CONSTRAINTS ON FORAGING AND THEIR CONSEQUENCES FOR EMPEROR PENGUINS

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CONSTRAINTS ON FORAGING AND THEIR CONSEQUENCES FOR EMPEROR PENGUINS

EINSCHRÄNKUNGEN BEI DER NAHRUNGSSUCHE UND DEREN KONSEQUENZEN FÜR KAISERPINGUINE

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SUMMARY

Emperor penguins are the largest living penguin and the only bird species that breeds during the Antarctic winter, on sea-ice around the Antarctic continent. They are fundamentally adapted to the high Antarctic sea-ice environment, showing radical breeding and foraging behaviour. High latitude-breeding exposes emperor penguins to extreme changes in sea-ice cover and light conditions over the course of the year, both factors that are likely to affect foraging success. This thesis examines some of the ecological and physiological constraints on emperor penguin foraging behaviour using birds from Pointe Géologie, Antarctica and considers how these birds modulate behaviour to cope with their extraordinary environment.

The trophic impact of emperor penguins on squid communities at Pointe Géologie was examined by analysing squid beaks obtained from the stomach of moribund chicks. Emperor penguins consumed primarily four squid species (*Psychroteuthis glacialis*, *Kondakovia longimana*, *Gonatus antarcticus*, *Alluroteuthis antarcticus*). Beak nitrogen stable isotope ratios (2.5–8‰ $\delta^{15}N$) indicated that squids consumed by the emperor penguin cover about two trophic levels. Emperor penguins feed primarily from the upper part of this range with 68% of squid prey being >6‰ $\delta^{15}N$. The trophic position of emperor penguins from different breeding colonies considerably differs because the principal components in the emperor penguin's diet; fish, krill and squid, differ in their average trophic level and also in their composition.

The foraging areas and depths used by 20 breeding emperor penguins at Pointe Géologie during winter, spring and summer in 2005/2006 (corresponding to incubation, early chick-brooding, late chick-rearing and the adult pre-moult period, respectively) were investigated using satellite telemetry and pressure transducers. Chick-provisioning penguins foraged over the Antarctic shelf in areas covered by winter pack-ice, using fissures in the ice although winter-foraging females compensated for limited water access by expanding their horizontal search component underwater. During the spring ice break-up, foraging ranges rarely exceeded the shelf slope and direct access to the sea was apparently almost unlimited. Spring-foraging birds showed higher area-restricted-search than birds in winter indicating more patchy prey abundance. During pre-moult trips, emperor penguins ranged much farther offshore than breeding birds, which augurs for particularly profitable oceanic feeding areas. These areas are presumably exploited because the time constraints imposed by having to return to a central place to provision the chick no longer apply.

Dive depth analyses were performed to determine how depth affects foraging efficiency. Penguins increased overall dive duration with increasing dive depth due to increasing transit (descent and ascent) durations as well as increasing duration of the bottom phase of the dive. Post-dive duration during which birds recovered at the surface was also positively correlated with both dive depth and dive duration, with accelerating recovery periods for dives in excess of 455 s. Consideration of efficiency, as the bottom duration divided by the dive cycle duration, showed that emperor penguins are less efficient during deeper dives, as predicted by physiological theory. Deeper dives are tenable if prey densities are appropriate, however, Application of an index of prey capture using the number of undulations in the bottom phase of the dive indicated that the most lucrative dive depths for the equipped birds were between 50 and 225 m, which were also the most frequently visited.

Since emperor penguins are considered to be visual hunters their foraging ability is believed to depend critically on light conditions. The influence of light on the foraging ability of breeding emperor penguins was examined during winter and spring, using light-recording depth loggers and combining results with models of light availability as a function of depth and time of year. Logger-measured light intensity decreased with increasing water depth while depth-specific values were higher at greater sun elevation angles. The virtually continuous daylight in spring/summer appears to provide penguins with more than double the depth-time availability of birds foraging in winter. A simple energetic model shows how reduced light levels led to increased foraging trip lengths for breeding birds in winter compared to spring-foraging birds.

This work highlights the dependence of the emperor penguin on particular conditions to survive but also alludes to sensitivity to environmental change. Further work is suggested to refine proposed models so that the effects of climate change may be postulated for this enigmatic and unique species.

ZUSAMMENFASSUNG

Kaiserpinguine sind die größten lebenden Pinguine und repräsentieren die einzige Art, die im antarktischen Winter auf dem Meereis brütet. Mit ihrem außergewöhnlichen Brut- und Nahrungssuchverhalten sind Kaiserpinguine an die hochantarktische Umwelt angepasst. Das Brüten in hohen Breiten setzt die Pinguine im Laufe des Jahres enormen Veränderungen in der Meereisbedeckung und den Tageslichtverhältnissen aus, die den Nahrungssucherfolg von Kaiserpinguinen beeinflussen dürften. Die vorliegende Arbeit untersucht einige ökologische und physiologische Einschränkungen bei der Nahrungssuche von Kaiserpinguinen der Brutkolonie „Pointe Géologie“ in Adélie Land, sowie die Verhaltensanpassungen der Vögel an ihre außergewöhnliche Umwelt.

Der trophische Einfluss von Kaiserpinguinen auf die Tintenfischgemeinschaft über dem Küstenschelf vor Adélie Land wurde anhand von Tintenfischschnäbeln untersucht, die den Mägen von verendeten Küken entnommen wurden. Kaiserpinguine konsumierten vier Tintenfischarten (*Psychroteuthis glacialis*, *Kondakovia longimana*, *Gonatus antarcticus*, *Alluroteuthis antarcticus*). Diese Tintenfische decken etwa zwei Trophiestufen ab (Verhältnis stabiler Stickstoffisotope 2.5–8‰ $\delta^{15}N$). Kaiserpinguine fressen bevorzugt am oberen Rand dieses Bereichs, denn 68% der konsumierten Tintenfische haben ein Isotopenverhältnis von >6‰ $\delta^{15}N$. Die trophische Stellung von Kaiserpinguinen verschiedener Brutkolonien unterscheidet sich beachtlich, da sich die wesentlichen Nahrungskomponenten (Fisch, Tintenfisch, Krill) in ihrer mittleren Trophiestufe sowie ihrer Komposition unterscheiden.

Von 20 Kaiserpinguinen wurden im Winter, Frühjahr und Sommer 2005/2006 die Ernährungsgebiete satellitentelemetrisch identifiziert und das Tauchverhalten mit Druckmessgeräten untersucht. Pinguine, die Küken versorgten, suchten über dem packeisbedeckten Schelf nach Nahrung, indem sie überwiegend Eisrisse als Zugang zum Meer nutzen. Im Winter kompensierten Weibchen bei ihren Tauchaktivitäten den eingeschränkten Meereszugang mit einer horizontalen Ausdehnung ihrer Nahrungssuche. Während des Eisaufbruches im Frühjahr führte die Nahrungssuche beider Geschlechter kaum über den Schelf hinaus, obwohl der Meereszugang nahezu uneingeschränkt war. Nahrungssuchende Pinguine zeigten im Frühjahr einen höheren „Area-Restricted-Search Index“ als im Winter, was auf ungleich verteilte Frühjahrsnahrung hinweist. Während der „pre-moult“ Periode wurde die Nahrungssuche beträchtlich weiter ausgedehnt als während der Kükenaufzucht, was auf lukrative ozeanische Ernährungsgebiete hinweist. Diese küstenfernen Gebiete können nun genutzt werden, weil die Küken selbständig sind, und somit die Notwendigkeit der Rückkehr zur Brutkolonie, dem „central place“, für die adulten Pinguine entfällt.

Tauchtiefenanalysen wurden durchgeführt um zu bestimmen, inwiefern die Tauchtiefe die Taucheffizienz von Kaiserpinguinen beeinflusst. Pinguine verlängerten die Gesamttauchzeit eines Tauchganges mit zunehmender Tauchtiefe, da sich dabei die Transitdauer (Ab- und Auftauchen) sowie die Bodentauchphase verlängert. Die „post-dive“ Dauer, in der sich Pinguine an der Wasseroberfläche erholten, nahm mit der Tauchtiefe und Tauchdauer zu, wobei die „post-dive“ Dauer für Tauchgänge länger als 455 s verstärkt anstieg. Untersuchungen der Taucheffizienz, als ein Quotient aus Bodentauchdauer und Tauchzyklusdauer (Summe von Gesamttauchdauer und „post-dive“ Dauer), zeigen dass Kaiserpinguine bei tiefen Tauchgängen weniger effizient sind als von der physiologischen Theorie bislang angenommen. Tiefe Tauchgänge sind dann zu rechtfertigen, wenn die Beutedichte angemessen ist. Tauchtiefen zwischen 50 und 225 m waren am lukrativsten für die Kaiserpinguine. Darauf weisen hohe Tauchfrequenzen für diesen Tiefenbereich und ein Beutefangindex hin, der auf der Anzahl von Unregelmäßigkeiten im Bodentauchprofil basiert.

Da Kaiserpinguine visuelle Jäger sind, dürfte ihr Nahrungssuchvermögen von den Tageslichtverhältnissen abhängen. Der saisonale Lichteinfluss auf das Nahrungssuchvermögen von Kaiserpinguinen wurde mit Hilfe von Licht registrierenden Tiefenloggern untersucht. Die Ergebnisse wurden mit Lichtverfügbarkeitsmodellen kombiniert, und zwar als Funktion von Tauchtiefe und Jahreszeit. Die vom Logger registrierte Lichtintensität nahm mit zunehmender Wassertiefe ab, während tiefenspezifische Werte bei größeren Sonnenstandswinkeln höher lagen. Das kontinuierliche Tageslicht im Frühjahr/Sommer scheint bei tauchenden Pinguinen zu einem mehr als doppelt so hohen „depth-time availability index“ zu führen als im Winter. Ein einfaches energetisches Modell zeigt, wie reduziertes Tageslicht im Winter, im Vergleich zum Frühjahr, zu einer Verlängerung der Nahrungstrips von Pinguinen führt.

Die vorliegende Arbeit hebt die Abhängigkeit des Kaiserpinguins von bestimmten Überlebensbedingungen hervor und verdeutlicht außerdem die Empfindlichkeit dieser Tiere gegenüber Umweltveränderungen. Die Arbeit sollte fortgeführt werden, um die erstellten Modelle zu verfeinern und somit mögliche Auswirkungen des Klimawandels auf diese einzigartige Spezies besser vorhersagen zu können.

SUMMARY

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1 PREFACE

Studies on top predators in the Antarctic sea-ice zone are conducted by research teams of different nations at a restricted number of locations where close collaboration is necessary in order to consolidate the results and to further our knowledge on the overall biology of these animals. Field research in Antarctica requires strong logistic support and necessitates team cooperation. The close collaboration with Dr. André Ancel's French research team was critical for the successful undertaking of this project at Pointe Géologie, Adélie Land. The French over-wintering station, Dumont d'Urville, and the team members who briefed me in field techniques to study emperor penguins were also invaluable. The field campaigns reported here were conducted during the austral springs of 2004 and 2005. In addition, winter foraging and diving data from the Pointe Géologie colony were collected by our over-wintering partner (Michaël Beaulieu) in 2005 and added to the overall data set. These data were included in my analysis as part of this study to obtain insights into the foraging behaviour of emperor penguins from this colony over a complete annual breeding cycle.

Field work required prior approval through the 'Ethics committee of the French Polar Institute'. The permit highlighted minimizing stress during handling and specified a maximum number of emperor penguins to be instrumented in this study. Despite a number of restrictions, the research project provided a rare opportunity to study the foraging ecology of emperor penguins from the Pointe Géologie colony. Previous information on birds from this colony consisted of limited data on foraging distribution and no studies had been conducted on the late chick-rearing and pre-moult foraging trips.

This thesis is a cumulative work consisting primarily of a series of papers, and as such, publications (Chapter 4) are presented as independent pieces of work. However there is extensive cross-referencing and there is some repetition of descriptions which is inevitable, given the format of the thesis. An initial 'Overview' (Chapter 2) and 'Material and methods' part (Chapter 3) provide important background and additional methodological information. In a synopsis (Chapter 5), I discuss the main findings of this study and assess the constraints on foraging and their consequences for emperor penguins in the high Antarctic sea-ice environment.

2 OVERVIEW

2.1 Penguins as marine predators

Penguins (Spheniscidae) are a specialised group of flightless pelagic seabirds (Williams 1995) comprising 17 species of six distinct genera. They are widely distributed in the colder waters of the Southern Hemisphere where they breed in harsh coastal environments while exclusively foraging at sea from where they obtain all their food and energy (Whittow and Rahn 1983). Distributions and population sizes are determined by the availability of suitable nesting habitats and the productivity of accessible ocean regions (Ashmole 1971; Croxall and Prince 1980). Typical characteristics of great body sizes (1-40 kg) and large populations (>30 million breeding pairs, Woehler 1995) make penguins a significant consumer of marine resources (Croxall et al. 1984; Williams 1995). The majority of penguin species are distributed between 45 and 60°S, whereas the greatest concentrations of penguins in total numbers occur around Antarctica and in the Subantarctic. South of the polar front there exist seven penguin species, their breeding being restricted to the isolated subantarctic islands and coastal areas of the Antarctic continent. Due to the extreme winter cold, penguins breed during summer in these regions with the exception of the two *Aptenodytes* species (Williams 1995). King penguins (*A. patagonicus*) which breed on subantarctic islands require 11-13 months for one breeding cycle. Emperor penguins (*A. forsteri*) breed around the Antarctic continent and have a nine months breeding period between late autumn and early summer (Stonehouse 1960; Prévost 1961).

Penguins display profound adaptations to the marine environment, for swimming and diving, including the loss of aerial flight, solid bones which result in high body density, a streamlined body for hydrodynamic shape and modified wings which serve as powerful flippers during swimming (Williams 1995). Furthermore they show development of insulative, circulatory and metabolic adaptations that allow them to live and breed in cold environments. Highly modified, short stiff feathers consist of downy under-feathers and main stiff feather parts which overlap each other and form a dense cover over the body surface. The waterproofed penguin feathers provide an effective insulation against heat loss at cold temperatures. The feet and parts of the flippers are unfeathered and served with a very abundant blood supply. In order to control heat loss in these peripheral body regions penguins possess circulatory arrangements (by counter-current heat exchange) in the flippers, feet and head (Frost et al. 1975). Penguins may increase their metabolic heat production by circulatory modifications, such as vasoconstriction, or when temperatures drop under their lower thermoneutral range by thermogenesis (shivering and non-shivering) as well as through locomotory activity. Penguins are air-breathing divers and rely entirely on the body oxygen storage in the lung and air-sacs, in haemoglobin in the blood and in myoglobin in their muscle tissue. The efficient utilisation of these stores during diving becomes increased by selective blood flow reduction to the main important organs such as the heart, the brain and the lung and by decreasing the heart rate (bradycardia). Furthermore, penguins frequently use anaerobic respiration for additional energy production during long dives which become metabolized or removed from the body during prolonged recovery periods at the water surface or proximate bouts of 'aerobic' shallow dives (Kooyman and Ponganis 1998).

2.2 Foraging

The term 'foraging' describes the animal's 'behaviour directed to acquiring food'. Breeding seabirds are central place foragers (Orians and Pearson 1979) and execute foraging trips to remote locations but consistently return to a central place, the colony, to deliver food to the brood. The penguin diet generally comprises a composition of pelagic and/or benthic fish, squid and crustacean. Penguins hunt prey in water depths ranging from near the surface to >500 m (Williams 1995; Wienecke et al. 2007) and concentrate their foraging effort where prey are most available, such as in regions where water bodies converge or where complex bottom topography induces the up-welling of nutrients, as occurs over submarine canyons and continental shelf breaks (Brown 1980; Hunt and Schneider 1987; Plötz et al. 1991).

Foraging behaviour of penguins can be broken down into four components: vertical movement (diving), horizontal movement or displacement, habitat use, and resultant prey capture (cf. Austin et al 2006). The allocation of time for different behaviours during foraging should translate into the foraging strategy which optimises the energy gain by adults and chicks as to enhance reproductive success. Generally penguins appear to allocate their foraging effort between searching for prey patches, with occasional feeding 'en route', and periods of intensive feeding once prey patches are located (Naito et al. 1990; Wilson 1995). Compared to volant seabirds which may forage at great distances from their breeding sites, penguins have a reduced foraging range during their breeding cycle which would tend to reduce predator-prey encounter rates. Penguins may compensate for this by maximizing horizontal speed while travelling and increasing dive depths and durations where prey density is high (Wilson and Wilson 1990). Generally, individuals can increase their probability of feeding success by spending more time underwater (Mori 1998; Mori and Boyd 2004). However, penguins are air-breathing animals and, while underwater, they only have access to oxygen via body stores which need to be replenished during subsequent surface periods. Extended dive durations consequently necessitate extended duration at the water surface for recovery (e.g. Ponganis et al. 1997). Penguins are assumed to find the optimal strategy to forage rather efficiently in dependency of prey availability but also of the seasonable energy demand of the brood.

In the past, observations of animal foraging behaviour at sea were constrained by the observers' remote incapability to follow the animals in their marine environment. Observations of animals from their own perspective were first provided by telemetry and remote-sensing technologies. The ultimate form of remote-sensing, where both the sensory and recording systems are attached to the animal itself, was termed 'bio-logging' (Naito 2004) and allows the simultaneous collection of different physical, physiological and environmental parameters (Wilson et al. 2002a; Ropert-Coudert and Wilson 2005). Parallel observations of the animals moving by satellite telemetry, which provides position fixes when the animal is at the sea surface, allow to study foraging behaviour at sea in both horizontal and vertical dimension (see Chapter 3 Material and methods).

2.3 The marine Antarctic habitat

Antarctica is a continental landmass surrounded by a generally narrow and unusually deep shelf. Beyond the Antarctic shelf the circumpolar Southern Ocean extends until a northward edge which is clearly marked by the Antarctic Polar Front where cold Antarctic waters interact with warmer subantarctic waters. The Antarctic Polar Front serves as a biological barrier to the dispersal of many marine species and consequently the Southern Ocean comprises several species are endemic (e.g. Fogg 1998).

The Antarctic environment is characterised by a high seasonal fluctuation in daylight. During winter the sun lies below the horizon for several weeks and sea-ice covers the sea surface for up to four hundred kilometres from the coast. In summer the opposite occurs when the sun remains up for several weeks and the sea-ice around coastal areas reaches its minimum extent (Zwally et al. 1983). The resulting seasonal fluctuation in incident solar energy in Southern Ocean waters leads to characteristically high seasonality in primary production (e.g. Whitaker 1982; Clarke 1988) which profoundly influences the biology of all consumers in the food webs of the Southern Ocean. Compared to more temperate marine systems the Southern Ocean is marked by low species diversity due to a simplified trophic structure, which is mainly centred around the Antarctic krill (*Euphausia superba*, Laws 1985; Nicol 1994; Moloney and Ryan 1995).

Emperor penguins have a special function as Antarctic predators and top consumers in the Southern Ocean food web among birds. Antarctic environmental features that greatly influence their foraging behaviour are the seasonal fluctuation in day length and the sea-ice cover extent. Southern Ocean sea-ice cover may fluctuate in area from less than 4×10^6 km^2 in austral summer up to 20×10^6 km^2 in winter (Zwally et al. 1983). Sea-ice which forms in situ and is fastened to the continental coast is the ‘fast-ice’. It builds seaward in early winter and breaks in early summer providing the breeding grounds for emperor penguins. The coastal sea-ice zone contains ice-free fissures and polynias, regions of open water within the sea-ice zone, which are formed by ice movement around glacier tongues and ice-bergs or by increases in water temperature due to areas of shallow up-welling water (Zwally et al. 1985). Sea-ice formation and fluctuation influences the foraging pattern and life cycle of winter breeding emperor penguins in the high Antarctic environment.

2.4 The emperor penguin

2.4.1 Distribution and abundance

Emperor penguins live year round in Antarctic waters and have a circumpolar distribution. So far 46 breeding colonies (Fig. 2.1) have been reported (Woehler 1993; Mellick and Bremers 1995; Messick et al. 1999; Coria and Montalti 2000; Todd et al. 2004) providing a minimum total population of 200 000 breeding pairs (Woehler 1993). The colonies are located between 66°S and 78°S with a remarkable concentration of about 80,000 breeding pairs of together six colonies in the Ross Sea sector, East Antarctica (160°E to 170°E, Harper et al. 1984). Emperor penguins are adapted to exploit shelf and offshore waters which are largely covered by sea-ice for most of the year. The breeding sites are located along the ice shelf coast where the sea-ice forms earliest in the year and remains stable from about March/April to mid January. Two colonies are on land, one being on Dion Island near the Antarctic Peninsula (67°52'S, 68°43'W) and the other, which is the only one on the Antarctic continent, is beside Taylor Glacier (67°28'S, 60°53'E) in McRobertson Land.

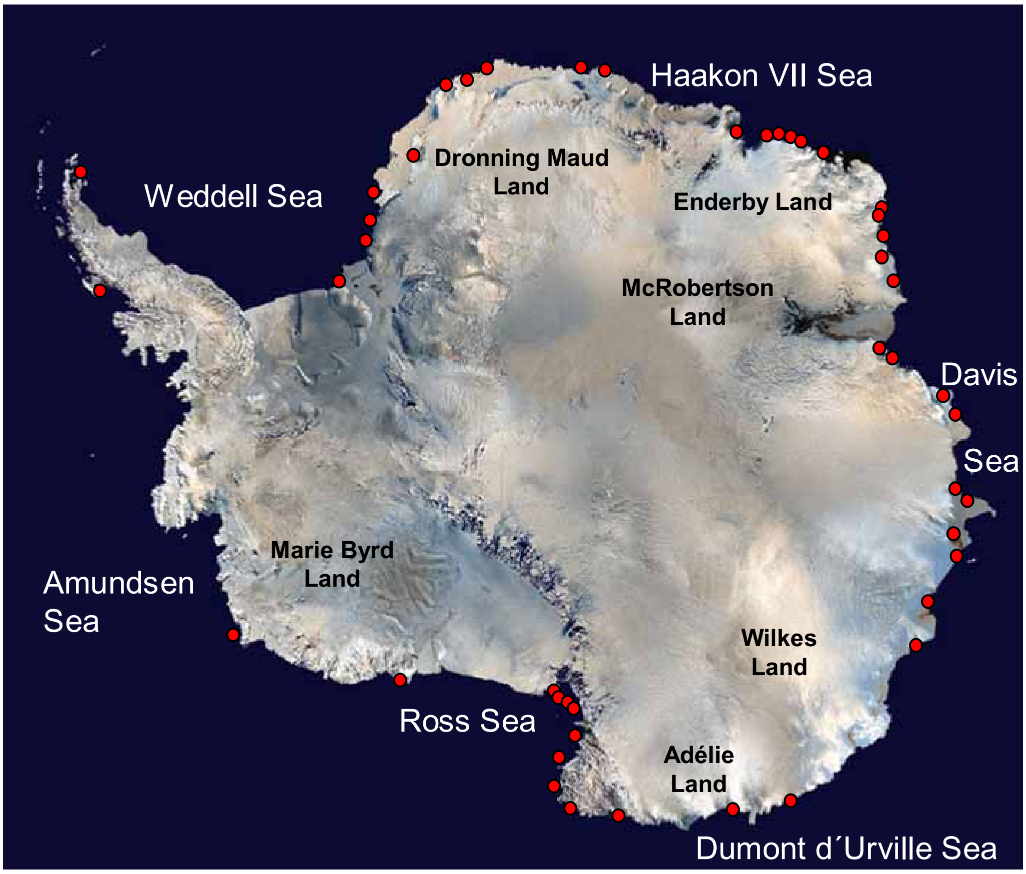

Fig. 2.1 Emperor penguin breeding colonies (n=46) indicated by red dots. Satellite image by NASA.

The emperor penguin is one of the most abundant Antarctic top predators (e.g. Woehler 1993). The foraging capacity and reproductive success of the emperor penguin, as with all upper trophic predator species, provides an indication of trends in the productivity of the marine ecosystem in which it lives (Croxall and Lishman 1990).

2.4.2 Special adaptations

Emperor penguins are the most specialized among penguins and well adapted in many aspects of their morphology, physiology, their behaviour and ecology (Le Maho 1977). They are the largest living penguin species, standing 115 tall and weighing up to 40 kg (Marchant and Higgins 1990), and they are the most extreme divers, with a measured maximum dive depth of 564 m and dive duration of 22 min (Robertson 1995; Wienecke et al. 2007).

Following the Bergmann's rule (Bergmann 1847) their size provides emperor penguins with a low surface-to-volume ratio and sufficient thermal mass to survive the extreme cold of the Antarctic winter with less than -40°C, wind speeds up to 40 m s^{-1} and extended periods of fasting (see breeding cycle below). Furthermore they have to 25% smaller extremities (flippers and beak) relative to their body size than do other penguins (Stonehouse 1967), an expanded plumage of higher density which provides about 85% of the emperor penguin insulation (Bougaeff 1972) and a more extensive heat conservation, counter-current system in the brachial arteries than was found in other penguin species (Trawa 1970). In addition to these physiological adaptations for the benefit of energy saving, emperor penguins are highly colonial by suppressing the penguin typical territorial aggressiveness (Jouventin 1971) and exhibit the unique huddling behaviour to minimize heat loss. Huddles are large compact groups of up to 5000 males, 10 birds standing per 1 m^{-2} (Prévost 1961) wherein males show minimum activity only to move between central and peripheral positions. This allows incubating males to maintain their body temperature at a constant high level (35°C) to support full embryonic development by a 16% reduction of field metabolic rate (Ancel et al. 1997). Huddling is one of the responsible key mechanisms for the emperor penguin breeding success during the Antarctic winter (Prévost 1961).

2.4.3 Breeding cycle

The emperor penguin is the only bird species which truly breeds in winter. The breeding biology summarized below is generally based on studies by Stonehouse (1953), Prévost (1961), Mougin (1966), Isenmann (1971) and Jouventin (1971).

Being a long lived species of up to 30 years, emperor penguins mature at 4-6 years of age. Mature male and female penguins arrive on their traditional breeding grounds in late autumn (March-April, Fig. 2.2). This is when the sea-ice cover, their breeding habitat, has formed and the moment of arrival in the colony is believed to ensure that chicks fledge until the ensuing ice break-up about 10 months later, in early summer. The arrival is followed by a six week courtship and egg production period and initiates a two month fast by females and a four month fast by males. In May, females lay a single egg (ca. 450 g) and pass it to the males for the entire incubation shift of about 65 days before departing the colony to forage at sea (Fig. 2.2). The emperor penguin incubation period is unique and the longest among birds.

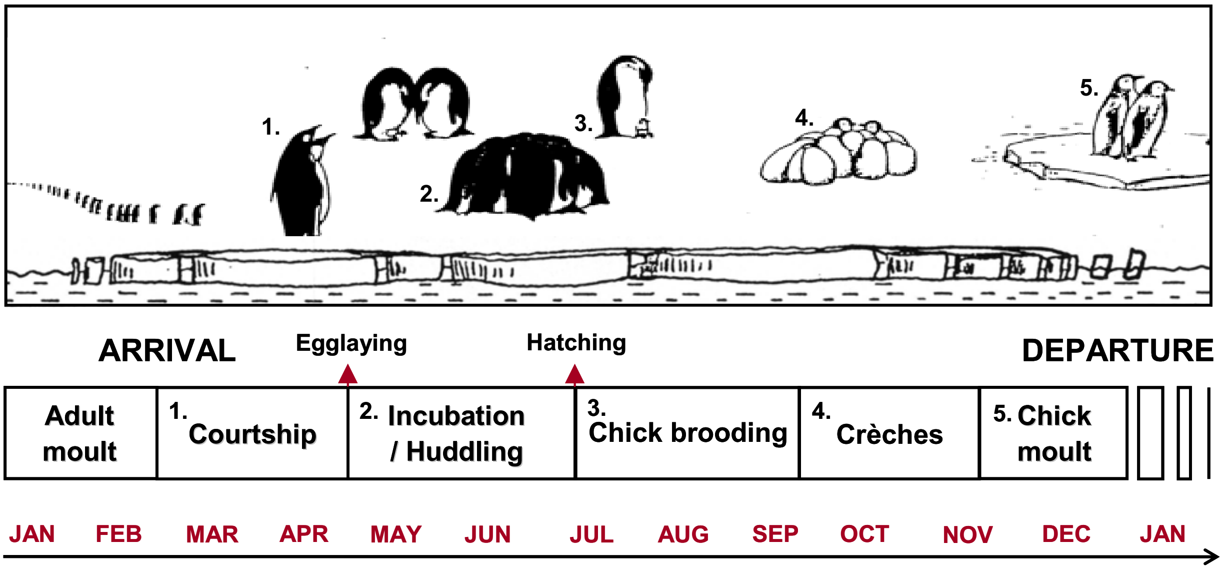

Fig. 2.2 Illustration of the annual breeding cycle of emperor penguins.

Males carry the egg on their feet, pressed up against a warm brood patch while being protected by an abdominal skin fold against the cold. Over much of the incubation period, males huddle together to minimize energy expenditure. Chicks hatch in July and may be fed by the males for a maximum of two weeks until females return from sea to relieve them, producing a milky secretion from the oesophagus (Prévost and Vilter 1963). Returning females locate their partner by vocal calling before overtaking and feeding the chick (Isenmann 1971). For the first 50 days of the chicks life adults share the brooding and feeding duties until about September when chicks become thermal independent and form crèches. After the cessation of brooding duties, when the chicks' food demand increases the most intensive feeding begins and both parents conduct up to eight foraging trips of several days to several weeks duration (Mougin 1966; Isenmann 1971). During this late chick-rearing period foraging adults attempt to balance their own food and energy requirements with those of the increasing demand of their offspring. In mid November chicks begin to moult into juvenile plumage and attained 10-15 kg, half the adult body mass, when they fledge around mid-December (Fig. 2.2). This is the time when adults leave the colony to forage for themselves in so-called pre-moult trips in preparation for their moulting fast. Adult moult commences in late January and last three to four weeks during which penguins need to select areas of heavy pack-ice which meet their requirement for stable ice floes during the moult. When penguins have renewed their plumage they gather new energy reserves during a post-moult foraging trip in preparation for the forthcoming breeding season.

3 MATERIAL AND METHODS

3.1 Study site

The emperor penguin colony of Pointe Géologie is located close to the French wintering station Dumont d'Urville (66°40'S, 140°01'E) in Adélie Land, Antarctica (Fig. 3.1). In the 'Baie des Empereurs' the emperor penguins mainly breed between two islands of the Pointe Géologie archipelo (Ile Rostand and Ile Le Mauguen) and the Nunatak du Bon Docteur aside the Antarctic continent in the protection of the islands, where the sea-ice shows its longest stability close to the continent. The continuous operation of Dumont d´Urville station since 1956, and its proximity to the breeding colony allowed the only existing long term observations of the emperor penguin breeding success for a period of 45 years with yearly counts since1963 (Woehler et al. 2001). The breeding colony almost halved between 1978 and 1984 due to a prolonged decrease in adult survival related to a period of warming and of reduced sea-ice extent (Barbraud and Weimerskirch 2001) and showed a slight decreasing tendency since then, providing a total of 2740 breeding pairs (Micol and Jouventin 2001).

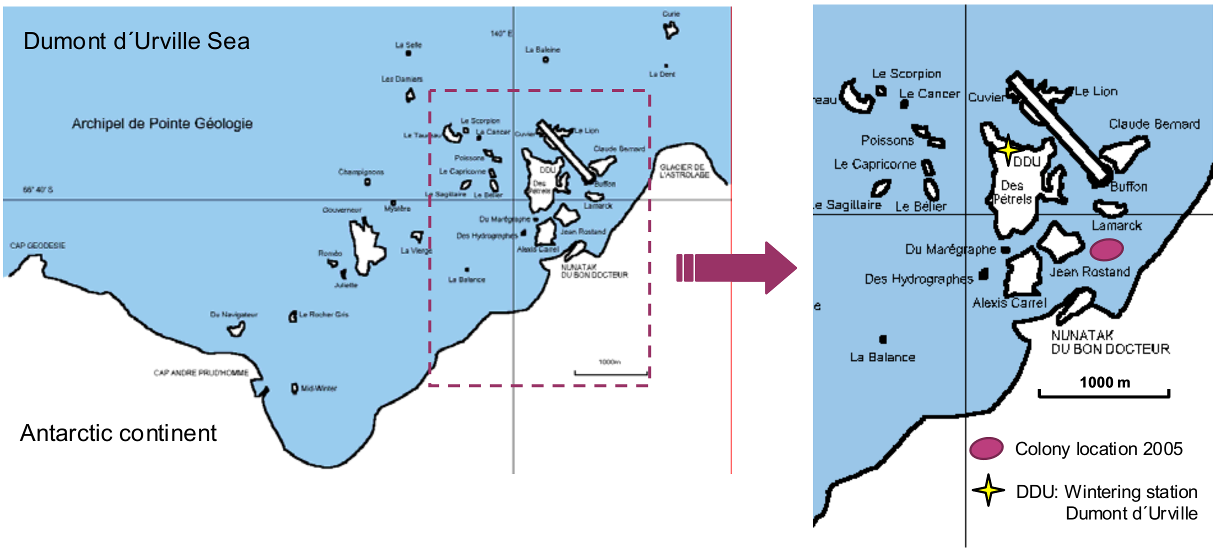

Fig. 3.1 The emperor penguin breeding colony at Pointe Géologie (66°40'S, 140°01'E), Adélie Land.

The continental shelf in this region is about 100 km wide and 100-200 m deep; the sea-floor is dissected by several marine canyons of up to 1000 m depth.

3.2 Field work

Ecological research is often restricted by harsh environmental factors of the studied species habitat. Field work in the high Antarctic sea-ice environment is especially dependent on good weather conditions and requires extensive logistical support. Studies on free-living animals in such habitat, especially on their at-sea behaviour, necessitate the equipment with satellite tags and/or data loggers which allow remote observation and the understanding of the animals' foraging behaviour. The present emperor penguin study required intensive monitoring of birds in their colony, since we attempted to choose successful breeders with a healthy chick for equipment. This should guarantee that birds return to the colony and devices are retrieved.

For dietary studies stomach samples of emperor penguin chick carcasses were collected in spring 2004 and 2005. Stomach contents (n = 20 in 2004; n = 12 in 2005) were sampled (by dissection) within 24 hours after demise of the chick and subsequently sieved and sorted in the laboratory. Undigested food remains predominantly consisted of squid beaks and provided only few fish otoliths. Squid beak measurements of the lower rostral length allowed for squid size and body mass calculation. Measurements of stable isotope signatures ($\delta^{15}N$, $\delta^{13}C$) in squid beaks furthermore enabled the reconstruction of the trophic range from squid prey consumed by emperor penguins in the Dumont d'Urville Sea (see Chapter 4, Publication I).

The foraging behavioural study in this thesis comprises data records from winter, spring and summer 2005/2006. Data records from spring 2004 could not be analysed due to technical difficulties. Twenty adult emperor penguins were studied during the breeding season in 2005, five penguins in winter and 15 penguins in spring. During the pairing period in early winter three breeding females and two breeding males were equipped with a satellite transmitter and an archival tag to track the post-egg-laying and post-incubating foraging trips and to record the penguins' diving behaviour (for technical details see Publications II, III). The 15 penguins in spring were either equipped with a conventional satellite transmitter or a device that combined such a satellite transmitter with an archival tag (see Publications II, III for device details, Fig. 3.2).

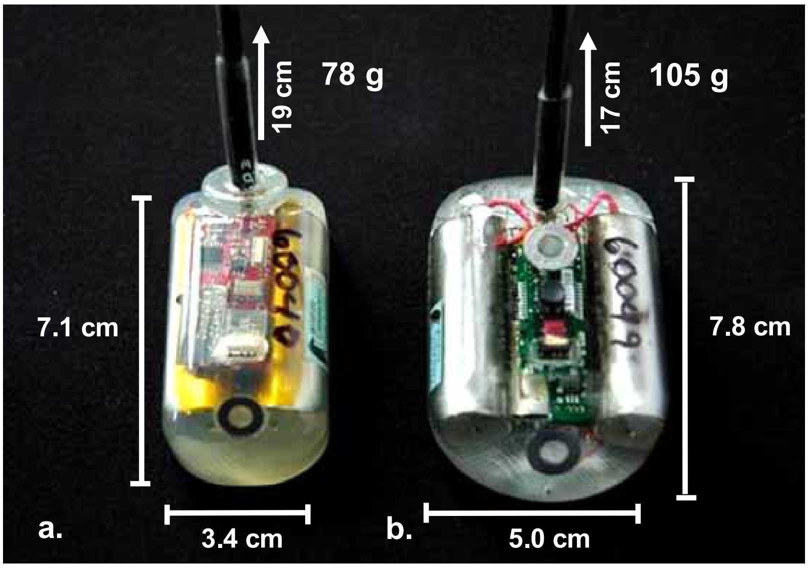

Fig. 3.2 Example of (a) a conventional satellite transmitter that provide animal positions (Spot5) and (b) a device that combined such a satellite transmitter with an archival tag to provide animal positins, dive depth, light and temperature data (Splash), both from Wildlife Computers, USA.

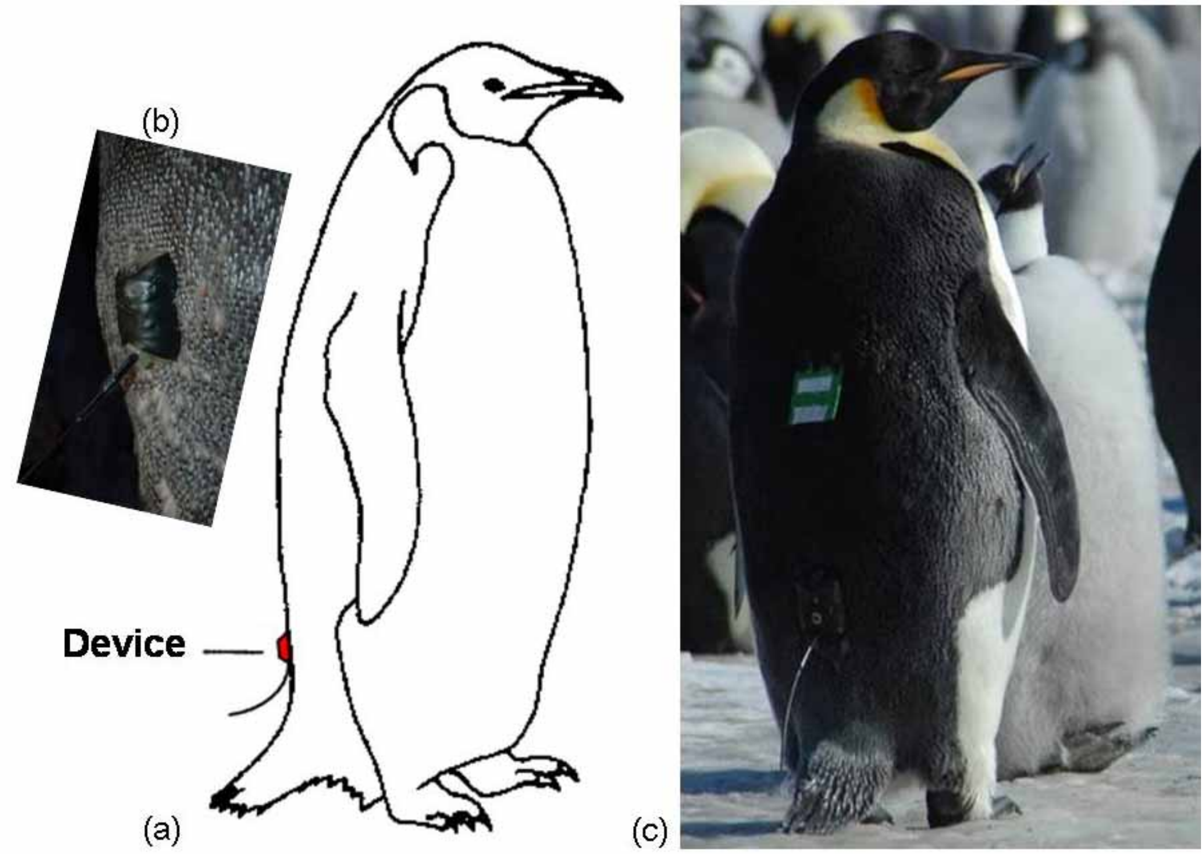

Fig. 3.3 (a) Satellite transmitter attached to the emperor penguin back-feathers with (b) the tape-method. (c) Chick-rearing emperor penguin equipped with a device that combined a satellite transmitter with an archival tag (Splash, Wildlife Computers, USA), colour marked with green-white Tesa tape.

Due to advances in technology miniaturisation no attached device exceeded 2.6% of a 24 kg penguin's cross-sectional area (Wienecke and Robertson 1997). To minimize drag (Bannasch et al. 1994) tags were hydrodynamic shaped and attached to the lower back feathers using either glue and hose clamps or Tesa tape (Fig. 3.3, Wilson et al. 1997). During the pairing period in winter, device attachment was conducted in a shelter where the penguins from the nearby colony were transported in a sledge. Several breeding pairs were colour marked using Nyanzol. About six months later, during the late chick-rearing study, we attempted to choose successful breeders among these marked birds for device attachment. Penguins were either equipped on their return from sea before reaching the colony, or after they had fed their offspring and were about to leave the colony again.

Individuals were caught by tackling them rugby-like (Robertson 1991) when they were dwelling at the margin of the colony or tobogganed on the sea-ice. In order to minimize stress experienced by birds, a penguin was caught by one person but further handling and device attachment required a team of two people at least. When caught, the bird was drawn up to its feet, eyes were covered by a tissue mask and wings physically restrained by a belt fixing jacket (Fig. 3.4). Now the equipment was conducted right in the field where the complete procedure lasted only about 15 min. Thereafter birds continued their way either to the sea-ice edge or to the colony for chick-feeding. Dive data records, stored in the memories of data loggers, were retrieved when equipped penguins returned from their foraging trips. Five birds remained equipped with satellite transmitters during summer for pre-moult trip and moult location documentation.

Fig. 3.4 (a) Catch of an adult emperor penguin by rugby-like tackling at the edge of the penguin colony of Pointe Géologie, Adélie Land. Before device attachment the penguins' eyes were covered by a tissue hat (b) and flippers were restrained by a belt fixing jacket (c).

3.3 Foraging distribution

The at-sea movements of emperor penguins were studied using satellite telemetry. The sole satellite transmission service for animal tracking is based on the Argos receiving system. The system is based on satellites with a polar orbit. This means, the number of passes effected per day, when a transmitter at a particular position can be localised, is greater at the poles (28 passes) than at the equator (8 passes) (Taillade 1992).

Argos satellite records (CLS Argos, Toulouse, France) were classified according to the size of the error radius of the location and the number of signals received by the satellite during a pass. The Argos system (Service Argos 1996) provides seven classes of accuracy, in order of decreasing accuracy from 3, 2, 1, 0, A, B to Z. Error radii, which were calculated for positions based on at least 4 signals, were 150, 350, 1000 and > 1000 m for class 3, 2, 1 and class 0 locations, respectively. For class A and B locations which were based on 3 or 2 signals, error radii were not calculated; class Z included signals for which the locations could not be determined. Thus class Z locations were excluded from data analyses. Data processing by speed-filter and distance calculations between valid positions were supported by the company Optimare (Bremerhaven, Germany). Thereafter emperor penguin foraging tracks were analysed concerning ecological aspects, such as the foraging range, the trip duration and the geolocation of satellite position fixes with dive depth records (see Chapter 4, Publication II).

3.4 Diving behaviour

Emperor penguin foraging trips consist of multiple dives being directed to different behaviours (see above, example Fig. 3.5a). The number of dives per foraging trip varies individually but also in dependence of the foraging trip duration which differs over a breeding cycle (see Chapter 4, Publication II, III). Single dives may be considered as a whole or divided into different dive phases. Most of the penguins' underwater forays consisted of three distinct phases: a descent phase, a phase when the birds swam horizontally (here termed 'bottom phase'), and an ascent phase. It is the bottom phase, during which penguins are most likely to hunt (Chappell et al. 1993; Wilson et al. 1995) and appear to capture most of their prey (Kirkwood and Robertson 1997bb; Simeone and Wilson 2003; Takahashi et al. 2004; Ropert-Coudert et al. 2006; Bost et al. 2007), indicated by irregularities in the dive profile (see Chapter 4, Publication III). Consequently, depending on the function of a dive, profiles differ characteristically from each other. Shallow dives of short duration generally provide travelling or recover from feeding dives. Search dives, performed for foraging purposes, are longer and deeper than travel dives. Characterized by smooth descent and ascent phases these (V-shaped) dives do not show bottom phases. The feeding dives contain a distinct descent phase followed by a ragged bottom phase (indicating prey pursuit) and the final ascent to the surface (example Fig. 3.5b).

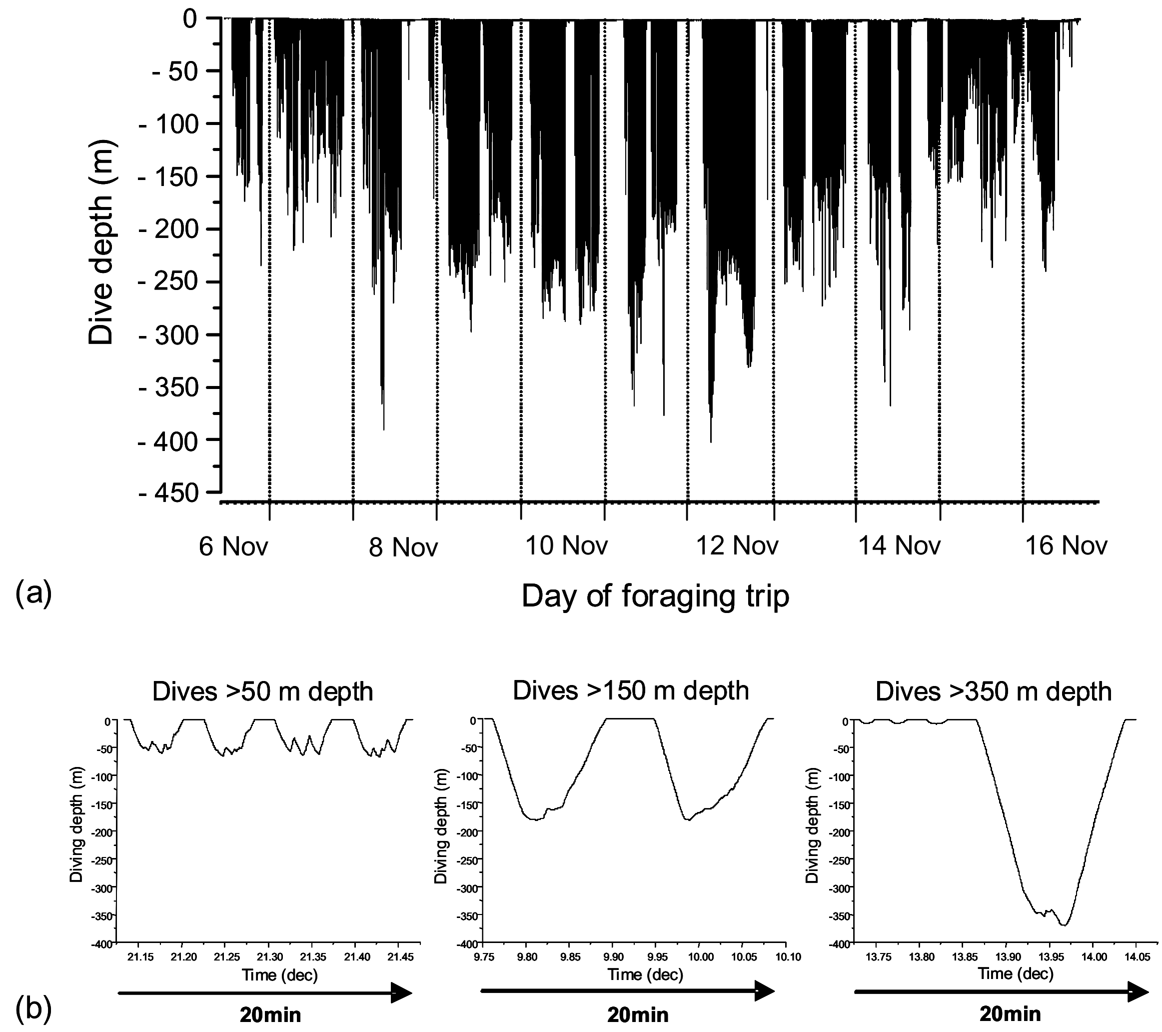

Fig. 3.5 Example of an emperor penguin foraging trip of 10 days duration during the late chick-rearing period comprising a total of n = 1,763 dives >2 m (a). The trip includes dives directed to foraging into different water depths (b).

Diving depth and ambient light intensity were logged at intervals of 5 s in winter and at intervals of 2 s (depth) and 10 s (light) in spring. Depth data recorded in 2 or 5 s intervals allowed for high resolution reconstruction of the penguin diving behaviour. Emperor penguin depth records of up to several thousand dives per foraging trip were displayed by special software (MT-dive, Jensen-Software, Kiel, Germany) which analysed all dives >2 m sequentially, and wrote, dive per dive, a number of defined parameters into an output file. These were: the time of the dive initiation, the overall dive duration, the maximum depth reached during the dive, the descent-, bottom-, and ascent-phase duration, the vertical velocities during the descent, bottom and ascent phases, the number of rapid succession short ascent/descent phases during the bottom phase, and the post-dive interval (for further details see Chapter 4, Publication II, III).

Satellite telemetry and dive record information allowed for different considerations of emperor penguin foraging behaviour as presented in the following papers (Chapter 4, Publication II, III, IV).

4 PUBLICATIONS

The cumulative dissertation entitled ‘Constraints on Foraging and their Consequences for Emperor Penguins’ consists of four peer reviewed publications in scientific journals and three parent sets of corresponding primary data publications in a digital library. The objective of this study was to examine the foraging ecology of the emperor penguin with a particular view to assessing constraints and their consequences. The thesis consists of four core publications and the publication of primary data. A dietary study examined the actual prey of the penguins, focusing on squid prey and examining the trophic impact of emperor penguins on the squid community at Pointe Géologie. The trophic position of the emperor penguin was compared between different breeding locations with different diets (Zimmer et al. 2007 PUBLICATION I). Satellite transmitters attached to free-living birds then allowed me to determine areas used by emperor penguins foraging at sea and parallel deployment of depth gauges permitted me to examine diving performance and its variation over the course of one breeding cycle (Zimmer et al. 2007 PUBLICATION II). Detailed examination of penguin diving behaviour necessitated analysis of every dive for high resolution (both in pressure and time) data. Results are used to consider how dive efficiency, ultimately determined by penguin physiology, varies with depth and the consequences that this has with respect to putative prey distribution and light availability, which may constrain foraging (Zimmer et al. 2007 PUBLICATIONS III, IV). Primary data are published for satellite and remotely-sensed data in the form of three parent sets which are related to publications II, III and IV in this thesis.

Publications are already published and registered by DOI or submitted and therefore citable. In all papers presented, I am first author and as the principal investigator being responsible for the field work planning, the preparation of scientific equipment used in the field, deployment of instruments and data collection in the field, analysis of the data and initialisation and preparation of the manuscripts.

All publications that constitute this thesis are listed below and my share thereof is explained in detail.

PUBLICATION I

Zimmer, I., Piatkowski, U., Brey, T. (2007) The trophic link between squid and the emperor penguin *Aptenodytes forsteri* at Pointe Géologie, Antarctica. *Marine Biology*, DOI:10.1007/s00227-007-0766-1

The initial idea originates from myself. Field work and collection of stomach samples for analyses were conducted by myself and colleagues who are mentioned in the acknowledgements. Squid beak identification and lower rostral length measurements for squid body size and mass calculations were accomplished in collaboration with the second author, and trophic analyses in collaboration with the third author. I conducted all analyses from the resulting data, wrote the initial draft manuscript and all further versions, which resulted from discussions with the second and third author.

PUBLICATION II

Zimmer, I., Wilson, R. P., Gilbert, C., Beaulieu, M., Ancel, A., Plötz, J. (2007) Foraging movements of emperor penguins at Pointe Géologie, Antarctica. *Polar Biology*, DOI:10.1007/s00300-007-0352-5

The initial idea for the seasonal comparison of emperor penguin foraging distributions and behaviour between different seasons originates from myself. The arithmetic procedure to calculate the area-restricted-search index which results in foraging hotspot identification was developed together with the second author. Field work and data acquisition were conducted by myself, the third, the fourth and the fifth author. I conducted all data analysis, wrote the initial draft manuscript and all further versions, which resulted from discussions with the second, the fifth and the sixth author.

PUBLICATION III

Zimmer, I., Wilson, R. P., Beaulieu, M., Ancel, A., Plötz, J. (submitted) Dive efficiency in relation to depth in foraging emperor penguins. *Aquatic Biology*

The initial idea originates from myself and the second author. Field work and data acquisition were conducted by myself, the third, and the fourth author. I conducted all data analysis, wrote the initial draft manuscript and all further versions, which resulted from discussions with the second, fourth and fifth author.

PUBLICATION IV

Zimmer, I., Wilson, R. P., Beaulieu, M., Ancel, A., Plötz, J. (submitted) Seeing the light: depth and time restrictions in the foraging capacity of emperor penguins at Pointe Géologie, Antarctica. *Aquatic Biology*

The initial idea originates from myself and the second author. Field work and data acquisition were conducted by myself, the third and the fourth author. I conducted all data analysis, wrote the initial draft manuscript and all further versions, which resulted from discussions with the second, fourth and fifth author.

PUBLICATION V Parent set of primary data to Publication II

Zimmer, I.; Wilson, R. P.; Gilbert, C.; Beaulieu, M.; Ancel, A.; Plötz, J.; Bornemann, H. (2007) At surface behaviour of emperor penguins from Pointe Géologie, Adélie Land, Antarctica, from expedition DDU 2005 [supplementary data to Publication II], *PANGAEA*, dataset #633712
(http://doi.pangaea.de/10.1594/PANGAEA.633712)

Data processing, archive and publication were conducted by myself and the seventh author.

PUBLICATION VI Parent set of primary data to Publication III

Zimmer, I.; Wilson, R. P.; Beaulieu, M.; Ancel, A.; Plötz, J.; Bornemann, H. (2007) Dive depth profile and at surface behaviour data of emperor penguins from Pointe Géologie, Adélie Land, Antarctica, from expedition DDU 2005 [supplementary data to Publication III], *PANGAEA*, dataset #633713
(http://doi.pangaea.de/10.1594/PANGAEA.633713)

Data processing, archive and publication were conducted by myself and the sixth author.

PUBLICATION VII Parent set of primary data to Publication IV

Zimmer, I.; Wilson, R. P.; Beaulieu, M.; Ancel, A.; Plötz, J.; Bornemann, H. (2007) Luminous intensity and dive depth profile data of emperor penguins from Pointe Géologie, Adélie Land, Antarctica, from expedition DDU 2005 [supplementary data to Publication IV], *PANGAEA*, (submitted)

Data processing, archive and submission were conducted by myself and the sixth author.

PUBLICATION I

THE TROPHIC LINK BETWEEN SQUID AND THE EMPEROR PENGUIN *APTENODYTES FORSTERI* AT POINTE GÉOLOGIE, ANTARCTICA.

Ilka Zimmer, Uwe Piatkowski, Thomas Brey

MARINE BIOLOGY

Mar Biol
DOI 10.1007/s00227-007-0766-1

RESEARCH ARTICLE

The trophic link between squid and the emperor penguin *Aptenodytes forsteri* at Pointe Géologie, Antarctica

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Abstract Cephalopod beaks retrieved from stomachs of dead emperor penguin chicks at Pointe Géologie, Terre Adélie, provide information on taxonomic and size composition of the penguin's squid diet, on the trophic range of the squid species preyed upon and on the fractional trophic impact of the penguin on the whole food web. Emperor penguins prey upon four squid species (*Psychroteuthis glacialis*, *Kondakovia longimana*, *Gonatus antarcticus*, *Alluroteuthis antarcticus*) and do not take squid larger than 480 mm mantle length. Larger squid live either below the penguin's diving range or are beyond its handling capacity. Nitrogen stable isotope ratios indicate that squids cover a range of about two trophic levels (2.5–8‰ δ^{15}N). The impact of the emperor penguin, however, concentrates on the upper part of this range, about 68% of its squid prey being >6‰ δ^{15}N. The principal components of the emperor's diet, fish, krill and squid, differ distinctly in average trophic level. Consequently the trophic position of the emperor penguin changes accordingly with diet composition and may differ by almost one trophic level between different emperor penguin colonies.

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Introduction

Cephalopods play an important role in the ecology of the Southern Ocean, having been identified as key species in the diets of many higher predators, including penguins, various seabird species, seals, cetaceans and fish (Collins and Rodhouse 2006 and References therein). Cephalopod beak samples from predator stomachs provide information on the trophic position of cephalopods in the Antarctic food web and on their migration patterns and ontogenetic dietary shifts (Cherel and Hobson 2005). Therefore, studies of predator diet and foraging are a major source of information on Southern Ocean cephalopod species composition and distribution (Clarke 1980; Cherel and Duhamel 2004; Cherel et al. 2004). Among the Antarctic penguins the deeper diving king and emperor penguins are thought to consume significant quantities of cephalopods (Williams 1995). Antarctic top predators such as emperor penguins catch larger specimens and a greater diversity of squid than fishing trawls during research cruises (Rodhouse 1990). The share of squid in the emperor penguin diet, however, is subject to substantial geographical variation, ranging from 3% at Pointe Géologie to 69% (wet mass) at Taylor glacier colony (Offredo and Ridoux 1986; Klages 1989; Gales et al. 1990; Robertson et al. 1994; Pütz 1995; Cherel and Kooyman 1998) and 74% in diet samples collected in the Weddell Sea (Ainley et al. 1992). Comprising about 3,000 breeding pairs, the emperor penguin colony of Pointe Géologie is average sized among the 46 documented colonies (Woehler 1993; Mellick and Bremers 1995; Messick et al. 1999; Coria and Montalti 2000; Todd et al. 2004). So far, feeding and alimentation of emperor penguins were studied once in this colony some 20 years ago (Offredo et al. 1985), a good reason to conduct our dietary study at this breeding site.

Table 1 Allometric equations relating lower rostral length (LRL, mm) of cephalopod beaks to mantle length (ML, mm) and wet body mass (WM, g)

Species	Allometric equation		Number, ML	Reference
	ML versus LRL	WM versus LRL		
P. glacialis	$ML = 50.6895\ LRL - 8.6008\ LRL^2 + 1.0823\ LRL^3 - 8.7019$	$\ln WM = 0.3422 + 2.1380 \ln (LRL) + 0.2214 \ln (LRL)^3$	I. $n = 10$; ML = 7–27 mm WM = <0.1–1.3 g II. $n = 186$; ML = 99–202 mm WM = 19–210 g III. $n = 15$; ML = 270–380 mm WM = 338–823 g	Gröger et al. (2000)
K. longimana	$ML = -22.348 + 37.318\ LRL$	$WM = 0.713\ LRL^{3.152}$	$n = 13$ (ML); $n = 22$ (WM)	Adams and Klages (1987)
G. antarcticus	$ML = -43.4 + 42.87\ LRL$	$WM = -0.0.655 + 3.33 \ln LRL$	$n = 20$	Clarke (1986)
A. antarcticus	$ML = -4.301 + 34.99\ LRL$	$WM = 1.229 + 2.944 \ln LRL$	$n = 22$; ML = 13–221 mm	Piatkowski et al. (2001)

Here, we use cephalopod beaks collected from stomach samples of dead emperor penguin chicks at the Pointe Géologie colony (a) to analyse species inventory, size and body mass distribution of the emperor penguin's cephalopod prey, (b) to reconstruct cephalopod trophic ranges in the Dumont d'Urville Sea food web, and (c) to estimate the trophic impact of the emperor penguin on the cephalopod community.

Materials and methods

Field sampling

Field work was conducted at the Pointe Géologie emperor penguin colony (66°40′S, 140°01′E), near Dumont d'Urville (DDU) station in Adélie Land, between November 3rd and December 16th 2004, and between September 25th and November 11th 2005. About 3,000 pairs of emperor penguins breed in this colony. Its size has remained constant since the early 1980s (Barbraud and Weimerskirch 2001). At this stage of the chick-rearing period, when chicks are 2–4 months old, the most intensive feeding occurs (Mougin 1966; Isenmann 1971). The colony was monitored regularly for chick carcasses and entire stomachs ($n = 20$ in 2004; $n = 12$ in 2005) were collected by dissection within 24 h after demise. Sampled stomachs were kept frozen until further analysis.

Laboratory methods

Stomach contents were sieved through a mesh size of 200 µm to collect all relevant dietary remains. Cephalopod beaks and fish otoliths were stored in 70% ethanol. We identified cephalopod species by comparing the lower beaks to a reference collection held at IFM-GEOMAR, Kiel and by reference to Clarke (1986). Lower rostral length (LRL) of the cephalopod beaks was measured with digital callipers (±0.1 mm). Small beaks (LRL < 2 mm) were measured by the stage micrometer installed in a stereo microscope. Dorsal mantle length (ML in millimetres) and wet body mass (in grams) were derived from LRL by means of published allometric relationships (Table 1).

Stable nitrogen and carbon isotope signatures (δ^{15}N, δ^{13}C) of body tissue provide important information on trophic relations within an ecosystem. δ^{13}C is commonly used as a carbon source tracer (e.g. Lesage et al. 2001), because it increases by ≤1‰ from one trophic level to the next (e.g. Peterson and Fry 1987; Michener and Schell 1994). Thus it can provide information on the geographical origin of migrating organisms, too, whereas δ^{15}N is indicative of the trophic distance of an organism from the primary food source of the corresponding food chain (e.g.

Rau et al. 1991, 1992; Jacob et al. 2006). Fractionation of δ^{15}N ranges between 1.4 and 3.3‰ per trophic level (Minagawa and Wada 1984; Post 2002; McCutchan et al. 2003). We determined stable isotope ratios (both δ^{15}N and δ^{13}C) in a sub-sample of 65 beaks from the sampling year 2004 ($n = 996$ beaks from 20 chicks). No beaks from 2005 were analysed, because of the smaller number of samples (12 chicks) and in order to avoid differential storage effects on isotope ratios. Squid beak sub-samples were selected to represent the available size ranges of the four cephalopod (squid) species (see results). In *Psychroteuthis glacialis* ten beaks were selected randomly from the density maximum (median 10% of beaks) of the two modes of the beak size distribution (Fig. 1a), in *Kondakovia longimana* ten beaks were selected randomly from the smallest 10%, the largest 10% and the medium sized 10% of beaks and in *Gonatus antarcticus* and *Alluroteuthis antarcticus* all beaks measured ($n = 10$ and $n = 5$ beaks, respectively) were analysed.

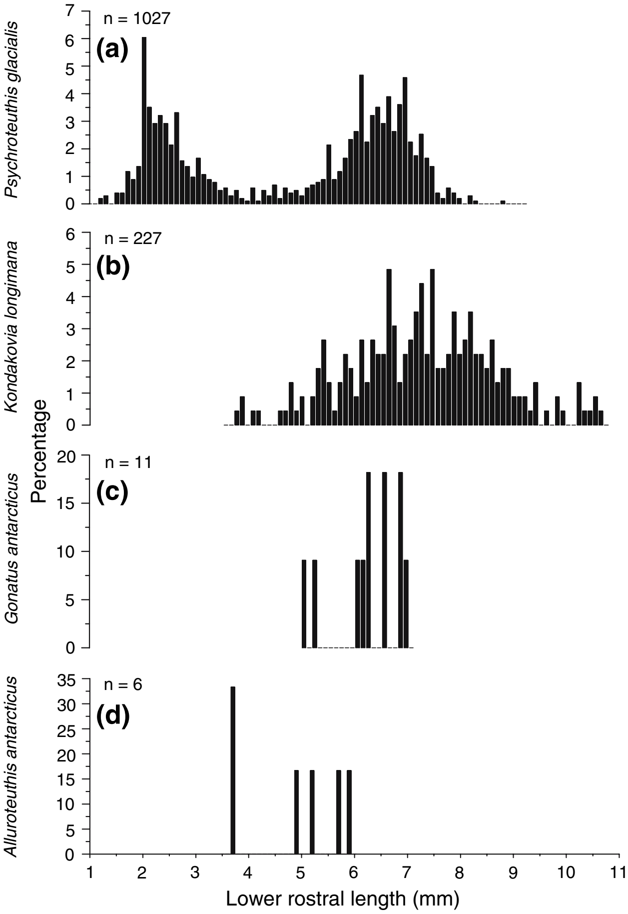


Fig. 1 Beak length-frequency distributions for **a** *P. glacialis*, **b** *K. longimana*, and **c** *G. antarcticus* and *A. antarcticus* based on stomach contents of 31 emperor penguin chick carcasses collected in 2004 ($N = 20$) and in 2005 ($N = 11$)

Prior to isotope analysis, samples were dried and ground to a fine powder using a pebble mill. Stable isotope analysis and concentration measurements of nitrogen and carbon were performed simultaneously with a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer, coupled to a THERMO NA 2500 elemental analyzer via a THERMO/Finnigan Conflo II-interface (GeoBio-Center at Ludwig-Maximilans-Universität, München). Stable isotope ratios are given in the conventional delta notation (δ^{13}C; δ^{15}N) relative to atmospheric N_2 (Mariotti 1984) and PDB (PeeDee Belemnite standard). Standard deviation for repeated measurements of lab peptone standard was <0.15‰ for nitrogen and carbon. Standard deviations of concentration measurements of replicates of our lab standard are <3% of the concentration analysed.

Trophic analysis

We used a full factorial analysis of covariance (ANCOVA) to establish linear models of the stable isotope ratio (δ^{15}N, δ^{13}C) versus the squid species and the covariate LRL, after checking the data for normality and homogeneity of variances. In order to evaluate whether δ^{13}C was affected by beak fat content, we included the C/N ratio that represents a lipid content proxy (McConnaughey and McRoy 1979) in the ANCOVA of δ^{13}C as a second covariate. The resulting δ^{15}N model was used to estimate the δ^{15}N value of each beak for the corresponding LRL collected from different species. Data were statistically analysed using the software JMP by Statistical Analysis System (SAS) Institute. Significance of the results was judged at level 0.05. Mean values are presented ±1 standard deviation.

We inferred trophic level distribution of the cephalopods from the δ^{15}N frequency distribution of the beaks and trophic impact of the emperor penguins on the cephalopod community from a cephalopod body mass weighted δ^{15}N frequency distribution.

Trophic level of emperor penguins at different breeding sites

In order to explore the relationship between diet composition (crustaceans, squid and fish as % of prey mass) and trophic level of emperor penguins, we compared data from seven different colonies, Amanda Bay (Gales et al. 1990), Pointe Géologie (Offredo et al. 1985), Cape Roget and Coulman Island (Cherel and Kooyman 1998), Auster Glacier and Taylor Glacier (Robertson et al. 1994) and the Drescher Inlet (Klages 1989). Emperor penguin trophic level in each colony was calculated from diet composition and average trophic level of the three diet items by means of a mass weighted mean:

$$\delta^{15}\mathrm{N}_{\mathrm{emperor}} = 3.3 + (\mathrm{Mass\%}_{\mathrm{crust}} \times \delta^{15}\mathrm{N}_{\mathrm{crust}} + \mathrm{Mass\%}_{\mathrm{squid}} \times \delta^{15}\mathrm{N}_{\mathrm{squid}} + \mathrm{Mass\%}_{\mathrm{fish}} \times \delta^{15}\mathrm{N}_{\mathrm{fish}})/100$$

where $\delta^{15}N_{crust} = 3.5$ (U. Jacob, unpublished data), $\delta^{15}N_{fish} = 9.04$ (U. Jacob, unpublished data) and $\delta^{15}N_{squid} = 5.93$ (this study, mass weighted mean) and 3.3 is the average tropic level step size (Minagawa and Wada 1984).

Results

Cephalopod prey composition

Stomach content was sampled from 32 emperor penguin chicks at Pointe Géologie and contained fish and crustacean remains, cephalopod beaks and pebbles. Fish eye lenses of up to several hundreds per sample indicated that fish had an important share in the penguin diet. Few otoliths were found, all coming from Nototheniidae. Lower cephalopod beaks occurred in 31 of 32 stomach samples with a total number of 1,327 (996 in 2004 and 331 in 2005). The average number of beaks per chick stomach content was 41 ± 51 and did not differ significantly between 2004 and 2005 ($P = 0.193$, ANOVA of log10 transformed data). A total of 1,317 lower beaks could be allocated to species. These beaks were still uneroded or at least did not show severe signs of digestion, i.e. the rostrum was still sharp albeit with partly broken and abraded wings. We identified four cephalopod (squid) species, *P. glacialis* (Psychroteuthidae; $N_{2004} = 736$, $N_{2005} = 322$), *K. longimana* (Onychoteuthidae; $N_{2004} = 227$, $N_{2005} = 5$), *G. antarcticus* (Gonatidae; $N_{2004} = 10$, $N_{2005} = 1$), and *A. antarcticus* (Neoteuthidae; $N_{2004} = 16$, $N_{2005} = 0$).

A total of 1,271 lower beaks were in sufficiently good condition to allow for measurement of lower rostrum length (LRL, Fig. 1). *P. glacialis* showed a distinct bimodal distribution of LRL, with one peak at 2–3 mm and a second one at 6–7 mm in both years. The LRL distribution of *K. longimana* was unimodal (7.09 ± 1.36 mm). The few beaks in *G. antarcticus* (6.20 ± 0.62 mm), and *A. antarcticus* (4.85 ± 0.96 mm) provided no clues on size distribution.

The corresponding mantle length ML amounted to 76 mm (left peak) and 251 mm (right peak) in *P. glacialis*, to a mean of 242 ± 51 mm in *K. longimana*, and to a mean of 222 ± 27 and 165 ± 34 mm in *G. antarcticus* and *A. antarcticus*, respectively. The corresponding wet body mass WM amounted to 10 g (left peak) and 322 g (right peak) in *P. glacialis*, to a mean of 384 ± 224 g in *K. longimana*, and to a mean of 233 ± 70 and 390 ± 201 g in *G. antarcticus* and *A. antarcticus*, respectively. The pooled frequency distribution of both mantle length and wet body mass were distinctly bimodal (Fig. 2).

Trophic levels and trophic relations

Nitrogen stable isotope ratio of the four examined squid species was significantly affected by squid species and beak size, as indicated by the multiple linear model (Fig. 3a):

$$\delta^{15}\mathrm{N} = 4.5569 + 0.1298 \times \mathrm{LRL} + 1.5238 \times \mathit{TaxonN} + 0.3521(\mathrm{LRL} - 6.2800) \times \mathit{TaxonN}$$

where $TaxonN = 1$ for *P. glacialis*, *G. antarcticus*, *A. antarcticus*, and –1 for *K. longimana*.

$\delta^{15}N$ values were indistinguishable in *P. glacialis* (range 4.68–8.02‰, mean = 6.60 ± 1.06‰), *G. antarcticus* (range 5.52–8.05‰, mean = 6.88 ± 0.74‰) and *A. antarcticus* (range 4.25–6.68‰, mean = 5.55 ± 0.91‰), but significantly lower in *K. longimana* (range 2.39–5.67‰, mean = 3.67 ± 0.88‰). Moreover, $\delta^{15}N$ decreased in *K. longimana* by about 1.2‰ from small to large beaks (Fig. 3a).

Carbon stable isotope ratio of the four examined squid species was significantly affected by squid species and

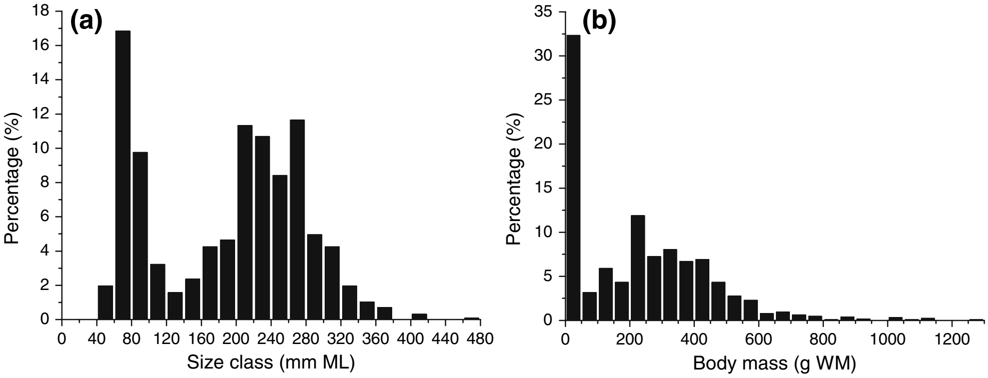


Fig. 2 **a** Size class (mm ML) and **b** body mass (g WM) of all four squid species combined ($n = 1{,}271$). ML and WM were calculated from beak length LRL by means of the allometric relations in Table 1

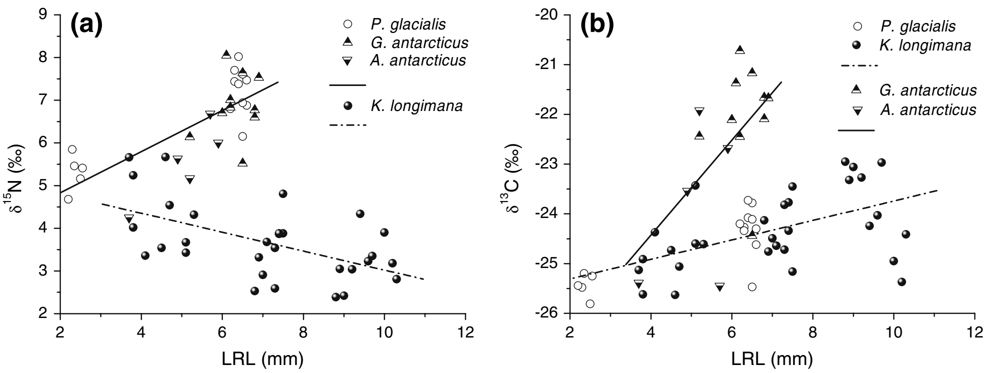


Fig. 3 Multiple linear models of stable isotope ratios versus lower rostral length of squid beaks (*LRL*) and squid taxon. Models were established by full factorial ANCOVA. **a** $\delta^{15}N = 4.5569 + 0.1298 \times \text{LRL} + 1.5238 \times \textit{TaxonN} + 0.3521(\text{LRL} - 6.2800) \times \textit{TaxonN}$ $N = 60$, $R^2 = 0.821$, $P < 0.001$. $\textit{TaxonN} = 1$ for *P. glacialis, G. antarcticus, A. antarcticus*, and –1 for *K. longimana*. **b** $\delta^{13}C = -26.9739 + 0.5756 \times \text{LRL} + 1.1099 \times \textit{TaxonC} + 0.3796(\text{LRL} - 6.2800) \times \textit{TaxonC}$ $N = 60$, $R^2 = 0.580$, $P < 0.001$. $\textit{TaxonC} = 1$ for *G. antarcticus, A. antarcticus*, and –1 for *P. glacialis, K. longimana*

beak size, too (Fig. 3b), but not by beak C/N ratio ($P = 0.493$):

$$\delta^{13}C = -26.9739 + 0.5756 \times \text{LRL} + 1.1099 \times \textit{TaxonC} + 0.3796(\text{LRL} - 6.2800) \times \textit{TaxonC}$$

where $\textit{TaxonC} = 1$ for *G. antarcticus*, *A. antarcticus*, and -1 for *P. glacialis*, *K. longimana*.

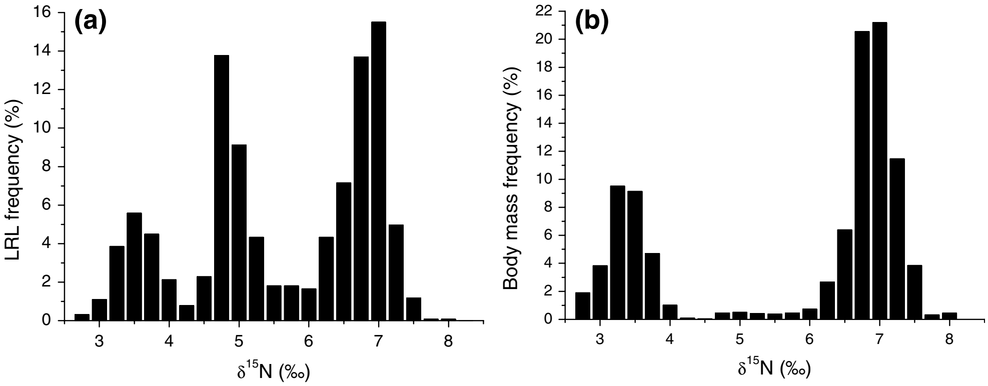
$\delta^{13}C$ values fell in two significantly different groups, *P. glacialis* (range –25.81 to –23.73‰, mean = –24.67 ± 0.70‰) and *K. longimana* (range –25.63 to –22.95‰, mean = –24.33 ± 0.78‰) on the one hand, and *G. antarcticus* (range –24.44 to –20.72‰, mean = –22.01 ± 1.02‰) and *A. antarcticus* (range –25.45 to –21.92‰, mean = –23.80 ± 1.59‰) on the other hand.

In terms of $\delta^{15}N$, the trophic spectrum of the four squid species combined covered a range from 2.5 to 8‰ (Fig. 4a). This spectrum exhibited three peaks at approximately 3.5, 4.75–5 and 6.75–7‰. Emperor penguins concentrated their feeding on the upper trophic range of their cephalopod prey. Squids with $\delta^{15}N$ above 6‰ contributed more than 68% to the squid body mass consumed by the penguins.

Trophic level of emperor penguins at different breeding sites

Emperor penguins trophic level clearly depends on its diet composition, as indicated by the ternary plot in Fig. 5. Trophic level was highest where the penguin diet was rich in fish such as in Amanda Bay (96.8% fish, $\delta^{15}N = 12.23$‰), Pointe Géologie (95.0% fish, 12.14‰), Cape Roget (93.0% fish, 12.12‰) and Coulman Island (88.0% fish, 11.97‰). When squid was dominant or of similar significance as fish, trophic position of penguins was distinctly lower, i.e. at Auster Glacier (44.7% squid, $\delta^{15}N = 10.95$‰) and Taylor Glacier (69.3% squid, 10.18‰). Emperor penguin trophic level was lowest when krill dominated the diet as in Drescher Inlet (52.1% krill, $\delta^{15}N = 9.15$‰, Fig. 5).

Fig. 4 $\delta^{15}N$ frequency distribution of **a** beak numbers and **b** squid body mass. $\delta^{15}N$ of each beak ($n = 1{,}271$) was estimated by the multiple linear model of $\delta^{15}N$ versus beak length and species (Fig. 3), and squid body mass was estimated from beak length by the species specific allometric relations (Table 1)



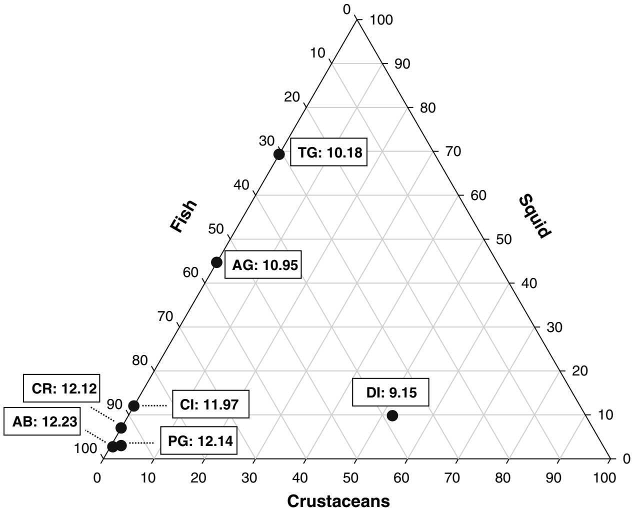


Fig. 5 Ternary plot showing diet composition (% mass) and corresponding calculated trophic level of emperor penguins at different breeding sites: Amanda Bay (*AB*), Pointe Géologie (*PG*), Cape Roget (*CR*), Coulman Island (*CI*), Auster Glacier (*AG*), Taylor Glacier (*TG*), Drescher Inlet (*DI*). *Numbers in rectangles* are emperor penguin δ^{15}N values estimated from diet composition and average trophic level of the three diet items fish, squid and crustaceans by means of a mass weighted mean (see "Materials and methods")

Discussion

Significance of squid in penguin alimentation at Pointe Géologie

Inferring diet composition from chick stomach contents has some disadvantages. We do not know whether the chick stomach content is a true reflection of adult feeding, because regurgitation may involve a bias related to prey item size or taxon, and digestion rate may differ between prey items, as observed by Wilson et al. (1985). Furthermore, the chick stomach content is in an advanced digestion state, making a quantitative weight based analysis difficult. These problems, however, do not seriously affect our analysis, because we do not aim at feeding rates, but on the composition of one particular prey group, squid. These are represented by their beaks which are more resistant to digestion than other hard part items such as fish otoliths in penguin diet (Pütz 1995) and thus reflect squid prey composition over a longer period of time.

The four cephalopod species identified in our chick stomach samples (*P. glacialis*, *K. lonigimana*, *A. antarcticum*, *G. antarcticum*) constitute the major squid prey of breeding emperor penguins all around the Antarctic (Offredo and Ridoux 1986; Piatkowski and Pütz 1994; Robertson et al. 1994; Cherel and Kooyman 1998). The share of each species differs from colony to colony, *P. glacialis* usually being the most frequent one (Collins and Rodhouse 2006). Other species, e.g. *Galiteuthis glacialis*, *Moroteuthis ingens*, *Mesonychoteuthis hamiltoni* or *Histoteuthis* sp. play a minor role in the emperor penguin diet (Offredo et al. 1985; Piatkowski and Pütz 1994; Robertson et al. 1994; but see also Ainley et al. 1992).

It remains uncertain whether the emperor penguins exploit the full size range of squid present off Adélie Land during the breeding season because independent information on squid size (ML) range in this region is lacking (but see below). Nevertheless, the population of the most abundant prey species, *P. glacialis*, is assumed to consist of a juvenile and an adult cohort (Offredo et al. 1985), which appears to be fully represented by the bimodal beak size-frequency distribution (Fig. 2). This may be different in the larger *K. longimana*, of which specimens up to 16.4 mm LRL (588 mm ML) have been reported from Crozet Island waters (Cherel et al. 2004).

Offredo and Ridoux (1986) reported a 3% (wet mass) share of squid in the diet of emperor penguins at Pointe Géologie which is quite low compared to other colonies (up to 69%, Robertson et al. 1994). Our findings of up to several hundred fish eye lenses in each chick stomach indicate that indeed finfish is of particular significance in the penguin diet at Pointe Géologie. Nototheniidae predominate, according to the otoliths found, as reported in earlier studies from this area (Offredo and Ridoux 1986). We presume that the Antarctic Silverfish *Pleuragramma antarcticum* is the major fish prey, as reported from other colonies (e.g. Offredo and Ridoux 1986; Klages 1989; Gales et al. 1990; Cherel and Kooyman 1998).

Trophic position and range of squid in the Dumont d'Urville Sea

P. glacialis (δ^{15}N 6.60 ± 1.06‰), *G. antarcticus* (δ^{15}N 6.88 ± 0.74‰) and *A. antarcticus* (δ^{15}N 5.55 ± 0.91‰), are positioned about one trophic level higher (assuming a 3‰ increase from one trophic level to the next) than *K. longimana* (δ^{15}N 3.67 ± 0.88‰). The increase of δ^{15}N in the former three species with beak size (about 2‰ from 2 to 7 mm LRL, Fig. 3a) indicates an ontogenetic shift in diet towards prey of higher trophic level, as observed in many marine predatory species (Cherel and Duhamel 2003; Phillips et al. 2003; Schmidt et al. 2003). Small and/or juvenile squid have been found to consume mostly crustaceans; they switch to a fish- and cephalopod-based diet as they grow larger (Breiby and Jobling 1985; Lipinski 1987; Ivanovic and Brunetti 1994; Pierce et al. 1994; Collins and Pierce 1996; Coelho et al. 1997; Quetglas et al. 1999). These changes in diet have been related to the energetic advantages of a fish diet compared to a crustacean diet (Pierce et al. 1994), in addition to the simple principle that a wider size-range of prey is available to larger squid (Rodhouse and Nigmatullin 1996).

Small individuals of *P. glacialis* have a trophic level slightly above euphausiids (about 3–5‰, U. Jacob et al., unpublished data), and large ones below pelagic fish (≥9‰, U. Jacob et al., unpublished data). In *K. longimana*, however, δ^{15}N decreases with beak size, contradictory to common wisdom as well as to observations in this species at Crozet Island (Cherel and Hobson 2005). We can only speculate how this isotope pattern and the overall low trophic level (Cherel and Hobson 2005 report a similar δ^{15}N range) of *K. longimana* may be explained. *K. longimana* is described as a pelagic predator (Lubimova 1985; Collins and Rodhouse 2006) feeding on zooplankton and micronekton (Nemoto et al. 1985), with a strong preference for krill (Nemoto et al. 1985, 1988; Lu and Williams 1994). Both large pelagic crustaceans and fish have similar or even higher trophic levels than *K. longimana* (U. Jacob et al., unpublished data), only small pelagics such as copepods and pteropods would fit into the picture. Seasonal variability of krill δ^{15}N may play a role too. Frazer (1996) reported δ^{15}N values ranging from –2 to +5‰ δ^{15}N, mainly dependent on changes in the isotopic composition of algal food resources exploited by krill offshore along the west coast of the Antarctic Peninsula and in the Weddell Sea. Lacking further detailed information on the feeding habits of *K. longimana*, trophic relations of this species remain enigmatic.

The four cephalopod species taken as a whole cover a trophic range from 2.5 to 8‰ δ^{15}N, corresponding to about two trophic levels (Fig. 4a). The lower end of the range is occupied by large *K. longimana* (see above), whereas large *P. glacialis* are positioned at the upper end. This is in accordance with their reported diet of mainly euphausiids, Nototheniidae and *P. antarcticum* (Kear 1992; Lu and Williams 1994; Collins et al. 2004).

We found a significant increase in δ^{13}C with beak size in all four species (Fig. 3b). This relation, however, should be taken with a grain of salt regarding *A. antarcticus* and *G. antarcticus*, because of the few values and small range of beak length data (Fig. 2). Thus, two sound findings have to be discussed, the significant higher δ^{13}C in *A. antarcticus* and *G. antarcticus* compared to *P. glacialis* and *K. longimana*, and the significant increase of δ^{13}C with beak size in the latter two species. In the Southern Ocean bulk phytoplankton δ^{13}C varies geographically by about 10‰ (Goericke and Fry 1994), and these differences should be traceable through the food web. Accordingly, the higher δ^{13}C values in *A. antarcticus* and *G. antarcticus* point towards migration from a remote location supplying a different plankton food base, either seasonal or ontogenetic, of these reportedly Antarctic and sub Antarctic (Collins and Rodhouse 2006) species. The comparatively lower δ^{13}C in small (young) *P. glacialis* and *K. longimana* indicate that these animals grew up in high-Antarctic waters. The increase of δ^{13}C with beak size, however, may be related to an ontogenetic shift in the diet—already indicated by the size related change in δ^{15}N—either to prey that undergoes seasonal migration, maybe coupled to the seasonal pattern in sea ice cover, or related to age dependent seasonal migration patterns (between pelagic, slope and shelf waters).

Trophic impact of the emperor penguin on the squid community

Provided that our beak samples are representative for the emperor penguin's squid catch in the Dumont d'Urville Sea, than the penguins prey on squids between 40 and 480 mm ML (Fig. 2a), i.e. between 2 and 1,272 g wet body mass (Fig. 2b). Several Antarctic cephalopod species, however, can grow distinctly larger, e.g. *K. longimana*, *A. antarcticus* and *M. hamiltoni*. Specimens up to 1,000 mm ML have been reported from stomach contents of Patagonian toothfish (Xavier et al. 2002), of southern bottlenose whales and sperm whales (Clarke 1980; Slip et al. 1995), of southern elephant seal (e.g. Piatkowski et al. 2002), and of wandering albatrosses who occasionally encounter surface drifting squid who lost neutral buoyancy (Lipinski and Jackson 1989). From the positive correlation of diving depth (up to 564 m in penguins, up to 2,000 m in toothfish, whales and elephant seals) and squid size, Collins and Rodhouse (2006) conclude that larger squid live deeper and thus cannot be reached by emperor penguins. This, however, remains an open question because it may well be that there is a size limit to the prey handling capacity of emperor penguins.

The cephalopod prey of the emperor penguin covers a wide trophic range (2.5–8.0‰ δ^{15}N, Fig. 4a, mean mass weighted δ^{15}N = 5.9‰, Fig. 4b), but their predatory impact concentrates on the upper part of this range (68% > 6‰ δ^{15}N, Fig. 4b). This is a consequence of squid species specific size range (Fig. 1) and size-trophic level relationship (Fig. 3). Assuming that average values for the trophic level of euphausiids (3.5‰ δ^{15}N, U. Jacob, unpublished data), *P. antarcticum* (9.0‰ δ^{15}N, U. Jacob, unpublished data) and squid (5.9‰ δ^{15}N, this study) are valid for the whole Antarctic, we can infer the trophic position of emperor penguins at different sites from diet composition (Fig. 5). Trophic level is high when diet is rich in fish, and low when diet is rich in krill, and intermediate when squid plays a major role. Overall the trophic level of the emperor penguin can vary by 2‰ δ^{15}N between colonies, rather a full trophic step (±3.3‰ for protein rich diet, Wada et al. 1987; McCutchan et al. 2003). So far, δ^{15}N has been determined in emperor penguins from the Weddell Sea only (U. Jacob, unpublished data), and this value, 10.28‰, is slightly above our calculated value of 9.15‰. Indeed this higher δ^{15}N value would be consistent with high proportions of fish and squid in stomach samples of emperor penguins collected in the marginal ice zone of the Weddell Sea (Ainley et al. 1992). It remains to be seen whether direct measurement in other colonies confirm our findings. If so, then the flexibility in alimentation of the emperor penguin translates in distinct variability of its position in the trophic hierarchy, a feature that should be kept in mind when comparing food webs of different Antarctic regions.

Conclusions

Emperor chick stomach contents yield valuable ecological information far beyond just the penguin's diet. The combined taxonomic, morphometric and trophic (by means of stable isotope ratios) analysis of cephalopod beaks from chick stomachs provides otherwise inaccessible data on squid trophic ecology, including indications of migration patterns and ontogenetic shifts in diet. Moreover, it enables us to infer (qualitatively) the trophic impact of a particular emperor penguin colony on the squid community in its feeding area. Our approach might be developed further along a number of different lines: (a) it may be used to compare squid trophic ecology as well as penguin trophic impact between different regions/colonies; (b) coupling with models of penguin metabolism it will allow to estimate quantitative trophic impact on the squid community (i.e. consumption); and (c) one might explore whether fish otoliths can be used in a similar way. Finally, collecting of dead chicks and preservation of their stomach contents could form the base of a regular monitoring programme in easily accessible colonies, in order to track long-term changes in penguin as well as squid trophic ecology which may be indicative of climate change induced modifications of the Antarctic food web.

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PUBLICATION II

FORAGING MOVEMENTS OF EMPEROR PENGUINS AT POINTE GÉOLOGIE, ANTARCTICA.

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ORIGINAL PAPER

Foraging movements of emperor penguins at Pointe Géologie, Antarctica

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Abstract The foraging distributions of 20 breeding emperor penguins were investigated at Pointe Géologie, Terre Adélie, Antarctica by using satellite telemetry in 2005 and 2006 during early and late winter, as well as during late spring and summer, corresponding to incubation, early chick-brooding, late chick-rearing and the adult pre-moult period, respectively. Dive depth records of three post-egg-laying females, two post-incubating males and four late chick-rearing adults were examined, as well as the horizontal space use by these birds. Foraging ranges of chick-provisioning penguins extended over the Antarctic shelf and were constricted by winter pack-ice. During spring ice break-up, the foraging ranges rarely exceeded the shelf slope, although seawater access was apparently almost unlimited. Winter females appeared constrained in their access to open water but used fissures in the sea ice and expanded their prey search effort by expanding the horizontal search component underwater. Birds in spring however, showed higher area-restricted-search than did birds in winter. Despite different seasonal foraging strategies, chick-rearing penguins exploited similar areas as indicated by both a high 'Area-Restricted-Search Index' and high 'Catch Per Unit Effort'. During pre-moult trips, emperor penguins ranged much farther offshore than breeding birds, which argues for particularly profitable oceanic feeding areas which can be exploited when the time constraints imposed by having to return to a central place to provision the chick no longer apply.

Keywords Foraging distribution · Central-place forager · Emperor penguin · Area-restricted-search · Foraging strategies

Introduction

During their breeding season, pelagic seabirds forage from a central place (sensu Orians and Pearson 1979) travelling outward to feeding patches, where their foraging behaviour is difficult, or impossible to observe. However, advances in solid-state technology in the form of animal-attached devices have done much to change this. There is now a suite of transmission and logging technologies available to help us examine the location and extent of feeding of seabirds (see Ropert-Coudert and Wilson 2005 for review).

The emperor penguin (*Aptenodytes forsteri*) is the largest (up to 40 kg mass, Williams 1995) and deepest diving of all breeding seabirds, feeding only at sea, with a maximum-recorded dive depth of 564 m (Wienecke et al. 2007). These extraordinary diving capabilities allow emperor penguins to forage deep in the open ocean and throughout the water column over the Antarctic shelf. Exploitation of prey at depth gives the emperor penguin access to a large water volume, which presumably helps counteract their low travelling speeds compared to volant seabirds (Meinertzhagen 1955; Wilson et al. 1989;

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Kooyman et al. 1992a; Weimerskirch et al. 1994b). A lower travelling speed compromises a breeding bird's ability to forage because it correspondingly reduces the range over which central place foragers may operate (Orians and Pearson 1979). This time spent foraging is determined by the necessary feeding frequency of the brood. The foraging efficiency achieved during the trip is constrained by prey encounter rate, which is itself affected by travelling speeds and depths (Ropert-Coudert et al. 2004).

The rate at which energy can be delivered to the brood, therefore, is dependent on these factors but also, critically, on the distance between foraging- and breeding sites (Weimerskirch et al. 1994a; Weimerskirch 1998; Ropert-Coudert et al. 2004). How far emperor penguins have to travel and whether they might feed over all, or simply part of, their foraging trips will likely depend on extrinsic conditions such as sea-ice cover and prey distribution, both vertically and horizontally. Indeed, observations at emperor penguin colonies have shown that foraging trips vary in duration as the breeding season goes on (Kirkwood and Robertson 1997a), with the suggestion being that this is brought about by changes in the environment. The complexity of environmental conditions, both biotic and abiotic, with which emperor penguins have to contend ultimately distil out into two major behavioural patterns which are expressed during foraging: (1) travelling behaviour, where birds move quickly and directly through regions inappropriate for foraging, and (2) searching behaviour, where a reduced rate of overall travel results from greater track tortuosity in regions where prey is most likely to be located (Wilson 1995; Leopold et al. 1996; Jaquet and Whitehead 1999; Nolet and Mooij 2002; Wilson 2002; Markman et al. 2004; Austin et al. 2006). The time allocated to each of these two behaviours results in a total foraging trip duration, which modulates the rate at which chicks can acquire food and thus grow appropriately.

At the colony of Pointe Géologie (Adélie Land) emperor penguins haunt areas of open water in the sea-ice such as polynias and light pack-ice zones during winter (Ancel et al. 1992; Rodary et al. 2000a). During summer, however, when sea-ice limitations diminish, their foraging extent is still unknown. From September on, when chicks become thermally independent, adults shuttle between the colony and the open water over about 100 days to forage. At this time each adult breeder may perform up to 8 or 9 foraging trips, lasting between 2 days and several weeks (Mougin 1966; Isenmann 1971; Offredo and Ridoux 1986; Kooyman and Kooyman 1995; Kirkwood and Robertson 1997a). The high energetic demands of adult penguins during the time that chicks are thermally independent (Robertson and Newgrain 1996) result from the birds having to acquire enough food for themselves as well as their brood in a period when much time and energy is invested in commuting between the central (breeding) place and the site of food acquisition. The situation is exacerbated because emperor penguins also have to gain enough body reserves to be able to moult (which lasts on average 30 days and during which no foraging occurs, e.g. Le Maho et al. 1976; Groscolas 1978). This occurs immediately after the chicks become fully independent.

The objectives of this study were: (1) to identify the foraging distribution of breeding emperor penguins from Pointe Géologie during winter, late chick-rearing and adult pre-moult periods, (2) to identify the moult location with a view to assessing how this location ties in with breeding and feeding constraints, (3) to examine depth utilisation of penguins during winter and late chick-rearing so as to (4) elucidate prey search strategies for the different stages of the birds' life cycle.

Materials and methods

Study colony, periods, instruments and fieldwork

The study was conducted at the Pointe Géologie colony (66°40′S, 140°01′E) near Dumont d'Urville station; (1) during austral winter between the end of May and the beginning of September 2005 and (2) in spring and summer between the end of October 2005 and the end of January 2006.

During the first study in winter, three females and two males were equipped during the pairing period (between 20 April and 11 May) with satellite transmitters to track their foraging trips and archival tags to record their diving behaviour. The satellite transmitters (Sirtrack, New-Zealand, 13 × 5 × 3 cm) weighed 230 g and had a 16 cm antenna (angled at 60° and facing backwards). They transmitted with a pulse repetition rate of 90 s, and were duty cycled to be 6 h on and 6 h off. The time depth recorders (Mk9, Wildlife Computers, USA, 6.7 × 1.7 × 1.7 cm, 0.5 m depth resolution, 0 to 1,000 m depth range) weighed 30 g, had a memory of 16 Mbytes and were set to record every 5 s.

For the second study period, during late chick-rearing, birds were either equipped on their return from sea before reaching the colony, or after they had fed the chick and were about to leave the colony again. Several couples were colour marked (using Nyanzol) during the pairing period in order to monitor breeding success. We attempted to choose successful breeders with a healthy chick among these marked birds for device equipment. Two types of Argos transmitter were used: between the 31 October and the 1 December; fifteen adult emperor penguins were equipped either with a conventional satellite transmitter (Spot5, Wildlife Computers, USA, 7.1 × 3.4 × 2.6 cm, 78 g) or a device that combined an Argos transmitter with an archival tag (Splash, Wildlife Computers, USA, 7.8 × 5.0 × 2.3 cm, 105 g, 0.1 m depth resolution, 0–1,000 m depth range, memory—14 Mbytes, set to record every 2 s). Six Spot5 tags were used to measure foraging tracks during late chick-rearing and during the pre-moult stage. The further deployment of five Splash tags allowed additional dive data records. Spot5 and Splash tags had 17 and 19 cm long antennae, respectively, that projected out at the back of the transmitters (angled at 60° and 65°, respectively, and facing backwards) both transmitting at 90 s intervals continuously but limited to a maximum of 320 transmissions per day.

In a third study, five birds remained equipped (Spot5 or Splash) beyond the chick-rearing period to enable us to record pre-moult trips. Here, we expected that the start of the moult would be the last position recorded before the loggers fell off with the old plumage.

The frontal area of 15 cm^2 (Sirtrack satellite transmitter) constituted about 2.6% of a 24 kg penguin's cross-sectional area (Wienecke and Robertson 1997), being only 0.5, 1.5 and 2% for MK9, Spot5 and Splash, respectively. To minimize drag (Bannasch et al. 1994) the devices were attached to the lower back feathers using either glue and hose clamps or Tesa tape (Wilson et al. 1997).

Sea-ice concentration maps were provided by the Advanced Microwave Scanning Radiometer for EOS (AMSR-E) and bathymetric data were derived from the ETOPO 1 min gridded evaluation database (GEBCO 1-min global bathymetric grid).

Analysis of transmitted location and archival dive data

Argos satellite records (CLS Argos, Toulouse, France) were classified according to the size of the error radius of the location and the number of signals received by the satellite during a pass. Satellite records were processed by the company OPTIMARE (Bremerhaven, Germany). Data were speed-filtered by comparison of two fixes in succession. The mean speed of travel was calculated by dividing the distance by the time difference between two fixes. When this value exceeded a predetermined maximum speed the point was eliminated from the dataset. We set the maximum speed at 15 km h^{-1} (Wienecke and Robertson 1997), which is slightly higher than the 14.4 km h^{-1} estimated by Kooyman et al. (1992b) for emperor penguins diving under the ice.

Following the distance classifications of Wienecke and Robertson (1997), the maximum distances from the nesting location at Pointe Géologie were measured in a straight-line between the colony and the penguin's most distant position. Minimum total travelling distances were considered to be the sum of all distances between valid locations.

Depth analysis

Depth data were corrected for surface drift in depth values recorded at the water's surface (which varied by ±2 m) using special software (MT-dive; Jensen Software, Kiel, Germany). This software analysed all dives sequentially, writing, dive per dive, a number of defined parameters into an output file. These were: the time of the dive initiation, the overall dive duration, the maximum depth reached during the dive, the descent-, bottom-, and ascent-phase duration, the vertical velocities during the descent, bottom and ascent phases, the number of rapid succession short ascent/descent phases during the bottom phase, and the post-dive interval.

All dives deeper than 2 m were considered as proper dives. The bottom phase, during which penguins are most likely to hunt (Chappell et al. 1993; Wilson et al. 1995) and appear to capture most of their prey (Takahashi et al. 2004; Ropert-Coudert et al. 2006; Bost et al. 2007), was defined by three conditions; it could only occur (1) at depths >85% of the maximum depth of the dive (cf. Kirkwood and Robertson 1997b), (2) if it was bounded by two points of inflection in the rate of change of depth and (3) if the overall rate of change of depth for the whole of the putative bottom period did not exceed 0.2 ms^{-1} (Rodary et al. 2000a). Short ascent/descent phases >2 m during the bottom phase of a dive were quantified according to the number of points of inflection (SPI) during the ascents and descents. Two or three SPI were described as a "wiggle". Such wiggles result in the capture of a single prey item pursued by Magellanic penguins *Spheniscus magellanicus* during the bottom phases of their dives (Fig. 1, cf. Simeone and Wilson 2003). They are also considered to be generally indicative of prey pursuit in penguins (Kirkwood and Robertson 1997b; Luna-Jorquera and Culik 1999; Hull 2000; Rodary et al. 2000b; Tremblay and Cherel 2000; Takahashi et al. 2004). Thus, although we could not derive absolute numbers of prey caught using the methodology, we considered that the number of wiggles occurring in the bottom phase of emperor penguin dives to be approximately linearly related to the number of prey caught. This SPI estimate was divided by the duration of the bottom phase to derive an estimate of prey abundance via 'catch-per-unit effort' (CPUE). Again, although our CPUE figures cannot give absolute abundance indices, higher CPUE values should generally relate to more abundant prey and *vice versa*.

To examine how emperor penguins allocate their time to foraging in certain areas, we examined location and depth data recorded for full foraging trips in winter ($n = 5$) and

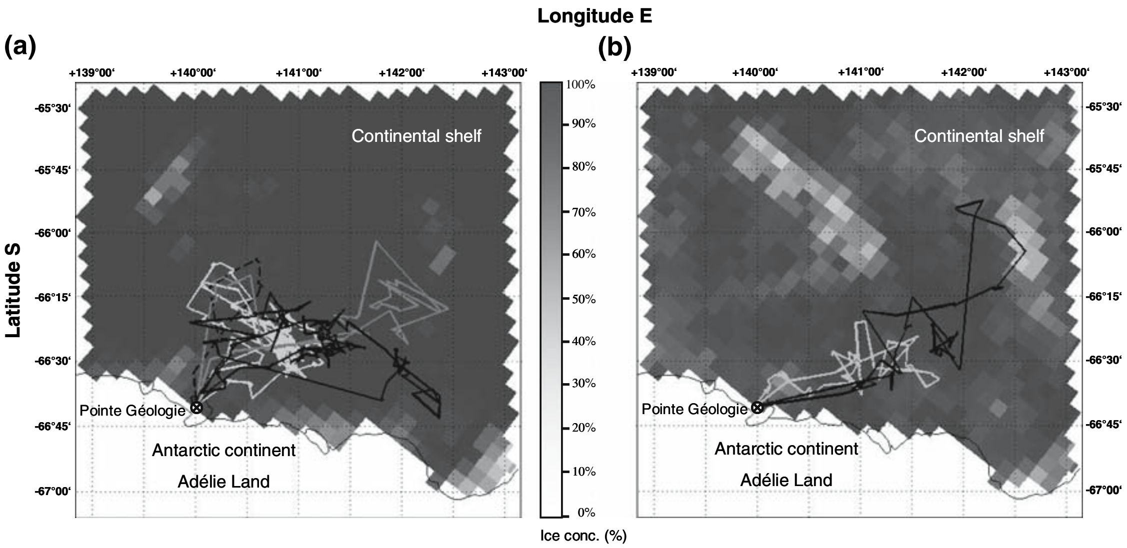

Fig. 1 Movements of **a** three females (a second trip recorded for female F-3a, see Table 1, is *dashed*) and **b** two males over the continental shelf of Adélie Land, monitored by satellite during winter between 15th May and 30th August 2005. Sea-ice data are displayed in percentage from 0 to 100% of ice cover provided by AMSR-E for **a** the 15 July 2005 and **b** the 2 August 2005

during late chick-rearing ($n = 4$). Foraging trips were cut into sections corresponding to periods in which a penguin spent a total ≥100 min underwater (although the precise duration varied according to the timing of satellite fixes). Two foraging parameters were defined relating to both the vertical and the horizontal movement. The extent of vertical movement (here termed vertical extent—VE) was defined by summing maximum depths from all dives between two defined time intervals so that:

$$\mathrm{VE} = \Sigma\, 2 \times \text{maximum dive depths}$$

(units m) over a specified period. Here, the doubling of maximum depths takes into account both the descent and ascent of the dives.

The horizontal movement was divided into two elements (1) the overall horizontal movement within any dive and (2) the tortuosity of the horizontal movement. In order to highlight the degree of the horizontal movement within any dive, cognisance needs to be taken of the extent of the vertical contribution in the dive (see VE above). Based on the fact that penguins travel at a relatively constant speed when underwater (Wilson et al. 2002), the extent of horizontal movement within any one dive can be alluded to via the normal swimming speed multiplied by the dive duration divided by the vertical extent for that dive. Thus, over a defined time period, within which numerous dives are conducted, the horizontal extent (HE):

$$\mathrm{HE}_{\text{underwater}} = \Sigma\,\text{Dive durations} \times \text{Swim speed}/\mathrm{VE},$$

(non-dimensional units) where a normal swim speed of 3 ms^{-1} was taken as standard (Kooyman et al. 1992b). Although this speed figure is based on rather observations from non-breeding birds, it is unlikely to differ greatly from that of foraging birds since penguins generally travel at their lowest cost of transport (Culik et al. 1994), showing remarkably little variation. Any errors in this figure will be consistent across groups and thus affect derived parameters similarly. Note that simple subtraction of the vertical extent from the total distance covered during a dive (nominally derived via the swim speed multiplied by the dive duration) does not take into account how overall distance, vertically travelled distance and horizontally travelled distance change with varying dive angles. For this reason, we opted for a simple ratio, with higher values indicating a greater proportion of the time underwater being dedicated to horizontal travel.

The horizontal tortuosity (HT) was derived by considering the extent of the HE in relation to the straight-line distance between two defined points in time:

$$\mathrm{HT} = \mathrm{HE}_{\text{underwater}}/\text{Straight} - \text{line distance},$$

(units m^{-1}), where the straight-line distance corresponded to the distance between two adjacent PTT fixes. However, this definition was standardized to encompass a defined period of a foraging trip (see above). For this, the sum of the straight-line distances between PTT fixes was taken to represent the overall distance.

Two other measures used to quantify foraging activity over a trip were:

(1) the "Area-Restricted-Search Index" (ARS-I), which was determined by dividing the total distance spent travelling underwater over a defined time interval

(given by the duration underwater multiplied by the normal swimming speed of 3 ms^{-1}) by the straight-line distance travelled during that period (see above) as follows:

$$\text{ARS - I} = \text{Total distance}_{\text{underwater}} / \text{Straight} - \text{line distance}$$

(non-dimensional units). Here, high values indicate high tortuosity (both vertical and horizontal).

(2) the CPUE (SPI min^{-1}), here derived by dividing the number of points of inflection in the bottom phases of dives, by the total time spent underwater for that defined time interval (see above).

Sexes

The two sexes of adult emperor penguins in winter adopt different roles during incubation and chick brooding during which time only one member of a pair gathers food at sea. During late chick-rearing, however, when chicks are thermally independent, adults shuttle almost continuously between the colony and the sea to forage. At this time the sex of inbound penguins could only be (sometimes) determined by voice differentiation by us (Jouventin 1982; Robisson 1992).

The pattern of foraging during trips at sea will be discussed for post-egg-laying females, post-incubating males and adults of both sexes during late chick-rearing with cognisance of the variability of the environmental conditions (such as sea-ice cover and seawater access) for these periods. Data of post-egg-laying females and post-incubating males were combined to compare winter-foraging birds with spring-foraging birds.

Statistics

In order to compare foraging activity parameters for penguin groups with regard to the trip duration, individual foraging trip durations (time at sea) were all taken to add up to 100% and the various trip sections (see above) within these transformed accordingly (cf. Ropert-Coudert et al. 2004). Data are presented as means, averaged over each 10% interval of foraging trip duration. ARS-I and CPUE mean values over foraging trips were defined to be high when they exceeded 60% of the individual parameter maximum. Mean values are presented ±1 standard error (SE). Significant differences between winter-foraging females and winter-foraging males or winter-foraging birds (both sexes) and spring-foraging birds were tested for all values in considered groups without regard to the trip duration by a parametric unpaired *t* test (*t*) or the non-parametric Mann–Whitney rank sum test (*U*), if data did not pass the Kolmogorov–Smirnov test ($P \leq 0.05$) for normal distribution. The significance level was $\alpha \leq 0.05$. Statistic tests were performed with SigmaStat version 3.5 (Systat Software, Point Richmond, USA).

Results

Winter (incubation and chick-provisioning)

Foraging distribution

The emperor penguins equipped in winter foraged exclusively over the coastal shelf. On their departure from Pointe Géologie in May, the three post-egg-laying females headed north-east of the colony where sea-ice images showed closed pack-ice of up to 100% (Fig. 1a). They travelled for 4–7 days (mean: 6 ± 1 day) across 22–96 km (mean: 56 ± 21 km) of fast-ice before entering the sea to forage. After their last dive at the end of the foraging trip, the birds travelled 1–4 days (mean: 2 ± 1 day) across the fast-ice to return to the colony. The walking distances could not be calculated due to a lack of positional fixes at the end of the trip. The three females' complete foraging trips lasted for 72 ± 7 days (range: 59–79 days, Table 1) of which 65 ± 7 days were spent actually gathering food (range: 51–72 days, resting periods on ice floes when the birds were ostensibly at sea were included here). Mean distance travelled over a foraging trip averaged 927 ± 175 km (range: 582–1,149 km) while the mean maximum distance to the colony was 94 ± 16 km (range: 62–116 km, Table 1).

The two equipped male penguins headed north-east after the incubation fast. One foraged where satellite images showed areas of open pack-ice and the other in open pack-ice and a polynia (Fig. 1b). Their complete foraging trips lasted for 24 ± 5 days (range: 19–29 days, Table 1) of which 22 ± 5 days were spent gathering food (range: 17–27 days, resting periods on ice floes when the birds were ostensibly at sea were included here). Males travelled mean foraging trip distances of 521 ± 62 km (range: 459–582 km) while the mean maximum distance to the colony was 106 ± 28 km (range: 78–133 km, Table 1). Both males travelled for two days before undertaking the first dive but covered different distances during that time, walking on the fast ice distances of 54 and 1 km.

The second winter foraging trip conducted by one of the three females (F-3a, Table 1, Fig. 1a) was recorded due to a failed recapture after the first return to the colony. F-3a restarted after 20 days of parental care and travelled for

Table 1 *Aptenodytes forsteri.* Summary of foraging data on monitored females and males in winter, birds in spring and summer (both sexes) at Pointe Géologie in 2005/2006. Emperor penguins were equipped with satellite transmitters

Penguins	Foraging trip records (*N*)	Trip dates (depart-return)	Trip duration (days)	Distance travelled (km)	Maximum distance To colony (km)
Winter-foraging females	3	15 May–2 Aug			
Median (range)			79 (59–79)	1,050 (582–1,149)	104 (62–116)
Mean (± SE)			72 ± 7	927 ± 175	94 ± 16
F-3a trip2	1	4 Aug–14 Aug	10	174	68
Winter foraging males	2	24 Jul–30 Aug			
Median (range)			25 (19–29)	521 (459–582)	105 (78–133)
Mean (±SE)			24 ± 5	521 ± 62	106 ± 28
Spring-foraging birds (both sexes)	21	31 Oct–17 Dec			
Median (range)			8 (2–19)	397 (81–859)	89 (21–163)
Mean (±SE)			7 ± 1	387 ± 48	85 ± 8
Summer-foraging birds (both sexes)	5	22 Nov–20 Jan			
Median (range)			42 (31–54)	3,056 (1,762–3,686)	649 (425–838)
Mean (±SE)			42 ± 5	2,862 ± 345	647 ± 72

10 days, of which 7 days were spent foraging at sea. This foraging trip covered a travelling distance of 174 km, reaching a maximum distance of 68 km to the colony (Table 1).

Diving behaviour

Depth data recorded for the three post-egg-laying females and the two post-incubating males totalled 19,082 dives (14,662 by females and 4,420 by males, Table 2). In winter males dived deeper than females (69.5 ± 10.8 for males and 55.6 ± 3.0 m for females; $U = 28{,}098{,}776$, $P < 0.001$; Fig. 2, Table 2) showing an absolute maximum depth of 438.4 vs. 338.8 m). While at sea, the females and males had days of no water entry. The three females took more of these “rest days” (sensu Kirkwood and Robertson 1997b) than did the two males and, therefore, foraged on proportionally fewer of their days at sea (84.1 ± 3.2 vs. 98.2 ± 1.9%; $t_3 = -3{,}194$, $P = 0.05$). On average, winter-foraging birds (sexes combined) foraged 91.2 ± 7.1% of their days at sea.

Mean and maximum dive durations were both higher for males than for females at 3.1 ± 0.4 versus 2.5 ± 0.1 min ($U = 26{,}697{,}777$, $P < 0.001$) and 16.1 versus 12.2 min, respectively (Table 2). The two males dived for 5.2 ± 0.3 h day^{-1} (range: 2.1–7.8 h day^{-1}) from 07h11 to 18h16 whereas the three females spent 3.5 ± 0.2 h day^{-1}

Table 2 Basic dive features of nine emperor penguins at Pointe Géologie, Adélie Land, in winter and spring 2005, recorded with archival tags and satellite transmitters

Penguins	N dives	Max. dive depth (m)	Mean max. dive depth (m)	Max. dive duration (min)	Mean dive duration (min)
Winter-foraging females	13,605				
Grand mean (± SE)		321.9 ± 19.8	55.6 ± 3.0	11.2 ± 0.8	2.5 ± 0.12
F-3aTrip2	1,057	242.5	47.3 ± 1.8	10.3	2.7 ± 0.02
Winter-foraging males	4,420				
Grand mean (± SE)		426.9 ± 11.6	69.5 ± 10.8	14.0 ± 2.2	3.1 ± 0.35
Winter-foraging birds (both sexes)	19,082				
Grand mean (±SE)		343.7 ± 30.6	58.8 ± 4.7	12.0 ± 0.9	2.7 ± 0.2
Spring-foraging birds (both sexes)	5,466				
Grand mean (±SE)		328.0 ± 42.2	99.0 ± 7.2	10.5 ± 0.7	4.1 ± 0.12

Mean values are given ±1 SE

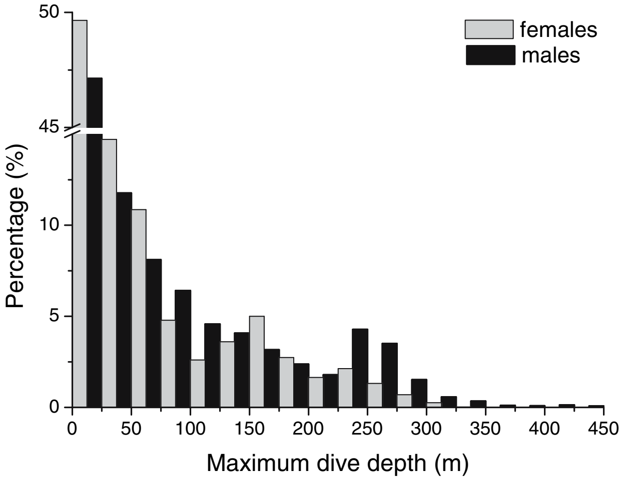

Fig. 2 Frequency distribution of maximum dive depths from foraging emperor penguin females and males, monitored in winter 2005 at Pointe Géologie, Adélie Land

(range: 0.4–6.3 h day^{-1}) in the water, all of which occurred from 08h06 to 17h27 (solar time) and showed higher dive frequencies per day than females (101 ± 5 vs. 85 ± 3 dives day^{-1}; $U = 5{,}546.5$, $P = 0.004$).

Allocation of time during foraging

Altogether, winter-foraging birds showed maximum horizontal tortuosity between 0 and 10% of the trip duration (Fig. 3a) and maximum vertical effort between 60 and 70% of the time into the trip (Fig. 3b). Horizontal tortuosity was significantly higher for females than for males ($U = 3{,}324$, $P = 0.05$), whereas the vertical extent was significantly higher for males than for females ($U = 4{,}591$, $P = 0.028$).

Measures for the overall foraging activity

The area-restricted-search index (ARS-I) showed highly variable values over the course of the foraging trip (Fig. 4a, b) as did the CPUE (Fig. 4c).

Winter-foraging birds (both sexes) showed maximum prey search activity between 70 and 80% of trip duration (Fig. 5a) and maximum CPUE between 60 and 70% of the time into the trip. There was no significant difference of the ARS-I between females and males ($U = 2{,}824$, $P = 0.677$). The CPUE, however was higher for males than for females ($U = 2{,}173$, $P = 0.009$).

Spring (chick provisioning)

Foraging distribution

The emperor penguins equipped during the late chick-rearing period ($n = 10$; 21 foraging trips) centred their foraging activity in shelf waters north-east of the colony covering an area of about 25,000 km^2 (Fig. 6). Foraging trips lasted for 2–19 days (mean: 7 ± 1 days) and rarely went beyond the slope region. The trip lengths of 81–859 km (mean: 387 ± 48 km) reached individual maximum distances of 21–163 km (mean: 85 ± 8 km) from the colony (Table 1). The penguins travelled up to 50 km per day.

Diving behaviour

Depth data recorded for four adults comprised 5,466 dives (Table 2). Mean maximum dive depth of spring-foraging birds was higher than for winter-foraging birds (99.0 ± 7.2 vs. 58.8 ± 4.7 m, $U = 34{,}031{,}782$, $P < 0.001$) although the ranges of maximum dive depth of both groups were

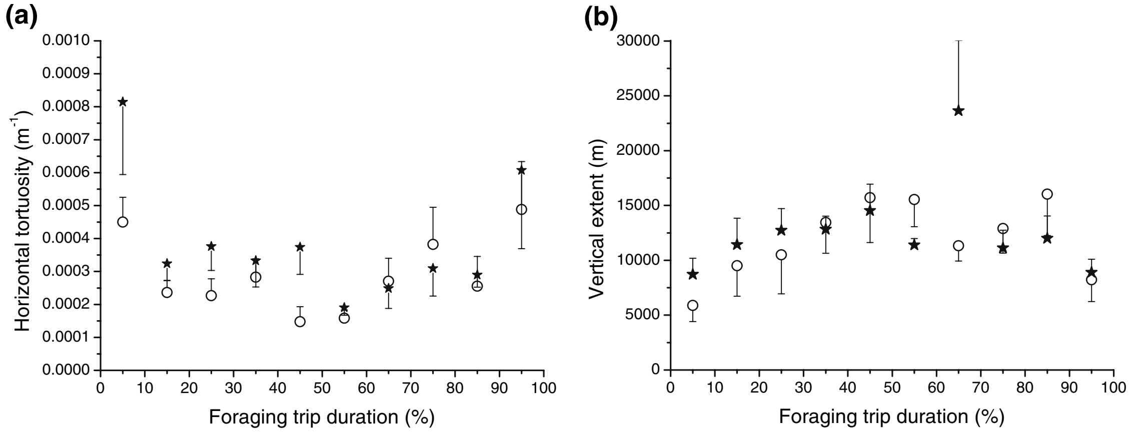

Fig. 3 **a** Horizontal tortuosity and **b** vertical extent of emperor penguins foraging during winter (*filled star* $n = 5$) and spring (*open circle*, $n = 4$). Data are presented as means with standard error (*SE*) per 10% classes over foraging trip duration

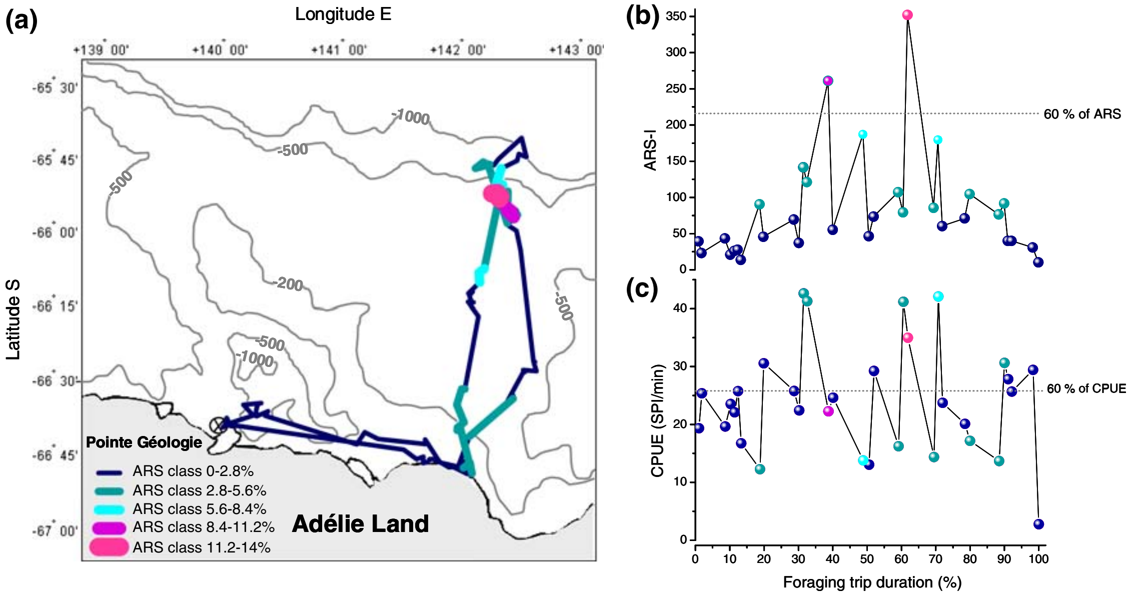

Fig. 4 **a** Area-restricted-search index (*ARS-I*) in percent of a breeding emperor penguin in spring over a complete foraging trip at Pointe Géologie over the Antarctic shelf and **b** ARS-I and **c** catch per unit effort (CPUE, SPI min^{-1}) as they vary with foraging trip duration. ARS-I intensity (in percent) is displayed in **a**, **b** and **c** by *different colour marks* that are explained in **a**. ARS-I **b** and CPUE **c** values were defined as maxima when exceeding 60% of the individual parameter maximum. **a** Shelf bathymetry was derived from the ETOPO 1 min gridded evaluation database (GEBCO 1-min global bathymetric grid)

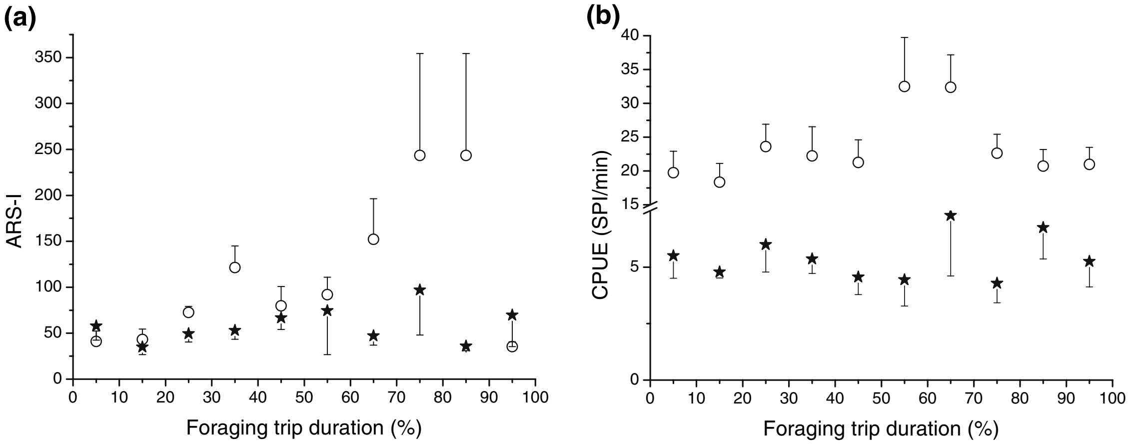

Fig. 5 **a** Area-restricted-search index (*ARS-I*) and **b** catch per unit effort (CPUE, SPI min^{-1}) of emperor penguins foraging during winter (*filled star* $n = 5$) and during spring (*open circle*, $n = 4$). Data are presented as means with standard error (*SE*) per 10% classes over foraging trip duration

almost identical (Table 2). In contrast to winter-foraging birds, the spring-foraging penguins did not take any rest-days. Mean dive duration for spring-foraging birds was 4.1 ± 0.1 min while maximum dive durations ranged from 9.0 to 13.0 min (Table 2). Spring-foraging birds showed a higher dive frequency than winter-foraging birds (126 ± 15 vs. 91 ± 5 dives day^{-1}, $U = 1{,}874$, $P < 0.001$) and spent more time underwater (8.7 ± 1.1 vs. 4.2 ± 0.4 h day^{-1}, $U = 932$, $P < 0.001$) at any hour of the day. Seventy-six percent of dives occurred from 03h00 to 17h00 solar time.

Allocation of time during foraging

Maximum horizontal tortuosity of spring-foraging birds occurred between 90 and 100% of trip duration (Fig. 3a) and maximum vertical effort between 80 and 90% of the time into the trip (Fig. 3b). There was no significant difference in either the horizontal tortuosity ($U = 9{,}750$, $P = 0.105$) or the vertical effort ($U = 9{,}496$, $P = 0.223$) between spring- and winter-foraging birds. Compared to winter females, however, spring-foraging birds showed a

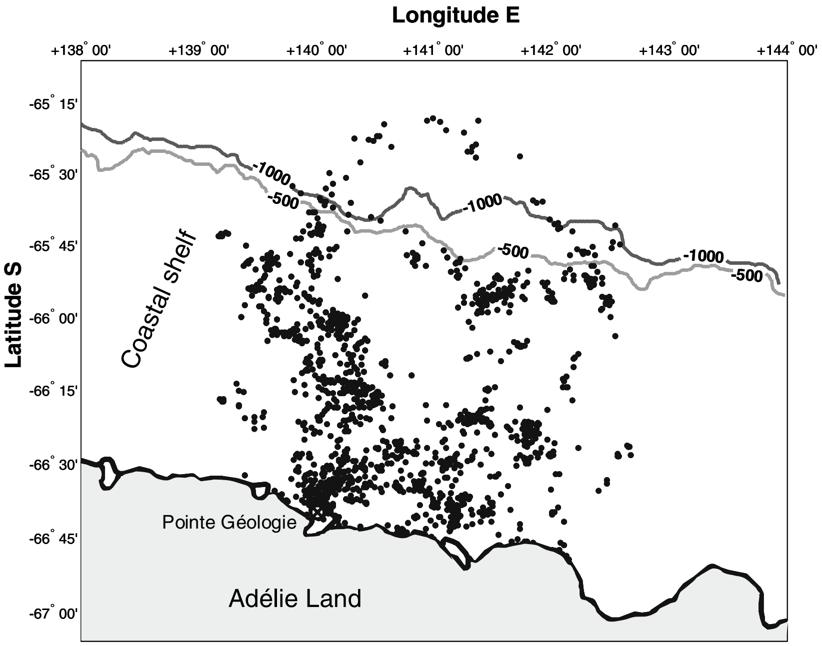

Fig. 6 Foraging trips ($n = 21$) of emperor penguins ($n = 10$) distributed over the Antarctic shelf of Adélie Land, monitored by satellite during late chick-rearing between 31 October and 17 December 2005. Shelf slope off the Adélie Land coast as calculated from ETOPO1 min gridded evaluation database (GEBCO 1-min global bathymetric grid)

significantly lower investment in horizontal tortuosity ($U = 7{,}153$, $P = 0.0042$).

Measures for the overall foraging activity

The maximum search behaviour occurred between 70 and 90% of trip duration (Fig. 5a) and the maximum CPUE occurred between 50 and 60% of the time into the trip (Fig. 5b). Spring-foraging birds showed a significantly higher ARS-I ($U = 5{,}524$, $P < 0.001$) as well as a higher CPUE ($U = 984$, $P < 0.001$) than winter-foraging birds. The latter significance concerning the CPUE, however, may be partially explained by the higher recording frequency of 2 s in spring compared to 5 s in winter.

Summer (pre-moult)

Foraging distribution

Five emperor penguins remained equipped from the breeding season right through into the moult. When leaving the colony after breeding, these birds headed north into the open ocean and dispersed widely to forage over deep water up to 660 km off the Adélie Land before turning back towards the Antarctic coast (Fig. 7). During this pelagic phase the trips lasted on average 42 ± 5 days (range: 31–54 days) and birds covered a total mean distance of 2,862 ± 345 km (range: 1,762–3,686 km) with a maximum distance of 647 ± 72 km (range: 425–838 km) from the colony (Table 1). The last positions of the five equipped penguins were recorded between 31 December 2005 and 20 January 2006 (Fig. 7).

After being equipped in early November 2005, four birds never returned to the colony. As non-breeders or unsuccessful breeders, they spent their time at sea (Fig. 8). Nevertheless, their travelling routes were similar to those of the pre-moult, previously breeding birds heading into the same moulting areas (Figs. 6, 7) with last positions being recorded between 21 December 2005 and 11 January 2006.

Discussion

Accuracy of the methods

Although air-breathing divers have to surface frequently during foraging, these resting periods vary greatly in length over the foraging trip. This affects the likelihood of obtaining a satellite fix as well as the potential quality of any given fix because satellite uplinks can only occur when the PTT is in air. In addition, the likelihood of signal transmission depends on the number of satellite passes over the PTT location, which varies with latitude, and is, in any event, not constant per unit time (Georges et al. 1997). Finally, the manner in which the tag is attached to the animal may also affect transmission properties. All these factors account for the variability in timing and quality of location fixes.

The travelled distance of a penguin between two valid position fixes was considered to be the minimum straight-line distance. As the number of positional fixes increases per unit time, the calculated travel distance will tend to

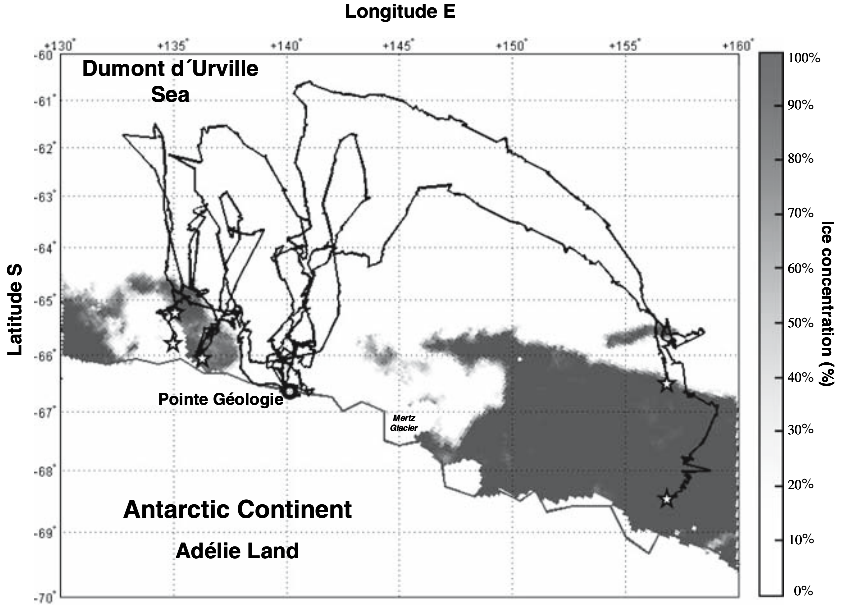

Fig. 7 Movements of five emperor penguins before the adult moult in the Dumont d́Urville Sea, monitored by satellite between 22 November 2005 and 20 January 2006. Sea-ice data are displayed in percentage from 0 to 100% of ice cover provided by AMSR-E for the 20 January 2006. Last at-sea positions are marked by a *star*

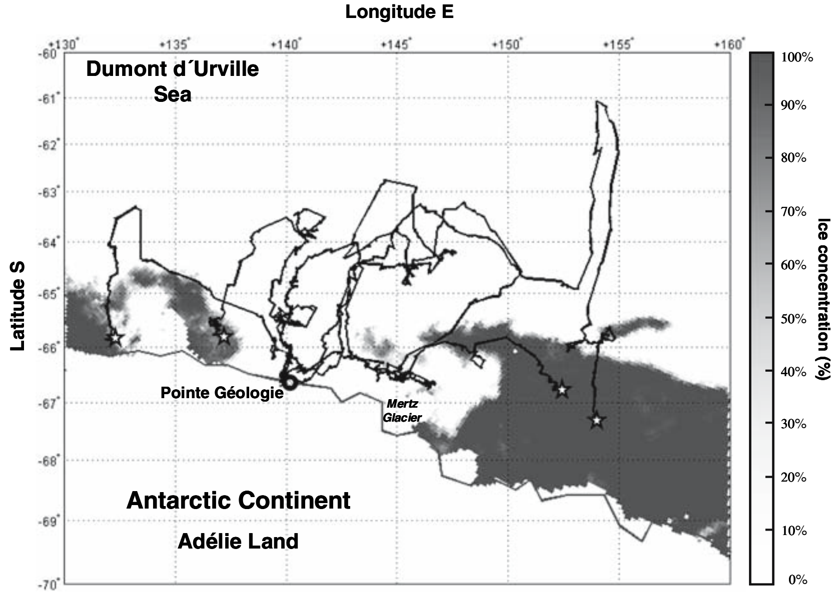

Fig. 8 Movements of four non- or unsuccessful breeding emperor penguins, before the adult moult in the Dumont d́Urville Sea, monitored by satellite between 2 November 2005 and 11 January 2006. Sea-ice data are displayed in percentage from 0 to 100% of ice cover provided by AMSR-E for the 20 January 2006. Last at-sea positions are marked by a *star*

increase because the deviations from a straight-line course will be incorporated. Since the number of valid positions over a foraging trip length varied, analyses were classified into defined time periods spent underwater. This meant that sections of comparable foraging activity (the time spent underwater) could be compared. However, the non-standardized way in which Argos positional fixes were acquired means that, even so, we had to consider different time periods and numbers of valid positions per defined trip section. The resolution of penguin foraging tracks and the analysis of horizontal tortuosity need to bear this in mind although we expect that our approach should broadly highlight trends.

Winter (incubation and chick-provisioning)

Movement at sea

When female penguins conducted their first foraging trip after egg-laying (May–July) the sea-ice extension off the Adélie Land coast was higher than at any other time during the emperor penguin breeding cycle (Metéo station of DDU and AMSR-E - Sea-Ice concentration maps). The female foraging trip length was about two months in winter (56–79 days), which appears typical for this species (Prévost 1961; Wienecke and Robertson 1997). This gives the birds ample time to move far from the colony. Despite this, the penguins' winter foraging range in our study was restricted to cracks and holes in the pack-ice, as has been reported in previous studies (Ancel et al. 1992; Kirkwood and Robertson 1997b; Rodary et al. 2000a). Trip durations of 56–79 days partially confirmed earlier observations for this colony (Prévost 1961) whereas females at Auster colony returned after 67–96 days to their breeding site (Wienecke and Robertson 1997). The foraging distribution within 120 km of the breeding colony at Pointe Géologie was similar to Auster females but, however, females at Auster travelled more than twice the distance during foraging trips compared to females from Pointe Géologie (mean 2617 ± 198 km at Auster vs. 927 ± 175 km at Pointe Géologie).

In late July, when male penguins moved to sea after their long incubation fast, sea-ice satellite images indicated that light pack-ice areas and polynias north and east of Pointe Géologie had extended (Fig. 1b). This resulted in better water access for departing males. The development of an eastward polynia and its exploitation by post-incubating males (one male in our study, Fig. 1b) concur with previous observations (Ancel et al. 1992) implying similar foraging conditions for penguins between years. Foraging trip durations of 19 and 29 days for both studied males, however, seem long compared to the 7–21 days recorded at Pointe Géologie by Ancel et al. (1992).

Foraging zones

The three females foraged intensively over a submarine plateau of about 200 m water depth as well as in areas of complex bathymetry with slopes ranging to more than 500 m water depth (depth data derived from ETOPO1). Complex bathymetry is often associated with upwelling, nutrient enrichment and thus high biological productivity, which may explain our data. The two males foraged in similar areas, whereas one male also foraged in a more distant (eastward) polynia. The higher incidence of deeper dives (>200 m) for males (44 vs. 27% for females) may have provided access to different prey such as krill, that has been suggested to inhabit areas deep in the water column during the late winter period (Wienecke and Robertson 1997).

Spring (chick provisioning)

Movement at sea

During late chick-rearing in October and November the sea-ice extent decreased rapidly until there was free seawater access close to the colony in mid November. Foraging in ice-free waters at distances far greater from the colony does not seem to be beyond the penguin capabilities. However, the present study shows that during the late chick-rearing period all 10 penguins confined their foraging activities to within 163 km of Pointe Géologie over the Antarctic shelf between 139 and 143°E, rarely exceeding the shelf break. This foraging pattern in a "central place forager" suggests that there was sufficient food availability close to the breeding site. Foraging duration of trips between 31 October and 17 December (7 ± 1 day) in this study roughly corresponded to the average durations of 9 days in early, and 7 days in late, November for penguins from Auster and Taylor Glacier (Kirkwood and Robertson 1997a). They were, however, only half those averaging 15 days in November for penguins from Coulman Island (Kooyman and Kooyman 1995). However, birds in this latter study moved between 81 and 859 km during a single of these short foraging trips (Table 1).

Foraging zones

The specific sites at which birds foraged during chick-rearing should have been a trade-off between the constraints of the animal phenotype (dive capacities, fitness as function of parental care, chick requirements, etc.) and the food supply, which presumably varied with depth and distance from the colony. However, the foraging activities during both winter and spring were concentrated in similar locations (Fig. 9a, b) although the open sea access in the latter period should have enabled penguins to exploit the entire shelf area off Pointe Géologie (Fig. 6).

Summer (pre-moult)

In December, when the constraints of chick-rearing no longer applied and emperor penguins left the breeding colony, they headed beyond the coastal shelf break towards the 3,000–4,000 m deep ocean where they apparently travelled continuously rather than concentrating foraging effort in a particular area. Here, studied birds ventured at least 300 km north of the coast, reaching distances of up to 838 km to the colony (Table 1). This foraging pattern was similar to those of pre-moult foraging penguins studied at the Mawson Coast, although some birds also foraged in dense pack-ice close to their colony (Wienecke et al. 2004). We did not observe this pattern.

Our study identified two moulting locations in the residual pack-ice east and west of the Pointe Géologie colony (Figs. 6, 7). The eastern pack-ice area was proposed as a potential moulting location by Kooyman et al. (2000) who based findings on predictable late-season pack-ice.

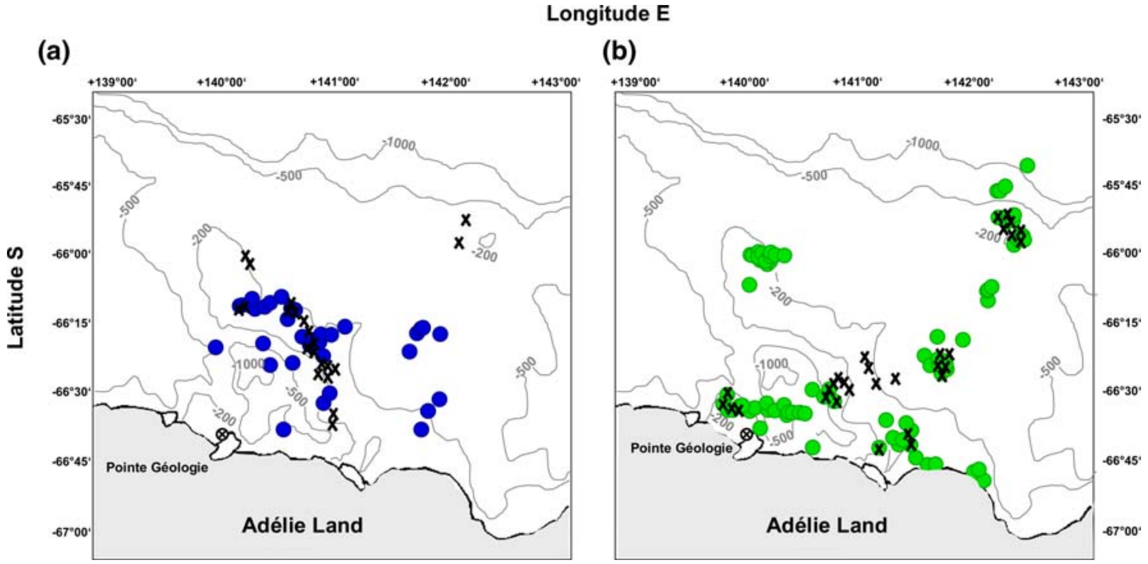

Fig. 9 Satellite locations of high catch per unit effort (*CPUE, dots*) and area-restricted-search index (*ARS-I, cross*) over the Antarctic shelf of monitored emperor penguins in **a** winter ($n = 5$ birds) and **b** spring ($n = 4$ birds). Locations were marked when CPUE and ARS-I values of single foraging trips exceeded 60% of the individual parameter maximum (see Fig. 4b, c). Shelf bathymetry was derived from the ETOPO1 min gridded evaluation database (GEBCO 1-min global bathymetric grid)

Foraging zones

Pre-moult trips of up to 3,686 km (Table 1) did not simply represent a direct transit to moult locations in the residual pack-ice (see Figs. 6, 7). Oceanic foraging over such a great radius off the shelf, as observed in our study and by Wienecke et al. (2004), suggests that there is more lucrative food supply over deep water and/or an enhanced opportunity to encounter prey by covering longer horizontal distances. The penguins offshore diet presumably relied on pelagic fish such as myctophid species or on Antarctic krill, *Euphausia superba*. Both of these were identified as a main pre-moult prey source for offshore feeding penguins in the eastern Ross Sea (Kooyman et al. 2004).

Commonalities and restrictions in foraging patterns

Since emperor penguins are sedentary birds returning to their traditional breeding site every year (Isenmann and Jouventin 1970; Isenmann 1971), they can be classed as central place foragers (Orians and Pearson 1979), although the duration that can be allocated to foraging varies greatly according to the time of year. These birds have essentially three major periods during the year, which have substantially different lengths of trips; (1) the moult period, when penguins leave the colony for a pre-moult foray lasting 3–7 weeks (this study, Wienecke et al. 2004), before moulting (ca. 4 weeks—Le Maho et al. 1976; Groscolas 1978), this being finally followed by a post-moult period (approximately one month), (2) the incubation period, lasting about 65 days (Prévost 1961; Isenmann 1971), which is only used by the females and (3) the chick-provisioning period, where forays away from the colony last between 2 days and several weeks depending on chick age (Mougin 1966; Isenmann 1971). As the time away from the central place increases, so too, does the potential for greater ranging movements. Indeed, it has been pointed out that even migration routes during the non-breeding season can be viewed as a particular form of foraging trip (Wilson et al. 2005) since all trips ultimately serve to enhance adult lifetime reproductive success. However, it is not necessarily of benefit to the foraging bird to spend extended time periods away from the central place at increasingly distant locations. This is because, although the Ashmole’s halo effect will tend to result in a reduced prey density in close proximity of the colony due to intra-specific competition (Birt et al. 1987), this effect will become negated, and ultimately irrelevant, with the exponentially increasing search area with linearly increasing distance to the colony. Thus, when time permits, penguins should be seeking feeding (and living) conditions that allow them to maximize the net energy gain per unit time spent away from their central place (Mori 1998; Weimerskirch 1998; Ropert-Coudert et al. 2004). Although there is likely to be only one best solution to this under any given conditions, birds have to modulate their behaviour so that they fare best in an environment where they have imperfect information.

Typically, animals searching for food from a central place have an initial period of rapid travel away from the central place (Jouventin et al. 1994). In most penguins, this occurs by swimming, where prey might, theoretically, be encountered at any time (Wilson 1995). The highly variable ice cover encountered by emperor penguins over the course of the year, however, has a profound effect on when, and how, foraging might occur. During winter, when the females go foraging during the incubation period, the sea ice edge is ca. 400 km distant from the colony. This distance, coupled with a slow walk (Pinshow et al. 1977) to reach it, appears to make attempts to reach the open sea untenable at this time. Rather, the birds apparently use small holes and cracks in the ice to access the water, and exploit prey in the immediate vicinity of them. Increasing distance swum by penguins tends to increase the likelihood of prey capture (e.g. Wilson 1985). Thus, in order to mitigate against probable space constrictions by having to return to their particular breathing sites, females apparently engage in highly tortuous tracks underwater, which should serve to increase the underwater distance travelled (see results). The constraints imposed by the position of breathing locations in the ice, which need not necessarily correspond to regions of high prey density, may also explain why it is that the CPUE of these birds is lower than at any other time of the year. Presumably, the wandering movements of the females over the ice during the incubation period reflect movements between ice holes as prey in particular vicinities become depleted.

By the time that the males go on their first foraging trip following incubation, the ice cover has broken down enough to expose larger cracks and polynias which appear to be an important site for food for these birds (Ancel et al. 1992). Such conditions, though spatially constrained, have much greater expanses of open water and likely allow penguins to concentrate their foraging at sites where prey concentration is highest.

The recession of the ice edge as spring and summer advance increases the area of open sea in the vicinity of the colony. This removes the limitations of ice cover and decreases travelling time between foraging and breeding sites and is appropriate for the feeding frequency of the brood. Interestingly though, the birds at this time still appear to exploit approximately the same areas as those used by penguins during the winter and early spring (Fig. 9a, b). This would augur for particular features of that area, which result in high prey abundance (see above). The relaxation of access to the water due to the removal of ice cover, however, means that area-restricted-search can increase (Fig. 5a), allowing late chick-rearing penguins to conduct shorter efficient foraging trips in a period when food demand of the offspring is high.

Pre-moult birds are the only group to move to a distinct foraging area, which is much farther offshore than at other times of the year. The extended time that penguins spend away from the colony around the moult period, coupled with potentially particular conditions necessary for a successful moult on the ice (Kooyman et al. 2004), apparently make it more profitable for these birds to move out of the normal foraging zone being used during the breeding period. The pre-moult period is critical for penguins since food has to be acquired at a high rate to ensure that body condition is good enough to take the birds through the extended fast (Adams and Brown 1990) which must occur at a well-defined period of the year. We speculate that the foraging areas used by emperor penguins during the pre-moult period are characterized by particularly high prey abundance. However, the distance between these sites and the colony precludes them as foraging sites for penguins at other times of the year due to the extended time and energy necessary to access this zone.

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PUBLICATION III

DIVE EFFICIENCY IN RELATION TO DEPTH IN FORAGING EMPEROR PENGUINS.

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AQUATIC BIOLOGY

DIVE EFFICIENCY IN RELATION TO DEPTH IN FORAGING EMPEROR PENGUINS.

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ABSTRACT: Air-breathing divers tend to increase their overall dive duration with increasing dive depth. In most penguin species, this occurs due to increasing transit (descent and ascent) durations but also because the duration of the bottom phase of the dive increases with increasing depth. We considered the efficiency with which birds can exploit different diving depths by using depth recorders on nine foraging emperor penguins (*Aptenodytes forsteri*) studied during the early and late chick-rearing period in Adélie Land, Antarctica. Dive- and post-dive duration positively correlated with diving depth but particularly long recovery durations were apparent for dives in excess of 455 s. This point of inflection (i.e. 455s) corresponded to a maximized theorized overall rate of gain of prey per dive cycle. By applying a simple model which used the number of undulations in the bottom phase of the dive as a measure of prey capture success, we determined that the most lucrative dive depths for our birds were between 50 and 225 m. Since these depths were also the most frequently visited, we conclude that emperor penguins tend to concentrate their dives to depths of highest profitability.

KEYWORDS: emperor penguin, foraging depth, bottom dive duration, dive efficiency

INTRODUCTION

Penguins are central place foragers (sensu Orians and Pearson 1979) in two respects; (1) when breeding they move out in forays from their central breeding site into the surrounding water and (2) during diving they also have to forage from the water surface to depth (Houston and McNamara 1985). The time constraints on the second of these are much more critical since inappropriate timing of foraging excursions from the breeding colony merely result in delayed growth or death of the chick while inappropriate timing with regard to diving would result in the death of the adult. Ideally, penguins provisioning chicks should organise the durations and depths underwater, and therefore the subsequent time spent recovering at the surface (Butler and Jones 1997), so that they maximize the rate of energy acquisition (Weimerskirch 1998; Ropert-Coudert et al. 2004), this rate of energy acquisition ultimately playing an important role in chick provisioning rates, and therefore brood survival (cf. Takahashi et al. 2003). The specific behaviour of a diving penguin (swim speed, rate of change of depth etc.) acts via its phenotypic physiology to determine the rate of oxygen usage underwater (e.g. Culik et al. 1994; Kooyman and Ponganis 1994) and the same phenotype also determines the rate of oxygen acquisition while the bird is at the surface between dives (Kramer 1988; Kooyman and Ponganis 1998). Both physiological processes affect durations at depths and the consideration of both together defines the ultimate efficiency of the penguin phenotype for exploiting prey at depth.

Emperor penguins (*Aptenodytes forsteri*) are the deepest diving birds with a maximum recorded dive depth of 564 m (Wienecke et al. 2007) and it is this remarkable dive capacity that allows them to exploit squid and fish at great depths in the Southern Ocean where no other avian species can compete (Ropert-Coudert et al. 2006a). Deeper dives, however, necessitate longer (and energetically more costly) transit phases to depth which result in longer surface durations (e.g. Butler and Jones 1997; Kooyman and Ponganis 1998) and a general supposed lowering of diving efficiency (Wilson 2003). Such a lowered diving efficiency can be justified, however, if there are appropriately greater gains in prey acquisition rates at these depths.

This paper examines the foraging behaviour of breeding emperor penguins. We analyse the depths at which this species operates, assess how diving efficiency varies according to foraging depth, and consider whether our depth-dependent, derived efficiencies correlate with putative prey ingestion rates.

MATERIAL AND METHODS

Study site and data records

Fieldwork was carried out at the emperor penguin colony at Pointe Géologie, Adélie Land, Antarctica (66°40'S, 140°01'E) during the 2005 breeding season, between 20 April and 31 August in winter and 2 to 21 November in spring.

Between 20 April and 11 May, in the pairing period, a time depth recorder (Mk9, Wildlife Computers, USA, 6.7 x 1.7 x 1.7 cm, 30 g) was deployed on three females and two males. The devices were attached with glue to the feathers on the midline of the lower back to minimize drag (Bannasch et al. 1994).

Between 2 and 13 November in the late-chick rearing period, a further four adult penguins were captured travelling to or from the colony (when the colony to sea distance was about 500 m). A data-collecting Argos tag (Splash, Wildlife Computers, USA, 7.8 x 5.0 x 2.3 cm, 105 g) was fixed with black Tesa-tape (Wilson et al. 1997b) on the penguins' lower back feathers.

The Mk9 archival tag had a relative depth resolution of 0.5 m, a memory of 16 Mbytes and was set to record depth every 5 s. The Splash had a relative depth resolution of 0.1 m, a 14 Mbyte memory, and was set to record depth every 2 s. Both devices recorded within the range of 0 to 1000 m depth.

Data analysis

The dive analysis was conducted on depth data that were corrected for surface drift (which varied by ± 2 m) using special software (MT-dive; Jensen Software, Germany) that analysed all dives sequentially, writing, per dive, a number of defining parameters into an ASCII output file. These were: the time of the dive initiation, the overall dive duration, the maximum depth reached during the dive, the descent-, bottom-, and ascent-phase duration, the vertical velocities during the descent, bottom and ascent phases, the number of rapid succession short ascent/descent phases during the bottom phase, and the post-dive interval (Fig. 1).

All dives deeper than 2 m were considered as proper dives. The bottom phase, during which penguins are most likely to hunt (Chappell et al. 1993; Wilson et al. 1995) and appear to capture most of their prey (Simeone and Wilson 2003;

Takahashi et al. 2004; Ropert-Coudert et al. 2006b; Bost et al. 2007), was defined by three conditions; it could only occur (i) at depths > 85% of the maximum depth of the dive (cf. Kirkwood and Robertson 1997), (ii) if it was bounded by two points of inflection in the rate of change of depth and (iii) if the overall rate of change of depth for the whole of the putative bottom period did not exceed 0.2 ms^{-1} (Rodary et al. 2000a). Short ascent/descent phases exceeding 2 m during the bottom phase of a dive were quantified according to the number of points of inflection during the ascents and descents (Fig. 1). Two or three serial points of inflection (SPI) were described as a "wiggle". Such wiggles result in the capture of a single prey item pursued by Magellanic penguins (*Spheniscus magellanicus*) during the bottom phases of their dives (Simeone and Wilson 2003) and are considered to be generally indicative of prey pursuit in penguins (Kirkwood and Robertson 1997; Luna-Jorquera and Culik 1999; Hull 2000; Rodary et al. 2000b; Tremblay and Cherel 2000; Takahashi et al. 2004). Consequently, we considered the number of wiggles occurring in the bottom phase of emperor penguin dives to be linearly related to prey abundance in that they represented a pursuit with, or without, prey catch. Thus, we derived an estimate of prey abundance via 'catch-per-unit effort' (CPUE, $SPI.min^{-1}$) statistics obtained by dividing the number of serial points of inflection during the bottom phase by the bottom dive duration. Likewise, the diving efficiency (DE) was calculated following the equation of Ydenberg and Clark (1989):

DE = bottom duration / (dive duration + post-dive duration)

being expressed as a non-dimensional fraction. As an overall measure for DE and CPUE the product of these parameters was calculated as the DE * CPUE index, being expressed as $SPI.min^{-1}$.

Dive data analyses were performed on individual datasets. The two different study periods of winter and spring in the breeding cycle of emperor penguins resulted in different foraging trip characteristics such as trip extension and direction, trip duration and thus the overall number of dives conducted (Table 1). A non-parametric Mann-Whitney Rank Sum test (U) was used to compare foraging trip durations of penguins in winter and spring, since data were not normally distributed. Results of the dive parameters (such as dive durations, dive efficiency and the CPUE, being variables that change with depth) were examined per individual before being converted to grand means, in order to correct for sample size biases. Grand means are presented ± 1 SE and averaged per 25 m maximum dive depth interval. All parameters were calculated for dives with post-dive durations of less than 25 min (this being delineated by a point of inflection in the frequency of post-dive duration graph, cf. bout-ending criterion Gentry and Kooyman 1986). The correlation of parameters was highlighted by linear functions $y = a + b\ x$ unless explained differently and tested for significance by a parametric one-way ANOVA (F). Data were processed using Excel, Origin 7.5, TableCurve 2D and SigmaStat 3.5 software packages.

RESULTS

Time-depth records were analysed from nine emperor penguins representing one complete foraging trip each. Additionally, dives of a second foraging trip were analysed for one of in winter foraging females, provided due to failed recapture. Foraging trips of post-egg-laying females and post-incubating males in winter were of longer durations (range: 19 to 79 days, Table 1) than the second recorded winter foraging trip of one female (10 days) and trip durations in spring (range: 8 to 10 days, Table 1) ($P = 0.008$, $U = 0$). Altogether trips provided 277 days foraging time at sea (Table 1). Dive records combined amounted to 24,403 dives (Table 1) with a maximum dive depth of 438 m (mean: 68.83 m ± 0.52) and a maximum dive duration of 16 min (mean: 3.00 min ± 0.02).

Dive duration and post-dive duration were examined for all dives with post-dive intervals <25 min (n = 24,068 dives). Both parameters were positively correlated with maximum dive depth (dive duration: $r^2 = 0.94$, $P < 0.0001$, $F_{17} = 267.95$, Fig. 2a and post-dive duration: $r^2 = 0.71$, $P < 0.0001$, $F_{17} = 38.28$, Fig. 2b):

$$\text{Dive duration} = 2.66 + 0.02\ (\text{max. depth}) \tag{1}$$

and

$$\text{Post-dive duration} = -0.06 + 0.01\ (\text{max. depth}) \tag{2}$$

Rate of increase of the post-dive duration was higher for deep dives between 225 to 450 m, being 1.7 $s.m^{-1}$, than for shallower dives between 0 to 225 m, being 0.35 $s.m^{-1}$ (Fig. 2b). The positive correlation of the post-dive duration with the dive duration (dive dur) was described by the following exponential function ($r^2 = 0.89$, $P < 0.0001$, $F_{17} = 131.09$, Fig. 3a):

$$\text{Post-dive duration} = \text{Exp}\,(4.14 + 1.00\text{E-08}\,(\text{dive dur})^3) \quad (3)$$

In order to better describe this correlation before and after a point of inflection which occurred at a grand mean of 455 ± 9 seconds dive duration, the relationship was described separately by non-linear functions for dive durations ≤455 s ($r^2 = 0.98$, $P < 0.001$, $F_{12} = 455.46$, Fig. 3b) and for dive durations ≥455 s ($r^2 = 0.99$, $P < 0.001$, $F_5 = 241.61$, Fig. 3c):

$$\text{Post-dive duration (dives} \leq 455\text{ s)} = 28.24 + 3.46\text{E-05}\,(\text{dive dur})^{2.5} \quad (4)$$

and

$$\text{Post-dive duration (dives} \geq 455\text{ s)} = 175.21 + 1.33\text{E-72}\,(\text{dive dur})^{26.91} \quad (5)$$

Descent and ascent durations were positively correlated to maximum depth ($r^2 = 0.97$, $P < 0.0001$, $F_{17} = 567.95$, Fig. 4a and $r^2 = 0.96$, $P < 0.0001$, $F_{17} = 406.29$, Fig. 4c) as follows:

$$\text{Descent duration} = 0.69 + 0.01\,(\text{max. depth}) \quad (6)$$

and

$$\text{Ascent duration: } 0.75 + 0.01\,(\text{max. depth}) \quad (7)$$

Of a total of 24,068 dives (with post-dive intervals <25 min) 80% (n = 19,248 dives) had a bottom phase. Bottom duration was shorter than descents and ascents during dives and accounted for 30% to the dive duration. It increased with increasing maximum dive depth for dives <225 m ($r^2 = 0.66$, $P < 0.01$, $F_8 = 13.78$, Fig. 4b) according to:

$$\text{Bottom duration (dives} < 225) = 0.74 + 0.01\,(\text{max. depth}) \quad (8)$$

but decreased thereafter ($r^2 = 0.71$, $P < 0.01$, $F_9 = 19.63$, Fig. 4b) according to:

$$\text{Bottom duration (dives} \geq 225\text{ m)} = 2.15 - 0.003\,(\text{max. depth}) \quad (9)$$

Dives with serial points of inflection (SPI dives, n = 13,915), indicating prey pursuit movements, occurred in 72% of dives with a bottom phase. The frequency distribution of all dives with SPIs showed two apparent peaks between depths of 25 – 75 m (23 % of dives) and 125 – 225 m (41 % of dives, Fig. 5a).

The catch per unit effort (CPUE) appeared relatively constant in dives to depths between 50 and 450 m (Fig. 5b) but actually increased significantly ($r^2 = 0.57$, $P < 0.001$, $F_{17} = 20.75$) with depth according to:

$$\text{CPUE} = 1.55 + 0.003\ (\text{max. depth}). \tag{10}$$

The dive efficiency (DE) only increased with maximum depth for dives up to 50 m before decreasing substantially with increasing dive depth ($r^2 = 0.93$, $P < 0.0001$, $F_{17} = 197.46$) to a minimum mean value of 0.06 ± 0.02 for dives terminating between 425 to 450 m (Fig. 5c). The relationship was best described by:

$$\text{DE}_1 = 0.28 - 4.95\text{E-}4\ (\text{max. depth}). \tag{11}$$

Dive efficiency was negatively correlated with the CPUE ($r^2 = 0.37$, $P < 0.01$, $F_{17} = 9.19$, Fig. 6) according to:

$$\text{DE}_2 = 0.22 - 0.13\ (\text{CPUE}) \tag{12}$$

The overall measure for diving efficiency and the effort of prey catch, the CPUE * DE index, increased with the maximum dive depth remaining high until 225 m, but then decreased with deeper dives (Fig. 7). Highest values for this occurred between 125 to 150 m.

DISCUSSION

Increases in dive duration with depth identified in our study (Fig. 2) have also been reported for emperor penguins by Kooyman and Kooyman (1995) and Kirkwood and Robertson (1997), and mirror patterns obtained for a suite of air-breathing, in diving endotherms (e.g. Schreer et al. 2001) and ectotherms (e.g. Hays et al. 2000). The reasons for this are essentially twofold: Firstly, travel to greater depths from the surface generally occurs at roughly constant speeds (Culik et al. 1994; Ropert-Coudert et al. 2001; Wilson et al. 2002) close to the minimum costs of transport (cf. Schmidt-Nielsen 1972; Culik et al. 1994) so that more time is necessary to cover the increasing vertical distance. This applies to both the descent and the ascent and is a pattern that is particularly obvious in the dive patterns of the penguins equipped in this study (Figs. 4a, c). It has also been pointed out, however, that penguins control the volume that they inhale prior to a dive so that they encounter conditions approaching neutral buoyancy during the extended bottom phase of their dives (Sato et al. 2002, Wilson and Zimmer 2004 – see also Hays et al. 2004 for turtles). A consequence of this is that penguins swimming near the surface inspire less in their final breath, which results in them having less oxygen in their respiratory air-spaces and reducing their capacity to stay underwater as long as deeper-diving birds (Wilson and Zimmer 2004).

Ultimately though, a major factor regulating the time spent underwater in relation to depth is the duration of the bottom phase of the dive. It is during this period that penguins are most likely to capture prey (Simeone and Wilson 2003; Takahashi et al. 2004; Ropert-Coudert et al. 2006b; Bost et al. 2007 - this paper) so it is of advantage for the birds to maximize this time in relation to all other phases of the dive cycle (Wilson et al. 1996). Our study shows an initial increase in bottom duration with increasing depth until maximum depths of 225 m are reached (Fig 4b), which corresponds to a total dive duration of about 6 min (Fig. 2a), after which bottom duration reduced overall with further increases in maximum dive depth (Fig. 4b, cf. Charrassin et al. 2002). The bottom duration decrease with deeper dives may reflect birds approaching the end of their total body oxygen stores during dives (cf. Butler and Jones 1997) so that increases in dive depth, which necessitate increases in descent and ascent duration (see above) can only occur by diminishing bottom duration. This can only strictly be true, however, if overall dive duration tends to reach a plateau at the time the bottom duration starts to decrease. This is clearly not the case in emperor penguins (Figs. 2a, 4b). Why then, do bottom durations decrease in our study?

A major, non-linear- with respect to depth, factor modulating the efficiency of dives (see earlier for definition) is the recovery duration at the surface following dives when the oxygen deficit is corrected in preparation for the next dive (Fig. 2b). Generally, the rate at which oxygen is taken up by a body is considered to be proportional to the difference in partial pressure between the body tissues and the air (Kramer 1988). Thus, birds with a high oxygen deficit acquire oxygen fast. However, long dives require high pre-dive oxygen partial pressures in the tissues and it is specifically the process of loading the oxygen to high levels that is so time consuming at the surface, making surface durations exceptionally long following deep (and therefore long) dives. In addition to this, exceptionally long dive durations may use anaerobic metabolism (Kooyman 1989; Kooyman and Ponganis 1998) necessitating even longer recovery periods to deal with the accumulated lactate (e.g. Ponganis et al. 1997).

The general premise, that oxygen uptake at the surface is proportional to the partial pressure difference between body tissues and air, allows us to construct a model curve for oxygen uptake over time at the surface, and to compare this with oxygen usage over time while the bird is underwater. This theoretical formulation needs to incorporate the complexity of the bottom duration, which first increases with increasing maximum depth before it decreases again (Fig. 4b). Why should this be? Firstly, given that most prey is caught during the bottom phase of the dive, increases in dive depth (and therefore transit duration) must be paralleled by increases in bottom duration if birds are to remain efficient (assuming constant rates of prey ingestion for any fixed prey density irrespective of depth) so this explains increasing bottom duration with increasing maximum dive depth. The subsequent decrease in bottom duration is more complex; if the efficiency of a bird is taken to be:

$$\text{Efficiency} = \text{Bottom dur} / (\text{Descent} + \text{Bottom} + \text{Ascent} + \text{Recovery dur}) \qquad (13)$$

and the prey encounter rate taken to be α per second spent in the bottom phase, then the overall rate of prey gain is given by:

$$\text{Rate} = (\text{Bottom dur} * \alpha) / (\text{Descent} + \text{Bottom} + \text{Ascent} + \text{Recovery dur}) \qquad (14)$$

The effect of various bottom durations on the rate of prey acquisition as a function of depth can be examined by putting these bottom duration values into equation (14), substituting values for the durations of the descent and ascent to specific depths derived from our results (Figs. 4a, c) and coupling these to an equation deriving the recovery duration as a function of dive duration. This approach shows that longer bottom durations are only profitable at shallower depths (Fig. 8a) and this is primarily a result of the accelerating surface recovery duration with increasing overall dive duration; this shows a point of inflection at a grand mean of 455 ± 9 seconds dive duration (Fig. 3a), which then leads to a corresponding point of inflection in the overall rate of gain of prey per dive cycle. The precise form of the rate of gain as a function of bottom duration for dives to different maximum depths is shown in Fig. 8b, which makes clear how the maximum rate of gain per dive cycle occurs at reduced bottom durations for the greater depths. This helps explain the downward trend in bottom duration observed in our data after depths of about 225 m (Fig. 4b).

Ultimately though, it is prey abundance as a function of depth that will dictate the profitability of dives, though this will be modulated by the manner in which birds have to allocate time to transit and recovery at the surface. Theoretically, the inverse of the dive efficiency should give a measure of the rate of prey ingestion needed to make dives profitable because dives to depths that result in low efficiency are only tenable if they can be balanced by an enhanced rate of prey ingestion. That emperor penguins adhere to only exploiting greater depths when they concur with increasing prey density is indicated by the significant relationship between dive efficiency and CPUE (Fig. 6). Similarly, we might derive a measure of how lucrative the different depths were for our study birds by multiplying the dive efficiency by the CPUE (Fig. 7) because where this value is high should indicate where gains per overall unit time should be highest (Fig. 7). This approach indicates a broad depth band of profitability between about 25 and 225 m, dropping off after that, although there appears to be a slight rise after 350 m (Fig. 7). As would be expected, this broadly concurs with the frequency of depth maxima exploited by the birds further indicating that emperor penguins tend to concentrate their dives to depths where overall gain is highest.

We note though, that predicted trends may be blurred by dives when prey are not encountered because it is not clear what birds do in terms of modulating their bottom duration during such dives, although for 20% of the time they return directly to the surface without any extension of the bottom phase at all. There is presumably a decision-making process by the birds as to whether to hunt prey at any particular depth and this is likely to be according to perceived prey density (cf. Krebs et al. 1974). Given the fairly strict form of the dive profile, consisting of a clear, single descent phase followed by equally clear bottom and finally ascent phases in emperors (e.g. Robertson 1995) and other penguin species like king penguins (e.g. Kooyman et al. 1992), chinstrap penguins (Bengtson et al. 1993; Wilson and Peters 1999), Adélie penguins (Rodary et al. 2000b), rockhopper penguins (Wilson et al. 1997a), Gentoo penguins (Wilson et al. 1996), *Spheniscus* species (Wilson and

Wilson 1990; Wilson 1995; Peters et al. 1998), it appears that these birds make a single decision relating to exploited bottom depth for each dive. There are never two bottom depths (i.e. two different depths) exploited within any one dive. This apparent inflexibility may, in part, be related to buoyancy problems. Other species of penguins (king, Adélie and Magellanic) inhale air preceding a dive according to the depth at which the bottom phase will occur (Sato et al. 2002; Wilson and Zimmer 2004), probably so that they can operate during the bottom phase at virtually neutral buoyancy and thus reduce swim costs (Wilson and Zimmer 2004) and extend the dive duration accordingly. While this approach is energetically sensible, it constrains birds to operate at particular depths that are chosen before the dive is initiated. Indeed, departures from the optimum foraging depth must be particularly energetically rewarding for them to be tenable. Variance in penguin exploitation of depth, and exploitation of prey at different depths is primarily based, therefore, on changes in maximum depth between dives (Wilson et al. 1996); we would expect the depth exploited in dive N to be highly dependent on the prey conditions encountered during dive N-1 (cf. Wilson 2003). Examination, therefore, of maximum dive depth sequentially (Wilson and Peters 1999) in relation to foraging success would seem to be an important next step in understanding the foraging strategies of these birds that have to make judicious decisions regarding how to allocate time in the acquisition of energy at a place far removed from that where they acquire their oxygen.

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Table 1 Emperor penguins satellite tagged at Pointe Géologie in winter and spring 2005; dive number, trip duration and actual foraging time at sea of post-egg-laying females (F), post-incubating males (M) and late chick-rearing birds of both (and unknown) sexes (F, M, ?).

Penguin	Dives (N)	Trip duration (days)	Foraging time (days)
Post-egg-laying females			
F-1a	4533	79	70
F-2a	5103	79	72
F-3aTrip1	3969	59	51
Mean (± SE)		72 ± 7	64 ± 7
F-3aTrip2	1057	10	7
Post-incubating males			
M-4a	2502	29	27
M-6a	1918	19	17
Mean (± SE)		24 ± 5	22 ± 5
Late chick-rearing birds			
?-5b	1129	9	8
?-8b	1168	8	7
M-10b	1763	10	10
F-18b	1261	9	8
Mean (± SE)		9 ± 0.4	8 ± 0.6

FIGURE CAPTIONS

Fig. 1. Example of a dive classified into descent, bottom and ascent phase. A wiggle during the bottom phase is defined by 2-3 registered serial points of inflection (SPI) counted during dive analysis (see text).

Fig. 2. (a) Dive and (b) post-dive duration as function of maximum dive depth for dives with post-dive durations <25 min (n = 24,068) of emperor penguins (n = 9). Grand means ± 1 SE.

Fig. 3. Post-dive duration as function of dive duration for dives with post-dive durations <25 min (n = 24,068) of emperor penguins (n = 9). The exponential correlation (a) was split in two parts (b and c) for detailed slope change description due to a point of inflection at 455 ± 9 s. Grand means ± 1 SE.

Fig. 4. Durations of descent (a), bottom (b) and ascent (c) phases of dives as function of maximum dive depth for dives with post-dive durations <25 min (n = 24,068) of emperor penguins (n = 9). Grand means ± 1 SE.

Fig. 5. (a) Serial point of inflection (SPI) frequency in percent, (b) catch per unit effort (CPUE, $SPI.min^{-1}$) and (c) dive efficiency (DE) as a function of maximum dive depth for dives with post-dive durations <25 min and a bottom phase (n = 19,248) of emperor penguins (n = 9). Grand means ± 1 SE.

Fig. 6. Dive efficiency (DE) as function of catch per unit effort (CPUE, $SPI.min^{-1}$) for dives with post-dive durations <25 min and bottom phase (n = 19,248) of emperor penguins (n = 9). Grand means ± 1 SE.

Fig. 7. (a) The frequency of the catch per unit effort * dive efficiency (CPUE * DE) index ($SPI.min^{-1}$) as function of maximum dive depth for dives with post-dive durations <25 min and bottom phase (n = 19,248) of emperor penguins (n = 9). Frequency bars presented ± 1 SE.

Fig. 8. Theoretical rate of gain of prey (assuming a constant rate of ingestion per unit time during the bottom phase of the dive), calculated over the whole dive cycle, as a function of (a) dive depth for different fixed bottom durations and (b) as a function of bottom duration for different fixed maximum dive depths. The overall rate of prey ingestion is calculated for particular conditions of bottom duration and depth by using known regressions for descent and ascent durations to that depth (equations 6 and 7, respectively – Fig. 4) and determining the total surface recovery duration necessary after the bottom duration has been added to these (using equations 4 and 5 – Fig. 3) – see text.

Figure 1

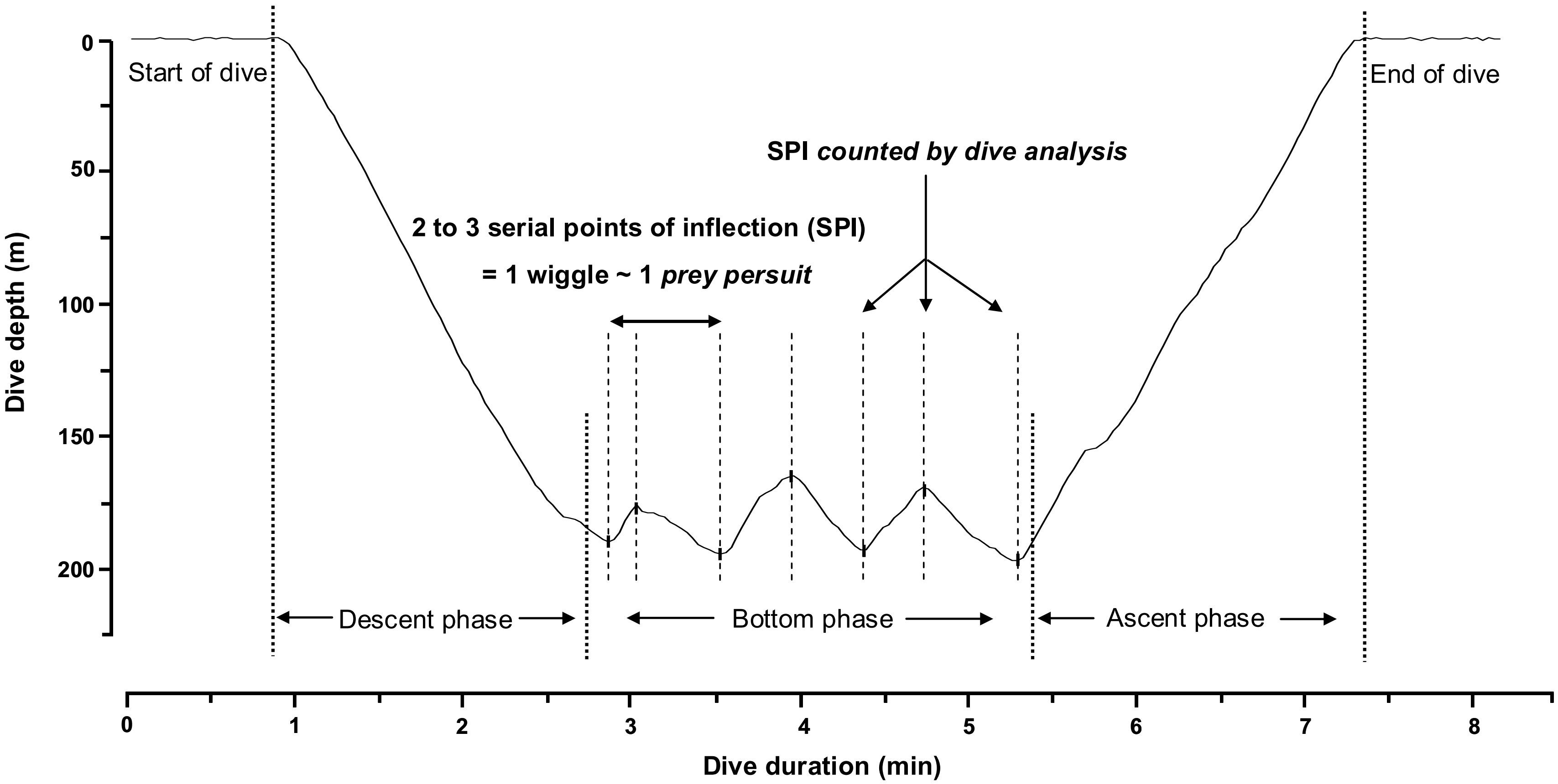

SPI counted by dive analysis
2 to 3 serial points of inflection (SPI)
= 1 wiggle ~ 1 prey persuit
Start of dive
End of dive
Descent phase
Bottom phase
Ascent phase
Dive depth (m)
0
50
100
150
200
Dive duration (min)
0
1
2
3
4
5
6
7
8

Figure 2

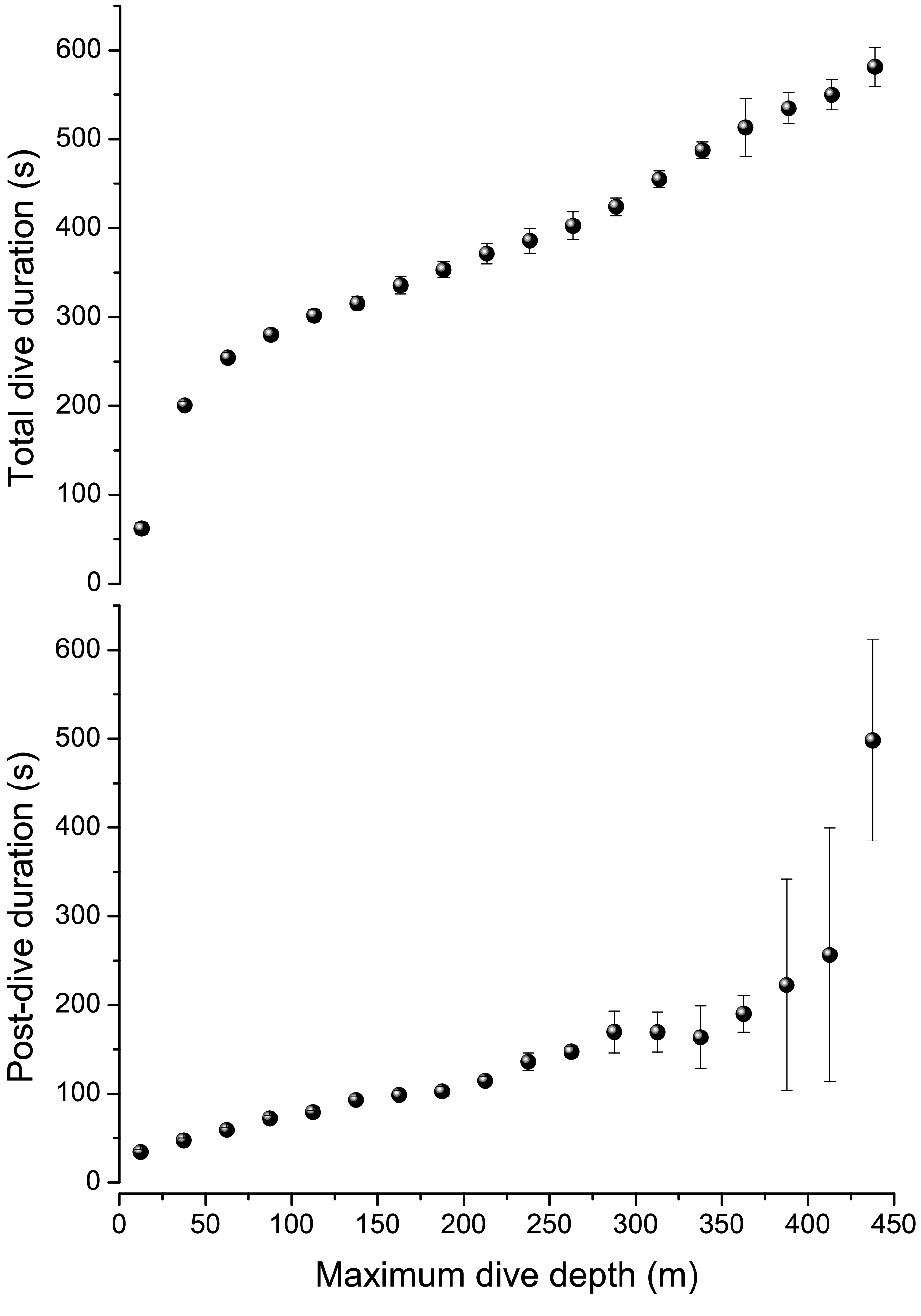

Total dive duration (s)
0
100
200
300
400
500
600
(a)
Post-dive duration (s)
0
100
200
300
400
500
600
(b)
0
50
100
150
200
250
300
350
400
450
Maximum dive depth (m)

Figure 3

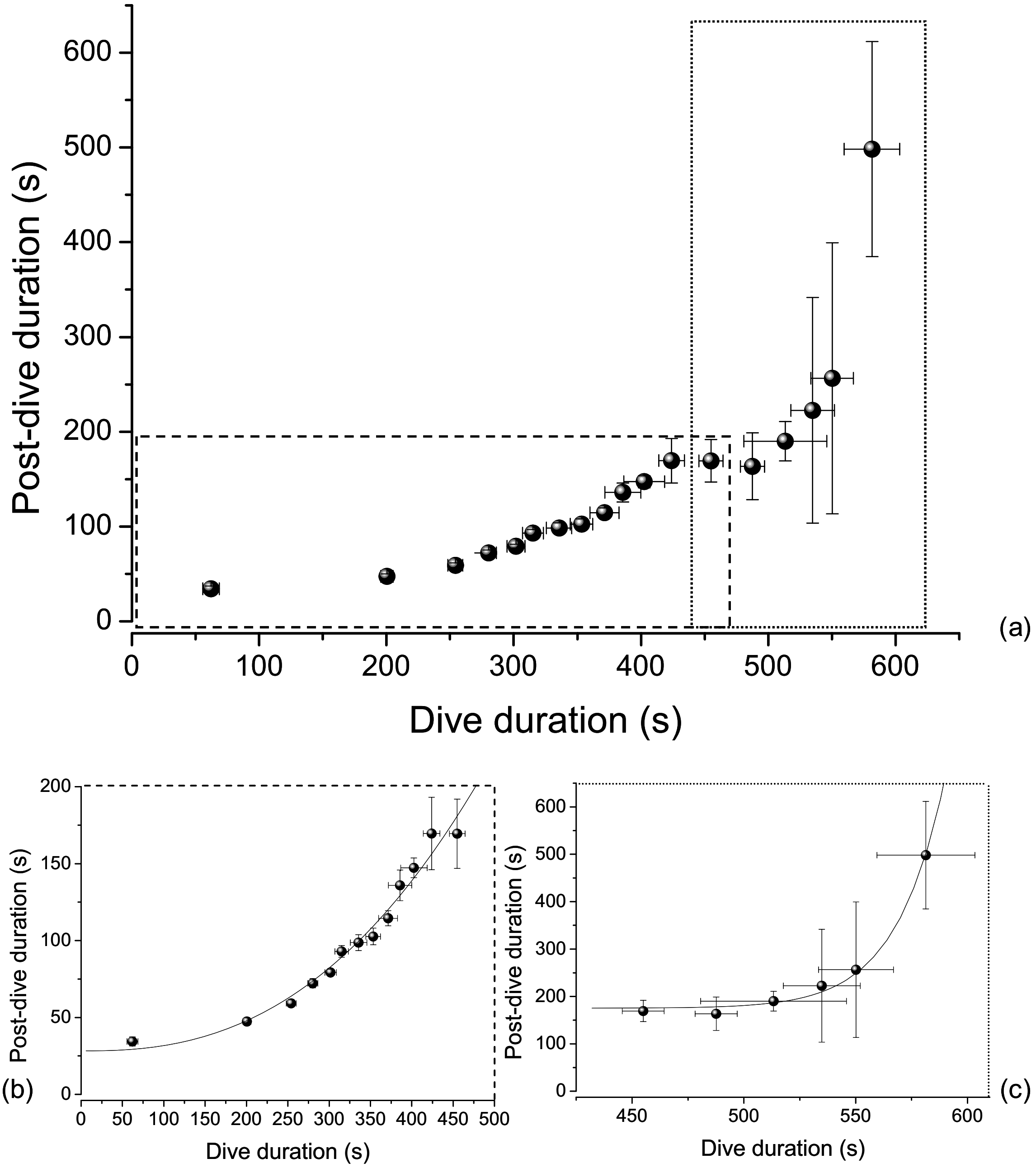

Post-dive duration (s)
0
100
200
300
400
500
600
Dive duration (s)
0
100
200
300
400
500
600
(a)
Post-dive duration (s)
0
50
100
150
200
Dive duration (s)
0
50
100
150
200
250
300
350
400
450
500
(b)
Post-dive duration (s)
0
100
200
300
400
500
600
Dive duration (s)
450
500
550
600
(c)

Figure 4

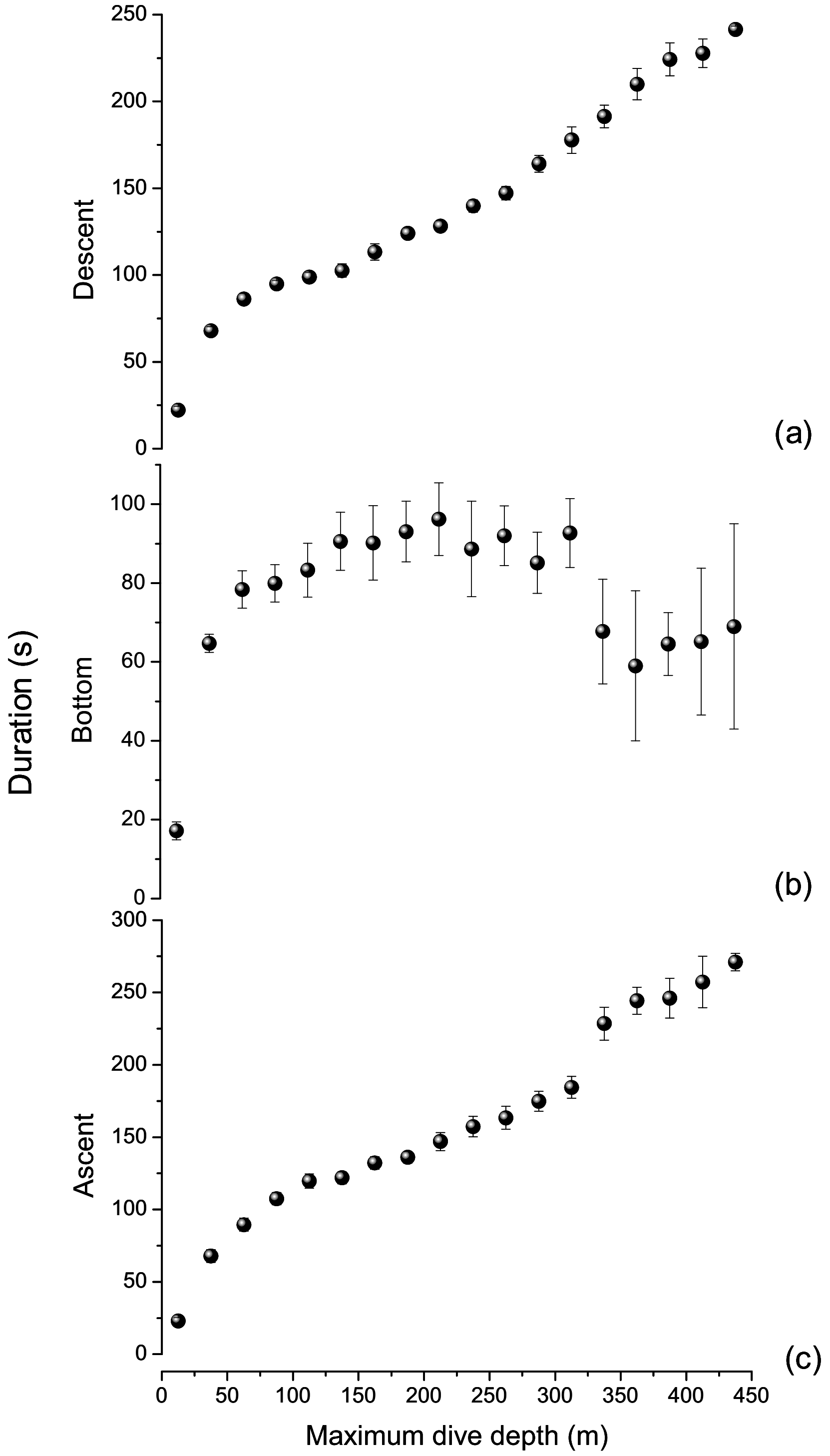

Duration (s)
Descent
250
200
150
100
50
0
(a)
Bottom
100
80
60
40
20
0
(b)
Ascent
300
250
200
150
100
50
0
(c)
0
50
100
150
200
250
300
350
400
450
Maximum dive depth (m)

Figure 5

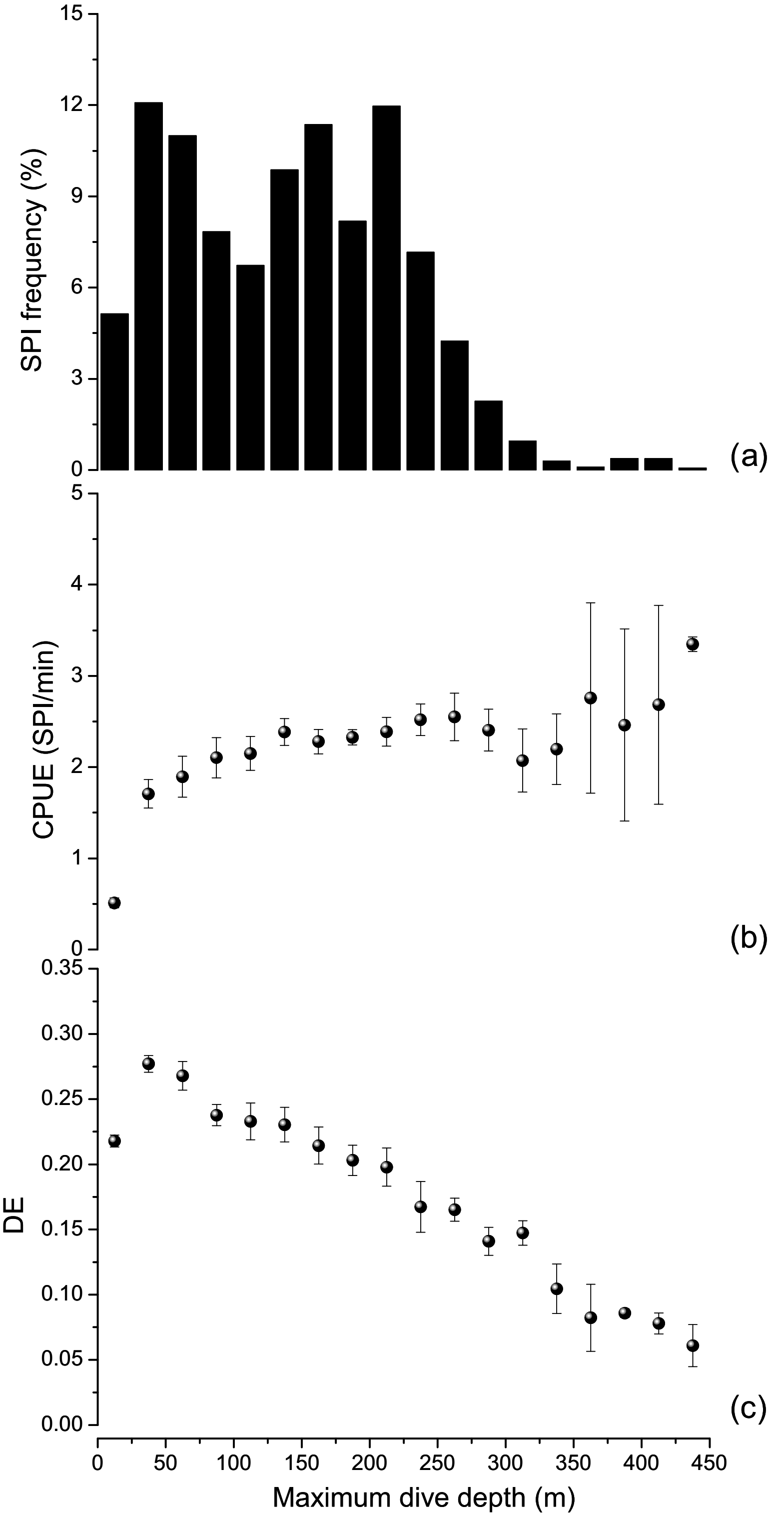

SPI frequency (%)
0
3
6
9
12
15
(a)
CPUE (SPI/min)
0
1
2
3
4
5
(b)
DE
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
(c)
0
50
100
150
200
250
300
350
400
450
Maximum dive depth (m)

Figure 6

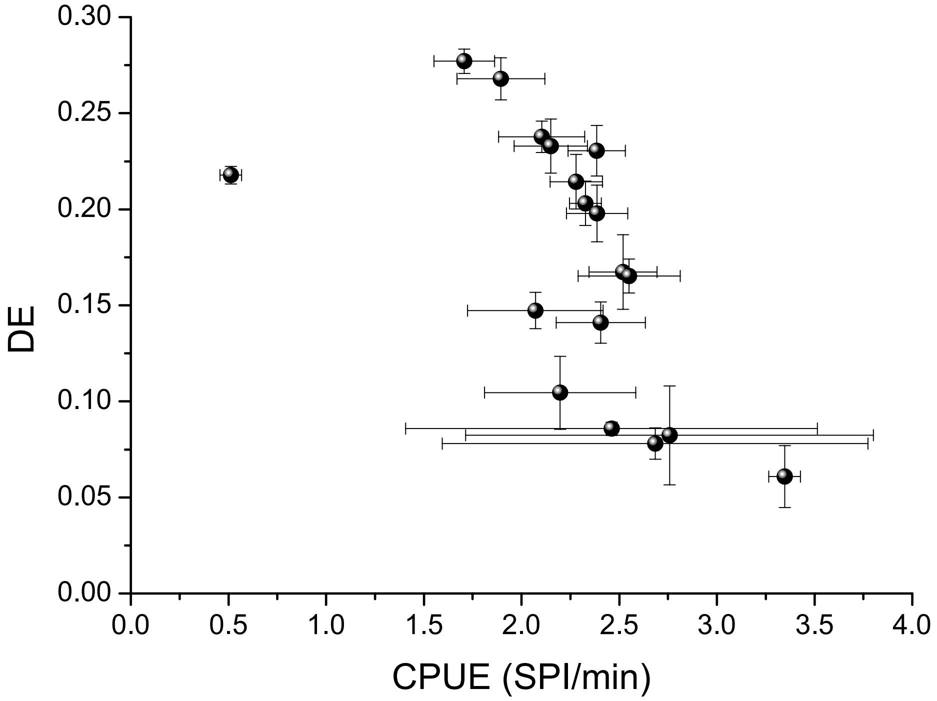


Figure 7

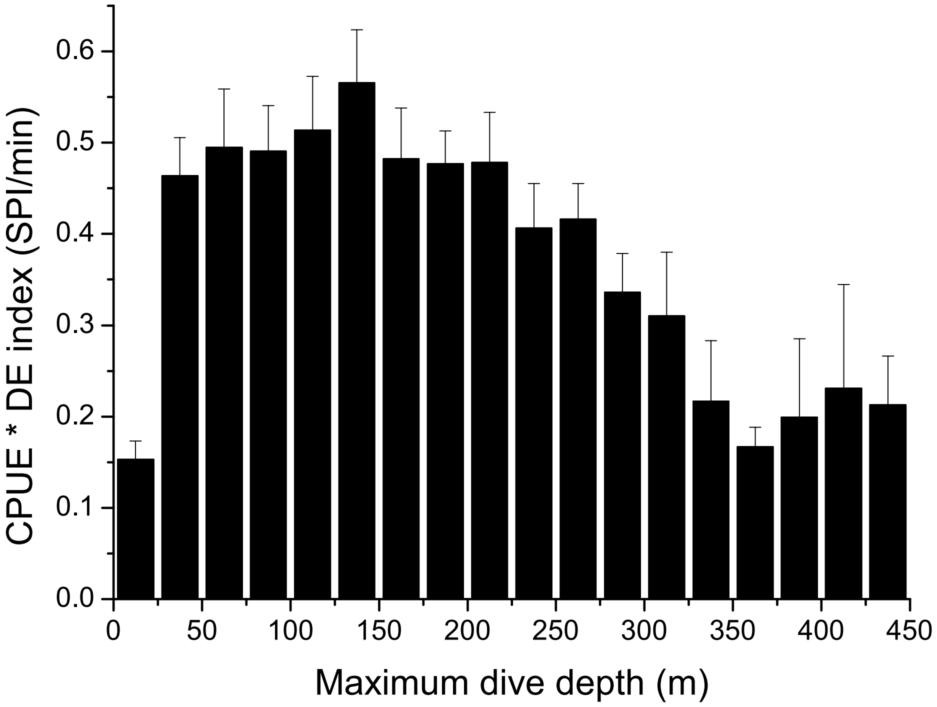
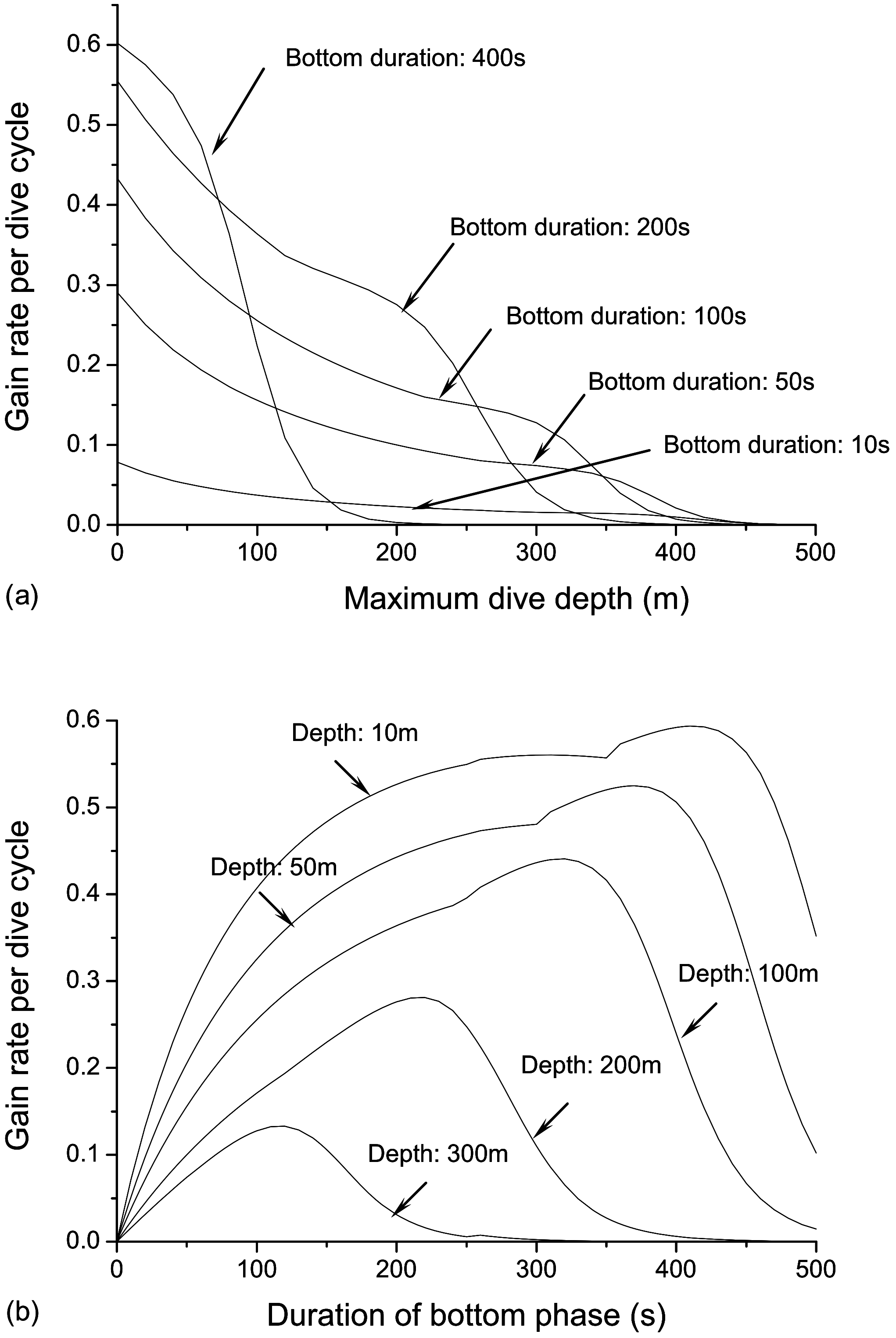


Figure 8


Gain rate per dive cycle
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Bottom duration: 400s
Bottom duration: 200s
Bottom duration: 100s
Bottom duration: 50s
Bottom duration: 10s
0
100
200
300
400
500
(a)
Maximum dive depth (m)
Gain rate per dive cycle
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Depth: 10m
Depth: 50m
Depth: 100m
Depth: 200m
Depth: 300m
0
100
200
300
400
500
(b)
Duration of bottom phase (s)

PUBLICATION IV

SEEING THE LIGHT: DEPTH AND TIME RESTRICTIONS IN THE FORAGING CAPACITY OF EMPEROR PENGUINS AT POINTE GÉOLOGIE, ANTARCTICA.

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André Ancel, Joachim Plötz

AQUATIC BIOLOGY

SEEING THE LIGHT: DEPTH AND TIME RESTRICTIONS IN THE FORAGING CAPACITY OF EMPEROR PENGUINS AT POINTE GÉOLOGIE, ANTARCTICA.

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ABSTRACT The foraging ability of visual hunters depends critically on light conditions. Emperor penguins are reported to be visual hunters but breed and forage at high latitudes and are thus exposed to extreme changes in light conditions in the course of the year. We examined how light influenced the foraging ability for breeding emperor penguins using loggers in winter (n = 5) and spring (n = 4) in 2005 at Pointe Géologie (140°01'E, 66°40'S), Antarctica, as well as by using models of light availability of the year and as a function of depth. The model showed that daylight was continuous between Julian days 350 and 363 and that the sun did not rise between Julian days of 166 and 180. Logger-measured light intensity decreased with water depth and depth-specific values were higher at greater sun elevation angles. Depth-time use (given by the maximum depth reached multiplied by the number of hours at which this depth could be achieved over 24 h) of spring-foraging penguins was 8,394.5 m.h which was more than twice that of winter-foraging birds at 3,845.4 m.h, showing the severe constraints imposed by winter. Average catch-per-unit effort was related to mean maximum diving depth and was highest around mid-day in winter and highest during dawn and dusk in spring. It is suggested that this relates to the behaviour of prey.

KEYWORDS: Light intensity, foraging, emperor penguins, depth-time availability

INTRODUCTION

The ability of marine animals to forage is often constrained by the physical characteristics of the environment. For example temperature (reptiles, e.g. Vitousek et al. 2007), depth (whales, e.g. Thode et al. 2002) and light (visual hunters, e.g. Wanless et al. 1999) have all been shown to enhance or compromise foraging ability. Although penguins are considered to be restricted in the maximum depth they can achieve for physiological reasons (Williams 1995), light has also been cited as important (Wilson et al. 1989; Wilson et al. 1993; Pütz and Bost 1994; Kooyman and Kooyman 1995; Kirkwood and Robertson 1997a; Wienecke and Robertson 1997; Cannell and Cullen 1998; Peters et al. 1998; Pütz et al. 1998; Luna-Jorquera and Culik 1999; Bost et al. 2002) since these birds are reputed to hunt by vision. Indeed, there are a number of studies that appear to show that the maximum dive depth achieved by penguins in the wild is often limited by the availability of light (e.g. Wilson et al. 1993; Pütz and Bost 1994; Cannell and Cullen 1998; Ropert-Coudert et al. 2006). Emperor penguins are the deepest diving of all the penguin species, an ability that has been linked to their large size (Ponganis and Kooyman 2000; Halsey et al. 2006). If these birds are indeed limited in the depths that they can exploit by light, it seems strange that they, coincidently, are the largest penguins species and forage under exceptional conditions of light. Perhaps, however, it is exceptional lighting conditions, illuminating greater depths down the water column that tended to select for larger-sized penguins because it is these that can dive deep? In fact, emperor penguins belong to the most southerly breeding birds (until 78°S, Woehler 1993) and forage in exceptionally clear waters (Jerlov 1968) in areas of light that varies from continuous daylight (with the sun above the horizon) to just few dimlight hours (without the sun above the horizon) per 24 h cycle (Iqbal 1983).

Data in the literature suggest that emperor penguins are indeed visual hunters seeing their prey items by shadow theatre and that their activity patterns, particularly as relates to foraging, are closely linked with the light/dark cycle (Wilson et al. 1989; Kooyman and Kooyman 1995; Kirkwood and Robertson 1997b; Wienecke and Robertson 1997).

This study focuses on the potential of light in modulating the foraging ability for emperor penguins. We examined the diurnal foraging activity of emperor penguins in winter and spring and analysed the light intensity over a whole year at Terre Adélie, Antarctica, in order to estimate the maximum depth availability over the breeding cycle. We consider the implications that this has for a species that breeds and forages at high latitudes, year-round, and is thus exposed to extremes in light availability.

MATERIAL AND METHODS

Dive patterns of emperor penguins were examined for nine emperor penguins during winter (n = 5) and spring (n = 4) 2005 at Pointe Géologie, Adélie Land (66°40’S, 140°01’E). In winter three females and two males were fitted with time-depth recorders (Mk9, Wildlife Computers, USA, 67 x 17 x 17 mm, 30 g) conducting foraging trips between 22 May and 29 August. In spring, four further birds were deployed with an archival data satellite transmitter (Splash, Wildlife Computers, USA, 7.8 x 5.0 x 2.3 cm, 105 g) recording foraging pattern between 2 and 21 November. Devices were fixed to the lower back feathers of penguins so as to minimize hydrodynamic drag (Bannasch et al. 1994) using tape (Wilson et al. 1997). Dive depth and light intensity were recorded at intervals of 5 s in winter and at intervals of 2 s (depth) and 10 s (light) in spring. Devices provided a depth range of 0 to 1000 m. Light sensors were pre-calibrated by Wildlife Computers and light level data (dimensionless) ranged from ~50 (when the light sensor was covered in a ‘bright room’) to ~180 (a ‘bright room’). Units were recovered after birds had been absent at sea for one or two foraging trips.

Measures for the extraterrestrial solar irradiation (W.m^{-2}) and sun angle (°) were processed for Pointe Géologie over the year 2005 based on calculations given in Iqbal (1983). The relative global radiation estimated after correcting for cloud cover (extraterrestrial irradiation divided by two; König-Langlo unpubl.), was used as a measure for light intensity at the water surface (Fig. 1a). Light availability underwater is a function of time of day and water depth and the ability to perceive prey for a visual predator can be defined by a critical light intensity which represents the lowest illumination at which prey can be perceived (Wilson et al. 1989). Theoretical changes in depth utilization over time by foraging emperor penguins (Fig. 2) were estimated by the following equation:

$$Light_{available} = Light_{Intensity} * Exp(-c_{\omega} * Depth),$$

where ‘Light intensity’ is the relative global radiation (after correcting for some cloud cover, W.m^{-2}) and c_{ω} the attenuation coefficient of 0.01 used for ‘non-productive seawater’ (Type 1; very good light transmission) taken from Jerlov (1968) (Fig. 1).

This calculation for available light at depth is optimistic since we assumed a water body of exceptional clarity. Derived values are intended to elucidate general trends which may differ in magnitude according to environmental factors e. g. sea-ice- and weather-conditions etc. (not noted in our study). We note also that we are unable to determine the effective sensitivity of the penguin eye to prey in the wild (cf. Martin and Young 1984; Sivak et al. 1987; Martin 1999). We derived a ‘depth-time availability index’ (DTAI) for each day of the year by assuming that emperor penguins need a critical light intensity of at least 30 $W.m^{-2}$ in order to perceive prey. DTAI values integrated the depths over which penguins could see prey (where light intensity >30 $W.m^{-2}$) over each full day and had units of meter x hour (m.h).

To examine the foraging activity of penguins in relation to the time of day recorded depth data were analysed by using special software (MT-dive; Jensen Software, Germany). All dives >2 m were analysed sequentially for the following parameters: the time of the dive initiation, the overall dive duration, the maximum depth reached during the dive, the descent-, bottom- and ascent-phase durations, the vertical velocities during the descent, bottom and ascent phases, the number serial points of inflection (SPI) during the bottom phase, and the post-dive interval. For specific details of this analysis see Zimmer et al. (2007b). As an attempt to derive a catch-per-unit effort index (CPUE), a measure for prey pursuit, we divided the number of SPI identified during the bottom phase of all dives by the respective bottom dive duration. Although the SPI estimate does not provide absolute prey abundance indices, we consider an approximate linear relationship to prey caught, so that CPUE values ($SPI.min^{-1}$) should relate to the extent of prey pursuit (cf. Kirkwood and Robertson 1997b; Luna-Jorquera and Culik 1999; Hull 2000; Rodary et al. 2000; Tremblay and Cherel 2000; Takahashi et al. 2004; Zimmer et al. 2007b). The diving efficiency (DE, dimensionless) was calculated following the equation of Ydenberg and Clark (1989):

$$DE = \text{bottom duration} / (\text{dive duration} + \text{post-dive duration})$$

being expressed as a non-dimensional fraction.

Measured light intensity at depth for different sun angles, the maximum dive depth, CPUE and DE over the day were examined per individual before being converted to grand means, in order to correct for sample size biases. Grand means are presented ± 1 SE, if not explained differently and averaged per 25 m maximum dive depth interval or per hour of the day. Light intensity was analysed for all dives >2 m. The latter three dive parameters were calculated for dives with post-dive durations of less than 25 min (this being delineated by a point of inflection in the frequency of post-dive duration graph, cf. bout-ending criterion, Gentry and Kooyman 1986) and the occurrence of a bottom dive-phase. Throughout the paper, time is expressed as local time i.e. UTC + 10 h. The correlation of parameters was examined using simple linear functions. Data were normally distributed and tested for significance by a parametric one-way ANOVA (F). Significance of the results was judged at level 0.05. Data were processed using Excel, Origin 7.5 and SigmaStat 3.5 software packages.

RESULTS

At Pointe Géologie, Adélie Land, the solar radiation was highest during the Antarctic summer on the 358 Julian day with a maximum global irradiation (estimated for mean cloud cover) of 514.5 $W.m^{-2}$ during a period of continuous daylight between 350 and 363 Julian day of the year 2005 (Fig. 1a). Light intensity and daylight hours declined over autumn, reaching a minimum dark period of 0 $W.m^{-2}$ at any hour of the day in the Antarctic winter between 166 and 180 Julian day. The estimated depth-time availability (DTAI in m.h) showed the extent to which light availability over the course of a year, coupled with attenuation in the water column, might compromise penguin foraging capacity (Fig. 1b). Following, DTAI for foraging penguins is highest in summer when daylight is maximal and lowest in winter when light availability is lowest.

Light intensity as recorded by devices from four emperor penguins during foraging in spring decreased with increasing water depth until the minimum value of 56.7 a.u., recorded for a single dive (Fig. 3). This trend was apparent at all times of the day, although light intensity was higher at greater sun elevation angles until greater depths (Fig. 3).

The diving patterns of the penguins equipped in winter (n = 5) and spring (n = 4) showed marked seasonality in their time-depth use, with the trend closely following the increase in availability of ambient light between the two seasons (Fig. 4). During winter between 22 May and 29 August 2005, penguins only dived between 7h00 and 19h00, with 78 % of all dives conducted between 10h00 and 15h00 (Fig. 5a). Dives were deepest when light was most intense (Fig. 4a). In spring between 2 and 21 November 2005, with almost continuous daylight, penguins dived at any hour of the day (to depths of up to 200 m, Fig. 4b) although dives deeper 350 m only occurred during periods of peak light intensity between 5h42 and 18h03. Maximum depths were reached between 12h00 and 13h00. The rate of dives was highest from 7h00 to 8h00 and from 19h00 to 20h00 (Fig. 4b). In spring-foraging birds the overall utilisation of the water column to maximum dive depth over the 24 hour cycle (depth-time availability index, DTAI) was more than twice that of winter-foraging penguins (8,394.5 *vs* 3,845.4 m.h, respectively, Fig. 6). The estimated DTAI over the yearly cycle 2005, showed minima and maxima during winter and summer, respectively (Fig. 7) that roughly corresponded to the trend observed in the wild birds. We do not expect absolute values to concur here due to our inability to determine proper thresholds for visual acuity in penguins (see above).

Since maximum depth varies over the diel cycle, it is little surprising to find that mean dive depth also varies systematically, and in a comparable manner (Fig. 8). Dive efficiency showed a trend that was the inverse of this (winter: $P < 0.01$, $F = 7.89$; spring: $P = 0.92$, $F = 0.01$; Fig. 8). CPUE during winter was maximal at mid-day, dipping towards dawn and dusk (Fig. 8a). By contrast, mean CPUE during spring was highest when light levels were lowest. Average CPUE was highly related to the mean maximum diving depth in winter and spring ($P < 0.0001$, $F = 56.09$; $P < 0.0001$, $F = 67.43$, respectively). CPUE was, however, negatively related to diving efficiency in winter ($P < 0.01$, $F = 7.89$) and positively in spring ($P < 0.01$, $F = 8.57$).

DISCUSSION

Estimation of the availability of light as a function of depth down the water column is complex. Although calculation of the amount of total solar radiation impinging on the earth's atmosphere is relatively straightforward, being dependent on the latitude, Julian day and local time of day (Iqbal 1983), this light is then modulated by filters in the atmosphere such as cloud cover and particulate matter (Iqbal 1983) according to circumstance. After reaching the sea surface, the angle of impingement (which is latitude, Julian day and time of day dependent) then determines the angle at which the light continues down the water column due to differences in refractive index between air and water. Finally, of the light travelling down the water column, the degree of attenuation with depth depends on the extent to which water filters out different wavelengths (Kirk 1994) and the optical properties of the water, such as the presence of particulate matter, which itself varies with depth (Jerlov 1968). The degree of particulate matter varies with weather and biological processes, particularly primary production (Jerlov 1968; Kirk 1994). Given these complexities, it would seem unwise to attempt to determine absolute values of light, but rather to use simplistic models to elucidate trends, as we have done. Actual measurement of light as a function of water depth is hardly less fraught with difficulty. Simple light transducers, such as the one we used on the penguins, respond in a general manner to the intensity of light energy, but do not react to all wavelengths equally and therefore give a biased view of light availability down the water column, which explains why the makers are imprecise in their specifications (see earlier). Proper assessment of light extinction with depth necessitates the use of complex instrumentation which assesses absolute energy values for all the different wavelengths (Jerlov 1968; Kirk 1994). Ultimately though, even such onerous procedures are of limited value for penguins if the spectral sensitivity of the animals is not known (e.g. Martin and Young 1984; Martin 1999). Despite these misgivings, there are a number of general trends that we can discern from our approach.

Our data clearly show that emperor penguins have variability in dive depth that accords with the general supposed availability of light (Fig. 4), and our crude measures of light intensity with depth and sun angle (Fig. 3) lend weight to this. This strengthens findings by Kooyman and Kooyman (1995), Kirkwood and Robertson (1997a) and Wienecke and Robertson (1997) for this species, and suggests that emperor penguins are typical of the Spheniscidae in being dependent on light to be able to forage (e.g. Cannell and Cullen (1998) for Little penguins, Wilson et al. (1993) for King, Chinstrap, Adélie, Gentoo and African penguins, Luna-Jorquera and Culik (1999) for Humboldt penguins, Peters et al. (1998) for Magellanic penguins). This has profound implications for a species that lives so far South because of the massive changes in appropriate foraging conditions over the course of the year (Fig. 1) which modulate both the number of hours per day that can be spent foraging as well as the depths at which prey can be exploited (Figs. 6 and 7). During summer, emperor penguins may apparently dive up to 200 m throughout the 24 h period, whereas during winter foraging is apparently only viable for a few hours (Fig 4). Theoretically, winter-foraging birds may increase the amount of light they have for foraging by travelling North (cf. Ancel et al. 1992; Kirkwood and Robertson 1997b; Wienecke and Robertson 1997, Fig. 9). The extended foraging trips of around 70 to

80 days undertaken by the females during winter should allow them time to do this although information on the areas exploited by females at this time shows that there is only limited movement North (Wienecke and Robertson 1997; Zimmer et al. 2007b). Clearly, the viability of movement North as a strategy will be a complex mix of energy and time invested travelling (and particularly the slow travel that involves walking over the ice), the real increase in time and depth available for foraging (Fig. 9) and the abundance of prey at sites farther North.

Systematic patterns in depth use according to hour of day have been noted for a number of marine vertebrates: fish (e.g. Sims et al. 2005), reptiles (e.g. Eckert et al. 1988), mammals (e.g. Croxall et al. 1985) and birds (e.g. Wilson et al. 1993; Bost et al. 2002), with the normal pattern consisting of deeper dives at mid-day than at night. This has been attributed variously to the animals exploiting prey which, itself, shows diel vertical migration, being nearer to the surface at night than during the day. The primary reason for prey movement up and down the water column is considered to relate to their exploitation of the productive surface waters at night when visual predators have difficulty foraging (McLaren 1974; Kalinowski and Witek 1980; Gliwicz 1986). Although the maximum depth boundaries over the course of the day identified in our study for emperor penguins (Fig. 4) appear to represent absolute maxima beyond which the birds cannot forage, the real issue facing birds is which depths, within these limits, are optimal. This will depend on the distribution of prey, given by the extent to which vertically migrating prey might be located within the penguins' limits, and the foraging efficiency of the penguins at that depth. Zimmer et al. (submitted) present data on the foraging efficiency of penguins as a function of depth. Generally, increases in maximum dive depth result in decreases in efficiency (Zimmer et al. submitted) because longer dives require longer recovery periods (e.g. Butler and Jones 1997; Kooyman and Ponganis 1998; Wilson and Quintana 2004) so it is little surprising to find that penguins diving deeper as light levels increase also become less efficient (Fig. 8). This decrease in efficiency can be justified, however, if prey concentrations in deeper waters are high enough. Our data on CPUE imply that the deep diving in winter at least accords with higher prey densities (Fig. 8a). During winter emperor penguins are known to feed predominantly on Antarctic krill *Euphausia superba* (Kirkwood and Robertson 1997a; 1997b). Indeed, krill is bentho-pelagic during the Antarctic winter and known to remain generally close to the seabed of the continental shelf (Kawaguchi et al. 1986; Taki et al. 2005) which may explain the deep diving effort according with high CPUE of foraging penguins in winter. The situation is reversed during spring, however, when CPUE values are highest during periods when light intensity appears to be lowest on any given day (although still high enough to allow birds to forage at depths of up to 200 m, Fig. 8b). We postulate that at this time the normal diel vertical migration of prey has been reinstated, and that the higher CPUE of birds foraging during the darkest hours corresponds to birds exploiting prey that are, themselves, feeding nearer the surface. In summer, the greatest densities of krill are found at 0-70 m depth (Siegel 1985; Higginbottom and Hosie 1989; Godlewska 1993). Moreover, the nototheniid *Pleuragramma antarcticum*, probably the main fish prey of emperor penguins from Pointe Géologie (cf. Offredo and Ridoux 1986; Cherel and Kooyman 1998; Zimmer et al. 2007a), shows diurnal vertical migration (Plötz et al. 2001). In the Antarctic summer, however, this species is most abundant in the upper 150 meters of the water column during night (Mintenbeck et al. in preparation). We suppose that emperor penguins in spring intensively fed on this prey source and that this explains some of the pattern that we observed particularly since the energy density of nototheniids is higher than of both krill or squid (cf. Zimmer et al. 2007a). This contrasts with what has been observed in other penguin species, where shallower dives at night correspond to the virtual cessation of feeding (Wilson et al. 1993). Indeed, based on this, such night-dives have been interpreted as representing travelling behaviour (Wilson et al. 1993).

The ability of the emperor penguin to exploit prey throughout the diel cycle, therefore, appears to be dependent on the continuous light conditions during the summer and undoubtedly enhanced by the exceptional water clarity in Antarctica (Jerlov 1968). It is this same clarity that lets greater light intensities down the water column at mid-day, making foraging technically feasible, from a sensory perspective, at depths in excess of 400 m. Such depths exceed the physiological capacities of the smaller penguin species (Wilson 1995; Ponganis and Kooyman 2000; Halsey et al. 2006). Indeed, where vertical movements of prey are extensive, and the light penetration down the water column substantial, we would expect there to be a strong selection pressure for penguins to have a larger body mass. Thus, aside from the thermal advantages in Antarctic penguins having a larger body mass (Schmidt-Nielsen 1993;

Ponganis and Kooyman 2000) the particular conditions of variation in light and prey behaviour may play a role in modulating the body size of the largest living penguin species.

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FIGURE CAPTIONS

Fig. 1. (a) Light intensity (global radiation estimated through cloud cover in W.m^{-2}) and (b) depth-time availability index (DTAI, m.h), derived by an assumed critical light intensity of 30 W.m^{-2}, representing the lowest illumination at which prey can be perceived, for local time of the day in 2005 in Adélie Land (66°40'S, 140°01'E), Antarctica. Parameters were calculated weekly. Light availability at depth was estimated as follows:

$Light_{available} = Light_{Intensity} * Exp(-c_{\omega} * Depth)$, where 'Light intensity' is the relative global radiation estimated through cloud cover (extraterrestrial irradiation divided by two) and c_{ω} the attenuation coefficient of 0.01 used for 'non-productive seawater' (Type 1; very good light transmission) taken from Jerlov (1968).

Fig. 2. Light intensity (W.m^{-2}) for different water depths for local time of Julian day 324 in 2005 in Adélie Land (66°40'S, 140°01'E), Antarctica. Light availability at depth was estimated as follows: $Light_{available} = Light_{Intensity} * Exp(-c_{\omega} * Depth)$, where 'Light intensity' is the relative global radiation estimated through cloud cover (extraterrestrial irradiation divided by two) and c_{ω} the attenuation coefficient of 0.01 used for 'non-productive seawater' (Type 1; very good light transmission) taken from Jerlov (1968).

Fig. 3. Light intensity (arbitrary units) for different sun angles showing the attenuation of light with water depth. Values are grand mean light records (without SE for the sake of clarity) from mean values of four emperor penguins studied between 2 and 21 November 2005 at Pointe Géologie, Adélie Land. Grey symbols show single records.

Fig. 4. Maximum dive depth as a function of time of day for dives >2 m conducted by (a) five emperor penguins in winter between 22 May and 29 August 2005 (n = 19,077 dives) and (b) four emperor penguins in spring between 2 and 21 November 2005 (n = 5,467 dives) at Pointe Géologie, Adélie Land.

Fig. 5. Frequency distribution of the number of dives conducted by emperor penguins as a function of time of day in (a) winter between 22 May and 29 August (n = 5 birds;

19,077 dives) and (b) spring between 2 and 21 November 2005 (n = 4 birds; 5,467 dives) at Pointe Géologie, Adélie Land.

Fig. 6. Depth-time availability index (DTAI) as a function of time of day of emperor penguins at Pointe Géologie, Adélie Land (see text) in (a) winter between 22 May and 29 August (n = 5 birds; 19,077 dives) and (b) spring between 2 and 21 November 2005 (n = 4 birds; 5,467 dives). The DTAI values (striped areas) are given in metre x hour (m.h).

Fig. 7. Depth-time availability index (DTAI, m.h) over the one year cycle 2005, derived by using an assumed critical light intensity of 30 $W.m^{-2}$, representing the lowest illumination at which prey can be perceived, at depth per hour over a day. Winter and spring marks (star symbols) stem from DTAI values from studied emperor penguins (sum for winter birds n = 5; sum for spring birds n = 4) during these periods (cf. Fig. 6).

Fig. 8. Diurnal pattern of the foraging parameters, maximum dive depth, catch per unit effort (CPUE, $SPI.min^{-1}$) and dive efficiency (DE) of emperor penguins in (a) winter (n = 5) and (b) spring (n = 4). Data are presented as grand mean values of penguin means per season and hour of day ± 1 SE, calculated for all dives with post-dive intervals <25 min and the existence of a bottom phase (winter: n = 14,395; spring: n = 4,853).

Fig. 9. Depth-time availability index (DTAI, m.h) for emperor penguins at Pointe Géologie longitude140°01’E, Terre Adélie, calculated for latitudes between 70 and 50°S. Presented is the example of Julian day 196 in winter.

Figure 1

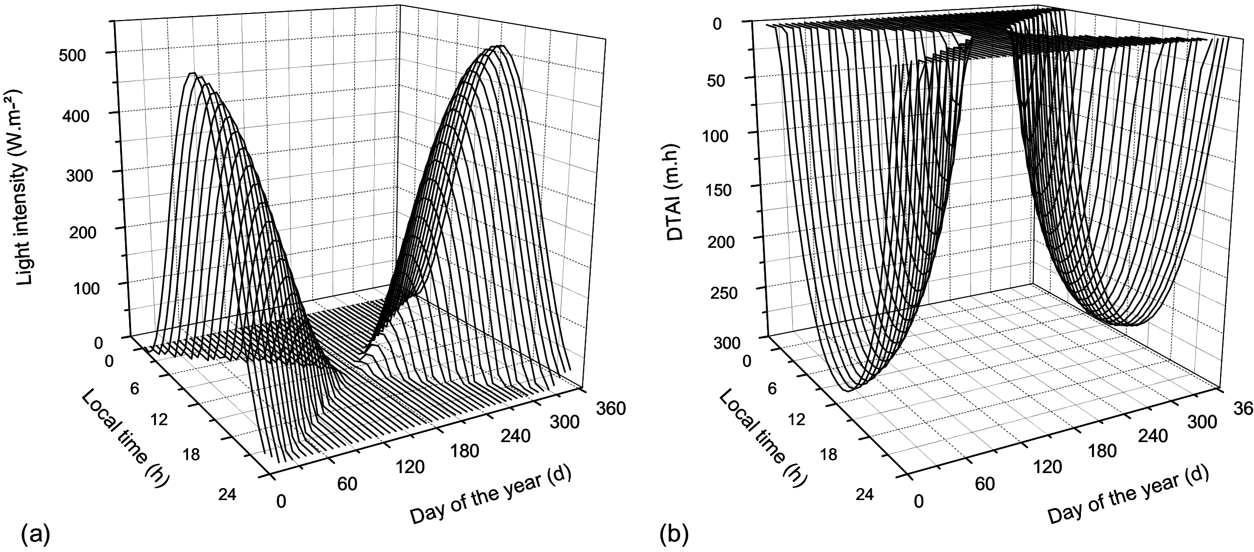
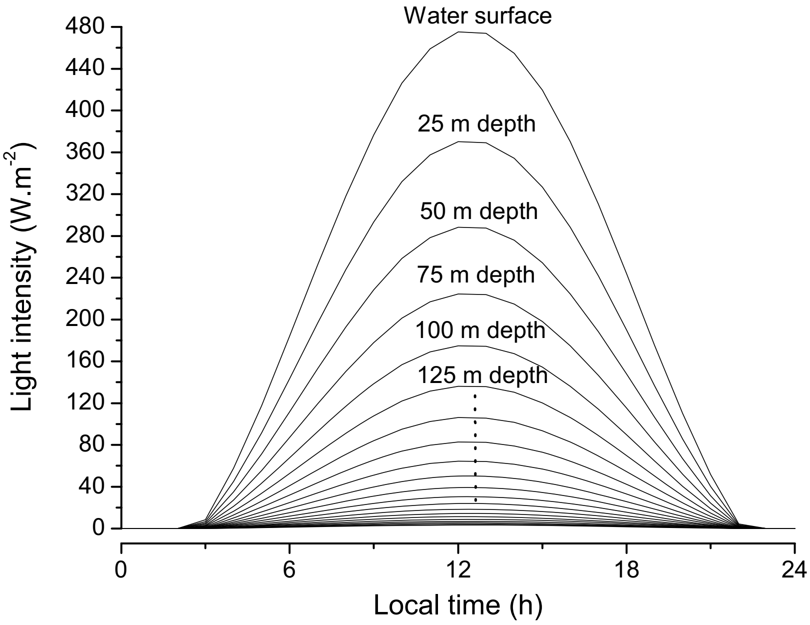


Figure 2



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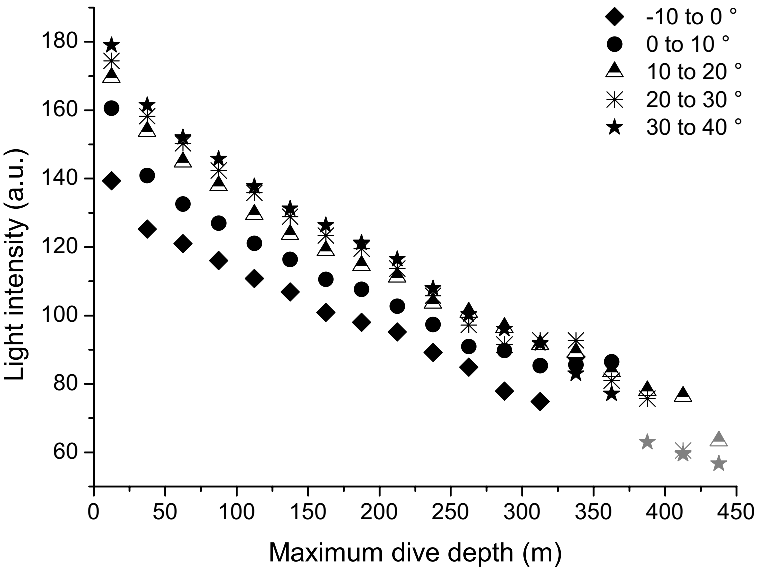

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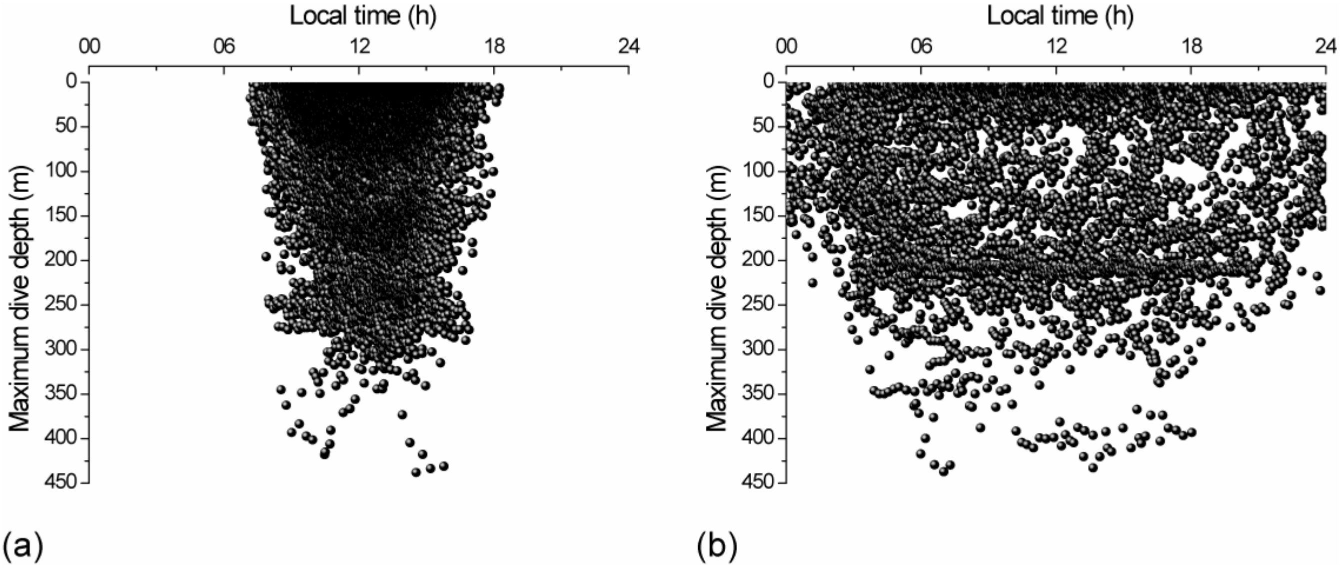

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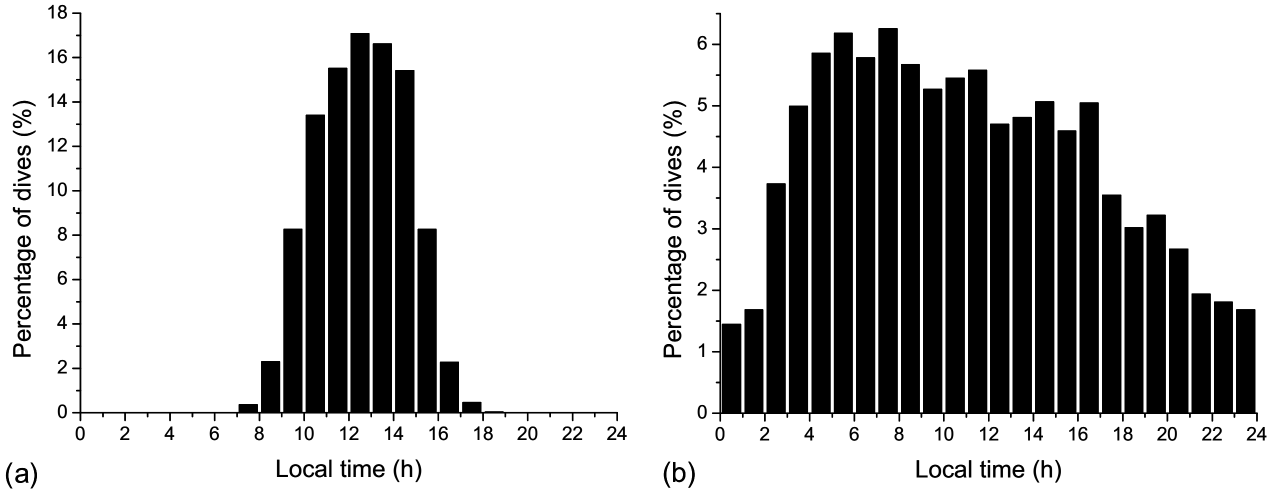

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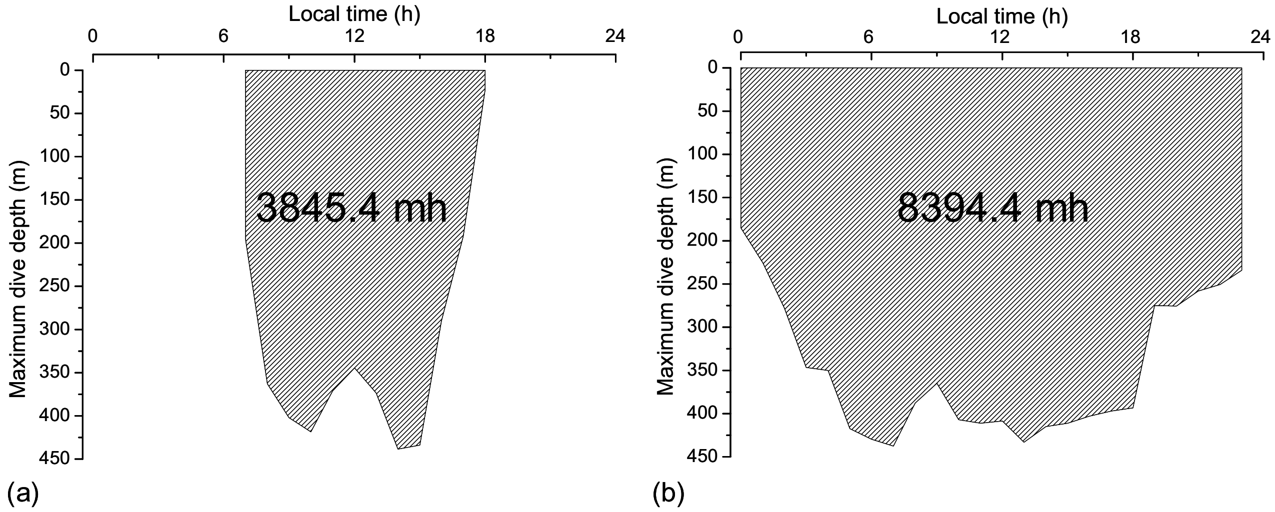


Figure 7

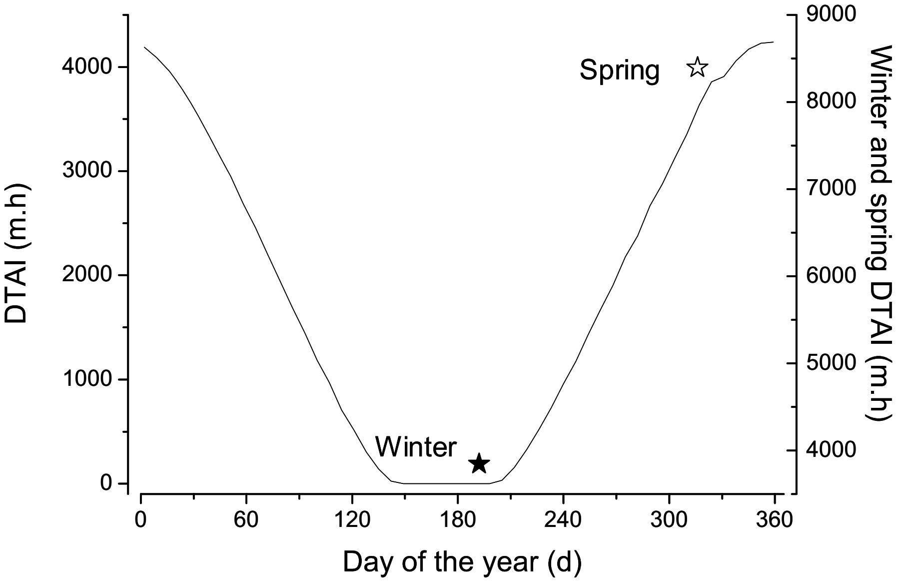

DTAI (m.h)
0
1000
2000
3000
4000
Winter and spring DTAI (m.h)
4000
5000
6000
7000
8000
9000
Day of the year (d)
0
60
120
180
240
300
360
Winter
Spring

Figure 8

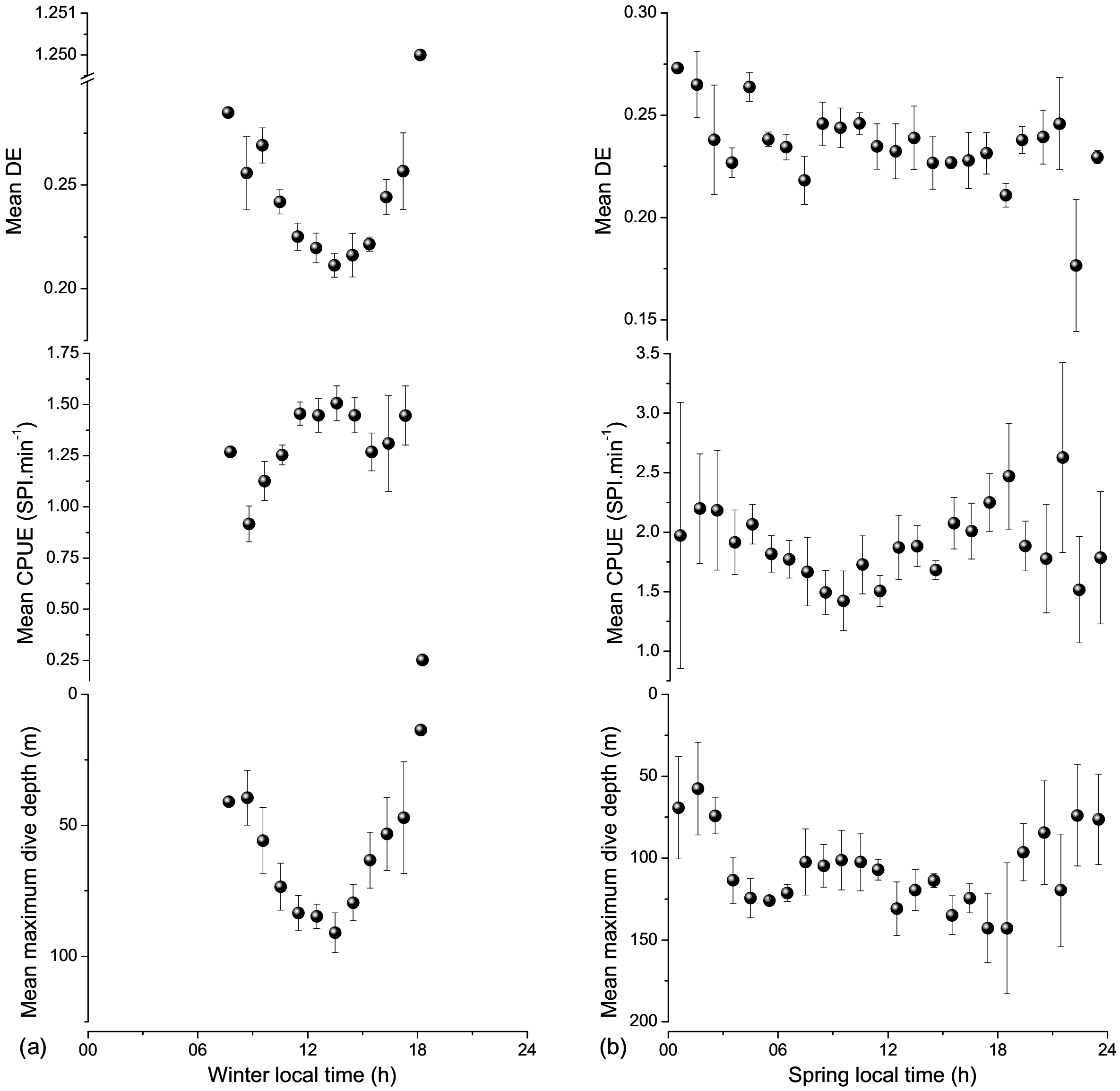
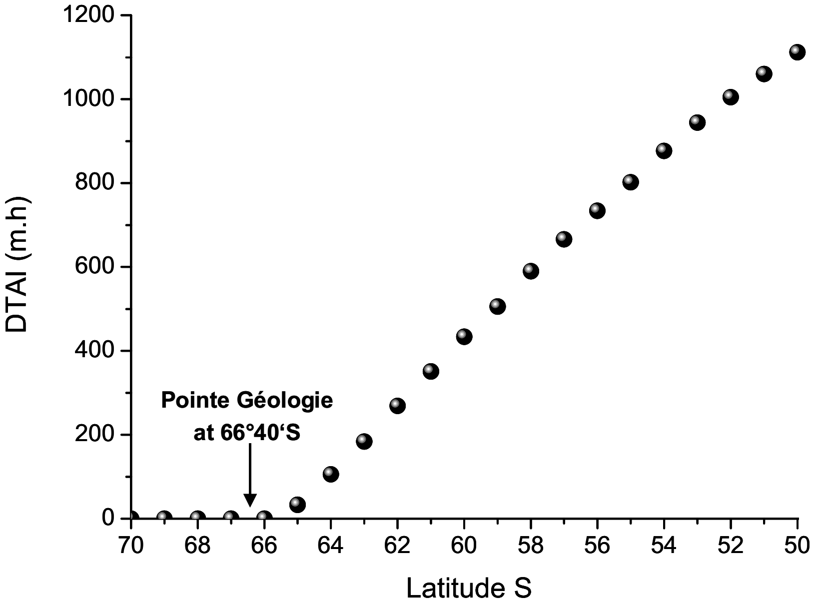

1.251
1.250
Mean DE
0.25
0.20
0.30
0.25
0.20
0.15
1.75
1.50
1.25
1.00
0.75
0.50
0.25
Mean CPUE (SPI.min^{-1})
3.5
3.0
2.5
2.0
1.5
1.0
0
50
100
Mean maximum dive depth (m)
0
50
100
150
200
(a)
00
06
12
18
24
Winter local time (h)
(b)
00
06
12
18
24
Spring local time (h)

Figure 9


DTAI (m.h)
1200
1000
800
600
400
200
0
Pointe Géologie
at 66°40'S
70
68
66
64
62
60
58
56
54
52
50
Latitude S

PUBLICATION V

PARENT SET OF PRIMARY DATA TO PUBLICATION II

Ilka Zimmer, Rory P. Wilson, Caroline Gilbert, Michaël Beaulieu,
André Ancel, Joachim Plötz, Horst Bornemann

PANGAEA

PUBLICATION V Parent set of primary data to Publication II

All primary data derived from emperor penguins satellite tagged during austral spring and summer in 2005/2006 at Pointe Géologie in Adélie Land, Antarctica, are available through the data library PANGAEA - Publishing Network for Geoscientific & Environmental Data (http://www.pangaea.de/). **PANGAEA** is a public digital library for science aimed at archiving, publishing and distributing geo-referenced data with special emphasis on environmental, marine and geological basic research. Publishing of archived datasets follows the "Berlin Declaration" (1998) towards making knowledge in the sciences and humanities accessible to the public. Access to primary data is in parallel with the publication of the respective scientific article. All data are archived in a consistent format, and are well documented along with their corresponding meta-information. Data listed in parent directories are referenced by their Digital Object Identifier (DOI) for direct access and citation. Yet unpublished data sets are archived in the same way but downloading is limited to the meta-data level only. All data can be retrieved by the PANGAEA search engine:
http://www.pangaea.de/

This parent set provides the primary dataset of publication II in this thesis.

Parent set:

Citation: Zimmer, I., Wilson, R. P., Gilbert, C., Beaulieu, M., Ancel, A., Plötz, J., Bornemann, H. (2007) At surface behaviour of emperor penguins from Pointe Géologie, Adélie Land, Antarctica, from expedition DDU 2005 [supplementary data to the reference given]. *PANGAEA*, dataset #633712
(http://doi.pangaea.de/10.1594/PANGAEA.633712)

Reference: Zimmer, I., Wilson, R. P., Gilbert, C., Beaulieu, M., Ancel, A., Plötz, J. (2007). Foraging movements of emperor penguins at Pointe Géologie, Antarctica. *Polar Biology*, DOI:10.1007/s00300-007-0352-5

Abstract: The foraging distributions of 20 breeding emperor penguins were investigated at Pointe Géologie, Terre Adélie, Antarctica, by using satellite telemetry in 2005 and 2006. Data derived from transmitter deployments in early and late winter, late spring and summer correspond to incubation, early chick-brooding, late chick-

rearing and the adult pre-moult period, respectively. ARGOS satellite location data of 15 emperor penguins correspond to spring and summer distribution of the birds. Data sets detailing the winter distribution (n = 5; archived elsewhere) were provided by A. Ancel, Centre d´Ecologie et Physiologie Energétiques, CNRS, Strasbourg France.

Project: Marine Mammal Tracking (MMT)

Size: 16 datasets (at surface behaviour)

Datasets listed in this collection:

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_02 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472121 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_07 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472122 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_18 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472124 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_18 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472125 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_19 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472126 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_10 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472128 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_13 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472130 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_14 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472131 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_15 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472132 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_03 from Pointe Géologie (SPOT 5). Alfred

Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472134 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_05 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472135 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_06 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472136 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_08 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472137 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_16 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472138 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_17 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472139 *(DOI registration in progress)*

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_04 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472140 *(DOI registration in progress)*

PUBLICATION VI

PARENT SET OF PRIMARY DATA TO PUBLICATION III

Ilka Zimmer, Rory P. Wilson, Michaël Beaulieu, André Ancel,
Joachim Plötz, Horst Bornemann

PANGAEA

PUBLICATION VI Parent set of primary data to Publication III

This parent set provides the primary dataset of publication III in this thesis.

Parent set:

Citation: Zimmer, I., Wilson, R. P., Beaulieu, M., Ancel, A., Plötz, J., Bornemann, H. (2007) Dive depth profile and at surface behaviour data of emperor penguins from Pointe Géologie, Adélie Land, Antarctica, from expedition DDU 2005 [supplementary data to the reference given], *PANGAEA*, dataset #633713 (http://doi.pangaea.de/10.1594/PANGAEA.633713)

Reference: Zimmer, I., Wilson, R. P., Beaulieu, M., Ancel, A., Plötz, J (0). Dive efficiency in relation to depth in emperor penguins. *Aquatic Biology* (submitted)

Abstract: Adult male and female emperor penguins (*Aptenodytes forsteri*) were fitted with satellite transmitters at Pointe-Géologie (Adélie Land), Dumont d´Urville Sea coast, in November 2005. Nine of 30 data sets were selected for analyses to investigate the penguins' diving behaviour at high resolution (#4 high resolution data sets). The profiles correspond to foraging trips of the birds during austral spring 2005 (#472171, #472173, #472164, #472160, #472161). Corresponding high resolution winter data (n = 5; archived elsewhere) were provided by A. Ancel, Centre d´Écologie et Physiologie Energétiques, CNRS, Strasbourg, France. Air-breathing divers tend to increase their overall dive duration with increasing dive depth. In most penguin species, this occurs due to increasing transit (descent and ascent) durations but also because the duration of the bottom phase of the dive increases with increasing depth. We interpreted the efficiency with which emperor penguins can exploit different diving depths by analysing dive depth profile data of nine birds studied during the early and late chick-rearing period in Adélie Land, Antarctica. Another eight datasets of dive depth frequency and duration (#472150, #472152, #472154, #472155, #472142, #472144, #472146, #472147), which backup the analysed high resolution profile datasets, as well as two further data sets of dive depth data of another bird (#472156, #472148) recorded in November 2005 did not match the requirement of high resolution. Eleven additional data sets provide information on the overall at surface behaviour during the period analysed (#472157, #472158,

#472162, #472163, #472166, #472167, #472168, #472170, #472172, #472174, #472175).

Project: Marine Mammal Tracking (MMT)

Size: 30 datasets

Datasets listed in this collection:

1. Four high resolution datasets:

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth profile of emperor penguin DDU2005_emp_a_f_18 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset # 633708 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth profile of emperor penguin DDU2005_emp_a_m_10 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset # 633709 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth profile of emperor penguin DDU2005_emp_a_x_05 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset # 633710 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth profile of emperor penguin DDU2005_emp_a_x_08 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset # 633711 (*DOI registration in progress*)

2. Five dive depth frequency histogram datasets:

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth frequency of emperor penguin DDU2005_emp_a_f_18 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472150 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth frequency of emperor penguin DDU2005_emp_a_m_10 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472152 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth frequency of emperor penguin DDU2005_emp_a_x_08 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472154 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth frequency of emperor penguin DDU2005_emp_a_x_05 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472155 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive depth frequency of emperor penguin DDU2005_emp_a_x_17 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472156 (*DOI registration in progress*)

3. Five dive duration frequency histogram datasets:

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive duration frequency of emperor penguin DDU2005_emp_a_f_18 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472142 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive duration frequency of emperor penguin DDU2005_emp_a_m_10 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472144 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive duration frequency of emperor penguin DDU2005_emp_a_x_08 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472146 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive duration frequency of emperor penguin DDU2005_emp_a_x_05 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472147 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) Dive duration frequency of emperor penguin DDU2005_emp_a_x_17 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472148 (*DOI registration in progress*)

4. 16 at surface behaviour (dive, time at surface, relative) datasets:

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_02 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472157 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_07 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472158 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_18 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472160 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_18 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472161 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_f_19 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472162 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_04 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472163 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_10 from Pointe Géologie (SPLASH). Alfred

Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472164 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_13 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472166 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_14 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472167 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_m_15 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472168 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_03 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472170 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_05 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472171 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_06 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472172 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_08 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472173 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_16 from Pointe Géologie (SPOT 5). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472174 (*DOI registration in progress*)

Zimmer, I., Ancel, A., Plötz, J., Bornemann, H. (2006) At surface behaviour of emperor penguin DDU2005_emp_a_x_17 from Pointe Géologie (SPLASH). Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, PANGAEA, dataset #472175 (*DOI registration in progress*)

PUBLICATION VII

PARENT SET OF PRIMARY DATA TO PUBLICATION IV

Ilka Zimmer, Rory P. Wilson, Michaël Beaulieu, André Ancel,
Joachim Plötz, Horst Bornemann

PANGAEA

PUBLICATION VII Parent set of primary data to Publication IV

This parent set provides the primary dataset of publication IV in this thesis.

Parent set:

Citation: Zimmer, I., Wilson, R. P., Beaulieu, M., Ancel, A., Plötz, J., Bornemann, H. (2007) Luminous intensity and dive depth profile data of emperor penguins from Pointe Géologie, Adélie Land, Antarctica, from expedition DDU 2005 [supplementary data to the reference given], *PANGAEA*, (submitted)

Reference: Zimmer, I., Wilson, R. P., Beaulieu, M., Ancel, A., Plötz, J (0). Seeing the light: depth and time restrictions in the foraging capacity of emperor penguins at Pointe Géologie, Antarctica. *Aquatic Biology* (submitted)

Abstract: The foraging ability of visual hunters depends critically on light conditions. Emperor penguins are reported to be visual hunters but breed and forage at high latitudes and are thus exposed to extreme changes in light conditions in the course of the year. We examined how light influenced the foraging ability for breeding emperor penguins using loggers in winter (n = 5) and spring (n = 4) in 2005 (see doi:10.1594/PANGAEA.633713) at Pointe Géologie (140°01'E, 66°40'S), Antarctica as well as by using models of light availability of the year and as a function of depth. The model showed that daylight was continuous between Julian days 350 and 363 and that the sun did not rise between Julian days of 166 and 180. Logger-measured light intensity decreased with water depth and depth-specific values were higher at greater sun elevation angles (4 light-depth Splash datasets). Time-depth use (given by the maximum depth reached multiplied by the number of hours at which this depth could be achieved over 24 h) of spring-foraging penguins was 8,394.5 m.h which was more than twice that of winter-foraging birds at 3,845.4 m.h, showing the severe constraints imposed by winter. Average catch-per-unit effort was related to mean maximum diving depth and was highest around mid-day in winter and highest during dawn and dusk in spring. It is suggested that this relates to the behaviour of prey.

Project: Marine Mammal Tracking (MMT)

Size: 4 datasets

5 SYNTHESIS

This study attempts to enhance our understanding of the foraging ecology of the emperor penguin with particular regard to the extraordinary high Antarctic marine environment in which it lives and breeds. Amongst birds, unusual life-history strategies appear to be promoted by extreme conditions and the extent to which these strategies themselves may be extreme has enabled these animals to inhabit a broad range of environments. It would be fair to say, though, that the emperor penguin embodies perhaps one of the most extreme avian examples of adaptation for an extreme environment on the planet. The core publications (parts I to IV) of this thesis examined some of the features of the foraging ecology of emperor penguins that enable them to provision chicks according to the standard avian central place scenario (Orians & Pearson 1979) despite initiating breeding at Pointe Géologie about 400 km from the sea-ice edge in near virtual conditions of darkness. Particular aims were to assess specific constraints on foraging and the consequences that these might have for emperor penguins.

5.1 General discussion

The unique habit of emperor penguins to reproduce on sea-ice during the austral winter provides them with a temporary breeding site which is initially far from the sea. This distance is particularly onerous, both in terms of time and energy, since emperor penguins swim much faster than they walk (e.g. Pinshow et al. 1977; Kooyman et al. 1992), and have lower costs of transport for swimming than walking (Pinshow et al. 1977) yet they have to traverse a substantial proportion of the distance between foraging and breeding site on foot. Once in an area where the conditions allow access to the sea, emperor penguins must generally forage from holes or fissures in the ice which restrict access to the water and search for food which is patchily distributed in the ocean, both horizontally and vertically. Extraordinary dive capacities, both in terms of dive duration and maximum dive depth, similar to those of marine mammals (such as Weddell seals, e.g. Burns and Kooyman 2001; Plötz et al. 2002) enable these birds to exploit marine food resources in the Antarctic sea-ice zone (Kooyman and Kooyman 1995; Kirkwood and Robertson 1997a; Kirkwood and Robertson 1997b; Wienecke and Robertson 1997; Rodary et al. 2000 - this thesis). These dive capacities owe much to the large size of the birds (Kooyman 1985; Butler and Jones 1997; Kooyman and Ponganis 1998; Ponganis and Kooyman 2000;

Halsey et al. 2006) and, aside from the standard Bergman's rule scenario (Bergmann 1847) cited as a reason for the exceptional mass of this species breeding at such high latitudes (cf. Meiri and Dayan 2007), may be a prime factor allowing the bird to breed in such difficult conditions. However, large size has disadvantages; specifically that there is a tendency for large species tending young to have a longer brood care period (Peters 1983). The implication in this is that, as an annual breeder, the emperor penguin has a reproductive cycle that occupies a larger proportion of the year than other penguin species (Fig. 4.1) despite the fact that it breeds at latitudes where annual variation in conditions is extreme.

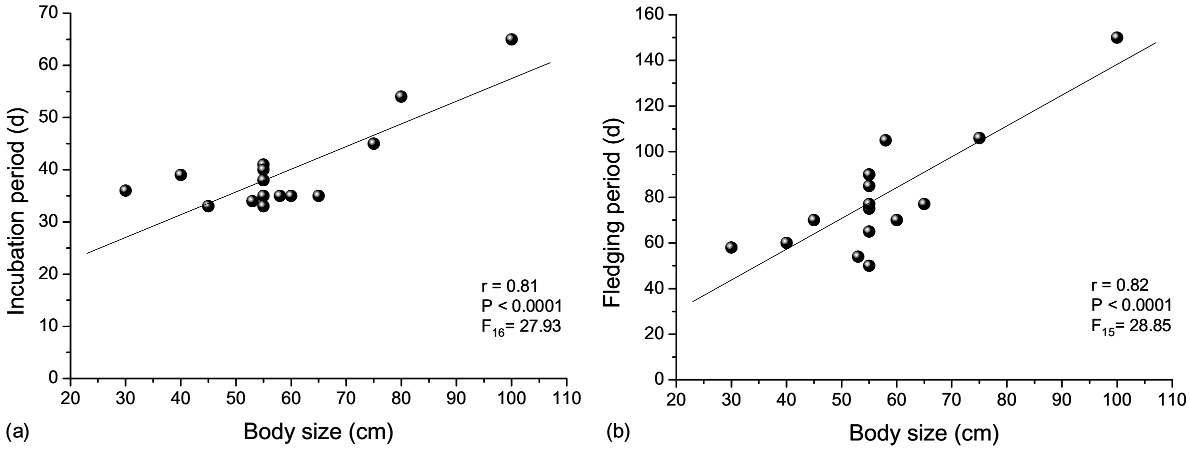


Fig. 5.1. (a) Incubation and (b) fledging period (days) as a function of body size (cm) for 16 penguin species, except the *Eudyptula minor* subspecies; (data taken from Williams 1995 and references therein). The relation in (b) does not include the king penguin because this species has an unusual breeding cycle that exceeds one year (Stonehouse 1960).

The overall time dedicated to the breeding cycle by emperor penguins is composed of between 1 to 10 days travel from the sea to the breeding area (depending on the breeding location and annual sea-ice extent), 45 days courtship and pair bonding, 65 days incubation and a further 150 days allocated to chick-rearing, making a total of about 270 days of the year (cf. Le Maho 1977). The brevity of the austral summer, which ideally should occur when the chicks need to be provisioned due to the enhanced prey abundance at this time (cf. Lack 1968), means that, in order to optimize chick growth, birds have to lay their eggs in the austral winter. Furthermore, due to the retreat of the sea-ice edge with the onset of spring, these eggs have to be laid far from the ice edge so that neither the eggs nor the chicks (which are only able to swim when they are about 150 days old) are at risk from the sea. Thus, when females conduct the post-egg-laying foraging trip, and subsequently, when males undertake their post-incubation trip, foraging is constrained by the extended sea-ice which prohibits the penguins from entering the water near the colony (Publication II). Accordingly, foraging trips are extended at this time. In this study the females had post-egg-laying foraging trips of mean 72 days while males had post-incubation trips of mean 24 days. Foraging trip durations became shorter as spring advanced until both breeding partners cycled to and from the colony for a mean of seven days to forage for themselves and their chick. During this latter period from late October to mid December, when the sea-ice cover breaks up, penguins could enter the sea close to the breeding colony and daylight becomes almost continuous.

The poor foraging situation in winter is exacerbated by the very restricted light conditions that prevail in such high latitudes at this time (Publication IV). It is notable that the studied emperor penguins, which like other penguin species appear to be uniquely visual hunters (Kooyman and Kooyman 1995; Kirkwood and Robertson 1997a; Wienecke and Robertson 1997), had foraging periods reduced to only 11 hours per day in winter compared to 24 hours in spring.

Emperor penguins have to equate restrictions in time available for foraging and restrictions in space due to the sea-ice cover with the temporal and spatial vagaries of prey distribution. In spring the foraging distribution of emperor penguins from Pointe Géologie suggests that enough prey was available in the vicinity of the breeding colony over the Antarctic shelf. Although the prey distribution and abundance could not be observed directly in this study, the incidence and distribution of specific foraging activity was examined by using an index based on area-restricted-search (Publication II) and also by examining preferred dive depths in the context of the emperor penguin diving efficiency (Publication III). Emperor penguins feed on fish, squid and krill (Offredo and Ridoux 1986; Klages 1989; Gales et al. 1990; Robertson et al. 1994; Pütz 1995; Kirkwood and Robertson 1997a; 1997b; Wienecke and Robertson 1997; Cherel and Kooyman 1998; Zimmer et al. 2007a) and may hunt in both pelagic and benthic environments, switching between them in response to the prey availability. Although emperor penguins are able to dive to extraordinary depths (in excess of 500 m - Kooyman and Kooyman 1995; Wienecke et al. 2007), depths between 50 and 225 m were determined to be the most lucrative for foraging birds (Publication III). Where deeper dives occurred, their occurrence could still be justified if the feeding rewards were appropriate and catch-per-unit-effort indices indicated that this was the case (Publications II to IV).

5.2 Generalized model

It is clear that the breeding and foraging strategies, employed by emperor penguins, are appropriate for the environment in which they live but it is not apparent the extent to which the birds are constrained by the environment to exhibit the patterns observed in this thesis (Publications I to IV) and by other researchers (Ancel et al. 1992; Kirkwood and Robertson 1997a; Kirkwood and Robertson 1997b; Wienecke and Robertson 1997; Rodary et al. 2000). This can be alluded to, however, by implementation of a simplistic model that considers the time and energy consequences of birds that are obliged to commute between breeding and foraging sites that can be made to vary in distance according to circumstance.

For this, I consider that penguins provision chicks by commuting between the colony and the foraging site and taking time that roughly corresponds to that observed in this work, namely eight days in the winter and one day in spring (Publication II). For this to be energetically tenable, the penguins have to acquire at least as much energy as they loose per trip as well as acquiring an extra of mean 4 kg of food stored in their stomachs for the chick (Kirkwood and Robertson 1997a). Penguins provisioning chicks may store up to 30% of their body mass as food (Wilson et al. 1989) and the mean mass of emperor penguins is taken to be 28 kg (this study). Thus, the energy recovered during foraging must, at least, equate with the costs of the travel as well as the costs of actively diving and the periods of rest both at the surface of the water between dives and on the ice, in addition to the energy acquired for the chick (calculated by multiplying the calorific value of primary prey by the mass of prey transported back to the chick – Table 5.1). Values for the metabolic costs of walking, diving and resting can be derived from the literature (Table 5.1). Finally, the amount of time that the birds can spend diving during the foraging trip depends on the time of year since the light only permits foraging for 11 hours per day during mid-winter while during spring birds may forage round the clock (Publication IV). The percentage times actually spent underwater and at the sea surface during active foraging (to allow birds to recover the oxygen debts incurred during diving) were set at 50% which is an approximate value derived from data in this study.

Table 5.1. Parameters used for a simple energetic model that considers time and energy consequences for emperor penguins assuming different foraging trip durations.

Parameter	Value	Reference
Emperor penguin body mass	28 kg	Mean; this study
Mass of food brought back to the chick per food delivery	4 kg	Mean, assuming 18-20 food deliveries during chick-rearing(Kirkwood and Robertson 1997a)
Winter – travel duration on sea-ice from/to colony to/from foraging site	8 d	Mean for winter-foraging females; this study Publications II, III
Spring – travel duration on sea-ice from/to colony to/from foraging site	1 d	Mean for spring-foraging penguins; this study Publications II, III
Winter – hours spent diving per day	11 h	This study Publication IV
Spring – hours spent diving per day	24 h	This study Publication IV
Percentage time spent at sea surface during active foraging	~ 50%	This study (unpublished data)
Basal Metabolic Rate (BMR)	1.58 W.kg^{-1}	5.7 kJ.kg^{-1}.h^{-1} (Nagy et al. 2001)
Metabolic rate during walking (2 km.h^{-1})	6.32 W.kg^{-1}	4.0 x BMR (Pinshow et al. 1977)
Metabolic rate during diving underwater	6.48 W.kg^{-1}	4.1 x BMR (Nagy et al. 2001)
Metabolic rate during resting at sea surface	2.21 W.kg^{-1}	(Kooyman and Ponganis 1994; Nagy et al. 2001)
Calorific value of food assuming fish and squid to be main components	6,200 kJ.kg^{-1}	(Robertson and Newgrain 1996)

Formulation of all the above parameters into a simple energetic model indicates that the necessary rate of energy gain for birds to balance energy output with energy input decreases with increasing trip duration during both winter and spring (Fig. 5.2). This is little surprising since longer trip durations result in a reduced proportion of the time devoted to travelling over the ice when no prey acquisition can take place. However, the necessary rate of energy gain of winter-foraging birds is considerably higher than of spring-foraging birds until about 32 days (Fig. 5.2). This is brought about by both the longer travelling times of winter birds and the reduced time available for foraging, due to poor light conditions, even when the birds are in the foraging area. The fact that the foraging trip durations for females during winter are about 72 days, and those of the males during late winter are 24 days presumably reflects the reduced prey abundance typical for the winter period. In other words, low prey availability does not allow emperor penguins to undertake short foraging trips (which would be primarily modulated by short periods within the foraging area) during the winter when the sea-ice conditions constrain the birds to undertake long periods of travel over the ice. The situation is reversed during spring when the short commuting periods resulting from the proximity of the sea to the colony and the enhanced light conditions allow birds to undertake much shorter trips with a reduced necessary rate of energy gain. This is enhanced by a presumed higher productivity of spring/summer waters (e.g. Whitaker 1982; Clarke 1988; Fogg 1998) leading to higher penguin prey abundance.

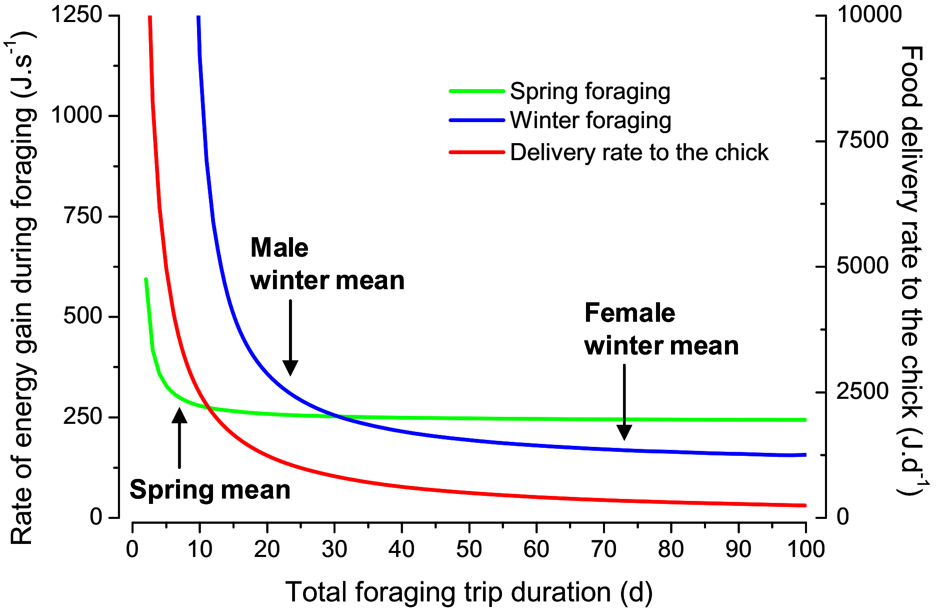


Fig. 5.2. Rate of energy gain during foraging modelled for emperor penguins as a function of foraging trip duration. The winter scenario (blue) considers eight days of travel on the ice to/from the colony and 11 hours diving activity per day. The spring scenario (green) considers one day travel on ice and 24 hours diving activity per day. The second y-axis shows the rate of delivery of energy to the chick assuming that adult birds may carry 4 kg food in their stomach (see text).

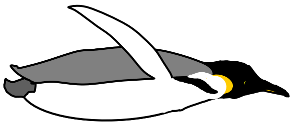
It is notable that the longer foraging trips for the adults result, overall, in them being exposed to a lower rate of necessary energy acquisition so, if adult well-being were the only consideration, one would expect long foraging trips to be the norm. However, as the duration of the foraging trip increases, the rate of energy delivery to the chick decreases, following a similar exponential decay-type curve (Fig. 5.2). This is because the adult can only deliver a certain mass of food to the chick per trip which is actually limited by the size of the adult stomach. There is thus a situation of ‘conflict’ whereby chick demands are best met by short foraging trips whereas adult demands are best met by long foraging trips and it is likely that what is observed is a compromise between the two. Specifically, if adults do not recover energy costs expended during the course of their foraging trips, they will decrease their own chances of survival in the long term. However, failure to provide energy to the growing chick at a rate commensurate with appropriate growth for survival means that reproductive output is compromised. The precise conditions of the sea-ice, with its effect of modulating the distance between foraging and breeding site, and the abundance and accessibility of prey at putative foraging sites will determine which foraging strategy is best at any one time during the breeding cycle or during any particular year.

The present study highlights two simplistic scenarios based on data that were gained during the course of this thesis. The literature, however, reports wide variation in foraging trip duration depending on year and site (Ancel et al. 1992; Kirkwood and Robertson 1997a; Kirkwood and Robertson 1997b; Wienecke and Robertson 1997; Rodary et al. 2000; Zimmer et al. 2007b). The extraordinary conditions under which the emperor penguin must breed make it likely that this species will be particularly sensitive to change. Global changes in temperature (e.g. Robinson et al. 2003; Zhen-Shan and Xian 2007) are considered likely to affect the distribution of sea-ice as well as putative distribution of penguin prey (e.g. Atkinson et al. 2004; Murphy et al. 2007) and climate change has already been invoked as responsible during the late 1970s for changes in the emperor penguin population at Pointe Géologie (Barbraud and Weimerskirch 2001). Modelling scenarios such as this demonstrate mechanisms by which adult or chick survival may be compromised but such attempts are only valid if the data used are good and the assumptions appropriate. This is reason enough to continue studying the emperor penguin so that, despite the difficulties in carrying out fieldwork (e.g. ‘Materials and methods’, this study), we can begin to understand how this remarkable species interacts with its environment. Hopefully, it would be nice to think that our understanding would reach a point that, if necessary, we could make viable suggestions to ensure that the emperor penguin, this most extraordinary of birds, continues to survive in its chosen habitat.

5.3 Perspectives

Although emperor penguins are difficult to study for logistic reasons, this study still managed to examine the foraging distribution of these birds during three major seasons (winter, spring, summer) of the annual cycle. Indeed, analyses of dive behaviour have enabled comparison of foraging strategies between the two main, yet different, chick-raising periods in winter and spring. I would like to think that the results presented in this thesis significantly enhance what we know and understand about emperor penguin foraging ecology and that this may allow insights into how postulated changes in the Antarctic ecosystem structure and functioning might impact the birds in a general sense. In the wider ecological context, however, the study was limited by two aspects: (1) by the fact that it was conducted at only one colony and (2) over a single breeding season. Consequently, the results may not be extended to other colonies or other years because biotic (e.g. changes in prey abundance and distribution) and abiotic (e.g. the sea-ice extent) factors, which effect the ecological performance of emperor penguins, are expected to vary between years and colonies. To speculate realistically on the effects of climate-induced changes to the Antarctic marine system we need prior knowledge of the magnitude of natural variation within the system and how it varies in time and space. A reasonable perspective would be the extension of this current study at more than one colony and over several years to quantify the variation in the emperor penguin foraging ecology.

A critical issue in this, and many other studies of animal feeding ecology, is our ability to determine the extent of feeding. An attempt was made at this via CPUE but ideally examination of diving should be supplemented by the direct measurement of prey ingestion such as has been proposed using beak sensors (Wilson et al. 2002b). It was unfortunate that, despite best attempts, this could not be realised over the course of this study. This highlights the difficulties of field work in the extreme environment of the Antarctic (and also at great water depth). I would advocate, however, that further work in this area should be attempted simply because definite knowledge regarding prey ingestion is so valuable for understanding foraging strategies. If such data were combined with additional measurements of animal dynamic acceleration (Wilson et al. 2006) it would pave the way for examination of the energetic cost of different foraging activities. Ultimately, since the ability of animals to balance energy input with output defines a large part of life history success, any data of this type combined with energy input data from beak sensors would enable models of the type proposed above to be much more realistic (and therefore useful in a predictive sense). Recent advances in solid-state technology in form of animal-attached devices should now enable parallel recording of multiple parameters in high resolution (Ropert-Coudert and Wilson 2005) in attempting to work towards this general aim. It would be naïve, however, to consider that any work of this nature will ever be easy. The vagaries of the sea-ice, variability in bird response to environmental change (intra- and inter-annually) and the simple draconian conditions experienced by emperor penguins in terms of temperature, pressure and time spent in, and out of, the water will always make work of this type a challenge. It is somewhat humbling to know that man’s greatest technological advances still do not allow us to unravel some of the basic biological secrets of some of the planet’s most enigmatic creatures. Our continued desecration of our world, bringing with it all the associated changes in complex ecosystems and their components, will, however, make it necessary that we find a way to provide the information that we need to protect this most remarkable of birds.



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APPENDIX

Tables 8.1 and 8.2 both refer to publication II providing detailed information on satellite and time-depth recorder equipped emperor penguins at Pointe Géologie in winter, spring and summer 2005/2006 which are only summarized therein.

Table 8.1 Total and mean (± SE) trip durations, maximum distances to the colony and distances travelled by winter female, winter male, spring and summer foraging emperor penguins at Pointe Géologie in 2005 and 2006 equipped with satellite transmitters.

Penguin	Foraging trip records (N)	Trip dates (depart-return)	Trip duration (days)	Distance travelled (km)	Maximum distance To colony (km)
Winter-foraging females					
F-1a*	1	15 May - 2 Aug	79	1149	62
F-2a*	1	15 May - 2 Aug	79	582	116
F-3a trip1*	1	17 May - 15 Jul	59	1050	104
Median (range)			79 (59 - 79)	1050 (582 - 1149)	104 (62 - 116)
Mean (± SE)			72 ± 7	927 ± 175	94 ± 16
F-3a trip2*	1	4 Aug - 14 Aug	10	174	68
Winter-foraging males					
M-4a*	1	31Jul - 30 Aug	29	582	133
M-6a*	1	24Jul - 13 Aug	19	459	78
Median (range)			25 (19 - 29)	521 (459 - 582)	105 (78 - 133)
Mean (± SE)			24 ± 5	521 ±62	106 ± 28
Spring-foraging birds (both sexes)					
F-2b	1	31 Oct - 09 Nov	8	416	92
?-3b	3	01 Nov - 29 Nov	9, 8, 11	420, 381, 593	58, 82, 101
M-4b	6	01 Nov - 17 Dec	19, 2, 11, 6, 2, 5	859, 121, 555, 396, 104, 326	123, 35, 117, 108, 41, 113
?-5b*	1	01 Nov - 10 Nov	9	511	89
F-7b	1	02 Nov - 2 Nov	14	555	81
?-8b*	1	02 Nov - 10 Nov	8	512	100
M-10b*	2	04 Nov - 16 Nov	2, 10	81, 667	21, 157
M-13b	4	05 Nov - 21 Nov	4, 3, 3, 3	167, 124, 169, 148	52, 49, 59, 55
?-17b	1	13 Nov - 23 Nov	10	626	163
F-18b*	1	13 Nov - 22 Nov	9	392	94
Median (range)			8 (2 - 19)	397 (81 - 859)	89 (21 – 163)
Mean (± SE)			7 ± 1	387 ± 48	85 ± 8
Summer-foraging birds (both sexes)					
?-3b		29 Nov - 30 Dec	31	2429	755
M-4b		17 Dec - 20Jan	34	1762	425
F-7b		23 Nov - 14 Jan	51	3378	568
F-18b		22 Nov - 15 Jan	54	3686	649
F-19b		1 Dec - 12 Jan	42	3056	838
Median (range)			42 (31 - 54)	3056 (1762 - 3686)	649 (425 - 838)
Mean (± SE)			42 ± 5	2862 ± 345	647 ± 72

* penguins providing depth records
a: penguins equipped in winter
b: penguins equipped in spring

Table 8.2 Basic dive features of nine emperor penguins at Pointe Géologie, Adélie Land, in winter and spring 2005, recorded with archival tags and satellite transmitters. Mean values are given ± 1 standard error (SE).

Penguin	N dives	Max. dive depth (m)	Mean max. dive depth (m)	Max. dive duration (min)	Mean dive duration (min)
Winter-foraging females					
F-1a	4533	338.8	60.0 ± 1.0	11.6	2.7 ± 0.03
F-2a	5103	344.5	56.8 ± 1.0	12.2	2.6 ± 0.03
F-3aTrip1	3969	282.5	50.0 ± 1.0	9.7	2.3 ± 0.03
Grand mean (± SE)		321.9 ± 19.8	55.6 ± 3.0	11.2 ± 0.8	2.5 ± 0.12
F-3aTrip2	1057	242.5	47.3 ± 1.8	10.3	2.7 ± 0.02
Winter-foraging males					
M-4a	2502	438.4	80.2 ± 1.9	16.1	3.4 ± 0.05
M-6a	1918	415.3	58.7 ± 1.7	11.8	2.7 ± 0.06
Grand mean (± SE)		426.9 ± 11.6	69.5 ± 10.8	14.0 ± 2.2	3.1 ± 0.35
Winter-foraging birds (both sexes)					
Grand mean (± SE)		343.7 ± 30.6	58.8 ± 4.7	12.0 ± 0.9	2.7 ± 0.2
Spring-foraging birds (both sexes)					
?-5b	1129	226.5	118.8 ± 2.6	10.5	4.4 ± 0.07
?-8b	1168	437.5	94.3 ± 3.3	13.0	3.7 ± 0.08
M-10bTrip1	146	238.0	75.0 ± 5.8	9.0	4.0 ± 0.21
M-10bTrip2	1763	400.0	101.8 ± 2.2	10.5	4.3 ± 0.06
F-18b	1261	338.0	105.0 ± 2.3	9.4	4.2 ± 0.06
Grand mean (± SE)		328.0 ± 42.2	99.0 ± 7.2	10.5 ± 0.7	4.1 ± 0.12