Fine-scale analysis of foraging strategies of free-ranging penguins.

Yan Ropert-Coudert

DOCTOR OF PHILOSOPHY

Department of Polar Science
School of Mathematical and Physical Science
The Graduate University for Advanced Studies

2000

"So long! And thanks for all the fish..."

Douglas Adams.

ABSTRACT

The large number of seabirds exploiting the Southern Ocean in relation to their status of potential competitors with human fisheries for key-species of commercial interests explain the prime importance of studies investigating the birds' feeding and foraging strategies. With this intention, progresses in the development of new technologies have allowed researchers to monitor the behaviour of animals while at sea using loggers that measure various parameters as a function of time.

In the past three years, deploying the most advanced technological devices in an integrative approach, multiple data per individual were recorded at a high sampling rate on free-ranging Adélie and King penguins. Depth utilization and swim speed as parameters of the foraging effort displayed by birds, were principally investigated in tandem with the monitoring of the oesophageal temperature, this latest being used to detect the ingestion of cold ectothermic prey, indicated by precipitous drops in the internal temperature of the predator. Thus, fine-scale foraging events could be related to feeding events.

Calibration experiments on captive penguins, handfed on land and swimming in an exhibit pool, showed that the upper the sensors in the oesophagus, the higher the detection rate. Moreover, the magnitude of the temperature drop increase with the mass fed and decrease with increasing frequency of ingestion. Deployed on free-ranging birds in tandem with swim speed and depth loggers, the oesophagus temperature recording gave precious indication about the depths at which prey were taken. In addition to the feeding behaviour, several foraging strategies that may enhance the prey detection and/or capture were also revealed.

Based on these data obtained on free-ranging penguins, the potential way birds locate the patch of prey within a foraging trip, possibly using chemoreception during shallow diving activity, as well as an updating of the classification of the role of dives using their depth profile will be described. Some of the most striking strategies displayed by both Adélie and King Penguins will also be discussed in the present thesis, these being i) the optimization of the commuting phase of the dive cycle (22% of the prey catches were observed during the ascent of the dives of Adélie penguins); ii) the use of an upwardly focused hunting strategy that may be related to the detection of prey in the deep using a backlighting effect; iii) the modification in the dive angles in relation to a prey encounter (birds descending the water column with a steeper angle when prey have been encountered in the previous dive); and iv) the intra- and interspecific adaptation of the swim speed to the status of the dive (feeding or non-feeding) and the type of prey pursued: Indeed, Penguins swam at a speed that accords closely to the minimum cost of transport during non-feeding dives and during commuting phases. On the other hand, the encounter with a prey led to an evolution in the range of speed used (the hunting speed of Adélie decreased, that of Magellanic increased and that of King Penguins became erratic), which depend on both the energetic advantages the birds might receive and the rate at which they could process prey.

Besides the optimization in the acquisition of food resources, the relevance of these adaptations to the reduction of the energy expended while foraging will be briefly evoked. The relevance of system for detection of prey intake, such as the oesophagus temperature recording, in tandem with other parameters to investigate the foraging behaviour and decision-making processes of free-ranging seabirds will be stated in a final conclusion.

Acknowledgements

I am very grateful to Professor Yasuhiko Naito for welcoming, supporting and advising me during my three years stay at the National Institute of Polar Research. He constantly provided me with the best encouragements he could and always keep an ear open to young people. Cafeteria chats with him were a constant source of interest... I am equally grateful to Professor Yvon Le Maho for, firstly, selecting me among the candidates to overwinter in Crozet archipelago, then welcoming me in his laboratory for the duration of my master thesis and finally for trusting me by allowing me to take a part in the collaboration between his laboratory in the CEPE of Strasbourg and the Japanese National Institute for Polar Research. I am also thanking him in advance for my forthcoming for his support in the realization of my French doctor thesis.

My five referees, Kawaguchi-sensei, Imafuku-sensei, Fukuchi-sensei, Kanda-sensei and Odate-sensei, should be especially acknowledged here for coping with the patient task of reading a large amount of pages written in English and providing me with useful comments.

Akiko Kato provided me (and most of the students of the NIPR) with more help and support than anyone could hope. She never refused to supervise, encourage, criticize, correct, comment my work, even when she was overwhelmed with other duties. Thanks for all you gave me, professionally and sentimentally.

This thesis would never had come to reality without the constant help, patience and friendship of Charles-André Bost who never ceased advising me since 1994 and this, even at great distances from each other (Antarctica or Japan).

The Monbusho of Japan, the Ministry of Foreign Affairs of France (especially Mme F. Gheno), the Terres Australes et Antarctiques Françaises (TAAF), the Institut Français pour la Recherche et la Technologie Polaire (IFRTP.) are acknowledged for their funding and/or logistic supports during field sessions. I would like here to express my gratitude to Pierrot, the logistic staffs and members of the 31st (1992-1994), 32nd (1994-1996), 33rd (1996-1998) missions in Crozet and the 41st (1998-1999) mission in Dumont d'Urville. At this occasion, I would also like to thank the Guillaume Froget (bonne chance pour ta thèse), Jean-Noel Clech (Gino), Jean-Benoît Charrassin (Jibi), Yannick Clerquin, Michel Gauthier-Clerc, Julien Baudat, Professor Claude Duchamp, Professor Hervé Barré, Frederique Denjean (Freda).

From the NIPR, I would give here my special thanks to Maki Kuroki, Eri Ayukawa, Kaori Iwao for ping-pong, beers and good times in general, Ueno Takeshi, Hideji Tanaka... well, to all of the NIPR students of the biology section and elsewhere. Gratitude are also due to Kani-sensei (especially for the unforgettable soft-ball game), Dohi-san, Ishii-san. Thanks also to the NIPR outsiders: Alan and Yuki Power and all the Dubliners' family, Dr. K. Saito, Dr. Y. Watanuki, Dr. Seiji Ohtani, the staff at Nagoya Public Aquarium and especially Kurita-san who authorized us to annoy his penguins in several occasions.

On an international scale now, I would thank the following friends. From France: André Ancel, Hughes Oudard, Cristina Sevenans, Sylvie Marchant, Cecile Thouzeau, Delphine Michard-Picamelot, JiPi Robin, Yves Handrich, and all the CEPE, Alexandra Amat, Yves Cherel, Christophe Guinet. A special thanks to my mother, my grandfather, my family and friends in France who always keep a seat for me at the table while I'm away. I also wish to thank all the "gaijins" that visited the laboratory during my stay (reading manuscripts, correcting, advising, modelling or even just sharing beers): Graham Hosie, Rory Wilson, Frank Pattyn, Graham Robertson, Harvey Marchant, John Kitchner, ... including people I met in various other places: Richard Bevan, Pat Butler, John Croxall, Alejandro Scolaro, Guillermo Luna-Jorquera, Gerry Kooyman...

Just a few words to the penguins: Thanks folks! I wouldn't be here without you!

-- TABLE OF CONTENT --

FINE-SCALE ANALYSIS OF FORAGING STRATEGIES OF FREE-RANGING PENGUINS

I – INTRODUCTION

I – 1. Biological background:

Analysis of the adaptations that animals display to optimize their food intake, and consequently their survival and reproductive success, are of prime importance in ecology studies (Collinvaux 1986, Stephen & Krebs 1986, Williams 1966). Since a given environment is generally heterogeneous at different scales (Begon *et al.* 1991), availability of food resources may show fluctuations. Natural selection will tend to favour the individuals capable of anticipating these changes and that can adjust their efficiency in gathering energy without altering significantly their condition (Carlisle 1982, Tolonen & Korpimäki 1996). For instance, it is expected that when prey availability is restricted, terrestrial predators should use the foraging strategies that are the less costly, energetically speaking (Norberg 1977). With this regards, one aim of studies on foraging ecology of animals is to highlight the behavioural strategies that animals might deploy to optimize the acquisition of food in a variable environment (Maurer 1996, Stephens & Krebs 1986).

In the present work, the fine-scale foraging strategies of predators were investigated. Since comparison between or within species, in parallel to optimality modelling (Stephens & Krebs 1986), is one of the methods to study the foraging strategies (*e.g.* Ridley 1984), this was applied to investigate the fine-scale behaviour displayed by various predators to detect and capture their specific food resources.

I – 2. Environmental background: the Southern Ocean:

The Southern Ocean is characterized by a zonation of the water masses (Deacon 1982) delimited by the following boundaries (going north from the continent): the Antarctic divergence; the Antarctic convergence (polar front); the sub-Antarctic front and the subtropical convergence. The zones between the boundaries, more or less foreseeable from one season to the next (Park *et al.* 1998), are characterized by vertical movements of water (upwelling), where cold Antarctic waters slip below and mixes with warmer waters (Kort 1967). These movements bring mineral elements to the upper layers, providing a basis for photosynthetic processes at the base of the Southern Ocean food webs (Jones *et al.* 1990). Consequently to the high primary production, these frontal zones are associated with high secondary productions (Laubscher *et al.* 1993, Lutjeharms *et al.* 1985, Pakhomov *et al.* 1994, Tynan 1998) and several studies have demonstrated the close correspondence between the abundance of top-predators and zooplankton in these zones (Ainley & DeMaster 1990, Knox 1994, Pakhomov & McQuaid 1996, Ricklefs 1983, Tynan 1998).

To summarize briefly the type and repartition of the marine resources of the Southern Ocean, the water masses can be divided into two areas, one north of the polar front, that present an important biodiversity and is rich in mesopelagic Myctophid fish (Hulley 1981, Kozlov *et al.* 1993) and another area south of the polar front. South of the polar front, the seasonal ice-cover plays a determinant role in the structure of the ecosystem: the biogeographical province permanently free of ice is dominated by zooplankton species (Tynan 1998) and mesopelagic fish (Gon & Heemstra 1990). Going closer to the continent, the food webs of the water masses seasonally covered by sea-ice – the richest region for primary production (Hempel 1985) – are dominated by the Antarctic Krill, *Euphausia superba* (Stemacek *et al.* 1990). Despite a smaller planktonic biomass, the area permanently covered by fast-ice also contributes to biological

productivity at different levels, Antarctic fast-ice probably providing refuges and feeding grounds for plankton (Andriashev 1968, see review in El-Sayed 1971).

I – 3. Animal model:

SEABIRDS OF THE SOUTHERN OCEAN: Among the abundant fauna of top-predators exploiting this vast ecosystem, seabirds are the largest by numbers (Croxall 1984, Croxall *et al.* 1984) and offer the advantage of a separation between feeding activities at sea and reproducting activities on sub-Antarctic islands or the Antarctic continent (see review in Marchant & Higgins 1993). In addition, they consumed marine resources in large quantity (Croxall & Prince 1987, Croxall *et al.* 1985, Furness 1990, Woehler 1995), especially species of commercial interests turning them into potential competitors with human fisheries (Birt-Friesen *et al.* 1989, Furness 1990, Furness & Cooper 1982). Using seabirds as bio-indicators of the marine resources (Bost & Le Maho 1993, Croxall *et al.* 1988, Furness & Nettleship 1990, Le Maho 1994, Guinet *et al.* 1998, Montevecchi 1993, Trivelpiece *et al.* 1990) could help improving the conservation and management of both the seabirds' community (Hunt 1991) and the stocks of the marine resources (CCAMLR 1985, 1986, Croxall *et al.* 1988).

Seabirds in the Southern Ocean show different feeding strategies (see Ashmole 1971, Harper *et al.* 1985) that allow them to exploit several ecological niches, reducing the overlapping between foraging grounds (Ashmole 1971). They can be separated into aerial feeders that fly from their colonies to the feeding zone and feed mainly in the surface and sub-surface waters (Storm Petrels, *Fregata grallaria*); plungers that use the momentum of fall to assist in catching prey without pursuit swimming (Terns, *Sterna vittata*) and finally, divers that submerged entirely their body to catch prey. This last category is further divided into surface divers (such as the Black-browded Albatross, *Diomedea melanophrys*) and pursuit divers that show the highest degree of adaptation to the aquatic environment (penguins Spheniscidae and some cormorants). In view of this paragraph, seabirds can browse from air to great depths, a large volume of the Southern Ocean ecosystem while foraging, most of the volume (from sub-surface to more than 500m) being attributed to penguins only.

PENGUINS: Penguins represent up to 90% of the bird biomass in the Antarctic regions (Mougin & Prévost 1980). Among seabirds, most of the penguins are large (exception of the Little Penguin, *Eudyptula minor*, Williams 1995) and greatly adapted to marine life (Croxall & Lishman 1987) with exceptional hydrodynamic features (Bannasch 1995, Hui 1988, Kooyman 1989, Nachtigall & Bilo 1980). These features allow them to exhibit impressive diving performances (see review in Wilson 1995), down to 534m for Emperor Penguin, *Aptenodytes forsteri* (Kooyman & Kooyman 1995). Being air-breathers, they are forced to return periodically to the surface to replenish their oxygen stores. Some physiological adaptations, still under investigations, might allow them to extend time underwater (Kooyman 1989, Handrich *et al.* 1997). Their foraging trips can be decomposed into various scales of analysis: travelling and feeding phases (Wilson 1990, 1995), dive bouts (Chappell *et al.* 1993, Kooyman 1989), dive cycle itself divided into commuting phases between the surface and the prey patch (descent and ascent phases) and phase of the dive devoted to hunting and prey capture activities (undulatory phases, Wilson 1995).

In relation to the huge number of penguins exploiting the Southern Ocean resources, studies on their feeding behaviour are of prime importance. Overall, the diet of penguins is limited to crustaceans, fish and squids (Croxall & Lishman 1987). They are known to be visual hunters (Croxall 1987) and visual observations of penguins feeding close to the shore suggested that they capture fish from beneath (Rand 1960). There are also some clues indicating that they feed frequently in group and may display synchronous diving, evoking a possible cooperation in

hunting strategies (Boswell & McYver 1975, Tremblay & Cherel 1999). However, the timing of prey intake, prey pursuit and capture by penguins remain poorly understood.

SPECIES INVESTIGATED: During the course of this thesis work, the analysis will focus on the foraging behaviour of free-ranging penguins, with a special emphasis on two species: Adélie Penguin, *Pygoscelis adeliae*, and King Penguin, *Aptenodytes patagonicus*, (see Williams 1995 for review on the breeding biology). Briefly, Adélie Penguins have a circumpolar distribution breeding during the short Antarctic summer (Croxall 1987, Williams 1995), while the King Penguin breed on most sub-Antarctic islands of the Southern Ocean (Williams 1995) and have the longest breeding cycle known in seabirds (Olsson 1996). The study of the feeding ecology of Adélie and King Penguins is of prime importance since these birds feed primarily on prey species that are important componenets of the Antarctic ecosystem: the Lanternfish, Myctophidae (Adams & Klages 1987, Cherel & Ridoux 1992, Klages *et al.* 1990, Olsson & North 1997) for King Penguins in the sub-Antarctic regions; and Krill, Crustacea, Euphausiacae (Coria *et al.* 1995, Kerry *et al.* 1995, Trivelpiece *et al.* 1987, Watanuki *et al.* 1997, Wilson *et al.* 1991) in the Antarctic for Adélie penguins. Besides Myctophids, the diet of King Penguins might comprise squids (Adams & Klages 1987, Cherel & Ridoux 1992, Klages *et al.* 1990), while the diet of Adélie Penguins can present an important proportion of Nototheniidae fish (Emison 1968, Endo *et al.* 2000, Ridoux & Offredo 1989). Myctophids and Krill are both schooling species (Gjosaeter & Kawaguchi 1980, Nicol & de la Mare 1993, Torres & Somero 1988, Zasel'sliy *et al.* 1985) and both Krill (Everson 1984, Everson & Murphy 1987, Kalinowski 1978, Marr 1962) and Myctophids (Gjosaeter & Kawaguchi 1980, Torres & Somero 1988, Zasel'slyi *et al.* 1985) undergo diel vertical migration.

I – 4. Technological background:

Studies of the foraging strategies deployed by seabirds while prospecting at sea are bound by a major constraint: the difficulty to collect data using direct observation of the animal in its milieu. Although seabirds or marine mammals need to replenish regularly their oxygen reserves at the water surface where they can be visually spotted from boats, the integrity of their foraging activity takes place underwater and visual observation ceases once they dive. However, in the early eighties the progresses in micro-technologies were applied to biology and opened a new area of science where the foraging behaviour of animals in an inaccessible environment can be monitored by devices that collect time-series data and are called loggers (Eckert *et al.* 1986, Kooyman & Davis 1982, Le Boeuf *et al.* 1988, Naito *et al.* 1990). These loggers are attached to the animals and record selected parameters during the animals' foraging trip. In the case of penguins, foraging trips take the form of a loop (Bost *et al.* 1997, Wilson 1995) that can be broken down into i) travel to the patch characterized by numerous shallow and few deep dives, ii) once the prey patch has been located, intense diving activity followed by iii) the travel back to the colony where almost no deep dives are recorded. Once retrieved (at the recapture of the animal), the data stored as a function of time in the memory are downloaded onto computers and subsequently used through purpose-written softwares to rebuilt the foraging behaviour. Following the pioneer works, the concept of loggers mounted on the animal has spread and various types data have been collected. The data collection rate, the data storage capacity, as well as the resolution of the measurement have increased proportionally to the recent advances in the technologies (see review in Le Maho 1994, Naito 1997). Over recent years, the use of these electronic recorders has consistently improved the understanding of the foraging behaviour of marine animals, such as diving activity (*e.g.* Davis *et al.* 1999, Kato *et al.* 1996, Peters *et al.* 1998), foraging area (*e.g.* Bost *et al.* 1997, Davis *et al.* 1996, Jouventin & Weimerskirch 1990) and energetics (*e.g.* Bevan *et al.* 1997, Butler & Jones 1997, Culik *et al.* 1996a, Grémillet *et al.*

1998, Handrich *et al.* 1997, Wilson & Grémillet 1996). Some of the most promising work on assessing the role of marine endotherms, however, has investigated the internal temperature of endothermic predators (Kato *et al.* 1996, Wilson & Culik 1991, Wilson *et al.* 1992) so as to determine when prey are ingested in tandem (Weimerskirch *et al.* 1994, Wilson *et al.* 1993, etc.).

I – 5. Aim of the thesis:

The main aim of this thesis is to present and compare the fine-scale foraging strategies of two different penguins species. Although the following works might sometimes appear like preliminary reports, especially regarding to the sample size of birds, the results obtained represents new findings and bring answers to questions and hypothesis raised in the past. In that sense, they reveal new tracks for future research on the foraging strategies of seabirds and how these might, in some instances, enhance food acquisition and, at a wider scale, help elucidating the complex interactions between prey and predators that occur in the Antarctic ecosystem.

This thesis aimed to address the following points

i) Technical aspect:
Development and application of a method to determine the exact timing of prey ingestion through the recording of the oesophagus temperature, in free-ranging diving seabirds.
In addition, improvement of the determination of the foraging behaviour by measuring swim speed at a fine-scale.

ii) Integrative biological application:
Using either fine-scale measurement of the foraging behaviour alone or in tandem with timing of prey intake (revealed by oesophagus temperature recording), determination of the foraging strategies of penguins and how they might enhance the prey capture while at sea.

iii) Ecological comparisons:
Evolution of these strategies interspecifically, when different predators seek different prey.

II – GENERAL METHODS

II – 1. Data collected during the present thesis:

Three different parameters were collected, *i.e.* swimming depth and speed and oesophageal temperature. Fine-scale swimming depth combined with the swim speed observed at the same time were used to describe the foraging activities, while oesophageal temperature data were used to detect the timing of prey intake. Because seabirds and marine mammals are endothermic – *i.e.* maintaining a high internal temperature independently from the ambient temperature – the ingestion of an exothermic prey (*i.e.* body temperature ≈ water temperature) induces a precipitous decrease in the internal body temperature of the predator (Wilson & Culik 1991, Wilson *et al.* 1992). Based on this principle a number of studies have been conducted using stomach temperature loggers in marine mammals and birds (Kato *et al.* 1996, Pütz 1994, Pütz & Bost 1994, Weimerskirch & Wilson 1992, Wilson & Culik 1991, Wilson *et al.* 1992, 1998), but several physiological factors tended to decrease the efficiency of these loggers to detect prey ingestion as the stomach fills and prey items cover the sensor (see review in Grémillet & Plös 1994, Wilson *et al.* 1995b). Furthermore, the accuracy of detection depends on the position of the logger inside of the stomach (Grémillet & Plös 1994, Wilson *et al.* 1995b) because body temperatures of diving seabirds can fluctuate independently of their feeding activity (Bevan *et al.* 1997, Culik *et al.* 1996b, Handrich *et al.* 1997, Wilson & Grémillet 1996). Recently, the monitoring of the internal temperature in the oesophagus of seabirds showed promising results in the detection of prey intake (Ancel *et al.* 1997). Here, prey items are thought not to cover the sensor and the time lag between ingestion and the detection of the drop is also considered minimal (Wilson *et al.* 1995b). In the present thesis, validation experiments of oesophageal temperature recording conducted on captive penguins, as well as use of this technique on free-ranging penguins in tandem with the recording of the foraging behaviour will be presented.

Localities where data were collected: All experiments on King penguins presented in section III were conducted at Possession Island, Crozet Archipelago, Southern Indian Ocean (46°25' S, 51°45' E, Fig. II – 1a) at the *Grande Manchotière* colony, where approximately 45 000 pairs of King Penguins are breeding (Weimerskirch *et al.* 1992). The experiments on Adélie penguins presented in section IV were conducted on a colony at *Ile des Pétrels*, Dumont d'Urville, Adélie Land (66°7' S, 140°0' E, Fig. II – 1b). Calibration experiments and video recordings were conducted during summer 1999 on captive Adélie Penguins swimming in a 21 x 4m pool (2.1-2.3m deep, water temperature: 6.2 – 6.4°C) at Port of Nagoya Public Aquarium (Nagoya, Japan).

II – 2. Logger description and attachment procedures:

All the loggers described below were manufactured and purpose-designed by Little Leonardo (Tokyo, Japan)*. A summary of the species equipped with the type of devices used are presented in Table II – 1.

* In the following sections, when other loggers were used in addition to those manufactured by Little Leonardo, technical information about these devices will be given in the text as footnotes.

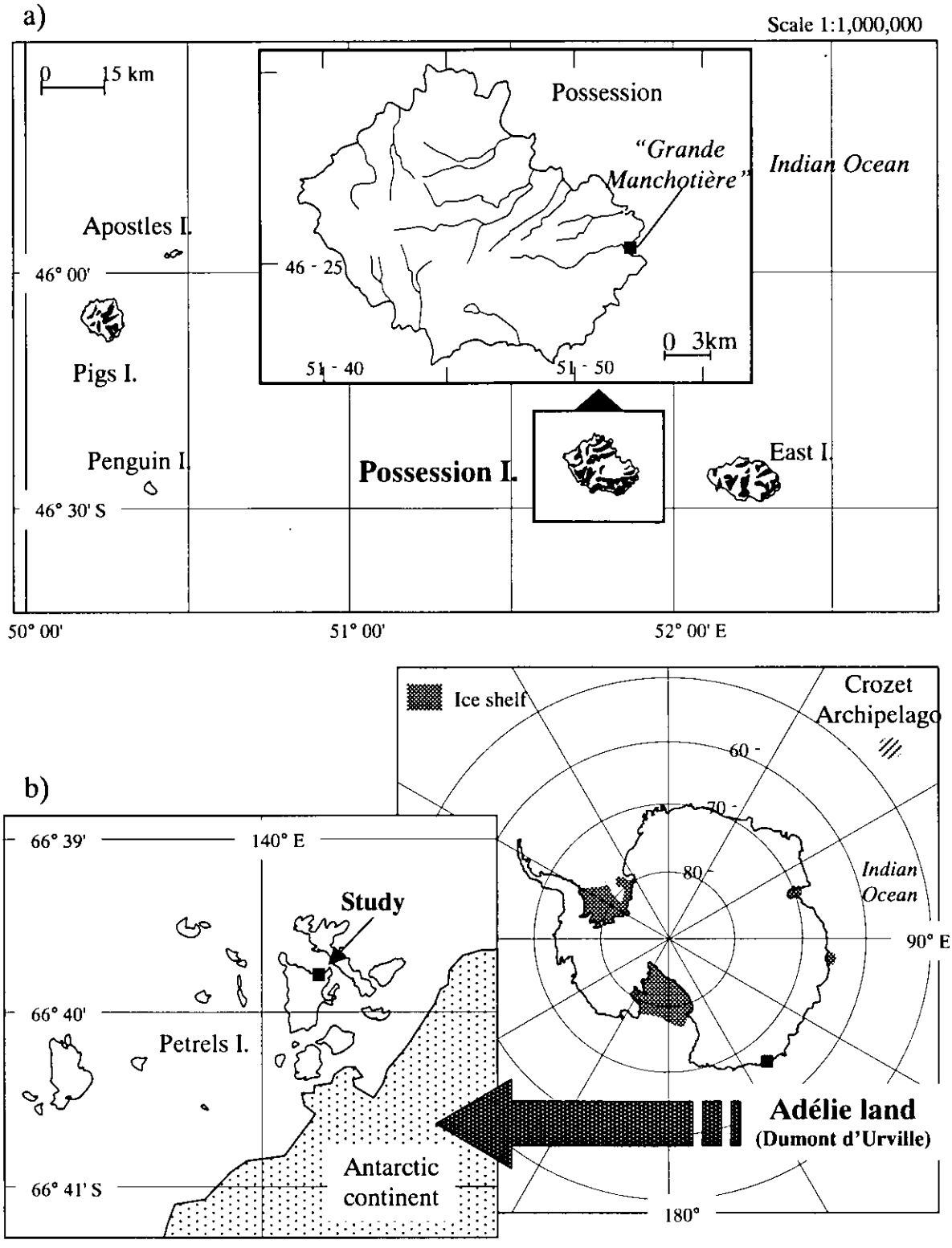


Fig. II – 1 : a) Possession Island in the Crozet Archipelago, Southern Indian Ocean and b) Petrel Island (Dumont d'Urville) in Adélie Land, Antarctica. The study colonies of King (Possession I.) and Adélie Penguins (Petrel I.) are indicated by black squares.

Table II – 1. Summary of the penguins species used, experiments sites, dates of logger deployment, type of logger deployed (parameters investigated) and related section in the manuscript. OT, D, 2T and SD stands for Oesophageal Temperature, Depth, Two-points Temperature and Swim speed – Depth data, respectively.

Localities	Birds	Deployment dates	Logger type	Thesis section
Crozet	King Penguins (captive)	Summer 1996	♦NIPR-QT (OT)	III – 1
	King Penguins (free-ranging)	Summer 1996/97	♦TDR MK5 (D) ♦UWE-DTT (2T) ♦Stomach T	III – 1
		Feb.-Mar. 1996	♦UWE-PDT (SD)	III – 2
Adélie Land	Adélie Penguins (captive)	Jan. 1999	♦UME-TT (OT)	IV – 1
	Adélie Penguins (free-ranging)	Summer 1998/99	♦UWE-PDT (SD) ♦UME-TT (OT)	IV – 2

OESOPHAGEAL TEMPERATURE:

♦**King model** (chapter III – 1): In captive birds, oesophageal temperatures were measured by a 1.2Mb, 8 bits, four-channels temperature NIPR-QT logger linked to an oesophageal probe with four thermistors; the logging unit was housed in an aluminium cylinder (90 x 14mm, resolution 0.1°C). Stomach temperature was recorded by a cylindrical 1.2Mb, 12 bits, two-channels logger (90 x 19mm, resolution 0.02°C, accuracy 0.1°C). Each captive King Penguin was induced to swallow a stomach sensor (1s sampling interval) attached to a thin plastic line (used to remove the unit after the experiment). The four-channels temperature logger (2s sampling interval) was then taped on the back feathers and the bird was induced to swallow the oesophageal probe that consisted in a 30cm flexible plastic tube, (diameter: 0.7cm), with four regularly spaced thermistors. In the oesophagus, the sensors were at 9, 16, 25, and 34cm from the beak junction (sensors A, B, C and D, respectively). In free-ranging birds, oesophageal temperature and dive depth in the 0-200m range were measured by a cylindrical 1.2Mb, 12 bits, three-channels UWE-DTT logger (90 x 20mm, *ca.* 50g, temperature and depth resolution 0.02°C and 0.1m, respectively). Cylindrical oesophagus thermistors (5 x 3mm) were plastic-coated, and had an accuracy of 0.3°C. Each thermistor was linked to a central unit by a 0.5 to 1m electric cable (diameter: 1.2mm). Birds were surgically implanted under halothane anaesthesia with an intra-luminal oesophageal and a tracheal temperature sensor, at 6-10cm from beak junction. The cables of the sensors were fixed with absorbable suture threads on the external walls of the oesophagus and trachea, at 15 and 5mm of the sensors respectively. The body of the unit was attached externally on the lower back with the cables tunnelled up to the upper oesophagus and the trachea (Fig. II – 2). The tunnellisation was performed using a special sterile stainless steel tube. Cutaneous wounds were closed using absorbable suture threads. The transcutaneous transition was protected and anchored by a non-absorbable suture thread.

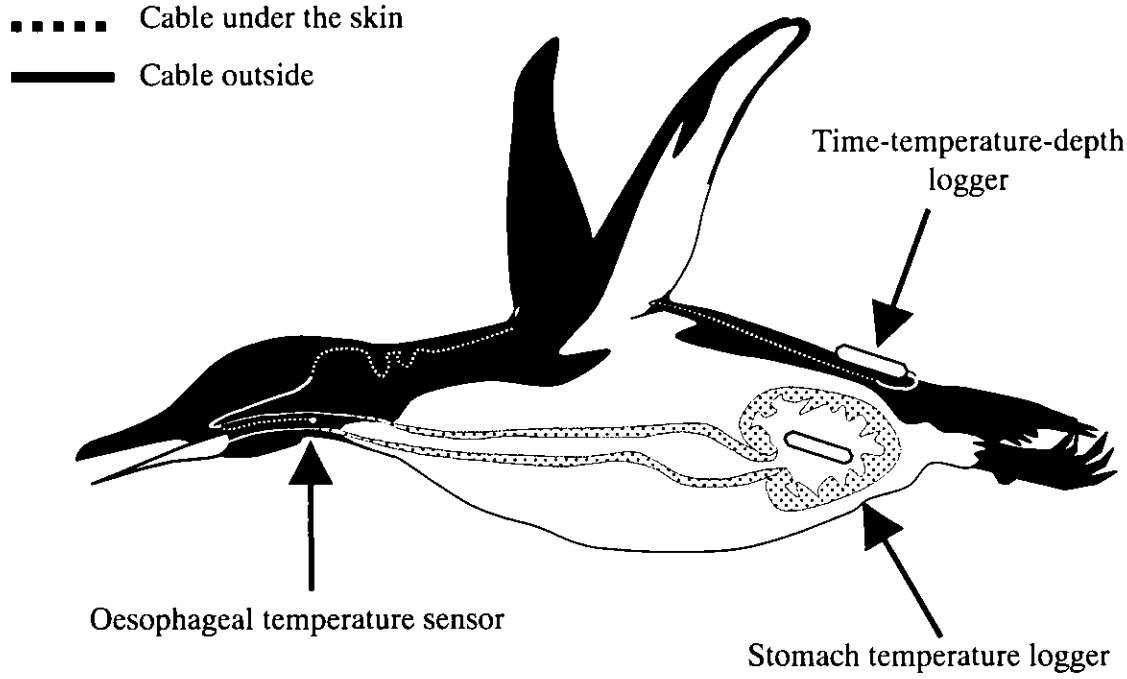


Fig. II – 2 : Position of the loggers and sensors deployed on a free-ranging King Penguin. Cables were tunnelled under the skin from the oesophagus to a logger unit taped on the feathers recording dive depth and oesophageal temperature. A second logger recorded the stomach temperature.

♦**Adélie model** (section IV): A 12 bit resolution, 2Mb, two-channels UME-TT loggers recorded the oesophageal temperature of Adélie Penguins every second (Fig. II – 3a). These devices consisted of a titanium cylinder (68 x 15mm, *ca.* 30g) containing the electronic components and battery from which two soft plastic cables, 27.5 and 2cm long (diameter: 1.2mm), respectively, emerged from one end. A temperature sensor (accuracy: 0.1°C) was incorporated at the end of each cable and set to record at a frequency of 1Hz. The longest cable was attached along its length to a thin filament, 50cm long (diameter: 0.5mm), itself also emerging from the logger with the cables.

During equipment, birds were induced to swallow the moistened logger first. The throat was gently rubbed until the logger reached the stomach and the filament emerging from the beak was glued (Loctite) on the feathers at three different points: 1cm from the mouth on the cheek and two points on the back of the head. The filament was multistranded to resist traction and thus avoid injury at the beak rictus. Using this system, the sensor at the end of the 27.5cm cable was held in the œsophagus lumen at the back of the throat while the other sensor recorded stomach temperature (Fig. II – 3b). The correct cable length had been determined by measuring the length of the œsophagus on Adélie Penguin carcasses. The position of the logger in the stomach was also verified by X-ray photography in one trial. At the end of the experiment, the logger was retrieved by pulling gently on the filament until the bird regurgitated the logger.

DEPTH UTILIZATION & SWIM SPEED: Depth utilization and swim speed of King Penguins were measured with KS-400PDT logger (Fig. II – 4a). These cylinder-shaped devices (110 x 25 x 25mm – 32mm at the thickest part of the recorder – 81.5g) have a depth resolution of 0.1m (depth range: 0 – 400m). Depth utilization and swim speed of Adélie Penguins were monitored at a frequency of 1Hz with a 12bit, 16Mb, three-channels, cylinder-shaped (102 x 20mm, *ca.* 50g) UWE-PDT logger (Fig. II – 4b). These loggers have an absolute accuracy of 0.5

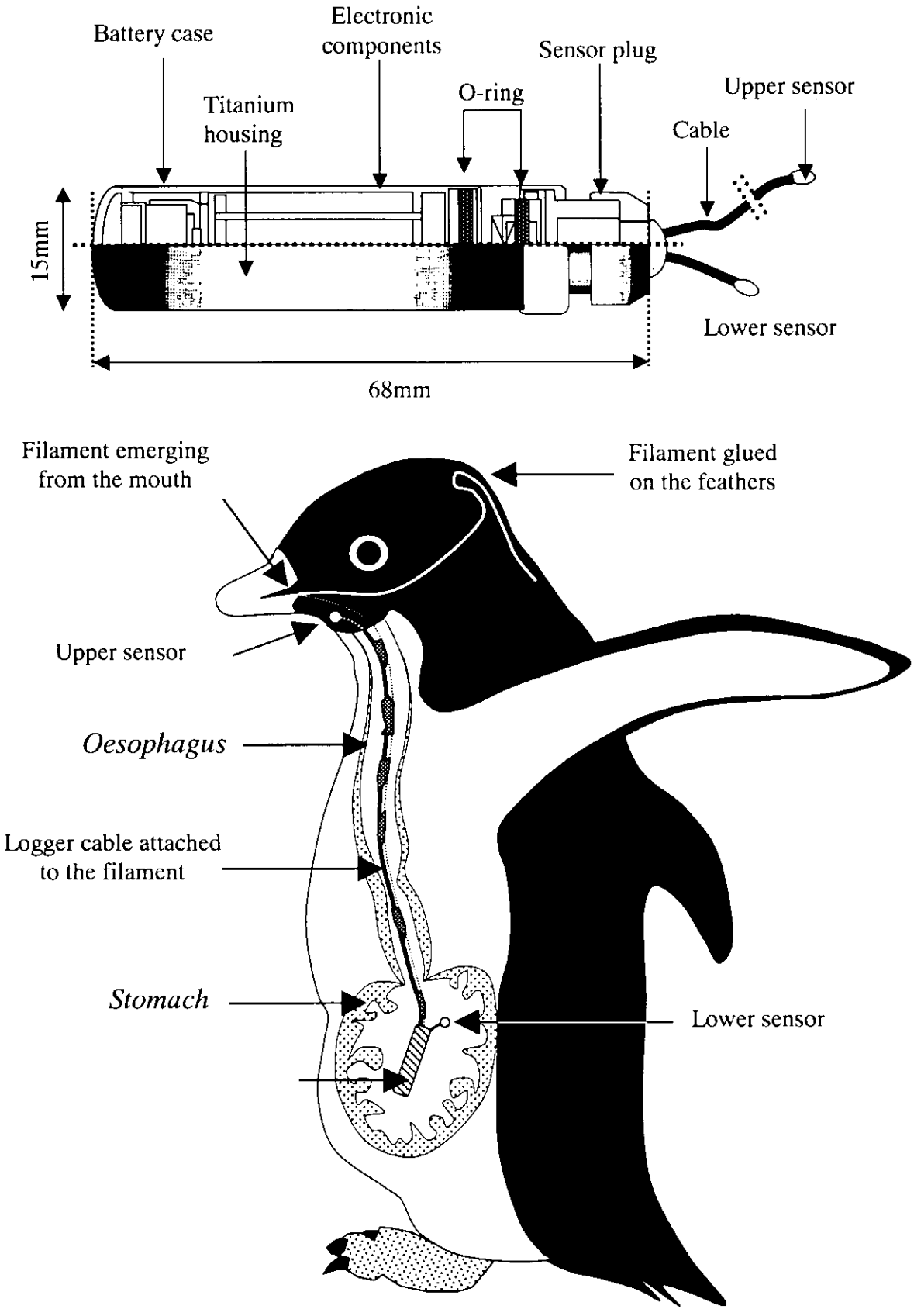


Fig. II – 3 : Technical scheme of UME-TT logger (Little Leonardo, Tokyo, Japan) and method of attachment on Adélie Penguins.

m for depth and 0.05m.s^{-1} for speed. External loggers were attached using tape (Wilson *et al.* 1997) or a system combining glue (Araldite) and plastic cable-ties to the birds' lower backs so as to reduce drag (Bannasch *et al.* 1994).

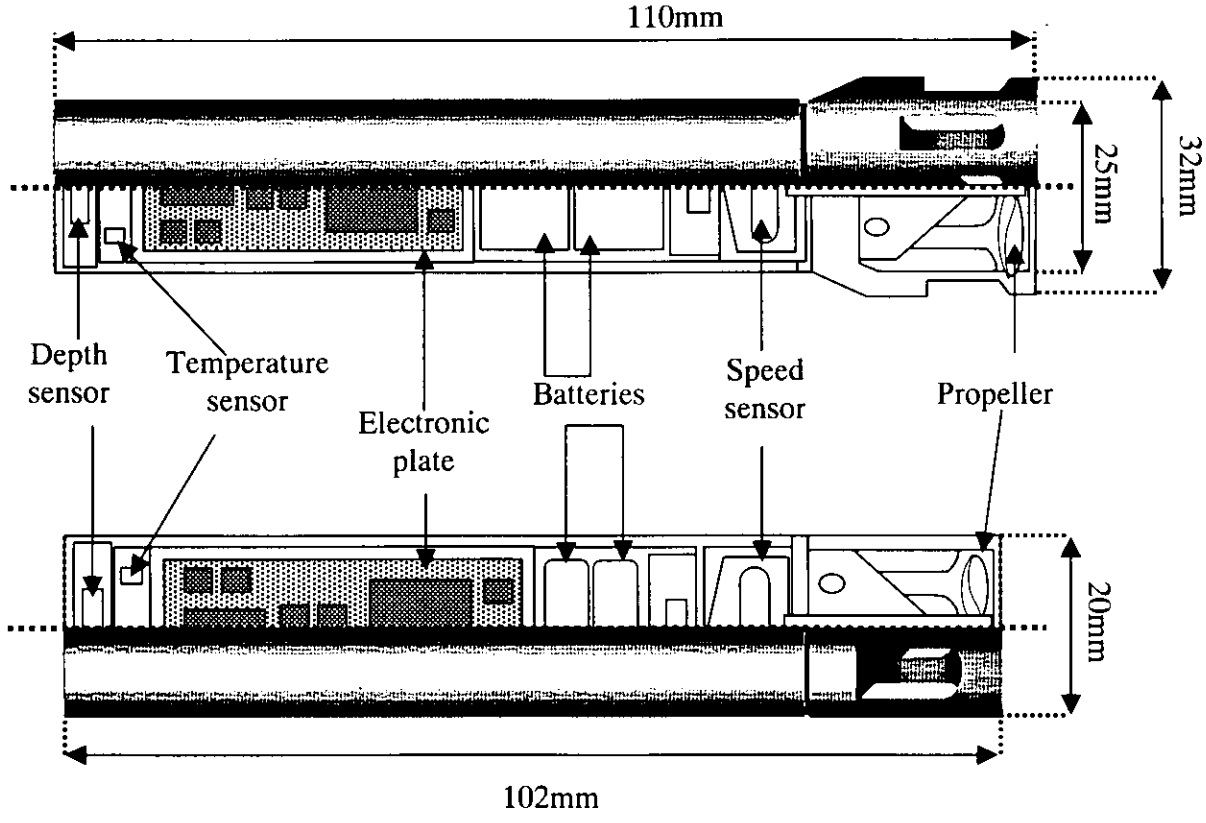


Fig. II – 4 : Technical details of a KS400-PDT (top) and a UWE-PDT loggers (bottom) measuring depth and swim speed data (Little Leonardo, Tokyo, Japan).

DATA PRE-TREATMENT: Swim speeds of King and Adélie Penguins were calculated from the number of revolutions of the propeller per second (RPS), which was converted into flow speed (m.s^{-1}) using the results obtained from calibration experiments. For King Penguins at Crozet Archipelago, these calibration experiments were made *in situ* by pulling the recorder in the water over a known distance at three different speeds using an electric fishing reel. The revolutions per distance relationship was linear at tow speeds of 0.3 to 2.5m.s^{-1} with the coefficient of determination for each recorder being greater than 0.98. For Adélie penguins at Dumont d'Urville, the RPS was converted into flow speed using the data obtained from the animal (Fletcher *et al.* 1993, Blackwell *et al.* 1999). Firstly, the RPS was plotted with the rate of change of depth calculated every second. Assuming that the lower RPS value for a given swim speed represents vertical diving, then the lowest swim speed for each vertical speed is equal to the rate of change in depth. A regression line through the lowest RPS value for each vertical speed is the calibration line to convert number of rotation of the propeller into flow speed. The linearity of the relationships between the RPS and the flow speed was also tested in a pool by towing the logger at several speeds using an electric fishing reel.

Diving depth data were treated mathematically to adjust the surface values of each dive to zero. Based on the depth profile (Le Boeuf *et al.* 1988, Wilson 1990, 1995), dives were separated into W- (feeding dives), V- (exploratory dives) and U-shaped dives (probably exploratory dives, Kirkwood & Robertson 1997, Kooyman *et al.* 1992). In this study, W-shaped dives were defined as such when two or more undulations (Wilson *et al.* 1996) with a magnitude

> 2m were observed in the depth profile. Subsequently, dives were divided into descent, ascent (sometimes regrouped as "commuting" phases) and undulatory phases (also termed "hunting" phases). Dives were grouped into dive bouts defined as periods during which a bird dived repeatedly to similar depths with minimal surface interval (Chappell *et al.* 1993), the end of a bout being defined by a bout end criterion (BEC). The BEC was determined as the point of inflexion of the log-survivor curve of post-dive surface intervals plotted for each individual (Gentry & Kooyman 1986).

STATISTICAL TREATMENT: Where data were normally distributed, parametric tests were used (Student t-test, One-way Analysis of variance, regression) following the procedures recommended by Sokal & Rohlf (1969). If the sample size was too small or if the data did not follow a Normal distribution, non-parametric tests (Mann-Whitney, Kruskall-Wallis, Spearman rank correlation) were preferred. Proportions were tested by χ^2 tests. For all statistical tests, the threshold was 5%.

II – 3. Ethical considerations:

In all experiments, the relevant permission for the work to be carried out had been obtained from the Commission of the Terres Antarctiques Australes Françaises. The procedure complied with current laws of French authorities: Authorisation of the Ministère de l'Agriculture et de la Forêt (n° 04196) followed by approbation of the surgical protocol by the ethics committee of the French Institute for Polar Research (IFRTP).

All birds were equipped following strict protocol procedures based on recommendations made regarding minimizing stress to birds. At Crozet and Dumont d'Urville, birds were caught on their departure to sea after exchange with partner using a blind net to decrease the stress of capture. After the foraging trip had taken place the birds were preferentially caught on the shore or, if the return was missed, at the nest site using the same blind net. Loggers were always deployed on breeding penguins (with chicks) for a minimum of one foraging trip. While the adults were at sea, the presence or absence of their mates in the colony and the status of their chicks were checked every day.

Surgical implantations of loggers in King Penguins at Crozet Archipelago were performed in a shelter within the colony site. All surgical equipment was placed and removed under halothane anaesthesia. The surgeries were planned so that it took place approximately seven days before the operated birds departed to sea. This gave the tissues sufficient time to recover from the surgical procedures (Bevan *et al.* 1995, 1998). After operations, birds were placed back on their breeding spot and were protected from neighbours and predators using a portable enclosure until full recovery from the anaesthesia. Every bird that underwent an operation continued to raise its chick normally and all birds were seen at the next moulting period.

In addition, guidelines recommended to minimize the effects of externally attached devices were adopted. This included particular device shapes (Bannasch *et al.* 1994, Culik *et al.* 1994b), colours (Wilson & Wilson 1989) and positions (Bannasch *et al.* 1994). Each penguin was individually recognized by a colored band of TESA tape on its flipper and picric acid dye mark on their chest. When the animals returned to the colony after a foraging trip, loggers were removed with the maximum care being taken to preserve the feathers around the point of attachment in order to maintain the thermoregulation efficiency of the birds (Wilson *et al.* 1997).

II – 4. Effect of logger deployment on birds:

IMPACT OF EXTERNALLY-ATTACHED LOGGER: Some experiments on captive penguins swimming in watertanks have demonstrated that externally-attached data loggers create additional drag which might affect the bird's swim speed and energy expenditure (Bannasch 1995, Kooyman 1989, Wilson & Culik 1992, Wilson *et al.* 1986). Previous studies on free-ranging seabirds have pointed out that an increase in the frontal area of loggers can affect the foraging behaviour of diving birds (Hull 1997). Using implantation technique (Bevan *et al.* 1994, 1995, Butler & Woakes 1979, Stephenson *et al.* 1986, Woakes *et al.* 1995), the diving performances of free-ranging King Penguins obtained from a group of birds implanted with depth recorder have been recently compared with those from a group that also had a dummy logger attached externally in order to determine the impact of the externally-attached logger (Ropert-Coudert *et al.* 2000a). These authors observed that birds with external dummies performed more shallow dives that interupted more frequently the sequences of deep dives and showed longer post-dive times than the birds implanted only. Such finding bears important consequences since an increase in the metabolic rate due to the externally-attached logger would reduce the aerobic dive limit (ADL, Butler & Jones 1997), defined as the diving duration beyond which blood lactate concentration increase above resting levels (Kooyman *et al.* 1983). This could force the bird either to rely on anaerobic metabolism for deep dives, especially during a consecutive sequence of deep dives, or to increase the number of longer resting periods and of shallow dives. These latter could therefore, be a way for the bird to decrease the level of lactate acid in their blood after a series of deep dives as has infrequently been observed on Weddell Seals, *Leptonychotes weddelli*, (Castellini *et al.* 1988).

The effect of externally attached logger would presumably be stronger and lead to a greater impact on bird's behaviour and energetics if the deployment is to be conducted over several consecutive foraging trips, or over the winter when there is a lack of marine resources (Adams & Klages 1987, Hindell 1988) due to a cumulative effect of the logger. The latter point could be even more pronounced in smaller bird's species, such as Adélie Penguins, or when the relative size of the logger is greater.

Despite its invasive nature, the implantation method would appear to open a new field of investigation by recording the diving behaviour of birds without increasing their hydrodynamic drag. The logger deployment on animals could be extended to several consecutive foraging trips and the monitoring could cover periods of the annual cycle that have not been possible until now, such as the pre-molting period. However, this method remains inadequate in the case of telemetric studies or swim speed measurements. Indeed, monitoring satellite-linked data depending on clear communication signals between the logger's antennae and a satellite, as well as recording of flow velocity by paddle wheels or propellers, implies that the logger should be externally attached. In the present study, the cross-sectional area of logger measuring swim speed on Adélie Penguins accounted for 1.6% of the bird's cross-sectional area so that the external loggers would probably have caused an increase in energy expenditures of less than 2.2%, this value being derived from experiments in a water canal with a logger with a cross-sectional area 1.8% that of the Adélie Penguin (Wilson *et al.* 1986, Culik & Wilson 1991b), although the loggers used by Culik & Wilson (1991b) were streamlined. The Adélie and King Penguins in the present study were swimming at speeds similar to the birds used by Culik & Wilson (1991b) and Culik *et al.* (1996), respectively, to derive their estimates.

STOMACH LOGGER EFFECT: Although several studies have extensively discussed the performances of the stomach logger in terms of prey or water ingestion (Gales & Renouf 1993, Hedd *et al.* 1996, Kato *et al.* 1996, Wilson *et al.* 1992, 1995b), the logger impact on the birds physiology and behaviour was poorly investigated. However, it is unlikely that the presence of a unit in the stomach of seabirds would lead to a deleterious effect on the birds'

condition. Indeed, seabirds may be able to tolerate such unit since they repetitively ingest large amounts of food under natural conditions. Moreover, the feeding processes of most of seabirds species involve frequent regurgitation of a part of the stomach content either in order to feed their chicks or to eliminate the indigestible fragments of prey (see Duffy *et al.* 1987). This may account for the high rejection rate of the logger more than any possible discomfort. In all studies using this type of technology, birds never had any apparent difficulties eating (Grémillet & Plös 1994), foraging or feeding their chicks (Wilson *et al.* 1992). Therefore, it can be assumed that the presence of a logger in the stomach caused only relatively little disturbance to the birds of the present study and that most of the effect may come from the stress due to capture and maintenance (Grémillet & Plös 1994, Le Maho *et al.* 1992).

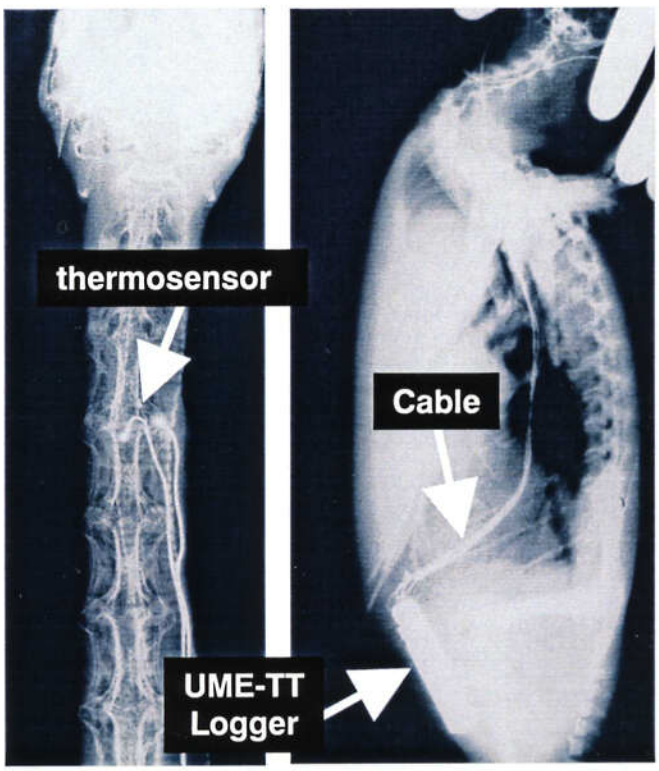


Fig. II – 6 : X-ray pictures of the upper body of a common goose implanted with thermosensors from a UME-TT logger. The body of the logger and the cables were externally attached on the goose.

OESOPHAGEAL CABLE: Intuitively, the main problem of oesophageal temperature logger is the cable that pass through the oesophagus and the throat, as illustrated by the X-ray picture showing the position of the cable in the oesophagus of a common goose (Fig. II – 5). During the pioneer study using such technique (Ancel *et al.* 1997), the logger did not seem to impair neither the eager to eat, nor the swallowing process of the equipped Brandt's Cormorants, *Phalacrocorax penicillatus Brandt*, although it seemed that the retention time of the logger may have been affected by the cable in the oesophagus. In the following experiments, captive birds equipped with such logger were nervous when released in the cage prior to feeding experiments, some trying to regurgitate the device by shaking their head and beak, while spasms of the digestive tracks were observed. However, after some hours of isolation, the birds remained relatively quiet and did not exhibit any behaviour that could indicate a discomfort due to the logger. After retrieval of the device, captive birds did not show any injuries at the beak rictus. In other words, oesophagus loggers did not impair the fitness of the birds.

However, the presence of the cable in the oesophagus might, in some instances, have impaired the ability of penguins to swallow prey. Indeed, on three Adélie Penguins equipped with such unit and presented with food items (Antarctic Krill) while swimming in a pool at the Port of Nagoya Public Aquarium, two birds refused to ingest the prey, while the last one ate several pieces at a rate of capture that was similar to non-equipped birds. For free-ranging Adélie, there was a high rejection rate of oesophagus logger. In some instances, the devices were retrieved hanging from beaks of birds covered with half-digested food. Consequently, it seems that most of birds undertaking foraging trips with the oesophagus logger, succeeded in ingesting prey and feeding their offspring. Similarly to Adélie, four King Penguins went to sea and showed normal foraging behaviour as judged by dive depth and food brought to the chick (Charrassin *et al.* 1998, Kooyman *et al.* 1992, Pütz *et al.* 1998) but two birds stayed at the

colony. Future work with a data transmission to the logger unit rather than a cable connection might help reducing the effect on birds' condition. In addition, implantation of the sensor in the oesophagus eliminates the possibility of losing the logger by regurgitation as it can occur for stomach sensors (chapter III – 1) or non-implanted oesophagus logger (chapter IV – 2), but this remains a costly operation that implies surgery and anesthesia.

III – FEEDING BEHAVIOUR OF KING PENGUINS

III – 1. Feeding behaviour of free-ranging King Penguins determined by œsophageal temperature recording

INTRODUCTION: As it has already been evoked in the chapter II – 1, the detection of prey ingestion has been estimated from drops in the internal temperature of top-predators (Grémillet & Plös 1994, Kato *et al.* 1996, Wilson & Culik 1991, Wilson *et al.* 1992, 1995b, 1998), the most recent and advanced technique involving the recording of the oesophageal temperature (Ancel *et al.* 1997, Ropert-Coudert *et al.* 2000b). The following chapter will summarize the results obtained during the first deployment of this promising technique on free-ranging King Penguins. The aims of the present work were 1) to validate this method in captive penguins, and 2) to assess the feeding activity at sea of birds.

MATERIAL & METHODS: The study was carried out at Possession Island (chapter II – 1) during the 1996 and 1997 breeding seasons.

♦**Captive birds**: Temperature changes in the oesophagus and the stomach in response to ingestion of meals of known size and temperature were examined in five non-breeding adults King Penguins equipped with NIPR-QT logger (chapter II – 2). A total of 220 fish pieces (mass: 1.6 – 14.7g; temperature: 0.5 – 9°C), simulating the temperature and the size of the prey usually caught by King Penguins (Cherel & Ridoux 1992), were handfed to the birds at 2-6min intervals, during sessions lasting *c.a.* 100min.

♦**Free-ranging birds**: Seven birds were surgically implanted with oesophageal and tracheal temperature sensors (UWE-DTT logger, chapter II – 2). Four of the seven individuals were implanted with a MK5 logger* in the abdominal cavity (see Handrich *et al.* 1997 for details). Six of the seven penguins were induced to swallow a stomach temperature sensor***.

Data were downloaded and analysed using Jensen System Software (Germany) and custom-made Fox-base programs. In the stomach and the oesophagus, the expected temperature signal following ingestion of a cold prey item by endotherms is a "precipitous drop" of the sensor temperature followed by an "exponential rise" to the body value (PDER), reflecting the cooling and rewarming of the sensor after contact with a cold item (Wilson *et al.* 1992, 1995b). However, because temperature changes in divers may reflect either prey ingestion (PDER), or non-feeding events (*i.e.* temperature changes due to diving *per se*, Handrich *et al.* 1997), oesophageal temperature drops were compared between the two main categories of dives previously observed in King Penguins (Charrassin *et al.* 1998, Kooyman *et al.* 1992, Pütz *et al.* 1998): shallow (≤ 30m) and deep (> 30m) dives.

---

* MK5: 65 x 38 x 15mm and *ca.* 50g, 2m resolution, 0.5Mb, sampling interval 4s, depth range 200-500m (Wildlife Computers, Washington, U.S.A).

*** Stomach temperature loggers: 105 x 16mm and *ca.* 80g, 0.1°C resolution, 0.25Mb, sampling interval 16s (Driesen + Kern GmbH, Germany).

colony. Future work with a data transmission to the logger unit rather than a cable connection might help reducing the effect on birds' condition. In addition, implantation of the sensor in the oesophagus eliminates the possibility of losing the logger by regurgitation as it can occur for stomach sensors (chapter III – 1) or non-implanted oesophagus logger (chapter IV – 2), but this remains a costly operation that implies surgery and anesthesia.

III – FEEDING BEHAVIOUR OF KING PENGUINS

III – 1. Feeding behaviour of free-ranging King Penguins determined by œsophageal temperature recording

INTRODUCTION: As it has already been evoked in the chapter II – 1, the detection of prey ingestion has been estimated from drops in the internal temperature of top-predators (Grémillet & Plös 1994, Kato *et al.* 1996, Wilson & Culik 1991, Wilson *et al.* 1992, 1995b, 1998), the most recent and advanced technique involving the recording of the oesophageal temperature (Ancel *et al.* 1997, Ropert-Coudert *et al.* 2000b). The following chapter will summarize the results obtained during the first deployment of this promising technique on free-ranging King Penguins. The aims of the present work were 1) to validate this method in captive penguins, and 2) to assess the feeding activity at sea of birds.

MATERIAL & METHODS: The study was carried out at Possession Island (chapter II – 1) during the 1996 and 1997 breeding seasons.

♦**Captive birds**: Temperature changes in the oesophagus and the stomach in response to ingestion of meals of known size and temperature were examined in five non-breeding adults King Penguins equipped with NIPR-QT logger (chapter II – 2). A total of 220 fish pieces (mass: 1.6 – 14.7g; temperature: 0.5 – 9°C), simulating the temperature and the size of the prey usually caught by King Penguins (Cherel & Ridoux 1992), were handfed to the birds at 2-6min intervals, during sessions lasting *c.a.* 100min.

♦**Free-ranging birds**: Seven birds were surgically implanted with oesophageal and tracheal temperature sensors (UWE-DTT logger, chapter II – 2). Four of the seven individuals were implanted with a MK5 logger* in the abdominal cavity (see Handrich *et al.* 1997 for details). Six of the seven penguins were induced to swallow a stomach temperature sensor***.

Data were downloaded and analysed using Jensen System Software (Germany) and custom-made Fox-base programs. In the stomach and the oesophagus, the expected temperature signal following ingestion of a cold prey item by endotherms is a "precipitous drop" of the sensor temperature followed by an "exponential rise" to the body value (PDER), reflecting the cooling and rewarming of the sensor after contact with a cold item (Wilson *et al.* 1992, 1995b). However, because temperature changes in divers may reflect either prey ingestion (PDER), or non-feeding events (*i.e.* temperature changes due to diving *per se*, Handrich *et al.* 1997), oesophageal temperature drops were compared between the two main categories of dives previously observed in King Penguins (Charrassin *et al.* 1998, Kooyman *et al.* 1992, Pütz *et al.* 1998): shallow (≤ 30m) and deep (> 30m) dives.

---

* MK5: 65 x 38 x 15mm and *ca.* 50g, 2m resolution, 0.5Mb, sampling interval 4s, depth range 200-500m (Wildlife Computers, Washington, U.S.A).

*** Stomach temperature loggers: 105 x 16mm and *ca.* 80g, 0.1°C resolution, 0.25Mb, sampling interval 16s (Driesen + Kern GmbH, Germany).

RESULTS:

♦**Experimental feedings**: All 220 items swallowed by the penguins were detected (temperature drop ≥ 0.3°C) by the sensor A, except for five meals that were not swallowed. The proportion of events showing a PDER at the upper sensor (A) was 20% (range 0 – 61%, N = 9 feeding sessions). Non-PDER events (*i.e.*, either a non-precipitous drop, or a slow rise) reflected a chaotic passage of the prey over the sensor. Indeed, birds often did not swallow the food at once, sometimes alternatively trying to regurgitate and swallow the food. It is further assumed that this does not occur in a free-ranging feeding bird. The response to ingestion was higher in the upper thermistor, and prey detection was less certain with increasing distance from the beak (Fig. III – 1). Ingestions were not detected by the stomach sensor although the temperature dropped from 38.2°C to 37.7°C during that period (Fig. III – 1). The progression velocity of prey items between the sensors A and B, B and C, and C and D averaged 0.6 ± 0.03 (N = 38), 0.3 ± 0.08 (N = 14) and 0.5 ± 0.1cm.s^{-1} (N = 4), respectively.

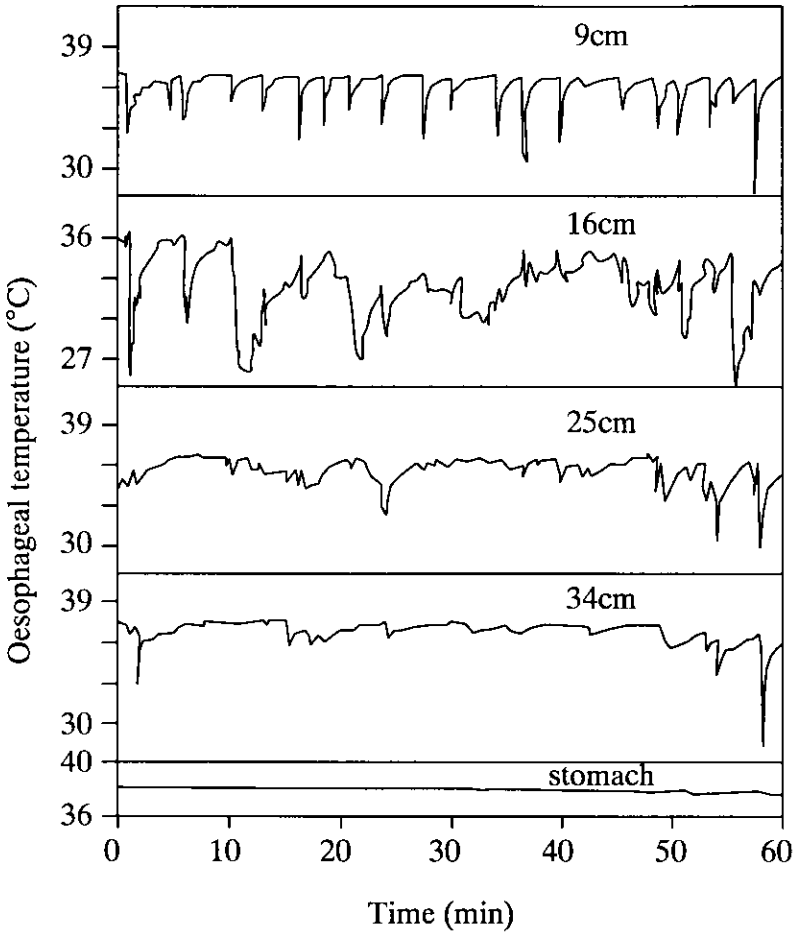


Fig. III – 1 : Changes in temperature of 4 thermistors located in the oesophagus of a captive King Penguin in response to the ingestion of 20 fish pieces. Thermistors were at 9, 16, 25 and 34cm from the beak. In addition, another thermistor recorded the temperature in the stomach.

♦**Prey ingestion and diving behaviour in free-ranging penguins**: Of the seven birds equipped, four remained at sea for 11.9 ± 0.9 days on average (range 10.1 – 14.5d). Stomach content upon return, ranging 0.5 – 1kg was sampled using the water off-loading technique (Wilson 1984). One bird spent 1.5d at sea, while two individuals stayed in the colony. Of the four birds which went to sea with a stomach logger, two regurgitated the unit at sea and two had retained it when they came back. Continuous oesophageal temperature records lasting 6 – 7d were obtained from three birds (a total of 4900 dives from 1 – 291m depth were recorded simultaneously; Table III – 1).

Table III – 1. Foraging characteristics of three King Penguins equipped with data loggers monitoring the oesophageal temperature and the diving behaviour, in early February 1997 at Crozet Archipelago. RTD stands for "rate of temperature decrease" (see text).

	Bird 1	Bird 2	Bird 3
Foraging dates	31 Jan-10 Feb	01-12 Feb	08-22 Feb
œsophageal temperature recording (d)	6.3	7.5	6.1
Mass stomach content (kg)	1	1	0.5
œsophageal temperature range (°C)	18.9 - 38.8	18.0 - 38.3	19.4 - 39.1
Number of prey ingestions (RTD ≥ 0.06°C.s^{-1})	1407	2342	580
Mean number of prey ingestions per day	187 ± 82	301 ± 121	91 ± 38
Mean number of dives > 30m per day	48 ± 12	82 ± 16	57 ± 11
Mean number of ingestions per dive (≤ 30m)	0.031 ± 0.004	0.017 ± 0.004	0.014 ± 0.005
Mean number of ingestions per dive (>30m)	3.94 ± 0.19	3.67 ± 0.14	1.55 ± 0.14
% of successful dives (≤ 30m)	3	2	1
% of successful dives (> 30m)	79	75	40

As shown in figure III – 2a, both stomach and oesophageal temperatures showed slow and regular variations which coincided with the dives. However, for oesophageal temperature, large and rapid drops which were not seen for stomach temperature were superimposed on these variations. Only when numerous rapid drops in oesophageal temperature occurred did stomach temperature decrease further. During the intensive diving that King Penguins make during their foraging trips at sea (Fig. III – 2b), their drops in oesophageal temperature did reach as much as 13.3°C. Still, dives with only minor changes in oesophageal temperature (Fig. III – 3a) contrasted with dives with large variations in oesophageal temperature (Fig. III – 3b).

For the 650 ± 60 temperature drops ≥ 0.02°C recorded on average per day for each of the three birds (N = 19 days), two groups of temperature drops were characterised according to their amplitude and duration (Fig. III – 4). The first group corresponded to slow drops, showing a small amplitude (1 – 2°C or below) and lasting for up to 3min. Based on their rate of temperature decrease (RTD, defined as the amplitude of the temperature drop divided by the drop duration), slow drops accounted for most of those occurring during shallow dives (95% of drops had a RTD < 0.06°C.s^{-1}) but were also observed during deep dives (Fig. III – 4). They corresponded to the cyclic variations already described in figure III – 2 which, occurring in relation to the dives, reflect the tissue cooling due to diving *per se* (Handrich *et al.* 1997).

The other group included large (up to 13.3°C) and short (< 30s) drops, which occurred mainly during deep dives (Fig. III – 4). During deep dives, 50% of these drops had a RTD > 0.06°C.s^{-1}. Because such rapid drops were much shorter than the duration of the dives during which they occurred, they indicate cooling by cold prey. Fast temperature drops (RTD ≥ 0.06°C.s^{-1}) were therefore assumed to reflect prey ingestion. Feeding events inferred from oesophageal temperature are shown in figure III – 3b.

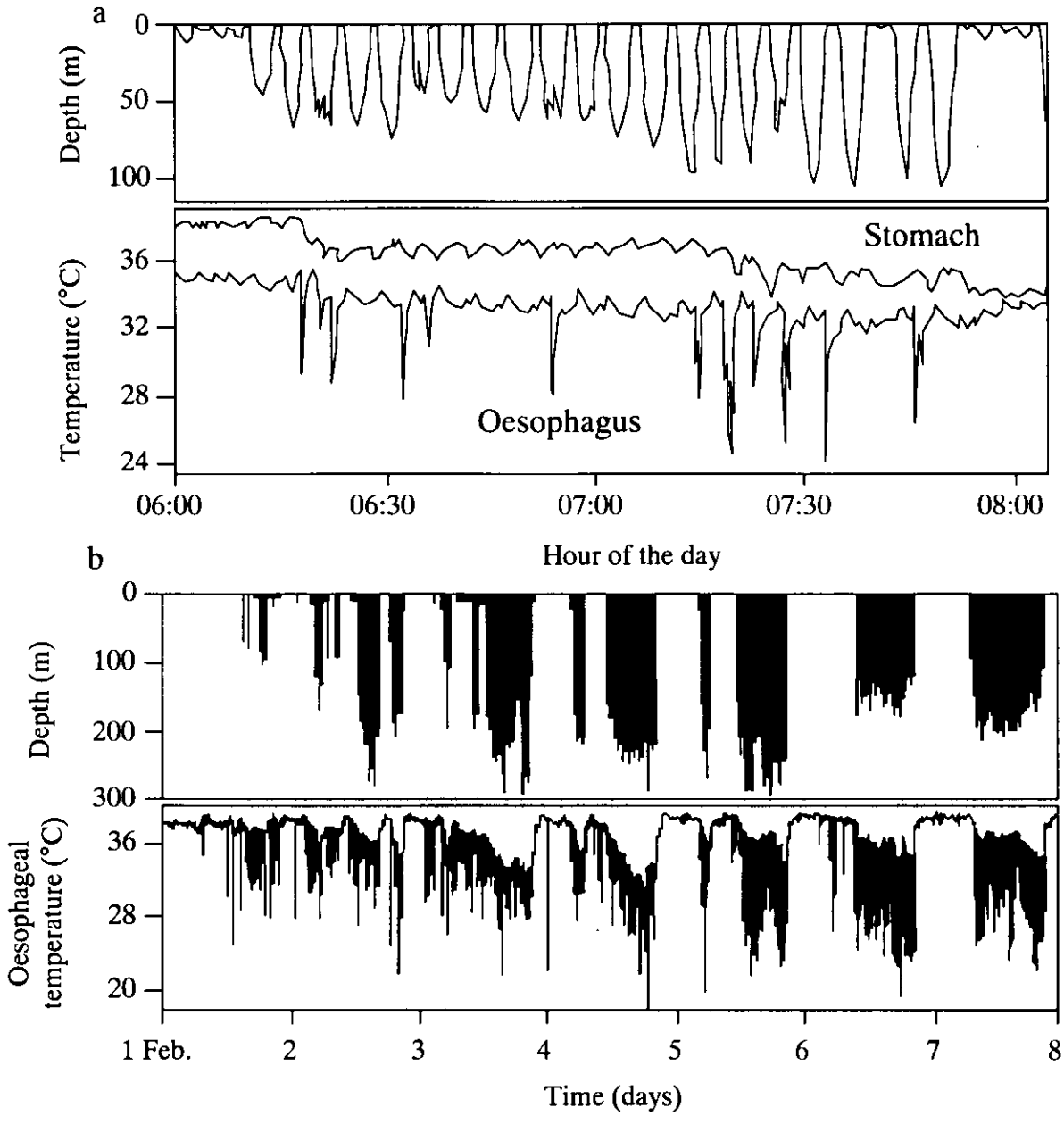


Fig. III – 2 : Changes in the upper oesophagus and stomach temperatures in relation to dive depths in a free-ranging King Penguin, a) during 2 hours, b) during 7 days (the total trip duration was 11 days).

♦**Feeding frequency and feeding depth**: The number of ingestion per day varied from 95 to 300 among the birds, and the number of ingestion per shallow dive (≤ 30m) was much smaller than for deep dives (Table III – 1). Bird 3 apparently experienced a much lower foraging success than the other birds did. Feeding depths were obtained from the dive profiles recorded simultaneously with oesophagus temperature. In bird 2, prey ingestion occurred mainly between 80 and 170m, where 70% of ingestion were detected (Fig. III – 5). During diving, 5 ± 3%, 41 ± 2%, and 54 ± 5% of prey ingestion took place during the descent, undulatory and ascent phases of dives, respectively (N = 3 birds, 4200 dives > 70m).

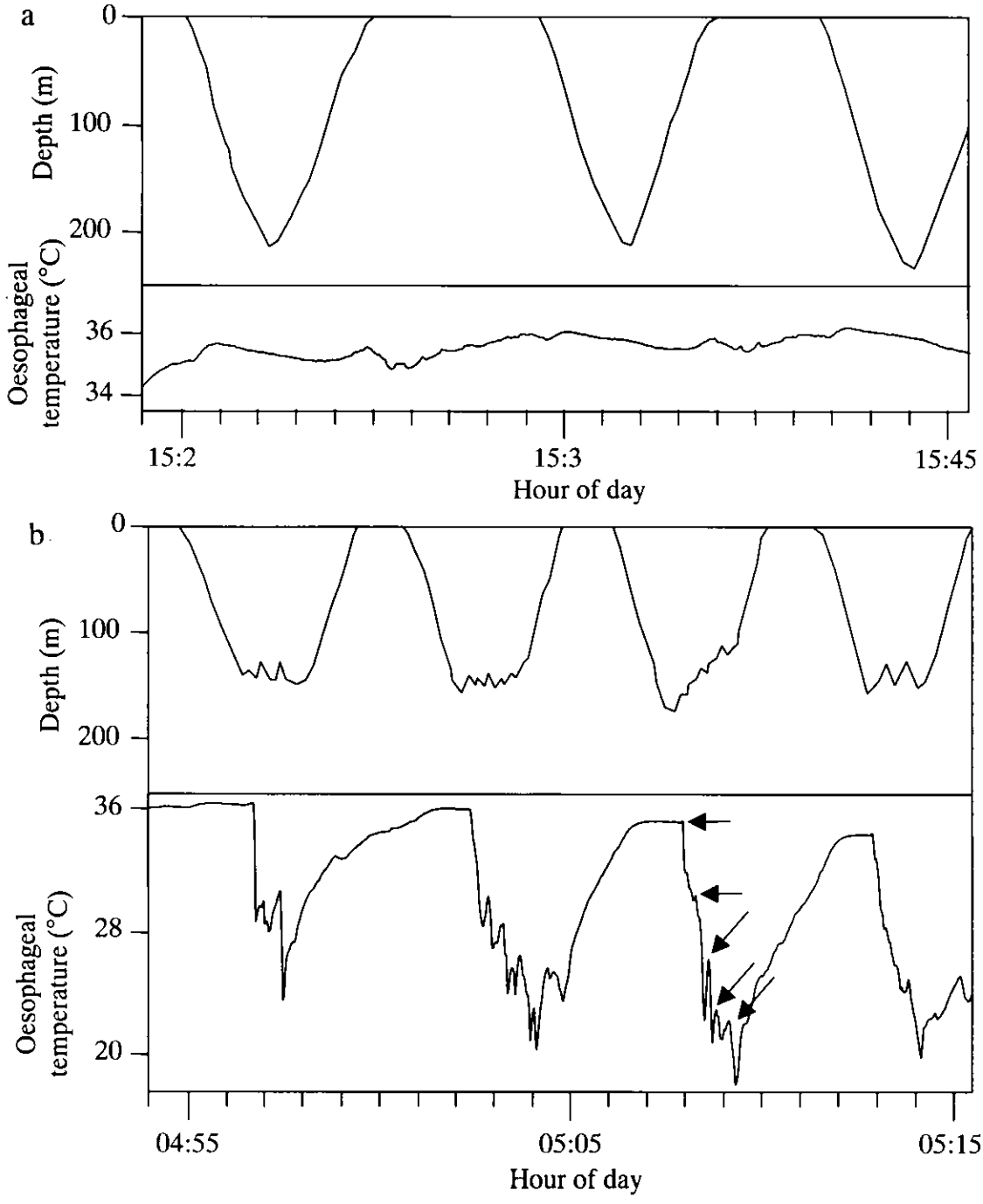


Fig. III – 3 : Changes in upper oesophageal temperature with dive during a) non-feeding and b) feeding dives in a foraging King Penguin. Arrows indicate the timing of prey ingestion.

DISCUSSION: Since all experimental feedings gave a detectable response, the system proved sensitive enough for small-sized prey items. The low thermal inertia of the small sensor accounts for its good sensitivity (Ancel *et al.* 1997). Such a small size reduces the probability of contact with prey but is counterbalanced by the small cross section area of the oesophagus. Prey items were less often detected with increasing distances from the beak, and detection was almost impossible in the stomach of captive penguins. However, prey detection in the stomach could be less reliable in captive individuals than in free-ranging birds, since movements during diving may continually change the sensor position in the stomach (Wilson *et al.* 1995b) thereby favouring contact with prey. Progression of food items is faster in the upper part of the

oesophagus. This lessens the time between prey ingestion and prey-sensor contact, and favours detection by reduced warming of the prey. Prey ingestion is then easier to distinguish from physiological changes due to diving (Handrich *et al.* 1997) if the probe is located in the upper oesophagus rather than deeper in the body (*e.g.* in the stomach). Based on the 0.6cm.s^{-1} displacement of prey items in the upper oesophagus found in captive birds, the delay for reaching a sensor located 9cm from the beak is 15s. Such a short interval allows a quasi real-time detection of food ingestion.

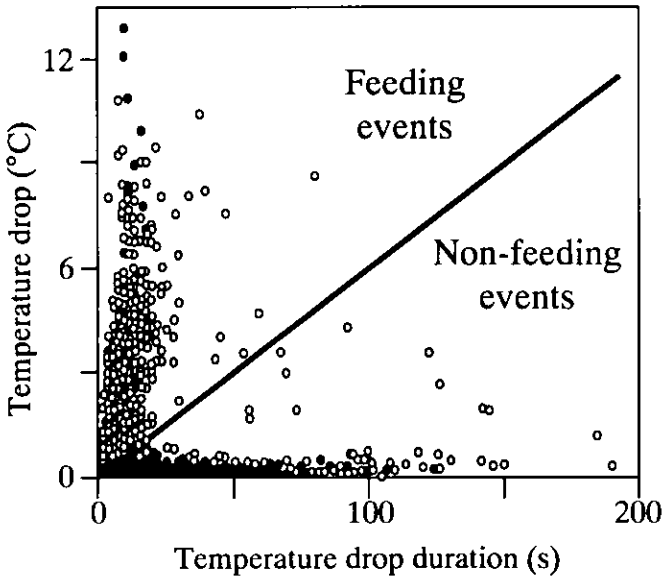


Fig. III – 4 : Amplitude and duration of temperature drops in the upper oesophagus of King Penguins during shallow dives (≤ 30m, black circles) and deep dives (> 30m, white circles). Drops below the solid line indicate prey ingestion (0.06°C.s^{-1}).

Oesophageal temperatures recorded in free-ranging birds showed large variations (>13°C) that indicated feeding events and feeding depths when combined with dive profiles. The typical fast, short and precipitous temperature drops clearly indicate prey ingestion, as opposed to the slow temperature variations corresponding to the tissue cooling due to physiological responses to diving (Handrich *et al.* 1997). These prey ingestions were furthermore confirmed as the rapid temperature drops mainly occurred during deep dives exclusively performed during daylight by King Penguins (Fig. III – 2b, Charrassin *et al.* 1998, Kooyman *et al.* 1992, Pütz *et al.* 1998), which correspond to the depths where Myctophids concentrate during the day (Duhamel 1998, Zasel'sliy *et al.* 1985).

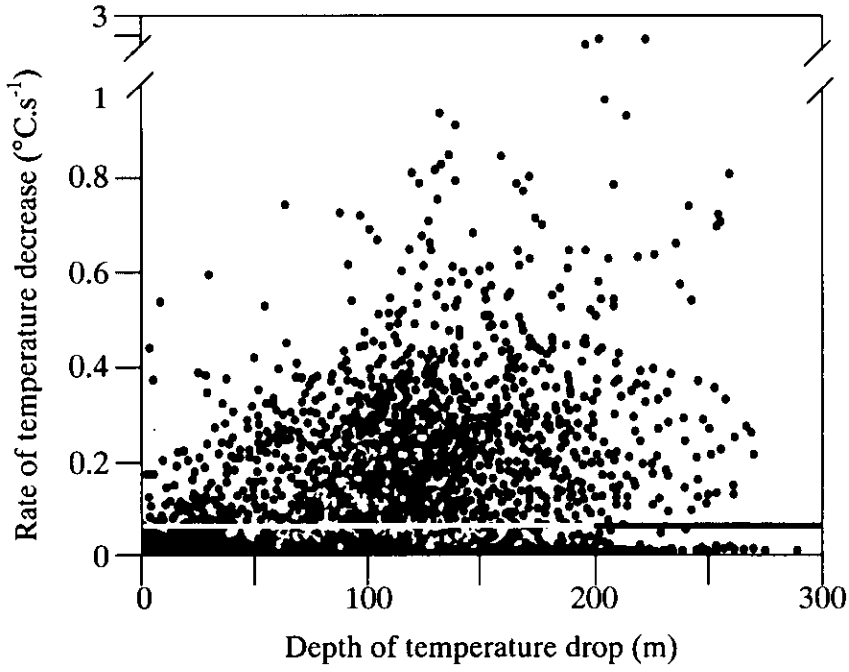


Fig. III – 5 : Depths at which temperature drops in the upper oesophagus occurred in King Penguin. The solid line indicates the drops with a rate of temperature decrease ≥ 0.06°C.s^{-1} (drops above this line represent feeding events).

Based on a penguin's average vertical velocity during diving of 1.3m.s^{-1} (Pütz *et al.* 1998) and with an ingestion-detection delay of 15s, the accuracy of depth where ingestion occurs is ≈20m, *i.e.* 10% of the dive depth if the bird reaches 200m. Being validated with concurrent application of a classical technique, such as hydroacoustic prey survey, or net trawl, this method may provide a unique means to assess the prey distribution over depth. For instance, one of the three birds fed mainly at 80 – 170m, where it likely encountered dense prey patches. Using average prey mass of King Penguins (7.4 and 1.7g for the two main prey species, in proportions of 75 and 15% of the diet, respectively (Cherel & Ridoux 1992)), the daily mass of fish ingested by birds 1 and 2 was about 1.6kg and was 0.6kg for bird 3. These values are comparable with those ranges found in studies based on energetics (Kooyman *et al.* 1992) and argue for the reliability of the method presented here.

III – 2. Prey pursuit and capture by King Penguins at sea

INTRODUCTION: Measurement of oesophageal temperature appears to be a promising tool for detecting prey ingestion by marine predators (*cf.* previous chapter). However, informations on the timing of prey intake are less valuable if they cannot be related to the foraging behaviour. Indeed, little is known about how King Penguins locate, pursue and capture prey in the dark deep-sea environment. In the present chapter, depth utilization and swim speeds were sampled on free-ranging King Penguins at a high sampling rate in order to determine accurately the birds' fine-scale underwater swimming and hunting behaviour.

MATERIAL & METHODS: Five King Penguins from Crozet Archipelago were equipped with KS-400PDT loggers that recorded depth and swim speed every second (Fig. II – 4a) in February – March 1996 (see chapter II – 2 for details). Data were analyzed using IGOR software (Wavemetrics, U.S.A.).

Previous studies indicated that 83% of the fishing behaviour of King Penguins occurs during deep dives (Pütz & Bost 1994). A bimodal distribution of the maximum depth frequencies is classically observed in King Penguins and is used to separate shallow from deep dives (Kooyman *et al.* 1992). Consequently, further analysis was performed only on dives to depths > 30m, this value representing the trough in the bimodal distribution of the maximum depth frequencies. Bottom times – the times spent at depths > 90% of the maximum depth of each dive – were calculated to provide estimates of hunting time (Kirkwood & Robertson 1997).

RESULTS: Two of the five devices deployed were recovered with reliable data, on birds PF141 and PF161. The recording periods occurred early in the foraging trips and lasted 2.9 (19 – 22 Feb.) and 2.5 days (16 – 19 Feb.) for birds PF141 and PF161, respectively. During these periods, 262 and 156 dives > 30m were recorded for birds PF141 and PF161, respectively. The average maximum depths of dives were 125 ± 53m (PF141) and 169 ± 59m (PF161).

During each deep dive, the speed increased rapidly from 0m.s^{-1} when at surface to a constant value of approximately 2m.s^{-1}, defined hereafter as cruising speed (Fig. III – 6a). Penguins maintained this cruising speed until the last 30s of the dive (Fig. III – 6a) when a short acceleration (up to 2.5m.s^{-1}) was observed followed by a rapid deceleration to 0m.s^{-1} when the bird emerged at the surface. The mean cruising speed was higher for bird PF161 (2.01 ± 0.11m.s^{-1}) than for bird PF141 (1.80 ± 0.05m.s^{-1}, Student $t_{32764} = 233.72$, $P < 0.0001$).

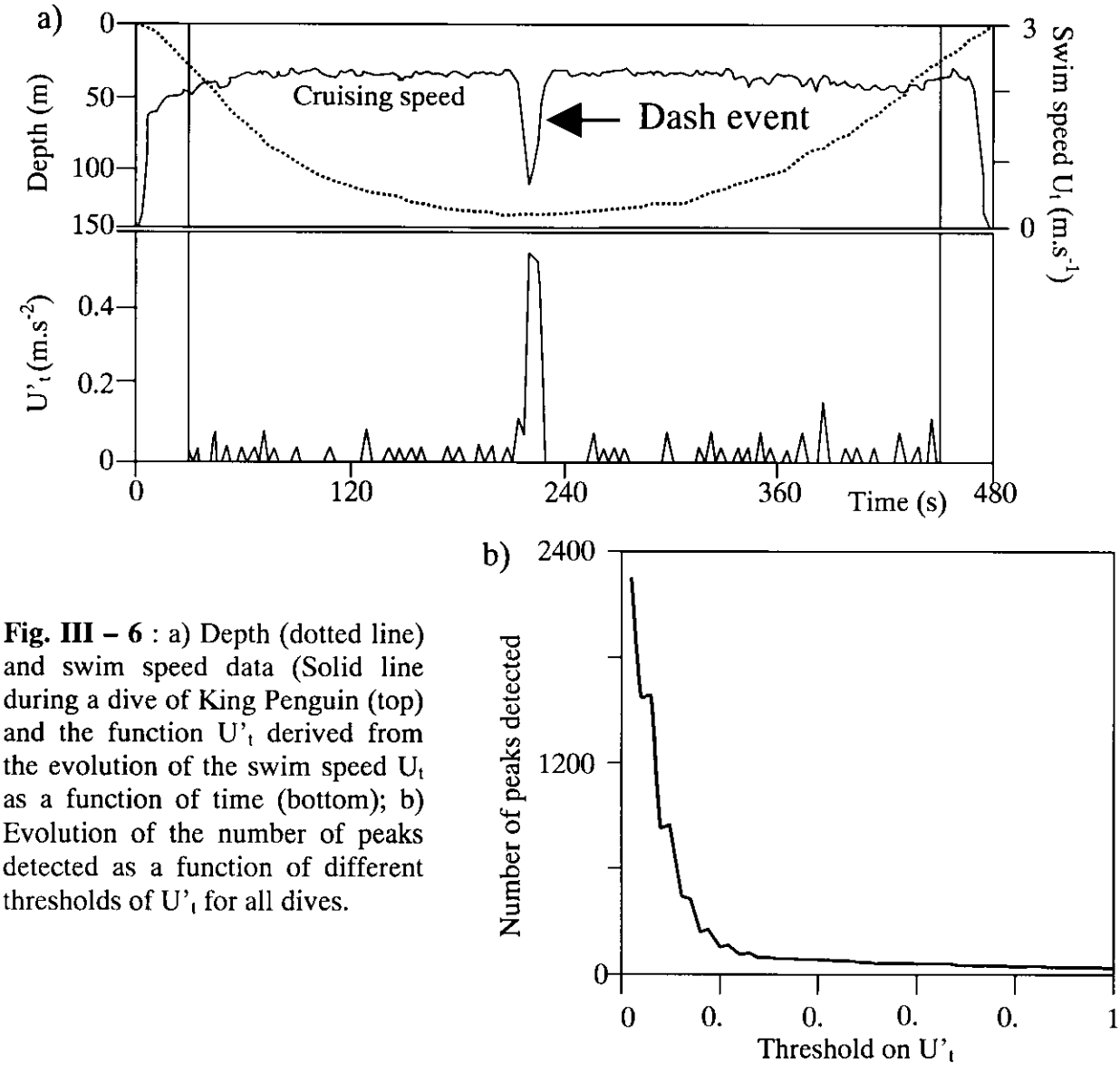


Fig. III – 6 : a) Depth (dotted line) and swim speed data (Solid line during a dive of King Penguin (top) and the function U'_t derived from the evolution of the swim speed U_t as a function of time (bottom); b) Evolution of the number of peaks detected as a function of different thresholds of U'_t for all dives.

Interrupting the constancy of the cruising speed, steep accelerations of speeds termed "dashes" were observed (Fig. III – 6a, top). In order to distinguish these pronounced dash events, a mathematical method was applied. The speed was first changed into accumulated values of acceleration using the following formulae:

$$U'_t = U'_{t-1} + (dU / dt) \qquad \text{if } (dU / dt) \geq 0$$

$$U'_t = 0 \qquad \text{if } (dU / dt) < 0$$

where U_t is the function describing the evolution of the cruising speed as a function of time (t). The function U'_t highlighted only the acceleration events (Fig. III – 6a, bottom). Thus, for all dives, the acceleration peaks were counted for different thresholds ranging from 0 to 1 with a step of 0.02 on U'_t (Fig. III – 6b). At first, the number of peaks was very high reflecting the noise due to variability. This number showed a sharp decrease before remaining constant after reaching a threshold value around 0.2. This stabilization corresponded to the detection of pronounced accelerations that were distinct from the variability. However, the limit between noise and clear peaks was difficult to estimate for all dives, as no clear break point was observed (Fig. III – 6b). Thus, this operation was repeated dive by dive, giving a threshold for each dive. Finally, the time of all peaks above a specific threshold indicated the position of the steep acceleration events in each dive, allowing accurate determination of dashes.

The dashes were separated into three categories based on their starting and ending values (Fig. III – 7, bottom). In 28% of all the dashes, these drastic accelerations arose from the cruising speed and were termed "Rush" events. In 59% of cases, following a brief deceleration, the dash events represented accelerations to return to the cruising speed and thus were termed "Adjust" events. Finally, there were "Intermediate" events (13% of the dashes) which were "Adjusts" that reached speeds greater than the cruising speed.

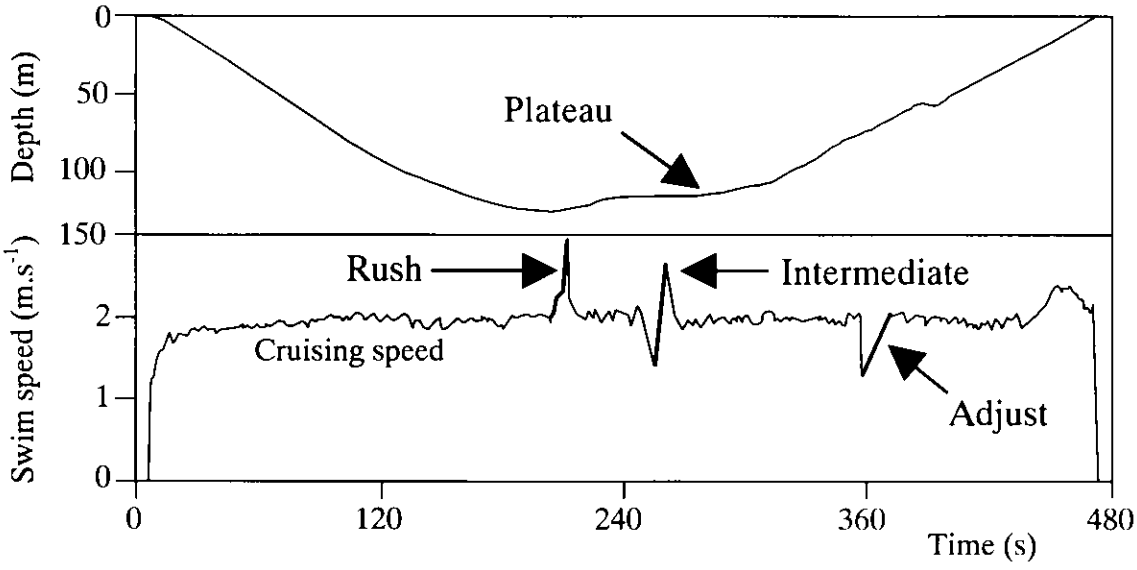


Fig. III – 7 : Depth (topr graph) and swim speed data (bottom graph) during a dive of a King Penguin. The dive represented in the top graph belongs to the category defined in this study as "Plateau" shaped dives. The three types of dash events ("Rush", "Intermediate" and "Adjust" events) interupting the constancy of the cruising speed are indicated.

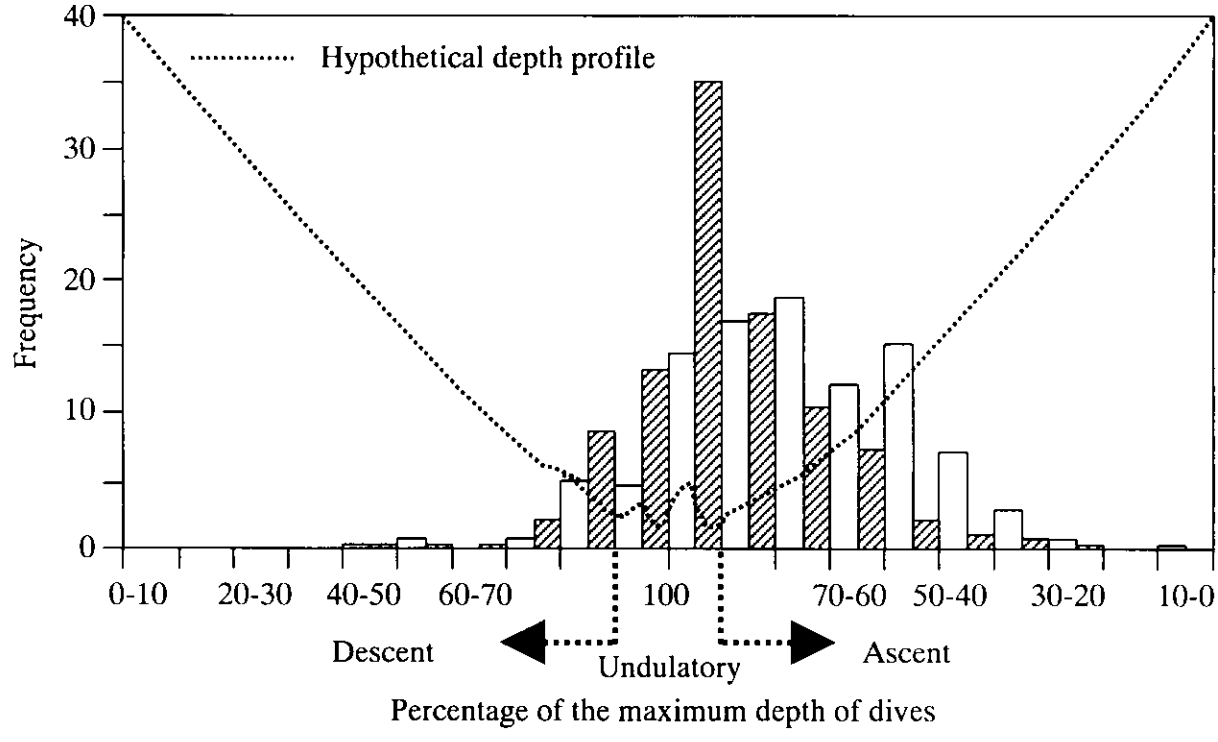


Fig. III – 8 : Frequency of occurrence of "Rush" (hatched bars) and "Adjust" events (white bars) in relation to the maximum depth of dives of King Penguins. "Intermediate" events were included in "Rush" as their distribution was similar.

Based on the depth profile of dives, a new category called "Plateau" dives (P-shaped dives) was added to the three classical ones: V-, U- and W-shaped dives (Wilson 1990, 1995). The P-dives had a portion of the ascending phase during which the depth remained constant (± 2m, Fig. III – 7, top). Dives were categorized as being with (DDE) and without (DW) "dash" events, then sub-categorized according to their depth profile (Table III – 2). There were three types of U-shaped dives, those without dashes (33% of dives), those with only "Adjusts" dashes (22%) and those with the three types of dashes combined together (8%). No dashes were performed during V-shaped dives. On the other hand, three W-shaped dives without dashes (N = 71) and 11 P-shaped dives without dashes (N = 56) were observed for the two birds. The number of dashes per dive category increased gradually from the U-shaped dives that had only "Adjusts" to the W-shaped dives.

Table III-2. Categorization of King Penguin dives based on both their depth profile and the presence (DDE) or absence (DW) of rapid acceleration events ("dashes") during the dives. See the text for description of the dive types.

Category of dives	Sub-category	Detailed percentages		Mean number of dash events for the 2 birds (± S.D.)
		PF141	PF161	
DW	"V" shaped	1.5%	2.6%	---
	"U" shaped	40.8%	24.4%	---
	"W" shaped	0.4%	1.3%	---
	"Plateau" shape	3.8%	0.6%	---
DDE	"U" shape with "adjust" only	13.4%	30.8%	1.5 (± 1.0, N = 83)
	"U" shape	11.8%	4.5%	2.5 (± 1.3, N = 38)
	"Plateau" shape	9.2%	14.1%	2.8 (± 2.7, N = 46)
	"W" shape	14.9%	18.6%	5.0 (± 3.6, N = 68)
Unclassified dives		4.2%	3.2%	---

Seventy-six percent of dash events (85, 80 and 71% for "Intermediates", "Rushes" and "Adjusts", respectively) were performed at depths > 100m. Moreover, half of the dashes detected at depths < 100m occurred during dives with maximum depths < 100m. Additionally, no clear dashes were observed during dives < 30m. "Rushes" and "Intermediates" occurred mainly during the early ascent phase of dives (Fig. III – 8). "Adjust" events were most prevalent during the ascent phase of dives, but generally were also performed later in the ascent than the other types of dashes. Finally, birds performed few dashes during the descending phase of dives. Overall, 65% of dashes corresponded to a movement of birds directed upward (Table III – 3). However, 58% of the "Intermediates" corresponded to downward movements.

Table III-3. Swimming directions of King Penguins during dash events.

Per dash type	Upward	Downward	No depth changes
"Rush" events	65%	26%	9%
"Adjust" events	74%	15%	12%
"Intermediate" events	28%	58%	14%
All dash type together	65%	24%	11%

The dashes were separated into straight, where a continuous increase in the speed was observed; and non-straight events, where the acceleration was briefly interrupted by a small deceleration (Fig. III – 9, top left). Straight events generally were shorter in duration (2.7 ± 1.9s, N = 560) than were non-straight events (7.2 ± 8.9s, N = 65, Mann-Whitney, U = 1914.5, P < 0.001, Fig. III – 9). Additionally, straight events were "Rushes" in 80% of cases. Correspondingly, the mean distance traveled during straight events (5.6 ± 3.1m, N = 560) was less than the distance traveled during non-straight events (17.3 ± 8.8m, N=65, Mann-Whitney U = 2401, P < 0.001). There was a linear relationship between the distance traveled during dashes D_{ist} and their duration D_{ur} (D_{ist} = 2.4 x D_{ur}, R^2 = 0.87).

"Rushes" were of longer duration than the other types of dashes (Kruskall-Wallis H_2 = 6.08, P = 0.048) whereas the penguins' rate of acceleration was greatest during "Intermediates" (Kruskall-Wallis H_2 = 60.74, P < 0.0001, Table III – 4).

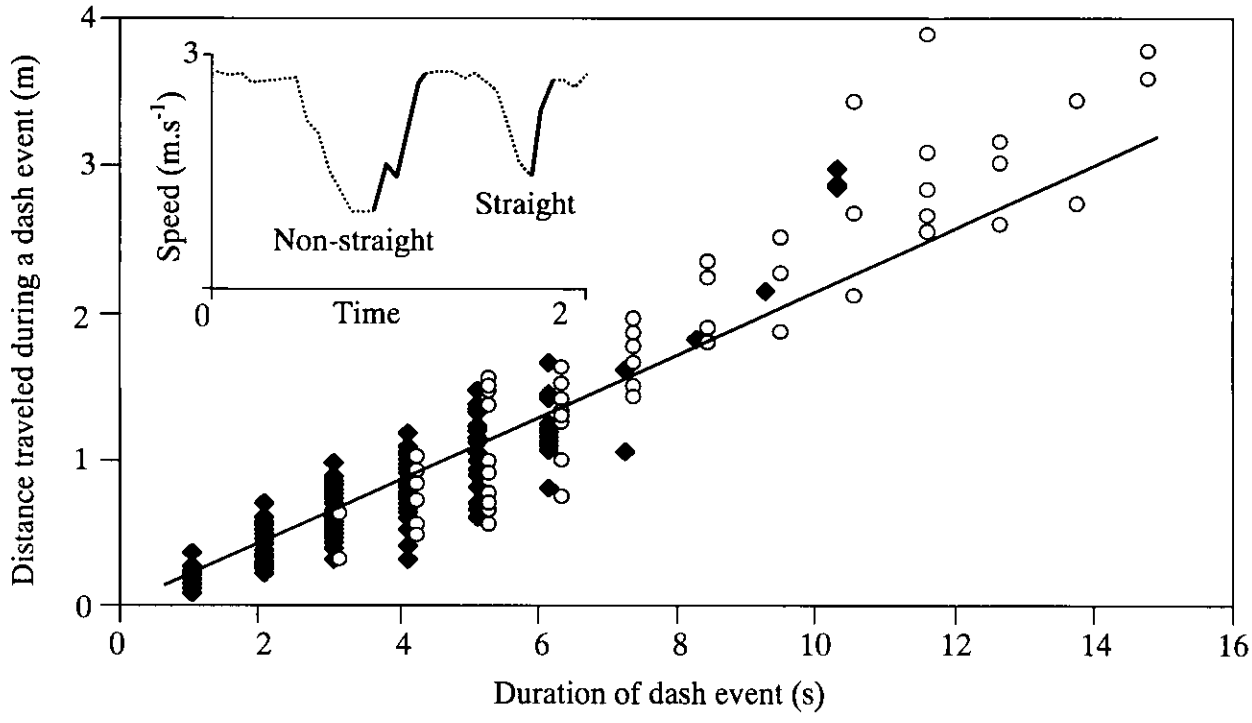


Fig. III – 9 : Distance traveled by King Penguins during dash events according to the events duration. Black squares and white circles represent straight and non-straight events, respectively. Straight and non-straight events are illustrated in the speed diagram (top-left figure).

Within a dive, 80% of "Rushes" were followed by another dash ("Rush", "Adjust", "Intermediate" or a combination). In one third of the cases, a "Rush" was followed by an "Adjust" while "Adjusts" represented single events in 48% of cases.

DISCUSSION: During most of each foraging dive, the penguins maintained constant speeds of approximately $2m.s^{-1}$, which may correspond to an optimal velocity at which the energetic cost of transport is at a minimum. Measurements of energetic and swim velocity performed on and King Penguins in artificial swim canals have suggested that these birds did possess such optimal speed, estimated to be around $2.2m.s^{-1}$ (Culik *et al.* 1996a), which is comparable with the mean cruising speed recorded in the present field study.

Table III – 4. Duration of dash events and acceleration rates of King Penguins during events.

Abrupt acceleration type	Duration (s)	Acceleration ($m.s^{-2}$)
"Rush"	4.1 (± 3.3)	0.35 (± 0.3)
"Adjust"	2.9 (± 1.3)	0.39 (± 0.2)
"Intermediate"	2.8 (± 1.7)	0.58 (± 0.3)

Penguins departed from the cruising speed to perform discrete dashes, which were postulated to be prey pursuit, capture and eventually recovery or swallowing events. Some dashes may indicate escapes from predators. However, the main predator of King Penguins while at sea is the Killer Whale, *Orcinus orca*, whose hunting seems to occur near the sea surface rather than at depths > 100m (Guinet 1991), where the majority of dashes were performed. Assuming that dashes represent hunting events, W-shaped dives do seem to represent active feeding dives, while V-shaped dives were probably exploratory dives. On another hand, the role of P-shaped dive remains unclear although 80% of them might have been feeding dives. Perhaps the most important observation, however, was the presence of dashes during 53% of the U-shaped dives, suggesting that they were not limited to exploration but were also feeding dives.

Few dashes were performed at shallow depths. When this happened, these shallow dashes occurred during dives performed at the beginning and end of each day. The maximum depth of these dives increases and decreases at dawn and dusk respectively, following the vertical migration of prey (Wilson *et al.* 1993). Among Myctophids, King Penguins at the Crozet Archipelago feed mainly on *Krefftichthys andersonii* and *Electrona carlsbergi* (Cherel & Ridoux 1992). The fine temporal scale of the recordings allows speculating on the actual detection, pursuit and capturing strategies of these prey by King Penguins.

Penguins are assumed to detect their prey by sight (Bowmaker & Martin 1985, Howland & Sivak 1984, Martin & Young 1984, Sivak 1976, Suburo & Scolaro 1988, Suburo *et al.* 1991). As such, prey recognition is dependent on their visibility at the depths where the penguins hunt. This visibility will vary with degrees of light penetration and characteristics of the prey such as bioluminescence. A dash was initialized once a potential prey was detected within a potential hunting range and ended once this prey was caught, in case of a successful capture. Therefore, in this study, the distance of prey detection by the King Penguins might equate to the distance traveled during constant acceleration (straight events), ranging 1 – 7m. This would be true except if the prey starts an escape using the same direction as the predator's attack. On the other hand, the non-straight events may represent active pursuits of either a single prey escaping in more than one direction or several trials of capture on more than one prey.

Most of the dashes corresponded to the ascent phase of the dives, suggesting that the penguins swam down to a depth where they expected to find prey, then foraged both at that depth and during the ascent back toward the surface. Moreover, two-thirds of the dashes were associated with upward movements, suggesting that most prey were detected and approached from below. Since an animal's eye looking upward in the sea would receive about 100 times more intense ambient flux light than an eye directed downward (Clarke & Denton 1962), observed from below, the prey would be silhouetted against a bright background, making them easier to locate.

However, using the counter-shade effect may be highly dependent on the light available at different depths, which would depend on the time of day, cloud cover and water clarity. A more recent study focusing on the underwater vision of Little Penguins (Cannell & Cullen 1998) has revealed the existence of a relationship between the light level and the efficiency of prey hunting. Since one third of dashes were performed while the birds were swimming downward or horizontally, King Penguins probably rely occasionally on bioluminescence to detect their prey as suggested by Martin (1999). This may be the case when the light level at the depths where prey are encountered decreases below the limit where the counter-shading effect can be used. However, the higher proportion of movements directed upward indicates that the detection of prey silhouette may play a more important role than the detection of bioluminescence for King Penguins' hunting behaviour in deep water (> 100m). The significance of an upwardly-focused hunting behaviour will be further discussed in the general synthesis (chapter V – 2)

Based on the variety of dashes distinguished, King Penguins may have several prey approaches and capture techniques. "Rushes" were the most common dashes performed and probably represented spontaneous movements toward a prey upon its detection. "Rushes" occurred singly, perhaps indicating a single prey capture, or in a series, which could reflect multiple prey captures or several unsuccessful "Rushes" prior to a successful capture.

"Adjusts" also were either single events or occurred within a series of other dashes. Single "Adjusts" may indicate the catching of a motionless prey such as torpid Myctophids (Barham 1966). The bird would sight the prey from a distance, slowing down so as to approach the prey undetected, and the "Adjust" would be a dash forward to capture the prey. When they occur within a series of other dashes, "Adjusts" may indicate returns to cruising speed following changes in direction (in which velocity was lost) or brief pauses to handle and/or swallow prey. "Intermediates" may have been "Adjusts" that over-shot cruising speeds or "Adjusts" that turned into "Rushes" as further pursuit was required to capture the prey.

This study reveals much about the possible hunting strategies of King Penguins but since these birds may vary their hunting strategies through foraging trips (Bost *et al.* 1997), between foraging trips at different times of the year, further studies with depth-speed loggers are required.

IV – FEEDING BEHAVIOUR OF ADELIE PENGUINS

IV – 1. Validation of oesophageal temperature recording for detection of prey ingestion in captive Adélie Penguins

INTRODUCTION: Since the oesophageal temperature recording method offered promising results on King Penguins (see section III), the same system was tested on a smaller bird, the Adélie Penguins, a key species among the top predators of the Antarctic food webs. The aim of the following experimental study was to test the efficiency and the reliability of this

Most of the dashes corresponded to the ascent phase of the dives, suggesting that the penguins swam down to a depth where they expected to find prey, then foraged both at that depth and during the ascent back toward the surface. Moreover, two-thirds of the dashes were associated with upward movements, suggesting that most prey were detected and approached from below. Since an animal's eye looking upward in the sea would receive about 100 times more intense ambient flux light than an eye directed downward (Clarke & Denton 1962), observed from below, the prey would be silhouetted against a bright background, making them easier to locate.

However, using the counter-shade effect may be highly dependent on the light available at different depths, which would depend on the time of day, cloud cover and water clarity. A more recent study focusing on the underwater vision of Little Penguins (Cannell & Cullen 1998) has revealed the existence of a relationship between the light level and the efficiency of prey hunting. Since one third of dashes were performed while the birds were swimming downward or horizontally, King Penguins probably rely occasionally on bioluminescence to detect their prey as suggested by Martin (1999). This may be the case when the light level at the depths where prey are encountered decreases below the limit where the counter-shading effect can be used. However, the higher proportion of movements directed upward indicates that the detection of prey silhouette may play a more important role than the detection of bioluminescence for King Penguins' hunting behaviour in deep water (> 100m). The significance of an upwardly-focused hunting behaviour will be further discussed in the general synthesis (chapter V – 2)

Based on the variety of dashes distinguished, King Penguins may have several prey approaches and capture techniques. "Rushes" were the most common dashes performed and probably represented spontaneous movements toward a prey upon its detection. "Rushes" occurred singly, perhaps indicating a single prey capture, or in a series, which could reflect multiple prey captures or several unsuccessful "Rushes" prior to a successful capture.

"Adjusts" also were either single events or occurred within a series of other dashes. Single "Adjusts" may indicate the catching of a motionless prey such as torpid Myctophids (Barham 1966). The bird would sight the prey from a distance, slowing down so as to approach the prey undetected, and the "Adjust" would be a dash forward to capture the prey. When they occur within a series of other dashes, "Adjusts" may indicate returns to cruising speed following changes in direction (in which velocity was lost) or brief pauses to handle and/or swallow prey. "Intermediates" may have been "Adjusts" that over-shot cruising speeds or "Adjusts" that turned into "Rushes" as further pursuit was required to capture the prey.

This study reveals much about the possible hunting strategies of King Penguins but since these birds may vary their hunting strategies through foraging trips (Bost *et al.* 1997), between foraging trips at different times of the year, further studies with depth-speed loggers are required.

IV – FEEDING BEHAVIOUR OF ADELIE PENGUINS

IV – 1. Validation of oesophageal temperature recording for detection of prey ingestion in captive Adélie Penguins

INTRODUCTION: Since the oesophageal temperature recording method offered promising results on King Penguins (see section III), the same system was tested on a smaller bird, the Adélie Penguins, a key species among the top predators of the Antarctic food webs. The aim of the following experimental study was to test the efficiency and the reliability of this

new methodology to detect ingestion events. For this, captive Adélie Penguins were equipped with the recording unit and fed prey of various sizes and supplied at various frequencies. In addition, experiments were conducted on captive birds in an aquarium in Japan to examine the delay between capture and swallowing by comparing the time of capture recorded by video-camera with the time a drop in the oesophageal temperature occurred.

MATERIAL & METHODS: One first set of experiments was conducted during the austral summer 1998-1999 on seven captive Adélie Penguins in Adélie Land (Fig. II – 1) equipped with UME-TT logger (chapter II – 2). Birds were caught in the morning, on the shore while departing for foraging trip with their stomachs presumed empty and were handfed in the afternoon.

Each feeding session consisted in the delivery of five pieces of dead shrimp (mass: 0.2 – 5.4g, N = 325) kept in icy water (0 – 2°C). The masses of each piece reflected as closely as possible the masses and volumes of juvenile to adult euphausids, the main prey of Adélie Penguins (Kerry *et al.* 1995, Ridoux & Offredo 1989, Trivelpiece *et al.* 1990, Watanuki *et al.* 1997, Wilson *et al.* 1991). During the sessions, penguins were held between the knees of an experimenter who opened the beak at specific times to allow the ingestion of pieces of shrimp. The time at which food was swallowed was noted. The feeding sessions alternated between high and low frequencies; high frequency sessions involved introduction of food items at intervals < 20s while low frequencies intervals were ≥ 20s. Feeding sessions were separated from each other by > 5min to let the oesophageal temperature reach normal values.

In a second set of experiments in July 1999, three captive Adélie Penguins at the Port of Nagoya Public Aquarium (chapter II – 1) were equipped with UME-TT loggers and released in the exhibit pool where they fed freely on dead *Euphausia superba*. One bird was equipped at a time to facilitate observation. During feeding sessions, bird behaviour was monitored by video-camera and the time of prey capture recorded. During feeding sessions, food items were delivered by throwing handfuls of Krill into the pool while several penguins were swimming. These feeding sessions ended when the basket of Krill, containing 10 – 15 handfuls, was empty. The mass of the individual pieces of Krill delivered was not measured but pieces ranged 0.5 – 1.2g. After the retrieval of the loggers in both series of experiments, data were analyzed with IGOR software (Wavemetrics, U.S.A).

RESULTS:

♦**Feeding experiments on land:** A total of 36 low and 27 high frequency feeding sessions were performed on the seven birds which corresponded to an average amount of Krill delivered per bird of 51.8 ± 41.5g (total number of pieces of shrimps seen swallowed by the seven birds = 309). The feeding experiments lasted a mean of 1.3 ± 0.4h. During the experiments, the body temperature of the birds increased by about one degree in response to the stress of being restrained (Boyd & Sladen 1971, Regel & Pütz 1997).

For three birds, the stomach temperature remained essentially constant at 40.8 ± 0.4°C, 39.5 ± 0.4°C and 40.9 ± 0.6°C so that prey ingestion could not be detected. The logger of another bird did not record reliable data for stomach temperature. Finally, in the three other birds 63 temperature drops corresponded to 129 prey swallowed (49%). The average magnitude of these stomach temperature drops was 2.4 ± 0.5°C (N = 63). Additionally, there was a substantial delay between the time the bird was seen swallowing and the initiation of the following temperature drop in the stomach. This delay was calculated for only one bird (5.6 ± 4.5s, N = 32) because it was impossible to relate the time of swallowing and the initiation of following temperature drop reliably.

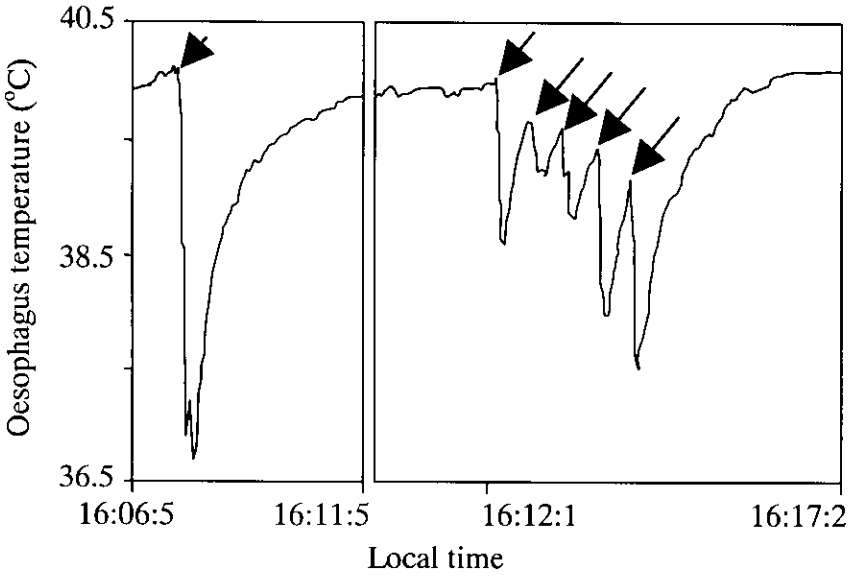


Fig. IV – 1 : Recording of the temperature of the oesophagus in captive Adélie Penguins. The arrows indicate the precipituous drops due to the ingestion of cold piece of shrimps delivered at a high frequency (left) and low frequency (right).

The recording of œsophagus and stomach temperatures revealed several drops of various magnitudes (Fig. IV – 1). Drops recorded by the sensors appeared to have various origins: ingestion of a prey at a lower temperature, variability in the internal temperature or variability in the measurements due to the logger itself. For each drop in the internal temperature, three parameters were collected: duration, magnitude and slope of drops. In the œsophagus, when these parameters were compared between drops directly following prey ingestion and drops due to other sources of variability, magnitude proved the most discriminating with 96% of temperature drops with a magnitude > 0.25°C directly following prey ingestion being detected (Fig. IV – 2). However, 12.7% of temperature drops > 0.25°C did not correspond to prey ingestion.

In order to separate drops due to ingestion of prey from others, an amelioration of the mathematical method detailed in chapter III – 2 was applied to the data bird by bird. Using this method, the number of drops in the œsophageal temperature were counted over the course of each bird (chapter III – 2).

Using this method, from the 309 food items seen swallowed, 176 drops in the œsophagus temperature were detected whatever the mass of prey or the frequency of ingestion. Of these, 3% (N = 5) were not associated with prey ingestion. Therefore, 171 temperature drops corresponding to food ingestion were taken into account by the mathematical method corresponding to 55.3% of the 309 food items seen swallowed. The average magnitude of temperature drops was 8.2 ± 3.3°C and the delay between the time of swallowing and the start time of the temperature drop was 4.0 ± 5.5s (N = 171).

Firstly, the success of detection was compared between high (< 20s) and low frequency (≥ 20s) of delivery using pieces of shrimps of similar masses ranging from 0.8 to 1.5g. For high frequency feeding sessions, 58.3% of the prey fed were detected; 76.7% being detected in the low frequency sessions. During high frequency feeding sessions, prey items were sometimes gathered in the beak and swallowed some seconds after the last piece of the feeding sequence was delivered. As a result, the œsophagus logger response to different masses of prey items was investigated using only low frequency sessions. Here, the initiation of a drop did not interfere with adjacent drops, *i.e.* items being isolated from each other. The likelihood that prey ingestion was detected increased with the corresponding mass fed (Fig. IV – 3a). Similarly, the magnitude of temperature drops M_t increased significantly with the mass fed M_f (Fig. IV – 3b) although the correlation coefficient between mass and magnitude was weak ($M_t = 0.8 \times M_f + 0.7$, $R^2 = 0.40$, $F_{118} = 79.4$, $P < 0.0001$). The magnitude of the temperature drop, was unaffected by position of the prey in the feeding sequence (One-way Anova $F_4 = 0.52$, $P = 0.72$).

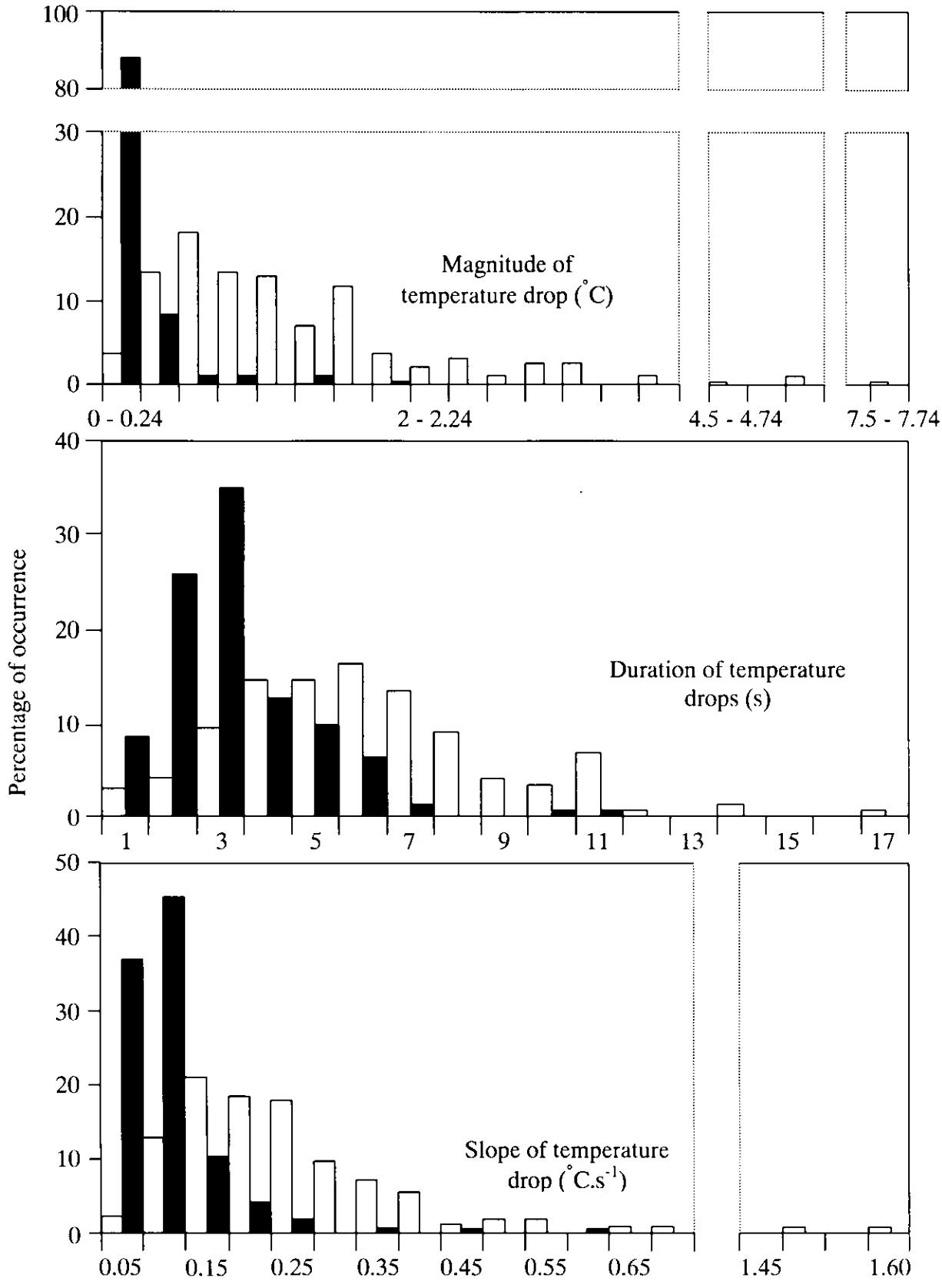


Fig. IV – 2 : Frequency of occurrence of the magnitude, duration and slope of temperature drops in the oesophagus of captive Adélie Penguins, corresponding to ingestion (black bars) and non-ingestion events (white bars).

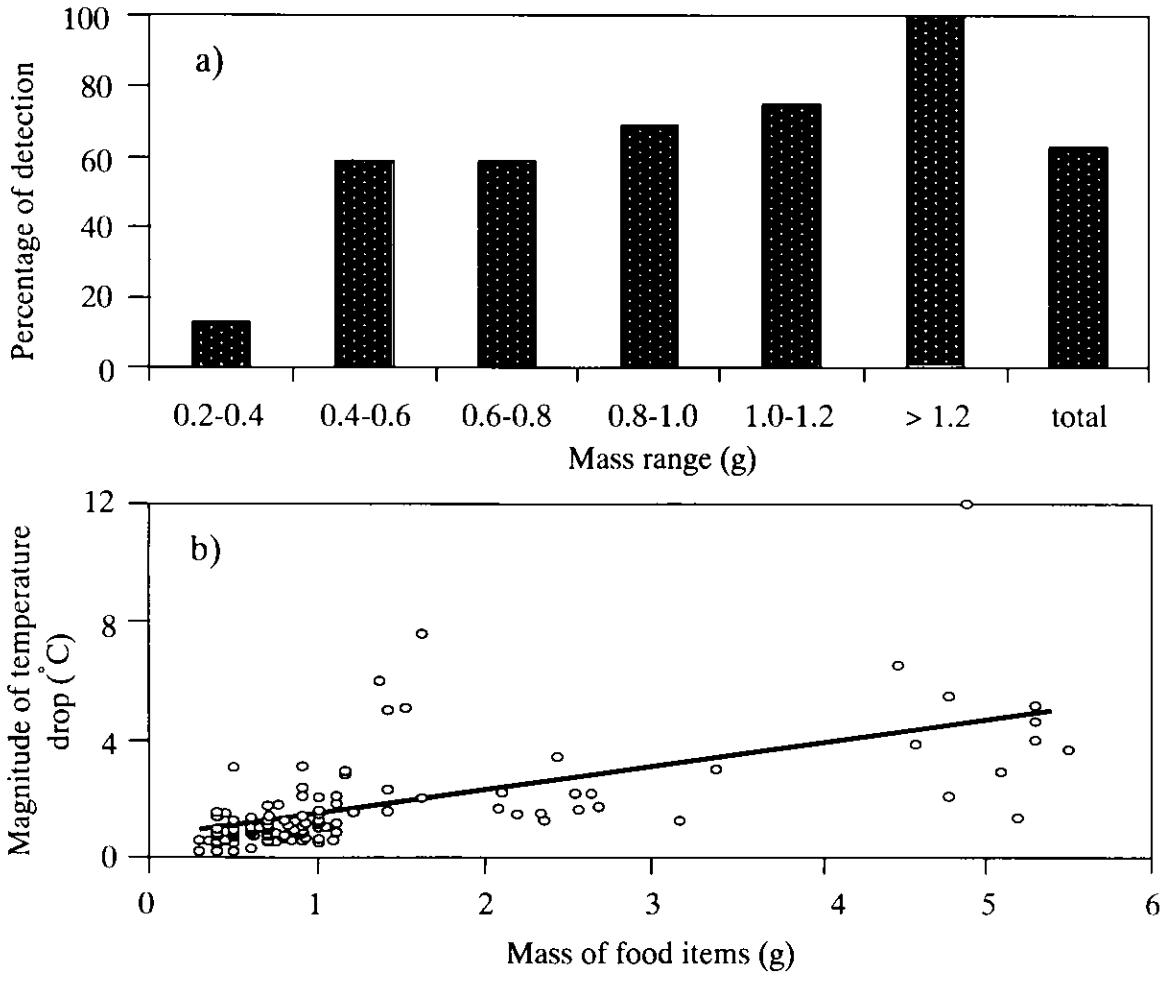


Fig. IV – 3 : a) Percentage of detection by oesophageal temperature sensor of different masses of cold food items delivered to captive Adélie Penguins at a low frequency (< 20s); b) Mass of food items swallowed and magnitude of the corresponding oesophageal temperature drops of captive Adélie Penguins.

♦**Feeding experiments in pool**: Of the three birds equipped, two caught few prey items (N = 12 and N = 3, respectively) and stayed mainly on land. The last bird, however, performed several underwater captures over three feeding sessions (duration: 15, 10 and 10min). This bird was seen to miss its prey five times and there was doubt about the success of five other events. In addition, the high concentration of birds in the pool during the feeding sessions might have masked several catches made by the equipped bird. Exactly, 100 prey captures were observed for this bird. Prey capture occurred at high frequencies since 83% of the food items were taken within 3s of each other, ingestion being grouped into 24 bouts, although 17% were taken in single isolated events. A bout ended when the following capturing event occurred after more than 3s. The bird captured on average 3.5 ± 1.9 prey per bout.

Comparison of the number of catches recorded by video-camera and the number of temperature drops recorded by the logger showed that 44.7% of the ingestion events were detected. Eleven isolated captures were followed by temperature drops after a delay of 3.8 ± 2.5s. Seventeen bouts of captures were followed by a temperature drop after a delay of 4.8 ± 3.6s. Five bouts had a temperature drop that occurred before the end of the bout. Finally, two bouts did not relate to any drop. On average, 2.2 ± 1.0 apparent ingestion events (range = 1 – 4) corresponded to one temperature drop which shows that prey were gathered in the beak before

swallowing. The mean magnitude of temperature drops following a single capture event (0.8 ± 0.5°C, N = 9) was statistically less than those following several catches (1.8 ± 1.1°C, N = 23, One-way Anova $F_1 = 6.6$, $P < 0.016$). Finally, the magnitude of the drop was independent of the pre-ingestion oesophageal temperature when the ingestion event occurred (Spearman coefficient $\rho = 0.20$, $P = 0.17$).

DISCUSSION : In the present study, the stomach temperature recordings of three birds did not show any substantial drops indicating that the temperature sensor was likely directly in contact with a portion of the stomach wall and thus unlikely to come into contact with recently-ingested prey. In the case of birds where drops were recorded in the stomach temperature, the detection rate might have been greater than that obtained on free-ranging animals since the stomach of captive birds was considered empty. This would lead to a greater probability that prey would touch the temperature sensor. In addition, the birds were on land and thus, stomach contents would not have been mixed due to swimming activity (Wilson *et al.* 1995b). Finally, since the birds were not in the water, there was no cooling of the internal tissues (Handrich *et al.* 1997) that could complicate the detection of prey ingestion. Prey were probably warmed up during the descent from the mouth to the stomach so that, the magnitude of temperature drops measured in the stomach was smaller than those recorded in the oesophagus.

The detection rate by the oesophagus sensor was considerably higher than that of the stomach sensor but still showed some limitations in the case of high feeding frequency. As Krill are patchily distributed in the wild (Nicol & de la Mare 1993), free-ranging penguins may be picking up prey at a high rate. Falla (1937, cited in Zusi 1975) quoted Sir Douglas Mawson who watched Adélie penguin feeding by saying "their heads darting from time to time to the left and to the right (...) and their beaks were going out just about as fast as barn-yard fowl feed on grain thrown on the floor". Similar behaviour was observed during the aquarium experiments where the prey delivery method led to a patchy distribution of Krill. The observation that birds collected several prey items over a few seconds, keeping them in the beak before swallowing, has superficial similarities to Puffin foraging behaviour (Harris 1984) and leads to several prey being registered as a single item. Furthermore, because prey gathered in the bill would be likely warmed up, the subsequent temperature drop measured by the sensor would lead to an underestimation of the mass ingested. In some instances, prey items were seen swallowed one by one during high feeding frequency sessions but the warming of the œsophageal temperature between two pieces was probably too slow to be registered, leading once again to a single temperature drop recorded for several prey items swallowed. This phenomenon depends mainly on the speed at which œsophageal temperature changes during the warming process and the rate at which the cold prey might pass through it.

Although the detection rate for isolated ingestion events was high for prey weighing more than 0.4g, it was low in the case of small mass items, especially, for prey ranging 0.2 – 0.4g (converted into length (Miller 1986), this corresponds to Krill 30 – 40mm long). Thus, oesophageal temperature loggers deployed on free-ranging Adélie Penguins would tend to underestimate the number of small isolated prey captured. This is likely to be the case for *Euphausia crystallorophias*, ranging 14 – 41mm in length (Coria *et al.* 1995, Davis & Miller 1990, Paulin 1975, Ridoux & Offredo 1989), immature euphausids (Miller & Hampton 1989) and some cephalopods (Coria *et al.* 1995, Ridoux & Offredo 1989). However, in the present experiment, the temperature of prey was probably higher than in the wild and the magnitude of the temperature drops correspondingly reduced. Nevertheless, around 70% of isolated prey > 0.4g are likely to be detected. In most localities, *E. superba* is the dominant prey of Adélie Penguins, with a body size ranging 32 – 59mm (Coria *et al.* 1995, Kerry *et al.* 1995, Ridoux & Offredo 1989, Trivelpiece *et al.* 1990, Watanuki *et al.* 1993, 1994, 1997, Wilson *et al.* 1989a, 1991), and mass of 0.8 – 1.5g for gravid females (Hosie 1994). In some instances, Adélie Penguins may switch from Krill to primarily fish (Kerry *et al.* 1995, Hopkins 1987, Ridoux &

Offredo 1989, Watanuki *et al.* 1993) although since the main fish prey is *Pleuragramma antarcticum* with lengths up to 75mm in length (Paulin 1975, Offredo *et al.* 1985, Watanuki *et al.* 1994), it is unlikely that the detection of this would be problematic. Thus, oesophageal temperature sensors may provide substantial information about the ingestion of large prey in other species such as King Penguins feeding mainly on Myctophid fish (Cherel & Ridoux 1992) or Spheniscus penguins feeding primarily on pelagic school fish (for review of penguin feeding habits see Croxall & Lishman 1987, Williams 1995).

This study demonstrates the potential of an oesophageal temperature sensor for the detection of feeding in Adélie penguins. Compared to stomach temperature recordings, the percentage of ingestion events detected as well as the clarity of the temperature drops has improved. Despite this, it is still impossible to separate temperature drops due to prey from those due to ice or water ingestion and to determine accurately the mass of the prey ingested (Hedd *et al.* 1996). The use of oesophageal temperature sensors in tandem with other loggers, such as time-depth recorders, might help eliminate some of these problems.

IV – 2. Underwater feeding behaviour of free-ranging Adélie Penguins using multiple data recording

INTRODUCTION: Following calibration experiments, the first data of oesophageal temperature recorded on free-living Adélie Penguins, simultaneously-equipped with depth, swim speed loggers will be presented. The rates of prey ingestion, and how these are related to water depth and swim speed will be considered. In addition, since the speed at which seabirds choose to swim during the ascent and the descent phases of dives is generally physiologically limited by the size of the animal (Wilson 1995), birds can optimize the commuting part of their dives by modifying the angle of descent and ascent. Therefore, analysis of the angle at which Adélie Penguins dive in relation to a successful or unsuccessful encounter with prey can help elucidate the decision-making in process and be used to examine how birds might enhance prey capture and minimise the energy or time expended.

MATERIAL & METHODS: The study was conducted in Adélie Land between Mid-December 1998 and Mid-January 1999, on 16 Adélie Penguins equipped with UWE-PDT loggers measuring depth and swim speed (chapter II – 2) and UME-TT loggers monitoring the oesophageal temperature (chapter II – 2), both loggers sampling every second. In order to maximize the number of data that can be stored in the memory, only one channel of the UME-TT was switched on. During the data analysis, drops in the oesophageal temperature and abrupt accelerations in the swim speed were treated mathematically using an amelioration of the method that counted the number of markedly decreasing or increasing events over the course of each dive (see chapter III – 2). This method of determination was successfully tested during feeding experiments performed on captive Adélie Penguins (see chapter IV – 1).

Angles of descent and ascent in radians (θ) were calculated as follows:

$$\sin(\theta) = \Delta D / Sp$$

where ΔD represents the absolute value of the depth changes calculated over 2s intervals and Sp, the swim speed. As the relative accuracy of depth and speed were 0.5m and 0.05m.s^{-1} respectively, the angle data were smoothed with a moving average calculated every 5s. Furthermore, as the accuracy of measurements of angles increase with descent or ascent duration, dives with short commuting phases (mainly dives < 20m) were excluded from the analysis.

The data were statistically treated using Systat (version 7.0, SPSS Inc. U.S.A.) and Statview (version 4.57, Abacus concepts Inc. U.S.A.) softwares.

RESULTS: Of the 16 free-ranging birds equipped, three regurgitated the devices on land prior to departure. Nine units were regurgitated at sea, six being retrieved hanging from the bill of the bird. These provided sporadic data. Another UME-TT logger leaked. Reliable swim speed, depth and œsophagus temperature data, therefore, were obtained for three birds (24, 28 and 07). The three parameters were logged for a full foraging trip in the case of bird 07 (Fig. IV – 4a). The œsophagus temperature was incorrectly recorded for three different portions of the trip in bird 28 accounting for 8.8% (N = 83) of the dives. This was due to temporary electrical shunts that reversed the polarity of the sensor at this time. In bird 24, the œsophagus temperature was recorded correctly for the first two-thirds of the foraging trip until the recorded temperature became constant although the bird continued to dive indicating a sensor malfunction at this time.

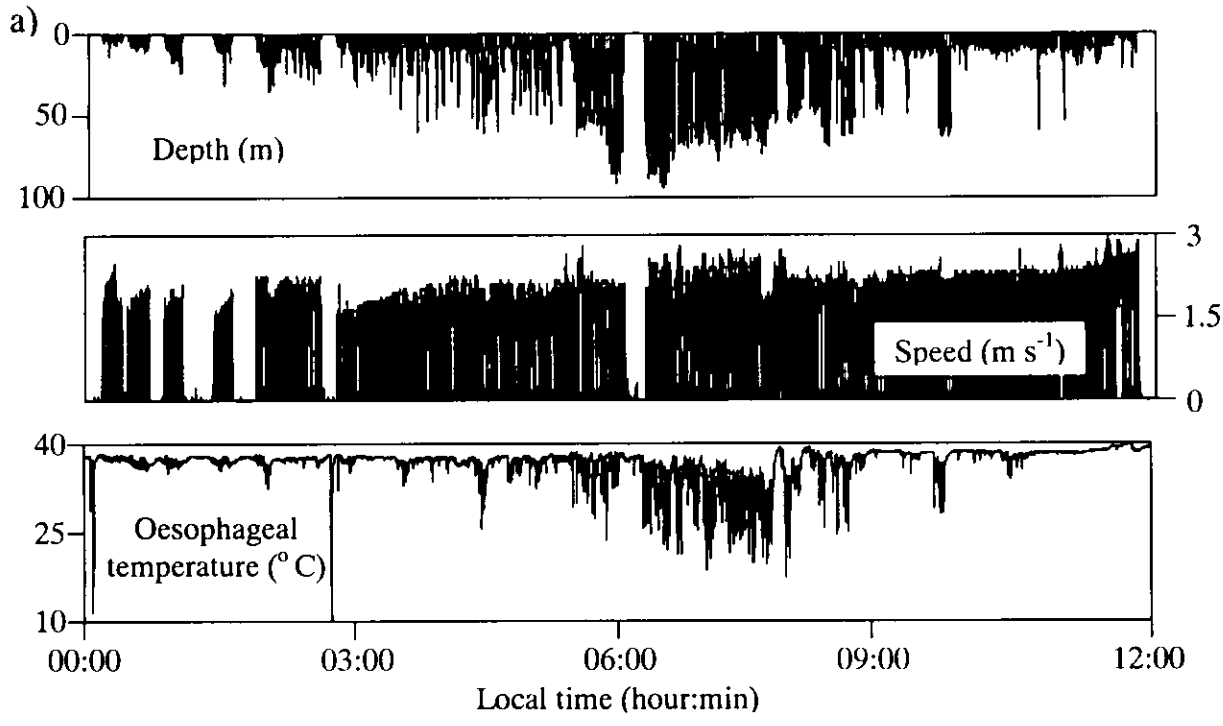
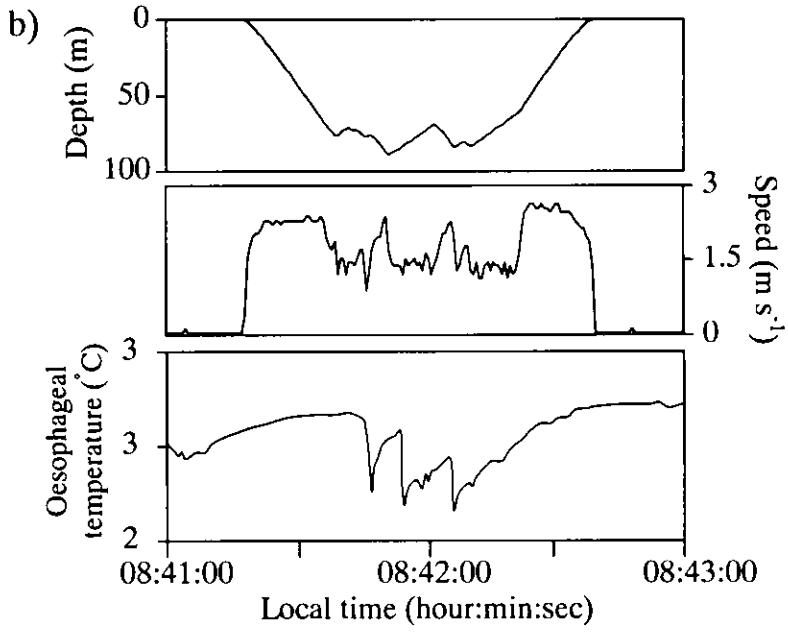


Fig. IV – 4 : Depth, swim speed and oesophageal temperature recorded during a) a complete foraging trip (~ 24h) and b) detailed on one deep feeding dive of a free-ranging Adélie Penguin.



Birds 28 and 07 had longer foraging trips incorporating more dives than bird 24 (Table IV – 1). Bird 07 dived on average significantly shallower than the other birds (One-way Anova $F_2 = 14.7$, $P < 0.0001$). The number of

temperature drops detected for birds 28 and 07 was similar and greater, respectively, than for bird 24. In penguin 24, the small number of temperature drops was certainly due to the shorter foraging trip duration associated with the default in the sensor. The occurrence of œsophageal temperature drops per dive bout was extremely variable within birds, temperature drops being concentrated in one or two dive bouts toward the middle of the foraging trip. However, for the three birds, the foraging trip was split into a similar number of dive bouts.

A total of 264 (16.28%) of the temperature drops occurred when the birds were at the surface. Most of these surface drops were small (0.7 ± 0.2°C, N = 203) and followed deep dives. However, 61 surface events were considered separately as they showed a greater than average magnitude of drop (4.3 ± 20.6°C, maximum magnitude = 19.5°C) and were only observed during the initial phase of the foraging trip.

Table IV – 1. General information on the foraging trip, dives and oesophageal temperature for the three equipped Adélie Penguins.

	Parameters	Bird 24	Bird 28	Bird 07
Bird	Body mass (kg)	4.8	4.4	4.9
Trip	Time spent at sea (h)	15	29	22
	Number of bouts (BEC* in min)	5 (7.5)	6 (7.5)	6 (6.5)
	Bout duration (h)	2.6 ± 3.5	4.5 ± 5.1	8.2 ± 4.0
Dive	Total number of dives	400	947	877
	Maximum depth (m)	93.2	67.0	58.4
	Mean maximum depth (m)	23.9 ± 26.62	24.8 ± 31.1	18.3 ± 22.3
	Ratio deep/shallow dives	0.31	0.4	0.2
Oesophageal temperature	Basal temperature* (°C)	38.3 ± 0.4	39.8 ± 1.1	37.8 ± 1.1
	Total Number of drops	269	545	568
	Number of drops per hour	22.1 ± 37.8	22.6 ± 28.7	19.5 ± 24.0
	Minimum temperature (°C)	22.7	18.7	10.2

* BEC stands for "bout end criteria" (see definition in section II)
**Temperature recorded before the departure to sea.

All other drops occurred during diving (Fig. IV – 4), most (64.6%) during bouts of dives > 40m. Deep dives were defined for dives with maximum depth > 40m, this value representing the trough in the bimodal distribution of the maximum depth frequencies of the three birds (Fig. IV – 5a). The average number of temperature drops per dive was higher for deep dives (4.1 ± 2.1, N = 310) than for shallow dives (1.7 ± 1.2, N = 50, One-way Anova $F_1 = 61.2$, $P < 0.0001$). Moreover, 99% of deep dives with temperature drops had an undulatory phase which started on

average at 91 ± 11% and ended at 85 ± 18% of the maximum depth (data for the three birds combined). Within W-shaped dives, 73% of the drops occurred during the undulatory phase although 23% and 4% occurred during the ascending and the descending phases, respectively (Fig. IV – 6). Single or sometimes multiple drops were occasionally observed between 40 and 50m during the ascent. However, the magnitude of these drops was significantly less than that observed during the undulatory phase (Table IV – 2).

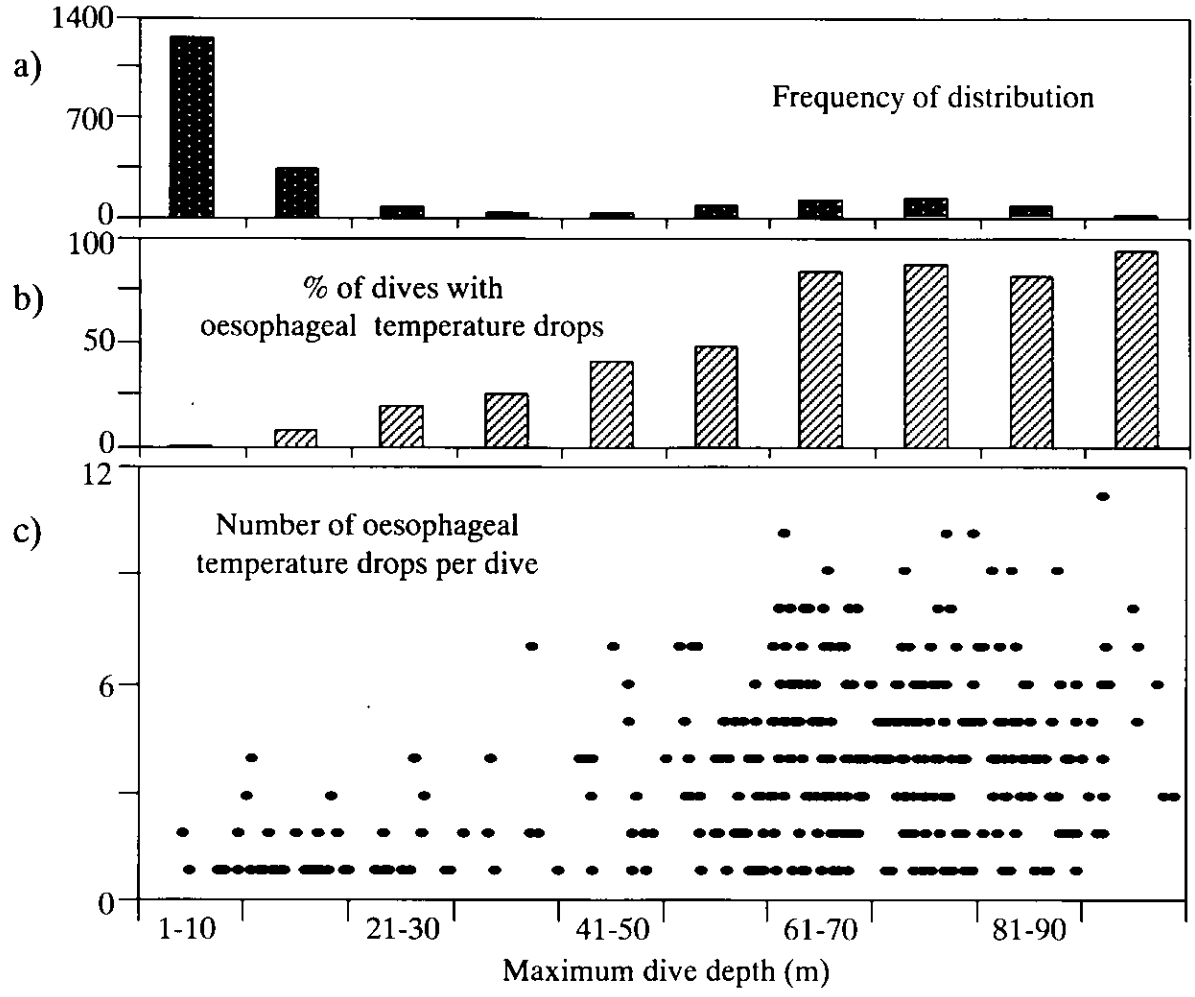


Fig. IV – 5 : a) Frequency of distribution, b) percentage of dives with oesophageal temperature drops and c) number of oesophageal temperature drops per dive according to the maximum dive depth of free-ranging Adélie Penguins.

Table IV – 2. Magnitude of oesophageal temperature drops during the different phases of dives and surface periods for the three equipped Adélie Penguins.

Phase	N	Average ± SE (°C)	One-way ANOVA
Descent	60	1.47 ± 0.93	
Undulatory	833	2.57 ± 2.03	$F_3 = 83.5$, $P < 0.0001$
Ascent	460	1.96 ± 1.44	

The mean number of undulations during W-shaped dive was 5.4 ± 2.0 (N = 122 dives), 7.4 ± 3.0 (N = 140 dives) and 10.8 ± 4.4 (N = 52 dives) for birds 07, 28 and 24, respectively. The number of temperature drops N_t per W-shaped deep dive was linearly related to the number of undulations N_u (N_t = 0.25 x N_u + 2.3, N= 360, F_1 = 63.7, P < 0.0001) but the coefficient of determination was poor (R^2 = 0.15). Within the undulatory phase of deep dives, drops were separated from each other by a mean of 14.9 ± 12.1s (N = 992).

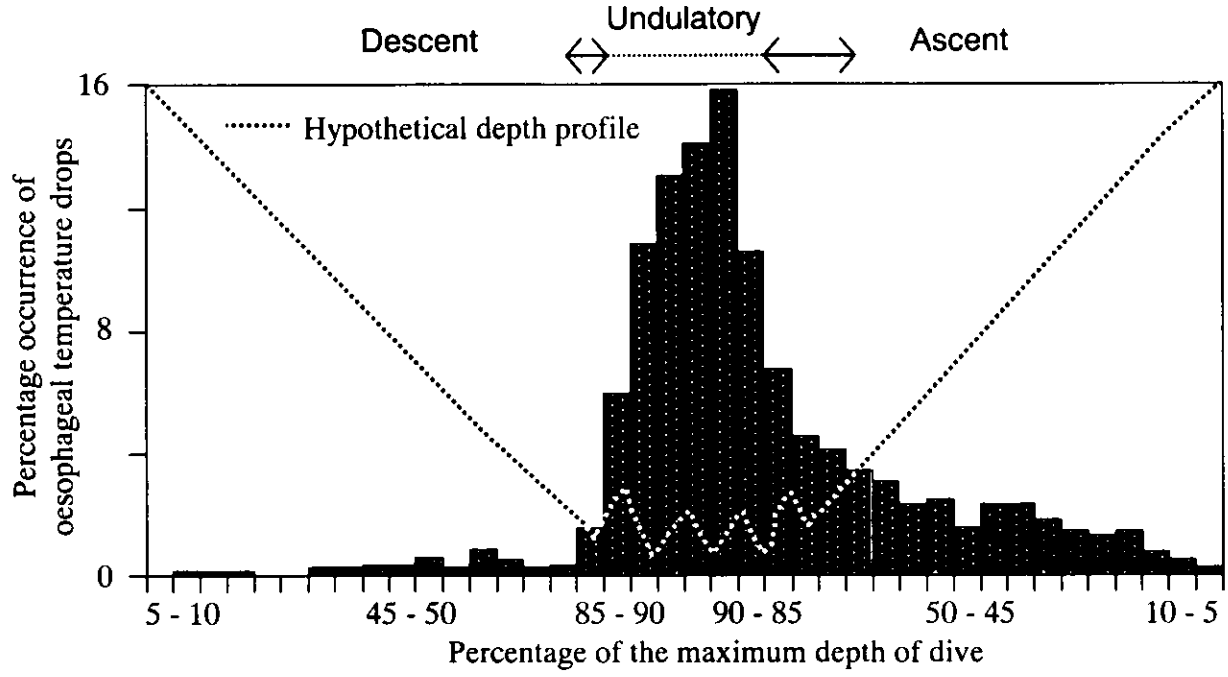


Fig. IV – 6 : Percentage of the maximum depth at which oesophageal temperature drops occurred in free-ranging Adelie Penguins. The average and standard deviation of the percentage of the maximum depth at which the undulatory period started and ended are indicated by dotted and solid arrows, respectively (see the Results in chapter IV – 2 for exact values).

Although statistically different from each other, the swim speed during shallow dives and during V-shaped deep dives remained approximately constant throughout the dive. For W-shaped deep dives the undulatory speed was significantly slower than the ascent and descent speeds (Table IV – 3).

Table IV – 3. Swim speed (m s^{-1}) during the descent, undulatory and ascent phases of Adélie Penguin's dives.

		Descent	Undulatory	Ascent	One-way ANOVA
Shallow dives		2.16 ± 0.37	2.13 ± 0.42	2.12 ± 0.38	F_2 = 38.2; P < 0.0001
Deep dives	V-shape	2.16 ± 0.28	---	2.00 ± 0.35	F_2 = 74.0; P < 0.0001
	W-shape	2.12 ± 0.29	1.71 ± 0.53	2.04 ± 0.40	F_2 = 4171.2; P < 0.0001

Here, birds decelerated sharply at the point of the first undulation whereupon the rest of the undulatory period was characterized by low speed with frequent abrupt acceleration and

deceleration. The number of abrupt speed changes N_a was linearly related to the number of undulations N_u in the undulatory phase ($N_a = 0.57 \times N_u + 2.47$, N = 316, $F_1 = 363.5$, $P < 0.0001$, $R^2 = 0.54$). During acceleration > 2s, the values of the depth change were summed in order to determine the preferred direction of swimming. Birds swam upward in 60% (N = 530) of the acceleration events and downward in 38% (N = 330). Swim depth apparently did not change in 2% of the cases. Summing data for all birds, 37.9% of the abrupt accelerations were followed by one temperature drop after 3.6 ± 3.2s (N = 772), 4.7% by two or more drops, with a second drop occurring 6.4 ± 3.1s (N = 108) after the first one and 57.5% were not followed by any drop.

In addition, 15% of the temperature drops began at the same time as an abrupt, but generally short, acceleration. In addition, accelerations that were followed by one or more temperature drops were statistically greater than those without subsequent temperature drops (Table IV – 4).

Table IV – 4. Magnitude of abrupt speed change events (m s^{-1}) for the three equipped Adélie Penguins according to the presence ("successful" speed changes) or absence ("unsuccessful" speed changes) of oesophageal temperature drops following them.

Bird #	# 24	# 28	# 07
"Unsuccessful" speed changes	0.68 ± 0.40 (N = 298)	0.62 ± 0.33 (N = 551)	0.51 ± 0.26 (N = 322)
"Successful" speed changes	0.91 ± 0.46 (N = 243)	0.75 ± 0.37 (N = 391)	0.66 ± 0.33 (N = 232)
One-way ANOVA	$F_1 = 38.7$, $P < 0.0001$	$F_1 = 32.1$, $P < 0.0001$	$F_1 = 34.4$, $P < 0.0001$

Two periods could be distinguished in the evolution of the angle during the descending phase of dives: Firstly, the descent angle remained constant or increased slightly during the main part of the descent (Figure IV – 7a). During this early period of the descent, variations in the angle were generally < 10° in both feeding and non-feeding dives (Table IV – 5). The descent angle increased with maximum depth and was affected by the presence or absence of prey capture in the previous dive (Figure IV – 8a). The slopes of the regression lines were non-significantly different (Ancova $F_1 = 1.29$, $P = 0.26$) but the intercepts were (Ancova $F_1 = 111.9$, $P < 0.0001$ and $F_1 = 271.7$, $P < 0.0001$ for covariate interactions for dive types and maximum depth, respectively).

Towards the end of the descent phase, most dives abruptly changed in descent angles (Fig. IV – 7a) which became more acute until the direction changed indicating the beginning of the undulatory phase of the dive. This abrupt point was observed in 68.5% of the cases (Table IV – 6). However, in 24% of the case, the descent angle appeared constant throughout the descent phase. This point at which the abrupt change occurred was significantly later in the descent phase of feeding dives (84.8 ± 13.4% of the descent time or at 81.2 ± 8.9% of the maximum depth) than for non-feeding dives (71.0 ± 15.7% of the descent time or at 75.7 ± 9.2% of the maximum depth, Anova for the percentage of the descent time $F_{1, 396} = 75.6$, $P < 0.0001$, Anova for the percentage of the maximum depth $F_{1, 396} = 29.2$, $P < 0.0001$).

Ascent phase: although 36% of the ascent angles of dives tended to have an oscillating pattern (Figure IV – 7b), the large proportion of angles with an irregular pattern (Table IV – 7) made further classification difficult. The ascent angles were affected by the presence or absence of prey capture during the undulatory phase of the dive (Figure IV – 8b); ascent angles of dives

where no prey were encountered increased less quickly with maximum dive depth than angles of dives with prey capture (Ancova $F_1 = 13.7$, $P < 0.0001$).

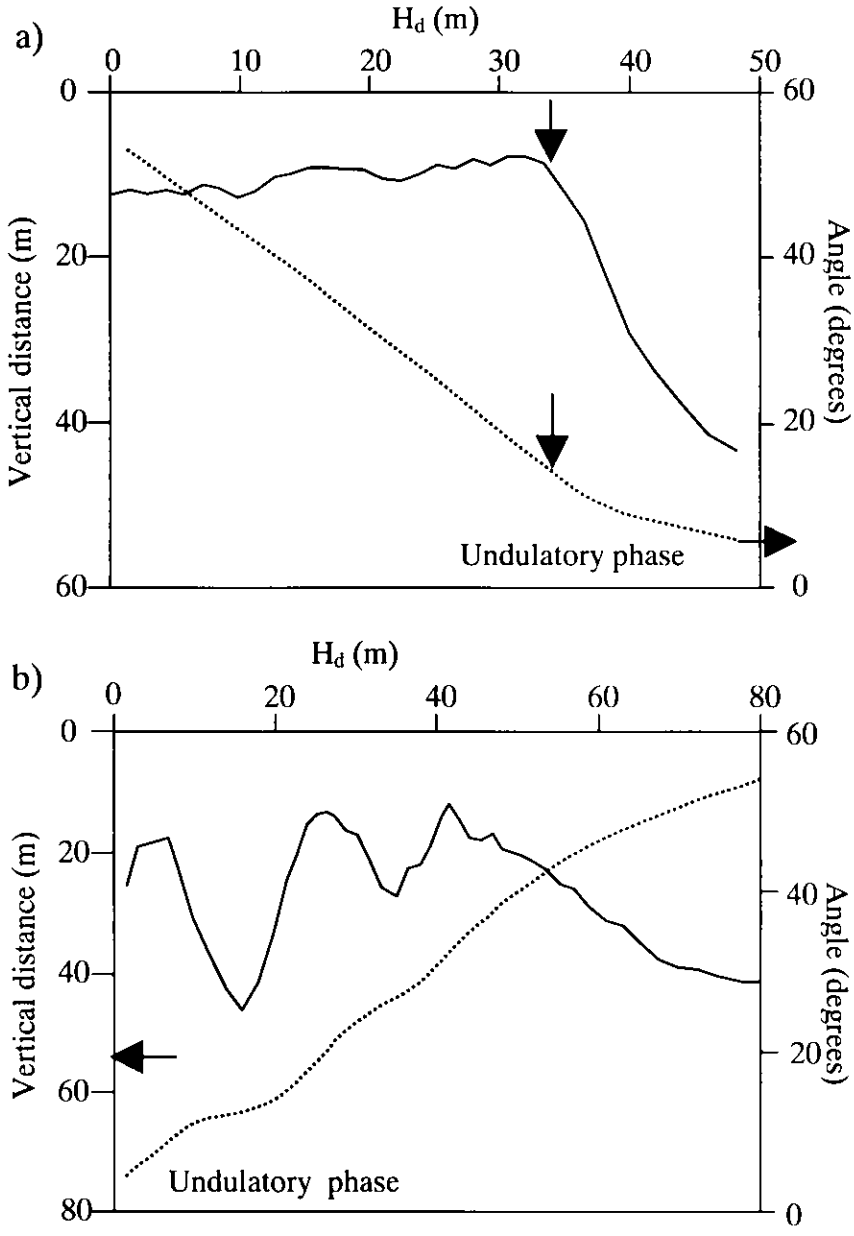


Fig. IV- 7 : a) Descent and b) ascent angles (solid lines) and profile of the distance traveled vertically and horizontally (dotted lines) during a feeding dive of free-ranging Adélie Penguins. Arrows indicate the abrupt change in the angle during the descent phase. Horizontal distance H_d was calculated as :

$H_d = Sp. Cos(\Theta)$,

where Sp is the swim speed and Θ the angle (in radians).

Table IV – 5. Descent angles of free-ranging Adélie Penguins calculated for dives with a maximum depth > 20 m.

Dive types	Angle constant (changes within 10°)	Steady increase of angle (< 30°)	Irregular pattern
Feeding	69% (N = 208)	26% (N = 77)	5% (N = 15)
Non feeding	57.5% (N = 81)	17% (N = 24)	25.5% (N = 36)
Total	65.5% (N = 289)	23% (N = 101)	11.5% (N = 51)

Table IV – 6. Percentage of dives with an abrupt drop in the descent angle of dives (for dives > 20m).

Dive type	Abrupt drop in the angle	No abrupt drop	Irregular pattern
Feeding	68% (N = 204)	30% (N = 90)	2% (N = 6)
Non feeding	69.5% (N = 98)	10% (N = 14)	20.5% (N = 29)
Total	68.5% (N = 302)	23.5% (N = 104)	8% (N = 35)

Table IV – 7. Pattern of the ascending angles of free-ranging Adélie Penguins calculated for dives with a maximum depth > 20 m.

Dive types	Oscillating pattern	Constant or increasing	Irregular pattern
Feeding	32% (N = 78)	40% (N = 98)	28% (N = 71)
Non feeding	43% (N = 56)	41% (N = 53)	16% (N = 21)
Total	36% (N = 134)	40% (N = 151)	24% (N = 92)

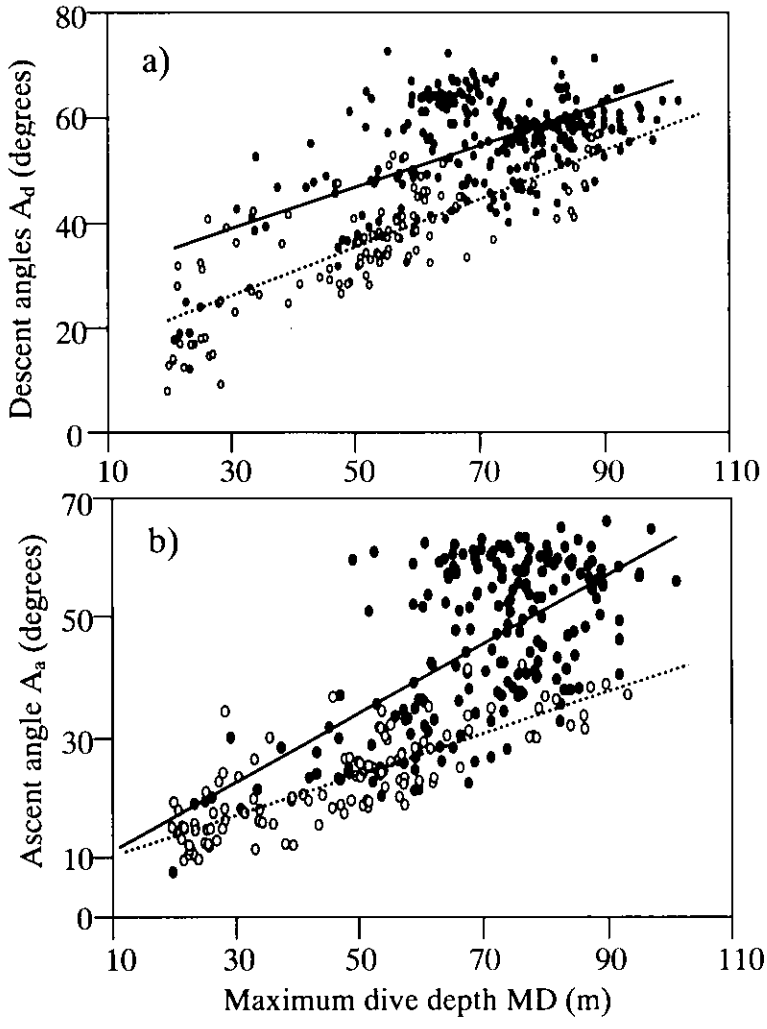


Fig. IV – 8 : a) Descent angles A_d according to the maximum depth of dive of free-ranging Adélie Penguins when the preceding dive was a feeding (black) or a non-feeding (white circle) dive.

Feeding dives:
$A_d = 0.40 \times MD + 27.9$
$R^2 = 0.36$ ($P<0.0001$)
Non-feeding dives:
$A_d = 0.46 \times MD + 13.2$
$R^2 = 0.61$ ($P<0.0001$)

Fig. IV – 8 : b) Ascent angles A_a according to the maximum depth of feeding (black) and non-feeding (white circles) dives

Feeding dives:
$A_a = 0.60 \times MD + 4.5$
$R^2 = 0.38$ ($P<0.0001$)
Non-feeding dives:
$A_a = 0.30 \times MD + 6.6$
$R^2 = 0.66$ ($P<0.0001$)

Best fit regressions are indicated by solid and dotted lines for feeding and non-feeding dives, respectively.

DISCUSSION:

♦Surface drops and prey ingestion rate: Substantial drops in the oesophageal temperature occurring in non-diving animals may represent snow ingestion while the birds rested on land or ice outside of the colony (Aoyanagi & Tamiya 1983, Wilson *et al.* 1989a). The small drops between dives may correspond to the cooling of the sensor during breathing events, especially since such events were observed within the two seconds after the birds emerged following deep dives. However, these small surface events were not always recorded and their observation may depend on several factors such as the air temperature. Field metabolic rate studies using double-labelled water indicate that penguins do not ingest a significant amount of seawater (Culik & Wilson 1992). Besides the high energetic cost of warming ingested water due to the high water specific heat capacity (Wilson & Culik 1991), it is unlikely that seabirds would ingest much water while at sea since they can derive the water from their prey (Gabrielsen & Melhum 1987, Birt-Friesen *et al.* 1989). Therefore, it is further assumed that temperature drops recorded during diving phases corresponded to prey ingestion. Small drops during the ascent might correspond to the capture of prey that, although not at the preferred depth, were easily accessible (no long pursuit phase required). The rare temperature drops occurring during descent might also correspond to the occasional ingestion of such small isolated prey.

Prey were either swallowed directly during, or few seconds after, acceleration. This pattern of capture and swallowing of prey has been observed on several occasions in free-ranging (Zusi 1975) or captive Adélie Penguins (chapter IV – 1), the delay between capture and swallowing corresponding to the prey manipulation. Most of the oesophageal temperature drops were recorded when the bird was swimming in an upward direction. This suggests the use of the backlighting effect to detect and capture prey as has been observed in Weddell Seals (Davis *et al.* 1999) and King Penguins (chapter III – 2).

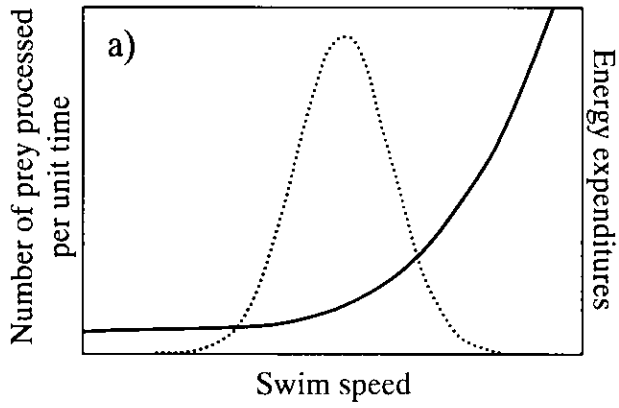
♦Swim speed during feeding and non-feeding dive: Consideration of the speed at which the penguins swam in relation to activity revealed some interesting departures from travel at minimum cost of transport COT_{min} (for definition see Schmidt-Nielsen 1972). During the descent and ascent phases of the dive cycle, birds swam at *ca.* $2.1 m.s^{-1}$, a value that accords closely with the COT_{min} of $2.2 m.s^{-1}$ calculated on captive Adélie Penguins in a swim canal (Culik & Wilson 1991a and b, Culik *et al.* 1991, 1994a). Under normal circumstances this should be the optimum speed to travel between the water surface and the preferred foraging depth if birds are to minimise energy expenditure per unit distance travelled but, by the same token, this speed also effectively extends the time that the birds may expend at their preferred foraging depth because less energy (and thus less oxygen reserves) would be wasted in the commuting process.

In dives where no prey were ingested the preferred swim speed during the bottom phase of the dive cycle also accorded closely with that corresponding to the COT_{min}. Again, this allows the birds to travel the maximum distance underwater at minimum cost, a feature which enhances the chances of detecting prey because the probability that prey will move into the bird's field of vision will be proportional to the distance swum underwater (Wilson *et al.* 1996).

However, once a prey patch was located, mean penguin swim speed during the undulatory phase decreased substantially. The periods of low speed at the undulatory phase presumably corresponded to prey manipulation by birds and/or search for the next target while acceleration phases probably resulted from the active pursuit of prey. This indicates that the speed at which Adélie Penguins effectively process encountered prey is substantially lower than the speed at the COT_{min}. Prey processing speed in penguins would be analogous to handling time (as defined in Krebs 1978, Piersma *et al.* 1988) but be modified by particular time constraints, over and above those discussed by Krebs (1978), because a reduction in swim speed also leads to a reduction in energy expenditure (Culik *et al.* 1994a) leading to potentially increased time underwater in the prey patch concerned. The effect of this can be simply

modelled by assuming that penguins exploiting a prey patch underwater have a particular swim speed at which they can fastest process prey items and that the form that this takes is approximately Gaussian (Fig. IV – 9a).

One underlying assumption, in this, is that there is no selectivity for particular prey sizes associated with particular speeds. Since the energy expended during swimming is approximately a cubed function of swim speed (Culik *et al.* 1994a, Fig. IV – 9a), the net energy gain by birds per unit time as a function of swim speed can be calculated as energy gained minus energy expended per unit time. This function has relatively high values more closely distributed about the peak than does the Gaussian curve and is skewed to the left (Fig. IV – 9b) although the optimum speed for maximising prey intake still corresponds to that of the Gaussian curve.



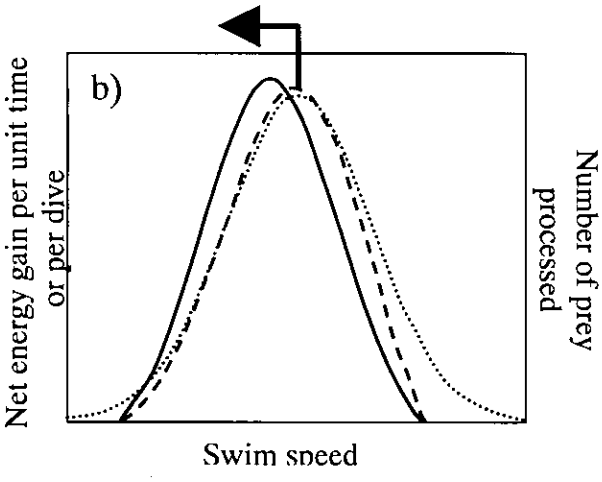


Fig. IV – 9 : Theoretical functions : a) number of prey processed / unit time (dotted line) and energetic cost of swimming (continuous line, from Culik & Wilson 1994) as a function of swim speed ; b) net energy gain / unit time (dashed line) and per dive (continuous line) by penguins exploiting a prey patch as a function of swim speed.

Net energy gain = energy gain (dotted line in a) – energy expenditures (continuous line in a).

However, the rapid increase in energy expenditure with increasing speed means that birds exhaust oxygen reserves disproportionately faster at higher speeds, leaving them less time to feed, so that the speed at which the total amount of energy gained per dive is maximised occurs at a lower speed than the optimum for maximising energy intake per unit time (Fig. IV – 9b).

Speeds at which penguins travel during prey capture must, however, be put in perspective with prey escape speeds. In species feeding on small prey, such as the Pygoscelid and many of the Eudyptid penguins (Croxall & Lishman 1987), escape speeds of the prey are essentially negligible compared to those of the penguins. Euphausids, for example, swim at average speeds ranging 0.13 – 0.15m.s^{-1} (Kanda *et al.* 1982) up to 0.4m.s^{-1} (Hamner 1984). Occasionally, euphausids can exhibit "tail-flip" escape behaviour where speeds can reach up to 1m.s^{-1} (O'Brien 1987) at a random heading or perhaps contralateral, as has been observed in Brown shrimp *Crangon crangon* (Arnott *et al.* 1999). This difference between prey and predator speeds results from massive differences in body size which tend to determine the limit of swim speed (Wardle 1975). Where prey become larger, birds may have to adjust capture speeds to be higher to minimise energetically costly extended chases.

♦**Depth utilisation:** The high concentration of capture events in deep dives illustrates the patchy distribution of euphausids, which aggregate in dense swarms (Nicol & de la Mare 1993).

A large number of studies on Krill distribution have focused on the horizontal component of the distribution (*e.g.* Brinton 1991, Ichii *et al.* 1998, Miller 1986). Investigations regarding to the Euphausid's vertical distribution showed that different stages of euphausids can be found at various depths in the water column (Hempel 1985, Hempel *et al.* 1979, Hosie 1994, Marr 1962) with, in some instances, a vertical diel migration that brings the euphausids close to the surface at night (Everson 1984, Everson & Murphy 1987, Kalinowski 1978). Hydroacoustic surveys off Adélie land region in 1996 showed that nearly all of the Krill was concentrated in the top 100m depth zone with about 80% being < 75m. (Pauly *et al.* 2000). This is similar to the range of depths observed by Watkins *et al.* in South Georgia (1985) or Brinton near the South Shetlands Islands (1991) and is in accordance with the observation in the present study of the oesophageal temperature drops being associated preferentially with dives > 40m, although there was no marked diel vertical migration of the maximum depth reached by the birds in the present thesis that would suggest that they followed the vertical migration of their prey. Hill *et al.* (1996) and Reid *et al.* (1996) compared the size of Krill caught by nets with that of Krill caught by free-ranging Macaroni Penguins *Eudyptes chrysolophus* and observed that the birds selected prey larger than that caught by net, although this may be biased by other factors such as size-differential net avoidance (Hovekamp 1989). Since gravid females, highly nutritional among Euphausids (Clarke 1984), may be the main target of Adélie Penguins (Endo *et al.* 2000), it is likely that Adélie Penguins in the present study were also selectively exploiting a category of size among the Euphausids that is confined in the depth zone > 40m. Due to diving constraints, the diving behaviour of bird in these depths will be dictated by the extent to which the penguins have to commute between the surface and the exploited depths, this itself being determined by the length of time that the birds can remain underwater. Since Adélie Penguins essentially only exploit prey during the bottom phase of W-shaped dives, the profitability of the dive will be determined by the length of time that the birds can remain in this phase compared to that consecrated to commuting between the surface and the point of maximum depth (Kooyman *et al.* 1992). The optimum strategy will thus be determined by the profitability of the various depths, the maximum dive duration and the rate at which birds move through the water column (Wilson *et al.* 1996). In having relatively short dive duration (Culik *et al.* 1994a), Adélie Penguins clearly have to spend a high proportion of their total time moving through shallower depths and thus accumulate much time at these depths, appearing, overall to be foraging non-optimally.

♦**Angles of diving during commuting process:** During the descent phase of feeding dives, the angle was steeper if the bird encountered prey in the previous dive. A typical feeding dive may be summarized as follows: birds descend directly to the depth where prey are to be found at a steep angle until an abrupt change in the angle that corresponds either to pursuit of the first prey encountered or a rapid deceleration in order to reduce speed in the prey patch (see above discussion on reduced speed during the undulatory phase). An abrupt decrease in the angle would modify the orientation of the vector of the positive lift force acting against negative buoyancy at these depths and thus contribute to deceleration. In this case, the birds may pass through the depth zone where the patch is located and then invert their angle quickly to approach the patch from under. This pattern of hunting is similar to that observed in other species of marine seabirds and mammals using vision to catch prey in a relatively dark environment (Davis *et al.* 1999, chapter III – 2).

Dive angle is a key parameter in determining the depths at which penguins invest foraging effort. To date, all penguins investigated appear to increase dive and return-to-the-surface angles with increasing maximum dive depth (see Wilson 1995 for review) which means that, since swim speed remains virtually unchanged, as maximum dive depth increases so birds spend proportionately less time per unit depth. This strategy differs markedly from that of benthic-feeding birds where descent and ascent angles are always very steep, a strategy which allows the birds to move as quickly as possible between the surface and the foraging depth

(Wilson & Wilson 1988, Grémillet *et al.* 1999). This latter strategy is a consequence of minimizing time spent in absolutely unprofitable zones. Penguin prey, however, is typically pelagic, and may occur at any depth. Thus, steep dive angles down to specific preferred depths tend to make the birds pass very quickly through the intermediate water layers and thus reduce the probability of prey encounter in these zones. It is to be expected, however, that the descent and ascent angles that penguins use may vary according to prey distribution in i) taking the birds to the depths where prey encounter is most considered likely and ii) ensuring, despite this, that an appropriate amount of time is dedicated to searching the upper water layers in case prey may occur there. This overall strategy should be tempered according to perceived circumstances. In particular, it is to be expected that where birds have located aggregating prey at depth it might be advantageous for birds to descend quickly and repeatedly to that depth during subsequent dives because of the greater likelihood that prey will be re-located. Although changes in descent and ascent angles in relation to foraging success have been rarely documented (but see Wilson & Wilson 1995), the present data show clearly this to be the case in Adélie Penguins.

During the ascent, the angle of the swim path was less well defined than in descending birds. This may be because the birds might engage in minor pursuit movements to catch prey encountered following the principle of 'lost-opportunities' (Stephen & Krebs 1986). This principle states that even less profitable prey, *e.g.* an isolated prey, is worth catching if it occurs during the course of the commuting process and does not require an extra energy expenditure. During the ascent the probability of perceiving a prey silouheted against the brighter background (Clarke & Denton 1962) is increased. It is also worth noting that the latter part of the ascent phase may be controlled by biomechanical forces since penguins use buoyancy to ascent passively (Sato *et al.* unpublished data).

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

V – SYNTHESIS

V – 1. Technological achievements:

The new technology that is now available has opened up a series of new tracks for biological investigations over the past decades and may emerge as a link between physiological, molecular or genetical models and their application in the wild. By deploying advanced technological devices on free-ranging animals in order to measure their behaviour, this thesis illustrates the potential offered by this new area of science. During the course of this work, the following discoveries and new steps were reached: