

Reconstruction of the feeding activity of marine top-predators foraging at sea

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Abstract: Top-predators in the Southern Ocean consume large quantities of marine resources and therefore, interact significantly with human fisheries. Thus, collection of information on seabird and marine mammal feeding activity is of prime importance but their behaviour at sea cannot be assessed directly. Consequently, over the last three decades researchers have attached micro-data recorders to marine predators. These units monitor various parameters as a function of time. The measurement of the feeding activity of seabirds and marine mammals while at sea has evolved from indirect to direct methods, the latest consisting of monitoring the internal temperature of these predators. Recently, substantial progresses were made when temperature was recorded in the upper part of the oesophagus of seabirds in tandem with the recording of other parameters. After a brief review of the various methods to determine the feeding activity of top-predators at sea, this article will discuss the results and potential of internal temperature recorders –with a special emphasis on oesophageal temperature recorders – for determining the foraging behaviour of seabirds and marine mammals.

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Investigating the feeding activity of marine animals: a key parameter to the management of marine resources.

Among the abundant fauna of top-predators exploiting the Southern Ocean, seabirds are the largest by number (CROXALL, 1984 ; CROXALL *et al.*, 1984), with penguins representing up to 90% of the bird biomass in the Antarctic regions (MOUGIN and PRÉVOST, 1980). In addition, both marine mammals and seabirds consume key species in the trophic chains of this ecosystem, which makes them potential competitors with human fisheries (FURNESS, 1990 ; FURNESS and COOPER, 1982). Over recent years, conflicts between fisheries and ecologists have sometimes resulted in controversial measures. Although “culls”, consisting of the removal of predators in order to optimize the development of prey stocks for fisheries, have been apparently successful in some instances, the underlying effects of organism removal is still incompletely controlled due to the complexity of trophic chains (see YODZIS, 2001). Thus, an understanding of the feeding ecology and the food requirements of marine top-predators is of prime importance. Using these predators as bio-indicators of marine resources (*e.g.* CROXALL *et al.*, 1988 ; FURNESS and NETTLESHIP, 1990) could help improve conservation and management of both the seabird community (HUNT, 1991) and the stocks of the marine resources (CCAMLR, 1986 ; CROXALL *et al.*, 1988).

In this respect, studies on the feeding behaviour of seabirds and marine mammals at sea have flourished despite the difficulty of directly observing the animal foraging in its natural environment: Although seabirds and marine mammals need to replenish regularly their oxygen reserves at the water surface, a large component, if not all (in the case of penguins or seals), of their foraging activity takes place underwater. In the early eighties, progress in the micro-chip technology branch was applied to marine biology and opened a new area of science where the activity of animals in an inaccessible environment could be monitored by

devices collecting time-series data (KOOYMAN, and DAVIS, 1982 ; Le BOEUF *et al.*, 1988 ; NAITO *et al.*, 1990). These devices, termed loggers, are attached to animals departing for a foraging trip and are recovered when the animals return to land to feed their offspring. Thanks to this technology, several insights in the “hidden” life of marine top-predators have been highlighted (*e.g.* WILSON, 1992 ; Le MAHO, 1994). Earlier pioneer works demonstrated the unexpected diving capacities of seabirds and marine mammals (KOOYMAN, 1989) and researchers have become aware of the large volume of water column that these animals can exploit.

However, despite an intensive use of loggers over the past three decades, the timing of prey intake, the amount of food ingested and the prey pursuit and capture by marine top-predators remain poorly understood. These parameters are extremely difficult to monitor and are in most of the case, estimated by indirect means. In this article, we wish to review briefly the different methods for determining the feeding activity of marine top-predators, with special emphasis on recent studies that involve recording the internal temperature in the upper part of the digestive system of seabirds (ANCEL *et al.*, 1997 ; ROPERT-COUDERT *et al.*, 2000a ; 2001a). In this regard, the accuracy of oesophageal temperature logger for detecting prey ingestion (especially in penguins), as well as estimating the amount of food ingested and the prey species ingested, will be discussed below. Finally, the potential of internal temperature recording for ecological studies concerning foraging strategies resulting in optimized prey detection and capture will be highlighted.

Indirect information about the feeding behaviour

Because visual observations of marine animals feeding close to the shore (*e.g.* WILSON, 1996) or from boats (KOOYMAN, 1975 ; KOOYMAN *et al.*, 1971) are few and the amount of information collected is necessarily restricted, the feeding activity of animals

have often been discussed based on indirect information. Two examples of investigations of the feeding behaviour through indirect evidence are discussed below:

1 – Where do top-predators feed? This question can be envisaged from two point of views, the horizontal (latitudinal and longitudinal) and vertical (depth zone in the water column) point of view. From an horizontal point of view, the preferred foraging grounds of animals at sea have been extensively investigated using remote-sensing methods such as satellite telemetry (WEIMERSKIRCH and WILSON, 1992 ; BOST *et al.*, 1997 ; KERRY *et al.*, 1995) or using loggers attached on the animals that record, for instance, the heading and swim speed in order to reconstruct the route taken by animals (see WILSON and WILSON, 1988). These studies showed that top-predators can travel astonishing distances at sea, flying up to 15,000km (as is the case for the Wandering albatross, *Diomedea exulans*, JOUVENTIN and WEIMERSKIRCH, 1990) or swimming regularly 400-600km from their colony (in the case of King penguins, *Aptenodytes patagonicus*, BOST *et al.*, 1997). After adopting a straight course to bring them to a foraging site, top-predators generally remain in specific areas where they concentrate their diving activity, revealing in this the location of their favorite food resources (BOST *et al.*, 1997 ; BORNEMANN *et al.*, 2000 ; PÜTZ *et al.*, 2000). In the Southern Ocean, these preferred feeding zones have been often shown to coincide with marine frontal structures where upwelling movements of water result in enhanced primary, and consequently, secondary and tertiary production (TYNAN, 1998). Substantial information on the status of a given ecosystem can be obtained when the preferred foraging grounds of top-predators can be directly correlated with prey availability (WEIMERSKIRCH *et al.*, 1994 ; BOYD *et al.*, 1994 ; KITAYSKY *et al.*, 2000 ; WIENECKE *et al.*, 2000 ; RODHOUSE *et al.*, 2000).

Among marine top-predators, marine mammals and a large proportion of seabirds prospect an important proportion of the water column, down to 500 m (in the case of emperor

penguin, *Aptenodytes forsterii*, KOOYMAN and KOOYMAN, 1995) or 600 m (in the case of Northern Elephant seals, *Mirounga augustirostris*, Le BOEUF *et al.*, 1988). Thus, studies about preferred foraging grounds of such deep diving species, should take into account their vertical distribution. Therefore, among the various parameters recorded by loggers over the past decades, diving depth recordings have revealed the depth where prey are caught (WILSON, 1989 ; SEDDON and VAN HEEZIK, 1990 ; WANLESS *et al.*, 1993). Moreover, analysis of the diving depth of marine animals gives indirect indications on the feeding behaviour, for example, using abrupt changes in depth – sometimes termed undulations, wiggles or zigzags – observed at the bottom part of the depth profile of diving seabirds (e.g. WILSON, 1995), as indicators of prey pursuit. On a finer scale, drastic accelerations recorded during swimming by King penguins are believed to represent active pursuit of prey and, as such, an indicator of feeding activity (Fig. 1, see ROPERT-COUDERT *et al.*, 2000b for details). However, it is necessary to confirm that a pursued prey is actually ingested. Moreover, although the capture speed displayed by predators is related to prey escape speed (WILSON and ROPERT-COUDERT, submitted), information on the species and amount captured are not provided by these types of data.

2 – What do top-predators consume? In parallel with the location of animals at sea, the assessment of the diet composition of marine seabirds and mammals has evolved from *post-mortem* analysis of the stomach contents, feces and pellet identification (See review in FURNESS and MONAGHAN, 1987 ; see also JACKSON and DUFFY, 1984), to the recovery of the stomach contents by non-mortal pumping and flushing methods (EMISON, 1968 ; DAHLGREN, 1982 ; WILSON, 1984). The evolution of the diet within individuals (e.g. KATO *et al.*, 1996) and/or during the breeding season (ADAMS and KLAGES, 1987 ; RIDOUX and OFFREDO, 1989) has helped highlight depletion in certain marine stocks (CROXALL *et al.*, 1999 ; IRVINE *et al.*, 2000) or environmental fluctuations (AINLEY *et al.*,

1998). However, all of these methods are subject to bias (see BEDARD, 1976 ; CROXALL and PRINCE, 1980 ; CARSS *et al.*, 1995), especially since a portion of the food ingested is digested while animals are at sea (WILSON *et al.*, 1989). Differential digestion, examined in the Jackass penguin, *Spheniscus demersus* (WILSON *et al.*, 1985 ; WILSON *et al.*, 1989) may lead to an underestimation of the amount of food ingested or the preferred prey type. In seals, the accumulation of prey remains add to the difficulty of an accurate estimate of the food consumption (see GALES and RENOUF, 1993).

The necessity of relating the location of the animals at sea to the type and amount of prey captured, as well as the incomplete information brought by collection of stomach contents, has meant that the direct measurement of the food intake of free-ranging animals is a particular challenge to researchers.

Direct recording of the feeding activity: internal temperature loggers.

Since most of the top-predators in the Southern Ocean are endotherms – *i.e.* maintain a high internal temperature independent of ambient temperature – the recent monitoring of the internal temperature of predators has revealed much about feeding habits (see BENGSTON, 1993 ; *e.g.* GALES and RENOUF, 1993 ; HEDD *et al.*, 1996 ; WILSON *et al.*, 1992), because these endotherms ingest mainly ectothermic prey (*i.e.* body temperature \square water temperature) which cause precipitous drops in the predator stomach temperature (WILSON and CULIK, 1991 ; WILSON *et al.*, 1992). In addition to feeding behaviour studies, the physiological adaptations to diving of marine mammals and birds has been investigated in a number of studies based on the principle of internal temperature recordings (HANDRICH *et al.*, 1997 ; WILSON and CULIK, 1991).

Temperature has been primarily monitored in the stomach of a variety of marine mammals and birds (KATO *et al.*, 1996 ; PÜTZ, 1994 ; PÜTZ and BOST, 1994 ;

WEIMERSKIRCH and WILSON, 1992 ; WILSON and CULIK, 1991 ; WILSON *et al.*, 1992 ; 1998). In such studies, animals were induced to swallow stomach temperature loggers, which are generally cylindrical devices built into an inert metal housing to resist digestive acids. One or two thermistors at the extremities of the device record the temperature. However, when placed in the stomach, several factors tended to decrease the efficiency of the loggers in detecting prey ingestion over time since the stomach fills and prey items may cover the sensor (see review in GRÉMILLET and PLÖS, 1994 ; WILSON *et al.*, 1995). In addition, the likelihood of detecting ingested prey depends on the position of the logger inside of the stomach (GRÉMILLET and PLÖS, 1994 ; WILSON *et al.*, 1995b) because body temperatures of diving seabirds may also fluctuate independent of feeding activity (*e.g.* BEVAN *et al.*, 1997 ; CULIK *et al.*, 1996 ; HANDRICH *et al.*, 1997 ; WILSON and GRÉMILLET, 1996). For example, if the sensor is in direct contact with the stomach wall, the temperature recorded can remain constant, or vary little, even when prey are ingested (ROPERT-COUDERT *et al.*, 2000a).

Recently, the monitoring of seabirds oesophageal temperature showed promising results for the detection of prey intake (ANCEL *et al.*, 1997 ; CHARRASSIN *et al.*, 2001 ; ROPERT-COUDERT *et al.*, 2000a ; 2001a). These loggers are similar to stomach temperature recorders but the thermistors are located in the anterior part of the oesophagus, at the end of a soft plastic cable of various sizes that emerge from the cylindrical body of the logger being placed in the stomach (Fig. 2). Calibration experiments showed that the higher a sensor was placed in the digestive system, the better the detection of prey ingestion (CHARRASSIN *et al.*, 2001) since prey items are not warmed up and do not cover the sensor. In addition, the time lag between ingestion and the detection of the drop is also considered minimal (ROPERT-COUDERT *et al.*, 2000a). In a study by CHARRASSIN *et al.* (2001) during deployment of oesophageal loggers on free-ranging King penguins, the sensor was

kept in position by suturing it to the wall of the oesophagus by surgery that necessitate animal anesthesie. This requires a substantial investment in term of logistics as well as time since a delay is necessary between the operation and the moment the animal can depart to resume normal foraging activity at sea. Therefore, in order to reduce the stress implicit in surgical procedures, a non-invasive method was initially tested on captive Brandts cormorants, *Phalacrocorax penicillatus* Brandt, (ANCEL *et al.*, 1997) and successfully applied to free-ranging Adélie penguins (ROPERT-COUDERT *et al.*, 2001a). Here, the body of the logger was placed in the stomach while the sensor was held suspended in the oesophagus just under the opening of the mouth by a filament externally attached on the plumage of the birds (see Fig. 2). The whole system can be placed on birds in less than 20 minutes and no delay is necessary between fitting and birds release. The main problem encountered with such systems is the substantial rejection rate of the logger in the stomach (ROPERT-COUDERT *et al.*, 2001a). However, this can be solved by incorporating a retaining system to the logger such as the anchor system described by WILSON *et al.* (1998). The reliability of the measurement and the ease of deployment and retrieval of oesophageal temperature devices, as experienced on seabirds, makes it a convenient tool for field studies. However, although the principle is theoretically applicable to any endotherms, oesophageal temperature recording method remains to be tested on pinnipeds. For such animal, surgery and anesthesie are still a necessity for deploying oesophageal temperature loggers.

Progress made due to internal, especially oesophageal, temperature loggers:

Internal temperature loggers have revealed much about the rate of prey ingestion at different scales. Following diel rhythm in vertical migration of prey (WILSON *et al.*, 1993), King Penguins ingest only 17% of the total prey catching during a foraging trip at night (BOST *et al.*, 1997). In being able to ascertain that prey are caught primarily during the day

confirmed, in many cases, that seabirds are essentially visual hunters, e.g. the Northern Gannet *Sula bassana* (GARTHE *et al.*, 1999). Finally, the identification of the rate of prey ingestion during a specific dive showed that, for instance, both King and Adélie, *Pygoscelis adeliae*, penguins optimize the hunting component of dives by catching a non-negligible percentage of prey during the ascent phase of dives (ROPERT-COUDERT *et al.*, 2000b ; 2001a), previously defined as a commuting phase only (see WILSON, 1995 for review).

By using internal temperature logger, it is possible to determine the exact number of prey ingested during a foraging trip and we are now reaching a stage where it is possible to determine the percentage of prey that is digested at sea. This could help elucidate how birds balance their own body maintenance with the provisioning to their offspring. However, since such investigations depend on the capacity of recording clear temperature drops, oesophageal temperature logger appears to be particularly suitable (Fig. 3, ROPERT-COUDERT *et al.*, 2000a). Internal temperature loggers offer another substantial advantage over other loggers in enabling the mass of food ingested to be more precisely estimated (WILSON *et al.*, 1992). It has been proposed that the energy invested to heat the prey items ingested in the stomach is directly related to the mass of the prey ingested (WILSON *et al.*, 1995). Thus, the mass of prey can be estimated by calculating the integral under the curve of the temperature drop (Fig. 4a; see WILSON *et al.*, 1995 for details), although one should bear in mind that problems occur when several prey are ingested in rapid succession (Fig. 4b ; GRÉMILLET and PLÖS, 1994). However, probably due to this confusion effect and in relation with the clearer signal obtained when the sensor is placed closer to the mouth, the magnitude of temperature drop monitored in the oesophagus, has also been shown to be a reliable estimator of the mass of prey swallowed (ROPERT-COUDERT *et al.*, 2000a). Such relationships not only provide information about the mass of prey ingested but can also be used to determine the species ingested. Seabirds, especially penguins, are mainly specialists (CROXALL and LISHMAN,

1987) consuming a limited number of prey species (see review in WILLIAMS, 1995). Within a particular prey species, birds seem even to select a specific category of the prey population, this being well illustrated by Adélie penguins which tend to capture, overall, a greater proportion of gravid females of Antarctic krill *Euphausia superba* (ENDO *et al.*, 2000). The fact that there is often a difference in mass between prey types means that the mass of prey ingested may help identify the prey species captured. By comparing the distribution of diverse prey caught in the three dimensions of a marine ecosystem it may be possible to map overall distribution using marine top-predators. Moreover, the capacity of top-predators to shift from one main target species to secondary ones can be analysed accurately.

In addition, knowledge of the exact amount of prey swallowed provides us with data for calculation of the energy gained by animals at sea. Energetic content of prey can be determined in calorimetric chambers and the corresponding value can be used to quantify the energy gained at sea. Furthermore, using internal temperature loggers, researchers can calculate indices of foraging efficiency, such as the catch per unit effort (abbreviated as CPUE) for marine top-predators (GRÉMILLET, 1997 ; GARTHE *et al.*, 1999), similar to indices used in fisheries. Such indices consider the percentage of prey caught at a particular depth in relation to the time spent by the predator at that depth and thus, relies on an accurate determination of all prey ingested. An example of a CPUE calculated on a free ranging Adélie penguin is shown in Fig. 5. In this figure the depth zones of maximum hunting success are easily visualized. Moreover, the amount of energy gained per unit of time at sea can be determined and examined with regards to the amount of energy expended by the birds and the amount of energy required by the offspring. This is relevant in the context of analysis of energy balances and of the breeding success of animals that are exploiting a fluctuating environment.

The previous paragraphs showed the potential in internal temperature loggers for the detection of the timing of prey intake and amount of food ingested. Such information can be used to estimate energy gained per individual and/or to quantify marine resources. However, determination of the exact moment a prey is swallowed also allows researchers to unravel the foraging strategies that lead to successful prey capture. Indeed, thanks to the timing of capture, it is possible to distinguish successful from unsuccessful dives and to compare their characteristics. To perform this type of analysis, one should be able to record multiple data per individual, including the internal temperature as direct indication of feeding. Although the technologies permitting large amount of data to be stored in loggers are relatively recent, some studies have clearly demonstrated the benefits derived from this integrative approach. Thus, the simultaneous recording of depth utilization, swim speed and oesophageal temperature of free-ranging Adélie penguins has demonstrated how these birds change their dive angle and swim speed according to prey encounter (ROPERT-COUDERT *et al.*, 2001a ; 2001b). Apart from confirming or refuting previous hypotheses about the marine top-predators foraging strategies based on simple observation of depth or speed profiles (cf. beginning of paragraph 3), the use of accurate, direct recording of the feeding activity of marine animals in tandem with the monitoring of other parameters, has meant that a whole new area of science is opened to investigation.

5 – Conclusions: Perspectives

Regarding the results presented in this review, direct measurement of the feeding activity is not only a parameter in itself, it is also a basis from which various parameters and information derive, offering several levels of analysis. To be complete, one should mention that further progress in the described methodology is still needed. Internal temperature drops can have various origins. For example, it remains difficult in some instances to differentiate between

the ingestion of prey and the ingestion of water or ice: this has been shown to occur in seals (GALES and RENOUF, 1993) as well as in Adélie penguins (ROPERT-COUDERT *et al.*, 2001a). Multiple data recording could thus be critical in helping address this problem. In addition, the effect of logger attachment has been carefully investigated and loggers have been constantly improved in order to reduce the stress incurred by the animals. However, development of less invasive methods is still regarded as important. In addition, ameliorations should be added to present methods so that their application can extend to various species of marine predators with different feeding and foraging habits.

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Figures Legends:

Fig. 1. Dive depth and swim speed recorded as a function of time in a free-ranging King penguin, *Aptenodytes patagonicus*. Arrows indicate undulations in the bottom part of the depth profile (top graph) and accelerations observed in the swim speed profiles (bottom graph) that are thought to represent prey pursuit.

Fig. 2. Presentation and attachment of oesophageal temperature logger (UME-TT generation, Little Leonardo, Tokyo, Japan) illustrated on an Adélie penguin, *Pygoscelis adeliae*. Technicals information about the logger can be found in ROPERT-COUDERT *et al.*, 2000b (see text).

Fig. 3. Internal temperature recordings in the oesophagus and the stomach of captive Adélie penguins, *Pygoscelis adeliae*, with several temperature drops corresponding to the ingestion of Antarctic krills, *Euphausia superba*. In a) the thermistor in the stomach is in direct contact with the stomach wall. In b) both the oesophageal and the stomach thermistors detect prey ingestion but the detection rate in the stomach decreases as the stomach filled. Note in b) the clarity of the temperature drops recorded in the oesophagus compared to that in the stomach.

Fig. 4. Schematic diagram showing the problems raised by the calculation of the mass of prey ingested using the integral method when multiple prey are ingested. In a) a single prey is ingested and the calculated integral (shaded area) is a good estimator of the mass of prey ingested. In b) and c) a second prey is swallowed before the asymptote reach the original temperature value and the utilization of the area might underestimate the actual mass of prey ingested. Graphs modified from WILSON *et al.*, 1995 with permission of the author.

Fig. 5. Catch per unit effort (CPUE, see text) in a free-ranging Adélie penguin, *Pygoscelis adeliae*, equipped with oesophageal temperature logger in tandem with a depth logger. X, Y and Z axis are the maximum diving depth (m), the time spent per depth unit (s) and the CPUE value, respectively.

Fig. 1. Roper-Couderc et al.

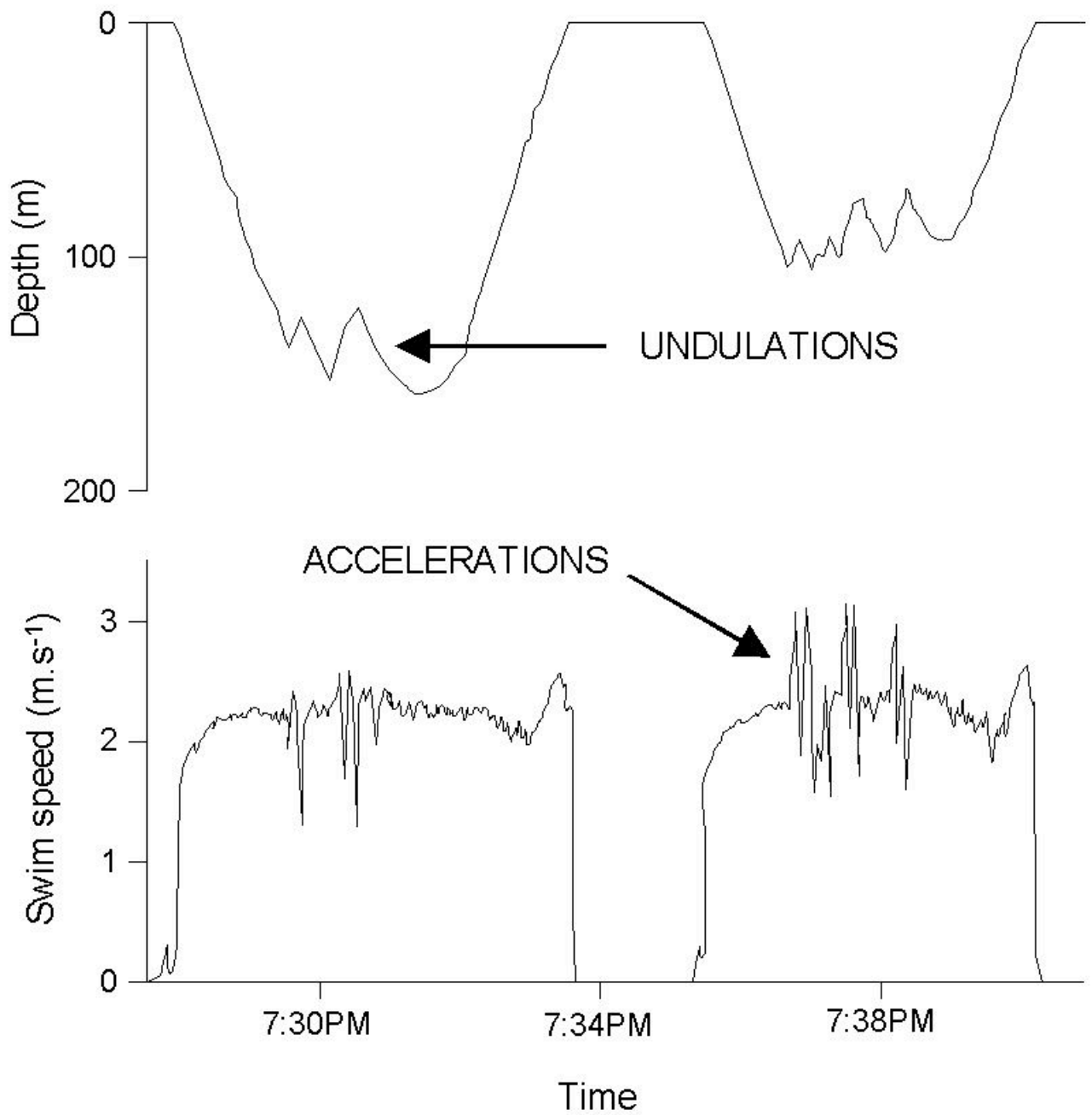
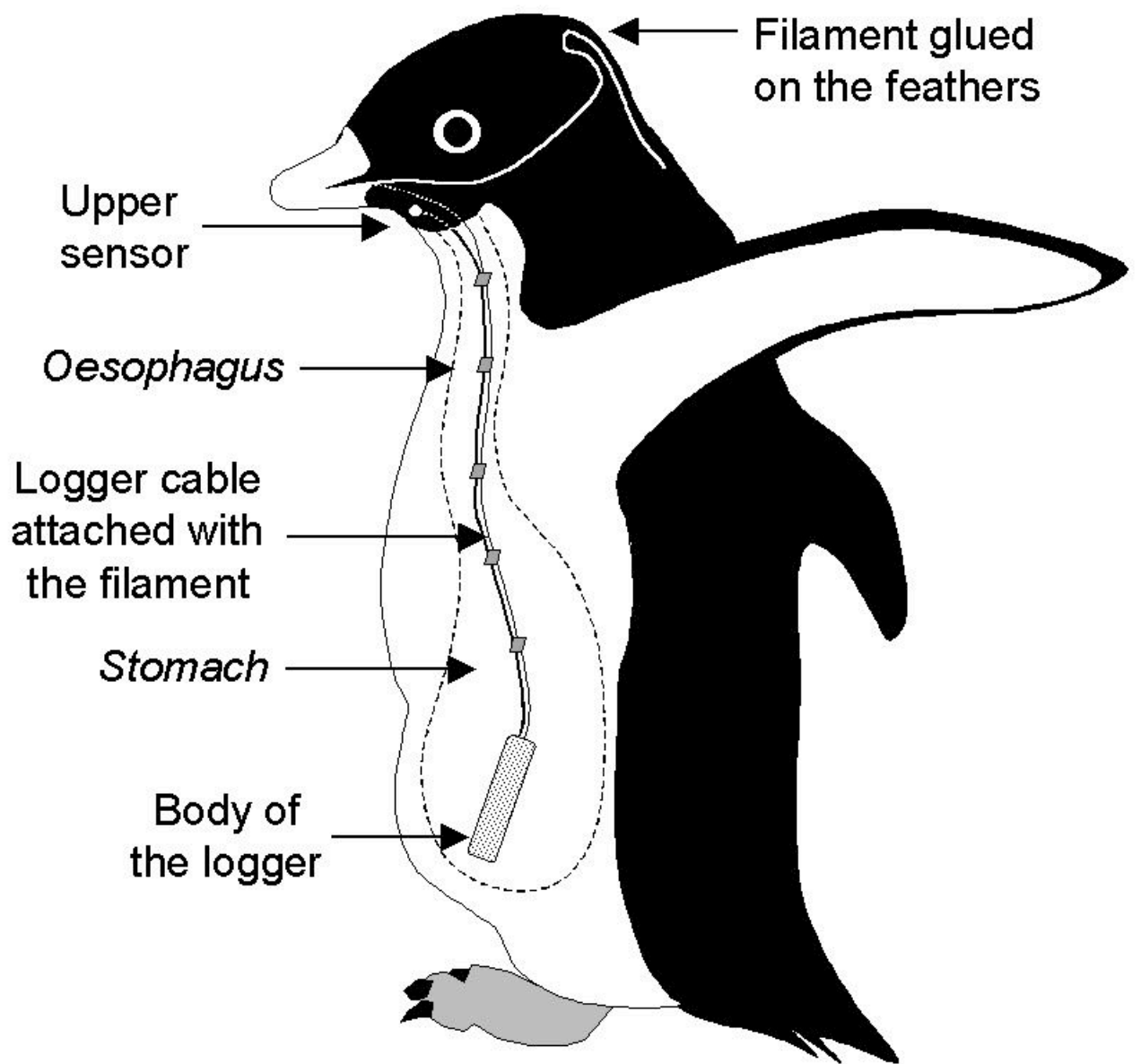


Fig. 2. Roper-Couderc et al.



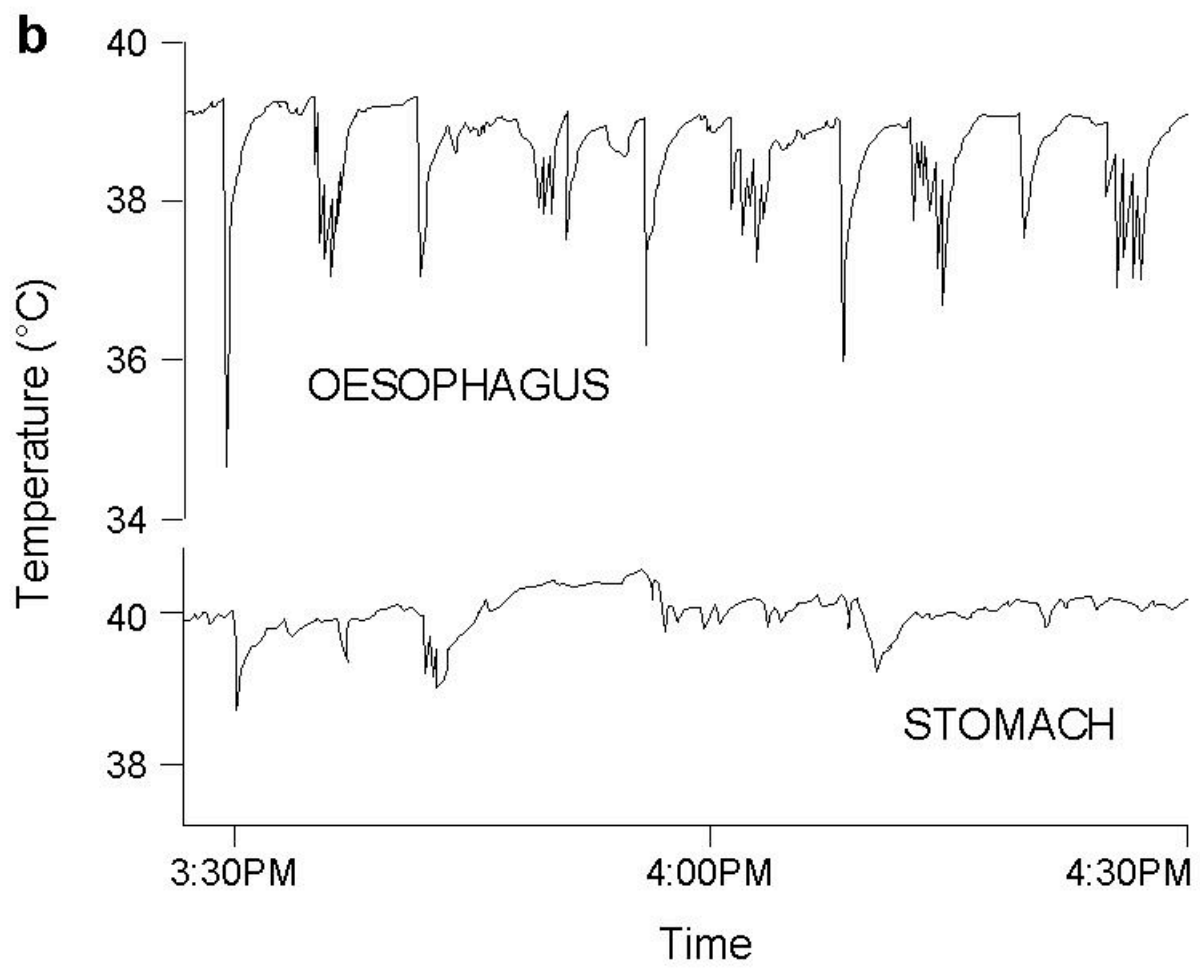
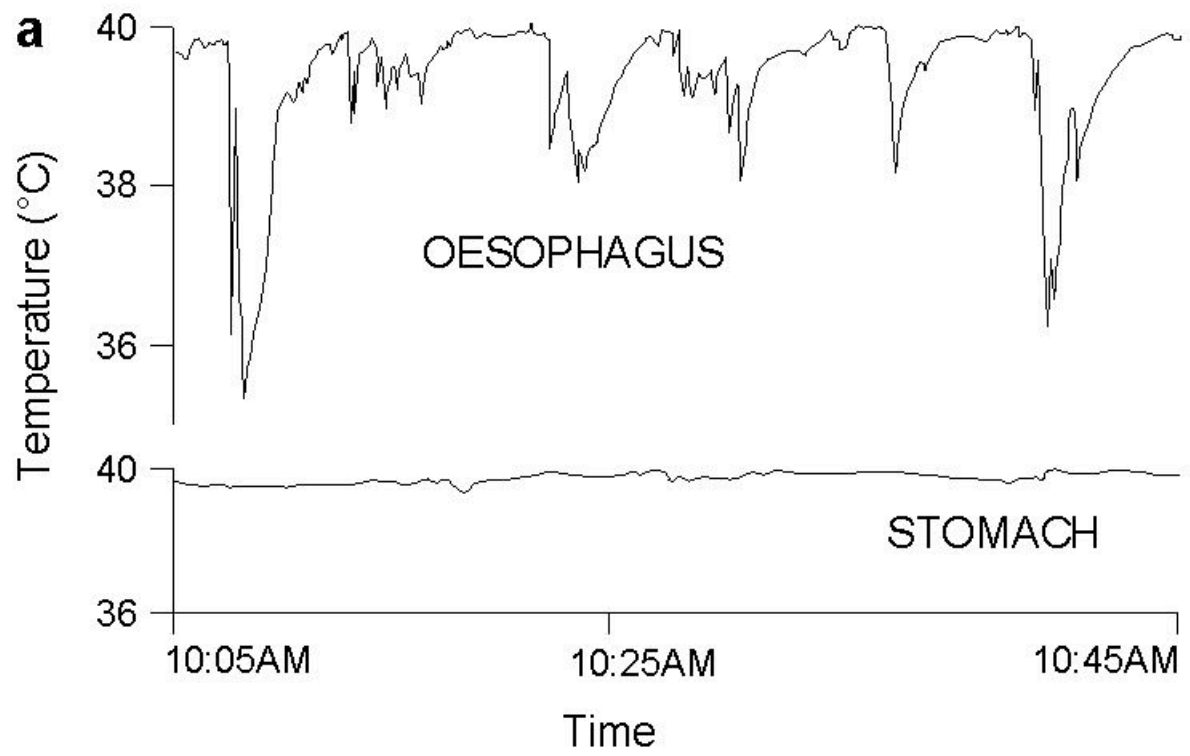
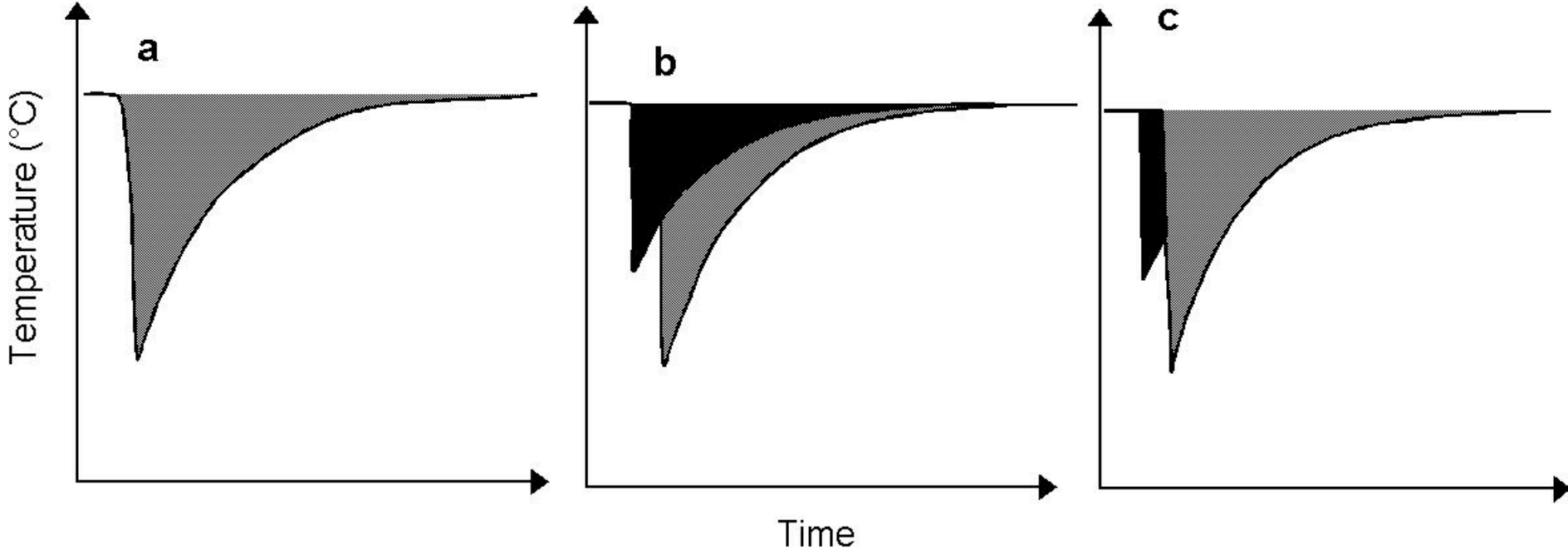


Fig. 4. Ropert-Coudert et al.



Modified from WILSON *et al.*, 1995

Fig. 5. Ropert-Coudert et al.

