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In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile?

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Abstract A new concept based on analysis of dive depth data was developed to help estimate prey consumption in ten free-ranging Magellanic penguins (*Spheniscus magellanicus*) that were brooding chicks. By simultaneously analysing the undulations in the dive depth profile (measured by time-depth recorders, TDRs) and beak opening (obtained from the recently developed intra-mandibular angle sensors, IMASEN), it was possible to determine the proportions of the undulations in the dive profile that resulted (or not) in prey capture. This methodology allowed the number of prey consumed to be estimated with a mean error of $10 \pm 6\%$ using TDR data alone. If the mean mass of prey is known, then the overall mass of prey consumed per unit time can be determined. Additionally, the method allows estimation of the depth at which prey is taken and thus indicates how penguins exploit the water column. Due to its simplicity, the proposed methodology has applications for other *Spheniscus* penguin species and should be considered for other marine endotherm divers that show undulations in the dive depth profile.

Introduction

Studies on the feeding habits of marine endotherms, particularly seabirds, are numerous and typically take one of primarily two forms: (1) those which look uniquely at the diet of the animals concerned using stomach content, scat or pellet analysis (e.g. Duffy and Jackson 1986) and (2) those that use devices on free-living animals. Of the latter, there are those which employ devices in the animal's stomach or oesophagus so as to determine prey ingestion via temperature changes (e.g. Wilson et al. 1992; Ropert-Coudert et al. 2000a) or those that attempt to determine the behaviours that animals use at sea in order to secure prey (e.g. Le Maho 1994; Ropert-Coudert et al. 2000b; Wilson et al. 2002a).

By far the most popular device being used in the latter studies is the time-depth recorder (TDR) which simply records hydrostatic pressure at set intervals and thus gives information on the depth usage by the animals over time (e.g. Kooyman 1989). Authors have been able to classify a number of different dive types based on the form of the dive profile (depth on the *y*-axis versus time on the *x*-axis; Schreer et al. 2001) and have speculated as to the function of such profiles (e.g. Wilson and Wilson 1990). The truth is, however, that there is little independent evidence that can confirm the assigned functions. Of particular help would be data reporting exactly when foraging animals ingest prey, since much of the TDR data on behaviour around such times could then be put into perspective.

Recently, there have been a number of developments that show promise in determining just this. In particular, a newly developed beak/jaw sensor (the intra-mandibular angle sensor, IMASEN) indicates precisely when the beak/jaw is opened, and thus when prey are taken (Wilson et al. 2002b). However, not all working groups have access to this rather specialised equipment, and its deployment is not considered to be particularly easy, since the sensor has to be fixed to the animals' mouthparts. Our methodological proposition in this paper is based on a rather simple premise: when initiated, dives follow a smooth course until the predator changes its heading abruptly (a point of inflection) due to an external stimulus, presumably, prey. If this is so, then undulations in the depth profile over time (which are obvious from TDR information) could be used to derive prey capture. Whether this proposition holds true depends on whether all undulations end with prey capture, whether a single undulation represents the capture of a single prey, and whether predators always produce an undulation when prey is captured.

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In an attempt to answer these questions we used the IMASEN on Magellanic penguins (*Spheniscus magellanicus*) in Argentina and looked to see the extent to which particular features in the depth profile recorded by a simultaneously deployed TDR might be used as an index of prey capture. Success in this would enable researchers without access to the IMASEN system to allude to prey capture by simply using depth profiles recorded by the ubiquitous and relatively easy to use TDRs.

Materials and methods

Study areas

Field work was conducted at three Magellanic penguin (*Spheniscus magellanicus*) colonies in Argentinean Patagonia: Estancia San Lorenzo (42°05′S; 63°51′W), Bahía San Julián (49°16′S; 67°40′W) and Cabo Vírgenes (52°22′S; 68°24′W). These colonies support breeding populations of ca. 17,000, 37,000 and 89,000 pairs, respectively (Yorio et al. 1998).

Technology used

Ten birds brooding chicks during late November were removed from their nests and fitted with IMASEN devices and TDRs (at Cabo Vírgenes three birds in 2000 and four birds in 2001, two at Bahía San Julián in 2001 and a single bird at Estancia San Lorenzo in 2002). The complete equipping procedure took ca. 30 min and was primarily dependent on the time it took for the glue used in the IMASEN attachment to set. Birds were then released back onto the nest where they continued brooding. The devices were recovered after the birds had been to sea for a single foraging trip, generally lasting <24 h. The data in the units were downloaded onto a computer using the appropriate software and interfaces provided by the manufacturer (see below).

The IMASEN consisted of a single-channel logger potted in resin (Driesen and Kern, Bad Bramstedt, Germany; dimensions: 70×35×20 mm, 45 g) and powered by a 3 V lithium battery. A Hall sensor (dimensions: 6×3×2 mm), also potted in resin, at the end of a 300×0.8 mm diameter cable leading from the device measured magnetic field strength at frequencies between 10 and 20 Hz in a 4 Mb flash RA memory with 12 bit resolution. The sensor was glued to the side of the upper mandible of birds' beaks using two-component epoxy glue (Poxypol, Argentina), and a small neodymium boron rare earth magnet (dimensions: 2×2×6 mm) was glued directly opposite on the lower mandibles in a similar manner. The sensor reacted to the magnetic field produced by the magnet, perceived field strength being dependent on the degree to which the beak was opened. After suitable calibration, the data recorded by the logger could be converted directly into beak angle (for details see Wilson et al. 2002b). The cable from the Hall sensor was run down the bird's back, being fixed in place periodically by spots of epoxy glue, until it reached the logger, which was attached to feathers using tape as described by Wilson et al. (1997).

Depth was sensed by one of two TDR types: (1) a three-channel logger (Driesen and Kern; max. dimensions: 93×16×17 mm, 48 g) recording temperature, light and depth in a 4 Mb flash RA memory with 16 bit resolution (absolute depth accuracy 3 cm) at frequencies of between 1 and 5 Hz. This unit was attached to feathers on the lower back of birds using tape as described in Wilson et al. (1997). And (2) the three-channel logger LTD 100 (Lotek Marine Technologies, St. John's, NF, Canada; dimensions: 57 mm long, 18 mm diameter, 22 g) recording temperature, light and depth in a 1.5 Mb memory with 12 bit resolution at a frequency of 1 Hz. This unit was attached to bird's legs on a plastic leg ring with a neoprene cover as described in Simeone et al. (2002).

Units attached with tape were placed along the mid-line of the bird's lower back so as to reduce drag during swimming (Bannasch et al. 1994). The caudal position of the leg-attached loggers on the birds was likely to produce little drag and, in any case, turbulence created at the rear of the bird is less important in hindering swimming (Bannasch et al. 1994). Finally, as reported by Simeone et al. (2002) for captive Humboldt penguins, there are no apparent ill effects while walking due to this attachment method.

Data analysis

Data on beak angle changes and depth were viewed using MT-BEAK (Jensen Software Systems, Laboe, Germany). This program allowed observation of both beak and depth data channels simultaneously with a synchronised time axis. The program accurately allowed determination of undulations and beak openings.

Undulations in the dive profile were characterised by both amplitude and duration. We considered an undulation to be initiated when an abrupt change in dive depth (hereafter, a point of inflection) was observed in the profile and ended when the prey was captured, evident by the beak opening and a new point of inflection. The duration of the undulation was determined following the same rationale. An undulation was considered to have occurred when a change in depth over any 1 s was >0.3 m (equivalent to ca. twice the maximum ventro-dorsal diameter of a Magellanic penguin) more than the mean rate of change of depth recorded over the previous 3 s, unless an undulation had already occurred within this 3-s time window. Undulations were measured with the program to the nearest 1 s and 0.1 m.

Prey ingestion was easily identified by examination of bird beak angle over time (Wilson et al. 2002b). Prey were considered to have been ingested if penguin beak angle exceeded 2° at any time while the bird was underwater (cf. Wilson 2003). Work with penguins in captivity (Wilson et al. 2002b) showed that birds that snapped at preferred prey, but failed to take it, had sudden beak openings and closures, whereas those that ingested even small prey invariably showed a tail in beak angle as the beak was closed, presumably due to the swallowing process. Such tails were apparent in all beak opening events made by Magellanic penguins underwater. We consider that these birds only open their beaks when prey capture is assured, perhaps for hydrodynamic reasons (see Bannasch et al. 1994), although there were occasions when prey were apparently pursued but not caught (see later).

Results

Duration and amplitude of undulations

Undulations lasted between 1 and 16 s, but 95% of them never exceeded 8 s (Fig. 1a). Undulations (only those >0.3 m) had an amplitude of up to 7 m, with 95% of them not exceeding 3.6 m (Fig. 1b).

Estimating prey consumption

By simultaneously analysing beak and dive data we were able to identify three different situations: type A events (Fig. 2a, c), in which an undulation was observed in the dive profile, but no beak opening was evident (i.e. no prey was captured); type B events (Fig. 2b, c), in which no undulation was evident, but the bird did open the beak (i.e. prey was captured); and type C events (Fig. 2a, c, d), in which both undulation and beak

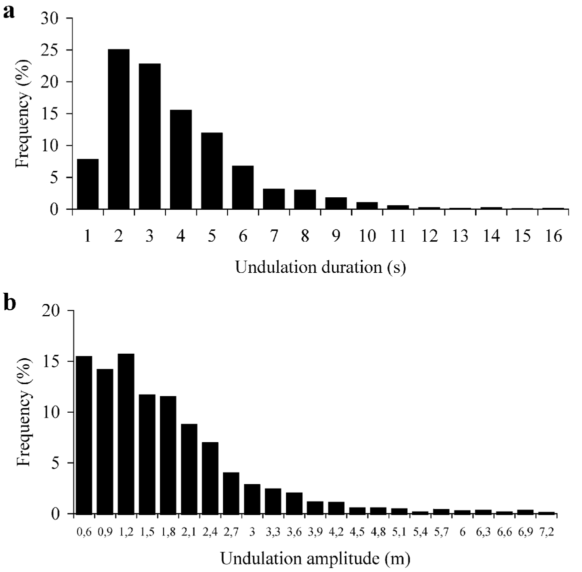


Fig. 1a, b *Spheniscus magellanicus*. Frequency distribution of: **a** undulation durations and **b** undulation amplitudes; $n = 1{,}721$ undulations from ten birds

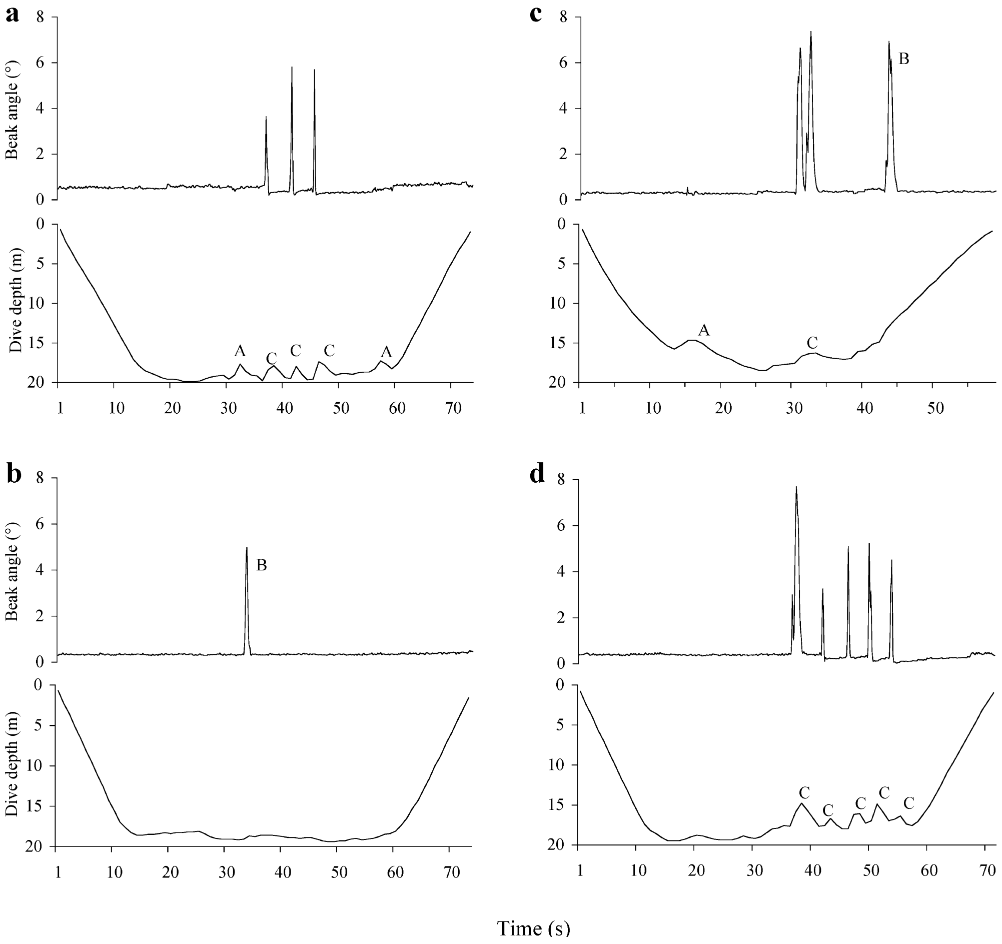
opening were recorded simultaneously (i.e. prey was captured). The frequency of occurrence of each of these events ascribed as being type A, B or C in the ten penguins (for 200 events per bird) is shown in Fig. 3.

As TDR data only allow identification of the undulations in the dive profile (i.e. events A + C), we attempted to test if these data could be used to predict the amount of prey ingested by the penguins. We know from A + C events, that only parameter C represents ingestion of prey, while parameter A represents undulations without prey capture. In addition, ideally, the number of B events, which are not accessible from TDR data, should be determined, since this represents captures without undulations. In order to determine the total number of capture events (TCE), we need to calculate:

$$\begin{aligned} \mathrm{TCE} &= [(A + C) - A] + B \\ &= B + C \end{aligned} \tag{1}$$

Note that the total numbers of undulations (A + C) are the only data accessible using TDRs. From our data on Magellanic penguins ($n = 10$ individuals) we were able to approximate the proportions of B and C events as a mean function of the total number of undulations as:

Fig. 2a–d *Spheniscus magellanicus*. Four examples (**a–d**) of events showing depth and beak data simultaneously [*A* events of dive undulations without prey capture; *B* events of beak openings (i.e. prey capture) without undulation in the dive profile; *C* events of beak openings coupled with undulations in the dive profile (see "Materials and methods" for details)]



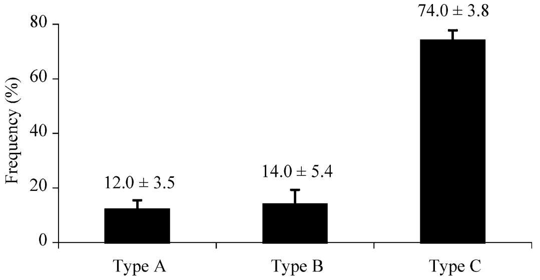


Fig. 3 *Spheniscus magellanicus*. Mean (± SD) frequencies at which A, B and C events occur; $n = 2{,}000$ events from ten birds

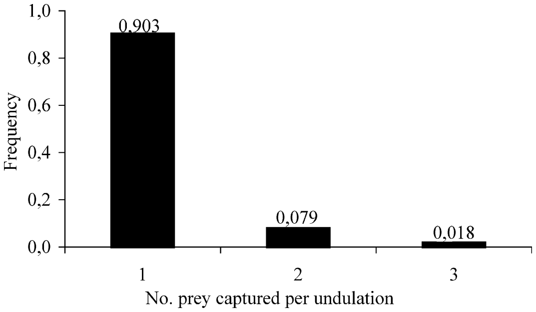


Fig. 4 *Spheniscus magellanicus*. Frequency at which Magellanic penguins capture one, two or three prey per undulation

$$\begin{aligned} B &= 0.166(A + C) \\ C &= 0.861(A + C) \end{aligned} \qquad (2)$$

In other words, on average, B and C events are 16.6% and 86.1% of the total undulations recorded, respectively. When the B parameter calculated by us was compared with the observed B parameters of each of the ten birds, we obtained a mean error of 47 ± 31% in its calculation. For parameter C, this error was only 3 ± 2%.

B events always resulted in the ingestion of a single prey, but C events could yield up to three prey per undulation (Fig. 4). Knowing the proportion of single undulations in which one, two or three prey are captured (Fig. 4), it is possible to correct these values so as to approximate the total number of prey captured (TPC) as:

$$\begin{aligned} \mathrm{TPC} &= B + C[0.903(1) + 0.079(2) + 0.018(3)] \\ &= B + C(1.115) \end{aligned} \qquad (3)$$

When we compared the TPC calculated by us with the observed TPC of each of the ten birds, we obtained a mean error of 10 ± 6% in its calculation.

Discussion

As is the case for other species of the genus *Spheniscus*, Magellanic penguins feed primarily on pelagic schooling fish such as anchovy (*Engraulis* spp.), sardine (*Sardinops* spp.) and silverside (*Odontesthes* spp., *Atherina* spp.), although squid (*Loligo* spp., *Ilex* spp.) are also taken (e.g. Rand 1960; Wilson 1985; Frere et al. 1996; Scolaro et al. 1999; Herling 2001). Boswall and MacIver (1975) report that squid are taken by birds driving at them from below, and Wilson et al. (1987), summarising data on the feeding habits of *Spheniscus* penguins, report that school fish are herded by the birds swimming round the prey in tight circles before diving underneath and swimming rapidly up through the fish catching individuals as they do so. This behaviour is thought to be advantageous to the penguins because pelagic school fish, which are particularly hard to see from most angles due to the orientation of light-reflecting crystals in their scales (Denton 1971), can be best viewed as a silhouette against the water surface and because fish perceive the penguins least well if they are attacked from below (Wilson and Duffy 1986). *Spheniscus* penguins are also known to pursue prey directly, without any apparent strategy (Rand 1960; Wilson 1996). In an attempt to flee the penguins, prey randomly swimming away are also quite likely to display some vertical movement; this would presumably produce an undulation in the depth profile exhibited by the penguin if the vertical movement is sufficient. Whatever the case, it is clear that most Magellanic penguin prey are caught during an undulation, and we assume that those prey caught without an undulation in the penguin depth profile involve simple pursuit without substantial vertical movement.

Some authors have suggested that irregular variation in the dive profiles of penguins might indicate feeding (e.g. Wilson and Wilson 1995; Kirkwood and Robertson 1997), and others suggest that undulations in the dive profiles together with variation in swim speed can be useful as indicators of prey pursuit and capture (Ropert-Coudert et al. 2000b; Wilson et al. 2002a). Our work indicates that, in Magellanic penguins at least, consideration of the number of undulations is a useful indicator of feeding in general. The utility of this depends, ultimately, on the extent to which consideration of undulations in the depth profile may enable us to determine how much prey is caught and over what period of time. Over the course of a single foraging trip, the total number of prey items caught can be estimated according to the equations given earlier, but, given the variability in the error margin and the fact that the proportion of A events is almost identical to the proportion of B events, a general rule of thumb might be to say that a single undulation results in a single prey item being captured. This certainly seems a reasonable approximation if the numbers of prey caught are to be summed over a long period of time. The situation becomes more critical as the time window is reduced. Any single undulation only has an 86% chance of being associated with a prey capture, but two adjacent undulations obviously increase the probability of at least one prey being taken to:

$$\begin{aligned} Ps &= 1-(0.14)^2 \\ &= 0.98 \end{aligned} \tag{4}$$

Simple probability theory can be used to calculate the running likelihood of prey being caught during any particular dive, although it should be noted that this approach does not help determine the position of B events.

Advantages of the methodology

The main advantage of this methodology is its simplicity. Dive depth over time is now commonly recorded by devices deployed on marine endotherms and used to classify dive types (usually V, U and W types) and, through these types, derive the proportion of searching and foraging dives (e.g. Wilson and Wilson 1990; Luna-Jorquera and Culik 1999; Schreer et al. 2001). Here, it should be noted that the W-shaped dives may be regarded as modified U dives, i.e. U-shaped dives with undulations. Calculation of the number of prey ingested will allow researchers to determine the proportion of dives that are actually likely to have been successful. In an extension of this, if the mean mass of prey is known (e.g. via dietary studies), then the overall mass of prey consumed per unit time can be determined (e.g. Kirkwood and Robertson 1997). This, in turn, can be used together with the dive data to derive catch per unit effort (CPUE) information. Determination of the depth at which undulations occur may help elucidate the vertical distribution of prey in the water column and which part of it penguins are exploiting.

Compared to other methods that use diet determination, which normally involves stomach pumping (e.g. Wilson 1984) or the ingestion of stomach temperature recorders (e.g. Wilson et al. 1992; Ropert-Coudert 2000a), our proposed method is less intrusive and with no additive effects to those already caused by the attachment of a TDR.

Disadvantages of the methodology

To determine whether an undulation, as defined by us, has actually occurred necessitates recording depth at a frequency of at least 0.5 Hz with an appropriate depth resolution. This will rule out studies looking at diving behaviour over long periods until solid state memories become appropriately large. For example, recent studies

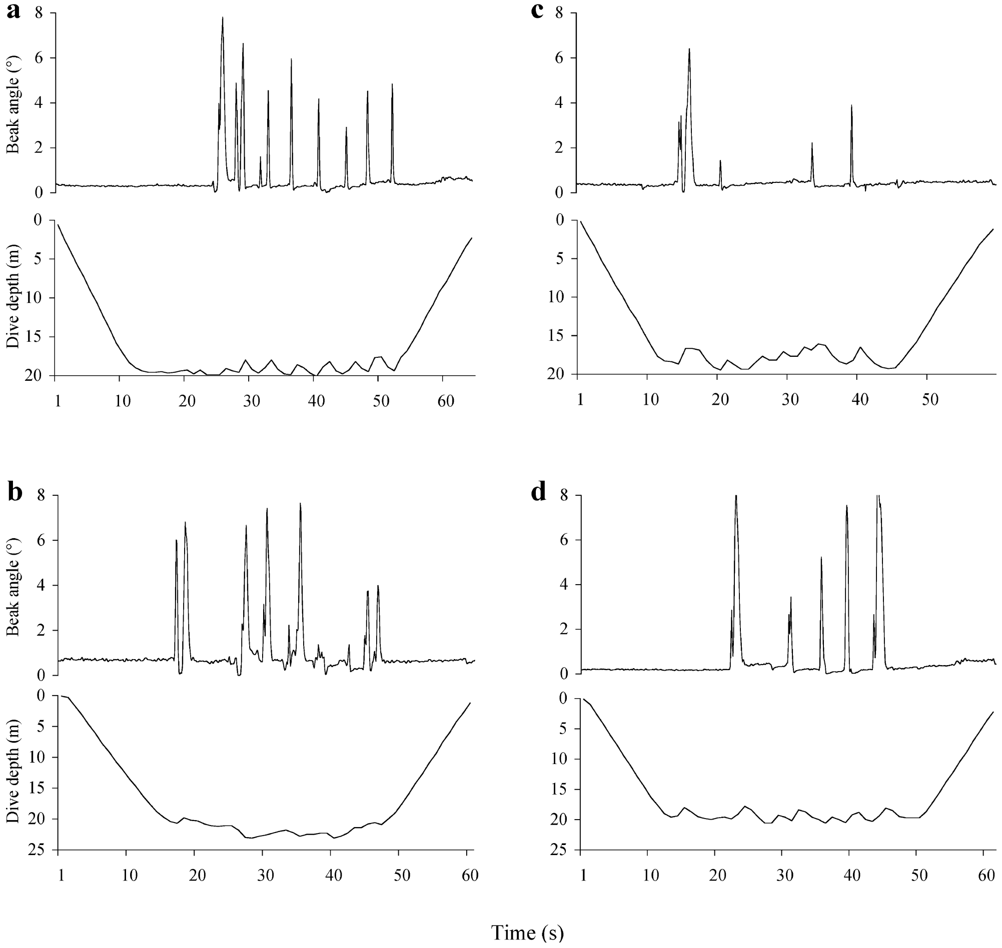


Fig. 5a–d *Spheniscus magellanicus*. Four examples (**a–d**) of complicated situations in the analysis of undulations in dive profiles with respect to prey capture

on the diving behaviour of *Spheniscus* penguins have used TDRs programmed to record depth every 5 s (e.g. Wilson and Wilson 1995; Luna-Jorquera and Culik 1999; Radl and Culik 1999; Mills 2000, but see Wilson 2003). This interval is clearly insufficient for determination of prey ingestion, since ca. 70% of the undulations last < 5 s (Fig. 1a), quite apart from consideration of the difficulties in determining rates of change of depth with such large recording intervals. The data in Fig. 1a show that a minimal logging interval of 2 s would allow recognition of ca. 90% of the undulations produced by a diving penguin.

Situations as shown in Fig. 2 are rather straightforward, but others, such as those illustrated in Fig. 5 are more complicated and could easily lead to overestimation of the amount of prey captured. In such cases, a conservative counting of undulations is recommended.

The application of the rather specialised equipment of the IMASEN technology is still in its infancy in the study of the foraging ecology of marine animals. It is, however, likely to become much more widespread, and its use will allow us to elucidate basic foraging patterns in a variety of diving species. Already, however, highly similar foraging behaviour for all penguins of the genus *Spheniscus* (Wilson and Wilson 1990) makes it likely that coarse patterns of feeding can be derived by simple examination of TDR data from these birds. On a broader scale, the use of the IMASEN on other marine endotherms in general (e.g. Wilson and Liebsch 2003) might help explain why it is that so many species show undulations in their dive profiles, including several marine mammal species (e.g. Le Boeuf et al. 1992; Harcourt et al. 1995; Martin et al. 1998; McCafferty et al. 1998), or at least to be able to confirm that such undulations are associated in some way with prey (pursuit and/or capture), as has been suspected by various authors for some time (e.g. Kirkwood and Robertson 1997). Once confirmed, simple inspection of TDR traces should be able to allow researchers to assign certain periods of diving to prey acquisition, while other periods can be considered as less fruitful. More detailed analysis, such as attempted above, may even allow prey consumption to be estimated from simple TDR data. This would ultimately simplify the work, cost and time for researchers and would reduce stress on the study animals.

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