

RESEARCH ARTICLE

Penguin head movement detected using small accelerometers: a proxy of prey encounter rate

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SUMMARY

Determining temporal and spatial variation in feeding rates is essential for understanding the relationship between habitat features and the foraging behavior of top predators. In this study we examined the utility of head movement as a proxy of prey encounter rates in medium-sized Antarctic penguins, under the presumption that the birds should move their heads actively when they encounter and peck prey. A field study of free-ranging chinstrap and gentoo penguins was conducted at King George Island, Antarctica. Head movement was recorded using small accelerometers attached to the head, with simultaneous monitoring for prey encounter or body angle. The main prey was Antarctic krill (>99% in wet mass) for both species. Penguin head movement coincided with a slow change in body angle during dives. Active head movements were extracted using a high-pass filter (5 Hz acceleration signals) and the remaining acceleration peaks (higher than a threshold acceleration of 1.0 g) were counted. The timing of head movements coincided well with images of prey taken from the back-mounted cameras: head movement was recorded within ± 2.5 s of a prey image on $89.1 \pm 16.1\%$ ($N=7$ trips) of images. The number of head movements varied largely among dive bouts, suggesting large temporal variations in prey encounter rates. Our results show that head movement is an effective proxy of prey encounter, and we suggest that the method will be widely applicable for a variety of predators.

Key words: accelerometry, chinstrap penguin, gentoo penguin, Antarctic krill, foraging effort, patch.

INTRODUCTION

Determining when and where predators capture prey is one of the most critical issues for studying mobile foraging animals (Perry and Pianka, 1997). Understanding the timing and rate of prey encounter and/or capture enables us to investigate how animals optimize their foraging behavior in the context of energy expenditure or habitat use (Stephens and Krebs, 1986). Furthermore, because foraging provides the link between the environment or lower trophic level and predators, quantifying top predator foraging behavior is necessary to understand their roles in both terrestrial and marine ecosystems (Spiller and Schoener, 1994; Boyd et al., 2006). Detecting the prey encounter and consequent feeding events of top predators at a fine scale is important for characterizing the habitat features associated with high foraging efficiency. This is particularly relevant for marine ecosystem given their high variability and poor demarcation (Hindell et al., 2010). Animal-borne data loggers, developed over the past 30 years, have provided great insight into the previously invisible underwater behavior. Nevertheless, precise detection of prey encounter rate is still challenging, especially for free-ranging small predators.

Some indicators of prey encounter and consequent feeding events have been explored, and each has advantages and disadvantages. The number of depth wiggles during a dive is a popular indicator of the number of prey encounter and/or foraging events (Simeone and Wilson, 2003; Bost et al., 2007), although the accuracy of this method is lower than that of other direct methods. More direct indicators such as drops in stomach or oesophageal temperature (Wilson et al., 1995; Ropert-Coudert et al., 2000; Hanuise et al.,

2010) and beak opening events (Wilson et al., 2002; Takahashi et al., 2004; Hanuise et al., 2010) have high accuracy. However, the disadvantages of these methods are the complex procedures for deployment, and the frequent failure to record because of regurgitation or dropout of the devices. An alternative method for quantifying the characteristics of aquatic animal behavior is the use of accelerometers (Yoda et al., 2001; Wilson et al., 2006). In particular, a new approach that uses mandible or head acceleration as a proxy for prey capture attempts has been developed in recent years (Naito, 2007). The utility of this approach was determined from experiments firstly with pinnipeds in aquariums (Suzuki et al., 2009; Skinner et al., 2009; Viviant et al., 2010), and secondly with free-ranging pinnipeds (Naito et al., 2010; Iwata et al., 2011). Furthermore, this method appears to be applicable to smaller free-ranging marine predators, as the size of the accelerometers has reduced in the last few years.

The medium-sized Antarctic penguins, such as Adélie, chinstrap, gentoo and macaroni penguins, are some of the major top predators in the Southern Ocean ecosystem, along with whales and pinnipeds (Brooke, 2004; Balance et al., 2006; Boyd, 2009). Measuring their at-sea foraging behavior is increasingly important in terms of understanding interspecific competition with whales and seals for the common resource Antarctic krill (*Euphausia superba*) (Ainley et al., 2010), or the effects of environmental change (Fraser and Hoffmann, 2003; Forcada et al., 2006) on their populations. Because penguins open their beak at frequent intervals when feeding in krill patches (Takahashi et al., 2004), we can assume that they move their heads to encounter, pursue and peck prey, as recorded in marine

mammals (Suzuki et al., 2009; Skinner et al., 2009). Although making the connection between head movement and successful/unsuccessful foraging events remains difficult, active head movement could act as a simple proxy of prey encounter. In this study we aimed to detect prey encounter rate of free-ranging penguins precisely, by monitoring their head movement using a recently developed small accelerometer, with simultaneous monitoring of underwater images using small cameras.

MATERIALS AND METHODS

Study site

The field study was conducted on Barton Peninsula, King George Island, South Shetland Islands, where chinstrap [*Pygoscelis antarcticus* (Forster 1781)] and gentoo penguins [*Pygoscelis papua* (Forster 1781)] breed sympatrically (Antarctic Specially Protected Area no. 171: Narębski Point). In the 2009–2010 austral summer season, 2278 breeding pairs of chinstrap penguins and 1759 breeding pairs of gentoo penguins were counted at the study colony. The study was conducted from 28 December 2009 to 2 February 2010, which covered the chick-guarding period of chinstrap and gentoo penguins.

Deployment of devices

Head movement and dive data were collected from 12 chinstrap and 12 gentoo penguins, using small accelerometers attached to the head (ORI-380 D3GT, housed in a pressure-resident cylindrical container: 12 mm diameter, 45 mm length, mass 10 g including batteries; Little Leonardo, Tokyo, Japan). Three axes of acceleration data (heave, surge and sway) were recorded at a frequency of 32 Hz, and dive depth data were recorded every second. Loggers were attached to the medial portion of the head using Tesa[®] tape and cyanoacrylate glue (Loctite[®] 401) to secure the end of the tape (Fig. 1). For eight chinstrap and six gentoo penguins, one more accelerometer was attached to the lower medial portion of the back to monitor the body angle of the individual (Fig. 1). Recording rates were the same as accelerometers attached to the head. Camera loggers (DSL-380, housed in a pressure-resident cylindrical container: 22 mm diameter, 133 mm length, mass 82 g including batteries; Little Leonardo) were attached to the back of three chinstrap and five gentoo penguins to visually monitor prey encounter in the sea. Still images were taken every 5 s and dive depth data were recorded every second. All loggers were attached to the birds just before their departure for a foraging trip. Mean handling time was 26.5 ± 5.4 min per bird. The body mass of the birds was also measured to the nearest 50 g using a Pesola[®] spring balance. Tagged birds were recaptured after they returned from their foraging trip, and the loggers were removed. The data were downloaded from the loggers to a laptop computer.

Effect of accelerometer deployments on penguin behavior

Accelerometers attached to the head of the penguins potentially affect their at-sea behavior, because of sensitivity of the birds or hydrodynamic drag caused by the loggers (Ponganis et al., 2000). The at-sea behavior of penguins without loggers was not observed in the present study. Instead, to evaluate the effect of accelerometer deployments, trip duration was compared between birds with and without head accelerometers, where the birds without head accelerometers had GPS depth loggers attached on their backs (Kokubun et al., 2010). No significant effect of the GPS depth loggers on the behavior of either chinstrap or gentoo penguins has been recorded (Kokubun et al., 2010). The GPS depth loggers were attached on the lower medial portion of nine chinstrap and 10 gentoo

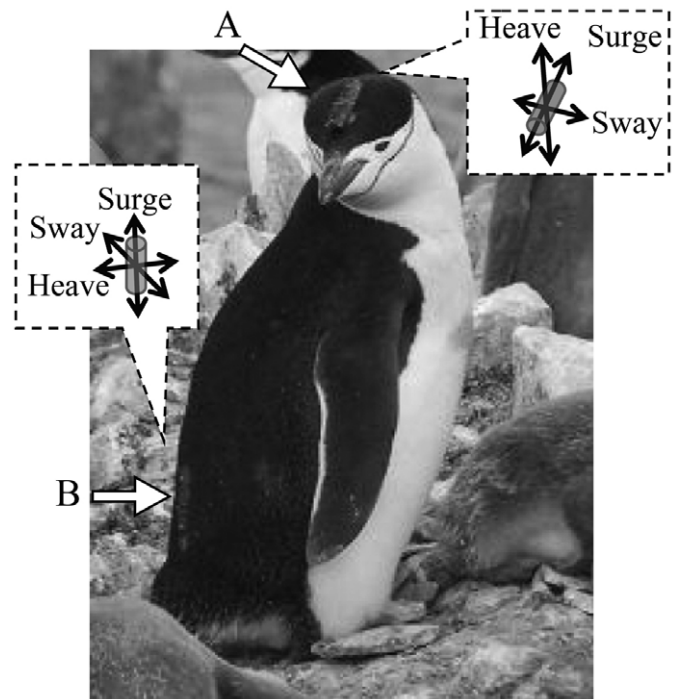


Fig. 1. Attachment of the accelerometers on (A) the head and (B) the back of a chinstrap penguin. The direction of the three axes recorded by the accelerometers is also shown.

penguins, during the period in which the accelerometers were deployed (28 December 2009 to 23 January 2010).

Analysis of head and body acceleration

Depth profiles were analyzed by examining dive depth, dive duration, diving bottom duration (the period between the start and end of the time when birds showed a depth change of 0 m) and the number of depth wiggles (number of changes in symbol of differential depth every second) for each dive. A dive was considered to occur when dive depth exceeded 1.0 m (Takahashi et al., 2003). Only data that covered a whole trip were used for subsequent analyses.

Acceleration data were analyzed with Ethographer (Sakamoto et al., 2009), with the analysis software Igor Pro version 6.0 (Wave Metrics Inc., Lake Oswego, OR, USA). Dominant frequencies and amplitudes of the three axes of acceleration from both head and back during each dive phase (descent, diving bottom and ascent) were examined visually on the spectrogram (Fig. 2). The minimum frequency resolution was set to 0.01 Hz. The calculated amplitude was expressed by color graphs. The spectrograms from both the head and back were compared and subsequently a high-pass filter of 5 Hz was applied on the three axes of head acceleration such that active head movements were highlighted (Fig. 2). Peaks in the filtered acceleration exceeding a threshold amplitude were counted within a 1.0 s time window. The minimum time interval of the peak was set to 0.2 s (i.e. the maximum peak number was set to five times per second). The number of the peaks was assumed to be the number of active head movements of the penguins.

Time series data for static acceleration were extracted using a low-pass filter of 1 Hz on surge acceleration from the back (Sato et al., 2004). Static acceleration was converted to body angle. Depth profiles and acceleration were analyzed using Igor Pro.

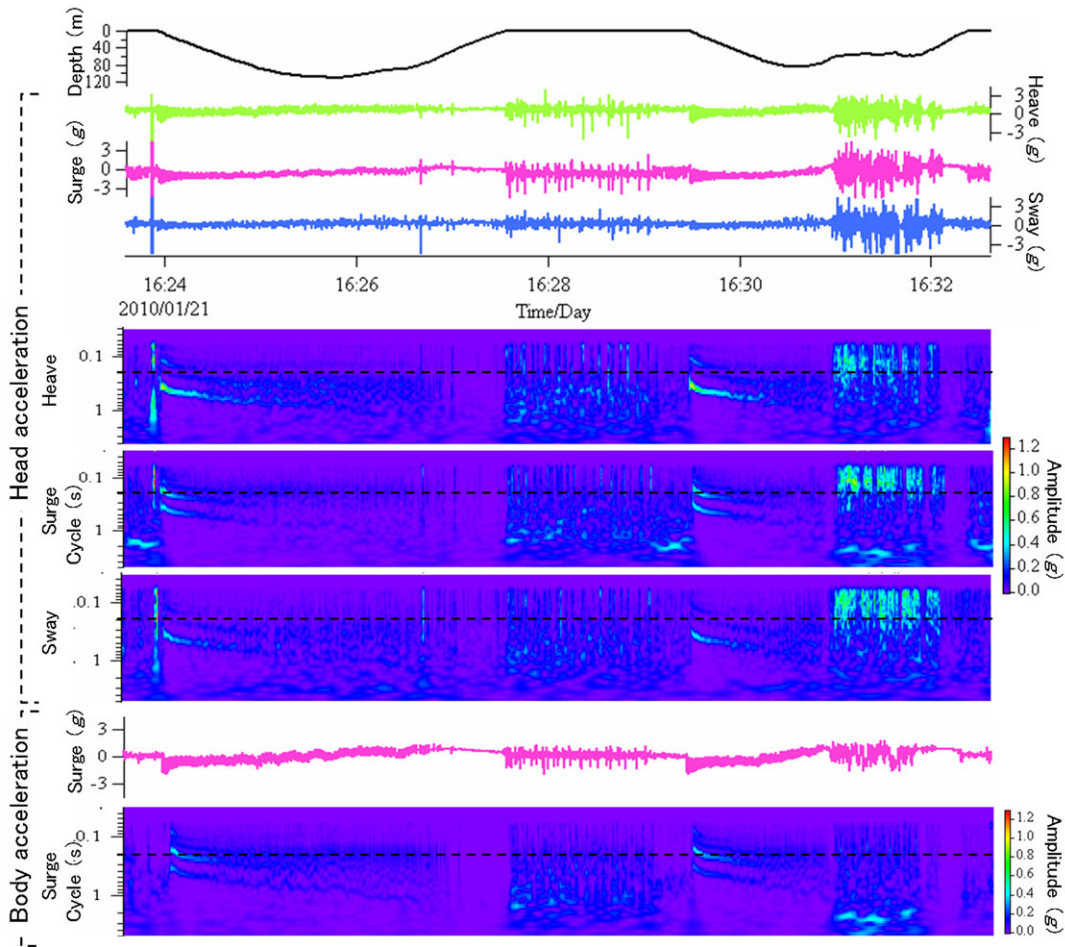


Fig. 2. Time series of diving depth, the three axes of head acceleration (heave, surge and sway), spectrogram of the three axes of head acceleration, body acceleration (surge) and the spectrogram of the body acceleration (surge) for two gentoo penguin dives (bird G054, 21 January 2010). The dashed lines in the spectrograms show a 0.2 s cycle (i.e. 5 Hz). Note that the amplitude of the high-frequency (>5 Hz) acceleration during the dives is larger for data from the head than those from the body. The high-frequency head acceleration during the dives was clearly observed in the second dive, but not in the first.

Analysis of still images

Still images taken by camera loggers were sorted visually. First, all images were classified as 'light' or 'dark' according to their light level. Dark images were unable to be used to determine prey presence or absence. Subsequently, all dives were classified as 'light' or 'dark' because darker images reflected deeper or nighttime dives, and the high proportion of dark images during a dive makes it difficult to estimate actual prey encounter rate. Dives were classified as 'light' when the proportion of light images was more than 50% of the images taken at depths greater than half of the maximum dive depth. Only data from the light dives were used for subsequent analyses. The number of images with prey in each dive was assumed to be the number of prey encounter events of the dive.

Correspondence between head movement and prey encounter

Active penguin head movement, detected using accelerometers, was compared with the prey encounter of individuals, as observed by camera loggers, using a regression model. The number of head movements varied according to the threshold detection amplitude. Therefore, a model was fitted for the number of head movements detected at various threshold amplitudes, ranging from 0.5 to 2.0 g ($g=9.8 \text{ ms}^{-2}$) in 0.1 g steps. The model was fitted for results from three axes of acceleration. In addition, the number of depth wiggles, which is a commonly used indicator of foraging effort (Simeone and Wilson, 2003; Bost et al., 2007), was also compared with the number of prey encounters using the same model. The statistical fit of the models was assessed using log likelihood values. Dive duration had a

significant effect on the number of head movements, prey encounter and depth wiggles. Thus the number of head movements per dive duration, the proportion of images with prey from all images during a dive, and the number of depth wiggles per dive duration were used in the model. A generalized linear mixed model (GLMM) with quasi-Poisson error distribution and logarithm link function was fitted: $y=a+bx+\text{random effect}$, where y is the proportion of images with prey from all images during a dive and x is either the number of head movements or the number of depth wiggles per dive duration. Bird identity was set as the random effect. The effect of species could not be included in the model because sample size for the chinstrap penguins was too low (only two birds). Regression analyses were performed with R 2.9 (R Development Core Team, 2009).

In addition, temporal concordance of both the images with prey and the head movement was examined. The two parameters were assumed 'concordant' if a head movement occurred within 2.5 s (i.e. time interval to previous/next image) of the time that the image with prey was taken.

Stomach contents

Stomach contents from six chinstrap and seven gentoo penguins were collected to examine the main prey species of the penguins, using the standard stomach-flushing method (CCAMLR, 1997). The samples were obtained from individuals with GPS depth loggers (see Effect of accelerometer deployments on penguin behavior). The wet mass of each stomach content sample was measured to the nearest 1 g using an electronic balance in the laboratory. Samples were then sorted and classified to taxonomic group. Fish species

Table 1. Sample size of each deployment type for chinstrap and gentoo penguins

Deployment type	Chinstrap			Gentoo		
	Deployments	Retrieves	Available trips	Deployments	Retrieves	Available trips
Accelerometer on the head	1	1	3	1	1	1
Accelerometer on the head and another on the back	8	8 ^a	7	6	6	7
Accelerometer on the head and a camera on the back	3	2	2	5	5	5
Total	12	11	12	12	12	13
GPS ^b	9	9	11	10	10	14

^aAmong the eight individuals, one bird did not depart for a trip. In addition, one back accelerometer and one head accelerometer did not work because of power supply problems (see Results).

^bThe behavior of individuals with GPS loggers was compared with that of individuals with head accelerometers, in the context of assessing impacts of the accelerometer attachment (see Materials and methods).

were identified based on the shape and/or size of the otolith or bones (Gon and Heemstra, 1990).

RESULTS

Device and data recovery

Eleven chinstrap and 12 gentoo penguins were recaptured in the 1 to 7 days after release, and the loggers were retrieved (Table 1). One chinstrap penguin with an accelerometer on the head and a camera logger on the back was not recaptured. Among the recaptured birds, one chinstrap penguin with accelerometers on the head and the back did not depart for a trip (Table 1). In addition, one accelerometer attached on the back of one chinstrap penguin and another accelerometer on the head of another chinstrap penguin did not work because of power supply problems (Table 1). Overall, records of 12 trips from nine chinstrap penguins (seven trips with a combination of head and back acceleration data, two trips with a combination of head acceleration and still image data, and three trips with only head acceleration data) and 13 trips from 12 gentoo penguins (seven trips with a combination of head and back acceleration data, five trips with a combination of head acceleration and still image data, and one trip with only head acceleration data) were available for the subsequent analyses (Table 1). The recording duration of the accelerometers on the head covered the entire periods of the trips. In 11 cases among these, the records continued until the memory capacity was full. The maximum mean recording duration was 33.9 ± 0.2 h ($N=11$ recorders). According to a full-logging test for the same type of loggers at a sampling rate of 16 Hz, mean recording duration should be 51.8 ± 1.2 h ($N=7$ recorders).

Effect of accelerometer deployments on penguin behavior

Trip duration did not differ between the birds with the accelerometer on the head ($N=12$ and 13 trips for chinstrap and gentoo penguins,

respectively) and the birds with GPS depth loggers on the back ($N=11$ and 14 trips for chinstrap and gentoo penguins, respectively) (chinstrap: accelerometer, 7.5 ± 2.8 h; GPS depth logger, 10.2 ± 5.2 h; ANOVA, $P=0.13$; gentoo: accelerometer, 8.2 ± 2.1 h; GPS depth logger, 9.8 ± 3.8 h; ANOVA, $P=0.19$). Thus we believe that the accelerometer attached to the head had no substantial negative effects on penguin behavior, and the effects were comparable to those of back-mounted GPS depth loggers.

Head and body accelerations

Simultaneous acceleration data from the head and the back of the penguins were compared with the spectrograms (Fig. 2). Active head movements along the surge, heave and sway axes at a frequency of >5 Hz (i.e. at a cycle of <0.2 s) occurred mainly at the bottom of the dive and, to a lesser extent, during the ascent phases of some dives (Fig. 2). The amplitude of active movement was greater for acceleration data from the head than for that from the back (Fig. 2). Active head movements (>5 Hz) were coincident with changes in body angle at a cycle of approximately 3 s at the bottom of the dive (Fig. 3).

Still images

A total of 19,648 underwater images were taken from two trips of chinstrap penguins and five trips of gentoo penguins (Table 1). Of these, 15,437 images had enough light to determine the presence/absence of prey. Some form of prey was observed in 998 light images. The data included an outlier from a chinstrap penguin for which only two images had prey from a total of 1802 light images. All identified prey species in the images were Antarctic krill (Fig. 4). The proportion of the 'light' dives (see Materials and methods) was 77.3% from a total of 1633 dives. The images showed that the penguins encountered krill patches for a mean of $23.1 \pm 16.1\%$ ($N=7$ trips) of the light dives.

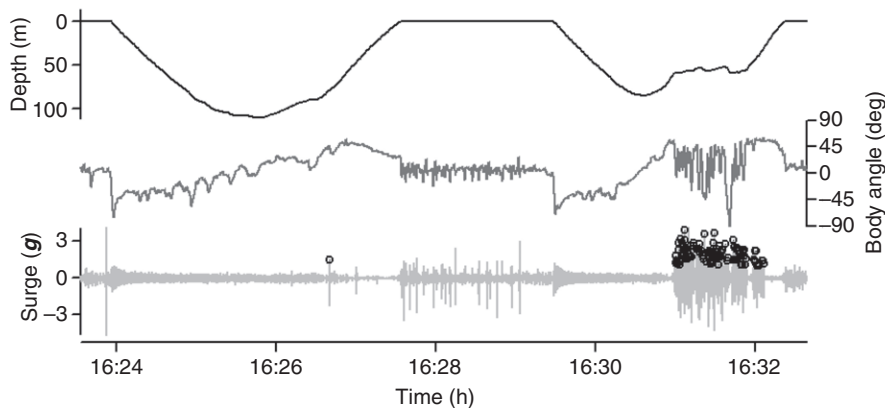


Fig. 3. Time series of diving depth, body angle and the high-frequency (>5 Hz) component of surge acceleration of the head for two gentoo penguin dives (bird G054, 21 January 2010). The time frame is the same as that shown in Fig. 2. The open circles indicate the timing of active head movements (amplitude >1.0 g). Note that the active head movements were observed many times in the second dive, but only a few times in the first.

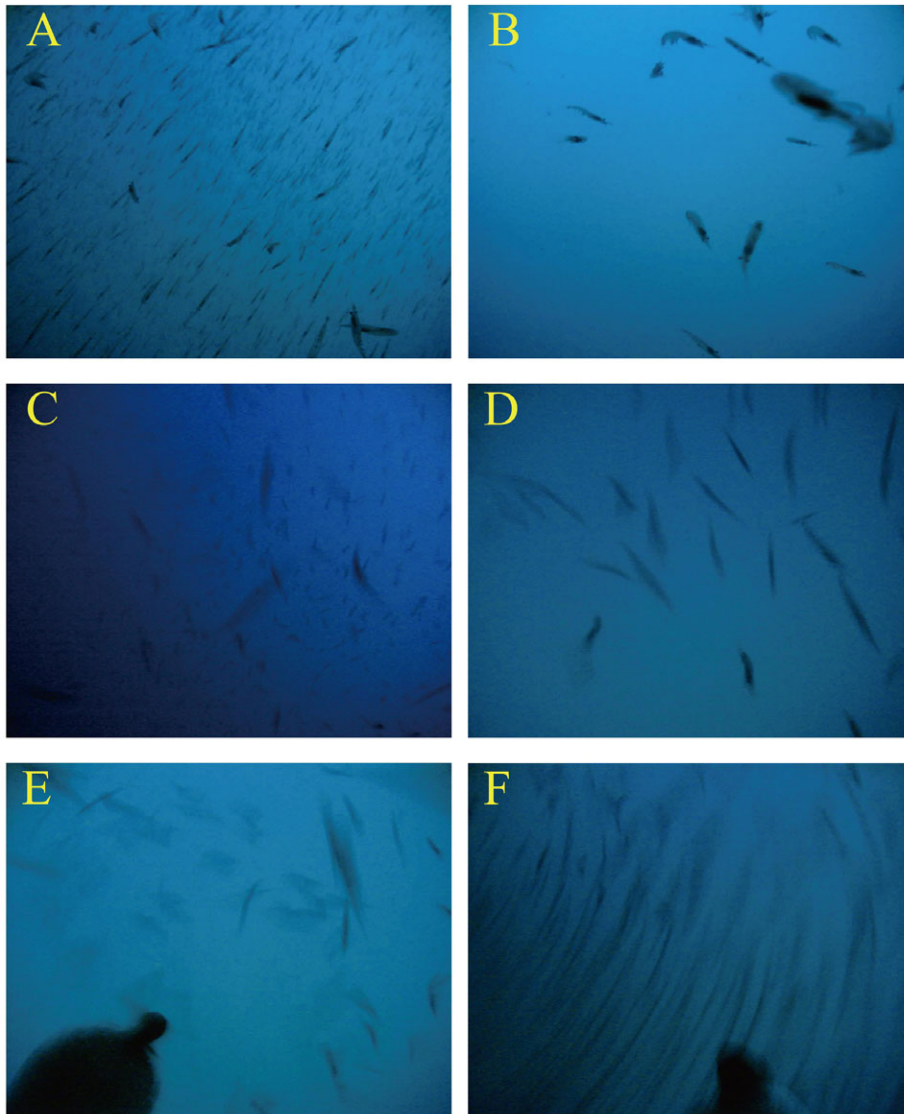


Fig. 4. Selected still images taken by camera loggers obtained from birds C043 (A,B), G038 (C), G044 (D) and G037 (E,F) where 'C' represents chinstrap and 'G' represents gentoo penguins. (A,B) Krill swarms at 20.7 and 19.8 m depth, respectively; (C,D) krill swarms at 92.8 and 73.2 m depth, respectively; and (E,F) penguins attempting to capture the krill at 43.7 and 35.4 m depth, respectively. The black shapes in front of the krill are the head of the penguin with an accelerometer attached.

Correspondence between head movement and prey encounter

Overall, the GLMM model showed that the number of head movements (determined by surge, heave and sway accelerations) was a better indicator than the number of depth wiggles in explaining the number of prey encounter events (Fig. 5). The statistical fit was highest using a threshold amplitude of 1.0 g for surge acceleration (Fig. 5). If heave acceleration was used, the statistical fit was lower than when the other two axes were used. If sway acceleration was used with a threshold amplitude >1.5 g, the statistical fit was greater than when the other two axes were used. Surge acceleration was used for subsequent analyses with a threshold amplitude of 1.0 g. Analysis of temporal concordance between images with prey and head movement indicated that penguins moved their heads within ± 2.5 s of an image with prey being taken for a mean of $89.1 \pm 16.1\%$ ($N=7$ trips) of cases.

We tentatively defined the number of the head movements per diving bottom duration as the prey encounter rate of the dive, and its typical time series during the trips is shown in Fig. 6. For comparison, the number of the depth wiggles per diving bottom duration is also shown (Fig. 6). The indicator of head movement rate varied largely among dive bouts, and did not always correspond with the occurrence of dives or the number of depth wiggles per

diving bottom duration (Fig. 6). The coefficient of variation (CV) during trips was greater using head movement rate as an indicator of prey encounter rate than the number of depth wiggles per diving

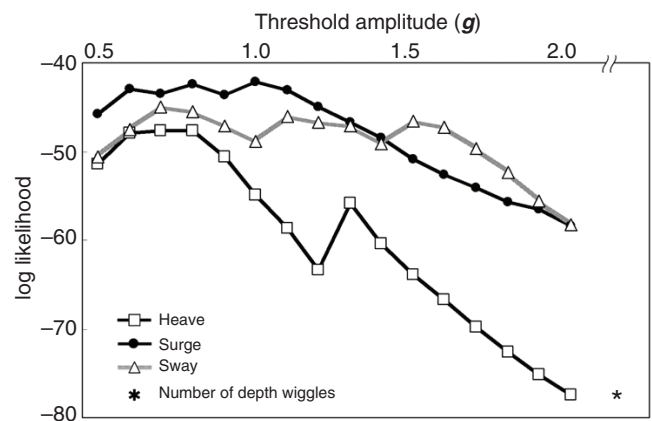


Fig. 5. Log likelihood values for models with different threshold acceleration amplitudes ranging from 0.5 to 2.0 g, obtained from the generalized linear mixed model (see Materials and methods) for three axes (heave, surge and sway) head acceleration and number of depth wiggles.

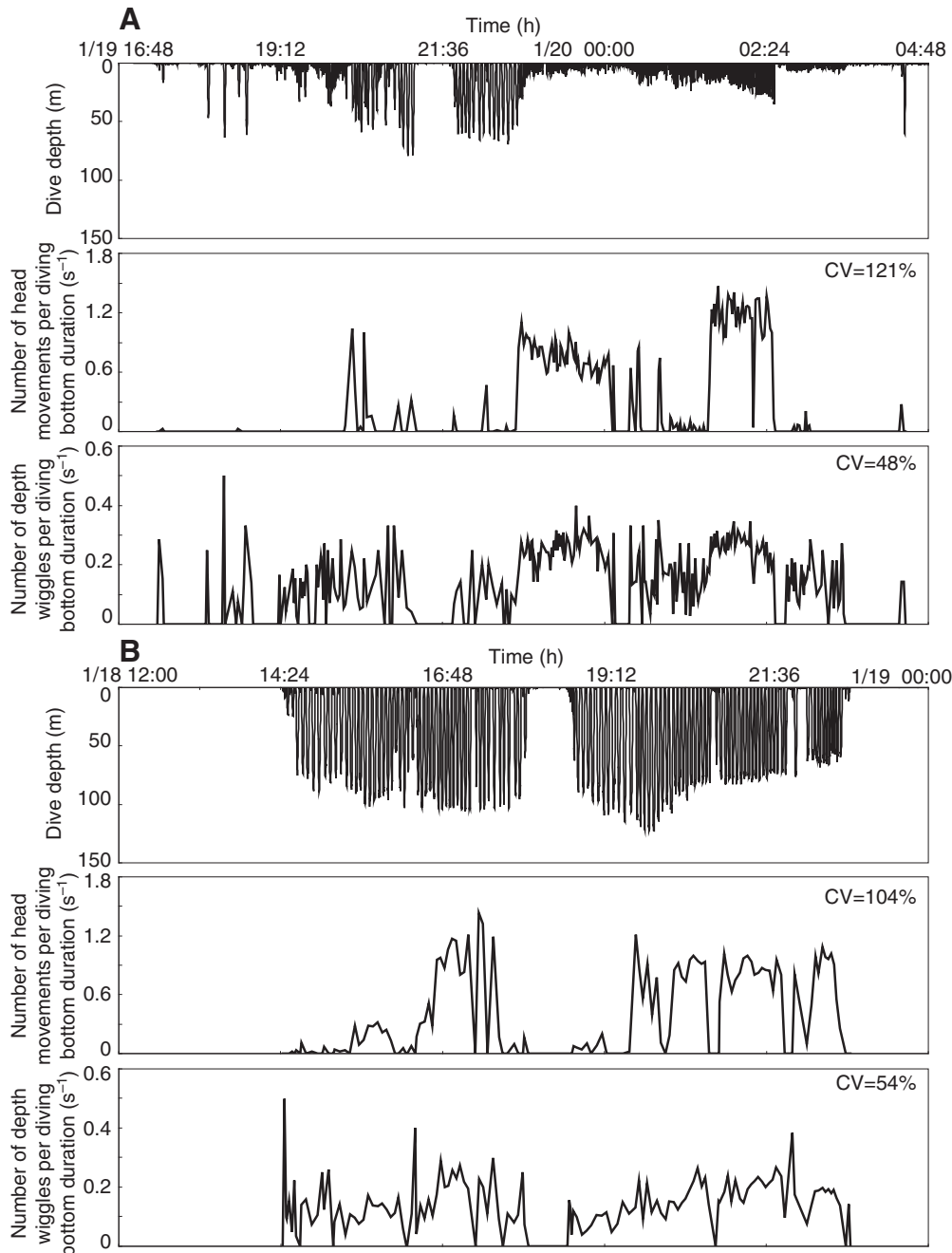


Fig. 6. Time series of (top) diving depth, (middle) number of head movements per diving bottom duration as a proxy of prey encounter rate and (bottom) number of depth wiggles per diving bottom duration for (A) chinstrap and (B) gentoo penguins. CV, coefficient of variation.

bottom duration (Fig. 6). Dives >5 m mostly had low values (<0.5 s⁻¹) of head movement rate for both species (Fig. 7A). This skewed distribution was not observed if the number of the depth wiggles per diving bottom duration was used (Fig. 7B).

Overall, in the present study, head movement rate did not differ between species (for dives >5 m, chinstrap: $0.41 \pm 0.13 \text{ s}^{-1}$; gentoo: $0.42 \pm 0.13 \text{ s}^{-1}$; GLMM with quasi-Poisson error distribution, $P=0.97$). Gentoo penguins dived a little deeper than chinstrap penguins, but the difference was not significant (for dives >5 m, chinstrap: $N=12$ trips, $44.5 \pm 13.9 \text{ m}$; gentoo: $N=13$ trips, $52.7 \pm 16.0 \text{ m}$; GLMM with gamma error distribution, $P=0.17$).

Stomach contents

The main prey item for both chinstrap and gentoo penguins was Antarctic krill (chinstrap: $99.8 \pm 0.2\%$ in wet mass, gentoo:

$99.4 \pm 1.1\%$). In addition, three and two *Pleuragramma antarcticum* were found in the stomach contents of three chinstrap and two gentoo penguins, respectively. The fishes were partially digested.

DISCUSSION

In this study we present a case for detecting prey encounter rates of predators by measuring their active head movements. The concept will be widely applicable for not only diving birds but also a variety of predators including terrestrial species, as long as prey encounter or feeding events associate with head movement. Therefore, together with other metrics, the present method is likely to enable a wide range of ecologists to investigate the foraging strategies of animals at an individual level, in relation to physiological and environmental constraints (Perry and Pianka, 1997). Here we presented results from the simultaneous recording

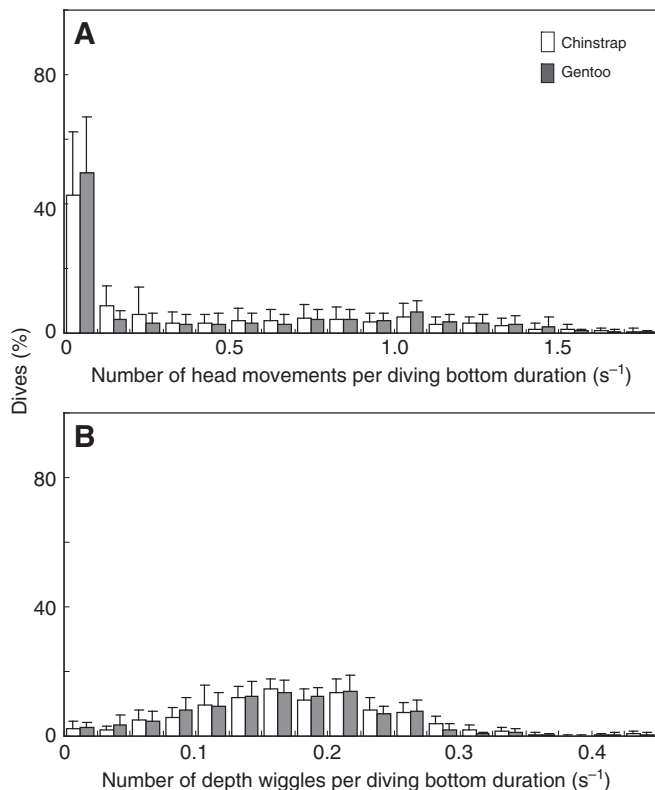


Fig. 7. Distribution of dives in relation to (A) the number of head movements per diving bottom duration and (B) the number of depth wiggles per diving bottom time. Data are means \pm s.d. ($N=12$ and 13 trips for chinstrap and gentoo penguins, respectively).

of underwater active head movement and prey encounter from free-ranging Antarctic penguins. Underwater head movement corresponded well with prey encounter rates detected by bird-borne cameras (Fig. 5), suggesting that head movement (especially in the surge axis) may be related to prey capture attempts in response to prey encounter opportunities.

A key challenge for analyzing top predator foraging strategies is how to increase the recording period as well as how to best detect signal motion relating to foraging (Halsey et al., 2009). The recording duration presented here (33.9 h) was not much longer than that of the beak opening sensor used in previous studies [>21 h (Wilson, 2003), 7.8 h (Takahashi et al., 2004) and 42 and 52 h (Hanuise et al., 2010)]. This is partly because three-axis head movement (>5 Hz) was recorded by a sampling rate of 32 Hz in the present study, although the movement will be detectable using a lower sampling rate of 16 Hz. Reduction of the sampling rate allows flexibility for total recording duration. For example, if only surge acceleration was recorded and the sampling rate of 32 Hz was reduced to 16 Hz, the amount of data recorded and hence the recording duration could be extended by at least three times. Another advantage of our method is that it is 'cable-free'. Although oesophageal temperature sensors (Hanuise et al., 2010) or beak opening sensors (Wilson, 2003) can detect foraging success accurately, these methods require cables that can cause problems with the operation of these devices *in situ*. The frequent regurgitation or dropout of devices and breakage of cables causes failure and/or reduced records (Hanuise et al., 2010). Thus, the precise detection of head movement presented here is an effective

tool for monitoring prey encounter and capture attempts continuously over long time periods (e.g. covering several foraging trips), especially for small diving predators.

Nonetheless, there should be caution in the use of head movement as an indicator of feeding success, for several reasons. First, unlike beak opening or oesophageal temperature drop events (Hanuise et al., 2010), every single head movement event does not necessarily indicate foraging success. However, active head movements along the surge axis (Fig. 2) were linearly correlated to and coincident with the number of prey encounters (Fig. 5). In other words, head movement in the surge axis reflects the sum of prey capture attempts in response to encounter with krill swarms. Second, the value of the filtering frequency or threshold amplitude significantly affects the number of head movements detected, consistent with other techniques to determine animal behaviors using acceleration data (Yoda et al., 2001; Sato et al., 2008). The optimum values of the filtering frequency or threshold amplitude will vary among target species, as well as prey species or foraging strategies. The high-pass filtering frequency of 5 Hz and the threshold amplitude $1.0g$ might be optimum for krill-feeding medium-sized penguins, but might this not be the case for other predators such as piscivorous penguins (Takahashi et al., 2004). Hence the method used here will need to be adapted and validated for other species.

Still images with prey are used as evidence for prey encounter events (Hooker et al., 2002; Takahashi et al., 2008), and we demonstrated here the utility of this method for the analysis of chinstrap and gentoo penguin foraging. Here we found that most foraging occurs in krill swarms (Fig. 4). Nonetheless, this method has the disadvantage that its success relies on the light level being high enough for prey to be visible. We found that 23% of the dives in the present study could not be used to determine prey presence or absence because of low light levels. Thus foraging behavior during overnight trips or at depth (more than 70% of dives occur at depths >70 m) could not be monitored continuously using the camera logger. Equipping camera loggers with flash facilities could result in biases because of the potential for attracting prey with the flash (Heaslip and Hooker, 2008). This highlights another advantage for using head movement data, as in the present study, because it allows prey encounters to be monitored continuously regardless of light level.

The pattern of prey encounter events such as those presented here (Fig. 6) offer the opportunity for exploring ecological context of prey distribution with the obvious step of further analyses of the temporal and spatial structure of foraging. In the present case, the large temporal fluctuations in head movement rate suggest temporal discontinuity of prey encounter rates, which may imply spatial and temporal patchiness in the distribution of the krill swarms (Fig. 6). Dives with high head movement rate sometimes occurred in clusters (Fig. 6). There was a better fit between head movement and prey encounter than the number of depth wiggles and prey encounter (Figs 5, 6) because depth wiggles can indicate diving activities without necessarily encountering prey. Combinations of head accelerometers with GPS depth loggers will add value to our approach by allowing precise three-dimensional monitoring of the prey encounter. The index for prey encounter rate was similar for both species, which suggests that they both feed on krill swarms in similar environments at this location.

In conclusion, we propose that recording the head movement of predators using small accelerometers would be useful for monitoring temporal variations in prey encounter rates over relatively long periods, covering foraging trips. Together with other information such as location (e.g. from GPS depth loggers), this method will

help advance our understanding of the relationship between the environment and the foraging behavior of small or medium-sized predators.

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