



Fine-scale feeding behavior of Weddell seals revealed by a mandible accelerometer

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Abstract

We used a mandible accelerometer to document feeding events in two free-ranging adult female Weddell seals in Atka Bay, Antarctica. Using spectral analysis, we isolated several patterns in the mandible acceleration data. The shorter, un-attenuated signals are thought to represent feeding. The longer, attenuating signals are thought to represent vocalizing activities. The depth data suggest that one seal dived under the base of the iceberg. During these dives we detected a unique type of feeding signal. These signals were characterized by patterns of low amplitude and irregular peaks. A second signal type, characterized by a larger amplitude, was observed 75 times at depths shallower than 60 m. The number of feeding signals per dive was higher for iceberg associated dives (>60 m, 11.3 signals/dive) than for dives to midwater depths (<60 m, 0.5 signals/dive). Our results support the hypothesis that underwater surface of icebergs serves as a habitat for marine fauna. We recorded the first vocalization related signals in seals using a mandible accelerometer. One seal spent significantly more time in shallow water and foraged less than the second seal. This seal also vocalized more often (135 events) than the second individual (29 events), possibly due to an emphasis on mating behavior.

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1. Introduction

Measurements of feeding events are essential to our understanding of the foraging ecology of marine mammals and seabirds. A variety of techniques have been developed to record prey ingestion by marine

endotherms. Stomach temperature recorders utilize the difference between the temperature of ectothermic prey and the stomach temperature of an endothermic predator to measure prey ingestion. This concept has been used extensively in seabirds (e.g. Wilson et al., 1992) and seals (e.g. Gales and Renouf, 1993; Kuhn and Costa, 2006). An alternative approach is based on fine-scale recordings of the movement of the beak or mandible when prey is caught and swallowed. The

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movement is detected by a strain-gauge, reed switch, or magnet-hall inter-mandibular angle sensor (IMASEN, Wilson et al., 2002). This approach has been used successfully to measure feeding behavior in seabirds (e.g. Simeone and Wilson, 2003; Takahashi et al., 2004) and seals (e.g. Bornemann et al., 1992; Plötz et al., 2001; Liebsch et al., 2007).

The “mandible movement method” is non-invasive and the potential loss or non-retrieval of instruments is of less concern regarding to animal health than for the instruments that measure stomach temperature. All techniques require retrieval of the data loggers. Handling and deployment of these loggers is often difficult under field conditions. Naito (2007) proposed a new method for recording feeding events based on a miniaturized acceleration data logger that could be attached to the mandibles of marine predators. The new mandible accelerometer was successfully tested in captive hooded seals, and provided an accurate record of feeding events (Suzuki et al., 2009). In addition, the accelerometer provides information on the posture and body movement of the animals (Yoda et al., 2001; Sato et al., 2003). This data is useful for the assessment of foraging tactics. Our objectives were to (1) examine the feasibility of deploying mandible accelerometers (MACs) in free-ranging Weddell seals and (2) to document the feeding behavior of seals under the iceberg in Atka Bay.

2. Materials and methods

The experiments were conducted in Atka Bay, near Neumayer Station (70°39'S, 08°15'W), in early December 2008. Atka Bay is located at the face of the Ekstrøm Ice Shelf in the eastern Weddell Sea and is flanked by floating ice shelf cliffs (see details: Klinck, 2008) (Fig. 1A). Water depths range from ~80 to 250 m (Schenke et al., 1997; Wegener, 1981). The sea ice in the bay provides a birthing site for many Weddell seals that gain access to the water via breathing holes and tidal cracks at the base of the icebergs located within the bay (Fig. 2). We captured three non-lactating female Weddell seals from a tidal crack (Wed 06) or in the immediate vicinity of an iceberg (Wed 12 and Wed 16) (Fig. 1C–E). The seals were anesthetized (see doi:10.1594/PANGAEA.710899 for dose rates) and the MAC (15 mm diameter, 53 mm length, 18 g in air; Little Leonard Co., Tokyo, Japan) was then glued to the hair below the center of the lower jaws using Araldite® epoxy resin and nylon mesh (Fig. 1B). In addition, we attached a digital still image logger (DSL: 22 mm diameter, 132 mm length, 82 g in air; Little

Leonard Co., Tokyo, Japan) to the head of each individual.

We obtained depth and environmental temperature data at 1 Hz and two way acceleration, heave (x), and surge (y) data at 32 Hz over three consecutive days from all seals. The depth data from Wed 12 suggested that this individual did not enter the water, therefore, the data from Wed 12 were excluded from the analysis. The majority of the still images were underexposed as the DSL was not equipped with a flash system. Thus, the images did not provide useful information on potential prey items.

We excluded data from dives that were <0.5 m in depth as the majority of jaw activity in this layer is likely related to the animals rearing the sides of their breathing holes (Liebsch et al., 2007). The acceleration data were processed and analyzed using the Ethographer package (Sakamoto et al., 2009) and Igor Filtering Design Laboratory (IFDL; ver.4, WaveMetrics) with Igor Pro software (6.30 J; Wave Matris, OR, United States). The Ethographer package is freely available at <http://bre.soc.i.kyoto-u.ac.jp/bls/index.php&Ethographer>.

To discriminate feeding behavior from miscellaneous acceleration records (e.g. body and head movements), we applied a continuous wavelet transformation to the Y axis data (longitudinal acceleration and pitch angle) using the Spectrum Analysis function in Ethographer with Igor Pro. We observed many high band signals between 0.4 and 10 Hz, suggesting the occurrence of behaviors that are characterized by periodicity of the mandibular acceleration signal. Based on these observations, and assuming that feeding behavior occurs underwater in quick motions that define the periodicity, duration, and the level of acceleration (Suzuki et al., 2009), we attempted to extract feeding events by filtering the depth and acceleration data with the mask manipulation function in the Ethographer. The acceleration data were further processed into dominant cycle (DC) and dominant amplitude (DA) data by filtering by amplitude and periodicity using the peak tracer function in Spectrum Analysis. The acceleration data for Wed 06 filtered using the following masks: depth > 0.5 m, DC > 0.4 Hz, DA > 1 G (9.8 m²/s), and duration > 1.5 s. We manipulated these masks and isolated feeding events using the mask calculation function. The data for Wed 16 was characterized by frequent acceleration changes with low peaks only occurring when the seal reached the bottom of dives that were deeper than 60 m. Therefore, the data for this individual were filtered through additional masks: depth > 0.5 m, <60 m, and >60 m; DC > 0.4 Hz; DA > 0.7 G and >1.5 G; and duration > 1.5 s. Combinations of these masks were then applied to isolate the quick motion signals (feeding

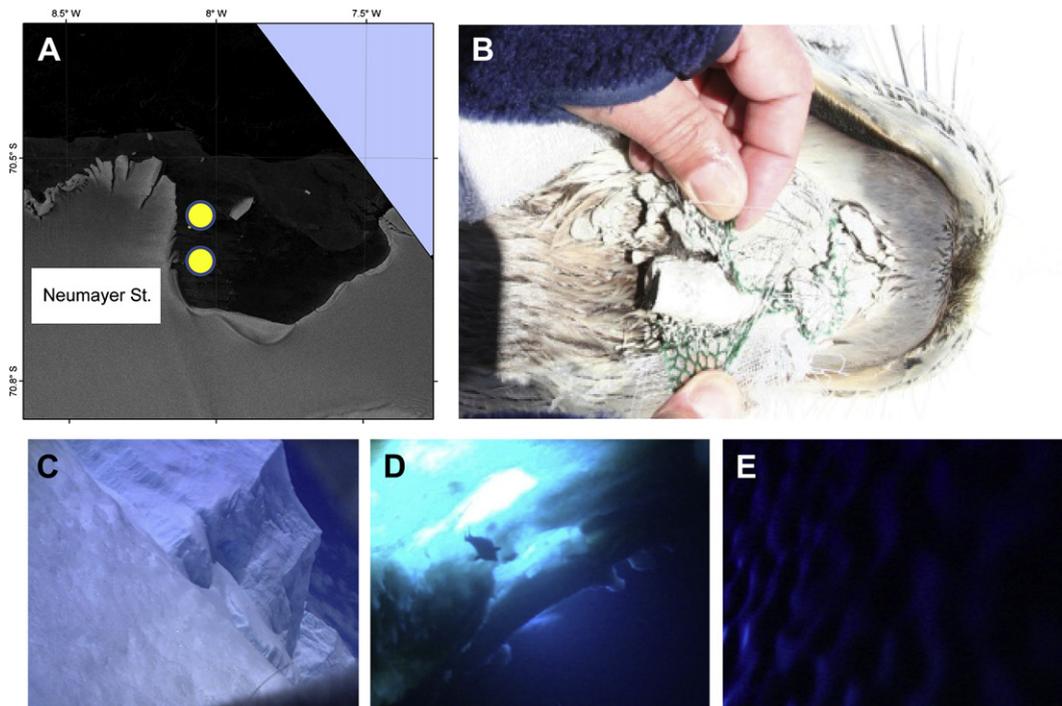


Fig. 1. (A) Envisat ASAR image showing the shelf ice contour around Atka Bay, including Neumayer Station ($70^{\circ}39'S$, $08^{\circ}15'W$), on 2008-11-15. Atka Bay is ~ 20 km long and wide, marking a permanent indentation in the front of the Ekström Ice Shelf on the coast of Queen Maud Land. The bay is flanked by floating ice shelf cliffs with an ice thickness of ~ 80 m at the outer ice margin, rising up to 200 m within the first 5 km to the south. Water depths inside the bay range from 80 to 250 m. Two Weddell seals (Wed 12 and Wed 16) were tagged at $70^{\circ}34.7160'S$ $8^{\circ}5.3940'W$ in the immediate vicinity of a stranded iceberg on 2008-12-11 (upper dot). Seal 06 was tagged close to a tidal crack in the sea ice (lower dot) on 2008-11-21. (B) The acceleration logger was glued below the center part of the lower jaws (right) and programmed for a 99-h delayed start. (C, D, E) The DSL attached to Wed 16 provided images of the environment encountered by the seal. The seal hauled out in the vicinity of the iceberg (C). The seals entered the water using a tidal crack near the iceberg. We observed a seal pup swimming in shallow water near the tidal crack (D). The underside of the sea ice near the tide crack was thin and contoured. The seal dived along the side wall of the iceberg (E).

events). We also defined quick motion signals that had an attenuating pattern (vocalization events) by constructing masks (e.g. dominant cycle > 0.4 Hz, dominant amp > 0.3 G, duration > 1 s) for both seals.

We compared the acceleration levels of the heave (x) and surge axes (y) in both positive and negative oscillations and found no significant differences between the x - and y -axes (Mann–Whitney rank sum test $P > 0.5$). Therefore, we only used the y axis for the analysis of events.

3. Results

3.1. Diving behavior beside the iceberg

Wed 06 spent the majority of the experimental period in the water in close proximity to the surface (≤ 0.5 m) and completed a total of 269 dives, some to midwater depths of up to 56 m (Fig. 2). Wed 16 performed a total of 167 dives during the two consecutive

days. The distribution of dive depths was bimodal and ranged from shallow to midwater (up to 79 m) (Fig. 2). Based on bathymetric data (water depth ~ 125 m; Schenke et al., 1997; Wegener, 1981), all the dives of both seals were classified as pelagic. Analysis of the DSL image data suggested that both individuals dived near the face of the iceberg (Fig. 1E).

3.2. Mandible movements

During the initial visual evaluation of the signal data we distinguished several events that were characterized by an attenuating pattern. Therefore, the signals were classified into two principal patterns, those that were short in duration (Type A) and those that were long in duration and had an attenuating pattern (Type B) (Table 1, Fig. 3). The Type B signal occurred with greater frequency (135 times) than Type A (16 times) in the data collected from Wed 06. Visual examination of the Type A signals from Wed 16, revealed a unique,

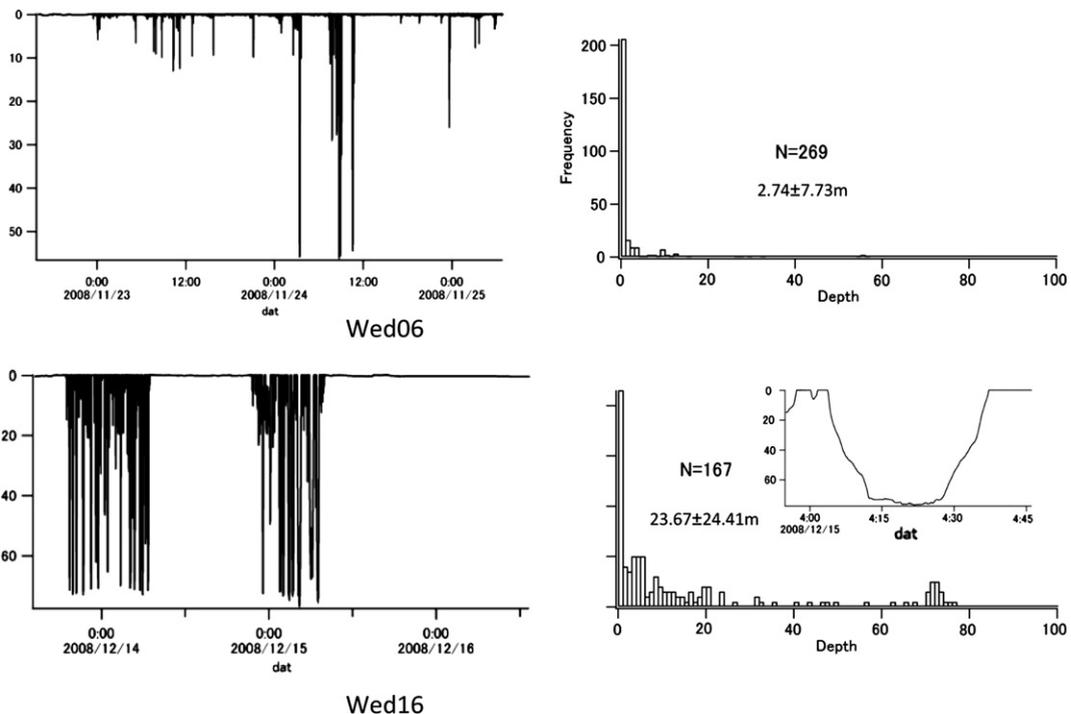


Fig. 2. Dive profiles and dive depth distribution for Wed 06 (upper), Wed 16 (lower), and an enlarged typical dive profile of Wed 16 (inset). Wed 16 foraged actively during the experimental period and the distribution of dive depths was bimodal. The dive profiles were characterized by a flat bottom for dives that were >60 m deep.

irregular pattern when the seal was swimming at depth (72.4 ± 3.6 m) (Fig. 3, middle). Thus, we divided the Type A signals into two subunits based on the depth and signal pattern, a shallow (<60 m) and a deep (>60 m) subunit. The deep subunit signal occurred with much greater frequency than the shallow subunit signal in the data from Wed 16 (shallow: 0.5/dive, deep: 11.3/dive, overall mean: 4.7/dive). Similarly, DA differed significantly ($P < 0.001$) between shallow (1.02 ± 0.42 m s⁻², $n = 231$) and deep (4.38 ± 2.68 m s⁻², $n = 75$)

subunits. The bimodal frequency distribution of the Type A events was even more pronounced in the data from Wed 16 than the distribution of dive depths (Fig. 4).

We isolated 135 Type B events in the 269 dives of Wed 06 (0.5/dive) and 29 events in the 167 dives of Wed 16 (0.17/dive). These events were only observed in shallow water (Wed 06: 2.1 ± 4.9 m; Wed 16: 6.8 ± 5.0 m). Due to gradual attenuation (fade-out) of the acceleration level (Fig. 3, bottom), the termination

Table 1

Duration, depth, and dominant amplitude of the Type A and B acceleration signals from Wed 06 and Wed 16. Differences between the two subunits were evaluated with a Mann–Whitney U-test.

	No.	Depth (m)	Duration (s)	Dominant amp (m/s ²)
<i>Wed 06</i>				
Type A	16	16.43 ± 23.73	0.83 ± 0.25	1.53 ± 0.15
Type B	135	2.16 ± 4.9	4.42 ± 2.62	1.30 ± 1.78
<i>U-test</i>	–	–	$P < 0.001$	$P < 0.001$
<i>Wed 16</i>				
Type A	313	57.48 ± 27.63	2.4 ± 1.67	1.8 ± 2.3
Type B	29	6.21 ± 6.42	4.08 ± 3.64	7.44 ± 4.80
<i>U-test</i>	–	–	$P = 0.087$	$P < 0.001$
Type A subunit	<60 m	10.21 ± 14.05	2.73 ± 2.43	4.28 ± 3.68
	>60 m	72.37 ± 3.64	2.30 ± 1.33	1.01 ± 0.42
<i>U-test</i>	–	–	$P = 0.758$	$P < 0.001$

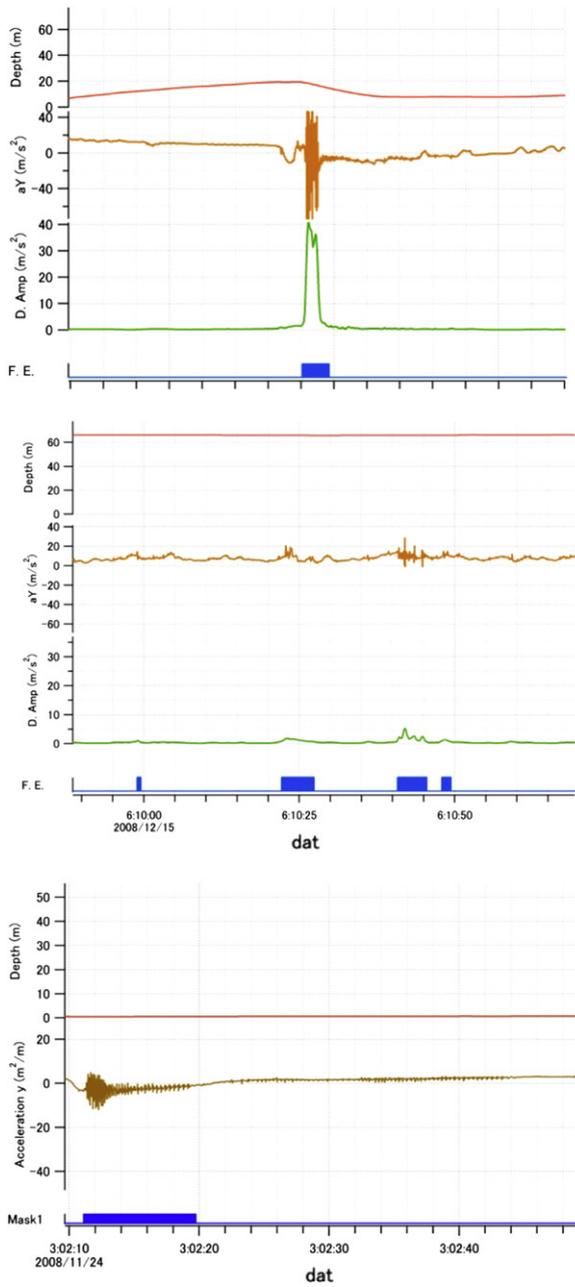


Fig. 3. The acceleration pattern in the Y axis (aY) was classified into two types, short duration (Type A) and long duration with attenuation (Type B). Type A signals were further separated into two subunits, a shallow type (upper), possibly caused during active biting motions, and deep type (middle) possibly caused during subsurface feeding under the iceberg. Type B (bottom) is thought to represent the head bobbing associated with vocalizations. Solid bars in the F.E. column indicate the duration of each event which was filtered by mask manipulation. F.E. = feeding event; D. Amp = dominant amplitude.

of these events was difficult to detect. However, the duration of Type B was longer than Type A (Table 1).

The accelerometer data also provided an indication of posture and stroking movements in the seals. For example, among the 75 Type A events in water depths of less than 60 m (Wed 16), we observed one strong distinctive Type A signal that was similar to a prey stalking and capture attempt reported by Davis et al. (1999). Based on their description, we hypothesize that Wed 16 began stalking a prey item at 15.2 m water depth. This was characterized by high amplitude and low frequency strokes in the accelerometer data (shown as “A” in Fig. 5). At a depth of 35.1 m the seal changed its head direction upward. A few seconds later the seal captured its prey during the period from 05:31:36 to 05:31:52 (“B”). Thereafter the seal appeared to carry the prey towards the surface, as indicated by abrupt changes in depth from 05:31:52 to 05:44:02 (“C”). Finally, the seal took 24 deep breaths

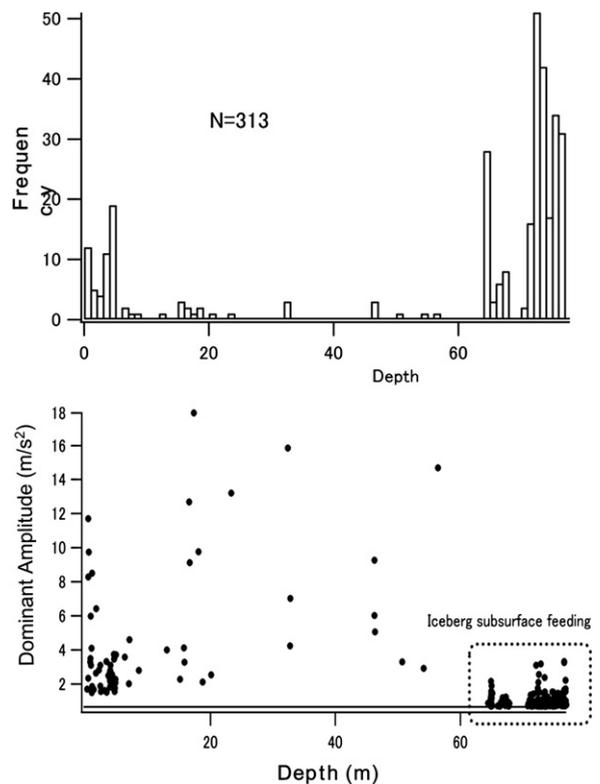


Fig. 4. Depth distribution of the acceleration signals (upper) and DA of the signals (lower) logged by the MAC attached to Wed 16. The depth data are bimodally distributed (<20 m and >60 m). The higher frequency of signals from depths between 60 and 80 m, and the lower DA at these depths, suggests that Wed 16 preferred to dive under the base of the iceberg to forage for small sized prey.

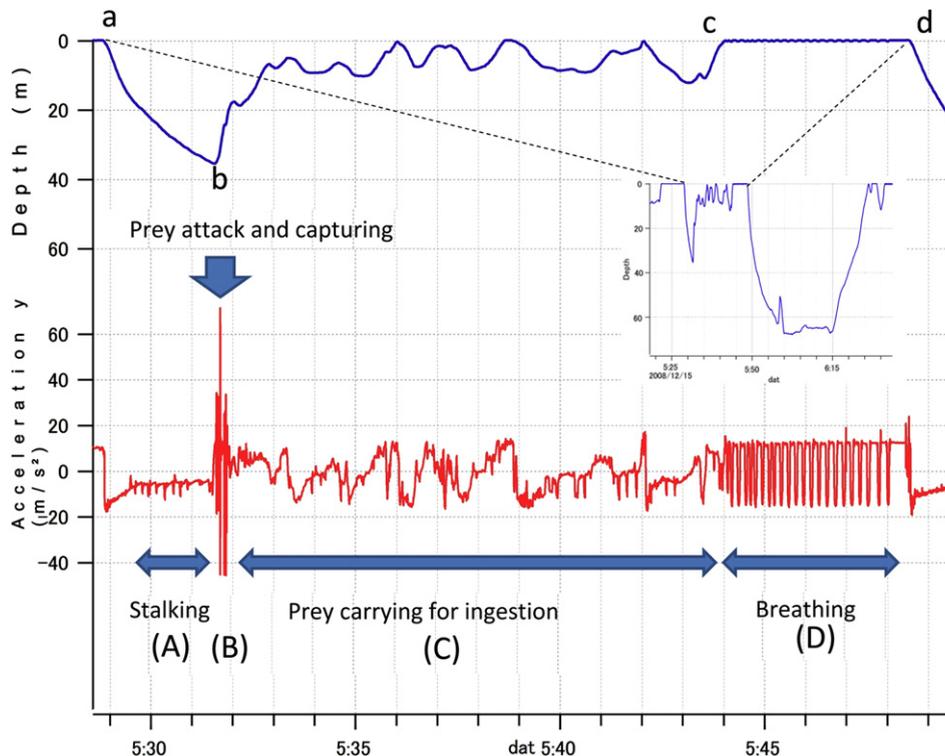


Fig. 5. Unique dive profile from Wed 16. The profiles of both depth and acceleration were enlarged to examine the behavioral process during this foraging dive. Wed 16 began the dive at (a). This was followed by strong but low frequency strokes (A). The descent phase ended at (b) coincident with a prey capture event (B). This was associated with a rapid change in acceleration followed by complicated prey carrying or manipulation behavior (C). This was followed by abrupt depth changes, with the seal visiting the surface once for 12 s (<0 m depth). The dive ended at (c) and was followed by breathing (24 times) with increasing intervals between the breaths (D). Wed 16 then began the next dive with regular strokes which were maintained at a lower level compared with the stalking strokes (A) in the previous dive.

with an increasing interval (“D”), characterized by static gravity changes caused by a change of head angle during breathing.

4. Discussion

The feeding behavior of free-ranging seals was documented by Liebsch et al. (2007). The authors used IMASEN to record the movement of the mandible in free-ranging Weddell seals. More recently, Suzuki et al. (2009) validated the use of MACs for measuring feeding activity in captive seals. The current study is the first to evaluate the use of MACs in free-ranging seals.

Using the MACs, we documented two types of movements, A and B. Type A behavior was further classified into two subunits, shallow and deep. We hypothesize that both shallow and deep subunits represent feeding related motions. Davis et al. (1999) reported midwater feeding using an animal-borne video system. The authors also reported blowing

behavior in Weddell seals near the undersurface of the sea ice. However, it is unlikely that the shallow subunit signals are representative of blowing behavior, because we excluded any data from dives <0.5 m. Furthermore, the signals were all acquired at midwater depths. The deep subunit included signals that were acquired while the seals were at the bottom of their dive profile at depths >60 m. The signals were characterized by a unique irregular pattern and occurred at a very high frequency relative to the shallow subunit (Fig. 3). This type of behavior was very different from those reported by Liebsch et al. (2007) and Suzuki et al. (2009).

The only other report of feeding rates in Weddell seals is by Liebsch et al. (2007). The feeding rates of Wed 06 (0.06 events/dive) and Wed 16 at depths <60 m (0.5 events/dive) were substantially lower than the 2.8 events/dive reported by Liebsch et al. (2007). However, the feeding rate was considerably higher during the deep type (irregular pattern) dives of Wed 16 (11.3 events/dive). Plötz et al. (2001) noted a bimodal distribution of dive depths in Weddell seals

that were foraging in the vicinity of the shelf ice edge in Drescher Inlet (Riiser-Larsen Ice Shelf). Watanabe et al. (2006) and Liebsch et al. (2007) also observed this bimodal pattern at the same location. The absence of normal up and down movements during the bottom phase of the pelagic dives of Wed 16, and side wall images taken by the seal-borne DSL, suggests that the seal may have followed the underwater contour of the iceberg (Figs. 1 and 2). The distribution of the irregular pattern is in congruence with the preferred dive depths of ~70 m. We hypothesize that Wed 16 selected this depth because of an abundance of prey associated with the underside of the iceberg. Feeding on cryo-benthic fauna attached to the iceberg (as described by Watanabe et al. (2006) for a floating ice shelf) would explain the low amplitude of irregular patterns and the increased number of events, which are indicative of irregular feeding (e.g. on small crustaceans). Images from the DSL and our own observations of the seal during deployment confirm that Wed 16 was diving in close proximity to a stranded iceberg (Fig. 1). Animal-borne CTD-casts of an adult male tagged with a CTD satellite-relay data logger at the same location (unpublished data) revealed precipitous temperature drops of 0.02–0.03 °C at depths between 60 and 100 m, consistent with predicted influence of the ice shelf or iceberg contours.

We hypothesize that the Type B behavior represents vocalization in Weddell seals. A number of vocalizations (e.g. chirps, trills, and guttural-glugs) have been reported in Weddell seals during the breeding season. It is well known that Weddell seals bob their heads repetitively while vocalizing at shallow depths (Evans et al., 2004). This head bobbing behavior is likely to be recorded by the MAC. Thus, the identification of mandible acceleration events at shallow depths may have been biased by vocalizations made by the study animals. Underwater vocalizations of Weddell seals are assumed to be related to mating (e.g. Green and Burton, 1998), and are generally attributed to males (see Van Parijs, 2003 for a review). However, female Weddell seals are also known to produce underwater vocalizations (Oetelaar et al., 2003). Thus, the comparatively low feeding rate and high vocalizing rate of Wed 06, relative to Wed 16, may be related to an emphasis on mating behavior.

Davis et al. (1999) documented the encounters of Weddell seals with large Antarctic cod, *Dissostichus mawsoni*, in midwater depths. The prey-stalking movements reported in their study are consistent with the dive profiles of seal Wed 16 (Fig. 5). Based on the image data, the dim light conditions are restricted to

the direct vicinity of ice cracks and breathing holes under the unbroken fast ice. However, scattered light reflections from the iceberg may offer enough back-light for seals to distinguish the silhouette of prey.

In summary, we successfully deployed mandible accelerometers for the first time on free-ranging Weddell seals. Our results suggest that this method may be used to document feeding behavior; however, the technique should be validated using video evidence. Despite the small sample size, our results support the hypothesis that Weddell seals forage along the underwater surface of icebergs (Plötz et al., 2001; Watanabe et al., 2006).

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