Identifying and quantifying prey consumption using stomach temperature change in pinnipeds

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Summary

For many marine predators knowledge of foraging behavior is limited to inferences based on changes in diving or movement patterns at sea. This results in an incomplete and potentially inaccurate view of the foraging ecology of a species. This study examined the use of stomach temperature telemetry to identify and quantify prey consumed in both a phocid (northern elephant seal *Mirounga angustirostris*) and an otariid (California sea lion *Zalophus californianus*) species. In addition, we used opportunistic water consumption by northern elephant seals to test a method to distinguish between prey and water ingestion. Over 96% of feedings could be identified based on a decline in stomach temperature, even when meals were separated by as little as 70 min. Water consumption was distinguishable from prey consumption, as the rate of recovery in stomach temperature was significantly faster for water ($F_{1,142}=79.2$, $P<0.01$). However, using this method, the overlap in recovery rates between prey and water resulted in 30.6% of water ingestion events being misclassified as prey ingestion. For both species, the integral calculated from the decline in stomach temperature over time (area above the curve) could be used to estimate mass consumed, when adjusted for the temperature difference between the prey and core body temperature. For California sea lions, there was a significant effect of individual on the ability to quantify prey consumed, which was not related to their mass or sex. Although many factors may influence the ability to use stomach temperature change to identify and quantify prey consumed, this study has shown measures of stomach temperature can accurately identify prey consumption and provide an estimate of meal mass, allowing for a greater understanding of the feeding behavior of marine mammals.

Key words: feeding behavior, stomach temperature, northern elephant seal, California sea lion, water ingestion.

Introduction

Knowledge of when and where predators forage is critical for understanding their role in the ecosystem and impacts on other species. With the development of time-depth recorders and satellite tracking transmitters, at-sea diving and movement patterns have been used to infer the foraging behavior of many marine predators (Boyd and Croxall, 1996; Costa, 1993; Kooyman, 1965; Kooyman, 1989; Shaffer and Costa, 2006). Previous studies examined changes in at-sea behavior, such as movement patterns (Le Boeuf et al., 2000; McConnell et al., 1999), dive shapes (Hindell et al., 1991; Lesage et al., 1999; Simeone and Wilson, 2003) and swim velocity (Le Boeuf et al., 1992; Lesage et al., 1999) to identify foraging. However, time-depth recorders and satellite transmitters cannot provide information about when and where prey are captured, and instead define putative foraging behavior. In order to truly understand the foraging ecology of a species, it is necessary to combine measures of feeding behavior with data collected on at-sea diving and movements.

To examine at-sea feeding behavior, technology to measure stomach temperature has been used with a variety of marine predators, such as seabirds (Catry et al., 2004; Grémillet and Plös, 1994; Weimerskirch et al., 2005; Weimerskirch and Wilson, 1992; Wilson et al., 1992), sharks (Klimley et al., 2001; Sepulveda et al., 2004), turtles (Tanaka et al., 1995), and marine mammals (Andrews, 1998; Austin et al., 2006; Hedd et al., 1995; Lesage et al., 1999). This technology is based on the assumption that ectothermic prey of marine endotherms is colder than the predators' core body temperature. Therefore, consumption results in a rapid decline in stomach temperature (Fig. 1).

Stomach temperature telemetry has been tested extensively with captive validations on a variety of seabird species (Ancel et al., 1997; Catry et al., 2004; Grémillet and Plös, 1994; Ropert-Coudert et al., 2000; Wilson et al., 1992; Wilson et al., 1995). These studies have shown that identifying both prey and water consumption is possible; however the best method to quantify prey consumed differs among species. These

instruments have been used frequently on free-ranging marine mammals (Andrews, 1998; Austin et al., 2006; Hedd et al., 1995; Lesage et al., 1999), but only limited effort has been made to validate the technique (Bekkby and Bjørge, 1998; Gales and Renouf, 1993; Hedd et al., 1996). Owing to the complicated nature of interpreting stomach temperature data, including the potential need to distinguish between prey and water ingestion, studies of feeding behavior can be misinterpreted in the absence of validation (Catry et al., 2004; Grémillet and Plös, 1994; Wilson et al., 1995).

Previous validation studies with marine mammals were limited by small numbers of study subjects or by small numbers of experiments per animal. Fish, ice, snow and free water intake could all be identified in four harp seals (*Phoca groenlandica*) using changes in stomach temperature (Gales and Renouf, 1993). In this study, using only 11 feedings, a significant linear relationship was found between meal mass and the time it took for stomach temperature to recover to pre-ingestion temperature. The effects of meal size, fish temperature and fish size on changes in stomach temperature were also investigated in two harbor seals *Phoca vitulina* (Bekkby and Bjørge, 1998). The response in stomach temperature was significantly different between these individuals and data from each animal had to be treated independently, further limiting sample size. Finally, a study re-examining the use of stomach temperature telemetry with harp seals (*N*=7), demonstrated that prey and water consumption could be identified and distinguished based on changes in stomach temperature (Hedd et al., 1996).

The previously described studies have attempted to measure the accuracy of both identifying and quantifying prey consumed, but they have all been limited to phocid seals (true seals). To date, we are unaware of published research that has validated the use of stomach temperature records to identify and quantify prey consumed by an otariid seal (fur seals and sea lions). With differences in body size, metabolic rate and core body temperature (Bartholomew, 1954; Bartholomew and Wilke, 1956; Nagy, 1987), it is possible that the changes in stomach temperature, resulting from feeding, differ between these families.

This study tested the accuracy of stomach temperature telemeters in identifying prey consumption in both a phocid (northern elephant seal *Mirounga angustirostris*) and an otariid (California sea lion *Zalophus californianus*) species. In addition, we examined changes in stomach temperature to determine if the mass of prey consumed could be estimated and whether estimates differ between species. Based on previous captive studies (Gales and Renouf, 1993; Hedd et al., 1996), we hypothesized meal mass will significantly affect the area above the curve (integral) created by the stomach temperature deflection (Fig. 1). In addition, based on the physics of heat transfer, the rate of the warming of stomach contents should be related to the temperature difference between the animal and the prey (Wilson et al., 1995). Therefore, we hypothesize that meal mass will also result in a significant difference in the area above the curve, adjusted for temperature difference between

the prey and core body temperature (Ancel et al., 1997). Finally, because of opportunistic water consumption by northern elephant seals, we hypothesized water consumption could be distinguished from prey consumption based on the rate of recovery of stomach temperature (Catry et al., 2004). By examining changes in stomach temperature in a controlled environment, it will be possible to better interpret similar data collected on free-ranging animals.

Materials and methods
Study subjects and instrumentation

Stomach temperature was measured using a stomach temperature recorder and stomach temperature telemeter (Wildlife Computers, Redmond, WA, USA). The stomach temperature recorder (10 mm $\times$ 50 mm $\times$ 70 mm) was attached to the dorsal pelage and stored temperatures at 4- or 10-s intervals. The stomach temperature telemeter (63 $\times$ 21.5 mm diameter) was placed in the stomach, *via* a stomach tube or hidden in a fish. The stomach temperature telemeter transmits a pulse that varies with temperature. The inter-pulse interval was measured by the recorder and converted to temperature ($\pm 0.2°C$). Previous laboratory calibrations found that these sensors differed from water temperature by $0.7\pm 0.6°C$ and response times averaged 6.0 ± 0.6 s (Lesage et al., 1999).

To increase retention time in some animals the telemeter was made bigger using an oval foam mount [northern elephant seals, 12 cm $\times$ 16 cm $\times$ 1.5 cm; California sea lions, 8 cm $\times$ 12 cm $\times$ 1.5 cm (Austin et al., 2006)]. In order to minimize influence on the telemeter, the foam mount covered less than 30% of the region of the telemeter that conducted heat to the internal thermistors. When stomach temperature telemeters were expelled, they were immediately re-administered following the methods described above.

Northern elephant seals, *Mirounga angustirostris* Gill (*N*=10) were transported from Año Nuevo State Reserve (CA, USA) to Long Marine Laboratory (LML, University of California, Santa Cruz, CA, USA). Sub-adult male and female elephant seals (approximately 2–3 years of age) were chosen after completion of the annual molt in May–June of 2003, 2004 and 2005. Seals were chosen based on condition, as thin seals with longer new hair growth were more likely to depart for the foraging migration and would potentially be more willing to eat while in captivity. Seals were housed individually in pens with access to haulout areas and saltwater pools (2.3 m $\times$ 2.3 m $\times$ 1.1 m or 4.6 m $\times$ 2.3 m $\times$ 1.1 m). Pool temperature ranged from 10.9 to 17.8°C, with an average of $14.6\pm 0.06°C$.

For transport, and to attach recording equipment, seals were sedated with an initial intramuscular injection of Telazol (Tiletamine hydrochloride and Zolazepam hydrochloride; Fort Dodge Animal Health, Fort Dodge, IA, USA) at 1.0 mg kg^{-1} based on a visual estimate of mass. Sedation was maintained with intravenous doses of ketamine hydrochloride when necessary (Fort Dodge Animal Health). At the completion of the study, stomach temperature recorders were removed

without sedation while the animal was held in a transport cage and animals were released at Año Nuevo State Reserve.

California sea lions *Zalophus californianus* Lesson (*N*=13) were rehabilitation animals from The Marine Mammal Center (TMMC, Sausalito, CA, USA). All animals were treated and deemed releasable by TMMC staff veterinarians before starting the study. Animals were held at either TMMC or LML. Adult females or sub-adult males of comparable body mass were selected for the study. To attach the stomach temperature recorder, sea lions were sedated using gas anesthesia (Isoflurane) from a portable anesthesia machine. Animals were briefly restrained to remove the recorder at the end of the study. Sea lions held at LML were returned to the care of TMMC for release or further treatment if necessary. Sea lions were housed individually with a haulout area and either a fresh (TMMC, range 2.2 m✕0.8 m to 3.1 m✕0.8 m) or saltwater pool (LML, 2.3 m✕2.3 m✕1.1 m or 4.6 m✕2.3 m✕1.1 m). Pool temperature ranged from 9.5 to 26.2°C, with an average of 17.5±0.2°C.

Feeding protocols

All animals were fed whole herring (*Clupea harengus harengus*), and to mimic natural feeding, all fish were warmed to pool temperature as determined by inserting a temperature probe into every fish (±0.1°C; Physitemp Instruments, NJ, USA). Feeding trials were conducted between 07:00 h and 23:30 h. Animals were fed in the water and had to consume all fish within 8 min for a trial to be considered successful. Most feedings were completed in less than 2 min. For each feeding, the times of first and last fish consumption were recorded. Animals were fed exact quantities of 0.5, 1.0, 2.0, 3.0 and 4.0 kg (±0.05 kg). Time to next feeding ranged from a minimum of 70 min to 6 h, depending on meal size and total food consumed for the day. To determine the minimum time between feedings, preliminary experiments were conducted with one captive sea lion. Time to recovery of stomach temperature was calculated and minimum time between feedings was determined as approximately two times the maximum recovery time for that animal. Based on this protocol we assumed that each feeding event was independent from previous feeds. Data from the preliminary experiments were not included in the analysis because the feeding protocol was modified for subsequent experiments. Number of feedings per day for northern elephant seals ranged from 1 to 6, with an average of 2.2±0.9. Sea lions ate on average 2.9±0.1 meals per day (range 1–6). Animals were not given access to food outside of feeding experiments.

Stomach temperature analysis

Stomach temperature changes were analyzed using Sable Systems DataCan V software (Sable Systems, NV, USA). For each drop in stomach temperature, a group of variables were defined for analysis (Fig. 1). Initial temperature was defined as the baseline temperature preceding the sharp decline resulting from feeding or drinking. Minimum temperature was identified and time to minimum was calculated as the interval between
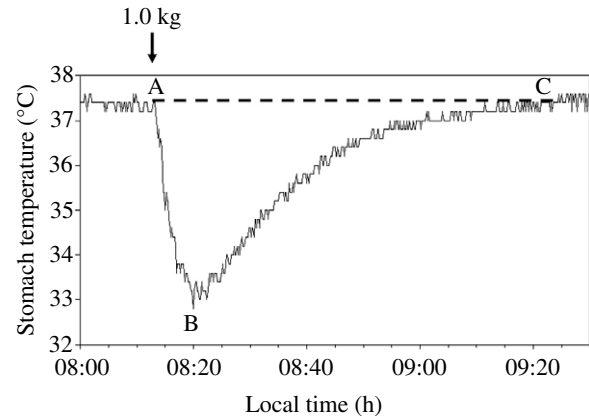

Fig. 1. Characteristic change in stomach temperature as a result of feeding (solid line). Data from a sub-adult male northern elephant seal fed 1.0 kg of herring at 08:12 h (denoted by arrow). Variables used to analyze stomach temperature change are A, initial temperature (°C); B, minimum temperature (°C); C, recovery (min). Area (s °C) was calculated from the broken line to the stomach temperature curve.

time at first fish consumption and the time at minimum temperature. Temperature difference (ΔT) was calculated as the difference between pre-ingestion body temperature and fish (water) temperature. Recovery in the stomach temperature was determined when temperature became stable over a 10 min period (±0.1°C). Time at recovery was then defined as the first temperature reading in the 10 min period. Area above the curve created by the decline in stomach temperature (area) was calculated using the Sable Systems software based on a trapezoidal integration algorithm from the initial temperature to the recovery temperature. When the initial and recovery temperatures were different, area was calculated based on the methods of Wilson et al. (Wilson et al., 1995). Essentially, area was calculated based on the lowest temperature (initial or recovery) and added to one half of the area above this curve (Fig. 2).

A general linear mixed model was used to test the hypotheses that mass consumed can be estimated by (1) area or (2) area/ΔT. We tested a random factor (individual) to examine whether this improved the models, as it is necessary to know the impact of individual variation when applying these models to field studies. Models with and without the random factor were compared using a log-likelihood ratio test. The model with the lowest AIC (Akaike's information criterion) was selected as the best model, unless there was no significant difference between models based on the likelihood ratio test (Burnham and Anderson, 2002). When no impact of individual was found, r^2 values were used to compare area and area/ΔT to determine which showed the stronger relationship to meal mass. In addition, when the random factor was considered significant we tested animal mass and sex as fixed factors.

To determine whether water and prey consumption could be distinguished from one another we followed published methods (Catry et al., 2004), using the equation:
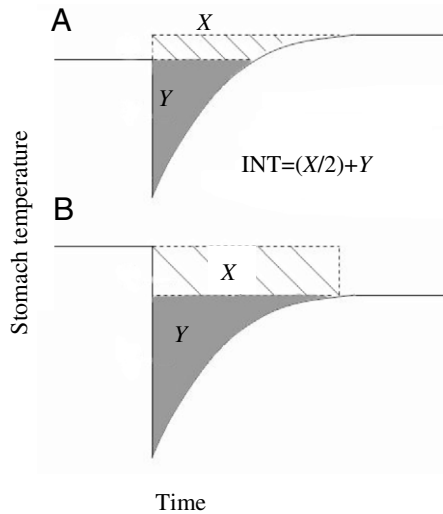
Fig. 2. Method used to calculate the area above the curve created by the drop in stomach temperature when initial temperature and recovery temperature were not equal. Following published methods (Wilson et al., 1995), area was calculated based on the lower temperature (initial or recovery) and added to half the area between the lower and higher temperature [INT=(X/2)+Y]. (A) Recovery temperature was greater than initial temperature. (B) Recovery temperature was lower than initial temperature.

$$I = t_{0.5} / (T_{\mathrm{initial}} - T_{\mathrm{minimum}}) ,$$

where I is an index of the rate of stomach temperature recovery (lower I corresponds with faster recovery), $t_{0.5}$ is the time (s) from the start of the temperature decline to the half-way point of temperature recovery, and T_{initial} is the stomach temperature prior to deflection from feeding or drinking. In albatross, I values for liquid consumption were found to be significantly lower than for prey consumption and I values of less than 30 s °C^{-1} always denoted water ingestion (Catry et al., 2004). I values were calculated for all water ingestion events and a subsample of feeding events.

Summary data are reported as means ± s.e.m. Statistical analysis was conducted using SYSTAT 10 (SPSS Inc., 2000) or R2.2.1 (R. Gentleman and R. Ihaka, http://www.r-project.org). All data were tested for normality and homogeneity of variance. Data that were non-normal or displayed unequal variances were log$_{10}$ or square root transformed. Contrasts were considered significantly different at $P<0.05$.

Results
Study subjects

Eight male and two female northern elephant seals ranging in mass from 132 to 218 kg (average 183.3±7.6 kg), and length from 192 to 277 cm (average 210.5±4.5 cm) were used in the study. There was no significant difference between sexes for mass or length. Seals retained stomach temperature telemeters for 7.1±1.3 days (range, 1–>22 days). Five animals retained

telemeters for the duration of the study (range 15–22 days) and were released without recovering the telemeters. For these individuals, the last day of known retention was used to calculate average retention times.

Nine adult female and four sub-adult male California sea lions were used for the feeding study. Sea lions ranged in mass from 63.0 to 102 kg (average 80.1±2.6 kg). Sub-adult males were significantly larger than females ($F_{1,12}$=21.6, P=0.001); however, these animals were within the range of free-ranging adult females and therefore, the difference was not considered biologically significant for the study. Sea lions retained stomach temperature telemeters for 11.8±2.5 days (range 1–53 days). Three animals retained telemeters for the duration of the study (range 10–22 days) and were released without recovering the telemeters.

Core body temperatures, in the absence of feeding or water ingestions, were variable for both species. Northern elephant seals had an average core body temperature of 36.7±0.2°C, with a range of 36.7–37.9°C. California sea lions had an average core body temperature of 38.1±0.1°C, with a range of 38.1–39.0°C. Average core body temperatures were significantly different between species ($F_{1,21}$=35.9, $P<0.001$).

Identifying feeding events

For the ten northern elephant seals, 432 feeding events were recorded. Data from 17 feedings (4.0%) were determined to be unusable because of missed data points, erroneous values, or instrument failure. Nine feedings (2.1%) showed no change in stomach temperature (range 0–7.3% per animal, N=6 individuals). Of the feedings that showed no change in stomach temperature, six were 0.5 kg and the largest meal not identified was 2.0 kg (N=2). Missed feeding occurred after one or two prior feedings (average 1.2±0.1), however multiple feedings per day were often easily identified (Fig. 3). This resulted in an average of 40.5±0.86 feedings analyzed per animal (range 36–46).

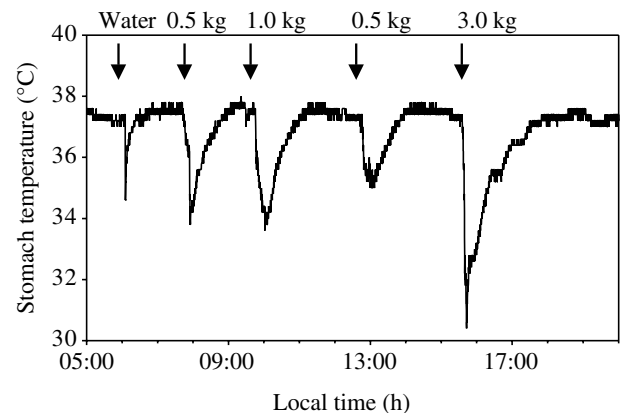For the California sea lions, 497 feeding events were

Fig. 3. Stomach temperature record for a sub-adult male northern elephant seal fed four meals (0.5 kg, 1.0 kg, 0.5 kg and 3.0 kg, denoted by arrows). First decline in stomach temperature was a result of water ingestion.

Table 1. *Summary of stomach temperature change variables for northern elephant seals and California sea lions for each quantity fed*

	Quantity fed					
	0.5 kg	1.0 kg	2.0 kg	3.0 kg	4.0 kg	Water
Elephant seals (N=10)						
T_{min} (°C)	33.6 (0.3)	32.8 (0.2)	31.9 (0.3)	31.6 (0.2)	30.4 (0.2)	32.9 (0.6)
ΔT (°C)	3.2 (0.3)	3.9 (0.2)	4.8 (0.2)	5.2 (0.2)	6.4 (0.2)	4.1 (0.5)
t_{min} (min)	12.2 (0.7)	11.0 (0.7)	13.2 (0.9)	12.5 (0.6)	11.8 (0.4)	–
t_{rec} (min)	61.7 (1.9)	69.8 (2.2)	77.7 (2.6)	87.2 (2.3)	88.1 (2.4)	35.2 (2.2)
Area (s °C)	5105 (507)	6429 (473)	7957 (579)	9779 (406)	11099 (464)	2843 (375)
Sea lions (N=13)						
T_{min} (°C)	34.3 (0.3)	34.0 (0.3)	33.4 (0.3)	33.5 (0.3)	32.8 (0.3)	–
ΔT (°C)	3.7 (0.2)	4.0 (0.2)	4.6 (0.2)	4.6 (0.2)	5.2 (0.2)	–
t_{min} (min)	10.0 (1.1)	12.3 (1.5)	10.1 (0.8)	14.3 (1.3)	10.9 (0.9)	–
t_{rec} (min)	55.2 (2.4)	73.1 (4.5)	81.2 (3.7)	95.2 (5.4)	93.4 (5.2)	–
Area (s °C)	4288 (225)	5657 (282)	7310 (383)	8513 (480)	9255 (458)	–

Values are means (± s.e.m.).

Owing to opportunistic water consumption by elephant seals, stomach temperature change ΔT for water ingestion is included. ΔT is the difference between initial body temperature and minimum temperature T_{min}. Time to minimum temperature t_{min} is the difference between time at minimum and the time of first fish consumption. Recovery time t_{rec} is the time for stomach temperature to return to stable body temperature. Area was calculated based on the stomach temperature change as depicted in Figs 1 and 2.

recorded. Data from 149 feedings (30.0%) were determined to be unusable due to missed data points, erroneous values, or instrument failure. Thirteen feedings (3.8%) showed no change in stomach temperature (range 0–25%, per animal, N=3 individuals). Eight of the feeds that showed no change in stomach temperature were from one individual. Of the feedings that showed no change, seven were 0.5 kg and 11 were less than or equal to 1.0 kg. The largest meal size not identified was 2.0 kg (N=2). Feedings that showed no change occurred after one to three prior feedings (average 1.9±0.2 meals). This resulted in an average of 38.2±2.4 feedings analyzed per animal (range 7–43).

Water consumption

Since sea lions were held at a rehabilitation facility employing numerous volunteers with access to the animals, we cannot be completely certain whether additional drops in stomach temperature were due to water ingestion or extra feedings by volunteers. These drops in stomach temperature only occurred five times for all animals in the 133 days of experiments. Conversely, access to northern elephant seals was limited and all drops in stomach temperature outside of feeding experiments were assumed to be water consumption (N=49, Fig. 3). One northern elephant seal showed no water ingestion events, while the other nine animals consumed water on average 5.8±1.3 times during the study (range 2–13). Water consumption occurred on 9.1 to 43.8% of the days in captivity (average 20.0±4.6%). When animals consumed water, it occurred 1.4±0.1 times per day (range 1–6 ingestions per day) and 70.1±8.2% of the time in the morning prior to the first feed (range for individuals 33.3–100%).

Water consumption (N=49) resulted in significantly lower I

values than fish consumption (N=97, $F_{1,142}$=79.2, $P<0.01$). I values for fish ranged from 55.1 to 4380.0 s °C^{-1} and water ranged from 37.8 to 764.0 s °C^{-1}. To distinguish between fish and water consumption we used a threshold of 250 s °C^{-1}, which resulted in the lowest error rate, with fish consumption being accurately identified 83.5% (N=81) of the time and water misidentified as fish 30.6% of the time (N=15). There was no relationship between meal size and misclassification (χ^2=3.4, P=0.50). Water ingestions showed a faster overall recovery time and smaller area than the smallest meal consumed (0.5 kg; Table 1).

Quantifying feeding events

Feeding events resulted in an average drop in temperature of 4.7±0.1°C and 4.4±0.1°C, for northern elephant seals and California sea lions, respectively. For both species, quantity consumed resulted in differences in all of the variables measured for both species (Table 1).

For northern elephant seals, there was a relationship between meal mass and both $\sqrt{area}$ and $\sqrt{area}/\Delta T$ (Table 2). There was no significant effect of individual for these relationships ($\sqrt{area}$: log-likelihood ratio=1.92, d.f.=1, P=0.17, $\sqrt{area}/\Delta T$: log-likelihood ratio=0.88, d.f.=1, P=0.35). Based on r^2 values $\sqrt{area}/\Delta T$ shows a slightly stronger relationship with meal size ($\sqrt{area}$: r^2=0.29, $\sqrt{area}/\Delta T$: r^2=0.30; Fig. 4). Therefore, the best equation to estimate quantity consumed is: quantity= 0.57($\sqrt{area}/\Delta T$)–0.12.

For California sea lions, both $\sqrt{area}$ and $\sqrt{area}/\Delta T$ were also related to meal mass. Unlike northern elephant seals, there was a significant effect of individual for both models ($\sqrt{area}$: log-likelihood ratio=131.9, d.f.=1, $P<0.01$, $\sqrt{area}/\Delta T$: log-likelihood ratio=53.0, d.f.=1, $P<0.01$). The impact of

Table 2. *Factors affecting the estimate of quantity consumed for each species*

Model	Animal	N		K	AIC	ΔAIC	AICW
√Area	Elephant seals	10	**Quantity***	**5**	**3695.2**	**3.7**	**0.14**
			Quantity + individual*	15	3691.5	0.0	0.86
	Sea lions	13	Quantity	5	2893.3	133.3	>0.01
			Quantity + individual	**18**	**2760.0**	**0.0**	**0.99**
√Area/Δ*T*	Elephant seals		**Quantity***	**5**	**1174.2**	**0.0**	**0.99**
			Quantity + individual*	15	1184.1	9.8	0.01
	Sea lions		Quantity	5	827.4	41.9	>0.01
			Quantity + individual	**18**	**785.4**	**0.0**	**0.99**

The lowest AIC (Akaike's information criterion) value was used to determine the best fitting model (indicated in bold), except when models were not significantly different (*). Included for each model is the Akaike weight (AICW), which can be regarded as the probability that a model is the best, given the set of models. K is the number of model parameters.

individual was not a result of animal mass or sex, as these parameters resulted in higher AIC values. Since it was not possible to account for the impact of individual, the two best models that explain quantity consumed are: quantity= $0.028(\sqrt{area})-0.13$ and quantity=$0.67(\sqrt{area/\Delta T})-0.54$. The equation based on area adjusted for temperature ($\sqrt{area/\Delta T}$) was not significantly different from the equation calculated for the northern elephant seals (Fig. 4; 95% confidence intervals for elephant seals: slope 0.56–0.79, constant $-1.02 - -0.06$).

To test the use of these equations to predict meal size we calculated the percentage error between actual mass and estimated mass. Owing to the variability in stomach temperature responses, the percentage error was high, at 76.9±4.8% for northern elephant seals, and 79.9±5.2% for California sea lions. However, the largest proportion of this error was for feedings of 0.5 kg and resulted from meal mass being overestimated for the smallest meals. When feedings of

1.0 to 4.0 kg were examined the error improves to 42.5±2.3% and 45.6±2.6%, for elephant seals and sea lions, respectively.

Discussion

Through the use of captive validations we have demonstrated that measurement of stomach temperature can accurately identify feeding events and provide an estimate of mass consumed in both a phocid and otariid species. Although stomach temperature telemeters have been used extensively in the lab and field with phocids (Austin et al., 2006; Bekkby and Bjørge, 1998; Gales and Renouf, 1993; Hedd et al., 1995; Hedd et al., 1996; Lesage et al., 1999), only one study used this technology with otariid seals (Andrews, 1998). Previous studies using stomach temperature measurement technology to measure feeding have described its challenges in detail (Ancel et al., 1997; Grémillet and Plös, 1994; Wilson et al., 1992; Wilson et al., 1995). Among these challenges are: retaining the stomach temperature telemeter in the animal, and identifying feeding as the stomach fills (Ancel et al., 1997; Austin et al., 2006; Grémillet and Plös, 1994; Wilson et al., 1995). In the present study, retention times for the stomach temperature telemeter averaged 7 days for elephant seals and 12 days for sea lions. Retention time varied among individuals as some regularly lost telemeters in 1 to 3 days, while others retained telemeters for the length of the study (greater than 22 days). Therefore, the successful use of stomach temperature telemetry in free-ranging animals requires further study to find a reliable method of increasing retention time.

The process of identifying and quantifying prey consumed could also be influenced by many factors such as the location of the telemeter in the stomach, the amount of stomach mixing, and the animals' activity level (Wilson et al., 1995). In addition, the prey species, and more specifically the composition of the prey (fish *versus* squid) is likely to influence the warming process in the stomach (Wilson et al., 1995). Both northern elephant seals and California sea lions consume fish and squid species (Antonelis et al., 1984; Antonelis et al., 1987; Condit and Le Boeuf, 1984; Lowry and Carretta, 1999; Lowry et al., 1991), which may have different thermal and digestive properties. For consistency, all animals in the present study
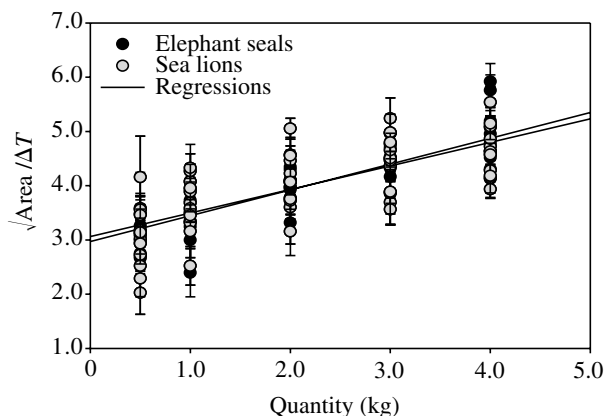

Fig. 4. Relationship between mass consumed and area above the curve created by the decline in stomach temperature, adjusted for temperature difference between animals' core body temperature and fish (Δ*T*). The regression lines for both species are not significantly different (northern elephant seals: $\sqrt{area/\Delta T}$=0.52×quantity+2.9; California sea lions: $\sqrt{area/\Delta T}$=0.41×quantity+3.1). Black circles denote mean values for each individual northern elephant seal (*N*=10), grey circles represent the mean values for individual California sea lions (*N*=13).

were fed the same fish (herring), which has a similar body composition as other prey species found in the diet these two animals (Antonelis et al., 1984; Antonelis et al., 1987; Condit and Le Boeuf, 1984; Lowry and Carretta, 1999; Lowry et al., 1991).

Despite the limitations of stomach temperature technology, its use can still provide valuable information about the foraging behavior of free-ranging seals and sea lions that is currently not available for many species (Andrews, 1998; Austin et al., 2006; Hedd et al., 1995; Lesage et al., 1999).

Identifying consumption

For both species, the identification of feeding occurred with high accuracy (97.9% northern elephant seals, 96.2% California sea lions). Feedings that were not identified tended to be small meals of 1.0 kg or less. Although it is not known what a 'normal' meal size is for either species in the wild, it appears that stomach temperature telemetry can accurately be used to identify prey consumed when feeding events are separated in time. Interestingly, the ability to identify ingestion appears to differ among individuals, as one sea lion had a much greater number of unidentified feedings than the others. In addition, although feeding regimes were similar for all animals, four elephant seals and seven sea lions did not have unidentified feedings. It is not known whether this variation was a result of differences in activity level between individuals, location of the telemeter in the stomach, or other factors not measured in this study.

In addition to identifying feeding events, it was possible to distinguish between prey and water consumption with a relatively high accuracy in northern elephant seals. In grey-headed albatross *Thalassarche chrysostoma*, an index of the rate of recovery of stomach temperature (*I*) was used to distinguish between prey and water ingestion, with 100% accuracy (Catry et al., 2004). However, with the small sample size evaluated (*N*=6 water, *N*=8 feeding), the authors may not have measured the full variation in recovery rates. Although our accuracy was not as high (16.5% of fish ingestion and 30.6% water ingestion misclassified), previous research suggests free-ranging phocids can maintain water balance without free water consumption (Depocas et al., 1971; Ortiz, 2004). Studies with northern elephant seals during both molt and lactation have also found that animals do not consume water during these fasting periods on land (Costa et al., 1986; Worthy et al., 1992). Therefore, the small possibility of misidentification of water consumption as prey may not be a problem when deciphering northern elephant seal stomach temperature data for free-ranging animals.

Quantifying consumption

Previous research with seabirds and marine mammals have used a variety of factors to quantify prey consumed, such as recovery time, total area created by the deflection, and area for only the recovery phase (Fig. 1B–C) (Ancel et al., 1997; Bekkby and Bjørge, 1998; Catry et al., 2004; Gales and Renouf, 1993; Grémillet and Plös, 1994; Hedd et al., 1996; Pütz et al.,

1998). Ancel et al. (Ancel et al., 1997) found a significant relationship when the difference between prey temperature and body temperature was incorporated in the estimate of meal mass (area=mass× Δtemp). For elephant seals this equation provided the best-fit model for estimating mass consumed [quantity=0.57($\sqrt{\text{area}}/\Delta T$)–0.12]. Given that it is possible to measure environmental temperature when dive recorders are used in conjunction with stomach temperature recorders, and fish temperature is similar to the temperature of the environment, all the necessary parameters can be acquired to estimate quantity consumed.

As observed for northern elephant seals, both the area under the curve created by the change in stomach temperature and the area adjusted for temperature difference, were related to mass consumed for sea lions. However, unlike elephant seals, there was a significant effect of individual in both models (Table 2). This difference between individuals was not related to sea lion mass or sex but could be a result of a variety of variables not measured in this study, including differences in metabolic rates, stomach churning, or activity levels. For sea lions, the model using area corrected for temperature difference was not significantly different from that for the northern elephant seals. Therefore, we suggest using area corrected for temperature to estimate mass consumed. Although the added uncertainty of individual differences makes the estimate of meal mass more variable, the similar relationship between stomach temperature change and quantity fed for both species provides support for the use of this technology to estimate mass consumed in free-ranging pinnipeds.

As previously stated, the goal of this study was to examine independent feeding events to test the accuracy of identifying consumption and to determine a method of estimating mass consumed. However, it is important to note that the nature of feeding behavior in the wild may strongly influence the ability to detect and quantify prey consumed when using stomach temperature. Both northern elephant seals and California sea lions show bout structure in their diving behavior, suggesting prey consumption occurs within distinct windows of time (Feldkamp et al., 1989; Le Boeuf et al., 1988; Le Boeuf et al., 1992). To estimate mass consumed using the equations presented in this study it is necessary to identify the time to recovery (Fig. 1C) as this is used to calculate area above the curve (Fig. 1). If animals feed during the recovery period this disrupts the recovery curve and could influence the ability to estimate mass consumed. By comparing recovery times with the diving behavior measured in free-ranging animals it is possible to examine the extent of feeding that might occur during the recovery period.

Northern elephant seal females dive on average for 20 min (Kuhn, 2006; Le Boeuf et al., 1988; Le Boeuf et al., 2000). Therefore, for the recovery period to be unaltered by further feedings, animals would have to feed only once every four dives, for the range of meal sizes examined. Although foraging success rates are not known for northern elephant seals, grey seals have been reported to feed on average just twice per day (Austin et al., 2006). For California sea lions dive times

average 2.2±0.2 min (Kuhn, 2006). In order to measure full recovery periods unaltered by additional feeding events, feedings for this species would have to be separated by 25–45 dives. Since females average 54 dives in a foraging bout (Feldkamp et al., 1989), it is unlikely that they would only successfully capture prey on one or two dives while foraging. Therefore, while consecutive feeding events may be identified (Fig. 3) (Austin et al., 2006; Grémillet and Plös, 1994; Pütz et al., 1998), it is necessary to consider the impacts of bout feeding when estimating quantity consumed by California sea lions.

Recent data from stomach temperature telemeters in free-ranging animals of both species show feeding does occur in bouts, but animals also display single feeding events separated in time by further consumption (Kuhn, 2006) (C.E.K. and D.P.C., unpublished). For these single feeding events the application of the equations presented here could provide an estimate of quantity consumed. For bout feeding periods, additional models are required if researchers are interested in estimating the mass of prey consumed (Wilson et al., 1995).

Conclusions

Without the ability to identify when and where an animal feeds it is difficult to truly understand foraging behavior. Using instruments to measure feeding events, it is possible not only to fill these gaps, but also to test the validity of the indirect methods currently used to examine foraging behavior, such as changes in dive shape or movement patterns. For northern elephant seals, a great deal of information has been gathered on at-sea behavior through the use of time-depth recorders and satellite telemetry (Crocker et al., 2006; Le Boeuf et al., 1988; Le Boeuf et al., 2000; Le Boeuf and Laws, 1994). Using specific changes in behavior, 'focal' foraging areas have been identified during foraging migrations (Le Boeuf et al., 2000). To date, the extent of foraging within these 'focal' areas *versus* outside these areas is still not known, and direct measures of feeding behavior can help provide the answer.

Because of the variability measured in stomach temperature change (Fig. 4) and the potential to overestimate small meals, we strongly suggest using these data as a tool to compare feeding behavior, rather than to calculate exact quantities consumed for both northern elephant seals and California sea lions. In addition, because of the challenges estimating mass consumed when animals bout feed, the use of stomach temperature change to estimate meal size appears to be most effective with animals that feed on single large prey, such as albatrosses or grey seals (*Halichoerus grypus*) (Weimerskirch et al., 2005; Weimerskirch and Wilson, 1992; Austin et al., 2006). For example, in grey seals significant sex differences were described for both feeding frequency and estimated meal size, using stomach temperature change (Austin et al., 2006). This type of analysis could provide a great opportunity to compare feeding behavior between sexes, individuals, seasons or years. In addition to addressing questions of foraging in the species of interest, measures of feeding behavior have also been used to examine prey distribution and behavior (Austin et al.,

2006; Fuiman et al., 2002; Hennicke and Culik, 2005; Weimerskirch et al., 2005), providing greater insight into the behavior of both marine predators and their prey.

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