

Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers

Morgane Viviant · Andrew W. Trites ·
David A. S. Rosen · Pascal Monestiez ·
Christophe Guinet

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Abstract We attached accelerometers to the head and jaw of a Steller sea lion (*Eumetopias jubatus*) to determine whether feeding attempts in a controlled setting could be quantified by acceleration features characteristic of head and jaw movements. Most of the 19 experimental feeding events that occurred during the 51 dives recorded resulted in specific acceleration patterns that were clearly distinguishable from swimming accelerations. The differential acceleration between the head-mounted and jaw-mounted accelerometers detected 84% of prey captures on the vertical axis and 89% on the horizontal axis. However, the jaw-mounted accelerometer alone proved to be equally effective at detecting prey capture attempts. Acceleration along the horizontal (surge)-axis appeared to be particularly efficient in detecting prey captures, and suggests that a single accelerometer placed under the jaw of a pinniped is a promising

and easily implemented means of recording prey capture attempts.

Keywords Prey capture · Accelerometers · Jaw movements · Foraging activity · Pinnipeds · Steller sea lion

Introduction

Observing and quantifying predation events is essential for determining when, where, and how top predators forage. Unfortunately, investigating foraging behavior of marine predators that feed at sea is challenging, and foraging studies with polar marine predators present additional challenges with respect to logistics and visibility. Given the divergent demographic trends detected between Steller sea lion (*Eumetopias jubatus*) populations in the North Pacific (Trites and Larkin 1996, NMFS 2008), such data would provide extremely valuable information on the foraging success and resource quality of the areas visited by these populations.

To date, most foraging behavior studies of marine predators have described spatial distributions and diving activities (Baechler et al. 2002; Boyd 1996; Guinet et al. 2001) using such characteristics as time on the bottom or the number of “wiggles” per dive as indirect proxies for foraging effort. It is only recently that new miniaturized electronic technologies have been developed to detect prey capture events and directly assess the foraging success and fine scale foraging behavior of top predators (Austin et al. 2006; Charrassin et al. 2001).

Early devices used to record predation events of seabirds and marine mammals included stomach (Wilson et al. 1992) and esophageal temperature sensors (Ancel et al. 1997) which detected temperature changes induced by prey

M. Viviant (✉) · C. Guinet
Centre d'Etudes Biologiques de Chizé,
CNRS, 79 360 Villiers en Bois, France
e-mail: viviant@cebc.cnrs.fr

C. Guinet
e-mail: guinet@cebc.cnrs.fr

A. W. Trites · D. A. S. Rosen
Marine Mammal Research Unit, Fisheries Centre,
University of British Columbia, 2202 Main Mall,
Vancouver, BC V6T 1Z4, Canada
e-mail: a.trites@fisheries.ubc.ca

D. A. S. Rosen
e-mail: rosen@zoology.ubc.ca

P. Monestiez
Institut National de la Recherche Agronomique,
Unité de Biostatistique et Processus Spatiaux,
Site Agroparc Domaine St Paul, 84914 Avignon, France
e-mail: Pascal.Monestiez@avignon.inra.fr

ingestion. However, these temperature loggers have certain limits—they are restricted to endotherms feeding on ectothermic prey, are quite invasive, fail to detect multiple rapid ingestions of small prey, and are often regurgitated (Ropert-Coudert and Kato 2006). External loggers such as the Inter-Mandibular Angle Sensor (IMASEN or “Hall Sensor”) record the mouth opening angle (Wilson et al. 2002), but are sometimes difficult to apply on animals with flexible lips (Liebsch et al. 2007; Ropert-Coudert et al. 2004).

Accelerometers are a new bio-logging device that records acceleration and were recently shown to record feeding events while mounted to the head and jaw of hooded seals, *Cystophora cristata* (Suzuki et al. 2009). We experimented with this new technology to detect jaw openings associated with ingesting fish using two accelerometers that simultaneously measured the differential acceleration between the upper and lower jaw of a Steller sea lion. We reasoned that jaw movements should be the only movement detected during prey capture attempts relative to the whole head because the lower jaw is the only mobile portion of a sea lion’s skull. The system we employed consisted of one accelerometer on top of the head and the other placed below the lower jaw of the animal (Fig. 1a). This enabled us to record mouth openings using the acceleration differential on the vertical axis between the two accelerometers. We also investigated whether failed and successful prey capture events could be detected using just one accelerometer, and whether the head-mounted or jaw-mounted logger yielded better results. Thus, we developed a method to detect prey capture attempts using head and jaw-mounted accelerometers, and validated their use with an otarid, the Steller sea lion.

Materials and methods

The trials were conducted at the Vancouver Aquarium (BC, Canada) in August and September 2007 using a single Steller sea lion (*Eumetopias jubatus*; Schreiber 1776) equipped with acceleration data loggers (M100L-D2GT) manufactured by the Little Leonardo Ltd (Tokyo, Japan). The loggers recorded accelerations on two axes (i.e., heave accelerations were measured along the vertical axis or dorso-ventral axis, while surge accelerations were measured along the horizontal axis or antero-posterior axis; Fig. 1a). All accelerometers were set to sample heave and surge accelerations at 32 Hz, and to sample water depth at 1 Hz using a pressure transducer (resolution of 0.1 m).

We used a digital video camera to record the trials from an underwater viewing window in the test tank, and synchronized recording times between the acceleration data loggers and the video camera. Synchronization between the two loggers was needed to properly calculate the acceleration

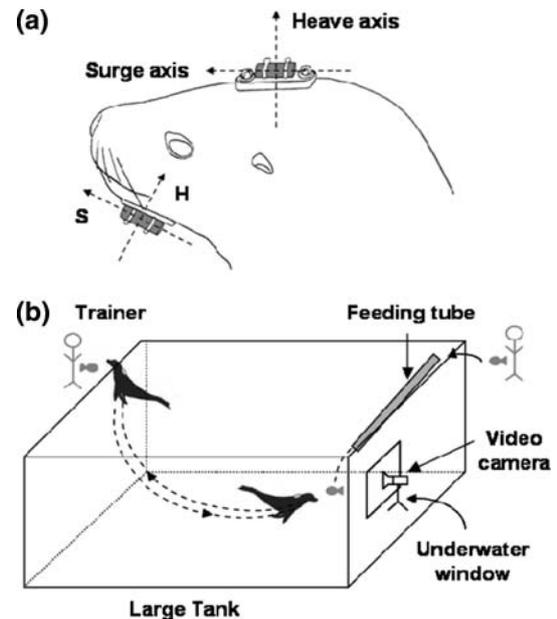


Fig. 1 **a** A Steller sea lion equipped with two accelerometers that measure heaving and surging accelerations. **b** The feeding experiment set up

differentials for both axes. We therefore carried out a small synchronization procedure for each trial (before attaching the accelerometers to the sea lion) by connecting the accelerometers together with tape and moving them quickly in different directions so that they recorded the same initial sequence of movements.

The accelerometers were secured to the sea lion using Velcro glued to the fur on top of the head and under the mandible while the sea lion was under anesthesia. One accelerometer was inserted into a Velcro-backed neoprene pocket that matched the Velcro strip previously glued under the mandible, while the second accelerometer was mounted on a small piece of neoprene using cable-ties, and secured to a piece of neoprene with swivel grommets that matched the head-mounted piece of Velcro (Fig. 1a). The Velcro, pocket, and swivel grommets allowed us to easily attach and remove the accelerometers without anesthetizing the animal following or prior to each trial.

The experiment consisted of feeding dead herring (*Clupea pallasii*) to the sea lion using a feeding tube placed 1 m below the surface of a large research pool equipped with an observation window (Fig. 1b). The sea lion was allowed to swim ~15 m (50 ft) to the feeding tube to catch one fish at a time before returning to the trainer at the opposite end of the pool where it was rewarded with a second fish as positive reinforcement. The time it took for the sea lion to reach the feeding tube was sufficient for the fish to sink in front of the underwater window, allowing us to record the prey capture on video. Two trials were carried out, with each trial consisting of feeding the sea lion 10 fish through

the feeding tube (one fish per dive), and 10 fish by the trainer for reinforcement. At the end of each trial, the loggers were carefully removed from the head and jaw of the sea lion and the data downloaded.

We recorded some swimming sequences without feeding events to better distinguish the mandible movements from other head and body movements. This was achieved by allowing the sea lion to swim freely in the tank while recording its behavior on video and with the accelerometers. The sea lion did not open its mouth while underwater, thereby providing acceleration signals representative of the swimming movements of the animal.

Data analysis

Accelerations on both axes that characterize mouth openings associated with catching a fish were analyzed using R software (R Development Core Team 2009). Time series recorded from the two accelerometers were first synchronized at 1 Hz, using the depth profiles of the two loggers while searching for the time lag that minimized the mean differences in depth (as the depth profile of the two loggers should have been nearly identical, Fig. 2a, b). The loggers were then synchronized at 32 Hz using the acceleration data.

We used the initial sequence of accelerations recorded by the two loggers during the synchronization procedure to calculate the time lag that minimized the mean difference in accelerations (both heave and surge) between the two time series. This time lag was then used to synchronize the time series of the two loggers (Fig. 2c), and was validated using the recorded sequences of the sea lion swimming with its mouth closed when the accelerometers had the same relative position and recorded the same signals. Data recorded over long periods could suffer from the two clocks drifting relative to each other, but was not an issue in our case due to the short duration of our experiments.

The accelerometers were not calibrated by the manufacturer and yielded different recorded accelerations for the same movements (Fig. 2a–c). We therefore calculated the offset in mean surge and heave acceleration between the two devices using the data recorded during the initial synchronization procedure. We then corrected the data of the mandible accelerometer with this value to match the offset of the data recorded by the head accelerometer (Fig. 2d).

Identifying individual feeding events from the accelerometry data was a six step process: (1) the signals for mandible movements were first isolated from head and body movements by calculating the differences in surge and heave accelerations between the two loggers, which corresponded to the differential movements between the mandible and the skull of the animal (Fig. 3b–d). (2) The resulting time series were then filtered with a high pass

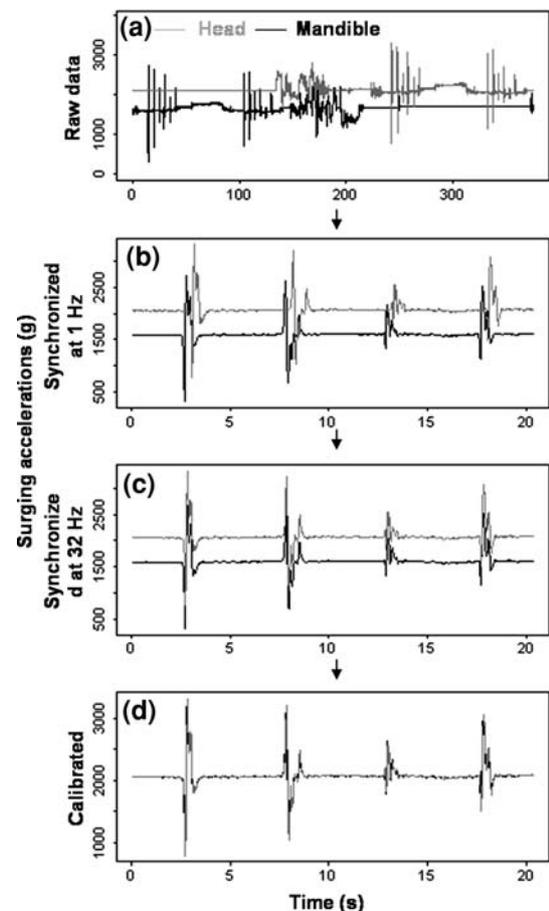


Fig. 2 Synchronization of two loggers (head and mandible accelerometers) shown for a sequence of acceleration data (a) recorded over 20 s during the “synchronisation procedure”. The raw data were filtered at 1 Hz (b) to remove noise and identify a time lag that minimized the mean differences in depths recorded by the two tags. The data were filtered again at 32 Hz to remove remaining noise before calculating the time lag that minimized the mean difference in accelerations (both heave and surge) between the two time series (c). This time lag was then used to synchronize the two time series and calibrate the two loggers (d)

filter of 3 Hz to remove the remaining noise corresponding to swimming movement, highlighting the peaks in acceleration representing mouth openings (Fig. 3e) (3) Only signals recorded below 1 m from the surface were retained to remove mouth opening events that occurred when the sea lion surfaced to breathe or grab the fish reward. (4) Variance was then calculated along a window of 1.5 s that moved over the time series to highlight extreme accelerations (Fig. 3f). (5) We next compared the distribution of variance obtained during the feeding trials to those obtained during the swimming sequences to determine the threshold value that distinguished the variance associated with swimming or mouth openings. We were thereby able to detect peaks of variance that exceeded the threshold value and were indicative of prey capture attempts (Fig. 3f). (6) Initial peaks of acceleration associated with capture attempts

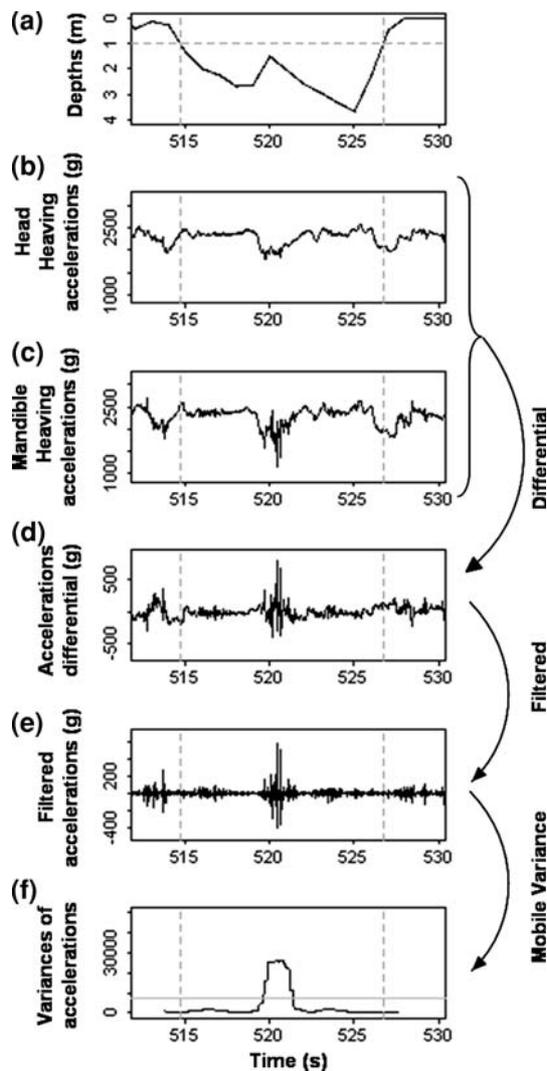


Fig. 3 An example of a prey capture within a 16 s dive by a Steller sea lion showing (a) the depth profile with corresponding heaving accelerations recorded on (b) the head and (c) lower mandible along with (d) the differentials between the two accelerometers. Data were then filtered (e) with a high pass 3 Hz filter to remove noise associated with swimming, and variance (f) was calculated along a moving window of 1.5 s to reveal the prey capture event

were usually followed by a succession of smaller peaks representing prey handlings. We therefore considered peaks within an interval of less than 1 s to be part of the same feeding event.

We compared the detected capture events to the actual prey captures recorded on video for each dive. Recorded dives were assigned to one of four categories: TP, true positives (events detected and actual prey captured); TN, true negatives (no events detected and no prey captured); FP, false positives (events detected but no prey captured); and FN, false negatives (no events detected but actual prey caught). We used these four categories to calculate four metrics that assessed the efficiency of our method to iden-

tify prey capture attempts from changes in acceleration (detection rate, specificity, precision and accuracy): detection rate ($=TP/[TP + FN]$) was the proportion of actual positives that were correctly identified as such (true positive rate); specificity ($=TN/[TN + FP]$) was the proportion of negatives that were correctly identified as such (true negative rate); precision ($=TP/[TP + FP]$) was the proportion of actual positives in the number of events classified as belonging to the positive class; and accuracy ($=[TP + TN]/[TP + TN + FP + FN]$) was the proportion of actual positives and negative events that were correctly identified. We also calculated a “weighted accuracy” ($=[TP + TN][TP + FN]/[TN + FP]/[[TP + FN] + [TN + FP][TP + FN]/[TN + FP]]$) because we had more dives without feeding events ($n = 32$) than dives with feeding events ($n = 19$). Thus, our weighted accuracy gave the same weight to feeding and non-feeding events, as for a balanced experiment.

Finally, we assessed whether a single accelerometer was sufficient to identify foraging behavior. We thus analyzed the heave and surge acceleration data of the head and mandible mounted accelerometers as standalone units following Steps 2–6.

Results

We intended for each of our two trials to consist of 10 feeding events (with a single feeding event per dive). Unfortunately, the head accelerometer fell off after the ninth fish ingestion during the first trial resulting in a total of 51 dives, consisting of 19 dives with feeding events (9 prey during Trial 1, and 10 during Trial 2) and 32 dives without feeding events. Most of the 19 feeding events were reflected by a specific acceleration pattern (Fig. 3). Results summarized in Table 1 show that the differential accelerations (using the two accelerometers) detected 84% of the 19 prey ingestion events on the heave-axis and had a weighted accuracy of 86% (i.e., the proportion of foraging type events recorded by the accelerometers that were correctly assigned into feeding or non-feeding events). Furthermore, 80% of the events detected to be feeding were actual feeding events (precision). Using the surge-axis, the differential acceleration correctly identified 89% of prey ingestion events with a precision of 81% and a weighted accuracy of 88%.

Both the head-mounted and jaw-mounted accelerometers detected more capture attempts (with greater precision and weighted accuracies) from surge accelerations than they did from the heave-axis. Furthermore, we found that the jaw-mounted accelerometer gave better results than the head-mounted accelerometer for every metric we used. The surge-axis of the jaw-mounted accelerometer detected 79% of the 19 ingestion events, whereas 88% of the calculated

Table 1 The number and percentage of times that prey ingestion events were or were not detected by the heave- and surge-axes of one or two accelerometers placed on a Steller sea lion consuming individual

herring during 19 feeding events (19 dives with feeding event and 32 dives without feeding event)

Accelerometers	Axis	TP	FP	TN	FN	Detection (%)	Specificity (%)	Precision (%)	Accuracy (%)	Weighted accuracy (%)
Two										
Acceleration differential	Heave	16	4	28	3	84.2	87.5	80	86.3	85.8
	Surge	17	4	28	2	89.5	87.5	80.9	88.2	88.4
One										
Head	Heave	10	8	24	9	52.6	75	55.5	66.7	63.8
	Surge	13	2	30	6	68.4	93.7	86.6	84.3	81.1
Jaw	Heave	14	5	27	5	73.7	84.4	73.7	80.4	79
	Surge	15	2	30	4	78.9	93.7	88.2	88.2	86.3

TP true positives, FP false positives, TN true negatives, FN false negatives

capture attempts were actual feeding events. The weighted accuracy for the surge-axis of the jaw-mounted accelerometer (86%) was on par with the differential acceleration measurement (88%) (Table 1). Weighted accuracies were within 1.6% of the unweighted accuracies in all cases.

Discussion

Our results show that head and mouth movements can be detected from acceleration along the surge- and heave-axes of accelerometers placed on the skull and mandible of a Steller sea lion. Acceleration along the surge-axis appeared to be particularly efficient at detecting prey captures as we could detect forward movement of the head at the instant of the grab, which corresponded to a brief and rapid extension of the sea lion's neck and a rapid extension of the lower jaw. These acceleration signals appeared to be the main features associated with prey capture events as suggested by Naito (2007) and observed in hooded seals (Suzuki et al. 2009) and harbour seals, *Phoca vitulina* (Bowen et al. 2002).

Using the differential acceleration between the two accelerometers improved the probability of detecting mouth openings of our study animal by reducing the miscellaneous signals associated with head and body movements. However, the surge-axis of a single accelerometer placed on the mandible provided good results with an accuracy on par with using the two accelerometer approach. The single jaw-mounted accelerometer had a lower detection rate than the two accelerometer differential method, but had greater precision, which was the metric that we most wanted to maximize. Thus, attaching a single accelerometer to the mandible seems sufficient for detecting probable prey captures, and agrees with the findings of Suzuki et al. (2009) for hooded seals.

Using a single accelerometer has the added benefit of reducing drag and financial costs associated with two instruments. A single instrument is easier to deploy and provides data that is simpler and faster to analyze compared to the two accelerometer approach. It also avoids needing to synchronize two loggers and negates possible issues associated with clocks drifting between the accelerometers over long periods. We did not specifically test how sample frequency influenced how well our method of detecting capture attempts performed. However, inspection of our data and pre-trial experimentation suggests that a sample frequency of 16 Hz should be sufficient for detecting prey capture attempts, and would allow for more data to be stored by the accelerometers.

Logistical considerations prevented us from carrying out our experiment with more sea lions or with live prey. Future studies should use live prey and more individual predators to examine individual variation and investigate the potential effects of sex and age. Our results nevertheless demonstrate that acceleration signals provide a valuable and easy way to implement a proxy of prey capture events. This is consistent with the findings of Suzuki et al. (2009) for the hooded seal, and suggests that the single jaw-mounted accelerometer method is potentially applicable to a variety of species.

The accelerometer method as we employed it could not distinguish actual prey captures from attempted catches and therefore does not give a precise quantitative measure of the number of prey ingested (Table 1). The accelerometers failed to detect some prey captures, while detecting some mouth opening events that did not correspond with ingestion. In our experiment, undetected prey captures occurred when the sea lion sucked down the fish with little movement of its mouth. Feeding by suction is known to occur in some pinniped species such as hooded seals (Suzuki et al. 2009) and bearded seals, *Erignathus barbatus* (Marshall

et al. 2008), but the behavior we observed could also have reflected the minimal effort required to catch a dead fish. The extent to which sea lions pursue their prey or ambush them in the wild is unknown, as is the understanding of the relative roles played in foraging by suction versus biting and manipulation of the prey in their mouths. We suspect that the percentage of captures detectable by accelerometers may be greater for wild animals foraging on live prey than the values we calculated from captive experiments using dead fish, which should improve the performance of the method. However, we recognize that other variables, such as prey species and size, could also affect the accuracy of this method. The influence of these factors on the intensity or duration of acceleration signals should be investigated in future studies.

False ingestion events identified by acceleration measurements from our captive study (Table 1) reflected occasions when the sea lion vocalized or grabbed at other objects at the bottom of the pool, or opened its mouth underwater for no apparent reason. The interaction with conspecifics in the wild could also induce mouth openings. Some of these events could be filtered out from the acceleration data using depth and swimming patterns as covariates to eliminate unlikely foraging behavior. Whether or not such events are rare or equally common among wild animals during dedicated foraging trips will require verification with supplemental bio-logging data that records other aspects of animal behavior. In this respect, the simultaneous deployment of video cameras and accelerometers would be particularly appropriate.

Overall, jaw acceleration analysis is a promising way to characterize foraging activity in pinnipeds. Despite the need for further validation to precisely quantify the number of prey ingested, the acceleration method provides useful information on the timing and location of prey encounters. In addition to the advantages of being externally mounted, accelerometers are also superior to internal data loggers (e.g., stomach and esophageal temperature sensors) or Hall sensors as they can provide additional information related to foraging activity (e.g., flipper beat frequency and turning angle with 3-dimensional accelerometers) (Ropert-Coudert et al. 2006; Sato et al. 2008) as well as detecting encounters with prey. The accelerometer method can also be applied to endothermic and exothermic predators seeking endothermic or exothermic prey, which expands the possible applications of this methodology. This method should be applicable to a wide range of animals, and the simultaneous deployment of accelerometers with tracking devices should contribute to improving knowledge about the foraging behavior of polar marine predators.

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References

- Ancel A, Horning M, Kooyman GL (1997) Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. *J Exp Biol* 200:149–154
- Austin D, Bowen WD, McMillan JI, Boness DJ (2006) Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *J Anim Ecol* 75:408–420. doi:10.1111/j.1365-2656.2006.01057.x
- Baechler J, Beck CA, Bowen WD (2002) Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*). *Can J Zool* 80:1569–1577. doi:10.1139/z02-150
- Bowen WD, Tully D, Boness DJ, Bulheier BM, Marshall GJ (2002) Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar Ecol Prog Ser* 244:235–245. doi:10.3354/meps244235
- Boyd IL (1996) Temporal scales of foraging in a marine predator. *Ecology* 77:426–434. doi:10.2307/2265619
- Charrassin JB, Kato A, Handrich Y, Sato K, Naito Y, Ancel A, Bost CA, Gauthier-Clerc M, Ropert-Coudert Y, Le Maho Y (2001) Feeding behaviour of free-ranging penguins determined by oesophageal temperature. *Proc R Soc Lond B* 268:151–157. doi:10.1098/rspb.2000.1343
- Guinet C, Dubroca L, Lea M-A, Goldsworthy SD, Cherel Y, Duhamel G, Bonadonna F, Donnay JP (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephallus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Mar Ecol Prog Ser* 219:251–264
- Liebsch N, Wilson RP, Bornemann H, Adelung D, Plötz J (2007) Mouthing off about fish capture: jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep-Sea Res II* 54:256–269. doi:10.1016/j.dsr2.2006.11.014
- Naito Y (2007) A new animal-borne digital still camera (DSL): Its functions and applications to marine mammal science. In: Marshall G (ed) Proceedings of the 2007 animal-borne imaging symposium. National Geographic Society, Washington D.C., pp 201–207
- NMFS (2008) Recovery plan for the Steller sea lion (*Eumetopias jubatus*). Revision. National Marine Fisheries Service, Silver Spring, p 325
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Ropert-Coudert Y, Kato A (2006) Are stomach temperature recorders a useful tool for determining feeding activity? *Polar Biosci* 20:63–72
- Ropert-Coudert Y, Kato A, Liebsch N, Wilson RP, Müller G, Baubert E (2004) Monitoring jaw movements: a cue to feeding activity. *Game Wildl Sci* 20:1–19
- Ropert-Coudert Y, Kato A, Wilson RP, Cannell B (2006) Foraging strategies and prey encounter rate of free-ranging little penguins. *Mar Biol* 149:139–148. doi:10.1007/s00227-005-0188-x
- Sato K, Daunt F, Watanuki Y, Takahashi A, Wanless S (2008) A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *J Exp Biol* 211:58–65. doi:10.1242/jeb.009811

- Suzuki I, Naito Y, Folkow LP, Miyazaki N, Blix AS (2009) Validation of a device for accurate timing of feeding events in marine animals. *Polar Biol* 32:667–671. doi:[10.1007/s00300-009-0596-3](https://doi.org/10.1007/s00300-009-0596-3)
- Trites AW, Larkin PA (1996) Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? *Aquatic Mammals* 22:153–166
- Wilson RP, Cooper J, Plotz J (1992) Can we determine when marine endotherms feed? A case study with seabirds. *J Exp Biol* 167:267–275
- Wilson RP, Steinfurth A, Ropert-Coudert Y, Kato A, Kurita M (2002) Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Mar Biol* 140:17–27