What a jerk: prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*)

Ydesen K.S.[1*], Wisniewska D.M. [1,2], Hansen, J.D.[3], Beedholm K.[1] Johnson M.[4], and Madsen P.T.[1]

1) Zoophysiology, Department of Bioscience, Aarhus University,
C. F. Moellers Alle 3, Build. 1131, 8000 Aarhus C, Denmark
2) Section for Marine Mammal Research, Department of Bioscience, Aarhus University,
Frederiksborgvej 399, 4000 Roskilde, Denmark
3) Fjord and Belt Centre, Margrethes Plads 1
5300 Kerteminde, Denmark
4) Sea Mammal Research Unit, University of St. Andrews, Scotland

* Author for correspondence: kristinaydesen@gmail.com

Revised for Journal of Experimental Biology methods

Summary

A key component in understanding the ecological role of marine mammal predators is to identify how, where and how much prey they capture in time and space. Satellite and archival tags on pinnipeds generally only provide diving and positioning information, and foraging is often inferred to take place in particular shaped dives or when the animal remains in an area for an extended interval. However, fast movements of the head and jaws may provide reliable feeding cues that can be detected by small low-power accelerometers mounted on the head. To test this notion, a harbour seal (*Phoca vitulina*) was trained to wear an OpenTag (sampling at 200 or 333 Hz with ±2 or ±16 g clipping) on its head while catching fish prey in front of four underwater digital high-speed video cameras. We show that both raptorial and suction feeding generate jerk (i.e., differential of acceleration) signatures with maximum peak values exceeding 1000 m/s^3. We conclude that reliable prey capture cues can be derived from fast-sampling, head mounted accelerometer tags thus holding a promising potential for long-term studies of foraging ecology and field energetics of aquatic predators in their natural environments.

Keywords

Harbour seal, pinniped, accelerometry, foraging, feeding, jerk, tag

Introduction

Pinnipeds are versatile top predators in marine food webs, and fine-scale information on their foraging behaviour is therefore critical for understanding top-down mediated energy cascades. However, it has proven challenging to detect feeding events in free-swimming aquatic animals and, as a result, relatively little is still known about the fine-scale feeding behaviour of many pinnipeds (Kuhn et al., 2009). With satellite and archival tags foraging is typically inferred from movement patterns (e.g., area restricted search) or from distinctive dive shapes (Kooyman, 2004), but without more detailed information, the accuracy of these methods may be difficult to assess. Moreover, such proxies provide little information about the quantity of prey taken. To directly observe foraging, cameras have been deployed on diving pinnipeds (Davis et al., 1999; Davis et al., 2001; Bowen et al., 2002; Hooker et al., 2002; Sato et al., 2002), but these are limited by battery power, and the need for a light source in deep dives may affect the behaviour of predator and prey. Actual prey ingestions have been measured with stomach temperature transmitters (Kuhn and Costa, 2006), but these sensors do not appear to be reliable for long intervals either due to changing conditions in the gut or due to passage of the sensor (Ropert-Coudert et al., 2000; Takahashi et al., 2004). Jaw opening and closing can be recorded by a mandibular sensor (Ropert-Coudert et al., 2004), but the logger may be unreliable over long recording periods where cabling to the jaw is likely to fail or affect the tagged animal.

Recent studies have shown promising use of head and jaw mounted accelerometers sampling at 32 Hz to measure head surge in foraging attempts of both pinnipeds (Skinner et al., 2009; Suzuki et al., 2009; Naito et al., 2010; Iwata et al., 2011; Naito et al., 2013) and penguins (Kokubun et al., 2011; Watanabe and Takahashi, 2013). Prey capture and engulfment involves rapid jaw movements in raptorial feeding and the retraction and lowering of the gular apparatus during suction feeding (Werth, 2000; Marshall et al., 2008). These movements are unique to feeding and should generate high frequency acceleration signatures that are distinctive and so readily detected against other head movements. Here we use fast super-cranial accelerometry on a trained male harbour seal catching prey to show that the differential of the three acceleration axes, jerk (m/s^3) (Simon et al., 2012), provides a reliable, easily-computed and orientation-independent measure of both raptorial and suction feeding that can be recorded or relayed over long time periods from wild animals at sea.

Results

Two experiments were conducted using different data collection parameters. In the first, an animal-attached triaxial accelerometer was set to sample at 200 Hz with a clipping level of +/- 2 g. A total of 124 trials were conducted over 27 days. After excluding prey captures in which engulfment was not visible on any of the video cameras, a set of 14 captures of dead fish, 10 of large live trout and 13 of small live trout was available for analysis. Due to the relatively low clipping threshold and the rapid head and jaw movements during capture (see video 1 in supplementary material), most of the captures had brief intervals in which the measured acceleration in one or more axes was clipped. Only 11 captures of dead fish, and one with a small live trout were unaffected by this limitation. In the second experiment, the tag was therefore configured for a sampling rate of 333 Hz and a clipping level of +/-16 g. A total of 20 trials were conducted with these settings, of which 9 captures of large 18-23 cm live trout happened in front of the cameras permitting analysis.

Based on visual analysis of all the prey captures, a total of 16 were judged to be primarily raptorial feeding, while 15 were categorized as suction feeding. Raptorial feeding occurred mostly in captures of large prey, whereas smaller prey were caught by suction (Table 1). In both feeding mechanisms the absolute jerk in the z-axis was highest, followed by the x-axis, then the y-axis. However, in suction feeding, the duration of the prey capture (t2-t0, see Material and methods) was shorter, and the amplitude of the jerk lower (Table 1). Fig. 1 shows an example of a raptorial prey capture of a large trout. Here, the jaw opening is followed by a sudden rise in jerk amplitude (Fig. 1A image 1 and 1C). Subsequent jerk peaks are associated with capture and handling of the fish (Fig. 1A images 2-8).

To test whether feeding jerks could be distinguished from the jerk recorded in intervals before and after feeding, we divided each capture session into three time windows of 250 ms each and computed the RMS of the norm jerk in each section: a pre-capture time window starting 1 sec before t0 (jaw opening), a capture window starting at t0, and a post-capture window starting 1 sec after t0. The RMS measure was chosen because it is relatively insensitive to brief intervals of clipping in the individual accelerometer signals (supplementary materials). Results of a one-way ANOVA and multiple comparison test show that the RMS jerk during the feeding window differed significantly from the before and after windows for all fish types (Fig. 2, Table 1). Furthermore, engulfment of live fish generated significantly larger RMS jerk values, compared to the RMS jerk during captures of dead fish (t-test, p-value < 0.005). A similar analysis of raptorial and

suction feeding did, however, not provide any significant difference. All data in the above analyses was found to be normally distributed by a Chi-square goodness-of-fit test.

The median sampling rate required to generate at least 90 % of the observed peak broadband jerk was 73, 95 and 64 Hz, for prey captures of dead fish, live fish (non-clipped data), and clipped live fish, respectively (Table 1).

Discussion

Foraging strikes in any predator targeting nekton inevitably involve sudden movements irrespective of the way in which prey are acquired. Here we tested if prey engulfment movements of the head and jaws of a pinniped produce fast, distinct changes in acceleration that can be measured by a small head-mounted tag sampling at high rates. We have identified the same surge (i.e., x-axis) acceleration signature reported to serve as a good proxy for successful prey captures in other studies, but we show also that the RMS of the norm-jerk over a short window (250 ms here) can provide a reliable and distinctive signal for detecting raptorial or suction feeding events (Fig. 1, Table 1). Movements were more powerful in trials with live fish which involved primarily raptorial feeding. Larger fish also required more handling as indicated by the comparably larger t1-t2 difference found in these trials (Table 1). Increased hunting and handling effort are also represented in the pre- and post-feeding RMS values in Fig. 2, opening the possibility that the magnitude and duration of the jerk signal may provide information about the type and size of prey, as well as the mode of capture, but utilisation of this potential would require confirmation across a number of animals.

Triaxial on-animal accelerometer data provide dense information about the movements of animals and can be, as a result, complex to analyse. Existing methods for detecting foraging impulses require various information about the orientation of the animal, the orientation of the tag on the animal, and the time scales of events in order to choose filters and axes to process. In comparison, the norm of the jerk is a very simple processing method that does not require explicit time-scale or tag orientation information. This makes the method both simple to implement for *in situ* processing and broadly applicable to other taxa.

The differentiation used in computing the jerk emphasises fast movements such as those produced by smaller muscles within the head during prey capture. Slower movements such as maneuvers and stroking tend to produce smaller jerk signals even though the amplitude of the movements and the muscle mass involved may be much greater. The norm of the jerk is also

completely independent of the orientation of the tag and so is unaffected by the direction of approach of the predator towards the prey or of the way the tag is attached to the head provided that the attachment is sufficiently rigid. As a result, the jerk signal associated with raptorial and suction feeding may provide a more easily detected and less ambiguous measure for prey captures than does head surge.

Compared to other methods for detecting foraging activity, triaxial accelerometers offer a number of important advantages. Many tags now include these miniature low-power devices and, as we demonstrate, foraging accelerations can be detected by a tag attached to the rear of the head obviating the need for jaw sensors and cables. A supra-cranial placement of a small tag is also ideal for other sensors such as GPS and for radio telemetry of data. Accelerometers are straightforward to use, but require the selection of two parameters: the sampling rate and the full-scale sensitivity (or clipping level). Key to reliable detection of rapid foraging movements is a wide sensing bandwidth necessitating a high sampling rate. Previous studies of accelerometry on pinnipeds have used a sampling rate of 32 Hz for which the bandwidth is < 16 Hz. Here, we used a sampling rate of 200 and 333 Hz, which enabled the detection of muscle movements with time constants of tens of milliseconds. Through decimation we can show that a sampling rate of more than 70 Hz is required on average, no matter the engulfment method, to capture 90 % of the jerk (Fig. 1C). Although the higher sampling rate means that more data is collected by the tag per unit of time, the benefit of more readily-detected foraging signals may mean that data compression methods such as event counting are more effective, increasing the quality of the data that is ultimately stored or telemetered.

The clipping level of an accelerometer determines both the maximum absolute acceleration that can be measured and, because the resolution of the sensor is fixed, the smallest change in orientation that can be detected. Accelerometers with clipping levels of 2 g are often used in tags as these provide detailed records of orientation. However, our results suggest that these devices will often clip during foraging strikes when head mounted. Although higher clipping level accelerometers are available, the RMS jerk processing method we propose appears to be robust to modest levels of clipping (see supplementary material).

We conclude that the RMS jerk calculated as the norm of the differential of the triaxial acceleration, provides a reliable and widely-applicable measure of both raptorial and suction feeding. Moreover, the duration and temporal sequence of jerks may offer the potential for separating prey sizes and feeding mechanisms, and provide quantitative measures of prey capture

success. Given the low power consumption of accelerometers, this processing method enables the timing and method of prey ingestion to be sampled over periods of months and relayed from the wild via low bandwidth telemetry. Such long records of foraging behaviour will help to understand how free ranging aquatic predators search for and acquire energy from their dynamic environment in time and space.

Materials and methods

Experiments were carried out at the Fjord&Belt in Kerteminde, Denmark, with a trained adult male harbour seal (*Phoca vitulina,* Linnaeus, 1758) (13years old, 80kg) housed in a net pen. Head accelerations during prey captures were measured using a triaxial accelerometer, "OpenTag" (Loggerhead Instruments, Sarasota, FL, USA), sampling at 200 Hz or 333 Hz (16 bits). The tag was calibrated for sensitivity and frequency response using a Brüel & Kjær Vibration Exciter Type 4809 and a pre-calibrated Brüel & Kjær Accelerometer Type 4381. The seal was trained to wear the datalogger (dimensions 7.5x3.5x2.2 cm, 55 g in air, 3 g in water) on top of its head attached by means of a small, custom-made elastic hood (Supplementary Fig. S1). The hood fit snugly around the head and neck holding the tag firmly against the dorsal surface of the skull. In each trial, the seal swam towards and acquired individual prey items released from a custom-made fish dispenser, and then returned to station. Both 12-13 cm small and 15-25 cm large live trout (*Oncorhynchus mykiss,* Walbaum, 1792), and 12-13 cm dead sprat (*Sprattus sprattus,* Linnaeus, 1758) and 15-16 cm capelin (*Mallotus villosus,* Müller, 1776) were used as prey in the experiments. The prey captures were filmed using four GoPro HD Hero2 cameras (120 fps) in underwater housings (Eye of Mine Action Cameras; Carson, CA, USA) arranged so as to image captures from different angles to ensure that timing of mouth opening and prey contact could be established. All recorders were synchronized before and after a session, and the data were subsequently analysed in Matlab 7.5 (Mathworks, MA, USA) with custom-written scripts. Three events were identified in the videos from each prey capture: the time of the first sign of jaw opening (t0), the time of first fish-seal contact (t1) and the time of complete engulfment (but not necessarily deglutition) of the fish (t2). Each prey capture was classified to be either primarily suction or raptorial feeding by five observers tasked with judging if the fish appearing in the videos were actively drawn into the mouth or not. Prey capture events were grouped according to fish type and feeding mechanism (suction or raptorial). The jerk was computed as the differential of the acceleration for each axis and the total

jerk was taken as the norm of the triaxial jerk (i.e., the square-root of the sum of the squared value in each axis) at each time instant. In Matlab, this is achieved with the following instruction:

```
Jerk = fs*sqrt(sum(diff(A).^2,2)) ;
```

where A is a three-column matrix containing the measured triaxial acceleration time series and fs is the sampling rate in Hz. The RMS jerk was calculated as the square-root of the sum of the squared jerk over an averaging window of 250 msec. Sampling rates required for generating 50 and 90% of the maximum jerk peaks were also calculated for each capture by decimating the sampled acceleration prior to jerk computation using a 12-length symmetric FIR filter (Orfanidis, 2010) with cut-off frequency of 0.4 of the new sampling rate.

Acknowledgements

Dr. D. Mann kindly shared prototypes of the OpenTag. We thank the Fjord&Belt staff for their dedicated help and support, and the staff at the workshop of Department of Bioscience, Aarhus University for assisting with the construction of the recording setup. The authors acknowledge helpful discussions on processing methods with A. Kato, T. Costa and Y. Ropert-Coudert and thank Alex Werth and an anonymous reviewer for helpful critique.

Funding

This work was funded by the Carlsberg Foundation through a grant to P.T. Madsen. MJ was funded by the Office of Naval Research and the Marine Alliance for Science and Technology Scotland. DMW was funded by the Oticon Foundation, Denmark.

Fig. legends

Fig. 1 Example of prey capture of a large live trout. The jaw opening time (t0) corresponds to time 0 on the x-axis. A) Still images of initial jaw opening (1), capture and handling (2-8). Measured triaxial acceleration (B) and jerk (C) over the same time interval. The timing of the images is marked on the jerk (C).

Fig. 2 Boxplot of pre (A), during (B) and post (C) jerks of all prey engulfments. Groups consist of dead, small and large fish, sampled at 200 Hz and large fish sampled at 333 Hz with a clipping level

of 2 and 16 g, respectively. The number of prey captures is indicated for each group. All groups during feeding that are significantly different from before and after feeding (one-way ANOVA) are marked by an asterix (*).

Table 1 Results for all fish. Non-clipped data: 12-13 cm dead sprat (DS), 15-16 cm dead capelin (DC), 12-13 cm small live trout (SLT), 18-23 cm large live trout (LLT). Clipped data: 12-13 cm small live trout (C-SLT) and 15-25 cm large live trout (C-LLT).

Abbreviations

t0: time of visible initial jaw opening

t1: time of seal-prey contact

t2: time of prey engulfment

x-jerk: x-axis jerk

y-jerk: y-axis jerk

z-jerk: z-axis jerk

References:

Bowen, W., Tully, D., Boness, D., Bulheier, B. and Marshall, G. (2002). Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series* **244**, 235-245.

Davis, R., Fuiman, L., Williams, T. and Le Boeuf, B. (2001). Three-dimensional movements and swimming activity. *Compartive Biochemistry and Physiology -Part A: Molecular & Integrative Physiology* **129**, 759-770.

Davis, R., Fuiman, L., Williams, T., Collier, S., Hagey, W., Kanatous, S., Kohin, S. and Horning, M. (1999). Hunting behavior of a marine mammal. *Science* **283**, 993-996.

Hooker, S. K., Boyd, I. L., Jessopp, M., Cox, O., Blackwell, J., Boveng, P. L. and Bengtson, J. L. (2002). Monitoring the prey-field of marine predators: combining digital imaging with datalogging tags. *Marine mammal science* **18**, 680-697.

Iwata, T., Sakamoto, K. Q., Takahashi, A., Edwards, E. W. J., Staniland, I. J., Trathan, P. N. and Naito, Y. (2011). Using a mandible accelerometer to study fine-scale foraging behavior. *Marine mammal science* **28**, 345-357.

Kokubun, N., Kim, J. H., Shin, H. C., Naito, Y. and Takahashi, A. (2011). Penguin head movement detected using small accelerometers. *The Journal of Experimental Biology* **214**, 3760-3767.

Kooyman, G. (2004). Genesis and evolution of bio-logging devices: 1963–2002. *Mem Natl Inst Polar Res* **58**, 15-22.

Kuhn, C. and Costa, D. (2006). Identifying and quantifying prey consumption. *Journal of Experimental Biology* **209**, 4524-4532.

Kuhn, C. E., Crocker, D. E., Tremblay, Y. and Costa, D. P. (2009). Time to eat: measurements of feeding behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris*. *Journal of Animal Ecology* **78**, 513-523.

Marshall, C. D., Kovacs, K. M. and Lydersen, C. (2008). Feeding kinematics, suction and hydraulic jetting capabilities in bearded seals (*Erignathus barbatus*). *Journal of Experimental Biology* **211**, 699-708.

Naito, Y., Bornemann, H., Takahashi, A., McIntyre, T. and Plötz, J. (2010). Fine-scale feeding behavior of Weddell seals. *Polar Science* **4**, 309-316.

Naito, Y., Costa, D. P., Adachi, T., Robinson, P. W., Fowler, M. and Takahashi, A. (2013). Unravelling the mysteries of a mesopelagic diet. *Functional Ecology*.

Orfanidis, S. (2010). Introduction to signal processing: Rutgers University.

Ropert-Coudert, Y., Kato, A., Liebsch, N., Wilson, R., Muller, G. and Baubet, E. (2004). Monitoring jaw movements. *Game and Wildlife Science* **21**, 1-20.

Ropert-Coudert, Y., Baudat, J., Kurita, M., Bost, C.-A., Kato, A., Le Maho, Y. and Naito, Y. (2000). Validation of oesophagus temperature recording for detection of prey ingestion. *Marine Biology* **137**, 1105-1110.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B., Watanabe, Y. and Naito, Y. (2002). Deep foraging dives in relation to the energy depletion of Weddell seal (*Leptonychotes weddellii*) mothers during lactation. *Polar biology* **25**, 696-702.

Simon, M., Johnson, M. and Madsen, P. T. (2012). Keeping momentum with a mouthful of water. *The Journal of Experimental Biology* **215**, 3786-3798.

Skinner, J. P., Norberg, S. E. and Andrews, R. D. (2009). Head striking during fish capture attempts by Steller sea lions. *Endangered Species Research* **10**, 61-69.

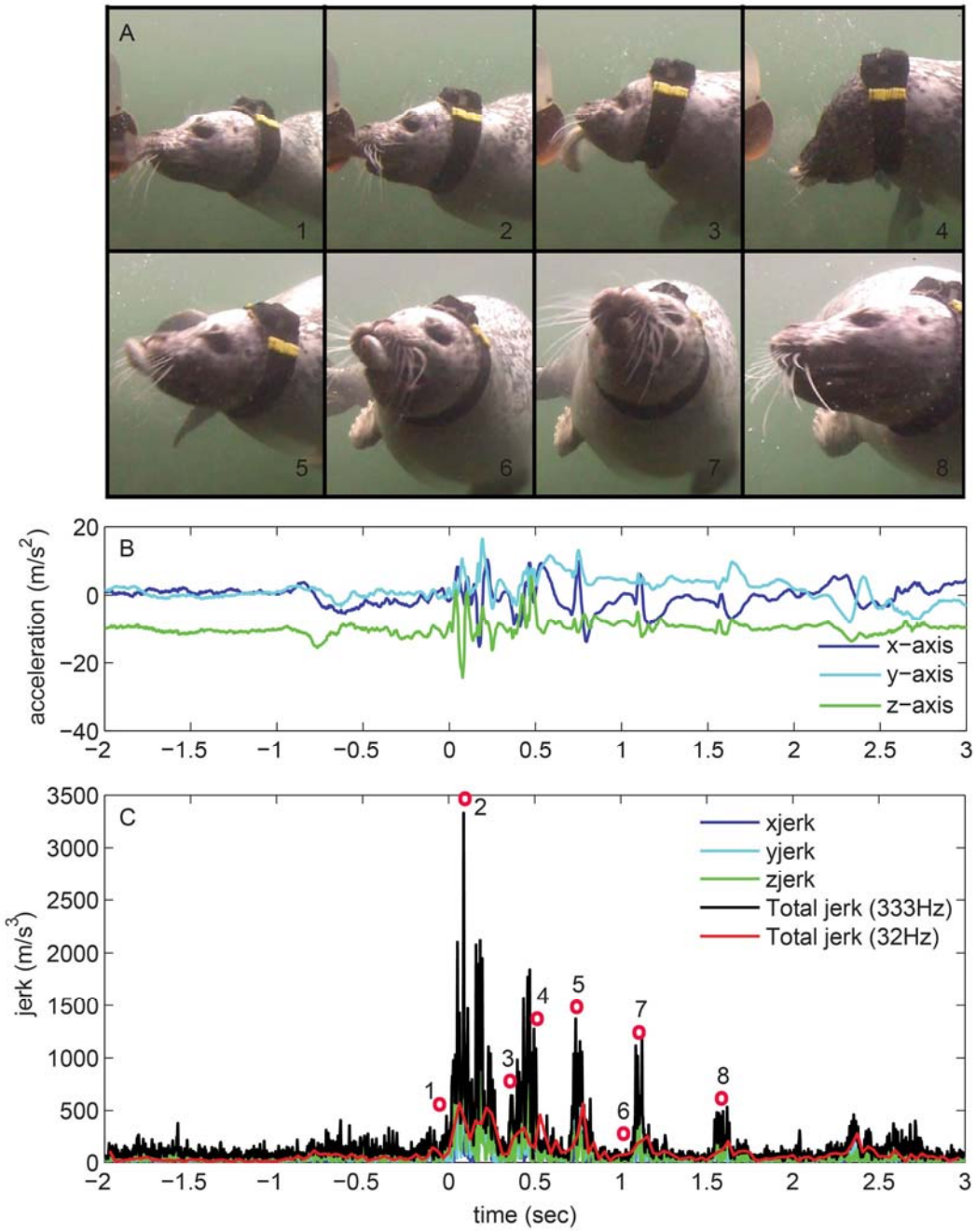
Suzuki, I., Naito, Y., Folkow, L. P., Miyazaki, N. and Blix, A. S. (2009). Validation of a device for accurate timing of feeding events. *Polar biology* **32**, 667-671.

Takahashi, A., Dunn, M., Trathan, P., Croxall, J., Wilson, R. P., Sato, K. and Naito, Y. (2004). Krill-feeding behaviour in a chinstrap penguin compared to fish-eating in Magellanic penguins: a pilot study. *Marine Ornithology* **32**, 47-54.

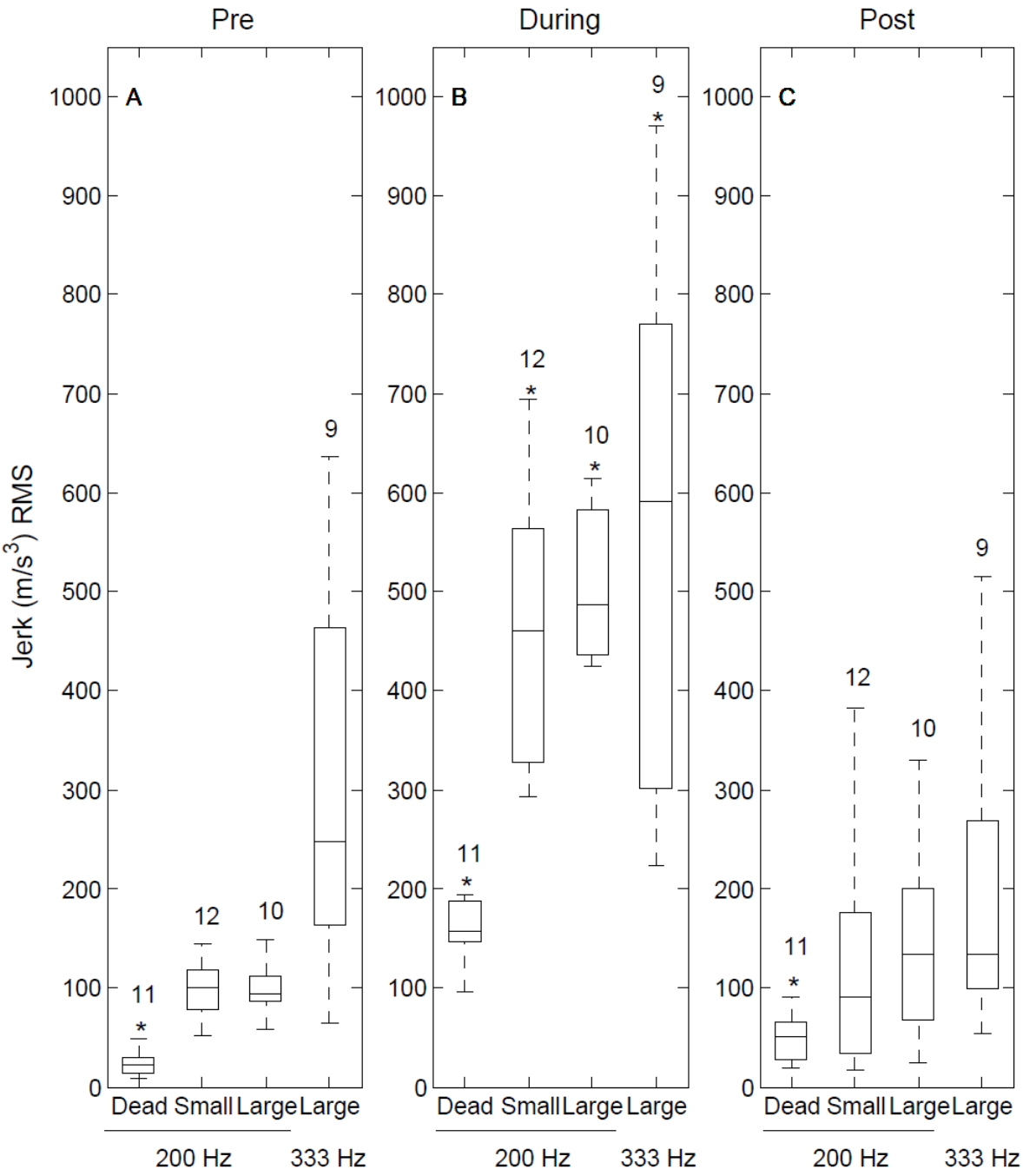
Watanabe, Y. Y. and Takahashi, A. (2013). Linking animal-borne video to accelerometers reveals prey capture variability. *Proceedings of the National Academy of Sciences* **110**, 2199-2204.

Werth, A. (2000). Feeding in marine mammals. *Feeding: form, function and evolution in tetrapod vertebrates*, 475-514.

Fig.1



359 **Fig. 2**



360
361
362
363
364
365

366 **Table 1**

	fish (samplingsrate)	no. of prey captures	mean total and mean per-axis peak jerk (m/s^3) total jerk (std) x-jerk (std) y-jerk (std) z-jerk (std)	median times of total and per-axis peak jerk (sec) total jerk x-jerk y-jerk z-jerk	median times of fish contact and engulfment (sec) t1 t2	RMS (m/s^3) of jerk in 250 ms windows 1st.Q median (p-value) 3rd Q pre	during	post	median sampling rate (Hz) required to generate 50 and 90 % of the peak jerk 50% 90%
non-clipped data	DS, DC (200 Hz)	11	573 (± 189) 371 (± 114) 326 (± 151) 416 (± 245)	100 150 120 130	30 190	13 21 29	146 157 * (p < 0.001) 188	27 50 65	11 73
	SLT (200 Hz)	1	1372 491 935 1364	0 130 80 0	30 80	56	300	52	12 96
	LLt (333 Hz)	9	3210 (± 1382) 2293 (±1285) 1920 (± 760) 2578 (± 1103)	156 158 170 7	0 1180	163 248 463	300 590 * (p < 0.001) 770	98 133 269	14 95
clipped data	C-SLT (200 Hz)	10	2689 (± 588) 1621 (± 617) 1521 (± 914) 2105 (± 412)	163 193 128 155	130 300	87 94 113	437 486 * (p < 0.001) 583	67 133 200	15 64
	C-LLT (200 Hz)	12	2373 (± 1174) 1708 (± 516) 1396 (± 471) 1710 (± 1350)	195 180 53 28	120 1000	78 100 119	328 462 * (p < 0.003) 563	34 91 176	15 79

367

Fig.1

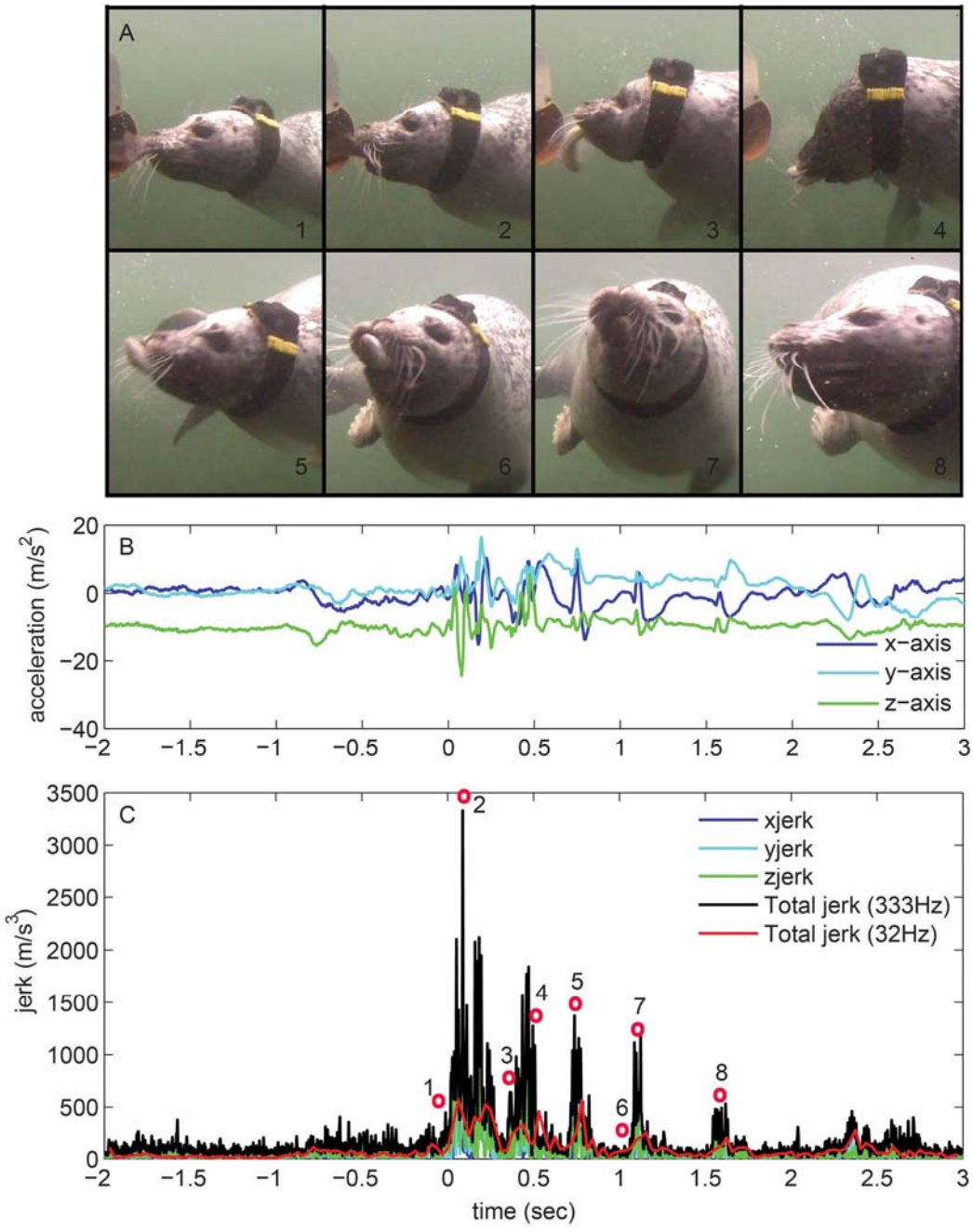


Fig. 2