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

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Revised for Journal of Experimental Biology methods

32 **Summary**

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

46

47 **Keywords**

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

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64 **Introduction**

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

82 Recent studies have shown promising use of head and jaw mounted accelerometers
83 sampling at 32 Hz to measure head surge in foraging attempts of both pinnipeds (Skinner et al.,
84 2009; Suzuki et al., 2009; Naito et al., 2010; Iwata et al., 2011; Naito et al., 2013) and penguins
85 (Kokubun et al., 2011; Watanabe and Takahashi, 2013). Prey capture and engulfment involves rapid
86 jaw movements in raptorial feeding and the retraction and lowering of the gular apparatus during
87 suction feeding (Werth, 2000; Marshall et al., 2008). These movements are unique to feeding and
88 should generate high frequency acceleration signatures that are distinctive and so readily detected
89 against other head movements. Here we use fast super-cranial accelerometry on a trained male
90 harbour seal catching prey to show that the differential of the three acceleration axes, jerk (m/s^3)
91 (Simon et al., 2012), provides a reliable, easily-computed and orientation-independent measure of
92 both raptorial and suction feeding that can be recorded or relayed over long time periods from wild
93 animals at sea.

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96 **Results**

97 Two experiments were conducted using different data collection parameters. In the first, an animal-
98 attached triaxial accelerometer was set to sample at 200 Hz with a clipping level of +/- 2 g. A total
99 of 124 trials were conducted over 27 days. After excluding prey captures in which engulfment was
100 not visible on any of the video cameras, a set of 14 captures of dead fish, 10 of large live trout and
101 13 of small live trout was available for analysis. Due to the relatively low clipping threshold and the
102 rapid head and jaw movements during capture (see video 1 in supplementary material), most of the
103 captures had brief intervals in which the measured acceleration in one or more axes was clipped.
104 Only 11 captures of dead fish, and one with a small live trout were unaffected by this limitation. In
105 the second experiment, the tag was therefore configured for a sampling rate of 333 Hz and a
106 clipping level of +/-16 g. A total of 20 trials were conducted with these settings, of which 9
107 captures of large 18-23 cm live trout happened in front of the cameras permitting analysis.

108 Based on visual analysis of all the prey captures, a total of 16 were judged to be
109 primarily raptorial feeding, while 15 were categorized as suction feeding. Raptorial feeding
110 occurred mostly in captures of large prey, whereas smaller prey were caught by suction (Table 1). In
111 both feeding mechanisms the absolute jerk in the z-axis was highest, followed by the x-axis, then
112 the y-axis. However, in suction feeding, the duration of the prey capture (t_2-t_0 , see Material and
113 methods) was shorter, and the amplitude of the jerk lower (Table 1). Fig. 1 shows an example of a
114 raptorial prey capture of a large trout. Here, the jaw opening is followed by a sudden rise in jerk
115 amplitude (Fig. 1A image 1 and 1C). Subsequent jerk peaks are associated with capture and
116 handling of the fish (Fig. 1A images 2-8).

117 To test whether feeding jerks could be distinguished from the jerk recorded in
118 intervals before and after feeding, we divided each capture session into three time windows of 250
119 ms each and computed the RMS of the norm jerk in each section: a pre-capture time window
120 starting 1 sec before t_0 (jaw opening), a capture window starting at t_0 , and a post-capture window
121 starting 1 sec after t_0 . The RMS measure was chosen because it is relatively insensitive to brief
122 intervals of clipping in the individual accelerometer signals (supplementary materials). Results of a
123 one-way ANOVA and multiple comparison test show that the RMS jerk during the feeding window
124 differed significantly from the before and after windows for all fish types (Fig. 2, Table 1).
125 Furthermore, engulfment of live fish generated significantly larger RMS jerk values, compared to
126 the RMS jerk during captures of dead fish (t-test, p-value < 0.005). A similar analysis of raptorial and

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

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

132

133 **Discussion**

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

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

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

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

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

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

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

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

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198 **Materials and methods**

199 Experiments were carried out at the Fjord&Belt in Kerteminde, Denmark, with a trained adult male
200 harbour seal (*Phoca vitulina*, Linnaeus, 1758) (13years old, 80kg) housed in a net pen. Head
201 accelerations during prey captures were measured using a triaxial accelerometer, “OpenTag”
202 (Loggerhead Instruments, Sarasota, FL, USA), sampling at 200 Hz or 333 Hz (16 bits). The tag was
203 calibrated for sensitivity and frequency response using a Brüel & Kjær Vibration Exciter Type 4809
204 and a pre-calibrated Brüel & Kjær Accelerometer Type 4381. The seal was trained to wear the
205 datalogger (dimensions 7.5x3.5x2.2 cm, 55 g in air, 3 g in water) on top of its head attached by
206 means of a small, custom-made elastic hood (Supplementary Fig. S1). The hood fit snugly around
207 the head and neck holding the tag firmly against the dorsal surface of the skull. In each trial, the seal
208 swam towards and acquired individual prey items released from a custom-made fish dispenser, and
209 then returned to station. Both 12-13 cm small and 15-25 cm large live trout (*Oncorhynchus mykiss*,
210 Walbaum, 1792), and 12-13 cm dead sprat (*Sprattus sprattus*, Linnaeus, 1758) and 15-16 cm
211 capelin (*Mallotus villosus*, Müller, 1776) were used as prey in the experiments. The prey captures
212 were filmed using four GoPro HD Hero2 cameras (120 fps) in underwater housings (Eye of Mine
213 Action Cameras; Carson, CA, USA) arranged so as to image captures from different angles to
214 ensure that timing of mouth opening and prey contact could be established. All recorders were
215 synchronized before and after a session, and the data were subsequently analysed in Matlab 7.5
216 (Mathworks, MA, USA) with custom-written scripts. Three events were identified in the videos
217 from each prey capture: the time of the first sign of jaw opening (t_0), the time of first fish-seal
218 contact (t_1) and the time of complete engulfment (but not necessarily deglutition) of the fish (t_2).
219 Each prey capture was classified to be either primarily suction or raptorial feeding by five observers
220 tasked with judging if the fish appearing in the videos were actively drawn into the mouth or not.
221 Prey capture events were grouped according to fish type and feeding mechanism (suction or
222 raptorial). The jerk was computed as the differential of the acceleration for each axis and the total

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

225
$$\text{Jerk} = \text{fs} * \text{sqrt}(\text{sum}(\text{diff}(\text{A}).^2, 2)) ;$$

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

232

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246 **Fig. legends**

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248 **Fig. 1** Example of prey capture of a large live trout. The jaw opening time (t_0) corresponds to time
249 0 on the x-axis. A) Still images of initial jaw opening (1), capture and handling (2-8). Measured
250 triaxial acceleration (B) and jerk (C) over the same time interval. The timing of the images is
251 marked on the jerk (C).

252

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

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

258
259 **Table 1** Results for all fish. Non-clipped data: 12-13 cm dead sprat (DS), 15-16 cm dead capelin
260 (DC), 12-13 cm small live trout (SLT), 18-23 cm large live trout (LLT). Clipped data: 12-13 cm
261 small live trout (C-SLT) and 15-25 cm large live trout (C-LLT).

262

263 **Abbreviations**

264 t0: time of visible initial jaw opening

265 t1: time of seal-prey contact

266 t2: time of prey engulfment

267 x-jerk: x-axis jerk

268 y-jerk: y-axis jerk

269 z-jerk: z-axis jerk

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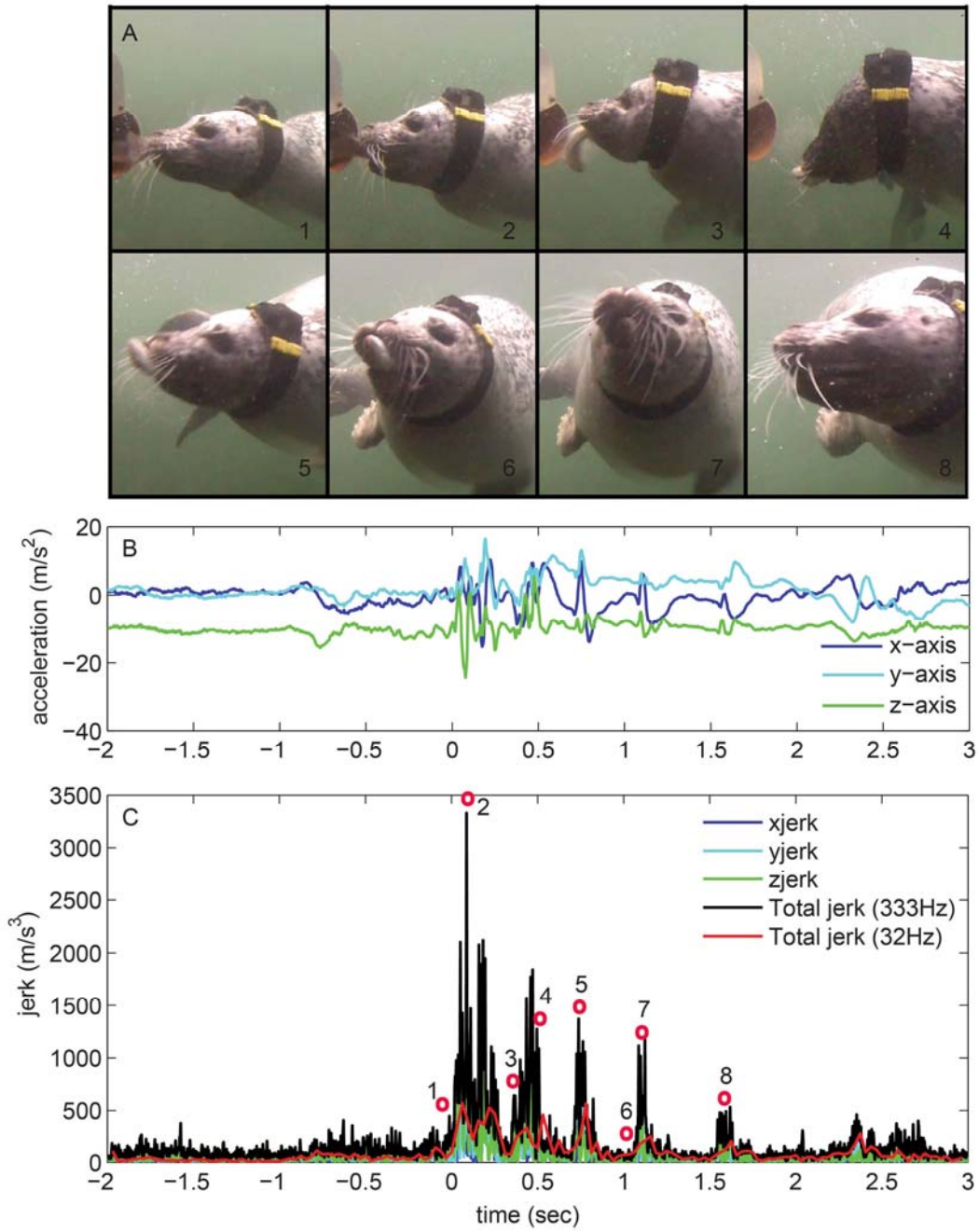
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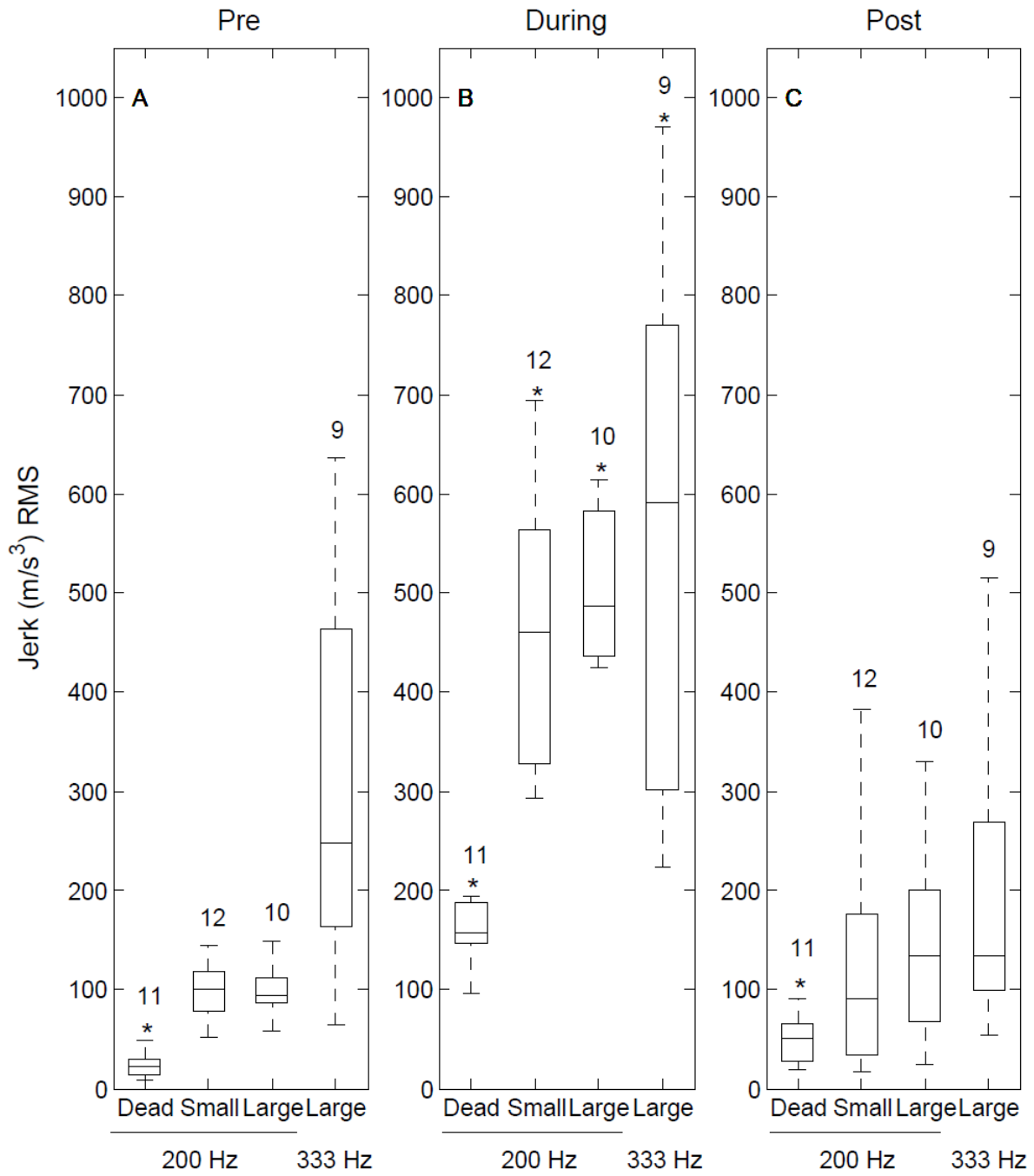
352 **Fig.1**



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359 **Fig. 2**



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366 **Table 1**

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

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Fig.1

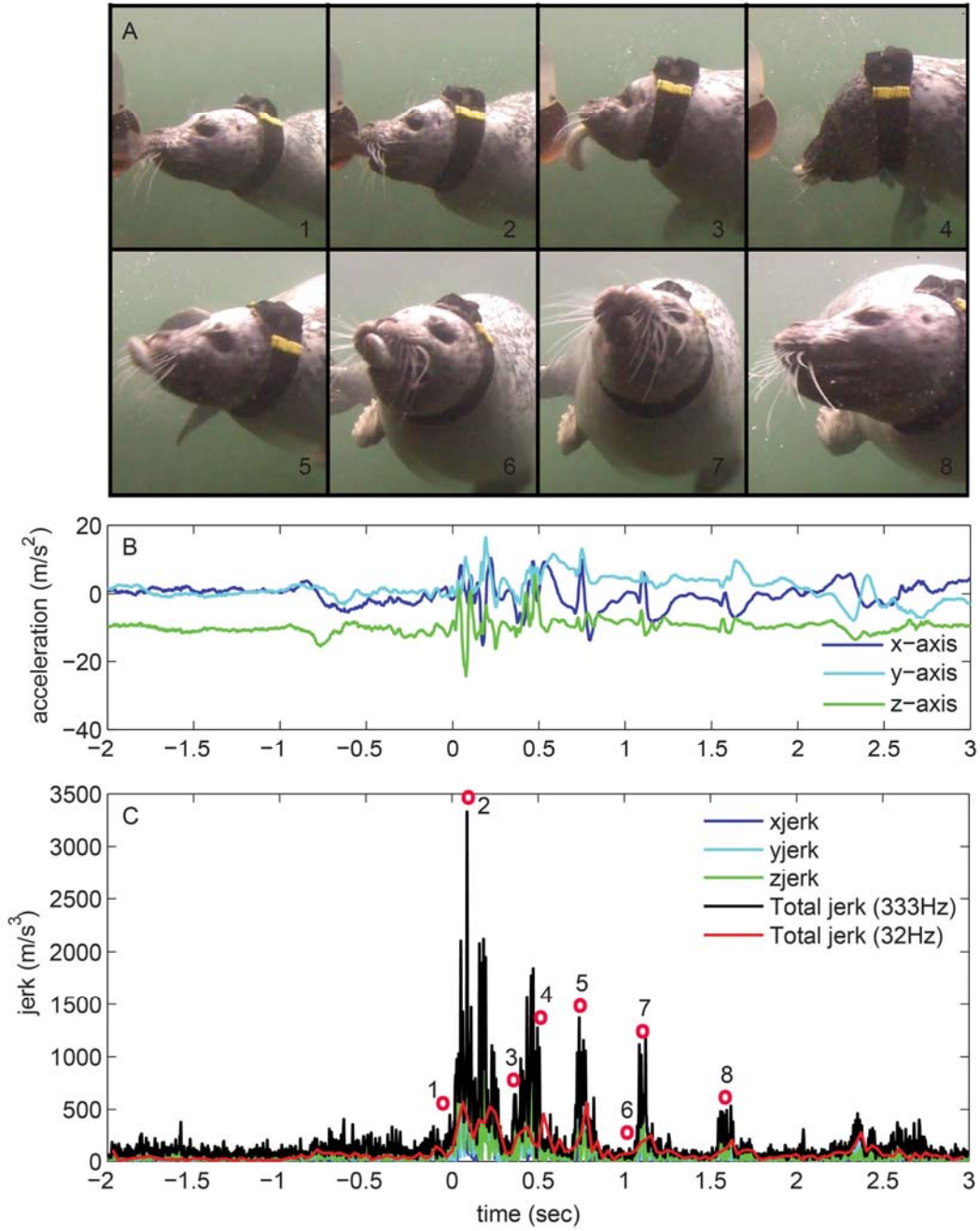


Fig. 2

