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Mathilde Chevally, Christophe Guinet, Didier Goulet-Tran, Tiphaine Jeanniard Du Dot. Sealing the deal – Antarctic fur seals’ active hunting tactics to capture small evasive prey revealed by miniature sonar tags. *Journal of Experimental Biology*, 2024, 227 (9), 10.1242/jeb.246937 . hal-04781582

HAL Id: hal-04781582

<https://hal.science/hal-04781582v1>

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Article in *Journal of Experimental Biology* · April 2024

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1 Sealing the deal – Antarctic fur seals’ active hunting tactics to 2 capture small evasive prey revealed by miniature sonar tags

3 **Running title:** Antarctic fur seal hunting tactics

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10 **Summary statement**

11 We describe fine-scale hunting tactics of Antarctic fur seals and show that fur seals
12 rely on their ability to perform bursts of acceleration to capture their small evasive prey.

13 **Abstract**

14 The ability of predators to adopt hunting tactics that minimise escape reactions from
15 prey is crucial for efficient foraging, and depends on detection capabilities and
16 locomotor performances of both predators and prey. Here we investigated the
17 efficiency of a small pinniped, the Antarctic fur seal (*Arctocephalus gazella*, AFS
18 hereafter) at exploiting their small prey by describing for the first time their fine-scale
19 predator-prey interactions. We compared them to those from another diving predator,
20 the Southern elephant seal (*Mirounga leonina*) that forage on the same prey type. We
21 used data recorded by a newly developed sonar tag that combines active acoustics
22 with ultra-high resolution movement sensors to study simultaneously the fine-scale
23 behaviour of both AFS and prey during predator-prey interactions in more than 1200
24 prey capture events for eight female AFS. Our results showed that AFS and their prey
25 detect each other at the same time, i.e. 1-2 seconds before the strike, forcing AFS to
26 display reactive fast-moving chases to capture their prey. In contrast, SES detect their
27 prey up to 10 s before the strike, allowing them to approach their prey stealthily without
28 triggering an escape reaction. The active hunting tactics used by AFS is likely very
29 energy consuming compared to the stalking tactics used by SES but might be
30 compensated by the consumption of faster-moving larger prey. We suggest that

31 differences in manoeuvrability, locomotor performances and detection capacities and
32 pace of life between AFS and elephant seals might explain their differences in hunting
33 styles.

34 **Key words**

35 Antarctic fur seals; *Arctocephalus gazella*; biologging; hunting tactics; predator-prey
36 interactions.

37 **Introduction**

38 Fine-scale predator-prey interactions, i.e. how predators find, select and capture their
39 prey, and alternatively how prey detect and react to imminent predation, are critical in
40 determining both predators' hunting efficiency and prey survival (Cooper Jr, 1997;
41 McHenry et al., 2009; Stewart et al., 2013), and in shaping their population dynamics
42 (Estes and Duggins, 1995; Frederiksen et al., 2006; Letnic et al., 2012). Sensory
43 capabilities and locomotor performances, i.e. manoeuvrability and acceleration
44 abilities, of both predators and prey are key factors in determining the outcome of
45 predator-prey interactions (Domenici and Blake, 1997).

46 In the three-dimensional marine environment, prey can escape in every direction
47 (Domenici and Blake, 1997), forcing predators to perform energy-expensive rapid
48 manoeuvres and bursts of accelerations. Predators are often larger than their prey,
49 and manoeuvrability being inversely proportional to body size (Henriques et al., 2021;
50 Tucker and Rogers, 2014), prey usually benefit from a greater manoeuvrability
51 (Domenici, 2001). Therefore, large vertebrate predators may be at disadvantage when
52 capturing small elusive prey. By adopting a stealthy approach, predators such as
53 Southern elephant seals (*Mirounga leonina*) and others can delay or even prevent prey
54 flight reaction, avoiding energy-expensive chase (Chevallay et al., 2023; Cooper Jr,
55 1997; Cooper Jr, 2003; Meager et al., 2006; Webb, 1984). However, this stalking tactic
56 implies that predators detect their prey far enough that they have time to adapt their
57 approach tactics before prey detect them (Chevallay et al., 2023; Snyder et al., 2007;
58 Vance et al., 2021). Conversely, if predators and prey detect each other at the same
59 time, predators must adopt a more reactive approach, with quick reactions being
60 essential to catch alerted prey (Snyder et al., 2007). This reactive hunting mode
61 requires predators to be able to perform fast-start manoeuvres.

62 In the aquatic environment, marine predators rely on different sensory systems to
63 locate their prey. Echolocating toothed whales can detect prey at long ranges (Jensen
64 et al., 2018; Tønnesen et al., 2020), while non-echolocating predators such as
65 pinnipeds must rely on vision or tactile cues (Adachi et al., 2022; Dehnhardt et al.,
66 1998; Levenson and Schusterman, 1999; McGovern et al., 2015) that may be only
67 detected at short ranges in the dark ocean. While forward motion of large predators
68 creates a bow wave that can be detected at distance by their prey (Blaxter and Fuiman,
69 1990; McHenry et al., 2009; Stewart et al., 2013), prey can easily go cryptic for non-
70 echolocating predators by staying motionless. This implies that, in most cases, prey
71 should detect their predators before being detected by them. Nevertheless, a recent
72 study highlighted unexpected detection abilities in Southern elephant seals, that were
73 found to be able to detect their prey several seconds before their prey detect them
74 (Chevallay et al., 2023). Prey detection capacities of free-ranging marine predators are
75 however poorly studied and it is not clear if other pinniped species benefit from the
76 same capacities as elephant seals.

77 Antarctic fur seals (*Arctocephalus gazella*, AFS hereafter) are small pinnipeds that
78 forage on mesopelagic prey, mostly myctophids (Jeanniard-du-Dot et al., 2017a; Lea
79 et al., 2002a). As air-breathing diving predators, they must regularly return to the
80 surface to breathe, limiting their time spent at the bottom of dives searching and
81 hunting for prey. Although foraging locations and diet of AFS are well known, fine-scale
82 characteristics of their prey (i.e. prey size and behaviour) and their hunting tactics to
83 subdue their prey are still poorly understood. Compared to hind-flipper thrusting and
84 low-expenditure swimming of elephant seals (Burkhardt and Frey, 2008), fast-
85 swimming AFS rely on their fore-flippers for propulsion (English, 1976). They are highly
86 manoeuvrable and able to perform fast bursts of accelerations. We thus hypothesize
87 that AFS rely on these abilities to target evasive, more reactive and faster moving prey
88 than the slow moving and less manoeuvrable elephant seals, which in turn likely rely
89 on highly sensitive sensory systems to surprise their prey (stalking approach,
90 Chevallay et al., 2023). The fact that female AFS from Kerguelen tend to forage mainly
91 on the fast-swimming lipid-rich *Gymnoscopelus sp.* myctophid species (Jeanniard-du-
92 Dot et al., 2017a; Lea et al., 2002a; Lea et al., 2008), capable of avoiding trawl nets
93 (Guinet et al., 2001), supports our hypothesis that they rely on active-hunting tactics to
94 target large calorific prey.

95 To better understand prey selection and hunting tactics in AFS and test the hypothesis
96 that AFS rely on their ability to perform fast manoeuvres to capture their evasive prey,
97 we took advantage of a newly developed miniature sonar and movement tag that
98 allows recording fine-scale information of prey characteristics simultaneously to fine-
99 scale AFS behaviour. Our objectives were (1) to describe characteristics of prey
100 targeted by female AFS to assess prey selection in this species; (2) to estimate the
101 timing of prey detection by AFS and prey reaction to the AFS approach, and (3) to
102 describe AFS hunting tactics, i.e. fine-scale AFS posture and swimming activity during
103 prey capture events to better understand how AFS efficiently exploit their small prey.
104 We then compared the predator-prey interactions to those from another diving predator
105 feeding on the same prey type, the Southern elephant seal.

106 Material and methods

107 **Device deployments and data collection**

108 Data were collected on eight lactating female AFS in January 2023 at Pointe Suzanne,
109 Kerguelen Island (49°26'S–70°26'E, Southern Ocean) under the ethical regulation
110 approval of the French Ethical Committee for Animal Experimentations (#37480-
111 2022052514544991v7) and the Committee for Polar Environment (A2021-48).
112 Females were captured with a hoop net, transported to a nearby handling station and
113 anaesthetised. Anaesthesia was achieved with isoflurane gas injected through a mask
114 placed over the snout. A flow rate of 3 to 5% isoflurane was used for the first 1 to 2
115 minutes, then the flow rate was reduced to 1 or 2% depending on the size of the animal.
116 Individuals were then measured (± 1 cm) and weighed (± 10 g). They were either
117 equipped with a head-mounted DTAG-4 sonar tag ($n = 5$, 85 x 45 x 20 mm, 120 g in
118 air, see Goulet et al. (2019) for further details) or a head-mounted DTAG-4 mini sound
119 tag ($n = 3$, 68.0 x 31.0 x 20.7 mm, 58 g in air). Tags were programmed to sample GPS
120 position (up to every minute), tri-axial acceleration (250 Hz), tri-axial magnetometer (50
121 Hz) and pressure (50 Hz). Mini sound tags also recorded audio data (96 kHz, 200 Hz
122 – 48 kHz bandwidth). The active sonar within the sonar tags recorded acoustic
123 backscatter returning from 10 μ s pings with a centre frequency of 1.5 MHz at a 25 Hz
124 ping rate. The active sonar operated with a 3.4° aperture beam width and a 6 m range
125 (Goulet et al., 2019). Tags were set to record only during night hours (from 6 P.M. to 6
126 A.M. local time, i.e. foraging periods of AFS (Boyd and Croxall, 1992)) to save battery.

127 Tags were glued to the fur using quick-setting epoxy glue (Araldite AW 2101, Ciba)
128 and recovered in January 2023 after a single foraging trip at sea when female returned
129 ashore to feed their pups using the same capture and sedation method. All deployed
130 tags were recovered.

131 **Data analyses**

132 Data recovered from tags were analysed using custom-written codes and functions
133 from www.animaltags.org in MATLAB version 2022b (The MathWorks, 2022).
134 Statistical analyses were conducted in R software version 3.5.1 (R Core Team, 2018).

135 *Prey capture attempt identification*

136 Prey capture attempts were detected from the 250 Hz tri-axial acceleration data
137 recorded by the sonar tags, by computing the norm of the differential of the tri-axial
138 acceleration (norm-jerk hereafter), as described in Chevallay et al. (2023). To establish
139 a threshold for detecting prey strikes, the maximum norm-jerk value over consecutive
140 10 s intervals was log-transformed and displayed as histograms for each seal. These
141 plots showed a bimodal distribution with a minimum at 3000 m.s⁻² for all individuals,
142 and was set as a threshold to identify strikes in the full norm-jerk series. Prey may be
143 encountered in patches or may elude capture, which might lead to several successive
144 strikes. Therefore, strikes occurring less than 15 s from the previous strike were
145 grouped in the same prey capture attempt bout (referred as bout hereafter) according
146 to the distribution of inter-strike interval (Chevallay et al., 2024).

147 *Sonar data analysis*

148 Sonar data recorded during bouts were displayed as echograms, showing the time on
149 the horizontal axis and the distance from the tag on the vertical axis, extending from
150 10 s before the bout start time to 2 s after the bout end (Chevallay et al., 2024). Different
151 variables describing predator-prey interactions were extracted manually from
152 echograms following the method described by Chevallay et al. (2024): number of prey,
153 prey evasive behaviour, prey acoustic size and echo intensity of the prey trace. The
154 number of prey were defined as the maximum number of independent echo traces
155 within a same ping (Jones et al., 2008). It was scored as one, i.e. a single prey, two,
156 or more than two, i.e. a school of prey. Prey evasive behaviour was identified from the
157 closing speed between predator and prey, which will vary in case of prey reaction,

158 resulting in a change in the slope of the prey echo trace (Goulet et al., 2019; Vance et
159 al., 2021). If a prey reaction was observed during the bout, prey was considered to be
160 evasive. Prey acoustic size was estimated from the -20 dB echo pulse width measured
161 on the widest part of the prey trace on evasive prey only (Burwen et al., 2003). Echo
162 intensity was defined as the maximum of the echo-to-noise ratio measured on the prey
163 trace. Echo-to-noise ratio was computed as the subtraction between the intensity of
164 the signal (in dB) and the noise level (in dB), defined as the 10th percentile of the signal
165 recorded in the last meter. It was measured only in prey traces visible in the 0.20-0.70
166 m range, to avoid measurement bias due to the distance between the target and the
167 transducer. This range was chosen because it is where most of prey traces were
168 visible.

169 *AFS hunting behaviour*

170 Metrics describing AFS fine-scale behaviour were extracted from the 250 Hz tri-axial
171 acceleration data and the 50 Hz tri-axial magnetometer data. Posture of AFS was
172 inferred from Euler angles (i.e. pitch angle (rotation around the left-right axis), roll angle
173 (rotation around the longitudinal axis) and heading angle (rotation around the dorso-
174 ventral axis, see Johnson and Tyack (2003) for details of the formulas). We also
175 described adjustments in travel direction during the approach as a proxy for prey
176 detection by computing the change in pointing angle, i.e. the angular change in
177 direction of the longitudinal axis from the second before (Chevallay et al., 2023; Miller
178 et al., 2004). Pointing angle was computed every second during the approach phase
179 and we then computed the change in pointing angle as the temporal evolution of the
180 pointing angle every second (Chevallay et al., 2023; Miller et al., 2004). Bouts were
181 characterised in term of duration (time elapsed from the first and last strike of the bout),
182 and intensity (RMS of the norm-jerk signal during the bout). AFS swim by propelling
183 themselves with their fore-flippers, resulting in an up and forward oscillating movement
184 synchronously visible on both the surge and the heave accelerometer axes (Jeanniard-
185 du-Dot et al., 2016). Therefore, flipper strokes were detected from the dynamic
186 acceleration of both the heave and the surge accelerometer axes by applying a high-
187 pass filter with a cut-off frequency of 1.6 Hz, i.e. 70% of the dominant stroke frequency,
188 on both axes. Absolute values of the dynamic heave and surge accelerations were
189 then summed to obtain the swimming effort, a proxy of the AFS swimming activity (Aoki
190 et al., 2011; Maresh et al., 2014).

191 **Statistical analyses**

192 Prey vertical distribution was compared between prey types using generalized mixed
193 models (GLMM hereafter, R package “MASS”, (Ripley et al., 2013)) with a gamma
194 distribution according to the distribution of the response variable, with depth (m) as a
195 response variable, prey type (schooling, single evasive or single non-evasive prey) as
196 fixed effects, and individual seal identities as random effects. Acoustic size and echo
197 intensity distribution of single and schooling prey traces were compared using
198 Kolmogorov-Smirnov test. Approach behaviour between prey types were compared
199 using GLMM with a gamma distribution, with bout duration (s), swimming effort ($\text{m}\cdot\text{s}^{-2}$),
200 pitch, roll and heading extent ($^{\circ}$) as response variables, prey type (schooling, single
201 evasive or single non-evasive prey) as fixed effects, and individual seal identities as
202 random effects. As the data represents a time-series, an autocorrelation structure of
203 order 1 was included in all the models. Results are all displayed as mean \pm sd.

204 **Results**

205 **Foraging behaviour**

206 Tags were deployed during a single foraging trip at sea. Six AFS travelled South, on
207 the edge of the Kerguelen plateau and two travelled East (Figure 1B).

208 Foraging trips lasted 8 ± 1 d (min-max 6-10 d) per individual, and tags were set to
209 record data only at night. During deployment, AFS performed 298 ± 129 dives per night
210 (min-max 160-541) at 26.5 ± 27.8 m (max 198.5 m) for 57.0 ± 53.6 s on average (max
211 267.2 s), with deeper dives performed at the beginning and the end of the night (Figure
212 1C). AFS performed 924 ± 165 bouts (min-max 622-1151 bouts) during the whole trip,
213 i.e. 142 ± 20 bouts per night (min-max 104-166 bouts per night).

214 **Prey characteristics and distribution**

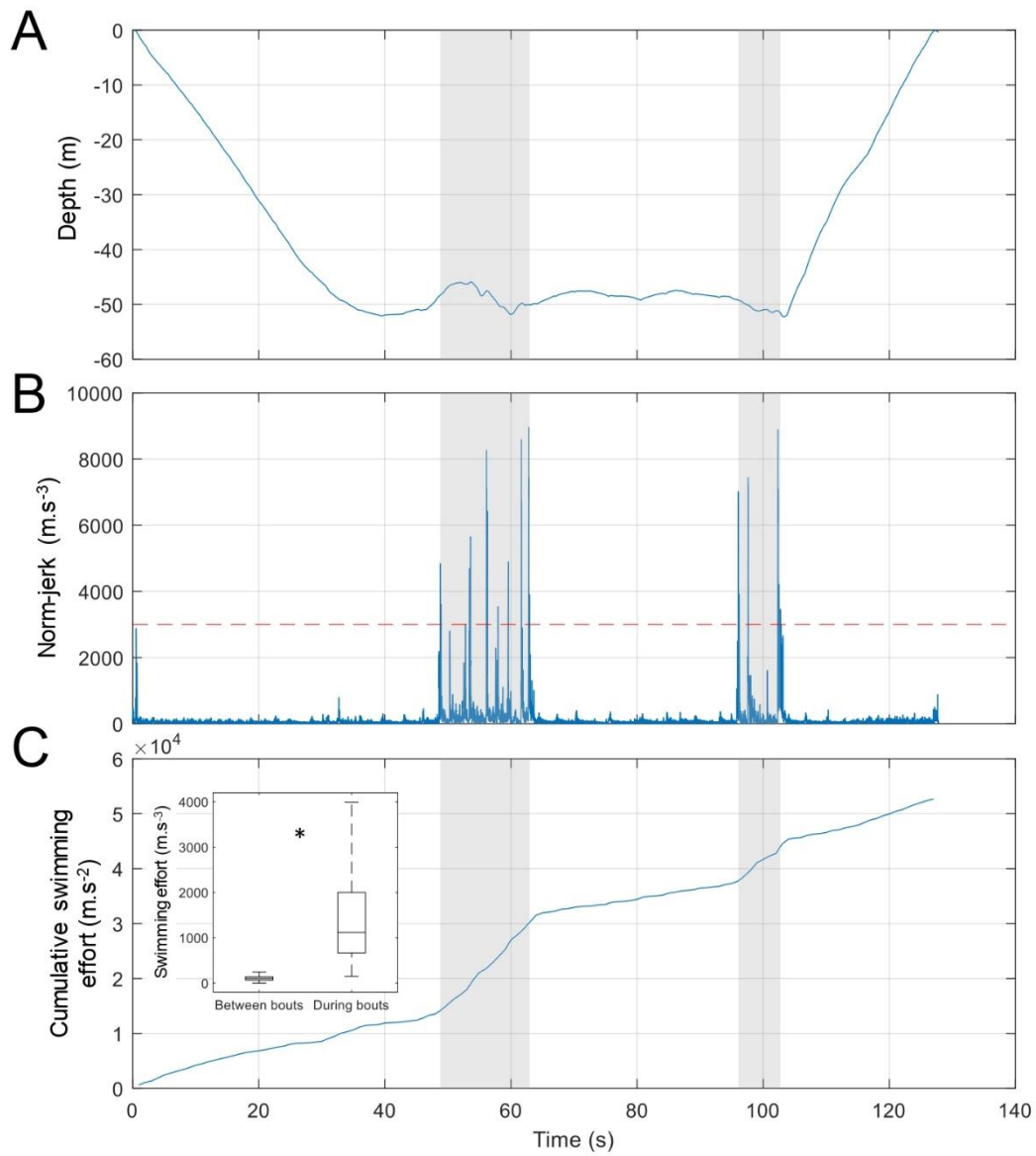
215 Prey characteristics and behaviour were inferred on 1117 echograms with clear prey
216 traces (Figure 2). Schooling prey represented 62% of targeted prey. Those prey usually
217 formed large diffuse schools showing evasive behaviour (Figure 2C). Single prey
218 represented 38% of targeted prey, among which 65% showed evasive behaviour
219 (Figures 2A&B). Prey reacted 1.0 ± 2.3 s before the first strike of the bout, at a distance
220 of 0.43 ± 0.21 cm from the AFS.

221 Prey acoustic size was estimated at 6.3 ± 5.6 cm for single prey (Q1-Q3: 3.1-7.0 cm,
222 Figure 3). Prey within schools had significantly lower acoustic sizes than single prey
223 (2.5 ± 1.1 cm, Q1-Q3: 1.6-3.1 cm, KS-test, $P < 0.001$, Figure 3). Echo intensity of single
224 prey traces was significantly higher than of schooling prey traces (61.6 ± 9.2 dB, Q1-
225 Q3: 55.9-67.7 dB for single prey; 50.3 ± 8.3 dB, Q1-Q3: 45.1-54.5 dB for schooling
226 prey, KS-test, $P < 0.001$, Figure 3). Schooling prey were encountered slightly shallower
227 than single prey (GLMM, $P < 0.001$, 42.1 ± 18.2 m vs. 49.3 ± 18.2 m respectively),
228 while no difference in depth was found between single evasive and non-evasive prey
229 (49.3 ± 23.0 vs. 48.2 ± 24.8 m, GLMM, $P = 0.1603$).

230 **Hunting behaviour**

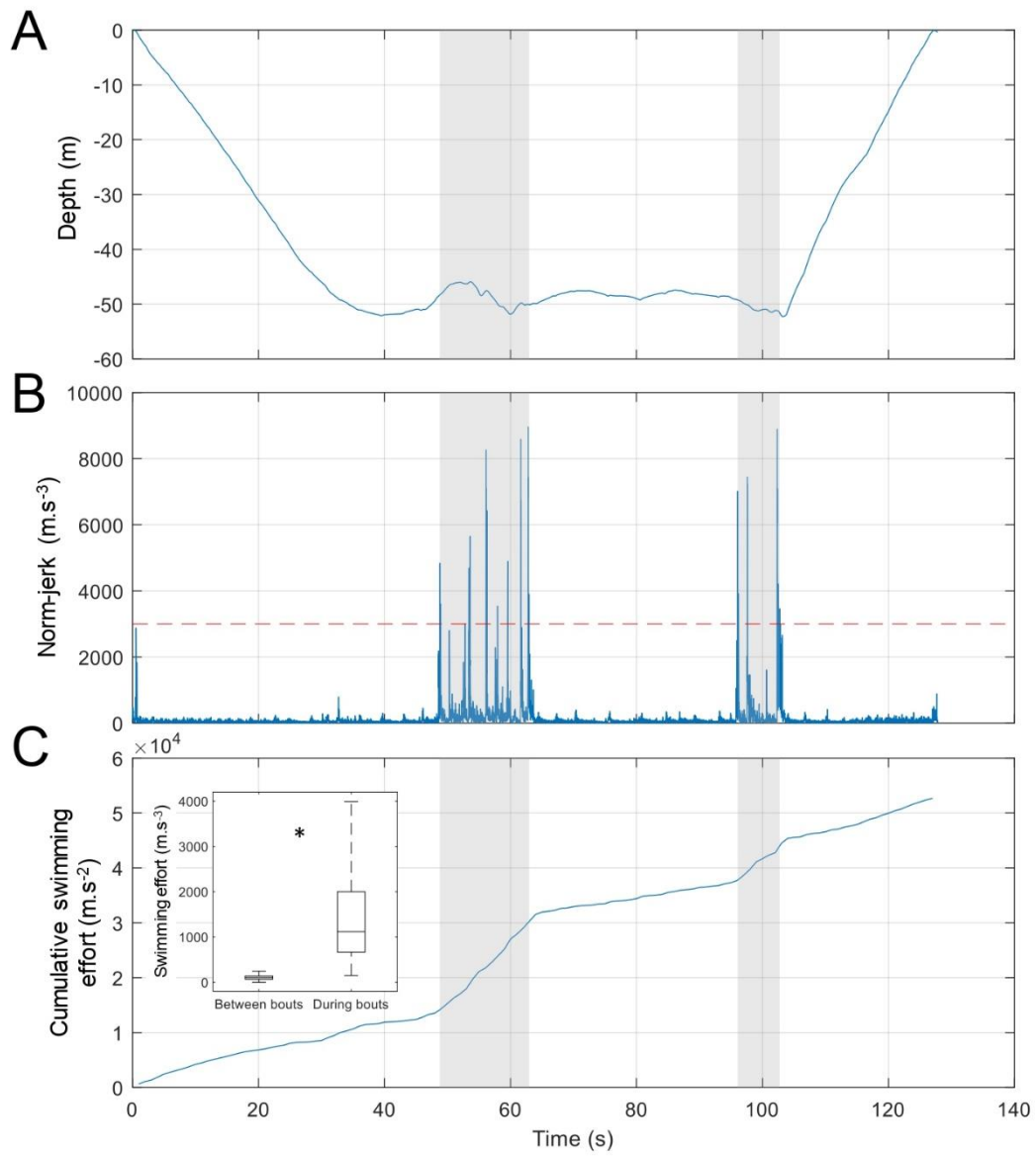
231 Between bouts, AFS generally glided resulting in a low swimming activity (Figure 4C),
232 with AFS only giving 0.2 ± 0.1 flipper strokes per second, i.e. 1 flipper stroke every 5 s
233 (Q1-Q3: 0.1 to 0.3 flipper strokes per second, i.e. 1 flipper stroke every 3 to 10 s).
234 During the approach phase, i.e. 10 seconds before the bout start, swimming activity
235 remained low (Q1-Q3: 0.1 to 0.6 flipper strokes per second), i.e. 1 flipper stroke every
236 1.6 to 10 s.

237 AFS usually adopted a horizontal posture (i.e. pitch angle close to 0° ,



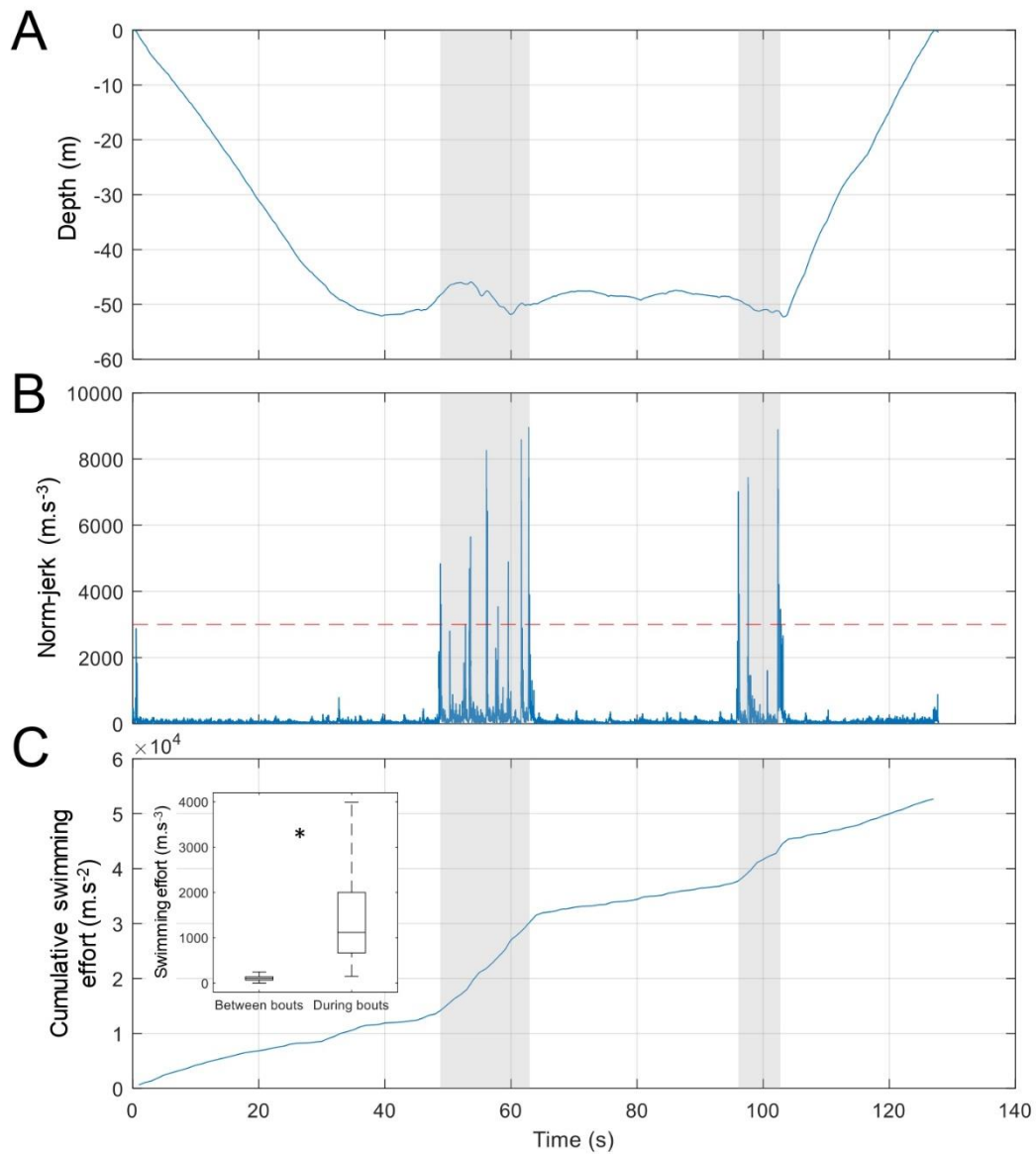
238

239 Figure 5) during the approach phase and maintained this posture during the whole
 240 approach. For all individuals, roll angles were mainly positive and varied between 0
 241 and 60° , meaning that the body of the animal leaned to the right (



242

243 Figure 5). AFS altered their direction of travel 1-2 s before the bout start (



244

245 Figure 5).

246 AFS actively stroke flippers during bouts, resulting in a steady increase in swimming
 247 activity throughout bout duration (Figure 4C). Swimming effort was significantly higher
 248 during bouts than during inter-bout periods (GLMM, $1672 \pm 1545 \text{ m.s}^{-3}$ vs. 112 ± 60
 249 m.s^{-3} , $P < 0.001$, Figure 4C). These bursts of acceleration lasted significantly longer
 250 for schooling prey and for single evasive prey than for single non-evasive prey (GLMM,
 251 $P < 0.001$, bout duration = $14.7 \pm 12.6 \text{ s}$, $13.6 \pm 10.3 \text{ s}$, and $7.2 \pm 7.5 \text{ s}$ respectively,
 252 Figure 6), with no difference observed between bouts targeting schooling prey or single
 253 evasive prey (GLMM, $P = 0.7745$). Similarly, bouts targeting both schooling prey and
 254 single evasive prey were characterised by a higher number of head strikes (GLMM, P

255 < 0.001, number of head strikes = 5.3 ± 4.6 , 4.4 ± 2.5 , 3.2 ± 2.0 respectively, Figure 6)
256 with no difference between schooling prey and single evasive prey (GLMM, $P =$
257 0.3563). AFS swimming effort during the bout was significantly higher for schooling
258 prey and single evasive prey than for single non-evasive prey (GLMM, $P < 0.001$,
259 swimming effort = $14311 \pm 12447 \text{ m}\cdot\text{s}^{-2}$, $12407 \pm 8077 \text{ m}\cdot\text{s}^{-2}$, and $7258 \pm 6270 \text{ m}\cdot\text{s}^{-2}$
260 respectively, Figure 6), but was not different between schooling prey and single
261 evasive prey (GLMM, $P = 0.1227$). Finally, posture of AFS was highly variable during
262 the bout regardless of the type of targeted prey, with pitch, roll and heading extents
263 being slightly inferior for single non-evasive prey, although not significantly (GLMM, P
264 > 0.2834 , Figure 6).

265 Discussion

266 Inferring fine-scale characteristics of the prey targeted by free-ranging diving predators
267 and their detailed hunting tactics has been a long-standing technical challenge. New
268 biologging devices combining ultra-high resolution movement sensors (i.e.
269 accelerometers and magnetometers) with a synchronously-sampled high-ping rate
270 active sonar have recently shed some light on predator-prey interactions in deep-diving
271 predators (Antoine et al., 2023; Chevallay et al., 2023; Goulet et al., 2019). Here, for
272 the first time on otariids, we deployed high-resolution sonar and movement tags on
273 AFS at Pointe Suzanne, Kerguelen Islands, to investigate prey selection and AFS
274 hunting tactics.

275 **AFS prey characteristics and behaviour**

276 Female AFS from Kerguelen Islands mainly forage on myctophids, mostly from the
277 genus *Gymnoscopelus* (Jeanniard-du-Dot et al., 2017a; Lea et al., 2002a; Lea et al.,
278 2008). Myctophids are small fish that are very abundant in the Southern Ocean,
279 particularly around Kerguelen Islands. While they can be found at 1000 m depth during
280 the day, most myctophid species perform diel vertical migration towards the surface at
281 night. This makes them accessible to AFS that dive to ~ 25 m depth on average (Boyd
282 and Croxall, 1992). The main prey species targeted by AFS females (i.e.
283 *Gymnoscopelus piabilis*, *G. nicholsi* and *Electrona subaspera*) usually form the upper-
284 part of the mesopelagic community in the Polar Frontal Zone at night, migrating to
285 deeper than 300 m during daytime.

286 Whilst the size of prey items found in AFS scats ranged from 4 to 15 cm (Lea et al.,
287 2002a), we acoustically estimated it to be between 3 and 7 cm. As the acoustic size
288 can vary greatly depending on the orientation of the target relative to the beam, the
289 smaller acoustic size of prey found might result from the non-optimal orientation of the
290 prey regarding the sonar beam. The inferred sizes of prey are minimal when the target
291 is perpendicular and maximal when oriented longitudinally to the beam. By measuring
292 the maximum length of evasive prey only, we assumed that prey were oriented
293 longitudinally to the sonar beam at some point during the escape manoeuvre. This
294 limits the target orientation bias. In addition to the orientation, the composition, such
295 as the presence of a gas-filled swimbladder in the target, can influence the measure of
296 the acoustic size (Burwen et al., 2003). For example, *Gymnoscopelus* species targeted
297 by AFS do not have a gas-filled swimbladder, which is responsible for most of the
298 reflected acoustic signal in many fish species (Dornan et al., 2019). Although the ultra-
299 high frequency of the sonar tag makes it sensitive to targets with low acoustic reflexion
300 properties (Goulet et al., 2019), the absence of gas-filled swimbladder might
301 underestimate the actual size of AFS prey. Despite this uncertainty regarding the actual
302 size of prey targeted by AFS using sonar recordings, this tag provides unique data on
303 fine-scale prey characteristics during each prey encounter event which have been
304 previously very difficult to obtain.

305 From sonar recordings, we also found that 62% of prey targeted by tagged AFS were
306 gathered in large diffuse and mobile schools encountered at shallower depths than
307 single prey. Individual targets within schools seemed to have lower acoustic size
308 compared to single prey items (i.e. 1-3 cm vs. 3-7 cm) and lower echo intensity (i.e.
309 45-54 dB vs. 56-68 dB). Differences in acoustic properties of single vs. schooling prey
310 items could indicate different prey species (Misund, 1997). The large number of small
311 individual targets within schools, and the evasive behaviour of schools could
312 correspond to krill, which is known to form very mobile swarms (Hamner and Hamner,
313 2000). Recent trawl sampling and acoustic surveys performed on the Kerguelen
314 plateau showed that one krill species, *Euphausia vallentini*, measuring 1-3 cm, is
315 particularly abundant in the first 200 m of the water column (Cotté et al., 2022). *E.*
316 *vallentini* is preyed upon by other Southern Ocean diving predators such as Macaroni
317 penguins (*Eudyptes chrysolophus*), rockhopper penguins (*Eudyptes chrysocome*
318 *moseleyi*) and Gentoo penguins (*Pygoscelis papua*) (Ridoux, 1988; Tremblay and

319 Cherel, 2003) as well as adult male AFS from Crozet Islands (Cherel et al., 2009). Fur
320 seals are characterised by a strong sexual dimorphism, with males being much larger
321 than females, leading to differences in physiological diving capacities, and therefore in
322 foraging preferences (Kernalleguen et al., 2012; Page et al., 2005; Staniland and
323 Robinson, 2008). While *E. valleritini* is preyed upon by adult males AFS from Crozet,
324 it has not been identified as a common prey species in the diet of female AFS from
325 Kerguelen Islands (Jeanniard-du-Dot et al., 2017a; Lea et al., 2002a; Lea et al., 2008).
326 This could be artefactual, however, as crustacean remains are less conspicuous, more
327 digestible and/or have a faster transit time more digestible than fish remains. DNA-
328 metabarcoding analyses on scats should be conducted to verify the presence of krill in
329 the diet of female AFS from Kerguelen (Jeanniard-du-Dot et al., 2017b). We cannot
330 also exclude a temporal shift in the diet, as the last dietary analyses were carried out
331 twelve years ago in this population.

332 **AFS fine-scale predator-prey interactions**

333 We hypothesized that compared to Southern elephant seals, a phocid seal also
334 feeding primarily on myctophids, AFS females adopt reactive fast-moving chases to
335 target their prey. To test this hypothesis, we identified the precise timing of prey strikes
336 and then described the AFS direction of travel during the approach to find when they
337 adjusted their course to intercept their prey (Chevallay et al., 2023; Miller et al., 2004).
338 We found that AFS consistently changed their direction of travel 1-2 s before the strike.
339 Swimming speed for AFS was estimated at less than 1 m/s during the bottom phase
340 of the dive (Boyd et al., 1995), which gives a prey detection distance inferior to 1-2 m
341 (Table 1). Tags increase drag forces on equipped animals, resulting in a slightly
342 reduced swimming speed (Rosen et al., 2018). Therefore, AFS might swim faster than
343 equipped animals and the prey detection distance might be slightly underestimated
344 here. Using sonar recordings, we also estimated prey reaction timing at approximately
345 1 s before the strike, i.e. at 0.4 m from the predator. Our results suggest that AFS
346 detect their prey very shortly before prey detect them as opposed to Southern elephant
347 seals which adjust their direction of travel up to 10 s before the strike, i.e. 7-17 m prior
348 the strike, with prey reacting 1 s before the strike, i.e. at 0.5 m from the predator
349 (Chevallay et al., 2023, Chevallay et al. unpublished data) (Table 1). Therefore, our
350 results suggest that, as opposed to elephant seals, AFS detect their prey very shortly

351 before prey detect them, suggesting that they might be constrained to adopt a more
 352 reactive mode of hunting compared to elephant seals.

353 Table 1: Comparison of foraging parameters (dive depth (m), dive duration (s), energy
 354 expenditure ($\text{kJ}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$)) and predator-prey interactions (prey acoustic size (cm),
 355 prey flight initiation distance (m) and prey detection distance (m)) in female Antarctic
 356 fur seals and female Southern elephant seals, two pinniped species foraging on
 357 myctophids, equipped with sonar and movement tags in Kerguelen Islands.

	Antarctic fur seals	Southern elephant seals
Dive depth (m)	26.5 ± 27.8^a	413 ± 89^c
Dive duration (s)	57.0 ± 53.6^a	1140 ± 180^c
At-sea energy expenditure ($\text{kJ}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$)	$\sim 590^b$	$\sim 100^d$
Prey acoustic size (cm)	6.8 ± 5.8^a	5.4 ± 3.0^e
Prey flight initiation distance (m)	0.43 ± 0.21^a	0.47 ± 0.23^e
Prey detection distance (m)	1-2 ^a	7-17 ^f

358 ^aThis study, ^bJeanniard du Dot et al. (2016), ^cChevallay et al. (2024), ^dMaresh et al.
 359 (2014), ^eChevallay et al. unpublished data, ^fChevallay et al. (2023).

360 Both elephant seals and AFS likely use a combination of whiskers and hearing to
 361 detect prey. In particular, pinnipeds have highly developed whiskers that can sense
 362 the mechanical vibrations created by a swimming prey (Adachi et al., 2022; Gläser et
 363 al., 2011; Miersch et al., 2011). They might also locate large prey aggregations by
 364 listening to fish choruses (McCauley and Cato, 2016), similar to killer whales (*Orcinus*
 365 *orca*, (Guinet, 1992)), Indo-Pacific humpback dolphins (*Sousa chinensis*, (Barros et al.,
 366 2004)) and bottlenose dolphins (*Tursiops truncatus*, (Gannon et al., 2005)). The acuity
 367 of these senses are likely different between environments, however, in shallow waters
 368 where AFS forage (20-40 m), surface turbulences and noise of waves might dampen
 369 tactile and acoustic cues and affect AFS senses. On the other hand, these turbulences

370 are attenuated under the mixed layer depth, where elephant seals forage (200-600 m).
371 These different environmental conditions may explain the shorter detection distance
372 observed in AFS compared to elephant seals. The smaller search swathe for AFS
373 suggests that they might need higher prey densities to have the same probability of
374 prey encounter as elephant seals. Therefore, they likely need to concentrate their
375 foraging activity on highly productive waters (Jeanniard-du-Dot and Guinet, 2021). AFS
376 concentrate their foraging activity at the edge of the Kerguelen plateau, where the
377 interactions between currents and continental slope enhance primary production and
378 promotes local aggregation of marine organisms (Lavoie et al., 2000; Meyer et al.,
379 2015; Park et al., 2008).

380 A reactive mode of hunting requires the predator to perform fast manoeuvres to capture
381 their evasive prey. We found that AFS rapidly increased their swimming effort and
382 accelerated quickly once interaction with prey began. Bursts of accelerations lasted
383 longer when foraging on evasive prey, likely reflecting prey pursuit. We also
384 consistently observed high variability in AFS roll and heading angles, indicating turning
385 and rolling manoeuvres during prey interactions. While AFS are highly mobile
386 underwater, their small prey might be more manoeuvrable (Domenici, 2001) but not as
387 fast as AFS (i.e. swimming speed of 0.1-0.3 m/s for myctophids (Ignatyev, 1996) vs.
388 cruising speed of 1-2 m/s for AFS (Boyd et al., 1995)). AFS higher locomotor
389 performances thus enable them to quickly surpass and catch up their prey. The
390 variability in AFS body angles during prey approaches indicates that single non-
391 evasive prey were approached in a straighter trajectory than evasive prey, and required
392 less quick and drastic manoeuvres from AFS. This result was not significant, however
393 our sample size was small and we observed a high inter-individual variability. This lack
394 of statistical power might explain lack of statistical differences in AFS posture between
395 evasive and non-evasive prey.

396 Bursts of acceleration and active pursuit are energetically costly especially for air-
397 breathing diving predators limited by their oxygen stores. For example, in sperm
398 whales, bursts of acceleration can be responsible for up to 50% of energy consumption
399 during dives (Aoki et al., 2012). In short-finned pilot whales, the energy spent in bursts
400 of acceleration might explain their relatively short dive duration compared to diving
401 predators of similar size (Soto et al., 2008). Similarly, AFS usually perform short dives
402 of approximately 1-2 min (Boyd and Croxall, 1992) which might be result in part from

403 their active-hunting tactics. Indeed, AFS have a field metabolic rate of $\sim 590 \text{ kJ.kg}^{-1}$.
404 day^{-1} (doubly-labelled water technique, Jeanniard-du-Dot et al., 2016) while it was
405 estimated at $\sim 100 \text{ kJ.kg}^{-1}.\text{day}^{-1}$ for Northern elephant seals (Maresh et al., 2014)
406 (Table 1). These differences in energy expenditure might be partly explained by their
407 respective hunting modes, even if other factors such as thermoregulation and diving
408 capacities, and oxygen stores also come into play. Nevertheless, this difference in
409 hunting mode between SES and AFS reflects nicely the respective pace of life between
410 otariids and phocids (Jeanniard-du-Dot and Guinet, 2021; Ponganis, 2015). Active
411 predators usually select highly nutritious prey such as large muscular squids to
412 compensate the high energy costs associated with bursts of acceleration or high pace
413 of life (Spitz et al., 2012). This is also the case for AFS who mainly forage on highly
414 nutritious lipid-rich myctophids (Lea et al., 2002b), mostly belonging to the
415 *Gymnoscopelus* genus measuring up to 16 cm (Lea et al., 2002a). Consequently, this
416 active mode of hunting seems compensated by the consumption of large calorific prey
417 (Table 1).

418 Bouts associated with schooling prey were long with several successive head strikes
419 (3 to 5), high swimming efforts and high turning rates. This suggests that AFS might
420 successively capture several prey within the school. We also observed similarities in
421 AFS behaviour during bouts associated with schooling prey and single evasive prey.
422 Given the limited range of the sonar, it is likely that only tight aggregations appear as
423 schools on echograms, while diffuse schools with a high inter-individual distance might
424 be classified as single prey. Bouts associated with single evasive prey were
425 significantly longer, associated with a higher swimming effort and a higher number of
426 head strikes than bouts associated with non-evasive prey, which might reflect
427 successive attempts to capture evasive prey. We found high variability in bout
428 durations, number of head strikes and swimming efforts for all prey types including
429 single non-evasive prey. While we would expect that these non-evasive prey would be
430 captured in a single head strike without a chase, the longer bouts with several head
431 strikes might correspond to multi-capture of non-mobile prey gathered in large
432 scattered aggregations. A fine-scale analysis of AFS three-dimensional trajectory
433 during bouts could help distinguishing between scattered schools and actual isolated
434 prey.

435 While bursts of acceleration are associated with prey capture attempts, AFS generally
436 displayed low swimming activity between bouts giving only one flipper stroke every 3
437 to 10 s. Similar gliding behaviour was observed in Southern elephant seals (Chevallay
438 et al., 2023) and sperm whales (Aoki et al., 2012) to reduce the bow wave generated
439 by their forward movement. Indeed, fish prey can detect turbulences produced by an
440 approaching predator using their lateral line. Consequently, AFS might avoid alerting
441 their prey by lowering their swimming activity (Blaxter and Fuiman, 1990; McHenry et
442 al., 2009; Stewart et al., 2013). Moreover, reducing body movements and associated
443 water turbulences might help AFS to better pick up tactile and acoustic cues of nearby
444 prey in the turbulent surface waters of the windy Southern ocean, as suggested for
445 rough-toothed dolphins (*Steno bredanensis*, (Götz et al., 2006)).

446 Conclusion

447 This study highlights fine-scale prey-predators interactions to an unprecedented level,
448 and shows how free-ranging Antarctic fur seals adjust hunting tactics to prey
449 characteristics in their specific environment. We found that AFS forage both on
450 individual prey and on smaller prey items gathered in large diffuse and evasive schools,
451 which may indicate a mixed diet between myctophids and krill. We suggest that AFS
452 adopt a reactive mode of hunting relying on their ability to perform fast manoeuvres
453 and bursts of acceleration. These active hunting tactics are likely very energy-
454 consuming but might be compensated by the consumption of highly nutritious prey.
455 We also highlight the differences in hunting styles and modes between two sympatric
456 marine top predators, AFS and the Southern elephant seals. In contrast with the active
457 pursuit used by highly manoeuvrable AFS to capture their prey, low-expenditure
458 swimming elephant seals rely on higher detection capacities to approach their prey
459 stealthily without triggering an escape reaction and without spending as much energy.
460 Differences in manoeuvrability, locomotor performances and detection capacities
461 between AFS and elephant seals might explain their differences in hunting styles.

462 Acknowledgments

463 Field work in Kerguelen was supported by the French Polar Institute (Institut Polaire
464 Français Paul Emile Victor) as part of the Ornithoeco programme (n. 109, PI C.
465 Barbraud). We thank Nicolas Bonetti, Lucas Bouland, Elie Castang, Pierre Guenot,
466 Lola Gilbert, Camille Henriët, Ludovic Ivars and Sébastien Picon for their help in

467 collecting the data. We want to thank Mark Johnson and Pauline Goulet for providing
468 tags, software and codes for data analysis. We thank Benjamin Dupuis for his help in
469 finding the title of this paper.

470 **Competing interests**

471 The authors declare that there is no conflict of interest.

472 **Funding**

473 Field work in Kerguelen was supported by the French Polar Institute (Institut Polaire
474 Français Paul Emile Victor) as part of the Ornithoeco programme (n. 109, PI C.
475 Barbraud).

476 **Data availability statement**

477 Data and codes used on the manuscript are available upon request from the
478 corresponding author, MC.

479 **Diversity and inclusion statement**

480 All authors were engaged early on with the research and study design to ensure that
481 the diverse sets of perspectives they represent was considered from the onset.
482 Whenever relevant, literature published by scientists from the region was cited.

483 **Author contributions**

484 MC, CG and TJDD conceived the ideas and designed methodology. MC and TJDD
485 collected the data. MC and DGT analysed the data. MC, CG and TJDD led the writing
486 of the manuscript. All authors contributed critically to the drafts and gave final approval
487 for publication.

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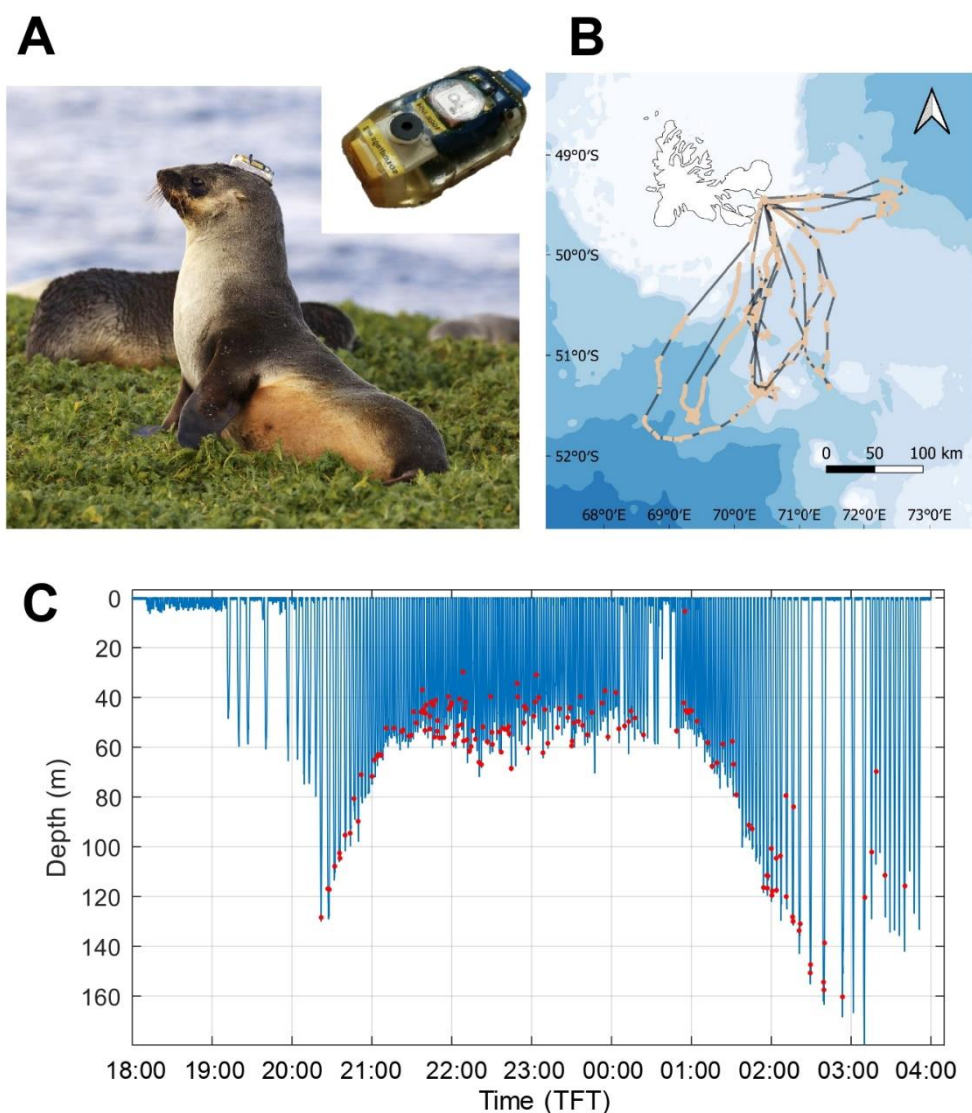
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717 **Figures**

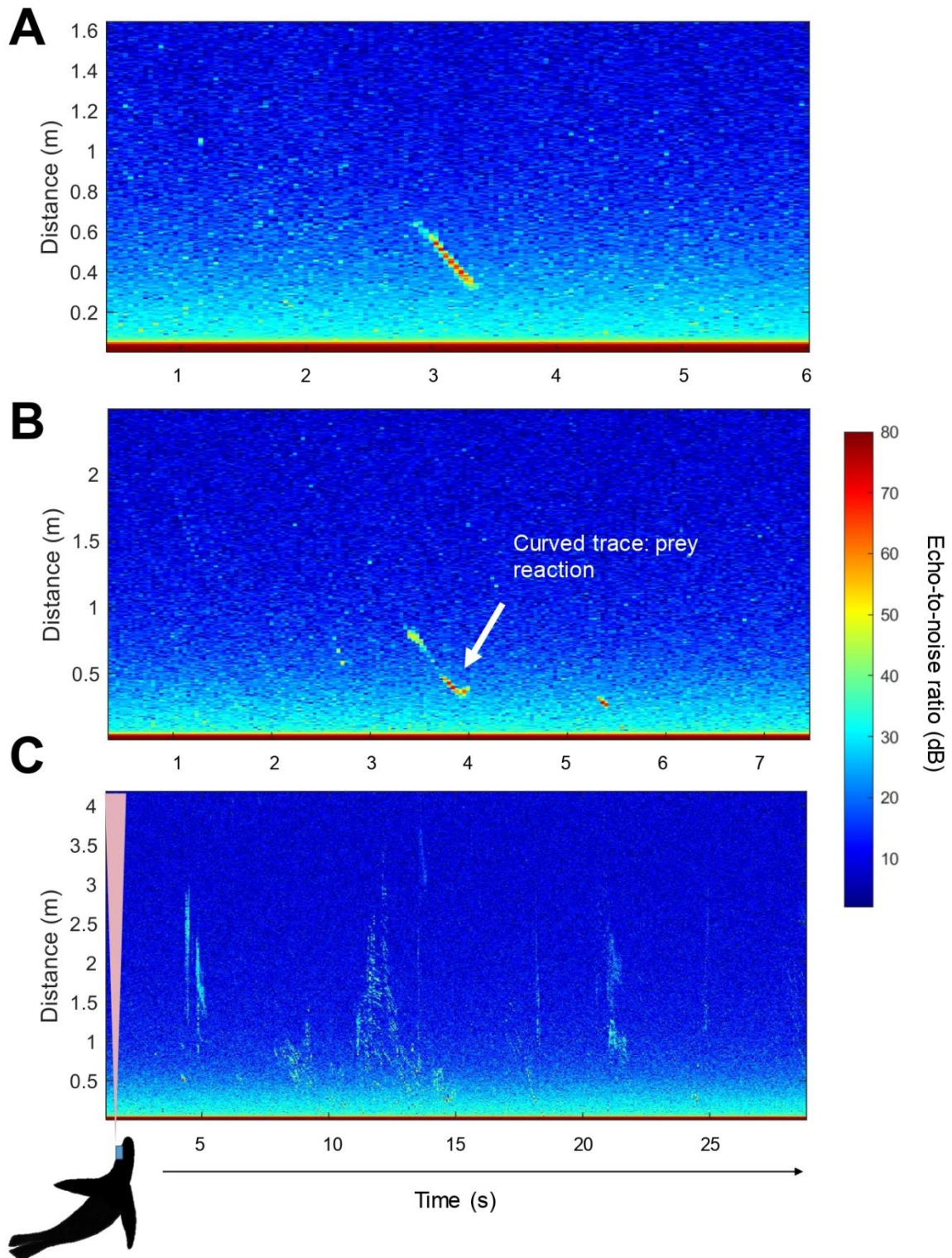
718 Figure 1: (A) Female Antarctic fur seals (AFS) equipped with a sonar tag, pictured in
719 the insert at the top right corner. (B) GPS track of eight female AFS from Pointe
720 Suzanne colony on Kerguelen Islands equipped with sonar and sound tags in January
721 2023 during a single foraging trip at sea. Grey lines corresponds to day periods when
722 the tag was switched off. (C) Example of a dive profile recorded during one foraging
723 night for a female AFS. Red dots indicate prey capture attempt bouts, identified as
724 spikes in the norm of the differential of the tri-axial acceleration.



725

726 Figure 2: Echograms showing sonar data recorded during a prey capture attempt bout
727 by a female AFS equipped with a sonar tag in January 2023 at Pointe Suzanne,

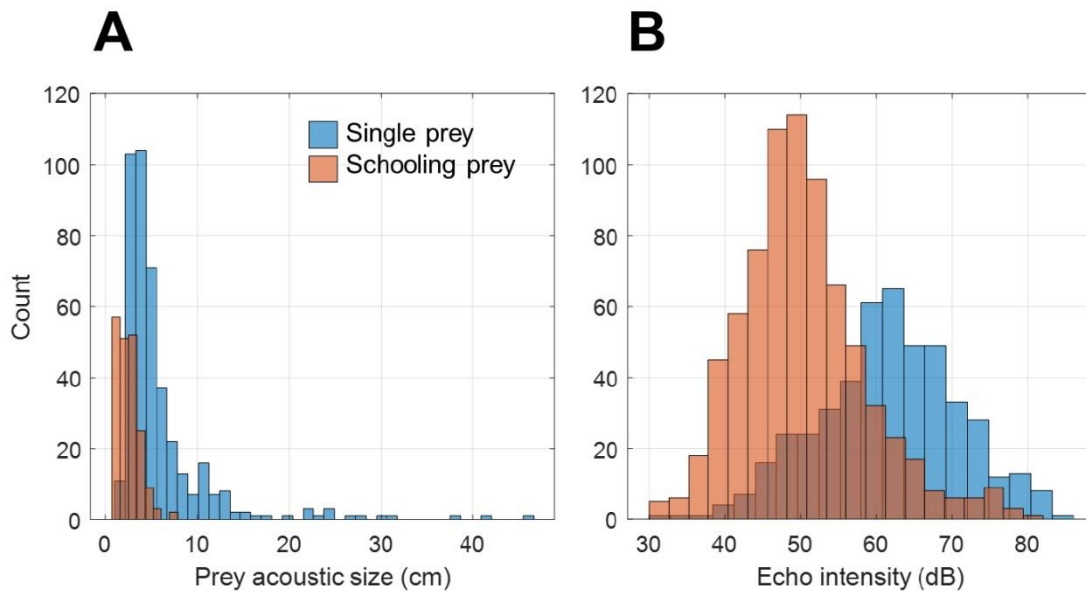
728 Kerguelen Island (time (s) on the horizontal axis and distance (m) from the sonar tag
729 on the vertical axis). For better visibility of the prey traces, the axes are not all at the
730 same scale. The colour scale indicates echo-to-noise ratio on a dB scale. Echograms
731 respectively display (A) a single non-evasive prey, (B) a single evasive prey and (C)
732 schooling prey insonified over successive sonar pings. When independent echo traces
733 were seen in the same ping, prey was considered as schooling prey. Prey evasive
734 behaviour was identified from the closing speed between predator and prey, which will
735 vary in case of prey reaction, resulting in a change in the slope of the prey echo trace.



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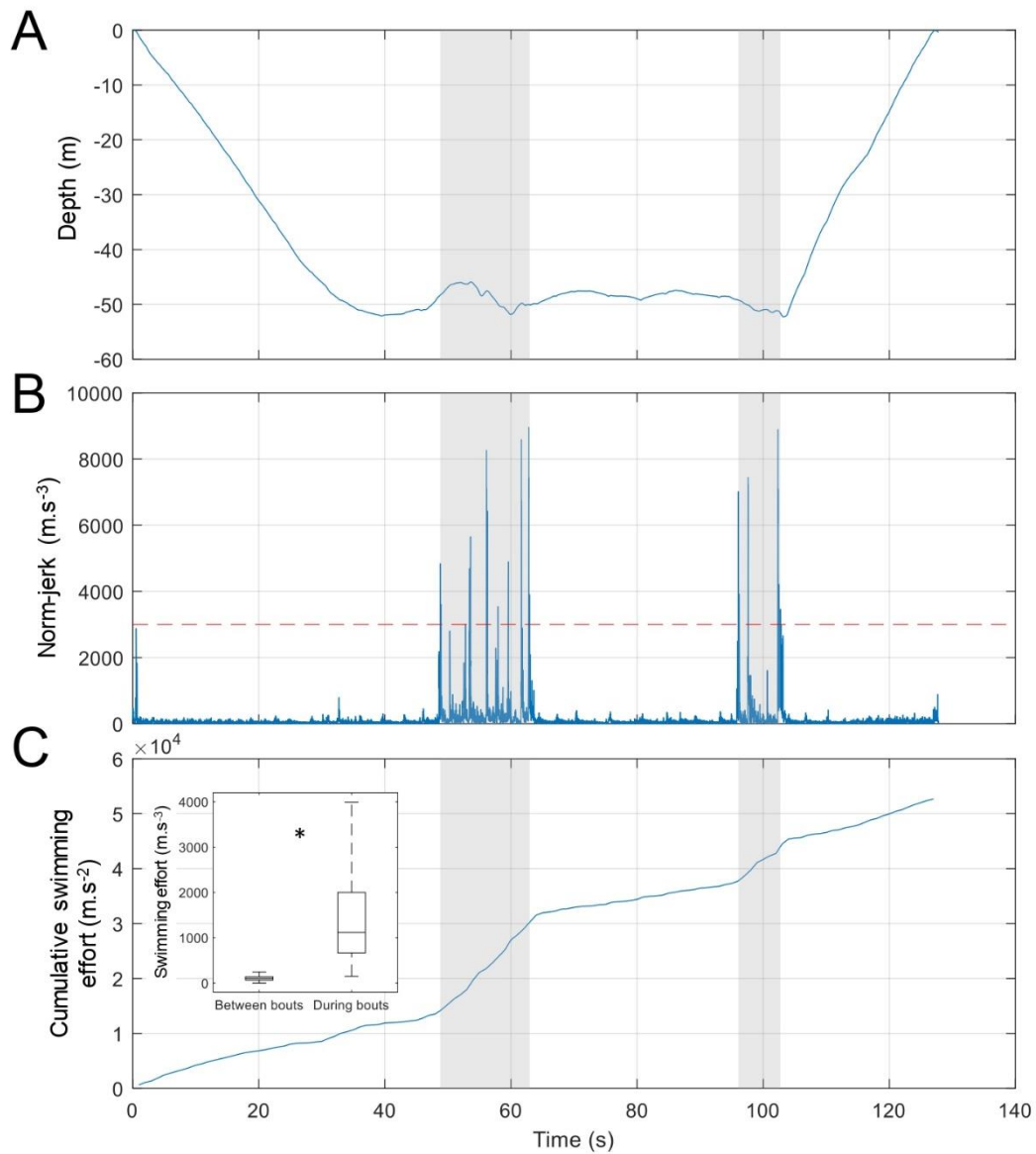
737 Figure 3: (A) Acoustic size and (B) echo intensity distributions of prey targeted by five
 738 female AFS equipped with sonar tags in January 2023 at Pointe Suzanne on Kerguelen
 739 Islands. Prey acoustic sizes were estimated on 419 single prey traces and on 199
 740 schooling prey traces from the -20 dB echo pulse width measured on the widest part

741 of the prey echo trace. Echo intensity was estimated on 467 single prey traces and 749
742 schooling prey traces and was defined as the maximum of the echo-to-noise ratio
743 measured on the prey trace.



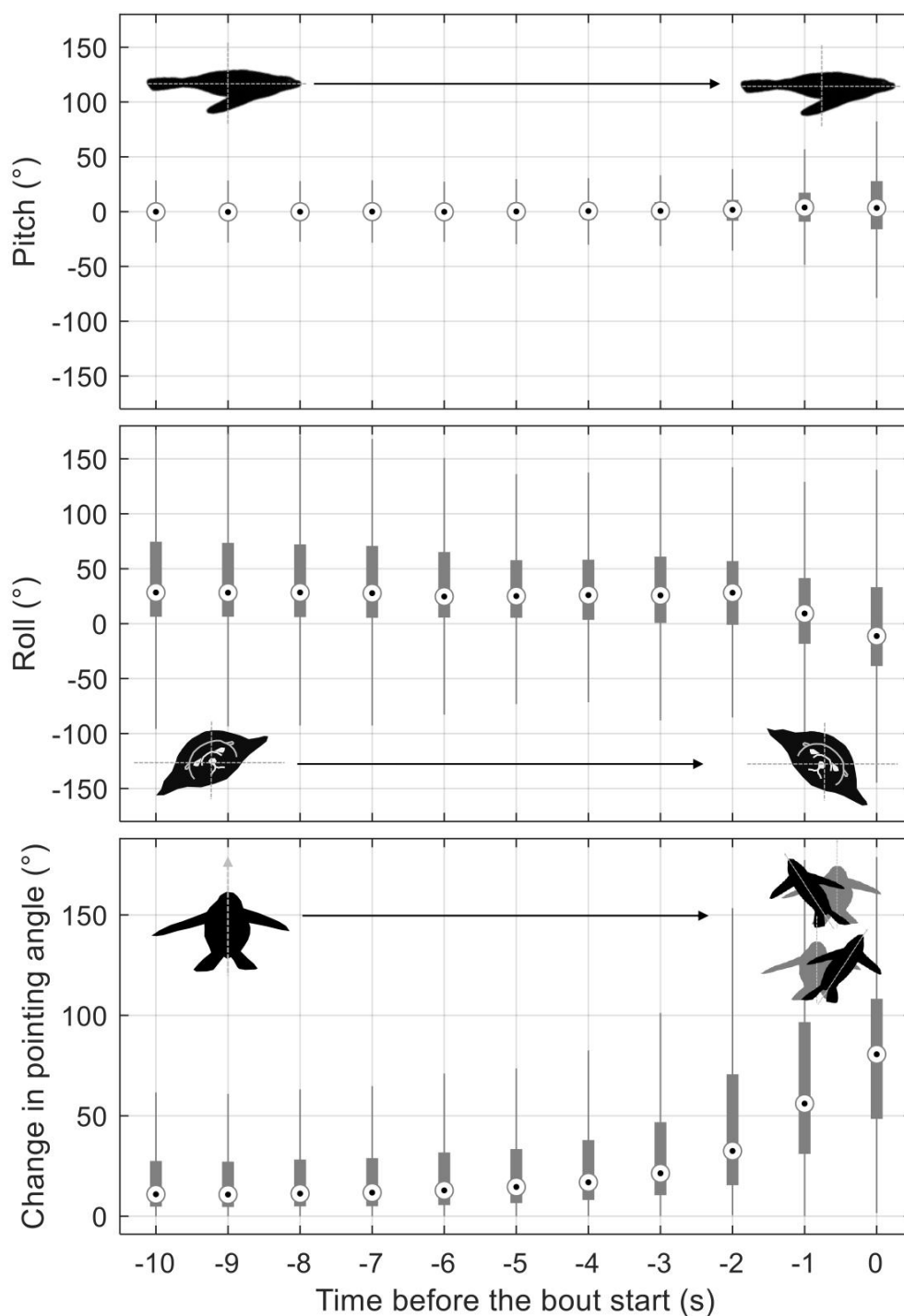
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745 Figure 4: Example of a dive of a female AFS equipped with a sonar tag in January
746 2023 at Pointe Suzanne on Kerguelen Island. (A) Depth profile recorded during a single
747 dive. (B) Norm of the differential of the tri-axial acceleration (norm-jerk) recorded during
748 the dive. Spikes higher than $3000 \text{ m}\cdot\text{s}^{-2}$ were classified as prey capture attempts.
749 Strikes occurring less than 15 s from the previous strike were grouped in the same
750 bout, indicated by the grey shaded region. (C) Cumulative swimming effort, i.e.
751 cumulative summed absolute values of the high-pass filtered surge and heave
752 accelerometer axes, used as a proxy of the swimming activity. The insert represents
753 the swimming effort per second between and during bouts. Asterisk indicates
754 significant difference in swimming effort between and during bouts (GLMM, $P < 0.001$).



755

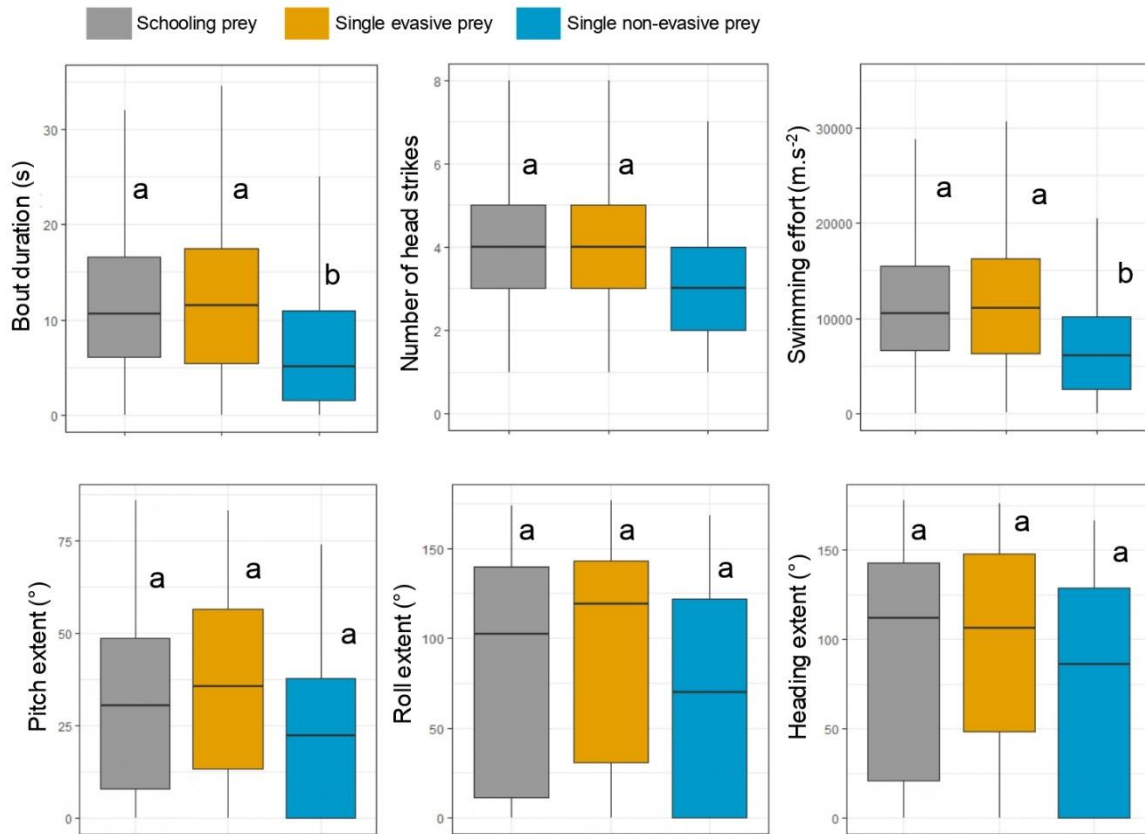
756 Figure 5: Posture of eight AFS equipped with sonar and sound tags in Kerguelen
 757 Islands in January 2023. Pitch and roll angles describe respectively the rotation around
 758 the left-right and longitudinal axes, while pointing angle reflects a change in direction
 759 of the longitudinal axis, likely associated with prey detection (Chevallay et al., 2023;
 760 Miller et al., 2004). Pointing angle was computed every second during the approach
 761 phase and we then computed the change in pointing angle relative to the previous
 762 second. They were computed on the static acceleration recorded by the tags during
 763 the approach phase, i.e. the 10 s preceding each bout (see Johnson and Tyack (2003)
 764 for details of the formulas).



765

766 Figure 6: Hunting behaviour of five female AFS equipped with sonar tags at Pointe
 767 Suzanne on Kerguelen Islands in January 2023. Behavioural metrics were derived
 768 from accelerometer and magnetometer data recorded during bouts and were
 769 compared between prey types encountered by AFS. Prey types, i.e. schooling prey (n
 770 = 746), single evasive prey (n = 239), and single non-evasive prey (n = 129) were

771 inferred visually from sonar data. Different superscript letters indicate significant
772 difference in behavioural parameters between prey types, i.e. schooling prey, single
773 evasive prey and single non-evasive prey (GLMM, $P < 0.05$).



774