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## Large sensory volumes enable Southern elephant seals to exploit sparse deep-sea prey

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## 3 **Main Manuscript for**

## 4 **Large sensory volumes enable Southern elephant seals to exploit** 5 **sparse deep-sea prey**

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23

### 24 **This PDF file includes:**

25 Main Text

26 Figures 1 to 3

27

28 **Abstract**

29 The ability of echolocating toothed whales to detect and classify prey at long ranges enables  
30 efficient searching and stalking of sparse prey in time-limited dives. However, non-echolocating  
31 deep-diving seals such as elephant seals appear to have much less sensory advantage over their  
32 prey. Both elephant seals and their prey rely on visual and hydrodynamic cues that may be  
33 detectable only at short ranges in the deep ocean, leading us to hypothesize that elephant seals  
34 must adopt a less efficient reactive mode of hunting that requires high prey densities. To test that  
35 hypothesis, we deployed high-resolution sonar and movement tags on 25 females to record  
36 simultaneous predator and prey behavior during foraging interactions. We demonstrate that  
37 elephant seals have a sensory advantage over their prey that allows them to potentially detect prey  
38 5-10 seconds before striking. The corresponding prey detection ranges of 7-17 m enable stealthy  
39 approaches and prey-specific capture tactics. In comparison, prey react at a median range of 0.7  
40 m, close to the neck extension range of striking elephant seals. Estimated search swathes of 150  
41 to 900 m<sup>2</sup> explain how elephant seals can locate up to 2000 prey while swimming more than 100  
42 km per day. This efficient search capability allows elephant seals to subsist on prey densities that  
43 are consonant with the deep scattering layer resources estimated by hydro-acoustic surveys but  
44 which are two orders of magnitude lower than the prey densities needed by a reactive hunter.

45 **Significance Statement**

46 The range at which predators detect prey strongly influences prey encounter rate and therefore the  
47 energy gained from foraging: predators with small sensory volumes require denser prey to meet  
48 their energy needs. If prey densities drop, predators rely increasingly on chance encounters with  
49 ephemeral prey aggregations making them vulnerable to changing prey distributions. Prey  
50 detection range of most marine predators, and the minimum prey density they can tolerate, are  
51 unknown. We show that Southern elephant seals can detect and classify prey at 10 m distance  
52 enabling efficient search, selection, and capture of small, sparse mesopelagic prey. This capability  
53 is critical for seals to maintain consistent high prey encounter rates as they roam over thousands  
54 of kilometers in the Southern Ocean.

55  
56 **Main Text**

57  
58 **Introduction**

59  
60 For active predators, sensory capabilities to detect, select and subdue prey are critical for efficient  
61 foraging (1). The ability to detect prey at longer ranges enables survival on sparse or diverse prey,  
62 expanding functional habitats and increasing resilience to disturbance. The relative sensory  
63 capabilities of predators and their prey also shape foraging interactions. If prey and predators detect  
64 each other at similar distances, predators must often hunt reactively (i.e. responding to the escape  
65 movement of the prey) and thus expend energy in chasing ever-alert prey (1, 2). Conversely, if  
66 predators have the sensory upper-hand, they can adopt a more efficient deliberative foraging mode,  
67 making stealthy approaches to unaware prey and adapting their attack tactics to each prey type to  
68 maximize capture success.

69 As endothermic, active predators, marine mammals have high metabolic requirements restricting  
70 the range of prey densities on which they can subsist. To meet these energy needs, more than 20  
71 species of large toothed whales target the largest ecosystem on the planet: the 4-10 gigatons of  
72 mesopelagic fish and squid that form the deep scattering layer (DSL hereafter) (3, 4). For these  
73 mega-predators, ultrasonic echolocation provides a private sensory channel allowing covert  
74 detection and classification of prey at long-ranges increasing the foraging efficiency of time-limited  
75 breath-hold dives (5, 6). In contrast, very few species of pinnipeds consistently rely on DSL food  
76 resources: likely only the hooded seal (*Cystophora cristata*) and the Northern and Southern  
77 elephant seals (*Mirounga angustirostris* and *M. leonina*) (7–9). These seals use passive visual and  
78 fluid disturbance stimuli to guide their hunting, the same sensory channels used by their prey to

79 detect predators. The massive size of elephant seals compared to their prey enables them to  
80 support the metabolic expense of large sensitive eyes (10), wide facial vibrissae that can pick-up  
81 the hydrodynamic trails of moving prey (11–13), and the cognitive faculties of a large warm brain  
82 to process the resulting sensory data flow. However, their size is also a disadvantage when  
83 approaching prey: they present a large visual stimulus and their forward motion creates a bow wave  
84 that can be detected at a distance by fish and squid (14–17). In comparison, their small nekton prey  
85 can go cryptic by simply staying motionless in the dark. This leads us to hypothesize that elephant  
86 seals and their prey detect each other at broadly similar short distances restricting the seals to a  
87 largely reactive (1) hunting style in stark contrast to echolocating whales. If so, the resulting small  
88 search swathe means that elephant seals must rely on high densities of prey, which they exploit  
89 relatively indiscriminately, raising the conundrum of how these large predators manage to  
90 consistently capture some 2000 small prey per day to meet their energy needs (18). Moreover,  
91 such strict reliance on dense prey would make the largest seal species highly vulnerable to  
92 changing prey distributions due to climate change and deep-sea fishing.

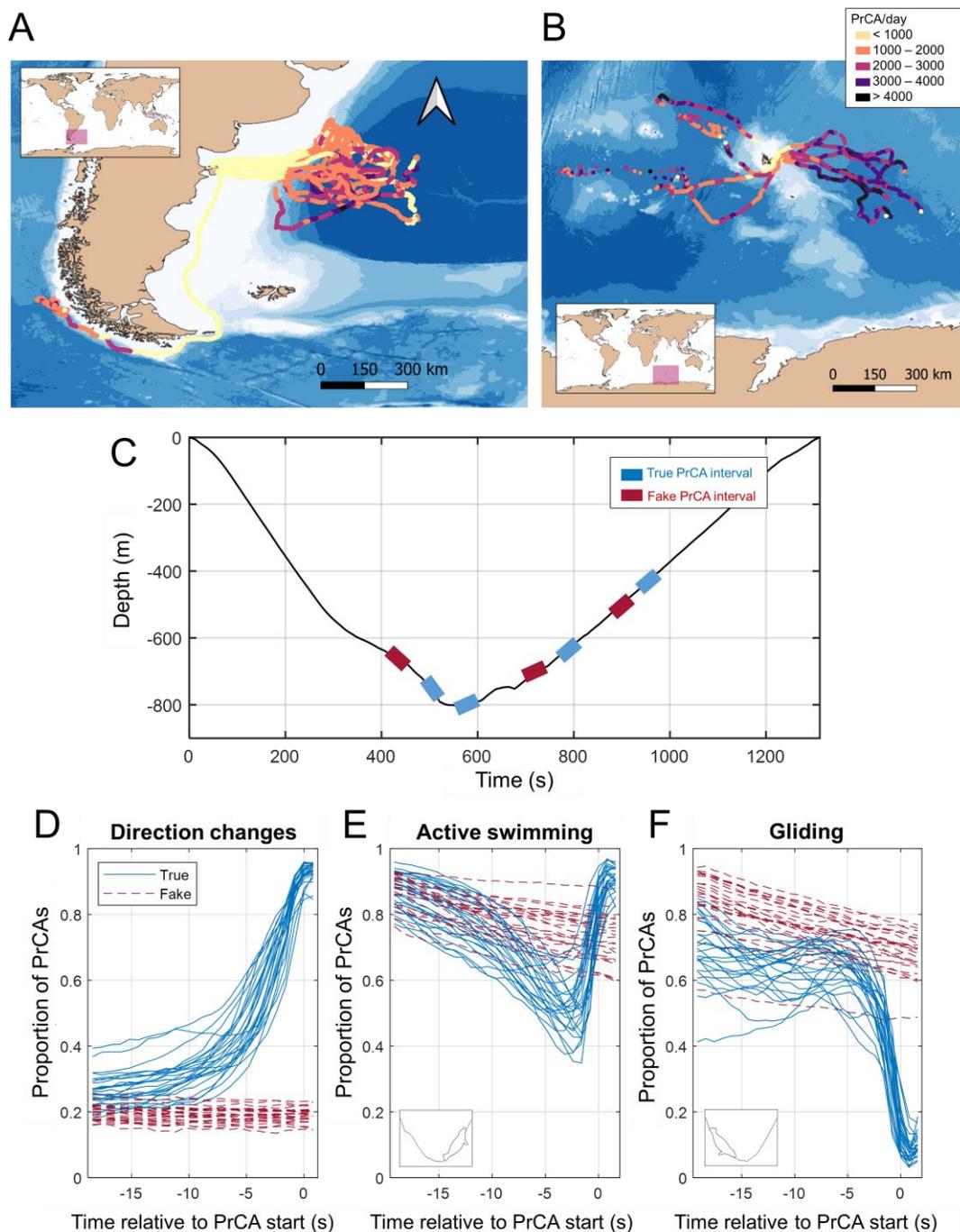
93 Studying the sensory volumes of predators and prey under ecologically relevant conditions has  
94 been a long-standing technical challenge but new biologging devices equipped with cameras or  
95 sonars now enable simultaneous sampling of hunting behavior and prey reactions for some wild  
96 marine predators (18–20). Here we use over 500 days of data from high-resolution sonar and  
97 movement tags to test the hypothesis that limited sensory capabilities oblige Southern elephant  
98 seals to hunt reactively.

99

## 100 **Results**

101

102 Female Southern elephant seals (SES hereafter) were tagged prior to their post-breeding foraging  
103 trip in two far-separated populations: Península Valdés, Argentina (PV hereafter, n=12) and  
104 Kerguelen Islands (KER hereafter, n=13) (Table S1). Differing oceanographic conditions mean that  
105 SES from these locations likely encounter different prey types and densities (21). Tags on all 25  
106 SES recorded triaxial accelerometry (200 Hz sampling) and magnetometry (50 Hz) continuously,  
107 while tags on 13 individuals additionally recorded echoes from high-frequency (1.5 MHz) sonar  
108 pings with 6 m range, up to 25 times per second (20). This unique combination of sensors samples  
109 simultaneously the fine-scale movements of both predator and prey during deep-sea hunting  
110 interactions allowing us to infer detection ranges for these large predators in the deep sea (Fig. 1).



111

112 **Figure 1. Prey detection by Southern elephant seals.** (A-B) Tracks of seals tagged with high-  
 113 resolution sonar and movement tags in (A) Peninsula Valdes, Argentina, and (B) Kerguelen Islands.  
 114 Tracks are colored by daily counts of prey capture attempts inferred from distinctive acceleration  
 115 transients. (C) Example of a dive profile with true PrCA and fake PrCA intervals. (D-F) Prey  
 116 detection behavior during the 20 seconds preceding each prey capture attempt. Each line  
 117 summarizes between 3093 and 20146 PrCAs for an individual seal ( $n = 25$ ). (D) Proportion of  
 118 PrCAs for each seal with above-threshold pointing angle changes in 1.6 s bins synchronized to the  
 119 prey strike. Pointing angle changes comprise changes in heading and/or pitch and the 1.6 s interval

120 is approximately the duration of one swimming stroke. The threshold was chosen from a  
121 comparable number of randomly-selected fake PrCAs for each seal (dashed red lines). A high  
122 proportion of pointing angle changes 5-8 s before the strike indicate the likely detection distance.  
123 This is supported by the swimming behavior prior to the strike (E-F). Being denser than seawater,  
124 tagged seals glide on descents and stroke on ascents. When seals are ascending 20 s before a  
125 PrCA (E), swimming activity, parameterized by the root-mean-square of the lateral acceleration  
126 averaged over 1.6 s bins, is initially high but seals often switch to gliding 4-8 s before the strike.  
127 Conversely, if seals are initially descending (F), they begin stroking just before the strike. In both  
128 cases, gliding prior to the strike increases stealth. See ESM for individual animal data.

#### 129 *Prey detection*

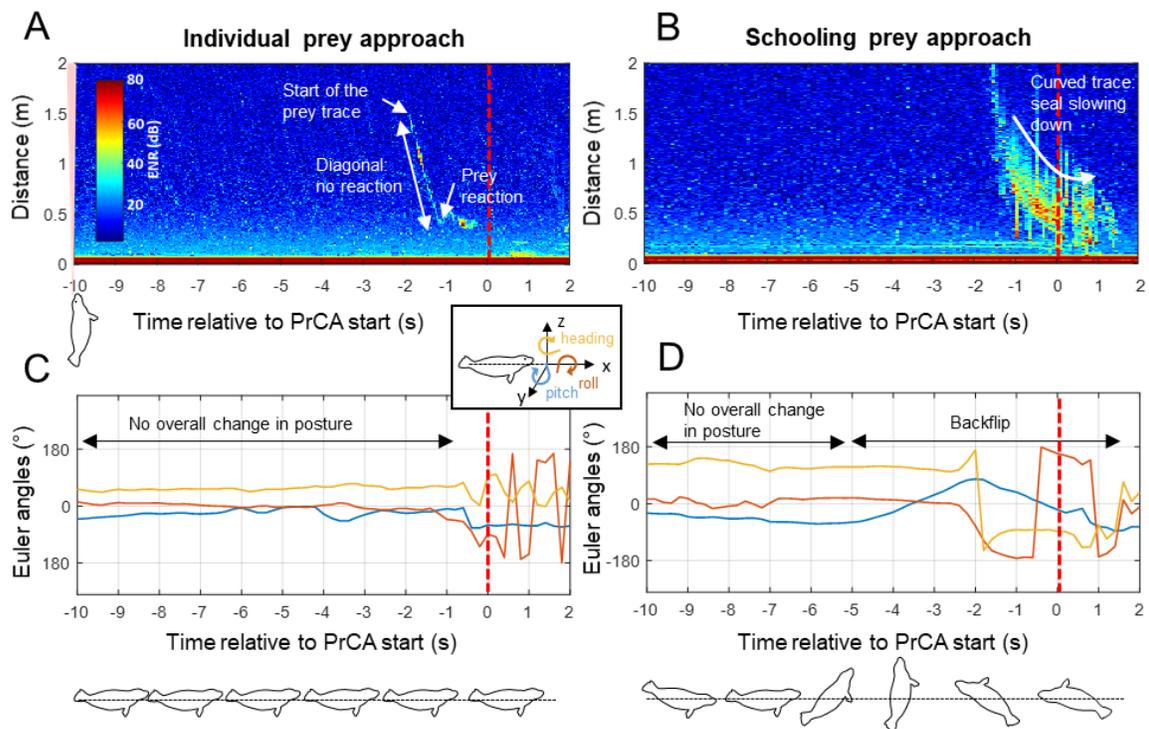
130 SES have extendable necks, which they use to accelerate the head forward when striking at prey.  
131 The head-mounted tags recorded distinctive strong transient acceleration signals during foraging  
132 dives consistent with these prey strikes (Fig. S1). We hypothesized that seals would change their  
133 direction of movement and/or their swimming activity preceding a strike when they detect prey (22).  
134 We accordingly looked for changes in pointing angle (i.e., the direction of the animal's longitudinal  
135 axis) and sway acceleration standard deviation (a proxy for swimming activity) in the seconds prior  
136 to strikes. We compared this against randomly-selected control intervals when SES were actively  
137 searching for, but not capturing, prey. Prey strikes often occur in bouts suggesting encounters with  
138 loose aggregations of prey. To ensure that seal movements prior to a strike were not influenced by  
139 a close preceding capture attempt, we only analyzed strikes that were at least 25 s apart. This  
140 resulted in a sample size of 230850 strikes, with between 3093 and 20146 strikes per individual.  
141 All tagged SES showed clear changes in movement direction and swimming activity about 5-10 s  
142 before strikes that were absent in control intervals (Fig. 1), indicating when prey were detected.  
143 Because seals are negatively buoyant in the first weeks of a foraging trip (23), the change in  
144 swimming activity related to prey detection depended on the vertical direction of travel: seals that  
145 were initially swimming actively to ascend tended to stop stroking prior to strikes. Conversely,  
146 descending seals tended to switch from gliding to powered swimming just before strikes in order to  
147 correct their course (Fig 1, Fig. S2).

148 Using the relationship between vertical speed and body pitch angle, we calculated an average  
149 swimming speed of 1.3 to 1.7 m/s for each individual. Applying these speeds to the approximate  
150 detection time prior to strikes gives prey detection distances,  $d$ , between 7 and 17 m. SES are  
151 expected to perform shallower foraging dives at night as they track the daily vertical migration of  
152 DSL fauna (24), and the visual and mechanical sensory cues from prey may vary accordingly. The  
153 13 PV animals followed the expected diel cycle in dive depth but showed no consistent change in  
154 detection distance between day and night nor with depth (Fig. S3). In contrast, the 12 seals tagged  
155 in Kerguelen often performed dives with similar depth during day and night, presumably reflecting  
156 attendance at gyres and fronts where vertical prey migration may be weak. These seals swam  
157 more and glided less during daytime prey approaches, but again day and night prey detection  
158 distances were comparable (Fig. S3).

#### 159 *Prey-dependent approach tactics*

160 Sonar data were examined in a subset of 57581 strikes (2158 to 8713 per individual) for the 13  
161 seals (6 KER and 7 PV) equipped with sonar tags, again selecting strikes that were at least 25 s  
162 apart. The sonar resolution (4 mm) is sufficient to distinguish isolated single prey versus preys  
163 aggregated in tight schools (20), providing the opportunity to test if seals approach shoals of prey  
164 differently. Although the 6 KER seals approached almost exclusively single prey, the 7 PV animals  
165 found more varied prey aggregations. Two PV seals in particular (m118\_295a and m119\_294b)  
166 targeted a high proportion of schooling prey (42.3% and 20.8% of analyzed strikes, respectively,  
167 with approximate school sonar cross-section of  $\sim 1$  m). These two seals performed a dramatically  
168 different movement pattern when approaching schooling versus single prey (Fig. 2): for single prey,  
169 the seals typically maintained a fixed horizontal posture, implying a direct approach style. In

170 contrast, when approaching schooling prey, both seals performed an upward backflip in which they  
 171 rotated through about 360° around their transverse axis, encircling the school. Backflips were  
 172 initiated some 5 seconds before the strike, indicating that the seals were able to both detect and  
 173 classify the prey as a group or singleton at a distance of about 7 m (25). Applying an automatic  
 174 pattern detector to the sonar and accelerometer data, we found that 95-99% of strikes targeting  
 175 schooling prey were associated with a backflip, compared to 26-30% of strikes on single prey. Data  
 176 from the other 7 sonar-equipped PV seals indicated less frequent capture attempts on schooling  
 177 prey (1-4% of strikes), however, the same distinctive backflip maneuver was performed by 5 of  
 178 these animals. For these seals, backflips were associated with 86-96% of strikes targeting  
 179 schooling prey and 11-17% of strikes on single prey.



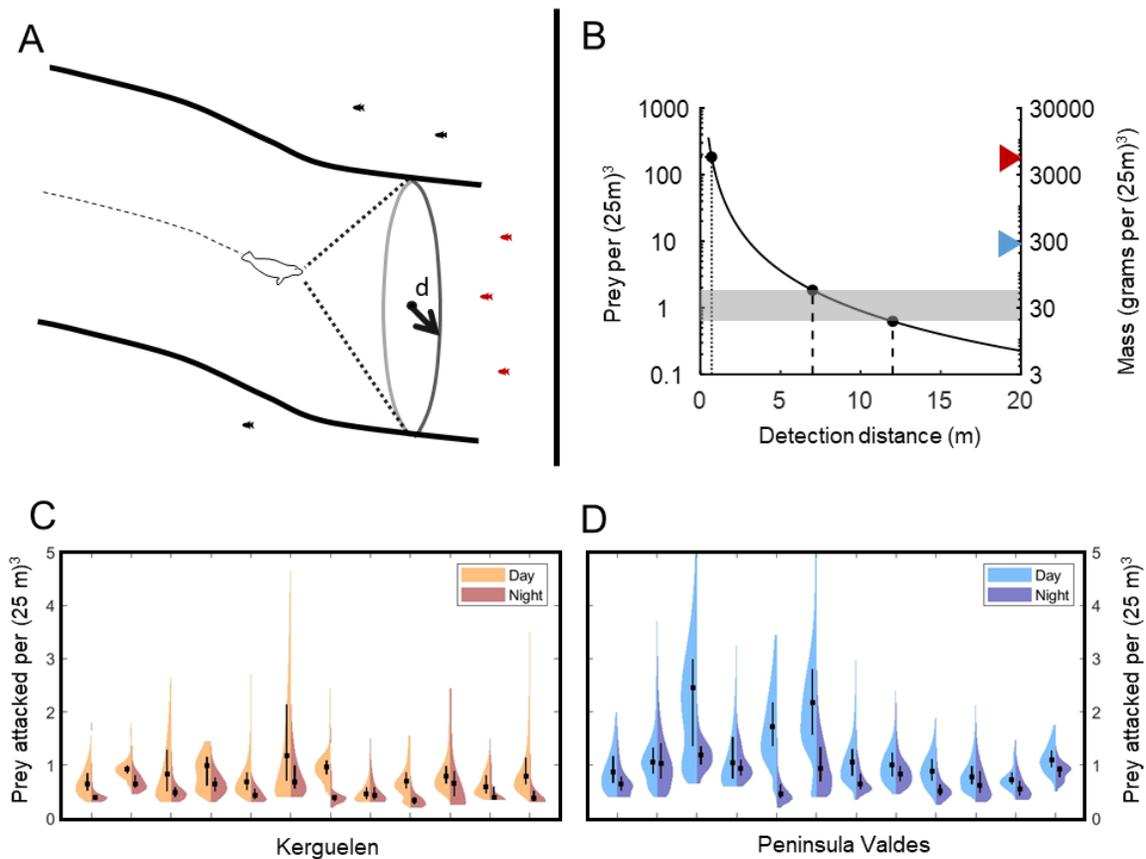
180

181 **Figure 2. Female elephant seals employ different capture tactics for individual and**  
 182 **schooling prey.** (A) Echogram displaying individual (left panel) or schooling prey (right panel)  
 183 insonified over successive sonar pings. The horizontal axis shows the time relative to PrCA start in  
 184 seconds, and the vertical axis shows the distance from the sonar tag in meters. The color scale  
 185 indicates echo-to-noise ratio (ENR) on a dB scale. (B) Pitch (rotation around the left-right axis), roll  
 186 (rotation around the longitudinal axis) and heading (rotation around the dorso-ventral axis) angles  
 187 showing prey-dependent approach tactics, illustrated by a schematic representation of SES  
 188 orientation. When approaching individual prey, SES generally maintained a fixed horizontal  
 189 posture, while when approaching schooling prey, some SES consistently made an upward backflip  
 190 maneuver.

191 *Prey escape behavior*

192 Prey escape behavior was assessed from sonar data by two expert assessors for a randomly-  
 193 selected subset of strikes for each seal equipped with sonar tags in 2018 (n = 5855 strikes, approx.  
 194 10% of eligible strikes per seal). Inter-rater agreement was high and 85% of individual prey were  
 195 judged to be reactive. Prey flight initiation distance, measured from echograms (Fig. 2), was a  
 196 median of 0.7 m (IQR: 0.5-1.0 m), and prey reactions occurred a median of 1.7 s (IQR: 0.5-3.6 s)  
 197 before the strike indicating a brief chase.

198 *Search volume*  
 199 Tagged SES travelled an average three-dimensional distance of 115 km/day (range 99-136  
 200 km/day) during foraging dives in which they attempted to capture some 2300 prey (range 1100-  
 201 3710 prey/day) or about one prey per 55 m of travel. The higher PrCA rate here compared to  
 202 previous reports from KER seals (7) is likely a result of wider accelerometer bandwidth which  
 203 enables clearer discrimination of strikes at prey versus swimming. The 7-17 m prey detection  
 204 distance suggests a search swathe, i.e., the area perpendicular to the trackline in which the seal  
 205 can presumably detect prey, of 150-900 m<sup>2</sup> (i.e.,  $\pi \cdot d^2$ ). Taking 10 m as a representative detection  
 206 distance and multiplying the corresponding swathe by the travel distance between prey gives an  
 207 apparent average prey density of one prey per 16500 m<sup>3</sup> within the foraging depth range of SES,  
 208 i.e., approximately one prey per 25 m cube of water (Fig. 3).



209

210 **Figure 3. Ecological significance of early prey detection.** (A) Schematic representation of a  
 211 female Southern elephant seal with estimated prey detection range, scaled with the seal body size.  
 212 (B) Required prey density to achieve the same prey encounter rate with varying detection distance.  
 213 The dotted and dashed lines show the estimated detection distances for a reactive forager and for  
 214 a SES, respectively. The grey shaded region represents the apparent prey density of SES based on  
 215 observed attack rates and travel distance, details of the calculation are given in the Methods  
 216 section "Search volumes". The blue arrow shows the estimated mesopelagic biomass obtained by  
 217 dividing the total predicted biomass (4) by the approximate volume of the mesopelagic. Only a  
 218 portion of this biomass is suitable SES prey. The red arrow shows the minimum biomass density  
 219 needed if SES had a prey detection range of 0.7 m. While SES attack rates are consistent with the  
 220 predicted mesopelagic resources, a reactive forager would require two orders of magnitude higher  
 221 prey density to achieve a similar rate. (C) and (D) Daily averaged apparent prey densities for each

222 seal, i.e. attack rate per (25 m)<sup>3</sup> searched, are relatively constant along their far-ranging foraging  
223 tracks, indicating a stable widely-distributed food resource.

224

## 225 **Discussion**

226

227 The range at which predators can detect prey is a key determinant of their foraging efficiency and  
228 therefore the minimum prey density they require to maintain fitness. Here we use a novel  
229 combination of two on-animal sensors to measure the detection capabilities of predators and prey  
230 in the wild. We use ultra-high-resolution accelerometry to determine the precise timing of prey  
231 strikes and then work backwards to find when the predator adjusts its course to intercept the prey.  
232 We combine this with a synchronously-sampled high-ping-rate active sonar to determine the  
233 distance to prey, their reactions, and whether prey are single or grouped. Our results show that  
234 SES have a strong sensory advantage over mesopelagic fish and squid, despite employing the  
235 same sensory modalities of vision and hydrodynamic wake detection. We show that SES can detect  
236 prey at ranges of about 10 m, an order of magnitude greater than the measured flight initiation  
237 distance of their prey, leading us to reject the hypothesis that SES are reactive hunters. The 5-10  
238 seconds between detection and strike provide SES with the possibility of deliberative sensorimotor  
239 operation during hunting thereby enabling efficient prey selection, tactical approaches, and precise  
240 strike timing. Conversely, prey flight initiation distances of around 0.7 m are close to the neck  
241 extension distance of SES. Thus, SES are often able to stalk prey until within striking distance,  
242 greatly reducing the possibilities of prey escape. For such large predators to capture some 2000  
243 individual small prey per day, energetically expensive fast maneuvers must be avoided. The ability  
244 to detect and classify prey at 2-3 predator body-lengths ahead of them enables movement planning  
245 and energy-saving slow motions, e.g., gliding approaches, which also minimize the hydro-dynamic  
246 signals available to prey. Thus, despite sharing the same sensory modalities, SES have information  
247 dominance over their prey, made possible by their vastly greater size, access to body oxygen stores  
248 and much superior cognitive capabilities of a large warm brain. This advantage may be key to  
249 understanding how these predators can make a living travelling thousands of kilometers in a  
250 feeding trip to find prey that are just 0.01% of their own mass (i.e. 10 g prey (ref) vs. 500 kg female  
251 SES, (26)).

### 252 *Sensory cues*

253 Tagged seals foraged at a wide range of depths enabling us to test how detection range varies with  
254 environmental conditions. The absence of a clear relationship between detection range and either  
255 depth or light (Fig. S3) suggests that SES use both vision and tactile sensing of wakes left by  
256 actively-swimming prey (11) to detect their vertically-migrating prey. Migrating mesopelagic  
257 organisms are expected to adopt a daytime depth that is a trade-off between predation risk from  
258 visual predators (primarily piscivorous fish), and access to their own prey which become scarcer  
259 with depth (27). Elephant seals have the most light-sensitive eyes of any mammal (10) and can  
260 likely still see prey at depths at which other visual predators cannot operate. Nonetheless, in both  
261 regions, seals detected prey at ranges of 5-10 m even in dives to 800 m where passive light cues  
262 (i.e visual cues that are dependent on downwelling light) are extremely attenuated (Fig. S2). At  
263 these depths, SES may pick up bioluminescent flashes from prey (28) or rely fully on tactile sensing.  
264 Passive detection of acoustic signals produced by prey such as the choruses of myctophids may  
265 also help SES to locate areas of high prey densities (29). However, tactile and acoustic cues may  
266 be difficult to detect in shallow dives amidst the turbulence and wave noise in the often-stormy  
267 Southern Ocean. Thus, the availability of multiple acute sensory systems likely increases foraging  
268 flexibility enabling SES to exploit prey throughout the water column, day and night (18).

269 Although detection ranges remained the same, SES from Kerguelen changed their approach tactics  
270 between day and night when hunting at the same shallow depths. Increased active swimming  
271 preceding daytime capture attempts suggests an effort to forestall prey reactions when these large  
272 predators are more visible to vigilant prey.

273 *Prey-dependent capture tactics*

274 SES not only detect prey well before intercepting them but can also classify prey and adopt prey-  
275 dependent capture tactics, further improving foraging efficiency. This was demonstrated in our data  
276 by Península Valdés seals that perform a backflip when they encounter small but dense shoals of  
277 prey. This maneuver is readily distinguished from the typically direct approach to single prey and  
278 may serve to aggregate prey into a tight ball enabling seals to engulf multiple prey at once with  
279 their wide gape akin to the prey aggregation behaviors of humpback whales and bottlenose  
280 dolphins (30, 31). Its apparent exclusive use by PV seals may indicate a prey type that is only  
281 available in this region. However, the stereotypicity of the backflip maneuver amongst PV seals is  
282 remarkable given that the solitary foraging trips and land-based breeding cycle of SES leave little  
283 apparent room for social learning of hunting styles.

284 *Ecological implications*

285 Ship-based hydroacoustic surveys of the DSL suggest a global mesopelagic biomass of around 5  
286 gigatons (4) albeit with a wide margin of error due to poorly-known and regionally-varying  
287 relationships between acoustic backscatter and biomass (4, 32). Nonetheless, the unquestioned  
288 vastness of the mesopelagic biomass and its global distribution as captured in biogeographic maps  
289 of the DSL (33) give the impression of a near-continuous layer of organisms that represent a  
290 treasure trove for any predator capable of diving deep enough. But taking the mesopelagic as  
291 occupying 20% of the world's oceans (i.e., a volume of  $2.6 \times 10^8 \text{ km}^3$ ), 5 GT of biomass translates  
292 into just  $0.017 \text{ g/m}^3$  or 270 g per 25 m cube of water (a volume of  $15625 \text{ m}^3$ ). Hydroacoustic surveys  
293 integrate acoustic backscatter from a wide size-range of organisms and assuming the usual log-  
294 normal distribution of organism sizes (32), this 270 g is composed of thousands of micro-nekton  
295 but only a few of the  $>10 \text{ g}$  organisms that are presumed to comprise the diet of elephant seals  
296 (18). Moreover, a portion of these larger organisms are low-nutrient cnidarians such as  
297 siphonophores which are unlikely to be eaten by elephant seals. Some regions of the Southern  
298 Ocean are predicted to have denser resources than the global average (34), potentially inflating  
299 these figures, but whatever the precise density, this analysis highlights that prey large enough to  
300 be worth hunting by air-breathing predators are sparse, notwithstanding the overall vastness of the  
301 mesopelagic biomass (Fig. 3).

302 The prey detection distances inferred here suggest that SES have an effective search swathe of  
303 some  $300 \text{ m}^2$  perpendicular to their direction of travel providing the search efficiency needed to  
304 target such dispersed mesopelagic resources. Judging from the rate at which seals attack prey,  
305 the average prey density, as perceived by seals, is low at around 1 per  $25 \text{ m}^3$  of water but is broadly  
306 consistent with the predicted density of mesopelagic resources (35). In contrast, a reactive forager  
307 with a prey detection distance of 0.7 m, i.e., the same distance at which prey can detect the  
308 predator, would require two orders of magnitude higher prey density to achieve a similar rate of  
309 prey capture attempts as the tagged seals (Fig. 3). Conversely, echolocating toothed whales can  
310 detect prey some 3-10 times further than SES (6) enabling efficient exploitation of even sparser  
311 food resources. This capability likely facilitated the radiation of toothed whales into warmer,  
312 oligotrophic waters where DSL biomass density is typically predicted to be low (33). It may have  
313 also enabled more selective diets thereby fostering niche segregation and, ultimately, speciation in  
314 a vast open environment without obvious barriers (36).

315 Southern elephant seals famously perform long meandering foraging trips that can span entire  
316 ocean basins and it has been posited that these may be guided by oceanographic phenomena  
317 such as fronts, gyres and eddies that tend to aggregate mesopelagic organisms (37). However,  
318 these aggregations are ephemeral and distributed throughout a vast water mass. Reliance on  
319 consistently finding such rich foraging areas would be a vulnerable strategy especially as changing  
320 ocean temperatures will inevitably impact the incidence and intensity of these oceanographic  
321 events. Moreover, reliance on dense food patches would drastically lower the absolute carrying  
322 capacity of the Southern Ocean for SES. In contrast, the high search efficiency of SES compared

323 to a reactive forager allows them to distribute their foraging, taking advantage of chance  
324 aggregations but subsisting on sparser prey in-between. Given a 10 m prey detection distance  
325 each SES samples, and potentially removes prey from, a water volume of about 3 km<sup>3</sup> in a typical  
326 three-month foraging trip. Thus, acute sensory capabilities lead SES to have a much larger  
327 ecological footprint and therefore exercise far greater top-down control over Southern Ocean food  
328 webs than they would as reactive predators. But even this robust foraging strategy is susceptible  
329 to large-scale changes in prey abundance and community structure due to industrial mesopelagic  
330 trawling and climate change (38).

331

## 332 **Materials and Methods**

333

### 334 *Fieldwork*

335 Data were collected in October 2017, October 2018 and October 2019 from 25 free-ranging post-  
336 breeding female Southern elephant seals (*Mirounga leonina*, SES hereafter) at Pointe du Morne,  
337 Kerguelen Island (KER hereafter, 49°20'S – 70°26'E, n = 3 in 2017, n = 4 in 2018 and n = 6 in  
338 2019) and at Peninsula Valdez, Argentina (PV hereafter, 42°57'S – 63°59'W, n = 5 in 2018 and n  
339 = 7 in 2019), Table S1. All experiments were conducted under the ethical regulation approval of  
340 the French Ethical Committee for Animal Experimentations and the Committee for Polar  
341 Environment.

342 SES were equipped with a neck-mounted Argos tag (SPOT-293 Wildlife Computers, 72x54x24  
343 mm, 119 g in air), a back-mounted CTD tag (SMRU-SRDL, 115x100x40 mm, 680 g in air) and a  
344 head-mounted DTAG-4 tag (configured as either a sound and movement tag, 97x55x33 mm, 200  
345 g in air, n = 10, or a sonar and movement tag, 95x55x37 mm, 200 g in air, n = 15, see (20) for  
346 further details on the devices). Equipment, animal treatment and retrieval procedures are detailed  
347 in (28). The DTAG-4 tags were programmed to sample GPS position (every minute when in air),  
348 tri-axial acceleration (200 Hz sampling rate), tri-axial magnetometer (50 Hz), and pressure (50 Hz).  
349 In addition, the sound tags recorded underwater sound (sampled at 48 kHz) and light (50 Hz) while  
350 the sonar tags recorded acoustic backscatter from 10  $\mu$ s pings with a center frequency of 1.5 MHz,  
351 a 3-4° half-power beamwidth and a 6 m range (20). The sonar ping rate was set to 12.5 Hz for PV  
352 seals in 2018 and 25 Hz for all other seals. To maximize coverage of the foraging trips, the sonar  
353 was turned off when near the surface and operated with a duty-cycle (6h on/off for KER, 24h on/off  
354 for PV) while all other sensors were recorded continuously. The tags start when the seal leaves the  
355 haul-out but end, due to low battery, in most cases before the seal returns to shore. Analyses of  
356 sonar and movement data were performed using custom-written codes and functions from  
357 www.animaltags.org in MATLAB version 2020b (The MathWorks, Natick, MA, USA).

### 358 *Prey capture attempt detection*

359 To detect prey capture attempts (PrCAs) we first computed the norm (i.e., vector magnitude) of the  
360 differential of the tri-axial acceleration (norm-jerk hereafter) using data at the full 200 Hz sampling-  
361 rate (39). The maximum of this norm-jerk signal over consecutive 10 s intervals was computed for  
362 each deployment, and plotted logarithmically in a histogram. These histograms were multi-modal  
363 for all animals with a clear high-jerk mode generated by brief strong jerk signals during foraging  
364 dives (Fig. S1). SES strike at prey by extending their necks leading us to interpret these high jerk  
365 transients as prey strikes. The high-jerk mode separated from lower modes in the histograms at a  
366 jerk of around 400 m/s<sup>3</sup> for all animals and this value was therefore used to detect PrCAs. A 25 s  
367 blanking time (i.e., the time which must elapse with the jerk below threshold before another PrCA  
368 can be detected) was used in the detector to identify well-separated bouts of foraging. The start  
369 time of each PrCA was taken as the time of the first threshold crossing. As the movements prior to  
370 the first PrCA of each dive may be a combination of transport and foraging, these initial PrCAs were  
371 removed from the analysis. Analysis intervals were defined as the 20 s preceding each remaining  
372 PrCA allowing a minimum 5 s gap from preceding PrCAs.

373 *Control intervals*

374 Fake PrCAs, used as controls, were selected from periods within foraging dives without PrCAs and  
375 falling between the first and last PrCA of a dive. We interpret these periods as comprising  
376 unsuccessful searching behavior. Dives with one or no PrCAs were excluded as they may be  
377 resting dives, short dives or with transitional behaviors. Long periods without PrCAs within dives  
378 were broken into a maximum of 5 control periods of length at least 37.5 s each (i.e. 1.5 times the  
379 blanking time). Periods without PrCAs lasting more than 10 min were excluded because they might  
380 comprise transport between different depth layers. A fake PrCA was selected from each of the  
381 resulting periods using uniformly-distributed random offset times, applying the same spacing rules  
382 as for true PrCAs, i.e., that each PrCA is separated by at least 25 s from any other fake or true  
383 PrCA.

384 *Prey approach movements*

385 Swimming activity: Phocid swimming involves sideways body undulations propelled from rear  
386 flippers which can be detected as oscillations in the y-axis (i.e. lateral) acceleration ( $A_y$  hereafter).  
387 To separate these from slower postural changes, the y-axis acceleration, decimated to 5 Hz, was  
388 high-pass filtered with a delay-free symmetric FIR filter with a cut-off frequency of 0.4 Hz (i.e. 70%  
389 of the typical stroking rate of female SES). Sections of the high-pass filtered  $A_y$  were extracted  
390 corresponding to each true and fake PrCA starting 20 s prior to the start time and ending 2.4 s after  
391 the start time. This 22.4 s interval was further divided into blocks of 1.6 s duration (i.e. 8 samples  
392 at 5 Hz) with 0.8 s overlap. This block length was chosen to be approximately equal to the duration  
393 of a swimming stroke allowing averaging over a full stroke. For each block, the root-mean squared  
394 (RMS) of the filtered  $A_y$  was computed as a proxy for swimming activity.

395 Change in movement direction: Animals hunting in a 3-dimensional environment can adjust their  
396 direction of travel by changing their yaw (i.e., azimuthal) angle and/or their pitch (or elevation)  
397 angle. We combined both adjustments into a single measure by computing the change in pointing  
398 angle, i.e., the angular change in direction of the longitudinal axis (the x-axis) of the seal (22). To  
399 compute this, segments of accelerometer and magnetometer data, sampled at 5 Hz, were first  
400 extracted for the same 22.4 s intervals starting 20 s before each true and fake PrCA. To avoid  
401 sensitivity to cyclic postural changes due to swimming, the accelerometer and magnetometer data  
402 were smoothed by computing the mean value on each axis over 1.6 s blocks with 0.8 s overlap.  
403 The longitudinal axis of the animal was then estimated from the smoothed acceleration and  
404 magnetometer data for each block using functions from animaltags.org. This resulted in a sequence  
405 of 3-element vectors,  $X_1, X_2, \dots$ , defining the temporal evolution of the longitudinal axis in 0.8 s time  
406 steps relative to each PrCA. Change in pointing angle was computed as the arc cosine of the dot  
407 product of pairs of vectors, skipping one vector to account for the 0.8 s overlap between consecutive  
408 vectors, i.e.,  $\phi_1 = \text{acos}(X_1^T X_3)$ ,  $\phi_2 = \text{acos}(X_2^T X_4)$ , etc.

409 *Biomechanical regimes*

410 Swimming activity depends on both the vertical movements of the seals and its buoyancy. Tag  
411 recordings for this study comprised the first few weeks of foraging trips during which seals were  
412 negatively buoyant, as judged from drift dives (23). Thus, seals are expected to glide when  
413 descending and swim actively when ascending. To avoid conflating these distinct biomechanical  
414 regimes when analyzing swimming activity, true and fake PrCAs were grouped according to the  
415 vertical movement prior to each PrCA. To do this, depth-rate was first computed over the full tag  
416 recordings as the differential of the pressure sensor data, low-pass filtered with a delay-free  
417 symmetric FIR filter (0.4 Hz cut-off frequency) to reduce noise. The depth-rate 20 s prior to each  
418 PrCA was then taken as indicative of the initial vertical movement. PrCAs with an initial depth-rate  
419 higher than 0.25 m/s and lower than -0.25 m/s were grouped as, respectively, descending and  
420 ascending PrCAs. We expect seals to glide and stroke, respectively, during these two groups of  
421 PrCAs, and any deviation from this default behavior prior to true PrCAs, relative to fake PrCAs,  
422 could indicate the onset of a prey approach behavior. PrCAs with initial depth-rates between -0.25

423 m/s and 0.25 m/s, i.e., implying close-to-horizontal movement, were not included in the swimming  
424 activity analysis as swimming is less predictable during horizontal movement making any difference  
425 between true and fake PrCAs difficult to interpret. As change in pointing angle is less clearly  
426 influenced by vertical direction, all PrCAs were analyzed for this parameter as a single group.

#### 427 *Data visualisation and summary*

428 Due to the long tag recording durations, several thousand PrCAs were detected for each seal which  
429 were matched with roughly equal numbers of fake PrCAs. To summarise the movement behaviour  
430 leading up to true and fake PrCAs, histograms of three the movement parameters (i.e. pointing  
431 angle change, and swimming activity in initially ascending and descending PrCAs) were computed  
432 at consecutive 1.8 s time steps relative to PrCAs. These histograms therefore provide a snapshot  
433 of the variety of movement behaviour at each moment prior to the strike. To represent the set of  
434 histograms visually, each histogram was converted into a vertical colored strip with the color scale  
435 indicating the height of the histogram (i.e. the proportion of PrCAs with a particular value of  
436 movement parameter). These colored strips are arranged vertically in the stack-plots of Fig. S2  
437 resulting in a set of 6 plots per animal comprising: the change in pointing angle prior to true and  
438 fake PrCAs (Fig. S2a,d); the swimming activity prior to initially ascending true and fake PrCAs (Fig.  
439 S2b,e); and the swimming activity prior to initially descending true and fake PrCAs (Fig. S2c,f). The  
440 color represents the proportion of PrCAs in which the parameter takes on the value given in the  
441 vertical axis of each plot.

442 To further summarise results for each seal and enable comparisons across animals, histograms  
443 were dichotomized using fixed thresholds, chosen for each seal. For change in pointing angle, the  
444 dichotomizing threshold was taken as 3 times the median change in pointing angle for the fake  
445 PrCAs in the first-time step. This threshold was chosen as representing a substantial deviation from  
446 the typical changes in pointing angle that occur during prey search. The number of true and fake  
447 PrCAs with changes in pointing angle above this threshold was counted at each time step and then  
448 normalized to the number of true and fake PrCAs, respectively. The ratio of these normalized counts  
449 was then plotted as a function of time step relative to time 0, i.e., the start time of the PrCAs. These  
450 plots therefore indicate the proportion of true and fake PrCAs with a large change in pointing angle  
451 at each time step (Fig. S2g). To dichotomize swimming activity, the consistent active swimming  
452 preceding upwards-directed fake PrCAs provides a natural threshold for distinguishing active  
453 swimming from gliding. This threshold was taken as one-half of the median activity measure  
454 recorded in the first-time interval prior to upward-directed fake PrCAs. Again, the normalized counts  
455 of true and fake PrCAs with activity levels above this threshold were plotted. These plots therefore  
456 indicate the proportion of true and fake PCAs for which the seal is swimming actively as a function  
457 of time relative to the start time of each PrCA. For descending PrCAs, the same threshold was  
458 used but the normalized counts were subtracted from 1 to give the proportion of gliding, the  
459 expected activity, as opposed to stroking (Fig. S2h-i).

#### 460 *Prey classification*

461 As demonstrated in a previous study (20), sonar tag recordings can be used to discriminate  
462 between schooling prey and individual prey. Visual analysis of echograms for a random subset of  
463 PrCAs indicated that prey schools with sonar cross-section of 1m or more were sometimes present  
464 before PrCAs for some seals. To establish the encounter rate of these schools in the full data set,  
465 we developed an automatic detector. This operated by first extracting the sonar data for the range  
466 interval of 0.5 to 2 m from the animal during the 20 s time interval preceding each PrCA, resulting  
467 in a matrix of 384 by 250 or 384 by 500 echo samples for each PrCA (i.e.,  $(1.5 \text{ m} \times 192\text{kHz} / (\text{sound}$   
468  $\text{speed} / 2))$  by  $(20 \text{ s} \times \text{ping rate})$ , where ping rate is 12.5 or 25 Hz). The median value of this matrix  
469 was taken as representing the prevailing noise level and a threshold was chosen relative to this  
470 noise level for each PrCA using a multiplying factor determined for each animal (described below).  
471 The sonar data matrix for each PrCA was then sub-divided into 1 m x 0.8 s blocks (i.e., 256 x 10  
472 or 20 samples) with 0.5 m and 0.4 s overlap. The 0.8 s block size was chosen to span a whole  
473 number of pings at both 12.5 and 25 Hz ping rates. The number of samples in each block with

474 echo level above threshold was then counted and the maximum value of these block counts for  
475 each PrCA, divided by the number of samples in the block, was defined as the schooling index.

476 As each sonar tag had slightly different transducer size and output level, the detection threshold  
477 was determined separately for each animal. To do this, the above analysis was first performed on  
478 the fake PrCAs, for which schooling prey are not expected, using a range of threshold multiplying  
479 factors. The multiplying factor giving a mean schooling index of 2% (i.e., a mean of 51 or 102  
480 samples above threshold per block for a ping rate of 12.5 or 25 Hz, respectively) was interpolated  
481 from the results and used in the schooling index analysis of the true PrCAs.

482 The schooling indices obtained with the automatic detector were compared with a subset of  
483 echograms that were inspected manually. Using a Receiver Operating Characteristic (ROC)  
484 analysis, we found that for a schooling index above 0.1, 86% of visually-detected schools were  
485 detected automatically, with a false alarm rate of 5% (sensitivity and specificity of 0.86 and 0.09,  
486 respectively). This threshold was therefore used to discriminate automatically between schooling  
487 and individual prey for all PrCAs with sonar data.

#### 488 *Prey-dependent approach behavior*

489 Only two seals (ml18\_295a and ml19\_294b, both from PV) encountered a high proportion of  
490 schooling prey. To investigate whether these seals adopted prey-dependent approach tactics, an  
491 exploratory analysis of SES orientation during the approach phase was made by computing the  
492 pitch, roll and yaw angles (the rotation around, respectively, the left-right axis, the longitudinal axis,  
493 and the dorso-ventral axis) from the tri-axial accelerometer and magnetometer data, decimated to  
494 a 5 Hz sampling rate (40). We found that both seals employed a stereotyped approach behavior  
495 for schooling prey that differed strongly from the approach behavior for single prey: when  
496 approaching schooling prey, the seals performed a backflip movement (i.e., a rotation of 180 or  
497 more degrees around the left-right axis) whereas approaches to single prey were typically made  
498 with a steady posture (Fig. 2). To establish the occurrence rate of this backflip maneuver in the full  
499 datasets, we developed an automatic detector based on its tri-axial acceleration signature. As the  
500 backflip involves a strong pitch change but little roll or yaw, we computed the rotation of the animal  
501 in the sagittal (i.e., x-z) plane in 0.2 s sampling intervals in the 20 s preceding each PrCA. The  
502 rotations were summed over the 20 s to give the cumulative directional pitching rotation in degrees.  
503 This number will be large and positive (or negative) if there are consistent clockwise (or counter-  
504 clockwise) pitching rotations prior to the PrCA. However a mix of clockwise and counter-clockwise  
505 rotations will give a sum close to zero. For the two seals that frequently encountered schooling  
506 prey, histograms of the directional pitching rotation were clearly bi-modal with large clockwise  
507 rotations associated with schooling prey (Fig. 2). An angular threshold was inferred from the  
508 histograms to discriminate backflip approaches from regular approaches and this was applied to  
509 all datasets to estimate the number of PrCAs for which this maneuver was used.

#### 510 *Prey reactivity*

511 Because of the large number of PrCAs detected per seal (ranging from 6000 to 16000 per animal),  
512 prey reactivity was assessed for a randomly-selected subset of approximately 10% of the PrCAs  
513 with sonar data for each female equipped with sonar tags in 2018. Sonar data were displayed as  
514 echograms, extending from 5 s before the PrCA start time to 2 s after the PrCA end time, and were  
515 manually analyzed by two trained assessors. Rapid accelerations made by prey when they react  
516 to the oncoming predator (41) are evident in echograms as a sudden change in the slope of the  
517 prey echo trace (2, 20). Echograms were therefore classified according to whether they (i)  
518 contained a clear echo trace, most likely representing the targeted prey), and (ii) evidence of a  
519 reaction by the prey. When a reaction was concluded, the distance and time of the first detectable  
520 prey response were recorded. The robustness of this subjective assessment across the two raters  
521 was verified using weighted Cohen's Kappa for reactivity (percentage agreement of 72%), and Lin's  
522 correlation coefficient for first reaction distance (0.6). See (20) for details.

523 *Search volumes*

524 The average swimming speed of each SES was taken from the slope of a scatter plot of depth rate  
525 versus pitch angle using data recorded throughout the foraging trip. Prey detection distance,  $d$ , was  
526 then estimated by multiplying the average swimming speed of SES by the time relative to a strike  
527 when the seal first changes its movement behavior, inferred from Fig. 1D-F. Little is known about  
528 the angle-dependency of fluid cue detection in whisking nor the visual acuity as a function of angle  
529 in SES. To get a rough idea of the search swathe, we assumed that SES have a hemispherical  
530 detection space with radius of  $d$  meters, giving a swathe area of  $\pi \cdot d^2$  m<sup>2</sup>. The apparent density of  
531 prey was then estimated by multiplying the search swathe by the average distance that SES move  
532 between prey encounters. This distance was estimated by dividing the three-dimensional distance  
533 travelled per day (i.e. the average swim speed multiplied by the time spent in foraging dives) by  
534 the number of prey strikes per day.

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536

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547 **References**

548

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