

Main Manuscript for

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

Mathilde Chevallay¹, Pauline Goulet¹, Peter T. Madsen², Julieta Campagna³, Claudio Campagna⁴, Christophe Guinet¹, Mark P. Johnson²

¹ CEBC-CNRS, Villiers-en-Bois, France, ² Zoophysiology, Aarhus University, DK-8000, Denmark.

³ CENPAT-CONICET, Puerto Madryn, Argentina, ⁴ Wildlife Conservation Society, Buenos Aires, Argentina

*Corresponding authors: Mathilde Chevallay, Mark P. Johnson

Email: mathilde.chevallay@outlook.fr; markjohnson@bio.au.dk

Author Contributions:

Conceptualization: MC, PG, PM, JC, CC, CG, MJ

Methodology: MC, PG, MJ

Formal analysis: MC, PG, MJ

Supervision: PG, CG, MJ

Writing—original draft: MC, PG, MJ

Writing—review & editing: MC, PG, PM, JC, CC, CG, MJ

Competing Interest Statement: All authors declare they have no competing interests.

Classification: Biological sciences – Ecology.

Keywords: deep-diving predators, prey detection, mesopelagic zone, bio-logging.

This PDF file includes:

Main Text

Figures 1 to 3

Abstract

The ability of echolocating toothed whales to detect and classify prey at long ranges enables efficient searching and stalking of sparse prey in time-limited dives. However, non-echolocating deep-diving seals such as elephant seals appear to have much less sensory advantage over their prey. Both elephant seals and their prey rely on visual and hydrodynamic cues that may be detectable only at short ranges in the deep ocean, leading us to hypothesize that elephant seals must adopt a less efficient reactive mode of hunting that requires high prey densities. To test that hypothesis, we deployed high-resolution sonar and movement tags on 25 females to record simultaneous predator and prey behavior during foraging interactions. We demonstrate that elephant seals have a sensory advantage over their prey that allows them to potentially detect prey 5-10 seconds before striking. The corresponding prey detection ranges of 7-17 m enable stealthy approaches and prey-specific capture tactics. In comparison, prey react at a median range of 0.7 m, close to the neck extension range of striking elephant seals. Estimated search swathes of 150 to 900 m² explain how elephant seals can locate up to 2000 prey while swimming more than 100 km per day. This efficient search capability allows elephant seals to subsist on prey densities that are consonant with the deep scattering layer resources estimated by hydro-acoustic surveys but which are two orders of magnitude lower than the prey densities needed by a reactive hunter.

Significance Statement

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

Main Text

Introduction

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

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

100 **Results**

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).

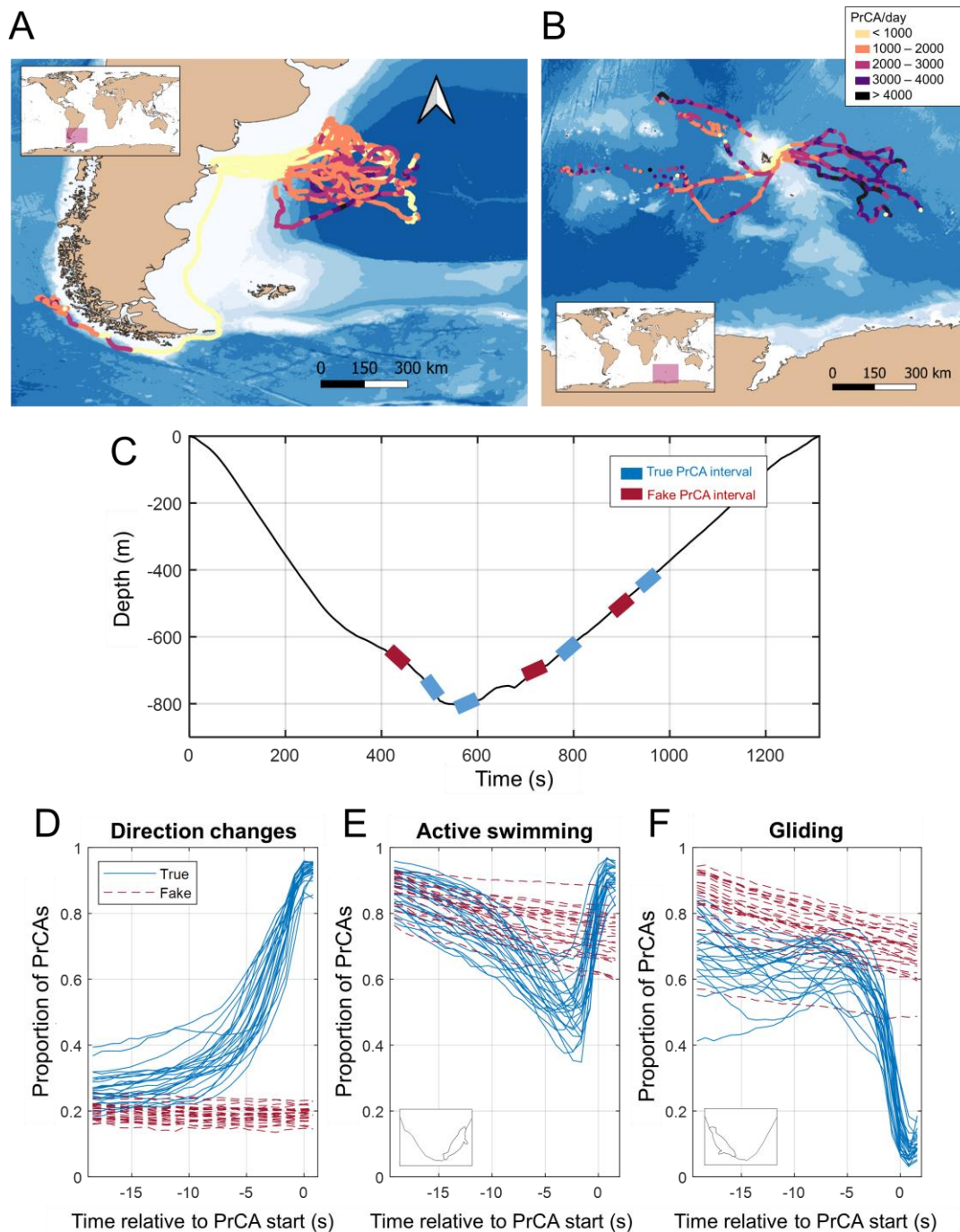


Figure 1. Prey detection by Southern elephant seals. (A-B) Tracks of seals tagged with high-resolution sonar and movement tags in (A) Peninsula Valdes, Argentina, and (B) Kerguelen Islands. Tracks are colored by daily counts of prey capture attempts inferred from distinctive acceleration transients.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

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

Prey detection

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

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

Prey-dependent approach tactics

Sonar data were examined in a subset of 57581 strikes (2158 to 8713 per individual) for the 13 seals (6 KER and 7 PV) equipped with sonar tags, again selecting strikes that were at least 25 s apart. The sonar resolution (4 mm) is sufficient to distinguish isolated single prey versus preys aggregated in tight schools (20), providing the opportunity to test if seals approach shoals of prey differently. Although the 6 KER seals approached almost exclusively single prey, the 7 PV animals found more varied prey aggregations. Two PV seals in particular (ml18_295a and ml19_294b) targeted a high proportion of schooling prey (42.3% and 20.8% of analyzed strikes, respectively, with approximate school sonar cross-section of ~1 m). These two seals performed a dramatically different movement pattern when approaching schooling versus single prey (Fig. 2): for single prey, the seals typically maintained a fixed horizontal posture, implying a direct approach style. In

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

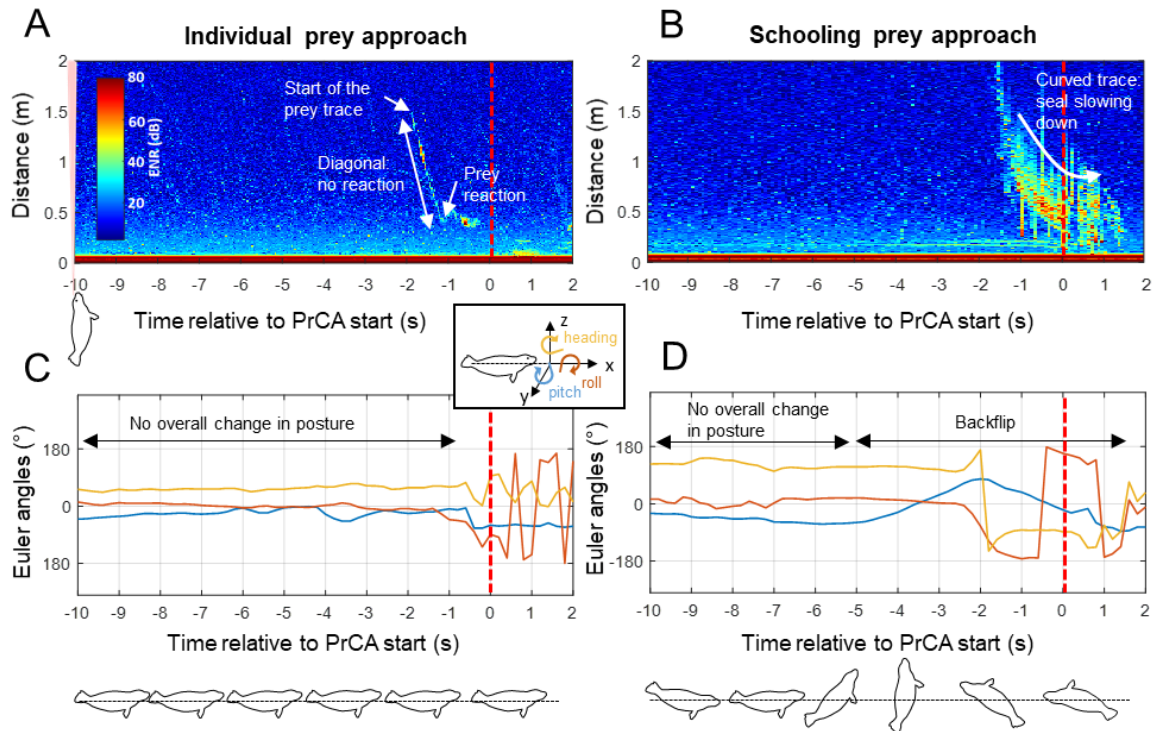


Figure 2. Female elephant seals employ different capture tactics for individual and schooling prey. (A) Echogram displaying individual (left panel) or schooling prey (right panel) insonified over successive sonar pings. The horizontal axis shows the time relative to PrCA start in seconds, and the vertical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

Prey escape behavior

Prey escape behavior was assessed from sonar data by two expert assessors for a randomly-selected subset of strikes for each seal equipped with sonar tags in 2018 ($n = 5855$ strikes, approx. 10% of eligible strikes per seal). Inter-rater agreement was high and 85% of individual prey were judged to be reactive. Prey flight initiation distance, measured from echograms (Fig. 2), was a 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) before the strike indicating a brief chase.

Search volume

Tagged SES travelled an average three-dimensional distance of 115 km/day (range 99-136 km/day) during foraging dives in which they attempted to capture some 2300 prey (range 1100-3710 prey/day) or about one prey per 55 m of travel. The higher PrCA rate here compared to previous reports from KER seals (7) is likely a result of wider accelerometer bandwidth which enables clearer discrimination of strikes at prey versus swimming. The 7-17 m prey detection distance suggests a search swathe, i.e., the area perpendicular to the trackline in which the seal can presumably detect prey, of 150-900 m² (i.e., $\pi \cdot d^2$). Taking 10 m as a representative detection distance and multiplying the corresponding swathe by the travel distance between prey gives an apparent average prey density of one prey per 16500 m³ within the foraging depth range of SES, i.e., approximately one prey per 25 m cube of water (Fig. 3).

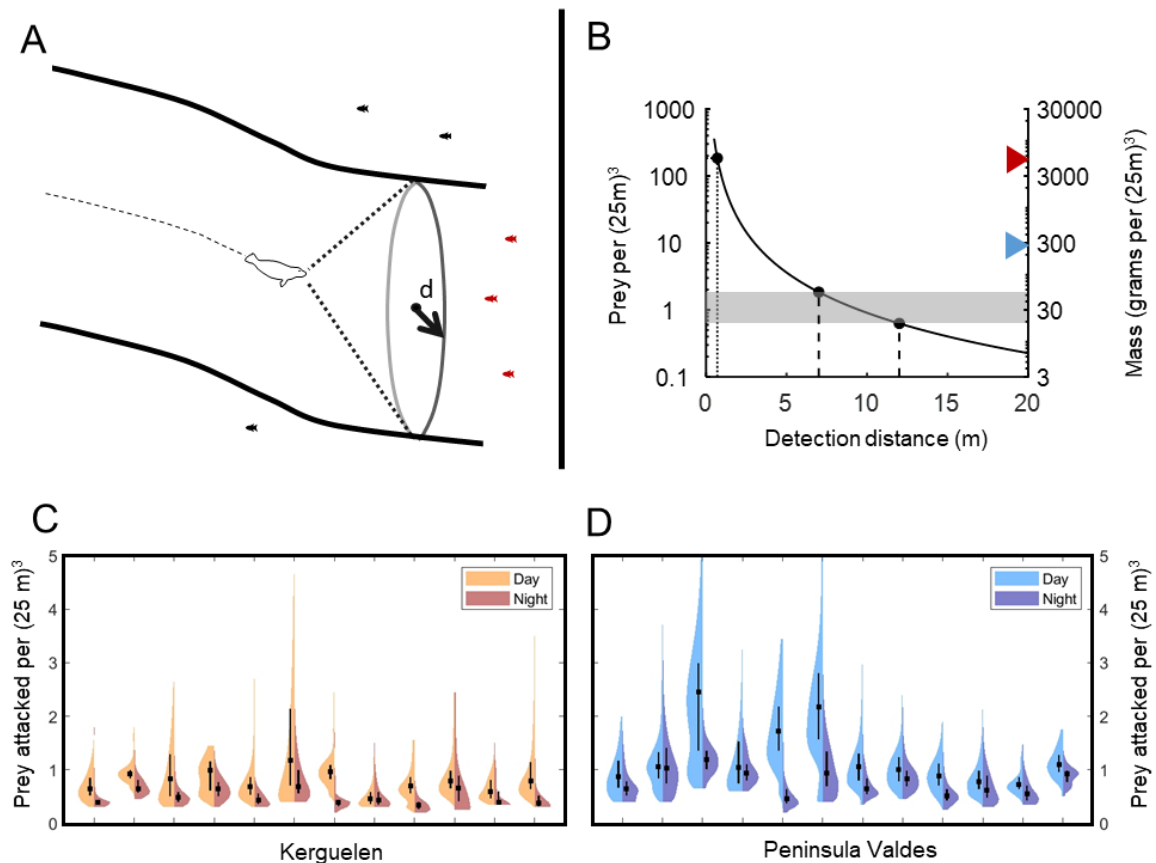


Figure 3. Ecological significance of early prey detection. (A) Schematic representation of a female Southern elephant seal with estimated prey detection range, scaled with the seal body size. (B) Required prey density to achieve the same prey encounter rate with varying detection distance. The dotted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

seal, i.e. attack rate per $(25\text{ m})^3$ searched, are relatively constant along their far-ranging foraging tracks, indicating a stable widely-distributed food resource.

Discussion

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

Sensory cues

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

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

Prey-dependent capture tactics

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

Ecological implications

Ship-based hydroacoustic surveys of the DSL suggest a global mesopelagic biomass of around 5 gigatons (4) albeit with a wide margin of error due to poorly-known and regionally-varying relationships between acoustic backscatter and biomass (4, 32). Nonetheless, the unquestioned vastness of the mesopelagic biomass and its global distribution as captured in biogeographic maps of the DSL (33) give the impression of a near-continuous layer of organisms that represent a treasure trove for any predator capable of diving deep enough. But taking the mesopelagic as 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 into just 0.017 g/m³ or 270 g per 25 m cube of water (a volume of 15625 m³). Hydroacoustic surveys integrate acoustic backscatter from a wide size-range of organisms and assuming the usual log-normal distribution of organism sizes (32), this 270 g is composed of thousands of micro-nekton but only a few of the >10 g organisms that are presumed to comprise the diet of elephant seals (18). Moreover, a portion of these larger organisms are low-nutrient cnidarians such as siphonophores which are unlikely to be eaten by elephant seals. Some regions of the Southern Ocean are predicted to have denser resources than the global average (34), potentially inflating these figures, but whatever the precise density, this analysis highlights that prey large enough to be worth hunting by air-breathing predators are sparse, notwithstanding the overall vastness of the mesopelagic biomass (Fig. 3).

The prey detection distances inferred here suggest that SES have an effective search swathe of some 300 m² perpendicular to their direction of travel providing the search efficiency needed to target such dispersed mesopelagic resources. Judging from the rate at which seals attack prey, the average prey density, as perceived by seals, is low at around 1 per 25 m³ of water but is broadly consistent with the predicted density of mesopelagic resources (35). In contrast, a reactive forager with a prey detection distance of 0.7 m, i.e., the same distance at which prey can detect the predator, would require two orders of magnitude higher prey density to achieve a similar rate of prey capture attempts as the tagged seals (Fig. 3). Conversely, echolocating toothed whales can detect prey some 3-10 times further than SES (6) enabling efficient exploitation of even sparser food resources. This capability likely facilitated the radiation of toothed whales into warmer, oligotrophic waters where DSL biomass density is typically predicted to be low (33). It may have also enabled more selective diets thereby fostering niche segregation and, ultimately, speciation in a vast open environment without obvious barriers (36).

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

to a reactive forager allows them to distribute their foraging, taking advantage of chance aggregations but subsisting on sparser prey in-between. Given a 10 m prey detection distance each SES samples, and potentially removes prey from, a water volume of about 3 km³ in a typical three-month foraging trip. Thus, acute sensory capabilities lead SES to have a much larger ecological footprint and therefore exercise far greater top-down control over Southern Ocean food webs than they would as reactive predators. But even this robust foraging strategy is susceptible to large-scale changes in prey abundance and community structure due to industrial mesopelagic trawling and climate change (38).

Materials and Methods

Fieldwork

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

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

Prey capture attempt detection

To detect prey capture attempts (PrCAs) we first computed the norm (i.e., vector magnitude) of the differential of the tri-axial acceleration (norm-jerk hereafter) using data at the full 200 Hz sampling-rate (39). The maximum of this norm-jerk signal over consecutive 10 s intervals was computed for each deployment, and plotted logarithmically in a histogram. These histograms were multi-modal for all animals with a clear high-jerk mode generated by brief strong jerk signals during foraging dives (Fig. S1). SES strike at prey by extending their necks leading us to interpret these high jerk transients as prey strikes. The high-jerk mode separated from lower modes in the histograms at a jerk of around 400 m/s³ for all animals and this value was therefore used to detect PrCAs. A 25 s blanking time (i.e., the time which must elapse with the jerk below threshold before another PrCA can be detected) was used in the detector to identify well-separated bouts of foraging. The start time of each PrCA was taken as the time of the first threshold crossing. As the movements prior to the first PrCA of each dive may be a combination of transport and foraging, these initial PrCAs were removed from the analysis. Analysis intervals were defined as the 20 s preceding each remaining PrCA allowing a minimum 5 s gap from preceding PrCAs.

Control intervals

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

Prey approach movements

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

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

Biomechanical regimes

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

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

Data visualisation and summary

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

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

Prey classification

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

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

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

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

Prey-dependent approach behavior

Only two seals (ml18_295a and ml19_294b, both from PV) encountered a high proportion of schooling prey. To investigate whether these seals adopted prey-dependent approach tactics, an exploratory analysis of SES orientation during the approach phase was made by computing the pitch, roll and yaw angles (the rotation around, respectively, the left-right axis, the longitudinal axis, and the dorso-ventral axis) from the tri-axial accelerometer and magnetometer data, decimated to a 5 Hz sampling rate (40). We found that both seals employed a stereotyped approach behavior for schooling prey that differed strongly from the approach behavior for single prey: when approaching schooling prey, the seals performed a backflip movement (i.e., a rotation of 180 or more degrees around the left-right axis) whereas approaches to single prey were typically made with a steady posture (Fig. 2). To establish the occurrence rate of this backflip maneuver in the full datasets, we developed an automatic detector based on its tri-axial acceleration signature. As the backflip involves a strong pitch change but little roll or yaw, we computed the rotation of the animal in the sagittal (i.e., x-z) plane in 0.2 s sampling intervals in the 20 s preceding each PrCA. The rotations were summed over the 20 s to give the cumulative directional pitching rotation in degrees. This number will be large and positive (or negative) if there are consistent clockwise (or counter-clockwise) pitching rotations prior to the PrCA. However a mix of clockwise and counter-clockwise rotations will give a sum close to zero. For the two seals that frequently encountered schooling prey, histograms of the directional pitching rotation were clearly bi-modal with large clockwise rotations associated with schooling prey (Fig. 2). An angular threshold was inferred from the histograms to discriminate backflip approaches from regular approaches and this was applied to all datasets to estimate the number of PrCAs for which this maneuver was used.

Prey reactivity

Because of the large number of PrCAs detected per seal (ranging from 6000 to 16000 per animal), prey reactivity was assessed for a randomly-selected subset of approximately 10% of the PrCAs with sonar data for each female equipped with sonar tags in 2018. Sonar data were displayed as echograms, extending from 5 s before the PrCA start time to 2 s after the PrCA end time, and were manually analyzed by two trained assessors. Rapid accelerations made by prey when they react to the oncoming predator (41) are evident in echograms as a sudden change in the slope of the prey echo trace (2, 20). Echograms were therefore classified according to whether they (i) contained a clear echo trace, most likely representing the targeted prey, and (ii) evidence of a reaction by the prey. When a reaction was concluded, the distance and time of the first detectable prey response were recorded. The robustness of this subjective assessment across the two raters was verified using weighted Cohen's Kappa for reactivity (percentage agreement of 72%), and Lin's 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 $\pi \cdot d^2$ m². 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.

535 Acknowledgments

536
537 The authors wish to thank all individuals who, over the years, have contributed to the fieldwork of
538 deploying and recovering tags at Kerguelen Island and in Valdes Peninsula. Southern elephant
539 seal data were gathered as part of the “Système National d’Observation: Mammifères
540 Echantillonneurs du Milieu Océanique” (SNO-MEMO, PI. C. Guinet), and was supported by CNRS,
541 Région Nouvelle Aquitaine (Development of new bio-logging technologies deployed on marine
542 animals to turn them into marine samplers), ANR HYPO2, CNES-(Centre National d’Études
543 Spatiales)-TOSCA as part of the projects elephant seals as high resolution oceanographic
544 samplers and SOS-Bio and IPEV (Institut Polaire Français Paul Emile Victor) as part of the
545 CyclEleph program (n. 1201, PI C. Gilbert).

546 547 References

- 548
549 1. J. B. Snyder, M. E. Nelson, J. W. Burdick, M. A. MacIver, Omnidirectional sensory and
550 motor volumes in electric fish. *PLoS Biol* **5**, e301 (2007).
- 551 2. H. Vance, *et al.*, Echolocating toothed whales use ultra-fast echo-kinetic responses to track
552 evasive prey. *Elife* **10**, e68825 (2021).
- 553 3. X. Irigoien, *et al.*, Large mesopelagic fishes biomass and trophic efficiency in the open
554 ocean. *Nature communications* **5**, 1–10 (2014).
- 555 4. R. Proud, N. O. Handegard, R. J. Kloser, M. J. Cox, A. S. Brierley, From siphonophores to
556 deep scattering layers: uncertainty ranges for the estimation of global mesopelagic fish
557 biomass. *ICES Journal of Marine Science* **76**, 718–733 (2019).
- 558 5. F. H. Jensen, M. Johnson, M. Ladegaard, D. M. Wisniewska, P. T. Madsen, Narrow
559 acoustic field of view drives frequency scaling in toothed whale biosonar. *Current Biology*
560 **28**, 3878–3885 (2018).
- 561 6. P. Tønnesen, C. Oliveira, M. Johnson, P. T. Madsen, The long-range echo scene of the
562 sperm whale biosonar. *Biology letters* **16**, 20200134 (2020).
- 563 7. C. Guinet, *et al.*, Southern elephant seal foraging success in relation to temperature and
564 light conditions: insight into prey distribution. *Marine Ecology Progress Series* **499**, 285–301
565 (2014).

- 566 8. Y. Le Bras, J. Jouma'a, C. Guinet, Three-dimensional space use during the bottom phase
567 of southern elephant seal dives. *Movement ecology* **5**, 18 (2017).
- 568 9. D. Saijo, *et al.*, Linking mesopelagic prey abundance and distribution to the foraging
569 behavior of a deep-diving predator, the northern elephant seal. *Deep Sea Research Part II:*
570 *Topical Studies in Oceanography* **140**, 163–170 (2017).
- 571 10. D. H. Levenson, R. J. Schusterman, Dark adaptation and visual sensitivity in shallow and
572 deep-diving pinnipeds. *Marine Mammal Science* **15**, 1303–1313 (1999).
- 573 11. G. Dehnhardt, B. Mauck, H. Bleckmann, Seal whiskers detect water movements. *Nature*
574 **394**, 235–236 (1998).
- 575 12. K. A. McGovern, C. D. Marshall, R. W. Davis, Are Vibrissae Viable Sensory Structures for
576 Prey Capture in Northern Elephant Seals, *Mirounga angustirostris*? *The Anatomical Record*
577 **298**, 750–760 (2015).
- 578 13. T. Adachi, *et al.*, Whiskers as hydrodynamic prey sensors in foraging seals. *Proceedings of*
579 *the National Academy of Sciences* **119**, e2119502119 (2022).
- 580 14. J. Blaxter, L. Fuiman, The role of the sensory systems of herring larvae in evading
581 predatory fishes. *Journal of the Marine Biological Association of the United Kingdom* **70**,
582 413–427 (1990).
- 583 15. M. McHenry, K. Feitl, J. Strother, W. Van Trump, Larval zebrafish rapidly sense the water
584 flow of a predator's strike. *Biology Letters* **5**, 477–479 (2009).
- 585 16. W. J. Stewart, G. S. Cardenas, M. J. McHenry, Zebrafish larvae evade predators by
586 sensing water flow. *Journal of Experimental Biology* **216**, 388–398 (2013).
- 587 17. M. Wilson, J. Å. R. Haga, H. E. Karlsen, Behavioural responses to infrasonic particle
588 acceleration in cuttlefish. *Journal of Experimental Biology* **221**, jeb166074 (2018).
- 589 18. T. Adachi, *et al.*, Forced into an ecological corner: Round-the-clock deep foraging on small
590 prey by elephant seals. *Science advances* **7**, eabg3628 (2021).
- 591 19. D. M. Wisniewska, *et al.*, Ultra-high foraging rates of harbor porpoises make them
592 vulnerable to anthropogenic disturbance. *Current Biology* **26**, 1441–1446 (2016).
- 593 20. P. Goulet, C. Guinet, R. Swift, P. T. Madsen, M. Johnson, A miniature biomimetic sonar and
594 movement tag to study the biotic environment and predator-prey interactions in aquatic
595 animals. *Deep Sea Research Part I: Oceanographic Research Papers* **148**, 1–11 (2019).
- 596 21. M. A. Hindell, *et al.*, Circumpolar habitat use in the southern elephant seal: implications for
597 foraging success and population trajectories. *Ecosphere* **7**, e01213 (2016).
- 598 22. P. J. Miller, M. P. Johnson, P. L. Tyack, Sperm whale behaviour indicates the use of
599 echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society of*
600 *London. Series B: Biological Sciences* **271**, 2239–2247 (2004).
- 601 23. M. Biuw, B. McConnell, C. J. Bradshaw, H. Burton, M. Fedak, Blubber and buoyancy:
602 monitoring the body condition of free-ranging seals using simple dive characteristics.
603 *Journal of Experimental Biology* **206**, 3405–3423 (2003).

- 604 24. J. Torres, G. Somero, Vertical distribution and metabolism in Antarctic mesopelagic fishes.
605 *Comparative Biochemistry and Physiology--Part B: Biochemistry and Molecular Biology* **90**,
606 521–528 (1988).
- 607 25. P. T. Madsen, N. A. de Soto, P. Arranz, M. Johnson, Echolocation in Blainville's beaked
608 whales (*Mesoplodon densirostris*). *Journal of Comparative Physiology A* **199**, 451–469
609 (2013).
- 610 26. V. Catul, M. Gauns, P. Karuppasamy, A review on mesopelagic fishes belonging to family
611 Myctophidae. *Reviews in Fish Biology and Fisheries* **21**, 339–354 (2011).
- 612 27. T. J. Langbehn, D. L. Aksnes, S. Kaartvedt, Ø. Fiksen, C. Jørgensen, Light comfort zone in
613 a mesopelagic fish emerges from adaptive behaviour along a latitudinal gradient. *Marine*
614 *Ecology Progress Series* **623**, 161–174 (2019).
- 615 28. P. Goulet, *et al.*, Flash and grab: deep-diving southern elephant seals trigger anti-predator
616 flashes in bioluminescent prey. *Journal of Experimental Biology* **223**, jeb222810 (2020).
- 617 29. R. D. McCauley, D. H. Cato, Evening choruses in the Perth Canyon and their potential link
618 with Myctophidae fishes. *The Journal of the Acoustical Society of America* **140**, 2384–2398
619 (2016).
- 620 30. J. L. Maresh, F. E. Fish, D. P. Nowacek, S. M. Nowacek, R. S. Wells, High performance
621 turning capabilities during foraging by bottlenose dolphins (*Tursiops truncatus*). *Marine*
622 *mammal science* **20**, 498–509 (2004).
- 623 31. D. Wiley, *et al.*, Underwater components of humpback whale bubble-net feeding behaviour.
624 *Behaviour*, 575–602 (2011).
- 625 32. P. C. Davison, J. A. Koslow, R. J. Kloser, Acoustic biomass estimation of mesopelagic fish:
626 backscattering from individuals, populations, and communities. *ICES Journal of Marine*
627 *Science* **72**, 1413–1424 (2015).
- 628 33. R. Proud, M. J. Cox, S. Wotherspoon, A. S. Brierley, A method for identifying sound
629 scattering layers and extracting key characteristics. *Methods in Ecology and Evolution* **6**,
630 1190–1198 (2015).
- 631 34. T. Dornan, S. Fielding, R. A. Saunders, M. J. Genner, Large mesopelagic fish biomass in
632 the Southern Ocean resolved by acoustic properties. *Proceedings of the Royal Society B* **289**,
633 20211781 (2022).
- 634 35. T. Dornan, S. Fielding, R. A. Saunders, M. J. Genner, Swimbladder morphology masks
635 Southern Ocean mesopelagic fish biomass. *Proceedings of the Royal Society B* **286**,
636 20190353 (2019).
- 637 36. S. Pompa, P. R. Ehrlich, G. Ceballos, Global distribution and conservation of marine
638 mammals. *Proceedings of the National Academy of Sciences* **108**, 13600–13605 (2011).
- 639 37. L. Siegelman, M. O'toole, M. Flexas, P. Rivière, P. Klein, Submesoscale ocean fronts act as
640 biological hotspot for southern elephant seal. *Scientific Reports* **9**, 5588 (2019).
- 641 38. A. Ariza, *et al.*, Global decline of pelagic fauna in a warmer ocean. *Nature Climate Change*
642 **12**, 928–934 (2022).

- 643 39. K. S. Ydesen, *et al.*, What a jerk: prey engulfment revealed by high-rate, super-cranial
644 accelerometry on a harbour seal (*Phoca vitulina*). *Journal of Experimental Biology* **217**,
645 2239–2243 (2014).
- 646 40. M. P. Johnson, P. L. Tyack, A digital acoustic recording tag for measuring the response of
647 wild marine mammals to sound. *IEEE journal of oceanic engineering* **28**, 3–12 (2003).
- 648 41. P. Domenici, *Fish locomotion: an eco-ethological perspective* (CRC Press, 2010).
- 649