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A miniature biomimetic sonar and movement tag to study the biotic environment and predator-prey interactions in aquatic animals

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ABSTRACT

How predators find, select and capture prey is central to understanding trophic cascades and ecosystem structure. But despite advances in biologging technology, obtaining in situ observations of organisms and their interactions remains challenging in the marine environment. For some species of toothed whales, echoes from organisms insonified by echolocation clicks and recorded by sound logging tags have provided a fine-scale view of prey density, and predator and prey behaviour during capture attempts, but such information is not available for marine predators that do not echolocate. Here the development and performance of a miniature biomimetic sonar and movement tag capable of acquiring similar data from non-echolocating marine predators is reported. The tag, weighing 200 g in air, records wide bandwidth sonar data at up to 50 pings a second synchronously with fast-sampling sensors for depth, acceleration, magnetic field and GPS. This sensor suite enables biotic conditions and predator behaviour to be related to geographic location over long-duration foraging trips by apex marine predators. The sonar operates at 1.5 MHz with a 3.4° beamwidth and a source level of 190 dB re 1 μPa at 1 m. Sonar recordings from a trial deployment of the tag on a southern elephant seal contained frequent targets corresponding to small organisms up to 6 m ahead of the tagged animal. Synchronously sampled movement data allowed interpretation of whether the seal attempted to capture organisms that it approached closely while the high sonar ping rate revealed attempts by prey to escape. Results from this trial demonstrate the ability of the tag to quantify the biotic environment and to track individual prey captures, providing fine-scale information on predator-prey interactions which has been difficult to obtain from non-echolocating marine animals.

1. Introduction

Information on the foraging preferences, and prey encounter and capture rates, of predators is fundamental to understanding habitat needs, trophic energy cascades, and ultimately in determining how populations may respond to environmental change (Reid and Croxall, 2001; Ribic et al., 2008). However, this type of information can be difficult to obtain for far-ranging predators especially in the marine environment. One approach is to combine visual sightings of predators with direct prey field measurements using net sampling, boat-mounted echosounders or cameras (Croll et al., 2005; Friedlaender et al., 2006; Waluda et al., 2010). While these methods can provide reliable estimates of species density, there is often a poor spatial and temporal overlap between visual observations and prey field measurements, which introduces uncertainty when linking datasets at fine-scale (Kuhn et al., 2015). Underwater cameras in particular have very short detection ranges due to rapid light attenuation in water and organisms may react to the light required to illuminate organisms in deep water. Net sampling is also biased towards slower organisms as energetic animals can out-swim nets (Kaartvedt et al., 2012).

In comparison, animal-borne biologging tags are able to record in-situ, fine-scale data on the movement, behaviour, and location of tagged predators, providing indirect information on where and how often they encounter prey. Transient signals recorded by three dimensional accelerometers on a range of species have been interpreted as resulting from sudden movements during prey capture attempts (Johnson et al., 2004; Gallon et al., 2013; Ydesen et al., 2014) although these may be difficult to separate from acceleration transients generated by other activities (Volpov et al., 2015). Jaw opening movements detected by accelerometers (Naito et al., 2013; Viviant et al., 2010) or magnetic sensors (Ropert-Coudert et al., 2004) provide less ambiguous indications of prey capture and handling, but remain sensitive to false

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detections from other jaw movements (Liebsch et al., 2007). However, neither of these methods provides a definitive indication of successful capture and ingestion. Prey ingestion has been measured using stomach temperature sensors which detect temperature drops associated with water and ectothermic prey ingestion. Although widely used with pinnipeds (Austin et al., 2006; Kuhn et al., 2009) and penguins (Bost et al., 2007; Ropert-Coudert and Kato, 2006) to infer actual foraging rates, these devices are frequently regurgitated and may therefore be unreliable for long deployments. In addition, rapid series of ingestions may be detected by stomach temperature loggers as a single cumulative event (Ropert-Coudert and Kato, 2006) leading to an underestimate of prey ingestion. These biologging methods thus offer powerful indications of where, when and how often predators attempt to capture prey but provide less information on the availability of organisms, including prey, and on capture success.

Biologging tags incorporating additional sensors have provided more direct observations of prey density and capture. Camera tags on penguins, pinnipeds and baleen whales have revealed prey types and capture tactics, while also validating foraging proxies inferred from other sensors (Goldbogen et al., 2017; Naito et al., 2013; Thiebot et al., 2016; Volpov et al., 2015; Watanabe and Takahashi, 2013). However, memory and power demands, especially if artificial illumination is needed in deep water, currently make cameras impractical for long-ranging, deep-diving predators.

Sound sampling tags deployed on some echolocating toothed whales have recorded echoes returning from insonified organisms (Johnson et al., 2004), enabling the quantification of biotic abundance (Arranz et al., 2011) as well as prey selection (Jones et al., 2008; Madsen et al., 2005), capture tactics and prey escape behaviour (Johnson et al., 2008; Wisniewska et al., 2016), effectively eavesdropping on the signals used by the sensory system of the predator. This approach is restricted to echolocating animals, but the technological equivalent of biosonar is widely used in fisheries science. Like biosonar, fisheries sonars emit high frequency sound pulses in narrow beams and use echoes from organisms to estimate their distance, density and distribution. While a single frequency sonar has limited ability to discriminate between different categories of organisms (e.g. Urmy et al. (2012)), newer multi-frequency (Brierley et al., 1998; Kloser et al., 2002) and broadband (Amakasu et al., 2017; Lavery et al., 2010; Ross et al., 2013) sonar systems exploit variations in echo intensity with frequency to discriminate categories, sizes and even species of pelagic organisms (McQuinn et al., 2013). For ship-borne sonar this quantification becomes increasingly coarse with depth due to beam spreading and acoustic attenuation of the high frequencies needed to study small organisms. This can be overcome by lowering the sonar to the depth of interest (e.g. (Kloser et al., 2016; Ryan et al., 2009) or deploying it in an autonomous vehicle (Dunlop et al., 2018; Moline et al., 2015). A number of studies have successfully recorded predators interacting with prey schools using sonars deployed from ships or underwater vehicles (Similä, 1997, Axelsen et al., 2001; Nøttestad et al., 2002; Benoit-Bird and Au, 2009; Benoit-Bird et al., 2017), providing valuable insight into anti-predator dynamics of schools and the harvesting tactics of predators. However, monitoring individual predators for longer intervals or when hunting sparsely-distributed prey remains a significant challenge.

Combining these approaches, a logical way to study prey from the predator's perspective would be to build the sonar into a biologging tag. Although the limited size of such a tag may dictate a relatively simple sonar that provides much coarser information than a camera, there are several potential advantages to an animal-borne sonar. Unlike a camera tag, an animal-borne sonar may be able to operate over longer and more predictable ranges independent of ambient light levels, and without the need for a light source in deeper waters that may modify the behaviour of both predator and prey. Importantly for long-duration deployments, sonar can use less power and memory than cameras because the transmit pulse can be very short and returning echo data are only collected in one dimension as compared to the two dimensions of a visual image.

The first reported animal-attached sonar was developed by Miyamoto et al. (2004) for detecting krill predation by penguins. This device used a 1 MHz centre frequency and was extremely compact (100 g weight in air). However, the 2004 paper did not report data from animal deployments and additional reports on this device could not be found. A decade later Lawson et al. (2015) developed a prototype sonar for use on wild northern elephant seals (*Mirounga angustirostris*). Using an off-the-shelf transducer with a working frequency of 200 kHz and a 1 Hz ping rate, this tag weighed around 4 kg in air due largely to the power source needed to record continuously for 8 days. The tag did not contain additional sensors and so was intended to be deployed with other tags to sample movement and position. Trial deployments of the tag successfully recorded discrete echoes during foraging dives, with some depth ranges also showing an increased backscatter strength suggesting a higher density of plankton and small nekton. This device therefore provided the first in situ profile of the biotic seascape on a non-echolocating animal. However, as acknowledged by the authors, the prototype required substantial miniaturisation to be suitable for deployment on wide-ranging or smaller species.

Here we describe the development and performance of a small, high-resolution sonar tag specifically designed to track predator-prey interactions and prey field density over long-duration foraging trips by marine predators. The tag builds on the approach of Lawson et al. (2015) but also takes inspiration from toothed whale biosonar: all studied toothed whales use a narrow (6–15°) forward-directed biosonar beam to detect prey (Jensen et al., 2018), relying on sequential scanning to inspect larger volumes of water (Wisniewska et al., 2012). A distinctive feature of toothed whale biosonar is the high click rate compared to their forward speed (Madsen et al., 2013), which leads to multiple insonifications of the same organisms (Arranz et al., 2011) potentially yielding information on their type and behaviour (Wisniewska et al., 2016). An additional goal of the tag was to integrate synchronous high-resolution position and movement sensors to relate biotic conditions with predator behaviour and geographic location. Preliminary results obtained from deployment on free-ranging southern elephant seals *Mirounga leonina* (SES hereafter) demonstrate the ability of the tag to detect biological targets and to track individual prey captures simultaneously from both sonar echoes and predator movements, providing new fine-scale information about the foraging ecology of this apex Southern Ocean predator.

2. Methods

2.1. Sonar tag design

The target application for the sonar tag is to collect foraging data for extended periods of time on wide-ranging marine species. With their post-breeding foraging trip lasting approximately 2 months, SES provide an appropriate test subject. The tag requires fine-scale sensors for movement (depth sensor, accelerometer and magnetometer) and location, in addition to the sonar, to facilitate inferences about behaviour. Given the relatively high data rate collected by these sensors, satellite telemetry is currently not feasible meaning that the tag must store data in on-board memory and be physically recovered when the seal returns to shore. The tag is mounted on the head of seals to ensure an unobstructed view of the water ahead of the mouth (Fig. 1 top right). This necessitates a small package size and a reasonably hydrodynamic shape to minimise the impact of the tag on the energy expenditure of the animal. Tags of size 105 × 70 × 40 mm (O'Toole et al., 2014) or larger are typically deployed on SES during post-breeding migrations with little apparent affect on foraging success (McMahon et al., 2008). Such dimensions therefore provide us with a maximum design envelope. This size constraints the battery volume to 3 × AA cells, i.e., a capacity of 25 Wh with lithium thionyl chloride (Li-SOCl2) batteries, dictating an

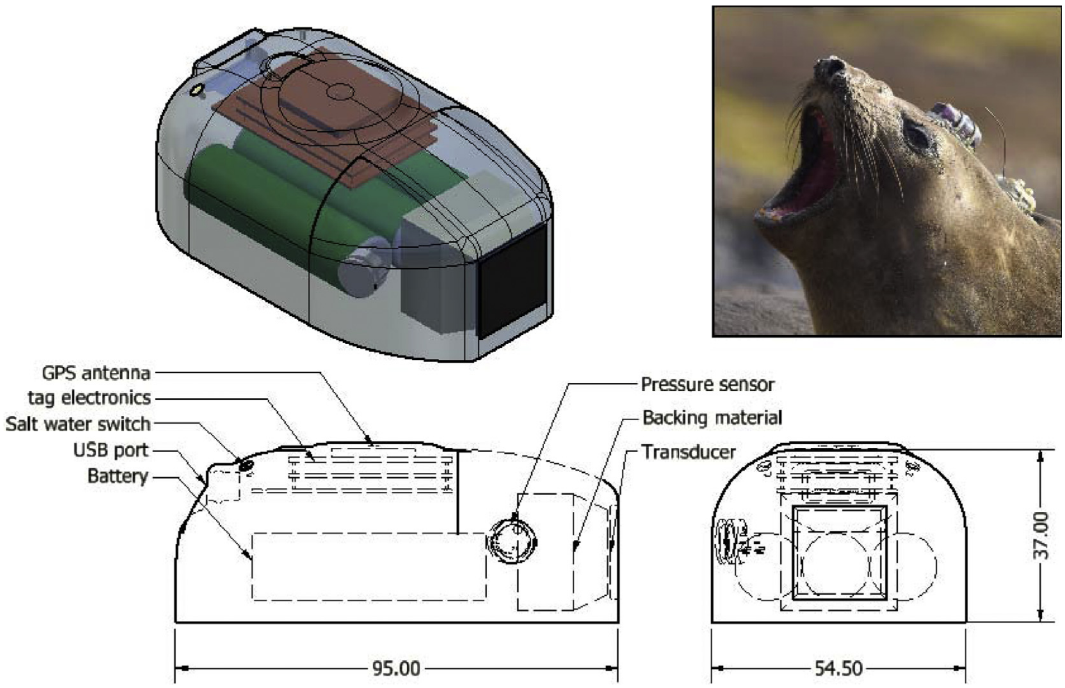

Fig. 1. Mechanical diagram of the sonar tag showing the location of the major components. The tag electronics, sonar transducer, sensors and battery are cast in epoxy to create a single compact pressure tolerant tag with dimensions 95 × 55 × 37mm. Top right: sonar tag deployed on an adult southern elephant seal female (photo: Joris Laborie).

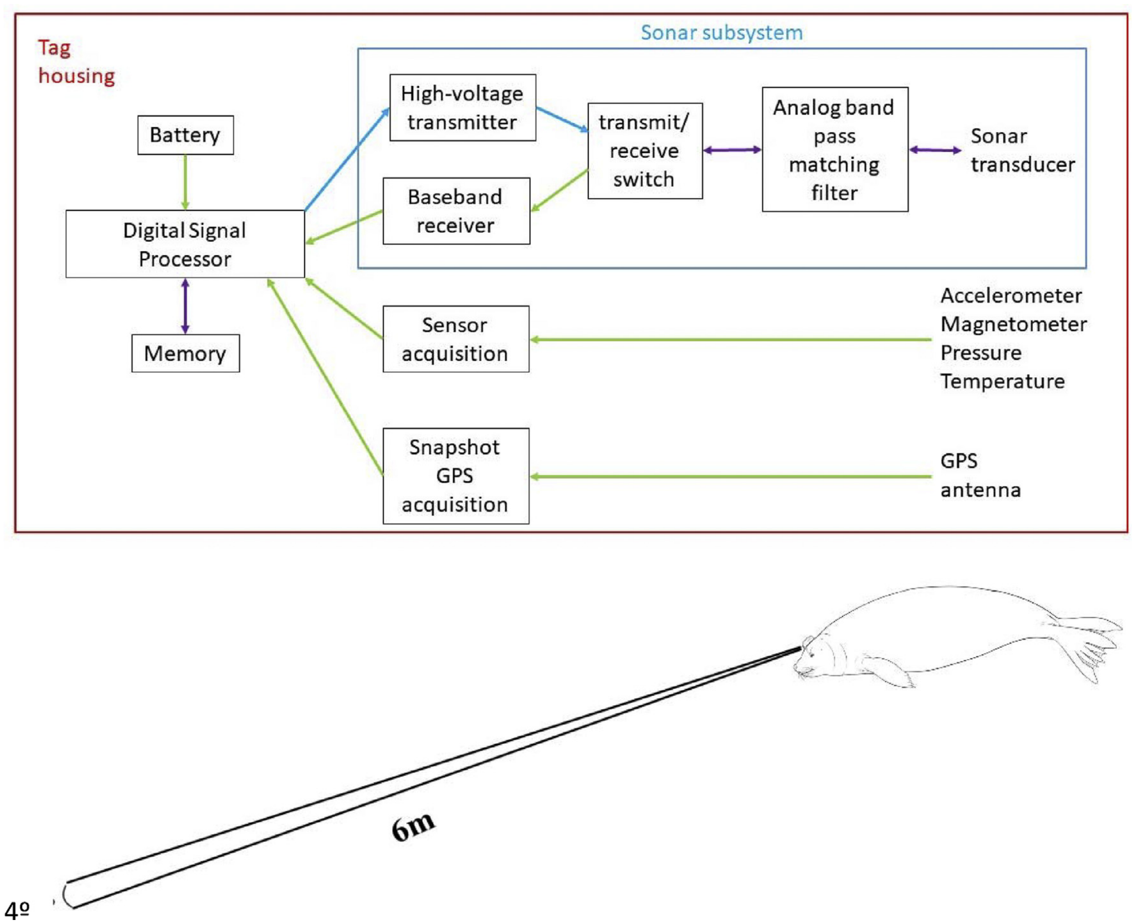

Fig. 2. Top: Simplified block diagram of the tag showing the sonar and movement sensor sub-systems. Bottom: Approximate position, beamwidth (4°) and operating range (6 m) of the sonar tag mounted on a female southern elephant seal.

Table 1
Sampling rate, resolution, data rate and power consumption of the sub-systems in the sonar tag assuming a GPS position every 5 min, accelerometer sampled at 200 Hz and the sonar operated at 12.5 pings per second, half power. The sonar produces 2 × 16-bit values per sample representing the in-phase and quadrature components of the complex demodulated signal.

Subsystem	Sampling rate	Resolution (approx.)	Data rate bytes/sec	Power consumption (mW)
Sonar	Programmable 6.25, 12.5, 25, 50 Hz ping rate 192 kHz receiver sampling rate	8 mm, 6 m max range	75 k (approx. 25 kB/s after compression)	16.3
GPS	Programmable, 128 kB per position	20 m RMS	440	3.4
Accelerometer (3-axes)	Programmable 100 Hz – 1 kHz	0.03 ms^{-2} RMS	1200	
Magnetometer (3-axes)	50 Hz	0.5 µT RMS	300	
Depth and temperature	50 Hz	0.05 m H_2O	200	
Processor	–	–	–	6.8

electronics design with high power efficiency. These function, size and power constraints lead directly to a number of design decisions for the sonar tag (see Fig. 2).

Due to the space and power requirements of supporting electronics, multibeam and multi-frequency sonar are not currently feasible in such a restricted footprint and so the design focused on a single beam sonar with a high ping rate to sample prey movements relative to the predator (Wisniewska et al., 2014). As echoes from each ping must return before emitting the subsequent ping for unambiguous ranging, the range of the sonar limits the ping rate. An ecologically relevant operating distance to sample prey targeted by seals is 5–10 m (Adachi et al., 2017) setting a maximum ping rate of 75 Hz (i.e., sound-speed/(2 × range)). However, ping rate also influences power and memory consumption, and was therefore left as a user-configurable option.

Off-the-shelf sonar transducers and hardware meeting the size and power constraints for the tag were not available and we therefore pursued a ground-up design centred around the development of a custom transducer. The centre frequency and size of the transducer control the beamwidth, range and sensitivity of the sonar. Using a high frequency enhances the echo strength from relatively small prey that could potentially be targeted by elephant seals (Naito et al., 2013) and would be missed with lower frequencies, but also results in increased echoes from smaller biotic and abiotic scatterers which may mask prey observations (Richards et al., 2004). Sound absorption also increases with frequency (Kinsler and Frey, 1962), limiting the range of a high frequency sonar (Miyamoto et al., 2004). However, for a given frequency, a larger transducer gives a narrower beam/field of view and a longer detection range because the acoustic energy is concentrated into a smaller volume. The relation between frequency, size and beamwidth for a flat piston transducer is: $\theta \approx 78.3^{\circ}/(Lf)$ where θ is the half power beamwidth in degrees, f is the centre frequency in kHz and L is the transducer side length in m (Lurton, 2002; Zimmer et al., 2005). As L is limited by the tag size, a relatively high centre frequency of 1.5 MHz was chosen, for which a 15 × 15 x 1 mm (width x height x thickness) transducer has a predicted −3 dB beamwidth of 3.5°.

To maximise power transfer to the water, a low impedance composite transducer composed of 60% piezoelectric ceramic rods in an epoxy matrix (Smart Material GmbH) was used. The front surface of the transducer has a polymer layer with thickness and impedance chosen to increase coupling efficiency. The transducer is backed with syntactic foam, a lightweight material able to withstand high pressure, in place of the typical metal or air backing.

A simple high-voltage square wave was chosen for the transmit signal to minimise board size and maximise efficiency. The transmit waveform comprises a burst of 16 cycles at 1.536 MHz, giving a pulse length of 10.4 µs. This short pulse was selected to reduce power consumption while giving a high spatial resolution of approx. 8 mm to track target movements and resolve close reflectors. An important consequence of using a rectangular windowed transmit pulse is that the very abrupt start and end of the signal produces sidebands over a wide frequency range. Although the sonar centre frequency is well beyond the nominal 100 kHz upper hearing limit of seals (Cunningham and Reichmuth, 2016), this sideband energy descends into the audible frequency range. A head-mounted tag is in close proximity to the seal's hearing system and must therefore produce very low emissions relative to ambient noise/hearing threshold to minimise disturbance (Lawson et al., 2015).

Low frequency emissions from the sonar were reduced in two ways: first the output drive circuit switched between closely matched positive and negative high voltage rails to avoid a low frequency transient due to pulse asymmetry. Remaining sidebands were attenuated using a passive 3-pole bandpass matching filter with components chosen to give an electrical match between the switcher and transducer at the centre frequency while also rejecting low frequencies. An additional way to reduce sideband emissions and power consumption was implemented as a user configurable option. This involves controlling the power level of the transmit signal by enabling the output switches for 1/4, 1/2 or the full halfcycle, corresponding to 25%, 50% and full power.

To further reduce power consumption, a receiving circuit with analog quadrature demodulation was used. The resulting in-phase and quadrature signals are sampled synchronously with 16-bit analog-to-digital convertors at a rate of 192 kHz to accommodate the transmit bandwidth (approx. 85 kHz for a 10.4 µs pulse). This approach avoids the high power consumption and memory usage of direct digital sampling of the received signal. The maximum acquisition range of the sonar is controlled by the amount of time that the receiver is enabled following each ping; the receiver is subsequently turned off to save power until the next ping. The sonar data are compressed losslessly (Johnson et al., 2013) and stored along with data from the movement sensors in non-volatile solid-state memory.

The recording time of the tag is determined not only by its power requirements but also by its memory capacity and sensor sampling rates (Table 1). With a sonar ping rate of 12.5 Hz, a maximum sonar acquisition range of 6 m and 50% output power, along with accelerometer sampling at 200 Hz and a GPS position acquired on average every 5 min, the tag generates data at a mean rate of 27 kB/s after compression with a power consumption of 27 mW. The tag has 64 GB of memory allowing about 30 days of continuous recording with these settings.

2.2. Audibility testing

Low frequency acoustic emissions from the sonar were quantified over a 1–100 kHz frequency range to assess its potential audibility to the tagged animal. A low-noise, autonomous sound recorder (DTAG), sampling at 576 kHz, was located 15 cm from the sonar transducer, and measurements were made 1 m below the water surface in a quiet pool filled with seawater. Sound level was measured below the tag, i.e., at 90° from the sonar beam centre, to be representative of sound reaching the animal's hearing system. Range gating was applied to the received signals to remove reverberation from the tank walls and water surface. The short transients produced by the sonar tag are well within the integration time of the seal hearing system (assumed to be about 125 ms (Kastelein et al., 2010),) and so the Root Mean Squared (RMS) level over this interval was calculated. Sound levels were measured with the sonar operating at ping rates of 6.25, 12.5 and 25 Hz, and at power levels of 1/4, 1/2 and full. Background noise levels were recorded with the sonar disabled. Measured sound levels from the sonar were compared against pinniped hearing thresholds as well as to predictions of the ambient noise in the Southern Ocean. Although the hearing range and sensitivity of southern elephant seals are unknown, measurements are available for northern elephant seals and harbour seals. Three published harbour seal audiograms (Kastelein et al., 2009; Reichmuth et al., 2013; Cunningham and Reichmuth, 2016) were used because thresholds at frequencies above 60 kHz are unavailable for northern elephant seals but their high-frequency hearing is reported to be similar to that of harbour seals (Reichmuth et al., 2013). Representative ambient noise levels for the Southern Ocean were extracted from a sound recording collected by a DTAG sound and movement recorder attached to a southern elephant seal on Kerguelen Island in November 2017. Sound samples were taken during drift dives, when the seal passively descended through the water column to minimise the confounding effect of flow noise on ambient noise estimates (Cazau et al., 2017). Both the sonar emissions and the ocean ambient noise were converted to third octave band levels to be comparable with hearing threshold data.

2.3. Calibration and validation

The sonar was calibrated for source level and beam pattern using a target with known target strength (TS) suspended at a known distance in the axis of the sonar beam (Foote and Martini, 2010). The narrow beam of the sonar makes the usual spherical calibration target impractical and a 0.1 mm radius stainless steel wire, stretched perpendicular to the beam, was used instead. This wire has a theoretical TS of −75 dB at a range of 40 cm (Sheng and Hay, 1993) and was chosen to produce clear echoes without overloading the receiver.

The echo level (EL) of the wire was measured with the sonar operating at 3 different power settings (Foote, 1990) and the sonar source level was back-calculated assuming an absorption of 0.5 dB/m at 1.5 MHz in 20 °C water (Ainslie and McColm, 1998). The transducer directivity pattern was estimated by rotating the sonar tag with respect to the target using a micrometer stage and measuring echo levels from the wire relative to off-axis angle in 0.2° increments. The noise floor of the sonar was estimated by operating the sonar in air and measuring the average echo level excluding the initial 2.5 ms after the out-going pulse.

To evaluate the capability of the sonar to detect small organisms, echoes were recorded from 3 to 4 cm long shrimps swimming in a 60 × 40 × 40 cm tank filled with seawater. The sonar was configured for a ping rate of 25 Hz and low power. A video camera, synchronised and co-located with the tag, was used to identify the source of echoes recorded by the sonar.

2.4. Field deployments

In October 2017, 4 post breeding female SES on the Kerguelen Islands were each equipped with a head-mounted sonar tag and a back-mounted CTD tag (SMRU-SRDL) (see Jouma'a et al. (2016) for details of similar fieldwork). Animals were anaesthetised using a 1:1 combination of tiletamine and zolazepam (Zoletil 100), injected intravenously (McMahon et al., 2000). Tags were glued to the pelage using quick-setting epoxy (Araldite AW 2101, Ciba). The sonar was configured for a 12.5 Hz ping rate at half power to reduce low frequency emissions. The tags were programmed to sample movement sensors continuously but to only operate the sonar with a 2.5 h on/off duty-cycle to facilitate detection of any movement responses to the sound output of the sonar (Lawson et al., 2015). Although this duty-cycling did not work as expected due to a software error, sets of complete descents were recorded with and without the sonar enabled. Potential behavioural responses to the sonar being switched on were examined as follows: For each dive in which the sonar operated continuously for at least 10 s (hereafter referred to as an exposure dive), dive characteristics including descent rate, dive duration and diving depth were quantified and compared with the closest dive during which the sonar was turned off (i.e., control dive). A Kolmogorov-Smirnov two-sample independent test was used to test whether each dive characteristic differed significantly between exposure and control dives. In addition, short-term reactions to the sonar startup were investigated by computing the RMS of the norm jerk, i.e., the vector magnitude of the rate of change in the 3-axis acceleration (Ydesen et al., 2014), each time the sonar started pinging during a descent. The RMS jerk was computed over 5 s intervals with a 0.04 s averaging time and these RMS levels were compared immediately before and after the startup of the sonar in exposure dives.

Echograms were produced from echoes recorded by the tag by first removing the mean values of the in-phase and quadrature received signals, and then computing the echo magnitude (i.e., the square-root of the sum of the in-phase and quadrature components squared), synchronised to each outgoing ping. The background noise level in decibels, approximated by the 5 percentile of the echo level, was subtracted to obtain the echo-to-noise ratio (ENR) which was then displayed as an image. Stationary or slow moving, individual organisms appear in these displays as sequences of echoes with decreasing range in successive pings due to the forward movement of the seal (Johnson, 2014). To measure the time that targets were within the sonar beam, targets with a peak ENR greater than 25 dB that were insonified for at least 2 successive pings were selected manually. This ENR threshold was chosen to avoid counting brief reflections from e.g., turbulence or planktonic scatterers. For each high ENR target, the number of successive pings during which the target was visible (i.e., with ENR > 3 dB) was determined. All data processing used custom scripts in Matlab (version R2016a, Mathworks).

3. Results

3.1. Low frequency emissions

Despite design efforts to reduce low frequency emissions, measured third octave sound levels from the sonar were above the presumed SES hearing threshold (Fig. 3). Below 10 kHz, emissions were about 10 dB above threshold but 1–5 dB below the measured Southern Ocean ambient noise level, so are unlikely to be audible to free-ranging SES. However, emissions above 10 kHz depended on both the ping rate and power setting: at maximum power level and 25 Hz ping rate, sound levels were 10–20 dB above hearing threshold, whereas decreasing either the ping rate or the power led to levels close to the noise floor of the recording device. Extrapolating the measured ambient noise level to higher frequencies suggests that the sonar emissions are unlikely to be perceivable in typical ambient noise conditions except possibly at the highest ping rate and power setting. . Intermediate settings (i.e., half power, 12.5 Hz ping rate) were therefore used in the deployments on wild SES as a compromise between sonar performance and audibility.

3.2. Calibration and validation

The measured beam pattern of the sonar was broadly similar to that of a circular piston with the same effective cross section (Fig. 4, Kinsler and Frey, 1962) with −3 dB and −10 dB beamwidths of 3.4° and 5.4°, respectively. The measured source level and noise floor of the sonar (Table 2) indicate a maximum echo attenuation (i.e., the 2-way transmission loss, TL, minus the target strength, TS) of 100 dB for an echo to noise ratio of > 10 dB at full power. Tank tests conducted on live invertebrates showed the potential of the sonar tag to register echoes from small, individual organisms (Fig. 4). The measured target strength of a 3 cm long live shrimp detected at a range of 0.4 m from the sonar tag operating at low power was −78 dB which is broadly similar to the values obtained by Richter (1985).

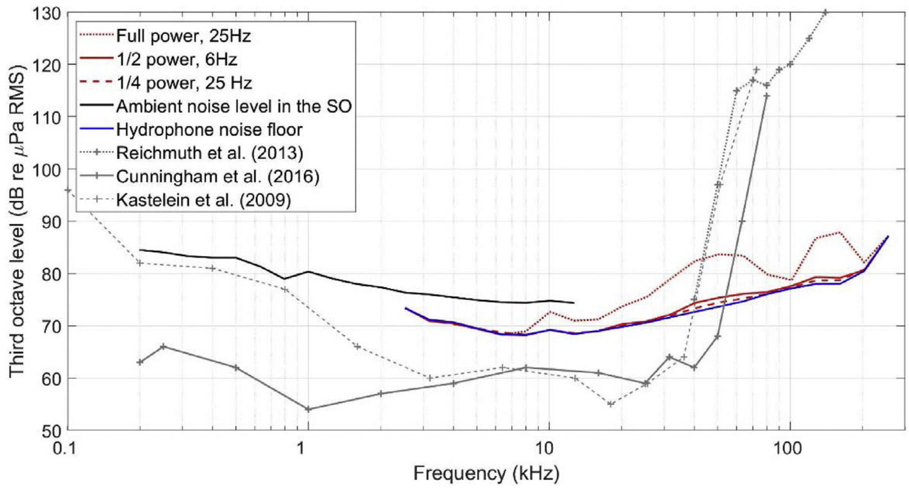

Fig. 3. Low frequency emissions of the sonar tag with different power and ping rate settings. The sound levels are compared against an ambient noise level measured in the Southern Ocean and harbour seal hearing thresholds (Kastelein et al., 2009; Reichmuth et al., 2013; Cunningham and Reichmuth, 2016). All levels are in dB re μPa RMS per 1/3 octave band.

3.3. Field deployments

Four sonar tags were deployed on post-breeding female SES in November 2017 of which only two devices were recovered in January 2018 (the other two animals returned to moult on inaccessible beaches in the Kerguelen Islands). The recovered tags recorded continuous high resolution movement and location data for 44 and 62 days. A software error prevented one tag from recording sonar data and limited the sonar collection of the other tag. Nonetheless, some 10 h of sonar data were recorded during 145 dives out of the 2371 dives performed by this animal.

Kolmogorov-Smirnov tests on the descent rate, duration and

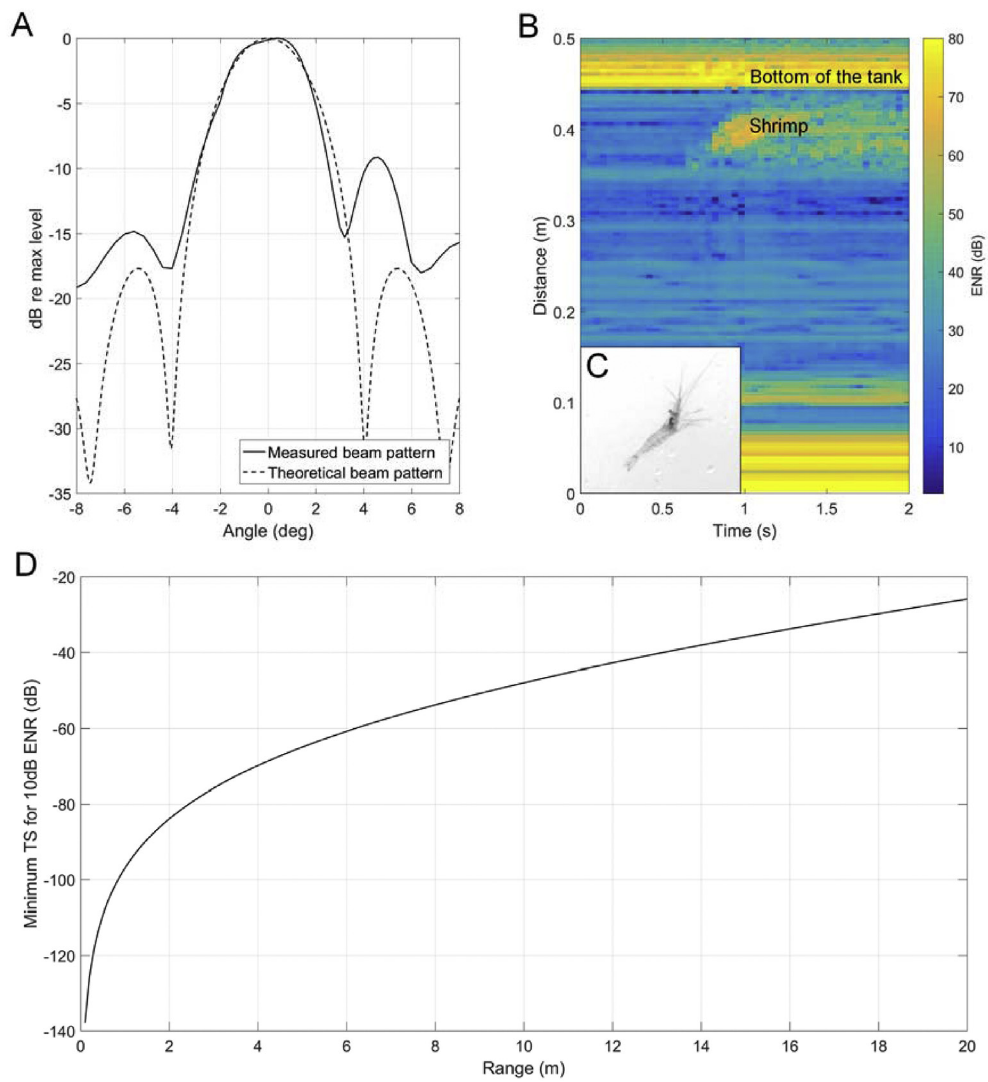

Fig. 4. A: Measured and theoretical beam patterns of the sonar tag. Echo levels were recorded from a target suspended 0.4 m from the sonar. The tag was mounted on a rotating platform and measurements were made in 0.2° increments. The theoretical beam pattern is for a circular piston with the same area as the transducer. B: Echogram produced from 50 consecutive pings showing the echo signature of a 3 cm long shrimp. Sonar settings: 1/4 power, ping rate 25 Hz. Time is on the horizontal axis and the vertical axis shows the distance from the sonar transducer (similar to an upside-down echosounder display). Echo to noise ratio (ENR) in dB is indicated by the colour. C: Still capture from the synchronised video camera showing the insonified shrimp (not to scale). D: Minimum target strength (TS) for an on-axis target as a function of range, to produce an ENR of > 10 dB with the sonar operating at half power. Transmission loss due to spherical spreading and absorption of 1 dB/m are assumed. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Sonar tag calibration results. Noise floor was measured in air. Source level was back-calculated from the on-axis echo level of a 0.1 mm radius stainless steel wire suspended 0.4 m from the transducer (expected TS -75 dB) and measured with the sonar operating at 3 different power settings. The on-axis sensitivity of the transducer is approximately −165 dB re V/μPa.

	Low (1/4 power)	Medium (1/2 power)	High (full power)
Noise floor (dB re μPa^2/Hz RMS)	26	26	27
Full band noise (dB re μPa)	79	79	80
Source level (dB re μPa RMS at 1 m)	184	187	189

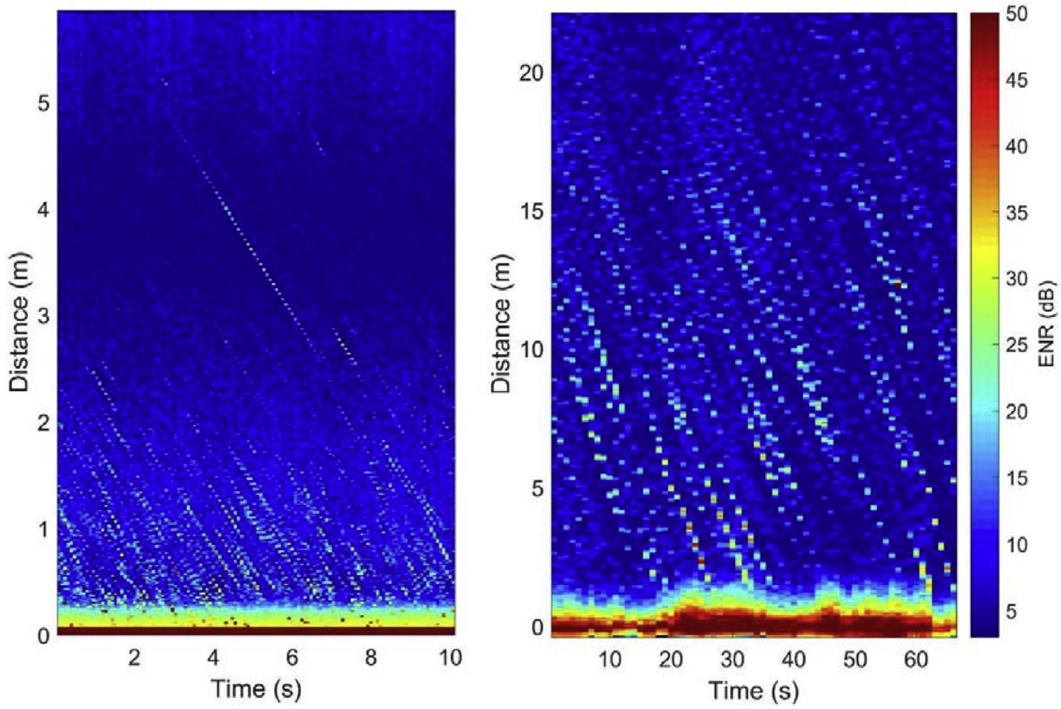

Fig. 5. Left: Echogram recorded by the sonar tag at 200 m depth on a descending southern elephant seal. Right: Echoes recorded passively by a DTAG deployed on a Blainville's beaked whale passing through a cloud of organisms (after Madsen et al., 2005). Note the different time and range scales in the two panels.

maximum depth showed no significant difference in dive parameters between dives with and without the sonar enabled. The maximum RMS jerk in 5 s intervals immediately before and after the sonar turned on was consistently lower than 100 ms^{-3} indicating no sudden head movement (such as a startle or flinch) or obvious change in behaviour when the sonar turned on. In comparison RMS jerk transients likely related to prey strikes were in the range 800–1500 ms^{-3}.

Sonar recordings from the SES contained frequent targets with range less than 2 m and occasional targets with ranges as far as 5 m (Fig. 5). The seal regularly swam through clouds of scatterers resulting in echograms similar to those obtained from passive acoustic tags on echolocating toothed whales (Madsen et al., 2005). The constant slope (i.e., closing speed, ms^{-1}) of echo traces in these echograms indicates stationary or slow-moving scatterers for which the forward movement of the seal dominates the closing speed. The duration that each target was insonified by the sonar, assessed by counting the number of visible echoes in 150 targets, was 4.6 ± 1.2 pings (0.4 ± 0.1 s at 12.5 pings/s).

Actively moving organisms were distinguishable from stationary objects by the varying slope of their echo trace (Supplementary Material). Synchronously sampled movement data helped to interpret the seal's behaviour towards these targets. The object in Fig. 6A was continuously insonified over the entire range of detection until very close to the seal's mouth yet the sensor data showed that the seal did not alter its diving behaviour nor produce a sudden acceleration while approaching it suggesting either that the seal did not attempt a capture or that the object was acquired with very little effort. In other cases, echo traces were associated with a sudden change in dive behaviour and a strong jerk peak (Fig. 6B and C), which may be due to head movement and/or the seal sucking the prey into its mouth (i.e. suction feeding - (Kienle and Berta, 2016)), leading us to interpret these as prey capture attempts. Prey strikes were also identifiable in some echograms by a change of closing speed in the echo trace. The high spatial resolution of the sonar allowed discrimination of closely separated targets such as the two distinct echo traces in Fig. 6B. The target trace in Fig. 6C appears to show a sequence of initial strike, prey escape attempt and final capture, illustrating the value of a high temporal resolution to track predator-prey interactions.

4. Discussion

Studying where free-ranging predators find prey and how they exploit it is especially challenging in the marine environment. Ship-based active sonar and animal-attached accelerometers provide valuable but incomplete and often decoupled information on prey availability and capture attempts by predators. Here, these two technologies are combined to produce a compact animal-attached sonar and movement tag that can directly monitor the biotic environment encountered by a predator as well as its fine-scale interactions with organisms within its close vicinity. Previous attempts to do this have either not been successfully deployed on animals (Miyamoto et al., 2004) or have been limited by size, power consumption and audibility issues (Lawson et al.,

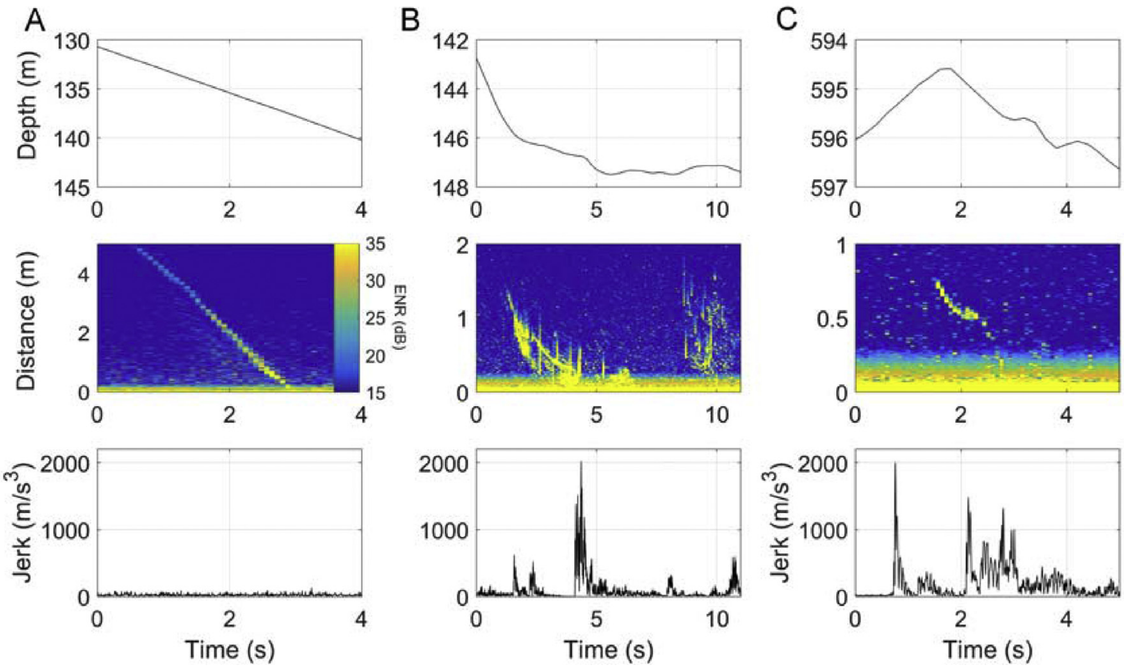

Fig. 6. Synchronised depth, sonar and acceleration data facilitate inferences on individual predator interactions with possible prey. Upper panels: dive profile; middle panels: echograms (vertical axis shows the distance of the target relative to the sonar transducer); bottom panels: jerk (i.e., rate of change in acceleration). A: A close target approach that is not associated with a depth change or acceleration suggesting that there is no attempt at capture. B: The high spatial resolution of the sonar allowed the discrimination of two close targets, or two glints from the same target, that were struck at by the seal. C: Target movement, indicated by a change in closing speed, suggests a sequence of strike, prey escape attempt and capture.

2015). In an attempt to overcome these problems, an integrated design approach was adopted, using a custom sonar transducer and low power sensor acquisition electronics. The resulting tag incorporates a sensitive short range sonar together with high rate motion and GPS sensors to provide data on where predators find prey, how they forage and with what success rate. With current settings and its built-in power supply of 3 AA batteries, the tag has the potential to record data during a period of 30 days, which can be modified by the user according to specific study requirements. We demonstrate with a deployment on a wild SES the ability of the device to record foraging interactions with high spatial and temporal resolution while producing very low sound levels that provoked no detectable behavioural responses by the animal carrying the instrument.

To reduce the size, frontal area and audibility of the sonar tag while maximising spatial resolution, a very high operating frequency (1.5 MHz) was chosen. Such high frequencies are rarely used for fisheries sonar, primarily because acoustic absorption would limit the range of ship-borne systems, but they are used to survey zooplankton where the short wavelength ensures scattering from small body sizes (Holliday and Pieper, 1980). This raises concern that the sonar tag may be strongly range-limited by acoustic absorption while at the same time being overly sensitive to small planktonic scatterers that will tend to mask echoes from the larger nekton targeted by SES. The short design range of the sonar tag reduces the impact of absorption: the predicted absorption in cold deep Southern Ocean water is about 1 dB per metre at 5 °C (Ainslie and McColm, 1998) summing to 12 dB for a target at 6 m range. In comparison, the transmission loss due to spherical spreading over the same distance is 31 dB (i.e., 40 $\log_{10}$(range)) making the absorption relatively less important. With the measured source level and noise floor of the sonar, a myctophid fish with a nominal TS of −50 dB (Benoit-Bird and Au, 2001) will, if on-axis, give an echo level that is 15 dB above the noise floor at a range of 6 m (i.e., SL-TL + TS-NF = 187-(31 + 12)-50-79 dB) which should be readily detectable. Tests of the sonar tag in an aquarium with pumped sea water showed considerable backscatter, presumably from planktonic organisms and turbulence in the water, but small invertebrates were nonetheless clearly visible in echograms (Fig. 4) albeit at short ranges limited by the tank dimensions. Data recorded by the tag on a SES showed less bulk backscatter, consistent with the lower micro-faunal density and absence of air bubbles in deep waters, and larger echoic objects were readily distinguished from the clutter of smaller targets throughout the operating range of the sonar (Fig. 5 and Supplementary Material).

A major advantage of using a high sonar frequency is that it makes possible the use of short transmit pulses which both reduce power consumption and give high spatial resolution. This is apparent on comparing echograms (Fig. 5) produced by the sonar tag (8 mm range resolution) with passive echograms computed for beaked whales (200 mm resolution, given their 270 μs duration clicks (Johnson et al., 2006)). Such high resolution enables discrimination of closely packed targets, making density estimates more precise. For organisms that react to the approaching seal by changing orientation rapidly, it may also be possible to distinguish echoes from multiple points along the body and thereby estimate prey size.

Another consequence of the high sonar frequency is a narrow beamwidth. At first glance, the 3.4° half-power beamwidth of the sonar tag may seem too narrow to be effective in tracking prey targeted by an agile predator. However, on animals such as seals that can be restrained for tag attachment, the tag may be rigidly mounted on the head, leading the narrow beam to be co-directed both with the sensory systems of the animal (the eyes and whiskers) and with the direction of approach towards prey. Moreover, the beam moves as the head moves, providing a wider effective field of view as the animal scans its surroundings. The narrow beam also reduces clutter and increases sensitivity: a 3.4° beam has a directivity index (DI) of 35 dB (Lurton, 2002), where the DI characterises the increase in on-axis transmit level and receive sensitivity compared to an omnidirectional transducer. Beamwidth depends on both the operating frequency and the transducer dimensions which are, in turn, limited by the size of the tag so that using a lower frequency would mean a wider beam. The larger (100 mm diameter) transducer used by Lawson et al. (2015) gave a beamwidth of 8° at their

200 kHz operating frequency. However, our smaller transducer size (15 × 15mm) would lead to a beamwidth of 26° and a corresponding DI of 17 dB at 200 kHz implying a 36 dB loss in echo-to-noise ratio for on-axis targets and the same power output (i.e., 35-17 dB for both transmit and receive). Such a wide beam would also result in an increased sensitivity to objects that are not directly ahead of the animal and which therefore show a variety of closing speeds. This could lead to ambiguity in judging whether an organism is itself moving away from the predator or simply has a lower approach speed because it is off the direction of travel. Thus our results on SES suggest that a narrow beam is effective in providing clear echoic information about the organisms approached and targeted by this deep water predator.

Modern fisheries sonars use multiple beams or frequencies to distinguish species but neither technique is currently compatible with the size constraints of an animal-borne sonar tag leading us to implement a simple single-beam sonar. Instead we designed the tag to use a high ping rate, inspired by toothed whale biosonar in which fast clicking yields detailed information on prey organisation, movements and size (Johnson et al., 2008; Wisniewska et al., 2016). The tag also samples wide bandwidth motion sensors synchronously with the sonar as a means of inferring whether echoic objects were targeted for capture by the seal. Data from the SES deployment of the sonar tag allowed us to test the effectiveness of these design strategies. Although limited to a single individual and a short operating time, the sonar recordings demonstrated the capability to measure the biotic density encountered by the predator, to sample prey escape behaviour, and to track predator strikes at prey. On average, echoic objects were detectable by our tag for just 0.4 s as they entered and exited the sonar beam, and so many would have been missed at the 1 Hz ping rate used by Lawson et al. (2015) despite the wider beam of that device. This highlights that a high ping rate is needed to track close range targets in a narrow beam as has been found for toothed whale biosonar (Jensen et al., 2018). The high ping rate used here also enabled detection of actively moving targets, e.g., exhibiting avoidance behaviour to the approaching seal. The synchronous movement sensors led to more definitive inferences about the fate of these targets: in several instances, organisms were tracked up to a few centimetres from the seal's mouth where a strong accelerative movement of the seal signalled a capture attempt. Sudden disappearance of the echo at this moment could be a robust indication of capture success, an inference which has been difficult to obtain reliably on marine predators (Dragon et al., 2012; Jouma'a et al., 2016; Le Bras et al., 2017).

An inevitable by-product of the pulsed signals generated by a sonar is sound emission at low frequencies which could be potentially audible to the tagged animal. This issue was identified by Lawson et al. (2015) where despite using a 200 kHz centre frequency which is well beyond the hearing range of pinnipeds, the authors measured low-frequency emissions from their sonar which would be audible. Lawson et al. (2015) sought to address the problem of audibility by reducing the output power of the sonar, and therefore the prey detection range, such that low frequency emissions were approximately 40 dB above the hearing threshold of northern elephant seals. No strong response to the resulting sonar emissions was found in that study either in terms of dive behaviour or stress hormone levels, although short-term or subtle responses could have passed undetected if they had little effect on dive parameters. Low frequency emission is a challenging design problem because the switched drive circuit which gives the most power-efficient transmitter also produces the most low frequency noise. The high operating frequency and incorporation of a passive filter in our design helped to reduce emissions to within 20 dB of published pinniped hearing thresholds. Programmable ping rate and output power settings gave us further flexibility in resolving the trade-off between audibility and sonar data quality. Given the relatively noisy acoustic environment in the windy Southern Ocean (Vinoth and Young, 2011; Cazau et al., 2017) we chose sonar settings (half power and 12.5 Hz ping rate) for which emissions would be no more than about 10 dB above the presumed hearing threshold and close to the prevailing ambient noise levels experienced by SES. As in Lawson et al. (2015), we found no evidence of reactions to the sonar with these settings, neither in terms of short-term acceleration nor longer-term dive behaviour suggesting that the low-level emissions from the tag had minimal impact on the animal.

The sonar settings chosen for low audibility restrict the sensitivity and temporal resolution of the sonar raising the question of whether useful information is being missed. Although echoes were detected up to the 6 m maximum range acquired by the sonar receiver, a higher power level would enable a longer sensing range if the receiving duration was extended accordingly. However, this would increase memory use per ping and therefore shorten recording times. Given the location of the tag on the head of the seal, a 6 m range seems sufficient to sample the organisms in the water mass immediately ahead of the seal and therefore available for capture. A longer range may be needed on species for which the tag must be mounted further back on the body. The ping rate of 12.5 Hz was found to be sufficient to track prey movements relative to the predator including escape attempts. However, using a still faster ping rate would enable tracking of rapid prey responses and give more accurate escape speed estimates at the cost of shorter recording duration. A higher ping rate may also allow detection of prey locomotory movements in taxa for which this leads to a modulation in target strength. The rate of these movements can give an indication of maximum prey size (Wisniewska et al., 2016).

In addition to detailed information about predatory interactions, an animal-borne sonar tag offers a means to sample biological conditions as a function of depth. The stereotyped deep-diving behaviour of SES over foraging trips that can cover 1000's of km enables collection of dense 3 dimensional data that would be extremely expensive to collect by a ship-borne echosounder. The sonar tag therefore provides a biological complement to temperature and salinity sampling tags on SES that have contributed much of the physical oceanographic data available from the Southern Ocean (Biuw et al., 2007; Charrasin et al., 2008; Fedak, 2013). The capability to record detailed echoic information over a well-defined water volume for extended time intervals opens the possibility of estimating the absolute density of organisms as a proxy for productivity akin to a video plankton recorder (McGillicuddy et al., 2007). The sampling volume of the sonar is defined by its beamwidth and the range limit of the receiver: with a 3.4° beamwidth and 6 m range limit, this volume is 0.2 m^3. The number of echoic targets in this volume could be quantified in terms of backscatter strength but can also be counted directly from the echogram taking advantage of the relatively high temporal and spatial resolution of the short-range sonar. This results in a density measurement in organisms per m^3 the accuracy of which is independent of the depth of the tagged animal. In comparison, a fisheries sonar deployed from a ship (but not a robotic vehicle, e.g., Benoit-Bird et al., 2017) must operate at a significantly lower frequency to sample the depth range attained by SES, and the concomitant lower resolution is unlikely to permit detection of individual small organisms throughout the depth range. As a consequence, a shipboard survey would likely need to quantify volume integrated backscatter intensity to estimate organism density requiring a species dependent calibration (Horne and Clay, 1998; Horne, 2000). On the other hand, a ship-based survey has the important advantage of providing a larger context on the distribution of prey which is lacking in an instrument attached to an animal. However, the small size and long duration of the sonar tag may also make it feasible to deploy as a productivity sensor on ocean gliders enabling directed surveys at the scale of ocean basins.

The combination of high resolution sonar and movement sensors in a tag therefore facilitates a broad range of ecological studies in the marine environment that have been hitherto difficult to conduct. The tag is potentially suitable for use on any large marine predator including baleen whales, diving birds, fish and sharks once logistical difficulties associated with attachment, placement with respect to the mouth, and transducer orientation have been solved, while further miniaturisation would be required to allow deployment on smaller animals. By recording dense information on the behaviour and movements of predators linked with the biological environment they encounter, the tag will provide information from the predator's perspective on prey availability, selection and capture manoeuvres. Moreover, individual variations in foraging behaviour in relation to biotic density will potentially help understand how populations of marine predators may be impacted by environmental changes.

Ethics statement

Ethical approval for the IPEV fieldwork was provided by the French Committee for Polar Environment and the University of St Andrews Ethics in Animal Use Committee.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2019.04.007.

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