open science

# A novel animal-borne miniature echosounder to observe the distribution and migration patterns of intermediate trophic levels in the Southern Ocean <br> Martin Tournier, Pauline Goulet, Nadège Fonvieille, David Nerini, Mark <br> Johnson, Christophe Guinet 

## To cite this version:

Martin Tournier, Pauline Goulet, Nadège Fonvieille, David Nerini, Mark Johnson, et al.. A novel animal-borne miniature echosounder to observe the distribution and migration patterns of intermediate trophic levels in the Southern Ocean. Journal of Marine Systems, 2021, 223, pp. 103608. 10.1016/j.jmarsys.2021.103608 . hal-03342311

HAL Id: hal-03342311
https://hal.science/hal-03342311
Submitted on 2 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

A novel animal-borne miniature echosounder to observe the distribution and migration patterns of intermediate trophic levels in the Southern Ocean

Martin Tournier ${ }^{1}$, Pauline Goulet ${ }^{2}$, Nadège Fonvieille ${ }^{1,3}$, David Nerini ${ }^{3}$, Mark Johnson ${ }^{4}$, Christophe Guinet ${ }^{1}$<br>${ }^{1}$ Centre d'Etudes Biologiques de Chizé, CNRS-La Rochelle Université, UMR 7372, 79360 Villiers-en-Bois, France<br>${ }^{2}$ Sea Mammal Research Unit, University of St Andrews, St Andrews, Fife KY16 8LB, UK<br>${ }^{3}$ Aix-Marseille Université, CNRS/INSU, Université de Toulon, IRD, Mediterranean Institute of Oceanography UM 110, 13288 Marseille cedex 09, France<br>${ }^{4}$ Aarhus Institute of Advanced Studies, Aarhus University, Høegh-Guldbergs Gade 6B, 8000 Aarhus C, Denmark<br>\section*{Highlights:}<br>- A novel sonar tag provides an acoustic scan of the elephant seal environment<br>- The sonar tag is able to detect common features such as the diel vertical migration of small organisms<br>- Contrasting oceanographic conditions affect the vertical distribution and abundance of midtrophic level organisms<br>- Areas of high particle abundances were observed over 500 m , potentially corresponding to marine snow events<br>\section*{Abbreviations:}<br>DSL: Deep-Scattering Layer, DVM: Diel Vertical Migration, FPCA: Functional Principal Component Analysis, KER: Kerguelen Islands, PV: Peninsula Valdes, MTL: Mid-Trophic Level, NSAF: Northern Sub-Antarctic Front, PCAs: Prey Capture Attempts, SAF: SubAntarctic Front, SO: Southern Ocean

## Abstract

Despite expanding in-situ observations of marine ecosystems by new-generation sensors, information about intermediate trophic levels remains sparse. Indeed, mid-trophic levels, while encompassing a broad range of zooplankton and micronekton organisms that represent
a key component of marine ecosystems and sustain large and diverse communities of marine predators, are challenging to sample and identify. In this study, we examined whether an animal-borne miniature active echosounder can provide information on the distribution and movements of mid-trophic level organisms. If so, such a sonar tag, harnessing the persistent diving behaviour of far-ranging marine mammals, could greatly increase the density of data on this under-studied biome. High-frequency ( 1.5 MHz ) sonar tags were deployed simultaneously with oceanographic tags on two southern elephant seals (Mirounga leonina), at the Kerguelen Islands and Valdés Peninsula (Argentina), and recorded acoustic backscatter while the seals foraged respectively in the Indian and the Atlantic sectors of the Southern Ocean. The backscatter varied widely over time and space, and the seals attempted to capture only a small fraction of the insonified targets. Diel vertical migration patterns were clearly identifiable in the data, reinforcing our confidence in the ability of the sonar tags to detect living mid-trophic organisms along with possibly sinking biological detritus. Moreover, CTD tags attached to the same animals indicated how the abundance, size distribution, and diel migration behaviour of acoustic targets varied with water bodies. These preliminary results demonstrate the potential for animal-borne sonars to provide detailed in-situ information. Further validation effort will make it a valuable tool to refine the estimation of carbon export fluxes as well as for assessing the variation of mid-trophic level biomass according to oceanographic domains and seasons.

Keywords: sonar tag, diel vertical migration, micronekton, marine acoustics, biologging, functional data analysis.

## Introduction

Marine ecosystems are manifesting multi-level responses to oceanographic changes related to global warming, from a suspected shift in phytoplankton communities (Montes-Hugo et al. 2009, Barton et al. 2016) to top-predator population-size variations (Bost et al. 2015, Sydeman et al. 2015). However, assessment of the biological consequences of a changing ocean is hampered by a scarcity of information on the intermediate or mid-trophic levels (MTLs) (Hidalgo and Browman 2019). The crucial MTLs linking phytoplankton to upper
marine predators are composed of zooplankton and micronekton (e.g. mesopelagic fishes and squids, euphausiids, siphonophores) (Handegard et al. 2009, Escobar-Flores et al. 2018) presenting a wide range of body structures (e.g. crustaceans with a chitinous exoskeleton, bony or gelatinous organisms), sizes (from a few millimetres for euphausiid larvae to a meter for some siphonophores) and behaviours (e.g. planktonic or nektonic) (Sutton 2013, St. John et al. 2016, Kloser et al. 2016). The mesopelagic biome, comprising a third of the globalocean volume, is one of the largest but least-known marine habitats (Reygondeau et al. 2018), and considerable uncertainties remain regarding the total biomass of mesopelagic fishes. Estimates of this biomass range from 2 to 20 gigatons (Irigoien et al. 2014, Kloser et al. 2016, Proud et al. 2019), the latter being some 100 times the annual catch of all existing fisheries ( Anderson et al. 2019, Hidalgo and Browman 2019). The resulting scantiness of information on the structure and turnover of mesopelagic food webs hinders accurate predictions about the consequences of environmental changes or industrial fishing on this biome, and on the numerous higher-level predators that it supports.

Information about the distribution and composition of MTLs is also critical for improved estimates of carbon export fluxes. The Southern Ocean (SO) in particular plays a crucial role in carbon sequestration, accounting for approximately $40 \%$ of global anthropogenic $\mathrm{CO}_{2}$ uptake (DeVries 2014). The biological carbon pump operating in the SO remains only partially explained due to the difficulty in monitoring its biotic environment, although recent programmes such as KEOPS or CROZEX have proposed, in some parts of the SO, a quantification of biological processes leading to carbon export (Blain et al. 2007, Pollard et al. 2009, Salter et al. 2012, Le Moigne et al. 2016). The biological carbon pump begins with primary production performed by phytoplankton, which represents the main source of organic carbon exported to mesopelagic layers (Buesseler et al. 2007). Gravitational sinking of
phytoplankton as individual cells and aggregates is responsible for a significant portion of carbon export in the SO (Leblanc et al. this issue, Laurenceau-Cornec et al. 2015a). However, alternative biological mechanisms transporting the carbon trapped by phytoplankton to deep waters are still poorly understood as they are likely to rely mainly on the behaviour of MTLs.

Of particular note with regard to MTL behaviour is the phenomenon of diel vertical migration (DVM), which is performed by a large majority of MTL organisms, from small zooplanktonic organisms to mesopelagic fish (Hays 2003, Sims et al. 2006, Watanabe et al. 2006), and is found across all oceans (Behrenfeld et al. 2019). Representing the largest daily migration observed in the biosphere (Brierley 2014), and presenting differences in migration patterns depending on both the species and its life stage (Atkinson et al. 1992), DVM participates in a massive carbon transfer across the mixed layers of the ocean (Buesseler and Boyd 2009, Cavan et al. 2015, Aumont et al. 2018, Hernández-León et al. 2020). This vertical migration pump results from MTL zooplankton and micronekton rising to the euphotic zone near the surface where they generally feed at night. Carbon acquired at the surface is then actively transported during the day to deeper waters where MTLs release rapidly-sinking faecal pellets that form large aggregates (Belcher et al. 2017). This biological detritus gravitational flux, in addition to active transport by MTL organisms, increases the transfer and transformation of carbon (Cavan et al. 2015, Belcher et al. 2017, Cavan et al. 2019b), and contributes directly to deep carbon sequestration. Preliminary estimates suggest that MTLs may be responsible for about a quarter of carbon transport to deeper waters, though large uncertainties persist and regional variability exists (Boyd et al. 2019). Achieving better quantification of the role played by MTLs in the biological carbon pump is therefore still one of the current challenges in oceanography.

Although advances in marine acoustics, especially in multi-frequency and multi-beam echosounders, have resulted in a coarse classification of micronektonic organisms (Escobar-

Flores et al. 2019), the understanding of MTL taxonomic composition, biomass, and behaviour remains limited due to the difficulty of sampling. This is especially true for the SO where logistics and weather constrain ship-based operations. Consequently, acoustic and nettow surveys of the mesopelagic layer, such as krill stock monitoring surveys (Fielding et al. 2014, Tarling et al. 2018, Manno et al. 2020), remain sparse for most SO sectors. In addition, although such surveys are highly valuable, they inevitably suffer from limited spatial and temporal coverage (Kloser et al. 2009). Each method also has its own sources of bias. Acoustic surveys are sensitive to regional differences in the relative abundance of mesopelagic species or in their body structure (Dornan et al. 2019). Net-tow sampling, which is often used to validate hydroacoustic surveys, suffers from an underestimation of energetic mesopelagic fishes that are able to escape the trawl (Kaartvedt et al. 2012, Proud et al. 2019), and rarely has sufficient spatial resolution to reveal mesoscale structuring (Davison et al. 2015). Although continuous ship-based acoustic surveys can sample over these larger spatial scales, they generally lack simultaneous sampling of fine-scale in-situ oceanographic profiles to investigate the coupling between physical and biological processes (Proud et al. 2019).

Helping to fill in the gaps left by ship-based surveys are autonomous ocean profilers (e.g. ARGO profilers and gliders), whose development has enabled extensive sampling of the physical properties of the water column. Recently some profilers were equipped to make continuous recordings of acoustic backscatter (Haëntjens et al. 2020). However, the relatively slow vertical movement of autonomous underwater robotic samplers may prevent reliable sampling of more rapid biological processes, such as the daily vertical migration of actively swimming larger-size micronekton species.

A creative approach to achieve dense sampling of physical oceanographic parameters in otherwise difficult-to-observe oceanographic regions has been to fit marine animals with
multi-sensor biologging tags so that they become ocean samplers (Fedak 2004, Hindell et al. 2016, Harcourt et al. 2019). Although this method does not provide systematic surveys, it offers the important advantage of providing simultaneous information about marine predator foraging ecology along with oceanographic conditions such as temperature, salinity or light level (Biuw et al. 2007, Guinet et al. 2014).

Biologging tags with sensors for temperature, salinity, chlorophyll- $a$ concentration, and dissolved oxygen have yielded fine-scale descriptions of oceanic processes in remote areas (Roquet et al. 2013, Bayle et al. 2015, Bailleul et al. 2015). Southern elephant seals (Mirounga leonina, SES hereafter) are particularly useful for such sampling as they perform long-range foraging trips with continuous diving to mesopelagic depths, routinely reaching 1000 m and in rare cases exceeding 2000 m (Roquet et al. 2009, Hindell et al. 2016). In recent years, animal-borne sensors have been developed to quantify the marine organisms encountered by deep-diving mammals. High-resolution accelerometers have been used to detect prey capture attempts by SES (Guinet et al. 2014, Jouma'a et al. 2016), providing critical insight into interactions between these top predators and the MTLs. Importantly, this approach has opened the possibility of indirectly mapping the distribution of mesopelagic prey targeted by SES, in particular myctophid fish (Cherel et al. 2008, Vacquié-Garcia et al. 2015). While more detailed information on MTL prey encountered by northern elephant seals has been collected by camera tags (Naito et al. 2013), the high energy consumption of these devices has limited the amount of data that can be collected (Watanabe and Takahashi 2013). More recently, measurements of bioluminescence from some SES prey (Vacquié-Garcia et al. 2017, Goulet et al. 2020) have provided a means to distinguish classes of prey and their distribution. However, although these biologging approaches provide insight into the specific MTL prey targeted by SES (Yoshino et al. 2020), they offer little general information about the distribution of other MTL organisms. New perspectives are now offered by the miniature
animal-attached echosounder used in our study. This sonar tag was deployed on female SES to study mesopelagic predator-prey interactions (Goulet et al. 2019). It can detect echoes from small organisms (ranging from a few millimetres to tens of centimetres) over a short distance (up to 6 m ) in front of the seal, resulting in detailed profiles of sonar backscatter as the animal dives. Here, we use data recorded by the tag on two SES females to assess the biological conditions as they forage in contrasting oceanographic regimes off Patagonia (Argentina) and the Kerguelen Islands. The goal of this study is to assess whether hydroacoustic data collected from deep-diving SES can contribute to understanding pelagic ecosystems in the SO by: 1) measuring the variation of MTL abundance and acoustic size within the water column; 2) documenting the diel vertical migration of MTLs; and 3) mapping spatial variations in MTL abundance and behaviour, and their relationships to local oceanographic conditions. While the aim of the present study is not to quantify carbon fluxes, which is beyond the scope of this paper and not possible at present, it can provide qualitative information on some processes that are involved in controlling these fluxes.

## Material and methods

1. Study sites and logger deployments

In October 2018, adult female SES breeding at Peninsula Valdes (Argentina, $42^{\circ} 57^{\prime}$ S, $63^{\circ} 59 \mathrm{~W}$, abbreviated to PV) and on the Kerguelen Islands $\left(49^{\circ} 21^{\prime} \mathrm{S}, 70^{\circ} 13^{\prime} \mathrm{E}\right.$, abbreviated to KER) were fitted with biologgers using a standard procedure (McMahon et al. 2008). The animals were captured and anaesthetised with an injection of Zoletil100 (1:1 mix of tiletamine and zolazepam). In each study location, three biologging devices were glued to the animal's fur using quick-setting epoxy (Araldite AW 1201): a head-mounted sonar tag (Goulet et al. 2019), a back-mounted Satellite Relayed Data Logger (CTD-SRDL, Sea Mammal Research

Unit, St Andrews, UK), and an ARGOS transmitting tag (SPOT, Wildlife Computers, USA). The CTD-SRDL recorded conductivity, temperature, and pressure at 1 Hz while also sending summary data via ARGOS messages. The SPOT tag was included to facilitate recovery of the tags when animals returned to land, in case the CTD-SDRL had stopped transmitting. At-sea movements were monitored using the ARGOS satellite-tracking system, and the loggers were recovered as soon as the seals hauled out for moulting. The three loggers had a total mass of under 800 g , representing less than $0.5 \%$ of the animal weight, and should therefore have minimal impact on the survival or foraging success of equipped animals (McMahon et al. 2008).

The sonar tag recorded high-resolution sonar, location, and movement data. GPS positions were obtained at each surfacing. Pressure and triaxial magnetometer data were recorded at a sampling rate of 50 Hz while triaxial acceleration was recorded at 200 Hz . The active sonar had a centre frequency of 1.5 MHz and emitted $10 \mu$ s pings at a rate of either $12.5(\mathrm{PV})$ or 25 (KER) pings per second, with a source level of approximatively 187 dB re $1 \mu \mathrm{~Pa}$ at 1 m (Goulet et al. 2019). Sound was transmitted and received via a transducer with a -3 dB beamwidth of approximately 3.4 degrees. The complex returning signal was demodulated and the resulting baseband signal was sampled at 192 kHz for intervals of 8 ms following each ping, giving a spatial resolution of about 3.9 mm and a maximum range of 6 m (see Goulet $e t$ al. 2019 for device specifications). The sonar transducer on the tag has a rigid backing which does not compress with depth. Therefore, we assume that the performance of the transducer remains reasonably constant over the depth range explored by SES. More in-depth validation approaches are still in progress and will be the subject of future papers

In order to extend the recording duration, the sonar was switched on and off on a regular basis with a cycle of 5.5 h on and 5.5 h off for Kerguelen and 24 h on and 24 h off in Argentina. Both protocols provided a homogenous sampling of all periods of the day throughout the
recording duration. The sonar was activated at depths deeper than 50 m for Kerguelen and 15 m for Argentina. The CTD and sonar tags were synchronised by matching the depth data sampled by their respective pressure sensors following Le Bras et al. (2016).
2. Sonar data processing and analysis

The echo level was calculated by first removing the mean values of the in-phase and quadrature received signals, and then computed as the root-mean square of these two signals. Echogram images were constructed from the log of the echo level, with each pixel representing a sonar sample (i.e. $1 / 192000 \mathrm{~s}$ or 3.9 mm of round-trip travel). Similar to echograms obtained from traditional fishery echosounders, the vertical dimension of the echogram represents the range to targets while the horizontal dimension represents successive pings (Figure 1). Hereafter, any insonified object giving an echo will be referred to as a scatterer, regardless of its nature or size. From the echograms, the two following metrics were derived:

## Scatterer count

The scatterer count is the number of pixels for which the echo level exceeds a threshold chosen to differentiate actual scatterers from background noise. For each sonar-on phase of the sonar data, the background noise level was calculated from the signal contained in the last meter of the sonar range. A visual inspection of the sonar data indicated that targets were rarely evident at this range due to high spreading and absorption losses. The echo level of all pixels in the $\sim 4.6-5.6 \mathrm{~m}$ range were therefore fit to a Rayleigh distribution to characterise the noise floor, and the detection threshold was set to the 99.9 percentile of this distribution (Figure 2, Supplementary Information). The scatterer number ( SN ) was then calculated as the total number of pixels above the detection threshold for each sonar ping, averaged over a 2 -second window, resulting in a proxy for
absolute particle abundance. Scatterer abundance was then calculated as the standardised SN divided by the nominal sampled volume, resulting in an approximate scatterer abundance value, i.e. number per $\mathrm{m}^{3}$. The sample volume was taken as the truncated cone of the sonar beam in the $1-1.5 \mathrm{~m}$ range assuming a $3.4^{\circ}$ beamwidth.

## Maximum apparent target size

Acoustic studies often use the echo level as a proxy of the target size. In this study, it is not possible to ascertain the position of small echoic targets in relation to the beam axis, meaning that the echo level is dependent on the location, with the echo strength of a given target decreasing as its position departs from the centre of the beam, and varying with the orientation of the targets as well as their size and composition. However, the high spatial resolution of the sonar data allowed measurement of the echo duration, which is related to the target cross-section, shape and composition (Burwen et al. 2003). Apparent size was therefore calculated for each detected scatterer using the duration $\Delta t(s)$ for which the echo intensity was above the detection threshold. This was converted to distance to give a size estimate in metres: $\Delta \mathrm{t} * \mathrm{ss} / 2=$ size, with ss $=$ sound speed in seawater, taken as a constant $1500 \mathrm{~m} / \mathrm{s}$ throughout the record. For each 2 -second period, the scatterer with the largest apparent size was retained as the Maximum Apparent Size (MAS). Although the smallest organic particle size detectable by the sonar tag is about 1 to 2 mm (L. Petiteau, personal communication, Supplementary Information, Figure 4), the smallest apparent size that can be calculated is 3.9 mm due to the limited sonar resolution. This spatial resolution allows, in theory, the detection of most mesozooplanktonic organisms of high ecological importance such as calanoids (e.g. Rhincalanus gigas), euphausiids (e.g. Euphausia vallentini), hyperiids (e.g. Themisto gaudichaudii), gelatinous organisms (e.g. Rosacea plicata). Considering that the sonar tag is able to detect targets as small as 1 mm (see Supplementary Information), it is also probable that smaller copepods (e.g. Calanus
simillimus, C. acutus) contribute to the signal obtained. The apparent size is dependent on many factors including the distance, orientation and composition of the target, and its position relative to the beam axis, making this a noisy proxy for the real size. We therefore graded the MAS into two broad size classes based on the 'Sieburth-scale' plankton classes (Sieburth et al. 1978): the first class contained small scatterers with MAS up to 20 mm which we considered as mesoplankton-like objects. The second class contained objects with MAS ranging from 20 to 50 mm which were considered as small macroplankton. Objects with MAS larger than 50 mm were rare (representing $2.2 \%$ and $2.9 \%$ of the signal for PV and KER respectively) and were often associated with a jerk (i.e. rapidly changing acceleration signal) which most likely indicates a prey capture attempt (Ydesen et al. 2014). These large targets are therefore likely to be macronekton, including the mesopelagic fish and squids preyed upon by SES (Daneri and Carlini 2002). This latter size class was therefore removed from the analysis to focus on potentially zooplanktonic organisms.

The above sonar metrics were calculated over non-overlapping 2 -second windows and extracted at distances ranging from 1 to 1.5 m ahead of the elephant seal's head. The lower distance limit was chosen to be beyond the sonar near-field and yet close enough to potentially detect echoes from the full-size range of MTL organisms. The 0.5 m analysis range was a trade-off between a narrower range, which may lead to too few detections for statistical evaluation, and a larger sampling range over which the probability of detection would vary substantially and hence complicate analysis.

Combining these acoustic metrics with the depth and GPS positioning collected by the tag resulted in a set of time-depth profiles similar to the oceanographic data profiles obtained with CTD loggers deployed on SES (Fedak 2004). The acoustic data were analysed with MATLAB R2019b, using custom functions.
3. Water body classification

A typology of the water bodies was established to investigate whether scatterer abundance on the one hand, and day versus night vertical distribution on the other hand, varied according to the oceanographic conditions encountered by the seal. Despite the good spatial and temporal resolution of SO fronts position estimation (Sallée et al. 2008), finer-scale structures, such as sub-mesoscale eddies or meanders, can have a strong impact on biological structure at a more local scale (Chapman et al. 2020), and by extension on the foraging behaviour of SES (Della Penna et al. 2015, Siegelman et al. 2019). Pauthenet et al. (2017) demonstrated that highresolution oceanographic data sampled by CTD tags on SES can be used to objectively define the geographical extents of water bodies by analysing joint variation of temperature $(\mathrm{T})$ and salinity (S). We therefore produced profiles of temperature and salinity for each dive, and fit B-splines to the sampled points. The structural variability between the splines was evaluated using the functional principal component analysis (FPCA) method developed by Ramsay and Silverman (2005), which is similar to a principal component analysis except that B-spline coefficients are used instead of raw data. Usage of FPCA enabled us to retain information about the shape of the temperature and salinity profiles (Nerini and Ghattas 2007, Pauthenet et al. 2017) while also allowing comparison between locations and individuals by smoothing out irregularities in data sampling.

Temperature and salinity profiles were generated on a constant vertical grid from 20 m to 200 m . This depth range was chosen to maximise temporal coverage especially at night when SES make shallower dives. As the objective of this analysis step was to describe near-surface mesoscale oceanic features that may influence MTL distribution, information loss on water structures below 200 m was not critical to our study. Dives shallower than 200 m were therefore removed. Oceanographic profiles were then decomposed on a B-spline basis with $c$ coefficients estimated by polynomial regression (see Ramsay and Silverman 2005). The

FPCA method was applied to the set of coefficients resulting in a compact representation of each profile according to its degree of similarity to the first principal components (PCs) generated by the FPCA.

Clusters of similar curves were discriminated using k-means supervised classification. The classification of temperature and salinity curves was achieved in the space of the 5 first PCs. These PCs account for more than $90 \%$ of the total inertia and $98 \%$ and $91.5 \%$ of the entire variability for KER and PV, respectively. Based on the Ward criterion, minimising the total within-cluster variance, we determined the number k of clusters for each SES track, with a maximum of five groups (Murtagh and Legendre 2014). Different clusters were considered as representing different water bodies and were then projected to their geographical positions along the track of the elephant seal, and did not necessarily correspond to the water bodies traditionally identified in these regions by other studies (Carter et al. 2008)
4. Analysis of vertical distribution

Each scatterer sampled by the sonar tag was assigned to a given water body as defined by the cluster analysis, according to the oceanographic conditions in which they were encountered. Although SES perform long-range foraging trips, they only travel a few tens of kilometres per day. This pace allows capturing large-scale phenomena such as mesozooplankton swarms (Fielding et al. 2014), and also the daily DVM, which is relatively consistent in the same water body (Behrenfeld et al. 2019). Migration behaviour, however, is suspected to be dependent on the organism type, which may lead to a time-varying vertical distribution of different-sized scatterers. We therefore determined the relative abundance in the water column of each scatterer size class (i.e. smaller than 20 mm and from 20 to 50 mm ) according to the period of the day. As the prey of SES performed DVM as well, and were shallower at night, the sampling effort for the lower depths was unbalanced between day and night. The
day period was determined using the sun angle for the current position of the seal (Guinet et al. 2014). Then, for each water body, the mean abundance of each scatterer class for each 10metre depth bin was calculated. The percentage difference between day and night means in each depth bin was computed to summarise the relative difference in migration behaviour for the two size classes.

The intensity of the DVM, for each water type, was determined by comparing the depth range of the migration (i.e. vertical amplitude), the total estimated abundance of scatterers present in the water column, and the mean acoustic size composition over the same depth range. For each profile, the depth with the highest abundance of scatterers was considered to represent the depth containing most of the organisms participating in the DVM. For each dive, the vertical distribution of the scatterers was determined by a simple peak-finding procedure. In most dives the vertical distribution of abundance was unimodal. In the case of a multimodal distribution, the largest mode was taken as the depth of maximum abundance. For each location, the range between the deepest and the shallowest abundance maximum was defined as the DVM range. Over these DVM ranges, the total abundance of scatterers was estimated by adding up interpolated values of the abundance for each depth meter. Finally, the mean size of the scatterers over the same depth ranges was compared between day and night in each water body. The numbers of samples for the different possible combinations of analysis categories (i.e. day period and water body) were unbalanced and heteroscedastic. Therefore, analyses assessing the effect of the period of the day and the water body were conducted using a multiway rank-based analysis (Rfit, Kloke and McKean 2012). Considering the large oceanographic differences between KER and PV regions, analyses were performed separately for each location, to compare DVM range, total abundance and size composition. Analyses were carried out with R software (R 3.5 R core team 2019).

## Results

1. Sonar observations

The maximum depth and mean ( $\pm$ standard deviation) diving depths were respectively 936 m and $413 \pm 136 \mathrm{~m}$ for KER individual with a mean diving depth of $321 \pm 109 \mathrm{~m}$ at night and $499 \pm 105 \mathrm{~m}$ during the day, and 1109 m and $392 \pm 249 \mathrm{~m}$ for PV individual with a mean diving depth of $218 \pm 108 \mathrm{~m}$ at night and $539 \pm 272 \mathrm{~m}$ during the day. A total of 313.8 and 408.8 hours of sonar data for KER and PV, respectively, were analysed. The abundance of scatterers ranged from 7 to 11940 scatterers. $\mathrm{m}^{-3}$ in KER (mean $=490 \pm 530$ and from 13 to 13800 scatterers. $^{-3}$ in PV (mean $=795 \pm 1465$ ). The echo signal was dominated by small objects ( $<20 \mathrm{~mm}$ ), representing $52.4 \%$ of scatterers in KER and $93.9 \%$ in PV, whereas the $20-50 \mathrm{~mm}$ size class represented $44.7 \%$ and $5.6 \%$ of the objects detected in KER and PV respectively.

The signals recorded by the sonar tag showed wide variability with time and depth (Figures 2 and 3). Scatterer abundance was the highest in the upper 200 m of the water column in both regions, for both day and night.

A portion of the KER recording (Nov $11^{\text {th }}-15^{\text {th }}$, Figure 2) showed an unusually high abundance of scatterers throughout the entire water column (from 70 m to 500 m ) (Figures 1.b \& 1.c). Over these 4 days, the mean size of the scatterers was $12 \pm 4.5 \mathrm{~mm}$.

A DVM pattern appeared to be the main driver of the vertical heterogeneity of the PV sonar signal data, in terms of scatterer abundance (Figures 3 and 5). This feature was not as clear for the KER dataset (Figures 2 and 4).
2. Classification of water bodies and scatterer size differences

A total of 2094 and 2819 dives for KER and PV, respectively, were used for the FPCA procedure (representing $96.9 \%$ and $85.5 \%$ of the available profiles; the remaining profiles did not reach 200 m ).

The first two principal components (PC) accounted for $80.1 \%$ and $89 \%$ of the variability in the individual profiles for PV and KER, respectively. CTD profiles were distributed within three water clusters for PV, with 226,1819 , and 364 profiles recorded for water clusters 1,2 , and 3 , respectively. The water bodies were distributed along both temperature and salinity gradients, with, for each location, colder and less salty waters for cluster 1 and warmer and saltier waters for cluster 3 (Figure 6).
3. Analyses of vertical distribution

When considering all scatterers regardless of size, the mean vertical extent of the abundance maximum ranged from 30 to 260 m in PV (Figure 7) while a narrower depth range from 70 m (i.e. the turn-on depth of the sonar) to 160 m was observed at KER (Figure 8).

For KER, there was a significant difference in the depth of peak abundance between day and night ( p -value $>0.001$ ), but no significant variation in depth between clusters (Figure 8). However, significant differences in scatterer abundance were found between water clusters (p-value $<0.005$ ). The mean size of scatterers differed significantly across water clusters, but no diel differences in this parameter were observed. Larger scatterer sizes were encountered in water clusters $1(14.7 \pm 5 \mathrm{~mm})$ and $2(14.8 \pm 3.7 \mathrm{~mm})$ compared to water cluster $3(11.8 \pm$ 3.8 mm ) (p-value < 0.001).

For PV, due to the 24-hour duty-cycle, no sonar profile was available for the night period of water cluster 1. For daylight hours, the depth of the main abundance peak differed significantly between the 3 water clusters ( p -value $<0.001$ ), with a deeper location in water clusters 2 and 3 compared to water cluster 1 (p-value < 0.001 ). Furthermore, the depth of the abundance maximum was significantly deeper during the day than the night for water clusters 2 and 3 (day: $113 \pm 56.5 \mathrm{~m}$, night: $42.3 \pm 18.9 \mathrm{~m}$, p-value $<0.001$, for water cluster 2; day: $126 \pm 49$ m, night: $40.1 \pm 13.1$ m, p-value $<0.001$ for water cluster 3; Figure 7b). The total number of scatterers, totalled over the depth range $30: 260 \mathrm{~m}$, was also significantly different between day and night for these water clusters (day: $194.10^{3} \pm 48.10^{3}$, night $185.10^{3} \pm 52.10^{3}$ for water cluster 2; day: $250.10^{3} \pm 68.10^{3}$, night $125.10^{3} \pm 46.10^{3}$ scatterers. ${ }^{-3}$, for water cluster 3, Figure 7c), but did not differ significantly between them. However, significant differences in scatterer size were found between the three clusters during the day ( p -value > 0.001 ) when they could be compared (water cluster 1: $15.4 \pm 6.6 \mathrm{~mm}$, water cluster2: $10.7 \pm$ 5.4 mm , water cluster 3: $11.5 \pm 5.4 \mathrm{~mm}$, Figure 7d).

The percentage difference between day and night for each scatterer size class in 10-metre depth bins showed a regular pattern of maximum abundance in upper layers at night, and in lower layers during the day (Figure 9). Depending on the water body, small (i.e. $<20 \mathrm{~mm}$ ) and medium-sized ( $20-50 \mathrm{~mm}$ ) scatterers exhibited some differences in their vertical distribution patterns (Figure 9).

Finally, clear differences were evident between KER and PV when looking at the complete depth range of 70 to 260 m that was sampled during the two surveys. Although the average scatterer abundance was similar in the two locations, PV data exhibited greater differences between the day and night vertical distributions of scatterers (p-value $<0.001$, Figure 10a). However, the mean size of scatterers was greater for $\operatorname{KER}(25.1 \pm 7.1 \mathrm{~mm}, \max =175 \mathrm{~mm})$ compared to PV data ( $17.4 \pm 6.2 \mathrm{~mm}, \mathrm{p}$-value $<0.05, \max =351 \mathrm{~mm}$, Figure 10b).

## Discussion

1. Horizontal and vertical heterogeneity in the acoustic backscatter

Two sonar tags were deployed in parallel on elephant seals from distinct oceanographic regions to assess their performance in capturing the sizes, vertical distribution and diel dynamics of MTL organisms. While a previous study showed that mesopelagic fish/squids were detected by the sonar tag during close prey encounters (Goulet et al. 2019), the present study quantifies the abundance of smaller acoustic targets, insonified by the tags as the seals dived through the water column. The primary aim of this study, presenting the first-ever application of the new biologger, is therefore to assess its potential for quantifying the vertical and horizontal distribution of the MTLs during the far-ranging foraging trips of SES.

It is important to note that using a free-ranging foraging animal as a sampling platform may ineluctably lead to some sampling bias. Foraging SES tend to target, and therefore oversample, highly dynamic areas such as fronts (Cotté et al. 2015, Della Penna et al. 2015, Rivière et al. 2019) characterised by complex hydrodynamic conditions, which are favourable for prey aggregation. In contrast, SES may tend to undersample areas of lower organism concentrations. However, this prey bias was reduced in this study by excluding portions of the sonar signal corresponding to prey catch attempts. As a result, only MTL organisms which were not targeted by the SES were investigated in the present study. Conversely, it should also be noted that some of the sampling biases associated with the use of non-biological platforms, such as gliders or Argo floats, are absent when using animal platforms. For example, Haëntjens et al. (2020) report a possible attraction of MTL organisms to the LEDs used on Argo floats, which is avoided by the sonar tag without LEDs. In addition, the slow
descent speed of a float is likely to cause a gathering of organisms in the echosounder beam, whereas the vertical speed of the elephant seal of about $1.4 \mathrm{~m} / \mathrm{s}$ prevents any flock formation.

A comparison between an underwater vision profiler and a sonar tag for measuring organism abundance has revealed the sonar tag's ability to detect organisms as small as 1 mm in diameter (unpublished data; Petiteau in prep., Supplementary Information). However, it is important to underline that the method used in this study cannot distinguish between several small, closely aggregated targets (i.e. separated by less than 3.9 mm , the spatial resolution of the sonar), and a single target of the same apparent size. Nevertheless, as the deep-water environments visited by foraging SES contain relatively few particles, the first scenario is rarely encountered, and should contribute only slightly to overall abundance estimates. Given the potential range of backscatter sources, the sonar tag data from SES in KER and PV likely include backscatter from a combination of objects whose nature cannot be determined, whether biological debris passively sinking to the ocean floor, or living organisms, some of them undertaking diel vertical migrations.

The main limitations being stated, we found that scatterers were more abundant and produced higher-intensity echoes in the upper part of the water column (i.e. above 250 m deep) in both locations. Temporal variations of the backscatter distribution were consistent with a daily cyclic movement in the water column corresponding to the daily migration of MTL organisms. However, this diel signal was not evident continuously throughout the datasets, and so is likely dependent on the nature of the scatterers present locally. Specifically, when the backscatter is dominated by small-size non-migrating items, we suggest that this could be indicative of biological detritus or else small-size non-vertically-migrating zooplankton, such as Calanus propinquus (Conroy et al. 2020), highly abundant in the eastern sector of the Kerguelen shelf (Carlotti et al. 2008).

We also found evidence that both the horizontal and vertical distributions of scatterers vary according to the oceanographic conditions encountered. Five distinct water bodies were identified along the seal tracks, corresponding closely with weekly estimates of SO fronts positions (Sallée et al. 2008). Only one of these water bodies, water body 3, corresponding to Sub-Antarctic Waters (SAW), was encountered by seals from both KER and PV. Each seal also encountered two other water types but these were distinct in each location.

For the PV seal, clear differences in the vertical distribution, abundance and size of scatterers were found between each oceanographic domain visited, evidencing a change in MTL community composition and/or abundance depending on the water body. The changes in water body along the track may indicate that the seal encountered sub-mesoscale oceanographic features. Such structures are frequently used by SES and are often linked with improved foraging conditions (Dragon et al. 2010, Della Penna et al. 2015, Siegelman et al. 2019). Currently, the datasets are too limited to investigate the commonalities and differences of scatterers among similar water bodies, or to investigate seasonal changes. We can nevertheless expect an increased number of deployments of this tag, and the large ranges covered by SES, to lead to studies comparing the different large-scale water bodies explored by SES.
2. Regional differences in sonar signal

In both study areas, the abundance of scatterers varied depending on the water body. For the PV seal, significantly higher scatterer abundance was found in water body 1 , which was close to the continental shelf, compared to the two other water bodies it encountered. This might be related to the highly productive waters of the Patagonian continental shelf, which receive nutrient-enriched inputs from the Malvinas current and support a large spring bloom (Lutz et al. 2018) with likely enhanced secondary production (Cepeda et al. 2018). However, the prey
catch rate of the seal is low within this water body compared to elsewhere along its track, suggesting that this high spring productivity may not lead to increased abundance of the prey targeted by SES, or with a delay, due to the temporal decoupling of primary producers and primary consumers (Latasa et al. 2014). Further offshore, within the Sub-Antarctic Front (SAF) northward inclusion, primary production tends to be lower and supports communities of small mesozooplankton with lower biomass (Thompson et al. 2013) - a tendency that appears to be supported by the sonar tag data, revealing fewer and smaller scatterers with a very clear DVM pattern.

Similarly, MTL abundance in KER differs according to water mass, with the lowest abundance observed for water body 3 and the highest for water body 1 . Water body 3 comprises profiles in the area around the North SAF and can be considered as a different bioregion than the other water bodies influenced by the subtropical regime (Godet et al. 2020). The warmer waters of this region tend to be associated with lower chlorophyll- $a$ concentration and overall lower productivity than the high-productivity shelf and off-shelf waters of the Kerguelen plateau (Godet et al. 2020). The high abundance of scatterers seen in water body 1 may be associated with these enriched plateau waters, with eastward advection by currents releasing soluble iron, and enhancing primary production (Robinson et al. 2016, Schallenberg et al. 2018).

Overall, a higher abundance of larger-sized scatterers was encountered in KER compared to PV waters while the DVM pattern is more obvious within the PV dataset. These findings exemplify the differences between these two distinct marine provinces (Longhurst 2010, Fay and McKinley 2014). Our results also highlight the wide variability in vertical distribution patterns of the MTLs, a finding consistent with recent fine-resolution studies (Pinti and Visser 2018, Conroy et al. 2020) and global ocean studies (Behrenfeld et al. 2019). More extensive
deployments of the sonar tag may therefore help improve our understanding of the environmental and biological factors that drive these differences.

## 3. Diel vertical migration

The current study also reveals fundamental differences in the vertical distribution and behaviour of zooplanktonic and micronektonic organisms according to their sizes. A dayscale cyclic vertical movement of a portion of the scatterers was evident in sections of the sonar recordings (see Figures $4 . \mathrm{b}$ \& 5.b) comprising an upward migration at dusk and a downward one at dawn. The presence of this diel pattern in our data confirms the ability of the sonar tag to detect mesopelagic organisms, such as macrozooplankton, or other small MTL organisms involved in the DVM.

The extent of the vertical migration recorded by the sonar tag in both regions, reaching 160 m deep in KER and 260 m deep in PV, does not match the migration range of mesopelagic fish such as myctophids, and squid (Davison et al. 2015, Bianchi and Mislan 2016, Béhagle et al. 2016, Kloser et al. 2016), which is also revealed by the day and night mean diving depth of the two seals. Therefore, the observed DVM likely represents the vertical movement of zooplankton (i.e. the prey of SES prey) although inferences about the size of scatterers from the sonar data require validation. However, the minimum spatial resolution of the sonar tag (approx. 3.9 mm ) means that smaller organisms will be lumped within the smallest size class resolved by the sonar tag. Nonetheless, the mean acoustic size ( 2 to 3 cm ) of the migrating scatterers, and the depth range at which they are detected, suggest large zooplanktonic organisms like euphausids. Indeed, the Kerguelen waters host high abundances of euphausids (Cuzin-Roudy et al. 2014, Koubbi et al. 2016, Godet et al. 2020) such as Thysanoessa macrura and Euphausia vallentini, both with an adult size close to 3 cm . The Argentinian Patagonian waters also host high densities of E. vallentini (Cepeda et al. 2018). This krill
species makes a diel migration between 100 and 250 m depth (Cuzin-Roudy et al. 2014), matching the vertical range of the migration detected by the sonar tag in this location.
4. A possible marine snow event recorded off Kerguelen

Between November $10^{\text {th }}$ and $14^{\text {th }}$, the sonar tag deployed in KER recorded anomalously high and constant scatterer abundances throughout the epipelagic layer to 500 m deep. This could have been caused by large concentrations of salps (Wiebe et al. 2010), and validation of the sonar tag is required to determine the typical echo signals generated by low-target strength targets such as salps and jellyfish. However, the homogeneous distribution along the vertical dimension could also indicate a mass sinking event of biological detritus, known as marine snow (Alldredge and Silver 1988, Turner 2015). Marine snow events follow periods of high productivity, when heavy phytoplankton cells and zooplankton faecal pellets sink downwards rapidly (Laurenceau-Cornec et al. 2015b). Some studies suggest that these events, occurring off the Kerguelen plateau twice a year during the seasonal blooms, represent, in the SO, one of the main contributions to the biological pump that exports particulate organic carbon (POC) to depth (Turner 2015, Rembauville et al. 2015). The spatial co-occurrence between such events and satellite-assessed POC from remote sensing may help resolve this question in the future (Tran et al. 2019).
5. Where is the Deep Scattering Layer?

A vast majority of the scatterers recorded by the sonar tags come from the epipelagic zone, whereas beneath 300 m , in the mesopelagic layer, echoes were scarce. One of the most notable acoustic features of the global ocean, the deep scattering layer (DSL), is therefore not immediately evident in the sonar tag data. The DSL, mainly composed of mesopelagic fish and squids (i.e. the main prey of SES), is found in the mesopelagic zone at a depth of around 400 to 500 m throughout the world oceans (Proud et al. 2018), and particularly in the SO
(Kloser et al. 2016, Béhagle et al. 2017). This depth is consistent with the mean diving depth of the SES, and the sonar tag's inability to detect the DSL as a clear pattern in the way that ship-based echosounders have been found to do, can possibly be explained by their different sampling resolutions. Ship echosounders are mainly designed to detect mesopelagic scatterers composed of organisms exceeding several centimetres while the high frequency sonar tag is well-suited to detect smaller-size organisms. Studies have established that the abundance of zooplankton and micronekton decreases linearly with size following a $\log / \log$ function (Heneghan et al. 2016)). Therefore, due to its narrow beam, the water volume sampled by the sonar tag is limited and may prevent the relatively low densities of micronektonic fish and squids from being properly assessed. In comparison, ship-based echo-sounders have a larger beam and are operated from the surface, leading to a much greater insonified volume of water at greater depths. Such sonars are well suited to sample bulk micronekton but are not so wellsuited to assess small-size and dispersed zooplankton. Therefore, these two approaches should be seen as complementary with one another. Nonetheless, the bottom phase of SES dives, and more specifically the depth of prey capture attempts (PCAs), provide a proxy for the DSL depth in the water column (Guinet et al. 2014, McMahon et al. 2019). Both the dive depth and the depth of PCAs, as inferred from acceleration transients recorded by biologging tags on SES, vary with a diel cycle, presumably tracking the daily vertical migration of components of the DSL (Figure 4.b and Figure 5.b). The sonar tags frequently recorded scatterers with a large apparent size simultaneously with PCAs. The focus of the study being smaller-size MTL organisms, and the time SES spend foraging being disproportionate, PCAs were excluded from this study. These larger scatterers however likely represent the DSL organisms targeted by SES and so provide some indication about the density and size distribution of the DSL that is the topic of a companion paper (Goulet et al., in prep).

## Conclusion

Although the sonar tag, aided by the persistent diving behaviour of SES, shows considerable promise for in situ studies of the biotic environment of the deep ocean, namely the distribution and movement of resident organisms, a recurring issue is the lack of certainty in inferring organism size and type from the echo returns. A key area for future work is therefore to assess how well the echo patterns associated with different sizes and categories of organisms can be distinguished with the current tag design. This information is critical for most trophic and carbon flux studies (Hernández-León et al. 2019). While careful tank-based validation studies can improve confidence in interpreting the sonar tag, ultimately in situ measurements will be most useful for the identification of unique deep-sea fauna that cannot be held in aquaria. One way to achieve in situ validation could be to combine the sonar tag with a camera tag in such a way that image capture is triggered by acoustic detections within a given detection range.

## Acknowledgements

Marine mammal data were gathered by the international MEOP Consortium, including the French National Observatory Mammals as sampler of the Ocean Environment (SNOMEMO). Fieldwork in Kerguelen was supported by the French Polar Institute (Institut Polaire Français Paul Emile Victor) as part of the CyclEleph programme (n. 1201, PI C.Gilbert). Fieldwork in Peninsula Valdes was supported by CNES-TOSCA (Centre National d'Études Spatial) as part of a French-Argentinian collaborative program (PI C. Guinet). This research was funded by the "Agence Innovation Défense" and the "Région Nouvelle-Aquitaine" to M.T.

The Kerguelen fieldwork team 2018-2019 as well as the Peninsular Valdes fieldwork team 2018-2019, who deployed and recovered the tags are gratefully acknowledged, with special thanks to J. Mestre, C. Vuillet, H. Allegue involved in the Kerguelen tagging, and to J. Campagna, C. Campagna, M.A. Hindell and C. Vera for the Argentinian deployments.

## Declaration of interest:

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Alldredge, A. L., and M. W. Silver. 1988. Characteristics, dynamics and significance of marine snow. Progress in Oceanography 20:41-82.

Anderson, T. R., A. P. Martin, R. S. Lampitt, C. N. Trueman, S. A. Henson, and D. J. Mayor. 2019. Quantifying carbon fluxes from primary production to mesopelagic fish using a simple food web model. ICES Journal of Marine Science 76:690-701.

Atkinson, A., P. Ward, R. Williams, and S. A. Poulet. 1992. Feeding rates and diel vertical migration of copepods near South Georgia: comparison of shelf and oceanic sites. Marine Biology 114:4956.

Aumont, O., O. Maury, S. Lefort, and L. Bopp. 2018. Evaluating the Potential Impacts of the Diurnal Vertical Migration by Marine Organisms on Marine Biogeochemistry. Global Biogeochemical Cycles 32:1622-1643.

Bailleul, F., J. Vacquie-Garcia, and C. Guinet. 2015. Dissolved Oxygen Sensor in Animal-Borne Instruments: An Innovation for Monitoring the Health of Oceans and Investigating the Functioning of Marine Ecosystems. PLOS ONE 10:e0132681.

Barton, A. D., A. J. Irwin, Z. V. Finkel, and C. A. Stock. 2016. Anthropogenic climate change drives shift and shuffle in North Atlantic phytoplankton communities. Proceedings of the National Academy of Sciences 113:2964-2969.

Bayle, S., P. Monestiez, C. Guinet, and D. Nerini. 2015. Moving toward finer scales in oceanography: Predictive linear functional model of Chlorophyll a profile from light data. Progress in Oceanography 134:221-231.

Béhagle, N., C. Cotté, A. Lebourges-Dhaussy, G. Roudaut, G. Duhamel, P. Brehmer, E. Josse, and Y. Cherel. 2017. Acoustic distribution of discriminated micronektonic organisms from a bifrequency processing: The case study of eastern Kerguelen oceanic waters. Progress in Oceanography 156:276-289.

Béhagle, N., C. Cotté, T. E. Ryan, O. Gauthier, G. Roudaut, P. Brehmer, E. Josse, and Y. Cherel. 2016. Acoustic micronektonic distribution is structured by macroscale oceanographic processes across $20-50^{\circ}$ S latitudes in the South-Western Indian Ocean. Deep Sea Research Part I: Oceanographic Research Papers 110:20-32.

Behrenfeld, M. J., P. Gaube, A. Della Penna, R. T. O’Malley, W. J. Burt, Y. Hu, P. S. Bontempi, D. K. Steinberg, E. S. Boss, D. A. Siegel, C. A. Hostetler, P. D. Tortell, and S. C. Doney. 2019. Global satellite-observed daily vertical migrations of ocean animals. Nature 576:257-261.

Belcher, A., C. Manno, P. Ward, S. Henson, R. Sanders, and G. Tarling. 2017. Copepod faecal pellet transfer through the meso- and bathypelagic layers in the Southern Ocean in spring. Biogeosciences 14:1511-1525.

Bianchi, D., and K. A. S. Mislan. 2016. Global patterns of diel vertical migration times and velocities from acoustic data: Global patterns of diel vertical migration. Limnology and Oceanography 61:353-364.

Biuw, M., L. Boehme, C. Guinet, M. Hindell, D. Costa, J.-B. Charrassin, F. Roquet, F. Bailleul, M. Meredith, S. Thorpe, Y. Tremblay, B. McDonald, Y.-H. Park, S. R. Rintoul, N. Bindoff, M. Goebel, D. Crocker, P. Lovell, J. Nicholson, F. Monks, and M. A. Fedak. 2007. Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. Proceedings of the National Academy of Sciences 104:13705-13710.

Blain, S., B. Quéguiner, L. Armand, S. Belviso, B. Bombled, L. Bopp, A. Bowie, C. Brunet, C. Brussaard, F. Carlotti, U. Christaki, A. Corbière, I. Durand, F. Ebersbach, J.-L. Fuda, N. Garcia, L. Gerringa, B. Griffiths, C. Guigue, C. Guillerm, S. Jacquet, C. Jeandel, P. Laan, D. Lefèvre, C. Lo Monaco, A. Malits, J. Mosseri, I. Obernosterer, Y.-H. Park, M. Picheral, P. Pondaven, T. Remenyi, V.

Sandroni, G. Sarthou, N. Savoye, L. Scouarnec, M. Souhaut, D. Thuiller, K. Timmermans, T. Trull, J. Uitz, P. van Beek, M. Veldhuis, D. Vincent, E. Viollier, L. Vong, and T. Wagener. 2007. Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. Nature 446:1070-1074.

Bost, C. A., C. Cotté, P. Terray, C. Barbraud, C. Bon, K. Delord, O. Gimenez, Y. Handrich, Y. Naito, C. Guinet, and H. Weimerskirch. 2015. Large-scale climatic anomalies affect marine predator foraging behaviour and demography. Nature Communications 6:8220.

Boyd, P. W., H. Claustre, M. Levy, D. A. Siegel, and T. Weber. 2019. Multi-faceted particle pumps drive carbon sequestration in the ocean. Nature 568:327-335.

Brierley, A. S. 2014. Diel vertical migration. Current Biology 24:R1074-R1076.
Buesseler, K. O., and P. W. Boyd. 2009. Shedding light on processes that control particle export and flux attenuation in the twilight zone of the open ocean. Limnology and Oceanography 54:1210-1232.

Buesseler, K. O., C. H. Lamborg, P. W. Boyd, P. J. Lam, T. W. Trull, R. R. Bidigare, J. K. B. Bishop, K. L. Casciotti, F. Dehairs, M. Elskens, M. Honda, D. M. Karl, D. A. Siegel, M. W. Silver, D. K. Steinberg, J. Valdes, B. V. Mooy, and S. Wilson. 2007. Revisiting Carbon Flux Through the Ocean's Twilight Zone. Science 316:567-570.

Burwen, D. L., S. J. Fleischman, J. D. Miller, and M. E. Jensen. 2003. Time-based signal characteristics as predictors of fish size and species for a side-looking hydroacoustic application in a river. ICES Journal of Marine Science 60:662-668.

Carlotti, F., D. Thibault-Botha, A. Nowaczyk, and D. Lefèvre. 2008. Zooplankton community structure, biomass and role in carbon fluxes during the second half of a phytoplankton bloom in the eastern sector of the Kerguelen Shelf (January-February 2005). Deep Sea Research Part II: Topical Studies in Oceanography 55:720-733.

Carter, L., I. N. McCave, and M. J. M. Williams. 2008. Chapter 4 Circulation and Water Masses of the Southern Ocean: A Review. Pages 85-114 in F. Florindo and M. Siegert, editors. Developments in Earth and Environmental Sciences. Elsevier.

Cavan, E. L., A. Belcher, A. Atkinson, S. L. Hill, S. Kawaguchi, S. McCormack, B. Meyer, S. Nicol, L. Ratnarajah, K. Schmidt, D. K. Steinberg, G. A. Tarling, and P. W. Boyd. 2019a. The importance of Antarctic krill in biogeochemical cycles. Nature Communications 10.

Cavan, E. L., E. C. Laurenceau-Cornec, M. Bressac, and P. W. Boyd. 2019b. Exploring the ecology of the mesopelagic biological pump. Progress in Oceanography 176:102125.

Cavan, E. L., F. A. C. Le Moigne, A. J. Poulton, G. A. Tarling, P. Ward, C. J. Daniels, G. M. Fragoso, and R. J. Sanders. 2015. Attenuation of particulate organic carbon flux in the Scotia Sea, Southern Ocean, is controlled by zooplankton fecal pellets. Geophysical Research Letters 42:821-830.

Cepeda, G. D., B. Temperoni, M. E. Sabatini, M. D. Viñas, C. M. Derisio, B. A. Santos, J. C. Antacli, and L. N. Padovani. 2018. Zooplankton Communities of the Argentine Continental Shelf (SW Atlantic, ca. $34^{\circ}-55^{\circ}$ S), An Overview. Pages 171-199 in M. S. Hoffmeyer, M. E. Sabatini, F. P. Brandini, D. L. Calliari, and N. H. Santinelli, editors. Plankton Ecology of the Southwestern Atlantic. Springer International Publishing, Cham.

Chapman, C. C., M.-A. Lea, A. Meyer, J.-B. Sallée, and M. Hindell. 2020. Defining Southern Ocean fronts and their influence on biological and physical processes in a changing climate. Nature Climate Change 10:209-219.

Cherel, Y., S. Ducatez, C. Fontaine, P. Richard, and C. Guinet. 2008. Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. Marine Ecology Progress Series 370:239-247.

Conroy, J. A., D. K. Steinberg, P. S. Thibodeau, and O. Schofield. 2020. Zooplankton diel vertical migration during Antarctic summer. Deep Sea Research Part I: Oceanographic Research Papers 162:103324.

Cotté, C., F. d’Ovidio, A.-C. Dragon, C. Guinet, and M. Lévy. 2015. Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current. Progress in Oceanography 131:46-58.

Cuzin-Roudy, J., J. Irisson, F. Penot, S. Kawaguchi, and C. Vallet. 2014. Southern Ocean Euphausiids. Biogeographic Atlas Southern Ocean:510.

Daneri, G., and A. Carlini. 2002. Fish prey of southern elephant seals, Mirounga leonina, at King George Island. Polar Biology 25:739-743.

Davison, P. C., J. A. Koslow, and R. J. Kloser. 2015. Acoustic biomass estimation of mesopelagic fish: backscattering from individuals, populations, and communities. ICES Journal of Marine Science 72:1413-1424.

Della Penna, A., S. De Monte, E. Kestenare, C. Guinet, and F. d'Ovidio. 2015. Quasi-planktonic behavior of foraging top marine predators. Scientific Reports 5.

DeVries, T. 2014. The oceanic anthropogenic $\mathrm{CO}_{2}$ sink: Storage, air-sea fluxes, and transports over the industrial era. Global Biogeochemical Cycles 28:631-647.

Dornan, T., S. Fielding, R. A. Saunders, and M. J. Genner. 2019. Swimbladder morphology masks Southern Ocean mesopelagic fish biomass. Proceedings of the Royal Society B: Biological Sciences 286:20190353.

Dragon, A.-C., P. Monestiez, A. Bar-Hen, and C. Guinet. 2010. Linking foraging behaviour to physical oceanographic structures: Southern elephant seals and mesoscale eddies east of Kerguelen Islands. Progress in Oceanography 87:61-71.

Escobar-Flores, P. C., Y. Ladroit, and R. L. O’Driscoll. 2019. Acoustic Assessment of the Micronekton Community on the Chatham Rise, New Zealand, Using a Semi-Automated Approach. Frontiers in Marine Science 6.

Escobar-Flores, P. C., R. L. O’Driscoll, and J. C. Montgomery. 2018. Predicting distribution and relative abundance of mid-trophic level organisms using oceanographic parameters and acoustic backscatter. Marine Ecology Progress Series 592:37-56.

Fay, A. R., and G. A. McKinley. 2014. Global open-ocean biomes: mean and temporal variability. Earth System Science Data 6:273-284.

Fedak M. 2004. Marine animals as platforms for oceanographic sampling: a "win/win" situation for biology and operational oceanography 58:133-147.

Fielding, S., J. L. Watkins, P. N. Trathan, P. Enderlein, C. M. Waluda, G. Stowasser, G. A. Tarling, and E. J. Murphy. 2014. Interannual variability in Antarctic krill (Euphausia superba) density at South Georgia, Southern Ocean: 1997-2013. ICES Journal of Marine Science 71:2578-2588.

Godet, C., M. Robuchon, B. Leroy, C. Cotté, A. Baudena, O. Da Silva, S. Fabri-Ruiz, C. Lo Monaco, S. Sergi, and P. Koubbi. 2020. Matching zooplankton abundance and environment in the South Indian Ocean and Southern Ocean. Deep Sea Research Part I: Oceanographic Research Papers 163:103347.

Goulet, P., C. Guinet, C. Campagna, J. Campagna, P. L. Tyack, and M. Johnson. 2020. Flash and grab: deep-diving southern elephant seals trigger anti-predator flashes in bioluminescent prey. The Journal of Experimental Biology 223:jeb222810.

Goulet, P., C. Guinet, R. Swift, P. T. Madsen, and M. Johnson. 2019. A miniature biomimetic sonar and movement tag to study the biotic environment and predator-prey interactions in aquatic animals. Deep Sea Research Part I: Oceanographic Research Papers 148:1-11.

Guinet, C., J. Vacquié-Garcia, B. Picard, G. Bessigneul, Y. Lebras, A. Dragon, M. Viviant, J. Arnould, and F. Bailleul. 2014. Southern elephant seal foraging success in relation to temperature and light conditions: insight into prey distribution. Marine Ecology Progress Series 499:285-301.

Haëntjens, N., A. Della Penna, N. Briggs, L. Karp-Boss, P. Gaube, H. Claustre, and E. Boss. 2020. Detecting Mesopelagic Organisms Using Biogeochemical-Argo Floats. Geophysical Research Letters 47.

Handegard, N. O., D. A. Demer, R. Kloser, P. Lehodey, O. Maury, and Y. Simard. 2009. Toward a Global Ocean Ecosystem Mid-trophic Automatic Acoustic Sampler (MAAS). 8 s.

Harcourt, R., A. M. M. Sequeira, X. Zhang, F. Roquet, K. Komatsu, M. Heupel, C. McMahon, F. Whoriskey, M. Meekan, G. Carroll, S. Brodie, C. Simpfendorfer, M. Hindell, I. Jonsen, D. P. Costa, B. Block, M. Muelbert, B. Woodward, M. Weise, K. Aarestrup, M. Biuw, L. Boehme, S. J. Bograd, D. Cazau, J.-B. Charrassin, S. J. Cooke, P. Cowley, P. J. N. de Bruyn, T. Jeanniard du Dot, C. Duarte, V. M. Eguíluz, L. C. Ferreira, J. Fernández-Gracia, K. Goetz, Y. Goto, C. Guinet, M. Hammill, G. C. Hays, E. L. Hazen, L. A. Hückstädt, C. Huveneers, S. Iverson, S. A. Jaaman, K. Kittiwattanawong, K. M. Kovacs, C. Lydersen, T. Moltmann, M. Naruoka, L. Phillips, B. Picard, N. Queiroz, G. Reverdin, K. Sato, D. W. Sims, E. B. Thorstad, M. Thums, A. M. Treasure, A. W. Trites, G. D. Williams, Y. Yonehara, and M. A. Fedak. 2019. Animal-Borne Telemetry: An Integral Component of the Ocean Observing Toolkit. Frontiers in Marine Science 6.

Hays, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Pages 163-170 in M. B. Jones, A. Ingólfsson, E. Ólafsson, G. V. Helgason, K. Gunnarsson, and J. Svavarsson, editors. Migrations and Dispersal of Marine Organisms. Springer Netherlands, Dordrecht.

Heneghan, R. F., J. D. Everett, J. L. Blanchard, and A. J. Richardson. 2016. Zooplankton Are Not Fish: Improving Zooplankton Realism in Size-Spectrum Models Mediates Energy Transfer in Food Webs. Frontiers in Marine Science 3.

Hernández-León, S., R. Koppelmann, E. Fraile-Nuez, A. Bode, C. Mompeán, X. Irigoien, M. P. Olivar, F. Echevarría, M. L. Fernández de Puelles, J. I. González-Gordillo, A. Cózar, J. L. Acuña, S. Agustí, and C. M. Duarte. 2020. Large deep-sea zooplankton biomass mirrors primary production in the global ocean. Nature Communications 11:6048.

Hernández-León, S., M. P. Olivar, M. L. Fernández de Puelles, A. Bode, A. Castellón, C. López-Pérez, V. M. Tuset, and J. I. González-Gordillo. 2019. Zooplankton and Micronekton Active Flux Across the Tropical and Subtropical Atlantic Ocean. Frontiers in Marine Science 6.

Hidalgo, M., and H. I. Browman. 2019. Developing the knowledge base needed to sustainably manage mesopelagic resources. ICES Journal of Marine Science 76:609-615.

Hindell, M. A., C. R. McMahon, M. N. Bester, L. Boehme, D. Costa, M. A. Fedak, C. Guinet, L. HerraizBorreguero, R. G. Harcourt, L. Huckstadt, K. M. Kovacs, C. Lydersen, T. McIntyre, M. Muelbert, T. Patterson, F. Roquet, G. Williams, and J. Charrassin. 2016. Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. Ecosphere 7.

Irigoien, X., T. A. Klevjer, A. Røstad, U. Martinez, G. Boyra, J. L. Acuña, A. Bode, F. Echevarria, J. I. Gonzalez-Gordillo, S. Hernandez-Leon, S. Agusti, D. L. Aksnes, C. M. Duarte, and S. Kaartvedt. 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. Nature Communications 5 .

Jouma'a, J., Y. Le Bras, G. Richard, J. Vacquié-Garcia, B. Picard, N. El Ksabi, and C. Guinet. 2016. Adjustment of diving behaviour with prey encounters and body condition in a deep diving predator: the Southern Elephant Seal. Functional Ecology 30:636-648.

Kaartvedt, S., A. Staby, and D. Aksnes. 2012. Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. Marine Ecology Progress Series 456:1-6.

Kloke, J. D., and J. W. McKean. 2012. Rfit: Rank-based estimation for linear models. The R journal 4:57-64.

Kloser, R. J., T. E. Ryan, G. Keith, and L. Gershwin. 2016. Deep-scattering layer, gas-bladder density, and size estimates using a two-frequency acoustic and optical probe. ICES Journal of Marine Science 73:2037-2048.

Kloser, R. J., T. E. Ryan, J. W. Young, and M. E. Lewis. 2009. Acoustic observations of micronekton fish on the scale of an ocean basin: potential and challenges. ICES Journal of Marine Science 66:998-1006.

Koubbi, P., C. Guinet, N. Alloncle, N. Ameziane, C. Azam, A. Baudena, C. Bost, R. Causse, C. Chazeau, and G. Coste. 2016. Ecoregionalisation of the Kerguelen and Crozet islands oceanic zone. Part I: Introduction and Kerguelen oceanic zone. CCAMLR Document WG-EMM-16/43.

Latasa, M., J. Henjes, R. Scharek, P. Assmy, R. Röttgers, and V. Smetacek. 2014. Progressive decoupling between phytoplankton growth and microzooplankton grazing during an ironinduced phytoplankton bloom in the Southern Ocean (EIFEX). Marine Ecology Progress Series 513:39-50.

Laurenceau-Cornec, E. C., T. W. Trull, D. M. Davies, S. G. Bray, J. Doran, F. Planchon, F. Carlotti, M.-P. Jouandet, A.-J. Cavagna, A. M. Waite, and S. Blain. 2015a. The relative importance of phytoplankton aggregates and zooplankton fecal pellets to carbon export: insights from freedrifting sediment trap deployments in naturally iron-fertilised waters near the Kerguelen Plateau. Biogeosciences 12:1007-1027.

Laurenceau-Cornec, E. C., T. W. Trull, D. M. Davies, C. L. D. L. Rocha, and S. Blain. 2015b. Phytoplankton morphology controls on marine snow sinking velocity. Marine Ecology Progress Series 520:35-56.

Le Bras, Y., J. Jouma'a, B. Picard, and C. Guinet. 2016. How Elephant Seals (Mirounga leonina) Adjust Their Fine Scale Horizontal Movement and Diving Behaviour in Relation to Prey Encounter Rate. PLOS ONE 11:e0167226.

Le Moigne, F. A. C. L., S. A. Henson, E. Cavan, C. Georges, K. Pabortsava, E. P. Achterberg, E. CeballosRomero, M. Zubkov, and R. J. Sanders. 2016. What causes the inverse relationship between primary production and export efficiency in the Southern Ocean? Geophysical Research Letters 43:4457-4466.

Leblanc, K., A. Lafond, V. Cornet, J. Legras, B. Marie, and B. Quéguiner. this issue. Leblanc, K., A. Lafond, A., V. Cornet, J. Legras, B. Marie, B. Quéguiner this issue). Deep particle stocks following the summer bloom around the Kerguelen islands: insights into diatoms physiological state, community structure and mortality modes. Journal of Marine Systems (under revision) This issue.

Longhurst, A. R. 2010. Ecological geography of the sea. Elsevier.

Lutz, V., V. Segura, A. Dogliotti, V. Tavano, F. P. Brandini, D. L. Calliari, A. M. Ciotti, V. F. Villafañe, I. R. Schloss, F. M. P. S. Corrêa, H. Benavides, and D. V. Cantonnet. 2018. Overview on Primary Production in the Southwestern Atlantic. Pages 101-126 in M. S. Hoffmeyer, M. E. Sabatini, F. P. Brandini, D. L. Calliari, and N. H. Santinelli, editors. Plankton Ecology of the Southwestern Atlantic: From the Subtropical to the Subantarctic Realm. Springer International Publishing, Cham.

Manno, C., S. Fielding, G. Stowasser, E. J. Murphy, S. E. Thorpe, and G. A. Tarling. 2020. Continuous moulting by Antarctic krill drives major pulses of carbon export in the north Scotia Sea, Southern Ocean. Nature Communications 11:6051.

McMahon, C. R., I. C. Field, C. J. A. Bradshaw, G. C. White, and M. A. Hindell. 2008. Tracking and data-logging devices attached to elephant seals do not affect individual mass gain or survival. Journal of Experimental Marine Biology and Ecology 360:71-77.

McMahon, C. R., M. A. Hindell, J.-B. Charrassin, S. Corney, C. Guinet, R. Harcourt, I. Jonsen, R. Trebilco, G. Williams, and S. Bestley. 2019. Finding mesopelagic prey in a changing Southern Ocean. Scientific Reports 9:19013.

Montes-Hugo, M., S. C. Doney, H. W. Ducklow, W. Fraser, D. Martinson, S. E. Stammerjohn, and O. Schofield. 2009. Recent Changes in Phytoplankton Communities Associated with Rapid Regional Climate Change Along the Western Antarctic Peninsula. Science 323:1470-1473.

Murtagh, F., and P. Legendre. 2014. Ward's Hierarchical Agglomerative Clustering Method: Which Algorithms Implement Ward's Criterion? Journal of Classification 31:274-295.

Naito, Y., D. P. Costa, T. Adachi, P. W. Robinson, M. Fowler, and A. Takahashi. 2013. Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. Functional Ecology 27:710-717.

Nerini, D., and B. Ghattas. 2007. Classifying densities using functional regression trees: Applications in oceanology. Computational Statistics \& Data Analysis 51:4984-4993.

Pauthenet, E., F. Roquet, G. Madec, and D. Nerini. 2017. A Linear Decomposition of the Southern Ocean Thermohaline Structure. Journal of Physical Oceanography 47:29-47.

Pinti, J., and A. W. Visser. 2018. Predator-Prey Games in Multiple Habitats Reveal Mixed Strategies in Diel Vertical Migration. The American Naturalist 193:E65-E77.

Pollard, R. T., I. Salter, R. J. Sanders, M. I. Lucas, C. M. Moore, R. A. Mills, P. J. Statham, J. T. Allen, A. R. Baker, D. C. E. Bakker, M. A. Charette, S. Fielding, G. R. Fones, M. French, A. E. Hickman, R. J. Holland, J. A. Hughes, T. D. Jickells, R. S. Lampitt, P. J. Morris, F. H. Nédélec, M. Nielsdóttir, H. Planquette, E. E. Popova, A. J. Poulton, J. F. Read, S. Seeyave, T. Smith, M. Stinchcombe, S. Taylor, S. Thomalla, H. J. Venables, R. Williamson, and M. V. Zubkov. 2009. Southern Ocean deep-water carbon export enhanced by natural iron fertilization. Nature 457:577-580.

Proud, R., M. J. Cox, C. L. Guen, and A. S. Brierley. 2018. Fine-scale depth structure of pelagic communities throughout the global ocean based on acoustic sound scattering layers. Marine Ecology Progress Series 598:35-48.

Proud, R., N. O. Handegard, R. J. Kloser, M. J. Cox, and A. S. Brierley. 2019. From siphonophores to deep scattering layers: uncertainty ranges for the estimation of global mesopelagic fish biomass. ICES Journal of Marine Science 76:718-733.

Ramsay, J., and B. Silverman. 2005. Principal components analysis for functional data. Functional data analysis:147-172.

Rembauville, M., I. Salter, N. Leblond, A. Gueneugues, and S. Blain. 2015. Export fluxes in a naturally iron-fertilized area of the Southern Ocean - Part 1: Seasonal dynamics of particulate organic carbon export from a moored sediment trap. Biogeosciences 12:3153-3170.

Reygondeau, G., L. Guidi, G. Beaugrand, S. A. Henson, P. Koubbi, B. R. MacKenzie, T. T. Sutton, M. Fioroni, and O. Maury. 2018. Global biogeochemical provinces of the mesopelagic zone. Journal of Biogeography 45:500-514.

Rivière, P., T. Jaud, L. Siegelman, P. Klein, C. Cotté, J. Le Sommer, G. Dencausse, and C. Guinet. 2019. Sub-mesoscale fronts modify elephant seals foraging behavior. Limnology and Oceanography Letters 4:193-204.

Robinson, J., E. E. Popova, M. A. Srokosz, and A. Yool. 2016. A tale of three islands: Downstream natural iron fertilization in the Southern Ocean. Journal of Geophysical Research: Oceans 121:3350-3371.

Roquet, F., Y.-H. Park, C. Guinet, F. Bailleul, and J.-B. Charrassin. 2009. Observations of the Fawn Trough Current over the Kerguelen Plateau from instrumented elephant seals. Journal of Marine Systems 78:377-393.

Roquet, F., C. Wunsch, G. Forget, P. Heimbach, C. Guinet, G. Reverdin, J.-B. Charrassin, F. Bailleul, D. P. Costa, L. A. Huckstadt, K. T. Goetz, K. M. Kovacs, C. Lydersen, M. Biuw, O. A. Nøst, H. Bornemann, J. Ploetz, M. N. Bester, T. McIntyre, M. C. Muelbert, M. A. Hindell, C. R. McMahon, G. Williams, R. Harcourt, I. C. Field, L. Chafik, K. W. Nicholls, L. Boehme, and M. A. Fedak. 2013. Estimates of the Southern Ocean general circulation improved by animal-borne instruments. Geophysical Research Letters 40:6176-6180.

Sallée, J., K. Speer, and R. Morrow. 2008. Southern Ocean fronts and their variability to climate modes. J. Clim 21:3020-3039.

Salter, I., A. E. S. Kemp, C. M. Moore, R. S. Lampitt, G. A. Wolff, and J. Holtvoeth. 2012. Diatom resting spore ecology drives enhanced carbon export from a naturally iron-fertilized bloom in the Southern Ocean. Global Biogeochemical Cycles 26.

Schallenberg, C., S. Bestley, A. Klocker, T. W. Trull, D. M. Davies, M. Gault-Ringold, R. Eriksen, N. P. Roden, S. G. Sander, M. Sumner, A. T. Townsend, P. van der Merwe, K. Westwood, K. Wuttig, and A. Bowie. 2018. Sustained Upwelling of Subsurface Iron Supplies Seasonally Persistent Phytoplankton Blooms Around the Southern Kerguelen Plateau, Southern Ocean. Journal of Geophysical Research: Oceans 123:5986-6003.

Sieburth, J. M., V. Smetacek, and J. Lenz. 1978. Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions 1. Limnology and Oceanography 23:1256-1263.

Siegelman, L., M. O’Toole, M. Flexas, P. Rivière, and P. Klein. 2019. Submesoscale ocean fronts act as biological hotspot for southern elephant seal. Scientific Reports 9.

Sims, D. W., V. J. Wearmouth, E. J. Southall, J. M. Hill, P. Moore, K. Rawlinson, N. Hutchinson, G. C. Budd, D. Righton, J. D. Metcalfe, J. P. Nash, and D. Morritt. 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. Journal of Animal Ecology 75:176-190.

St. John, M. A., A. Borja, G. Chust, M. Heath, I. Grigorov, P. Mariani, A. P. Martin, and R. S. Santos. 2016. A Dark Hole in Our Understanding of Marine Ecosystems and Their Services: Perspectives from the Mesopelagic Community. Frontiers in Marine Science 3.

Sutton, T. T. 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives: vertical ecology of the pelagic ocean. Journal of Fish Biology 83:1508-1527.

Sydeman, W. J., E. Poloczanska, T. E. Reed, and S. A. Thompson. 2015. Climate change and marine vertebrates. Science 350:772-777.

Tarling, G. A., S. E. Thorpe, S. Fielding, T. Klevjer, A. Ryabov, and P. J. Somerfield. 2018. Varying depth and swarm dimensions of open-ocean Antarctic krill Euphausia superba Dana, 1850 (Euphausiacea) over diel cycles. Journal of Crustacean Biology 38:716-727.

Thompson, G. A., E. O. Dinofrio, and V. A. Alder. 2013. Structure, abundance and biomass size spectra of copepods and other zooplankton communities in upper waters of the Southwestern Atlantic Ocean during summer. Journal of Plankton Research 35:610-629.

Tran, T. K., L. Duforêt-Gaurier, V. Vantrepotte, D. S. F. Jorge, X. Mériaux, A. Cauvin, O. Fanton d'Andon, and H. Loisel. 2019. Deriving Particulate Organic Carbon in Coastal Waters from Remote Sensing: Inter-Comparison Exercise and Development of a Maximum Band-Ratio Approach. Remote Sensing 11:2849.

Turner, J. T. 2015. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. Progress in Oceanography 130:205-248.

Vacquié-Garcia, J., C. Guinet, C. Laurent, and F. Bailleul. 2015. Delineation of the southern elephant seal's main foraging environments defined by temperature and light conditions. Deep Sea Research Part II: Topical Studies in Oceanography 113:145-153.

Vacquié-Garcia, J., J. Mallefet, F. Bailleul, B. Picard, and C. Guinet. 2017. Marine Bioluminescence: Measurement by a Classical Light Sensor and Related Foraging Behavior of a Deep Diving Predator. Photochemistry and Photobiology 93:1312-1319.

Watanabe, H., T. Kubodera, M. Moku, and K. Kawaguchi. 2006. Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. Marine Ecology Progress Series 315:187-197.

Watanabe, Y. Y., and A. Takahashi. 2013. Linking animal-borne video to accelerometers reveals prey capture variability. Proceedings of the National Academy of Sciences 110:2199.

Wiebe, P. H., D. Chu, S. Kaartvedt, A. Hundt, W. Melle, E. Ona, and P. Batta-Lona. 2010. The acoustic properties of Salpa thompsoni. ICES Journal of Marine Science 67:583-593.

Ydesen, K. S., D. M. Wisniewska, J. D. Hansen, K. Beedholm, M. Johnson, and P. T. Madsen. 2014. What a jerk: prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (Phoca vitulina). Journal of Experimental Biology 217:2239-2243.

Yoshino, K., A. Takahashi, T. Adachi, D. P. Costa, P. W. Robinson, S. H. Peterson, L. A. Hückstädt, R. R. Holser, and Y. Naito. 2020. Acceleration-triggered animal-borne videos show a dominance of fish in the diet of female northern elephant seals. Journal of Experimental Biology 223.


Figure 1: (a) Echogram with a schematic representation of the metrics calculations. Red lines mark the analysis range. The orange line shows the range used for Background Noise Level estimation. (b) Echogram from a regular area. (c) Echogram from the high-intensity signal region.

977


Figure 2: (a) Time-depth series of scatterer abundance, expressed in scatterers. ${ }^{-3}$, detected by the sonar tag on a seal tagged on Kerguelen Island (KER). The coloured rectangles above the plot indicate the position of inferred water body types 1 (purple), 2 (green) and 3 (light orange). (b) Water temperature profiles recorded by a tag on the same animal. Pink points indicate prey capture attempts inferred from acceleration transients.


Figure 3: (a) Time-depth series of scatterer abundance, expressed in scatterers.m ${ }^{-3}$, detected by the sonar tag on a seal tagged on Peninsula Valdes (PV). The coloured rectangles above the plot indicate the position of inferred water body types 1 (purple), 2 (green) and 3 (light orange). (b) Water temperature profiles recorded by a tag on the same animal. Pink points indicate prey capture attempts inferred from acceleration transients. The colour scales have different ranges than in Figure $\mathbf{2}$ to accommodate the differing conditions in this oceanographic region.


Figure 4: (a) Time-depth representation of the relative abundance of scatterers, expressed in scatterers. ${ }^{-3}$, detected by the sonar tag, zoomed over a one-day period for KER. The coloured rectangles represent the light angle with yellow and grey for day and night, respectively, and the shaded grey for twilight. The sonar was operated on a 5.5 -hour on/off duty-cycle. (b) Temperature profiles, in ${ }^{\circ} \mathrm{C}$ for the same time interval. The dotted black lines in both plots represent the isotherms, with an increment of $1^{\circ} \mathrm{C}$.


Figure 5: (a) Time-depth representation of the relative abundance of scatterers, expressed in scatterers. ${ }^{-3}$, detected by the sonar tag, zoomed over a one-day period for PV. The coloured rectangles represent the light angle with yellow and grey for day and night, respectively, and the shaded grey for twilight. The sonar was operated on a 12-hour on/off duty-cycle. (b) Temperature profiles, in ${ }^{\circ} \mathrm{C}$ for the same time interval. The dotted black line represents the isotherms, with an increment of $3^{\circ} \mathrm{C}$.


Figure 6: Average temperature (A, C) and salinity (B, D) profiles of KER and PV datasets. The three clusters are shown in blue (cluster 1), green (cluster 2) and orange (cluster 3). For each profile, the envelopes are bounded by the first and last quartile and thus contain $50 \%$ of the profiles.


Figure 7: (a) Track of the SES tagged on Peninsula Valdes during the interval recorded by the sonar tag (FPCA cluster colours as in Figure 6). The solid grey line shows the 1000 m isobath. Blue lines indicate the mean position of oceanic fronts over the study period, as given by the Centre for Topographic studies of the Ocean and Hydrosphere (see Sallée et al. 2008). Lower panels: (b) mean day (yellow) and night (blue) DVM depth (maximum abundance of profiles) for the 3 water clusters for the PV seal, (c) sum of the scatterers' abundances over the depth range $30-260 \mathrm{~m}$ (matching the vertical extent of the DVM depth for each cluster), (d) average scatterers' size distribution for each cluster. Grey dots and error bars respectively indicate the mean of each violin plot and the standard deviation.




Figure 8: (a) Track of the SES tagged on Kerguelen Island during the interval recorded by the sonar tag (FPCA cluster colours as in Figure 6). The solid grey line shows the 1000 m isobath. Blue lines indicate the mean position of oceanic fronts over the study period, as given by the Centre for Topographic studies of the Ocean and Hydrosphere (see Sallée et al. 2008). Lower panels: (b) mean day (yellow) and night (blue) DVM depth (maximum abundance of profiles) for the 3 water clusters for the KER seal, (c) sum of the scatterers' abundances over the depth range 70-160 m (matching the vertical extent of the DVM depth for each cluster), (d) average scatterers' size distribution for each cluster. Grey dots and error bars respectively indicate the mean of each violin plot and the standard deviation.


Figure 9: Percentage difference, for small- (left) and medium- (right) size scatterers between day (yellow) and night (grey), calculated over 10-m depth bins, for the three water clusters (colours as in Figure 6) for KER (upper panel) and PV (lower panel). Positive values correspond to higher abundances during daytime than at night, and conversely a negative difference indicates higher abundances at night than during daytime for this depth bin.


Figure 10: (a) Mean day (yellow) and night (blue) DVM depth for the $\mathbf{2}$ locations. The DVM depth is the depth with the maximum density over a profile. (b) Mean particle size distribution over thedepth range (70:260). Grey points indicate the mean and the error bars represent +/-1 standard deviation.

## 1061 Supplementary information

## 1062 Calculation of the sonar tag metrics:

## Intensity threshold definition:

The noise intensity threshold is set on the last meter of the sonar detection range ( 5 to 6 m ), assuming that the entire signal in this range is ambient noise, and designated as the Background Noise Level (BNL). The amplitude fluctuations in the signal obtained from a shadow area (i.e. area behind a target) or from out-of-range detections are essentially electronic noise. The signal amplitude $X$ is thus noised with a Gaussian distribution function.

$$
G(X)=\frac{1}{\sqrt{2 \pi \sigma}} \exp \frac{-(X-\mu)^{2}}{2 \sigma^{2}}
$$

where $\mu$ is the mean of the amplitude and $\sigma$ the standard deviation.
The acoustic signal recorded by the sonar tag is the result of a combination of elementary signals, which can be for example caused by a strong scattering phenomenon. For the sonar tag, two signal channels of different amplitudes are considered, the sum of these constituting the acoustic signal. The signal amplitude R resulting in the sum of the channels is described as a Rayleigh law.

$$
R=\sqrt{X^{2}+Y^{2}}
$$

$$
\begin{aligned}
& \text { with } X \sim \mathcal{N}\left(0, \sigma^{2}\right) \text { and } Y \sim \mathcal{N}\left(0, \sigma^{2}\right) \\
& \text { Then } R \sim \text { Rayleigh }(\sigma)
\end{aligned}
$$

A random sampling of the BNL is operated over the entire record, with 1000 pixels values (acoustic power) sampled over a continuous sonar record sequence of at least 10 minutes. The sizes of the samples for KER and PV records are $10.10^{7}$ and $13.10^{7}$ respectively. The cumulative distribution function of the Rayleigh law is fitted upon the BNL samples (Figure 2). The threshold is set as the acoustic power value ( $\mu \mathrm{Pa}$ ) corresponding to the $99.9^{\text {th }}$ percentile of the Rayleigh distribution ( for KER and PV), allowing the discrimination between the actual target detection and the white noise in the studied range $1-1.5 \mathrm{~m}$ of the sonar beam.


1091
1092
1093
1094
1095
1096 1097 1098 1099 1100

Figure 1: Time series of the Background Noise Level (BNL) for (a) KER and (b) PV. The interval between the red lines contains $99,9 \%$ of the sampled echoes, which are used to fit the Rayleigh distribution.

The far range of the sonar beam is unlikely to insonify target. But it could sometimes happen that the far range contains a few targets, particularly in regions with high target densities. The evolution of the background sampled values is represented in Figure 1. To prevent the influence of peaks or trends in the signal, the $1 \%$ of extreme values are removed to prevent 1101 the influence of peaks or trends in the BNL threshold calculation.



## 1102 Figure 2: Rayleigh fit of the data for KER (a) and PV (b) Background Noise Level (BNL)

1103 sampled in the last meter of the signal range. The green line represents the density probability for 1104 a theoretical Rayleigh distribution, and the blue lines the fitted distribution of the samples. The 1105 vertical dotted red lines represent the defined threshold, set as the quantile $99,9 \%$ of the Rayleigh 1106 distribution.

1107
1108 Echo Intensity distribution
1109 The echo intensity presented in figure 3 is expressed as the echo-integration of each ping of the 1110 records. The echo-integration is performed by summing the echo power of each 4 mm bin
1111 insonified in the range $1 \mathrm{~m}-1.5 \mathrm{~m}$.
1112


1113 Figure 3: Distribution of the echo integrated intensities for (a) KER and (b) PV sonar records.
1114
1115 Minimum size detected
1116 The ability of the sonar to detect small targets at the limit of the sensor resolution depends
1117 primarily on its position in the beam and the acoustic backscattering properties of its body.
1118 However, size is the most common measure to discriminate organisms, but fluid-like organisms
1119 - even of large size - cannot be observed, thus we propose a limit of detectability for small
1120 targets with high Signal-to Noise-Ratio.
1121
1122 The sonar was deployed simultaneously with an optical sensor (Underwater Vision Profiler
1123 UVP5) in the Mediterranean Sea for an efficient measurement of the size of the targets. The

1124 density profiles show a maximum correlation for a target size class greater than 1 mm , with the 1125 same density peaks at 47.5 m and 147.5 m deep for both instruments (Figure 4). Targets
1126 identified as detritus from the UVP images contribute to a large part of the signal and suggest 1127 that they are detectable by sonar for sizes larger than 1 mm .

1128


1129
1130 Figure 4: Relative density of detected targets simultaneously by (a) an Underwater Vertical
1131 Profiler (UVP) and (b) the sonar tag attached to the UVP along a vertical profile. Colored curves 1132 represent the relative density of detected targets belonging to a specific size class.
1133
1134
1135 Dives clustering:
1136 A dive is considered when the animal is continuously deeper than 15 m . After the B-spline 1137 reconstruction and the FPCA performed on the B-spline coefficients, the observations (profiles) were projected in the space of the first two PCs (Figure 5). The five first components explained $98 \%$ and $91.5 \%$ of the total inertia for KER and PV respectively. By adding or subtracting the eigenfunctions to the mean profile, one can assess the effect of the principal components on the curve shape (Figure 6). For each component, if an observation is in the positive part of the PC axis, the shape of this observation should be close

1143 to the one described by the ' + ' curve. Inversely, negatives observations on the PC axis would 1144 have a curve close to the one described by the '-'.
1145 Before the $k$-means classification, the optimal number of $k$ clusters was determined using the 1146 Ward distance, minimizing the total within-cluster variance, on the observations. A visual 1147 assessment of the cluster tree allowed retaining 3 clusters for both KER (Figure 7) and PV 1148 (Figure 8).

1149


1152 Figure 5: Left: Temperature-Salinity profiles represented over the space of the first two modes of 1153 the FPCA for KER (a) and PV (b). Right: Percentage of the variance explained by the first 5 1154 eigenfunctions of the FPCA.
1155


1156 Figure 6: Representation of the effects of the first two eigenfunctions on temperature and salinity 1157 mean profiles, for $\operatorname{KER}(\mathrm{a}, \mathrm{b})$ and $\mathrm{PV}(\mathrm{c}, \mathrm{d})$. The curves show the mean profile (solid) and the 1158 effect of adding $(+)$ and subtracting $(-)$ the first $(\mathrm{a}, \mathrm{c})$ and the second (b,d) eigenfunctions. The 1159 percentages indicated in the x -axis label are the variance contained by each variable ( T and S ) 1160 for the corresponding component.


1162 Figure 7: Cluster resulting of the $k$-means classification for KER. The hierarchical clustering 1163 tree, defined by the Ward distance, suggesting an optimal clustering in 3 groups: cluster 1
1164 (purple), cluster 2 (orange), and cluster 3 (green). (b) T-S diagrams of all profiles contained in 1165 each cluster, associated with the mean 200 m -deep and the standard deviation of the temperature.


1167
1168 Figure 8: Cluster resulting of the $k$-means classification for PV. The hierarchical clustering tree, 1169 defined by the Ward distance, suggesting an optimal clustering in 3 groups: cluster 1 (purple),
1170 cluster 2 (orange), and cluster 3 (green). (b) T-S diagrams of all profiles contained in each
1171 cluster, associated with the mean 200m-deep and the standard deviation of the temperature.
1172
1173
1174
1175
Table 1: Mean temperature and salinity with standard deviations recorded at 200 m deep for each water masses in both locations.

| Location | KERGUELEN |  |  | PENINSULA VALDES |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Cluster (water <br> mass) | 1 | 2 | 3 | 1 | 2 | 3 |
| Temperature | $3.1^{\circ} \mathrm{C}$ | $5.7^{\circ} \mathrm{C}$ | $8^{\circ} \mathrm{C}$ | $4.8^{\circ} \mathrm{C}$ | $6.4^{\circ} \mathrm{C}$ | $7.9^{\circ} \mathrm{C}$ |


| (T200m) | $( \pm 0.1)$ | $( \pm 1.1)$ | $( \pm 0.6)$ | $( \pm 0.7)$ | $( \pm 0.6)$ | $( \pm 1.4)$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Salinity | $33.9 \%_{0}$ | $34.1 \%_{0}$ | $34.4 \%_{0}$ | $34.2 \%_{0}$ | $34.4 \%_{0}$ | $34.6 \%_{0}$ |
| (S200m) | $( \pm 0.08)$ | $( \pm 0.14)$ | $( \pm 0.1)$ | $( \pm 0.07)$ | $( \pm 0.2)$ | $( \pm 0.3)$ |

1176
1177
1178

