



MESOPP

Use of micronekton data and models to improve ecology of top predators

Deliverable Lead:	University of St Andrews
Reference:	MESOPP-18-0011
Dissemination Level:	Confidential
Issue:	2.0
Date:	2018,Nov.30

Chronology Issues:

Issue:	Date:	Reason for change:	Author
0.0	01/09/2018	Documentation start draft outline	Proud
1.0	26/11/2018	First draft	Proud
1.1	28/11/2018	Comments on draft	Brierley
2.0	30/11/2018	Update and new version	Proud

Distribution:

Company	Means of distribution	Names
All MESOPP partners	Notification and sharepoint	

This report can be cited as follows:

Proud R., Brierley A. S. (2018). Use of micronekton data and models to improve ecology of top predators. Report from the EU-H2020 MESOPP project, MESOPP-18-0011. 23 pp.

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Overview of MESOPP project

The underlying concept of MESOPP is the creation of a collaborative network and associated e-infrastructure (marine ecosystem information system) between European and Australian research teams/institutes sharing similar interests in: the Southern Ocean (SO) and Antarctica, its marine ecosystem functioning and the rapid changes occurring with the climate warming and the exploitation of marine resources.

In the past 30 years – facing global knowledge issues, lacking data and addressing huge modelling challenges – we observed the successful world organisation of meteorology. These past 15 years, Europe has kick started and achieved successful structuring of the operational oceanography fostered by the Copernicus initiative (<http://marine.copernicus.eu/>). Today, this structure is used and recognised worldwide and is integrated in GOOS (Global Ocean Observing System), IOOS (Integrated ocean observation system), SOOS (Southern Ocean Observing System), GODAE (the International Global Ocean Data Assimilation Experiment), and IMBER (Integrated Marine Biogeochemistry and Ecosystem Research).

The next major R&D strategic challenge is to connect the marine ecosystem community across the fields of meteorology, climate, oceanography and biology. This is a critical pre-requisite to overcoming (i) the domain's lack (or patchiness) of data, (ii) development of accurate high end to end models, (iii) global coverage and the need for exchange.

The objective of the MESOPP project is to meet this challenge and create links across the fields, pulling the marine ecosystem together. In particular, to:

1. Make an inventory of science challenges, stakes and existing policies and develop tools to federate and structure the community;
2. Start to organise the related marine ecosystem community between the EU and Australia through two implementation actions
3. Propose a R&D roadmap to support a large international cooperation on marine ecosystems based on an e-infrastructure, adding additional countries such as USA, New Zealand, Canada (in the Frame of the Galway statement), Brazil and all active countries already involved in large organisations such as IMBER, CCAMLR or IMOS.

MESOPP will focus on the enhancement of collaborations by eliminating various obstacles in establishing a common methodology and a connected network of databases of acoustic data for the estimation of micronekton biomass and validation of models. It will also contribute to a better predictive understanding of the SO based on furthering the knowledge base on key functional groups of micronekton and processes which determine ecosystem dynamics from physics to large oceanic predators.

This first project and associated implementation (science network and specification of an infrastructure) should constitute the nucleus of a larger international program of acoustic monitoring and micronekton modelling to be integrated in the general framework of ocean observation following a roadmap that will be prepared during the project.

1. Introduction

Typically, studies that focus on mid-to-high trophic-level species, such as fish and marine mammals, analyse data collected using instruments designed specifically to observe only a partial aspect of a single or small group or related species. For instance, mid-trophic level mesopelagic (200 to 1,000 m) organisms, which form deep scattering layers (DSLs), can be observed using echosounders, but these instruments do not enable elucidation of food web structure. Recent developments in data collection, storage and accessibility (via online data centres and project portals), have enabled observations collected by a wide range of instruments to be integrated and analysed concurrently. The Pelagic Ecology Research Group (PERG) at the University of St Andrews has collated a global dataset of 38 kHz echosounder observations. The Southern Ocean component of this collated data were obtained primarily from the Integrated Marine Observing System (IMOS, ww.imos.org.au) and the MESOPP data portal (www.mesopp.eu), which include observations made from both fisheries and research vessels. In parallel to these developments, a database of Southern elephant seal diving data has been established, providing both CTD and time-depth data collected via bio-logging (Roquet et al. 2014). In this study, we link together a decade's worth (between 2004 and 2017) of Southern elephant seal dive data and echosounder observations of sound scattering layers (SSLs) to investigate fine-scale (10's m) vertical predator-prey interactions in the Indian ocean sector of the Southern Ocean.

1.1. Southern elephant seals

Southern elephant seals, *Mirounga leonine*, referred to from here on as SES, are the largest phocid. They are long-lived, deep-diving (up to 2000 m; McIntyre *et al.*, 2010) air-breathing vertebrates. Adult female SES, spend 10 months of the year at sea, covering vast distances (100's to 1,000s of km), repeatedly (c. 90% of their time) performing foraging dives, only resting in-between at the surface, for periods of c. 2-3 minutes (McConnell et al. 1992). Despite these long migrations and foraging trips, SES remain faithful to their colonies and return to land to moult and breed. Each dive on average lasts c. 20-30 minutes, foraging at depths between 300 and 500 m (McConnell et al. 1992). During the dive, SES perform most of their feeding during the so called 'bottom phase' (Bras et al. 2017). SES, particularly in the Indian ocean sector of the Southern Ocean, mainly feed on myctophids (Guinet et al. 2014), whilst males are thought to principally feed on cephalopods.

1.2. Monitoring Southern elephant seals

Technological advancements and the miniaturisation of instruments over the last few decades have driven the development of bio-logging, in which, animals are tagged with instruments that monitor their behaviour and also the surrounding environment. SES are perfect candidates for bio-logging due to their large size, and hence, their capacity for carrying instruments with large processing and storage capabilities. To monitor foraging behaviour, time-depth recorders (TDR, Kooyman, 1965) and high-sampling rate accelerometers (Yoda et al. 1999) are used. Head mounted (Gallon et al. 2013, Foo et al. 2016) or triaxial jaw-mounted

(Viviant et al. 2010, Naito et al. 2010, Watanabe & Takahashi 2013) accelerometers are used to detect prey encounter events. GPS data collected using Argos satellites provide accurate information in regards to important feeding grounds (Robinson et al. 2007, Hindell et al. 2016), which is of particular use in studies that aim to identify area-restricted search behaviour (ARS, e.g. Kareiva and Odell, 1987). By analysing vertical speeds and swimming effort across different phases (e.g. drift, decent, bottom and ascent phases) of SES dives (resting or foraging), variability in body density can be estimated, which is a proxy for fitness or lipid-to-lean body tissue ratio (Richard et al. 2016).

1.3. Foraging behaviour of Southern elephant seals

By monitoring foraging trips and dive behaviour of tagged animals, we have gained invaluable insight into the ecology of top predators. After all, foraging success is critical to the survival of these animals and the efficiency of their diving strategy is key in optimising net-energy gain, balancing expenditure between prey consumption, body maintenance and locomotion (Bras et al. 2016, Richard et al. 2016). The diving behaviour of marine mammals, turtles and seabirds changes in accordance with changes in prey patch quality and depth (Thompson & Fedak 2001, Sparling et al. 2007, Doniol-Valcroze et al. 2011). For SES, and for some penguins, this includes modulation of their dive duration, especially during the bottom phase where most feeding takes place (Le Bras et al. 2016); this is also true of other species e.g. Antarctic fur seals, northern elephants seals, grey seals, and leatherback turtles. SES forage across a wide range of water masses, ranging from Antarctic shelf waters to north of the sub-Tropical front, encountering water temperatures of between -1 and 13°C at 200 m depth (Guinet et al. 2014). The rate of prey encounter events and dive depth of adult female SES has been related to environmental properties, such as water temperature and light level both at depth and at the surface (Guinet et al. 2014), and also to time of day, where prey encounter events per unit time are lowest during the day and highest around twilight (Guinet et al. 2014). The fitness or body condition of SES has been shown to be related to habitat type as well as number of prey encounter events and body activity (Biuw et al. 2007, Richard et al. 2016). For instance, SES foraging north of the sub-Antarctic front improve their body density when compared to those foraging south of the sub-Antarctic and polar fronts (Richard et al. 2016); this suggests that prey in these areas are either easier to catch and/or more energetically rich.

1.4. Predator-prey interactions

SES dive on average to depths of c. 300 to 500 m, which coincides with the depths of deep scattering layers (DSLs), which are comprised of mesopelagic organisms e.g. fish, squid and zooplankton etc. It is perhaps not that surprising that the diets of adult SES have been found to mostly consist of fish and squid (Le Bras et al. 2016), and for females associated with Kerguelen, mainly myctophids (e.g. *Gymnoscopelus nicholsi*, *Electrona antarctica* and *Electrona calbergi*) (Cherel et al. 2008, Naito et al. 2013, Guinet et al. 2014), which are the most abundant and diverse mesopelagic fish in the global ocean. Furthermore, SES are believed to rely mainly on sight for predation, and their visual acuity is optimised for wavelengths within the range of those produced by myctophid bioluminescence (Vacquié-Garcia et al. 2015). Components of DSLs perform daily migrations to the surface at night to

feed, shifting a proportion of seal prey biomass closer to the surface. This is consistent with studies that have observed that SES dive deeper during the daytime, adjusting their dive patterns in response to changes in prey depth (Biuw et al. 2010, McIntyre et al. 2011, Jaud et al. 2012, Guinet et al. 2014). Since DSL depth, biomass and species composition vary in relation to changes in environmental conditions, e.g. across frontal boundaries and towards continental shelves, then the diving depth of SES that may feed on these layers is also likely to vary (e.g. Boersch-Supan et al., 2012). Furthermore, a reduction in DSL intensity has often been observed in deeper or 'secondary DSL's (Proud et al. 2017), which is consistent with observations of decreases in SES prey encounter rate with increasing bottom phase depth (Bras et al. 2016); this could also be related to the reduced accessibility that is associated with greater water-column depths. In response to changes in prey density, SES change their diving behaviour by steepening their ascent and decent dives, reducing transit time, and also by increasing the duration of the sinuous bottom, or feeding, phases (Bras et al. 2016).

1.5. This report

SES, according to optimal foraging theory, seek out high-density (or high-reward, subject to effort) patches of prey, whilst prey seek to avoid high-density predator patches. Their foraging success is therefore dependent on their diving strategy, which is a learned behaviour that has evolved over time through natural selection. In this study, we aim to assess spatial changes in foraging behaviour of SES by analysing the characteristics of targeted prey-patches i.e. targeted deep scattering layers. We focus on analysing data collected in the Indian Ocean sector of the Southern Ocean, as an abundance of both echosounder observations and SES dive records are available for this region.

The objectives of this report are as follows: i.) obtain collocated and concurrent SES dive data and echosounder observations for the Indian Ocean sector of the Southern Ocean; ii) derive a method to extract fine-scale (10's m) metrics (e.g. echo intensity, thickness and depth) of sound scattering layers; iii.) match concurrent dive records with sound scattering layers observed in similar environments/water masses, and iv.) determine if SES are selectively foraging on specific sound scattering layers (characterised by layer metrics).

2. Fine-scale characteristics of deep scattering layers

Deep Scattering layers (DSLs), i.e. sound scattering layers (SSLs) that are deeper than 200 m, are comprised primarily of mid-trophic level species, e.g. fish and zooplankton, and are a ubiquitous feature of the world ocean (Proud et al. 2017, Proud, Cox, Le Guen, et al. 2018). They are typically observed using echosounders operating at 38 kHz, and the majority of the received backscattering intensity is produced by gas-bladdered fish and siphonophores (Proud et al. 2018). Since mesopelagic fish are a key prey-item for Southern elephant seals (SES), it is reasonable to assume that DSL depth and dive depth of SES are, to some extent, correlated. However, traditional techniques of DSL detection and extraction typically involve isolating vertically extensive (10's to 100's m) layers that likely comprise of a mixed assemblage of species (including both prey and non-prey species of SES), and any calculated mean depths may not correspond to the target dive depth of SES. To this end, and before comparing DSL metrics to the dive behaviour of SES, we develop a fine-scale SSL extraction method. The method developed, builds on previous work, the sound scattering layer extraction method (SSLEM; Proud *et al.*, 2015), and is simply referred to as SSLEM2 from here on.

2.1. Study region and echosounder observations

For our study region (see Figure 1), 38 kHz echosounder observations were obtained from IMOS, MESOPP and PERG. Data were calibrated using the best available calibration parameters and were pre-processed to remove transient noise, noise spikes, dropped pings and surface noise. Data consisted of 12,285 echograms, collected between 2009 and 2017 across all months. Since in this study we are primarily interested in SES prey e.g. squid and fish, we set a conservative echo intensity threshold of -80 dB re 1m⁻¹ to remove observations of assemblages of weakly scattering organisms such as zooplankton, which are not targeted by SES.

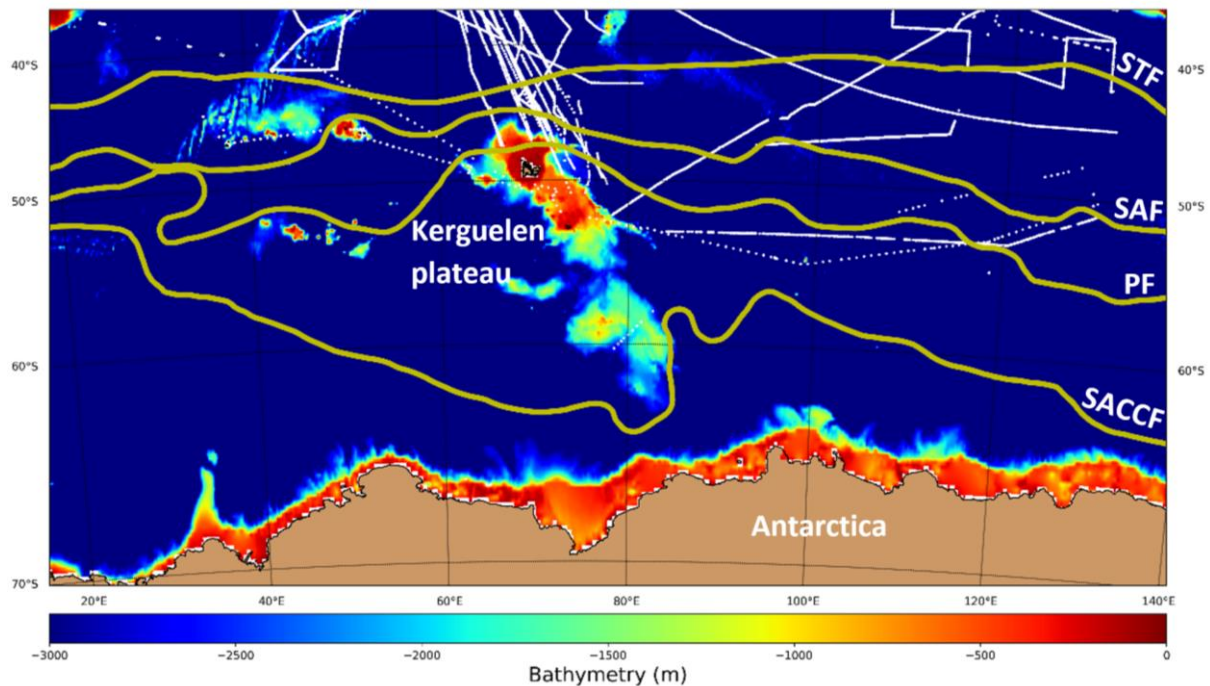


Figure 1: Study region: Echosounder observations (white lines) obtained from the Integrated Marine Observing System (IMOS, www.imos.au.org), the MESOPP project (www.mesopp.eu) and pelagic ecology research group (PERG, University of St Andrews). Bathymetry is mapped over the study region using data from the latest GEBCO chart (Weatherall et al. 2015). Orsi fronts are shown by gold lines (Orsi et al. 1995), where STF is the sub-Tropical front, SAF is the sub-Antarctic front, PF is the Polar front and SACCF is the Southern Antarctic Circumpolar Current front.

2.2. Deep Scattering Layers

On average, DSLs (see Figure 2) reside at c. 500 m in the water column and are between 50 and 300 m thick (Proud et al. 2015, 2017). They are comprised of organisms that undertake daily migrations to the surface at dawn to feed, and other organisms that take up residency within the mesopelagic zone. Whilst some mesopelagic communities have been observed to aggregate into a single layer, others form more complex arrangements formed of many layers. The arrangement and characteristics of DSLs are dependent upon the species composition, the environment, and the frequency at which you observe them; DSLs can appear very different, particularly in echo intensity, when, for example, observing them both at 18 and 38 kHz. DSLs are typically observed at a frequency of 38 kHz, this provides optimum resolution (i.e. a relatively small wavelength) for an observation range of c. 1,000 m i.e. covering the full extent of the mesopelagic zone. At this frequency, DSL echo intensity has been related to primary production (PP) at the surface and water temperature at both the surface and at depth (Proud et al. 2017), and DSL depth has been related to oxygen concentration, light level, wind stress and PP (Klevjer et al. 2016, Aksnes et al. 2017, Proud et al. 2017).

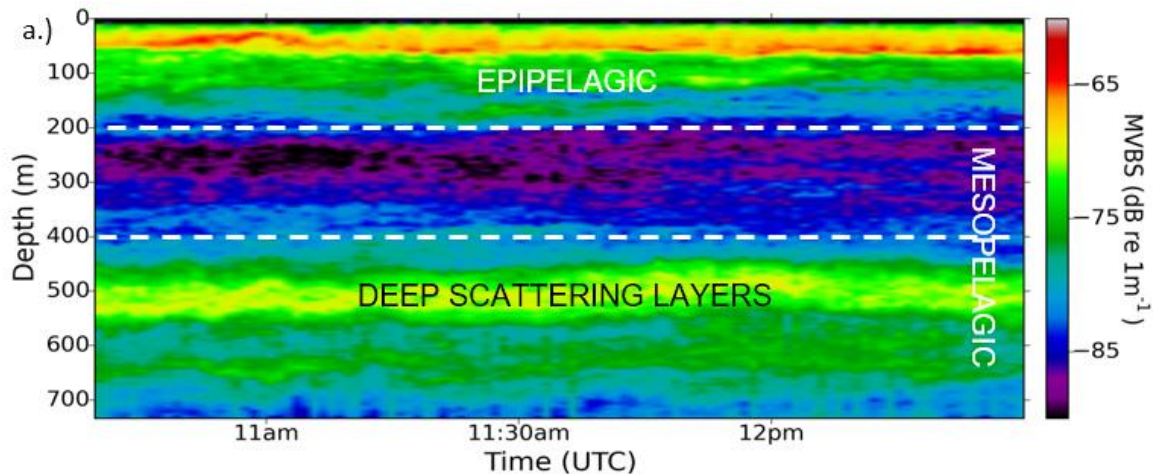


Figure 2: Example of sound scattering layers. Multiple deep (> 200 m) sound scattering layers reside between 450 and 700 m. Underlying data were 38 kHz echosounder observations extracted from the IMOS database, recorded by a fisheries vessel in the Indian Ocean.

2.3. Sound Scattering Layer Extraction Method (SSLEM)

The Sound Scattering Layer Extraction Method (SSLEM, see Figure 3) has been used to extract SSLs across a range of frequencies and echo intensities (Proud et al. 2017, Proud, Cox, Le Guen, et al. 2018). It is essentially an image processing technique that iteratively attempts to isolate layers, within predefined spatial and temporal limits, by applying a range of thresholds to the data. Unlike previous methods to isolate SSLs that use a single value to threshold the data, this method is able to detect SSLs over a wide range of echo intensity values, meaning that both strong (consistent of densely packed organisms or stronger scatterers e.g. fish) and weak (consistent of diffusely packed organisms or weaker scatterers such as zooplankton) are detected. In other studies, the depth of the DSL has been calculated by using a weighted mean depth of echo intensity over the mesopelagic zone. This method should be used with caution, as in situations where more than one DSL is observed, which is often the case, then a WMD may result in a calculated DSL depth that resides in between layers and therefore has little significance or relation to the surrounding environment.

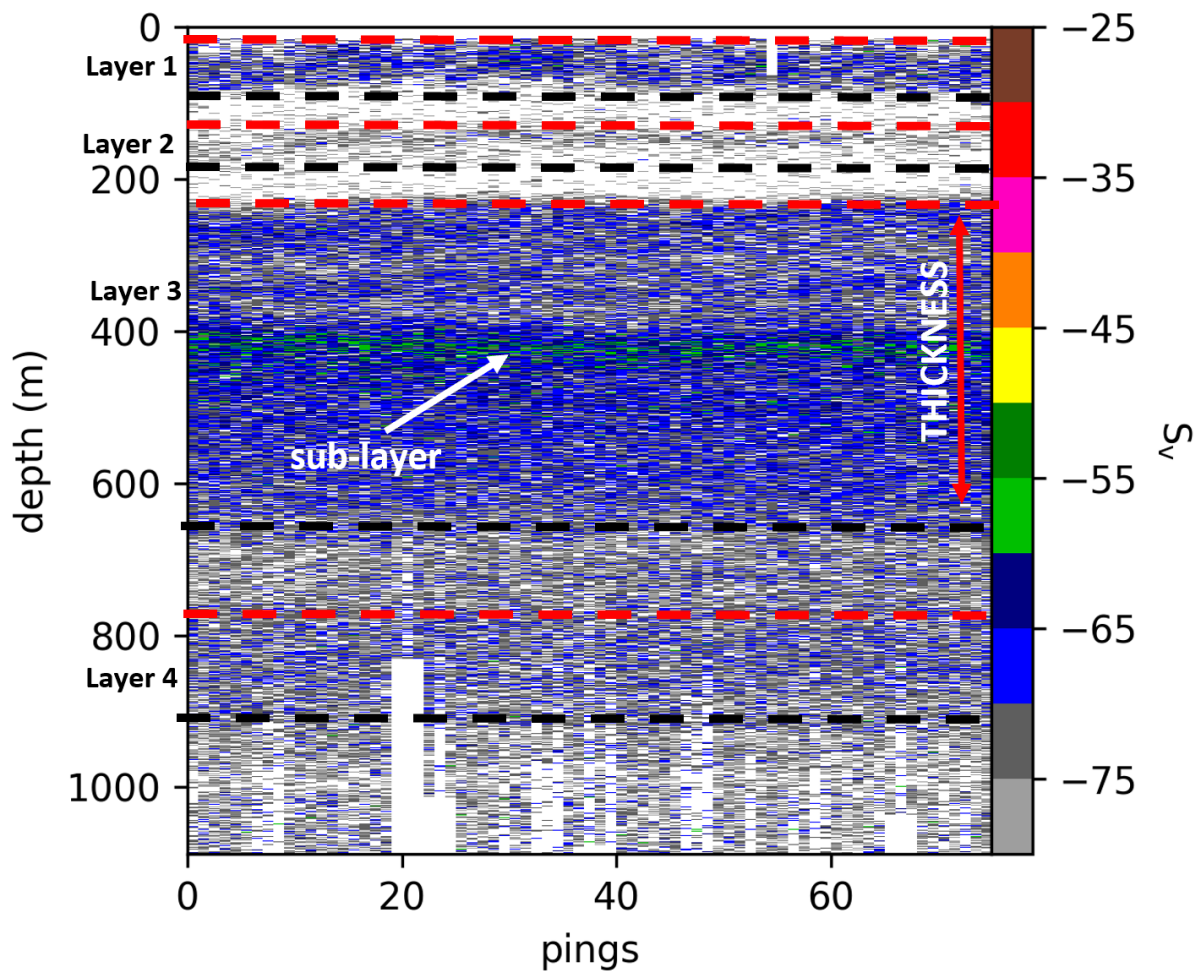


Figure 3: Isolated 38 kHz scattering layers using the sound scattering layer extraction method (SSLEM). The start and end depths of each layer are indicated by dashed red and black lines respectively.

Models that predict DSL depth are often based on thresholding techniques or weighted mean depths, both of which do not resolve fine-scales DSL structures such as sublayers i.e. layers of relatively high echo intensity that are found within larger but weaker DSLs (See Figure 3). Since SES are known to target and repeatedly forage at specific depths, a SSL extraction method is required that is capable of drilling down into the sub-layers of these communities.

2.4. Sound Scattering Layer Extraction Method 2 (SSLEM2)

The SSLEM method is useful for broad-scale analyses and studies that integrate echo intensity over depth ranges. However, to extract fine-scale sub-layers, the method needs to be adjusted, such that SSLs are isolated over a range of echo intensity thresholds. The SSLEM2 was developed by using the same logic as applied in SSLEM, but instead of pooling all of the detected layer pixels into a single group, identified layer pixels for different echo intensity ranges were labelled separately. This resulted in a large number of detected layers that overlapped in space and time, referred to as a layer set. To select the optimum arrangement of layers for each echogram, 1,000 echograms were built by randomly selecting layers from

the layer set and stopping when no more layers could be added. The optimum arrangement was selected by considering both the amount of layer space filled (total vertical extent) and the complexity of the layer arrangement (total number of layers). An example of an optimum arrangement of layers derived from a layer set is given in Figure 4.

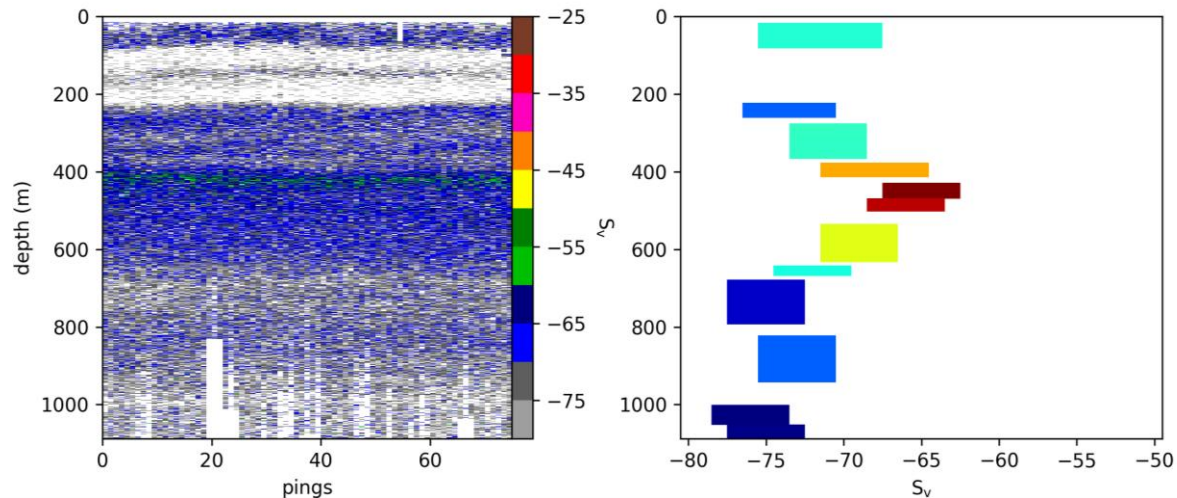


Figure 4 Sound Scattering Layer Extraction Method 2: sound scattering layers are extracted across a range of Sv ranges to separate out layers that have distinct echo intensity values and ranges. The stronger layers are likely to be consistent of stronger/more densely packed scatterers e.g. fish. The faintly visible SSL at c. 180 m was not extracted as it fell below the minimum echo intensity value of $-80 \text{ dB re } 1\text{m}^{-1}$.

SSLs extracted using SSLEM2 were generally thinner and had shorter echo intensity ranges than SSLs extracted using SSLEM. In total, 77,904 layers from the 12,285 echograms were extracted using SSLEM2, applying a minimum threshold of $-80 \text{ dB re } 1\text{m}^{-1}$. Each extracted SSL was defined by its mean echo intensity value (S_v ; $\text{dB re } 1\text{m}^{-1}$), thickness (m), start depth (m), end depth (m), minimum echo intensity (S_v ; $\text{dB re } 1\text{m}^{-1}$), maximum echo intensity (S_v ; $\text{dB re } 1\text{m}^{-1}$), data quality (number of good data samples divided by the total number of data samples) and persistence (length in km and duration in minutes).

2.5. Conclusions

In this section of the report we have described the echosounder observations that are available for analysis in our study region. These were obtained from online data centres and through our own lab. To isolate and extract fine-scale scattering layers from within these data, which SES may target, we adapted a layer extraction method to provide finer-scale detection of SSLs across a range of echo intensity thresholds. This method, SSLEM2, can resolve sub-layers that have relatively high echo intensity values (see Figure 4), which could potentially be formed of myctophids - the primary prey item of female SES. Given that these layers are invariant over short-timescales and small areas, we can now compare them to the dive depths of SES.

3. Interactions between deep scattering layers and foraging Southern elephant seals

In section 2, 77,904 fine-scale sound scattering layers were extracted using SSLEM2 from 12,285 echograms and summarised by a set of SSL metrics (e.g. SSL depth and echo intensity). In this section, we match extracted SSLs with SES dive records, which were obtained through the Marine Mammals Exploring the Oceans Pole-to-pole (MEOP) database (<http://www.meop.net>), both in space and in time. Matching was carried out at a frontal zone scale spatially and on a monthly time-scale temporally. We also compare the distributions of SSL metrics for layers detected across different frontal zones, with those targeted by seals whilst foraging and feeding.

3.1. Southern elephant seal dive data distribution

SES dive data were obtained from the MEOP database. In this study, only SES associated with Kerguelen were considered (see Figure 5 for SES dive tracks); other data for SESs are available, see Rodríguez et al. (2017). Although the tagging of the animals was not carried out as part of this work, it is worth briefly describing the process. Tags were applied at the end of the annual moult haul-out or at the end of the annual breeding haul out. Data were transmitted via Argos platform transmitting terminals. Before gluing the satellite relay data logger (SRDL, Sea Mammal Research Unit, University of St Andrews) to the head or back of the seal, they were chemically sedated (McMahon et al. 2000), weighed and measured (Field et al. 2002, Rodríguez et al. 2017).

In total, 595,452 dive records, collected between 2004 and 2016 including observations made day and night across all months except January, November and December (see Figure 5) were obtained from the database. Records include dives made by both females and males, between 1.66 and 3.75 m in length, and are split into 3 different age classes: female-adult, male-sub-adult and juvenile. Dives ranged between 20 and 2,389 m and were broken into 5 depth components (each constituting a single dive record) using the so-called broken-stick method (see Fedak 2002).

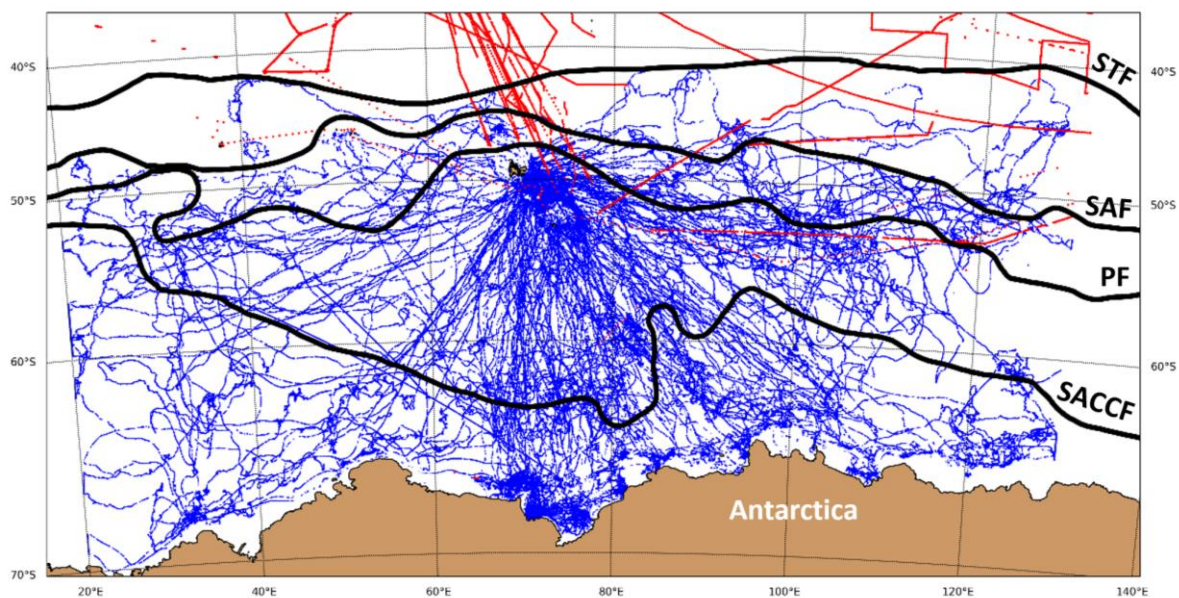


Figure 5: Spatial distribution of Southern elephant seal dive tracks (blue) and echosounder observations (red). Orsi fronts are shown by black lines (Orsi et al. 1995), where STF is the sub-Tropical front, SAF is the sub-Antarctic front, PF is the Polar front and SACCF is the Southern Antarctic Circumpolar Current front.

3.2. Assigning scattering layers to dive records

DSL depth and echo intensity are driven by environmental variables. It is therefore reasonable to expect that DSL properties vary less within similar environments (e.g. within the same frontal zone) than they do between them.

Since the two datasets analysed in this study do not overlap exactly in time and space, we have chosen to assign extracted SSLs to SES dive records by using the following method: 1.) group data by year and month; 2.) assign a frontal zone to both dive records and extracted SSLs (see Table 2) using the temperature field from the Simple Ocean Data Analysis (SODA; Carton *et al.*, 2017) data product ; 3.) determine distance between all dives and SSLs, and 4.) assign the closest SSL to each dive record where the dive depth is between the start and end depth of the SSL.

Table 1: Frontal zone names, definitions and observation counts. T_x corresponds to temperature at a water depth of X taken from the SODA (Carton et al. 2017) reanalysis dataset. Concurrent numbers refer to the total number of observations/records that occur in the same time periods i.e. the same month and year.

Zone	Acronym	Description	Logic	All dive records	All SSLs	Concurrent SSLs	Concurrent dive records
1	NSTF	North of STF	$T_{200} > 8^{\circ}\text{C}$	13,081	70,247	1,188	556
2	SAF-STF	Between SAF and STF	$T_{300} > 4^{\circ}\text{C}$ and $T_{200} < 8^{\circ}\text{C}$	21,139	3,385	537	1,711
3	PF-SAF	Between PF and SAF	$T_{200} > 2^{\circ}\text{C}$ and $T_{300} < -4^{\circ}\text{C}$	118,150	2,140	845	7,152
4	SACCF-PF	Between SACCF and PF	$T_{200} \leq 2^{\circ}\text{C}$ and $T_{500} > 1.8^{\circ}\text{C}$	192,199	953	731	4,005
5	SSACCF	South of SACCF	$T_{200} \leq 2$ and $T_{500} \leq 1.8^{\circ}\text{C}$	250,883	1,179	119	2,204

The frontal zones defined in Table 1 correspond to the averaged Orsi fronts (Orsi et al. 1995) shown in Figures 1 and 5. These definitions (pers. comm. Lars Boehme), however, are based on temperature and are therefore dynamic, changing continuously over time. For each zone listed in Table 1, the corresponding number of echosounder and SES dive observations are given. Unfortunately, the zone with the most echosounder observations also happens to be the zone with the fewest dive records (Zone 5) and vice-versa. This is because most of the echosounder data collated originates from IMOS, the majority of which are collected by fisheries vessels that operate north of the sub-Tropical front.

3.3. SES foraging by frontal zone

To determine whether SES were targeting specific SSLs, we compared the distributions of SSL metrics of those assigned to dive records against distributions drawn from the entire dataset. We represented the available prey for a particular frontal zone by pooling all of the detected SSLs that were located within the zone (see Table 1) during months and years where SES dive records were also available. This avoided any bias that would occur if SSL observations from specific month-year combinations, where no concurrent dive record was available, were to be included. The matched dataset of SES-targeted-SSLs were classified as ‘foraging’ SSLs, where SES may be feeding, searching or transiting. This dataset was further reduced into ‘feeding’ SSLs, where the time spent at the record depth was greater than 33% of the time of the entire dive. This was calculated from the output provided by the broken-stick method,

where each dive is broken into 5 depth components and the total elapsed proportion of the dive duration is calculated.

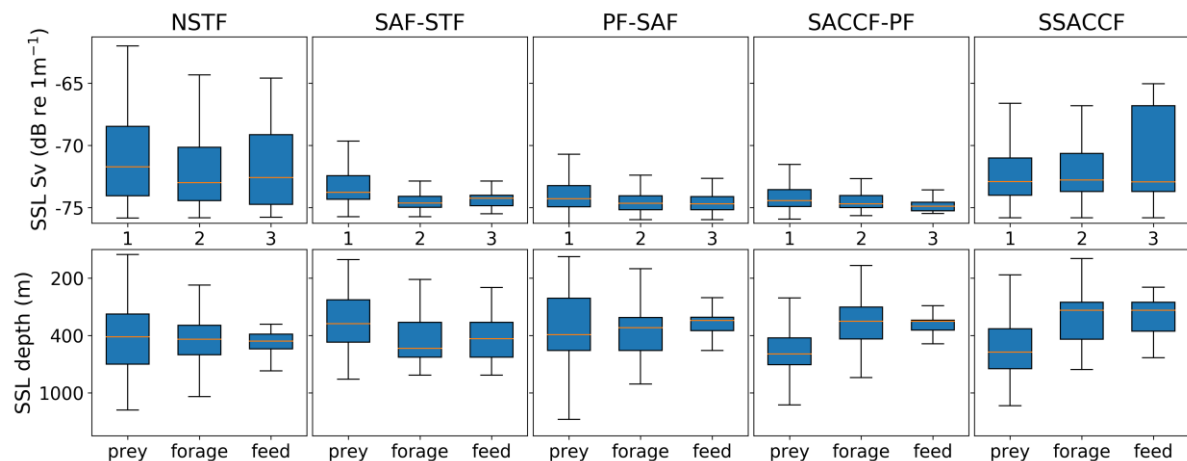


Figure 6: Boxplots of sound scattering layer depth and echo intensity for seal foraging dives across different frontal zones. X-axis labels are defined as follows: ‘prey’ represents all sound scattering layers observed within the zone, ‘forage’ represents the layers that have been assigned a dive record (in the same month and year) and ‘feed’ represents layer matches where the seal has spent at least 33% of the dive at that depth. STF is the sub-Tropical front, SAF is the sub-Antarctic front, PF is the Polar front and SACCF is the Southern Antarctic Circumpolar Current front.

Echo intensity of SSLs is strongest and most variable at the boundaries of our study site, north of the sub-Tropical front (STF) and South of the southern Antarctic Circumpolar Current front (Figure 6). This is typical of what has been observed previously i.e. concentration of biomass (and hence increase in echo intensity) where cold water front’s meet warm waters and towards continental shelves. Within the frontal zones, the SSL echo intensity range is weaker and narrower, and the SES tend to focus on weaker SSLs that are relatively shallow (c. 400 m) in the water-column. Interestingly, whilst SES tend to forage over a wide depth range and focus on a narrower depth range to feed, the Sv range for both foraging and feeding is similar.

3.4. Conclusions

A large volume of SES dive data exists and is available via the MEOP database. Echosounder observations are also becoming available through online databases making complimentary data analysis such as this possible. We have defined 5 frontal zones based on temperature to spatially partition our data (Table 1) and assumed that SSL characteristics do not change significantly over small time-scales (less than a month). We have linked dive records, which represent different stages of SES dives (segmented via the broken stick method), to nearby SSL observations. By comparing SES-targeted-SSLs to all the observed SSLs in a given frontal zone, we were able to determine firstly, that SESs do indeed target 38 kHz SSLs and secondly, what type of SSLs they preferentially feed on: SES forage on relatively weak and shallow SSLs and will search for these specific layers over a wide depth range (Figure 6).

4. Discussion and Summary

In this report we have collated echosounder data and SES dive data for the Indian Ocean sector of the Southern Ocean. We have extracted fine-scale sound scattering layers from the echosounder observations and matched them with SES dive records from within the same frontal zone, during the same month and year. We have then compared the SES-targeted-SSLs with SSLs observed in different Southern Ocean frontal zones. This work is the first attempt to link spatially and temporally coincident SSLs with dive records of SESs.

4.1. Linking deep scattering layers to the diving behaviour of Elephant Seals

A surprising result of this analysis is that Southern elephant seals target weaker SSLs. Echo intensity will typically increase as biomass increases, for a given DSL depth, and hence, this finding is contrary to optimal foraging theory, which assumes predators should spend most of their time in high-density/high-reward prey patches (Bras et al. 2017). However, there is not necessarily more prey biomass in DSLs with higher echo intensities. A significant proportion of DSL echo intensity is produced by siphonophores and very small fish that produce resonant backscatter (Proud, et al. 2018). Weaker DSLs could actually be formed of larger fish that have fat-invested swimbladders, which makes them weaker acoustic targets; the volume of gas within swimbladders is responsible for producing the majority of the observed backscattering intensity. This would then conform to optimal foraging theory, since an assemblage of low echo intensity and high-lipid content large fish, would provide more energy per unit effort for a predator than that of an assemblage of high echo intensity low-lipid content small fish. This discovery is important, since traditionally DSL depth is often estimated using a weighted mean (weighted by echo intensity), which is biased towards high intensity DSLs and may not relate to the dive depths of predators.

It has been observed that SES improve their body condition at a higher rate when feeding north of the sub-Antarctic front (SAF), when compared to SES south of the front (Richard et al. 2016). As the authors point out, this observations suggests that prey in the north are easier to catch or more energetically rich (Richard et al. 2016). Our results indicate that north of the SAF, i.e. in the STF-SAF zone (see Figure 6 and Table), SES feed on deeper layers, when compared with the other between-zone regions (Figure 6). Deeper layers often consist of larger fish that have relatively high-lipid stores, and therefore, could provide a more energetically-rich food source than shallower layers, which are likely to be comprised of younger/smaller fish with relatively low-lipid stores.

4.2. Future work

The SES database is extensive and holds an incredible amount of information relating to SES foraging strategy and behaviour. To utilise its full potential, supplementary data are required to provide information regarding prey species. Echosounder observations are now being collated in large volumes at numerous data centres. In this study, we were only able to obtain a relatively small sample of these data. To progress this work and improve our understanding of predator-prey interactions of deep-diving predators and the mesopelagic community, more echosounder data are required, especially towards the Antarctic continent (see Figure 1),

south of the polar front. Also, to resolve species composition, multi-frequency and/or broadband data are needed, coupled with visual validation of prey from deep-water probes and trawl samples, along with seal gut-content analyses. SES have the ability to learn (Rodríguez et al. 2017) and therefore it would be interesting to study changes in SSL selection throughout their lifecycles to see if their layer/prey preference changes at any stage. Also, studies should investigate the relation of other SSL metrics to SES dive behaviour. For instance, it has been observed that prey encounter rate decreases when the bottom phase (i.e. the feeding phase) of SES dives is spread across a larger vertical range (Bras et al. 2016). This could be investigated by comparing total SSL thickness (summed thickness of each SSL) against vertical extent of the broken stick depths. Such approaches are already in progress (e.g. Kloser et al., 2016) and will be critical in improving our understanding of the ecology of deep-diving predators such as elephant seals.

5. References

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