

Spatial and temporal distribution patterns of acoustic backscatter in the New Zealand sector of the Southern Ocean

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ABSTRACT: Mid-trophic level organisms (MTLO) of open-ocean marine ecosystems play a key role linking primary and tertiary consumers. Despite their importance, characterisation of MTLO is limited due to sampling difficulty, and is largely obtained through active acoustics. Acoustic data collected from vessels of opportunity transiting across the Southern Ocean between New Zealand and the Ross Sea provided the opportunity to study distribution and abundance of MTLO over 7 yr. Analyses were performed to identify spatial (vertical and horizontal) and temporal (annual, seasonal and diel) patterns in 28 acoustic transects collected between 2008 and 2014. Mean acoustic backscatter (s_a) at 38 kHz varied between years, but overall was reasonably stable, being in the same order of magnitude across all transects. Backscatter consistently and significantly decreased from north to south. Although this latitudinal pattern could be related to MTLO abundance, trawl samples collected in 3 research voyages suggest that it may also reflect differences in species composition and size distribution; consequently, indices based on bulk backscatter must be interpreted with caution. Vertical distribution of backscatter showed clear diel vertical migration patterns and 4 distinct vertical bands (i.e. epipelagic, transition, mesopelagic and deep mesopelagic), with seasonal differences in concentration and behaviour. Deep mesopelagic layers stopped north of the Ross Sea, which may relate to the temperature limitation of contributing organisms. Predicted climate change effects in the Southern Ocean could modify the spatial distribution of MTLO and have impacts on top predators relying upon the mid-trophic level as their main food source.

KEY WORDS: Mid-trophic levels · Mesopelagic zone · Epipelagic zone · Acoustic backscatter · Southern Ocean · Mesopelagic fish · Myctophids · Diel vertical migration

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INTRODUCTION

Mid-trophic level organisms (MTLO) of open-ocean ecosystems include small fish, squids, crustaceans and gelatinous zooplankton, but as shown by net sampling, are usually dominated by mesopelagic fishes (e.g. Williams & Koslow 1997, Kloser et al. 2009). Lanternfish (Myctophidae) and bristlemouths (Gonostomatidae) are the principal component of the mesopelagic fish community in the subantarctic, transitional and subtropical waters (Gjøsaeter & Kawaguchi 1980, Brodeur & Yamamura 2005, Nelson 2006,

Irigoien et al. 2014). MTLO play a key role in the ecology and biochemical cycles of the open-ocean ecosystems, linking primary consumers and higher trophic levels (Kloser et al. 2009, Catul et al. 2011). Likewise, they facilitate energy transfer and carbon fluxes across the water column through diel vertical migration (DVM) (Irigoien et al. 2014), and affect oxygen consumption at different depths (Bianchi et al. 2013).

Despite their crucial role in the open-ocean ecosystem, our ecological knowledge of the MTLO is limited (Brodeur & Yamamura 2005, Lehodey et al. 2010, 2015, Handegard et al. 2013). MTLO are difficult to

sample, in part due to their ability to avoid plankton nets and escape from fishing gear because of their swimming capabilities and small size (e.g. Kaartvedt et al. 2012). Driven by the need to parameterize and validate ecosystem models, recent papers have stressed the need for better data on the mid-trophic levels (MTLs) (e.g. Lehodey et al. 2010). It is also important to understand how the MTLO behave and are distributed spatially and temporally, since these patterns in marine communities could be affected by climate change (McFarlane et al. 2000, Roessig et al. 2004, Constable et al. 2016) and resource exploitation (Greenstreet & Hall 1996, Garrison & Link 2000).

Fisheries acoustics is commonly used for studying fish abundance and distribution (Simmonds & MacLennan 2005) and can provide an effective way of characterising MTLO. Many myctophids have a physoclistous gas-filled swimbladder (Marshall 1960), making them good acoustic targets (e.g. Kloser et al. 1997). Acoustics has previously been used for studying abundance (e.g. Koslow et al. 1997), vertical distribution, behaviour (e.g. Godø et al. 2009), and horizontal patterns (e.g. Escobar-Flores et al. 2013) of mesopelagic fish. Additionally, acoustics has been used to detect oceanographic physical structures (e.g. internal waves, submesoscale and mesoscale eddies) by observing the multiscale coupling between organisms and clines (e.g. Bertrand et al. 2010, 2014) and/or internal waves (e.g. Haury et al. 1979, Lavery et al. 2003, Bertrand et al. 2014), and to demonstrate the aggregating power of mesoscale eddies (Godø et al. 2012). Since most vessels are equipped with echosounders, acoustic data can sometimes be collected opportunistically over broad spatial and temporal scales (Karp 2007). Though regarded as the most suitable method for abundance estimation of MTLO (e.g. Gjøsaeter & Kawaguchi 1980), recent studies have also highlighted some caveats for interpreting and converting acoustic energy into density due to issues such as resonance scattering by siphonophores and small mesopelagic fish (e.g. Lavery et al. 2007, Davison et al. 2015a, Kloser et al. 2016).

In this paper, we describe a time series of return acoustic transects collected annually from vessels of opportunity transiting between New Zealand (NZ) and the Ross Sea (RS). This provided the opportunity to study distribution of backscatter as a proxy for MTLO abundance (i.e. mesopelagic fish and other organisms responsible for scattering layers), in the Southern Ocean (SO) over 7 yr from 2008 to 2014. Our main focus was to describe patterns of spatial and vertical distribution of backscatter using descrip-

tive statistics, statistical modelling, and analytical comparisons. The consistency of the acoustic time series also allowed us to study changes in distribution over time, to explore the potential of using acoustic backscatter from vessels of opportunity to uncover impacts of climate change on the SO ecosystem.

MATERIALS AND METHODS

Acoustic data set

Our acoustic dataset consisted of 28 acoustic transects collected opportunistically between NZ and the RS between November and March from 2008 until 2014 (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m592p019_supp.pdf for additional information on the timing, duration and length of the transects). This period corresponds to the fishing season of Antarctic toothfish *Dissostichus mawsoni*, when the ice retreats close to the Antarctic continent allowing access to the toothfish fishing grounds. A transect is defined as a group of raw files collected by a vessel during its transit from NZ to the SO or upon its return, excluding data recorded on the fishing grounds (which is commercially sensitive). For instance, transect SAO 2013 NZ-SO refers to the transit of vessel 'San Aotea II', between NZ and the SO in fishing year 2013. Fishing year was used to group transects rather than calendar year (i.e. November 2009 to March 2010 defined as 2010 fishing year). Transects were grouped into 6 fishing years and each classified as either spring (Nov and Dec) or summer (Jan to Mar) (Table 1). The acoustic dataset used in this research is available through the Integrated Marine Observing System (IMOS) portal (<https://portal.aodn.org.au/>).

Transects were collected by 3 toothfish fishing vessels (TFV) and the RV 'Tangaroa' continuously during their transits to and from the RS (Fig. 1, see Figs. S1–S4 in the Supplement for individual transects). The TFV 'San Aotea II' (SAO), 'San Aspiring' (SAS) and 'Janas' (JAN) collected 38 kHz single frequency data, using Simrad split-beam ES60 echosounders. The RV 'Tangaroa' (TAN) collected multi-frequency data: 2 frequencies (38 and 70 kHz) in 2008; and 5 frequencies (18, 38, 70, 120 and 200 kHz) in 2010 and 2013, using Simrad split-beam EK60 echosounders. Since acoustic transects were most consistently collected at 38 kHz, the analysis and results are largely focussed on transects at this frequency. Transceiver settings used in the 38 kHz single frequency systems during data collection were typically 2 milli-

Table 1. Summary of acoustic transects grouped by fishing year and season. NZ: New Zealand; SO: Southern Ocean

Fishing year	Spring	Summer	No. of transects
2008	–	San Aotea II 2008 SO-NZ, Tangaroa 2008 NZ-SO and Tangaroa 2008 SO-NZ	3
2010	Janas 2010 NZ-SO, San Aspiring 2010 NZ-SO and San Aotea II 2010 NZ-SO	San Aotea II 2010 SO-NZ, Tangaroa 2010 NZ-SO and Tangaroa 2010 SO-NZ	6
2011	Janas 2011 NZ-SO, San Aspiring 2011 NZ-SO and San Aotea II 2011 NZ-SO	Janas 2011 SO-NZ, San Aspiring 2011 SO-NZ and San Aotea II 2011 SO-NZ	6
2012	San Aotea II 2012 NZ-SO	San Aotea II 2012 SO-NZ and San Aspiring 2012 SO-NZ	3
2013	Janas 2013 NZ-SO, San Aspiring 2013 NZ-SO and San Aotea II 2013 NZ-SO	San Aotea II 2013 SO-NZ, Tangaroa 2013 NZ-SO and Tangaroa 2013 SO-NZ	6
2014	Janas 2014 NZ-SO and San Aotea II 2014 NZ-SO	Janas 2014 SO-NZ and San Aotea II 2014 SO-NZ	4

seconds (ms) pulse length and 2000 Watts (W) power. The TAN's multi-frequency system had 1 ms pulse length for all frequencies, with 2000 W power for 18 and 38 kHz frequencies, and 1000, 500 and 300 W for the 70, 120 and 200 kHz respectively.

for reducing the effect of common types of signal degradation, described by Ryan et al. (2015) as impulsive noise, transient noise, background noise and signal attenuation. These filters were applied following Ryan et al. (2015), with modifications described by

Calibrations were carried out on the TFV on a semi-regular basis, and at least annually on TAN, following procedures as per Demer et al. (2015) using a 38.1 mm tungsten carbide sphere. Like most vessels used for opportunistic acoustic data collection (Karp 2007), TFV have not been built for minimising noise, therefore considerable data grooming is required to reduce bias due to noise and signal attenuation. Our grooming protocols for processing acoustic data were based largely on those developed for the IMOS, which operates through COM port objects to control the software Echoview (v.5.4; Myriax 2013) using Matlab routines. These protocols include 4 filters

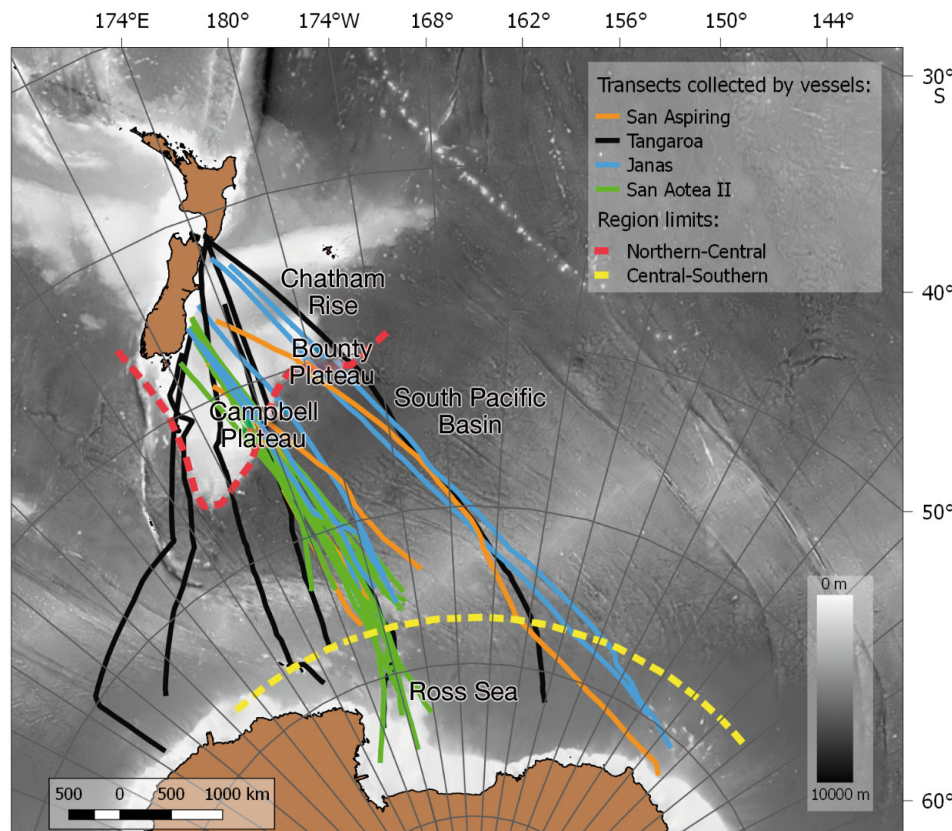


Fig. 1. Acoustic transects ($n = 28$) collected between 2008 and 2014 along the transit between New Zealand and the Southern Ocean from fishing ('San Aotea', 'San Aspiring' and 'Janas') and research ('Tangaroa') vessels. Red and yellow dotted lines: limit between the Northern and Central regions and Central and Southern regions, respectively, in which transects were split for descriptive analysis (see 'Results' section and the Supplement at www.int-res.com/articles/suppl/m592_p019_supp.pdf)

Escobar-Flores (2017), and Echoview's implementation of the De Robertis & Higginbottom (2007) background noise filter. For a complete description of the acoustic data processing, noise handling and performance of the grooming filters, see Escobar-Flores (2017). The total amount of backscatter (signal plus noise) removed during the grooming process varied between transects (mean \pm SD: $62.9 \pm 30\%$), with the main reductions due to the removal of double bottom echoes and transient noise (visually verified by comparing echograms of the transects pre- and post-processing).

The mean volume backscattering strength (S_v ; dB re 1 m) and area backscattering coefficient, referred to here as acoustic backscatter (s_a) were echo-integrated in 1 km long by 10 m high elementary distance sampling units (EDSU; referred to as bins). Although the system of physical units for s_a is $\text{m}^2 \text{m}^{-2}$, s_a was scaled by 1×10^6 for practicality (units in $\text{m}^2 \text{km}^{-2}$), and should be interpreted as the sum of all acoustic backscatter per km^2 of ocean surface. Bins were defined from 10 m from the surface down to 1200 m or the maximum range where data quality was high enough to achieve a minimum of 70% of accepted acoustic samples per echo-integration bin (Escobar-Flores 2017). This minimum percentage of accepted samples per bin criterion—defined so that only bins retaining a high number of samples after the acoustic data processing (i.e. noise and attenuated pings removal) were used for analysis—retained more than half of the bins of all transects for echo-integration, avoiding substantial changes in mean backscatter.

Description of spatial distribution

Descriptive statistics were used to compare s_a between transects, geographical regions and depth zones. Mean s_a for each transect was obtained by vertically summing s_a across all depth zones per bin, and secondly by averaging all the bins along the transect.

Horizontal distribution patterns were described based on visual interpretation of vertically summed s_a at bin resolution, and overall trends and their significance were numerically evaluated by fitting linear regressions as a function of latitude for each transect, using the statistical software R (R Core Team 2013).

Cubic spline smoothers (CSS) were fitted to each transect using the 'smooth.spline' function of the R 'stats' package to assess semi-systematic fluctuations of s_a along transects (e.g. DVM), while removing the

bin-to-bin variability. CSS are mainly used for interpolation between adjacent points by fitting third-order polynomial sections conditioned to be continuous at the knots or joining points on its first and second derivatives (Pollock 1999).

Description of vertical distribution

The water column was divided into an epipelagic and mesopelagic zone, defined as between 10 and 200 m, and 200 and 1200 m, respectively (all descriptive and spatial analyses of this paper follow these definitions). Mean s_a was estimated separately for both zones, as well as for the total pelagic zone (i.e. 10 to 1200 m). Due to the lack of normality in the backscatter distribution, we used non-parametric bootstrapping (1000 replicates) to generate 95% confidence intervals (defined using the percentile method in the bootstrapped distribution) to test whether there were statistically significant differences in mean backscatter by pelagic zone, time of day and season. Vertical profiles of S_v were plotted by averaging 10 m depth layers along the transects' bins. All the averaging of S_v in our paper was done in the linear domain and back-transformed into the logarithmic domain for plotting. To measure homogeneity of S_v within a depth layer, 90% confidence intervals for the mean S_v were calculated using a *t*-distribution.

Vertical distribution was summarised by time of day (discretised as 'day' or 'night') and season. To classify day or night, sunrise and sunset times were estimated along the transect for each bin using the 'sunrise' function from the R package 'maptools' (Bivand & Lewin-Koh 2015). Sunrise and sunset times were estimated based on the civil twilight definition (6° below the horizon). The mean projected latitude and longitude of each bin was calculated using the 'SpatialPoints' function from the R package 'sp' (Pebesma & Bivand 2005, Bivand et al. 2013), and used in the 'sunrise' function along with the date of data collection. Bins with a time stamp between sunrise and sunset were flagged as day, and between sunset and sunrise as night (i.e. dawn and dusk transition periods were not specifically excluded). In summer within the Antarctic Circle ($66^\circ 33' 46.9''$ S), the light period extends up to 24 h due to the earth's rotation and angle of inclination, therefore bins collected within the 24 h of light period were flagged as day.

Day and night profiles of mean S_v were used to evaluate effects of diel cycles on vertical distribution of MTLO. Similar to the analysis of horizontal spatial

distribution patterns, CSS were fitted to S_v horizontally averaged at 10 m depth resolution in the Central region (see region definition below) for each transect, to summarise temporal and vertical distribution patterns while removing the small-scale stochasticity. Vertical bands of backscatter of varying depth were defined by season and time of day, using a subjective assessment of the shape of the CSS fitted to the backscatter profile and the depth that the main CSS features occupy, allowing a minimum difference in mean S_v between adjacent bands (i.e. >0.9 dB). To obtain the mean S_v in each band, we first averaged the mean S_v of each CSS within a vertical band, and then calculated mean S_v across the CSS of the transects grouped by day and night and season.

Acoustic transects were split into 3 latitudinal regions to remove bottom depth effects on s_a detected in the northern region (see Escobar-Flores et al. 2018, this volume), and to focus the analyses in the most consistently sampled and topographically uniform region of the area of study (see Figs. 1 & S5 in the Supplement). Transects were split into Northern and Central regions using the 1500 m depth beyond the shelf break into the South Pacific Basin as cut-off point. The southern limit of the Central region

was defined by data availability, with data from almost all transects available to 67° S. The Southern region was defined from 67° S to the southernmost limit of the transect, which was variable and determined by the start of the fishing operation. The Southern region was defined so the southernmost end of the long transects would not affect the comparison of backscatter in the Central region. Mean s_a by pelagic zone, region, day/night, and season is summarised in Tables S2 & S3 in the Supplement. Analyses of vertical distribution of backscatter were focussed on the Central region only.

Biological sampling

Biological information on mesopelagic organisms was opportunistically collected by TAN on 3 research voyages (voyage codes: TAN0802, TAN1116 and TAN1502) carried out within the area of study by the National Institute of Water and Atmospheric Research (NIWA) in 2008, 2011 and 2015, respectively. A total of 51 trawls were used to characterise species' composition in the Northern (25), Central (7) and Southern (19) regions (Fig. 2, Table S4). Sampling

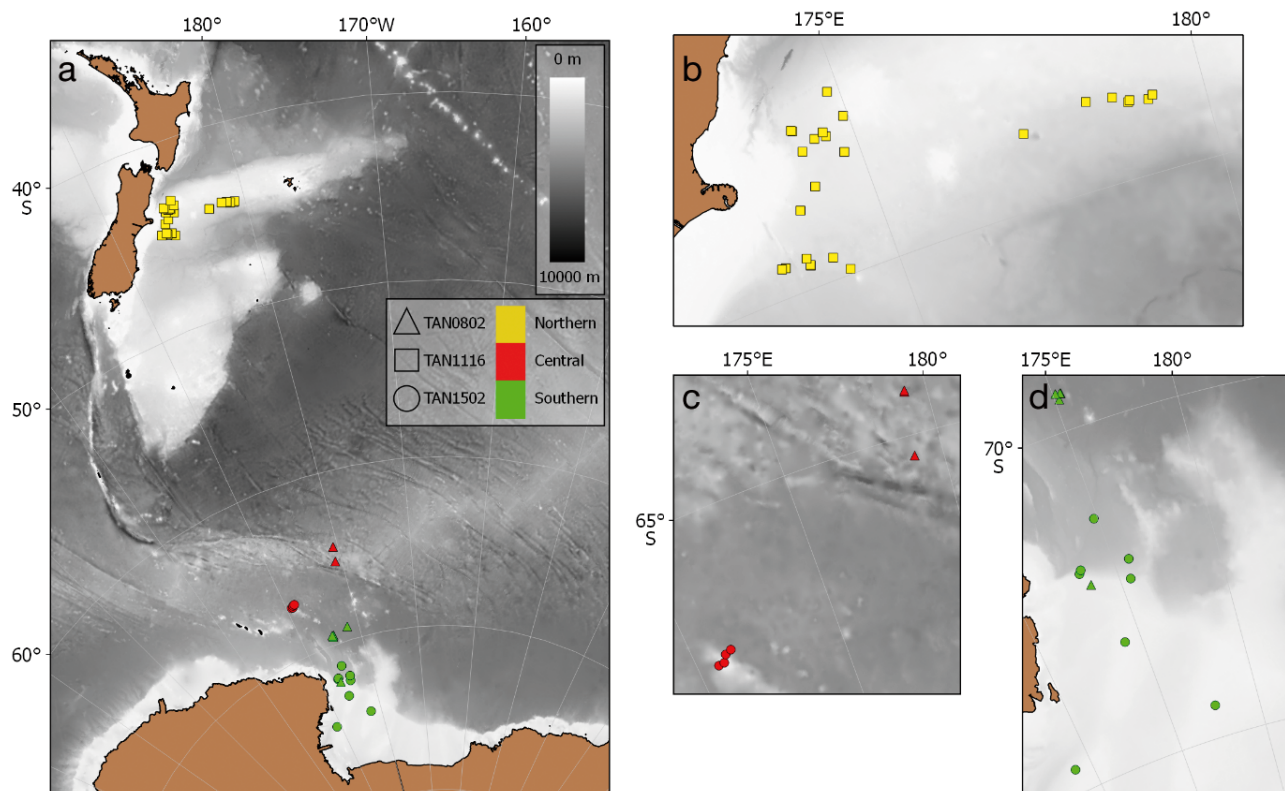


Fig. 2. Location of trawls in the area of study from (a) the 3 research voyages: TAN0802 (triangles), TAN1116 (squares) and TAN1502 (circles), and within each region: (b) Northern (yellow), (c) Central (red) and (d) Southern (green)

gear was a fine mesh midwater trawl net with a 10 mm cod-end mesh and a headline height of 12 to 15 m, with a door spread of around 140 to 160 m. This midwater gear is similar to the International Young Gadoid Pelagic Trawl (IYGPT), recommended by the Census of Antarctic Marine Life for sampling pelagic fish layers (www.caml.aq). Two types of tows were carried out: those used for acoustic mark identification (referred hereinafter as mark ID); and oblique (OB) tows. Mark ID tows were carried out during day or night and had variable duration (10 to 40 min). For mark ID, the net was towed at the depth of the scattering layer of interest at speeds of 3 to 4 knots. Most OB tows were carried out at night-time to characterise MTLO diversity, from 50 m off the seabed up to the surface, at an ascent speed of 20 m min^{-1} , and vessel speed of 3 knots. Details of all tows is provided in Table S4.

Trawl catches were sorted and identified to species' taxonomic level. The information from both trawl types was used to characterise the species composite of each region, though we focussed on the dominant mesopelagic fish species (by number and occurrence across tows). We assumed that the species composition drawn from the tows was representative of each region. Species having only an incidental occurrence in the catches and those poorly represented in the catches were excluded.

RESULTS

Comparison of backscatter amongst transects and temporal variability

A complete summary of mean s_a for all transects is provided in Table S1 in the Supplement. In the TAN multifrequency data, mean s_a in the epipelagic zone was within one order of magnitude across frequencies and was generally higher when measured at lower frequencies (i.e. 18, 38 and 70 kHz). In the mesopelagic zone, the comparison of mean s_a showed that transects collected at 18 and 38 kHz showed typically higher backscatter, which was expected due to the shorter range reached at 70 kHz due to attenuation. Mean s_a varied by less than one order of magnitude when excluding transects collected at 70 kHz, with the maximum and minimum observed in transects collected at 38 kHz in TAN 2008 SO-NZ and SAS 2011 NZ-SO, respectively.

When averaged over the whole transect, mean s_a (epi- and mesopelagic zones vertically summed) varied amongst all the 38 kHz transects but was still within one order of magnitude (transect mean $s_a \pm \text{SD}$: $13.8 \pm 3.31 \text{ m}^2 \text{ km}^{-2}$; Fig. 3, Table S1). Mean s_a in the most consistently sampled latitudinal region (i.e. Central; see Fig. 1) was also within one order of magnitude (transect mean s_a : $12.6 \pm 3.36 \text{ m}^2 \text{ km}^{-2}$;

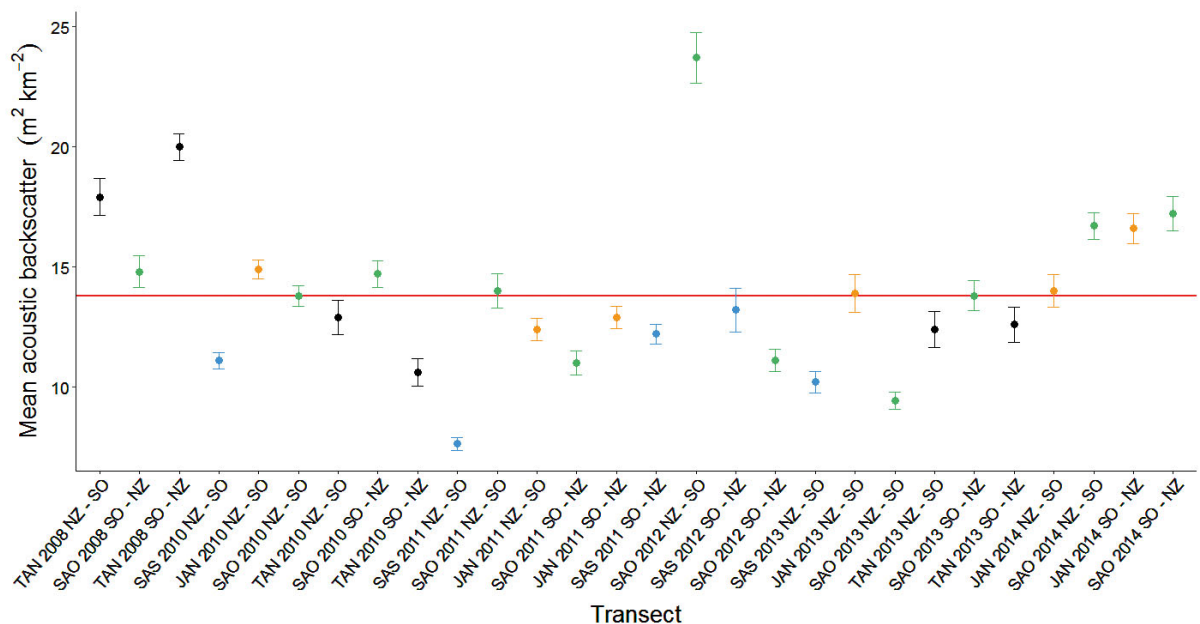


Fig. 3. Transect mean acoustic backscatter ($\text{m}^2 \text{ km}^{-2}$) in chronological order (see transect collection dates in Table S1 in the Supplement) by vessel: 'Janas' (JAN; orange), 'San Aotea II' (SAO; green), 'San Aspiring' (SAS; blue) and 'Tangaroa' (TAN; black). Whiskers: 2 times the SE of the mean; red line: grand mean (across all transects) acoustic backscatter (s_a) ($13.8 \text{ m}^2 \text{ km}^{-2}$)

Table S3). This suggests an overall consistency of s_a levels over the 7 yr period. Maximum mean s_a was observed along transect SAO 2012 NZ-SO, which was more than 3 times higher than the lowest mean s_a detected on transect SAS 2011 NZ-SO. Along transect SAO 2012 NZ-SO, high mean s_a was heavily influenced by the presence of strong levels of backscatter in the epipelagic zone over the Campbell Plateau (Fig. 4). The low mean s_a observed along transect SAS 2011 NZ-SO was due to signal degradation, likely caused by inclement weather conditions leading to the presence of different types of noise and signal attenuation (Fig. 4). Noise- and attenuation-filtering algorithms were applied to the data; however, evidence suggests that even after the application of filters, backscatter reductions can still be as high as 50% (ICES 2017). This transect also only started close to 50° S, missing areas of apparent high s_a concentration shown by other transects located farther north.

Latitudinal distribution of backscatter

Acoustic transects collected at 38 kHz showed a consistent and well defined decrease in vertically

summed s_a from north to south (see Fig. S6 in the Supplement). Out of 28 transects, 27 showed a highly significant negative slope from north to south for the total pelagic zone ($p < 0.001$). The only transect that did not show a significant north–south pattern (SAS 2013 NZ-SO) did not extend very far north or south (transect latitudinal extend 49 to 61° S) in relation to the other transects of our data set (see Fig. 1). All linear models fitted to epipelagic zone s_a showed a highly significant negative slope ($p < 0.001$), but only 25 transects showed a statistically significant negative trend in the mesopelagic zone ($p < 0.001$), and one transect (SAS 2013 NZ-SO) showed a significant positive north–south slope ($p < 0.001$). The significant positive north–south slope in SAS 2013 NZ-SO was again likely due to transect location, which did not extend far enough south of NZ.

Two further latitudinal patterns were detected by fitting the CSS. The first was a peak in the vertically summed s_a around 47° S followed by a drop around 50° S (Fig. 5). This was related to bathymetry, with lower backscatter usually measured in shallow areas (<1000 m) over the Campbell Plateau. The second feature was an undulating pattern along the transect (see Fig. 5) which was due to DVM. DVM effects on s_a are discussed in the ‘DVM pattern’ section.

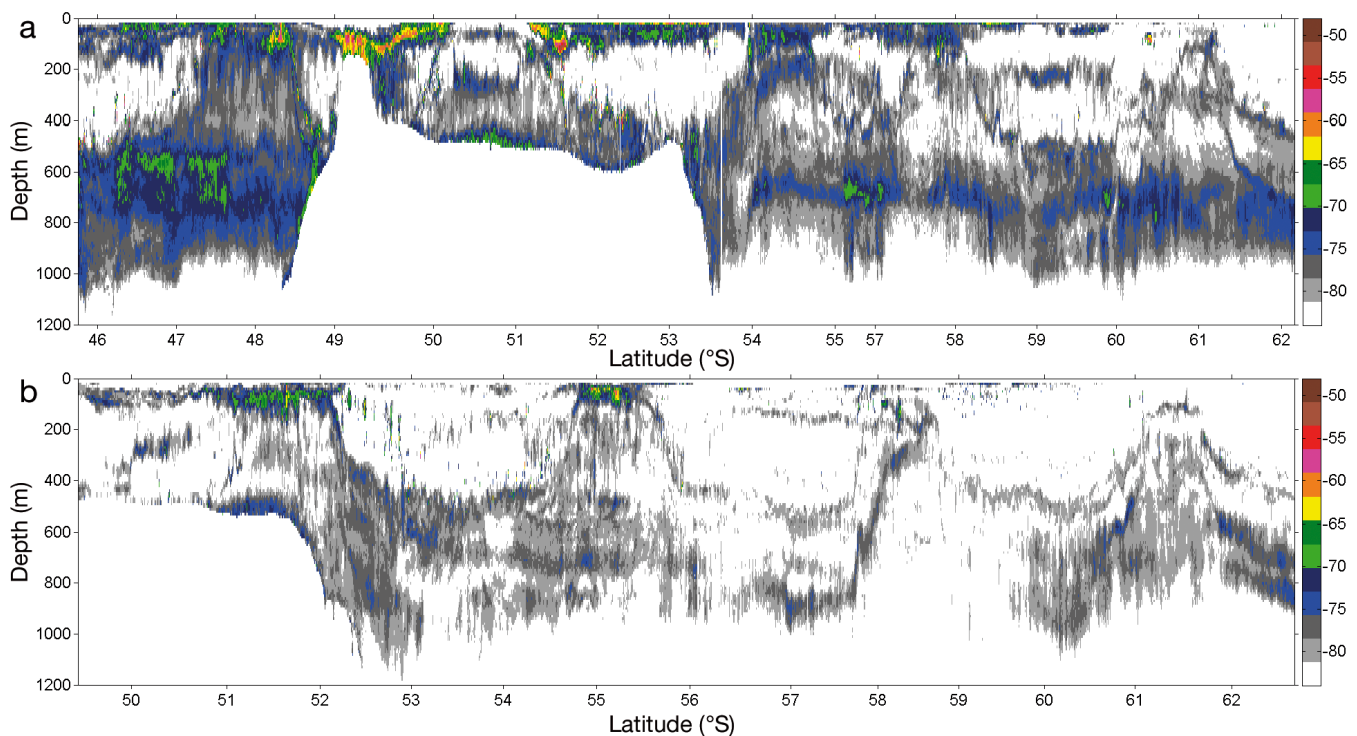


Fig. 4. Echogram of transects collected by vessels (a) ‘San Aotea II’ (SAO) in 2012 and (b) ‘San Aspiring’ (SAS) in 2011 between New Zealand (NZ) and the Southern Ocean (SO) showing particularly high (SAO) and particularly low (SAS) levels of mean backscatter. Each pixel represents mean volume backscattering strength (S_v) in decibels (dB) echo-integrated in 1 km long and 10 m depth bins. Echogram threshold: -84 dB. Note difference in latitude scale on x-axes

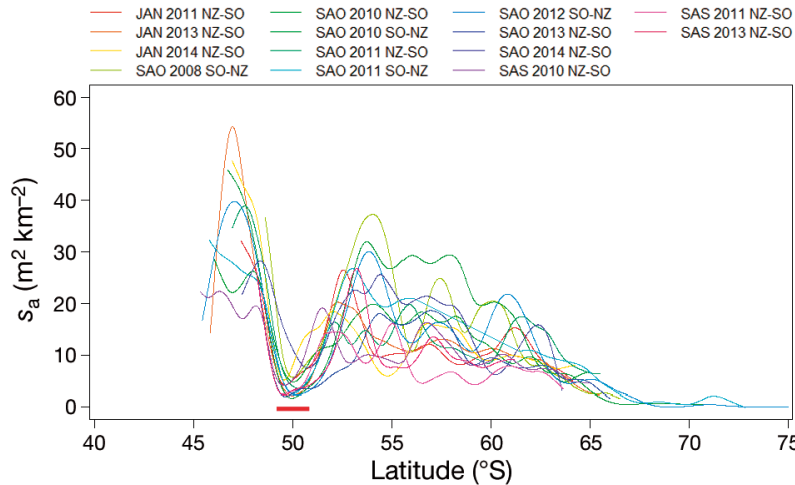


Fig. 5. Cubic spline smoothers fitted to vertically summed acoustic backscatter (s_a) in $\text{m}^2 \text{km}^{-2}$ per bin to a group of transects collected at 38 kHz centred longitudinally around 175°E (see Fig. 1). Red bar: approximate location of the Campbell Plateau (around 50°S), located between the Bounty Trough (north) and the South Pacific basin (south). See Table S1 in the Supplement for transect collection dates and vessel abbreviations

Vertical distribution of backscatter

Analysis of vertical distribution focussed on the Central region because it had the most consistent sampling effort over time and is a deep ocean basin (deeper than 1500 m), allowing mean s_a comparisons which were not impacted by varying integration depth. There was a statistically significant difference between mean s_a during the day (lower) and at night (day, 11.6 and night, $14.6 \text{ m}^2 \text{km}^{-2}$) (Fig. 6). In the epipelagic zone, night mean s_a was about 2.5 times higher than day mean s_a . Conversely, mean s_a in the mesopelagic zone at night was only marginally higher ($10.3 \pm 8 \text{ m}^2 \text{km}^{-2}$) than mean s_a measured during the day ($9.9 \pm 9.3 \text{ m}^2 \text{km}^{-2}$), though the bootstrapping test showed that the difference was still statistically significant.

DVM pattern

As already noted, DVM behaviour was clearly visible in echograms (see Fig. 4), and plots of vertical distribution of backscatter in the Central region further highlighted day/night effects (Fig. 7). Vertical distribution of S_v was variable between the surface and 1200 m, but there were consistent patterns. The key vertical features present in all transects were the presence of peaks, normally below 400 m, which were indicative of s_a associated with deep scattering layers (DSLs); and the consistent difference between day and night vertical distribution, characterised by a higher night mean S_v in the upper 400 m (e.g. Fig. 7). DSLs are defined as continuous acoustic layers formed by organisms that cannot be individualised, showing migratory, semi-migratory or stationary behaviours

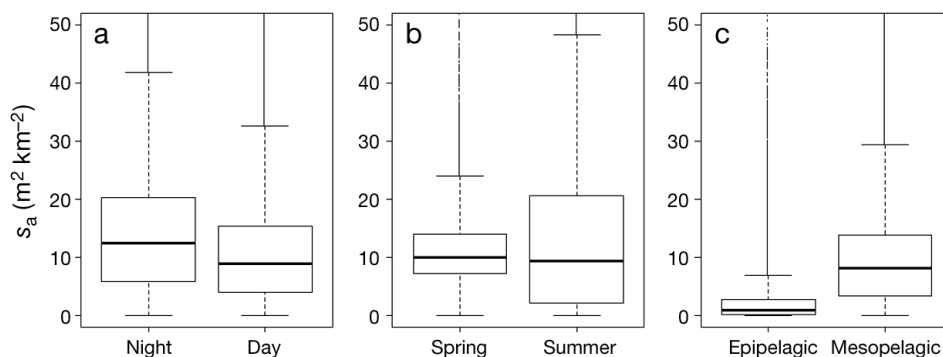


Fig. 6. Acoustic backscatter (s_a ; in $\text{m}^2 \text{km}^{-2}$) in the Central region by (a) day and night, (b) season and (c) pelagic zone, combining all transects' elementary distance sampling units (EDSU) or bins within the region. Bars: median; boxes: interquartile range (IQR); whiskers: range of data within $1.5 \times \text{IQR}$ of lower/upper quartiles; data beyond whiskers: outliers

Seasonally (day and night, and both pelagic zones combined), summer mean s_a ($13.2 \pm 13.5 \text{ m}^2 \text{km}^{-2}$) was higher than spring mean s_a ($11.4 \pm 7.3 \text{ m}^2 \text{km}^{-2}$) (Fig. 6), and this difference was statistically significant as shown by bootstrapping at the 95% level. The observed summer increase in mean s_a occurred across the entire water column but mostly in the epipelagic zone during the day. Interannual variability in mean s_a was lower in the epipelagic zone than in the mesopelagic zone (see Fig. S7). Mean backscatter per transect and bootstrap generated backscatter distributions with 95% confidence intervals for statistical tests in the central region are available in the Supplement (Table S3, Figs. S8 & S9).

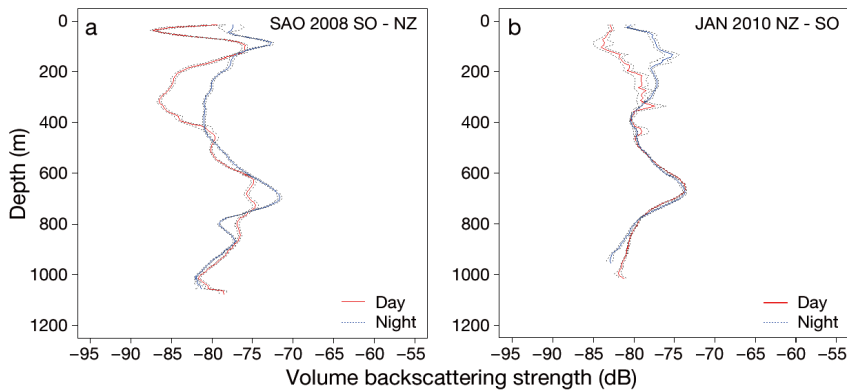


Fig. 7. Vertical distribution (between the surface and 1200 m) of mean volume backscattering strength (S_v ; in dB) in the Central region along transects collected by vessels (a) 'San Aotea II' (SAO) and (b) 'Janas' (JAN), during fishing years 2008 (summer) and 2010 (spring), correspondingly. Red line: day; blue line: night; dotted grey lines: 90% confidence intervals (Student's t -test, 0.90). Panels correspond to individual transects

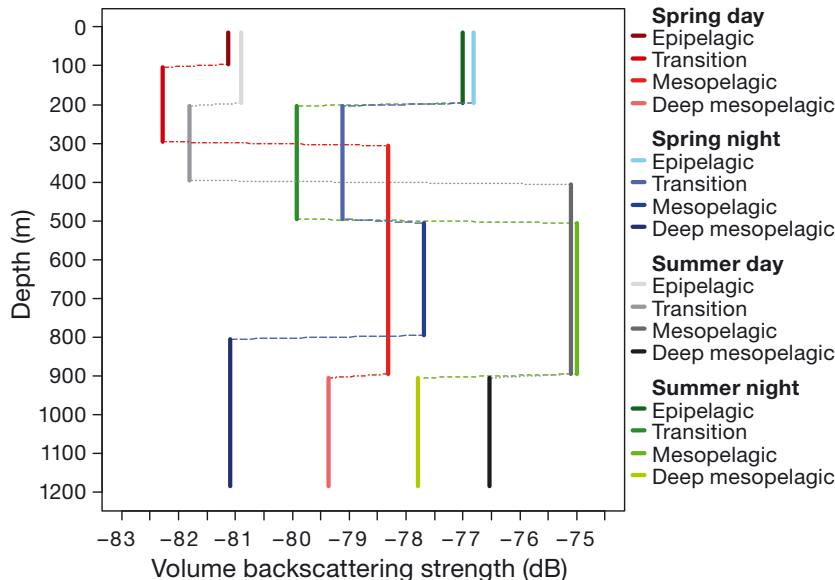


Fig. 8. Vertical distribution of backscatter in 4 vertical bands by season and day and night. Vertical bands were defined using the dominant patterns of vertical distribution observed by fitting cubic spline smoothers to the vertical distribution of volume backscattering strength (S_v) for individual transects

(Tont 1976). Plots of vertical distribution of mean S_v for all transects are available in Fig. S10.

Summary of the vertical distribution of acoustic backscatter using CSS

A CSS was fitted to day and night vertical mean S_v (horizontally averaged at 10 m depth resolution) of each transect (vertical CSS fits for all transects available in Figs. S11–S14). The CSSs suggested 4 distinc-

tive vertical bands of backscatter, which described not only the main features of the vertical distribution by day and night but also highlighted the seasonal differences, and are summarised in Fig. 8. The terminology used to define the vertical bands does not follow the traditionally accepted depth range definitions for epi- and mesopelagic zones (based on light penetration) or our extended definition for the mesopelagic zone (i.e. 1200 m), but was based upon the zones that the bands of backscatter mostly occupied.

The first vertical band was the 'epipelagic band'. This band, always located within the epipelagic zone, usually extended down to 200 m but during the day in spring it only reached down to 100 m (Fig. 8). This band showed moderate levels of backscatter which were higher at night in both seasons (mean S_v in spring and summer around -80 and -76 dB at day and night).

The second, 'transition band', was characterised by a convex curvature in CSS fits as mean S_v declined vertically between 100 and 500 m. At night in both seasons the transition band extended between 200 and 500 m, while during the day in spring it was shallower (100 to 300 m). The transition band normally had relatively low backscatter, with mean S_v levels around -82 and -79 dB during day and night in both seasons (Fig. 8).

The third band, the 'mesopelagic band', was in the mesopelagic zone, and had the highest backscatter levels reaching mean S_v values of -75 dB in

summer and more moderate values in spring (approx. -77 and -78 dB). This band extended between 300 and 400 m, down to 900 m during the day in spring and summer, and down to between 500 and 800 m at night in spring, and 900 m in summer (Fig. 8).

The deepest band was named the 'deep mesopelagic band'. This band showed variable backscatter values and was affected by range limitation of the 38 kHz echosounder. In general, levels of mean S_v in this band were higher in the day than at night in a given season (Fig. 8).

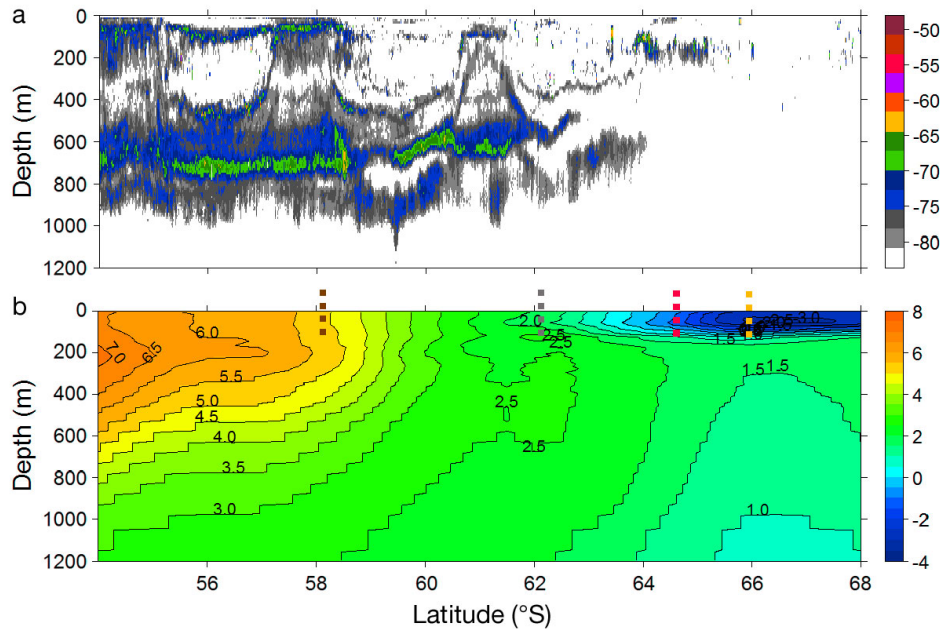


Fig. 9. (a) Acoustic echogram of transect collected by vessel ‘San Aotea II’ in 2010 between the Southern Ocean (right) and New Zealand (left). Each pixel represents mean volume backscattering strength (S_v) in decibels (dB) echo-integrated in 1 km long and 10 m depth bins. Minimum echogram threshold: -84 dB for visualisation purposes only. (b) Profile of mean temperature for the period of data collection and along the acoustic transect, retrieved from regional hydrographic climatologies using the CSIRO Atlas of Regional Seas (CARS). Dotted line segments on the top of panel (b) indicate the approximate position of Southern Ocean fronts as defined by Sokolov & Rintoul (2009): Sub-Antarctic front (brown), Polar front (grey), and the northern (red) and southern (yellow) branches of the Southern Antarctic Circumpolar Current (ACC) front

Latitudinal effects of temperature in mesopelagic layers

Mesopelagic scattering layers deeper than 200 m stopped in the northern area of the RS (e.g. Fig. 9). This was observed consistently over time and across transects, regardless of the longitude where transects reached the northern area of the RS. The latitude where mesopelagic layers stopped was always within 1 or 2 degrees of latitude around 62°S . Temperature profiles (e.g. Fig. 9) suggest that scattering layers could be negatively affected by water masses colder than 2.0°C at depths >200 m. Although the confounding negative temperature–depth effect seems to affect all layers equally (see Fig. 9a), the layer centred around 600 m depth typically stopped farther north at slightly warmer temperatures (approx. 2.5°C). Using boosted regression tree models (BRT) (Elith et al. 2008), following Escobar-Flores et al. (2018, this volume), we explored the relationship between backscatter and temperature (from climatologies) in the mesopelagic zone. We found that temperature had a significant effect on backscatter (95% confidence intervals using 500 bootstrap samples) and explained 20% of the deviance. The rela-

tionship depicted by the models supports a drop in mesopelagic backscatter around 2°C (see Fig. S15 in the Supplement), though more dedicated studies including *in situ* biological and physical sampling are needed for validation. Our findings suggest that organisms making up these layers or their targeted prey species might be physiologically limited by water temperatures.

Species composition

As inferred from trawl catches, species diversity in the 3 regions was dominated by fish, followed by crustaceans and squids (Table 2). In the Northern region, the myctophid *Lampanyctodes hectoris* and the stomiiform *Maurollicus australis* were the dominant species by number in 19 and 2 trawls, respectively. The myctophid *Electrona antarctica* was the dominant species in 5 out of 7 trawls in the Central region. In the Southern region, the Antarctic krill *Euphausia superba* and *E. antarctica* dominated in 5 trawls, and the myctophid *E. carlsbergi* and the Antarctic silverfish *Pleuragramma antarctica* in 4 and 3 trawls, respectively. Although the split of the area

Table 2. Number of trawl-caught species collected by the National Institute of Water and Atmospheric Research (NIWA) in 3 research voyages in 2008, 2011 and 2015 in the study area by taxonomic group and region

Taxonomic group	Species collected		
	Northern region	Central region	Southern region
Fish	61	28	23
Crustacean	13	6	4
Squid	8	9	9
Jelly ^a	1	3	3
Siphonophore ^a	1	–	–
Ctenophore ^a	1	–	–
Salps ^a	1	–	–
Tunicate ^a	1	1	1
Gastropods ^a	1	–	–
Leptocephali	1	–	–
Total	90	37	40

^aOrganisms not taxonomically identified to species level

of study into 3 regions was not based on biological or ecological factors primarily, each region was dominated by different species and had at least one species that was not present elsewhere (e.g. *L. hectoris* was only present in the Northern region and *P. antarctica* only present in the Southern region), which supported our split. Detailed information of species composition by region is available in the Supplement (Tables S5–S7).

The most commonly caught fish species, based on their average contribution across trawls in number, weight and occurrence per region, are shown in Table 3. By number and weight, myctophids dominated the fish fauna in the Northern (*L. hectoris*) and Central (*E. antarctica*) regions, while the notothenioid *P. antarctica* had the highest average contribution in the Southern region. Despite being only the third most important species in number, the myctophid *E. antarctica* was the fish species most commonly caught (11 trawls) in the Southern region. In addition to latitudinal changes in species dominance, the individuals of the most commonly caught species in the Central and Southern regions were typically of larger size than those from the Northern region. Other than fish, the Northern and Central regions were dominated by salps (average contribution when present of 20.3 and 35.8%, respectively), and the Central and Southern regions were dominated by weight by jellyfish (average contribution when present of 42.6 and 23.2%, respectively). Similarly, *E. superba* had the highest average contribution by number in the Southern region (64.1%).

DISCUSSION

This paper presents the first time series of data on acoustic backscatter in the SO, based on 7 yr of opportunistically collected data. Consistent spatial and vertical distribution patterns were detected, which were related to latitude, bathymetry, diel cycles, seasonality and water temperature. As our data collection and analysis protocols were consistent over time, we assume that 38 kHz backscatter provide a useful relative abundance index for MTLO, as long as the species composition and behaviour do not change substantially over time.

Resonance scattering, a well described and studied phenomenon in gas-bearing organisms (e.g. Kloser et al. 2016), might invalidate our assumption of backscatter as a proxy for MTLO abundance (see Davison et al. 2015a). Some studies have associated resonance of mesopelagic species to low frequencies (i.e. 18 kHz; e.g. Kloser et al. 2002, Godø et al. 2009); however, species whose swimbladders regress in adult stages or individuals of small size (<4 cm) might still resonate at depth at 38 kHz (Peña et al. 2014, Davison et al. 2015a, Kloser et al. 2016). For example, Kloser et al. (2016) showed that organisms 3.5 cm long with an equivalent spherical radius gas-bladder size of 0.7 mm could resonate at 750 m depth. The limited biological information derived from our trawl data indicated that most mesopelagic fish caught were larger than 4 cm. The incidence of small mesopelagic fish (<4 cm) (e.g. bristlemouths *Cyclothone* spp.) and fragile organisms (e.g. siphonophores) capable of resonating at 38 kHz (Kloser et al. 2002, 2016, Godø et al. 2009, Peña et al. 2014) in our samples was negligible, but this could represent bias due to our sampling gear (relatively large midwater trawl). Further acoustic sampling and modelling as well as biological sampling using different gears are needed to disentangle whether backscatter trends observed represent MTLO density or transitions between species and communities or differences in spatial size distribution, or a combination of these factors.

Variability was observed between transects, years and seasons, but no trends in backscatter were evident over the 7 yr study period, which is supported by statistical analyses presented in Escobar-Flores et al. (2018, this volume). This relative stability could suggest that mesopelagic fish populations in the SO have not been affected by climate-induced effects, but our time series is probably too short to capture such effects. Continuous plankton recorder data from 2002 to 2013 in the NZ sector of the SO (Robinson et al. 2014), estimates of mesopelagic fish biomass on

Table 3. Fish species that contributed on average >2% by number across trawl catch and were present in at least 2 trawls (Occurrence)

Species	Mean contribution in number (%)	Mean contribution in weight (%)	Occurrence	Mean length (cm)
Northern region				
<i>Lampanyctodes hectoris</i>	70.8	39.2	22	5.2
<i>Maurolicus australis</i>	11.7	6.9	24	4.4
<i>Protomyctophum</i> spp.	8.2	2.3	20	5.5
<i>Gymnoscopelus piabilis</i>	6.9	4.8	10	9.2
<i>Electrona carlsbergi</i>	4.3	3.6	15	7.2
<i>Lampanyctus</i> spp.	3.3	5.0	16	9.3
<i>Symbolophorus boops</i>	1.7	5.0	14	8.7
<i>Diaphus</i> spp.	1.0	3.1	19	9.6
Central region				
<i>Electrona antarctica</i>	38.2	18.7	6	6.7
<i>Protomyctophum</i> spp.	18.5	10.1	2	4.1
<i>Bathylagus antarcticus</i>	12.5	18.7	3	12.2
<i>E. carlsbergi</i>	10.3	12.4	4	7.3
<i>Gymnoscopelus braueri</i>	9.2	7.5	4	21.7
<i>Cyclothone microdon</i>	8.5	3.7	4	5.9
<i>Gymnoscopelus nicholsi</i>	5.8	13.8	6	14.9
<i>Notolepis coatsi</i>	3.5	5	5	15.4
<i>G. opisthopterus</i>	2	4.4	3	14.9
Southern region				
<i>Pleuragramma antarctica</i>	51.4	44.4	7	13.2
<i>E. carlsbergi</i>	37.0	23.2	7	7.9
<i>E. antarctica</i>	21.4	8.4	11	7.4
<i>B. antarcticus</i>	15.9	18.7	9	12.2
<i>Neopagetopsis ionah</i> ^a	12.9	35.3	5	38.5
<i>C. microdon</i>	12.9	4.5	5	6.3
<i>G. braueri</i>	11.8	10.7	5	22.9
<i>N. coatsi</i>	9.6	6.6	10	15.5
<i>G. opisthopterus</i>	6.0	13.1	7	13.6
<i>G. nicholsi</i>	5.1	8.1	9	14.9
<i>G. hintonoides</i>	2.1	5.7	5	11.3
<i>G. bolini</i>	1.8	14.4	2	22.9

^aInfluenced by 2 trawls with 11 and 13 individuals of *N. ionah* over a total catch of 21 and 111 individuals, respectively. When these trawls were removed contribution dropped to <0.2%

the Chatham Rise (east of NZ) between 2001 and 2007 (O'Driscoll et al. 2009), and primary productivity in the SO between 1997 and 2006 (Arrigo et al. 2008) have also shown variability but no temporal trends. However, our study provides a baseline for detecting potential future changes in the levels of backscatter in the NZ sector of the SO. If opportunistic acoustic data collection and post-processing continues, it will be possible to deliver a consistent acoustic data set for studying MTLO. Ideally, we would like to establish a long-term (multi-decadal) ecological time series. Such series are rare but can provide the basis for establishing long-term scientific strategies for marine ecosystem management (Edwards et al. 2010).

Acoustic backscatter decreased significantly from north to south for almost all transects collected across the SO. A north–south latitudinal pattern between tropical and Antarctic waters was also described in the southern Indian Ocean (Béthagle et al. 2016). This suggests that the overall latitudinal pattern may extend across the SO. However, our limited trawl information showed that the composition of the MTL community also varied from north to south between the regions, so the apparent north–south decrease in backscatter may be related to the changes in species' composition as well as abundance. Similarly, Fielding et al. (2012) concluded that latitudinal trends in backscatter in the Scotia Sea, with higher levels in the north than farther south, were most likely due to differences in species composition.

DVM, observed in all transects, is a common behaviour of mesopelagic fish, which occur between the bathy-, meso- and epipelagic zones (Catul et al. 2011). In general, organisms ascend around sunset and descend around sunrise, although different DVM patterns have been described. For example, Watanabe et al. (1999) described 4 types of DVM patterns in the western North Pacific Ocean: migrant (surface and midwater), with clear differences between day and night distribution; semi-migrant, where part of the population migrates; passive-migrant, in which the limits of the daytime vertical

distribution of the organism expand but there is no separation of the layer as such; and non-migrant. Conversely, in the Canary Islands (Northeast Atlantic) Ariza et al. (2016) identified 4 distinct DSLs and described only 2 DVM patterns (migrant and non-migrant).

In the whole water column (down to 1200 m) night s_a was higher than day s_a because of DVM cycles, which could be related to migration of organisms from deeper waters, and/or changes in scattering properties. We observed evidence of migration of organisms into and out of the mesopelagic zone from deeper zones, but this was limited to one transect (see Fig. S16 in the Supplement). Because DVM alters swimbladder volume (pressure-induced), it

changes acoustic target strength (TS) (Johnson 1977, Huse & Ona 1996, Godø et al. 2009). DVM may influence fish tilt angle (but see Janssen et al. 1986), which also changes TS (MacLennan & Holliday 1996, MacLennan et al. 2002, Godø et al. 2006). Higher backscatter observed at night in the mesopelagic zone could also relate to resonance scattering (e.g. Hersey et al. 1961, Godø et al. 2009).

Four characteristic vertical bands were described in the Central region: epipelagic, transition, mesopelagic and the deep mesopelagic band. Backscatter in all bands likely consists of nektonic and planktonic organisms with different acoustic properties, including fish, squid and zooplankton.

In the SO, there are no true epipelagic fish families (Sabourenkov 1990, Rodhouse & White 1995), and only near the Antarctic continent (e.g. Southern region) a few nototheniids have adapted to the pelagic habitat (e.g. *Pleuragramma antarctica*) (Rodhouse & White 1995). In the oceanic area of the SO meso- and bathypelagic, pelagic fish dominated the catches, and this was in agreement with previous research (e.g. Kock 1992, Pusch et al. 2004). Limited information from NZ waters suggest that mesopelagic fish are the main contributors of backscatter measured at 38 kHz in the epipelagic zone (e.g. Robertson et al. 1978, McClatchie & Dunford 2003, Gauthier et al. 2014). For example, *Symbolophorus boops* and *Electrona carlsbergi* are species that during the day distribute in the upper 200 m (McGinnis 1982), and both species were commonly caught in the Northern (*E. carlsbergi* and *S. boops*) and Central (*E. carlsbergi*) regions. Myctophid larvae could also contribute to epipelagic backscatter in spring and summer. After spending their pre-larvae and egg stages in the mesopelagic zone over autumn and winter, myctophid larvae migrate to the epipelagic zone in spring (Efremenko 1986, Sabourenkov 1990), where more than half of the zooplankton biomass within the first 1000 m concentrates (Atkinson et al. 2012).

Fish such as myctophids and gonostomatids are consistently recognised as the most important component of mesopelagic layers worldwide (Catul et al. 2011, Peña et al. 2014). In the SO, the biomass, abundance and diversity of mesopelagic fish is dominated by myctophids (Gjøsaeter & Kawaguchi 1980, Pusch et al. 2004), which are mostly located below 400 m during the day (Torres & Somero 1988, Collins et al. 2012). In our samples, myctophids were also the most commonly caught mesopelagic fish in all regions, and were represented mainly by the genera *Lampantodes*, *Electrona* and *Gymnoscopelus*. However, in diverse MTL communities, trawl sampling effi-

ciency and selectivity can heavily misrepresent community composition, and bias catches towards larger specimens (more likely to be caught) (Brodeur & Yamamura 2005, Pakhomov & Yamamura 2010). For example, Peña et al. (2014) showed that the main source of backscatter and most abundant mesopelagic fish in waters of the western Mediterranean were bristlemouths *Cyclothone* spp., which were only caught by MOCNESS (multiple opening and closing net, with an environmental sensing system). These limitations make it difficult to obtain unbiased net-derived estimates of MTLO abundance, and interpret backscatter as a measure of their density and partition it into particular taxa without comprehensive sampling (Kaartvedt et al. 2012, Davison et al. 2015b, Kloser et al. 2016).

There are strong seasonal patterns in environmental conditions in the SO that affect temperature and light level regimes (Okada & Yamanouchi 2002), which restrict positive conditions for primary productivity and the higher trophic levels that rely on this seasonal productivity for reproducing and energy storage (Laws 1983, Murphy et al. 2007). Although seasonal differences in productivity and vertical distribution patterns of MTLO could be expected, the seasonal differences in backscatter in the epi- and mesopelagic zones were not large (e.g. Fig. 6). However, our transects only covered a short period in late spring and mid-to-late summer, so we were not able to observe the whole seasonal cycle.

Mesopelagic layers stopped consistently at latitudes south of 62° S and water depths greater than 200 m. Except for *Electrona antarctica*, which appear to have adapted to colder environments being widely distributed south of the Polar front in cold waters (-1 to 3°C) (Hulley 1981, Saunders et al. 2014), myctophids and other mesopelagic fish families lack anti-freezing glycoproteins or peptides. Circumpolar Deep Water (CDW) surrounds the RS between 150 and 2000 m depth, intruding up the continental slope (Russo 2000). From temperature profiles and echograms, we argue that warm CDW at intermediate depths is the last reservoir for mesopelagic fish species inhabiting these latitudes, since scattering layers stopped near waters colder than 1.5°C, located close to the southern branch of the Southern Antarctic Circumpolar Current front (SACCF) (Sokolov & Rintoul 2002).

A similar relationship has been proposed in other regions of the SO. Warm CDW waters hold higher species diversity (Pusch et al. 2004) and abundance than Antarctic surface waters (Piatkowski et al. 1994). When CDW intrudes into the shelf, the habitat

of species such as *E. antarctica* and *Gymnoscopelus braueri* expands (Donnelly & Torres 2008). Lancraft et al. (2004) found that myctophid species (other than *E. antarctica*) were only found sporadically or were absent in deep basins of the Croker Passage, which they linked to limited input of CDW warm water ($>1.5^{\circ}\text{C}$ at 200 m). Unlike at other locations of the Antarctic shelf, in the Western Antarctic Peninsula (WAP), myctophids are part of the fish community (Donnelly & Torres 2008). This has also been related to the intrusion of the CDW into cold shelf waters (Martinson et al. 2008), which also occurs periodically in the RS shelf (Orsi & Wiederwohl 2009). In the WAP, temperatures around 1.5°C coincide with sharp and distinctive changes in community assemblages. When CDW temperatures drop below 1.3°C , neritic and oceanic communities are very distinctive, but when temperatures are between 1.4 and 1.3°C near the shelf these 2 communities overlap. Conversely, water temperatures of 1.5°C seem to limit neritic species at their upper temperature limit (Donnelly & Torres 2008). Donnelly et al. (2006) also related low incidence of myctophids to cold temperatures (approx. 0°C) in the presence of favourable trophic conditions at the pack ice area at the marginal ice zone in the Weddell Sea.

Climate change has been linked to southward shifts of the Antarctic Circumpolar Current (ACC) and its fronts (Constable et al. 2014). Mesopelagic fishes that show preference for, or are physiologically limited by, certain water temperature ranges could expand their ecological niche within the SO as temperature fronts move south (Constable et al. 2014). These changes might have cascading effects on higher trophic levels. For example, a southward displacement of mesopelagic prey might mean predators that reside on the Antarctic continent have shorter feeding journeys to more abundant feeding grounds, with potential positive effects on their breeding performance.

Unfortunately, water temperature from *in situ* CTD casts or Argo buoys are not available for this southern region of the NZ sector of the SO, preventing further analysis of this apparent environmental limitation. As different mesopelagic layers disappear at different latitudes, it may be indicative of different temperature tolerances and therefore different species composition. Future research voyages to this region should include combined biological and physical sampling to help determine the environmental constraints on species' distribution.

Further research on acoustic methods is also needed. If the data collection and processing error in

the methodology is large, we will not be able to detect biological change. Common sources of process error in the collection and processing of acoustic data include physical calibration, hydrographic conditions (temperature and salinity affecting sound speed and absorption), transducer motion, attenuation due to surface bubbles and subjective decisions made during the grooming process (see Escobar-Flores 2017). There are also biological sources of uncertainty (e.g. species composition, survey timing and detectability). Future research should try to further quantify the different sources of uncertainty in the acoustic observations.

CONCLUSIONS

Acoustic data collected opportunistically over 7 yr between NZ and the SO was analysed and latitudinal (horizontal), vertical, annual, seasonal and diel pattern of s_a were described and discussed. Backscatter between NZ and the SO was reasonably stable, being on the same order of magnitude across all transects collected at 38 kHz. Vertically summed backscatter showed a negative, statistically significant north–south trend, which could be related to abundance but also to changes in species composition, size distribution and resonance scattering effects. Vertical distribution of backscatter provided compelling evidence of DVM patterns, suggesting that at night organisms migrate into the epipelagic and mesopelagic zones from deeper waters, or that the scattering properties of semi-migrant or passive migrant mesopelagic organisms change. Averaged backscatter by depth strata showed 4 distinctive vertical bands. These 4 bands captured the DVM effects, and showed seasonal differences/consistencies on backscatter in the epi- and mesopelagic zones. Mesopelagic scattering layers stopped consistently near the northern area of the RS, which may be linked to water temperature. More biological and physical information in this region is needed to establish the limiting temperatures and the species responsible of these scattering layers.

Our study demonstrated that acoustic data collected on-board vessels of opportunity provide useful information for studying and monitoring the MTLs of open-ocean marine ecosystems, and it established a baseline for future studies. We recommend endeavours for acoustic data collection, management and storage be continued and expanded, and encourage more ecological studies of the composition, structure and dynamics of the MTLs in the SO.

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