

Contents lists available at ScienceDirect

Deep-Sea Research Part II



journal homepage: http://www.elsevier.com/locate/dsr2

An acoustic method to observe the distribution and behaviour of mesopelagic organisms in front of a trawl

Melanie J. Underwood^{*}, Eva García-Seoane, Thor A. Klevjer, Gavin J. Macaulay, Webjørn Melle

Institute of Marine Research, PO Box 1870 Nordnes, NO-5817, Bergen, Norway

ARTICLE INFO	A B S T R A C T
<i>Keywords:</i> Forward-facing Trawl-mounted echosounder Mesopelagic Density Distribution Behaviour	We describe a method to allow acoustic sampling at depths not reachable by the higher frequencies of ship hull- mounted echosounders and observe the abundance and behaviour of individual organisms in front of trawls. A self-contained scientific echosounder with a 120 kHz transducer was mounted forward-facing on the headline of a macrozooplankton trawl that was obliquely towed from 0 to 1000 m depth, to investigate the mesopelagic fauna. With the use of a forward-facing echosounder, we were able to estimate organism densities in front of the trawl, the vertical profiles of organism target strength and the movement of organisms in front of the trawl. We demonstrate that a forward-facing trawl-mounted echosounder is a simple and useful method to investigate the distribution of mesopelagic fauna at depth.

1. Introduction

The mesopelagic zone is broadly defined as the part of the ocean located between 200 and 1000 m depth (Sutton, 2013), although recently it has been suggested that light intensity (ranging from 10^{-9} to 10^{-1} µmol quanta m⁻²s⁻¹) could be a better definition (Kaartvedt et al., 2019). Many of the macroplankton and micronekton (~2–20 cm length fish, shrimps and squids) found at these depths during daytime actively migrate to the epipelagic layer (0–200 m depth) at night, thereby contributing to the "biological pump" (Drazen et al., 2011; Davison et al., 2013; Sutton, 2013). Over the course of these diel vertical migrations, many mesopelagic organisms feed near the surface, and subsequently may release carbon in the form of defecation, respiration, and mortality below the depth zone in which most remineralisation occurs (Robinson et al., 2010; Davison et al., 2013).

The global mesopelagic fish biomass (primarily using net catch data) was estimated to be around 10⁹ t wet mass (Gjøsæter and Kawaguchi, 1980; Lam and Pauly, 2005). Net sampling has the advantage of allowing a precise taxonomic identification and also allows for length measurements of the individuals caught (Béhagle et al., 2016). However, all nets have selectivity issues due in part to avoidance and extrusion through meshes (Sutton, 2013). Recent acoustic-based estimates indicate a much higher abundance of mesopelagic fish, possibly up to 7–10 higher (Koslow et al., 1997; Kaartvedt et al., 2012), and if so,

mesopelagic fishes probably dominate the global fish biomass (Irigoien et al., 2014). Acoustic methods are useful for estimating mesopelagic organism biomass but require refinements to produce reliable and accurate results (Kloser et al., 2009). For example, reflected acoustic energy is not necessarily directly proportional to biomass (a basic assumption of many acoustic biomass surveys). Some organisms reflect very strongly due to frequency-dependent acoustic backscattering (e.g., resonance scattering), while other non-fish organisms such as siphonophores can contribute to the acoustic backscatter (Barham, 1963; Stanton et al., 1998). Knowledge of the composition and acoustic properties of the mesopelagic community is most likely necessary to accurately estimate mesopelagic fish biomass (Davison et al., 2015).

Ground-truthing of hull-mounted acoustic data by net sampling is a common method used for estimating biomass. This method has been widely applied for many species since the 1980's (Simmonds and MacLennan, 2005; ICES, 2015a; ICES, 2015b). However, methodological limitations occur when sampling small and weakly scattering species, especially at depth (Kloser, 1996; Kloser et al., 2009). For example, only low frequency (<100 kHz) hull-mounted echosounders have the measurement range necessary to reach mesopelagic depths which limits the use of multifrequency techniques (Simmonds and MacLennan, 2005), and sufficient data quality requires low sea states (Kloser, 1996). Echosounders mounted on towed vehicles have been used to reduce the range to the targets (e.g., Kloser, 1996; Moline et al., 2015; Knutsen

* Corresponding author. E-mail address: melanie.underwood@hi.no (M.J. Underwood).

https://doi.org/10.1016/j.dsr2.2020.104873

Received 31 December 2019; Received in revised form 28 August 2020; Accepted 2 September 2020 Available online 10 September 2020

0967-0645/© 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

et al., 2013). Although towed vehicles are beneficial, they increase survey time due to deployment and retrieval operations and often require a slower vessel speed than would be used for hull-mounted echosounders (e.g., 2.5 ms^{-1} compared to 5 ms^{-1}).

A method that can obtain higher frequency acoustic data at depth without consuming extra time is to attach echosounders to the trawls during the routine trawl hauls that are part of existing trawl-acoustic surveys. Such attachments with downward-looking echosounders have been used to improve the estimates of deep-water species (Ryan et al., 2009; Kloser et al., 2011). However, a downward-looking echosounder only detects individuals that are entering or are below the trawl, and hence only images organisms that have potentially reacted to the presence of the trawl. Changing the echosounder to forward-facing instead of downward-looking could measure individual organism behaviours in front of the trawl and provide estimates of density prior to any avoid-ance of the trawl.

Here, we describe a novel method to observe the reaction of mesopelagic species in front of a trawl, and to study the vertical and spatial distribution of these organisms. We discuss the potential uses of a forward-facing trawl-mounted echosounder and suggest improvements for future use.

2. Material and methods

A forward-facing trawl-mounted echosounder was attached to the headline of a macrozooplankton trawl (Fig. 1) deployed from R.V. "G.O. SARS" when operating to the east of the Reykanes Ridge in June 2018. The trawl was lined from the 5 m \times 8 m opening to the codend with 8mm mesh (stretched mesh, knot to knot, 3×3 mm square opening). A self-contained scientific echosounder system (SIMRAD Wide-Band Autonomous Transceiver (WBAT); SIMRAD Kongsberg Maritime AS, Horten, Norway) contained within a protective plastic cylinder was attached to the headline of the trawl (Fig. 1). This equipment was deployed on three hauls. The trawl was obliquely towed from the surface to 1000 m depth at an average trawling speed through water of 1 ms^{-1} . The echosounder was manually programmed to start recording soon after the trawl was deployed, to stop recording after 90 min, and to record data out to a range of 100 m. This arrangement provided data for most of the downward cast but typically only part of the upward cast due to the 90 min cut-off. Therefore, analysis was limited to the downward cast. A split-beam 120 kHz transducer with nominal 7° opening angle (ES120-7CD, SIMRAD Kongsberg Maritime AS, Horten, Norway) was used and operated in continuous wave (CW) mode with a ping interval

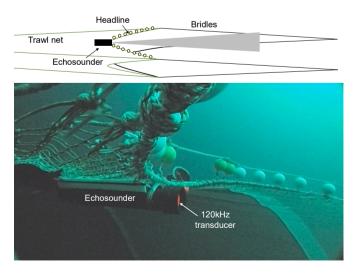


Fig. 1. The location of the trawl-mounted echosounder on the trawl headline (upper) and matching image from a trawl-mounted camera (lower). The shaded region (upper) shows the 3dB beamwidth of the transducer beam (7° beam).

of about 2 Hz, pulse duration of 0.256 ms and transducer power of 400 W.

The echosounder was calibrated using the standard sphere method (Demer et al., 2015) in Bjørnafjorden, Hordaland, Norway at the end of the G.O. Sars cruise (Fig. 2). The echosounder was calibrated using a tungsten carbide (with 6% cobalt binder) sphere of diameter 38.1 mm. The sphere was suspended approximately 6 m below the transducer (which itself was about 2 m below the surface) and moved throughout the beam while recording data. Subsequent to the data collection, the recorded files were processed using the calibration utility in the Simrad EK80 v1.12.2 program. The WBAT operated with a 100 W transmit power level and a pulse duration of 0.256 ms⁻¹. Measurements of seawater temperature and salinity were taken and used to derive a calibration-specific sound speed value. No correction was made for changes in calibration with depth, but this is expected to be less than 1 dB (Haris et al., 2017).

The hull-mounted Simrad EK80 echosounders were calibrated on April 30, 2018 in Sandvikflaket using the procedures set out in Demer et al. (2015). Trawl-mounted internally-logging pressure sensors (RBR Solo³, RBR Ltd, Ottawa, Canada) recorded the depth of the trawl during the oblique hauls. Two cameras (GoPro HERO6, GoPro Inc, San Mateo, USA) in pressure rated housings (Benthic 3; Group B Distribution Inc, Florida, USA) were mounted on the footrope and headrope of the trawl to observe the echosounder and other sensors on the trawl.

2.1. Data analysis

Data from one representative station were processed and analysed (station 419 on June 15, 2018 at 59° 21′ N, 22° 41' W, Fig. 2). This station had the best coverage of all sensors on the trawl throughout the haul.

2.1.1. Estimation of densities from single echo detections and comparisons with s_ν data

The Large Scale Survey System software (LSSS; Korneliussen et al., 2006; Korneliussen et al., 2016) was used to detect single echoes from mesopelagic organisms using a single echo detection algorithm (Ona, 1999; with settings of: minimum target strength = -90 dB re 1 m⁻², pulse length determination level = 6 dB, minimum echo length ratio = 0.6, maximum echo length ratio = 1.4, maximum beam compensation = 3 dB and maximum phase deviation = 10) and to calculate the volume backscattering coefficient (s_v; m⁻¹) in 20 m range bins.

We used single echo detections within the 3 dB beamwidth (i.e. with a 1-way beam compensation of less than 3 dB) to estimate organism densities per ping (ρ):

$$p = \frac{n_{sed}}{n_{ping} \times V_{obs}} \tag{1}$$

where n_{sed} is the number of detected single echoes. n_{ping} is the number of transmitted sound pulses and V_{obs} is the sampled volume, which was estimated as the volume of a cone, based on the nominal transducer 3 dB beamwidth, extending from the minimum to maximum sampling range (4–15 m). Densities were binned by 30 pings and then averaged per 20 m depth bin.

The volume backscattering coefficient (s_v ; m^{-1}) for the hull-mounted 38 and 120 kHz data was calculated after using the noise removal module in LSSS (Korneliussen, 2000). The average s_v per 20 m depth bin (between 14:23–14:57) was used to create a vertical profile. The vertical profile was compared with the direct density estimates from the echo counts and the s_v from the trawl-mounted 120 kHz data (per 20 m depth bin). The s_v for the hull-mounted 120 kHz was calculated to 300 m depth due to the range limitations of the frequency (see lower echogram in Fig. 3).

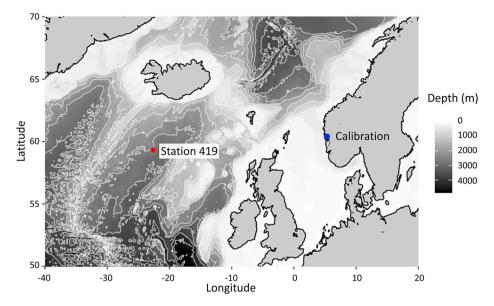


Fig. 2. Map of the trawl-mounted echosounder deployment and calibration locations. The blue diamond indicates the location of the deployment. The red circle shows the calibration location. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

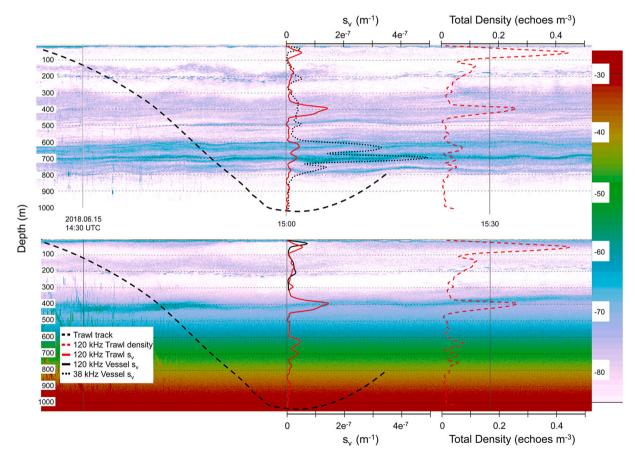


Fig. 3. Trawl-mounted (red solid and dashed lines) and hull-mounted (black dotted and solid lines) acoustically-derived vertical profiles of organism density. The background images are the echograms (upper 38 kHz and lower 120 kHz) used to produce the black dotted and solid curves, respectively. Total density (echoes m^{-3}) from the trawl-mounted 120 kHz acoustics is illustrated by the red dashed line, while the red solid line indicates the volume backscattering coefficient s_v (m^{-1}). The black dashed line indicates the trawl path. The colourbar on the right indicates the backscatter magnitude (S_v , dB re $m^2 m^{-3}$) for the echogram. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.1.2. Tracking individuals in front of the trawl

Tracks of individual organisms were extracted using the aggregation tracking module in LSSS (see Handegard (2007) for detailed description)

using settings of: minimum target strength = -90 dB, maximum gain compensation = 6 dB, track association settings of $\alpha_G = 1.5^\circ$, $\beta_G = 1.5^\circ$, $r_G = 1.2$ m, $I_G = 20$ dB, and target initialisation settings of $\alpha_0 = 1.5^\circ$, β_0

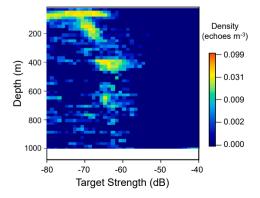
 $= 1.5^{\circ}, r_0 = 1.2 \text{ m}, I_0 = 20 \text{ dB}$. The α and β are the maximum alongship and athwartship angles within the beam accepted for subsequent target detection in a track (α_G , β_G) or initiating a new track (α_0 , β_0). r_G is the maximum change in range between subsequent target detection in a track, while r_0 is the maximum difference in range when initiating a new track. I_G is the maximum difference in sample energy between subsequent target detection in a track and I_0 is the maximum difference in sample energy when initiating a new track. The maximum number of successive missing pings within a track was set to 1 and tracks were manually scrutinized afterwards to verify appropriate tracking. Track length was limited to eight pings or greater to enable an individual to be tracked for an extended time (minimum track length = 8). Range from the echosounder was limited to 30 m. The swimming speed of the individual was corrected for trawl speed by subtracting the instantaneous mean movement of small targets (target strength of -65 dB or less, averaged per second) from the individual track speeds. Only the range from the trawl-mounted echosounder was included in the calculations of individual speed (vertical and horizontal movement were excluded). Individual speeds were also standardised to the beam area (total count/beam area for each 1-m range).

3. Results

3.1. Estimation of densities from single echo detections and comparisons with s_{ν} data

Two distinct layers (at 50 and 400 m depth) were observed during daylight with the trawl-mounted echosounder (Fig. 3). The densities inside the layers reached a maximum of about 0.44 echoes m^{-3} , whereas densities outside the scattering layers were on average 0.02 echoes m^{-3} . In addition, the target strength distributions differed between the two layers, with more weak targets (Fig. 4) at shallower depths (from 40 to 200 m). Most of the targets counted (95%) in the shallow layer were weak targets (lower than -65 dB), compared to 23% in the scattering layer around 400–440 m and 21% from 600 to 750 m (i.e., 77–79% of targets in the deep layers were stronger than -65 dB).

The vertical profiles from the trawl-mounted echosounder (density estimates and s_v) were markedly different to the vertical profile from the 38 kHz hull-mounted echosounder (upper echogram in Fig. 3). We assume that the peaks (higher values) are comparable and indicate a detected layer even though different frequencies and measures of density were used. The highest densities measured by the 120 kHz trawl-mounted echosounder occurred in the shallower layer (around 50 m), while the strongest scattering at 38 kHz came from the deeper layer at 700 m (Fig. 3). The position of the layers also differed between the two methods, for the shallower and deeper scattering layers (Fig. 3). Two distinct layers (around 50 m and 400 m) were observed in the 120 kHz trawl-mounted data, with some increase in density at 650–700 m, while



three distinct layers (150–200, 300–500 and 600–800 m), appeared on the 38 kHz channel. However, the vertical profiles from the trawlmounted echosounder were similar to the vertical profile from the 120 kHz hull-mounted echosounder to 300 m depth (lower echogram in Fig. 3). Both methods showed peaks around 50 m. In addition, some stronger scattering was seen over the noise on the 120 kHz hull-mounted echogram when the trawl moved through the 400 m depth mark. Though the scattering at 400 m was unable to be quantified, the stronger scatterings corresponded with the distinct layer observed in the 120 kHz trawl-mounted data.

3.2. Tracking individuals in front of the trawl

A total of 1007 individuals were tracked in front of the trawl. Individual tracks were first detected at distances of up to 30 m and then appeared at shorter ranges as the trawl moved through the water (down to a range of 5 m from the trawl; Fig. 5). Organisms were observed for up to 25 s (ranged from 3.8 to 25.0 s, mean = 10.9 s, standard deviation (SD) = 4.3 s) within the acoustic beam and were rarely observed closer than 4 m. Track lengths ranged from 3.1 to 24.4 m (mean = 10.9 m, SD = 4.7 m). The average speed of an individual (speed for the whole track minus the trawl speed) ranged between moving towards the trawl at 0.6 ms⁻¹ and moving away from the trawl at 0.5 ms⁻¹ (mean = 0.0 m, SD 0.1 m). When each track was separated into pings (N = 9932), the pingto-ping speeds had a higher range ($-0.9 - 0.9 \text{ ms}^{-1}$).

The ping-to-ping speeds (standardised to the beam area) were similar to the total track speeds (highest counts around 0 ms⁻¹; Fig. 6). The ping-to-ping speeds for the whole cast did not appear to change as the distance between the individual and the trawl became shorter (Fig. 6). Some tracks were observed inside the layers; however, it was difficult to follow single tracks due to the high organism densities. The few tracks (30 in the first layer and 38 in the second) indicated that there could be a difference in the ping-to-ping speeds of organisms between the layers (Fig. 6). The first layer contained targets of lower target strengths (Fig. 4), had lower ping-to-ping speeds and the speeds were less variable as distance to the trawl decreased. On the other hand, organisms observed in the second layer (higher target strengths; Fig. 4) recorded higher ping-to-ping speeds and appeared to move away from the trawl $(-0.3 \text{ ms}^{-1}; \text{ Fig. 6})$.

3.3. Catch data

The catch consisted mainly of mesopelagic fish and crustaceans (Table 1). *Cyclothone* spp. dominated the mesopelagic fish by number of individuals with *Benthosema glaciale* and *Maurolicus muelleri* also present in numbers. Two groups of jellyfish were also present in the catch (*Atolla* sp. and *Periphylla periphylla*) and though they were not high in numbers, contributed to most of the catch weight.

4. Discussion

This paper describes a method to allow acoustic sampling at depths that are not accessible to the higher frequencies of hull-mounted echosounders, and hence to observe the behaviour of individuals in front of the trawl. We were able to estimate the densities inside and outside the mesopelagic layers in front of the trawl, the vertical profiles of target strengths and the movement of organisms with a forwardfacing trawl-mounted echosounder. This method was easy to implement, can be used in conjunction with traditional acoustic-trawl surveys, and does not adversely affect the time required to carry out trawls.

4.1. Potential uses and limitations

Our results demonstrate that a trawl-mounted echosounder is a useful tool to investigate the vertical and spatial distribution of mesopelagic organisms. The trawl catches showed that the organisms ahead

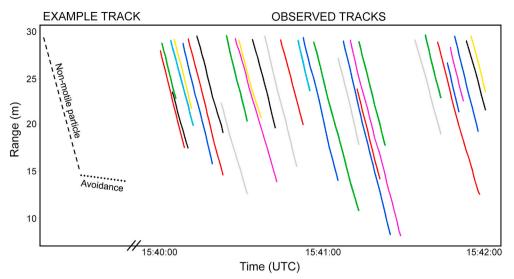


Fig. 5. Individual tracks from the organisms detected by the trawl-mounted echosounder at 120 kHz over a 2-min period. Example tracks are illustrated on the left with the dashed line indicating the track of a non-motile particle and the dotted line illustrates a track of an individual moving away from the trawl. Observed tracks are represented by solid lines (colour indicates different tracks). Each track includes the movement of the organism as well as the movement of the trawl. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of the trawl were a mixture of crustacean as well as teleost macroplankton and micronekton, thus giving a good indication that the method works in a typical mixed mesopelagic setting. Unlike methods based on data from hull-mounted echosounders, our method gives direct estimates of densities of organisms inside and outside mesopelagic scattering layers, and the measured acoustic scattering strengths may provide information on scatterer taxonomy. Since the density estimates are based on counts of individual scatterers rather than integrated acoustic energy, these density estimates are not affected by resonance effects. The main strength of the method, however, lies in the ability to assess if the trawl catches are affected by pre-trawl avoidance, which can bias size and weight composition of the trawl. Mesopelagic scattering layers are comprised of mixed aggregations of diverse taxa such as myctophid and stomiiform fish, shrimps, squids and gelatinous zooplankton (Pakhomov and Froneman, 2000; Lehodey et al., 2010). Thus, results from hull-mounted, low-frequency echosounders can be expected to give a biased view of *in situ* organism densities, in the sense that it mainly shows organisms that generate strong echoes. The results can therefore be of limited use towards an overall understanding of the patterns of distribution of mesopelagic macroplankton and micronekton. We note, however, that the method is very effective for mapping distribution of organisms with strong echoes, such as many species of mesopelagic fish. Broadband or multi-frequency measurements are more appropriate for separating mixed targets in mesopelagic layers.

Mesopelagic biomass estimates are challenging due to uncertainty in the conversion of acoustic backscatter into biomass (Koslow et al., 1997; Kaartvedt et al., 2012). Not enough is known about the population characteristics (such as species morphology, length distribution and acoustic properties), or the relative influence of resonance and siphonophores at 38 kHz to make a more precise estimate (Godø et al., 2009; Proud et al., 2019). Lower frequencies (such as 38 kHz) are desirable for the detection of gas-bearing animals (such as siphonophores and many mesopelagic fishes) since the scattering of fluid-like organisms (for example krill, squid, and jellyfish) are often negligible at 38 kHz (Warren et al., 2001; Proud et al., 2019). Our results showed differences in the position and intensity of the layers detected from the trawl-mounted and hull-mounted echosounders. This can be explained by the different frequencies employed in each method (120 and 38 kHz respectively). The 400 m layer apparent in the trawl-mounted echosounder data is clearly composed of organisms with low targets strengths at 38 kHz, since the high densities found here did not result in high backscattering levels at 38 kHz but was visible in the 120 kHz hull-mounted echogram (Fig. 3). The 700 m layer visible in the 38 kHz suggests strong scattering strengths for these organisms, since very low

counts were obtained from the 120 kHz echosounder on the trawl (Fig. 3). By combining the moderate target strengths found in this layer at 120 kHz with the strong backscatter seen at 38 kHz, our data strongly suggests that these organisms are close to their resonant frequency at 38 kHz (Fig. 3). The high frequency trawl-mounted echosounder provides information that is complementary to the hull-mounted data and has proven to be useful for investigations of vertical and fine-scale spatial distribution of mesopelagic organisms, including mesopelagic micro-zooplankton that are not detectable using hull-mounted echosounders.

Observing behavioural responses of fish in front of the trawl net has previously been challenging. Video observations at the mouth of the trawl are generally only useful at short ranges (within meters; Graham et al., 2004) and require the use of artificial light at mesopelagic depths. A forward-facing trawl-mounted echosounder can provide in situ behavioural observations of organisms in front of the trawl, at a greater distance than video cameras and has the potential to show the behavioural sequence before an individual reacts to the trawl net. Here, we observed mesopelagic organisms up to 30 m in front of the trawl net but the trawl-mounted echosounder has the potential to record tracks further away from the trawl when densities are low. Generally, organisms throughout the cast did not avoid the trawl (an overall speed of 0 ms⁻¹) but larger organisms in the second layer showed some avoidance as the trawl got closer. However, the number of larger organisms recorded in the second layer was low and more observations are needed to be confident of this. Several previous studies have inferred that pre-trawl avoidance is an important factor (e.g., Gjøsæter and Kawaguchi, 1980; Kaartvedt et al., 2012; Davison et al., 2015). Since the avoidance in this paper was recorded close to the trawl, this suggests that net extrusion could be an important factor for larger, graded trawls. Although avoidance may occur in front of the trawl, the little to no observed reactions within 30 m indicates that this method (echosounder attached to a non-graded trawl) has potential to be used for density estimates.

A forward-facing echosounder is expected to generally record lower average target strengths than a downward-looking echosounder (Miyashita et al., 1996; Pedersen et al., 2009) which could lead to misidentification of individuals or an assumption that smaller organisms are present. When the transducer is closer to the head (or tail) of asymmetrical targets (e.g., fish with long and thin swim bladders or krill), the transmitting energy reflected decreases (Simmonds and MacLennan, 2005). Therefore, for organisms that primarily swim horizontally with the dorsal side up, target strength distributions are expected to be more varied than what would be measured with a vertically aligned transducer. More information on side-aspect target strengths

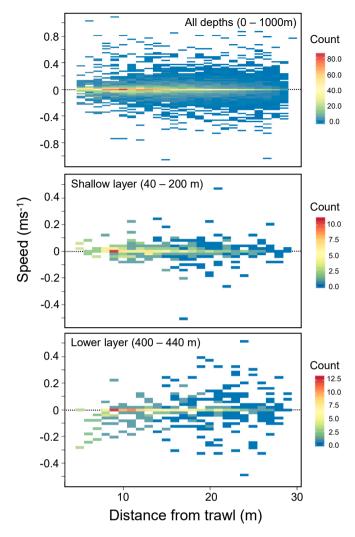


Fig. 6. Individual speed (individual speed – mean echo movement per second) of organisms as a function of distance from the trawl-mounted echosounder for all depths (top panel, N = 9932 pings), the upper (middle panel, N = 458 pings) and lower layers (bottom panel, N = 570 pings). A positive speed represents movement towards the trawl, while a negative speed represents movement away from the trawl. The colour scale indicates the number of organisms (normalised by beam area at range). The dotted line is 0 ms⁻¹. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

will be needed to fully utilize TS data from forward-looking echosounders. Optics can be used to verify target strengths and species identification (Ryan et al., 2009). Though, we did not have optics near the echosounder at the front of the trawl, a camera system was attached to the aft of the trawl (Deep Vision; Rosen and Holst, 2013), which could identify when (and at what depth) species entered the codend.

4.2. Application of this method to the study of mesopelagic organisms and implication in fisheries management

Traditional sampling methods such as acoustic-trawl surveys have limitations when sampling small, deep-water species (Kloser, 1996; Kloser et al., 2009). A trawl-mounted echosounder can improve the sampling of mesopelagic species by providing acoustic density estimates and distribution of species. In addition, it provides insight on the behaviour of mesopelagic individuals to help identify improvements to the effectiveness of sampling gear. Using the method described in this work, we can observe the behaviour of species in front of the trawl and

Table 1

Trawl catch composition for station 419.

Species/Group	Total count	Total weight (kg)	Average Length (mm)	
Fish	2705	2.223		
Argyropelecus hemigymnus	5	0.002	23	
Bathylagus euryops	46	0.746	102	
Benthosema glaciale	844	0.346	30	
Borostomias antarcticus	1	0.029	169	
Caristius sp.	1	0.010	61	
Chauliodus danae	6	0.055	12	
Chiasmodon bolangeri	1	0.018	141	
Coryphaenoides sp.	1	0.001	21	
Cyclothone braueri	130	0.021	31	
Cyclothone microdon	1365	0.377	37	
Holtbyrnia anomala	1	0.001	47	
Lampanyctus macdonaldi	10	0.027	63	
Leucobrotula adipata	1	0.001	47	
Macrouridae unknown	1	0.001	20	
Maurolicus muelleri	205	0.132	37	
Melanolagus bericoides	9	0.025	55	
Normichthys operosus	3	0.043	105	
Parabrotula plagiophthalmus	1	0.000	34	
Poromitra megalops	6	0.016	51	
Protomyctophum arcticum	23	0.015	32	
Scopelogadus beanii	32	0.325	73	
Searsia koefoedi	1	0.000	31	
Serrivomer beanii	6	0.022	298	
Stomias boa	4	0.007	107	
Xenodermichthys copei	2	0.003	58	
Crustaceans	2243	0.931		
Cephalopods	21	0.019		
Gonatus sp.	21	0.019		
Chaetognatha		0.489		
Jellyfish	182	9.531		
Atolla sp.	99	4.217		
Periphylla periphylla	83	5.314		
Other		1.958		

estimate their densities and depth distribution without increasing the survey sampling time. As interest in establishing a commercial industry for mesopelagic species evolves, it is crucial to obtain sufficient information to allow for the potential establishment of a sustainable and economical fishery, such as unbiased and accurate abundance estimates. The use of forward-looking trawl-mounted echosounders can help to estimate densities of organisms and detect the target strengths of separate organisms in a layer. Refining the acoustic density estimates is a first step of calculating accurate abundance estimates and reliable mesopelagic fish biomass values, which will assist fishery managers to determine the sustainability of a potential mesopelagic fishery. To date, there have been few commercial and trial mesopelagic fisheries (for example Shilat and Valinassab, 1998; Valinassab et al., 2007; Remesan et al., 2016). However, these have either been subsequently closed or stopped due to, in the main, low catches and processing and operating difficulties. Kaartvedt et al. (2012) noted that avoidance of the sampling gear may in fact underestimate the abundance of mesopelagic species and therefore sampling gears that are tailored more towards mesopelagic species are needed. Identifying areas of high escapement or potential improvements to the herding efficiency and species selection of commercial gears could help increase the catch rates to provide an economical mesopelagic fishery.

CRediT authorship contribution statement

Melanie J. Underwood: Investigation, Formal analysis, Visualization, Data curation, Writing - original draft. Eva García-Seoane: Formal analysis, Visualization, Data curation, Writing - original draft. Thor A. Klevjer: Methodology, Investigation, Formal analysis, Data curation, Writing - review & editing. Gavin J. Macaulay: Methodology, Investigation, Writing - review & editing. Webjørn Melle: Methodology, Supervision, Writing - review & editing.

Declaration of competing 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.

Acknowledgements

The authors wish to thank the officers and crew of RV "G.O. Sars" for their assistance and cooperation. We also thank the anonymous reviewers for their comments on earlier versions. The research was funded by HARMES, Research Council of Norway project number 280546 and MEESO, EU H2020 research and innovation programme, Grant Agreement No 817669.

References

- Barham, E.G., 1963. Siphonophores and the deep scattering layer. Science 140, 826–828. https://doi.org/10.1126/science.140.3568.826.
- Béhagle, N., Cotté, C., Ryan, T.E., Gauthier, O., Roudaut, G., Brehmer, P., Josse, E., et al., 2016. Acoustic micronektonic distribution is structured by macroscale oceanographic processes across 20–50°S latitudes in the South-Western Indian Ocean. Deep Sea Res. Oceanogr. Res. Pap. 110, 20–32. https://doi.org/10.1016/j. dsr.2015.12.007.
- Davison, P.C., Checkley Jr., D.M., Koslow, J.A., Barlow, J., 2013. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. Prog. Oceanogr. 116, 14–30. https://doi.org/10.1016/j.pocean.2013.05.013.
- Davison, P.C., Koslow, J.A., Kloser, R.J., 2015. Acoustic biomass estimation of mesopelagic fish: backscattering from individuals, populations, and communities. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 72, 1413–1424. https://doi.org/10.1093/ icesjms/fsv023.
- Demer, D., Berger, L., Bernasconi, M., Bethke, E., Boswell, K., Chu, D., Domokos, R., et al., 2015. Calibration of Acoustic Instruments. ICES Cooperative Research Report No. 326. https://doi.org/10.25607/OBP-185, 133pp.
- Drazen, J.C., De Forest, L.G., Domokos, R., 2011. Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon. Deep Sea Res. Oceanogr. Res. Pap. 58, 557–566. https://doi.org/10.1016/j.dsr.2011.03.002.
- Gjøsæter, J., Kawaguchi, K., 1980. A review of the world resources of mesopelagic fish. FAO Fish. Tech. Pap. 193, 1–153.
- Godø, O.R., Patel, R., Pedersen, G., 2009. Diel migration and swimbladder resonance of small fish: some implications for analyses of multifrequency echo data. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 66, 1143–1148. https://doi.org/10.1093/icesjms/ fsp098.
- Graham, N., Jones, E.G., Reid, D.G., 2004. Review of technological advances for the study of fish behaviour in relation to demersal fishing trawls. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 61, 1036–1043. https://doi.org/10.1016/j. iccsims.2004.06.006.
- Handegard, N.O., 2007. Observing individual fish behavior in fish aggregations: tracking in dense fish aggregations using a split-beam echosounder. J. Acoust. Soc. Am. 122, 177–187. https://doi.org/10.1121/1.2739421.
- Haris, K., Kloser, R.J., Ryan, T.E., Malan, J., 2017. Deep-water calibration of echosounders used for biomass surveys and species identification. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 75, 1117–1130. https://doi.org/10.1093/icesjms/fsx206. ICES, 2015a. Manual for International Pelagic Surveys (IPS). Series of ICES Survey
- Protocols SISP 9 IPS, p. 92. ICES, 2015b. Report of the workshop on scrutinisation procedures for pelagic ecosystem
- surveys (WKSCRUT). ICES Document ICES CM2015/SSGIEOM 18, 103.
- Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A., et al., 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. Nat. Commun. 5 https://doi.org/10.1038/ncomms4271.
- Kaartvedt, S., Langbehn, T.J., Aksnes, D.L., 2019. Enlightening the ocean's twilight zone. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 76, 803–812. https://doi.org/10.1093/ icesjms/fsz010.
- Kaartvedt, S., Staby, A., Aksnes, D.L., 2012. Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. Mar. Ecol. Prog. Ser. 456, 1–6. https://doi.org/10.3354/meps09785.
- Kloser, R., Knuckey, I., Ryan, T., Pitman, L., Sutton, C., 2011. Orange Roughy Conservation Program: Eastern Zone Surveys and Trials of a Cost-Effective Acoustic

Headline System. Final report to the South East Trawl Fishing Industry Association, p. 153.

- Kloser, R.J., 1996. Improved precision of acoustic surveys of benthopelagic fish by means of a deep-towed transducer. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 53, 407–413. https://doi.org/10.1006/jmsc.1996.0057.
- Kloser, R.J., Ryan, T.E., Young, J.W., Lewis, M.E., 2009. Acoustic observations of micronekton fish on the scale of an ocean basin: potential and challenges. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 66, 998–1006. https://doi.org/10.1093/icesjms/ fsp077.
- Knutsen, T., Melle, W., Mjanger, M., Strand, E., Fuglestad, A.-L., Broms, C., Bagøien, E., et al., 2013. MESSOR-A towed underwater vehicle for quantifying and describing the distribution of pelagic organisms and their physical environment. In: 2013 MTS/ IEEE OCEANS - Bergen, pp. 1–12. https://doi.org/10.1109/OCEANS-Bergen.2013.6608177.
- Korneliussen, R.J., 2000. Measurement and removal of echo integration noise. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 57, 1204–1217. https://doi.org/10.1006/ jmsc.2000.0806.
- Korneliussen, R.J., Heggelund, Y., Macaulay, G.J., Patel, D., Johnsen, E., Eliassen, I.K., 2016. Acoustic identification of marine species using a feature library. Methods in Oceanography 17, 187–205. https://doi.org/10.1016/j.mio.2016.09.002.
- Korneliussen, R.J., Ona, E., Eliassen, I., Heggelund, Y., Patel, R., Godø, O.R., Giertsen, C., et al., 2006. The large scale survey system-LSSS. In: Proceedings of the 29th Scandinavian Symposium on Physical Acoustics. Ustaoset, 29 January – 1 February 2006.
- Koslow, J.A., Kloser, R.J., Williams, A., 1997. Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. Mar. Ecol. Prog. Ser. 146, 21–35. https://doi.org/ 10.3354/meps146021.
- Lam, V., Pauly, D., 2005. Mapping the global biomass of mesopelagic fishes. Sea Around Us Project Newsletter 30, 4.
- Lehodey, P., Murtugudde, R., Senina, I., 2010. Bridging the gap from ocean models to population dynamics of large marine predators: a model of mid-trophic functional groups. Prog. Oceanogr. 84, 69–84. https://doi.org/10.1016/j.pocean.2009.09.008.
- Miyashita, K., Aoki, I., Inagaki, T., 1996. Swimming behaviour and target strength of isada krill (*Euphausia pacifica*). ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 53, 303–308. https://doi.org/10.1006/jmsc.1996.0039.
- Moline, M.A., Benoit-Bird, K., O'Gorman, D., and Robbins, I.C. 2915. Integration of scientific echo sounders with an adaptable autonomous vehicle to extend our understanding of animals from the surface to the bathypelagic. Journal of Atmosheric and Ocean Technology, 32: 2173-2186. doi:10.1175/JTECH-D-15-0035.1.
- Methodology for target strength measurements (with special reference to in situ techniques for fish and micro-nekton). ICES cooperative research report No. In: Ona, E. (Ed.), 1999. https://doi.org/10.17895/ices.pub.5367, 235. 59 pp.
- Pakhomov, E.A., Froneman, P.W., 2000. Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997. Polar Biol. 23, 410–419. https://doi.org/ 10.1007/s003000050462.
- Pedersen, G., Handegard, N.O., Ona, E., 2009. Lateral-aspect, target-strength measurements of in situ herring (Clupea harengus). ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 66, 1191–1196. https://doi.org/10.1093/icesjms/fsp121.
- Proud, R., Handegard, N.O., Kloser, R.J., Cox, M.J., Brierley, A.S., 2019. From siphonophores to deep scattering layers: uncertainty ranges for the estimation of global mesopelagic fish biomass. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 76, 718–733. https://doi.org/10.1093/icesjms/fsy037.
- Remesan, M.P., Prajith, K.K., Raj, F.D., Joseph, R., Boopendranath, M.R., 2016. Investigations on aimed midwater trawling for myctophids in the arabian sea. Fish. Technol. 53, 190–196.
- Robinson, C., Steinberg, D.K., Anderson, T.R., Arístegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.-F., et al., 2010. Mesopelagic zone ecology and biogeochemistry – a synthesis. Deep Sea Res. Part II Top. Stud. Oceanogr. 57, 1504–1518. https://doi. org/10.1016/j.dsr2.2010.02.018.
- Rosen, S., Holst, J.C., 2013. DeepVision in-trawl imaging: sampling the water column in four dimensions. Fish. Res. 148, 64–73. https://doi.org/10.1016/j. fishres.2013.08.002.
- Ryan, T.E., Kloser, R.J., Macaulay, G.J., 2009. Measurement and visual verification of fish target strength using an acoustic-optical system attached to a trawlnet. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 66, 1238–1244. https://doi.org/10.1093/icesjms/ fsp122.

Shilat, A.Z., Valinassab, T., 1998. Trial Fishing for Lantern Fishes (Myctophids) in the Gulf of Oman (1989-1990). FAO Fisheries Circular No. 935, 66 pp.

- Simmonds, J., MacLennan, D.N., 2005. Fisheries Acoustics: Theory and Practice. Blackwell Science Ltd, Oxford, p. 437.
- Stanton, T.K., Chu, D., Wiebe, P.H., 1998. Sound scattering by several zooplankton groups. II. Scattering models. J. Acoust. Soc. Am. 103, 236–253. https://doi.org/ 10.1121/1.421110.
- Sutton, T.T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. J. Fish. Biol. 83, 1508–1527. https://doi.org/10.1111/jfb.12263.
- Valinassab, T., Pierce, G.J., Johannesson, K., 2007. Lantern fish (*Benthosema pterotum*) resources as a target for commercial exploitation in the Oman Sea. J. Appl. Ichthyol. 23, 573–577. https://doi.org/10.1111/j.1439-0426.2007.01034.x.
- Warren, J.D., Stanton, T.K., Benfield, M.C., Wiebe, P.H., Chu, D., Sutor, M., 2001. In situ measurements of acoustic target strengths of gas-bearing siphonophores. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 58, 740–749. https://doi.org/10.1006/ jmsc.2001.1047.