



Vertical distribution, composition and migratory patterns of acoustic scattering layers in the Canary Islands



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ABSTRACT

Diel vertical migration (DVM) facilitates biogeochemical exchanges between shallow waters and the deep ocean. An effective way of monitoring the migrant biota is by acoustic observations although the interpretation of the scattering layers poses challenges. Here we combine results from acoustic observations at 18 and 38 kHz with limited net sampling in order to unveil the origin of acoustic phenomena around the Canary Islands, subtropical northeast Atlantic Ocean. Trawling data revealed a high diversity of fishes, decapods and cephalopods (152 species), although few dominant species likely were responsible for most of the sound scattering in the region. We identified four different acoustic scattering layers in the mesopelagic realm: (1) at 400–500 m depth, a swimbladder resonance phenomenon at 18 kHz produced by gas-bearing migrant fish such as *Vinciguerria* spp. and *Lobianchia doleini*, (2) at 500–600 m depth, a dense 38 kHz layer resulting primarily from the gas-bearing and non-migrant fish *Cyclothone braueri*, and to a lesser extent, from fluid-like migrant fauna also inhabiting these depths, (3) between 600 and 800 m depth, a weak signal at both 18 and 38 kHz ascribed either to migrant fish or decapods, and (4) below 800 m depth, a weak non-migrant layer at 18 kHz which was not sampled. All the diel migrating layers reached the epipelagic zone at night, with the shorter-range migrations moving at $4.6 \pm 2.6 \text{ cm s}^{-1}$ and the long-range ones at $11.5 \pm 3.8 \text{ cm s}^{-1}$. This work reduces uncertainties interpreting standard frequencies in mesopelagic studies, while enhances the potential of acoustics for future research and monitoring of the deep pelagic fauna in the Canary Islands.

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1. Introduction

Acoustic scattering from marine organisms is caused by body structures with densities notably different from water, such as gas bladders or lipid inclusions (Aguilar et al., 2008). Thanks to this phenomenon, the vertical distribution of pelagic animals can be easily monitored using scientific echosounders (Kloser et al., 2002; Kaartvedt et al., 2009; Cade & Benoit-Bird, 2015). Two reflecting regions are normally visible in the ocean, the shallow and the deep scattering layer (SSL and DSL) occurring respectively in the epipelagic and the mesopelagic domains (0–200 and 200–1000 m depth), with the latter often partitioned into multiple layers. Part of the biota forming the DSLs feed between dusk and dawn in the epipelagic zone, producing a thicker and more intense SSL during the night. This displacement is known as

diel vertical migration (DVM), occurring on a daily basis around the world's oceans and performed by a large variety of zooplankton and micronekton species (Tucker, 1951; Barham, 1966; Roe, 1974; Pearre, 2003).

DVM promotes trophic interactions and biogeochemical exchanges between the upper layers and the deep ocean (Ducklow et al., 2001; Robinson et al., 2010), and its study is therefore important for understanding pelagic ecosystems functioning. The micronekton component, mainly fishes, decapods and cephalopods between 2 and 10 cm in length (Brodeur et al., 2005), is expected to account for a substantial export of carbon to the deep ocean as they comprise a significant fraction of the migrant biomass (Angel & Pugh, 2000), and cover more extensive depth ranges than zooplankton (Badcock & Merrett, 1976; Roe, 1984b; Domanski, 1984). In fact, the importance of fishes and decapods in mediating carbon export has been recently highlighted by several studies (Hidaka et al., 2001; Davison et al., 2013; Schukat et al., 2013; Hudson et al., 2014; Ariza et al., 2015). Therefore, using acoustic observations

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for monitoring their distribution and migrations may be a powerful tool for the ocean carbon pump assessment.

The present study focus on micronekton from mesopelagic waters nearby the Canary Islands, a region in the subtropical northeast Atlantic exhibiting open-ocean and oligotrophic gyre characteristics (Barton et al., 1998; Davenport et al., 2002; Neuer et al., 2007). Due to its position between temperate and tropical waters, this faunal province presents a high diversity of mesopelagic micronekton in comparison to other latitudes (Backus & Craddock, 1977; Badcock & Merrett, 1977; Landeira & Franssen, 2012). In the Canary Islands, the vertical distribution of fishes (Badcock, 1970), decapods (Foxton, 1970a; Foxton, 1970b), cephalopods (Clarke, 1969) and euphausiids (Baker, 1970) was thoroughly studied in the SOND cruise during the mid-sixties (Foxton, 1969), providing valuable knowledge about DVM in the area. More recent studies have contributed to a more detailed catalogue of mesopelagic micronekton illustrating community differences between neritic and oceanic realms around the Canary Islands (Bordes et al., 2009; Wienerroither et al., 2009). However, the lack of integrated studies combining acoustic data and biological information from net sampling has prevented the identification of the specific organisms responsible for each scattering layer occurring in the archipelago. Acoustic properties of midwater fauna may help in this task. For instance, the swimbladder of fishes produce resonance under certain frequencies and pressure conditions, depending on its size and internal structure (Andreeva, 1964; Capen, 1967; Weston, 1967; Kloser et al., 2002). Thus, the swimbladder features of dominant mesopelagic fishes can be used in combination with resonance models to investigate the origin of acoustic scattering.

This study describes the acoustic properties and the vertical distribution of scattering layers at 18 and 38 kHz occurring from the surface to 1000 m depth in the Canary Islands, as well as their diel migrant movements between the epipelagic and the mesopelagic zone. We also present the first attempt to identify organisms causing these layers by trawling. The assessment of species composition of the scattering biota was complemented with a swimbladder resonance model, and also contrasted with previous reports of the micronekton vertical distribution in the region.

2. Methods

2.1. Survey

The survey was conducted in two locations southwest of La Palma and Tenerife Islands (Canary Islands), between the 1000 and 2000 m isobaths (Fig. 1). From the 9th to the 18th of April 2012, hydrographic and acoustic data, as well as micronekton samples were collected on board the R/V *Cornide de Saavedra*.

2.2. Hydrography

Vertical profiles of conductivity and temperature were collected using a SeaBird 9/11-plus CTD equipped with dual conductivity and temperature sensors. CTD sensors were calibrated at the SeaBird laboratory before the cruise. A sensor for measurements of dissolved oxygen (SeaBird SBE-43) and fluorometer for chlorophyll *a* estimations (WetLabs ECO-FL) were linked to the CTD unit. Seawater analyses of dissolved oxygen (Winkler titrations) and chlorophyll *a* extractions were performed to calibrate the voltage readings of both sensors. Analyses were carried out in accordance with the JGOFS recommendations (UNESCO, 1994). Temperature, dissolved oxygen and chlorophyll *a* profiles were averaged from 3 CTD casts performed within each sampling area off La Palma and Tenerife Islands (Fig. 2).

2.3. Acoustics

Hull-mounted SIMRAD EK60 echosounders operating at 18 and 38 kHz (11° and 7° beam width, respectively) were used for recording

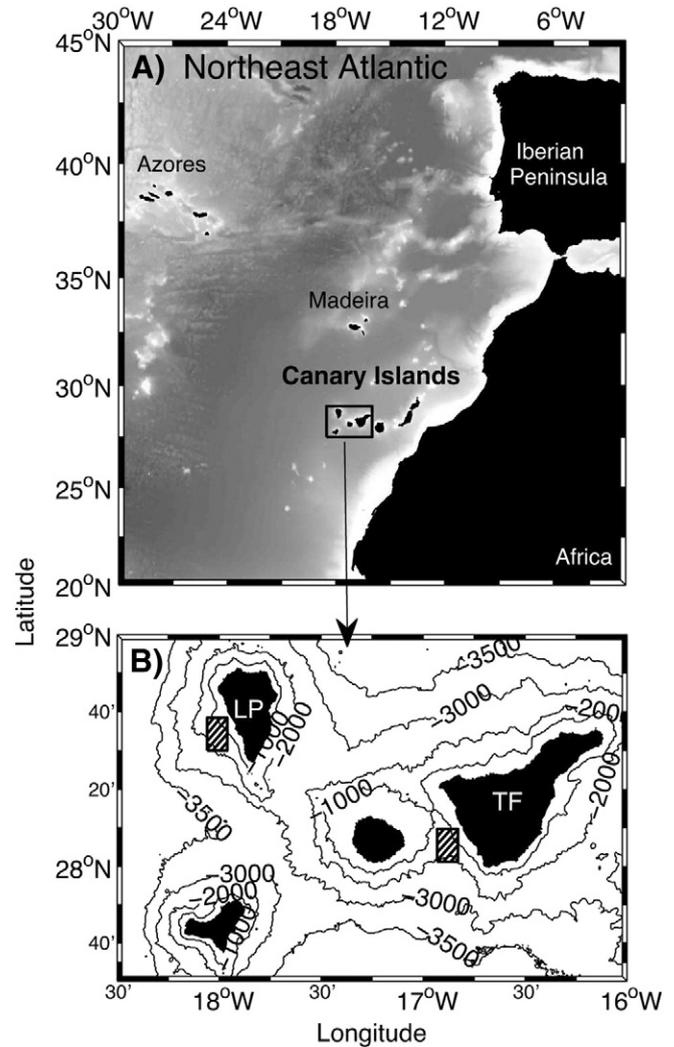


Fig. 1. (A) Map showing the situation of the Canary Islands west off Africa. (B) Study areas southwest of La Palma and Tenerife Islands where acoustic recordings and net trawling were conducted (striped rectangles).

acoustic data. Configuration was set at 1024 μ s pulse duration and one ping every 3 s. Due to the draft of the transducer and to prevent near-field effects (Simmonds & MacLennan, 2005), acoustic data for the first 10 m depth were not available. In order to avoid the range-increasing noise (Korneliusson, 2000), maximum depth of data used was 1000 m, and minimum threshold was set to -80 dB. The echosounders were calibrated *in-situ* by standard techniques (Foote et al., 1987). Since acoustic records covered several days while trawling in each location, we opted for showing a composite echogram per location, which were obtained by averaging the daily acoustic data every minute (Figs. 3 and 4). Fragments with scattering layers visibly affected by steaming noise or interferences from other acoustic devices were removed before averaging. Echograms were shown at 18 kHz and 38 kHz, and also as the difference between both frequencies (18 kHz minus 38 kHz). In order to calculate approximate vertical migration velocities, we manually marked sets of points over different migratory traces observed at 18 and 38 kHz. The velocities were extracted by averaging the slopes along the curves fitted to these points. All acoustic data were processed using customized applications in Matlab software.

2.4. Biological sampling

Micronekton was captured using a pelagic trawl with a 300 m² mouth area and 45 m length. The mesh size was 80 cm near the opening,

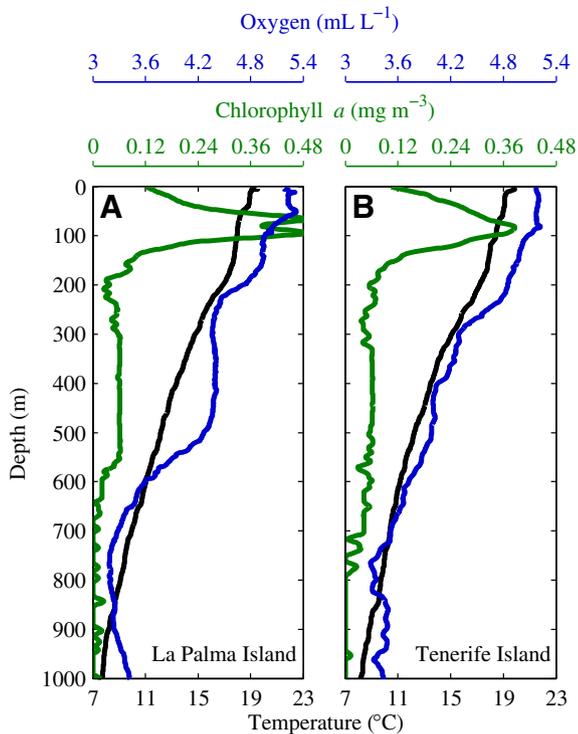


Fig. 2. Averaged profiles of temperature, dissolved oxygen and chlorophyll *a* near (A) La Palma and (B) Tenerife Islands.

decreasing to 1 cm in the cod end. Hauls were performed within the different scattering regions according to information provided by the echosounders and the Scanmar depth sensor attached to the trawl headline. Depth and time of each haul were pointed out by boxes overlaying the 24 h echogram shown in Fig. 3. Since the trawl had no opening-closing system, deploying and lifting were conducted without towing to reduce the by-catch from non-desired strata. The towing speed was maintained near 3 knots, with effective fishing times of one hour and approximate distances of three nautical miles. Samples were frozen on board at -20°C . Once in the laboratory, they were fixed in 4% buffered formalin and later transferred to 70% ethanol for species identification, enumeration, weighing and length measurements. Catch results were not standardized by water volume filtered since the effective mouth size was uncertain due to the decreasing meshes along the trawl. Abundance data was instead shown as “individuals per haul”, without the need of standardization since the differences in both fishing times and distances among hauls were below 5%. Non-migrant species were excluded from abundances and biomass of the nocturnal epipelagic hauls (Table 1). For this, we checked the diel vertical distribution of micronekton species consulting the existing literature in the region (Clarke, 1969; Badcock, 1970; Foxton, 1970a,b; Badcock & Merrett, 1976; Roe, 1984a; Clarke & Lu, 1995). We also excluded other non-migrant species that were detected in shallow waters during hauling tests performed at daytime.

The naming convention for hauls was, a first letter depicting whether the tow was conducted during the day (D) or during the night (N), followed by a 3-digit number indicating the averaged depth, and finally

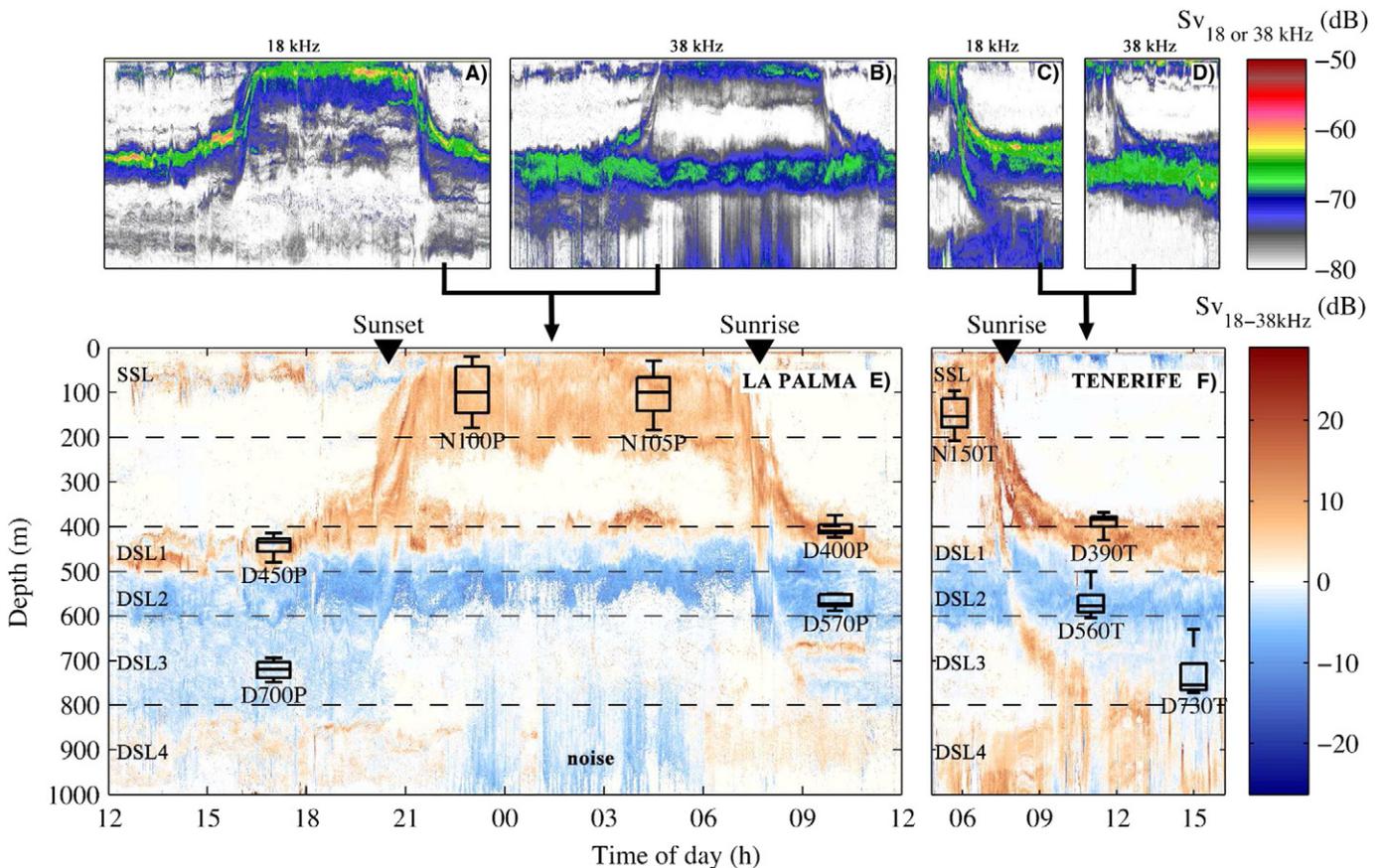


Fig. 3. Echograms at 18 and 38 kHz in waters nearby La Palma (A and B) and Tenerife (C and D) Islands, and differential echograms (18 minus 38 kHz) from the same locations (E and F). Acoustic scattering layers are indicated according to frequency response and the depth of occurrence; one shallow scattering layer in the epipelagic (SSL), and four deep scattering layers in the mesopelagic (DSL1, DSL2, DSL3 and DSL4). Time and depth of fishing hauls are indicated with boxes, where the central lines are trawling depth medians, the edges of the box are the 25th and 75th percentiles and the whiskers extend to the most extreme trawling depths not considered outliers.

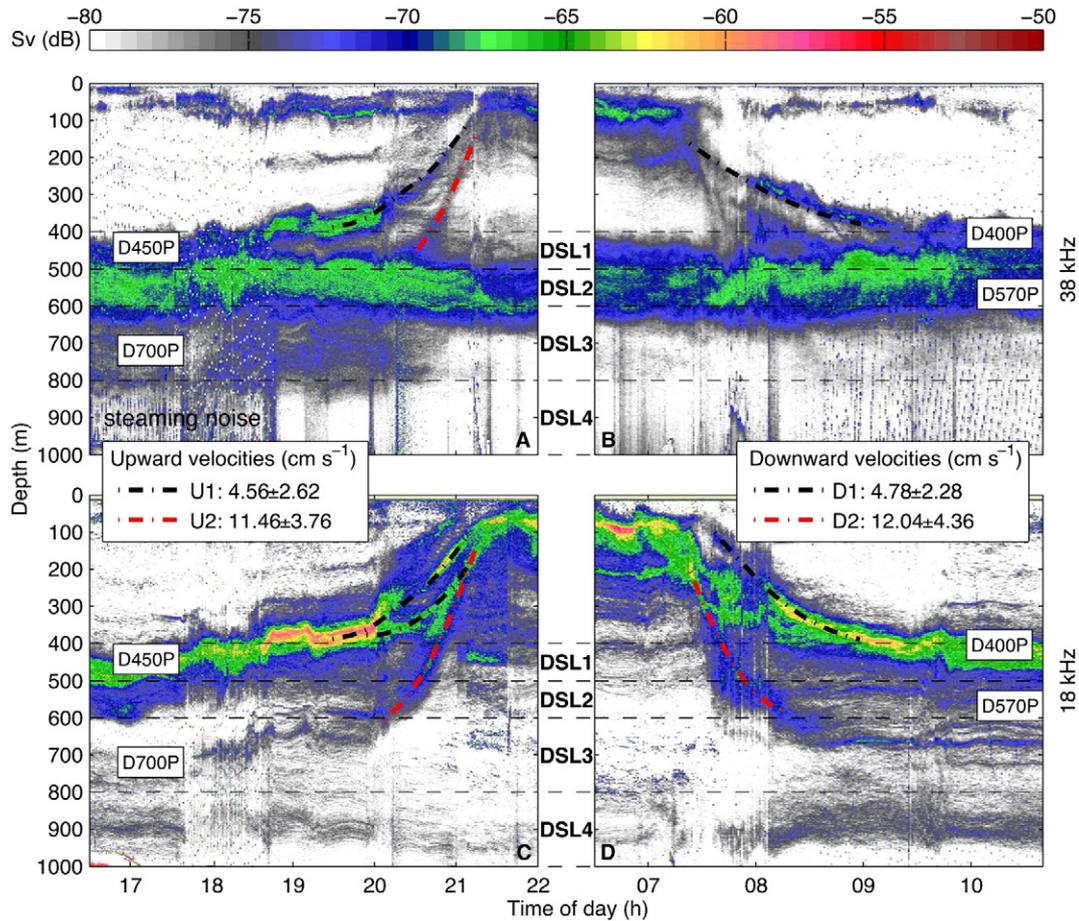


Fig. 4. Same echograms at 38 (A and B) and 18 kHz (C and D) showing migratory pathways near La Palma Island. Different upward (U1, U2) and downward (D1, D2) tracks are indicated with dashed lines and their averaged migrant velocities are given in the legends. Distinct acoustic scattering layers (DSL1, DSL2, DSL3 and DSL4) are indicated according to divisions proposed in Fig. 3e and f. Text boxes over the echograms indicate depth and time of fishing hauls.

a letter indicating if the location was La Palma (P) or Tenerife (T). For example, D450T would be a daytime haul conducted at an averaged depth of 450 m depth in Tenerife.

2.5. Community analyses

Community assemblage structure was analyzed through hierarchical agglomerative and unweighted arithmetic average (UPGMA) clustering based on the Bray–Curtis similarity matrix (Bray & Curtis, 1957). Significant clusters were afterwards tested using the similarity profile procedure (SIMPROF, (Clarke et al., 2008)). The high diversity of the sampled community posed difficulties for illustrating catch results for all the species identified in this study (152). Many of these species showed very low abundances, presumably contributing poorly to acoustic scattering and migrations. For this reason, after clustering we focused the graphical results on dominant fishes, decapods and cephalopods involved in diel vertical migrations in the region, and also on the most abundant non-migrant species occupying the mesopelagic domain. Nevertheless, raw data of the entire community are also provided in Supplementary material. Multivariate analyses were performed with Fathom toolbox for Matlab (Jones, 2014).

2.6. Source of scattering analysis

A target much smaller than its incident wavelength produces a weak echo that increases rapidly with higher frequencies. On the

contrary, for large targets the frequency has little effect (Simmonds & MacLennan, 2005). Besides, targets with densities very different from those of seawater resonate when their dimensions are shorter but near the wavelength of a given frequency. This is typically caused by “gas-bearing organisms”, which produce very high backscattering. On the other hand, those with densities similar to seawater are known as “fluid-like organisms”, producing much weaker echo (Stanton & Chu, 2000; Lavery et al., 2002; Korneliusson & Ona, 2003). In this study, fishes with gas-filled swimbladders would be the main cause of resonance according to trawl data, while crustaceans, squids or non gas-bearing fishes probably behaved as fluid-like targets.

In order to identify potential species producing resonance, we assigned a swimbladder condition (gas-filled, contracted or fat-invested) for the dominant fishes inhabiting each scattering layer. This was determined for each species and according to their standard lengths consulting the swimbladder catalogues of (Marshall, 1960; Kleckner & Gibbs, 1972; Badcock & Merrett, 1977). The equivalent spherical radii (ESR) were as well estimated on the basis of standard lengths using species-specific equations given by (Saenger, 1989). If equations were not available from a given specie, the radius was obtained from swimbladder spherical volumes of the same size fishes given by (Kleckner & Gibbs, 1972) and using simple sphere calculations.

Once collected the swimbladder features and sizes of the main targets forming each layer, we modeled the swimbladder resonance from surface to 1000 m depth at 18 and 38 kHz. This was achieved

following the model developed by Andreeva (1964), later adapted for prolate spheroids by Weston (1967), and applied as in Kloser et al. (2002).

$$TS = 10 \log_{10}(\sigma_{bs}) \quad (1)$$

$$\sigma_{bs} = a_{es}^2 \left(\left(\left(\frac{f_p}{f} \right)^2 - 1 \right)^2 + \frac{1}{Q^2} \right)^{-1} \quad (2)$$

$$f_p = f_o 2^{\frac{1}{2}} e^{-\frac{1}{2}} (1 - e^2)^{\frac{1}{4}} \left(\ln \left(\frac{1 + (1 - e^2)^{\frac{1}{2}}}{1 - (1 - e^2)^{\frac{1}{2}}} \right) \right)^{-\frac{1}{2}} \quad (3)$$

$$f_o = \frac{1}{2\pi a_{es}} \left(\frac{3\gamma P + 4\mu_1}{\rho} \right)^{\frac{1}{2}} \quad (4)$$

$$P = (1 + 0.103D)10^5 \quad (5)$$

TS is the target strength of the swimbladder. σ_{bs} is the acoustic backscattering cross-section at the incident acoustic frequency (f) of an equivalent spherical swimbladder volume of radius a_{es} with a prolate resonant frequency (f_p), and a resonance quality factor of Q . The prolate resonant frequency is a function of the prolate spheroid roundness (e) and the spherical resonant frequency (f_o) at a hydrostatic pressure (P) for fish depth (D) and fish tissue density (ρ), with a ratio of specific heats for the swimbladder gas (γ) and the real part of the complex shear modulus of the fish tissue defined by μ_1 . The values assumed

Table 1

Relative abundance (%) and biomass (%) of species found in the nocturnal shallow scattering layer. Values were averaged from hauls N100P, N105P and N150T (see Fig. 3). Only organisms identified to the species level and with relative abundances above 0.5% are shown.

Group	Family	Abundance (%)	Biomass (%)
Fis	Myctophidae	53.56	51.65
	<i>Lepidophanes gaussi</i>	10.64	6.54
	<i>Lobianchia dofleini</i>	8.73	4.66
	<i>Ceratoscopelus warmingii</i>	7.57	18.53
	<i>Hygophum hygomii</i>	7.26	3.95
	<i>Lobianchia</i> spp.	3.36	1.36
	<i>Hygophum taaningi</i>	2.49	0.94
	<i>Hygophum reinhardtii</i>	2.41	1.70
	<i>Bolinichthys indicus</i>	1.74	1.00
	<i>Diaphus rafinesquii</i>	1.47	0.83
	<i>Lobianchia gemellarii</i>	1.11	0.48
	<i>Notoscopelus resplendens</i>	0.88	3.70
	Phosichthyidae	8.80	4.05
	<i>Vinciguerria attenuata</i>	6.35	3.18
	<i>Vinciguerria nimbaria</i>	1.31	0.50
	<i>Vinciguerria poweriae</i>	1.14	0.37
	Gonostomatidae	2.58	4.83
	<i>Gonostoma elongatum</i>	1.85	4.09
	<i>Gonostoma nudatum</i>	0.54	0.64
	Sternoptychidae	1.43	1.01
	<i>Argyropelecus aculeatus</i>	1.43	1.01
Dec	Oplophoridae	8.56	5.83
	<i>Oplophorus spinosus</i>	7.08	4.58
	<i>Systellaspis debilis</i>	1.48	1.25
	Sergestidae	5.04	1.22
	<i>Deosergestes corniculum</i>	1.90	-
	<i>Sergia splendens</i>	0.55	-
<i>Sergestes</i> spp.	0.51	-	
Cep	Pyroteuthidae	9.22	14.21
	<i>Pyroteuthis margaritifera</i>	7.38	6.83
	<i>Pterygioteuthis giardi</i>	1.84	7.39
	Onychoteuthidae	1.76	3.34
	<i>Onychoteuthis banksii</i>	1.76	3.34

were: $\mu_1 = 105$ Pa, $\gamma = 1.4$, $\rho = 1.075$ kg m³, and $Q = 5$, following Kloser's et al. (2002) settings. We assumed e to be 0.3 according to swimbladder roundness values ranging from 0.2 to 0.4 for most mesopelagic fish species found in this study (Kleckner & Gibbs, 1972; Brooks, 1977). Resonance was modeled for ESRs ranging from 0.3 to 1.8 mm.

The frequency response of echograms at 18 and 38 kHz, the species composition, their acoustic properties, and their theoretical resonance along depth was used to investigate the species most likely causing scattering in the region.

3. Results

3.1. Hydrography

Both fishing areas were placed leeward of the islands presenting therefore similar hydrographical features (Figs. 1 and 2). Sea surface temperature ranged between 19.5 and 19.8 °C while seasonal thermoclines were not present in any location (mixing period). Subsurface chlorophyll maxima appeared between 50 and 100 m depth with values of 0.48 and 0.40 mg m⁻³ near La Palma and Tenerife Islands, respectively. Oxygen minima of about 3.3 mL L⁻¹, well above hypoxia levels (<1.4 mL L⁻¹, Ekau et al., 2010), were located between 700 and 800 m depth in both places.

3.2. Distribution of acoustic scattering layers and migrations

According to the different responses shown at 18 and 38 kHz and the depth of occurrence, we distinguished one shallow scattering layer (SSL) in the epipelagic zone and four deep scattering layers (DSLs) in the mesopelagic zone. All of them occurring in waters around La Palma and Tenerife Islands (Figs. 3 and 4). The SSL became denser and thicker at night as a consequence of the aggregation of migrant layers coming from deeper waters. This occurred roughly between the surface and 200 m depth coinciding with chlorophyll and oxygen maxima (Fig. 2).

In the mesopelagic we identified (Fig. 3): a zone characterized by a high backscattering at 18 kHz roughly between 400 and 500 m depth (DSL1), a zone mainly visible at 38 kHz between 500 and 600 m depth (DSL2), a weak backscattering zone at 18 and 38 kHz between 600 and 800 m depth (DSL3), and finally, a weak echo at 18 kHz approximately from 800 to 1000 m depth (DSL4). As exemplified in the echograms registered near La Palma, some scattering layers also exhibited diel vertical movements between the mesopelagic and the epipelagic zone. At sunset (Fig. 4A and C), shallow upward migrations (U1) were registered from DSL1, moving at an averaged velocity of 4.6 ± 2.6 cm s⁻¹. Simultaneously, deeper upward migrations (U2) moved from DSL3 to shallow waters at 11.5 ± 3.8 cm s⁻¹. At sunrise (Fig. 4B and D), shallow and deep migrations were observed following similar patterns but moving downwards (D1, D2). DSL1 at 18 kHz and DSL3 at 38 kHz practically disappeared during nighttime (signal close or below the minimum threshold, -80 dB). On the contrary, DSL2 at 38 kHz and DSL4 at 18 kHz apparently did not exhibit vertical movements. DSL2 was however slightly weaker during nighttime. These migratory patterns were visible at both frequencies everyday and everywhere regardless the location surveyed (La Palma or Tenerife Islands).

3.3. Taxonomic composition of acoustic scattering layers

A total of 8199 individuals were classified, resulting in 104, 26 and 22 identified species of fishes, decapods and cephalopods, respectively. The number of individuals per haul for all species captured during the survey is shown in Supplementary material.

Fishes were the prevailing group captured within the nocturnal SSL (Table 1), contributing more than 70% in both abundance (%A) and

biomass (%B). Myctophidae was the dominant fish family (54%A and 52%B), followed by Phosichthyidae (9%A and 4%B), Gonostomatidae (3%A and 5%B) and Sternoptychidae (1%A and 1%B). Among all fish species, only *Ceratoscopelus warmingii*, *Lobianchia dofleini*, *Hygophum hygomii* and *Vinciguerria attenuata* accounted for more than 30% of the migratory fish, both in abundance and biomass. Decapods were the second most important group in shallow waters at night (15%A and 9%B), dominated by the families Oplophoridae (9%A and 6%B) and Sergestidae (5%A and 1%B). The most abundant decapods were *Oplophorus spinosus*, *Systellaspis debilis* and *Deosergestes corniculum*. Cephalopods were the least frequent taxon in terms of abundance but occupied the second place in biomass (13%A and 20%B). This group was dominated by the families Pyroteuthidae (9%A and 14%B) and Onychoteuthidae (2%A and 3%B), with *Pyroteuthis margaritifera*, *Pterygioteuthis giardi* and *Onychoteuthis banksii* as the prevalent migrating species.

Cluster analyses of the faunistic composition revealed 4 significant groups (SIMPROF routine, $P < 0.001$) at a similarity distance of 0.8. Further, the clusters grouped according to the towing depth and time, but regardless of the location surveyed (Fig. 5). Nocturnal catches in shallow waters showed the highest abundances of vertical migrants, assembling separately from the rest of hauls (red cluster). In the meso-pelagic zone, the hauls conducted within the DSL1 were almost

exclusively composed by the myctophid *L. dofleini* and other small fishes from the genus *Vinciguerria* (green cluster). The DSL2 was characterized by the occurrence of the non-migratory fish *Cyathothone braueri* and also the presence of vertical migrants such as the lanternfish *H. hygomii*, the dragonfish *Chauliodus danae* or the decapod *O. spinosus* (blue cluster). The deepest hauls conducted within the DSL3 also clustered together. Here, the most remarkable feature was the massive presence of the non-migratory fish *Cyathothone microdon*, but also the relative high abundances of lanternfishes such as *Lepidophanes gaussi* or *Hygophum reinhardtii*, and also several decapods species from the family Sergestidae.

3.4. Dominant targets and their acoustic properties

Despite the high diversity, each scattering region was numerically dominated by a few species for which we collected information about their swimbladder, if present (Table 2). According to catch data, most of the organisms in the DSL1 were fishes near 30 mm in length, bearing gas-filled swimbladders with ESR from 0.6 to 1.2 mm. In the DSL2, the catches were dominated either by fishes or decapods with sizes ranging from 23 to 133 mm, and with *C. braueri* being the only specie susceptible to bear gas in the swimbladder. In the case of the DSL3, *C. microdon*

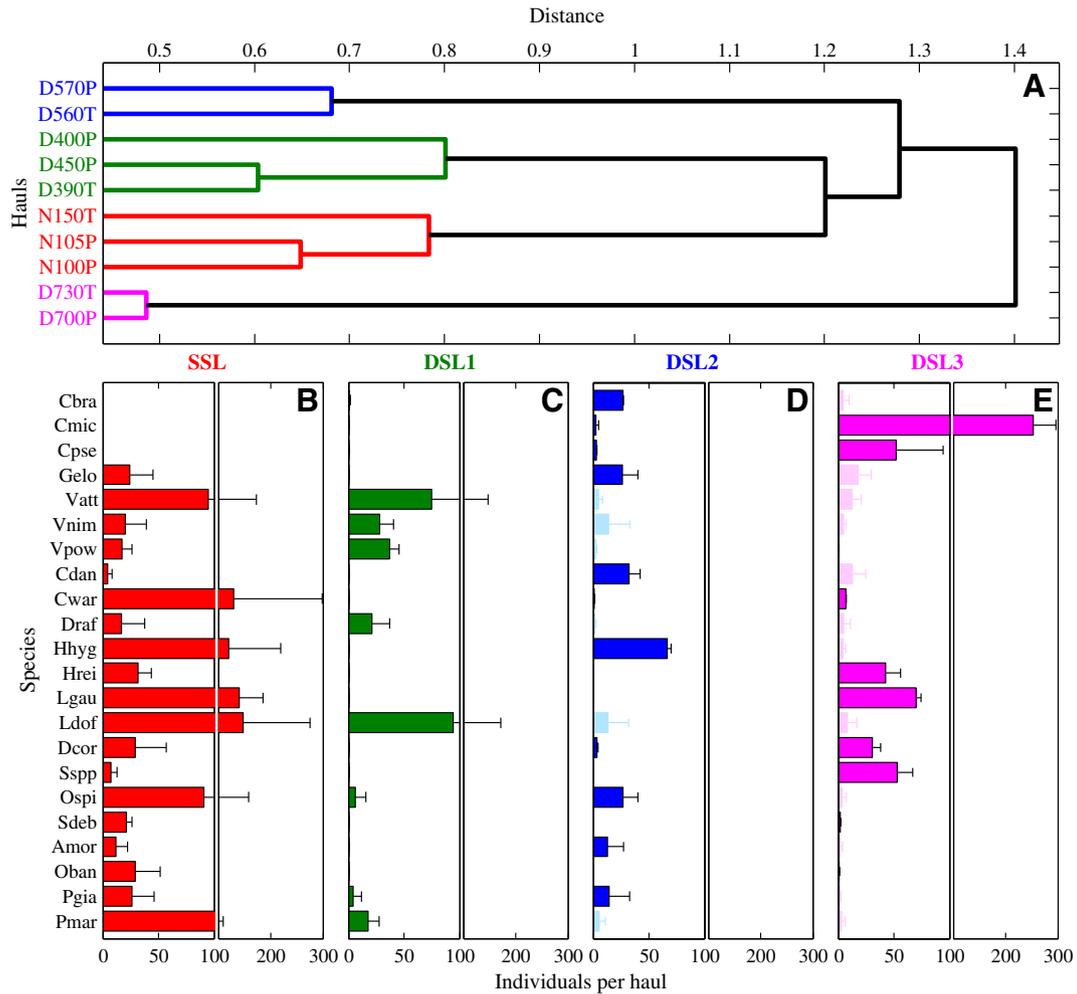


Fig. 5. (A) Dendrogram showing classification of fishing hauls according to Bray-Curtis dissimilarity distances. Time and depth of each haul can be checked in Fig. 3e and f. (B-E) Individuals per haul of dominant species contributing to differences among clusters. Light-colored bars indicate possible contamination from upper strata (see discussion). Error bars indicate standard deviations. Species abbreviations: Cbra = *Cyathothone braueri*; Cmic = *Cyathothone microdon*; Cpse = *Cyathothone pseudopallida*; Gelo = *Gonostoma elongatum*; Vatt = *Vinciguerria attenuata*; Vnim = *Vinciguerria nimbaria*; Vpow = *Vinciguerria poweriae*; Cdan = *Chauliodus danae*; Cwar = *Ceratoscopelus warmingii*; Draf = *Diaphus rafinesquii*; Hhyg = *Hygophum hygomii*; Hrei = *Hygophum reinhardtii*; Lgau = *Lepidophanes gaussi*; Ldof = *Lobianchia dofleini*; Dcor = *Deosergestes corniculum*; Sspp = *Sergestes* spp.; Osp = *Oplophorus spinosus*; Sdeb = *Systellaspis debilis*; Amor = *Abraliopsis moriisi*; Oban = *Onychoteuthis banksii*; Pgia = *Pterygioteuthis giardi*; Pmar = *Pyroteuthis margaritifera*.

Table 2
Dominant species forming each scattering layer with indications of relative abundances within catches, lengths, and if present, the swimbladder condition according to the literature. “None” means that the organism has no swimbladder. ESR depicts the equivalent spherical radius of the swimbladder, as estimated from the modal standard length of fishes using species-specific equations given by (Saenger, 1989), or calculated from swimbladder spherical volumes given by (Kleckner & Gibbs, 1972). Relative abundances are given as means while lengths refer to modal values. In both cases, minimum and maximum values are also noted between parentheses.

		Abundance (%)	Length (mm)	Swimbladder condition	ESR (mm)
DSL1	<i>Lobianchia dofleini</i>	24 (6–43)	22 (16–37)	Gas-filled ^b	0.6 ^d
	<i>Vinciguerria attenuata</i>	18 (8–36)	35 (21–43)	Gas-filled ^{a,b}	1.2 ^d
	<i>Vinciguerria poweriae</i>	10 (7–16)	33 (20–36)	Gas-filled ^b	1.1 ^d
	<i>Vinciguerria nimbaria</i>	8 (4–14)	32 (22–35)	Gas-filled ^a	–
	<i>Diaphus rafinesquii</i>	6 (1–8)	49 (27–61)	Gas-filled ^{a,b}	2.2 ^d
DSL2	<i>Hygophum hygomii</i>	20 (15–25)	35 (24–45)	Contracted ^b	0.9 ^d
	<i>Chauliodus danae</i>	9 (9–10)	120 (43–134)	None	–
	<i>Oplophorus spinosus</i>	9 (4–13)	25 (23–33)	None	–
	<i>Cyclothone braueri</i>	8 (7–9)	23 (16–29)	Gas-filled ^{a,c} Fat-invested ^b	0.7 ^b
	<i>Gonostoma elongatum</i>	7 (6–8)	133 (61–135)	Fat-invested ^a	–
DSL3	<i>Cyclothone microdon</i>	46 (38–54)	54 (29–56)	Fat-invested ^{a,c}	–
	<i>Lepidophanes gaussi</i>	13 (11–14)	41 (28–47)	Unknown	1.4 ^d
	<i>Cyclothone pseudopallida</i>	10 (4–16)	43 (25–46)	Fat-invested ^{a,c}	–
	<i>Sergestes spp.</i>	10 (7–12)	–	None	–
	<i>Hygophum reinhardtii</i>	8 (6–10)	34 (22–39)	Unknown	–

^a Marshall (1960).

^b Kleckner and Gibbs (1972).

^c Badcock and Merret (1977).

^d Saenger (1989).

accounted for most of the catches, a fish with a modal length of 54 mm and bearing a fat-invested swimbladder. Myctophids and sergestids were also well represented in the DSL3.

4. Discussion

Scientific echosounders are a powerful tool to study the distribution and behavior of pelagic biota (Kloser et al., 2002; Kaartvedt et al., 2009; Cade & Benoit-Bird, 2015). The potential to extract information of biological significance is enhanced when acoustic data are validated with net sampling, as in this study. However, trawling data should be interpreted with caution in order to accurately identify the animals most likely causing sound scattering in the region. First, as expected, a high diversity of mesopelagic species was found here in the subtropical Atlantic (152 species identified in this survey). This introduces a broad list of likely targets, each one with different acoustic properties. Secondly, it is possible that some species found in deep hauls came from contamination of upper layers due to the lack of an opening-closing system in our trawl. This contamination should be reduced according to the velocity of deploying and lifting maneuvers, where the trawl crossed other scattering layers within less than 5 min and not in an adequate fishing position. This represented less than 10% of the effective fishing time. With analogous trawling settings, (Watanabe et al., 1999) calculated a contamination of less than 2% in the northwestern Pacific. In spite of this, we adopted the precautionary principle of considering susceptible of contamination all the species with less than 50 individuals per haul, as long as these species also occurred at higher abundances in upper strata (see light-colored bars in Fig. 5D and E). This did not apply therefore to hauls conducted in shallow waters, or those in the DSL1 at daytime. Contaminated or not, this approach only excludes non-dominant species, which on the other hand, are expected to poorly contribute to sound scattering due to their low abundances.

Therefore, in order to find the main cause of reverberation, here we focused on the acoustic properties of the dominant species captured within each scattering layer. It should be noted, however, that these scattering zones must also be inhabited by many species not visible in our echograms, either because their weak signal is easily masked by dominant sound reflectors, or because they do not respond at all under the insonifying frequency.

The distribution of scattering layers as well as their species composition was quite similar regardless the location surveyed, which in fact,

also presented similar hydrographic conditions (Fig. 2). We systematically observed two strong layers between 400 and 600 m depth (Fig. 3), the upper one responding higher at 18 kHz (DSL1), and the lower one at 38 kHz (DSL2). This layout has been previously documented at other latitudes, where the upper layer at 18 kHz has been ascribed to the resonance of small swimbladdered fishes such as the pearlside *Maurolicus muelleri* (Kaartvedt et al., 2008; Godø et al., 2009) or different species of myctophids (Olivar et al., 2012; Peña et al., 2014). According to the model developed by Kloser et al. (2002), animals bearing gas bladders of ESR about 1.2–1.4 mm are susceptible to resonate at 18 kHz when inhabiting waters between 400 and 500 m depth (see Fig. 6A). In our study the DSL1 was mainly inhabited by gas-filled swimbladdered animals, the lightfishes *Vinciguerria* spp. being the most likely targets producing resonance at 18 kHz (ESR = 1.2 mm, Table 2). According to the same model, *L. dofleini* might be causing swimbladder resonance at similar depths but at 38 kHz (ESR = 0.6 mm, Table 2 and Fig. 6B).

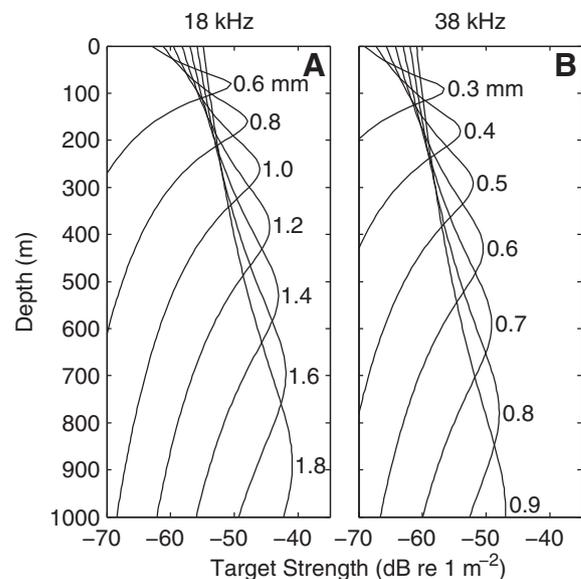


Fig. 6. Modeled swimbladder resonance at (A) 18 and (B) 38 kHz along depth according to Kloser et al., (2002). Each line represents expected target strengths for swimbladders of different equivalent spherical radius (ESR, mm).

Another clue supporting that these layers are mainly caused by swimbladder resonance is the changing backscattering during vertical migration (averaged Sv from -65 dB to -59 dB, see Fig. 4C and D). This is because the effective scattering cross section of fishes varies substantially due to little variations of the swimbladder dimensions when changing depth, typically showing maximum values between 150 and 400 m depth (Andreeva, 1964; Godø et al., 2009).

Even though there were migrations coming from or passing by the DSL2, this layer itself did not exhibit diel vertical movements. This layer remained visible at the same depth range during all day long. Notwithstanding the foregoing, the DSL2 also became less dense at night (Fig. 4A and B). This implies that the main targets producing the DSL2 must be non-migrant animals, albeit the migrant fauna also contributed to a lesser extent. Among the dominant species inhabiting the DSL2, the fish *C. braueri* is the only one not performing vertical migrations (Goodyear et al., 1972; Badcock & Merrett, 1976) and the best sound reflector according to their swimbladder features (Table 2). It is difficult to predict the size range over which fat-investment occurs in *C. braueri* since there is a considerable variability between individuals (Marshall, 1960; Kleckner & Gibbs, 1972; Badcock & Merrett, 1977). Here, the swimbladder condition was determined for individuals of 23 mm (modal length), not being clear whether gas was displaced by fat at this stage or later (see Table 2). However, it should be taken into account that sizes of *C. braueri* ranged from 16 to 29 mm, and that our trawl probably biased the abundances towards large specimens (see paragraph below). It is probably therefore that both gas-filled and fat-invested swimbladders occur in the population of *C. braueri* inhabiting near the DSL2. According to our catch results, the most common sizes of *C. braueri* would have swimbladders of ESR near 0.7 mm, which could be responsible of the acoustic resonance at 38 kHz (see Table 2 and Fig. 6B).

We are aware that our trawl data showed species more abundant than *C. braueri* at the DSL2, such as the lanternfish *H. hygomii* or the decapod *O. spinosus* (Fig. 5D). However, they are vertical migrants and behave as bad sound reflectors due to the atrophy or the absence of the swimbladder (Table 2). This migrant fauna could be instead the secondary cause of the DSL2 and responsible of its weakening at night. In

addition to this, *C. braueri* might be the dominant fish species within the DSL2, even though its presence was not the most prominent in our catches (Fig. 5D). According to previous studies, *C. braueri* is extremely abundant at the DSL2 when using sampling gears with smaller meshes, about one to two orders of magnitude more abundant than other species of the same sample (Badcock, 1970; Badcock & Merrett, 1976; Roe & Badcock, 1984). We think therefore that this fish was widely underestimated due to the large meshes of our trawl. Based on the above, we prioritized in this case acoustic insights such as the non-migrant behavior of the DSL2 or the optimal scattering features of *C. braueri* rather than our catch results. Obviously, other small animals belonging to species different to *C. braueri* could have been as well underestimated with our trawl, this would remain a possibility. However, we have no clue in this respect when consulting earlier studies. The most noticeable change when using smaller sampling gears within the DSL2 is the dominance of *C. braueri* (Badcock, 1970; Badcock & Merrett, 1976; Roe & Badcock, 1984).

Acoustic scattering was notably lower below 600 m depth, where differences in the frequency response suggested the existence of different community strata. From 600 to 800 m depth (DSL3) sound reflection was mainly caused by migrant biota as evidenced by the diel vertical movements of both the 18 and 38 kHz scattering layers (Fig. 4). Here the captures were clearly dominated by *C. microdon* (Fig. 5F), a fish which could in principle be a likely target causing scattering if it were not for the fact that this species does not conduct migrations (Goodyear et al., 1972; Badcock & Merrett, 1976). Besides, *C. microdon* and other species of the genus inhabiting below 600 m depth, are no longer potential sound reflectors due to the fat investment of their swimbladders during earlier stages in shallower waters (Badcock & Merrett, 1976; Badcock & Merrett, 1977). Therefore, dominant migrants in the DSL3 must be the most likely acoustic targets. Among others, the myctophids *L. gaussi*, *H. reinhardtii*, or many species of sergestids which were abundant at these depths. According to the literature, *L. gaussi* and *H. reinhardtii* bear swimbladders which in case of being functional (gas-filled) could cause resonance at 18 kHz (Fig. 6A). Although we lack such information (Table 2), the scattering levels below 600 m depth are not indicative of swimbladder resonance.

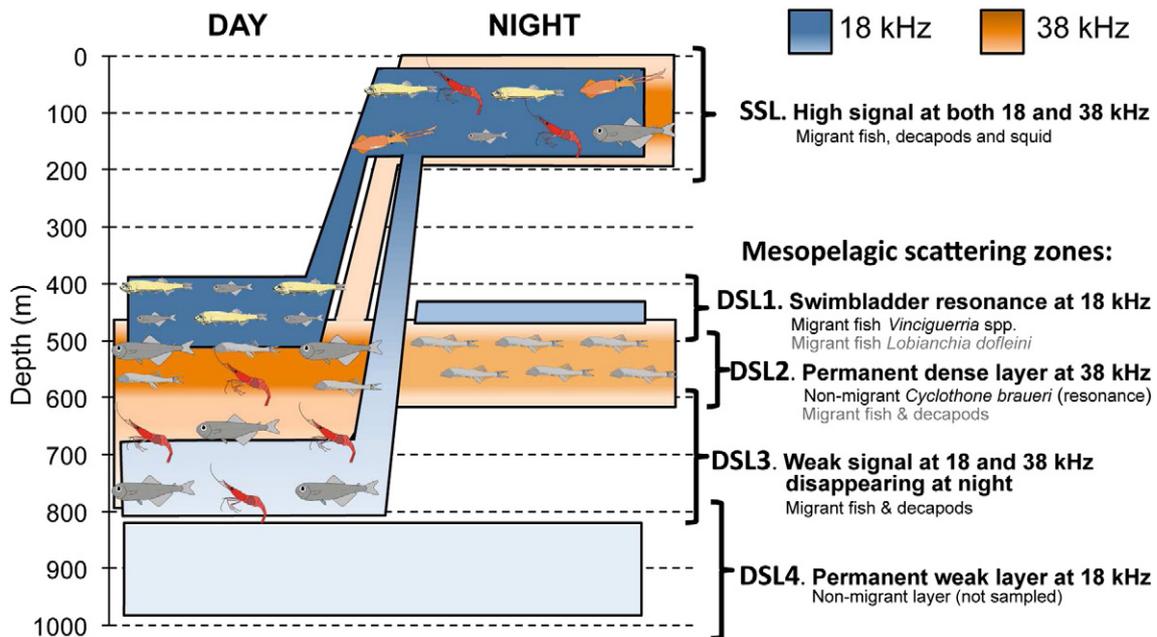


Fig. 7. Distribution of shallow and deep scattering layers (SSL and DSLs) based on observations at 18 and 38 kHz in waters around the Canary Islands (threshold -80 to -50 dB). Only dominant animals likely to contribute more to backscattering are indicated (main scatterers in black, and secondary ones in gray). Blue and orange depict 18 and 38 kHz frequencies respectively, with dark colors indicating high backscattering and light colors representing weak backscattering. See Discussion for further details.

This is consistent with the fact that swimbladders are usually contracted (atrophied) in myctophids reaching these depths (see Discussion below). Therefore, it is probably that both fishes and decapods inhabiting this strata behave as fluid-like targets, but uncertain which one causes more reflection.

Contracted swimbladders are a common feature in large myctophids, which is the same as saying that the functionality of the swimbladder decreases with migration depth (Marshall, 1960; Butler & Percy, 1972; Davison, 2011). This is especially true in our study area, where the smallest myctophid *L. dofleini* exhibits the shallower migration depth while largest species such as *C. warmingii* or *Notoscopelus resplendens* reach bathypelagic waters (Badcock & Merrett, 1976). Since a “cottony tissue” (expanded fibrous submucosa) fills most of the lumen in contracted swimbladders, the external size of the organ is probably not an accurate indication of the gas volume contained (Capen, 1967; Kleckner & Gibbs, 1972). According to swimbladder catalogues, gas-bearing fishes occurred in our study only above 600 m depth, while swimbladders regressions in both *Cyclothone* species and myctophids are a common feature at deeper waters (see Table 2). In acoustic terms, this means that the deep mesopelagic zone must be dominated by fluid-like targets, where resonance models are hardly applicable. It would also explain why the relative high abundances from net sampling does not result in a higher backscattering at these depths.

The DSL4 (800–1000 m depth) was out of reach of our trawl and this impeded the assessment of the species producing reflection. Although the deeper migrations observed in this study were somewhat associated with the DSL3 and DSL4, the later was clearly visible both during day and night. This suggests that the DSL4 would mainly be caused by non-migrating organisms. In this respect, literature may provide clues about the likely targets. Below 800 m depth, there is a peak of not only non-migrant fishes such as *Cyclothone pallida* and *Sternoptyx diaphana*, but also large migrant fishes such as *C. warmingii* or *N. resplendens* which are abundant at these depths according to Badcock (1970). Both migrant species dominated at night in the SSL (specially *C. warmingii*) but were scarce in our daytime mesopelagic hauls (< 800 m depth). Besides, the DSL4 is the most frequented daytime foraging zone by short-finned pilot-whales in the Canary Islands (*Globicephala macrorhynchus*), whose diet is known to be mainly composed by squid but also large fishes (Aguilar et al., 2008). Hence, both fishes or squid might be responsible of the DSL4 but also other targets. Deeper hauls with concurrent acoustic records are therefore required to unveil the specific origin of this reflection.

Overall, the association of scattering layers and animals proposed here (Fig. 7) is consistent with the vertical distribution previously observed during the SONDA expedition in the Canary Islands and other surveys in nearby oceanic waters (Foxton, 1969; Badcock & Merrett, 1976; Roe et al., 1984). Specifically, Badcock (1970) and Badcock & Merrett (1976) noted that most myctophid species inhabited between 400 and 600 m depth, while less species of larger sizes appeared deeper than 700 m depth. Their abundance tables also evidenced the shallower distribution for *L. dofleini* and *Vinciguerria* spp., and showed a prominent peak of *Cyclothone braueri* between 500 and 600 m depth. This matches with our description of the DSL1 and the DSL2. On the other hand, (Foxton, 1970a) and (Foxton, 1970b) reported maximum densities of decapods below 650 m depth. In this respect, both Badcock's and Foxton's studies proposed a distinction between “shallow and deep mesopelagic fauna”, which they ascribed to adaptations for different light conditions. Based on the above, the interphase of high and weak scattering seen here around 600 m depth might be outlying this “biocline” (Lezama-Ochoa et al., 2014), with small and gas-bearing animals above, and larger and fluid-like organisms below. In fact, the increased migrant velocity of the deeper scattering biota (about 11–12 cm s⁻¹) also supports the idea of larger and non gas-bearing animals. They can move faster not only because of their increased size, but also for not requiring gas volume adjustments during vertical migrations (Marshall, 1960), (Butler & Percy, 1972), (Kleckner & Gibbs, 1972).

In conclusion, this study has revealed a high diversity within the micronekton mesopelagic community (152 species identified), yet with few dominant species likely being responsible for most of the acoustic phenomena in the region. We suggest that the DSL1 (400–500 m depth) is largely formed by swimbladder resonance, produced by the migrant fishes *Vinciguerria* spp. and *Lobianchia dofleini*. We primarily ascribe the DSL2 (500–600 m depth) to the gas-bearing and non-migrant fish *Cyclothone braueri*, and to a lesser extent, to fluid-like migrant fauna also inhabiting these depths. The DSL3 (600–800 m depth) was caused either by migrant fish or decapods, but as for other layers occurring deeper, the specific target identities remain unknown. All layers exhibiting diel vertical movements reached the epipelagic zone at night, with the shorter migrations moving near 5 cm s⁻¹ and the large ones near 12 cm s⁻¹. This work reduces uncertainties interpreting acoustic scattering, although more accurate results will be obtained with deeper and higher vertical resolution trawling, using multifrequency lowering echosounders, as well as improving the scattering models for the mesopelagic fauna in the region.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jmarsys.2016.01.004>.

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