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From coast to slope: Zooplankton communities shift in the Northern Alboran Sea

Ana Ventero *, Magdalena Iglesias, Joan Miquel

Instituto Español de Oceanografía. Centro Oceanográfico de Baleares, Spain

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A B S T R A C T

The zooplankton composition of the Sound Scattering Layer (SSL) detected at multiples frequencies, 18, 38, 120 and 200 kHz, along the continental shelf of the Northern Alboran Sea (Mediterranean Sea) has been identified in July 2013 and 2014 by means of different plankton nets and the SSL dominant scatterers have been identified using zooplankton scattering models.

Three acoustic patterns, based on their distinctive relative frequency response (r(f)), have been detected along the continental shelf, matching with three zooplankton communities; in coastal areas (25–40 m bottom depth), a homogeneous community composed by Fluid-like zooplankton, mainly crustaceans, exhibiting a r(f) peak at 120 kHz, (ii) in intermediate areas (40–190 m) a heterogeneous community composed by Fluid-like (crustaceans, chaetognaths, larvaceans, doliolids, Calycophora siphonophores), Elastic-shelled (heteropods) and Gas-bearing (fish larvae) zooplankton, exhibiting a r(f) peak at 38 kHz (iii) in the continental shelf edge (180–250 m), a zooplankton community dominated by *Maurolicus muelleri* fish larvae, exhibiting a r(f) peak at 18 kHz. Scattering models results showed that stronger scatterers as fish larvae (Gas-bearing), although scarce in samples, dominated the backscattering energy at almost all frequencies and locations. Fluid-like zooplankton contribution was only significant in coastal areas at high frequencies (120 and 200 kHz).

The application of these findings to all echograms collected over the study area made it possible to obtain, the macro scale spatial distribution of the zooplankton communities as well as the SSL backscatter energy all over the continental shelf, highlighting the suitability of the use of acoustic data as an indicator of secondary production.

1. Introduction

Plankton and micronekton form dense and geographically extensive layers, which are observed acoustically using echosounders, known as Sound Scattering Layers (SSLs). These layers may present a monospecific composition such as occurs with euphausiids aggregations (Everson, 2000; Everson et al., 2007; Ventero et al., 2019); they may be composed by organisms belonging to the same taxonomic family such as copepods (Mutlu, 2003) or mesopelagic fishes (Peña et al., 2014) or they may present a heterogeneous and multispecific organisms composition (Lavery et al., 2007). Echosounders let us determine the vertical (Benoit-Bird et al., 2010) and the horizontal (Moline et al., 2010) structure of the SSLs in a remote, no invasive and synoptically way (Simmonds and MacLennan, 2005) and enable the collection of information simultaneously from different pelagic communities (plankton and nekton) on a spatial and temporal scale, an almost impossible task with the use of traditional sampling methods (Godo et al., 2014).

Technology evolution from single to multiple frequency systems (Chu, 2011) has provided scientists with an additional capability to characterize or classify the scattering targets according to the strong frequency dependence of signals backscattered by marine animals (Chu et al., 1992; Holliday et al., 1989). Planktonic organisms can be classified, based on the dispersion model that explains their acoustic reflection, according to the categorization principle (Fernandes et al., 2006). This principle discriminates organisms in three different categories, namely: Fluid-like, Elastic-shelled, and Gas-bearing (Martin et al., 1996; Simmonds and MacLennan, 2005; Stanton et al., 1996). The Fluid-like class includes organisms with tissues composition causing a low contrast of density and sound speed compared to sea water; e.g., copepods, euphausiids, or chaetognaths. The Elastic-shelled class is composed by organisms with an external shell made of calcium carbonate, such as pteropodes. Finally, in the Gas-bearing class are included organisms with gaseous vesicles, such as some siphonophores, adult jellyfish, and fish larvae. The relative frequency response measured at

* Corresponding author. Muelle de Poniente s/n, 07015, Palma de Mallorca, Balearic Islands, Spain.
E-mail address: ana.ventero@ieo.es (A. Ventero).

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different acoustic frequencies is an important acoustic feature used to characterize the acoustic targets (Korneliussen and Ona, 2003). Fluid-like zooplankton backscatter is characterized by increasing the acoustic backscatter from low to high frequencies considering the frequency range (18–200 kHz) commonly employed during acoustic surveys focus on stock assessment. All Gas-bearing zooplankton displays resonant scattering at a frequency that depends on the depth and the size of the gas inclusion. Backscatter from Elastic-shelled zooplankton is characterized by the smooth transition between low frequencies and high frequencies.

Fisheries acoustic water-column data is a currently underused data source for monitoring changes in pelagic ecosystem state, in particular for deriving indicators making use of the distinctive acoustic frequency response of different organism groups (Trenkel et al., 2011). Routine assessment acoustic surveys data contain information about the entire water column and can provide large scale reference maps of the distribution of acoustic scattering groups (Trenkel and Berger, 2013). In addition, knowledge of the spatial and temporal variation of the distribution of different pelagic communities (mainly fish and plankton) is essential to achieve efficient management of fishery resources based on the ecosystem approach (Bertrand et al., 2014; FAO, 2008).

The main difficulty when several frequencies are used to characterize zooplankton is the diverse array of organisms present in the water column (Lavery et al., 2007). Direct identification of organisms, by means of biological samples, is needed in order to interpret correctly the echotraces (Simmonds and MacLennan, 2005). The zooplankton is composed by a multitude of organisms that live their entire life (holoplankton) or part of it (meroplankton) suspended in the water column, presenting an extraordinary diversity of taxa (Alcaraz and Calbet, 2007) shapes, sizes (Sieburth et al., 1978) and body structures that prevent their sinking. The high degree of biodiversity and sizes makes it difficult to determine its composition using a single sampling device, so it is necessary to use several of them to know the global composition of the community (Skjoldal et al., 2013). Moreover, the distribution of the zooplankton community is strongly influenced by climatic factors (Fernández de Puelles et al., 2004, 2008; Siokou-Frangou et al., 2010), thus the SSLs has to be framed into their environmental context to determine its principal environmental forcing.

In this study, our main objective was to determine the macroscale spatial distribution of the different zooplankton communities present in the Northern Alboran Sea. The achievement of this objective was carried out by verifying our working hypothesis which implied that the changes in the acoustic frequency response (Korneliussen and Ona, 2003) observed along the continental shelf (from coast to the edge) were due to changes in the composition of the zooplankton community. In order to be able to interpret the echograms collected at different frequencies (18, 38, 120 and 200 kHz) in terms of zooplankton communities, the SSL biological composition was determined by analyzing zooplankton samples collected by plankton nets. In addition, the suitability of acoustic methods for generating secondary production indicator maps is discussed.

The main contribution of this study is the application of acoustic methods, for the first time in the Mediterranean Sea, to obtain the spatial distribution of different zooplankton communities. This fact has a great ecological importance because it shows the different levels of complexity and organization of zooplanktonic communities on the continental shelf. The scope of this work does not subscribe only to the limits of the study area but also gives the keys to interpret echograms in terms of the zooplankton community collected in previous years in the same area and/or in adjacent areas. In addition, the distribution of zooplankton determines the presence and distribution of upper links of the trophic chain thus having a map of the distribution of possible prey can help to understand the distribution and behavior of potential predators. With the results provided, it is possible to interpret the data collected in acoustic stock assessment surveys, such as MEDIAS (MEDiterranean International Acoustic Survey) in a global context, integrating the main components of the ecosystem, fish and zooplankton.

2. Material and methods

2.1. Study area and sampling design

The study area (Fig. 1), the Northern Alboran Sea, is located in the Western part of the Mediterranean Sea and includes the Gulf of Vera and the North Alboran Sea continental shelf, characterized by a very narrow margin, ranging between 0.7 km and 17 km, and locally dissected by submarine canyons (Durán et al., 2018). The predominant circulation pattern in this area within the upper 150–200 m involves an incoming meandering buoyant Atlantic jet through the Strait of Gibraltar (Oguz et al., 2014; Renault et al., 2012). Moreover, a strong ocean front, called Almeria-Oran Front, is present between Almeria (Spain) and Oran (Argelia). This front is part of the easternmost segment of the Eastern Alboran Gyre, and constitutes a large scale density front formed by the convergence of two different water masses (Atlantic and Levantine Intermediate Waters) and it is controlled by the geographic position and strength of the Eastern Alboran Gyre (Tintore et al., 1988). Alboran Sea represents a high productive area due to the costal upwelling near the Malaga Bay, the inflow of nutrient-enriched Atlantic waters, riverine influences from the mountainous coastline and a front presence which promote formation of zones of concentrated distributions of small organisms (Agostini and Bakun, 2002).

The acoustic survey design included the continental shelf and the first 50 m of continental slope (from 25 to 250 m) and it was based on a systematic sampling by parallel transects running along the greatest gradient in bottom topography, normally perpendicular to the coastline/bathymetry. The inter-transect distance was 4 nautical miles (Fig. 1). Survey transects were acoustically sampled at a vessel speed of 10 knots (nautical mile/hour) in a standardized way, each summer (July), during the daytime hours.

2.2. Acoustic data

During the MEDIAS acoustic survey conducted during July 2013 and 2014 on board R/V Miguel Oliver (70 m long), acoustic data were collected following the sampling design (Fig. 1) by means of a scientific echosounder Simrad EK60 with 4 split-beam transducers (18, 38, 120 y 200 kHz). All transducers were hull mounted, positioning 5.3 m below the water surface. Nominal half-power beam widths were 7° for the 38, 120 and 200 kHz transducers and 11° for the 18 kHz transducer. All the recommendation to collect spatial and temporal comparable acoustic data were considered (Korneliussen et al., 2004; Korneliussen et al., 2008) taking into account that although the 18 kHz sampling volume was greater than the rest of the frequencies, the scattering quantities were comparable between frequencies since the zooplankton SSL formed a continuous layer. Prior to sampling, the echosounder was calibrated by standard sphere techniques (Foote et al., 1987). Pings were transmitted every 1 s (s) with a pulse duration of 1 ms (ms).

Three different acoustic patterns regarding the zooplankton SSL strongest frequency (maxima acoustic scattering quantity recorded at 120, 38 or 18 kHz) were observed along the continental shelf when sailing at 10 knots and their identification by means of plankton nets (see section 2.3) were carried out sailing between 2.2 and 3.1 knots. The Echoview software (v.5.4; Myriax Ltd.) was employed for the acoustic data processing. For each frequency, acoustic data were corrected for the background noise effect (De Robertis and Higginbottom, 2007) and the zooplankton SSL S_V (volume backscattering strength data) values (Maclennan et al., 2002) were calculated. The SSL vertical limits were determined and the respective mean depth was calculated.

Echograms recorded during the net tows were used to define the relative frequency response (r(f)) of a specific acoustic pattern and to determine their zooplankton composition. The relative frequency

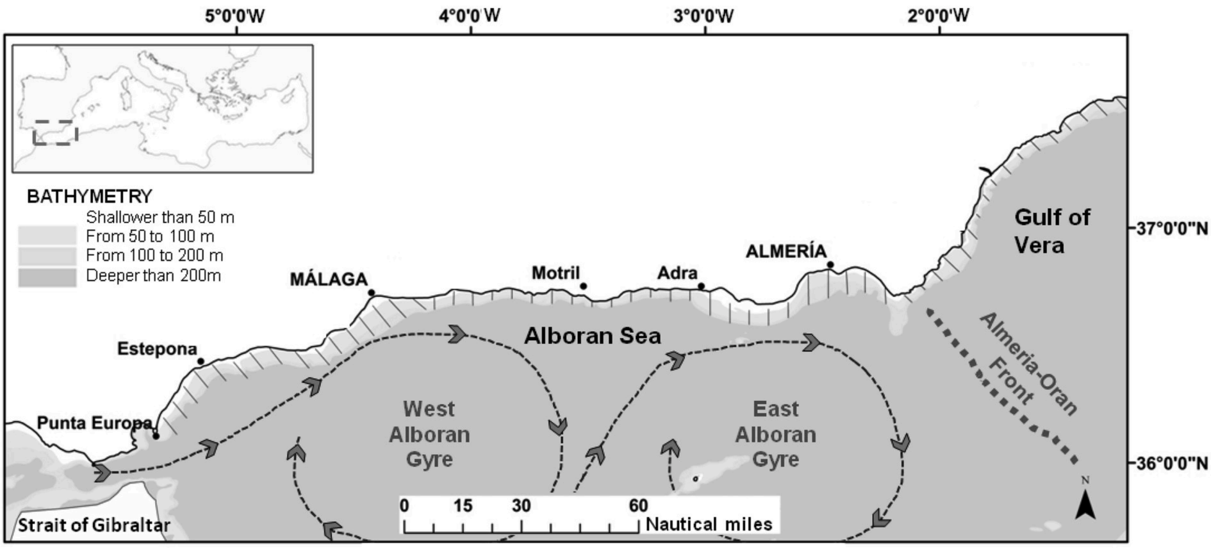

Fig. 1. Study area, Alboran Sea, showing the main oceanographic features: main current, gyres and the position of the Almeria-Oran density front, and the systematic sampling design based on parallel transect (black lines) perpendicular to bathymetry from 25 to 250 m, covering the continental shelf and the first meters of the shelf break.

response, (Korneliussen and Ona, 2003), the acoustic feature used to characterize the acoustic targets, was calculated for all the echograms recorded during the net tows. This relative frequency response has been defined as the s_v value for a specific frequency relative to that of a reference frequency (e.g. 38 kHz). The r(f) was determined using the equation: $r(f) \equiv s_v(f)/s_v(38\ \text{kHz})$, where s_v is the volume backscattering coefficient and "f" is the reference acoustic frequency. In addition, the vertical homogeneity of the zooplankton sound scattering layer was tested in a previous experiment dividing the layer into 5 m strata and comparing its frequency response.

Echograms recorded over the systematic survey design were used to characterize the entire study area and to mark off the spatial distribution of the different acoustic patterns in terms of zooplankton communities. A non-metric multidimensional scaling (nMDS) analysis was carried out in order to group the zooplankton SSL detected in the entire study area into classes of similar frequency response based on the S_V values registered at multiples frequencies. The zooplankton SSL S_V values registered by frequency, 18, 38, 120 and 200 kHz, along each transect and averaged each 1 m following the bathymetric range, from 20 to 224 m depth, constitute the predictor variable. The S_v values were square root transformed and the Euclidean distance was used to calculate the distance matrix. Finally the factor "depth" was superimposed in the nMDS graph to highlight bathymetric gradients in the zooplankton SSL frequency response. Moreover, a two-way analysis of variance (ANOVA) was performed in order to examine the influence of two factors "frequency", with four levels: 18, 38, 120 and 200 kHz, and "depth", with three levels: coastal areas (depth $<$ 40 m), intermediate areas (depth $>$ 40 and $<$180 m) and edge areas (depth $>$ 180 m), in the zooplankton SSL nautical area scattering coefficient (s_A values) (Maclennan et al., 2002). The null hypothesis tested were (i) no differences in the population mean (s_A values) due to the first factor, (ii) no differences in the population mean due to the second factor and (iii) no interaction effects between the first and second factors. As it could not be assumed that the data fit a normal distribution, necessary assumption to apply the ANOVA test, the data were log transformed before performing the analysis. A *post hoc* Tukey multiple pair wise-comparison test was performed to determine if the mean difference between specific pairs of group were statistically significant.

Finally, in order to map the general distribution of the zooplankton SSL in the study area, the s_V values averaged by nautical mile were represented by means of a Kernel spatial density analysis using the ArcGIS 10.4 software (ESRI). The distribution spatial centre was calculated for each year in order to detect possible East-West displacement of the zooplankton sound scattering layer preferential concentration areas. Finally, once the biological composition of each of the three different acoustic patterns were determined, the echograms were interpreted in term of zooplankton communities obtaining the zooplankton communities distribution map in the study area.

2.3. Biological data

The identification of the zooplankton SSL was carried out by net tows employing two different plankton nets: a 40 cm opening Bongo net with 250 μm and 333 μm meshes and a 90 cm opening Bongo net with 500 μm and 2000 μm meshes. These four different mesh sizes were chosen to sample a wide range of organism sizes covering from meso to macrozooplankton (Sieburth et al., 1978) since they were expected to generate the observed acoustic signal at the frequencies used.

The Bongo nets were positioned at the stronger scattering depths of the zooplankton SSL observed on live-viewed echograms, corresponding to the maximum zooplankton individual density, and they were towed horizontally for 6 minutes (min). The tow duration was established based on a previous experiment, in which 6 min tow fitted to the compromise between getting a zooplankton community representative sample and avoiding the net clogging. Bongo nets were equipped with a depth sensor (Scanmar or ITI) that allowed monitoring the net track in real time, and enabled the Bongo net to be accurately placed in the position where the stronger signal was detected. The filtered volume was calculated according to the mouth opening, the research vessel's speed and the tows duration (Olivar et al., 2012), considering a cent per cent filtering efficiency. Once the Bongo net was on-board, the sample of each mesh was filtered, concentrated, placed in 250-ml plastic bottles and fixed using formalin buffered with 4% borax.

Analysis of zooplankton samples was performed at the laboratory, after the survey, using a binocular microscope. For the purpose of this study, and after considering the acoustic properties of different types and sizes of scatterers, nine zooplankton groups were considered: "small crustaceans" that grouped cladocerans and copepods with a size smaller than 1.2 mm, "big crustaceans" that mainly grouped developmental stages of decapods and mysids with a size larger than 1.2 mm, chaetognaths, larvaceans, doliolids, siphonophores, heteropods, fish eggs and fish larvae. Three replicates of 10 ml (one eighth of the sample) were analyzed for each net at each station. The number of individuals belonging to each zooplankton group per cubic meter was calculated from the number of animals caught and the volume of water filtered.

Finally, the different zooplankton taxa were grouped according to the general zooplankton acoustic classification (Martin et al., 1996; Simmonds and MacLennan, 2005; Stanton et al., 1996) in order to infer the dominant scatterers in each acoustic pattern. Small crustaceans, big crustaceans, chaetognaths, larvaceans, doliolids, siphonophores and fish eggs were grouped within the acoustic category Fluid-like, heteropods and fish larvae were the only representatives of the Elastic-shelled and Gas-bearing acoustic categories, respectively. In contrast to other areas (Stanton et al., 1996; Warren et al., 2001), siphonophores found in the study area belonged to the Calycophora genus characterized by the absence of gas vesicles (Madin, 1991), for that reason were classified as Fluid-like.

In addition, in order to determine the main environmental forcing of the zooplankton sound scattering layer, the thermo-haline properties of the water column were determined for each net tow by using a Seabird 19 plus CTD with a fluorescence sensor coupled. The instrument used was self-contained, storing data of depth (m), temperature (°C), and conductivity (S/m) to determine the salinity (PSU), as well as chlorophyll-a (mg/m^3).

2.4. Zooplankton modelling: solving the forward problem

The forward problem was solved to determine the dominant scatterer in the biological samples. In order to link the net tows related backscatter (observed volume backscattering) to net tows derived backscatter (predicted volume backscattering) it was necessary integrate the contribution of each taxa at each frequency calculated using published scattering models appropriate for each zooplankton taxa (Table 1).

All models required biological measures, and assumptions about the material properties of the organisms. To determinate the mean length and weight of the main taxa, random samples were measured to the lowest 0.1 mm from the samples collected using the 500 μm mesh size in 2014 (Table 2). The 500 μm mesh size was selected because it was considered the most representative of the shapes, sizes and body structures of the zooplankton community present in the study area.

Five taxa were considered for the modelling approach, as they represented more than 95% of the total abundance in the samples: Crustacean, chaetognats, siphonophores heteropods and fish larvae (Tables 1 and 2). Values for "g" (the ratio of the density of the organism to the density of sea water) and "h" (the ratio of the speed of sound in the organism to the speed in sea water) were taken from literature. For the application of Stanton's models (Stanton, 1989) $g = 1.043$ and $h = 1.052$ (Greenlaw, 1979) were set for crustaceans, $g = 1.03$ and $h = 1.03$ (Mair et al., 2005) were set for chaetognats and siphonophores and $g = 2.8$ and $h = 4.38$ (Stanton, 1989) for heteropods. For the swimbladder model (Kloser et al., 2002), the following specific values were assumed: $\mu_1 =$ 105 Pa, $\gamma = 1.4$, $\rho = 1.075$ kg/m^3, $Q = 5$ and $e = 0.2$ (Kloser et al., 2002). It was assumed that sound scattering from larval fish would be due to the swimbladder alone, and that the swimbladder diameter would be 5% of the fish length (Simmonds and MacLennan, 2005). All models were parameterized with a sound velocity in water of 1500 ms^{-1}.

Table 1
Scattering model according to the taxa applied to solve the forward problem. *For all k*a, being "k" the acoustic wavenumber (= 2•π/ƛ, where ƛ is acoustic wavelength) and "a" is the spherical radius (sphere), length of semi-minor axis (spheroid), or cylindrical radius (cylinder).

Taxa	Equivalent shape	Acoustic category	Model	Reference
Crustaceans	Irregular Prolate spheroid	Fluid-like	High pass*	Stanton (1989)
Chaetognats	Irregular Straight cylinder	Fluid-like	High pass*	Stanton (1989)
Siphonophores	Irregular Straight cylinder	Fluid-like	High pass*	Stanton (1989)
Heteropods	Irregular sphere	Elastic-shelled	High pass*	Stanton (1989)
Fish larvae	Regular sphere	Gas-bearing	Swimbladder	Kloser et al. (2002)

To compare the observed and predicted acoustic quantities, the predicted data were converted to volume backscattering strength (Maclennan et al., 2002) using:

$$\text{Volume backscattering strength}_{\text{pred}} = \text{TS} + 10\text{Log}_{10}(\text{n})$$

Volume backscattering strength$_{\text{pred}}$ is the predicted mean volume backscattering strength (dB), TS target strength output from the relevant model (dB) and n is the number of individuals per cubic meter of the relevant taxa. This calculation was performed for all five scattering categories and the resultant values added in the linear domain to give a total Volume backscattering strength$_{\text{pred}}$ for each net tow. Finally, the dominant acoustic group was identified as that which made the greatest contribution to the total Volume backscattering strength$_{\text{pred}}$.

3. Results

3.1. SSL acoustic patterns

The analysis of the acoustic data collected at the identification tows, verified the existence of three clearly defined acoustic patterns independent of the year (Fig. 2), and based on their distinctive frequency response (Fig. 3).

In coastal areas, less than 40 m (m) bottom depth, the dominant pattern was a prominent 120 kHz SSL (pattern 1), located between the surface and 15 m depth. The relative frequency response of the echograms corresponding to the identification tows showed that the 120 kHz frequency detected the maximum S_V value, followed by the 38 kHz frequency. At intermediate zones, between 40 and 190 m bottom depth, the dominant pattern was a prominent 38 kHz SSL located, on average, between 5 m below the surface and 50 m depth (pattern 2). The relative frequency response of the echograms corresponding to the identification tows showed that the 38 kHz frequency detected the maximum S_V value, followed by the 120 and 200 kHz frequencies, being the 18 kHz frequency the one that detected the lowest S_V values. In the continental shelf edge echograms, corresponding to the identification tows carried out at bottom depth greater than 180 m, the dominant pattern was a prominent 18 kHz SSL (pattern 3) located, on average, between 60 m below the surface and 140 m depth. The relative frequency response of the echograms corresponding to the identification tows showed that the 18 kHz frequency detected the maximum S_V value, followed by the 38 and 120 kHz frequencies, being the 200 kHz frequency the one that detected the lowest S_V value. As the identification tows were carried out proportionally to the area where the different acoustic patterns were detected, it was found that the most common pattern was the second one described (pattern 2) located in the intermediate areas of the continental shelf, which was sampled in 14 of the 18 stations. Patterns 1 and 3 that presented a restricted spatial distribution were sampled in 2 stations respectively (Fig. 2).

The multivariate analysis carried out for all the transects acoustically sampled in the study area showed the existence of three homogeneous groups segregated by depth (Fig. 3), reinforcing the hypothesis of the existence of a succession of communities from the coast to the contineta1 shelf edge. Moreover, from the ANOVA test we could conclude that both "area" and "frequency" were statistically significant, as well as their interaction (Table 3). Tukey test results hightligthed that all pairwise comparisons were significant with an adjusted p-value < 0.05,

Table 2
Mean values (mm) ± standard deviation (sd) of the physical dimensions, length and width or diameter, estimated from the Bongo-90 (500 μm mesh size) collected in 2014 and the number of individual measured (n) employed to resolve the forward problem applying scattering models. St: net tow station.

	Variable	St01	St02	St03	St04	St05	St06	St07	St08
Crustaceans	Length	5.45 ± 2.83	3.12 ± 1.86	2.49 ± 1.55	2.79 ± 1.11	2.03 ± 0.46	4.88 ± 1.02	5.15 ± 2.43	2.84 ± 1.52
	Width	1.16 ± 0.37	1.26 ± 0.70	1.56 ± 0.70	1.11 ± 0.32	1.00 ± 0.00	1.18 ± 0.39	1.26 ± 0.45	1.19 ± 0.42
	n	64	37	77	72	77	100	100	100
Chaetognats	Length	13.07 ± 3.27	10.67 ± 1.67	–	–	8.00 ± 0.50	–	9.03 ± 0.39	8.52 ± 0.50
	Width	1.00 ± 0.10	1.50 ± 0.03	–	–	0.50 ± 0.00	–	0.39 ± 0.21	0.50 ± 0.00
	n	60	30	–	–	15	–	38	33
Siphonophores	Length	8.38 ± 4.13	5.11 ± 3.03	5.87 ± 3.46	2.10 ± 0.61	1.39 ± 0.58	5.58 ± 4.21	3.91 ± 3.01	–
	Width	2.97 ± 1.38	2.62 ± 0.83	3.46 ± 2.40	1.87 ± 0.35	1.03 ± 0.17	2.79 ± 2.28	2.77 ± 2.47	–
	n	34	100	67	30	66	86	93	–
Heteropods	Diameter	0.68 ± 0.10	0.50 ± 0.08	0.50 ± 0.10	–	–	0.66 ± 0.09	0.74 ± 0.10	–
	n	29	20	30	–	–	30	6	–
Fish larvae	Length	7.05 ± 4.47	6.68 ± 3.17	8.53 ± 2.59	6.05 ± 1.87	5.00 ± 2.05	11.01 ± 3.81	9.80 ± 4.14	12.23 ± 3.70
	Width	1.41 ± 0.79	1.34 ± 0.95	1.71 ± 0.59	1.21 ± 0.54	1.00 ± 0.00	2.22 ± 0.89	1.96 ± 1.32	2.45 ± 0.60
	n	39	34	17	55	8	86	96	100

indicating that, for the frequency of response in coastal, intermediate and edge areas, it was different for the entire study area.

Each acoustic pattern was characterized by presenting different proportions of the zooplankton acoustic categories: Fluid-like, Elastic-shelled and Gas-bearing. Pattern 1 was composed solely by Fluid-like organisms (mainly crustaceans, but also siphonophores, chaetognats, doliolids, larvaceans and fish eggs). Pattern 2 was mainly composed by Fluid-like organisms although organisms belonging to Gas-bearing (fish larvae) and Elastic-shelled (heteropods) also appeared. Pattern 3 was composed by organisms belonging to the three acoustic categories; however it presented the highest proportion of Gas-bearing organisms and the lowest of Elastic-shelled organisms respect to the pattern 2.

3.2. Zooplankton SSL layer composition

A total of 18 zooplankton identification tows were performed: 10 in 2013 and 8 in 2014 (Table 4). The two Bongo nets (Bongo 40 and 90) were used in all of the identification tows, except in the tow 9 in 2013 (St13.9), where it was only sampled with the Bongo 90 (Table 1) making a total of 70 biological samples. In order to determine the sampling abundance and its associated uncertainty, 3 replicates of every sample were analyzed (10 bongo-90 tows, 2 mesh sizes and 9 bongo-40 tows 2 mesh sizes give a total of 38 samples in 2013 and 8 bongo-90 tows, 2 mesh sizes and 8 bongo-40 tows 2 mesh sizes give a total of 32 samples in 2014), then a total of 210 (38*3 + 32*3) biological analyses were performed at the laboratory.

The nets with the smallest mesh size (250 and 333 μm) captured the greatest organism's abundance (Fig. 4), dominated by small crustaceans, mainly cladocerans and copepods, followed by larvaceans. In 2014 a significant increase in the abundance of doliolids and small crustaceans was detected. Moreover, an evidenced East–West gradient in the crustacean size was detected, being bigger in the western area of Alboran Sea as compared to that in the Gulf of Vera, cladocerans and copepods were most abundant in the Eastern part and decapods larvae in the Western part of the study area.

The 500 and 2000 μm mesh size nets mainly captured large crustaceans and siphonophores (all belonging to the *Calycophora* order), respectively (Fig. 4). The spatial distribution of abundance collected by the 500 μm mesh size net showed two East-West gradients, (i) related with the zooplankton abundance, being the greatest abundance concentrated in the vicinity of the Strait of Gibraltar (W), and (ii) related with the community composition, moving from a diverse and heterogeneous community (E) to a crustacean dominated community (W).

The biological samples collected in coastal areas, corresponding to the acoustic pattern 1 (Fig. 4, net tows 13.1 and 14.5), presented a low abundance of individuals, dominated by crustaceans, mainly copepods and cladocerans as indicate the 250 and 333 μm mesh size nets, although also fish eggs, doliolids and siphonophorae were present. The biological samples collected in intermediate areas, corresponding to the acoustic pattern 2 (Fig. 4, net tows from 13.3 to 13.10 and 14.1, 14.2, 14.3, 14.4, 14.6 and 14.7), showed the presence of a heterogeneous zooplankton community were all the zooplankton groups considered in this study were presented in different proportions. Finally, the samples collected in the continental shelf edge, corresponding to the acoustic pattern 3 (Fig. 4 net tows 13.2 and 14.8), were the only ones in which the larvae of mesopelagic fish were found, mainly *Maurolicus muelleri* species.

3.3. Zooplankton communities distribution

In the study area, the zooplankton SSL was continuous, vertically homogeneous and located parallel to the sea surface, spreading all over the continental shelf. Although the zooplankton SSL was distributed over the entire area, zones of higher acoustic density associated with higher zooplankton abundance were detected, in particular in Almeria and Malaga bays as showed by the 38 kHz echograms taken as reference (Fig. 5A).

The zooplankton SSL relative frequency response changed from coast (25 m bottom depth) to the shelf edge (250 m) due to the presence of different zooplankton communities, as reflected the acoustic and biological data collected during the net tows. The biological interpretation of the echograms recorded during the systematic sampling, allowed to generate a distribution map of the main zooplankton communities present in the study area, from a coastal community dominated by crustaceans, through a heterogeneous zooplankton community located in the intermediate areas of the continental shelf to a community formed by mesopelagic fish larvae, at the end of the continental shelf (Fig. 5B). The acoustic pattern 1 characterized by a 120 kHz prominent scattering layer was distributed in coastal areas from 25 m to 40 m depth and was associated to the mixed water column layer where the temperature was uniform. This 120 kHz prominent SSL was composed by a crustacean dominated zooplankton community. From 40 m to 190 m bottom depth, the 38 kHz prominent SSL was found and its vertical extent was associated with the water column vertical gradient, being restricted to the thermocline limits (from 15 m to 55 m depth from the water surface in average). This layer appeared at 40 m bottom depth masking the presence of the 120 kHz prominent SSL and was detected to the edge of the continental shelf where its intensity decreased until it disappeared. This 38 kHz prominent SSL was composed by a heterogeneous zooplankton community. In addition to the 38 kHz prominent SSL, a 18 kHz prominent SSL located below the 38 kHz prominent SSL and out of the thermocline limits appeared at the continental shelf edge, from 180 m to more than 250 m bottom depth. This 18 kHz prominent SSL was composed by mesopelagic fish larvae.

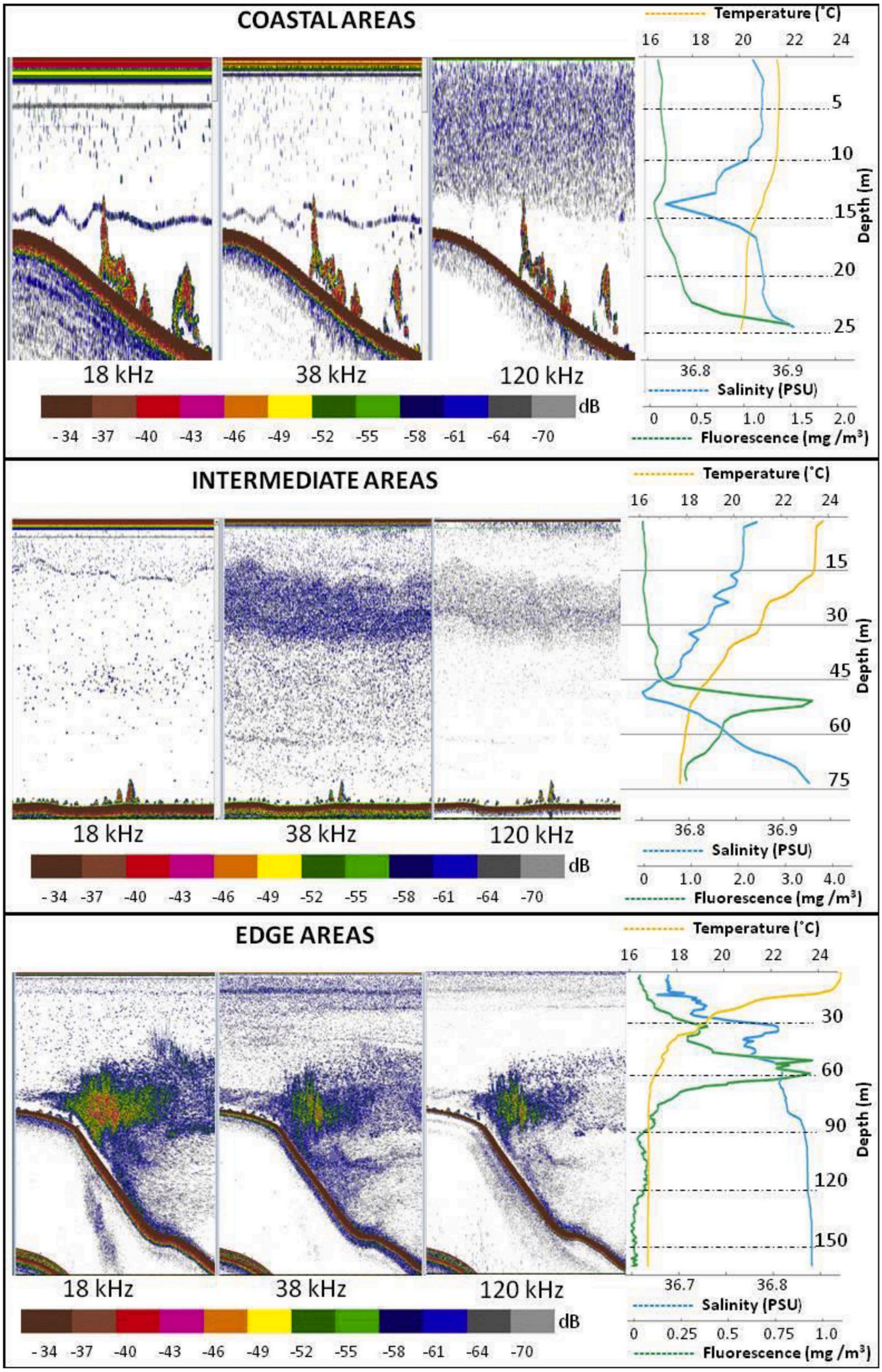

Fig. 2. Example of echograms at 18, 38 and 120 kHz frequencies showing the acoustic patterns identified along the continental shelf. In coastal areas a 120 kHz prominent scattering layer (pattern 1), in intermediated areas a 38 kHz prominent layer (pattern 2) and in edge areas an 18 kHz scattering layer (pattern 3). Colorbar indicates values of volume backscattering strength (dB), the applied threshold from −34 to −75 dB was used only for visualizing echograms and no threshold was set for the analysis. Moreover the temperature (yellow line), salinity (blue line) and fluorescence (green line) CTD profiles of each area are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

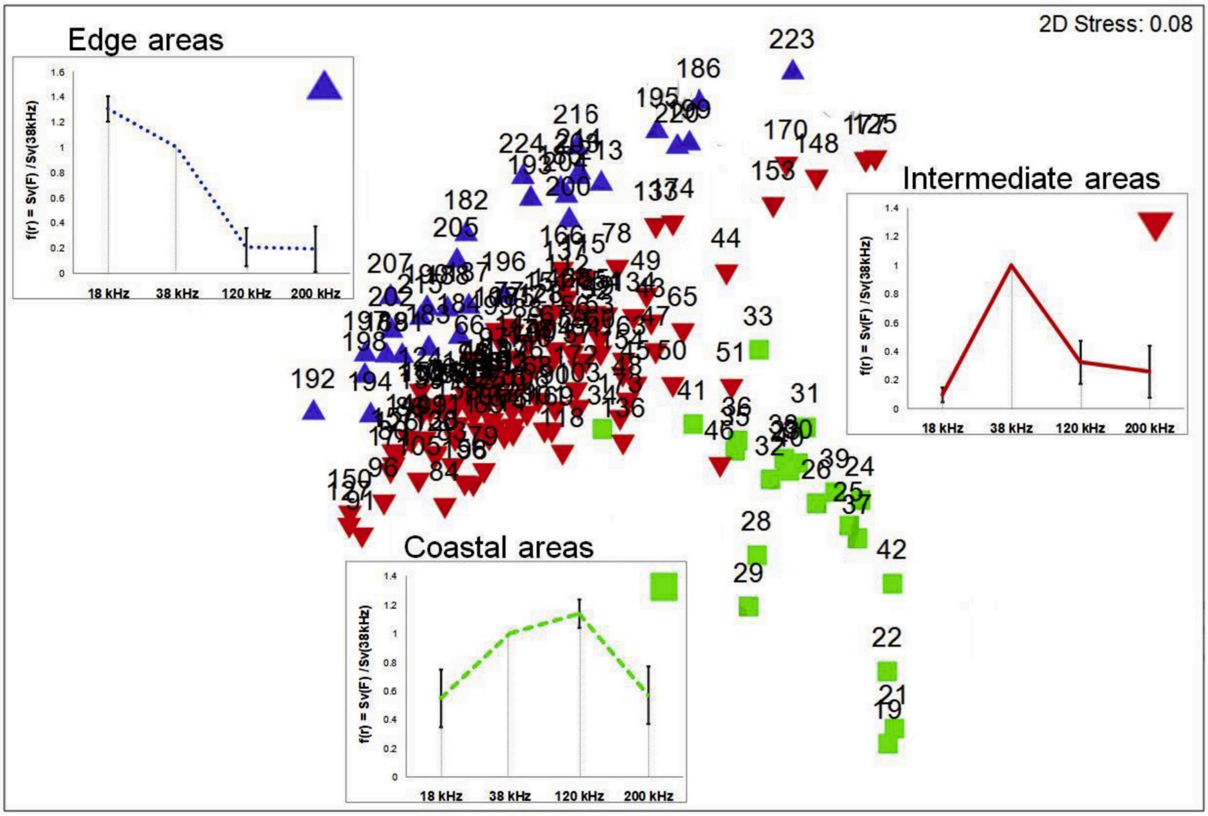

Fig. 3. Results of the Non-metric multidimensional scaling (nMDS) analysis using S_V data at 18, 38, 120 and 200 kHz from the entire study area (all transects) averaged each 1 m bottom depth from 19 to 250 m (n = 232), with the bottom depth superimposed and the frequency response graphs corresponding to each homogeneous group. The green, red and blue lines represent the frequency response graph derived from empirical observations which match with the acoustic pattern detected in coastal (pattern 1, green squares), intermediate (pattern 2, inverted red triangles) and edge areas (pattern 3, blue triangles) respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Results of the two way ANOVA test, using s_A values as dependent variable and "frequency" and "Area" as factors, with 18, 38, 120 and 200 kHz and coast, intermediate and edge as level respectively. Df: degrees of freedom; SS: sum square; MS: mean square; F: F value; Pr (>F): p value for the test, the probability of observing an F ratio greater than that given the null hypothesis is true.

Sources of variation	Df	SS	MS	F	Pr (>F)
Frequency	3	325.4	108.47	110.94	<2e-16***
Area	2	214.8	107.42	109.85	<2e-16***
frequency*area	6	324.5	54.09	55.32	<2e-16***
Residuals	676	661	0.98		

3.4. Zooplankton dominant scatterers

According to the scattering models, the total predicted scattering of zooplankton was strongly dominated by swimbladder fish larvae at most of the frequencies (Table 5) regardless the depth and the location of the samples. This fact was especially evident at station number 8 (St08) located at the edge of the continental shelf, indicating the great capacity to disperse sound of this type of scatterers, due to the presence of swimbladder. The contribution of the Fluid-like organisms, mainly crustaceans, to total predicted scattering became apparent at 120 and 200 kHz in St05 and 200 kHz in St03. The relative contribution of Elastic-shelled organisms was almost negligible at all frequencies and locations. According to the scattering models, the relative contribution to total predicted scattering from swimbladder fish larvae (Gas-bearing zooplankton), decreased with increasing frequency, while the contribution from Fluid-like and Elastic-shelled zooplankton increased. Though there was a significant contribution to the total abundance from crustaceans at some locations, their relative contribution to scattering was small at all frequencies.

Frequency response curves derived from model predictions (Fig. 6) showed that in the Alboran Sea continental shelf the strongest scatterer were the fish larvae, dominating the acoustic signal in almost all locations and frequencies. In coastal areas the stronger scatterer shifted from larvae to crustaceans with increasing frequency. The low values estimated, compared to the observed, could be pointed out the importance of the smaller crustaceans fraction in shallow waters. In intermediated areas, fish larvae were the main scatterer at all frequencies, although the contribution of the others components of the zooplankton community increase with frequency. In edge areas the contribution of the larvae was higher than the rest of the scatterers at all frequencies. The Kloser's model (Kloser et al., 2002) application to estimate fish larvae backscatter energy was adequately adjusted to the empirical data observed in edges areas, while in intermediate areas although the values registered at 18 kHz frequency showed a minimum, it did not reflected the market empirical difference between the backscatter energy at 18 and 38 kHz. According to the model, smaller larvae would be detected at higher frequencies, which would explain that the smallest fish larvae had been associated with a 38 kHz predominant scattering layer, while the largest fish larvae had been associated with an 18 kHz predominant scattering layer.

Comparison between the observed and predicted backscattering based on the bongo-90 500 μm net tows samples (Fig. 7) showed a slight trend to over predicting the observed scattering in the net tows located at intermediate areas at 18 and 120 kHz frequencies and a clear over estimation in the continental shelf edge (St08) at all frequencies. On the contrary, in the more coastal areas (St05) the observed values were under predicted by the models. This fact was strongly conditioned by the

Table 4
Year, geographical position (decimal degrees, WGS 1984 geographic system), dates (dd-mm), time (hh:mm), bottom depth (meters), net tow speed (nautical miles/hour), and net tow depth (meters) of the Bongo 40 and 90 tows performed during the MEDIAS surveys in 2013 and 2014.

							Bongo 40		Bongo 90	
Year	St	Latitude	Longitude	Date	Hour (GMT)	Bottom depth (m)	Speed (mn/h)	Sampling depth (m)	Speed (mn/h)	Sampling depth (m)
2013	**St13.1**	37.3019 N	1.6478 W	20-Jul	17:04	48	2.2	15.6	2.2	13.9
	St13.2	37.3220 N	1.6595 W	20-Jul	14:57	200.6	2.2	82	2.2	80
	St13.3	36.8161 N	1.9226 W	21-Jul	16:23	112.5	2.2	27.9	2.2	26.2
	St13.4	36.7474 N	2.3000 W	22-Jul	17:17	95	2.2	15	2.2	13.4
	St13.5	36.6585 N	2.6332 W	23-Jul	17:01	57.5	2.2	41.8	2.2	30.2
	St13.6	36.7183 N	3.2676 W	24-Jul	16:02	97.5	2.2	11.9	2.2	10.7
	St13.7	36.6947 N	3.6518 W	25-Jul	15:47	114.5	2.2	24.8	2.2	22.6
	St13.8	36.6803 N	4.1024 W	26-Jul	15:08	99	2.2	11.7	2.2	11.3
	St13.9	36.4200 N	5.0041 W	28-Jul	17:26	33	–	–	2.2	10.5
	St13.10	36.1844 N	5.3062 W	29-Jul	15:26	92.5	2.2	11.1	2.2	9
2014	**St14.1**	36.8799 N	1.8959 W	12-Jul	15:33	90	2.3	33.5	2.4	24.5
	St14.2	36.7740 N	2.3407 W	14-Jul	16:06	83	2.5	30.5	2.5	34
	St14.3	36.6037 N	2.7639 W	15-Jul	16:46	90	2.6	37.5	2.7	38.5
	St14.4	36.6986 N	4.1360 W	17-Jul	17:19	40	2.6	22	2.7	20.4
	St14.5	36.6294 N	4.4622 W	18-Jul	16:03	35	2.9	22	2.7	23.5
	St14.6	36.4222 N	4.8941 W	19-Jul	16:57	102	2.2	55.5	2.6	47
	St14.7	36.2047 N	5.2580 W	20-Jul	15:23	95	2.5	46.5	2.4	45
	St14.8	36.3971 N	5.0599 W	21-Jul	08:41	215	3.1	88.5	2.6	85

presence and abundance of Gas-bearing organisms. In coastal areas where the fish larvae were scarce, the predicted scatter fitted almost perfectly to that observed at 200 kHz frequency, highlighting the ability of the higher frequencies to detect Fluid-like organisms even when a small amount of Gas bearing organisms were present in the water collum.

4. Discussion

Our work hypothesis on the basis of changes in the acoustic relative frequency response (Korneliussen and Ona, 2003) observed along the continental shelf were due to changes in the composition of the zooplankton community has been verified in 2013 and 2014 in the Northern Alboran Sea. Three acoustic patterns, based on its distinctive relative frequency response, have been detected along the continental shelf and their match with three zooplankton communities has been confirmed by means of biological samples. The distance to the coast, related to the bottom depth, constituted the main factor of variation in the acoustic responses observed at multiple frequencies. The models application to predict the dominant scatterers showed that when the zooplankton community is heterogeneous a single scatterer not dominate the scattering at all frequencies, as occurred in coastal areas where scattering at 18 was dominated by Gas-bearing organisms while at 200 kHz it was dominated by Fluid-like organisms. Moreover, low abundances of strong scatterers, as swimbladder fish larvae, dominated the scattering at all frequencies in the intermediate areas and the continental shelf edge. In addition, areas where a greater amount of acoustic energy was detected concurred with areas of greater abundance of zooplanktonic individuals, which makes it possible to interpret the backscattering acoustic energy as an indicator of secondary production.

4.1. Coastal areas

In the coastal areas, from 25 to 40 m depth, mainly in the vicinity of Almeria and Malaga Bays, an almost exclusively crustaceans dominated zooplankton community was found. The smaller meshes (250 and 333 μm) pointed out that the most abundant group was "small crustaceans", mainly cladocerans which can be related to sampling season, since cladocerans reach their maximum abundance in summer (Mafalda et al., 2007; Terbiyik Kurt and Polat, 2015; Calbet et al., 2001).

MVBS values derived from the 120 kHz frequency represents appropriately "Fluid-Like" scatterers dominated zooplankton communities when compared to lower frequencies (Ballón et al., 2011; Lezama-Ochoa et al., 2011; Madureira et al., 1993), and MVBS values derived from the 200 kHz frequency has been employed to determine the total zooplankton contribution mainly composed by euphausiids and copepods (Sato et al., 2015). In the easternmost part of the Mediterranean Sea has been proved that 120–200 kHz frequencies effectively detect copepods and other crustaceans (Mutlu, 2003). Therefore, it can be deduced that the backscattered quantity estimated from the 120 kHz frequency in coastal areas was proportional to the abundance of "Fluid-Like" zooplankton, mainly composed by crustaceans. Even though, the 120 kHz resonance peak could also reflect the presence of other scatterers as fish eggs, very common in coastal areas as reflected the smaller mesh sizes (250 and 333 μm). The presence of oil globules in fish eggs, as occur with the summer spawner *Trachurus mediterraneaus* (Rodriguez et al., 2017), could slightly modify the typical crustaceans frequency response peaked at 200 kHz (Fernandes et al., 2006).

Moreover, this coastal zooplankton community was associated to areas where thermocline has not been developed, due to the shallow depth, so that it is distributed vertically throughout the water column.

4.2. Intermediate areas

In the intermediate areas of the continental shelf, from 40 to 190 m depth, distributed throughout the study area, a heterogeneous zooplankton community was detected forming a continuous and parallel to sea surface SSL with an average vertical thickness of 44 m. The main environmental forcing factor was the thermocline, which is characteristic of the non-migrating zooplankton community in the Mediterranean Sea (Mutlu, 2005).

Although some authors have suggested that 38 kHz peak in the relative frequency response correspond to zooplankton organisms but neither adult fish nor crustaceans (Ballón et al., 2011; Lezama-Ochoa et al., 2011), our results pointed out that a peak at the 38 kHz frequency correspond to a heterogeneous zooplankton community which biological composition is likely dominated by crustaceans and others Fluid-like weak scatterers, whose presence is masked by others stronger scatterers as Elastic-shelled (heteropods) or Gas-bearing (fish larvae) which is in accordance with predictions based on the forward and inverse model (Mair et al., 2005).

When the zooplankton community is formed by multiple taxonomic groups or species with different anatomical characteristics, it is difficult to attribute the acoustic signal to a single taxonomic group (Stanton et al., 1987). Since the ability of organisms to reflect sound depends on their abundance in the medium, their size, and their body characteristics

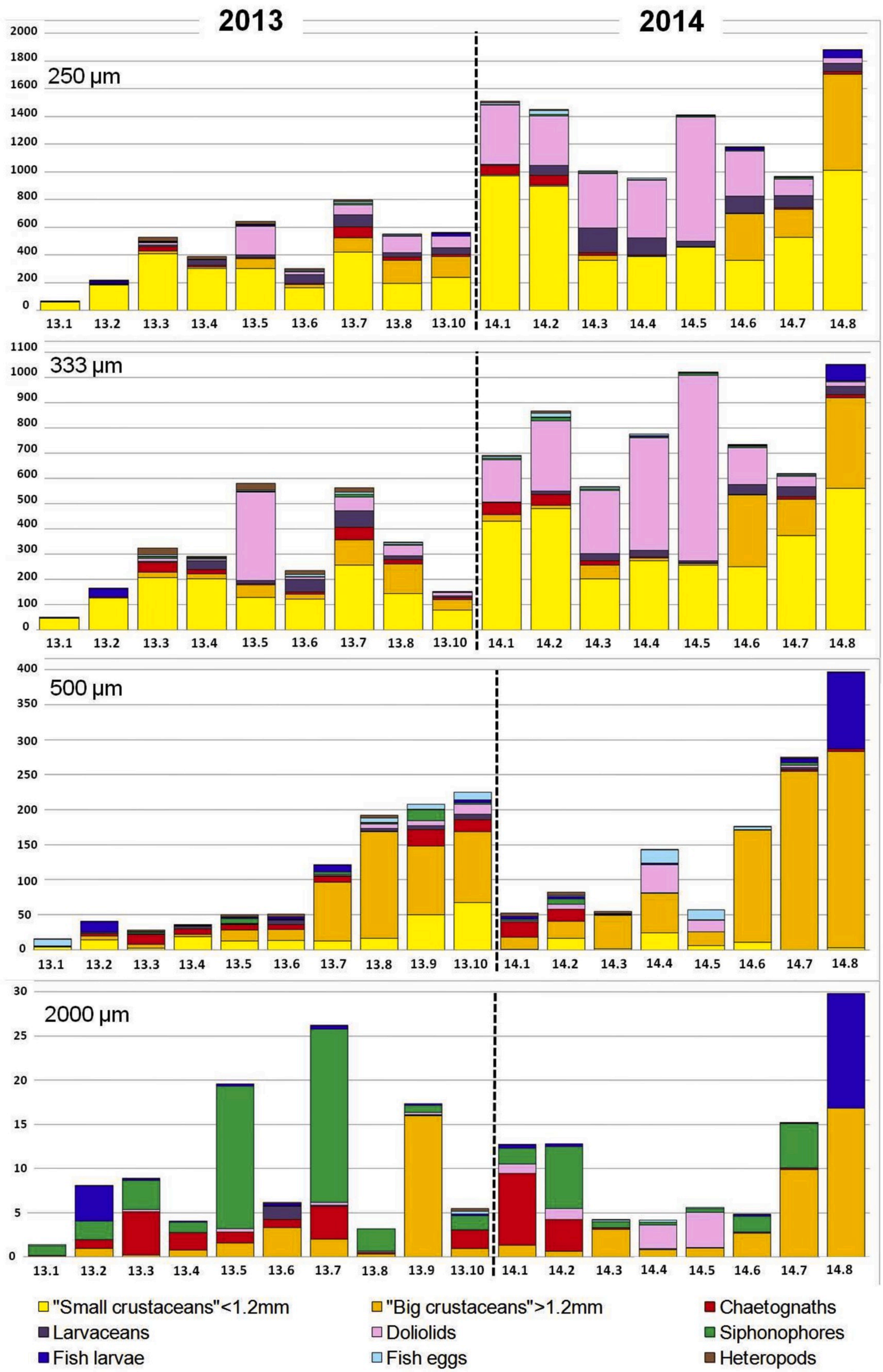

Fig. 4. Abundance (ind/m^3) of the main zooplankton groups collected by the Bongo 40 with 250 and 333 µm mesh sizes and by the Bongo 90 with 500 and 2000 µm mesh sizes in 2013 and 2014. For both years, the identification tows were placed from East to West. Net tows 13.1, 14.4 and 14.5 matched the acoustic pattern 1 (120 kHz prominent scattering layer located in coastal areas), 13.2 and 14.8 matched the acoustic pattern 3 (18 kHz prominent scattering layer located in edge areas) and the rest of them matched the pattern 2 (38 kHz prominent scattering layer located in intermediate areas).

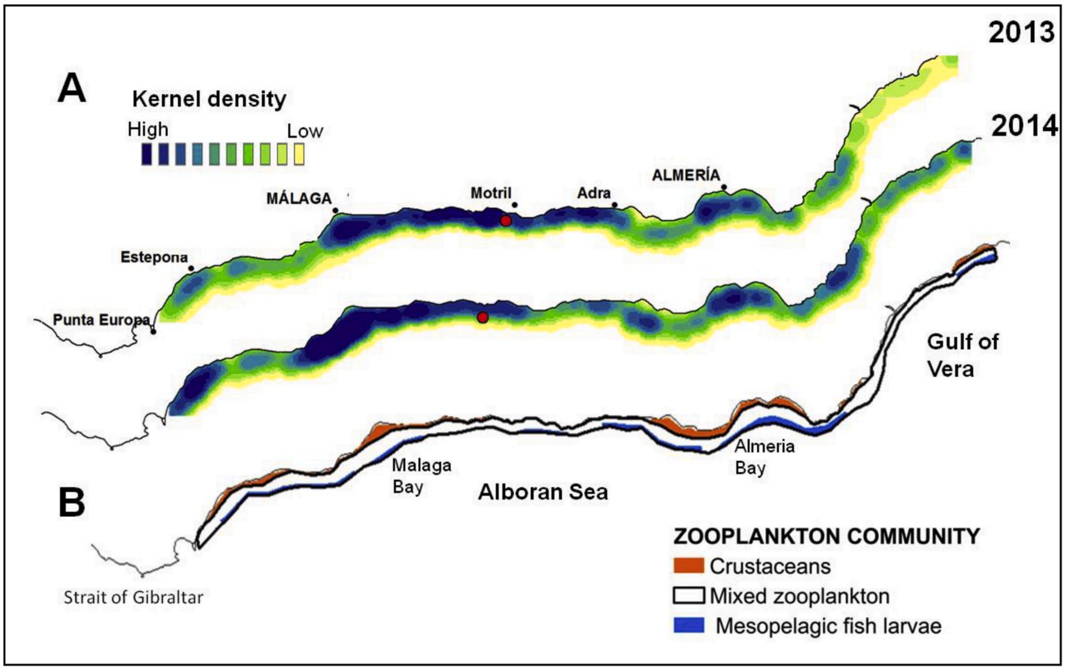

Fig. 5. A: Zooplankton scattering layer spatial distribution inferred from the 38 kHz frequency in the study area in 2013 and 2014. Colour scale represents the gradient of the kernel density values estimated using the acoustic quantities at 38 kHz in the lineal domain from the highest (dark blue) to the lowest (yellow). The red circle represents the gravity centre of the zooplankton distribution. B: Zooplankton communities distribution in the study area. In orange, mainly crustaceans located in shallow coastal areas. In hollow with black contour, mixed zooplankton located in intermediated areas. In blue, mesopelagic fish larvae (*Maurolicus muelleri*). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 5
Model predicted volume backscattering S_v values at 18, 38, 120 and 200 kHz for the main 5 taxa from each net tow samples and the dominant scatterer type at each frequency. FL: Fluid-like; GB: Gas-bearing; ES: Elastic-shelled. In bold the total S_v value per scatterer type.

Taxa	Frequency	St01	St02	St03	St04	St05	St06	St07	St08
Crustaceans (FL)	18	−118.1	−119.9	−115.2	−119.4	−128.5	−108.9	−105.2	−111.0
Chaetognaths (FL)	18	−122.5	−118.2	-	-	−159.4	–	−151.4	−146.0
Siphonophores (FL)	18	−116.1	−118.3	−122.6	−141.9	−156.4	−125.9	−123.2	–
Total FL	18	**−113.4**	**−114.0**	**−114.5**	**−119.4**	**−128.5**	**−108.8**	**−105.2**	**−111.0**
Fish larvae (GB)	18	**−56.2**	**−63.6**	**−66.1**	**−66.1**	**−105.6**	**−56.8**	**−45.0**	**−30.8**
Heteropods (ES)	18	**−129.8**	**−137.8**	**−139.6**	-	-	**−138.6**	**−132.4**	-
Dominant scatter category	18	GB	GB	GB	GB	GB	GB	GB	GB
Crustaceans (FL)	38	−105.1	−106.9	−102.2	−106.4	−115.6	−95.9	−92.3	−98.0
Chaetognaths (FL)	38	−109.3	−104.8	-	-	−146.4		−138.3	−133.0
Siphonophores (FL)	38	−101.8	−104.2	−108.0	−128.3	−143.2	−111.7	−109.0	–
Total FL	38	**−99.6**	**−100.4**	**−101.2**	**−106.4**	**−115.6**	**−95.8**	**−92.2**	**−98.0**
Fish larvae (GB)	38	**−60.5**	**−60.3**	**−73.4**	**−64.8**	**−93.9**	**−67.1**	**−56.7**	**−41.8**
Heteropods (ES)	38	**−116.8**	**−124.8**	**−126.7**	-	-	**−125.7**	**−119.5**	-
Dominant scatter category	38	GB	GB	GB	GB	GB	GB	GB	GB
Crustaceans (FL)	120	−85.2	−87.0	−82.3	−86.5	−95.6	−76.0	−72.3	−78.1
Chaetognaths (FL)	120	−87.6	−82.0	-	-	−125.9		−118.0	−112.5
Siphonophores (FL)	120	−77.6	−80.1	−83.9	−104.9	−121.4	−87.5	−84.9	–
Total FL	120	**−76.6**	**−77.4**	**−80.0**	**−86.4**	**−95.6**	**−75.7**	**−72.1**	**−78.1**
Fish larvae (GB)	120	**−63.3**	**−64.4**	**−75.9**	**−68.5**	**−100.6**	**−68.7**	**−58.7**	**−43.9**
Heteropods (ES)	120	**−96.8**	**−104.8**	**−106.7**	-	-	**−105.7**	**−99.5**	-
Dominant scatter category	120	GB	GB	GB	GB	FL	GB	GB	GB
Crustaceans (FL)	200	−76.4	−78.2	−73.6	−77.7	−86.8	−67.2	−63.6	−69.3
Chaetognaths (FL)	200	−76.9	−71.1	-	-	−116.1		−108.5	−102.7
Siphonophores (FL)	200	−67.9	−70.1	−74.6	−94.2	−110.6	−77.7	−75.0	–
Total FL	200	**−66.9**	**−67.2**	**−71.1**	**−77.6**	**−86.8**	**−66.8**	**−63.3**	**−69.3**
Fish larvae (GB)	200	**−63.4**	**−64.6**	**−76.0**	**−68.7**	**−100.9**	**−68.8**	**−58.8**	**−44.0**
Heteropods (ES)	200	**−87.9**	**−95.9**	**−97.8**	-	-	**−96.8**	**−90.6**	-
Dominant scatter cate Ory	200	GB	GB	FL	GB	FL	GB	GB	GB

(i.e., shape, composition, presence of air or oil vesicles) (Simmonds and MacLennan, 2005), if organisms that are not abundant in the medium are very efficient in reflecting the acoustic energy, for example, because they contain air in their internal structures, they can be responsible for the acoustic signal (Lavery et al., 2007). In addition, even if an isolated animal is acoustically detectable but it appears next to another one that

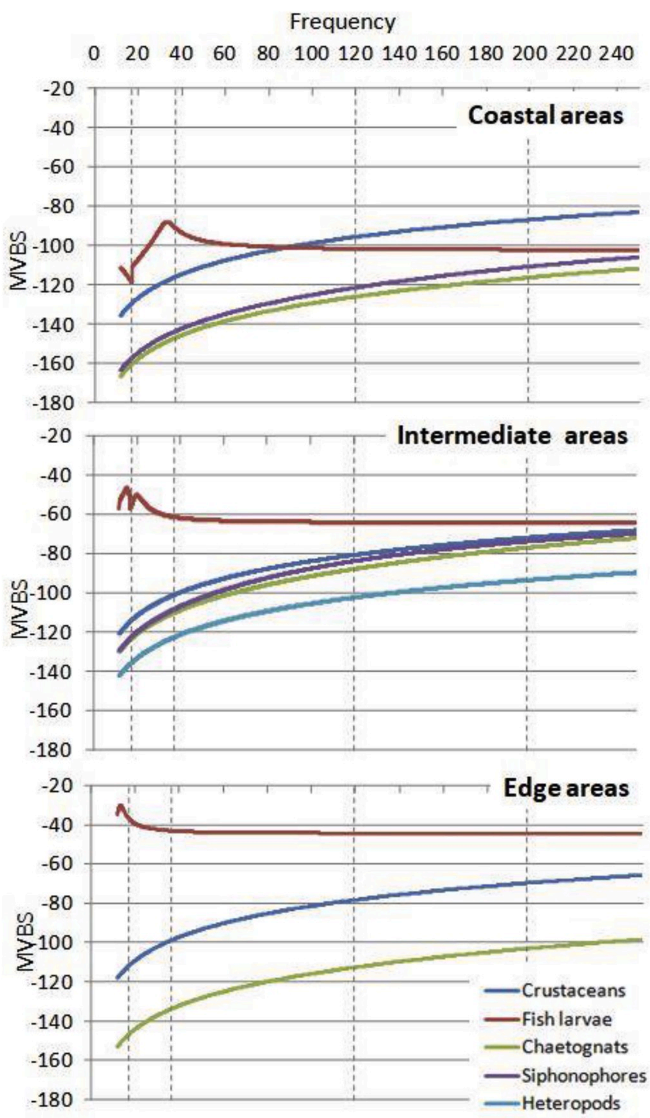

Fig. 6. Frequency response curves derived from predictions based on physic-based scattering models estimated through empirical measures corresponding to coastal, intermediate and edge continental shelf areas. The vertical dotted lines show the punctual frequencies employed in this study (18, 38, 120 and 200 kHz). The colour lines indicate the taxonomical group. For coastal areas; the blue line shows a 2.0 mm crustacean with a mean density of 20 ind/m^3, the red line shows a 5.0 mm swim-bladder fish larvae with a mean density of 0.001 ind/m^3, the green line shows a 8 mm chaetognat with a mean density of 0.2 ind/m^3 and the purple line shows a 1.4 mm siphonophore with a mean density of 0.7 ind/m^3. For intermediate areas; the blue line shows a 3.5 mm crustacean with a mean density of 93 ind/m^3, the red line shows a 8.2 mm swim-bladder fish larvae with a mean density of 2.4 ind/m^3, the green line shows a 13.5 mm chaetognat with a mean density of 13.2 ind/m^3, the purple line shows a 5.2 mm siphonophore with a mean density of 2.6 ind/m^3 and the cyan line shows a 0.3 mm radius heteropod with a mean density of 2.4 ind/m^3. For edge areas; the blue line shows a 2.8 mm crustacean with a mean density of 279 ind/m^3, the red line shows a 12.2 mm swim-bladder fish larvae with a mean density of 108 ind/m^3, the green line shows a 8.5 mm chaetognat with a mean density of 3.7 ind/m^3. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

has a higher capacity to scatter sound, the latter will be detected, masking the presence of the former (Mutlu, 2005). Resonance peak at 38 kHz frequency has been related to massive concentrations of salps species as *Iasis zonaria* (Alvarez Colombo et al., 2003), and with the presence of the jellyfish *Pelagia noctiluca* (Peña et al., 2014), however in our study area neither jellyfishes nor salps were found. The massive collection of doliolid in 2014 suggests that they are weaker scatters compared to salps. The most likely candidate scatterers to generate the strong echoes detected at 38 kHz are fish larvae (Cabreira et al., 2006; Lavery et al., 2007; Mair et al., 2005; Warren and Wiebe, 2008) and heteropods (Fernandes et al., 2006).

4.3. Edge areas

At the edge of the continental shelf, an incursion of a mesopelagic SSL was detected in a patched way in the study area from 180 m depth to beyond the end of the continental shelf. Although, the migratory mesopelagic fish SSL is located during the day at 200 m, it can ascend the continental slope to stand on the platform (Godo et al., 2014). The relative frequency response showed a peak in 18 kHz frequency as expected in a community dominated by Gas-bearing organisms, due to the air filled swimbladder (Fernandes et al., 2006).

The nets tows carried out in order to identify this SSL revealed the presence of "big crustaceans" and *Maurolicus muelleri* fish larvae. It must be taken into account that the plankton nets lacked an opening and closing system, thus it is likely that part of the crustaceans collected were not part of the 18 kHz prominent layer, but rather that they were collected in the rest of the water column, thus it is suspected that the 18 kHz prominent layer could be entirely formed by mesopelagic fish. As occurs in other areas where *Maurolicus muelleri* has been identified as the main component of the mesopelagic 18 prominent SSL between 150 and 200 m depth (Kaartvedt et al., 2008; Staby et al., 2013). Moreover, verification hauls carried out by means of pelagic trawl as part of the routine of the MEDIAS survey confirmed that this SSL presented a monoespecific composition of *Maurolicus muelleri*. Therefore, the frequency response peak at 18-kHz frequency was related to a larger-size of the Gas-bearing organisms, confirming that organisms with swimbladder are better detected at 18 kHz than at 38 kHz, from a certain size (Fernandes et al., 2006).

4.4. Forward model predictions

The scattering levels predicted by use of the models and net tow information were between 0.1 and 10 dB higher than the observed scattering at most frequencies and depths in intermediate areas, roughly 20 dB higher than the observed at all frequencies in the continental shelf edge areas and from 27 dB at 38 kHz to 3 dB at 200 kHz lower than the observed in the coastal areas. If the influence of the swimbladder had not been included in the model, the predictions would have been under estimated in all cases. For this reason, the choice of the model and the model constant parameters is crucial to get results adjusted to reality. In our case, the models used for Fluid-like and Elastic-Shelled organisms (Stanton, 1989) have been adjusted adequately to the zooplankton community, obtaining quite reliable predictions at high frequencies. The model used to predict the fish larvae contribution to the observed scattering (Kloser et al., 2002) provided results very adjusted to the observed values when the abundance of fish larvae was very small, from 2 to 5 ind/m^3, however it overestimated the scattering at the edge of the continental shelf where the massive presence of larvae of *Maurolicus muelleri* was sampled. This mismatch between the observed and predicted scattering may be due to different factors such as, the choice of the spherical radius equivalent to the volume swimbladder, in this case it has been estimated per each net tow as 5% of the average length of larvae (Simmonds and MacLennan, 2005), but in other studies we have used fixed values (Kloser et al., 2002; Peña et al., 2014) or proportionately bigger values than that in this study, 9% of the larvae length (Brierley et al., 2005) or based on empirical relationships between the length of the larvae and its bladder (Álvarez-Colombo et al., 2011). Moreover, It must be taken into account that the swimblader is not a perfect sphere and the fish behavior causing a tilt angle distribution would yield lower intensity backscattering values than a regular

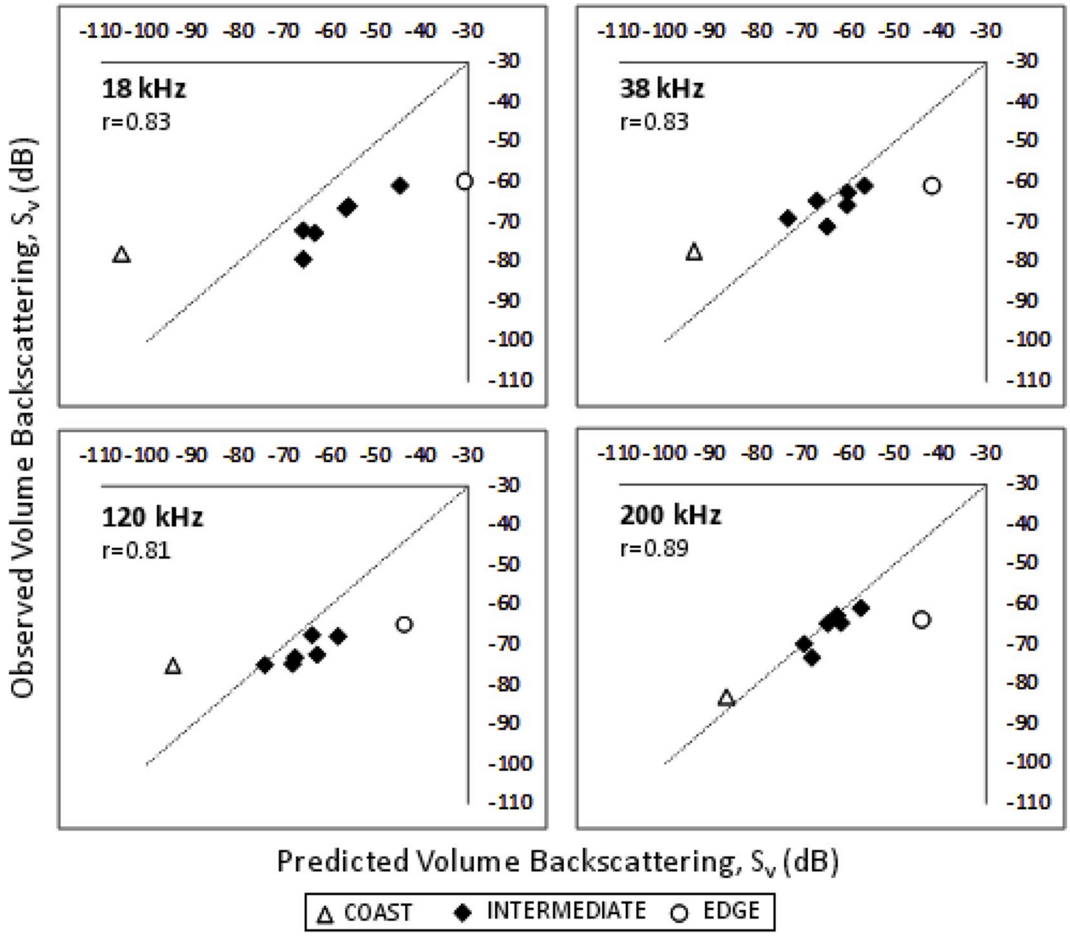

Fig. 7. Observed *versus* predicted mean volume backscattering strength at 18, 38, 120 and 200 kHz frequencies for all bongo-90 net tows (500 μm mesh size) carried out in 2014, considering all the zooplankton groups presented in samples (crustaceans, chaetognats, siphonophores, fish larvae and heteropods). A line corresponding to a 1:1 relationship is shown on each plot. The triangle (coastal areas) corresponds to St05; the circle (edge areas) corresponds to St08; the diamonds (intermediate areas) correspond to St01, 02, 03, 04, 06 and 07.

dorsal-aspect larvae aggregation (Warren et al., 2002). Another factor of uncertainty is the structure of the net, lacking opening and closing systems, which was able to collect organisms during its rise to surface, thus overestimating the abundance of larvae in that particular station. Finally, it must be considered the roll of physical structures, such as microstructure, in the observed backscatter, since it can contribute highly to the backscatter in some areas (Lavery et al., 2007; Warren et al., 2003). In the study area, where astronomical tides have no effect, internal waves occur with the entry of Atlantic water (Vázquez et al., 2009) and their influence on water bodies, although it affects up to about 150 m deep, it is more pronounced in the part Central of the Alboran Sea (Mojica et al., 2018), thus microstructure effect can be considered as negligible in the study area.

4.5. Acoustic data as secondary production indicator

The zooplanktonic backscattered energy spatial distribution, presented a high variability along the study area and showing four zones (from East to West) of high acoustic density: Almería Bay, Adra, the area located between Motril and Malaga Bay, and that from Estepona to Punta Europa These zones coincide with zones of high primary production (Mercado et al., 2013). The high productivity of these areas can be attributed to the coastal upwelling induced by the wind and to the circulation of the bodies of water in the Alboran Sea (Oguz et al., 2014; Renault et al., 2012; Sarhan et al., 2000). The upwelling processes, both influenced by persistent NW component winds and the position of the Atlantic front (Renault et al., 2012; Vargas-Yáñez et al., 2002) favor the proliferation of zooplankton in nearby areas to Punta Europa and in the bay of Malaga (Vargas-Yáñez and Sabatés, 2007). The zooplankton abundance density gradient in the East-West direction detected in this study, which has been described in previous works and related to the oceanographic conditions of the Alboran Sea (Agostini and Bakun, 2002; Mercado et al., 2013; El-Geziry and Bryden, 2010, Sampaio de Souza et al., 2005), is in accordance with the increment of the backscatter energy.

Our results pointed out that the density maps developed in the frame of this study can be used as a tool to represent zones of higher zooplankton production, and once the organisms producing the sound records have been defined, they can be interpreted in terms of the ecological groups or surrogate species (Trenkel and Berger, 2013). Moreover, they could be used as indicators of the secondary production.

5. Conclusions

The combined use of acoustic and biological data has allowed detecting a succession of zooplankton communities following the bathymetric gradient in Alboran Sea in summer (July). Community complexity increased with depth, moving from a predominantly crustacean-dominated community (120 kHz prominent scattering layer) located in coastal areas to a heterogeneous one where fish larvae turned out to be the dominant scatterers (38 kHz prominent scattering layer). Finally, at the edge of the continental shelf, the massive presence of larvae and juveniles of the *Maurolicus muelleri* species was detected (18 kHz prominent scattering layer).

The application of dispersion models has revealed the complexity associated with heterogeneity in zooplankton populations. Strong scatterers as fish larvae, even if they are not very abundant in the samples, dominate the acoustic signal in a wide frequency range. In order to the models reflect accurately reality, all the elements present in the environment must be taken into account, which is extremely complicated in the pelagic habitat due to both abiotic factor as turbulence, density fronts, internal waves and also biotic factors related with the diversity of sizes, shapes, body structures and swimming capacity of the zooplankton community.

Echograms collected in Alboran Sea in July 2013 and 2014 have been scrutinized in terms of zooplankton communities based on their frequency response, establishing their spatial distribution on the continental shelf at a macro-spatial scale not addressed to date in the Mediterranean Sea. In addition, it has been found that the acoustic energy associated with SSL can be interpreted as an indicator of secondary production in the study area.

These evidences represent a great step towards the integrated study of the pelagic ecosystem, since simultaneous data from pelagic fish and zooplankton has been collected, highlighting the potential of MEDIAS surveys to generate indicators of the different pelagic trophic levels. In addition, standardized data has been collected in the MEDIAS survey time series throughout the Mediterranean Sea since 2009, so this work will allow the retrospective study to zooplankton community in relation to climate changes and could be the key to understand the fluctuations of the main pelagic species of commercial interest.

Declaration of competing interest

The authors declare that they have no conflict of interest. All applicable institutional and national guidelines for the care and use of animals were followed in this study.

CRediT authorship contribution statement

Ana Ventero: Data curation, Formal analysis, Writing - original draft. **Magdalena Iglesias:** Data curation, Formal analysis, Writing - original draft. **Joan Miquel:** Data curation, Formal analysis.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.106854.

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