First description of the shelf epipelagic plankton layers at a Mediterranean basin-scale

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Abstract

This research represents the first approach to the study of the shelf zooplankton community at a Mediterranean scale, using acoustic standardized data collected in June-July in 10 different geographical sub-areas (GSAs) established by the General Fisheries Commission for the Mediterranean (GFCM) within the framework of the MEDiterranean International Acoustic Survey (MEDIAS). The analysis of the zooplankton layers based on their acoustic characteristics has revealed the potential of these surveys for the study of zooplankton at a Mediterranean basin scale and, also, the need to collect biological samples to interpret the acoustic records in terms of species. The fish population's direct assessment is established in the MEDIAS framework, but the integration of zooplankton community data would constitute a qualitative step for the understanding of the fluctuations of fish populations and therefore to achieve the objective of an ecosystem-based management. Results have revealed the ubiquity of the zooplankton layers and its ability to form layers detectable by scientific echosounders throughout the Mediterranean at the common fish assessment frequency (38 kHz). In addition, the use of two frequencies (38 and 120 kHz) has allowed to apply the dB difference method, observing changes in the difference of the Mean Volume Backscattering Strength (ΔMVBS) at 38 and 120 kHz frequencies, which would be related to changes in the composition of the zooplankton community.

Introduction

Continental shelves and coastal areas have been called "Large Marine Ecosystems", occupying coastal ocean space around the margins of the continents. In contrast to the open sea areas, they have a high biodiversity of organisms and habitats and a great primary productivity, hosting the main upwelling areas. Moreover, they constitute areas of recruitment and distribution of a multitude of commercial species and produce 80 per cent of the world's annual marine fish catch (Sherman 2015). Due to its strategic interest, it is subjected to a multitude of impacts and threats, both climate and anthropogenic: accelerated warming from climate change, acidification, overfishing, loss of habitats, pollution, eutrophication...(He and Silliman 2019)

The Mediterranean Sea has been shown as an area of important recent changes. Most fish stocks have decreased (Machias et al. 2008; Vasilakopoulos et al. 2014; Van Beveren et al. 2016; Colloca et al. 2017; FAO 2020) and while overexploitation is a fact, the synergy with environmental changes probably represents a big part of the explanation. In certain cases, other more ecological reasons have been proposed for declining small pelagic fish populations. For instance, several studies have shown that the variations observed in sardines and anchovies in the Gulf of Lion (smaller size, lower body condition, and changes in age structure) might result from changes in the plankton community (reviewed in Saraux et al. 2019). Further, the size and condition of sardine and anchovy decreased in most areas of the Mediterranean Sea (Brosset et al. 2015), which could reflect a modification in the available resources for small pelagic, namely changes in the zooplankton abundance, composition or distribution. Given the extremely high dependence of small pelagic species development on the zooplankton community, the integration of its study in scientific surveys such as MEDiterranean International Acoustic Survey

(MEDIAS) could be crucial to explain the fluctuations in distribution or biological parameters of the fish populations under study.

The pelagic habitat is the largest biome on Earth, key for temperature regulation, oxygen, and food production. Its physical and biological components and processes vary spatially and temporally depending on multiple drivers. Understanding this variability, processes and interactions is fundamental to identify the drivers of changes and properly assess pelagic habitats and communities (Magliozzi et al. 2021). Traditionally, the study of the pelagic environment has been approached regionally, making intercomparison and benchmarking difficult. This fact is especially relevant in the Mediterranean Sea, where there is a lack of knowledge related to the spatial coverage of the pelagic community studies, which makes the conclusions difficult to be extrapolated to the entire basin (Varkitzi et al. 2018). Macroscale studies are essential to understand the peculiarities of each area in a common frame, to determine general reference points and to achieve the basin scale management. In this context, the MEDIAS survey, whose main strengths are: (i) the standardization of data collection and processing across the Mediterranean (same methodology, same time of year), (ii) the common historical series and (iii) and its temporary continuity (monitoring), can constitute an essential tool to describe and analyze the pelagic ecosystem at basin scale and contribute to its integrated management.

In the framework of fisheries acoustics, the goal target usually is the precise estimation of fish abundance, so that plankton echotraces have been considered as reverberation or undesired elements, systematically removed from the echograms (Simmonds and MacLennan 2005). However, as fisheries acoustics are changing toward an ecosystem based management, zooplankton has become a key component in ecology assessment models (Möllmann et al. 2014). Although fisheries acoustic data can still be considered as underused (Trenkel and Berger 2013), they present a high potential for the study of the pelagic ecosystem as a whole, integrating concurrent information both on pelagic fish and zooplankton assemblages. The joint treatment of the pelagic fish data collected in the MEDIAS has made it possible to reveal differences in the growth and maturity of anchovies in the Mediterranean Sea (Ferreri et al. 2021), to detect displacements of small pelagic species forced by climatic changes (De Felice et al. 2021), to determine the influence of the nycthemeral migration of pelagic fish on their abundance determination (Bonanno et al. 2021), to estimate the correlation between the small pelagic body size variation with temperature (Hattab et al. 2021) or to assess the effects of sampling intensity and biomass levels on the precision of acoustic surveys (Barra et al. 2021). Nonetheless, the study of the zooplankton community has not been jointly addressed to date.

Acoustic methods can be an adequate tool for monitoring and studying the zooplankton community, complementary to traditional zooplankton sampling methods. Acoustic instruments permit remote and quasi-continuous sampling of fish and plankton throughout the water column and consequently offer a spatio-temporal resolution similar to that of physical oceanographic data, therefore they have been proposed to generate new ecosystem indicators (Trenkel et al. 2011) in the frame of marine ecosystem acoustics (Godo et al. 2014). However, they require a large investment on infrastructure and technology for groundtruthing echotraces *i.e*. identify or verify the identity of the acoustic targets (Simmonds and

MacLennan 2005; Chu 2011). Furthermore, modelling the acoustic properties of zooplankton is a complex process, making it difficult to infer the specific composition of zooplankton from acoustic data alone (Stanton et al. 1998; Warren and Wiebe 2008; Jech et al. 2015). In the other hand, traditional methods determine the exact zooplankton taxonomic composition and seasonal variations in short time intervals and small spatial scales (Fernández de Puelles et al. 2007; Fernández de Puelles and Molinero 2008; García-Comas et al. 2011). While they constitute a systematic, standardized and robust methodology to study the zooplankton communities, they remain very time consuming, despite great strides being made to develop automatic processes (*e.g.* zooscan), almost prohibiting a spatio-temporal monitoring at high resolution (Pitois et al. 2018). Most long-term zooplankton time-series are indeed sampled at a single location (*e.g.* Fernández de Puelles et al. 2007; Fernández de Puelles and Molinero 2008; García-Comas et al. 2011). Uniting the strengths of each method, is a challenge that could be addressed in the future to understand marine ecosystem in the Mediterranean Sea and MEDIAS surveys can play a strategic role in its achievement.

Plankton organisms are extremely abundant in the water column often forming dense layers, so when they are insonified, their echoes overlap to form the diffuse cloud-like marks frequently seen on echograms (Simmonds and MacLennan 2005). Moreover, due to the wide variety of shapes, structures and sizes of plankton, the acoustic identification of planktonic targets to species or even genera level is difficult (Martin et al. 1996; Stanton et al. 1996). The evolution of underwater acoustics technology from single frequency (narrow band) to multiple frequency systems provided scientists with additional capability to characterize or classify scattering targets (Chu 2011). Since then, numerous studies on the distribution (Lebourges-Dhaussy et al. 2009, 2014; Lezama-Ochoa et al. 2014), migration (Mutlu 2007; Benoit-Bird et al. 2013; Benoit-Bird and McManus 2014) and biological composition (Lavery et al. 2007; Mutlu 2007) of zooplankton have been carried out using acoustic methods all over the world. Nevertheless, studies regarding zooplankton scattering layers are scarce in the Mediterranean Sea, mainly focusing on mesopelagic fish (Peña et al. 2014) or fish larvae (Bonanno et al. 2006; Ventero et al. 2021) or displaying a limited spatial coverage (Kačić, 1973; Mutlu, 2005; Ventero, 2016).

The purpose of this study is to contribute to the plankton knowledge at a Mediterranean Sea scale. The general framework is the first jointly characterization of the plankton acoustic layers present on the continental shelf of ten GSAs along the Mediterranean Sea. The main objectives were (i) to describe and compare the acoustic structures associated to the Mediterranean plankton layers at two frequencies (38 and 120 kHz), with emphasis on the influence of the enrichment process of each study area, (ii) to apply the dB different method (Madureira et al. 1993) in order to infer the most likely zooplankton acoustic category (Madureira et al. 1993; Stanton et al. 1996) that form the plankton layers and, (iii) to establish a reference point for evaluating future zooplankton community changes in the Mediterranean Sea.

Material And Methods

Study area

The area covered by the MEDIAS survey is the European continental shelf of the Mediterranean Sea. In this study, 900 nautical miles of ten geographical sub-areas (GSAs) established by the General Fisheries Commission for the Mediterranean (GFCM) in 2009 (GFCM, 2009) were analyzed (Table 1).

Table 1
Study areas: General Fisheries Commission for the Mediterranean (GFCM) geographical sub-areas (GSAs) considered in this study and the extension of the analysed sample.

GSA	Country	Institution	Transects	Nautical miles
GSA01 (Northern Alboran Sea)	Spain	COB-IEO,CSIC	6	29
GSA06 (Northern Spain)	Spain	COB-IEO, CSIC	6	162
GSA07 (Gulf of Lions)	France	IFREMER	1	24
GSA10 (South and Central Tyrrhenian Sea)	Italy	CNR-IAS	6	61
GSA16 (South of Sicily)	Italy	CNR-IAS	5	59
GSA17-Western (Northern Adriatic)	Italy	CNR-IRBIM	5	150
GSA17-Eastern (Northern Adriatic)	Croatia	IOF	9*	53
GSA18 (Southern Adriatic)	Italy	CNR-IRBIM	4	151
GSA20 (Eastern Ionian Sea)	Greece	HCMR	15	56
GSA22 (Aegean Sea)	Greece	HCMR	5	155

*Partially covered.

Acoustic data

Acoustic data were collected exclusively during daytime, according to the MEDIAS protocol (MEDIAS handbook, 2019). Data recorded by the scientific echosounders (EK60 or EK80, Simrad) at 38 and 120 kHz frequencies were used in this study. The 38 and 120 kHz 7*7 split beam transducers were calibrated at the beginning of each survey following the international standard protocol (Demer et al. 2015). The general survey design was based on parallel transects perpendicular to bathymetry up to 200 m, modified according to the specific characteristics of each area. Research Vessel (R/V) speed during acoustic sampling was between 8 and 10 knots. The main features of the collected data are summarised in Table 2.

Table 2
Parameter and echosounder setting for data acquisition. EDSU: Elementary Distance Sample Unit. In the case of CNR-IRBIM, the back slash (/) indicates the use of two scientific echosounders, EK60 and EK80, each operating at a frequency, 38 and 120 kHz respectively.

Institution	**IEO**	**IFREMER**	**CNR-IRBIM**	**CNR-IAS**	**IOF**	**HCMR**
Echosounder	EK60	EK60	EK60/EK80	EK60	EK80	EK80
Frequency (kHz)	38, 120	38, 120	38/120	38, 120	38,120	38,120
Transducer depth (m)	5.3	3.5	3.5	3.5	3.1	2.3
Year	2018	2017	2018	2018	2018	2016
Near field limit (m)	4.5 for 38 kHz,1.8 for 120 kHz					
Pulse length	1 ms					
Ping rate	max					
Acquisition threshold	No threshold					
Analysis threshold	-100 dB					
Transducer	7*7 split beam					
EDSU	200 m					
Vertical cell	10 m					

Acoustic data (echograms) analysis was carried out using the Echoview software Pty Ltd (formerly Myriax Pty Ltd). Planktonic community echotraces were extracted for the entire water column from 10 m below the sea surface to 1 m above the sounder detected bottom, therefore, the first ten meters of the water column and the first one on the bottom were not considered in this study. The upper limit of 10 meters was established to avoid making estimates in the near field, where acoustic values are unstable (Simmonds and MacLennan 2005), based on the most restrictive conditions, i.e. Maximum transducer depth (5.3 m in the Spanish R/V) and near field limit (4.5 m at 38 kHz frequency). The data acquisition was standardized in all cases, including six steps: First step: background noise determination at each frequency (De Robertis and Higginbottom 2007). Second step: background noise elimination and subtraction from the primary echogram in the linear domain. Third step: region determination: a two-dimensional analysis area was delimited for each analysed transect, in the vertical plane from 10 m below the sea surface to 1 m above the sounder detected bottom and in the horizontal plane from 20 m to 200 m bottom depth. Fourth step: fish schools detection and codification as “Bad data” to compute solely zooplankton acoustic values. In order to detect schools, the general setting parameters were; minimum total school length = 10 m, minimum total school height = 10 m, minimum candidate length = 5 m, minimum candidate height = 5 m, maximum vertical linking distance = 5 m, maximum horizontal linking distance = 5 m, distance mode = GPS distance. When necessary, these parameters were adjusted according to the specific schools characteristics in each study area. Fifth and sixth steps: two-dimensional analysis grid definition and acoustic values estimation. To define the grid, a horizontal dimension of 200 m and a vertical dimension of 10 m were established, dividing each region (defined in step 3) into rectangles or cells of 200*10 m. In each of these cells, the Mean Volume Backscattering Strength (MVBS, MacLennan *et al.*, 2002) values at 38 and 120 kHz frequencies were estimated. The size of the cell was defined, based on previous experiences, according to the commitment to obtain the maximum information with the shortest calculation time. The MVBS at 38 and 120 kHz frequencies were explored and statistically compared between GSAs using the non-parametric Kruskal-Wallis test.

Then, the dB difference method was applied, estimating the MVBS differences according to the equation proposed by Madureira (1993), in order to categorize each cell (200*10 m). The ΔMVBS was derived by subtracting the MVBS of 38 kHz from the MVBS of 120 kHz, when the MVBS of both frequencies were larger than a given MVBS threshold, -100 dB, in this study. When the MVBS of both or either frequency was smaller than the MVBS threshold, we assumed that there was no echo.

ΔMVBS = MVBS120 kHz - MVBS38 kHz

In general terms, considering the three acoustic categories established for zooplankton organisms (Martin et al. 1996; Stanton et al. 1996), a negative ΔMVBS would indicate the presence of Gas-Bearing organisms, while a positive ΔMVBS would indicate a community dominated exclusively by Fluid-Like organisms.

Finally, in order to assess the spatial distribution of the planktonic community acoustically detected in the Mediterranean Sea, the MVBS values at 38 and 120 kHz frequencies were vertically averaged each 200 m (horizontal dimension of the grid) for each transect and spatially represented using the Arc Map 10.4.1 software. In addition, to assess the existence of a depth-dependent change in zooplankton community along the continental shelf, the results of the dB difference method application was represented by 10 m depth strata (vertical dimension of the grid) from 10 to 50 m. The first four depth strata (10–20, 20–30, 30–40 and 40–50 m) were chosen for the representation since they presented the highest spatial variability in terms of MVBS and dB difference values.

Results And Discussion

The joint study of ten different areas of the Mediterranean has made it possible to count a great diversity of geomorphological, oceanographic and productive scenarios that condition the composition of the zooplankton community. Figures 1 and 2 show onshore (40 m depth) and offshore (from 100 to 200m depth) echograms representative of the plankton scattering layers commonly detected in each considered GSA. For all GSAs, the onshore plankton echotraces were commonly dispersed through the water column, except in GSA17-E, GSA18 and GSA22 where they were concentrated forming a clearly visible layer between 20 and 30 m depth in GSA17-E and GSA18, and from the transducer face to 20 m depth in GSA22. In addition, 120 kHz frequency showed the highest MVBS compared to 38 kHz, except in GSA17-W, GSA17-E, GSA20 and GSA22. In the case of GSA17-W, this could be due to the large number of scattered fish presented in the water column, which made it difficult to distinguish between fish and plankton echotraces. In the offshore area, the plankton echotraces formed a well defined layer in most GSAs at both frequencies. The strongest frequency resulted 38 kHz. It is noteworthy that GSA10, GSA 17-W and GSA 18 presented a vertical gradient in the strongest frequency, shifted from 120 kHz in the first 15–20 m of the water column to 38 kHz in the rest of the water column. In addition, extremely low values were evident, especially at 120 kHz frequency, in the easternmost GSAs (GSAs 16, 17-E, 18, 20 and 22), which could indicate a difference in the offshore communities between the eastern and western Mediterranean sub-basins or a lower abundance in the event that the communities were similar.

The average water column MVBS (S_v dB re 1 m^{-1}) at 38 kHz and 120 kHz frequency showed statistically significant differences at a basin scale (Kruskal-Wallis test for $MVBS_{38\ kHz}$, H = 9881.3, df = 10, p-value < 2.2e-16, Kruskal Wallis test for $MVBS_{120\ kHz}$, H 16396, df = 10, p-value < 2.2e-16). For the GSAs considered in this study, the MVBS values, regardless of the frequency considered, showed an east-west gradient, with higher values found in the western GSAs compared to the eastern ones. The difference in the strongest frequency seems to be related to the fertilization mechanism and the productivity of the GSA. It is known that GSA01, which connects the Atlantic Ocean with the Mediterranean Sea, is one of the most productive areas of the Mediterranean along with the main river discharge areas such as GSA06 Ebro river), GSA17-E (Po river) or GSA18 (Agostini and Bakun 2002; D´Ortenzio and Ribera d'Alcala 2009; Macias et al. 2018). On the contrary, the GSA16 is an especially oligotrophic zone of great hydrodynamism and exchange of water masses where deep water upwelling processes take place. (Bonanno et al. 2014; Jouini et al. 2016; Rumolo et al. 2016). Moreover, areas with a high amount of acoustic energy would coincide with those that present a high primary productivity (Mercado et al. 2013; Colella et al. 2016).

The highest average water column MVBS at 38 kHz were detected in GSA01 followed by GSA18, while the lowest were detected in GSA16 (Fig. 3). In the case of the average water column MVBS at 120 kHz, the highest values were detected in GSA18, 10 and 16, while the lowest were detected in GSA20 (Fig. 3). Broadly, except GSA10 and 16, plankton echotraces backscattered a greater amount of acoustic energy at 38 than at 120 kHz, so the dB difference resulted negative in most GSAs. The maximum negative difference ($MVBS_{38kHz} > MVBS_{120kHz}$) was found in GSA20 and the maximum positive one ($MVBS_{38kHz} < MVBS_{120kHz}$) in GSA16. This fact would indicate different acoustic characteristics of the plankton communities depending on the GSAs. In most of them the plankton community resonated predominantly at 38 kHz, while in GSA10 and 16 the plankton community resonated at 120 kHz. This could indicate the unique presence of Fluid-Like class organisms in GSA16 (Martin et al. 1996; Fernandes et al. 2006).

The vertical average water column MVBS showed a decreasing onshore-offshore gradient, with the highest values found in the areas closest to the coast regardless the frequency (Fig. 4). In addition, five GSAs stand out for the high values of MVBS associated to the plankton community, GSA01, 06, 17-W and 18 at 38 kHz and GSA16 at 120 kHz.

The onshore-offshore gradient was not only due to an uneven distribution of MVBS decreasing with increasing distance from shore, but also to differences in the stronger frequency (Fig. 5). In general, 120 kHz frequency turned out the strongest one in coastal areas (ΔMVBS > 0), while offshore the strongest frequency was 38 kHz (ΔMVBS < 0). This fact would indicate that the resonant community at 120 kHz would decrease its presence with increasing distance from the coast and depth except in GSA16.

The main conclusion of this study is that the planktonic community present in June-July in the Mediterranean Sea forms scattering layers detectable at the common fish assessment frequencies (Leonori et al. 2021), therefore MEDIAS survey constitutes an ideal platform for monitoring the zooplankton community at a macro scale. Nevertheless, efforts must be made to collect biological samples that allow echograms to be interpreted in terms of species composition rather than acoustic categories. The use of two different frequencies has made it possible to apply the dB difference method and interpret the echograms in terms of zooplankton acoustic categories (Martin et al. 1996; Fernandes et al. 2006). In general, for the ten studied GSAs, the ΔMVBS was positive (38 kHz frequency recorded a lower MVBS value than 120 kHz frequency) in the areas closest to the coast, becoming negative (38 kHz frequency recorded a higher MVBS value than 120 kHz frequency) as the distance to the coast and the depth increased. This fact has already been observed in GSA01 and associated with a change in the zooplankton community (Ventero et al. 2020). In addition, the ΔMVBS was negative for all GSAs except GSA16, where a community dominated by Fluid-Like organisms presumably dominates (Ballón et al. 2011). Finally, it is worth highlighting the existence of a MVBS longitudinal gradient that would coincide with the gradient of primary production existing in the Mediterranean (Mercado et al. 2013; Colella et al. 2016). This work provides new information on the spatial distribution and acoustic characteristics of zooplankton communities in the Mediterranean Sea, determining a starting point with which to compare future scenarios. In addition, it aims to promote multidisciplinary research by combining the strengths of remote sensing with planktonic sampling, to contribute to a better understanding of the pelagic ecosystem and its processes.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Ana Ventero, Magdalena Iglesias, Marianna Giannoulaki, Maria Myrto Pyrounaki, Iole Leonori, Andrea de Felice, Vjekoslav Tičina, Claire Saraux, Simona Genovese, Josep Baeza, Pilar Córdoba, Zacharias Kapelonis, Stylianos Somarakis, Tarek Hattab, Ilaria Biagiotti, Sara Malavolti, Tea Juretić, Jean-Hervé Bourdeix, Gualtiero Basilone, Rosalia Ferreri and Salvatore Aronica. The first draft of the manuscript was written by Ana Ventero and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets analysed during the current study, due to the large number of countries involved, are available from the corresponding author on request.

Ethics approval

All applicable institutional and national guidelines for the care and use of animals were followed in this study.

References

1. Agostini VN, Bakun A (2002) 'Oceantriads'in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, Engrauli sencrasicolus). Fish Oceanogr 11:129–142
2. Ballón M, Bertrand A, Lebourges-Dhaussy A, Gutiérrez M, Ayón P, Grados D, Gerlotto F (2011) Is there enough zooplankton to feed forage fish populations off Peru? An acoustic (positive) answer. Prog Oceanogr 91:360–381. doi: 10.1016/j.pocean.2011.03.001
3. Barra M, Bonanno A, Hattab T, Saraux C, Iglesias M, Leonori I, Tičina V, Basilone G, De Felice A, Ferreri R, Machias A, Ventero A, Costantini I, Juretic T, Pyrounaki MM, Bourdeix JH, Gašparević D, Kapelonis Z, Canduci G, Giannoulaki M (2021) Effects of sampling intensity and biomass levels on the precision of acoustic surveys in the Mediterranean Sea. Mediterr Mar Sci 22:769–783. doi: 10.12681/mms.26100
4. Benoit-Bird KJ, McManus MA (2014) A critical time window for organismal interactions in a pelagic ecosystem. PLoS ONE 9:E97763. doi: 10.1371/journal.pone.0097763
5. Benoit-Bird KJ, Shroyer EL, McManus MA (2013) A critical scale in plankton aggregations across coastal ecosystems. Geophys Res Lett 40:3968–3974. doi: 10.1002/grl.50747
6. Bonanno A, Goncharov S, Mazzola S, Popov S, Cuttitta A, Patti B, Basilone G, Di Nieri A, Patti C, Aronica S, Buscaino G (2006) Acoustic evaluation of anchovy larvae distribution in relation to oceanography in the Cape Passero area (Strait of Sicily). Chem Ecol. doi: 10.1080/02757540600670307

7. Bonanno A, Placenti F, Basilone G, Mifsud R, Genovese S, Patti B, Bitetto M, Di, Aronica S, Barra M, Giacalone G, Ferreri R, Fontana I, Buscaino G, Tranchida G, Quinci E, Mazzola S (2014) Variability of water mass properties in the Strait of Sicily in summer period of 1998–2013. Ocean Sci 10:759–770. doi: 10.5194/os-10-759-2014
8. Bonanno A, Barra M, De Felice A, Giannoulaki M, Iglesias M, Leonori I, Ventero A, Aronica S, Biagiotti I, Tičina V, Canduci G, Genovese S (2021) Acoustic correction factor estimate for compensating the vertical diel migration of small pelagic species. Mediterr Mar Sci 22:784–799. doi: 10.12681/mms.25120
9. Brosset P, Menard F, Fromentin J, Bonhommeau S, Ulses C, Bourdeix J, Bigot J, Van Beveren E, Roos D, Saraux C (2015) Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. Mar Ecol Prog Ser 529:219–231. doi: 10.3354/meps11275
10. Chu D (2011) Technology evolution and advances in fisheries acoustics. J Mar Sci Technol 19:245–252
11. Colella S, Falcini F, Rinaldi E, Sammartino M, Santoleri R (2016) Mediterranean ocean colour chlorophyll trends. PLoS ONE. doi: 10.1371/journal.pone.0155756
12. Colloca F, Scarcella G, Libralato S (2017) Recent trends and impacts of fisheries exploitation on Mediterranean stocks and ecosystems. Front Mar Sci doi. 10.3389/fmars.2017.00244
13. D´Ortenzio F, Ribera d'Alcala M (2009) On the trophic regimes of the Mediterranean Sea: a satellite analysis. Biogeosciences 6:139–148
14. De Felice A, Iglesias M, Saraux C, Bonanno A, Tičina V, Leonori I, Ventero A, Hattab T, Barra M, Gašparevic D, Biagiotti D, Bourdeix JH, Genovese S, Juretic T, Aronica S, Malavolti S (2021) Environmental drivers influencing the abundance of round sardinella (Sardinella aurita) and European sprat (Sprattus sprattus) in different areas of the Mediterranean Sea. Mediterr Mar Sci 22:812–826. doi: 10.12681/mms.25933
15. De Robertis A, Higginbottom I (2007) A post-processing technique to estimate the signal-to-noise ratio and remove echosounder background noise. ICES J Mar Sci 64:1282–1291. doi: 10.1093/icesjms/fsm112
16. Demer DA, Berger L, Bernasconi M, Bethke E, Boswell KM, Chu D, Domokos R, Dunford A, Fassler S, Gauthier S, Hufnagle LT, Jech JM, Bouffant N, Lebourges-Dhaussy A, Lurton X, Macaulay GJ, Perrot Y, Ryan T, Parker-Stetter S, Stienessen S, Weber T, Williamson N (2015) Calibration of acoustic instruments
17. Fernandes PG, Korneliussen RJ, Lebourges-Dhaussy A, Massé J, Iglesias M, Diner N, Ona E, Knutsen T, Gajate J, Ponce R (2006)Species Identification Methods From Acoustic Multi-frequency Information
18. Fernández de Puelles ML, Alemany F, Jansá J (2007) Zooplankton time-series in the Balearic Sea (Western Mediterranean): Variability during the decade 1994–2003. Prog Oceanogr 74:329–354. doi: 10.1016/j.pocean.2007.04.009

19. Fernández de Puelles ML, Molinero JC (2008) Decadal changes in hydrographic and ecological time-series in the Balearic Sea (western Mediterranean), identifying links between climate and zooplankton. ICES J Mar Sci 65:311–317. doi: 10.1093/icesjms/fsn017
20. Ferreri R, Genovese S, Barra M, Biagiotti I, Bourdeix JH, De Felice A, Gašparević D, Hattab T, Iglesias M, Juretić T, Leonori I, Malavolti S, Raykov VS, Saraux C, Tičina V, Ventero A, Basilone G (2021) Variability in size at maturity of the European anchovy (Engraulis encrasicolus) in the Mediterranean Sea. Mediterr Mar Sci 22:858–870. doi: 10.12681/mms.25995
21. García-Comas C, Stemmann L, Ibanez F, Berline L, Mazzocchi MG, Gasparini S, Picheral M, Gorsky G (2011) Zooplankton long-term changes in the NW Mediterranean Sea: Decadal periodicity forced by winter hydrographic conditions related to large-scale atmospheric changes? J Mar Syst 87:216–226. doi: 10.1016/j.jmarsys.2011.04.003
22. General Fisheries Commission for the Mediterranean (2020) The State of Mediterranean and Black Sea Fisheries 2020. FAO
23. GFCM (2007) Resolution GFCM/31/2007/2 on the establishment of Geographical. Sub-Areas in the GFCM Area
24. Godo OR, Handegard NO, Browman HI, Macaulay GJ, Kaartvedt S, Giske J, Ona E, Huse G, Johnsen E (2014) Marine ecosystem acoustics (MEA): quantifying processes in the sea at the spatio-temporal scales on which they occur. ICES J Mar Sci 71:2357–2369. doi: 10.1093/icesjms/fsu116
25. Hattab T, Gucu A, Ventero A, De Felice A, Machias A, Saraux C, Gašparević D, Basilone G, Costantini I, Leonori I, Bourdeix JH, Iglesias M, Barra M, Giannoulaki M, Ferreri R, Ayoubi S, El, Malavolti S, Genovese S, Somarakis S, Juretic T, Tičina V, Certain G (2021) Temperature strongly correlates with regional patterns of body size variation in Mediterranean small pelagic fish species. Mediterr Mar Sci 22:800–811. doi: 10.12681/mms.26525
26. He Q, Silliman BR (2019) Climate Change, Human Impacts, and Coastal Ecosystems in the Anthropocene. Curr Biol 29:R1021–R1035. doi: 10.1016/j.cub.2019.08.042
27. Jech JM, Horne JK, Chu D, Demer DA, Francis DTI, Gorska N, Jones B, Lavery AC, Stanton TK, Macaulay GJ, Reeder DB, Sawada K (2015) Comparisons among ten models of acoustic backscattering used in aquatic ecosystem research. J Acoust Soc Am 138:3742–3764. doi: 10.1121/1.4937607
28. Jouini M, Bérange, Karine, Arsouze T, Beuvier J, Thiria S, Crépon M, Taupier-Letage I (2016) The Sicily Channel surface circulation revisited using a neural clustering analysis of a high-resolution simulation. J Geophys Res Ocean 121:4545–4567. doi: 10.1002/2015JC011472.Received
29. Kacic I (1973) Preliminary observations on seattering layer in the Adriatic
30. Lavery AC, Wiebe PH, Stanton TK, Lawson GL, Benfield MC, Copley N (2007) Determining dominant scatterers of sound in mixed zooplankton populations. J Acoust Soc Am 122:3304–3326. doi: 10.1121/1.2793613
31. Lebourges-Dhaussy A, Coetzee J, Hutchings L, Roudaut G, Nieuwenhuys C (2009) Zooplankton spatial distribution along the South African coast studied by multifrequency acoustics, and its

relationships with environmental parameters and anchovy distribution. ICES J Mar Sci 66:1055–1062. doi: 10.1093/icesjms/fsp129

32. Lebourges-Dhaussy A, Huggett J, Ockhuis S, Roudaut G, Josse E, Verheye H (2014) Zooplankton size and distribution within mesoscale structures in the Mozambique Channel: A comparative approach using the TAPS acoustic profiler, a multiple net sampler and ZooScan image analysis. Deep Res 100:136–152. doi: 10.1016/j.dsr2.2013.10.022
33. Leonori I, Tičina V, Giannoulaki M, Hattab T, Iglesias M, Bonanno A, Costantini I, Canduci G, Machias A, Ventero A, Somarakis S, Tsagarakis K, Bogner D, Barra M, Basilone G, Genovese S, Juretic T, Gašparević D, De Felice A (2021) History of hydroacoustic surveys of small pelagic fish species in the European Mediterranean Sea. Mediterr Mar Sci 22:751–768. doi: 10.12681/mms.26001
34. Lezama-Ochoa A, Irigoien X, Chaigneau A, Quiroz Z, Lebourges-Dhaussy A, Bertrand A (2014) Acoustics reveals the presence of a macrozooplankton biocline in the bay of Biscay in response to hydrological conditions and predator-prey relationships. PLoS ONE 9:e88054. doi: 10.1371/journal.pone.0088054
35. Machias A, Stergiou KI, Somarakis S, Karpouzi VS, Kapantagakis A (2008) Trends in trawl and purse seine catch rates in the north-eastern Mediterranean. Mediterr Mar Sci 9:49–66. doi: 10.12681/mms.143
36. Macias D, Garcia-Gorriz E, Stips A (2018) Major fertilization sources and mechanisms for Mediterranean Sea coastal ecosystems. Limnol Oceanogr 63:897–914. doi: 10.1002/lno.10677
37. Madureira LSP, Ward P, Atkinson A (1993) Differences in backscattering strength determined at 120 and 38 kHz for three species of Antarctic macroplankton. Mar Ecol Prog Ser 93:17–24. doi: 10.3354/meps093017
38. Magliozzi C, Druon J-N, Palialexis A, Artigas LF, Boicenco L, González-Quirós R, Gorokhova E, Heyden B, McQuatters-Gollop A, Varkitzi I (2021) Pelagic habitats under MSFD D1: current approaches and priorities. Publications Office of the European Union, Luxembourg, 2021
39. Martin LV, Stanton TK, Wiebe PH, Lynch JF (1996) Acoustic classification of zooplankton. ICES J Mar Sci 53:217–224. doi: 10.1121/1.413130
40. Mercado JM, Cortés D, Gómez F, León P, Putzeys S, Sallés S, Yebra L, Español I, Centro DO, Málaga D (2013) A method based on satellite imagery to evaluate the eutrophication at MSFD scale in the Alboran Sea. 2013
41. Möllmann C, Lindegren M, Blenckner T, Bergström L, Casini M, Diekmann R, Flinkman J, Müller-Karulis B, Neuenfeldt S, Schmidt JO, Tomczak M, Voss R, Gårdmark A (2014) Implementing ecosystem-based fisheries management: from single-species to integrated ecosystem assessment and advice for Baltic Sea fish stocks. ICES J Mar Sci 71:1187–1197. doi: 10.1093/icesjms/fst123
42. Mutlu E (2005) A comparison of the contribution of zooplankton and nekton taxa to the near-surface acoustic structure of three Turkish seas. Mar Ecol 26:17–32. doi: 10.1111/j.1439-0485.2005.00039.x
43. Mutlu E (2007) Compared studies on recognition of marine underwater biological scattering layers. J Appl Biol Sci 1:113–119

44. Peña M, Olivar MP, Balbín R, López-Jurado JL, Iglesias M, Miquel J, Jech JM (2014) Acoustic detection of mesopelagic fishes in scattering layers of the Balearic Sea (western Mediterranean). Can J Fish Aquat Sci 71:1–12. doi: 10.1139/cjfas-2013-0331
45. Pitois SG, Tilbury J, Bouch P, Close H, Barnett S, Culverhouse PF (2018) Comparison of a Cost-Effective Integrated Plankton Sampling and Imaging Instrument with Traditional Systems for Mesozooplankton Sampling in the Celtic Sea. Front Mar Sci 5:1–15. doi: 10.3389/fmars.2018.00005
46. Rumolo P, Bonanno A, Barra M, Fanelli E, Calabrò M, Genovese S, Ferreri R, Mazzola S, Basilone G (2016) Spatial variations in feeding habits and trophic levels of two small pelagic fish species in the central Mediterranean Sea. Mar Environ Res 115:65–77. doi: 10.1016/j.marenvres.2016.02.004
47. Saraux C, Van Beveren E, Brosset P, Queiros Q, Bourdeix JH, Dutto G, Gasset E, Jac C, Bonhommeau S, Fromentin JM (2019) Small pelagic fish dynamics: A review of mechanisms in the Gulf of Lions. Deep Res Part II Top Stud Oceanogr 159:52–61. doi: 10.1016/j.dsr2.2018.02.010
48. Sherman K (2015) Sustaining the world's large marine ecosystems. ICES J Mar Sci 72:2521–2531. doi: 10.1093/icesjms/fsv136
49. Simmonds J, MacLennan D (2005) Fisheries acoustics: theory and practice, 2nd edn. Blackwell Science Ltd a Blackwell Publishing company Editorial, Oxford
50. Stanton T, Chu D, Wiebe PH (1996) Acoustic scattering characteristics of several zooplankton groups. ICES J Mar Sci 53:289–295
51. Stanton TK, Chu D, Wiebe PH (1998) Sound scattering by several zooplankton groups. II. Scattering models. J Acoust Soc Am 103:236–253. doi: 10.1121/1.421110
52. Trenkel VM, Berger L (2013) A fisheries acoustic multi-frequency indicator to inform on large scale spatial patterns of aquatic pelagic ecosystems. Ecol Indic 30:72–79. doi: 10.1016/j.ecolind.2013.02.006
53. Trenkel VM, Ressler PH, Jech M, Giannoulaki M, Taylor C (2011) Underwater acoustics for ecosystem-based management: State of the science and proposals for ecosystem indicators. Mar Ecol Prog Ser 442:285–301. doi: 10.3354/meps09425
54. Van Beveren E, Fromentin J-M, Rouyer T, Bonhommeau S, Brosset P, Saraux C (2016) The fisheries history of small pelagics in the Northern Mediterranean. ICES J Mar Sci 73:1474–1484. doi: 10.1093/icesjms/fsw023
55. Varkitzi I, Francé J, Basset A, Cozzoli F, Stanca E, Zervoudaki S, Giannakourou A, Assimakopoulou G, Venetsanopoulou A, Mozetič P, Tinta T, Skejic S, Vidjak O, Cadiou JF, Pagou K (2018) Pelagic habitats in the Mediterranean Sea: A review of Good Environmental Status (GES) determination for plankton components and identification of gaps and priority needs to improve coherence for the MSFD implementation. Ecol Indic 95:203–218. doi: 10.1016/j.ecolind.2018.07.036
56. Vasilakopoulos P, Maravelias CD, Tserpes G (2014) The alarming decline of mediterranean fish stocks. Curr Biol 24:1643–1648. doi: 10.1016/j.cub.2014.05.070
57. Ventero A (2016) Estudio biologico de la capa de dispersion acustica estival en el mar de Alboran y su implicacion en la evaluacion de pelagicos costeros

58. Ventero A, Iglesias M, Miquel J (2020) From coast to slope: Zooplankton communities shift in the Northern Alboran Sea. Estuar Coast Shelf Sci 242:106854. doi: 10.1016/j.ecss.2020.106854
59. Ventero A, Marcos I, Iglesias M (2021) Acoustic evidences of the beginning of anchovy (Engraulis encrasicolus) schooling in the Northern Alboran Sea (Mediterranean Sea). Fish Res 239:105950. doi: 10.1016/j.fishres.2021.105950
60. Warren JD, Wiebe PH (2008) Accounting for biological and physical sources of acoustic backscatter improves estimates of zooplankton biomass. Can J Fish Aquat Sci 65:1321–1333. doi: 10.1139/F08-047

Figures

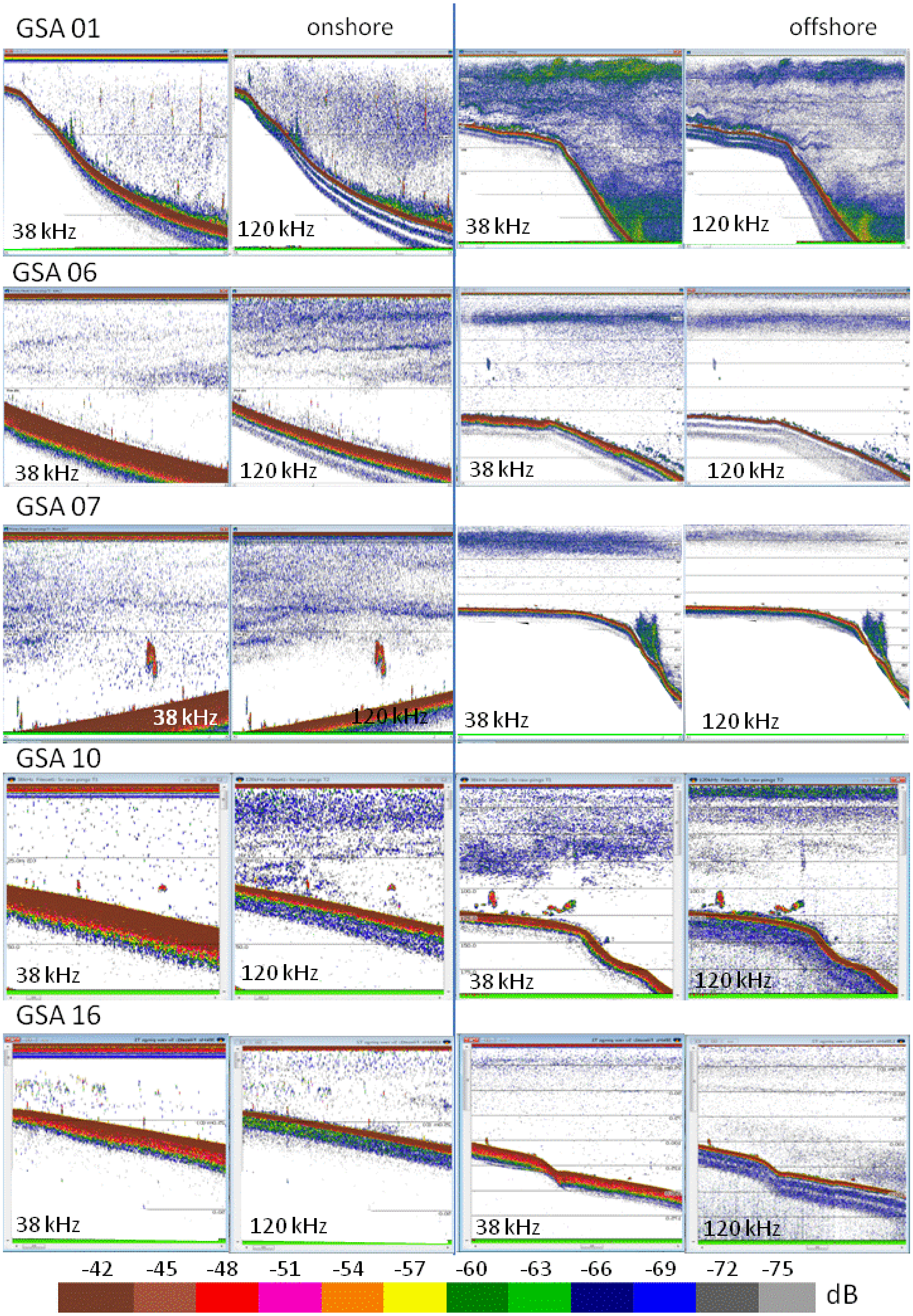

Figure 1

Examples of echograms (S_v dB re 1 m^{-1}, -75 dB threshold) collected onshore, till 40 m bottom depth and offshore, from 100 to 200 m bottom depth at 38 and 120 kHz frequencies in GSA01 (Northern Alboran Sea), GSA06 (Northern Spain), GSA07 (Gulf of Lion), GSA10 (South and Central Tyrrhenian Sea) and GSA16 (South of Sicily).

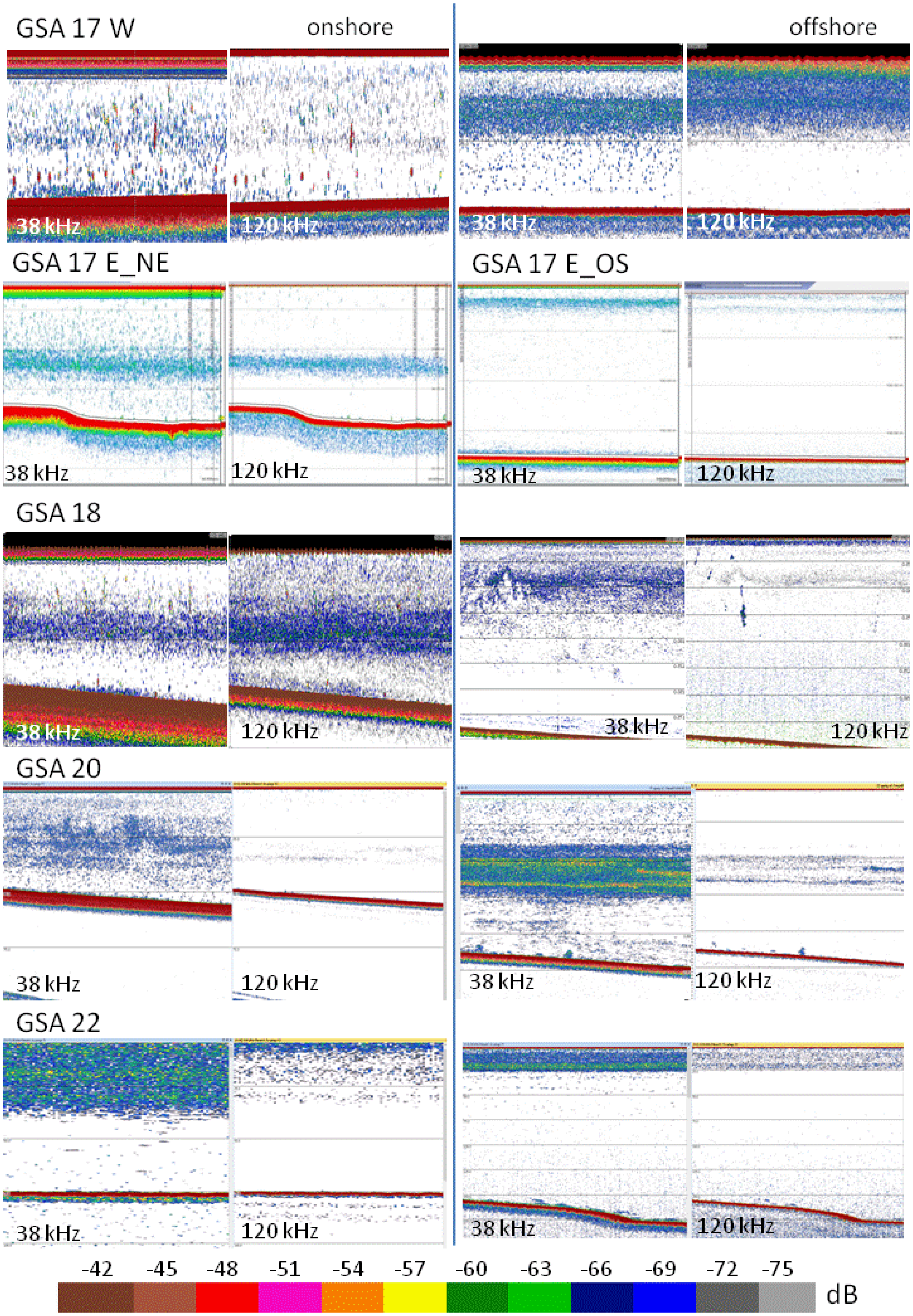

Figure 2

Examples of echograms (S_v dB re 1 m^{-1}, -75 dB threshold) collected onshore, till 40 m bottom depth and offshore, from 100 to 200 m bottom depth at 38 and 120 kHz frequencies in GSA17- Western (Northern Adriatic), GSA17- Eastern (Northern Adriatic), GSA18 (Southern Adriatic), GSA20 (Eastern Ionian Sea) and GSA22 (Aegean Sea).

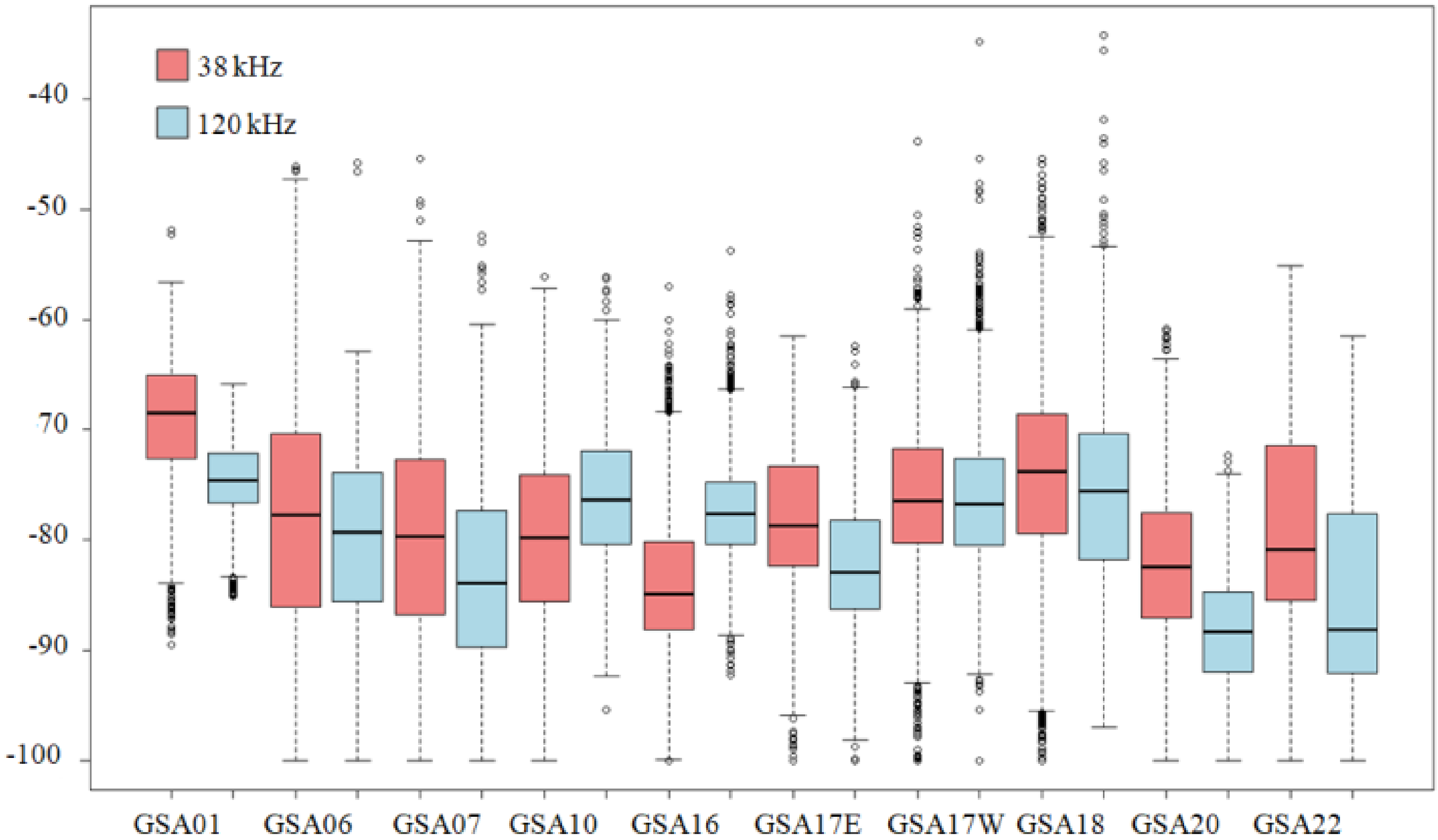

Figure 3

Average water column Mean Volume Backscattering Strength (S_v dB re 1 m^{-1}) at 38 kHz and 120 kHz for the analyzed GSA's.

Figure 4

Spatial distribution of the vertical average water column MeanVolume Backscattering Strength (S_v dB re 1 m^{-1}) at 38 kHz and 120 kHz frequencies.

Figure 5

Spatial distribution of the results of the application of the dB difference method, according to the equation ΔMVBS=MVBS120 kHz - MVBS38 kHz (Madureira et al. 1993). Negative values are represented in orange, indicating that the Mean Volume Backscattering Strength (MVBS, S_v dB re 1 m^{-1}) value recorded at the 38 kHz frequency was greater than that recorded at the 120 kHz frequency. Positive values of the difference are represented in blue, indicating that the MVBS value recorded at the 38 kHz frequency was lower than that recorded at the 120 kHz frequency.