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ORIGINAL ARTICLE

Krill spatial distribution in the Spanish Mediterranean Sea in summer time

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We documented krill distribution in the Spanish Mediterranean Sea for the first time using acoustic methods, highlighting the method's suitability to study marine communities restricted to specific areas with patchy aggregation behavior. The 2009–2017 acoustic time series analysis revealed that krill distribution, mainly located on the continental shelf edge, was driven by the presence of fronts and submarine canyons. On the other hand, areas of persistent krill distribution included from Cape La Nao to the eastern part of Almeria Bay, although an interannual northwards increase of krill presence had been detected in 2015–2017 likely related to the position of the Balearic front. We provide information on the aggregation characteristics and biological parameters of three krill species, *Nyctiphanes couchii*, *Nematoscelis megalops* and *Meganyctiphanes norvegica*. *N. couchii* and *N. megalops* formed patchy pelagic aggregations in the neritic and oceanic zone, respectively, and they were the most common species in the net tows. By contrast, *M. norvegica* formed a large demersal aggregation on the continental shelf edge and was only found in 2017; nevertheless, its 861-kg catch represented a unique milestone in the Mediterranean. Finally, krill species shared distribution area with *Maurolicus muelleri*; thus, coexistence between them are also described.

KEYWORDS: krill; frequency response; biological parameters; Western Mediterranean Sea; spatial distribution

INTRODUCTION

Euphausiids, commonly called krill, are small holoplanktonic shrimp-like crustaceans, fundamental in marine food webs because they link the lower and higher trophic levels. Krill is an intrinsic part of the diet of pelagic, mesopelagic and demersal fish (Šantić *et al.*, 2003; Valls *et al.*, 2011Šantić *et al.*, 2013Fanelli *et al.*, 2014) as well as cetaceans (Canese *et al.*, 2006) and birds (Louzao *et al.*, 2015). Krill distribution determines the distribution of higher predators like cetaceans (Bentaleb *et al.*, 2011).

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In the Mediterranean Sea, 13 krill species have been found (Mauchline and Fisher, 1969; Casanova, 1970), namely *Euphausia brevis*, *Euphausia hemigibba*, *Euphausia krohni*, *Meganyctiphanes norvegica*, *Nematoscelis atlantica*, *Nematoscelis megalops*, *Nyctiphanes couchii*, *Stylocheiron abbreviatum*, *Stylocheiron longicorne*, *Stylocheiron maximum*, *Stylocheiron suhmi*, *Thysanoessa gregaria* and *Thysanopoda aequalis*.

In the Western Mediterranean, *N. megalops* and *E. krohni* are the most abundant species (Cartes *et al*., 1994) and, together with *M. norvegica* and *S. abbreviatum*, form the principal krill assemblage (Wiebe and D'Abramo, 1972).

In the Mediterranean Sea, studies related to krill distribution are scarce, outdated or dealing with very limited spatial samples (Wiebe and D'Abramo, 1972; Cartes *et al*., 1994), with the main focus being the population dynamics (Labat and Cuzin-Roudy, 1996) and vertical distribution (Andersen *et al*., 1998, 2004; Gangai *et al*., 2012). Moreover, studies are based on punctual samples collected by means of plankton nets or suprabenthic sledges. There is then a lack of acoustic studies, which are the most common method for the study and assessment of krill, e.g. Antarctic krill (*Euphasia superba*), northern krill (*M. norvegica*) and Arctic krill (*Thysanoessa raschii*) (Everson *et al*., 2007; McQuinn *et al*., 2013; Krafft *et al*., 2015; Fallon *et al*., 2016). Furthermore, there is a knowledge gap with regard to krill distribution in the epipelagic zone, especially on the continental shelf, as well as a need for updated information regarding biological parameters of these species.

As krill tend to aggregate in monospecific aggregations (Ritz, 1994), acoustic techniques are suitable to study their spatial distribution and hence are widely used for assessment of these stocks (Everson, 2000; Hewitt and Demer, 2000). The main advantage of using acoustic techniques is that they enable the characterization of large marine areas within a short time period (Lebourges-Dhaussy *et al*., 2009; Lezama-Ochoa *et al*., 2014) and permit collection of information from various pelagic communities (e.g. plankton and fish) simultaneously on fine spatial and temporal scale, an hitherto almost impossible task when the traditional sampling methods were used (Godo *et al*., 2014). However, identification of the biological composition of the krill aggregations by means of hauls is necessary in order to properly interpret the echograms. Once the biological composition of the echotraces is known, it can be extrapolated to other echotraces that share the same acoustic characteristics, making it possible to characterize extended areas (Simmonds and MacLennan, 2005).

When several frequencies are used, acoustic multifrequency classification can be applied based on the acoustic frequency responses of the aquatic organisms (Korneliussen and Ona, 2003). Moreover, given a sufficient range of frequencies and a restricted number of species, the identity and size composition of the aquatic organisms can be inferred (Greenlaw and Johnson, 1983; Holliday *et al*., 1989; Holliday and Pieper, 1995).

Krill resonance usually occurs at high frequencies, mainly between 120 and 200 kHz (Korneliussen *et al*., 2008; McQuinn *et al*., 2013). This specific feature of krill, along with their tendency to form monospecific aggregations, can be exploited for distinguishing them from other pelagic organisms in a remote and noninvasive way, employing the dB difference method (Madureira *et al*., 1993).

The Mediterranean International Acoustic Survey (MEDIAS; http://www.medias-project.eu) carried out annually in the Spanish Mediterranean Sea with the goal of estimating the anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) stock biomass has been used as a platform to study the krill distribution over the continental shelf in the time series 2009–2017 and to contribute with new biological and acoustic data of the aggregations of *N. couchii*, *N. megalops* and *M. norvegica*, since an increase of krill abundance has been observed during the past years. In addition, the coexistence of the predator *Maurolicus muelleri* and krill species is presented and its role in the krill aggregation pattern is discussed.

Our main working hypothesis was that krill species in the Spanish Mediterranean Sea are not restricted to the near bottom slope areas but they are also distributed over the continental shelf, both near the bottom and in the water column, and that interannual changes in krill presence/absence and abundance along the shelf edge are related to changes in the general thermohaline circulation.

METHOD

Study area and sampling design

The study area is located in the Spanish Mediterranean Sea and includes the Balearic Sea and the Alboran Sea (Fig. 1). These two areas have different hydrological and geomorphologic characteristics. The dominant circulation feature in the Balearic Sea is the Northern Current, a slope current that passes along the continental slope bounding and controlling the shelf circulation, effectively separating the typically nutrient-rich shelf from the oligotrophic Mediterranean open ocean (Robinson *et al*., 2001). Regarding geomorphology, the shelf has distinct sectors. In the Northern sector, from Cape Creus to Ebro Delta, the continental shelf width is highly variable, ranging between 9.5 and 41 km, and submarine canyon is present. In the middle sector, from Ebro Delta

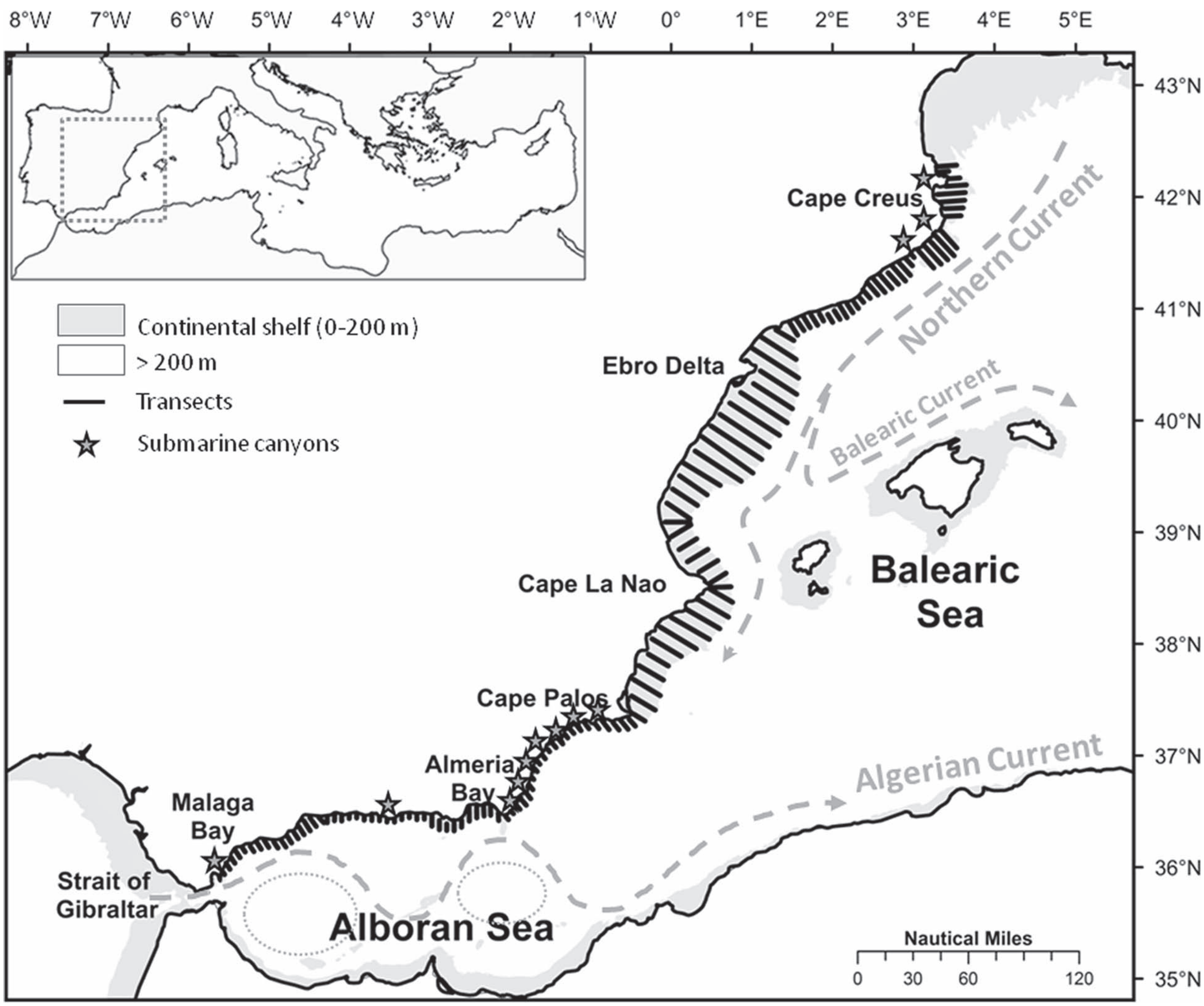

Fig 1. Study area. The Spanish Mediterranean Sea is zoomed to show the main geographical features, the sampling design and the general bathymetry, indicating the continental shelf and continental slope boundary as well as the general water masses circulation.

to Cape Palos, the shelf ranges between 43 and 92 km (Durán *et al.*, 2018). On the other hand, the predominant circulation pattern in the Alboran Sea within the upper 150–200 m involves an incoming meandering buoyant Atlantic jet through the Strait of Gibraltar (Renault *et al.*, 2012; Oguz *et al.*, 2014). The shelf in the Alboran Sea constitutes the Southern sector of the Spanish shelf, and it is characterized by a very narrow margin, ranging between 0.7 and 17 km, and locally dissected by submarine canyons (Durán *et al.*, 2018). The confluence of the saltier surface water that has stayed longer in the Mediterranean Sea (salinity > 37.5) and the fresher water recently arrived through the Strait of Gibraltar (salinity < 37.5) generate a salinity-driven oceanic front called Balearic Front (Lopez Garcia *et al.*, 1994; Balbín *et al.*, 2014). The Balearic Front position in July for the time series (Fig. 2) has been mapped based on salinity maps provided by the European Earth Observation Programme (Simoncelli *et al.*, 2014), known to be useful to detect salinity fronts structures as Balearic Front (Balbín *et al.*, 2014).

This study was conducted during the annual acoustic MEDIAS surveys. The study area prospected by the surveys included the continental shelf and the first 50 m of continental slope (from 30 to 250 m depth), from the French border (North) to the Strait of Gibraltar (South) (Fig. 1). Acoustic surveys were performed on board the research vessels (R/V) “Cornide de Saavedra” (2009−2013) and “Miguel Oliver” (2014–2017), 67 and 70 m in length, respectively. The survey design was based on parallel transects running along the greatest gradient in bottom topography, normally perpendicular to the coastline/bathymetry. The inter-transect distances were

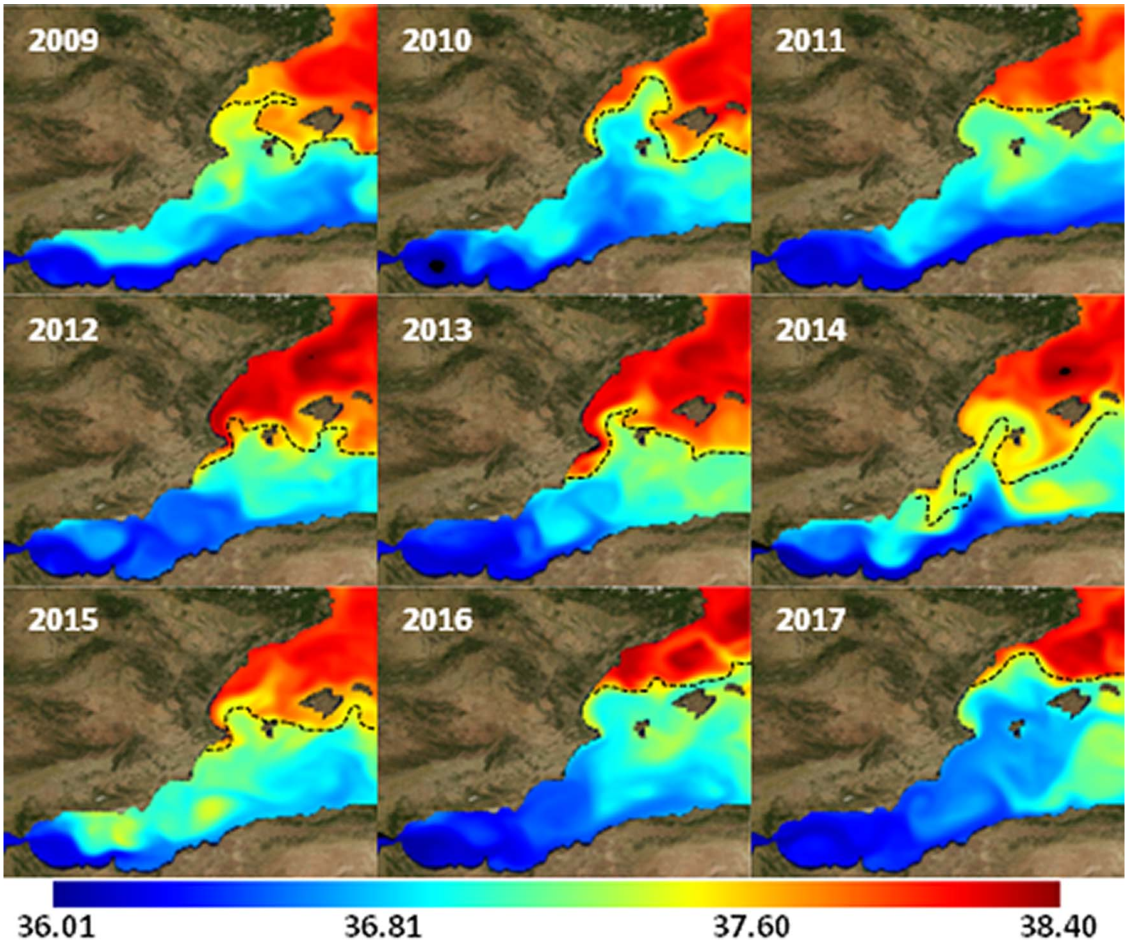

Fig. 2. Salinity maps provided by The European Earth Observation Programme (Simoncelli *et al.*, 2014) showing the Balearic Front position in July for the time series. The boundary between new ($S < 37.5$ ups) and resident (S > 37.5 ups) Atlantic water that constitute the Balearic Front position (Balbín *et al.*, 2014) is represented by a dotted black line mark.

8 nautical miles, where the continental shelf was wide (15−33 nautical miles), and 4 nautical miles, where the continental shelf was narrow (2−8 nautical miles). Transects extended from 30 to 250 m in depth (Fig. 1). Survey transects were sampled at a vessel speed of 10 knots (nautical mile/hour) in a standardized way, each summer (June–July), from 2009 to 2017, during the daytime hours.

Acoustic sampling

Acoustic data were collected following a systematic survey design, covering an area of 24.428 km^2, using a hull-mounted Simrad EK60 scientific echosounder, equipped with five transducers, operating at 18, 38, 70, 120 and 200 kHz frequencies. At the start of each survey, all the transducers were calibrated implementing the standard procedures (Foote *et al.*, 1987; Demer *et al.*, 2015). Once the equipment was calibrated, the multi-frequency data were spatially and temporary comparable. All the frequencies had identical pulse length (1 ms) and pulse shape, with no interference between the frequencies. Individual pings were identifiable in the data files at all times. The transmission pulses were simultaneous and synchronized (Korneliussen *et al.*, 2004; Korneliussen *et al.*, 2008). Acoustic data were recorded on a computer and were analyzed using the Echoview 5.4 software.

Net sampling

During the surveys MEDIAS_2015, MEDIAS_2016 and MEDIAS_2017, net tows were carried out simultaneously with the acoustic data collection to verify the identity of krill-like aggregations detected by the echosounder (Table I). As the objective of the MEDIAS surveys is the assessment of the small pelagic fish stocks and krill is not a target species, the krill identification net tows were taken when the krill aggregations were clearly visible at least

Table I: Net tows details

St	Date	Latitude	Longitude	Bottom mean depth	Swarms mean depth	Time UTC	Sampling device	Species
1	2015/07/16	37.6735° N	0.4914° W	133	60	14:30	Bongo 90	*N. couchii*
2	2015/07/18	37.3349° N	1.5488° W	190	87	13:12	Bongo 90	*N. megalops*
3	2016/07/10	38.9639° N	0.2892° E	155	48	13:09	Bongo 90	*N. couchii*
4	2016/07/16	37.4917° N	1.0991° W	250	76	14:15	Bongo 90	*N. megalops*
5	2016/07/17	37.3157° N	1.6096° W	240	96	11:32	Bongo 90	*N. megalops*
6	2017/07/10	39.2866° N	0.0248° W	115	30	16:25	Bongo 90	*N. couchii*
7	2017/07/17	37.3244° N	1.5836° W	243	87	09:11	Bongo 90	*N. couchii*
8	2017/07/13	38.2021° N	0.0324° E	163	157	12:30	Pelagic trawl	*M. norvegica*

Date values are in year/month/day format, geographical positions in decimal degrees and depths in meters and time in HH:MM.

at 120 and 200 kHz applying a −70 dB threshold and appeared continuously during 2 km at least to maximize the identification success.

Biological samples were taken using a quadrangular double Bongo net (90-cm opening) fitted with 500-μm mesh size and a pelagic trawl (25-m vertical and 15-m horizontal opening) with a 20-mm cod end.

The sampling devices (Bongo net and pelagic trawl) were positioned at the krill aggregation maximum scattering quantity (s_A) depth, corresponding to the maximum krill individual density, and they were towed horizontally for 10−15 min. Both devices were equipped with a depth sensor, a PI (Simrad) for the Bongo net and a netsonder FS20/25 (Simrad) for the pelagic trawl net. The depth sensors allowed monitoring the net track in real time and enabled the sampling device to be accurately placed in the position, where the krill aggregations were detected.

Once on board, krill samples were concentrated and relative biomass was determined as wet weight in kilograms and they were placed in 500 mL bottles. The first taxonomical analysis, using a stereomicroscope, was performed on live krill individuals at the taxonomic level of species, following the ICES Identification Leaflets for Plankton for euphausiids (Mauchline, 1971). The samples were then fixed in 2% formaldehyde buffered with borax and stored. After the survey, in the lab, a second taxonomist verified the krill species. Finally, the total length (from the rostral tip to the telson) of a representative krill individuals subsample from each net tow was measured to the nearest 0.5 mm.

Acoustic data analysis

In order to compare the echograms from different frequencies, the ping number and position between the echograms were synchronized using the matching ping number algorithm from the Echoview software. We excluded the surface noise (5-m depth from the transducer) and the bottom echo. To prevent the beam spreading and acoustic absorption associated noise, we created a new acoustic field for each frequency using a data generator algorithm from Echoview, based on a noise function, using the formula

$$20\log(R) + 2\alpha R + \mathit{offset},$$

where R is the range (in m), α is the frequency absorption coefficient (in dB m^{-1}) and the *offset* value (in dB) is the assumed initial noise in the first meter from the transducer face. To generate the noise field, we required the initial input values of α and the offset. The absorption coefficients were automatically calculated by the EK60 software during the calibration process, considering the local values of temperature and salinity collected by a Conductivity Temperature Depth (CTD) cast. The offset values were estimated from an echogram recorded in passive mode, in a 1-m wide region, located at 1 m from the transducer face. The noise field generated from the previous equation was subtracted from the echogram in the linear domain. Finally, we resampled the echograms in the common elementary cells 1 ping long and 0.75-m high.

In the case of the 200-kHz frequency, an electromagnetic sinusoidal noise of unknown origin was identified in the echograms from 150 to 250 m depth. To avoid an overestimation of krill species scattering quantities, the noise was estimated and its contribution scattering was removed from the echogram. We determined the electromagnetic noise by analyzing a 1.500-m long region, between 160 and 240 m depth, of an echogram recorded in passive mode.

Krill species acoustic identification

For each net tow, Bongo net or pelagic trawl trajectories were reconstructed from the time–depth sensors and overlain on the echograms with appropriate spatial lagging between the transducers and the net to determine which aggregations were sampled. Employing the Echoview “School module,” krill aggregation outline was defined on the 200-kHz echograms and applied to the rest of the frequencies. A 200-kHz echogram was chosen because it detected the maximum amount of krill scattering in the all cases. The parameter settings for automatic detection of krill aggregations included a minimum total length of 2 m, a minimum total height of 2 m, a maximum vertical linking distance of 2 m and a maximum horizontal linking distance of 5 m. The mean depth, morphometric characteristics (height and length) and energetic parameters (mean, maximum and minimum), volume backscattering coefficient (s_V), mean value backscattering strength (MVBS) and nautical area backscattering coefficient (s_A) (Maclennan *et al.*, 2002) of the krill aggregations were extracted from each frequency. The observed aggregation height was determined directly from the echogram scale and the true aggregation length (L_t) was estimated by means of the follow equation: $L_t = L_m - 2z\tan(\varphi/2)$, where "$L_m$" is the observed length calculated from the distance traveled by the ship as it passes the school (Lm = Vt, being "V" the ship's speed and "t" the time between the first and last detections of the aggregation), "z" is the aggregation mean depth and "φ" is the nominal beam width specified by the manufacturer, namely the angle between the half-power points of the beam pattern (Simmonds and MacLennan, 2005). The backscatter quantities of krill aggregations at different frequencies associated with their biological composition formed the basis of the data for subsequent analysis.

The relative frequency response, *r*(*f*) (Korneliussen and Ona, 2003), which is an acoustic feature used to characterize the acoustic targets, was calculated for all the krill aggregations biologically identified (ground-truthed) in 2015, 2016 and 2017, employing the s_v values at 18, 38, 70, 120 and 200 kHz frequencies. This response has been defined as the s_v value for a specific frequency relative to that of a reference frequency (38 kHz). The *r*(*f*) was determined using the equation: $r(f) \equiv s_v(f)/s_v$ (38 kHz), where s_v is the volume backscattering coefficient and "f" is the response at the acoustic frequency.

Krill spatial distribution

Once the relative frequency response was established for each krill species and it was verified that the MVBS registered at 200 kHz was always higher than the MVBS recorded at 38 kHz, the dB difference method was applied to the echograms collected during the MEDIAS 2009–2017 acoustic surveys, in order to detect the krill aggregations during the time series. An aggregation belongs to the krill category if the $\Delta MVBS_{200-38}$ was positive (up to +4 dB); else, the echotraces were indicative of fish schools or "others." Krill aggregations were isolated from the echograms using a Boolean mask (true for values above the +4 dB threshold), and their geographical positions were extracted and plotted on a GIS application (ESRI ArcGIS10.4). Data flow was followed until isolated krill aggregations were identified, as outlined in Fig. 3.

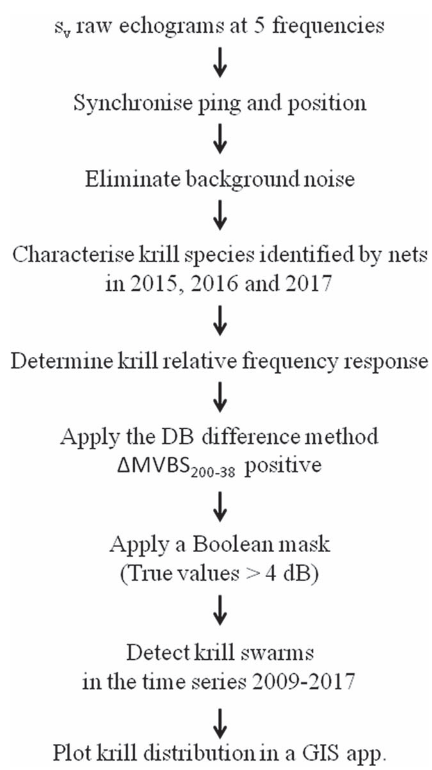

Fig. 3. Data flow followed in the data analysis.

RESULTS

During the MEDIAS 2015, 2016 and 2017, krill-like aggregations were detected using the scientific echosounder mainly in the first 60 m of the water column on the shelf, the shelf edge and the slope. In MEDIAS 2017, krill-like aggregations were also detected close to the bottom on the shelf edge. Eight net tows were performed (Table I), highlighting that the aggregations were monospecific and composed of *N. couchii*, *N. megalops* or *M. norvegica* (Fig. 4). The first two species formed pelagic aggregations, while *M. norvegica* formed demersal aggregations. The most abundant species regarding acoustic quantities and collected biomass was *M. norvegica* (Table II). *Nyctiphanes couchii* was found in each survey on the shelf and in 2017 also on the slope, reaching its maximum acoustic quantities and biomass in 2016 (Table II). *Nematscelis megalops* was found in 2015 and 2016 mainly on the slope, reaching its maximum acoustic quantities and collected biomass in 2016 (Table II). The coexistence of krill and *M. muelleri* was detected. As *N. megalops* was placed 50 m above *M. muelleri*, no interaction between them was evident during daytime, whereas

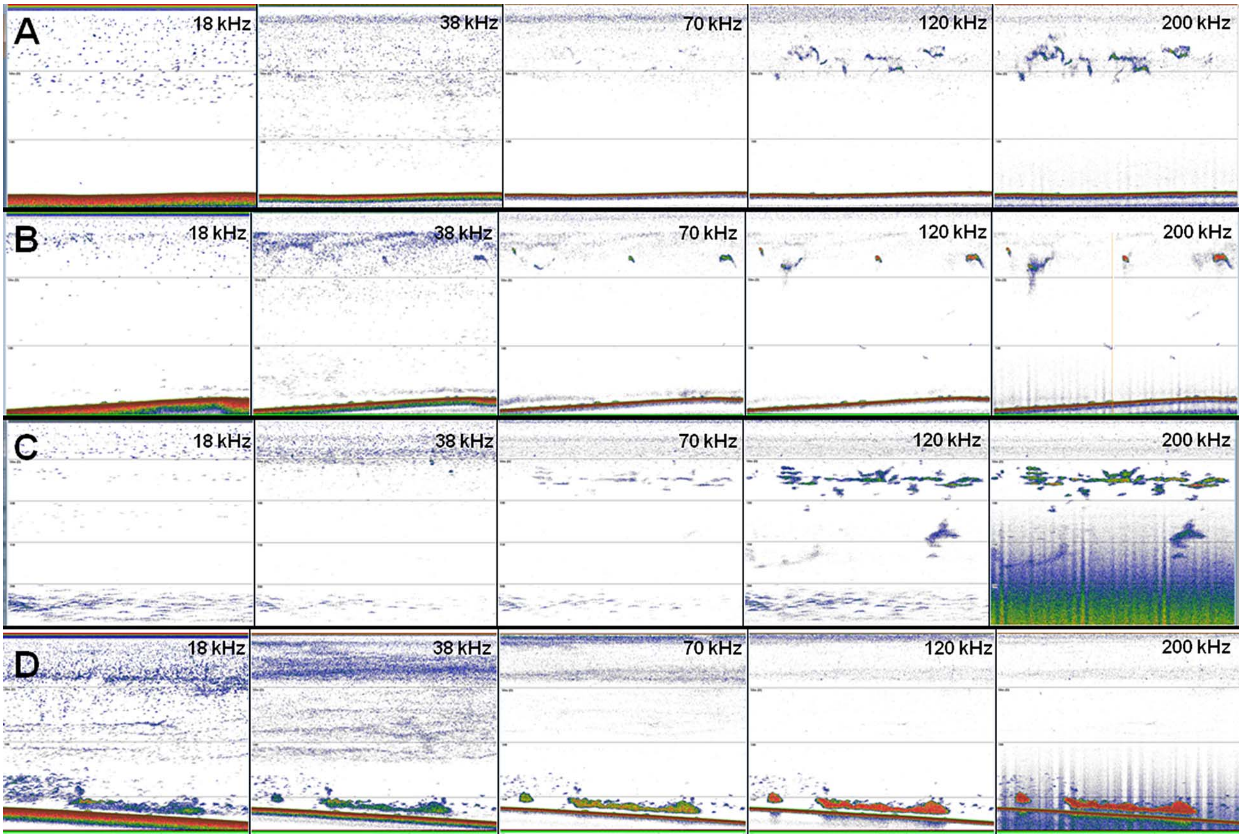

Fig. 4. Identification of echograms at five frequencies (−70 dB threshold), the horizontal marks of each echogram represents a depth stratum of 50 m. (**A**) *Nyctiphanes couchii* in 2015. (**B**) *Nyctiphanes couchii* in 2017. (**C**) *Nematoscelis megalops* in 2015. (**D**) *Meganyctiphanes norvegica* in 2017.

Table II: Mean s_A values [dB re 1 (m^2 nmi^{-2})] at multiple frequencies per krill species and year corresponding to the net tows

	18 kHz	38 kHz	70 kHz	120 kHz	200 kHz	BIOMASS	Localization
N. couchii							
2015	3	8	11	33	125	0.7	shelf
2016	2	20	67	645	1 723	4.7	shelf
2017	6	44	115	260	785	2.1	shelf
2017	4	8	12	28	162	1.1	slope
N. megalops							
2015	6	4	10	43	159	0.9	Shelf and slope
2016_1	<1	7	12	50	170	1.2	slope
2016_2	1	14	15	80	223	1.9	slope
M. norvegica							
2017	155	195	628	2 919	7 595	861.0	shelf

Estimate biomass collected in wet weight (kg) and localization: "shelf" indicates that krill aggregations were found at bottom depths shallower than 200 m and "slope" indicates that krill aggregations were found at bottom depths >200 m. All values are background noise corrected; the *M. norvegica* values at 200 kHz frequency are also electromagnetic noise corrected.

M. norvegica was surrounded by *M. muelleri* (Fig. 5). The time series analysis showed an increase in krill presence and mean abundance in the continental shelf in the study area in 2015–2017 (Figs. 6 and 7). Finally, an apparent krill preference area extended from the Ebro Delta to the eastern part of the Almeria Bay, reaching a hot spot between Cape La Nao and Cape Palos (Fig. 6).

Krill species characteristics

Nyctiphanes couchii

Nyctiphanes couchii was detected in 2015, 2016 and 2017 surveys as discrete and continuous aggregations along the bathymetric stratum between 110 and 160 m, in a 2.5-km area in the direction of the coastline slope and of

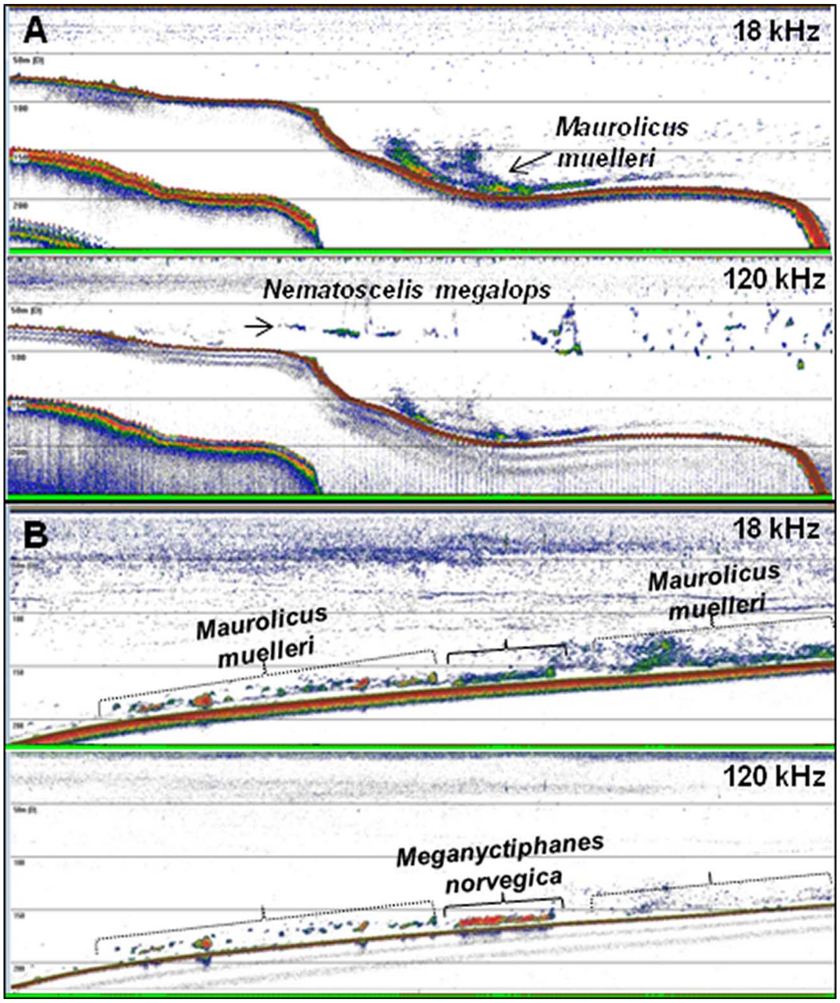

Fig 5. Echograms at two frequencies (18 and 120 kHz) showing the coexistence of krill species and *M. muelleri*. (**A**) *Nematoscelis megalops*. (**B**) *Meganyctiphanes norvegica*.

20 km along the bathymetric stratum. In 2017, they were also found at the slope, from a bottom depth from 190 to 250 m. The mean true length of the aggregations was 320 m and the mean height 10 m. In the vertical plane, the *N. couchii* aggregations located in the continental shelf appeared within a restricted strip of 45 m depth, from 25 to 70 m in depth, while in the continental slope they were located within a deeper and wider strip, from 30 to 110 m.

The *N. couchii* aggregations were clearly visible at 120 and 200 kHz, when the −70-dB threshold was applied (Fig. 4A). In 2017, the *N. couchii* aggregations presented a high density of individual being also visible at 70 kHz (Fig. 4B). The maximum biomass was collected in 2016 when the maximum acoustic values were detected (Table II). In all the cases, the relative frequency response value showed a rising acoustic response as the frequency increased (Table III). The *r*(*f*) values escalated gradually to 120 kHz and then sharply increased to reach the maximum value for the 200-kHz frequency.

Nyctiphanes couchii total length was found to be from 4.5 to 14.5 mm. In 2015, the total length frequency distribution was bimodal, with 6.5 mm being the first and main modal value and 9.5 mm the secondary modal value. The mean value was 7.3 ± 1.8 mm (Table IV). In 2016, the total length frequency distribution was unimodal, with a modal value of 11.5 mm and mean value of 11.5 ± 1.5 mm (Table IV). For both years, the largest females carried the eggs attached to the rearmost pair of their thoracic legs. In 2017, two different length frequency distributions were identified, depending upon the sample location, in which the individuals found in the continental shelf presented a bimodal frequency distribution with a mean total length of 11.3 ± 1.7 mm, while those found in

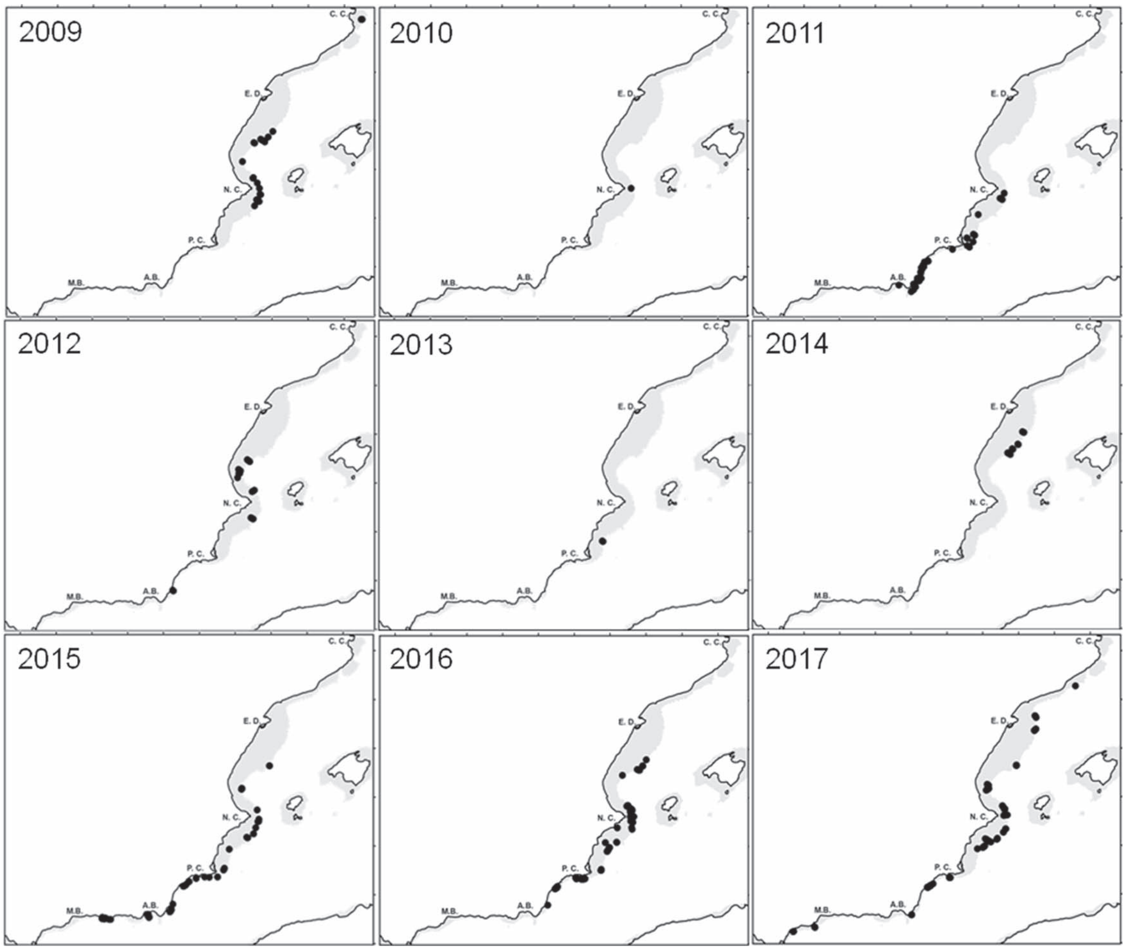

Fig. 6. The presence of krill aggregations in the time series 2009–2017 inferred from the acoustic data, using the dB difference method.

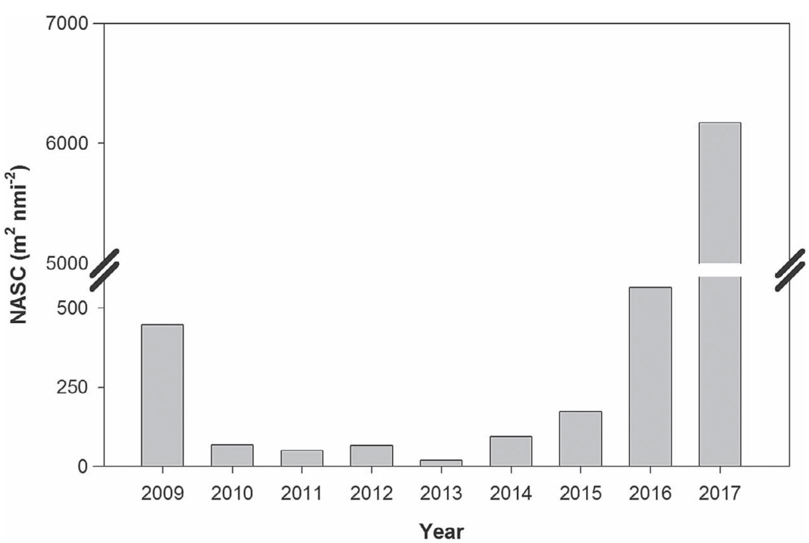

Fig. 7. Mean NASC [s_A value (m^2/nmi^2)] at 200-kHz frequency integrated per year.

Table III: Relative frequency response values, r(f), per krill species determined using the equation: $r(f) \equiv s_v(f)/s_v$ (38 kHz), where s_v is the volume backscattering coefficient and "f" is the response at the acoustic frequency (18, 38, 70, 120 and 200 kHz)

	18 kHz	38 kHz	70 kHz	120 kHz	200 kHz
M. norvegica	0.90	1.00	2.26	9.36	17.58
N. couchii	0.24	1.00	1.99	8.08	23.37
N. megalops	0.17	1.00	0.77	2.98	10.50

the shelf break presented a unimodal distribution with a mean length of 6.3 ± 1.2 mm (Table IV).

Nematoscelis megalops

Nematoscelis megalops aggregations were found from 40 to 160 m depth in the water column, along 2 km in the coastline-slope direction and for 24 km along the bathymetric stratum from 190 to >250 m. The *N. megalops* aggregation mean dimensions were 457-m long (true length) and 47-m height.

Nematoscelis megalops aggregations were clearly visible at 70, 120 and 200 kHz when the −70-dB threshold was applied (Fig. 4C). Moreover, the highest s_A values were found in 2016, indicating a denser swarm structure compared to 2015 (Table II). It is noteworthy that the presence of *M. muelleri* below them was found in the sampled area in 2016 (Fig. 5A). In all the cases, the frequency response values showed the increase in acoustic response with increasing frequency (Table III).

Nematoscelis megalops total length frequency distribution was bimodal in 2015, being the main modal value 12 mm and the secondary 15 mm, with a mean value of 13.4 ± 1.6 mm (Table IV). In 2016, it was unimodal, with a modal value of 12.5 mm and the mean being 11.9 ± 1.3 mm (Table IV).

Meganyctiphanes norvegica

In 2017, a huge *M. norvegica* aggregation (1810-m length and 27-m height) was found at the end of the continental shelf close to the bottom. The school was detected at all the frequencies (Fig. 4D) with extremely high s_A values (Table II). It was the only species that was affected by the presence of electromagnetic noise in the 200-kHz echograms (Fig. 4D), so its values were corrected considering the maximum calculated value. The mean and maximum S_V noise value estimates were −66.36 and −48.42 dB, respectively.

Meganyctiphanes norvegica was found in a place commonly occupied by *M. muelleri* in the study area and appeared surrounded by them (Fig. 5B). These two species were clearly distinguishable because they have distinct frequency responses, *M. norvegica* acoustic values rising with the increasing frequency (Table III) whereas *M. muelleri* acoustic values decreasing with the increasing frequency (Fig. 5B).

Given the uniqueness of the echotraces and the high density, the pelagic trawl was employed to identify it. The trawl catch included 861 kg of *M. norvegica* mixed with 10 kg of *M. muelleri*. As the pelagic trawl cod end was 20 mm, a large number of krill individuals were assumed to be lost through the mesh. The length frequency distribution *M. norvegica* was bimodal, the main mode being 18.5 mm and the secondary one being 23.0 mm (Table IV), ranging from 16.5 to 25 mm. The mean total length was 20.0 ± 2.2 mm.

Krill spatial distribution

Based on the relative frequency response values of the krill aggregations identified by net tows in 2015, 2016 and 2017 surveys (Table III), the automatic isolation of krill aggregations was carried out applying the dB difference method, in the time series (2009–2017) stored echograms.

The suitability of utilizing the dB difference method to automatically isolate krill aggregations was supported from an echogram expert. It was estimated that more than the 95% of the krill aggregations detected in the time series were correctly isolated and assigned to krill. The mapping of the positions of the krill aggregation per year (Fig. 6) highlights that they occurred mainly at the edge of the continental shelf and in the continental slope, between 150- and 250-m bottom depth, although in 2011, 2012, 2015, 2016 and 2017 they were occasionally found in shallower locations. In all the cases, the krill aggregations exhibited a pelagic behavior, being located from 25 to 160 m in depth in the water column. It is noteworthy that only in 2017, within a restricted area, demersal behavior was identified, which coincided with the huge capture of *M. norvegica*. Krill was located mainly from the southern part of the Ebro Delta to the eastern part of the Almeria Bay, although interannual changes were detected. In 2009 and 2014, krill aggregations were found in the vicinity of Cape Creus as well. In 2017, krill was detected farther in the south, in the Malaga Bay, and its distribution was scattered throughout the study

Table IV: The length frequency distribution of krill species, N. couchii, N. megalops *and* M. norvegica *in millimeters derived from the net tows*

	2015		2016		2017		
Total length	*N. couchii*	*N. megalops*	*N. megalops*	*N. couchii*	*M. norvegica*	*N. couchii*_shelf	*N. couchii*_slope
4.5	2	0	0	0	0	0	0
5	4	0	0	0	0	0	6
5.5	6	0	0	0	0	0	10
6	15	0	0	0	0	0	4
6.5	18	0	0	0	0	0	2
7	13	0	0	0	0	0	2
7.5	7	0	0	0	0	0	2
8	5	0	0	1	0	0	3
8.5	2	0	0	2	0	1	2
9	3	0	2	2	0	4	1
9.5	4	0	5	4	0	7	0
10	3	0	5	5	0	9	0
10.5	2	1	10	6	0	5	0
11	3	5	11	7	0	4	0
11.5	2	9	19	9	0	3	0
12	2	11	21	7	0	6	0
12.5	0	4	26	5	0	4	0
13	0	2	12	8	0	3	0
13.5	0	3	8	3	0	2	0
14	0	5	5	2	0	2	0
14.5	0	7	2	1	0	3	0
15	0	9	1	1	0	2	0
15.5	0	8	0	0	0	0	0
16	0	2	0	0	0	0	0
16.5	0	1	0	0	1	0	0
17	0	0	0	0	5	0	0
17.5	0	0	0	0	7	0	0
18	0	0	0	0	8	0	0
18.5	0	0	0	0	11	0	0
19	0	0	0	0	9	0	0
19.5	0	0	0	0	6	0	0
20	0	0	0	0	5	0	0
20.5	0	0	0	0	3	0	0
21	0	0	0	0	3	0	0
21.5	0	0	0	0	1	0	0
22	0	0	0	0	3	0	0
22.5	0	0	0	0	5	0	0
23	0	0	0	0	6	0	0
23.5	0	0	0	0	4	0	0
24	0	0	0	0	3	0	0
24.5	0	0	0	0	2	0	0
25	0	0	0	0	1	0	0
TOTAL	91	67	127	63	83	55	32

area, while in 2010 and 2013 it was restricted to a single point (Fig. 6).

Interannual changes in krill abundance have been detected (Fig. 7). In 2015–2017, krill presence (Fig. 6) and abundance (Fig. 7) have increased substantially in the study area, reaching the maximum value in 2017 due to the presence of *M. norvegica*.

DISCUSSION

Krill aggregations identified in 2015, 2016 and 2017 were verified, by net tows, as *N. couchii*, *N. megalops* and *M. norvegica*. *Nyctiphanes couchii* formed discrete aggregations mainly located at a mean depth of 50 m in the water column over the continental shelf, which confirming its pelagic and neritic distribution (Everson, 2000). *Nyctiphanes couchii* aggregations were composed of one or two cohorts, and when two cohorts were identified, the biggest females carried eggs, which suggest, according with previous studies, overlapping size ranges due to a prolonged spawning period over the year (Lindley, 1982). *Nematoscelis megalops* formed discrete aggregations mainly located at a mean depth of 85 m in the water column in the continental shelf edge and the continental slope and behaved as oceanic pelagic species. *Nematoscelis* *megalops* aggregations were composed of one or two cohorts, and in both cases, their mean length was larger than that of the previous ones reported for the same season period (Cartes *et al.*, 2010), maybe bigger specimens form pelagic aggregations while smaller ones form benthic aggregations. Although *N. couchii* and *N. megalops* have been found in the water column, *N. couchii* appeared closer to the surface being more accessible to seabirds than *N. megalops*, which can explain that Balearic Shearwaters feed on krill during their breeding season in our study area (Louzao *et al.*, 2015). *Meganyctiphanes norvegica* showed the opposite behavior, forming a large aggregation close to the bottom as previously has been reported (Cartes *et al.*, 2010), related to its feeding habits (Pond *et al.*, 2012). *Meganyctiphanes norvegica* length frequency distribution was bimodal; the first mode we interpret as the born-in-the-year cohort (0+), whereas the second is a pool of the older age classes (1+) (Labat and Cuzin-Roudy, 1996). The detection and catch of *M. norvegica* is a punctual and unprecedented event in the study area; thus, we cannot affirm that it is the most abundant species, since we have caught more than 860 kg, but it is possible that under certain oceanographic conditions part of the population ascend by the slope and be located on the continental shelf. The ecological implication of the massive presence of *M. norvegica* in the area is not restricted to the change not only in the migration pattern or distribution of cetaceans or tuna searching for prey (Canese *et al.*, 2006; Logan *et al.*, 2011) but also in the carbon flux to the deep sea communities (Hirai and Jones, 2012).

The use of multiple frequencies has facilitated the detection of the co-occurrence of species belonging to different trophic levels. The highest frequencies have detected krill and the lowest their predator, *M. muelleri* (Young and Blaber, 1986; Rasmussen and Giske, 1994). In the MEDIAS surveys time series *M. muelleri* has been commonly detected during the day close to the bottom in the continental shelf edge, coinciding with *N. megalops* and *M. norvegica*, although only interaction with *M. norvegica* was detected since *M. muelleri* surrounded *M. norvegica*. This finding could explain the formation of very compact swarms as an anti-predator mechanism, although further efforts are required in this direction to understand the actual mechanisms that govern the behavior of these species.

Nyctiphanes couchii, *N. megalops* and *M. norvegica* share the shape of the frequency response graph, which records the maximum scattering quantity at 200 kHz. In the case of *N. couchii* and *N. megalops*, no specific study has been done regarding the acoustic features because the majority of the bibliography refers to the Antarctic, *E. superba*, or Northern krill, *M. norvegica*, due to their commercial importance (Everson *et al.*, 2007; Reiss *et al.*, 2008; Krafft *et al.*, 2015; Watkins *et al.*, 2016). Regarding *M. norvegica* relative frequency response, our results concur with the data presented in the frame of the SIMFAMI project (Fernandes *et al.*, 2006) and with multi-frequency target strength measured using the *ex situ* mesocosm experiments (Calise and Knutsen, 2012), as well as with the recent wideband data (Jech *et al.*, 2017). However, they do not coincide with those reported for the Gulf of Saint Lawrence (McQuinn *et al.*, 2013), possibly due to the difference in the aggregation size, structure, behavior exhibited (pelagic or demersal) and presence of predators.

The dB difference method, based on the relative frequency response, was applied to identify krill aggregations in the study area along the time series 2009–2017, and our results showed that krill in the Spanish Mediterranean Sea aggregate over the continental shelf edge and slope and its spatial distribution is related to bathymetric and oceanographic structures as other places around the world (Santora *et al.*, 2012); moreover, its distribution is not only restricted to open-ocean bottom areas (Cartes *et al.*, 1994, 2010) but also inhabited in the epipelagic neritic area. Based on our results, the species most likely to have been detected during the 2009–2017 time series were *N. couchii* or *N. megalops* given their pelagic habits. Krill distributions have been associated with frontal zones (Tarling *et al.*, 1995) and submarine canyons (Santora *et al.*, 2018), which represent regions of enrichment (Howatt and Allen, 2013). In our study area, the krill presence observed along the shelf edge in the Balearic Sea can be explained by the North Current front position, while in Alboran Sea by the upwelling from the submarine canyons due to the specific orographic and oceanographic characteristics (Robinson *et al.*, 2001; Oguz *et al.*, 2014; Durán *et al.*, 2018). North Current variability is mainly related to intensity and wind direction (Berta *et al.*, 2018); moreover, North Current front displacement toward the continental shelf has been described in the Gulf of Lyon (Barrier *et al.*, 2016), and it can favor krill detection during the MEDIAS over the continental shelf. On the other hand, the interannual increase of the krill in the study area, especially in 2015–2017, can be explained by the northward displacement of the Balearic front as can be deduced by the salinity maps predicted by the European Union Copernicus Marine Service Information (Simoncelli *et al.*, 2014). The position of the Balearic front has been reported as the main physical feature that influences the latitudinal species distribution in the Balearic Sea (Gaertner *et al.*, 2005; Garcia *et al.*, 2005; Balbín *et al.*, 2014).

Our study confirms that krill are part of Spanish Mediterranean Sea continental shelf pelagic community and the presence of krill has increased in recent years. In addition, the suitability of the use of acoustic methods for the study of krill in areas where it forms patchy aggregations, where its presence is punctual and where its distribution is restricted to specific zones has been demonstrated. Although we have made progress in knowledge about krill distribution and the possible role of the thermohaline currents in the krill populations interannual changes, specific and multidisciplinary studies aimed at the simultaneous study of the krill distribution related to the mesoscale oceanographic structures, as fronts or eddies, are still needed in the study area. Finally, the verification of the krill relative frequency response in the Mediterranean for the first time will facilitate gaining knowledge, in the near future, about the interannual krill distribution, at least from 2009 onwards, when the MEDIAS surveys had commenced.

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