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**Insights from a multibeam echosounder to survey pelagic fish shoals and their
spatio-temporal distribution in ultra-shallow waters**

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Abstract

Surveying pelagic fish population dynamics in ultra-shallow waters (< 20m) is often
limited by research vessel size, which not usually navigate in shallow waters. Here, we use a
multibeam echosounder to detect fish shoals and assess their characteristics (acoustic density
and 3-D morphology) in ultra-shallow waters to follow European Marine Strategy Framework

Directive (MSFD) request. Surveys were made in two coastal areas in French Brittany during different seasons (spring, summer, autumn) in 2020. Our surveying methodology applying portable multibeam echosounder on small vessels allowed us to successfully survey pelagic fish spatio-temporal distributions in ultra-shallow waters. Numerous shoals have been observed which could account for important biomass and they were significantly denser and larger in ultra-shallow waters compared to shoals in deeper areas for both study sites. Shoal surfaces and volumes were also significantly lower in autumn compared to spring and summer. In addition, Atlantic mackerels (*Scomber scombrus*) were observed in ultra-shallow waters areas during summer in both study sites. Consequently, the multibeam echosounder is a workable and relevant tool for setting up long-term surveying of pelagic fish in ultra-shallow waters (coastal and estuarine ecosystems) as required by the MSFD to better assess pelagic fish ecological status.

Key-words. Pelagic fish, multibeam, echosounder, ultra-shallow waters, coastal ecosystems

1. INTRODUCTION

Shallow coastal waters, and in particular ultra-shallow waters (< 20m), provide many biological and ecological functions for fish species at different stages and throughout their life cycle (Beck et al. 2001, Franco et al. 2006, Pihl et al. 2007). Numerous fish species (sardines, European anchovies, Atlantic mackerels, etc.) are also known to migrate to coastal and estuarine areas for various reasons which can vary extensively between fish species, *e.g.*, for spawning, feeding reasons or environmental conditions (Bellier et al. 2007, Morais et al. 2010, Nøttestad et al. 2016). In addition, shallow waters are subjected to many anthropogenic

pressures, such as urbanization of coasts, fisheries, pollution, physical disturbance of habitats, etc. (Jackson et al. 2001, Halpern et al. 2007, Dauvin 2008). To study marine ecosystems, acoustic methods are often effective as they allow rapid sampling with high spatial and temporal coverage and are non-invasive and non-extractive techniques to observe several marine organisms (Simmonds & MacLennan 2006, Benoit-Bird & Lawson 2016). However, ultra-shallow waters ($< 20\text{m}$) are less regularly acoustically surveyed because scientific monitoring of pelagic fish populations using active acoustic methods are usually conducted by research vessels which are restricted to work in ultra-shallow areas for safety reasons (Brehmer et al. 2006b). Consequently, knowledge on the pelagic fish spatio-temporal distributions in ultra-shallow waters are still scarce although crucial for effective management and conservation of marine and coastal ecosystems.

Split-beam echosounders associated with trawl catches are widely used to assess pelagic fish population distributions and abundances in order to estimate fish stocks in offshore waters (Doray et al. 2010, 2018, Demer et al. 2012). However, the use of multibeam echosounders has gained increasing attention (Melvin & Cochrane 2015, Brehmer et al. 2019a, Lamouret et al. 2019). They have been developed to operate with frequencies ranging from 12 up to $>500\text{ kHz}$ allowing them to be used in different water depths from shallow to deep waters (Colbo et al. 2014), and could transmit either continuous wave (CW) signals or frequency modulated (FM) signals. Multibeam echosounders sample a larger volume of waters compared to split-beam echosounders and should provide more information about the distribution and movement of targets in the field of view (Gerlotto et al. 1999, Trenkel et al. 2008). In particular, in ultra-shallow waters ($< 20\text{m}$), where the sampled volume is restricted by the bottom, sampling a higher volume is interesting. Multibeam echosounders have thus been used to survey schooling fish on artificial and natural reefs (Holland et al. 2021). They could also limit the bias in fish biomass estimations due to avoidance reaction to boats (Reid

2000). This could be particularly relevant in shallow waters where the avoidance reaction are supposed to be higher than in deeper areas due to the noise and visual effects of the vessel (Draštík & Kubečka 2005, Brehmer et al. 2019b). Finally, multibeam echosounders allow 3-D observations of the entire fish shoals which could have implications for behaviour studies (Reid 2000) as well as help for species identification (Guillard et al. 2011).

Fish shoals refer to aggregated social assemblages, and can display synchronized and/or polarized behaviors (Pitcher 1986). The ability of fish to form shoals depends on many factors including species-specific features such as behaviour, physiology and/or biology, and the environment. For example, fishes could form shoals for physiological reasons (*i.e.* feeding and reproduction), due to interactions with other species (*i.e.* anti-predator response), or environmental conditions (*i.e.* diurnal cycles, seasons) (Bahri & Fréon 2000). Consequently, surveying fish shoals by a multibeam echosounder could help to better understand population spatio-temporal distributions as well as ecological interactions with their environment (Benoit-Bird & Lawson 2016, Innangi et al. 2016). Especially, the marine habitat features (rocky substrate, sediments, etc.) should be better investigated as they would likely influence the fish shoal distributions (Lamouret et al. 2019, 2020). In addition, analyzing the distribution of a species along environmental or anthropic gradients can help identifying geographic areas considered suitable, or on the opposite, unsuitable for the presence of this species (Guisan & Thuiller 2005), which is necessary for the management of the marine environment.

Our study was made in the framework of the context of the Marine Strategy Framework Directive (MSFD) which requires the Member States of the European Union to put measures in place to achieve and maintain good environmental status of all marine waters (Long, 2011), including shallow coastal waters. This study focuses on shallow water areas in French Brittany which are poorly known. We used a multibeam echosounder to estimate the spatio-

temporal distributions of fish shoals from shallow waters to ultra-shallow water areas (< 20m) in two French Brittany areas at different seasons (spring, summer, autumn) in 2020. Fish shoal detections and characteristics were analysed related to environmental gradients. Finally, we concluded on the insight of the multibeam echosounder to detect pelagic fish shoals in ultra-shallow waters and assess and their characteristics and spatio-temporal distributions.

2. MATERIAL AND METHODS

2.1. Survey area description

Data were collected in two coastal areas near Brest and Douarnenez located in the North of the Bay of Biscay (called Bay of Biscay area), and near Roscoff, in the Celtic Sea (called Celtic Sea area) (Figure 2a). In the Bay of Biscay area, two surveys were conducted in early summer 2020 and again in early autumn 2020. The transects designed for this area covered a total of 99.0 nautical miles (nmi) and the same transects were made during each season (See supplementary information, Figure S1a). In the Celtic Sea area, three surveys were conducted in spring 2020, summer 2020 and autumn 2020. The defined transects for this area covered a total of 63.7 nautical miles and the same transects were made during each season (See supplementary information, Figure S1b).

The transects have been designed to cover a range of 5 to 70 m bathymetry and different seafloor substrate types in order to assess the impact of environmental factors on pelagic fish distributions. A sampling effort was made in the ultra-shallow water areas (< 20m) as they are not traditionally surveyed. Surveys were made with two small vessels, the Albert Lucas and Neomysis, dedicated respectively for the study sites (in the North of Bay of Biscay and in the Celtic Sea) by the French Oceanographic Fleet (<https://www.flotteoceanographique.fr/Nos-moyens/Navires-engins-et-equipements-mobiles/Navires-de-station>). Due the availability of

these vessels, surveys were made only during the day. The speed of the vessels was set to 5 knots.

2.2. Recorded data

Water column was sampled along the transects by a Simrad M3 multibeam echosounder (Kongsberg M3 Sonar, 922-20007011), side mounted and used in vertical beaming. We used a multibeam echosounder with a high frequency (500 kHz, 128 beams in imaging mode, 120° swathe, 1.6° angular resolution, 30° vertical beam widths, detection up to 150 m) and a relatively short pulse duration (200 µs) giving a vertical resolution of 15 cm. The “Time Variable Gain” was adjusted in the M3 software following the manufacturer’s recommendations. In order to have absolute backscattering strength levels, the multibeam echosounder was previously calibrated *in situ* with a 22-mm tungsten sphere (Foote et al. 2005, Perrot et al. 2014). This operation was carried out at quayside in quiet weather. The calibration coefficients were calculated as in Cochrane et al. (2003). Hence, when the sphere’s echo was stable, the difference between the theoretical and measured responses of the calibration sphere was estimated. In addition, due to the difficulty of positioning the sphere in all beams, the equivalent two-way beam angle was calculated theoretically from the geometry of the elementary sensors of the transmitting and receiving antennas. For fish shoals, by making empirical comparisons with results from another calibrated split-beam echosounder (Simrad EK80, not presented in this study), our calibration was relevant.

Seawater temperature, salinity and dissolved oxygen were measured with Conductivity-Temperature-Depth (CTD) (SeaBird SBE *19plus* V2) casts at the extremities of the transects (See Supplementary Information Figures S4 and S6). Data on the seafloor substrates came from the Naval Hydrographic and Oceanographic Service (SHOM) in which the substrate were classified in different categories dependent on the grain size (rock, stone: > 20 mm, gravel: 2-20 mm, sand: 0.05-2 mm and mud: < 0.05 mm).

2.3. Acoustic data processing

For data processing, we adapted the Matecho open-source tool which is implemented in Matlab (Perrot et al. 2018). Matecho is an automated tool which allows fish shoal extractions. Routine analyses have been developed to import the multibeam data into Matecho and convert them into a HDF5 file format, detect the seafloor to create a bottom line which can be manually corrected as well as remove the noise coming from potential interferences. In particular, the bottom depth is estimated for each ping by Matecho only for the beam perpendicular to the bottom. Indeed, a disadvantage of using multibeam echosounder is the bottom echo, which reverberates in all beams at distances larger than the depth. Consequently, the analysed volume of water excludes the area where the bottom echo was reverberated (Figure 1). The shoal number in this area was nevertheless negligible. After applying the algorithms of bottom and noise detections on multibeam data, all filter results were manually checked using the graphical interface of Matecho. When necessary, we manually corrected the bottom line, as usually made for all acoustic data.

The automatic extraction process of shoals in Matecho for multibeam data is the same than for split-beam data (Perrot et al. 2018). It is based on the Movies3D algorithm (Trenkel et al. 2009) and used a threshold for the (i) volume backscattering strength S_v in decibels, (ii) a maximum along-ping-axis integration distance in m and (iii) a depth integration distances in m. For our analyses, these parameters were set to -55 dB for the S_v threshold, 0.61 m for the maximum integration length for the distance and 0.6 m for the maximum integration length for the depth. This high S_v threshold was chosen to facilitate automatic extraction of fish shoals and exclude macrozooplankton (Petitgas 2003, Brehmer et al. 2007). In addition, the extractions were made up to 0.3 m from the bottom. Compared to the former version of Matecho, a visualization of the beam fan was added (Figure 1) as well as a 3-D view of the

169 shoals. Hence, all extracted fish shoals have been visually checked using the graphical
170 interface.

171 To keep only the fish shoals and avoid big individual fish, only the extractions with a
172 minimum volume of 1 m^3 were kept for the analyses. Number of shoal detections were
173 recorded and corrected by the sampling effort per study sites (transects of 97.4 and 63.7 nmi
174 for the Bay of Biscay and Celtic Sea areas, respectively). The fish shoal descriptors
175 automatically calculated are the maximal height in m (along the depth-axis), maximal width
176 in m (along the athwart distance), total length in m (along the ping distance), surface in m^2 ,
177 volume in m^3 , percentage of holes under the threshold (Guillard et al. 2006, 2011, Paramo et
178 al. 2007), mean acoustic volume backscattering strength S_v in dB (MacLennan et al. 2002)
179 and mean distance from the bottom in m (Scalabrin & Massé 1993), expressed in percentage
180 to the bottom depth. In particular, the percentage of or holes was calculated by dividing the
181 number of samples under the extraction threshold in dB by the total number of samples from
182 the shoals and multiplied it by 100. Other information are also provided for each shoal like the
183 GPS coordinates (GPS with a circular error probable of 3m), the sampling time and the vessel
184 speed. Finally, the environmental factors such as the bottom depth (given by Matecho) and
185 the seafloor substrate types (from the SHOM data) where the shoals were detected were
186 added.

187 For species allocation, we tried to capture fish using longlines (having five hooks with a
188 shank of 3 cm) to identify the species responsible of observed detections in the multibeam
189 echosounder's field of view. The species, total fish length, and weight of each individual fish
190 was recorded before releasing it into the water. Probability of error in the shoal identification
191 was reduced as shoals were observed at the same localization and fishing identification
192 operation was done directly after the detection with the multibeam echosounder. The places to

do the species allocation were chosen based on the acoustic observations (numerous and/or large detections).

2.4. Statistical analysis

All statistical analyses were made with the R software (R version 3.6.2) (R Development Core Team 2019) and the significance threshold was set to 0.05. The number of detected shoals was analysed in function of the seafloor substrate types and the bathymetry, taking into account the frequency in which the different categories of seafloor substrates as well as the bathymetric ranges (< 10, 10-20, 20-30, 30-40, 40-50, 50-60 and 60-70 m) were encountered along the entire transects for both study sites.

Test correlations were made using the Spearman methods to analyse the correlations between fish shoal descriptors (mean acoustic volume backscattering strength S_v as well as the percentage of holes, their maximum width, maximum height, length, surface area and volume and the distance from the bottom in percentage). Fish shoal descriptors were also analysed in function of the environmental variables (bottom depth, season) using linear models (“lm” function). The seafloor substrate type was excluded from the model as it was correlated to the bathymetry (see Supplementary Information, Figure S2). The tested equation was:

$$Y_i = \beta_0 + \beta_1 Bathymetry_i + \beta_2 Season_i + \beta_3 Bathymetry_i \times Season_i + \varepsilon_i \quad \text{Eq. 1}$$

With Y_i the different fish shoal descriptors, β_0 to β_3 are the regression coefficients, Bathymetry and Season the environmental variables and ε_i the error independent and normally distributed. The maximal width, maximal height, length, surface and volume were log-transformed for the analyses. For each shoal descriptor, the fitting model was chosen based upon the Aikake Information Criterion (AIC) selection (Akaike 1974). Two models were considered different if their Δ_{AIC} was higher than 2, in which case the lowest AIC defined the best model. However, if the Δ_{AIC} was lower than 2, we used the Akaike weight

(Anderson et al. 2000). In addition, we also made multiple pairwise comparisons using t-test using the Bonferroni correction to further analyse the differences between seasons.

For those shoals where species was identified based on longline sampling, 3-D morphological characteristics of the fish shoals (maximal height, maximal width, length, surface, volume) as well as the percentage of holes, the mean acoustic volume backscattering strength S_v and the distance from bottom in percentage were compared for the same species and for the different areas where they were caught. In addition, we also compared the environmental factors (seafloor substrate, bottom depth). Finally, we performed a Multiple Factor Analysis (package R “FactoMineR”) (Pagès 2014) which allows to take into account both quantitative (fish shoal descriptors and bathymetry) and qualitative data (seafloor substrate type, season and study site) to compare the shoal groups identified by the species to the other shoals.

3. RESULTS

3.1. Physical-chemical parameters

For the Bay of Biscay area, mean surface (1-m depth) water temperature, salinity and dissolved oxygen were respectively $16.7 \pm 0.90^\circ\text{C}$, 34.3 ± 1.08 and $8.33 \pm 0.66 \text{ mg L}^{-1}$ in early summer and $17.8 \pm 0.83^\circ\text{C}$, 35.1 ± 0.40 and $7.86 \pm 0.32 \text{ mg L}^{-1}$ in early autumn (1-m depth) (see Supplementary information, Figures S3 and S4). The mean surface water temperature and salinity were significantly higher in early autumn compared to early summer 2020 whereas the dissolved oxygen was significantly lower (ANOVA, p -value < 0.05). Water temperature decreased with depths, *i.e.* the mean temperature difference being below 1.5°C between surface and bottom for both seasons. Dissolved oxygen decreased within the water column with depths (mean difference of 0.9 and 1.2 for both early summer and autumn respectively).

For the Celtic Sea area, mean surface water temperature, salinity and dissolved oxygen were respectively $14.6 \pm 0.67^{\circ}\text{C}$, 34.8 ± 0.13 and $7.67 \pm 0.34 \text{ mg L}^{-1}$ in spring, $16.0 \pm 0.75^{\circ}\text{C}$, 34.7 ± 0.42 and $7.0 \pm 0.7 \text{ mg L}^{-1}$ in summer and $14.9 \pm 0.52^{\circ}\text{C}$, 34.2 ± 1.89 and $6.45 \pm 0.22 \text{ mg L}^{-1}$ in autumn (1-m depth) (Supplementary information, Figures S5 and S6). Mean surface water temperature were significantly higher in summer compared to spring and autumn 2020 (Pairwise comparisons using t tests, p -values < 0.05) whereas no difference was found between spring and autumn 2020. No statistical differences were found for the mean surface water salinity between the seasons. Dissolved oxygen significantly decreased throughout the seasons (Pairwise comparisons using t tests, p -values < 0.05). Temperature slightly decreased with depths, i.e. the mean temperature difference being below 0.3°C between surface and bottom for all seasons in Celtic Sea area and dissolved oxygen was more homogeneous throughout the water column.

For both study sites, water temperature was higher close to the coast with a maximal difference of 3.2°C in summer for the Bay of Biscay area (see Supplementary information, Figures S4 and S6). Salinity did not vary with bathymetry, except in some particular locations near the coast where surface salinity was lower due to freshwater arrivals and was homogeneous throughout the water column (mean salinity differences below 1 between the surface and bottom).

3.2. Acoustic results

Shoal number and characteristics for the Bay of Biscay area

In Bay of Biscay area, 14.3 and 5.38 shoals nmi^{-1} having a minimum volume of 1 m^3 were detected in summer and autumn 2020, respectively (Figure 2b,c). The shoals were mainly located where the seafloor was composed of mud (21 %) or fine sand (20 %) in early summer 2020. However, shoals were mainly located above sand (31 %) and sand mixed with mud (24

264 %) in autumn 2020 (Figure 3a). In addition, the shoals were detected in similar bathymetry
265 during summer and autumn, except for depths under 10 m where 26 % of the detected shoals
266 where observed in summer compared to 3 % in autumn (Supplementary Information, Figure
267 S7a).

268 According to the AIC criteria and Akaike weights, the chosen models explaining
269 respectively the mean acoustic volume backscattering strength S_v of the shoals, the percentage
270 of holes, the distance from bottom in percentage and the maximal height included an
271 interaction effect between bathymetry and season (Table S2 given the AIC values and Akaike
272 weights per models in Supplementary Information). In particular, the acoustic energy
273 decreased with increasing bathymetry (Figures 4 and S8) and the acoustic energy was
274 significantly higher in summer than autumn (p -value < 0.05) (see Supplementary Information,
275 Table S1). The models explaining the length, maximal surface area and volume included
276 bathymetry and season without an interaction effect and the model explaining the maximal
277 width included only the season effect (Table S2).

278 Shoals in shallow waters were significantly larger (vertically and horizontally elongated
279 with larger surface areas and volumes) compared to shoals in deeper areas (Figures 4 and S8).
280 The maximal width, maximal height, length, maximal surface and volumes were all positively
281 correlated (> 66.7 , Spearman method, p -value < 0.05). They were also significantly closer to
282 the bottom in deeper areas compared to shallower areas as seen with the distance from bottom
283 in percentage. Shoals in shallow waters had also less holes as shown by the percentage of
284 holes which was inversely correlated to the acoustic volume backscattering strength S_v of the
285 shoals (-93.1 , Spearman method, p -value < 0.05). Finally, shoals were significantly smaller
286 (smaller length, maximal surface area, and volume) in autumn than in summer (Figure 5).

287 *Shoal number and characteristics for the Celtic Sea area*

For the Celtic Sea area, 10.3, 6.8 and 11.0 shoals nmi^{-1} having a minimum volume of 1 m^3 were detected in spring, summer and autumn 2020, respectively (Figure 2d,e,f). Shoals were mainly located above sand (46 %) and sand mixed with gravel (17 %) in spring 2020 whereas they were mainly located above gravel mixed with stone (59 %) and fine sand (17 %) in summer 2020 and above fine sand (28 %) and rock (19 %) in autumn 2020 (Figure 3b). In addition, 41 % of the detected shoals were observed in depths $<10 \text{ m}$ in summer compared to 0% in spring and autumn (Supplementary Information, Figure S7b).

According to the AIC criteria and Akaike weights, the chosen models explaining mean acoustic volume backscattering strength S_v of the shoals, the percentage of holes and the distance from bottom in percentage included an interaction effect between bathymetry and season (See Table S3 given the AIC values and Akaike weights per models in Supplementary Information). In particular, the mean acoustic volume backscattering strength S_v was significantly higher in autumn than in spring and summer but no differences were found between spring and summer (pairwise comparisons using t tests, p -values < 0.05). The models explaining the length, maximal height and maximal width included bathymetry and season without an interaction effect and the models explaining the maximal surface and volume included only the season effect (Table S3).

Shoals in shallower areas were significantly larger (length, width and height) compared to the shoals in deeper areas (Figures S9 to S11). The maximal width, maximal height, length, maximal surface and volumes were all positively correlated (> 55.1 , Spearman method, p -value < 0.05). Shoals in shallow waters had also less holes as shown by the percentage of holes which was inversely correlated to the acoustic volume backscattering strength S_v of the shoals (-93.2 , Spearman method, p -value < 0.05). The position in the water column varied with seasons as they were closer to the bottom in deeper areas compared to shallower areas in summer whereas they were closer to the surface in deeper areas in spring and autumn. Finally,

shoals were significantly smaller (smaller maximal width, maximal surface area and volume) in autumn than in summer and spring (Figure 5) but no differences were found between summer and spring (pairwise comparisons using t tests, p -values < 0.05). The length and maximal width were also significantly lower in autumn compared to spring and summer and in summer compared to spring for the length whereas it was higher in summer compared to spring for the maximal width (pairwise comparisons using t tests, p -values < 0.05).

3.3. Observations of coastal Atlantic mackerels

Fish measurements

Overall, we succeeded to fish in few places (Figure S1 for the localization of the fishing sites on both study sites). A total of 35 Atlantic mackerels (*S. scombrus*) were caught in the Bay of Biscay area, specifically in the Douarnenez bay, during the summer survey in 2020. Total lengths ranged from 15.0 cm to 41.5 cm (mean: 28.0 cm and standard-deviation (SD): 5.3) and wet weights ranged from 23.0 to 500.0 g (mean: 212.9 g and SD: 96.6) (Supplementary Information, Figure S12a). Fishing was not successful during the autumn survey.

A total of 56 Atlantic mackerels (*S. scombrus*) have been caught in the Celtic Sea area, specifically in the Lannion bay, during the summer survey in 2020. Total lengths ranged from 10.8 to 34.3 cm (mean: 24.5 cm and standard-deviation (SD): 6.2) and wet weights ranged from 15.0 to 340.0 g (mean: 152.4 g and SD: 91.6) (Supplementary Information, Figure S12b). The Atlantic mackerels caught in the Celtic Sea area were significantly smaller than the Atlantic mackerels caught in the Bay of Biscay area (t-test, p -value < 0.05). Fishing was not successful during the spring and autumn surveys.

Atlantic mackerels shoals

A total of 19 and 24 shoals were observed in the area where Atlantic mackerels (*S. scombrus*) were caught in the Bay of Biscay and Celtic Sea areas, respectively. In the Bay of Biscay area, these shoals were mainly located above fine sand (87 %) and all these shoals were found in depths of 10-20 m (87 %). In the Celtic Sea area, these shoals were also mainly located above fine sand (99 %) and in depths of 10-20 m (97%). Finally, we observed that the shoals were static which facilitated their catch and allowed a relevant species allocation.

Examples of echotraces of presumed Atlantic mackerel shoals can also be visualized in Supplementary Information (Figures S13 and S14). General shape of the echotraces were the same for both study areas. No statistical differences were found between the minimum and maximum width, minimum and maximum height, total length, maximum surface, volume and distance from bottom in percentage between the Atlantic mackerel echotraces found in both study areas (t-test, p -value > 0.05) (see Supplementary Information Figure S15). However, the mean acoustic volume backscattering strength S_v was significantly higher and the percentage of holes significantly lower for the echotraces in the Celtic Sea area compared to the Bay of Biscay area (p -value < 0.05), and these two variables were significantly inversely correlated (-93.8, Spearman test, p -value < 0.05).

The Multiple Factor Analysis indicated that the 3-D morphological characteristics of the shoal (maximal height, maximal width, length, surface and volume) fell out along the first axis and represented 16% of the total variance, whereas the variables related to the position of the shoal in the water column and the environmental variables fell out along the second axis and represented 13% of the total variance (Figure 6). All presumed shoals of Atlantic mackerels from both study areas were grouped together and the second axis was more discriminating since the distribution of the data had a low variability on this axis.

4. DISCUSSION

Pelagic fish shoal descriptors according to environmental gradients

Overall, fish shoals observed on the whole surveys are probably due to different fish species. Indeed, small fish species as European sprats (*Sprattus sprattus*), smelts (*Atherina sp.*) and sand eels (*Ammodytes tobianus*) are frequent in the studied areas (O’Connell & Fives 1995, Limborg et al. 2009) and account for important biomass. These small pelagic fish form inshore shoals and are important prey for top predators such as the European shag (*Phalacrocorax aristotelis*) or the Northern gannet (*Morus bassanus*) (Harris & Wanless 1991, Hamer et al. 2000). In addition, from personal exchanges with local fishermen, European sea bass (*Dicentrarchus labrax*), Atlantic horse mackerel (*Trachurus trachurus*), black seabream (*Spondyliosoma cantharus*), pollack (*Pollachius pollachius*), Atlantic mackerels, pout whiting (*Trisopterus luscus*) and Ballan wrasse (*Labrus bergylta*) are frequently present in these areas in French Brittany. In our study, Atlantic mackerels were indeed observed during the summer in both the Bay of Biscay and Celtic Sea areas in shallow waters.

For both study sites and for all seasons, the mean acoustic volume backscattering strength S_v linearly decreased with deeper depths. Similar results was found by Brehmer et al. (2006b) in the Mediterranean Sea showing larger acoustic densities where bathymetry was lowest (< 20m) compared to deeper areas. In addition, shoals were also significantly larger in shallow waters compared to deeper areas as seen with several 3-D shoal morphological variables (maximal width, maximal height, length, maximal surface and volume) depending on the study sites. Furthermore, detections of shoals in shallow areas with a bathymetry under 10 m were important during summer (26 % and 41 % for the Bay of Biscay and Celtic Sea areas respectively). Consequently, these results confirm the importance of surveying pelagic fish populations as they could count for important biomass in shallow waters, which are not surveyed by the conventional research vessels in order to enhance a better management of pelagic fish populations.

Different assumptions could be made to explain the decrease of the fish shoal descriptors with deeper depths. Firstly, the efficiency of which an individual organism scatters sound varies with its acoustic properties (e.g., swim bladder, backbone) as well as with its length, shape and behaviour (Benoit-Bird & Lawson 2016). Hence, species and sizes of the individuals could have varied with bathymetry as the acoustic energy was significantly impacted. In addition, shoal in shallow water areas had higher acoustic energy and a lower percentage of holes compared to deeper areas structures, suggesting that they were denser. Shoals were also closer to the bottom with increasing depths, especially in the North of Bay of Biscay. Shoal structure could vary to exhibit an anti-predator response, especially during daytime as they could be spotted more easily by predators (Gerlotto 1997, Nøttestad et al. 2001). Here, the shoals in ultra-shallow water areas could be more vulnerable to visual predators. However, shoal structure could also result from a predatory behaviour. For example, small pelagic fish could form schools for foraging purpose, especially during daytime (Gerlotto 1997, Brehmer et al. 2007). The influence of the water column depth on the shoal formation was also seen in Kaltenberg & Benoit-Bird (2009). Indeed, in shallow water areas, individuals may less disperse vertically which facilitates organization of individuals into shoals. However, in larger depths, the diel vertical migrations of zooplankton with a pattern of ascent at dusk and descent at dawn could explain that the shoals were mainly observed near the bottom during the day (Kaltenberg & Benoit-Bird, 2009).

Our study focused on pelagic shoals located in the water column, consequently shoals close to the bottom (under 0.3 m from bottom) were not considered. We observed that pelagic shoals were detected above all type of substrates but were predominant over sand and mud. Preference of fish schools for seabed with finer granulometry such as mud was observed for small pelagic fish species (D'Elia et al. 2009) and gravel and sand bottoms were also suggested as preferred habitats for shoals in several studies (Maravelias et al. 2000, Manik et

al. 2006). In addition, shoals were found in all bathymetric ranges but numerous shoals were detected in areas with bathymetry under < 10 m only during summer, which could then represent suitable areas during this period. Overall, understanding the combined environmental factors, which structure the fish species distributions, is challenging as species–environmental relationships can be remarkably complex in shallow waters (Beck et al. 2001, Staveley et al. 2017). In the future, the development of more autonomous techniques to directly classify the seabed and analyse fish shoals using multibeam echosounders could improve the understanding of the distribution patterns of fish in different shallow-water habitats (Lamouret et al. 2019). Other environmental variables could influence the fish distribution in shallow waters. Especially, we observed that surface sea water temperature was higher in shallower areas close to the coast compared to deeper areas, particularly during summer in both study areas. Finally, additional data like chlorophyll-*a* concentration would be relevant to analyse at small-scale to study the pelagic fish distribution (Diogoul et al. 2021).

Data showed a seasonal variability as the mean morphological characteristics of the shoals (width, height, length, surface and volume) significantly decreased in autumn compared to spring and summer 2020 for both study sites. The motivation to form shoals could vary considerably between species and relies on different reasons (reproduction, feeding, size of the individuals) (Freon & Misund 1999, Pavlov & Kasumyan 2000) which could vary seasonally. Indeed, at the beginning of the reproductive season, clupeid fishes such as Atlantic herring (*Clupea harengus*) are known to regularly mass in large shoals for spawning at specific times and locations which could be due to initial conditions on population density and external stimuli such as light level (Makris et al. 2009). For Atlantic mackerels in Celtic Sea and west of Ireland, Dawson (1986) observed that the size of the individuals in populations decreased throughout the spawning season and, at the end of the spawning season,

predominantly young fish remain in the populations. For European sardine in Atlantic, spatio-temporal variability in school morphology was related to length and age of individuals of the populations (Muiño & Carrera-López 2007).

Changes in the fish communities according to the bathymetry and with the seasons of the surveys could also have occurred as interactions between those two variables were found for several fish shoal descriptors, especially for the mean acoustic volume backscattering strength (S_v). Indeed, several pelagic species are known to exhibit migration patterns. For example, distribution of European sea bass changes seasonally as they migrate between feeding and spawning grounds (Quayle et al. 2009). Furthermore, migratory species such as anchovies, sprats, sardines, mackerels often exhibit schooling behaviour (Pavlov & Kasumyan 2000) and their migration were suggested to be driven by abiotic parameters like sea surface temperatures (Berge et al. 2015, Diankha et al. 2015, Twatwa et al. 2005). However, the effects of environmental factors on their migration at small local scales, especially in ultra-shallow water areas are still poorly understood. Brehmer et al. (2006a) suggested that decrease of temperature and salinity could have influenced the migration of several fish species including *D. labrax* in two lagoons in the Mediterranean Sea during the autumn migration period. Here, we also observed significant seasonal variations in several abiotic parameters (sea water temperature, salinities and dissolved oxygen). Especially, the dissolved oxygen decreased throughout the seasons for both study sites which could have also impacted the spatial distribution of fish (Roman et al. 2019).

Atlantic mackerel shoals in ultra-shallow waters

During the surveys, Atlantic mackerels were observed in both the Bay of Biscay and Celtic Sea areas during summer in ultra-shallow waters. The Atlantic mackerels were concentrated at a narrow range of depth (10-20m) near the coast and above the same substrate (fine sand) for both study areas. They were caught at the end of their spawning period

(Dawson 1986) which is consistent as we observed both juvenile Atlantic mackerels (less than 28.7 cm) and adults (higher than 28.7 cm) (Froese & Pauly 2021). Indeed, Atlantic mackerels are known to spawn from January to July along the continental shelf edge from Portuguese to Scottish waters and in the North Sea. In autumn, less shoal detections were observed in this same areas. This could suggest that the shoals dispersed or move toward deeper areas, or that the populations were lower at this season as mackerels migrate toward the North Sea and Norwegian Sea after the spawning season (Reid et al. 1997, Bruge et al. 2016).

Furthermore, the 3-D morphological characteristics of the mackerel shoals were similar between the two study sites as no significant differences were found for the width, height, length, surface and volume of the shoals. All presumed shoals of Atlantic mackerels were grouped together according to the Multiple Factor Analysis highlighting the similarities of the shoals between both study areas. The position of the shoal in the column water as well as the environmental variables were the most discriminant variables. However, Atlantic mackerel shoals were denser in the Celtic Sea area compared to the Bay of Biscay area as the S_v was higher and the percentages of holes inside the detections lower. As mackerels were significantly smaller in Celtic Sea than in the North of Bay of Biscay, the higher energetic acoustic values could not be directly related to their size. However, fish abundances could have been larger in Celtic Sea. Another possible explanation is that avoidance reaction to the boat could have been higher in the Celtic Sea areas as the boat was larger and louder compared to the one used in the North of Bay of Biscay (Draštík & Kubečka, 2005, Brehmer et al. 2019b). Hence, the same boat should be used for further surveys to avoid this bias. In addition, as longlines used to catch mackerels does not provide exhaustive view of the shoals, the use of alternative methods such as underwater cameras (Langlois et al. 2010, Mallet & Pelletier, 2014, Brehmer et al. 2019a) would be highly interested in shallow waters where visibility is improved compared to larger depth.

Atlantic mackerels are supposed to be highly sensitive to environmental conditions such as sea water temperature (Jansen et al. 2012, Hughes et al. 2014). In our study, mean sea surface temperature during summer was 16.7°C in the North of Bay of Biscay and 16.0°C in the Celtic Sea respectively which was consistent to the fact that they could be present in temperatures up to 15°C, although they are supposed to prefer areas with temperatures between 9 and 13°C (Olafsdottir et al. 2019). Observations of mackerel schools during the summer feeding migration between the surface and a depth of 40 m were suggested to be due to temperature preferences as well as their foraging strategy and food availability (Godø et al. 2004, Nøttestad et al. 2016). Especially, shoals were found static in both areas and Atlantic mackerels, as they were supposed to reduce their swimming speed when they reach the most productive area (Nøttestad et al. 2016). Overall, our data could help understanding the Atlantic mackerels population dynamics in ultra-shallow waters where they are not traditionally surveyed (Brehmer et al. 2006b) which is important for conservation. Indeed, observations of shifted distributions of the mackerel populations in response to climate change were already observed (Berge et al. 2015, Bruge et al. 2016).

5. CONCLUSION

Overall, our study showed the interest of surveying fish populations in shallow waters areas and especially ultra-shallow waters (< 20m) using a multibeam echosounder. Especially, numerous shoals were detected in ultra-shallow waters and could account for important biomass. Seasonal variations were also observed on the maximal surfaces and volumes of shoals as they significantly decreased in autumn for both study sites. In addition, observations of Atlantic mackerels in ultra-shallow waters in summer were made in both study sites and exhibit similar shoal characteristics, which could be related to their feeding strategy. Finally, it should be noted that the first surveys in both study sites were made when the restrictions due to the COVID-19 pandemic were being lifted. Especially, the lock down may have

resulted in reduced anthropogenic pressures and especially fisheries pressure. Hence, a long-term survey over several years would be necessary to investigate if the fish shoal descriptors during this period were similar to other years. Finally, the multibeam echosounder is a workable and relevant tool for setting up long-term surveying of pelagic fish in ultra-shallow waters such as coastal and estuarine areas which are potentially exposed to high anthropogenic pressures. We thus suggest the interest of this method to better assess pelagic fish ecological status and enable conservation management.

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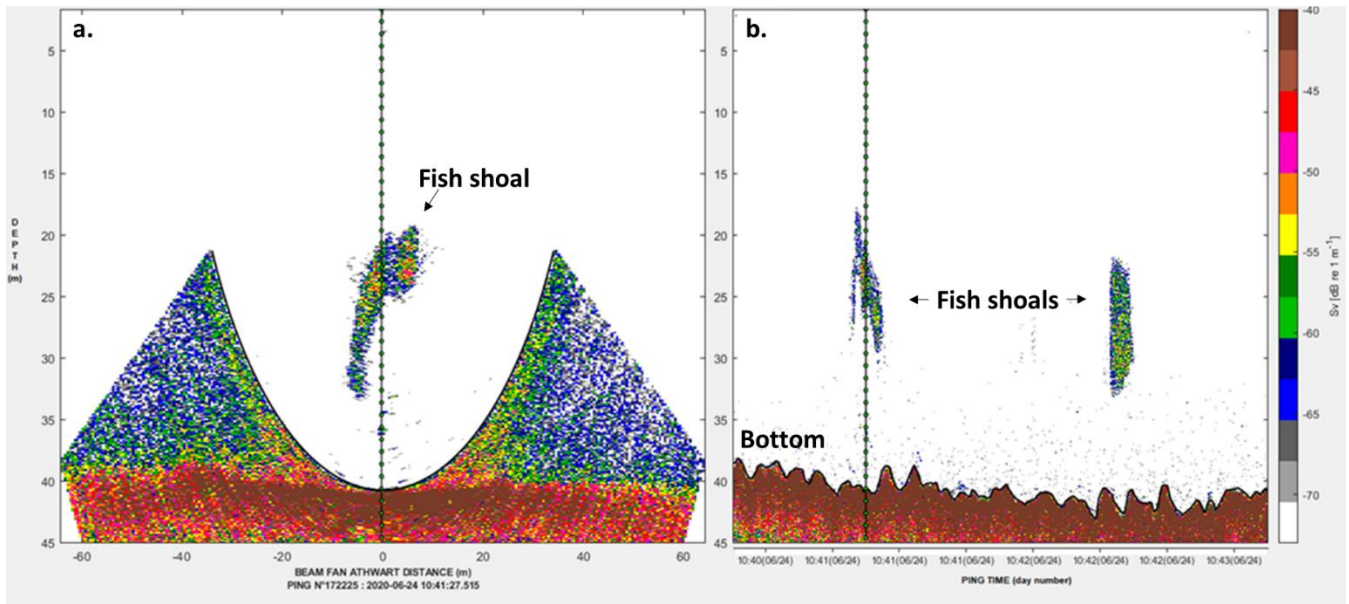
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8. FIGURES AND TABLES

Figure 1. Screenshot of the Matecho software (Perrot et al. 2018), an automated tool which allows fish shoal extractions using data from the Simrad M3 multibeam echosounder (frequency: 500 kHz). Visualization of a water column ping including a fish shoal (a) and of two fish shoals along several pings (b). The black line represent the bottom line on the panel b. The colored scale represents the S_v values.

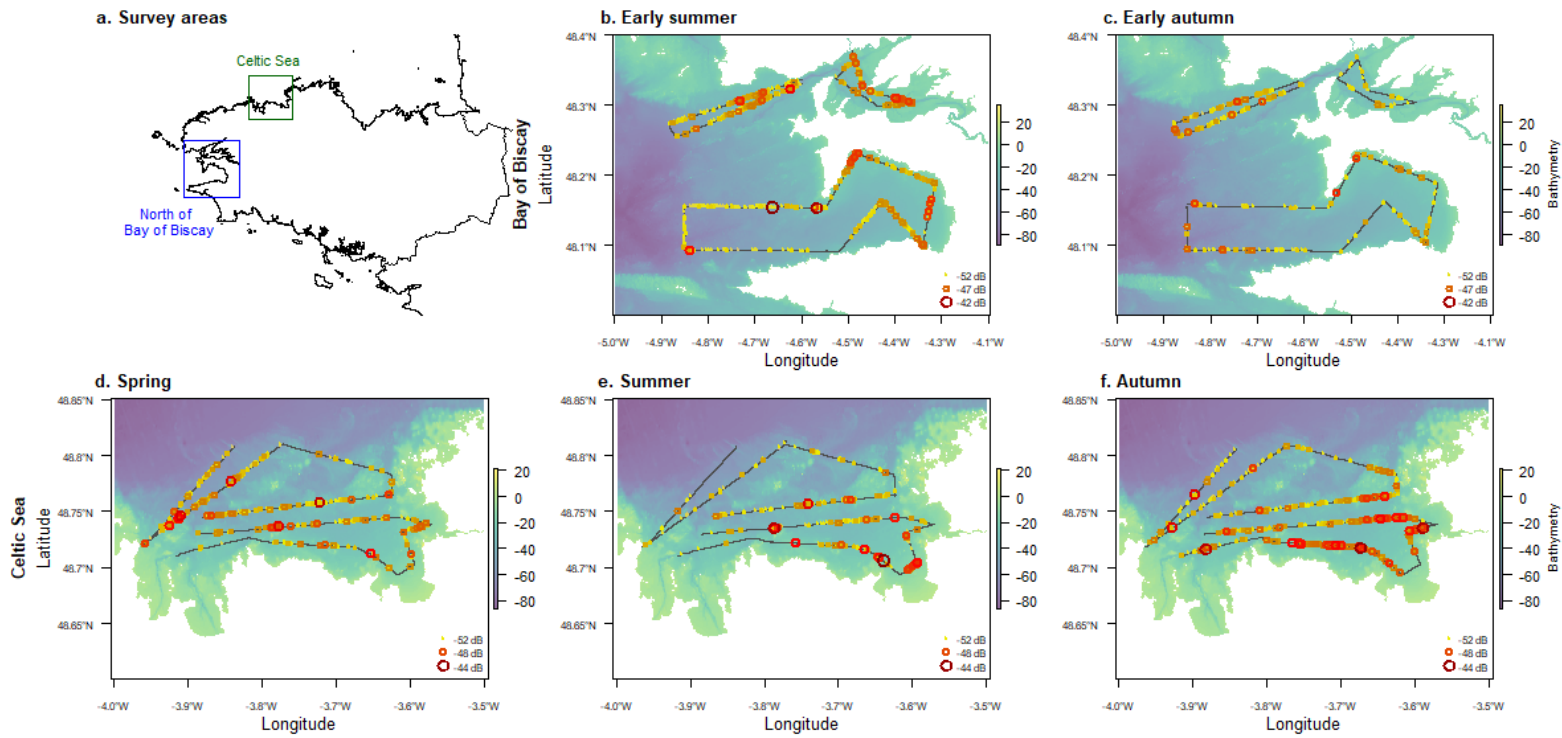


Figure 2. Detected shoals observed by the multibeam echosounder during the surveys in 2020. Surveys areas in the North of the Bay of Biscay and in the Celtic Sea can be viewed on panel a. For the Bay of Biscay area, the b and c panels represent the detected shoals respectively during the beginning of the summer and autumn 2020. For Celtic Sea area, panels d, e and f represent the detected shoals respectively during spring, summer and autumn 2020. Circle sizes and colors are dependent on the acoustic volume backscattering strength S_v (dB). Only shoals with a minimum volume of 1 m^3 was represented in order to avoid single targets. Colors of the map are dependent on the bathymetry.

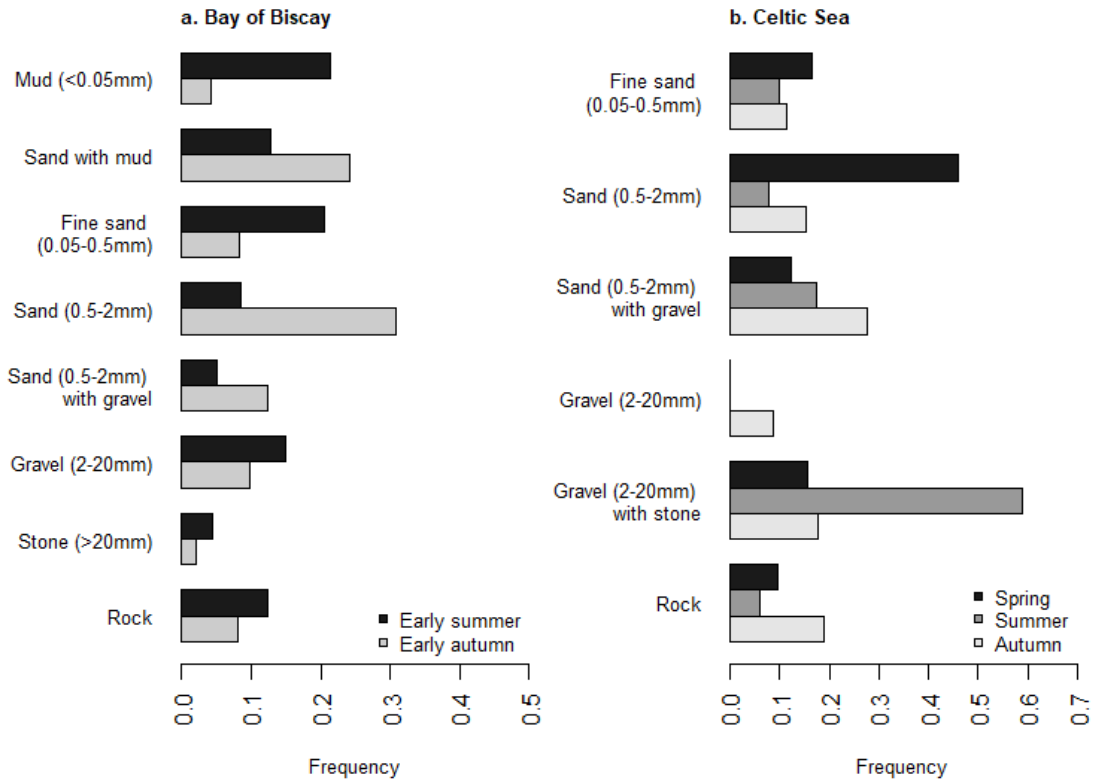


Figure 3. Frequency of occurrence of detected shoals according to seafloor substrate type in the North of Bay of Biscay (a) and in the Celtic Sea (b). Colors of the barplots depend on the surveyed season. Results were reported taking into account the frequency in which the different categories of the seafloor substrate type were encountered along the entire transects.

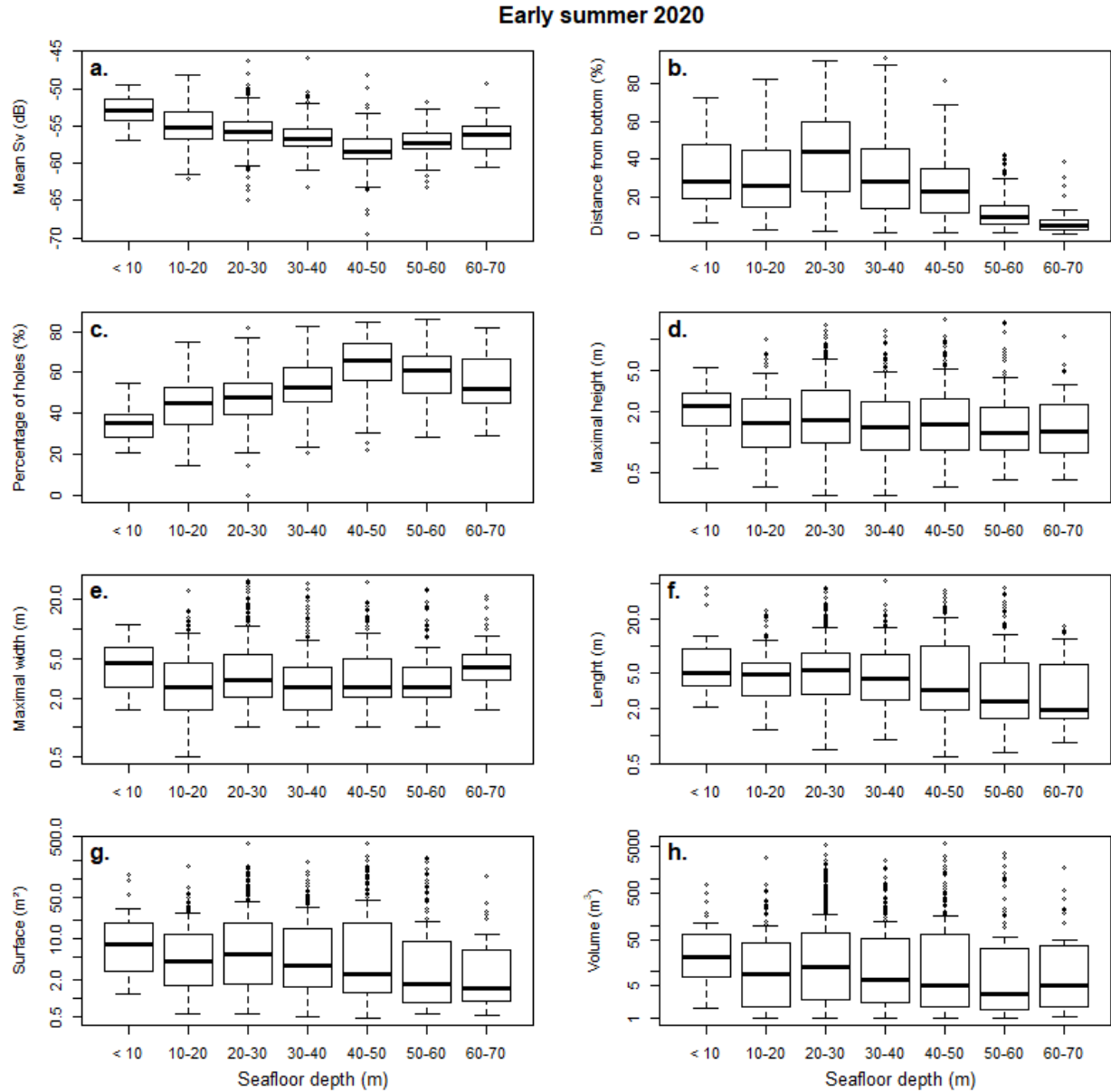


Figure 4. Fish shoal characteristics as a function of the seafloor depth (m) for the shoal detected during early summer 2020 in the North of Bay of Biscay. Graphs (a) represent the mean volume backscattering strength S_v in dB, (b) the distance from bottom in percentage compared to the bottom depth, (c) the percentage of holes, (d) the maximal height in m, (e) the maximal width in m, (f) the total length in m, (g) the maximum surface in m^2 and (h) the volume in m^3 . Results for the height, width, total length, maximum surface and volume are presented in log. The boxplots present the median, the 25th and 75th percentiles with a 1.5 interquartile range and the outliers.

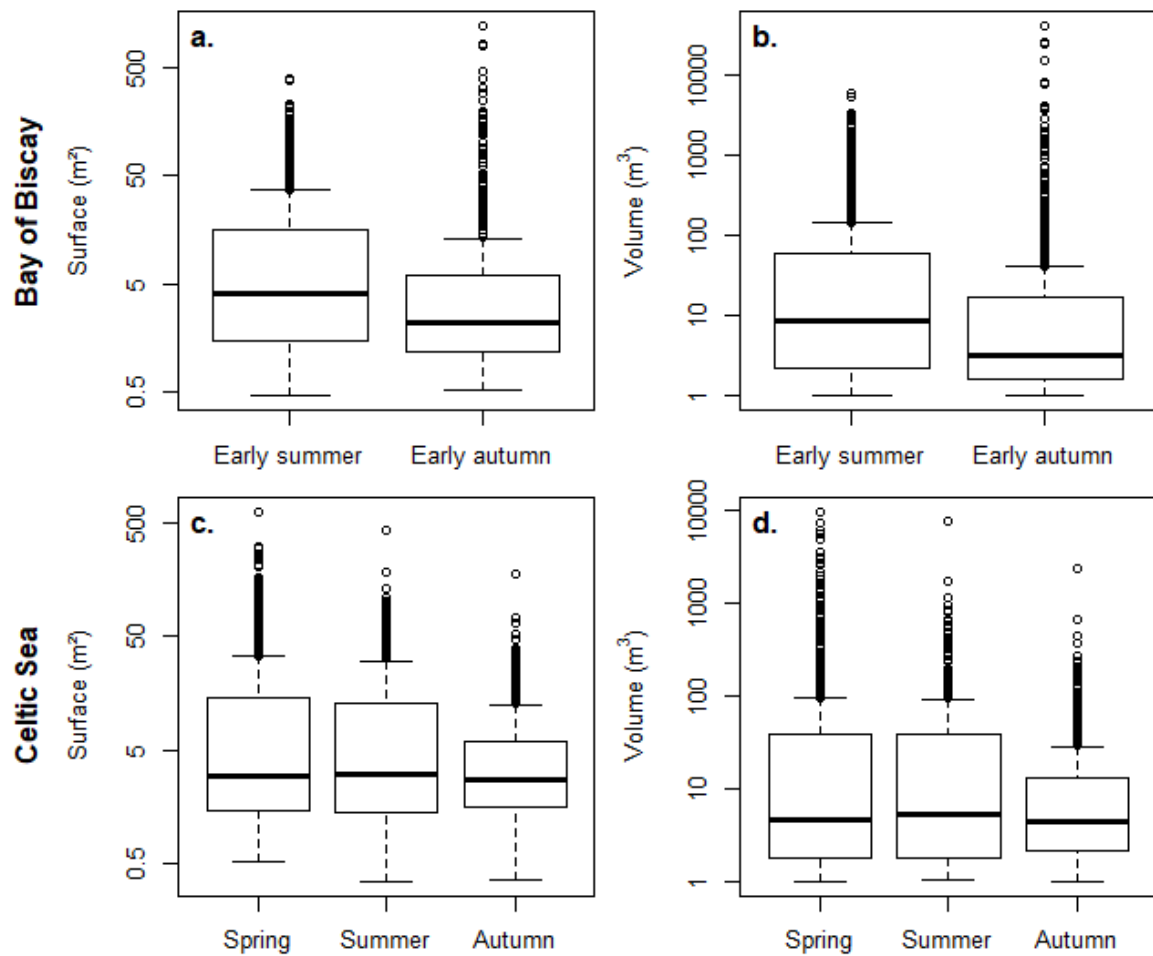


Figure 5. Fish shoal characteristics as a function of the seasons. The top panels represent the maximum surface (a) and the volume (b) for the Bay of Biscay area. The bottom panels represent the maximum surface (c) and the volume (d) for the Celtic Sea area. The boxplots present the median, the 25th and 75th percentiles with a 1.5 interquartile range and the outliers.

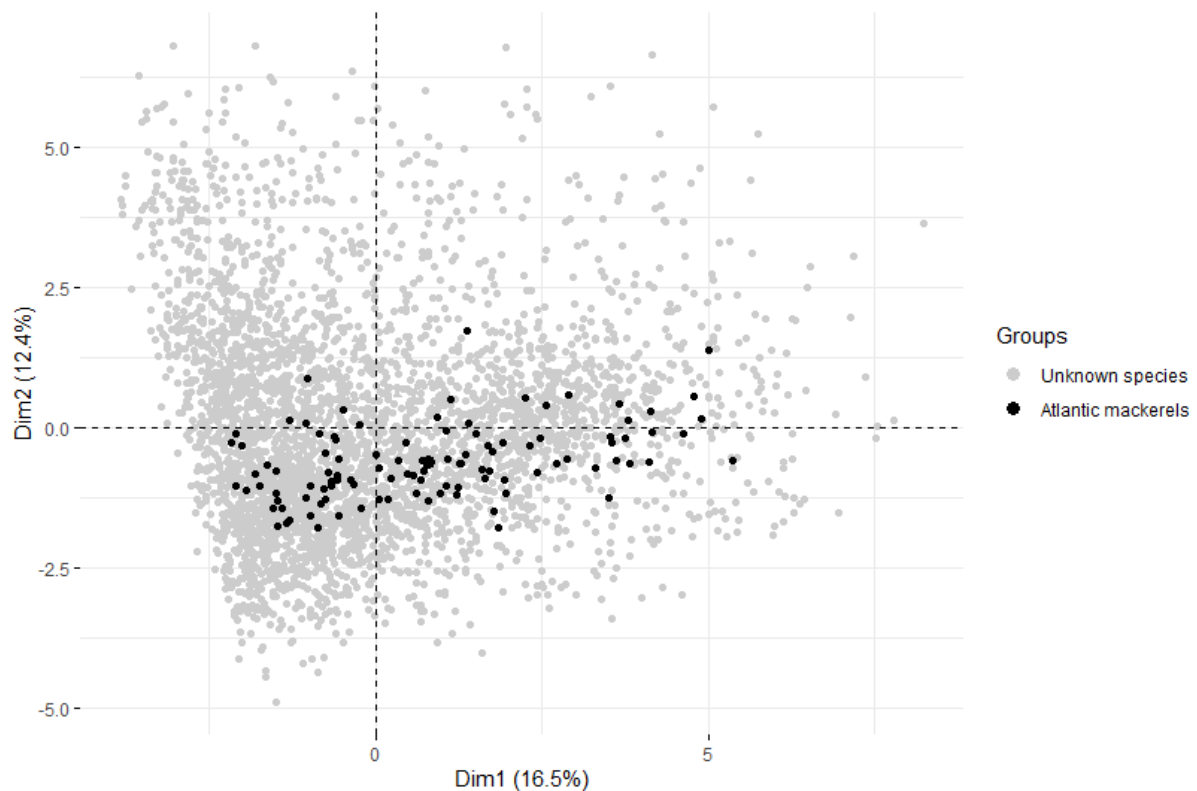


Figure 6. Multiple Factor Analysis taking into account both quantitative and qualitative data: all the fish shoal descriptors as well as the environmental variables (bottom depth, seafloor substrate type, season and study site). The maximal height, maximal width, length, surface and volume fell out along the first axis whereas the variables related to the position of the shoal in the water column and the environmental variables fell out along the second axis.