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

Viviane David, Anne Mouget, Yannick Perrot, Loïc Le Goff, Pierre Thiriet, Ndagoue Diogoul, Eric Feunteun, Anthony Acou, Patrice Brehmer

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

3  
4 Viviane David<sup>1,2,\*</sup>, Anne Mouget<sup>4,5</sup>, Yannick Perrot<sup>2</sup>, Loïc Le Goff<sup>1</sup>, Pierre Thiriet<sup>1</sup>, Ndague  
5 Diogoul<sup>2,3</sup>, Eric Feunteun<sup>4,5</sup>, Anthony Acou<sup>1</sup>, Patrice Brehmer<sup>2,6</sup>

6  
7 <sup>1</sup> UMS 2006 Patrimoine Naturel – OFB, CNRS, MNHN – Station Marine de Dinard,  
8 CRESCO, 38 rue de Port Blanc, Dinard, France

9 <sup>2</sup> IRD, Univ Brest, CNRS, Ifremer, UMR Lemar, Plouzané, France

10 <sup>3</sup> ISRA, CRODT, PRH, BP 2221, Dakar, Senegal

11 <sup>4</sup> Laboratoire BOREA (Museum National d’Histoire Naturelle, CNRS, Sorbonne Université,  
12 IRD, UniCaen, Univ Antilles Guadeloupe), 57 rue de cuvier, 75005 Paris, France

13 <sup>5</sup> Station Marine de Dinard, CRESCO, 38, rue du port Blanc, 35800 Dinard, France

14 <sup>6</sup> Commission Sous Régional des Pêches, CSRP, SRFC, Dakar, Sénégal

15  
16 \*Corresponding author: [viviane.david@mnhn.fr](mailto:viviane.david@mnhn.fr)

17  
18                   **Abstract**

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

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

35

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

38

## 39 **1. INTRODUCTION**

40 Shallow coastal waters, and in particular ultra-shallow waters (< 20m), provide many  
41 biological and ecological functions for fish species at different stages and throughout their life  
42 cycle (Beck et al. 2001, Franco et al. 2006, Pihl et al. 2007). Numerous fish species (sardines,  
43 European anchovies, Atlantic mackerels, etc.) are also known to migrate to coastal and  
44 estuarine areas for various reasons which can vary extensively between fish species, *e.g.*, for  
45 spawning, feeding reasons or environmental conditions (Bellier et al. 2007, Morais et al.  
46 2010, Nøttestad et al. 2016). In addition, shallow waters are subjected to many anthropogenic

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

58 Split-beam echosounders associated with trawl catches are widely used to assess pelagic  
59 fish population distributions and abundances in order to estimate fish stocks in offshore  
60 waters (Doray et al. 2010, 2018, Demer et al. 2012). However, the use of multibeam  
61 echosounders has gained increasing attention (Melvin & Cochrane 2015, Brehmer et al.  
62 2019a, Lamouret et al. 2019). They have been developed to operate with frequencies ranging  
63 from 12 up to >500 kHz allowing them to be used in different water depths from shallow to  
64 deep waters (Colbo et al. 2014), and could transmit either continuous wave (CW) signals or  
65 frequency modulated (FM) signals. Multibeam echosounders sample a larger volume of  
66 waters compared to split-beam echosounders and should provide more information about the  
67 distribution and movement of targets in the field of view (Gerlotto et al. 1999, Trenkel et al.  
68 2008). In particular, in ultra-shallow waters (< 20m), where the sampled volume is restricted  
69 by the bottom, sampling a higher volume is interesting. Multibeam echosounders have thus  
70 been used to survey schooling fish on artificial and natural reefs (Holland et al. 2021). They  
71 could also limit the bias in fish biomass estimations due to avoidance reaction to boats (Reid

72 2000). This could be particularly relevant in shallow waters where the avoidance reaction are  
73 supposed to be higher than in deeper areas due to the noise and visual effects of the vessel  
74 (Draštík & Kubečka 2005, Brehmer et al. 2019b). Finally, multibeam echosounders allow 3-D  
75 observations of the entire fish shoals which could have implications for behaviour studies  
76 (Reid 2000) as well as help for species identification (Guillard et al. 2011).

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

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

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

## 102 **2. MATERIAL AND METHODS**

### 103 **2.1. Survey area description**

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

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

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

## 122 **2.2. Recorded data**

123 Water column was sampled along the transects by a Simrad M3 multibeam echosounder  
124 (Kongsberg M3 Sonar, 922-20007011), side mounted and used in vertical beaming. We used  
125 a multibeam echosounder with a high frequency (500 kHz, 128 beams in imaging mode, 120°  
126 swathe, 1.6° angular resolution, 30° vertical beam widths, detection up to 150 m) and a  
127 relatively short pulse duration (200  $\mu$ s) giving a vertical resolution of 15 cm. The “Time  
128 Variable Gain” was adjusted in the M3 software following the manufacturer’s  
129 recommendations. In order to have absolute backscattering strength levels, the multibeam  
130 echosounder was previously calibrated *in situ* with a 22-mm tungsten sphere (Foote et al.  
131 2005, Perrot et al. 2014). This operation was carried out at quayside in quiet weather. The  
132 calibration coefficients were calculated as in Cochrane et al. (2003). Hence, when the sphere’s  
133 echo was stable, the difference between the theoretical and measured responses of the  
134 calibration sphere was estimated. In addition, due to the difficulty of positioning the sphere in  
135 all beams, the equivalent two-way beam angle was calculated theoretically from the geometry  
136 of the elementary sensors of the transmitting and receiving antennas. For fish shoals, by  
137 making empirical comparisons with results from another calibrated split-beam echosouder  
138 (Simrad EK80, not presented in this study), our calibration was relevant.

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

### 145        **2.3. Acoustic data processing**

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

159        The automatic extraction process of shoals in Matecho for multibeam data is the same  
160        than for split-beam data (Perrot et al. 2018). It is based on the Movies3D algorithm (Trenkel  
161        et al. 2009) and used a threshold for the (i) volume backscattering strength  $S_v$  in decibels, (ii)  
162        a maximum along-ping-axis integration distance in m and (iii) a depth integration distances in  
163        m. For our analyses, these parameters were set to -55 dB for the  $S_v$  threshold, 0.61 m for the  
164        maximum integration length for the distance and 0.6 m for the maximum integration length  
165        for the depth. This high  $S_v$  threshold was chosen to facilitate automatic extraction of fish  
166        shoals and exclude macrozooplankton (Petitgas 2003, Brehmer et al. 2007). In addition, the  
167        extractions were made up to 0.3 m from the bottom. Compared to the former version of  
168        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  $1 \text{ m}^3$  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  $\text{m}^2$ ,  
177 volume in  $\text{m}^3$ , 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

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

#### 195 **2.4. Statistical analysis**

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

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

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

209 With  $Y_i$  the different fish shoal descriptors,  $\beta_0$  to  $\beta_3$  are the regression coefficients,  
210 Bathymetry and Season the environmental variables and  $\varepsilon_i$  the error independent and  
211 normally distributed. The maximal width, maximal height, length, surface and volume were  
212 log-transformed for the analyses. For each shoal descriptor, the fitting model was chosen  
213 based upon the Aikake Information Criterion (AIC) selection (Akaike 1974). Two models  
214 were considered different if their  $\Delta_{AIC}$  was higher than 2, in which case the lowest AIC  
215 defined the best model. However, if the  $\Delta_{AIC}$  was lower than 2, we used the Akaike weight

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

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

## 228 **3. RESULTS**

### 229 **3.1. Physical-chemical parameters**

230 For the Bay of Biscay area, mean surface (1-m depth) water temperature, salinity and  
231 dissolved oxygen were respectively  $16.7 \pm 0.90^\circ\text{C}$ ,  $34.3 \pm 1.08$  and  $8.33 \pm 0.66 \text{ mg L}^{-1}$  in  
232 early summer and  $17.8 \pm 0.83^\circ\text{C}$ ,  $35.1 \pm 0.40$  and  $7.86 \pm 0.32 \text{ mg L}^{-1}$  in early autumn (1-m  
233 depth) (see Supplementary information, Figures S3 and S4). The mean surface water  
234 temperature and salinity were significantly higher in early autumn compared to early summer  
235 2020 whereas the dissolved oxygen was significantly lower (ANOVA,  $p$ -value  $< 0.05$ ). Water  
236 temperature decreased with depths, *i.e.* the mean temperature difference being below  $1.5^\circ\text{C}$   
237 between surface and bottom for both seasons. Dissolved oxygen decreased within the water  
238 column with depths (mean difference of 0.9 and 1.2 for both early summer and autumn  
239 respectively).

240 For the Celtic Sea area, mean surface water temperature, salinity and dissolved oxygen  
241 were respectively  $14.6 \pm 0.67^{\circ}\text{C}$ ,  $34.8 \pm 0.13$  and  $7.67 \pm 0.34 \text{ mg L}^{-1}$  in spring,  $16.0 \pm 0.75^{\circ}\text{C}$ ,  
242  $34.7 \pm 0.42$  and  $7.0 \pm 0.7 \text{ mg L}^{-1}$  in summer and  $14.9 \pm 0.52^{\circ}\text{C}$ ,  $34.2 \pm 1.89$  and  $6.45 \pm 0.22$   
243  $\text{mg L}^{-1}$  in autumn (1-m depth) (Supplementary information, Figures S5 and S6). Mean surface  
244 water temperature were significantly higher in summer compared to spring and autumn 2020  
245 (Pairwise comparisons using t tests,  $p$ -values  $< 0.05$ ) whereas no difference was found  
246 between spring and autumn 2020. No statistical differences were found for the mean surface  
247 water salinity between the seasons. Dissolved oxygen significantly decreased throughout the  
248 seasons (Pairwise comparisons using t tests,  $p$ -values  $< 0.05$ ). Temperature slightly decreased  
249 with depths, i.e. the mean temperature difference being below  $0.3^{\circ}\text{C}$  between surface and  
250 bottom for all seasons in Celtic Sea area and dissolved oxygen was more homogeneous  
251 throughout the water column.

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

## 258 **3.2. Acoustic results**

### 259 *Shoal number and characteristics for the Bay of Biscay area*

260 In Bay of Biscay area, 14.3 and 5.38 shoals  $\text{nmi}^{-1}$  having a minimum volume of  $1 \text{ m}^3$  were  
261 detected in summer and autumn 2020, respectively (Figure 2b,c). The shoals were mainly  
262 located where the seafloor was composed of mud (21 %) or fine sand (20 %) in early summer  
263 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*

288 For the Celtic Sea area, 10.3, 6.8 and 11.0 shoals  $\text{nmi}^{-1}$  having a minimum volume of  $1 \text{ m}^3$   
289 were detected in spring, summer and autumn 2020, respectively (Figure 2d,e,f). Shoals were  
290 mainly located above sand (46 %) and sand mixed with gravel (17 %) in spring 2020 whereas  
291 they were mainly located above gravel mixed with stone (59 %) and fine sand (17 %) in  
292 summer 2020 and above fine sand (28 %) and rock (19 %) in autumn 2020 (Figure 3b). In  
293 addition, 41 % of the detected shoals were observed in depths  $<10 \text{ m}$  in summer compared to  
294 0% in spring and autumn (Supplementary Information, Figure S7b).

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

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

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

### 319 **3.3. Observations of coastal Atlantic mackerels**

#### 320 *Fish measurements*

321 Overall, we succeeded to fish in few places (Figure S1 for the localization of the fishing  
322 sites on both study sites). A total of 35 Atlantic mackerels (*S. scombrus*) were caught in the  
323 Bay of Biscay area, specifically in the Douarnenez bay, during the summer survey in 2020.  
324 Total lengths ranged from 15.0 cm to 41.5 cm (mean: 28.0 cm and standard-deviation (SD):  
325 5.3) and wet weights ranged from 23.0 to 500.0 g (mean: 212.9 g and SD: 96.6)  
326 (Supplementary Information, Figure S12a). Fishing was not successful during the autumn  
327 survey.

328 A total of 56 Atlantic mackerels (*S. scombrus*) have been caught in the Celtic Sea area,  
329 specifically in the Lannion bay, during the summer survey in 2020. Total lengths ranged from  
330 10.8 to 34.3 cm (mean: 24.5 cm and standard-deviation (SD): 6.2) and wet weights ranged  
331 from 15.0 to 340.0 g (mean: 152.4 g and SD: 91.6) (Supplementary Information, Figure  
332 S12b). The Atlantic mackerels caught in the Celtic Sea area were significantly smaller than  
333 the Atlantic mackerels caught in the Bay of Biscay area (t-test,  $p$ -value  $< 0.05$ ). Fishing was  
334 not successful during the spring and autumn surveys.

#### 335 *Atlantic mackerels shoals*

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

342 Examples of echotraces of presumed Atlantic mackerel shoals can also be visualized in  
343 Supplementary Information (Figures S13 and S14). General shape of the echotraces were the  
344 same for both study areas. No statistical differences were found between the minimum and  
345 maximum width, minimum and maximum height, total length, maximum surface, volume and  
346 distance from bottom in percentage between the Atlantic mackerel echotraces found in both  
347 study areas (t-test,  $p$ -value  $> 0.05$ ) (see Supplementary Information Figure S15). However, the  
348 mean acoustic volume backscattering strength  $S_v$  was significantly higher and the percentage  
349 of holes significantly lower for the echotraces in the Celtic Sea area compared to the Bay of  
350 Biscay area ( $p$ -value  $< 0.05$ ), and these two variables were significantly inversely correlated (-  
351 93.8, Spearman test,  $p$ -value  $< 0.05$ ).

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

#### 359 **4. DISCUSSION**

360 *Pelagic fish shoal descriptors according to environmental gradients*



361 Overall, fish shoals observed on the whole surveys are probably due to different fish  
362 species. Indeed, small fish species as European sprats (*Sprattus sprattus*), smelts (*Atherina*  
363 *sp.*) and sand eels (*Ammodytes tobianus*) are frequent in the studied areas (O'Connell & Fives  
364 1995, Limborg et al. 2009) and account for important biomass. These small pelagic fish form  
365 inshore shoals and are important prey for top predators such as the European shag  
366 (*Phalacrocorax aristotelis*) or the Northern gannet (*Morus bassanus*) (Harris & Wanless  
367 1991, Hamer et al. 2000). In addition, from personal exchanges with local fishermen,  
368 European sea bass (*Dicentrarchus labrax*), Atlantic horse mackerel (*Trachurus trachurus*),  
369 black seabream (*Spondyliosoma cantharus*), pollack (*Pollachius pollachius*), Atlantic  
370 mackerels, pout whiting (*Trisopterus luscus*) and Ballan wrasse (*Labrus bergylta*) are  
371 frequently present in these areas in French Brittany. In our study, Atlantic mackerels were  
372 indeed observed during the summer in both the Bay of Biscay and Celtic Sea areas in shallow  
373 waters.

374 For both study sites and for all seasons, the mean acoustic volume backscattering strength  
375  $S_v$  linearly decreased with deeper depths. Similar results was found by Brehmer et al. (2006b)  
376 in the Mediterranean Sea showing larger acoustic densities where bathymetry was lowest (<  
377 20m) compared to deeper areas. In addition, shoals were also significantly larger in shallow  
378 waters compared to deeper areas as seen with several 3-D shoal morphological variables  
379 (maximal width, maximal height, length, maximal surface and volume) depending on the  
380 study sites. Furthermore, detections of shoals in shallow areas with a bathymetry under 10 m  
381 were important during summer (26 % and 41 % for the Bay of Biscay and Celtic Sea areas  
382 respectively). Consequently, these results confirm the importance of surveying pelagic fish  
383 populations as they could count for important biomass in shallow waters, which are not  
384 surveyed by the conventional research vessels in order to enhance a better management of  
385 pelagic fish populations.

386 Different assumptions could be made to explain the decrease of the fish shoal descriptors  
387 with deeper depths. Firstly, the efficiency of which an individual organism scatters sound  
388 varies with its acoustic properties (e.g., swim bladder, backbone) as well as with its length,  
389 shape and behaviour (Benoit-Bird & Lawson 2016). Hence, species and sizes of the  
390 individuals could have varied with bathymetry as the acoustic energy was significantly  
391 impacted. In addition, shoal in shallow water areas had higher acoustic energy and a lower  
392 percentage of holes compared to deeper areas structures, suggesting that they were denser.  
393 Shoals were also closer to the bottom with increasing depths, especially in the North of Bay of  
394 Biscay. Shoal structure could vary to exhibit an anti-predator response, especially during  
395 daytime as they could be spotted more easily by predators (Gerlotto 1997, Nøttestad et al.  
396 2001). Here, the shoals in ultra-shallow water areas could be more vulnerable to visual  
397 predators. However, shoal structure could also result from a predatory behaviour. For  
398 example, small pelagic fish could form schools for foraging purpose, especially during  
399 daytime (Gerlotto 1997, Brehmer et al. 2007). The influence of the water column depth on the  
400 shoal formation was also seen in Kaltenberg & Benoit-Bird (2009). Indeed, in shallow water  
401 areas, individuals may less disperse vertically which facilitates organization of individuals  
402 into shoals. However, in larger depths, the diel vertical migrations of zooplankton with a  
403 pattern of ascent at dusk and descent at dawn could explain that the shoals were mainly  
404 observed near the bottom during the day (Kaltenberg & Benoit-Bird, 2009).

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

411 al. 2006). In addition, shoals were found in all bathymetric ranges but numerous shoals were  
412 detected in areas with bathymetry under  $< 10$  m only during summer, which could then  
413 represent suitable areas during this period. Overall, understanding the combined  
414 environmental factors, which structure the fish species distributions, is challenging as  
415 species–environmental relationships can be remarkably complex in shallow waters (Beck et  
416 al. 2001, Staveley et al. 2017). In the future, the development of more autonomous techniques  
417 to directly classify the seabed and analyse fish shoals using multibeam echosounders could  
418 improve the understanding of the distribution patterns of fish in different shallow-water  
419 habitats (Lamouret et al. 2019). Other environmental variables could influence the fish  
420 distribution in shallow waters. Especially, we observed that surface sea water temperature was  
421 higher in shallower areas close to the coast compared to deeper areas, particularly during  
422 summer in both study areas. Finally, additional data like chlorophyll-*a* concentration would  
423 be relevant to analyse at small-scale to study the pelagic fish distribution (Diogoul et al.  
424 2021).

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

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

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

#### 456 *Atlantic mackerel shoals in ultra-shallow waters*

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

461 (Dawson 1986) which is consistent as we observed both juvenile Atlantic mackerels (less than  
462 28.7 cm) and adults (higher than 28.7 cm) (Froese & Pauly 2021). Indeed, Atlantic mackerels  
463 are known to spawn from January to July along the continental shelf edge from Portuguese to  
464 Scottish waters and in the North Sea. In autumn, less shoal detections were observed in this  
465 same areas. This could suggest that the shoals dispersed or move toward deeper areas, or that  
466 the populations were lower at this season as mackerels migrate toward the North Sea and  
467 Norwegian Sea after the spawning season (Reid et al. 1997, Bruge et al. 2016).

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

486 Atlantic mackerels are supposed to be highly sensitive to environmental conditions such  
487 as sea water temperature (Jansen et al. 2012, Hughes et al. 2014). In our study, mean sea  
488 surface temperature during summer was 16.7°C in the North of Bay of Biscay and 16.0°C in  
489 the Celtic Sea respectively which was consistent to the fact that they could be present in  
490 temperatures up to 15°C, although they are supposed to prefer areas with temperatures  
491 between 9 and 13°C (Olafsdottir et al. 2019). Observations of mackerel schools during the  
492 summer feeding migration between the surface and a depth of 40 m were suggested to be due  
493 to temperature preferences as well as their foraging strategy and food availability (Godø et al.  
494 2004, Nøttestad et al. 2016). Especially, shoals were found static in both areas and Atlantic  
495 mackerels, as they were supposed to reduce their swimming speed when they reach the most  
496 productive area (Nøttestad et al. 2016). Overall, our data could help understanding the  
497 Atlantic mackerels population dynamics in ultra-shallow waters where they are not  
498 traditionally surveyed (Brehmer et al. 2006b) which is important for conservation. Indeed,  
499 observations of shifted distributions of the mackerel populations in response to climate  
500 change were already observed (Berge et al. 2015, Bruge et al. 2016).

## 501 **5. CONCLUSION**

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

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

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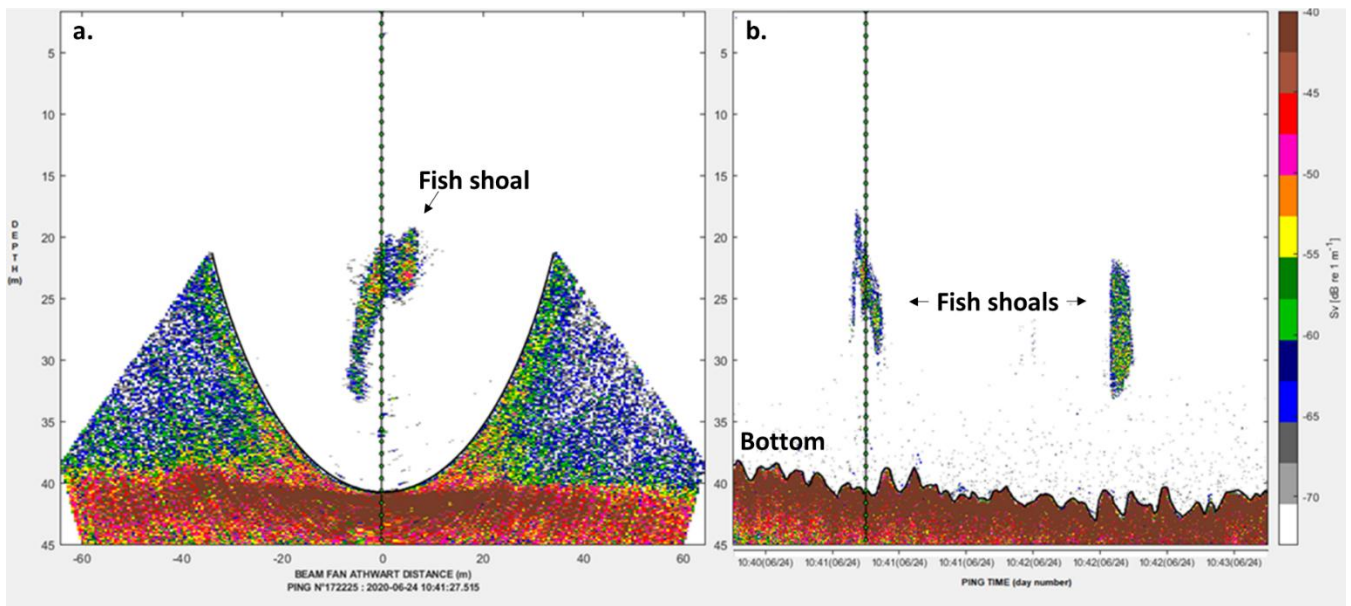
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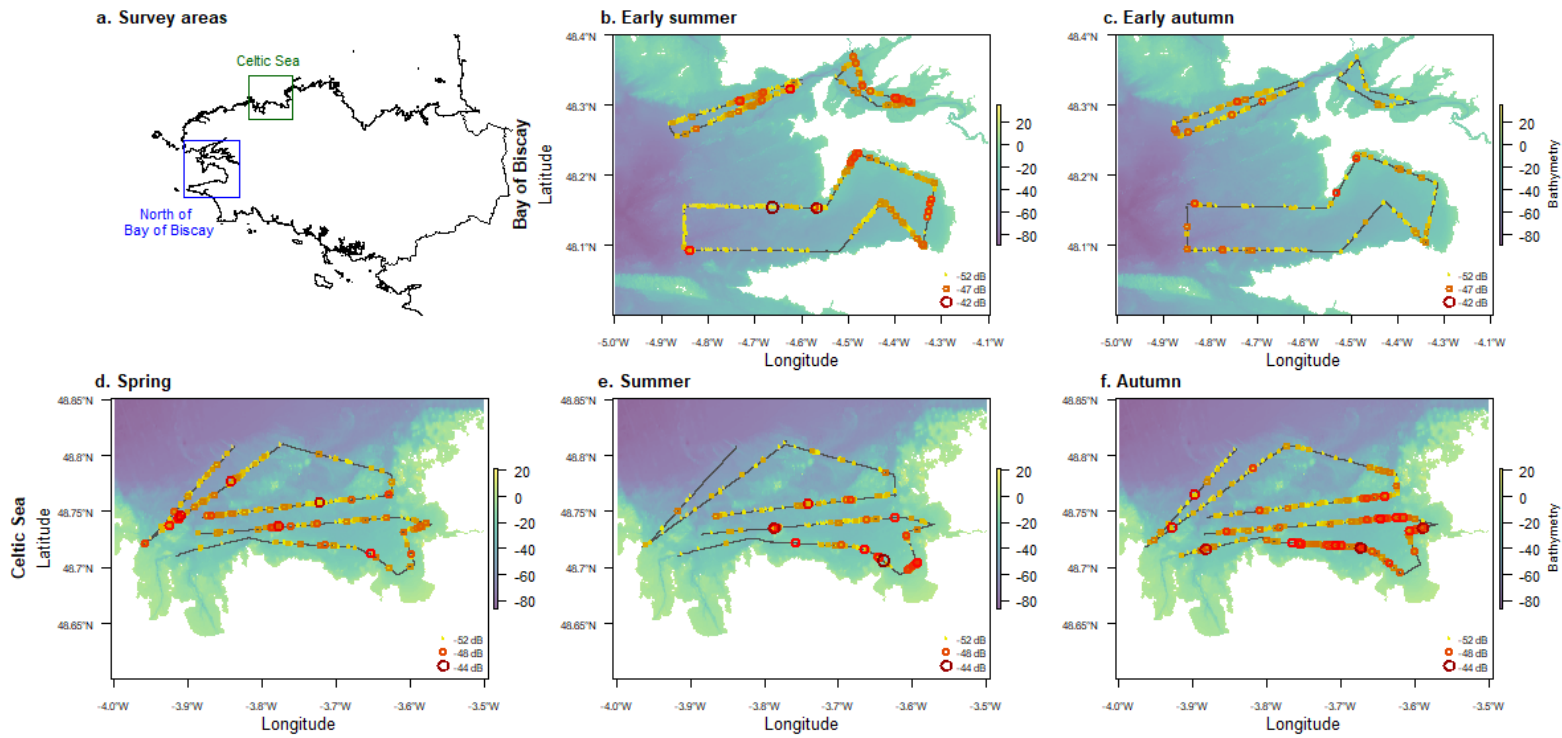
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740 **8. FIGURES AND TABLES**

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

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747 **Figure 2.** Detected shoals observed by the multibeam echosounder during the surveys in  
 748 2020. Surveys areas in the North of the Bay of Biscay and in the Celtic Sea can be viewed on  
 749 panel a. For the Bay of Biscay area, the b and c panels represent the detected shoals  
 750 respectively during the beginning of the summer and autumn 2020. For Celtic Sea area,  
 751 panels d, e and f represent the detected shoals respectively during spring, summer and autumn  
 752 2020. Circle sizes and colors are dependent on the acoustic volume backscattering strength  $S_v$   
 753 (dB). Only shoals with a minimum volume of  $1 \text{ m}^3$  was represented in order to avoid single  
 754 targets. Colors of the map are dependent on the bathymetry.

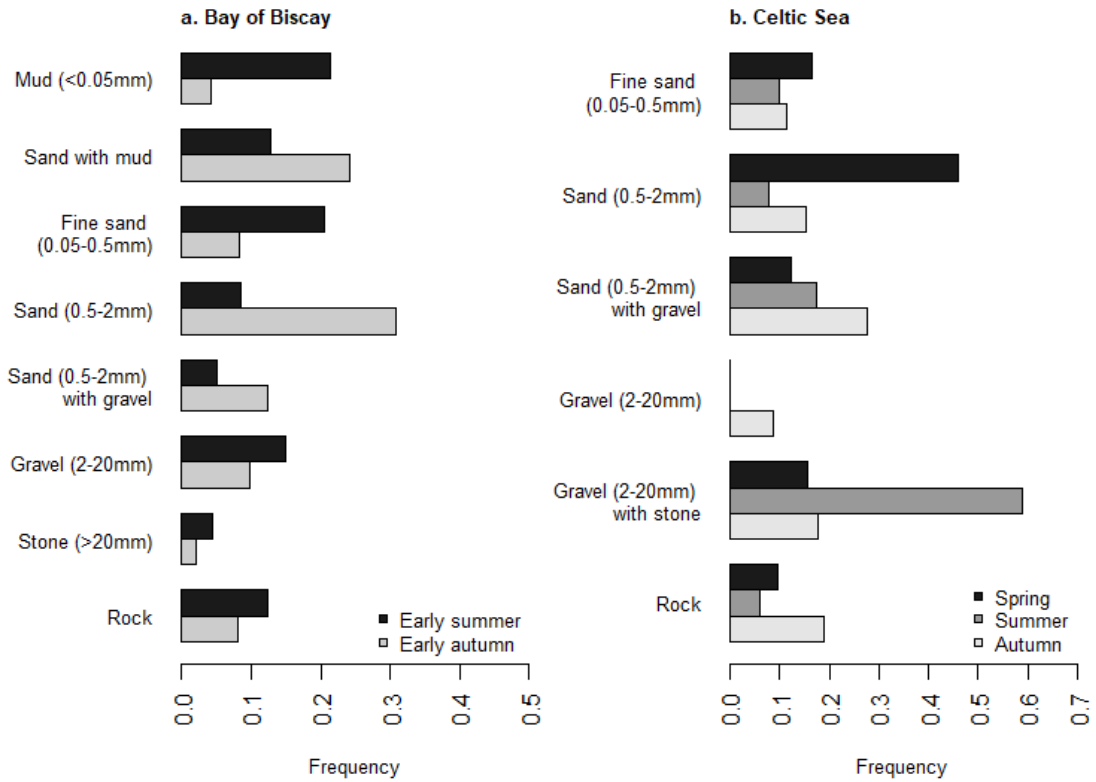
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761 **Figure 3.** Frequency of occurrence of detected shoals according to seafloor substrate type in  
 762 the North of Bay of Biscay (a) and in the Celtic Sea (b). Colors of the barplots depend on the  
 763 surveyed season. Results were reported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

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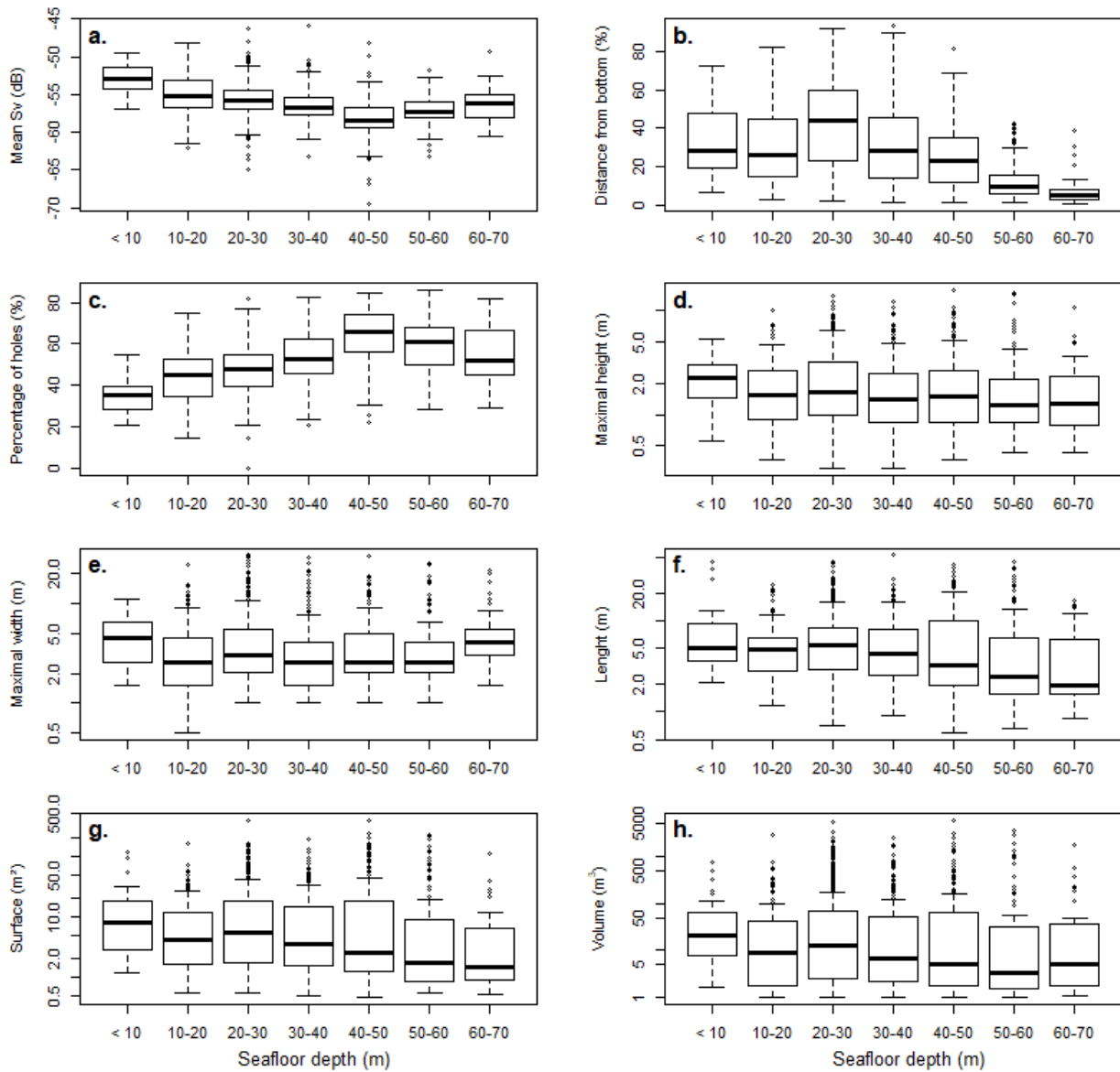
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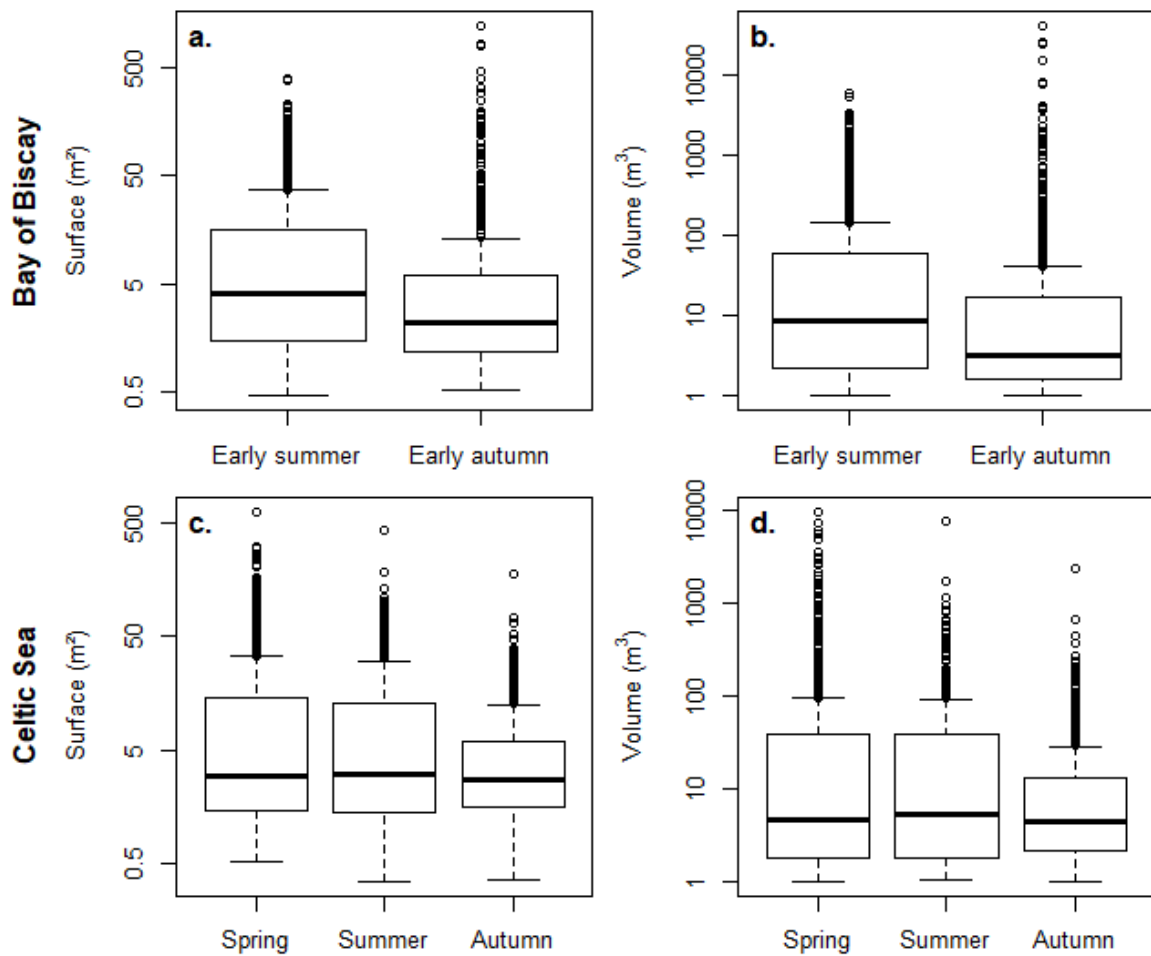
Early summer 2020



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

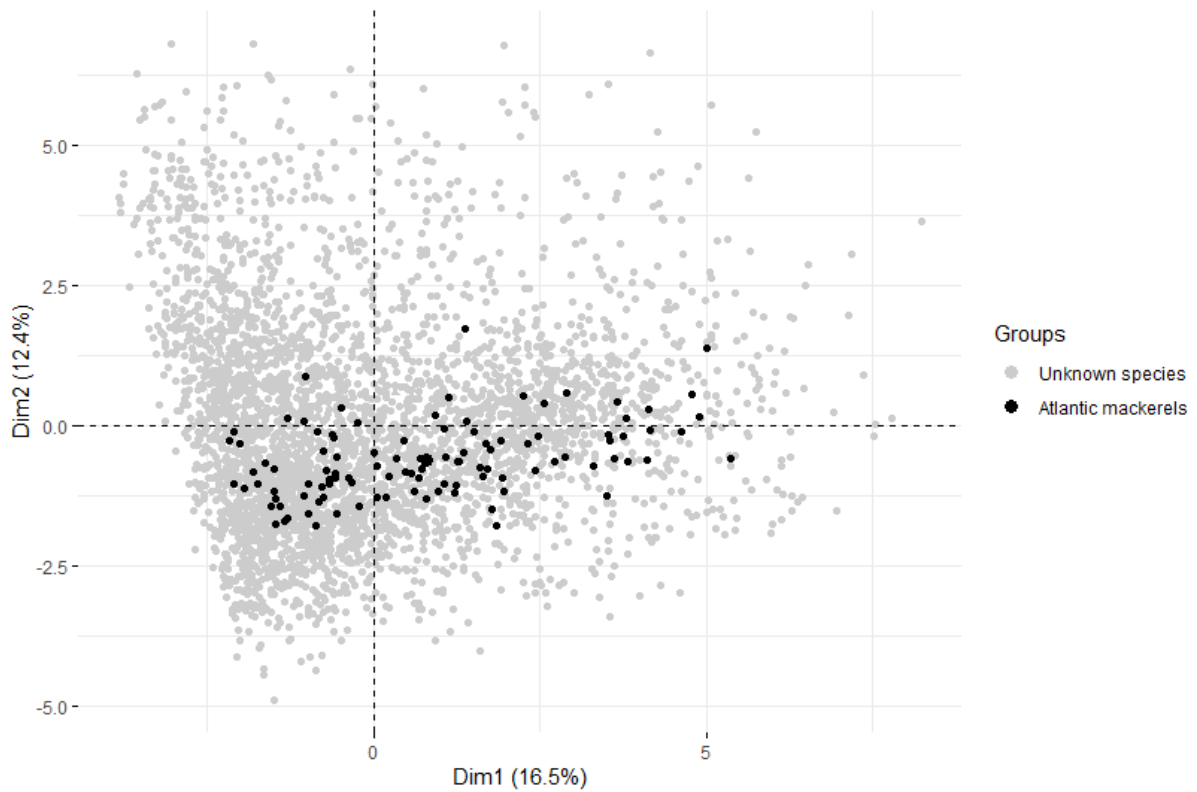






781 **Figure 5.** Fish shoal characteristics as a function of the seasons. The top panels represent the  
 782 maximum surface (a) and the volume (b) for the Bay of Biscay area. The bottom panels  
 783 represent the maximum surface (c) and the volume (d) for the Celtic Sea area. The boxplots  
 784 present the median, the 25th and 75th percentiles with a 1.5 interquartile range and the  
 785 outliers.  
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789 **Figure 6.** Multiple Factor Analysis taking into account both quantitative and qualitative data:  
 790 all the fish shoal descriptors as well as the environmental variables (bottom depth, seafloor  
 791 substrate type, season and study site). The maximal height, maximal width, length, surface  
 792 and volume fell out along the first axis whereas the variables related to the position of the  
 793 shoal in the water column and the environmental variables fell out along the second axis.

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