



HAL
open science

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

► To cite this version:

Viviane David, Anne Mouget, Yannick Perrot, Loïc Le Goff, Pierre Thiriet, et al.. Insights from a multibeam echosounder to survey pelagic fish shoals and their spatio-temporal distribution in ultra-shallow waters. *Estuarine, Coastal and Shelf Science*, 2021, 264, pp.107705. 10.1016/j.ecss.2021.107705 . hal-03831015

HAL Id: hal-03831015

<https://hal.science/hal-03831015v1>

Submitted on 19 Jan 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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^{1,2,*}, Anne Mouget^{4,5}, Yannick Perrot², Loïc Le Goff¹, Pierre Thiriet¹, Ndague
5 Diogoul^{2,3}, Eric Feunteun^{4,5}, Anthony Acou¹, Patrice Brehmer^{2,6}

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

9 ² IRD, Univ Brest, CNRS, Ifremer, UMR Lemar, Plouzané, France

10 ³ ISRA, CRODT, PRH, BP 2221, Dakar, Senegal

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

13 ⁵ Station Marine de Dinard, CRESCO, 38, rue du port Blanc, 35800 Dinard, France

14 ⁶ Commission Sous Régional des Pêches, CSRP, SRFC, Dakar, Sénégal

15
16 *Corresponding author: 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 μ 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 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

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, β_0 to β_3 are the regression coefficients,
210 Bathymetry and Season the environmental variables and ε_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 Δ_{AIC} was higher than 2, in which case the lowest AIC
215 defined the best model. However, if the Δ_{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 ± 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 ± 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°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 ± 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 ± 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 ± 0.22
243 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°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°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 nmi^{-1} having a minimum volume of 1 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 nmi^{-1} having a minimum volume of 1 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 echotracés of presumed Atlantic mackerel shoals can also be visualized in
343 Supplementary Information (Figures S13 and S14). General shape of the echotracés 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 echotracés 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 echotracés 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.

518 **6. ACKNOWLEDGMENTS**

519 This project was funded by the measure 80 of the FEAMP agreement
520 (PFEA800219DM0530003). The authors wish to thank all people who contributed to the
521 surveys including the crew members of the Albert Lucas (Univ Brest, IRD, CNRS) and
522 Neomysis (MNHN). We also thank Gildas Roudaut (IRD, UMR Lemar), Fabrice Roubaud
523 (IRD, US Imago) and Laurent Berger (Ifremer) for their help and the Naval Hydrographic and
524 Oceanographic Service (SHOM) for their data (data.shom.fr). We also thank Eva Russier for
525 her exchange with local fishermen and Gaëtan Richard for his helpful proofreading. We thank
526 administrative supports of the MNHN (Dinard and Paris) and the IRD Delegation Regional
527 West. Finally, we thank the anonymous reviewers for their helpful suggestions of
528 improvements.

529 **7. REFERENCES**

- 530 Akaike H (1974) A New Look at the Statistical Model Identification. *IEEE Transactions on Automatic*
531 *Control* 19:716–723.
- 532 Anderson DR, Burnham KP, Thompson WL (2000) Null Hypothesis Testing: Problems, Prevalence,
533 and an Alternative. *The Journal of Wildlife Management* 64:912–923.
- 534 Bahri T, Fréon P (2000) Spatial structure of coastal pelagic schools descriptors in the Mediterranean
535 Sea. *Fisheries Research* 48:157–166.
- 536 Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG,
537 Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The Identification,
538 Conservation, and Management of Estuarine and Marine Nurseries for Fish and
539 Invertebrates A better understanding of the habitats that serve as nurseries for marine species

540 and the factors that create site-specific variability in nursery quality will improve conservation
541 and management of these areas. *BioScience* 51:633–641.

542 Bellier E, Planque B, Petitgas P (2007) Historical fluctuations in spawning location of anchovy
543 (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the Bay of Biscay during 1967-73
544 and 2000-2004. *Fisheries Oceanography* 16:1–15.

545 Benoit-Bird KJ, Lawson GL (2016) Ecological Insights from Pelagic Habitats Acquired Using Active
546 Acoustic Techniques. *Annu Rev Mar Sci* 8:463–490.

547 Berge J, Heggland K, Lønne OJ, Cottier F, Hop H, Gabrielsen GW, Nøttestad L, Misund OA (2015)
548 First Records of Atlantic Mackerel (*Scomber scombrus*) from the Svalbard Archipelago,
549 Norway, with Possible Explanations for the Extensions of Its Distribution. *Arctic* 68:54–61.

550 Brehmer P, Chi TD, Mouillot D (2006a) Amphidromous fish school migration revealed by combining
551 fixed sonar monitoring (horizontal beaming) with fishing data. *Journal of Experimental*
552 *Marine Biology and Ecology* 334:139–150.

553 Brehmer P, Gerlotto F, Laurent C, Cotel P, Achury A, Samb B (2007) Schooling behaviour of small
554 pelagic fish: phenotypic expression of independent stimuli. *Marine Ecology Progress Series*
555 334:263–272.

556 Brehmer P, Guillard J, Guennegan Y, Bigot J-L, Liorzou B (2006b) Evidence of a variable unsampled
557 pelagic fish biomass in shallow water (<20 m): the case of the Gulf of Lion. *ICES Journal of*
558 *Marine Science* 63:444–451.

559 Brehmer P, Sancho G, Trygonis V, Itano D, Dalen J, Fuchs A, Faraj A, Taquet M (2019a) Towards an
560 Autonomous Pelagic Observatory: Experiences from Monitoring Fish Communities around
561 Drifting FADs. *Thalassas* 35:177–189.

562 Brehmer P, Sarré A, Guennégan Y, Guillard J (2019b) Vessel Avoidance Response: A Complex
563 Tradeoff Between Fish Multisensory Integration and Environmental Variables. *Reviews in*
564 *Fisheries Science & Aquaculture* 27:380–391.

565 Bruge A, Álvarez P, Fontán A, Cotano U, Chust G (2016) Thermal Niche Tracking and Future
566 Distribution of Atlantic Mackerel Spawning in Response to Ocean Warming. *Front Mar Sci*.

567 Cochrane NA, Li Y, Melvin GD (2003) Quantification of a multibeam sonar for fisheries assessment
568 applications. *The Journal of the Acoustical Society of America* 114:745–758.

569 Colbo K, Ross T, Brown C, Weber T (2014) A review of oceanographic applications of water column
570 data from multibeam echosounders. *Estuarine, Coastal and Shelf Science* 145:41–56.

571 Dauvin J-C (2008) The main characteristics, problems, and prospects for Western European coastal
572 seas. *Marine Pollution Bulletin* 57:22–40.

573 Dawson WA (1986) Changes in Western mackerel (*Scomber scombrus*) spawning stock composition
574 during the spawning season. *Journal of the Marine Biological Association of the United*
575 *Kingdom* 66:367–383.

576 D’Elia M, Patti B, Bonanno A, Fontana I, Giacalone G, Basilone G, Fernandes PG (2014) Analysis of
577 backscatter properties and application of classification procedures for the identification of
578 small pelagic fish species in the Central Mediterranean. *Fisheries Research* 149:33–42.

579 D’Elia M, Patti B, Sulli A, Tranchida G, Bonanno A, Basilone G, Giacalone G, Fontana I, Genovese
580 S, Guisande C, Mazzola S (2009) Distribution and spatial structure of pelagic fish schools in
581 relation to the nature of the seabed in the Sicily Straits (Central Mediterranean). *Marine*
582 *Ecology* 30:151–160.

583 Demer D, Zwolinski J, Byers K, Cutter G, Renfree J, Sessions T, Macewicz B (2012) Prediction and
584 confirmation of seasonal migration of Pacific sardine (*Sardinops sagax*) in the California
585 Current Ecosystem. *Fishery Bulletin* 110:52–70.

586 Diankha O, Thiaw M, Sow BA, Brochier T, Gaye AT, Brehmer P (2015) Round sardinella (*Sardinella*
587 *aurita*) and anchovy (*Engraulis encrasicolus*) abundance as related to temperature in the
588 senegalese waters. *Thalassas* 31:9–17.

589 Diogoul N, Brehmer P, Demarcq H, El Ayoubi S, Thiam A, Sarre A, Mouget A, Perrot Y (2021) On
590 the robustness of an eastern boundary upwelling ecosystem exposed to multiple stressors. *Sci*
591 *Rep* 11:1908.

592 Doray M, Massé J, Petitgas P (2010) Pelagic fish stock assessment by acoustic methods at Ifremer.
593 <https://archimer.ifremer.fr/doc/00003/11446/> (accessed April 2, 2020)

- 594 Doray M, Petitgas P, Romagnan JB, Huret M, Duhamel E, Dupuy C, Spitz J, Authier M, Sanchez F,
595 Berger L, Dorémus G, Bourriau P, Grellier P, Massé J (2018) The PELGAS survey: Ship-
596 based integrated monitoring of the Bay of Biscay pelagic ecosystem. *Progress in*
597 *Oceanography* 166:15–29.
- 598 Draštik V, Kubečka J (2005) Fish avoidance of acoustic survey boat in shallow waters. *Fisheries*
599 *Research* 72:219–228.
- 600 Foote KG, Chu D, Hammar TR, Baldwin KC, Mayer LA, Hufnagle LC, Jech JM (2005) Protocols for
601 calibrating multibeam sonar. *The Journal of the Acoustical Society of America* 117:2013–
602 2027.
- 603 Franco A, Franzoi P, Malavasi S, Riccato F, Torricelli P, Mainardi D (2006) Use of shallow water
604 habitats by fish assemblages in a Mediterranean coastal lagoon. *Estuarine, Coastal and Shelf*
605 *Science* 66:67–83.
- 606 Freon P, Misund OA (1999) *Dynamics of Pelagic Fish Distribution and Behaviour: Effects on*
607 *Fisheries and Stock Assessment*. Oxford: Blackwell Science.
- 608 Froese R, Pauly D (2021) www.fishbase.org
- 609 Gerlotto F (1997) Gregariousness and school behaviour of pelagic fish: impact of the acoustics
610 evaluation and fisheries. In: *Proceedings of acoustics seminar AKUSTIKAN 2*. Petit D, Cotel
611 P, Nugroho D (eds) Union Européenne, Luxembourg, p 233–252
- 612 Gerlotto F, Soria M, Fréon P (1999) From two dimensions to three: the use of multibeam sonar for a
613 new approach in fisheries acoustics. *Can J Fish Aquat Sci* 56:6–12.
- 614 Godø OR, Hjellvik V, Iversen SA, Slotte A, Tenningen E, Torkelsen T (2004) Behaviour of mackerel
615 schools during summer feeding migration in the Norwegian Sea, as observed from fishing
616 vessel sonars. *ICES Journal of Marine Science* 61:1093–1099.
- 617 Guillard J, Brehmer P, Colon M, Guennégan Y (2006) Three dimensional characteristics of young-of-
618 year pelagic fish schools in lake. *Aquatic Living Resources* 19:115–122.
- 619 Guillard J, Fernandes P, Laloe T, Brehmer P (2011) Three-dimensional internal spatial structure of
620 young-of-the-year pelagic freshwater fish provides evidence for the identification of fish
621 school species. *Limnology and Oceanography Methods* 9:322–328.
- 622 Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat
623 models. *Ecology Letters* 8:993–1009.
- 624 Halpern BS, Selkoe KA, Micheli F, Kappel CV (2007) Evaluating and ranking the vulnerability of
625 global marine ecosystems to anthropogenic threats. *Conserv Biol* 21:1301–1315.
- 626 Hamer K, Phillips R, Wanless S, Harris M, Wood A (2000) Foraging ranges, diets and feeding
627 locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry.
628 *Marine Ecology Progress Series* 200:257–264.
- 629 Harris MP, Wanless S (1991) The Importance of the Lesser Sandeel *Ammodytes marinus* in the Diet
630 of the Shag *Phalacrocorax aristotelis*. *Ornis Scandinavica (Scandinavian Journal of*
631 *Ornithology)* 22:375–382.
- 632 Holland MM, Becker A, Smith JA, Everett JD, Suthers IM (2021) Fine-scale spatial and diel dynamics
633 of zooplanktivorous fish on temperate rocky and artificial reefs. *Marine Ecology Progress*
634 *Series* 674:221–239.
- 635 Hughes KM, Dransfeld L, Johnson MP (2014) Changes in the spatial distribution of spawning activity
636 by north-east Atlantic mackerel in warming seas: 1977–2010. *Mar Biol* 161:2563–2576.
- 637 Innangi S, Bonanno A, Tonielli R, Gerlotto F, Innangi M, Mazzola S (2016) High resolution 3-D
638 shapes of fish schools: A new method to use the water column backscatter from hydrographic
639 MultiBeam Echo Sounders. *Applied Acoustics* 111:148–160.
- 640 Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke
641 R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM,
642 Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent
643 collapse of coastal ecosystems. *Science* 293:629–637.
- 644 Jansen T, Campbell A, Kelly C, Hátún H, Payne MR (2012) Migration and Fisheries of North East
645 Atlantic Mackerel (*Scomber scombrus*) in Autumn and Winter. *PLOS ONE* 7:e51541.
- 646 Kaltenberg A, Benoit-Bird K (2009) Diel behavior of sardine and anchovy schools in the California
647 Current System.

648 Lamouret M, Abadie A, Viala C, Boissery P, Thirion-Moreau N (2019) Measuring fish activities as
649 additional environmental data during a hydrographic survey with a multi-beam echo sounder.
650 Lamouret M, Boissery P, Viala C, Thirion-Moreau N, Abadie A (2020) Coupling the map of marine
651 habitats and fish accumulation zones: a three-dimensional spatial approach for the
652 management of halieutic resources. *Vie et Milieu / Life & Environment* 70.
653 Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL (2010) Cost-efficient
654 sampling of fish assemblages: comparison of baited video stations and diver video transects.
655 *Aquatic Biology* 9:155–168.
656 Limborg MT, Pedersen JS, Hemmer-Hansen J, Tomkiewicz J, Bekkevold D (2009) Genetic
657 population structure of European sprat *Sprattus sprattus*: differentiation across a steep
658 environmental gradient in a small pelagic fish. *Marine Ecology Progress Series* 379:213–224.
659 Long R (2011) The Marine Strategy Framework Directive: A New European Approach to the
660 Regulation of the Marine Environment, Marine Natural Resources and Marine Ecological
661 Services. *Journal of Energy & Natural Resources Law* 29:1–44.
662 Maclellan DN, Fernandes PG, Dalen J (2002) A consistent approach to definitions and symbols in
663 fisheries acoustics. *ICES J Mar Sci* 59:365–369.
664 Makris NC, Ratilal P, Jagannathan S, Gong Z, Andrews M, Bertsatos I, Godø OR, Nero RW, Jech JM
665 (2009) Critical Population Density Triggers Rapid Formation of Vast Oceanic Fish Shoals.
666 *Science* 323:1734–1737.
667 Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: A
668 review of sixty years of publications (1952–2012). *Fisheries Research* 154:44–62.
669 Manik HM, Furusawa M, Amakasu K (2006) Quantifying Sea Bottom Surface Backscattering
670 Strength and Identifying Bottom Fish Habitat by Quantitative Echo Sounder. *Jpn J Appl Phys*
671 45:4865.
672 Maravelias CD, Reid DG, Swartzman GL (2000) Seabed substrate, water depth and zooplankton as
673 determinants of the prespawning spatial aggregation of North Atlantic herring.
674 Melvin GD, Cochrane NA (2015) Multibeam Acoustic Detection of Fish and Water Column Targets
675 at High-Flow Sites. *Estuaries and Coasts* 38:227–240.
676 Morais P, Babaluk J, Correia AT, Chícharo MA, Campbell JL, Chícharo L (2010) Diversity of
677 anchovy migration patterns in an European temperate estuary and in its adjacent coastal area:
678 Implications for fishery management. *Journal of Sea Research* 64:295–303.
679 Muiño R (Ramón), Carrera-López P (Pablo) (2007) Sardine (*Sardina pilchardus* Walbaum)
680 characterisation off the Spanish Atlantic coast.
681 Nøttestad L, Axelsen B, Anker-Nilssen T, Fossum P, Kvamme C (2001) Pretty patterns but a simple
682 strategy: predator-prey interactions between juvenile herring and Atlantic puffins observed
683 with multibeam sonar. *Canadian Journal of Zoology* 79:1586–1596.
684 Nøttestad L, Diaz J, Penã H, Søliland H, Huse G, Fernö A (2016) Feeding strategy of mackerel in the
685 Norwegian Sea relative to currents, temperature, and prey. *ICES Journal of Marine Science*
686 73:1127–1137.
687 O’Connell M, Fives JM (1995) The Biology of the Lesser Sand-Eel *Ammodytes tobianus* L. In the
688 Galway Bay Area. *Biology and Environment: Proceedings of the Royal Irish Academy*
689 95B:87–98.
690 Olafsdottir AH, Utne KR, Jacobsen JA, Jansen T, Óskarsson GJ, Nøttestad L, Elvarsson BP, Broms C,
691 Slotte A (2019) Geographical expansion of Northeast Atlantic mackerel (*Scomber scombrus*)
692 in the Nordic Seas from 2007 to 2016 was primarily driven by stock size and constrained by
693 low temperatures. *Deep Sea Research Part II: Topical Studies in Oceanography* 159:152–168.
694 Pagès J (2014) Multiple Factor Analysis by Example Using R, Chapman and Hall/CRC.
695 Paramo J, Bertrand S, Villalobos H, Gerlotto F (2007) A three-dimensional approach to school
696 typology using vertical scanning multibeam sonar. *Fisheries Research* 84:171–179.
697 Pavlov D, Kasumyan A (2000) Patterns and mechanisms of schooling behavior in fish: A review.
698 *Journal of Ichthyology* 40:S163–S231.
699 Perrot Y, Brehmer P, Habasque J, Roudaut G, Behagle N, Sarre A, Lebourges Dhaussy A (2018)
700 Matecho : an open-source tool for processing fisheries acoustics data. *Acoustics Australia*
701 46:241–248.

702 Perrot Y, Brehmer P, Roudaut G, Gerstoff P, Josse E (2014) Efficient multibeam sonar calibration and
703 performance evaluation. *International Journal of Engineering Science and Innovative*
704 *Technology* 3:808–820.

705 Petitgas P (2003) A method for the identification and characterization of clusters of schools along the
706 transect lines of fisheries-acoustic surveys. *ICES J Mar Sci* 60:872–884.

707 Pihl L, Cattrijsse A, Codling I, Mathieson S, McLusky D, Roberts C (2007) Habitat use by Fishes in
708 Estuaries and Other Brackish Areas. p 10–53

709 Pitcher TJ (1986) Functions of Shoaling Behaviour in Teleosts. In: *The Behaviour of Teleost Fishes*.
710 Pitcher TJ (ed) Springer US, Boston, MA, p 294–337

711 Quayle VA, Righton D, Hetherington S, Pickett G (2009) Observations of the Behaviour of European
712 Sea Bass (*Dicentrarchus labrax*) in the North Sea. In: *Tagging and Tracking of Marine*
713 *Animals with Electronic Devices*. Reviews: Methods and Technologies in Fish Biology and
714 Fisheries, Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J (eds)
715 Springer Netherlands, Dordrecht, p 103–119

716 R Development Core Team (2019) R: a language environment for statistical computing.

717 Reid DG (2000) Report on Echo Trace Classification.

718 Reid DG, Turrell WR, Walsh M, Corten A (1997) Cross-shelf processes north of Scotland in relation
719 to the southerly migration of Western mackerel. *ICES Journal of Marine Science* 54:168–178.

720 Roman MR, Brandt SB, Houde ED, Pierson JJ (2019) Interactive Effects of Hypoxia and Temperature
721 on Coastal Pelagic Zooplankton and Fish. *Front Mar Sci* 6.

722 Scalabrin C, Massé J (1993) Acoustic detection of the spatial and temporal distribution of fish shoals
723 in the Bay of Biscay. *Aquat Living Resour* 6:269–283.

724 Simmonds J, MacLennan D (2006) *Fisheries Acoustics: Theory and Practice*, 2nd Edition. Wiley-
725 Blackwell.

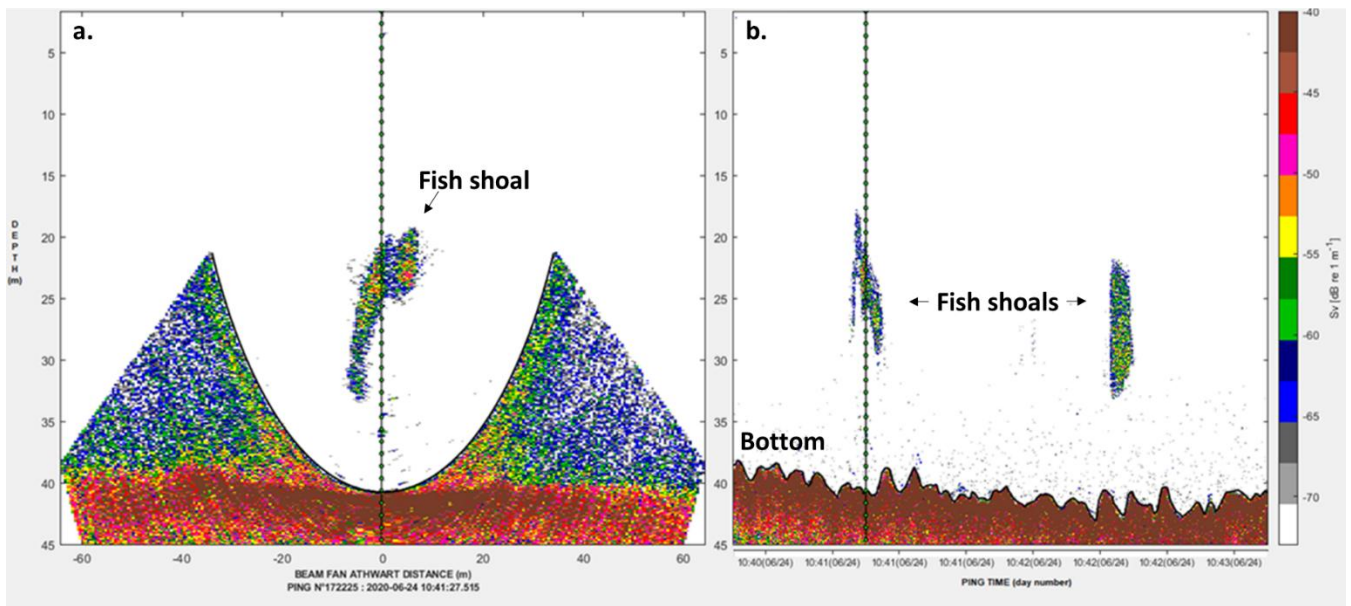
726 Staveley TAB, Perry D, Lindborg R, Gullström M (2017) Seascape structure and complexity influence
727 temperate seagrass fish assemblage composition. *Ecography* 40:936–946.

728 Trenkel V, Mazauric V, Berger L (2008) The new fisheries multibeam echosounder ME70:
729 description and expected contribution to fisheries research. *ICES Journal of Marine Science*
730 65:645–655.

731 Trenkel VM, Berger L, Bourguignon S, Doray M, Fablet R, Massé J, Mazauric V, Poncelet C,
732 Quemener G, Scalabrin C, Villalobos H (2009) Overview of recent progress in fisheries
733 acoustics made by Ifremer with examples from the Bay of Biscay. *Aquatic Living Resources*
734 22:433–445.

735 Twatwa NM, van der Lingen CD, Drapeau L, Moloney CL, Field JG (2005) Characterising and
736 comparing the spawning habitats of anchovy *Engraulis encrasicolus* and sardine *Sardinops*
737 *sagax* in the southern Benguela upwelling ecosystem. *African Journal of Marine Science*
738 27:487–499.

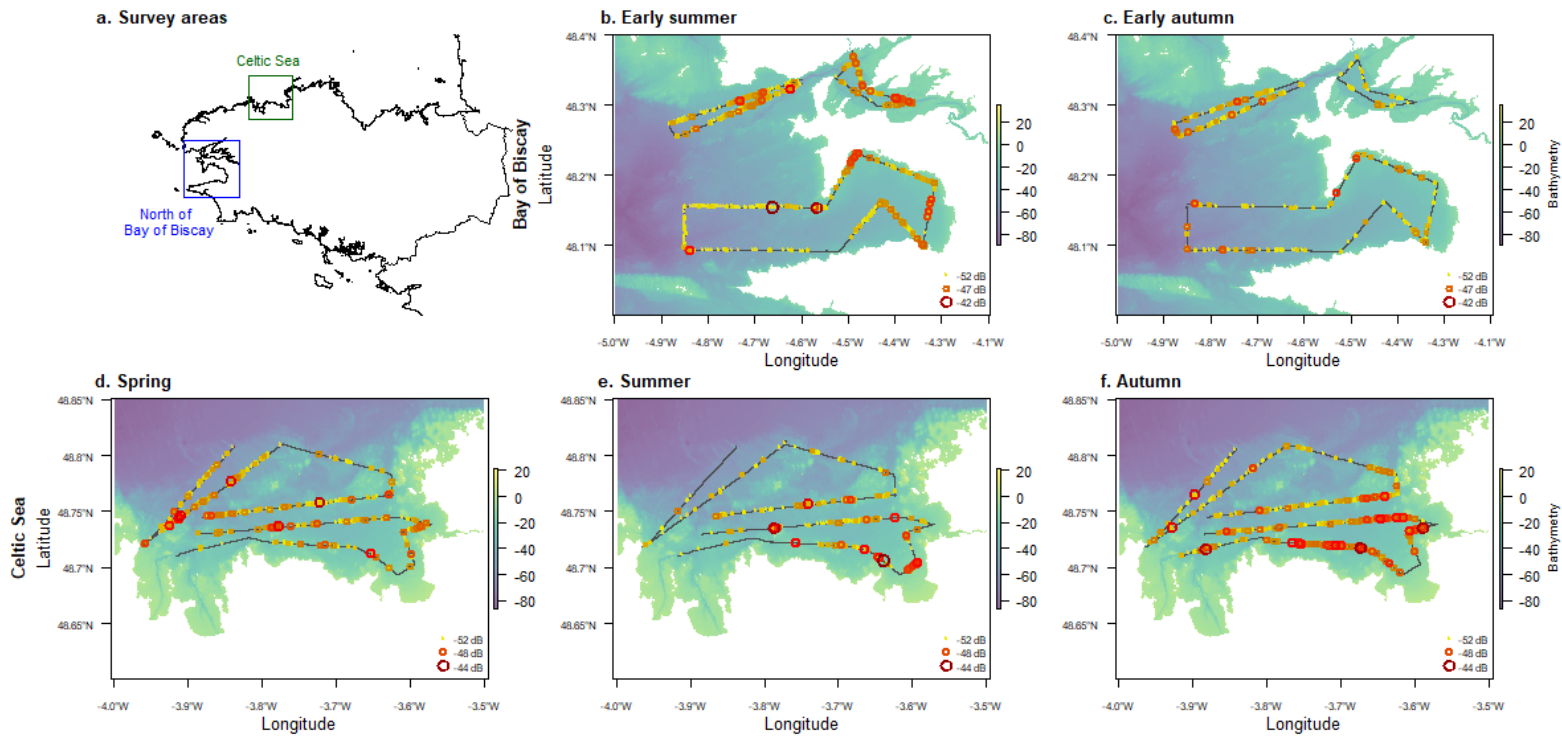
739



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.

746



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 m^3 was represented in order to avoid single
 754 targets. Colors of the map are dependent on the bathymetry.

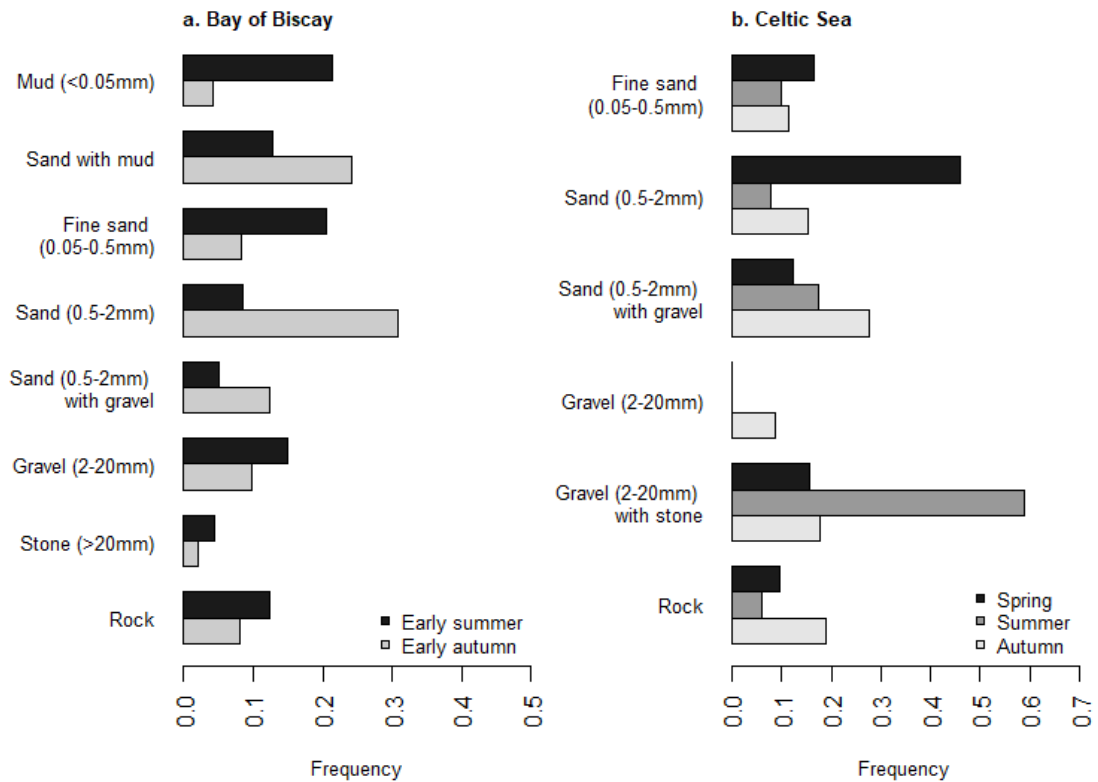
755

756

757

758

759



760

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.

765

766

767

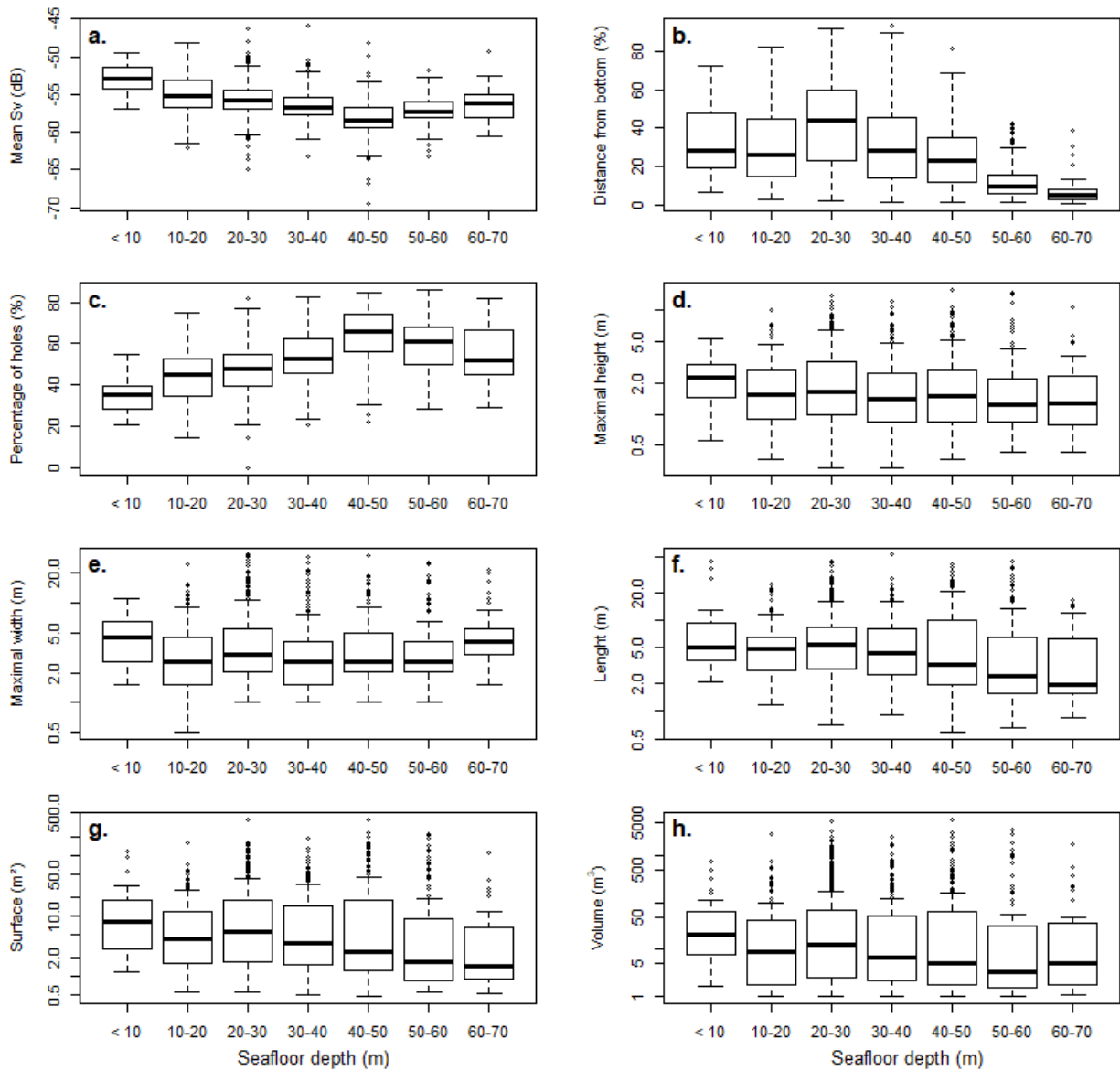
768

769

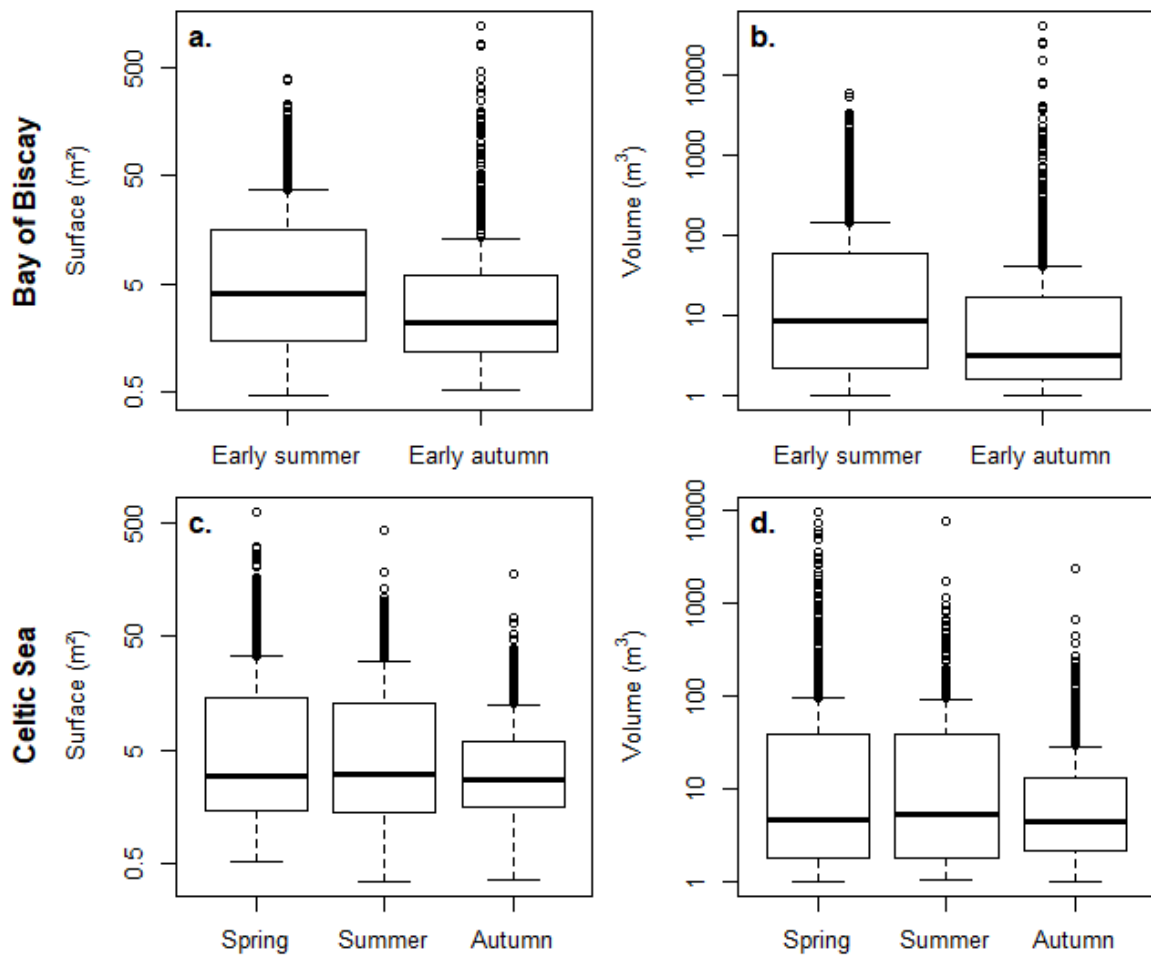
770

771

Early summer 2020

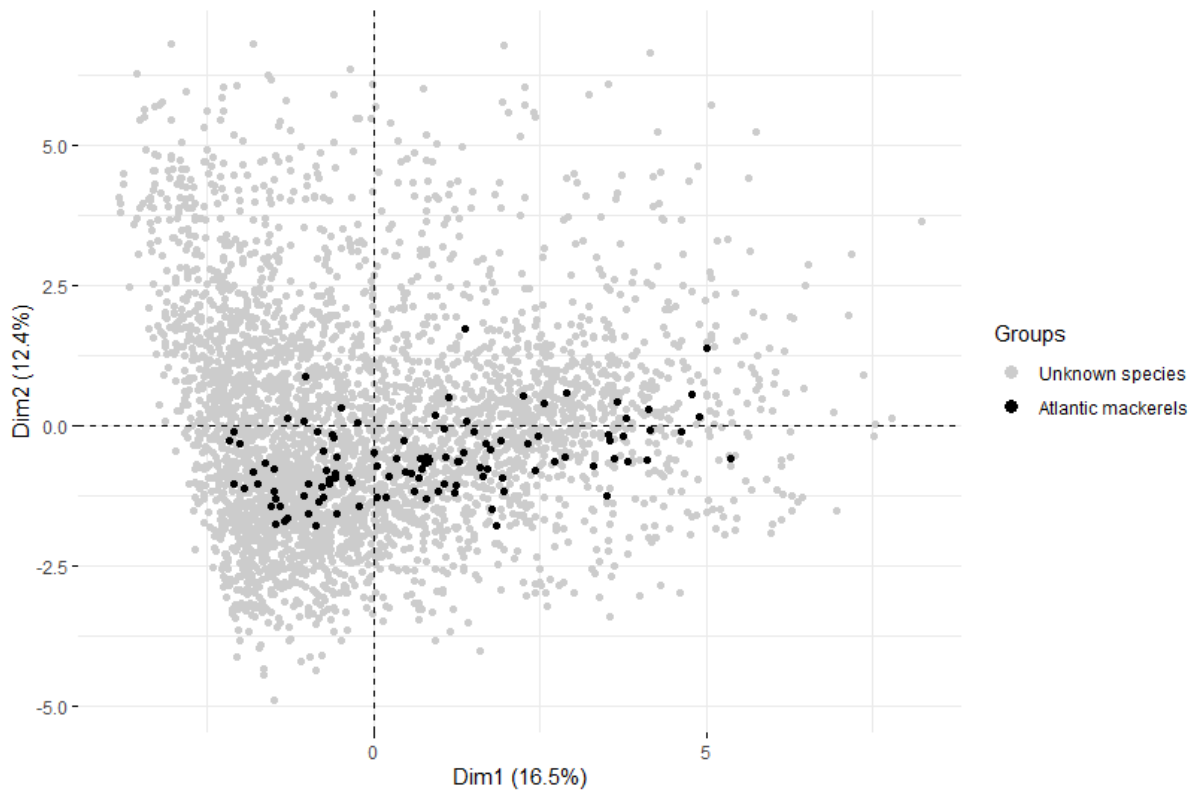


772 **Figure 4.** Fish shoal characteristics as a function of the seafloor depth (m) for the shoal
 773 detected during early summer 2020 in the North of Bay of Biscay. Graphs (a) represent the
 774 mean volume backscattering strength S_v in dB, (b) the distance from bottom in percentage
 775 compared 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 25th and 75th percentiles with a 1.5
 779 interquartile range and the outliers.



781
 782 **Figure 5.** Fish shoal characteristics as a function of the seasons. The top panels represent the
 783 maximum surface (a) and the volume (b) for the Bay of Biscay area. The bottom panels
 784 represent the maximum surface (c) and the volume (d) for the Celtic Sea area. The boxplots
 785 present the median, the 25th and 75th percentiles with a 1.5 interquartile range and the
 786 outliers.

787



788

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.

794