

1 Article

# 2 Larval fish community in the northwestern Iberian 3 upwelling system during the summer period.

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11 **Abstract:** The Galician shelf (northwestern Iberian Peninsula) is a highly dynamic area with an  
12 important multi-species fisheries industry that exploits resources from several habitats,  
13 characterized by being not only very diverse, rich, and productive but also seasonally and  
14 inter-annually variable. Early life stages of different species are distributed throughout the year,  
15 with fluctuating abundances and community composition. Likewise, the influence of  
16 environmental factors and processes on larval production and survival remains unknown.  
17 Sampling was carried out in July of 2012, and all the larvae obtained were identified to establish the  
18 specific composition of the community in a typical summer upwelling scenario. The results show  
19 no zonation in the species distribution, a consequence of the mixing effects of the upwelling and  
20 eddies, with high diversity but low abundance, which render in a slight predominance of a few  
21 species. Due to the dependence of planktonic populations on upwelling events, which was not very  
22 pronounced in 2012, we cannot conclude that this was a typical conformation of the Galician  
23 summer larval fish community, but it is the first approach to comprehend the community  
24 composition.

25 **Keywords:** Ichthyoplankton; upwelling system; larval fish community; Northwest Atlantic Ocean;  
26 Galicia; summer.

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## 28 1. Introduction

29 The fluid environment in which marine populations live offers a wide variety of ways for  
30 individuals to disperse within and among populations. The extent of successful dispersal is one of  
31 the major determinants of population dynamics but is poorly understood for most marine species.  
32 Understanding the drivers of fish larval dispersal is a bio-physical problem that comprises processes  
33 that influence offspring production, growth, development, and survival, as well as advection,  
34 diffusion, and other physical properties of water circulation and their interactions with larval traits  
35 (e.g., vertical migrations) and that operate at various scales [1].

36 Understanding the influence of environmental variables on fish larval ecology is even more  
37 relevant in highly dynamic areas, such as those affected by upwelling events. The Galician shelf,  
38 located in the north-western corner of the Iberian Peninsula, marks the northern boundary of the  
39 Iberian-Canary current upwelling system. During summer, wind typically blows southward along  
40 the coast, inducing upwelling events and associated southward currents [2]. In addition, a  
41 subsurface front occurs off Cape Finisterre between two modes (subtropical and subpolar) of the  
42 Eastern North Atlantic Central Water (ENACW) [3]. These modes can mix in an area of convergence,  
43 a situation that is intensified by northerly winds [4–7].

44 Shoreline also plays a role in upwelling conditions, and changes in orientation between the  
45 western and northern coasts modulate wind direction and intensity and are mainly responsible for

46 the differences observed along the two coasts; upwellings are generally more prevalent in the west  
47 and more discontinuous and distant from the coast (occurring near the edge of the continental shelf)  
48 in the north [8–10]. The Galician margin is characterized by a system of terraces up to 30 km wide  
49 that form a stepped slope followed by an abrupt lower slope affected by large-scale rotational  
50 failures [11], which differs from the surrounding Cantabrian and Portuguese margins.

51 The predictive models for environmental changes in the area hypothesize a future scenario in  
52 which the frequency and intensity of upwelling events will increase due to the increasing northerly  
53 winds, especially in the region of the north-western coast [9]. Changes in upwelling frequency or  
54 intensity have consequences for ecosystem productivity and composition. For example, the  
55 reduction in the intensity and length of upwelling events in the area during the last 40 years has had  
56 a significant impact on the abundance, distribution, and species composition of zooplankton,  
57 although this influence has been delayed for several years [12–14]. Linking the environmental  
58 conditions to the characteristics of the larval fish community in Galicia could be important for  
59 improving the understanding of variations in fish recruitment in present and future environmental  
60 scenarios. The cold nutrient-rich deeper water pumped by the upwelling from the ENACW  
61 generates a large amount of primary productivity [15], which supports the high amount of fishery  
62 and aquaculture activity in this region. The Galician fisheries industry is multi-specific and exploits  
63 a resource comprising several habitats (from coastal pelagic to demersal, benthic, or oceanic species),  
64 with high diversity, richness and biomass, and seasonal and inter-annual variability in abundance  
65 and spawning seasons [16, 17]. Hence, comprehensive larval fish community (LFC) knowledge  
66 related to the spatial and temporal structures of the community and the associated environmental  
67 factors is required.

68 Several studies were accomplished in the past, most of them focused on more restricted areas of  
69 the same region [18], adjacent regions [19, 20], different seasons [21–25], or even with different  
70 methodologies [26]. This study contributes to the knowledge of the region adding seasonal  
71 information of the summer conditions and with a more detailed set of data, given the high level of  
72 segmentation of the sample grid in relation with other studies that may comprehend the same area.  
73 The ecosystem approach to fisheries has been advocated as one way forward because it considers the  
74 holistic complexity of linkages across ecosystems, identifies conflicts between ecosystem services  
75 and considers the impacts of fisheries on marine ecosystems. [27]. However, it needs a  
76 comprehensive understanding of ecosystem structure and function – the ecosystem approach to  
77 fisheries advances as fast as the empirical support of science allows.

78 In fisheries ecology, the unit of study is the population; communities are composed of fish  
79 populations and operate within ecosystems that comprise all other levels of ecological organization  
80 [28]. Given the lack of successful attempts to manage fisheries based on single populations  
81 (maximum sustainable yield), fisheries management has turned its attention to the highest level of  
82 ecological organization [29–30]. Therefore, there is an interest in matching the practical management  
83 scales with those of ecosystem dynamics, while maintaining awareness that there is enormous  
84 variability between all the key components of fisheries ecosystems [27].

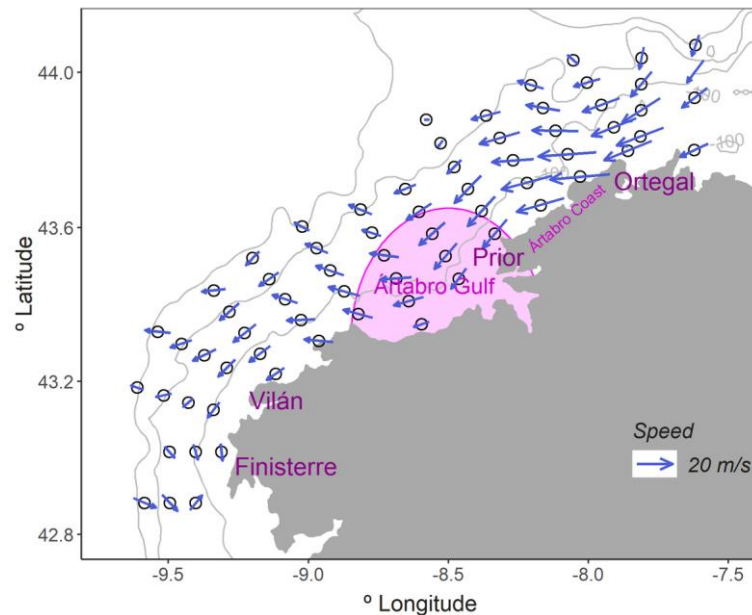
85 The causes of variation in recruitment have not led to annual predictive power, however,  
86 predictions at a community- (or larval fish assemblage) and ecosystem-level dynamics are more  
87 powerful [30]. Thus, it is critical to understand the composition and distribution of fisheries and  
88 other ecological setups related to ecosystem functioning (e.g., phenology, population dynamics,  
89 trophic relationships) because it provides relevant information on fisheries management in the  
90 context of climate change.

91 The goal of this study is to describe the composition and structure of the larval fish community  
92 in Galicia during a summer upwelling period which will serve as a reference for current and future  
93 fishery management efforts. We hypothesize that upwelling has the dominant influence on the  
94 horizontal and vertical distributions of the LFC.

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## 96 2. Materials and Methods

97 The CRAMER1207 survey was conducted aboard the Spanish research vessel Cornide de  
 98 Saavedra along the Galician coast from July 17 till July 31, 2012. Ninety-two stations were  
 99 established in a sampling grid with the stations being distributed along fifteen transects  
 100 perpendicular to the coastline and separated by eight nautical miles (nm), with a distance between  
 101 stations of four nm (Figure 1). The transects extended from the 50 m isobath to the 500 m isobath,  
 102 although due to weather conditions several stations were not sampled. Sampling elapsed for 7 days  
 103 around the clock, from south to north. Temperature, salinity, and fluorescence were measured at  
 104 every station with a conductivity-temperature-depth sensor (CTD, SBE25, Seabird Electronics, Inc.),  
 105 coupled to a Turner fluorometer. CTD's casts and net hauls were performed at depths of 200 m at  
 106 deeper stations or 5-10 m above the bottom at shallower stations.



107

108 Figure 1. Distribution of the sampled stations (black circles). The pink-shaded area is the Artabro  
 109 Gulf, an important spawning area for many commercial species. The main capes in the area are  
 110 shown in blue. Blue arrows are the geostrophic velocity of currents at each sampling station.

111 Ichthyoplankton sampling was performed with a MultiNet (Midi, 0.50 m<sup>2</sup> mouth opening)  
 112 consisting of 5 nets of 200 μm mesh. The MultiNet was equipped with a Scanmar depth sensor as  
 113 well as an electronic flowmeter located at the mouth. The depth strata, defined by the different  
 114 depths at which each net was open, were 0–20 m, 21–40 m, 41–60 m, 61–100 m, and 100–200 m. At the  
 115 stations located in depths shallower than 200 m the programmed terminal depth was adjusted  
 116 and/or the number of strata reduced. The net was towed obliquely at 2 knots. The duration of the  
 117 hauls was approximately one hour and the mean volume filtered for each depth stratum was 25 L  
 118 for the first three strata, 57 L for the fourth stratum, and 87 L for those at depths deeper than 100 m.  
 119 Samples were preserved in a 4% seawater/formalin buffered solution with borax.

120 In the laboratory, all fish larvae were sorted and identified to the lowest possible taxonomic  
 121 level. When identification at the species level was impossible, individuals were identified to the  
 122 family level. Selected taxa (those with ≥20 larvae caught, both day and night) were photographed  
 123 and, when possible, measured for standard length (±0.01 mm) using ImageJ (v. 1.53a).

124 Zooplankton was also sampled at each station from 200 m depth through vertical hauls using a  
 125 CalVET net (25 cm diameter, 53 μm mesh size) equipped with an electronic flowmeter at its mouth.  
 126 At shallower stations, hauling started 10 m above the bottom. Samples were filtered upon collection  
 127 through 55 and 200 μ mesh sieves to separate micro (55–200 μm) and mesozooplankton (>200 μm).  
 128 Both fractions were frozen in liquid nitrogen. In the lab, both fractions were dried in an oven at 60 °C  
 129 to estimate obtain their weight [31]. Then, micro- and mesozooplankton weight were standardized  
 130 with the total volume of filtered water to obtain biomass m<sup>-2</sup>. Mesozooplankton abundance

131 (zooAbd) was calculated in the laboratory from the multinet samples for every depth stratum in  
132 each station by using a semi-automatic image analysis technique [32]. For that purpose, a subsample  
133 of 5 ml from each sample was stained with 0.1% eosin for 24 h and scanned; the resulting images  
134 were processed using Zoolmage and ImageJ software.

135

## 136 **Data**

### 137 Environmental data

138 Chlorophyll fluorescence, temperature, and salinity at 10 m depth (referred to as chlorophyll;  
139 Chlor,  $\text{mg}\cdot\text{m}^{-3}$ ), sea surface temperature (SST,  $^{\circ}\text{C}$ ), and sea surface salinity (SSS, practical salinity  
140 scale) were extracted from the CTD data and used for most statistical analyses. Thermocline was  
141 obtained from the CTD data with the R packages *oce* and *rLakeAnalyzer*. The micro- and  
142 mesozooplankton biomass (MiB and MeB) values were referred as  $\text{mg}\cdot\text{m}^{-2}$ , mesozooplankton counts  
143 (Abdzoo) were standardized to  $\text{ind}\cdot\text{m}^{-3}$ , and depth stratum were also integrated for the sampled  
144 water column to obtain a value per station. Dynamic height (DH) was integrated over the water  
145 column and calculated from vertical profiles of temperature, salinity, and pressure using the 400 m  
146 depth as the reference level of no motion. At shallower stations, or when data were recorded only to  
147 200 m, the density anomaly at the closest 400 m station was assigned to the deepest level sampled by  
148 the CTD. As DH and integrated water column density are inversely proportional [33], areas of high  
149 DH correspond to low salinity, warm seawater and anticyclonic regions [34], whereas locations with  
150 low DH correspond to salty, cool seawater and cyclonic eddy regions, showing gradients in frontal  
151 regions [36,37]. Geostrophic velocities (GVs) were obtained by the first derivative of the DH profiles  
152 analysed on a regular grid of  $3 \times 3$  nautical miles, and extracting manually the closest value for each  
153 sampling point. Geostrophic velocities were used as an indicator of eddy boundaries and frontal  
154 regions because GV should be higher in these regions [38, 39]. Finally, Spiciness was estimated,  
155 which is defined as a state variable and constructed to characterize water masses and indicate  
156 double-diffusive stability [39], being higher in warm and salty (spicy) waters [40]. Spiciness was  
157 calculated using R software v.3.5.1 [41] and the package *oce* [42].

158 We used published data on upwelling and wind regimes to understand the environmental  
159 scenario prevailing during the survey. The upwelling index and information about eddies was  
160 obtained from Instituto Español de Oceanografía [43]. Winds regime were obtained from 'Puertos  
161 del Estado' database [44], specifically from the buoy located at Cabo Vilano ( $43.29^{\circ}\text{N}$  and  $9.12^{\circ}\text{W}$ ).

162 The maps of the physical and biological variables were constructed from the fitted variogram  
163 and posterior kriging of the values per station with the R packages *gstat* [45] and *automap* [46].

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### 165 Community

166 Fish larval abundance was standardized to the number of larvae found beneath a  $10 \text{ m}^2$  area of  
167 sea surface [ $\text{ind}\cdot 10 \text{ m}^{-2}$ ]. Similarly, larval densities were standardised to individuals  $1000 \text{ m}^{-3}$  and  
168 calculated using flowmeter measurements [47]. Larval fish diversity (Shannon-Wiener index) and  
169 species richness were calculated for each station. Densities were also calculated for each depth  
170 stratum.

### 171 Horizontal distribution

172 Several regression models were tested to assess the influence of the biological and  
173 environmental variables (MiB, MeB, Chlor, zooAbd, depth, SSS, SST, DH and GV) on the parameters  
174 of the LFC: larval abundance, diversity (Shannon index), and richness of species at every sampled  
175 station. These parameters were obtained integrating the number of larvae at every depth stratum in  
176 each sampling station.

177 Data exploration was carried out after testing for collinearity [48, 49]. When the correlation  
178 between pairs of variables was  $>0.6$ , one of the variables was removed from analyses. Finally, the  
179 covariables included in the models were depth, SST, SSS, GV, Chlor, MeB, and MiB. Chlor and depth  
180 were log transformed to reduce the influence of very high values. The fish larval abundance was  
181 modeled using General Additive Model (GAM), given the nonlinear behaviour of some covariates in

182 relation to the response variables. Richness and abundance were adjusted to a negative binomial  
 183 distribution with a logistic link function, and diversity was adjusted to a normal distribution. To  
 184 model larval abundance, we added the volume of water filtered at every station as an offset in the  
 185 equation. The final model was selected following a forward stepwise procedure based on the AIC  
 186 minimization. The model assumptions were verified by plotting the residuals against the fitted  
 187 values, each covariate in the model, and each covariate not included in the model. The R package  
 188 mgcv [50] was used to fit the model. The same procedure was used for the other LFC parameters.

189 Cluster and ordination methods were used to analyse the structure of the LFC using the matrix  
 190 of the larval fish abundances, but selected taxa had to have abundances greater than 0.2 larvae·10 m<sup>-2</sup>  
 191 and be present at more than 5% of the stations, resulting in a matrix of twenty-one species. The  
 192 abundance data were log (x+1) transformed to dampen the influence of the most abundant species  
 193 prior to obtaining the dissimilarity (Bray-Curtis) matrix [51, 52]. R package NbClust [53] was used to  
 194 find the more appropriated number of clusters, while ANOSIM (Analysis of Similarities) was  
 195 performed to test the significance of the clusters. Hierarchical agglomerative clustering with average  
 196 linking in conjunction with non-metric multidimensional ordination (nMDS) was used to identify  
 197 assemblages.

198 The relationship between environmental factors and community structure was assessed with  
 199 canonical correspondence analysis (CCA). The environmental data matrix included the values of the  
 200 biological and oceanographic variables at a depth of 10 m. The selection of variables included in the  
 201 CCA followed a forward stepwise procedure. Significance (p<0.05) was tested with an ANOVA-like  
 202 permutation test. Only those variables that significantly explained the species distribution pattern  
 203 were included in the model. The canonical axes were also tested for significance with the same  
 204 permutation test. All the ordinations were performed using the vegan package in R [54,55].

205 The relative length distribution was explored to assess the direction that the most influential  
 206 currents were having in the LFC. Lengths were standardized to each species maximum length  
 207 registered during the entire survey, as a proxy of age to infer the spawning area since smaller  
 208 specimens will likely be nearer to the spawning area.

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#### 210 Vertical distribution

211 A matrix with the densities of species with more than 20 individuals (adding the day and night  
 212 collections) was created for the analysis of vertical and daily (day/night) distributions. This resulted  
 213 in a matrix of fifteen species, 5 depth strata, and two light regimes. The depth strata were 0-20 m,  
 214 21-40 m, 41-60 m, 61-100 m, and >100 m. For the light regime analysis, the day period was defined as  
 215 7:30 am till 9:30 pm GMT, and the night period was defined as 10:30 pm till 6:30 am GMT,  
 216 considering the sunrise and sunset time in the study area during sampling. Samples between  
 217 6:30-7:30 am and 9:30-10:30 pm were considered as transitional and discarded for this analysis. The  
 218 weighted mean depths (WMDs) of the larvae in each (MultiNet) haul were calculated as the centre of  
 219 masses of the larval distribution:

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$$\text{WMD} = \sum_{i=1}^5 \frac{n_i \times d_i}{n_i} \quad (1)$$

221 where  $n_i$  is the density of fish larvae [ind·1000 m<sup>3</sup>] in the  $i$ th stratum, and  $d_i$  is the mid-depth of the  
 222  $i$ th stratum [56].

223 The amplitude of the diel vertical migrations (DVM) was calculated as the difference between  
 224 the average WMDs for the day and night periods (DVM= WMD<sub>day</sub> – WMD<sub>night</sub>). Positive values of  
 225 DVM (type I) correspond to species that move towards the surface during the night, whereas  
 226 negative values indicate downward movement at night (type II) [57]. A t-test was used to test for the  
 227 significance of the DVM for each species.

228 The larval densities were used to calculate the Bray-Curtis matrix of distances from the log  
 229 x+1-transformed data, these distances were used for the clustering and nMDS. ANOSIM was

230 performed to test if the vertical structure of larval assemblages existed depending on depth and time  
231 of day.

232 Differences between depth strata and day/night abundances were tested using Permutational  
233 Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA) with the R package  
234 vegan.

235 Because DVM is often a size-related (ontogenetic) phenomenon, with larvae starting to migrate  
236 after yolk sac absorption [57], differences in larval length between day and night and depth strata  
237 were also assessed, for the selected taxa, by using a two-factor ANOVA. When significant  
238 differences were found, the Tukey post-hoc test was conducted to identify which groups were  
239 significantly different from the other. The ANOSIM, NMDS, and distance matrix calculations were  
240 done using the R package vegan.

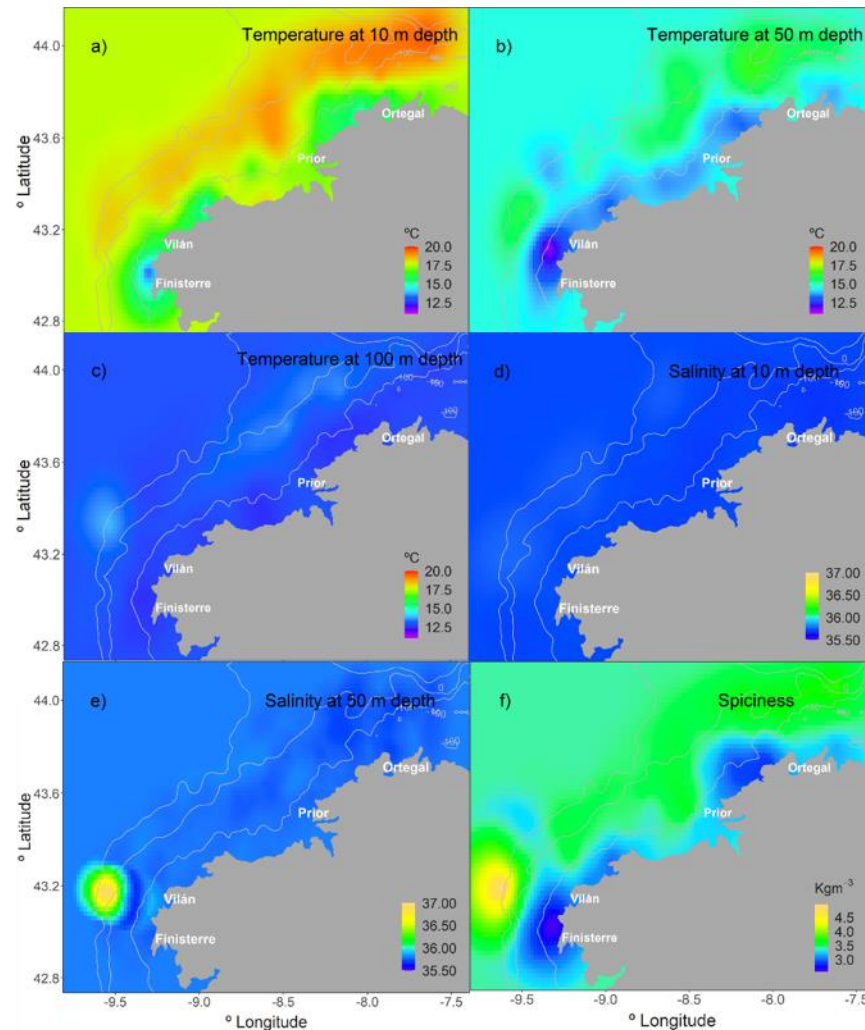
241 The standard deviation and standard error were used to describe the dispersion of  
242 environmental and biological data.

### 243 3. Results

#### 244 Environmental variables

245 There was a north-prevailing wind regime during the sampling period, increasing its intensity  
246 towards the end of the cruise, although in the preceding days of the survey, northerly and southerly  
247 pulses were alternating. The change of wind direction resulted in an average upwelling index (UI)  
248 for the month of July below the historical average value for this period ( $21 \text{ m}^3 \cdot \text{s}^{-1} \cdot \text{km}^{-1}$  and  $370 \text{ m}^3 \cdot$   
249  $\text{s}^{-1} \cdot \text{km}^{-1}$ , respectively). However, the dominant upwelling conditions prevailed during the cruise and  
250 during the four previous days – the mean UI was  $191 \text{ m}^3 \cdot \text{s}^{-1} \cdot \text{km}^{-1}$ .

251 The hydrographic structure along the sampled area changed due to the wind regime and  
252 coastal orientation. Upwelling events occurred south and north of the grid area during the survey,  
253 although they were slightly weaker in the north. In the Artabro Gulf area, the average temperatures  
254 were higher than those in the surroundings, and linked to the higher GV which suggests the  
255 presence of an anticyclonic eddy. Nevertheless, the upwelling event was not strong enough to  
256 completely break the stratification (except partially in the inner shelf), as the water column was  
257 stratified in the upper ~60 m, according to CTD's profiles, except when the wind-driven mixed layer  
258 reach the top 30 m.



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**Figure 2.** Temperature at depths of a) 10 m, b) 50 m, and c) 100 m; salinity at depths of d) 10 m and e) 50 m; and f) spiciness. The plot of salinity at 100 m is not shown due to its very low standard deviation (2.9).

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The SST showed an along-shelf temperature front with colder waters occupying the inner shelf; it varied between 13.2°C next to Cape Finisterre and 19.5 °C west of Cape Ortegal (Figure 2a). The lowest SSS (35.6) were associated with freshwater masses from river runoff near Cape Ortegal, although other coastal low values were found south of Artabro Gulf (35.7). The maximum SSS (35.8) was recorded near the Cape Finisterre over the 200 m isobath (Figure 2d). Temperature and salinity at different depths show cross-shelf gradients. Temperature gradient was from minimum to maximum, from coast, outwards. It ranged from 12.5 °C to 17.8 °C (between bathymetris 10 m and 150 m) and reached its minimum north of Finisterre cape and maximum in the north of the area, over the 200-500 bottom isobaths (Figure 2a,b). Salinity had minute variations with depth, except off Finisterre cape where salinity reached 36.9 at 50 m depth, over the 200-500 isobath (Figure 2e).

A front separates the colder and fresher waters of the inner shelf from the warmer and saltier offshore waters. This front is well reflected by the spiciness, which ranged from 2.3 to a maximum of 5.5 kg.m<sup>-3</sup> offshore of Cape Finisterre, that reveals the presence of a subsurface thermohaline front (Figure 2f).

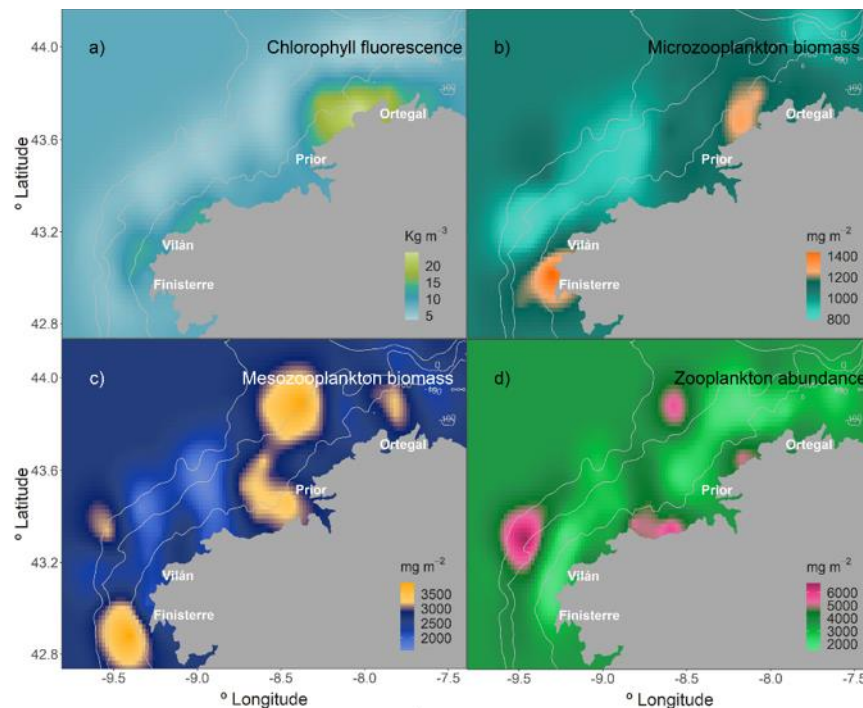
The gradient between the cold freshwater and warm salty water resulted in an area of low dynamic heights along the inner shelf (over grounds < 100 m) and a geostrophic current flowing south-westwards along the 100 m isobath. The dynamic height ranged from -3.1 to 3.4 cm in the whole area, and geostrophic velocities were weak (< 10 cm.s<sup>-1</sup> in the upper levels and < 5 cm.s<sup>-1</sup> at depths under 100 m) but exceeded 30 cm.s<sup>-1</sup> at some points near Cape Ortegal (Figure 1). The general



282 currents in the area informed of an anticyclonic mesoscale feature associated with high temperature  
 283 and salinity, stacking in the gulf during the entire period.

#### 284 Biological variables

285 Regarding the biological variables, the average superficial chlorophyll fluorescence was  $8.4 \pm$   
 286  $7.7 \text{ mg}\cdot\text{m}^{-3}$ , microzooplankton biomass was  $1033.1 \pm 220.4 \text{ mg}\cdot\text{m}^{-2}$ , mesozooplankton biomass was  
 287  $2661.5 \pm 916.2 \text{ mg}\cdot\text{m}^{-2}$ , and mesozooplankton abundance was  $3320.4 \pm 1472 \text{ ind}\cdot\text{m}^{-3}$ . Primary  
 288 production (Chlor) at 10 m depth was higher near the coast than in the shelf break. The mean Chlor  
 289 at the stations below the 100 m isobath was  $12.3 \pm 9.5 \text{ mg}\cdot\text{m}^{-3}$  and  $5.8.1 \pm 4.8 \text{ mg}\cdot\text{m}^{-3}$  in stations between  
 290 100-200 m isobaths (Figure 3a). The MiB maximum ( $1836.3 \text{ mg}\cdot\text{m}^{-2}$ ) were located below the 100 m  
 291 isobaths off the Finisterre coast and in a small area of the Artabro coast (Figure 3b), while the MeB  
 292 maximum ( $4990.5 \text{ mg}\cdot\text{m}^{-2}$ ) were observed between the 100-200 m isobaths in the Finisterre area and  
 293 over the 200 m isobath in front of the Artabro coast (Figure 3c). Zooplankton abundance show its  
 294 maximum ( $7405.2 \text{ ind}\cdot\text{m}^{-3}$ ) between 200-500 isobaths north of Finisterre cape and in some stations in  
 295 the Artabro Gulf ( $6945.1 \text{ ind}\cdot\text{m}^{-3}$ ). Concerning the vertical distribution of chorophyll, the maximum  
 296 was concentrated in the 20-60 m layer ( $74.1 - 0.6 \text{ mg}\cdot\text{m}^{-3}$ , max-min), while the maximum zooplankton  
 297 abundance was mainly in the 0-60 m layer ( $3635.9 - 101.2 \text{ ind}\cdot\text{m}^{-3}$ , max-min).



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299 **Figure 3.** a) Chlorophyll fluorescence b) microzooplankton biomass c) mesozooplankton biomass d)  
 300 mesozooplankton abundance.

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#### 302 Descriptors and structure of the larval fish community

303 A total of 2189 larvae belonging to 64 taxa and grouped into 31 families were collected and  
 304 identified (Table 1). The percentage of unidentified larvae (2.4%) was due to a lack of early life  
 305 history descriptions of the regional species, damaged specimens, and to a major extent due to the  
 306 early development stage of the larvae and lack of characteristic features. The abundance per station  
 307 ranged from 5.7 to 749.6 larvae $\cdot$ 10 m<sup>-2</sup>, and averaged  $217.2 \pm 189.1$  larvae $\cdot$ 10 m<sup>-2</sup>, with a maximum of  
 308 139 larvae collected in one sampling station (Figure 4a). The most diverse family represented was  
 309 Sparidae, with six species (one identified to the genus level) and Gobiidae was the most abundant



310 (specimens were grouped into the family level due to the high difficulty in their classification). Two  
 311 coastal species, *Trachurus trachurus* (pelagic) and *Serranus cabrilla* (demersal), were the most  
 312 abundant and ubiquitous species, and the unique mesopelagic (oceanic slope) species that was  
 313 among those with relative abundance higher than 1% was *Maurolicus muelleri* (Table 1).

314 The maximum abundance (749.6 larvae·10 m<sup>-2</sup>) of larvae was recorded on the Artabro coast and  
 315 it was mainly due to the contribution of the family Gobiidae (161.8 larvae·10 m<sup>-2</sup>) and non-identified  
 316 larvae (275 larvae·10 m<sup>-2</sup>). The second highest value of abundance (668.3 larvae·10 m<sup>-2</sup>) was made  
 317 south of Artabro Gulf, where *T. trachurus* contributed the most to the total larvae abundance (244  
 318 larvae·10 m<sup>-2</sup> (Figure 4a) . Regarding diversity of the community, the highest value was recorded  
 319 between Cape Prior and Cape Ortegá; for richness the maximum was registered near the Artabro  
 320 coast (Figure 4b, c). The species richness values ranged from 0 to 20 (11.9 ± 4.7), and the Shannon  
 321 index ranged from 0 to 2.7 (1.9 ± 0.5).

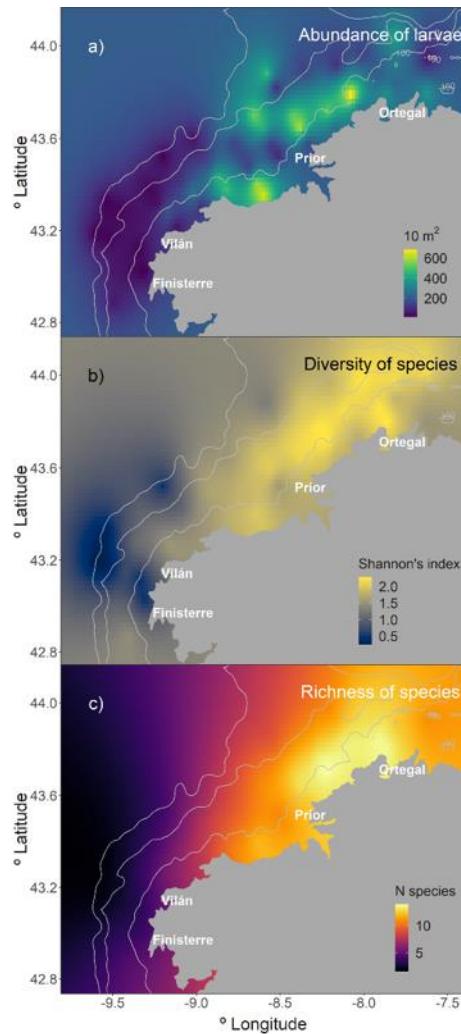
322 The mean standard length of *T. trachurus* was 3 ± 1.3 mm, ranging from 1.1 to 7.0 mm; for *S.*  
 323 *cabrilla* it was 3.7 ± 1.2 mm, ranging from 1.4 to 6.8 mm; for *M. muelleri* it was 7 ± 2.1 mm, ranging  
 324 from 1.6 to 11.2 mm; and for *C. julis* it was 3.2 ± 1.3 mm, ranging from 1.2 to 10.7 mm (Table 5)

325 **Table 1.** List of larval fish species grouped by families collected off the Galician coast during the Cramer1207  
 326 research survey. The families are ordered by decreasing abundance. Code: taxon code; Oc: percentage of  
 327 occurrence (%); RA: relative abundance (%). The taxa written in blue are those with relative abundances > 0.2  
 328 larvae 10·m<sup>-2</sup> and that were present in >5% of the stations, therefore were included in subsequent analyses.

Family/species	Code	% Oc	% RA	Family/species	Code	% Oc	% RA
<b>Family Gobiidae</b>	G	58.2	11.4	<b>Family Trachinidae</b>			
<b>Family Carangidae</b>				<i>Trachinus draco</i>	Td	22.4	2.3
<i>Trachurus trachurus</i>	Tt	62.7	9.2	<i>Echiichthys vipera</i>	Ev	6	0.4
<i>Trachurus mediterraneus</i>	Tm	11.9	1.5	<b>Family Gadidae</b>			
<b>Family Labridae</b>				<i>Gadiculus argenteus</i>	Ga	11.9	1.8
<i>Coris julis</i>	Cj	49.3	6.2	<i>Pollachius pollachius</i>	Ppll	1.5	0.3
<i>Ctenolabrus rupestris</i>	Cr	19.4	2.3	<i>Raniceps raninus</i>	Rr	3	0.2
<i>Symphodus melops</i>	Sm	7.5	0.5	<b>Family Scorpaenidae</b>			
Unidentified spp.	L	1.5	0.2	<i>Scorpaena porcus</i>	Spr	26.9	2.2
<i>Labrus bergylta</i>	Lb	1.5	0.1	<b>Family Merlucciidae</b>			
<b>Family Serranidae</b>				<i>Merluccius merluccius</i>	Mm	19.4	2.1
<i>Serranus cabrilla</i>	Scb	76.1	8.5	<b>Family Caproidae</b>			
<i>Serranus hepatus</i>	Sh	3	0.1	<i>Capros aper</i>	Ca	19.4	1.7
<b>Family Sparidae</b>				<b>Family Cepolidae</b>			
<i>Pagellus acarne</i>	Pa	35.8	3.0	<i>Cepola macrophthalmia</i>	Cmc	11.9	1.1
<i>Pagrus pagrus</i>	Ppgr	17.9	1.3	<b>Family Mugilidae</b>			
<i>Boops boops</i>	Bb	9	1.0	<i>Mugil cephalus</i>	Mc	9	1.0
Unidentified spp.	S	9	1.1	<b>Family Mullidae</b>			
<i>Diplodus</i> spp.	Dspp	9	0.5	<i>Mullus surmuletus</i>	Ms	10.4	1.0
<i>Pagellus bogaraveo</i>	Pb	3	0.4	<b>Family Triglidae</b>			
<i>Pagellus erythrinus</i>	Pe	3	0.4	<i>Eutrigla gunardus</i>	Eg	4.5	0.5
<b>Family Sternoptychidae</b>				<i>Lepidotrigla cavillone</i>	Lcv	3	0.3
<i>Maurolicus muelleri</i>	Mmll	62.7	6.4	<b>Family Pleuronectidae</b>	P		
<i>Argyropelecus hemigymnus</i>	Ah	6	0.3	Unidentified spp.		1.5	0.3
<b>Family Blenniidae</b>				<i>Pleuronectes platessa</i>	Ppl	1.5	0.2
<i>Parablennius pilicornis</i>	Pp	40.3	4.3	<b>Family Scombridae</b>			
<i>Parablennius tentacularis</i>	Pt	4.5	0.3	<i>Scomber colias</i>	Sc	3	0.4
<i>Lipophrys pholis</i>	Lp	1.5	0.2	<b>Family Scophthalmidae</b>	Scph	1.5	0.1
<i>Coryphoblennius galerita</i>	Cg	1.5	0.1	Unidentified spp.			
<i>Parablennius gattorugine</i>	Pg	1.5	0.1	<i>Zeugopterus punctatus</i>	Zp	1.5	0.2
<b>Family Bothidae</b>				<b>Family Soleidae</b>			

<i>Arnoglossus thori</i>	At	35.8	3.7	<i>Pegusa lascaris</i>	PI	1.5	0.2
<i>Arnoglossus laterna</i>	Al	10.4	1.0	<i>Microchirus variegatus</i>	Mv	1.5	0.1
<i>Arnoglossus imperialis</i>	Ai	1.5	0.1	<b>Family Gobiesocidae</b>			
<i>Arnoglossus</i> spp.	Aspp	1.5	0.0	<i>Diplecogaster bimaculata</i>	Db	1.5	0.1
<b>Family Myctophidae</b>				<i>Lepadogaster candollei</i>	Lcn	1.5	0.03
<i>Ceratoscopelus maderensis</i>	Cmd	14.9	1.3	<b>Family Gonostomatidae</b>			
<i>Lampanyctus crocodilus</i>	Lc	10.4	1.3	<i>Cyclothone braueri</i>	Cb	3	0.1
<i>Myctophum punctatum</i>	Mp	17.9	1.2	<b>Family Paralepididae</b>			
<i>Benthoosema glaciale</i>	Bg	13.4	0.7	<i>Lestidiops sphyrenoides</i>	Ls	1.5	0.1
Unidentified spp.	M	1.5	0.1	<b>Family Syngnathidae</b>			
<i>Notoscopelus elongatus</i>	Ne	3	0.0	<i>Nerophis lumbriciformis</i>	Nl	1.5	0.1
<b>Family Callionymidae</b>	Cspp	40.3	4.3	<b>Family Lotidae</b>			
Unidentified individuals	U	29.9	4.2	<i>Gaidropsarus vulgaris</i>	Gpv	1.5	0.1
<b>Family Clupeidae</b>				<b>Family Argentinidae</b>			
<i>Sardina pilchardus</i>	Sp	28.4	3.2	<i>Argentina spyraena</i>	As	1.5	0.04
<b>Family Engraulidae</b>							
<i>Engraulis encrasicolus</i>	Ee	26.9	2.7				

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**Figure 4.** Distribution of the LFC parameters of a) abundance, b) diversity, and c) richness.

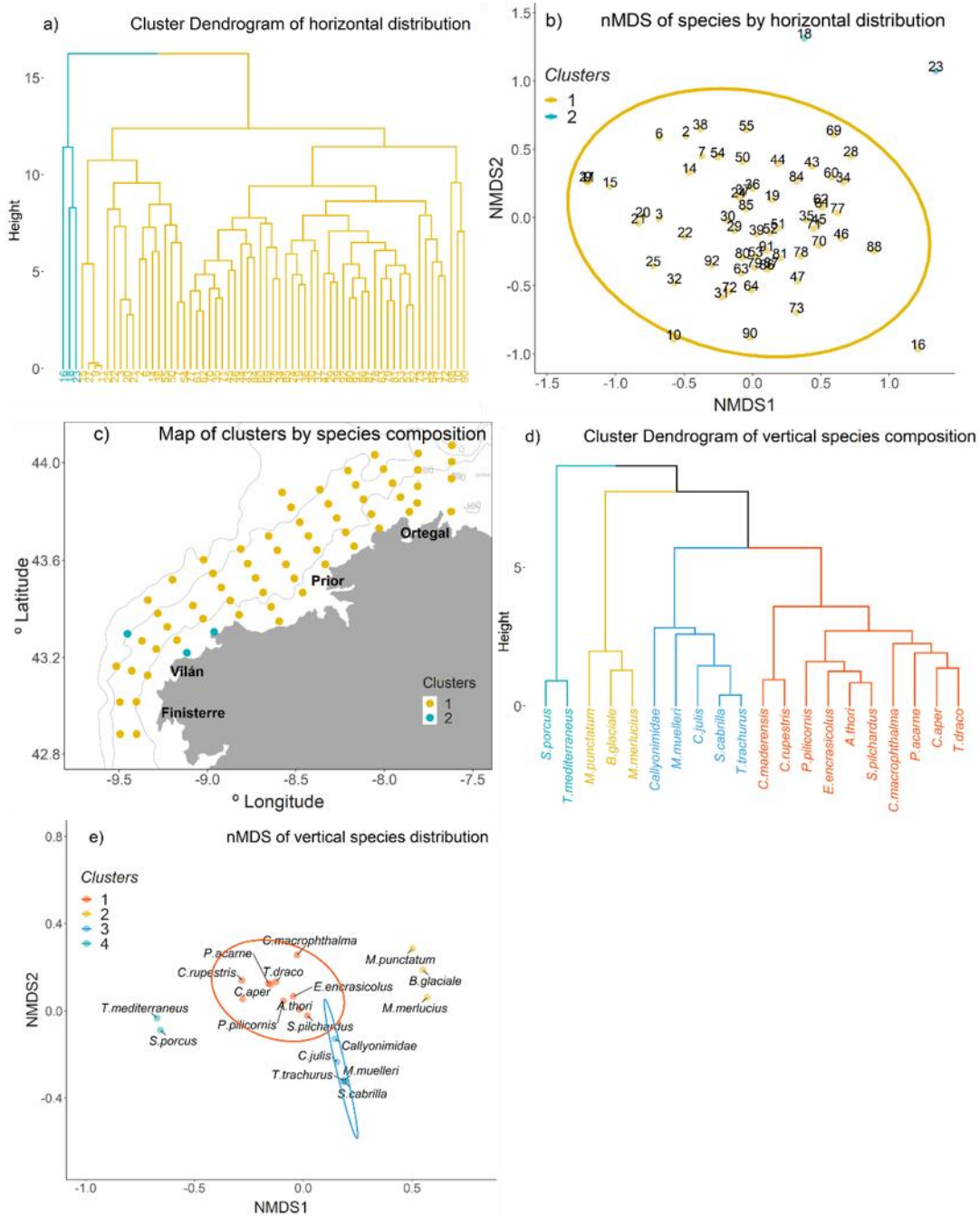
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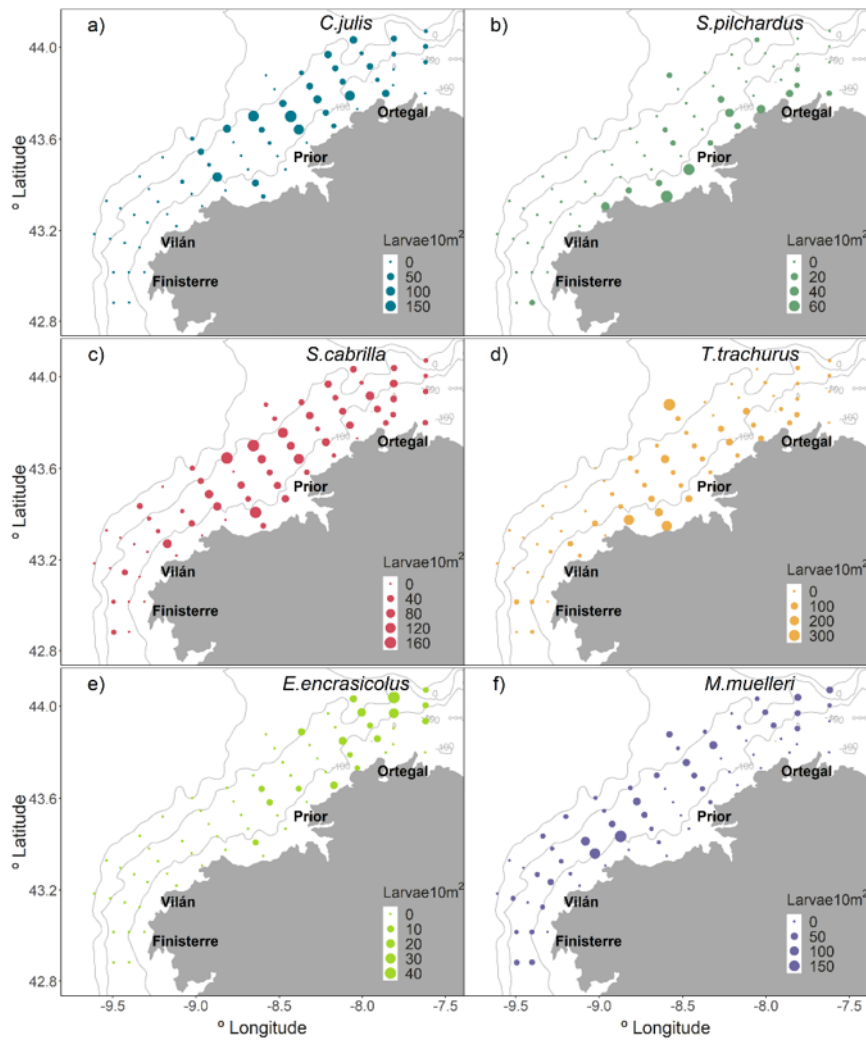
The species that define the summer LFC did not show any horizontal structure (Figure 5); they were not differentially grouped, even among coastal-, shelf- or slope-spawning species as indicated by cluster analysis. The method used to find the best grouping for the dissimilarity matrix identified

335 two clusters as the best result for the matrix of dissimilarities (Figure 5a, c), which was corroborated  
 336 by the nMDS ordination (Figure 5b). Groups separated at a similarity level of 85%. ANOSIM was  
 337 performed as well and confirmed this grouping (R statistic=0.8,  $p < 0.005$ ). ANOSIM was also used to  
 338 test the three clusters option but results did not supported (R statistic=0.3,  $p < 0.005$ )



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 340 **Figure 5.** a) Dendrogram, b) NMDS ordination and c) map of the clustering of the horizontal species  
 341 composition, d) dendrogram, and e) nMDS ordination of the vertical species composition.

342 In general, no differential pattern was evident when mapping the most abundant taxa, except  
 343 for *S. pilchardus* (Figure 6b) and *E. encrasicolus* (Figure 6e) which were concentrated in shallow waters  
 344 and almost entirely near to Cape Ortegá, respectively. *Serranus cabrilla* was widespread over the  
 345 study area but dominating north of Artabro Gulf (Figure 6c), while *M. muelleri* had no clear  
 346 distribution pattern (Figure 6f). *Trachurus trachurus* and *C. julis* were more abundant in the Artabro  
 347 Gulf, although *C. julis* showed a more northward distribution (Figure 6a).



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**Figure 6.** Geographical distribution of the most abundant species.

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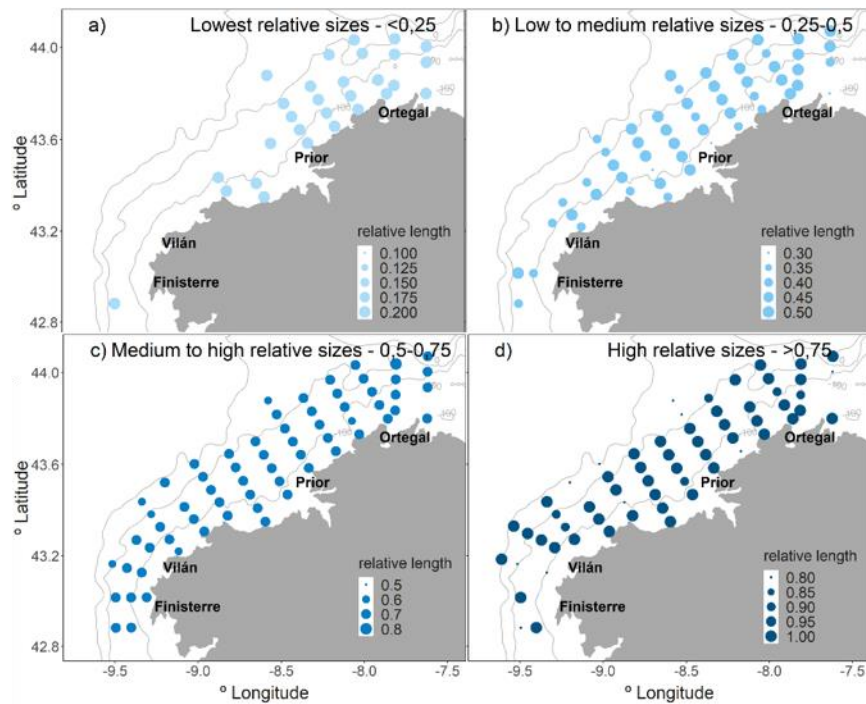
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From the ontogenic point of view, the horizontal distribution of the larvae of the most abundant species did not show any trend, except for *S. pilchardus* which appears to be concentrated by the coast (Figure 6b). Overall, the horizontal distribution of larvae according to relative length showed that smaller larvae accumulated in the northern area, from the Artabro Coast to Cape Ortegál, while bigger larvae were distributed between Cape Vilán and Cape Ortegál and towards the slope (Figure 7).



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**Figure 7.** Larval fish community distribution by relative length: a)  $\leq 0.25$ , b)  $[0.25-0.5]$ , c)  $[0.5-0.75]$ , and d)  $>0.75$ .

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In contrast, according to the multinet samples results, the vertical distribution larvae appeared well structured, showing higher abundances in the first 40 m. The PERMANOVA analysis ( $R^2=0.27$ ,  $p \leq 0.001$ ) and Tukey post-hoc confirm these differences (Table 2b). Mesozooplankton abundance was higher in the first 60 m (min-max, mean: 101.2-3635.9, 988.7 ind.m<sup>-3</sup>), both day (101.2-3635.9, 913.3 ind.m<sup>-3</sup>) and night (155.0-3566.1, 1056.8 ind.m<sup>-3</sup>) (Table 2a). Most of the species were almost absent from the 60–200 m depth stratum (except some myctophids) during the day and night. The vertical distribution of the most abundant species was not significantly correlated with mesozooplankton, except for *A. thori* and *S. pilchardus* (Table 3). For their distribution in the water column, cluster and ordination analyses (Figure 5d, e) showed four groups (ANOSIM R statistic= 0.95,  $p < 0.005$ ) of larvae at a similarity level of 40% (Figure 5d, e). The resulting groups are as follows: 1) *S. porcus* and *T. mediterraneus*; 2) *M. punctatum*, *B. glaciale*, and *M. merluccius*; 3) *M. muelleri*, *C. julis*, *S. cabrilla*, *Callionymidae*, and *T. trachurus*; and 4) *C. maderensis*, *C. rupestris*, *C. macrophthalma*, *P. acarne*, *P. pilicornis*, *E. encrasicolus*, *A. thori*, *S. pilchardus*, *C. aper*, and *T. draco*. However, the ANOSIM detected only a slight segregation along the water column (ANOSIM R statistic= 0.3,  $p > 0.005$ ), and no differences in community composition between day and night (R statistic= 0.06  $p < 0.005$ ). No significant correlation between the vertical migrations of the pool of fish larvae and the mesozooplankton was observed, except for *M. muelleri*, *C. julis*, and *S. cabrilla* that performed significant type I DVMs (i.e., upward movement at night) (Table 4). The mean vertical displacement was  $7.8 \pm 6.5$  m for the selected species, with *M. muelleri* being the species that had a wider migration (27 m).

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385**Table 2a.** Mean density (standard error) of the larval fish species (larvae·1000 m<sup>-3</sup>), mesozooplankton (individuals·m<sup>-3</sup>), and all fish larvae (larvae·1000 m<sup>-3</sup>) in each depth stratum and period (day and night).

Species	0-20 m		20-40 m		40-60 m		60-100 m		>100 m	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
<i>A. thori</i>	55.0 ±6.6	72.2 ±12.2	88.4 ±53.6	38.1 ±6.6	38.4 ±6.4	47.6	13.9	20.0		
<i>C. aper</i>	70.1 ±30.3	60.0 ±40.0	94.0 ±54.1	34.5	32.3			14.1		
<i>C. maderensis</i>	39.2 ±13.5	160.1 ±88.3	32.1 ±6.4	84.8 ±24.0		62.7 ±28.2				
<i>C. julis</i>	184.6 ±58.6	286.0 ±98.3	127.5 ±38.1	58.2 ±5.6	84.2 ±28.1	41.1 ±6.6	21.9 ±4.1	21.7	6.3	
<i>E. encrasicolus</i>	34.3 ±8.7	76.1 ±30.2	40.8 ±6.6	45.2 ±6.1	34.0 ±1.7	53.4 ±18.8	14.9 ±1.0			
<i>L. crocodilus</i>	43.5	73.8 ±26.2	35.7	123.7 ±59.1		90.6 ±60.9				
<i>M. muelleri</i>	58.4 ±13.0	223.9 ±163.5	53.2 ±5.6	98.7 ±56.4	39.2 ±0.8	63.2 ±13.7	24.4 ±4.3	34.9 ±5.7	40.2 ±18.2	43.6 ±24.1
<i>M. merluccius</i>			35.7	51.1 ±13.3	26.0 ±9.4	34.6 ±2.4	13.5 ±5.3	17.0 ±2.0	33.3	
<i>M. punctatum</i>			45.5	40.0	47.0 ±15.4	94.7 ±33.4	11.4	27.8 ±10.1		
<i>P. acarne</i>	81.5 ±16.9	52.8 ±10.3	37.0	45.5	32.3		18.5			
<i>P. pilicornis</i>	72.5 ±12.2	63.5 ±8.9	44.7 ±20.8	76.3 ±7.3	32.3	34.5	20.4	20.0		
<i>S. pilchardus</i>	108.8 ±18.1	104.3 ±24.5	90.1 ±28.9	127 ±79.0	44.4 ±12.4	29.3 ±3.0	46.8 ±24.6	17.9		
<i>S. cabrilla</i>	158.7 ±26.8	251.7 ±45.2	152.6 ±37.4	86.4 ±29.0	86.5 ±19.8	18.2	22.8 ±6.1			27.0
<i>T. draco</i>	55.2 ±9.0	113.9 ±43.5	29.4 ±6.2	69.0	41.0 ±4.7		13.0			
<i>T. trachurus</i>	134.1 ±44.5	142.8 ±44.8	254.1 ±89.2	58.7 ±12.1	79.3 ±20.5	75.1 ±21.2	16.2 ±1.8	60.0	31.3	
<b>All fish larvae</b>	89.7 ±1.0	127.1 ±7.3	109.8 ±14.0	97.8 ±14.9	81.5 ±18.5	65.9 ±13.5	30.8 ±8.4	30.2 ±5.6	34.1 ±3.6	48.6 ±10.9
<b>Mesozoo-plankton</b>	1037.0 ±106.3	1277.4 ±148.1	975.1 ±98.4	1136.0 ±136.9	723.0 ±78.0	719.5 ±70.4	327.6 ±29.2	347.0 ±26.8	219.5 ±25.9	236.8 ±39.3

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**Table 2b.** Tuckey post-hoc test for the differences between larval abundances, per strata (p<0.05).

	diff	lwr	upr	p adj
[0-20 m]-[20-40 m]	0,07	-0,03	0,18	0,300
[0-20 m]-[40-60 m]	0,14	0,02	0,25	0,008
[0-20 m]-[60-100 m]	-0,01	-0,13	0,10	0,996
[0-20 m]- >100 m	0,31	0,19	0,42	0,000
[20-40 m]-[40-60 m]	0,06	-0,05	0,18	0,522
[20-40 m]-[60-100 m]	-0,09	-0,20	0,02	0,205
[20-40 m]- >100 m	0,38	0,26	0,49	0,000
[40-60 m]-[60-100 m]	-0,15	-0,27	-0,03	0,006
[40-60 m]- >100 m	0,44	0,32	0,57	0,000
[60-100 m]- >100 m	0,29	0,17	0,41	0,000

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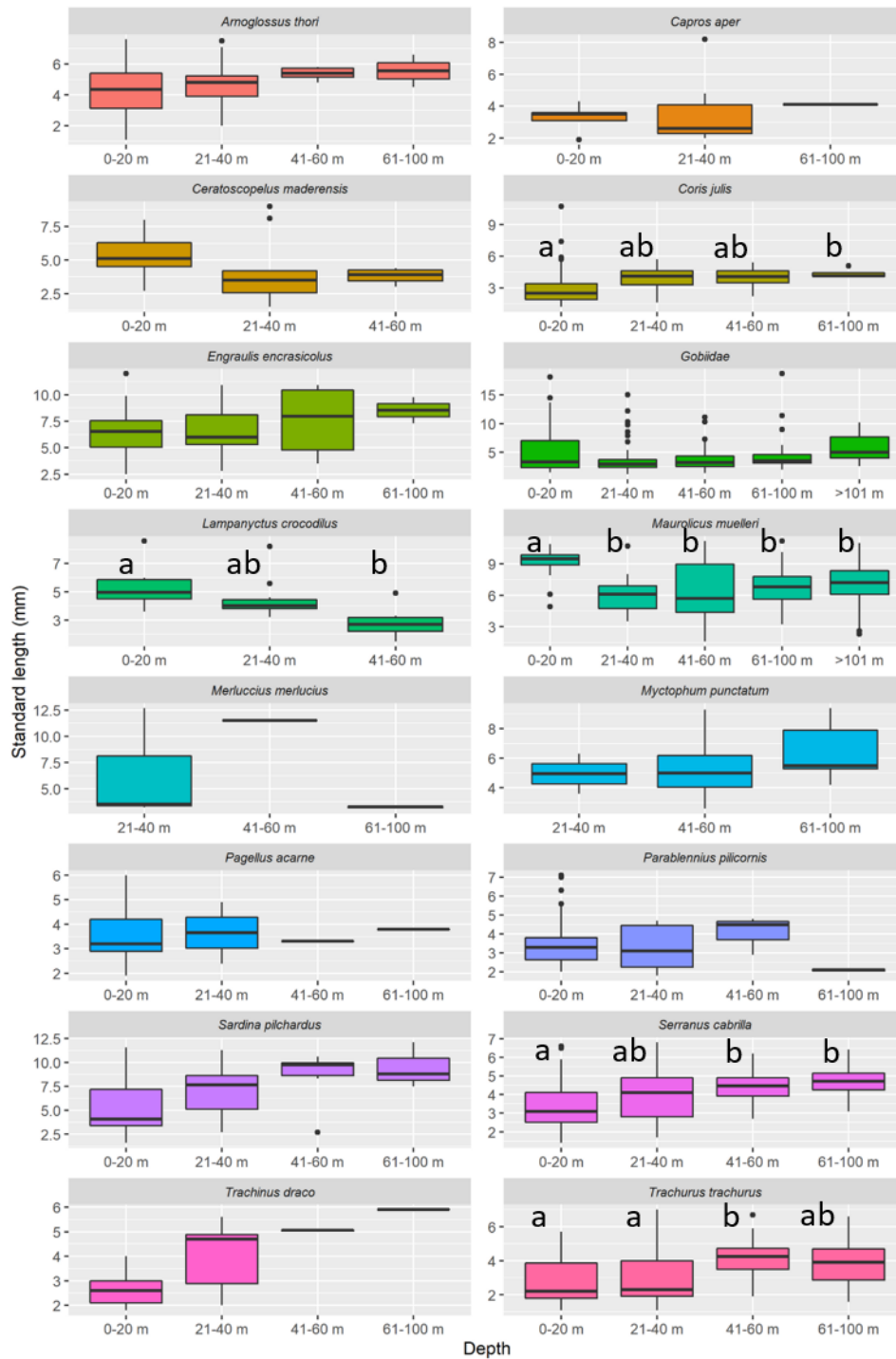
389 **Table 3.** Pearson's correlation coefficients between the vertical distributions (weighted mean depth,  
 390 WMDs) of fish larvae and mesozooplankton, where the \* stands for  $p < 0.01$ .

Species	R
<i>A. thori</i>	0.54*
<i>C. aper</i>	0.19
<i>C. maderensis</i>	-0.3
<i>C. julis</i>	0.15
<i>E. encrasicolus</i>	0.32
<i>L. crocodilus</i>	0.19
<i>M. muelleri</i>	0.37
<i>M. merluccius</i>	-0.08
<i>M. punctatum</i>	-0.29
<i>P. acarne</i>	-0.04
<i>S. pilchardus</i>	0.39*
<i>S. cabrilla</i>	-0.01
<i>T. draco</i>	0.21
<i>T. trachurus</i>	0.35
<b>All fish larvae</b>	<b>0.53*</b>

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392 **Table 4.** Results of the day and night weighted mean depth analysis and respective t-test analysis.  
 393 The data show the diel vertical migration (DVM) of the dominant species. Positive DVM indicates  
 394 species ascending at night and descending during the day (DVM type I). Negative DVM indicates  
 395 species descending at night and ascending during the day (DVM type II).

Species	DVM	t-statistic	p-value	Low C.I.	High C.I.
<i>A. thori</i>	3.6	0.4	0.7	-16.6	23.9
<i>C. aper</i>	-9.5	-0.6	0.6	-60.6	41.6
<i>C. maderensis</i>	-5.9	-1.1	0.3	-19.2	7.33
<i>C. julis</i>	11.4	3.3	0.0**	4.33	18.5
<i>E. encrasicolus</i>	7.1	1.3	0.2	-4.52	18.8
<i>M. muelleri</i>	27.1	2.7	0.0*	6.42	47.8
<i>M. punctatum</i>	-1.9	-0.2	0.9	-24.8	21.1
<i>P. acarne</i>	2.1	0.4	0.7	-8.76	13.0
<i>P. pilicornis</i>	-4.8	-0.8	0.4	-17.9	8.29
<i>S. pilchardus</i>	-4.7	-0.4	0.7	-31.9	22.6
<i>S. cabrilla</i>	9.5	2.3	0.0*	1.13	17.9
<i>T. draco</i>	13.3	1.9	0.1	-2.34	28.9
<i>T. trachurus</i>	5.2	1.2	0.2	-3.61	14.0
<b>All fish larvae</b>	<b>3.9</b>	<b>0.6</b>	<b>0.5</b>	<b>-8.4</b>	<b>16.2</b>
<b>Mesozooplankton</b>	<b>1.2</b>	<b>0.2</b>	<b>0.8</b>	<b>-9.4</b>	<b>11.8</b>



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**Figure 8.** Length distribution of fish larvae at varying depths. Line: median; box: 1<sup>st</sup> and 3<sup>rd</sup> quartiles; whiskers: maximum and minimum values; black dots: outliers. The results of the Tukey post-hoc test ( $\alpha=0.01$ ) for differences in larval length of the most abundant taxa by depth are indicated by the letters a and b to define the groups that are significantly different from each other, groups sharing a letter are not significantly different.

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Regarding the analysis of length distributions by depth (Figure 8) and day/night period, the results of the two-factor ANOVA showed significant differences in day/night larval length for only two species. In the case of *M. Muelleri*, larvae caught at night were significantly larger than larvae caught during the daytime, while the inverse pattern was observed for *S. cabrilla*. Differences in larval length in relation to depth were significant for five taxa; *C. julis*, *M. muelleri*, *S. pilchardus*, and *T.*

407 *trachurus* were larger at deeper strata, while the opposite trend was observed for *L. crocodilus*. The  
 408 interaction between daytime and depth was significant only for *T. trachurus* (Table 5).

409 **Table 5.** Mean ( $\pm$  standard error) of larval length (mm) and number of individuals per depth stratum  
 410 and time (D: day, N: night). The results of the two-factor ANOVA for differences in the larval length  
 411 of the most abundant taxa between time and depth are also shown. Legend: ns- not significant.

Species	Mean larval length per depth stratum										two-way ANOVA p-values		
	0-20 m		21-40 m		41-60 m		61-100 m		> 100 m		D/ N	Depth	Time x Depth
	D	N	D	N	D	N	D	N	D	N			
<i>A. thori</i>	3.7 $\pm$ 0.6 (8)	4.7 $\pm$ 0.6 (10)	4.9 $\pm$ 0.3 (16)	4.4 $\pm$ 1.0 (4)	5.4 $\pm$ 0.2 (5)	5.1 (1)	6.6 (1)	4.5 (1)			ns	ns	ns
<i>C. aper</i>	3.1 $\pm$ 0.3 (5)	4 $\pm$ 0.3 (2)	3.5 $\pm$ 0.5 (13)	2.3 (1)				4.1 (1)			ns	ns	ns
<i>C. maderensis</i>	3.6 $\pm$ 0.5 (3)	5.7 $\pm$ 0.3 (14)	4.4 $\pm$ 1.9 (3)	3.8 $\pm$ 0.7 (9)	3.6 (1)	3.9 $\pm$ 0.4 (3)					ns	ns	ns
<i>C. julis</i>	2.7 $\pm$ 1 (40)	2.9 $\pm$ 1.6 (85)	3.9 $\pm$ 0.1 (61)	2.8 $\pm$ 0.8 (4)	3.9 $\pm$ 0.2 (14)	4.4 $\pm$ 1.0 (2)	4.5 $\pm$ 0.3 (3)	4.1 (1)	2.4 (1)		ns	<0.01	ns
<i>E. encrasicolus</i>	5.2 $\pm$ 0.9 (4)	7.1 $\pm$ 0.8 (10)	6.7 $\pm$ 1.1 (6)	6.1 $\pm$ 1.7 (3)	8.3 $\pm$ 2.6 (2)	7.2 $\pm$ 1.8 (4)	8.6 $\pm$ 1.2 (2)				ns	ns	ns
<i>L. crocodilus</i>	5.4 (1)	5.4 $\pm$ 0.9 (5)	5.6 (1)	4.3 $\pm$ 0.4 (10)	4.9 (1)	2.6 $\pm$ 0.2 (9)					ns	<0.01	ns
<i>M. muelleri</i>	7.2 $\pm$ 2.3 (2)	9.3 $\pm$ 0.4 (13)	4.2 $\pm$ 0.6 (2)	6.5 $\pm$ 0.5 (12)	4.5 $\pm$ 0.7 (3)	6.9 $\pm$ 0.8 (13)	5.9 $\pm$ 0.4 (16)	7 $\pm$ 0.3 (37)	7 $\pm$ 0.2 (53)	7.3 $\pm$ 0.3 (34)	<0.05	<0.01	ns
<i>M. merluccius</i>				6.5 $\pm$ 3.1 (3)		11.5 (1)	3.1 (1)	3.4 (1)			-	-	-
<i>M. punctatum</i>	3.6 (1)	6.3 (1)			6.5 $\pm$ 1.4 (4)	4.7 $\pm$ 0.3 (12)	9.4 (1)	6.0 $\pm$ 0.6 (6)			ns	ns	ns
<i>P. acarne</i>	3.5 $\pm$ 1.9 (29)	3.1 $\pm$ 2.8 (8)	4.9 (1)	2.4 (1)	3.3 (1)		3.8 (1)				ns	ns	ns
<i>P. pilicornis</i>	3.5 $\pm$ 0.3 (21)	3.7 $\pm$ 0.3 (18)	2.9 $\pm$ 0.5 (6)	3.8 $\pm$ 0.3 (5)	4.8 (1)	3.7 $\pm$ 0.8 (2)	2 (1)	2.2 (1)			ns	ns	ns
<i>S. pilchardus</i>	4.9 $\pm$ 0.8 (14)	5.8 $\pm$ 0.9 (10)	7.5 $\pm$ 0.7 (12)	6.8 $\pm$ 1.0 (8)	9.5 $\pm$ 0.4 (4)	6.7 $\pm$ 3.9 (2)	9.5 $\pm$ 1.4 (3)				ns	<0.01	ns
<i>S. cabrilla</i>	3.4 $\pm$ 0.9 (99)	3.2 $\pm$ 1.3 (93)	4 $\pm$ 1.3 (83)	3.6 $\pm$ 0.4 (10)	4.6 $\pm$ 0.2 (25)	2.7 (1)	4.7 $\pm$ 0.3 (12)				<0.01	ns	ns
<i>T. draco</i>	2.7 $\pm$ 1.0 (6)	2.6 $\pm$ 0.4 (7)	4.1 $\pm$ 1.4 (4)	3.9 $\pm$ 2.3 (2)	5.1 $\pm$ 0.0 (2)		5.9 (1)				ns	ns	ns
<i>T. trachurus</i>	2.6 $\pm$ 0.2 (53)	3 $\pm$ 0.2 (49)	2.8 $\pm$ 0.1 (127)	3.9 $\pm$ 0.4 (9)	4.5 $\pm$ 0.2 (25)	3.4 $\pm$ 0.3 (11)	3.9 $\pm$ 0.8 (5)	3.6 $\pm$ 1.0 (3)	2.0 (1)		ns	<0.01	<0.01

412

### 413 Relationship between the LFC and environmental variables

414 The regression models constructed to explain the variation in the abundance, diversity, and  
 415 richness of the fish larvae community in relation to the biotic and abiotic variables explained 66.1%,  
 416 59%, and 51.5% of the variability, respectively. In the case of fish larvae abundance, depth,  
 417 abundance of zooplankton, and GV were the most important drivers followed by SST. For diversity,  
 418 SSS and GV were the most relevant drivers followed by SST. For richness, only SSS and GV had a  
 419 significantly influence in setting its variability (Table 6). In general, fish larvae abundance, diversity,  
 420 and richness increase with increasing temperature, salinity, and geostrophic velocities, while  
 421 zooplankton abundance has a positive relationship with fish larvae abundance, despite decreasing  
 422 with depth.

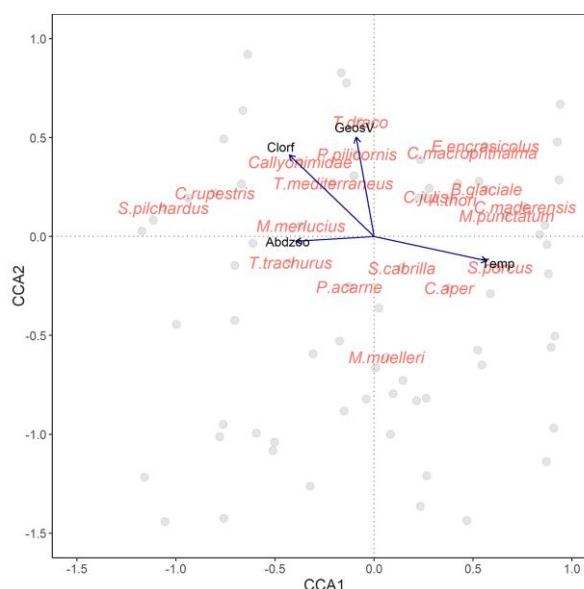
423 From a multivariate perspective, the CCA resulted in a simplified model (significant  $p < 0.01$ )  
 424 that included three environmental variables: GV, SST, zooplankton abundance (Figure 9). However,  
 425 the proportion of total variance explained by the environmental constraints was only 18% from  
 426 which the first two constrained axis explained 11%, and 7%, respectively. Among the species more

427 influenced by temperature were some oceanic myctophids (*B. glaciale*, *M. punctatum*, *C. maderensis*),  
 428 while the abundance of coastal species, such as *S. pilchardus* (Figure 6b), was more influenced by  
 429 higher values of chlorophyll. However, in general, there was no clear pattern or evident association  
 430 between species and environmental conditions, and none of the variables showed great influence on  
 431 the species distribution, as reflected by the small percentage of variation explained by the constrains.

432 **Table 6.** Parameters of the best regression model for explaining the relative influence of the  
 433 environmental variables on the larval fish community descriptors. Abiotic (logarithm of depth  
 434 (logDepth), sea surface temperature (SST), sea surface salinity (SSS), geostrophic velocity (GV) and  
 435 biotic variable (logarithm of chlorophyll (LogChlor) and zooplankton abundance (Abdzoo)) had an  
 436 influence on diversity (Shannon-Wiener index), species richness and abundance of fish larvae.  
 437 Legend: Coeff= regression coefficients, SE= Standard error, p=p-value, Edf=Estimated degrees of  
 438 freedom for the predictor with smoothers.

	Diversity index				Species richness				Larval fish abundance			
	Coeff	SE	Edf	p	Coeff	SE	Edf	p	Coeff	SE	Edf	p
Intercept	-0.99	0.98		0.317	-1.57	1.56		<0.001	-1.57	1.67		0.347
SSS			2.28	<0.001	0.33	0.12	2.5	<0.001				
SST	0.11	0.05		<0.1	0.17				0.31	0.10		<0.01
LogDepth									-1.44	0.25		<0.001
GV	0.03	0.01		<0.01	0.03	0.011		<0.001	0.09	0.02		<0.001
Abdzoo											5.36	<0.001
Deviance Explained		59%			51.5%			66.1%				
Dispersion parame		0.21			1.12			1.01				

439



440

441 **Figure 9.** Canonical correspondence analysis (CCA) biplot for the environmental variables (arrows),  
 442 larval fish taxa (red labels), and sampling stations (grey dots). Arrows indicate the relative  
 443 importance (length) and correlation (angle with axis) between each variable retained in the model  
 444 and the canonical axes. The significant environmental variables were temperature (Temp),  
 445 zooplankton abundance (Abdzoo) and geostrophic velocity (GeosV).

446 **4. Discussion**

## 447 Environmental conditions and their influence on the summer LFC

448 The abiotic conditions in the Artabro Gulf pointed that this zone was a transition area between  
449 two water masses during the summer of 2012, as indicated by the sea surface temperature and  
450 salinity and of spiciness which showed a subsurface front off Cape Finisterre. In front of Finisterre  
451 cape there was a point which can be reflecting the emergence of water from the subtropical ENACW  
452 (Figure 2f), defined as a spicy water [4, 15, 53]

453 The upwelling conditions were fully established during the sampling period (predominant  
454 northern winds), despite that northerly and southerly wind pulses were alternating in the weeks  
455 preceding the survey. Usually, the response time off between wind conditions and oceanographic  
456 changes in the Galician coast is of 3 days [59]. The water column, which had conditions consistent  
457 with summer stratification in temperate regions [60], a mixed layer of variable depth that was  
458 narrower in the Artabro Gulf area. Also, an anticyclonic eddy in front of the Gulf was constant  
459 during the cruise as indicated by the higher geostrophic velocities along the north-western coast and  
460 in a southward surface flow that moved parallel to the coast and changing direction with coastal  
461 orientation (Figure 1). Both, CCA and GAMs elucidated the influence of the environment in the  
462 structure and descriptors of the LFC, point to the upwelling and currents, as the main forces  
463 conforming the summer community. In both analyses, zooplankton abundance showed a positive  
464 relationship with the larvae abundance and the LFC species distribution.

465 Primary production was higher along the coast than offshore, especially along the Artabro coast  
466 next to Ortegal, where the highest superficial chlorophyll concentrations reached  $40 \text{ mg}\cdot\text{m}^{-3}$ .  
467 Regarding secondary production, Fletcher [61] analysed the egg distribution in the same area and  
468 period, and marked the cape next to Ortegal (Estaca de Bares) as the point with the highest egg  
469 abundance and Finisterre cape as the point with the lowest egg abundance. These results coincided  
470 with the larval distribution seen in this work. An analysis of the LFC in a different environmental  
471 regime (spring) also found the same areas to have the highest abundances of eggs and larvae [22],  
472 coincident with a cross-shelf frontal region.

473 This studies about egg distribution plus the distribution of larvae by relative length, point to the  
474 Artabro coastal area as a spawning ground for many of the species detected in the present study.  
475 This distribution highlights the existence of a current that transports fish eggs southwards from the  
476 northern spawning area, and following the clockwise direction of the eddy and the offshore  
477 superficial current of the upwelling, which was stronger in the south. Young larvae were gathered  
478 by the currents and transported south-westwards with the surface current as they developed. The  
479 Artabro coast coincides with the change in orientation of the Galician coast (north to north-west),  
480 which makes it more sensitive to northern winds and hence more prone to upwelling events in  
481 summer. The presence of a single larval fish assemblage was already seen in spring and then was  
482 attributed to offshore Ekman transport associated with a coastal upwelling event, which  
483 homogenized the LFC in the cross-shelf direction [22].

484 For the upwelling areas, the vertical position of fish larvae throughout the day and night also  
485 determines if they are retained in shallow and productive waters or advected offshore [62]. Larvae  
486 with near-surface distributions are more susceptible to offshore transport associated with coastal  
487 upwelling than larvae with deeper distributions, which are moved shoreward [62]. Thus, larval  
488 transport across the shelf depends on the horizontal location of the spawning ground and vertical  
489 position at which eggs were spawned. The vertical summer distribution of the LFC in the surface  
490 layer suggests that most taxa with neritic spawning (e.g., *S. pilchardus*, *E. encrasicolus*, *T. trachurus*)  
491 should spread over the shelf and oceanic larvae (Sternoptychidae: *M. muelleri*, Myctophidae: *M.*  
492 *punctatum*), which spawn at greater depths, should be driven shoreward by the cold bottom flow [24]  
493 . It was been noted that the highest densities of eggs above the mixed layer [61]. Eggs from neritic  
494 species (*S. pilchardus*, *E. encrasicolus*, *T. trachurus*) were found in higher abundancies at depth lower  
495 than 50 m, while eggs from mesopelagic species, as *M. muelleri*, were found at depths between 50 to  
496 150 m on the Artabro coast [61]. The horizontal distribution of the most abundant species seems to  
497 indicate that larvae were transported passively southwards from a spawning area along the  
498 north-western coast.

499 Regarding the cross-shelf distribution, the abundance of neritic species (Gobiidae, Blenidae,  
500 Cupleidae) decreased from the coast to the 200 m isobaths, while oceanic species had the opposite  
501 distribution. It had been reported that the spatial distribution of larvae could be quite heterogeneous  
502 in coastal areas with a highly variable shelf structure, and that the existence of a shelf slope front  
503 associated with a current flow parallel to the coast would contribute to larval concentrations of  
504 mesopelagic and shelf species over the shelf break [63], as we observed in this study. Thus, the front  
505 detected in the Galician shelf in the summer of 2012 could act as a barrier preventing offshore  
506 dispersion. The importance of frontal regions for fish spawning and the concentration of fish larvae  
507 has already been documented [30, 59]. Settlement and recruitment of the coastal species will be  
508 favoured by retention structures; and here lies the importance of the knowledge of seasonal  
509 environmental conditions to understand the mechanisms that affect fish larval stages.  
510

### 511 Seasonal LFC in Galician waters

512 The LFC was highly diverse and rich with lower abundances than in winter or spring and  
513 without dominant species [23-24]. The LFC was made up of a mixture of coastal, neritic, and oceanic  
514 mesopelagic species, which coincides in to a great extent with the composition and diversity of  
515 coastal and transitional assemblages found in the central Cantabrian Sea in summer [52]. The  
516 Galician summer assemblage seems to differ from the spring assemblage. Diversity was lightly  
517 higher in the summer of 2012 compared to spring (summer: 0-2.7, mean 1.9, spring: 0-3.1, mean 1.8)  
518 but richness lightly lower (summer: 0-20, mean 11.9, spring: 1-32, mean 13.8), and abundance  
519 considerably lower (summer: 5.7-749.6, mean 217.2 larvae·10 m<sup>-2</sup>, spring: 4.6 - 26147.3, mean of 939.8  
520 larvae 10m<sup>-2</sup>) [65]. However, due to the markedly different seasonal environmental conditions and  
521 the impact that it has on communities and poor knowledge about its dynamics, it is impossible to  
522 evaluate if such differences or similarities are permanent or due to specific seasonal fluctuations or  
523 to species protracted reproductive period or adaptations.

524 There are some descriptions about the spawning season for some of the dominant species. The  
525 spawning period of *T. trachurus* begins in March-April and ends November [66], while for *S. cabrilla*  
526 it begins in February and ends in July in southern latitudes [67]. Regarding *E. encrasicolus*, its  
527 spawning season increases with decreasing latitude from Bay of Biscay to Gulf of Cádiz in  
528 April-August to April-November [68]. *Sardina pilchardus* has the main spawning period during  
529 October-June peaking in December-March but with longer duration and earlier peak at lower  
530 latitudes [69]. Unfortunately, there are no reproductive studies for most species – including *C. julis*,  
531 *P. acarne*, *P. pilicornis*, and *T. draco* – in the Galician waters. Regarding the alongshore composition,  
532 there are different structures of the LFC between the northern and north-western coasts of Galicia in  
533 the spring of 2012 [23], which were not evident in the summer. Yet, more data should be collected to  
534 obtain more robust conclusions.  
535

### 536 5. Conclusion

537 The larval fish community of the Galician coast seems to be shaped by the interaction between  
538 fish spawning location, concurrence of two water masses, coastal upwelling, and an anticyclonic  
539 eddy. This interaction resulted in a lack of structure in the across and along the shelf. The eddy  
540 circulation may have transported fish eggs and larvae from a spawning area in the north, which  
541 with the help of winds (and consequent upwelling) pushed larvae southwards and offshore while  
542 avoiding oceanic dispersion. This scenario kept the larvae retained in the same area, either if they  
543 were spawned by shelf-, coastal-, or slope-spawning species. Similarly, changes in the seasonal  
544 environmental conditions could result in major changes affecting interspecific competition and  
545 reproductive success, which finally would be reflected in recruitment and stock abundance.  
546



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