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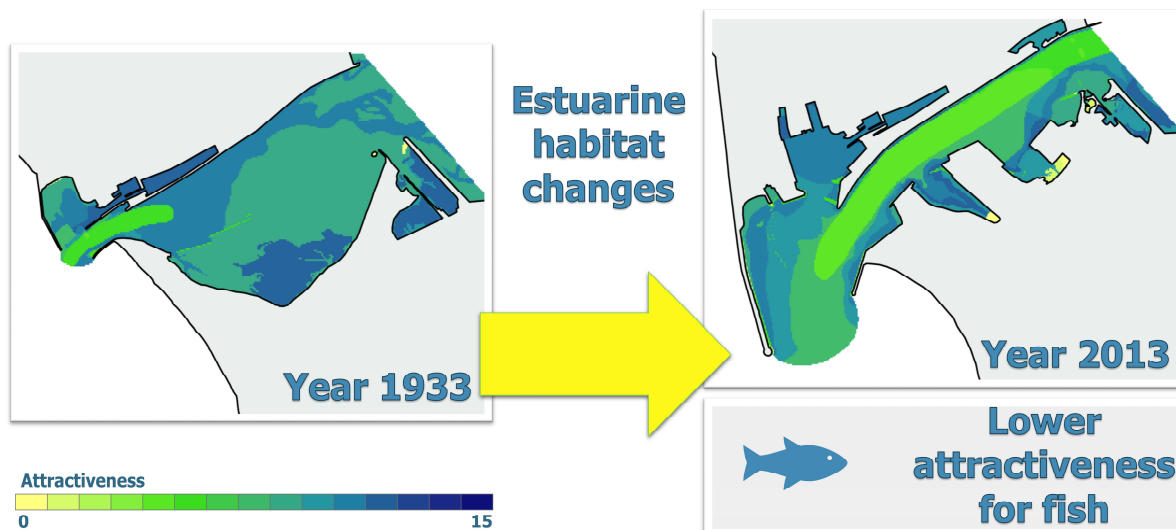
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1 Habitat loss and gain: influence on habitat 2 attractiveness for estuarine fish communities

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10 Abstract

11 Habitat structure and complexity influence the structuring and functioning of fish communities.
12 Habitat changes are one of the main pressures affecting estuarine systems worldwide, yet the
13 degree and rate of change and its impact on fish communities is still poorly understood. In order
14 to quantify historical modifications in habitat structure, an ecohydrological classification system
15 using physiotopes, i.e. units with homogenous abiotic characteristics, was developed for the
16 lower Lima estuary (NW Portugal). Field data, aerial imagery, historical maps and interpolation
17 methods were used to map input variables, including bathymetry, substratum (hard/soft),
18 sediment composition, hydrodynamics (current velocity) and vegetation coverage. Physiotopes
19 were then mapped for the years of 1933 and 2013 and the areas lost and gained over the 80
20 years were quantified. The implications of changes for the benthic and demersal fish
21 communities using the lower estuary were estimated using the attractiveness to those
22 communities of each physiotope, while considering the main estuarine habitat functions for fish,
23 namely spawning, nursery, feeding and refuge areas and migratory routes. The lower estuary
24 was highly affected due to urbanisation and development and, following a port/harbour
25 expansion, its boundary moved seaward causing an increase in total area. Modifications led to
26 the loss of most of its sandy and saltmarsh intertidal physiotopes, which were replaced by
27 deeper subtidal physiotopes. The most attractive physiotopes for fish (defined as the way in

28 which they supported the fish ecological features) decreased in area while less attractive ones
29 increased, producing an overall lower attractiveness of the studied area in 2013 compared to
30 1933. The implications of habitat alterations for the fish using the estuary include potential
31 changes in the nursery carrying capacity and the functioning of the fish community. The study
32 also highlighted the poor knowledge of the impacts of habitat changes on fish due to coastal
33 development and urbanisation and emphasises that ecosystem management and conservation
34 will benefit from a wider understanding of habitat functional roles and habitat changes
35 influencing the functioning and structure of the fish communities.

36 Keywords: Estuaries; habitat changes; fish habitat attractiveness; physiotores

37 **1. Introduction**

38 Habitat destruction has been taking place on a large scale over the past 300 years in many
39 estuaries and coastal areas (Elliott and Cutts, 2004; Lotze et al., 2006) and it is recognised as
40 one of the major threats to biodiversity, structure and functioning of marine ecosystems (Airoldi
41 et al., 2008; Halpern et al., 2008; Wolanski and Elliott, 2015). In addition to supporting cities and
42 harbours having a large economic and social importance (Airoldi and Beck, 2007), estuaries
43 also have great ecological value and are among the most biologically productive and valuable
44 habitats in temperate aquatic areas (Costanza et al., 1997). However, increasing human activity
45 over recent centuries has increased the vulnerability of estuarine and coastal marine
46 ecosystems to habitat degradation and loss (Lotze et al., 2006) and affected several critical
47 ecosystem services (Barbier et al., 2011).

48 The modification of shorelines and the introduction of large amounts of physical materials and
49 man-made structures adversely changes the functioning of the system. This is regarded as
50 permanent habitat loss or change, given that it requires large-scale engineering works to be
51 reversed; similarly it is a form of pollution under the definition of materials added to the natural
52 system which result in harm to the biology of the system or to human welfare (Wolanski and
53 Elliott, 2015). The impact of land claim in estuarine areas (i.e. the anthropogenic removal of
54 estuarine area, such as wetlands, for space for urban or agricultural use; older literature use the
55 term reclamation but it is argued here that an area is being claimed from the sea rather than re-

56 claimed from it), causing habitat loss, has been greater than the effects of any polluting
57 discharges (McLusky and Elliott, 2004). Major impacts to wetlands, including saltmarshes,
58 seagrasses and soft-sediment habitats, have been caused by coastal development (e.g.
59 construction of marinas, the widening and dredging of channels for navigation, tourist
60 developments and infrastructures, aquaculture, etc.), and defence (e.g. breakwaters, seawalls,
61 jetties, dykes) (Airoldi and Beck, 2007; Elliott et al., 2016; Wolanski and Elliott, 2015).

62 Estuaries are important as essential fish habitats providing nursery grounds, migration corridors,
63 refuge and feeding areas for many species, as well as supporting their own resident fish
64 community (Able and Fahay, 2010; Elliott and Hemingway, 2002; Potter et al., 2015). These
65 functions are closely related to the physical and ecological structure of the estuary, which
66 comprises a complex mixture of distinctive habitat types (Pihl et al., 2002). Alterations to
67 estuarine habitats, or to the hydrophysical linkages between them, are likely to compromise the
68 ability of fish larvae or young juveniles to reach favourable nursery habitats, which can have
69 negative population effects, such as reduced recruitment success or near complete failure of a
70 year class (Peterson, 2003). Additionally, the loss of structurally complex habitats, such as
71 seagrasses and marshes, often leads to lower abundances and declines in species richness
72 (Airoldi et al., 2008). Morphological pressures (i.e. changes to the shape, size and physical
73 complexity of the areas such as seagrass habitat loss, bathymetric changes) have also had a
74 main role in affecting potential habitat productivity in transitional waters through effects on
75 biomass of resident and marine migrant fish (Franco et al., 2009a; Zucchetta et al., 2016).

76 Despite these evident changes, there is still limited knowledge and understanding of the
77 magnitude and importance of habitat losses in coastal systems (Airoldi et al., 2008). The
78 historical losses of soft-bottom habitats are poorly known (Airoldi and Beck, 2007), as well as
79 the impacts of engineering structures on coastal habitats and their communities, such as how
80 they change or introduce new ecosystem functions and services (Bulleri and Chapman, 2010;
81 Dugan et al., 2011; Elliott et al., 2016; Perkins et al., 2015). Knowledge of the extent of changes
82 is especially relevant given the fact that the implementation of conservation and management
83 goals for the marine and estuarine ecosystems requires identifying baselines acting as
84 reference conditions (Borja et al., 2012). Yet, this is often limited by the lack of historical data
85 prior to large-scale human impacts and by the lack of information on the drivers of change

86 (Airoldi and Beck, 2007; Bianchi et al., 2014; Claudet and Fraschetti, 2010). Without long-term
87 data series, change has been assessed by alternative means, such as anecdotal knowledge
88 (Al-Abdulrazzak et al., 2012; Alleway and Connell, 2015; Katikiro, 2014) or expert opinion
89 (Halpern et al., 2008).

90 Given the need to further understand the drivers and the level of habitat change, to help
91 ecosystem management and conservation and restoration efforts, the present study aimed to
92 test the hypothesis that historical habitat changes have the potential to affect the overall
93 attractiveness of estuarine habitats for fish communities. To achieve this, the study quantified: i)
94 the changes in habitat structure of an estuarine area over a period of 80 years, and ii) the
95 attractiveness of each habitat and overall estuarine area for fish communities and potential
96 implications of the changes observed.

97 **2. Material and Methods**

98 **2.1. Methodological approach**

99 The historical changes to an estuarine area were studied by applying an ecohydrological
100 classification system in order to produce ecologically meaningful habitat maps for fish
101 communities. The habitats created by this approach are units of homogenous physical
102 characteristics that are referred to as physiotope, after Bouma et al. (2005). The classification
103 system was based on a hierarchical integration of variable-layers, allowing for an increasingly
104 detailed level of description of habitat (Bouma et al., 2005; Stevens et al., 2008). The
105 classification system was used to compare the habitat structure of the estuarine area between
106 past (1933) and present (2013) scenarios, and estimate the area lost or gained for each
107 physiotope. Due to the lack of historical data on fish communities using the estuary, and to
108 further understand the potential implications of the changes observed on those fish
109 communities, the attractiveness of the lower estuary to fish communities in both years (1933
110 and 2013) was estimated using a qualitative method, based on available information from
111 literature review and expert judgment. This method scored each physiotope considering the
112 main estuarine habitat functions for estuarine representative fish species, and its relative cover
113 area. Finally, the physiotope were clustered according to their attractiveness (see Fig. 1).

114 **2.2. Study area**

115 The Lima estuary (NW Portugal) is a small North Atlantic temperate system (approximately 20
116 km length) (Fig. 2) draining an international river basin. The tidal regime is mesotidal (average
117 range of 3.7 m) and semidiurnal, with an annual average freshwater flow of 70 m³ s⁻¹,
118 regulated upstream by two hydroelectric dams. The estuary has three distinct morphological
119 areas: the lower estuary (0-3 km from the mouth) is a narrow, deep and navigational channel
120 with artificial banks; the middle estuary (3-7 km) is a broad shallow zone with salt marshes and
121 tidal sandy islands; and the upper estuary (7-20 km) is a shallow and narrow channel with small
122 sandy islands (Ramos et al., 2010). Historically, the middle and upstream areas have retained
123 most of their natural banks (being part of the EU Natura network), while the lower estuary has
124 been subject to extensive modification within the last century, with the building of walled banks,
125 a large shipyard, a fishing harbour, a commercial seaport, two marinas and two jetties
126 protecting the river mouth. Aerial photographs of the estuary comparing the past with the
127 present situation have shown that the major modifications in the Lima estuary have occurred in
128 the lower part. Additionally, given that more detailed historical information was available for this
129 area (because it is the most urbanised), the ecohydrological classification system was applied
130 to the lower estuary only (Fig. 2).

131 **2.3. Ecohydrological classification system**

132 The ecohydrological classification system used the following variables based on their
133 importance to benthic and demersal fish communities: depth, substratum type, hydrodynamics
134 (namely, water velocity) and vegetation cover. As the lower estuary covers from the mouth to 3
135 km upstream, salinity was considered to be homogeneous within a euhaline area. The variables
136 and their threshold values selected were adapted from Bouma et al. (2005) and Stevens et al.
137 (2008). Different methodologies (see below) were applied to obtain data layers of the spatial
138 variability of each variable based on the available data. The spatial grid resolution for all
139 variables was 9 x 9 m.

140 **2.3.1. Present scenario - 2013**

141 Depth

142 Bathymetric data were obtained as point records collected by a single beam echo sounder
143 during 2013. Additionally, contour lines of the mean high water of spring tides and mean low
144 water of spring tides were digitized from RGB orthophotos of the estuary obtained from public
145 web mapping services of aerial and satellite imagery. The low water contour was obtained from
146 the historical imagery of Google Earth (year of 2006) and the high water contour was obtained
147 from the Portuguese Geographic Institute (IGP) imagery provided by ESRI online map service.
148 The axial tidal influence was corrected from bathymetric data based on hydrodynamic models
149 built for the Lima estuary (Falcão et al., 2013; Mazzolari et al., 2013; Rebordão and Trigo-
150 Teixeira, 2009). Data were interpolated to a contiguous grid of 9 m resolution using ANUDEM
151 (version 5.3) algorithm (Hutchinson, 1989; Hutchinson et al., 2011), which is implemented in
152 ArcGIS 10.2 (ESRI, Redlands, CA) (Topo to Raster tool). This method was designed for
153 creating hydrologically-correct DEMs (Digital Elevation Models) by using a discretized thin plate
154 spline technique (data points and contour data lines were used). To evaluate the performance
155 of the interpolation method, a subset of the input data points (100 out of 3428) were randomly
156 removed from the dataset and later compared against the predicted values using the root mean
157 squared error (RMSE) measure. Depth classes were chosen as follows to characterise the
158 physiotores: supratidal (above mean high water of spring tides); intertidal (between mean high
159 water and mean low water of spring tides), and 3 subtidal classes, between mean low water of
160 spring tides and 2 m depth ("shallow"), between 2 m and 5 m depth ("moderately deep"), and
161 greater than 5 m depth ("deep").

162 Hydrodynamics

163 Water velocity was used to describe the hydrodynamic conditions of the estuary, as a forcing
164 function for many benthic species and fish ontogenetic development stages. Two classes were
165 used: >0.8 m s⁻¹ ("high dynamics") and <0.8 m s⁻¹ ("low dynamics"), 0.8 m s⁻¹ being the
166 boundary at which sediment is frequently stirred or suspended and the formation of megaripples
167 occurs (Bouma et al., 2005). Water velocity in the estuary was determined from hydrodynamic
168 models (Falcão et al., 2013; Mazzolari et al., 2013; Rebordão and Trigo-Teixeira, 2009) to show
169 areas where depth averaged current velocity exceeds the above threshold.

170 Substratum

171 “Hard substrata” (rock, boulders) were delineated based on aerial imagery and field
172 observations. In order to further characterise soft substratum, sediments were also classified
173 using data from previous research projects from the Lima estuary. Samples were collected in
174 2010 (Mendes et al., 2014), 2013 and 2015, using a Petit Ponar grab and dried at 100 °C. Grain
175 size was analysed by sieving (CISA Sieve Shaker Mod. RP.08) and the sediments were divided
176 into three fractions: mud (<0.063 mm), sand (0.063–2.000 mm), and gravel (> 2.000 mm). Each
177 fraction was weighed and expressed as a percentage of the total weight. These data were
178 complemented with those from literature for 2002 (Sousa, 2003). A permutational multivariate
179 analysis of variance (PERMANOVA), based on Euclidean distance matrices, was applied to test
180 temporal differences between the years and seasons of the collections for the coincident
181 sampling sites. No significant temporal differences ($p>0.05$) were detected between the
182 sediment composition of the remaining non-coincident sites, and all datasets were used to
183 create sediments maps. The spatial interpolation of the three fractions was performed using the
184 Empirical Bayesian Kriging (EBK) method implemented in ArcGIS 10.2 (ESRI, Redlands, CA).
185 While the classical kriging methods use a single semivariogram to predict the values at
186 unknown locations, the EBK accounts for the uncertainty of semivariogram estimation, by
187 estimating several semivariograms models through a process of subsetting and simulations
188 (Krivoruchko, 2012). Cross-validation was used to assess the accuracy of the interpolations by
189 evaluating the root mean square error (RMSE) and root mean square standardized error
190 (RMSSE) values. Since kriging is not an exact interpolator, under- or over-estimations may
191 occur, and the sum of the interpolated sediment fractions might not be 100 %. Therefore, each
192 grid map was standardized (Jerosch, 2013), according to the following:

$$193 \quad (\textit{interpolated fraction map} / \textit{sum of the 3 fractions}) \times 100.$$

194 Finally, and to match with the classification of historical sediment data, sediment types were
195 characterised using a simplified version of the Folk (1954) textural classification for soft
196 sediment (as adapted from the classification of Connor et al. (2006), into the following classes:
197 “coarse sediment”, “sand” and “mud”.

198 Vegetation cover

199 Vegetation cover, namely saltmarsh presence, was delineated based on aerial imagery and
200 field expert knowledge. Two classes were used: “non-vegetated” and “saltmarsh”.

201 **2.3.2. Past scenario – 1933**

202 Historical data were retrieved from aerial imagery and cartography from 1933 of the Marinha
203 Portuguesa (Portuguese Navy) and Instituto Geográfico do Exército (Geographic Institute of the
204 Portuguese Army) (Fig. 2c). Information on currents, sediment, and depth (data points and
205 contour lines, including low and high water contours) were retrieved from a hydrographic chart.
206 Saltmarshes were delineated based on aerial imagery (black and white photogrammetric
207 restitution), collected at low tide. The imagery were georeferenced using recognisable control
208 points present on the imagery of both years (1933 and 2013) (e.g. road intersections, buildings,
209 etc.). The relevant variables were digitised and classified according to the criteria described
210 above.

211 **2.3.3. Physiotopes**

212 To obtain the final classification system, the layers of each variable were hierarchically
213 integrated in the following order: depth, hydrodynamics, substratum and vegetation. The code
214 for each physiotope was built by shortening the class name to one or two letters and adding
215 them in hierarchical order. For example the physiotope Sh.ID.M.nV is composed of the classes
216 “Shallow” (Sh), “low Dynamics” (ID), “Mud” (M) and “non-Vegetated” (nV).

217 **2.4. Fish habitat attractiveness**

218 The habitat attractiveness was evaluated based on a score attributed to all the physiotopes
219 identified in the lower estuary. Each physiotope was scored for five estuarine habitat functions:
220 nursery, feeding, refuge, spawning and migratory route. These were adapted from Pihl et al.
221 (Pihl et al., 2002): spawning – areas with simultaneous presence of ripe adults and production
222 of eggs; nursery – areas with high concentration of early juvenile stages, which are suitable for
223 settlement, feeding and growing; feeding - habitats used by older juveniles and adults as a
224 feeding ground (seasonal or permanent); refuge – areas used by older juveniles and adults to
225 avoid predation and/or inter-species competition; and migratory route/corridors - use of a habitat
226 as a migration route for diadromous species and marine migrants. Scores from 0 to 3 reflected

227 the role that each physiotope plays for the different estuarine functions: 0 – not occurring; 1 –
 228 low; 2 – medium; and 3 – high. The scores were allocated based on the generic attractiveness
 229 of the physiotope, based on information derived from a literature review and expert knowledge
 230 (see S1 Table for the criteria used for each class composing the physiotope).

231 The scoring system was applied to five species, chosen due to their representativeness of the
 232 benthic and demersal fish occurring in estuaries, the main ecological guilds (Franco et al., 2008)
 233 and because they are typical of the study area and nearby estuaries (França et al., 2011;
 234 Ramos et al., 2012). The species chosen were: *Platichthys flesus* and *Dicentrarchus labrax*
 235 (marine migrants), *Pomatoschistus microps* (estuarine resident), *Callionymus lyra* (marine
 236 straggler) and *Anguilla anguilla* (catadromous) (see Table 1 for the scientific literature used to
 237 derive the attractiveness scores).

238 The resulting attractiveness scores were calculated for the years of 1933 and 2013, as follows:

239 (1) Species (z) attractiveness = $\sum_j [(\sum_i f_{ijz}) \cdot area_j]$;

240 (2) Overall attractiveness (lower estuary) = $\frac{\sum_z \text{Species attractiveness}_z}{Z}$;

241 Where f_{ijz} is the score given to the estuarine function i for physiotope j and species z , $area_j$ is
 242 the proportion of the estuarine area occupied by physiotope j in the Lima lower estuary in a
 243 given year and Z is the number of species considered for the assessment. Species (z)
 244 attractiveness (1) is the estuarine attractiveness for species z , and overall attractiveness (2) is
 245 the estuarine attractiveness for all the species considered.

246 2.5. Data analysis

247 Habitat areas in 1933 and 2013 were calculated using ArcGIS 10.2 (ESRI, Redlands, CA).
 248 Number of total physiotopes, physiotope density (number of physiotopes per 100 ha), patch
 249 density (number of physiotope patches per 100 ha, where a patch is an homogeneous area of a
 250 specific physiotope class that differs from its surroundings) and proportion of landscape
 251 occupied by each physiotope were calculated using FRAGSTATS (McGarigal, 2012). To
 252 understand the similarities between physiotopes regarding their generic attractiveness scores

253 by function (using the average species scores), a hierarchical cluster analysis was performed in
254 R (R Core Team, 2016) using the pvclust package (Suzuki and Shimodaira, 2006). Pvclust
255 assesses the uncertainty in hierarchical cluster analysis by calculating approximately unbiased
256 (AU) probability values for each cluster by multiscale bootstrap resampling (as an indication of
257 how strong the cluster is supported by data). The cluster analysis was performed using
258 Euclidean distances with Ward's minimum variance method and 10,000 bootstrap replicates.
259 Cluster significance was assumed for AU probability values higher than 95 %.

260 The attractiveness assessment developed in this study may suffer from some degree of
261 subjectivity from the evaluator allocating the scores, albeit supported by evidence from the
262 literature. Therefore, a sensitivity analysis (Alvarez et al., 2013) was undertaken to assess how
263 the attribution of scores to each function influenced the final attractiveness scoring. Two tiers of
264 simulation were defined: tier 1 where f_{ijz} was changed, and tier 2 considering scenarios where
265 the changes in the overall function scoring were applied to a different number of physiotopes
266 amongst those contributing to the overall assessment of the lower estuary in a given year. In tier
267 1, as f_{ijz} could range between 0 and 3, and given that the allocation of each score was based
268 on expert judgement supported by the literature, the maximum change of f_{ijz} allowed for the
269 analysis was 1 point. Simulations included the best (B) and worst (W) case scenarios of
270 change, i.e. only one of the five functions changes its score (hence $\sum_i f_{ijz}$ increases or
271 decreases by 1 point; B(+) and B(-), respectively), or all the functions change their score (hence
272 $\sum_i f_{ijz}$ increases or decreases by 5 points; W(+) and W(-), respectively). In tier 2, the four
273 scenarios above were applied to (i) all the physiotopes included in the final assessment (All); (ii)
274 only the physiotope with the largest cover area in 1933 and in 2013 (L1933 and L2013,
275 respectively); and (iii) only the physiotope with the smallest cover area in 1933 and in 2013
276 (S1933 and S2013, respectively). This resulted in a total of 20 permutations of the scenarios
277 that were applied to each assessment year (1993 and 2013). The scenarios were applied to by
278 keeping all other scores as the average scores of the five representative species used in this
279 study. The effect of each scenario on the performance of the attractiveness assessment was
280 analysed by evaluating the relative response of each assessment (1933 and 2013), measured

281 as a percentage deviation from its original value. The effect of each scenario was also
282 evaluated on the difference of attractiveness between both years.

283 **3. Results**

284 **3.1. Habitat loss and gain**

285 **3.1.1. Total area**

286 Between 1933 and 2013, the lower estuary increased by 32.4 % in total area (Table 2). The
287 north bank was moved forward by claiming area from the estuary (Fig. 2b). As a result, the
288 mouth of the estuary was repositioned south, eliminating part of the southern sand bar and
289 seashore beach that were located in the coastal area around the former estuary mouth. Also,
290 the port was further developed, by building infrastructures on top of the northern rocky shore
291 and developing a northern arm that terminates in a jetty parallel to the coast. Thus, the mouth of
292 the estuary and its plume were deflected to the south. On the southern bank, the intertidal area
293 was mostly dredged, to build a commercial port and industrial sand storage facilities. These
294 changes led to an overall loss of 80 ha (73%) of intertidal habitat from the lower estuary, with
295 additional loss also from the former adjacent coastal area (not estimated here). This loss was
296 overcompensated by a marked increase (130 ha) in the extent of subtidal habitats (Table 2). In
297 particular, there was an increase of the depth of the estuarine subtidal area, with the deep areas
298 (higher than 5 m depth) and the moderately deep areas (between 2 and 5 m) occupying now
299 82 % of the subtidal, while previously, in 1933, they only occupied 9 % of the total estuarine
300 subtidal (Table 2). Together with the changes in depth, there was an increase in the areas with
301 high hydrodynamics (high energy areas) and an increase in the muddy areas, whereas sandy
302 areas decreased overall. The saltmarsh coverage also decreased by 18.7 ha (87.8 %) between
303 1933 and 2013.

304 **3.1.2. Physiotores**

305 The hierarchical integration of the variables identified 21 physiotores in 1933 and 23
306 physiotores in 2013 (Table 3), of which 16 were in common to both scenarios (Fig. 3).
307 Physiotope density, however, was higher in 1933, with 12.5 physiotores per 100 ha, against

308 10.3 physiotopes per 100 ha in 2013. The most common physiotope present in the lower
309 estuary in 1933 was In.ID.S.nV (intertidal; low hydrodynamics; sand; non-vegetated) (Fig. 4),
310 which covered 50.9 % of the total area, followed by Sh.ID.S.nV (shallow; low hydrodynamics;
311 sand; non-vegetated), covering 25.1 %. In 2013, the most common physiotope was Md.ID.S.nV
312 (moderately deep; low hydrodynamics; sand; unvegetated) followed by D.ID.S.nV (deep; low
313 hydrodynamics; sand; unvegetated) (Fig. 4), covering 17.1 % and 13.2 % of the lower estuary,
314 respectively. Patch density, representing the number of patches per 100 ha in the lower estuary,
315 increased between 1933 and 2013 (Table 3).

316 **3.2. Habitat attractiveness**

317 The results obtained with the final weighted scores of habitat attractiveness for the lower Lima
318 estuary were 9.25 in 1933 and 8.12 in 2013 (maximum of 15) (Table 3). In general, the
319 attractiveness of estuarine habitats was highest in 1933, for all species. *P. microps* presented
320 the largest difference in attractiveness (with 10.71 and 8.10 for 1933 and 2003, respectively),
321 while *C. lyra* presented the closest values of attractiveness between 1933 and 2013 (8.46 and
322 8.40, respectively) (Table 3; S1-S5 Figures; Tables A-E in S2 Table). The scientific literature
323 compiled in order to support the attribution of scores showed that the amount information
324 available on estuarine habitat use is species specific: *P. flesus* and *A. anguilla* were the species
325 with the highest amount of available information, while there was a lack of information for *C. lyra*
326 (Table 1).

327 Physiotopes were grouped into four clusters (with AU probability values >95 %) according to
328 their individual attractiveness scores (Group I to IV; see Fig. 5). The lowest scores were
329 registered by the supratidal physiotopes, which are habitats that are rarely flooded and
330 therefore can rarely be accessed by fish. Supratidal physiotopes were clustered as a group
331 (Group IV) and separated first (Fig. 5). Group III, with the second lower scores, included all the
332 physiotopes with high hydrodynamics. The highest scores were obtained for Sh.ID.M.nV
333 (shallow; low dynamics; mud; non-vegetated), In.ID.M.Sm (intertidal; low dynamics; mud;
334 saltmarsh) and In.ID.S.Sm (intertidal; low dynamics; mud; saltmarsh), with 12, 11.4 and 11.4
335 respectively (Fig. 5; S2 Table). These, together with the other intertidal soft substratum
336 physiotopes and the shallow sandy and moderately deep muddy physiotopes were included in

337 the group of higher attractiveness to fish (Group I). Of the four clusters, only Group I showed a
338 net reduction (by 48 %) in total area between 1933 and 2013, while the cumulative area of the
339 physiotoypes in the remaining clusters increased (Fig. 5; S3 Table).

340 **3.3. Sensitivity of the habitat attractiveness**

341 **assessment**

342 The manipulation of scores in the habitat attractiveness showed the strongest response when a
343 change was applied to all the functions of all physiotoypes included in the assessment (W – All,
344 worst case scenario applied to all physiotoypes; Fig 6), as it would be expected. The sensitivity of
345 the assessment was also shown to be highly dependent on the annual area cover of the
346 physiotope to which change is applied. The worst case scenario applied only to In.ID.S.nV (i.e.
347 the most extensive physiotope present in 1933; W-L1933), elicited a weaker response of the
348 final attractiveness score in 2013 (with a deviation of 3.8 %, positive or negative depending on
349 the scenario) than in 1933 (deviation of 27.5 %) and this was due to the higher proportion of
350 estuarine area covered by this physiotope in 1993 (50.9 %) compared to 2013 (6.2 %) (Fig.
351 6a,b). When the worst case scenario was applied to Md.ID.S.nV (i.e. the largest physiotope in
352 2013, with 17.1 % area cover in this year; W-L2013), the response deviation of the habitat
353 attractiveness assessment score of 2013 was 10.5 %, whereas the deviation was 0.3 % in
354 1933, when this physiotope covered only 0.5 % of the lower estuary area.

355 The difference between the final scores of habitat attractiveness of the Lima estuary between
356 1933 and 2013 was 1.14 (Table 3). A positive difference (i.e. the final attractiveness score was
357 higher in the 1933 assessment than in 2013 assessment) was observed for all the scenarios of
358 change, except for scenario W – All (Fig. 6c). Under this scenario, that represents the very
359 worst case of underestimation of all the function scores for all the physiotoypes included in the
360 assessment, there would have been an increase of habitat attractiveness for fish in the lower
361 Lima estuary between 1933 and 2013.

362 **4. Discussion**

4.1. Estuarine habitats and their attractiveness for fish

Estuaries have long been regarded as highly attractive areas for fish, which use them in a variety of ways (Elliott and Hemingway, 2002; Potter et al., 2015). The scoring system used in this study aimed to reflect the role of different estuarine habitats for fish, while taking into account the different estuarine functions. As a result, saltmarshes and sandy and muddy intertidal and shallow areas were identified as being highly attractive (all clustered in Group I). Sandy and muddy intertidal and shallow areas are suitable as nursery grounds and usually carry high abundances of juveniles (Cabral and Costa, 2001; Le Pape et al., 2003; Trimoreau et al., 2013; van der Veer et al., 2001). The preference for such habitats appears to be related to the interaction between refuge from predation, which is assumed to be low in shallow waters (Manderson et al., 2004; Ryer et al., 2010), and availability of food resources (Whitfield and Patrick, 2015), which is assumed to be high in intertidal and shallow waters with fine sediments (Phelan et al., 2001; Vinagre et al., 2005). Benthic intertidal primary production has been shown to sustain juvenile fish food webs and therefore contribute to maintaining the nursery function of estuarine and coastal tidal ecosystems (Le Pape et al., 2013). The higher scores allocated to intertidal and shallow habitats, in contrast to deeper areas, reflect, therefore, the habitat use of the species considered in this study (e.g. *Pomatoschistus microps*, *Platichthys flesus*, *Dicentrarchus labrax*), which are representative of the small sized or young demersal fish species that dominate fish communities in the Lima and other European estuaries (França et al., 2011; Franco et al., 2008; Ramos et al., 2012). Estuarine saltmarshes are very productive ecosystems that convert nutrients into plant biomass, are an important source of organic matter to the estuary, and they trap sediments and absorb wave energy (McLusky and Elliott, 2004; Wolanski and Elliott, 2015). Their high productivity associated with a complex structure make saltmarshes important habitats for many fish and crustaceans, functioning as sites for reproduction, nursery, enhanced feeding, and refuge from predation and stressful environmental conditions (França et al., 2009; Franco et al., 2009b; Minello et al., 2003; Rountree and Able, 2007). For these reasons, saltmarshes are very attractive for fish and are usually areas of high fish densities within estuaries (França et al., 2009). High hydrodynamics

392 were identified in the cluster group with the second lowest scores of attractiveness for benthic
393 and demersal fish. Hydrodynamics are known to influence the distribution of fish in the estuary
394 (Thiel et al., 1995) and, depending on the estuarine currents and species behaviour, can have a
395 positive effect on transport towards inner nursery areas (Forward et al., 1999; Harrison et al.,
396 2014; Jager, 1999). However, and given that estuaries have a net flow of water to the ocean,
397 high current velocities may also have the opposite effect and reduce the access of the marine
398 migrant early life stages to the vital estuarine nursery areas. While larvae have developed
399 behaviour to overcome strong currents that frequently exceed larval swimming velocities
400 (Forward et al., 1999), such as selective tidal stream transport (STST), they are still sensitive to
401 increased river flow (Ramos et al., 2012) and can be easily flushed back to the ocean and
402 prevented from reaching settlement areas.

403 **4.2. How has the estuary changed?**

404 As with many coastal and wetland areas, the Lima estuary has been modified over time by
405 increased urbanisation and coastal development. In the past 80 years, the geomorphology of
406 the lower Lima estuary has been altered, and its area has increased by claiming area from the
407 ocean and estuary. The modifications have removed most of its sandy and saltmarsh intertidal
408 areas, replaced by deeper areas continuously dredged to allow the operation of the port,
409 commercial harbour and marina. In general, the attractiveness of the estuarine area decreased
410 for fish, as shown by the scores obtained for each species and the final score. The results were
411 calculated taking into account that, in addition to the presence (or absence) of certain types of
412 physiotopes, the proportion of seascape occupied by each physiotope also contributes to the
413 final attractiveness of the estuarine area. Although the lower estuarine area increased between
414 1933 and 2013, the density of physiotopes (number of physiotopes per 100 ha) has decreased.
415 Patch density increased between the two dates. These results show a change in the spatial
416 configuration of the lower estuary and suggest a potential fragmentation of habitats. Patch
417 density is one of the basic descriptors of habitat subdivision, although it is limited as a habitat
418 fragmentation quantitative indicator, given its correlation with habitat abundance (Wang et al.,
419 2014). Fragmentation is regarded here as a complex and dynamic process that is the net result
420 of interlinked changes such as habitat loss, increased isolation of patches and changes in the

421 number, shape, size and quality of patches (Bostrom et al., 2011). Nevertheless, spatial
422 features of habitat patches play an important role in structuring associated fish communities
423 (Nagelkerken et al., 2015) and habitat fragmentation and the resulting loss of connectivity can
424 potentiate the consequences of habitat loss.

425 Vegetated areas, i.e. saltmarsh areas, of the lower Lima estuary were reduced by 88 %. As in
426 many other estuaries worldwide (Wolanski and Elliott, 2015), França et al. (2012) recognised
427 land claim, together with nutrient input and changes in river flow, as the highest threats in other
428 Portuguese estuarine sites and habitats. The impact of land claim was especially high for
429 saltmarshes and mudflats, due to historical and current pressures claiming wetlands for
430 agriculture, aquaculture and the construction of shoreline structures. Moreover, shoreline
431 development may also lead to a decrease in densities of benthic prey and predators on the
432 adjacent subtidal areas, when compared to the adjacent subtidal areas of natural saltmarshes
433 (Seitz et al., 2006). Recently, a study carried in the sub-estuaries of Chesapeake Bay and the
434 Delaware Coastal Bays, USA, showed that shoreline hardening (hard engineering structures at
435 the top of the shore) affects adjacent local fish and crustacean assemblages, and that
436 cumulative shoreline hardening negatively affects fauna at the sub-estuary system scale (Kornis
437 et al., 2017). The attractiveness score system identified saltmarsh habitats present in the Lima
438 lower estuary as highly attractive to fish (the second highest) and hence the loss of 88 % of
439 these habitats is likely to have negatively affected the fish assemblages. Additionally, from 1933
440 to date there has been a large increase in coastal urbanisation. Land use of the southern bank
441 changed from natural habitats (essentially pine forest with a low extent of corn and vegetables
442 cultivated areas) to an urbanised area with hardened shorelines. The amount of urbanisation
443 influences nekton assemblages, and intact natural saltmarsh landscapes support a nekton
444 assemblage significantly different from those in partially or completely urbanised saltmarsh
445 landscapes (Elliott et al., 2016; Lowe and Peterson, 2014).

446 The physiotopes of the lower Lima estuary (saltmarshes, intertidal and shallow subtidal habitats
447 with fine sediments) were clustered in the group of physiotopes with higher attractiveness for
448 fish. However, these were also the physiotopes that lost more area between 1933 and 2013.
449 Given their high productivity, it is likely that these changes reduced the carrying capacity of the
450 system for juvenile fish. Rochette et al. (2010) used a habitat suitability model based on

451 bathymetry and sediment structure to hindcast the effect of nursery habitat degradation of the
452 Seine estuary on *Solea solea* population. They suggested that, since 1850, the estuary nursery
453 capacity has decreased by 42 % due to habitat loss. Considering that the physiotopes lost in the
454 lower Lima were highly attractive for juveniles, the estuary is likely to have also lost some of its
455 nursery capacity. The extent of available nursery area has a considerable influence on the
456 recruitment level of marine fish populations (Rijnsdorp et al., 1992; Schmitt and Holbrook,
457 2000), therefore the protection of these essential fish habitats has currently high priority in
458 conservation and management strategies (Beck et al., 2001; Nagelkerken et al., 2015).

459 In contrast, highly hydrodynamic areas increased in the lower Lima estuary, probably as an
460 effect of the deepening of the channel and of the increasing of engineered structures in the
461 estuary. Typically, engineered structures placed in a coastal site are expected to modify the
462 hydrodynamics of the area, by altering the water flow, currents, sediment dynamics, grain size
463 or depositional processes (Dugan et al., 2011; Gonzalez et al., 2001; Lesourd et al., 2001;
464 Walker et al., 2008).

465 **4.3. Implications of habitat changes for the structure** 466 **and functioning of the fish communities**

467 Habitats differ in their productivity and ecological services and functions that they deliver
468 (Peterson and Lowe, 2009; Turner and Schaafsma, 2015). Thus, the loss of different habitats
469 will have different impacts on the fish communities although functional redundancies among
470 habitat types could decrease the negative effects of habitat changes (Camp et al., 2013). The
471 ability to recreate habitats as compensation or biodiversity offsets for those lost during
472 development has been increasing (Elliott et al., 2016; Wolanski and Elliott, 2015). In the lower
473 Lima estuary, the physiotopes most attractive to fish decreased by 48 % in their total area and
474 the loss of saltmarshes and intertidal areas cannot be compensated by the gain of deep subtidal
475 physiotopes, given their different functional roles for fish. Hence, even if the total carrying
476 capacity of the system had increased with the increase in total area, the structure of the fish
477 community will probably have changed. However, the functional roles of many habitats are not
478 yet fully understood and therefore the consequences of habitat changes become difficult to
479 predict (Camp et al., 2013).

480 Villéger et al. (2010) showed that, following habitat degradation in a tropical estuary, there was
481 a loss of functional diversity resulting from a loss of functional specialisation in fish communities,
482 and that the species turnover observed was determined by habitat-trait relationships. Habitat
483 changes can, therefore, alter the functional structure of the community by removing species with
484 traits that are poorly adapted to the new habitat and allowing colonization by better adapted
485 species (Mouillot et al., 2013). Baptista et al. (2015) reported changes in the structure and
486 function of an estuarine fish community in a temperate estuary due to hydrological changes
487 caused by man-induced alterations and weather extremes. Zucchetta et al. (2016) also
488 identified the potential of changes in habitat morphology (e.g. bathymetric changes, loss of
489 intertidal or seagrass habitat) to affect the functioning of transitional water habitats (namely their
490 secondary production) by affecting the biomass of estuarine resident and migratory species
491 (including also the European Eel *Anguilla anguilla*) in a temperate lagoon system. On the other
492 hand, areas that have been modified due to the introduction of man-made structures have
493 started to receive attention as potential artificial habitats, combining engineering and ecological
494 principles in an attempt to minimize their negative impacts (Browne and Chapman, 2011; Elliott
495 et al., 2016).

496 Although it was not possible to quantitatively evaluate the extent of changes to the ecosystem
497 functioning following the extensive habitat changes observed in the lower Lima estuary due to
498 the lack of reference data, it is hypothesised that functional changes of the fish community had
499 occurred.

500 **4.4. Limitations of the approach**

501 The lack of historical data hinders direct empirical studies evaluating the impacts of habitat loss
502 on diversity changes (Airoldi et al., 2008). Given the lack of historical data on fish assemblages
503 of the studied area, historical comparisons of fish community data were not possible. Under
504 these conditions, that may be also common in other estuarine systems, the present study aimed
505 to define an alternative approach to investigate changes in the estuarine functioning for fish as
506 associated with changes in the physical habitat of the estuary. Physical habitat change was
507 assessed by a snapshot of two points in time (year of 1933 and year of 2013), using historical
508 and contemporary data sources to create the physiotopes. While historical map data, such as

509 military maps are unlikely to contain systematic biases (Vellend et al., 2013), data acquisition
510 strategies and processing, such as determination of bathymetry, characterisation of sediments
511 and currents, were most likely different between 1933 and 2013. Therefore, the observed
512 changes in area of each physiotope could be confounded, to an extent, by differences in data
513 sources.

514 The method for evaluating the attractiveness of habitats was based on the knowledge of a few
515 representative species using the estuary. Although it covered the major estuarine use guilds
516 (Elliott et al., 2007; Potter et al., 2015), it does not entirely reflect the complexity of the whole
517 assemblage and functional diversity. In fact, ecological guilds are only one of the functional
518 traits that can be used to evaluate functional diversity. In addition to the ecological guilds, the
519 trait vertical distribution (Elliott and Dewailly, 1995) was considered by choosing two species to
520 cover the benthic and demersal guild (*Platichthys flesus* and *Dicentrarchus labrax*) as these are
521 more likely to be linked the structure of the habitat. Nevertheless, the attribution of
522 attractiveness scores highlighted the scarcity of information available about the functional roles
523 of the different habitats to individual species, as indicated elsewhere (Seitz et al., 2014). The
524 present study showed this was evident for the least commercially important species (therefore
525 least studied).

526 The study gives a partial representation of the estuarine habitats, by investigating the lower
527 estuary only. Although natural habitats in the upper/middle estuary have undergone minor
528 changes, their exclusion from the analysis does not account for their relative importance (in
529 terms of area and functionality) compared to the lower estuary, therefore the understanding of
530 the overall loss of attractiveness of the whole estuary is limited. Furthermore, attractiveness has
531 been associated to physiotopes, irrespective of their location within the estuary. The location of
532 a physiotope along the estuarine gradient, or in relation to its adjacent habitats, might affect this
533 value. For example, the attractiveness of intertidal, low dynamics physiotopes in brackish areas
534 might be different from those in the lower euhaline estuary, as juveniles of some marine migrant
535 species, like *Platichthys flesus*, may be attracted by freshwater cues (Amorim et al., 2016;
536 Zucchetta et al., 2010). Given that a generic assessment of the habitat attractiveness has been
537 undertaken and the literature review/expert knowledge used is also likely to include information
538 from brackish habitats that are not presented in this study, attractiveness might be over- or

539 under-estimated. The lower estuary was assumed homogenous within a euhaline area in both
540 years, however it is likely that in 2013 the estuary presented a greater saline penetration than in
541 1933 due to the deepening of the channel. Therefore, this likely salinity change between 1933
542 and 2013 might have also affected the habitat attractiveness in the lower estuary, a factor that
543 could not be accounted for by the assessment in the present study.

544 The sensitivity analysis showed that the habitat attractiveness assessment can be sensitive to
545 the choice of the function scores allocated to the physiotopes, although only the worst-case
546 scenarios led to high deviations from the original result. These scenarios assumed that the
547 experts undertaking the assessment misjudged the scores of all habitat functions for all the
548 physiotopes (by either always underestimating or overestimating them), and therefore are
549 considered to be very unlikely cases. When considering individual physiotopes, those with the
550 bigger area cover in the estuary appeared to be most influential in the assessment, as it would
551 be expected given that area cover was used to weight the contribution of each physiotope to the
552 overall estuarine attractiveness. One way to avoid these types of errors could be, for example,
553 to use a Delphi approach by asking multiple experts to attribute scores to the functions of the
554 physiotopes and use averaged scores in the assessment.

555 Based on the major functions of estuarine habitats, the Lima estuarine area became less
556 attractive for fish representing the major ecological groups using the estuary. However, it is also
557 of note that habitat attractiveness may be determined by features and/or environmental
558 parameters additional to the physical attributes that were used in this approach to define
559 physiotopes. These may be biotic factors (e.g. species interactions such as competition or
560 predation) or other abiotic factors that may affect the physiotope attractiveness to fish. For
561 example, anthropogenic pressures such as dredging, regulated river flow and water quality may
562 reduce habitat attractiveness for fish. The lower Lima estuary is subjected to constant dredging
563 for navigation, which is known to affect macrobenthic assemblages, modify sediment and
564 biogeochemical characteristics and resuspend fine sediment, nutrients and pollutants (Gray and
565 Elliott, 2009; Ponti et al., 2009; Quigley and Hall, 1999). The river flow of the Lima is regulated
566 by two large hydroelectrical dams and the freshwater inputs are recognized to affect estuarine
567 fish communities (Ramos et al., 2006) by influencing salinity fluctuations in estuaries (Drake et
568 al., 2002; Wolanski and Elliott, 2015). Water quality, nutrient inputs, hypoxia or eutrophication

569 symptoms restrict fish access to suitable habitats (Elliott and Hemingway, 2002). A lack of
570 historical and quantitative information on these pressures prevented the use of such additional
571 factors in defining physiotopes in this study, and hampered further knowledge of their impacts
572 on habitat attractiveness and degradation, and changes to the structure and functional
573 properties of fish communities of the estuary. The potential contribution of these additional
574 factors however cannot be disregarded and future research efforts should aim at integrating
575 these elements in the assessment of fish habitat attractiveness.

576 **5. Conclusions**

577 Hydrophysical factors are a major determinant of habitat structure and may therefore influence
578 the establishment, development and functioning of fish communities. The availability of food,
579 shelter and refuge from predation allow for different uses of each habitat (Wolanski and Elliott,
580 2015). The lower Lima estuary suffered extensive modifications in its habitat structure between
581 1933 and 2013, mostly due to the increase of the total area and the change of the system from
582 one dominated by intertidal and shallow subtidal habitats with soft sediment and saltmarsh, to
583 one dominated by moderately deep / deep subtidal habitats. Considering the main estuarine
584 habitat functions, the physiotopes lost were the most attractive to the benthic and demersal fish
585 communities using the estuary. These physiotopes were replaced by others with lower
586 attractiveness and different functional roles for fish, for example hard substrata. Consequently,
587 these decreased the overall attractiveness of the estuarine area since 1933.

588 This study highlights the importance of understanding and tracking habitat loss and gains,
589 particularly as habitat alterations also occur widely in many other nearshore environments as
590 well as estuaries. These types of cumulative impacts are challenging because they are not
591 immediately noted and build up over time to produce a more substantial impact at larger scales
592 (Peterson and Lowe, 2009). Management and conservation strategies of coastal areas rely on
593 a better understanding of habitat functional roles for fish species and further research is needed
594 to identify how habitats are related to functional traits of the fish community to understand the
595 consequences of habitat changes.

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Figure 1. The methodological framework to show the influence of historical habitat changes on the attractiveness of estuarine habitats for estuarine fish communities.

Flowchart shapes: parallelogram – input/output data; rectangle - process; hexagon – preparation/initialisation; diamond – decision; rounded rectangle – terminator.

Figure 2. The lower Lima River Estuary. a) Location of the Lima Estuary in the Iberian Peninsula (*); **b)** Lima lower estuary presently – the orange line represents the delimitation of the lower estuary in 1933 and the arrows indicate the sites where major modifications occurred (basemap source: ESRI, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community). **c)** Photogrammetric restitution of the lower Lima estuary in 1933 (provided by Câmara Municipal de Viana do Castelo).

Figure 3. Physiotypes of the lower Lima estuary: 1933 and 2013. Class code names: Sp - supratidal; In – intertidal; Sh - shallow subtidal (<2 m); Md - moderately deep (2 – 5 m); D – deep (>5 m); ID - low dynamics (water velocity <0.8 m s⁻¹); hD - high dynamics (water velocity >0.8 m s⁻¹); R - hard substrata; G - Coarse sediment; S – sand; M – mud; Sm – saltmarsh; nV – non-vegetated.

Figure 4. Area (ha) of the physiotypes of the lower Lima estuary in 1933 and 2013. Class code names: Sp - supratidal; In – intertidal; Sh - shallow subtidal (<2 m); Md - moderately deep (2 – 5 m); D – deep (>5 m); ID - low dynamics (water velocity <0.8 m s⁻¹); hD - high dynamics (water velocity >0.8 m s⁻¹); R - hard substrata; G - Coarse sediment; S – sand; M – mud; Sm – saltmarsh; nV – non-vegetated.

Figure 5. Dendrogram of the results of the hierarchical cluster analysis performed on the attractiveness scores of Lima estuary physiotypes. Red boxes indicate clusters with unbiased (AU) probability values >95 %. GI – Group I; GII – Group II; GIII – Group III; and GIV – Group IV. Numbers in brackets show cumulative percentage (%) increase (positive values) or

decrease (negative values) in the area of the physiotopes of the corresponding group. Class code names: Sp - supratidal; In - intertidal; Sh - shallow subtidal (<2 m); Md - moderately deep (2 - 5 m); D - deep (>5 m); ID - low dynamics (water velocity <0.8 m s⁻¹); hD - high dynamics (water velocity >0.8 m s⁻¹); R - hard substrata; G - Coarse sediment; S - sand; M - mud; Sm - saltmarsh; nV - non-vegetated.

Figure 6. Results of the sensitivity analysis applied to the habitat attractiveness assessment. **a)** Tornado diagram showing the percentage of deviation of the habitat attractiveness assessment of the lower Lima estuary in 1933 under twenty scenarios of change; **b)** Tornado diagram showing the percentage of deviation of the habitat attractiveness assessment of the lower Lima estuary in 2013 under twenty scenarios of change; **c)** Radar plot showing how the difference between habitat attractiveness assessments in 1933 and 2013 (with a baseline value of 1.14, represented by the dashed line) changes under the twenty scenarios of change. W - worst case scenarios (tier 1); B - best case scenarios (tier 1); (+) and (-) - positive and negative scenarios of change (tier 1); All - tier 1 scenarios applied to all the physiotopes in the annual assessment; L - tier 1 scenarios applied to the physiotope with the largest cover area in a given year; S - tier 1 scenarios applied to the physiotope with the smallest cover area in a given year.

Table 1. Literature references used to derive the physiotopes attractiveness scores of the Lima estuary for the species *Anguilla anguilla*, *Callionymus lyra*, *Dicentrarchus labrax*, *Platichthys flesus* and *Pomatoschistus microps*.

<i>A. anguilla</i>	<i>C. lyra</i>	<i>D. labrax</i>	<i>P. flesus</i>	<i>P. microps</i>
Barry et al. (2015)	Griffin et al. (2012)	Cabral and Costa (2001)	Dando (2011)	Hampel and Cattrijsse (2004)
Bouchereau et al. (2009)	King et al. (1994)	Dando and Demir (1985)	Kristensen et al. (2014)	Nellbring (1986)
Harrison et al. (2014)	Prista et al. (2003)	Dufour et al. (2009)	Le Pichon et al. (2014)	Nellbring (1993)
Laffaille et al. (2004)	Van Der Veer et al. (1990)	Kelley (1988)	Mendes et al. (2014)	Polte et al. (2005)
Laffaille et al. (2003)		Laffaille et al. (2001)	Souza et al. (2013)	Tallmark and Evans (1986)
Schulze et al. (2004)		Martinho et al. (2007)	Vinagre et al. (2005)	
Walker et al. (2014)			Zucchetta et al. (2010)	

Table 2. Total area (ha) for each class variable of the Lima estuary and their change (ha and %) between 1933 and 2013. The abbreviation for each class used in the final physiotope codes is shown in square brackets [].

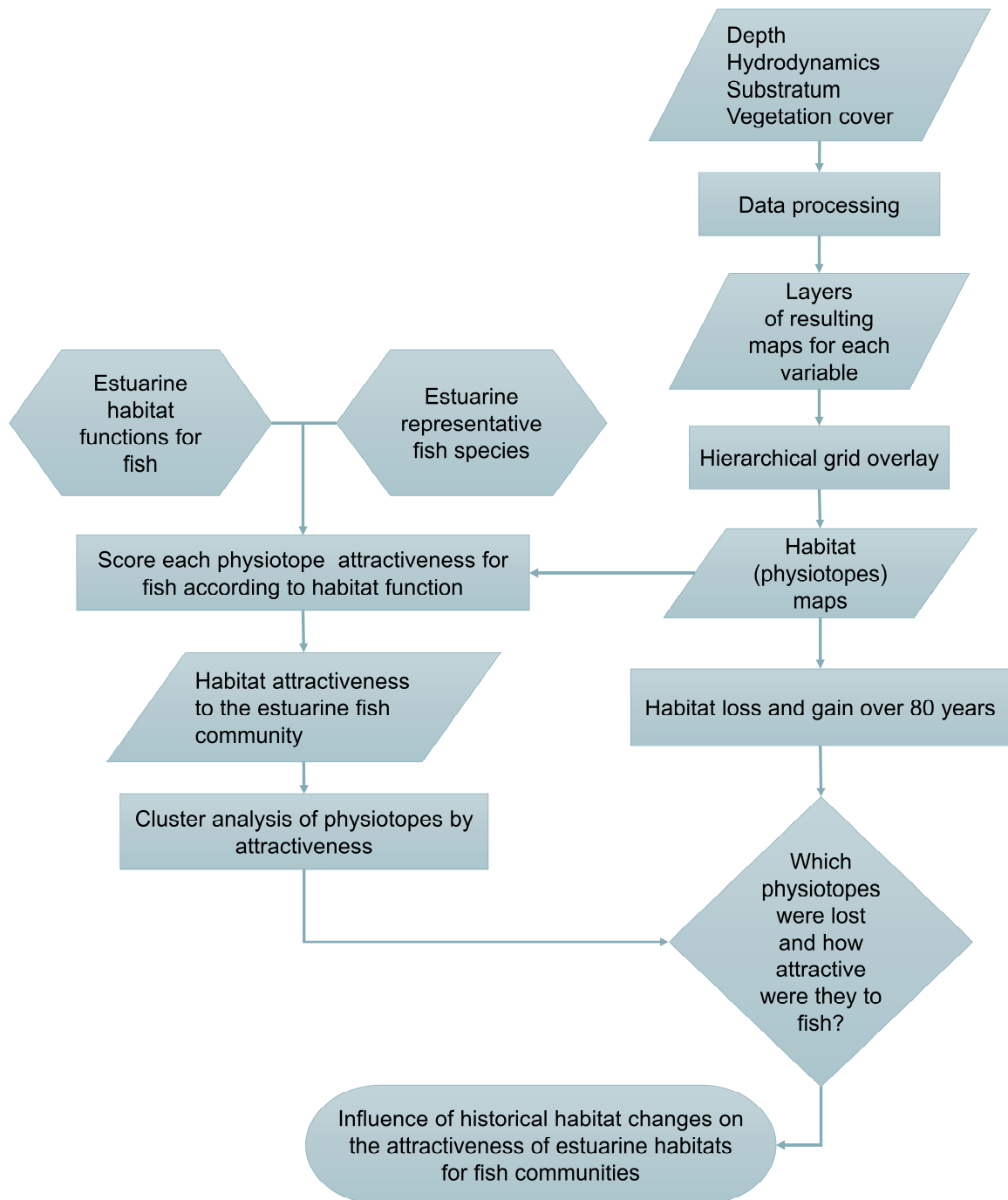
	Area (ha) 1933	Area (ha) 2013	Change (ha)	Change (%)
Total estuarine area	169.1	223.2	54.1	32
Supratidal [Sp]	0.4	4.5	4.1	945
Intertidal [In]	110.2	30.2	-79.9	-73
Subtidal	58.5	188.5	130.0	222
Shallow [Sh]	53.5	33.0	-20.5	-38
Moderately deep [Md]	4.9	74.5	69.6	1416
Deep [D]	0.1	81.0	80.9	71300
High hydrodynamics [hD]	7.2	51.7	44.5	616
Low hydrodynamics [lD]	162.0	171.5	9.6	6
Coarse sediment [G]	0.8	0.0	-0.8	-100
Sand [S]	150.7	136.7	-14.1	-9
Mud [M]	15.3	80.8	65.5	429
Hard substrata [R]	2.2	5.7	3.5	158
Saltmarsh [Sm]	21.3	2.6	-18.7	-88
Non-vegetated [nV]	147.7	220.6	72.9	49

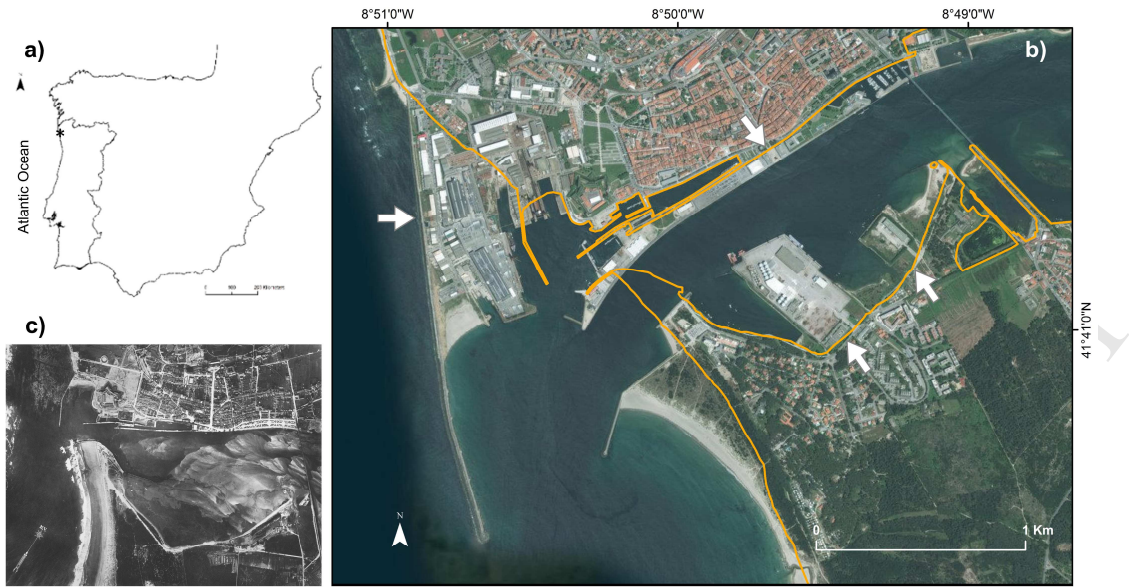
Positive values represent increase and negative values decrease.

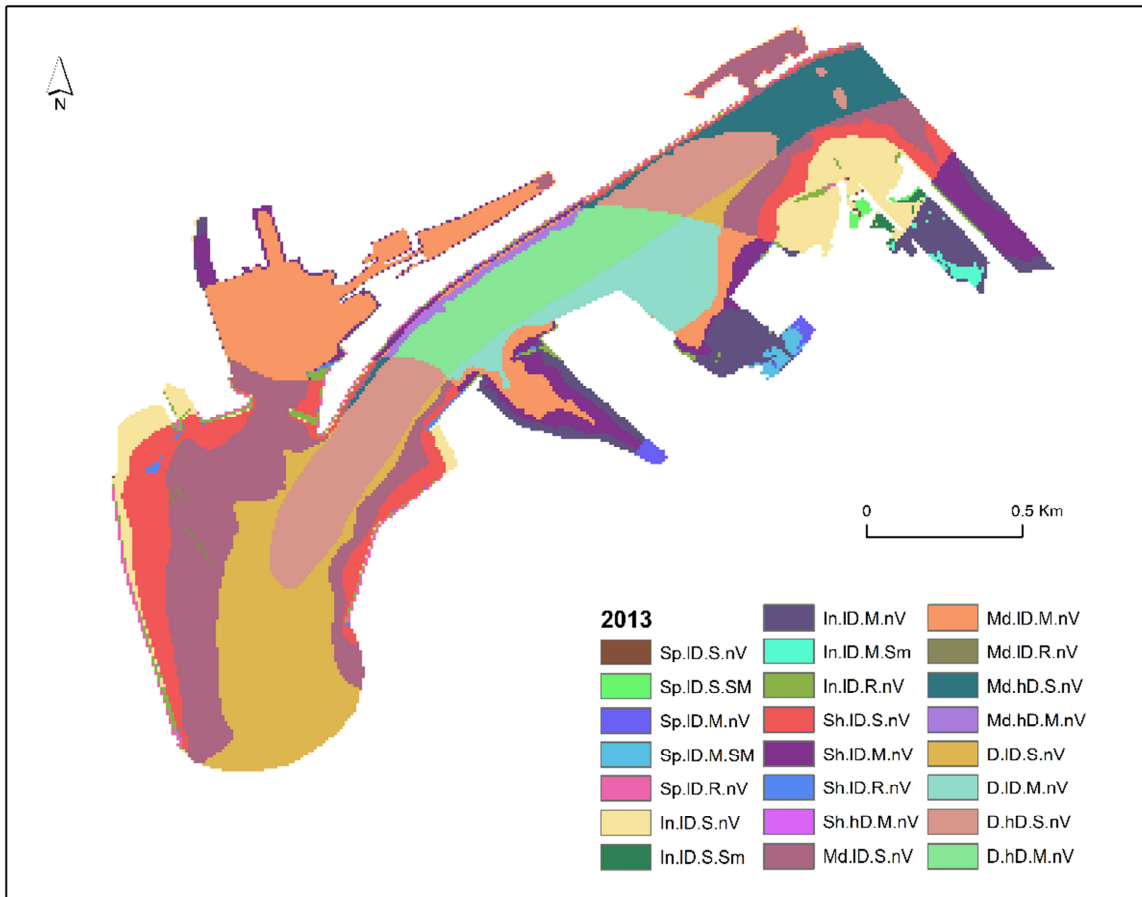
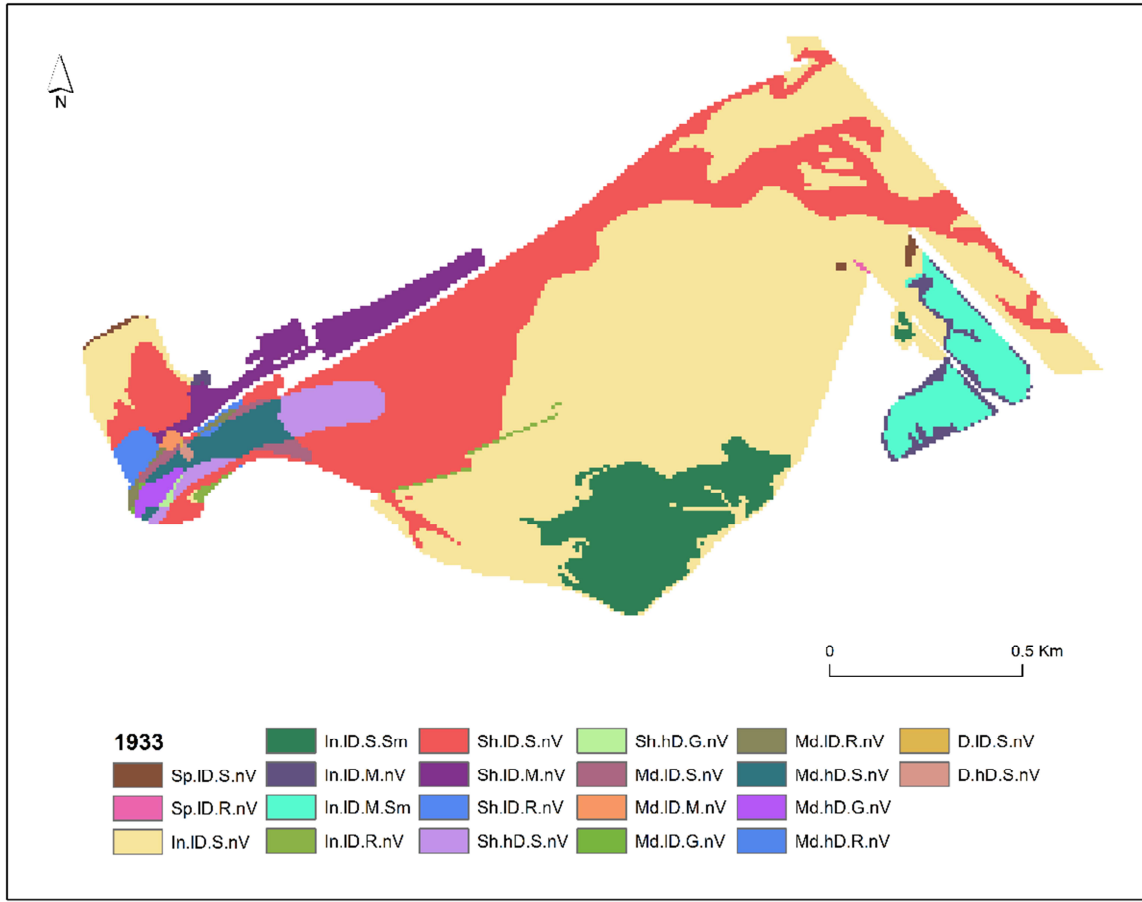
Table 3. Number and density of physiotopes (number per 100 ha), patch density (number per 100 ha) and attractiveness of the Lima estuary for fish (total and by species) for the years of 1933 and 2013.

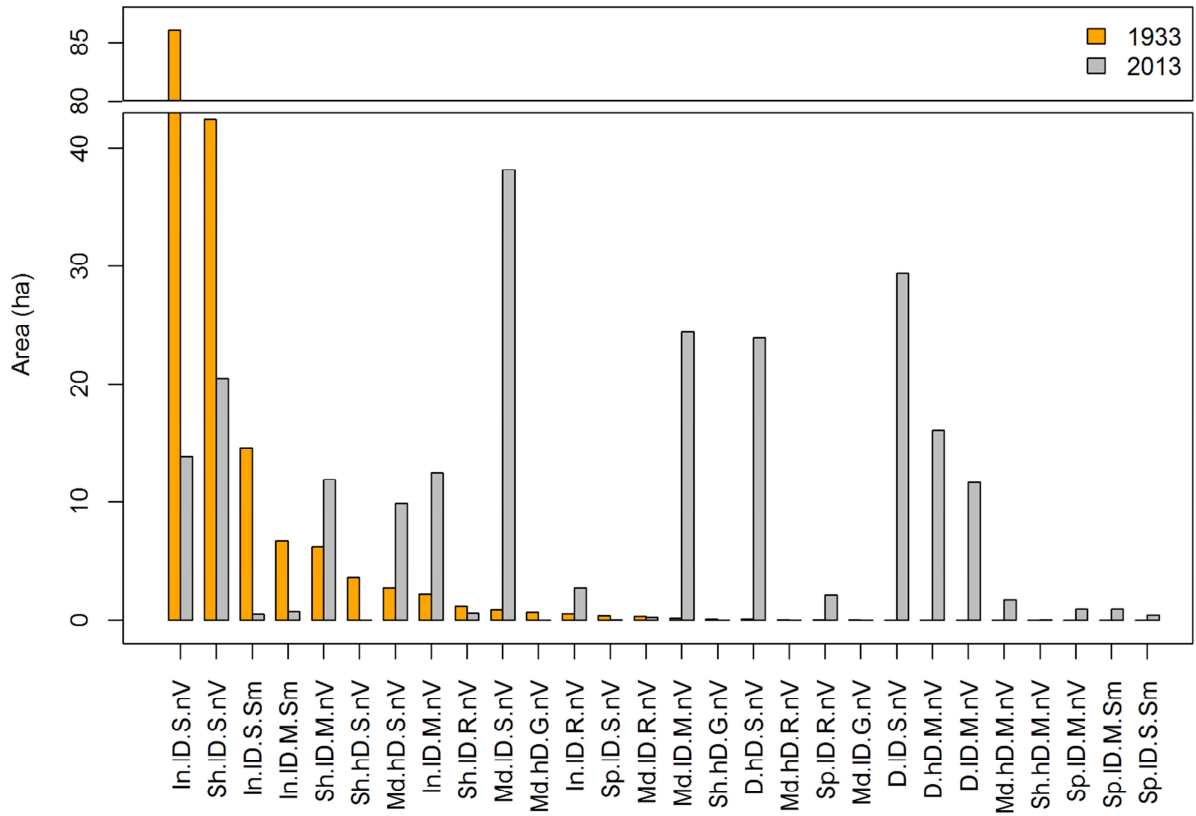
	1933	2013
Number of physiotopes	21	23
Physiotopes density (number per 100 ha)	12.5	10.3
Patch density (number per 100 ha)	55.0	300.6
Attractiveness	9.26	8.12
<i>Anguilla anguilla</i>	8.66	8.21
<i>Callionymus lyra</i>	8.46	8.40
<i>Dicentrarchus labrax</i>	8.88	7.98
<i>Platichthys flesus</i>	9.58	7.93
<i>Pomatoschistus microps</i>	10.71	8.10

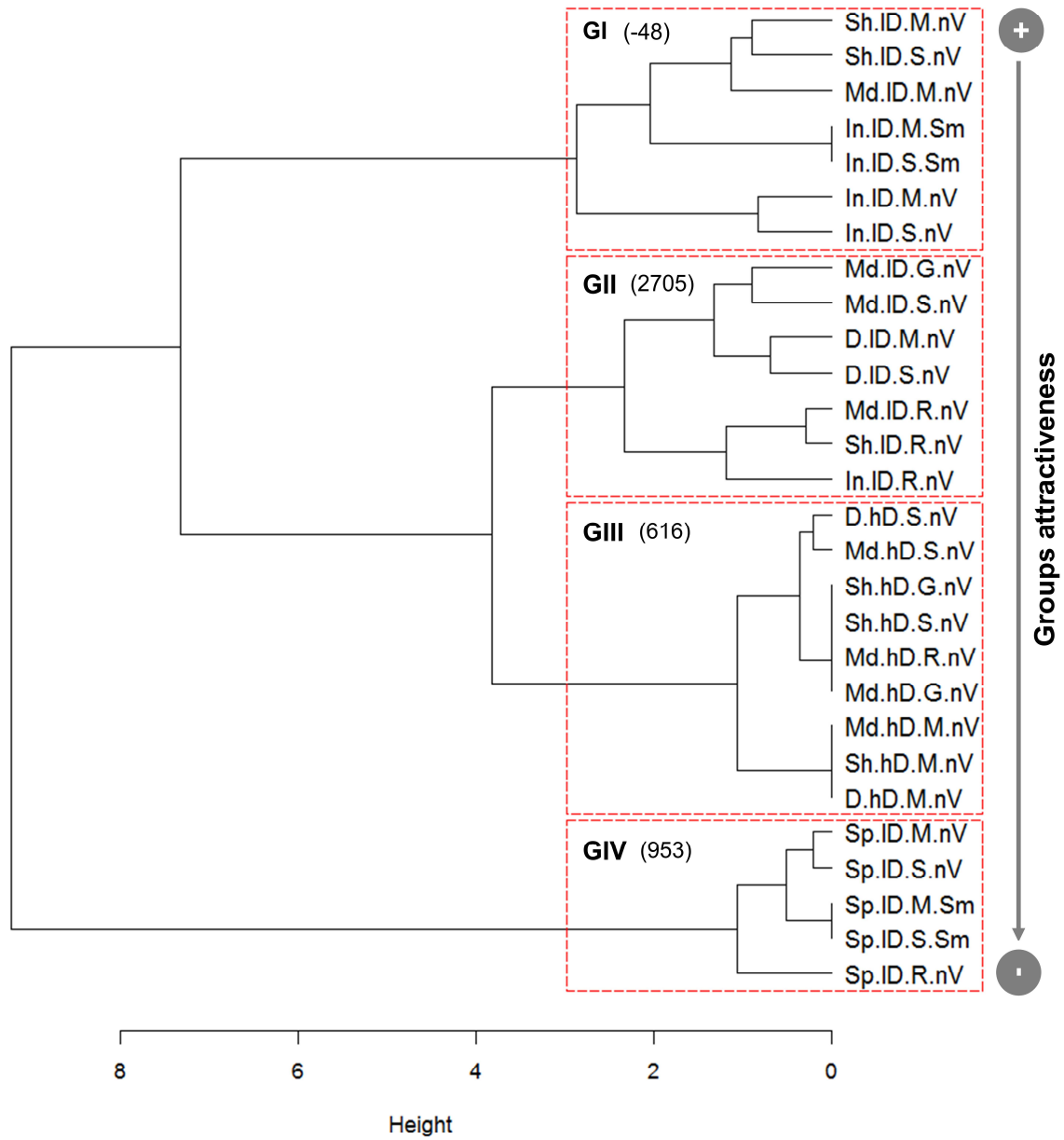
Note that the potential range of variability of the attractiveness score is 0-15.



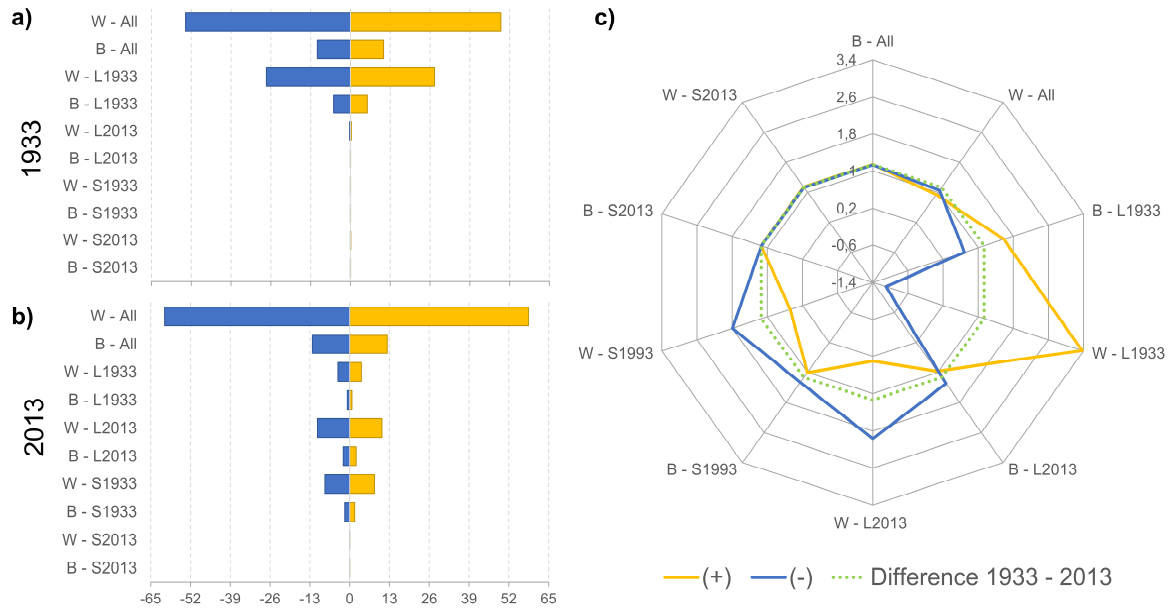








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Highlights

- Investigation of the habitat loss and gain of an estuarine area over 80 years.
- An ecohydrological classification system was used to quantify changes.
- The lower estuary was highly affected due to urbanisation and development.
- The most attractive physiotopes for fish decreased in area.
- Overall lower attractiveness of the studied area for fish in 2013 compared to 1933.

ACCEPTED MANUSCRIPT