

1 **Decapod crustacean larval communities in the Balearic Sea (western**
2 **Mediterranean): seasonal composition, horizontal and vertical distribution**
3 **patterns**

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14 **Abstract**

15 Decapod crustaceans are the main target species of deep water bottom trawl fisheries in
16 the Balearic Sea but little is known about their larval stages. This work focuses on the
17 species composition of the decapod larval community, describing the main spatio-
18 temporal assemblages and assessing their vertical distribution. Mesozooplankton
19 sampling was carried out using depth-stratified sampling devices at two stations located
20 over the shelf break and the mid slope, in the north-western and southern of Mallorca in
21 late autumn 2009 and summer 2010. Differences among decapod larvae communities,
22 in terms of composition, adult's habitat such as pelagic or benthic, and distribution
23 patterns were observed between seasons, areas and station. Results showed that for both
24 seasons most species and developmental stages aggregated within the upper water
25 column (above 75 m depth) and showed higher biodiversity in summer compared to late
26 autumn. Most abundant species were pelagic prawns (e.g., Sergestidae) occurring in
27 both seasons and areas. The larval assemblages' distributions were different between
28 seasonal hydrographic scenarios and during situations of stratified and no-stratified
29 water column. The vertical distributions patterns of different larval developmental
30 stages in respect to the adult's habitat were analyzed in relation to environmental
31 variables. Fluorescence had the highest explanatory power. Four clearly different
32 vertical patterns were identified: two corresponding to late autumn, which were
33 common for all the main larval groups and other two in summer, one corresponding to
34 larvae of coastal benthic and the second to pelagic species larvae.

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36 Key words: larval assemblages, Decapoda, adult habitats, developmental stage, vertical
37 distribution patterns, western Mediterranean.

38 1. Introduction

39 Most species of decapod crustaceans produce planktotrophic pelagic larvae that in some
40 areas and seasons can constitute a dominant group of the meroplankton (Beaugrand,
41 2005; Highfield et al., 2010). During their planktonic life they pass through many larval
42 stages whose complexity varies among species, spending from hours to months in the
43 pelagic environment before joining the parental population. Descriptions of decapod
44 larvae communities are still rare for most places around the world (e.g., Brandão et al.,
45 2012; Landeira et al., 2013). When available, they usually describe the nearshore
46 communities (e.g., Fusté, 1982, 1987; Paula, 1987) because studies focusing on the
47 spatial and temporal distribution of decapod larvae on estuarine or coastal waters are
48 more accessible and hence monitoring less costly. Besides, there has been a worldwide
49 interest to explain variations in larval supply rates in productive shelf areas, where
50 physical processes such as seasonal upwelling can drive large larval mass to settle (e.g.,
51 Queiroga et al., 2007).

52 Decapod species associated with the continental shelf and slope tend to have a wide
53 spatial offshore distribution, while those of coastal and nearshore species are usually
54 found much closer to the coast (e.g., Dos Santos et al., 2008; Miller and Morgan, 2013).
55 The temporal spawning patterns tend to vary among species with some species
56 reproducing in cold, some in warm months and others all year around (e.g., González-
57 Gordillo and Rodríguez, 2003; Pessani, 1993).

58 Decapod larvae feed on phytoplankton, detritus and other zooplankton (Anger, 2001).
59 Therefore, we may expect rich communities of decapod larvae associated to areas of
60 high primary productivity e.g. in coastal upwelling (Fusté and Gili, 1991) or in eddies
61 around oceanic islands (Landeira et al., 2009, 2010). Surface fronts and mesoscale
62 eddies may act as spatial hotspots of larval densities since these structures may increase
63 the availability of trophic resources to biological organisms (Bakun and Weeks, 2006).
64 Furthermore, protozoal stages of the Dendrobranchiata are capable of retaining
65 particles such as microorganisms, which can be crucial in oligotrophic waters where
66 bacteria biomass is dominant over phytoplankton biomass and most carbon and nitrogen
67 occur sequestered in bacteria (Cho and Azam, 1990).

68 Within the general oligotrophic environment of the western Mediterranean, the waters
69 around the Balearic Islands show an even more pronounced oligotrophy (Bosc et al.,
70 2004; Fernández de Puelles et al., 2007). However, the biological production around the
71 Balearic Sea during summer is partly associated to mesoscale oceanographic features,
72 fronts and eddies which may result in punctual productive zones (Alcaraz et al., 2007;
73 Estrada et al., 1993; Jansà et al., 1998). This could explain the relatively high
74 abundances of other meroplanktonic groups, as fish larvae, aggregating in the area,
75 especially during summer (Alemany et al., 2006; Torres et al., 2011). Therefore, we may
76 expect the presence of high abundances of decapod crustacean larvae as well. In the
77 western Mediterranean, most surveys targeting meroplankton have been conducted
78 during summer, when the water column is stratified with a well defined thermocline.
79 Below the thermocline a deep chlorophyll maximum (DCM) is temporally found
80 (Estrada et al., 1993; Jansà et al., 1998), coinciding with the maximum concentration of
81 zooplankton (Alcaraz et al., 2007; Saiz et al., 2007). In Mediterranean waters few
82 studies address together all groups that constitute the meroplankton concluding that
83 their abundance in general decreases in autumn (e.g., Vives, 1966; Olivar et al., 2010).

84 In the Balearic Islands, the mesozooplankton community shows a clear seasonal pattern
85 with highest abundances during summer and lowest numbers during winter. However,
86 significant peaks can be recorded in autumn, mainly due to an increase in copepod
87 abundances (Fernández de Puelles et al., 2003).

88 Some macro-zooplankton crustacean species are believed to be capable of utilizing
89 dominant currents and maintain their vertical position in the water column to avoid food
90 limitation in the general oligotrophic environment (Andersen et al., 2004). Vertical
91 ontogenetic migration has been shown to play an important role in larvae of benthic
92 species since they are hatched from eggs carried by bottom-dwelling females, after
93 release into the water column they tend to feed in the upper layers and return to the
94 adult habitat to settle. In the case of benthic species, an ontogenetic final migration from
95 upper layers of the water column to settle in the bottom near adults' habitats is also well
96 established (see review Queiroga and Blanton, 2004). Vertical migration behavior has
97 been described for larvae that develop in estuarine, shelf, and oceanic waters (Queiroga
98 and Blanton, 2004) and is considered to be mainly performed by the need to feed and, at
99 the same time, avoid predation (Pearre, 2003).

100 In the western Mediterranean Sea some studies have considered the annual distribution
101 of decapod larvae (e.g., Fusté, 1982, 1987; Pessani, 1993). Other studies have focused
102 primarily on the summer season (Olivar et al., 1998). In an important area for
103 crustacean fisheries, such as Balearic Islands, studies thus far have only focused on
104 individual single species (Carbonell et al., 2010; Marco-Herrero et al., 2013; Torres et
105 al., 2012; Torres et al., 2013).

106 The southern part of Balearic Islands, that forms part of the Algerian sub-basin, during
107 summer, receives new lower salinity surface water from the Atlantic (AW) and the
108 hydrodynamics of this area are thus strongly influenced by this density gradient. To the
109 northern, the Balearic sub-basin consists of colder and more saline Atlantic surface
110 waters that has remained longer in the Mediterranean (resident AW), and its dynamics is
111 affected by notable atmospheric forcing, mainly wind. The Western Intermediate Water
112 (WIW) is a modification of the Atlantic waters, formed only during winter in the Gulf
113 of Lion and the northern continental shelves of the north-western Mediterranean (from
114 the Ligurian Sea to the Catalan coast), and is not a consistent feature found every year
115 around at the Balearic channels (Monserrat et al., 2008; Vargas-Yáñez et al., 2012). As a
116 consequence, there are significant differences between the general hydrodynamic
117 conditions that affect the north and the south of the islands.

118 The present study is the first specific research on the decapod larval community off the
119 Balearic archipelago. Our aim is to describe seasonal patterns in the composition of the
120 decapod larvae community and assess differences between the shelf break and the slope
121 regions and between Balearic and Argelian sub-basins. We characterize these
122 communities according to their adult habitats i.e. if the adult stages have a pelagic or
123 benthic life mode, their taxonomic group and their larval development stage. Our
124 hypothesis is that decapod larvae communities will be different for the two seasons and
125 that both will be characterized mainly by larvae of pelagic species. In addition, the
126 northern study area where the shelf is narrower and the slope is quite pronounced, the
127 currents over the shelf created mixed conditions. In this case we expect to have an
128 important component of larvae from coastal species in the northern stations, at least
129 during warm season. Taking into account the resources availability for the oligotrophic

130 Mediterranean Sea we analyze and discuss environmental variables vertical distribution
131 and their effect on the larval vertical distribution from pelagic or benthic adult's habitat
132 in relation with the main oceanographic features of the area.

133 **2. Material and methods**

134 *2.1. Sampling methodology*

135 Two multidisciplinary research surveys were conducted off the Balearic archipelago
136 (western Mediterranean; Fig. 1) during late autumn (29th November to 18th December
137 2009) and summer (11 to 30th July 2010) on board the R/V *Sarmiento de Gamboa*. We
138 sampled a total of 4 stations during each cruise. One station was located over the shelf
139 break (250 m depth) and the other over the mid slope (900 m depth) off the north-
140 western (N), in Balearic sub-basin. The other two stations were also located in the shelf
141 break and the mid slope but in the southern (S) of the Mallorca Island, in Algerian sub-
142 basin. In each station we conducted repeated stratified hauls continuously during 36
143 hours. A total of 34 hauls resulting in 218 depth-stratified samples were sampled for
144 decapod larvae. The hauls were distributed as: 5 hauls in the northern during late
145 autumn, 13 hauls in the southern during late autumn, 8 hauls in the northern during
146 summer and 8 hauls in the southern during summer (Fig. 1).

147 The samples were collected in late autumn using an HYDRO-BIOS MultiNet sampling
148 five depth strata and in summer with a Multiple Opening-Closing Net and
149 Environmental Sensing System (MOCNESS) sampling seven depth strata (Olivar et al.,
150 2012). The net mouth openings were 0.25 and 1 m², respectively, and the mesh size was
151 333 μ m for both nets. Both devices were towed at ~2 knots. The volume of water
152 filtered in each layer varied from 44 to 2414 m³, depending on the depth range of the
153 layer sampled. The whole water column from a given depth relatively close to the
154 bottom was sampled and the thickness of each layer varied depending on the
155 bathymetry and the season (Table 1). Immediately after collection all samples were
156 preserved in ~5 % borax-buffered formaldehyde, prepared using seawater. Once in the
157 laboratory, samples were subsequently sorted for crustacean decapod larvae, which were
158 identified to species level and developmental stage, whenever possible, using available
159 descriptions (Dos Santos and Lindley, 2001; Dos Santos and González-Gordillo, 2004).

160 Geostrophic velocities at surface were obtained for both seasons from satellite altimetry
161 data (Fig. 2a and 2b), which were downloaded from MyOcean (Baharel et al., 2009).
162 Delay Time data gridded into a Map of Absolute Dynamic Topography (DT-MADT)
163 was used (Aviso, 2012). Hydrographic measurements were recorded using a CTD
164 (SBE911) at the four plankton stations (Fig. 3a-3h). A salinity value of < 37.0 is the
165 criterion used to identify the fresher Atlantic water (AW), and that of > 37.5 was used to
166 identify resident AW. We refer to water with intermediate salinity values between 37.0 –
167 37.5 as mixed AW.

168 Vertical profiles of potential temperature, salinity and fluorescence were averaged at 1
169 m intervals to depict the vertical structure of the 200 first meters of water column and
170 also $\theta - S$ diagrams were performed, based on potential temperature and salinity, to
171 describe the water masses. The fluorescence concentration at the different depths was
172 used as a proxy for food availability. Temperature values were used to describe the
173 position of the thermocline and the thermal characteristics of the water column. Salinity
174 was used to identify different water masses.

175 2.2. *Spatial and seasonal larval distribution analysis*

176 The species richness has been analyzed by means of dominance plots usually used
177 evaluate ecosystem status. Cumulative dominance percentage of species were calculated
178 as the proportion of total hauls, by season, areas and sampling stations, where a species
179 was present.

180 Density estimates of the organisms at each depth stratified sample were standardized to
181 number of individuals per 100 m³ at lowest taxonomic level identified, for each area and
182 season. The frequency of occurrence of each taxonomic level was calculated. The
183 species were grouped by their taxa group and their adult habitat to analyze their
184 contributions to the larval community. Regarding their corresponding taxa group the
185 decapod larval species were grouped in 7 categories as presented in Table 2 under the
186 taxa column. According to their adult's habitat the larvae were assigned to 11 groups as
187 presented in the column Adults Habitat in Table 2. To assess the vertical distribution of
188 the larvae, besides the adult habitat classification we separated the larvae by ontogenetic
189 developmental stage.

190 Differences in the composition of the assemblages of the larval community in the first
191 200 m, during late autumn and summer and at the four stations per season, were
192 analyzed using nonparametric multivariate analysis applied to densities of the larvae
193 (Clarke, 1993). Prior to the analysis, data were squared root transformed in order to
194 prevent the dominant larval species from masking the responses of those with low
195 densities (Clarke and Warwick, 2001). The Bray–Curtis similarity index was chosen as
196 the similarity coefficient and the group average was used as the clustering algorithm
197 (Clarke and Warwick, 2001). Cluster analysis and their corresponding two-dimensional
198 representations by Multidimensional scaling ordination (MDS) were used to identify
199 larval assemblages during both seasons. Stress coefficients with values <0.15 indicate
200 that the data are portrayed well (Clarke and Gorley, 2006). We calculated the percentage
201 contribution of average densities of the dominants groups by adult's habitat for main
202 larval assemblage described by Cluster (SIMPER analysis).

203 Decapod larvae pass through several developmental stages that were merged in 2 groups
204 to analyze their vertical distribution. A first group named *stage 1* included the first zoeal
205 stages (*Z*) and a second group named *stage 2* included the advanced zoeal stages. The
206 second developmental group (*stage 2*) never included megalopal or decapodite stages.

207 2.3. *Vertical larval distribution analysis*

208 The seasonal vertical distribution patterns for the main larval taxa belonging to the more
209 representative adults' origin (coastal epibenthic, coastal nektobenthic, epipelagic and
210 mesopelagic) were analyzed within the first 200 meters of the water column, where
211 most decapod larvae were found (up to 90.7 % and 93.7 % of the total density in
212 autumn and summer, respectively). General Linear Models (GLMs) were used to
213 analyze the environmental variables that could drive the larval vertical distributions.
214 Temperature, salinity and fluorescence were used as continuous co-variables and larval
215 density as the independent variable. Area (northern and southern) and station (shelf
216 break and mid slope) were included in the model as factors.

217 3. **Results**

218 3.1. *Hydrographic conditions*

219 In the upper layers, during late autumn, a well defined anticyclonic gyre at the north of
220 Ibiza deflected Northern Current waters (Fig 2a). The southern area was mainly under
221 the influence of a cyclonic gyre formed by resident Atlantic waters (AW) re-circulated
222 from the Balearic sub-basin and flowing from coastal areas at the east of Mallorca (Fig.
223 2a). During summer, we observed an anticyclonic gyre in the northern area, but situated
224 slightly northwards and affecting mostly the slope and a cyclonic meander to the south-
225 western. In contrast, the southern area was mostly occupied by an anticyclonic gyre of
226 recent Atlantic Waters, detached from the main current of recent Atlantic Waters flowing
227 in SW-NE direction at the south of the archipelago, trapped at the east of Ibiza Island
228 (Fig. 2b). The geostrophic currents during late autumn reached higher values than
229 during summer (Fig. 2a and 2b).

230 Therefore, there were contrasting hydrographic conditions between the late autumn and
231 summer seasons (Fig. 2 and 3) due to (a) the income of new AW in the upper layers in
232 summer, (b) the seasonal differences in the presence / absence of Western Intermediate
233 Waters (WIW) and (c) the stratification of the water column (Fig. 3). The water masses
234 found at the surface during both surveys were different. Thus, during late autumn we
235 could find only resident surface Atlantic Waters in both areas (Fig. 3a) whereas in
236 summer we also observed mixed Atlantic waters in the southern (Fig. 3b). The seasonal
237 differences in WIW are clearly observed in the $\theta - S$ diagrams, indicating absence of
238 WIW (Fig. 3a) during autumn, whereas during summer three of the stations showed the
239 presence of WIW (Fig. 3b).

240 The water column was stratified in summer whereas in late autumn conditions were of
241 mixed layer without clear clines. More specifically, the temperature in the upper layers
242 was colder in late autumn, around 17°C, whereas in summer temperatures up to 26°C
243 and 27°C were recorded (Fig. 3c and 3d). In late autumn the surface waters were saltier
244 (~38) than during summer, when the income of recent AW resulted in the presence of
245 less saline waters (37.5 – 37.9) (Fig. 3e and 3f). Regarding surface fluorescence values,
246 in autumn (range between 0.1 – 0.3; Fig. 3g) were higher than in summer (~0.05; Fig.
247 3h). The vertical profiles of the environmental variables during the late autumn survey
248 were homogeneously distributed down to the mixing layer depth (MLD), located at 60
249 and 80 m depth in the southern and the northern, respectively (Fig. 3c, 3e and 3g).

250 In summer, environmental variables showed strong gradients in the upper 100 meters. A
251 shallow MLD of around 10-13 m and a thermocline located between 10 to 50 m depth
252 was observed in the summer, in both areas (Fig. 3d). During late autumn no halocline
253 was detected and in summer halocline was located between 5 to 25 m depth, when
254 surface waters were influence by wind (Fig. 3e and 3f). Deep fluorescence maximums
255 with values between 0.4 and 1 were found below the MLD between 50 and 80 m depth
256 in summer (Fig. 3h). The maximum fluorescence peak was located over slope in the
257 southern study area, at 80 m depth, and the minimum in northern area also over the
258 slope, at 55 m depth, which in addition represented the shallowest registered depth of
259 such fluorescence peak.

260 3.2. *Assemblage composition, seasonal and horizontal larval distribution*

261 The list of all taxa identified in the samples with total individuals identified for each
262 season and the mean densities for same season and in the same area are given in Table
263 2. From the total of 121 taxa found, 19 were identified at family level (or higher), 27 at
264 genus level and 75 at species level. Most of them appeared only in summer (63),
265 whereas only 7 were exclusively present in late autumn. In terms of the main decapod
266 taxa groups, the most abundant in the samples were shrimps (Dendrobranchiata) larvae
267 that accounted for 63 % of the total decapod larvae sampled during late autumn and 52
268 % in summer, followed by crabs species (Brachyura) for late autumn, with 18 %, and in
269 summer by caridean shrimps, with 32 %. The minor groups during both seasons were,
270 in order of abundance, hermit crabs, squat lobsters, slipper lobster and ghost shrimps.
271 Regarding the origin of the larvae, they were mainly constituted by species from
272 mesopelagic and epipelagic habitats, comprising around 57 % of the total captures.

273 Shrimps larvae during autumn were mainly *Gennadas elegans*, whereas in summer
274 *Parasergestes vigilax* and *Eusergestes arcticus* were the most abundant ones. Mean
275 densities of *G. elegans* during late autumn were about 14.5 ind. per 100 m³ (± 8.7) in
276 northern stations to 6.1 ind. per 100 m³ (± 3.8) in southern stations (Table 2). The crab
277 species *Goneplax rhomboides*, second in order of abundance during the fall season,
278 appeared only in the southern, with mean abundances of 2.9 ind. per 100 m³ (± 4.3). *E.*
279 *arcticus* and *Plesionika* spp. registered important abundances as well in this season. The
280 summer most abundant species was *Parasergestes vigilax*, showing densities from 1.8
281 ind. per 100 m³ (± 2.6) in the northern area to 2.2 ind. per 100 m³ (± 3.4) in the southern.
282 Three crab taxa exclusively found in summer and relatively abundant were *Parthenope*
283 spp., *Ebalia* spp. and *Xantho* spp., followed by hermit crabs such as *Calcinus tubularis*.

284 The species rank plots showed that the decapods larval community was most diverse
285 during summer, especially in the northern area, and higher species dominance were
286 registered in late autumn (Fig. 4). In late autumn, the southern area showed the highest
287 diversity, having the “southern shelf break” station similar species richness, as the ones
288 found at summer stations.

289 The analysis of the horizontal distribution of larvae grouped considering the adult’s
290 habitats showed no clear pattern between areas. During late autumn the larvae were
291 mainly from mesopelagic species, which dominated in the northern area, whereas in the
292 southern a mixed assemblage was observed, with high percentage of larvae from coastal
293 epibenthic species (Table 3). In summer, at the northern area the assemblage was mixed,
294 with larvae from all types of species, whereas in the southern area the community was
295 mainly constituted by larvae belonging to pelagic, coastal nektobenthic and oceanic
296 epibenthic species (Table 3). Moreover, significant differences between seasons, areas
297 and station for the second group of development stage were detected for larvae from
298 coastal epibenthic and nektobenthic adult’s, which are summarized in Table 4.
299 Furthermore, for the first group of development stage differences between area and
300 station were significant for late autumn for pelagic and for pelagic and coastal species at
301 summer (Table 5).

302 The inter-relationships by season, determined by means of the cluster analysis
303 considering the available data from the hauls carried out at different depth ranges
304 between 0 and 200 m, are presented in Fig. 5a and 5c. The SIMPER analysis was used
305 to identify those adults habitats, used as a proxy for the origin of the larvae, primarily
306 responsible for the differences among larval assemblages. The adult habitats explained

307 more than 50 % of the analyzed cluster variability. In both seasons, larvae from
308 mesopelagic species were the dominant group, despite the larvae of epipelagic species
309 were also important in summer (Table 3). The “late Autumn Southern shelf break”
310 cluster group (ASshelf; Fig. 5a, b) was the most diverse, with a predominance of coastal
311 benthic species (epibenthic plus nektobenthic) and with an important contribution of
312 mesopelagic species. Nevertheless, the rest of the hauls in “late Autumn” (A; Fig. 5a,
313 5b) were clearly dominated by larvae of mesopelagic species. At “Summer the Southern
314 slope” Cluster assemblage (SSslope; Fig. 5c, d) grouped hauls from southern slope,
315 whereas the rest of summery hauls were grouped in the “Summer” cluster assemblage
316 (S; Fig. 5c, d). The similarity analysis for summer season revealed that about 50 % of
317 the variability was explained by larvae from coastal benthic species (coastal epibenthic
318 and nektobenthic), grouped in summer cluster assemblage “S”, except in the “Summer
319 Southern slope” cluster assemblage “SSslope“, which was exclusively formed by larvae
320 of mesopelagic and epipelagic species.

321 3.3. Vertical larval distribution

322 A general vertical distribution pattern, characterized by the aggregation of individuals
323 within the upper 75 m of water column, was followed by all taxa and larval stages.
324 However, two different vertical distribution patterns were identified in each season for
325 the main larval groups according to the adult’s habitat and the larval developmental
326 stage.

327 For late autumn, the non-stratified season, the general pattern (pattern 1) shows that the
328 larvae were mainly concentrated at depths between the 25 and 75 m. It happened in both
329 zoal groups (pattern 1a, see Fig. 6a, 6c and pattern 1b, see Fig. 7c), being fluorescence
330 the variable that explained most of the vertical distribution variability (Fig. 6b, 6d, 7d).
331 However, during late autumn this pattern differed for stage 1 (early protozoae) by
332 larvae belonging to pelagic species, which were mainly found between 60 and 200 m
333 depth (pattern 2 see Fig. 7a) and showed a strong relation to temperature and salinity
334 (Fig. 7b).

335 In addition, during fall season in southern area the highest densities of early zoeae of
336 coastal benthic species were situated over shelf break (Fig. 7c). At this station (southern
337 shelf break) the temperature and fluorescence presented the highest values during the
338 season (Fig. 3d, 3f) coinciding with the depth of densities’ peak of larvae (around 25-
339 75m). At this point we found the highest abundances of developmental larval group 1
340 from coastal epibenthic and nektobenthic taxa, composed mainly by *Goneplax*
341 *rhomboides* and *Plesionika* spp., respectively.

342 During summer, when the water column was stratified, showing a marked thermocline,
343 halocline and fluorescence peak, two different patterns were identified also. All larval
344 stages of coastal epibenthic and nektobenthic species presented a decreasing density
345 from surface down to 75 m (pattern 3, see Fig. 6f, 7g). Temperature, salinity and
346 fluorescence explained the stage 2 (late zoeae) distribution pattern (Fig. 6g). For the
347 stage 1 group, fluorescence and salinity were the main variables explaining the vertical
348 distribution of the larvae (Fig.7h), corresponding to the minimum observed values,
349 recorded at surface, to the maximum larval abundance.

350 The larvae of the mesopelagic and epipelagic species showed two clear peaks in
351 summer (pattern 4), one at the surface layers, from 0 m to 25 m depth, and the other
352 from 50 m to 75 m depth (Fig. 6e, 7e). The surface peak was mainly attributable to
353 *Parasergestes vigilax*, and was best explained by temperature, suggesting that these
354 larvae preferred warm waters above the thermocline. On the other hand, fluorescence
355 was the environmental variable that best explained the deep peak, where the main
356 abundances were of *Eusergestes arcticus*, suggesting that these larvae concentrate at the
357 maximum fluorescence peak (Fig. 7f).

358 The highest larval abundances in late autumn were registered at the southern shelf break
359 station. The highest values of temperature and fluorescence during late autumn at this
360 station (17.6 °C and 0.43, Fig. 3c, 3g) agree well with the depth in which the highest
361 densities of larvae were found (around 25-75 m, Fig. 6 and 7). The highest abundances
362 in summer were found at the surface layers of the northern mid slope station (Fig. 6 and
363 7). The highest values of temperature during warm season (27 °C; Fig. 3d) at this station
364 agree with the depth in which the highest densities of larvae were registered.

365 4. Discussion

366 4.1. Seasonal and horizontal larval distribution

367 We found decapod larval densities around 100 times lower than those reported for
368 productive upwelling nearby coastal Atlantic areas (e.g., Dos Santos et al., 2008; Fusté
369 and Gili, 1991). This agrees well with the oligotrophic characteristics of the
370 Mediterranean Sea nevertheless the sampled area of the present study is located on the
371 shelf break where recurrent mesoscale eddy activity is observed. However, late autumn
372 larval densities were similar to those found off Canary Islands (23.7 ind. per 100 m³ ±
373 22.9; Landeira et al., 2010). This could be related to the 'island mass effect' (Doty and
374 Oguri, 1956), which cause and enhancement of primary productivity around islands in
375 relation to open ocean waters (Gilmartin and Revelante, 1974; Hernández-León, 1991),
376 increasing preys availability and, in consequence, we could expect higher abundances of
377 decapod larvae. Mesoscale oceanographic features such as fronts and eddies are key
378 mechanisms to enhance the biological productivity in specific areas (Alcaraz et al.,
379 2007; Estrada, 1996). The Balearic Sea, due to the interaction among different water
380 masses and of those with the island's topography, is a hydrodinamically complex area
381 (López-Jurado et al., 1995, 1996; Pinot et al., 2002). Moreover, we found the maximum
382 peak of larval density during summer in the northern area, associated to strong
383 geostrophic currents and an anticyclonic eddy. The continuous current system that runs
384 from the mainland to the Balearic archipelago in some years could result, in local
385 enrichment processes derived from the more productive area linked to the Spanish
386 mainland rivers (López-Jurado et al., 2008; Pinot et al., 2002).

387 The dominance of shrimps (Dendrobranchiata species) in our assemblages is in
388 agreement with those observed for offshore waters around oceanic islands (e.g., Brandão
389 et al., 2012 off Saint Paul's Rocks, Southwest Atlantic Ocean; Landeira et al., 2009 off
390 Canary Islands). On the contrary, crab larvae usually dominate decapod larvae
391 assemblages from continental shelf areas (e.g., Dos Santos et al., 2008) or neritic areas
392 around Atlantic islands (Koettker and Freire, 2006). In our study, crabs were the second
393 most abundant group during late autumn and the third in summer, suggesting some
394 degree of mixing between typical offshore, such as mesopelagics, and nearshore, such

395 as coastal-benthic species. Specifically, information on the casual occurrence and
396 morphology of larval stages of the red shrimp *Aristeus antennatus*, the rose shrimp
397 *Parapenaeus longirostris*, the slipper lobster *Scyllarides latus* and the Mediterranean
398 spider crab *Maja squinado*, species that are important for fisheries management and
399 conservation purposes have been published recently (Torres et al., 2013).

400 The most abundant taxon in our samples at late autumn, *Gennadas elegans*
401 (Dendrobranchiata), presented its highest densities at the northern of the Balearic
402 Islands (14.5 ind. per 100 m³ ± 8.7) coinciding with the highest velocity currents. This
403 high density in Balearic oligotrophic waters could be explained by the capacity of
404 Dendrobranchiata early life stages to retain picoplankton which tend to dominant over
405 phytoplankton biomass. Thus picoplankton could act as source for carbon and nitrogen
406 (Cho and Azam, 1990). It must be pointed out that in autumn the maxima of dissolved
407 organic carbon are found in surface waters, where it is continuously removed from
408 surface waters by diffusive processes during the stratified period in north-western
409 Mediterranean (Copin-Montégut and Avril, 1993).

410 A review of the relevant literature shows that Mediterranean pelagic shrimps have not
411 been thoroughly studied and information on their adult distribution is poor (e.g.,
412 Casanova, 1977; Koukouras, 2000; Koukouras et al., 2000). Within this context, the
413 present study allows us to reveal some ecological traits for these pelagic species that
414 currently are of no commercial interest to the fishing industry and for which no previous
415 information of this type exists for the western Mediterranean (Simão et al., 2013-this
416 issue).

417 According to Champalbert (1996) zooplankton communities in the western
418 Mediterranean present low diversity at inshore waters, especially when the continental
419 shelf is narrow. Contrastingly, in our case decapod larval k-dominance curves showed
420 different behavior, in the northern shelf in summer, since our highest diversity and
421 density values were registered there, despite the shelf is narrower than in the southern
422 area. The larvae of coastal nektobenthic and epibenthic species dominated the decapod
423 larvae community in this area and season, showing the maximum values of biodiversity
424 registered for Mediterranean Sea (Fusté, 1987; García-Comas et al., 2011; Pessani,
425 1975). In late autumn larvae of these groups dominated also the communities over the
426 shelf break in the southern part of the Balearic Islands. However, overall the larvae of
427 pelagic species dominated in the majority of our samples, comprising 57 % of total
428 decapod larvae.

429 Our data revealed the highest densities and biodiversity of decapod larvae in summer,
430 coinciding with the major reproductive season for most decapods species in the western
431 Mediterranean (García Raso, 1982; Zariquiey, 1968). The seasonal pattern described for
432 pelagic shrimps (Dendrobranchiata and Caridea) larvae agrees with the seasonality in
433 species composition of the neighboring Ligurian Sea, where the species maximums
434 were registered in June and the minimum in autumn-winter (Pessani, 1993). As
435 mentioned above, in our samples taken off the Balearic Islands, the most abundant
436 species were the mesopelagic shrimp *Gennadas elegans*. In a study carried out on the
437 shelf of Catalanian coast all the year round, *G. elegans* larvae showed their maximum
438 abundance during February, and the minimum in October, but no larvae were found in
439 December and July (Fusté, 1987). On the contrary, we registered the presence of *G.*
440 *elegans* larvae in both months, being present in abundance in December. Therefore we

441 can conclude that this species reproduces during all year in the western Mediterranean,
442 and that late autumn – winter potentially being their most important reproductive
443 season.

444 4.2. *Hydrographic effect on larval assemblages*

445 Larval densities during the autumn season differed between the two study zones
446 (northern and southern). The highest densities were observed in the southern shelf break
447 and the lowest at the northern slope stations. The larval assemblages were mainly
448 constituted by larvae of mesopelagic species, except for the southern shelf break station,
449 where coastal benthic species larvae dominated. The observed differences were
450 probably related with the currents registered in the area.

451 There was a strong north-south flowing current during late autumn, originated in
452 offshore areas of Balearic sub-basin and associated to a front perpendicular to the shelf
453 located in the northern sampling area, which swept both northern area and southern
454 slope stations (Balbín et al., 2012). This current could explain why the majority of
455 decapod larvae at the northern and in the outer southern stations (autumn cluster group)
456 belonged to mesopelagic species. The larvae of coastal benthic species were
457 concentrated over the southern shelf break station (Autumn Southern shelf cluster
458 group) where a cyclonic gyre could promote its retention. Species richness and also
459 larval densities were highest at this southern shelf break station. This fact could also be
460 a consequence of the aforementioned gyre; it not only would retain larvae, but would
461 produce the mixing of larvae of more coastal and deeper upper slope species, increasing
462 the diversity of such mixed larval assemblage.

463 In summer, both the northern stations and the southern shelf break station with a high
464 similarity, showed a mixed larval assemblage, and composed by mesopelagic,
465 epipelagic and coastal nektobenthic species, without any clear dominance of one group
466 over the others. On the contrary, almost only larvae from pelagic species were found at
467 the southern slope station coinciding with an anticyclonic input of lower salinity
468 Atlantic, since up to 80 % of specimens were *Parasergestes vigilax* early protozoae
469 (stage 1). Most of the late protozoae of this species were caught over the northern
470 slope, in the front side of an anticyclonic eddy.

471 Currents in summer were in general less intense than in late autumn, which could allow
472 spatial retention of larvae close to the area of their release. However, in the northern
473 area, the cyclonic gyre located over the shelf break sampling station should promote the
474 advection of coastal larvae to the nearby offshore stations, favoring the existence of the
475 mixed assemblage with the highest biodiversity. In fact, in the north of Mallorca where
476 the shelf is narrower and the slope is quite pronounced, the currents over the shelf
477 created mixed conditions, that could explain the important component of larvae from
478 coastal species. Specifically, over the northern shelf break the highest larval densities of
479 *Plesionika* spp. and *Xantho* spp. swept from coastal benthic zones were caught. In the
480 northern slope station, the only with surface resident AW, had been influenced by a
481 heavy anticyclonic feature which would also favour the mixing of larvae. The highest
482 larval density value was registered, corresponding mainly to larvae of epipelagic adults
483 (e.g., Sergestidae), as those of *P. vigilax* mentioned above.

484 Mesoscale advective processes (surface fronts and eddies) affect planktonic
485 communities and may offer opportunities for exceptional local productivity and growth
486 of species. Owing to the complex hydrodynamic situation and topographic features in
487 the study area, mesopelagic species were also relatively abundant in stations located
488 over the shelf break, being found together with larvae of neritic species.

489 The general structure of decapod larvae community found off the Balearic Islands is
490 similar to that reported in nearby Spanish continental coast by Fusté (1987), with
491 pelagic taxa being more dominant. The mesopelagic species dominance during both
492 seasons in our study area was expected as all sampling stations were not located close to
493 the shore, the shelf in this area is relatively narrow and hence the distance between shelf
494 break and slope stations is short, and also because the existence of mesoscale features as
495 eddies favor the advection of offshore species larvae to shelf.

496 4.3. *Environmental effect on vertical larval distribution*

497 Most decapod larvae were distributed between the 0-75m and followed well the vertical
498 pattern in fluorescence during both seasons. The early and late protozoae are mostly
499 phytotrophic and they can adapt their movements in the water column to stay by the
500 fluorescence peak and optimize their feeding. Increasing food abundance enhances
501 feeding rates and resulting developmental rates in decapod larvae (Dawirs, 1985).
502 Therefore, observed larval distribution may reflect an optimization of their behavior in
503 the water column to favor the encounter of food. Decapod larvae show positive
504 phototaxis in the laboratory (e.g., Sulkin, 1975), which is supported by the finding of
505 the current study that found mainly larvae within the euphotic layer (0 – 200 m).

506 The earliest stages of the pelagic species (mesopelagic and epipelagic) in late autumn
507 were distributed between the 60-200 meters. These developmental stages could have
508 been caught during their first ontogenetic migration upwards from the deepest layers
509 were they were probably born since the adults of these species, e.g., *Gennadas elegans*,
510 are mostly located in the mid slope within the Deep Scattering and the Benthic
511 Boundary Layers around 400 m depth close to the bottom (Ramón et al., 2013-this
512 issue; Simão et al., 2013-this issue). Another example is the case of *Eusergestes*
513 *arcticus*. The adults inhabit the mesopelagic waters whereas the larvae were located
514 mostly between 50-75 m depth. For the epipelagic shrimp *Parasergestes vigilax* most
515 larvae were located in the first 25 m of the water column.

516 Crustacean larvae are able to swim across environmental gradients in the water column
517 such as the thermocline (Dos Santos et al., 2008; Lindley et al., 1994). They can
518 perform diel vertical migrations though patterns can vary among the successive
519 developmental stages and species (e.g., Andersen et al., 2004; Dos Santos et al., 2008;
520 Lindley et al., 1994). We have observed larvae above the thermocline during the
521 summer supporting these previous findings. Though some of the larvae were found at
522 the highest temperatures, most larvae were not located in the warmest layers. The
523 occurrence of the larvae of the same species across temperatures ranges of 13-27 °C
524 reinforces the conclusion that temperature is not a main variable defining the vertical
525 distribution of the early life stages of decapod crustaceans.

526 Migratory behavior in crustacean larvae has been related to predator-avoidance, hunger
527 and adaptations to optimize dispersal by currents (Queiroga and Blanton, 2004;

528 Landeira, 2009; Pearre, 2003). At surface, potential predators such as fish larvae (Olivar
529 et al., 2013-this issue) coexist with crustacean larvae. On the other hand, late stages can
530 predate on zooplankton while earlier stages prey mostly on phytoplankton. The vertical
531 position of the crustacean larvae may reflect strategies considering a trade-off between
532 the optimization of food availability and survival. Further research on the overlap in the
533 water column of crustacean and fish larvae can help to describe such trade-offs.

534 **5. Conclusions and perspectives**

535 Our study provides for the first time an accurate analysis of the decapod larvae structure
536 and vertical distribution over shelf break and mid slope in two seasons at two areas off
537 the Balearic Islands. The community of decapod larvae in the study area is composed
538 mainly of larvae of mesopelagic shrimp species (Dendrobranchiata). Our results show
539 also that the complex surface water circulation patterns around the Balearic
540 Archipelago, characterized by the presence of mesoscale structures as fronts and
541 eddies, can lead to local larval retention over the adult populations. The oceanography
542 causes the mixing of coastal and mesopelagic species larvae in the area.

543 The analyses of the vertical distribution of larvae show most larvae concentrate in the
544 first 75 m of the water column though differences are observed among species mostly
545 related to the vertical distribution of different ontogenetic developmental stages. The
546 main factor explaining the observed vertical distributions is food availability. The larvae
547 are concentrated in the depth ranges of the water column where the fluorescence values
548 confirm higher concentration of potential preys, considering that decapod larvae feed on
549 picoplankton and phytoplankton. Within this context, the vertical position of the
550 crustacean larvae may reflect strategies considering a trade-off between the optimization
551 of food availability and survival. However, further improvements on the knowledge of
552 ecology and vertical distribution of autotrophic and heterotrophic plankton,
553 communities are deemed necessary in the area to achieve a better understanding of the
554 biological processes affecting decapod larvae survival.

555 The positioning of the larvae along the water column could be related to species specific
556 strategies developed to optimize recruitment processes, since transport of decapod
557 larvae throughout their pelagic larval stages is a key determinant of adult population
558 dynamics. The larval vertical migration behaviors may couple with vertically stratified
559 flows to retain larvae nearshore. Thus, by varying their vertical position in relation to
560 mesoscale hydrological structures, they could control in a certain way their transport
561 from spawning to nursery areas. In order to identify better their effect on life history
562 traits our results underline the need for further detailed studies, with new data taken
563 concurrently on both physical and biological parameters. These kinds of studies would
564 allow developing biophysical models which require not only accurate 3D hydrodynamic
565 models but reliable information on larval distribution, ecology and behavior. Thus, the
566 knowledge on larval assemblage's structure, distribution and ecology will be essential in
567 improving our understanding of population's dynamics and population connectivity
568 aspects that will be important to inform management strategies.

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808

809 **Figure legends:**

810 Fig. 1. The study area and main hydrographic features. The Mallorca and Ibiza
811 channels, the Northern and Balearic Currents, and the Algerian Gyres are indicated.
812 Study area (framed and dotted) with haul's position during late autumn (A) 2009 (black)
813 and summer (S) 2010 (grey), at four plankton stations located over shelf break (250
814 isobath) and mid slope (900 isobath) off the northwest(N) (Balearic sub-basin) and
815 southern (S)(Algerian sub-basin) of Mallorca Island. Grey lines indicate isobaths (200,
816 400, 600, 800 and 1000 m).

817 Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (\blacklozenge) Southern shelf break; (\square) Southern mid slope.

818

819 Fig. 2. Map of absolute dynamic topography and surface derived geostrophic currents at
820 study area during late autumn in 2009 (a) and summer in 2010 (b) with hydrographic
821 stations and structures (A: Anticyclonic eddie; C: Cyclonic eddie)

822 Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (\blacklozenge) Southern shelf break; (\square) Southern mid slope

823 Fig 3. Seasonal $\theta - S$ diagram with gray boxes indicating the different water masses (a,
824 b), potential temperature (c, d), salinity (e, f) and fluorescence (g, h) vertical profiles at
825 four stations. For TS profiles below 50 m to bottom were plotted and the rest of
826 variables from surface down to 200 m.

827 Stations lines: black: Northern mid slope; black dotted: Northern shelf break; gray: Southern mid slope; gray dotted: Southern shelf
828 break

829 Water masses: Levantine Intermediate Water (LIW), Western Mediterranean Intermediate Water (WIW) and Western Mediterranean
830 Deep Water (WMDW)

831 Fig. 4. Multiple k-dominance curves with cumulative dominance percentage of species
832 described at four plankton stations during late autumn (black) and summer (grey).

833 Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (\blacklozenge) Southern shelf break; (\square) Southern mid slope.

834 Fig. 5. Seasonal cluster analysis (on the left) and Multidimensional scaling (MDS) of
835 BrayCurtis similarities (on the right) of hauls based on adults habitat densities and their
836 assemblages at 50 % similarity during late autumn (a and b) and 65 % during summer (c
837 and d). Clusters groups in bubbles, two during late autumn (AS shelf: late Autumn
838 Southern over shelf break; A: Autumn rest of the samples) and other two during summer
839 (S: Summer rest of the samples; SS slope: Summer Southern over mid slope). Samples
840 legends N: Northern stations and S: Southern stations.

841 Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (\blacklozenge) Southern shelf break; (\square) Southern mid slope.

842 Fig. 6. Scatterplots of observed (a, c, e, f) and predicted (b, d, g) larval densities (n/m^3)
843 with explanatory variables, of adult habitat epipelagic (Ah_7), mesopelagic (Ah_8),

844 coastal epibenthic (Ah_3) and coastal nektobenthic (Ah_4) of late development stage
845 group (stage 2), at four plankton stations during autumn and summer. Environmental
846 variables fluorescence (fluo), temperature (temp) and salinity (sal).

847 Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (◆) Southern shelf break; (□) Southern mid slope. nd= not
848 enough data

849 Fig. 7. Scatterplots of observed (a, c, e, g) and predicted (b, d, f, h) larval densities
850 (n/m^3) with explanatory variables, of functional groups epipelagic (Ah_7), mesopelagic
851 (Ah_8), coastal epibenthic (Ah_3) and coastal nektobenthic (Ah_4) of group 1 of early
852 stages (stage 1), at four plankton stations during autumn and summer. Environmental
853 variables fluorescence (fluo), temperature (temp) and salinity (sal).

854 Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (◆) Southern shelf break; (□) Southern mid slope

1 TABLES

Late autumn (2009)		Summer (2010)		2
Shelf break (m)	Mid slope (m)	Shelf break (m)	Mid slope (m)	3
0-30	0-60	0-25	0-25	4
30-60	60-200	25-50	25-50	5
60-90	200-350	50-75	50-75	6
90-120	350-600	75-100	75-125	7
120-200	600-850	100-125	125-200	
		125-150	200-400	
		150-200	400-500	

7

8 Table 1. Depth strata level with the thickness of each layer in meters during the late
9 autumn and summer surveys over the shelf break and the mid slope stations.

10

Taxa	Adults Habitat	Late autumn						Summer							
		N	Northern			Southern			N	Northern			Southern		
			F (%)	$\rho \pm SD$		F (%)	$\rho \pm SD$			F (%)	$\rho \pm SD$		F (%)	$\rho \pm SD$	
SHRIMPS (Dendrobranchiata)															
<i>*Allosergestes sargassi</i>	mesopelagic							7	50.00	0.02	± 0.02	50.00	0.01	± 0.02	
<i>*Aristeus antennatus</i>	oceanic epibenthic							3	25.00	0.01	± 0.02	25.00	0.01	± 0.01	
[^] Dendrobranchiata n. id.	-	1	20.00	0.02	± 0.05										
<i>Deosergestes corniculum</i>	epipelagic	2				15.38	0.02	± 0.05	70	100.00	0.14	± 0.11	75.00	0.12	± 0.22
<i>Deosergestes henseni</i>	mesopelagic	2	20.00	0.02	± 0.05	7.69	0.01	± 0.05	162	87.50	0.26	± 0.25	100.00	0.48	± 0.55
<i>Eusergestes arcticus</i>	mesopelagic	256	100.00	3.92	± 2.98	61.54	0.46	± 0.51	616	100.00	1.94	± 2.61	100.00	0.97	± 0.87
<i>Gennadas elegans</i>	mesopelagic	1445	100.00	14.53	± 8.73	100.00	6.05	± 3.81	132	75.00	0.10	± 0.11	100.00	0.57	± 0.50
<i>*Lucifer typus</i>	epipelagic								1	12.50	0.01	± 0.01			
<i>Parapenaeus longirostris</i>	oceanic epibenthic	1	0.00			7.69	0.01	± 0.05	1				12.50	0.01	± 0.02
<i>Parasergestes vigilax</i>	epipelagic	4	20.00	0.04	± 0.08	23.08	0.03	± 0.06	887	100.00	1.77	± 2.67	100.00	2.21	± 3.43
<i>Sergestes atlanticus</i>	epipelagic	12	20.00	0.28	± 0.64	23.08	0.04	± 0.09	23	62.50	0.05	± 0.06	62.50	0.04	± 0.04
<i>Sergestes spp.</i>	epipelagic	12	40.00	0.05	± 0.06	46.15	0.13	± 0.18	277	100.00	0.72	± 0.33	87.50	0.49	± 0.48
Sergestidae n.id.	-	116	100.00	1.83	± 0.68	53.85	0.29	± 0.39	97	87.50	0.23	± 0.37	100.00	0.26	± 0.17
<i>Sergia robusta</i>	mesopelagic	140	80.00	2.35	± 3.03	69.23	0.47	± 0.47	160	87.50	0.49	± 0.54	87.50	0.20	± 0.20
<i>*Sergia splendens</i>	mesopelagic								2	12.50	0.01	± 0.03			
<i>Sergia spp.</i>	mesopelagic	22	80.00	0.44	± 0.48	23.08	0.03	± 0.06	1	12.50	0.01	± 0.01			
<i>Solenocera membranacea</i>	coastal nektobenthic	28	20.00	0.05	± 0.11	69.23	0.32	± 0.37	126	100.00	0.52	± 0.66	50.00	0.24	± 0.28
CARIDEAN SHRIMPS (Caridea)															
<i>Acanthephyra spp.</i>	meso/bathypelagic	27	80.00	0.32	± 0.36	76.92	0.17	± 0.17	102	87.50	0.36	± 0.22	75.00	0.05	± 0.06
<i>*Aegaeon spp.</i>	cosmopolite epibenthic								22	62.50	0.12	± 0.15	25.00	0.02	± 0.04
<i>Alpheus glaber</i>	cosmopolite nektobenthic	32	40.00	0.05	± 0.08	53.85	0.44	± 0.63	144	87.50	0.54	± 0.46	75.00	0.22	± 0.24
<i>Alpheus spp.</i>	cosmopolite nektobenthic	10				30.77	0.13	± 0.35	185	100.00	0.61	± 0.96	50.00	0.05	± 0.11
<i>Athanas nitescens</i>	coastal epibenthic	7	20.00	0.01	± 0.03	30.77	0.11	± 0.17	24	75.00	0.09	± 0.15	25.00	0.04	± 0.07
[^] <i>Brachycarpus biunguiculatus</i>	coastal epibenthic	1				7.69	0.02	± 0.07							
Caridea n. id.	-	12				23.08	0.08	± 0.17	5	12.50	0.01	± 0.02	37.50	0.02	± 0.04
<i>*Caridion steveni</i>	coastal epibenthic								1				12.50	0.01	± 0.02
<i>*Chlorotocus crassicornis</i>	oceanic epibenthic								1	12.50	0.01	± 0.02			
<i>Eualus cranchii</i>	coastal epibenthic	3				23.08	0.05	± 0.10	45	75.00	0.17	± 0.32	37.50	0.11	± 0.16
<i>*Eualus occultus</i>	coastal epibenthic								7	25.00	0.04	± 0.10	12.50	0.01	± 0.02
<i>Eualus spp.</i>	coastal epibenthic	1				7.69	0.02	± 0.08	28	75.00	0.05	± 0.04	50.00	0.11	± 0.18
<i>Hippolytidae n.id.</i>	coastal epibenthic	8	20.00	0.02	± 0.05	46.15	0.08	± 0.11	24	75.00	0.10	± 0.13	62.50	0.05	± 0.06
<i>*Lysmata seticaudata</i>	intertidal nektobenthic								1	12.50	0.01	± 0.01			
<i>*Lysmata spp.</i>	intertidal nektobenthic								20	75.00	0.08	± 0.07	12.50	0.01	± 0.01
<i>*Palaemon elegans</i>	intertidal nektobenthic								1	12.50	0.01	± 0.02			
<i>*Palaemon macrodactylus</i>	intertidal nektobenthic								7	12.50	0.02	± 0.06			
<i>*Palaemon spp.</i>	intertidal nektobenthic								1	12.50	0.01	± 0.01			
<i>*Palaemonidae n.id.</i>	intertidal nektobenthic								1	12.50	0.01	± 0.02			
Pandalidae n.id.	-	9				38.46	0.09	± 0.19	44	87.50	0.12	± 0.12	75.00	0.14	± 0.18
<i>Pandalina brevisrostris</i>	coastal nektobenthic	8				46.15	0.09	± 0.12	78	62.50	0.35	± 0.47	87.50	0.15	± 0.13
<i>*Pasiphaea sivado</i>	cosmopolite epibenthic								3	25.00	0.01	± 0.02	12.50	0.01	± 0.02
[^] <i>Philocheras echinulatus</i>	oceanic epibenthic	6	20.00	0.04	± 0.08	30.77	0.09	± 0.17							
<i>*Philocheras fasciatus</i>	intertidal epibenthic								2	25.00	0.01	± 0.02			
<i>Philocheras sculptus</i>	coastal epibenthic	5				38.46	0.09	± 0.12	3	12.50	0.01	± 0.04	12.50	0.01	± 0.02
[^] <i>Philocheras spp.</i>	oceanic epibenthic	2				7.69	0.04	± 0.16							
<i>Philocheras trispinosus</i>	intertidal epibenthic	2				15.38	0.03	± 0.08	1	12.50	0.01	± 0.02			
<i>*Pleocyemata n. id.</i>	-								1				12.50	0.01	± 0.02
<i>Plesionika spp.</i>	coastal nektobenthic	103	60.00	0.11	± 0.12	100.00	1.54	± 1.85	370	100.00	1.32	± 1.33	100.00	0.85	± 1.03
<i>*Pontonia spp.</i>	coastal epibenthic								3	12.50	0.01	± 0.01	12.50	0.01	± 0.02
<i>*Pontoninae n.id.</i>	coastal epibenthic								14	50.00	0.04	± 0.06	50.00	0.02	± 0.03
<i>Processa canaliculata</i>	oceanic epibenthic	6	40.00	0.04	± 0.05	23.08	0.06	± 0.13	42	62.50	0.29	± 0.40	12.50	0.01	± 0.02
<i>Processa edulis edulis</i>	intertidal epibenthic	13				53.85	0.20	± 0.24	51	100.00	0.25	± 0.23	50.00	0.03	± 0.05
<i>*Processa macrodactyla</i>	coastal epibenthic								5	25.00	0.04	± 0.08			
<i>*Processa modica caroli</i>	coastal epibenthic								8	25.00	0.04	± 0.08	12.50	0.01	± 0.01
<i>Processa modica modica</i>	coastal epibenthic	1	20.00	0.02	± 0.05				1	12.50	0.01	± 0.01			
<i>Processa noveli</i>	coastal epibenthic	3				23.08	0.05	± 0.10	27	87.50	0.12	± 0.13	50.00	0.03	± 0.03
<i>Processa spp.</i>	oceanic epibenthic	35	20.00	0.07	± 0.16	61.54	0.50	± 0.57	78	87.50	0.40	± 0.53	87.50	0.11	± 0.11
<i>Processa? elegantula</i>	coastal epibenthic	3				15.38	0.06	± 0.16	7	37.50	0.04	± 0.07			
<i>*Stenopus spinosus</i>	cosmopolite epibenthic								4	37.50	0.02	± 0.02			
HERMIT CRABS (Paguridae and Diogenidae)															
<i>Anapagurus spp.</i>	cosmopolite epibenthic	25	20.00	0.01	± 0.03	38.46	0.42	± 0.71	20	50.00	0.02	± 0.02	50.00	0.10	± 0.12
<i>*Calcinus tubularis</i>	intertidal epibenthic								144	87.50	0.44	± 0.89	12.50	0.01	± 0.02
<i>*Clibanarius erythropus</i>	intertidal epibenthic								2	12.50	0.01	± 0.02			
<i>*Dardanus arrosor</i>	coastal epibenthic								7	37.50	0.02	± 0.03	12.50	0.01	± 0.02
<i>*Diogenes pugilator</i>	intertidal epibenthic								6	37.50	0.03	± 0.05			
<i>*Nematopagurus longicornis</i>	oceanic epibenthic								8	12.50	0.01	± 0.02	37.50	0.05	± 0.07
<i>*Pagurus cuanensis</i>	coastal epibenthic								1	12.50	0.01	± 0.02			
<i>Pagurus spp.</i>	cosmopolite epibenthic	16	20.00	0.04	± 0.08	53.85	0.24	± 0.27	11	50.00	0.03	± 0.04	25.00	0.01	± 0.02
GHOST SHRIMPS (Axidea and Gebiidea)															
<i>*Callianassa subterranea</i>	endobenthic								1	12.50	0.01	± 0.01			
<i>Callianassidae n.id.</i>	endobenthic	1				7.69	0.01	± 0.03	6	50.00	0.04	± 0.05			
<i>*Necallianassa truncata</i>	endobenthic								7				37.50	0.05	± 0.08
<i>*Upogebia deltaura</i>	endobenthic								2	12.50	0.01	± 0.04			
<i>*Upogebia pusilla</i>	endobenthic								1	12.50	0.00	± 0.01			
<i>*Upogebia spp.</i>	endobenthic								1	12.50	0.01	± 0.01			

14 Table 2. The seasonal number of decapods larvae (N), their seasonal and area (northern
15 and southern stations) frequency of occurrence (F) and the average density (ρ) over the
16 water column (number of larvae/100 m³ \pm SD) of the different taxa identified, during
17 late autumn (2009) and summer (2010). A classification of the different taxa according
18 to their adult habitats is provided.

19 ([^])*Exclusively autumn appearance and* (^{*}) *exclusively summer appearance*

20

21

Adult habitat	Cluster A	Cluster ASshelf	Cluster S	Cluster SSslope
Mesopelagic	74.78%	22.55%	18.83%	48.78%
Epipelagic			16.10%	16.62%
Coastal necktobenthic		17.73%	16.46%	
Coastal epibenthic		18.86%		

22

23 Table 3. Similarities among cluster assemblages regarding taxa composition grouped by
24 their adult habitat. Only the groups that represent more than 50% of the cumulative
25 contribution to explain the variability of each seasonal Cluster group (SIMPER) are
26 included.

27 (*A:late Autumn; ASshelf:late Autumn Souternh shelf break; S: Summer; SSslope: Summer Southern mid slope*)

28

Season	Adult habitat	Factor		Variables		
		area	station	fluo	temp	sal
Late autumn	Mesopelagic & epipelagic	***	ns	***	***	ns
	Coastal epibenthic & nektobenthic	***	***	***	ns	ns
Summer	Mesopelagic & epipelagic	ns	ns	***	ns	***
	Coastal epibenthic & nektobenthic	***	***	***	***	***

30

31 Table 4. Effect of fluorescence (fluo), temperature (temp) and salinity (sal) on the
 32 density of late zoeas/protozoas (stage 2) over the water column as estimated from a
 33 generalized linear model. Area and station (shelf break or mid slope) are included in the
 34 model as factors. Results are shown for late autumn and summer for the larvae
 35 classified by their adult habitat. The asteriscus *** indicate significant effects ($p < 0.001$)

36 *No significance "ns" = $p > 0.001$*

37

38

39

Season	Functional group	Factor		Variables		
		area	station	fluo	temp	sal
Autumn	Mesopelagic & epipelagic	***	***	ns	***	***
	Coastal epibenthic & nektobenthic	***	ns	***	ns	ns
Summer	Mesopelagic & epipelagic	***	***	***	***	ns
	Coastal epibenthic & nektobenthic	***	***	***	ns	***

40

41 Table 5: Effect of fluorescence (fluo), temperature (temp) and salinity (sal) on the
42 density of early zoeas/protozoas (stage 1) estimated from a generalized linear model.

43 Area and station (shelf break or mid slope) are included in the model as factors. Results
44 are shown for late autumn and summer for the larvae classified by their adult habitat.

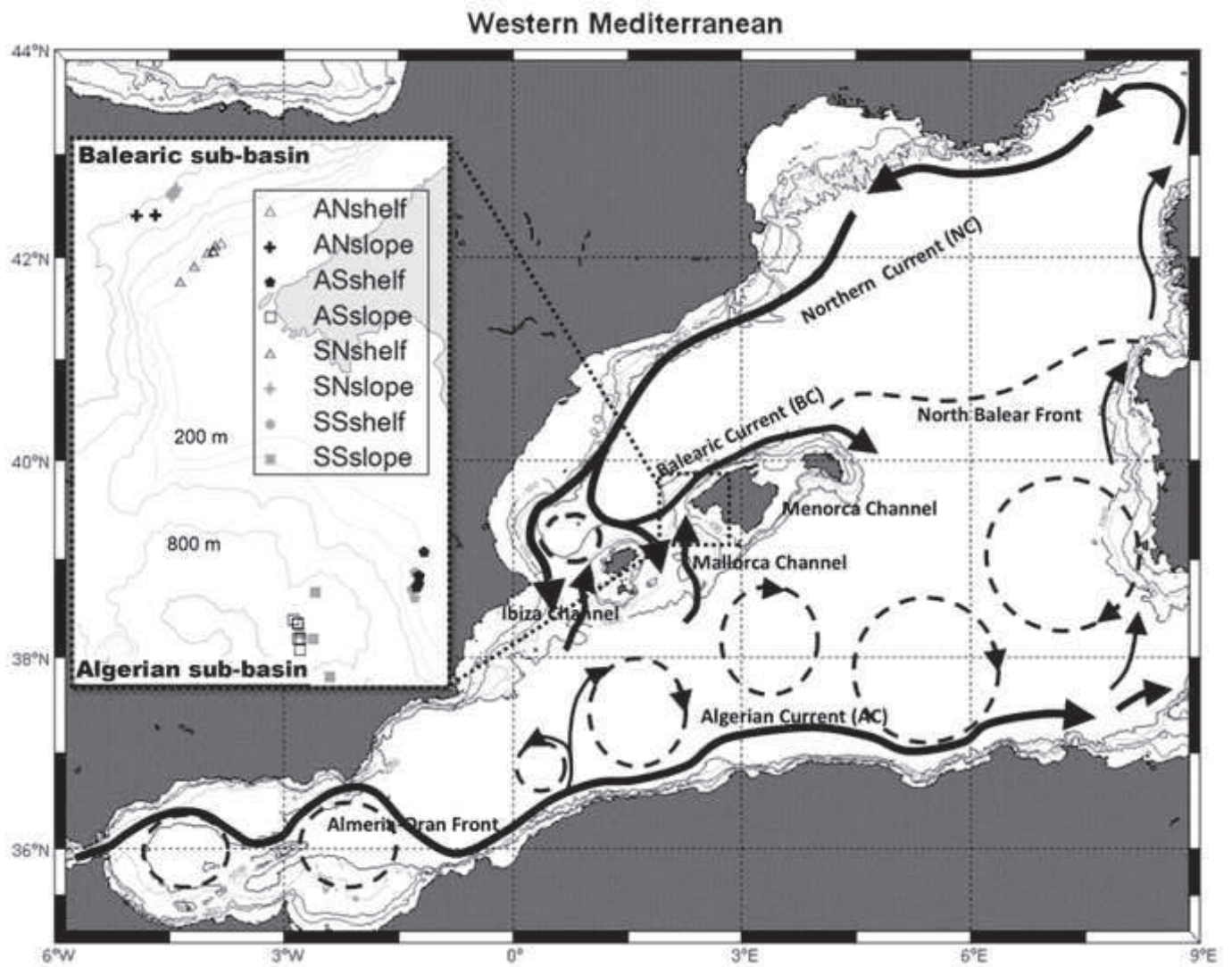
45 The asteriscus *** indicate significant effects ($p < 0.001$)

46

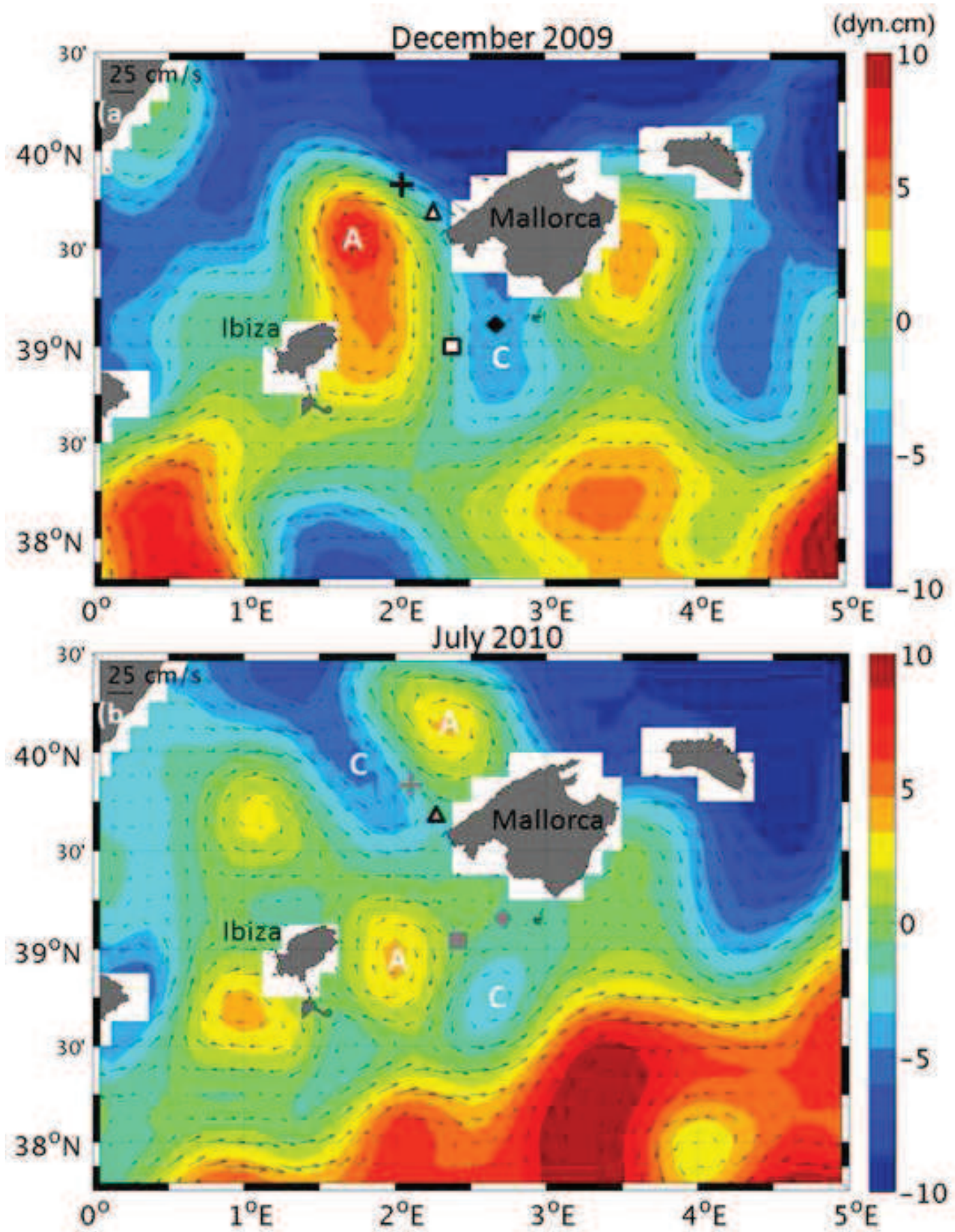
47 *No significance "ns" = $p > 0.001$*

48

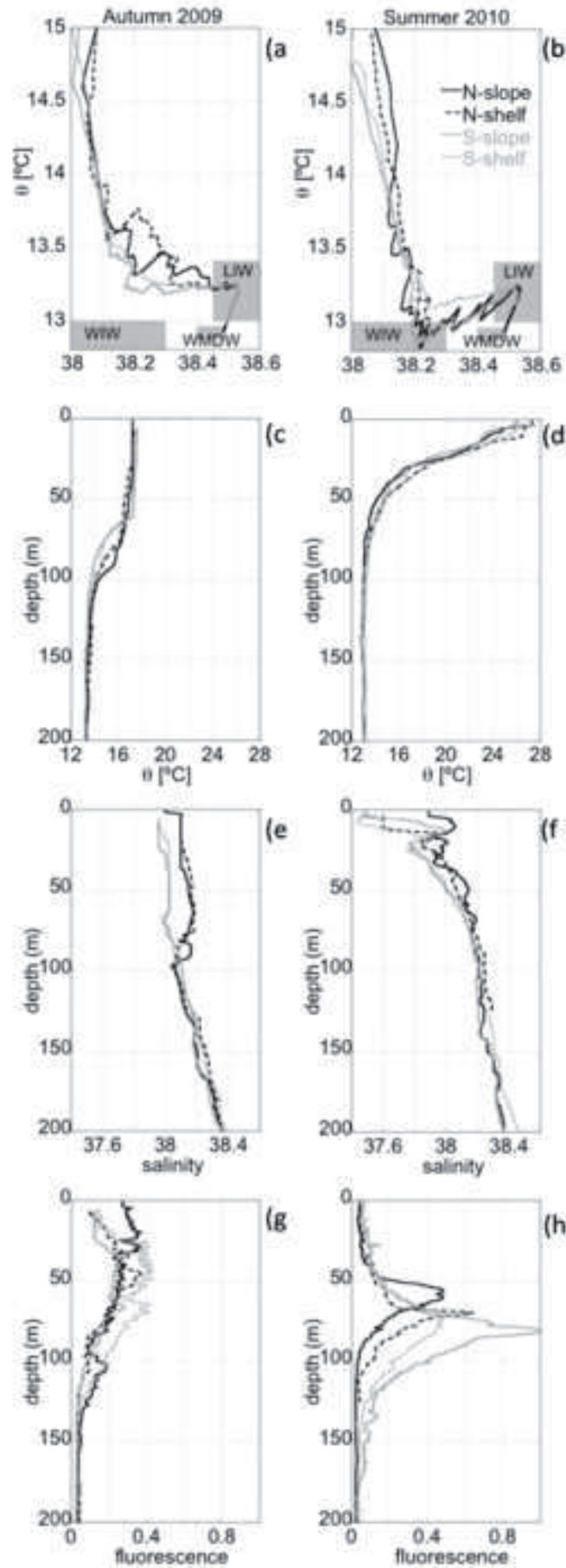
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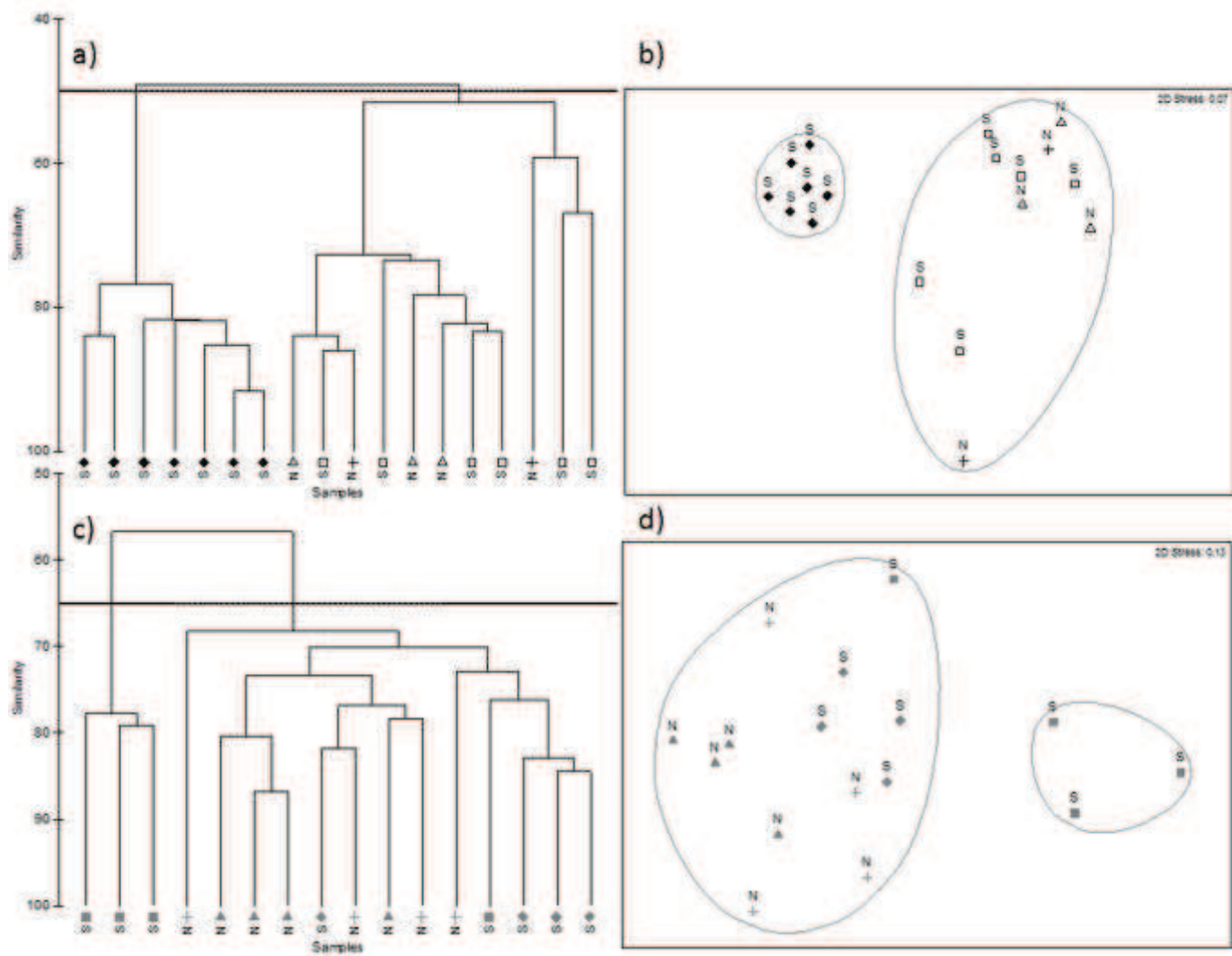
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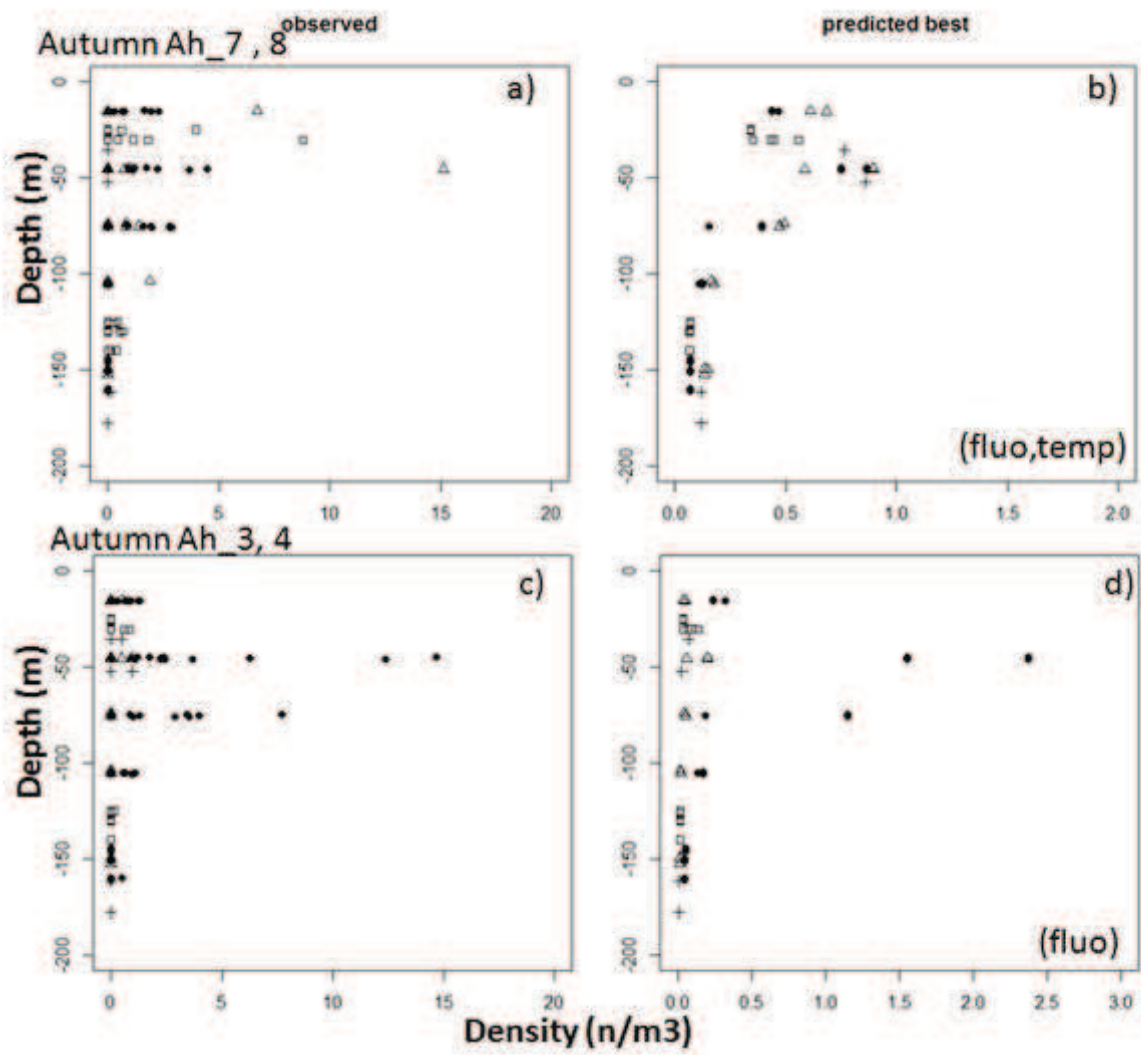
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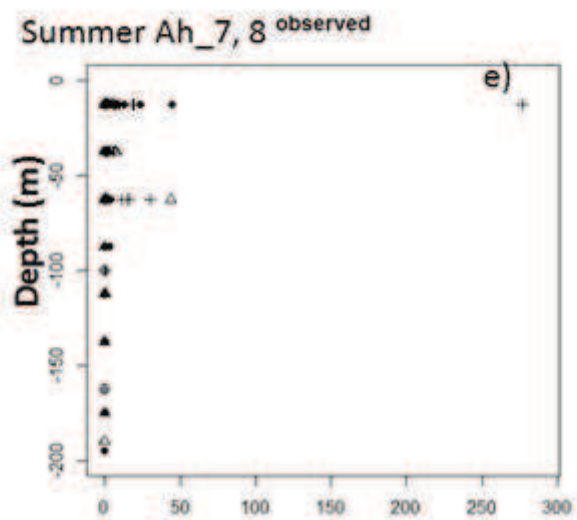
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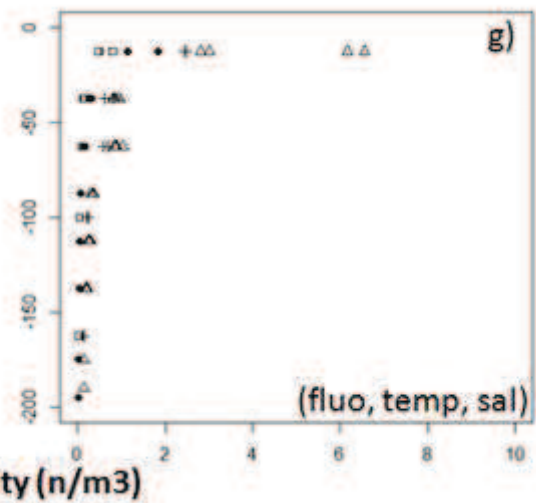
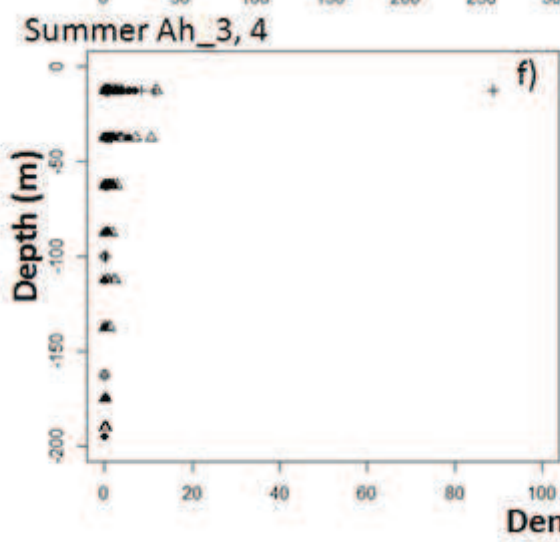
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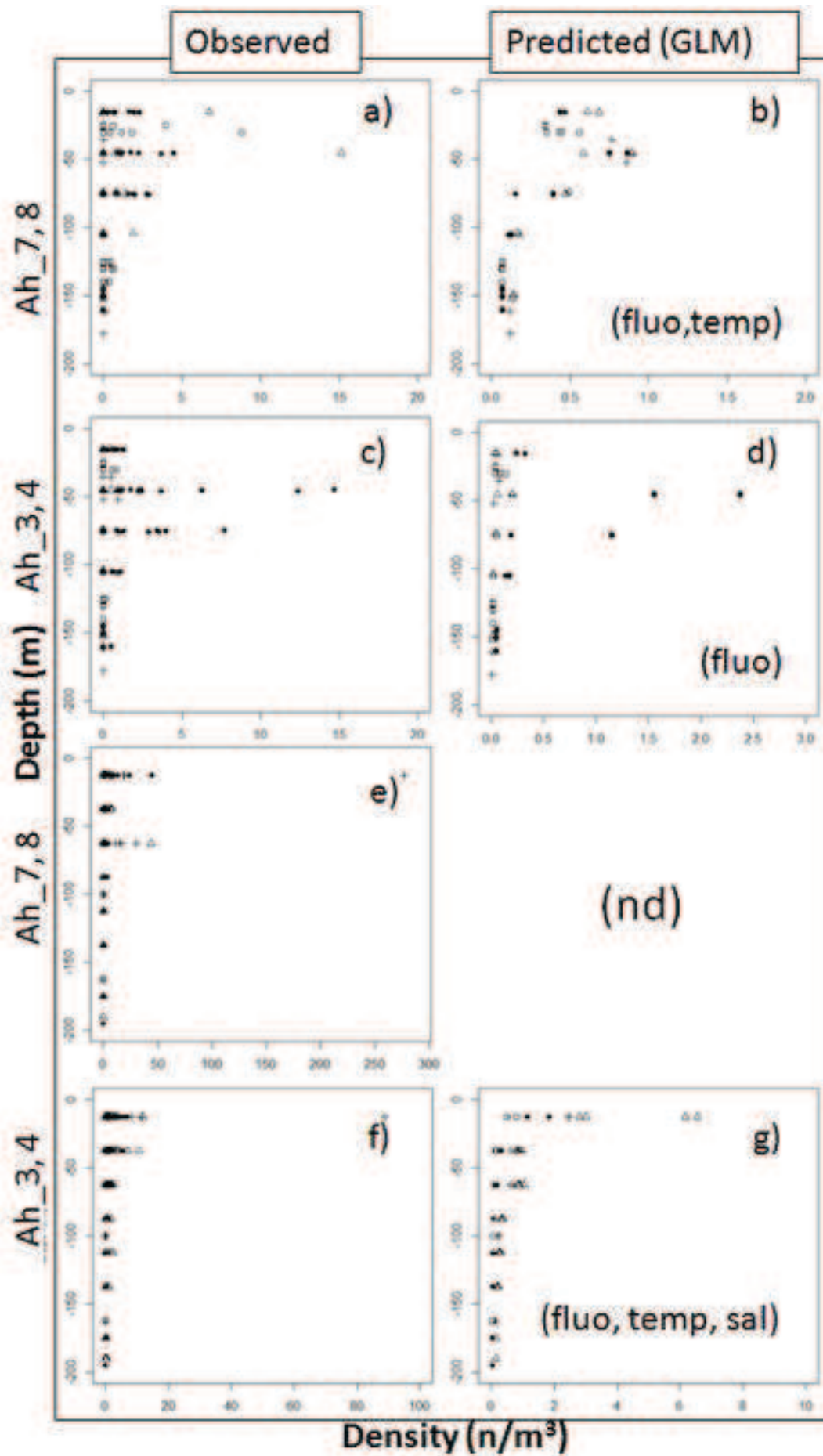
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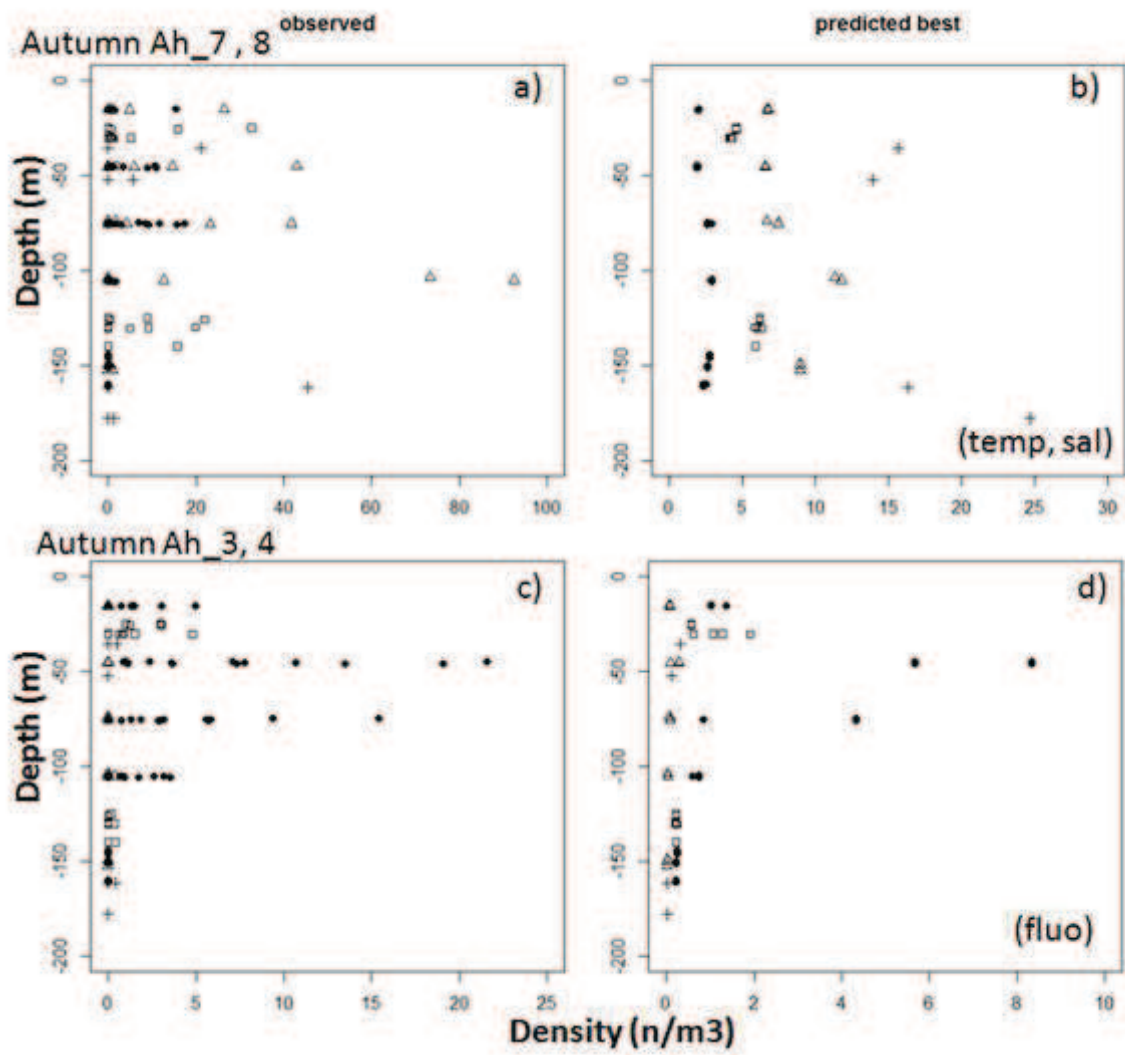
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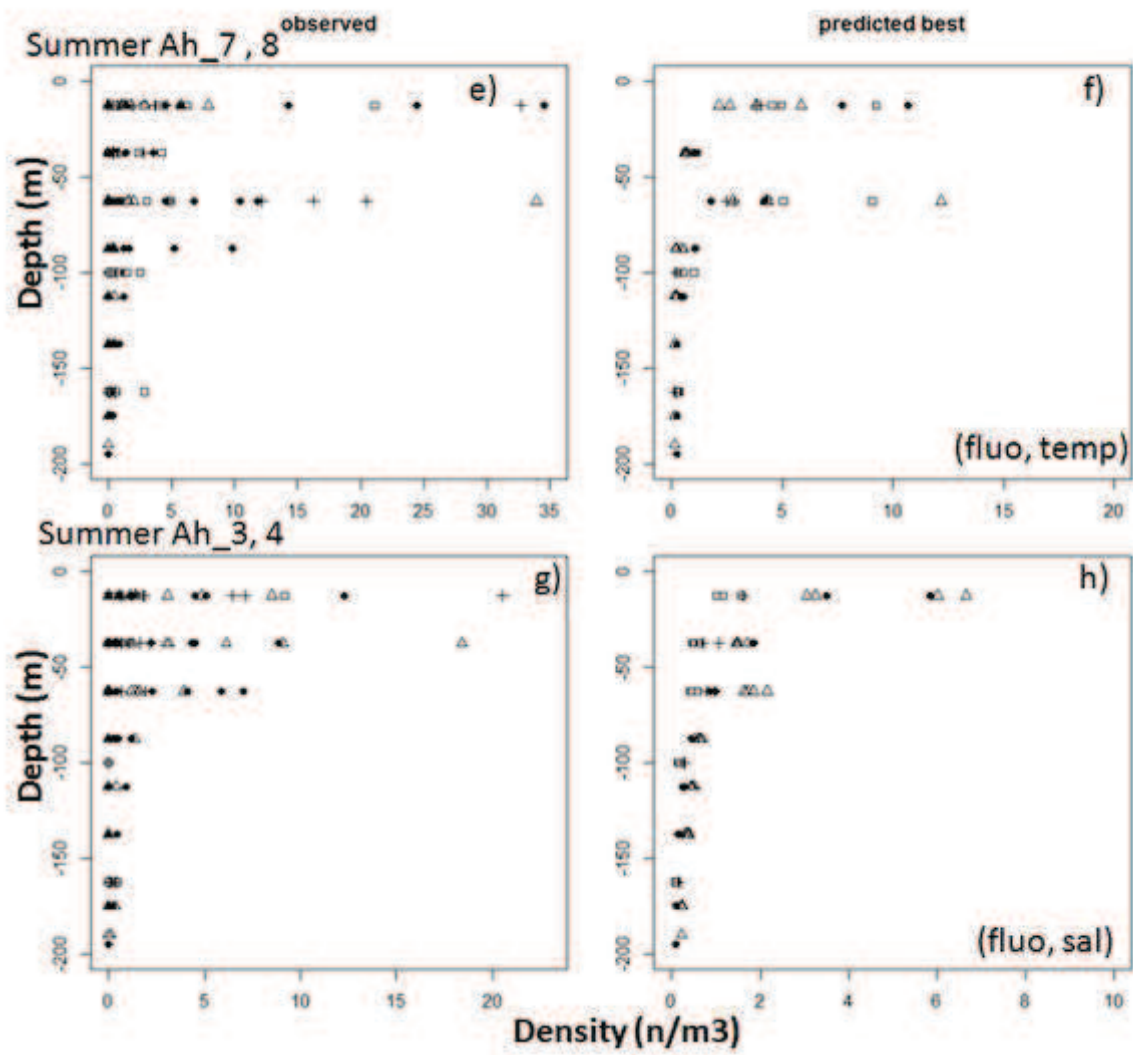
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