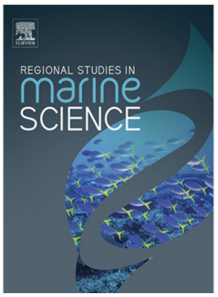
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The three-dimensional structure of *Cymodocea nodosa* meadows shapes juvenile fish assemblages at Fornells Bay (Minorca Island)

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Abstract

The role of the meadows of the Mediterranean seagrass *Cymodocea nodosa* as nursery habitats for fish remains largely unknown and there are only few studies investigating the influence of their structure on juvenile assemblages. Here, we monitored juvenile fish assemblages among shallow *Cymodocea nodosa* meadows (0 – 1 meter) in Minorca Island (north-western Mediterranean Sea) in both July and September 2013. To assess the influence of structural components on juvenile fish assemblages, we selected two different meadow structure types: heterogeneous with intermingled boulders and homogeneous meadows, i.e. without boulders. Juvenile fish assemblages varied significantly among these two meadow structures. Heterogeneous meadows had higher total juvenile density and species richness, where some species were only found in these portions, such as *Coris julis* and *Serranus* spp. Other species, such as *Symphodus* spp. and *Sarpa salpa*, were also more abundant within heterogeneous meadows. However, densities of some species were not increased in heterogeneous meadows demonstrating a specific response to habitat structure. For instance, *Diplodus annularis* displayed similar abundances in both heterogeneous and homogeneous portions of the meadow. Our study reveals that the intrinsic structural variability of seagrass meadows plays a key role for the assemblage of several fish species that are characterized by different early life history strategies.

Key words: fish nursery; habitat structure; seagrass meadows; *Cymodocea nodosa*; Balearic Islands; Mediterranean Sea

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1. Introduction

Among coastal habitats used by juvenile fish, those which provide a greater than average contribution to adult populations are called "nursery habitats" (Beck et al., 2001). Nurseries are key habitats among the seascape, essential for the renewal of populations. Seagrass meadows are considered as nursery habitats for many juvenile fishes and invertebrates worldwide (Heck et al., 2003; Nagelkerken et al., 2001). In the Mediterranean Sea, such ecological function has been notably highlighted for meadows of *Posidonia oceanica* (L.), Delile 1813 (Garcia-Rubies and Macpherson, 1995; Guidetti, 2000; Harmelin-Vivien et al., 1995; Kalogirou et al., 2010). Another study has also suggested that shallow mixed meadows composed by the seagrasses *Cymodocea nodosa* (Ucria), Ascherson 1870, and *Zostera noltii*, Hornemann 1832, have a functional importance for juvenile fishes (Guidetti and Bussotti, 2000). Native macroalgae meadows (e.g. *Caulerpa prolifera* (Chlorophyta)) and Fucoid forests (e.g. *Cystoseira* spp.) can also mediate juvenile fish assemblages (Cheminée et al., 2013; Koulouri et al., 2016). This nursery role has been explained due to the influence of their habitat structure (Verwey et al., 2006). Evaluating how the structure of these nursery habitats determines juvenile fish assemblages has important implications for conservation biology. In particular, in the case of *Cymodocea nodosa* meadows which role in juvenile assemblages has been poorly investigated.

The habitat structure is defined as the amount, composition and three-dimensional arrangement of structural components (both abiotic and biotic) at a given location under a determinate spatio-temporal scale (Beck, 2000; Bell et al., 1991; Byrne, 2007). There are two principal aspects that determine the habitat structure, its complexity (absolute

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abundance of individual structural components) and heterogeneity (relative abundance of different structural components) (Beck, 2000). Accordingly, habitats with higher degrees of structuration are considered as the ones that are more "complex" and/or more "heterogeneous". As a consequence, seagrass meadows produce a higher number of juveniles per unit of surface, i.e. display a higher nursery value, *sensu* Beck et al. (2001), compare to less structured habitats, such as un-vegetated bottoms (Beck et al., 2001; Heck et al., 2003; Kalogirou et al., 2012) and compared to less structurally complex macrophyte meadows (Verdiell-Cubedo et al., 2007). Previous studies have shown the evidence of a positive correlation between the habitat three-dimensional structure and juvenile fish density, which is most likely related to the higher availability of food and/or shelters in highly structured and complex habitats (Thiriet et al., 2014; Verwey et al., 2006).

The three-dimensional structure can vary spatially among distinct seagrass habitats, as well as within a single seagrass meadow (Bell and Westoby, 1986; Guidetti and Bussotti, 2000; Gullström et al., 2008). Many studies have related the differences in meadow three-dimensional structure to both the vertical stratification (presence and height of the canopy) and horizontal distribution of macrophytes (shoot density, percent coverage and patchiness) (August, 1983; García-Charton et al., 2004; Guidetti and Bussotti, 2002; Wilson et al., 2007). In seagrass meadows, the density of juvenile fishes has been reported to be correlated with the height and/or shoot density of the seagrass and with its patchiness (Bell and Westoby, 1986; Guidetti and Bussotti, 2000; Gullström et al., 2008). On the other hand, several studies have shown that the actual relationship between juvenile density and meadow structure is species-specific (Bussotti and Guidetti, 2010). Some fish species display life history strategies (e.g. anti-predator or foraging tactics) that contribute to their ecological success in highly structured

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96 meadows, whereas others species colonize habitats that are less structured. Some
97 species can also colonize opened areas that are adjacent to the meadow. In addition,
98 there are fishes whose densities are not influenced by seagrass meadow structure; these
99 species are habitat generalists (Elliott and Dewailly, 1995; Horinouchi, 2007; Kalogirou
100 et al., 2010; Orth et al., 1984). Furthermore, a recent study has revealed that abiotic
101 structural components found in some meadows, such as intermingled boulders, play a
102 determinant role for fish recruitment (Cheminée et al., 2016). For that reason, it is
103 crucial to determine to what degree the density of juvenile fishes depends on the
104 presence/absence of such structural components.

105 In the Mediterranean Sea, *Cymodocea nodosa* meadows are common in subtidal (0 to
106 20 meters depth) and sheltered to semi-exposed marine, polyhaline or hypersaline water
107 masses (Borum et al., 2004; Guiry and Guiry, 2015; Mascaro et al., 2009). These
108 meadows are known to display a high nursery value (Espino et al., 2011; Guidetti and
109 Bussotti, 2002, 2000; Verdiell-Cubedo et al., 2007), although information regarding the
110 influence of its three dimensional structure on juvenile assemblages remains scarce.

111 By quantifying juvenile fish assemblages in shallow *C. nodosa* meadows (0.5 – 1 meter
112 depth) at Fornells Bay, Minorca Island (Mediterranean Sea), in both summer and fall
113 seasons, we investigated the effect of a specific habitat trait, the meadow three
114 dimensional structure, on juvenile fish assemblages. To do so, we specifically compare
115 the relative densities of juveniles that settle on heterogeneous (i.e. scattered with
116 intermingled boulders) *versus* homogeneous portions of the meadow (i.e. without
117 boulders).
118

119 **2. Material and methods**

120 ***2.1 Studied area***

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121 The study was conducted on the northern coast of Minorca Island (Balearic
122 Archipelago) at Fornells Bay (Fig. 1), which is located in the marine protected area
123 "Reserva del Nord de Menorca"(Coll et al., 2012). A previous study has suggested that
124 Fornells Bay is an important area for the settlement and recruitment of many fishes
125 (Manent and Abella, 2005). The bay is semi-enclosed and 4.4 km long by 1.5 km wide
126 with an average depth of 5.5 m. Fornells Bay is connected to the Mediterranean Sea by
127 a 300 m wide strait opened towards the north. Phyto-benthic communities are
128 characterized by dense meadows dominated by the seagrasses *Posidonia oceanica* and
129 *Cymodocea nodosa*. Some green macroalgae (Chlorobionta) are scattered within the
130 meadows (Delgado et al., 1997). The extensive areas of *Cymodocea nodosa* meadows
131 thrive from 0 to 10 m depth. Boulders (sizing from 15 cm x 15 cm up to 20 cm x 20 cm)
132 are scattered in some portions of the *C. nodosa* meadows and are mainly covered
133 (approximately 60%) by perennial Fucales, mostly *Cystoseira* spp., or alternatively by
134 shorter (< 3 cm tall), shrubby and seasonal macroalgae that belong to the orders
135 Dictyotales and Sphacelariales (see Supplementary Table ST1a).

136 ***2.2 Sampling design and data collection***

137 Three sites (S1, the outermost site within the bay, and S2 and S3, the innermost sites)
138 were selected after a broad exploration of Fornells Bay (Fig. 1). In order to avoid
139 confounding effects between our study variables and other environmental variables, the
140 selected sites were similar in terms of depth (0.5 – 1 m) and slope (< 15º). For each site,
141 we selected two types of meadow structure: i) heterogeneous meadow portions, where
142 sparse intermingled boulders cover 20 to 40% of the total meadow area, and ii)
143 homogeneous meadow portions without boulders. For each meadow structure type,
144 within each of the three sites, random replicates were monitored by performing both
145 habitat description and juvenile fish visual censuses. Surveys were conducted in 2013 at

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two sampling months: July (between the 13th and 29th) and September (between the 9th and 23th).

For each replicate, meadow structure was described by recording habitat components (i.e. boulders, seagrass and algae canopy) and characteristics (cover percentage and maximum height to the nearest cm) (Cheminée, 2012; Cheminée et al., 2013; Garcia-Rubies and Macpherson, 1995). The two sampled months coincide with high juvenile occurrences of many Mediterranean littoral fish species within the meadows (Bussotti and Guidetti, 2010; Garcia-Rubies and Macpherson, 1995; Raventos and Macpherson, 2001). Juvenile fish assemblages were surveyed by means of underwater visual census (UVC) techniques (Bussotti and Guidetti, 2010; Cuadros et al., 2017; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995, 1985; Thiriet et al., 2016). For each taxa, all individuals smaller than one third of adult maximum total length were considered as juveniles (Cheminée, 2012; Louisy, 2015). Abundance and total length (TL) of juvenile fishes were recorded during daylight (between 9 am and 4 pm). Moderate or rough sea conditions with poor visibility were avoided to perform our surveys. Censuses were carried out by three previously trained divers, using snorkels, and the TL of juveniles was estimated with the help of fish silhouettes of different sizes (5 mm TL size-classes) on a plastic slate (Cuadros et al., 2017; Macpherson, 1998; Pastor et al., 2013). Belt-transects of 6 m x 3 m were used for juvenile counts and twelve random replicates were performed within both heterogeneous and homogenous portions of the meadow.

Furthermore, we pooled the juveniles into broad taxonomical groups as some juvenile fish species are difficult to identify on the field (Cheminée et al., 2013). Crypto-benthic fish species (including different taxa belonging to Blenniidae, Gobiidae and Tripterygiidae) were pooled as a single group due to their apparent low densities. Other

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groups were as follows: *Symphodus* spp. (including *S. roissali*, *S. tinca* and *S. ocellatus*); *Serranus* spp. (including S. *cabrilla* and *S. scriba*); *Mullus* spp. *(M. barbatus* and *M. surmuletus*); *Pagellus* spp.; and Mugilidae. For the purpose of this study, we are now referring to these groups as "taxa". Taxa accounting for equal or more than 10 % of the juvenile total abundance were considered as "dominant". Those accounting for 5 to 10% were considered as "common". All other taxa were considered "occasional" (see results, Table 1).

2.3 Statistical analyses

The effect of meadow structure types, sampling months and sites on habitat descriptors (combination of cover and height of meadow components) was assessed using a PERMutational multivariate ANalysis Of VAriance (PERMANOVA), since assumptions of parametric testing could not be met. PERMANOVA model included three factors: i) "meadow structure" was fixed and included two levels; homogeneous and heterogeneous, ii) "sampling month" was also fixed and included two levels; July and September, and iii) "site", was random and included three levels; S1, S2 and S3. PERMANOVA results were visualized using a non-metric Multi-Dimensional Scaling (nMDS) biplot of samples (Clarke and Gorley, 2006). Arrows that represent Spearman's rank correlations between samples and meadow characteristics were superimposed to nMDS biplots (Clarke and Warwick, 2001). For this analysis, multivariate descriptors of meadow structure were previously standardized and the Euclidean distance was used as measure of dissimilarity due to the different nature and variation range of the two descriptors used herein (cover and height) (Anderson and Gorley, 2008).

Then, we assessed the effect of meadow structure types, sampling months and sites on juvenile assemblage descriptors using PERMANOVAs with the aforementioned model.

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Two analyses were performed: i) univariate assemblage structure: total density and richness of juvenile fishes, and ii) multivariate assemblage structure: the comparative densities of each taxa. In order to represent dissimilarities between juvenile assemblages, we performed a Principal Coordinate Analysis (PCoA) ordinations plot of centroids of juvenile assemblage samples of the dummy factor combining meadow structure, sampling month and site (Clarke and Gorley, 2006). Arrows were once more superimposed to PCoA biplots to represent the Spearman's rank correlations between biplot axes and taxa-specific densities (Clarke and Warwick, 2001). The Euclidean distance was used as measure of dissimilarity for univariate response variables (total density and richness), while we used the modified-Gower (base 2) as measure of dissimilarity for multivariate juvenile assemblage structure. The PCoA with modified-Gower dissimilarity was well suited to analyze our dataset (see results) since this measure has the advantages to reduce heterogeneity of variance and down-weight the most abundant species, and this without altering the data with any prior transformation (Anderson and Gorley, 2008).

Finally, we assessed the effect of meadow structure types, sampling months and sites on taxa specific univariate descriptors (juvenile fish density) using univariate PERMANOVAs with Euclidian distances and the previously described model.

Sums of squares (SS) for all PERMANOVA designs were performed as a fully partial analysis (type III). P-values were obtained by 999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (< 200). Terms were pooled as suggested by Anderson and Gorley (2008). Due to the intrinsic variability of ecological data, tests were considered significant for P-values < 0.1. Multivariate exploratory analyses and both multivariate and univariate inferential tests were performed using the PRIMER 6 software and

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PERMANOVA + B20 package (Anderson and Gorley, 2008; Clarke and Gorley, 2006). Dataset manipulations and others graphical visualizations were performed in R Environment (R Development Core Team, 2013) using the library ggplot2 (Wickham, 2009).

3. Results

3.1 Meadow descriptors

The relative cover and height of meadow components varied significantly according to the interaction between meadow structure types, sampling months and sites (PERMANOVA, P = 0.01, Supplementary Table ST1b). Accordingly with our sampling design, heterogeneous meadow samples were characterized with the presence of boulders (27±2.23 to 37.7±3.12 % cover, mean ± standard error (SE)), absent in the homogeneous ones. Such boulders were mostly covered by *Cystoseira* and shrubby algae (~60%) (Supplementary Figure SF1). Furthermore, meadow descriptors varied among the two sampling months. Samples collected in July, mostly those found in heterogeneous meadows, were characterized by a high *C. nodosa* cover (~1.11 to 2.40 times higher coverage than in September, Supplementary Figure SF1 and Table ST1a). The lowest *C. nodosa* cover was recorded in the innermost sites of the bay (sites S2 and S3) (~ 1.6 times lower coverage than in S1), while the cover of the green macroalgae *Caulerpa prolifera* was the highest at these sites (~30±1.75 max cover *versus* 2.17 ±0.66 max cover in S1, Supplementary Figure SF1).

3.2 Juvenile fish assemblages and taxa-specific trends

A total of 2592 m² of *Cymodocea* meadows was surveyed in Fornells Bay, where 411 juveniles belonging to 17 taxa were recorded in July against 498 of 11 different taxa in

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September (18 different taxa in total and 10 shared among seasons) (Table 1). Overall, juvenile fish assemblages in these meadows were dominated by three taxa, *Symphodus* spp., *Sarpa salpa* and *Diplodus annularis*, and all together corresponded to 64% of the total juvenile density (Table 1). Although less abundant, three other taxa were commonly observed in the meadow: *Diplodus sargus*, *D. vulgaris* and *Oblada melanura* (Table 1). The total density of juveniles and species richness significantly differed between meadow structure types for both sampling months (PERMANOVAs, P-values < 0.1, Table 2). Heterogeneous portions of the meadow had systematically higher mean total densities (S1: 0.81±0.12, S2:0.31±0.04, S3:0.37±0.06, mean ± standard error (SE)) and richness (S1: 3.75±0.55, S2: 1.50±0.30, S3: 2.08±0.36) than the homogeneous ones (density- S1: 0.34±0.07, S2: 0.09±0.03, S3: 0.19±0.05; richness-S1: 2.42±0.53, S2: 0.33±0.14, S3: 1.17±0.39) for all sites surveyed (Fig. 2, Table 1). Furthermore, the outermost site of the bay (S1) had a significantly higher mean total density (0.57±0.08) and juvenile species richness (3.63±0.33) than the two innermost sites (density-S2: 0.20±0.03, S3: 0.28±0.04; richness-S2: 1.21±0.14, S3: 1.50±0.17) (PERMANOVAs, P-values < 0.1, Table2, Fig. 2). In the contrary, the sampling month seemed to have no effect on patterns of total density and species richness, although the interaction term 'meadow structure x sampling month x site' was significant for the total density (PERMANOVAs Table 2, Fig. 2).

Juvenile assemblage structure significantly differed between meadow structure types and sampling months (see PERMANOVAs, P-values < 0.1, Table 2, Fig. 2 and Fig. 3). These results first reflect the different mean taxa composition among meadow structure types with a significantly higher mean taxa number (i.e. richness described above) in heterogeneous portions of the meadow. *Coris julis* and *Serranus* spp. were observed only in heterogeneous meadows, while juveniles of *Sphyraena viridensis* and few

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269 individuals of *Lithognathus mormyrus* and *Pagellus* spp. (two and one, respectively)
270 were observed only in homogeneous meadows (Fig.3, Table 1). However, this
271 assemblage difference is most likely due to the 10 species that are found in both
272 meadow structure types (mostly dominant and common species), while characterized by
273 a higher density in heterogeneous portions (Fig. 3, Table 1).

274 Secondly, our results reveal distinct patterns of juvenile fish assemblages between the
275 two sampling months for some species. Marked dissimilarities were noticed among
276 dominant taxa. Although *D. annularis* displayed similar densities in heterogeneous and
277 homogeneous portions of the meadow (PERMANOVA, $P > 0.1$), their juveniles were
278 more abundant for the three sites in September (mean densities, S1: 0.1±0.02, S2:
279 0.05±0.02, S3: 0.16±0.04) compare to July (mean densities, S1: 0.06±0.02, S2:
280 0.01±0.01, S3: 0.02±0.01) (PERMANOVA, P-value = 0.032, Table 2, Fig. 2, Fig. 3).
281 *Symphodus* spp. were also more abundant in September (mean total density, September:
282 0.13±0.03; July: 0.03±0.01), but they were more abundant in heterogeneous portions
283 than in homogeneous ones for 4 of the 6 combinations of season x site (PERMANOVA,
284 $P = 0.004$, Table 2, Fig. 2, Fig. 3). Although low frequencies of *S. salpa* did not allow
285 accurate testing, their juveniles seemed to be more abundant in July *versus* September
286 (mean total density, July: 0.15±0.03, September: 0.01±0.00), as well as in
287 heterogeneous portions of the meadow *versus* homogeneous ones (mean total density,
288 heterogeneous: 0.10±0.02, homogeneous: 0.05±0.02). See Fig. 2, Fig. 3, Table 1 and
289 PERMANOVAs in Table 2.

290

291 **4. Discussion**

292 **4.1 *Relative influence of the studied factors***

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Determining how the three-dimensional structure of seagrass meadows mediates the assemblage of juvenile fishes is needed to better understand the ecological role of this habitat trait on the maintenance and replenishment of adult assemblages. In this study, we analyzed the effect of various habitat traits of the *Cymodocea nodosa* meadow, a common nursery habitat in the Mediterranean Sea, on the density and species richness of juvenile fishes. We found marked differences in total juvenile densities among heterogeneous (i.e. scattered with intermingled boulders) and homogeneous (i.e. without boulders) portions of the meadow, while these contrasting habitat structures had a significant, but slight influence on juvenile richness. Such patterns were found for the two sampling months, July and September, as well as for the three sites surveyed. The assemblage composition in homogeneous meadows was characterized by lower abundances of juvenile fishes, while the distribution of taxa between dominant, common and occasional species was similar among the two meadow structure types. Whereas the influence of the sampling month on the total density of juvenile fishes was limited, this factor promoted great changes in the relative abundance and/or presence of some taxa, which resulted in a poorer juvenile fish assemblage composition in September on Fornells Bay's meadows. Total abundances and richness of juvenile fishes varied as well among the three sites surveyed within the bay, while no marked difference in assemblage composition was noticed among them.

4.2 Effect of the three-dimensional structure of meadows

Our results showed that juvenile fish assemblages varied among homogeneous and heterogeneous habitats regardless of the meadow's location within the bay. Overall, higher densities and species richness were found in heterogeneous meadows. For that reason, our results demonstrate the importance of meadow structure in determining the

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318 assemblage of juvenile fishes at the scale of a few meters, as suggested in Bell and
319 Westoby (1986). The occurrence of boulders in heterogeneous habitats may facilitate
320 the colonization of species with life history traits that are well suited for seagrass
321 meadows and rocky reefs covered by macroalgae, such as *Coris julis* and *Serranus* spp.
322 (Bussotti and Guidetti, 2010; Garcia-Rubies and Macpherson, 1995).

323 Dahlgreen and Eggleston (2000) stated that the best fitted juvenile habitat provides
324 trade-offs between the availability of foods and shelters. Juvenile fishes inhabiting
325 heterogeneous meadows may benefit from diversified food and shelter resources due to
326 the variety of ecological niches that this complex habitat structure supports (Dorenbosch
327 et al., 2005; Horinouchi, 2007). For instance, boulders create small open areas (i.e.
328 edges) within the meadow resulting in small ecotones (Kolasa and Zalewski, 1995).
329 These edges can provide a great amount of food for omnivorous juvenile fish as they
330 support high abundances of crustaceans and other invertebrates (Macreadie et al., 2009;
331 Warry et al., 2009). In addition, many studies have reported that predators are less
332 efficient at the meadow edges (Hovel and Lipcius, 2001; Smith et al., 2011). However,
333 another study has shown a different pattern where juveniles have the ability to forage
334 efficiently in risky meadow habitats and can find shelter at the edges when predators are
335 detected (Thiriet, 2014). The alternate use of these adjacent micro-habitats therefore
336 allows organisms to optimize their acquisition of resources within a single meadow
337 (Cheminée, 2012; Thiriet et al., 2014). It must be noted that highly complex and
338 structured meadows may not necessarily impact all fish species. Although the densities
339 of *Symphodus* spp. and *S. salpa* increased in heterogeneous portions of the meadows,
340 there was no difference in the density of *D. annularis* among the two structure meadow
341 types. Such findings corroborate with previous studies demonstrating that juvenile fish
342 responses to seagrass structure is taxa-specific, which is most likely related to species

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343 life history strategies (e.g. anti-predator and foraging tactics) (Horinouchi, 2007; Orth et
344 al., 1984).

345 *Symphodus* spp. are highly sedentary necto-benthic fishes, characterized by a small
346 home range (Harmelin, 1987) and often associated with complex habitats (Cheminée,
347 2012). Their morphology is characteristic of maneuverable epibenthic foragers.
348 Nonetheless, there are some species within this genus (e.g. *S. ocellatus*) with juveniles
349 that mostly feed on planktonic, epibenthic and bentic meiofauna (e.g. copepods) that are
350 commonly found on boulder substratum and/or nearby (Levi, 2004). Furthermore,
351 *Symphodus* spp. juveniles, and Labrids in general, are not fast speed swimmers (Leis et
352 al., 2011; Motta et al., 1995; Recasens et al., 2006). They are characterized by a pale
353 brown color, which provides them with great camouflage abilities, and they also display
354 cryptic behaviors by hiding in the algae canopy. The success of such anti-predator
355 tactics is thus largely influenced by the habitat structure. Consequently, the occurrence
356 of boulders in the meadow may further benefit both their foraging abilities and
357 survivorship.

358 On the other hand, juveniles of both *S. salpa* and *D. annularis* are considered as necto-
359 benthic fish with a high capability for swimming by medium lateral and vertical
360 movements (Harmelin, 1987). *S. salpa* is characterized by a silver color with yellow
361 golden bands and *D. annularis* changes color while growing up, from yellow to silver
362 (Bianco, 1931; Crec´hriou et al., 2015). Such color patterns may enhance their
363 camouflage abilities in the seagrass meadows, where solar irradiance generates golden
364 reflections in the water (Marshall et al., 2003). Such species would therefore not depend
365 on boulders as shelter resources. Moreover, *S. salpa* juveniles feed on seaweed
366 fragments and photophilous epilithic algae, such as *Halopteris scoparia*, whereas sub-
367 adults and adults feed on seagrass leafs (Verlaque, 1990). On the contrary, *D. annularis*

368 juveniles are omnivorous, but mostly feed on Chlorophyte algae (Matić-Skoko et al.,
369 2004). In *C. nodosa* meadows at Fornells Bay, *C. prolifera* is the most extensive
370 Chlorophyte and has similar distribution patterns and abundances among both
371 heterogeneous and homogeneous meadows. Because epilithic algae, mostly Dictyotales
372 and Sphacelariales, predominantly grow on boulders within the Fornells Bay's
373 meadows, the colonization success of *S. salpa* should be increased in heterogeneous
374 habitats where boulders are found compare to *D. annularis*. Our data thus suggest that
375 feeding strategies can drive juvenile assemblage differences between meadow structure
376 types.

377 ***4.3 Effect of the sampling month***

378 Differences in the season during which the sampling was performed (i.e. July or
379 September) can also contribute in the variations of juvenile assemblages observed in
380 this study. It is known that meadow complexity decreases in September when *C. nodosa*
381 cover declined due to the decrease in water temperature (Marba et al., 1996). However,
382 changes in juvenile fish assemblages between sampling months may depend on the
383 species-specific reproduction timing (e.g. settlement processes) rather than on the
384 variability of seagrass structure among seasons. For instance, *S. roissali* and *S. tinca*
385 reproduce in April and then settle on the substratum from June to July. *S. ocellatus*
386 reproduces in June and settles in August-September. Consequently, it further results in
387 higher densities of *Symphodus* spp. in September (Cheminée et al., 2013; Garcia-Rubies
388 and Macpherson, 1995; Lejeune, 1984). *D. annularis* settles from June to September in
389 the north-western Mediterranean Sea, which most likely results in the higher densities
390 of juveniles observed in September at the end of the settlement period (Bussotti and
391 Guidetti, 2010; Harmelin-Vivien et al., 1995). *S. salpa* was more abundant in July as the
392 first settlement pulse usually occurs early in May-June (Bussotti and Guidetti, 2010;

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Garcia-Rubies and Macpherson, 1995). Such distinctions in reproduction timing among species strongly suggests once again that juvenile fish densities are determined by specific life history strategies

4.4 Effect of the meadow location within the bay

Our results show that the meadow location within Fornells Bay can affect species richness and density of juvenile fishes, as both increased in the site closer to the opening of the bay. Variations in the structure of *C. nodosa* meadows within Fornells Bay were also observed among the outermost and innermost sites due to the variable environmental conditions of sites, e.g. temperature and sedimentation patterns (as previously described in Delgado et al., 1997; Fàbregas, 2007). *C. prolifera* cover was higher at the innermost sites, while lower for *C. nodosa* at these sites. Variations in fish assemblages among the three sites surveyed can be related to these marked differences in *C. prolifera* and *C. nodosa* covers. However, the influence of the site location itself within the bay on juvenile assemblage patterns has to be considered as well. Site S1, where the highest fish density and richness was recorded, is located near the opening of the bay on the sea. Such a location can enhance the egg and larvae supplies within this site and can even be accentuated due to frequent north winds that characterize the hydrodynamics of Fornells Bay (Fornos et al., 1992). Previous studies also suggested that the location of a nursery habitat within an enclosed landscape, such as *C. nodosa* meadow, can affect the abundance of juvenile fishes and decapods (Cuadros et al., 2017; Jenkins et al., 1998). This nursery characteristic may be more determinant for fish assemblages than the size, shape, leaf height and/or leaf density of the seagrass meadow (Bell et al., 1988).

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5. Conclusions

Juvenile fish assemblages of *Cymodocea nodosa* meadows varied with habitat structure types (i.e. presence or absence of boulders). Richness and total abundance increased in heterogeneous portions of the meadow (i.e containing boulders). Juvenile fish responses to differences in meadow structure (i.e. higher density, lower density or no response) varied among taxa due to specific trade-offs for the acquisition of foods and shelters. Overall, this work demonstrates that the maximum production of juvenile fish in a semi-enclosed bay can be reach through intrinsic structural variability of seagrass seascape by displaying a mosaic of various micro-habitats. They can allow a spatial partitioning of resources, fulfilling the species-specific requirements. Finally, differences in seasons and sites can also influence juvenile fish assemblages in terms of composition and richness. Both sampling months and sites seem to play an important role in determining larval supply and settler survivorship due to their influence on the reproduction timing and environmental conditions.

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Contributions of authors:

Conceived and designed the experiments: ACU, ACH; Performed the experiments / field works: ACU, EV, JS, NS, ACH; Analyzed the data: ACU, ACH, PT, JM, LC; Wrote the paper: ACU, ACH, PT, JM, LC.

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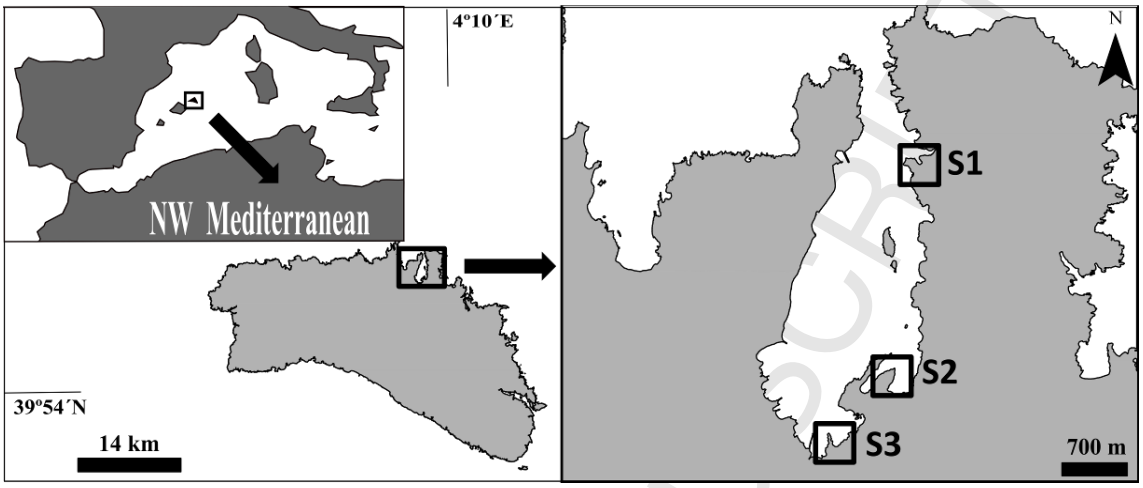
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683 **Figures and Tables**

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686 **Figure 1.** Location of the three surveyed sites in Fornells Bay (Minorca, NW
687 Mediterranean). Sites were: S1 (40.0544°N, 4.1386°E), S2 (40.0343°N, 4.1377°E) and
688 S3 (40.0284°N, 4.1287°E) (coordinates in the WGS 84 geodesic system). The map was
689 drawn using free and open source software Inkscape 0.91 (https://inkscape.org/en/) and
690 QGIS 2.14 (http://www.qgis.org/). Public domain source of background maps:
691 OpenStreetMap contributors, available under ODbL licence at
692 http://www.openstreetmap.org/.

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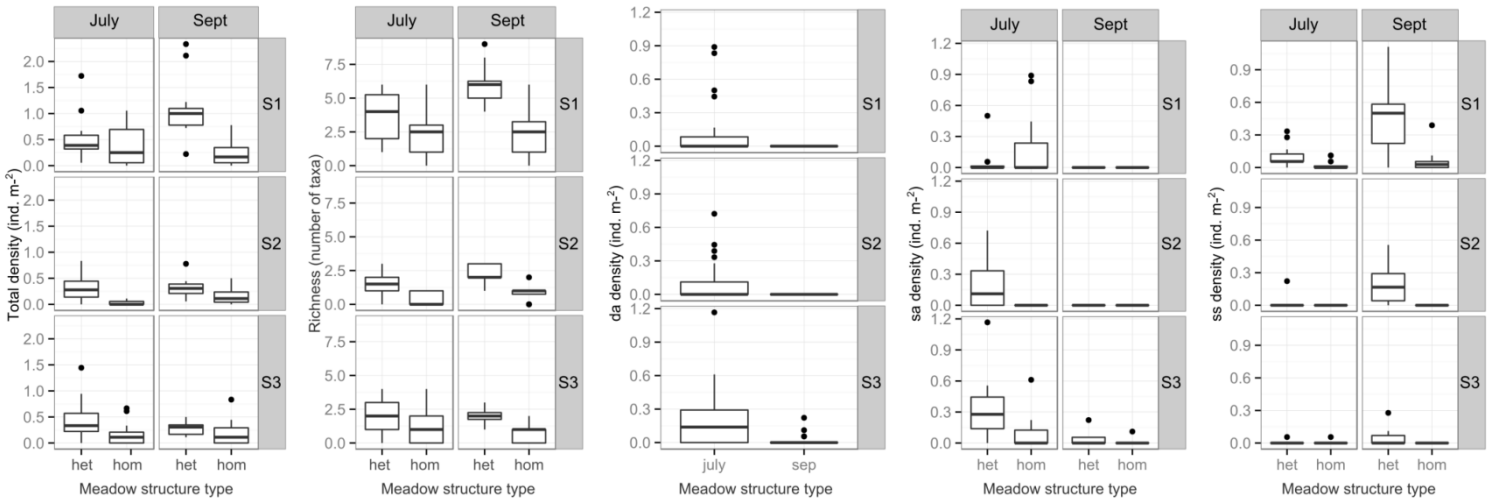
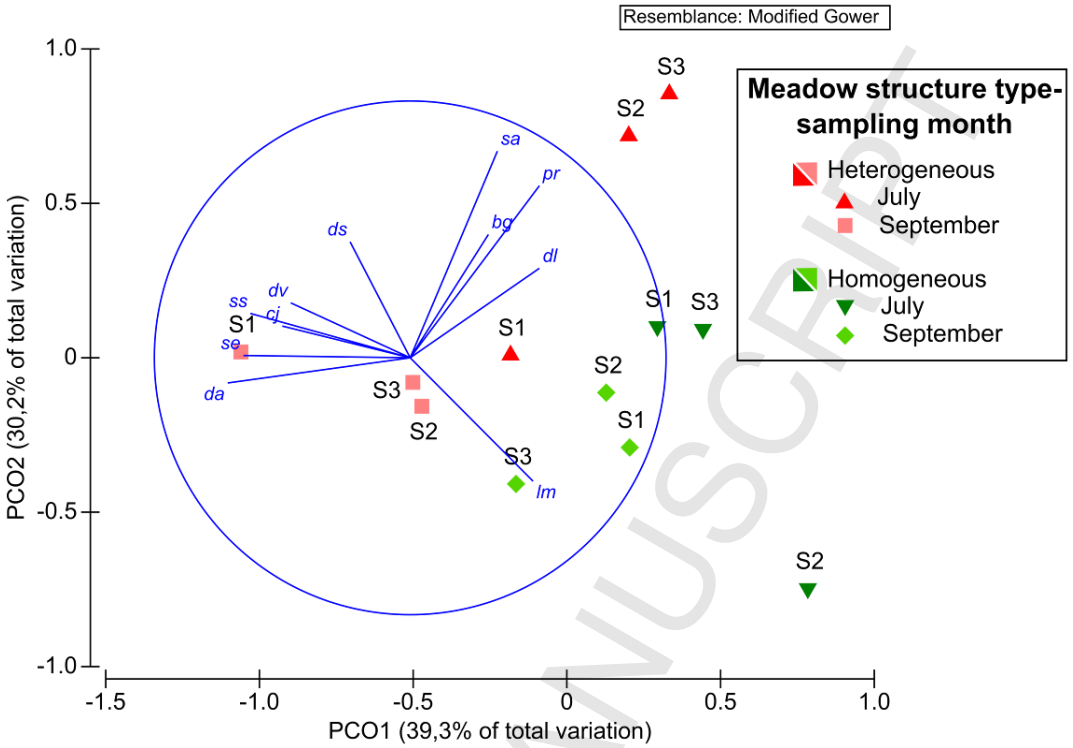


Figure 2. Tuckey boxplots of descriptors of juvenile fish assemblage (total fish density and richness) and taxa-specific densities of juvenile *Diplodus annularis* (da), *Sarpa salpa* (sa) and *Symphodus* spp. (ss) in *Cymodocea nodosa* meadows according to significant terms (see PERMANOVA Table 2). Meadow structure types: heterogeneous (het) and homogeneous (hom); sampling months: July and September (sep); sites: S1, S2 and S3 (see Fig. 1). Box plots indicate the median (bold line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the inter-quartile range (whiskers), and remaining outliers (dark circles).

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707 **Figure 3.** Principal coordinate analysis (PCoA) ordinations plot of centroids of fish
708 juvenile assemblage samples within *Cymodocea nodosa* meadows according to meadow
709 structure types (heterogeneous and homogeneous), sampling months (July and
710 September) and sites (S1, S2, S3). Correlation vectors (Spearman) of taxa specific
711 densities are plotted (for correlations > 0.4). Taxa: bg = Blenniidae-Gobiidae-
712 Tripterygiidae; da = *Diplodus annularis*; dl = *Dicentrarchus labrax*; ds = *Diplodus*
713 *sargus;* dv = *Diplodus vulgaris;* cj = *Coris julis;* lm = *Lithognathus mormyrus;* mu =
714 *Mullus* spp.*;* om = *Oblada melanura;* pr = *Pagrus pagrus;* sa = *Sarpa salpa;* se =
715 *Serranus* spp.; ss = *Symphodus* spp.

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Table 1. Juvenile fishes observed in the *Cymodocea* meadows in summer 2013. Number of juvenile fish in heterogeneous portions of the meadow (n he), number of juvenile fish in homogenous portions (n ho), number of juvenile fish in July (n july), number of juvenile fish in September (n sept), number of juvenile fish in sites (n S1, n S2, n S3), total number of juvenile counted (n tot), contribution (%) to total abundance (cont), cumulated contribution (%) to total abundance (cum), dominance categories (dom: d = dominant, c = common, o = occasional), mean TL (mm ± se), minimum (Min) and maximum (Max) TL (mm). Total sampled area = 2592 m². BGT = Blenniidae – Gobiidae – Tripterygiidae.

Taxa	**n he**	**n ho**	**n july**	**n sept**	**n S1**	**n S2**	**n S3**	**n tot**	**cont**	**cum**	**dom**	**mean TL**	**Min TL**	**Max TL**
Symphodus spp.	187	19	34	172	148	45	13	206	22,7	22,7	d	49.58±1.31	15	65
Sarpa salpa	132	69	192	9	56	43	102	201	22,1	44,8	d	50.00±2.91	15	100
Diplodus annularis	109	71	42	138	76	27	77	180	19,8	64,6	d	45.60±1.20	10	70
Diplodus sargus	49	35	35	49	38	33	13	84	9,2	73,8	c	58.09±2.51	25	90
Diplodus vulgaris	41	27	33	35	40	14	14	68	7,5	81,3	c	56.80±2.32	20	90
Oblada melanura	48	10	0	58	58	0	0	58	6,4	87,7	c	48.82±2.37	30	60
Coris julis	27	0	14	13	27	0	0	27	3,0	90,6	o	49.67±3.18	15	60
Mullus spp.	18	9	18	9	26	1	0	27	3,0	93,6	o	76.00±4.76	40	90
Mugiilidae	7	5	7	5	0	0	12	12	1,3	94,9	o	51.67±7.26	40	65
Sparus aurata	5	5	4	6	7	0	3	10	1,1	96,0	o	87.86±8.85	45	120
Dicentrarchus labrax	7	2	9	0	0	5	4	9	1,0	97,0	o	68.00±10.20	40	90
Spondyliosoma cantharus	5	2	7	0	7	0	0	7	0,8	97,8	o	52.50±10.31	30	70
Serranus spp.	6	0	2	4	5	1	0	6	0,7	98,5	o	71.67±4.01	60	80
Sphyraena viridensis	0	6	6	0	6	0	0	6	0,7	99,1	o	70	70	70
Pagrus pagrus	2	2	4	0	0	1	3	4	0,4	99,6	o	78.33±21.67	35	100
Lithognatus mormyrus	0	2	2	0	0	2	0	2	0,2	99,8	o	77.50±12.50	65	90
Pagellus spp.	0	1	1	0	1	0	0	1	0,1	99,9	o	50	50	50
BGT	1	0	1	0	0	0	1	1	0,1	100,0	o	45	45	45
Total	644	265	411	498	495	172	242	909	100					

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ACCEPTED MANUSCRIPT

Table 2. PERMANOVA results: effect of *Cymodocea nodosa* meadow structure and sampling month on univariate descriptors of juvenile fish assemblage (total density and richness), multivariate juvenile assemblage structure and univariate taxa-specific densities of juvenile dominant species.

Response variable:	Source of variation	Df	MS	Pseudo-F	P(perm)
Total density	Meadow structure (me)	1	60.47	83.21	**0.015***
	Sampling month (sm)	1	3.97	2.05	0.271
	Site (si)	2	21.30	16.00	**0.001*****
	me x sm	1	0.57	$9.36 \cdot 10^{-2}$	0.785
	me x si	2	0.73	0.55	0.558
	sm x si	2	1.94	1.46	0.228
	me x sm x si	2	6.14	4.61	**0.015***
	Res	132	1.33		
	Total	143			
Richness	Meadow structure (me)	1	90.25	14.25	**0.073·**
	Sampling month (sm)	1	8.03	1.47	0.345
	Site (si)	2	83.53	51.32	**0.001*****
	me x sm	1	7.11	1.92	0.320
	me x si	2	6.33	3.89	**0.021***
	sm x si	2	5.44	3.35	**0.04***
	me x sm x si	2	3.69	2.27	0.118
	Res	132	1.63		
	Total	143			
Assemblage structure	Meadow structure (me)	1	19.37	3.80	**0.064·**
	Sampling month (sm)	1	19.61	3.14	**0.084·**
	Site (si)	2	3.58	2.20	**0.039***
	me x sm	1	6.44	1.45	0.328
	me x si	2	5.09	3.13	**0.006****
	sm x si	2	6.25	3.84	**0.001*****
	me x sm x si	2	4.45	2.73	**0.009***
	Res	132	1.63		
	Total	143			
***D. annularis* density**	Meadow structure (me)	1	3.05·10-2	3.18	0.239
	Sampling month (sm)	1	0.20	5.71	0.162
	Site (si)	2	5.40·10-2	5.62	**0.004****
	me x sm	1	2.55·10-2	2.14	0.251
	me x si	2	9.61·10-3	1.00	0.371
	sm x si	2	3.51·10-2	3.65	**0.032***
	me x sm x si	2	1.20·10-2	1.24	0.304
	Res	133	9.61·10-3		
	Total	144			
***S. salpa* density**	Meadow structure (me)	1	$7.69 \cdot 10^{-2}$	0.54	0.533
	Sampling month (sm)	1	0.70	21.40	**0.048***
	Site (si)	2	$6.76 \cdot 10^{-2}$	2.50	**0.069·**
	me x sm	1	$5.33 \cdot 10^{-2}$	0.43	0.62
	me x si	2	0.14	5.32	**0.006****
	sm x si	2	$3.25 \cdot 10^{-2}$	1.21	0.304
	me x sm x si	2	0.12	4.59	**0.007****
	Res	133	$2.70 \cdot 10^{-2}$		
	Total	144			
***Symphodus* spp. density**	Meadow structure (me)	1	0.61	3.57	0.174
	Sampling month (sm)	1	0.41	3.60	0.193
	Site (si)	2	0.32	22.29	**0.001*****
	me x sm	1	0.33	4.85	0.161
	me x si	2	0.17	11.82	**0.001*****
	sm x si	2	0.11	7.96	**0.002****
	me x sm x si	2	$6.88 \cdot 10^{-2}$	4.78	**0.004****
	Res	133	$1.44 \cdot 10^{-2}$		
	Total	144			

Significance= · $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

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