Fish nursery value of algae habitats in temperate coastal reefs

Hilmar Hinz Corresp., 1, 2 , **Olga Reñones** 2 , **Adam Gouraguine** 3 , **Andrew F Johnson** 4 , **Joan Moranta** 2

1 Instituto Mediterraneo de Estudios Avanzados (IMEDEA; CSIC-UIB), Esporles, Illes Balears, Spain

2 Centre Oceanogràfic de les Balears, Instituto Español de Oceanografía (IEO), Palma de Mallorca, Illes Balears, Spain

3 School of Biological Sciences, University of Essex, Colchester, United Kingdom

4 MarFishEco, Portland, Oregon, United States

Corresponding Author: Hilmar Hinz
Email address: hhinz@imedea.uib-csic.es

The nursery function of coastal habitats is one of the most frequently mentioned and recognized ecosystem services in the valuation of coastal ecosystems. Despite its importance our understanding of the precise habitat parameters and mechanisms that make a habitat important as a nursery area is still limited for many species. The study aimed to establish the importance of different algae morphotypes in providing shelter and food for juvenile coastal fish during the main settlement peaks in early spring and late summer in littoral rocky reef systems in the Northwestern Mediterranean. The results of our study showed strong seasonal differences in algae cover, composition and height between the two sampling periods. Overall, during spring the algae were well developed, while in late summer, both density and height, of most algae decreased considerably. Equally, prey biomass, in form of suitable sized invertebrate fauna associated to the algae, decreased. Accordingly, the shelter and food for the fish settling in this habitat during late summer were less abundant, indicating a mismatch between the observed presence of juvenile fish and optimal habitat conditions. Differences in prey densities were detected between algae morphotypes, with structurally more complex algae, such as *Cystoseira* spp. and *Halopteris spp* consistently contain more prey independent of season compared to simpler structured morphotypes such as many *Dictoytales*. The study furthermore related juvenile fish density to habitats dominated by different algae morphotypes. Out of the three-study species (*Diplodus vulgaris, Symphodus ocellatus, Coris julis*) only *S. ocellatus* showed a significant association with an algae habitat. *S. ocellatus* related positively to habitats dominated by *Dictoytales* which provided the highest cover during late summer but had the lowest prey densities. A strong association of this species with *Cystoseira* as reported by other studies could not be confirmed. *Cystoseira* was abundant within the study area but in a state of dieback showing loss and reduced height of foliage, typical for the time of year within the study area. It is therefore likely that algae-fish

associations are context dependent and that several algae species may fulfil similar functions. We also discovered that prey biomass did not appear to have an important effect on juvenile abundances. Nevertheless, the availability of prey may influence juvenile fish condition, growth performance and ultimately long-term survival. We therefore suggest that future studies on habitat quality should also include, besides abundance, indicators related to the condition and growth of juveniles.

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5   Hilmar Hinz [a,b], Olga Reñones[b], Adam Gouraguine[c], Andrew F. Johnson[d] and Joan Moranta[b]

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7   *[a]Instituto Mediterráneo de Estudios Avanzados, IMEDEA, (CSIC-UIB), C/Miquel Marqués 21, 07190 Esporles, Illes*
8   *Balears, Spain*

9   *[b]Instituto Español de Oceanografía (IEO), Centre Oceanogràfic de les Balears, Moll de Ponent sn, 07015 Palma,*
10   *Spain*

11   *[c]University of Essex, School of Biological Sciences, Colchester CO4 3SQ, United Kingdom,*

12   *[d], MarFishEco, 5645 N Denver Avenue, Portland Oregon, 97217*

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14   *Corresponding author: Hilmar Hinz*

15

16   **Abstract**

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18   ecosystem services in the valuation of coastal ecosystems. Despite its importance our understanding of

19   the precise habitat parameters and mechanisms that make a habitat important as a nursery area is still

20   limited for many species. The study aimed to establish the importance of different algae morphotypes in

21   providing shelter and food for juvenile coastal fish during the main settlement peaks in early spring and

22   late summer in littoral rocky reef systems in the Northwestern Mediterranean. The results of our study

23   showed strong seasonal differences in algae cover, composition and height between the two sampling

24   periods. Overall, during spring the algae were well developed, while in late summer, both density and

25   height, of most algae decreased considerably. Equally, prey biomass, in form of suitable sized

26   invertebrate fauna associated to the algae, decreased. Accordingly, the shelter and food for the fish

27   settling in this habitat during late summer were less abundant, indicating a mismatch between the

28   observed presence of juvenile fish and optimal habitat conditions. Differences in prey densities were

29   detected between algae morphotypes, with structurally more complex algae, such as *Cystoseira* spp. and

30   *Halopteris spp* consistently contain more prey independent of season compared to simpler structured

31   morphotypes such as many *Dictoytales*. The study furthermore related juvenile fish density to habitats

32   dominated by different algae morphotypes. Out of the three-study species (*Diplodus vulgaris, Symphodus*

33   *ocellatus, Coris julis*) only *S. ocellatus* showed a significant association with an algae habitat. *S. ocellatus*

34   related positively to habitats dominated by *Dictoytales* which provided the highest cover during late

35   summer but had the lowest prey densities. A strong association of this species with *Cystoseira* as reported

36   by other studies could not be confirmed. *Cystoseira* was abundant within the study area but in a state of

37   dieback showing loss and reduced height of foliage, typical for the time of year within the study area. It is

38   therefore likely that algae-fish associations are context dependent and that several algae species may fulfil

39   similar functions. We also discovered that prey biomass did not appear to have an important effect on

40   juvenile abundances. Nevertheless, the availability of prey may influence juvenile fish condition, growth

41   performance and ultimately long-term survival. We therefore suggest that future studies on habitat quality

42   should also include, besides abundance, indicators related to the condition and growth of juveniles.

43   **Introduction**

44   The provision and value of nursery habitats by the coastal zone is one of the most frequently mentioned

45   and recognized ecosystem services in the valuation of coastal marine ecosystems (Duarte, 2000; Jackson

46   et al., 2001, 2015). As many coastal habitats are under increasing human pressures from urbanisation,

47   fishing, climatic change and the introduction of alien species (Sala et al., 2011, 2012, Vergés et al.,

48   2014a,b), the provisioning of this ecosystem service is progressively also under threat. While the large-

49   scale importance of nursery habitats for ecosystem functioning, food production and integrity of
50   ecosystems is recognized, a detailed understanding over which habitat types constitute to this function is
51   still lacking (Beck et al., 2001). Seagrass meadows and estuarine systems have been the focus of marine
52   nursery habitat research (e.g. Heck et al., 2003; Seitz et al., 2013; Woodland et al., 2012; Ruiz-Frau et al.,
53   2017) , while studies that focus on littoral rocky reef systems appear less frequently in the literature (but
54   see Cheminée et al., 2017; Guidetti, 2000; Harmelin-Vivien et al., 1995). Although spatially less
55   extensive compared to seagrass meadows, littoral rocky reef systems harbour a wide variety of different
56   algae species, providing shelter and food, in the form of associated fauna, to juvenile fish (Harmelin-
57   Vivien, Harmelin & Leboulleux, 1995; Cheminée et al., 2013; Félix-Hackradt et al., 2014).

58   In the Mediterranean, littoral rocky reef habitats are used by a variety of commercial and non-commercial
59   species that utilise these habitats for part, or during their entire life cycle (Harmelin-Vivien, Harmelin &
60   Leboulleux, 1995; Guidetti, 2000; La Mesa et al., 2011; Félix-Hackradt et al., 2014; Cheminée et al.,
61   2017). In general, coastal species with smaller body sizes, such as many Labridae, Blenniidae and
62   Gobiidae, complete their entire life cycle within this habitat. Several other, larger, commercial species,
63   such as various Sparid species e.g. *Pagelus spp* or *Dentex dentex*, often only use it as a nursery habitat,
64   with the larger juvenile and adult life stages moving further offshore. Settlement of juvenile fishes in
65   rocky littoral habitats occurs throughout the year but most species have a settlement peak between early
66   spring and late summer (García-Rubies & Macpherson, 1995; Biagi, Gambaccini & Zazzetta, 1998;
67   Bussotti & Guidetti, 2011). The survival of recently settled juveniles within a habitat through to their
68   recruitment to the adult population depends to a large extent on the environmental conditions encountered
69   at the site of settlement (Beck et al., 2001). Intolerance to physical extremes, starvation and predation are
70   among the broad, major causes of juvenile mortality in these habitats (Sogard, 1997; Guidetti, 2001;
71   Thierret et al., 2016; Cuadros et al., 2018). High nursery value is thus conferred through a combination of
72   factors that provide adequate physical conditions, refuge space and a sufficient food supply. Highly
73   structured habitats are thought to provide both, shelter and an abundance of food, that may facilitate
74   juvenile survival and growth processes and thus contribute to overall production and population stability
75   (Cheminée et al., 2016; Dahlgren and Eggleston, 2014; Leslie et al., 2017; Parsons et al., 2015; Scharf et
76   al., 2006). Although the importance of habitat complexity is well documented, it should be noted that it is
77   likely to be context dependent related to spatial scale and species-specific habitat requirements. For
78   example, highly complex habitats have been reported to negatively affect juvenile fish by reducing
79   feeding efficiency (Tátrai & Herzig, 1995) and increasing mortality by harbouring ambush predators
80   (Canion & Heck, 2009).

81   Nursery habitats harbouring large numbers of juvenile fish are important to ensure future recruitment into

82   adult populations. They also contribute to the maintenance of essential food web links and energy transfer

83   processes within many coastal systems (Gee, 1989; Schückel et al., 2013; Tito de Morais and Bodiou,

84   1984), consuming the associated micro-fauna (mesograzers e.g. micro crustaceans such as Harpacticoids,

85   Isopods and Amphipods) associated with macroalgae and seagrasses (Bologna & Heck, 2002; Jaschinski

86   & Sommer, 2008; Vázquez-Luis, Sanchez-Jerez & Bayle-Sempere, 2008). Macrophytes often have

87   morphological or chemical deterrents that inhibit direct herbivory by larger consumers such as fish and

88   urchins (Cruz-Rivera & Villareal, 2006). Therefore meso-grazers that can directly utilize macrophytes are

89   thought to represent an important link in the energy transfer between macro-algae and fish (Lewis &

90   Anderson, 2012; Duffy & Hay, 2016). Many juveniles are also, in turn, consumed by larger higher trophic

91   level predators (Doherty & Sale, 1986; Sogard, 1997), thus representing the intermediate stage of energy

92   transfer from primary producers to higher trophic level fish.

93   Perennial algae species belonging to the genus *Cystoseira* (Fucales, Phaeophyceae) are thought to

94   represent habitats of high quality for juvenile coastal fish in the Mediterranean (Ruitton, Francour &

95   Boudouresque, 2000; Sala et al., 2012; Cheminée et al., 2013). *Cystoseira* are macrophytes with a tree-

96   like morphology that can form dense meadows over rocky substrates, aggregations of which are often

97   referred to as *Cystoseira* forests. This habitat generally shows high primary productivity, is

98   morphologically highly complex and harbours a diverse invertebrate and fish fauna. Therefore, *Cystoseira*

99   forests, in addition to the seagrasses, have been recognised as a central foundation species (as defined by

100   Dayton, 1972) of the euphotic zone in the Mediterranean (Irving et al., 2009; Vergés, Alcoverro &

101   Ballesteros, 2009). Past declines of subtidal *Cystoseira* forests (Thibaut et al., 2005; Sala et al., 2012)

102   may have had a negative effect on the fish nursery value of coastal rocky reef habitats in many regions of

103   the Mediterranean. Nevertheless, the role and importance of other macroalgae-dominated habitats for

104   juvenile fish has not been fully explored and these could also provide adequate shelter and food for

105   juvenile fish production. Thus far the services or functions that littoral macroalgae may provide to

106   juvenile fish, i.e. shelter and food, have only been suggested and only partially tested and quantified

107   scientifically (Sala & Ballesteros, 1997; Ruitton, Francour & Boudouresque, 2000; Cheminée et al.,

108   2013). Thus, overall, we know little about the real habitat value of the littoral macroalgae and the

109   consequences their loss has on the functioning of coastal ecosystem as fish nursery habitats. Furthermore,

110   we are still unaware if there may be other macro-algae habitats, equivalent to *Cystoseira* forests, that may

111   provide a similar function and compensate for their loss. Such knowledge will be of importance for the

112   development of management and conservation strategies against the backdrop of the currently observed

113   acute environmental change experienced in coastal rocky shores in the Mediterranean, due to chronic

114   pollution, urbanisation, fishing and the introduction of non-native macro-algae species (Sala et al., 2012)

115   and herbivorous fish (Sala et al., 2011; Vergés et al., 2014a) that have the potential to rapidly modify
116   coastal habitats.

117   The present study aims to quantify the importance of the Mediterranean littoral habitats of varying algal
118   morphotype composition with respect to its functions for commonly occurring juvenile fish.In particular,
119   the study focused on measuring habitat parameters related to the key habitat requirements for juveniles
120   i.e. shelter and food. Prey availability in macroalgae has generally been inferred by past studies on
121   nursery habitat quality in the Mediterranean (Cheminée et al., 2013, 2017), but thus far has not been
122   quantified for different algae morphotypes. The study examined the relationship between juvenile density
123   and physical and biological habitat parameters, over two distinct settlement periods (Spring and late
124   Summer) and geographical areas (Mallorca and Menorca). Sampling on these two neighbouring islands
125   was conducted as to investigate the generality of any findings within the context of the Balearic Islands.
126   The algae habitats sampled included areas dominated by *Cystoseira* forest and therefore provided the
127   opportunity to contrast this habitat type, with respect to its nursery value, with other habitats dominated
128   by other macroalgae. Against the background of rapidly changing algae habitats this study thus aimed to
129   contributes towards understanding if a loss of *Cystoseira* habitats will disproportionally affect the nursery
130   function of littoral habitats or if other algae could provide similar functions

131   **Methods**

132   *Fish study species*

133   The study focused on three common and abundant fish species of littoral rocky reefs in the
134   Mediterranean, namely *Diplodus vulgaris* (common two-banded seabream), *Symphodus ocellatus*
135   (ocellated wrasse), *Coris julis* (Mediterranean rainbow wrasse). These species were chosen as they
136   occurred at sufficiently high abundances to engage with the posed research questions. Settlement of the
137   two-banded seabream, occurs in very shallow rocky coastal areas and seagrass meadows but are thought
138   to migrate quickly to deeper waters following settlement (Harmelin-Vivien, Harmelin & Leboulleux,
139   1995). Settlement peaks for this species have been reported to occur in two settlement pulses, one in early
140   November and the other in January-through to march (Vigliola et al, 1998; Garcia Rubies & Macpherson
141   1995, Harmelin-Vivien et al.1995). Biaggi et al., (1998) describes the settlement periods to occur in
142   December-January and March. Within the Balearic Islands the authors observed the presence of recently
143   settled juveniles in early spring (April-May).

144   The settlement period of the two wrasse species have been reported to occur during late summer between
145   July to August (García-Rubies & Macpherson, 1995; Biagi, Gambaccini & Zazzetta, 1998; Bussotti &
146   Guidetti, 2011) while Raventos et al. (2005) reports settlement of *S. ocellatus* slightly early during June

147 until mid-July. Within the present study the presence of recently settled juveniles was observed at the end
148 of August by the authors. The two species of wrasse have been reported to settle predominantly in rocky
149 habitats with high algal cover (García-Rubies & Macpherson, 1995; Biagi, Gambaccini & Zazzetta, 1998;
150 Bussotti & Guidetti, 2011, Félix-Hackradt et al., 2014). Juveniles of *D. vulgaris* have been reported to
151 feed predominantly on micro-crustaceans (Altin et al., 2015). Adults of the ocellated wrasse feed
152 predominantly on small crustaceans and molluscs with a suspected tendency towards herbivory
153 (Kabasakal, 2001)and adults of rainbow wrasse feed on gastropods, sea urchins and small crustaceans
154 (Sinopoli, Chemello & Vaccaro, 2016). Presently there is no information on the diet of the juvenile stages
155 of these two wrasse species.

156 *Study area and sampling design*

157 Littoral habitats were studied in the Balearic Archipelago, in the western Mediterranean . Surveys were
158 conducted in early spring (April-May) and late summer (August-September) of 2014 on the islands of
159 Mallorca and Menorca. Sampling in Mallorca took place around the north western part, while sampling in
160 Menorca was primarily conducted around the western part (see Figure 1). Sampling at each island and
161 during each period was conducted in 10 consecutive day surveys. The sampling stations comprised rocky
162 reef zones with a depth of 7-10 meters. The same depth range was chosen as not to introduce any
163 confounding effects related to depth. Furthermore, at this depth we encountered extensive algae
164 communities and juvenile fish. From an operational point of view this depth allow for comfortable diving
165 and sufficiently long bottom time for surveying. Maintaining the depth range, stations were haphazardly
166 chosen to cover a variety of habitats, including different physical (geomorphology) and biological (algae
167 cover) properties. Eight stations were sampled per sampling period and island.

168 The linear distance between consecutive stations was 4 km on average in Mallorca and the survey area
169 extended over a coastal strip of approx. 55 km. In Menorca, the distance between consecutive stations
170 was 7 km on average and the survey area covered a coastal strip of approximately 75 km. Some of the
171 survey sites were sampled both in spring and late summer, while other sites were only sampled within one
172 season. The overall number of samples was however balanced between the two seasons and islands (see
173 above)

174 *.Fish and habitat census*

175 At each sampling station the fish community and the habitat were assessed by diver underwater visual
176 census. The fish assemblage was assessed in 6 replicates of 15 x 2m transects with a horizontal gap
177 between each of at least 20m. All fish sighted along the transect were recorded and their size was
178 estimated to the nearest cm (Harmelin-Vivien et al., 1985). Benthic composition along the transects was

179   characterized using the following categories: sand, pebbles and gravel, seagrass and rock. The habitat

180   complexity of the substrate was also assessed, using a five-point scale index for rugosity, presence of

181   different sized boulders and amount of refuge spaces (see S1 for field sampling protocol.

182   The second diver measured algae cover, composition and height in three haphazardly placed 50 x 50cm

183   quadrats along the transect. Quadrats were further subdivided into 25, 10 x10 cm squares using nylon

184   string. These sub-squares were used to estimate the % cover of 8 algae morphotypes (Figure 2)and

185   unvegetated barren patches. If a morphotype occurred in a sub-square, the square was counted. For each

186   morphotype the total number of squares it occurred in was recorded as well as their average height in cm

187   form the rock surface. Algae morphotype cover in m^2 within transects was calculated by taking the m^2

188   recoded for rocky reef habitats overgrown by algae (as opposed to being occupied by sand or pebble

189   substratum) and divide this area proportionally according to the % cover of each morphotype obtained by

190   the quadrate samples. The following algae morphotypes represented by various related species that are

191   commonly encountered in the rocky littoral zone were used (Figure 2): erect tree like **1-ET** (*Cystoseira*

192   *spp.*), soft leaf like **2-SL** (*Dictyopteris polypoides* and *Dictyota spp.,*), filamentous **3-FI** (*Dictyota*

193   *dichotoma* var. intricate, Dictyota spp*.* and occasional *Hincksia spp.*), tubular **4-TU** (*Cladostephus*

194   *spongiosus*), plumose **5-PL** (*Asparagopsis spp.*), bulbous tree like **6-BT** (*Halopteris spp.*), leathery bands

195   **7-LB** (*Padina pavonica*), turf forming **8-TF** (dominated by Corallinaceae such as *Haliption vigatum*). For

196   data from dive transect see S2.

197   *Sampling of algae associated fauna and prey communities*

198   To determine prey availability for juvenile fish, the associated fauna of dominant macroalgae was

199   sampled for each station. At each site, the three most dominant algae types were sampled by collecting 6

200   x 113 cm^2 samples. A circular tube of 5 cm height and 11.5 cm diameter was used to define the surface

201   area for algae cuttings (0.01 m^2). A 0.55 µm meshed sampling bag was draped over the piece of tube to

202   collect algae cuttings and to retain associated fauna. The samples were transferred to plastic bags and

203   stored frozen. Once defrosted, the samples were pooled and rinsed into a receptacle using fresh water.

204   The algae were blotted dry with kitchen paper and the wet weight recorded from each station. The water

205   from the receptacle was passed through a 300 µm mesh sieve and any retained fauna was processed. All

206   large fauna (>5mm) were preserved in 70% ethanol. Using a Folsom plankton sample splitter, the

207   remaining, depending on its overall volume, was split up to 4 times. The final split fraction of the sample

208   was re-sieved over a 300 µm mesh and preserved in 70% ethanol. The number of sample splits was

209   recorded for each faunal sample to later enable calculation of faunal abundance and biomass of the whole

210   sample.

211 All fauna retained from the samples was sorted into large taxonomic groups (see S3 for full list of
212 groups). A photograph was taken of each taxonomic group using a standard digital camera (Canon
213 powershot G7) for the large fraction and a Leica stereo microscope (MZ16) with a digital camera (EC3)
214 for the small fraction. The photograph served to measure the size of the organisms and to quantify their
215 abundance. Image analysis software, ImageJ (Rueden et al., 2017), was used to measure the size of all
216 organisms using the polyline measurement tool. The pixel length of each measurement line was converted
217 to µm using values attained from calibration images. Length measurements were furthermore converted
218 to biomass using published length weight relationships of respective taxonomic groups (see S3 and S4 for
219 more details on the size-mass conversion and S5 for data on associated invertebrate fauna size
220 measurements).

221 Since not all invertebrates collected can be consumed by juvenile fish, due to their size, stomach content
222 analyses were carried out on a subset of fish. This allowed to determine the taxonomic composition and
223 size of the fauna consumed to more accurately estimate prey densities within algae at each station.
224 Approximately 50 fish of each species were used. These were selected at random, from different stations
225 at which fish samples were available (see protocol of fish sampling below). The taxonomic group and size
226 of taxa were determined from photographs in the same manner as for the determination of algae
227 associated fauna. Only prey items that had an intact body outline were measured. For data of prey sizes
228 found in stomachs see S6.

229 To determine the upper size limit of suitable prey for juveniles of each study species (those below 60 mm
230 total length) of the study species we used quantile regressions analysis (Cade & Noon, 2003). Only
231 significant upper quantiles were considered starting from the 95th quantile moving down in steps of 5.
232 Since some invertebrate taxa had an elongated, while other had compact body shape, the first significant
233 upper quantile was considered the upper limit of prey size for compact and elongated prey for each fish
234 species. The cutoff point for prey sizes to be considered for the determination of prey availability in algae
235 was the value where the upper quantile regression line intersected with the 60 mm total length of the
236 study species (i.e. juvenile fish) (Cade and Noon, 2003). Furthermore, we only considered prey taxa that
237 cumulatively contributed to at least 90% of the prey taxa found in stomachs as to exclude rare species that
238 may only occasionally or accidentally were ingested. Not all algae morphotypes were sampled in both
239 islands, the data on the abundance and biomass of prey per algae morphotype was therefore presented
240 using pooled data from both islands for the season in which juvenile fish of respective study species
241 occurred i.e. *Diplodus vulgaris* spring and summer for *Coris julis* and *Sympodus ocellatus*.

242 The abundance and biomass of prey within a transect was estimated using the area cover (m²) by different
243 algae morphotypes multiplied abundances and biomass of prey items found (per m²) within these from

244 algae cuttings (see above). Organisms were only considered prey if they were of the relevant taxa and

245 sizes as identified by the stomach content analysis described above.

246 *Sampling of juvenile fish*

247 Using hand-held nets, a sample of approx. 30 juvenile fish of each of the study species were collected

248 from each of the 32 sampling stations (see S7 for fish size data). In addition to the stomach content

249 analysis, the fish sample was used to evaluate the size distribution of juvenile fish.

250 *Wave exposure data*

251 As juvenile fish may experience higher dispersal from habitats with high wave action, and algae may be

252 influenced by physical wave stress, wave exposure was considered in the study (Spatharis et al., 2011).

253 Wave stress data for each station was calculated from a dynamical coastal wave model provided by the

254 Coastal Ocean Observing and Forecasting System located in the Balearic Islands (SOCIB) using past real

255 weather events. The mean wave exposure as well as the wave exposure of the 4 months prior to sampling

256 was used as an environmental parameter in the analysis of data.

257 *Statistical analysis*

258 *Algae community analysis over temporal and spatial scales*

259 Algae morphotype cover composition was analyzed using a Principal Component Analysis (PCA) based

260 on Euclidian distance. The resulting ordination was explored through investigating the correlation of

261 algae morphotypes with the two first Principle Component (PC) axes. Furthermore, the loading of each

262 variable was superimposed as arrows over the ordination. The length of the arrow corresponds to the

263 strength of influence on the ordination while its orientation provides information on the direction of

264 influence. ANOSIM pairwise comparisons were used to test for significant differences in algae cover

265 composition between the transects sampled between different seasons and islands. Distance based linear

266 models (DistLM) were used to investigate the environmental variables that best explained the observed

267 ordination patterns in algae composition. The following five environmental variables were used: Mean

268 depth, Slope, rugosity, Temperature, herbivore (density of *Salpa salpa* and urchins), along with the

269 modelled wave stress for each site. All multivariate analyses were conducted with the Software Package

270 Primer-E version 6 (Clarke & Gorley, 2006).

271 The height of different algae morphotypes was compared on an island scale using a two-way ANOVA

272 with morphotype and season as main factors. A Post-hoc Tukey-test was used to identify height

273 differences between morphotypes within seasons and the height of the same morphotype between

274   seasons. Height data was log-transformed prior to analysis to meet model assumptions regarding

275   normality and homogeneity of variance.

276   *Potential prey availability in different algae morphotypes for juvenile fish*

277   Potential prey availability was calculated considering prey sizes, taxonomic groups and the season

278   relevant to the juveniles of the respective fish species (<60 mm). Potential prey availability was compared

279   between morphotypes using a one-way ANOVA and post-hoc Tukey pairwise comparison tests. The data

280   of both islands were pooled to compare all algae morphotypes as for some algae morphotypes insufficient

281   specimens were sampled to be able to consider both islands separately in the analysis. Potential prey

282   density was log-transformed prior to analysis to meet model assumptions regarding normality and

283   homogeneity of variance.

284   *Relationship between different algae morphotypes and juvenile fish abundances.*

285   The relationship between juvenile fish abundance and algae morphotype cover (m^2), as well as total prey

286   biomass per transect, was modeled using a Generalized Linear Mixed Model (GLMM) with a negative

287   binomial error distribution and a log-link function. Within the model the station was considered a random

288   factor to address the dependency structure of dive transect from the same station. The cover by

289   morphotypes, as well as total prey biomass per transect, were considered as fixed factors. All variables

290   introduced to the model were correlated prior to analysis to identify any collinear variables to be removed

291   or pooled prior to modelling. Model selection procedures were adopted whereby non-significant variables

292   were removed until only significant variables were contained in the final model, using the drop-one

293   procedures in R. Models were checked for over dispersion and the residuals were visually examined

294   (Zuur, A.F. et al., 2009; Zuur, Ieno & Elphick, 2010).

295   **Results**

296   *Algae morphotype composition and height across sampling seasons and islands*

297   Algae morphotype composition within sampling areas and season were compared by PCA ordination of

298   the dive transects sampled. The PCA explained 60.5% of the variability of the algae cover data (Figure 3,

299   Table S8). The ANOSIM pairwise comparisons analysis verified that there were significant differences in

300   composition of morphotypes between all island and season combinations ($p < 0.001$, Figure 3). The largest

301   differences were found between transects surveyed in summer in Menorca and all other island-season

302   combinations (see Figure 3 and Table S8). Algae cover was most similar between spring and summer in

303   Mallorca (see Figure 3). Transects sampled in spring in Menorca were similar to those sampled in

304   Mallorca (see overlap of PCA space Figure 3 and lower summed Euclidian squared distance Table S9).

305   Overall, seasonal changes in algae cover for both islands were similar for most morphotypes (Table 1). In
306   both islands the average transects cover of 1-ET (*Cystoseira spp.)* were lower in summer compared to
307   spring as was the cover of 2-SL and 3-FI (*Dictyota spp*. and similar). In contrast, the cover of 7-LB
308   (*Padina pavonia*) was higher in both islands during summer as did the occurrence of barren patches (no
309   vegetation over rock) (Table 1). However, the magnitude of seasonal change was more pronounced in
310   Menorca. Furthermore, transects surveyed in summer were significantly different to those sampled in
311   Mallorca (Figure 3 and table S9) with higher cover in morphotype 7-LB (*Padina pavonia*) and lower turf
312   forming morphotypes 8-TF (Corallinaceae) compared to Mallorca (Figure 3 and Table 1). Morphotypes
313   2-SL and 3-FI (*Dictyota* spp. and similar) formed part of many transects in Mallorca in late summer,
314   while these morphotypes were almost absent from transects in Menorca (Figure 1 and Table 1).

315   The distance based linear model (DistLM) relating environmental variables to the PCA ordination of
316   algae cover showed that of the 6 environmental variables considered, three (Temperature, wave stress and
317   rugosity) proved to show significant relationships with the PCA ordination pattern (Figure 3 and Table
318   S10). The model with the best fit (lowest AIC) containing these three variables had an r^2 of 0.2 thus
319   explaining about 20% of the variability. Mean depth, slope and herbivore density (*Salpa salpa* and
320   urchins) were not significantly correlated with the ordination (S10). Temperature and waves stress were
321   associated with PC1 as indicated by the horizontal orientation of the eigenvectors in Figure 3 and thus
322   could be related to the distinct algae cover in Menorca over the summer period. In general, average wave
323   stress was higher (H_s 0.7) and temperature lower (25.8˚C) in Menorca compared to Mallorca during
324   summer surveys (H_s 0.4) and 26.9˚C respectively).

325   Additional to the surface cover, the height of algae varied between morphotypes, seasons and islands
326   (Figure 4). In general, the height of morphotypes was higher in Mallorca compared to Menorca. Seasonal
327   changes in the height of cover were however relatively consistent over both areas. In general, *Cystoseira*
328   *spp.* (1-ET) decreased height between spring and summer surveys (Figure 4). In Mallorca *Cystoseira spp.*
329   decreased in height from spring to late summer from an average 11.2 cm to 4.3 cm, while in Menorca it
330   decreased from 7.6 cm to 5.1 cm. These reported changes were statistically significant (S11 and S12).
331   Other morphotypes decreased less in height (2-SL) or approximately maintained their height (3-FI, 6-BT
332   and 8-TF). In summer, *P. pavonia* (7-LB) was the only algae that significantly increased in height in both
333   areas from 4.2 to 6.9 cm in Mallorca and 3.8 to 6.8 in Menorca. During the summer period in Mallorca
334   filamentous morphotype algae (3-FI) were found to be the highest with 10.6 cm while in Menorca both
335   filamentous (3-FI) and bulbus tree like (6-BT) were the highest with 7.8 and 7.9 cm respectively.

336   *Taxonomic composition and size of prey items found in juvenile fish stomachs*

337   Stomach samples of the three-study species showed that. All three species shared many prey taxa (see

338   Figure 5). *Diplodus vulgaris* and *Sympodus occelatus* diets were dominated by harpacticoids (both 53%)

339   while stomachs of *Coris julis* predominantly by gastropods (50%) and to a lesser extent by Harpacticoids

340   (34%). *Diplodus vulgaris* stomach samples were furthermore dominated by Ostracods (14%), Amphipods

341   (9%) and Gastropods (9%) while *Symphodus occelatus* also contained sea mites (Acari 34%) and

342   Gastropods (15%).

343   For all species significant upper quantiles (p<0.05) were found determining the upper limit of prey sizes

344   that were consumed at a certain size (Figure 5). Comparing the upper limit of prey sizes consumed with

345   increasing size of fish showed that fish below 60 mm, the chosen cutoff point to determine the upper limit

346   for juvenile prey size, of the three-study species consumed very similar size prey when considering

347   compact body prey such as Harpacticoids or Amphipods. In general prey sizes were between 1.33- 1.61

348   mm. Both *Diplodus vulgaris* and *Coris julis* consumed elongated prey consisting mainly of Polychaetes

349   reflected in the % contribution to the diet, 3% and 6% respectively (Figure 5). Other elongated taxa such,

350   *Diptera* larvae, *Caprellidea* and *Tanaidacea* contributed less to this prey category. Stomachs of

351   *Sympodus occelatus* also had too few elongated prey items to perform an upper quantile regression

352   analysis. The size of elongated prey found in *Coris julis* were slightly larger for fish at a size of 60mm

353   compared to *Diplodus vulgaris*. The size elongated taxa consumed was below 6.18mm and 7.83mm

354   respectively (see Figure 5). Overall the stomach content reflected well the dominant taxa found in the

355   different algae morphotypes (S13)

356   *Potential prey availability in different algae morphotypes for juvenile fish*

357   Comparing potential prey abundance and biomass by algae morphotype using one-way ANOVA analysis

358   showed that there were significant differences considering the three-study species (S14 and Figure 6).

359   Post-hoc Tukey tests showed that in general 1-ET, 6-BT held significantly higher prey densities and

360   biomass compared to other algae morphotypes (S15 and Figure 6). In general, the highest prey densities

361   or biomasses in absolute terms were irrespective of season and fish species found in the three structurally

362   complex algae's 1-ET, 6-BT and 8-TF compared to the more structurally simple algae such as 2-SL, 3-FI

363   and 7-LB. The general pattern between islands and seasons observed in prey abundances and biomass

364   were reflective of patterns when considering all associated fauna (S16). Note that overall abundances and

365   biomass of associated fauna were considerable higher within all algae morphotypes in spring compared to

366   summer (S16).

367   *Relationship between different algae morphotypes and juvenile fish abundances.*

368   The total number of juvenile fish observed over the visuals transect surveyed varied considerably between
369   islands and species. For *Diplodus vulgaris* we only encountered 39 fish in 96 transects during the spring
370   period of which 35 were recorded in Mallorca (mean size 43.8mm Mallorca and 46.1 mm Menorca). In
371   contrast, similar numbers of *Coris julis* were recorded at both islands during the summer sampling period
372   see Table 2 (mean size 48.7mm Mallorca and 32.7mm Menorca). However, for *Symphodus ocellatus* the
373   number of juveniles varied considerably between islands. In 48 transect dives we observed 486 fish in
374   Mallorca as opposed to only 63 in Mallorca (mean size 28.1mm Mallorca and 33.3 mm in Menorca). This
375   island scale difference was also reflected in other *Symphodus* species (see Table 2).

376   Due to the low abundance of *Diplodus vulgaris* juveniles in visual census transects we did not investigate
377   its relationship with algae cover, rugosity and total prey biomass within transects using a Generalized
378   Linear Mixed Modelling (GLMM) approach. Furthermore, we restricted this type of analysis to Mallorca
379   for *Symphodus ocellatus* where we had a sufficiently large sample size. *Coris julis* was analyzed
380   considering data from both islands.

381   Prior to the GLMM analysis we correlated the explanatory variables to detect any collinearity. As we
382   found a positive correlation between 2-SL and 3-FI (Pearson correlation coefficient 0.68), two algae
383   morphotypes that are were many cases structurally and taxonomically similar, their cover was pooled to
384   avoid collinearity.

385   For *Coris julis* neither algae cover, nor the total prey biomass had a significant effect on juvenile
386   abundances. For *Symphodus ocellatus* the best model including only the significant variables contained
387   the algae morphotypes 2-SL+3-FI and 7-LB. While 2-SL+3-FI had a positive effect on fish abundances 7-
388   LB had a negative effect (Table 3 and Figure 7).

Discussion

390   High quality habitats for juvenile coastal fish have generally been characterized by both, high sheltering
391   opportunities and food for the resident juvenile fish (Cheminée et al., 2013, 2017). In our study, we
392   however observed that recently settled juveniles in summer appear to occur at a suboptimal time. Our
393   results showed strong seasonal variations in algae cover between sampling seasons. Algae morphotype
394   cover and height had changed considerably on both islands between the two sampling events that
395   coincided with the two major settlement peaks of juvenile fish documented for the Mediterranean
396   (García-Rubies & Macpherson, 1995; Biagi, Gambaccini & Zazzetta, 1998; Bussotti & Guidetti, 2011).
397   During the settlement period of *Diplodus vulgaris* the extent and height of the forest forming algae
398   *Cystoseira spp*. was considerably greater compared to the summer period in which *Symphodus ocellatus*
399   and *Coris julis* settled. Similarly, most other algae decreased in cover and to some extend in height except

400   for *Padina pavonica*, which increased both in cover and height during this period. Concurrent with these
401   cessation patterns of algae, the associated fauna was also found to undergo a sharp seasonal decline in
402   abundance and biomass, from spring to summer. However, this was not restricted to algae that decreased
403   in height but was a consistent pattern which was also found to affect algae that increased in height, such
404   as *Padina pavonica*. Thus, when comparing overall prey availability per unit area between fish species,
405   there were considerably more prey available in algae during the spring period during *Diplodus vulgaris*
406   settlement, compared to prey available for the other species during the late summer period. These
407   seasonal patterns between algae and associated fauna have also been demonstrated by other authors (e.g.
408   Guerra-García et al., 2011). An apparent mismatch exists between the period of high shelter and food
409   provision by habitats and the settlement and growth period of juvenile fish. Summer settlement of
410   juveniles results from spawning during early spring and the mismatch may be caused by evolutionary
411   processes favoring the match of earlier larvae stages with planktonic production processes, ensuring
412   higher larval survival. Certainly, for *Coris julis* there appear to be strong links between primary
413   production processes and the amount of larval settlement (Fontes et al., 2016), which may also apply to
414   other fish species with summer settlement peaks in the Mediterranean. This mismatch therefore does not
415   suggest that shelter and food are not important for juveniles, but that they do not appear to have a strong
416   selective influence on the timing of spawning. The decrease of shelter and food provisioning from spring
417   to summer shows that coastal habitats and the services they provide for juveniles are not a constant and
418   that they can undergo notable changes in a relatively short amount of time. With this in mid, it is plausible
419   that climate change may further increase the mismatch between algae habitat provisioning properties and
420   summer settlers, if higher temperatures increase the speed of seasonal cycles causing earlier cessation in
421   algae communities. Little is currently known about the influence of climate change on the timing of
422   seasonality in macro-algae, several studies argue that warming can affect the phenology and reproduction
423   of macroalgae (Kraufvelin et al., 2012; Andrews, Bennett & Wernberg, 2014), thus suggesting that early
424   cessation processes could be triggered by seasonally early or extreme warming events. For example, in
425   the Baltic, increased seawater temperature and light during early springs accelerate receptacle growth of
426   *Fucus vesiculosus*, causing earlier reproduction (Kraufvelin et al., 2012). As cessation processes generally
427   follow reproduction in many marco-algae species (Liu et al., 2017) climate change has the potential to
428   shorten macro-algae cycles potentially causing a mismatch between the provision of shelter and food for
429   juvenile fish (Durant et al., 2007). Both the timing of spawning and the rate of larvae and juvenile
430   development may however also be affected by temperature (Pankhurst & Munday, 2011). Therefore, it is
431   also conceivable that both juvenile fish and habitat may be affected synchronously. The precise effect of
432   temperature on reproduction and larvae development of fish is however complex and highly species
433   specific. Thus, for example warming may advance or delay the maturation and ovation depending on

434   species specific thermal endocrine triggers (Pankhurst & Munday, 2011). Climate induced mismatches

435   between fish and their food resources have been reported for pelagic fish illustrating that climate warming

436   may not affect larval development and prey production equally (Gröger, Hinrichsen & Polte, 2014; Illing

437   et al., 2018). Whether the match/mismatch hypothesis, i.e. the synchronized/desynchronized timing of

438   seasonal activities, as described by Cushing (1969, 2019), is important with respect to algae habitats

439   provisions for juvenile fish is currently unknown and requires further scientific attention.

440   When considering the potential prey availability in different macro-algae morphotypes, we found that

441   structurally more complex algae contained more prey, in particular algae such as *Halopteris* spp. and

442   *Cystorceria* spp., but also turf forming *Corallinaceae* such as *Haliption vigatum*, that have a complex

443   internal structure. In contrast, *Dictyotales*, with flat leafs or filamentous algal species contained fewer

444   prey. This pattern of distribution of prey amongst algae was persistent during both settlement periods.

445   Whether algae containing higher prey biomasses also provide higher quality habitats is unclear. The term

446   potential prey availability was used throughout as we did not examine whether this prey was readily

447   available to the juvenile fish. It is possible that, due to the complex structure of some algae, feeding

448   efficiency of juveniles may be decreased or less optimal (Tátrai & Herzig, 1995). Thus, the higher

449   amounts of associated invertebrate fauna in morphologically complex algae could reflect reduced

450   predation by fish. Equally, lower biomass of potential prey within less complex algae morphotypes could

451   be the result of increased feeding on less protected and thus easier to feed upon prey. As a result, it is

452   possible that juveniles are responsible for structuring the associated algal fauna. Further research into

453   juvenile feeding behavior will be required to explain observed prey distributions among algae

454   morphotypes.

455   Within our study, no tangible indication appeared within the data that juvenile fish densities are strongly

456   linked to prey densities. For example, *Symphodus ocellatus*, was associated to algae with the least prey

457   and thus, prey availability may not be a central factor in determining juvenile fish densities. It is likely

458   that food availability is of secondary importance to fish abundance, but it may, nevertheless, affect

459   juvenile body condition and growth rate and thus, their long term-survival (Lloret et al., 2002, 2012). To

460   assess and compare nursery qualities of habitatsand move away from using solely abundance estimates

461   for habitat suitability, these parameters should be considered by future studies.

462   Analyzing the association of juvenile fish abundance and algae morphotype cover, we discovered that,

463   while for *Coris julis* there was no clear association to any particular algae morphotype, *Symphodus*

464   *ocellatus* had a positive association with *Dictyotales* and a negative association with *Padina pavonica*. No

465   analyses were carried out for *Diplodus vulgaris*, as too few individuals were observed within transects.

466   The absence of a clear relationship of *C. julis* with algae morphotype appears consistent with findings by

467   Cheminée et al. (2017) who reported an association of this species with sparser algae cover. However, we

468   did not found a clear relationship between the abundance of *S. ocellatus* and *Cystoseria* contrary to the

469   patterns observed by other studies (e.g. Cheminée et al., 2013, 2017; Thiriet et al., 2016). These studies

470   stress the importance of *Cystoseira* forests as a prime juvenile habitat for *Symphodus* spp., due to their

471   structure. These discrepancies could be due to different factors such as: i) the different UVC methodology

472   used in the different studies (15*2 m transects this study, 1 m² point-count Cheminée et al., 2013, 2017

473   and 9-m² stationary-point snapshotcount Thiriet et al., 2016), which can have an effect on the total

474   amount of fish counted; ii) different geographical and temporal settlement peaks of local populations,

475   which can produce a mismatch between the time of the study and the time of the settlement in each study

476   area and year of sampling (Cheminée et al., 2017 sampled slightly earlier in July-August as opposed to

477   August-September as in this study); iii) seasonal and annual differences in the development of height and

478   cover of *Cystoserira* between the mentioned studies caused by the delay or advance in their development.

479   Within our study *Dictyotales* provided considerably higher cover, compared to *Cystoseira*, and may have

480   therefore been more important in providing shelter to *Symphodus* spp. The low numbers of individuals of

481   this species in Menorca were not only restricted to juveniles but also fewer adults were observed, possibly

482   indicating that habitats surveyed in this island were altogether less suitable for this species. Apart from

483   potentially having provided better sheltering opportunities, *Dictoytales* were observed to be an important

484   nest building material for male *Symphodus occelatus*, during spring in Mallorca. Many labridae species

485   build nests in which the male protects and broods the fertilized eggs (Raventós, 2006). Thus, it is possible

486   that the higher abundances of juveniles observed in *Dictoytales* dominated habitats may be related to a

487   higher number or quality of nests, subsequently providing a locally larger numbers of settlers in summer.

488   However, a study on the related species *Symphodus roissali* found no significant relationship between the

489   indirect measure of successful nests (larval output) and the number of recruits within a three year period

490   (Raventos, 2009). It remains unclear if the shelter, or better nesting conditions, are responsible for higher

491   abundances of *Symphodus ocellatus* in *Dictoytales*.

492   Overall, more effort needs to be made to study the behavioral relationship and interaction of fish with

493   their habitats. This and other studies focused on measuring the percentage cover of algae for shelter and

494   food provisioning. Shelter, however, may be used in different configurations. For example, fish may use

495   banks/patches of algae to hide from predators behind or hide within the algae matrix. Hiding behind

496   would require high cover but in a fragmented format, with open spaces, whereas hiding within would

497   require a more continuous cover. Within our study, while catching juvenile fish, we observed that

498   *Symphodus ocellatus* hid within the algae matrix, while *Diplodus vulgaris* avoided entering any algae or

499   *Posidonia* patches but instead used these as a parkour of obstacles to outpace and loose human pursuers.

500   In the case of *Diplodus vulgaris,* a continuous dense algae forest cover, may due to this behavior, not

501 represent an ideal habitat. This type of behavioral shelter use may explain why no trends were observed

502 for this species and shows that future study also needs to consider the spatial configuration of cover

503 depending on the behavioral needs of a species.

504 **Conclusion and recommendations for future studies**

505 The results of this study show that in many ways we still have a relatively rudimentary understanding of

506 what represents a good nursery habitat for juvenile fish. Algae species such as *Cystoseira* that appear to

507 have high importance in one area and season for a specific species may not necessarily have the same

508 importance in another area or season. This may be due to the context dependent nature of juvenile

509 occurrence and the habitat composition at the time of the study. The results suggest that fish can adapt to

510 local situations and use algae morphotypes/species that offer the required function at the time. While at

511 the time of our study we detected an association of *S. ocellatus* juveniles (3-4cm) with *Dictyotales* these

512 results do not implicate that *Cystoseira* habitats are not important for juvenile fish. Settlers that arrived in

513 July-early August may well have used *Cystoseira* to shelter within the first two month of their lives.

514 Equally likely, those new settlers of other species arriving in the area during the spring, when the

515 *Cystoseira* forest are better developed with higher cover and canopy height may have a preference for this

516 algae than others. While providing new insights, the present study is not able to evaluate the importance

517 of *Cystoseira* habitats as a nursery habitat with certainty and as such the effect of the continuing loss of

518 this habitat. Considerably more focused research will be required to address this question.

519 Abundance of juvenile fish may vary considerably in time, at any one location, due to natural stochastic

520 processes, causing a high degree of variability. Scenarios are imaginable in which, due to a strong

521 settlement pulse and fishery-depleted predators, there are many juveniles in a habitat. However, because

522 of the lack of food provided by the habitat fish may have low long-term survival potential (e.g.

523 Macpherson et al. 1997; Planes et al. 1998; Cuadros et al., 2018). Using abundance indices alone as a tool

524 to assess habitat quality has limitations as these do not consider the effect of different habitat conditions

525 on the individual fish i.e. how a habitat affects parameters such e.g. growth and survival potential. Thus,

526 when combined with abundance estimates, methodologies that assess fish condition, growth performance

527 and health status may provide a more accurate picture of the prevailing conditions for fish living at a

528 certain location. Habitat quality for juveniles should not be measured on the level of "settlement success"

529 alone i.e. the maximum number of recently settled individuals, which may be largely a function of

530 stochastic hydrodynamic processes (Beck et al. 2001). A better measure of habitat quality would be to

531 estimate the survival rate of newly settled fish to reach a certain arbitrary size in good condition.

532 However, measuring this type of "recruitment success" would be time consuming and financially costly

533 as it would require intensive temporal sampling of juveniles from their settlement phase to their

534 recruitment to the adult population. To increase our understanding of what constitutes high quality
535 nursery habitats it is important to have workable and cost-effective sampling solutions. Therefore, future
536 studies should aim to incorporate methods and develop indicators that link both abundance estimates and
537 population fitness parameters of juvenile fish at an agreed, predefined size range (by species)to evaluate
538 habitat quality.

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730

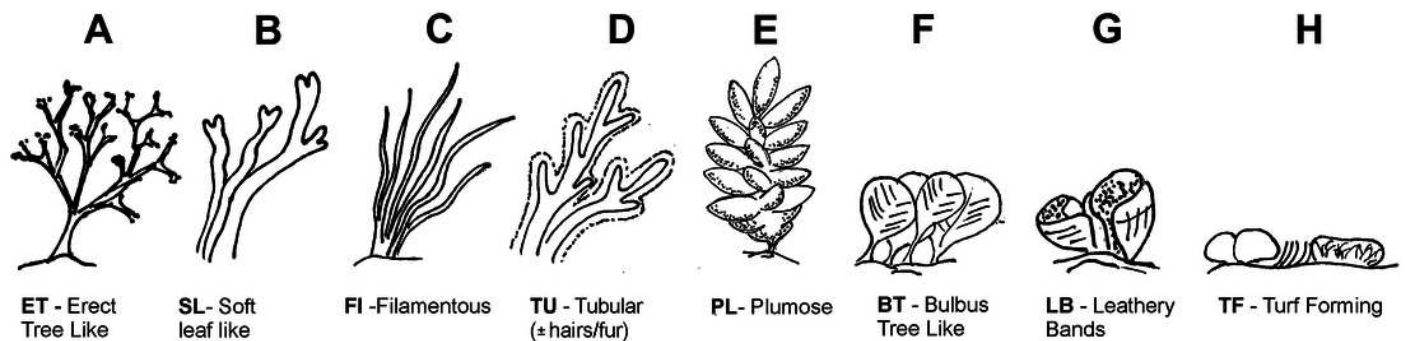# Figure 1

Survey area and sampling locations.

Sampling stations surveyed in Mallorca (A) and Menorca (B). White circles denote stations sampled in spring and black circles denote stations sampled during the summer
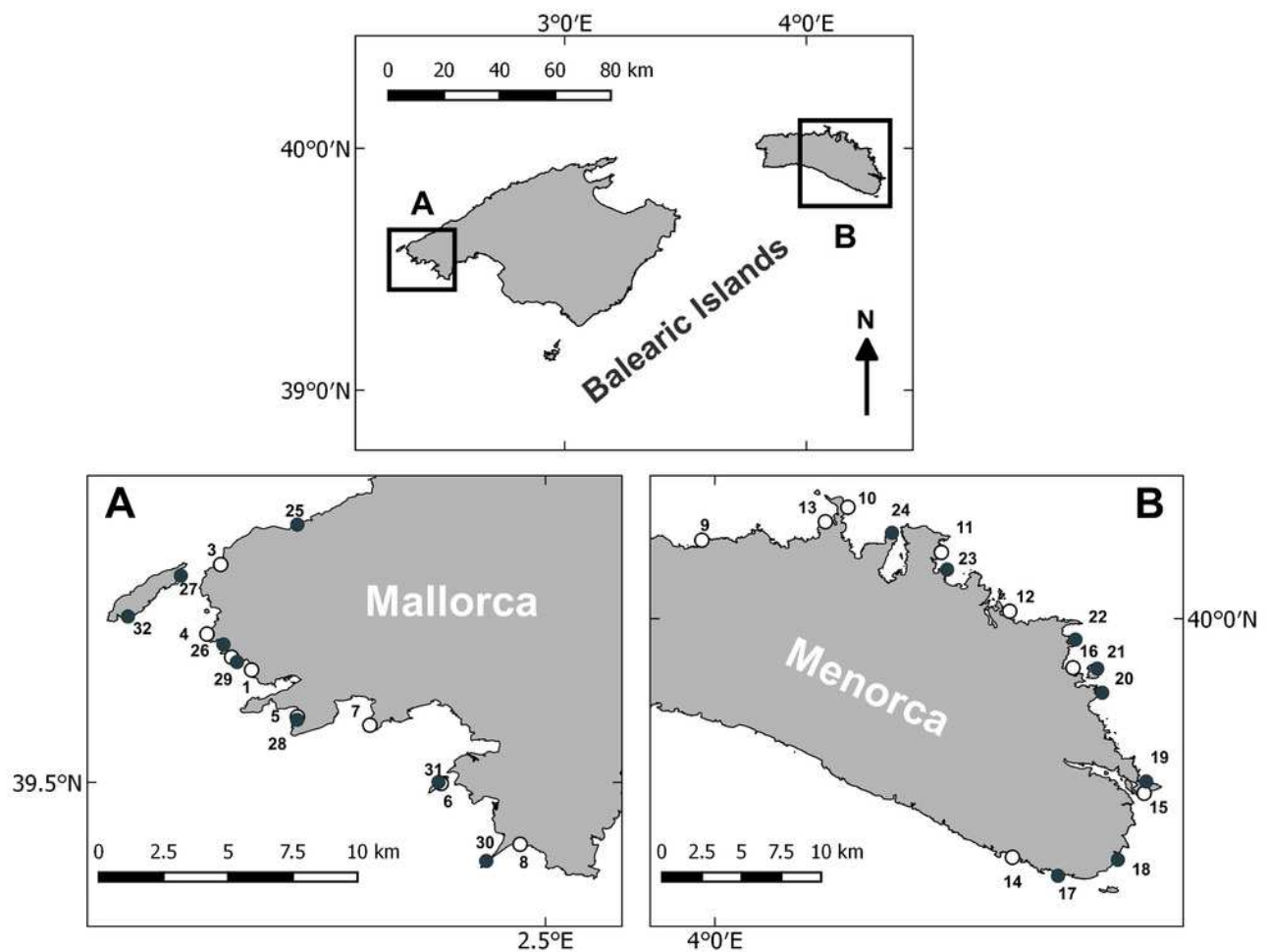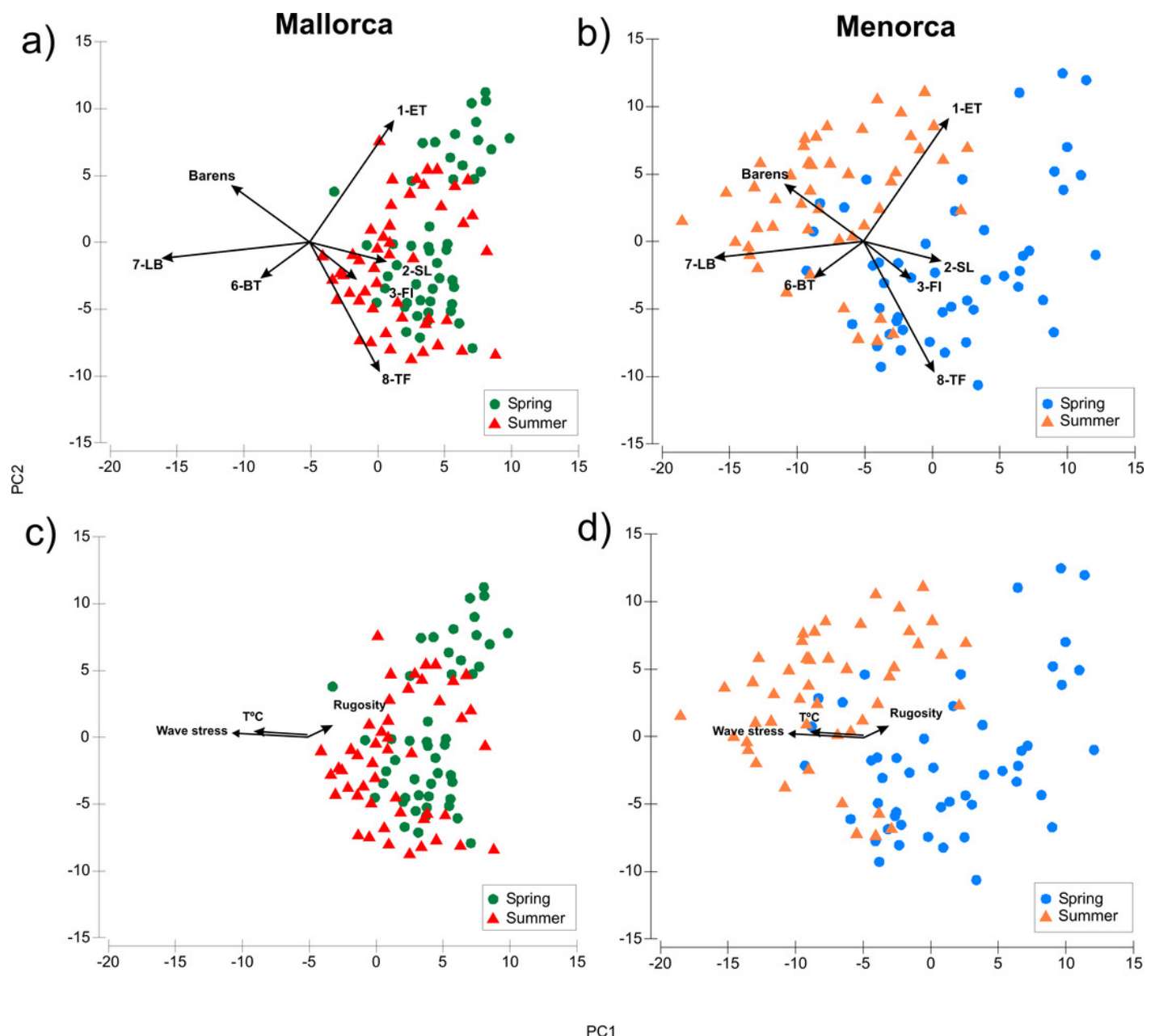
Figure 2

Algae morphotype

Algae morphotypes surveyed along dive transects corresponded to different species complexes with similar morpholog; (A) Erect tree like (*Cystoseira spp*.), (B) soft leaf like (*Dictyopteris spp. and Dictyota spp*),(C) filamentous *Dictyota dichotoma* var. *intricate, Dictyota spp.* and occasional *Hincksia spp*.), (D) tubular (*Cladostephus spongiosus*), (E) plumose (*Asparagopsis spp.*), (F) bulbous tree like (*Halopteris spp* .), (G) leathery bands (*Padina pavonica*),(H) turf forming (dominated by Corallinaceae such as *Haliption vigatum*). Copyright figure H.Hinz.

Figure 3

Comparison of algae morphotype composition in dive transects sampled during spring and summer in Mallorca and Menorca

PCA showing the composition of algae morphotype cover over dive transects surveyed in summer and spring (a: Mallorca, b: Menorca) as well as the potential environmental drivers in the variation of algae morphotype cover. (c: Mallorca, d: Menorca).

Figure 4

Height of algae morphotypes during spring and summer in Mallorca and Menorca

Mean height of algae morphotypes during spring (May 2014) and summer (August 2014) in a) Mallorca and b) Menorca measured within 0.5 m^2 quadrats located within dive transects. Error bars are S.E.
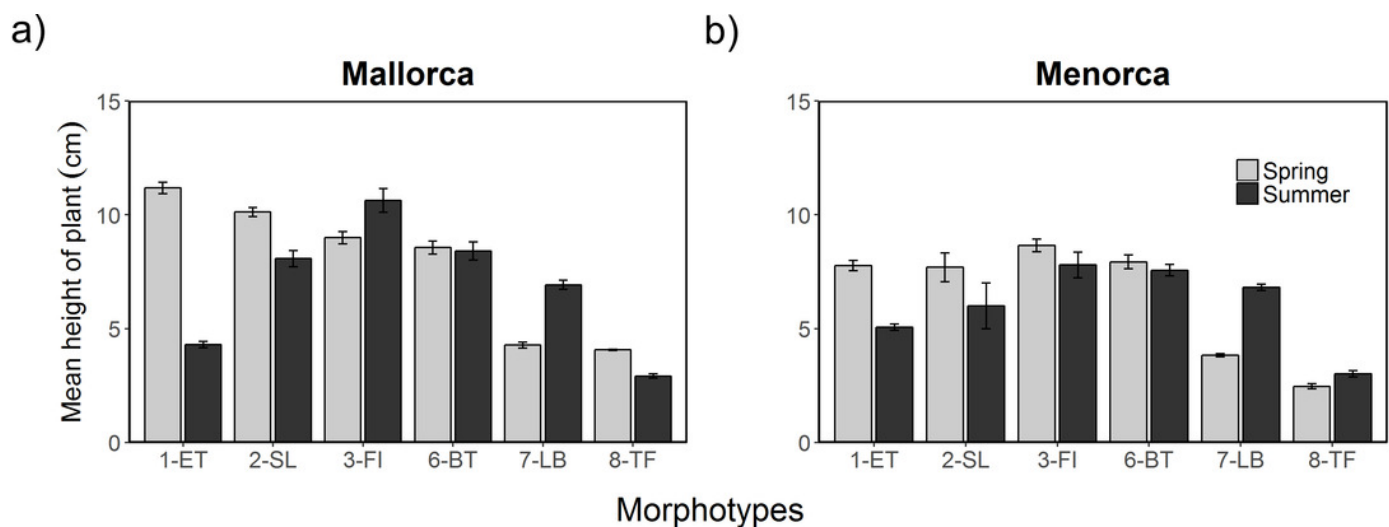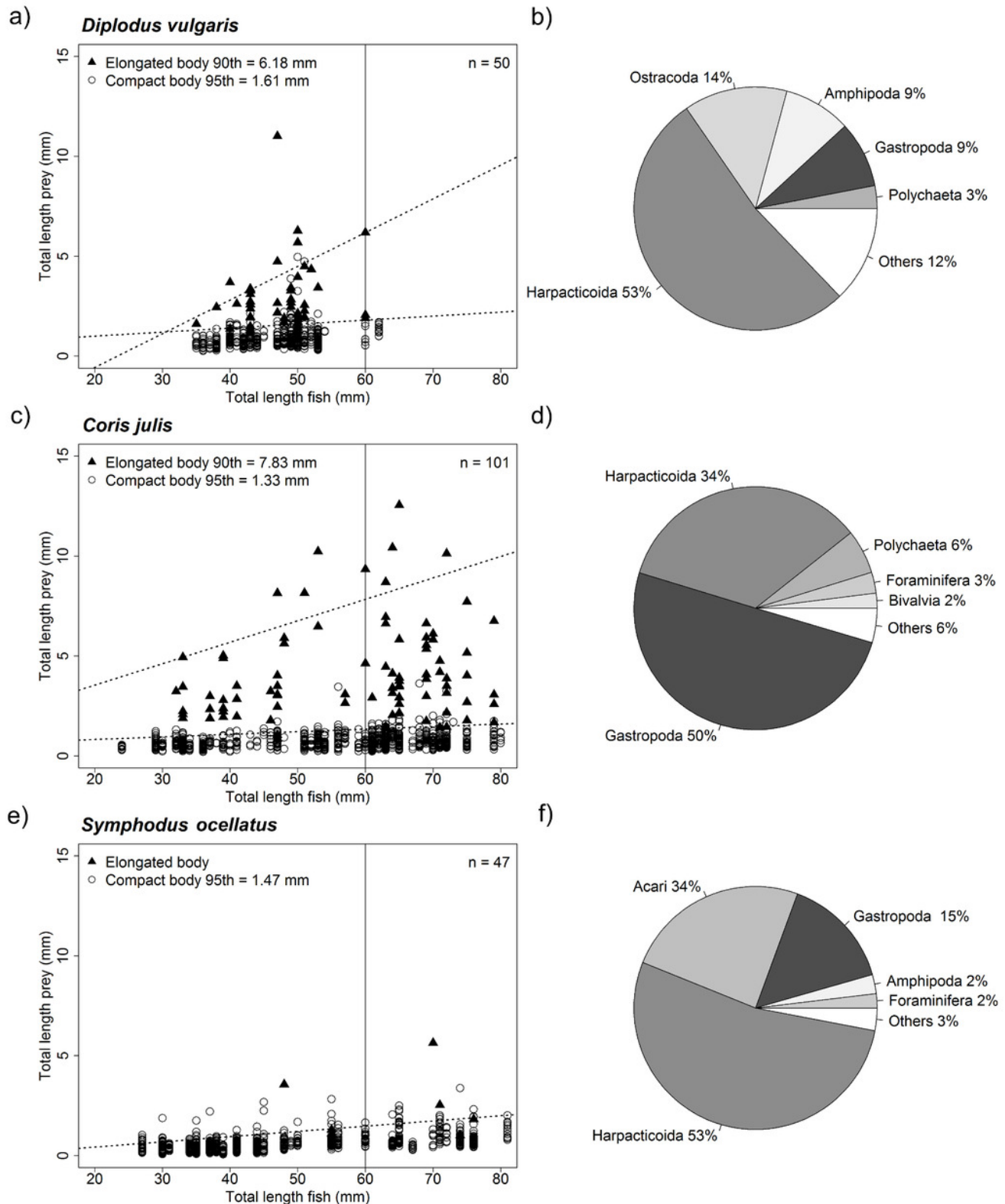
Figure 5

Relationship of fish size and prey size as well as overall taxonomic composition of prey ingested

Relationship of fish size and prey size as well as overall taxonomic composition of prey ingested. Graph (a,c and e) showing size distribution of ingested pey for different sized predators. The upper pey size limit for fish of up to 60mm was determined by quantile regression for both elongated body prey (i.e. Polychaetes, Diptera larvae, Caprellidea and Tanaidacea) and compact body prey. Only significant upper quantiles were considered starting from the 95th quantile moving down in steps of 5 points. The first significant upper quantile was considered the upper limit. Due the rare occurrence of elongated prey in *Symphodus ocellatus* stomachs no specific upper boundary could be established for elongated prey for this species. Size limits of prey for fish below 60mm total length for both prey body shapes are given in the graphs (intersect of upper quantile regression with 60mm vertical line), as well as the number of fish analyzed (n). Pie charts (b, d and f) showing the proportional contribution of taxa found in fish stomachs analyzed. The five most dominant taxa are shown, all other taxa were pooled under the category others.
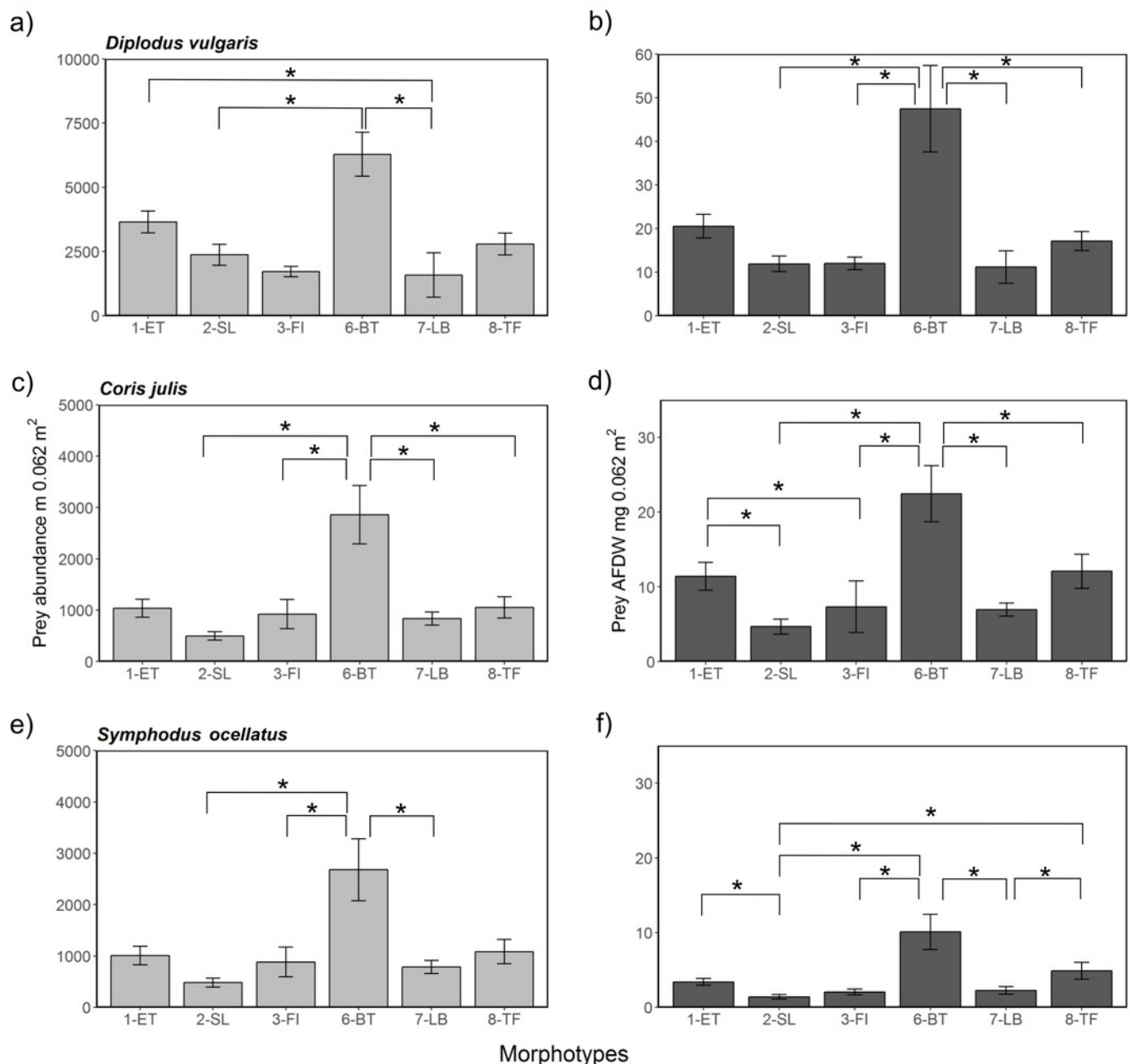
Figure 6

Prey availability in different algae morphotypes

Figure 6. Prey availability with respect to abundance (A,C,E) and biomass as AFDW (B, D, F) per 0.067 m^2 within different algae morphotypes. Significant ($p<0.05$) pairwise comparisons of from the post-hoc analysis are marked with a bracket and an asterisk.

Figure 7

Density of *S. ocellatus* with algae cover of FI+SL

Results of the generalized mixed variable intercept model. Relationship shown signify significant relationship of juvenile fish density of *S. ocellatus* and algae cover of the analysis presented in table 3. Solid line represents predicted juvenile abundances of the GLMM model and dashed lines the 95% C.I.. Data points represent individual transects
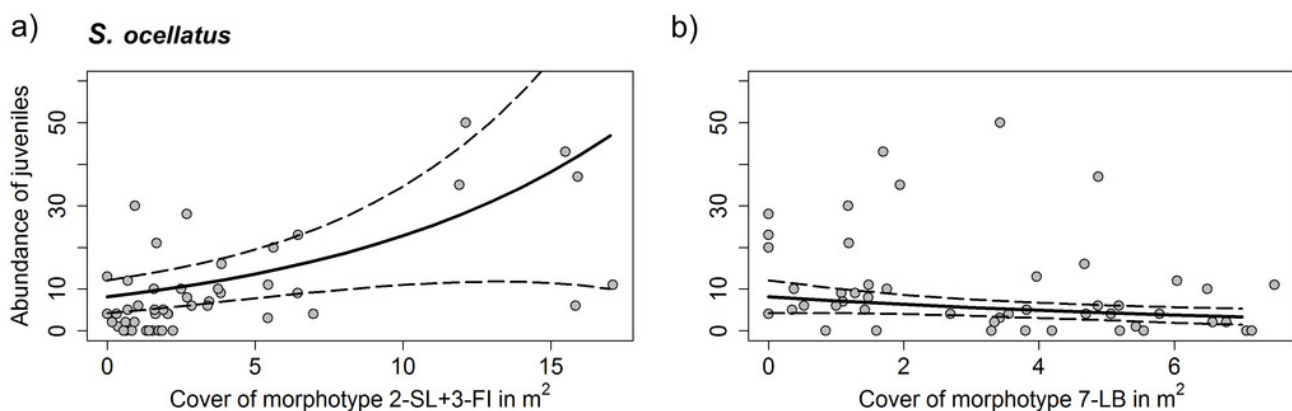
Table 1(on next page)

Morphotype cover during spring and summer in Mallorca and Menorca

Percentage occurence of algae in dive transects and mean algae morphotype cover (m^2) in Mallorca and Menorca during spring and summer sampling. Arrows indicate average increases or decreases in algae cover between sampling seasons at respective Islands.

1

	Mallorca						Menorca						
Season	**Spring**				**Summer**		**Spring**				**Summer**		
Morphotypes	% occ. T.	Mean	S.D.		% occ. T.	Mean	S.D.	% occ. T.	Mean	S.D.		% occ. T.	Mean	S.D.
1-ET	89.6	5.8	5.1	>	79.2	3.0	3.7	64.6	5.6	6.0	>	60.4	4.0	4.1
2-SL	100.0	4.1	2.6	>	18.8	2.6	2.6	2.1	0.2	0.8	>	87.5	0.1	0.8
3-FI	95.8	3.5	2.1	>	83.3	1.9	2.9	35.4	3.5	3.3	>	56.3	0.6	1.1
4-TU	56.3	1.5	2.8	>	12.5	0.4	1.4	6.3	0.0	0.1	>	16.7	0.1	0.6
5-PL	45.8	0.5	1.0	>	14.6	0.0	0.0	0.0	0.1	0.2	>	0.0	0.0	0.0
6-BT	85.4	1.7	1.6	>	66.7	0.4	1.2	64.6	1.9	2.6	<	27.1	2.4	3.3
7-LB	95.8	2.7	1.8	<	97.9	4.0	2.7	100.0	6.8	4.0	<	91.7	12.2	5.1
8-TF	100.0	6.8	3.5	>	100.0	9.4	4.0	72.9	9.9	4.5	>	100.0	3.2	3.8
Barens	37.5	0.5	1.0	<	33.3	5.6	3.5	97.9	0.7	2.2	<	91.7	5.8	3.7

2

Table 2(on next page)

Number and sizes of juvenile fish observed during spring and summer in Mallorca and Menorca

Summary table of the total number of fish observed in visual censuses and their sizes in mm measured from a capture subsample (see method section). The table also includes the number of other Sympodus species encountered and the number of adults observed over transects by sampling season and island.

1

		Spring		Summer	
		Mallorca	**Menorca**	**Mallorca**	**Menorca**
D. vulagris	No. of juveniles	**35**	**4**	-	-
	Size of juveniles in mm (caught)	43.8 (3.8) n=105	46.1(5.7) n=46		
	No. of adults	188	168	508	229
C. julis	No. of juveniles	-	**-**	**181**	**245**
	Size of juveniles in mm (caught)			48.7 (5.2) n=19	32.7 (10.3) n=168
	No. of adults	314	373	743	528
S. ocellatus	No. of juveniles	-	-	**486**	**63**
	Size of juveniles in mm (caught)			28.1 (14.6) n=371	33.3 (9.7) n=51
	No. of adults	220	90	186	34
	No juveniles other *S. spp.*			**48**	**20**

Table 3(on next page)

Relationship of *S. occelatus juvenile density with algae morphotypes*

Summary table of the total number of fish observed in visual censuses and their sizes in mm measured from a capture subsample (see method section). The table also includes the number of other Sympodus species encountered and the number of adults observed over transects by sampling season and island.

GLMM						
Species	Conditional model:	Estimate	Std.Error	z-value	p-value	
S. ocellatus	(Intercept)	2.10	0.28	7.37	0.0000	***
	2-SL + 3-FI	0.12	0.03	3.72	0.0002	***
	7-LB	-0.15	0.06	-2.38	0.0172	*

1