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Fish nursery value of algae habitats in temperate coastal reefs

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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.
The fish nursery value of algae habitats in temperate coastal reefs

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Abstract

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 fulfill 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.

Introduction

The provision and value of nursery habitats by the coastal zone is one of the most frequently mentioned and recognized ecosystem services in the valuation of coastal marine ecosystems (Duarte, 2000; Jackson et al., 2001, 2015). As many coastal habitats are under increasing human pressures from urbanisation, fishing, climatic change and the introduction of alien species (Sala et al., 2011, 2012, Vergès et al., 2014a,b), the provisioning of this ecosystem service is progressively also under threat. While the large-
scale importance of nursery habitats for ecosystem functioning, food production and integrity of 
ecosystems is recognized, a detailed understanding over which habitat types constitute to this function is 
still lacking (Beck et al., 2001). Seagrass meadows and estuarine systems have been the focus of marine 
nursery habitat research (e.g. Heck et al., 2003; Seitz et al., 2013; Woodland et al., 2012; Ruiz-Frau et al., 
2017), while studies that focus on littoral rocky reef systems appear less frequently in the literature (but 
see Cheminée et al., 2017; Guidetti, 2000; Harmelin-Vivien et al., 1995). Although spatially less 
extensive compared to seagrass meadows, littoral rocky reef systems harbour a wide variety of different 
algae species, providing shelter and food, in the form of associated fauna, to juvenile fish (Harmelin- 
Vivien, Harmelin & Leboulleux, 1995; Cheminée et al., 2013; Félix-Hackradt et al., 2014).

In the Mediterranean, littoral rocky reef habitats are used by a variety of commercial and non-commercial 
species that utilise these habitats for part, or during their entire life cycle (Harmelin-Vivien, Harmelin & 
Leboulleux, 1995; Guidetti, 2000; La Mesa et al., 2011; Félix-Hackradt et al., 2014; Cheminée et al., 
2017). In general, coastal species with smaller body sizes, such as many Labridae, Blenniidae and 
Gobiidae, complete their entire life cycle within this habitat. Several other, larger, commercial species, 
such as various Sparid species e.g. *Pagelus spp* or *Dentex dentex*, often only use it as a nursery habitat, 
with the larger juvenile and adult life stages moving further offshore. Settlement of juvenile fishes in 
rocky littoral habitats occurs throughout the year but most species have a settlement peak between early 
spring and late summer (García-Rubies & Macpherson, 1995; Biagi, Gambaccini & Zazzetta, 1998; 
Bussotti & Guidetti, 2011). The survival of recently settled juveniles within a habitat through to their 
recruitment to the adult population depends to a large extent on the environmental conditions encountered 
at the site of settlement (Beck et al., 2001). Intolerance to physical extremes, starvation and predation are 
among the broad, major causes of juvenile mortality in these habitats (Sogard, 1997; Guidetti, 2001; 
Thierret et al., 2016; Cuadros et al., 2018). High nursery value is thus conferred through a combination of 
factors that provide adequate physical conditions, refuge space and a sufficient food supply. Highly 
structured habitats are thought to provide both, shelter and an abundance of food, that may facilitate 
juvenile survival and growth processes and thus contribute to overall production and population stability 
(Cheiminée et al., 2016; Dahlgren and Eggleston, 2014; Leslie et al., 2017; Parsons et al., 2015; Scharf et 
al., 2006). Although the importance of habitat complexity is well documented, it should be noted that it is 
likely to be context dependent related to spatial scale and species-specific habitat requirements. For 
example, highly complex habitats have been reported to negatively affect juvenile fish by reducing 
feeding efficiency (Tátrai & Herzig, 1995) and increasing mortality by harbouring ambush predators 
(Canion & Heck, 2009).
Nursery habitats harbouring large numbers of juvenile fish are important to ensure future recruitment into adult populations. They also contribute to the maintenance of essential food web links and energy transfer processes within many coastal systems (Gee, 1989; Schüeckel et al., 2013; Tito de Morais and Bodiou, 1984), consuming the associated micro-fauna (mesograzers e.g. micro crustaceans such as Harpacticoids, Isopods and Amphipods) associated with macroalgae and seagrasses (Bologna & Heck, 2002; Jaschinski & Sommer, 2008; Vázquez-Luis, Sanchez-Jerez & Bayle-Sempere, 2008). Macrophytes often have morphological or chemical deterrents that inhibit direct herbivory by larger consumers such as fish and urchins (Cruz-Rivera & Villareal, 2006). Therefore meso-grazers that can directly utilize macrophytes are thought to represent an important link in the energy transfer between macro-algae and fish (Lewis & Anderson, 2012; Duffy & Hay, 2016). Many juveniles are also, in turn, consumed by larger higher trophic level predators (Doherty & Sale, 1986; Sogard, 1997), thus representing the intermediate stage of energy transfer from primary producers to higher trophic level fish.

Perennial algae species belonging to the genus *Cystoseira* (Fucales, Phaeophyceae) are thought to represent habitats of high quality for juvenile coastal fish in the Mediterranean (Ruitton, Francour & Boudouresque, 2000; Sala et al., 2012; Cheminée et al., 2013). *Cystoseira* are macrophytes with a tree-like morphology that can form dense meadows over rocky substrates, aggregations of which are often referred to as *Cystoseira* forests. This habitat generally shows high primary productivity, is morphologically highly complex and harbours a diverse invertebrate and fish fauna. Therefore, *Cystoseira* forests, in addition to the seagrasses, have been recognised as a central foundation species (as defined by Dayton, 1972) of the euphotic zone in the Mediterranean (Irving et al., 2009; Vergés, Alcoverro & Ballesteros, 2009). Past declines of subtidal *Cystoseira* forests (Thibaut et al., 2005; Sala et al., 2012) may have had a negative effect on the fish nursery value of coastal rocky reef habitats in many regions of the Mediterranean. Nevertheless, the role and importance of other macroalgae-dominated habitats for juvenile fish has not been fully explored and these could also provide adequate shelter and food for juvenile fish production. Thus far the services or functions that littoral macroalgae may provide to juvenile fish, i.e. shelter and food, have only been suggested and only partially tested and quantified scientifically (Sala & Ballesteros, 1997; Ruitton, Francour & Boudouresque, 2000; Cheminée et al., 2013). Thus, overall, we know little about the real habitat value of the littoral macroalgae and the consequences their loss has on the functioning of coastal ecosystem as fish nursery habitats. Furthermore, we are still unaware if there may be other macro-algae habitats, equivalent to *Cystoseira* forests, that may provide a similar function and compensate for their loss. Such knowledge will be of importance for the development of management and conservation strategies against the backdrop of the currently observed acute environmental change experienced in coastal rocky shores in the Mediterranean, due to chronic pollution, urbanisation, fishing and the introduction of non-native macro-algae species (Sala et al., 2012).
and herbivorous fish (Sala et al., 2011; Vergés et al., 2014a) that have the potential to rapidly modify coastal habitats.

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

**Methods**

**Fish study species**

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

The settlement period of the two wrasse species have been reported to occur during late summer between July to August (Garcia-Rubies & Macpherson, 1995; Biagi, Gambaccini & Zazzetta, 1998; Bussotti & Guidetti, 2011) while Raventos et al. (2005) reports settlement of *S. ocellatus* slightly early during June.
until mid-July. Within the present study the presence of recently settled juveniles was observed at the end of August by the authors. The two species of wrasse have been reported to settle predominantly in rocky habitats with high algal cover (García-Rubies & Macpherson, 1995; Biagi, Gambaccini & Zazzetta, 1998; Bussotti & Guidetti, 2011, Félix-Hackradt et al., 2014). Juveniles of *D. vulgaris* have been reported to feed predominantly on micro-crustaceans (Altin et al., 2015). Adults of the ocellated wrasse feed predominantly on small crustaceans and molluscs with a suspected tendency towards herbivory (Kabasakal, 2001) and adults of rainbow wrasse feed on gastropods, sea urchins and small crustaceans (Sinopoli, Chemello & Vaccaro, 2016). Presently there is no information on the diet of the juvenile stages of these two wrasse species.

**Study area and sampling design**

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

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

**Fish and habitat census**

At each sampling station the fish community and the habitat were assessed by diver underwater visual census. The fish assemblage was assessed in 6 replicates of 15 x 2m transects with a horizontal gap between each of at least 20m. All fish sighted along the transect were recorded and their size was estimated to the nearest cm (Harmelin-Vivien et al., 1985). Benthic composition along the transects was
characterized using the following categories: sand, pebbles and gravel, seagrass and rock. The habitat complexity of the substrate was also assessed, using a five-point scale index for rugosity, presence of different sized boulders and amount of refuge spaces (see S1 for field sampling protocol).

The second diver measured algae cover, composition and height in three haphazardly placed 50 x 50cm quadrats along the transect. Quadrats were further subdivided into 25, 10 x10 cm squares using nylon string. These sub-squares were used to estimate the % cover of 8 algae morphotypes (Figure 2) and unvegetated barren patches. If a morphotype occurred in a sub-square, the square was counted. For each morphotype the total number of squares it occurred in was recorded as well as their average height in cm form the rock surface. Algae morphotype cover in m² within transects was calculated by taking the m² recoded for rocky reef habitats overgrown by algae (as opposed to being occupied by sand or pebble substratum) and divide this area proportionally according to the % cover of each morphotype obtained by the quadrate samples. The following algae morphotypes represented by various related species that are commonly encountered in the rocky littoral zone were used (Figure 2): erect tree like 1-ET (Cystoseira spp.), soft leaf like 2-SL (Dictyopteris polypoides and Dictyota spp.), filamentous 3-FI (Dictyota dichotoma var. intricate, Dictyota spp. and occasional Hincksia spp.), tubular 4-TU (Cladostephus spongiosus), plumose 5-PL (Asparagopsis spp.), bulbous tree like 6-BT (Halopteris spp.), leathery bands 7-LB (Padina pavonica), turf forming 8-TF (dominated by Corallinaceae such as Haliption vigatum). For data from dive transect see S2.

**Sampling of algae associated fauna and prey communities**

To determine prey availability for juvenile fish, the associated fauna of dominant macroalgae was sampled for each station. At each site, the three most dominant algae types were sampled by collecting 6 x 113 cm² samples. A circular tube of 5 cm height and 11.5 cm diameter was used to define the surface area for algae cuttings (0.01 m²). A 0.55 µm meshed sampling bag was draped over the piece of tube to collect algae cuttings and to retain associated fauna. The samples were transferred to plastic bags and stored frozen. Once defrosted, the samples were pooled and rinsed into a receptacle using fresh water. The algae were blotted dry with kitchen paper and the wet weight recorded from each station. The water from the receptacle was passed through a 300 µm mesh sieve and any retained fauna was processed. All large fauna (>5mm) were preserved in 70% ethanol. Using a Folsom plankton sample splitter, the remaining, depending on its overall volume, was split up to 4 times. The final split fraction of the sample was re-sieved over a 300 µm mesh and preserved in 70% ethanol. The number of sample splits was recorded for each faunal sample to later enable calculation of faunal abundance and biomass of the whole sample.
All fauna retained from the samples was sorted into large taxonomic groups (see S3 for full list of groups). A photograph was taken of each taxonomic group using a standard digital camera (Canon powershot G7) for the large fraction and a Leica stereo microscope (MZ16) with a digital camera (EC3) for the small fraction. The photograph served to measure the size of the organisms and to quantify their abundance. Image analysis software, ImageJ (Rueden et al., 2017), was used to measure the size of all organisms using the polyline measurement tool. The pixel length of each measurement line was converted to µm using values attained from calibration images. Length measurements were furthermore converted to biomass using published length weight relationships of respective taxonomic groups (see S3 and S4 for more details on the size-mass conversion and S5 for data on associated invertebrate fauna size measurements).

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

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

The abundance and biomass of prey within a transect was estimated using the area cover (m²) by different algae morphotypes multiplied abundances and biomass of prey items found (per m²) within these from
algae cuttings (see above). Organisms were only considered prey if they were of the relevant taxa and sizes as identified by the stomach content analysis described above.

Sampling of juvenile fish

Using hand-held nets, a sample of approx. 30 juvenile fish of each of the study species were collected from each of the 32 sampling stations (see S7 for fish size data). In addition to the stomach content analysis, the fish sample was used to evaluate the size distribution of juvenile fish.

Wave exposure data

As juvenile fish may experience higher dispersal from habitats with high wave action, and algae may be influenced by physical wave stress, wave exposure was considered in the study (Spatharis et al., 2011). Wave stress data for each station was calculated from a dynamical coastal wave model provided by the Coastal Ocean Observing and Forecasting System located in the Balearic Islands (SOCIB) using past real weather events. The mean wave exposure as well as the wave exposure of the 4 months prior to sampling was used as an environmental parameter in the analysis of data.

Statistical analysis

Algae community analysis over temporal and spatial scales

Algae morphotype cover composition was analyzed using a Principal Component Analysis (PCA) based on Euclidian distance. The resulting ordination was explored through investigating the correlation of algae morphotypes with the two first Principle Component (PC) axes. Furthermore, the loading of each variable was superimposed as arrows over the ordination. The length of the arrow corresponds to the strength of influence on the ordination while its orientation provides information on the direction of influence. ANOSIM pairwise comparisons were used to test for significant differences in algae cover composition between the transects sampled between different seasons and islands. Distance based linear models (DistLM) were used to investigate the environmental variables that best explained the observed ordination patterns in algae composition. The following five environmental variables were used: Mean depth, Slope, rugosity, Temperature, herbivore (density of Salpa salpa and urchins), along with the modelled wave stress for each site. All multivariate analyses were conducted with the Software Package Primer-E version 6 (Clarke & Gorley, 2006).

The height of different algae morphotypes was compared on an island scale using a two-way ANOVA with morphotype and season as main factors. A Post-hoc Tukey-test was used to identify height differences between morphotypes within seasons and the height of the same morphotype between
seasons. Height data was log-transformed prior to analysis to meet model assumptions regarding normality and homogeneity of variance.

Potential prey availability in different algae morphotypes for juvenile fish

Potential prey availability was calculated considering prey sizes, taxonomic groups and the season relevant to the juveniles of the respective fish species (<60 mm). Potential prey availability was compared between morphotypes using a one-way ANOVA and post-hoc Tukey pairwise comparison tests. The data of both islands were pooled to compare all algae morphotypes as for some algae morphotypes insufficient specimens were sampled to be able to consider both islands separately in the analysis. Potential prey density was log-transformed prior to analysis to meet model assumptions regarding normality and homogeneity of variance.

Relationship between different algae morphotypes and juvenile fish abundances.

The relationship between juvenile fish abundance and algae morphotype cover (m²), as well as total prey biomass per transect, was modeled using a Generalized Linear Mixed Model (GLMM) with a negative binomial error distribution and a log-link function. Within the model the station was considered a random factor to address the dependency structure of dive transect from the same station. The cover by morphotypes, as well as total prey biomass per transect, were considered as fixed factors. All variables introduced to the model were correlated prior to analysis to identify any collinear variables to be removed or pooled prior to modelling. Model selection procedures were adopted whereby non-significant variables were removed until only significant variables were contained in the final model, using the drop-one procedures in R. Models were checked for over dispersion and the residuals were visually examined (Zuur, A.F. et al., 2009; Zuur, Ieno & Elphick, 2010).

Results

Algae morphotype composition and height across sampling seasons and islands

Algae morphotype composition within sampling areas and season were compared by PCA ordination of the dive transects sampled. The PCA explained 60.5% of the variability of the algae cover data (Figure 3, Table S8). The ANOSIM pairwise comparisons analysis verified that there were significant differences in composition of morphotypes between all island and season combinations (p< 0.001, Figure 3). The largest differences were found between transects surveyed in summer in Menorca and all other island-season combinations (see Figure 3 and Table S8). Algae cover was most similar between spring and summer in Mallorca (see Figure 3). Transects sampled in spring in Menorca were similar to those sampled in Mallorca (see overlap of PCA space Figure 3 and lower summed Euclidian squared distance Table S9).
Overall, seasonal changes in algae cover for both islands were similar for most morphotypes (Table 1). In both islands the average transects cover of 1-ET (*Cystoseira spp.*) were lower in summer compared to spring as was the cover of 2-SL and 3-FI (*Dictyota spp.* and similar). In contrast, the cover of 7-LB (*Padina pavonia*) was higher in both islands during summer as did the occurrence of barren patches (no vegetation over rock) (Table 1). However, the magnitude of seasonal change was more pronounced in Menorca. Furthermore, transects surveyed in summer were significantly different to those sampled in Mallorca (Figure 3 and table S9) with higher cover in morphotype 7-LB (*Padina pavonia*) and lower turf forming morphotypes 8-TF (Corallinaceae) compared to Mallorca (Figure 3 and Table 1). Morphotypes 2-SL and 3-FI (*Dictyota spp.* and similar) formed part of many transects in Mallorca in late summer, while these morphotypes were almost absent from transects in Menorca (Figure 1 and Table 1).

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

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

*Taxonomic composition and size of prey items found in juvenile fish stomachs*
Stomach samples of the three-study species showed that. All three species shared many prey taxa (see Figure 5). *Diplodus vulgaris* and *Symphodus occelatus* diets were dominated by harpacticoids (both 53%) while stomachs of *Coris julis* predominantly by gastropods (50%) and to a lesser extent by Harpacticoids (34%). *Diplodus vulgaris* stomach samples were furthermore dominated by Ostracods (14%), Amphipods (9%) and Gastropods (9%) while *Symphodus occelatus* also contained sea mites (Acari 34%) and Gastropods (15%).

For all species significant upper quantiles (p<0.05) were found determining the upper limit of prey sizes that were consumed at a certain size (Figure 5). Comparing the upper limit of prey sizes consumed with increasing size of fish showed that fish below 60 mm, the chosen cutoff point to determine the upper limit for juvenile prey size, of the three-study species consumed very similar size prey when considering compact body prey such as Harpacticoids or Amphipods. In general prey sizes were between 1.33- 1.61 mm. Both *Diplodus vulgaris* and *Coris julis* consumed elongated prey consisting mainly of Polychaetes reflected in the % contribution to the diet, 3% and 6% respectively (Figure 5). Other elongated taxa such, *Diptera* larvae, *Caprellidea* and *Tanaidacea* contributed less to this prey category. Stomachs of *Symphodus occelatus* also had too few elongated prey items to perform an upper quantile regression analysis. The size of elongated prey found in *Coris julis* were slightly larger for fish at a size of 60mm compared to *Diplodus vulgaris*. The size elongated taxa consumed was below 6.18mm and 7.83mm respectively (see Figure 5). Overall the stomach content reflected well the dominant taxa found in the different algae morphotypes (S13)

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

Comparing potential prey abundance and biomass by algae morphotype using one-way ANOVA analysis showed that there were significant differences considering the three-study species (S14 and Figure 6). Post-hoc Tukey tests showed that in general 1-ET, 6-BT held significantly higher prey densities and biomass compared to other algae morphotypes (S15 and Figure 6). In general, the highest prey densities or biomasses in absolute terms were irrespective of season and fish species found in the three structurally complex algae’s 1-ET, 6-BT and 8-TF compared to the more structurally simple algae such as 2-SL, 3-FI and 7-LB. The general pattern between islands and seasons observed in prey abundances and biomass were reflective of patterns when considering all associated fauna (S16). Note that overall abundances and biomass of associated fauna were considerable higher within all algae morphotypes in spring compared to summer (S16).

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

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

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

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

**Discussion**

High quality habitats for juvenile coastal fish have generally been characterized by both, high sheltering opportunities and food for the resident juvenile fish (Cheminée et al., 2013, 2017). In our study, we however observed that recently settled juveniles in summer appear to occur at a suboptimal time. Our results showed strong seasonal variations in algae cover between sampling seasons. Algae morphotype cover and height had changed considerably on both islands between the two sampling events that coincided with the two major settlement peaks of juvenile fish documented for the Mediterranean (García-Rubies & Macpherson, 1995; Biagi, Gambaccini & Zazzetta, 1998; Bussotti & Guidetti, 2011).

During the settlement period of *Diplodus vulgaris* the extent and height of the forest forming algae *Cystoseira* spp. was considerably greater compared to the summer period in which *Symphodus ocellatus* and *Coris julis* settled. Similarly, most other algae decreased in cover and to some extend in height except
for *Padina pavonica*, which increased both in cover and height during this period. Concurrent with these cessation patterns of algae, the associated fauna was also found to undergo a sharp seasonal decline in abundance and biomass, from spring to summer. However, this was not restricted to algae that decreased in height but was a consistent pattern which was also found to affect algae that increased in height, such as *Padina pavonica*. Thus, when comparing overall prey availability per unit area between fish species, there were considerably more prey available in algae during the spring period during *Diplodus vulgaris* settlement, compared to prey available for the other species during the late summer period. These seasonal patterns between algae and associated fauna have also been demonstrated by other authors (e.g. Guerra-García et al., 2011). An apparent mismatch exists between the period of high shelter and food provision by habitats and the settlement and growth period of juvenile fish. Summer settlement of juveniles results from spawning during early spring and the mismatch may be caused by evolutionary processes favoring the match of earlier larvae stages with planktonic production processes, ensuring higher larval survival. Certainly, for *Coris julis* there appear to be strong links between primary production processes and the amount of larval settlement (Fontes et al., 2016), which may also apply to other fish species with summer settlement peaks in the Mediterranean. This mismatch therefore does not suggest that shelter and food are not important for juveniles, but that they do not appear to have a strong selective influence on the timing of spawning. The decrease of shelter and food provisioning from spring to summer shows that coastal habitats and the services they provide for juveniles are not a constant and that they can undergo notable changes in a relatively short amount of time. With this in mind, it is plausible that climate change may further increase the mismatch between algae habitat provisioning properties and summer settlers, if higher temperatures increase the speed of seasonal cycles causing earlier cessation in algae communities. Little is currently known about the influence of climate change on the timing of seasonality in macro-algae, several studies argue that warming can affect the phenology and reproduction of macroalgae (Kraufvelin et al., 2012; Andrews, Bennett & Wernberg, 2014), thus suggesting that early cessation processes could be triggered by seasonally early or extreme warming events. For example, in the Baltic, increased seawater temperature and light during early springs accelerate receptacle growth of *Fucus vesiculosus*, causing earlier reproduction (Kraufvelin et al., 2012). As cessation processes generally follow reproduction in many macro-algae species (Liu et al., 2017) climate change has the potential to shorten macro-algae cycles potentially causing a mismatch between the provision of shelter and food for juvenile fish (Durant et al., 2007). Both the timing of spawning and the rate of larvae and juvenile development may however also be affected by temperature (Pankhurst & Munday, 2011). Therefore, it is also conceivable that both juvenile fish and habitat may be affected synchronously. The precise effect of temperature on reproduction and larvae development of fish is however complex and highly species specific. Thus, for example warming may advance or delay the maturation and ovation depending on
species specific thermal endocrine triggers (Pankhurst & Munday, 2011). Climate induced mismatches between fish and their food resources have been reported for pelagic fish illustrating that climate warming may not affect larval development and prey production equally (Gröger, Hinrichsen & Polte, 2014; Illing et al., 2018). Whether the match/mismatch hypothesis, i.e. the synchronized/desynchronized timing of seasonal activities, as described by Cushing (1969, 2019), is important with respect to algae habitats provisions for juvenile fish is currently unknown and requires further scientific attention.

When considering the potential prey availability in different macro-algae morphotypes, we found that structurally more complex algae contained more prey, in particular algae such as Halopteris spp. and Cystoserica spp., but also turf forming Corallinaceae such as Halioption vigatum, that have a complex internal structure. In contrast, Dictyotales, with flat leafs or filamentous algal species contained fewer prey. This pattern of distribution of prey amongst algae was persistent during both settlement periods. Whether algae containing higher prey biomasses also provide higher quality habitats is unclear. The term potential prey availability was used throughout as we did not examine whether this prey was readily available to the juvenile fish. It is possible that, due to the complex structure of some algae, feeding efficiency of juveniles may be decreased or less optimal (Tátrai & Herzig, 1995). Thus, the higher amounts of associated invertebrate fauna in morphologically complex algae could reflect reduced predation by fish. Equally, lower biomass of potential prey within less complex algae morphotypes could be the result of increased feeding on less protected and thus easier to feed upon prey. As a result, it is possible that juveniles are responsible for structuring the associated algal fauna. Further research into juvenile feeding behavior will be required to explain observed prey distributions among algae morphotypes.

Within our study, no tangible indication appeared within the data that juvenile fish densities are strongly linked to prey densities. For example, Symphodus ocellatus, was associated to algae with the least prey and thus, prey availability may not be a central factor in determining juvenile fish densities. It is likely that food availability is of secondary importance to fish abundance, but it may, nevertheless, affect juvenile body condition and growth rate and thus, their long term-survival (Lloret et al., 2002, 2012). To assess and compare nursery qualities of habitats and move away from using solely abundance estimates for habitat suitability, these parameters should be considered by future studies.

Analyzing the association of juvenile fish abundance and algae morphotype cover, we discovered that, while for Coris julis there was no clear association to any particular algae morphotype, Symphodus ocellatus had a positive association with Dictyotales and a negative association with Padina pavonica. No analyses were carried out for Diplodus vulgaris, as too few individuals were observed within transects. The absence of a clear relationship of C. julis with algae morphotype appears consistent with findings by...
Cheminée et al. (2017) who reported an association of this species with sparser algae cover. However, we did not found a clear relationship between the abundance of *S. ocellatus* and *Cystoseria* contrary to the patterns observed by other studies (e.g. Cheminée et al., 2013, 2017; Thiriet et al., 2016). These studies stress the importance of *Cystoseira* forests as a prime juvenile habitat for *Symphodus* spp., due to their structure. These discrepancies could be due to different factors such as: i) the different UVC methodology used in the different studies (15*2 m transects this study, 1 m² point-count Cheminée et al., 2013, 2017 and 9-m² stationary-point snapshot count Thiriet et al., 2016), which can have an effect on the total amount of fish counted; ii) different geographical and temporal settlement peaks of local populations, which can produce a mismatch between the time of the study and the time of the settlement in each study area and year of sampling (Cheminée et al., 2017 sampled slightly earlier in July-August as opposed to August-September as in this study); iii) seasonal and annual differences in the development of height and cover of *Cystoserira* between the mentioned studies caused by the delay or advance in their development.

Within our study *Dictyotales* provided considerably higher cover, compared to *Cystoseira*, and may have therefore been more important in providing shelter to *Symphodus* spp. The low numbers of individuals of this species in Menorca were not only restricted to juveniles but also fewer adults were observed, possibly indicating that habitats surveyed in this island were altogether less suitable for this species. Apart from potentially having provided better sheltering opportunities, *Dictyotales* were observed to be an important nest building material for male *Symphodus ocellatus*, during spring in Mallorca. Many labridae species build nests in which the male protects and broods the fertilized eggs (Raventós, 2006). Thus, it is possible that the higher abundances of juveniles observed in *Dictyoctales* dominated habitats may be related to a higher number or quality of nests, subsequently providing a locally larger numbers of settlers in summer. However, a study on the related species *Symphodus roissali* found no significant relationship between the indirect measure of successful nests (larval output) and the number of recruits within a three year period (Raventos, 2009). It remains unclear if the shelter, or better nesting conditions, are responsible for higher abundances of *Symphodus ocellatus* in *Dictyotales*.

Overall, more effort needs to be made to study the behavioral relationship and interaction of fish with their habitats. This and other studies focused on measuring the percentage cover of algae for shelter and food provisioning. Shelter, however, may be used in different configurations. For example, fish may use banks/patches of algae to hide from predators behind or hide within the algae matrix. Hiding behind would require high cover but in a fragmented format, with open spaces, whereas hiding within would require a more continuous cover. Within our study, while catching juvenile fish, we observed that *Symphodus ocellatus* hid within the algae matrix, while *Diplodus vulgaris* avoided entering any algae or *Posidonia* patches but instead used these as a parkour of obstacles to outpace and loose human pursuers. In the case of *Diplodus vulgaris*, a continuous dense algae forest cover, may due to this behavior, not
represent an ideal habitat. This type of behavioral shelter use may explain why no trends were observed for this species and shows that future study also needs to consider the spatial configuration of cover depending on the behavioral needs of a species.

**Conclusion and recommendations for future studies**

The results of this study show that in many ways we still have a relatively rudimentary understanding of what represents a good nursery habitat for juvenile fish. Algae species such as *Cystoseira* that appear to have high importance in one area and season for a specific species may not necessarily have the same importance in another area or season. This may be due to the context dependent nature of juvenile occurrence and the habitat composition at the time of the study. The results suggest that fish can adapt to local situations and use algae morphotypes/species that offer the required function at the time. While at the time of our study we detected an association of *S. ocellatus* juveniles (3-4cm) with *Dictyotales* these results do not implicate that *Cystoseira* habitats are not important for juvenile fish. Settlers that arrived in July-early August may well have used *Cystoseira* to shelter within the first two month of their lives. Equally likely, those new settlers of other species arriving in the area during the spring, when the *Cystoseira* forest are better developed with higher cover and canopy height may have a preference for this algae than others. While providing new insights, the present study is not able to evaluate the importance of *Cystoseira* habitats as a nursery habitat with certainty and as such the effect of the continuing loss of this habitat. Considerably more focused research will be required to address this question.

Abundance of juvenile fish may vary considerably in time, at any one location, due to natural stochastic processes, causing a high degree of variability. Scenarios are imaginable in which, due to a strong settlement pulse and fishery-depleted predators, there are many juveniles in a habitat. However, because of the lack of food provided by the habitat fish may have low long-term survival potential (e.g. Macpherson et al. 1997; Planes et al. 1998; Cuadros et al., 2018). Using abundance indices alone as a tool to assess habitat quality has limitations as these do not consider the effect of different habitat conditions on the individual fish i.e. how a habitat affects parameters such e.g. growth and survival potential. Thus, when combined with abundance estimates, methodologies that assess fish condition, growth performance and health status may provide a more accurate picture of the prevailing conditions for fish living at a certain location. Habitat quality for juveniles should not be measured on the level of “settlement success” alone i.e. the maximum number of recently settled individuals, which may be largely a function of stochastic hydrodynamic processes (Beck et al. 2001). A better measure of habitat quality would be to estimate the survival rate of newly settled fish to reach a certain arbitrary size in good condition. However, measuring this type of “recruitment success” would be time consuming and financially costly as it would require intensive temporal sampling of juveniles from their settlement phase to their
recruitment to the adult population. To increase our understanding of what constitutes high quality nursery habitats it is important to have workable and cost-effective sampling solutions. Therefore, future studies should aim to incorporate methods and develop indicators that link both abundance estimates and population fitness parameters of juvenile fish at an agreed, predefined size range (by species) to evaluate habitat quality.

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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.
Algae morphotype

Algae morphotypes surveyed along dive transects corresponded to different species complexes with similar morphology: (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).

a) Mallorca

b) Menorca

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 m² quadrats located within dive transects. Error bars are S.E.

a) Mallorca

b) Menorca
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 prey for different sized predators. The upper prey 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 to 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 m² 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 occurrence of algae in dive transects and mean algae morphotype cover (m²) in Mallorca and Menorca during spring and summer sampling. Arrows indicate average increases or decreases in algae cover between sampling seasons at respective Islands.
| Season Morphotypes | Mallorca | | | | Menorca | | | |
|---|---|---|---|---|---|---|---|---|
| | Spring | Summer | Spring | Summer | | | | |
| | % 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 |
| Baren | 37.5 | 0.5 | 1.0 | < 33.3 | 5.6 | 3.5 | 97.9 | 0.7 | 2.2 | < 91.7 | 5.8 | 3.7 |
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.
|                   | 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  *  |