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Does habitat complexity influence fish recruitment?

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Abstract

Human activities facilitate coastal habitat transformation and homogenization. The spread of marine invasive species is one example. This in turn may influence fish recruitment and the subsequent replenishment of adult assemblages. We tested habitat complexity effect on fish (Teleostei) recruitment by experimentally manipulating meadows of the habitat-forming invasive macroalga *Caulerpa taxifolia* (Chlorophyta). Among the fourteen fish species recorded during the experiment, only two labrids (*Coris julis* and *Symphodus ocellatus*) settled in abundance among these meadows. Patterns in the abundance of these juveniles suggested that reduced tri-dimensional meadow complexity may reduce habitat quality and result in altered habitat choices and / or differential mortality of juveniles, therefore reducing fish recruitment and likely the abundance of adults.

Keywords: Mediterranean, Habitat complexity, fish settlement, nursery, *Caulerpa, Coris, Symphodus*.

Introduction

Habitat complexity (i.e. the three-dimensional arrangement of structures that form habitat, *sensu* August (1983)) exerts a strong influence on species diversity, abundance (Harborne *et al.*, 2011a) and behavior (Harborne *et al.*, 2011b). Atrill *et al.* (2000) and Horinouchi & Sano (1999) described that habitats with greater complexity typically support more species and individuals. For a given species, at a given life stage, differences in complexity between two habitats may result in differences in habitat quality in terms of the tradeoff between food availability and predation risk (Dahlgren & Eggleston, 2000). This may lead to active habitat selection aiming at minimizing this tradeoff and maximizing survival, or to differential mortality between habitats (Thiriet *et al.*, 2014). Consequently, many species have very specific microhabitat requirements, which vary among species and life history stages (i.e. ontogenetic shift in habitat use) (Vigliola & Harmelin-Vivien, 2001).

As a consequence, altering habitat complexity can have cascading effects on species composition and abundance. Many shallow subtidal habitats in the Mediterranean Sea have been modified by anthropogenic impacts (Sala *et al.*, 1998; Francour *et al.*, 1999; Milazzo *et al.*, 2004; Mangialajo *et al.*, 2008; Rovere *et al.*, 2009; Coll *et al.*, 2010; Montefalcone *et al.*, 2010). These modifications include alteration of habitat complexity, by changing the composition of biotic and abiotic structural components. One Mediterranean example of such changes is the fragmentation and/or shoot density reduction of *Posidonia oceanica* (Linnaeus) Delile seagrass meadows due to repeated anchoring (Francour *et al.*, 1999; Montefalcone *et al.*, 2010); inversely, others examples illustrate the homogenization of seascapes through anthropogenic stressors. For example, beach artificial nourishment is known to homogenize the mixed heterogeneous bottoms of pebbles, boulders and rocks, therefore reducing their habitat quality for Sparidae fish juveniles (Cheminée *et al.*, 2014). Among macrophytes, seascape homogenization has been as well reported through the introduction and dominance of invasive habitat-forming species, such as *Caulerpa taxifolia* (Vahl) C. Agardh and *C. cylindracea* Sonder, two benthic macroalgae (Chlorophyta) that have been introduced into the Mediterranean (Levi & Francour, 2004; Longepierre *et al.*, 2005; Klein & Verlaque, 2008; Francour *et al.*, 2009; Molenaar *et al.*, 2009; Box *et al.*, 2010; Tomas *et al.*, 2011). In many coastal sites, heterogeneous habitats such as rocky reefs (Cebrian *et al.*, 2012), sandy bottoms, or seagrass meadows tend consequently to be replaced by homogenous *Caulerpa* spp. meadows. In such areas, it has been suggested

that the simple structure, i.e. low complexity of *Caulerpa* spp. meadows reduces the three-dimensional complexity of habitats relative to natural heterogeneous rocky reef habitats (Harmelin-Vivien *et al.*, 2001). This habitat simplification should be detrimental to fish assemblage (Francour *et al.*, 1995) because of the associated loss of diversity and amount of shelter and food (Levi & Francour, 2004), which in turn reduces habitat quality (Dahlgren & Eggleston, 2000; Hindell *et al.*, 2000). Similarly, in the case of the Mediterranean *Cymodocea nodosa* seagrass meadows, another study (Cuadros, 2015) revealed that heterogeneous sectors of these meadows (i.e. scattered with boulders) supported more diversified and abundant juvenile fish assemblages. The author suggested that this is probably related to the diversified food and/or shelter resources, obtained through complementarity and/or synergy between patch-types among the more complex sectors of the meadow.

In this context, it is crucial to understand the effect of habitat complexity on fish settlement and recruitment, because they are key events in the life history of individuals and therefore determine the replenishment of fish assemblages. In our study, settlement is defined as the arrival of early juvenile (post-larval) fishes (referred as "settlers") within benthic habitats after their pelagic larval phase; recruitment corresponds to the subsequent incorporation of these juvenile fish into adult populations after their survival in nurseries and migration towards adult habitats (referred as "recruits") (Levin, 1994; MacPherson, 1998; Beck *et al.*, 2001). We use the term "juvenile" to encompass individuals present in the nursery habitats after settlement and until their dispersal (Cheminée *et al.*, 2011). The maximum density of settlers is the best metric for the intensity of settlement events, i.e. the number of new individuals joining the benthic habitat in a given area (Macpherson *et al.*, 1997). However it does not necessarily reflect the final abundance of juveniles that recruit into the adult population: indeed, the initial number of settlers might be highly depleted through mortality (Macpherson *et al.*, 1997; Arceo *et al.*, 2012). Macpherson (1998) defined recruitment level as the number of juveniles remaining at the end of the post-settlement period. However, this does not take into account mortality of juveniles during their transition from nurseries toward adult habitats (Beck *et al.*, 2001). A proxy of recruitment level is the number of juveniles surviving arbitrary periods of time after settlement (Macpherson & Zika, 1999). These variables can be assessed by monitoring abundance of juveniles over the post-settlement period in the nursery until their dispersal towards adult habitats (Macpherson *et al.*, 1997; Arceo *et al.*, 2012).

In this paper, the tri-dimensional structural complexity of a given habitat (here *Caulerpa taxifolia* meadow) was manipulated in order to test the effect of the complexity degree of this habitat on fish settlement and recruitment. We hypothesized that any increase in complexity within an homogenous meadow should result in an increase in juvenile survival and therefore densities (Connell & Jones, 1991). We experimentally manipulated the degree of habitat complexity in a *Caulerpa* meadow, using arrangements of concrete blocks. In order to test our hypothesis we studied temporal trends of densities of fish juveniles in these manipulated habitats of different complexities.

Material and Methods

Ethics statement

The observational protocol was submitted to regional authority 'Direction interrégionnale de la mer Méditerranée' (the French administration in charge of the Maritime affairs) who did not require a special permit since no extractive sampling or animal manipulations were performed (only visual censuses in natural habitats), since the study did not involve endangered or protected species, since no works within any marine protected area were performed and since accessed field was not privately owned.

Study site, treatments and experimental design

The study was carried out along the coast of Cap Martin, near Menton, France (north-western Mediterranean; 43.75073° N, 7.48010° E). The study site was composed of flat, gently-sloping sandy bottoms, covered by a dense and continuous *Caulerpa taxifolia* meadow, at 10 meter depth. After its first appearance in the Mediterranean in 1984 in Monaco (Meinesz & Hesse, 1991), *C. taxifolia* invaded the study site in the 1990's (Francour *et al.*, 1995; Meinesz *et al.*, 1998) and formed large homogenous meadows (more than 90% cover) from 5 to 15 m depth.

We used concrete blocks (20x20x50 cm) to manipulate habitat complexity within the *Caulerpa* meadow. Blocks were arranged on the bottom, in the meadow, and we manipulated the density of blocks, to create treatments of four complexities (Fig. 1). Each treatment was built by randomly spreading the blocks over a 2x20 m area parallel to the coast. Treatments were arranged in two parallel lines separated by 10 meters; each line contained one replicate for each treatment, and each replicate was separated by 3 meters. In one line the treatments were arranged from the highest to the lowest complexity; in the other line, the order was reversed. Overgrowing *Caulerpa taxifolia* fronds were regularly removed by SCUBA divers.

Fish counts

Fish counts were performed weekly from August 2000 to February 2001 (N = 18) when weather and diving conditions permitted. Counts were done by means of underwater visual census (UVC) (Harmelin-Vivien *et al.*, 1985), by SCUBA divers at 0.5 m above the substrate; each replicate was censused in less than 5 minutes. All

counts were made when visibility exceeded 3 m, and between 9 am and 11 am, a timeframe within which studied species were active. Fish abundance was recorded in units of 1 up to 10 individuals; when more than 10 individuals were observed, abundance was recorded in classes: 10-20, 20-50, 50-100 individuals (Francour, 1999).

A total of 14 species belonging to the families Labridae, Serranidae and Sparidae were recorded (Table 1). Two species of labrids, *Coris julis* and *Symphodus ocellatus*, were the only two species to settle in high abundances on treatments (see next section); we therefore focused analyses on these two species. We categorized individuals into three size classes (small, medium and large; each class encompasses 1/3 of the total maximum length), and further subdivided the "small" size class into "settlers", "post-settlers" and "recruits", as defined in the previous section.

Data analysis

Relative densities of each species among treatments (habitat complexity: H>M>L>V; see Fig. 1) and through time, for the period following the abundance peak of a given size-class were analyzed. To standardize for differences in fish abundance between treatments (n=2 for a complexity level), we expressed abundances as the percentage of the maximum abundance per treatment to avoid density-dependent effect (Macpherson *et al.*, 1997).

Because assumptions of data normality were not met, the Scheirer-Ray-Hare test (SRH), a non-parametric alternative to two-way ANOVA (Sokal & Rohlf, 1995), was used to test the null hypothesis H_0 of no difference in relative abundances between the four treatments and between sampling dates after the abundance peak. Sampling dates were considered independent because, given the mobility of species, abundances at *t* time did not influence abundances at *t*+1. If H_0 was rejected, *i.e.* that at least one treatment or date was different from another, SRH test was followed by a non-parametric post-hoc test for pairwise comparisons (Siegel & Castellan, 1988) in order to determine which treatment(s) and date(s) was(were) different from each other. Separate analyses were conducted for each size class of each species. All statistical analyses were performed using the R 2.12.2 statistical software (R_Development_Core_Team, 2013).

Table 1 Frequency of occurrence of the species recorded on each habitat complexity treatment between August 2000 and February 2001 (n = 18 censuses) – Habitats treatments (replicates n = 2): High complexity (H), Medium complexity (M), Low complexity (L), Very low complexity (V).

		Treatments			
		H	**M**	**L**	**V**
Family	**Species**				
Labridae	*Coris julis*	1.00	1.00	0.89	0.92
	Symphodus ocellatus	0.97	0.94	0.83	0.83
	Symphodus tinca	0.58	0.36	0.33	0.19
	Symphodus roissali	0.03	0.06	0.03	0.08
	Symphodus melanocercus	-	-	0.03	-
	Symphodus rostratus	0.17	0.08	0.06	0.03
	Symphodus cinereus	0.14	0.11	0.03	0.06
	Labrus spp.	0.28	0.14	0.19	0.19
Serranidae	*Serranus cabrilla*	0.61	0.58	0.53	0.39
	Serranus scriba	0.36	0.28	0.33	0.25
Sparidae	*Diplodus annularis*	0.14	0.19	0.19	0.22
	Diplodus vulgaris	0.08	0.14	0.03	-
	Diplodus puntazzo	-	-	0.03	-
	Spondyliosoma cantharus	-	-	0.06	-
No. Species		**11**	**11**	**14**	**10**

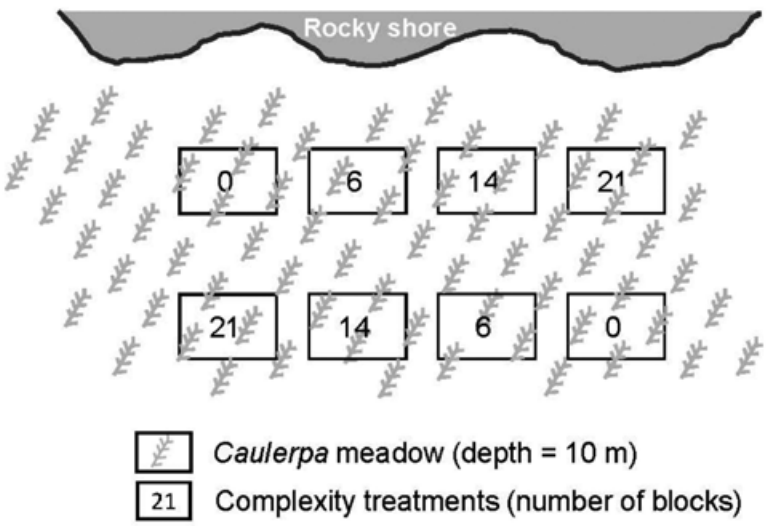


Fig. 1: Schematic view of the study site and experimental layout. Concrete blocks (20x20x50 cm) were used to manipulate habitat complexity within the *Caulerpa* meadow. High complexity (H, number of blocks (nb) = 21), Medium complexity (M, nb = 14), Low complexity (L, nb = 6), Very low complexity (V, nb = 0).

Results

For both *Symphodus ocellatus* and *Coris julis*, peaks in the abundance of settlers, post-settlers and recruits succeeded each other sequentially from the start of the study (Fig. 2). The peak of *C. julis* abundance was recorded on the 27th September (day 56) for settlers, the 3th October (day 62) for post-settlers and 24th October (day 83) for recruits. For *S. ocellatus*, these maxima were recorded on the 19th September (day 48), 3th October (day 62) and 24th October (day 83), respectively. Individuals belonging to medium and large size classes were recorded during the entire survey period (August to February) and their mean abundances did not show significant differences between treatments or dates (Scheirer-Ray-Hare test; $p > 0.05$). The maximum densities recorded for medium and large size classes were 1.62 and 0.37 ind./10 m² for *C. julis* and 3.50 and 0.50 ind./10 m² for *S. ocellatus*.

Following the peak abundance for each size class of each species, significant differences in relative abundance between complexity treatments were revealed only for recruits of *Coris julis* (Scheirer-Ray-Hare test, H=11.06, Df=3, p = 0.011, Table 2); besides, at peak abundance for this size class (recruits, day 83), initial recruits densities did not differ between treatments (Kruskal-Wallis,

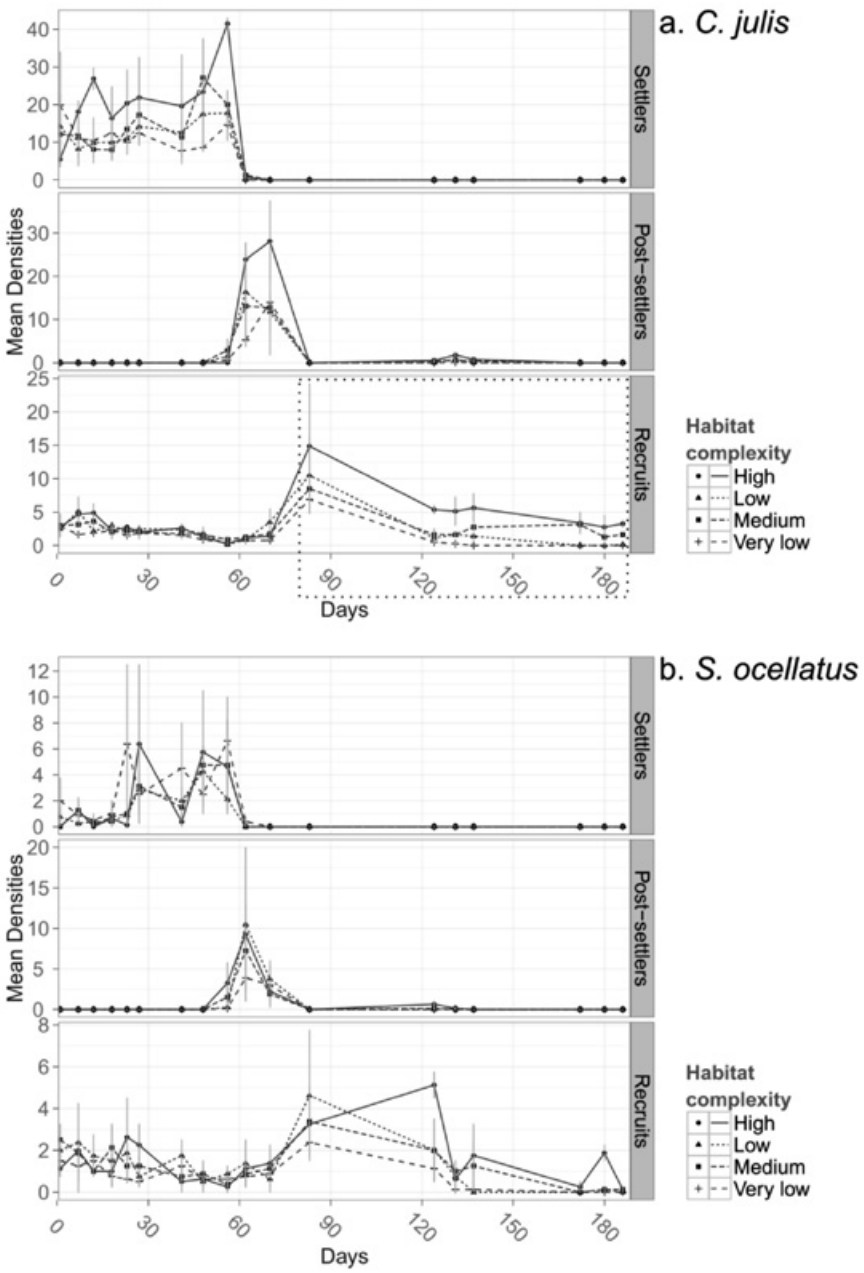


Fig. 2: Mean densities of *Coris julis* (a) and *Symphodus ocellatus* (b) settlers, post-settlers and recruits. Mean densities are given for various survey dates in each habitat complexity treatment. Error bars as standard error (n=2). Dashed-line rectangle: see detailed view for *C. julis* recruits on Figure 3.

Chi²= 0.7256, Df = 3, p = 0.867). Relative abundances of other size classes for this species and all size classes of *Symphodus ocellatus* differed among dates, but not complexity treatments (Table 2). Pairwise comparisons of the density of recruits of *C. julis* revealed that relative abundances in habitats H and M (the most complex) were significantly higher than in habitats L and V (the least complex) (post hoc test, $p < 0.0001$, Fig. 3); they did not differ significantly between habitats H and M, or between habitats L and V respectively (post hoc test, $p > 0.05$).

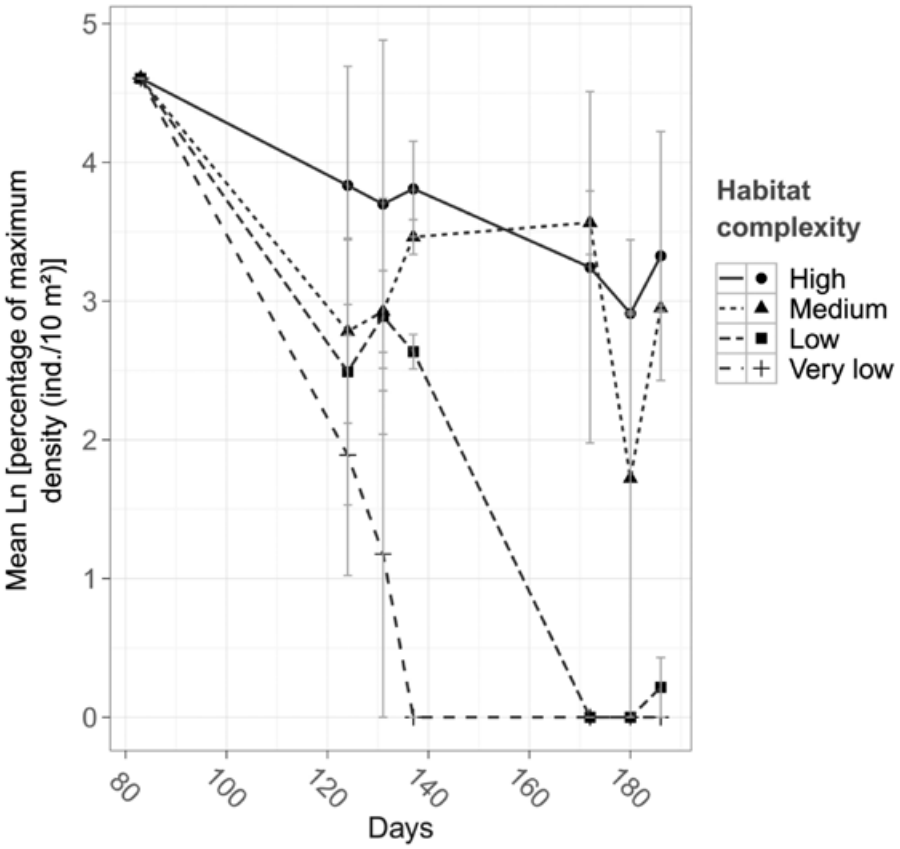


Fig. 3: Relative abundance of *Coris julis* recruits from the date of peak abundance for each treatment. The Y-axis is expressed as the mean of Ln-transformed proportion of the initial density at the peak (day 83) – error bars as standard error (n = 2).

Table 2 Results of Scheirer-Ray-Hare tests analyzing effects of habitat complexity treatments and date on abundances of *Coris julis* and *Symphodus ocellatus* for the settlers, post-settler and recruits size classes. Significant effect ($p < 0.05$) is marked by an asterisk. Df refers to degrees of freedom.

Species	Size class	Explanatory variables	Df	Mean Sq.	*H*	*p* value
		Habitat complexity	1	6.91	0.04	0.838
	Settlers	Date	10	340.35	20.63	0.024*
		Residuals	32	12.82	2.49	1.000
		Habitat complexity	3	29.78	0.80	0.848
Coris Julis	Post-settlers	Date	8	353.17	25.45	0.001*
		Residuals	24	12.49	2.70	1.000
		Habitat complexity	3	249.43	11.06	0.011*
	Recruits	Date	6	133.42	11.83	0.066
		Residuals	18	13.51	3.59	0.999
		Habitat complexity	3	12.64	0.23	0.973
	Settlers	Date	10	324.20	19.65	0.033*
		Residuals	30	7.84	1.42	1.000
		Habitat complexity	3	12.57	0.34	0.952
Symphodus ocellatus	Post-settlers	Date	8	291.25	20.99	0.007*
		Residuals	24	15.10	3.26	1.000
		Habitat complexity	3	103.14	4.57	0.206
	Recruits	Date	6	211.54	18.76	0.005*
		Residuals	18	11.91	3.17	1.000

Discussion

In our study only two species (*Coris julis* and *Symphodus ocellatus*), among the fourteen species we observed, settled in *C. taxifolia* meadows in substantial abundance. Comparing our treatments, for *S. ocellatus* the absence of significant differences between levels of complexity might be due to low initial densities of individuals. In contrast, recruits of *C. julis* varied significantly with habitat complexity. We infer that this pattern is due to a lower habitat quality for the lowest complexity treatments, i.e. a higher mortality risk due to increased predation rate and/or reduced food availability (Dahlgren & Eggleston, 2000; Hindell *et al.*, 2000), which in turn results in active habitat selection and/or differential mortality of juveniles (Thiriet, 2014; Thiriet *et al.*, 2014) .

In our experiment, treatments differed by the number of refuges available (related to the number of concrete blocks) but probably did not differ in food availability because blocks were regularly cleaned of any epibiota. We therefore hypothesize that the lower *C. julis* juvenile densities we observed in the less complex habitats are due to higher predation risk in less complex habitat, resulting in higher mortality or active movement towards more suitable habitats. Previous studies in the Mediterranean on the deployment among *P. oceanica* meadows of anti-trawling reefs showed an increase in species richness and abundance of already present species (Ramos-Espla *et al.*, 2000). Similarly, the presence of scattered boulders among *Cymodocea nodosa* meadows (resulting in more complex meadow sectors, *versus* homogeneous ones) resulted in more diversified and abundant juvenile fish (Cuadros, 2015). It was attributed to the more diversified food and/or shelter resources (diversified ecological niches), through complementarities and/or synergy (e.g. edge effects) between patch-types of the more complex sectors of the meadow. Furthermore, in our study, the absence of significant differences between complexity treatments for the smallest (settlers and post-settlers) size classes suggests that this did not equally affect fishes of all size classes, as previously shown for other species (Fisher *et al.*, 2007). This might be because the smallest size classes (e.g. settlers, about 10-15 mm TL) may still find sufficient shelter despite the lower complexity, while larger individuals (e.g. recruits, >40 mm TL) cannot. Larger recruits of *C. julis* may not find sufficient space between thalli of *C. taxifolia* meadows; as a result they may not be able to use it as a shelter habitat in the same way that they use *Posidonia oceanica* meadows (Garcia-Rubies & Macpherson, 1995), although we did not test it directly; in addition, nor may they be able to use *C. taxifolia* meadows understory as a foraging habitat as they do in habitats dominated by Dictyotales and Sphacelariales (Guidetti, 2004; Cheminée, 2012; Cheminée *et al.*, 2013). Therefore they may be more exposed to mortality by predation and/or starvation. For the "recruits" size class of *C. julis*, these abundance patterns were consistent through time during our study. Altogether, our results for *C. julis* are consistent with our initial hypothesis: least complex habitat may have a lower habitat quality and therefore lower juvenile fish's survivorship, resulting in increased mortality and/or active movements toward more complex habitats.

Abundances of *C. julis* were consistently higher than those of *S. ocellatus* in all treatments. In other macrophyte-formed habitats, e.g. *Cystoseira* spp. forests or in *P. oceanica* meadows, the reverse has been observed: juveniles of *S. ocellatus* were consistently more abundant than those of *C. julis* (Francour & Le Direac'h, 2001; Cheminée, 2012; Cheminée *et al.*, 2013). We hypothesize that the thicker body shape of *S. ocellatus* impairs their ability to hide between *Caulerpa* thalli; this restriction might not apply to the thinner *C. julis* individuals. The inter-thalli void (spaces between and under thalli) may indeed be larger below a *Cystoseira* or *Posidonia* canopy than a *C. taxifolia* canopy, although this has not been measured. If this hypothesis is correct, *C. taxifolia* habitat may offer suitable refuges only for the slim-bodied individuals such as *C. julis*. Studies are needed to quantify the habitat complexity differences, and their putative impact on juvenile assemblages, between *Caulerpa* invaded and non-invaded Mediterranean substrates. Although our design did not allow us to test it, we hypothesize that our experimental set up may reflect the natural complexity differences between totally invaded sites (i.e. substrate homogeneously covered by *C. taxifolia* = our low complexity treatment) *versus* non-invaded (or partially invaded) ones (substrate with heterogeneous habitat characteristics = our complex treatment). Consequently we hypothesize that in sites totally invaded and covered by *C. taxifolia*, the low habitat complexity -*sensu* August (1983)- resulting from habitat homogenization at both micro-habitat scale (inter-thalli void) and seascape scale (loss of habitat diversity), is detrimental for at least some species and might be detrimental to the nursery role of coastal habitats, notably because of decreased habitat quality in terms of shelter and/or food availability. If this hypothesis would be validated, active habitat selection and/or higher mortality of recruits could explain the lower densities of adults that have been previously observed in *C. taxifolia* meadows in comparison with un-invaded (and more complex) habitats (Francour *et al.*, 1995; Harmelin-Vivien *et al.*, 2001). Consequently, as proposed by Harmelin (1996), artificial habitats superimposed on large homogenous *C. taxifolia* meadows could allow mitigation of these invasions by increasing survival of fish recruits.

As a conclusion, we argue that Mediterranean fish assemblages rely on a complex mosaic of habitats and microhabitats suitable as nurseries for juveniles of different species (Cheminée *et al.*, 2013; Thiriet *et al.*, 2014). Alien species introduction is one of the main anthropogenic stressors acting in Mediterranean marine seascapes. In the *Caulerpa* spp. case, the invading species act as exotic engineers and tend to homogenize the sea-

scape and reduce the diversity of habitats and microhabitats available (Harmelin-Vivien *et al.*, 2001; Molenaar *et al.*, 2009). Our study suggests it is relevant to bring new information about the fish recruitment patterns that operate in these transformed systems, as well as about their causes. Additional manipulative studies, including more species, comparing sites before and after invasion or comparing invaded *versus* un-invaded natural sites are required to assess if the relative low diversity of fishes that settled in our *Caulerpa* meadows (compared to references in native habitats) is an artifact of studied site/year or is truly and impact of habitat transformations. This can help us understanding the role that can play the expansion of *Caulerpa* (and other structurally similar exotic species) in the recruitment of littoral fishes.

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Supporting information: full relevant data set of field observations.

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