



Macrophyte complexity influences habitat choices of juvenile fish

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Abstract

The nursery function of littoral habitats for juvenile fish is widely recognized, but data on the specific habitat features that contribute to this function is sparse for many species, in part related to the difficulty of studying juvenile fish in their natural environment. However, this information is required to understand the potential risks of environmental change to the nursery functions of habitats. In this context, the habitat choice behaviour, with respect to differences in structural features, was evaluated for three Mediterranean littoral fish species known to be associated to macrophytes as juveniles. The overarching aim of this experiment was to determine if juveniles actively choose between different macrophyte configurations of varying complexity and height. Juveniles were exposed simultaneously to multiple visual habitat stimuli within an experimental choice arena, and their swimming behaviour was tracked by video recordings to determine the amount of time they spent near each habitat configuration. All three species showed a clear association in their occupancy towards more complex habitat configurations demonstrating that juveniles distinguished and actively selected habitats using visual cues. Subtle differences in species' affinity for complex habitats allowed us to appraise their potential vulnerabilities to habitat loss in the Mediterranean under environmental change scenarios. Furthermore, the results of this study provided evidence that differences in juvenile distribution between habitats found in previous observational studies may indeed be caused by active habitat selection, as well as through differential survivorship rates.

Keywords Ecosystem functions · Algae habitats · Nursery habitats · Juvenile fish behaviour · Environmental change

Introduction

Following the planktonic dispersal phase, many littoral fish larvae metamorphose and become juvenile benthic settlers (Almany and Webster 2006; Garcia-Rubies and Macpherson

1995; Juanes 2007). The survival of these juvenile fish is determined by both the suitability of the overarching environmental conditions and the smaller-scale habitat choices made at an individual level (Igulu et al. 2011; Lecchini et al. 2007). The principal requirements in this phase, considering environmental parameters are favourable, are the avoidance of predators and the detection of food, to optimize growth during this vulnerable development stage (Grol et al. 2011; Juanes 2007; Rozas and Odum 1988; Shulman 1985). Other requirements such as water quality (e.g. temperature, dissolved oxygen levels, pH, and pollutants), social interactions or competition may also influence the well-being of juvenile fish (Juanes 2007; Naidoo and Glassom 2019). The level of importance of these various requirements may vary considerably between species, development stages and environmental context (Laegdsgaard and Johnson 2001).

The littoral rocky reefs in the Mediterranean contain a variety of habitat-forming macrophytes that can create complex structures, thought to be important nursery habitat features for the local fish fauna (Cheminée et al. 2013, 2016, 2020;

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Hinz et al. 2019). Macrophytes that have a high structural complexity, such as the Genus *Cystoseira*, have been highlighted as important for predator avoidance and for holding high abundances of prey, such as Harpacticoids, Amphipods and Molluscs (Cheminée et al. 2013, 2017a, b; Cuadros et al. 2019; Hinz et al. 2019). In terms of “high-quality nursery habitats”, there has been a general consensus that complex habitats are likely the most suitable (Beck et al. 2001; Heck Jr. et al. 2003). However, there is little quantitative data about the features that make a habitat complex and if fish can recognize this complexity. With respect to macrophytes, height, volume, leaf/stem structure and ramification have been shown to contribute to their overall complexity (Corbit and Garbary 1995; Hacker 2011; Thomaz and Cunha 2010; Warfe et al. 2008). However, considerable uncertainty exists over the species-specific affiliation of juvenile fish to specific macrophyte species or morphotypes (structurally similar species). Nevertheless, several field studies have related higher abundances of juvenile fish to macrophyte volume (Cheminée et al. 2017a, b; Cuadros et al. 2019) and height of cover (Cheminée et al. 2013, 2020) suggesting that these features are important in defining nursery quality. In part, the lack of available information for certain habitats and juvenile fish species is related to the difficulty in studying these at adequate temporal and spatial scales. Field studies often rely on differences in population densities between habitat types or features to infer juvenile fish preferences and habitat suitability (Cheminée et al. 2013; Cuadros et al. 2017; Garcia-Rubies and Macpherson 1995; Hannan and Williams 1998; Levin 1994b; MacPherson 1998; Stunz et al. 2002). However, while fish density has been extensively used to identify essential fish habitats (Beck et al. 2001; Kraufvelin et al. 2018), as a sole indicator it can struggle in identifying which precise habitats features or configurations are preferred (Hinz et al. 2006). This is because the abundance of fish may vary considerably in time at any location due to natural stochastic processes, causing a high degree of variability in observations (false positives and negatives), which is a particular concern in studies that rely on low spatial or temporal replication in sampling (e.g. Dulčić et al. 1997; Levin 1994a). Scenarios are imaginable, where due to strong settlement pulses and/or the absence of predators (e.g. due to fishing), juveniles may be found in high densities in poor or otherwise unsuitable habitats. Additionally, abundance-based field observations are often limited by local context dependence of habitat configurations, with the potential of not containing all possible combinations or configurations of habitat features to assess their relative importance. While spatially extensive and temporally highly detailed field surveys could address these limitations, they come with the inherent trade-off of being extremely costly. Therefore, additional complementary methodologies such as behavioural habitat selection experiments, as presented here, can provide important additional insights into the relevance of specific habitat features.

Juvenile fish may, among other senses, use visual cues to detect suitable microhabitats (Igulu et al. 2011). Specific habitat features may offer superior sheltering or feeding opportunities over others, and, therefore, have a different attractiveness. Juvenile fish may therefore show directed movement towards such preferred habitat features and spend more time in or around these. Following this premise, choice experiments may be a suitable methodology to investigate the preference of juvenile fish for specific habitat features (i.e. species or morphotypes) and configurations (i.e. height, density or diversity).

The present study explores the choices of juveniles of three common temperate reef fish species of the Mediterranean when presented with different macrophyte morphotypes and configurations. The juvenile fish were exposed simultaneously to multiple visual stimuli within a tank arena, and their swimming behaviour was tracked by video recordings, to later determine the amount of time each individual spent near a particular macrophyte habitat configuration. The principal factors tested were macrophyte complexity, measured through fractal dimensions, and height. Understanding the importance of macrophyte habitat to juvenile fish is of significant ecological relevance, especially against the backdrop of environmental change in the Mediterranean, which appears to significantly affect macrophyte habitats through eutrophication, climate change and the introduction of non-native species (Katsanevakis et al. 2011; Pickholtz et al. 2018; Sempere-Valverde et al. 2021). Consequences are the loss and alteration in the composition of macrophyte cover, which in turn affect fish that rely heavily on these habitats during their juvenile stages. Without suitable habitats such species may experience reduced access to food resources, increased vulnerability to predation, and limited opportunities for growth and development (Aarts et al. 2004; Hughes et al. 2002; McCormick et al. 2010). Fundamental changes in macrophyte communities in the littoral zone are not limited to the Mediterranean region alone. Similar transformations in macrophyte-dominated habitats have been documented in various other regions around the world, e.g. South Africa (Sheppard et al. 2011), North America (Hughes et al. 2002), Australia (Pessarrodona 2022), and China (Titlyanov et al. 2015), underscoring the significance of such shifts and emphasizing the need to understand their ecological consequences.

Methods

Selected species, their capture and husbandry

The choice experiment was carried out with juveniles of three littoral fish species: *Coris julis* and *Symphodus ocellatus* during August–September 2020, and *Diplodus vulgaris*

during May 2021. These fish species were selected due to their abundance, ecological importance, and distinct behaviour in the littoral rocky reef systems in the Mediterranean. All three species have been described to settle predominantly in littoral rocky habitats, and an association with macrophyte cover have been mentioned for all three (Cheminée et al. 2017a, b; Cuadros et al. 2019; Ventura et al. 2015). However, past studies appear to suggest a slight difference in their affinity to macrophyte cover in general and to specific species or morphotypes. *S. ocellatus* has been consistently mentioned to be found in higher abundances in structurally complex macrophyte forests, such as *Cystoseira* and *Dictyota* forests, for both juveniles and adults (Cheminée et al. 2013; Thiriet et al. 2016). While macrophytes are mentioned in connection with juveniles of *C. julis* (Cheminée et al. 2016; Guidetti 2000; Letourneur et al. 2003), there are few studies that suggest a clear positive association (but see Cuadros et al. 2019). *D. vulgaris* juveniles have been associated with heterogeneous coastal habitats in general, which may include macrophytes (Mercader et al. 2019; Ventura et al. 2015), but other structuring habitats features such as pebbles, rocks or seagrasses have equally been mentioned as important (García-Rubies and Macpherson 1995; Harmelin-Vivien et al. 1995; Mercader et al. 2019; Ventura et al. 2015).

Experimental fish were captured with hand nets by scuba divers, authorized by the responsible government agency (DGPM/JMT/agj, April 15th, 2019, Conselleria de Agricultura, Pesca i Alimentació). Approximately 100 individuals of each species were caught for this study. All individuals were fished close to Port d'Andratx (Mallorca, Spain), in depths between 1 and 6 m. To reduce stress, individuals caught by divers were first transferred to a holding net underwater and later transported via boat in a large 90 l coolbox

filled with seawater to the nearby Laboratory facilities (Laboratori d'Investigacions Marines i Aqüicultura – LIMIA). Fish were kept for a minimum of 24 h in a 200L opaque maintenance tank with filtered seawater circulation and aeration, and without being fed for 24 h to acclimatise. After that, fish were fed pellets and frozen mysids and shrimps. Each fish was only used in a single trial. After the experiment, fish were euthanised following established authorized protocols. The experimentation underwent an ethical review and was authorized by the local authorities (Conselleria de Agricultura, Pesca i Alimentació by the permit code 2019/19/AEXP). Fish used for the experiment were of similar size, and variations were kept to a minimum (*Coris julis* 3.81 cm SD \pm 0.44, *Diplodus vulgaris* 3.2 cm SD \pm 0.28 and 3.59 cm SD \pm 0.52 *Symphodus ocellatus*, sizes are averaged total length).

Experimental arena

A square aquarium was used for the choice experiment, as described by Igulu et al. (2011). The aquaria had the following dimensions 0.8 \times 0.8 \times 0.5 m with four smaller closed side-compartments in each corner and a central arena (Fig. 1A). The four equally sized corner-isolated areas served for the presentation of visual stimuli, and the larger central area as the choice arena, in which the fish could move freely (Fig. 1B). Parts of the choice arena were considered as undetermined choice areas (Fig. 1C, see below for more details). Different from Igulu et al. (2011), the central arena base and side walls were covered with white plastic foil. The white base served to increase the contrast of the fish against the background when filming the movement of the juvenile fish from above, while side coverings served to exclude any

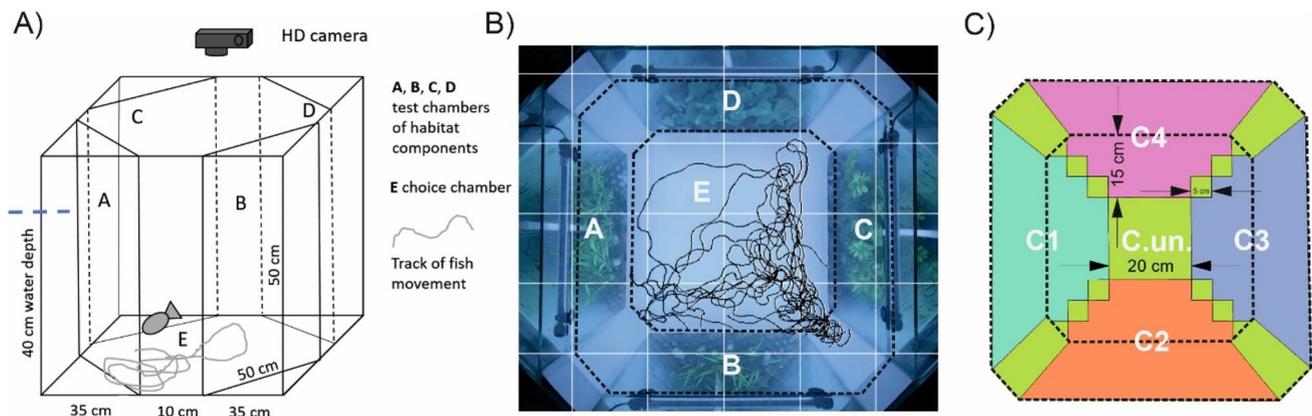


Fig. 1 **A** Schematic representation of the experimental aquaria with four closed side compartments for visual habitat presentation (A–D) and one choice chamber (E); **B** photograph of the choice arena with the movement track of a fish superimposed; **C** showing the 5 analysis areas: 4 choice areas (C1–C4) and the undetermined choice areas

(C.un., green). The undetermined choice areas C.un. were located in the centre of the square aquarium and laterally next to the C1–C4 choice areas. Dotted lines to aid visual comparison of B and C. Distances marked by two opposing arrowheads in cm providing the dimensions of aquarium choice areas at the base of the aquarium

unwanted visual stimuli from the outside. The aquarium was lit by four submersible led lights (MF-21U DOCEAN) that were placed in each corner. This setup limited light reflections on the water surface allowing high-resolution filming of fish movements with a GoPro Hero 7 Black at 1440/30fps (4:3) positioned above the tank (93.5cm from the base of the tank to the camera). The central and side compartments of the tank were filled with filtered UV-sterilized seawater so that they had a water depth of 40 cm. Prior to filming the aquaria was cleaned, wiping it with ethanol. This was done daily prior to trial runs. On average, a total of 10 fish were tested per day. Each complete experimental trial consisted of 30 fish being individually exposed to 4 different visual habitat stimuli (configurations).

Experimental treatments and workflow

Individual fish were presented with different configurations of macrophyte habitats. Habitats were presented simultaneously to the fish through the 4 corners of the aquarium. For each trial, the location of the 4 habitat configurations tested was changed, to randomise their positions between trials, aiming to eliminate potentially confounding effects related to the orientation of the aquarium. The macrophytes presented were artificial macrophytes of different morphologies and complexities. Macrophyte mimics were used, that to some extent mirrored morphologies encounter in the field, although their height and colour may differ significantly due to experimental needs. Mimics were chosen in this experiment following various rationales: (a) since we were interested in the general response of fish to complexity and height of macrophyte a true replication of natural conditions was thought less important to the experiment; (b) some of the macrophyte species are long-lived and uprooting them for the experiments was thought a disproportional intervention; (c)

within the experimental setup mimics were less fragile and easier to maintain and manipulate, compared to their natural counterparts. Mimics have been used in other habitat choice experiments of juvenile fish (e.g. see Ottmar and Hurst (2012) and Stoner and Titgen (2003).

The mimics chosen all had a similar green colour. For each species, three experiments with different configurations of macrophytes were run: Experiment A.) Complex macrophytes (Complex ramification, tree-like similar to *Cystoseira*, 8 macrophyte units per habitat) with three different height levels (28, 12 and 6 cm) and a control (a corner without habitat). Experiment B.) Simple macrophytes (Simple ramification, tree-like with some resemblance to *Dictyotales*, 8 macrophyte units per habitat) again with testing three height levels (28, 12 and 6 cm) and a control. Experiment C.) Macrophytes of four different morphologies (6 units per habitat) but of the same height (12 cm): 1. Complex tree-like similar to *Cystoseira* (C2 in Fig. 2); 2. Simple tree-like similar to *Dictyotales* (D2 in Fig. 2); 3. Strait leaves, non-ramified similar to the phanerogam *Cymodocea nodosa* (Cym. in Fig. 2); and 4. Broadleaf or band-like, similar to *Padina pavonica* (Pad. in Fig. 2). However, note the height used in this experiment for *P. pavonica* was modified for experimental purposes (max. height 8 cm in the Balearic Island). For each fish species, 30 individuals were used for each experiment. Individual fish taken from the holding tank were introduced into the experimental aquarium as close as possible to its centre. Fish movements were recorded for 15 min similar to Igulu et al. (2011). The first 5 min served as acclimation and were therefore excluded from the analysis, and the remaining 10 min represented the time of the choice experiment. All experimental runs were performed in an isolated space in the absence of the experimenter thereby limiting external noise and disturbances.

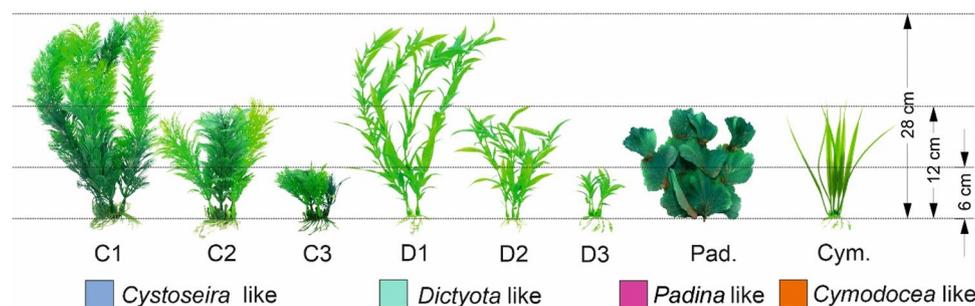


Fig. 2 Macrophyte morphotypes mimics used within the three experiments. In experiment 1, fish had the choice between 3 habitats composed of C1–C3 (*Cystoseira* like) that varied in height and one control area without any macrophyte. In experiment 2, fish were exposed to D1–D3 (*Dictyota* like) that varied in height and a control area without macrophyte. For experiment 1 and 2 eight plants were used

within each habitat choice chamber expect for the control. In experiment 3, the fish were exposed to four different morphotype mimics that all had the same height 12 cm [C2, D2, Pad. (*Padina* like) and Cym. (*Cymodocea* like)]. In this experiment, six plants were used within each choice habitat chamber. Colour legend below plants indicate the different morphotypes represented in the boxplots of Fig. 3

Complexity measures of macrophyte morphotype mimics

To quantify the complexity of macrophyte habitats offered as visual stimuli, we calculated the fractal dimensions of images composed of single and multiple macrophyte shoots. Photographs of macrophytes were taken in a lightbox (61 × 61 × 61 cm) to ensure indirect homogenous lighting with a Canon EOS 2000D. To isolate the image of the individual macrophyte from the background and remove any shadows, CorelDRAW Graphics Suite 2020 was used. Subsequently, we converted macrophyte images into vectors to scale and manipulate images without losing image quality. Once vectorised, macrophyte images were duplicated creating the number of macrophyte images replicas necessary to recreate experimental habitats. ImageJ software (Schneider et al. 2012) was used to convert images into binary and calculate fractal dimensions (D) using the FracLac plugin (Karperien 1999). A Boxcount scan was used with 12 different grid locations, in power series 2^2 and a calibre (overlap) of 45%. Thus, we obtained the (D) for the different morphotype habitat compositions tested. The visual surface area occupied by the habitats was calculated as an additional parameter using binary images and the area occupied by the silhouette of the habitats.

Tracking fish movements from video recordings

The movement patterns of individual fish video recordings were analysed using the open-source artificial intelligence-based tracker software idtracker.ai (Romero-Ferrero et al. 2019). For the analysis, we used an Intel i7 PC equipped with a GPU NVIDIA GeForce GTX 1660 SUPER. Prior to analysis the mpg4 videos files of individual trials were stitched together using ffmpeg (<https://www.ffmpeg.org/download.html>) and converted to avi format with VSDC Free Video Editor (<https://www.videosoftdev.com/>), the required format for idtracker.ai. The idtracker.ai software tracked fish movement and converted it into positional information. The recorded positional tracks were subsequently analysed in R (<https://www.R-project.org/>), plotting the fish trajectories and calculating time spent by each fish near the tested habitat configurations (the frequency of the points recorded was equal to the number of frames recorded i.e. 30 points per second). For the allocation of tracks to the experimental habitat treatments, the recorded visual area of the aquarium was divided into 5 choice zones: 4 side areas C1 to C4, where the 4 different habitats were offered simultaneously, and a 5th undefined choice zone (C.un) which consisted of the central area and the 4 small lateral corner areas situated between habitat choice sides (green colour in Fig. 1C). The idtracker.ai software detected movements of fish near the base of the aquarium well, however,

the software had difficulties detecting fish swimming higher in the water column near the habitat choice areas, due to the complexity of the background introduced by the habitat. The loss of detection did not place a problem with respect to calculating the time spent in different zones, as the time and location of signal loss and gain could be identified and hence force allocated to corresponding areas. This process was helped by the four white background lateral corner areas, that separated the habitat choice areas. In these areas, idtracker.ai also detected fish higher up in the water column due to the high contrast between the fish and the white background. Fish that demonstrated no movement and remained at the release point during the whole experimental trials were excluded from the analysis. This was predominately observed in *C. julis* with 32 out of 90 individuals that showed this behaviour, contrasted with 2 and 1 individuals observed for *S. ocellatus* and *D. vulgaris* respectively.

Statistical analysis

To compare for statistical significance in differences of occupancy for respective species and choices within the three experiments PERMANOVA multiple comparison tests were used. Due to the interdependence of individual proportional occupancy observations, assumptions of standard parametrical statistical tests were not met, and we, therefore, opted for a non-parametric analysis approach. The significance level of the p-value for these tests was adjusted to 0.005 after Bonferroni correction, considering the 10 possible comparisons within each experimental run.

Additionally, we compared the pattern of occupancies by the three species for each of the three experiments, through a multivariate means plot and associated PERMANOVA using Primer-e v.7. This approach facilitated the investigation of potential variations in the overall occupancy patterns of choice areas at species level. Additionally, we added a random response dataset to each of the three analyses, to assess whether the observed habitat occupancy for each species significantly deviated from randomly expected responses. The random response datasets were created using the random function in R, creating 30 random habitat choices, reflecting the variance introduced by the selected sample size of fish within experiments. The multivariate means plot is essentially an MDS plot of grouped data (in our case observed species and randomly generated occupancy), that provides a visual summary of the mean centroid of each group and its deviation following bootstrap runs. The bootstrap runs of each group are represented by point clouds of different shapes and colours. Additionally, a coloured area underlying each point clouds represents the 95% smoothed confidence envelopes of bootstrapped centroids of respective groups. The extent by which point clouds of individual groups overlap or are separated within the MDS plot indicates if they

are similar or distinct, respectively. The PERMANOVA performed, provided the statistical test, to verify, if the visually observed differences in the plots were statistically significant.

Additionally, we correlated the fractal dimension and 2D visual surface area occupied by macrophytes for each habitat configurations as a univariate predictors of the proportion of time spent near a particular habitat type. Regression slopes of the different species were compared via ANCOVA. Prior to this analysis, the data was arcsine transformed. Due to the narrow range of fractal dimension values calculated (see Table 1), the control treatment with its zero value (no habitat), had a disproportional leverage on the rest of the data and was therefore removed, prior to analysis.

Results

Complexity measures of macrophyte morphotype mimics

Fractal dimension as a complexity index varied between macrophytes habitat treatments (see Table 1). Both, increases in height and density, caused increases in fractal dimension values of *Cystoseira* and *Dictyota*-like habitats used in the experimentation. Considering habitats composed of 6 units at medium height (12 cm) as a reference baseline, the complexity ranking of macrophyte morphotypes was as follows: *Cystoseira* like >> *Dictyotales* like >> *Cymodocea* like >> *Padina* like. With respect to the 2D visual surface area occupied, the following rank order was evident *Padina* like >> *Cystoseira* like >> *Dictyotales* like >> *Cymodocea* like.

Macrophyte habitat choices of juvenile littoral fish

The analysis of the movement tracks in the choice experiment with complex macrophyte of different heights C1-C3 and a control habitat without macrophyte mimics (Experiment 1) showed that all three species spent more time in the habitat selection area of the macrophyte C1, the tallest macrophyte mimic (Fig. 3). The post-hoc analysis demonstrated significant differences between the tallest (C1) and other treatments for all three species (Table 2). The multivariate analysis of habitat occupancy of experiment 1, comparing the choices of all three species in and MDS plot, showed that the habitat occupancy of all three species, *C. julis*, *S. ocellatus* and *D. vulgaris* was significantly different from random (Table 3, Fig. 4a).

Amongst the selection pattern, *S. ocellatus* was significantly separated from both *C. julis* and *D. vulgaris*, that showed highly similar occupancy responses (Fig. 4). This is explained by *S. ocellatus* showing a higher affiliation to the tallest macrophyte while avoiding the non-vegetated control area and undetermined choice areas (Fig. 3).

In experiment 2, we tested the macrophyte mimic type D1-D3 (*Dictyota*-like) and an un-vegetated control habitat. While individuals of *C. julis* and *S. ocellatus* spent most time near the tallest mimics D1 and D2, *D. vulgaris* showed no clear selection for any of the macrophyte or un-vegetated habitats and spent most time in the undetermined choice area (C.un.) in the centre of the arena (Figs. 3 and 4b). For *C. julis* and *S. ocellatus*, the post-hoc analysis showed significant differences for both high (D1) and medium height (D2) mimics with other treatments (Table 2). For *D. vulgaris* significant differences were detected between the undetermined choice areas and all other choices (Table 2).

Table 1 Configuration, mean fractal dimension of the different macrophyte habitat treatments used in the 3 experimental setups

Experiment	Treatment (morphotype like)	Height cm	N ^o of units	Fractal dimension of hábitat (D)	D mín	D máx	SD (σ)	2D surface area cm ²
1	C1 <i>Cystoseira</i> like	28	8	1.65	1.64	1.65	0.00	1661.48
	C 2 <i>Cystoseira</i> like	12	8	1.58	1.57	1.58	0.00	392.33
	C-3 <i>Cystoseira</i> like	6	8	1.49	1.48	1.50	0.01	113.52
2	D-1 <i>Dictyota</i> like	28	8	1.52	1.52	1.52	0.00	1016.41
	D-2 <i>Dictyota</i> like	12	8	1.51	1.50	1.51	0.00	224.83
	D-3 <i>Dictyota</i> like	6	8	1.44	1.43	1.46	0.01	57.11
3	C 2 <i>Cystoseira</i> like	12	6	1.58	1.57	1.58	0.00	311.92
	D-2 <i>Dictyota</i> like	12	6	1.52	1.51	1.52	0.00	171.23
	Pa. <i>Padina</i> like	12	6	1.43	1.42	1.44	0.01	560.31
	Cym. <i>Cymodocea</i>	12	6	1.46	1.45	1.47	0.01	112.84

D max, D min and SD were calculated from box count runs. The names of the treatments are the same as in Fig. 2

H height (cm); N number of units; D fractal dimension of habitat; 2D visual surface area (cm²) occupied by the habitat configuration

There was a significant difference in the pattern of occupancy of all three fish species compared to random as demonstrated by the MDS means plot (Table 3, Fig. 4b). Furthermore, *C. julis* and *S. ocellatus* occupancy were significantly different from that of *D. vulgaris*.

In experiment 3, where fish were exposed to different macrophyte mimics of the same height (C2, D2, Padina like and Cymodocea-like), there appeared to be a tendency for both *C. julis* and *S. ocellatus* to spend a higher proportion of time near the C2 habitat (i.e. *Cystoseira* like mimic) compared to other morphotypes (Fig. 3). The post-hoc analysis showed significant differences between C2 and D2 (*Dictyota* like) for both these species. For *S. ocellatus*, also significant differences between C2 and Cym. (*Cymodocea*-like) were detected (Table 2). *S. ocellatus* furthermore, spent more time near the *Padina*-like mimics compared to the remaining two morphotype choices (Fig. 3), reflected by significant differences between Pad. and Cym. in the post-hoc analysis (Table 2). In the case of *D. vulgaris*, no clear selection for any of the macrophyte types or the undetermined choice area (C.un.) was evident (Fig. 3, Table 3). *C. julis* and *S. ocellatus* habitat occupancy differed significantly from random, while for *D. vulgaris* no such difference was detected (Table 3,

Fig. 4c). Furthermore, no significant difference was detected among species (Table 2, Fig. 4c).

The calculation of fractal dimensions (D) and visual surface area, as proxies of macrophyte complexity, (see Table 1) allowed us to relate them with the habitat occupancy of the fish from across the experiments. Both fractal dimensions and surface area demonstrated the same pattern of positive trends for the three species (see Fig. 5a and b). All relationships were statistically significant, except for the relationship of *S. ocellatus* occupancy and fractal dimensions up (Appendix Table 1 in supplementary material). While the slopes for *D. vulgaris* were less steep compared to the other two species, the ANCOVA demonstrated no significant difference in the slopes for both analyses (Fig. 5a, b Appendix Table 2 in supplementary material).

Discussion

Within our experiments, all three species showed a clear association in their occupancy towards more complex habitat configurations, demonstrating that juveniles distinguished and actively selected habitats using visual cues.

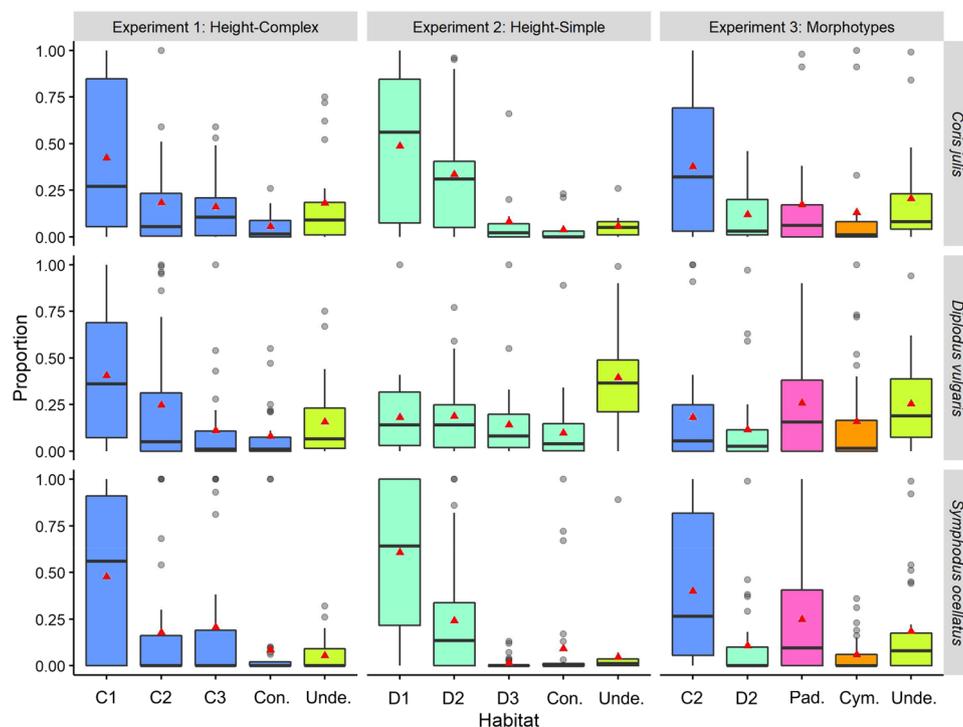


Fig. 3 Proportional occupancy of the different habitat selection areas for the three species *Coris julis*, *Diplodus vulgaris* and *Symphodus ocellatus* amongst the experimental habitat choice experiment. Experiment 1 Height-complex: Macrophyte of *Cystoseira*-like mimics were used (C1–C3). Experiment 2 Height-simple: Macrophyte of *Dictyota* like mimics were used (D1–D3). In Experiment 3 the habitat occupancy of fish with respect to four different macrophyte morphotype mimics of the same height were tested (C2, D2, and Pad.=Padina

like and Cym.=Cymodocea like). In Experiments 1 and 2 Con. corresponds to un-vegetated controls. C. un corresponds to choice undetermined, signified the central and lateral areas of the choice arena, where the habitat choice could not be determined (see Fig. 1C). The names of the morphotype treatments and colours are the same as in Fig. 2, but also include the undetermined choice area=Unde.in lime green. Table 2 provides the corresponding statistical test results of this figure

Table 2 Post-hoc multiple comparison of habitat choices of the three study species and experiments. Table relates to results shown in Fig. 3

Experiment 1			<i>C. julis</i>		<i>D. diploodus</i>		<i>S. ocellatus</i>	
Treatments			<i>t</i>	<i>p</i> (perm)	<i>t</i>	<i>p</i> (perm)	<i>t</i>	<i>p</i> (perm)
C1	<>	C2	2.401	0.019	1.704	0.104	2.895	0.006
C1	<>	C3	2.823	0.005	3.810	0.001	2.546	0.010
C1	<>	Con	4.286	0.001	4.573	0.002	4.791	0.001
C1	<>	C.un	2.45	0.016	3.262	0.004	4.958	0.001
C2	<>	C3	0.338	0.736	1.775	0.082	0.306	0.800
C2	<>	Con	2.243	0.024	2.381	0.021	1.201	0.226
C2	<>	C.un	0.024	0.988	1.187	0.261	1.954	0.057
C3	<>	Con	2.404	0.019	0.685	0.509	1.473	0.145
C3	<>	C.un	0.32	0.749	0.862	0.424	2.202	0.026
Con	<>	C.un	2.304	0.026	1.751	0.092	0.610	0.537
Experiment 2			<i>C. julis</i>		<i>D. diploodus</i>		<i>S. ocellatus</i>	
Treatments			<i>t</i>	<i>p</i> (perm)	<i>t</i>	<i>p</i> (perm)	<i>t</i>	<i>p</i> (perm)
D1	<>	D2	1.131	0.246	0.129	0.899	3.944	0.001
D1	<>	D3	3.680	0.004	0.730	0.492	8.085	0.001
D1	<>	Con	4.365	0.001	1.690	0.091	6.008	0.001
D1	<>	C.un	4.194	0.001	3.585	0.002	7.134	0.001
D2	<>	D3	2.548	0.018	0.879	0.381	3.876	0.001
D2	<>	Con	3.257	0.002	1.883	0.071	2.021	0.053
D2	<>	C.un	3.060	0.005	3.546	0.003	2.997	0.002
D3	<>	Con	0.917	0.462	0.905	0.380	1.703	0.133
D3	<>	C.un	0.524	0.773	4.251	0.002	1.031	0.420
Con	<>	C.un	0.745	0.482	5.306	0.001	0.862	0.476
Experiment 3			<i>C. julis</i>		<i>D. diploodus</i>		<i>S. ocellatus</i>	
Treatments			<i>t</i>	<i>p</i> (perm)	<i>t</i>	<i>p</i> (perm)	<i>t</i>	<i>p</i> (perm)
C2	<>	D2	3.006	0.004	0.969	0.348	3.434	0.003
C2	<>	Pad	2.071	0.046	0.992	0.296	1.571	0.106
C2	<>	Cym	2.469	0.020	0.300	0.773	4.442	0.001
C2	<>	C.un	1.757	0.087	1.071	0.315	2.381	0.025
D2	<>	Pad	0.737	0.478	2.058	0.052	1.867	0.073
D2	<>	Cym	0.141	0.899	0.685	0.496	1.062	0.341
D2	<>	C.un	1.244	0.231	2.342	0.022	1.166	0.245
Pad	<>	Cym	0.475	0.628	1.331	0.178	2.888	0.004
Pad	<>	C.un	0.392	0.691	0.043	0.965	0.777	0.440
Cym	<>	C.un	0.871	0.430	1.467	0.163	2.289	0.024

Significant differences were marked in bold. Significance level of *p* values were adjusted for each species and experiment to ≤ 0.005 following Bonferroni correction for multiple comparison tests

Previous studies investigating links between specific habitat features and juvenile fish have predominantly relied on differences in abundances to determine their functional importance. However, non-random use of habitats after settlement may be a consequence of various factors affecting distribution patterns at a small scale (e.g. abundance of prey, presence of predators, or shelter opportunities) (Hixon and Beets 1993; MacPherson 1998; Shulman 1984; Steele 1999; Vigliola et al. 1998). Thus far these studies could not distinguish if differences in abundances were caused by the active movement and choice by the

juveniles or if they reflected differences in juvenile fish's survivorship related to habitat properties (Cheminée et al. 2016; Cuadros et al. 2019; Thiriet et al. 2013). While differential survivorship has been experimentally confirmed as a potential mechanism for observed distribution patterns for some juveniles (Scharf et al. 2006), few studies investigated and demonstrated active habitat selection (but see Mercader et al. 2019; Yeager and Hovel 2017 or Laegdsgaard and Johnson 2001). Within the present study, we therefore focused on the visual recognition of macrophyte habitat structure (i.e. height and complexity) by the

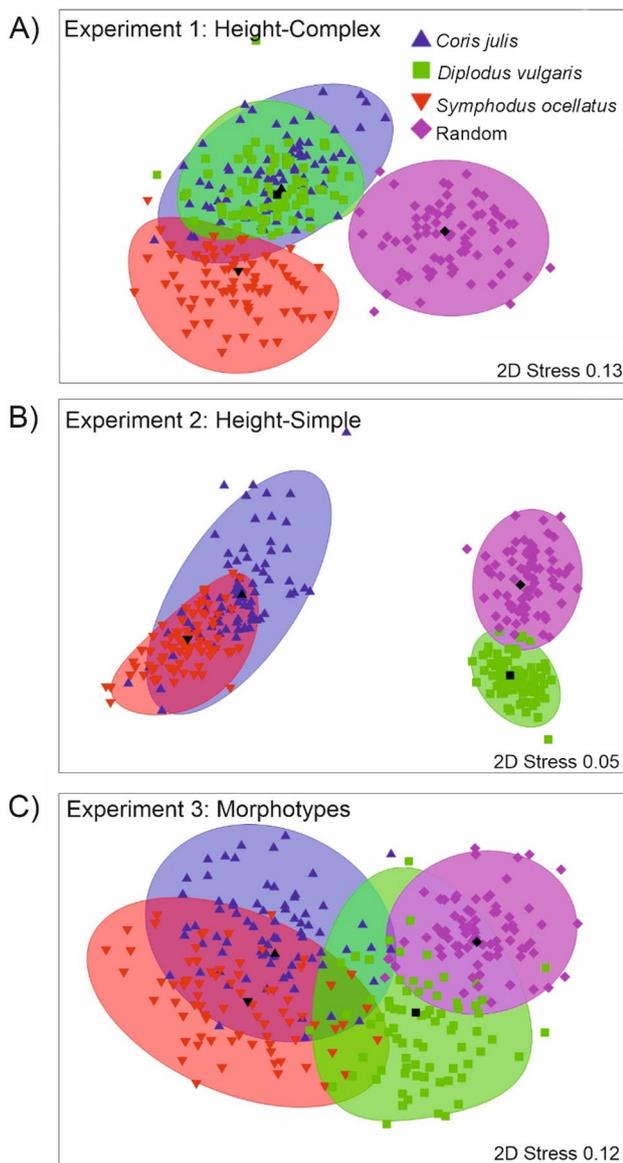


Fig. 4 Multivariate bootstrap average plot showing the difference between the choices of the three fish species tested against a random choice scenario for the three experiments conducted (**A**: experiment 1, **B**: experiment 2, **C**: experiment 3). The points for each species and the random scenario within plots represent bootstrapped centroids following 100 permutations. The plots also show 95% smoothed confidence envelopes for the distribution of bootstrapped centroids of each fish species and the simulated random choice. For the associated PERMANOVA results see Table 3

selected juvenile fish species. In experiments 1 and 2 we varied the height of two macrophyte mimics, one complex and one slightly simpler, respectively. All three species responded similarly to experiment 1, testing the most complex macrophyte mimic type (*Cystoseira*-like), with fish spending more time swimming near the tallest habitat and less in any of the other treatments or control. The positive response towards the tallest macrophyte mimic was

repeated in experiment 2, where fishes were exposed to structurally simpler macrophyte mimics (*Dictyota*-like), by *C. julis* and *S. ocellatus*. In fact, the selection of the tallest habitat appeared to be more pronounced in these species compared to experiment 1. In contrast, for *D. vulgaris* in experiment 2 no clear choice appeared to be visible, with individuals spending equal amounts of time near the three choices and the control habitats. Indeed, individuals of *D. vulgaris* passed proportionally more time in the central and lateral undetermined choice areas.

Comparing the responses of the three species in experiments 1 and 2, it appears that the selection of macrophyte height is context-dependent. For *C. julis* and *S. ocellatus*, attraction towards height appears to be stronger when exposed to simpler macrophyte mimics. For *D. vulgaris* this relationship appears to be reversed, with fish only selecting for height when exposed to complex plants, while when exposed to simpler plants no clear choice was evident. The difference in the choice patterns may be derived from the differences in shelter requirements and behaviour of the three fish species. Hinz et al. (2019) reported that *C. julis* and *S. ocellatus* are fish that appear to avoid predators by hiding within macrophyte meadows, while *D. vulgaris* appears to use macrophyte patches or other objects like rocks to hide behind, with some free space for swimming to outpace potential predators. These contrasting behaviours between species observed in the wild, to some extent may be reflected by the results of experiments 1 and 2. In experiment 1 the structure provided by the complex macrophyte was sufficient for *D. vulgaris* to provide shelter to hide behind, whereas the other lower treatments providing more open space. In experiment 2, the macrophyte may not have had sufficient complexity to serve as cover and thus *D. vulgaris* spent equal amounts of time in the 4 choice areas and substantially more time in the central area.

In the 3rd experiment, the height of macrophyte was maintained, but the complexity of the habitats offered to the fish varied. *C. julis* and *S. ocellatus* appeared to spend most time near the most complex habitats. *C. julis* predominantly occupied the C2 habitat (*Cystoseira*-like habitat), while *S. ocellatus* also spent most time near habitat C2, it also showed some affiliation to habitat type Pad (*Padina*-like), the least complex macrophyte mimic considering its fractal dimensionality. However, visually this macrophyte mimic appeared as the densest or most solid structure and thus occupied, due to its large oval-shaped leaves, the largest visual 2D surface area. Interestingly, although *D. vulgaris* spent most time in this experiment in the undefined area, there were indications of a slightly higher occupancy near this habitat, potentially being more attractive as cover to hide behind, compared to the other macrophyte mimics. The only other habitat choice experiment with respect to this species (Mercader et al.

Table 3 Results of the three macrophyte habitat choices experiments of juvenile of *Coris julis*, *Diplodus vulgaris* and *Symphodus ocellatus*. Table shows differences in choice patterns between the three study species in respective experiments. It furthermore shows the difference in choice pattern of the three species versus a simulated random habitat choice. Results correspond to data shown in Fig. 4

	Species	<i>t</i>	<i>P</i> (perm)	<i>Df</i>	Perms
Experiment 1	<i>C. julis</i> vs Random	17.697	0.015	50	997
	<i>D. vulgaris</i> vs Random	19.376	0.006	58	998
	<i>S. ocellatus</i> vs Random	22.458	0.001	57	999
	<i>C. julis</i> vs <i>D. vulgaris</i>	0.24615	0.971	50	999
	<i>S. ocellatus</i> vs <i>D. vulgaris</i>	11.349	0.263	57	999
	<i>C. julis</i> vs <i>S. ocellatus</i>	11.128	0.295	49	998
Experiment 2	<i>C. julis</i> vs Random	2.917	0.001	43	998
	<i>D. vulgaris</i> vs Random	17.889	0.016	58	999
	<i>S. ocellatus</i> vs Random	42.179	0.001	58	999
	<i>C. julis</i> vs <i>D. vulgaris</i>	32.199	0.001	43	997
	<i>S. ocellatus</i> vs <i>D. vulgaris</i>	45.522	0.001	58	999
	<i>C. julis</i> vs <i>S. ocellatus</i>	10.811	0.297	43	999
Experiment 3	<i>Coris julis</i> vs Random	16.632	0.035	49	999
	<i>D. vulgaris</i> vs Random	11.534	0.267	57	999
	<i>S. ocellatus</i> vs Random	21.647	0.002	56	999
	<i>C. julis</i> vs <i>D. vulgaris</i>	12.892	0.14	48	998
	<i>S. ocellatus</i> vs <i>D. vulgaris</i>	15.347	0.068	55	999
	<i>C. julis</i> vs <i>S. ocellatus</i>	0.59319	0.844	47	998

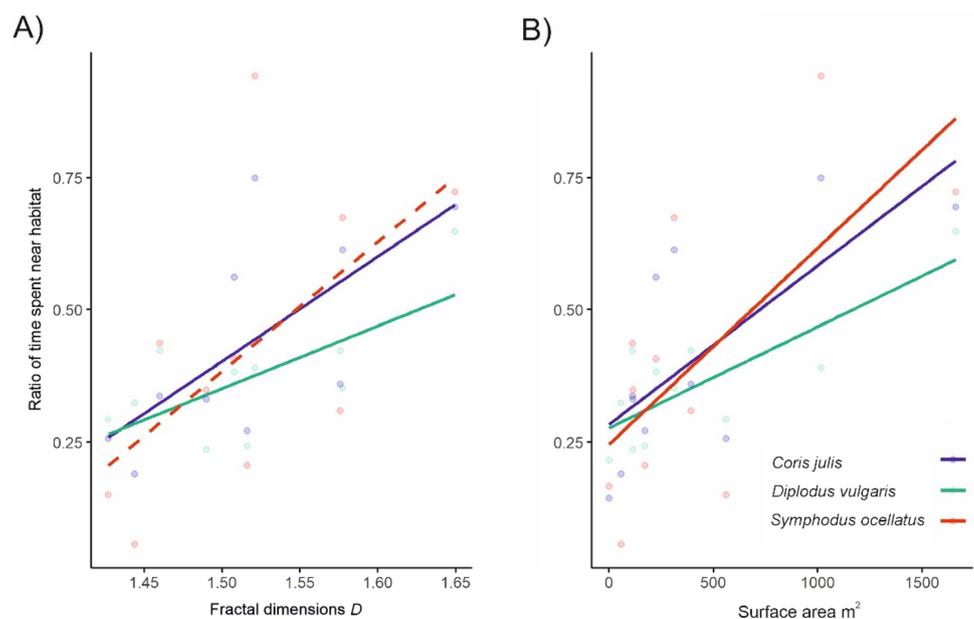
Values shown in bold are statistically significant at $P < 0.05$

T statistic; *P* significance; *Df* degrees of freedom; *Perms* number of permutations

2019) demonstrated that juveniles positively selected artificial habitat (PVC tube) and rocks, while dismissing seagrass meadows, where survival was also found to be lower. These findings appear to concur to some extent with the results of this study, which suggest that more solid structures serving as cover may be important for this species.

While within the experimental design, we made a distinction between habitat complexity and height, it is evident from the fractal dimension calculated for the different macrophyte treatments, that this is an arbitrary distinction. An increase in the macrophyte height always resulted in an increase in the fractal dimensions (i.e. complexity). This is

Fig. 5 Regression plots showing the relationship of both fractal dimensions (A) and visual surface area (B), as habitat complexity measures, with the proportion of time fish spent near habitats for the three species studied. Regression plot A excludes zero complexity control areas, see “Methods” section above for justification, while plot B contains all data



somewhat self-evident, as larger macrophyte plants will tend to overlap much more with neighbouring individuals, creating a more complex habitat, compared to smaller individuals with short stems and leaves. Thus, the results of the experiment should be interpreted with this aspect in mind. To some extent, we tried to address this issue by also providing the relationship between fractal dimensions and 2D surface area as explanatory variables for occupancy, which proved to be positive and statistically significant in most instances (except for the relationship between fractal dimensions and *S. ocellatus* occupancy).

Conclusion

Considering these and past results, the nursery function of macrophytes of the littoral zone in Mediterranean has been further highlighted. However, this coastal zone is currently undergoing fundamental changes related to the invasion of non-native herbivorous tropical fish (Pickholtz et al. 2018), pollution (Pedrotti et al. 2016), physical impact (Sánchez-Arcilla et al. 2011) and climate change (Paireud et al. 2014). All of these have the potential to reduce or change macrophyte cover, leading to fundamental structural changes that may ultimately affect the survivorship of dependent juveniles. One of the projected threats to macrophyte cover in the Mediterranean is the increasing spread of the non-native herbivorous rabbit fish species (Pedrotti et al. 2016). These species have the potential to significantly diminish macrophyte cover, and its impact has been likened to the detrimental effects of deforestation (Verges et al. 2014). Reflecting on the potential level of vulnerability from macrophyte cover loss or structural simplification on the three species studied (considering here primarily the need for predator avoidance), *S. ocellatus* would be the most vulnerable to such changes, followed by *C. julis*, with the least vulnerable being *D. vulgaris*, as this species may use other objects such as rocks to find cover. It is evident that from the behavioural choices we cannot deduct the demographic consequences on these species. However, animal behaviour is partly a reflection of selective processes and learning, aimed at maximizing survival. Thus, we assumed within this study that distinct preference for a particular habitat type is linked with species-specific requirements, that if not fulfilled may ensue negative consequences. We want to emphasize that we are not implying that behavioural preference studies can serve as a substitute for demographic studies. However, these studies can assist us in directing our scientific focus toward species that are more susceptible to experiencing adverse effects in the face of habitat change.

The experimental approach taken by this study and its results, demonstrate clear complementarity to traditional observational studies that deduct habitat affiliations from

distributional differences. While the latter could not establish if fish actively choose habitats, the current study provides some basis to support this notion. Tank experiments are intrinsically limited in their ability to fully replicate natural environmental conditions and consequently can influence fish behaviour. In this particular study, the chosen experimental setup imposed restrictions on fish movement, utilized artificial lighting and habitats, and potentially induced stress through the process of capture, acclimation and experimental handling. Nevertheless, the coherence between conclusions drawn from past observational studies and current results provide some basis for confidence that the behaviours observed reflected genuine habitat choice patterns.

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Author contributions All authors contributed to the study's conception and design. Material preparation, data collection and analysis were performed by HH, PA, AGV, OR, GC, JC-F, MMG, AG and JM. The first draft of the manuscript was written by HH and JC-F, all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval Ethical approval for the capture and experimentation on juvenile fish was provided by the responsible local authorities, Conselleria de Agricultura, Pesca i Alimentació, by the permit code 2019/19/AEXP. All field activities were carried out in compliance with national laws.

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