

# Local habitat and seascape structure influence seagrass fish assemblages in the Venice lagoon: the importance of conservation at multiple spatial scales

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## Abstract

Seagrass meadows are a critical component of estuarine and coastal seascapes, and their structure influence fish assemblages at multiple spatial scales. The patch mosaic model, which defines the seascape as a collection of interacting habitat types, is increasingly adopted to prioritise protected areas and design ecological restoration schemes, hence helping to preserve seagrass meadows and the associated fish assemblages. Despite that, there are few studies investigating the relative contribution of environmental characteristics measured at different spatial scales in determining the distribution of seagrass fish. This study collects fish and environmental observations taken at both site and seascape scales in seagrass meadows in the Venice lagoon (Adriatic Sea, Italy). By means of Generalised Linear Models, it aims to disentangle the relative influence of local water quality and habitat characteristics from that of habitat mosaic properties, investigating the response of whole fish assemblage descriptors, feeding guilds and dominant species. While confirming the primary importance of local habitat quality, the study highlights that also seagrass habitat structure at the seascape scale is relevant for seagrass fish assemblages, influencing total biomass, biomass of macrobenthivorous and hyperbenthivorous/piscivorous species and seagrass specialists such as syngnathids. Conservation of seagrass fish assemblages can therefore be promoted in Mediterranean coastal lagoons by preserving or restoring some features of the habitat mosaic, namely the extension of seagrass patches and their shape complexity, in addition to local water quality and seagrass cover.

**Keywords:** transitional waters, patch mosaic, seagrass meadows, management, restoration

## 1. Introduction

Coastal ecosystems, including lagoons and estuaries, are characterised by a high spatial variability in abiotic and biotic conditions (McLusky and Elliott 2004). The complex arrangement of different habitats (e.g. seagrass meadows, saltmarshes, mud flats, oyster reefs) and the presence of gradients in water physico-chemical parameters and hydromorphological characteristics are typical features of these environments (Sheaves 2009; Barbier et al. 2011). For such reasons, coastal and estuarine ecosystems are effectively studied from a seascape ecology point of view, where a seascape can be defined as a spatially heterogeneous area that can be perceived and described as a mosaic of homogeneous elements (i.e. patches) (Boström et al. 2011). Distribution of faunal organisms could be particularly influenced by mosaic composition and spatial configuration of habitat patches (Pittman et al. 2004), due to the capability of many species to exploit different resources during their life cycle by actively moving and/or disperse as larvae from a habitat to another (Nagelkerken et al. 2015). In these terms the patch mosaic model, which characterises the seascape as a collection of interacting habitat types providing complementary resources for motile fauna (Wiens 1995; Davis et al. 2014), is particularly useful to investigate the role of seascape attributes in determining fish distribution and movements in estuarine and coastal marine environments (Irlandi and Crawford 1997; Pittman et al. 2004; Pittman et al. 2007; Nagelkerken et al. 2015).

Along with the increase in popularity of such an approach in coastal research, the implications of a seascape perspective in ecosystem conservation and restoration are also emerging. In general, a seascape-based approach to habitat and species conservation would fit well into the context of coastal zone management, which usually operates at the scale of administrative water bodies, and would allow to take into account the high spatial diversity that characterises coastal ecosystems (Grober-Dunsmore et al. 2009). Management and conservation of fish fauna in particular, could take advantage of the concepts and tools developed from seascape ecology. The study of the coastal mosaic would help managers to identify essential habitat characteristics for fish (Betzabeth and de los Ángeles 2017), and decision tools based on seascape composition and configuration are currently being developed to prioritise areas for the creation of coastal reserves (Engelhard et al. 2016). Insights from seascape ecology also assisted the choice of sites where mangrove forests

could be restored in order to improve habitat connectivity for reef fish (Mumby 2006), and guided the design of large-scale restoration schemes aimed to enhance fish populations in saltmarsh ecosystems (Rozas and Minello 2007; Weinstein and Litvin 2016). The application of management strategies at the seascape scale would be particularly critical in estuaries and coastal lagoons. These ecosystems are indeed typically affected by multiple anthropogenic pressures that may lead to the degradation and loss of habitats and associated faunal assemblages, as well as to the depletion of important ecosystem services such as the nursery function for commercially important species, the maintenance of water quality and carbon stocking (Vasconcelos et al. 2007; Elliott and Quintino 2007; Franco et al. 2009; Solidoro et al. 2010; Lotze et al. 2011).

Many studies conducted at the seascape level targeted seagrass meadows (Robbins and Bell 1994; Salita et al. 2003; Boström et al. 2006; Connolly and Hindell 2006). Seagrasses are a critical component of coastal seascapes, being a major primary producer, supporting detritus-based trophic webs and stabilising sediments (Nordlund et al. 2016). Among the number of ecosystem functions they supply, seagrass meadows also provide an essential habitat for a variety of faunal assemblages, including fish (Whitfield 2016). Seagrass habitat structure can significantly affect the distribution of seagrass-associated fish species at multiple spatial scales. For instance sheltering, food availability, larval recruitment and predator-prey interactions can be influenced by both microhabitat characteristics such as shoot density, canopy height and epiphytal load (Jackson et al. 2006a; Horinouchi 2007) and seascape properties such as edge complexity and patchiness of meadows (Ford et al. 2010; Smith et al. 2010; Thistle et al. 2010; Smith et al. 2011). Furthermore, seagrass meadows play a fundamental role as part of the seascape nursery in coastal ecosystems (Nagelkerken et al. 2008; Nagelkerken et al. 2015), and represent a focal habitat in coastal mosaics for a variety of species of commercial and conservation interest (Jackson et al. 2006b; Smith et al. 2008; Macreadie et al. 2010; Ryan et al. 2012; Staveley et al. 2017).

Despite the increasing interest in the role of seascape structure as potential driver of seagrass fish distribution (e.g. Jackson et al. 2006b; Ford et al. 2010; Smith et al. 2010; Moore et al. 2011; Staveley et al. 2017), fewer works have taken into account the potential effect of site-scale water quality, in addition to seascape characteristics (Dance and Rooker 2015; Gilby et al. 2016). There are also few examples of studies including different candidate mosaic extents (e.g. Pittman and Brown 2011; Pittman et al. 2007). In addition, since most

of the studies are carried out in tropical and northern European temperate ecosystems, there is a general lack of knowledge on the influence of the coastal seascape on fish assemblages in the Mediterranean Sea, which in turn represents a biodiversity hotspot for marine fauna (Abdul Malak et al. 2011).

The present work aims to bridge these knowledge gaps by investigating the potential influence of the seascape on seagrass fish in the Venice lagoon (Adriatic sea, Italy), taking into account two different spatial scales and disentangling the relative influence of local water quality and habitat characteristics (i.e. the site scale) from that of mosaic properties (i.e. the seascape scale). This study tested the hypothesis that properties of seagrass meadows measured at the seascape scale influence seagrass fish, and hence that seascape characteristics should be taken into account in conservation and restoration actions. In particular, this approach allowed us to i) understand whether the seagrass fish assemblage responds to the seascape structure in the Venice lagoon, and ii) identify which environmental characteristics at both site and seascape scale are critical for management, conservation and restoration of seagrass ecosystems in Mediterranean transitional waters.

## 2. Methods

### 2.1. Study area and definition of spatial scales

The Venice lagoon is the largest Mediterranean coastal lagoon (approximately 550 km<sup>2</sup>) and is located in the northern Adriatic sea (Fig. 1). It is connected to the sea by three inlets, and experiences a tidal range of  $\pm 0.50$  m during spring tides (Umgiesser et al. 2004). It is mostly composed of shallow water areas, with an average depth of 1.2 m (Molinarioli et al. 2007), which are intersected by a network of channels up to 30 m deep (Solidoro et al. 2004). Shallow water areas usually experience strong spatial and temporal variations in environmental conditions such as salinity, dissolved oxygen, turbidity, trophic status and sediment granulometry, these being driven by both natural processes and multiple anthropogenic pressures (Solidoro et al. 2010). The geomorphological heterogeneity and the strong spatial gradients contribute to forming a highly diverse seascape of islands, saltmarshes, creeks, mud- and sandflats, channels, man-made structures and seagrass meadows. Three species of seagrasses are present in the Venice lagoon, namely *Cymodocea nodosa*,

*Zostera marina* and *Z. noltei*, forming very different meadows in terms of shoot density, canopy height and blade dimensions (Sfriso and Ghetti 1998).

For the purposes of this study, we assumed that two different spatial scales influence fish assemblages, namely site scale and mosaic scale. The site scale corresponded to the area within which fish were actually sampled (see next paragraph for details on fish sampling). The mosaic scale corresponded to the portion of seascape in which each sampling site is located, and was spatially defined as circular buffers surrounding each sampling site. We created mosaic buffers of 50, 100, 300, 500 and 800 m-radius. These extents corresponded to circular areas of different sizes (approximately 0.8, 3, 28, 79 and 201 hectares respectively), thus allowing to include seascape properties that may emerge at different extents.

**Fig. 1** Study area and examples of the habitat mosaics considered

## 2.2. Fish sampling

We gathered data from nine years of fish surveys in the Venice lagoon (between 2002 to 2015) and included observations performed either in spring (April to June; n=114), summer (July to September; n=59) or autumn (October to December; n=85) depending on the specific survey. A total of 258 observations were included in the dataset. Throughout the years, all surveys were made so as to explore the same typologies of lagoon areas, i.e. shallow water seagrass beds along the confinement gradient created by each one of the three sea inlets (Fig. 1). As a result, the dataset employed for the analyses included observations from 75 different seagrass sites. All observations were conducted with a standardised methodology. Fish were caught by means of a small beach seine net, following the protocol described in Franco et al. (2006b). We photographed caught fish on millimeter paper and then we released them. Only when necessary, we sacrificed a representative subsample of fish with an excess of 2-phenoxyethanol, preserving it in 8% buffered formaldehyde and then identifying it in the laboratory. We identified fish at the species level, and registered abundance (number of individuals) and biomass (g) at all sites. Biomass was always estimated from measures of standard length. We standardised all data over an area of 100 m<sup>2</sup>.

### 2.3. Site scale characterisation

We characterised each sampling location at the site scale by taking into account a set of environmental parameters. Together with fish sampling, we measured water temperature (°C), dissolved oxygen (percentage of saturation), salinity (PSU) and turbidity (FNU) by means of a multi-parameter probe (HANNA HI-929829) positioned in the water column above the seagrass canopy. We also recorded some features of the seagrass habitat within the area sampled. We estimated the average seagrass cover by visual census following the Braun-Blanquet method (Braun-Blanquet 1972), and subsequently expressed it as percent cover. We identified three meadow typologies, according to the observed floristic composition at the moment of sampling, and based on the resulting differences in canopy height as indicated in the literature for the Venice lagoon (Sfriso and Ghetti 1998). We classified as “tall meadows” either pure or mixed meadows including *C. nodosa* or *Z. marina*, always without *Z. noltei*; pure *Z. noltei* meadows as “short meadows”; mixed meadows of *C. nodosa* or *Z. marina* and always including *Z. noltei* as “mixed meadows”. We also associated a value of sediment grain size (percentage of sand in the 10 cm surface layer) to each sampling site using data from previous studies (ARPAV, 2012; MAG.ACQUE - SELC, 2005; MAG.ACQUE - THETIS, 2005). As a measure of confinement, we calculated the distance of each site from the nearest sea inlet along the lagoon channel network. We standardised all the numerical variables, allowing direct comparison between them.

### 2.4. Mosaic scale characterisation

In order to characterise the seascape of the Venice lagoon we took into account nine habitat typologies: seagrass meadows (either tall, short or mixed meadows, following the same method used to categorise seagrass habitat at the site scale), natural saltmarshes, saltmarsh creeks, intertidal flats and subtidal shallows (without seagrasses but potentially covered by macroalgal beds), artificial marshes/flats and shallower portions of lagoon channels (up to -3.5m deep). We included in the seascape characterisation also the mainland, islands and deeper portions of lagoon channels, and classified them as “no habitat”, assuming them to represent physical obstacles for shallow water fish. We derived all habitat typologies from land cover maps. We considered the temporal variation of some habitats (namely natural saltmarshes, creeks, intertidal/subtidal flats and channels) negligible within the study period, and therefore we used the same maps over the entire time span of the analysis (MAG.ACQUE, 2002). By contrast, we took into account the temporal variation of

dynamic habitats (namely seagrass meadows and artificial habitats created in different occasions over the study period), and used different temporal maps (Curiel et al., 2014; MAG.ACQUE, 2002; Rismondo et al., 2003) (see also Fig. S1 in Online resource for an overview of the temporal coverage of habitat maps).

We then calculated a set of seascape metrics for each one of the five mosaic extents considered (50, 100, 300, 500 and 800 m-radius buffers). Metrics were based on the relative surface occupied, number and spatial arrangement of habitat typologies (McGarigal et al. 2002) and allowed to quantify both composition and spatial configuration of circular habitat mosaics surrounding each sampling site (Table 1; see also Fig. S2 in Online resource for a graphical representation of seascape metrics). In order to manage the collinearity between seascape variables, and to summarise seascape properties with independent components, we performed a Principal Component Analysis (PCA) on standardised seascape metrics at each buffer extent and extracted metric loadings on PC axes. After checking the screeplots for changes in slope, we selected the first four axes of each PCA to characterise the mosaic scale.

## 2.5. Data analysis

### *Selection of mosaic extents*

We carried out a preliminary analysis of mosaic scale variables, in order to identify the most relevant buffer extents in terms of expression of seascape characteristics among the whole range of extents considered. We took the proportion of variance explained by the first four PC axes as a proxy for the amount of information that each buffer extent could provide. In addition, we visually inspected the PCA bi-plots based on each extent, in order to assess whether PC axes could be interpreted in terms of meaningful seascape patterns.

### *Response variables*

This study investigated the influence of site and mosaic scales on three components of the seagrass fish assemblage. We considered total fish biomass density, total number of species and Margalef's species richness calculated on biomass density, in order to characterise the seagrass assemblage as a whole. Adopting the approach of Franco et al. (2008), we grouped all the species (with the exception of marine stragglers, only occasionally found within the lagoon) into feeding guilds, and considered the biomass density of each guild. Since one species could be allocated to multiple feeding guilds, we expressed the contribution of each species to each guild as a proportion (0 to 1), by identifying the importance of different food resources within the diet

on the basis of literature (Froese and Pauly 2015) and of available data for the Venice lagoon (Franzoi, unpublished data). Finally, we included in the analysis the densities of biomass of species accounting for 95% of cumulative fish assemblage biomass. A complete list of the species caught and the respective allocation to feeding guild is reported in Table S1 (see Online Resource). We then used whole fish assemblage indicators, feeding guilds and single species densities as independent response variables in GLMs.

Table 1: Seascape metrics used to characterise the habitat mosaics surrounding fish sampling sites. Each metric quantifies a property of the seascape composition or configuration, and can be computed for each habitat typology and/or for the whole habitat mosaic. All the metrics are described after McGarigal et al. (2002).

<b>Category</b>	<b>Metric</b>	<b>Description</b>	<b>Computed for each habitat type in the mosaic</b>	<b>Computed for the whole mosaic</b>
Composition	PROP	Proportion of the whole mosaic represented by each habitat type	x	
Composition	DENS	Patch density: the numbers of patches divided by total mosaic area	x	x
Composition	DIV	Diversity calculated as the Shannon's index on habitat area		x
Composition	EVE	Evenness calculated as the Pielou's index on habitat area		x
Composition	ARE	Average area of all patches		x
Composition	LARG	Largest patch index: percentage of mosaic occupied by the largest patch		x
Configuration	SHP	Landscape shape index: a standardised measure of edge density that adjusts for the size of the mosaic	x	x
Configuration	FRC	Perimeter-area fractal dimension: a measure of sinuosity of patch geometries. It equals 2 divided by the slope of regression line obtained by regressing the	x	x



logarithm of patch area against the logarithm of patch  
perimeter

Configuration COHE Patch cohesion index: a measure of the physical  
connectedness of patches

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x

### *Model calibration*

In order to understand how the variability in the response variables is explained with different combinations of environmental predictors, we fitted Generalized Linear Models (GLMs; McCullagh and Nelder, 1989) by independently modelling each response variable, using the most appropriate distribution family. We fitted negative binomial GLMs for species and feeding guild densities, and zero-inflated Poisson GLMs for the number of species. We adopted a hierarchical approach, and used different model structures (Table 2) so as to hypothesise different contributions of variables measured at the site and at the mosaic scale, ultimately allowing to disentangle the relative influence of each spatial scale on response variables.

Given the importance of seasonal variations for fish in coastal and transitional waters (Elliott and Hemingway 2002; Green et al. 2009; Franzoi et al. 2010; Ribeiro et al. 2012; Perry et al. 2017), we took into account both sampling season and year in all the GLM formulations. The interaction between season and year hence represented the temporal factor in the models. We included three model formulations in the analysis, investigating the following hypotheses (Table 2): the response variable is affected by temporal factor only (seasonal and inter-annual variability; category m0); the response variable is affected by both temporal factor and site scale predictors (category m1); the response variable responds to temporal factor, site scale and mosaic scale predictors (the latter quantified at each mosaic extent, hence yielding five models; category m2). We then calculated the explained deviance for each model formulation.

### *Selection of best models and effect estimation*

For each response variable, we selected the best candidate model by using the Akaike Information Criterion corrected for small samples (AICc; Burnham and Anderson, 2002). To perform the selection, we chose for each set of models the one with the lower AICc value and the higher probability (i.e. higher AICc weight) of being the best formulation (Burnham and Anderson, 2002). We selected an AICc weight threshold of 0.7 (i.e.

the selected model has at least 70% of chance of being the best formulation in each set) and, following Burnham and Anderson (2002), considered models with a difference in AICc lower than 2 as undistinguishable. This allowed us to explore each hypothesis formulated, by verifying if progressive addition of predictor terms would improve the overall fit of the model. We derived the sign and the magnitude of the effect of each site scale predictor directly from the parametric coefficients estimated by the best model. In contrast, we calculated the effect of each seascape metric as the sum of the metric loadings on each PC axis, weighted with the estimated coefficients of the respective axis.

Table 2: Structure of GLMs considered in the analysis. Model formulas and respective hypotheses investigated are also shown. c: constant term (model intercept);  $\varepsilon$ : error term.

<b>Model</b>		
<b>category</b>	<b>Model structure</b>	<b>Hypothesis</b>
m0	$Y_i \sim$ season • year + c + $\varepsilon_i$	Response variable is influenced by temporal factor only
m1	m0 + t + sal + do + turb + sand + dist + cover + canopy	Response variable is influenced by both temporal factor and site scale variables
m2 <sub>j</sub>	m1 + PC1 <sub>j</sub> + PC2 <sub>j</sub> + PC3 <sub>j</sub> + PC4 <sub>j</sub>	Response variable is influenced by temporal factor, site scale and mosaic scale variables (the latter quantified at each extent <i>j</i> , hence yielding <i>j</i> models)

### 3. Results

#### 3.1. Emerging properties of the seagrass seascape

The first four axes of PCAs based on 500 and 800 m extents explained a larger proportion of cumulative variance (68 and 67% respectively) compared with the other extents considered (58, 62 and 65% of variance explained by the first four axes of PCAs based on 50, 100 and 300 m extents respectively). Bi-plots of PC axes at 500 and 800 m extents were also more easily interpretable in terms of patterns in seascape properties (see also Fig. S3 in Online Resource for an example of biplots, Fig. S4 for the loadings matrix and Fig. S5 for an estimation of collinearity between seascape variables). For these reasons, we selected 500 and 800 m-radius buffers (corresponding to 79 and 201 ha mosaics respectively) as the most relevant mosaic extents from which to infer the main properties of the seascape. The choice of the most appropriate mosaic extent should be carried out while taking into account the scale of movements of the target species. However, home ranges of seagrass fish in Mediterranean lagoons are largely unknown, this severely limiting any a priori selection of a particular mosaic extent (Pittman et al. 2004; Pittman and Brown 2011). As a result, in order to take into account the potential differences in species mobility, we included both the two alternative buffers in the following analysis. A series of patterns in seascape characteristics could be easily identified in PCAs based on 500 and 800m-radius extents. We found such patterns to be highly similar between alternative mosaic extents, allowing a single interpretation of each PC axis (see Fig. S3 in Online Resource).

The first PC axis of PCAs based on both 500 and 800 m-radius extents highlighted a major pattern of seagrass vegetation, with mosaics characterised by higher proportion and shape complexity of tall canopy meadows, opposed to mosaics dominated by natural saltmarshes and intertidal flats. The second axis of both PCAs was related with complexity, with overall habitat diversity, overall shape index and fractal dimension as well as proportion, density and shape index of mixed and short canopy meadows being negatively correlated with average patch area and largest patch index in mosaic. The third axis was associated with proportion and shape

index of non-habitat typologies (i.e. mainland, islands and deep channels), these being negatively correlated with proportion of artificial habitats, subtidal flats and whole mosaic largest patch index. Finally, the fourth axis was associated with lagoon channel habitats, these being positively correlated with whole mosaic diversity and negatively with largest patch index and average patch area (Fig. S3 and Fig. S4 in Online Resource).

### 3.2. Model selection

Both site and mosaic scale (quantified at 800m) were relevant in explaining the variability of the overall fish biomass density (best model belonging to category m2), while overall species richness responded only to site scale (m1). It was not possible to identify a single best model for total number of species (Fig. 2). The best model for overall biomass explained 59% of deviance, while a smaller proportion (43%) was explained by the best model for species richness.

Among feeding guilds, model formulations could only be selected for biomass densities of macrobenthivorous and hyperbenthivorous/piscivorous, while there was not enough support to identify single best models for the other guilds. Macrobenthivorous responded only to site scale (m1), with 58% of deviance explained, whereas hyperbenthivorous/piscivorous responded to both site and 800 m-mosaic scale (m2), with 63% of deviance explained (Fig. 2).

In this work, eight lagoon resident species accounted for 95% of fish biomass in seagrass sites: sand smelt *Atherina boyeri* (family Atherinidae), pipefishes *Nerophis ophidion*, *Syngnathus abaster* and *Syngnathus typhle* (Syngnathidae), large gobies *Gobius niger* and *Zosterisessor ophiocephalus*, the small goby *Pomatoschistus marmoratus* (family Gobiidae) and the blenny *Salaria pavo* (family Blenniidae). The three species of syngnathids all responded to both site and mosaic scale (m2; Fig. 2). While the best model for *S. abaster* included the 500 m mosaic extent, those for both *S. typhle* and *N. ophidion* included the 800 m extent. The respective selected models all explained between 50 and 60% of deviance. Also the small goby *P. marmoratus* responded to the two spatial scales (m2), with the selected best model including both site and 500m-mosaic scale and explaining 68% of deviance. Conversely, *A. boyeri* and *Z. ophiocephalus* responded only to site scale (m1), with models explaining respectively 38 and 61% of deviance. Biomass of *G. niger* was not influenced by environmental variables at any scale, the specie responding only to temporal factor (m0).

Finally, we could not carry out a clear model selection for *Salaria pavo*, since formulations including only the site scale (m1) and both site and 800m-mosaic scale (m2) were undistinguishable (Fig. 2).

**Fig. 2** Output summary of GLMs fitted for the response variables. For each alternative model formulation (m0, m1 and m2, the latter at two mosaic extents) the AICc weight (bars) and the respective difference in AICc value from the best model are shown. The AICc weight threshold of 0.7 for the selection of the best model is also shown as a vertical dashed line. Intensity of colour scale is proportional to the amount of deviance explained by each model formulation. Feeding guilds are labelled as follows. Bmi: Microbenthivorous; Bma: Macrobenthivorous; OV: Omnivorous; HZ: Hyperbenthivorous/Zooplanktivorous; HP: Hyperbenthivorous/Piscivorous; DV: Detritivorous; PL: Planktivorous

### 3.3. Effects of environmental variables at two spatial scales

Sampling season influenced all seagrass fish attributes considered in this work, with no significant interaction with sampling year. Overall, we detected a greater positive effect of summer and autumn compared with spring (figure not shown). The effect of temperature was negative for most of the response variables considered (Fig. 3 and Fig. 4) when including the aforementioned effect of seasonality in the model. Among other variables characterising the site scale, we could observe an overall relevant positive effect of dissolved oxygen, seagrass percentage cover, turbidity and distance from sea inlets for total biomass, macrobenthivorous and hyperbenthivorous/piscivorous guilds, as well as for some species (e.g. *S. abaster*, *S. typhle* and *Z. ophiocephalus*). By contrast, dissolved oxygen and seagrass cover had a smaller effect on biomass density of *N. ophidion*, compared to both other site scale variables and some properties of the seascape. This species also showed a strong negative link with distance (i.e. larger densities found in seagrasses near sea inlets). By contrast, seagrass cover showed a strong negative effect on biomass density of *P. marmoratus* and whole species richness. *A. boyeri* showed a mixed response to site scale variables, its biomass density being positively related to dissolved oxygen and seagrass percent cover and negatively to turbidity.

In addition to site-scale variables, some features of the seagrass fish assemblages were influenced by properties of the seascape (Fig. 3 and Fig. 4). Proportion, patch density and shape index of seagrass meadows in the mosaic played an overall positive effect on biomass density of the whole assemblage, hyperbenthivorous/piscivorous and syngnathid species. Among syngnathids, we could detect some differences in the response to seagrass properties at the mosaic scale. *N. ophidion* and *S. typhle* were both markedly influenced by proportion, patch density and shape index of seagrass habitats, with the former showing a greater response to tall and mixed meadows, and the latter to mixed and short meadows. Conversely, the overall intensity of the response of *S. abaster* to seagrass properties at the mosaic scale was weaker. Density of biomass of *S. typhle* and *N. ophidion* were positively associated also with overall habitat cohesion and largest patch index in the mosaic, and negatively with overall mosaic shape index and fractal dimension. Mosaics with greater proportion of natural saltmarshes and unvegetated substrata showed a negative effect for most of the seagrass fish metrics considered. As opposed to this pattern, biomass density of *P. marmoratus* was positively related to the proportion of intertidal flats and natural saltmarshes in the mosaic, and negatively to proportion, density and shape index of seagrass meadows. Artificial marshes and flats played overall a minor role in affecting seagrass fish fauna, showing both positive and negative effects. Overall habitat diversity in mosaic did not affect markedly the response variables considered.

**Fig. 3** Standardised effects of site-scale (light grey) and mosaic-scale (dark grey) predictors on whole assemblage indicators and feeding guilds, derived from the best GLM formulations. Effect magnitudes are sorted in descending order. Only a subset of mosaic properties is shown, excluding the most collinear variables in PCA (i.e. showing very similar effects). Abbreviations for mosaic variables are described in Table 1

**Fig. 4** Standardised effects of site-scale (light grey) and mosaic-scale (dark grey) predictors on considered species, derived from the best GLM formulations. Effect magnitudes are sorted in descending order. Only a subset of mosaic properties is shown, excluding some highly collinear variables in PCA (i.e. showing very similar effects). Abbreviations for mosaic variables are described in Table 1

## 4. Discussion

The present results confirm the primary importance of site-scale water and habitat quality for seagrass fish assemblages. Nonetheless, they emphasise that also some seagrass habitat features at the seascape scale are influential for seagrass fish assemblages, affecting overall fish biomass and some common species and feeding guilds. This work thus highlights how environmental characteristics at two spatial scales together contribute to determine the distribution of fish in seagrass meadows within coastal lagoons.

The role of local physico-chemical parameters in driving the distribution of fish in estuaries and coastal lagoons is well documented. Estuarine species are usually well adapted to spatial and temporal variability in water quality; nevertheless temperature, dissolved oxygen and salinity (among other factors) exceeding tolerance thresholds can act as barriers to fish movements, hence determining significant differences in assemblage structure and composition along environmental gradients (Blaber and Blaber 1980; Marshall and Elliott 1998; Elliott and Hemingway 2002). Habitat architecture is also a major environmental factor affecting fish distribution at the small scale in estuarine and coastal ecosystems. Highly cryptic species such as syngnathids and gobies associated to seagrasses rely on habitat complexity (Howard and Koehn 1985; Steffe et al. 1989; Malavasi et al. 2007). Greater seagrass cover, taller canopies and greater epiphytial load also represent more suitable feeding habitats, in particular for larger hyperbenthivorous and piscivorous species (i.e., in this work, *S. typhle* and *Z. ophiocephalus*) (Jackson et al. 2006b; Horinouchi 2007; Schultz et al. 2009). Degree of confinement strongly affects biological communities in coastal lagoons, not only by influencing water and sediment properties but also explaining the patterns of larval and juvenile dispersal (Quignard 1984; Franco et al. 2006b; Pérez-Ruzafa et al. 2011). For the purpose of this work, we could not consider the whole confinement gradient of the Venice lagoon (i.e. from sea inlets to mainland) in the sampling scheme, mainly due to the absence of seagrass meadows in very confined areas near the mainland. However, distance from the sea inlets markedly influences many of the species included in the analysis, with the majority of them and overall fish biomass being present with greater biomass densities in seagrass habitats located at greater distances from the sea inlets. More confined meadows of the lagoon are generally characterised by greater nutrient availability (Sfriso et al. 2005a), thus sustaining greater fish biomasses.

The overall fish biomass in studied seagrass habitats is largely composed by habitat specialists such as syngnathids, as already noted for seagrass meadows in the Venice lagoon by Scapin et al. (2016; 2018). Such species are influenced by properties of the habitat mosaic in addition to site-scale environmental parameters. Proportion of the seascape occupied by seagrass meadows, seagrass edge density and larger mosaic patches have a positive effect on overall biomass as well as on syngnathid species, highlighting the importance of a lagoon seascape dominated by seagrass habitats with a substantial presence of ecotones between meadow cores and contiguous unvegetated habitat patches. In addition, the notable differences among *N. ophidion*, *S. abaster* and *S. typhle* in the intensity of the response to seagrass mosaic features highlight the different sensitivity to habitat quality of the three syngnathids. In particular, *N. ophidion* and *S. typhle* show a greater response to extent and spatial arrangement of seagrass meadows in the seascape, as well as a positive response to larger mosaic patches. This emphasises their role as seagrass specialists that could be employed as indicators of seagrass habitat status, as already pointed out for the Venice lagoon (Scapin et al. 2016; Scapin et al. 2018). Syngnathids exhibit preferences for different canopy heights in seagrass meadows at the site scale in the Venice lagoon (Malavasi et al. 2007; Scapin et al. 2018). This paper emphasises that species of this family show a different response to canopy height also at the mosaic scale. Morphological adaptations and recruitment strategies may both contribute to explain the observed preference of *N. ophidion* for taller meadows in the mosaic compared to *S. typhle*. For instance, *N. ophidion* is specifically adapted to entwine median and top portions of seagrass leaves with caudal peduncle, and explore the surroundings in search of prey. Furthermore, this species exhibits planktonic early-life stages for dispersal (Riccato et al. 2003). It can be hypothesised that, in the Venice lagoon, seagrass mosaics with larger proportions of taller canopies (i.e. meadows dominated by *C. nodosa* and *Z. marina*, located in areas with higher hydrodynamism) can provide both greater availability of suitable holdfasts and increased chance to settle for this species. Differences in body morphology and feeding strategies could also explain the observed differences in the response to mosaic extents by syngnathids. *S. typhle* for instance, a larger species feeding on larger, more motile prey including nekton (Campolmi et al. 1996; Franzoi et al. 2004; Vizzini and Mazzola 2004; Oliveira et al. 2007), is indeed influenced by mosaic characteristics at larger (800 m-radius) extents. Nevertheless, our analysis does not allow us to verify such hypotheses. Ad hoc studies should be designed, in order to investigate in detail the response of syngnathids to



seagrass mosaic composition and structure over different extents, taking into account population-level metrics such as age structure and sex ratio.

More generally, such evidences suggest that seagrass fish assemblages, despite including large proportions of species with low mobility (such as pipefishes), can indeed be influenced by seagrass habitat structure also at considerably large extents (tens or even hundreds of ha). Accordingly, Staveley et al. (2017) pointed out that syngnathids in seagrass meadows of Swedish west coast are predicted with higher abundances in simpler rather than more diverse mosaics, taking into account a mosaic extent of ca. 28 ha (300m-radius circular buffer). Syngnathids could indeed benefit from seascapes with little habitat diversity, with mature and well-established meadows forming larger patches providing the most suitable conditions for settlement and survival and greater connectivity between populations (Bell and Westoby 1986; Jackson et al. 2006b; Sato et al. 2016; Staveley et al. 2017). Greater prey availability and/or better foraging efficiency in ecotonal patches (such as at meadows edges) may explain the positive effect of seagrass shape index on syngnathids that emerges from this work, as already noted by several authors (Flynn and Ritz 1999; Jelbart et al. 2006; Smith et al. 2008; Macreadie et al. 2010).

Compared to fish biomass, no influence of the seascape can be found on species richness in the seagrass sites investigated. The present study focuses on  $\alpha$ -diversity, i.e. diversity measured at different sites within the same habitat typology. Congruent results were obtained by Yeager et al. (2011), who found that differences in mosaic structure have no significant effect on fish  $\alpha$ -diversity measured among artificial reefs located in different seagrass seascapes. Similarly, Staveley et al. (2017) showed that species richness among seagrass sites is not influenced by seascape composition and spatial configuration. However, while  $\alpha$ -diversity is affected only by environmental characteristics at the site scale, both total fish diversity in the lagoon seascape ( $\gamma$ -diversity) and diversity turnover among sites ( $\beta$ -diversity) could be linked to seascape variability, as already demonstrated for coastal benthic communities (Harborne et al. 2006). Thus, metrics based on  $\gamma$ - and  $\beta$ -diversity should be taken into account in future studies investigating the influence of seascape structure on fish assemblage diversity.

The inclusion of feeding guilds in the analysis provides relevant insights into scale-dependent trophic functions of seagrass habitats. In this study, macrobenthivorous (Bma) species are influenced only by site scale, while

hyperbenthivorous/piscivorous (HP) respond to both site and mosaic scales. This could reflect the different motility of fish prey in seagrasses; larger prey that swim actively, such as hyperbenthic organisms (e.g. decapods) and fish are likely to be influenced by environmental factors at larger spatial scales compared with smaller and less motile ones, such as macrobenthic organisms (e.g. gastropods and amphipods). In addition, both Bma and HP guilds are composed of relatively few abundant species, with large gobies and *S. typhle* accounting for ca. 70% of Bma and HP biomass respectively (see Fig. S6 in Online Resource) and partly explaining the response of the respective guilds.

While found in the seagrass assemblage, *A. boyeri* and *P. marmoratus* are not considered as seagrass specialists in the Venice lagoon (Franzoi et al. 2010). *A. boyeri* is widespread throughout a large variety of lagoon habitats, both structured and unstructured, this partly explaining the lack of species response at the habitat mosaic scale. *P. marmoratus*, in turn, is often found outside seagrass meadows, showing a particular preference for mud- and sand-flats (Malavasi et al. 2005; Franco et al. 2006b; Franzoi et al. 2010). This species is indeed positively associated with mosaics dominated by unvegetated habitats, such as saltmarshes and intertidal flats.

Although it was beyond our aim to investigate in detail the temporal variability of the studied assemblages, it is worth noting that season played a relevant role in explaining the variability of assemblage biomass. The observed positive effect of summer and autumn, compared to spring, can be explained by the general patterns of reproduction and recruitment in seagrass fish of the Venice lagoon. Spring and early summer are the periods of major reproductive investment in most of the resident species found in seagrass habitats, including pipefish *S. abaster* and *S. typhle* (Franzoi et al. 1993; Riccato et al. 2003) and grass goby *Z. ophiocephalus* (Malavasi et al. 2005; Franco et al. 2012; Zucchetto et al. 2012). Subsequently, fish abundance and biomass increase due to juvenile recruitment and growth during the following months and until autumn (Franco et al. 2006a; Franco et al. 2006b; Franzoi et al. 2010).

### *Implications for conservation*

As one of the first studies applying the seascape approach in the Mediterranean region, this work emphasises the importance of a two-scale (i.e. at site and seascape level) perspective for management and conservation of coastal lagoon biodiversity in this area. Like most transitional water ecosystems in the Mediterranean, the

Venice lagoon is subjected to a variety of anthropogenic pressures, with changes in lagoon morphology and alterations to water and sediment quality being some of the major issues (Curiel et al., 2014; Molinaroli et al., 2009; Sarretta et al., 2010; Sfriso and Facca, 2007; Solidoro et al., 2010). Fish fauna can significantly be affected by the impacts deriving from human activities, including habitat loss (Franco et al. 2009; Zucchetta et al. 2016). Seagrass habitat in particular has been critically impacted in the Venice lagoon as well as in other Mediterranean transitional waters, which faced important regime shifts from benthic macrophytes- to phytoplankton-dominated conditions during the last decades (Sfriso et al. 2005a; Viaroli et al. 2008). Human-induced sediment disturbance and nutrient enrichment in the Venice lagoon, for instance, led to the decline of water quality followed by extensive losses of *Z. marina* and *Z. noltei* meadows at least since the 1990s, in particular within the central and northern sub-basins (Sfriso et al. 2005b; Sfriso et al. 2005a; Sfriso and Facca 2007). This brought major changes in the distribution of seagrasses across the seascape, hence in the structure of the habitat mosaic (Caniglia et al. 1990; Curiel et al. 2014). Seagrass meadows are now starting to recover due to enhanced environmental conditions (Facca et al. 2014b). However, the effects of past habitat changes on seagrass fish assemblages are poorly known.

As demonstrated in this study, the reduction of seagrass habitat coverage at both site and seascape scales should be regarded as an issue for the conservation of associated fish in coastal lagoons. Restoration actions aiming to recreate stable meadows across impacted seascapes may be needed, especially in those areas where direct human activities have triggered a fragmentation process followed by a loss of seagrass cover (e.g. in the northern Venice lagoon) (Sfriso and Facca 2007). The effects of habitat fragmentation on seagrass fish can vary, according to species-specific habitat preferences, the magnitude of the phenomenon and the existence of threshold levels (Bell et al. 2002; Jackson et al. 2006a; Macreadie et al. 2009; Masonjones et al. 2010). When accompanied by a reduction in the habitat extent, however, fragmentation could cause the decline of species that benefit from greater seagrass cover at the site scale and from greater proportion and larger patches of meadows in the mosaic, such as syngnathids (Pérez-Ruzafa et al. 2006). At the seascape scale, seagrass specialists are indeed more likely to be impacted by habitat loss compared with habitat opportunists and species associated with unvegetated gaps between seagrass patches (Horinouchi 2009), such as *P. marmoratus* in the Venice lagoon. Conservation of seagrass specialists could be promoted also by limiting direct human stressors

such as dredging and anchoring, which can significantly concur to seagrass loss in shallow water ecosystems (McCloskey and Unsworth 2015).

Despite that, the conservation objectives towards seagrass fish may not entirely correspond to those towards seagrass meadows themselves. Seagrass restoration schemes often operate to reduce habitat patchiness, aiming to recreate continuity in seagrass meadows over large areas (Campbell 2002; Uhrin et al. 2009). This may not always be desirable in terms of conservation of seagrass fish fauna in coastal lagoons. Overall fish assemblage, as well as species of conservation interest such as *N. ophidion* and *S. typhle* (Pollom 2016a; Pollom 2016b) would indeed benefit from the recovery of seagrass edge complexity (hence patchiness), in addition to habitat extent in the seascape. Seagrass patch complexity could be enhanced by adopting a “diffuse” transplantation scheme, in which a large number of small seagrass sods are transplanted at several locations, hundreds or thousands metres apart, over a large project area. This approach has been followed since 2014 in the northern Venice lagoon to restore seagrass meadows (Facca et al. 2014a). By providing a large number of points of origin for rhizomial propagation, it is expected to create a complex mosaic of seagrass patches at the seascape scale after restoration. Similarly, the use of different plant species both within each transplantation site and between them (Facca et al. 2014a) would enhance the complexity at the mosaic scale due to the different morphology and periods of growth of the species, as in the case of *Z. marina* and *Z. noltei* in the Venice lagoon (Sfriso and Ghetti 1998). Such measures would not only favour the associated fish assemblage through enhanced seagrass patch complexity, but also make an effective and viable restoration strategy for seagrass meadows themselves, by spreading of risks and limiting the impact on donor sites (van Katwijk et al. 2009; Facca et al. 2014a). Moreover, beyond direct restoration actions, the conservation of the lagoon morphological heterogeneity is required for the development of seagrass habitats suitable for fish fauna. Preserving the overall lagoon mosaic of intertidal and subtidal flats, saltmarshes and channels would indeed prevent seagrasses to uniformly spread across the lagoon basin, hence helping to maintain a level of patch complexity similar to that of natural meadows.

Compared with seagrass habitat characteristics, whole mosaic properties (e.g. overall habitat diversity, whole cohesion and complexity) play a minor role in influencing seagrass fish at the seascape scale in the Venice lagoon. The importance of identifying seascape features more relevant for target species and the potential

advantages of such an approach for the management of coastal fauna have been already emphasised for tropical ecosystems (e.g. Pittman and Brown 2011; Betzabeth and de los Ángeles 2017). Similarly, the relative amount of seagrass habitat and its edge density could be taken as practical indicators in Mediterranean coastal lagoon seascapes, to guide the prioritisation of conservation areas for fish and to identify sites where active restoration is needed.

This work underlines how a more efficient management of coastal lagoons should incorporate strategies operating at both spatial scales. In such context, the usually adopted approach based on monitoring and control of environmental quality (e.g. trophic status, oxygen levels and chemical pollutants) at the site scale should be integrated with a seascape perspective, in particular when designing monitoring and conservation schemes that involve seagrass habitats and associated fish fauna. Similarly, criteria for designing seagrass restoration schemes and evaluating their success as fish habitat should not be solely based on the analysis of site-scale conditions (e.g. physico-chemical water and sediment parameters, seagrass floristic composition, percent cover and canopy height) (Short et al. 2000; Bell et al. 2008), but in addition main seagrass seascape features (e.g. spatial continuity and edge density) should be taken into account. Other large-scale factors, such as the morphology of deep areas and the connectivity between these and shallow water habitats, should also be considered in future studies aiming to guide the management of coastal fish assemblages, as suggested by Perry et al. (2017).

A two-scale point of view in conservation should hence be adopted, allowing to take into account the differences in the spatial scale of fish response to different environmental factors (Pittman et al. 2007; Pittman and Brown 2011). However, if a more complete understanding of the influence of broad-scale environmental variables on fish is to be reached, studies on species home ranges and habitat use patterns in coastal and estuarine ecosystems are also needed. They would greatly reinforce any approach taking into account explicitly defined spatial scales, by linking species response at multiple scales with their ecology and behaviour.

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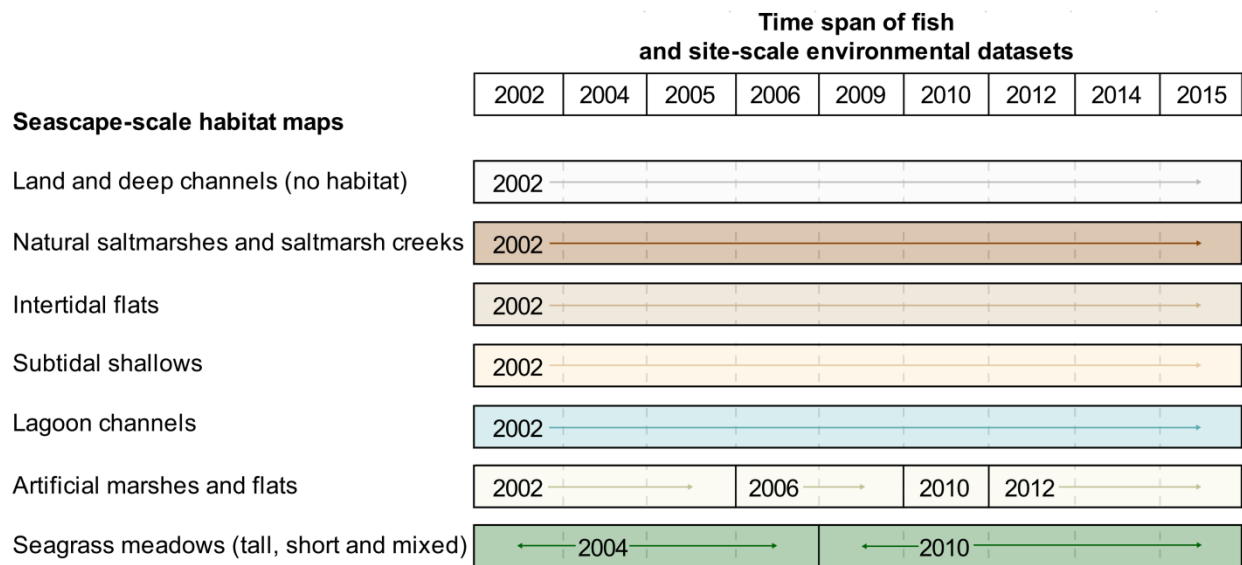
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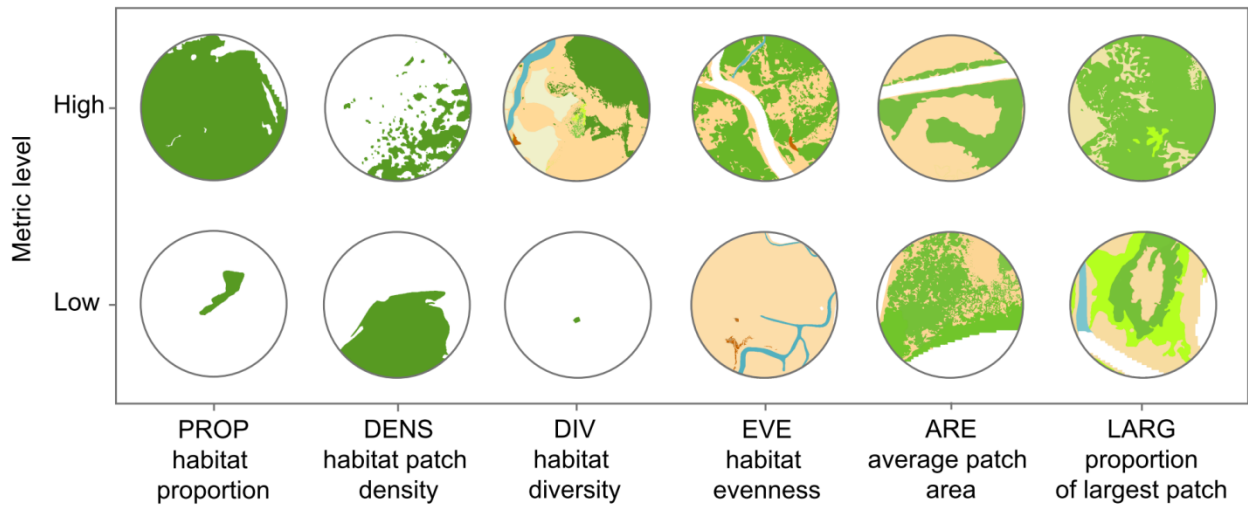
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## Electronic supplementary material

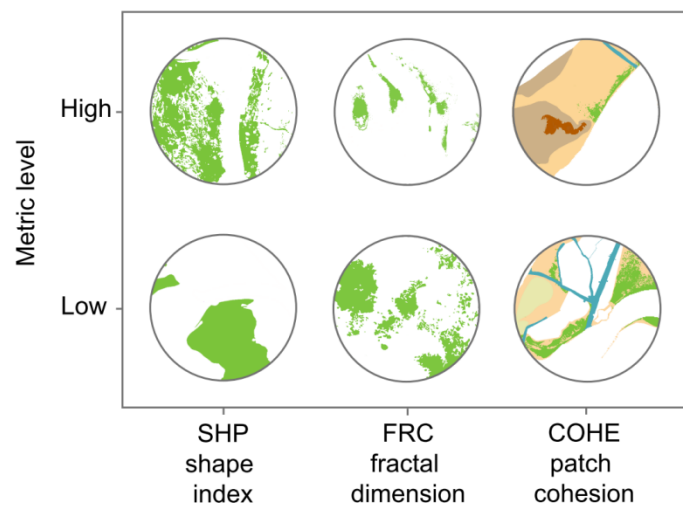


**Fig. S1** Temporal coverage of habitat maps used to characterise the seascape scale, in relation to fish and site-scale environmental sampling. For each habitat map the year of creation is reported, and the time span for which the map was used in the model analysis was indicated with arrows.

### A. Seascape composition



### B. Seascape configuration



**Fig. S2** Graphical representation of metrics employed to characterise seascape composition (panel A) and configuration (panel B). For each metric a mosaic exemplifying high and low metric values is included. Each colour in mosaics represents a different habitat type.



**Tab. S1** List of species caught in the present study. For each species the ecological guild, summarising the main use of the Venice lagoon ecosystem, and the feeding guilds (modified from Franco et al., 2008) are shown. Guilds are abbreviated as follows. ES: estuarine residents; D: diadromous; MM: marine migrants; MS: marine stragglers; DV: detritivorous; Bmi: microbenthivorous; Bma: macrobenthivorous; HZ: hyperbenthivorous/zooplanktivorous; HP: hyperbenthivorous/piscivorous; PL: planktivorous; OV: omnivorous. Proportion of species diet allocated to each feeding guild is shown. Marine straggler species were not grouped into feeding guilds due to their occasional presence within the lagoon.

Family	Species	Ecological guild	Feeding guild						
			DV	Bmi	Bma	HZ	HP	PL	OV
Atherinidae	<i>Atherina boyeri</i>	ES				1			
Belonidae	<i>Belone belone</i>	MM				0.5	0.5		
Blennidae	<i>Parablennius sanguinolentus</i>	MS							
Blennidae	<i>Parablennius tentacularis</i>	MS							
Blennidae	<i>Salaria pavo</i>	ES		0.5					0.5
Bothidae	<i>Arnoglossus laterna</i>	MS							
Callionymidae	<i>Callionymus risso</i>	MS							
Carangidae	<i>Trachurus trachurus</i>	MS							
Clupeidae	<i>Sardina pilchardus</i>	MM							1
Clupeidae	<i>Sprattus sprattus</i>	MM							1
Cyprinodontidae	<i>Aphanius fasciatus</i>	ES		0.5					0.5
Engraulidae	<i>Engraulis encrasicolus</i>	MM							1
Gobiidae	<i>Gobius cobitis</i>	MS							
Gobiidae	<i>Gobius niger</i>	ES		0.4	0.4		0.2		
Gobiidae	<i>Gobius paganellus</i>	ES		0.4	0.4		0.2		
Gobiidae	<i>Knipowitschia panizzae</i>	ES		0.7		0.3			
Gobiidae	<i>Pomatoschistus canestrinii</i>	ES		0.7		0.3			
Gobiidae	<i>Pomatoschistus marmoratus</i>	ES		0.7		0.3			
Gobiidae	<i>Pomatoschistus minutus</i>	MM		0.7		0.3			
Gobiidae	<i>Zebrus zebrus</i>	MS							
Gobiidae	<i>Zosterisessor ophiocephalus</i>	ES		0.3	0.3		0.3		
Labridae	<i>Labrus viridis</i>	MS							
Labridae	<i>Symphodus cinereus</i>	MS							
Labridae	<i>Symphodus melops</i>	MS							

**Tab. S1** (continued).

Family	Species	Ecological guild	Feeding guild						
			DV	Bmi	Bma	HZ	HP	PL	OV
Mugilidae	<i>Chelon labrosus</i>	MM	0.5			0.5			
Mugilidae	<i>Liza aurata</i>	MM	0.5			0.5			
Mugilidae	<i>Liza ramada</i>	D	0.5			0.5			
Mugilidae	<i>Liza saliens</i>	MM	0.5			0.5			
Mugilidae	<i>Mugil cephalus</i>	D	0.5			0.5			
Mullidae	<i>Mullus surmuletus</i>	MM		0.7	0.3				
Pleuronectidae	<i>Platichthys flesus</i>	MM		0.4	0.4		0.2		
Poeciliidae	<i>Gambusia gr. affinis</i>	ES		0.5		0.5			
Sciaenidae	<i>Sciaena umbra</i>	MS							
Sciaenidae	<i>Umbrina cirrosa</i>	MS							
Scophthalmidae	<i>Scophthalmus rhombus</i>	MS							
Soleidae	<i>Solea solea</i>	MM		0.7	0.3				
Sparidae	<i>Boops boops</i>	MS							
Sparidae	<i>Diplodus annularis</i>	MS							
Sparidae	<i>Diplodus puntazzo</i>	MS							
Sparidae	<i>Diplodus sargus</i>	MS							
Sparidae	<i>Diplodus vulgaris</i>	MS							
Sparidae	<i>Lithognathus mormyrus</i>	MS							
Sparidae	<i>Oblada melanura</i>	MS							
Sparidae	<i>Sparus aurata</i>	MM		0.4	0.2	0.4			
Sphyraenidae	<i>Sphyraena sphyraena</i>	MS							
Syngnathidae	<i>Hippocampus guttulatus</i>	ES		0.5		0.5			
Syngnathidae	<i>Hippocampus hippocampus</i>	ES		0.5		0.5			
Syngnathidae	<i>Nerophis maculatus</i>	MS							
Syngnathidae	<i>Nerophis ophidion</i>	ES		1		0			
Syngnathidae	<i>Syngnathus abaster</i>	ES		0.7		0.3			
Syngnathidae	<i>Syngnathus acus</i>	MS							
Syngnathidae	<i>Syngnathus taenionotus</i>	ES		0		1			
Syngnathidae	<i>Syngnathus tenuirostris</i>	MS							
Syngnathidae	<i>Syngnathus typhle</i>	ES		0.2		0.4	0.4		
Triglidae	<i>Chelidonichthys lucernus</i>	MM		0.4	0.4		0.2		

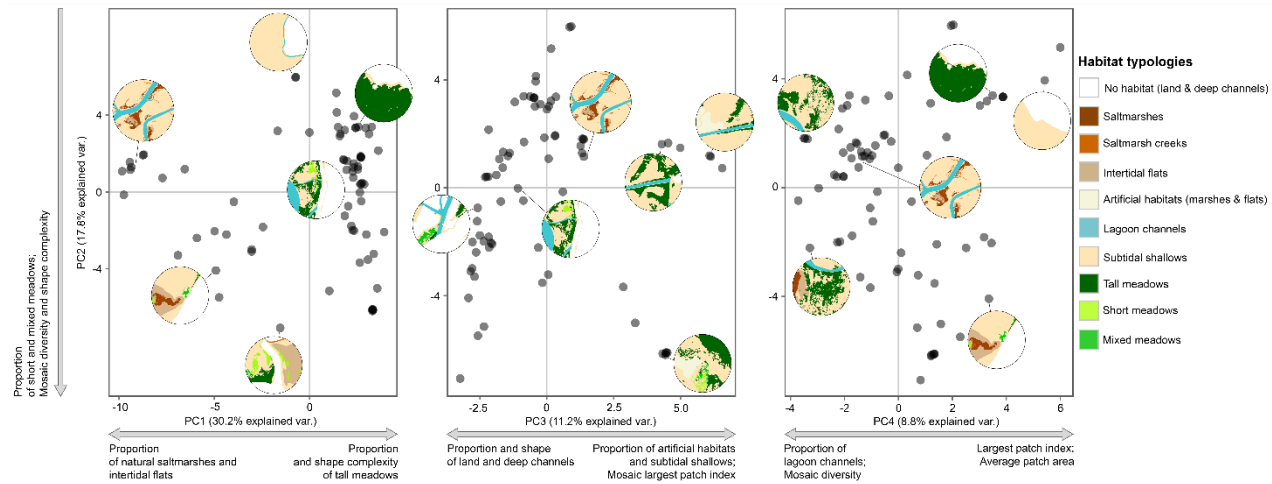
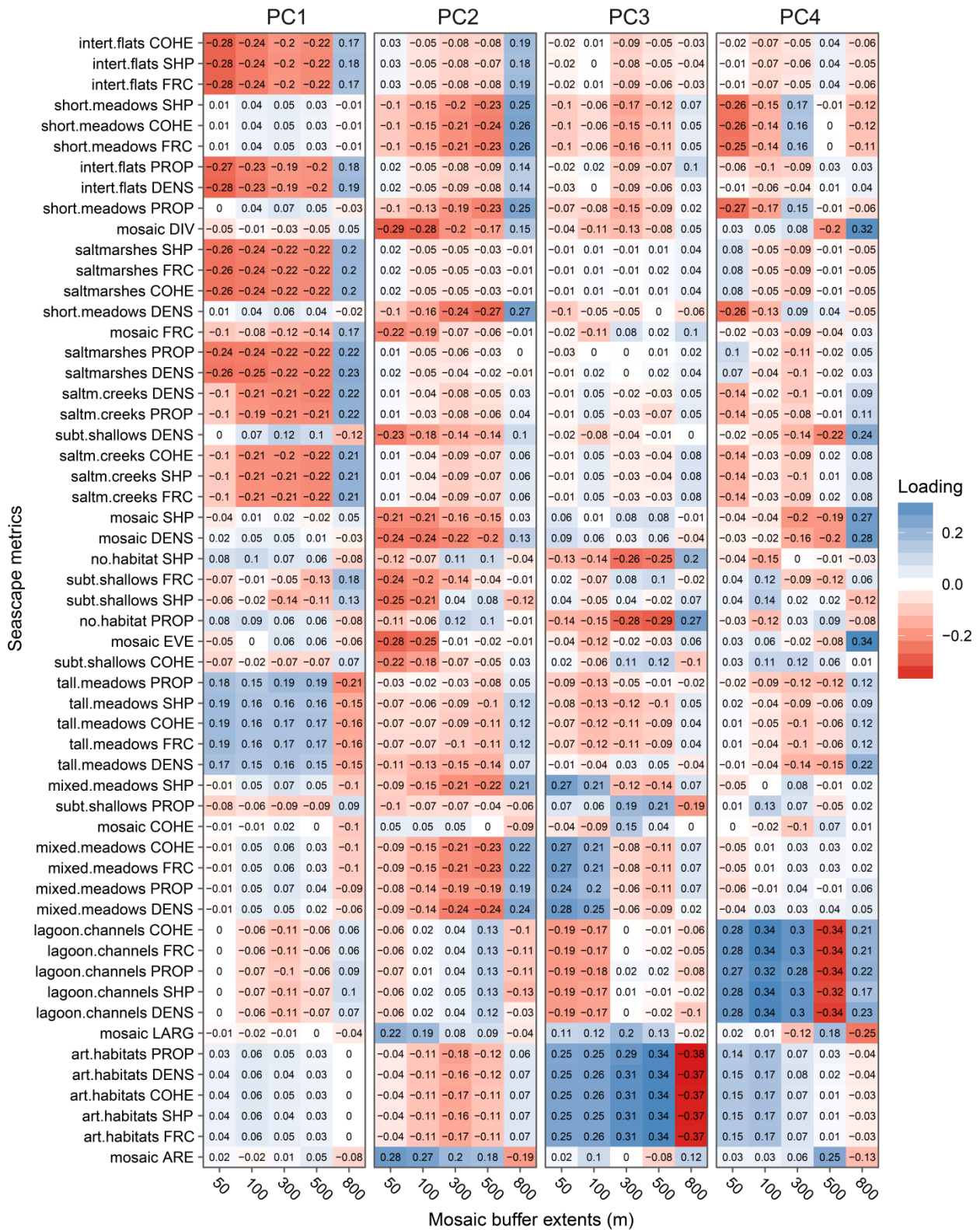


Fig. S3 Example of biplots produced with the first four axes of PCA based on mosaics quantified for 500m-radius buffer extents. Points represent observations.

Some mosaics are highlighted to exemplify the patterns in seascape properties along the axes, which are described at box margins.



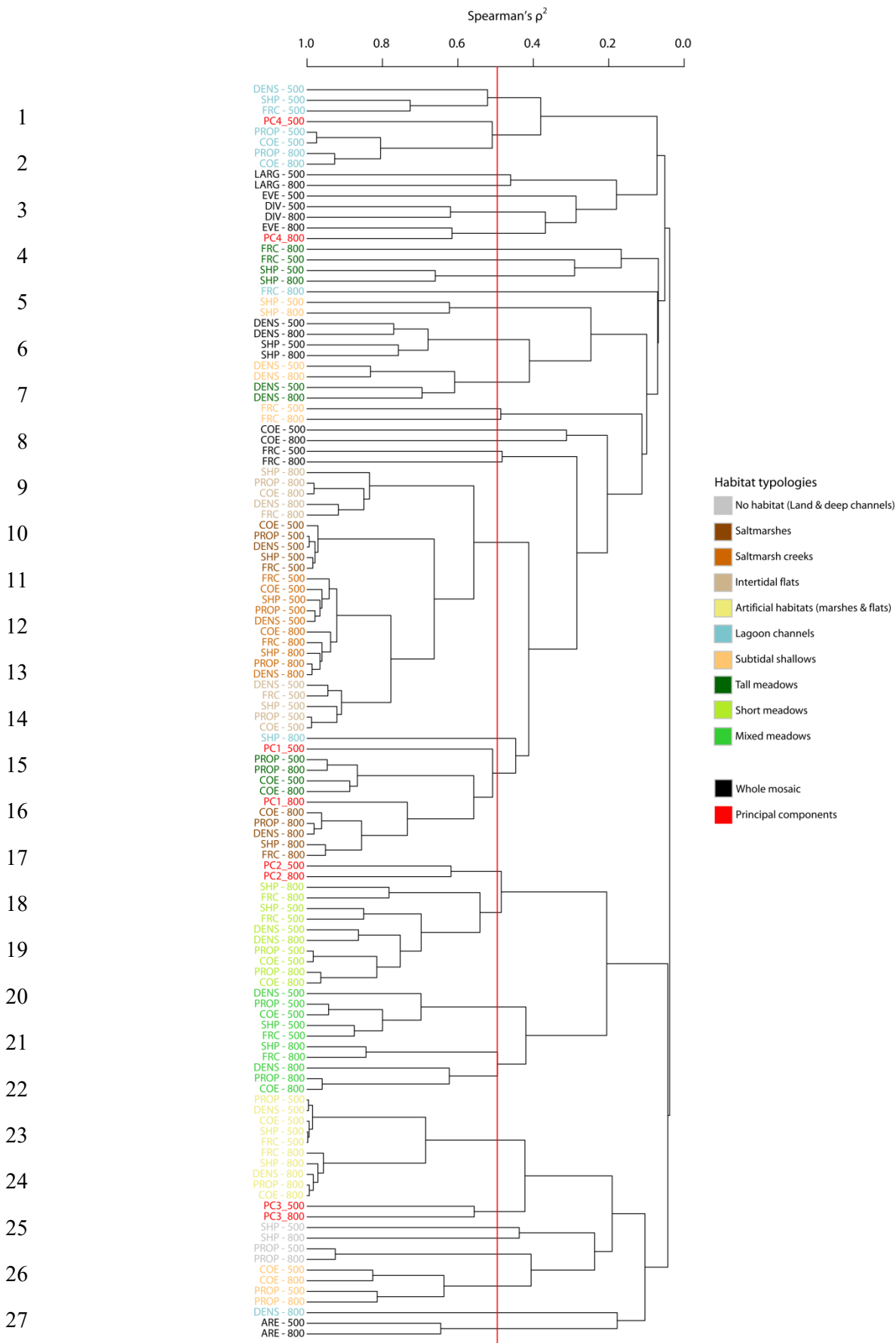
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2 **Fig. S4** Correlations (loadings) of seascapes metrics with the first four PC axes calculated for each buffer extent.

3 See Table 1 in manuscript for variables abbreviations

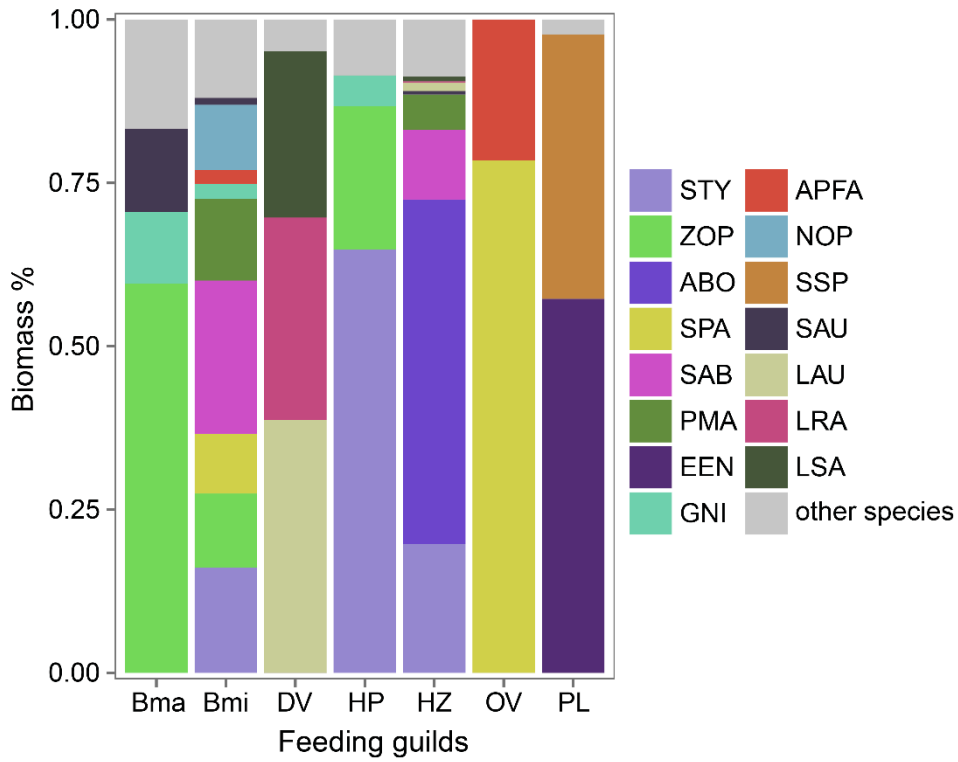
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5



28 **Fig. S5** Similarity (expressed as Spearman's correlation coefficient) between seascape variables included in  
 29 the model analysis. Principal components calculated on these variables and included in category m2 models  
 30 are also shown. For each variable, the buffer extent (either 500 or 800 m) is provided. The red line corresponds  
 31 to a Spearman's correlation coefficient of 0.5. See Table 1 in manuscript for variables abbreviations

1



2

3 **Fig. S6** Species composition (biomass %) of feeding guilds considered. Bma: Macrobenthivorous; Bmi:  
4 Microbenthivorous; DV: Detritivorous; HP: Hyperbenthivorous/Piscivorous; HZ:  
5 Hyperbenthivorous/Zooplanktivorous; OV: Omnivorous; PL: Planktivorous. Species are abbreviated as  
6 follows: STY: *Syngnathus typhle*; ZOP: *Zosterisessor ophiocephalus*; ABO: *Atherina boyeri*; SPA: *Salaria*  
7 *pavo*; SAB: *Syngnathus abaster*; PMA: *Pomatoschistus marmoratus*; EEN: *Engraulis encrasicolus*; GNI:  
8 *Gobius niger*; APFA: *Aphanius fasciatus*; NOP: *Nerophis ophidion*; SSP: *Sprattus sprattus*; SAU: *Sparus*  
9 *aurata*; LAU: *Liza aurata*; LRA: *Liza ramada*; LSA: *Liza saliens*.

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