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Habitat use of fish in seagrass meadows of the Venice lagoon: implications for seagrass restoration and for conservation of the lagoon seascape

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ABSTRACT

Seagrass meadows play a primary role in supporting ecosystem services in coastal lagoons. Still, their importance as habitat for fish in transitional waters is poorly understood. Moreover, the persistent loss of seagrass beds during the last decades requires conservationists to provide scientifically sound plans to enhance their preservation. The objectives of this work are i) to investigate the influence of environmental factors, including habitat and seascape characteristics, on seagrass fish assemblages in the Venice lagoon (northern Adriatic Sea, Italy); ii) to evaluate the suitability of fish fauna as indicator of the effectiveness of seagrass restoration. Ultimately, this work aims at presenting approaches for planning efforts for the conservation of seagrass and associated fish, and assessing their outcomes.

This work features three main sections. Firstly, the role of different floristic composition and habitat structure of seagrass beds was linked to distribution of pipefishes and seahorses (Syngnathidae), highlighting the importance of enhancing conservation of *Zostera marina* meadows in shallow coastal lagoon waters and the potential role of syngnathids as flagships species and indicators of habitat health. Secondly, the role of seagrass fish and other nekton fauna as indicator of the success of conservation actions was investigated. A seagrass restoration scheme that recently started in the Venice lagoon allowed to test a model-based method, to predict reference conditions for nekton fauna in *Z. marina* and *Z. noltei* transplantation sites, and provide an assessment of the progress of restoration towards designed goals. Thirdly, the potential role of habitat mosaic structure in influencing seagrass fish in the Venice lagoon was evaluated. The study highlighted the importance of conservation of seagrass habitat quality at multiple spatial scales for the preservation of the associated fish assemblages, and the need for including seascape ecology in seagrass restoration projects.

On the whole, this thesis provides some new insights into the critical role of seagrass conservation for the maintenance of biodiversity, and suggestions for more successful management strategies in coastal lagoons.

INTRODUCTION

Seagrasses as fish habitat in coastal lagoons

Coastal lagoons play a fundamental role in supporting the diversity of fish and other nekton organisms (i.e. swimming crustaceans and molluscs). For instance, numerous marine species during early life stages use lagoons and other transitional water ecosystems, which serve as nursery grounds (Beck et al., 2001; Sheaves et al., 2014). The nursery potential of coastal lagoons and estuaries may vary considerably among habitats, with saltmarshes, reed beds and seagrass meadows exhibiting a different role in supporting juveniles, depending upon the ecosystem and species considered (Nagelkerken et al., 2015; Whitfield, 2016). Coastal lagoons and estuaries, due to their unique sets and heterogeneity of environmental conditions, host also highly specialised organisms, which spend most of their life cycle in transitional water habitats (e.g. estuarine resident fish sensu Franco et al., 2008; Potter et al., 2013). Many of such taxa, due to their constrained distribution, constitute species of high conservation interest and are protected by national and international regulations (Caldwell and Vincent, 2012; Cavraro et al., 2017; Franzoi et al., 2010; Pérez-Ruzafa et al., 2005; Verdiell-Cubedo et al., 2012).

Seagrasses (marine angiosperm plants) are a critical component of coastal and transitional water ecosystems, which modifies the environment and directly affects the fitness of other organisms (Jones et al., 1997). They represent the major primary producer in shallow water environments, hence supporting detritus-based trophic webs (Vizzini et al., 2002) and contributing significantly to carbon sequestration (Duarte et al., 2013). In addition, they stabilise sediments and contribute to nutrient cycling (Bos et al., 2007; Nordlund et al., 2016). Compared to unvegetated substrata, angiosperms form structurally complex habitats, providing enhanced survival potential for many fish and invertebrate species thanks to increased prey and/or shelter availability (Horinouchi, 2007; Jackson et al., 2006a). For these reasons, seagrass meadows support diverse nekton assemblages, often featuring a large proportion of habitat specialists as well as endangered and iconic species (Browne et al., 2008; Franco et al., 2006; Franzoi et al., 2010; Shokri et al., 2009; Vincent et al., 2011). Seagrass beds are also acknowledged as important nursery grounds for juveniles of commercially important species in some areas of the world (Blandon and Zu Ermgassen, 2014; Pihl et al., 2006; Whitfield, 2016).

Accounting for spatial complexity in coastal lagoons: a multi-scale perspective for the study of seagrass fish

Coastal ecosystems, including lagoons and estuaries, are characterised by a high spatial variability in abiotic and biotic conditions (McLusky and Elliott, 2004). The presence of gradients in water physico-chemical parameters such as salinity, turbidity and nutrient concentrations, in hydromorphological characteristics such as bathymetry and confinement as well as the complex arrangement of different habitats (e.g. seagrass meadows, saltmarshes, mud flats, oyster reefs) are typical features of these environments (Barbier et al., 2011; Sheaves, 2009). 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 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 (Davis et al., 2014; Wiens, 1995), 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; Nagelkerken et al., 2015; Pittman et al., 2004; Simon J. Pittman et al., 2007).

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 (Horinouchi, 2007; Jackson et al., 2006a) and seascape properties such as edge complexity and patchiness of meadows (Ford et al., 2010; Smith et al., 2011, 2010; Thistle et al., 2010). Furthermore, seagrass meadows play a fundamental role as part of the seascape nursery in coastal ecosystems (Nagelkerken et al., 2015, 2008), and represent a focal habitat in coastal mosaics for a variety of species of commercial and conservation interest (Jackson et al., 2006b; Macreadie et al., 2010; Ryan et al., 2012; Smith et al., 2008; Staveley et al., 2016).

Loss and conservation of seagrass habitats

At the same time, estuaries and coastal lagoons are also subjected to multiple human pressures (Elliott & Quintino, 2007; Marchand et al., 2002; Pérez-Ruzafa et al., 2011). Habitat loss, due to land claim, bank regulation and negative impacts of pollution and other human activities on biogenic structures, is one of the most significant threats to biodiversity in these ecosystems (Cattrijsse et al., 2002; Vasconcelos et al., 2007).

Despite being recognised as a priority subject for conservation in international frameworks (e.g. Rio Convention, EU's Habitats Directive; (Borum et al., 2004), seagrass meadows are declining at both local and global scale (Airoldi & Beck, 2007; Short et al., 2011; Waycott et al., 2009). In many Mediterranean coastal lagoons, seagrass meadows are threatened by eutrophication processes triggered by increased nutrient inputs from watersheds, and by sediment disturbance due to anthropogenic activities such as fishery, aquaculture, navigation and boat anchoring. Such pressures determined important regime shifts from benthic macrophytes- to phytoplankton-dominated conditions (Curiel et al., 1998; Piccoli, 1998; Sfriso & Facca, 2007; Viaroli et al., 2006), with significant seagrass losses being recorded in coastal lagoons from Italy, France, Spain and Greece at least since 1970s (Viaroli et al., 2008 and citations therein).

The persistent loss of seagrass habitat may severely damage marine biodiversity, including fishes, especially in coastal lagoon ecosystems (Franco et al., 2009b; Pérez-Ruzafa et al., 2006; Zucchetta et al., 2016), where meadows have limited distribution and serve as nursery habitat (Bertelli & Unsworth, 2014; Pihl et al., 2006). In this light, it is critical to acquire information on seagrass habitat characteristics that support fish biodiversity, in order to develop effective conservation measures to preserve both habitat and associated fauna (Freyhof, 2016; Ouyang & Pollom, 2016; Pollom, 2016a, b).

Removing or reducing the anthropogenic pressures affecting directly and indirectly seagrass beds is acknowledged as the most viable way to implement seagrass conservation in coastal lagoons and estuaries (Cunha et al., 2012). Nonpoint source pollution, such as nutrient and organic matter loadings, is a major cause of degradation of seagrass meadows, hence requiring particular attention and the adoption of management strategies at the watershed scale (Borum, Duarte, Krause-Jensen, & Greve (eds.), 2004). Direct seagrass disturbance due to coastal development projects could be avoided, or at least minimised, by careful planning and site selection, while a more effective enforcement of regulations is required, to prevent resource use activities (e.g. fishery, aquaculture) to damage seagrass meadows (Cunha et al., 2012).

When all conservation efforts aiming to foster the natural recovery potential of seagrasses are ineffective, restoration should be considered. Reversing the underlying causes of habitat loss is essential to successfully restore seagrasses. In addition, selecting suitable donor and transplantation sites, as well as spreading the risk of failure (e.g. by designing large-scale interventions and including spatial and temporal transplantation replicates), are suggested as measures to increase the chances of success (van Katwijk et al., 2015, 2009).

The Venice lagoon: a case study to understand functions, loss and recovery potential of seagrass habitats

The Venice lagoon is the largest Mediterranean coastal lagoon (approximately 550 km^2) and is located in the northern Adriatic sea. It is connected to the sea by three inlets, and experiences a tidal range of ±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 (Molinaroli 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). In most confined areas of the lagoon, along the saltmarsh edges and in proximity to freshwater outflows, the genus of aquatic angiosperms *Ruppia* is also present (Curiel et al., 2012).

In the Venice lagoon, seagrass meadows support greater fish abundances and biomasses compared to unvegetated habitats. Seagrass fish assemblages also exhibit greater diversity, and are dominated by estuarine resident species such as pipefish and seahorses (Syngnathidae), and large gobies (Gobiidae), which use seagrass beds as foraging and spawning grounds (Franco et al., 2006; Franzoi et al., 2010; Malavasi et al., 2005; Riccato et al., 2003).

Since the early works describing its trophic conditions and floral assemblages (Vatova, 1940), the Venice lagoon experienced some marked decrease in the overall surface occupied by *C. nodosa*, *Z. marina* and *Z. noltei* meadows (Curiel et al., 2014; Sfriso & Facca, 2007). Although their distribution being highly dynamic and characterised by significant interannual variations (Rismondo & Mion, 2008), populations of *Z. marina* and *Z. noltei* have been particularly affected by eutrophication, macroalgal blooms and perturbation of sediments (Sfriso et al., 2005a, 2005b; Solidoro et al., 2010). These species showed an overall decline in the northern and central sub-basins at least since 1990s (Curiel et al., 2014). Despite the recovery of trophic status and the overall enhancement of ecological conditions since 2010s, which is leading to the progressive recolonisation by seagrasses in some areas, the distribution of *Z. marina* and *Z. noltei* is still very limited in the central and northern lagoon sub-basins (Curiel et al., 2014; Sfriso & Facca, 2007).

The LIFE project SERESTO (acronym for SEagrass RESTOration: www.lifeseresto.eu; Facca et al., 2014a) is being implemented since 2014 in the northern sub-basin of the Venice lagoon, in order to reverse the degradation of seagrass meadows in this area. The project operates through the diffuse, small-scale transplantation of *Z. marina* and *Z. noltei* sods and rhizomes over a large area. This, according to the stated objectives of the scheme, would trigger the natural re-colonisation of meadows and the long-term stabilisation of seagrass populations. The ultimate goal of the project is to enhance the overall status of the ecosystem and increasing the floral and faunal diversity associated with seagrass habitats. Seagrass transplant activities started in autumn 2014 at 17 sites, with 18 additional sites included in 2015. A total of 35 sites were subjected to seagrass transplantations in the northern Venice lagoon.

Aims and structure of the research

The research, operating in the Venice lagoon, aims to increase the knowledge on the role of seagrass meadows as habitats for fish and other nekton fauna in Mediterranean coastal lagoons. The work is expected to give new insights into the critical role of seagrass conservation and restoration for the maintenance of biodiversity. At the same time, it would provide new perspectives for more successful management strategies in lagoon ecosystems.

The specific objectives of the research are: i) to investigate the influence of environmental factors, including habitat characteristics at different spatial scales, on seagrass fish and other nekton assemblages in the Venice lagoon; ii) to evaluate the progress of nekton recovery after seagrass restoration; and iii) to discuss the implications for management and conservation of biodiversity associated to seagrass habitats. Subsequently, the research helped to test the following general hypotheses: i) distribution of fish and other nektonic organisms associated with seagrass meadows in Mediterranean coastal lagoons is driven not only by physico-chemical properties of water and sediment, but also by habitat composition and structure, at multiple spatial scales; ii) the preference of nekton species towards particular habitat properties can be exploited in conservation studies, to evaluate the effectiveness of restored seagrass habitats in supporting associated faunal assemblages.

Three main sections are featured in this work. In the first section, the composition and structure of main habitat typologies found in shallow waters of the Venice lagoon are linked to the distribution of a key component of lagoon fish assemblages, which plays both an ecological and flagship role in seagrass meadows: pipefish and seahorses (Syngnathidae). The analysis highlights the relevance of implementing conservation measures towards seagrass habitats for syngnathids. On these bases, the second section investigates the potential role of fish and other nekton taxa as indicators of seagrass restoration. By developing and testing a method to identify reference conditions for nekton assemblages in seagrass habitats, the analysis provide a first description of the progress of faunal colonisation at newly-recreated seagrass sites in the Venice lagoon under the project SERESTO. The third and last section aims to broaden the perspective on habitat use by fish, by including seascape-scale habitat characteristics in the analysis of seagrass fish distribution in the Venice lagoon.

Overall, this research work provides major implications for conservation and restoration of seagrass habitats and associated fish in transitional water ecosystems.

GENERAL METHODS

All the analyses carried out during the research relied on consistent procedures of data collection and manipulation, including biological and environmental sampling as well as statistical approaches. As a result, this chapter provides a description of field and numerical methods employed throughout the research. Conversely, specific methodologies that only apply to each one of the sections composing this work (e.g. variations of sampling design; particular models used) are separately illustrated within the respective sections.

This work partly relied on fish and environmental data collected in the past under different monitoring activities, which were carried out in the shallow waters of the Venice lagoon from 2002 to 2014 following the same field procedures described in this chapter.

Sampling and analysis of nekton fauna

Fish and other nekton fauna in shallow waters of the Venice lagoon was sampled during daylight hours, following the approach described in Franco et al. (2006), by means of a nylon seine net 10 m long and 2 m tall, with a knot-to-knot mesh size of 2 mm. The net was provided with float and lead lines, allowing to explore the entire volume of water from above the sediment to the water surface. During each sampling action, the net was deployed by two operators walking in parallel and pulled across a fixed distance. The distance covered by fishing action might vary (20 to 50 m) according to the specific requirement of each sampling design and to the site-specific environmental conditions.

Fish caught were collected by bringing the two ends of the net together and retrieving the seine into a boat. Individuals were then identified at the species level, counted, photographed on millimetre paper and released. Only in the presence of larval and juvenile stages of non endangered species, a representative subsample was sacrificed with an excess of 2-phenoxyethanol, preserved in 8% buffered formaldehyde and subsequently returned in the laboratory. Subsamples were sorted and identified by species, and individuals weighed (± 0.001 g). The total abundance (no of individuals) and biomass (g) of each species in each sample were calculated and standardised by area (100 m^2).

Although usually correlated, abundance and biomass in fish studies provide different, and sometimes complementary, information. While abundance is often employed as response variable to investigate the structural aspects of the nekton assemblages, it has been recently emphasised that biomass-based metrics can effectively be used as proxies for ecological functions mediated by nekton, such as secondary production, trophic structure and overall ecological status (Zucchetta et al., 2016). In this light, descriptors based on nekton abundance were employed in the first and second main sections of the research, since the main focus was to investigate the environmental and habitat influence on structural attributes of syngnathid and overall nekton assemblages. Conversely, biomass was used in the third section, in order to emphasise the importance of environmental features at multiple spatial scales on functional aspects (e.g. trophic guild composition) of seagrass fish assemblages.

Environmental characterisation of sampling sites

An environmental characterisation of sampling sites was generally carried out during fishing activities, considering both physico-chemical properties of water and sediment as well as habitat structure. Water temperature (°C), salinity (PSU), dissolved oxygen (saturation %) and turbidity (FNU) were measured using a multi parameter probe at the moment of fish sampling. Sediment granulometry in each sampling location (sand % in the 10 cm surface layer) was derived from interpolation of sediment monitoring sites (ARPAV, 2012; MAG.ACQUE - SELC, 2005; MAG.ACQUE - THETIS, 2005).

Structural characteristics of the substrate at the moment of sampling were considered, taking into account the attributes of shallow water habitats that may affect fish fauna. Presence of seagrass vegetation and macroalgae was recorded, together with floral composition and total percentage of cover of seagrass habitat within the sampling area. The methods of habitat definition varied according to the specific purposes and hypotheses formulated in each of the sections of this work.

Data analysis

Statistical analyses mainly relied on the recently proposed model-based approach, which allows to explicitly answer ecological questions by means of Generalised Linear Models (GLMs) or Generalised Additive Models (GAMs). The main advantages of this approach are: i) to explicitly formulate a priori hypoteses on the role of the different environmental variables in influencing nekton distribution; ii) to build a set of models of increasing complexity (e.g. by progressively adding new predictors to models), based on the stated hypotheses; iii) to select the best formulation(s), hence allowing to support or reject the different hypotheses; iv) to estimate the magnitude of the effect of each variable included in the selected models, considering also the sign of the response (i.e. to evaluate if a given predictor positively or negatively affects the response variable).

The model analysis generally features three main phases (see also Table 1). In the *hypotheses formulation and model calibration* phase, a set of models are formulated, including different combinations of predictor variables according to the formulated hypotheses. The *model selection* allows to identify the best formulations, thus the predictor variables that are relevant to explain the variability in the response variable. Selection is made by comparing couples of formulations, either following the Akaike's An Information Criterion (AIC; (Akaike, 1973; Burnham and Anderson, 2002)) approach, or using Likelihood Ratio Tests. Finally, the *evaluation of the effect(s)* is carried out by estimating model coefficients, allowing to interpret the models and compare the magnitude of the contribution of each variable included.

Table 1: Main phases constituting the model analyses employed in the research.

Phase		Example
1	**Hypotheses formulation and model calibration**	Response variable Y is influenced by variable A only: $Y \sim \beta \cdot A + \varepsilon$ Response variable Y is influenced by variable B only: $Y \sim \beta \cdot B + \varepsilon$ Response variable Y is influenced by both variables A and B: $Y \sim \beta \cdot A + \beta \cdot B + \varepsilon$
2	**Model selection**	Ranking according to AIC values, or Likelihood Ratio Tests. $Y \sim \beta \cdot A + \beta \cdot B + \varepsilon$ is the best model: A and B together influence Y
3	**Evaluation of the effect(s)**	Variable A shows a positive effect on Y ($\beta = 2.1$), while B shows a negative effect ($\beta=-1.3$)

1.

LINKING PIPEFISHES AND SEAHORSES TO SEAGRASS MEADOWS IN THE VENICE LAGOON: IMPLICATIONS FOR CONSERVATION

Previous page: female *Nerophis ophidion* among *Zostera marina* (© Luca Scapin)

Introduction

Pipefishes and seahorses (family Syngnathidae) are a major feature of the fish biodiversity in the Venice lagoon, and account for a large proportion of species density and diversity in seagrass meadows and other structured habitats in this ecosystem, as well as in other Mediterranean transitional waters (Campolmi et al., 1996; Franco et al., 2006; Franzoi et al., 1993; Riccato et al., 2003). Among the ten species of Mediterranean syngnathids, nine can be found in the Venice lagoon (Franzoi et al., 2010), this being an ecosystem of primary importance for the conservation of this family. Two of the nine species are assessed as Near Threatened (NT) by IUCN at the Mediterranean scale, namely *Hippocampus guttulatus* (Pollom, 2016a) and *H. hippocampus* (Pollom, 2016b), and three species are Data Deficient (DD), including *Syngnathus taenionotus* (Allen, 2016), *S. tenuirostris* (Papakonstantinou et al., 2016) and *Nerophis maculatus* (Wiswedel, 2016). Moreover, at the global scale, five of the species are assessed as DD, namely *H. guttulatus* (Woodall, 2012a), *H. hippocampus* (Woodall, 2012b), *N. maculatus* (Wiswedel, 2015), *S. taenionotus* (Tunesi and Czembor, 2014) and *S. tenuirostris* (Papakonstantinou et al., 2014). Some species are also protected under European and international regulations. In particular, all species of the genus *Hippocampus* are strictly protected species under the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), and their trade is regulated under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES: www.cites.org). However, the overall lack of information regarding habitat use, population dynamics and life history severely limits effective management actions towards syngnathid conservation (Vincent et al., 2011). While there is a relatively larger amount of knowledge about some of the species in the Mediterranean, it is still not clear how and to what extent habitat loss may affect their populations (Freyhof, 2016; Ouyang & Pollom, 2016; Pollom, 2016a, 2016b). For instance, a better understanding of habitat requirements would benefit the assessment of the status of species like *S. typhle* and *N. ophidion*, for which the monitoring of habitat trends is regarded as a conservation priority (Pollom, 2016c, 2016d).

Syngnathids share some body adaptations as well as feeding and reproductive behaviours that make them highly specialised organisms (Ahnesjö & Craig, 2011). Most of them are cryptic species that live in highly structured coastal environments such as coral reefs, algal beds, kelps and seagrass meadows (Browne et al., 2008; Kuiter, 2000; Lourie et al., 1999). Together with their specific environmental requirements, their typically low mobility and slow reproductive rates could make syngnathids particularly sensitive to degradation or loss of their habitat (Vincent et al., 2011). Thanks to their unique appearance and behaviour, however, syngnathids are charismatic fish that may attract sympathy and help raise public awareness of biodiversity conservation in coastal environments. Therefore, they are sometimes regarded as effective flagship species, which could be used to select Marine Protected Areas and enhance the conservation of coexisting less charismatic taxa and associated habitats (Browne et al., 2008; Shokri et al., 2009). Despite that, no information is available regarding the potential use of syngnathids as flagships for the protection of seagrass meadows in Mediterranean coastal lagoons. Similarly, while some species exhibit a marked dependence on seagrass meadows for survival, growth and reproduction and many are considered to be highly sensitive to seagrass loss, syngnathids are rarely employed as indicators to assess habitat health, conservation status or restoration success in the Mediterranean (Deudero et al., 2008; Scapin et al., 2016). Investigating the meadow characteristics influencing their distribution could thus also help identifying the species that are more sensitive to changes in seagrass habitat.

The present work gathers observations on syngnathids distribution, environmental parameters and habitat characteristics collected during eight years of monitoring and research in the Venice lagoon, from 2002 to 2014. Data from 186 sites were analysed. The work examines the role of habitat characteristics in affecting the distribution of syngnathids in the Venice lagoon shallow waters. In particular, the aims were to i) disentangle the influence of environmental characteristics and habitat features on the distribution and abundance of syngnathid assemblage; ii) highlight the dependence of these species on seagrass meadows with particular characteristics; and iii) find which habitat characteristics contribute most to supporting syngnathid species densities and diversity. The following hypotheses were tested: i) seagrass meadows are the most important habitat for overall syngnathid abundance and diversity in the Venice lagoon; ii) seagrass meadows are not all equivalent habitats for syngnathids, with different floristic composition and structure influencing species distribution.

This work would thus help coastal lagoon managers in prioritizing habitats for conservation and provide some insights into the potential role of syngnathids as indicator and flagship species in these environments.

Methods

Fish and environmental sampling

This work collected observations on syngnathids distribution, environmental parameters and habitat characteristics performed during eight years of monitoring and research in the Venice lagoon, from 2002 to 2014. Data from 186 sites were analysed (Figure 1). All sampling sites were located in shallow water environment, with a water depth ranging between approximately 20 to 150 cm at the time of sampling.

Together with fish sampling, water and sediment parameters were measured at each site following the methodology described in "General methods – Environmental characterisation of sampling sites" (pag. 12). In addition, information on bottom characteristics was collected in each site. The presence of seagrass vegetation (i.e. epigeous parts of *C. nodosa*, *Z. marina* and *Z. noltei*) was recorded by visual census, and its relative coverage within the sampled area was estimated following the Braun-Blanquet method and subsequently expressed as percent cover. Presence of macroalgae (mainly laminar Ulvaceae and branched Gracilariaceae and Soleriaceae) was also recorded by visual census.

Data analysis

Each sampling site was allocated to one of three habitat typologies, defined according to the main bottom cover recorded in the field. Substrata without any macroalgae or seagrass vegetation were classified as "bare substratum". Substrata without seagrass vegetation but covered by macroalgae were classified as "macroalgal bed". Finally, substrata characterised by presence of seagrasses, with or without macroalgae, were classified as "seagrass meadow".

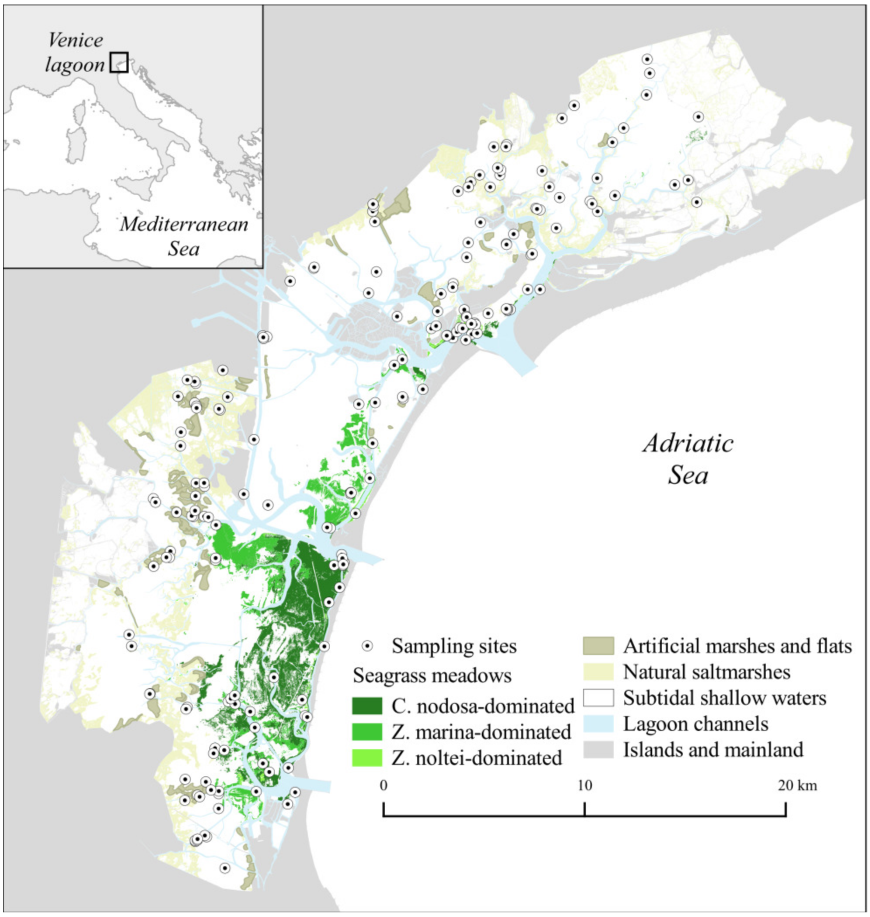

Figure 1: Study area and locations of sampling sites. Distribution of seagrass meadows (as in 2010) is also shown (Curiel et al., 2014).

Fish abundance data were standardised by area, in order to obtain comparable density measures (number of individuals · 100 m^{-2}). A set of indicators based on the whole syngnathid assemblage were also calculated: total number of species, total density, species richness (Margalef's index calculated on density of abundance), species diversity (Shannon's index calculated on density of abundance) and species evenness (Pielou's index calculated on density of abundance). Mean and standard deviation values for density of abundance of each species, as well as for all indicators, were calculated per habitat typology.

A model approach (*sensu* Warton et al. (2014)) was adopted in order to study the effect of environmental descriptors on syngnathid distribution. Density of abundance was used as response variable for most abundant species, while presence/absence data were used for rarer species (i.e. those with a large proportion of zeros in dataset). Indicators of the whole syngnathid assemblage were also considered as response variables. Species and indicators were independently modelled with Generalised Additive Models (GAMs). A negative binomial distribution was used to model response variables based on density, species richness and species diversity. A binomial distribution was chosen to model presence/absence data, while a zero-inflated Poisson distribution was used to model the number of species.

Three categories of models were developed for each response variable separately, in order to test three different hypotheses on the contributions of predictor variables. Model categories were hierarchical, i.e. were built by progressively adding new predictors, to represent an increasingly level of complexity. This allowed to explore the following *a-priori* made hypotheses (Table 2): response variable is affected by seasonal factor alone (category m1); response variable is affected by environmental parameters when seasonal factor is already accounted for (category m2); response variable is affected by habitat characteristics, including habitat types and seagrass percent cover, if seasonal factor and environmental parameters are already accounted for (category m3). Since the present study did not aim at investigating the temporal trends, potentially present in the dataset, we did not included the year of sampling in the model analysis. The possibility to include sampling year as random factor in a Generalised Additive Mixed Model (GAMM) framework was also explored, but eventually not included in the analysis due to the relative homogeneity of residuals among years. The possibility to include sampling year as random factor in a Generalised Additive Mixed Model (GAMM) framework was also explored, but eventually not included in the analysis due to the relative homogeneity of residuals among years.

Category m1 included only one model, while more than one GAM formulation was made for the others, resulting in a series of candidate alternative models for each category (Table 2). Category m2 was built by adding to category m1 either water physico-chemical parameters (m2.1), water depth and sediment granulometry (m2.2) or all such predictors together (m2.3). Category m3 was built by adding to category m2 either habitat types (m3.1) or both habitat types and seagrass percentage cover (m3.2).

For each response variable and starting from category m1, the best candidate model within each category was selected by using the Akaike Information Criterion (AIC) approach, choosing the model with the lower AIC value. In case of model comparisons with an inadequate support for the identification of the best model (AIC difference lower than 2) the most parsimonious formulation (i.e. the model retaining less predictors) was selected. Then, each following category was built adding predictors to the best model selected from the preceding category. This stepwise procedure allowed to explore each hypothesis formulated, by verifying if progressive addition of predictor terms would improve the overall fit of the model (Table 2).

Following this method, a best model was selected for each response variable and results were interpreted. In particular, the sign (either positive, null or negative) and magnitude of the effect of presence of a specific habitat typology, as estimated by the best fitted GAMs, were used to interpret habitat influence on response variables.

Seagrass morphological features (e.g. leaf and shoot length and width) determine the structural characteristics of meadow habitat (e.g. canopy height), hence they may influence habitat choice in cryptic species that mimic seagrass leaves or use them as holdfasts to feed and hide (Malavasi et al., 2007; Schultz et al., 2009). Thus, the potential effect of seagrass species composition was investigated for those species predicted with greater mean densities/probability of presence in seagrass meadows (i.e. whose best model belong to model category m3). The respective best GAMs were modified so that the three-level factor for habitat typology was replaced by a five-level factor, maintaining the "bare substratum" and "macroalgal bed" levels and adding "*C. nodosa*-meadow", "*Z. marina*-meadow" and "*Z. noltei*-meadow" in replacement of "seagrass meadow" level, depending on the seagrass species dominating the habitat (in terms of percent cover) in each sampling site. This allowed to test the hypothesis that each response variable is affected by habitat characteristics, including habitat/meadow types and seagrass percent cover, if seasonal factor and environmental parameters are already accounted for (category m4; Table 2).

Table 2: Structure of models used to link syngnathid species and assemblage indicators to temporal factor, environmental factors and habitat characteristics. The stepwise procedure of model fitting is also described. Yi = response variables; temp. = water temperature; diss.oxy. = water dissolved oxygen; sal. = water salinity; turbid. = water turbidity; depth = water depth; sand% = percent of sand in surface sediments; habitat = main habitat typology; seagrass% = percent cover of seagrass vegetation; meadow = seagrass meadow typology.

Model category	**Label**	**Model structure**	**Description**
1. Temporal factor	m1	$Y_i \sim$ season + constant + ε_i	Response variable is affected by seasonal effect only
			Category-1 model is improved by adding the effect of:
2. Environmental factors	m2.1	m1 **+ temp. + diss.oxy. + sal. + turbid.**	Water physico-chemical parameters
	m2.2	m1 **+ depth + sand%**	Water depth and sediment granulometry
	m2.3	m1 **+ temp. + diss.oxy. + sal. + turbid. + depth + sand%**	All environmental parameters
			Best category-2 model is improved by adding the effect of:
3. Habitat characteristics	m3.1	m2.X **+ habitat**	Presence of habitat types (either bare substratum, macroalgal bed or seagrass meadow)
	m3.2	m2.X **+ habitat + seagrass%**	Habitat types and seagrass % cover

Additional analysis - effect of seagrass meadow types on species

(only when best models belong to category m3)

Meadow types	m4	best **+ meadow**	Best model is modified by replacing seagrass as a whole with seagrass meadow types (either *C. nodosa*-, *Z. marina*- or *Z. noltei*-dominated meadows)

Results

Habitat types distribution

A total of 579 observations were included in the fish and environmental dataset. The observations were relatively well distributed among habitat typologies, with seagrass meadows accounting for 37% of the records, bare substrata accounting for 36% and macroalgal beds for 27%. Within seagrass habitat, *Z. noltei* was found to be dominant in terms of percentage cover in 40% of observations (14% of the total), *C. nodosa* in 31% (11% of the total) and *Z. marina* in 29% (11% of total observations).

Syngnathids distribution

Overall, syngnathid species accounted on average for 47% of the total fish density of abundance and 39% of the total number of species sampled in seagrass meadows. In turn, they played a minor role in structuring the fish assemblage of both bare substrata and macroalgal beds. Syngnathids accounted on average for 3% of the total fish density and 14% of the total number of species in unvegetated habitats, and for 10% of the total fish density and 19% of the total number of species in macroalgae habitats.

Nine species of syngnathids were caught in the Venice lagoon during the study period, including seven species of pipefishes (*Nerophis maculatus*, *N. ophidion*, *Syngnathus abaster*, *S. acus*, *S. taenionotus*, *S. tenuirostris* and *S. typhle*) and two species of seahorses (*Hippocampus hippocampus* and *H. guttulatus*). Six species were found in all three habitat typologies (all the species excluding *S. acus*, *H. hippocampus* and *N. maculatus*), and showed overall greater densities in seagrass meadows compared with other habitats (Figure 2). Three species were the most abundant, namely *S. abaster*, *S. typhle* and *N. ophidion*, which accounted for more than 80% of total syngnathid density in all habitats.

All indicators based on the syngnathid assemblage varied markedly between seagrass meadows and other habitat types (Figure 2). On average, seagrass habitats were characterised by greater values of total density, total number of species Shannon's diversity and Pielou's evenness, while Margalef's richness showed similar mean values between habitats.

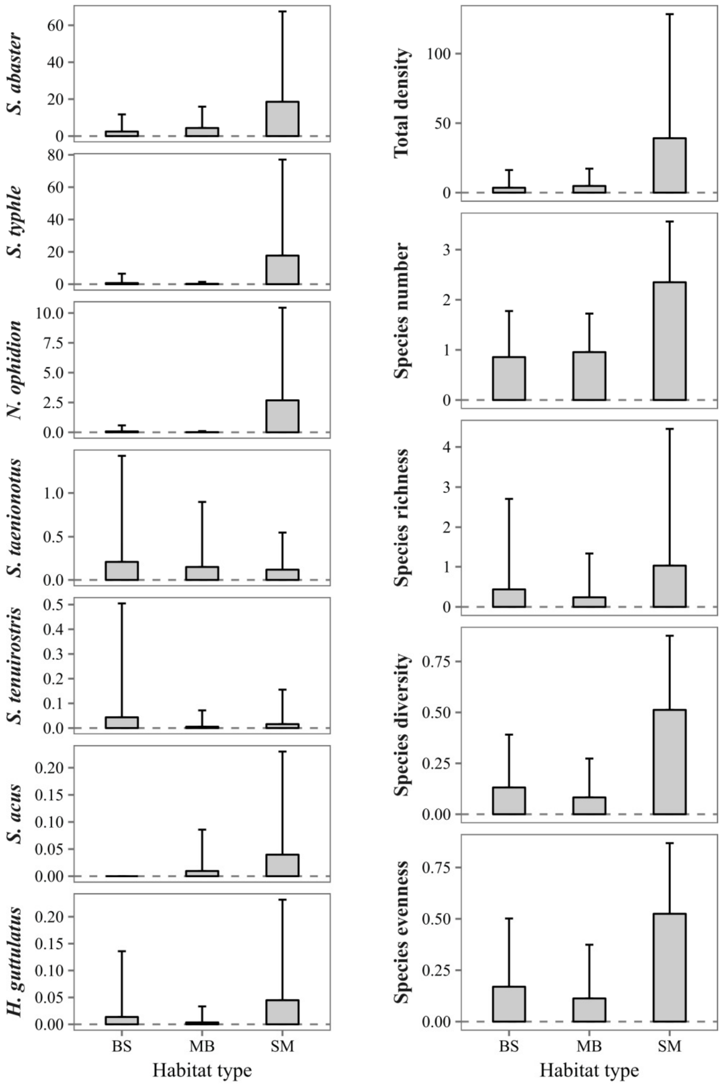

Figure 2: Mean values and standard deviations among habitat typologies for species density (no. of individuals·100 m-2) and syngnathid assemblage indicators. BS: bare substrata; MB: macroalgal beds; SM: seagrass meadows. Densities of Hippocampus hippocampus (n=2) and Nerophis maculatus (n=1) are not shown.

Habitat use by syngnathids

S. abaster, *S. typhle* and *N. ophidion* were the most abundant species in the syngnathid assemblage, hence their response to environmental conditions were modelled using density of abundance. In turn, presence/absence data were used to model the response of *H. guttulatus*, *S. acus*, *S. taenionotus* and *S.*

tenuirostris. Due to the very few observations of both *H. hippocampus* and *N. maculatus* (n=2 and n=1 respectively), these species were excluded from further analyses.

Importance of predictors for species

Seasonal factor, physico-chemical descriptors and habitat characteristics were all included in best models explaining the distribution of five species of syngnathids in the Venice lagoon (Table 3). In particular, density of abundance of *S. abaster*, *S. typhle* and *N. ophidion* and presence/absence of *H. guttulatus* responded to both habitat typology and seagrass cover, when seasonal factor and physico-chemical descriptors were already taken into account (m3.2). In terms of physico-chemical descriptors, water parameters, water depth and sediment granulometry were all relevant for *S. abaster*, *S. typhle* and *N. ophidion*, while only water parameters were relevant for *H. guttulatus*. Similarly, presence/absence of *S. acus* responded to seasonal factor, physico-chemical descriptors (water depth and sediment granulometry only) and habitat typology, while it was not affected by seagrass cover (m3.1). Conversely, presence/absence of *S. taenionotus* was affected only by seasonal factor and physico-chemical descriptors (including water parameters, water depth and sediment granulometry; m2.3), while presence/absence of *S. tenuirostris* was predicted by seasonal factor alone (m1).

Importance of predictors for indicators

According to the fitted GAMs (Table 3), the variability of all syngnathid assemblage indicators was explained by seasonal factor, physico-chemical descriptors and habitat characteristics (both habitat typology and seagrass cover) (m3.2). While all the considered physico-chemical descriptors (i.e. water parameters, water depth and sediment granulometry) explained total syngnathid density of abundance, total number of species and species richness, only water depth and sediment granulometry were included in the best models explaining species diversity and evenness.

Table 3: AIC values computed on models fitted for syngnathid species and assemblage indicators. Response variable (either density of abundance or presence/absence) is also specified for the species. AICs values of best models selected within each model category are underlined, while AICs of the final model formulations are underlined and highlighted in bold.

	Model category	1. Temporal	2. Environmental			3. Habitat	
	Label	m1	m2.1	m2.2	m2.3	m3.1	m3.2
Response variable							
Species							
Syngnathus abaster	density of abundance	2890.98	2837.91	2875.44	2805.87	2723.30	**2712.49**
Syngnathus typhle	density of abundance	1929.45	1882.69	1797.19	1754.06	1661.78	**1622.36**
Nerophis ophidion	density of abundance	928.41	865.91	810.63	797.20	742.85	**706.72**
Syngnathus taenionotus	presence/absence	456.51	404.15	447.48	**391.30**	390.64	390.44
Syngnathus acus	presence/absence	136.80	136.06	111.81	110.63	**104.07**	104.07
Hippocampus guttulatus	presence/absence	217.13	204.35	213.83	204.35	199.60	**188.92**
Syngnathus tenuirostris	presence/absence	**94.81**	94.81	95.17	95.17	97.40	97.40
Assemblage indicators							
Total density of abundance		3447.33	3381.80	3377.85	3318.93	3201.30	**3174.40**
Total number of species		1754.24	1689.59	1688.79	1676.38	1566.62	**1552.01**
Species richness		1157.14	1094.86	1118.80	1082.81	1080.84	**1060.62**
Species diversity		666.51	652.94	636.51	634.61	612.67	**600.50**
Species evenness		708.27	697.60	687.60	686.65	673.17	**656.54**

Effects of physico-chemical parameters

The selected models for the most common species *S. abaster*, *S. typhle* and *N. ophidion* all showed how sites with relatively higher salinity and located at greater depths support greater abundance densities of the species. Moreover, *S. typhle* and *N. ophidion* showed a positive response to coarser sediments. On the contrary, species like *S. taenionotus* showed a slightly negative relationship with salinity and depth, and a positive response to turbidity. Assemblage indicators responded more weakly to these physico-chemical parameters, with only Margalef's species richness showing a marked positive relationship with salinity (see also Figure S1 and Figure S2 in supplementary materials).

Habitat influence on syngnathids

S. abaster was predicted with greater mean densities in both macroalgal beds and seagrass meadows, compared with bare substrata (Figure 3). However, standard errors associated to each effect did not allow to infer a preference for one or other of the two vegetated habitats, which seemed to have equivalent importance for this species. On the contrary, *S. typhle* and *N. ophidion* showed a marked preference for seagrass meadows compared with both unvegetated substrata and macroalgal beds (Figure 3). The effect of habitat typology on probability of presence of *H. guttulatus* and *S. acus* was characterised by large standard errors. However, an overall preference for seagrass meadows can be highlighted for *H. guttulatus*. In addition, it is interesting to note that macroalgal beds show a negative effect on both density of *N. ophidion* and probability of presence of *H. guttulatus* (Figure 3).

A linear effect of seagrass percentage cover was found for mean density of both *S. abaster* and *N. ophidion*. Conversely, non-linear effects of vegetation cover were estimated for mean density of *S. typhle* and presence/absence of *H. guttulatus* (Figure 4). In particular, *S. typhle* showed a steeper response to the increase in seagrass percent cover up to *ca.* 30%, while *H. guttulatus* showed a steeper response from 50 to 100% cover.

According to the respective best models, greater mean values of total syngnathid density, number of species and species diversity are predicted in seagrass meadows compared with both bare substrata and macroalgal beds (Figure 3). Total density and number of species are also positively affected by the presence of macroalgal beds, compared with bare substrata. Regarding species richness, diversity and evenness, a negative effect of unvegetated substrata could be observed, compared with vegetated habitats on the whole (i.e. macroalgal beds and seagrass meadows) (Figure 3). Within seagrass habitat, vegetation percent cover had a positive linear effect on mean values of all indicators except for species evenness, which varied non linearly and reached a plateau at approximately 40% of seagrass cover (Figure 4).

Effect of floral composition in seagrass meadows

Best models fitted for *S. abaster*, *S. typhle*, *N. ophidion* and *H. guttulatus* showed an overall positive effect of seagrass habitat on species distribution. Hence, the relative importance of each meadow typology for such species was investigated (Figure 5). *S. typhle*, *N. ophidion* and *H. guttulatus* all showed a similar response pattern to the presence of a particular meadow typology. They were all predicted with greater mean densities or probability of presence in meadows dominated by both *C. nodosa* and *Z. marina*, without marked differences between the two habitats (only *N. ophidion* showed a clear preference for *C. nodosa*) and meadows dominated by *Z. noltei* showing an overall less positive effect. In addition, all these species were negatively affected by the presence of both bare substrata and macroalgal beds when considering different meadow types in models, hence suggesting their avoidance of such habitats. On the contrary, while a preference of *S. abaster* for *C. nodosa* can be observed, the effects of *Z. marina* and *Z. noltei* meadows, as well as of macroalgal beds, were similar and positive, compared to bare substrata.

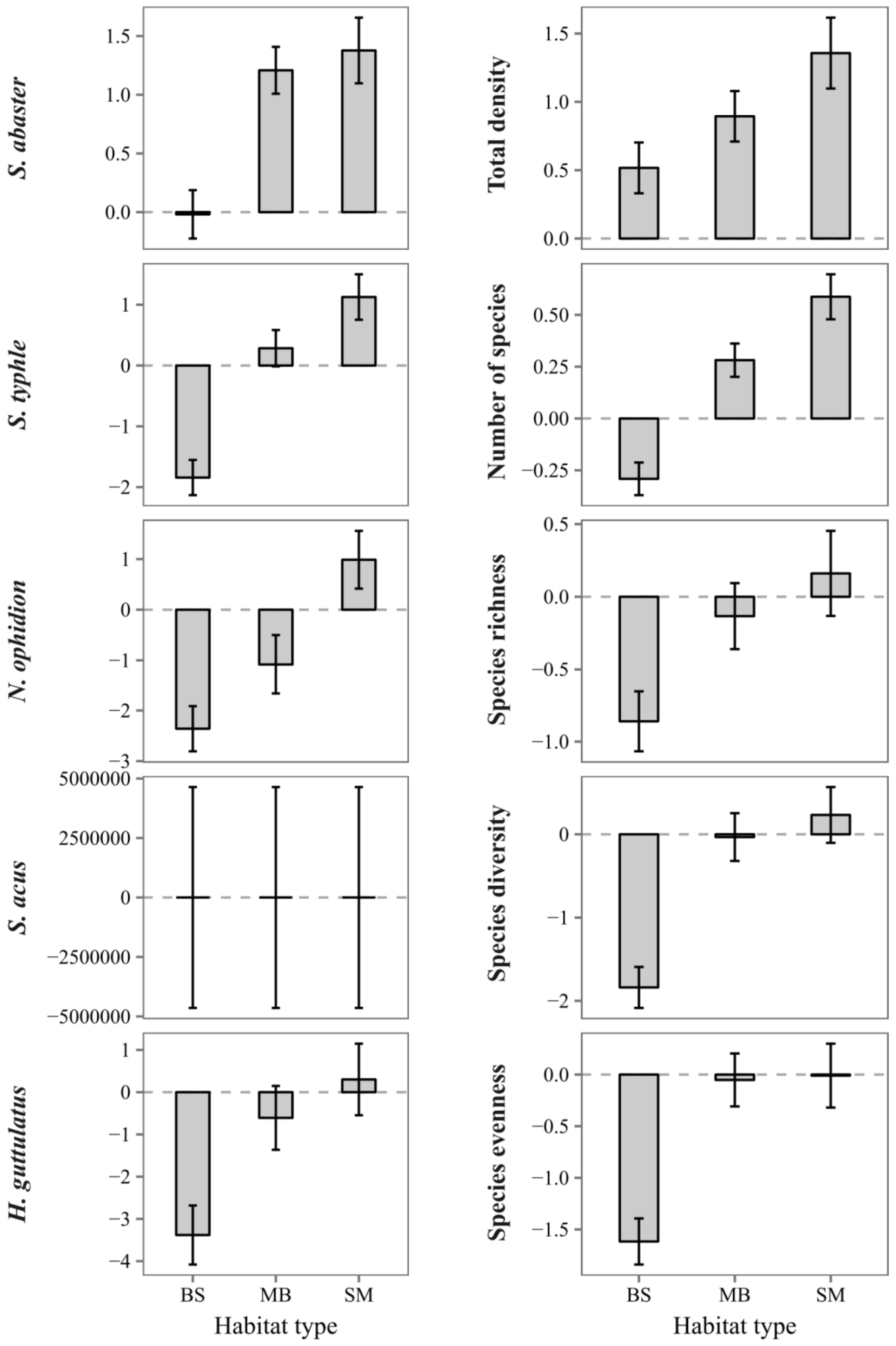

Figure 3: Parametric coefficients of habitat typology as estimated by the best models selected for syngnathid species. BS = bare substrata; MB = macroalgal beds; SM = seagrass meadows.

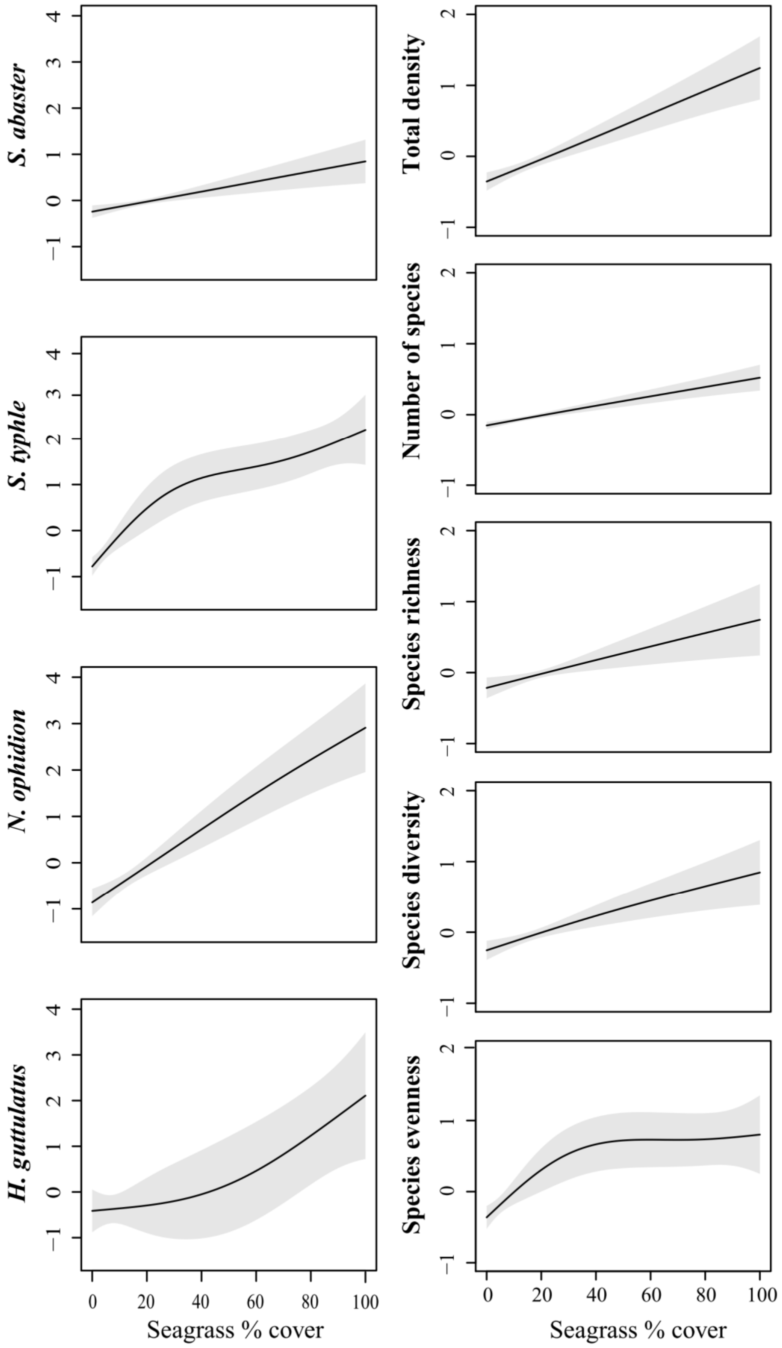

Figure 4: Smoothers of seagrass percent cover as estimated by the best models selected for syngnathid species and assemblage indicators. The fitted values are adjusted to average zero and the shaded areas indicate 95% confidence intervals.

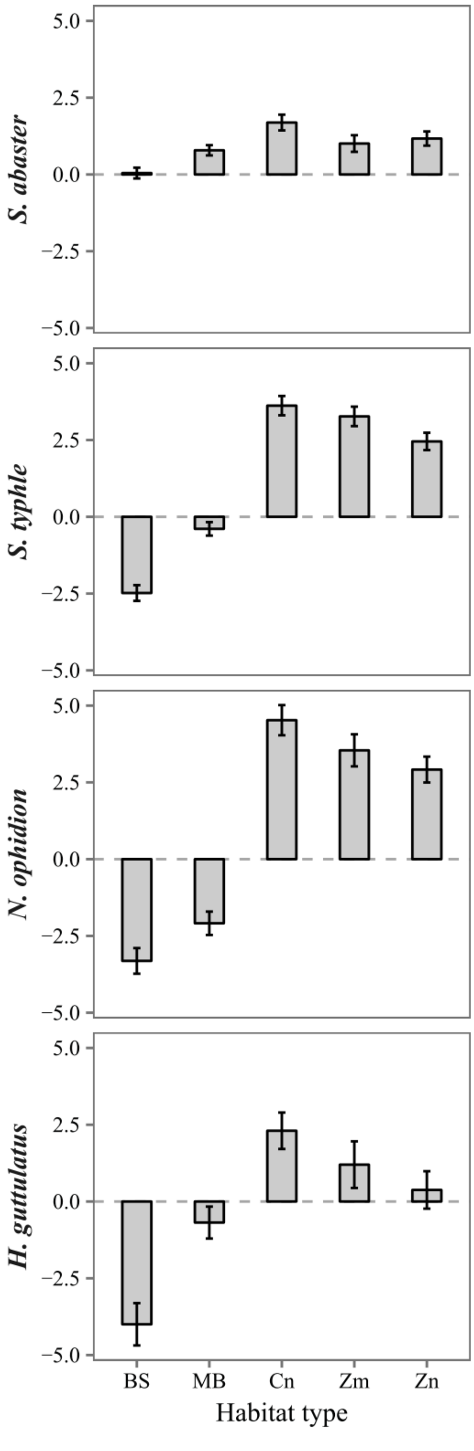

Figure 5: Effect of habitat typology including seagrass meadow types on syngnathid species according to the selected best models. BS = bare substrata; MB = macroalgal beds; Cn = C. nodosa-dominated meadows; Zm = Zostera marina-dominated meadows; Zn = Zostera noltei-dominated meadows.

Discussion

Linking syngnathids to their habitat in the Venice lagoon

The present study showed that seagrass meadows in the Venice lagoon support significantly greater densities of common syngnathid species, total syngnathid densities and species richness compared with unvegetated areas and macroalgal dominated areas, thus confirming the overall importance of seagrasses for the family. In addition, a positive relationship with the increase in seagrass percentage cover was observed in these species as well as in all the assemblage indicators considered, Many studies have investigated the effect of meadow structure on seagrass fish. Bell and Westoby (1986) for instance, drawn similar conclusions to those reported here, suggesting the important role for Syngnathids of more mature and continuous meadows. Indeed, they found that *Hippocampus whitei* and *Syngnathus margaritifer* responded negatively to a reduction in seagrass density in *Posidonia australis* and *Zostera capricorni* meadows.

This study highlighted that the variability in floral composition of seagrass meadows influences syngnathid distribution. Seagrass species composition determines some fundamental characteristics of meadow architecture such as canopy height, leaf and shoot densities as well as leaf width, which could consequently affect the availability of suitable microhabitats for syngnathids (Hyndes et al., 2003; Malavasi et al., 2007). In the Venice lagoon, *Z. marina* and *C. nodosa* meadows are usually characterised by taller canopies and larger leaves compared with meadows dominated by *Z. noltei*, which in turn show the highest shoot densities (Sfriso & Ghetti, 1998). *S. typhle* and *N. ophidion* in particular, appeared to avoid non-seagrass habitats and have a preference for tall canopy meadows dominated by either *C. nodosa* or *Z. marina*. Longer and broader leaves could enhance the crypsis in the relatively large and broad-nosed *S. typhle* (Jackson et al., 2006a; Malavasi et al., 2007; Steffe et al., 1989), which assumes a vertical posture in order to locate and capture their prey among seagrass leaves. Similarly *N. ophidion*, which often entwines seagrass leaves and explores the surroundings in search of prey, may need longer and more robust leaves for physical support, as already suggested by Malavasi et al. (2007).

H. guttulatus was not abundant in shallow waters, probably preferring deeper and more stable environments such as subtidal meadows and other hard substrata at greater depths (Gristina et al., 2017). Despite being relatively uncommon, this species resulted associated with tall and spatially continuous seagrass habitats.

Macroalgal beds are actively avoided by *Nerophis* and *Hippocampus* species in the shallow waters of the Venice lagoon. While macroalgae may host great densities of invertebrate prey and serve as habitat for some syngnathid species (Polte & Buschbaum, 2008), they usually lack structures that are robust enough to serve as holdfast, especially in the case of laminar Ulvaceae. Unlike *Nerophis* and *Hippocampus*, *Syngnathus* species are not provided with prehensile tail and do not need to grasp or entwine holdfasts, showing instead an active swimming behaviour for most of the time. For this reason, also macroalgae may be selected as habitat by *Syngnathus* species.

In particular for *S. abaster,* macroalgal beds serve as a suitable habitat, possibly due to the increased chance to feed on associated fauna and to hide from predators. *S. abaster* is a common component of fish assemblages of the Italian coastal lagoons, and it is found in a variety of habitat typologies including macroalgae (Campolmi et al., 1996; Franco et al., 2006; Franzoi et al., 1993; Riccato et al., 2003). The differences in seagrass association between *S. abaster*, *S. typhle* and *N. ophidion* shown in the present study highlighted the more generalist behaviour in habitat choice of *S. abaster* compared to *S. typhle* and *N. ophidion*, which in turn appear to be seagrass specialists.

Unlike other syngnathids in the Venice lagoon, *S. taenionotus* feeds almost exclusively on zooplankton (Franzoi et al., 1993); hence, the less strict association with any particular habitat that was highlighted in the present study might increase the foraging efficiency in the water column. This species is indeed documented to live in Northern Adriatic lagoons on seagrass meadows, bare mud- and sand-flats and within drifting macroalgae (Franco et al., 2006; Franzoi et al., 1993). Similarly, other syngnathid species modelled in this study did not show any clear response to habitat typology, probably due to their relatively scarce presence in shallow water environments, due to their preference for other habitat types. As regarding the two species of *Hippocampus*, Curtis and Vincent (2005) suggest that *H.*

hippocampus tends to use bare sandy bottoms and hard biogenic structures, while Caldwell and Vincent (2012) highlighted the preference of *H. hippocampus* for slightly deeper water (>3m) and habitats with high current speed.

Implications for species and habitat conservation

Alterations of lagoon morphology, including habitat loss, and deterioration of water and sediment quality are currently the major factors of human-induced change in the Venice lagoon (Curiel et al., 2014; Molinaroli et al., 2009; Sarretta et al., 2010; Sfriso & Facca, 2007; Solidoro et al., 2010), which can have a negative effect on fish fauna (Franco et al., 2009a; Zucchetta et al., 2016). Traditional fishing activities in the shallow waters of the lagoon at the present level of effort can be considered not harmful for syngnathids, since these species have no commercial value and levels of by-catch are usually very low (Zucchetta et al., 2016). In turn, it can be argued that habitat loss is the biggest threat to syngnathids in the Venice lagoon, as well as in other coastal waters around the world (Curtis & Vincent, 2005; Harasti et al., 2014; Lim et al., 2011; Pihl et al., 2006; Vincent et al., 2011).

In this context, populations of *S. typhle*, *N. ophidion* and *H. guttulatus* in the Venice lagoon may be the most damaged by fragmentation and loss of *C. nodosa* and *Z. marina* meadows, due to their strong association with this habitat. Other syngnathids, such as *S. abaster*, could also be directly affected by an overall loss of suitable habitat, as well as a number of other fish species of conservation and commercial value that are strongly associated with seagrasses in this ecosystem (Franco et al., 2006; Franzoi et al., 2010; Scapin et al., 2016). The indirect consequences of habitat loss however may be difficult to predict, and reach also species that do not rely directly on meadows, since the degradation of this habitat could alter the whole nutrient and detritus chains on which all fish species and the entire ecosystem is based (Vizzini et al., 2002; Vizzini & Mazzola, 2004).

Seagrass meadows composed of long- and broad-leaved species are known to provide more substantial and a wider variety of ecosystem services compared with meadows dominated by small species (Nordlund et al., 2016). As the present work highlighted, the long- and broad-leaved *C. nodosa* and *Z.*

marina also support greater densities of seagrass specialist syngnathid taxa in the Venice lagoon, in particular in less confined areas subjected to a greater influence of the sea. Managers in Mediterranean coastal lagoons should then regard the reduction of human pressures that lead to the depletion of these meadow typologies as a priority in ecological conservation. Ad hoc measures may include the limitation of direct pressures and impacts, such as anchoring practices or other disturbance that determine the mechanical destruction of meadows, but a more comprehensive coastal planning approach should be followed, in order to prevent alterations to the morphology and hydrodynamics of shallow water areas at the ecosystem scale (McCloskey & Unsworth, 2015). Furthermore, actions aiming to restore meadow structure and functionality for syngnathids should be promoted in these ecosystems (Scapin et al. (2016). While continuous and well structured meadows (e.g. those successfully restored) are able to support overall greater densities of species such as *N. ophidion* and *H. guttulatus*, early restoration stages, which may be characterised by lower seagrass densities, could be more important for species such as *S. abaster* and *S. typhle*, as well as for the overall syngnathid species diversity and evenness, which all appear to be less affected by seagrass percent cover. This, while highlighting the importance of seagrass population dynamics and diversity for associated fish, also confirms that different levels of seagrass restoration success would determine significant differences in the associated syngnathid assemblages.

Syngnathids are usually considered one of the most typical fish groups associated with seagrass meadows, and are subsequently viewed as one of the flagships of this habitat. However, as this study demonstrates, different syngnathid species can coexist in highly heterogeneous ecosystems such as coastal lagoons by selecting different habitats, according to the species specific adaptations. In the Venice lagoon shallow waters, of the nine species recorded only *S. typhle* and *N. ophidion* are truly seagrass specialists, and may serve as suitable flagships for *C. nodosa* and *Z. marina* meadows. Any initiative aiming at raising the public attention on seagrass conservation in Mediterranean coastal lagoons could hence adopt such species as iconic representatives of a threatened habitat and its associated fauna; both *S. typhle* and *N. ophidion* are easily identifiable organisms, which could easily play this role. In addition to the flagship function, because of their strong association with particular seagrass meadow typologies, it is suggested that such species could also be employed as sensitive indicators of the conservation status of these habitats in the Mediterranean, e.g. by monitoring attributes of population structure (Pollom, 2016c, d). *H. guttulatus*, while being associated with tall and highly structured meadows as well, accounts for a very small proportion of the overall catches of syngnathids in the shallow waters of the Venice lagoon, and conversely could represent a key feature of fish assemblages in other structured habitats at greater depths, as suggested by other studies (Gristina et al., 2017, 2014). For this reason, despite the obviously charismatic function of this species, it may not be as effective a flagship for shallow water seagrass meadows as *S. typhle* and *N. ophidion*.

A monitoring programme of fish assemblages is currently ongoing in the northern sub-basin of the Venice lagoon, which is revealing early signals of re-colonisation of shallow water habitats by one of the identified seagrass specialists, namely *S. typhle*. These preliminary findings, although not yet confirmed by numerical analyses, are probably linked to the reinstatement of *Z. marina* meadows currently observed in the area, as a consequence of both natural dynamics and restoration (Facca et al., 2014a; Scapin et al., 2016). The presence of *S. typhle* within an area that was subjected during the last decades to extensive seagrass loss suggests that the conservation status of meadows in a large portion (approximately 260 km^2, Cucco & Umgiesser, 2002) of the Venice lagoon ecosystem is now starting to recover. Specifically designed studies are however needed, in order to quantify the rates of such recovery in terms of both seagrass habitat development and syngnathid populations enhancement.

Future goals of research and conservation

Of the nine species recorded in the lagoon, only three (*S. abaster*, *S. typhle* and *N. ophidion*) are very abundant and frequent in shallow waters, with a fourth one (*H. guttulatus*) being relatively frequent but found in lower densities. It is therefore urgent to investigate the role of other lagoon habitats, such as seagrass meadows, oyster reefs and other hard substrata located at greater depths, which could possibly play a role in supporting syngnathid species that are only occasionally found in shallower environments. Indeed, deep estuarine environments have been proven to be important yet poorly known fish habitats elsewhere (Bradley et al., 2017), and in particular for some syngnathids such as the genus *Hippocampus* (Caldwell & Vincent, 2012; Curtis & Vincent, 2005; Gristina et al., 2017, 2014).

Despite the primary importance of seagrass meadows for syngnathids in Mediterranean coastal lagoon shallow waters, future studies should focus on investigating the attributes of syngnathid assemblages in deeper lagoon areas, in order to understand the habitat characteristics affecting their distribution and provide more comprehensive and effective management tools towards their conservation.

Given the indicator role of *S. typhle* and *N. ophidion*, it is also suggested that data on population structure of these species should be collected, in order to detect potential declining trends and provide insights into the conservation status of Mediterranean coastal lagoons. These surveys could be standardised and incorporated in periodic sampling programmes of fish assemblages, such as surveillance monitoring under the Water Framework Directive (2000/60/EC), allowing to extend to other Mediterranean transitional water ecosystems this approach.

Acknowledgments

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Supplementary materials

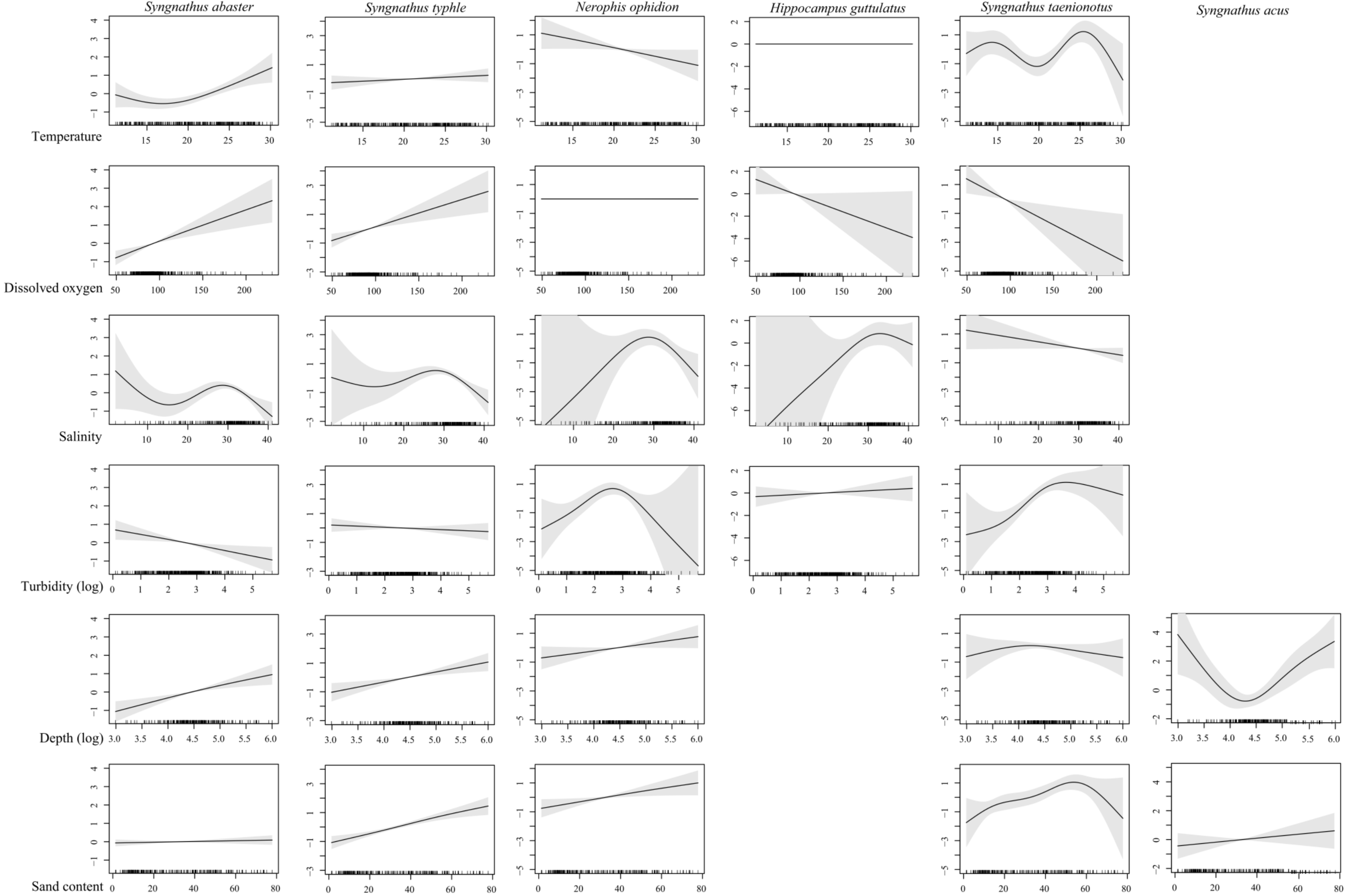


Figure S1: Smoothers of physico-chemical parameters as estimated by the best models selected for syngnathid species. Only species responding to one or more parameters are shown. The fitted values are adjusted to average zero and the shaded areas indicate 95% confidence intervals. Tick marks along the x- axis show the location of observations along the variable range.

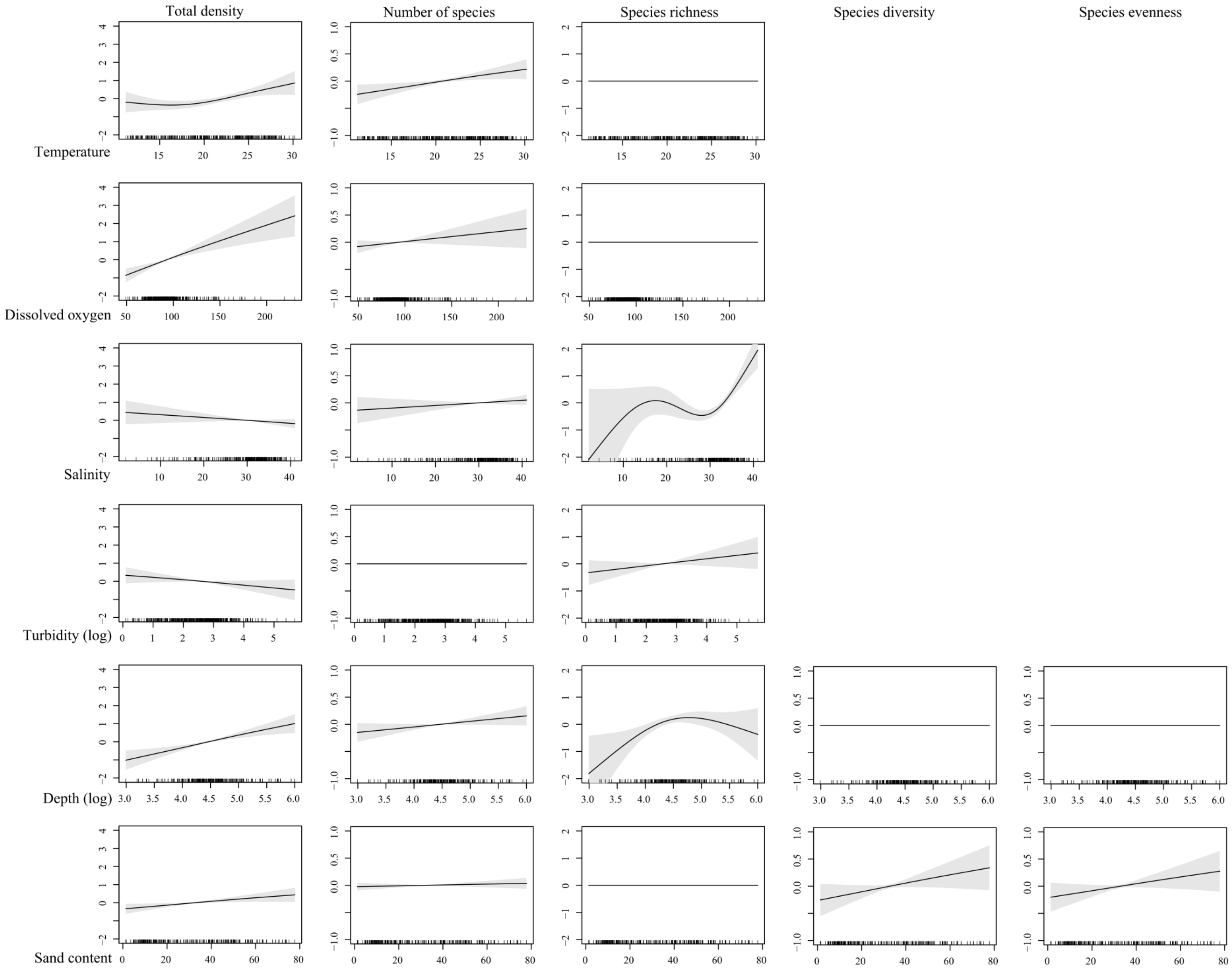
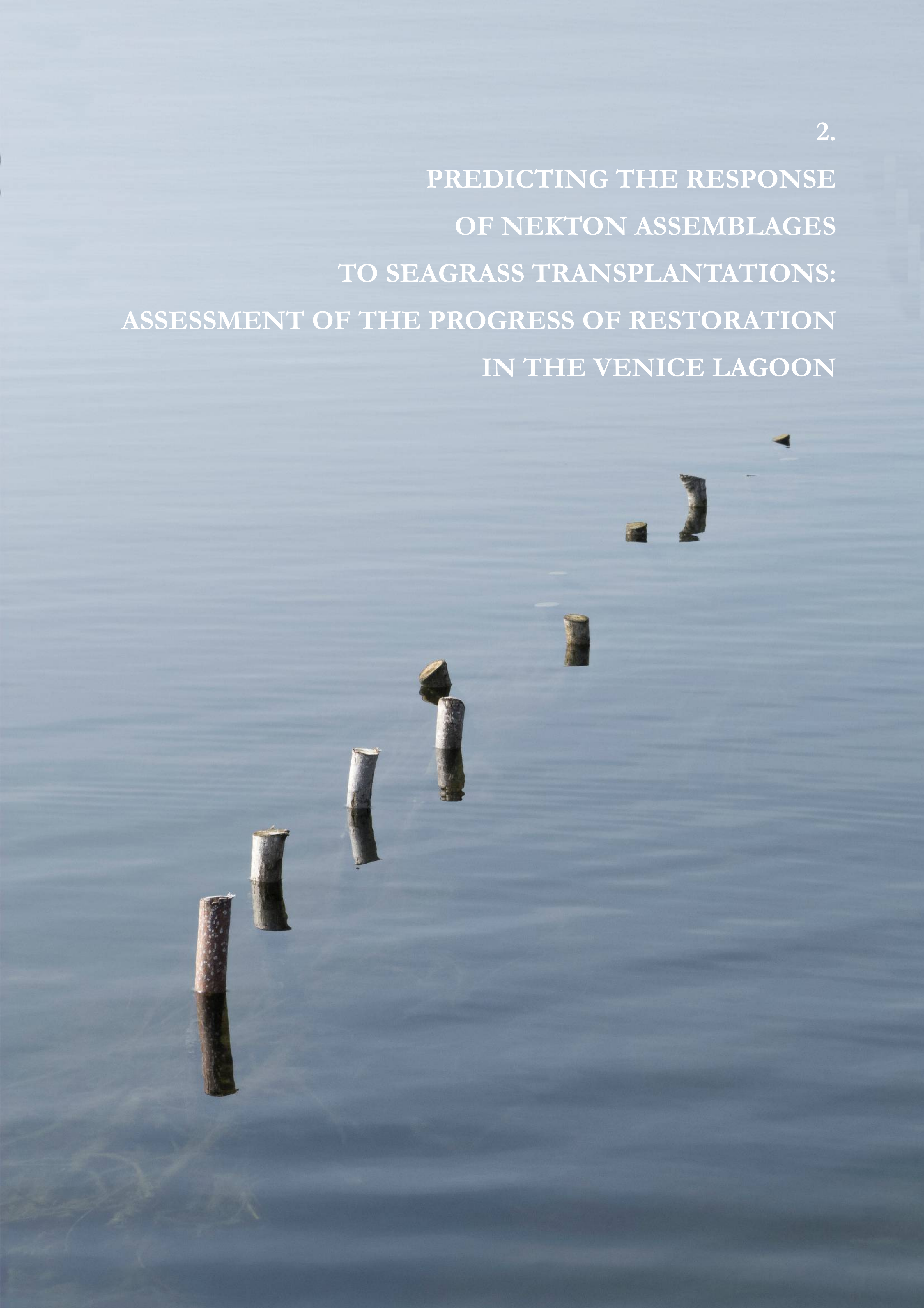


Figure S2: Smoothers of physico-chemical parameters as estimated by the best models selected for syngnathid assemblage indicators. The fitted values are adjusted to average zero and the shaded areas indicate 95% confidence intervals. Tick marks along the x- axis show the location of observations along the variable range.

2.

PREDICTING THE RESPONSE OF NEKTON ASSEMBLAGES TO SEAGRASS TRANSPLANTATIONS: ASSESSMENT OF THE PROGRESS OF RESTORATION IN THE VENICE LAGOON



Previous page: protective wooden barriers at a seagrass restoration site in the northern Venice lagoon (© Luca Scapin)

Introduction

Restoration of ecosystems is considered a strategic approach to successfully implement management and conservation of biodiversity (Menz et al., 2013; Perring et al., 2015; Suding, 2011). A major task in restoration ecology is to evaluate the progress (or success, although terms are not equivalent) of re-created habitats towards desired ecological goals (*sensu* Zedler, J.B. & Callaway, 2000). To quantitatively assess whether a restoration scheme is successful, is for many reasons often a challenging duty. Definition of progress criteria can be biased, as it depends upon which measurable targets are selected and subsequently upon how monitoring schemes are designed (Kentula, 2000; Short et al., 2000). The selection of targets itself may be problematic, since the different stakeholders involved in a project may be interested in different restoration outcomes (Kentula, 2000; Suding, 2011). Historically, restoration schemes have primarily focused on the re-establishment of vegetation, hence adopting plant-based success criteria that rely on e.g. plant morphometrics, vegetation cover and diversity, primary productivity (McAlpine et al., 2016). However, this approach could lead to simplistic and/or incomplete assessments, since it does not take into account other fundamental ecological functions, such as the trophic role of recreated habitats for faunal assemblages and their capability to support overall biodiversity (Bourque and Fourqurean, 2014; Dolbeth et al., 2013; Fraser et al., 2015). Coastal and transitional water ecosystems pose additional challenges to the evaluation of restoration success, since many ecological compartments and processes are known to follow complex patterns of recovery and exhibit hysteresis after restoration (Borja et al., 2010; Duarte et al., 2015; Elliott et al., 2007).

Seagrass loss has been observed worldwide, this being caused by both natural and human-induced pressures (Airoldi & Beck, 2007; Short et al., 2011; Waycott et al., 2009). The loss of seagrass beds has induced scientists and practitioners in many countries to directly intervene with restoration programmes (van Katwijk et al., 2015). However, there are still few examples of seagrass transplantations in the Mediterranean, which are mainly represented by experimental trials instead of being actual management strategies (Jahnke et al., 2015; Pirrotta et al., 2015; Pranovi et al., 2000). On the contrary, in the Venice lagoon, the seagrass restoration programme SERESTO started in 2014 in order to revert the status of the northern lagoon sub-basin (Facca et al., 2014a), which was subjected to extensive loss of *Zostera marina* and *Z. noltei* seagrass species at least since 1990s (Curiel et al., 2014; Sfriso et al., 2005a). The project involved the transplantation of seagrass sods and rhizomes within 100 m^2 sites of the northern lagoon sub-basin, aiming to trigger a natural process of re-colonisation of shallow water substrata by *Z. marina* and *Z. noltei* through the increase of vegetation cover within the area. Together with the recreation of the seagrass meadows, the scheme also aims to restore the associated nekton faunal assemblages, which are expected to progressively colonise the newly-created habitats and eventually acquire structural and functional traits similar to those of natural seagrass beds (Scapin et al., 2016).

In seagrass restoration studies, great attention is given to measure the success of vegetation recovery, in terms of survival and growth of transplantations and expansion of seagrass patches (Bell et al., 2014; Suykerbuyk et al., 2016; Uhrin et al., 2009; van Katwijk et al., 2015). Conversely, fewer works adopt a faunal-based perspective in assessing the success of seagrass restoration (Lefcheck et al., 2017; McSkimming et al., 2016; Sheridan et al., 2003), partly due to the fact that the time span covered by monitoring programmes is often insufficient to track changes in animal colonisation of created habitats (Cunha et al., 2012; McSkimming et al., 2016). The seagrass restoration project taking place in the Venice lagoon included the monitoring of plant survival and growth, but also of associated nekton assemblages, acknowledging that, through the reinstatement of habitat structural attributes, ecological restoration must also sustain the trophic web dynamics and enhance the overall ecosystem biodiversity (Facca et al., 2014a; Scapin et al., 2016).

Recently, a call for making restoration ecology a truly predictive science has been advocated. The use of forecasting techniques would allow to overcome some of the uncertainty associated with the assessment of restoration success, ultimately supporting the design and management of more effective habitat creation schemes (Brudvig, 2017). Embracing this perspective, in this study we carried out a model analysis based on nekton observations in natural and transplanted seagrass meadows, aimed to predict the characteristics of fish and invertebrate assemblages that are expected in successfully restored seagrass habitats in the Venice lagoon.

The ultimate goal of this chapter is to propose a model-based approach to assess the progress of nekton fauna in restored seagrass habitats, using the transplantation project in the Venice lagoon as case study. The work, after describing the general methods employed, illustrates the three focal steps involved in the analysis: i) in the first phase, a model explaining the variability of nekton assemblage observed at natural seagrass sites is developed; ii) in the second phase, the target environmental and habitat scenarios expected at the end of the restoration process are defined, and the reference nekton assemblages expected according to such scenarios are predicted using the models developed in the first phase; iii) in the third and last phase, the nekton assemblages observed at a set of seagrass restoration sites are compared with the respective reference assemblages as predicted in the second phase. The following hypotheses were tested: i) water and sediment properties and seagrass habitat characteristics can explain the distribution of nekton fauna in natural meadows of the Venice lagoon; ii) such environmental drivers can be employed in a predictive way to assess the progress nekton assemblages in sites subjected to seagrass restoration.

Thus, an example of how it could be possible to assess the progress of nekton assemblages towards reference conditions is provided.

Methods

Study area

The northern sub-basin (Figure 6) is the widest in the Venice lagoon (approximately 260 km^2), and exchanges with the Adriatic sea ca. 10 m^3 of water per second through the Lido inlet (Cucco and Umgiesser, 2002). It comprises the majority of inhabited islands, including the city of Venice, and is characterised by greater freshwater inputs compared to the other sub-basins due to the presence of many tributaries (Solidoro et al., 2002). Such conditions produce strong environmental gradients within the sub-basin, with water salinity, trophic status, turbidity and sediment granulometry experiencing relevant spatio-temporal variations. In addition, the northern sub-basin is characterised by the presence of a strong confinement gradient between the inlet and the mainland and by a higher degree of morphological and habitat heterogeneity compared with other lagoon areas. It features a mosaic of saltmarshes, intertidal flats, channels and subtidal shallows, the latter with or without seagrass meadows (Solidoro et al., 2010).

Field data collection and sampling sites

Sampling sites and definition of calibration and evaluation datasets.

The sampling design included five natural seagrass sites located along a gradient of confinement and of water and sediment physico-chemical conditions within the northern sub-basin (Figure 6). Natural sites were all characterised by stable seagrass meadows, featuring different plant species composition and habitat structure, hence allowing to represent the heterogeneity of seagrass habitats found in the lagoon northern sub-basin. Sampling was carried out on five occasions, from late March to late June 2016 (23/03/2016, 18/04/2016, 03/05/2016, 24/05/2016 and 22/06/2016), this period coinciding with the phase of major development of epigeous parts of seagrass plants (Sfriso and Ghetti, 1998) and of recruitment of most of the lagoon nekton species (Franco et al., 2006). During each sampling occasion, at each one of the five natural sites, data on nekton fauna, abiotic variables and habitat characteristics were recorded employing the methodologies described in the following paragraphs. Such data constituted the calibration dataset.

In addition, eight of the 35 sites subjected to restoration under the project SERESTO, which were representative of the environmental variability in the whole northern sub-basin (Facca et al., 2014a), were included in the sampling design. Sampling at eight sites was carried out in spring 2014, 2015, 2016 and 2017, allowing to track changes in assemblages from the moment of seagrass transplantations (year

0) for the following three years. Together with restoration sites, two stable natural seagrass meadow sites ("independent control sites") located near the sea inlet and in a highly confined area were also monitored in 2015, 2016 and 2017 (Figure 6). This additional sampling at natural seagrass sites, providing data independent from that included in the calibration dataset, allowed to describe how the structure of seagrass nekton assemblage may vary under two very different abiotic and habitat conditions. Data from both restoration and independent control sites constituted the evaluation dataset.

Nekton and abiotic sampling

At all types of site, nekton fauna was collected with the same methodology, and described in "General methods – Sampling and analysis of nekton fauna", pag. 11. Specimes were identified at the species level. Only for individuals belonging to the family Hippolytidae (Crustacea Decapoda), identification was limited to family level. All data were then standardised over an area of 100 m^2, allowing direct comparison between samples.

Only for sites constituting the calibration dataset, a set of abiotic variables was also measured, following the methodologies described in "General methods - Environmental characterisation of sampling sites", pag. 12. In addition, water residence times (days) were attributed to each sampling site from thematic raster maps (Ghezzo et al., 2010).

Habitat characterisation

In addition to abiotic parameters, a set of seagrass habitat characteristics was recorded at each site constituting the calibration dataset. Total seagrass percent cover was estimated for each site by visual census at five fixed distances along the transect swept by the seine net and then averaged. Three to five replicate quadrats (0.25 x 0.25 m) were placed at fixed distances on the substratum along the transects. A total of 52 seagrass samples were collected, and then taken in the laboratory for additional analysis. Canopy height (cm), shoot density (no. of shoots . m^{-2}), leaf area index (LAI; half-leaf area . m^{-2}), epiphytal load (percent weight of all epibiota relative to the 15 cm apical portion of leaves) and epigeous biomass (g) were measured separately for seagrass species *C. nodosa*, *Z. marina* and *Z. noltei* and for each replicate. Values were then averaged per species, site and sampling occasion. Overall properties of the seagrass habitat were also calculated for each site and sampling occasion, by averaging species values.

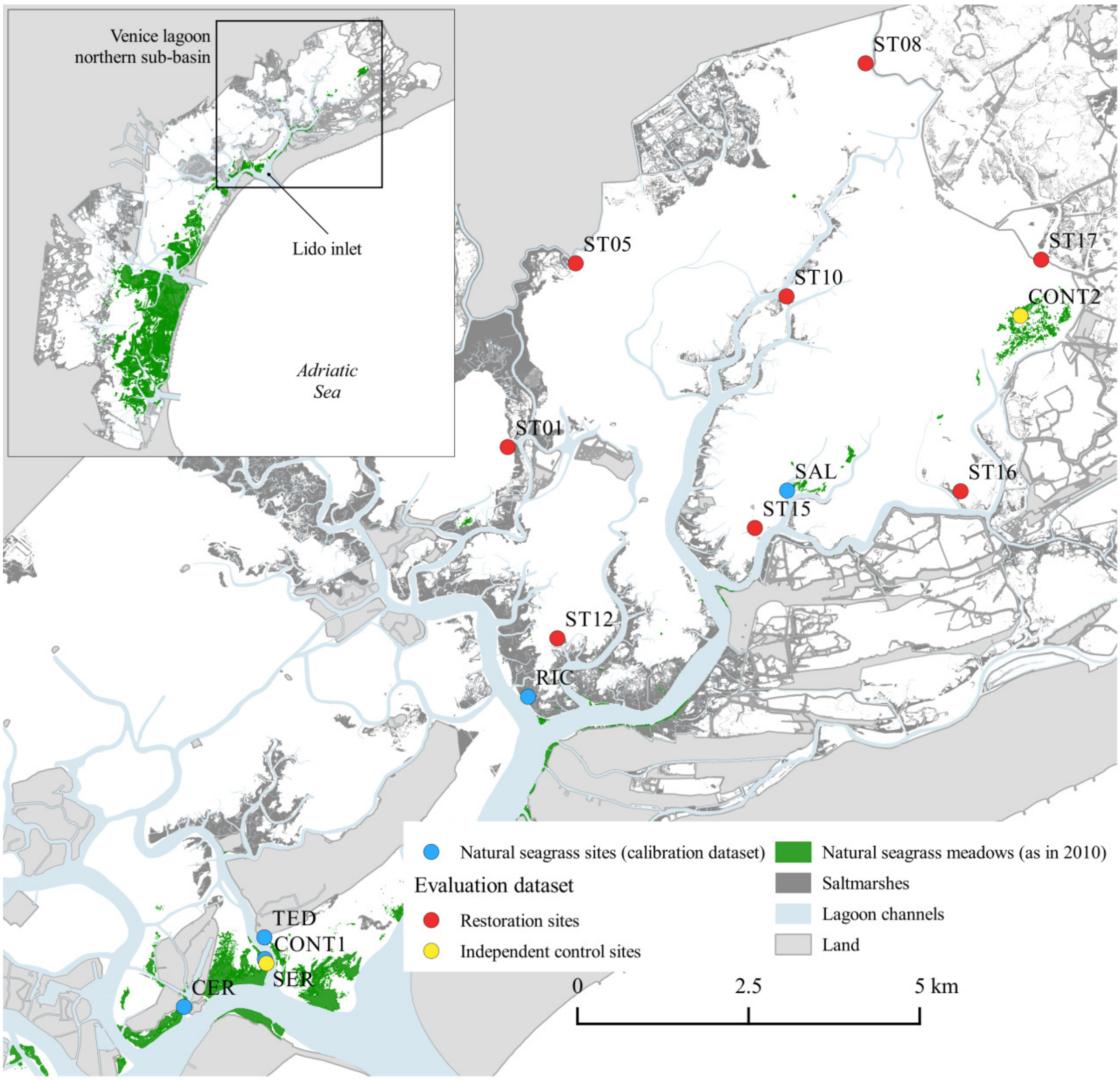


Figure 6: Study area and location of sampling sites constituting the calibration and evaluation datasets.

Data analysis

Modelling the calibration dataset

Two separate Principal Component Analyses (PCAs) were performed on standardised abiotic and habitat variables measured for the calibration dataset, and variable loadings on PC axes were extracted. The first two axes of each PCA were then used to summarise abiotic and seagrass habitat properties of natural sites.

Negative binomial GLMs were fitted on density of abundance of each species contributing to 95% of total abundance in the calibration dataset, while binomial GLMs were fitted on presence/absence data of all the species. Different model formulations were considered, including different combinations of temporal, abiotic and habitat predictors (Table 4). Sampling date was included as temporal factor; the first two principal components calculated on abiotic and habitat variables were included to represent respectively abiotic and seagrass predictors. The relative influence of abiotic and habitat factors on structure of nekton assemblage was then tested by performing Likelihood Ratio tests (with 1000 bootstrap iterations) between GLM formulations (Table 5). Following the approach of the *manyglm* software package (Wang et al., 2012), inference was carried out at the assemblage level by combining species-specific results in a global analysis (Wang et al., 2012; Warton et al., 2012). This allowed to investigate various hypotheses on the different contribution of each type of predictor to overall assemblage variability. Test t1 allowed to test the hypothesis that habitat predictors (respectively) improved a model only including temporal factor. Test t2 tested the significance of including abiotic variables, to a model considering both temporal and habitat factors. Ultimately, this method permitted to disentangle the influence of habitat structure on nekton fauna from the temporal effect (test t1), and to investigate if physico-chemical and geographical characteristics of sites played an additional role (test t2). According to the results of the tests, the most parsimonious model formulation (i.e. that including the smallest number of relevant factors) for both abundance density and presence/absence was selected, and employed in the last section of this work to evaluate the success of restoration for seagrass fauna.

The predictive capabilities of the chosen model formulations were evaluated by calculating Spearman's r coefficient and Area Under the ROC Curve (AUC; Fielding and Bell, 1997), for GLMs based on species density and presence/absence respectively. To compute the coefficients, both the whole dataset (i.e. using sampling sites, occasions and species as replicates) and each species separately (i.e. using sampling sites and occasions as replicates) were considered. Coefficients were calculated between observed and predicted values, with the latter obtained by means of a k-fold cross-validation (k=5), allowing to compute average and standard deviation values for r and AUC calculated for the whole dataset and for each species. This procedure ultimately allowed to evaluate the overall model prediction performances, and to identify which species were better predicted by the chosen models.

Table 4: GLMs formulations considered in this study. PC1 and PC2 refer to first two axes extracted from PCAs performed on abiotic and habitat variables.

Model	**Formula**	**Factors included**
m0	$Y_i \sim date + c + \varepsilon_i$	Temporal
m1	$m0 + PC1_{habitat} + PC2_{habitat}$	Temporal + habitat
m2	$m0 + PC1_{abiotic} + PC2_{abiotic} + PC1_{habitat} + PC2_{habitat}$	Temporal + abiotic + habitat

Table 5: Summary of Likelihood Ratio tests performed between pairs of GLM formulations. For each comparison, the respective factor (*abiotic* or *habitat*) being tested is specified.

Test		**Testing the effect of:**
t1	m0 vs m1	*Habitat* factor, when only temporal factor was considered before
t2	m1 vs m2	*Abiotic* factor, when both temporal and habitat factors were considered before

Definition of target scenarios and prediction of reference assemblages

In order to identify the reference assemblage using the predictive approach, it was necessary to define the state of predictor variables as expected at the end of restoration process, i.e. the target scenarios. Three target scenarios were defined, each one accounting for different floristic composition and habitat structure. This allowed to set site-specific (i.e. different for each one of the restoration sites evaluated) target environmental conditions, based on the different habitat characteristics that were designed for each restoration site. The first scenario represented a target seagrass meadow dominated by *Z. marina*, while the second one represented a seagrass meadow dominated by *Z. noltei* and the third one a seagrass meadow with mixed characteristics. Seagrass characteristics estimated at natural sites were used for this purpose, and set according to the three different scenarios proposed. For the first scenario, parameters measured on *Z. marina* (and overall seagrass parameters correlated with them) were set at the best values recorded (e.g. maximum observed *Z. marina* cover, canopy height, density etc.). Conversely, parameters measured on *Z. noltei* (and overall seagrass parameters correlated with them) were set at average values. For the second scenario, parameters measured on *Z. noltei* (and overall seagrass parameters correlated with them) were set at the best recorded values, while parameters measured on *Z. marina* (and overall seagrass parameters correlated with them) were set as average. For the third scenario, parameters of both *Z. marina* and *Z. noltei* were set at average values. In all cases, parameters measured on *C. nodosa* were set at the lowest observed values, since this species was not subjected to transplantations at the considered sites.

Abiotic conditions were also included in target scenarios, and defined based on the assumption that, within the temporal range considered in this study (three years after restoration), temperature, salinity, dissolved oxygen and sediment granulometry would not be influenced by the development of new seagrass habitat. In turn, the assumption was made that values of turbidity and of chlorophyll concentration in water and sediments would change in response to changed habitat characteristics, and become similar to those observed at natural seagrass meadow sites in comparable condition of confinement within the study area. As a result, abiotic variables not influenced by seagrass restoration (including geographical variables distance from sea inlets and water residence time) were included in the three scenarios using values measured at each restoration site during each monitoring campaign. On the contrary, variables expected to change as a consequence of seagrass restoration were included using values measured at natural seagrass sites "SAL" and "RIC", the most similar to restoration sites in terms of degree of confinement. Finally, date of sampling was used as temporal factor. A synthesis of temporal, abiotic and habitat conditions used to define target scenarios is provided in (Table 6). Scenarios selected for each restoration and independent control site are shown in (Table 7).

For each site and year, both abundance density and probability of presence of each species was predicted, using the selected GLM formulations and each site-specific scenario. The site-specific reference nekton assemblage, i.e. that expected in target scenarios, was finally composed by weighting predicted abundance density values with respective predicted probability of presence. This allowed to take into account the influence of temporal and environmental predictors simultaneously on both species densities and probability of presence during the evaluation phase.

Table 6: Target scenarios for the prediction of reference nekton assemblage. Target scenarios for seagrass habitat parameters are defined for each seagrass species. ZMA: parameters related to *Z. marina* and overall habitat parameters correlated with this species. ZNO: parameters related to *Z. noltei* and overall habitat parameters correlated with this species. CNO: parameters related to *C. nodosa* and overall habitat parameters correlated with this species. See Figure 7 in Results section for the overall habitat parameters correlated with parameters measured for each seagrass species.

		Abiotic variables		**Seagrass habitat parameters**		
Target scenarios	**Temporal factor**	**not influenced by restoration**	**influenced by restoration**	**ZMA**	**ZNO**	**CNO**
S1	Date of sampling	Site-specific water and sediment parameters (measured during nekton sampling); site-specific distance from the inlet and water residence time	Average values of turbidity and chlorophyll concentration in water and in sediments measured at SAL and RIC natural seagrass sites	maximum	average	minimum
S2				average	maximum	minimum
S3				average	average	minimum

Table 7: Floristic composition of seagrass habitats designed for each transplantation site and respective scenario selected. Scenarios selected for the two independent control sites are also shown. Scenarios are described in Table 6.

Seagrass site	**Target seagrass habitat**	**Selected scenario**
Transplantation		
ST01	*Z. noltei* dominant	S2
ST05	*Z. noltei* dominant	S2
ST08	*Z. marina* dominant	S1
ST10	*Z. noltei* dominant	S2
ST12	Mixed meadow	S3
ST15	*Z. marina* dominant	S1
ST16	*Z. marina* dominant	S1
ST17	Mixed meadow	S3
Control		
CONT1	*Z. marina* dominant	S1
CONT2	*Z. marina* dominant	S1

Applying the model-based approach to the evaluation dataset

Abundance density of nekton assemblage collected at each restoration site and year was compared with the respective site-specific reference assemblage, as predicted following the procedure described in the previous method sections. A scatterplot of observed versus predicted (weighted) density values of all the species caught was produced for each restoration site. A similar graph was produced for the two independent control sites. Scatterplots allowed to rapidly assess the status of nekton assemblages with respect of the reference one: points located above the diagonal indicated those species occurring in restoration sites with greater densities than expected in the reference assemblage; vice versa, points located below the diagonal indicated those species observed with lower densities than expected. The absolute (i.e. without sign) differences between observed and predicted (weighted) densities of each species were averaged, in order to visualise the yearly average distance of each restoration site from the reference conditions. This allowed to track the restoration trajectories of the overall nekton assemblage at each site, eventually performing a preliminary evaluation of the success of seagrass transplantations for nekton fauna.

Results

Model calibration

The first axis of PCA performed on abiotic variables explained 39% of variance, with the second axis explaining an additional 17% of variance (56% of total variance explained by the two axes) (Figure 7). The first principal component showed a positive correlation with sediment granulometry and a negative correlation with distance from inlet, water residence time, chlorophyll concentration in sediments and turbidity, thus highlighting a major confinement gradient. The second axis, being positively correlated with temperature and chlorophyll concentration in water and negatively with dissolved oxygen and salinity, was associated with the temporal dimension, with observations made in late spring and early summer being positively correlated with the axis. PCA performed on seagrass variables allowed to explain 65% of variance with the first two principal components (Figure 7). The first axis (40% of variance explained) separated habitats dominated by *Z. noltei* and located near the inlet, from mixed habitats with both *Z. noltei* and *Z. marina* at intermediate distance from the inlet, and from more confined habitats dominated by *Z. marina*. In addition, the first component was negatively correlated with overall seagrass cover, canopy and LAI, as well as (partially) with overall seagrass epigeous biomass. The second axis (25% of variance explained) was positively correlated with *Z. noltei* epigeous biomass and (partially) with all the other variables related to *Z. noltei*. In turn, it was negatively correlated with variables related to *C. nodosa* and (partially) with overall seagrass epigeous biomass.

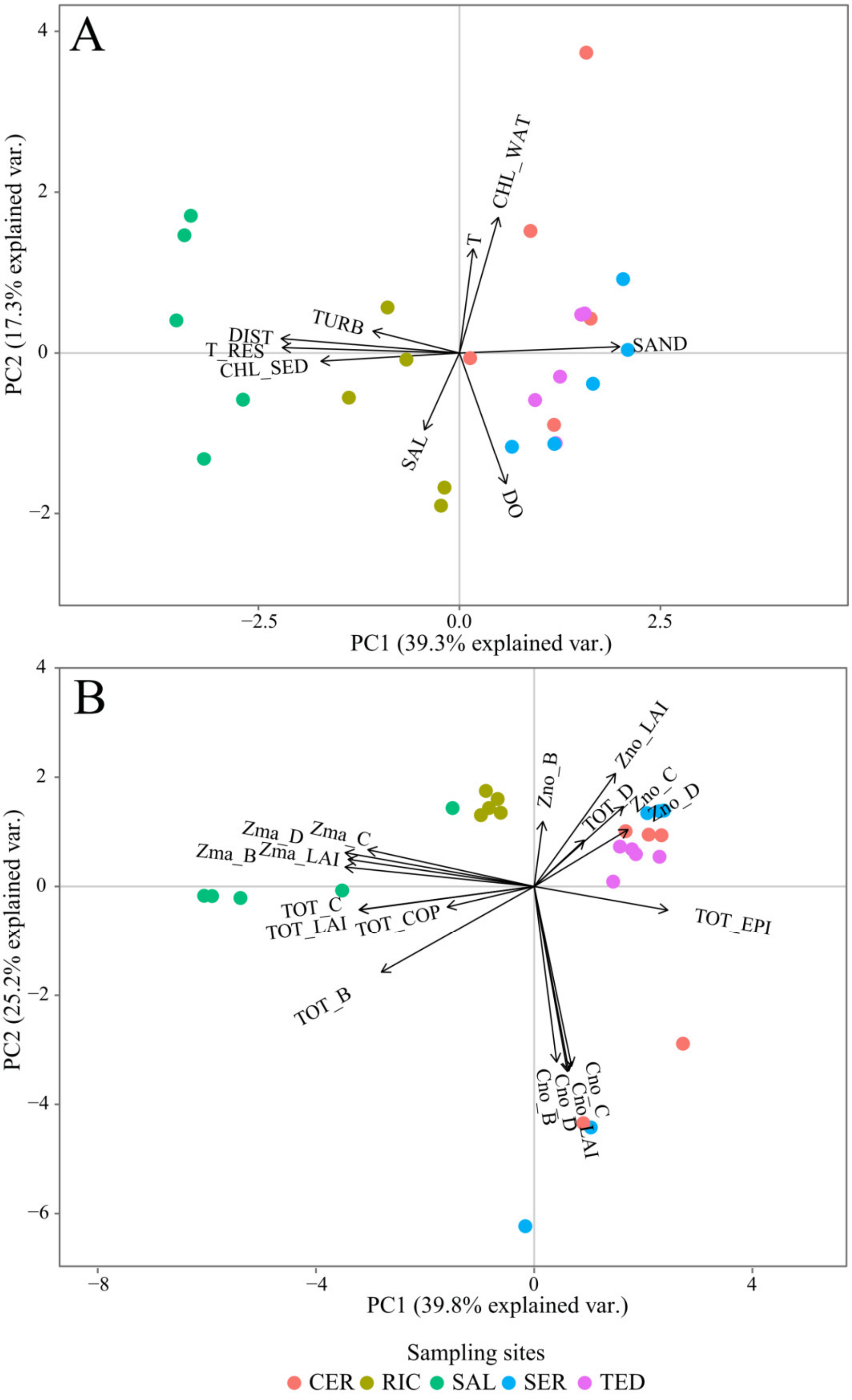


Figure 7: Biplots of PCAs calculated on abiotic variables (A) and seagrass variables (B). Points are observations. Abiotic variables are abbreviated as follows. CHL_SED: chlorophyll concentration in sediments; CHL_WAT: chlorophyll concentration in water; DIST: distance from sea inlet; DO: dissolved oxygen; SAL: salinity; SAND: sediment granulometry; T: temperature; T_RES: water residence time; TURB: turbidity. Seagrass variables were measured for C. nodosa (Cno), Z. marina (Zma), Z. noltei (Zno) and for the overall seagrass habitat (TOT), and are abbreviated as follows. B:

epigeous biomass; C: canopy height; COP: percent cover; D: shoot density; EPI: epiphytal load; LAI: leaf area index.

The species accounting for 95% of total nekton abundance in the natural seagrass assemblage were 13 (11 species of fish and two taxa of decapods). Fish species included *Atherina boyeri* (Atherinidae), *Liza aurata* and *L. ramada* (Mugilidae), *Syngnathus typhle*, *S. abaster* and *Nerophis ophidion* (Syngnathidae), *Sprattus sprattus* (Clupeidae), *Salaria pavo* (Blenniidae) and *Pomatoschistus marmoratus*, *Zosterisessor ophiocephalus* and *Knipowitschia panizzae* (Gobiidae). Among decapods, *Palaemon adspersus* (Palaemonidae) and family Hippolytidae were present. The complete checklist of species caught, and included as presence/absence in the analysis, is reported in supplementary materials (Table S1). Likelihood Ratio tests among pairs of model formulations (Table 8) highlighted that seagrass habitat variables significantly explained both assemblage density and probability of presence ($p<0.05$), when added to a model already including temporal factor (t1). Conversely, the additional inclusion of abiotic variables to a model already accounting for temporal and habitat factors significantly explained only assemblage density (t2).

Table 8: Results of the Likelihood Ratio tests comparisons between pairs of multivariate GLM formulations. For each test, the models compared and the effect tested are indicated. Significant tests (p-value<0.05) on both abundance density and probability of presence are marked with an asterisk.

Test		**Testing the effect of:**	**abundance density**	**probability of presence**
t1	m0 vs m1	*Habitat* factor, when only temporal factor was considered before	0.011 *	0.026 *
t2	m1 vs m2	*Abiotic* factor, when both temporal and habitat factors were considered before	0.038 *	0.155

GLM formulation including all the considered predictors (temporal, abiotic and habitat factors; m2) was then selected as the best model explaining the variability of abundance density of nekton assemblage. In turn, the formulation including only temporal and habitat factors (m1) was selected as the best model explaining the variability of species probability of presence.

Average Spearman's r coefficient values calculated for each species density ranged between -0.091 and 0.863, and were all characterised by a relevant amount of variability among cross-validation folds (Table 9). Species predicted more accurately in terms of density were *S. sprattus* (0.863), *S. abaster* (0.528), *S. typhle* (0.502) and *N. ophidion* (0.401). Conversely, density of *K. panizzae* (-0.091), *S. pavo* (-0.016), *L. aurata* (0.036) and *P. marmoratus* (0.056) were predicted with less accuracy and larger variability. Average correlation calculated on the whole dataset was 0.384 (Table 9). Average AUC scores calculated for each species presence/absence ranged from 0.5 to 0.88 (Table 9). *S. typhle* (0.88), *S. sprattus* (0.875), *S. pavo* (0.853) and Hippolytidae (0.85) were predicted with more accuracy in terms of probability of presence. In turn, *A. boyeri* (0.5), *P. adspersus* (0.55) and *S. abaster* (0.617) were the species predicted with less accuracy according to AUC. Average AUC calculated on the whole dataset was 0.832 (Table 9).

Table 9: Results of the cross-validation (k=5) employed to assess predictive performances of selected models. Average and standard deviation values of Spearman's r coefficients (calculated on species density) and AUC (calculated on presence/absence) for each species and for the whole dataset are shown. Only dominant species in terms of density are reported.

	Spearman's r		**AUC**	
Species	**mean**	**sd**	**mean**	**sd**
Atherina boyeri	0.271	0.472	0.500	-
Hippolytidae	0.203	0.476	0.850	0.149
Knipowitschia panizzae	-0.091	0.641	0.775	0.263
Liza aurata	0.036	0.275	0.687	0.197
Liza ramada	0.382	0.625	0.656	0.150
Nerophis ophidion	0.401	0.215	0.673	0.205
Palaemon adspersus	0.162	0.573	0.550	0.100
Pomatoschistus marmoratus	0.056	0.312	0.670	0.194
Salaria pavo	-0.016	0.325	0.853	0.202
Sprattus sprattus	0.863	0.194	0.875	0.250
Syngnathus abaster	0.528	0.336	0.617	0.126
Syngnathus typhle	0.502	0.341	0.880	0.217
Zosterisessor ophiocephalus	0.226	0.395	0.833	0.118
Whole assemblage	0.384	0.078	0.832	0.019

Evaluation of restoration success

Nekton assemblage differed markedly in species composition and structure between the two independent controls investigated (Figure 8). Assemblage at CONT1, located near the sea inlet, featured large abundances of *S. abaster*, *S. typhle*, *N. ophidion*, *P. adspersus* and Hippolytidae. *S. pavo*, *Z. ophiocephalus* and *A. boyeri* additionally characterised the assemblage. On the contrary, the assemblage at CONT2, located in a very confined area, was dominated by Hippolytidae, *A. boyeri* and *K. panizzae*, with also *Crangon crangon* and *Palaemon elegans* being abundant.

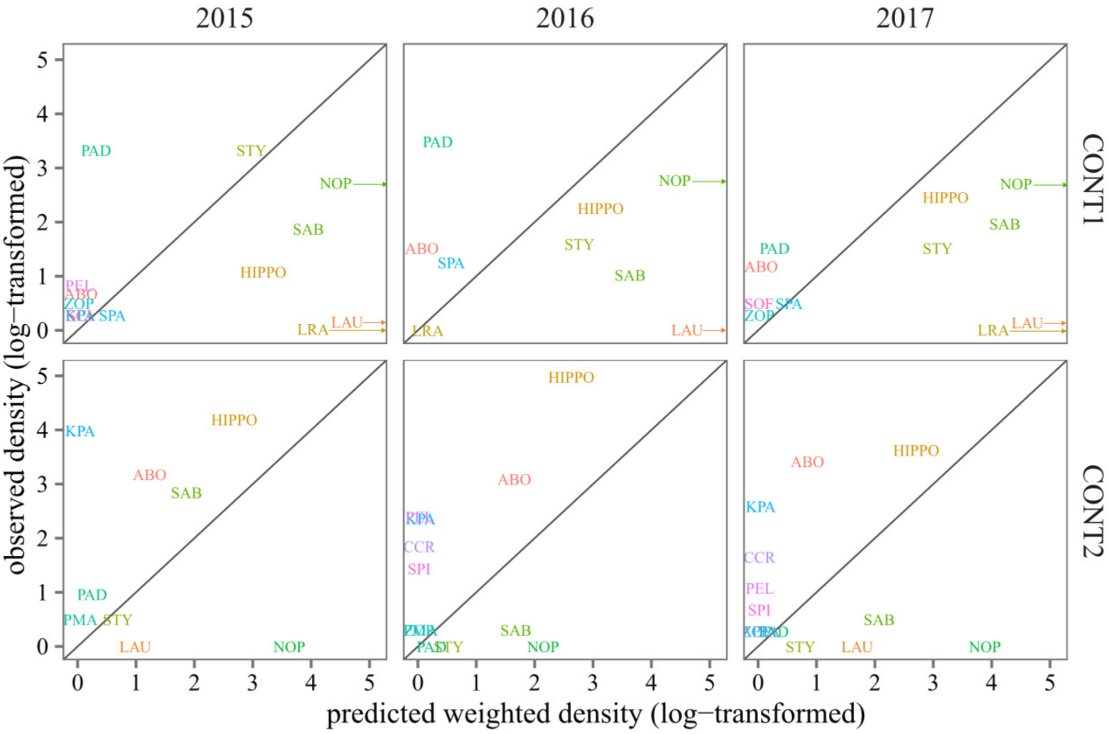


Figure 8: Scatterplots of observed versus (weighted) predicted abundance densities of species constituting nekton assemblages at independent control sites. The distance of species plots from the diagonal on y-axis is the difference from the reference species density. Species plots located above the diagonal are observed with greater densities than expected in the reference assemblage, while species plots located below the diagonal are observed with smaller densities than expected. Position of species located beyond the scale is indicated with an arrow. Key for species labels is provided in supplementary materials (Table S1).

Overall, restoration sites were dominated in terms of abundance density by *A. boyeri*, *K. panizzae* and *P. marmoratus* (Figure 9 and Figure 10). In addition, sites ST08, ST10 and ST17 included *S. abaster* and Hippolytidae among most abundant species, which in turn were scarcer at sites ST01, ST05, ST12 and ST15. *A. boyeri*, *S. abaster* and Hippolytidae were on the whole observed with densities more similar to the respective reference values, being located closer to the diagonal in scatterplots (i.e. being characterised by smaller differences between observed and reference values). This pattern was clearer for sites where such species were more abundant, i.e. ST08, ST10 and ST17 (Figure 9 and Figure 10). Overall, dominant species *A. boyeri*, *K. panizzae* and *P. marmoratus*, but also locally abundant *C. crangon*, *S. abaster* and *A. fasciatus* were found in restoration sites with greater densities than expected in the respective reference assemblages, being located above diagonal in scatterplots. On the contrary, Hippolytidae, *N. ophidion*, *S. typhle*, *S. abaster* and *L. aurata* were found with smaller densities than expected, being located below the diagonal (Figure 9 and Figure 10).

On average, the nekton assemblages observed at sites ST08, ST10 and ST17 were characterised by smaller differences with the respective reference assemblages (Figure 11), indicating an overall more successful recovery of seagrass fauna at such sites. In turn, greater differences between observed and reference assemblages (hence suggesting an overall less successful restoration three years after transplantations) could be detected at sites ST01, ST05, ST12 and ST15, with ST16 being characterised by intermediate conditions. In turn, some sites showed, on average, marked temporal variations in difference between observed and reference assemblages. Stronger variations could be detected for less successful sites, i.e. ST01, ST05, ST12 and ST15, with an overall decrease in difference between observed and reference assemblages over the first two years after restoration (2015 and 2016), followed by an increase in the third year (2017).

Despite such differences among transplantation sites, no clear patterns of progress towards reference conditions could be detected, i.e. nekton fauna did not show an increase in similarity with reference assemblages through time (Figure 11). Indeed, single species temporal trajectories did not highlight any marked trend, with some exceptions. Most notably, at sites ST10 and ST17 Hippolytidae, *Syngnathus abaster*, *Atherina boyeri*, *Pomatoschistus marmoratus* and *Palaemon elegans* showed converging patterns towards reference conditions (see Figure S3 in supplementary materials for differences between observed and reference densities of individual species).

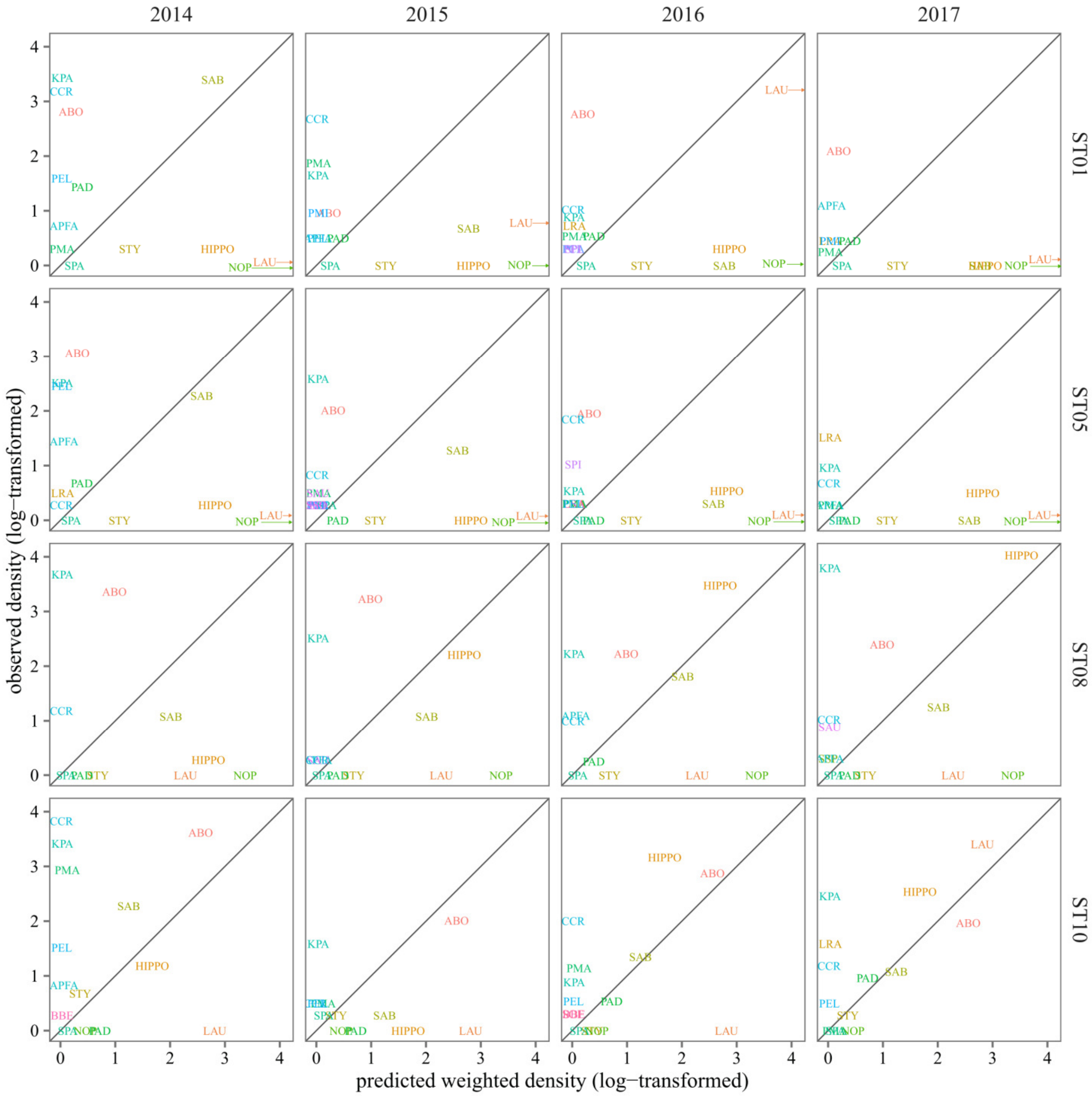


Figure 9: Scatterplots of observed versus (weighted) predicted abundance densities of species constituting nekton assemblages at restoration sites (ST01 to ST10). The distance of species plots from the diagonal on y-axis is the difference from the reference species density. Species plots located above the diagonal are observed with greater densities than expected in the reference assemblage, while species plots located below the diagonal are observed with smaller densities than expected. Position of species located beyond the scale is indicated with an arrow. Key for species labels is provided in supplementary materials (Table S1).

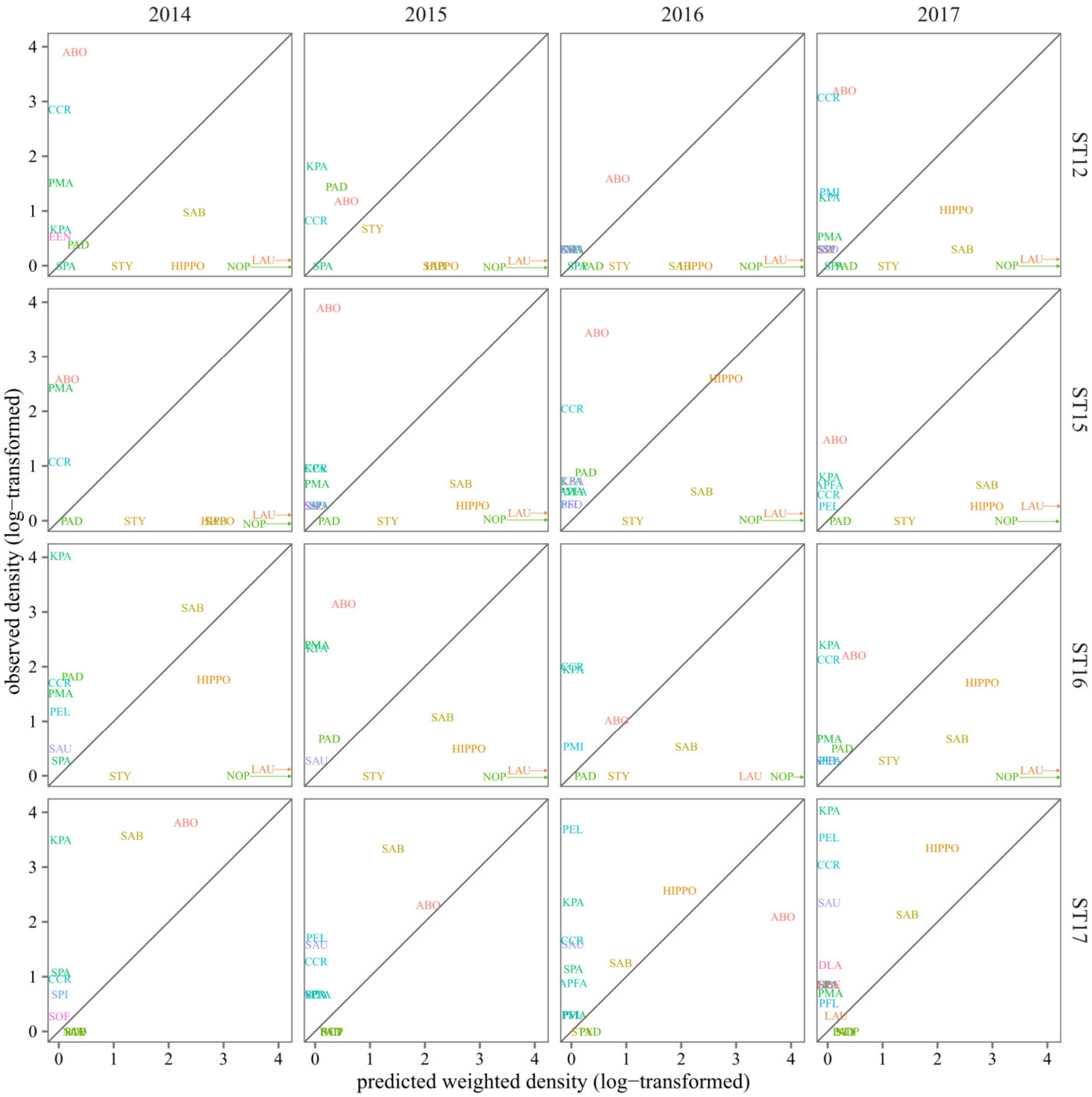


Figure 10: Scatterplots of observed versus (weighted) predicted abundance densities of species constituting nekton assemblages at restoration sites (ST12 to ST17). The distance of species plots from the diagonal on y-axis is the difference from the reference species density. Species plots located above the diagonal are observed with greater densities than expected in the reference assemblage, while species plots located below the diagonal are observed with smaller densities than expected. Position of species located beyond the scale is indicated with an arrow. Key for species labels is provided in supplementary materials (Table S1).

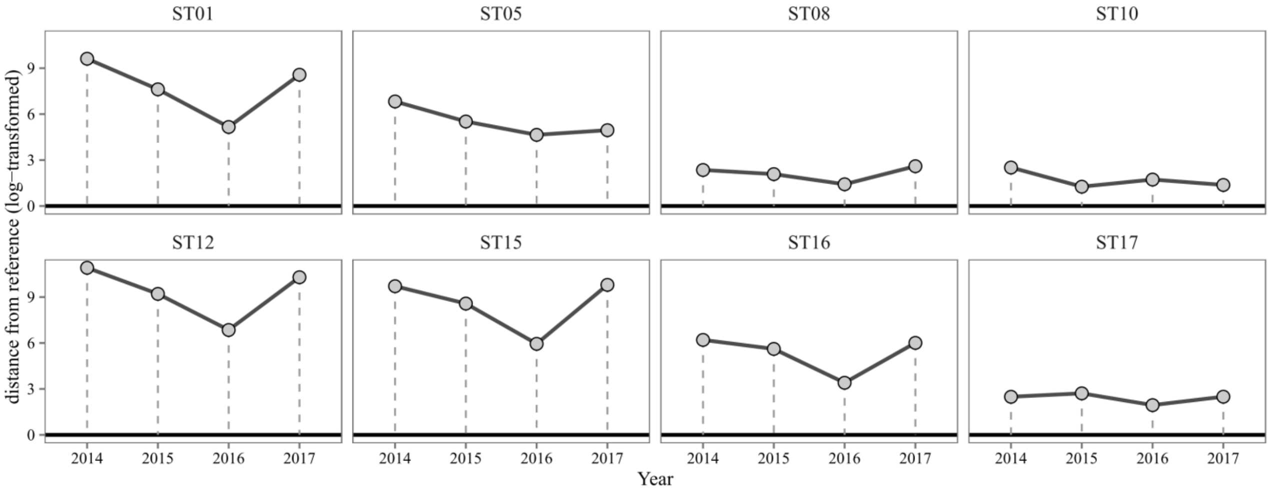


Figure 11: Average difference between observed and reference species densities at each restoration site. Reference values are kept as zero to highlight the distance of each observed assemblage.

Discussion

Predicting reference conditions for the restoration of seagrass nekton fauna

Predicting species composition and its dynamics in biological communities as a response of environmental factors is increasingly required by managers and conservationists in aquatic ecosystems, in order to prevent or mitigate degradation of biological resources and loss of biodiversity (Troia and Gido, 2013). Predictions carried out at the community level, by integrating the effects of both environmental and biotic interactions, are particularly effective for management purposes, especially when applied to highly heterogeneous systems such as large rivers (Wilkes et al., 2016) or coral reefs (Brokovich et al., 2006; Darling et al., 2017). In restoration ecology, however, predictive approaches are still uncommon (Brudvig, 2017).

While few works investigated the progress of epifaunal and macrobenthic assemblages following seagrass restoration (Dolbeth et al., 2013; Lefcheck et al., 2017; McSkimming et al., 2016), the response of nekton (fish and motile invertebrates) to transplantations still remains largely unknown (Fonseca et al., 1996; Sheridan et al., 2003). However, assessing the value of restored meadows as habitat for the associated fauna (hence, their functionality) rather than their structure per se is likely to be more appropriate, especially in dynamic environments such as estuaries and coastal lagoons (Palmer et al., 1997). In this light, this work proposed and tested a novel approach to identify reference conditions and track early changes in nekton fauna at newly-created seagrass habitats in a Mediterranean coastal lagoon.

The variability in spring nekton assemblage associated with natural seagrass meadows in the Venice lagoon was linked to abiotic and habitat determinants using a multivariate GLM framework. The models allowed to predict the assemblage composition (i.e. the presence of the species) and structure (i.e. the densities of the species), under different conditions of water, sediment and seagrass habitat. When such conditions correspond to the target of a restoration programme, in terms of e.g. recovery of water quality and seagrass habitat structure, it is argued that the predicted nekton assemblage can be considered as a reference assemblage, against which evaluating the progress of fauna in restored habitats towards designed goals. This approach allowed to identify the species driving the assemblages towards particular compositions and structures, hence informing on the causes of variation in restoration outcomes among transplanting sites (Brudvig et al., 2017).

Due to the high natural and human-induced variability that typifies estuaries and coastal lagoons, any attempt to define or evaluate the state of the ecosystem can be challenging. This is true for setting reference conditions in restoration programmes (Duarte et al., 2015), as well as for other ecological applications, such as the assessment of ecological status under the Water Framework Directive (Dir. 2000/60/EC; Elliott & Quintino, 2007). In the case study considered here, the strong gradients and high heterogeneity characterising the northern area of the Venice lagoon made necessary to identify site-specific reference conditions to evaluate progresses of nekton fauna following habitat recreation. Seagrass transplantations were indeed designed to match the site-specific environmental characteristics, involving the use of the most suitable species for each location, as suggested by van Katwijk et al. (2009). In general terms, a greater proportion of sods of *Z. noltei* was transplanted in shallower sites, more frequently exposed at low tides, with muddier and more anoxic sediments and in closer proximity to saltmarshes. Conversely, deeper, more open and dynamic sites were restored using a greater proportion of Z. *marina*. Finally, at two of the considered sites, both the species were transplanted in similar proportions (Facca et al., 2014a). As a consequence, three target scenarios were considered in this study to reflect such differences in the restoration design. Ultimately, the use of the abiotic (i.e. temperature, salinity, dissolved oxygen and sediment granulometry) and geographical (i.e. confinement) variables of each restoration site resulted in the definition of site-specific reference conditions. This also allowed to overcome the potential flaws in the assessment of success, deriving from directly comparing restored and reference habitats characterised by different environmental backgrounds (Brinson and Rheinhardt, 1996; Moorhead, 2013).

This study, far from providing a definitive predictive method for ecological restoration studies, aimed to test the applicability of an experimental approach to a real-world case study of seagrass restoration, emphasising both its strong points and limits. Due to the very limited dataset available (n=25), prediction accuracy of models employed varied markedly among species. In particular, taxa observed in few occasions but with great abundances, such as *Nerophis ophidion* and *Liza aurata*, showed poor correlation with respective predicted values. Conversely, frequently observed species such as Hippolytidae, *Atherina boyeri*, *Knipowitschia panizzae* and *Syngnathus abaster* were predicted with high accuracy and detected both spatial (i.e. among transplantation sites) and temporal (i.e. among years after transplantation) differences in the restoration outcomes.

Assessing the progress of nekton fauna in restored seagrass habitats

The influence of environmental variables on seagrass fish and invertebrates in estuarine and lagoon ecosystems has been widely studied, and distance to the sea, water quality and seagrass habitat structure are all recognised as major drivers of nekton distribution (Franco et al., 2006; Malavasi et al., 2007, 2005; Schultz et al., 2009; Taylor et al., 2017). This hypothesis was tested by the model analysis carried out in this study, and emphasised by its application to the nekton assemblages sampled at two independent control seagrass sites, located at the opposite ends of a confinement gradient and characterised by different seagrass canopy height and percent cover. The predicted assemblages, fitting well the respective observed values, differed noticeably in species composition and density among sites. Seagrass habitat in closer proximity to sea inlet, with a taller canopy and higher cover supported greater densities of seagrass specialists such as syngnathids, palaemonids and hippolytids as well as higher assemblage diversity, compared with the confined habitat with shorter canopy and lower percent cover. The latter site, in turn, featured greater densities of typical estuarine species, such as *Atherina boyeri*, *Syngnathus abaster* and *Knipowitschia panizzae*, which are commonly found also in macroalgal beds and bare sediment habitats (Franzoi et al., 2010). In the Venice lagoon, confinement plays a fundamental role in determining not only the distribution of nekton species, but also that of seagrass meadows themselves (see also Figure 6; Curiel et al., 2014). In more confined areas, meadows are generally scarcer, patchier and less structured (i.e. characterised by smaller shoot density and canopy height), this additionally contributing in shaping the nekton assemblages (as already noted in section 1, pag. 15; Scapin et al., 2017).

It can hence be argued that different outcomes in terms of nekton assemblage structure and composition must be expected among transplantation sites, when restoring seagrass habitats in highly heterogeneous environments such as coastal lagoons. As a result, location and design of transplantations must be programmed on the basis of the known influence of environmental drivers, which should be taken into account in tools (such as indices and models) to guide the design of restoration plans (Short et al., 2002; Valle et al., 2015; van Katwijk et al., 2009). Subsequently, as this study demonstrates, success criteria for the associated fauna should be set allowing for the potential differences in the structure of the target assemblages. In the absence of a sufficient number of reference habitats to be compared with restored ones, predicting a set of site-specific reference conditions to match the variability in the local environmental context seems then a suitable solution.

In the present study, the nekton assemblages at the investigated transplantation sites exhibited different degrees of similarity with the respective predicted reference conditions. Estuarine and non-seagrass species were overall the most abundant among sites, and were in many cases predicted with greater densities than expected. Three sites (namely ST08, ST10 and ST17) showed greater densities of typical seagrass species, and, overall, greater similarity with reference assemblages. This pattern broadly corresponded to the progress of habitat development after transplantation. The same sites exhibited higher survival of seagrass sods and rhizomes, as well as greater increase in seagrass percent cover (Sfriso et al., unpub. data), which explain the observed greater proportion of seagrass nekton species. Overall, site location and temporal variations in abiotic conditions are likely to have affected habitat development and the subsequent recovery of nekton assemblages. For instance, sites in closer proximity to the mainland (namely ST01 and ST05) were particularly influenced by freshwater inflows, and showed little to none seagrass survival after transplantation due to high nutrient inputs and turbidity (Sfriso et al., unpub. data). Nekton assemblages at these sites were characterised by very low proportion of seagrass species, and overall showed the greatest dissimilarity with the respective reference conditions. Moreover, marked differences in local weather conditions, such as the yearly succession of low and high temperatures, frequent and scarce precipitations that characterised the 2014-2017 period, are likely to have affected both seagrass habitat development and faunal rate of recovery. This may have contributed to the observed temporal oscillations in the progress trajectories of nekton assemblages. As Stuble, Fick and Young (2017) pointed out for grassland habitats, outcomes of restoration efforts can vary dramatically according to yearly changes in weather conditions. The potential effects of unmanageable, although measurable, environmental contingencies should be considered also in seagrass habitat restoration, and appears to be crucial also for the recovery of associated fauna.

The present study investigated the nekton assemblages at the time zero of seagrass restoration and during the following three years. In few instances (e.g. at sites ST10 and ST17), species showed progresses towards reference weighted densities during the study period. Nevertheless, none of the eight assemblages considered exhibited, as a whole, clear temporal trajectories towards restoration targets. On a similar temporal scale, Sheridan et al. (2003) showed similar results from a restoration scheme in Galveston Bay (USA). Authors observed that, although progresses of some nekton species towards reference conditions could be detected at transplanted seagrass sites, the overall assemblage composition would take longer than the study period to reach equivalence with natural habitats. In other seagrass faunal communities, such as epifauna, also assemblage richness and total abundance can recovery fast after seagrass restoration. However, species composition and relative abundance would still take longer to fully resemble reference conditions (McSkimming et al., 2016). In general terms, organisms with rapid life cycles and occupying lower trophic levels, such as small epifaunal and benthic invertebrates, could be expected to rapidly re-colonise transplanted seagrass sites (Lefcheck et al., 2017; McSkimming et al., 2016). Conversely, as confirmed in this work, more time may be needed for higher-order consumers such as fish and decapods (Sheridan et al., 2003).

Future developments

The present study reported the first four years of nekton observations at seagrass transplantation sites. Despite highlighting major differences in assemblages among sites as a consequence of different habitat recovery rates, it failed at detecting clear progress trajectories towards reference conditions. With seagrass fauna in the project area not having reached the expected restoration goals yet, it is strongly emphasised that nekton monitoring should continue in the Venice lagoon. There is indeed a general lack of studies following the reinstatement of seagrass meadows for longer than 3-4 years (Cunha et al., 2012), although these may have increased chances to detect progresses of both ecosystem structure and functions that usually require at least a decade to fully recover (McGlathery et al., 2012). Furthermore, long-term monitoring could reveal unexpected developments of restored habitats, hence potentially reversing assessments made in early-stage studies (Bell et al., 2014).

While the approach presented in this study focused on structural aspects of nekton fauna, it is suggested that future works should aim to investigate also the response of functional attributes of assemblages. Ecological and trophic guild composition, as well as species functional traits and their diversity (e.g. following Dolbeth et al., 2013), could be included as response variables in the proposed methodology, and predicted according to specific target scenarios. Incorporating functional aspects into predictive models would also provide insights into how biological communities and whole ecosystems function (Brudvig, 2017; Lavorel and Garnier, 2002). In addition, some functional aspects of ecosystems may be relatively more predictable than taxonomic composition itself (Brudvig et al., 2017), since they can result from many different combinations of redundant species (e.g. trophic guild composition). As a result, focusing on functional features of nekton assemblages could result in more robust assessments of their recovery progresses.

Acknowledgements

This work partly relied on data collected under the project LIFE12 NAT/IT/000331 – SERESTO (*Habitat 1150* (Coastal lagoon) recovery by SEagrass RESTOration. A new strategic approach to meet HD & WFD objectives*). SERESTO is funded by the European Union's LIFE+ financial instrument and contributes to the environmental recovery of a Natura 2000 site (SCI IT3250031/– Northern Venice Lagoon/SPA IT3250046 – Venice lagoon).

Supplementary materials

Table S1: Checklist of all nekton species collected in this study. Presence at natural seagrass sites, independent control sites and transplantations sites is reported.

Family	**Species**	**Label**	**Natural seagrass sites (calibration dataset)**	**Independent control sites (evaluation dataset)**	**Transplantation sites**
Atherinidae	*Atherina boyeri*	ABO	x	x	x
Belonidae	*Belone belone*	BBE	x		x
Blennidae	*Parablennius tentacularis*	PTE	x		
Blennidae	*Salaria pavo*	SPA	x	x	x
Bothidae	*Arnoglossus kessleri*	AKE	x		
Clupeidae	Clupeidae postlarvae n.d.		x		
Clupeidae	*Sardina pilchardus*	SPI	x	x	x
Clupeidae	*Sprattus sprattus*	SSP	x		x
Crangonidae	*Crangon crangon*	CCR	x	x	x
Crangonidae	*Philocheras monacanthus*	PHMO	x		
Cyprinodontidae	*Aphanius fasciatus*	APFA	x	x	x
Engraulidae	*Engraulis encrasicolus*	EEN			x
Gobiidae	Gobiidae postlarvae n.d.		x		
Gobiidae	*Gobius niger*	GNI	x	x	
Gobiidae	*Gobius sp.* juvenile		x		
Gobiidae	*Knipowitschia panizzae*	KPA	x	x	x
Gobiidae	*Pomatoschistus canestrinii*	PCA			x
Gobiidae	*Pomatoschistus marmoratus*	PMA	x	x	x
Gobiidae	*Pomatoschistus minutus*	PMI	x		x
Gobiidae	*Zebrus zebrus*	ZZE			x
Gobiidae	*Zosterisessor ophiocephalus*	ZOP	x	x	x
Hippolytidae	Hippolytidae n.d.	HIPPO	x	x	x
Labridae	*Symphodus cinereus*	SCI		x	
Moronidae	*Dicentrarchus labrax*	DLA			x
Mugilidae	*Liza aurata*	LAU	x		x
Mugilidae	*Liza ramada*	LRA	x		x
Mugilidae	*Liza saliens*	LSA	x		x

Table S1 (continued).

Family	**Species**	**Label**	**Natural seagrass sites (calibration dataset)**	**Independent control sites (evaluation dataset)**	**Transplantation sites**
Palaemonidae	*Palaemon adspersus*	PAD	x	x	x
Palaemonidae	*Palaemon elegans*	PEL	x	x	x
Palaemonidae	*Palaemon macrodactylus*	PAMA			x
Palaemonidae	*Palaemon serratus*	PSE	x		
Palaemonidae	*Palaemonetes sp.*				x
Peneidae	*Melicertus kerathurus*	MKE			x
Pleuronectidae	*Platichthys flesus*	PFL	x		x
Processidae	*Processa edulis*	PRED	x		x
Scophthalmidae	*Scophthalmus rhombus*	SRH	x		
Sepiidae	*Sepia officinalis*	SOF	x	x	x
Soleidae	*Monochirus hispidus*	MHI	x		
Soleidae	*Solea solea*	SSO	x		x
Sparidae	*Boops boops*	BBO	x		
Sparidae	*Diplodus vulgaris*	DVU	x		
Sparidae	*Sparus aurata*	SAU	x		x
Sparidae	*Spicara sp.* juvenile		x		
Syngnathidae	*Hippocampus guttulatus*	HGU	x		x
Syngnathidae	*Hippocampus hippocampus*	HHI	x		
Syngnathidae	*Nerophis ophidion*	NOP	x	x	
Syngnathidae	*Syngnathus abaster*	SAB	x	x	x
Syngnathidae	*Syngnathus taenionotus*	STA	x		
Syngnathidae	*Syngnathus typhle*	STY	x	x	x
Trachinidae	*Echiichthys vipera*	EVI	x		
Triglidae	*Chelidonichthys lucernus*	CLU	x		

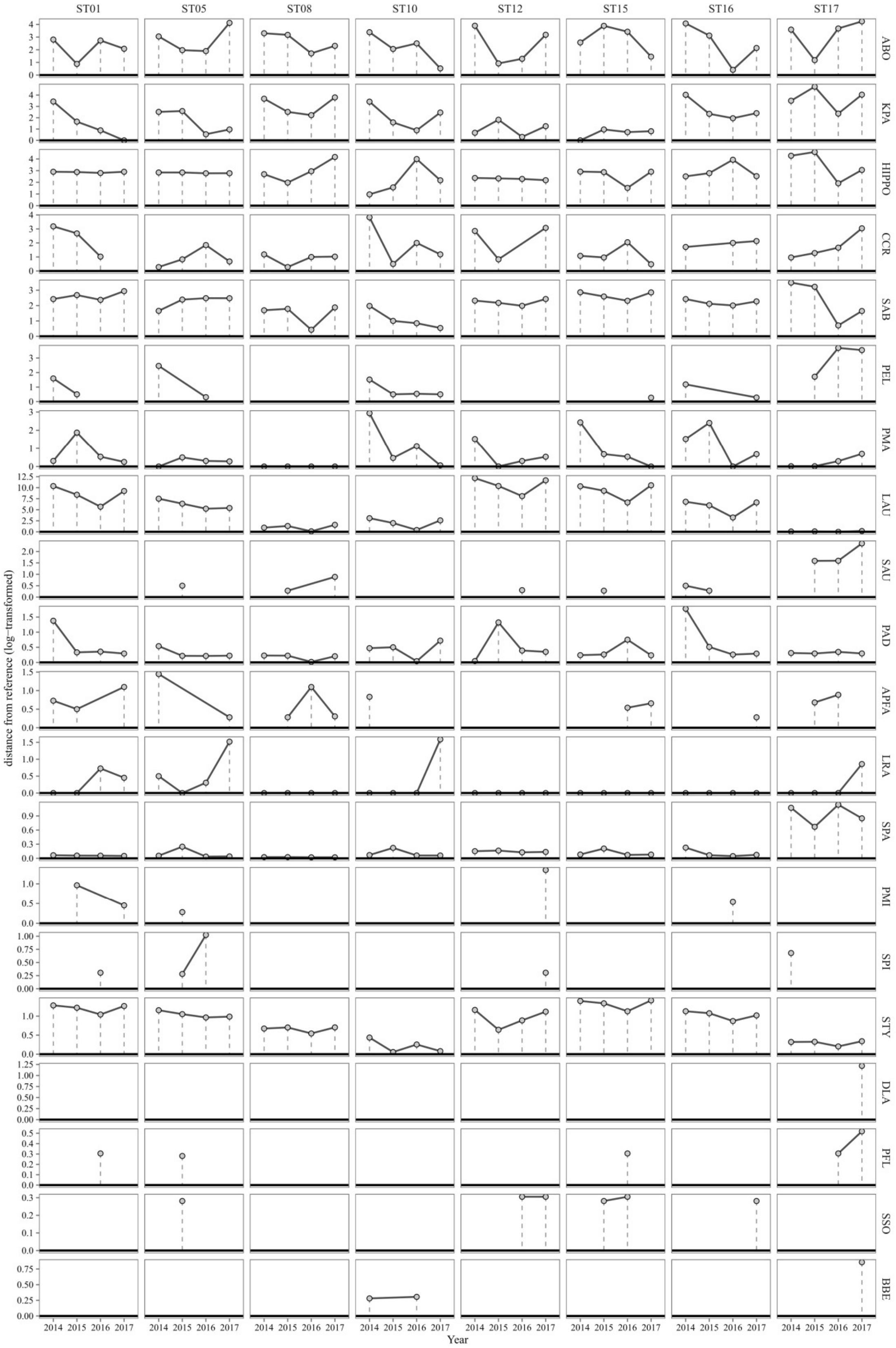
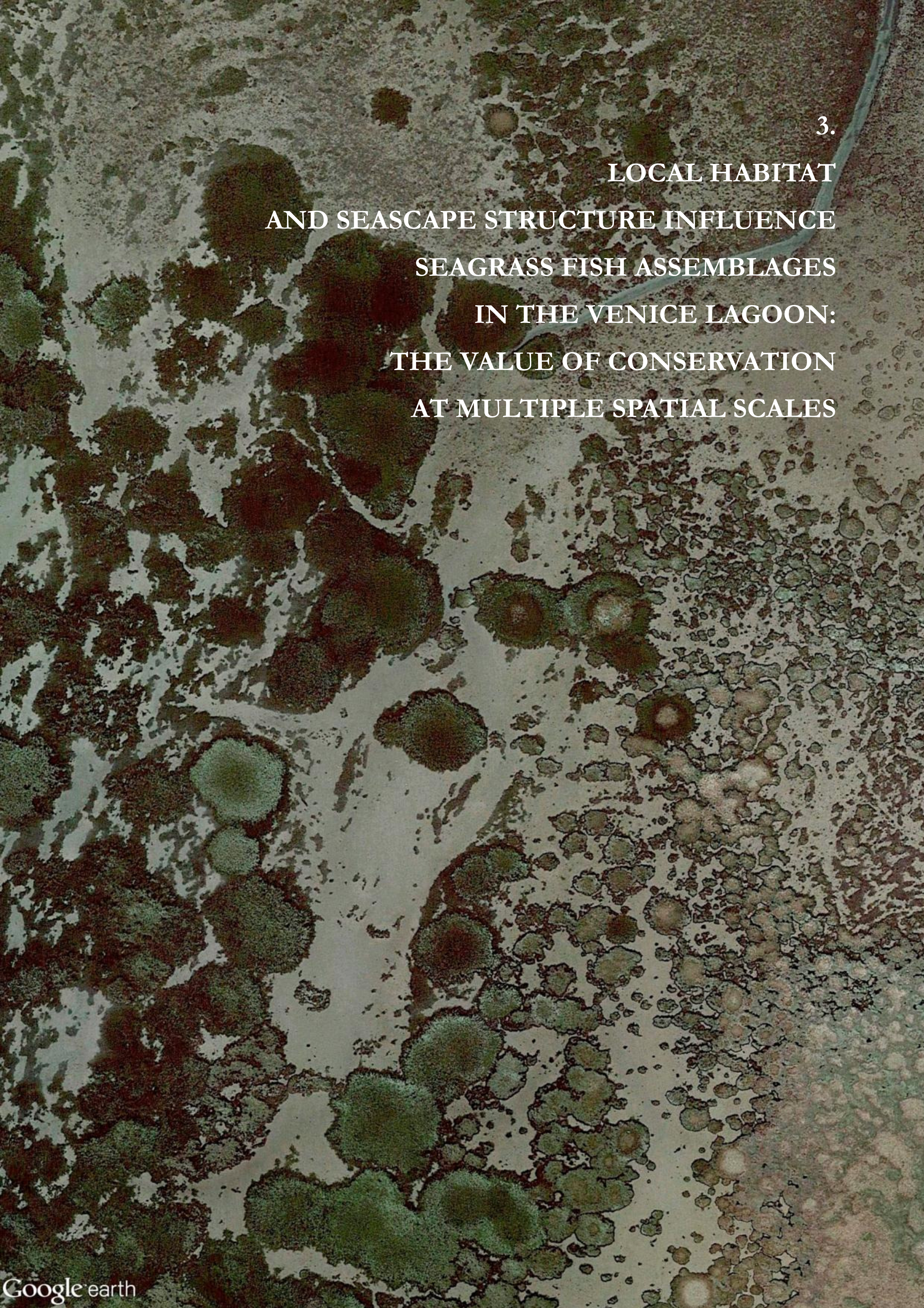


Figure S3: Difference between observed and reference species densities at each restoration site. Reference values are kept as zero to highlight the distance of each observed assemblage. Only the first 20 most abundant species in the restoration dataset are shown.



3.

LOCAL HABITAT AND SEASCAPE STRUCTURE INFLUENCE SEAGRASS FISH ASSEMBLAGES IN THE VENICE LAGOON: THE VALUE OF CONSERVATION AT MULTIPLE SPATIAL SCALES

Previous page: satellite view of a seagrass habitat mosaic in the Venice lagoon (© Google Earth)

Introduction

Along with the increase in popularity of the seascape approach in coastal research, the implications of such a perspective in ecosystem conservation and restoration are also emerging. In general, a seascape-based approach to habitat and species conservation would better fit into the context of coastal zone management, which usually operates at the scale of administrative waterbodies, 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 estuarine and coastal lagoons, which are typically affected by multiple anthropogenic pressures that may lead to the degradation and loss of habitats and associated species, as well as to the depletion of important ecosystem services (Elliott and Quintino, 2007; Franco et al., 2009a; Lotze et al., 2011; Solidoro et al., 2010; Vasconcelos et al., 2007).

Many studies conducted at the seascape level targeted seagrass meadows (Boström et al., 2006; Connolly and Hindell, 2006; Robbins and Bell, 1994; Salita et al., 2003). Despite the increasing interest in the role of seascape structure as potential driver of seagrass fish distribution, few works have compared the influence on fish of multiple, explicitly defined spatial scales (e.g. site and seascape scale) (Jackson et al., 2006a; Staveley et al., 2016), or taken into account the potential effect of water quality (Dance and Rooker, 2015; Gilby et al., 2016). Works allowing for potential differences in mobility of different target species, hence including different candidate mosaic extents, are also few (Simon J.

Pittman et al., 2007; Pittman and Brown, 2011). 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, which in turn represents a biodiversity hotspot for marine fauna (Abdul Malak et al., 2011).

The present work aims to understand the potential influence of the seascape on seagrass fish in the Venice lagoon (Adriatic sea, Italy), taking into account multiple spatial scales and disentangling the relative influence of local water quality and habitat characteristics from that of mosaic properties. 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. This study allowed 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 local and seascape scale are critical for management, conservation and restoration of seagrass ecosystems in Mediterranean transitional waters.

Methods

Definition of spatial scales

Fish and environmental data at multiple spatial scales were collected at 75 shallow water seagrass sites (Figure 12). For the purposes of this study, two spatial scales were assumed to have an influence on fish assemblages, which were referred to as site scale and mosaic scale. The site scale corresponded to the area within which fish were actually sampled. The mosaic scale was identified as the portion of seascape in which each sampling site is located, and was spatially defined as circular buffers surrounding each sampling site. Buffers of 50, 100, 300, 500 and 800 m-radius were created. 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, for instance according to the differences in spatial resolution at which different habitats were mapped.

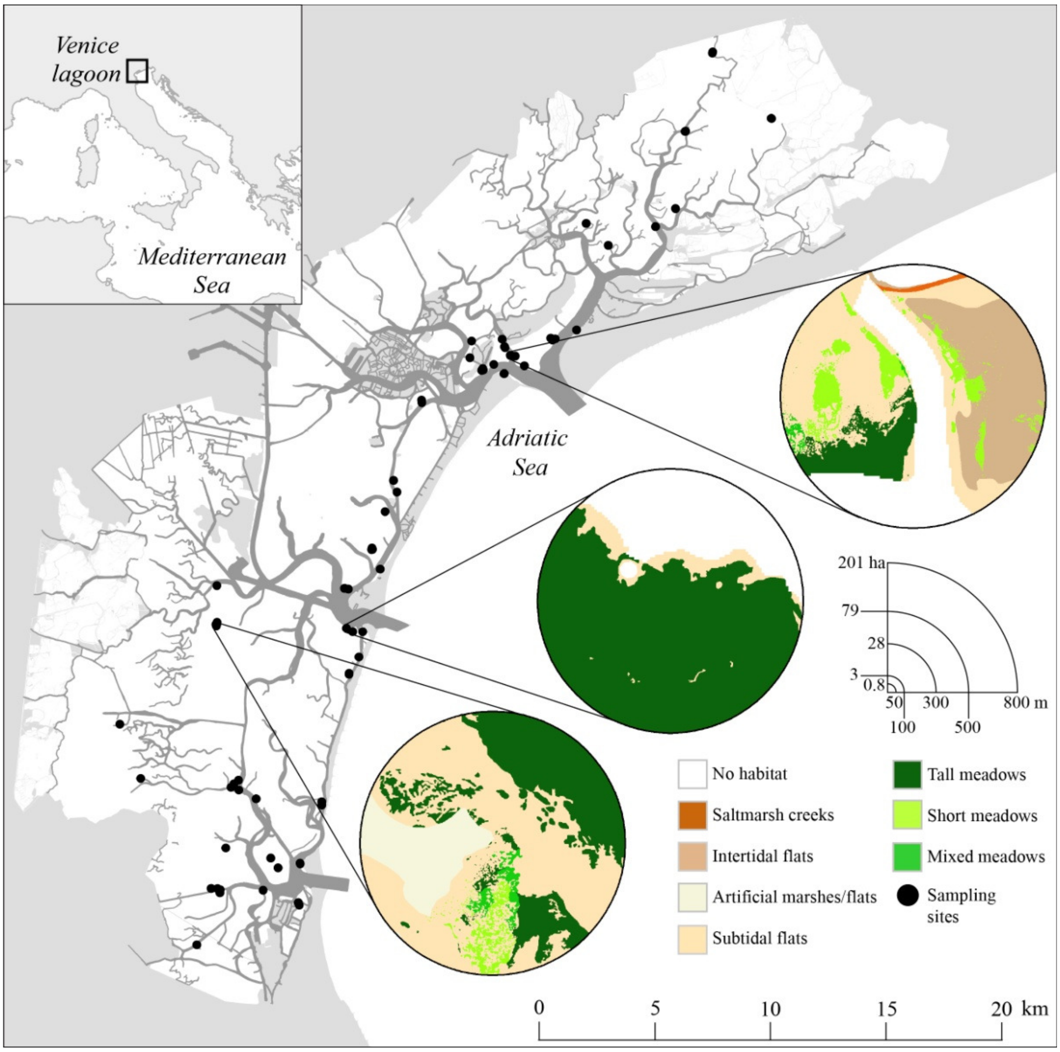


Figure 12: Study area and examples of the habitat mosaics considered.

Site scale characterisation

Each sampling location was characterised at the site scale by taking into account a set of environmental parameters. Water and sediment parameters were quantified as described in "General methods - Environmental characterisation of sampling sites", pag. 12. Some features of the seagrass habitat within the area sampled were also recorded. The average seagrass cover was estimated by visual census following the Braun-Blanquet method and subsequently expressed as percent cover. Three meadow typologies were identified, 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). Either pure or mixed meadows, including *C. nodosa* or *Z. marina* always without *Z. noltei*, were classified as "tall meadows"; pure *Z. noltei* meadows were classified as "short meadows"; mixed meadows of *C. nodosa* or *Z. marina* and always including *Z. noltei*, were classified as "mixed meadows". Finally, the distance of each site from the nearest sea inlet along the lagoon channels was calculated via a network analysis. All the numerical variables were standardised, allowing direct comparison between them.

Mosaic scale characterisation

Nine habitat typologies were taken into account to characterise the seascape of the Venice lagoon: 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). The mainland, islands and deeper portions of lagoon channels were also included in the seascape characterisation and classified as "no habitat", assuming them to represent physical obstacles for shallow water fish. All habitat typologies were derived from land cover maps (Curiel et al., 2014; MAG.ACQUE, 2002; Rismondo et al., 2003). The temporal variation of some of the habitats (namely natural saltmarshes, creeks, intertidal/subtidal flats and channels) was considered to be negligible within the study period, and therefore the same maps were used over the entire time span of the analysis. By contrast, different maps were considered over time for highly dynamic habitats such as seagrass meadows, as well as for artificial habitats created in different occasions over the study period.

For each one of the five mosaic extents considered (50, 100, 300, 500 and 800 m-radius buffers), a set of seascape metrics was then calculated. 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 10). A Principal Component Analysis (PCA) was performed on standardised seascape metrics at each buffer extent and metric loadings on PC axes were extracted. The first four PC axes were then used to summarise the properties of the seascape and to characterise the mosaic scale.

Table 10: 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).

Category	**Metric**	**Description**	**Computed for each habitat type in the mosaic**	**Computed for the whole mosaic**
Composition	PROP	Proportion of the whole mosaic represented by each habitat type	x	
	DENS	Patch density: the numbers of patches divided by total mosaic area	x	x
	DIV	Diversity calculated as the Shannon's index on habitat area		x
	EVE	Evenness calculated as the Pielou's index on habitat area		x
	ARE	Average area of all patches		x
	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
	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 logarithm of patch area against the logarithm of patch perimeter	x	x
	COHE	Patch cohesion index: a measure of the physical connectedness of patches		x

Data analysis

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

The influence of site and mosaic scales was investigated on three components of the seagrass fish assemblage. Total fish biomass density, total number of species and Margalef's species richness calculated on biomass density were considered to characterise the seagrass assemblage as a whole. Adopting the approach of Franco et al. (2008) all the species (with the exception of marine stragglers, only occasionally found within the lagoon) were grouped into feeding guilds, and biomass density of each guild was considered. Since one species could be allocated to multiple feeding guilds, the contribution of each species to each guild was assigned as 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, densities of biomass of species accounting for 95% of cumulative fish assemblage biomass were also included. A complete list of the species caught and the respective allocation to feeding guild is reported in supplementary materials (Table S2). Whole fish assemblage indicators, feeding guilds and single species densities were then used as independent response variables in GLMs.

Generalized Linear Models (GLMs; (McCullagh and Nelder, 1989)) were fitted in order to understand how the variability in the response variables is explained with different combinations of environmental predictors. All response variables were independently modelled, using the most appropriate distribution family. Negative binomial GLMs were fitted for species and feeding guild densities, while zero-inflated Poisson GLMs were used for the number of species. A hierarchical approach was adopted and different model structures were used (Table 11) 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.

The interaction between seasons and years was included in all the GLM formulations in order to represent the temporal factor. Three model formulations were included in the analysis, investigating the following hypotheses (Table 11): the response variable is affected by temporal factor only (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). For each model, the explained deviance was calculated.

For each response variable, the best candidate model was selected by using the Akaike Information Criterion corrected for small samples (AICc; Burnham & Anderson, (2002)), choosing the model with the lower AICc value and with an AICc weight equal or higher than 0.7. Hence, models with a difference in AICc lower than 2 were considered as undistinguishable. This let to explore each hypothesis formulated, by verifying if progressive addition of predictor terms would improve the overall fit of the model. The sign and the magnitude of the effect of each site scale predictor was derived directly from the parametric coefficients estimated by the best model. In contrast, the effect of each seascape metric was calculated as the sum of the metric loadings on each PC axis, weighted with the estimated coefficients of the respective axis.

Table 11: Structure of GLMs considered in the analysis. Model formulas and respective hypotheses investigated are also shown.

Model category	Model structure	Hypothesis
m0	$Y_i \sim$ season $\cdot$ year + c + ε_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
$m2_j$	m1 + $PC1_j + PC2_j + PC3_j + PC4_j$	Response variable is influenced by temporal factor, site scale and mosaic scale variables (the latter quantified at each extent *j*, hence yielding j models)

Results

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; Figure 13) compared with the other extents considered. Bi-plots of PC axes at 500 and 800 m extents were also better interpretable in terms of patterns in seascape properties (see also supplementary materials, Figure S4 for an example of biplots and Figure S5 for the loadings matrix). For these reasons, 500 and 800 m-radius buffers (corresponding to 79 and 201 ha mosaics respectively) were selected 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, the two alternative buffers were both included in the following analysis.

A series of patterns in seascape characteristics could be easily identified in PCAs based on 500 and 800m-radius extents. Such patterns were found to be highly similar between alternative mosaic extents, allowing a single interpretation of each PC axis.

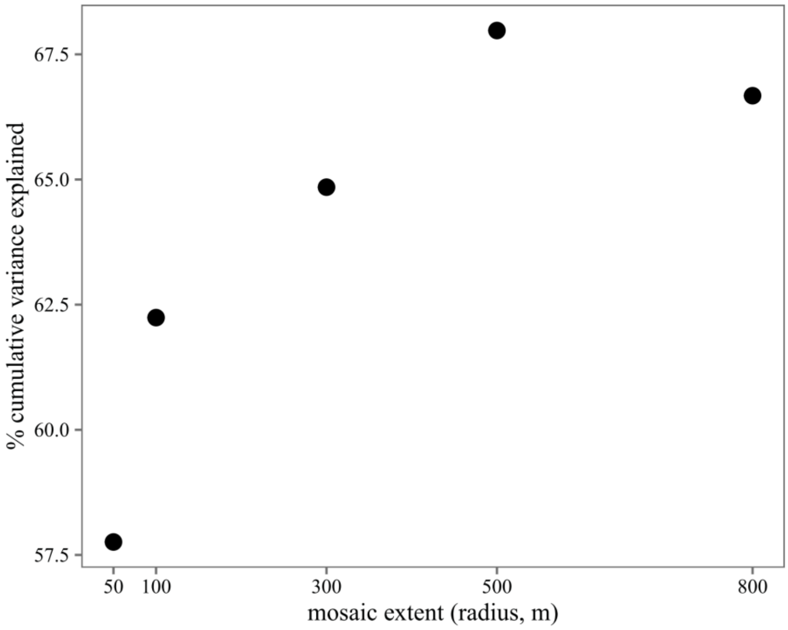


Figure 13: Cumulative variance (percentage values) explained by the first four axes of PCAs based on each mosaic extent.

The first PC axes 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 axes were 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 axes were 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 axes were associated with lagoon channel habitats, these being positively correlated with whole mosaic diversity and negatively with largest patch index and average patch area.

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). No model could be identified for total number of species (Figure 14). 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, best model formulations could only be selected for biomass densities of macrobenthivorous and hyperbenthivorous/piscivorous (i.e. models formulations for the other guilds were undistinguishable). 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 (Figure 14).

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*, small goby *Pomatoschistus marmoratus* (family Gobiidae) and blenny *Salaria pavo* (family Blenniidae). The three species of syngnathids all responded to both site and mosaic scale (m2; Figure 14). 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 best 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, no model could be selected for *Salaria pavo*, since formulations including only the site scale (m1) and both site and 800m-mosaic scale (m2) were undistinguishable.

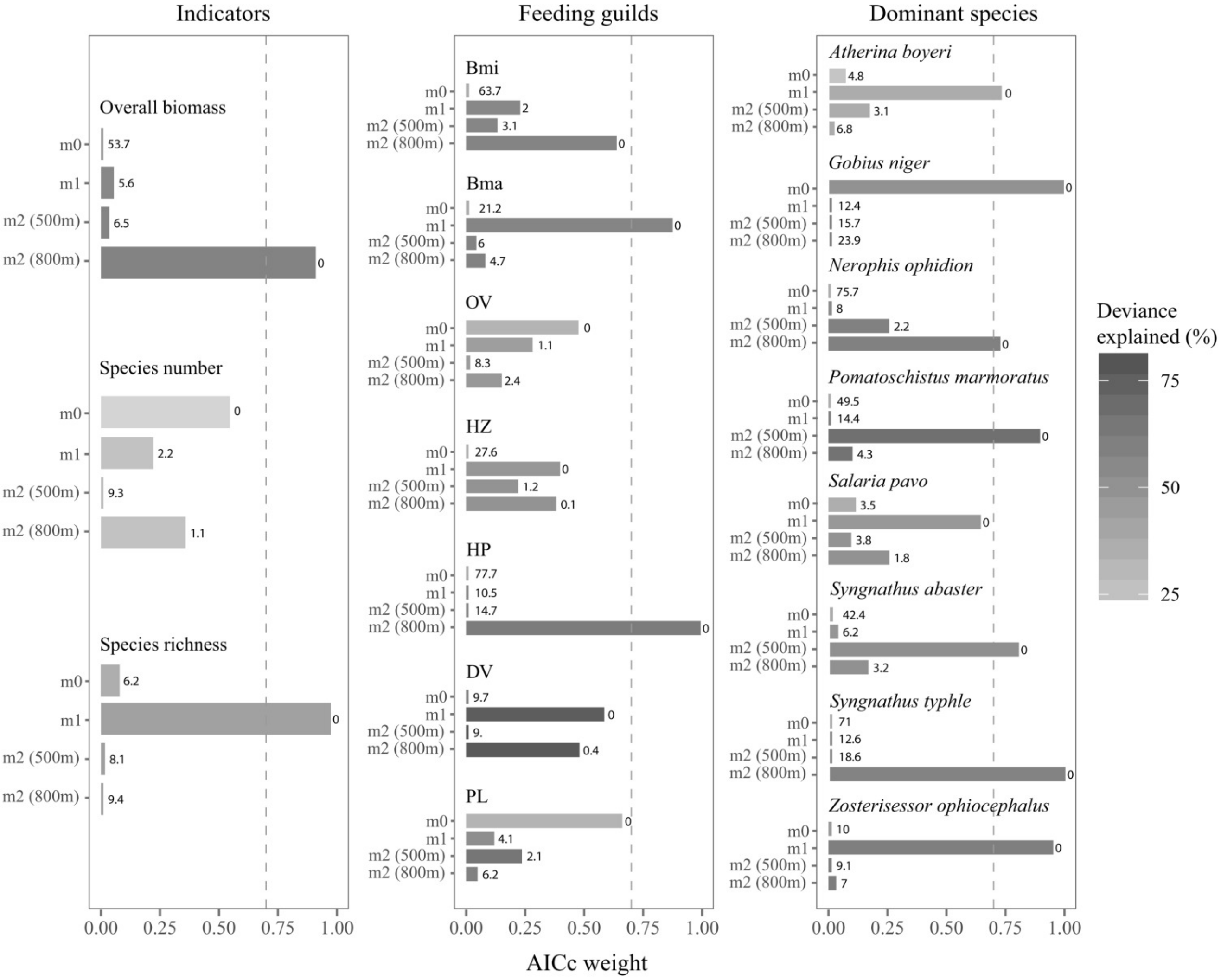


Figure 14: Output summary of GLMs fitted for the response variables. For each alternative model formulation (m0, m1 and m2, the latter at two mosaic extents) the AICc weight (bars) and the respective difference in AICc value from the best model are shown. The AICc weight threshold of 0.7 for the selection 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.

Effects of environmental variables at two spatial scales

Among environmental properties characterising the site scale, an overall relevant positive effect of dissolved oxygen, seagrass percentage cover, turbidity and distance from sea inlets could be observed for overall biomass, macrobenthivorous and hyperbenthivorous/piscivorous guilds, as well as for some species (e.g. *S. abaster*, *S. typhle* and *Z. ophiocephalus*) (Figure 15 and Figure 16). 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). Furthermore, 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. 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, some differences in the response to seagrass properties at the mosaic scale could be detected. *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.

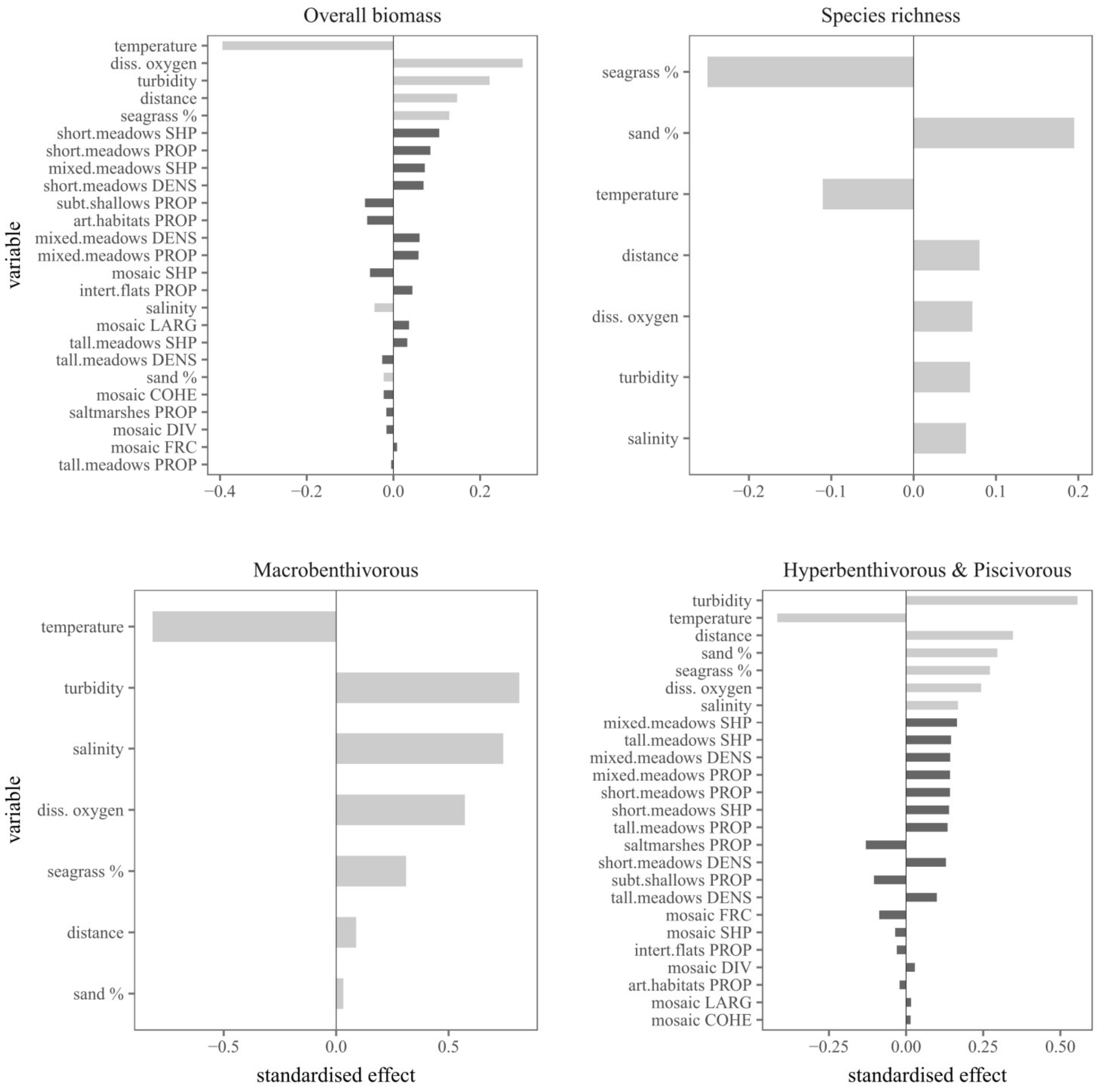


Figure 15: Standardised effects of site-scale (light grey) and mosaic-scale (dark grey) predictors on whole assemblage indicators and feeding guilds, derived from the best GLM formulations. Effect magnitudes are sorted in descending order. Only a subset of mosaic properties is shown, excluding the most collinear variables in PCA (i.e. showing very similar effects). Abbreviations for mosaic variables are described in Table 10.

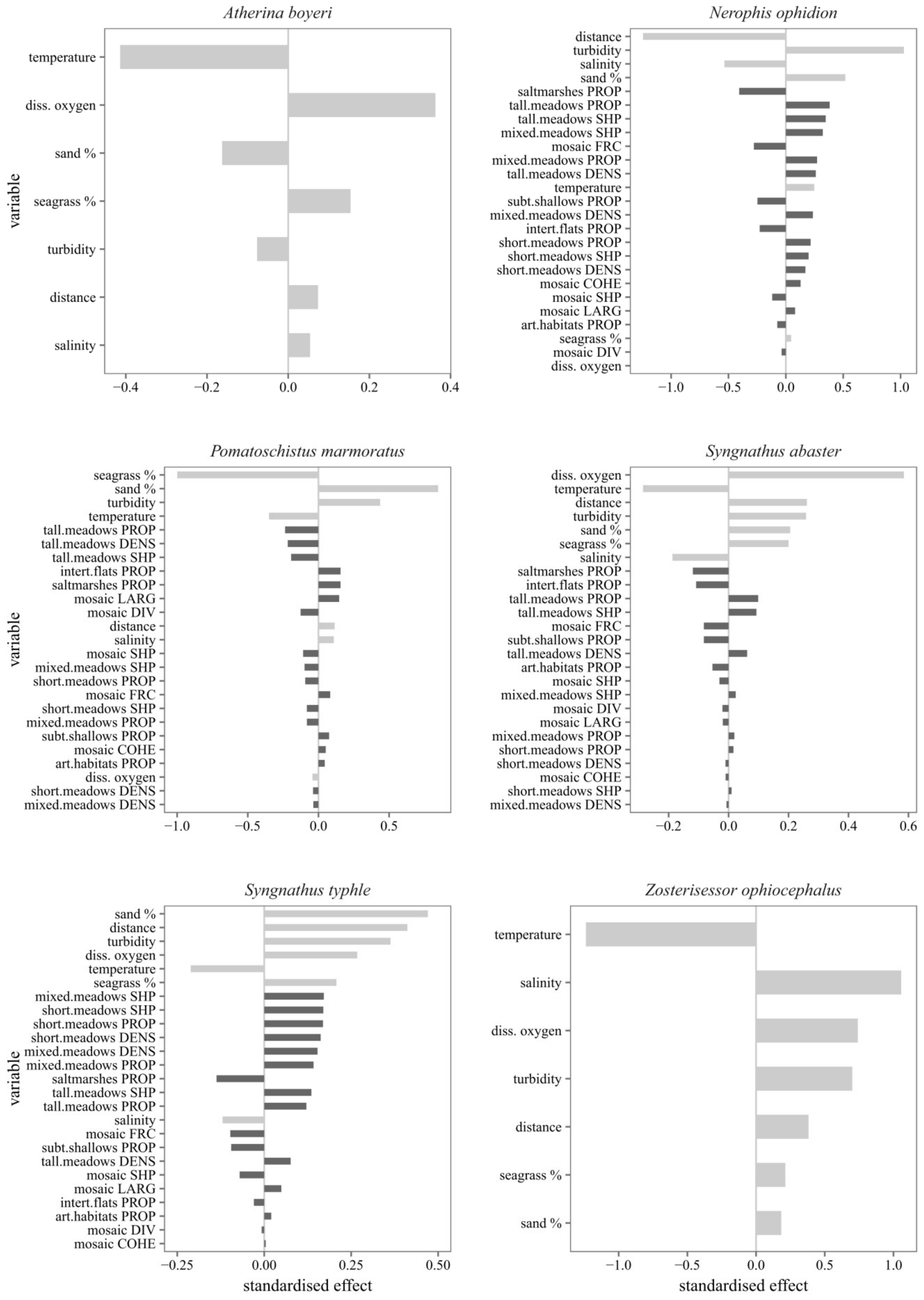


Figure 16: Standardised effects of site-scale (light grey) and mosaic-scale (dark grey) predictors on considered species, derived from the best GLM formulations. Effect magnitudes are sorted in descending order. Only a subset of mosaic properties is shown, excluding some highly collinear variables in PCA (i.e. showing very similar effects). Abbreviations for mosaic variables are described in Table 10.

Discussion

Influence of local- and broad-scale seagrass habitat structure on fish

The present results confirm the primary importance of in situ water and habitat quality for seagrass fish assemblages. Nonetheless, they emphasise that also some seagrass habitat features at the seascape scale are influent for overall fish biomass and for some common species and feeding guilds. This work thus highlights how environmental characteristics at multiple spatial scales 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; Elliott and Hemingway, 2002; Marshall and Elliott, 1998). 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 to shelter and ambush their prey (Howard and Koehn, 1985; Malavasi et al., 2007; Steffe et al., 1989). Greater seagrass cover, taller canopies and greater epiphytal 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*), and enhance foraging efficiency (Horinouchi, 2007; Jackson et al., 2006b; 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 (Franco et al., 2006; Pérez-Ruzafa et al., 2011; Quignard, 1984). For the purpose of this work the whole confinement gradient of the lagoon (i.e. from sea inlets to mainland) was not entirely included 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 influenced many of the species included in the analysis, with the majority of them together with overall fish biomass being supported with greater biomass densities in seagrass habitats located at greater distances. 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 seagrass sites investigated was largely composed by habitat specialists such as syngnathids (see also section 1, pag. 15; Scapin et al., 2017), which were influenced by properties of the habitat mosaic in addition to small-scale environmental parameters. Proportion of the seascape occupied by seagrass meadows and seagrass edge density had a positive effect on overall biomass as well as on syngnathid species, highlighting the importance of a lagoon seascape featuring 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 highlighted the different sensitivity to habitat quality of the three syngnathids. In particular, *N. ophidion* and *S. typhle* showed a greater response to extent and spatial arrangement of seagrass meadows in the seascape. This emphasises their role as seagrass specialists that could be employed as indicators of seagrass habitat status, as already pointed out in this work (see section 1, pag. 15; Scapin et al., 2017).

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. (2016) pointed out that syngnathids in seagrass meadows of western Swedish 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 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., 2016). 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 emerged in this work, as already noted by several authors (Flynn and Ritz, 1999; Jelbart et al., 2006; Macreadie et al., 2010; Smith et al., 2008).

Compared to fish biomass, no influence of the seascape was found on species richness in the seagrass sites investigated. The present study focused on α-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 α-diversity measured among artificial reefs located in different seagrass seascapes. Similarly, Staveley et al. (2016) showed that species richness among seagrass sites is not influenced by seascape composition and spatial configuration. However, while α-diversity is affected only by environmental characteristics at the site scale, both total fish diversity in the lagoon seascape (γ-diversity) and diversity among sites (β-diversity) could be linked to seascape variability, as already demonstrated for coastal benthic communities (Harborne et al., 2006).

The inclusion of feeding guilds in the analysis provided relevant insights into scale-dependent trophic functions of seagrass habitats. In this study, macrobenthivorous (Bma) species were influenced only by site scale, while hyperbenthivorous/piscivorous (HP) responded 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. gasteropods and amphipods). In addition, both Bma and HP guilds were composed of relatively few abundant species, with large gobies and *S. typhle* accounting for ca. 70% of Bma and HP biomass respectively (see Figure S6 in supplementary materials) and partly explaining the response of the respective guilds.

While found abundant 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 (Franco et al., 2006; Franzoi et al., 2010; Malavasi et al., 2005). This species was indeed positively associated with mosaics dominated by unvegetated habitats, such as saltmarshes and intertidal flats.

Implications for conservation

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 & Facca, 2007; Solidoro et al., 2010). 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 local and seascape scales should be regarded as an issue for the conservation of associated fish in coastal lagoons. Restoration actions aimed 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 local scale and from larger proportion of meadows in the mosaic, such as syngnathids. 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).

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. Palafox-Juárez and Liceaga-Correa, 2017; Pittman and Brown, 2011). 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 local 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 local conditions (e.g. physico-chemical water and sediment parameters, seagrass floristic composition, percent cover and canopy height) (Bell et al., 2008; Short et al., 2000), but in addition main seagrass seascape features (e.g. spatial continuity and edge density) should be taken into account.

A multi-scale point of view in conservation should hence be adopted, allowing to take into account the differences in the 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.

Acknowledgements

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Supplementary materials

Table S2: 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 also 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	*Atherina boyeri*	ES	HZ	0	0	0	1	0	0	0
Belonidae	*Belone belone*	MM	HZ; HP	0	0	0	0.5	0.5	0	0
Blennidae	*Parablennius sanguinolentus*	MS								
Blennidae	*Parablennius tentacularis*	MS								
Blennidae	*Salaria pavo*	ES	Bmi; OV	0	0.5	0	0	0	0	0.5
Bothidae	*Arnoglossus laterna*	MS								
Callionymidae	*Callionymus risso*	MS								
Carangidae	*Trachurus trachurus*	MS								
Clupeidae	*Sardina pilchardus*	MM	PL	0	0	0	0	0	1	0
Clupeidae	*Sprattus sprattus*	MM	PL	0	0	0	0	0	1	0
Cyprinodontidae	*Aphanius fasciatus*	ES	Bmi; OV	0	0.5	0	0	0	0	0.5
Engraulidae	*Engraulis encrasicolus*	MM	PL	0	0	0	0	0	1	0
Gobiidae	*Gobius cobitis*	MS								
Gobiidae	*Gobius niger*	ES	Bmi; Bma; HP	0	0.4	0.4	0	0.2	0	0
Gobiidae	*Gobius paganellus*	ES	Bmi; Bma; HP	0	0.4	0.4	0	0.2	0	0
Gobiidae	*Knipowitschia panizzae*	ES	Bmi; HZ	0	0.7	0	0.3	0	0	0
Gobiidae	*Pomatoschistus canestrinii*	ES	Bmi; HZ	0	0.7	0	0.3	0	0	0
Gobiidae	*Pomatoschistus marmoratus*	ES	Bmi; HZ	0	0.7	0	0.3	0	0	0
Gobiidae	*Pomatoschistus minutus*	MM	Bmi; HZ	0	0.7	0	0.3	0	0	0
Gobiidae	*Zebrus zebrus*	MS								
Gobiidae	*Zosterisessor ophiocephalus*	ES	Bmi; Bma; HP	0	0.3	0.3	0	0.3	0	0
Labridae	*Labrus viridis*	MS								
Labridae	*Symphodus cinereus*	MS								
Labridae	*Symphodus melops*	MS								
Labridae	*Symphodus roissali*	MS								
Mugilidae	*Chelon labrosus*	MM	DV; HZ	0.5	0	0	0.5	0	0	0
Mugilidae	*Liza aurata*	MM	DV; HZ	0.5	0	0	0.5	0	0	0
Mugilidae	*Liza ramada*	D	DV; HZ	0.5	0	0	0.5	0	0	0
Mugilidae	*Liza saliens*	MM	DV; HZ	0.5	0	0	0.5	0	0	0
Mugilidae	*Mugil cephalus*	D	DV; HZ	0.5	0	0	0.5	0	0	0
Mullidae	*Mullus surmuletus*	MM	Bmi; Bma	0	0.7	0.3	0	0	0	0
Pleuronectidae	*Platichthys flesus*	MM	Bmi; Bma; HP	0	0.4	0.4	0	0.2	0	0
Poeciliidae	*Gambusia* gr. *affinis*	ES	Bmi; HZ	0	0.5	0	0.5	0	0	0
Sciaenidae	*Sciaena umbra*	MS								
Sciaenidae	*Umbrina cirrosa*	MS								
Scophthalmidae	*Scophthalmus rhombus*	MS								

Table S2 (continued).

Family	**Species**	**Ecological guild**	**Feeding guild**	**DV**	**Bmi**	**Bma**	**HZ**	**HP**	**PL**	**OV**
Soleidae	*Solea solea*	MM	Bmi; Bma	0	0.7	0.3	0	0	0	0
Sparidae	*Boops boops*	MS								
Sparidae	*Diplodus annularis*	MS								
Sparidae	*Diplodus puntazzo*	MS								
Sparidae	*Diplodus sargus*	MS								
Sparidae	*Diplodus vulgaris*	MS								
Sparidae	*Lithognathus mormyrus*	MS								
Sparidae	*Oblada melanura*	MS								
Sparidae	*Sparus aurata*	MM	Bmi; Bma; HZ	0	0.4	0.2	0.4	0	0	0
Sphyraenidae	*Sphyraena sphyraena*	MS								
Syngnathidae	*Hippocampus guttulatus*	ES	Bmi; HZ	0	0.5	0	0.5	0	0	0
Syngnathidae	*Hippocampus hippocampus*	ES	Bmi; HZ	0	0.5	0	0.5	0	0	0
Syngnathidae	*Nerophis maculatus*	MS								
Syngnathidae	*Nerophis ophidion*	ES	Bmi	0	1	0	0	0	0	0
Syngnathidae	*Syngnathus abaster*	ES	Bmi; HZ	0	0.7	0	0.3	0	0	0
Syngnathidae	*Syngnathus acus*	MS								
Syngnathidae	*Syngnathus taenionotus*	ES	HZ	0	0	0	1	0	0	0
Syngnathidae	*Syngnathus tenuirostris*	MS								
Syngnathidae	*Syngnathus typhle*	ES	Bmi; HZ; HP	0	0.2	0	0.4	0.4	0	0
Triglidae	*Chelidonichthys lucernus*	MM	Bmi; Bma; HP	0	0.4	0.4	0	0.2	0	0

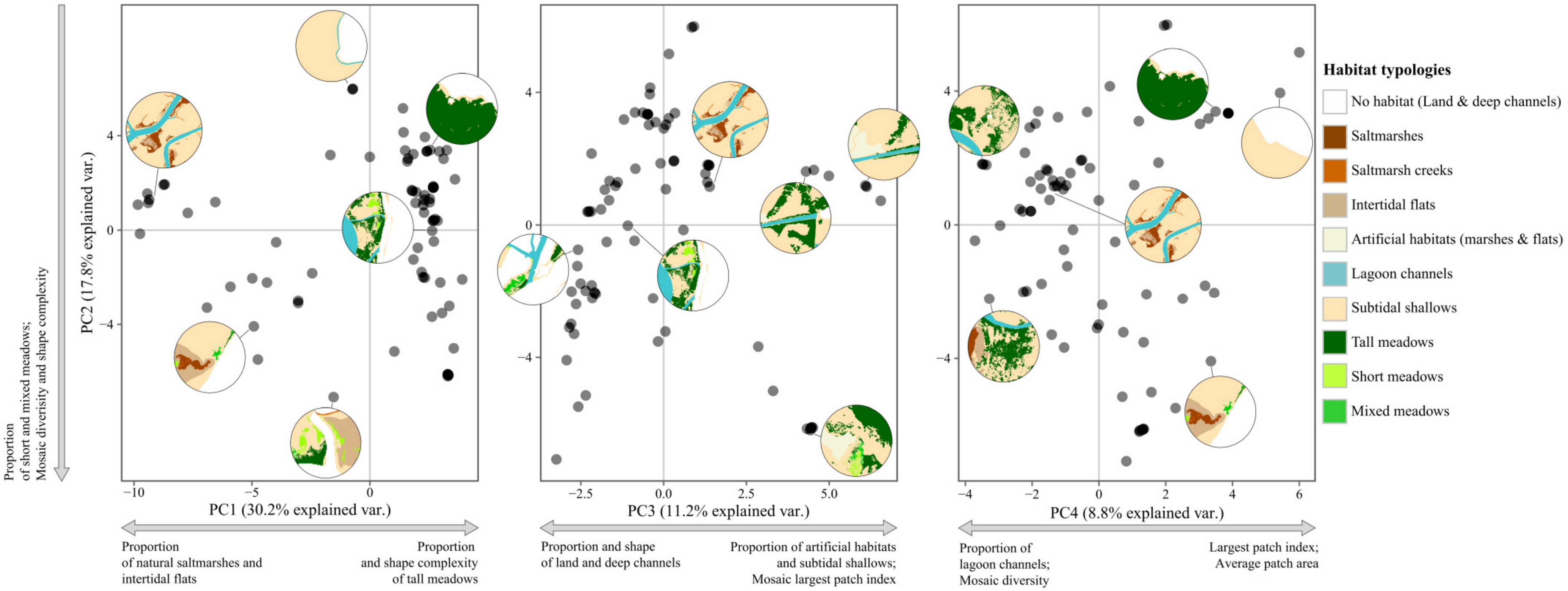
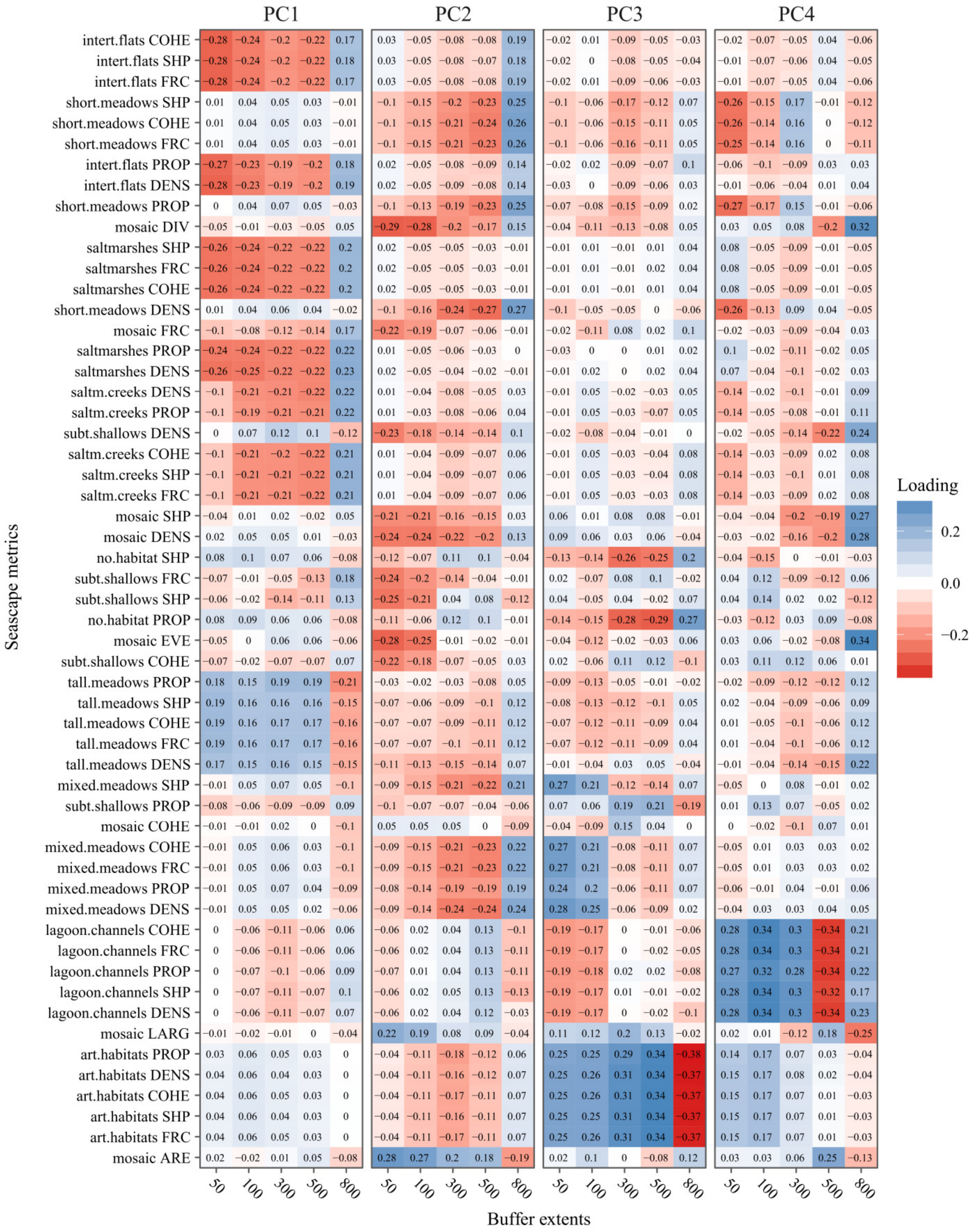


Figure S4: Example of biplots produced with the first four axes of a PCA based on mosaics quantified in 500m-radius buffer extents. Points represent observations. Some mosaics are highlighted to exemplify the patterns in seascape properties along the axes, which are described at box margins.



Seascape metrics	PC1					PC2					PC3					PC4				
	50	100	300	500	800	50	100	300	500	800	50	100	300	500	800	50	100	300	500	800
intert.flats COHE	−0.28	−0.24	−0.2	−0.22	0.17	0.03	−0.05	−0.08	−0.08	0.19	−0.02	0.01	−0.09	−0.05	−0.03	−0.02	−0.07	−0.05	0.04	−0.06
intert.flats SHP	−0.28	−0.24	−0.2	−0.22	0.18	0.03	−0.05	−0.08	−0.07	0.18	−0.02	0	−0.08	−0.05	−0.04	−0.01	−0.07	−0.06	0.04	−0.05
intert.flats FRC	−0.28	−0.24	−0.2	−0.22	0.17	0.03	−0.05	−0.08	−0.08	0.19	−0.02	0.01	−0.09	−0.06	−0.03	−0.01	−0.07	−0.05	0.04	−0.06
short.meadows SHP	0.01	0.04	0.05	0.03	−0.01	−0.1	−0.15	−0.2	−0.23	0.25	−0.1	−0.06	−0.17	−0.12	0.07	−0.26	−0.15	0.17	−0.01	−0.12
short.meadows COHE	0.01	0.04	0.05	0.03	−0.01	−0.1	−0.15	−0.21	−0.24	0.26	−0.1	−0.06	−0.15	−0.11	0.05	−0.26	−0.14	0.16	0	−0.12
short.meadows FRC	0.01	0.04	0.05	0.03	−0.01	−0.1	−0.15	−0.21	−0.23	0.26	−0.1	−0.06	−0.16	−0.11	0.05	−0.25	−0.14	0.16	0	−0.11
intert.flats PROP	−0.27	−0.23	−0.19	−0.2	0.18	0.02	−0.05	−0.08	−0.09	0.14	−0.02	0.02	−0.09	−0.07	0.1	−0.06	−0.1	−0.09	0.03	0.03
intert.flats DENS	−0.28	−0.23	−0.19	−0.2	0.19	0.02	−0.05	−0.09	−0.08	0.14	−0.03	0	−0.09	−0.06	0.03	−0.01	−0.06	−0.04	0.01	0.04
short.meadows PROP	0	0.04	0.07	0.05	−0.03	−0.1	−0.13	−0.19	−0.23	0.25	−0.07	−0.08	−0.15	−0.09	0.02	−0.27	−0.17	0.15	−0.01	−0.06
mosaic DIV	−0.05	−0.01	−0.03	−0.05	0.05	−0.29	−0.28	−0.2	−0.17	0.15	−0.04	−0.11	−0.13	−0.08	0.05	0.03	0.05	0.08	−0.2	0.32
saltmarshes SHP	−0.26	−0.24	−0.22	−0.22	0.2	0.02	−0.05	−0.05	−0.03	−0.01	−0.01	0.01	−0.01	0.01	0.04	0.08	−0.05	−0.09	−0.01	−0.05
saltmarshes FRC	−0.26	−0.24	−0.22	−0.22	0.2	0.02	−0.05	−0.05	−0.03	−0.01	−0.01	0.01	−0.01	0.02	0.04	0.08	−0.05	−0.09	−0.01	−0.05
saltmarshes COHE	−0.26	−0.24	−0.22	−0.22	0.2	0.02	−0.05	−0.05	−0.03	−0.01	−0.01	0.01	−0.01	0.01	0.04	0.08	−0.05	−0.09	−0.01	−0.05
short.meadows DENS	0.01	0.04	0.06	0.04	−0.02	−0.1	−0.16	−0.24	−0.27	0.27	−0.1	−0.05	−0.05	0	−0.06	−0.26	−0.13	0.09	0.04	−0.05
mosaic FRC	−0.1	−0.08	−0.12	−0.14	0.17	−0.22	−0.19	−0.07	−0.06	−0.01	−0.02	−0.11	0.08	0.02	0.1	−0.02	−0.03	−0.09	−0.04	0.03
saltmarshes PROP	−0.24	−0.24	−0.22	−0.22	0.22	0.01	−0.05	−0.06	−0.03	0	−0.03	0	0	0.01	0.02	0.1	−0.02	−0.11	−0.02	0.05
saltmarshes DENS	−0.26	−0.25	−0.22	−0.22	0.23	0.02	−0.05	−0.04	−0.02	−0.01	−0.01	0.02	0	0.02	0.04	0.07	−0.04	−0.1	−0.02	0.03
saltm.creeks DENS	−0.1	−0.21	−0.21	−0.22	0.22	0.01	−0.04	−0.08	−0.05	0.03	−0.01	0.05	−0.02	−0.03	0.05	−0.14	−0.02	−0.1	−0.01	0.09
saltm.creeks PROP	−0.1	−0.19	−0.21	−0.21	0.22	0.01	−0.03	−0.08	−0.06	0.04	−0.01	0.05	−0.03	−0.07	0.05	−0.14	−0.05	−0.08	−0.01	0.11
subt.shallows DENS	0	0.07	0.12	0.1	−0.12	−0.23	−0.18	−0.14	−0.14	0.1	−0.02	−0.08	−0.04	−0.01	0	−0.02	−0.05	−0.14	−0.22	0.24
saltm.creeks COHE	−0.1	−0.21	−0.2	−0.22	0.21	0.01	−0.04	−0.09	−0.07	0.06	−0.01	0.05	−0.03	−0.04	0.08	−0.14	−0.03	−0.09	0.02	0.08
saltm.creeks SHP	−0.1	−0.21	−0.21	−0.22	0.21	0.01	−0.04	−0.09	−0.07	0.06	−0.01	0.05	−0.03	−0.04	0.08	−0.14	−0.03	−0.1	0.01	0.08
saltm.creeks FRC	−0.1	−0.21	−0.21	−0.22	0.21	0.01	−0.04	−0.09	−0.07	0.06	−0.01	0.05	−0.03	−0.03	0.08	−0.14	−0.03	−0.09	0.02	0.08
mosaic SHP	−0.04	0.01	0.02	−0.02	0.05	−0.21	−0.21	−0.16	−0.15	0.03	0.06	0.01	0.08	0.08	−0.01	−0.04	−0.04	−0.2	−0.19	0.27
mosaic DENS	0.02	0.05	0.05	0.01	−0.03	−0.24	−0.24	−0.22	−0.2	0.13	0.09	0.06	0.03	0.06	−0.04	−0.03	−0.02	−0.16	−0.2	0.28
no.habitat SHP	0.08	0.1	0.07	0.06	−0.08	−0.12	−0.07	0.11	0.1	−0.04	−0.13	−0.14	−0.26	−0.25	0.2	−0.04	−0.15	0	−0.01	−0.03
subt.shallows FRC	−0.07	−0.01	−0.05	−0.13	0.18	−0.24	−0.2	−0.14	−0.04	−0.01	0.02	−0.07	0.08	0.1	−0.02	0.04	0.12	−0.09	−0.12	0.06
subt.shallows SHP	−0.06	−0.02	−0.14	−0.11	0.13	−0.25	−0.21	0.04	0.08	−0.12	0.04	−0.05	0.04	−0.02	0.07	0.04	0.14	0.02	0.02	−0.12
no.habitat PROP	0.08	0.09	0.06	0.06	−0.08	−0.11	−0.06	0.12	0.1	−0.01	−0.14	−0.15	−0.28	−0.29	0.27	−0.03	−0.12	0.03	0.09	−0.08
mosaic EVE	−0.05	0	0.06	0.06	−0.06	−0.28	−0.25	−0.01	−0.02	−0.01	−0.04	−0.12	−0.02	−0.03	0.06	0.03	0.06	−0.02	−0.08	0.34
subt.shallows COHE	−0.07	−0.02	−0.07	−0.07	0.07	−0.22	−0.18	−0.07	−0.05	0.03	0.02	−0.06	0.11	0.12	−0.1	0.03	0.11	0.12	0.06	0.01
tall.meadows PROP	0.18	0.15	0.19	0.19	−0.21	−0.03	−0.02	−0.03	−0.08	0.05	−0.09	−0.13	−0.05	−0.01	−0.02	−0.02	−0.09	−0.12	−0.12	0.12
tall.meadows SHP	0.19	0.16	0.16	0.16	−0.15	−0.07	−0.06	−0.09	−0.1	0.12	−0.08	−0.13	−0.12	−0.1	0.05	0.02	−0.04	−0.09	−0.06	0.09
tall.meadows COHE	0.19	0.16	0.17	0.17	−0.16	−0.07	−0.07	−0.09	−0.11	0.12	−0.07	−0.12	−0.11	−0.09	0.04	0.01	−0.05	−0.1	−0.06	0.12
tall.meadows FRC	0.19	0.16	0.17	0.17	−0.16	−0.07	−0.07	−0.1	−0.11	0.12	−0.07	−0.12	−0.11	−0.09	0.04	0.01	−0.04	−0.1	−0.06	0.12
tall.meadows DENS	0.17	0.15	0.16	0.15	−0.15	−0.11	−0.13	−0.15	−0.14	0.07	−0.01	−0.04	0.03	0.05	−0.04	−0.01	−0.04	−0.14	−0.15	0.22
mixed.meadows SHP	−0.01	0.05	0.07	0.05	−0.1	−0.09	−0.15	−0.21	−0.22	0.21	0.27	0.21	−0.12	−0.14	0.07	−0.05	0	0.08	−0.01	0.02
subt.shallows PROP	−0.08	−0.06	−0.09	−0.09	0.09	−0.1	−0.07	−0.07	−0.04	−0.06	0.07	0.06	0.19	0.21	−0.19	0.01	0.13	0.07	−0.05	0.02
mosaic COHE	−0.01	−0.01	0.02	0	−0.1	0.05	0.05	0.05	0	−0.09	−0.04	−0.09	0.15	0.04	0	0	−0.02	−0.1	0.07	0.01
mixed.meadows COHE	−0.01	0.05	0.06	0.03	−0.1	−0.09	−0.15	−0.21	−0.23	0.22	0.27	0.21	−0.08	−0.11	0.07	−0.05	0.01	0.03	0.03	0.02
mixed.meadows FRC	−0.01	0.05	0.06	0.03	−0.1	−0.09	−0.15	−0.21	−0.23	0.22	0.27	0.21	−0.08	−0.11	0.07	−0.05	0.01	0.03	0.03	0.02
mixed.meadows PROP	−0.01	0.05	0.07	0.04	−0.09	−0.08	−0.14	−0.19	−0.19	0.19	0.24	0.2	−0.06	−0.11	0.07	−0.06	−0.01	0.04	−0.01	0.06
mixed.meadows DENS	−0.01	0.05	0.05	0.02	−0.06	−0.09	−0.14	−0.24	−0.24	0.24	0.28	0.25	−0.06	−0.09	0.02	−0.04	0.03	0.03	0.04	0.05
lagoon.channels COHE	0	−0.06	−0.11	−0.06	0.06	−0.06	0.02	0.04	0.13	−0.1	−0.19	−0.17	0	−0.01	−0.06	0.28	0.34	0.3	−0.34	0.21
lagoon.channels FRC	0	−0.06	−0.11	−0.06	0.06	−0.06	0.02	0.04	0.13	−0.11	−0.19	−0.17	0	−0.02	−0.05	0.28	0.34	0.3	−0.34	0.21
lagoon.channels PROP	0	−0.07	−0.1	−0.06	0.09	−0.07	0.01	0.04	0.13	−0.11	−0.19	−0.18	0.02	0.02	−0.08	0.27	0.32	0.28	−0.34	0.22
lagoon.channels SHP	0	−0.07	−0.11	−0.07	0.1	−0.06	0.02	0.05	0.13	−0.13	−0.19	−0.17	0.01	−0.01	−0.02	0.28	0.34	0.3	−0.32	0.17
lagoon.channels DENS	0	−0.06	−0.11	−0.07	0.07	−0.06	0.02	0.04	0.12	−0.03	−0.19	−0.17	0	−0.02	−0.1	0.28	0.34	0.3	−0.34	0.23
mosaic LARG	−0.01	−0.02	−0.01	0	−0.04	0.22	0.19	0.08	0.09	−0.04	0.11	0.12	0.2	0.13	−0.02	0.02	0.01	−0.12	0.18	−0.25
art.habitats PROP	0.03	0.06	0.05	0.03	0	−0.04	−0.11	−0.18	−0.12	0.06	0.25	0.25	0.29	0.34	−0.38	0.14	0.17	0.07	0.03	−0.04
art.habitats DENS	0.04	0.06	0.04	0.03	0	−0.04	−0.11	−0.16	−0.12	0.07	0.25	0.26	0.31	0.34	−0.37	0.15	0.17	0.08	0.02	−0.04
art.habitats COHE	0.04	0.06	0.05	0.03	0	−0.04	−0.11	−0.17	−0.11	0.07	0.25	0.26	0.31	0.34	−0.37	0.15	0.17	0.07	0.01	−0.03
art.habitats SHP	0.04	0.06	0.04	0.03	0	−0.04	−0.11	−0.16	−0.11	0.07	0.25	0.25	0.31	0.34	−0.37	0.15	0.17	0.07	0.01	−0.03
art.habitats FRC	0.04	0.06	0.05	0.03	0	−0.04	−0.11	−0.17	−0.11	0.07	0.25	0.26	0.31	0.34	−0.37	0.15	0.17	0.07	0.01	−0.03
mosaic ARE	0.02	−0.02	0.01	0.05	−0.08	0.28	0.27	0.2	0.18	−0.19	0.02	0.1	0	−0.08	0.12	0.03	0.03	0.06	0.25	−0.13

Figure S5: Correlations (loadings) of seascape metrics with the first four PC axes calculated for each buffer extent.

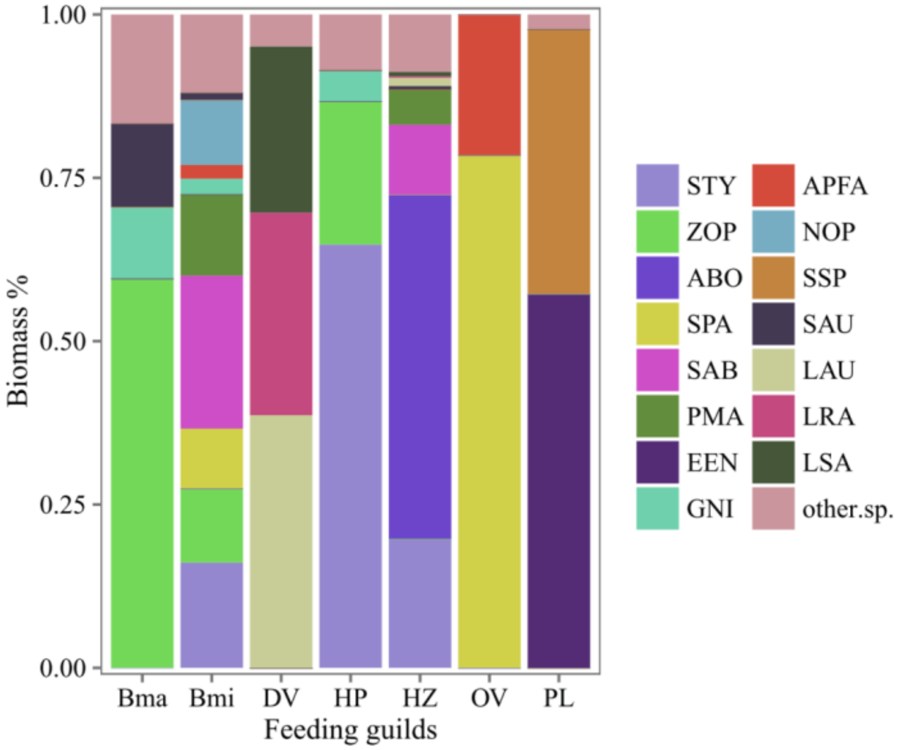


Figure S6: Species composition (biomass %) of feeding guilds considered. Bma: Macrobenthivorous; Bmi: Microbenthivorous; DV: Detritivorous; HP: Hyperbenthivorous/Piscivorous; HZ: Hyperbenthivorous/Zooplanktivorous; OV: Omnivorous; PL: Planktivorous. Species are abbreviated as follows: STY: *Syngnathus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

DISCUSSION

Understanding habitat use of fish in seagrass meadows for biodiversity conservation in Mediterranean coastal lagoons

Despite the importance of Mediterranean sea as a biodiversity hotspot at the global scale, and the recognised role of seagrass habitat for the Mediterranean (Campagne et al., 2014; Nordlund et al., 2016), there are few applications targeting the conservation of seagrass habitats and associated fauna in Mediterranean coastal lagoons (Borum et al., 2004; Facca et al., 2014a; Jahnke et al., 2015; Pirrotta et al., 2015; Pranovi et al., 2000).

This work ultimately aims to raise the profile of seagrass meadows as habitats for fish and other nekton fauna in Mediterranean coastal lagoons. Through the three main sections of the study, it has been emphasised how habitat characteristics and variability have a profound influence on structure and composition of associated fish assemblages, and proposed insights, approaches and tools for planning conservation efforts and assessing their outcomes.

Are all seagrass habitats equal for fish? Insights into conservation from pipefish and seahorses

Most of the studies investigating habitat use by fish contrast broad habitat typologies, such as unvegetated sandy bottoms, hard substrata, macroalgal beds and seagrass meadows (Franco et al., 2006; Franzoi et al., 2010; Whitfield, 2016). The generally high habitat selectivity of syngnathid fish, however, often allowed to perform studies taking into account different variations of a single habitat type (e.g. seagrass habitat) (Bell and Westoby, 1986; Hyndes et al., 2003; Malavasi et al., 2007). The Venice lagoon permitted such an approach, thanks to the presence of seagrass meadows of highly variable species composition and bottom cover (Curiel et al., 2014; Rismondo et al., 2003). While seagrasses as a whole are essential for the conservation of many species of syngnathids in coastal lagoons, some structural features of meadows enhance the habitat attractiveness for some of them. Overall, larger and broaderleaved species, such as *Cymodocea nodosa* and *Zostera marina*, with greater plant bottom cover, characterised the preferred habitats for most abundant syngnathid species in the Venice lagoon.

The actual conservation status and population trends of *C. nodosa* and *Z. marina* are however different. While the former shows stable populations within its range (Pergent-Martini et al., 2015; Short et al., 2010a), the latter is declining in many areas of the world as well as in the Mediterranean (Buia and Pergent-Martini, 2015; Short et al., 2010b). From a fish conservation point of view, these evidences should encourage managers to pay a particular attention to the conservation of *Z. marina* habitats, possibly prioritising areas of coastal lagoons hosting larger meadows, and carrying out direct transplantations when other efforts are insufficient.

Communicating effectively the needs, methods and outcomes of conservation efforts is essential, both for obtaining funding opportunities and growing public awareness, and flagship species are increasingly employed to draw attention on conservation of habitats and ecosystems (Melero, 2017; Veríssimo et al., 2017). Unquestionably, seahorses are among the most iconic animals, and are employed around the world to raise the public awareness of coastal marine environments, their value, threats and preservation (Shokri et al., 2009; Vincent et al., 2011). For a successful conservation of seagrass meadows in the Venice lagoon (and possibly in other Mediterranean transitional waters where seagrass habitats contribute to local biodiversity, e.g. Pérez-Ruzafa et al. (2006)), it is suggested that a similar role can be played by seagrass specialist pipefish.

Nekton fauna as indicator of restoration outcomes: the case of seagrass transplantations in the Venice lagoon

As previously pointed out, many seagrass fish are strongly linked to the structural attributes and status of seagrass habitats. As a result, it is proposed that nekton assemblages (also including swimming invertebrates in addition to fish) could be used to assess the outcomes of conservation efforts, such as restoration (Fonseca et al., 1996; Sheridan et al., 2003).

The Venice lagoon, through the project SERESTO, offers one of the few examples of restoration programmes currently tackling seagrass loss in the Mediterranean and setting specific criteria for the evaluation of its success (Jahnke et al., 2015; Pirrotta et al., 2015; Pranovi et al., 2000), which are based also on the recovery of associated faunal assemblages. In addition, being carried out in a highly heterogeneous area, the project provides an ideal case study to demonstrate how different sets of abiotic parameters and seagrass habitat characteristics are able to affect the colonisation of nekton fauna.

Understanding and managing the variability of restoration outcomes is arguably one of the grandest challenges to be addressed by scientists and practitioners dealing with conservation of habitats and associated fauna in transitional water ecosystems (Borja et al., 2010; Duarte et al., 2015; Elliott et al., 2007). In the context of this work, this task translates into the capability to predict which species composition has to be expected in different restored habitats, and whether the restoration goals designed under the project SERESTO are met. By means of a predictive approach, the present work provided a first attempt to achieve these results.

Most of the seagrass restoration studies compare the outcomes of transplantations with one or few "natural" or "undisturbed" sites, taken as reference (van Katwijk et al., 2009). However, the present analysis emphasised how measuring restoration success against a single reference condition would be inevitably too simplistic and flawed in coastal lagoon ecosystems. Indeed, while it would be ideal to have at disposal a rich and diverse reference dataset, encompassing the whole heterogeneity of abiotic, floristic and structural conditions found in the studied ecosystem, this is rarely the case. Different nekton assemblages must be expected, according to the degree of confinement, water physico-chemical characteristics, sediment granulometry and relative abundance of *Z. marina* and *Z. noltei* in transplanted sites. In these terms, the predictive approach to define reference conditions may significantly improve the assessment of restoration success.

The results obtained have profound implications for the forthcoming evaluation of the success of the project SERESTO, as well as for future seagrass restoration schemes carried out in Mediterranean coastal lagoons. They indicate that not all transplantation sites in the northern Venice lagoon will have an equal conservation potential for nekton fauna, regardless of the recovery of habitat structure. They also suggest that is critical to take into account the ecosystem spatial heterogeneity, when both designing restoration schemes and identifying project goals towards effective seagrass conservation in coastal lagoons.

Broadening the view: should the habitat mosaic be considered in seagrass conservation programmes?

The influence of site location, water and sediment quality and habitat structure on the distribution of fish in seagrass meadows of the Venice lagoon has been demonstrated, as well as their role in determining the recovery of seagrass nekton following habitat restoration. Accounting for spatial heterogeneity in conservation of coastal lagoons, however, also implies that both scientists and managers should operate at the level of whole water bodies, taking into account ecosystem processes only measurable and manageable at the seascape scale (Grober-Dunsmore et al., 2009).

As verified by the multi-scale approach followed in the third section of this work, habitat mosaic structure, quantified at the scale of tens/hundreds of hectares, is indeed as much important as local-scale environmental and habitat characteristics for some seagrass specialist fish in the Venice lagoon. In particular, species of high conservation value like syngnathids, were influenced by seagrass meadows features at the mosaic level, this suggesting that they could be employed as indicators of seagrass conservation status not only at the local level, but also across whole lagoon seascapes. If seagrass fish assemblages in Mediterranean coastal lagoons are to be protected, conservationists should focus on preserving and, if necessary, restoring *Z. marina* habitat coverage at the local scale, as well as overall seagrass meadows extent and patch complexity at the seascape scale.

These conclusions suggest that, in some cases, 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, for which a certain degree of edge complexity (hence patchiness) should also be maintained in addition to habitat extent in the seascape.

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LIST OF PUBLICATIONS, MANUSCRIPTS IN PREPARATION AND CONTRIBUTIONS TO SCIENTIFIC CONGRESSES

Publications

- Scapin, L., Cavraro, F., Malavasi, S., Riccato, F., Zucchetta, M., Franzoi, P., 2017. *Linking pipefishes and seahorses to seagrass meadows in the Venice lagoon: Implications for conservation.* Aquat. Conserv. Mar. Freshw. Ecosyst. (in press). doi:10.1002/aqc.2860
- Scapin L., Cavraro F., Zucchetta M., Franzoi P. (2016). *Effects of fishery and other anthropogenic pressures on artisanal fishery catches in the Venice lagoon.* Biologia Marina Mediterranea 23 (1), 45-46
- Zucchetta M., Scapin L., Cavraro F., Pranovi F., Franco A., Franzoi P. (2016). *Can the effects of anthropogenic pressures and environmental variability on nekton fauna be detected in fishery data? Insights from the monitoring of the artisanal fishery within the Venice lagoon.* Estuaries and Coasts 39, 1164. doi:10.1007/s12237-015-0064-y
- Scapin L., Zucchetta M., Facca C., Sfriso A., Franzoi P. (2016). *Using fish assemblage to identify success criteria for seagrass habitat restoration.* Web Ecology 16, 33–36. doi:10.5194/we-16-33-2016
- Scapin L., Facca C., Zucchetta M., Bonometto A., Oselladore F., Boscolo R., Franzoi P., Sfriso A. (2015). *First assessment of the ecological status in seagrass restoration sites of the northern Venice lagoon: application of macrophyte, macrozoobenthos and fish indices.* Biologia Marina Mediterranea 22 (1), 144-145

Manuscripts submitted/in preparation

- Scapin L., Zucchetta M., Franzoi P. *Local habitat and seascape structure influence seagrass fish assemblages in the Venice lagoon: the value of conservation at multiple spatial scales.* Oecologia (submitted)
- Scapin L., Zucchetta M., Sfriso A., Franzoi P. *Predicting the response of fish and invertebrate assemblages to seagrass transplantations: assessment of the progress of habitat restoration in the Venice lagoon.* (in preparation)

Contributions to scientific congresses

- Facca C., Bonometto A., Boscolo Brusà R., Buosi A., Franzoi P., Oselladore F., Ponis E., Rampazzo F., Scapin L., Zucchetta M., Sfriso A. *Biodiversity changes after seagrass transplantation in coastal lagoons (habitat 1150*): LIFE SeResto project results in Venice lagoon.* 52nd European Marine Biology Symposium, Pirano, Slovenia, 25-29 Settembre 2017
- Scapin L., Zucchetta M., Sfriso A., Franzoi P. *How habitat structure affects nekton fauna in seagrass meadows: identifying success criteria for seagrass restoration in the Venice lagoon.* 27° Congresso della Società Italiana di Ecologia, Napoli 12-15 settembre 2017
- Scapin L., Zucchetta M., Franzoi P. *Habitat use of fish in seagrass meadows of the Venice lagoon: multi-scale analysis and implications for conservation and restoration of the lagoon seascape.* 13° Incontro dei Dottorandi in Ecologia e Scienze dei Sistemi Acquatici, Palermo, 3-5 Maggio 2017

- Scapin L., Buosi A., Zucchetta M., Bonometto A., Oselladore F., Boscolo R., Sfriso A., Franzoi P. *Two years of seagrass restoration in the northern Venice lagoon (Italy) under the LIFE SeResto project: environmental constraints at multiple spatial scales to restoration of seagrass fish assemblages.* 12th International Seagrass Biology Workshop, Nant Gwrtheyrn, Gwynedd, Regno Unito, 16-21 Ottobre 2016
- Scapin L., Zucchetta M., Franzoi P. *The importance of habitat mosaic for seagrass fish assemblages: a study at multiple spatial scales in the meadows of the Venice lagoon.* 1° Congresso Nazionale Congiunto SITE - UZI – SIB, Milano, 30 Agosto-2 Settembre 2016
- Scapin L., Cavraro F., Zucchetta M., Franzoi P. *Effects of fishery and other anthropogenic pressures on artisanal fishery catches in the Venice lagoon.* 47° Congresso della Società Italiana di Biologia Marina, Torino 13-17 Giugno 2016
- Scapin L., Facca C., Zucchetta M., Oselladore F., Rampazzo F., Berto D., Franzoi P., Sfriso A. *Two years of seagrass restoration in the northern Venice lagoon (Italy): detecting changes in macrophytes, macrozoobenthos and fish of recreated habitats under the LIFE SeResto project.* 7th European Coastal Lagoon Symposium, Murcia, Spagna, 1-4 Marzo 2016
- Scapin L., Zucchetta M., Franzoi P. *Accounting for spatial complexity in transitional waters: a multi-scale approach to study fish distribution in the Venice lagoon.* 7th European Coastal Lagoon Symposium, Murcia, Spagna, 1-4 Marzo 1-4 2016
- Scapin L., Zucchetta M., Facca C., Sfriso A., Franzoi P. *Using fish community to identify success criteria for seagrass habitat restoration.* The 13th European Ecological Federation (EEF) and 25th Italian Society of Ecology (SItE) joint conference. Roma, 21-25 Settembre 2015
- Franzoi P., Scapin L., Cavraro F., Malavasi S., Riccato F., Zucchetta M. *Linking pipefishes and seahorses to their habitat: implications for species conservation in the Venice lagoon.* 15th European Congress of Ichthyology. Porto, Portogallo, 7-11 Settembre 2015
- Scapin L., Facca C., Zucchetta M., Bonometto A., Oselladore F., Boscolo R., Franzoi P., Sfriso A. *First ecological status assessment in some seagrass restoration sites of the northern Venice lagoon: application of macrophyte, macrozoobenthos and fish indices.* 46° Congresso della Società Italiana Biologia Marina. Roma, 10-12 Giugno 2015

Following page: *Cymodocea nodosa* meadow in the Venice lagoon (© Luca Scapin)