Linking pipefishes and seahorses to seagrass meadows in the Venice lagoon: implications for conservation

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Abstract

1. Seagrass meadow degradation and loss is one of the major threats to fish biodiversity in coastal marine and lagoon ecosystems in the Mediterranean. Pipefishes and seahorses (family Syngnathidae) are particularly affected by loss of seagrass meadows and other structured habitats, on which they rely for survival and reproduction. Despite their charismatic appearance and peculiar behaviour, their habitat ecology is still poorly understood in Mediterranean coastal waters.

2. This study focuses on syngnathid assemblage composition and diversity in the shallow waters of the Venice lagoon (Italy), aiming at highlighting habitat preferences and providing insights into the conservation of biodiversity in these ecosystems. Generalized Additive Models were used in order to disentangle the potential effect of habitat typologies and different architectures of seagrass meadows from that of other environmental parameters.

3. Most abundant taxa and whole syngnathid assemblage indicators were positively associated with seagrass meadows. Only few species, however, were seagrass specialists in shallow waters, and preferred meadows with taller canopies.

4. Despite that, other structured habitats including short-leaved seagrass meadows and macroalgal beds were important for some species and overall assemblage diversity.

1   5. Managers in Mediterranean coastal lagoons should thus limit human pressures that lead to the depletion of

2   seagrass meadows, with particular attention to long- and broad-leaved species in less confined areas.

3   Nevertheless, syngnathid assemblages would benefit from the preservation and restoration of the overall

4   habitat diversity characterizing shallow waters in coastal lagoon.

5   6. Future studies should aim at investigating the potential role of habitats at greater depths in supporting

6   syngnathids.

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8   **Keywords**: biodiversity, coastal, endangered species, fish, habitat management, transitional water

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11   # 1. Introduction

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13   With more than 600 marine fish taxa, accounting for approximately 7% of the total world fish species, the

14   Mediterranean Sea is a biodiversity hotspot (Abdul Malak et al., 2011). Coastal lagoons play a fundamental

15   role in supporting fish biodiversity, acting for instance as nursery grounds for commercially important species

16   and hosting taxa of conservation interest (Franco et al., 2006; Franco, Franzoi, & Torricelli, 2008; Quignard,

17   1984). At the same time, these environments are also subjected to high and multiple human pressures (Elliott

18   & Quintino, 2007; Marchand et al., 2002; Pérez-Ruzafa, Marcos, C., & Pérez-Ruzafa, 2011), with degradation

19   and loss of seagrass meadows being one of the most significant threats for fish fauna (Franco, Riccato,

20   Torricelli, & Franzoi, 2009; Vasconcelos et al., 2007). Seagrass meadows are declining at both local and global

21   scales (Airoldi & Beck, 2007; Short et al., 2011; Waycott et al., 2009). This may severely damage marine

22   biodiversity, including fishes, especially in ecosystems where meadows have limited distribution and serve as

23   nursery habitat (Bertelli & Unsworth, 2014; Pihl et al., 2006). In this light, it is critical to acquire information

24   on seagrass habitat characteristics that support fish biodiversity, in order to preserve both habitat and associated

25   fauna.

26   In the Venice lagoon (northern Adriatic Sea), the largest transitional water body in the Mediterranean, seagrass

27   meadows (*Cymodocea nodosa*, *Zostera marina* and *Z. noltei*) have reduced during the last 30 years due to

1   multiple anthropogenic causes, such as the increase in nutrient inputs from the drainage basin and the sediment

2   resuspension caused by the mechanized clam fishery and sediment dredging and disposal (Sfriso, Facca,

3   Ceoldo, & Marcomini, 2005; Sfriso, Facca, & Marcomini, 2005). Despite the recovery of trophic status and

4   the overall enhancement of ecological conditions in recent years, which is leading to the progressive

5   recolonization by seagrasses in some areas, the distribution of *Z. marina* and *Z. noltei* is still very limited in

6   the central and northern lagoon sub-basins (Curiel et al., 2014; Sfriso & Facca, 2007).

7   The Venice lagoon ecosystem supports diversified fish communities thanks to a highly heterogeneous mosaic

8   of habitats that includes seagrass meadows, saltmarshes, bare mud- and sandflats and macroalgal beds.

9   Pipefishes and seahorses (family Syngnathidae) are a major feature of the fish biodiversity in this environment,

10 and account for a large proportion of species density and diversity in seagrass meadows and other structured

11 habitats in the Venice lagoon, as well as in other Mediterranean transitional waters (Campolmi, Sarà, Galioto,

12 Baratta, & Franzoi, 1996; Franco et al., 2006; Franzoi, Maccagnani, Rossi, & Ceccherelli, 1993; Riccato et al.,

13 2003). Among the ten species of Mediterranean syngnathids, nine can be found in the Venice lagoon (Franzoi,

14 Franco, & Torricelli, 2010), this being an ecosystem of primary importance for the conservation of this family.

15 Two of the nine species are assessed as Near Threatened (NT) by IUCN at the Mediterranean scale, namely

16 *Hippocampus guttulatus* (Pollom, 2016a) and *H. hippocampus* (Pollom, 2016b), and three species are Data

17 Deficient (DD), including *Syngnathus taenionotus* (Allen, 2016), *S. tenuirostris* (Papakonstantinou et al.,

18 2016) and *Nerophis maculatus* (Wiswedel, 2016). Moreover, at the global scale, five of the species are assessed

19 as DD, namely *H. guttulatus* (Woodall, 2012a), *H. hippocampus* (Woodall, 2012b), *N. maculatus* (Wiswedel,

20 2015), *S. taenionotus* (Tunesi & Czembor, 2014) and *S. tenuirostris* (Papakonstantinou et al., 2014). Some

21 species are also protected under European and international regulations. In particular, some species of the

22 genus *Hippocampus* are strictly protected under the Convention on the Conservation of European Wildlife and

23 Natural Habitats (Bern Convention), and their trade is regulated under the Convention on International Trade

24 in Endangered Species of Wild Fauna and Flora (CITES: www.cites.org). However, the overall lack of

25 information regarding habitat use, population dynamics and life history severely limits effective management

26 actions towards syngnathid conservation (Vincent, Foster, & Koldewey, 2011). While there is a relatively

27 larger amount of knowledge about some of the species in the Mediterranean, it is still not clear how and to

28 what extent habitat loss may affect their populations (Freyhof, 2016; Ouyang & Pollom, 2016; Pollom, 2016a,

1   b). For instance, a better understanding of habitat requirements would benefit the assessment of the status of

2   species like *S. typhle* and *N. ophidion*, for which the monitoring of habitat trends is regarded as a conservation

3   priority (Pollom, 2016c, d).

4   Syngnathids share some body adaptations as well as feeding and reproductive behaviours that make them

5   highly specialized organisms (Ahnesjö & Craig, 2011). Most of them are cryptic species that live in highly

6   structured coastal environments such as coral reefs, algal beds, kelps and seagrass meadows (Browne, Baker,

7   & Connolly, 2008; Kuiter, 2000; Lourie, Vincent, & Hall, 1999). Together with their specific environmental

8   requirements, their typically low mobility and slow reproductive rates could make syngnathids particularly

9   sensitive to degradation or loss of their habitat (Vincent et al., 2011). Thanks to their unique appearance and

10   behaviour, however, syngnathids are charismatic fish that may attract sympathy and help raise public

11   awareness of biodiversity conservation in coastal environments. Therefore, they are sometimes regarded as

12   effective flagship species, which could be used to select Marine Protected Areas and enhance the conservation

13   of coexisting less charismatic taxa and associated habitats (Browne et al., 2008; Shokri, Gladstone, & Jelbart,

14   2009). Despite that, no information is available regarding the potential use of syngnathids as flagships for the

15   protection of seagrass meadows in Mediterranean coastal lagoons. Similarly, while some species exhibit a

16   marked dependence on seagrass meadows for survival, growth and reproduction and many are considered to

17   be highly sensitive to seagrass loss, syngnathids are rarely employed as indicators to assess habitat health,

18   conservation status or restoration success in the Mediterranean (Deudero, Morey, Frau, Moranta, & Moreno,

19   2008; Scapin, Zucchetta, Facca, Sfriso, & Franzoi, 2016). Investigating the meadow characteristics influencing

20   their distribution could thus also help identify the species that are more sensitive to changes in seagrass habitat.

21   The paper examines the role of habitat characteristics in affecting the distribution of syngnathids in the Venice

22   lagoon shallow waters. It gathers observations on syngnathids distribution, environmental parameters and

23   habitat characteristics collected during eight years of monitoring and research in the Venice lagoon, from 2002

24   to 2014. Data from 186 sites were analysed. In particular, the objectives of the present work were to i)

25   disentangle the influence of environmental characteristics and habitat features on the distribution and

26   abundance of syngnathid assemblage; ii) highlight the dependence of these species on seagrass meadows with

27   particular characteristics; and iii) find which habitat characteristics contribute most to supporting syngnathid

28   species densities and diversity. This work would thus help coastal lagoon managers in prioritizing habitats for

1 conservation and provide some insights into the potential role of syngnathids as indicator and flagship species

2 in these environments.

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5 ## 2. Methods

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7 <u>Study area</u>

8 The Venice lagoon is a large (approximately 550 km^2) transitional water body located in the northern Adriatic

9 Sea (Figure 1). It is connected to the sea by three sea inlets, and experiences a tidal range of ±0.50 m during

10 spring tides (Umgiesser, Melaku canu, Cucco, & Solidoro, 2004). It is mostly composed of shallow water

11 areas, with an average depth of 1.2 m (Molinaroli, Guerzoni, Sarretta, Cucco, & Umgiesser, 2007) and is

12 characterized by high spatial and temporal variability in environmental conditions such as salinity, dissolved

13 oxygen, turbidity, trophic status and sediment granulometry, these being driven by both natural processes and

14 multiple anthropogenic pressures (Solidoro et al., 2010).

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16 <u>Field data collection</u>

17 All sampling sites were located in water depth ranging between approximately 20 to 150 cm at the time of

18 sampling. Following the methodology described in Franco et al. (2006), fish were collected during daylight

19 hours by means of a small beach seine net of 10 m length, 2 m height and 2 mm knot-to-knot mesh size.

20 Samplings (one to three replicates per site) were performed either in spring (April to June), summer (July to

21 September) or autumn (October to December).

22 Sampled fish were photographed on millimetre paper and then released. Only when necessary (e.g. larval and

23 juvenile stages) and always excluding rare and endangered species, a representative subsample of fish was

24 sacrificed with an excess of 2-phenoxyethanol, preserved in 8% buffered formaldehyde and subsequently

25 identified in the laboratory. Fish were identified at the species level, and abundance (number of individuals)

26 was recorded for each species at all sites.

1   Together with fish sampling, water temperature (°C), dissolved oxygen (percentage of saturation), salinity

2   (PSU) and turbidity (FNU) were measured with a multi-parameter probe at each site. In addition, information

3   on bottom characteristics was collected in each site. The presence of seagrass vegetation (i.e. epigeous parts

4   of *C. nodosa*, *Z. marina* and *Z. noltei*) was recorded by visual census, and its relative coverage within the

5   sampled area was estimated following the Braun-Blanquet method and subsequently expressed as percentage

6   cover. Presence of macroalgae (mainly laminar Ulvaceae and branched Gracilariaceae and Soleriaceae) was

7   also recorded by visual census. Finally, sediment granulometry (percentage of sand in the 10 cm surface layer)

8   was associated to each sampling site from granulometry maps (ARPAV, 2012; MAG.ACQUE - SELC, 2005;

9   MAG.ACQUE - THETIS, 2005).

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11   Data analysis

12   *Definition of habitat typologies*

13   Each sampling site was allocated to one of three habitat typologies, defined according to the main bottom cover

14   recorded in the field. Substrata without any macroalgae or seagrass vegetation were classified as "bare

15   substratum". Substrata without seagrass vegetation but covered by macroalgae were classified as "macroalgal

16   bed". Finally, substrata characterized by presence of seagrasses, with or without macroalgae, were classified

17   as "seagrass meadow".

18   *Descriptive statistics*

19   Fish abundance data were standardized by area, in order to obtain comparable density measures (number of

20   individuals · 100 m^{-2}). A set of indicators based on the whole syngnathid assemblage were also calculated:

21   total number of species, total density, species richness (Margalef's index calculated on density), species

22   diversity (Shannon's index calculated on density) and species evenness (Pielou's index calculated on density).

23   Mean and standard deviation values for density of each species, as well as for all indicators, were calculated

24   per habitat typology.

25   *Model calibration*

26   A model approach was adopted in order to study the effect of environmental descriptors on syngnathid

27   distribution. Density was used as response variable for most abundant species, while presence/absence data

28   were used for rarer species (i.e. those with a large proportion of zeros in dataset). Indicators of the whole

1   syngnathid assemblage were also considered as response variables. Species and indicators were independently

2   modelled with Generalized Additive Models (GAMs; Hastie & Tibshirani, 1990; Wood, 2006). A negative

3   binomial distribution was used to model response variables based on density, species richness and species

4   diversity. A binomial distribution was chosen to model presence/absence data, while a zero-inflated Poisson

5   distribution was used to model the number of species.

6   Three categories of models were developed for each response variable separately, in order to test three different

7   hypotheses on the contributions of predictor variables. Model categories were hierarchical, i.e. were built by

8   progressively adding new predictors, to represent an increasing level of complexity. This allowed to explore

9   the following *a-priori* hypotheses (Table 1): response variable is affected by seasonal factor alone (category

10   m1); response variable is affected by environmental parameters when seasonal factor is already accounted for

11   (category m2); response variable is affected by habitat characteristics, including habitat types and seagrass

12   percentage cover, if seasonal factor and environmental parameters are already accounted for (category m3).

13   Since the present study did not aim at investigating the temporal trends, potentially present in the dataset, we

14   did not included the year of sampling in the model analysis. The possibility to include sampling year as a

15   random factor in a Generalized Additive Mixed Model (GAMM) framework was also explored, but eventually

16   not included in the analysis due to the relative homogeneity of residuals among years.

17   Category m1 included only one model, while more than one GAM formulation was made for the others,

18   resulting in a series of candidate alternative models for each category (Table 1). Category m2 was built by

19   adding to category m1 either water physico-chemical parameters (m2.1), water depth and sediment

20   granulometry (m2.2) or all such predictors together (m2.3). Category m3 was built by adding to category m2

21   either habitat types (m3.1) or both habitat types and seagrass percentage cover (m3.2).

22   *Selection of best models*

23   For each response variable and starting from category m1, the best candidate model within each category was

24   selected by using the Akaike Information Criterion (AIC; Burnham & Anderson, 2002) approach, choosing

25   the model with the lower AIC value. In case of model comparisons with an inadequate support for the

26   identification of the best model (AIC difference lower than 2) the most parsimonious formulation (i.e. the

27   model retaining less predictors) was selected. Then, each following category was built adding predictors to the

28   best model selected from the preceding category. This stepwise procedure allowed to explore each hypothesis

1   formulated, by verifying if progressive addition of predictor terms would improve the overall fit of the model

2   (Table 1).

3   Following this method, the best model was selected for each response variable and results were interpreted. In

4   particular, the sign (either positive, null or negative) and magnitude of the effect of presence of a specific

5   habitat typology, as estimated by the best fitted GAMs, were used to interpret habitat influence on response

6   variables.

7   *Effect of floral composition in seagrass meadows*

8   Seagrass morphological features (e.g. leaf and shoot length and width) determine the structural characteristics

9   of meadow habitat (such as canopy height), hence they may influence habitat choice in cryptic species that

10 mimic seagrass leaves or use them as holdfasts to feed and hide (Malavasi et al., 2007; Schultz, Kruschel, &

11 Bakran-Petricioli, 2009). Thus, the potential effect of seagrass species composition was investigated for those

12 species predicted with greater mean densities/probability of presence in seagrass meadows (i.e. whose best

13 model belong to model category m3). The respective best GAMs were modified so that the three-level factor

14 for habitat typology was replaced by a five-level factor, maintaining the "bare substratum" and "macroalgal

15 bed" levels and adding "*C. nodosa*-meadow", "*Z. marina*-meadow" and "*Z. noltei*-meadow" in replacement

16 of "seagrass meadow" level, depending on the seagrass species dominating the habitat (in terms of percentage

17 cover) in each sampling site. This allowed to test the hypothesis that each response variable is affected by

18 habitat characteristics, including habitat/meadow types and seagrass percentage cover, if seasonal factor and

19 environmental parameters are already accounted for (category m4; Table 1).

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26 ## 3. Results

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2 <u>Habitat types distribution</u>

3 A total of 579 observations were included in the fish and environmental dataset. The observations were

4 relatively well distributed among habitat typologies, with seagrass meadows accounting for 37% of the records,

5 bare substrata accounting for 36% and macroalgal beds for 27%. Within seagrass habitat, *Z. noltei* was found

6 to be dominant in terms of percentage cover in 40% of observations (14% of the total), *C. nodosa* in 31% (11%

7 of the total) and *Z. marina* in 29% (11% of total observations).

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9 <u>Syngnathids distribution</u>

10 Overall, syngnathid species accounted, on average, for 47% of the total fish density and 39% of the total

11 number of species sampled in seagrass meadows. In turn, they played a minor role in structuring the fish

12 assemblage of both bare substrata and macroalgal beds. Syngnathids accounted on average for 3% of the total

13 fish density and 14% of the total number of species in unvegetated habitats, and for 10% of the total fish

14 density and 19% of the total number of species in macroalgal habitats.

15 Nine species of syngnathids were caught in the Venice lagoon during the study period, including seven species

16 of pipefishes (*Nerophis maculatus*, *N. ophidion*, *Syngnathus abaster*, *S. acus*, *S. taenionotus*, *S. tenuirostris*

17 and *S. typhle*) and two species of seahorses (*Hippocampus hippocampus* and *H. guttulatus*). Six species were

18 found in all three habitat typologies (all the species excluding *S. acus*, *H. hippocampus* and *N. maculatus*), and

19 showed overall greater densities in seagrass meadows compared with other habitats (Figure 2). Three species

20 were the most abundant, namely *S. abaster*, *S. typhle* and *N. ophidion*, which accounted for more than 80% of

21 total syngnathid density in all habitats.

22 All indicators based on the syngnathid assemblage varied markedly between seagrass meadows and other

23 habitat types (Figure 2). On average, seagrass habitats were characterized by greater values of total density,

24 total number of species Shannon's diversity and Pielou's evenness, while Margalef's richness showed similar

25 mean values between habitats.

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28 <u>Habitat use by syngnathids</u>

1   *S. abaster*, *S. typhle* and *N. ophidion* were the most abundant species in the syngnathid assemblage, hence their

2   response to environmental conditions were modelled using density. In turn, presence/absence data were used

3   to model the response of *H. guttulatus*, *S. acus*, *S. taenionotus* and *S. tenuirostris*. Due to the very few

4   observations of both *H. hippocampus* and *N. maculatus* (n=2 and n=1 respectively), these species were

5   excluded from further analyses.

6   *Importance of predictors for species*

7   Seasonal factor, physico-chemical descriptors and habitat characteristics were all included in best models

8   explaining the distribution of five species of syngnathids in the Venice lagoon (Table 2). In particular, density

9   of *S. abaster*, *S. typhle* and *N. ophidion* and presence/absence of *H. guttulatus* responded to both habitat

10 typology and seagrass cover, when seasonal factor and physico-chemical descriptors were already taken into

11 account (m3.2). In terms of physico-chemical descriptors, water parameters, water depth and sediment

12 granulometry were all relevant for *S. abaster*, *S. typhle* and *N. ophidion*, while only water parameters were

13 relevant for *H. guttulatus*. Similarly, presence/absence of *S. acus* responded to seasonal factor, physico-

14 chemical descriptors (water depth and sediment granulometry only) and habitat typology, while it was not

15 affected by seagrass cover (m3.1). Conversely, presence/absence of *S. taenionotus* was affected only by

16 seasonal factor and physico-chemical descriptors (including water parameters, water depth and sediment

17 granulometry; m2.3), while presence/absence of *S. tenuirostris* was predicted by seasonal factor alone (m1).

18 *Importance of predictors for indicators*

19 According to the fitted GAMs (Table 2), the variability of all syngnathid assemblage indicators was explained

20 by seasonal factor, physico-chemical descriptors and habitat characteristics (both habitat typology and seagrass

21 cover) (m3.2). While all the considered physico-chemical descriptors (i.e. water parameters, water depth and

22 sediment granulometry) explained total syngnathid density, total number of species and species richness, only

23 water depth and sediment granulometry were included in the best models explaining species diversity and

24 evenness.

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 characterized 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 percentage 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

1   and seagrass meadows) (Figure 3). Within seagrass habitat, vegetation percentage cover had a positive linear

2   effect on mean values of all indicators except for species evenness, which varied non- linearly and reached a

3   plateau at approximately 40% of seagrass cover (Figure 4).

4   *Effect of floral composition in seagrass meadows*

5   Best models fitted for *S. abaster*, *S. typhle*, *N. ophidion* and *H. guttulatus* showed an overall positive effect of

6   seagrass habitat on species distribution. Hence, the relative importance of each meadow typology for such

7   species was investigated (Figure 5). *S. typhle*, *N. ophidion* and *H. guttulatus* all showed a similar response

8   pattern to the presence of a particular meadow typology. They were all predicted with greater mean densities

9   or probability of presence in meadows dominated by both *C. nodosa* and *Z. marina*, without marked differences

10   between the two habitats (only *N. ophidion* showed a clear preference for *C. nodosa*) and meadows dominated

11   by *Z. noltei* showing an overall less positive effect. In addition, all these species were negatively affected by

12   the presence of both bare substrata and macroalgal beds when considering different meadow types in models,

13   hence suggesting their avoidance of such habitats. In contrast, while a preference of *S. abaster* for *C. nodosa*

14   can be observed, the effects of *Z. marina* and *Z. noltei* meadows, as well as of macroalgal beds, were similar

15   and positive, compared to bare substrata.

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4. 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, Kendrick, MacArthur, & Stewart, 2003; Malavasi et al., 2007). In the Venice lagoon, *Z. marina* and *C. nodosa* meadows are usually characterized 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, Attrill, & Jones, 2006; Malavasi et al., 2007; Steffe, Westoby, & Bell, 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).

1   *H. guttulatus* was not abundant in shallow waters, probably preferring deeper and more stable environments

2   such as subtidal meadows and other hard substrata at greater depths (Gristina et al., 2017). Despite being

3   relatively uncommon, this species resulted associated with tall and spatially continuous seagrass habitats.

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5   Macroalgal beds are actively avoided by *Nerophis* and *Hippocampus* species in the shallow waters of the

6   Venice lagoon. While macroalgae may host great densities of invertebrate prey and serve as habitat for some

7   syngnathid species (Polte & Buschbaum, 2008), they usually lack structures that are robust enough to serve as

8   holdfast, especially in the case of laminar Ulvaceae. Unlike *Nerophis* and *Hippocampus*, *Syngnathus* species

9   are not provided with prehensile tail and do not need to grasp or entwine holdfasts, showing instead an active

10   swimming behaviour for most of the time. For this reason, also macroalgae may be selected as habitat by

11   *Syngnathus* species.

12   In particular for *S. abaster,* macroalgal beds serve as a suitable habitat, possibly due to the increased chance

13   to feed on associated fauna and to hide from predators. *S. abaster* is a common component of fish assemblages

14   of the Italian coastal lagoons, and it is found in a variety of habitat typologies including macroalgae (Campolmi

15   et al., 1996; Franco et al., 2006; Franzoi et al., 1993; Riccato et al., 2003). The differences in seagrass

16   association between *S. abaster*, *S. typhle* and *N. ophidion* shown in the present study highlighted the more

17   generalist behaviour in habitat choice of *S. abaster* compared to *S. typhle* and *N. ophidion*, which in turn appear

18   to be seagrass specialists.

19   Unlike other syngnathids in the Venice lagoon, *S. taenionotus* feeds almost exclusively on zooplankton

20   (Franzoi et al., 1993); hence, the less strict association with any particular habitat that was highlighted in the

21   present study might increase the foraging efficiency in the water column. This species is indeed documented

22   to live in Northern Adriatic lagoons on seagrass meadows, bare mud- and sand-flats and within drifting

23   macroalgae (Franco et al., 2006; Franzoi et al., 1993). Similarly, other syngnathid species modelled in this

24   study did not show any clear response to habitat typology, probably due to their relatively scarce presence in

25   shallow water environments, due to their preference for other habitat types. As regarding the two species of

26   *Hippocampus*, Curtis and Vincent (2005) suggest that *H. hippocampus* tends to use bare sandy bottoms and

27   hard biogenic structures, while Caldwell and Vincent (2012) highlighted the preference of *H. hippocampus* for

28   slightly deeper water (>3m) and habitats with high current speed.

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4   *Implications for species and habitat conservation*

5   Alterations of lagoon morphology, including habitat loss, and deterioration of water and sediment quality are

6   currently the major factors of human-induced change in the Venice lagoon (Curiel et al., 2014; Molinaroli et

7   al., 2009; Sarretta et al., 2010; Sfriso & Facca, 2007; Solidoro et al., 2010), which can have a negative effect

8   on fish fauna (Franco et al., 2009; Zucchetta et al., 2016). Traditional fishing activities in the shallow waters

9   of the lagoon at the present level of effort can be considered not harmful for syngnathids, since these species

10 have no commercial value and levels of by-catch are usually very low (Zucchetta et al., 2016). In turn, it can

11 be argued that habitat loss is the biggest threat to syngnathids in the Venice lagoon, as well as in other coastal

12 waters around the world (Curtis & Vincent, 2005; Harasti et al., 2014; Lim et al., 2011; Pihl et al., 2006;

13 Vincent et al., 2011).

14 Loss of aquatic angiosperms has been reported from coastal lagoons throughout the Mediterranean (Viaroli et

15 al., 2008 and citations therein), and particularly in the North Adriatic since the mid 1970s, where transitional

16 water ecosystems faced important regime shifts from benthic macrophytes- to phytoplankton-dominated

17 conditions (Curiel et al., 1998; Piccoli, 1998; Sfriso & Facca, 2007; Viaroli et al., 2006). Since the early works

18 describing its trophic conditions and floral assemblages (Vatova, 1940), the Venice lagoon has experienced

19 some marked decrease in the overall surface occupied by *C. nodosa*, *Z. marina* and *Z. noltei* meadows (Curiel

20 et al., 2014; Sfriso & Facca, 2007), although their distribution is highly dynamic and characterized by

21 significant interannual variations (Rismondo & Mion, 2008). Populations of *Z. marina* and *Z. noltei* have been

22 the most affected by eutrophication, macroalgal blooms and perturbation of sediments (Sfriso, Facca, Ceoldo,

23 et al., 2005; Sfriso, Facca, & Marcomini, 2005; Solidoro et al., 2010), showing an overall decline in the

24 northern and central sub-basins at least since the 1990s (Curiel et al., 2014).

25 In this context, populations of *S. typhle*, *N. ophidion* and *H. guttulatus* in the Venice lagoon may be the most

26 damaged by fragmentation and loss of *C. nodosa* and *Z. marina* meadows, due to their strong association with

27 this habitat. Other syngnathids, such as *S. abaster*, could also be directly affected by an overall loss of suitable

28 habitat, as well as a number of other fish species of conservation and commercial value that are strongly

1 associated with seagrasses in this ecosystem (Franco et al., 2006; Franzoi et al., 2010; Scapin et al., 2016). The

2 indirect consequences of habitat loss, however, may be difficult to predict, and reach also species that do not

3 rely directly on meadows, since the degradation of this habitat could alter the whole nutrient and detritus chains

4 on which all fish species and the entire ecosystem is based (Vizzini et al., 2002; Vizzini & Mazzola, 2004).

5 Seagrass meadows composed of long- and broad-leaved species are known to provide more substantial and a

6 wider variety of ecosystem services compared with meadows dominated by small species (Nordlund, Koch,

7 Barbier, & Creed, 2016). As the present work highlighted, the long- and broad-leaved *C. nodosa* and *Z. marina*

8 also support greater densities of seagrass specialist syngnathid taxa in the Venice lagoon, in particular in less

9 confined areas subjected to a greater influence of the sea. Managers in Mediterranean coastal lagoons should

10 then regard the reduction of human pressures that lead to the depletion of these meadow typologies as a priority

11 in ecological conservation. Ad hoc measures may include the limitation of direct pressures and impacts, such

12 as anchoring practices or other disturbance that cause the mechanical destruction of meadows, but a more

13 comprehensive coastal planning approach should be followed, in order to prevent alterations to the morphology

14 and hydrodynamics of shallow water areas at the ecosystem scale (McCloskey & Unsworth, 2015).

15 Furthermore, actions aiming at restoring meadow structure and functionality for syngnathids should be

16 promoted in these ecosystems (Scapin et al. 2016). While continuous and well structured meadows (e.g. those

17 successfully restored) are able to support overall greater densities of species such as *N. ophidion* and *H.*

18 *guttulatus*, early restoration stages, which may be characterized by lower seagrass densities, could be more

19 important for species such as *S. abaster* and *S. typhle*, as well as for the overall syngnathid species diversity

20 and evenness, which all appear to be less affected by seagrass percentage cover. This, while highlighting the

21 importance of seagrass population dynamics and diversity for associated fish, also confirms that different levels

22 of seagrass restoration success would determine significant differences in the associated syngnathid

23 assemblages.

24 Syngnathids are usually considered one of the most typical fish groups associated with seagrass meadows, and

25 are subsequently viewed as one of the flagships of this habitat. However, as this study demonstrates, different

26 syngnathid species can coexist in highly heterogeneous ecosystems such as coastal lagoons by selecting

27 different habitats, according to the specific adaptations. In the Venice lagoon shallow waters, of the nine

28 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., 2014,

2017). 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., 2014; 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 the northern part 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 with 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

1   environments have been proven to be important yet poorly known fish habitats elsewhere (Bradley, Baker, &

2   Sheaves, 2016), and in particular for some syngnathids such as the genus *Hippocampus* (Caldwell & Vincent,

3   2012; Curtis & Vincent, 2005; Gristina et al., 2017, 2014).

4   Despite the primary importance of seagrass meadows for syngnathids in Mediterranean coastal lagoon shallow

5   waters, future studies should focus on investigating the attributes of syngnathid assemblages in deeper lagoon

6   areas, in order to understand the habitat characteristics affecting their distribution and provide more

7   comprehensive and effective management tools towards their conservation.

8   Given the strong relationship between *S. typhle* and *N. ophidion* and well structured, mature meadows, they

9   could be considered indicators of the seagrass fish assemblage, as well as the seagrass habitat itself. Hence,

10 the collection of data on population structure of these species should be considered, in order to detect possible

11 impacts on syngnathids population and seagrass fish assemblage more in general, providing insights into the

12 conservation status of Mediterranean coastal lagoons. These surveys could be standardised and incorporated

13 in periodic sampling programmes of fish assemblages, such as surveillance monitoring under the Water

14 Framework Directive (2000/60/EC) and purposely designed surveys under the Habitat Directive (92/43/EEC).

15 Such monitoring protocols based on seagrass indicator species could then be adopted in other transitional water

16 environments in the Mediterranean.

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6. References

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Tables

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3 Table 1: Structure of models used to link syngnathid species and assemblage indicators to temporal factor,

4 environmental factors and habitat characteristics. The stepwise procedure of model fitting is also described. Y_i

5 = response variables; temp. = water temperature; diss.oxy. = water dissolved oxygen; sal. = water salinity;

6 turbid. = water turbidity; depth = water depth; sand% = percent of sand in surface sediments; habitat = main

7 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)

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5 Table 2: AIC values computed on models fitted for syngnathid species and assemblage indicators. Response

6 variable (either density or presence/absence) is also specified for the species. AICs values of best models

7 selected within each model category are underlined, while AICs of the final model formulations are underlined

8 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	2890.98	2837.91	2875.44	<u>2805.87</u>	2723.30	**<u>2712.49</u>**
Syngnathus typhle	density	1929.45	1882.69	1797.19	<u>1754.06</u>	1661.78	**<u>1622.36</u>**
Nerophis ophidion	density	928.41	865.91	810.63	<u>797.20</u>	742.85	**<u>706.72</u>**
Syngnathus taenionotus	presence/absence	456.51	404.15	447.48	**<u>391.30</u>**	390.64	390.44
Syngnathus acus	presence/absence	136.80	136.06	<u>111.81</u>	110.63	**<u>104.07</u>**	104.07
Hippocampus guttulatus	presence/absence	217.13	<u>204.35</u>	213.83	204.35	199.60	**<u>188.92</u>**
Syngnathus tenuirostris	presence/absence	**<u>94.81</u>**	94.81	95.17	95.17	97.40	97.40
Assemblage indicators							
Total density		3447.33	3381.80	3377.85	<u>3318.93</u>	3201.30	**<u>3174.40</u>**
Total number of species		1754.24	1689.59	1688.79	<u>1676.38</u>	1566.62	**<u>1552.01</u>**
Species richness		1157.14	1094.86	1118.80	<u>1082.81</u>	1080.84	**<u>1060.62</u>**
Species diversity		666.51	652.94	<u>636.51</u>	634.61	612.67	**<u>600.50</u>**
Species evenness		708.27	697.60	<u>687.60</u>	686.65	673.17	**<u>656.54</u>**

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