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Identifying key environmental variables of two seahorse species (*Hippocampus guttulatus* and *Hippocampus hippocampus*) in the Ria Formosa lagoon, South Portugal

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Abstract Recent findings reported a significant decrease in abundance of two seahorse species (*Hippocampus guttulatus* and *H. hippocampus*) in the Ria Formosa lagoon (South Portugal) and no direct causes have been, so far, clearly identified. This study aimed to describe fluctuations in the local seahorse populations through monthly surveys over a course of a year, in order to identify some of the potential drivers behind the seasonal fluctuations. A total of six sites were chosen based on their habitat characteristics. The highest *H. guttulatus* abundances were recorded at sites with higher holdfast availability and depth ranging from 3 to 6 m, while *H. hippocampus* were observed at highest numbers in sites with lower holdfast availability and patchy distribution. In most sites, seahorse density decreased during the summer months (from May to August) and increased from August to December. Holdfast use changed across the surveyed sites, according to the respective habitat characteristics. This study identified environmental variables that influenced the abundance of seahorse population, i.e., holdfast availability, depth and temperature in the Ria Formosa lagoon, underlining the importance of monitoring populations over a course of no less than a year in order to avoid bias due to seasonal fluctuations. Identifying critical habitats will provide valuable information for local authorities in order to implement protective measures towards seahorse conservation.

Keywords *Hippocampus guttulatus* · *Hippocampus hippocampus* · Syngnathidae · Long term survey · Population abundance · Seasonal changes

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Introduction

Seahorses have been reported as flagship species for lagoon and estuarine conservation areas (Martin-Smith and Vincent 2005) that are affected by overfishing (either as targeted species or by-catch), degradation and habitat loss (Vincent 1996; Baum et al. 2003; Bell et al. 2003; Martin-Smith and Vincent 2006). Seahorses are globally threatened as they are overexploited to be used in traditional oriental medicine, as curios and as ornamental fish for the aquarium trade (Vincent 1996; Koldewey and Martin-Smith 2010). All *Hippocampus* species were included in the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species in 2004. Of the 38 seahorse species assessed by the IUCN Red List, most are described as Data Deficient (26), while others are considered as Vulnerable (10), Least Concerned (1) and Endangered (1) (IUCN 2014). In recognition of

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the threats faced posed by the global seahorse trade, all species are listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), which was implemented in May 2004. These species' vulnerabilities are mostly due to their sparse distributions, low mobility, small home ranges, low fecundity, lengthy parental care and mate fidelity, which make them vulnerable to overfishing and habitat damage (Foster and Vincent 2004).

Significant declines in the abundance of other seahorse species (e.g., *H. abdominalis* Lesson 1827) have been reported in the absence of fishing pressure through long term monitoring programs (Martin-Smith and Vincent 2005). Environmental variables, natural fluctuations and/or recruitment were suggested as possible causes for that decline. Likewise, other authors have reported fluctuations in the abundance of White's seahorses (*H. whitei* Bleeker, 1855) during the breeding season, suggesting that the search for mates could be the driver for those fluctuations (Harasti et al. 2012), and found a negative correlation between seahorses and their predators (Harasti et al. 2014). Population fluctuations have also been reported and attributed to seahorse movement patterns (Vincent 1994, 1995; Masonjones et al. 2010). Notwithstanding, no data-supported causes were reported for these fluctuations in seahorse abundance.

The Ria Formosa lagoon (South Portugal) is a multi-inlet barrier island system and a highly productive ecosystem sustaining a great variety of commercial species of high economic value (Ribeiro et al. 2006). The use of fishing gear has a direct (by-catch) and indirect (habitat degradation) impact on the local seahorse species (Curtis et al. 2007). In addition, South Portugal is a renowned area for tourism and many human related activities occur in the Ria Formosa, including aquatic sports, boat traffic and boat anchoring. Clam farming is also a common activity in the lagoon and has led to the removal of natural *Zostera noltii* (Hornemann, 1832) seagrass beds (Guimarães et al. 2012). Harbours and coastal development, combined with periodical dredging to open and maintain navigation channels, have also destroyed vast areas of seahorse habitat (Cunha et al. 2013). Overall, along with anthropogenic activities, natural events (e.g. silting events) are known to alter the condition of seahorses' natural habitat and reduce holdfast availability, essential for seahorse settlement (2010; Correia pers. obs.). Inlets influence the water dynamics within the Ria Formosa, shaping channels and creeks. These areas are particularly vulnerable to the occurrence of periods of high energy winter waves, which leads to severe erosion problems, with frequent over-wash of the barrier islands (Martins et al. 1996). Silting events along with sand deposition change water flow, shaping the channels and creeks, and alter the physical conditions of particular areas in the lagoon (Pacheco et al. 2010). In certain areas, these events also contribute to changes in depth and bottom coverage, which can have a direct impact on local fish communities, including seahorses (Correia 2015). This highly dynamic nature of the Ria Formosa lagoon, combined with a temperate climate and variations in seahorse populations reported elsewhere, makes it important to assess whether seasonal events might influence seahorse abundance in certain areas within the lagoon.

The first field studies conducted in the Ria Formosa documented the largest seahorse populations ever recorded globally (Curtis and Vincent 2005). Recent findings, however, have identified a dramatic decrease in abundance of both seahorse species, the long-snout seahorse *H. guttulatus* (94%) and the short-snout seahorse *H. hippocampus* (Linnaeus, 1758) (73%) (Caldwell and Vincent 2012), but no clear causes identified. Nevertheless, changes in habitat, water quality, and population fluctuations linked to species interactions were hypothesized as contributing factors to population declines (Correia et al. 2015a).

Although Caldwell and Vincent (2012) have highlighted overall trends in abundance of *H. guttulatus* and *H. hippocampus*, it is important to understand the reasons for the observed declines. Also, the seahorse population surveys were done from July to November (Curtis and Vincent 2005; Caldwell and Vincent 2012), thus no information was made available on seahorse abundance from January to June and December. Therefore, in order to overcome the existing gaps in seahorse population surveys, this study aimed (1) to describe and quantify the spatial and temporal distribution of *H. guttulatus* and *H. hippocampus* over a one year period, and (2) to identify the environmental variables that might influence their population dynamics.

Material and methods

Species description

The long-snouted seahorse (*H. guttulatus*) and the short-snouted seahorse (*H. hippocampus*) are two species that

occur in the Ria Formosa lagoon (South Portugal). These species have distinctive morphological traits including coronet shape, number of trunk rings and skin colour patterns (Lourie et al. 2004). Although these species have overlapping areas of distribution in the Ria Formosa lagoon, they have distinct habitat preferences, as *H. guttulatus* is generally associated with shallow waters and prefers higher habitat complexity, while *H. hippocampus* favors deeper areas with lower holdfast availability (Curtis and Vincent 2005; Correia et al. 2015a; Gristina et al. 2015; Woodall et al. 2018).

Site description

Spatial and temporal seahorse distributions were assessed using underwater surveys (Correia et al. 2016) carried out in the Ria Formosa lagoon (36°59'N, 7°51'W, Fig. 1). Six locations were chosen based on their different habitat characteristics (Table 1) and were representative of all potential seahorse habitats in the lagoon. These sites were monthly surveyed from January to December 2012.

Underwater visual census

In each sampling occasion, a standardized underwater visual census technique (UVC) was used. At each of the predetermined locations, the UVC protocol consisted of two 30 m transect belts, placed in parallel, 4 m apart. Each diver surveyed each transect belt, first covering the right side and then the left side, with a 2 m range visibility. In this process, each diver covered an area of 120 m^2, with a total combined area of 240 m^2 at each location. In order to minimize observational bias surveys were always performed by the same divers. All surveys were conducted at slack high tide for optimal visibility and diminished tidal currents. This UVC protocol has been proven effective to monitor seahorse populations by Correia et al. (2016). In each survey, seahorses were identified for species, sexed, counted and measured with a ruler (vertical distance from the tip of the coronet to the tip of the outstretched tail), and classified into four different size classes, i.e., 0–5 cm, 5–10 cm, 10–15 cm and 15–20$^+$ cm. These four size classes were chosen to allocate each individual in one of the four age categories considered for *H. guttulatus*: 0 to 2 months (0–5 cm), 2 to 5 months (5–10 cm), 5 to 12 months (10–15 cm) and 12$^+$ months (15 to 20$^+$ cm). For *H. hippocampus*, three size classes were considered due to the maximum size that was recorded for this species (<15 cm). Size classes for both species were based on previous studies (Curtis and Vincent 2005). Seahorses with a full brood pouch were considered as pregnant males and recorded as such. Habitat characteristics, including holdfast availability, depth and water
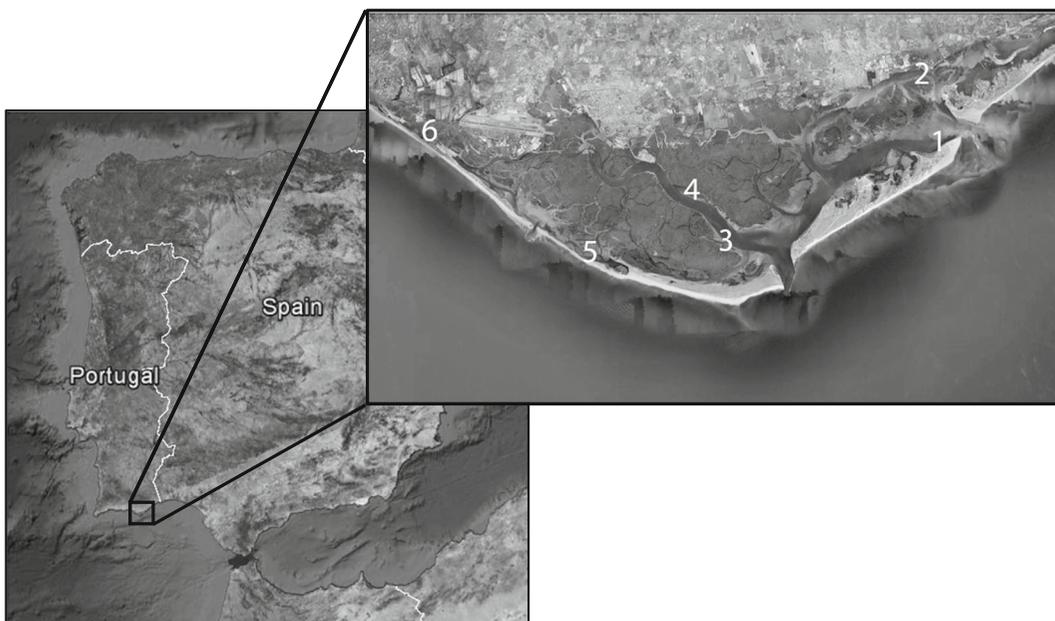

Fig. 1 Sites location in the Ria Formosa lagoon. Site 1 (1), Site 2 (2), Site 3 (3), Site 4 (4), Site 5 (5) and Site 6 (6)

Table 1 Description of each surveyed site regarding depth (meters); hydrodynamics (water flow); substrate type; habitat complexity (holdfast availability) and holdfast distribution

Location	Depth (m)	Hydrodynamics (m.s^{-1})	Substrate	Habitat complexity	Holdfast distribution
Site 1	4–6	Medium (0.3–0.7)	Sand	High	Homogeneous
Site 2	2–5	Medium (0.3–0.7)	Mud	Low	Patchy
Site 3	6–10	High (0.5–1)	Sand	Medium	Patchy
Site 4	3–5	Medium (0.3–0.7)	Mud	High	Homogeneous
Site 5	2–3	Low (0.1–0.5)	Sand/Mud	Medium	Patchy
Site 6	3–4	Low (0.1–0.5)	Sand	High	Homogeneous

temperature were also recorded. Depth and temperature were recorded using a dive computer Suunto® Mosquito (http://www.suunto.com). Holdfast availability was visually estimated within a 1 m^2 area surrounding each sighted seahorse. Holdfasts, i.e., structure that seahorses were grasping when sighted, were included throughout the study and are presented in Table 2.

Habitat complexity was considered low if bottom coverage (i.e., number of holdfasts available) was less than two holdfasts m^{-2}; medium for 2 to 10 holdfasts m^{-2}; and high for more than 10 holdfasts m^{-2}. Holdfast distribution was considered patchy when the distance between holdfasts was greater than a three-meter radius. A GPS unit was used to accurately determine the location of each study area and during site delineation. Some surveys could not be completed due to adverse weather conditions during the winter season: Site 2 was not surveyed in October and November, Site 5 was not surveyed in January, February and September and Site 6 was not surveyed in January and September.

Statistical analysis – Seahorse density and environmental variables

The relationship between the seasonal (monthly) distribution of seahorses' abundance (number per m^2) at six locations (sites 1—6) in the Ria Formosa, and several abiotic predictors (temperature, depth, and %holdfasts) was modelled using generalized additive models (GAM) (Hastie and Tibshirani 1990; Wood and Augustin 2002; Wood 2006).

When using GAM, the relationship between a dependent variable Y and a set of predictor variables X_1, X_2, …, X_p is modelled as

$$Y = \alpha + \sum_{j=1}^{p} f_j(X_j) + \varepsilon$$

where f_j are relatively general (unspecified, possibly nonlinear) functions x_j that can be estimated in a flexible manner, using a scatterplot smoother [herein *spline*

Table 2 Relative abundances (%) of bottom coverage for all sites surveyed

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Pooled
Artificial	0.2	13.0	76.8	0.9	0.8	1.8	18.6
Tunicates	15.6	35.9	–	78.6	21.8	7.6	28.6
Barren	1.1	16.3	3.0	0.9	17.3	4.7	3.8
Bryozoan	–	–	1.5	0.9	0.8	2.9	0.9
Codium	1.7	0.0	4.0	–	15.8	3.5	2.9
Rock	–	–	9.7	0.0	–	0.0	2.2
Polychaete	1.3	10.9	0.0	1.1	3.0	5.3	2.0
Seagrass	–	5.4	–	–	13.5	31.8	4.3
Sea Urchin	0.0	–	0.0	0.5	0.0	0.0	0.1
Shell	78.2	17.4	1.2	17.1	15.0	36.5	33.5
Ulva	1.9	1.1	3.7	0.0	12.0	5.9	2.9

functions, which impose smoothness directly on $f(x)$] and the estimated function $\hat{f}_j(x_j)$ can then reveal possible nonlinearities in the effect of x_j. The model was fitted through R package "mgcv" (Wood 2001) by iteratively smoothing the partial residuals using *spline* functions. Herein, raw data on seahorses' abundance was used as the response variable and a Poisson distribution together with a log link function were used to describe the error structure because it is often appropriate for count data (fish abundance was estimated as numbers per m^2) (Swartzman et al. 1992). Inclusion or deletion of predictor variables obeyed the marginality principle and the effect of adding or removing individual terms from a model was first assessed visually using the model's effects plot and then using sequential analysis of deviance – using the generalized cross-validation criterion, (GCV score; Wood 2006) – and the Akaike's Information Criterion (AIC). The model where residuals sum of squares and AIC are minimized can be selected as the best for the empirical data at hand. Spearman's rank correlation coefficients between observed and predicted values of shad density were used to assess the predictive potential of the models.

The level of significance was set at 0.05 and *p*-values greater than 0.10 were considered as indicative of nonsignificance. All statistical procedures described above were implemented in R (R Core Team 2016).

Results

The data collected during the monthly surveys were used to calculate seahorse abundance (Fig. 2), size class distribution (Fig. 3a, b) and relative holdfast abundance (%).

Seahorse abundance

Overall, a total of 1760 seahorses, of which 1675 were *H. guttulatus* and 85 were *H. hippocampus,* were found at the six sites surveyed. After pooling all sites and all monthly surveys, *H. guttulatus* was 20 times more abundant than *H. hippocampus*. The highest *H. guttulatus* abundances were recorded in November at Site 1 (122 seahorses) and Site 4 (72 seahorses), while *H. hippocampus* were observed in its highest numbers in May at Site 2 (6 seahorses) and in Site 5 (9 seahorses). No *H. hippocampus* were ever observed at Site 6 in all survey events. Pregnant males, both *H. guttulatus* and *H. hippocampus,* were first observed in May, and the young-of-the-year classes were recorded from July onwards at most sites. *H. guttulatus* density ranged from 0.004 (Site 2) to 0.508 seahorse m^{-2} (Site 1) and *H. hippocampus* density ranged from 0 to 0.038 seahorse m^{-2} at Site 5. As for juveniles, a total of 102 *H. guttulatus* and 14 *H. hippocampus* were found
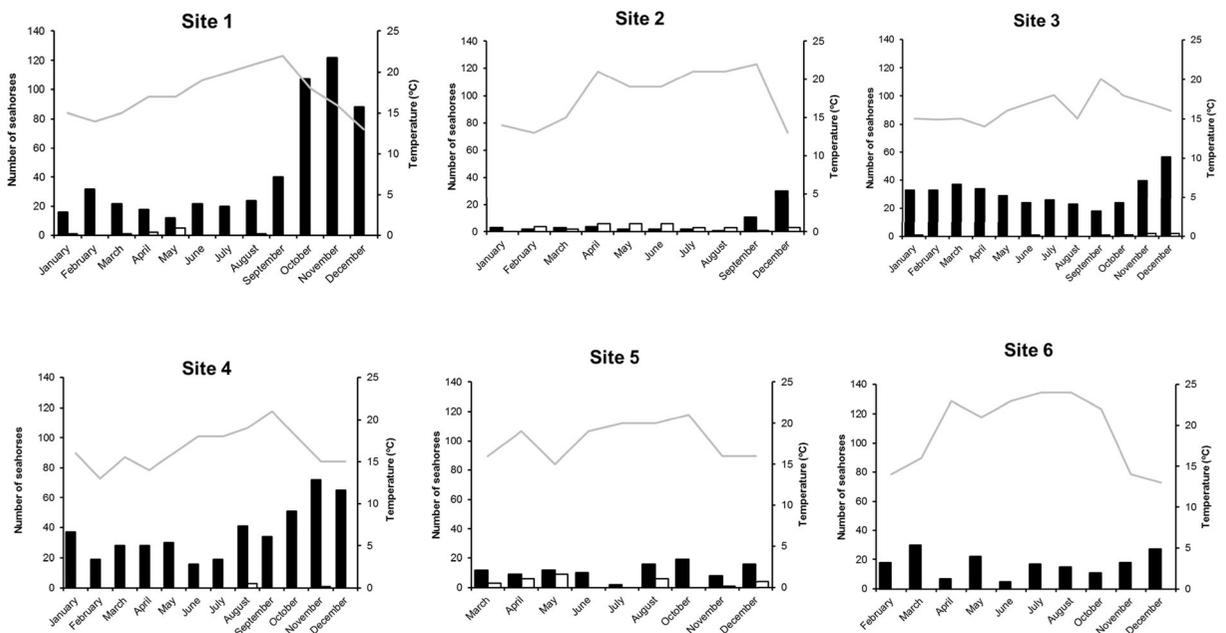

Fig. 2 Seahorse abundance at Site 1, Site 2, Site 3, Site 4, Site 5 and Site 6, for *H. guttulatus* (■) and *H. hippocampus* (□). Temperature (°C) is shown in 2nd axis
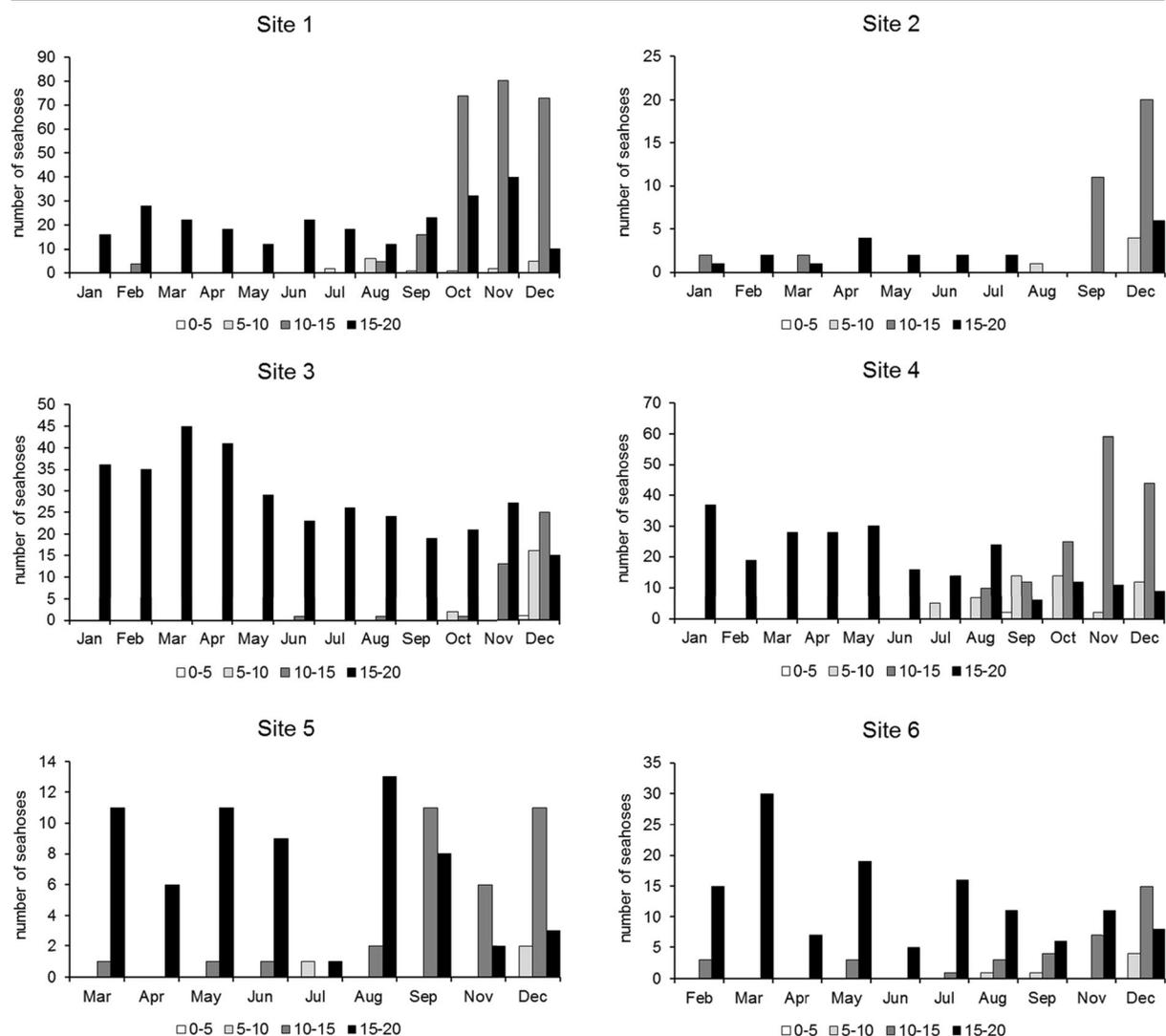
Fig. 3 **a** Number of seahorses per size class (cm) of *H. guttulatus* at different sites in all survey events. **b** Number of seahorses per size class (cm) of *H. hippocampus* at different sites in all survey events

throughout this study (Fig. 3a, b). Pooled average seahorse density was 0.107 and 0.005 seahorse m^{-2} for *H. guttulatus* and *H. hippocampus*, respectively.

Seahorse density and environmental variables

Seahorses were found in 2.0 m to 10.1 m depths at temperatures ranging from 13 °C to 24 °C. In the case of *H. guttulatus* the full GAM, i.e. including all the explanatory variables studied, fitted the data well (adjusted R-squared = 0.939, Deviance explained = 97.5% and AIC = 440.31). There were distinct differences in the seasonal and temporal distributions of specimens of *H. guttulatus* (Fig. 4, upper left

plots). Fish were significantly more abundant between August and December, particularly in Site 3. Water temperature in the range 14–16 °C and depths >5 m favoured the occurrence as did sites with lower % of artificial holdfasts (<20%) but higher % of holdfasts consisting of tunicates and shells (>50%; Fig. 4, lower plots).

The GAM fitted to *H. hippocampus* abundance data included only as significant explanatory variables those related to % holdfasts (adjusted R-squared = 0.352, Deviance explained = 53.7%, and AIC = 207.74). Higher number of fish are expected to be present in sites where the % holdfasts is <20% tunicates, 20–40% artificial and mostly (>90%) shells (Fig. 5).
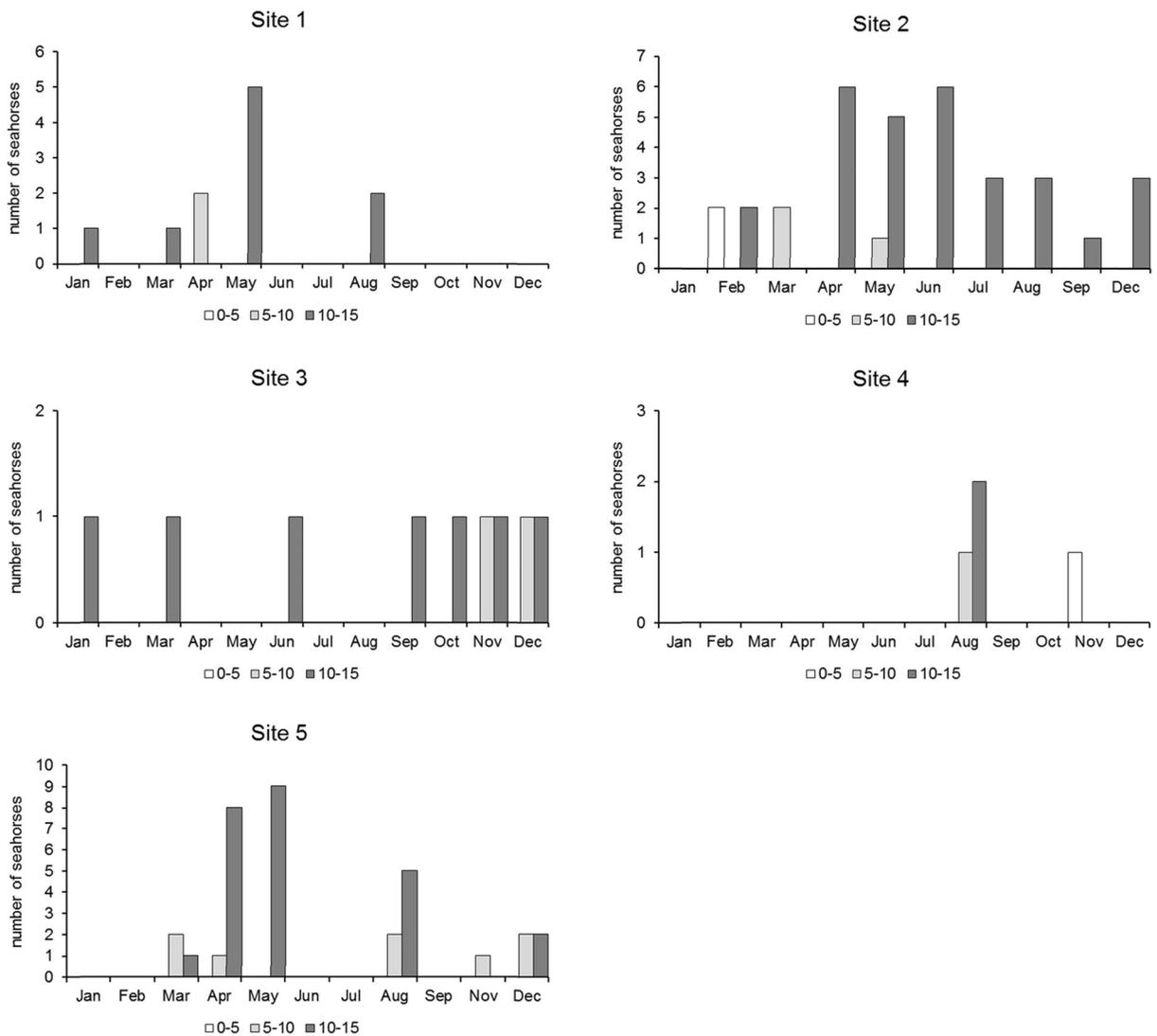
Site 1

Site 2

Site 3

Site 4

Site 5

Fig. 3 (continued)

Seahorses were found grasping a variety of holdfasts in all surveys and their use varied among the different sites surveyed, from shells (Site 1, 5 and 6), tunicates (Site 2, 4 and 5) and seagrass (Site 5 and 6) to artificial structures (Site 3).

Discussion

In this study, the six locations were chosen based on the seahorse abundance reported in previous surveys (Curtis and Vincent 2005; Caldwell and Vincent 2012), so that enough data were made available to track seasonal changes in seahorse abundance. Site selection also included in consideration habitat characteristics and geographical location in order to represent a range of environmental variables that occur in the Ria. As the selected sites are representative of most seahorse habitats, the results can help to understand the potential environmental variables responsible for the fluctuations in seahorse abundance. Previous studies reported mean densities ranging from 0.001 to 0.330 seahorse m^{-2} (Table 3). Considering that this study focused on seasonal dynamics, the sites selected for this study were chosen based on seahorse presence, however, with no minimum threshold of seahorses per site.

H. guttulatus density correlated positively with depth and negatively with temperature. This fact agrees with
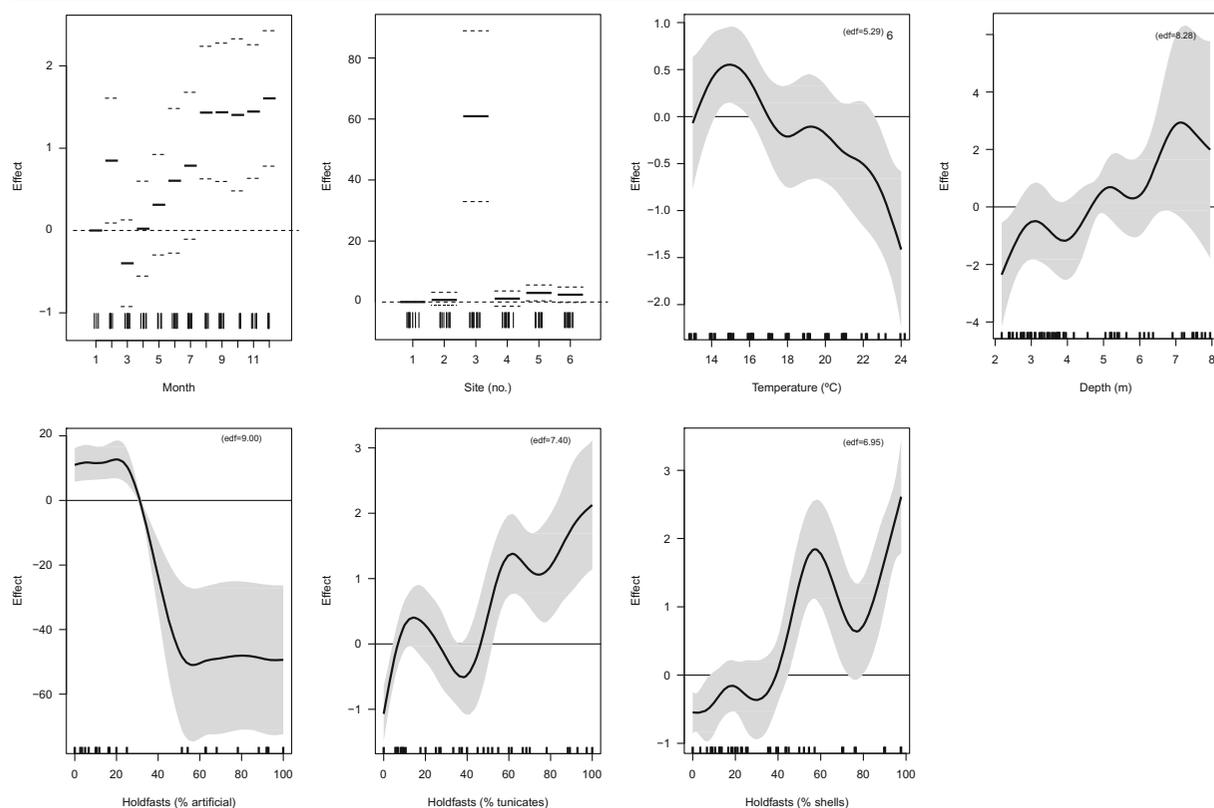
Fig. 4 Results of fitting GAM to the seasonal data on seahorses' *H. guttulatus* abundance. The vertical axis corresponds to predicted values of abundance, centered so that function values add to zero. Positive values denote more specimens than expected from a random distribution. Conversely for negative values. The effect of month and site (as factors) on seahorses' number is represented as a whisker plot. Horizontal lines indicate mean response with 95% confidence intervals. Effects on the number of seahorses are also represented as smoothing functions of temperature, depth and %holdfast (artificial, tunicates and shell). Effects are standardized because the estimated abundance at a given value of a variable is dependent upon levels of all other variable. The grey areas are approximate 95% pointwise confidence intervals. The estimated degrees of freedom (edf) for the model parameters are the numbers at top-right of each plot and approximate the complexity of the curve (a polynomial regression of degrees = edf-1), i.e. express the smoothness of function. The tick marks (rugs) close to the x-axis show the location of the observations on that variable

the findings of Caldwell and Vincent (2012). During the surveys, depth ranged from 2 to 10 m and higher *H. guttulatus* abundances were registered in the range of 4 to 6 m depth. Moreover, areas of just 2 m depth at high tide can be considered as intertidal zones and therefore unsuitable for seahorse settlement. The negative correlation found between temperature and *H. guttulatus* might reflect a seasonal pattern. In fact, in the summer months there was an overall decrease in seahorse density, when the temperature tend to be higher. Temperature was higher overall at Site 6, probably due to a combined factor of low depth and low water flow. Although this site has high holdfast availability, which should favor *H. guttulatus* abundance (Correia 2015), the temperature might be the driver for seahorse paucity.

H. guttulatus abundance decreased during May to July and then increased from August to December, particularly in Sites 1, 3 and 4, where highest densities were observed. This decrease in abundance occurred during the species' breeding season, when *H. guttulatus* pregnant males were observed (from May to late August, which agrees with Lourie et al. (2004)). According to Woodall et al. (2011), *H. guttulatus* is a serial monogamous species, which might suggest that the search for mates could be the driver for this decrease. In fact, *H. guttulatus* has a reported home range of 20 m^2 (Curtis and Vincent 2006) but they have been observed travelling longer distances (Caldwell and Vincent 2013) perhaps due to environmental factors, reproductive behaviour or unsuitable habitat. The young-of-the-year classes were
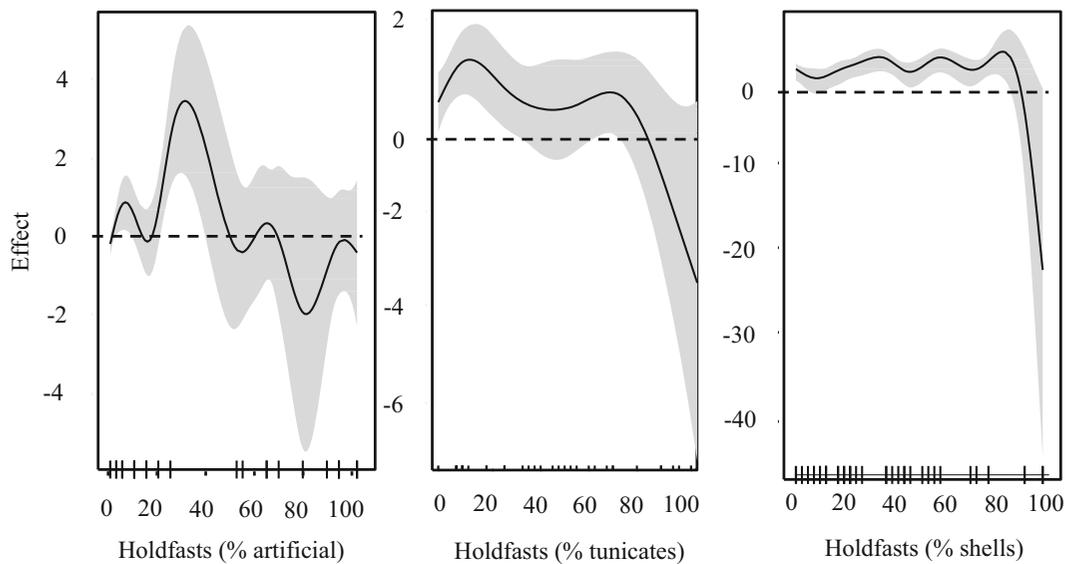
Fig. 5 Results of fitting GAM to the seasonal data on seahorses' *H. hippocampus* abundance

observed from July onwards which suggests a new recruitment to those areas, contributing to the increase in seahorse abundance. Following the same pattern as the adults, the younger *H. guttulatus* seem to recruit not only to areas with higher habitat complexity, but also to locations where the species is more abundant.

In this study, Site 5 (located next to the Ancão's inlet) is more vulnerable to silting events. During January and February, winter storms were responsible for physical changes in the area, creating a sediment inflow that lead to a decrease in the local water currents. This reduction in water flow promoted a progressive sand deposition,

with a direct impact on the seagrass bed coverage. Roughly 17% of the seahorses found at Site 5 were located in barren areas, i.e., not grasping to any holdfast. This percentage may be due to diminished holdfast availability and low current which collectively may have forced seahorse to move in search of nearby holdfasts.

The GAM highlighted the optimal environmental variables, and particularly habitat choice for each species, considering the monthly data collected. *H. guttulatus* seemed to prefer areas with higher percentage of holdfast consisting of tunicates and shells,

Table 3 Seahorse species densities in previous studies

Species	Density (seahorse.m^{-2})	Location	Year	Author(s)
Hippocampus abdominalis	0.010	Derwent estuary, Australia	2001–2014	(Martin-Smith and Vincent 2005)
Hippocampus reidi	0.026	Brazil	2002–2006	(Rosa et al. 2007)
Hippocampus reidi	0.180	Ilha Grande, Brazil	2002–2004	(Freret-Meurer and Andreata 2008)
Hippocampus zosterae	0.080	Tampa Bay, USA	2005–2007	(Masonjones et al. 2010)
Hippocampus capensis	0.330	Knysna Estuary, South Africa	2001	(Teske et al. 2007)
Hippocampus guttulatus	0.018	Mar Piccolo di Taranto, Italy	2011	(Gristina et al. 2015)
Hippocampus guttulatus	0.073	Ria Formosa, Portugal	2001–2002	(Curtis and Vincent 2005)
Hippocampus guttulatus	0.004	Ria Formosa, Portugal	2008–2009	(Caldwell and Vincent 2012)
Hippocampus guttulatus	0.107	Ria Formosa, Portugal	2012	Current study
Hippocampus hippocampus	0.007	Ria Formosa, Portugal	2001–2002	(Curtis and Vincent 2005)
Hippocampus hippocampus	0.001	Ria Formosa, Portugal	2008–2009	(Caldwell and Vincent 2012)
Hippocampus hippocampus	0.005	Ria Formosa, Portugal	2012	Current study

whereas *H. hippocampus* prefers areas with higher percentage of shells. This information is not in line with what was reported by Curtis and Vincent (2005), which suggested a strong influence of seagrass as the main habitat for seahorses in the Ria Formosa. Although seahorses are known as limited swimmers and sedentary fish, they can adapt to progressive habitat changes by moving to more suitable areas (Masonjones et al. 2010). Nevertheless, this dispersal might fragment local populations and have a direct impact on relative reproductive success, therefore affecting that year's recruitment, and ultimately, overall seahorse abundance. Habitat changes have been reported in the Ria Formosa, where seagrass beds have been declining in the past 20 years, with 75% reduction in the distribution of *Zostera noltii* (Cunha et al. 2014). Moreover, the distribution of seagrass beds has been reported to migrate in response to natural and human-induced activities (Cunha et al. 2005). Considering that seahorses have been reported to favor seagrass as preferred habitat (Curtis and Vincent 2005), this decrease in seagrass abundance should have a negative impact on seahorse populations, particularly for *H. guttulatus* (Ribeiro et al. 2006). In face of seagrass depletion, seahorses might occupy alternative habitats facing a consequent population dispersal (Correia et al. 2015b). It is therefore likely that local seahorse populations had to adapt to these habitat changes, opting for an alternative habitat which eventually became their first choice, and it is a clear indication of seahorse plasticity to habitat changes.

The highest *H. guttulatus* density (0.51 seahorse m^{-2}) was reported in November 2012 at Site 1. This density was similar to the highest density reported in 2002 by Curtis and Vincent (2005). Nevertheless, lower seahorse densities were observed at the same site in different months (0.05 seahorse m^{-2} in May 2012). This fact highlights the importance of an extended surveying effort to avoid bias due to seasonal fluctuations in the local seahorse population densities. Other factors such as water current and holdfast distribution might influence the distribution of the seahorses in an area. Thus, higher water flows might promote seahorse holdfast grasping for longer periods, whereas slower water current situations might allow seahorses to move and eventually to disperse. These are important aspects to consider when doing a seahorse population census in a particular area.

In conclusion, this study showed that highly dynamic areas are more prone to physical habitat changes that lead to benthic species abundance shifts. The seagrass

declines over the last decades has led to a significant reduction in the available seahorse habitats. Seahorses have showed resilience and adaptability to these adverse conditions by changing their habitat choice. Habitat availability is a key factor with direct influence on seahorse abundance, therefore the implementations of protective measures (e.g. Marine Protected Areas) is of paramount importance to maintain healthy habitats and high standard biodiversity.

Compliance with ethical standards

Ethical compliance All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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

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