

Distribution of sympatric seahorse species along a gradient of habitat complexity in a seagrass-dominated community

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ABSTRACT: We present estimates of local population abundance, distribution and habitat preference for 2 European seahorse species, *Hippocampus guttulatus* and *H. hippocampus*. We predicted that these sympatric species would partition their habitat into 2 broadly defined habitat types: complex vegetated habitats and sparsely vegetated sand flats. We sampled populations using underwater visual census techniques over landscape (100s to 1000s m) and microhabitat scales (<1 m). Over landscape scales, we estimated abundance and quantified habitat associations using generalized linear models. Over microhabitat scales, we tested for holdfast (attachment site) preferences using selection indices. Both species were patchy in distribution, but *H. guttulatus* mean density (0.073 ind. m⁻²) was one order of magnitude greater than that of *H. hippocampus* (0.007 ind. m⁻²). At a landscape scale, *H. guttulatus* abundance was positively correlated with an index of habitat complexity, the percentage of substrate covered by flora and sessile fauna. Conversely, *H. hippocampus* used more open and less speciose habitats that were subjected to greater oceanic influences. At microhabitat scales, both species significantly preferred grasping holdfasts over barren surfaces, but the species differed in holdfast preferences: *H. guttulatus* grasped all prospective holdfast types with equal probability while *H. hippocampus* significantly avoided both fauna and flora that formed large colonies or tracts of dense vegetation. Patterns in habitat use were consistent with differences in morphology and foraging strategy. Despite similar life histories, these sympatric species may respond differently to disturbances that modify habitat structure and complexity over landscape or microhabitat scales.

KEY WORDS: Habitat selection · Habitat complexity · *Hippocampus* · Syngnathidae · Habitat suitability models · Underwater visual census · Foraging strategy

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INTRODUCTION

Seagrasses are productive, biogenic habitats (Pollard 1984, Sheperd et al. 1989, Short & Wyllie-Escheverria 1996) that usually support a greater abundance and diversity of fishes than surrounding unvegetated habitats (Heck et al. 1989, Edgar & Shaw 1995, Jenkins et al. 1997). This pattern has been attributed to lower predation risk (Choat 1982, Orth et al. 1984, Hindell et al. 2000), greater food availability (Edgar 1990), increased sediment stability, and refuge from hydrodynamic forces within seagrasses (Lewis 1984, Dean & Connell

1987). While hydrodynamic processes influence recruitment patterns (Jenkins et al. 1997, Stoner 2003), many marine species actively select seagrass beds over unvegetated habitats, as well as microhabitats of different complexities within seagrasses (Bell & Westoby 1986b, Edgar 1990). Higher densities inside versus outside seagrass beds were noted for many species in the family Syngnathidae (seahorses, pipefishes, pipehorses and seadragons) (Teixeira & Musick 1995, Diaz-Ruiz et al. 2000, Kendrick & Hyndes 2003).

As heterogeneous habitats that vary in the degree of structural complexity and exposure to tidal regimes

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(Bell & Westoby 1986a,b, Hovel et al. 2002), seagrasses provide opportunities for sympatric species to partition their habitat over multiple spatial scales. The effects of habitat structure and complexity on the diversity and abundance of seagrass-associated species are well documented (e.g. Lewis 1984, Bell & Westoby 1986a,b, Dean & Connell 1987, Heck et al. 1989, Edgar 1990, Hovel et al. 2002, Hyndes et al. 2003). However, few studies have contrasted the effects of seagrass bed structural complexity on the habitat partitioning of closely related species with similar life histories.

Within the Syngnathidae, sympatric species of pipefish partition habitat both within and among seagrass beds according to their morphology, mobility, foraging technique and prey use (Howard & Koehn 1985, Kendrick & Hyndes 2003). Seagrass-dwelling syngnathids are generally cryptic and sedentary, and either occupy the canopy or reside at the sediment-water interface (Bell & Westoby 1986a, Teixeira & Musick 1995). Howard & Koehn (1985) showed that less mobile syngnathid species (inferred from prehensile tails) consumed mainly planktonic prey and may have relied more on dense macrophyte canopies, while more mobile species (inferred from well developed caudal fins) consumed both planktonic and epibenthic prey and likely used a wider range of microhabitats including bare substrate.

Seahorse species (genus *Hippocampus*) in temperate regions are typically associated with seagrass habitats (Foster & Vincent 2004). Seagrasses allow for crypsis, provide holdfasts (attachment sites for prehensile tails) and harbour abundant food for syngnathids, such as small crustaceans (Howard & Koehn 1985, Tipton & Bell 1988, Foster & Vincent 2004). However, anecdotal observations suggest that some species also exploit bare substrates: *Hippocampus abdominalis*, *H. capensis*, *H. guttulatus*, *H. hippocampus* and *H. kuda* have been encountered on open tracts of sand and/or distant from potential holdfasts (Bell et al. 2003, Garrick-Maidment & Jones 2004, S. Lourie pers. comm., K. Martin-Smith pers. comm.). Laboratory experiments also show that seahorses employ different foraging strategies in vegetated and unvegetated habitats (James & Heck 1994). Thus, some seahorse species may use barren surfaces as well as more complex vegetation.

Hippocampus guttulatus (Cuvier 1829) and *H. hippocampus* L. appear to partition their habitat over both landscape and microhabitat scales (Boisseau 1967, Lythgoe & Lythgoe 1971, Whitehead et al. 1986, Reina-Hervás 1989). Both species occur in the northeastern Atlantic Ocean and Mediterranean Sea (Boisseau 1967, Whitehead et al. 1986, Reina-Hervás 1989, Lourie et al. 1999). While *H. guttulatus* is usually reported from seagrass beds, *H. hippocampus* is re-

ported from soft bottoms among rocks and algae. *Hippocampus guttulatus* tends to be dark green or brown in colouration and commonly bears skin filaments, suggesting that this species employs vegetated microhabitats. Conversely, *H. hippocampus* is variable in colouration with fewer or no skin filaments, suggesting that this species relies less on flora or filamentous structures for crypsis. Recreational diver surveys support these inferences (Garrick-Maidment & Jones 2004). However, no previous studies have examined the extent to which local abundances of these sympatric species can be predicted by habitat structure.

Our study examined the distribution and abundance of *Hippocampus guttulatus* and *H. hippocampus* in a coastal lagoon along a habitat gradient from sheltered seagrass and macroalgae to largely unvegetated sand flats exposed to increased tidal flow and water depth. Despite conservation concern (Santos et al. 1995, Foster & Vincent 2004, IUCN 2004), this is one of few ecological studies of either *H. guttulatus* or *H. hippocampus*. Our objectives were to (1) estimate local population abundances, (2) quantify differences in habitat preference over landscape and microhabitat scales and (3) identify components of habitat structure for predicting local abundances. Given the biological characteristics of the study species, we predicted that *H. guttulatus* uses vegetated areas, while *H. hippocampus* uses more open sandy habitats over landscape scales. We further predicted that within these 2 broadly defined habitat types, both species would prefer microhabitats with potential holdfasts. We expected that habitat partitioning over both landscape and microhabitat scales would reflect interspecific differences in morphology and foraging strategy. We evaluated these predictions through a multi-scale sampling program covering the lagoon system.

MATERIALS AND METHODS

Species descriptions. We adopted the taxonomy of the genus *Hippocampus* as outlined in Lourie et al. (1999), recognizing that *H. guttulatus* was historically synonymized with *H. ramulosus* (Leach 1814). Further research is required to clarify whether *H. ramulosus* represents a different species (Lourie et al. 1999). *Hippocampus guttulatus* and *H. hippocampus* are readily distinguished *in situ* by differences in head, snout and trunk shape (Lourie et al. 1999).

Measuring seahorses precisely is challenging because of the curvature of the trunk and tail and because the head is held at an angle to the trunk. We used the measurement protocol outlined in Lourie et al. (1999) with one important distinction: we measured lengths as straight lines between the appropriate reference

points, with the head held at a right angle to the body. All measurements reported in our paper are standard lengths, except where stated otherwise.

Published details about the life histories of *Hippocampus guttulatus* and *H. hippocampus* are sparse (Boisseau 1967, Foster & Vincent 2004). In our study, adult *H. guttulatus* ranged in size from 108 to 210 mm ($n = 384$). *H. hippocampus* was on average ~40% smaller, with adults ranging from 87 to 146 mm ($n = 41$). Juveniles of both species were planktonic (Boisseau 1967, Pérez-Ruzafa et al. 2004). The smallest settled *H. guttulatus* and *H. hippocampus* encountered in this study were 65 mm and 62 mm, respectively.

Site description. We carried out our study in the western and central parts of the Ria Formosa lagoon (36°59'N, 7°51'W), in southern Portugal (Fig. 1). The Ria Formosa is a productive coastal lagoon (Sprung 1994a) characterized by high water turnover rates, sand flats, salt marshes and a network of channels and tidal creeks (Sprung 1994a, Machás & Santos 1999, Newton & Mudge 2003). From July 2001 to September 2002, water temperature varied seasonally from 10 to 28°C. Salinity ranged very little (36 to 38 ppt) among our sampling sites, but had declined occasionally to 33 ppt in the Ria Formosa during previous winters (Monteiro 1989). Water is exchanged with the open ocean through 6 tidal inlets, 2 of which have been dredged. Tides are semidiurnal and mean depth varies from 2 to 3 m, but can be as great as 15 m in the main Faro-Olhão channel (between Sites 11 and 22, Fig. 1). Total lagoon area is ~170 km² (Machás & Santos 1999) with an estimated subtidal area of 26.7 km² (A. Rodrigues de Matos, Parque Natural da Ria Formosa, pers. comm.).

Underwater visual census. We surveyed 32 sites (Fig. 1) using SCUBA: 16 sites were surveyed from 13 August to 19 September 2001 and 16 were surveyed from 14 June to 22 August 2002. In 2001, coincident

with another study (Erzini et al. 2002), sites were selected along a gradient of ocean influence. To verify 2001 results, sites were selected in 2002 from throughout the subtidal area. We did not stratify random sampling by habitat type (e.g. seagrass, macroalgae, sand flat) in either year because the distribution of vegetation had not been mapped at the time of our study and we could not discern habitat type from the surface because of low water clarity (usually <1 m). Some parts (~20%) of the subtidal area were not accessible because of sand bars, strong currents (e.g. near inlets) or high volumes of boat traffic, therefore sites were surveyed as close to the pre-selected coordinates as possible. Surveys were carried out using standard underwater visual census (UVC) techniques (Samoilys 1997). Three randomly placed 2 m × 30 m belt transects, placed >5 m apart, were surveyed per site (total surveyed area = 5760 m²). Data were averaged among transects within sites. All sites were >100 m apart.

Fish counts and observations. The species, sex, trunk length, life history stage (juvenile, adult), holdfast, appearance (colouration, presence of skin filaments) and behaviour were recorded for all seahorses encountered on transects. We used trunk lengths (cleithral ring to the last trunk ring) to measure live seahorses *in situ* because the precision was greater than when measuring standard length (tip of the snout to the cleithral ring, and from the cleithral ring to the tip of the straightened tail), as the tail did not need to be straightened. Trunk lengths were converted to standard lengths using regression equations developed for both species (Table 1). *Hippocampus guttulatus* and *H. hippocampus* were considered subadults if they were <50% size at maturity, corresponding to 109 mm and 78 mm SL, respectively (Curtis 2004). In order to characterize interspecific differences in activity patterns associated with habitat use, behaviour was noted upon detection

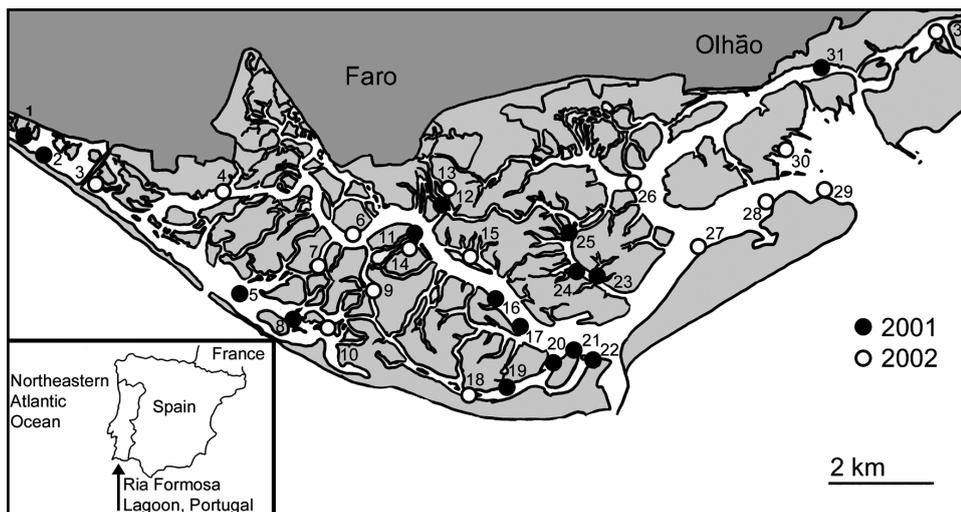


Fig. 1. Western and central part of the Ria Formosa lagoon in southern Portugal (inset). Solid (2001) and open (2002) circles correspond to the location of 32 underwater visual census (UVC) sites (site numbers given)

Table 1. *Hippocampus guttulatus* and *H. hippocampus*. Regression equations for predicting standard length (SL) from trunk length (TrL) for males (m) and females (f) (Curtis 2004)

Species	Sex	Equation	n	r ²	p-value
<i>H. guttulatus</i>	m	$\log\text{TrL} = -0.325 + 0.872 \times \log\text{SL}$	703	0.86	<0.0001
	f	$\log\text{TrL} = -0.474 + 0.950 \times \log\text{SL}$	637	0.85	<0.0001
<i>H. hippocampus</i>	m	$\log\text{TrL} = -0.232 + 0.811 \times \log\text{SL}$	56	0.90	<0.0001
	f	$\log\text{TrL} = -0.593 + 1.008 \times \log\text{SL}$	47	0.92	<0.0001

and was classified into 4 categories: (1) stationary, (2) swimming, (3) ambush predation, when individuals were observed rapidly flicking their heads and sucking from the plankton while in a stationary position, and (4) active foraging, when individuals were observed feeding from the plankton, sediments or vegetation while actively searching for prey.

Few individuals (<1%) swam away from observers during UVCs; therefore surveys were not time constrained. Using the same experienced observer (J.M.R.C.) for all UVCs further reduced observer bias. Population sizes were estimated by extrapolating mean densities to the subtidal area. Confidence intervals (95% CI) were estimated by bootstrapping the density estimates (Efron & Tibshirani 1993).

Benthic community and habitat characteristics. The abundance of conspicuous (>2.5 cm in height, length or width) seagrasses, macroalgae, invertebrates (sessile and relatively immobile) and artificial structures was estimated as percent cover, defined here as the percentage of the seafloor that was overlaid by a given habitat component. Percent cover was quantified using three 30 m line intercepts (line-intercept method, Samoilys 1997) per site (averaged within sites). These line intercepts corresponded to the same transects used during fish counts. Microhabitat patch sizes (e.g. bryozoan colonies, tufts of macroalgae) were estimated by measuring the length of the transect line that covered patches. The mean density of seagrass short shoots and mean leaf height were estimated using 5 randomly placed quadrats of 0.01 m² per transect searched. The presence of mobile benthic invertebrates (e.g. *Aplysia* spp., *Sepia officinalis*) and fishes (e.g. *Halobatrachus didactylus*) was recorded to estimate total species richness (flora and fauna) at each site. Two composite variables were also considered: (1) an index of habitat complexity, C_t/A_t (Bartholomew et al. 2000), which corresponded to the area surveyed within a site (A_t) that was covered by vegetation or sessile invertebrates (C_t), and (2), M_t/A_t , which denotes the proportion of A_t that was covered by all species of macroalgae (M_t).

Depth was measured at the beginning and end of each transect and averaged within sites (all UVCs

were carried out within 2 h of low tide). Distances to the nearest tidal inlet were estimated planimetrically. Substrate particle size structure was characterized by fractionating 3 randomly placed sediment cores (0.02 m diameter \times 0.01 m depth) per site into 4 size classes (<110 μm , 110–1000 μm , 1000–1800 μm and >1800 μm), drying them to constant weight, and estimating percent composition by weight.

Potential covariates were recorded and included date, tidal and lunar phases, start time, horizontal visibility, current strength and prevailing weather conditions (wind strength and % cloud cover).

Landscape level habitat use. The abundance of *Hippocampus guttulatus* approximated a Poisson distribution and we assumed the same for *H. hippocampus*. The landscape level relationships between seahorse counts and habitat variables were therefore characterized using generalized linear models (GLMs), assuming a Poisson distribution (McCullagh & Nelder 1989) with a log link function. Prior to model selection, the data from both years were summarized in Spearman rank correlation matrices to identify collinear variables as well as suites of variables that were broadly correlated with seahorse abundance. Poisson regressions were carried out for both species in 2001, but only for *H. guttulatus* in 2002, when few *H. hippocampus* were observed. To evaluate the predictive accuracy of our GLMs, we compared the densities of *H. guttulatus* observed in 2002 to expected values based on the 2001 GLM for *H. guttulatus*. We used a jackknife resampling procedure to test whether the correlation coefficient between observed and expected values differed significantly from unity (Manly 1997). In all cases, model selection was carried out using both forward and backward selection, which produced the same results. Variables were retained in the model if p-values associated with type III Wald tests were <0.05. Final regression models are reported. Data were examined for sex- and stage-specific differences in habitat associations.

Microhabitat and holdfast preferences. Habitat preference is a measure of the strength of selection of one habitat component over others (Johnson 1980). The standardized selection index (Krebs 1999) was used to test whether *Hippocampus guttulatus* and *H. hippocampus* preferred using microhabitats that offered potential holdfasts (covered substrate) to using bare surfaces. The selection index was estimated as $U_t/(C_t/A_t)$, where U_t was the proportion of individuals grasping a holdfast. A selection index >0.5 indicated relative preference for covered substrate, while a selection index <0.5 indicated a relative pref-

erence for bare substrate (Krebs 1999). Rank preference indices (Johnson 1980, Krebs 1999) for using different microhabitats as holdfasts were calculated using PREFER 5.1 (Pankratz 1994). Data were examined for sex and stage-specific differences in microhabitat preferences.

Table 2. *Hippocampus guttulatus* and *H. hippocampus*. Indices of abundance. Occupancy (%) refers to the percentage of sites where a species was detected and n denotes number of individuals encountered during UVCs (CI = bootstrap-estimated confidence limit)

Abundance index	<i>H. guttulatus</i>			<i>H. hippocampus</i>		
	2001	2002	Pooled years	2001	2002	Pooled years
Total n	168	216	384	39	2	41
Juveniles n	26	22	48	1	0	1
% Occupancy	87.5	93.8	90.6	62.5	12.5	37.5
Max. density (m ⁻²)	0.27	0.51	0.51	0.072	0.008	0.072
Mean density (m ⁻²)	0.060	0.085	0.073	0.013	0.001	0.007
Lower 95% CI			0.039			0.003
Upper 95% CI			0.110			0.014
Population size			1895 700			186 900
Lower 95% CI			1 041 300			80 100
Upper 95% CI			3 043 800			373 800

RESULTS

Seahorse abundance and distribution

Pooling across years and sites, *Hippocampus guttulatus* was 10 times more abundant than *H. hippocampus* and occupied more than twice the number of survey sites (Table 2). *Hippocampus guttulatus* was encountered at all but 3 of the 32 UVC sites. By contrast, *H. hippocampus* occurred primarily in large channels that were influenced by water flowing through tidal inlets (Fig. 2a).

Site characteristics

Survey sites were located from 1.0 to 6.9 km from the open Atlantic Ocean in 0.25 to 6.75 m of water depth. Horizontal visibility ranged from 0.3 to 6.0 m. Approximately 70% of the total surveyed area (all sites pooled) was bare substrate (fine sand, coarse sand or shell fragments). Of the total area that was covered, 58.6% was seagrass, 20.8% was macroalgae and 17.8% was invertebrates (Table 3). Fourteen sites were on sand flats, 7 sites were dominated by the seagrass *Cymodocea nodosa*, 4 sites were dominated by a mixture of *C. nodosa* and macroalgae (mostly *Ulva lactuca* and *Codium* spp.) and 7 sites were dominated by a mixture of macroalgae and colonies of benthic invertebrates (mostly the bryozoan *Zoobotryon verticillatum*) interspersed with sand flats (Fig. 2b). Where seagrass (*C. nodosa*) was present, mean leaf height ranged from 11.1 to 34.2 cm and mean short shoot density ranged from 233.3 to 848.3 shoots m⁻².

Landscape level habitat use

Hippocampus guttulatus and *H. hippocampus* were broadly associated with different suites of variables (Table 4). After applying a sequential Bonferroni correction to adjust p-values for multiple correlations, the only significant correlation was be-

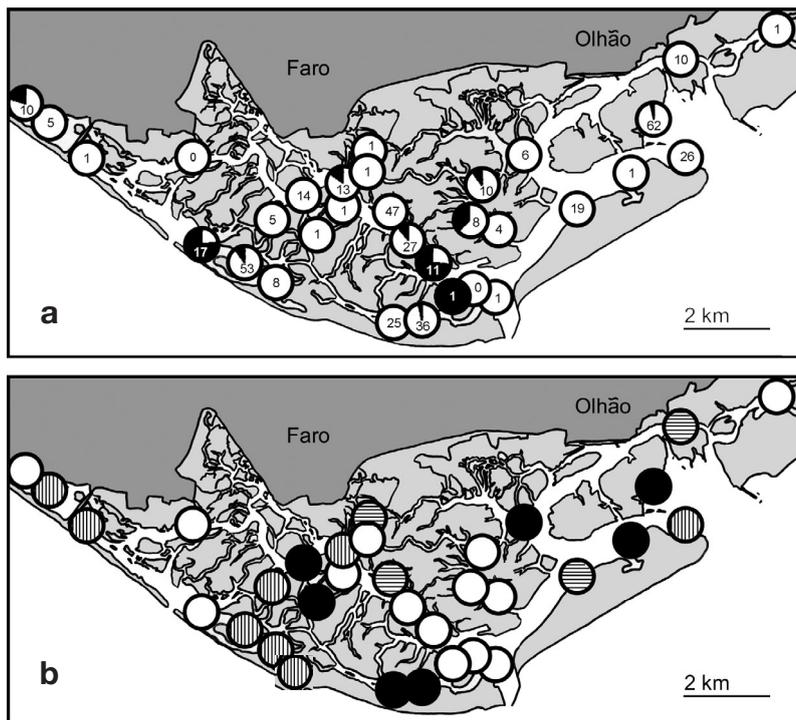


Fig. 2. (a) Relative frequencies of *Hippocampus guttulatus* (white) and *H. hippocampus* (black) at each site. The total number of seahorses encountered per site is given. (b) The dominant habitat type at 32 UVC sites: sand flats (O), seagrass beds (●), mixed seagrass and macroalgae (⊙) and mixed macroalgae and sessile invertebrates interspersed with bare sand (⊖)

tween *H. guttulatus* density and the % cover of *Ulva lactuca*. However, by examining the direction of the correlations, the correlation matrix suggested that *H. guttulatus* density was greater at sites with greater habitat complexity (i.e. sites with greater seagrass shoot density, vegetation cover and sessile inverte-

Table 3. Primary producers and benthic invertebrates encountered during underwater visual censuses in the Ria Formosa lagoon. Relative abundances (%) are a percentage of the total surveyed area (32 sites pooled) that was covered by benthic flora and fauna. Only taxonomic groups covering >1% of the pooled transects are reported

Habitat component	Dominant species	%
Seagrasses	<i>Cymodocea nodosa</i>	54.2
	<i>Zostera noltii</i>	4.4
Macroalgae	<i>Chaetomorpha</i> sp.	1.43
	<i>Chondrus crispus</i>	1.09
	<i>Codium</i> spp.	2.24
	<i>Dictyopterus</i> sp.	1.29
	<i>Dictyota dichotoma</i>	1.19
	<i>Ulva lactuca</i>	9.03
	<i>Ulva rigida</i>	2.43
Bryozoans	<i>Zoobotryon verticillatum</i>	8.4
	<i>Bugula neritina</i>	1.61
Tunicates (<i>Ciona intestinalis</i> , <i>Clavelina lepadiformis</i> , <i>Phallusia mammillata</i> , <i>Styela plicata</i>)		3.77
Tube-dwelling polychaetes	<i>Sabella</i> spp.	2.9
Sea urchins	<i>Paracentrotus lividus</i>	1.12
Total		95.1

Table 4. Non-parametric Spearman rank correlations (r_s) between habitat variables and seahorse density (data pooled across all sites). Included are habitat variables that were most highly correlated ($r_s > 0.3$, $p < 0.1$) with at least one of the species (other variables are not shown). *Significant after applying a sequential Bonferroni correction to adjust p-values for the multiple tests in this table

Habitat variable	<i>Hippocampus guttulatus</i>		<i>Hippocampus hippocampus</i>	
	r_s	p	r_s	p
% <i>Cymodocea nodosa</i>	0.406	0.021	0.196	0.282
<i>C. nodosa</i> shoot density	0.408	0.100	-0.197	0.305
% <i>Ulva lactuca</i>	0.557*	0.001	-0.059	0.750
% Anemone	-0.334	0.064	-0.193	0.289
M_t/A_t	0.438	0.012	0.233	0.199
C_t/A_t	0.512	0.003	-0.263	0.145
Species richness	0.220	0.226	-0.386	0.029
% Sand	-0.249	0.169	0.333	0.063
% Shell fragments	-0.433	0.013	0.142	0.437
Horizontal visibility	-0.162	0.376	0.373	0.035
Water temperature	-0.264	0.144	-0.372	0.036
Depth	0.195	0.284	0.423	0.002
Current strength	0.164	0.379	0.542	0.002
Latitude	-0.110	0.556	-0.304	0.096
Lunar phase	-0.011	0.952	0.321	0.074

brates), and thus less abundant at sites with lower habitat complexity (i.e. sites with a greater amount of bare sand and shell fragments). Conversely, *H. hippocampus* was generally more abundant in sites that had low habitat complexity (i.e. less speciose sites with a greater amount of bare sand). *H. hippocampus* density was also greater in sites with stronger oceanic influences, reflected in positive correlations with horizontal visibility, depth and current strength, and a negative correlation with water temperature.

In the GLMs, C_t/A_t was the most significant predictor of *Hippocampus guttulatus* abundance in both years, but M_t/A_t was also retained in the 2001 model and % *Ulva lactuca* was retained in the 2002 model (Fig. 3a, Table 5). There was a significant correlation between the observed and expected *H. guttulatus* densities for 2002 ($r = 0.471$, $p = 0.033$), but the correlation was significantly less than unity (jackknifed $r = 0.488$, $SE = 0.203$, $t = 2.52$, $p < 0.02$), meaning that the predicted values were significantly greater than densities

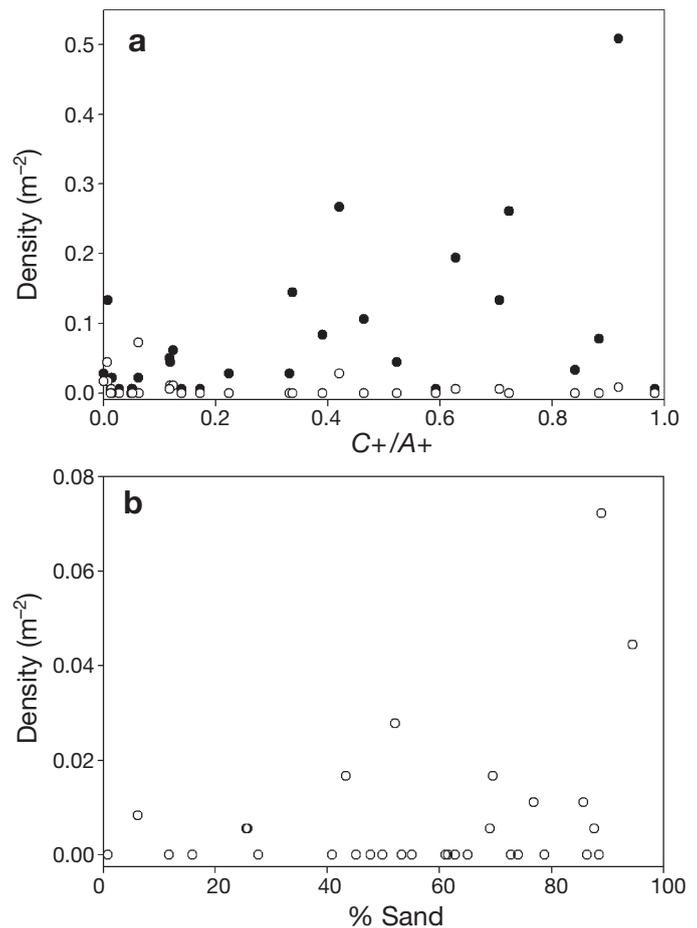


Fig. 3. (a) Density of *Hippocampus guttulatus* (●) and *H. hippocampus* (○) plotted against C_t/A_t (see text for details). (b) *Hippocampus hippocampus* density plotted against % sand

Table 5. Significant explanatory variables retained in generalized linear models for *Hippocampus guttulatus* and *H. hippocampus* density. Regression coefficients (Coeff), corresponding standard errors (SE) and p-values (p) are given

Species (year)	Variable(s)	Coeff	SE	p
<i>H. guttulatus</i> (2001)	% covered substrate	3.10	1.00	0.002
	% macroalgae	3.37	1.66	0.042
<i>H. guttulatus</i> (2002)	% covered substrate	2.17	0.96	0.023
	% <i>Ulva lactuca</i>	7.69	2.94	0.009
<i>H. hippocampus</i> (2001)	% sand	25.22	0.00	<0.0001

observed in 2002. The density of *H. hippocampus* was significantly explained by (and positively associated with) % bare sand in 2001 (Fig. 3b, Table 5). Within years, qualitatively results were robust to the exclusion of the 2 sites that supported the highest densities of *H. guttulatus* and *H. hippocampus*, respectively, and robust to the exclusion of sites with densities of zero. There were no significant correlations or significant interactions among variables retained in the regression models (even when no sequential Bonferroni corrections were used to adjust critical p-values).

Microhabitat and holdfast preferences

Despite differences in habitat use over landscape scales, both species significantly preferred covered substrate to bare surfaces at microhabitat scales. Approximately 89% of all seahorses employed holdfasts such as seagrass blades, macroalgae, tunicates, bryozoans, polychaete tubes, sea urchins, and artificial structures (e.g. ropes, nets, bricks). The selection index for covered substrate was >0.5 for *Hippocampus*

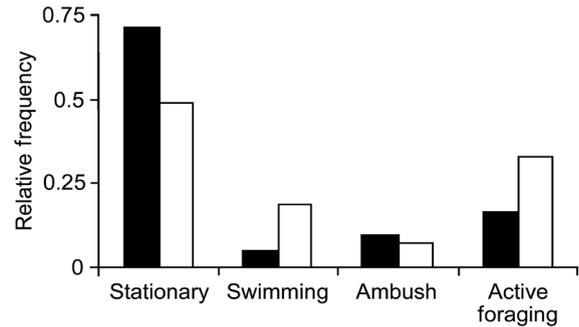


Fig. 5. Relative frequency of *Hippocampus guttulatus* (black bars, $n = 382$) and *H. hippocampus* (white bars, $n = 41$) individuals observed stationary, swimming, using ambush predation techniques or actively foraging

guttulatus at all occupied sites (mean SI = 0.87 ± 0.25 SD, Fig. 4a) and >0.5 for *H. hippocampus* at 80% of occupied sites (mean SI = 0.82 ± 0.36 SD, Fig. 4b). *H. guttulatus* did not exhibit a preference for any holdfast type ($F_{19,18} = 1.16$, $W = 3.13$, $K = 100$, all pairwise comparisons <3.13). Conversely, *H. hippocampus* significantly preferred grasping artificial structures, the small tuft-forming bryozoan *Bugula neritina*, sea urchins, and small or tuft-forming macroalgae (e.g. *Colpomenia sinuosa*, *Dictyota dichotoma*, *Padina pavonia* and *Ulva rigida*) to the abundant bryozoan *Zoobotryon verticillatum*, which generally formed large colonies (mean \pm SD patch length = 1.25 ± 1.32 m, $n = 50$). *H. hippocampus* also significantly preferred using small or tuft-forming macroalgae to colonial ascidians, and to seagrasses (patch length = 5.03 ± 4.09 m, $n = 22$) and *Ulva lactuca* (patch length = 1.12 ± 1.28 m, $n = 47$), which generally formed large tracts of densely vegetated substrates.

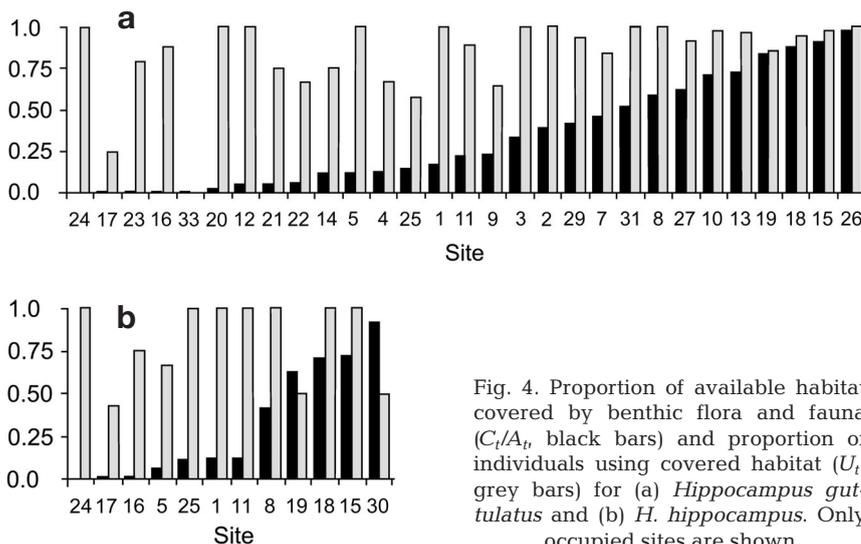


Fig. 4. Proportion of available habitat covered by benthic flora and fauna (C_t/A_t , black bars) and proportion of individuals using covered habitat (U_t , grey bars) for (a) *Hippocampus guttulatus* and (b) *H. hippocampus*. Only occupied sites are shown

Morphology and foraging strategies

The 2 seahorse species differed significantly in their appearance and foraging strategies. Colouration varied both within and between species (Fisher Exact test, $p < 0.0001$): *Hippocampus guttulatus* primarily occurred in shades of brown (69.0%) and green (28.7%) and *H. hippocampus* occurred in shades of mottled brown (61.6%), yellow (26.3%), maroon (7.9%) and rust (4%). A greater percentage (70.3%) of *H. guttulatus* bore skin filaments on their heads and trunks than *H. hippocampus* (36.0%; $\chi^2 = 48.28$, $p < 0.001$). The 2 species also differed in mobility and predation technique (Fig. 5). *H.*

hippocampus swam significantly more frequently than *H. guttulatus*, which tended to sway passively with the currents while grasping holdfasts ($\chi^2 = 33.24$, $p < 0.001$). *H. hippocampus* was also more active when feeding; a greater proportion was observed actively foraging for planktonic and epibenthic prey than *H. guttulatus* ($\chi^2 = 3.24$, $p = 0.072$). We found no evidence of sex- or stage-specific differences in habitat associations, holdfast preferences, appearance or foraging technique within species.

DISCUSSION

Temperate seagrass communities support diverse and abundant populations of syngnathids (Pollard 1984, Howard & Koehn 1985, Hindell et al. 2000, Hyndes et al. 2003), which generally prefer complex vegetated habitats to unvegetated habitats (Howard & Koehn 1985, Flynn & Ritz 1999, Kendrick & Hyndes 2003). Our study revealed that 2 sympatric seahorse species, *Hippocampus guttulatus* and *H. hippocampus*, with similar life histories (reviewed in Foster & Vincent 2004) differed markedly in their habitat use over multiple spatial scales and along a gradient of habitat complexity: one species was positively associated with habitat cover at both landscape and microhabitat scales, whereas the other species used more open and less speciose habitats at the landscape scale despite preferring covered microhabitats. As predicted, habitat associations over both spatial scales were linked to differences in morphology (size, colouration, presence of skin filaments), activity and foraging strategy.

Abundance

The density of *Hippocampus guttulatus* was one order of magnitude greater than mean densities observed in similar transect surveys of *H. abdominalis* in Australia (K. Martin-Smith pers. comm.), *H. capensis* in South Africa (Bell et al. 2003) and *H. comes* and *H. barbouri* in the Philippines (A. Maypa pers. comm.). High seahorse abundance in the Ria Formosa may be attributable to high local productivity (Sprung 1994a) and plankton biomass (Sprung 1994b). In some aquatic ecosystems, fish biomass responds positively to increases in primary production (Garg & Bhatnagar 2000). Seahorses, which prey primarily on small vagile crustaceans (Howard & Koehn 1985, James & Heck 1994), may be less prone to food limitation in growth and reproduction in productive habitats such as the Ria Formosa than in less productive coastal habitats. However, mechanisms underlying differences in abundance between *H. guttulatus* and *H. hippocampus*

within the Ria Formosa require further study. Our sampling constraints may have caused us to miss areas of high *H. hippocampus* abundance, which appeared to be linked with greater depths and stronger currents (see below).

Landscape level habitat associations

The amount of total habitat covered by vegetation and sessile invertebrates, C_t/A_t , appeared to influence the distribution and abundance of *Hippocampus guttulatus*. This is consistent with the distributions of many marine organisms, which are positively correlated with the amount of habitat structure (Heck et al. 1989, Kendrick & Hyndes 2003), drift algae (Kulczycki et al. 1981) or seagrass (Kupschus 2003). Although the predation efficiency of predators typically decreases in more complex habitats (Choat 1982), increased habitat complexity either had no impact on (James & Heck 1994) or increased (Flynn & Ritz 1999) the predation efficiency of syngnathids practicing ambush predation. By contrast, *H. hippocampus* exploited sparsely vegetated sand flats, which were less speciose and subject to stronger oceanic influences. The 3 sparsely covered sites where *H. hippocampus* outnumbered its congener (5, 17 and 20) were located close to tidal inlets where horizontal visibility, current strength and depth—all positively correlated with *H. hippocampus* abundance—were the greatest. *H. hippocampus* also outnumbered *H. guttulatus* in more open and exposed coastal habitats near Barcelona (sand flat) and Malaga (seagrass bed), in Spain (J.M.R.C. pers. obs.), but were not reported from seahorse samples collected from a coastal lagoon in the Mediterranean Sea (Pérez-Ruzafa et al. 2004).

Fish distribution and abundance are often predicted by multiple habitat variables including salinity and temperature (e.g. Brown et al. 2000, Kupschus 2003). Despite having quantified 60 habitat variables, the GLMs retained only 1 or 2 explanatory variables that were related to the extent of local habitat complexity. This may reflect (1) low variance in other important ecological variables within the Ria Formosa lagoon (e.g. salinity; Monteiro 1989), (2) the influence of additional ecological processes (e.g. predation, hydrodynamic processes, recruitment dynamics) on local patterns of abundance (Choat 1982, Orth et al. 1984, Hindell et al. 2000, Hovel et al. 2002, Stoner 2003), (3) low power to detect weakly correlated variables, or (4) the potential influence of unmeasured habitat variables (e.g. size of seagrass beds, distance between suitable habitat patches). Examining patterns of abundance and habitat use over regional spatial scales may reveal other variables for predicting seahorse distribution and abundance, including salinity and water temperature.

Microhabitat and holdfast preference

Both European seahorse species preferred using covered microhabitats as holdfasts to using bare substrate, although *Hippocampus hippocampus* was observed more frequently on bare surfaces than *H. guttulatus*. Our results were consistent with an experimental study showing that captive *H. abdominalis* preferred using artificial seagrass microhabitats to bare substrate (Flynn & Ritz 1999). The use of holdfasts with prehensile tails likely helps these relatively poor swimmers to stabilize themselves in strong currents. Seahorses encountered on bare substrate (e.g. *H. capensis*, *H. guttulatus*, *H. hippocampus*, *H. kuda* and *H. abdominalis*) may be temporarily exploiting open habitats, be in transit between covered microhabitats or have been displaced from their home ranges by strong wave action during storms (as inferred for *H. breviceps* in Moreau & Vincent 2004).

Although both *Hippocampus guttulatus* and *H. hippocampus* in this study used prehensile tails to grasp structures, they differed significantly in the types of holdfasts they preferred, as reflected by interspecific differences in appearance. Syngnathids mimic vegetation in color, shape and behaviour (Howard & Koehn 1985, Kendrick & Hyndes 2003), which likely reduces their visibility to both predators and prey. The skin filaments and predominantly brown and green colouration of *H. guttulatus*, a holdfast generalist, was consistent with its use of seagrasses, macroalgae and colonial invertebrates (e.g. *Zoobotryon verticillatum*) for camouflage. The colour patterning of *H. hippocampus*, a holdfast specialist, was similar in colour to sand, shell fragments and some sessile invertebrates. This colouration was consistent with *H. hippocampus* being less reliant on vegetation for camouflage than *H. guttulatus*.

Interspecific differences in habitat preferences between *Hippocampus guttulatus* and *H. hippocampus* were also linked to differences in foraging strategy and prey use. *H. guttulatus* was relatively sedentary and ambushed planktonic prey more frequently than its more active congener. *H. hippocampus* swam more often and actively foraged for both planktonic and epibenthic prey. Differences in activity and foraging strategy between these 2 species were consistent with a study in which *H. erectus* adopted different prey capture techniques in complex and bare habitats: *H. erectus* tended to ambush prey in artificial seagrass habitats and actively forage for prey while on bare substrates (James & Heck 1994). These results were also consistent with observations of 4 sympatric pipefishes within a seagrass bed: less mobile species consumed mainly planktonic prey and were associated with dense macrophytes, while more mobile species

consumed both planktonic and epibenthic prey and probably used a variety of habitats, including bare substrate (Howard & Koehn 1985). Differences in microhabitat use and behaviour coupled with size-selective prey use resulted in little diet overlap among pipefishes during most of the year.

Implications for conservation

While our results suggest that the 2 European seahorse species may respond differently to an overall reduction in seagrass cover, both species would likely be affected by a loss of holdfasts, and reductions in exported drift (Melville & Connolly 2003, Vanderklift & Jacoby 2003). Habitat loss has been linked to the extirpation of several marine fish populations (Wolff 2000, Dulvy et al. 2003) and is assumed to threaten populations of temperate seahorses including *Hippocampus hippocampus* (Santos et al. 1995, Musick et al. 2000, Pogonoski et al. 2002, IUCN 2003). Moreover, syngnathids are incidentally captured in non-selective, bottom-dragged fishing gears, especially trawls (Vincent 1996), which may also reduce habitat structure (Watling & Norse 1998, Turner et al. 1999) and holdfast availability.

Seagrasses are threatened marine habitats (Shepherd et al. 1989, Short & Wyllie-Escheverria 1996) and have declined along some European coasts (Pasqualini et al. 1999, Wolff 2000). Excessive seagrass damage within the Ria Formosa and in other parts of the North Atlantic Ocean or Mediterranean Sea could result in a reduction of *Hippocampus guttulatus* habitat, and hence local population sizes. Although *H. hippocampus* does not rely on seagrasses per se for refuge or camouflage, its response is difficult to predict. This is because the implications of seagrass loss reach beyond the physical provisioning of refuge and camouflage for both predators and prey: the production of many marine fishes stems from detritus exported from seagrass beds (Melville & Connolly 2003).

Because fisheries-independent data are often scant and costly to obtain, the development of habitat suitability models for predicting species distributions and responses to environmental change is appealing (Brown et al. 2000, Kupschus 2003). Our preliminary models were strengthened by qualitative concordance between GLMs for *Hippocampus guttulatus* from 2 sequential years: C_t/A_t was included in GLMs from both years and densities observed in 2002 were significantly correlated with predicted values. The index of habitat complexity, C_t/A_t , may thus be useful in a habitat suitability model for predicting the relative abundance of *H. guttulatus* in similar areas that have not yet been surveyed. Recently, habitat use models extra-

polated to broader spatial and temporal scales successfully predicted the relative abundances of several marine fishes (e.g. Brown et al. 2000, Kupschus 2003). However, our results also underscore the importance of examining habitat associations over multiple spatial scales as habitat preferences are not necessarily consistent over a range of spatial scales.

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