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When natural history collections reveal secrets on data deficient threatened species: Atlantic seahorses as a case study

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Abstract Natural history collections from museums and private institutions can play an important role supporting decisions in biodiversity conservation. Seahorse populations have suffered a worldwide decline, while many areas remain data deficient including areas subjected to heavy commercial trading, such as the coasts of West Africa. In this work, seahorse collections from museums and public institutions in Macaronesia (Azores, Madeira and the Canary Islands) were initially reviewed (1) to identify specimens not previously determined, and (2) to correct species determinations from Macaronesia and adjacent West African coasts. The morphological data (3) were tested for phenotypic variation of seahorses within and between Macaronesia and adjacent West African coasts. The presence of *Hippocampus hippocampus* (short-snouted seahorse) and *Hippocampus algiricus* (West African seahorse) was confirmed for the area, including new sightings

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along previous geographical distribution ranges. Morphological analyses partitioned sea-horse species and several morphotypes within and between Macaronesia and adjacent West African coasts. This phenotypic plasticity was associated with cranial morphology. Such differences are a useful tool for tracking seahorse populations of varying species and origins. New information presented here, is valuable for improving the management and conservation of seahorses, particularly in areas threatened by illegal trading or other anthropogenic activities.

Keywords Atlantic Ocean · Biodiversity conservation · *Hippocampus* · Phenotypic plasticity · Preserved specimens · Polymorphisms

Introduction

Seahorses (Fishes: *Syngnathidae*: *Hippocampus*) are widely distributed, colonizing a large range of marine habitats, e.g. rocky and coral reefs, seagrass meadows, and supporting sudden changes of environmental conditions (e.g. hydrodynamics, food availability or salinity) (Foster and Vincent 2004). Marine organisms have developed morphological adaptive responses to varying biotic and/or abiotic conditions. Despite this, phenotypic plasticity has been documented in marine organisms, from algae to vertebrates (Smith and Palmer 1994; Padilla 1998; Baldridge and Smith 2008; Abaad et al. 2016), but whether is common for seahorses remains elusive.

Seahorse populations have suffered a worldwide decline in the last decades (Vincent et al. 2011; Foster et al. 2016). Seahorse life traits (i.e. low population densities, parental care, low fecundity and small home ranges) promote their vulnerability to overexploitation (Foster and Vincent 2004; Foster et al. 2016). In fact, millions of animals are traded worldwide, dried for traditional medicine, and collected for the ornamental aquarium industry (Koldewey and Martin-Smith 2010; Vincent et al. 2011). The Convention on International Trade of Endangered Species of wild fauna and flora (CITES) included seahorses in the Appendix II to regulate their international trade. The CITES database is useful as a conservation tool to redefine species quotas, capture minimum sizes, or even to infer population dynamics (Foster et al. 2016). However, this database has problems with species identification and their taxonomy, including misidentifications; there is an urgent need to obtain accurate biological information. Despite these efforts, some seahorse species are heavily exploited and their populations are threatened near extinction (Foster et al. 2016).

In the Macaronesian ecoregion (Azores, Madeira and Canary Islands), within the Lusitanian Province, and the adjacent West African coasts, two species of seahorses have been catalogued. The information about these species is scarce and comes mainly from reports and checklists from the last 30 years. The long-snouted seahorse *Hippocampus guttulatus* Cuvier 1829 (also recorded as *Hippocampus ramulosus*) and the short-snouted seahorse *Hippocampus hippocampus* (Linnaeus 1758) have been regarded as originating from the Azores; however, nowadays the presence of both species at this archipelago is considered rare (Santos et al. 1997; Woodall et al. 2009; Afonso et al. 2013). Moreover, one specimen of the lined seahorse, *Hippocampus erectus* (Perry 1810), was caught in the Azores Bank; representing the first record of this species in the central and eastern Atlantic and denoting its northernmost distribution limit (Woodall et al. 2009). Observations in the

wild and preserved collection specimens of *H. hippocampus* at Madeira Island confirm its presence around this archipelago (Wirtz et al. 2008). The presence of *Hippocampus ramulosus*, reported from Madeira in some manuscripts, has not been verified (Dawson 1986, 1990). In the Canary Islands, *H. hippocampus* seahorses have also been recorded (Otero-Ferrer 2012).

Wirtz et al. (2013) reported on the presence of the West African seahorse *Hippocampus algiricus* Kaup 1856 in the Cape Verde Islands. This species is distributed from Senegal to Angola, including the Cape Verde archipelago and possibly Saint Helena (Afonso et al. 1999; Wirtz et al. 2007, 2014; Lourie et al. 2016).

Despite significant decreases of wild stocks at certain locations through Macaronesia and adjacent regions (Otero-Ferrer et al. 2015b) data are still insufficient to assess their risk of extinction. *H. algiricus* and *H. hippocampus* dominate catches by artisanal fleets in West Africa. Both species appear mixed in Asian markets, reflecting a growing commercial interest for this African region (Kaczynski and Looney 2000; Woodall et al. 2011; Cisneros-Montemayor et al. 2015). West Africa populations of both species have been severely depleted, with more than 700,000 specimens traded each year; this is one of the most relevant seahorse trading industry worldwide (Cisneros-Montemayor et al. 2015; Foster et al. 2016). For these species, taxonomic collections are a potentially important tool for assessing the extent of past species distributions, and therefore to inform and redefine potential conservation strategies (Newbold 2010).

Natural history collections from museums and private institutions have been shown to play an important role supporting decisions in the conservation of a range of species (McCarthy 1998; Ponder et al. 2001). These collection specimens can provide a view into the past, for example, by using samples to follow temporal changes in pollutants (e.g. mercury contamination) through marine food chains (Monteiro and Furness 1997), or providing data for estimating genetic diversity, and changes in population size and connectivity (Wandeler et al. 2007). In particular, historical records can be compared with present-day information to detect changes in the distribution of species; this may help us to understand how species have responded to environmental changes (Shaffer et al. 1998; Tingley and Beissinger 2009; Newbold 2010).

In this work, seahorse collections from museums and public institutions in Macaronesia were reviewed (1) to identify specimens not previously determined, and (2) to correct species determinations, if pertinent. Morphological data were then obtained (3) to test for phenotypic variation of seahorses within and between Macaronesia and adjacent West African coasts. This data fill gaps on their distribution and allows identification of polymorphisms (phenotypic plasticity); such information is valuable to define conservation strategies.

Methods

Biological sampling

Seventy-eight dried seahorse specimens, collected between 1953 and 2013, from collections at museums and universities throughout Macaronesia were identified, including: 'Universidad de Las Palmas de Gran Canaria' (ULPGC, Spain), 'Museo de Ciencias Naturales de Tenerife' (TFMC, Spain), 'Instituto Español de Oceanografía' at Tenerife (IEO, Spain), 'Museu Municipal do Funchal' (MMF, Madeira, Portugal) and 'Universidade dos Açores' (UAç, Azores, Portugal). Sixty individuals were collected throughout the

entire Macaronesia, but also from adjacent West African regions, such as Cape Verde archipelago, Western Sahara, Senegal, Guinea Bissau and Liberia. Among them, forty individuals were originally determined as *H. hippocampus*, *H. ramulosus* or *H. algiricus*, whereas 20 were unidentified. A set of 18 specimens from the collections at ULPGC and TFMC, retrieved in the early 1980s, had no data about their origin or species identification (Appendix 1).

Morphological analysis and species identification

To identify seahorse species, 14 morphometric and 3 meristic variables (Lourie 2003; Otero-Ferrer et al. 2015a) were taken from each individual, with the exception of 4 specimens (from the MMF collection) that were partially damaged and, therefore, excluded. One individual missed parts of the body, while the other three had been recovered from stomach contents; one from a small-tooth sand tiger shark *Odontaspis ferox* (Risso 1810) in 2001, and the two others from loggerhead sea turtles, *Caretta caretta* (Linnaeus 1758) in 1999. Morphological variables included were: standard length (SL), defined as the sum of the head (HL), trunk (TrL) and tail length (TaL); length of pectoral (PL) and dorsal (DL) fin base; trunk depth between the 4th and 5th (TD4) and the 9th and 10th (TD9) trunk rings; and snout depth (SnD). In addition, snout length (SnL), head depth (HD), orbital diameter (OD), post-orbital length (PO) and coronet height (CH) were selected as proportions of the HL. Regarding meristic variables, counts included the number of tail rings (TaR), and dorsal (DF) and pectoral (PF) fin rays. All morphometric and meristic descriptors were obtained following Lourie (2003), using manual callipers and a binocular microscope (Leica M-125, Wetzlar, Germany). If necessary, counts were verified from X-ray radiographs.

Species identification was based on morphological attributes following Lourie et al. (2004). To verify species identification, a Canonical Analysis of Principal coordinates (CAP, Anderson and Willis 2003) was performed, as a constrained ordination method to visualize differences among species (Tuya and Haroun 2009). CAP found axes in the multivariate space to maximize the separation among seahorse species. The analysis was based on a Euclidean distance matrix from a morphological dataset matrix; the 'trace statistic' was used to test (via 9999 permutations of the data) the significance of differences among species. The CAP routine also estimated miscalculation errors for species identifications using the 'Leave-one-out Allocation success' (LoA): each specimen was removed from the dataset, the CAP analysis re-run using the remaining observations, and then the removed individual classified to the nearest group centroid (i.e. species) in the canonical space (Anderson and Willis 2003). Pairwise comparisons between each pair of species were carried out through one-way ANOSIM, using 999 permutations, via calculation of the R statistic.

Phenotypic variation

The CAP and one-way ANOSIM routines were used to visualize and test for phenotypic variability of both *H. hippocampus* and *H. algiricus* between individuals collected from the Macaronesia and adjacent African coasts (Fig. 1). Euclidean distances were calculated from standardized and square root transformed data. A similar routine was carried out to test for phenotypic variation of *H. hippocampus* among Macaronesian archipelagos. The Similarity Percentages breakdown procedure (SIMPER, Clarke, 1993) partitioned the contribution of morphological and meristic variables to dissimilarities among species and
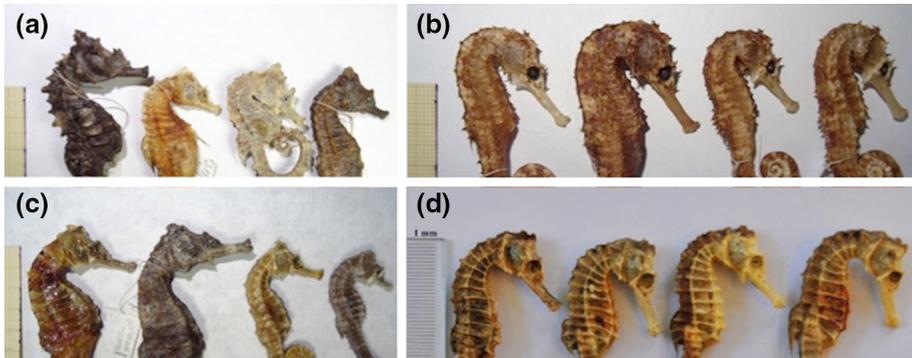
Fig. 1 Head ant trunk morphology of seahorse species: **a** *Hippocampus hippocampus*, **b** *H. comes*, **c** *H. algiricus*, and **d** *H. trimaculatus*

regional morphotypes. All multivariate analyses were computed using the PRIMER-E 6.0 package (Clarke and Warwick 2001).

Results

Species identification

From the 40 previously identified specimens, only one was incorrectly determined (as *H. ramulosus* instead of *H. hippocampus*). Among the 20 unidentified specimens whose locations were known, 18 individuals collected from Gran Canaria (Canary Islands), Liberia and São Miguel (Azores) were identified as *H. hippocampus*. The remaining two specimens collected off the Western Sahara were identified as *H. algiricus*. All collected *H. hippocampus* and *H. algiricus* specimens belonged to various zones across Macaronesia and West African coasts (Appendix 1). Of the 18 unidentified specimens whose locations were unknown, 9 animals from the ULPGC collection showed low coronets with five distinct rounded points, double cheek spines and long slender snouts, matching the description of the tiger tail seahorse, *H. comes* Cantor, 1850 (Lourie et al. 2004) (Fig. 1). The other 9 from the MCNT showed the main morphological attributes of the three-spot seahorse *H. trimaculatus* Leach, 1814, including low coronets and narrow heads, but with the distinctive dark spots in their necks (Lourie et al. 2004) (Fig. 1).

The CAP ordination efficiently separated specimens of the four seahorse species along the first and second canonical axis (Fig. 2, $\delta^2 = 0.964$, $p < 0.001$); all species significantly differed from a morphological perspective (Table 1, $p < 0.001$ in all cases). The main morphological variables contributing to the separation of the two West African native species (*H. hippocampus* and *H. algiricus*) were skull-related variables (>80% of dissimilarities, Table 2), including: pectoral fin rays, HL:SnL, CH:HL, SnD:SnL, HD:HL, OD:HL, PO:HL, HL:SL, PL:SL. The number of pectoral fin rays and the snout related variables (SnL and SnD) accounted for >61% of dissimilarities between species (Table 2). *H. hippocampus* showed a lower number of pectoral fin rays, and shorter and wider snouts compared to *H. algiricus* (Fig. 1).
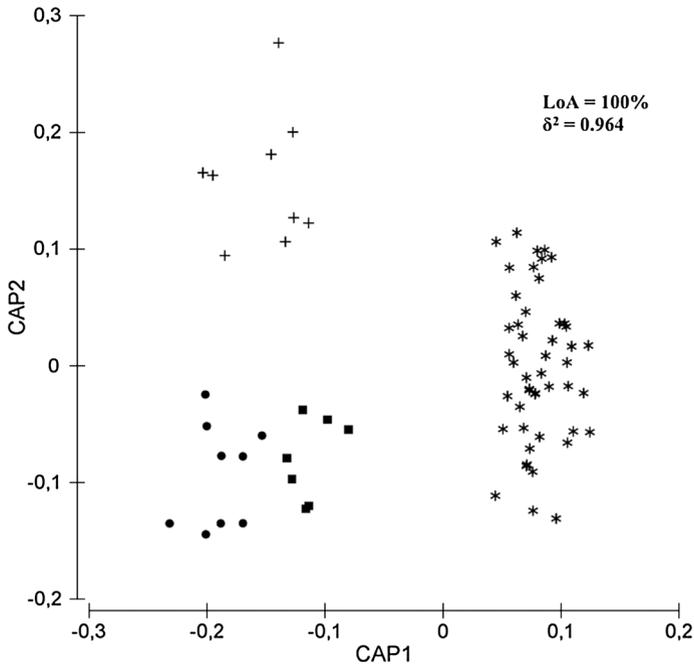
Fig. 2 Constrained canonical ordination plot (CAP) of seahorse species throughout Macaronesia: *Hippocampus algiricus* (*filled square*), *H. comes* (*filled circle*), *H. hippocampus* (*asterisk*), and *H. trimaculatus* (*plus symbol*). The 'Leave-one-out Allocation' success is indicated (LoA, i.e. indicates the percentage of samples correctly allocated to each group). δ^2 square canonical correlation with CAP-I

Table 1 Pairwise comparisons of morphometric variation between seahorse species (R statistic from ANOSIM)

	H. algiricus	*H. hippocampus*	*H. trimaculatus*
H. algiricus			
H. hippocampus	0.967*		
H. trimaculatus	0.730*	0.933*	
H. comes	0.764*	0.999*	0.581*

* $p < 0.001$

Phenotypic variations in seahorse species

H. hippocampus showed phenotypic differences between Macaronesia and West African coasts; the CAP analysis separated specimens along the first and second canonical axis (Fig. 3, $\delta^2 = 0.71$, $p < 0.001$); almost all records were well allocated into each archipelago (LoA = 93.8%), which were further corroborated by the one-way ANOSIM (R = 0.22, $p = 0.02$). The size of the snout was the main morphological variable contributing to split these morphotypes, with also an important contribution of skull-related variables (>70%, Table 2). In contrast, *H. algiricus* did not show phenotypic variation between Macaronesia and West African coasts (one-way ANOSIM: R = −0.27, $p = 0.86$).

Table 2 Morphological and meristic variables contributing to dissimilarities (%) in morphology between seahorse species and regional morphotypes of *H. hippocampus*

| *H. hippocampus* versus *H. algiricus*	*H. hippocampus* Macaronesia versus West Africa	*H. hippocampus* Canaries versus Azores	*H. hippocampus* Canaries versus Madeira
Pectoral fin rays (31.93)[a]	HL:SnL (19.54)[a]	Dorsal fin rays (16.22)	Pectoral fin rays (20.86)[a]
HL:SnL (21.06)[a]	Pectoral fin rays (13.16)[a]	HD:HL (15.03)[a]	Dorsal fin rays (18.18)
CH:HL (9.80)[a]	Dorsal fin rays (12.64)	Pectoral fin rays (11.70)[a]	TD9:TrL (15.53)
SnD:SnL (8.02)[a]	PO:HL (12.23)[a]	SnD:SnL (11.24)[a]	PO:HL (9.78)[a]
HD:HL (7.07)[a]	HD:HL (6.73)[a]	TD9:TrL (9.46)	HL:SnL (7.51)[a]
Dorsal fin rays (5.79)	SnD:SnL (5.90)[a]	HL:SnL (7.56)[a]	CH:HL (6.41)[a]
TD9:TrL (4.95)	OD:HL (5.83)[a]	CH:HL (5.42)[a]	TD9:SL (3.79)
OD:HL (3.34)[a]	TD9:TrL (5.80)	TaL:SL (4.27)	SnD:SnL (3.55)[a]
PO:HL (1.79)[a]	CH:HL (4.36)[a]	TrL:SL (3.61)	HD:HL (2.95)[a]
TD4:SL (1.46)	DL:SL (3.54)	PO:HL (3.35)[a]	TrL:SL (2.39)
TD9:SL (1.35)	HL:SL (2.63)[a]	OD:HL (3.21)[a]	TaL:SL (1.87)
HL:SL (0.94)[a]	TD9:SL (1.96)	HL:SL (3.01)[a]	OD:HL (1.70)[a]
TaL:SL (0.81)	TaL:SL (1.90)	TD9:SL (2.65)	DL:SL (1.69)
TrL:SL (0.64)	TrL:SL (1.53)	DL:SL (1.26)	TD4:SL (1.41)
PL:SL (0.56)[a]	PL:SL (1.49)[a]	PL:SL (1.23)[a]	PL:SL (1.23)[a]
DL:SL (0.49)	TD4:SL (0.74)	TD4:SL (0.77)	HL:SL (1.13)[a]

[a] Skull related variables
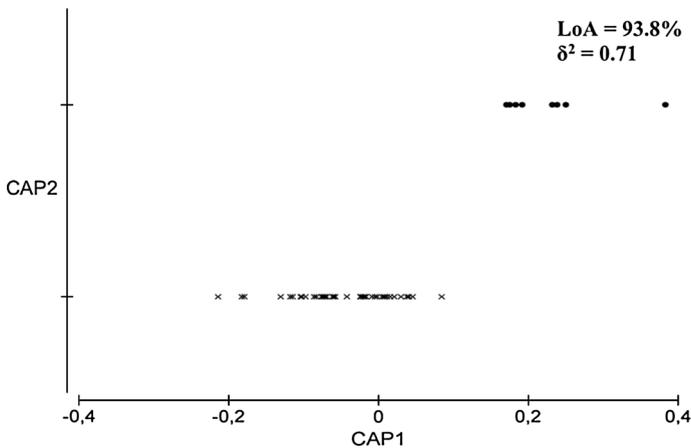
Fig. 3 Constrained canonical ordination plot (CAP) of *Hippocampus hippocampus* from Macaronesia (*multiplication symbol*) and adjacent West African coasts (*filled circle*). The 'Leave-one-out Allocation' success is indicated (LoA, i.e. the percentage of samples correctly allocated into each group). δ^2 square canonical correlation with CAP-I

H. hippocampus also showed varying morphology through Macaronesia (Fig. 4, $\delta^2 = 0.70$, $p < 0.001$). Specimens from the Azores and Canary Islands separated along the first and second canonical axis and significantly differed (Fig. 4, R = 0.484, $p = 0.0003$).
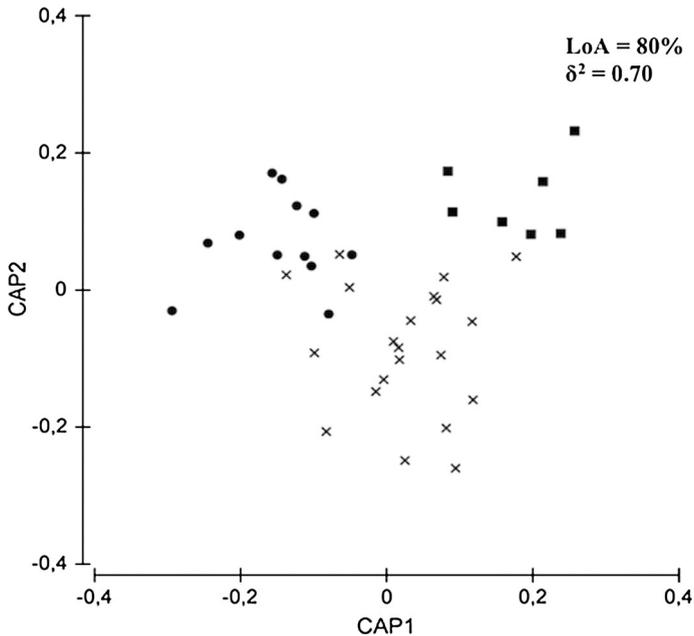
Fig. 4 Constrained canonical ordination plot (CAP) of *Hippocampus hippocampus* throughout Macarone-sia: Azores (*filled square*), Madeira (*multiplication symbol*) and Canary Islands (*filled circle*). The 'Leave-one-out Allocation' success is indicated (LoA, i.e. the percentage of samples correctly allocated into each group). δ^2 square canonical correlation with CAP-I

Similarly, specimens from Madeira also differed relative to those from the Canary Islands (Fig. 4, R = 0.194, p = 0.007). Yet, individuals from the Azores and Madeira archipe-lagos did not morphologically differ (R = 0.131, p = 0.11). The number of dorsal and pectoral fin rays and the head and snout shape were the most important morphological variables contributing to the separation of specimens from the Canary Islands and those from the Azores (Table 2). The number of dorsal and pectoral fin rays and the trunk shape were the most important variables to discriminate specimens from Canary Islands and those from Madeira (Table 2).

Discussion

This study has demonstrated the value of natural history collections for assessing the distribution and polymorphism of threatened species, seahorses in particular. This is especially relevant when available data are scarce and limit proper decisions about the conservation and management of these species. The present results have firstly filled some knowledge gaps about the distribution of the short-snouted seahorse, *H. hippocampus*, including specimens recorded at Madeira Island, as well as at Fuerteventura and Tenerife (Canary Islands), which had not been recorded in the last global seahorse taxonomic revision (Lourie et al. 2016). The present results have not confirmed the presence of *H. guttulatus*, previously known as *H. ramulosus* (Lourie et al. 2016), in Macaronesia (Dawson 1986, 1990).

The unexpected presence of *H. comes* and *H. trimaculatus* in various collections (here at TFMC and ULPGC), which inhabit the Indo-Pacific tropical areas (Lourie et al. 2016), could be related to private donations linked to aquarium trade activities in the early '80s from the Philippines to the Canaries. In this sense, the morphological data obtained for *H. comes* and *H. trimaculatus* showed similar range sizes and so low variation, i.e. low standard deviations (Appendix 1; Fig. 1), in agreement with homogenous animal stocks, typically involved in aquarium trade (Koldewey and Martin-Smith 2010; Vincent et al. 2011).

The present analyses confirmed the presence of both *H. hippocampus* and *H. algiricus* along their previous geographical distribution ranges (Lourie et al. 2004, 2016). Both species are in a precarious situation; *H. hippocampus* has been catalogued as an IUCN data deficient species, while *H. algiricus* is listed as an IUCN vulnerable species (Czembor 2012). The present morphological study revealed that *H. algiricus* could be distinguished from *H. hippocampus* by their snout (larger and thicker) and coronet shape (rounded overhanging at the back of their head). In living organisms, this information could be supplemented by the *H. algiricus* dark body colour pattern and the presence of tiny white dots or larger brown spots (Lourie et al. 2004; Wirtz et al. 2007; Cisneros-Montemayor et al. 2015; Otero-Ferrer et al. 2015a). Such criteria could be used to separate both species in those West African regions involved in commercial trade. In Macaronesia, commercial trade does not affect seahorse wild stocks; threats to seahorses are linked to overfishing (Castro et al. 2015) and habitat destruction including the deterioration of seagrass meadows (Tuya et al. 2014). However, the low abundances of wild populations and the recent expansion trend of *H. algiricus* towards northern latitudes, with some specimens recorded from the Canary Islands, may create a sympatric scenario with a potential risk of hybridization with *H. hippocampus* (Otero-Ferrer et al. 2015a, b). Even if genetic studies should confirm species identification, morphology could additionally help to distinguish both species, for example to detect abnormal animal sightings out of their distribution ranges.

The most abundant seahorse in the studied region, *H. hippocampus*, showed polymorphism between locations in and out of Macaronesia. Individuals from Macaronesia (Azores, Madeira and Canary Islands) may be differentiated from those in West Africa (Western Sahara, Senegal and Liberia) by their cranial and snout characteristics. These results agreed with the three well-defined genetic units established by Woodall et al. (2011), where West African populations could be separated from those inhabiting the Mediterranean and Atlantic European coasts (including the Iberian Peninsula, Madeira and Canary Islands) and the English Channel and Bay of Biscay. In addition, Lourie et al. (2004) described several morphotypes; *H. hippocampus* specimens inhabiting Western African zones showed larger and angular heads compared to northern specimens. Surprisingly, some morphological differences were also found for *H. hippocampus* within Macaronesia. The head shape separated specimens from the Canary Islands and the Azores, i.e. between the most distant areas within Macaronesia. Individuals from Madeira are, from a morphological point of view, somehow half way between the Azores and Canary Islands. Sporadic dispersal events could explain a connection between individuals from Madeira and the Azores and Canary Islands. Seahorses are relatively sedentary fishes and weak swimmers with a low dispersion rate (Foster and Vincent 2004). However, they have the potential to establish viable populations from rare colonization events, e.g. males are able to produce large number of well-developed offspring sporadically (Foster and Vincent 2004; Novelli et al. 2017).

In general, those variables related to seahorse skull morphology were the major contributors to the differentiation of seahorse species and several of their morphotypes. As toothless species, seahorse-feeding mechanisms are highly dependent on head and snout shape (Van Wassenbergh et al. 2009). The skull morphology plays a key role during feeding, involving the coordination of highly complex musculoskeletal systems and linking head rotation with the rapid snout suction of prey (Van Wassenbergh et al. 2009). The performance of this movement is supported by seahorse skull hydrodynamic shape avoiding prey alert systems (Gemmell et al. 2013). Several studies have demonstrated that different prey regimes in seahorse parents can alter the body plan development and modulate morphology (snout and head sizes) of their offspring (Otero-Ferrer et al. 2014). Morphological variations of seahorse species through their geographical distribution ranges can be, therefore, conditioned by the availability, abundance and quality of their prey (Wikelski and Thom 2000; Doughty and Reznick 2004). This diet-induced phenotypic plasticity affecting cranial and body shape has been described for other fishes, where various prey sizes lead to modification of snout and body morphometric patterns (Hegrenes 2001; Wintzer and Motta 2005; Heermann et al. 2007). The present study, however, does not confirm the connection between morphological (phenotypic) variation of seahorses and varying regimes in the quantity and quality of prey.

Skull variables, especially snout shape, were useful for distinguishing between *H. algiricus* and *H. hippocampus* specimens. In addition, these variables can also help to separate *H. hippocampus* at inter-regional scales, even though they were less important for separating morphotypes within Macaronesia. Globally, 95% of the seahorse trade involves dried specimens for use in traditional medicine (Vincent et al. 2011); therefore these morphological differences could be potentially employed as a traceability tool to partition not only seahorse species, but also the origin of seahorse populations. Such valuable information could be used to optimize seahorse conservation actions, particularly in areas where specimens are critically threatened by trading or anthropogenic activities.

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