SEAHORSES -MASTERS OF ADAPTATION

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From Marine Ecology to Developmental Biology
In Honour of Pierre Tardent (1927-1997)

SEAHORSES – MASTERS OF ADAPTATION

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SEAHORSE
HIPPOCAMPUS
ADAPTATION
EVOLUTION
REPRODUCTION

ABSTRACT. – Seahorse habitats are hard substrates (rocks, gravel, corals, gorgonians, sponges). Special adaptations are needed for survival in such an environment. Seahorses show adaptations in body shape, appearance, locomotion and behaviour as well as (most outstanding) in reproductive biology. In contrast to the majority of marine teleosts, seahorses avoid a planktonic larval phase. Males develop a brood pouch in which, after mating, the eggs are fertilized and kept for cleavage and embryonic development. Like this, a maximum degree of protection is provided for the clutch. This paper gives an overview on seahorse biology, emphasizing most important features and discussing them with reference to the benthonic way of life of these extraordinary animals.

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RÉSUMÉ. – Les Hippocampes vivent sur fonds durs (roches, graviers, Coraux, Gorgones, Eponges). Des adaptations spéciales sont nécessaires pour survivre dans un tel biotope. Elles concernent leur morphologie, leur locomotion et leur comportement aussi bien que leur reproduction. Contrairement à la plupart des Téléostéens marins, les Hippocampes évitent la phase larvaire planctonique. Les mâles possèdent une poche abdominale d'incubation dans laquelle (après l'accouplement) les œufs sont fécondés et maintenus pendant leur segmentation et leur développement embryonnaire, ce qui leur assure une protection maximale. Cette étude présente une vue d'ensemble de la biologie des Hippocampes et fait ressortir les points les plus importants liés à la vie benthique de ces Poissons extraordinaires.

INTRODUCTION

Teleosts represent the modern type of fish among the ray-finned fishes (Actinopterygii). Their body structure shows differentiations referring to a light construction, maneuverability and swift swimming. Even generalized teleosts (Greenwood *et al.* 1973, Arratia 1996), the type of herring-like fishes (Clupeomorpha), have thin and light scales; furthermore they get perfect buoyancy by an adjustable swim-bladder in order to move in the three-dimensional environment of the open ocean. The fusiform-shaped body (Hertel 1966, Senn 1997) permits an efficient and energy-saving locomotion. Some reproductive patterns emphasize that the modern fish differentiated for a high degree of mobility. Eggs and larvae develop as part of the drifting plankton. When clupeomorph (herring-like) teleosts radiated during Cretaceous and early Tertiary they primarily populated the pelagic environment.

However, teleosts as the richest group of vertebrates did not only adapt to open waters. Numerous independent lines secondarily led to bottom-dwelling life-styles. Such substrate-dwelling fishes developed different body shapes and structures. Not speed and swiftness became important but adaptations to the substrate and to slower swimming. Some fishes differentiated flattened bodies in order to get in intimate contact with the bottom. Others developed skin structures resembling the ground in order to obtain a perfect camouflage. Some forms show an astonishing ability to change coloration; they produce rapid adaptations while frequently changing the substrate. Flounders and plaices are perfectly invisible on sandy bottoms (Portmann 1956, Bürgin 1986).

On hard substrates adaptations are a bit special. Here on rocks, gravel, corals and gorgonians, which are frequently overgrown by calcifying red algae (Lithophyllum), sponges, tubeworms and Bryozoa, camouflage is more elaborate. A variety of structures contribute to make fishes (scorpion fish, stone fish, file fish etc.) invisible. In terms of camouflage on structured hard bottoms as well as in sea-grass the tubemouth fishes (Syngnathiformes) are unsurpassable (Kuiter 2001).

The pipe fishes of the genus *Syngnathus* resemble a sea-grass leaf in shape and coloration; thus they are perfectly camouflaged in their environment of Posidonia fields. Leafy pipe fishes

(*Phyllopteryx*) seamlessly imitate all irregular parts of thalli (stalks and phylloids) of brown algae in Australian waters. And the seahorses (genus *Hippocampus*), with the earliest representatives known from the Pliocene of Fiume Merecchia, Italy (Frickhinger 1991), show enormous adaptations for their living on hard substrate bottoms of Mediterranean and North Atlantic coastal waters.

Hippocampus shows various adaptations to the hard substrate. We observe adaptations in body shape, appearance and behaviour in order to move safely and get a perfect camouflage on the richly structured bottom. Body shape does not at all resemble a fish; there is no need for a hydrodynamic, fast swimming animal. Secondly locomotion is neither swift nor buoyant. The seahorse rather creeps on the substrate while bending its body and, if there is low current, uses the dorsal fin to hover slowly to the next structure. It then gets firmly fixed on a hard object by its seizing tail in order to harvest plankton by suction feeding. Among the most surprising adaptations to a substrate dwelling biology is the pattern of reproduction. In contrast to most marine teleosts seahorses (and other syngnathids e.g. pipe fish) avoid a planktonic larval phase in their life history. Males develop an incubating pouch in which, after mating, the eggs are fertilized and kept for cleavage and embryonic development under a maximum degree of protection.

MATERIAL AND METHODS

All observations (*H. hippocampus, H. bleekeri* and *H. reidi*) have been realised thanks to the Vivarium of the Zoological Gardens in Basle. Big thanks are expressed to the whole team of the Vivarium for their help in various respects.

The seahorses used for paraffin and alcohol preparation were taken from the clutch of *H. hippocampus* on January 2nd, 2001. On the first day after hatching few specimens were taken out of the salt-water aquarium and given into the fixation solution AFE (90 % alcohol, 10 % formaldehyde, 10% glacial acetic acid) for two days. After that all specimens were given into alcohol (80 %) for storage. Living animals were taken, though, individuals that already had serious problems with keeping themselves upright in the water column, helplessly drifting on the water surface.

RESULTS AND DISCUSSION

The entire biology of seahorses is harmonized with their benthonic habitat (Bellomy 1969). The aspect of adaptation can be seen as the key to the understanding of seahorse biology. Subsequently, the most important parts in seahorse biology will be emphasized and discussed in the context of the benthonic way of life of these animals.

A. Morphologic adaptations

One of the most outstanding changes with reference to the morphology of original teleosts is the transformed and now prehensile tail of seahorses. As a consequence, the tail fin was lost. Most of the time this prehensile tail works as anchorage in the highly structured sea-grass habitat. While swimming it fulfils balance and steering duties. Additionally the tail takes action during the greeting rite (performed daily), the mating dance of pairs (reproductive season) as well as in the competition of males. If not more or less stretched out during swimming, adult seahorses do generally keep their tail rolled up towards their belly. The morphology of the tail tells us more about the phenomena of grasping (according to Hale 1996) and the impossibility of lateral and s-ward bending in adults.

In the context of tail structure and function the existing exoskeleton is worth a glance. It is built by dermal bones (joint pieces of the skeleton, located right below the skin), evolving directly from embryonic connective tissue (desmic way of bone formation). The trunk of seahorses is surrounded by 7 longitudinal rows of these plates (forming 3 pairs of bony ridges to both sides and one ridge to the front). Four rows of bony plates do lie around the tail. This is how the striking appearance of seahorses and pipe fishes is created. Every segment of the tail consists of 4 bony plates. They overlap their anterior neighbors at any time, even at maximum bending (Fig. 1). Overlapping parts of succeeding plates are joined by connective tissue. The vertebrae attach to the plates with connective tissue at the lateral processes and the hemal spines (Hale 1996).

In comparison to our model of the 'classic' teleost the muscular apparatus in seahorses shows considerable modification. We find a redistribution and new orientation of muscular tissue within the myomeres. Fast and powerful contractions become possible by this special kind of muscle formation. Every single plate is connected to a myomere by a thick band of connective tissue (muscular tendon). During axial bending ventral tendons and plates project myomere-generated forces to the backbone. Ventral bending of the tail can therefore be achieved by simultaneous and evenly strong contraction of the left and right hypaxial muscle of a segment (Fig. 2a). Median ventral muscles are involved in axial bending, too. In this latter case the transformation of forces runs over the hemal spines of the vertebrae (Fig. 2b).

In the whole mechanism of bending we find a division of labor between myomeres and median ventral muscle groups. Myomeres do act in fast,

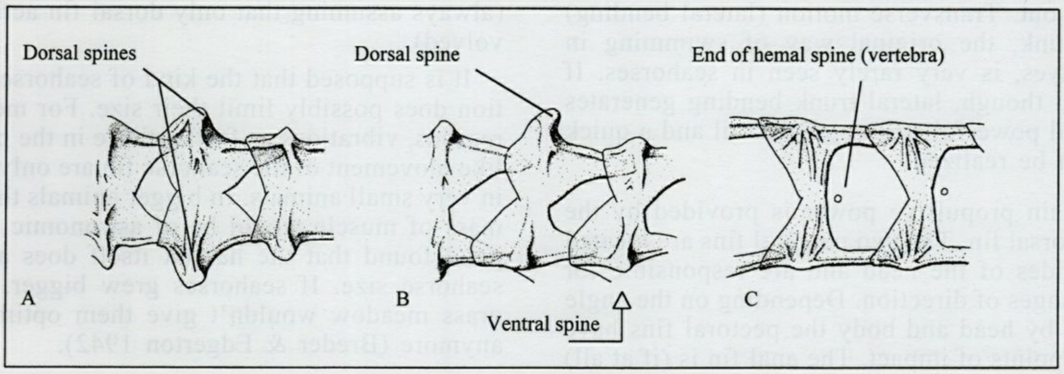

Fig 1. – Overlapping plates in the tail segments of *H. Kuka* (from Hale 1996): dorsolaterally and ventrolaterally the plates from edges, which dorsolaterally end in spiny projections. A, Dorsal view; B, Lateral view; C, Ventral view.

powerful tail movements. Median muscles (composed of tonic fibers) do generate rather small forces but seem to be responsible for maintaining a bent tail position for a longer period. The heavy plating of the seahorse tail plays a prominent role in the transmission of forces during axial bending. The plates provide rigid structures for the myomeres to pull upon. Therefore the plating can eventually even be seen as a necessary prerequisite for this extreme kind of force transmission and tail bending (Hale 1996).

According to Hale studies, the arrangement of plates and skin connective tissues prevents strictly lateral movement of the tail. Additionally, the overlapping of plates helps control the twisting of the tail in adults. In newborns the development of plating and connective tissues is still incomplete. This might be the/a reason for the extended lateral bending abilities in newborn seahorses (personal observation M Schmid 2001). In adults lateral grasping can only be achieved by controlled twisting of the tail. As in the normal grasping movement, the ventral side of the tail becomes the inside of the curl, when lateral grasping is necessary.

Most of the time seahorses keep themselves in an upright position. Like their relatives, the pipe fishes, they manage to maintain this position by the cooperation of air bladder and tail. For a change of position the gas mixture of the bladder can be moved to its anterior or posterior part. For animals depending on the ability of fast swimming (either for hunting of flight) only very few changes in the shape of their body are possible without suffering losses in velocity. In the habitat of seahorses, though, no advantage can be derived from fast swimming. For this reason a spindle-shaped body, as present in fast hunters like sharks, is no longer attractive for seahorses. Alternatively they count on optimized maneuverability which is much more advantageous in their complex habitat of sea-grass meadows.

Basically four modes of progression can be distinguished (Blake 1976 and personal observations).

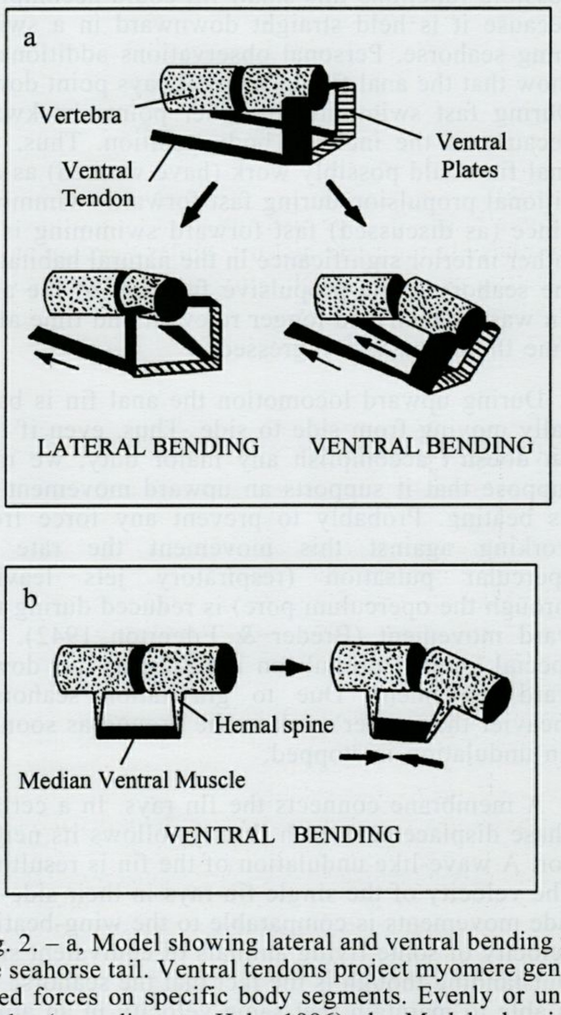

Fig. 2. – a, Model showing lateral and ventral bending in the seahorse tail. Ventral tendons project myomere generated forces on specific body segments. Evenly or unevenly (according to Hale 1996). b, Model showing ventral bending in the seahorse tail by contraction of median ventral muscles and transmission of forces over the hemal spines of the vertebrae (according to Hale 1996).

These are: slow forward, fast forward, turning and vertical movement. The faster the animal swims, the more its body will be inclined towards swimming direction and the more the tail will be stretched out. Transverse motion (lateral bending) of the trunk, the original way of swimming in Osteichthyes, is very rarely seen in seahorses. If demanded though, lateral trunk bending generates strong and powerful strokes of the tail and a quick flight can be realized.

The main propulsive power is provided by the waving dorsal fin. The two pectoral fins are located at both sides of the head and are responsible for small changes of direction. Depending on the angle produced by head and body the pectoral fins have different points of impact. The anal fin is (if at all) only present in a reduced, tiny form and has almost no function with respect to locomotion (Vincent 1990). Breder & Edgerton (1942) consider a slightly lifting force or rudder-like action the only possible functions this small fin could accomplish because it is held straight downward in a swimming seahorse. Personal observations additionally show that the anal fin does not always point down. During fast swimming it rather points backward because of the inclined body position. Thus, the anal fin could possibly work (have worked) as additional propulsion during fast forward swimming. Since (as discussed) fast forward swimming is of rather inferior significance in the natural habitat of the seahorses, the propulsive function of the anal fin was probably no longer relevant and time after time the organ was regressed.

During upward locomotion the anal fin is basically moving from side to side. Thus, even if this fin doesn't accomplish any major duty, we may suppose that it supports an upward movement by its beating. Probably to prevent any force from working against this movement the rate of opercular pulsation (respiratory jets leaving through the operculum pore) is reduced during upward movement (Breder & Edgerton 1942). No special kind of propulsion is necessary for downward movement. Due to gravitation seahorses (heavier than water) sink to the ground as soon as fin undulation is stopped.

A membrane connects the fin rays. In a certain phase displacement each fin ray follows its neighbor. A wave-like undulation of the fin is resulting. The velocity of the single fin rays in their side-to-side movements is comparable to the wing-beating velocity of some flying animals of equivalent size. Outstanding though is the fact that the seahorse fin is able to maintain that same velocity in an atmosphere (water) that is far more dense than the one (air) in which the insect wing beats ! If there wasn't the connecting membrane, the force produced by the beating fin rays would carry the animal horizontally forward. The posterior moving waves do additionally create a force that works vertically downward. The cooperation of the two force vectors of waves and fin rays produces the actual propulsion that pushes the animals diagonally upward (always assuming that only dorsal fin action is involved).

It is supposed that the kind of seahorse locomotion does possibly limit their size. For mechanical reasons, vibrations as fast as those in the propeller-like movement of the seahorse fin are only possible in very small animals. In bigger animals the needed mass of muscle would be of astronomic size. Experts found that the habitat itself does also limit seahorse size. If seahorses grew bigger, the seagrass meadow wouldn't give them optimal cover anymore (Breder & Edgerton 1942).

B. Adaptations in reproductive biology

Syngnathidae are the only vertebrate group in which males literally get pregnant. The male seahorse carries the clutch either at the base of its belly or tail (male ghost fish), separated by thin walls at the bottom of its body, completely surrounded by folded skin or even in tightly closed brood pouches. This gives us an idea of how the brood pouch in seahorse males has evolved (Vincent 1990). Further development probably proceeded past the open pouch in pipe fish (at the back or tip of the tail) ending up with the pouch at the belly of seahorse males, which represents the version of highest development. Apart from a small pore this brood pouch is completely closed.

In an impressive way seahorse reproductive biology is tuned with habitat conditions. In the majority of species mating pairs are faithful. At least for the course of a breeding season, probably even longer. In natural habitats, seahorses don't live in big colonies. Mating pairs are spread in a patchy way and in low density. Therefore, finding a partner is a rather difficult attempt, requiring a great deal of energy. In contrast, living in pairs helps saving time and energy that would otherwise have to be spent when searching for new mates. Additionally, predation risk is reduced since the animals do have to leave their cryptic state less often.

When it comes to caring for the clutch we find an exchange of duties in seahorse pairs. The female deposits a set of eggs (several hundreds in most species!) into the pouch of the male who is responsible for all further care. The brood pouch with its ion-rich fluid is of optimal nutritional value and works as osmotic adaptation chamber for the developing embryos (Linton & Soloff 1964). The duration of egg and embryo incubation within the pouch does strongly depend on the species. The finally hatching newborns are miniatures of their parents and right from the start independent in every respect (Fig. 3).

A new clutch of eggs can already mature in the belly of the female while the male is carrying the previous breed in his pouch. This means that the male seahorse increases his own rate of reproduc-

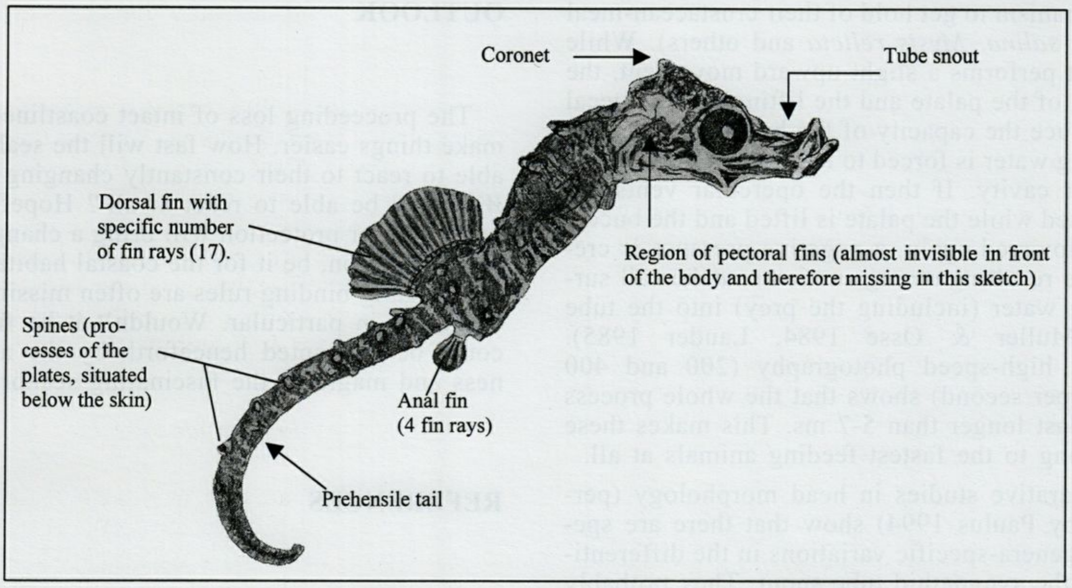

Fig. 3. – Newborn *H. hippocampus*, Zoo Basle (almost one day old, after fixation in AFE, kept in 70 % alcohol for storage). Body development comparable to an adult, though proportions are different. Total body length: 7 mm (Drawing by M Schmid 2001).

tion by breeding the young in his pouch (Woodruffe & Vincent 1994). Additionally a male seahorse can be sure of his paternity at 100 percent because the eggs of the female are only fertilized after they've reached his (and no other) brood pouch.

Literature tells us of daily-performed greeting rites at daybreak. The choice of this particular time of day might be connected to the attempt of keeping the rite unnoticed by enemies. Eventually we can talk of a so-called 'trade-off' effect. Minimal predation risk on one side and more or less good lighting conditions on the other side. As changes of body color are part of this morning rite some active role of the optic sense can be assumed. Considering this, it obviously makes sense to meet and 'dance' early in the morning before hiding away in the seagrass when the sun rises. Probably for the same reasons of protection the birth of the young is set in the early morning, too, or does even happen at night. In their natural habitat, the newborn seahorses are subject to a high mortality caused by predators and their hatching during darkness does certainly benefit their chances of survival.

C. Appearance – A factor for survival

The development of a brood pouch in the male seahorse provides optimal security for the clutch. Anyway, it would be useless if the fabulous camouflage wouldn't have been invented simultaneously. There is no exaggeration in calling the camouflage of seahorses 'close to perfection'. Seahorses are able to adapt their looks to their environment in a way that an unpracticed eye will have difficulties to spot a specimen in the wild. By their changing body color and by their ability to grow tufts, seahorses imitate sea-grass or gorgonians on which and in which they hide. The shield of bony plates below their skin is part of their subtle tactics of passive defense. The hard casing alone makes them relatively uneatable already and therefore less attractive to some potential predators.

Naturally the just hatched youngsters do face an elevated degree of danger. The risk of predation is reduced by the birth in darkness and by the transparency of the newborn. In contrast to many other adult features (which are already present at birth), pigmentation patterns are developed during the first weeks *after* birth.

D. 'Cool' hunters

Following the aim of optimum camouflage, seahorses are ambush-hunters. Remaining motionless they let their prey (small crustaceans) come to them. Their eyes can move chamaeleon-like and independently from each other, allowing the seahorse to observe a large part of the vicinity while remaining perfectly hidden. Problems arise when the water is troubled by a storm or by human water pollution along the coastline. Reduced visibility is problematic since the optic sense of seahorses is of great importance when it comes to localizing and catching the prey. Even newborns do already use their tube snout and their specialized pipet-feeding-mechanism to get hold of their crustacean-meal (*Artemia salina, Mysis relicta* and others). While the snout performs a slight upward movement, the lowering of the palate and the lifting of the buccal floor reduce the capacity of the buccal cavity. The remaining water is forced to leave the mouth by the opercular cavity. If then the opercular vents are kept closed while the palate is lifted and the buccal floor is lowered again, a negative pressure is created. The resulting strong suction snatches all surrounding water (including the prey) into the tube snout (Muller & Osse 1984, Lauder 1985). Lauder's high-speed photography (200 and 400 pictures per second) shows that the whole process doesn't last longer than 5-7 ms. This makes these fish belong to the fastest feeding animals at all.

Comparative studies in head morphology (performed by Paulus 1994) show that there are species- or genera-specific variations in the differentiation of the syngnathid tube snout. They probably reflect a secondary specialization according to the adaptation to various food ressources. Sympatric living species (species, living in the same habitat) such as the syngnathids of the Jordanian Red Sea coastal waters are forced to use different niches when feeding. This is because of the enormous interspecific pressure by competition. Specialized differentiations in the tube snout with regards to a certain food item are favoured (Brauch 1966). These specializations are shown in the bones of the tube snout and, within the species, overall in lateral snout elements (Paulus 1994).

CONCLUSION

With regard to all the adaptations to the benthonic habitat, the biology of seahorses may without a doubt be of great fascination for evolution scientists. Unfortunately, some aspects of the seahorses specialized way of living are about to become their ruin. Several peculiarities in behaviour and ecology render seahorses extremely sensitive for disturbances. Their small density in natural populations would be an example. Additionally, seahorse territories are small as well. Males stay on a territory of only one square meter during breeding season. Seahorses are tied to their home territory and their mobility (particularly the mobility of males during pregnancy) is restricted. All this makes them an easy catch for fishermen. Their strong faithfulness means that widowed animals do have to face serious problems when looking for a new mate. From this point of view all the fascinating adaptations discussed above do unfortunately turn to a multitude of fatal facts with regards to seahorse survival.

OUTLOOK

The proceeding loss of intact coastlines doesn't make things easier. How fast will the seahorses be able to react to their constantly changing habitat ? *Will* they be able to react at all ? Hopefully new programs for protection will bring a change for today's situation, be it for the coastal habitat in general (legally binding rules are often missing) or for seahorses in particular. Wouldn't it be fine if we could be enchanted henceforth by the attractiveness and magic of the fascinating seahorses... ?

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