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ARTICLE

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Feeding behavior of the longsnout seahorse *Hippocampus reidi* Ginsburg, 1933

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Abstract *Hippocampus reidi* is a threatened species and one of the most heavily traded seahorses in the aquarium trade. Nevertheless, little is known about its biology and ecology. This study encompasses the first description of the feeding behavior of *H. reidi*, with emphasis on preferred feeding time, feeding frequency, feeding behavior during nonreproductive and reproductive periods, and prey choice. Underwater observations were made in NE Brazil from May 2003 to September 2004, and the behavior of 57 specimens was recorded during 118 feeding events. In the laboratory, 8 specimens and 176 feeding events were recorded. Prey choice was tested among carideans, amphipods, live and frozen brine shrimp, with the most consumed prey being the caridean *Hyppolyte curacoensis*. *H. reidi* fed both at diurnal and crepuscular hours, its feeding frequency being directly proportional to luminous intensity. No feeding was observed at night. Males with a fully developed pouch exhibited a significantly higher feeding frequency than nonreproductive males. *H. reidi* generally is a "sit-and-wait" predator that occasionally pursues prey.

Key words *Hippocampus reidi* · Feeding behavior · Feeding preference · Brazil · Seahorse

Introduction

More than 24 million seahorses are traded each year among at least 77 nations (Project Seahorse 2004). The seahorse trade is almost exclusively based on wild-caught specimens, as seahorse aquaculture still faces some challenges, among them limited knowledge of most species' biology.

Brazil is one of the main exporters of fishes for the aquarium trade, and the longsnout seahorse *Hippocampus reidi* Ginsburg, 1933 is one of the country's most exported marine ornamental fish species (Monteiro-Neto et al. 2003). *H. reidi* is a threatened species (Appendix II of CITES 2004; IUCN 2004; Instrução Normativa 05/2004, Ministry of the Environment, Brazil) that has been poorly studied in the wild (e.g., Dauwe 1992; Nijhoff 1993; Rosa et al. 2002; Dias and Rosa 2003). As a result, it is presently listed by The World Conservation Union under the category Data Deficient (IUCN 2004). *H. reidi* is recognized as a difficult species to raise in captivity (Giwojna 2002), feeding being one of the aspects that still needs to be better understood. Studies on the biology and ecology of *H. reidi* are necessary not only to support the conservation of wild populations but also to generate data that can be used to improve the survival of captive specimens.

This study focused on the feeding behavior of *H. reidi* and addressed the following questions: (1) Is there a preferential feeding time for the species? (2) Does its feeding frequency change during the day? (3) Are there changes in its feeding behavior during the reproductive period? (4) What is the species' feeding behavior repertoire? (5) Is there a preference for a certain prey type?

Materials and methods

Field sampling and observations

Field observations were made from May 2003 to September 2004, during low-tide periods between 0600 and 1200, at two protected areas in northeastern Brazil: Reserva Estadual de Desenvolvimento Sustentável Ponta do Tubarão, Rio Grande do Norte State (05°04′37″S; 36°28′31″W) and Área de Proteção Ambiental Barra do Rio Mamanguape, Paraíba State (06°43′02″S; 35°07′46″W). The selected

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observation points consisted of shallow areas (maximum depth 1 m) bordered by mangrove forest, mainly *Rhizophora mangle*.

Specimens of *H. reidi* were observed through snorkeling, using the "focal animal" method (Lehner 1998). Each specimen was observed for 30 min, during which the number of feeding events and the associated behaviors were recorded. Specimens were then filmed, photographed and measured underwater (height) by leaning them against an underwater slate equipped with a ruler. Subsequently they were marked with a piece of colored cotton ribbon (tied around the base of their tails) to avoid observing the same specimen twice. Marks were removed after completion of the total experiment.

Each specimen was visually identified according to its reproductive stage and sex, following Lourie et al. (1999). Specimens were grouped into four categories: "pregnant" male (PM), nonpregnant male (NM), reproductive female (RF), nonreproductive female (NF).

Laboratory sampling and observations

Maintenance of seahorse specimens

Specimens of *H. reidi* were obtained on loan from a licensed ornamental fish retailer, on the day of their capture in the wild. Eight nonreproductive adult specimens (height 15 ± 0.5 cm) were kept in individual glass aquaria (24 l) under natural light and photoperiod. Tanks were provided with continuous aeration, biological filter, artificial plants and 2 cm of a calcareous shell substrate. Abiotic factors were controlled weekly (Marine Lab, Red Sea). Temperature was maintained at 27°C, salinity at 35 ppt; alkalinity at 2.5 mEq/l; NO_2 at 0.1 ppm; NO_3 at 0 ppm; pH ranged from 8.1–8.4, and NH_3 from 0–0.01 ppm. Specimens were fed ad libitum with caridean shrimp, amphipods and brine shrimp. Frozen brine shrimp were not manually agitated and sank to the bottom as soon as they were placed in the tank.

Collection and maintenance of prey

Seahorse feeding ecology has been poorly studied, however some works have shown that crustaceans such as copepods, amphipods, caridean shrimp and mysid shrimp constitute the main items of their diet (e.g., Tipton and Bell 1988; Teixeira and Musick 2001; Woods 2002). Based on that information, four groups of prey were tested in the present study: caridean shrimp (*Hyppolyte curacoensis*) ranging from 1.0–2.0 cm in length; amphipods (*Ampithoe ramondi*) ranging from 0.5–1.0 cm in length; live brine shrimps (*Artemia* sp.) ranging from 0.8–1.0 cm in length; and frozen brine shrimps (*Artemia* sp.) ranging from 0.8–1.0 cm in length.

The caridean and amphipods were collected in association with algae at Praia do Cabo Branco (João Pessoa City, Paraíba State). The live adult brine shrimp were acquired from aquarium shops. Live prey were kept separately, in three glass aquaria (6 l), under the same conditions as the seahorses. The frozen brine shrimp specimens were thawed out before being presented to the seahorses.

Experimental design

Preliminary trials were carried out to define the amount of time required by seahorses to fully explore the tanks and the number of prey items of each category to be used per experiment. Eight seahorses (four nonreproductive males, four nonreproductive females) were tested after acclimatizing in individual tanks for 48 h. Prior to the observations, a vertical plastic blinder was placed in the middle of the aquarium to separate the seahorse from the area where 40 prey (10 per category) were released. Subsequently the blinder was removed and observations began. After 1 h, prey that had not been captured by the seahorse were removed from the tank and identified. Feeding frequency was quantified as the difference between the initial and the final number of prey per category (adapted from James and Heck 1994).

To test if luminous intensity interfered with the feeding pattern of *H. reidi*, specimens were fed at four times: dawn (DA), from 0500 to 0600 (0.1–100 lux); high light intensity (HI), from 1100 to noon (1,400–1,600 lux); dusk (DU), from 1700 to 1800 (100–0.1 lux); and dark (DK), from 2300 to midnight.

Luminous intensity was measured with a luxmeter and corresponded to the values obtained by McFarland (1986) in the wild. Nocturnal observations were recorded through a digital camera with infrared light, and prey behavior was recorded at DA, HI, DU and DK.

Syngnathids have a very simple stomach, which consists of a slight widening of the intestine, and an undifferentiated alimentary tract (Michael 2001). Ryer and Boehlert (1983) stated that the time required by the pipefish *Syngnathus fuscus* to complete gastric evacuation was 10.3 h at 27°C. This would mean that a minimum interval of 11 h (maximum 17 h) should be kept between feeds to prevent seahorses from being satiated prior to prey presentation. Feeding preference experiments are summarized in Table 1.

Statistical analyses

Feeding frequency and specimens' height according to the reproductive stage were compared using Kruskal-Wallis and *Q*-test. Data on prey selection, preferential feeding time and prey size were analyzed using Kruskal-Wallis and Nemenyi test. The Statistic 4.0 package was used for the statistical analyses, except for the *Q*-test and Nemenyi test, which were performed according to Zar (1999). Data were interpreted considering $\alpha = 0.05$.

Table 1. Experimental design used to observe the feeding behavior of *Hippocampus reidi* at dawn, high light, dusk and dark

	Dawn	High light	Dusk	Dark	Dawn	High light	Dusk	Dark	Dawn
Male A	First		Second			Third		Fourth	
Male B		First		Second			Third		Fourth
Male C	First		Second			Third		Fourth	
Male D		First		Second			Third		Fourth
Female A	First		Second			Third		Fourth	
Female B		First		Second			Third		Fourth
Female C	First		Second			Third		Fourth	
Female D		First		Second			Third		Fourth

Ordinal numbers refer to the sequence in which specimens ($n = 8$) were tested at each light period

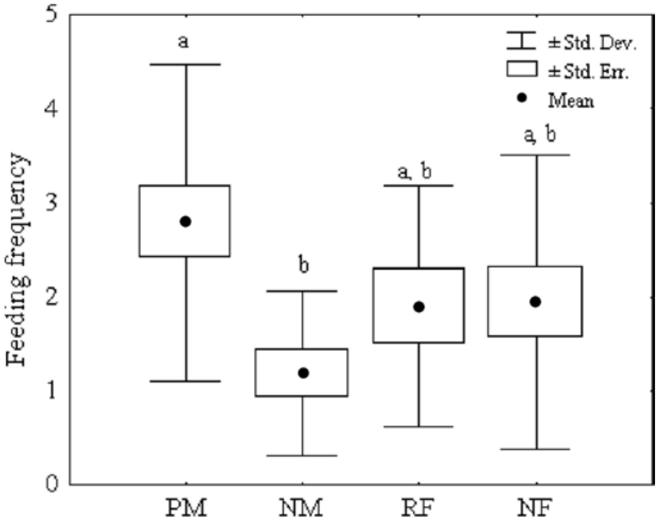

Fig. 1. Feeding frequency in the four groups of *Hippocampus reidi* during 30 min of observations. *PM* Pregnant male ($n = 19$), *NM* nonpregnant male ($n = 11$), *RF* reproductive female ($n = 10$) and *NF* nonreproductive female ($n = 17$). *Different letters* represent significant differences among groups

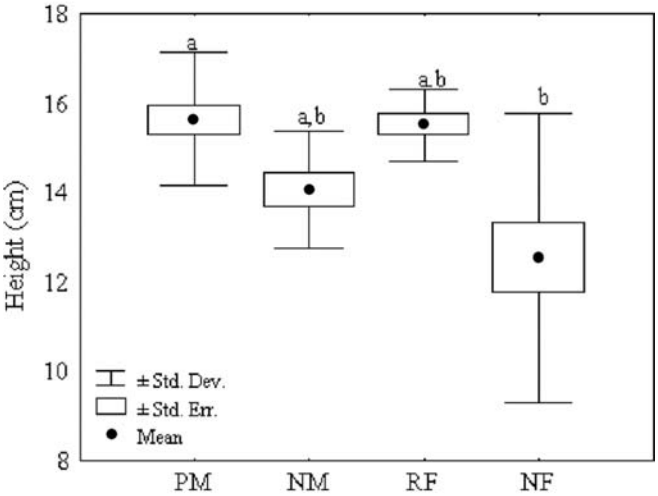

Fig. 2. Height (cm) of the four groups of *Hippocampus reidi*. *PM* Pregnant male ($n = 19$), *NM* nonpregnant male ($n = 11$), *RF* reproductive female ($n = 10$) and *NF* nonreproductive female ($n = 17$). *Different letters* represent significant differences among groups

Results

Feeding frequency

In the field 57 specimens (19 PM, 11 NM, 10 RF and 17 NF) and 126 feeding events were recorded, of which eight did not result in capture of prey. Feeding frequency significantly differed among the tested groups (Kruskal-Wallis; $H = 8.15$ and $P < 0.05$), with the feeding frequency of group PM being significantly higher than the NM group ($Q_{calc} = 2.83 > Q_{0.05,4} = 2.64$). On the other hand, no significant difference was found between the feeding frequency of the PM group with respect to the RF and NF groups ($Q_{calc} = 1.29 < Q_{0.05,4} = 2.64$ and $Q_{calc} = 1.41 < Q_{0.05,4} = 2.64$, respectively), the NM group with respect to the RF and NF groups ($Q_{calc} = 1.43 < Q_{0.05,4} = 2.64$ and $Q_{calc} = 1.38 < Q_{0.05,4} = 2.64$, respectively), or between the RF and NF groups ($Q_{calc} = 0.09 < Q_{0.05,4} = 2.64$; Fig. 1).

Height significantly differed among some of the tested groups (Kruskal-Wallis; $H = 13.93$ and $P < 0.01$). PM significantly differed from NF ($Q_{calc} = 3.28 > Q_{0.05,4} = 2.64$), but not from NM and RF ($Q_{calc} = 2.33 < Q_{0.05,4} = 2.64$ and $Q_{calc} = 0.26 < Q_{0.05,4} = 2.64$, respectively). No significant differences were found between NM with respect to RF and NF ($Q_{calc} = 1.78 < Q_{0.05,4} = 2.64$ and $Q_{calc} = 0.55 < Q_{0.05,4} = 2.64$, respectively) or between RF and NF ($Q_{calc} = 2.49 < Q_{0.05,4} = 2.64$; Fig. 2).

In the laboratory, 193 feeding events were recorded, of which 17 did not result in capture of prey.

Experimental data

Relationship between feeding frequency and luminous intensity

During the in vitro experiments, all tested specimens fed at luminous intensities above 0.8 lux (DA, HI, DU), with no feeding behavior observed at night. The total number of prey consumed per specimen ranged from 14–36. The highest consumption of prey consumed in one 60-min period ($n = 16$) occurred at HI, while the lowest ($n = 3$) occurred at DU (Table 2).

Table 2. Number of prey items consumed by *Hippocampus reidi* in aquaria at dawn, high light and dusk, over a 60-min observation period

	Dawn (DA)	High light (HI)	Dusk (DU)	Total
Male A	7	16	9	32
Male B	5	9	4	18
Male C	4	11	4	19
Male D	4	7	3	14
Female A	6	10	5	21
Female B	5	7	3	15
Female C	5	10	6	21
Female D	11	13	12	36
Total	47	83	43	176

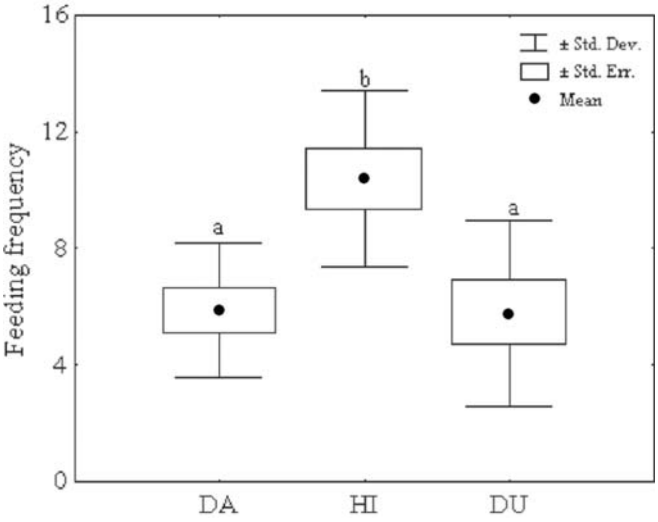

Fig. 3. Feeding frequency of *Hippocampus reidi* throughout the day. *DA* Dawn ($n = 8$), *HI* high light intensity ($n = 8$), and *DU* dusk ($n = 8$). *Different letters* represent significant differences among distinct luminous intensity periods

Significant differences were found when comparing the feeding frequency in the three tested luminous intensities (Kruskal-Wallis; $H = 9.2$ and $P < 0.01$). Feeding frequencies at DA and DU were lower than at HI (Nemenyi; $q_{\text{calc}} = 3.43 > q_{0.05,\infty,3} = 3.31$ and $q_{\text{calc}} = 3.93 > q_{0.05,\infty,3} = 3.31$, respectively). No significant difference was found between DA and DU (Nemenyi; $q_{\text{calc}} = 0.5 < q_{0,05,\infty,3} = 3.31$; Fig. 3).

Feeding preference

Caridean shrimp were the most consumed prey (66%), followed by live brine shrimp (21%) and amphipods (13%). None of the tested seahorses consumed frozen brine shrimp.

Significant differences were found when comparing the different prey categories (Kruskal-Wallis; $H = 12.4$ and $P < 0.01$). Consumption of amphipods and live brine shrimp was significantly lower than of caridean shrimp (Nemenyi; $q_{\text{calc}} = 4.23 > q_{0.05,\infty,3} = 3.31$ and $q_{\text{calc}} = 4.33 > q_{0.05,\infty,3} = 3.31$, respectively). No significant differences were found in the consumption of amphipods and live brine shrimp (Nemenyi; $q_{\text{calc}} = 0.1 < q_{0.05,\infty,3} = 3.31$; Fig. 4).

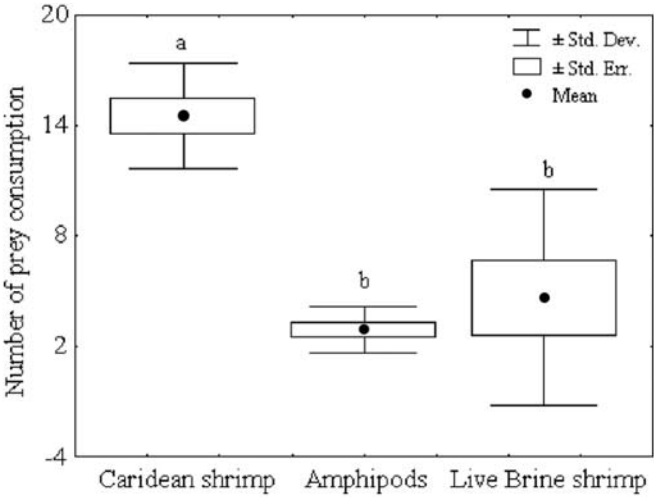

Fig. 4. Number of prey consumed by *Hippocampus reidi*, by tested category ($n = 8$). *Different letters* represent significant differences among groups

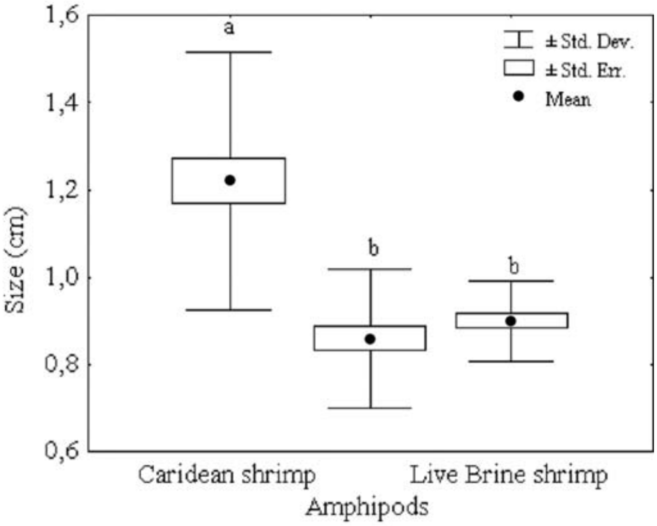

Fig. 5. Size of prey (cm) consumed ($n = 30$) by *Hippocampus reidi* in aquaria. *Different letters* represent significant differences among groups

When comparing the size of the prey used per category, significant differences were found (Kruskal-Wallis; $H = 49.1$ and $P < 0.01$). Amphipods and live brine shrimp were significantly smaller than carideans (Nemenyi; $q_{\text{calc}} = 7.45 > q_{0.05,\infty,3} = 3.31$ and $q_{\text{calc}} = 7.01 > q_{0.05,\infty,3} = 3.31$, respectively). No significant differences were found between amphipods and live brine shrimp (Nemenyi; $q_{\text{calc}} = 0.44 < q_{0.05,\infty,3} = 3.31$; Fig. 5).

Behavior of prey

No change in prey behavior was visually detected. Caridean shrimp mostly rested on the substrate or on the glass and only rarely moved from one place to another; on the other hand, brine shrimp constantly moved throughout the tank; amphipods buried themselves in the gravel and only rarely changed places. They were only captured when partially exposed or while moving.

The feeding behavior of *Hippocampus reidi* in the wild and in captivity

Observations made during 319 feeding events (193 in aquaria and 126 in the field) resulted in a description of five feeding phases for *H. reidi*, summarized in the ethogram below:

1. Inspection: Close visual inspection of the substrate, while swimming or using a holdfast.
2. Visual orientation: Both eyes are directed to the prey; the animal may lower the snout, positioning it close to the ventral region of the body.
3. Approach: The animal slowly approaches the prey, by swimming or by stretching the body while using a holdfast.
4. Positioning: The animal assumes a vertical, horizontal, oblique or upside-down position, while using a holdfast (by wrapping its tail around it or by leaning against it).
5. Strike: The animal moves very fast and directs the snout to the prey; prey is sucked into the snout, and this normally is accompanied by a characteristic noise (click).

Two strategies to capture prey were recorded in the field: (1) "sit-and-wait" – the animal remains still, with the tail wrapped around a holdfast. In this strategy, observed in 84% of the feeding events, only stages 2 and 5 of the ethogram took place. (2) The second feeding strategy was observed when the animal swam in areas with little vegetation; in this case the five stages of the ethogram were recorded. In the field, a failed attempt to capture prey was never followed by its pursuit, while in the aquaria pursuit of prey was recorded. *H. reidi* was sighted feeding from the surface to the maximum depth of the study sites (1 m), and the shortest interval between strikes was 2.5 min.

In the aquaria, during all 193 feeding events, specimens of *H. reidi* fully inspected the area and did not use the "sit-and-wait" strategy. On two occasions specimens of *H. reidi* were observed to dismantle larger prey items (2-cm caridean shrimps) before ingesting one piece at a time.

Discussion

Relationship between feeding frequency and reproductive stage

Although height did not significantly differ between PM and NM, the former exhibited a higher feeding frequency. It is known that pregnancy represents a high energetic cost for the male seahorse (Teixeira and Musick 2001) as males have been shown to be responsible for the osmoregulation and nutrition of the embryos (Strawn 1958; Haresign and Shumway 1981; Masonjones 2001).

Since the seahorse digestive system is simple and not very efficient in terms of nutrient absorption (Michael 2001), the pre-pregnancy storage of nutrients would seem unlikely. Nevertheless, Lyons and Dunne (2004) showed that in the worm pipefish *Nerophis lumbriciformis* post-brooding males had significantly lower values for the hepato-somatic index than either egg-bearing or nonmated males.

With regard to female seahorses, no significant difference was found in the feeding frequency between the reproductive and nonreproductive specimens, and this was probably related to an equivalency in energy costs for producing and maturing follicles. Selman et al. (1991) showed that female seahorses continuously produce mature follicles; Masonjones and Lewis (2000) remarked that females may be physiologically capable of mating immediately after encountering a sexually receptive male, but require at least 2 days to prepare a clutch of eggs and became sexually receptive.

Relationship between feeding frequency and luminous intensity

Vision is the primary sense used in prey detection and capture in many teleost fish (Blaxter 1980), therefore luminous intensity influences their feeding activity. Seahorses are active predators, feeding exclusively on live prey (Wilson and Vincent 1998), and like most fish species, they depend on vision in their search for prey (Guthrie 1986). It is accepted for many fishes that visual predation in the aquatic environment is strongly correlated with ambient light levels (Vinyard and O'Brien 1976; Howick and O'Brien 1983; McFarland 1986) and that feeding is reduced when intensity falls to 10 lux, i.e., at dawn and dusk (Blaxter 1965).

However, James and Heck (1994) showed that *Hippocampus erectus* fed equally well at dawn and dusk and at high light intensities, although it is not a nocturnal predator. Most studied seahorse species are considered diurnal predators, an exception being *Hippocampus comes*, which was shown by Perante et al. (2002) to be a nocturnal species, being active from dusk to dawn.

Our results showed that *H. reidi* feeds at dawn and dusk and high light intensities, but not at night. Its feeding frequency peaked at the highest luminous intensity (1,400–1,600 lux), suggesting the existence of a direct relationship between those two parameters. Similarly to what has been reported for *H. erectus* by James and Heck (1994), *H. reidi* was able to locate prey at low luminous intensity (0.8 lux), an expected characteristic for a species known to feed in estuarine areas where water visibility generally is low. Nevertheless at night *H. reidi* not only ceases feeding, but also stops swimming and wraps its tail around a holdfast, sometimes remaining in that position until the onset of dawn.

Regarding behavior of prey in relation to luminous intensity, although some studies have shown that some crustaceans may experience changes in behavior due to light levels (e.g., Hooks et al. 1976; Greening and Livingston 1982; Bauer 1985), no behavioral change was visually detected in this study, suggesting that prey behavior did not interfere with the feeding behavior of *H. reidi* at the different luminous intensities tested.

Consumption of prey per unit of time is a poorly studied topic in the whole genus *Hippocampus*. Published data are limited to James and Heck (1994), who showed that *H. erectus* could consume 20 prey items offered within a 3-h period and never consumed all 20 prey items within 2 h. In the present study, the maximum number of prey consumed per hour was 16, a figure that approaches the results obtained by James and Heck (1994). Among other aspects, this relatively high daily prey consumption should be taken into consideration by those who wish to keep seahorses in aquaria.

Feeding preference in the laboratory

Caridean shrimp were the largest prey items offered to *H. reidi* and also the most consumed prey. Fish tend to consume the most accessible prey – that which requires the lowest energy expenditure on the part of the predator. This strategy, known as the optimum foraging theory, constitutes the basis for the field of feeding ecology (DeLoach 1999). Selection of prey by a predator may be a result of accessibility of prey and not of preference, because factors such as prey size and mobility are fundamental to the visual detection of prey by the predator (Main 1985). This may explain why the cover-seeking amphipods were the least captured food item (13%). However, other factors were also relevant. Caridean shrimp and live and frozen brine shrimp were equally accessible in the tank, but unequally consumed. No frozen brine shrimp were consumed, possibly due to seahorses' preference for live food, and the lack of artificial agitation of the frozen food provided in the experiments. Collin and Collin (1999) showed that the structure of syngnathid eyes may make them adapted to moving and carotenoid-rich prey, and Woods (2003) pointed out that the weaning of seahorses onto frozen foods may take time and can depend on the appearance of frozen food after the freezing/thawing process.

Capture of the highly mobile live brine shrimp was relatively low, while the more sedentary caridean shrimp were consumed most frequently. This suggests that size and not only mobility influenced the prey choice of *H. reidi*. Although still inconclusive, our observations suggest that *H. reidi* may select less mobile, relatively larger prey (1–2 cm).

Similarly to what was observed in this study, Woods (2002) has shown that *H. erectus* is capable of breaking larger prey into smaller pieces, which are then ingested by the seahorse. This disagrees with the view that gape limitation constitutes a constraining factor for seahorses that limits them to exploiting only smaller prey species (Teixeira and Musick 2001), and suggests that at least some seahorse species have adapted to making use of prey larger than their mouth gape.

Feeding behavior

A study of syngnathid feeding kinematics described three phases in their strikes: preparatory, expansive and recovery. In the preparatory phase, the seahorse slowly approaches the prey in an upright orientation, slowly flexing its head ventrally. During the expansive phase, prey capture is accomplished by simultaneous elevation of the head and expansion of the buccal cavity: the prey item is sucked in. In the recovery phase, the jaws, head and hyoid apparatus return to their starting positions (Bergert and Wainwright 1997).

The preparatory phase described by Bergert and Wainwright (1997) corresponds to the orientation phase described in the present study, while the expansive phase corresponds to the strike phase. The other phases described in the present study focused on movements of the body that were not analyzed by Bergert and Wainwright (1997), and therefore do not correspond to the phases described by them. James and Heck (1994) described the various phases of the feeding behavior of *H. erectus*, and these coincide with the phases described in our ethogram for *H. reidi*, suggesting that their feeding behaviors resemble each other, at least in captivity conditions. The characteristic snapping sound during feeding produced by protusion of the jaws in seahorses (Lourie et al. 1999) and observed in *H. erectus* (James and Heck 1994; Colson et al. 1998) and *Hippocampus zosterae* (Colson et al. 1998) was also observed in the present study. Prey pursuit behavior in aquaria described in this study, and also observed by James and Heck (1994) differed from prey capture in the field, where no pursuits occurred. Water conditions in aquaria (e.g., transparent, no currents) and the absence of predators possibly explain the observed differences.

The amount of available coverage also seemed to influence the feeding behavior of *H. reidi*. In the field, in areas with little vegetation, *H. reidi* not only captured prey through a "sit-and-wait" strategy, as described for some syngnathids, such as *H. zosterae* (Tipton and Bell 1988) and *Urocampus carinorostris* (Howard and Koehn 1985), but also exhibited a high degree of inspection of the surroundings, and fed while swimming. In aquaria with little vegetation, the specimens fully inspected the area, and never used a "sit-and-wait" strategy to capture prey. James and Heck (1994) found no differences in the feeding frequency of *H. erectus* in aquaria with different densities of vegetation, due to a change in the strategy of prey capture. Similarly to what has been observed for *H. reidi* in the present study, the specimens of *H. erectus* observed by James and Heck (1994) in aquaria with low density of vegetation spent most of their feeding period moving, while those in the tank with a high density of vegetation used holdfasts during feeding.

Feeding ecology of most seahorse species is still poorly studied, and much remains to be done to better understand the interactions between these animals and their habitat. As pointed out by Foster and Vincent (2004), biological knowledge along with population monitoring and fisheries management are required to better understand the impacts of the harvesting and trade of seahorses.

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