



Biology of a seahorse species, *Hippocampus comes* in the central Philippines

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Based on 16 months of field observations on tagged seahorses *Hippocampus comes* in the Philippines, adults were found to be nocturnal, to maintain small home ranges, and to live mostly among corals. Prolonged pair associations suggested that *H. comes*, like many other seahorse species, were probably monogamous, a conclusion consistent with their low density and sparse distribution. Site and mate fidelity suggest that *H. comes* populations may fare poorly under current high levels of exploitation.

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INTRODUCTION

About 70% of the world's estimated 32 seahorse species (genus *Hippocampus*) are found in the Indo-Pacific (Lourie *et al.*, 1999a,b), but none has ever been studied in the wild. Moreover, no research has yet been published on habitat choice or movement in any seahorse species around the world. Existing studies focus on reproductive behaviour of seahorses in the laboratory (Fiedler, 1955; Vincent, 1990, 1994a,b, 1995; Masonjones & Lewis, 1996, 2000; Masonjones, 2001) or on reproductive ecology of temperate seahorse species in the wild (Vincent & Sadler, 1995; Jones *et al.*, 1998; Kvarnemo *et al.*, 2000). It would be inappropriate to infer reproductive behaviour and ecology of tropical seahorses from research on temperate species. For example, seahorses at lower latitudes may produce smaller eggs (Vincent, 1990), and reproductive seasons in the tropics tend to be triggered by monsoons rather than by photoperiod as in temperate zones (McClanahan, 1988; Reichenbach, 1999).

Certain elements of reproductive ecology are common to all seahorse species. In particular, male seahorses exhibit specialized paternal care of young. The female seahorse deposits her eggs into the male's brood pouch, where they are fertilized. The male then protects the young in the pouch, provides oxygen through a capillary network, osmoregulates the developing embryos (Leiner, 1934; Linton & Soloff, 1964), and transfers nutrients (some of them maternally derived) to his offspring (Boisseau, 1967; Haresign & Shumway, 1981;

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Masonjones, 1997). After *c.* 10 days to 6 weeks, depending on species and water temperature, the male releases young that are thereafter entirely independent of the adults.

Laboratory experiments on an Indo-Pacific species, *Hippocampus fuscus* Rüppell, indicated that males competed more to receive eggs, by snapping and tail wrestling, than females did to transfer eggs (Vincent, 1994b). After mating, however, it took longer for a male than a female to be ready to mate again (Vincent, 1994a). This apparent contradiction between predominant competition for mates and relative reproductive rates of the two sexes probably arises from the long-term sexual monogamy in many species (Dauwe, 1993; Nijhoff, 1993; Vincent & Sadler, 1995; Masonjones, 1997). The only study of movement patterns in seahorses, on the temperate Australian species, *Hippocampus whitei* Bleeker, found that both sexes or paired individuals ignored non-partners they encountered (Vincent & Sadler, 1995) in their small home ranges (A. Vincent, unpubl. data). Thus, significant competition for mates will presumably only occur if at least three seahorses lack partners, and hence recent matings.

The Indo-Pacific has both the greatest diversity of seahorses and the greatest threats to persistence of their populations. A large and growing trade in seahorses for traditional medicines, aquarium fishes and curiosities appears to be contributing to declines in their populations across the region (Vincent, 1996). In addition, these fishes are frequently taken in trawl bycatch, and are vulnerable to destruction and degradation of their coastal habitats (seagrasses, mangroves, corals and estuaries). Asian fishers repeatedly cited reductions in the wild catch of 15–50% over 5 years from 1990 (Vincent, 1996). An understanding of the biology of these species would greatly assist in their management and conservation.

The present study concentrates on *Hippocampus comes* Cantor, a seahorse species found in the Philippines. This species is of medium height (maximum *c.* 15 cm from top of coronet to tip of straightened tail), usually black and yellow coloured, and commonly distinguished by a striped tail (Lourie *et al.*, 1999b; Fig. 1). No field studies have previously been conducted on *H. comes*, yet this is a heavily exploited seahorse (Vincent, 1996). Fishers in north-western Bohol in the central Philippines reported catch declines of *c.* 70% for the 10 years from 1985 (A. Vincent, unpubl. data). The aim of the research was to provide information on the biology of wild *H. comes*, that could assist in the development of management and conservation measures for threatened populations.

MATERIALS AND METHODS

STUDY SITE

Research was conducted off the village of Handumon, Jandayan Island on the north-western edge of Bohol (Fig. 2). Jandayan is in the southern part of the Camotes Sea, in one of the densest areas of coral reefs in the Central Philippines. These coral reefs form part of the Danajon Bank, a double barrier reef; the outer barrier stretches 148 km along the coast of Bohol, the inner barrier is 28 km long, and each barrier is *c.* 2.8 km wide (Pichon, 1977).

Hippocampus comes had been heavily fished throughout the region, leaving no populations unexploited. A study site was therefore established in Handumon's new

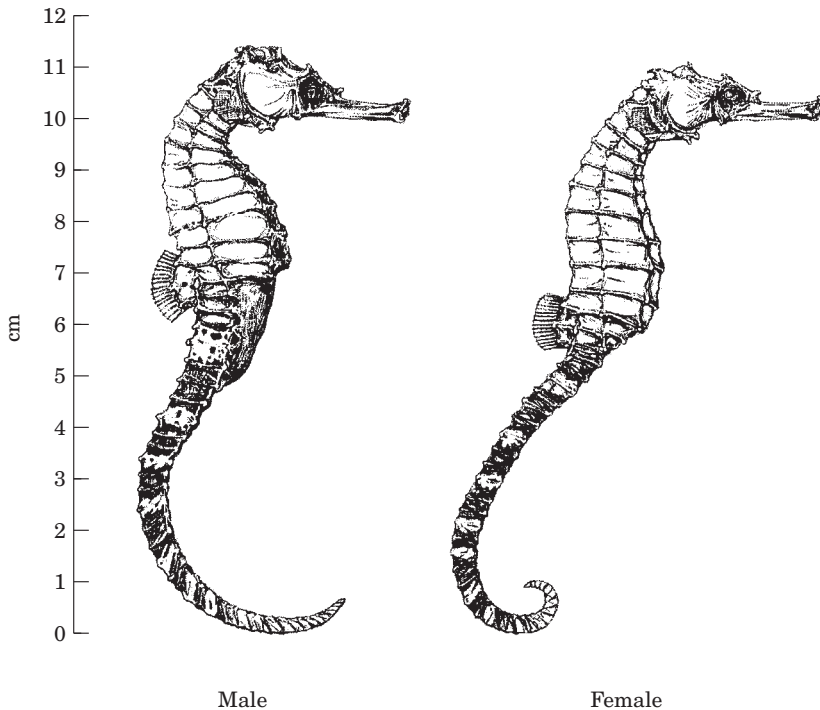


FIG. 1. Male and female *Hippocampus comes*, showing the striped tail found in many individuals. Used with permission of L. Richardson.

33 ha no-take marine protected area (MPA; Fig. 2). The MPA was created in 1995 by the community of Handumon, and community patrols have since protected it from fishing (Vincent & Pajaro, 1997). Extending 1 km along Jandayan Island, the MPA consisted of the following habitats: (a) a shoreline of mangroves; (b) a shallow flat of *Sargassum* and coralline rocks, mostly exposed at low tide; (c) a narrow coral reef flat; (d) a reef slope with an average depth at the crest of 2 m at high tide and <1 m during spring low tides; (e) a sandy bottom at *c.* 8 m depth. Horizontal visibility usually ranged from 3 to 5 m, but heavy rains or typhoons reduced this to <1 m.

The study site was based around the greatest density of seahorses in the MPA, covering a 110 m stretch along the reef crest and the full 15 m width of the subtidal reef crest area, for a total area of *c.* 1650 m². The original seahorse populations on the reef had been depleted by decades of heavy exploitation before the MPA was declared, but repopulation was occurring in four ways: (a) reproduction in the remnant resident seahorse population; (b) natural recruitment from other areas in the region; (c) restocking by fishers, who haphazardly released some of the seahorses they caught elsewhere in an attempt to revive local populations; (d) settlement of the young released by males that had been caught elsewhere, and placed in cages on the MPA to give birth.

FIELD SAMPLING AND OBSERVATIONS

Research carried out for 8 months after the implementation of the MPA (April–December 1995) was treated as a pilot study (April–December 1995) which allowed the population to recover partially from its previous disturbance, and allowed methods to be tested. Data gathered during this pilot phase were excluded from data analyses but are cited anecdotally. The main study was from January 1996 to April 1997.

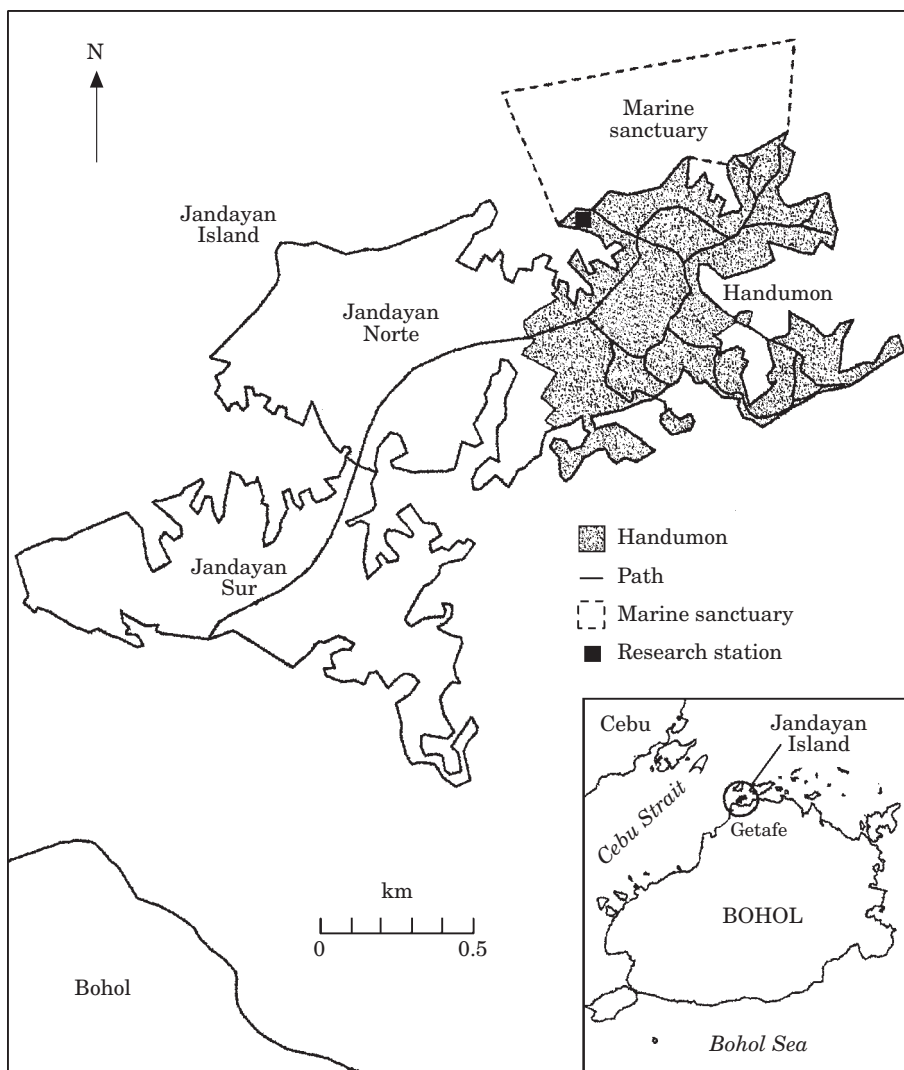


FIG. 2. Map of Jandayan Island in the central Philippines, and the location of Handumon's 33 ha no-take marine protected area. Used with permission of J. Villasper.

Mapping and tagging

Two 50 m line transects were laid over the study site and the benthic community and possible holdfasts (branching coral or sponge, *Sargassum*, twig or any other appropriately narrow object) were mapped for representative benthic covers.

Local spearfishers helped to survey the study area in January 1996 and every 3 months thereafter, in order to ensure that all seahorses within the study site were discovered and tagged. Fishers are highly skilled at spotting seahorses because of their many years of experience catching them by hand (A. Vincent, unpubl. data).

All seahorses found from January 1996 to April 1997 were tagged with yellow oval PVC discs, measuring 5.5×3.0 mm with a number on one side and a symbol on the other. These were hung on a thread (or later fine nylon gut) which was then tied loosely around the seahorse's neck. The tags became covered with algae and probably did not

affect seahorse crypsis. The collars were checked on each visit and loosened or replaced as the seahorse grew. This method of tagging (Vincent & Sadler, 1995) is only suitable for populations that are closely monitored.

The location of each seahorse found in the study site was marked by a small concrete block (12 × 12 cm) with a small styrofoam float attached. The markers were submerged, and rapidly grew a covering of algae that helped them blend with the underwater environment.

Observations

The site was monitored 55 times during the 16 month main study period (mean ± s.d. = 3.8 ± 2.4 visits per month) for a total of *c.* 156 h of observations. Surveys were undertaken by snorkel during low tides or by SCUBA during high tides. All observations were made at night because the reports of fishers, the 8 month pilot study, daytime surveys and 24 h watches all confirmed that seahorses could not be found by day. Night lasted from *c.* 1830 to 0530 hours, and most observations were made between 0230 and 0500 hours although some were between 1700 and 1900 hours.

Each survey involved finding all seahorses on the site, whether tagged or new recruits, then recording their identity, location on the grid, holdfast type, reproductive state (Table 1) and associations with other animals. Previous monitoring of seahorse matings and births has shown that shape of the male's pouch and the female's trunk provides a robust index of reproductive state (Vincent & Sadler, 1995).

Home range size was calculated as the mean distance a seahorse was located from its typical holdfast; home range sizes were too small to make more detailed analysis biologically meaningful. A seahorse had to spend a minimum of 7 days (to allow repeated sightings on the study survey schedule) on or within 1 m of a given holdfast before it was judged to have established a home range.

Associations with other animals included pairing and other groupings. Putative pairs of seahorses were inferred through: (a) proximity, with animals <0.5 m apart listed as possible partners and (b) synchrony of reproductive state between putative partners.

DATA ANALYSES

The number of observations, site fidelity, home range fidelity and size, and proximity by sex and pair status were compared using *t*-tests (Zar, 1999). χ^2 goodness of fit was used to assess holdfast preference (Zar, 1999). Logistic regression was used to evaluate seasonal variation in reproductive state (Tabachnick & Fidell, 1996). All values are reported as mean ± s.d. except where otherwise stated.

RESULTS

POPULATION

Densities on the study site were low. A total of 32 seahorses was tagged within the 1650 m² site, for a mean of 0.019 seahorses m⁻² or one seahorse for every 52 m². Mean distance among seahorse locations throughout the study was 5.8 ± 8.9 m (Fig. 3). Mean distance among seahorses themselves was, however, greater (8.2 ± 8.1 m) because a maximum of 15 seahorses was resident on the study site at any one time (Fig. 3). The number of seahorses observed on the study site neither increased nor decreased during the course of the study (Fig. 4).

The ratio of males to females on the study site was equal. The total study population included 13 females (264 total observations), 15 males (234 total observations) and four juveniles of uncertain sex (18 total observations). Each male seahorse was seen on 15.6 ± 15.9 nights while each female was seen on 20.3 ± 18.7 nights, but the mean number of observations of males and females during the study did not differ significantly (*t*=0.7, d.f.=26, *P*=0.47). The

TABLE I. Possible combinations of reproductive status (RS) of male and female seahorses

Male RS	Male	Female RS	Female	Event
0	Pouch empty and taut	1 or 2	ITR sunken, eggs just transferred	Ready to mate
1*	Pouch full of embryos, brooding	0	ITR flat, developing eggs	Just mated and eggs transferred
1	Pouch full of embryos, brooding	1	ITR bulging, sometimes visible eggs	Brooding
2*	Pouch very distended	2	ITR bulging, sometimes visible eggs	Soon to release young and transfer eggs
3*	Pouch empty and flaccid	2	ITR bulging, sometimes visible eggs	Just released young, ready to mate

ITR, Females intertrunk ridge. *States that signify important synchronies: (a) male from 0 to 1 and female from 2 to 0 when mating, and (b) male and female both changing from 1 to 2 when nearing end of pregnancy and remating.

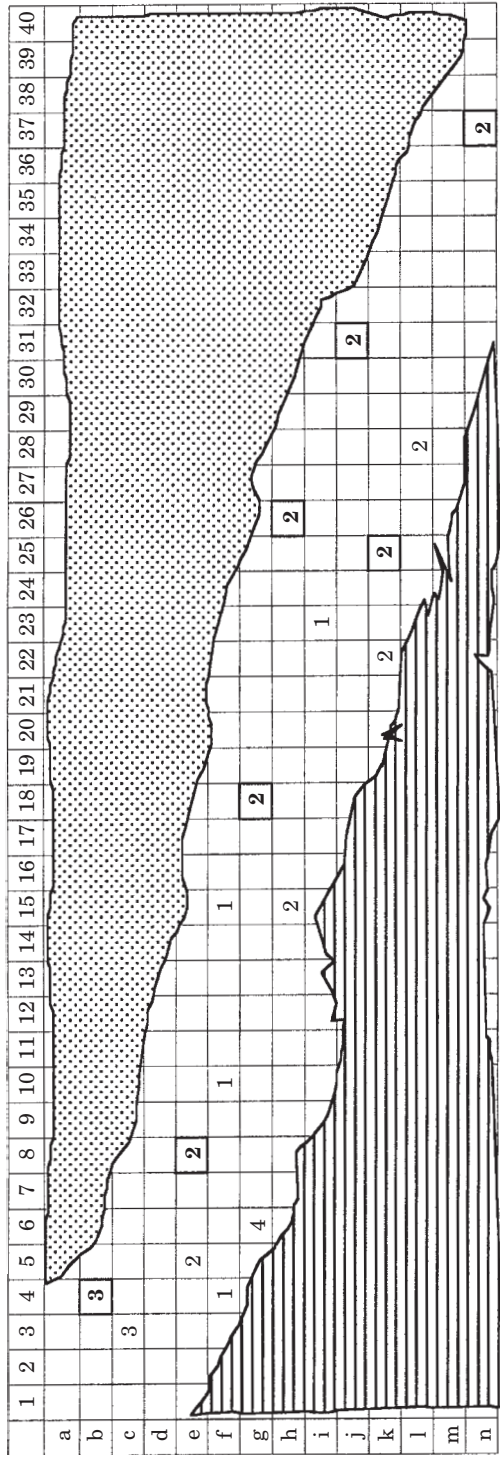


FIG. 3. Location of 17 seahorse stations in the 1650 m² study area from January 1996 to April 1997, indicated by alphabetic (a-n) and numeric (1-40) co-ordinates. The number of seahorses typically found at each station is indicated as singles (1), putative pairs (2), trios including putative pairs (3), and quartets (4). There are more than 32 locations because some seahorses moved. The locations of all individuals on one particular representative day, 7 September 1996, is shown in bold and in boxes ($n=15$). Scale: one grid-square=9 m². ☐, Sandy bottom at 6 m; □, reef crest; ▨, shallow flat.

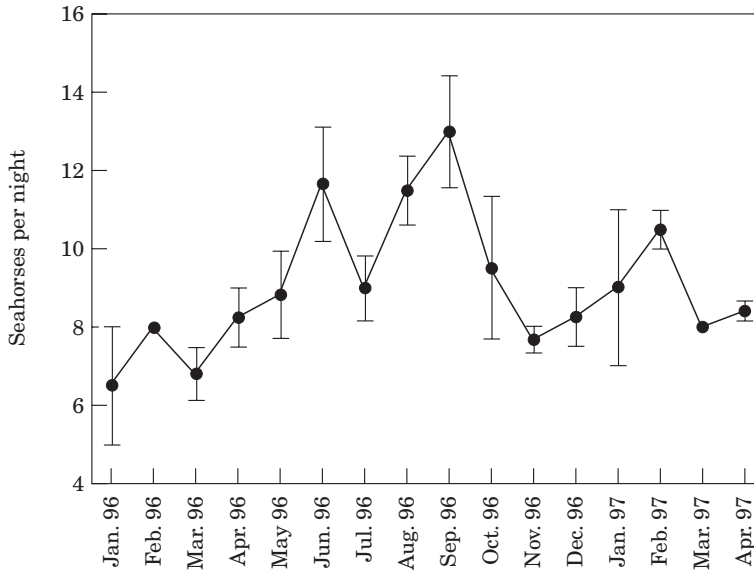


FIG. 4. Mean (\pm S.E.) number of seahorses observed per night during the study.

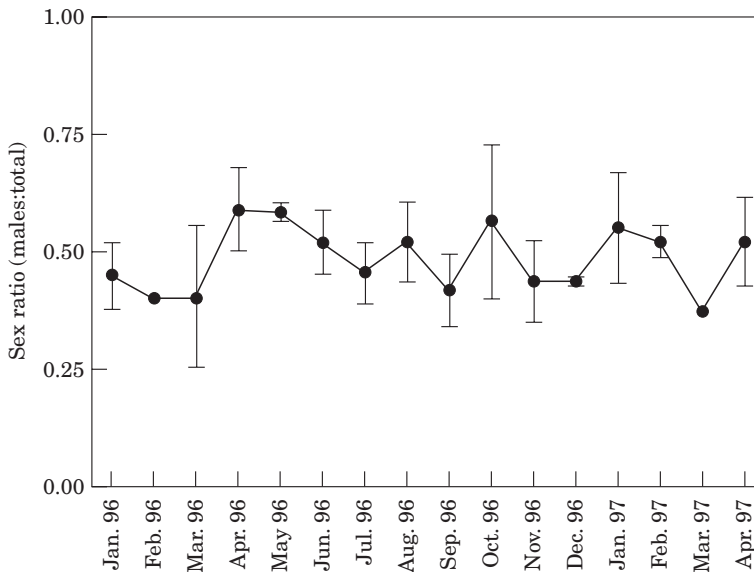


FIG. 5. Mean (\pm S.D.) sex ratio (proportion of males) by month ($n=1$ to 7 depending on the month).

proportion of males of the total adult population in the study site ranged between 0.38 and 0.59 by month (Fig. 5) with a mean proportion of 0.49 ± 0.07 males: regression analysis indicated no trend in the sex ratio through time ($n=16$ months, $P=0.87$).

TABLE II. Availability and use of three major habitat types on the study site

Habitat	Habitat availability (%)	Habitat use (%)			
		First observation Frequency	%	All observations Frequency	%
Branching and massive corals	86	26	81	425	88
Sponges	12	4	13	55	11
Mangrove twigs	2	2	6	3	1

HABITAT

Seahorses were distributed according to holdfast availability, with no apparent preference for any particular holdfast. Within the entire study site, 54% of the area contained potential holdfasts, most of which were corals (Table II). Seahorses used these potential holdfasts in proportion to their availability within the area, whether only the first observation for each seahorse ($\chi^2=3.99$, $n=32$, $P=0.136$; Table II) or all observations throughout the study period ($\chi^2=3.68$, $n=483$ $P=0.159$; Table II) were considered.

Seahorses apparently spent the day hidden among the corals, then moved out from crevices among the corals at dusk. Visits to the study site during the day ($n=20$) yielded no sightings of seahorses, even at known locations. At night, each animal usually positioned itself on the same part of its particular holdfast, and was only rarely seen elsewhere (17 of 516 observations, involving 11 of the 32 seahorses). Seahorses were observed to remain still for at least 2 h, apart from occasional ambush feeding. They moved back into the corals at dawn, usually to a retreat within 0.5 m of their regular holdfast ($n=32$ observations involving 10 seahorses), where their activities remained unknown.

FIDELITY IN SITE, HOME RANGE AND HOLDFAST

Hippocampus comes exhibited considerable fidelity to the study site, remaining within its 1650 m² for 7–486 days of the 16 month (486 days) main study period, with a mean of 177 ± 162 days (Fig. 6). Females were resident for 223 ± 181 days ($n=13$ seahorses), males were resident for 163 ± 157 days ($n=15$ seahorses) and juveniles were resident for 75 ± 37 days ($n=4$). Males and females did not differ in their residency period ($t=0.62$, d.f.=26, $P=0.453$). These figures probably underestimate site fidelity as they do not take into account the time that seahorses were on the site both before and after the study (Fig. 6). For instance, two pairs were tagged on the study site at the beginning of the main study period, so probably spent more time on the study site than the 10 months noted during the study. The corollary is that two later arriving pairs were recorded as spending only 2 and 3 months, respectively, on the study site but may well have remained at the same location after the study ended. This problem with study methodology is reflected in the large standard deviations.

Within the site, each seahorse maintained a small home range focused around a particular holdfast, again for at least 7–486 days ($n=41$ home ranges for 32 seahorses, with five seahorses relocating at least once). At night, each seahorse was generally found within a particular area with a diameter of <1 m ($n=499$ of

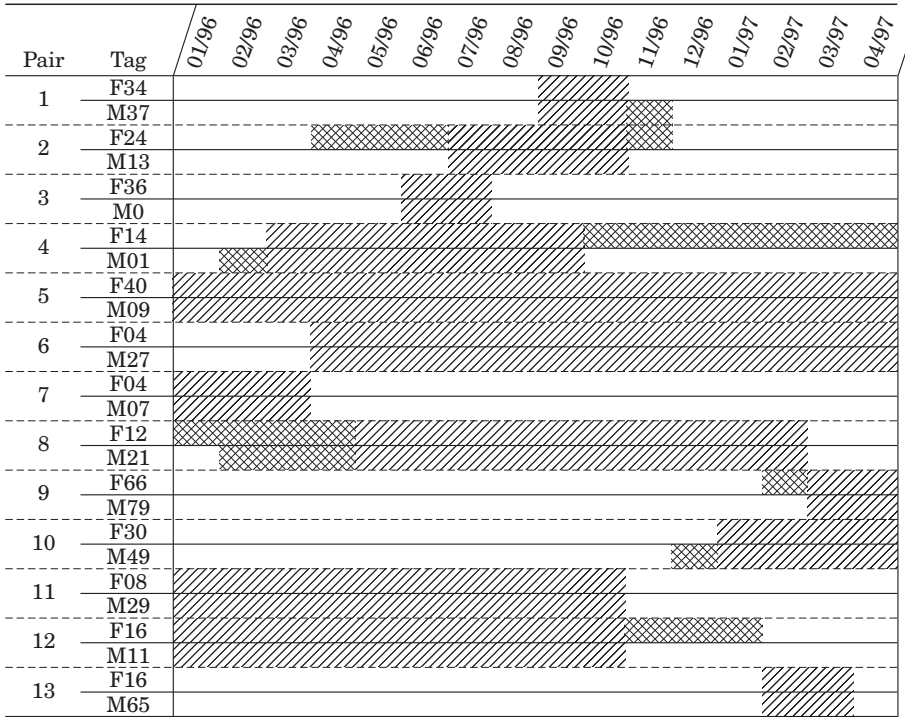


FIG. 6. Duration of pairing by female and male seahorses from January 1996 to April 1997, giving sex (F, female; M, male) and tag number. ▨, Dates on which the individuals were inferred to be paired (i.e. repeated sightings in a shared home range); ▩, continuous dates on which only one individual could be found in a home range.

the 516 observations, including all observations for those that had two home ranges). Mean duration of home range fidelity was 147 ± 141 days ($n=32$) with females staying 168 ± 150 days ($n=13$), males staying 148 ± 150 days ($n=15$), and juveniles sighted repeatedly in the same location for 75 ± 37 days ($n=4$ seahorses); males and females did not differ significantly in fidelity to their home ranges ($t=0.6$, d.f.=26, $P=0.58$). As with site fidelity, these are probably underestimates as seahorses may well have held the same home range before the study began or after it ended. For instance, one pair was still on the same home range 21 months after being tagged during the pilot study, while another pair had been in the same home range for 12 months by the end of the main study period.

Paired seahorses were more faithful to home ranges than were unpaired seahorses (Table III). Seahorses that had relocated were excluded from this analysis, in order to avoid pseudo-replication by including them more than once. Taking mean values for these seahorses was also inappropriate because their pair status sometimes changed with relocation. The data suggest that, among unpaired seahorses, males had a much lower home range fidelity than females, but the sample size was too small for formal analysis ($n=4$). Among paired seahorses, males and females were faithful to a home range for about the same length of time. The means and number of males and females differed slightly

TABLE III. Mean and s.d. for home range fidelity (days) as a function of sex and pair status for 23 non-relocating seahorses

Pair status	Sex	<i>n</i>	Mean	s.d.
Paired	M	11	176	163
Paired	F	8	194	181
Unpaired	M	2	30	6
Unpaired	F	2	62	56

M, males; F, females.

(Table III) because the relocation of some partners precluded a direct match of males and females.

Sexes did not differ in the extent to which they moved more widely. Seahorses found outside the 1 m diameter home range included seven females (10 observations) with inferred home ranges of (mean \pm s.e.) 5.2 ± 1.8 m in diameter and four males (seven observations) with inferred home ranges of 5.7 ± 1.3 m diameter ($t=0.3$, d.f.=9, $P=0.762$).

CHANGING HOME RANGES AND HOLDFASTS

Five of the 32 seahorses relocated to new home ranges within the study site, then remained faithful to their new home range and holdfast. The three females relocated a mean distance of 10.8 ± 9.3 m from their previous home range centres, with the longest move measuring 21.5 m. The two males both moved 6.0 m from their previous home range centres. Juveniles that left locations they had briefly occupied were never seen again.

Seahorses relocated when they had lost either their holdfast and their partner. Four of the five relocating seahorses moved once while one female moved three times, making four home ranges for herself ($n=51$ total observations). One pair of seahorses moved when its sponge holdfast of 3 months was destroyed, one female moved when she lost her partner after the same sponge was destroyed, and one female changed home ranges within the site when her partner disappeared from the study site. Whether abandonment of home range resulted in short or long migrations appeared partly to depend on pair status: (i) one pair moved only 6 m away to a coral holdfast where they stayed for a further 7 months; (ii) the newly single female moved 21.5 m across the study site, found a smaller male, formed a pair with him, and settled on his home range with a coral holdfast for at least 12 months; (iii) the other newly single female disappeared from the study site and the second male was unpaired when he relocated.

SOCIAL ASSOCIATIONS

Seahorses were most commonly sighted in pairs (60% of 516 observations). Putative partners in a pair were found distinctly closer to each other (<0.5 m) than to non-partners (9 ± 10 m: $P=0.009$, $n=13$ pairs; see Fig. 3 for distribution of animals). Male and female putative partners were sometimes observed with their tails coiled together on a particular holdfast for >2 h ($n=30$ out of 516 observations). Seahorses were also observed on their own, with no other

TABLE IV. Social association of seahorses

	Single	Grouping		Quartet
		Pair	Trio	
No. of observations of seahorses	97	310	57	52
No. of observations of groups	97	155	19	13
No. of different groups	na	13	2	2
No. of sightings per group	na	11.9	9.5	6.5

TABLE V. Synchrony between the reproductive state of a seahorse (F, female; M, male) and its putative partner (PP) and its next nearest neighbour

Female association	F match PP only	F match PP and other M	F match other M only	F not match any seahorse	Total
Pair	126	0	0	4	130
Trio	15	4	0	1	20
Quartet	15	4	0	0	19
Male association	M match PP only	M match PP and other F	M match other F only	M not match any seahorse	Total
Pair	125	0	0	5	130
Trio	16	5	0	1	22
Quartet	15	1	0	1	17

seahorse within the 1 m diameter home range, in trios or in quartets (Table IV). The higher number of sightings per pair-wise combination of seahorses suggested that these were probably more stable than the quartets. Indeed, social groups of more than two animals were fluid: one often sighted trio evolved after 4 weeks into a quartet of two males and two females, and one set of trio sightings represented a quartet which one individual was sometimes missing.

The synchrony of reproductive state between putative male and female partners suggests that they really were stable pairs. Where only two seahorses were close together (putatively considered partners), the reproductive state of the female matched that of her putative mate at least 97% of the time ($n=126$ recorded states), while a male's reproductive state matched that of his putative partner at least 96% of the time ($n=125$) (Table V). No seahorse's reproductive state ever matched that of its next nearest neighbour (Table V). Where three or four seahorses were present (trios and quartets), putative partners were defined as the male and female nearest one another within the group. As with the pairs, reproductive state of these putative female and male partners generally matched (>73% of observations, Table V). Within these larger groups, a seahorse's reproductive state sometimes matched that of a putative non-partner as well as

that of his or her putative partner, but never matched only the non-partner (Table V).

All male seahorses brooded young all year round during the time that they were paired, with 75–100% of males reproductively active in any given month. However, logistic regression indicated a strong seasonality in male reproductive activity ($P < 0.001$, McFadden's $Rho^2 = 0.21$, $n = 180$): peaks in reproductive activity (brooding *v.* not brooding) occurred between July and December.

DISCUSSION

This study, the first of an Indo-Pacific seahorse population, shows that individuals were faithful to one partner and one site, similar to that of *H. whitei*, a temperate Australian species (Vincent & Sadler, 1995; A. Vincent, unpubl. data) and *Hippocampus reidi* Ginsburg, a tropical Caribbean species (Dauwe, 1993; Nijhoff, 1993). In contrast, however, preliminary studies have revealed no mate fidelity in *Hippocampus breviceps* Peters (M.-A. Moreau & A. Vincent, unpubl. data) and neither mate nor site fidelity in *Hippocampus abdominalis* Lesson (K. Martin-Smith & A. Vincent, unpubl. data), both from south-eastern Australia. More research is needed to understand factors determining spatial and social structure in seahorse populations.

The nocturnal habits of *H. comes*, not previously documented in seahorses, may be of fairly recent origin. Fishers reported that some *H. comes* seahorses could be seen and caught by day when seahorse fishing started in the late 1960s, but not by the time this study began. They speculate that direct fishing pressure may have selected for a nocturnal behavioural shift in *H. comes*. Previous fishing pressure probably also explained the low density of seahorses in the study site. In semi-structured interviews, older fishers reported they had been able to find 20 seahorses m^{-2} on similar habitat of corals and 10 seahorses m^{-2} on *Sargassum* in 1969 (pre-exploitation), 5–10 seahorses m^{-2} on good reef or *Sargassum* in 1985 (after low exploitation), and far fewer than one seahorse m^{-2} in 1995 (after heavy exploitation) (A. Vincent, unpubl. data). On the other hand, protection under the MPA probably explains why densities of *H. comes* on the study site were higher than elsewhere in the region (0.02 m^{-2} in the MPA *v.* 0.004 m^{-2} outside; N. Perante, unpubl. data).

Adult *H. comes* generally grasped coral, the most abundant subtidal holdfast within the study site. Fishers reported that adult *H. comes* outside the study site also held corals and sponges, even though the region was rich in mangroves and seagrasses. Corals probably provided good holdfasts for seahorses' prehensile tails, crevices for protection from predators, and shelter from strong water movements. The precise holdfast may have been influenced by mate availability. For example one tagged female seahorse changed its holdfast from coral to sponge in a successful bid to mate with a potential partner on a sponge. The lack of *Sargassum* in the reef flat of the MPA may help explain the dearth of settled young seahorses in this study, as they tend to be associated with this macroalgae (Perante *et al.*, 1998).

The fidelity of *H. comes* to a small home range was probably associated with their limited swimming speed, but may also have provided other advantages. First, familiarity with their surroundings may have increased their feeding

success and survival, as in other fishes (Coleman & Wilson, 1996). Second, home range fidelity may have made it easier to relocate their mate: seahorse partners routinely emerged from different hiding places to grasp a common holdfast. Third, retaining the same home range and holdfast may have facilitated crypsis, given that seahorses adopt colours and camouflage quite specific to their location. Finding a mate may be a precursor to site fidelity: seahorses were observed to relocate when without a partner, and become site faithful when in a pair. The similar home range duration for male and female *H. comes* was expected: putative pairs were first recognized by noting their shared home ranges, although the pairings were later validated by matching reproductive states. It should be noted that home ranges for all seahorses may be larger than those described in this study, as animals' movements were not tracked all night, or every night, or under the corals during the daytime.

No aggressive behaviour (e.g. snout snapping and tail wrestling) was observed in this study, either in defence of the seahorses' home ranges or during other social behaviour. The low density and sparse distribution of *H. comes*, and their small home ranges, may have made aggression unnecessary. Indeed, aggressive behaviour has only rarely been documented among other wild seahorses (e.g. *H. whitei*; Vincent & Sadler, 1995) although it has been elicited under experimental conditions in the laboratory (e.g. *H. fuscus*; Vincent, 1994b).

Hippocampus comes seahorses formed partnerships that were apparently sexually monogamous: (i) both putative partners had small, overlapping, home ranges <1 m diameter; (ii) distance between putative partners was <0.5 m as against non-partner distances of 9 ± 10 m; (iii) reproductive synchrony between putative partners was very high (at least 96% of sightings). Both sexes apparently remained monogamous even when they had choices (as with *H. whitei*; A. Vincent, unpubl. data). Whenever trios and quartets of seahorses were observed, only two of the seahorses were reproductively synchronized with one another, and trios eventually evolved into quartets comprising two pairs.

Sexual fidelity to a partner may have been promoted by the sparse distribution and small home ranges of seahorses in the study site. Sexual fidelity has been recognized in other seahorse species: *H. fuscus* (Vincent, 1994a); *H. reidi* (Dauwe, 1993; Nijhoff, 1993); *H. whitei* (Vincent & Sadler, 1995) and *Hippocampus zosterae* Jordan and Gilbert (Masonjones & Lewis, 1996). It has also been documented in several species of *Corythoichthys* pipefish (Gronell, 1984; Matsumoto & Yanagisawa, 2001). Unlike *H. comes*, however, none of these other syngnathids has yet been reported to occur repeatedly in a quartet of two putative pairs. One temperate Australian species, *Hippocampus subelongatus* Castelnau, may change partners among matings, but field data remain limited (Jones *et al.*, 1998).

Why might *H. comes* seahorses be monogamous? The question seems likely to be more important for females. The relative potential reproductive rates of *H. comes* males and females are unknown, but male *H. fuscus* (an Indo-Pacific seahorse with similar reproductive behaviour) that had mated were marginally slower to finish their pregnancy than females were to prepare another clutch (Vincent, 1994a). If this were also the case in *H. comes*, then monogamy might not impair the rate at which males can reproduce (Vincent & Sadler, 1995).

Female *H. comes* may have remained with the same partner because finding a new mate would be energetically expensive and dangerous in terms of predation and physical damage. Once pairing became widespread in the population, it would take time for a widow to find a lone male, even if seahorse density were considerably higher than in this study site (e.g. *H. whitei*; Vincent & Sadler, 1995). The penalty for monogamy may not be high given that female potential reproductive rate only slightly exceeded that of males in other species, even under experimental conditions (e.g. *H. fuscus*; Vincent, 1994a). In the end, monogamy, and hence familiarity, may be advantageous to both partners in enhancing their reproductive efficiency and their brood size (as seems possible in *H. fuscus*; Vincent, 1994a).

CONSERVATION

Monogamy and site fidelity may render *H. comes* particularly vulnerable to over-exploitation. Removal of one partner would compromise the reproductive rate of the other, and over-fished areas would probably not be replenished quickly through immigration from elsewhere. On the other hand, its continuous breeding and nocturnal activity might make *H. comes* less vulnerable to fishing than other seahorses with seasonal breeding and diurnal activity.

Modelling length-frequency catch data of *H. comes* indicated that local seahorse populations were indeed over-exploited (Perante *et al.*, 1998), consistent with fishers' reports that seahorse catch had declined 70% from 1985 (Vincent, 1996). Moreover, this study showed that adult seahorses were slow to recruit into the MPA; there was no obvious directional change in seahorse numbers on the site during the 16 month study, even though the area had historically been a good fishing ground for seahorses.

Seahorses may recover particularly slowly if inferences that their limited mobility and dispersal anchor the continuum of fish movement hold true (Jennings, 2000). Nonetheless, the small home ranges of *H. comes* reported here should mean that existing populations will be secure within MPAs, since only animals on the edge should be vulnerable to fishing pressure (Chapman & Kramer, 2000).

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