REVIEW PAPER

Life history and ecology of seahorses: implications for conservation and management

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We present the first synthesis of the life history and ecology of seahorses, compare relationships for seahorses with other marine teleosts and identify research needs. Seahorses occurred primarily amidst temperate seagrasses and tropical coral reefs. Population densities were generally low, ranging from 0 to 0·51 individuals m^{-2}, but reached $10 m^{-2}$ in some patches. Inferred life spans ranged from 1 to 5 years. Seahorses consumed live prey and possibly changed diet as they grew. Growth rates are poorly investigated to date. Reproduction and mating systems are the best-studied aspects of seahorse ecology. The relationship between size at first maturity and maximum size in seahorses conformed to that for other marine teleosts. All seahorse species were monogamous within a cycle, but some were polygamous across cycles. Direct transfer of clutches to the brood pouch of the male fish made it difficult to measure clutch size in live seahorses. After brooding, males released from *c.* 5 to 2000 young, depending on species and adult size. Newborn young measured from 2 to 20 mm in length, which was a narrower size range than the 17-fold difference that occurred in adult size. Newborn body size had no relationship to adult size. Both eggs and young were larger than expected among marine teleosts, even when considering only those with parental care, but brood size at release was lower than expected, perhaps because the young were more developed. The size of adults, eggs and young increased with increasing latitude, although brood size did not. Considerable research is needed to advance seahorse conservation and management, including (a) fisheries-dependent and fisheries-independent abundance estimates, (b) age- or stage-based natural and fishing mortalities, (c) growth rates and age at first maturity, and (d) intrinsic rates of increase and age- or size-specific reproductive output. Current data confirm that seahorses are likely to be vulnerable to high levels of exploitation. © 2004 The Fisheries Society of the British Isles

Key words: growth; *Hippocampus*; movement; reproduction; survival; syngnathid.

INTRODUCTION

Sound knowledge of the life history of species is essential for their conservation and management. Theoretical and empirical analyses show that certain life-history characteristics make species more vulnerable to overexploitation (Jennings *et al.*,

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1999; Sadovy, 2001; Denney *et al.*, 2002). For example, comparative studies have indicated that, all else being equal, species with low rates of natural population increase and small geographic ranges, complex social behaviour and distributions in vulnerable habitats are more likely to be overfished (Sadovy, 2001). In general, populations of species that are common and widely distributed with broad dietary and breeding needs (generalists) are more likely to be resilient to exploitation and disturbance than populations of species with limited distributions and specific needs (specialists). As well as providing an indication of vulnerability, a knowledge of the detailed life-history traits of target species may influence the effectiveness of different management approaches. For example, marine reserves are thought to be most effective for animals with intermediate levels of juvenile and adult movement (Botsford *et al.*, 2003). As another example, stage class modelling of the loggerhead sea turtles (*Caretta caretta*) indicated that juveniles were the most vulnerable life-history stage and that conservation efforts, often focused on eggs and nesting beaches, would be more effective if refocused to reduce by-catch (Crouse *et al.*, 1987).

Seahorses (*Hippocampus* spp.) are among the many genera whose life histories might render them vulnerable to overfishing or other disruptions such as habitat damage. They are generally characterized by a sparse distribution, low mobility, small home ranges, low fecundity, lengthy parental care and mate fidelity. In addition, the male seahorse, rather than the female, becomes pregnant. Indeed, curiosity about this phenomenon explains why currently more is known about reproduction than about other life-history parameters. Such life-history characteristics (notwithstanding exceptions to these generalities) may help explain why 10 seahorse species are listed as 'Vulnerable' or 'Endangered' on the 2003 IUCN Red List of Threatened Species (IUCN, 2003). The other 23 species are listed as 'Data Deficient', which reflects substantial gaps in knowledge even for heavily exploited seahorses.

The existing information on seahorse life history and ecology was synthesized, to promote management derived from the best-available biological knowledge. Understanding seahorse life history becomes particularly important now that the entire genus *Hippocampus* has been added to Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). This listing requires the 166 signatory nations to manage international trade to enable the persistence of wild populations. To better understand the impacts of the harvesting and trade of seahorses requires knowledge of their biology, along with population monitoring and fisheries management.

Throughout this review, an attempt was made to predict unquantified life-history variables by comparing seahorses with other marine teleosts. Empirical relationships across life-history parameters in fishes are often consistent across taxonomic groups (Beverton & Holt, 1959; Jennings *et al.*, 1999; Froese & Binohlan, 2000; Pope *et al.*, 2000; Frisk *et al.*, 2001). Comparative analyses allow us to estimate life-history parameters that are difficult to measure (such as growth and mortality) from parameters that are more easily assessed (such as maximum body size) (Jennings *et al.*, 1999). Where seahorses conform to empirical relationships known within and across other species, we can make crude estimates of the unknown life-history parameters needed for management.

Seahorses comprise one genus (*Hippocampus*) of the family Syngnathidae, which otherwise consists of about 55 genera of pipefishes, pipehorses and seadragons (Kuiter, 2000). The entire family Syngnathidae falls within the order Gasterosteiformes (Vari, 1982; Fritzsche, 1984; Palsson & Pietsch, 1989; Nelson, 1994; Orr, 1995) (Fig. 1). Seahorse species are distributed circumglobally, leading to the suggestion that the genus is pre-Tethyan in origin, and at least 20 million years old (Fritzsche, 1980). Such ageing is supported by genetic evidence, although the origin of many species is believed to be much more recent. For example, *Hippocampus algiricus* and *Hippocampus reidi* are thought to have diverged 0·5 to 1·3 million years ago (Casey *et al.*, 2003). Recent attempts to resolve the entire phylogeny of seahorses using the cytochrome *b* gene of mitochondrial DNA concluded that several species designations needed re-evaluation and that further studies would be required to assess patterns and processes of seahorse dispersal (Casey *et al.*, 2003).

The taxonomy of seahorses still requires clarification. Lourie *et al.* (1999) recognized 32 species in the genus *Hippocampus*, yet Kuiter (2000, 2001) believed there might be over 50 species. The difficulties with species identification and the large number of names (>120) used in the early literature meant that the names given to seahorses were often unreliable. Taxonomic confusion surrounded two species in particular: the designations *Hippocampus histrix* and *Hippocampus kuda* were used for virtually any spiny or smooth seahorse respectively in the Indo-Pacific (Lourie *et al.*, 1999). We chose to use the taxonomy of Lourie *et al.* (1999) and Lourie & Randall (2003) for the purposes of this review, as this list of 33 species has been adopted by the IUCN Species Survival Commission.

METHODS

In collating this review, a wide array of sources were canvassed to assemble as much data as possible. Primary literature was supplemented with information from field guides
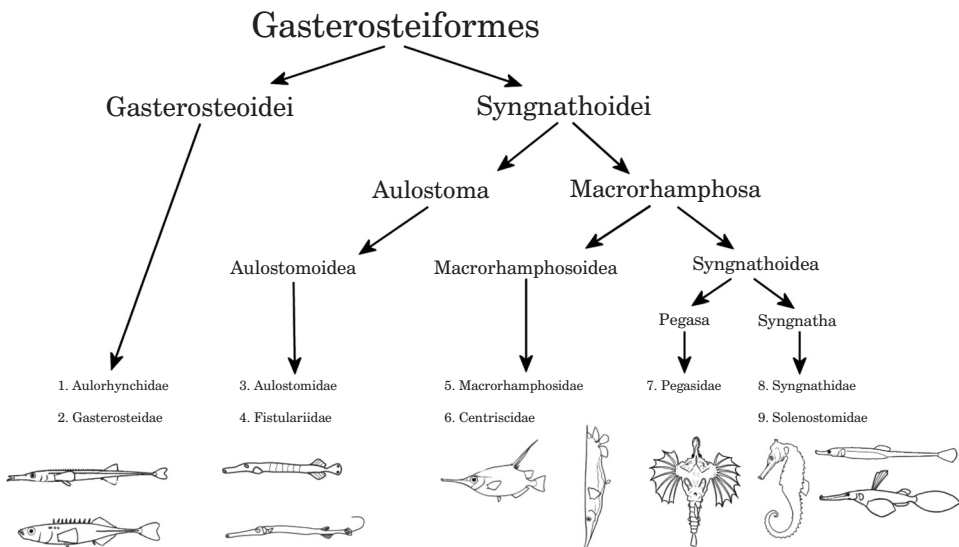

FIG. 1. Phylogeny of the order Gasterosteiformes (based on Orr, 1995; drawings from Nelson, 1994, reproduced with permission from John Wiley and Sons).

and other books, grey literature (reports, theses), and communications with syngnathid researchers and aquarists worldwide. Even with such extensive coverage, this required the integration and comparison of data collected under quite different conditions. Unfortunately, *in situ* and *ex situ* research could not be separated (although studies were labelled accordingly for each comparison), nor was it possible to control for a wide suite of other environmental variables that may have influenced findings reported within each study.

This paper relied heavily on measures of seahorse size, especially maximum observed body length, a strong predictor of life-history variables in fishes (Beverton, 1963; Charnov, 1993; Sadovy, 1996; Pauly, 1998). Seahorse measurements were most commonly given as height (Ht) or standard length (SL). Height was measured from the top of the coronet to the tip of the straightened tail, while SL was measured as head + trunk +
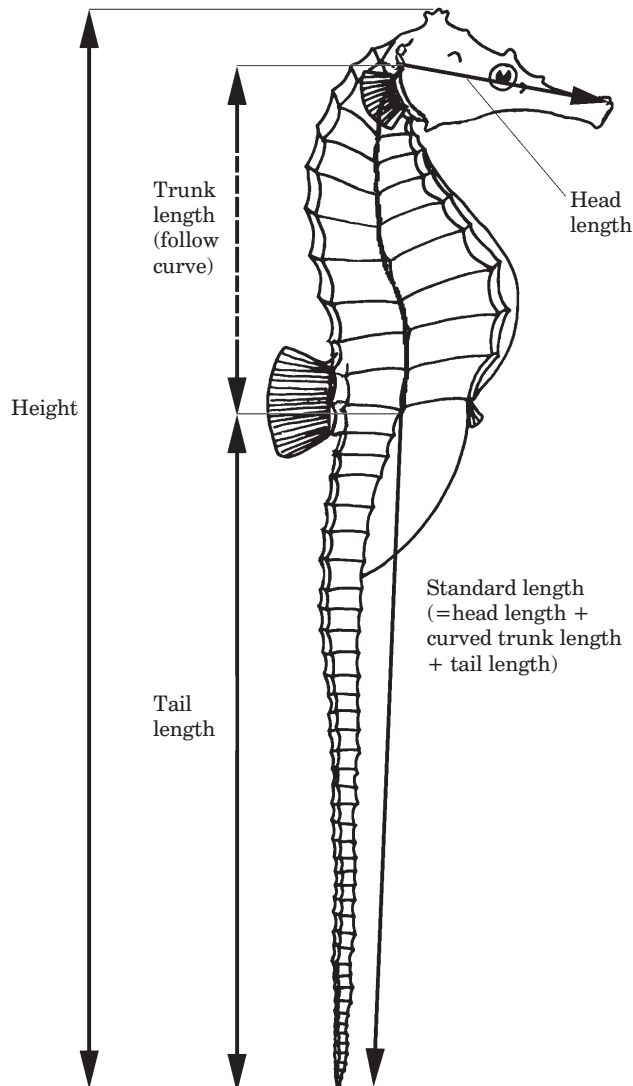

Fig. 2. Height (Ht) and standard length (SL) as measured on a seahorse (figure by S. A. Lourie, published with permission).

tail length (Lourie *et al.*, 1999; Fig. 2). Total length (TL) cannot be measured in seahorses because they lack a caudal fin; researchers who claimed to have measured TL had probably recorded height. For the purposes of this study, all SL measurements were converted to Ht using metric conversions provided by researchers. This measure is shorter than the SL used for other fish, but is valid for comparative purposes. Undefined 'lengths' were assumed to equate to heights, as these are the easiest and most commonly used seahorse measurements. The different, and often undefined, means of measuring used across studies made it difficult to standardize information on seahorses' maximum adult height (Ht_{max}) or height at onset of sexual maturity (Ht_{mat}).

A relationship between latitude and many life-history variables was expected, mainly because environmental factors such as temperature and photoperiod that vary with latitude are known to affect physiological function in many species (Thresher, 1988). Where possible, the actual latitude of the study site was used. For cases where the location of the study was not given, the latitude of the mid-range of the species distribution was used, as reported in Lourie *et al.* (1999) (Table I), a source which was highly conservative in its designations of species' ranges. Some species, such as *Hippocampus erectus*, have such extensive latitudinal ranges that intraspecific differences may be due to geographic location, not detectable by using the mid-point of their occurrence. Nonetheless, available data for *H. erectus*, and other wide-ranging species, were included in the analyses.

Two approaches were used for extracting a single value from diverse sources. For egg diameter, gestation duration and length at birth, the arithmetic mean of available values (*n*) were used, as given in Tables VIII and X. The mean latitude across all studies was used to calculate the final latitude for analysis. In contrast, however, maximum recorded brood sizes (number of young released by a male in any one cycle) were used for comparisons with Ht_{max}. Such analyses were based on the assumption that brood size increases with adult size (Nguyen & Do, 1996; Teixeira & Musick, 2001; Vincent & Giles, 2003), but such clutch and brood sizes may have underestimated reproductive output at Ht_{max}, if the counts came from smaller animals. When required, life-history variables were log$_e$-transformed for analyses to reduce heterogeneity of variance.

Data on multiple species are always presented in alphabetical order, by specific name. The authorities for all species are given in Table I. References for specific life-history parameters cited are found in the appropriate table if not individually cited in the text. In reference to the release of young from the pouch of the male fish, the term 'born' is used.

Life-history data for marine teleosts other than seahorses were extracted from tables in FishBase (July 2003 edition, Froese & Pauly, 2003). Teleost species were those designated as belonging to the class Actinopterygii (ray-finned fishes) as indicated by class number '6' in the FAMILIES table, and marine fishes were defined as those species with a 'yes' entry under the 'marine' field in the ECOLOGY table. The maximum reported length (L_{max}) for a species was obtained from the SPECIES table. Length at first maturity (L_{mat}, defined by FishBase as the mean or median length at onset of sexual maturity) was taken from the MATURITY table, and the fecundity (FecundityMax, defined as the absolute fecundity in number of eggs found in a female which is not the same as released from a female, especially for batch or fractional spawners) was taken from the SPAWNING table. The maximum reported length at first maturity and fecundity were used so the data would be comparable to the measures of first maturity and reproductive output used for seahorses (the maximum reported height at first maturity, or the maximum reported brood size respectively). Similarly, the mode of the reported egg diameters (Eggdiammod, the most frequently reported value for egg diameter from the EGGS table) and length at birth (LBirthmod, the most frequently reported value for length upon hatching from the LARVAE table) were used to allow comparison with the mean egg diameters and lengths at birth used for seahorses in the analyses.

Analysis of Covariance (ANCOVA) was used to test for differences between seahorses and other marine teleosts for certain life-history parameters, controlling for differences in maximum size. Where appropriate, the life-history variable was tested against two subsets of data from FishBase: (a) all marine teleosts with $L_{max} <51$ cm (except in the case of L_{mat} where all available data were used) and (b) all marine teleosts that exhibit some

TABLE I. Latitude of the mid-range of the species distribution (− = south), maximum recorded adult height (Ht_{max}) and height at first maturity (Ht_{mat}) for seahorses (*Hippocampus* spp.). Ht_{mat} is the largest value recorded for that species (which may be a mean within the particular source study). * indicates species for which the smallest recorded adult Ht was used as an estimate because no records of Ht_{mat} could be found. The values for Ht_{max} in this table are the values used for all regression analyses involving seahorse maximum adult Ht as a variable

Species	Latitude	Ht_{max} (cm)	Reference	Ht_{mat} (cm)	Reference
H. abdominalis (Lesson 1827)	−43	35·0	Francis, 1988	8·7	C. Woods, unpubl. data
H. algiricus (Kaup 1856)*	50	19·2	Lourie *et al.*, 1999	9·0	Lourie *et al.*, 1999
H. angustus (Günther 1870)*	−19	16·0	Kuiter, 2000	7·8	Lourie *et al.*, 1999
H. barbouri Jordan & Richardson 1908	1	15·0	Perez-Oconer, 2002	8·0	Perez-Oconer, 2002
H. bargibanti (Whitley 1970)	6	2·4	Gomon, 1997	1·3	Whitley, 1970
H. borboniensis (Duméril 1870)*	−18	14·0	Lourie *et al.*, 1999	8·0	Lourie *et al.*, 1999
H. breviceps (Peters 1869)	−37	10·0	Kuiter, 2000	4·6	Moreau & Vincent, in press
H. camelopardalis (Bianconi 1854)*	−18	10·0	Lourie *et al.*, 1999	6·5	Lourie *et al.*, 1999
H. capensis (Boulenger 1900)	−34	12·1	Lockyear *et al.*, 1997	5·1	Whitfield, 1995
H. comes (Cantor 1850)	7	18·7	J.J. Meeuwig, unpubl. data	8·1	Perante *et al.*, 1998
H. coronatus (Temmick & Schlegel 1850)*	35	12·7	Kaup, 1856	6·0	Lourie *et al.*, 1999
H. denise (Lourie & Randall 2003)*	−3	2·1	Lourie & Randall, 2003	1·1	Lourie & Randall, 2003
H. erectus (Perry 1810)	27	19·0	Lourie *et al.*, 1999	5·6	Baum *et al.*, 2003
H. fisheri (Jordan & Evermann 1903)*	21	8·0	Lourie *et al.*, 1999	5·0	Lourie *et al.*, 1999
H. fuscus (Rüppell 1838)*	11	14·4	Golani & Fine, 2002	8·0	Lourie *et al.*, 1999
H. guttulatus (Cuvier 1829)	48	18·0	Lourie *et al.*, 1999	9·9	J. Curtis, unpubl. data
H. hippocampus (Linnaeus 1758)	38	15·0	Neil Garrick-Maidment, unpubl. data	7·7	J. Curtis, unpubl. data

H. histrix (Kaup 1856)*	5	17·0	Masuda et al., 1984	7·9	Lourie et al., 1999
H. ingens (Girard 1859)	10	31·0	Miller & Lea, 1972	5·4	Groves & Lavenberg, 1997
H. jayakari (Boulenger 1900)*	24	14·0	Kuiter, 2000	11·0	Lourie et al., 1999
H. kelloggi (Jordan & Snyder 1902)*	11	28·0	Kuiter, 2000	15·0	Lourie et al., 1999
H. kuda (Bleeker 1852)	6	17·0	Lourie et al., 1999	14·0	Jiaxin, 1990
H. lichtensteinii (Kaup 1856)*	21	4·0	Lourie et al., 1999	3·0	Lourie et al., 1999
H. minotaur (Gomon 1997)	−35	5·0	Lourie et al., 1999	—	
H. mohnikei (Bleeker 1854)	28	8·0	Lourie et al., 1999	5·5	Jiaxin, 1990
H. reidi (Ginsburg 1933)	5	17·5	Lourie et al., 1999	8·0	Vari, 1982
H. sindonis (Jordan & Snyder 1902)*	35	8·0	Lourie et al., 1999	4·0	Lourie et al., 1999
H. spinosissimus (Weber 1913)	7	17·2	Nguyen & Do, 1996	10·4	Nguyen & Do, 1996
H. subelongatus (Castelnau 1873)*	−41	20·0	Lourie et al., 1999	13·0	Lourie et al., 1999
H. trimaculatus (Leach 1814)	−5	17·0	Masuda et al., 1984	14·0	Jiaxin, 1990
H. whitei (Bleeker 1855)*	−32	13·0	Lourie et al., 1999	6·0	Lourie et al., 1999
H. zebra (Whitley 1964)*	−16	9·4	Whitley, 1964	7·0	Lourie et al., 1999
H. zosterae (Jordan & Gilbert 1882)	27	2·5	Lourie et al., 1999	2·0	Lourie et al., 1999

form of parental care (either egg bearing or guarding, Balon, 1975). In ANCOVA, the life-history parameter was specified as the dependent variable, group (seahorses versus marine teleost subset a or b) as a fixed factor, and L_{max} (or Ht_{max} for seahorses) as the covariate. All tests were performed on $\log_e$-transformed data.

RESULTS

MORPHOLOGY AND CRYPSIS

Seahorses ranged in size from the tiny *Hippocampus denise* (<20 mm Ht) to the large *Hippocampus abdominalis* (>300 mm Ht) (Table I). Across species, seahorse maximum adult height (Ht_{max}) did not appear to vary by latitude; a regression of Ht_{max} on the latitude of the mid-range of the species was not significant (*t*-test: slope $= 0.03 \pm 0.10$, $n = 33$, $P = 0.72$). Within *H. abdominalis*, however, Ht_{max} of seahorses in New South Wales was considerably smaller than those in New Zealand, at higher latitudes (Francis, 1988; K. Martin-Smith, pers. comm.).

All seahorses have the same basic body morphology and function: a horse-like head positioned at a right angle to an erect body; eyes that swivel independently; a long tubular snout (no teeth) that sucks food; a digestive tract without a differentiated stomach (Rauther, 1925; Stoskopf, 1993); skin (no scales) stretched over a series of bony plates visible as obvious rings around the trunk and tail; and a prehensile tail (Gill, 1905). Adult seahorses have no pelvic and caudal fins, and retain only one propulsive dorsal fin, two small ear-like pectoral fins used for stabilization and steering, and a reduced anal fin. Very young *Hippocampus comes* (S. Morgan, unpubl. data), *Hippocampus mohnikei* (Kanou & Kohno, 2001) and *Hippocampus spinosissimus* (S. Morgan, unpubl. data) have a reduced caudal fin that is subsequently lost in adults.

Male and female seahorses were commonly the same size: in total, 45% of species were sexually monomorphic in terms of weight, and 73% with respect to length (Table II). Analyses of sexual dimorphism in weight were, however, confounded by the inclusion of animals with different reproductive states in the same analyses: both sexes gained and lost considerable weight through the reproductive cycle. The occurrence of sexual dimorphism in seahorse length may have arisen from sex-specific differences in mortality rates; such dimorphism was relatively rare across species, even though most studies explicitly sought it.

All studies established sexual dimorphism in body proportions beyond the distinct sexual difference of the caudal brood pouch, found only on males (Table II). Males consistently had a relatively longer tail, while females had a relatively longer body trunk. A longer tail may enable a male to support a large caudal pouch while still grasping a holdfast, or may give males an advantage in the tail-wrestling exhibited during mating competition (Vincent, 1990). Males had shorter snouts in two species (*H. abdominalis* and *Hippocampus fuscus*), while females of *Hippocampus zosterae* had a shorter snout. The use of snouts to snap at competitors may explain the shorter and thicker snouts in male *H. fuscus* (Vincent, 1990), but any foraging differences between the sexes might also have helped select for different snout lengths (Shine, 1991).

TABLE II. Occurrence of sexual dimorphism in weight, length, weight/length (W/L) and proportions (trunk length/tail length and snout length/head length) for 16 seahorse species (*Hippocampus* spp.). The majority finding of the cited sources is presented, and in cases where studies were evenly divided the result is reported as 'split'. * indicates an *ex situ* study with a small sample size

Species	Weight	Length	W/L	Proportions	Notes	Reference(s)
H. abdominalis	Yes	No	Yes	Yes	Male heavier, tail longer, snout shorter	Vincent, 1990; Woods, 2000a
H. barbouri	No	No	No	Yes	Male tail longer	Vincent, 1990*
H. breviceps	–	No	Yes	Yes	Male tail longer	Moreau & Vincent, in press
H. capensis	Yes	Yes	–	Yes	Male longer and heavier, tail longer	Lockyear et al., 1997; Bell et al., 2003
H. comes	Yes	No	Yes	–	Male heavier	Meeuwig & LaFrance, 2001
H. erectus	Split	No	Yes	Yes	Males W/L greater, tail longer	Vincent, 1990; Teixeira & Musick, 2001; Baum et al., 2003
H. fuscus	No	No	No	Yes	Male tail longer, snout shorter	Vincent, 1990
H. guttulatus	–	–	–	Yes	Male tail longer	J. Curtis, unpubl. data
H. kelloggi	–	No	–	–		Choo & Liew, 2003
H. kuda	Yes	Split	–	–	Males heavier	Job et al., 2002; Choo & Liew, 2003
H. reidi	No	No	No	Yes	Male tail longer	Vincent, 1990*
H. spinosissimus	–	Yes	–	–	Male longer	Nguyen & Do, 1996; Choo & Liew, 2003; J.J. Meeuwig, unpubl. data
H. subelongatus	No	No	No	Yes	Male tail longer	Jones & Avise, 2001
H. trimaculatus	–	Yes	–	–	Male longer	Nguyen & Do, 1996; Choo & Liew, 2003; J.J. Meeuwig, unpubl. data
H. whitei	Yes	No	Yes	–	Males heavier	Vincent & Giles, 2003
H. zosterae	No	No	No	Yes	Male tail and snout longer	Vincent, 1990
TOTAL	11	15	10	10		
YES	5	3	5	10		
NO	5	11	5	0		
SPLIT	1	1	0	0		

Seahorses have excellent camouflage capabilities, with crypsis probably facilitating both prey capture and predator avoidance. They remain virtually immobile for much of the time, can change colour over a few days or weeks to match their background better, and sometimes have long skin filaments to blend better with their habitats. Most seahorses are beige, brown or black, but species-specific colour changes include fluorescent orange and deep purple (A. Vincent, pers. obs.). For example, *Hippocampus capensis* individuals were usually mottled brown with darker patches, but were also found in black, green, orange, white or yellow colour forms (Bell *et al.*, 2003). *Hippocampus bargibanti* mimics in colour and form the stalks and polyps of the gorgonian coral (*Muricella* sp.) to which it clings using its tail (Whitley, 1970). Encrusting organisms sometimes grow on the skin of a seahorse, improving the fish's camouflage (Rauther, 1925).

Seahorses often changed colour rapidly when interacting with each other. Both sexes of *Hippocampus whitei* brightened in colour from a dark brown or grey to a pale yellow or off-white during pair-wise encounters in the wild (Vincent & Sadler, 1995). On an Australian algal reef, *Hippocampus breviceps* were observed to brighten their pouches and body front to a flashing silver or white when approaching another seahorse (Moreau & Vincent, in press). Similarly, aquarium observations of *H. fuscus* males (Vincent, 1995), and field observations of *Hippocampus guttulatus* and *Hippocampus hippocampus* males (J. Curtis, pers. comm.), indicated that they brightened in colour when courting females.

DISTRIBUTION AND HABITAT

Seahorses are exclusively marine, generally living in coastal habitats in shallow temperate and tropical waters. They are distributed from *c.* 50° north to 50° south, while the highest diversity of species occur in the IndoPacific region (Table III, based on Lourie *et al.*, 1999). While individuals of most seahorse species were found in shallow waters (<30 m depth), many have been found between depths of 40 and 100 m (Table IV); *Hippocampus kelloggi* were reported to depths of 90 m in Malaysian waters (Choo & Liew, 2003), and *Hippocampus minotaur* were reported from trawls at 100 m in Australia (Gomon, 1997). Overall, the most commonly reported seahorse habitat was seagrass, and mangroves were the least reported (Table IV). Temperate species predominantly inhabited seagrasses and algae, while tropical species were primarily found among coral reefs (see Tables I and IV). Some estuarine species, such as *H. abdominalis* (K. Martin-Smith, pers. comm.), *H. capensis* (Whitfield, 1995), *H. kuda* (Munro, 1967; Nguyen & Do, 1996; Kuiter, 2000) and *H. reidi* (Rosa *et al.*, 2002), appear to tolerate fluctuating salinities, although they could experience high rates of mortality during freshwater flooding (Russell, 1994; Bell *et al.*, 2003).

Seahorse species in soft-bottom habitats differed in the complexity of habitats they occupied. In an *ex situ* experimental situation, *H. abdominalis* preferred areas of vegetated habitat to open water (Flynn & Ritz, 1999). Similarly, *H. whitei* were found in areas of longer seagrasses, as opposed to open areas or short

TABLE III. Distributions of seahorse species (*Hippocampus* spp.) by FAO statistical area. ? indicates unconfirmed distribution. Based on Lourie *et al.*, 1999

Species	Atlantic- northwest (21)	Atlantic- northeast (27)	Atlantic- western central (31)	Atlantic- eastern central (34)	Atlantic- southwest (41)	Atlantic- southeast (47)	Mediter- ranean + Black Sea (37)	Indian Ocean western (51)	Indian Ocean eastern (57)	Pacific- northwest (61)	Pacific- northeast (67)	Pacific- western central (71)	Pacific- eastern central (77)	Pacific- southwest (81)	Pacific- southeast (87)
H. abdominalis									*					*	
H. algiricus				*											
H. angustus									*			*			
H. barbouri												*			
H. bargibanti									*	*		*			
H. borboniensis								*							
H. breviceps									*						
H. camelopardalis						*		*							
H. capensis						*									
H. comes									*			*			
H. coronatus										*					
H. erectus	*		*		*?										
H. fisheri												*?	*		

TABLE III. Continued

Species	Atlantic-northwest (21)	Atlantic-northeast (27)	Atlantic-western central (31)	Atlantic-eastern central (34)	Atlantic-southwest (41)	Atlantic-southeast (47)	Mediterranean + Black Sea (37)	Indian Ocean western (51)	Indian Ocean eastern (57)	Pacific-northwest (61)	Pacific-northeast (67)	Pacific-western central (71)	Pacific-eastern central (77)	Pacific-southwest (81)	Pacific-southeast (87)
H. fuscus					*?		*	*	*						
H. guttulatus		*		*?			*								
H. hippocampus		*		*?			*								
H. histrix								*	*	*		*			
H. ingens													*		*
H. jayakari								*							
H. kelloggi								*	*	*		*			
H. kuda								*	*	*		*	*		
H. lichtensteinii								*	*						
H. minotaur														*	
H. mohnikei										*					
H. reidi			*		*										
H. sindonis										*					
H. spinosissimus									*	*		*			
H. subelongatus									*						
H. trimaculatus								*	*	*		*			
H. whitei												*		*	
H. zebra													*		
H. zosterae			*												
Totals	1	2	3	3	3	2	3	8	13	9	0	11	3	3	1

TABLE IV. Maximum recorded depths and all documented habitat types for seahorse species (*Hippocampus* spp.)

Species	Max depth (m)	Algal reef	Algae/macroalgae	Coral	Mangrove	Rocks/gravel	Seagrass	Soft bottom	Sponges
H. abdominalis	104	●	●			●	●	●	●
H. angustus	63	●							
H. barbouri	10			●			●		
H. bargibanti	40			●					
H. borboniensis	60						●	●	
H. breviceps	15	●	●				●		●
H. camelopardalis	45		●				●		●
H. capensis	20	●	●				●		
H. comes	20		●	●			●		●
H. coronatus	–		●						
H. denise	90			●					
H. erectus	73		●				●	●	●
H. fisheri	–								
H. fuscus	10	●	●			●			
H. guttulatus	12	●	●			●			
H. hippocampus	60		●			●	●	●	
H. histrix	20			●			●	●	●
H. ingens	60			●			●	●	●
H. jayakari	20		●			●	●	●	●
H. kelloggi	152			●				●	●

TABLE IV. Continued

Species	Max depth (m)	Algal reef	Algae/macroalgae	Coral	Mangrove	Rocks/gravel	Seagrass	Soft bottom	Sponges
H. kuda	55		•		•	•	•	•	
H. minotaur	100								
H. reidi	55		•	•	•		•		
H. spinosissimus	70			•					•
H. subelongatus	25			•		•	•	•	
H. trimaculatus	100			•		•		•	•
H. whitei	25		•	•			•	•	
H. zebra	69			•					
H. zosterae	2						•		
Totals		6	13	12	2	8	19	11	11

References: A. Kendrick, pers. comm. in Lourie *et al.*, 1999; Al-Hassan & Al-Badri, 1986; Barnard, 1925; Bell *et al.*, 2003; Boisseau, 1967; Burgess & Axelrod, 1984; Choo & Liew, 2003; Coleman, 1980; J. Curtis, unpubl. data; Dauwe, 1992; Eschmeyer & Herald, 1983; Fish & Mowbray, 1970; Flynn & Ritz, 1999; Francis, 1988; Fritzsche, 1980; N. Garrick-Maidment, pers. comm.; Golani & Fine, 2002; J. Gomezjuardo, pers. comm. in Lourie *et al.*, 1999; Gomon & Neira, 1998; Gomon *et al.*, 1994; Gomon, 1997; Groves & Lavenberg, 1997; Hardy, 1978; Hildebrand & Schroeder, 1927; Holley, pers. comm. in Lourie *et al.*, 1999; Hubbs & Hinton, 1963; Hutchins & Swainston, 1986; Jones *et al.*, 1998; Kuiter, 1997, 2000; Kuiter & Debelius, 1994; Kuronuma & Abe, 1972; Last *et al.*, 1983; Lee, 1983; Lieske & Myers, 1994; J. Lockyear, pers. comm. in Lourie *et al.*, 1999; Lourie, 2001; Lourie & Randall, 2003; Lourie *et al.*, 1999; Lovett, 1969; Lythgoe & Lythgoe, 1971; Masuda *et al.*, 1984; Matlock, 1992; D. McAllister, pers. comm.; Moreau & Vincent, in press; Munro, 1967; Nguyen & Do, 1996; Paulin & Roberts, 1992; Paxton *et al.*, 1989; Perante *et al.*, 1998, 2002; Randall, 1996; A.K. Riley, unpubl. data; Rosa *et al.*, 2002; Scarratt, 1996; Strawn, 1953; Strawn, 1958; Tabb & Manning, 1961; Tackett & Tackett, 1997; Teixeira & Musick, 2001; Toefy, 2000; Trommelen, 2001; Vari, 1982; Walls, 1975; Weber & de Beaufort, 1922; Wheeler, 1969, 1985; Whitehead, 1986; Whitfield, 1995; Whitley, 1964, 1970; Wilson & Vincent, 1998; Woods, 2000*a*; Woods, 2002.

seagrasses (Vincent *et al.*, in press). Long seagrasses may have maximized prey density and capture efficiency, as well as predator avoidance (Bell & Westoby, 1986; Flynn & Ritz, 1999). In contrast, *H. capensis* were most commonly associated with relatively sparse vegetation, with greater water exchange and feeding opportunities suggested as a reason for the choice of habitat (Bell *et al.*, 2003). Sympatric species may have occupied different habitats at the same geographic location; within a Portuguese lagoon *H. hippocampus* were associated with more open habitat, while *H. guttulatus* were positively and significantly correlated with the percentage cover of vegetation and immobile benthic invertebrates (J. Curtis & A. Vincent, unpubl. data). The differences in occupancy suggest either that feeding opportunities or predation risk must have varied among species or that they did not determine habitat choice.

Some seahorses change habitat and depth choice as they grow. *H. comes* were thought to prefer *Sargassum* spp. beds in shallow subtidal environments as juveniles, and then moved to adjacent communities composed of hard corals and sponges when older (Perante *et al.*, 1998). In a Portuguese lagoon, juvenile *H. guttulatus* only began occupying the same habitat as adults when they neared maturity (J. Curtis, pers. comm.). Among adults, size classes may also have differed in habitat occupancy, with larger individuals of some species found in deeper waters (*H. comes*, J.J. Meeuwig, unpubl. data; *H. reidi*, Dauwe, 1992).

Most seahorses grasped holdfasts with their tail, although individuals in some populations, such as that of *H. abdominalis* in Derwent Estuary, Australia, were on occasion found distant from any structure, nestled in small depressions in the substratum (A. Vincent, pers. obs.). Holdfasts could be anything from a sponge to a branching coral, a piece of seagrass or a submerged tree branch. Some species exhibited preferences for particular holdfasts – for example, *H. comes* usually grasped sponges in communities dominated by seagrasses (J. Anticamara, unpubl. data), while others exhibited no obvious preference [*H. comes* on a Philippines' coral reef (Perante *et al.*, 2002); *H. guttulatus* in a Portugal lagoon (J. Curtis, unpubl. data)]. Some seahorses also grasped artificial structures; *H. abdominalis* and *H. whitei* held onto shark nets in Sydney Harbour, and large populations of *H. abdominalis* could be found on salmon cages in Tasmania (K. Martin-Smith, pers. comm.). Other species known to use artificial habitats included *H. kuda* (fishnets and cages, Choo & Liew, 2003), *H. reidi* (wooden piers, Dias & Rosa, 2003) and *Hippocampus subelongatus* (jetty piles, Coleman, 1980).

Most seahorse species studied to date were active during the day. Documented diurnal species included *H. breviceps* (Moreau & Vincent, in press, *in situ*), *H. capensis* (Lockyear *et al.*, 1997, *ex situ*), *H. erectus* (Hardy, 1978, *in situ*), *H. guttulatus*, *H. hippocampus* (J. Curtis, pers. comm., *in situ*), *H. kuda* (Do *et al.*, 1998, *ex situ*), *H. whitei* (Vincent & Sadler, 1995, *in situ*) and *H. zosterae* (Tipton, 1987 in Tipton & Bell, 1988, *in situ*). Nocturnal species included *Hippocampus ingens* (J. Gomezjurado, pers. comm., *in situ*). *Hippocampus abdominalis* was reportedly active during both day and night (K. Martin-Smith, pers. comm., *in situ*). *Hippocampus comes* may also have been active during both day and night, but were most commonly seen at night on reefs, when they emerged from the corals (Perante *et al.*, 2002; A. Vincent, pers. obs.).

DENSITY AND MOBILITY

The literature indicated that seahorse density tended to be low and that they were patchy in distribution (Table V). For example, *H. guttulatus* mean density was generally $0.07 \, \text{m}^{-2}$ (range 0 to $0.51 \, \text{m}^{-2}$), but reached $10 \, \text{m}^{-2}$ in small patches on the edges of seagrass beds over a transect survey covering $3324 \, \text{m}^2$ of the Ria Formosa Lagoon, Portugal (J. Curtis, unpubl. data). Likewise, *H. whitei* were found at a density of $0.08 \, \text{m}^{-2}$ in one area of seagrass in Sydney Harbour, and $0.215 \, \text{m}^{-2}$ in a very similar patch of *Posidonia* and *Zostera* seagrasses only 20 m away, with no other seahorses for hundreds of metres around (Vincent *et al.*, in press). Given the variation in seahorse densities, it is important to document and assess the manner in which seahorse population densities were extracted: bias in site selection means that they were likely to be greater on focal study grids than in transect surveys. For example, *H. capensis* were recorded at a mean density of $0.22 \, \text{m}^{-2}$ on a focal study grid

TABLE V. Recorded seahorse (*Hippocampus* spp.) densities

Species	Mean density (m^{-2})	Range (m^{-2})	Locality	Study type	Reference
H. abdominalis	0.007		Tasmania, Australia	Transect	K. Martin-Smith, unpubl. data
H. breviceps	0.17		Port Philip Bay, Australia	Focal grid	Moreau & Vincent, in press
	0.31		Port Philip Bay, Australia	Focal grid	Moreau & Vincent, in press
H. capensis	0.0089	0–0.25	Knysna Estuary, South Africa	Transect	Bell *et al.*, 2003
	0.22		Knysna Estuary, South Africa	Focal grid	Bell *et al.*, 2003
H. comes	0.02		Bohol, Philippines	Focal grid	Perante *et al.*, 2002
H. guttulatus	0.07	0–0.51	Ria Formosa Lagoon, Portugal	Transect	J. Curtis, unpubl. data
	1.1		Ria Formosa Lagoon, Portugal	Focal grid	J. Curtis, unpubl. data
H. hippocampus	0.007	0–0.07	Ria Formosa Lagoon, Portugal	Transect	J. Curtis, unpubl. data
H. reidi	0.51		Rio Grande do Norte State, Brazil	?	Dias & Rosa, 2003
	0.006		Rio Grande do Norte State, Brazil	?	Dias & Rosa, 2003
H. whitei	0.08		Sydney, Australia	Focal grid	Vincent *et al.*, in press
	0.215		Sydney, Australia	Focal grid	Vincent *et al.*, in press

and $0.0089\,m^{-2}$ in randomly placed transect surveys that covered a total of $4920\,m^2$ of a South African estuary (Bell *et al.*, 2003).

Reported densities for seahorses were comparable with those found for temperate pipefish and seadragon species (all syngnathids): five pipefish species in a Swedish seagrass bed had a total density of $0.04\,m^{-2}$ (grid survey, Vincent *et al.*, 1995); *Syngnathus leptorhynchus* Girard occurred at densities ranging from 0.02 to $0.1\,m^{-2}$ in an Oregon seagrass bed (transect survey, Bayer, 1980); densities of *Stigmatopora argus* Richardson were 0.036–$0.107\,m^{-2}$ in Southeastern Tasmania (transect survey, Jordan *et al.*, 1998); and *Phycodurus eques* Günther, the leafy seadragon, was calculated to occur at a density of $0.006\,m^{-2}$ in South Australia (Connolly *et al.*, 2002). Reported seahorse densities could be similar in fished and unfished populations, but the low densities in at least some populations probably derived from overexploitation. For example, Filipino fishers reported patchy *H. comes* densities as high as $20\,m^{-2}$ on coral, or $10\,m^{-2}$ in seagrass in the 1960s (A. Vincent & M. Pajaro, unpubl. data), while they were found at only $0.02\,m^{-2}$ in the late 1990s (Perante *et al.*, 2002).

Most seahorse species studied thus far maintained individual home ranges, at least during the breeding season. As three examples, *H. comes* often ranged only $1\,m^2$ on coral reefs at night (Perante *et al.*, 2002) although they moved considerably more on seagrass beds (J. Anticamara, unpubl. data), *H. kuda* had overlapping home ranges of $32.35\,m^2$ in a tropical eelgrass bed (C.K. Choo, unpubl. data), and *H. subelongatus* also had home ranges, although the sizes were not specified (Jones & Avise, 2001).

Sex differences in home range size have been documented for some species. A field study on *H. whitei* showed that females had significantly larger home ranges than males, with means of $14.4\,m^2$ (range 6–$21\,m^2$) and $9\,m^2$ (range 4–$17\,m^2$), respectively (Vincent *et al.*, in press). In Australia, female *H. breviceps* had average home ranges of $8.1\,m^2$ (s.d. $= 2.7\,m^2$), while those of males averaged $4.4\,m^2$ (s.d. $= 1.6\,m^2$) (Moreau & Vincent, in press). In Bonaire, as well, *H. reidi* females had larger home ranges than males ($13.3\,m^2$ and $3.5\,m^2$ respectively, Dauwe, 1992). On the other hand, *H. guttulatus* and *H. hippocampus* showed no apparent sex differences in home ranges: both sexes covered a mean of $12.1\,m^2$ (range 0.005–$67\,m^2$) and $7.8\,m^2$ (range 0.7–$18.1\,m^2$) in *H. guttulatus* and *H. hippocampus* respectively (J. Curtis, unpubl. data).

The small home ranges of *H. breviceps*, *H. guttulatus*, *H. hippocampus*, *H. reidi* and *H. whitei* indicate limited daily movements similar to those in other monogamous syngnathid species (Vincent *et al.*, in press). Small home ranges may have enabled the seahorses to adopt camouflage appropriate for their environment, and to maintain a stable social structure (Vincent *et al.*, in press). However, not all seahorses had small home ranges. Individual *H. abdominalis*, for example, ranged over hundreds of metres in the course of a day (Vincent, 1990; K. Martin-Smith, unpubl. data).

No seahorses demonstrated any territorial defense of the home range (*H. whitei*, Vincent *et al.*, in press), unlike most fish with limited home ranges (Barlow 1984; Roberts & Ormond 1992; Grant 1997). The difference may reflect the fact that seahorses had no need to defend their oviposition sites or young, and presumably did not find it necessary or energetically expedient to defend the area in which their partners or prey were found (Vincent *et al.*, in press).

Such a situation might arise if partnerships were maintained in some other manner and prey were either indefensible or abundant relative to size of the seahorse population.

While most species studied to date made limited daily movements, adults of some species may have made seasonal migrations to deeper waters in the winter months. Such moves have been inferred for *H. comes* (J.J. Meeuwig, unpubl. data), *H. erectus* (Hardy, 1978), *H. guttulatus* (Boisseau, 1967), *H. hippocampus* (Boisseau, 1967), *H. subelongatus* (G. Moore, pers. comm.), and *H. whitei* (Vincent & Sadler, 1995), as well as for the pipefishes *Syngnathus fuscus* Storer (Lazzari & Able, 1990) and *Syngnathus leptorhynchus* (Bayer, 1980).

Adult dispersal over large distances appeared primarily to occur when adults were cast adrift by storms or carried away while grasping floating debris. Adult *Hippocampus fisheri* have been caught at the surface in the open sea (as cited in Lourie *et al.*, 1999), while the occurrence of *H. ingens* in the stomachs of tuna suggests they were occasionally found in the pelagic zone (Alverson, 1963), possibly associated with rafts of drifting seaweed.

Young seahorses are more likely to disperse than adults. Some species were clearly planktonic immediately after birth, as juveniles were found in plankton samples (Table VI). Of the six species with a confirmed planktonic stage, information on the size of specimens found in the plankton was available only from studies of *H. abdominalis* (Kingsford & Choat, 1985; Hickford, 2000), *H. comes* (S. Morgan, unpub. data), *H. mohnikei* (Kanou & Kohno, 2001) and *H. spinosissimus* (S. Morgan, unpubl. data). It is likely that seahorses were overlooked in many ichthyoplankton studies because of their low abundance in tows when compared to other plankton types (S. Morgan, pers. comm.). Juveniles of other seahorse species were inferred to be planktonic because they were positively phototactic immediately after leaving the pouch, rising to the surface of the water column in captivity, or not settling immediately after birth in the wild (Table VI); such inferences may be questionable in the case of *ex situ* studies. Similarly, *H. fuscus* was inferred to lack a planktonic stage as they settled immediately after release *ex situ* (Golani & Fine, 2002), but it is not known how transferable this observation is to wild animals.

The extent of juvenile dispersal by passive means is unknown but may explain some gene flow among populations. Juvenile dispersal by currents was suggested for *H. capensis* (Whitfield, 1995), while juvenile *H. kuda* (Mi *et al.*, 1998) and *H. subelongatus* (Lawrence, 1998) were observed to drift passively as water circulated in aquaria. While in the water column, young seahorses attach themselves to floating *Sargassum* weed as in *H. erectus* (Fish & Mowbray, 1970). *Hippocampus abdominalis* (Gomon & Neira, 1998) and *H. zosterae* (Vari, 1982) were occasionally found attached to drifting macroalgae.

Recent studies of seahorse population genetic structure over a range of dispersal distances produced conflicting results, according to species, the geographic region and the molecular marker used. For example, populations of *H. capensis* appeared to have limited contemporary exchange among three South African estuaries separated by <100 km based on D-loop sequencing (Teske *et al.*, 2003), and *H. comes* in the central Philippines appeared to have restricted gene flow based on microsatellites over a distance of 135 km, through isolation by distance (Casey, 1999). Deep genetic breaks were found among

TABLE VI. Presence or absence of a planktonic life-history stage immediately after release for seahorse species (*Hippocampus* spp.). 'yes' = species in which newly released young were found in plankton nets or observed drifting in the water column *in situ*; 'inferred' = species in which newly released young were observed to rise to the surface, without settling after birth; 'no?' = species in which newly released young were observed to settle immediately after birth *ex situ*. Where possible the duration of the planktonic stage, in either duration of time or length of juvenile, is given

Species	Planktonic	Pelagic duration	*In*/*ex situ*	Reference
H. abdominalis	Yes	4–6 weeks (inferred)	*In situ*	Lovett, 1969
	Yes	12·5–73 mm	*In situ*	Hickford, 2000
	Inferred		*In situ*	Gomon & Neira, 1998
	Inferred		*In situ*	Graham, 1939
	Inferred	2–4 weeks, to 25 mm	*Ex situ*	Woods, 2000a
H. bargibanti	Inferred		*In situ*	D. Tackett, pers. comm.
H. breviceps	Inferred		*In situ*	Kuiter, 2000
H. capensis	Yes		*In situ*	Whitfield, 1995
H. comes	Yes	9·66–16·58 mm	*In situ*	S. Morgan, unpubl. data
H. erectus	Inferred		Not stated	Smith, 1907 as cited in Hardy, 1978
H. fuscus	No?		*Ex situ*	Golani & Fine, 2002
H. guttulatus/ H. hippocampus assemblage	Yes	6–8 weeks (inferred)	*In situ*	Boisseau, 1967
H. hippocampus	Inferred		*Ex situ*	Golani & Fine, 2002
H. kuda	Inferred	19–22 days	*Ex situ*	Mi, 1993; Mi *et al.*, 1998
H. mohnikei	Yes	15·1–45·5 mm	*In situ*	Kanou & Kohno, 2001
H. reidi	Inferred		*In situ*	Dauwe, 1992
H. spinosissimus	Yes	6·52–23·8 mm	*In situ*	S. Morgan, unpubl. data
H. subelongatus	Inferred	14–21 days	*Ex situ*	Lawrence, 1998

individuals of both *H. kuda* and *Hippocampus trimaculatus* collected only 800 km apart in Southeast Asia based on cytochrome *b* sequencing (Lourie, 2004). In contrast, however, the same study of *H. trimaculatus* revealed identical genetic haplotypes across distances of up to 10 000 kms along the Asian

continental shelf, suggesting extensive gene flow over the last 10 000 years (Lourie, 2004). A similar study, also using cytochrome *b* sequencing across Southeast Asia, shows distinct phylogenetic breaks within *Hippocampus barbouri*, but extensive gene flow in *H. spinosissimus* (Lourie, 2004).

LIFE SPAN AND MORTALITY

The life spans of seahorses, and the parameters that influenced them such as predation and disease, were virtually unknown for most species. Most survival estimates came from *ex situ* observations or cohort analysis, with uncertainties as to how comparable these estimates were to actual life spans of seahorses *ex situ*. Inferred life spans for seahorse species ranged from about 1 year in the very small species *H. zosterae* (Strawn, 1953, *in situ*) to an average of 3 to 5 years for larger species (*H. capensis*, Lockyear *et al.*, 1997, *ex situ*; *H. comes*, J.J. Meeuwig, unpubl. data, *in situ*; *H. guttulatus*, Boisseau, 1967, *in situ*; *H. hippocampus*, N. Garrick-Maidment, pers. comm., *ex situ*).

As with life span, natural mortality rates were unknown for almost all seahorse species. About 86% of individually identified adult *H. whitei* that had been tagged on a study grid in November were still present in March, suggesting a low rate of natural mortality (Vincent & Sadler, 1995). In another study, *H. comes* was estimated to have a high rate of natural mortality ($M = 0.83–1.5$, J.J. Meeuwig, unpubl. data; $M = 2.81$, Perante *et al.*, 1998). Other mortality estimates include $M = 1$ for *H. erectus* (Herald & Rakowicz, 1951) and $M = 2–3$ for *H. zosterae* (Strawn, 1958), but it is not clear how these estimates were determined and therefore whether they were low or high.

Sub-adult and adult seahorses are presumed to have few natural predators because of their camouflage capabilities, and unpalatable bony plates and spines (Lourie *et al.*, 1999). Seahorses were, however, found in the stomachs of large pelagic fishes such as red snapper (Jordan & Gilbert, 1882), dorado, rays, skates, tuna (Herald 1949; Alverson, 1963; Wilson & Beckett, 1970) and dolphin fish (Sharpe, 1998), and were preyed upon by anglerfish, flatheads and sea urchins (Kuiter, 2000). In New Zealand, seahorses were reputedly taken by blue cod, ling, red cod, sea perch, skate and trumpeter (Whitley & Allan, 1958). A seahorse was also recorded from the stomach of a loggerhead sea turtle (Burke *et al.*, 1993), and seahorses were taken by cormorants, penguins and other water birds (Kuiter, 2000). Partial predation by crabs may be a threat to seahorses, as indicated by direct observations of seahorses with shortened tails (Baum *et al.*, 2003; A. Vincent, pers. obs.). Predation mortality was probably greatest in juveniles that were highly vulnerable to piscivorous fish and planktivorous organisms (J. Curtis, pers. comm., A. Vincent, pers. obs.).

Reports of disease in seahorses arose from laboratory and aquaculture observations. Health ailments included those caused by bacteria (*H. kuda*, Alcaide *et al.*, 2001; Greenwell, 2002), cestodes (*H. abdominalis*, Lovett, 1969), microsporidians (*H. erectus*, Blasiola, 1979; Vincent & Clifton-Hadley, 1989), fungi (*H. erectus*, Blazer & Wolke, 1979), ciliates (*H. erectus*, Cheung *et al.*, 1980; *H. trimaculatus*, Qingxian & Kaikang, 1985), trematodes

(*H. trimaculatus*, Jiwei, 1982) and marine leeches (*H. kuda*, de Silva & Fernando, 1965).

FEEDING AND GROWTH

Seahorses are ambush predators, and consume primarily live, mobile prey types (James & Heck, 1994; Bergert & Wainwright, 1997). When feeding within the water column, they wait until prey come close to the mouth, whereupon, they are drawn up into the long snout with a rapid intake of water. At least one seahorse was observed feeding from the sediment, suspending it in the water column by jetting water into the substratum (*H. guttulatus*, J. Curtis, pers. comm.). Seahorse eyes move independently of each other, enabling the seahorse to maximize its search area and/or to monitor its environment (Ocken, 1994). They ingest any organism small enough to fit into their snout; mostly small crustaceans such as amphipods, but also fish fry and other invertebrates (Boisseau 1967; Tipton & Bell, 1988; Do *et al.*, 1998; Teixeira & Musick, 2001). *Hippocampus abdominalis* were observed to dismantle larger prey items before ingestion (Woods, 2002). Wild seahorses do not appear to target plants or algae (*H. trimaculatus*, Do *et al.*, 1998), but pieces of seagrass were found in the stomachs of *H. guttulatus* (D'Entremont, 2002), perhaps indirectly ingested when eating small prey such as molluscs attached to the grass blades. *Hippocampus zosterae* were credited with eating sufficient invertebrate prey to affect the structure of at least some benthic invertebrate communities, although trophic dynamics were not fully explored (Tipton & Bell, 1988). It appears that *H. erectus* were able to obtain prey over a wide range of habitat complexities although they preferred to grasp a holdfast when feeding (James & Heck, 1994). Among pipefish relatives, a pregnant male *Syngnathus typhle* Linnaeus ate more than twice the number of small prey that an egg-bearing female did, perhaps because the former were too slow to chase larger prey (Svensson, 1988). However, preliminary data on *H. guttulatus* indicated no difference in dominant prey types among pregnant males, non-pregnant males and females (D'Entremont, 2002).

Seahorses may change their diet ontogenetically. Gut content analyses of a wild population of *H. abdominalis* indicated that smaller individuals (9·52–13·75 cm Ht) consumed a greater proportion of amphipods, while larger seahorses (>13·84 cm Ht) consumed more caridean shrimp more often (Woods, 2002). Given a choice of amphipods and smaller copepods, *ex situ H. erectus* smaller than 6 cm Ht ate both prey types, whereas those larger than 6 cm Ht ate only amphipods (Teixeira & Musick, 2001). Wild *H. mohnikei* also showed prey division among size classes with smaller individuals selecting smaller prey items (Kanou & Kohno, 2001).

Growth rates for seahorse species have not been investigated in any detail. There were few data on growth rates in captivity, and even fewer in the wild, with none of the data covering enough of a size range to give a clear picture of lifetime patterns of seahorse growth. Available growth rate information was mostly for juveniles, with inconsistent results among studies as to the relationship between size and age (Table VII). The best long-term study of growth was

TABLE VII. Seahorse species (*Hippocampus* spp.) for which some growth rate data are available

Species	Reference(s)
H. abdominalis	Lovett, 1969; Filleul, 1996; Woods, 2000*a*, *b*; Woods, 2003; Weymouth Sea Life Park, unpubl. data
H. barbouri	Wilson & Vincent, 1998
H. capensis	Le Cheminant, 2000; London Zoo, unpubl. data
H. comes	Perante *et al.*, 1998
H. erectus	Herald & Rakowicz, 1951; Correa *et al.*, 1989; Matlock, 1992; Scarratt, 1996
H. fuscus	Wilson & Vincent, 1998
H. guttulatus	J. Curtis, unpubl. data; Weymouth Sea Life Park, unpubl. data
H. kuda	Jiaxin, 1990; Wilson & Vincent, 1998; Job *et al.*, 2002; Hilomen-Garcia *et al.*, 2003
H. mohnikei	Jiaxin, 1990
H. subelongatus	Lawrence, 1998
H. trimaculatus	Jiaxin, 1990

for *H. abdominalis* from birth through to onset of sexual maturity (52 weeks) and showed a quadratic increase of length over time (Woods, 2000*a*).

REPRODUCTIVE TIMING

Most available information on age at onset of sexual maturity (a_m) was from *ex situ* observations on only a few species, and it was unclear how transferable the results were to populations *in situ*. Smaller seahorse species, such as *H. zosterae*, appeared to mature at 3 months (Strawn, 1953). *Hippocampus barbouri*, *H. fuscus* (Wilson & Vincent, 1998), *H. hippocampus* (N. Garrick-Maidment, pers. comm.) and *H. ingens* (J. Gomezjurado, pers. comm.) reached maturity at 4 or 5 months, while many other species were thought to start breeding in the season after birth, at 6 months to 1 year (*H. kuda* and *H. mohnikei*, Jiaxin, 1990; *H. spinosissimus*, *H. trimaculatus*, Truong & Nga, 1995; *H. capensis*, Whitfield, 1995; *H. erectus*, Gardiner, 1998; *H. abdominalis*, Woods, 2000*a*; *H. comes*, J.J. Meeuwig, unpubl. data).

Size served as a better predictor of first maturity than age. For example, *H. trimaculatus* populations in the South China Sea and North China Sea both matured at the same size, but the former were 3 months old while the latter were 5 months old (Cai *et al.*, 1984*a*). Across seahorse species, $\log_e Ht_{mat}$ increased with $\log_e Ht_{max}$ (*t*-test: slope $= 0.79 \pm 0.08$, $n = 32$, $P < 0.001$) (Fig. 3).

Seahorses showed the same relationship between size at first maturity and maximum size as other marine teleosts (Fig. 3). For marine teleost data and seahorse data combined, there was an overall significant positive linear relationship between $\log_e L_{mat}$ and $\log_e L_{max}$ (*t*-test: slope $= 0.86 \pm 0.02$, $n = 354$, $P < 0.001$) with no evidence of difference in slopes between seahorses and other marine teleosts ($L_{max} \times$ group interaction: *F*-test: $F = 0.49_{1,350}$, $P = 0.486$). Seahorses came very close to differing significantly from other
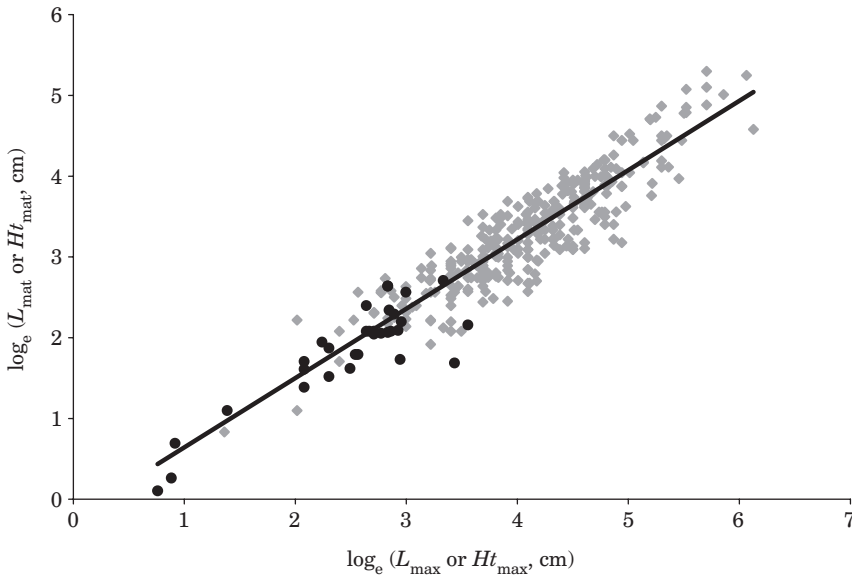
FIG. 3. Maximum recorded size at first maturity (L_{mat} for other teleosts, Ht_{mat} for seahorses) *v.* maximum recorded adult size (L_{max} for teleosts, Ht_{max} for seahorses) for 322 marine teleosts species and 32 seahorse species (*Hippocampus* spp.). Regression through seahorses only: $\log_e(Ht_{mat},$ cm$) = 0.79 \times \log_e(Ht_{max},$ cm$) - 0.11$ ($r^2 = 0.76$). Regression through all points: $\log_e$(length at maturity, cm$) = 0.86 \times \log_e$(maximum length, cm$) - 0.22$ ($r^2 = 0.86$). References for seahorses in Table I. Data for other marine teleosts from FishBase (Froese & Pauly, 2003). ◆, marine teleosts; ●, seahorses.

marine teleosts in L_{mat}, controlling for L_{max} (*F*-test: $F = 3.15_{1,351}$, $P = 0.08$); however addition of group explained no additional variation in the data set (r^2 with group $= 0.86$, without group $= 0.86$). These results indicate that the relationship between maximum reported length at onset of maturity and maximum length found for other teleosts could be used to predict length at first maturity for seahorse species for which data were lacking.

Marine fish species that exhibited parental care were examined next, comparing the size of seahorses at first maturity to that of other fishes. For marine teleosts with parental care and seahorses combined there was a significant linear relationship between $\log_e$ average length at first maturity and $\log_e$ maximum length (*t*-test: slope $= 0.80 \pm 0.54$, $n = 43$, $P < 0.001$) with no evidence of difference in slopes between seahorses and other marine teleosts with parental care ($L_{max} \times$ group interaction: *F*-test: $F = 0.003_{1,39}$, $P = 0.96$). Similar to comparisons with all marine teleosts (Fig. 3), seahorses did not differ significantly from other marine teleosts with parental care in L_{mat}, controlling for L_{max} (*F*-test: $F = 0.086_{1,40}$, $P = 0.77$).

For teleosts in general, maximum length was a good predictor of length at first maturity (Froese & Binohlan, 2000; Frisk *et al.*, 2001). One study found that asymptotic length (which was highly correlated with maximum reported length) explained 85–91% of the variation in the relationship between length at first maturity and asymptotic length across 265 species of fish, indicating that

length at first maturity was primarily a function of size (Froese & Binohlan, 2000).

In seahorses, methodological challenges meant that size at first maturity was commonly underestimated in studies. For teleosts in general, this parameter was measured as the size at which 50% of the animals have reached sexual maturity (developed ripe gonads: Froese & Pauly, 2003). In seahorses, however, the most commonly used (and somewhat subjective) determinant of sexual maturity was the presence of a fully developed brood pouch in the males (Perante *et al.*, 1998; Wilson & Vincent, 1998; Baum *et al.*, 2003). The only species that lack externally obvious pouches are the pygmy seahorses *H. bargibanti* and *H. denise* (Lourie & Randall, 2003). While this variable allowed one to infer maturity without having to kill the animals, the developed brood pouch may not have indicated physiological maturity. In *H. trimaculatus*, for example, the first fully developed brood pouch appeared at 80–90 mm Ht, but dissection of the testes revealed the size at first maturity to be 120 mm Ht (Cai *et al.*, 1984a). As an alternative, some studies defined sexual maturity as the size of the smallest recorded pregnant male (Nguyen & Do, 1996). This method also presented problems as males may have matured some time before they mated, especially where low seahorse densities or a skewed sex ratio reduced mating opportunities. Such error would result in an overestimation of size at onset of maturity. In order to resolve such problems, size at first maturity should be defined as size when 50% of the males in a population first bred; this point can be deduced from meticulous behavioural analysis in the field or dissection of testes in destructive sampling. However, conservation concern and pragmatism will dictate that the presence of a fully developed pouch will still be a key index of sexual maturity.

So few studies reported sex-specific lengths at first maturity that we had to assume that both sexes matured at much the same size. Methods for determining onset of female maturity were even more varied than those for males, and include the size at which ovaries appeared (Kanou & Kohno, 2001), the size of the smallest recorded female with hydrated eggs (Nguyen & Do, 1996) and the size of the smallest recorded female to release her eggs (Cai *et al.*, 1984a).

The timing and length of the breeding season for seahorses varied with location, and could be influenced by environmental parameters such as light, temperature and food availability (Bye, 1984). The breeding season for *H. zosterae* appeared to be correlated more with day length than with temperature (Strawn, 1953; Vari, 1982). *Hippocampus trimaculatus* had a peak in breeding from March to May in the China Sea (Truong & Nga, 1995), but bred consistently year round *ex situ* if temperatures were kept constant (Cai *et al.*, 1984a). Pregnant *H. comes* were found year round in the Philippines, where water temperatures were fairly constant, but with a peak in the number of pregnant males between July and December, corresponding to the rainy season (Perante *et al.*, 2002). Peak periods of reproduction were correlated with the full moon for *H. guttulatus* in the Arcachon Basin, France (Boisseau, 1967), but not in a Portuguese lagoon (J. Curtis, unpubl. data). Any one individual animal may have mated for only a portion of the entire breeding period.

The duration of the breeding season was longer in tropical than temperate waters, with the apparent exception of *H. abdominalis* (Table VIII, Fig. 4)

TABLE VIII. Breeding season (*in situ*), duration of breeding season (*in situ*) and average reported gestation (pregnancy) duration for seahorse species (*Hippocampus* spp.). Where more than one reported value was found per species (indicated by $n > 1$, where $n =$ the number of sources consulted) the results were averaged with the mean given in the table

Species	Breeding season	Breeding duration (months)	Reference(s)	Gestation duration (days)	Range (days)	n	Reference(s)
H. abdominalis	Year round	12	Woods, 2003	30	28–34	6	Graham, 1939; Lovett, 1969; Francis, 1988; Gomon & Neira, 1998 in Lourie *et al.*, 1999; Woods, 2000*a*; Sobolewski, unpubl. data
H. barbouri	–	–		13	12–14	1	Warland, 2003
H. bargibanti	Year round	12	D. Tackett, pers. comm.	14	–	1	D. Tackett, pers. comm.
H. capensis	Summer	4	Whitfield, 1995; Lockyear *et al.*, 1997	28	18–45	3	Grange & Cretchley, 1995; Whitfield, 1995; J. Lockyear, pers. comm.
H. comes	Year round	12	A.D. Macansantos, unpubl. data	14	9–18	3	A.D. Macansantos, unpubl. data; M. Pajaro, unpubl. data; N. Perante, unpubl. data
H. erectus	May to October	6	Teixeira & Musick, 2001	21	–	1	Herald & Rakowicz, 1951
H. guttulatus	March to October	8	Reina-Hervas, 1989	26	21–28	4	Boisseau, 1967; Cabo, 1979; Kuiter, 200l; N. Garrick-Maidment, unpubl. data

TABLE VIII. Continued

Species	Breeding season	Breeding duration (months)	Reference(s)	Gestation duration (days)	Range (days)	n	Reference(s)
H. hippocampus	April to October	7	Wheeler, 1969; Tortonese, 1970; Wheeler, 1985; Whitehead, 1986; Reina-Hervas 1989	25	21–32	4	Boisseau, 1967; Lythgoe & Lythgoe, 1971; Cabo, 1979; N. Garrick-Maidment, unpubl. data
H. kuda	Year round	12	Truong & Doan, 1994	17	10–24	5	Xu, 1985; Mi et al., 1998; Mi, 1993; Truong & Doan, 1994; Truong, 1994
H. spinosissimus	Year round	12	Truong & Nga, 1995; Nguyen & Do, 1996	–	–	–	–
H. subelongatus	Seasonal	4	Jones & Avise, 2001	18	14–21	1	G. Moore, pers. comm. in Lourie et al., 1999
H. trimaculatus	Year round	12	Truong & Nga, 1995	16	11–20	5	Cai et al., 1984a, b; Xu, 1985
H. whitei	October to April	6	Vincent & Sadler, 1995	21	–	1	Vincent & Sadler, 1995
H. zosterae	February to November	10	Strawn, 1958	11	10–13	5	Strawn, 1954, 1958; Masonjones & Lewis, 1996; Masonjones, 1997; Masonjones & Lewis, 2000
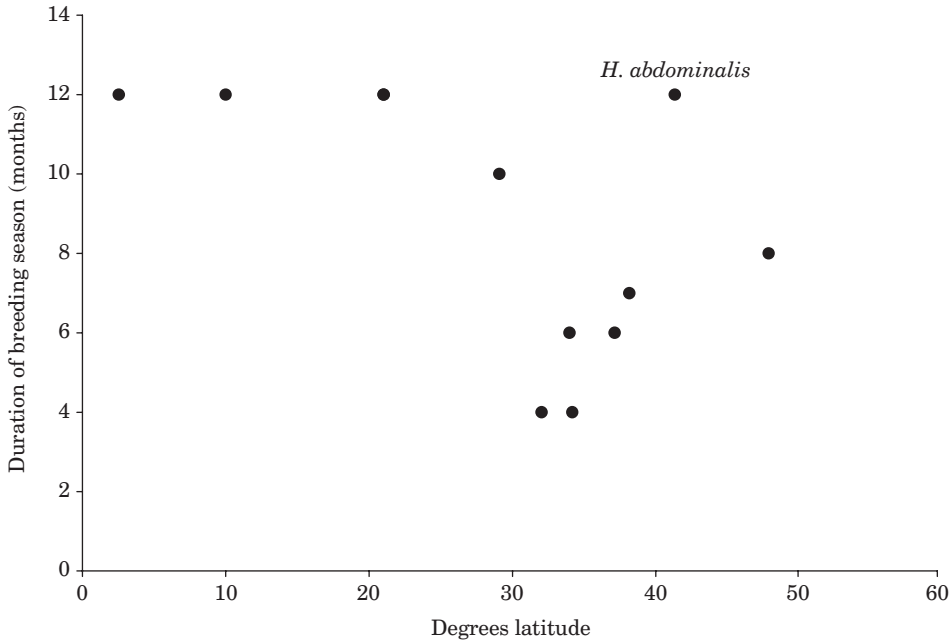
FIG. 4. Duration of breeding season (months *in situ*) *v.* latitude for 12 species of seahorse (*Hippocampus* spp.). In general, the number of breeding months decreases with increasing latitude. *Hippocampus abdominalis*, however, may breed year round at high latitudes. References in Table VIII.

(Pearson's correlation coefficient: with *H. abdominalis* $P = 0.04$; without *H. abdominalis* $P = 0.01$): *H. abdominalis* may have reproduced year round at high latitudes in Australia (Poortenaar *et al.*, 2001). In contrast, most fishes that inhabited temperate latitudes reproduced during a limited season when their young were most likely to benefit from improvements in climate and food supplies (Wootton, 1990; Bromage *et al.*, 1994).

MATING PATTERNS

All seahorse species appeared to be monogamous within a single breeding cycle, the male accepting eggs from only one female, based on observations made *in situ*. Of the 12 reported studies on social structure, nine reported that the seahorses formed pair bonds that endured through multiple matings, while seahorses in only three species formed larger groups (Table IX). When it came to mating patterns, four studies found that seahorses mated exclusively with one partner in a single breeding season (monogamy), while one study found evidence that seahorses mated with several partners in a single breeding season (polygamy) (Table IX). The results of one study showed variation in mating patterns, with apparent low-level sexual polygamy: seven of 15 wild male *H. subelongatus* were shown to remain faithful throughout the study period, five other males switched mates but it was not known if the original partners were available, and one re-mated when its original partner was still accessible (Kvarnemo *et al.*, 2000). In a similar *in situ* study, most of the observed

TABLE IX. The occurrence of social groupings and mating patterns for seahorse species (*Hippocampus* spp.). The nature of the study is indicated (*ex situ*, *in situ*)

Species	Social grouping	Mating pattern	Reference(s)
H. abdominalis	Groups (*in situ*)	Polygamous (*ex situ*)	Woods, 2000a
H. bargibanti	Pairs (*in situ*)		Tackett & Tackett, 1997
H. breviceps	Groups (*in situ*)		Moreau & Vincent, in press
H. capensis	Pairs (*in situ*)	Monogamous (*in situ*)	Grange & Cretchley, 1995
H. comes	Pairs (*in situ*)		Perante *et al.*, 2002
H. fuscus	Pairs (*ex situ*)	Monogamous (*ex situ*)	Vincent, 1990
H. guttulatus	Groups (*in situ*)		J. Curtis, unpubl. data
H. hippocampus	Pairs (*in situ*)		J. Curtis, unpubl. data
H. histrix	Pairs (*in situ*)		Kuiter & Debelius, 1994
H. reidi	Pairs (*in situ*)		Dauwe, 1992; Nijhoff, 1993; Trommelen, 2001
H. subelongatus		Variable (*in situ*)	Kvarnemo *et al.*, 2000; Jones *et al.*, 2003
H. whitei	Pairs (*in situ*)	Monogamous (*in situ*)	Vincent & Sadler, 1995
H. zosterae	Pairs (*ex situ*)	Monogamous (*ex situ*)	Masonjones & Lewis, 1996

H. subelongatus males ($n = 9/12$) remained faithful to a single female over two broods, whereas the other males switched partners (Jones *et al.*, 2003).

Given the generally monogamous mating pattern in seahorses, their sexual monomorphism in size is not surprising; sexual dimorphism is generally associated with polygamy (Emlen & Oring, 1977; Jones & Avise, 2001). In support of such an association, polygamous pipefishes tended to be highly dimorphic in size, colour and ornamentation (*Nerophis ophidion* Linnaeus, *Syngnathus typhle*, Berglund *et al.*, 1989), while monogamous pipefishes were monomorphic (*Corythoichthys* spp., Gronell, 1984). Sexual dimorphism in body proportions is commonly related to competition for mates, primarily among males, but such competition among seahorses was probably limited to accessing desirable partners when pairs were originally formed.

Monogamy probably acts to increase the reproductive success of fishes found in low densities, that have low mobility, and that depend on camouflage as a defense against predation (Barlow, 1984, 1988; Vincent & Sadler, 1995). However, monogamous *H. whitei* had temporal and spatial opportunities for extra

pair mating, commonly encountering non-partner seahorses (Vincent & Sadler, 1995; Vincent *et al.*, 2004). Seahorses may have experienced increased reproductive efficiency from mating with the same partner, resulting in larger broods and reduced time spent on courtship. In *H. fuscus*, for example, *post hoc* analysis showed that pairs that spent greater than half a pregnancy together prior to mating had significantly larger brood sizes than otherwise (Vincent, 1990). Sexual fidelity may have also shortened interbrood intervals (Kvarnemo *et al.*, 2000).

Monogamy, where it occurred, appeared to be reinforced by daily greetings (*H. fuscus*, Vincent, 1995; *H. whitei*, Vincent & Sadler, 1995; *H. zosterae*, Masonjones & Lewis, 1996). This was true for most monogamous syngnathid species studied to date, including certain pipefishes (*Corythoichthys intestinalis* Ramsay, Gronell, 1984; *Hippichthys penicillus* Cantor, Watanabe *et al.*, 1997). In a wild population of *H. whitei*, the female seahorse travelled to her mate each morning and they interacted for 6–10 min, performing the first few movements of courtship (Vincent & Sadler, 1995). Morning interactions continued all through the pregnancy, and may have helped synchronize female egg preparation to the end of male pregnancy. On the day the male gave birth, or the next day, the routine greeting was prolonged into a courtship and mating. Given their inferred dependence on camouflage, it was surprising that seahorse courtships *in situ* were colourful, active and lengthy, lasting up to 9 h (*H. whitei*, Vincent & Sadler, 1995). After this long courtship the seahorses mated (see Fiedler, 1954 and Masonjones & Lewis, 1996 for detailed descriptions of seahorse mating behaviour in other species). Neither sex within an established pair bond responded to displays by non-partners (Vincent & Sadler, 1995). Similar behaviours were observed with captive pairs of *H. fuscus* (Vincent, 1995) and *H. zosterae* (Masonjones & Lewis, 1996).

Polygamy in seahorses may have derived from a combined effect of greater population density, and higher rate of movement. Very high densities were reported for populations of *H. guttulatus* in a Portuguese seagrass bed, where large group sizes may lead to an inference of polygamy (J. Curtis, pers. comm.). As well, the socially and sexually polygamous *H. abdominalis* were highly mobile when compared to other seahorse species (K. Martin-Smith, pers. comm.), increasing chances of extra-pair encounters.

Contrary to expectations (Trivers, 1985), seahorses studied to date maintained conventional sex roles with males competing most intensely for mates, and females selecting mates most carefully (*H. capensis*, Fourie, 1997; *H. fuscus*, Vincent, 1994a; *H. subelongatus*, Jones *et al.*, 1998; *H. zosterae*, Masonjones & Lewis, 1996). Sex role reversal had been predicted on the basis that high male parental investment in pregnancy would depress the male reproductive rate below that of the female; in such a case, more intense female competition for mates and greater sexual selection pressure imposed on females would be expected (Clutton-Brock & Vincent, 1991; Vincent *et al.*, 1992; Berglund, 2000; Matsumoto & Yanagisawa, 2001). The finding that unmated seahorses maintained conventional sex roles was explained by the relative time it took seahorses to prepare for mating: unmated males could prepare their pouches more quickly than a female could ready eggs, and unmated males could also remain ready to mate for longer than could unmated females. Consequently, among seahorses first seeking mates, the sex ratio of receptive seahorses was

male-biased (Vincent *et al.*, 1992). In fact, competition for mates was very rare in a monogamous and low-density population of wild *H. whitei* (Vincent, 1994*a*; Vincent & Sadler, 1995), probably because three or more unpaired seahorses rarely encountered each other simultaneously.

As in pipefishes, mate selection in seahorses appeared to be assortative, with breeding pairs comprising males and females of similar size (Berglund *et al.*, 1989 *ex situ*; Berglund, 1994 *ex situ*; Vincent & Sadler, 1995 *in situ*; Watanabe *et al.*, 1997 *ex situ*). Evidence of size-assortative mating was seen in a wild population of *H. whitei*, in which partners' lengths were significantly and positively correlated (Vincent & Giles, 2003). Similarly, a microsatellite-based study of mating patterns in wild populations of *H. subelongatus* and *H. whitei* confirmed that their offspring were derived from size-matched pairs (Jones *et al.*, 2003). In the pipefish *Syngnathus schlegeli* Kaup, the size relationship between mates was related to effective use of pouch space (Watanabe & Watanabe, 2002) but similar data were not available for any seahorse species. Assortative mating was coincident with little or no dimorphism in size, and was argued to contribute to the sympatric speciation of seahorse species (Jones *et al.*, 2003).

EGG AND CLUTCH SIZE

Seahorse eggs are oval or pear-shaped, semi-transparent, and orange as a result of the carotenoids from their crustacean-dominated diet (Boisseau, 1967; Hardy, 1978; Vincent, 1990; Woods, 2000*b*; Poortenaar *et al.*, 2001). Seahorse ovaries are unusual: when sliced transversely (dorso-ventrally), they appear as spirals, with developing oocytes moving to the outer edge of the ovary as they mature (Boisseau, 1967; Selman *et al.*, 1991). The female hydrates part of her post-vitellogenic clutch at each mating, transferring all such eggs to the male. In contrast, other fishes might spawn all oocytes from the ovary and began again with primary oocytes (Wallace & Selman, 1981). Ovarian length was roughly proportional to trunk length but the diameter reflected reproductive state, expanding greatly with ripe eggs (Boisseau, 1967). Ovaries of seahorses had relatively few oocytes for their size (Boisseau, 1967).

No significant relationship was found between egg size (diameter: Table X) and adult size (Ht_{max}) in seahorses (*t*-test: slope $= 0.01 \pm 0.01$, $n = 12$, $P = 0.52$). This lack of relationship was common across marine teleosts (Fig. 5): for marine teleosts with an $L_{max} < 51$ cm (including seahorses), there was no linear relationship between $\log_e$ average egg diameter and $\log_e$ maximum length (*t*-test: slope $= 0.02 \pm 0.08$, $n = 78$, $P = 0.79$) and there was no difference in the slopes between seahorses and other marine teleosts ($L_{max} \times$ group interaction: *F*-test: $F = 0.006_{1,74}$, $P = 0.94$). These findings support the theory that optimal egg size was independent of the size of the parent (Wootton, 1990). Seahorses did, however, have larger diameter eggs than did marine teleosts, controlling for L_{max} (*F*-test: $F = 6.43_{1,75}$, $P = 0.013$). Such an investment in reproduction was not surprising given that species with parental care tended to have larger eggs than species that broadcast spawn into open waters (Bagarinao & Chua, 1986; Goodwin *et al.*, 2002). Small sample sizes precluded repetition of the analyses with marine teleosts that exhibited forms of parental care.

TABLE X. Egg diameter and length at birth for seahorse species (*Hippocampus* spp.). Where more than one reported value was available per species (indicated by $n > 1$, where $n =$ the number of studies consulted) the results were averaged and the mean given in the table

Species	Egg diameter (mm)	n	Reference(s)	Length at birth (mm)	n	Reference(s)
H. abdominalis	1·8	4	Graham, 1939; Vincent, 1990; Woods, 2000a; Poortenaar et al., 2001	16·2	12	Young, 1926; Graham, 1939; Lovett, 1969; Francis, 1988; Vincent, 1990; Gomon & Neira, 1998; Sobolewski, manuscript in Lourie et al., 1999; Woods, 2000a, b; Poortenaar et al., 2001; J. Le Cheminant, unpubl. data; C. Woods, unpubl. data
H. barbouri				5·0	1	B. Burhans, unpubl. data
H. bargibanti				2·0	1	S. Lourie, unpubl. data
H. breviceps	1·6	1	Vincent, 1990	8·9	1	Vincent, 1990
H. capensis				11·1	3	Whitfield, 1995; Lockyear et al., 1997; J. Lockyear, pers. comm. in Lourie et al., 1999
H. comes	1·4	1	Vincent, 1990	9·5	2	Vincent, 1990; N. Perante, unpubl. data
H. erectus	1·5	1	Vincent, 1990	11·0	4	Herald & Rakowicz, 1951; Vari, 1982; Correa et al., 1989; Vincent, 1990

TABLE X. Continued

Species	Egg diameter (mm)	n	Reference(s)	Length at birth (mm)	n	Reference(s)
H. fuscus	1·7	1	Vincent, 1990	7·5	2	Vincent, 1990; Golani & Fine, 2002
H. guttulatus	2·0	2	D'Ancona, 1932; Whitehead, 1986	11·8	3	Cabo, 1979; Whitehead, 1986; N. Garrick-Maidment, unpubl. data
H. hippocampus	1·6	1	D'Ancona, 1932	9·3	3	Cabo, 1979; Golani & Fine, 2002; N. Garrick-Maidment, unpubl. data
H. ingens				8·5	2	Jones *et al.*, 1998; J. Gomezjurado, unpubl. data in Lourie *et al.*, 1999
H. kuda	1·8	1	Mi *et al.*, 1998	7·0	2	Mi, 1993; Mi *et al.*, 1998; J. Mitchell, unpubl. data
H. reidi	1·2	1	Vincent, 1990	6·7	1	Vincent, 1990
H. subelongatus				11·3	2	Lawrence, 1998; Payne & Rippingale, 2000
H. trimaculatus	0·9	1	Cai *et al.*, 1984a	6·1	1	Cai *et al.*, 1984a
H. whitei	1·8	1	Vincent, 1990	8·5	1	Vincent, 1990
H. zosterae	1·3	1	Vincent, 1990	7·9	4	Breder, 1940; Strawn, 1958; Vincent, 1990; Lourie *et al.*, 1999
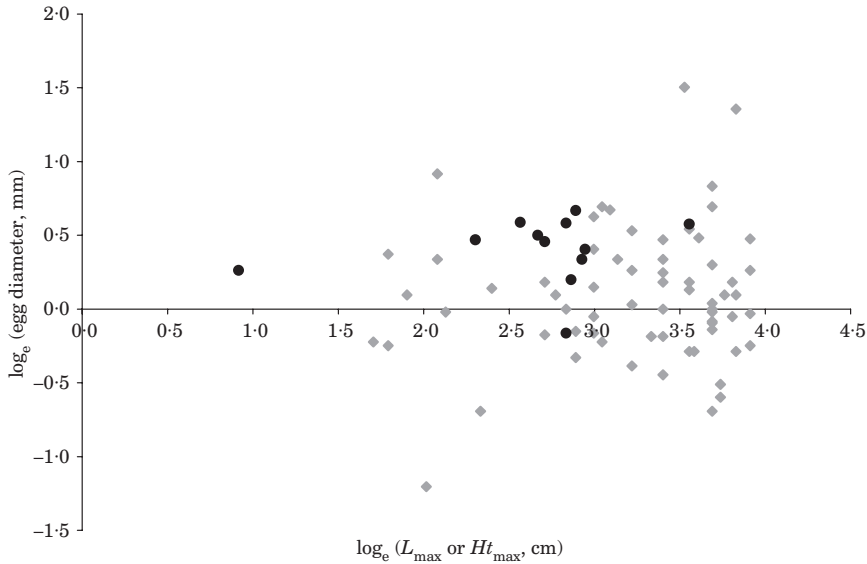
FIG. 5. Average egg diameter (mode for teleosts, mean for seahorses) v. maximum recorded adult size (L_{max} for teleosts, Ht_{max} for seahorses) for 66 marine teleosts species less than 51 cm in maximum reported length and 12 seahorse species (*Hippocampus* spp.). References for seahorses in Table X. Data for other marine teleosts from FishBase (Froese & Pauly, 2003). ◆, marine teleosts; ●, seahorses.

In seahorses, as in most fish species, interspecific differences in egg size were more dependent on latitude than on adult size; the nearer the species was found to the equator, the smaller the eggs (Thresher, 1988). When the average egg diameter of seahorse species was regressed against latitude, the regression was significant (*t*-test: slope $= 0.01 \pm 0.005$, $n = 12$, $P = 0.015$) (Fig. 6). For teleosts in general, eggs of species living at lower latitudes were generally smaller than those at higher latitudes (Bagarinao & Chua, 1986). A similar trend was observed in pipefishes of the North Atlantic (Thresher, 1988), perhaps because offspring from larger eggs had a greater chance of survival in higher latitudes than those from smaller eggs (Lack, 1954; Williams, 1966; Capinera, 1979). Arguably, larger eggs produced larger offspring that were better able to swim, to survive food deprivation, to compete for resources and better equipped for thermoregulation (Marshall, 1953; Blaxter & Hempel, 1963; Mann & Mills, 1979; Calow, 1981). Field and laboratory studies of juvenile fish have supported the hypothesis that survival is size dependent (Sogard, 1997).

In general, larger eggs produced larger young. A meta-analysis of 135 teleost species from a wide variety of habitats found that egg diameters were positively correlated with larval lengths and weights at hatching (Bagarinao & Chua, 1986). Similarly, a study of 11 seahorse species found that the dry weight of individual eggs was positively correlated with the dry weight of individual young (Vincent, 1990). The current study also showed a positive interspecific relationship between $\log_e$ mean egg size and $\log_e$ average size at birth (Fig. 7, *t*-test: slope $= 0.70 \pm 0.31$, $n = 12$, $P = 0.05$); the small sample size, and the
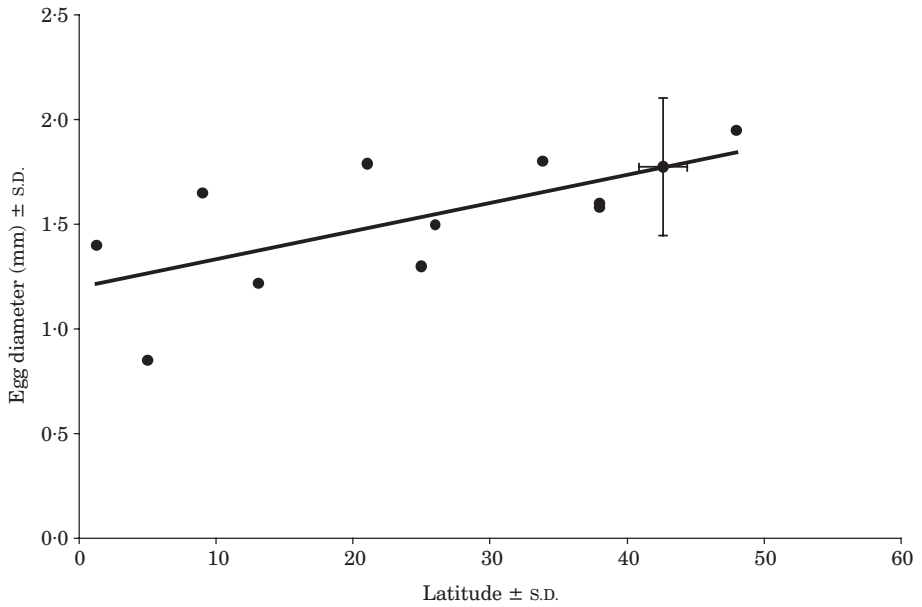
FIG. 6. Mean* egg diameter *v.* mean latitude for 12 species of seahorse (*Hippocampus* spp.). Egg diameter increases with increasing latitude: egg diameter (mm) $= 0.01 \times$ (latitude) $+ 1.20$ ($r^2 = 0.46$). *Data points without error bars are single estimates ($n = 1$ study). References in Table X.
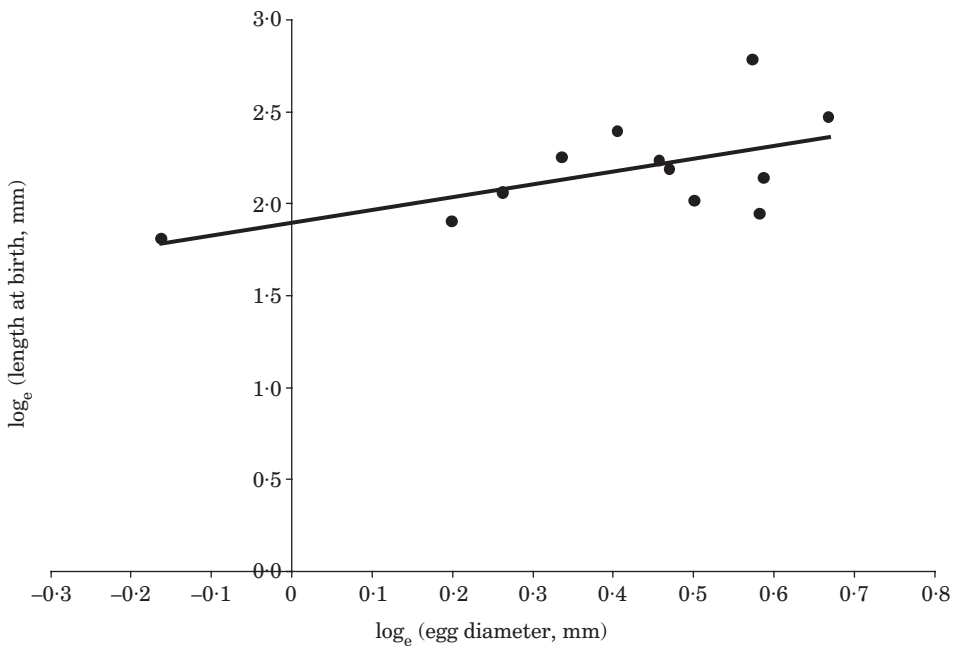

FIG. 7. Mean length at birth *v.* mean egg diameter for 12 species of seahorse (*Hippocampus* spp.). The length at birth increases with increasing egg diameter: Log$_e$(length at birth, mm) $= 0.70 \times$ log$_e$(egg diameter, mm) $+ 1.90$ ($r^2 = 0.34$). References in Table X.

potential for inconsistency in measurement techniques among studies may contribute to the marginal level of significance.

A comparison of egg sizes from different studies was problematic because different researchers used eggs in differing states of development, and measured them differently. Eggs were obtained from spills during copulation (Graham, 1939; Woods, 2000*a*), dissection of the male's pouch (Whitehead, 1986; Mi *et al.*, 1998) or from the ovaries (Selman *et al.*, 1991; Poortenaar *et al.*, 2001). Size was determined when the eggs were fresh (Graham, 1939; Woods, 2000*a*), preserved (Vincent, 1990), or using histology after fixation (Cai *et al.*, 1984*a*; Poortenaar *et al.*, 2001). If fresh, it was not always clear if only the yolk was measured or the chorion as well. Egg measurements have been obtained across the long and short axes of the eggs, or with formulae using both.

Recorded female clutch sizes (total number of eggs deposited or dropped in one mating) ranged from 5 (*H. zosterae*, Vincent 1990) to over 1000 eggs (*H. erectus*, Teixeira & Musick, 2001; *H. reidi*, Vincent, 1990) (Table XI). Comparative analyses of clutch size were precluded by the great variation in methods used to determine clutch size, with some studies reporting the size of dropped clutches (Vincent, 1990; Lawrence, 1996), and others using histology of the ovaries (Strawn, 1958; Boisseau, 1967); this latter approach is problematic because seahorse ovaries spiral out, with eggs constantly maturing and being shed from the outer layer (Wallace & Selman, 1981). Direct measurements of egg transfer would only be possible by intrusion into the male's pouch, probably through destructive sampling. The difficulty in measuring clutch size was clear from the fact that three of the five estimates of maximum clutch size were smaller than the maximum brood size (Table XI), despite monogamy within a particular reproductive cycle, for all species.

PREGNANCY

Seahorses invest heavily in the development of each of their young. During mating the female seahorse deposits her entire clutch of eggs in the male's brood pouch, where they are fertilized (ensuring paternity), whereupon the male seals the pouch shut. Both male and female seahorses exhibit visible evidence of having mated, as the female girth diminishes and the male pouch fills (Vincent & Sadler, 1995). In a monogamous population of *H. whitei*, male and female reproductive state changes were always synchronized exclusively within a pair, thereby confirming mate fidelity (Vincent & Sadler, 1995). Not all transferred eggs were successfully fertilized and/or developed properly. For example, $1\cdot23 \pm 0\cdot19\%$ of eggs were non-viable in the pouches of wild *H. abdominalis* (C. Woods, unpub. data), 2–33% of eggs were found to be sterile in *H. erectus* pouches *in situ* (Teixeira & Musick, 2001), and there was an inferred loss during *H. fuscus* pregnancy of approximately 45% *ex situ* (Vincent, 1994*b*).

Seahorse embryos develop in a marsupium that acts much like the mammalian uterus. The developing embryos are protected and provided with oxygen through a capillary network, while the pouch acts as an adaptation chamber with the osmolarity of the fluid inside the pouch changing from that of body fluids to that of salt water as pregnancy progresses (Linton & Soloff, 1964). The male hormone prolactin in the pouch initiates enzymatic conversion of proteins

TABLE XI. Reported maximum clutch and brood sizes for seahorse species (*Hippocampus* spp.). Both the nature of the reported study (*ex situ*/*in situ*, where *in situ* includes wild-caught pregnant males whose broods are released in captivity) and the total number of sources consulted (*n*) are given

Species	Maximum clutch	Reference	n	Clutch sampling methods	Maximum brood	Reference(s) (*in situ*/*ex situ*)	n
H. abdominalis					1116	R. Hawkins, pers. comm. (*ex situ*)	10
H. barbouri					250	Warland, 2003	1
H. bargibanti					34	D. Tackett, unpubl. data (*in situ*)	1
H. breviceps	63	A. Kendrick, unpubl. data (?)	1	Unknown	100	Kuiter, 2000 (*in situ*)	3
H. capensis					120	Whitfield, 1995 (?)	4
H. comes					350	N. Perante, unpubl. data (*in situ*)	2
H. erectus	1313	Teixeira & Musick, 2001 (*in situ*)	2	Pre-hydrated oocytes, counted in ovaries	1552	Teixeira & Musick, 2001 (*in situ*)	5
H. fuscus	157	A. Vincent, unpubl. data (*ex situ*)	1	Hydrated oocytes, counted after release	150	Golani & Fine, 2002 (*in situ*)	2
H. guttulatus					581	Boisseau, 1967 (*in situ*)	3
H. hippocampus					865	Boisseau, 1967 (*in situ*)	3
H. ingens					2000	B. Burhans, unpubl. data (*ex situ*)	3
H. kuda					1405	Truong & Doan, 1994 (*in situ*)	2
H. reidi					1572	Vincent, 1990 (*ex situ*)	2
H. spinosissimus					683	Nguyen & Do, 1996 (*in situ*)	2
H. subelongatus	600	Lawrence, 1996 (*ex situ*)	1	Hydrated oocytes, counted after release	700	Jones & Avise, 2001 (*in situ*)	5
H. trimaculatus					1783	Nguyen & Do, 1996 (*in situ*)	3
H. whitei					250	Vincent, 1990 (*in situ*)	3
H. zosterae	69	Strawn, 1958 (*in situ*)	1	Mature oocytes, counted in ovaries	55	Strawn, 1958 (*in situ*)	7

of vitellogenic (maternal) origin which nourish the embryos (Boisseau, 1967), along with male-contributed inorganic compounds (Linton & Soloff, 1964). Waste products diffuse out into the male's blood stream for removal (Linton & Soloff, 1964). After fertilization, the pouch becomes spongy, vascularized and distended (Wetzel & Wourms, 1991). The eggs induce pits in the wall of the pouch which become compartmentalized and then are enveloped in epithelial tissue until the end of yolk absorption (Boisseau, 1967; Wetzel & Wourms, 1991).

The duration of the male's pregnancy (gestation duration) ranged from approximately 9 to 45 days, depending on species and water temperature (Table VIII). Across the genus, gestation duration was positively and significantly correlated with latitude (t-test: slope $= 0.28 \pm 0.08$, $n = 15$, $P = 0.005$) (Fig. 8). The relationship between gestation duration and latitude probably reflected changes in water temperature; $H.$ $trimaculatus$ had gestation durations of 19 days at $22.5°$ C, 16 days at $24°$ C and 11 days at $28.5°$ C (Cai et $al.$, 1984b). Gestation duration also decreased with increasing temperature for captive $H.$ $abdominalis$ (Woods, 2000a) and for $H.$ $whitei$ in $situ$ (Vincent & Sadler, 1995). Gestation duration did not vary with Ht_{max} across the genus (t-test: slope $= 0.26 \pm 0.19$, $n = 14$, $P = 0.19$).

Males of all species studied to date went through several pregnancies in a single breeding season, the number of pregnancies depending on the length of brooding and the length of the season: individual male $H.$ $comes$ were observed
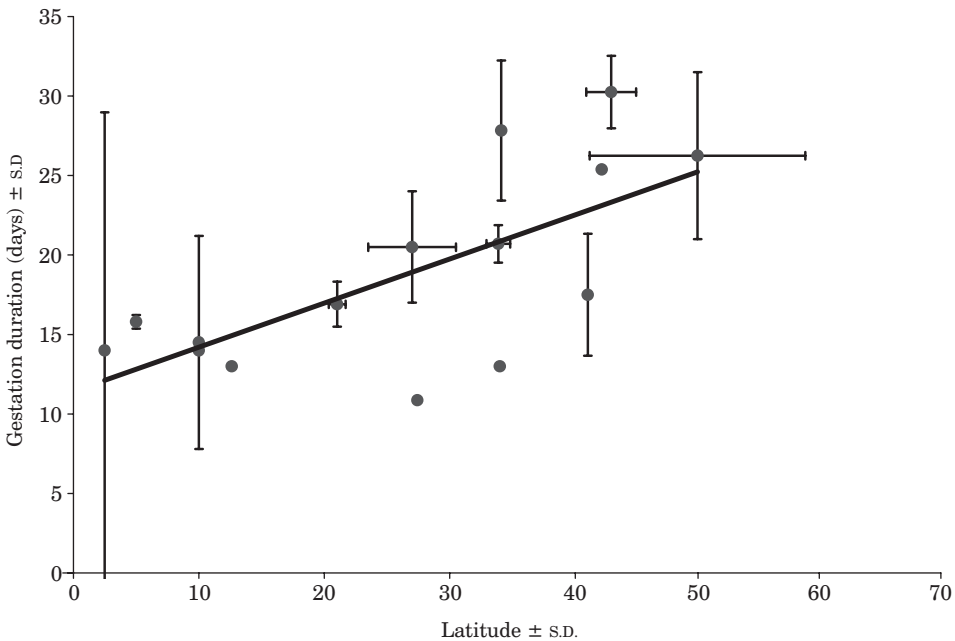

FIG. 8. Mean* gestation duration $v.$ mean latitude for 12 species of seahorse ($Hippocampus$ spp.). Gestation duration increases with increasing latitude: gestation duration (days) $= 0.28 \times$ (latitude) $+ 11.43$ ($r^2 = 0.47$). *Data points without error bars are single estimates ($n = 1$ study). References in Table VIII.

to undergo repeated pregnancies during a year (Perante *et al.*, 2002); *H. subelongatus* males had more than one pregnancy per breeding season (Kvarnemo *et al.*, 2000); *H. whitei* pairs mated every 3 weeks over a study period lasting from November to April (Vincent & Sadler, 1995); and *H. zosterae* were reported to carry two broods per month (Vari, 1982). In addition, studies of the oocytes of female *H. abdominalis* indicated that they mated many times during the reproductive season (Poortenaar *et al.*, 2001).

It was possible to calculate the maximum possible number of young produced by a pair of seahorses. Assuming that males became pregnant the day after giving birth, as was observed for wild *H. whitei* (Vincent & Sadler, 1995), then the number of days available for breeding divided by average gestation duration (from Table VIII) produced an estimate of the maximum possible number of pregnancy events per year for a species. When this was multiplied by the maximum possible brood size (from Table XI), this gave maximum annual reproductive outputs that ranged from approximately 500 young per pair of *H. capensis*, to over 29 000 young for *H. kuda*.

YOUNG AND BROOD

At the end of pregnancy the male went into labour (usually at night), actively forcing the brood out of his pouch for hours (Vincent, 1990). Young resembled miniature adult seahorses, complete with hardened fin rays, trunk rings and pigmentation (Boisseau, 1967; Gomon & Neira, 1998; Mi *et al.*, 1998). They were independent from birth and received no further parental care. Known newborn sizes ranged from approximately 2 mm (*H. bargibanti*, S. Lourie, unpubl. data) to 20 mm (*H. abdominalis*, Young, 1926), or a eight-to 10-fold increase from smallest to largest young (Table X). In contrast, adult Ht_{max} ranged from 21 mm (*H. denise*, Lourie & Randall, 2003) to 350 mm (*H. abdominalis*, Francis, 1988), a 17-fold increase from smallest to largest species (Table I).

Similar to egg size, length of seahorses at birth was correlated with latitude and not adult size, a common relationship across fishes (Bagarinao & Chua, 1986). When the log_e of the averaged values for length at birth were regressed against log_e Ht_{max} across species, the relationship was significant (Fig. 9, *t*-test: slope $= 0.41 \pm 0.13$, $n = 17$, $P = 0.006$). However, the relationship between length at birth and Ht_{max} was largely driven by the values for *H. abdominalis* and *H. bargibanti*; removing these species from the analysis caused the effect of Ht_{max} to become insignificant (Fig. 9 – dashed trend line, *t*-test: slope $= 0.05 \pm 0.12$, $n = 15$, $P = 0.72$). Length at birth then varied significantly and positively with latitude (*t*-test: slope $= 0.16 \pm 0.04$, $n = 17$, $P < 0.001$) (Fig. 10). As with eggs, this relationship between length at birth and latitude could have derived (directly or indirectly) from the influence of photoperiod or temperature; decreased photoperiod and temperature found at higher latitudes may have resulted in an increased egg size or gestation duration, and final size at birth (Bagarinao & Chua, 1986; Thresher, 1988).

The lack of relationships between size at birth (size at hatching for most teleosts) and adult size observed across seahorse species in this study was consistent with the pattern observed across marine teleosts (Fig. 11). For marine teleosts less than 51 cm L_{max} and seahorses combined there was no linear
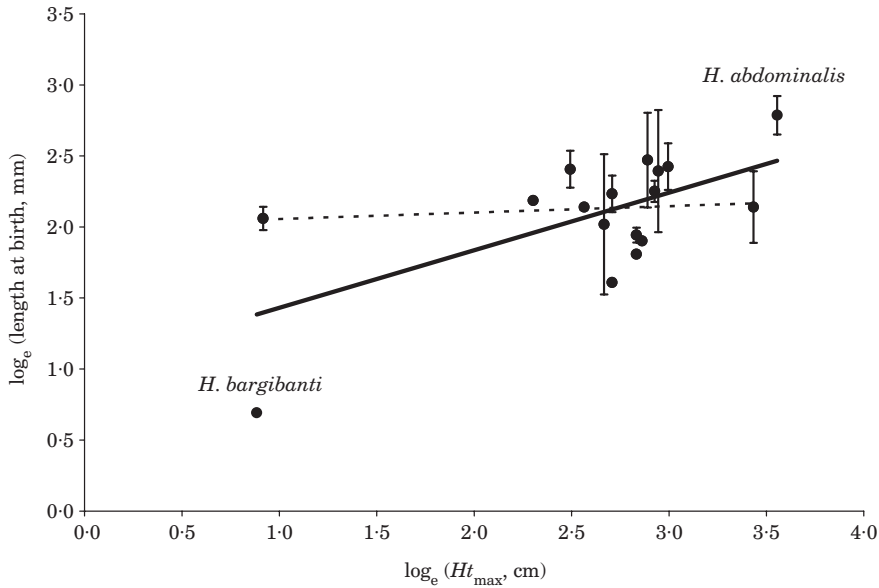
FIG. 9. Mean* length at birth $v.$ maximum recorded adult height (Ht_{max}) for 17 species of seahorse (*Hippo-campus* spp.). Length at birth increases with max Ht, but this relationship is driven by *H. bargibanti* and *H. abdominalis* (solid trendline): Log_e(length at birth, mm) = $0.41 \times Log_e$(Ht_{max}, cm) + 1.02 ($r^2 = 0.40$). When *H. abdominalis* and *H. bargibanti* are excluded from the analysis ($n = 15$), length at birth shows no significant relationship with Ht_{max} (dashed trendline) ($r^2 < 0.001$). *Data points without error bars are single estimates ($n = 1$ study). References in Tables I and X.
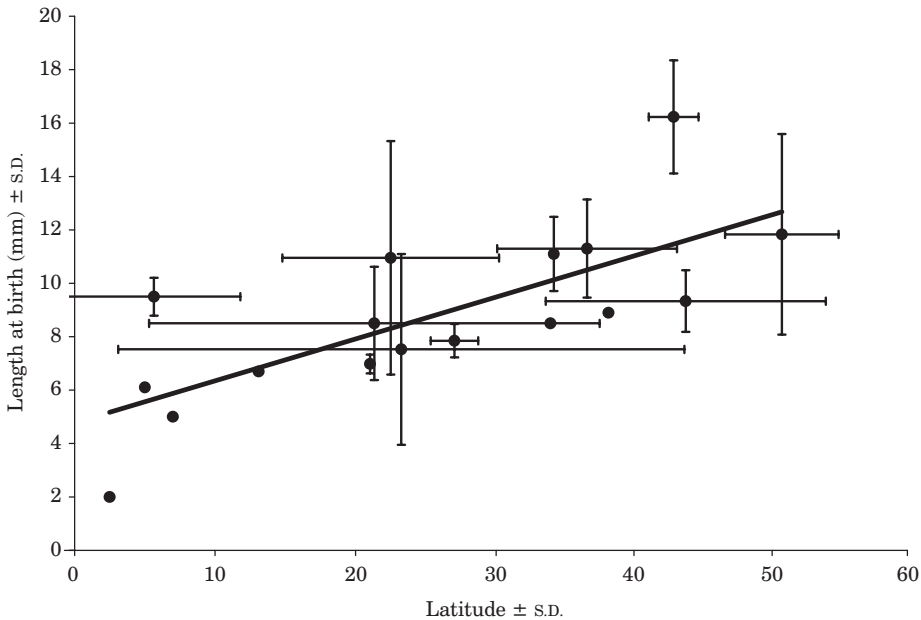
FIG. 10. Mean* length at birth $v.$ mean latitude for 17 species of seahorse (*Hippocampus* spp.). Length at birth increases with increasing latitude: length at birth (mm) = $0.16 \times$ (latitude) + 4.78 ($r^2 = 0.55$) *Data points without error bars are single estimates ($n = 1$ study). References in Table X.
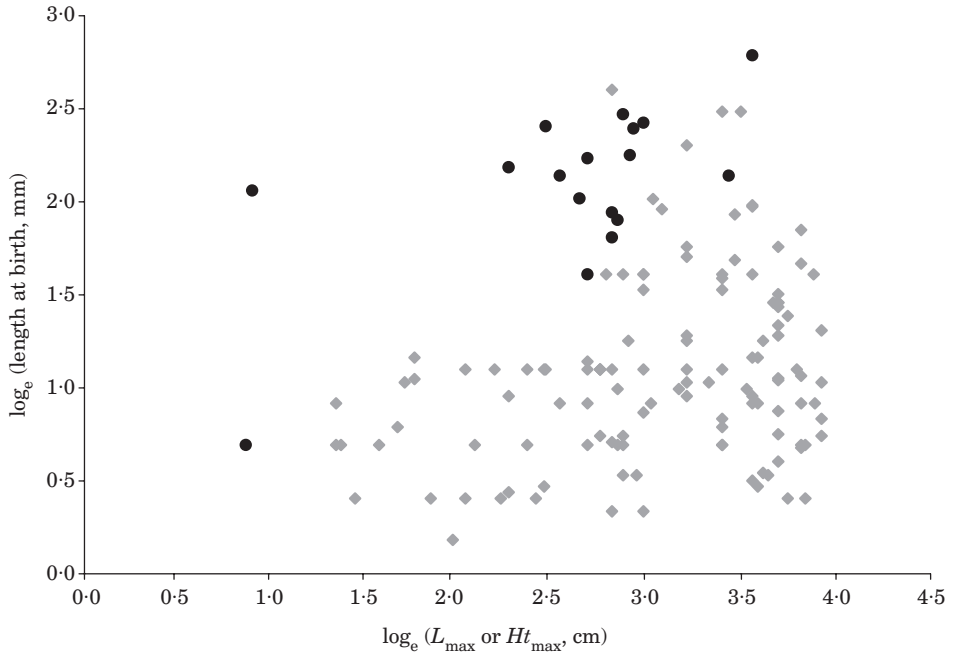
FIG. 11. Average length at birth (mode for teleosts, mean for seahorses) *v.* maximum recorded adult size (L_{max} for teleosts, Ht_{max} for seahorses) for 121 marine teleosts species less than 51 cm in maximum reported length and 17 seahorse species (*Hippocampus* spp.). References for seahorses in Table X. Data for other marine teleosts from FishBase (Froese & Pauly, 2003). ◆, marine teleosts; ●, seahorses.

relationship between $\log_e$ average length at birth and $\log_e$ maximum length (*t*-test: slope $= 0.09 \pm 0.07$, $n = 138$, $P = 0.224$) with no evidence of difference in slopes between seahorses and other marine teleosts ($L_{max} \times$ group interaction; *F*-test: $F = 0.012_{1,134}$, $P = 0.93$). At birth, seahorses were longer than other marine teleosts were at hatching, controlling for L_{max} (*F*-test: $F = 89.61_{1,135}$, $P < 0.001$); the difference presumably derived from the longer developmental period before seahorse young emerge from the pouch.

For marine fish species that exhibited parental care, a comparison was made of the size of seahorses at birth with the size at hatching of other fishes (Fig. 12). For marine teleosts with parental care and seahorses combined there was no linear relationship between $\log_e$ average length at birth and $\log_e$ maximum length (*t*-test: slope $= 0.10 \pm 0.12$, $n = 39$, $P = 0.39$) with no evidence of difference in slopes between seahorses and other marine teleosts ($L_{max} \times$ group interaction: *F*-test: $F = 0.08_{1,35}$, $P = 0.78$). Seahorses were, however, larger at birth than the young of other marine teleosts with parental care, controlling for L_{max} (*F*-test: $F = 21.83_{1,36}$, $P < 0.001$). Again, it may be that seahorses were developmentally more advanced than the newly released young of other bearers and guarders, highlighting the investment by seahorse parents in each offspring. In general, live bearing teleosts were found to have larger offspring than egg layers (Goodwin *et al.*, 2002). A size advantage experienced by seahorses upon independence could translate into an increased survival advantage, as mortality rates generally decrease with increasing body size (Houde, 1997).
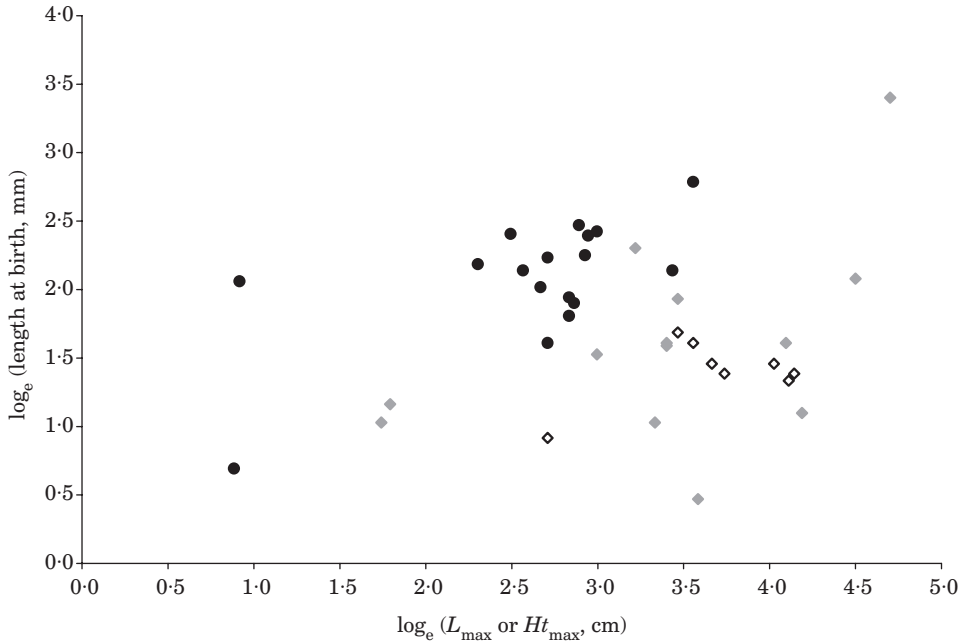
FIG. 12. Average length at birth (mode for teleosts, mean for seahorses) *v.* maximum recorded adult size (L_{max} for teleosts, Ht_{max} for seahorses) for 22 marine teleost species with parental care (either egg bearing or guarding) and 17 seahorse species (*Hippocampus* spp.). References for seahorses in Table X. Data for other marine teleosts from FishBase (Froese & Pauly, 2003). ◇, bearers; ◆, guarders; ●, seahorses.

Total reproductive success is ideally calculated as the total number of offspring that reach sexual maturity from the lifetime output of an individual. This is the product of the number of offspring produced per mating event, number of mating events per season, number of reproductive seasons and offspring survival (Clutton-Brock, 1988). The latter two components are very difficult to measure for wild fish because an individual can seldom be tracked throughout its life. As a result, presumed indicators of reproductive success that are easier to measure are employed, such as number and size of offspring (Wootton, 1990; Cole & Sadovy, 1995; Vincent & Giles, 2003).

Brood size is the number of young per pregnancy released by a male in one birth cycle. Males of most seahorse species produced about 100–300 young per pregnancy, although smaller species released only about five offspring per cycle (*H. zosterae*, Masonjones & Lewis, 1996). The maximum known brood size for seahorses was approximately 2000 young, by one *H. ingens* male (B. Burhans, unpubl. data).

Seahorses did not conform to predictions that fish brood size decreases with increasing latitude, as a trade-off for larger egg size (*cf.* Mann & Mills, 1979; Thresher, 1988). There was no relationship between maximum brood size and latitude (Table XI, *t*-test: slope $= -10{\cdot}53 \pm 10{\cdot}16$, $n = 18$, $P = 0{\cdot}32$). Possibly the seahorse data from the literature were not precise enough to detect a trend; the maximum reported brood sizes reported in Table XI may themselves be means.

The results might have been confounded by the absence of a significant relationship between Ht_{max} and latitude in this study, since maximum brood size is dependent on Ht_{max} across species (Fig. 13). However, repeating the analysis on size-specific fecundity (max brood size/Ht_{max}) still indicated that there was no relationship with latitude (t-test: slope $= -0.64 \pm 0.47$, $n = 18$, $P = 0.19$). In addition, the estimates of latitude may have been sufficiently crude to obscure relationships.

Maximum reported brood size was positively related to Ht_{max} across species (Fig. 13). The relationship between brood size and Ht_{max} across species was significant, with $\log_e$ brood size increasing with $\log_e Ht_{max}$ (t-test: slope $= 1.50 \pm 0.26$, $n = 18$, $P < 0.001$). A correlation between brood size and body size has been found in most ectotherms and invertebrates (Breder & Rosen, 1966; Tilley, 1968; Ridley & Thompson, 1979). The relationship between brood size and maximum reported height appeared to reach an asymptote at 23 cm (when seahorse data were plotted alone, not visible in Fig. 13). This finding can probably be explained by a possible bias in the data used in the current analysis, as the two variables (brood size and Ht_{max}) were never obtained from the same study and the maximum brood size was not necessarily from an animal of Ht_{max}. For example, the maximum reported brood size of 1116 young for *H. abdominalis* (R. Hawkins, pers. comm., Table XI) came from a male that was much smaller than the 35 cm maximum reported Ht_{max} (Francis, 1988, Table I).
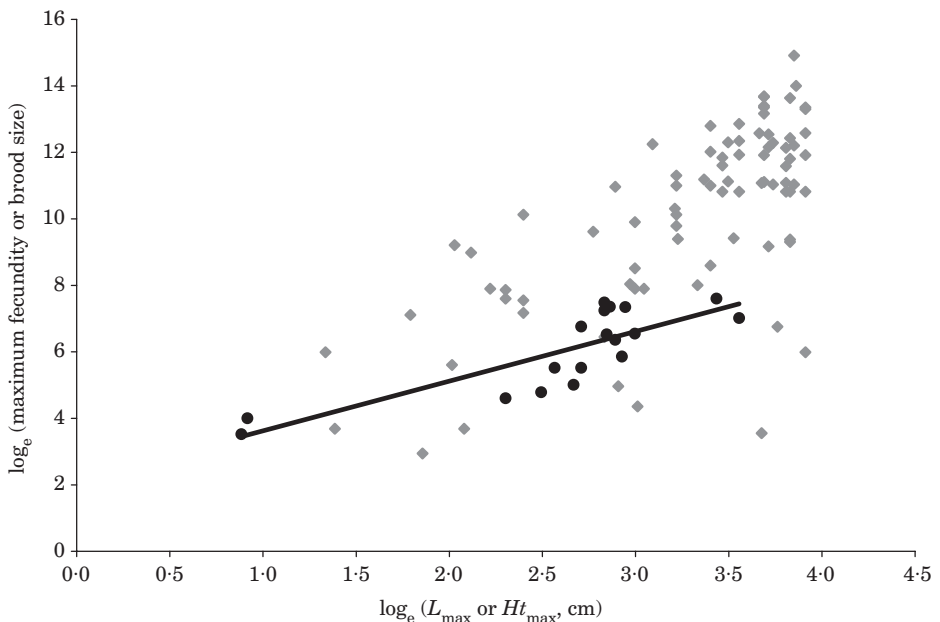

FIG. 13. Maximum reproductive output (fecundity for teleosts, brood size for seahorses) v. maximum recorded adult size (L_{max} for teleosts, Ht_{max} for seahorses) for 83 marine teleosts species less than 51 cm L_{max} and 18 seahorse species (*Hippocampus* spp.). Regression for seahorses: Log_e(maximum brood size) $= 1.50 \times \text{Log}_e(Ht_{max}, \text{cm}) + 2.13$ ($r^2 = 0.67$). References for seahorses in Tables I and XI. Data for other marine teleosts from FishBase (Froese & Pauly, 2003). ◆, marine teleosts; ●, seahorses.

Reproductive output as measured by brood size was low compared to the fecundity of other teleosts of similar size (Fig. 13). For data on marine teleosts <51 cm L_{max} and seahorses combined, there was an overall significant positive linear relationship between $\log_e$ maximum fecundity and $\log_e$ maximum length (*t*-test: slope $= 3.08 \pm 0.30$, $n = 101$, $P < 0.001$) with no evidence of difference in slopes between seahorses and other marine teleosts ($L_{max} \times$ group interaction: *F*-test: $F = 3.62_{1,97}$, $P = 0.06$). Seahorse broods were, however, smaller than the maximum reported fecundity of other marine teleosts controlling for L_{max} (*F*-test: $F = 20.21_{1,98}$, $P < 0.001$). Comparisons of seahorse brood size and other teleost fecundity were potentially flawed because the developed young released by seahorses had a greater chance of survival than the eggs released by other teleosts. Nevertheless, the current dearth of information on seahorse clutch sizes made it impossible to compare reproductive output among teleosts in any other way.

Even among marine teleosts with parental care, seahorse brood sizes appeared to be lower than the fecundity of other fishes (Fig. 14); while there was no evidence of difference in slopes between seahorses and other marine teleosts with parental care ($L_{max} \times$ group interaction: *F*-test: $F = 0.702_{1,38}$, $P = 0.407$), seahorse brood sizes were smaller than the maximum reported fecundity of other teleosts, controlling for L_{max} (*F*-test: $F = 2.92_{1,39}$, $P = 0.095$). While the difference in intercepts between the two groups was only
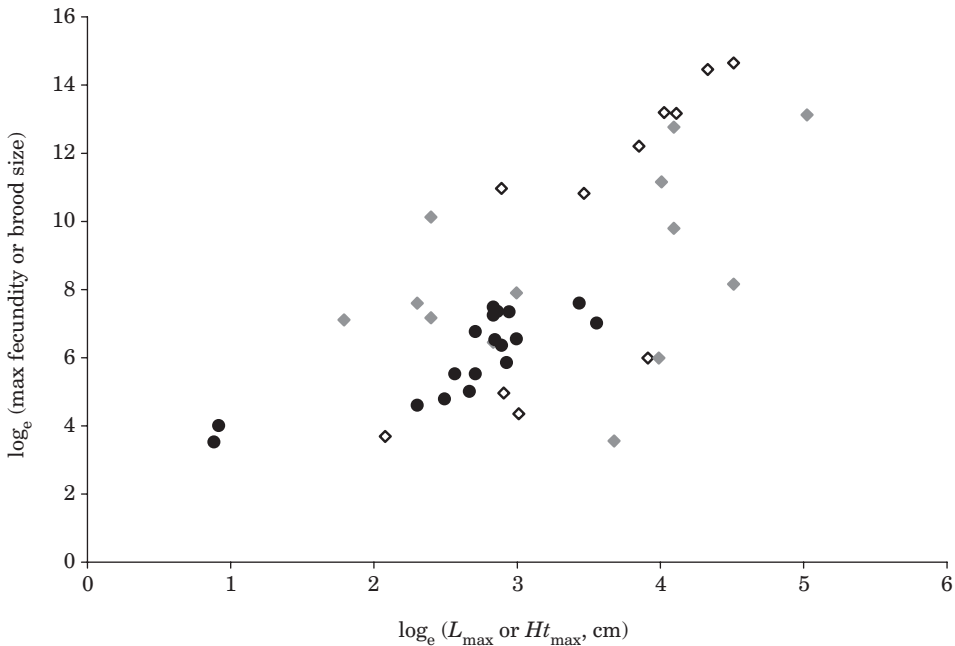

FIG. 14. Maximum reproductive output (fecundity for teleosts, brood size for seahorses) *v.* maximum recorded adult size (L_{max} for teleosts, Ht_{max} for seahorses) for 25 marine teleosts species with parental care (either egg bearing or guarding) and 18 seahorse species (*Hippocampus* spp.). References for seahorses in Table X. Data for other marine teleosts from FishBase (Froese & Pauly, 2003). ◇, bearers; ◆, guarders; ●, seahorses.

marginally non-significant, group only explained an additional 4% of the variation in the data (r^2 with group $= 0.53$, without group $= 0.49$), and therefore the effect of group was not likely to be biologically relevant. The level of significance was likely to be reduced even further as not all fishes with parental care released their young to independence at the same developmental stage as seahorses. While it is beyond the scope of this paper, it would be interesting to collect information on the exact stage at which other teleost larvae become independent and incorporate that information into comparisons of seahorses and other teleosts.

RESEARCH NEEDED FOR CONSERVATION AND MANAGEMENT

Seahorses are exploited and traded for use in traditional medicine (particularly traditional Chinese medicine), for the aquarium trade, and for sale as curiosities (Vincent, 1996). Seahorses are also frequently brought up by non-selective fishing gear such as trawl nets (Haysom, 1985; Vincent, 1996; Flaherty, 1998 in Lane, 1999; Baum *et al.*, 2003) and are vulnerable to degradation of their inshore habitats (IUCN, 2003). Management guidelines and initiatives are required to ensure the persistence of seahorse populations, with each venture relying on an understanding of seahorse biology and ecology, within and across species. Understanding the socio-economic aspects of a fishery is also important for the development of any successful management plan, but these issues are beyond the scope of this paper.

Seahorses have much in common with other small marine fish species, both in the threats they face and in our general lack of knowledge about their biology. The vast majority ($>95\%$) of seahorses in international trade were obtained as by-catch in shrimp trawl fisheries (A. Vincent, unpubl. data). Indeed, small species that mature at sizes under 20 cm and that predominantly weigh under 100 g constituted a significant proportion of discards from most tropical shrimp fisheries (Alverson *et al.*, 1994). It seems unlikely that potentially unsustainable exploitation of these small species in non-selective fisheries will be resolved by gear modifications or other technological changes. A dearth of information on life-history variables of small- to medium-sized fishes (<51 cm maximum reported length) was apparent in our survey of FishBase (Froese & Pauly, 2003) for this paper, and should provoke concern. Small species contribute to marine biodiversity, ecosystem function and food security, with the latter role becoming more important as we fish down the food web (Pauly *et al.*, 1998). Without knowledge of their life-history and population parameters, it will be difficult to assess the effects of incidental catch or to develop management strategies to ensure their population persistence in the wild.

Results of this review suggest that seahorses conform to empirical relationships between life-history parameters across other marine teleost species. Such a finding implies that patterns previously identified for other fish species (Beverton & Holt, 1959; Jennings *et al.*, 1999; Froese & Binohlan, 2000; Pope *et al.*, 2000; Frisk *et al.*, 2001) could be used to estimate missing life-history variables for seahorses, with later refinement as data become available. As a corollary, the potential similarities between seahorses and other fishes also indicate that seahorses might serve as useful models for the study of individual

and population effects of direct and incidental catch (as well as habitat disturbance) on marine fishes. Such extrapolations would be especially apt for those fishes that share similarities in life history with seahorses (*e.g.* gobies, Reavis & Barlow, 1998). Seahorses provide more tractable study taxa than many species because their limited movement and site fidelity might enable individual-based assessments and models of the effects of exploitation and disturbance (DeAngelis & Gross, 1992).

In order to ensure the persistence of seahorse populations worldwide, researchers ideally need to recreate the past, assess the present and plan for the future. Reconstructing past population estimates is particularly important in setting bounds for future goals in conservation (Jackson *et al.*, 2001; Pitcher, 2001; Roman & Palumbi, 2003). Identification of the upper limits of population size is necessary to avoid the syndrome of shifting baselines, wherein contemporary depleted populations (often still in decline) become the accepted normal scenario (Pauly *et al.*, 1998). An understanding of changing seahorse populations in the longer term will require analysis of genetics and other technical information (Roman & Palumbi, 2003), traditional knowledge (Johannes, 2002), historical documents, and archaeology (Pitcher, 2001).

A population's conservation status is deduced by comparing past abundance with current population size and structure. For *H. comes* in the central Philippines, accounts of historic population densities cast current numbers into sharp relief: fishers reported finding up to 20 seahorses per m^{-2} in the 1960s and $5–10 \, m^{-2}$ in 1985 (A. Vincent & M. Pajaro, unpubl. data), while densities in the 1990s were only about $0 \cdot 02 \, m^{-2}$ (Perante *et al.*, 2002). Such a contrast raises questions about whether the low densities of many seahorse populations around the world (see Table V) might be the result of severe exploitation and/or environmental change, as was reputedly the case for marine turtles in the Caribbean (Jackson, 1997).

Broad empirical surveys, using rapid assessment techniques (of populations and of fisheries) should allow analyses of the relationships among (i) current population size and structure, (ii) current exploitation rates, and (iii) population responses to exploitation. Such responses will largely depend on how pressures affect seahorse survival, growth, reproduction and movement, requiring us to garner just such an understanding. Information is required regarding seahorse habitat choice to ensure that their habitats are protected. Habitat degradation is a threat to seahorse populations, as they usually inhabit shallow coastal areas that are highly influenced by anthropogenic activities (Pogonoski *et al.*, 2002). Even removal or alteration of artificial structures (*e.g.* moorings, aquaculture pens, or shark nets) might affect seahorse populations, where they harbour high densities of these fish (Coleman, 1980; Choo & Liew, 2003; Dias & Rosa, 2003; K. Martin-Smith, pers. comm.). The recognized importance of understanding temporal change emphasizes the necessity of assessing current population status and structure, as benchmarks for future reference.

Having identified the scale of any conservation problem, goals must be set for population recovery. Such goals derive from a pragmatic comparison of past populations with present situations, recognizing current constraints (such as phase shifts or habitat loss). For seahorses, goals will be needed on three levels. First, management strategies should be implemented for populations whose

primary pressure is target catch, such as *H. comes* in the Philippines (Vincent & Pajaro, 1997). Second, there is a great need to address the challenge of managing seahorse populations caught in non-selective gear, such as *H. erectus* populations in the Gulf of Mexico (Baum *et al.*, 2003). Third, it is important to identify populations for which the primary threat may be habitat degradation – such as the Endangered species, *H. capensis* (Lockyear, 1999) – for which another set of management objectives must be devised. Goals may take the form either of trends (a defined percentage increase) or of targets (a defined number of individuals), and should conserve the evolutionary potential of the species, not just a viable population size. Once goals have been decided, regular monitoring of index (or 'sentinel') populations, fisheries and trades may well offer the most pragmatic approach to assessing the impact of conservation action. Such monitoring should also provide opportunities to document life-history characteristics, and their forcing agents that are important for population management.

A good understanding of a wide array of life-history parameters is a major asset in planning for long-term persistence and recovery of depleted populations. Robust information on taxonomy, global occurrence and habitat suitability would be helpful. Data on individual movement, survival, growth and reproduction, by age and stage – and how these parameters respond in the face of exploitation pressure and habitat change – could then contribute to the construction of models of possible management schemes, and the evaluation of population level responses to such scenarios (Caswell 1989; Akcakaya 2000). For example, important parameters related to survival might include natural mortality, age at first maturity, age at entry into the fishery and generation time (Froese & Binohlan, 2000; Reynolds *et al.*, 2001). Ecological interactions affecting seahorses (*e.g.* competitors, prey, predators) and the gene flow that may connect and sustain populations are also priority areas for research.

DISTRIBUTION AND MOVEMENT

The distribution of most seahorse species remains poorly defined (Lourie *et al.*, 1999; Kuiter, 2001; Choo & Liew, 2003). An important step in determining the global occurrence of seahorse species will be to reach a consensus on seahorse taxonomy. Accurate identification of different species based on a reliable set of characteristics (*e.g.* number of tail rings or spines, rather than colour or filaments, Lourie *et al.*, 1999) will promote the effective implementation of domestic and international management, the accuracy of global trade data and future research on the genus. In this context, it would be valuable if, when referring to seahorses, researchers provided (a) the standard species name, (b) the reference identification guide used to designate the species name, and (c) information about the geographic locality of the individuals: for example, *H. comes* (Lourie *et al.*, 1999; central Philippines).

Both fisheries-independent and fisheries-dependent abundance estimates are required for many populations worldwide. Published population estimates for seahorses are few and limited and usually buried in reports on fish community assemblages (Monteiro, 1989) such that population inferences must instead often be drawn from trade surveys (Vincent, 1996). While fishers' and traders'

reports and records of changes in trade volumes are invaluable, they often lack information on the effort involved in obtaining the animals, thus diminishing the worth of the data for population estimates.

Since populations of marine fauna are usually connected into metapopulations, and are reinforced through such connections (Gilpin & Hanski, 1991; Crowder *et al.*, 2000; Hixon *et al.*, 2002), more research is required on seahorse movement and dispersal, particularly for newly released young. Small sub-adult and adult home ranges may mean that seahorses are slow to recolonize heavily fished areas (Vincent, 1996), unless such minimal adult movement is offset by high dispersal of newly released young. The corollary, however, is that small home ranges may allow small protected areas to support viable seahorse populations (Kramer & Chapman, 1999).

Understanding partitioning of habitat by size and/or age classes, or life-history stage, can be important for developing management strategies, especially when addressing the effects of non-selective fishing gear (Vincent, 1996). For example, a greater understanding of how seahorses segregate by size or sex would enable spatial management of trawling and use of other non-selective gear to reduce indiscriminate fishing pressure on vulnerable cohorts or classes. If reproductively active animals were concentrated in particular areas (Baum *et al.*, 2003), then trawling could be redirected away from these regions during important breeding periods. Also, if sub-adult seahorses were found in shallower water than adult seahorses (Dauwe, 1992; Perante *et al.*, 1998), then elimination of trawling activities from shallow zones might reduce the risk of recruitment overfishing.

SURVIVAL

Data on natural mortality/survival rates of seahorses, particularly if age or stage specific, are important parameters for modelling population viability and devising management plans (Macpherson *et al.*, 2000), but are virtually non-existent for seahorses. In the absence of direct estimates of survival, analyses of population age or size structure would permit survival to be modelled, for the purposes of management. For example, a minimum size limit might be set where the trade-off between growth and mortality maximizes yield per recruit (Beverton & Holt, 1957).

Fishing mortality remains virtually unknown for most seahorse populations, despite the importance of such data in formulating catch guidelines for a sustainable fishery. Some research indicates that fishing mortality of fish that have spawned once must be lower than natural mortality for the fishery to be sustainable (Myers & Mertz, 1998). For *H. comes*, even with high estimates of natural mortality in some parts of their range, fishing mortality exceeded those rates (Martin-Smith *et al.*, in press; J.J. Meeuwig, unpubl. data). Presumably as a consequence, fishers reported that *H. comes* catches on one Philippines barrier reef had declined 70% in the 10 years from 1985 to 1995 (Vincent, 1996), with associated changes in the length–frequency distribution of the catch (Perante *et al.*, 1998); more data of greater precision are needed to determine whether fishers had begun targeting smaller seahorses or whether the size structure of the seahorse populations had changed under exploitation.

GROWTH

Age- or stage-specific survival rates could be married to an improved knowledge of growth rates to fill a significant gap in our biological understanding of seahorses. The von Bertalanffy equation provides the most commonly used model for growth in fishes: $L_t = L_{inf} (1 - \exp^{(-K \ (t - t_0))})$ where $L_t =$ length at age t in years, $L_{inf} =$ maximum theoretical length, $K =$ growth coefficient (yr^{-1}) and $t_0 =$ theoretical age at zero length (von Bertalanffy, 1938). Age-based population assessments would enable researchers to determine K, and then to compare growth rates among species while applying them to management models. Ageing will, however, require analyses of seahorse otoliths or application of other ageing methods not yet validated on seahorses.

Age at first maturity (a_m) is a common biological reference point in fisheries models (Hilborn & Walters, 1992), and therefore determining a_m in the wild for various seahorse populations should be a research priority. Estimates of a_m would involve accurate determination of age in the wild. An understanding of a_m has been useful for determining other important life-history parameters, such as life expectancy, in other fish species (Frisk et al., 2001).

REPRODUCTION

A greater understanding of seahorse mating patterns and reproduction is important for conservation. Exploitation could disrupt seahorse social structure by disturbing pairs more quickly than they are established. Removing a member of a monogamous pair could decrease short-term reproductive output, by leaving the remaining animal without a partner, and possibly by reducing the size of its later broods if familiarity enhances brood success (H. fuscus, Vincent, 1994a). Sex-selective fishing would also have important effects, especially in monogamous populations where members of the more abundant sex might be less likely to find a mate thereafter. More needs to be discovered about how mating patterns respond to environmental and social parameters. For example, three pipefishes of the genus Corythoichthys were shown to be strictly monogamous on the Great Barrier Reef where an equal number of males and females was available to mate (Gronell, 1984). However, a fourth Corythoichthys species, in Japan, exhibited a highly polyandrous mating pattern, in a situation where more females than males were available to mate (Matsumoto & Yanagisawa, 2001).

The lack of estimates of intrinsic rate of increase for seahorse populations poses a great challenge in conservation management. Fecundity rates are difficult to measure and do not necessarily determine resilience to exploitation (Sadovy, 2001; Denney et al., 2002). Rather, great effort should be dedicated to estimating recruitment rates of seahorses to the breeding population and to the fishery, in order to understand population dynamics and to predict response to exploitation, such as recruitment compensation (Goodyear, 1980). Too little is known about survival rates of seahorse juveniles compared to other fishes, although the considerable parental care probably enhances survival in early life (McCann & Shuter, 1997).

More research on age- or size-specific reproductive output could allow us to tailor fisheries plans more usefully. For example, if further research confirmed

that brood size increased with male size, then maximum size limits might be considered for fisheries, in order to allow the most fecund animals to continue reproduction. Realistically, however, such a management measure, no matter how apparently desirable, might prove politically difficult to implement given that larger seahorses fetch a higher price (Vincent, 1996).

ONE POSSIBLE MANAGEMENT TOOL AMONG MANY

Implementation of the CITES Appendix II listing for seahorses, in effect as of May 2004, requires immediate application of existing biological knowledge and provokes particular calls for more information on maximum adult size (Ht_{max}) and size at first maturity (Ht_{mat}). All 166 signatory countries to CITES (as of May 2004) are legally obliged to manage seahorse exports for sustainability. Many potential tools, such as a maximum permissible size or slot sizes, could prove useful for managing seahorses in international trade, but the successful restrictions will be those that interested groups can and will accept. Six different sets of stakeholders (from Philippines fishers to Hong Kong traditional Chinese medicine traders to North American aquarium professionals) agreed that setting a minimum permissible height (minHt) for seahorses in trade would be both biologically appropriate and socially acceptable as an initial means to meet CITES requirements (Martin-Smith *et al.*, in press). Such a proposal was endorsed by the (technical) CITES Animal's Committee in April 2004 as a useful means of moving towards adaptive management of seahorse trade. A minHt above Ht_{mat} but below Ht_{max} should allow animals to reproduce before being caught, thus reducing the problem of recruitment overfishing, while still allowing trade (Nowlis, 2000). The effectiveness of such a measure will, however, depend on the form of stock-recruitment curve as well as the intensity of fishing (Beverton & Holt, 1957). Further research is urgently needed to refine the minHt for seahorse species. At present, cross-species comparisons suggest that seahorses are sufficiently similar to other species to allow us to recommend minimum size limits based on existing data and established relationships among life history parameters.

CONCLUSIONS

Patterns in seahorse biology revealed by limited current research should be interpreted with caution. In particular, much of the research has been conducted *ex situ* (in public aquaria, laboratory and aquaculture situations) and results may differ *in situ*, for wild populations. Greater confidence in the findings could come from augmenting the sample size of studies on all life-history parameters *in situ* and *ex situ*, and under variable environmental conditions. Further, there is a need for sufficient data to repeat the interspecific analyses in this paper within single species, especially for those with large geographic ranges (*e.g.* *H. erectus*).

While present knowledge of seahorse life history is incomplete, existing information indicates that seahorse populations are commonly vulnerable to overexploitation, whether direct or indirect: low population densities mean that seahorses may have trouble finding a new partner (Allee effects: *e.g.* Knowlton,

1992); low mobility and small home range sizes mean that seahorses may be slow to recolonize overexploited areas (although this may be offset by planktonic dispersal of juveniles); possible low rates of natural mortality mean that heavy fishing will place unsustainable pressure on the population; monogamy in most species means that a widowed partner may stop reproducing, at least temporarily; male brooding means that survival of the young *in marsupio* depends on the survival of the male; and a small brood size limits the potential reproductive rate of the pair (although this may be offset by frequent spawning and enhanced juvenile survival through parental care). Even if seahorses are returned to the water after being caught in non-selective gear, they may still experience deleterious effects that include physical injury, habitat damage, removal from home ranges and disturbance of pair bonds (Davis, 2002; Baum *et al.*, 2003). In the context of conservation management, variation in life-history parameters across the genus requires thorough analysis, in order to assess the relative vulnerability of different species to exploitation and habitat damage. With such information, management initiatives can be improved for the long-term security of wild seahorse populations.

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