Growth and reproduction of double-ended pipefish, *Syngnathoides biaculeatus*, in Moreton Bay, Queensland, Australia

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Synopsis

Life-history characteristics of the double-ended pipefish, *Syngnathoides biaculeatus* (Bloch), were investigated to determine growth rate, degree of sexual dimorphism, size at maturity, and reproductive biology. Growth rates of wild juveniles and adults calculated from monthly progression of length-frequency modes ranged from $0.8 \, \text{mm d}^{-1}$ (fish lengths 120–145 mm standard length (SL)) in summer to $0.2 \, \text{mm d}^{-1}$ in winter (185–200 mm SL). Growth of laboratory-reared juveniles up to 63 d old was greater, ranging from 0.8 to $2.3 \, \text{mm d}^{-1}$. The von Bertalanffy growth constant K was estimated at $0.0076 \, \text{d}^{-1}$, or $2.8 \, \text{year}^{-1}$. Morphological differentiation between the sexes based upon abdominal pattern was possible for fish larger than 120 mm SL, with females possessing a zigzag pattern on the abdomen. The association between this pattern and sex was confirmed by histological gonad analysis. Males were significantly longer than females during four of seven seasons examined, and a 1 : 1 sex ratio was determined for all seasons except autumn when the ratio was female biased. The breeding season was marked by the appearance of pregnant males between October and April, and during courtship both species exhibited increased pigmentation. The minimum paternal size at maturity was 185 mm, the maximum length recorded 260 mm. Clutch size ranged between 60 and 200 eggs, with a mean of 153. Ovaries had a sequential pattern of egg development, resulting in egg batches that approximated the number of eggs carried by brooding males. Additionally, all eggs in a brood were at the same developmental stage. This suggests that one female provides all of the eggs for one male per breeding event in a monogamous mating system.

Introduction

Syngnathids are among the most abundant and ubiquitous fish inhabiting seagrass habitats (Pollard 1984). Anecdotal evidence has indicated that syngnathids are declining in abundance in some parts of the world as a result of heavy exploitation for traditional Chinese medicine (Vincent 1996). Concerns regarding syngnathid conservation are further compounded by the degradation of their inshore habitats (Vincent 1996), particularly in Australia where seagrass loss in the past century has been extensive (Short & Wyllie-Echeverria 1996).

There has been a recent increase in the knowledge of syngnathid biology, partly due to the characteristic breeding biology of syngnathids. Males exclusively brood and care for offspring (Vincent et al. 1992), providing an excellent opportunity to investigate the implications of male brooding on the evolution of sexual differences and the mating system. Syngnathids exhibit a range of brood 'pouch' morphologies, ranging from exposed eggs attached externally to the tail, to eggs completely enclosed within brood pouches (Wilson et al. 2001). The mating system is similarly varied, ranging from strict monogamy, typified by seahorses (Vincent & Sadler 1995, Masonjones & Lewis 1996,

Jones et al. 1998) and some pipefishes (Gronell 1984, Berglund et al. 1989, Vincent et al. 1995, Matsumoto & Yanagisawa 2001), to sequential or simultaneous polygamy identified in other pipefish species (Berglund et al. 1989, Berglund and Rosenqvist 1990, 1993, Vincent et al. 1995, Jones & Avise 1997a,b, Jones et al. 2000, McCoy et al. 2001). The extent of secondary sexual characteristics exhibited among species also varies, with a suggested trend of monogamous species exhibiting 'conventional' sex roles and polygamous species being 'sex-role reversed' (Vincent et al. 1992). Only an examination of the biology of additional species can give a clearer understanding of such trends.

The double-ended pipefish, *Syngnathoides biaculeatus,* is widely distributed throughout the Indo-Pacific region in seagrass meadows (Dawson 1985), in which they are well camouflaged. The life-history characteristics of *S. biaculeatus* are virtually undocumented (Dawson 1985). The aim of the present study was to provide information on the life-history characteristics of *S. biaculeatus* within Moreton Bay, Queensland, Australia, and specifically to establish the growth rate, degree of sexual dimorphism, size at maturity, clutch size and breeding characteristics of the species.

Materials and method

Field sampling

We sampled *S. biaculeatus* individuals from four subtidal seagrass meadows located in Pumicestone Passage and the Broadwater, within Moreton Bay, Queensland (Figure 1). At each location we identified two sites. From April 1997 to March 1998, we sampled
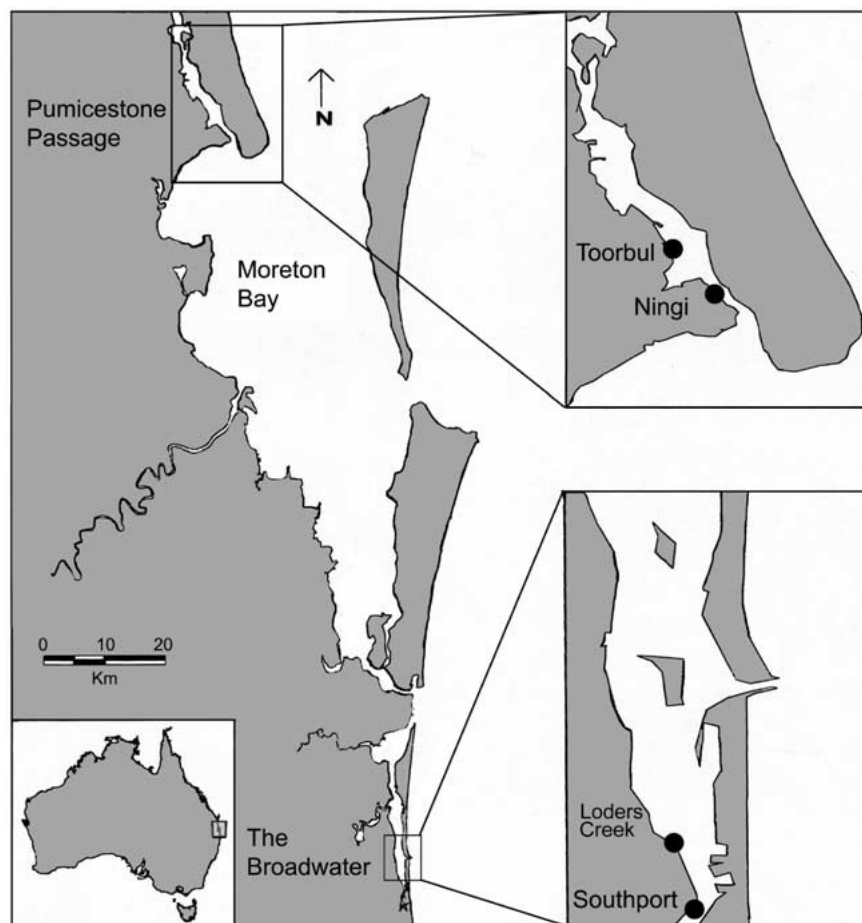

Figure 1. Map of study sites and locations within Moreton Bay, Queensland, Australia.

one site at each location monthly, whereas we collected samples from both sites every month from April 1998 to June 1999. Sampled locations comprised meadows of the seagrass *Zostera capriconi,* with interspersed *Halophila ovalis* and *H. spinulosa.* Water temperature recorded at the time of sampling ranged between 21°C and 31°C. We caught fish using seine nets 5 m long and 2 m high with a mesh size of 2 mm. Sampling was typically done for 3 h, from 1 h prior to low tide to 2 h after low tide, at a water depth of 0.5–1.5 m. The average effort was 13 nets during each low tide, ranging from 7 to 22 nets per low tide.

Field measurements

For every fish caught (n = 853) we measured standard length (SL – from tip of snout to tip of tail, ±1 mm) using a ruler and wet mass was measured on site using a spring balance. Fish were classified morphologically as male, female or indeterminate (based on the presence of eggs and the pattern on the abdomen) to determine the sex ratio of the population. We measured trunk depth (TD – narrowest distance between the superior and inferior trunk ridges) and spine width (SpW – the distance between lateral trunk ridges) (refer to Lourie et al. 1999) (n = 484), and calculated the ratio of SpW : TD. Measurements of SpW and TD were restricted in number to decrease the handling time of fish prior to their release. We estimated clutch size for all pregnant males caught. Eggs on pregnant males are arranged roughly in lines, allowing an estimate of clutch size to be made by multiplying the number of rows of eggs by the number of columns. We retained 50 fish for further analysis in the laboratory.

Growth rates

For field-collected fish we plotted relative length-frequency distributions at monthly intervals and identified the modal length. We used modal progression to estimate the growth rate between months. We compared male and female length frequency distributions each season using Kolmogorov–Smirnov (K–S) tests.

In January 1999 a pregnant male was obtained from the field, and 26 newly hatched juveniles from this male were separated evenly into two tanks. From day 3 to 43, the juveniles were fed daily on cultured rotifers, *Brachionus plicatilis*, and 1–2-day-old brine shrimp, *Artemia franciscana*, nauplii reared in the laboratory. Zooplankton caught from the wild were also fed to the fish every 2–3 days. From day 43, fish were fed

daily with field-caught zooplankton. Tanks were kept at 25.5°C (the average temperature of the sites at the time of sampling), and a light regime of 14 h light : 10 h dark. The lengths of three live fish haphazardly collected from each tank were measured every second day up to day 63. The growth coefficient K was calculated using the von Bertalanffy equation, $L_t = L_\infty - (L_\infty - L_0)e^{-kt}$ where L_t = length at time t, L_∞ = maximum length observed and L_0 = size at hatch.

Sex determination

Histological analysis of gonads was done on 49 fish ranging between 125 and 230 mm SL, collected between April and November 1997. Gonads were preserved in 10% formalin for a minimum of 5 days, after which one gonad from each fish was placed in a biopsy cassette. Gonad tissues were embedded in paraffin wax and sectioned (Culling 1974). Three to six longitudinal sections were prepared from each fish and placed onto slides. Samples were stained using haematoxylin to detect sperm cells and then counter-stained with eosin to detect egg cells. Slides were observed using a compound light microscope at 40× and 100× magnification. Four characteristics were noted: the colour of stain picked up by the cells, gonad diameter, gamete diameter and the structural arrangement of the gametes in the gonads. Gametes were measured with a calibrated stage micrometer at five different locations for each gonad section. The mean diameter of gametes in each section was calculated, and data for each section pooled to give a mean diameter for each fish.

Gonads from 13 other females collected during the breeding season and not used for histological analysis were dissected and the eggs counted. At least two size classes were observed in each female. The diameters of five eggs selected randomly from each size class were measured using a light microscope where necessary. In addition, 44 pregnant males were collected, the eggs counted, and divided into three categories based on colour. Eggs were dissected to remove the embryos, and the lengths of the embryos measured.

To establish whether sexes could be determined morphologically, snout length (SnL – from the tip of the snout to the nose spine) and head depth (the distance from the depression behind the coronet to immediately behind cheek spine) (refer to Lourie et al. 1999) were measured. Following observations by Dawson (1985) that coloured dots present on the abdomen of *S. biaculeatus* may be a sexually dimorphic characteristic, the pigmentation and pattern on the abdomen

were recorded. The accuracy of sexing fish using morphological comparisons was verified with fish sexed using histological gonad analysis.

Results

Growth rates

We used modal progression between January and June 1999 to calculate growth rates in the field. The greater sampling effort and numbers of fish meant the data (Figure 2) were more reliable than those measured prior to this period, when modes represented few fish and consequently the length-frequency did not display consistent progression over time. Growth between January and February was $0.83 \, \text{mm} \, \text{d}^{-1}$ (120–145 mm SL) and slowed steadily as the fish exceeded 170 mm SL, to $0.17 \, \text{mm} \, \text{d}^{-1}$ between May and June (185–190 mm SL) (Figure 3). Modes mostly represented fish larger than 120 mm SL, preventing growth estimation in fish smaller than 120 mm SL. Males were significantly longer than females in four out of seven seasons (summer 1997/98 and spring 1998 to autumn 1999, K–S test: $p < 0.05$).

In comparison, the growth of juveniles reared in laboratory tanks was faster than larger fish in the field and was characterised by three distinct phases (Figure 4). Growth rate was rapid for the first 25 days ($1.8 \, \text{mm} \, \text{d}^{-1}$), then slowed markedly ($0.8 \, \text{mm} \, \text{d}^{-1}$) before increasing again after 44 days ($2.3 \, \text{mm} \, \text{d}^{-1}$) (Figure 4). The first changes in the rate of growth rate at day 24 occurred at approximately the same time as changes in food type (from laboratory-reared rotifers and newly hatched brine shrimp to zooplankton caught from the wild) and feeding frequency. The second change in the rate of growth at day 45 coincided with an increase in feeding frequency from every 2–3 days to daily.

The growth coefficient, K, was calculated using field and laboratory data. L_∞ obtained from field data was 260 mm and L_0 obtained from laboratory data was 21 mm. L_t and t were obtained from modal progression of the length-frequency distribution of field fish (Figure 3), and K-values were calculated for t = 90, 120, 150, 180 and 540 days. The average K-value was $0.0076 \, \text{d}^{-1}$ (s.d. = 0.0008) or $2.8 \, \text{year}^{-1}$.

Sex determination

Two distinct types of gonads were observed: Type A gonads were 350–500 μm in width and possessed small gametes with an average diameter of 3.8 μm and range of 2–5 μm (s.d. = 1.25 μm). Gametes representing all sizes were clumped around the gonad walls. These gametes stained blue with haematoxylin, and in conjunction with their small size were classified as sperm (Culling 1974).

Type B gonads were 900–1125 μm in diameter. The gametes spanned a wide range of sizes (25–1375 μm), but on average were 75 times larger than type A gametes (average diameter = 287 μm, s.d. = 12.5 μm). (The maximum gamete size was from a fish for which the gonad burst and was unable to be measured, hence maximum gonad size is less then maximum gamete size.) Gametes were arranged in longitudinal chains, with each chain consisting of similar sized gametes. Chains were arranged sequentially with larger, more developed gametes occurring toward the periphery of the gonad. These gametes stained with eosin rather than haematoxylin and in conjunction with their relatively large size were classified as eggs (Culling 1974).

Sexual dimorphism was not distinguishable from any of the morphometric measurements alone. Abdominal pigmentation was similarly ineffectual in distinguishing between sexes. Red dots occurred on both sexes, and although blue dots occurred only on females, they were not present on all mature females. Abdominal pattern was the only morphological characteristic observed which differed consistently between sexes. Females, as identified histologically, possessed a white zigzag pattern on the abdomen not present in males (Figure 5). A 1 : 1 sex ratio was determined for all seasons except autumn when the ratio was female biased. Individuals that could not be sexed histologically lacked the zigzag abdominal pattern, but instead had transverse straight lines. Of the 853 fish examined, 126 were classified indeterminate and could not be sexed morphologically. The smallest fish that could be sexed morphologically using the abdomen pattern was 144 mm SL for males and 122 mm SL for females. The length distribution (Figure 6) and SpW to TD distribution (Figure 6) of males was greater than females, with indeterminate fish occurring at the lower end of the range. Indeterminate fish were subsequently considered immature and categorised as juveniles.

Reproduction

Pregnant males were caught between October and April (Figure 7), when water temperatures in the shallow subtidal zone ranged from 28°C to 31°C. Most recruitment of juveniles to the sampled areas occurred
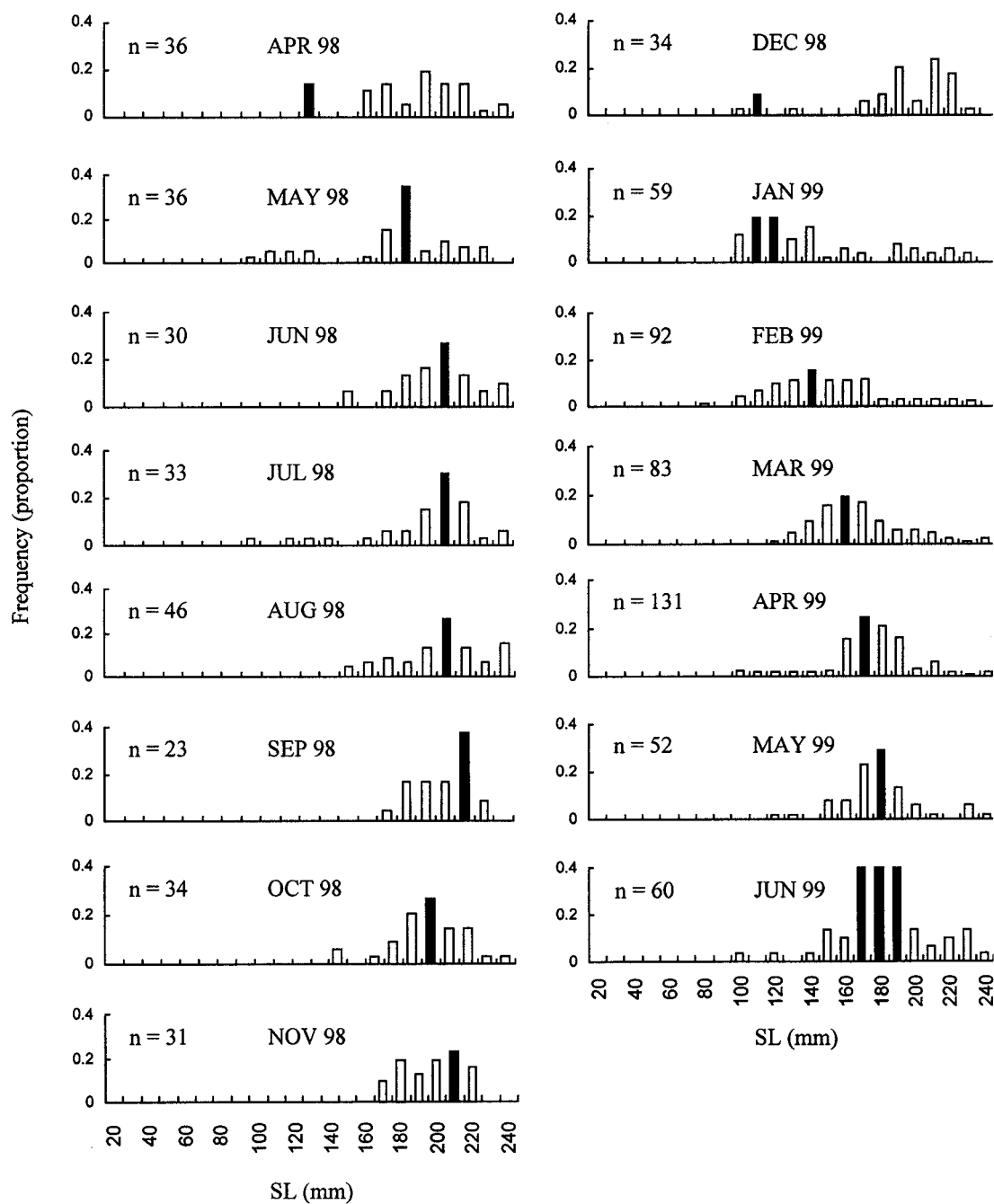
Figure 2. Length-frequency distributions of field-collected fish between April 1998 and June 1999. Shaded columns indicate mode of smallest cohort for each month. SL = standardised length.

between December and May, with a small amount in June (Figure 7).

A total of 44 pregnant males were caught, ranging from 185 to 235 mm SL (mean = 206 mm).

No significant difference (K–S test, p = 0.12) was detected between the length distribution of pregnant and non-pregnant males collected during the breeding season (Oct–Apr). Size at maturity, based
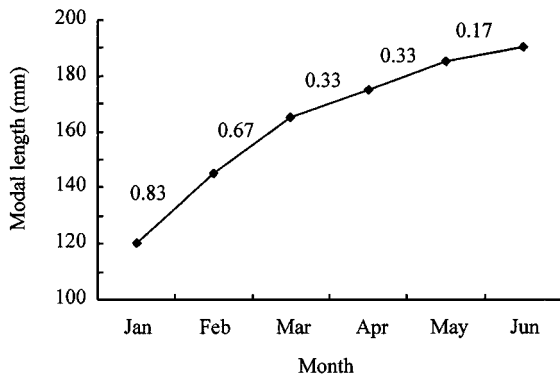
Figure 3. Growth rate of field-collected fish between January and June 1999. Numbers above the line indicate growth rate (mm d^{-1}) calculated using modal progression between sampling periods.
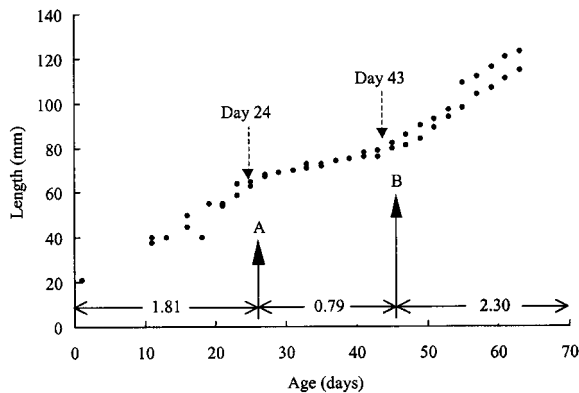

Figure 4. Growth (mm d^{-1}) of laboratory-reared juveniles. Points A and B show where growth rate changed. Dotted arrows mark the days when the quality and types of food changed.

Figure 5. Abdomen patterns of (a) juvenile, (b) male, (c) female and (d) close up of female abdomen (height of box = 10 mm).

category at any one time, but at any one time all three egg categories were present in the population.

Discussion

Growth rates

Growth rates of wild *S. biaculeatus* (0.2–0.8 mm d^{-1}) are lower than those of the northern pipefish, *Syngnathus fuscus* (1.2 mm d^{-1}), also estimated from modal progression analysis (Campbell & Able 1998). The faster growth of *S. biaculeatus* coincides with warmer water temperatures in summer and a relatively young age structure of the population. *S. biaculeatus* growth slows as water temperatures decline coming into winter and fish approach adult size, as for *S. fuscus* (Campbell & Able 1998).

The use of modes of length-frequency distributions to calculate growth rates assumes that mortality is even within a cohort at any one time, no size-selective emigration out of the sampling area occurred, and no size-selective gear bias was introduced. There are no known fishing pressures on the populations sampled in this study, however, natural mortality is probably greatest in young syngnathids, which are vulnerable to piscivorous fishes (Lourie et al. 1999). No pipefish less

on the minimum size of a pregnant male caught, was 185 mm, which is 71% of the maximum length recorded (260 mm).

Counts of eggs in female *S. biaculeatus* gonads during the breeding season identified at least two non-overlapping egg class sizes, averaging 155 eggs at 1.5 mm diameter for the first batch and 91 eggs at 0.5 mm diameter for the second batch (Table 1). Brood size estimated from the number of eggs observed on pregnant males ranged between 60 and 260 eggs with a mean of 153 eggs. Out of the three egg categories observed, there was a trend from clear to white to brown, of decreasing eggs numbers and increasing embryo size (except embryos were not evident in clear eggs) (Table 1). Each male brooded only one egg
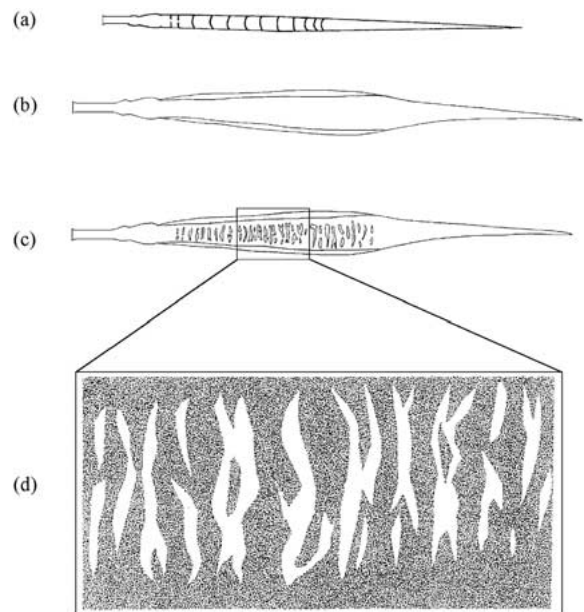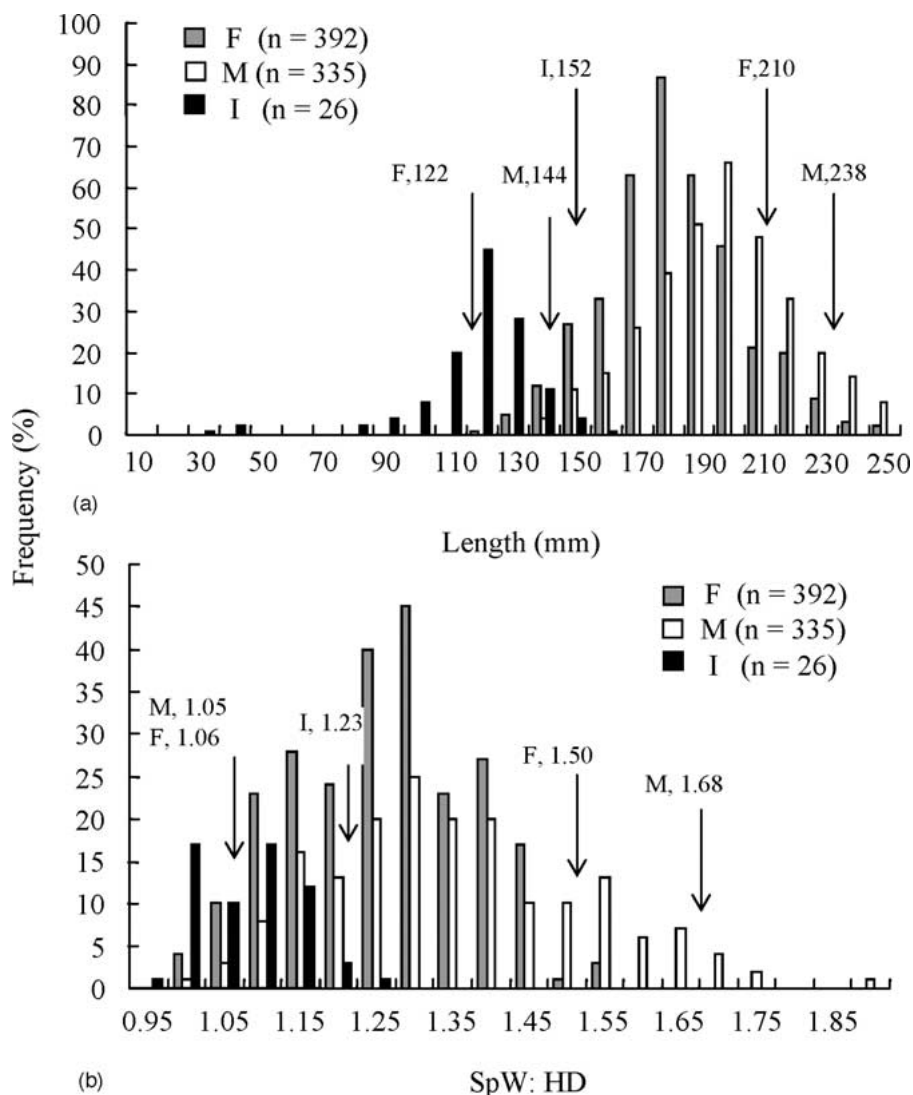
Figure 6. Comparison of morphology by sex, (a) length-frequency distributions, and (b) ratio of spine width : trunk depth (SpW : TD), of wild fish, classified morphologically as female (F), male (M) and indeterminate (I). The 95% upper and lower confidence limits are shown for males and females and upper confidence limit for indeterminate.

than 80 mm were collected, suggesting such small fish occur in other habitats and migrate into seagrass once they are larger. Migrations have been observed in other species of the family including *Entelurus aequoreus, Nerophis ophidion*, *Syngnathus acus*, *Syngnathus rostellatus, Syngnathus typhle* (Vincent et al. 1995) and *Syngnathus fuscus* (Lazzari & Able 1990), therefore *S. biaculeatus* are assumed to be capable of some migration, however the extent of movement is unknown. The samples obtained are believed to accurately represent the size–structure of *S. biaculeatus* in

the field, as it is unlikely that juveniles escaped collection, given that juveniles of other species (*Urocampus carinirostris* and *Stigmatopora nigra*) were caught in large numbers during the study. Furthermore, *S. biaculeatus* lacks a caudal fin and is considered a weak swimmer (Dawson 1985), and juveniles are unlikely to be able to avoid capture in a seine net.

The growth rate of laboratory-reared fish was more than double that for wild fish. Such a difference was also observed in Strawn's (1958) study of *Hippocampus zosterae*. In the current study, the water
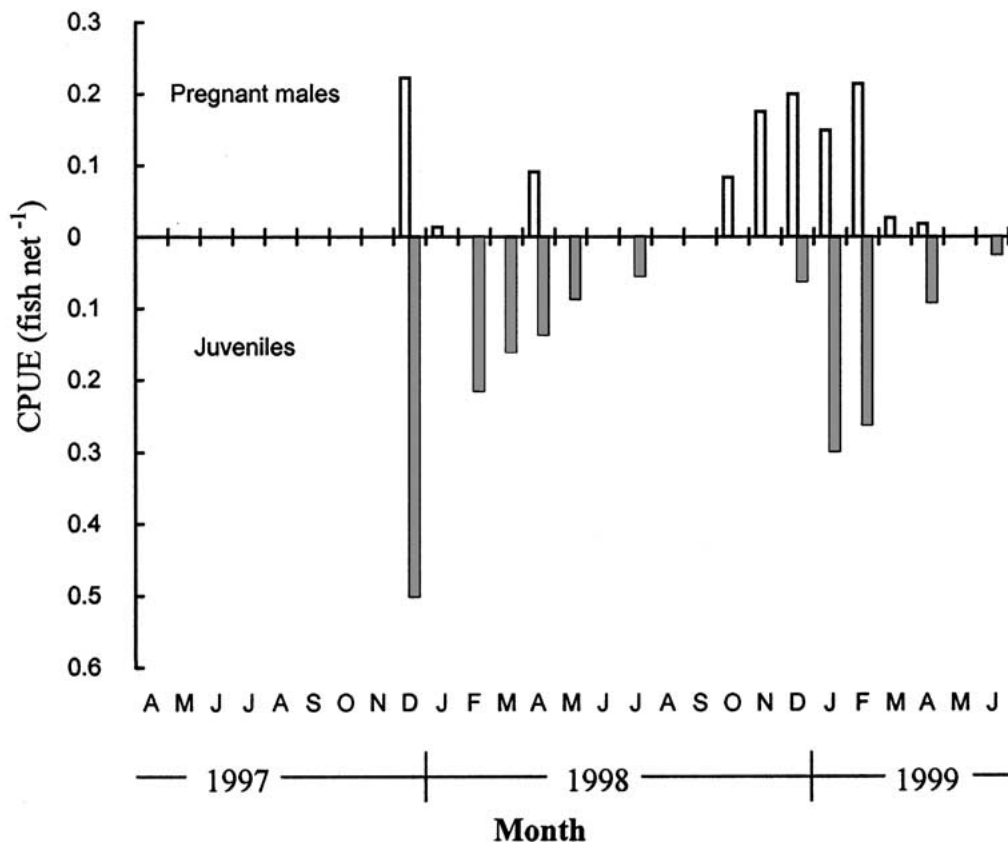
Figure 7. Abundance (CPUE) of pregnant males and juveniles between April 1997 and June 1999, from all locations.

Table 1. Egg numbers and sizes from female gonads and male abdomens. All numbers are means, size is gamete diameter (mm) for females and embryo length (mm) for males. Number of fish examined is in parenthesis.

Sex	Batch	Number of eggs	Size
Female	1	155 (13)	1.5
	2	91 (7)	0.5
Male	Brown	120 (21)	17.4
	White	153 (7)	10.4
	Clear	185 (16)	n/a

temperature in aquaria was adjusted to reflect that in the sea, so any difference in growth rate must have been a result of some other factor such as food availability. It should also be noted that the wild growth rate was estimated monthly over 6 months for fish larger than 100 mm SL whereas the laboratory growth rate was calculated every second day for fish less than 120 mm SL. The difference in laboratory and wild growth rates might, therefore, simply represent the higher rates expected for smaller fish based on the von Bertalanffy equation.

For the laboratory-reared fish, the slower growth between days 25 and 45 may have been attributable to a lack of adequate food (both quantity and type) provided during this period, since growth accelerated once feeding frequency was increased. Young seahorses are known to exhibit growth inflection points as they switch between prey types (Boisseau 1967). The influence of food availability on growth of *S. biaculeatus* needs further clarification, as this experiment was not designed to investigate the effects of food abundance and quality on growth. The K-value of 2.8 year^{-1} for *S. biaculeatus* was similar to 2.5 year^{-1} for *Hippocampus erectus*, but higher than those of other pipefish species (Table 2).

The monthly field data provided an indication of longevity in *S. biaculeatus*. Two cohorts can be identified on several occasions, notably between December 1998 and February 1999. Since the breeding season of *S. biaculeatus* is restricted to once a year, the presence

Table 2. Life-history characteristics of syngnathid species. Dash – data not available. Sources: (1) Lourie et al. (1999), (2) Froese & Pauly (2001)*, (3) Perante et al. (1998), (4) Vincent (1996), (5) Strawn (1958), (6) Bayer (1980), (7) Target (1984), (8) Watanabe (1999), (9) Berglund et al. (1989), (10) Campbell & Able (1998), (11) Present study. K = growth coefficient, in d^{-1}.

Species	Location	Breeding season	Breeding period (months)	Clutch size	K	Source
Hippocampus abdominalis	Australia	Oct.–Jan.	5	300–700		1, 2
Hippocampus bargibanti	Australia	Mar.–Nov.	9	—		1, 2
Hippocampus breviceps	Australia	—	—	48		1, 2
Hippocampus capensis	South Africa	Sep.–Apr.	8	7–95		1, 2
Hippocampus comes	Pacific	—	—	200	1.7	3
Hippocampus coronatus	Japan	Jun.–Aug.	3	200–300		1, 2
Hippocampus erectus	Europe	Jul.–Sep.	3	250–300	2.5	1, 2
Hippocampus fuscus	Indian ocean	—	—	30–140		1
Hippocampus guttulatus	Europe	Apr.–Oct.	7	—		1, 2
Hippocampus hippocampus	Europe	Apr.–Oct.	7	—		2
Hippocampus kuda	Indo-Pacific	—	—	20–200		1
Hippocampus reidi	W Atlantic	—	—	1572		4
Hippocampus triaculatus	Japan	May.–Sep.	5	400–1000		1
Hippocampus whitei	Solomon Is.	Oct.–Apr.	7	100–250		1, 2
Hippocampus zosterae	Florida	Feb.–Oct.	9	3–25	12.0	2, 5
Nerophis ophidon	E Atlantic	—	—	—	1.1	2
Syngnathoides biaculeatus	Indo-Pacific	Oct.–Apr.	7	120	2.8	11
Syngnathus leptorhynchus	E Pacific	Feb.–Jul.	7	NA		2, 6
Syngnathus rostellus	Europe	Jul.–Oct.	4	NA	0.8	2
Syngnathus scovelli	Florida	Mar.–Jul.	5	175–296		2, 7
Syngnathus schlegeli	Japan	Jun.–Jan.	8	1000		8
Syngnathus typhle	Europe	Apr.–Oct.	7	—	0.6	2, 9
Syngnathus fuscus	W Atlantic	—	—	45–1380		10

*Froese, R. & D. Pauly (eds.) 2001. FishBase. www.fishbase.org.

of two length-frequency modes indicates fish from at least two year classes were present, with the large mode representing fish at least 18 months old. As fish reached maximum length, modes became difficult to distinguish, making it impossible to estimate longevity. Future studies on otolith ageing may help clarify growth rates and longevity of this species.

Sex determination

Based upon the abdominal pattern, differentiation between the sexes was possible for fish larger than 120 mm SL, whilst all smaller fish displayed a transverse pattern on the abdomen excluding the possibility of distinguishing morphologically between sexes in young fish. A further characteristic in mature fish was the pigmentation of dots on the abdomen, which became very distinctive during courtship, indicating that they may be used for sexual display, as observed in female straight-nosed pipefish, *N. ophidion,* which

develop increased colouration on their body during mating (Berglund et al. 1989).

Reproduction

The summer breeding pattern observed in *S. biaculeatus* is similar to that of other syngnathid species. Fourteen out of 15 syngnathid species for which breeding season has been recorded bred between early summer and late spring (Table 2). *S. biaculeatus* males carrying eggs were observed over 7 months of the year, which is within the range observed for other syngnathid species (Table 2).

Male *S. biaculeatus* are reproductively mature at 71% of the maximum length recorded, as estimated from the length of the smallest pregnant male. Female syngnathids typically mature at much the same size as males, but physical manifestation is much less obvious (Vincent 1996). Further gonad analysis throughout the year is required to confidently establish the size at maturity for female *S. biaculeatus*. Male size

estimated for *S. biaculeatus* at maturity is similar to that of *Doryrhamphus baldwini*, which matures at 76% of the maximum length.[1] However, the size at maturity of *H. erectus* and *H. bargibanti* is as small as 50% and 58% of the maximum size, respectively (Lourie et al. 1999). Results from the calculation of field growth rates, and the timing of the breeding season, suggest that *S. biaculeatus* could potentially reach the estimated length at maturity within 6 months of hatching. Since the breeding season is restricted to once a year, most fish would not breed until closer to 12 months old.

Clutch sizes of pregnant *S. biaculeatus* of 60–200 eggs are comparable to those reported for other syngnathids (Table 2). Clutch size in syngnathids depends largely on body size and pouch structure (Lourie et al. 1999), and ranges from 3 to 25 embryos in *H. zosterae* up to 1572 embryos in *H. reidi* (Table 2). In comparison to males, very little work has been done on female egg counts. The presence of at least two distinct size classes of gametes in *S. biaculeatus* indicates that batches of eggs develop sequentially throughout the reproductive season (Wallace & Selman 1981), similar to the development of gametes in *Syngnathus scovelli* (Begovac & Wallace 1987) and *Syngnathus schlegeli* (Watanabe 1999). The similar number of eggs in female gonads and brooding males implies that females produce approximately the same number of mature eggs as the males brood. Furthermore, in *S. biaculeatus*, the stage of development of all eggs in a brood is equal, implying that males most likely receive eggs from only one female. The similarity of egg numbers between the sexes and the apparent provision of a single clutch of eggs from one female to one male indicates that this species is probably monogamous. Monogamy in syngnathids is well established, with some pipefishes (Gronell 1984, Berglund et al. 1989, Vincent et al. 1995) and all seahorses studied to date exhibiting this mating system (Vincent et al. 1992, 1995, Vincent 1994a,b, Masonjones & Lewis 1996, Vincent & Sadler 1995, Jones et al. 1998). In contrast, egg counts from dropped clutches following unsuccessful mating attempts in *N. ophidion* and *S. typhle* showed that females produced twice as many eggs as the males could brood, suggesting these species are polyandrous (Rosenqvist 1990, Berglund 1991). Polygamy has also been established for other pipefish species (Berglund et al. 1989, Berglund and Rosenqvist 1990, 1993,

Vincent et al. 1995, Jones & Avise 1997a,b, Jones et al. 2000, McCoy et al. 2001) by behavioural and/or genetic investigation. Confirmation of the mating system in *S. biaculeatus* would best be established using microsatellite DNA markers to verify maternity of embryos.

In summary, *S. biaculeatus* exhibits weak sexual dimorphism and is likely to be monogamous. The growth rates and densities recorded here provide valuable information on a widely distributed shallow water pipefish species occurring in coastal habitat vulnerable to degradation from human activities.

Acknowledgements

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