The life history of weedy seadragons, *Phyllopteryx taeniolatus* (Teleostei : Syngnathidae)

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Abstract. The aim of this study was to provide a detailed description of the life history of weedy seadragons, *Phyllopteryx taeniolatus*. Weedy seadragon development was described based on morphological characters and categorised into four periods: incubation, larval, juvenile and sub-adult. Hatching occurred 35–42 days post-fertilisation, most hatchlings exhibited juvenile characteristics upon hatching or shortly thereafter. The von Bertalanffy growth parameters generated from weedy seadragon length-at-age data were $L_\infty = 285 \pm 3$ mm standard length (SL; mean $\pm$ s.e.) and $k = 2.20 \pm 0.05$ year^{-1}. Females possessed a higher gonosomatic index (GSI; $1.25 \pm 1.18\%$; mean $\pm$ s.d.) than males ($0.34 \pm 0.20\%$), which increased substantially for females over 230 mm in length. Mature female weedy seadragons (290 ± 32 mm SL) ovulated 110 ± 27 eggs per female per spawning. Additionally, three females produced more than one clutch per season. Male weedy seadragons (319 ± 9 mm SL) successfully incubated 91 ± 40 eggs per spawning event. In addition to improving our understanding of the life history of weedy seadragons, this information can be used to estimate population demography and develop management strategies.

Extra keywords: Australia, development, growth, reproduction, syngnathid.

Introduction

The family Syngnathidae includes the seahorses, pipefishes and seadragons, a unique group of small cryptic fishes found worldwide in coastal temperate and tropical waters (Foster and Vincent 2004). Aside from their unique appearance, syngnathids are characterised by their reversed sex roles in which the male incubates eggs received from the female in a brood pouch located on the trunk (seahorses) or on a brood patch on the underside of the tail or abdomen (pipefishes and seadragons) (Herald 1959). As a result, offspring survival is dependent on paternal investment (Foster and Vincent 2004). In addition, syngnathids produce relatively few young and tend to have low population densities, making them susceptible to overexploitation (Foster and Vincent 2004). Significant markets have developed for both dead and live animals, particularly seahorses, for curios, traditional medicines and aquarium displays (Salin *et al*. 2005). Shrimp trawling in certain regions has resulted in significant seahorse bycatch and damage to critical habitat (Baum *et al*. 2003).

Owing to the paucity of information on the life history and population dynamics of syngnathids and the growing need to protect these vulnerable species, the majority of syngnathids have been listed by the International Union for the Conservation of Nature and Natural Resources (IUCN) as 'Data Deficient', a classification attributed to impacted species where there is insufficient information on the life history or population status for adequate management (IUCN 2004).

Weedy seadragons, *Phyllopteryx taeniolatus*, are endemic to kelp forests off southern Australia from Port Stephens, New South Wales to Geraldton, Western Australia and Tasmania (Hutchins and Swainston 1986). Although they are not harvested for the traditional medicine trade, weedy seadragons are collected for private and public aquarium displays (Pogonoski *et al*. 2002). Regional commercial harvest of weedy seadragons is managed by allowing only a few collectors export permits each year; however, over 510 live fish were exported between February 1998 and May 2000 (Pogonoski *et al*. 2002). The weedy seadragon has been listed as 'Data Deficient' by the IUCN (Vincent 1996). Weedy seadragons are also listed as a 'Protected Species' in New South Wales, 'Protected Aquatic Biota' in Victoria, and are protected in Tasmania, which is indicative of the concern for this species, and is necessary given this species' commercial value (Pogonoski *et al*. 2002). Additionally, leafy seadragons, a closely related species, are accidental bycatch in the trawl fishery and could

also be a potential threat to weedy seadragons (Connolly *et al*. 2002).

Although anecdotal information on aspects of weedy seadragon biology is abundant (e.g. Kuiter 2003), only a few studies have been conducted in the wild (Sanchez-Camara and Booth 2004; Sanchez-Camara *et al*. 2005) and a systematic and detailed description of their life history has not been documented. Advances in captive animal husbandry resulting in the successful breeding and rearing of weedy seadragons have provided an opportunity to study the life history of this species. The objectives of this study were to describe the developmental stages (embryo through sub-adult), growth and reproduction of weedy seadragons. In addition to improving our understanding of the life history of weedy seadragons, this information could be used to assist in estimating demographic parameters and better determine the vulnerability of this species.

Materials and methods

Animal husbandry

The weedy seadragon collection at the Aquarium of the Pacific in Long Beach, CA was used to describe this species' developmental stages, growth and reproduction. Nine adult and 10 juvenile wild-caught weedy seadragons were collected in the Sydney, New South Wales area and imported from Australia from 1997 to 2001, and maintained at the aquarium. Environmental data from Sydney ($37°49'$S, $144°58'$E) were used as a guideline to create a water temperature and daylength schedule to simulate regional conditions (CSIRO Marine and Atmospheric Research 2000; Australian Government Geoscience Australia 2000).

Sub-adult and adult weedy seadragons were fed thawed frozen mysids (*Mysis relicta*; 8–12 mm TL; Tropical Marine Centre Ltd, Chorleywood, England) supplemented with vitamins and fatty acids (VitaFish, Marine Enterprises Intl., Baltimore, MD) twice daily. Live adult mysids (*Mysidopsis bahia*; 10–12 mm TL) fed brine shrimp nauplii (*Artemia salina*; 400–500 μm TL) enriched with Selco (Inve Aquaculture, Dendermonde, Belgium) were also fed to sub-adult and adult weedy seadragons 1–3 times a week.

Captive-bred and raised weedy seadragons were fed different diets according to their stage of development. Newly hatched weedy seadragons (hatching to 3 weeks of age) were fed enriched brine shrimp nauplii (as above) to satiation, which was directly observed when fish stopped striking at prey. Juvenile weedy seadragons (3–6 weeks of age) were fed enriched mysids (1–4 mm TL) to satiation, and weedy seadragons 6–10 weeks of age were fed larger mysids (4–10 mm TL) 3–4 times a day. Older weedy seadragons (3–6 months of age) were fed adult mysids 2–3 times daily. Enriched frozen and live adult mysids were fed to sub-adult weedy seadragons after 6 months of age (as above).

Developmental stages

Weedy seadragon developmental stages were described based on offspring raised from three successful reproductive events at the Aquarium of the Pacific from 2001 to 2003, and one reproduction at the Tennessee Aquarium in Chattanooga, TN. Digital photographs of weedy seadragons were taken daily to closely examine the progression of development, and were used to create drawings of the developmental stages. Because of the unique reproductive strategy and early life history of syngnathids, standard teleost developmental stages could not be applied. However, the same template for describing teleost development was used for characterising development of weedy seadragons (Fuiman and Werner 2002).

The stages of development before and after hatching were described by establishing one or more dominant morphological characters such as eye and heart development, fleshy appendages, somites and bony plates. To describe pre-hatching development, live embryos from two males that died during the incubation period were removed from the epithelial cups on the brood patch upon the male's death and reared independently of the male as prematurely hatched embryos, which were defined as those embryos with >6% of the yolk sac remaining.

Somatic growth

Calcified structures (opercula, vertebra, bony plates and bony plate spines) were removed from six weedy seadragons that died of natural causes to establish a method of determining the age of wild-caught fish. No animals were purposefully sacrificed during this study; additionally, non-sacrificed animals were not likely to have influenced calcification results. Calcified structures were also removed from 11 animals bred in captivity (known age) to validate annual calcium banding patterns. Structures were cleaned of excess tissue by soaking in warm water and brushing gently with a soft bristle brush. The structures were mounted on glass slides with a clear casting resin (TAP Plastics, Dublin, CA) for examination. Longitudinal and sagittal sections of all structures were made using a diamond-blade isomet saw and polished with 30-μm grit wet sandpaper. In addition, a subsample of the vertebrae and bony plates were stained with 0.1% alizarin red, 0.1% alcian blue, and some with both stains to enhance banding patterns (Presnell and Schreibman 1997). All structures were examined under a dissecting light microscope.

Body lengths of weedy seadragons bred in captivity, and thus of a known age, were monitored over time. Owing to the fragility of live weedy seadragons, a novel method of measuring seadragons *in situ* was developed with all length measurements made while fish were in holding tanks. Length measurements were spatially referenced by placing a millimetre grid in the water and taking a digital image of the fish in a lateral position while in contact with the grid. Digital images of weedy seadragons of known age were collected daily from hatching to 3 weeks of age, weekly to 6 weeks of age, and monthly thereafter from June 2001 through November 2004. Hatchlings were treated as a cohort until they could be individually identified by natural facial markings and fleshy appendage patterns at ~6–7 months of age. Wild-caught adult weedy seadragons of unknown age were also photographed and measured.

Spatially referenced digital images were transferred into Scion Image for Windows, an imaging analysis program (Rasband 2000). The length of weedy seadragons was calibrated using the millimetre scale. The standard length (SL; mm) of each weedy seadragon was determined by measuring along the dorsal ridge of the fish from the tip of the snout to the tip of the tail (Fig. 1). Key body features, such as fleshy appendages, were used as reference points to allow for consistent measurements within and among individuals. To quantify the precision of length measurements of individuals, five independent measurements of the same individual were made. Percentage change in yolk volume was quantified by measuring the area of the yolk in each digital image over the various stages of development.

The mean rate of growth for weedy seadragons from hatching to 4 days of age, from 4 to 7 days of age and from 7 days of age to the beginning of the sub-adult period (6 months of age) was determined. Captive weedy seadragon length-at-age data was fit to the von Bertalanffy growth model with a nonlinear least-squares regression algorithm to estimate growth parameters (Sigma Plot, SPSS Inc., Chicago, IL). The von Bertalanffy growth equation used was:

$$L_t = L_\infty(1 - be^{-kt}) = L_\infty - (L_\infty - L_0)e^{-kt}$$
$$b = (L_\infty - L_0)/L_\infty = e^{kt_0}$$

L_t = predicted length at time, L_∞ = theoretical asymptotic length, L_0 = length at birth, k = the growth coefficient, t_0 = time when length
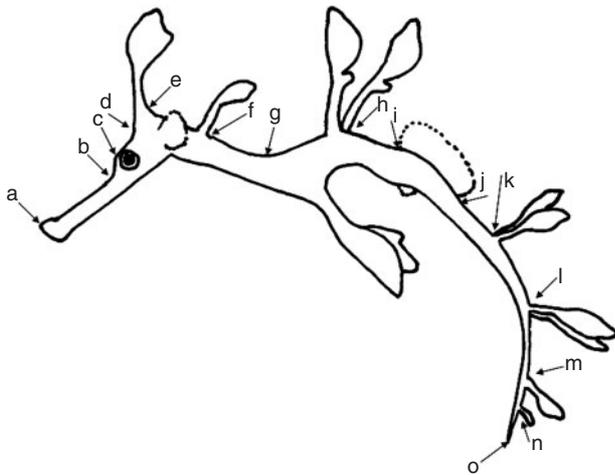
Fig. 1. Key body features used as reference points for determining the standard length (mm) measurement for captive weedy seadragons (*Phyllopteryx taeniolatus*). The standard length was measured along the dorsal ridge from the tip of the snout to the tip of the tail using body features (indicated by arrows) as reference points to allow for consistent measurements within and among individuals: (a) tip of snout; (b) end of snout; (c) ridge of eye; (d) anterior base of fleshy head appendage; (e) posterior base of fleshy head appendage; (f) base of fleshy nape appendage; (g) nape; (h) base of pair of fleshy dorsal appendages; (i) anterior end of dorsal fin; (j) posterior end of dorsal fin; (k) base of first pair of fleshy tail appendages; (l) base of second pair of fleshy tail appendages; (m) base of first single tail appendage; (n) base of second single tail appendage; and (o) tip of tail.

theoretically equals zero (von Bertalanffy 1938; Fabens 1965). All individuals were pooled for the von Bertalanffy growth model because the sex of individuals could not be determined externally until they exhibited breeding behaviour.

Reproduction

A gonosomatic index (GSI) was used to determine whether wild-caught and captive-bred weedy seadragons that died in captivity of natural causes were sexually mature. The GSI was determined by the following equation: (gonad weight/bodyweight) × 100 (Cailliet *et al.* 1986) for six male weedy seadragons and six female weedy seadragons.

Sexual dimorphism of live animals was only discernable during the breeding season when a mature male's brood patch became soft and swollen in appearance and a female's abdomen became swollen. The collection of wild-caught seadragons was maintained together and included eight males and five females at any given time. Individual weedy seadragons were identified using natural facial markings and fleshy appendage patterns. Courtship and mating behaviours of mature wild-caught and maturing captive-bred individuals were described during the breeding season from 2001 to 2003. Female fecundity was measured by the number of eggs per spawning event each season, and male fecundity was measured by the number of eggs that were accommodated by each male successfully receiving eggs.

Results

Developmental stages

The development of weedy seadragons was categorised into four periods: incubation, larval, juvenile and sub-adult based

on the appearance of dominant morphological characters. In addition, four major developmental stages were described during the incubation period. All eggs that became partially enclosed by the epithelial tissue of the brood patch were viable and hatched. However, because embryos within the epithelial cups that were still attached to the male's brood patch were difficult to observe, and no males died between 7 and 20 days post-fertilisation, no detailed descriptions were made for weedy seadragon embryos during this time.

Stage I – Incubation Period

Embryonic development of eyes was the first major morphological feature observable within the eggs, while still attached to the male's brood patch, and were apparent 5–7 days after fertilisation. This was the only major character observable from embryos within the epithelial cup.

Stage II – Incubation Period

Stage II embryos were between 20 and 24 days post-fertilisation, and were 20 ± 2 mm SL (mean $\pm$ s.d.; $n = 4$; Fig. 2*a*). Embryos at this stage had a very large, pink yolk connecting to the abdomen of the embryo, with the head and body separated from the yolk. The embryos were transparent, with the exception of the cardiovascular system and the eyes. The heart was discernable and the yolk vein was clearly visible. The eyes were large and darkly coloured with iridescent irises. The brain was also visible as a dark shadow.

Stage III – Incubation Period

Stage III embryos were between 25 and 29 days post-fertilisation, and were 22 ± 2 mm SL (mean $\pm$ s.d.; $n = 4$; Fig. 2*b*). No mortality occurred between stage II and stage III. At this stage of development, 6% of the yolk had been absorbed. Melanocytes were visible on the body at locations where fleshy appendages later developed, and a single fleshy cranial appendage was the first to emerge. The dorsal, pectoral, and anal fins were beginning to develop and some fin rays were discernable. At this stage, the gills were visible and the snout was beginning to develop. Somites were clearly visible throughout the trunk, and there was an increase in body-trunk movements.

Stage IV – Incubation Period

Stage IV embryos were between 30 and 34 days post-fertilisation, and were 24 ± 4 mm SL (mean $\pm$ s.d.; $n = 30$; Fig. 2*c*). Thirty-seven per cent mortality was observed between stages III and IV. The yolk decreased by 52% in size and was lighter in colour than previous stages of development. Additional brown and silver pigmentation was present on the dorsal surface of the body. With the exception of the cranial appendage, which first appeared during stage III, all of the fleshy body appendages began to emerge during stage IV. Body appendages include a pair of ventrally oriented fleshy pectoral appendages, a pair of fleshy dorsal
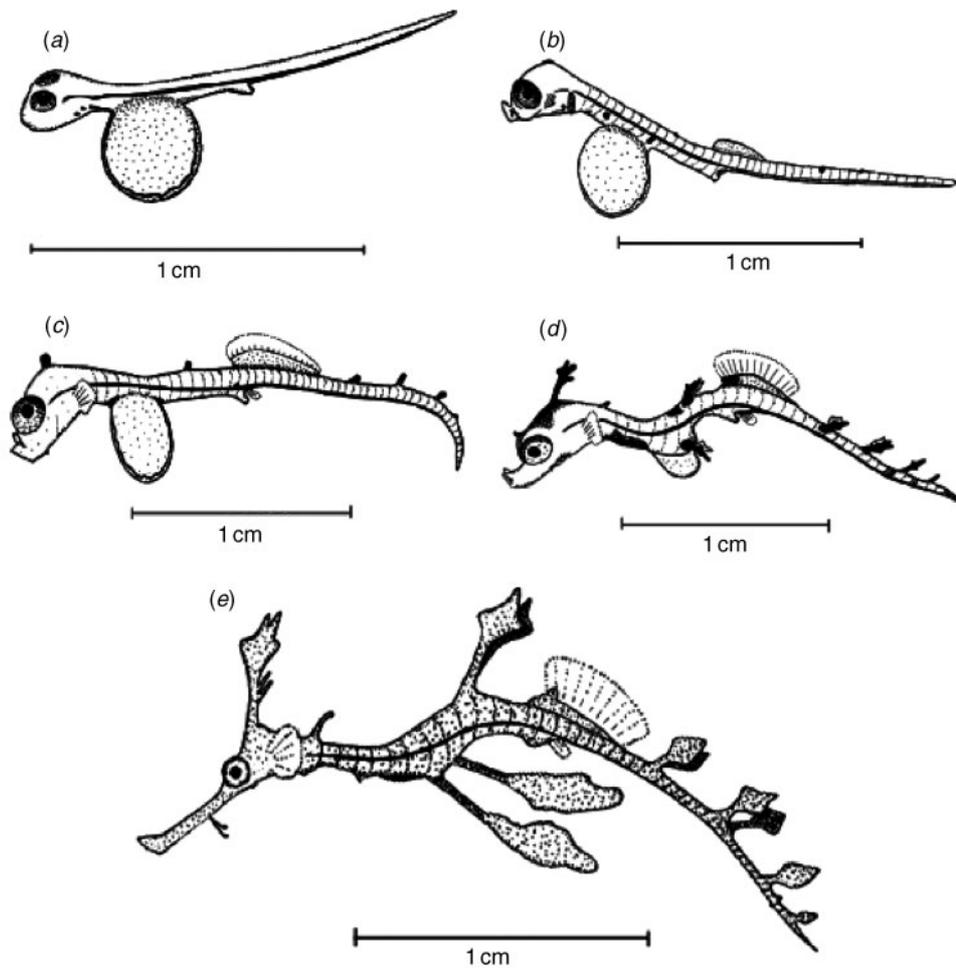
Fig. 2. Weedy seadragon (*Phyllopteryx taeniolatus*) developmental stages. Stages included: (*a*) Stage II –
Incubation Period; (*b*) Stage III – Incubation Period; (*c*) Stage IV – Incubation Period; (*d*) Larval Period;
and (*e*) Juvenile Period.

appendages between the nape and dorsal fin, a series of two
median paired fleshy appendages after the dorsal fin on the
tail and two single median fleshy appendages that developed
posterior to the paired tail appendages. The embryos were
increasingly active during this stage of development.

Larval Period

The larval period occurred from 35 to 39 days post-
fertilisation; larvae were 27 ± 3 mm SL (mean $\pm$ s.d.; $n = 55$;
Fig. 2*d*). The larval stage was characterised by the pres-
ence of a full complement of fin rays: the dorsal fin (34
fin rays); the pectoral fin (21 fin rays); and the anal fin (5
fin rays). Twenty-six per cent mortality occurred between
stage IV and the larval period. The yolk had decreased by
94% in size and was very light pink in colour. The fleshy
body appendages were beginning to elongate and a pair of
fleshy snout appendages were beginning to bud. Snout and

mouth development continued. The bony plates had begun to
develop on the body.

Hatching began at the end of this stage as a result of
increased activity by the larvae. Larvae were able to break out
of the egg capsule by thrusting the tail through the capsule
wall, and were thus expelled from the male's tail. Hatchlings
were able to swim weakly for short periods of time and rest
on the bottom in between swimming intervals.

Juvenile Period

The juvenile period occurred 40–42 days post-fertilisation;
juveniles were 32 ± 3 mm SL (mean $\pm$ s.d.; $n = 55$; Fig. 2*e*).
The mortality observed between the larval and juvenile peri-
ods was 10%. At this stage, 98% of the yolk had been
absorbed. Larvae that hatched at the end of the larval period
took an additional 3–5 days post-hatching to develop juvenile
characteristics, although the majority of the individuals did

not hatch until the juvenile period. All remaining eggs hatched by 42 days post-fertilisation.

The juvenile period was characterised by squamation of the bony plates so that they completely covered the body. A single spine developed from the centre of each bony plate, and the body was heavily pigmented with black, brown, and silver. The fleshy body appendages were well developed and extended with club-shaped tips. The snout had elongated and the mouth was well developed. Juvenile fish swam continuously and actively searched for food, feeding partially on yolk sac supplies that were maintained up to 4 days after the juvenile period, in addition to exogenous food sources. Five to 7 days after hatching, juveniles developed a pair of ventrally oriented fleshy snout appendages and a single median appendage on the nape (Fig. 2*e*).

Sub-adult Period

The sub-adult period was defined when the pair of ventrally oriented fleshy snout appendages fell off the snout at approximately 6 months after hatching. Individuals were 184 ± 22 mm SL (mean $\pm$ s.d.; $n = 44$). Twenty per cent mortality occurred between the juvenile and the sub-adult periods. During this period, individuals were sexually immature and did not illicit mating behaviours.

Somatic growth

Banding patterns were present on the edges of vertebra, bony plates and opercula removed from both wild-caught and captive-bred weedy seadragons; however, none of the banding patterns were indicative of age. In addition, inconsistencies in the banding patterns were observed in different structures removed from the same individual. For example, different numbers of bands were observed on multiple hard structures removed from the same individual resulting in an unreliable method of ageing. The skulls of six wild-caught weedy seadragons and two captive-bred animals were dissected to locate otoliths. However, no otoliths were located or recovered, even after microscopic examination of the cranium.

The standard lengths of 112 captive-bred weedy seadragons were measured from three sets of cohorts, of which nine individuals could be identified and re-measured over time. The low number of weedy seadragons repeatedly sampled over the study was attributed to natural mortality and the exchange of sub-adult animals with other public aquaria. Standard lengths of captive-bred weedy seadragons ranged from 29 to 324 mm ($n = 431$ length measurements). Adult animals of unknown age were also monitored but, because their ages could not be determined, these measurements were not included in the length-at-age analysis.

The rate of growth (mean $\pm$ s.d.) for weedy seadragons from hatching to 4 days of age was 0.22 ± 0.03 mm day^{-1} ($n = 55$). The rate of growth from 4 to 7 days was 0.91 ± 0.30 mm day^{-1} ($n = 55$) and 0.72 ± 0.17 mm day^{-1} ($n = 44$) from 7 days of age to the sub-adult period, $\sim$220 mm SL.
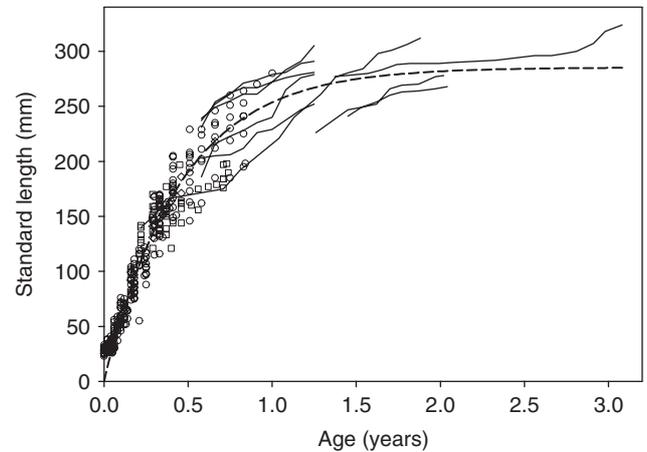

Fig. 3. The von Bertalanffy growth model fit to length-at-age data for captive-bred weedy seadragons (*Phyllopteryx taeniolatus*) of known age. Fish were monitored from hatching to 3.5 years of age ($n = 431$ length measurements) and the estimated parameters were: $L_\infty = 285 \pm 3$ mm SL (mean $\pm$ s.e.) and $k = 2.20 \pm 0.05$ year^{-1}. The dashed curve represents the growth model, whereas the data points represent actual length measurements of cohorts: $\diamond$ = cohort 2001 ($n = 21$); $\square$ = cohort 2002 ($n = 43$); and $\bigcirc$ = cohort 2003 ($n = 291$); and solid lines represent individuals ($n = 9$) that could be identified and monitored over time.

Known length at birth was 32 ± 3 mm SL (mean $\pm$ s.d.; $n = 55$) and was therefore used as L_0 in the growth equation. The von Bertalanffy growth parameters generated from the length-at-age data for weedy seadragons were $L_\infty = 285 \pm 3$ mm SL (mean $\pm$ s.e.) and $k = 2.20 \pm 0.05$ year^{-1} ($n = 431$ length measurements; Fig. 3). The largest animal of known age was 324 mm SL, and the largest individual of unknown age in the collection was 386 mm SL.

Reproduction

A gonosomatic index (GSI) was calculated for six male weedy seadragons and for six female weedy seadragons (Fig. 4). The GSI for all weedy seadragons was low, with females ($1.25 \pm 1.18\%$; mean $\pm$ s.d.) having a greater GSI than males ($0.34 \pm 0.20\%$). Because GSI was only determined for animals as a result of natural mortality and no animals died during the breeding period, a seasonal peak in GSI indicative of breeding condition could not be determined.

Breeding behaviours and sexual dimorphism were observed in wild-caught weedy seadragons when the photoperiod exceeded 12.5 h daylength and water temperature exceeded 14°C. Courtship behaviours typically lasted for 2–4 weeks before the time of breeding. Weedy seadragons exhibited a tail curling behaviour in which adult males approached an adult female curling their tail away from the female. If responsive, the female curled her tail away from the male. Early in the breeding season, females were less responsive, but become more responsive to male approaches as the breeding season continued. When more than one male courted
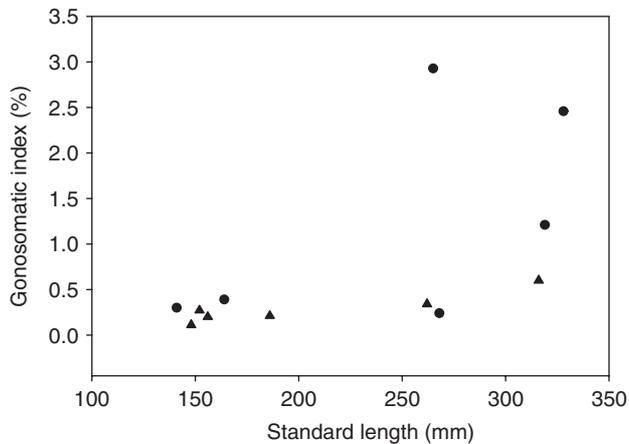
Fig. 4. The gonosomatic index (GSI) and standard length (mm) for male and female captive wild-caught weedy seadragons (*Phyllopteryx taeniolatus*). The GSI was greater for females ($1.25 \pm 1.18\%$; mean $\pm$ s.d.) than for males ($0.34 \pm 0.20\%$), this difference was not significant ($t = 1.99$, $P = 0.07$). Data: ● = females and ▲ = males.

a female, both males approached the female on either side with their tails curled outward; the female, in the middle, curled her tail away from the male she selected and the other male withdrew. The pair then swam parallel maintaining the curled tail posture while moving their heads back and forth towards one another, without making contact. After a few moments, the female swam away and the courtship behaviour was repeated, occasionally with a different male. No physical contact was made during this phase of courtship display. Tail curling behaviour between courting individuals occurred 15–20 times per hour during the morning hours (0730–1200 hours), 1–3 times per hour during the afternoon (1200–1700 hours) and only 1–2 times per night (1700–0730 hours).

Males also exhibited the tail curling behaviour towards other males. The display between males differed from that of females in that males maintained the outward tail curling for longer periods of time, which may be indicative of male–male competition and occurred year-round. Male–female tail curling interactions only occurred during the breeding season and became more intense before mating.

Approximately 2 weeks after courtship began, the underside of the male's tail (brood patch) became soft and swollen in appearance. Originally light pink in colour, it turned deep red before mating. The female's abdomen became increasingly swollen, presumably during egg hydration and ovulation. Three to 4 days before mating, the female's response to male tail curling courtship changed, and when the male approached the female, she swam upward in the water column. If the male did not follow the female, she swam away and waited for the male to approach her again. The female continued this behaviour until the male followed her into the water column, at which time the pair progressively became closer in proximity to one another. During this time, the

female's cloaca became enlarged and the eggs could be seen. As the pair swam upward with tails curled outward, the male positioned his brood patch anterior to the female's cloaca. This behaviour was repeated continuously for 3–4 days, primarily during the morning hours. If the individuals became separated, they repeated the upward swimming behaviour. Once the male properly contacted the female, the female rapidly transferred the eggs to the male's brood patch, the upward swimming behaviour ceased and the pair separated.

After the male received the eggs, he shook his tail and swam in tight circles, possibly after the release of sperm to facilitate fertilisation. Although sperm clouds were not observed, dissection indicated that the vas deferens duct opened just anterior to the cloaca, which was located directly above the brood patch of the tail (K. L. Forsgren, personal observation). Tail shaking also resulted in the removal of loose eggs or eggs not directly attached to the brood patch so that only a single layer of eggs remained in contact with the brood patch. The number of eggs lost appeared to be dependent upon male size, with larger males able to accommodate more eggs than smaller males.

The eggs were bright pink, spherical and 4–5 mm in diameter. Eggs were released in a large cluster arranged in several chains of 15–25 eggs per chain and covered in thick, sticky mucus. An egg mass of 75–100 eggs weighed 450–500 mg. Within 24 h from the time of egg transfer and fertilisation, the epithelial tissue of the male's brood patch formed a cup around each egg. The male incubated the eggs for 35–42 days. After hatching, egg cup scars were visible on the male's tail for several weeks.

Five wild-caught adult female weedy seadragons (290 ± 32 mm SL; mean $\pm$ s.d.) ovulated 110 ± 27 eggs per female per spawning (Table 1). Three wild-caught adult male weedy seadragons (319 ± 9 mm SL) successfully incubated 91 ± 40 eggs per egg transfer (Table 1).

Discussion

Developmental stages

Weedy seadragon development is unique compared with other teleost species. The majority of teleosts produce inconspicuous planktonic larvae that develop without the influence of parental care (comprehensive review of teleost larvae – Fuiman and Werner 2002), whereas weedy seadragon embryos remain within the epithelial cup attached to the male's brood patch throughout the larval period. This additional paternal care allows for advanced development within the egg, so that individuals become juveniles at the time of hatching or soon thereafter.

One of the first signs of differentiation in most teleost species occurs within the caudal fin. During development, the urostyle, the final segment of the vertebral column, turns upward in a process known as flexion, and is characteristic of the larval period (Fuiman and Werner 2002). Soon

Table 1. Fecundity data for captive wild-caught weedy seadragons (*Phyllopteryx taeniolatus*) collected over three breeding seasons (2001–2003) at the Aquarium of the Pacific, Long Beach, CA, USA

Female	Female length (mm SL)	Breeding season	Number eggs per spawning	Number eggs incubated by male	Male length (mm SL)
F1	251	2001	75	N/A	N/A
		2001	114	N/A	N/A
F2	262	2001	100	47	310
		2001	75	N/A	N/A
F3	315	2002	150	125	328
	300	2002	110	N/A	N/A
F4	322	2003	134	100	319
		2003	125	N/A	N/A

after flexion, the fins begin to develop. The flexion stage of development may be absent in the weedy seadragon because they do not possess a caudal fin. Additionally, fin development begins during stage III of the incubation period rather than during the larval period. However, one syngnathid (*Hippocampus mohnikei*) has been reported to possess a minute caudal fin with two vestigial fin rays during development, which later disappear (Kanou and Kohno 2001). The examination of larval and juvenile captive-bred weedy seadragon embryos revealed no evidence of a caudal fin or caudal fin rays. If the caudal fin is also vestigial in weedy seadragons, it may be lost early in development.

Weedy seadragon larvae also become heavily pigmented while still inside the epithelial cup and attached to the male, which is different than most teleost species. Attaining pigmentation early in development may help camouflage the developing embryos during incubation, while attached to the male's brood patch. In addition, the presence of pigmentation before hatching may be critical for neonatal predator avoidance in this cryptic species (Fuiman and Werner 2002).

Somatic growth

Attempts to age weedy seadragons using hard structures were unsuccessful. Although banding patterns were observed in the calcified structures examined (opercula, vertebra and bony plates), no consistent banding periodicity was discernable resulting in a reliable method of ageing wild-caught fish. Otoliths, which are the most common hard structures used to age teleosts, were not located or removed from the weedy seadragons examined, even after microscopic examination of the cranium. Paxton (2000) suggested that elongate epipelagic species have very small otoliths as a result of excessive background noise in turbulent waters that would interfere with an acute sense of hearing. These organisms generally have large eyes to compensate for the lack of acute hearing (Paxton 2000). Weedy seadragons have large well-developed eyes; therefore, a keen sense of hearing may not

be as important for these ambush predators as precise vision, and as a result, otoliths may be absent or microscopic in weedy seadragons.

The rates of growth of captive-bred weedy seadragons varied over the span of time in which fish were monitored. Immediately after hatching, weedy seadragons grew slowly (0.22 ± 0.03 mm day^{-1}; mean $\pm$ s.d.). This slow growth rate occurred during the period when animals were transitioning between endogenous nutrition via yolk sac supplies and active feeding on nauplii. Juvenile growth increased 7 days after hatching (0.91 ± 0.31 mm day^{-1}) when weedy seadragons feed exogenously. Growth from the juvenile to the sub-adult period remained high (0.71 ± 0.17 mm day^{-1}) until $\sim$220 mm SL, after which growth began to slow. Because growth of individuals could be continuously monitored after 6–7 months of age, individual growth trajectories were determined and indicated brief periods of accelerated growth (Fig. 3). Periods of accelerated growth occurred during times of increased water temperature and daylength, which has also been observed in weedy seadragons in the field (Sanchez-Camara *et al.* 2005).

The theoretical asymptotic length ($L_\infty = 285 \pm 3$ mm SL; mean $\pm$ s.e.; Fig. 3) generated by the von Bertalanffy growth model for captive-bred weedy seadragons resulted in a lower estimate of standard length than that seen in the captive population studied and that reported for weedy seadragons in the wild. The maximum length of captive-bred weedy seadragons was 324 mm SL, and the largest wild-caught fish was 386 mm SL. In the wild, weedy seadragons have been reported to reach 460–470 mm SL (Dawson 1985). Because larger animals of known age (greater than 3.5 years) were not available in the current study, the growth curve generated by the von Bertalanffy growth model underestimates the asymptotic length for the species; however, it accurately represents the growth of younger animals. Additionally, the growth of captive-bred weedy seadragons is similar to that of weedy seadragons monitored in the field (Table 2; Sanchez-Camara *et al.* 2005).

**Table 2.   Length-at-age data for captive-bred weedy seadragons
(*Phyllopteryx taeniolatus*) compared to data collected in the wild
by Sanchez-Camara *et al*. (2005)**

Means, standard deviations (mean ± s.d.) and sample sizes (*n*)
provided for captive data

Captive-bred weedy seadragons		Wild weedy seadragons	
Known age (months)	Standard length (mm)	Estimated age (months)	Standard length (mm)
0	32 ± 3 (*n* = 55)	0	30
1	49 ± 6 (*n* = 11)	1	60
2	91 ± 9 (*n* = 15)	2	95
3	105 ± 9 (*n* = 11)	3	125
4	152 ± 16 (*n* = 17)	4	150
6	198 ± 28 (*n* = 13)	6	200
10	238 ± 27 (*n* = 12)	10	270
12	262 ± 22 (*n* = 6)	12	300

Reproduction

A gonosomatic index (GSI) was calculated to assess the repro-
ductive maturity of weedy seadragons. The GSI for male
and female weedy seadragons was low, but indicated that
females likely mature around 230 mm SL. A wild-caught
female 265 mm SL that died just before the breeding season
had the highest GSI value (2.93%), whereas another wild-
caught female 268 mm SL had a low GSI (0.24%) after the
breeding season (Fig. 4). Because GSI was determined as
a result of natural mortality, no individuals were available
for analysis during the breeding season; therefore, GSI could
not be determined throughout the year. As a result, a sea-
sonal pattern could not be discerned. A larger sample size of
individuals over a wider range of sizes and seasons may help
further resolve seasonal differences in GSI. Since only ani-
mals that died of natural causes were sampled, body condition
may have an affect on gonadal condition; however, animals
that perished after breeding are not likely to not have affected
these results since death may be indicative of the end of the
final breeding season of older adults.

Male GSI analysis did not show an increase in gonad mass
to body size with increased length (Fig. 4). Seahorses and
pipefishes produce smaller volumes of sperm compared with
other teleosts (Kornienko 2001). Because male weedy sea-
dragons are guaranteed paternity of the eggs they are carrying
and the relatively few numbers of eggs that are incubated, it
may not be necessary to produce large amounts of sperm;
therefore, testis size would be small, and a low GSI would be
expected even during the breeding season.

No captive-bred weedy seadragons were observed to ovu-
late in captivity or successfully mate in captivity during the
study period. However, a wild-caught female weedy sead-
ragon (251 mm SL) ovulated twice in a single breeding
season, producing 75 and 114 eggs respectively (Table 1),
but released her eggs into the water column on both occa-
sions without attempting to mate. Only larger wild-caught

females (262–326 mm SL) successfully mated (Table 1).
Females greater than 230 mm SL were sexually mature, but
may not have successfully mated if an appropriate mate was
not available.

Although the age at first maturity of male weedy seadrag-
ons is unknown, individuals as small as 214 mm SL have
been observed brooding eggs in the wild (Dawson 1985) and
Sanchez-Camara *et al*. (2005) observed one individual
∼300 mm SL brooding eggs. Although weedy seadragons of
similar size did not incubate eggs in captivity, one captive-
bred weedy seadragon (298 mm SL, three years of age)
was observed displaying courtship behaviour during the last
breeding season studied. Based on the types of behaviours
elicited by this individual during the breeding season, it was
suspected that it was a male, and approached both male and
female weedy seadragons. When it approached competing
males it exhibited the same tail curling behaviour as other
mature males; however, the other males ignored this indi-
vidual. When this individual approached a mature female, it
was also ignored. These failed attempts to ward of competing
males and mate with a female may be common among naive
animals during their first year of breeding.

Female syngnathids typically produce more eggs than can
be accommodated by a male; therefore, the male limits the
reproductive success of the female (Kornienko 2001). As a
result, variable mating patterns were observed over the breed-
ing season in weedy seadragons. Female weedy seadragons
have the ability to ovulate more than once in a breeding sea-
son, and may mate with more than one male per season, but
do not mate with more than one male per mating event. There-
fore, weedy seadragons appear to be monogamous during any
one particular spawning event, which is similar to other syn-
gnathid species (comprehensive review of syngnathid mating
behaviour – Foster and Vincent 2004). When courtship began,
more than one male may have approached a female; however,
once a male was selected, the female continuously courted
the same male until mating occurred. Similarly, males were
also monogamous within a single breeding event and did not
attempt to acquire eggs from another female at the time of
mating. Females that ovulated more than once in a breed-
ing season had an opportunity to mate with a different male;
therefore, females may be polygamous across the breeding
season, which is also similar to other syngnathids (Foster
and Vincent 2004). Likewise, after a male's first clutch has
hatched there is evidence that he may brood a second clutch
(Sanchez-Camara *et al*. 2005); in this case males may also be
polygamous during the breeding season.

The brood patch of male weedy seadragons becomes
soft and swollen in appearance and reddened in colour just
before mating; this morphological change has also been
observed in the pipefish *Syngnathus abaster* (Carcupino *et al*.
1997). The increase in the size and numbers of capillar-
ies is thought to play an osmoregulatory role in developing
embryos (Carcupino *et al*. 1997). After mating, eggs were

organised in rows of several eggs and covered in thick, sticky mucus. The mucilaginous coating may allow the eggs to temporarily attach to the brood patch until the epithelial tissue of the brood patch forms a cup around each egg, adhering them to the tail until hatching while providing osmoregulatory tissue to the developing embryos.

After mating, the male weedy seadragon shakes off the extra eggs that he is not able to accommodate on the brood patch; therefore, the surface area of the brood patch may be the limiting factor in male reproductive success. If male weedy seadragon size limits female reproductive success, then there should be strong sexual selection towards larger males. In pipefish (*Syngnathus typhle*) mate choice experiments, larger mates were preferred and fecundity increased with size in both sexes (Berglund *et al*. 1986). Because the reproductive success increased equally in both sexes, it was determined that sexual dimorphism was absent in *S. typhle* (Berglund *et al*. 1986). The same mode of sexual selection may also occur in the weedy seadragon, since males and females of similar sizes were observed to breed first during the breeding season. Interestingly, sexual dimorphism is also absent in weedy seadragons except during the breeding season when the males' brood patches swell and become reddened and the females' abdomens become swollen. Additionally, because females can produce multiple clutches per year, smaller males may have an opportunity to mate towards the end of breeding season when larger males are already incubating eggs. Berglund *et al*. (1986) noted that *S. typhle* female–female interactions were less important in breeding behaviours and this appeared to be the case with weedy seadragons. Weedy seadragon mating behaviour is also similar to that of *S. typhle* and *Hippocampus breviceps*, which involves the mating pairs rising to the surface during mating (Berglund *et al*. 1986; Moreau and Vincent 2004).

This represents the first comprehensive study of the early life history and description of breeding of weedy seadragons. The life history of weedy seadragons appears to be similar to that of other syngnathids. Several syngnathid species have been characterised as having few young resulting in low population densities with offspring survival dependent upon male survivorship (Foster and Vincent 2004). The leafy seadragon (*Phycodurus eques*) has low levels of dispersal in the field (Connolly *et al*. 2002), and it is likely that weedy seadragons exhibit a similar pattern of hatchling dispersal. Low population densities may impact the variable mating strategies of weedy seadragons, making it difficult to find suitable mates, or sequential mates. Additionally, weedy seadragons show site fidelity and have limited home ranges, but migrate to specialised breeding and nursery grounds (Sanchez-Camara and Booth 2004). Low densities and fecundity, a long incubation period, and high larval mortality may increase the susceptibility of weedy seadragons to habitat loss and overexploitation, further supporting the need for protection of weedy seadragon populations in the wild. Marine protected areas for weedy

seadragons have been proposed and would be justified given this species life history characteristics and endemism to southern Australian waters (Pogonoski *et al*. 2002).

Captive breeding programs utilising wild-caught weedy seadragons may be beneficial in supplying the public and private aquarium industry with display animals, which conveys the importance of conservation while reducing the pressure on wild populations. However, breeding programs of this nature are extremely difficult and expensive.

In addition to significantly advancing our understanding of the early life history of weedy seadragons, this novel information (growth rates, larval mortality and fecundity) can be used to develop population demography models. These models are essential for evaluating the 'Data Deficient' status of weedy seadragons and can be used to improve management of this protected species by better assessing the number of animals that can be collected from the wild or impacts of habitat destruction.

Acknowledgments

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