Invertebrate Biology 127(1): 98–107.

DOI: 10.1111/j.1744-7410.2007.00110.x

Brooding of pelagic-type larvae in *Ophiopeza spinosa:* reproduction and development in a tropical ophiodermatid brittlestar

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Abstract. *Ophiopeza spinosa,* a small ophiodermatid ophiuroid, is locally abundant in shallow water rubble habitat at Lizard Island, northern Great Barrier Reef, Australia. This species is a protantric hermaphrodite. The switch from reproduction as a male to a female is progressive, involving a simultaneous hermaphrodite as a transitional stage. Members of *O. spinosa* brood their young in the respiratory bursae. Cohorts of eggs (280 μm diameter) develop synchronously in the gonad and are spawned as a group into the bursa. Despite non-pelagic development, the larvae of *O. spinosa* are a vitellaria type typical of broadcast-spawning ophiodermatids, providing a link to an ancestral form with a dispersive larva. The vitellaria has prominent ciliary bands and swims in the same manner as pelagic vitellaria. *In vitro,* the larvae developed to the juvenile stage independent of the parent. There was no evidence of extraembryonic nutrition; a proportion of the maternal provisions were retained through metamorphosis. This is the first ophiuroid known to brood a pelagic-type vitellaria larva. Juveniles appear to leave the parent at the two- to three-arm segment stage, slightly larger than the newly settled juveniles of ophiodermatids with pelagic vitellariae. The presence of functional larvae in the bursa suggests a recent switch to the incubatory life history in *O. spinosa* and the possibility of a reversal back to a dispersive life history. *O. spinosa* have the potential to both brood and broadcast their young.

Additional key words: Ophiuroidea, life history, evolution

Echinoderms are a conspicuous component of the marine invertebrate fauna of tropical regions. In particular, ophiuroids (brittle stars) are common shoreward of coral habitats, where they are often found aggregated in mixed species assemblages under slabs of coral rubble and in crevices (Sloan et al. 1979; Sloan 1982; Byrne et al. 2004b; Oak & Scheibling 2006). In the tropical Indo-West Pacific, these assemblages are comprised of large-bodied brittlestars, including those of *Ophiocoma, Ophiarachnella,* and *Macrophiothrix* species (Sloan 1982; Byrne et al. 2004b; Oak & Scheibling 2006). Of ~170 species of Ophiuroidea reported from the Great Barrier Reef (GBR), most of these have a broad distribution in the Indo-West Pacific and most species that have been studied have a pelagic stage in their life history (Mortensen 1921, 1931; Endean 1957; Clark & Rowe 1971; Rowe 1985; Guille et al. 1986; Hendler 1991; Byrne et al. 2004a; Cisternas et al. 2004). Their dispersive life history undoubtedly contributes to their pan-tropical Indo-West Pacific distribution, as shown for other Indo-West Pacific echinoderms (Lessios et al. 1998; Uthicke & Conand 2005). Some ophiuroid genera are characterized by a feeding ophiopluteus larva (e.g., *Ophiocoma, Macrophiothrix*) and others have a non-feeding vitellaria larva (e.g., *Ophiarachnella, Ophiomastix*) (Cisternas et al. 2004; Cisternas & Byrne 2005; Fourgon et al. 2005; Podolsky & McAlister 2005). Larval type (ophiopluteus, vitellaria) is clade-related, indicating the influence of phylogeny on life-history evolution in ophiuroids (Byrne & Selvakumaraswamy 2002; Cisternas & Byrne 2005; Selvakumaraswamy & Byrne 2006). Brooding ophiuroids lack a pelagic larva and only three species from the Indo-West Pacific are reported to have this life-history, including the cosmopolitan species *Amphipholis squamata* (Mortensen 1933a,b; Fell 1946; Clark & Rowe 1971; Falkner & Byrne 2006). The paradox of the widespread distribution of *A. squamata,* despite the absence of a dispersive

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larva, is discussed in a number of studies (see Le Gac et al. 2004). Here, we report a fourth brooding ophiuroid from the region, *Ophiopeza spinosa* Ljungman 1867, an ophiodermatid with a broad distribution in the Indo-West Pacific (Vail & Rowe 1988).

In the Ophiuroidea, parental care is most prevalent in small-bodied species that incubate their embryos in ten respiratory bursae, thin-walled invaginations at the base of each arm (Mortensen 1920; Byrne 1991; Hendler 1991). The body profile in *O. spinosa,* with its small disc (maximum diameter 9 mm) and short arms (≤30 mm) (Vail & Rowe 1988), indicates that this species might brood its young, and this was confirmed here. A link between small size, hermaphroditism, and brooding has been identified for ophiuroids (Mortensen 1920; Byrne 1991; Hendler 1991) and this was examined for *O. spinosa*. Development through a pelagic feeding larva is considered to be the ancestral-type life-history mode in echinoderms (Strathmann 1978; Smith 1997), and so evolution of benthic development in *O. spinosa* would have involved a loss of the ancestral-type pelagic feeding larva, a switch to a lecithotrophic mode of larval nutrition, and the loss of a dispersive stage. Development in *O. spinosa* is compared with that of other ophiuroids to assess the modifications associated with the evolution of lecithotrophic development and brooding. Despite its benthic life-history, development in *O. spinosa* is similar to that seen in planktonic developers, and thus provides a link to an ancestral form with a dispersive larva.

Methods

Specimens of *Ophiopeza spinosa* were collected at low tide from a shallow water (1–2 m depth) rubble habitat at Coconut Beach (145°28′24″E; 14°40′25″S), Lizard Island in October 2005 ($n = 32$) and March 2006 ($n = 11$). The disc diameter of each specimen was measured and the bursae were examined for the presence of developing young. Late vitellogenic eggs and embryos were measured with an ocular micrometer. The eggs were dissected from the gonad for measurement. The stage of maturation of the gonads was scored on dissection as in previous studies (Byrne 1991) and the embryos were staged and counted. Following removal of the aboral body wall to score gonad maturity, the discs were placed in Bouin's fluid for histology. The tissue was embedded in paraffin, sectioned (7 µm thick), and the slides were stained with hematoxylin and eosin.

To document development, larvae from entire broods were removed from the bursa and placed in glass culture dishes (200 mL) with filtered seawater (1-µm filter, Millepore, Billerica, MA) at 28°–29°C. Approximately 50 larvae were placed in each dish. The water was renewed every second day, and reared to the juvenile stage. Whole specimens and sections were photographed using an Olympus SZX9 stereomicroscope and digital camera (Olympus, Tokyo, Japan).

Results

As is typical of its occurrence elsewhere (Vail & Rowe 1988), *Ophiopeza spinosa* is a secretive ophiuroid occurring under coral rubble at the Coconut Beach site. It is common at this location, where it co-occurs with a diverse assemblage of large ophiuroids, including *Ophiocoma scolopendrina, Ophiocoma dentata, Ophiocoma schoenlenii, Ophiomastix mixta, Ophiarthrum elegans, Ophiarachnella gorgonia,* and *Macrophiothrix* species.

Reproduction

The disc diameter in *O. spinosa* ranged 3.5–9.0 mm (Fig. 1). In October 2005, the population had mature gonads, attached to the genital plates alongside the respiratory bursa (Figs. 2A,B, 3A,B). The smallest specimens appeared to lack identifiable gonads on dissection and this was verified by histology. On

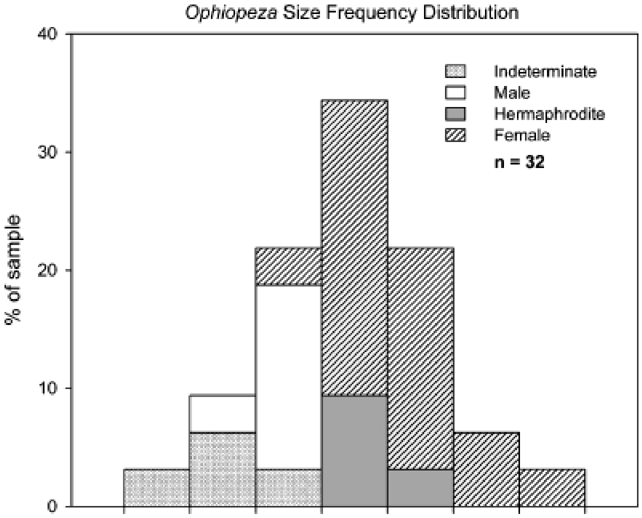

Fig 1. Size–frequency histogram showing the distribution of indeterminate (no gonad), male, female, and hermaphroditic individuals of *Ophiopeza spinoza.* This species is a protandric hermaphrodite with small and large specimens being male and female, respectively. The switch from male to female reproduction occurs at a 5–8 mm disc diameter.

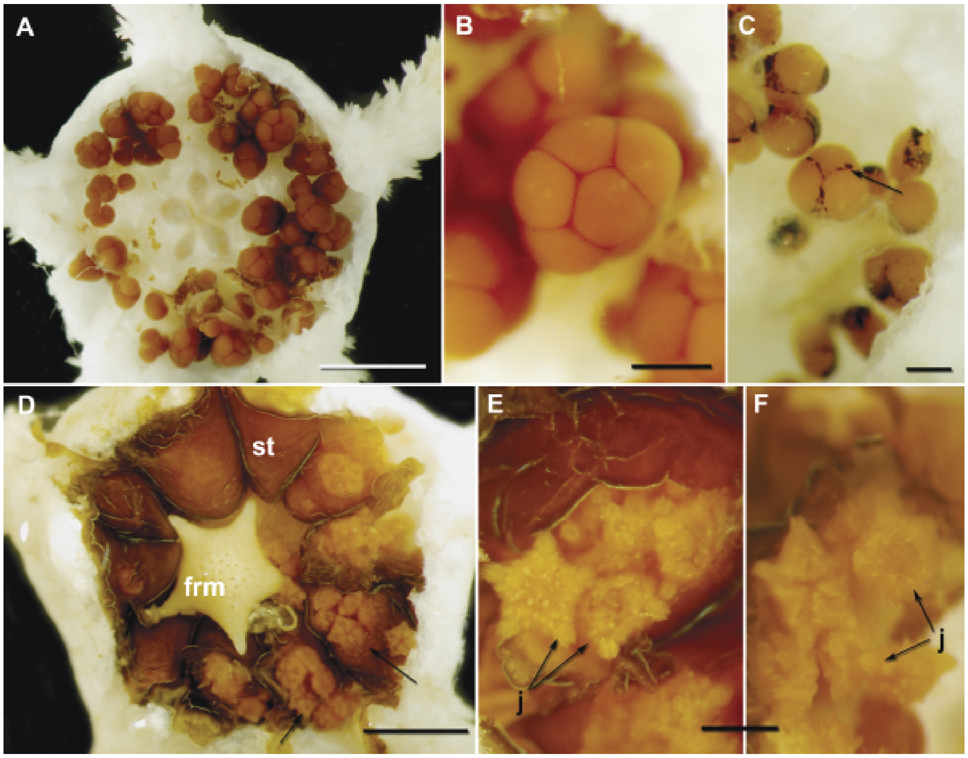

Fig 2. Specimen of *Ophiopeza spinosa* with the aboral surface of the disc removed to view the gonads and bursae. **A.** Two to four ovaries are associated with each bursa. **B.** Mature ovaries with fully grown eggs. **C.** Partially spawned ovary with an accumulation of brown pigment (arrow) around the remaining eggs. **D.** Female with the bursae filled with juveniles (arrows). The stomach (st) has been removed in places to show developing young (arrows). A large foraminiferan (frm) is present in the stomach. **E, F.** Juveniles (j) in the bursae (arrows) with one arm segment and the terminal arm plate. Scale bars, A, D = 1 mm; B, C, E, F = 300 μm.

dissection, individuals appeared to be a protandric hermaphrodite with small individuals (4–5.5 mm disc diameter) being male and large individuals (5–9 mm disc diameter) being female (Fig. 2A). One simultaneous hermaphrodite (6.0 mm disc diameter) was found that had both ovaries and testes evident. Histological sections revealed that some gonads scored as testes contained developing oocytes and that some individuals scored as female had a few small (~100 μm diameter) testes distributed among the ovaries (Fig. 3C–F). These observations indicate that small and large specimens are predominantly male and female, respectively, although both sexes occur over the size range of 5–8 mm disc diameter. The switch from reproduction as a male to a female in most individuals occurs at 5–6 mm disc diameter and involves a simultaneous hermaphrodite as a transitional stage (Fig. 1).

Each bursa had two to four testes, ovaries, or ovotestes (Figs. 2A, 3A). Ovotestes had developing oocytes along the germinal epithelium and spermatozoa in the gonad lumen (Fig. 3D–F). Some large individuals that appeared female had minute testes and so may also function as males. For these specimens, the presence of testes was only detected by histology (Fig. 3C–F).

Within individuals, the ovaries were at the same stage of development and these varied in size depending on the stage of oogenesis (Figs. 2A, 3A). Mature ovaries contained large brown-orange eggs, ranging in diameter 150–300 μm ($n = 20$) (Fig. 2b). The largest eggs dissected from the ovaries had a mean diameter of 278 μm (SE = 8.25; $n = 20$). Some mature ovaries also contained developing previtellogenic and midvitellogenic oocytes (Fig. 3B). Ovary development proceeded in parallel with embryonic development (Fig. 3H). Brooding individuals had ovaries with eggs at various stages of development and young in the bursae (Fig. 3H). Each ovary contained groups of synchronously developing oocytes. These oocytes appear to be spawned as a group into the bursa, as indicated by the presence of embryos at the same stage of development.

Partly spawned ovaries contained fewer large eggs and had an accumulation of dark brown lipid-like droplets in the gonad lumen and around the remaining large eggs (Figs. 2C, 3G). This brown pigment resembled lipofuscin (Fig. 3G). Post-spawned and spent ovaries contained material from relict oocytes and accumulations of brown pigment (Fig. 3G). All the specimens examined in March 2006 had small gonads in a post-spawning state.

Development

The eggs are fertilized in the bursa. Of the 18 females examined in October 2005, six were brooding. The number of young brooded by individual females

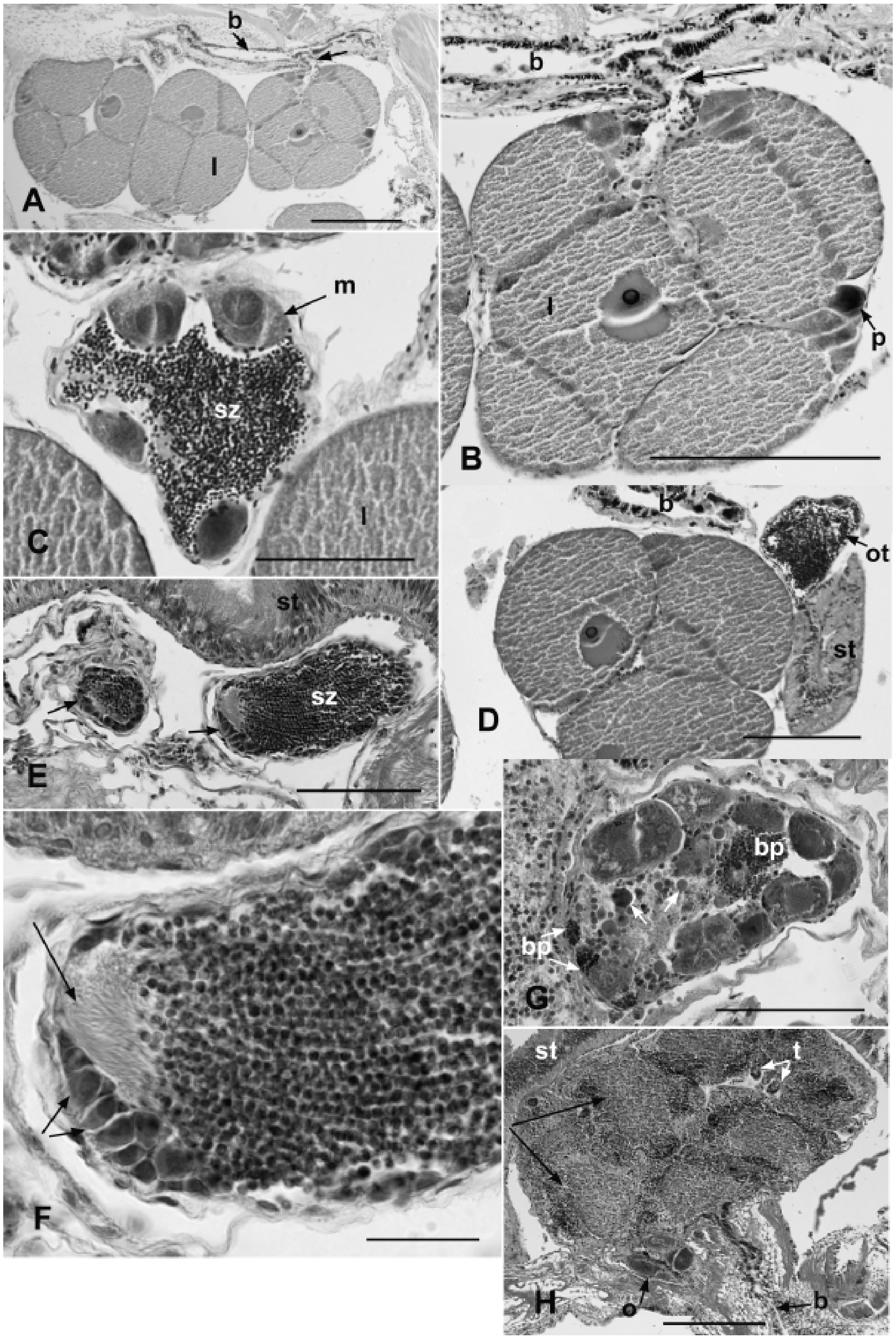

Fig 3. Histology of *Ophiopeza spinosa*. **A, B.** Ovaries filled with late vitellogenic oocytes (l) alongside the bursa (b). p, previtellogenic oocyte; arrow, gonoduct. **C.** Ovotestis with midvitellogenic oocytes (m) and spermatozoa (sz). **D.** Ovotestes (ot) and ovary in a hermaphrodite. st, stomach. **E, F.** Ovotestis with oocytes (small arrows) developing in the germinal epithelium and spermatozoa (sz) in the lumen. Large arrow, aligned spermatozoa and sperm tails. **G.** Post-spawned ovary with material from lysed oocytes (arrows) and brown pigment (bp). **H.** Bursa filled with developing embryos (arrows). b, bursal slit; o, ovary; t, developing tube feet. Scale bars, A, B, H = 250 μm; C, D, E, G = 100 μm; F = 25 μm.

summed over all bursae ranged 83–189 (mean = 125.8; SE = 22.4, $n = 6$). All the bursae in an individual female contained a similar suite of embryos. The earliest embryos observed were midvitellariae. There were no vestigial ophiopluteal features evident. The most advanced young in the bursae were juveniles with two arm segments and the terminal arm plate. Some females had larvae and juveniles at different stages of development in the bursae and others had embryos at the same stage of development (Fig. 2D,E). Sections of brooding females show the close packing of the developing juveniles in the bursa and the narrow bursal slit (Fig. 3H). The embryos were not attached to the parent's tissue at any stage of development. Newly metamorphosed juveniles had a pentagonal shape and a mean disc diameter of 283 μm (SE = 7.2; $n = 14$). The similar size of the eggs and juveniles indicates that development does not depend on extraembryonic (post-vitellogenic) nutrition. The nutrients laid down in the egg support development to the crawl-away juvenile stage. The juveniles were strongly pigmented an orange-amber color due to the presence of maternal reserves in their stomach (Fig. 4D,E).

Members of *O. spinosa* develop through a vitellaria larva (Fig. 4). When released from the bursa, the larvae swam in culture dishes in the same manner as the vitellariae of non-brooding species. Development of embryos reared *in vitro* was identical to that of embryos in the bursa. The fully developed larva is a

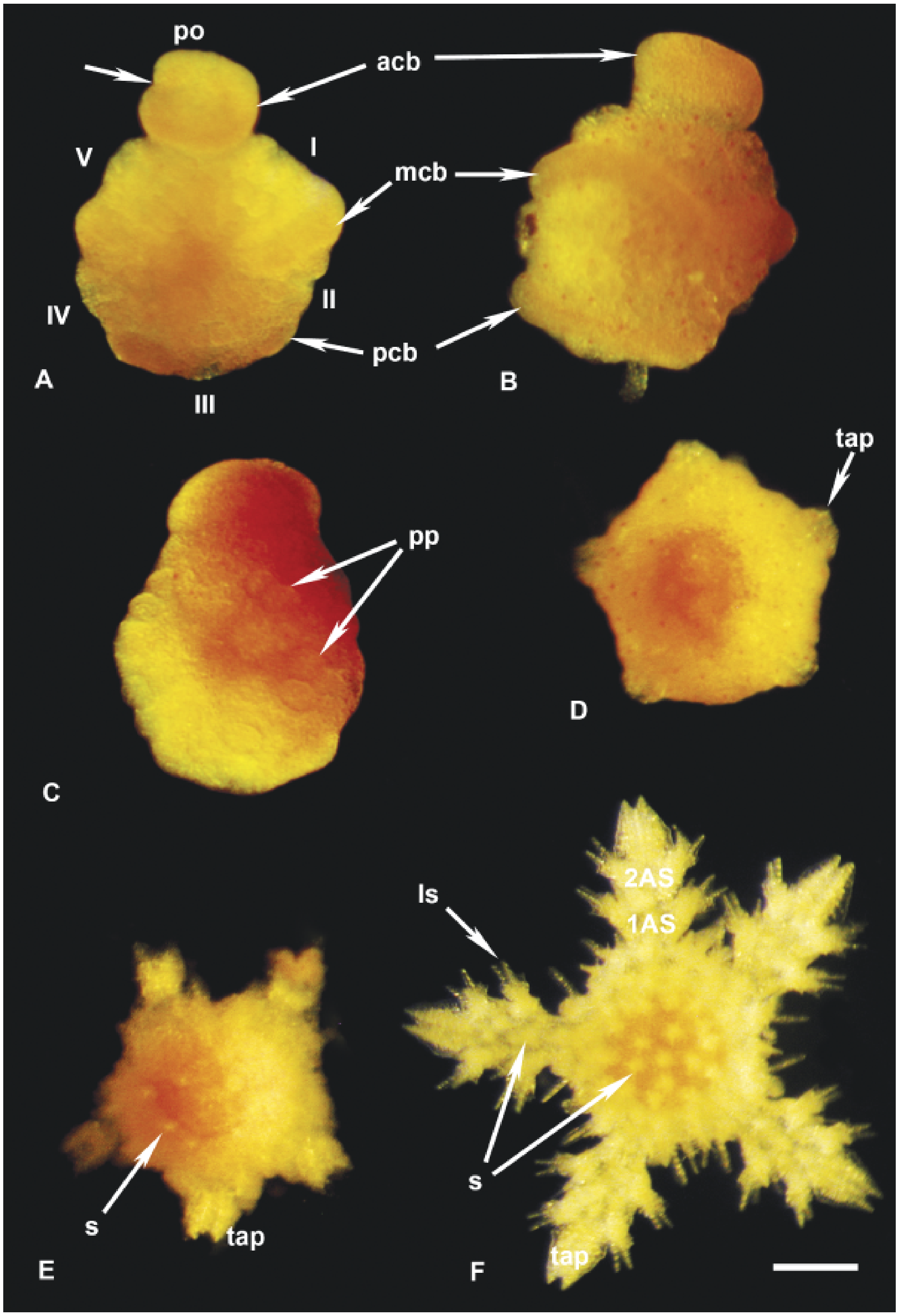

Fig 4. Vitellaria and juveniles of *Ophiopeza spinosa*. **A.** Oral and **B.** aboral views of vitellaria larva showing the location of transverse ciliated bands: the anterior ciliated band (acb) on the pre-oral lobe (po), mid-ciliated band (mcb), and posterior ciliated band (pcb). Developing juvenile arm buds numbered I–V. **C.** Advanced vitellaria, the pre-oral lobe is reduced and the primary pair of buccal podia (pp) is evident. **D.** First juvenile stage with developing terminal arm plates (tap). **E.** Juvenile with one arm segment and the terminal arm plate (tap). s, developing spines. **F.** Advanced juvenile reared *in vitro* with the first and second arm segments (1as, 2as), and the terminal arm plate (tap). ls, lateral arm spines; s surface spines. Scale bar, 100 μm.

typical vitellaria, with three transverse ciliary bands and the developing juvenile rudiment in the mid-larval region. The ciliary bands were located on prominent epithelial elevations. In advanced larvae, the first pair of buccal podia was evident in the mouth region of the developing juvenile (Fig. 4C). The nomenclature of the developing arm buds used in Fig. 4 follows the numbering system of Brooks & Grave (1899).

Three ciliary bands cross the aboral side of the vitellaria: the anterior, mid-, and posterior ciliary bands. The anterior ciliary band loops around the pre-oral lobe (Fig. 4A,B). The mid-ciliary band extended from the right oral side between developing juvenile arm buds IV–V, across the aboral surface to the left oral side between arm buds I and II (Fig. 4A,B). This ciliary band has a distinct curve in its path on the aboral surface (Fig. 4B). The posterior ciliary band bordered the edge of the posterior larval region aborally and extended orally, in the regions between arm buds II–III and III–IV (Fig. 4A,B).

Vitellariae metamorphose in the bursa by resorption of the larval body. Larvae reared *in vitro* settled onto the bottom of the culture dishes with their primary podia, followed by metamorphosis. As the terminal arm plates formed, the early pentagonal juveniles became star-shaped (Fig. 2D). The mouth skeleton was not fully formed. During development, maternal reserves are sequestered to the developing gut, giving the central region an orange color (Fig. 4D–F). These juveniles also had small spots of red pigment scattered over the aboral surface. The first pair of buccal podia was present.

Juveniles with one arm segment and the terminal arm plate were the most common stage seen in the bursae (Fig. 2E,F). As they developed, the arms increased in length with addition of arm segments. The most advanced juveniles in the bursae had two arm segments and the terminal plate (Fig. 4F). These juveniles still had extensive maternal reserves as indicated by the orange color of their stomach. The mouth was not yet open.

Larvae reared *in vitro* developed from the early vitellaria stage to the juvenile stage in 3 d. Juveniles with three arm segments and the terminal arm plate had reduced pigment as their maternal reserves were diminished. Their mouth was open and the second pair of buccal podia had developed. These juveniles were competent to feed. Juveniles appear to leave the bursa with two to three arm segments, but this was not observed. The aboral surface of exotrophic juveniles was covered with thorny spines that extended along the mid-dorsal aboral surface of the arms and on the oral shields (Fig. 4F). The lateral arm spines also had thorny projections. The armature of the disc and spines are juvenile characters as they are not present in the adults.

Discussion

The Ophiodermatidae is an important tropical ophiuroid family comprising 23 genera with one genus in the tropical Atlantic and ten genera in the Indo-West Pacific (Clark & Rowe 1971; Hendler et al. 1995). Their members are scavengers and predators, and are among the largest ophiuroids on coral reefs (disc diameter >45 mm) (Morin 1988). As typical of brooding ophiuroids, specimens of *Ophiopeza spinosa* are small (disc diameter <10 mm) in comparison with confamilial ophiodermatids (Hendler 1991; Hendler & Tran 2001). Several echinoderm taxa on the GBR have been discovered to be species complexes, with new species discerned by differences in morphology, life history, and molecular phylogeny (O'Hara et al. 2004; Byrne & Walker 2007). Several morphs appear to exist within *O. spinosa* and these may prove to be different species (T. O'Hara, unpubl. data). Examination of populations of *O. spinosa* for the presence or the absence of brooding, across its broad range, may aid in distinguishing cryptic species. Robust taxonomy is required to confirm the apparently broad distribution of this ophiuroid in the absence of a dispersive stage. The problem of the presence of cryptic species has been highlighted for other pan-Indo-West Pacific echinoderms and molluscs (O'Hara et al. 2004; O'Loughlin & Rowe 2005; Paulay & Meyer 2006; Byrne & Walker 2007).

Development through a non-feeding vitellaria appears to be a synapomorphy for the Ophiodermatidae and most species have a planktonic phase in their life history (for a review, see Cisternas & Byrne 2005). In addition to *O. spinosa,* brooding in the Ophiodermatidae is known from *Ophiopeza cylindrica,* two species of both *Cryptopelta* and *Ophiurochaeta,* and one species of *Ophioconis* (Mortensen 1924, 1925, 1933a,b; Hotchkiss 1982; Byrne 1991; Hendler 1991). Most of these are temperate species, with the exception of *Cryptopelta granulifera* from the Indo-West Pacific and *Ophiurochaeta* sp. from the Caribbean (Mortensen 1933a; Hotchkiss 1982). Only four shallow water ophiuroids from the tropical Indo-West Pacific, comprising two species in two families (Ophiodermatidae: *O. spinosa, C. granulifera;* Amphiuridae: *Amphiura constricta, Amphipholis squamata*), are known to brood their young (Mortensen 1933a; Fell 1946; Clark & Rowe 1971; Falkner & Byrne 2006). Detailed examination of the shallow water ophiuroid fauna of the GBR failed to locate other brooding species (M. Byrne, unpubl. data). In contrast, brooding ophiuroids are common in shallow water reef and back reef habitats in the Caribbean (Hendler 1979; Hendler & Littman 1986; Byrne 1991). Brooding has evolved independently numerous times in Caribbean ophiuroids and includes approximately ten species from five families (Mortensen 1920; Hendler 1979; Hotchkiss 1982; Hendler & Littman 1986; Byrne 1989, 1991; Schoppe & Holl 1994). The rationale underlying this difference in life-history evolution of the ophiuroid fauna of the two coral reef regions is not known.

The link between small size, hermaphroditism, and brooding in ophiuroids has been noted for some time (Mortensen 1920; Hendler 1991). These features were also exhibited in *O. spinosa*. Small and large individuals of *O. spinosa* were largely male and female, respectively, and so this ophiuroid is protandrous. The detection of ovotestes and minute testes in histological sections indicated that the switch from reproduction as a male to a female involves a transitional stage of simultaneous hermaphrodism, similar to that described for several other brooding ophiuroids (Hendler 1979; Schoppe & Holl 1994). Some large specimens of *O. spinosa* that appeared to be female had minute testes, and so retained some capacity to produce sperm. A similar trend in increased allocation to ovary production with increasing size occurs in the brooding Caribbean ophiuroid, *Ophiolepis paucispina* (M. Byrne, unpubl. data). In this species, however, simultaneous hermaproditism is readily detected (Byrne 1989). Most ophiuroids that brood their young are simultaneous hermaphrodites (Mortensen 1920; Byrne 1991, 1994; Hendler 1991).

Oogenesis in *O. spinosa* involved synchronous development of groups of oocytes, followed by their release into the bursa. The eggs are fertilized in the bursa, presumably by sperm drawn in by the respiratory current created by this structure, although self-fertilization remains a possibility. Through the brooding season, release of eggs may be triggered by departure of clutches of juveniles. Very early embryos and juveniles were not present in the same bursae. Embryogenesis and gametogenesis occurred in parallel in *O. spinosa,* a feature described for several other brooders (e.g., *O. paucispina*), but contrasts with *Ophionereis olivacea* where gametogenesis, gamete release, and incubation of progeny are temporally separate events (Byrne 1989, 1991; Hendler 1991). Partly spawned and spent gonads in *O. spinosa* had material from lysed oocytes and an accumulation of a brown lipid-like pigment. These lipfuscin-like deposits occur in the ovaries of other ophiuroids at the end of the spawning season (Falkner & Byrne 2003).

Except for *A. squamata* and *Ophionotus hexactis,* which have small eggs (120 and 200 μm diameter, respectively) and support their embryos with extraembryonic nutrition (Mortensen 1921; Turner & Dearborn 1979; Walker & Lesser 1989), most ophiuroids that brood their young have large eggs (400+ μm diameter) and the embryos are not dependent on exogenous nutrients (Byrne 1991, 1994; Hendler 1991). The egg in *O. spinosa* (280 μm diameter) is one of the smallest known for brooding ophiuroids and is similar in size to those of ophiodermatids with pelagic larvae (*Ophioderma brevispinum:* 300 μm diameter; *Ophiarachnella gorgonia:* 320 μm diameter) (Hendler 1991; Cisternas & Byrne 2005). Juveniles of *O. spinosa* appear to leave the parent at the two to three arm segment stage, similar to that seen in *O. olivacea,* but considerably smaller than that in other species, where advanced juveniles are retained in the bursae well beyond metamorphosis (seven to 12 arm segment juveniles) (Byrne 1989, 1991; Hendler 1991). Release of large juveniles is likely to enhance the survival of newly independent juveniles (Hendler 1991). The evolution of an incubatory life history in *O. spinosa* is not associated with release of advanced juveniles. At a disc diameter of 283 μm and with two to three arm segments, juveniles of *O. spinosa* are only slightly larger than the newly settled juveniles of ophiodermatids with pelagic vitellariae (Cisternas & Byrne 2005).

Juveniles of *O. spinosa* have a prominent spinous cover over the disc and the lateral arm spines have thorny projections. These features are not present in adults and are likely to be defensive structures for the juveniles to deter predators during the early benthic stage. Newly settled juveniles of several ophiuroid species have a similar armature, also putatively defensive (Turon et al. 2000; Stöhr 2005; Falkner & Byrne 2006). As seen here in *O. spinosa,* juvenile ophiuroids often look different from the adults and lack the defining morphological characters required for identification to species (Stöhr 2005; Falkner & Byrne 2006).

In the Type II (ophiopluteus+vitellaria) pattern of ophiuroid development, the vitellaria is the metamorphic larval form, contrasting with the Type I pattern (ophiopluteus only), where the ophiopluteus is the metamorphorphic larva (Byrne & Selvakumaraswamy 2002; Cisternas & Byrne 2005; Selvakumaraswamy & Byrne 2006). Development in *O. spinosa* follows the Type II pattern, as characteristic of the Ophiodermatidae (Cisternas & Byrne 2005). A recent study, however, showed that some ophiuroids have features of both patterns in their development, indicating that there may be a continuum of developmental patterns in the Ophiuroidea and that the Type

I–Type II dichotomy may not be appropriate (Selvakumaraswamy & Byrne 2006).

The feeding ophiopluteus larva is considered to be the ancestral larval form for the Ophiuroidea (Strathmann 1978). Several species with non-feeding lecithotrophic development have vestiges of the feeding pluteus in their development, providing a link with an ancestral feeding larva (Selvakumaraswamy & Byrne 2000, 2004). The ciliary bands in reduced ophioplutei and vitellaria larvae are considered to have originated from the ciliary bands of an ancestral feeding ophiopluteus (Mladenov 1985; Selvakumaraswamy & Byrne 2000, 2006; Cisternas & Byrne 2005; Fourgon et al. 2005). The larva of *O. spinosa* is typical of ophiuroid vitellariae in possessing three well-developed ciliary bands and a central region where the juvenile rudiment develops. Vestigial ophiopluteal features were not evident. The ciliary bands of *O. spinosa* are positioned on prominent epithelial elevations, a feature that facilitates efficient swimming (Emlet 1991). In contrast, the short-lived pelagic vitellaria larva of the sympatric ophiodermatid *O. gorgonia* has reduced ciliary bands that are not positioned on prominent epithelial elevations (Cisternas & Byrne 2005). These features are suggested to reflect a decrease in selection for swimming capacity in the larva of *O. gorgonia* and prompt settlement (Cisternas & Byrne 2005). The earliest stage encountered in the bursa of *O. spinosa* was mid-vitellaria and, based on the development in the sympatric species *O. gorgonia,* these larvae are estimated to be 3 d old. Development to the juvenile stage in *O. spinosa* is estimated to take ~5 d.

Ophiuroid bursae are densely ciliated, thin-walled, body-wall invaginations used for respiration and are considered to be preadaptive features for the evolution of brooding (Hendler 1979). In this scenario, the shift to brooding involved a relatively simple change in reproduction: the retention of eggs in the bursa rather than release of eggs through the bursal slit as occurs in broadcast spawners. Several ophiuroids that brood their young have a number of vestigial larval features in their development (Mortensen 1921; Fell 1946; Byrne 1991). Intragonadal larvae occur in *O. hexactis,* and intrabursal larvae have been observed in *A. squamata* and *O. olivacea* (Mortensen 1921; Fell 1946; Byrne 1991). The intragonadal larva in *O. hexactis* develops through a rudimentary pluteus stage with a ciliary band and larval skeleton, and the intrabursal larva in *A. squamata* is minute and highly reduced (Mortensen 1921; Fell 1946). The intrabursal larvae in *O. olivacea* lack ciliary bands, although they can swim due to their ciliary cover (Byrne 1991). In contrast to these three species, the brooded larvae in *O. spinosa* are well developed, and their morphology and behavior are typical of pelagic larvae.

Ophiopeza spinosa is the first brooding ophiuroid known to incubate a pelagic-type larva in its bursae. This larva provides a connection to an ancestral form that had a dispersive life history and indicates that the switch to benthic development by *O. spinosa* may have been an evolutionarily recent change. It also indicates that the loss of pelagic larval characters in the ontogeny of other ophiuroids that brood their young may have occurred following the evolution of intrabursal development. Ciliary bands are not needed in the bursa, as evidenced by the reduced larva in *O. olivacea.* The reduced ciliary bands of the vitellaria in *O. gorgonia,* however, show that morphological features used for larval swimming can be reduced within a planktonic life history (Cisternas & Byrne 2005).

The presence of a functional vitellaria larva and juveniles in the bursae of *O. spinosa* is similar to the observation of functional brachiolaria larvae and juveniles in the gonads of *Cryptasterina* species, viviparous asterinid sea stars that give birth to juveniles (Byrne 2005). Like that seen in *O. spinosa,* the larvae of these asterinids can develop *in vitro* to the juvenile stage with no dependence on extraembryonic nutrition. These observations indicate the potential for a reversal back to a pelagic dispersive life stage by *O. spinosa* and the *Cryptasterina* species. The brooding sea star, *Pteraster militaris,* releases some of its progeny as larvae and retains others to the juvenile stage (McClary & Mladenov 1989). *Pteraster tesselatus* may have made the complete reversal to a pelagic larval stage from a brooded one (McEdward & Janies 1993). *O. spinosa, Cryptasterina* species, and *P. militaris* are thus far the only echinoderms with the potential to both brood and broadcast their young.

Acknowledgments. An Australian Research Council Discovery Grant to M. Byrne and grant from the Australian Geographic Society to T. O'Hara supported this research. P. Selvakumaraswamy, J. Lee, and T. Prowse provided technical assistance. Thanks are due to S. Uthicke and B. Schaffelke for assistance with specimen collection. The Directors and Managers of the Lizard Island Research Station, a facility of the Australian Museum, are thanked for assistance and use of facilities. Two reviewers are thanked for helpful comments.

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