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Reproduction, spawning, and development of 5 ophiuroids from Australia and New Zealand

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Abstract. Reproduction and development in 5 brittle stars: *Ophiactis resiliens, Ophionereis fasciata, Ophiothrix caespitosa, Ophiothrix spongicola,* and *Ophionereis schayeri* were investigated in a series of laboratory spawning and fertilization trials. *Ophiactis resiliens* spawned in 90% of trials, both spontaneously (in response to disturbance) and after temperature and light shock. *Ophiothrix caespitosa* and *Ophiothrix spongicola* spawned in 100% of trials, largely due to spontaneous gamete release. In contrast, *Ophionereis fasciata* and *Ophionereis schayeri* spawned in only 32% and 50% of trials respectively, and only in response to temperature and light shock. All 5 species required an aggregation of males and females for spawning and fertilization. The breeding periods of each species, estimated from the spawning trials, are reported. Eggs of *Ophiactis resiliens, Ophionereis fasciata, Ophiothrix caespitosa,* and *Ophiothrix spongicola* were 83 μm, 99 μm, 105 μm, and 128 μm in diameter, respectively, and all underwent planktotrophic development through an ophiopluteus. Eggs of *Ophionereis schayeri* were 241 μm in diameter and underwent lecithotrophic development through an armless bilateral larva that secondarily transformed into a radial vitellaria. The two *Ophionereis* species, with differing modes of development, provide an ideal opportunity to examine life-history evolution within a clade; however, these species were the most difficult to spawn. *Ophiactis resiliens* and the two *Ophiothrix* species spawned readily when they were visually mature at collection, and are thus useful species for developmental studies.

Additional key words: Echinodermata, *Ophiactis, Ophionereis, Ophiothrix*

Echinoid and asteroid echinoderms are an important resource for developmental biologists because their gametes are readily obtained through use of spawning inducers such as potassium chloride for echinoids and 1-methyladenine for asteroids. In contrast, reliable methods to induce gamete release in ophiuroids, holothuroids, and crinoids are not available (Strathmann 1987) and so development of these echinoderms is less well known. Although numerous attempts have been made, few ophiuroids have been induced to spawn in the laboratory (Hendler 1991). Manipulation of temperature or light, however, has been useful in inducing spawning in several ophiuroids (Stancyk 1973; Heatwole & Stancyk 1982; Yamashita 1983; Hendler 1991; Balser 1998). An increase in cyclic AMP induces maturation of ophiuroid eggs, but use of this compound to obtain eggs for fertilization trials results in abnormal development (Yamashita 1986, 1988).

We report the results of spawning trials in 4 ophiuroids from Australia—*Ophiactis resiliens, Ophiothrix caespitosa, Ophiothrix spongicola,* and *Ophionereis schayeri*—and 1 ophiuroid from New Zealand, *Ophionereis fasciata,* with the aim of identifying reliable spawning methods and assessing the seasons of gamete availability for developmental studies. Although all 4 Australian species are abundant in southeastern Australia (Clark 1946; Baker 1982), their reproduction and life histories have not been recorded. The only previous studies on reproduction for an Australian ophiuroid are for *Ophionereis schayeri,* which spawns lipid-rich eggs (241 μm) and has lecithotrophic development (Moloney & Byrne 1994; Selvakumaraswamy & Byrne 1995, 2000). *Ophionereis fasciata* is common in the intertidal in Northern New Zealand; however, only one study on the general biology and ecology of ophiuroids, including *O. fasciata,* exists (Pentreath 1968). We documented several life-history traits for each species, including spawning behavior, fecundity, fertilization, egg size, and mode of development. The species that spawned most readily were identified for use in future developmental studies.

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Mode of development is described for each species and their potential role for obtaining insights into the evolution of development in ophiuroids is assessed.

Methods

Ophiactis resiliens LYMAN 1879, *Ophiothrix caespitosa* LYMAN 1879, *Ophiothrix spongicola* STIMPSON 1855, and *Ophionereis schayeri* MÜLLER & TROSCHEL 1844 were collected from several sites in New South Wales, Australia—including Sydney, (33°54′S, 151°17′E), Shell Harbor (34°36′S, 150°54′E), and Jervis Bay (35°5′S, 150°43′E). *Ophiothrix spongicola* was found only at sites living on sponge-covered boulders. *Ophiactis resiliens, Ophiothrix caespitosa,* and *Ophionereis schayeri* were found at all sites under boulders. *Ophionereis fasciata* HUTTON 1872 was collected from Echinoderm Reef (36°18′S, 174°48′E), Leigh, New Zealand, and was found under boulders.

Mature specimens of *Ophiactis resiliens, Ophiothrix caespitosa,* and *Ophiothrix spongicola* could be identified in the field by the color of the gonads, which were visible through the body wall on the oral surface. Thus, these species were collected when they were visually mature (Table 1). *Ophionereis schayeri* is mature from January to April (Selvakumaraswamy & Byrne 1995) and specimens were collected during these months. *Ophionereis fasciata* has mature gonads from December through February (Selvakumaraswamy, unpubl. data) and specimens were collected in January. Collection dates and sizes for the 5 species are given in Tables 1 and 2.

Upon collection, ophiuroids were placed in a bucket and transported immediately to the laboratory. No attempt was made to separate males and females. The ophiuroids either spawned spontaneously in response to collection disturbance and heating of water in the collection bucket, or were induced to spawn on the same day as collection. If specimens did not spawn spontaneously after 3 h in the laboratory, temperature and light shock were used to induce spawning. A temperature of 34°C was chosen as the highest temperature for the shock treatment because it usually induced immediate sperm release by the males of all species and a few seconds at this temperature did not cause mortality. For these trials, ≥ 6 (range 6–45) individuals were transferred repeatedly between 34°C and ambient temperature (19–23°C) seawater and then kept in the dark for ~30 min in a container with aerated seawater at ambient temperature. Specimens were then exposed to laboratory light and further disturbed by shaking their container. This temperature shock and light/dark shock was repeated every 30 min for ~2–3 h. No attempt was made to remove cloudy water due to sperm release.

Ophionereis fasciata and *Ophionereis schayeri* were the most difficult species in which to induce spawning. Several other spawning methods were tried, including treatment of ovaries in 1-methyladenine, placing sperm suspensions in dishes containing gravid females, and continuous exposure of males and females together to natural sunlight, but none of these induced spawning. Attempts to fertilize eggs dissected from ripe ovaries of these two species also failed.

The diameter of freshly spawned eggs was measured for all 5 species, whether the eggs were released spontaneously or in response to temperature and light shock. Because females could not be induced to spawn in isolation, the number of eggs spawned per female was estimated by suspending all released eggs in a measuring cylinder and counting the number of eggs in replicate 100-μl aliquots. This figure was then divided by the number of females observed to spawn, but only when it was clear how many females had spawned. Fecundity is reported as the number of eggs released by a female in one spawning episode, not the total number of eggs produced over the breeding season.

The embryos were cultured at 19–23°C in filtered (1 μm) seawater in 500-ml beakers that were kept constantly stirred (Strathmann 1987). Cultures were stocked at densities of 5 embryos/ml. Larvae of *Ophiactis resiliens, Ophiothrix caespitosa,* and *Ophiothrix spongicola* were fed *Chaetoceros calcitrans* (strain CS-178, CSIRO Australia). Larvae of *Ophionereis fasciata* were fed a mixture of *Dunaliella tertiolecta* and *Isochrysis* sp. All 4 species were fed at concentrations of 2×10^4 cells/ml every second day and the seawater in cultures was changed every fourth day through the use of aspiration.

Results

Ophiactis resiliens

Ophiactis resiliens is gonochoric and the sex of mature specimens was identified in the field by the gonad color visible through the body wall, with females possessing pink ovaries and males possessing orange testes. Specimens spawned spontaneously in the collection bucket from 1–3 h after collection. Spawning occurred during the day and after dark. No pumping action or disc elevation was observed during spawning, however the bursal slits of males widened whilst spawning, making the area through which the sperm was released larger than normal. In males, 10 strings of sperm were released, one from each bursal slit. Females also released their eggs in strings that broke up

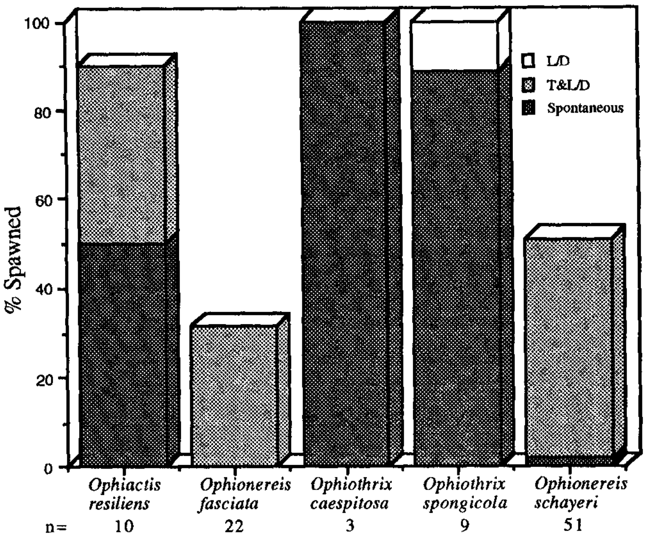


Fig. 1. Percentage of successful spawning trials for each species. The total number of spawning trials carried out for each species (years are pooled) is indicated below each bar. L/D = light/dark shock; T & L/D = temperature and light/dark shock.

within seconds. Gonads examined after spawning contained few gametes, indicating that one spawning event evacuated most of the gametes.

Ophiactis resiliens spawned in May, July, August, September, and November 1997 and August 1999. Out of 10 trials, spawning occurred spontaneously in 5 and after temperature and light shock in 4 (Table 1, Fig. 1). In December 1997, specimens examined were spent, whereas in 1999 all specimens were spent by October. Individual females released a mean of 28,618 eggs (range 24,920–31,500, SE = 2333, n = 3 spawning events each by 1–4 females). The pink, negatively buoyant eggs had a mean diameter of 83 μm (range 77–91 μm, SE = 0.66 μm, n = 3 females).

Ophiactis resiliens was placed in a bucket with *Ophiothrix spongicola* on one occasion and with *Ophiothrix caespitosa* on another. Both species spawned together on both occasions, resulting in competent larvae of both species. Hybrid larvae were not evident.

In *Ophiactis resiliens,* development was planktotrophic via an 8-armed ophiopluteus (Fig. 2). All 4 pairs of arms had formed by 8–10 days. The long posterolateral arms had red pigment along their length.

Table 1. Sampling record and total number of spawning trials for each species. The methods used to induce spawning consisted of: none (spontaneous spawning followed disturbance of collection and transportation), temperature and light/dark shock of both males and females (T & L/D), temperature shock of males and light/dark shock of females (T(M) & L/D(F)), and light/dark shock of both males and females (L/D).

Species	Date of trials	Method	# trials	# trials spawned
Ophiactis resiliens	May–Dec 1997	Spontaneous	4	4
		T & L/D	2	1
		Dissected (Dec)		all spent
	Aug and Oct 1999	Spontaneous	1	1
		T & L/D	3	3
		Dissected (late Oct)		all spent
Ophionereis fasciata	Jan 1997	T & L/D	15	5 no fert
		T & L/D (daylight)	1	0
		T (M) & L/D (F)	3	1 no fert
		L/D	2	0
	Jan 2000	T & L/D	1	1 <5% fert
Ophiothrix caespitosa	July 1992	Spontaneous	2	2
	July and Dec 1997	Spontaneous (July)	1	1
		Dissected (Dec)		mature males only
Ophiothrix spongicola	Apr 1996	Spontaneous	1	1
	Apr–June 1997	Spontaneous	6	6
		L/D	1	1
	Mar and June 1998	Spontaneous	1	1
		Dissected (June)		all spent
Ophionereis schayeri	Dec 1995	T & L/D	5	2
	Jan–Apr and Dec 1996	T & L/D	16	9
	Jan–Apr 1997	T & L/D	24	13
		Spontaneous	1	1
	Jan–Feb 1998	T & L/D	5	2

Plutei developed prominent epaulette-like ciliary ridges after 3–4 weeks and had, at the posterior end of the larval body at the base of the end rods, 3 spheres whose appearance suggested lipid. Settlement occurred after 2 months.

Ophionereis fasciata

Ophionereis fasciata is gonochoric. The color of gonads was generally visible through the body wall, with females bearing pale pink ovaries and males bearing white testes. However, identifying the sex of specimens in the field by color was not always possible. This species proved difficult to spawn and although temperature and light shock induced spawning in 32% of trials, only one trial resulted in any fertilization (Table 1, Fig. 1). In the other 6 trials, the eggs spawned had an intact germinal vesicle (Table 1). To determine if temperature shock was affecting the viability of the eggs, we ran 3 trials in which only males were exposed to temperature shock to induce sperm release (Table 1). These males were then placed into the same container as females and light shock was performed. This method induced spawning in 1 of 3 trials (Table 1), but no fertilization resulted, indicating that the temperature shock probably does not affect egg viability. Spawning in *O. fasciata* occurred during the day and at night, but release of eggs was not directly observed. The pale pink, negatively buoyant eggs had a mean diameter of 99 μm (range 90–110 μm, SE = 1.2 μm, n≥2 females).

In *Ophionereis fasciata,* development was planktotrophic and the larvae were raised to the 4-armed stage, after which they died. By day 5, plutei had developed posterolateral and anterolateral arms, and postoral arm rods were also present (Fig. 2).

Ophiothrix caespitosa

Ophiothrix caespitosa is gonochoric, and the sex of mature specimens was identified in the field by yellow ovaries and white testes, visible through the body wall. Specimens spawned soon after collection in July 1992 and 1997. Two males collected in December 1997 were mature. Specimens were only collected 3 times in July 1992 and 1997, and on each occasion they spawned spontaneously in the collection bucket (Table 1, Fig. 1). Spawning occurred during the day, but release of gametes was not directly observed. The yellow, negatively buoyant eggs had a mean diameter of 105 μm (range 100–110 μm, SE = 1 μm, n = 1 female).

In *Ophiothrix caespitosa,* development was planktotrophic via an 8-armed ophiopluteus (Fig. 2). All 4 pairs of arms had formed after 7 days and plutei had long posterolateral arms. The cultures did not develop beyond 26-day plutei.

Ophiothrix spongicola

Ophiothrix spongicola is gonochoric, and the sex of mature specimens was identified in the field by red ovaries and orange–yellow testes, visible through the body wall. Specimens spawned spontaneously in the collection bucket 3–8 h after collection. Spawning occurred both during the day and after dark. No pumping action or disc elevation was observed during spawning; however, the bursae of males appeared to expand during spawning, releasing 10 strings of sperm, as was observed in *Ophiactis resiliens.* Females released their eggs in strings that broke up within seconds after release. Gonads examined after spawning contained few gametes, indicating that one spawning event evacuated most of the gametes.

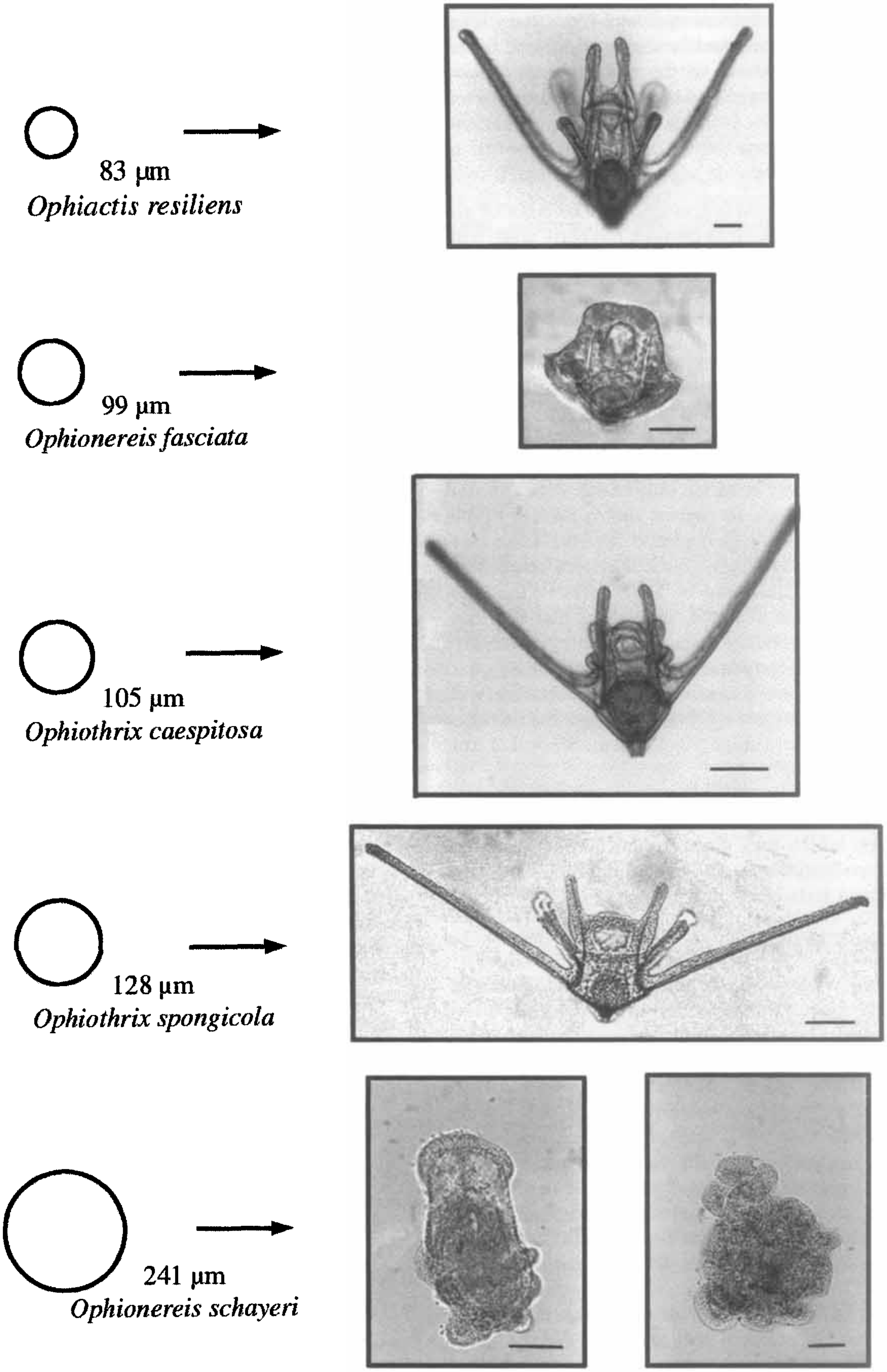
Ophiothrix spongicola spawned in April 1996, April, May, and early June 1997, and late March 1998 (Table 1). The sex of specimens could not be determined by direct observation in early June 1998, and dissection of gonads revealed that specimens were spent. Out of 9 collections, 8 spawned spontaneously, and 1 spawned after light shock (Table 1, Fig. 1). Females of *Ophiothrix spongicola* released a mean of 58,630 eggs (range 30,500–87,500, SE = 10,666, n = 5 spawning events each by 2–4 females). The red, negatively buoyant eggs had a mean diameter of 128 μm (range 122–131 μm, SE = 0.4 μm, n = 3 females).

In one trial, 3 females were kept separate to determine whether the presence of males was essential to induce spawning in females. These females spawned in isolation and their eggs had polar bodies, indicating that at least the first meiotic division had occurred before or during spawning. Several attempts to fertilize these eggs failed. The same females, which were still spawning, were placed in a container with males that subsequently spawned, resulting in 100% fertilization. In another trial one female in a group of 8 spawned before the males, and the eggs had similarly undergone meiosis with an extruded polar body.

In *Ophiothrix spongicola,* development was planktotrophic via an 8-armed ophiopluteus (Fig. 2). All 4 pairs of arms had formed after 4 days and plutei had long posterolateral arms with orange–red pigment along their length. Settlement occurred after one month.

Ophionereis schayeri

Ophionereis schayeri is gonochoric. The color of gonads was generally not visible through the body wall of specimens, and males and females could seldom be


83 µm
Ophiactis resiliens
99 µm
Ophionereis fasciata
105 µm
Ophiothrix caespitosa
128 µm
Ophiothrix spongicola
241 µm
Ophionereis schayeri

distinguished in the field. Therefore, ≥8 specimens were used for spawning trials to increase chances of including some mature males and females. This species was difficult to spawn and spawned spontaneously on only 1 out of 51 attempts (Table 1). Use of temperature and light shock to induce spawning was successful only 51% of the times attempted (n = 51) (Table 1, Fig. 1). Males could be induced to spawn at any time of day whereas females spawned only after dark, between 18:00–2:00 h. Individual males released sperm from the bursae in strings, in short bursts over several hours. In contrast, individual females released their eggs from the bursae in just one burst that lasted a few seconds. The eggs did not seem to be clumped, as they were in *Ophiactis resiliens* and *Ophiothrix spongicola.* Males and females raised the disc slightly off the substrate when spawning and held this posture for a few seconds.

Initial temperature and light shock trials involving placement of males and females in isolation or in pairs never resulted in spawning. Trials were successful only when aggregations of males and females were used in combination with temperature and light shock. Males usually released sperm when exposed to light after being in the dark for ~30 min, in combination with disturbance by shaking the container they were in. In contrast, females did not release eggs until 3–8 h after the start of temperature and light shock. As soon as females started to release eggs, males usually spawned immediately, resulting in fertilization.

Females of *Ophionereis schayeri* released a mean of 6164 eggs (range 1564–9720, SE = 844, n = 9 spawning events each by 1–4 females). The cream-colored, negatively buoyant eggs had a mean diameter of 241 μm (range 231–270 μm, SE = 1.7 μm, n = 4 females). In fertilized eggs, the vitelline space between the oolemma and fertilization envelope was 50 μm wide. Although looked for, polar bodies were never observed.

Ophionereis schayeri spawned from December–February in 1995, January–April in 1996, February–April in 1997, and January–February in 1998.

In *Ophionereis schayeri,* development was planktonic and lecithotrophic. Gastrulae elongated to form a bilateral, barrel-shaped larva after 36 hours. This larva was characterized by a reduced stomodeum, even though it is a non-feeding larva, and by a red-pigmented, ciliated band. After 3–4 days, the larva transformed into a vitellaria with 5–6 ciliated ridges and radial symmetry. Settlement of the metamorphosed juvenile occurred after 6–7 days (Fig. 2).

Discussion

Of the 5 ophiuroid species examined here, the 2 *Ophiothrix* species spawned most readily, releasing gametes spontaneously in response to collection and transportation disturbance in most trials. *Ophiactis resiliens* spawned in most trials, either spontaneously or after temperature and light shock. In contrast, *Ophionereis fasciata* and *Ophionereis schayeri* were difficult to spawn, requiring a combination of temperature and light shock, and even this treatment was often ineffective.

In the laboratory, all 5 species required an aggregation of males and females for spawning and fertilization. Female *Ophionereis schayeri* released eggs only in the presence of sperm. As is typical of ophiuroids, the eggs of *Ophionereis schayeri* are encased in a follicle throughout oogenesis (Byrne 1994; Moloney & Byrne 1994), and the presence of sperm may initiate a hormonal cascade, similar to that documented for asteroids: the follicle cells release a hormone that induces meiosis, ovulation, and spawning (Kanatani 1969; Schroeder 1981). In contrast to *Ophionereis schayeri,* females of *Ophiothrix spongicola* released eggs in the absence of males. These eggs did not fertilize when sperm suspensions were added, but eggs released in the presence of spawning males did fertilize. As these observations were from a single trial, further controlled experiments are needed to determine if the presence of spawning males is essential for fertilization in *Ophiothrix spongicola.* Male pheromones associated with spawning might be required for the final meiotic division to produce fertile eggs. Evidence for the induction of spawning by the release of sperm attractants has been presented for asteroids (Miller 1989).

The presence of polar bodies in the spawned eggs of *Ophiothrix spongicola* prior to fertilization indicates that meiosis occurred in association with ovulation and spawning. This may explain why eggs stripped from the mature ovaries of this and other ophiuroids are not

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Fig. 2. Egg diameter and larval form of 5 ophiuroid species. All images are oriented with anterior towards the top of the page. The 4 species with the smallest eggs develop through 8-armed ophioplutei. The pluteus of *Ophiactis resiliens* is 1 month old, *Ophionereis fasciata* 3.5 days old, *Ophiothrix caespitosa* 9 days old, and *Ophiothrix spongicola* 6 days old. *Ophionereis schayeri,* with the largest eggs, develops through a non-feeding armless larva (left, 3 days old) that later transforms into a vitellaria larva (right, 4 days old), which has radial symmetry. Scale bars, 100 μm.

Table 2. Summary of the general reproductive and developmental characteristics for each species. Spawning was either spontaneous or induced by temperature and light/dark shock (T & L/D). Yes (Y) or no (N) indicates the presence or absence of polar bodies in the fertilized eggs. Mean fecundity is the number of eggs released by one female during one spawning event.

	Disc diam. (mm)	Gonad/gamete color		Spawning season	Method of spawning	Mean egg diam. (µm)	Polar bodies	Mean fecundity	Larval type	Time to settlement
		Female	Male							
Ophiactis resiliens	5–7	pink-red	orange	May–Nov	spontaneous	83	Y	28,618	Ophiopluteus	2 months
Ophionereis fasciata	10–18	pale pink	white	Jan–?	T & L/D	99	?	?	Ophiopluteus	?
Ophiothrix caespitosa	5–7	yellow	white	July–?	spontaneous	105	?	?	Ophiopluteus	>26 days
Ophiothrix spongicola	10–35	red	orange-yellow	Mar–June	spontaneous	128	Y	58,630	Ophiopluteus	1 month
Ophionereis schayeri	13–22	beige	white	Jan–Apr	T & L/D	241	N	6164	Reduced pluteus and vitellaria	6–7 days

fertile (Strathmann 1987; Stewart 1998). Since the other 4 species would not spawn eggs in the absence of sperm, it was not possible to detect whether meiosis occurred during ovulation and spawning. Although searched for, polar bodies were not evident after fertilization in the yolky eggs of *Ophionereis schayeri.*

Most observations of ophiuroid spawning events in situ and in the laboratory have been serendipitous (Mortensen 1921; Hendler 1991). However, temperature and/or light/dark shock has been used to spawn and fertilize eggs of *Ophiolepis elegans, Amphipholis kochii,* and *Ophiopholis aculeata* (Stancyk 1973; Yamashita 1983; Balser 1998). The combination of temperature shock together with light/dark stress used in this study has also been used to induce gamete release in *Ophiarachnella ramsayii* (453 µm diameter eggs) and *Clarkoma pulchra* (282 µm diameter, positively buoyant eggs) from Australia (Selvakumaraswamy, unpubl. obs.). In these trials active sperm were added to the eggs, but fertilization was not successful.

Females of *Ophionereis schayeri* could be induced to spawn only in the late evening or night. Nocturnal spawning has been observed in the field and in the laboratory for several other ophiuroids (Grave 1916; Hendler 1977, 1991; Hendler & Meyer 1982). In contrast, massive spawning by *Ophiactis resiliens, Ophiothrix caespitosa,* and *Ophiothrix spongicola* occurred during the day and night. The disturbance caused by collection of these species, however, was responsible for inducing spontaneous gamete release and thus the timing of spawning in these species was influenced by stress.

Spawning trials indicate that *Ophiactis resiliens* has a breeding season from winter to late spring (May–November). *Ophiothrix spongicola* reproduces from late summer to early winter (March–June), and *Ophiothrix caespitosa* spawns in winter (July). The ease of identification of mature specimens of these species and the success of spawning trials makes them ideal for use in future developmental studies. Extended seasonal sampling of each species, however, is required to further define their reproductive cycles, particularly in the case of *Ophiothrix caespitosa,* for which only 3 trials were conducted, all within July. The two sympatric *Ophiothrix* species with planktotrophic development may avoid hybridization by temporal differences in spawning periods. Further examination of each species' reproductive cycle together with laboratory based hybridization experiments are required to test this suggestion.

Examination of the gonads of *Ophionereis fasciata* over a one-year period indicated that mature gametes were present during December–March (Selvakumaraswamy, unpubl. data). Spawning was induced only once, in late January, despite efforts to obtain gametes earlier in the month. Future spawning induction trials for this species from January through March may be more successful. *Ophionereis schayeri* was induced to spawn from December/January–April. This species has mature gametes from December–April, although a few late vitellogenic oocytes remain in the ovaries through August (Selvakumaraswamy & Byrne 1995). This species did not spawn in the laboratory after April, suggesting that unspawned oocytes remaining in the ovary after April were relict eggs bound for resorption.

The fecundity estimates for *Ophiactis resiliens* and *Ophiothrix spongicola* are lower than those estimated for other ophiuroids with small eggs and planktotrophic development (range: 2.5×10^5–10^6 eggs; Hendler 1975, 1991). Our estimates are based on single spawning events and are likely to underestimate total egg production over the breeding season. When fecundity is assessed with respect to adult body size, however, the small size of *Ophiactis resiliens* (5–7 mm disc diameter), is similar to that of viviparous species that brood their young and generally have large eggs and low fecundities (Mortensen 1920; Hendler 1975; Strathmann et al. 1984; Hendler & Littman 1986; Byrne 1991). The comparatively low fecundity of *Ophiactis resiliens* (28,618 eggs) may reflect its small size. However, this explanation cannot be envoked for *Ophiothrix spongicola,* which is a relatively large ophiuroid (10–35 mm disc diameter, fecundity 58, 630 eggs) and would be expected to have a fecundity more typical of ophiuroids with planktotrophic development. The fecundity estimate for *Ophionereis schayeri* (6164 eggs, 13–22 mm disc diameter) is typical for ophiuroids with intermediate-sized eggs and lecithotrophic development (Hendler 1975, 1991).

The 4 planktotrophic species had small egg sizes (83–128 μm diameter) whereas *Ophionereis schayeri,* with lecithotrophic development, had large eggs (241 μm diameter) (Fig. 2, Table 2). Egg diameter of *Ophionereis schayeri* was previously reported as 200 μm diameter in ovary sections (Selvakumaraswamy & Byrne 1995); this was an underestimate due to shrinkage of tissue from fixation. A strong correlation between egg size and developmental mode has long been recognized in echinoderms (Thorson 1950; Hendler 1975; Emlet et al. 1981). Echinoid, asteroid, and holothuroid egg size distributions are bimodal (Emlet et al. 1981; Sewell & Young 1997), a trend used to suggest a strong selection for either small eggs (<200 μm) and planktotrophic development or larger eggs (generally >280 μm) and lecithotrophic development (Emlet et al. 1981).

In contrast to the model proposed by Vance (1973), that selection drives egg sizes towards the extremes, McEdward (1997) has shown that selection can in fact favor intermediate-sized eggs in marine invertebrates. The egg size distribution for ophiuroids is indeed unimodal, with 53% of species possessing eggs of intermediate size, 150–350 μm diameter (Sewell & Young 1997; present study). This suggests that ophiuroids with intermediate-sized eggs may have features of development that are transitional between the extremes of planktotrophy and lecithotrophy. Indeed, although the development of *Ophionereis schayeri* is lecithotrophic, the larvae retain a continuous ciliated band, larval skeleton, and larval gut (Selvakumaraswamy & Byrne 2000). The ability to obtain ophiuroid eggs of a range of sizes, albeit with some effort, may be used to extend our knowledge of ophiuroid development. Emphasis on species with intermediate-sized eggs may lead to the discovery of a range of developmental modes and provide insights into the evolution of development in the Ophiuroidea.

One of the most interesting findings from this study was the discovery of 2 *Ophionereis* species with different modes of development. *Ophionereis fasciata* from New Zealand develops via an ophiopluteus, whereas *Ophionereis schayeri* from Australia develops via a non-feeding armless larva that transforms into a vitellaria. If planktotrophy is considered the ancestral state for echinoderms (Strathmann 1974), then these species provide an ideal opportunity to investigate the evolution of non-feeding development within an ophiuroid clade. Unfortunately, these 2 species proved most difficult to spawn, making such evolutionary comparisons a challenge.

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