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RESEARCH ARTICLE

Uncommon diversity in developmental mode and larval form in the genus *Macrophiothrix* (Echinodermata: Ophiuroidea)

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Abstract Development mode in the ophiuroid genus *Macrophiothrix* includes an unusual diversity of planktonic larval forms and feeding types. The modes of development for seven congeners that coexist in coral reef habitats at Lizard Island, Australia were compared using larvae generated from crosses over several reproductive seasons from 1999 to 2003. Three species (*Macrophiothrix koehleri* Clark, *Macrophiothrix longipeda* Lamarck, *Macrophiothrix lorioli* Clark) develop from small eggs (<170 μm) into typical obligately feeding planktonic (planktotrophic) pluteus larvae with four larval arm pairs. The remaining four species develop from larger eggs (≥230 μm) into either facultatively-feeding or non-feeding (lecithotrophic) larval forms. The facultative planktotroph (*Macrophiothrix rhabdota* Clark) retains the ability to digest and benefit from food but does not require particulate food to complete metamorphosis. Among the lecithotrophic species, *Macrophiothrix caenosa* Hoggett retains the pluteus morphology with four pairs of larval arms, but is incapable of feeding, depending instead on maternal provisions for larval development. The remaining two lecithotrophs have simplified larval morphologies with only a single pair of full length (*Macrophiothrix nereidina* Lamarck) or highly reduced (*Macrophiothrix belli* Doderlein) larval arms and no functional mouth or gut. This genus includes the first example of facultative planktotrophy in ophiuroids, the first example in echinoderms of a complete pluteus morphology retained by a lecithotrophic larva, and three degrees of morphological simplification among lecithotrophic larval forms. Egg volume varies 20-fold among species and is related to variation in feeding mode, larval form, and development time, as predicted for the transition from planktotrophic to lecithotrophic development.

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Introduction

To understand patterns of life-history variation, marine invertebrate biologists have steadily accumulated information about taxonomic diversity in development mode and larval form (Young 1990; Levin and Bridges 1995). These comparative data have challenged the view that early development is conservative and suggested that a major component of functional diversity is found at early life-history stages (Strathmann 1988). When coupled with phylogenetic information, they also provide the means to test predictions and assumptions about how life histories evolve (Strathmann and Eernisse 1994; Hart 2000; Levitan 2000). Such analyses benefit from the combination of phylogenetic resolution and developmental diversity among closely related taxa; extensive examples of such data sets, however, are relatively rare (Jeffery and Swalla 1992; Kohn and Perron 1994; Hart et al. 1997; Jeffery and Emlet 2003).

One widespread life-history pattern among marine invertebrates involves the relationship between egg size and mode of development. In echinoderms, for example, species with small eggs (<200 μm diameter) tend to produce morphologically-complex, feeding (planktotrophic) larvae with extended larval periods, while species with larger eggs tend to produce non-feeding (lecithotrophic) larvae with simple morphologies and abbreviated larval periods (Emlet et al. 1987; Hendler 1991; Smiley et al. 1991). Planktotrophic development from small eggs is thought to be ancestral and non-feeding development to have arisen many times independently (Strathmann 1985; Wray 1996). The evolutionary transition between these modes is hypothesized to involve increases in egg size that lead through a series of intermediate larval forms, including a facultative-planktotrophic larva that can benefit from feeding but does not require particulate food to complete metamorphosis (Wray 1996). Although an explicit model for this transition has been proposed (Wray 1996), intermediate forms are rare (Perron 1981; Kempf and Hadfield 1985; Emlet 1986; Kempf and Todd 1989; Hart 1996b) and few examples exist of broad intrageneric diversity—including both highly-derived and intermediate forms—that could be used to address predictions of the model.

In addition to its relationship with development mode, the relationship between egg size and the size, shape, and growth of larvae is important for understanding changes in larval form during the hypothesized transition from feeding to non-feeding development. The larval morphometrics of several species of echinoderms with pluteus larval forms have been reported (McEdward 1986a; McEdward and Herrera 1999; Morgan and Jangoux 2005) but these studies have been limited to species with the typical, ancestral development mode, obligate planktotrophy.

Here we describe and compare development for seven ophiuroid echinoderms in the genus *Macrophiothrix*. In contrast with more extensive data on echinoids and asteroids, larval development has been described for fewer than 5% of the 2000+ ophiuroid species (Hendler 1975; Sewell and Young 1997). To facilitate further analysis of evolutionary changes in mode of development (Podolsky and Allen, in preparation) here we document differences in egg size, development time, larval form, and larval nutritional requirements in a diverse genus for which phylogenetic relationships have been recently inferred (Hart and Podolsky 2005).

Materials and methods

Adult collection

Individuals of the seven species (*Macrophiothrix koehleri* Clark, *Macrophiothrix longipeda* Lamarck, *Macrophiothrix lorioli* Clark, *Macrophiothrix rhabdota* Clark, *Macrophiothrix caenosa* Hoggett, *Macrophiothrix nereidina* Lamarck, *Macrophiothrix belli* Doderlein) described here were collected by SCUBA and snorkeling in shallow waters (<15 m) on coral reefs surrounding Lizard Island, Queensland, Australia (S14°40′12″, E145°28′12″). Species co-occurred in fields of coral rubble, although typically only a single individual was found under a given piece of rubble. After collection, adults were maintained in flow-through aquaria at the Lizard Island Research Station (LIRS). Species identifications are based on Hoggett (1990, 1991) and were verified on location by that author. Data on egg size, spawning, and larval culture were accumulated during parts of reproductive seasons (November to March) from 1999 to 2003 (Tables 1, 2).

Spawning and larval culture

The sex of *Macrophiothrix* spp. adults in ripe condition is indicated by the color of gonads visible through the

Table 1 Summary of egg, embryo, and larval trait averages for seven *Macrophiothrix* species

Species	Egg diameter (±SE) (μm)	First cell cycle (min)	Hatching (h)	Larval form (no. of arms)	Feeding mode
M. koehleri	147 (±2.2)	25–30	8	Pluteus (8)	Planktotroph
M. longipeda	155 (±2.9)	25	8	Pluteus (8)	Planktotroph
M. lorioli	166 (±3.3)	25–30	7.5–8	Pluteus (8)	Planktotroph
M. rhabdota	230 (±2.5)	40	9	Pluteus (8)	Facultative planktotroph
M. caenosa	242 (±3.8)	30	7.5	Pluteus (8)	Lecithotroph
M. nereidina	266 (±5.9)	30	7–7.5	Reduced (2)	Lecithotroph
M. belli	406 (±11.6)	25	6	Reduced (2)	Lecithotroph

First cell cycle is the time between first appearances of first and second cell divisions among embryos in culture at 28–29°C; hatching times similarly represent time of first appearance of hatched embryos in culture. Definitions and sample sizes in text

Table 2 Summary of trait averages at metamorphosis for seven *Macrophiothrix* species under different feeding conditions

Species	Food	Start of metamorphosis (d)	Time to settlement(d)	Juvenile disk diameter(μm)
M. koehleri	D	–	32	294
M. longipeda	D	>>14	–	–
M. lorioli	D	–	23	201
M. rhabdota	D	4.5	5.75	327
	I	6.25	7.25	298
	U	6.25	7.25	238
M. caenosa	D	4	5.25	326
	U	4	5.25	314
M. nereidina	U	2	3.25	275
M. belli	U	2	3.25	342

Metamorphosis and settlement times are medians for all larvae that underwent metamorphosis. Disk diameters are averages measured on day of settlement. Definitions, sample sizes, and estimates of variance are reported in text. Cultures of *M. caenosa* reared with *D. tertiolecta* did not appear to ingest the alga

D Dunaliella tertiolecta, *I Isochrysis galbana*, *U* unfed

ventral body wall; testes appear cream, and ovaries vary among species from orange to pink, red, or purple. In *M. belli*, the ovaries are grayish and can be distinguished from the whitish testes only under magnification. Ripe males of all species spawned following coelomic injection with a trace volume (<<0.1 ml) of 0.5 M KCl; sperm were pipetted from bursal slits and stored cool until use. Methods for inducing spawning in female ophiuroids are not consistent among species (Strathmann 1987). We attempted several methods to induce spawning or egg maturation, including: repeated temperature shock, light shock, and water changes (Selvakumaraswamy and Byrne 2000a); rapid water flow; exposure to conspecific gametes; coelomic injection of 1-methyladenine (Sigma) or crude extracts of radial nerves from *Macrophiothrix* spp. or the seastar *Acanthaster planci*, prepared according to Strathmann (1987); and exposure of dissected eggs and ovaries to cAMP, caffeine, or theophylline (Yamashita 1988). Measurements of unfertilized (spawned or dissected) eggs are reported as the mean diameter ± SE among females, not including jelly coats. Approximately 20 eggs were measured female^{-1}.

Containers used for fertilization and larval culture were maintained at ambient seawater salinity (~35 ppt) and temperatures (28–29°C) in a circulating heated water tray. Seawater was 0.45-μm filtered (FSW) before use. Spawned eggs were transferred to large containers and dilute conspecific sperm were added to test samples every 15–30 min to detect the optimal time for inseminating whole clutches. A pilot study determined that fertilizability of eggs initially increased but then declined within 2 h of spawning although sperm could be stored concentrated at 4°C for several hours. Throughout this paper, the term "culture" refers to larvae established from one male–female cross, and "containers" represent subsets of those larvae reared separately. Replicate containers were established for most cultures, but some were lost to mortality during development.

Early development

For each container we measured the time from insemination to first cleavage, to second cleavage, and to hatching from the vitelline membrane. Every 10 or 15 min starting 30 min post-insemination, we collected 50–100 eggs from the bottom of each container and rapidly scored the proportion of eggs that had begun first or second cleavage. Every 30 or 60 min starting 6 h post-insemination, we stirred containers, collected 50–100 suspended embryos, and scored the percentage that had hatched. For each of these measures, we report the first time point at which the first embryos had completed cleavage or hatching. At hatching, cultures were partitioned into 1–l containers for rearing at densities of no more than 1 larva ml^{-1}.

Containers were cleaned every other day by aspirating water through a submerged 75-μm filter, transferring larvae to a new container, and adding fresh FSW. Food was added to containers after cleaning, except for cultures of *M. nereidina, M. belli* and unfed containers of *M. caenosa* and *M. rhabdota*. Unless specified, larvae were fed the unicellular alga *Dunaliella tertiolecta* (CSIRO strain CS-175) at initial densities of 7.5 cells μl^{-1}. In one culture of *M. rhabdota*, two additional containers received a different alga, *Isochrysis* sp., at the same density (both algae supplied by DPI, Cairns, Australia). Algae were cultured at room temperature in filtered, autoclaved seawater enriched with a modified Guillard's f/2 medium (Florida Aqua Farms, Inc.) and were centrifuged and resuspended in fresh seawater

before use. Larvae and food were kept suspended by stirring containers gently with paddles at 7 strokes min^{-1} (Strathmann 1987).

Larval morphometrics

Larvae were removed at irregular intervals from containers and fixed briefly for morphological measurements in 2% formalin buffered with $CaCO_3$. The pluteus larval form gains its shape from an internal calcite skeleton that projects the body wall into a set of arms, which support a narrow, continuous ciliated band that is used in swimming and feeding. The fully developed pluteus skeleton includes a pair of body rods and four pairs of arm rods (Fig. 1a). Using a compound microscope, camera lucida drawings were made of 11 landmarks on the larval body, allowing measurement of five skeletal elements on the left side of the body [posterolateral arm rod (PL), anterolateral arm rod (AL), postoral arm rod (PO), posterodorsal arm rod (PD), and body rod (BR)], one soft-tissue body length (BL), and stomach width (SW). Five or ten larvae per container were measured at each time point. Measurements were calculated using digitized *x* and *y* coordinates from drawings and *z* coordinates recorded at the time of drawing using a rotary encoder (Ledex Corp.) coupled to the fine focus of the microscope (McEdward 1985). Because the node connecting the PL and BR, which form a continuous axis, could not be visualized through the opaque tissue of *M. nereidina* embryos, in order to compare growth of this arm among species we report the sum of the two skeletal rods. BR growth is negligible during development (see Results), so PL arm growth accounts for all of the change in the sum PL + BR. All measurements of larval arm and BLs are reported as means ± SE.

Cultures were checked every 12–24 h to record metamorphosis and settlement. Larvae were scored as beginning metamorphosis when juvenile skeletal elements were first visualized under polarized light, and as settled when they had completely resorbed three pairs of larval arms and had dropped to the bottom of the container. Settlement occurred in culture containers without the addition of substrate or additional cues. Several metamorphs were collected on the day of settlement, and disk diameter was measured from digital images or camera lucida drawings by outlining the disk as a pentagon, with the corners at the center of each interambulacrum, and then calculating the average of the five diameters bisecting the pentagon.

Results

Spawning and fertilization

The seven Macrophiothix species described are dioecious; of several hundred ripe or partly ripe brittlestars examined, only four were hermaphrodites (one *M. caenosa*, one *M. nereidina*, and two *M. lorioli*). Fertilization and development occurred externally in all species without brooding or other forms of parental care.

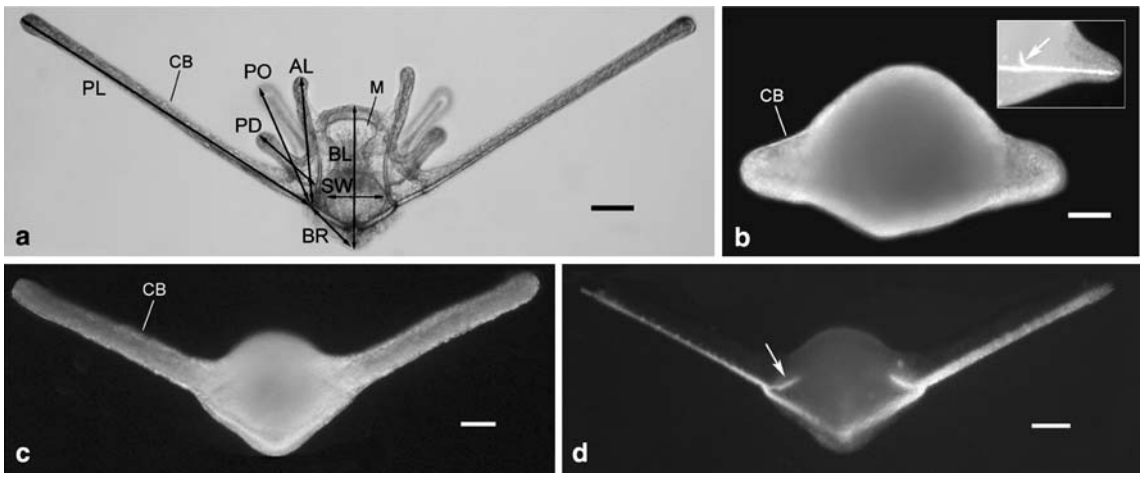


Fig. 1 **a** *Macrophiothrix longipeda.* Four day-old pluteus larva showing soft-tissue and skeletal landmarks used for measurements of larval form. Although some landmarks are out of the plane of focus in this image, measurements reported were reconstructed in three dimensions as described in the text. **b** *M. belli*, darkfield image of 2-day old larva. *Inset* shows internal skeletal rods under polarized light with larva slightly compressed under coverslip. **c** *M. nereidina*, darkfield and **d** polarized-light darkfield images of 1.5-day old larva showing body and skeletal rods. *Arrows* in **b** and **d** indicate vestigial skeletal rods. *PL* posterolateral arm, *AL* anterolateral arm, *PO* postoral arm, *PD* posterodorsal arm, *BR* body rod, *BL* body length, *SW* stomach width, *M* mouth, *CB* ciliated band. *Scale bar* (all images other than inset) = 0.1 mm

Females sometimes spawned spontaneously within a few hours of collection or after combinations of repeated temperature shock, light shock, and water changes, but these methods were not as reliable as for other local ophiuroids (cf. Selvakumaraswamy and Byrne 2000a). No other method tried (see Materials and methods) yielded fertilizable eggs. Ripe males of a given species were not always available when females spawned spontaneously, and spawned eggs did not always fertilize. As a result, we could not obtain replicate cultures for some species, although data among containers within a culture and across replicate cultures for other species were highly repeatable. In addition to the seven species for which we gained developmental data, females of three additional *Macrophiothrix* species (*M. demessa* Lyman, *M. leucosticha* Hoggett, and *M. propinqua* Lyman) failed to spawn.

Spawning events were directly observed on a few occasions. In some cases females released tens to hundreds of thousands of eggs in a brief pulse (<10 s) while elevating the disk above the substrate and twisting or thrashing from side to side. In other cases females elevated the disk without much further motion and released eggs more slowly over several minutes.

In all seven species, (a) fertilized eggs developed a fertilization envelope within 2 min and underwent radial cleavage (Fig. 2), (b) embryos hatched from the fertilization envelope at the swimming blastula stage, and (c) larvae underwent Type 1 metamorphosis (Mladenov 1985), in which three arm pairs, if present, were resorbed, but the PL arms were retained through metamorphosis and ultimately cast off by the settled juvenile. Descriptions of further development below are for individual species in order of increasing egg size.

Larval form and development mode

Macrophiothrix koehleri

Eggs were negatively buoyant and 146.7 ± 2.2 μm in diameter (n = 10 females). First cleavage began after 40–50 min, second cleavage after 70–75 min, and hatching 8 h after insemination for three cultures. After hatching, larvae developed skeletal rods in a pattern typical of planktotrophic ophiopluteus larvae (Strathmann 1987). A single pair of BRs, which support the soft tissue of the body, developed first in association with a pair of PL arms at the anterior end of the BR, followed closely by initiation of AL and post-oral (PO) arm rods at the PL-BR node, and then by PD arm rods at a proximal position along the AL rods (Fig. 1a). Arms grew simultaneously once initiated. A ciliated band formed a continuous loop along the sides of each arm and between adjacent arms. The eight-arm pluteus larva was largely transparent except for reddish pigment on the distal portion of the PL arms and at the base of the larval body.

Starting at the two-arm stage, the pluteus had a functional mouth, esophagus, stomach, and intestine and fed readily on unicellular algae. Larvae were obligate planktotrophs and did not develop past 18 days in culture without food. Fed larvae underwent metamorphosis after 30–42 days in culture, with a median time of 32 days. Settled juveniles had disks that measured 294.9 ± 7.7 μm in diameter (n = 4 juveniles).

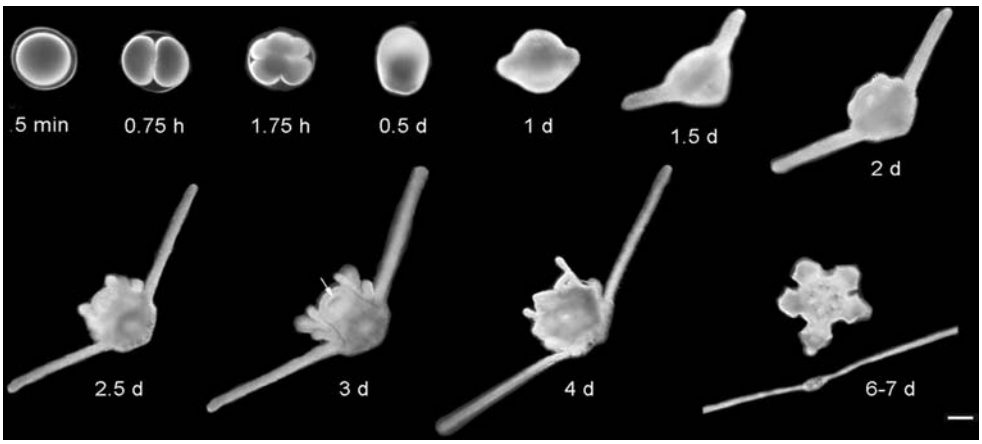


Fig. 2 *Macrophiothrix caenosa*. Development from fertilized egg through metamorphosis and settlement. Embryos display radial cleavage and hatch at the swimming blastula stage. The first pair of larval arms, as well as an indentation at the normal site of the larval mouth, are visible by 1 day. By 2.5 days larvae have developed all four arm pairs. Larvae begin Type 1 metamorphosis around 4 days, releasing a pair of PL arms at settlement after 5.25 days. *Arrow* shows position of non-functional mouth indentation on oral field. *Scale bar* = 0.1 mm

Macrophiothrix longipeda

Eggs were negatively buoyant and 155.0 ± 2.9 μm in diameter (n = 10 females). First cleavage began after 60 min, second cleavage after 85 min, and hatching after 8 h post-insemination for two cultures. Pluteus larvae were similar in form to those of *M. koehleri* except that the reddish body pigment apparent in *M. koehleri* and other *Macrophiothrix* species was sparse in *M. longipeda*. Plutei of *M. longipeda* (Fig. 1a) were obligately planktotrophic and did not develop past 10 days in unfed cultures. Because cultures were started near the end of a field season, we were not able to rear larvae through metamorphosis, but after 2 weeks larvae had not developed juvenile structures.

Macrophiothrix lorioli

Eggs were negatively buoyant and 166.6 ± 3.3 μm in diameter (n = 13 females). First cleavage began after 40–50 min, second cleavage after 60–80 min, and hatching after 7.5–8 h for three cultures. Pluteus larvae were similar in form but larger than those of the other two small-egg species (Fig. 3). Larvae did not develop past 18 days without particulate food. Only one culture was reared to settlement, which occurred after 18–29 days, with a median time to settlement of 23 days (n = 33 juveniles). Disk size for two juveniles whose settlement dates were uncertain was 200.9 ± 10.9 μm.

Macrophiothrix rhabdota

Eggs were negatively buoyant and 229.6 ± 2.5 μm in diameter (n = 10 females). For two replicate containers of a single culture, first cleavage began after 50 min, second cleavage after 90 min, and hatching after 9 h post-insemination. Larvae had a pluteus form, but the larval body was more opaque than in species with smaller eggs. Embryos quickly began to develop internal skeletal rods and within 3 days possessed four pairs of larval arms. Larvae of *M. rhabdota* were similar in size to those of *M. lorioli*, but larger than those of the other two planktotrophic species (Fig. 3). They possessed a functional gut and readily ingested algal cells, though larvae in unfed cultures also completed metamorphosis, indicating that facultative planktotrophy was the developmental mode.

Larvae of *M. rhabdota* reared under different feeding conditions varied in time to and size at metamorphosis as well as survival to metamorphosis. Larvae in all feeding treatments showed signs of metamorphosis by 5 days. Unfed larvae in two replicate containers had identical median settlement times of 7.25 days (n = 62 and 64 larvae) and mean disk diameters of 240.0 ± 4.1 and 235.8 ± 10.5 μm (n = 10 from each container; SE for container means). Larvae in two replicate containers fed *Isochrysis galbana* also had median times to settlement of 7.25 days (n = 173 and 127) but newly settled juveniles were larger, with disk diameters of 298.6 ± 4.4 and 297.5 ± 8.3 μm in two replicate containers (n = 5 per container). Larvae in two replicate containers fed *D. tertiolecta* settled within a 12-h period between 5.5 and 6 days (n = 192 and 101) and were larger than in the other two treatments, with disk diameters of 342.7 ± 14.4 and 311.5 ± 15.0 μm (n = 5 and 3, respectively). Survival percentage was 45.3 ± 0.1% in unfed containers, 80.4 ± 6.2% in containers with *I. galbana*, and 100% in containers with *D. tertiolecta*.

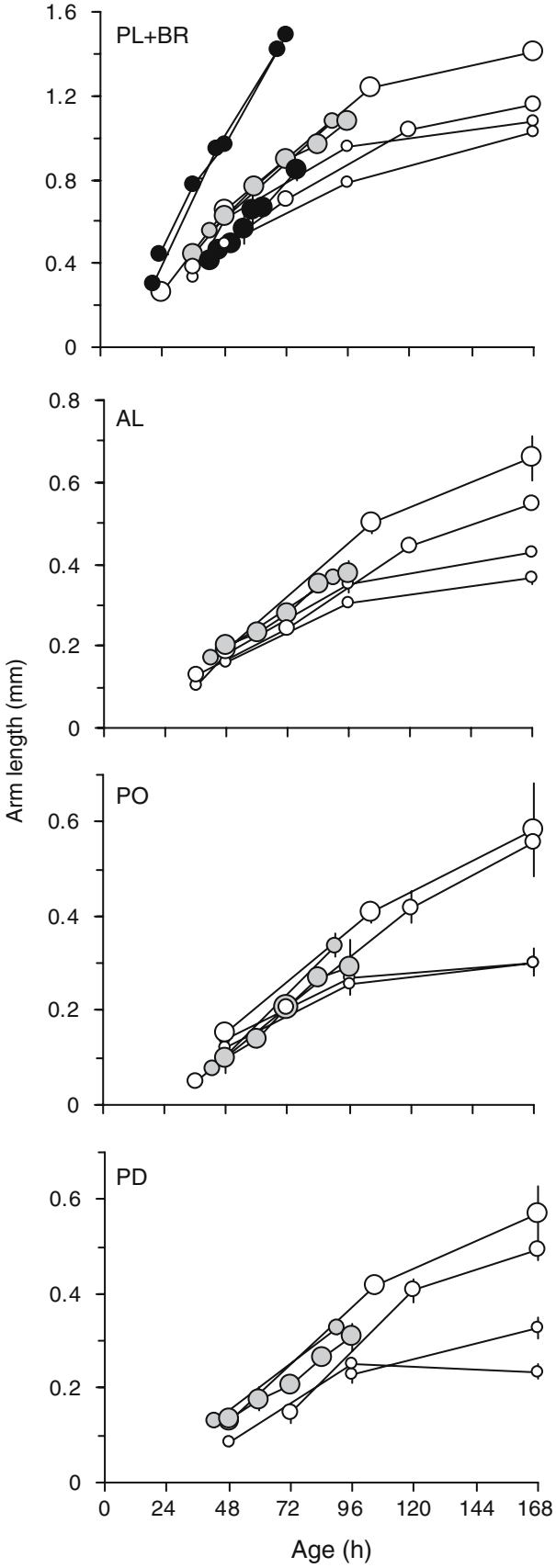
Macrophiothrix caenosa

Eggs were negatively buoyant and 241.9 ± 3.8 μm in diameter (n = 7 females). For two replicate containers from a single culture, first cleavage began after 45 min, second cleavage after 75 min, and hatching after 7.5 h post-insemination.

Larvae of *M. caenosa* developed features of a planktotrophic pluteus including all four arm pairs, a ciliated band, an indentation at the site of the mouth and anus, and outlines of a digestive system. The four pairs of larval arms grew at rates similar to the four species with plutei capable of feeding (Fig. 3). Internal features were difficult to examine through the larval body, which was significantly more opaque than in smaller-egg species (Fig. 2), and we could not determine if the gut was complete without sectioning. However, when compressed under a cover slip, the stomach regions of larvae from cultures with added food were not observed to contain algal cells under transmitted light or epifluorescence. In addition, the presence of particulate food in larval cultures had no effect on time to or size at metamorphosis. Fed and unfed larvae both began to show signs of metamorphosis (juvenile skeletal elements) by 4 days, and settled within a 12-h period between 5 and 5.5 days. Newly settled juveniles had disk diameters of 313.9 ± 5 μm in unfed cultures, and 323.9 ± 5.2 μm in larval cultures where *D. tertiolecta* was added (n = 5 per container; all containers from a single culture). The absence of ingested food in the body and lack of substantial difference in time to or size at metamorphosis from containers with and without food indicate lecithotrophy as the likely developmental mode.

Macrophiothrix nereidina

Eggs were negatively buoyant and 265.9 ± 5.9 μm in diameter (n = 11 females). First cleavage began after 40 min, second cleavage after 70 min, and hatching



◀ **Fig. 3** Growth of four larval arms for seven *Macrophiothrix* species. Measurements after 1 week (not shown) for the three species with longer development times tended to plateau and become more variable. *Symbols* correspond to species in the following order of increasing egg size: three obligate planktotrophs (*Macrophiothrix koehleri*, *M. longipeda*, *Macrophiothrix lorioli*; small, medium, and large *open circles*, respectively), two transitional forms (*Macrophiothrix rhabdota* and *M. caenosa*; medium and large *shaded circles*, respectively) and two non-pluteus lecithotrophs (*M. nereidina* and *M. belli*; medium and large *filled circles*, respectively). Each *line* represents a single male–female cross, with five to ten larvae measured at each time point. Standard *error bars* (most smaller than *symbols*) are for larvae pooled across containers. Note differences in scale among arms. *PL + BR* posterolateral arm L arm plus body rod, *AL* anterolateral arm, *PO* postoral arm, *PD* posterodorsal arm

after 7–7.5 h for two cultures. Embryos were opaque and heavily pigmented, but began to develop skeletal BRs within 24 h. After 36 h larvae had developed a prominent pair of PL arms (Fig. 1c). A pair of developing AL skeletal rods was visible under polarized light (Fig. 1d), but these arm rods did not lengthen to extend arms from the larval body. No other skeletal rods formed, and there were no signs of a mouth or gut. Juvenile skeletal elements and other signs of metamorphosis appeared by 2 days and larvae settled and cast off the PL arms within a 12-h period 3.5–4 days after insemination. Newly metamorphosed juveniles had mean disk diameters of 266.3 ± 6.9 for one culture and 283.9 ± 8.1 μm for a second (n = 5 each culture). Similar measures taken approximately 24 h before settlement, however, found disk diameters of 331.4 ± 5.4 and 321.9 ± 4.0 (n = 5 each culture), respectively, suggesting that disk size may change substantially around the time of settlement.

Macrophiothrix belli

Eggs were 406.0 ± 11.6 μm in diameter (n = 5 females) and, unlike in the other six species, positively buoyant. For a single culture derived from a spontaneous spawning event where the time of insemination was not recorded precisely, second cleavage began about 25 min after first cleavage, and hatching began approximately 6 h after insemination. The large embryos were opaque, but skeletal rods were visible under polarized light within 24 h. As in *M. nereidina*, larvae formed BRs and PL arms. Under polarized light they also showed evidence of vestigial AL arm rods that did not reach the body wall (Fig. 1b). No other arms formed during larval development, and there were no signs of a digestive system. Metamorphosis began after approximately 2 days, and settlement began around 3 days. At settlement, juveniles had a mean disk diameter of 342.8 ± 17.1 μm (n = 4).

Larval growth

Both the rate and duration of arm growth contributed to interspecific differences in the ontogeny of larval form (Fig. 3). Species that metamorphosed within 10 days (*M. belli*, *M. nereidina, M. caenosa*, and *M. rhabdota*) maintained a constant rate of PL arm growth during their brief development, whereas PL arm growth in species with smaller eggs and longer development (*M. lorioli, M. longipeda, M. koehleri*) began to plateau. PL arms grew at the fastest rate and to the greatest length in *M. nereidina*, the species with the second largest egg size, and were slower growing and shorter in *M. koehleri* and *M. longipeda*, the species with the smallest egg sizes (Fig. 3). Growth rate of PL arms was similar in *M. caenosa*, *M. rhabdota*, and *M. lorioli*, but growth was truncated by an earlier metamorphosis in the former two species. AL and PD arms followed the same relative growth rate pattern among species. Growth rates of PO arms were similar, except that the slower growth rates for *M. koehleri* distinguished it from the other four species. Arm growth rates were unaffected by the presence of external food for *M. rhabdota* and *M. caenosa*, the two species with intermediate egg sizes that completed metamorphosis in unfed cultures (Fig. 4).

Three body size measures–BR length, BL, and SW–provided somewhat different pictures of species differences in growth (Fig. 5). Interspecific differences in BL support the idea that larger eggs produce larger embryos that grow at a faster rate before the onset of feeding (Fig. 5). As seen in patterns of arm growth,

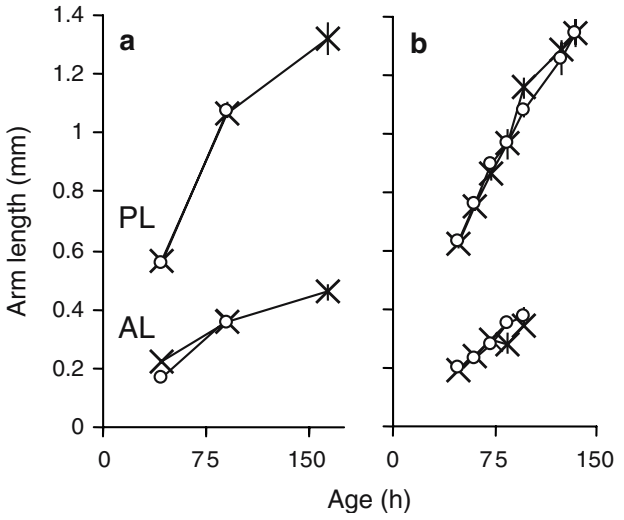


Fig. 4 Growth of *PL* and anterolateral (*AL*) arms for larvae in fed (*open circles*) and unfed (*cross symbols*) containers of **a** *M. rhabdota* and **b** *M. caenosa*. Each pair of *lines* from a single male–female cross, with *error bars* showing SE among container means

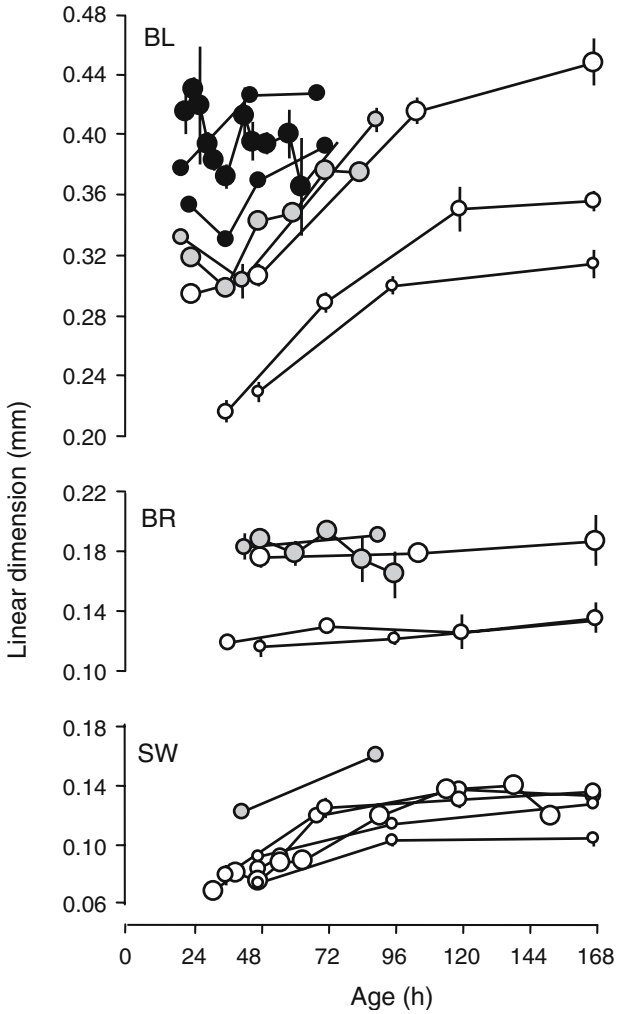


Fig. 5 Growth of larval body features (*BR* body rod, *BL* body length, *SW* stomach width), for seven *Macrophiothrix* species. *Broken axes* are shown on the same absolute scale. *Symbols* correspond to species in the following order of increasing egg size: three planktotrophs (*M. koehleri*, *M. longipeda*, *M. lorioli*; small, medium, and large *open circles*), two transitional pluteus forms (*M. rhabdota* and *M. caenosa*; medium and large *shaded circles*) and two non-pluteus lecithotrophs (*M. nereidina* and *M. belli*; medium and large *filled circles*). Each *line* represents measures a single male–female cross, with five to ten larvae measured at each time point. Standard *error bars* (most smaller than *symbols*) are for larvae pooled across containers. Measurements of BR were unavailable for *M. nereidina* and *M. belli* because BR was not distinguishable from PL. SW measurements were unavailable for the same two species and *M. caenosa*, all of which lacked a functional digestive system

M. lorioli larvae started at a larger BL than the two species with smaller eggs and grew at a rate comparable to the larger-egg species. Species differences in BR were similar, but this skeletal rod did not change substantially during development and was therefore a poor indicator of body growth (Fig. 5). Initial SW and growth of SW were similar among small-egg species, but SW was about 50% greater in *M. rhabdota* than in

the three small-egg species. Among body size measures, SW showed the greatest relative increases, nearly doubling in some cultures over the first few days of planktonic feeding (Fig. 5).

Discussion

The diversity of planktonic developmental modes within *Macrophiothrix* is more extensive than is known from within the best-studied genera of ophiuroid echinoderms, from across the class Ophiuroidea, or even from genera of the more extensively studied echinoids and asteroids (McEdward and Miner 2001). In echinoids, for example, transitional and highly derived forms have been described only from separate genera (Wray 1996). However, the range of egg diameters among the seven *Macrophiothrix* species (147–406 μm) is not unusually large; at least four other ophiuroid genera include egg diameters with ranges >300 μm (*Amphiura*, 100–1,000 μm; *Ophiacantha*, 400–750 μm; *Ophiomyxa*: 250–880 μm; *Ophiura*: 90–400 μm) (Hendler 1991). The present study and other recent work (Selvakumaraswamy and Byrne 2004) suggest that developmental diversity within this class may ultimately prove useful for comparative life-history analyses as have patterns in more thoroughly studied classes (Arndt et al. 1996; Wray 1996; Hart et al. 1997).

Currently, three modes of development are recognized for ophiuroids: planktotrophic development, abbreviated lecithotrophic development, and direct development (Hendler 1975; Mladenov 1979; see Strathmann 1987 for an alternative classification). Planktotrophic species produce small diameter (<200 μm) eggs that undergo planktonic development as pluteus larvae for extended periods (19–216 days). Abbreviated development occurs in species with intermediate egg sizes (130–350 μm) and reduced times to metamorphosis (3–5 days), and typically involves a planktonic larval form with a reduced number of larval arms or a barrel shaped, armless vitellaria larva, which may represent an extreme reduction of pluteus form (Fenaux 1963; Stancyk 1973; Hendler 1975, 1977, 1982; Mladenov 1979; Komatsu and Shosaku 1993; Selvakumaraswamy and Byrne 2000b). Direct developers include species with a broad range of egg sizes (100–1,000 μm) and development times and offspring are often brooded within the adult bursae.

In the present study, three *Macrophiothrix* species are clearly identifiable as obligate planktotrophic developers. *M. koehleri*, *M. longipeda*, and *M. lorioli* develop from small eggs and spend several weeks in the plankton as feeding pluteus larvae prior to settlement. At the other end of the spectrum, *M. nereidina* and *M. belli* are both abbreviated developers that arise from large eggs and develop into non-feeding larvae with one arm pair over short development times. *M. belli* significantly extends the upper limit of egg sizes (from 350 to 406 μm) reported for abbreviated developers (Hendler 1991), especially those with vestiges of pluteus morphology. Other ophiuroid species with two-arm larval forms most closely resembling those of *M. nereidina* and *M. belli* are *Amphiura chiajei* and *Ophiothrix oerstedi*, which have egg diameters of 140 and 252 μm, respectively (Fenaux 1963; Hendler 1975; Mladenov 1979). Fell (1945) reported that *Ophiura affinis* also develops from a two-arm pluteus, but did not report an egg size. More extreme simplification of the pluteus morphology has been described in *Amphioplus abditus* (Hendler 1977), *Ophionereis annulata* (Hendler 1982), and *Ophionereis schayeri* (Selvakumaraswamy and Byrne 2000b), which have egg sizes of 132, 240, and 241 μm, respectively, and retain only vestigial skeletal elements within the larval body. All other ophiuroids with abbreviated development and eggs larger than 250 μm develop via a barrel shaped vitellaria larva (Grave 1916; Mortensen 1938; Hendler 1979; Komatsu and Shosaku 1993). It is therefore unusual that both species of *Macrophiothrix* with eggs >250 μm in diameter developed via a reduced pluteus with no vitellaria stage. Given that reduced plutei can develop from large eggs (e.g., *M. belli* at 406 μm) and that vitellaria can develop from eggs as small as 200 μm (e.g., Ophionereis squamulosa, Mortensen 1921), egg size does not dictate the larval form of lecithotrophic ophiuroids.

Two species in the present study, *M. rhabdota* and *M. caenosa*, have modes of development that do not fit traditional categories. One of those modes, facultative planktotrophy, was defined by Chia (1974) by the presence of a functional digestive system in larvae that do not require particulate food to complete metamorphosis. We found that *M. rhabdota* larvae can ingest phytoplankton cells and benefit from larval feeding, but can reach metamorphosis in the absence of particulate food, albeit in smaller numbers and at smaller size. Although facultative planktotrophy is predicted as a stage in the evolutionary transition from planktotrophic plutei to simplified, lecithotrophic larvae (Wray 1996), *M. rhabdota* is the first documented case of facultative planktotrophy in ophiuroids (McEdward and Miner 2001). Similar to *M. rhabdota*, *M. caenosa* develops the full pluteus morphology and completes metamorphosis without particulate food, but does not appear capable of algal ingestion or digestion or of benefiting from the presence of food. We conclude that

M. caenosa has an obligately lecithotrophic pluteus larva, a second mode of development that is predicted by theory (Wray 1996), but has not been previously described in echinoderms. The reduced, non-feeding larval form of the echinoid *Phyllacanthus imperialis* is similar to that of *M. caenosa* but is simplified to a greater extent, lacking two of the four pairs of larval arms (Olson et al. 1993). The larval condition of *M. caenosa* also resembles the persistence of feeding structures in some non-feeding polychaete (Pernet 2003) and mollusc (Kempf and Todd 1989) larvae.

Facultative planktotrophy has been described in only seven other animal species, including two echinoid echinoderms, four molluscs, and two amphibians (Perron 1981; Kempf and Hadfield 1985; Emlet 1986; Crump 1989; Kempf and Todd 1989; Hart 1996b; Doughty 2002). In another mollusc, *Tritonia hombergi*, larvae can ingest algae but appear to be incapable of digesting it (Kempf and Todd 1989). Other reports describe species with brief pelagic stages that may ingest planktonic food as larvae, but it is unclear whether feeding is necessary to complete development. These species include the abalone *Haliotis tuberculata* (Crofts 1937), the bivalve *Pandora inaequivalvis* (Allen 1961), the snapping shrimp *Alpheus heterochaelis* (Knowlton 1973), and several other species of polychaetes, prosobranch molluscs, and opisthobranch molluscs (Thorson 1950).

The benefits of larval feeding for *M. rhabdota* included increased survivorship, development rate, and metamorph size. These benefits differed from those measured for the two echinoid species with facultative planktotrophy. For both *Clypeaster rosaceus* and *Brisaster latifrons*, feeding as larvae had little effect on larval survival or growth, but in the former it enhanced juvenile size, growth, and survival (Emlet 1986), while in the latter it produced juveniles that were slightly larger (Hart 1996b). Effects of feeding in *M. rhabdota* were more similar to those in the nudibranch mollusc *Adalaria proxima*, which metamorphosed earlier and in greater numbers, and had greater mass and higher energy content at metamorphosis, when fed as larvae (Kempf and Todd 1989). In another nudibranch, *Phestilla sibogae*, larval feeding extended the length of the competent period (Kempf and Hadfield 1985) and increased larval survivorship and mass, juvenile survivorship and mass, and adult mass and reproductive output (Miller 1993). Similarly, in the cone snail *Conus pennaceus*, feeding increased both larval and juvenile survival when metamorphosis was artificially delayed relative to unfed larvae (Perron 1981). In contrast, in the bivalve *Codakia orbicularis*, although individuals took phytoplankton into the gut, larval development and survivorship were unaffected by the presence of food (Berg and Alatalo 1982; Alatalo et al. 1984). This diverse set of taxa and results indicate that food typically provides a measurable benefit to facultative planktotrophs, but that effects on early life-history processes vary among the few species with this uncommon mode of development.

In echinoid echinoderms, an experimental reduction of egg size results in smaller larval body size, shorter larval arms, and a shorter ciliated band (Sinervo and McEdward 1988; McEdward 1996), characteristics that correlate with a lower maximum rate of food clearance from suspension (Hart 1996a). Our comparative results for *Macrophiothrix* spp., as well as comparative work in echinoids (McEdward 1986b), similarly reflect a positive relationship between egg size and larval body size. In addition, for six of the seven *Macrophiothrix* species, the rate of PL arm growth was positively related to egg size. The one exception was *M. belli*, which underwent exceptionally rapid development, but whose PL arms grew at a relatively slow rate and to a relatively short length. In the five species that developed all four arm pairs there was also an association between egg size and the initial growth rate of each arm pair.

The pattern of arm growth in these *Macrophiothrix* spp. shows both similarities with and differences from those of other ophiuroid and echinoid plutei. For example, PL arm growth follows a similar early trajectory of rapid growth and a subsequent plateau in the planktotrophic ophiuroid *Ophiothrix fragilis*, which develops over 3–4 weeks in the plankton from 100 μm-diameter eggs (MacBride 1907; Morgan and Jangoux 2005). However, a second spurt of arm growth closer to the time of metamorphosis seen in both *O. fragilis* (Morgan and Jangoux 2005) and echinoplutei (McEdward 1986a), was not observed in *Macrophiothrix* spp. This latter period of arm growth has been suggested to relate to the use of PL arms for navigation near the time of settlement. If so, it is unclear why the larvae of *Macrophiothrix* spp. lack this second phase.

The reduced arm number of *M. nereidina* and *M. belli*, associated with the absence of feeding, could also have a significant impact on swimming abilities (Emlet 1994). In larvae of *M. nereidina*, the decline in swimming capacity could be compensated for by growth of exceptionally long PL arms. One model of pluteus swimming suggests that investment in a single pair of long PL arms could actually increase swimming speed and weight-carrying capacity relative to multiple arm pairs, especially given their low angle of elevation (Grunbaum and Strathmann 2003). The PL arms of ophioplutei, which are typically longer than those of

echinoplutei, can become especially long in species that resorb other arm pairs before settlement (Type I metamorphosis, Strathmann 1987; Hendler 1991). In contrast, *M. belli*, which had the largest egg size, had the shortest PL arms at settlement. We hypothesize that reduced reliance on PL arms for swimming by larvae of *M. belli* is associated with its positive buoyancy throughout most of development, which could reduce the importance of a ciliated band for remaining suspended (Kelman and Emlet 1999). The rapid emergence of PL arms close to settlement—and relatively late in development for its egg size—could reflect the need for *M. belli* to swim downward, to compensate for the developmental loss of buoyancy or to aid navigation among potential settlement sites.

In the genus *Macrophiothrix*, egg size appears to be related both to larval body size and to size at metamorphosis. Independence of juvenile size from egg size has been established for a much larger set of echinoid echinoderms (Levitan 2000), while asteroids appear to show a positive relationship between the two (Emlet et al. 1987). Because only a handful of values for ophiuroid disk size at metamorphosis have been published, it is difficult to establish a clear relationship between egg size and juvenile size.

In addition, we found an inverse relationship among *Macrophiothrix* species between egg size and time to metamorphosis; the latter ranged over more than an order of magnitude. Species with small eggs required several weeks of feeding to complete development, while the four species with larger eggs metamorphosed within 1 week and in order of decreasing egg size. As in other invertebrates with planktonic larvae, development time can have important consequences for a number of other time-dependent processes, including planktonic mortality (Rumrill 1990) dispersal distance (Strathmann 1974; Scheltema 1986), geographic range (Strathmann 1985; Emlet 1995) and genetic exchange among populations (McMillan et al. 1992).

McEdward and Miner (2001) cited the paucity of knowledge of both phylogenetics and developmental diversity as factors limiting the analysis and understanding of life cycle evolution in echinoderms and other marine invertebrate taxa. With development described for only 7 of >40 species in the genus, *Macrophiothrix* already provides an unusually diverse collection of development modes and a promising opportunity for further study of evolutionary relationships involving developmental processes and life-history patterns (Jeffery and Swalla 1992; Kohn and Perron 1994; Hart et al. 1997; Hart 2000). We are currently using phylogenetic (Hart and Podolsky 2005) and developmental information for this genus to analyze how differences in egg size are related to stepwise changes in larval form and function (Wray 1996) during the widespread and ecologically important transition from planktotrophy to lecithotrophy.

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