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Sexual reproduction, larval development and benthic planulae of the solitary coral *Monomyces rubrum* (Scleractinia: Anthozoa)

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Abstract The reproductive biology of the solitary ahermatypic coral *Monomyces rubrum* was studied in northeastern New Zealand between January 1996 and January 1998. The period of oogenesis lasted around 11 months, from late January to December, while spermatogenesis was more rapid, starting in late August and culminating in a spawning period in early December. Reproduction commenced at a polyp size of around 1,000 mm^3 (5–6 years old) and the maximum estimated fecundity of the largest corals (7,000 mm^3) was no more than 200 eggs. Oocytes were probably fertilized while within the mesentery and were shed into the coelenteron where they developed, via a solid blastula stage, for approximately 1 month. Planulae were relatively large, 3–4 mm in length and 1–2 mm diameter at the time of release, and crawled or swam immediately to the substratum. Peaks of planula shedding were semi-lunar in January 1997, but only one peak was observed in January 1998. The production of a few large rapidly settling larvae by this member of the family Flabellidae is consistent with the trend for solitary short-lived corals from other families to brood larvae rather than spawn gametes.

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Introduction

Reproductive and larval behaviour of solitary scleractinians has been studied for over 100 years (Gardiner 1902; Tranter et al. 1982). Early investigations focused primarily on brooding corals, thus promoting the misconception that brooding was the main form of larval development (Fadlallah 1983). More recent work has shown broadcast spawning to predominate (Harrison and Wallace 1990). In the past 15 years there have been few studies of the reproductive and larval behaviour of solitary corals (Beauchamp 1993), and most of the literature covering this subject focuses on colonial scleractinians (Willis et al. 1985; Babcock et al. 1986; Szmant 1986). It is apparent that sufficient comparative information on the reproductive and larval behaviour for solitary corals is lacking in comparison with colonial forms. Reproduction and recruitment are also central components of life history and a broader understanding of these traits will help provide a basis for comparisons of life history adaptations within the Scleractinia and between colonial and solitary forms of organisms in general.

Among solitary scleractinians various reproductive behaviours can be found, ranging from year-round brooding of larvae as seen in *Balanophyllia elegans* (Fadlallah and Pearse 1982a), to brief annual spawning periods as seen in *Paracyathus stearnsii* (Fadlallah and Pearse 1982b). Solitary corals such as *Caryophyllia smithi* are known to release large brooded larvae (Tranter et al. 1982) while *Heteropsammia cochlea* releases very numerous small eggs (Fisk 1981). It has even been speculated that *Flabellum rubrum* (former synonym of *Monomyces rubrum*) spawned once and then died (Gardiner 1902). Thus within the solitary corals there is a need for further information on which to base any attempts to generalize patterns of reproductive traits, larval behaviour and life histories. Broadly speaking, comparisons of life history within the Scleractinia have supported the suggestion that smaller, presumably

shorter-lived, species of corals tend to be more likely to produce larger gametes or brood larvae (Szmant 1986; Babcock 1991). There are exceptions to this, however, for example *Heterocyathus* and *Heteropsammia* spawn numerous small gametes (Fisk 1981). Solitary corals form one extreme of this continuum in terms of their size and life span. Among other marine invertebrates with both solitary and colonial forms, the opposite trends seem to be found, with solitary forms tending to release externally developing gametes (Jackson 1985).

The overall aim of this study was to examine the reproductive biology of *Monomyces rubrum* so that it could be compared with other solitary and colonial scleractinians. We provide information on size at first reproduction, fecundity, and annual cycles of gametogenesis and larval release for this shallow water solitary coral.

Materials and methods

Field work and collections were carried out on subtidal rocky reefs along the northeast coast of New Zealand, adjacent to the Leigh Marine Laboratory (174°46′ to 49′E: 36°16′N). *Monomyces rubrum* was conspicuous in caves, crevices, overhangs and under rock formations at depths of 5–20 m. The epithecae of individual *M. rubrum* were frequently overgrown with sponges, bryozoans, tunicates, brachiopods and other sessile invertebrates along with various types of encrusting calcareous algae. *M. rubrum* was formerly known as *Flabellum rubrum* and has recently been placed in the genus *Monomyces* by Cairns (1994). The coralla are solitary conical to cylindrical in form, and usually laterally compressed. They are always attached and when dislodged from the substratum do not appear to survive long.

Gametogenic cycles

Observations of reproductive status of freshly dissected polyps were made during the summer of 1993–1994 in order to roughly establish reproductive timing. Further observations of gamete developmental stage were made using freshly dissected polyps over the summer of 1997–1998. Regular monthly samples were taken by SCUBA from January 1996 to August 1997. From 20 to 60 solitary corals were collected per sample and preserved in 10% (v/v) concentrated formalin in sea-water for at least 5 days. Each individual coral was measured (height, greatest diameter and orthogonal diameter) to estimate its volume, assuming that their shape was approximately cylindrical. The corals were then placed into 70 ml jars and decalcified in a solution of 10% (v/v) concentrated HCl in distilled water. Each decalcified polyp was washed in water and stored in 70% ethanol. Polyps were then divided into two equal sections, one for dissection and the other for histology. Sexes are separate in *M. rubrum* and for each sample date, 10 males and 10 females were examined. In female polyps, oocytes are found in a single row immediately behind the mesenterial filament. The number of oocytes were counted for 10 randomly selected mesenterial filaments, and the longest diameter and the orthogonal diameter of each oocyte were then measured by ocular micrometer under a dissecting microscope. The mean radius was used to calculate the volume of each oocyte according to the formula for the volume of a sphere and these were then averaged to obtain a mean oocyte volume for each coral. Then the mean oocyte volume for each coral was averaged to obtain a mean oocyte volume for each sample date.

Using the same dissection methods as for the female corals, the length, width and thickness of testes in male corals were measured to obtain volumes. The volumes of testes were calculated according to the formula for a cuboid (volume = length × width × thickness). Mean testes volume for each sample date was determined using the same procedure as described for oocytes.

For histological analysis, polyps were dehydrated through an ethanol series, cleared in xylol, and embedded in Paraplast. Samples were sectioned at 4–8 μm, stained with Mallory's Trichrome, and examined for the presence of developing gametes.

Size-specific fecundity

Corals of a range of sizes, including both the largest and the smallest individuals available, were sampled haphazardly at the main study site as well as at several sites on reefs at the northeastern entrance to Leigh Harbour to establish how fecundity of individuals changed with size. The volumes of the corals collected ($n = 124$) were measured using the methods described above prior to placing them into bleach to decompose the organic material. Within the corallite is a series of vertically radiating skeletal septa that alternate with the mesenteries. The number of primary and secondary septa, corresponding to the number of mesenteries, for each coral was counted and recorded to obtain an estimate of the number of mesenteries an individual of a given size would possess.

Dissections of preserved corals collected in December 1996 ($n = 68$) were made to obtain an average number of oocytes per mesentery for each individual. The fecundity and septal density data were combined to provide a means of relating fecundity to volume for all corals dissected.

Fertilization experiment

Mature oocytes and testes were dissected from adults of *M. rubrum* on 8 December 1997. Twenty oocytes still bound within the mesogleal lining and 20 free oocytes that had been removed from the mesentery were placed into a deep-well dissection dish containing fresh seawater. Mature testes were placed in the same dish, squashed and broken apart, then stirred for 1 min to distribute the gametes. Oocytes were checked for fertilization every hour for 24 h.

Periodicity of larval release

Female corals planulated freely in laboratory conditions. In January 1996, 100 corals were haphazardly collected and placed in an aquarium with running seawater at ambient temperature and photoperiod. These corals were maintained throughout the year as a source of larvae for use in future experiments. Another 57 corals were maintained in individual flow-through containers. These corals were also supplied with flowing seawater, at ambient temperature and photoperiod. Water flowed from the individual containers into 70 ml jars fitted with 250 μm plankton mesh that allowed water to pass and larvae to be trapped. The number of larvae released by individual females was recorded 3 times a day, approximately 0800, 1300 and 1800 hours from 1 January to 1 April 1997. These corals were replaced on 24 December 1997 with freshly collected corals collected from the field and records were kept from 1 January to 31 January 1998 in the same fashion as for early 1997. From these observations the number of larvae released per individual was measured and the frequency of larval release obtained.

Results

Oogenesis

The earliest stages of oocyte development were found in late January/early February 1997. Histological preparations revealed primordial oocytes developing within the mesogleal layer of the mesenteries in samples from

January and February 1997. These oocytes were small, approximately 0.01 $mm^3 \pm 0.006$, and were presumably from females that had already released larvae in January and started a new oogenic cycle. At that time oocytes were undeveloped with scattered yolk granules and uncondensed nuclei and were surrounded by a thick layer of endodermal tissue. A synchronous annual cycle of oocyte growth was found from polyp dissections (Fig. 1).

Between one and seven oocytes were seen attached to each mesentery and positioned distally with respect to the mesenterial filament. Oocytes began to increase in volume in May 1996, and by August–September had a volume of 1 ± 0.5 mm^3 (approximately 0.5 mm diameter) and with an increased density of yolk granules and a more condensed, centrally located nucleus. Oocytes reached a mean volume of 4.2 mm^3 (2 ± 0.5 mm diameter) in October 1996. Oocytes maintained this volume until December 1996, which coincided with peak testis volume (see below Fig. 2).

Oocytes matured between October and December with a decreased amount of surrounding endodermal tissue. Nuclei of mature oocytes became concave and were located on the extreme periphery of the oocyte. There was a sharp decline in oocyte volume in early December, coinciding with the appearance of developing larvae in the coelenteron. No developing oogonia were found within polyps containing embryos and conversely no developing embryos were seen in polyps containing oogonia. From April to August 1997, oocytes once more increased in size as they entered another growth cycle (Fig. 1).

During the early stages of gametogenesis of *Monomyces rubrum*, gonads from different individuals could be found at different stages of development. As gametogenesis proceeded developmental stages became progressively more synchronized within the sample populations and growth rates of oocytes (and testes) seemed to accelerate as temperatures began to increase during spring.

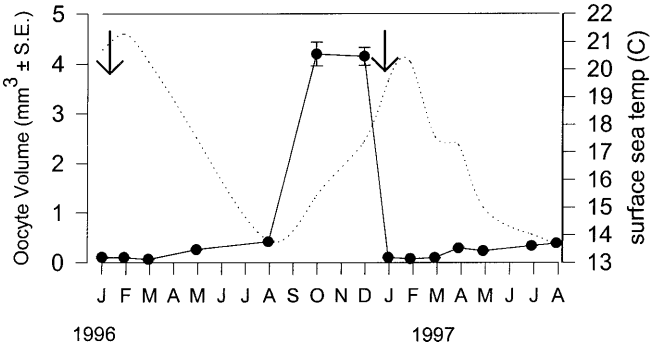

Fig. 1 Oogenic cycle of *Monomyces rubrum*. Values are mean oocyte volumes based on dissections of preserved specimens. *Arrows* indicate periods when brooded larvae were present. Seawater temperatures (*dotted line*) are monthly averages from daily thermometer readings of surface seawater samples taken at 0900 hours at the shore adjacent to the Leigh Marine Laboratory

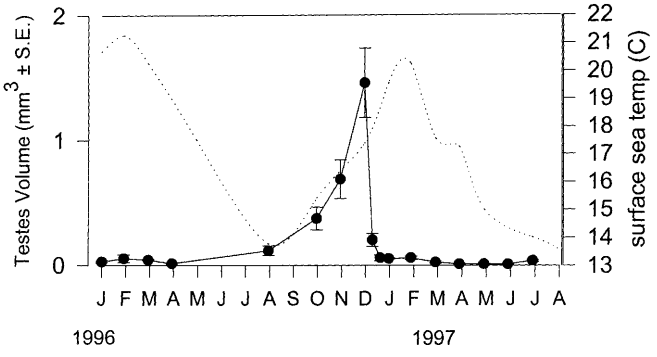

Fig. 2 Spermatogenic cycle of *M. rubrum*. Values are mean testes volumes based on dissections of preserved specimens. Seawater temperatures (*dotted line*) are monthly averages from daily thermometer readings of surface seawater samples taken at 0900 hours at the shore adjacent to the Leigh Marine Laboratory

Spermatogenesis

M. rubrum displayed an annual cycle of testis growth and released gametes in the summer (Fig. 2). Results from dissections showed testes started growth in August 1996, increased in size through October and November and reached their maximum volume on 6 December, with testes size reaching a mean volume of 1.3 mm^3. By 16 December, the testes showed a dramatic decrease in size, indicating a spawning event, and by 26 December the testes were spent with few residual sperm bundles present. This data was consistent with observations made in 1993 when motile, mature sperm were observed on 7 December (Table 1). Changes in sperm morphology were closely related to changes in testis size. Histological analysis showed that from January to August, the gonads were small, less than 0.5 mm thick, with primary germ cells seen developing within the endoderm and mesogleal lining of the gonads. At the end of this period, spermatogonia aggregated in spherical clusters within the gonads but were maintained by the mesogleal lining. The number and thickness (> 0.7 mm) of clusters increased during the gonadal growth season (September–December) prior to spawning.

Spermatogenesis was synchronous within and among clusters and gonads of the same polyp. Squash preparations of live material were examined from early October through the end of November 1997 (Table 1) and by early October primordial germ cells or spermatogonia were evident. The first sign of spermatids with uncondensed spherical heads (7 ± 1 μm), no tail and conspicuous nucleus was observed on 20 October 1997. Samples from 27 October contained spermatids as well as spermatozoa with uncondensed heads, a flagellum and slight movement. The first sign of condensing spermatozoa was seen in samples from 19 November. At that time, sperm showed increased motility with further development of the flagellum and sperm-heads showed signs of elongation. Samples from the last week of

Table 1 Descriptions of spermatogenic changes in *Monomyces rubrum* for 1993 and 1997. Stages are characterized by the following: *spermatogonia* primordial germ cells; *spermatocytes* round with developing nucleus; *spermatid* developing flagellum with conspicuous nucleus; *spermatozoa* mature sperm with fully developed flagellum, condensed head, and elongated anterior process. Lunar phases: 1993, three-quarter moon 6 December; 1997, first-quarter moon 7 December

Date	Spermatogenic stage
1993–1994	
9 September 1993	Spermatogonia
8 October 1993	Spermatogonia
9 November 1993	Spermatids
16 November 1993	Spermatids/early spermatozoa
7 December 1993	Spermatozoa
5 January 1994	Sperm absent
1997–1998	
8 October 1997	Spermatogonia
20 October 1997	Spermatogonia/spermatids
27 October 1997	Spermatids
19 November 1997	Early spermatozoa/spermatozoa heads starting to condense
22 November 1997	Early spermatozoa
25 November 1997	Early spermatozoa and first sign of fully developed spermatozoa
30 November 1997	Early spermatozoa/spermatozoa
1 December 1997	Mature spermatozoa
5 December 1997	Mature spermatozoa
8 December 1997	Spermatozoa/half-spent gonads
9 December 1997	Sperm absent/residual loculi still present

November revealed mature motile spermatozoa, with fully developed flagellum (4 ± 1 μm). These mature spermatozoa had developed long pointed processes at the tip of their heads. Testes appeared full of spermatozoa on 5 December, but many testes appeared spent or half-full when examined on 8 December. Gonads were fully spent by 9 December 1997. The date of the first-quarter moon was 7 December 1997.

Sex ratio and size-specific fecundity

The sex ratio of *M. rubrum* did not deviate from 1:1 (158 males and 133 females, $\chi^2 = 0.9088$, $df = 1$, $P = 0.3404$) among all the individuals dissected in monthly samples. The number of septa was described by the regression: $septa = 20.28\ 5\ volume + 8.27$ [Fig. 3, ANOVA, $F_{(1),1,123} = 230.69$, $P < < 0.001$, $r^2 = 0.6541$]. Fecundity showed a positive linear correlation with individual volume [Fig. 4, ANOVA, $F_{(1),1,66} = 44.046$, $P < < 0.001$, $r^2 = 0.4003$]. An estimation of fecundity for a coral of any given size was obtained using the equation: $fecundity = 0.0193\ 5\ volume + 26.013$. Based on this formula the largest coral collected (7,000 mm^3) would have produced less than 200 eggs. However, even the smallest corals sampled (~1,000 mm^3) contained some eggs. Fecundity at this size was low, between 17 and 56 eggs per coral or an average of between 1 and 2 eggs per mesentery (Fig. 4), suggesting that the size at first reproduction was not much smaller than this.

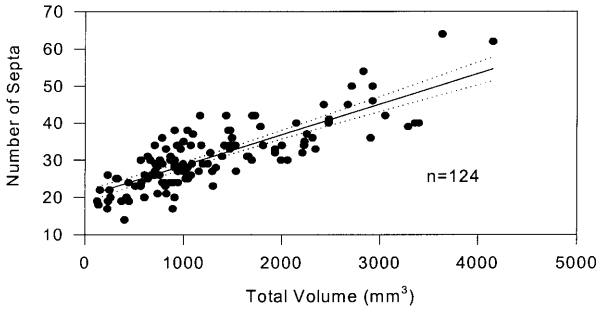

Fig. 3 Corallum volume and number of septa for *M. rubrum*. Total number of septa for coralla of a given volume. Regression line ± 95% confidence interval

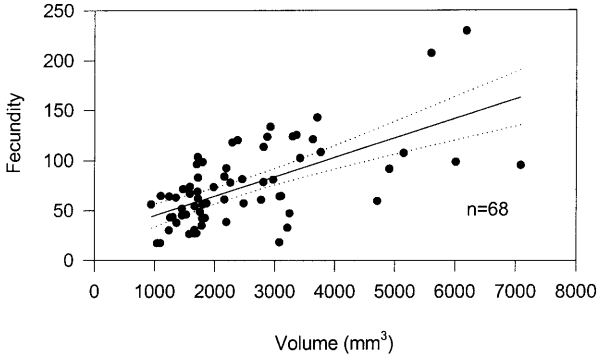

Fig. 4 Polyp fecundity and corallum size in *M. rubrum*. Fecundity is expressed as total number of eggs per individual, based on mean number of eggs per septa and mean number of septa for a corallum of a given volume. Regression line ± 95% confidence interval

Fertilization experiment

Of those oocytes dissected from polyps and mixed with spermatozoa, fertilization was seen only in mesogleal bound oocytes. Five of these oocytes divided to the two-cell stage over a period of 5 h. Once it was evident that division had commenced, oocytes were shed from the mesogleal lining. Only one oocyte developed to the four-cell stage, which took 18 h.

Embryogenesis and larval development

The earliest developmental stages seen in histological sections were four-cell embryos from samples taken on 6 December 1996. The timing of this sample corresponded with the time of peak testis volume. Developing planulae were first seen within 16 December samples, and fully developed larvae were not seen until 5 January 1997. All mature oocytes were found bound within mesenteries, while embryos showing early stages of division (Fig. 5a) were only found within the coelenteron in the proximity of their original mesogleal lamella (Fig. 5b). Initial cleavage followed an irregular radial pattern (Fig. 5b). Gastrulation appeared to be by delamination rather than invagination since development showed no evidence of a hollow blastula stage. Embryogenesis was

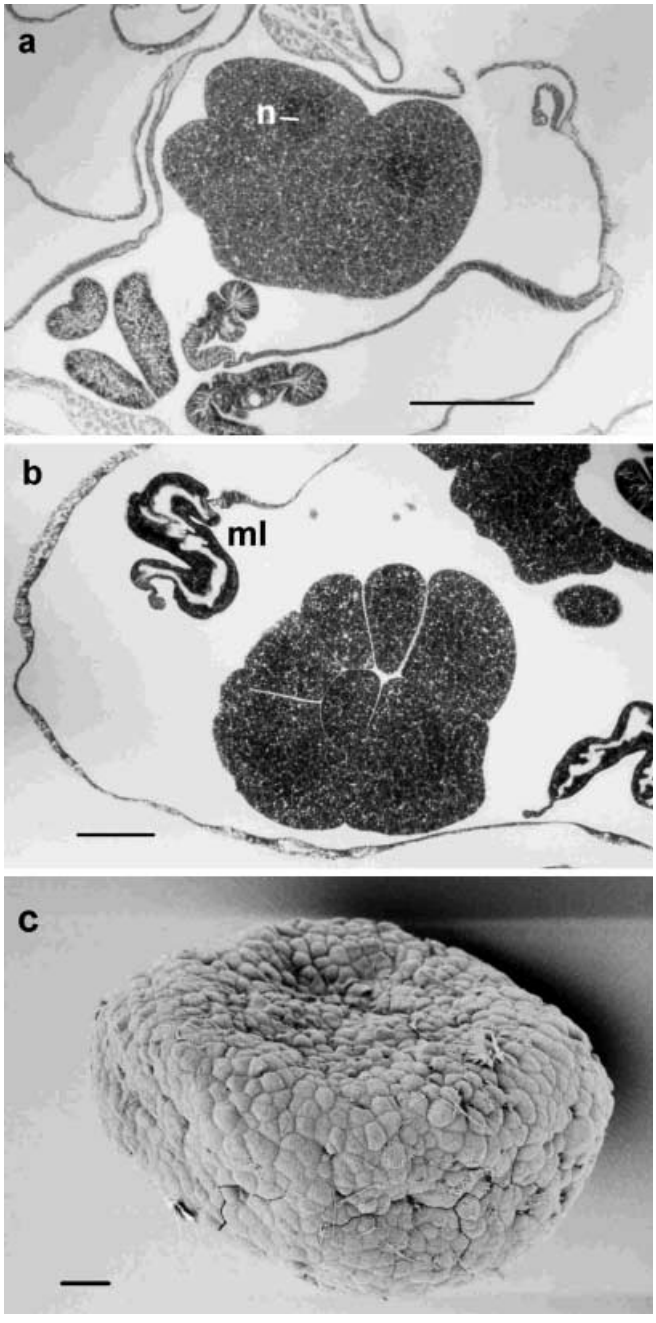

Fig. 5a–c Embryogenesis of *M. rubrum*. **a** Section of a developing embryo within the coelenteron of a female polyp. Cleavage shows an irregular radial pattern. Notice nuclei (*n*) with two larger cells. **b** Section of a developing embryo within the coelenteron of a female polyp. The embryo has undergone several divisions and displays significant polarity in the size of blastomeres. Note mesentery (*ml*) from which developing embryos have recently emerged. **c** Scanning electron micrograph of a solid steroblastula. *Bar* = 100 μm. Other *bars* = 0.5 mm

somewhat asynchronous within the coelenteron; hence embryos at different developmental stages could be found within the same polyp. Development proceeded to a solid blastula, (Fig. 5c) and a fully differentiated ectoderm, mesoglea and endoderm (Fig. 6 a) characterized early stages of larval development. Development of the mouth, pharynx and gut cavity followed, and the mouth was initiated through invagination of the ectoderm and mesoglea. During development of the mouth, two lobes were found at the base of the invagination, presumably the start of the pharynx. The ectoderm and mesoglea were continuous throughout these lobes (Fig. 6b). Further development led to mature larvae, still within the gastrovascular cavity of the parent coral, with full development of the mouth, pharynx, gut cavity and developing mesenteries. Brooded embryos of *M. rubrum* took approximately 2 weeks to develop into fully formed larvae. Once embryos reached full size and maturity, they filled the coelenteron and could become deeply indented by projecting septa. Based on data from the 1996-1997 season, the minimum developmental period for brooded larvae would be approximately 1 month, from the time of sperm release on 6 December until 5 January, when the first peak of larval release was seen. During this time larvae grew from mature oocytes of 2 ± 0.5 mm mean diameter, to planulae 3–4 mm long and 1–2 mm thick (mean diameter of approximately 2.5 mm).

Planulation and timing of larval release

Observations on planulation both in the field (0800–1200 hours) and laboratory showed that when polyps were ready to release larvae they filled with water and assumed a puckered position. The planulae were then extruded from the mouth (Fig. 7a), fully developed and ready for settlement and metamorphosis. Once released, larvae observed in the field drifted in the water column approximately 15 cm above the parent then sank to the bottom after a few seconds. Larvae were also seen crawling out the parent's mouth on their own accord and down the side of the parent to the substratum. In more turbulent areas larvae were also seen drifting up to 1 m above the substratum. Once larvae had sunk or crawled to the substratum they immediately began crawling, presumably searching for a settlement site. Planulae had a conspicuous bright orange color which was maintained during settlement (Fig. 7b) and metamorphosis (Figs. 7c).

M. rubrum planulated from early January 1997 through February, and larvae were seen in the field and the laboratory as late as the beginning of March 1997. This seasonality of release was very similar for both field and laboratory populations in January 1998. In the laboratory, larvae were found during all three monitoring periods (including the summer of 1993-1994). While there did not appear to be a particular time of day during which larval release took place, slightly higher numbers were found during the midday period (6.4 ± 0.4 SE larvae polyp^{-1} day^{-1}) than at other times of day (between 4 ± 0.2 and 4.4 ± 0.1 larvae polyp^{-1} day^{-1}).

A roughly semi-lunar pattern of planulation was seen, with three main pulses of larval release occurring in January 1997 (Fig. 8a). In January 1998 only one main

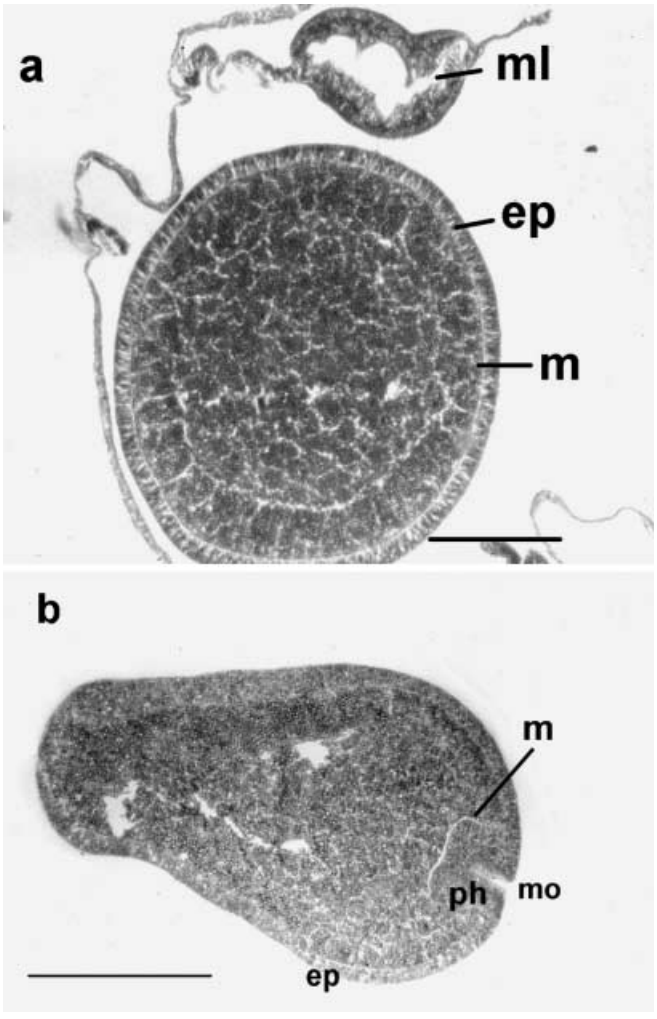

Fig. 6a, b Larval development of *M. rubrum*. **a** Cross-section of a female polyp showing the early stage of development of a planula larva within the coelenteron. Note the fully differentiated ectoderm (*ep*), and mesogleal layer (*m*). The central portion of the larvae is filled by the developing endoderm. The larva is still near the mesentery (*ml*) from which it has been released. *Bar* = 0.5 mm. **b** Longitudinal section of a larva showing the first development of the mouth (*mo*) and pharynx (*ph*) by the invagination of mesoglea (*m*) and ectoderm (*ep*) surrounding the mouth. *Bar* = 1 mm

pulse of planulation was recorded, 2 days before the full moon (Fig. 8b). Only 10 out of the 57 corals in the flow-through traps planulated in 1997 and only 12 planulated in 1998 (possibly due to expulsion of planulae during transport from the field to the laboratory). The number of larvae released by each individual female ranged from 1 to 59 in January 1997 and from 1 to 40 in January 1998.

Discussion

Gametogenesis

Observations of the sexual reproduction of *Monomyces rubrum* showed this coral to be a typical member of its class with respect to a number of basic reproductive characteristics. Both primordial oocytes and spermatocyte bundles first appeared within the mesoglea, thus displaying morphological similarities with other members of the anthozoa, for example *Tubastrea willeyi*, *Flabellum rubrum* (Gardiner 1902), *Balanophyllia elegans* (Fadlallah and Pearse 1982a), *Xenia umbellata* (Benayahu et al. 1988), and *Porites porites* (Tomascik and Sander 1987).

Size at first reproduction was found to be less than 1,000 mm^3, although fecundity was low at this size. Based on measured growth rates (Heltzel 1998) the age of *Monomyces* of this size is estimated to be no more than 6 years. Despite *Monomyces*' small size, its age at first reproduction may not be greatly different than those of colonial corals, which are estimated to range between 1 and 10 years, though most commonly at around 4 years old (Harrison and Wallace 1990).

Oogenesis preceded the initiation of spermatogenesis by 6 months. Gonads in both sexes subsequently matured together during spring and early summer, a common attribute in coral species with single annual gametogenic cycles (Harrison and Wallace 1990). Synchronous development and release of gametes within solitary gonochoristic organisms has potential advantages, as it may increase gamete concentrations and the probability of fertilization. However, other solitary corals, such as *Balanophyllia* (= *Leptopsammia*) *pruvoti*, have been found to planulate seasonally and yet contain eggs and embryos of different sizes, as well as mature sperm, all year round (De Lacaze-Duthiers 1897, cited in Fadlallah and Pearse 1982a).

Water temperature, lunar cycles, salinity, food, day length, moonlight, tidal cycles and daily light/dark cycles (Harrison and Wallace 1990) have been suggested as mechanisms for synchronizing gamete development within the anthozoa. Experimental studies of the effects of environmental variables on gametogenesis and planulation in *B. elegans* have shown that temperature is the major factor controlling reproductive seasonality (Beauchamp 1993). A correlation was also observed between the rate of gamete development of *M. rubrum* in the field and seasonal increase in seawater temperature. The timing of sperm release and oocyte maturation of *M. rubrum* that have lived their entire existence in large, completely enclosed seawater supply tanks at Leigh Marine Laboratory were not different from those observed in the field (Heltzel 1998). These findings suggest that for shade-loving ahermatypes such as *Monomyces* and *Balanophyllia*, seawater temperature regulates reproductive timing.

Embryogenesis

It can be inferred from histological evidence, and the fertilization experiment, that mature oocytes remained within the mesogleal lining until fertilized and entered the gastrovascular cavities of the polyps only after fertilization. Once fertilized, embryogenesis in *M. rubrum*

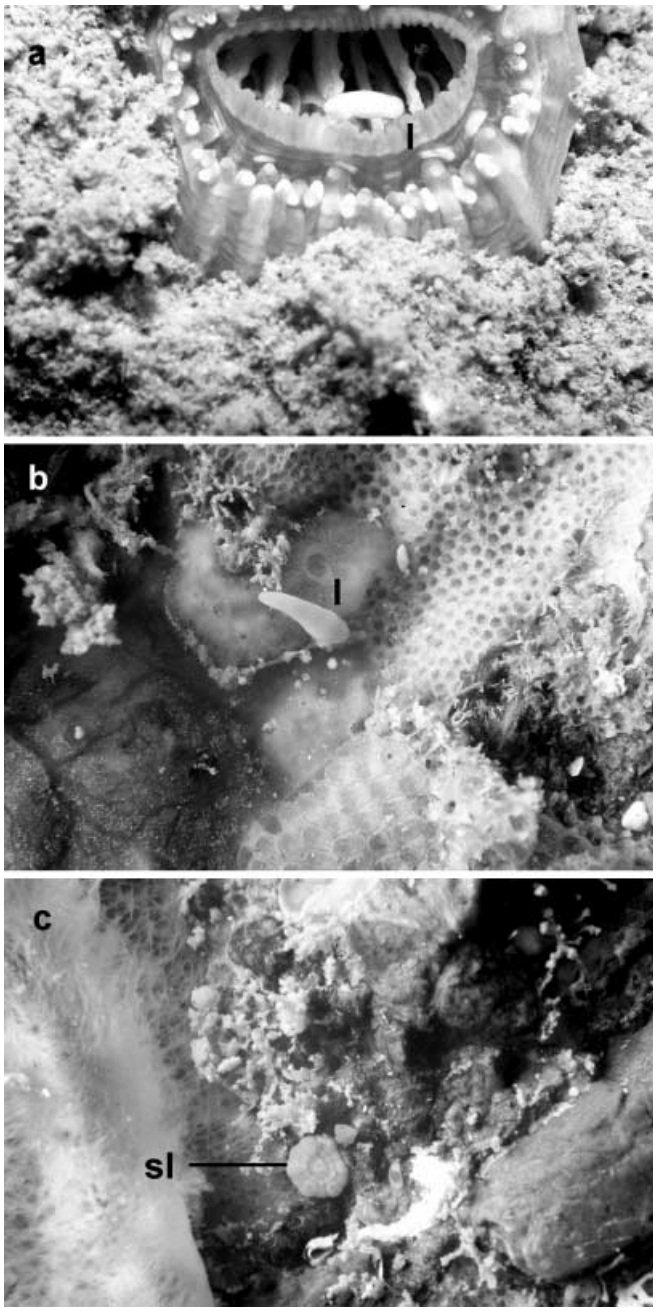

Fig. 7a–c Planulation and settlement of *M. rubrum*. **a** A fully developed larva (*l*) at the point of leaving the maternal polyp (*p*). **b** Larva of *M. rubrum* crawling on the substratum at 10 m depth. **c** Newly settled and metamorphosed larva (*sl*) in the field. Note that the initial development of the polyp is into 12 segments

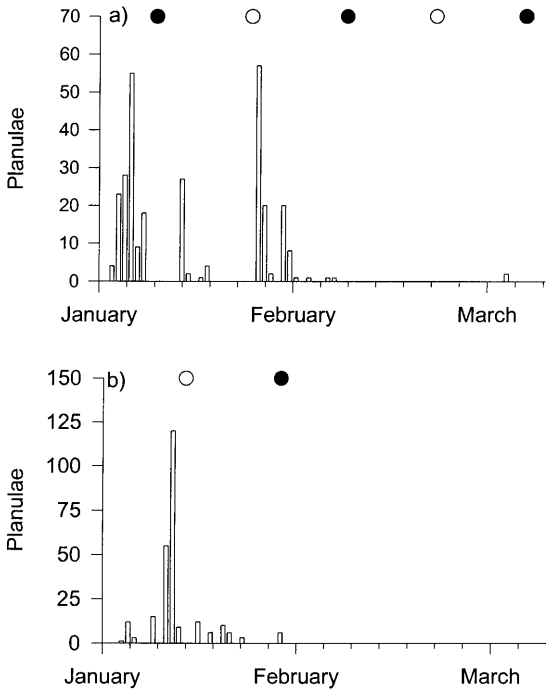

Fig. 8a, b Frequency of planula release in *M. rubrum*. Data are total numbers of planulae trapped per day in corals held in laboratory aquaria. *Open circles* represent full moons, *filled circles* new moons. **a** 1997, **b** 1998

showed no evidence of a hollow blastula stage and, as in *Favia fragum* (Szmant-Froelich 1985), the only other brooding scleractinian whose embryology has been fully described, embryonic development proceeded via stereoblastulae with gastrulation occurring by delamination, rather than invagination. In *B. elegans* it has also been suggested that initial cell divisions were probably superficial and that endoderm formed by delamination (Fadlallah and Pearse 1982a). Similarly, in many alcyonarians with internal fertilization, development has been observed to proceed via a solid stereoblastulae (*Parerythropodium fulvum fulvum*, Benayahu and Loya 1983; *Xenia umbellata*, Benayahu and Loya 1984; *X. macrospiculata*, Benayahu et al. 1988).

In contrast, developmental patterns in externally fertilizing scleractinians followed a trend of developing via a hollow blastulae, such as *Astrangia danae,* (Szmant-Froelich et al. 1980)and *Favia pallida*, *Goniastrea favulus* and *Montipora digitata* (Babcock and Heyward 1986). *Meandra areolata* had a hollow blastula stage with both internal and external development (Wilson 1888). Internal fertilization may constrain larvae to develop via a solid blastula, due to restricted availability of space, while development in external fertilized species may proceed via a hollow blastula (Babcock and Ryland 1990). Anemones, many of which are quite large, such as *Metridium senile* and *Anthopleura elegantissima*, are not constrained by growth form or calcareous skeletons. Therefore, for them space in the coelenteron may be less limiting and these species, e.g. *Tealia crassicornis* (Chia and Spaulding 1972), may not have to follow the trend for solid stereoblastulae.

The larvae of brooding corals are known to develop slowly through embryogenesis and larval development and *M. rubrum* appears to be no exception. For example, *Balanophyllia elegans* had a very long brooding cycle that lasted for 14–15 months (Fadlallah and Pearse 1982a). Brooded embryos of *F. fragum* take about 4 days to develop into planulae and stay within the polyp for

around 3 weeks before being released (Szmant-Froelich et al. 1985). In contrast, embryogenesis can be quite rapid in externally fertilized embryos, with swimming larvae developing within 6–8 h as in *Astrangia danae* (Szmant-Froelich et al. 1980), and 48 h for *Platygyra sinensis* (Babcock and Heyward 1986). We postulate that externally fertilized corals rapidly develop to the larval stage in order to minimize the time spent in the plankton and decrease mortality by facilitating quicker settlement. Internally fertilized corals such as *M. rubrum*, *F. fragum* and *Pocillopora damicornis* may have longer development because embryos and larvae are protected and perhaps nourished by the parent coral.

Timing of planulation

Planulation of individuals maintained in aquaria followed a semi-lunar release pattern in 1997 and a lunar pattern in 1998. All individuals for both 1997 and 1998 were collected at least 1 week prior to planulation and the pattern of release suggested a biological rhythm was maintained. Semi-lunar reproductive patterns are known in other brooding corals (Richmond and Jokiel 1984) and work by Hunter (1988) has shown that these can be experimentally manipulated and possibly entrained by artificial moonlight.

Many scleractinians posses lunar patterns of gametogenesis, spawning and planulae release (Harrison and Wallace 1990). Release of sperm by *M. rubrum* coincided with the first-quarter moon phase in 1997. Based on the observations from 1997 mature spermatozoa are only present in the testes for approximately 1 week. If this were true during 1993 (Table 1), then sperm release would have taken place some time during the week following three-quarter moon, or new moon at the latest. Lunar patterns of both spawning and larval release exist for *F. fragum* (Szmant-Froelich et al. 1985), and *M. rubrum* may also display these patterns of behavior. The timing of planula release could be regulated to some degree by the maturation of individual larvae. Dissections and histological examination of polyps revealed that not every egg was fertilized at the same time and as a result individual larvae could be found at different stages of maturation within samples. Larvae could crawl out of the parent coral on their own accord, hence there may be some sort of signaling process between larvae that were ready to be expelled and the adult coral.

Life history observations for *M. rubrum* support the trend for solitary or small and short-lived scleractinians to produce brooded, rapidly settling larvae. Nevertheless, there are exceptions to this trend, such as in the life histories of the corals *Paracyathus stearnsii* (Fadlallah and Pearse 1982b) and *Caryophyllia smithi* (Tranter et al. 1982), solitary forms that produce numerous small externally developing larvae. Further comparisons of these groups may provide insights into the demographic processes, environmental and phylogenetic constraints that determine life history variation in the Scleractinia.

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