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Reproduction in *Anthelia glauca* (Octocorallia: Xeniidae). I. Gametogenesis and larval brooding

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Abstract *Anthelia glauca* Lamarck, 1816 is a gonochoric, external-brooding soft coral found in KwaZulu-Natal. It is reproductively active in the summer months. The development of gametes produced in late summer is arrested in winter. Several stages of gametes are found at the base of the polyps, and female polyps produce several cycles of larvae over an extended breeding period of 4 to 5 months. Larvae are brooded in a unique pharyngeal brooding pouch not yet described in other coral species. The brood pouch consists of an expansion of the pharynx with constrictions proximal and distal to the embryos and larvae. Our data suggest that egg transfer and fertilization occur at full moon and the mature larvae are released after new moon. Zooxanthellae are absent in *A. glauca* oocytes, but zooxanthella infestation commences at the immature larval stage.

Introduction

Anthelia glauca has a wide Indo-Pacific distribution on littoral and sublittoral coral reefs from the Red Sea and the African east coast to the islands of the Pacific Ocean (Williams 1993). The small, pale, grey-brown colonies consist only of non-retractile, gonochoric autozooids that bear gonads. Limited studies on reproduction in *A. glauca* have only mentioned its reproductive mode of brooding (Gohar 1940) and that oocytes are found in female polyps in the Red Sea (Benayahu 1991).

Several genera of the family Xeniidae brood their planulae internally or on the surface of the colony, each involving various structural adaptations (Benayahu and Loya 1984a, b; Benayahu 1991). *Xenia umbellata* Savigny, *Sympodium caeruleum* Ehrenberg and *Anthelia glauca* are gonochoric internal brooders in the Red Sea (Benayahu et al. 1990) and on the Great Barrier Reef (Alino and Coll 1989). *Xenia macrospiculata* Gohar was initially believed to be an internal brooder (Benayahu and Loya 1984a, b), but a later study showed that it is an external brooder (Achituv et al. 1992). Its brooding sites are formed by invaginations of the epidermis which remain in contact with the external environment and are interconnected in the coenenchyme. *Heteroxenia fuscescens* Ehrenberg embryos develop inside the tentacles; they are extruded into intersiphonozooid spaces on the surface of the colony for final larval maturation when they reach the immature planula stage (Benayahu et al. 1989; Benayahu 1991). *Clavularia hamra* Gohar and *Parerythropodium fulvum fulvum* Forskål are external surface brooders as they entangle cleaving eggs in mucus on the surface of the female colonies (Benayahu and Loya 1983; Benayahu 1989).

Apart from the two brooding modes and the different adaptations found in each, there is also variability in the reproductive strategies followed by these species; these have been reviewed by Benayahu et al. (1990). Gonadal development may be seasonal or continuous and may be synchronized within a colony or population (Benayahu and Loya 1983, 1984a; Benayahu 1991). Spawning, embryogenesis and planulation may be synchronized or sporadic depending on several factors, and these activities differ in duration. Some species also employ different reproductive modes in different localities, e.g., the brooding *Heteroxenia coheni* Verseveldt is hermaphroditic in the Red Sea and gonochoric on the Great Barrier Reef (Benayahu et al. 1990). The present paper deals with the annual gonadal development, embryogenesis, brooding mode and planulation of *Anthelia glauca* on the marginal reefs off KwaZulu-Natal, South Africa, and was part of a more comprehensive study of coral reproduction in the region (Kruger 1996; Schleyer et al. 1997).

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Materials and methods

Anthelia glauca Lamarck, 1816, colonies were collected on Ninemile Reef at Sodwana Bay in KwaZulu-Natal on the east coast of South Africa (27°24.9′S; 32°43.6′E). Colonies were randomly sampled by SCUBA diving at a depth between 12 and 17 m from September 1991 to November 1994. Monthly sampling was undertaken in 1992 to ascertain the reproduction season in this species. Samples were collected during the weeks of full moon and new moon to ensure collection of the various gametogenic stages and to elucidate the spawning and planulation events during the peak of the breeding season (January to March) in 1993 and 1994. The samples comprised 5 to 12 colonies (usually 10), each with at least 50 polyps, and these were fixed in 4% formaldehyde in seawater for up to a week. The samples were rinsed in freshwater in the laboratory until all traces of the formal-saline were removed, and then preserved in 70% ethyl alcohol. Subsamples of each colony (three sections, each 2 mm thick) were decalcified in a formol-nitric acid solution (Mahoney 1966), washed and transferred to 70% ethyl alcohol. The gonads of five polyps of each decalcified subsample were dissected for examination under a compound microscope. The diameters of the oocytes and spermaries were measured with a micrometer and the number of gonads in each polyp noted. Embryos and planulae were also measured and counted. Histological sections were prepared to assess the gamete development. The tissues were dehydrated in a series of alcohols, cleared with isopropanol and then infiltrated with Paraplast using a Biorad microwave processor. Microwave processing ensured good reproducibility due to faster, better diffusion of chemicals at controlled, accurate temperatures. The tissues were embedded in histological paraffin wax (melting point 57 to 60 °C) and oriented so that longitudinal sections could be obtained. Sections of 4 to 6 μm were cut using a microtome and mounted on glass slides. The sections were stained with Ehrlich's haemalum stain (Drury and Wallington 1967) and aqueous eosin solution (Mahoney 1966). The stained slides were rendered permanent, using a mounting medium and coverslips.

The gametogenic stages and their frequency of occurrence in five polyps in each subsample were recorded. Oocyte and spermary developmental stages were based on the classification of Glynn et al. (1991). Embryonic and larval stages were based on the descriptions given by Achituv et al. (1992). The chi-squared goodness-of-fit formula (Zar 1974) was used to test for deviations from a 1:1 sex ratio.

Results

Sex ratio and gonadal development

Of the 302 colonies analysed, 149 were female, 136 were male, 4 contained hermaphroditic polyps and 13 contained polyps with no gonads. The sex ratio did not differ from 1:1 ($\chi^2 = 0.593$; $0.5 > P > 0.25$; $df = 1$).

The earliest gametes found in histological preparations were embedded in the basal parts of six of the eight mesenteries (Fig. 1a). The later stages were separately attached to the basal parts of the mesenteries by pedicels (Fig. 1b) and formed clusters. As the gonads matured they gradually filled the gastrovascular cavity.

All four stages of gamete development were found, often simultaneously, in a single polyp from November to June (Fig. 1a, b, c). Stage I oocytes had little ooplasm and large nuclei, and had a mean diameter of 14 ± 3 μm ($n = 25$). The mean diameter of Stage II oocytes increased to 47 ± 14 μm ($n = 25$) due to the accumulation of ooplasm. Vacuoles developed in the ooplasm of later Stage II oocytes. Nuclei were centred in the ooplasm and contained one conspicuous nucleolus. The onset of vitellogenesis and the migration of the nucleus to the periphery of the oocyte were characteristic of Stage III oocytes. The yolk droplets were small, giving the ooplasm a fine granular appearance (Fig. 1b). The mean diameter of Stage III oocytes increased to 171 ± 10 μm ($n = 25$). Mature Stage IV oocytes were characterised by an indented nucleus, a pronounced purple follicular layer and azooxanthellate ooplasm filled with large yolk droplets (Fig. 1b) that were a mottled pink and white when stained. Mature Stage IV ova had a mean diameter of 390 ± 39 μm ($n = 25$). The follicular layer thickened throughout oocyte development and remained azooxanthellate at all stages.

The unpreserved oocytes were light beige, but they became darker when preserved in formal-saline.

Oogenic cycle

Although oocytes were present throughout the year during the study (Fig. 2), the production of primordial oocytes was seasonal as there was an increased presence of Stage I oocytes in the female polyps during the months of November to March. Several cycles of oocytes were produced in each polyp in the summer months from November to March, this being indicated by the presence of several oocyte stages, each with a specific size range. There was a marked increase in the size range of oocytes, from 375 to 750 μm, as they underwent maturation over a period of 4 to 6 months from December or January. Two size classes were present in the polyps from January to June (Figs. 2, 5), with primordial oocytes developing between the large oocytes. The smaller oocyte size class corresponded to the Stage I to III oocytes, and the larger oocyte size class to Stage IV oocytes. The mean diameters of the small and large oocytes during this period were 143 ± 85 μm ($n = 7669$) and 492 ± 70 μm ($n = 1895$), respectively (Fig. 2). Stage IV oocytes were predominantly found during December to April. The maximum diameter attained by a mature Stage IV ovum was 787 μm. Gonadal development was synchronous within a colony but not necessarily between colonies.

In July to October or November the oocytes ranged in size from 50 to 375 μm with a mean diameter of 127 ± 73 μm ($n = 4748$) (Fig. 2). The small oocytes were mainly found in the polyps during this period; Stage III and IV oocytes were low in numbers or nearly absent.

Spermary development

Three spermatogenic stages were usually found in a single polyp (Fig. 1c, d); Stages I and II with Stage III or IV. The clusters of spermatogonia (Stage I spermaries) were embedded in the basal parts of the mesenteries in

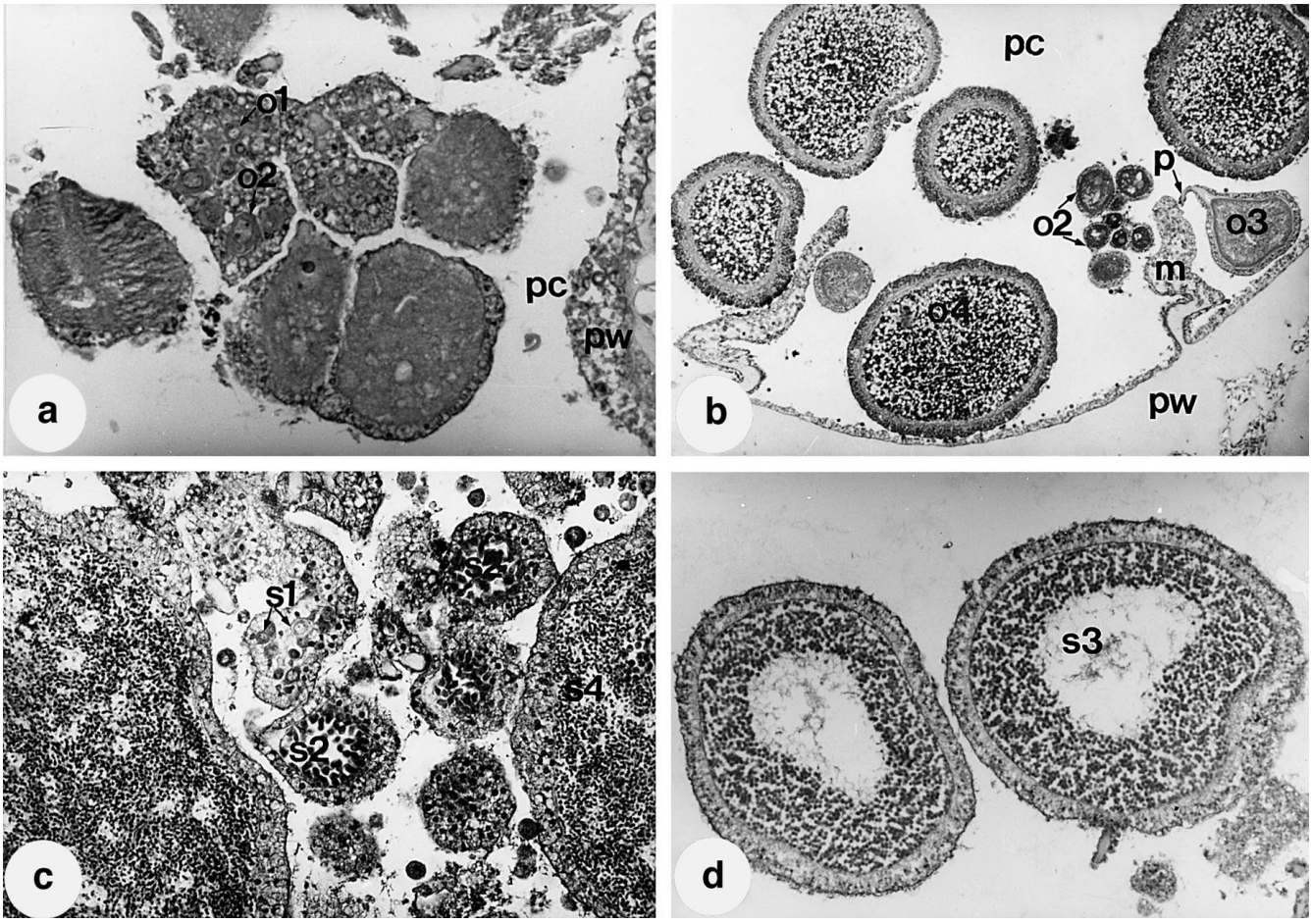

Fig. 1 *Anthelia glauca.* Gametogenesis. **a** Stage I and II oocytes embedded in the mesentery (1400×). **b** Oocytes in various stages of development are found in the same polyp. A Stage III oocyte is connected to the mesentery by a pedicel (350×). **c** Spermaries with spermatogonia, spermatocytes and mature sperm are found in a single polyp during the summer months (1000×). **d** Spermaries containing spermatids or Stage III spermatocytes (400×).(*m* mesentery; *o1* Stage I oocyte; *o2* Stage II oocyte; *o3* Stage III oocyte; *o4* Stage IV oocyte; *p* pedicel; *pc* polyp cavity; *pw* polyp wall; *s1* spermatogonia; *s2* Stage II spermary with spermatocytes; *s3* Stage III spermary with spermatids; *s4* Stage IV spermary with mature sperm)

the aboral part of the polyp. Spermatogonia (mean diameter 14 ± 2 μm, $n = 25$) had conspicuous nuclei, but the cytoplasm was not well-defined (Fig. 1c). Stage II spermaries had distinct boundaries and contained spermatocytes with large nuclei (Fig. 1c). The mean diameter of the Stage II spermaries was 65 ± 60 μm ($n = 25$). Stage III spermaries contained spermatids which were more numerous and smaller than spermatocytes. The nuclei of the spermatids were small and stained a conspicuous dark purple. A lumen formed in each Stage III spermary just before the transformation of spermatids into spermatozoa, with the spermatids arranged on the periphery of the spermary (Fig. 1d). The mean diameter of Stage III spermaries was 121 ± 2 μm ($n = 25$). Stage IV spermaries (247 ± 28 μm) contained mature spermatozoa that were half the size of the spermatids. Tails were usually visible and stained pink. The sperm were arranged in clusters inside the spermaries with the tails projecting inwards

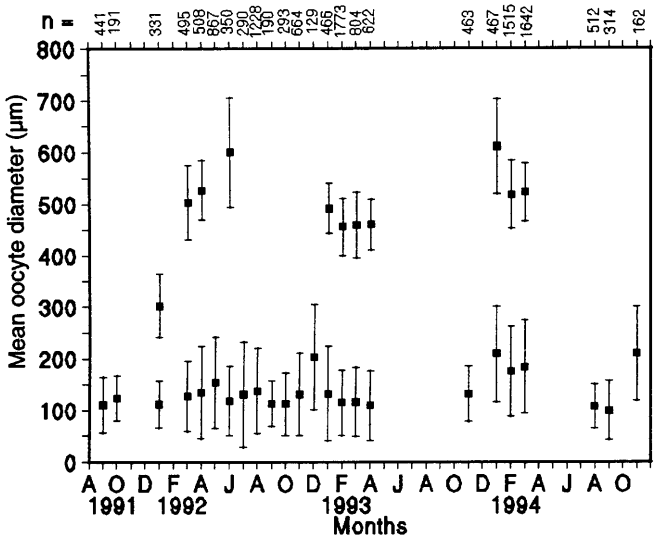

Fig. 2 *Anthelia glauca.* Monthly mean diameter ± SD (μm) of oocytes in female polyps. Two oocyte size classes are found during the breeding season from January to June. Gaps occur in the graph when no samples were collected ($n = 14\,717$)

(Fig. 1c). The preserved spermaries were beige, transparent and appeared granular.

Spermatogenic cycle

Spermaries were present throughout the year. The mean number of spermaries per polyp increased to 121 ± 105 ($n = 9925$) in November, maintaining this level for 6 months. Their mean diameter simultaneously increased (Fig. 3), and the spermaries matured throughout the breeding season within the population. Their mean diameter was 153 ± 105 μm ($n = 9925$). Two spermary size classes were found in the colonies from January to June in 1992 and 1994 and December 1992 to April 1993. Polyps usually contained both small and large spermaries filled with early spermatocytes or spermatids/mature sperm, respectively. As in the case of female polyps, spermary development was synchronised within a colony but not necessarily between colonies. Outside the breeding season (July to September), the mean diameter of the spermaries was 48 ± 31 μm ($n = 1545$); the mean spermary count per polyp was 32 ± 37 ($n = 1545$), and only Stage I and II spermaries were found.

Larval development

Embryos and larvae were brooded in the pharynx of *Anthelia glauca* in a brooding pouch formed by constrictions in the pharyngeal wall proximal and distal to the brood. The embryos and larvae were thus isolated from both the external environment and the developing oocytes at the base of the polyp cavity (Fig. 4a, b). The embryos and larvae were in contact with the epidermal layer of the pharynx but contained within the polyp cavity.

Histological analyses provided evidence for four stages of embryogenesis. The embryos were azooxanthellate in Stages I (fertilized oocytes without a follicular layer; Fig. 4c) and II (divisional stage; Fig. 4d). Stage III embryos comprised immature planulae, with zooxanthellae in the ectoderm and mesogloea as well as yolk in the lumen. Later Stage III larvae had distinct layers of ectoderm, mesogloea and endoderm (Fig. 4e), with most zooxanthellae in the latter. The acquisition and transfer of the algae are described by Benayahu and Schleyer (1998). Preserved Stage III larvae were greenish-brown owing to the symbiotic zooxanthellae. Their shape varied from round to elongated, with the majority being barrel-shaped.

The mean diameter of the embryos was 620 ± 51 μm ($n = 992$), and the planula length was 1008 ± 144 μm ($n = 614$). The maximum length attained by an immature larva was 1665 μm. No larvae were found that were similar to Achituv et al.'s (1992) description of mature Stage IV larvae, i.e., larvae containing three distinct layers of endoderm, mesogloea and ectoderm, with zooxanthellae only in the endoderm. During the breeding months, embryos and planulae were present in 22 and 18.2% of the female polyps ($n = 351$), respectively. Embryos and larvae appeared in the polyps in late February 1993 and 1994 and were also present in May 1992, February to April 1993 and February to March 1994. Various developmental stages were found in each polyp. Embryogenesis was loosely synchronised in the polyps within a colony and between colonies in terms of the development of the dominant embryo stage (Table 1).

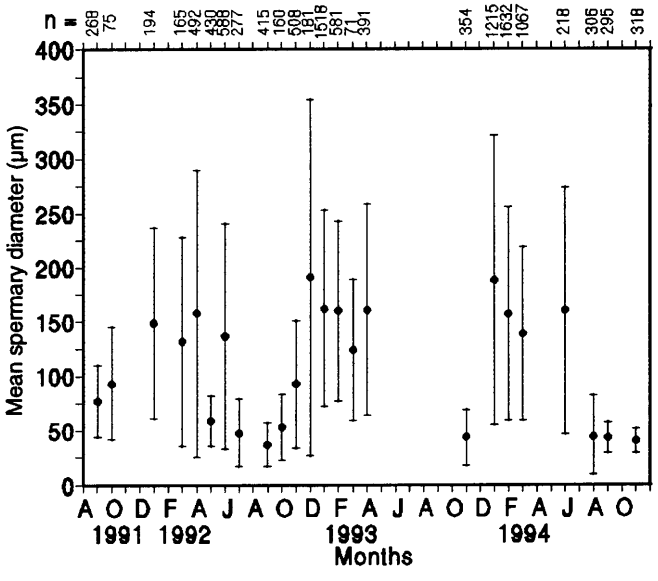

Fig. 3 *Anthelia glauca*. Monthly mean diameter ± SD (μm) of spermaries in male polyps. Gaps occur in the graph when no samples were collected ($n = 11\ 719$).

Lunar phase, embryogenesis and planulation

The abundance of gametes, spermaries, embryos and larvae found in *Anthelia glauca* polyps at full moon and new moon is summarised in Table 2. Small and large oocytes attained a mean diameter and abundance per polyp that was higher during full moon than at new moon (Table 2). Polyps contained both oocyte size classes during the new moon phase; the large oocytes were still present at full moon after which they disappeared (Fig. 5). Both the mean diameter and number of spermaries per polyp were lower at full moon than at new moon (Table 2). Embryos were found in higher numbers at full moon (19 May 1992, 29 March 1994) than during new moon while, in contrast, the planulae were more numerous during new moon (21 February 1993, 12 February 1994, 12 March 1994; Tables 1, 2). Only Stage I and Stage II embryos were present at full moon (Table 1). Both were present at new moon, but 76% ($n = 347$) of the contents of the brood pouch consisted of Stage III immature planulae (Table 1).

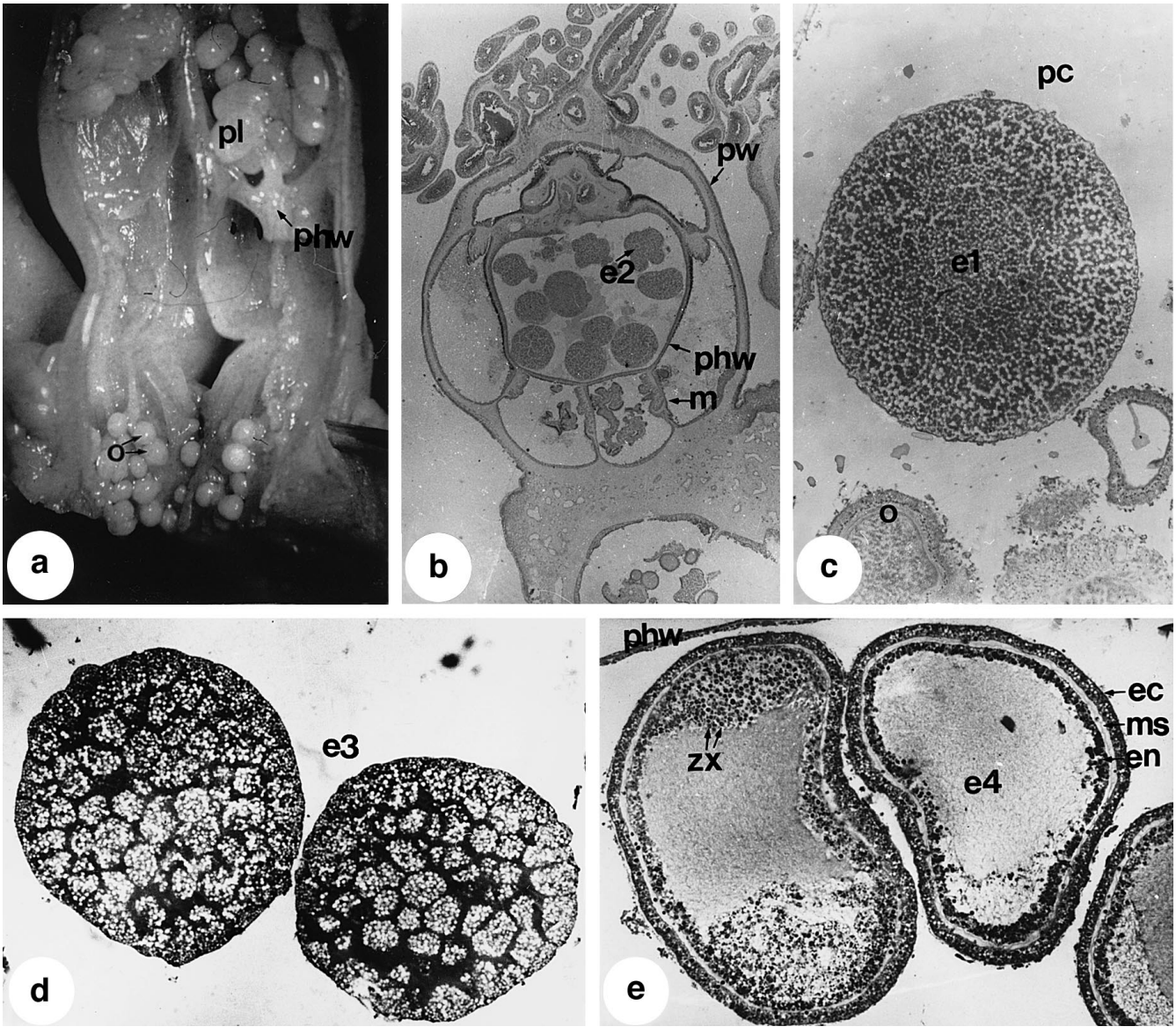

Fig. 4 *Anthelia glauca*. Embryogenesis. **a** Dissected female polyp with planulae in the pharyngeal brood pouch (*top*), and oocytes in various stages of development at the base of the polyp (70×). **b** A histological longitudinal section of Stage II embryos undergoing division in the pharyngeal pouch, with mesenteries in the polyp cavity (130×). **c** Stage I embryo (fertilized ovum), in which the maternal epithelium has been lost, in the polyp cavity (350×). **d** Late Stage II embryos (blastomeres) (400×). **e** Late Stage III planulae with fully differentiated tissues (250×) (*e1* Stage I embryo; *e2* early Stage II embryo; *e3* late Stage II embryos; *e4* Stage III larva; *ec* ectoderm; *en* endoderm; *m* mesentery; *ms* mesoderm; *o* oocyte; *phw* pharyngeal wall; *pl* planulae; *pc* polyp cavity; *pw* polyp wall; *zx* zooxanthellae)

Discussion

Gamete development in *Anthelia glauca*

Gametes are present throughout the year in *Anthelia glauca*; however, gamete development is seasonal. Several cycles of oocytes develop within female polyps each year (Figs. 1b, 2), but only one or two spermary cycles develop in each male polyp in the austral summer

Table 1 *Anthelia glauca*. Percentage abundance of embryo and larval stages in female polyps at full moon and new moon (n = 1045)

Lunar phase	Stage I fertilized oocytes (%)	Stage II early embryos (%)	Stage III immature planulae (%)	Stage IV mature planulae (%)
Full moon	37.7	62.3	–	–
New moon	7.7	16.5	75.8	–

Table 2 *Anthelia glauca*. Abundance of gametes, embryos and larvae in polyps at full moon and new moon ($n = 56$)

Lunar phase, reproductive product	Mean diameter (μm)	Mean number per active polyp	Mean number per polyp with that product	Brooding stage
Full moon				
Small oocytes	186	69.0	69.0	
Large oocytes	633			
Spermaries	94	84.9	84.9	
Embryos	589	12.4	22.4	I & II
Planulae	1110	0.02	1.0	III
New moon				
Small oocytes	124	48.7	48.7	
Large oocytes	567			
Spermaries	249	141.5	141.5	
Embryos	634	1.9	10.2	I & II
Planulae	1002	4.7	17.5	III

(Figs. 1c, 3). Ova that are formed in the late austral summer (March) appear to undergo a period of arrested development from autumn to early spring (April to October) irrespective of their stage of development; no evidence was found of gamete maturation during winter (Fig. 2). Gametes which overwinter in the polyp appear to mature in the next summer at the onset of the production of new gamete cycles. The full oogenic cycle of *Anthelia glauca* may take as little as 8 months if an egg completes its development within one season (e.g. November to July). However, the development of oocytes produced late in the season, if arrested during the winter months (July to October), would take 13 to 15 months to mature before transfer to the brood pouch.

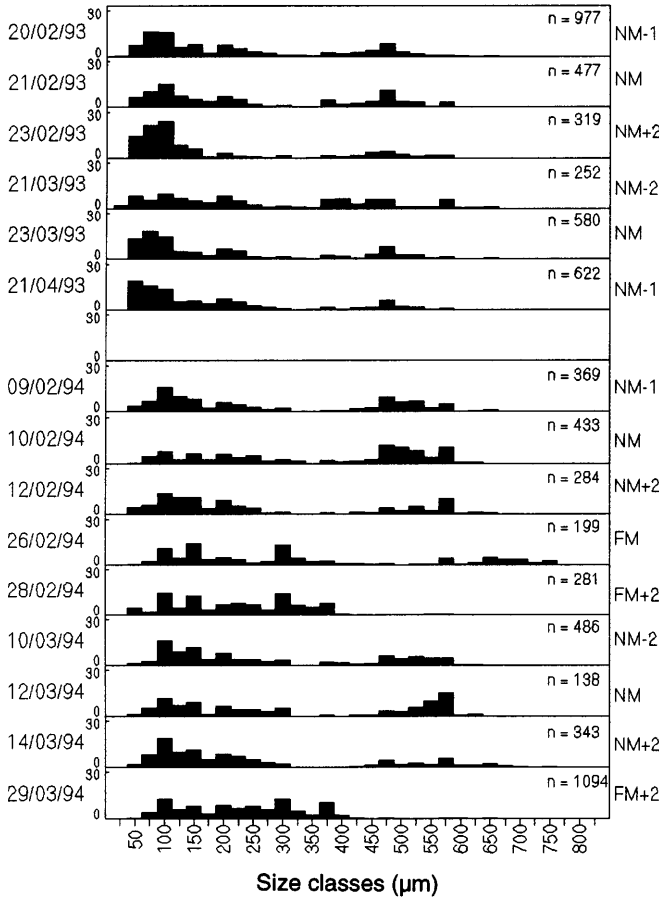

Fig. 5 *Anthelia glauca*. Incidence of oocytes relative to the lunar cycle in February and March 1993 and 1994 (*FM* full moon; *NM* new moon; *numerals* number of days before or after lunar period)

There are similarities between oocyte development in *Anthelia glauca* and *Xenia macrospiculata*; both produce several cycles of oocytes in their polyps over an extended period each year, and these mature cyclically. However, in the former, both oocyte production and maturation occur simultaneously in the summer months, whereas in the latter the oocyte cycles are produced over a period of 7 to 8 months followed by a period of cyclical maturation of 4 to 5 months (Benayahu and Loya 1984a). Spermaries are produced in *Anthelia glauca* during a 6-month period in summer (November to April). The development of a spermary may take as little as 3 months if produced during the breeding season, from November to January when the first spawning event occurs. However, the development may take 8 months if a spermary is produced in late summer and arrested development occurs during winter. *A. glauca* adheres to a pattern commonly found amongst alcyonaceans and scleractinians in which spermary development occurs more rapidly than oocyte development (Benayahu and Loya 1983, 1984a; Harriott 1983; Benayahu 1989, 1991; Benayahu et al. 1990; Harrison and Wallace 1990).

The majority of the stony coral species which spawn gametes for external fertilization and development undergo a single cycle of gametogenesis each year, with the gametes taking less than 12 months to develop, culminating in a short spawning period during spring or summer (Harrison and Wallace 1990). There are exceptions, however; the broadcast-spawning scleractinian coral *Paracyathus stearnsii* Verrill and the soft coral *Sarcophyton glaucum* Quoy and Gaimard have extended oogenic cycles of 14 and 23 months, respectively (Fadlallah and Pearse 1982; Benayahu and Loya 1986). Studies by Szmant-Froelich et al. (1980) also suggest that, under favourable conditions, certain broadcast-spawning species may be capable of producing multiple oogenic cycles each year.

Brooding soft corals and some brooding stony corals tend to have multiple gametogenic cycles (Harrison and Wallace 1990), e.g., the soft corals *Xenia macrospiculata*, *Xenia umbellata*, *Heteroxenia fuscescens* and the hard corals, *Acropora palifera* Lamarck and *A. cuneata* (Benayahu and Loya 1984a; Kojis 1986a, b; Benayahu 1991). In contrast, the brooding soft corals *Parerythropodium fulvum fulvum* and *Clavularia hamra* have a single gametogenic cycle each year (Benayahu and Loya 1983; Benayahu 1989).

Two oocyte size classes are found in the *Anthelia glauca* polyps in summer, with all four developmental stages present (Figs. 1, 2). Stage IV oocytes appear to mature together within a polyp. Indirect evidence of this is the similar degree of embryo development within the colonies found at each full moon during the breeding season (Table 1). However, development is asynchronous within the population as less than a third of the female polyps in the population were found to contain embryos and larvae during the breeding season. Various developmental stages of gametes are found in polyps of a number of brooding soft and stony corals which have multiple overlapping gametogenic cycles; these undergo synchronous maturation within the colony but not within the population (Rinkevich and Loya 1979; Benayahu and Loya 1984a; Kojis 1986a; Benayahu 1991).

It was suggested by Harrison and Wallace (1990) that large oocytes are often associated with longer oogenic development. Large oocytes are, however, commonly found in soft corals (Benayahu and Loya 1986), irrespective of whether the duration of oogenesis is 12 or 24 months (Benayahu and Loya 1983, 1984a, 1986) and there are hard corals with extended oogenic cycles that only produce small eggs (e.g. *Paracyathus stearnsii*: Fadlallah and Pearse 1982). Oocyte diameter appears to be generally consistent within some hard coral families. The stony coral families manifest variation in egg sizes (Harrison and Wallace 1990), e.g., Acroporidae have large eggs (400 to 800 μm), Faviidae have intermediate-sized eggs (300 to 500 μm) and Pocilloporidae have small eggs (100 to 250 μm). Small eggs are also evident in the families Agariciidae and Poritidae (Glynn et al. 1994, 1996). Benayahu and Loya (1986) suggested that large egg size is not the consequence of a prolonged egg development, but that prolonged gametogenesis is found in species with high fecundity, synchronized maturation and brief spawning periods.

The hypothesis of Rinkevich and Loya (1979) that broadcast-spawning stony corals produce large oocytes and brooders produce small oocytes is clearly not applicable to soft corals (Benayahu and Loya 1986). Both the brooders (Benayahu and Loya 1983, 1984a; Benayahu 1989; Benayahu et al. 1989) and the broadcast-spawners (Benayahu and Loya 1986; Alino and Coll 1989) produce large oocytes ranging between 400 and 900 μm.

The significance of larger eggs in brooding species, as in *Anthelia glauca,* is not immediately obvious, other than their possession of greater nutrient stores (Wallace 1985) for larval development. It is thus possible that large eggs may thus be associated with non-feeding planulae and vice versa, but there is, thus far, no information on planular feeding. In broadcast-spawning soft corals, the greater nutrient stores in the larger oocytes may result in longer-living larvae, increasing their competency period and thus the amount of time available for dispersal before settling (Richmond 1981).

Developing *Anthelia glauca* planulae deplete their yolk supply until they become hollow inside, attaining an appearance similar to the mature larvae of *Xenia macrospiculata* (Achituv et al. 1992). Zooxanthellae infesting the *A. glauca* larval layers might supplement their nutrition, thus allowing the brooding polyps to conserve energy for gamete production on attaining maturity. *Xenia umbellata* embryos were found to acquire symbionts that may support their development to the mature planula stage (Benayahu et al. 1988)

Fertilization and embryogenesis

Non-gastrovascular brooding seems to be the rule in alcyonaceans (Achituv et al. 1992), however, internal or gastrovascular brooding has been found in *Sympodium caeruleum* and *Lithophyton arboreum* (Benayahu et al. 1990; Benayahu 1991). In the external-surface brooders the embryos can be attached to the colony surface with mucus as in *Parerythropodium fulvum fulvum*, *Clavularia hamra* and *Efflatounaria* sp. (Benayahu and Loya 1983; Dinesen 1985; Benayahu 1989). Temporary brooding cavities can be formed by invagination of the colony surface as in *Xenia macrospiculata*; or, after initial brooding in the gastrovascular cavity, the embryos may be transferred to intersiphonozooid spaces on the colony surface as in *Heteroxenia fuscescens*; the final brooding is therefore external (Benayahu et al. 1989; Achituv et al. 1992).

Anthelia glauca is a brooder in South African waters with an adaptation which has not been recorded in other brooding species (Kruger 1996; Schleyer et al. 1997). The brood pouch is formed by an expansion of the pharynx with constrictions proximal and distal to the embryos and larvae. The embryos and larvae are loose inside the brood pouch, surrounded by the epidermal lining of the pharynx. *A. glauca* is thus not a true internal-brooder, despite appearances, but an external-brooder as are *Xenia macrospiculata* and *Heteroxenia fuscescens*.

Internal fertilization is suspected in *Anthelia glauca* as it probably occurs within the gastrovascular cavity. Fertilization may, however, take place while oocytes are within the pharyngeal pouch, an "external" structure, although oocytes have not been found within the pouch. The mode of fertilization varies in the external-brooding soft corals, being external and internal, respectively, in the external-surface brooders *Parerythropodium fulvum fulvum* and *Clavularia hamra,* and is suspected to be internal in the external-brooder *Xenia macrospiculata*

(Benayahu and Loya 1983; Benayahu 1989; Achituv et al. 1992).

The formation of a solid stereoblastula during division, the maturation of planulae with three distinct layers and the presence of microvilli on the surface of the ectoderm are consistent features in all the brooding species studied; *Parerythropodium fulvum fulvum*, *Clavularia hamra*, *Xenia macrospiculata* and *Anthelia glauca* (Benayahu and Loya 1983; Benayahu 1989; Achituv et al. 1992; Kruger 1996; Schleyer et al. 1997).

Synchronicity in embryogenesis varies between the brooding soft coral species. Embryogenesis is highly synchronised within *Xenia macrospiculata* colonies, but not between colonies (Benayahu and Loya 1984b). It is highly synchronous within populations of the external-surface brooders *Clavularia hamra* and *Parerythropodium fulvum fulvum*, but asynchronous in populations of *Heteroxenia fuscescens* (Benayahu and Loya 1983; Benayahu 1989, 1991). Embryogenesis is loosely synchronised within and between *Anthelia glauca* colonies, with a few embryos lagging in development; however, the general degree of development is similar within and between the colonies (Table 1) (Kruger 1996).

The estimate of 14 d for embryogenesis in *Anthelia glauca* is derived from the appearance of Stage I or fertilized oocytes in the polyps at full moon, and the dominance of immature planulae at the following new moon (Tables 1, 2). This also provides evidence for synchrony in embryogenesis. Earlier studies implied that the period of embryogenesis is longer in the brooding species than in broadcasting species (Benayahu and Loya 1986). Benayahu and Loya (1983, 1986) suggested that the embryos of broadcast-spawners need to develop rapidly as they are exposed to predation, damage by wave action and erosion by sediment. Rapid embryogenesis will therefore increase survival of the sexual offspring in broadcasting species, while the protection embryos enjoy in brooding species provides the opportunity for slower development.

Larval development in *Anthelia glauca* is seasonal and occurs in the summer months. The presence of oocytes at different stages of development in the same polyp due to prolonged oogenesis with successive maturation of the oocytes suggests that each female polyp broods larvae several times during the breeding season. *A. glauca* appears to be a successive spawner with an extended planulation period of at least 4 months. This is possibly extended to a fifth month, as large oocytes were found in female polyps in June 1992 and these may have been fertilized and brooded (Fig. 2).

The duration of planulation varies between soft corals, depending on the number of gametogenic cycles produced by individual polyps and colonies. The planulation period can be as short as a few days if spawning and embryogenesis are highly synchronised within the population as in the external brooder *Clavularia hamra* and broadcast-spawner *Sarcophyton glaucum* (Benayahu and Loya 1986; Benayahu 1989). Planulation can also occur over several months as in the external brooders *Xenia macrospiculata*, *X. umbellata* and *Heteroxenia fuscescens* (Benayahu and Loya 1984b; Benayahu 1991).

Embryogenesis and planulation versus lunar phase

Coral reproduction studies have revealed that corals may react to several cues to spawn, be they tidal or lunar cycles, daylight, temperature, etc. (Babcock et al. 1986; Harrison and Wallace 1990). The best example of this is the mass-spawning of corals which occurs with spring tides on the Great Barrier Reef during full moon in late spring or early summer (Harrison and Wallace 1990). This includes both soft and hard corals (Alino and Coll 1989). Spawning and planulation appear to be synchronised by lunar periodicity in several soft coral species, although at different lunar phases (Benayahu and Loya 1983, 1984b; Benayahu 1989; Kruger 1996). Others, e.g. *Heteroxenia fuscescens*, are not influenced in this way and planulate independently of such factors (Benayahu 1991).

There is indirect evidence that sperm release and planulation in *Anthelia glauca* are influenced by lunar phase. Spawning and fertilization occur at full moon; the number of spermaries per polyp decreases and the mature oocytes are fertilized and transferred to the brooding pouch, becoming Stage I and II embryos during this period. At full moon, only Stage I and II embryos are found inside the brood pouch (Table 1). Rapid maturation of the next cycle of oocytes then begins. Larval development in *A. glauca* appears to take a minimum of 14 d. Mainly immature planulae are found in the brood chamber 2 weeks after fertilization at new moon (Table 2). Planulation appears to occur at new moon or soon thereafter as the larvae then disappear from the brood pouch. This allows the next cycle of oocytes to enlarge and mature in the base of the female polyp, ready for fertilization during the following full moon. The provision of more space for developing oocytes is also found in *Heteroxenia fuscescens* when immature larvae are transferred into intersiphonozooid spaces on the colony surface, allowing for further oocyte development in the polyp cavities (Benayahu et al. 1989).

Sexuality, sex ratio and fecundity

Anthelia glauca is a gonochoric-brooder in the Red Sea (Benayahu et al. 1990) and on South African reefs, as are most brooding soft corals (Benayahu et al. 1990; Benayahu 1991). A few xeniid brooding species have, however, been found to be hermaphroditic, e.g. *Heteroxenia fuscescens* and *H. coheni* (Benayahu et al. 1990). Sexuality can differ in the same species, e.g. *H. elizabethae* Kölliker is hermaphroditic in the Red Sea, but gonochoric in Australia (Benayahu et al. 1990). Hermaphroditic stony corals can alternate between protandry or protogyny, and certain species contain

both male and female polyps within the colonies (Harrison and Wallace 1990). However, these hermaphroditic patterns have not yet been found in brooding soft corals.

The fecundity of a coral species can be influenced by several factors. The activity of the colonies may be seasonal or continuous (Benayahu 1991); the number of oocytes or planulae per polyp can vary, according to the thickness of the coenenchyme and the length of the polyps (Benayahu and Loya 1983, 1984a, b; Benayahu 1991), and structural modifications may permit a more efficient use of the polyp cavity for oocyte development, oocyte production and brooding capabilities, e.g., encrusting species maximise their fecundity by being external-surface brooders (Benayahu and Loya 1983; Benayahu 1989).

Such factors are evident in *Anthelia glauca*. The majority of the *A. glauca* polyps contain gonads throughout the year, but they are only reproductively active in summer. Female colonies/polyps produce several generations of oocytes each year. This is also the case in *Xenia macrospiculata*, *Heteroxenia fuscescens* and *X. umbellata*, resulting in an annual production of several hundred eggs by each polyp (Benayahu and Loya 1984a; Benayahu 1991).

The mean number of oocytes (in various stages of development) per *Anthelia glauca* polyp in South African waters at any given time is 49 ± 33 ($n = 742$). Benayahu (1991) found only 8 to 12 oocytes per polyp in *A. glauca* in the Red Sea and suggested that the thin encrusting coenenchyme limited the egg count. The difference in the number of oocytes per polyp between the Red Sea and KwaZulu-Natal is not easily explained. However, Margalef (1984), as cited by Coma et al. (1995), proposed that more offspring are produced in temperate and climatically less stable waters than in the tropics, and this may account for the difference; KwaZulu-Natal certainly appears to have a variable climate and turbulent sea (Schleyer 1995) when compared to the more sheltered and environmentally stable conditions of the Red Sea.

In *Anthelia glauca*, the oocytes are produced along the entire length of the mesenteries, and small oocytes are scattered between the large maturing oocytes using the available space efficiently (Benayahu and Loya 1986; Kruger 1996; Schleyer et al. 1997). An alternation between the rapid maturation of oocytes and brooding of embryos and larvae during the reproductive season increases the scope for continuous reproduction. The reproductive potential and success of *A. glauca* is thus enhanced by the reproduction of several gamete cycles in each female polyp with larvae being produced throughout the breeding season.

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