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Gonad development and the planulae of the temperate Australian soft coral *Capnella gaboensis*

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Abstract

Capnella gaboensis Verseveldt, 1977 was sampled at four sites in Sydney Harbour, during 1981–1984. This soft coral has an annual cycle of gonad development, with gonad number reaching a peak in May several weeks prior to spawning, and gonad size reaching a peak in May–June at spawning. The gonads develop during the warm months, and colonies spawn their gametes in late autumn and early winter. Gonad development is neither synchronous within colonies nor within populations, possibly reflecting the protracted nature of spawning. The histology of the developing oocytes and spermaries is described in detail. *C. gaboensis* is a surface-brooder. The planulae are similar in structure to the larvae of other octocorals. The larvae are benthic, settling quickly upon suitable substratum, metamorphosing into polyps with mouths, tentacles and spicules, approximately one week after settling.

Introduction

Capnella gaboensis Verseveldt, 1977 is an abundant and widespread soft coral (Octocorallia, order Alcyonacea, family Nephtheidae) which grows in temperate Australian waters. *C. gaboensis* is dioecious; the sex ratio is biased in favour of males in the Sydney population; colonies become sexually mature at 2 to 3 yr of age; the species has an annual cycle of gonad development and the colonies spawn their gametes in early winter; it is a surface-brooder and the larvae are benthic.

This paper presents a detailed account of gonad development and the development and settlement of the planulae of *Capnella gaboensis*. The aims of this study were: to investigate the annual changes in gonad number and size in *C. gaboensis;* to investigate variation in gonad development between branches of colonies, between colonies, and between populations of *C. gaboensis;* to describe the developmental stages of the female and male gonads of *C. gaboensis* and the time of year and timespan of such stages; and to describe the development of the planulae.

Materials and methods

Most material for the study was sampled from Fairlight, Cobblers, Dobroyd, and Manly Point, four study sites in Sydney Harbour (33°50′S; 151°15′E) during 1981–1984.

Sampling of colonies of *Capnella gaboensis* Verseveldt, 1977 (Table 1) involved the removal of randomly chosen healthy branches (never more than 5% of an individual colony). Each branch was used for dissection of whole gonads, with small portions being used for histological and ultrastructural observations (Farrant, 1985). From May 1981 to May 1982, sections from the top, mid, and base regions of colony branches were used to record number of gonads; the three largest gonads in each section were measured, thus giving a rough measure of the changes in gonad number and size through the year for different regions of the coral branches.

For each colony sampled over the entire sampling period, the sample branch was cut longitudinally into 1 to 2 mm-thick slices, and at least five randomly chosen mesenterial filaments were dissected-out from different polyps. The following information was recorded: abundance of gonads in the coral branch (an estimate on a scale of 0 to 10, where 10 was allocated to the maximum occupation of polyp space by the gonads); number of gonads per filament (note that this may underestimate the true number of gonads per filament because of the difficulty in dissecting-out intact filaments); gonad diameter; sex and stage of development of gonads. Gonad measurements for each sex were totalled to obtain mean diameter (and standard deviation) for each collection. For each collection, the abundance of gonads in coral branches, and the number of gonads per filament in branches, were

Table 1. *Capnella gaboensis.* Sampling schedule at four sites in Sydney Harbour

Sampling period	Site (s)	Sampling frequency	No. of colonies sampled	Sampling protocol
May 1981–May 1982	Fairlight	fortnightly	5	Random, from numbered population of 100 colonies
May 1982–Oct. 1982	Fairlight mainly; Other 3 sites sometimes	fortnightly	5	Random, not from mapped populations
Nov. 1982–Oct. 1984	Fairlight	3-monthly	12	Same 12 mapped colonies at each site, in order to pick up early stages of gametogenesis in colonies whose sex was known
	Cobblers		12	
	Dobroyd		12	
	Manly Point		12	
May 18, 1983	Cobblers	once only	49	All whole colonies collected from a given area of substratum at a time when they could be easily sexed; 10 branches from each of 5 large female colonies and 5 large male colonies from each site were sampled in order to check homogeneity of gonad number and size in populations, colonies and branches
	Fairlight		106	
	Dobroyd		552	
	Manly Point		56	
Occasional sampling	Other localities on N.S.W. coast			Deep sites in Sydney Harbour, Jervis Bay and offshore; shallow sites in other bays and offshore

averaged separately for total female and total male colonies.

Nested analyses of variance were carried out on material collected from all sites on the same day (18 May, 1983; Table 1). Five randomly chosen, whole, large colonies of each sex, from each site, were used. Gonads from ten branches (randomly selected, but from all sides of the colony) were counted and measured for each colony. All data were checked for homogeneity of variance using the F_{max} test applied to residuals, and data were not transformed. The statistical methods of Sokal and Rohlf (1969) and the statistical tables of Rohlf and Sokal (1969) were used.

Branches of ripe female and male *Capnella gaboensis* colonies were kept in dishes and allowed to spawn naturally in the laboratory. The development of larvae resulting from the fertilization of the eggs by the sperm was monitored.

Seawater temperature was measured at Fairlight (at 6 m depth, using a thermometer) at fortnightly intervals during the first year of the study. Seawater temperatures for Manly ocean beach, 1 km away, were obtained from the local newspaper for the entire study period.

Results

The gonads of *Capnella gaboensis* develop on the ventral and lateral mesenterial filaments, in the part of the polyps below the level of the coenenchyme. Histological sections and dissections indicate that gonads are located on two or three, rarely more, of the filaments in any one polyp. The development of both female gonads (ovaries, each consisting of a single oocyte) and male gonads (spermaries) follows an annual cycle.

Gonad abundance

In *Capnella gaboensis* colonies, gonad abundance is greatest in May and least in July to November (Fig. 1). The number of spermaries per filament is much greater than the number of oocytes per filament, especially in the period November to May (Fig. 2). The maximum numbers of oocytes and spermaries recorded on a filament were 14 and 55, respectively, with average numbers per filament of approximately 8 (female) and 15 (male) several weeks prior to spawning, when gonads were still attached to the filaments. At this time the polyps contain up to about 40 ova or over a hundred spermaries. The number of ripe ova or spermaries in the polyps at spawning is not as great, which may indicate resorption of small gonads by larger ones. Female colonies generally spawn about 5 to 10 ova per polyp, and males about 10 to 20 spermaries per polyp.

Gonad size

Spermaries are smaller than oocytes throughout most of the year (Fig. 3). The average sizes of gonads at spawning are: $492 \pm 69\,\mu m$ (ova, $n = 1\,000$) and $287 \pm 74\,\mu m$ (spermaries, $n = 1\,000$). The variation in gonad size at any one time is due to the presence of several gametogenic stages. The smaller gonads appear to be resorbed prior to spawning.

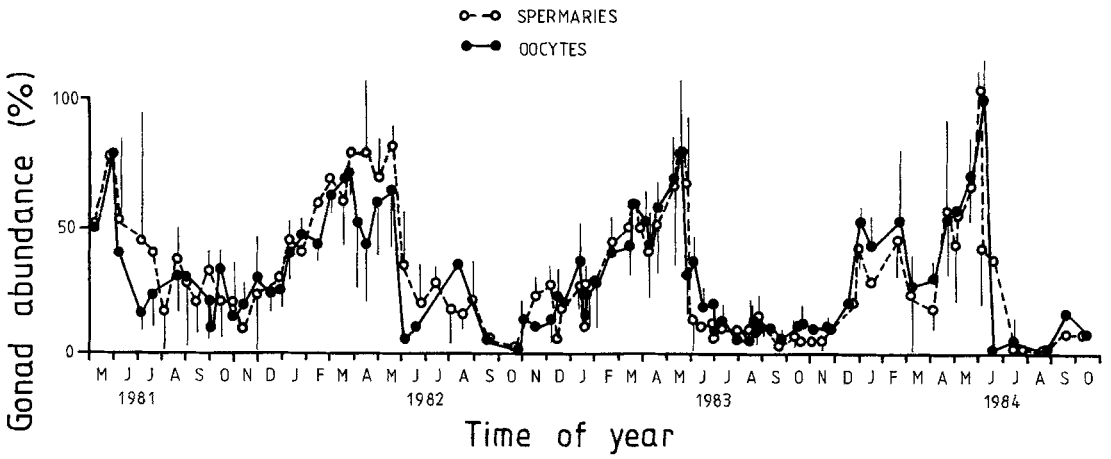

Fig. 1. *Capnella gaboensis.* Abundance of female and male gonads 1981–1984 as percentage of maximum gonad abundance observed. Standard deviation lines are shown to one side only. Each point represents mean (usually for 3 colonies) of one collection. All data are for collections from the four study sites in Sydney Harbour

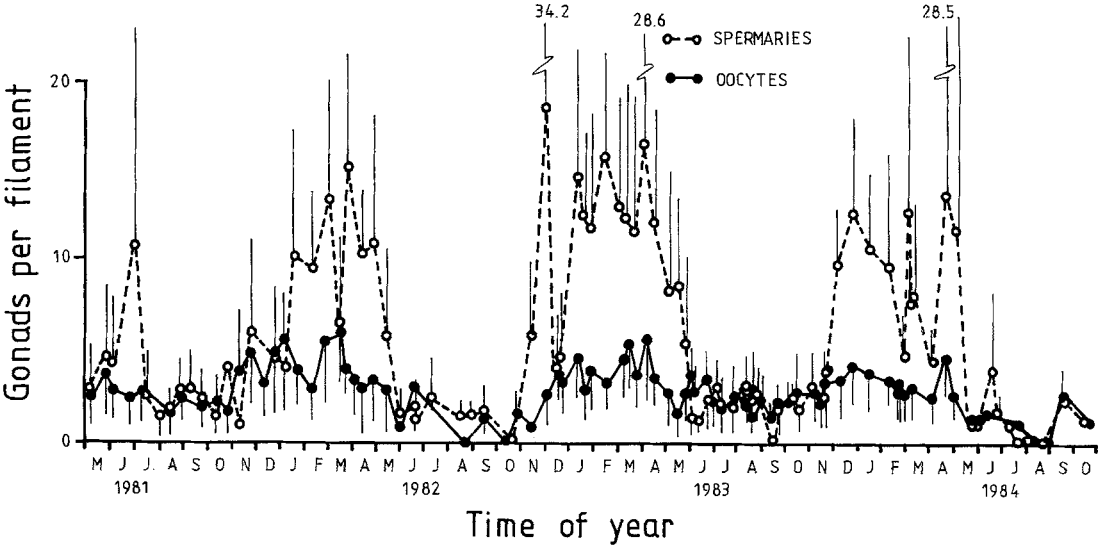

Fig. 2. *Capnella gaboensis.* Number of female and male gonads per mesenterial filament, 1981–1984. Standard deviation lines are shown to one side only. Each point represents mean (usually for filaments from 3 colonies) of one collection. All data are for collections from the four study sites in Sydney Harbour

Fig. 4 shows the size-frequency distribution of gonads from the same female colony and the same male colony, from July 1983 to October 1984. Swellings were observed on some filaments soon after spawning. Histological sections revealed that these were the very early stages of gonad development, consisting of "clusters" of primordial generative cells, oogonia/spermatogonia and spermatocytes, and young primary oocytes/spermaries. The occurrence of the clusters was infrequent until November. In these individual colonies, therefore, most of the gonads developed over a period of 6 to 7 mo. Likewise, in the overall population, few colonies contain gonads in September or October (Fig. 1), and the main growth period of the gonads is from November to May. The start of this growth period corresponds with the rise in seawater temperatures in late spring–early summer (Fig. 5). Spawning in populations coincides with the fall in seawater temperature in late autumn–early winter.

Variation of gonad development between colonies and between branches

Table 2 lists the results obtained from nested analyses of variance calculated from gonad abundance estimates and gonad diameter measurements. The differences in gonad diameter between branches (i.e., within colonies) were found to be significant for most female and male colonies at most sites. The differences in gonad diameter between branches were not as great as the differences between colonies (i.e., within populations at each study site; Table 2). There were also significant differences in gonad

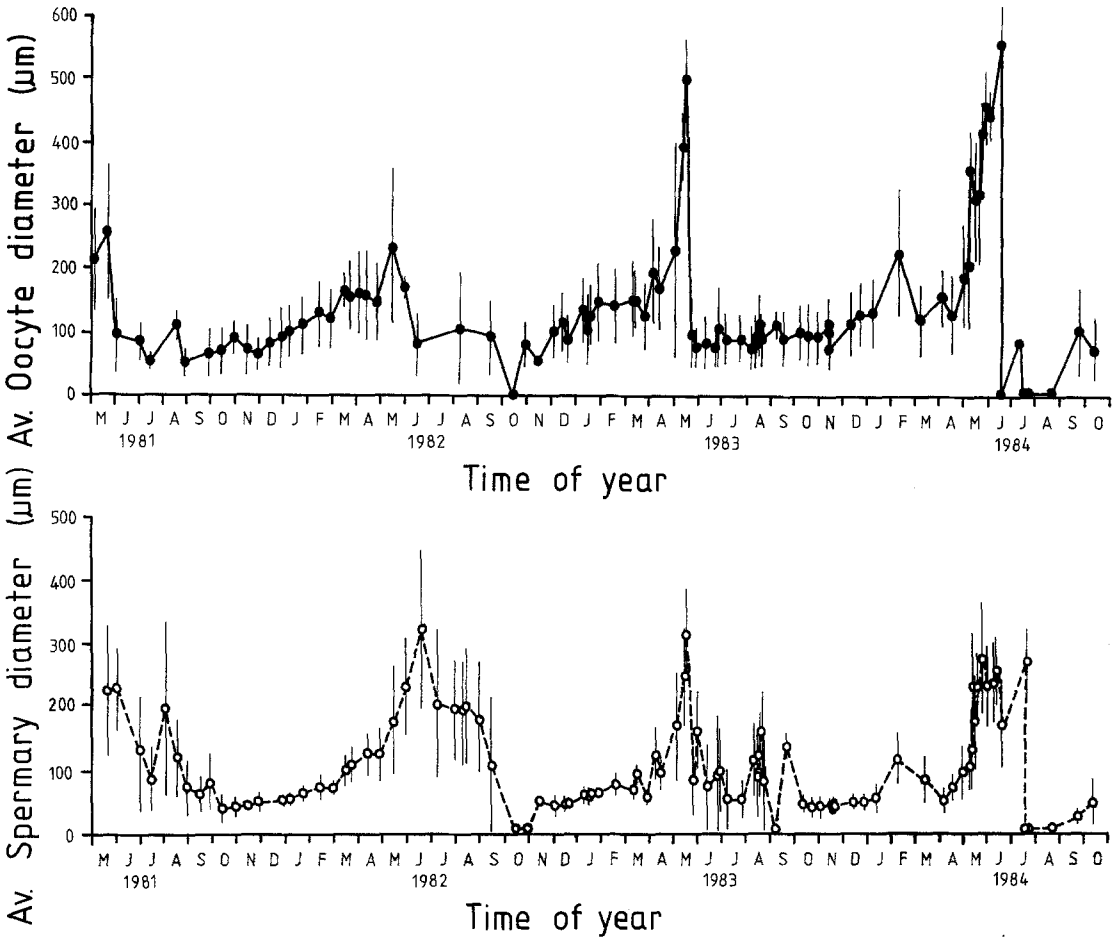

Fig. 3. *Capnella gaboensis.* Average diameter of oocytes and spermaries, 1981–1984. Vertical lines indicate standard deviations. Each point represents mean (usually for filaments from 3 colonies) of one collection. All data are for collections from the four study sites in Sydney Harbour

Table 2. *Capnella gaboensis.* Results of nested analyses of variance on probabilities of the variation in gonad diameter and gonad abundance, between sites, colonies and branches being due to chance alone

	At each site			
Location	Gonad diameter			
	Between colonies		Between branches	
	♀	♂	♀	♂
Fairlight	0.05–0.10	$\ll 0.001$*	0.01–0.025*	0.1–0.25
Cobblers	$\ll 0.001$*	0.001–0.005*	>0.75	$\ll 0.001$*
Dobroyd	0.005–0.10	$\ll 0.001$*	0.001–0.005*	0.025–0.05*
Manly Point	$\ll 0.001$*	0.001–0.005*	<0.001*	<0.001*

	For all sites:			
	Gonad abundance		Gonad diameter	
	♀	♂	♀	♂
Between sites	>0.75	$0.1<p<0.25$	0.25–0.5	0.01–0.025*
Between colonies	<0.001*	<0.001*	$\ll 0.001$*	$\ll 0.001$*

* Significant at the 5% level

abundance between colonies. These results indicate that the cycle of gonad development is not at an equivalent stage for all the colonies, even when the gonads are ripe, making a single spawning event unlikely. The collection on 18 May 1983 contained ripe females, females with embryos and females with larvae, providing further evidence for protracted spawning in populations.

Variation of gonad development between sites

For the material collected on 18 May 1983, there were no significant differences in gonad abundance between the populations at the four study sites. Male gonad size differed significantly between sites, whereas female gonad size did not (Table 2). Material collected from other shallow sites in Botany Bay (Bare Island), Jervis Bay, and offshore (Elephant Rock), from two deep sites (North Head, Colours Reef) and from Coffs Harbour, was also consistent with the annual cycle displayed by the populations in Sydney Harbour. The only exception to this pattern was a single female colony from deep water at Long Reef, which still contained numerous ripe eggs in August, several months after eggs had been spawned by the

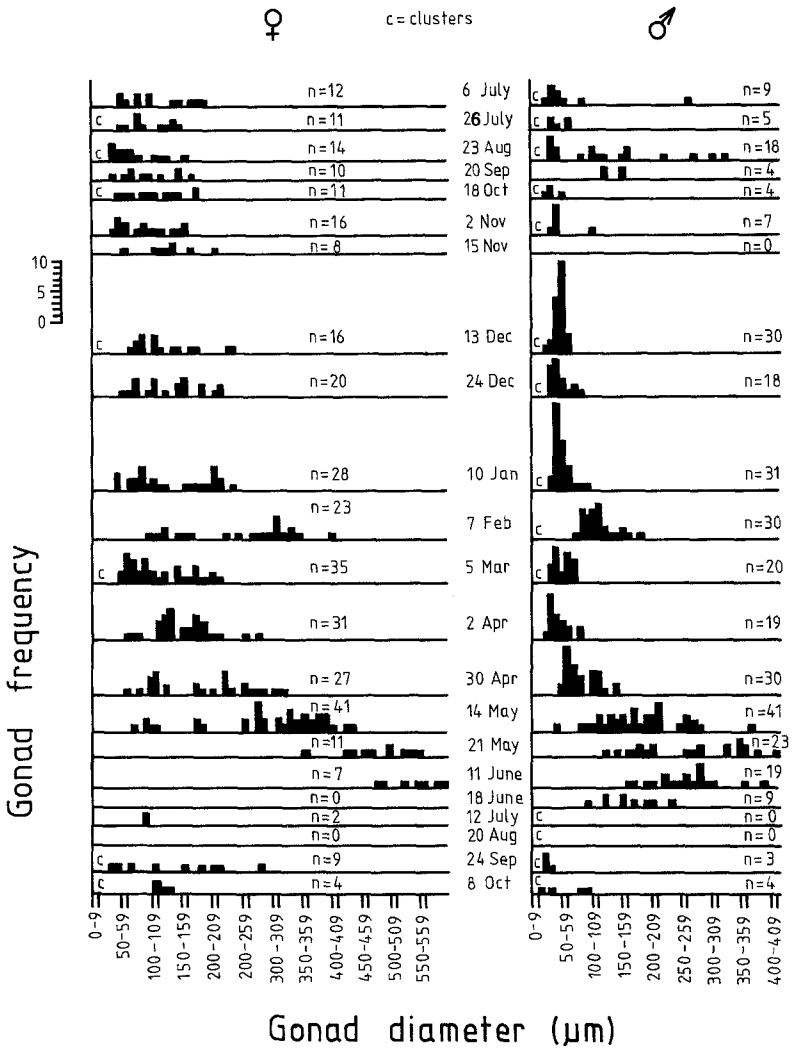

Fig. 4. *Capnella gaboensis.* Size-frequency distribution of gonads from the same female colony (left) and the same male colony (right), both at Fairlight, Sydney Harbour, July 1983–October 1984

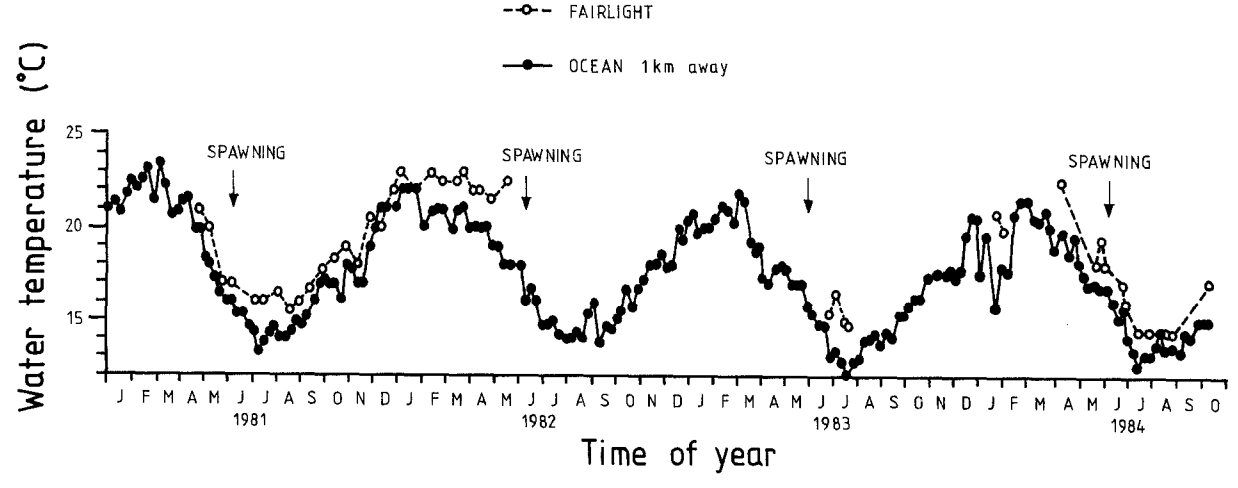

Fig. 5. Seawater temperature at Manly ocean beach and Fairlight, 1981–1984

Table 3. *Capnella gaboensis.* Gametogenic stages of ova and spermaries. Diameters include endoderm; width of endoderm is shown in parentheses; cl: clusters. + indicates presence of stage in that month. Fig. nos. are those figures in which the respective stages are illustrated

Description of stage	Fig. no.	Max. diam (μm)	Duration (month) J F M A M J J A S O N D
Female			
(A) *Clusters of primordial generative cells, oogonia and young primary oocytes:* primordial generative cells divide to form oogonia which develop into primary oocytes by growth, enlargement of nucleus, appearance of a nucleolus. Individual oocytes cannot be seen in dissections	6 a	20 (cl)	+ + + + + + +
(B) *Clusters where small primary oocytes (=young ova) can be seen in dissected colonies:* cluster is embedded in mesogloea and surrounded by cuboidal endoderm. Oocytes bulge into gastrovascular cavity, large central nucleus, dark staining nucleolus, slightly granular cytoplasm	6 b	45 (cl, 4)	+ + + + + + + + + + + +
(C) *Large stalked oocytes:* covered with dense mesogloea, squamous-cuboidal endoderm, finely granular cytoplasm	6 c	300 (4)	+ + + + + + + + + + + +
(D) *Mature oocytes (ova):* with peripheral nuclei, darkly staining basement membrane and columnar non-ciliated endoderm. Ova detach from the mesentery and move to the polyp mouth. Yellow-orange ova easily seen in polyps	6 d, 6 e	520 (18)	+ + + + + +
(E) *Spent ovaries:* the endodermal layers which are left behind in the female parent colony after spawning	6 f	spent	+
Male			
(A) *Clusters of primordial generative cells, spermatogonia, spermatocytes and young spermaries:* the primordial generative cells divide to form the spermatogonia, which develop into spermatocytes and become spermaries by many divisions. Spermaries cannot be seen in dissections	7 a	20 (cl)	+ + + + + + + + + +
(B) *Clusters in which the young spermaries can be seen, although still within a common endodermal covering:* each contains a number of large spermatocytes. The endoderm is cuboidal or columnar. Nuclei are large, stain lightly	7 b	50 (cl, 6)	+ + + + + + + + + + + +
(C) *Stalked spermaries:* containing many spermatocytes so the separate spermaries bulge into gastrovascular cavity, joined by stalks to the mesentery. Tall endodermal cells	7 c	95 (6)	+ + + + + + + + + + + +
(D) *Small spermary:* spermatocytes divide to increase the number of cells. Columnar-cuboidal endodermal cells	7 d	180 (7)	+ + + + + + + + +
(E) *Large spermary:* with central cavity or darkly staining central spermatids, and with squamous endoderm	7 e, 7 f	235 (9)	+ + + + + + +
(F) *Spermary with spermatids:* small round darkly staining cells, usually in radial rows. Squamous endoderm	7 g	350 (9)	+ + + + + +
(G) *Ripe spermary:* containing radial rows of sperm with conical heads (1 μm × 5 μm) and long tails (50 μm). Endoderm squamous, spermaries visible inside polyps. Spermaries or free sperm may be shed (evidence for both)	7 h, 7 i	400 (5)	+ + + + + + + + +

females in all the other populations. This may indicate either that spawning is delayed in deeper water, or that this particular colony was an oddity.

Histology of the gonads

The gonads develop in *Capnella gaboensis,* as in other soft corals, from cells in the mesogloea of the ventral and lateral mesenteries (the two dorsal ones are sterile), and the ripe gonads bulge from the septa into the gastrovascular cavities. As Hickson (1895) found for *Alcyonium digitatum,* the very young testes of *C. gaboensis* cannot be distinguished from the very young ovaries, since both consist simply of a number of small round cells on the mesenteries covered by a layer of endodermal cells. In *C. gaboensis,* the gonads are first observed as clusters (of primordial generative cells, oogonia/spermatogonia and

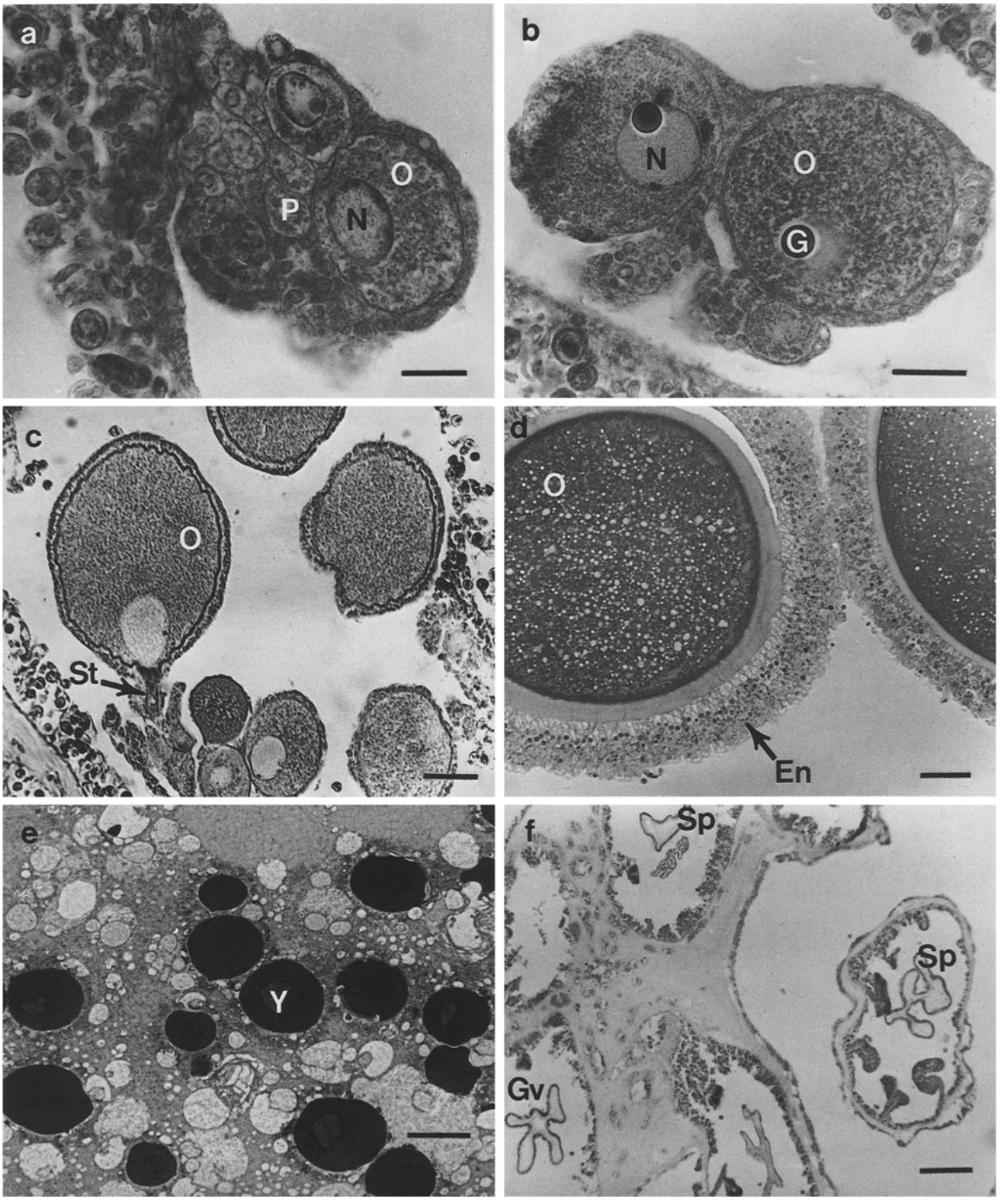

Fig. 6. *Capnella gaboensis.* Stages of oogenesis. (a) Stage A: cluster of primary genital cells (oogonia; P), and small primary oocytes (O) with large nuclei (N); scale bar = 15 μm. (b) Stage B: cluster of small primary oocytes (O) with large nuclei (N) and deeply stained nucleoli (germinal spots; G); scale bar = 15 μm. (c) Stage C: large stalked oocytes (O); St: stalk; scale bar = 30 μm. (d) Stage D: mature oocytes (ova; O); with columnar endodermal covering (En); scale bar = 20 μm. (e) Stage D: transmission electron micrograph showing yolk granules (Y) inside a mature egg; scale bar = 2 μm. (f) Stage E: spent ovaries (Sp) in gastrovascular cavities (Gv) of polyps in a female colony which has spawned; scale bar = 10 μm

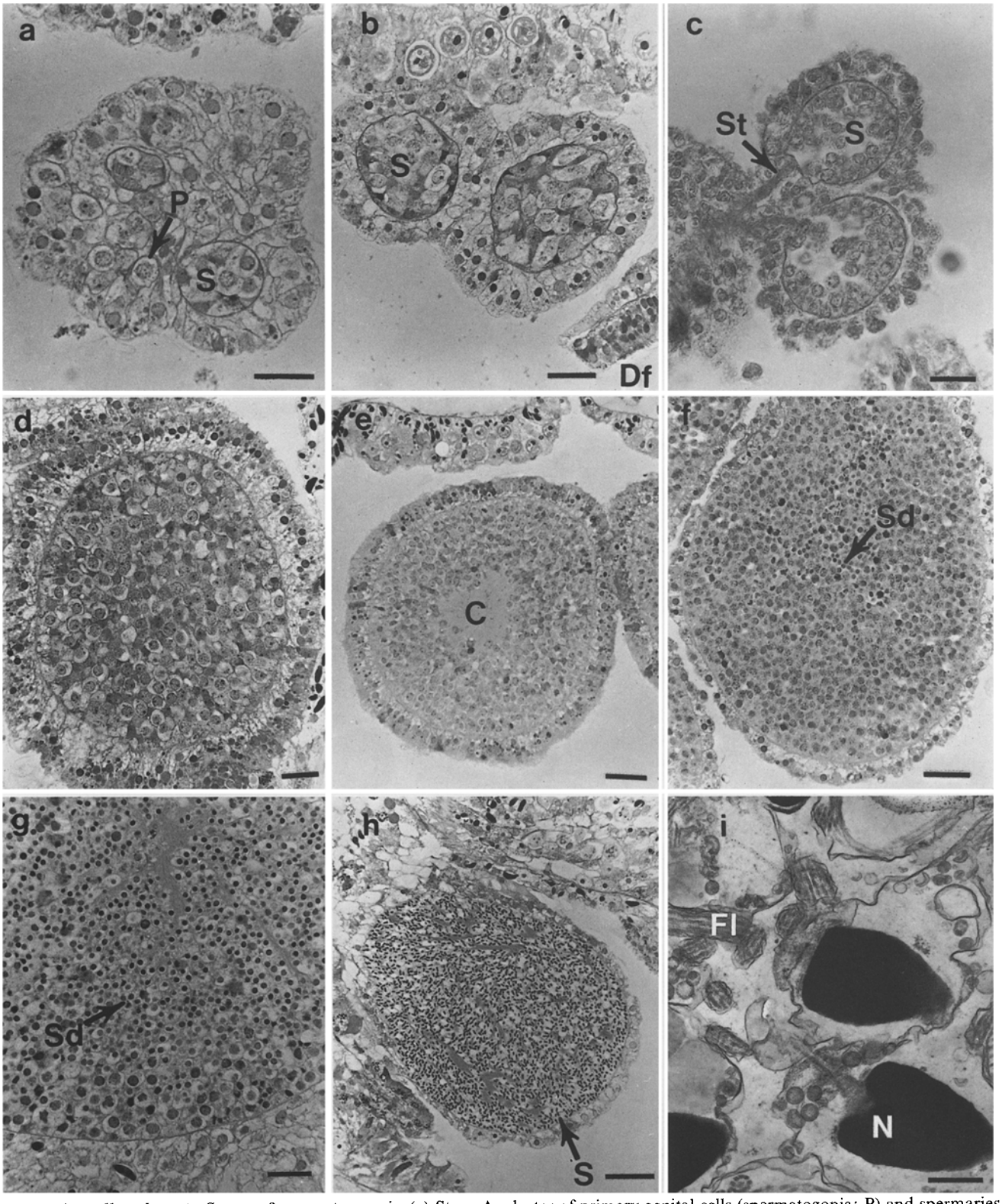

Fig. 7. *Capnella gaboensis.* Stages of spermatogenesis. (a) Stage A: cluster of primary genital cells (spermatogonia; P) and spermaries (S) containing spermatocytes; scale bar = 20 μm. (b) Stage B: two young spermaries (S) in a cluster, and dorsal mesenterial filament (Df); scale bar = 20 μm. (c) Stage C: stalked spermaries (S); St: stalk; scale bar = 15 μm. (d) Stage D: small spermary (and part of an adjacent one) in gastrovascular cavity; scale bar = 20 μm. (e) Stage E: large spermaries, one with a central cavity (C); scale bar = 30 μm. (f) Stage E: large spermary with central small darkly stained spermatids (Sd); scale bar = 30 μm. (g) Stage F: part of spermary almost filled with spermatids (Sd); scale bar = 15 μm. (h) Stage G: ripe spermary with sperm (S); scale bar = 25 μm. (i) Stage G: transmission electron micrograph showing sperm, with condensed conical darkly stained nuclei (N) and flagella (Fl); scale bar = 0.5 μm

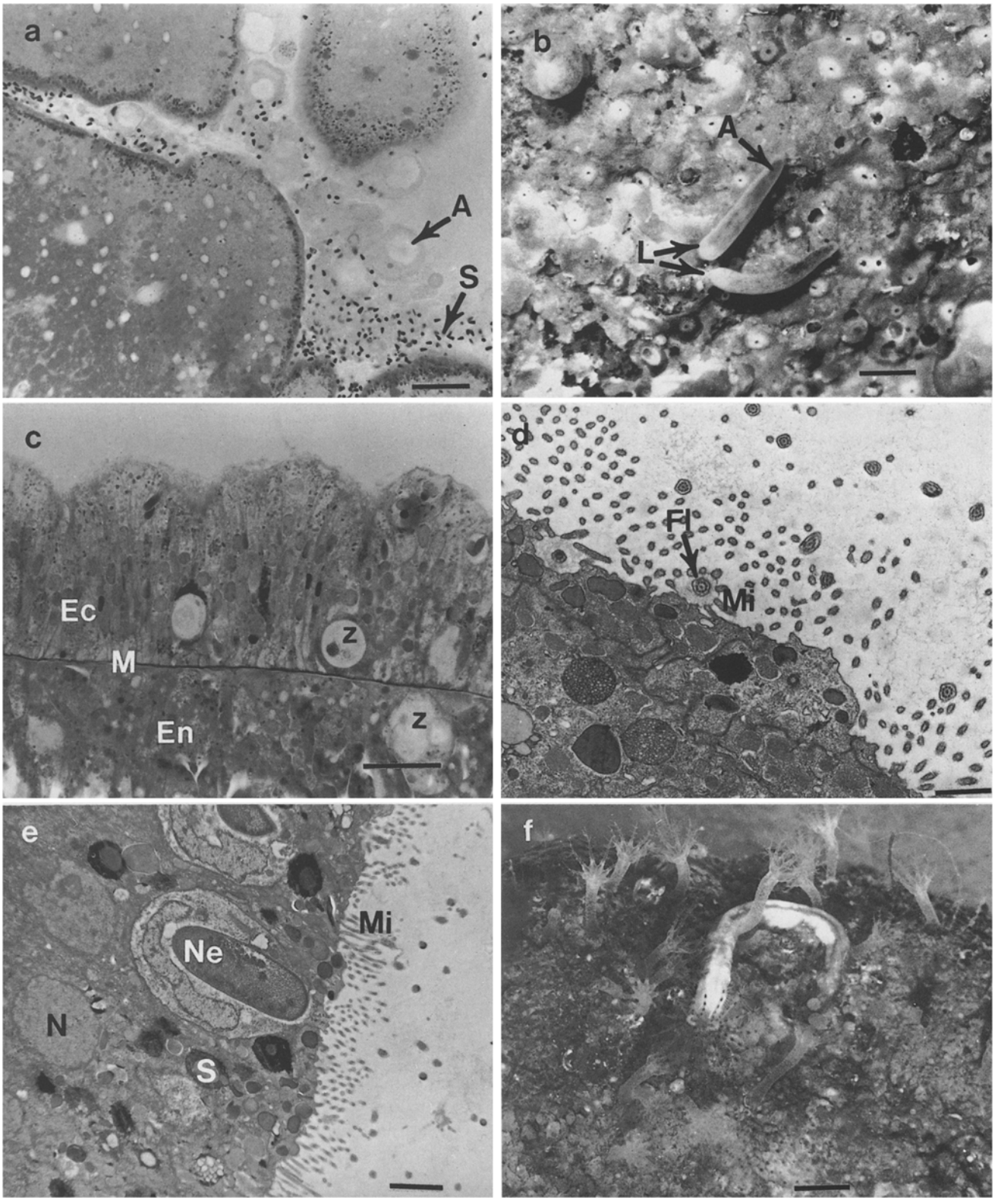

Fig. 8. *Capnella gaboensis.* Development of larvae. (a) Section through edge of an early embryo showing sperm (S) and algae (zooxanthellae; A) on outside; scale bar = 10 μm. (b) Larvae (L) with algae (A) visible as dark patches inside; scale bar = 1 mm. (c) Section through edge of a larva showing endoderm (En), mesogloea (M), and ectoderm (Ec); z: zooxanthellae; scale bar = 10 μm. (d) Transmission electron micrograph showing flagellate collar region of a cell in the larval ectoderm; flagellum (Fl) is surrounded by collar of microvilli (Mi); scale bar = 1 μm. (e) Transmission electron micrograph showing nematocysts (Ne), secretory granules (S), nuclei (N), and microvilli (Mi) in larval ectoderm; scale bar = 2 μm. (f) Polyps 13 d after settling, with well developed tentacles and pinnules; scale bar = 2 mm

spermatocytes, and young primary oocytes/spermaries), with several clusters per mesentery, as for other octocorals. The gametogenic stages recognized for *C. gaboensis* are given in Table 3, which also lists the figures illustrating the various stages, the maximum size of each stage (including the endodermal layer), the mean width of the endodermal layer, and the time of the year during which the stages are present. Stages of oogenesis are shown in Fig. 6, and stages of spermatogenesis in Fig. 7.

Larval development

The eggs of *Capnella gaboensis* are fertilized on the outside of the female colonies: sperm were never seen along the mesenterial filaments of recently spawned female colonies as they are in *Parerythropodium fulvum fulvum* (Benayahu and Loya, 1983), although they were plentiful around embryos on the outside of the colonies (Fig. 8 a); nor were embryos ever observed inside polyps in sections. *C. gaboensis* is a surface-brooder, and the polyps of the parent colony bend over to conceal the embryos during their development. The larvae of *C. gaboensis* are 1.0 to 2.0 mm long and up to 0.4 mm wide, and they contain numerous zooxanthellae (Fig. 8 b). Abnormally shaped larvae were observed, including several which appeared to have resulted either from two fused eggs or two fused larvae. The larvae consist of an endoderm, which is continuous with the central yolk material, a thin mesogloea, and an ectoderm (Fig. 8 c). Ultrastructurally, the columnar ectoderm has microvilli and contains flagellate collar cells (Fig. 8 d), secretory cells, and nematocysts (Fig. 8 e). Zooxanthellae are frequently seen in the ectoderm of immature larvae (Fig. 8 c), although they occur only in the endoderm of mature larvae. Zooxanthellae adhering to the sticky spawned eggs may be trapped in the bulges of dividing embryos (Fig. 8 a).

Larval settlement and metamorphosis

Capnella gaboensis planulae are fully benthic and crawl with the blunt (aboral) end forward. The larvae are slow moving, and are also able to contract and change shape. In the laboratory the larvae begin to settle within 1 to 2 d of leaving the parent colony, providing they find suitable substratum. They remain viable (i.e., capable of settling) for at least one month after leaving the parent colony. The larvae attach to the substratum by the aboral end. They become wrinkled, then flatten, metamorphosing into polyps with mouths after several days. The polyps have spicules and tentacles after approximately one week, and the tentacles are well developed and pinnate after one-and-a-half weeks (Fig. 8 f). *C. gaboensis* polyps in the laboratory did not grow as rapidly as those in the field, and they did not produce buds. One small colony in the field was observed to consist of four polyps approximately ten weeks after spawning.

Discussion and conclusions

Capnella gaboensis has an annual cycle of gonad development, with ova and spermaries developing in less than one year. Gonad development in octocorals generally, ranges from several months to two years. When development takes longer than one year, two size classes of gonads will be present simultaneously. This occurs in the soft coral *Lobophytum crassum* (Yamazato *et al.*, 1982), and the gorgonian *Corallium rubrum* (Vighi, 1972). In *Capnella gaboensis*, female and male gonads take almost the same time to develop, whereas for most octocorals the spermaries develop in a much shorter time than the ova (Vighi, 1972; Yamazato *et al.*, 1982; Benayahu and Loya, 1983). *C. gaboensis* colonies do not go through an annual cycle of expansion and contraction activity corresponding with the annual cycle of gonad development, as has been reported for *Alcyonium digitatum* (Hartnoll, 1975).

The ripe eggs and spermaries of *Capnella gaboensis* are similar in size to those of other soft corals (Ashworth, 1899; Hartnoll, 1975; Yamazato *et al.*, 1982; Benayahu and Loya, 1983, 1984 a). There is little published data concerning the numbers of oocytes and spermaries within soft coral polyps during gonad development. In corals generally, the number of gonads produced in polyps of different species seems to depend upon the size of the polyps, the size reached by the gonads, and whether or not the coral is a brooder. In *C. gaboensis*, resorption of small gonads during the annual cycle appears to be responsible for a decline in the number of gonads as they approach maturity.

Gonad development was generally not synchronized in different branches of *Capnella gaboensis* colonies, even just prior to spawning. Usually gonad development within coral colonies is synchronized, e.g. *Parerythropodium fulvum fulvum* (Benayahu and Loya, 1983) and *Porites* species (Kojis and Quinn, 1982). Nevertheless, gonad development in *C. gaboensis* showed even less synchrony at a population level. This is related to the protracted nature of spawning within *C. gaboensis* populations. *Alcyonium digitatum*, another soft coral with protracted spawning, also shows variation in gonad development between colonies close to spawning (Hickson, 1895). When colonies in a population all spawn at once, gonad development usually becomes synchronized at this time, whereas there is usually no synchronization between coral colonies in populations which breed for much of the year, e.g. *Stylophora pistillata* (Rinkevich and Loya, 1979 b).

Gonad development in *Capnella gaboensis* populations at different sites was synchronized. Spawning may be delayed in deeper populations of *C. gaboensis*, as it is for two gorgonians, *Muricea californica* and *M. fruticosa* (Grigg, 1977) and for *Parerythropodium fulvum fulvum* (Benayahu and Loya, 1983), although this aspect requires further investigation.

The histological development of *Capnella gaboensis* gonads is similar to that reported for other soft corals (Ashworth, 1899; Gohar, 1948; Gohar and Roushdy, 1961)

and other octocorals (e.g. Chia and Crawford, 1973). In *C. gaboensis,* not all the primordial oocytes in an ovary develop into oocytes. Eventually each ovary is spherical and contains only one oocyte. Ovaries in *C. gaboensis* never contain two oocytes in their later stages in the manner described for the hard coral *Stylophora pistillata* (Rinkevich and Loya, 1979a). In *C. gaboensis,* the eggs are attached by a stalk to the mesentery, as for other octocoral eggs, and they contain nuclei up until the time they are spawned. The eggs are probably not fertilized inside the parent colony. Ripe *C. gaboensis* oocytes are similar in ultrastructure to those of *Hydra* sp. (Thorington and Margulis, 1980), with a border of microvilli, cortical lipid globules and yolk spheres, abundant mitochondria, rough endoplasmic reticulum and Golgi bodies. The endoderm surrounding *C. gaboensis* oocytes is not ciliated as in other octocoral eggs, e.g. *Xenia macrospiculata* (Benayahu and Loya, 1984a). The sperm of *C. gaboensis* are similar in size to those of other octocorals, e.g. *X. hicksoni* (Ashworth, 1899) and *Heteroxenia fuscescens* (Gohar and Roushdy, 1961).

Capnella gaboensis larvae are similar in structure to other octocoral larvae (e.g. *Alcyonium digitatum,* Matthews, 1917) and do not have an oral aperture or gastrovascular cavity at this stage. The collar cells in *C. gaboensis* larvae are similar to those in the octocoral *Veretillum cynomorium* (Bilbaut and de Ceccatty, 1971) and in the ectoderm of larvae of the hard coral *Balanophyllia regia* (Lyons, 1973). Collar cells usually have a sensory or feeding function (Lyons, 1973). Other benthic soft coral larvae include those of *Xenia macrospiculata* (Benayahu and Loya, 1984b) and *Alcyonium siderium* (Sebens, 1983a, b). Given that *C. gaboensis* larvae move slowly and settle quickly, they would not normally disperse far from parent colonies. For benthic larvae, long-range dispersal probably relies upon strong water motion to dislodge them from the substratum, as well as an ability to delay metamorphosis.

Capnella gaboensis larvae have an apparent preference for aged substrata such as sandstone (own unpublished data). Large numbers of new recruits were observed in the field, especially near to parent colonies, and they had settled upon rock, red algae (encrusting coralline and frondose) and shells. The triggering factors for settlement of *C. gaboensis* larvae appear to be similar to those recorded for other octocorals: natural, rough substratum covered with other living organisms (Cary, 1914; Matthews, 1917; Gohar, 1940; Weinberg and Weinberg, 1979; Sebens, 1983a, b; Benayahu and Loya, 1984b); the presence of other larvae (Matthews, 1917) and the absence of certain other organisms (Sebens, 1983a). The degree of water movement might also be important in substratum selection, as for *Alcyonium siderium* larvae (Sebens, 1983b), although this was not investigated for *C. gaboensis.* Symbiont-containing larvae like those of *C. gaboensis* would be not expected to settle in dark places, and metamorphosis may even be inhibited in the dark (Sebens, 1983a). Investigations of octocoral planulae in general have shown that selection of substratum varies considerably among species. Metamorphosis of *C. gaboensis* larvae is similar to that recorded for other octocorals (Weinberg and Weinberg, 1979; Benayahu and Loya, 1984b).

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