

REPRODUCTION IN THE TEMPERATE AUSTRALIAN  
SOFT CORAL *CAPNELLA GABOENSIS*

LA REPRODUCTION CHEZ LE CORAIL MOU  
*CAPNELLA GABOENSIS* DES EAUX TEMPEREES AUSTRALIENNES

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ABSTRACT

*Capnella gaboensis* is probably the most abundant and widely distributed octocoral growing in temperate Australian waters. This study, the first on reproduction of any temperate Australian coral, involved an investigation of : general features of sexual reproduction in *C. gaboensis*; development of the gonads, spawning, fertilization and embryo-development; transmission of zooxanthellae; aspects of larval life; and importance of asexual reproduction.

*C. gaboensis* reproduces primarily by sexual means. It is dioecious, with a low incidence of hermaphroditism and relatively early onset of sexual maturity. It is a small-polyped coral, highly fecund, with protracted spawning of relatively large gonads in winter following a period of 6-7 months gametogenesis. *C. gaboensis* eggs remain on the outside of the female parent colony where fertilization and development of the embryo take place. Planulae are demersal. Since they generally do not move far from parent colonies, and since they settle rapidly upon suitable substrate, this leads to aggregated populations of *C. gaboensis*. Dispersal of the species into new habitats is probably achieved during storms when water movement is sufficient to sweep larvae off the substrate and carry them away. Larvae are still capable of settling for at least one month after they have left the parent colony.

No aposymbiotic forms of *C. gaboensis* have been observed. Zooxanthellae are present in large numbers in all larvae. Developing oocytes never contain algae. When they are spawned, a sticky coating ensures that eggs carry with them a covering of zooxanthellae. The algae enter the fertilized egg during the later stages of segmentation, ensuring that the mature larva has a full complement of zooxanthellae in its endoderm before it leaves the parent colony.

RESUME

*Capnella gaboensis* est probablement le plus abondant et le plus répandu des Octocoralliaires vivant dans les eaux tempérées australiennes. Ce travail, le premier réalisé sur la reproduction d'un corail des eaux tempérées d'Australie, comprend une étude des traits généraux de la reproduction sexuée chez *C. gaboensis*, du développement des gonades, de la ponte, de la fécondation et du développement de l'embryon, de la transmission des zooxanthelles, de certains aspects de la vie larvaire, et de l'importance de la reproduction asexuée.

*C. gaboensis* se reproduit surtout par voie sexuée; il est dioïque, plus rarement hermaphrodite, et arrive relativement tôt à maturité sexuelle. C'est un corail à petits polypes, très fécondes, avec des gonades relativement développées et une longue saison de reproduction en hiver, après une période de gamétogenèse de 6-7 mois. Les oeufs de *C. gaboensis* restent accrochés à l'extérieur de la colonie-mère femelle où la fécondation et le développement de l'embryon ont lieu. Les planula sont benthiques. Comme ces larves ne s'éloignent en général pas de la colonie-mère, et se fixent rapidement en présence d'un substrat adéquat, elles constituent des populations aggr de *C. gaboensis*. La colonisation de nouveaux habitats par cette espèce se produit probablement au cours de tempêtes, lorsque le mouvement de l'eau est suffisant pour balayer les larves de leur substrat et les transporter au loin. Les larves sont toujours capables de se fixer, au moins un mois après avoir quitté la colonie-mère.

Aucune forme d'aprosymbiose n'a été observée. Les zooxanthelles sont présentes en grand nombre chez toutes les larves. Les ovocytes ne renferment jamais d'algues. Lors de la ponte, les oeufs sont recouverts d'une muqueuse riche en algues. Les algues pénètrent l'oeuf fécondé au cours des derniers stades de la segmentation, et se retrouvent dans l'endoderme. La larve quittera la colonie-mère, dotée de son complément algal.

## INTRODUCTION

*Capnella gaboensis* is the most abundant and widely distributed octocoral growing in temperate Australian waters. The species was described only recently (Versveldt, 1977), and little is known about its life history. There have been no studies of reproduction in any temperate Australian corals (octocorals or hard corals). There have been several studies of reproduction in the northern hemisphere cool temperate soft coral *Alcyonium digitatum* (eg Hartnoll, 1975), and of warm temperate soft corals in the Red Sea (Gohar, 1940, 1948; Gohar and Roushdy, 1961; Benayahu and Loya, 1983, 1984) and in Japan (Yamazato *et al.*, 1981). Recently the number of studies on hard coral reproduction in both temperate and tropical locations has increased.

*Capnella gaboensis* is widely distributed in the temperate waters of south-eastern Australia. Colonies inhabit rocky reefs from depths of 5m to at least 28m. The species is extremely abundant in shallow bays, and estuaries such as Sydney Harbour, where aggregations reach densities of 60 colonies per square metre. In this study, the annual water temperature range recorded at the main study site in Sydney Harbour was 13°C - 23°C.

*Capnella gaboensis* belongs to the soft coral family Nephtheidae. Colonies are small-polyped, grey-brown in colour, up to 40cm tall, upright and branched in form, and up to about 1 kg wet weight. *C. gaboensis* harbours zooxanthellae.

This paper describes the sexual reproductive cycle of *Capnella gaboensis*, and examines the importance of asexual reproduction for the species.

## MATERIALS AND METHODS

**Sampling schedule:** most material for the study of reproduction in *Capnella gaboensis* was sampled from four study sites in Sydney Harbour (New South Wales, Australia): Fairlight, Cobblers, Dobroyd, and Manly Pt (figure 1). Table 1 outlines the sampling schedule. Sampling of colonies involved the removal of branches (never more than 5% of an individual colony). Samples were prepared for histological and ultrastructural observations, and part of each sample was used for dissection of whole gonads. Spawning and recruitment were

monitored in field populations (table 1). Larval settlement and longevity were studied in the laboratory. The age of first reproduction was established from a collection of colonies growing upon an artificial reef of known age.

**Light microscopy:** material was fixed either in Bouin's fixative (for several days) or in 3% glutaraldehyde in cacodylate buffer, pH 7.1, at 4°C (12 hours). Corals fixed in Bouin's were embedded in Paraplast and sectioned to 7 µm. Corals fixed in glutaraldehyde were decalcified in cacodylate buffer, pH 7.1 (0.1M) containing 3% EDTA (ethylenediamine-tetra-acetic acid) for several days at 4°C, then embedded in glycol methacrylate (Cole and Sykes, 1974) and sectioned to 2 µm.

Histological sections of ova at all stages of development were observed for the presence of zooxanthellae. Similar observations were made for embryos and for planulae larvae from colonies collected 18/05/83 and in 1984. During the 1984 spawning period, fresh squashed ova were observed as frequently as possible using fluorescence microscopy, since the zooxanthellae were easily distinguished by the red chlorophyll fluorescence during UV excitation (Muscatine and McAuley, 1982). This was done in order to establish the stage at which reinfection of the new generation occurred.

**Electron microscopy:** pieces of corals for transmission electron microscopy were fixed with 3% glutaraldehyde in 0.1M cacodylate buffer pH 7.1, at 4°C (1-2 hours), decalcified in the same buffer containing 3% EDTA at 4°C (1-2 days), post-fixed in 2% osmium tetroxide in the same buffer at 4°C (1-2 hours), embedded in Spurr's (1969) resin, and stained with uranyl acetate and lead citrate (Reynolds, 1963). Ultrathin sections were viewed with a Phillips EM-300 at Sydney University.

Figure 1: location of the study sites in Sydney Harbour (Fairlight, Dobroyd, Cobblers, Manly Pt), and other collecting sites.

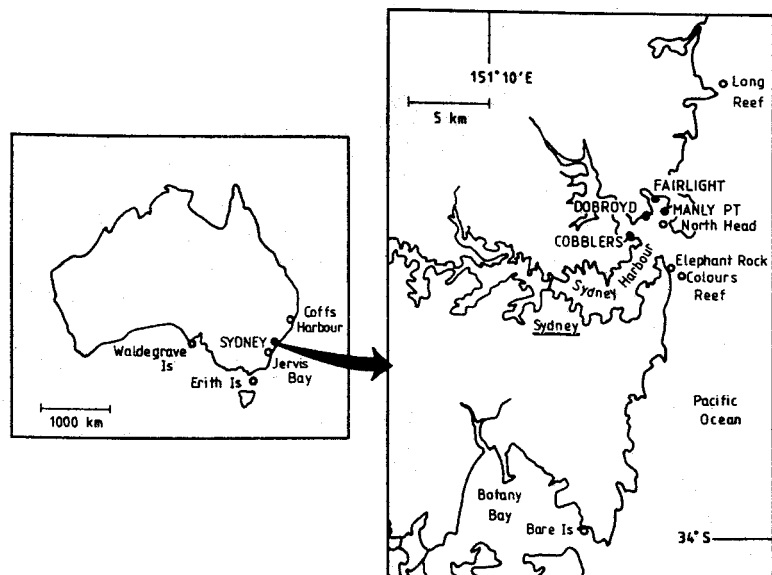


Table 1: sampling schedule

Sampling Period	Site(s)	Frequency	No. of Colonies	Sampling Protocol
May 81-May 82	Fairlight	fortnightly	5	Random, from numbered populations of 100 colonies.
May 82-Oct 82	Fairlight mainly, and other sites	fortnightly	5	Random, not from mapped populations.
Nov 82-Oct 84	Fairlight	fortnightly (more often at spawning)	12	Same 12 mapped colonies at each site, in order to pick up early stages of gamete maturation in colonies whose sex was known, to determine onset and duration of spawning, and to see if colonies changed sex with time. Large mapped populations (>100 colonies) at each site were monitored for spawning and recruitment. All whole colonies collected from a given area of substratum at a time when they could be easily sexed, for size-frequency distribution, sex ratio, onset of sexual maturity. Deep sites in Sydney Harbour, Jervis Bay, and offshore; shallow sites in other bays and offshore.
	Cobblers	3-monthly	12	
	Dobroyd	3-monthly	12	
	Manly Pt	3-monthly	12	
May, 1983	Cobblers	once only	49	All whole colonies collected from a given area of substratum at a time when they could be easily sexed, for size-frequency distribution, sex ratio, onset of sexual maturity. Deep sites in Sydney Harbour, Jervis Bay, and offshore; shallow sites in other bays and offshore.
	Dobroyd	once only	552	
	Fairlight	once only	112	
	Manly Pt	once only	56	
Occasional sampling	other localities NSW coast			

Dissecting microscope counts and measurements: for each colony sampled over the entire sampling period, one or more pieces of the colony were cut longitudinally into 1-2 mm thick slices, and at least five mesenterial filaments containing gonads were dissected out from different polyps, and mounted onto a slide for examination under a compound microscope. The following information was recorded: general abundance of gonads, number of gonads on mesenterial filaments, diameter of gonads, sex and stage of development of gonads.

Larvae: branches of ripe male and female *Capnella gaboensis* colonies were kept in dishes and allowed to spawn naturally. Embryos and larvae were also obtained from field-collected female colonies. Some of the larvae were transferred into boxes made from glass microscope slides, for settling (Reed, 1971). These boxes were kept in 2 l glass dishes (with lids) and the boxes were transferred into new dishes during seawater changes. Some of the larvae which had settled on glass slides were transferred to coplin staining jars, but these larvae were much more difficult to maintain. Larvae were also transferred into 2 l glass dishes containing other substrata (dead coral, sandstone, sandstone with coralline algae and other organisms). Water was aerated continuously and changed every two days for two weeks, thereafter once per week. Freshly collected seawater was used, and light and temperature conditions were ambient. Larval settlement was recorded.

## RESULTS

(1) Sexuality of colonies: *Capnella gaboensis* is dioecious, with a low incidence of hermaphroditism. Of 1031 colonies examined between May 1981 and October 1984, 487 (47%) were male, and 378 (37%) were female. Only six hermaphrodites were found and 160 colonies had no gonads. Only one of the hermaphrodites had male and female gonads in the same polyp, the others had male and female gonads in separate polyps.

Regular sampling of the same 48 colonies (12 at each site) showed clearly that colonies did not change sex during the yearly reproductive cycle.

(2) Sex ratio: the sex ratio for *Capnella gaboensis* colonies in the Sydney area was 1.3:1.0 (males:females), n=865 reproductive colonies. A chi-square test showed that there was a significant excess of males in the population ( $p < 0.05\%$ ). Hermaphrodites accounted for only 0.7% of the reproductive population.

(3) Onset of sexual maturity: sixteen percent of *Capnella gaboensis* colonies examined during the study contained no gonads. Figure 2 shows the size-frequency distribution of colonies collected on the 18th of May 1983. In these large collections, very small colonies generally were found to contain no gonads. One or two immature gonads were present in some small colonies, but these gonads were much smaller than the mature ones present in large colonies collected at the same time. Of colonies without gonads, approximately 90% were under 2 g wet weight (4 cm contracted height). Measurements of colonies growing upon substrata of known age indicated that colonies of this size would be 2-3 years of age.

(4) Annual reproductive cycle: in some *Capnella gaboensis* colonies gamete maturation began soon after spawning (June), but the main period of maturation was during a period of 6-7 months between November and May. This corresponded with falling seawater temperatures in late autumn-early winter. Gonad abundance was least in the period July to November, and reached a peak in May (figure 3). There were many more spermaries per filament than oocytes, especially from November to May, and the maximum number of gonads per mesenterial filament was 14 (female) and 55 (male). Prior to spawning the gonad number decreased, so that female polyps contained 5-10 ova and male polyps contained 10-20 spermaries when ripe. Spermaries were smaller than oocytes through most of the year. Ripe ova were  $492 \pm 69 \mu\text{m}$  (n=1000), and ripe spermaries were  $287 \pm 74 \mu\text{m}$  (n=1000). There was considerable variation in gonad size at all stages of gamete maturation, and even at spawning there were significant differences in colonies and between colonies.

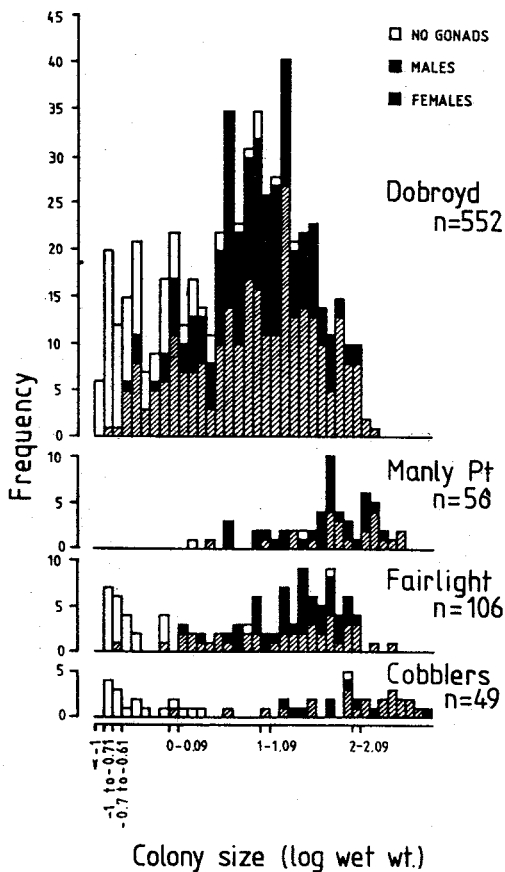


Figure 2: size-frequency distribution of *Capnella gaboensis* colonies collected at each study site on the 18th of May, 1983.

(5) Fecundity and reproductive output: *Capnella gaboensis* colonies have a large number of small polyps, each producing 5-10 eggs. The annual egg production by a medium-sized (200 g) female colony with an estimated 60000 polyps, each producing 6 eggs, would be 360000. The numbers of larvae on female colonies corresponded with this order of magnitude predicted for egg production. A medium-size male colony was estimated to produce around one million spermaries per year.

(6) Spawning, fertilization and planulae larvae: *Capnella gaboensis* populations spawned gametes during a protracted period of 3-4 weeks in early winter, when seawater temperatures were falling. Spawning of individual colonies lasted for several days. Ripe eggs, detached from the mesenterial filaments, were extruded slowly through polyp mouths, leaving spent ovaries inside polyps. The eggs were negatively buoyant and sticky. They remained adhering to the outside of the female colonies where they were fertilized and where the embryos developed into planulae larvae. The larvae were concealed amongst polyps during their development.

*Capnella gaboensis* larvae were ciliated, wormlike, opaque, and lacked mouths and spicules. They were fully demersal, and crawled slowly along the substratum. Planulae began to settle within 1-2 days of leaving the parent colony, but they were still capable of settling for at least a month (and probably longer). Planulae showed a preference for natural substratum with other organisms. They preferred horizontal rough surfaces. Upon settling, they metamorphosed reasonably quickly to become polyps with mouth, pinnate tentacles and spicules after 2-3 days.

(7) Transmission of zooxanthellae: developing *Capnella gaboensis* oocytes never contained zooxanthellae, even in the epithelial covering. Spawmed eggs, no longer enclosed in the gastrodermal epithelium, were sticky and took with them a dense covering of zooxanthellae. Early embryos occasionally had zooxanthellae in them, and sometimes the algae appeared to be trapped in between bulging segments. By the time the embryos consisted of two clear cell layers, many zooxanthellae could be seen in the outer layer (ectoderm). At a later stage, the zooxanthellae could be seen in both the outer and inner layers (ectoderm and endoderm). The mature larvae, however, only contained zooxanthellae in the endoderm. The algae appeared to be transferred within animal cells to the endoderm of the developing larva via the ectoderm and mesogloea (figure 4). All larvae contained populations of zooxanthellae.

(8) Asexual reproduction: asexual recruitment in field populations of *Capnella gaboensis* was by means of fission. In comparison with sexual recruitment, asexual recruitment was relatively unimportant: of 226 recruits (in two years), only nine were the result of asexual reproduction.

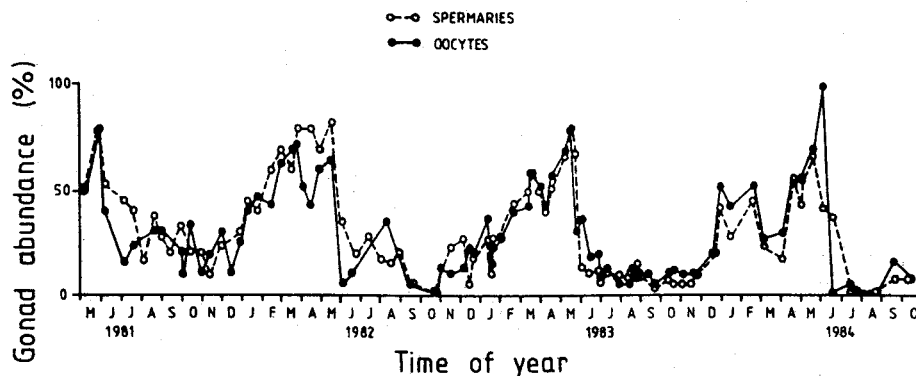


Figure 3: abundance of *Capnella gaboensis* male (o) and female (●) gonads, as % of maximum abundance.

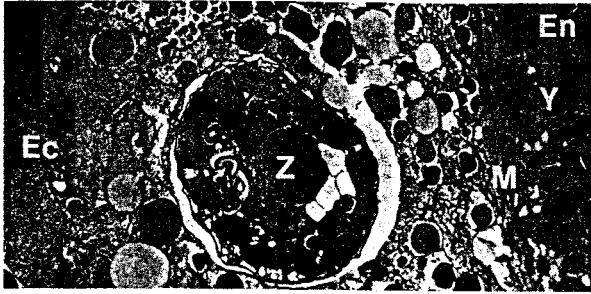


Figure 4: transmission electron micrograph showing a zooxanthella (Z) in the ectoderm (Ec) of a developing *Capnella gaboensis* larva. The mesogloea (M) is thin, and the endoderm (En) contains numerous yolk granules (Y). ——— 5µm

#### DISCUSSION

*Capnella gaboensis* is dioecious, like most soft corals studied (Hartnoll, 1975; Yamazato et al., 1981; Gohar, 1948; Benayahu and Loya, 1983, 1984). *C. gaboensis* has a low incidence of hermaphroditism, which is comparable with figures given for other dioecious soft corals (Hartnoll, 1975; Benayahu and Loya, 1984). Amongst hard corals, many of the temperate species which have been studied are dioecious (Szmant - Froelich et al., 1980; Fadlallah, 1982; Tranter et al., 1982), while the majority of tropical hard corals are simultaneous hermaphrodites (Harrison et al., 1983). There is a slight but significant excess of males in the Sydney *C. gaboensis* population. An excess of males might be advantageous for the species since only sperm are broadcast, the eggs remaining on the outside of the female colony for fertilization. *Xenia macrospiculata* also has a sex ratio skewed towards males, and this soft coral is fertilized internally (Benayahu and Loya, 1984).

The mode of brooding of *Capnella gaboensis* is unusual. Colonies spawn gametes, but the eggs are fertilized and the embryos brooded on the outside of the female colonies. This type of brooding is also shown by *Parerythropodium fulvum fulvum* (although this coral spawns fertilized eggs), and has been termed "surface brooding" by Benayahu and Loya (1983). This mode of brooding affords protection to the developing larvae and avoids the heavy losses associated with a planktonic phase. The erect growth form of *C. gaboensis*, however, suggests that surface brooding of eggs may not necessarily represent an adaptation to an encrusting growth form as suggested by Benayahu and Loya (1983).

The main period of gonad maturation in *Capnella gaboensis* corresponds with the highest seawater temperatures. Maximum gonad growth also corresponds with rising seawater temperatures for some other species: Vighi (1972) reported that temperature had an accelerative effect on the development of gonads of *Corallium rubrum*, and Ottaway (1979) reported that the main period of development of the gonads shown by the anemone

*Actinia tenebrosa* in New Zealand was between November and April, coinciding with the warmest annual sea temperatures.

In *Capnella gaboensis* the small gonads observed from June to August may be remnants of the previous year's gonad population in the process of resorption. Kojis and Quinn (1981) reported that some remnant oocytes were left in colonies of *Porites lutea* until two months after spawning. At all times during gamete maturation in *C. gaboensis*, different sizes of ova are found, an indication that small ones may be re-sorbed by larger ones.

Annual spawning appears to be the rule for the majority of corals, whether temperate or tropical. *Capnella gaboensis* spawns annually over a period of several weeks in early winter. The northern hemisphere cool temperate soft coral *Alcyonium digitatum* also spawns over several weeks (Hartnoll, 1975). On the other hand, most tropical corals spawn annually, but in spring-summer, and often for a very short and predictable time. For tropical corals which release both eggs and sperm into the seawater during very brief periods, simultaneous spawning is necessary.

*Capnella gaboensis* spawns when the seawater temperature falls in late autumn - early winter. Very few corals, soft or hard, have been reported to spawn in winter (Hill and Oxon, 1905; Tranter et al., 1982; Fadlallah and Pearse, 1982). For *C. gaboensis*, storms and big seas might increase the chances of dispersal of the demersal larvae, by sweeping them off the substratum and carrying them further away from parent colonies. Chances of dispersal would be aided by the protracted nature of spawning within populations, and by the ability of larvae to postpone metamorphosis. *C. gaboensis* larvae move slowly and settle quickly, and therefore they would not normally disperse far from parent colonies.

*Capnella gaboensis* has a mode of reproduction which ensures transmission of zooxanthellae to the embryos before they leave the parent colonies. *C. gaboensis* eggs, like coral eggs generally, do not contain algae in their early stages. Although transmission is surest when the eggs are infected with algae before fertilization, this does not occur with *C. gaboensis*. *C. gaboensis* eggs carry an algal population on the outside similar to the way in which the extruded egg cases of the flatworm *Convoluta roscoffensis* have algae adhering to their surfaces (the algae are then available for ingestion by the young worms: Oschman, 1966), and similar to the manner in which "autobleaching" of green *Hydra* provides the sexual generation with a source of zoochlorellae (Thorington and Margulis, 1980). Transmission of zooxanthellae via the embryos appears to be obligatory for *C. gaboensis*, since all the larvae contain zooxanthellae, and since no aposymbiotic adults of this soft coral are ever observed in the field.

Sexual reproduction is the primary mode of localized recruitment for *Capnella gaboensis*, and of dispersed recruitment through chance events. Unlike other members of the Nephtheidae, colonies of *C. gaboensis* in the field populations were never observed to reproduce by means of fragmentation or the production of stolons or runners. Asexual reproduction occurred only by means of fission, and the resulting colonies did not actively move apart as those of *Nephtea brassica* are able to do (La Barre and Coll, 1982).

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