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ORIGINAL PAPER

Multiple spawning events and sexual reproduction in the octocoral *Sarcophyton elegans* (Cnidaria: Alcyonacea) on Lizard Island, Great Barrier Reef

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Abstract *Sarcophyton elegans* is a common symbiotic (zooxanthellate) octocoral species in the shallow waters of the Great Barrier Reef (GBR). Study of a population at Lizard Island (14°40′S, 145°28′E) on the GBR from October 1991 to January 1994 revealed that, as is typical of tropical alcyonarian corals, *S. elegans* is a gonochoric broadcast spawner with a 1:1 sex ratio. Sexual reproduction was closely correlated with colony size, with first reproduction at 13-cm basal stalk circumference for females and 12 cm for males. Oogenesis took 19–24 months, with a new cycle commencing every year, and spermatogenesis took 10–12 months. The majority of gametes were released during the annual austral mass coral spawning event after the full moon in November, but gametes were also released after the full moon in each month between August and February. All autozooid polyps participated in reproduction, but those at the outer edge of a colony released their gametes first. During subsequent months, the polyps closer to the center of the colony released their gametes. This is a novel strategy of gamete release, reported here for the first time, which accommodates the demands of feeding and reproduction in a different way than other corals where individual polyps have separate feeding or reproductive roles. Colonies upstream in the prevailing current spawned up to 1 month earlier than those downstream and ceased 1 month earlier. The mechanism controlling this spatial differentiation in spawning time, repeatedly observed over three seasons, is unknown. *Sarcophyton elegans* appears to have a dual strategy of providing protection for its gametes by releasing most of them concurrently with the single, annual mass spawning of a large number of cnidarians, while also hedging its bets by individual colonies spawning a fraction of their gametes over an extended period of 6 months.

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Introduction

The mode and timing of reproduction are key life history characteristics that influence the population dynamics, ecology and evolution of organisms (Stearns 1992), but major characteristics of reproduction remain unknown for many marine species. For example, while most hard corals are hermaphroditic (Carlon 1999), it has only been established relatively recently that alcyonarian octocorals are primarily gonochoric (having separate males and females), (reviewed by Benayahu 1997; Hwang and Song 2007). Timing of reproduction is variable among corals, but the limited data

available show that alcyonarians have continuous gametogenesis, internal fertilization and brooding of developing embryos more frequently in temperate waters (Gohar 1940; Hartnoll 1975; Farrant 1986; Cordes et al. 2001; McFadden et al. 2001). In contrast, the tropical octocorals studied to date more frequently exhibit short seasonal synchronous spawning periods with external fertilization (Benayahu and Loya 1984; Alino and Coll 1989; Benayahu et al. 1990; Benayahu 1997; Slattery et al. 1999).

Octocorals (Cnidaria: Alcyonacea) have several modes of asexual reproduction including budding, colony fragmentation and asexual production of planulae (Fautin 2002), as well as three different modes of sexual reproduction including internal brooding (Achituv and Benayahu 1990), external surface brooding of planular larvae (Dinesen 1985; Benayahu et al. 1990; Coma et al. 1995), and broadcast spawning of gametes with fertilization taking place in the water column (Alino and Coll 1989; Babcock et al. 1990; Benayahu 1997). The mode of reproduction and length of breeding season vary both within a genus (Hartnoll 1975; Dahan and Benayahu 1997; Hwang and Song 2007) and within a species (Benayahu and Loya 1986; Schleyer et al. 2004) depending on the geographical location of the corals.

The variety of modes of reproduction revealed by a relatively small set of studies, usually limited in spatial and temporal extent, suggests that more detailed studies are required to better document the reproductive strategies of octocoral species. However, comprehensive long term datasets on timing and mode of coral reproduction are extremely rare (Bastidas et al. 2002; Fuchs et al. 2006).

The fleshy octocorals of the order Alcyonacea comprise a major component of the benthic community, second only to the scleractinian reef-building corals, on the GBR (Dinesen 1983; Fabricius and Alderslade 2001). *Sarcophyton* species in the GBR region are widespread, and *S. elegans* is a common member of the alcyonarian community found in shallow lagoons and reef flats throughout the GBR, often appearing in large monospecific aggregations (Hellström, unpublished data). While larvae of alcyonarians are not easy to identify, adults and juveniles of *S. elegans* are relatively easy to distinguish from other *Sarcophyton* species by morphology and by examining the microscopic sclerites, which are species specific (Fabricius and Alderslade 2001). The colonies are mushroom shaped, and the disc-like polyp-bearing region (the polypary) has two different kinds of polyps; large autozooids that bear tentacles and smaller, more numerous siphonozooids lacking obvious tentacles (Fabricius and Alderslade 2001).

This study documents in detail the sex, sex ratio, gametogenesis, and mode of sexual reproduction in a Lizard Island population of this ecologically important species of octocoral on Australia's GBR over 2.5 years.

Materials and methods

Study sites

This study sampled two sites with high abundance of *Sarcophyton elegans* near Lizard Island (14°40′S, 145°28′E) on the northern GBR (Fig. 1). Site A was on shallow Loomis Reef at the western entrance of the Lizard Island lagoon. Site B was on a small wave-exposed patch reef between South Island and Palfrey Island of the Lizard Island group. The water depth at both sites ranged from 3 m at high tide to total exposure during maximum low tide in the austral spring. All field observations and collections were performed by snorkeling or SCUBA.

At each study site, three 1×10 m belt-transects, marked by metal rods at each corner, were laid down end to end on the reef where the density of *S. elegans* colonies seemed highest (Fig. 1). The transect lines were oriented parallel to the current direction in order to assess the effects of spawning by upstream colonies on the reproductive behavior of those downstream (e.g., see Slattery et al. 1999). In December 1991, sizes of all the colonies within the transects were measured to determine colony size distribution. The 50 colonies collected to determine the size at first reproduction, and the 20 colonies subjected to detailed histological analysis, were collected from aggregations of octocorals outside the transects on the study reef.

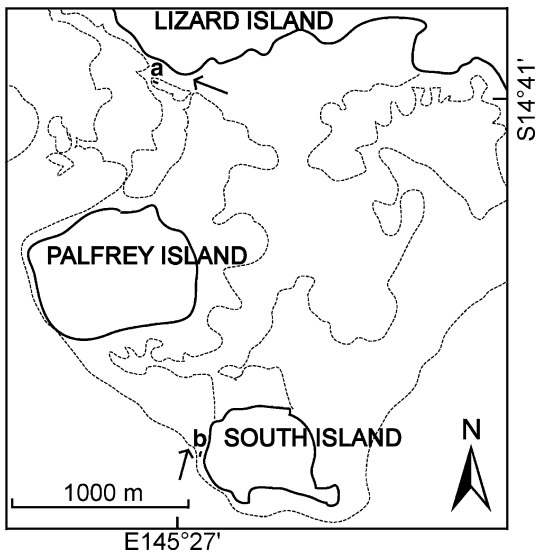

Fig. 1 Map of study sites on Lizard Island, Great Barrier Reef, Australia. **a** (Lagoon site); **b** (Exposed site, close to South Island). *Lines* show position of belt transects and *arrows* indicate net current direction during observed spawning events. *Dashed lines* indicate the outline of the coral reefs

Colony sexual identity, sex ratio, and size at onset of sexual reproduction

Since certain members of the genus *Sarcophyton* exhibit regional variation in reproductive modes (Benayahu and Loya 1986; Alino and Coll 1989; Schleyer et al. 2004), the first priority was to determine whether the corals were gonochoric or hermaphroditic. In October 1991, several weeks before the predicted coral annual mass spawning (e.g., Harrison and Wallace 1990), a small incision was made in the polypary of each colony within all transects (a total of 334 colonies), thereby exposing the mesenteries containing white sperm sacs or pink/red oocytes (Alino and Coll 1989) allowing the colonies to be sexed. Sex of the colonies was recorded, and sex ratio was tested for any deviation from 1:1 using the Chi-square test.

To determine the minimum colony size at onset of first reproduction and sexual maturity, 50 colonies of different size classes were collected outside the transect lines prior to the spawning season in 1992. The basal circumferences of the stalks of the colonies were used to compare colony size because polypary diameter and height within colonies varied considerably with tidal levels and time of day (Hellström, unpublished data). The collection was biased toward smaller colonies in order to detect the smallest size at maturity. The colonies were sectioned in the laboratory with a scalpel, and their sexual condition was established by examining them under a light microscope to detect the presence of gametes. Histological samples in the smaller colonies were processed as described below in order to confirm the absence of gametes in the colonies that appeared to be immature.

Gametogenic cycle

To determine the length of the gametogenic cycle, 10 large male colonies and 10 large female colonies (>20 cm in stalk circumference) outside the transects at sites A and B were numbered with plastic markers and subjected to detailed histological analysis. The marked colonies were sampled approximately monthly between October 1991 and January 1994, by cutting off a small rectangular piece of tissue (1 cm^3) from the polypary with a sharp scalpel, as outlined by Benayahu and Loya (1986). All samples were preserved in 10% formalin in seawater (v/v) for 3 days and then transferred to 70% ethanol for further analysis. The samples were decalcified for 10 min using formic acid and sodium citrate (Winsor 1984). Diameters of the oocytes and spermaries were measured with a micrometer under a compound microscope. Fresh samples were examined under a stereomicroscope to establish the color difference between mature and immature gonads. Three paraffin sections from each sample (6 µm) were stained with hematoxylin and eosin following Winsor (1984) for histological analysis to determine the stages of gonadal development. The gametogenic cycle was determined according to descriptions by Glynn et al. (1991) and Schleyer et al. (2004).

The effects of frequent cutting were examined using 10 mature colonies tagged with plastic markers. A cut in the oral disc (1 cm long and 1 cm deep) was made in five of these colonies every third day for 4 weeks, and five were left intact as controls. At the end of 4 weeks, gamete production was measured in both groups, and a *t*-test was used to determine whether there was any significant effect of cutting on colony gamete production.

Temporal spawning dynamics

The positions of the colonies along the belt transects were recorded and their reproductive state was noted monthly from October 1991 to January 1994. The colonies were monitored every 2 weeks for spawning activity after both the full moon and new moon, between August and March 1992 and 1993 and in January 1994, as higher reproductive activity occurred in those months. To obtain information on the spatial distribution of immature, mature and spawned mesenteries in individual polyparies, incisions were made at several points along the radius of the polypary to expose the mesenteries. These were then identified as either translucent with undeveloped gametes, white with mature sperm sacs, pink/red with mature oocytes or as spent mesenteries with no gametes. A colony was recorded to have released its gametes when ripe gametes were recorded as present during a census and absent at the next sampling event. Colonies were observed releasing eggs and sperm on three separate dates, and the detailed times of gamete release within the transects were recorded at site A only, for logistic reasons.

Results

Colony sexual identity, sex ratio, and size at onset of reproduction

Gross anatomical and histological examinations revealed that the study population of *Sarcophyton elegans* was gonochoric; that is, individual colonies were either male or female. Of the 334 colonies that fell within the transects at both study sites, 121 were females, 162 were males, and 51 were inactive and therefore could not be sexed. At the end of the survey 285 of the 334 mapped colonies remained, indicating 85% survival. The mean number of females over all transects was 40 (to nearest whole number), and mean number of males was 54. The ratio of males to females,

using the mean from the six transects, did not significantly deviate from 1:1 (1-proportion analysis, $x = 40$, $n = 94$, $P = 0.180$).

The minimum basal circumference of females containing their first batch of white immature oocytes was 13 cm at site B and 14 cm at site A. The minimum basal circumference of sexually mature males was 12 cm at both sites. However, many colonies 14 and 15 cm in basal circumference were not sexually mature, whereas most colonies measuring 16 cm and above were sexually mature (Fig. 2). During the study, many of the colonies underwent vegetative growth by either binary fission or by the production of buds that developed at the edges of the polypary. Bud formation was observed during every census, seemed to be independent of season, and took about 6 months. Buds developed into miniature colonies and, after forming high densities of sclerites at the bases, fell off the parent colonies. The buds landed upright on the substratum as a result of their heavy, sclerite-dense base, and some of the buds contained gametes of mature color. However, during the following spawning season, buds that measured 8–13 cm in basal circumference did not contain mature gametes.

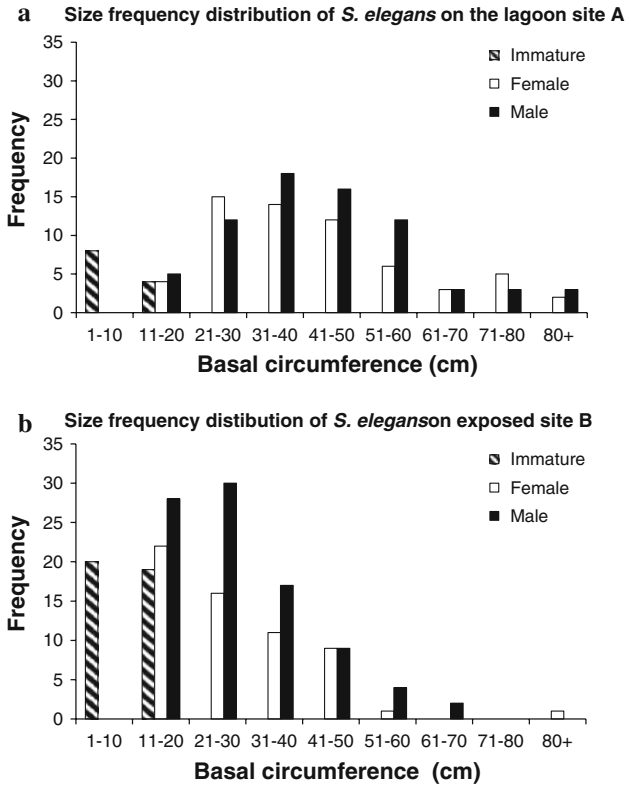

Fig. 2 Size frequency distribution of *Sarcophyton elegans* colonies within study sites, measured as basal stalk circumference. **a** Lagoon site; **b** South Island, exposed site. *Shaded bars* sexually immature colonies; *white bars*, females; *black bars* males

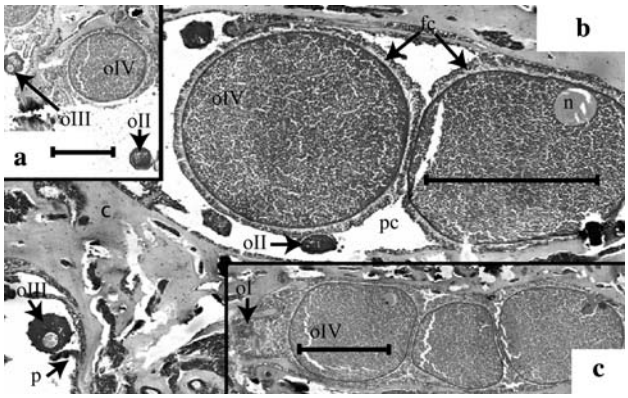

Fig. 3 Oogenic development of *Sarcophyton elegans*. **a** Stage II, III and IV oocytes. **b** Stages II, III and IV oocytes in polyp cavities **c** Stage I and IV oocytes in polyp cavity. *c* coenenchyme, *f* follicular layer (under the coenenchyme), *oI* stage I primordial oocyte, *oII* stage II oocyte, *oIII* stage III oocyte, *oIV* stage IV mature oocyte, *p* pedicle, *pc* polyp cavity. Stages as in Glynn et al. (1991) and Schleyer et al. (2004). *Scale bars* = 500 μm

Gamete development

Gametogenic cycles of 10 colonies of each sex were followed in detail. In a pilot test, there was no significant difference in production between cut and intact colonies ($n = 10$, $t = 0.35$, $P > 0.05$) indicating that repeated tissue sampling did not affect gamete production.

Fresh oocytes were white when immature, changing to pink, or occasionally dark red, at maturity. The immature sperm sacs were translucent-gray and turned white at maturity. After preservation in formalin, both male and female gonads became pale orange. The gonads were found in the autozooids only. At early developmental stages, the gonads were attached to the mesenteries by pedicles.

The oocytes could be differentiated into four oogenic stages (as described by Glynn et al. 1991 and Schleyer et al. 2004) and oocytes of different developmental states occurred simultaneously (Fig. 3a). Stage I oocytes appeared in the autozooid polyps in February and were present until July. The Stage II oocytes were present between April and November and were attached to the mesenteries by pedicles (Fig. 3b). The Stage III oocytes were present in all months, were not connected to the mesenteries by pedicles and were close to the polyp cavity. Stage IV oocytes were granular in texture as a result of evenly distributed vacuoles (Schleyer et al. 2004), with the nucleus at the periphery of the cell (Fig. 3b, c). The Stage IV ova were observed in polyps at the outer edge of the colonies just before the full moon in August and September; during subsequent months, Stage IV oocytes were found in polyps closer to the center of the polypary (Table 1). The Stage IV oocytes were not observed after the last spawning event of the season in February. Each month between October 1991 and February

Table 1 Monthly observations of gamete release from different parts of polyparies (edge, intermediate, or center) of *Sarcophyton elegans*., within spawning groups at two sites (lagoon, A and exposed, B)

Group	Oct 91	Nov 91	Dec 91	Jan 91	Feb 91	Aug 92	Oct 92	Nov 92	Dec 92	Jan 93	Feb 93	Aug 93	Sept 93	Nov 93	Dec 93	Jan 94	Feb 94
	D5	D5–6	D6	D6	D6	D5	D5	D6	D6	D5	D5–6	D6	D6	D6	D6	D5	D5
Site A																	
1	EI	IC	C	C	*	E	EI	IC	C	C	*	E	EI	IC	C	*	*
2	EI	IC	C	C	*	E	EI	IC	C	*	*	E	EI	IC	C	*	*
3	EI	IC	C	C	*	E	EI	IC	C	*	*	E	EI	IC	C	C	*
4	EI	IC	C	C	*	E	EI	IC	C	C	*	E	EI	IC	IC	C	*
5	EI	IC	IC	C	*	E	EI	IC	C	C	*	E	EI	IC	IC	C	*
6	EI	IC	IC	C	C	*	EI	IC	IC	C	*	*	EI	IC	IC	C	*
7	EI	IC	IC	C	C	*	EI	IC	IC	C	C	*	EI	IC	IC	C	*
8	EI	IC	IC	C	C	*	EI	IC	IC	C	C	*	E	IC	IC	C	*
9	EI	IC	IC	C	C	*	EI	IC	IC	C	C	*	E	IC	IC	C	C
10	EI	IC	IC	C	C	*	EI	IC	IC	C	C	*	E	IC	IC	C	C
Site B																	
11	EI	IC	C	C	*	E	EI	IC	C	C	*	E	EI	IC	C	C	*
12	EI	IC	C	C	*	E	EI	IC	C	*	*	E	EI	IC	C	C	*
13	EI	IC	C	C	*	*	EI	IC	C	*	*	E	EI	IC	IC	*	*
14	EI	IC	C	C	*	E	EI	IC	C	C	*	E	EI	IC	IC	C	*
15	EI	IC	C	C	*	*	EI	IC	C	C	*	E	EI	IC	IC	C	*
16	EI	IC	C	C	*	*	EI	IC	IC	C	*	*	EI	IC	IC	C	*
17	EI	IC	IC	C	*	*	EI	IC	IC	C	C	*	EI	IC	IC	C	*
18	EI	IC	IC	C	C	*	EI	IC	IC	C	C	*	E	IC	IC	C	C
19	EI	IC	IC	C	C	*	EI	IC	IC	C	C	*	E	IC	IC	C	C
20	EI	IC	IC	C	C	*	EI	IC	IC	C	C	*	E	IC	IC	C	C

Note that no observations were made in September 1992 and October 1993

G1–G20 Spawning group 1–20 (see Fig. 6), *D5* Spawning 5 days after full moon, *D6* Spawning 6 days after full moon, *E* Gamete release by polyps at edge of polypary, *I* Gamete release by polyps in intermediate region of polypary, *C* Gamete release by polyps at center of polypary, * No gamete release

1994, there were two distinct size cohorts of oocytes, with the diameters of both cohorts increasing over time. This pattern indicates that a new oogenic cycle commences every year (Fig. 4a) and that oogenesis takes 20–22 months. The oocytes along the margins of colonies matured and were spawned up to 5 months earlier than gonads in the center of the same colony (Table 1). Mature ova were 450–620 μm in diameter.

The spermaries developed in 10–12 months, and the mature sperm sacs measured 300–450 μm prior to spawning (Fig. 4b). The reproductive male polyps mainly contained spermaries at similar stages of development in contrast to the female colonies, which had two parallel cohorts of developing oocytes. Classification of spermary development was determined according to Glynn et al. (1991) and Schleyer et al. (2004). Stage I and Stage II spermaries appeared in February and March and increased slowly in size until August when they reached Stage III (Fig. 5). The spermaries in polyps at the edge of the polypary reached Stage IV by August and September and did not contain gametes in October through February. The spermaries in polyps closer to the center of the colonies matured into Stage IV gradually from October until January or February.

Temporal spawning dynamics

Visual observations in the field and laboratory revealed that spawning occurred 5 and 6 days after a full moon, approximately 4–5 h after sunset each month from August to February. The positively buoyant eggs from the female colonies ascended first, followed by clouds of sperm from the male colonies. Gamete release from a colony during a spawning event lasted for up to 2 h.

Assessment of the mesenteries from incisions into a polypary showed that polyps at the edges of the polypary released a fraction of their gametes in August, and had released all gametes by after the full moon in October. This was 1 month before the annual mass spawning event in November, and no gametes could be observed in this region of the polypary in the weeks prior to the annual mass spawning event. Partial gamete release continued from autozooids located progressively closer to the center of the polypary until the mass-spawning event after the full moon

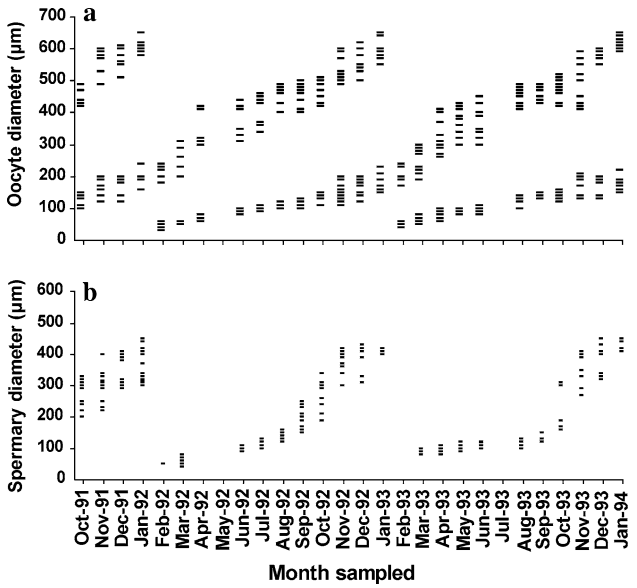

Fig. 4 Monthly measurements of diameters (µm) of **a** oocytes ($n = 520$) and **b** spermaries ($n = 460$) of *Sarcophyton elegans* colonies between October 1991 and February 1994. Months start at October 1991 through January 1994. No data were collected in May 1992 and July 1993 due to bad weather

in November, when large quantities of eggs and sperm were released into the surrounding water. The remaining mature gametes were released 5 days after the full moons in December and January, as determined by underwater observations.

Male and female colonies were not randomly dispersed, but were found in groups of the same sex (Fig. 6). The close proximity of many colonies of the same sex suggests that these were clones produced by vegetative propagation. Each group contained 5–34 mature colonies, adding up to 20 groups in total over both sites. Five to six days after each full moon from August through February each of these colony-groups spawned in synchrony (releasing gametes relatively slowly over approximately 2-h periods). Direct observation of spawning showed that gamete release occurred first in upstream colony-groups and progressively later in downstream colony-groups in every spawning period. Each subsequent group started spawning about 10 min after the adjacent upstream one (Fig. 6). Although tidal flows around Lizard Island are not well understood, the net current over the transects, while varying in intensity, was in the same direction at each spawning observation.

Spawning also differed between upstream and downstream colony-groups on longer time scales (Table 1).The colonies furthest downstream made their first gamete release of the season 1 month after the ones upstream (i.e. the upstream colony-groups first spawned in August, but further downstream colony-groups started the spawning season in September). Similarly, the downstream colony-groups continued spawning until February, while the final

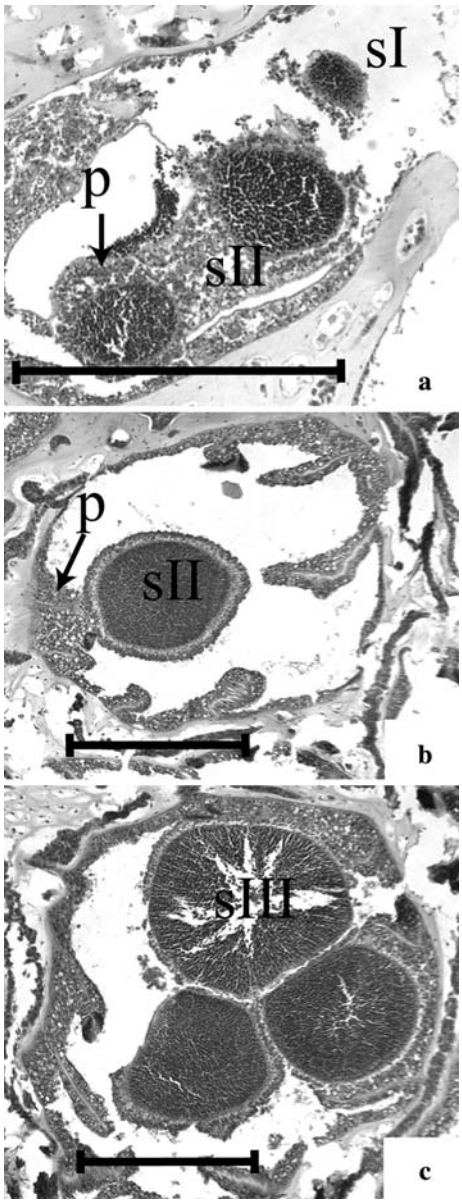

Fig. 5 Spermatogenic development of *Sarcophyton elegans*. **a** Spermatogonia and spermatocysts **b** Spermatocyst attached with pedicle **c** Spermaries with spermatids. *p* pedicle, *sI* stage I spermatogonia, *sII* stage II spermaries, *sIII* stage III spermaries with spermatids. *Scale bars* = 250 µm

spawning of the upstream colony-groups occurred in January (Table 1).

Discussion

This study showed that *Sarcophyton elegans* on the GBR is a broadcast spawner with stable gonochorism (sensu Giese and Pearse 1974) and an overall sex ratio that did not deviate significantly from 1:1. In this respect, the GBR populations of *S. elegans* are like the majority of alcyonarian

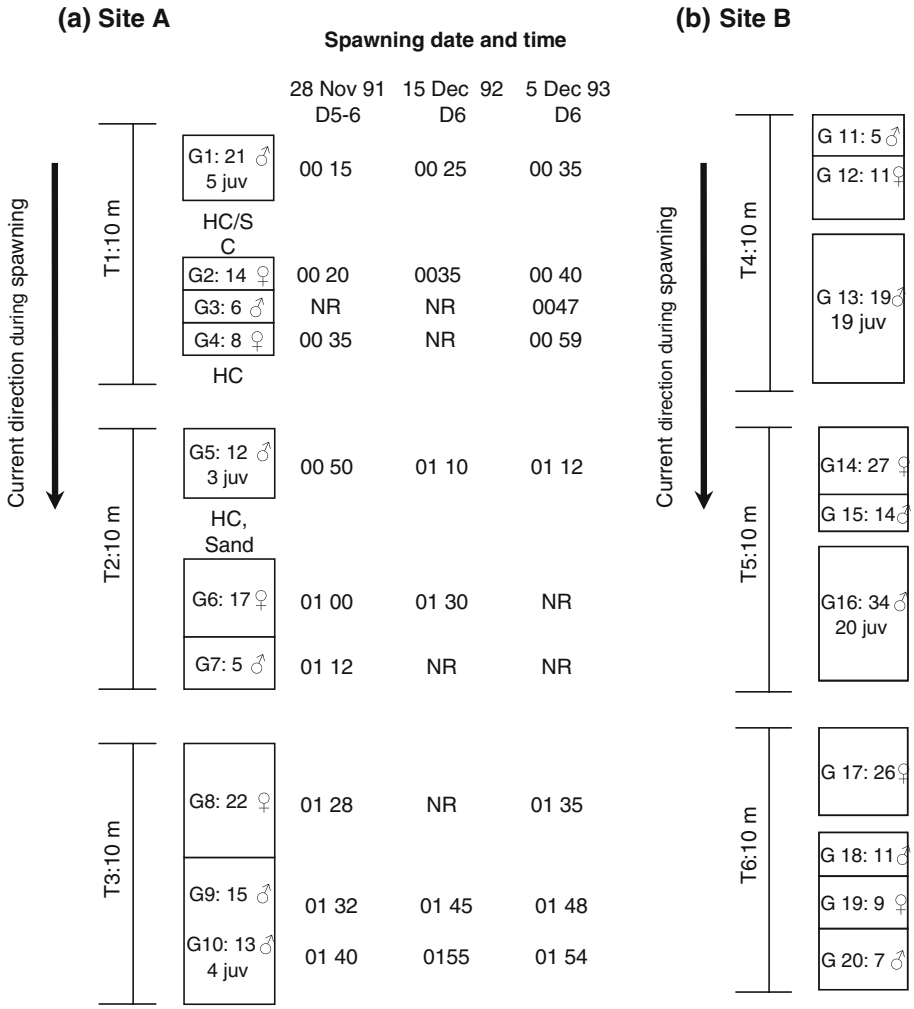

Fig. 6 Position of *Sarcophyton elegans* colonies within six 10-m belt transects from sites A and B (see Fig. 1), and record of observed downstream spawning at three different spawning events at site A (28 Nov 91, 15 Dec 92, and 5 Dec 93). Number of colonies and gender within each group (G1-G20) are given. Times are records of spawning initiation of each group. Groups 9 and 10 were of the same sex. Site B; spawning initiation only observed for group G11 (28 Nov 91 at 00.25 h, 15 Dec 92 at 00.30 h and 5 Dec 93 at 00.45 h). Belt transect 1–3 on site A, T1–T3; Transects 4–6 on site B, T4–T6; Distinct spawning groups, G1–G10 at site A and G11–G20 at site B; 5 days after full moon, D5; 6 days after full moon, D6; *NR* not recorded, *HC* hard corals, *SC* soft corals, *Sand* sandy substrate

octocorals where gonochorism is the rule than the exception (Benayahu 1997), 1:1 sex ratios are usually observed (e.g., Grigg 1977; Benayahu and Loya 1986; Ribes et al. 2007), and, as in the majority of species in the Alcyoniidae and Nephtheidae, the gametes are released by broadcast spawning (reviewed by Benayahu 1997; Hwang and Song 2007). The gonad structures in *S. elegans* were similar to *S. glaucum* in the Red Sea (Benayahu and Loya 1986) and South Africa (Schleyer et al. 2004). However, no hermaphroditic colonies were detected within the GBR study sites. Either they were so few that they were not discovered or they did not exist. In contrast, data from a South African population of *S. glaucum* (Schleyer et al. 2004), a Mediterranean population of the stable gonochoric gorgonian octocoral *Eunicella singularis* (Ribes et al. 2007) and the octocoral *Carijoa riisei* in Hawaii (Kahng et al. 2008) showed a low incidence of hermaphroditism in predominantly gonochoric populations.

Most sex ratio estimates in octocorals are based on sampling a single location, but it has been shown in the gorgonian corals *Paramuricea clavata* and *E. singularis* that sex ratios can vary between locations (Gori et al. 2007). A higher frequency of females to males has been reported in some octocoral species (summarized by Ribes et al. 2007) and in the Mediterranean octocoral *Corallium rubrum* (Santangelo et al. 2003). Higher frequencies of males to females have also been documented, for example in *Xenia macrospiculata* (Benayahu and Loya 1984), *Briaerum asbestinum* (Brazeau and Lasker 1992) and in some populations of *P. clavata* (Gori et al. 2007).

Sexual reproduction appears strictly size dependent in *S. elegans* in the GBR population, demonstrated in this study by a minimum size for sexually mature colonies (12 cm basal circumference in males and 13 cm in females), the absence of gametes from many larger colonies with stalks up to 15 cm diameter, and the absence of gametes in colonies derived from buds <15 cm diameter that had possessed mature gametes in the previous year when they first detached from their parent colony. Size dependent sexual maturity is relatively common in colonial marine invertebrates and may be a strategy to allocate energy resources to growth in young colonies, and hence avoid the high risk of

mortality associated with small colony size (e.g. Harvell and Grosberg 1988; Babcock 1991; Gutierrez-Rodriguez and Lasker 2004). Rapid early growth would also reduce the possibility of being shaded by nearby larger colonies. Although size-specific predation mortality is not reported for any octocorals, overall predation mortality can be high. On the outer GBR, predation as a known cause of death accounted for 69% of mortality in *Sarcophyto*n spp. colonies (Fabricius 1995). Species such as the gastropod *Ovula ovum* (Coll et al. 1983) and the butterflyfish *Chaetedon unimaculatus* (Slattery et al. 2001) are reported octocoral predators.

Sarcophyton elegans on the GBR exhibited prolonged oogenesis over 20–22 months, which gave rise to two main cohorts of oocytes of different developmental stages in female colonies at any given time, and a spermatogenic cycle of only 10–12 months. These features are shared with *S. glaucum* in the Red Sea (Benayahu and Loya 1986, Fig. 3), *Lobophyton crassum* in Okinawa (Yamazato et al. 1981), and *Sinularia polydactyla* in Guam (Slattery et al. 1999).

A trade-off between feeding and reproduction has been proposed in cnidarians, in which the polyps on the outer edge of the colony are not gametogenic and are involved in feeding, while polyps nearer to the center are gametogenic (e.g., Hall and Hughes 1996). This differentiation is distinct in anemones (Francis 1976) and hydrozoans (Harvell 1984) but less apparent in corals (Veron 1993). A study on scleractinian corals less than a month prior to the mass spawning event in Australia indicated that some coral species showed no gametogenic activity in peripheral polyps (Hall and Hughes 1996). Zones of active growth in octocorals have also been associated with reduced fecundity (Brazeau and Lasker 1990). The reproductive cycle in mature octocorals can reduce feeding activity, as the mature oocytes in the brooding coral obstruct the coelenteron and thus limit polyp feeding, as described for *Heliopora coerulea* (Babcock 1990) and the brooding octocoral, *Thouarella variabilis*, where a single larva may occupy up to 80% of the polyp cavity (Brito et al. 1997).

The discovery that all autozooids in *S. elegans* are involved in reproduction but show differential timing of development and release of gametes across the polypary represents a new way of accommodating the demands of feeding and reproduction. Previous studies either do not indicate that they have sampled different parts of the polyparies, or have specifically stated that they did not. The lack of previous reports of this pattern of gamete release in other species may therefore reflect differences in methods of observation rather than reflecting its absence.

In free-spawning marine invertebrates with sexual dimorphism, female reproductive success is limited by sperm availability and male reproductive success by fertilization rates (Levitan 1996). In *S. elegans* on Lizard Island, gamete release was synchronized over the shorter time scales of gamete release by the spawning of one colony appearing to stimulate others downstream to release their gametes, thereby possibly increasing the probability of fertilization success in the colonies. Progressive downstream spawning over short time scales has been observed previously in scleractinian (Atkinson and Atkinson 1992) and alcyonarian corals (Slattery et al. 1999), and is thought to result from pheromone signaling between colonies (Atkinson and Atkinson 1992; Slattery et al. 1999; Tarrant 2005).

In the GBR *S. elegans* population, however, upstream colonies started to spawn earlier in the season by up to 1 month, and the downstream colonies continued to spawn for up to a month after the most-upstream colonies had completed spawning. The mechanism controlling this spatial differentiation in spawning time, repeatedly observed over three seasons, is unknown.

The period over which *S. elegans* spawns on the GBR fits with reproductive modes typically ascribed to tropical species of alcyonarians. The tropical spawning pattern is generally characterized by short, seasonal, synchronous spawning periods with external fertilization as opposed to the temperate pattern of continuous gametogenesis, internal fertilization and brooding of developing embryos (Kruger et al. 1998). However, in *S. elegans* the spawning was spread over a significantly longer period (7 months) than is reported for most tropical alcyonarians. Alino and Coll (1989) reported that many ocotocorals on the GBR take part in the short, synchronized annual mass spawning event in the austral spring. This event typically takes place 2–6 days after the full moon in November, although a split-spawning over two consecutive lunar cycles when the full moon fell late or early in the month has been reported (Harrison et al. 1984; Babcock et al. 1986). More recently, protracted spawning patterns in mass spawning scleractinian corals have been reported from Japan where spawning occurred after the full moon during two consecutive months (Hayashibara et al.1993), as well as from Barrow Island and Dampier Archipelago in Western Australia where four *Acropora* spp. spawned both in the austral fall, i.e. March to April and in the spring to early summer, i.e. October to December (Rosser and Gilmour 2008) and in Palau multiple spawning events took place two to three times in different months (Penland et al. 2004). In Venezuela, Bastidas et al. (2005) reported two to three spawning events in scleractinian corals and in gorgonian octocorals over 2–3 months.

Synchronous development and release of a large number of gametes by individuals in a population may reduce the risk of predation by overwhelming the predators' capacity to feed on the gametes and by diluting the individual risk of predation (Babcock et al. 1986; Richmond and Hunter

1990). The synchronization of spawning may also be important to facilitate higher fertilization success (Lasker et al. 1996; Levitan 1996). Conversely, a presumed advantage of multiple spawning events is to escape the effects of a single catastrophic event on a population's reproductive success (Richmond and Hunter 1990). *Sarcophyton elegans* appears to have both strategies, and to have achieved this by differential gamete release over the polypary and differential timing of spawning among colonies.

The extremely high level of temporal and spatial structuring in sexual reproduction seen in only a 30-m transect of octocoral colonies is remarkable. The novel aspects of sexual reproduction in *S. elegans*, including a prolonged, 7-month, split-spawning from August to February and a progressively more central release of gametes across the polypary, suggest that many fundamental aspects of coral ecology are yet to be discovered.

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