Sexual reproduction of a low-temperature tolerant coral *Oulastrea crispata* (Scleractinia, Faviidae) in Hong Kong, China

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ABSTRACT: In December 1993, an experimental artificial reef made of pulverised fuel ash (PFA) and concrete was deployed at Hoi Ha Wan Marine Park, Hong Kong. The reproductive biology of *Oulastrea crispata*, the pioneer species recruited onto the structure, was studied to ascertain its reproductive strategies, including its gametogenic cycle in terms of oocyte and spermary development and timing of planula release. A histological study showed that *O. crispata* was hermaphroditic and had an annual gametogenic cycle with an extended spawning period from July to October. Planulae were released in the resting period of the gametogenic cycle. With an opportunist life history trait, including a wide range of reproductive strategies, *O. crispata* is able to colonize a variety of substrata, including those unfavourable to other corals, and to flourish as the pioneer colonizer of newly immersed structures.

KEY WORDS: Coral · *Oulastrea crispata* · Reproduction · Gametogenesis · Planula release

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INTRODUCTION

Coral reproduction has been reviewed by Fadlallah (1983), Harrison & Wallace (1990), Richmond & Hunter (1990) and Richmond (1997). According to these reviews, the majority of such work has been undertaken in the Caribbean, the Great Barrier Reef, the Central Pacific (Guam, Marshall Islands, Palau and Hawaii) and the Red Sea. Examples from the Southeast Asian Pacific Rim are restricted to Okinawa (Japan), Taiwan, and the Philippines. There is little information on the reproductive status of corals in Hong Kong, China and the islands of the South China Sea. Liang (1985) has listed 325 species in 62 genera of common scleractinian corals from China, including regions of the South China Sea, Taiwan, Hainan and along the mainland coast. Reproductive seasonality has been demonstrated for 64 species (Dai et al. 1993). Of these, 27 species have been identified as spawners and 3 as brooders (Dai et al. 1993). The sexual status of these

corals has not, however, been recorded (Dai et al. 1993, Richmond 1997). Of the 50 known species of local scleractinians (Scott & Cope 1982, Thompson & Cope 1982, Cope 1984, Scott 1984, Cope & Morton 1988, Zou et al. 1992), only *Platygyra sinensis*, *Goniopora colomna*, *Acropora tumida*, *Favia speciosa*, *Goniastrea aspera* and *Porites lobata* (Clark 1997, Collinson 1997) have been studied in terms of their reproductive biology. There are no studies of asexual reproduction in local corals.

Throughout the first 2 yr study on the epibiotic colonization of an experimental pulverised fuel ash (PFA)-concrete artificial reef at Hoi Ha Wan, Hong Kong, *Oulastrea crispata* (Fig. 1) was the only coral to show significant recruitment (Lam 1998). *O. crispata* is a member of the Faviidae (Scleractinia). Its special morphology of a chocolate brown skeleton with overlaying white septa gives it its common name of zebra coral (Kawaguti & Sakumoto 1952). The geographical distribution of *O. crispata* is restricted to the Eastern Pacific. It extends from the Great Barrier Reef in the southern hemisphere to Japan in the north (Nemenzo 1986, Veron 1986, Yajima et al. 1986). It has been

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Fig. 1. *Oulastrea crispata* recruited on concrete blocks retrieved from the experimental artificial reef at Hoi Ha Wan, Hong Kong (colony size ~15 mm in diameter)

reported as common in the Philippines and some Japanese waters. Locally, it is distributed near the low tide mark and occurs on bare subtidal boulder surfaces in Hoi Ha Wan, Port Shelter, Ping Chau and Cape d'Aguilar (author's pers. obs.). Preliminary observations suggest it is resistant to adverse environmental conditions. Japanese *O. crispata* are reported to live on shallow reef depressions and on turbid bay bedrocks inhabited by only a few other corals (Yajima et al. 1986, Nakano & Yamazato 1992). This species is also tolerant of low temperatures. It has been recorded from the shores of the Noto Peninsula, Japan, where the winter water temperature is usually between 7 and 10°C, and air temperatures are several degrees below freezing for about 20 d (Yajima et al. 1986). Studies on this tolerant and common species are, however, rare and restricted to the Japanese con-specific. The skeletal pigmentation is unique among reef corals and was the first interest of study. The pigment is thought to be a tetrapyrrol derivative (Kawaguti & Sakumoto 1952). Yamashiro (1992) recorded

high concentrations of Fe, Al and minor elements such as Sc, V, Cr, Br, Ag, I, La, Ce, Sm, Hf, Th and U associated with the skeletal pigment and suggested, therefore, that the coral tissues are involved in the active uptake of these elements during calcification. Nakano & Yamazato (1992) have given a brief description of sexual reproduction by *O. crispata*.

In this paper, the reproductive ecology of *Oulastrea crispata*, a pioneer species in the present coral recruitment study, was examined to ascertain its reproductive strategy, including its gametogenic cycle in terms of oocyte and spermary development and fecundity. Planula brooding was also observed. These were analysed in an attempt to explain why and how this, and only this, scleractinian was able to colonize such new habitats.

MATERIALS AND METHODS

Spawning activity. The spawning of *Oulastrea crispata* was monitored in the summers of 1994, 1995 and 1996. Colonies were collected from Hoi Ha Wan, Hong Kong, each summer. They were kept in the outdoor flow-through aquarium of the Swire Institute of Marine Science and observed intensively during periods of potential spawning (from June to September), especially on nights around full moon periods. The colonies were returned to their original sites after the investigation ended (October). No spawning was observed for any colonies in 1994, 1995 and 1996.

Gametogenic cycle. *Oulastrea crispata* was studied for its seasonal pattern of reproduction, gonadal structure, and sizes of the oocytes and spermaries to obtain a picture of its reproductive strategy. Sampling of *O. crispata* was conducted approximately every month from September 1995 to September 1996, along the western shoreline of Hoi Ha Wan in the vicinity of the artificial reef site (Fig. 2). Colonies >20 mm in diameter were chosen to avoid individuals which might be sexually immature. Three to 5 colonies were collected at each time interval. Specimens of *O. crispata* were obtained by chipping off the colony with a hammer and chisel. As this coral ranges in size from 5 mm (with a single polyp) to about 50 mm at Hoi Ha Wan, and because of its encrusting growth form, entire colonies were often broken when hit. Monthly sampling of the same colony to follow the gametogenetic cycle, as in other studies (Clark 1997), was therefore impossible.

Samples obtained from the field were immediately placed in 10% seawater formalin and fixed for a period of 48 h. The decalcification of coral samples was achieved by using 10% HCl for a period of 5 to 6 d with frequent changes of acid. Polyyps from the sterile edges were not used. Several undamaged polyyps were re-

moved and stored in Bouin's solution. Standard methods (Szmant-Froelich et al. 1980) for coral histological preparations were used. Decalcified coral tissue was dehydrated, cleared, embedded in paraffin and subsequently sectioned at 6 μm . Tissues were then stained with Mayer's haematoxylin and eosin. Longitudinal (LS) and transverse (TS) sections were obtained. The former were used to study oocyte diameter and numbers, whereas the latter were used to locate the position of ovaries and testes in the coelenteron.

The reproductive organs of 30 polyps from between 3 and 5 colonies were investigated monthly, for 13 mo, from September 1995 to September 1996, i.e. a total of 390 polyps were examined. Gametogenesis was deduced from the monthly changes in the development of the reproductive organs. For each polyp studied, a longitudinal section approximating its transverse axis was chosen. The numbers of oocytes in this section were counted. The maximum diameter of the 5 largest

oocytes and their diameters perpendicular to this were measured using a calibrated eyepiece micrometer on a light-microscope. Geometric diameter was calculated from the following equation:

$$\sqrt{\text{max. oocyte diam.} \times \text{diam.} \perp \text{ to max. diam.}}$$

The mean geometric diameters of 5 oocytes in each polyp were used in subsequent statistical analyses.

The relative quantities of the reproductive structures (oocytes and spermaries), in terms of a monthly scale, were also obtained by surface area measurements of the longitudinal sections (Collinson 1997). Quantification of surface area was conducted using an image analysis technique (Leica Instruments 1991). An image of the photographed longitudinal section was converted and loaded into a computer via a Sony CCD video camera. The resulting digitised colour image was subsequently analysed using a Leica Quantimet 500 Image

Analyser to obtain surface area values for the oocytes and spermaries. This was done for each monthly sample collected.

Planula release. Planulae were observed in coral recruits (Lam 1998) on the concrete blocks retrieved from the artificial reef at Hoi Ha Wan and specimens were collected from the same bay for spawning observations. These corals were kept in the outdoor aquarium at the Swire Institute of Marine Science from September 1994 to 1997. Sizes, in terms of geometric diameters and numbers of polyps, of these colonies were recorded. Histological slides prepared for studying gametogenic development were also examined for signs of planula brooding.

RESULTS

Gametogenetic cycle

The histological examination of colonies from Hoi Ha Wan indicate that *Oulastrea crispata* is a simultaneous hermaphrodite, with both ovaries and spermaries intermingling within the mesoglea of the same mesentery, but developing separately. Transverse sections show that these reproductive organs were present in all 12 mesenteries of a single polyp. The testes occupied a position above the ovaries. The eggs were generally spherical and without zooxanthellae.

Oocyte development took between 6 and 7 mo, whereas spermary development took approximately 3 mo. Gametes of both sexes

Fig. 2. Map of Hoi Ha Wan showing the location of the experimental artificial reef and sampling site ($\triangleright$) of *Oulastrea crispata*

reached maturity at approximately the same time, in June and July 1995. Figs. 3 & 4 represent the changes in gamete sizes, in terms of oocyte and spermary surface area per standard longitudinal section of a single polyp, and oocyte diameter from September 1995 to September 1996, respectively.

Oogenesis commenced in February 1996, 4 mo after late spawning in September 1995. Oocytes then developed in the following months, reaching a maximum size and maturity from July to August. The smallest detectable primordial oocytes in the mesoglea had a mean diameter of $17.3 \pm 6.1 \mu\text{m}$ (range = 4 to 30 μm ; $n = 5$) and an area of $0.58 \pm 0.3 \text{ mm}^2$ (range = 0 to 0.9 mm^2 ; $n = 30$) and were first observed in February 1996. Oocytes at this stage were small, with a relatively large germinal vesicle and a prominent nucleus. Sampling in subse-

quent months showed continued oocyte growth in terms of both size and surface area, characterised by an increase in the distance between the cytoplasm and nucleus, in addition to an increasing cytoplasm to nucleus ratio. There was a gradual increase in both oocyte surface area and diameter during early summer. Between March and July, the oocyte diameter and surface area increased from $26.6 \pm 7.2 \mu\text{m}$ (range = 13 to 38 μm ; $n = 5$) and $0.58 \pm 0.3 \text{ mm}^2$ (range = 0 to 0.9 mm^2 ; $n = 30$), respectively, to $117.5 \pm 14.8 \mu\text{m}$ (range = 100 to 142 μm ; $n = 5$) and $1.88 \pm 0.16 \text{ mm}^2$ (range = 1.6 to 2.1 mm^2 ; $n = 30$), again respectively. Oocytes were fully developed in samples obtained between August and September 1996, i.e. with diameters of $131.5 \pm 6.1 \mu\text{m}$ (range = 120 to 143 μm ; $n = 5$) and $131.7 \pm 3.4 \mu\text{m}$ (range = 126 to 140 μm ; $n = 5$), respectively. In July, August

Fig. 3. Gametogenetic cycles of *Oulastrea crispata* from Hoi Ha Wan between September 1995 and September 1996. (A) Changes in oocyte and spermary area (mm^2). Values are the mean of 30 polyps from between 3 and 5 colonies at each time interval. (B) Oocyte geometric diameter (μm). Values are the mean of the 5 largest oocytes in 30 polyps. Vertical bars denote standard deviations

Fig. 4. Transverse sections through the gonads of *Oulastrea crispata*. (A) Primordial oocytes in March 1996 ($\times 140$). (B) Developing oocytes in June 1996 ($\times 140$). (C) Mature oocyte in July 1996 ($\times 140$). (D) Empty space in mesoglea after egg release in September 1996 ($\times 140$). (E) Primordial spermary in June 1996 ($\times 200$). (F) Developing spermaries in July 1996 ($\times 140$). (G) Mature spermaries in August 1996 ($\times 200$). (H) Empty testes after spawning in September 1996 ($\times 140$). ec: ectoderm; en: endoderm; m: mesoglea; nu: nucleus; o: oocyte; s: spermary. Scale bars = 1 mm

and September 1996, mature oocytes with maximum diameters of 142, 143 and 140 μm , respectively, were recorded. In the mature oocytes, the germinal vesicles had migrated to the periphery, as is characteristic of anthozoan eggs. At later development stages, yolk granules, presumably consisting of lipids, occupied more space in the cytoplasm and were seen in histological sections as light-coloured vacuoles. There was also a reduction in the number of oocytes present in each mesentery during this period. In August and September 1996, oocyte surface area declined dramatically to $1.52 \pm 0.18 \text{ mm}^2$ (range = 0.9 to 1.7 mm^2 ; $n = 30$) and $1.06 \pm 0.2 \text{ mm}^2$ (range = 0.4 to 1.4 mm^2 ; $n = 30$), respectively. In August and September 1996, empty female gonads were observed, indicating egg release.

At the end of the previous cycle of oogenesis in September and October 1995, mature oocytes were still present, with no indication of breakdown, i.e. being resorbed. These oocytes had surface areas of $0.58 \pm 0.43 \text{ mm}^2$ (range = 0.1 to 1.3 mm^2 ; $n = 30$) and $0.1 \pm 0.11 \text{ mm}^2$ (range = 0 to 0.3 mm^2 ; $n = 30$), respectively. This shows that egg release can extend into October. From November to January 1995, no oocytes were present in the mesenteries.

Spermaries were first observed during May and June 1996, as small elongate structures in the mesoglea of the mesenteries. While the oocytes were usually situated near the polyp base, developing spermaries were usually at either a similar or a higher position in the same mesentery, i.e. they were nearer to the stomodeum. The spermary area was $0.31 \pm 0.18 \text{ mm}^2$ (range = 0 to 0.6 mm^2 ; $n = 30$) in June 1996 and gradually increased to $0.45 \pm 0.19 \text{ mm}^2$ (range = 0.2 to 0.9 mm^2 ; $n = 30$) by August 1996. Mature spermaries were observed in August and September 1996 as darkly stained, elongate, oval clusters. Spermaries, after releasing sperm, were seen in September 1995, August and September 1996 and appeared as kidney-shaped structures composed of rows of empty elongate sacs.

Planula release

A total of 154 colonies of *Oulastrea crispata* were investigated for signs of planula release. From January to May 1996, newly settled polyps of <1 mm in diameter ($n = 4$) were seen on concrete blocks, which had been previously colonized by *O. crispata* and had obtained geometric diameters of between 6 and 15 mm. These new recruits seemed to be derived from planulae, as the time of settlement was the resting phase in the annual spawning cycle of the adults. Histological observations also showed that planulae occurred in polyps without gonads, i.e. during the resting phase of gametogenesis (Fig. 5).

DISCUSSION

Gametogenesis and planula release

The sexual status of *Oulastrea crispata* determined in this study agrees with the observations of Nakano & Yamazato (1992) which stated that it is a simultaneous hermaphrodite. *O. crispata* is thus similar to its faviid relatives (Richmond & Hunter 1990, Richmond 1997). The gonadal arrangement also follows that of other species in this family, such as *Platygyra sinensis*, *Favia speciosa* and *Goniastrea aspera*, in which both spermaries and oocytes develop in the same mesentery (Clark 1997, Collinson 1997).

The gradual but slow decrease in oocyte surface area together with an increase in oocyte diameter, from July to September 1996, suggested that the spawning of mature eggs had occurred during this period. The cycle of oogenesis in 1995 seemed to end in October when surface area decreased to a minimum. The potential spawning period for local *Oulastrea crispata*, therefore, appears to extend from July to October. This is similar to some other faviids in the Caribbean and Central Pacific (Guam, Marshall Islands, Palau, Hawaii), which have spawning periods that may extend over the whole summer and even year round (Richmond & Hunter 1990). In contrast, the 3 local faviids studied (*Platygyra sinensis*, *Favia speciosa* and *Goniastrea aspera*) spawn over a short period in either June or July only (Clark 1997, Collinson 1997). In Okinawa, *O. crispata* was observed to release non-zooxanthellic eggs every few days from July onwards, regardless of the lunar phase (Nakano & Yamazato 1992). The exact spawning time of *O. crispata*, however, could not be monitored in this study, making it difficult to prove whether it is related to other environmental factors such as water temperature and lunar (and tidal) rhythms. Hong Kong *O. crispata* seems to have a similar spawning period to Japanese conspecifics. There are, however, species in the Acroporidae, Faviidae, Fungiidae, Pocilloporidae and Poritidae which exhibit different reproductive periodicities over their geographical ranges (Richmond & Hunter 1990).

Atrophy and resorption of oocytes have been reported for some coral species (Rinkevich & Loya 1979, Kojis & Quinn 1984). In this study of *Oulastrea crispata*, the number of oocytes present in each mesentery decreased between July and September. A possible reason for this could be resorption of source materials from smaller oocytes to maturing ones (Bermas 1996). Oocytes were visible after the peak spawning period (in October), but did not exhibit degeneration as described in other studies. Therefore, the resorption of oocytes after the spawning period presumably did not occur, but atrophy, which involves the release of immature eggs, may be possible.

Fig. 5. Cross sections through *Oulastrea crispata* polyps. (A) Young planula in the gastric cavity of a polyp ($\times 70$). (B) Close-up of a young planula in the gastric cavity ($\times 140$) (ec: ectoderm; en: endoderm; m: mesoglea; p: planula). (C) Appearance of a newly settled planula on a concrete block

Nakano & Yamazato (1992) showed that *Oulastrea crispata* is capable of releasing eggs and sexual planulae (without zooxanthellae) and asexual planulae (with

zooxanthellae) and, thus, is presumably both a broadcast spawner and a planula brooder. Mixed strategies of both broadcast spawning and brooding are not com-

mon, and *Pocillopora damicornis* is the only known example existing (Ward 1992). Histological study did not show any clear connection between planula development and gametogenesis. A cross section of the planulae also showed a layer of zooxanthellae at their perimeters. This suggests the planulae were produced asexually.

The recruitment of *Oulastrea crispata* first occurred on the artificial reef in September 1994, 9 mo after deployment (Fig. 6). There was a distinct increase in recruit density from June to September 1994, from 0 to 3.47 recruits m^{-2} . Coral recruitment densities were highest in June and September 1995. An expected significantly higher density of recruits in September 1995, as compared to the previous June before the presumed spawning period, was, however, not observed. There was also a general increase in accumulated recruit density between autumn and spring, i.e. September 1994 to June 1995. Such evidence suggests that sexual reproduction in *O. crispata* mainly occurs during the period from July to September. The poor relationship between spawning period and subsequent recruitment may arise from the occurrence of asexual reproduction in the form of either planula release or polyp bailout so that the relative degree of importance in sexual and asexual recruitment for this species is close. Asexual reproduction, through planula release, may not be seasonal because between January and May 1996, newly settled polyps of <1 mm ($n = 4$) were observed on concrete blocks previously used for growth investigations (author's pers. obs.). Dispersal by asexual planula release, thus,

seems to occur in Hong Kong as well as Japan (Nakano & Yamazato 1992). The sizes of colonies from which planulae could have been released were between 6 and 15 mm in geometric diameter. This study therefore concludes that, locally, *O. crispata* is a broadcast spawner and a planula brooder. Japanese *O. crispata* have also been shown to release asexual planulae during rest periods between spawning (Nakano & Yamazato 1992). These asexual planulae possess zooxanthellae, in contrast to those produced sexually, which do not (Nakano & Yamazato 1992). None of the polyps on the studied *O. crispata* colonies were lost. This eliminates the possibility of polyp bailout. Settlement failure by coral larvae during the spawning period in summer can also cause a lost link between sexual reproduction and observed recruitment. A lowering of larval viability may be brought about by sedimentation (Hodgson 1990, Rogers 1990, Te 1992), water turbidity (Kojis & Quinn 1984, Jokiel 1985, Tomascik & Sander 1987), nutrient enrichment (Tomascik 1991, Ward & Harrison 1997), water pollution (Loya & Rinkevich 1979), lower salinity (Richmond 1993a,b) or competition with fast-growing sessile invertebrates (Birkeland 1977, 1988) and macroalgae (Tanner 1995). Water quality at Hoi Ha Wan in summer is characterised by low dissolved oxygen levels, wide fluctuations in salinity and water transparency, all of which may, therefore, decrease the rate of coral settlement. Furthermore, juvenile mortality of *O. crispata* may balance recruitment locally, resulting in the observed no distinct net increase in recruits from December 1994 to December 1995.

Fig. 6. Accumulated density of *Oulastrea crispata* recruits (recruits m^{-2}) onto the test blocks retrieved from the experimental artificial reef at Hoi Ha Wan, from February 1994 to December 1995. All test blocks were deployed in December 1994. Density was calculated from the total number of *O. crispata* colonies recruited onto a surface area (total = 1.44 m^2) of 16 test blocks. Data were obtained from Lam (1998)

Coral spawning

The expected local spawning period, i.e. from June to August, is also Hong Kong's rainy season. Because of Hoi Ha Wan's enclosed topography, its water quality is easily affected by heavy terrestrial runoff, resulting in an increase in sedimentation and a decrease in salinity and dissolved oxygen levels (Fig. 7). These unfavourable conditions may cause reproductive failure of the corals in the bay. Previous studies have shown that the entire process of reproduction, such as reproductive timing, synchronisation and egg-sperm interactions, are all chemically mediated and susceptible to changes in water quality (Richmond 1997). Kojis & Quinn (1984) showed that the fecundity of *Acropora palifera* was depressed by high sedimentation rates and low water transparency. Under high sedimentation rates, coral colonies need more energy for cleaning, at the expense of maintenance, growth and reproduction (Kojis & Quinn 1984, Tomascik

Fig. 7. Hydrography of the surface and bottom waters recorded monthly (n = 5), for 35 mo, from January 1994 to December 1996, at the Hoi Ha Wan artificial reef site (after Lam 1999). B.O.D.₅: biological oxygen demand

& Sander 1987). Jokiel (1985) showed that changes in salinity, water temperature and light intensity affect planula production in *Pocillopora damicornis*. A decrease in water clarity, either by eutrophication or sedimentation, also has a negative effect on fecundity as photosynthetic products in the zooxanthellae contribute to egg and larva production (Rinkevich 1989). Even if mass spawning could occur locally, it would be difficult to observe. Possible reasons, or a combination of such factors, for this are as follows: (1) gamete numbers in each spawning event may not be high enough to see in the field, and (2) eggs may also be too small. In contrast, mass spawning on the Great Barrier Reef results in slicks of coral eggs and sperm above the reefs which may extend for hundreds, even thousands of metres (Oliver & Willis 1987). An hypoxic event in the summer of 1994 destroyed approximately one-half of Hoi Ha Wan's coral communities, but left the shallow ones at approximately -3 m Chart Datum relatively undisturbed (Collinson 1997, Lam 1999). Therefore, the number of possible colonies contributing to a spawning event decreased further after 1994. Most Hong Kong corals are under stress from water pollution (Morton 1992, 1994, 1995, Hodgson 1994, Collinson 1997), resulting in a decrease in energy invested in sexual reproduction, i.e. producing mature gametes. Another possibility accounting for the lack of mass spawning locally is the non-presence of chemical messengers, which could be triggered by either other invertebrates or different coral species. Coll et al. (1989, 1990, 1994) and Atkinson & Atkinson (1992) have shown that coral spawning may be chemically mediated. On Japanese reefs, contagious spawning events occur as the gametes from 1 coral colony stimulate others of the same species downcurrent to release their eggs and sperm upon contact with the gamete cloud (Richmond 1997). Hayashibara et al. (1993) tentatively suggested that a chemical cue may be produced by spawning colonies, to induce spawning of nearby corals.

Although 36 species of scleractinian corals are known to be present in Hoi Ha Wan (Cope & Morton 1988, Collinson 1997), only *Oulastrea crispata* was successfully recruited onto the artificial reef. Chou & Hsu (1987) stressed the importance of assessing reef resources at sites identified for artificial reef establishment in order to predict the significance of such deployment. However, fecundity and recruitment rate of these reef invertebrates, especially corals, should also be studied in order to better predict the final community structure. This pioneer scleractinian species has a complex reproductive strategy to assist it in colonizing new structures in the sea, such as hermaphroditism, an extended spawning period from summer to autumn and the release of planulae in the resting pe-

riod of the gametogenic cycle. These adaptations suggest that it is an opportunist, being able to colonize a new open surface in a relatively short period of time.

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