Diurnal periodicity in planula release by the reef coral *Pocillopora damicornis*

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Abstract

The hourly planula production rates of the common hermatypic coral *Pocillopora damicornis* in Kaneoke Bay, Hawaii were measured for three 24 h periods in order to detect any ordered periodicity that might exist in the daily cycle. A single peak in daily production was found. This peak occurred during periods of low tide and appeared to be independent of photoperiod.

Introduction

With the increasing amount of attention which is being focused on the subject of planula production in corals, the occurrence of periodicity in planulation (in some species) is becoming more thoroughly documented. Lunar periodicity in the reef coral *Pocillopora damicornis* (Linnaeus, 1758) has been described particularly well (Marshall and Stephenson, 1983; Abe, 1983; Atoda, 1987; Harigian, 1972; Richardson and Jokiel, 1984). Only a limited amount of research, however, has been done on the subject of diurnal variation in planula production. Harrigan (1972) found no evidence of diurnal variation in *Pocillopora damicornis*, but these studies were done using an artificially induced photoperiod under laboratory conditions. Richardson (personal communication), however, observed evidence of a peak in planula release immediately following sunset by *P. damicornis* at Al dewatik. The current study was designed to investigate the possibility of the existence of periods of peak planula production in the diurnal cycle.

Materials and Methods

In order to monitor the lunar cycle of planulation, daily observations of planula production by *P. damicornis* colonies from Kaneoke Bay, Hawaii (21° 50′ N; 157° 47′ W) were made. These colonies were maintained in containers of 3 l volume with a continuous flow of non-toxic sea water, which overflowed into collecting cups constructed of 100 micron plankton netting.

Two different morphological variations of *P. damicornis* were collected and monitored. These two types vary in appearance, in that type "Y" exhibits yellow animal pigment and type "W" exhibits only the brown color of the symbiotic zooxanthellae and has a different growth form. The lunar cycles of planula release of these two types also showed dimorphism in that they were asynchronous (Richardson and Jokiel, 1984). Two approximately equal sized colonies of each type were collected. These colonies were replaced with fresh colonies on alternate days so that they might represent the planula activity in the field more accurately. This method has been shown to be effective (Richardson and Jokiel, 1984).

The numbers of planula produced daily were monitored until an approaching peak in the lunar cycle of planula production was indicated. At this time, hourly observations were made for several days during peak production. In the first experiment (Exp. 1), these observations were carried out at an approximate peak in production by the "Y" type corals. This peak in production normally occurs after the time of full moon (Richards and Jokiel, 1984). Due to an extended period of cloudy weather, however, peak numbers of planula were unusually low. Lack of planulae of the normal time of production prompted us to attempt an experiment. We decided to try to stimulate production with artificial light illumination. Five of the 10 coral heads were subjected to an artificial light
of approximately full lunar intensity on the first night of the 48 h period of observation. The light was then placed over the other set of coral heads on the second night. Exp. 2 was also performed using "P" type corals, and Exp. 3 was performed using "T" type corals (Fig. 1). No artificial illumination was needed in either case due to lack of cloud cover. Natural moonlight was quite high.

The results were plotted using several different methods. Daily production of planulæ varied by three orders of magnitude. Therefore, in the case of the lunar variation in production (Fig. 2), the results were plotted as log (mean ± SEM) as a function of the time of month. For the diurnal data, mean number of planulæ produced in a given hour was plotted as a function of the time of day (Figs. 2 and 3). A plot of the tide levels was superimposed in order to facilitate comparison in Fig. 2.

Results

The data obtained in Exp. 1 (Fig. 2) indicated a definite peak in planulæ production near midnight. The 5 colonies that were subjected to the light treatment all showed mid-night peaks. However, peaks exhibited by the light treated colonies were much more dramatic than the other half of the set were treated with light on the second night, they also showed a dramatic increase in production on the following day. The colonies subjected to night light treatment on the first night but not on the second night still exhibited a pronounced peak on the second day.

In Exp. 2 (Fig. 2), the peak was indicated around 0300 h which again was coincident with low tide. Exp. 3 (Fig. 2) involved the "P" type corals, but still produced results indicating a peak near low tide. In this case, the peak occurred around 0200 h.

Discussion

Results of this investigation indicate a definite daily periodicity in larval production. All three experiments produced data showing extremely well defined daily peaks in production (Fig. 2). Because the peaks occurred at different times of the day, the possibility of the periodicity being controlled by the diurnal photoperiod is doubtful. The only obvious correlation between the periodicity and an environmental factor is that which occurs with the tide. In each case, peak production occurred within 3 h of low tide. A possible mechanism might be one in which changing tidal pressure is responsible for regulation of the period. Forringer (1977) describes a similar mechanism for the regulation of bimonthly periodicity in 2 corals. In this case, the colonies still followed this rhythm after they were isolated from the tidal stimulus suggests that the cycle has become entrained in a tidal time is still regulated by the tide. This lack of tidal stimulus in the collecting bowls may explain the slight observed deviations from low tide.

The data for Exp. 1 shows that the use of artificial light to induce planulæ production did not alter the periodicity, but rather the amplitude as compared to the control (Fig. 3). The fact that the colonies did respond to the light treatment can be attributed to the fact that night illumination is the main controlling factor in periodicity for this species (Jokiel, in prep.).

There are at least two possible selective advantages for peak release of planulæ at low tide. It may serve to retain those planulæ which settle almost immediately (Richardson, personal communication) on the same reef by way of the current patterns produced when the tide rises. This could increase survival of the larvae that are released during the period of rising tide. The idea that the number of planulæ released per day is supported by the findings of Ringer that the number of planulæ in the water is highest when the water is most turbid. This would indicate that the number of planulæ released throughout the period of rising tide is accumulated near the reef until the tide started dropping, at which time the number of planulæ in the water is greatest. The second possible advantage is that the larvae that are released and survive, in this case the state of release or state of tide is unimportant. The observations raise interesting questions as to how mechanisms and adaptive value of diurnal periodicity of larvae release.

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Fig. 1. Lunar variation of planulation during period of study showing the point in the cycle at which each experiment was carried out.
Fig. 1. Diurnal periodicity during the three different experiments (solid line) and the corresponding tide levels (dashed line).
Fig. 3. (A) Diurnal planula production by the set of corals exposed to artificial illumination on the first night of Exp. 1 and (B) on the second night of Exp. 1.
Literature Cited


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The relationship between colony size and larva production in the reef coral *Porites damicornis*

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Abstract

The planulation rates of *Porites damicornis* colonies from throughout the size range in which they occur in Kaneohe Bay, Hawaii were experimentally determined. It was found that the planulation rate increased with colony size until a size of 6 cm in radius was reached. The planulation rate in colonies greater than 8 cm decreased with increasing colony size.

Introduction

In the field of coral research, relatively little work has been done on the relationship of fecundity to coral colony age (as implied from size). Several reports are available which relate various species to a minimum reproductive size or age. Abe (1973) noted that *Pocillopora acuta* extended planulae only after growing to a size of 7 cm in diameter. Harrigan (1972) found that *Porites damicornis* colonies were reproductively mature in as little as 1 to 2 years. A few other reports also relate various species to a minimum reproductive size or age (Loya, 1972; Polacheck, 1978; Stimson, 1978). There is no available literature, however, which relates reproduction rates to colonies over the whole size range in which they are found. This investigation was designed to define this relationship through measurement of planulation rates of *Pocillopora damicornis* colonies throughout the size range in which they occur in Kaneohe Bay, Hawaii.

Materials and Methods

In Hawaii, *Porites damicornis* colonies are commonly found in sizes which range from single polyps, newly settled planulae to colonies with a radius of 10 cm. A few larger colonies can be found, but these are comparatively rare. At least two different morphological variations of *P. damicornis* occur in Hawaii (see Richmond and Jokiel, 1980, for descriptions). The "A" type coral was chosen for this study because it is more sturdy and easier to work with than the "B" type coral. Colonies ranging in size from 2 cm to 10 cm in radius were collected from the Coconut Island reef. These colonies were then placed in appropriately sized containers (from 1 to 5 liters) through which a continuous flow of seawater was maintained. The overflow from these containers flowed into collecting cups constructed of 180 micron plankton netting. The planulae which were collected were removed and counted daily and the numbers recorded.

The experiments were always carried out within a period of three days from a peak in the lunar cycle of planula production (Bolloran and Ritteeman, this volume). Data was taken on ten different days. In each case, 5 colonies from the stated size range were used.

Results

Daily planula production rates are reported in Table 1. The results suggest that there is an optimum colony size in terms of numbers of planulae produced. All of the colonies which were sampled produced planulae, although the numbers produced by the smallest colonies (2 cm radius) were rather low. Maximum production occurred in colonies which were approximately 8 cm in radius. Colonies which were greater than 8 cm in radius exhibited a decline in production.
Table 1. *Pocillopora fasciculata* daily larva production as a function of colony size.

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Discussion

The initial rise in the numbers of planulae which are produced is related to the increasing colony size (up to 8 cm in radius) can be expected. The relationship to increasing colony size (up to 8 cm in radius) can be expected. The numbers of polyps on the larger colonies could account for this initial linear increase. This same linear increase has also been found in *P. fasciculata* colonies of similar sizes at Enevetak (Richmond, personal communication).

The downwond trend in larva production which was observed in the larger colonies supports recent studies of canopy-understory effects in this species (Jekiel and Morrissey, in prep.). This suggests that the canopy which is formed by the larger colonies of this highly branched species severely shades the understory (inner regions of the colony). This, in turn, limits the light which is available to these inner regions and therefore could limit the energy which is available for reproduction. For this reason, these colonies would have a smaller number of reproductive polyps even though the colonies themselves are larger.

Literature Cited


Sexual reproduction in five species of the coral *Montipora*

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Abstract

The timing and mode of sexual reproduction were investigated in five Hawaiian corals of the genus *Montipora*. All species were simultaneous hermaphrodites. *M. verrucosa* and *M. dilatata* were observed to shed gametes following the new and full moons, respectively, in July. Spawning was also inferred for *M. studeri* and *M. verrucosa* following the July full moon. Oocytes contained zooxanthellae when released. Fertilization and development were external.

Introduction

Descriptive studies on reproduction in corals appear to be undergoing a renaissance. The importance of sexual reproduction in population dynamics has been demonstrated for several species (Jokiel et al., 1983; Weigel and Irvine, 1983; Heyward and Collins, in press: Stoddart, this volume). Furthermore, the most recent research (Harrison et al., 1984) into sexual reproduction suggests that the majority of coral species release eggs for external fertilization. Abandonment of the planulation paradigm (e.g. Hyman, 1940) has also focused attention on previously investigated species where planulation was not observed.

Stimson (1978) noted developing gonads in many species of Hawaiian corals, particularly in spring and summer, yet did not detect planulation in the majority. He hypothesized that many of these species may not breed planulae. Certainly if such corals culminated their gametogenic cycles with the brief summer spawning of many broadcasting species (Jokiel, 1983; Harrison et al., 1984) the ‘planulation’ event would easily escape notice.

The majority of the Acroporidae are broadcast spawners (Bothwell, 1972; Oliver, 1977; pers. obs.) and this is true of many species of *Montipora* in Australia (Robertson, 1981; Heyward and Collins, in prep.). In the present study five species of *Montipora* were studied in Hawaii during the summer months to determine the mode and timing of their reproduction.

Materials and Methods

Site and Sampling

*G. floridiana* and *G. studeri* were found in zones of high wave energy along the barrier reef crest, while *G. verrucosa*, *G. dilatata* and *G. verrucosa* were sampled from the more sheltered patch reefs within the bay. All species exhibited considerable morphological plasticity but were typically encrusting or plate-like. *G. verrucosa* and *G. dilatata* often had branch-like projections arising from the plates while *G. studeri* typically took a low thick branching form. All colonies were collected at approximately weekly intervals, commencing on 25 May, 1983. *G. studeri* was first sampled on the 21 June. Pieces of each colony were broken off with hammer and chisel, transported to the laboratory in seawater and immediately fixed in 10% formalin seawater for 24 h.

The arrangement and size of gonads were studied using a stereo-dissecting microscope with ocular micrometer, by dissecting soft tissues following decalcification in 5% formalin - 20% formic acid solution. The identification of oocytes and spermatogonia was confirmed from histological sections. In treatment for histology, fixed tissue was decalcified in 5% formalin - 2% formic acid solution, processed to paraffin, sectioned on a rotary microtome at 5 μm and stained with Haematoxylin and Eosin as per Winkler (1981).

Synchrony and Sampling

A field survey on 26 May revealed that every adult (i.e. > 20 cm diameter) colony had gonads at an early stage of development. In order to determine sampling procedure, 5 colonies of each species were collected and investigated for
synchronous gamete maturity. Ten polyps were dissected from the edge, middle and center of each colony. Mean oocyte diameters and numbers per polyp showed considerable but non-significant (p<0.05) differences within and between colonies of each species. However, a sterile zone of varying width was present at the plate edges and branch tips. Consequently, 5 colonies (>50 cm diameter) of M. verrucosa and M. dilatata and 2 colonies of the less abundant M. verrucosa were tagged and sampled sequentially each week. M. strigosa and M. flabelifera occurred in a wave swept environment where relocation of individuals was difficult. Subsequently, 3 untagged colonies of each were sampled at random each week.

Fixed and decalcified specimens were only used for histology. Number of eggs per mesenterium and egg size were recorded from live material which was fractured using wire cutters and supported in seawater under the stereo-dissecter. This avoided fixation artifacts when measuring oocytes and gave a better feeling for macroscopic changes in the gonads. Thirty eggs per species were measured on two diameters each week.

Spawning and embryogenesis

When fresh squashes of spermatogonia from the weekly samples revealed motile spermatids, some colonies were placed in flow through aquaria for close observation. Individual colonies were isolated in buckets or aquaria when spawning appeared imminent. Immediately following spawning the buoyant egg spars bundles of each species were collected. In four dishes gametes of individual colonies were isolated to test for self fertilization while four other dishes contained a mixture of gametes from several colonies.

Results

 Gonad structure and development

The five species of Porites were simultaneous hermaphrodites with male and female reproductive structures on separate mesenteries in the same polyp. Gonads were arranged on eight mesenteries, two side alternating with two female (Fig. 7). The appearance of the gonads was very similar for all species although M. verrucosa was always more advanced in development.

On 25 May ovaries were prominent with 3-5 oocytes along the oral-aboral axis of each mesenterium. Testes also developed within the mesenteries but at this stage were translucent, strap-like bodies and were of smaller volume than the ovaries. Oocytes increased steadily in size until spawning (Fig. 2). Testes increased markedly in volume in the month prior to spawning when testes and ovaries were similar in volume and both structures were cream to white. At this stage, density of zoanthellae in the mesenteries surrounding the gonads increased, particularly around the ovaries. A week prior to spawning the oocytes were surrounded by a dense accumulation of zoanthellae, making them appear brown. Zooanthellae had invaded some oocytes up to 12 d prior to spawning (Fig. 3). Testes were usually quite locular 1 week prior to spawning, with spermatids developing tails as the locules developed. Some spermatids were maturing at this stage but the sperms heads appeared spherical and translucent. A week prior to spawning, squashes revealed very active spermatids and many had a condensed, well-defined acrosomal body. The white testes were the most prominent, macroscopic reproductive structure immediately prior to spawning.

Spawning

M. verrucosa broadcast gametes on the 10th, 11th and 12th of July following the new moon on the 10th. M. dilatata, M. verrucosa and M. strigosa spawned throughout the week following the full moon on July 25th. Spawning of M. verrucosa and M. dilatata occurred simultaneously in the aquaria and in the field, where polyps began spawning behavior approximately 30 min after sunset. Each polyp elongated, gathered the gonads under the oral disc, then contracted the body wall. The gametes were forced into a siphon which disturbed the oral disc. This posture was maintained for 30 minutes before the gametes were ejected. Egg and sperm release were simultaneous, each polyp releasing a single cluster of eggs, packaged around the spars (Fig. 4). It appeared that each gamete cluster represented the entire reproductive complement of the polyp, containing 12-26 ova. At release, all the eggs contained zooanthellae. The inheritance of parental zooanthellae was also noted for Porites compressa which
Fig. 1. Transverse section of *Mertensia dilatata* polyp.
Fig. 2. Mean oocyte diameter for five species of *Hysterothyla* throughout the summer.
Fig. 3. Coelenterae in oocyte (12 d prior to spawning).
Fig. 9. Transverse section of *Montipora* *dilata* s. gamete cluster.
spawned on the new and full moons throughout the summer. Presence of zoanthellae was checked with fluorescence microscopy.

During spawning the gamete cluster was usually propelled clear of the colony and floated quickly to the surface where it broke up within 30 min. In M. verrucosa and M. dilatata, release of gametes commenced between 2045 h and 2100 h, individual colonies continued to release gametes until 2145 h. A particular colony would release most of its gametes during one evening. The major population spawning occurred on 11 July for M. verrucosa and on 27 July and 28 July for M. dilatata. However, small areas of a colony might retain some gravid gonads for M. dilatata. Spawings on successive nights always occurred at about 2100 h, suggesting some photoperiod cue as the final trigger.

Following spawning, up to 50 colonies of each species were collected from the field. No gravid colonies were found after the colonies kept in aquaria had spawned. Indicating a synchronous population spawning. M. verrucosa and M. dilatata were not observed to spawn. Spawning time was inferred by the absence of zoa in the weekly samples following the spawning of M. dilatata. M. flabellata still contained gonads in August and early September, although not M. dilatata. The species may have a multiple spawning during the late summer and fall. It was noted that small pieces of M. flabellata which had become separated from their original colony by an area of dead skeleton were sterile, while the larger parts of the original were fertile. This suggests the importance of not only age but size in reproductive status.

Embryogenesis

Gametes collected from isolated colonies were mixed together at 2230 h. The first cell divisions were noted at 2345 h, however, by 0045 h less than 1% of the population were at 2 or 3 cell stage. Some embryos at 2 cell stage were isolated for observation. Cell divisions occurred every 45-60 min in irregular radial development (Giese and Pearse, 1976, pg. 176). Cell divisions were complete and equal, although not always synchronous beyond the 8 cell stage. Lumen 12 h after spawning, sorus were common and gastrulae were apparent within 12 h. At 14 h many embryos were ciliated, but the cultures were deteriorating rapidly. Many embryos developing at the surface formed irregular shapes, probably due to surface tension effects, and ceased to divide. Agitation is a key factor in maintaining the embryos through to viable planulae (Heyward and Hancock, in prep.).

Cells in the settling experiments lysed by 0800 h and only one egg showed signs of dividing. Although inconclusive, this suggests that settling, if at all possible in these populations, has a lower probability of occurring than cross fertilization.

Discussion

These species of Montipora in Hawaii broadcast spawn after the new or full moon during summer and fall. This is a common reproductive pattern for scleractinian corals (Harriott, 1953; Ershiken, 1981; Krupp, 1983; Yalden, 1983; Szant-Froelich et al., 1983; and others). The sequence of gametogenesis and the timing of spawning is very similar to Montipora ramosa on the Great Barrier Reef in Australia (Heyward and Collins, in prep.).

Although the energetics of reproduction in corals are poorly understood, the annual cycles of water temperature and insolation are likely to affect reproductive effort (Jokiel and Sutker, 1978; Szant-Froelich et al., 1983) and have been suggested as a major trigger for gonad maturation and spawning (Harriott, 1983). Like Pachyseria scutellaris in Hawaii (Krupp, 1983), the Montipora spp. spawn at the time of maximum water temperature and solar irradiance.

There was no evidence of a second reproductive cycle commencing following spawning. However, the study was terminated at the start of fall. Simmons (1978) noted eggs present in one colony as late as October, and Robertson (1983) found some suggestion of a bimodal spawning during summer and fall for Montipora spp. in Australia. If light and temperature permit, (Szant-Froelich et al., 1983) a second cycle may well appear and this possibility should be investigated more comprehensively. Similarly, the sequential spawns of the dinocyst Porites compressa on the new and full moons throughout the summer lend themselves to a detailed quantitative study.
The incorporation of parental zooxanthellae into the oocytes at least 12 d prior to spawning is notable. It would appear to be characteristic of the genus Acropora but many other Acroporidae do not acquire zooxanthellae until after settlement (Heyward and Babcock, in prep; Harrison, personal communication). One day old Montipora plumosa collected from the plankton have as extensive symbiont loads (see Hodgson, this volume). If these zooxanthellae are translocated to their planktonic hosts (Richmond, 1971) dispersal potentials may be quite high. Porites and Montipora both inherit parental zooxanthellae and are widespread in the Hawaiian archipelago, in contrast to the restricted occurrence of Acropora (Grigg, 1983).

At the time of spawning, no germinal vesicle was apparent in the ova, suggesting that these eggs were mature and ready for fertilization. Considering the proximity of eggs and sperm in the gamete bundles (Fig. 4), selfing had every chance of occurring. Outcrossing mixtures were far more successful than selfing trials at producing cleavages and embryos. Recent observations on the Great Barrier Reef (Heyward and Babcock, in prep.) were larvae of broadcast spawners were successfully raised to settlement for several species, suggest that some mechanisms must exist which reduce the probability of selfing. Investigations into coral self-fertilization need to be continued on a rigorous basis to clarify the issue.

This study, while only of short duration, confirms Stimson's (1978) proposal that many corals broadcast gametes. It is likely that many do this in summer and fall. Recent work in the Caribbean (Szmant-Froelich et al., 1983) reveals similar patterns for the timing of coral reproduction but also indicate the diversity of coral reproductive modes. Many species of Hawaiian coral await long-term investigation of their reproductive patterns.

Acknowledgements

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Aspects of reproduction and planula development in the reef coral *Cup珊瑚* ocellata

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Abstract

Gametogenesis and planulae development and production were followed in small and large colonies of the hermatypic coral, *Cup珊瑚* ocellata. This species is a viviparous, simultaneous hermaphrodite and planulae are produced continuously and asynchronously in the Coconut Island population. Ovaries and testes are intermingled within the same mesenteries by hollow vessels. The potential for self-fertilization and the possible nutritive function of the vessels are discussed.

Introduction

Traditional views of reproduction in hermatypic corals (Nyma, 1940; Vaugh and Wells, 1943; Wells, 1956) have been revised in the light of recent research, and it is now recognized that scleractinians may display a variety of sexual characteristics and timing in reproduction (Pedaliathan, 1983). Despite the current interest in coral reproductive studies, the origin of planulae is an issue which remains largely unresolved. The question of whether planulae are produced sexually or asexually has rarely been addressed. Pioneer electrophoretic studies (Stoddart, 1983; Stoddart, this volume) have shown that the planulae of *Pocillopora damicornis* may be generated asexually, thereby revealing a further uncharted dimension to the propagative capabilities of corals. Patterns of coral gametogenesis are poorly known, and crucial developmental studies of planulae remain undocumented, although they are of profound importance to the understanding of coral reef ecology and demography.

The paper focuses on the gametogenesis and development of planulae in *Cup珊瑚* ocellata (a shallow water species of Hawaiian coral) known to produce larvae throughout the year (Edmondson, 1946; Stimson, 1978), together with observations on the timing of planula release, in an attempt to provide an insight into the reproductive system underlying the propagation and brooding of planulae.

Materials and Methods

The study site was located on the southern portion of the fringing reef surrounding Coconut Island, in Kaneohe Bay, Oahu, Hawaii. The reef flat zone is about 75 m wide and is covered by 1-2 m of water but may become emergent at low tide. *Cup珊瑚* ocellata is a massive species of coral restricted to shallow water habitats. Typically, *C. ocellata* colonizes dead coral substrates, predominantly *Porites compressa* (the dominant structural reef coral) forming irregular "knob shaped" colonies or encrustations which reach 10-15 cm in diameter. Commonly, *C. ocellata* is a sandy brown coloration at the top of the colony, becoming darker at the base.

Several approaches were adopted to study the reproduction of this species. Firstly, the polyps of the coral were examined histologically for evidence of gametogenesis. Secondly, since *C. ocellata* is viviparous, an attempt was made to follow the frequency and timing of reproduction by monitoring the release of planulae from individual colonies.

Histological preparations

Each week, over a period of two months, three large colonies (8-10 cm diameter) and three small colonies (2-4 cm diameter) were collected in order to study the development of genital cells. The colonies were fixed in seawater containing 4% formalin for a period of 48 h. Large fixed colonies were sectioned on a diamond wheel. and live samples were extracted from the top and lower regions of each colony. Samples were decalcified in either 10% Brandy decalcifying solution or a solution of 3% formalin with 1% formic acid. Decalcified specimens
revealed a mat of algal material directly beneath the coral tissues, apparently ramifying the skeletal framework. The identity of this algal tissue and its possible significance to the growth is unknown. The remaining coral tissue was separated from the underlying algal mat, and rinsed in distilled water.

Dehydration, clearance and paraffin infiltration of tissue samples was automatically by a Technicon Tissue Processor. Six micron serial sections were prepared and stained with Mayers, Haematoxylin and Eosin.

Planulation

Fifteen colonies (of approximately equal size) were collected from different locations on the reef site. Each colony was placed in individual "planula collection boxes" supplied with running seawater and maintained in ambient sunlight. Planulae were collected each day from overflow water, in 180 micron mesh cups. The captured planulae were counted, and settlement activity was observed periodically under a dissection microscope. Those planulae which had settled within the mesh cups were counted before removal. The production of planulae from these colonies was monitored over a period of six weeks, during which the colonies showed no signs of deterioration. Some planulae were fixed in 1% formalin/seawater solution for histological preparations.

Preparations for scanning electron microscopy

Free-swimming and newly settled planulae were fixed in 2% glutaraldehyde in Millipore-filtered seawater. Whole polyps were dissected from decalcified formalin-fixed material to reveal their internal anatomy. Fixed tissues were dehydrated to 70% alcohol, in which they were stored. Final dehydration was performed using a series of alcohols before subsequent critical point drying. The samples were plated with gold and viewed under a scanning electron microscope.

Results

Reproduction

From the histological study, it is apparent that C. ocellata is hermaphroditic. Ova and testes are found intermingled on the same mesenteries throughout the polyp body (Fig. 1a). Mature eggs reach a size of 150-160 micron mean diameter. The mean polyp diameter of this species is 1.8 micron, and each of the twelve gonads per polyp may contain two or three eggs. There is a marked asynchrony in the development of genital cells between colonies. Planulae develop to an advanced state within the adult polyp, suspended from the mesenteries.

Female gonads

Ovaria are found with testes within the same gonad on each mesentery. Sexually mature polyps. Early stages of egg development are first seen as small ovoid gonial structures developing within the mesenterial tissue (Fig. 1b). Two or three eggs may grow in the plane of the mesentery, intermingled between testes within each gonad. Zooxanthellae may be found in the endodermal tissue surrounding the eggs but the eggs themselves do not contain these algal cells. The eggs are ovoid in shape, and contain globules of yolk material which have a high affinity for eosin, staining pink (Fig. 1c). Mature eggs grow to 160 microns diameter, with an oval nucleus (60 micron diameter) and a dark red stained nucleolus (6 micron diameter).

Male gonads

Testes develop in the same gonad as the ovary, throughout the polyp from the base to the pharynx, but were not observed within the tentacles. The testes consist of variously shaped sacs of different sizes. The gonad, incorporating both ovary and testes, is enveloped by a layer of endoderm extending from the mesenteries. Each testes may have several lobes in which different stages of development may be observed. The male gonads may reach a diameter of 100 microns. The development of male gonads is initiated with a primary spermatocyte within the endoderm of the mesenteries (Fig. 1d). The spermatocyte increases in size by successive division, and gradually fills up with spermatagonia (Fig. 1e). The caudally typically seen in immature spermatocytes is progressively lost with the growth of the spermatids and spermatocytes. The spermatogonium (6 micron diameter) appear ovoid or circular in shape showing dark staining activity. Spermatids and
Fig. 1. *Crithidia ocellata*. Scale bar = 50 microns. Abbreviations: BQ = Sperm "Bouquet"; E = Egg; En = Endoderm; N = Nucleus; S = Spermaties; M = Mesentery.

A) Transverse section through intermingled testes and ova on the same mesentery.

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Fig. 1b. Transverse section of early female *C. ocellata* oozing gonad.
Fig. 1c. Transverse section of *Euphasia ocellata* egg.

Fig. 1d. Transverse section of early male *Euphasia ocellata* gonad.
Fig. 1a. Transverse section of immature _Orchestrea ocellata_ testes with characteristic lumen.

Fig. 1b. Longitudinal section through mature _Orchestrea ocellata_ gonad illustrating the sperm "bouquet" arrangements adjacent to mature eggs.
spermatocysts also show such staining. As development progresses the spermary becomes densely packed with sperm. The sperm heads are darkly stained from which extend long tails, which stain pink in eosin, forming "bouquet" type arrangements (Fig. 1f).

Planula development

Cyclostrea ocellata is viviparous and breeds its planulae to an advanced state of development before release. The primordial planula is first observed within breeding colonies containing mature eggs and sperm (Fig. 2a) beyond which no gonads were present in polyps containing planulae. The early planula which develops on the mesenteries consists of an ovoid structure, composed of two layers of cells: the endoderm and an outer layer of columnar ectoderm. Few zooxanthellae are present within the tissues of the early planula. As development progresses, attachment structures extend from several mesenteries abutting the planula laterally as well as at the base (Fig. 2b, 2c). Typically the planula grows suspended at one side of the polyp, where there is an intimate association of adult polyp and planula tissues. Several layers of tissue enclose the planula. In transverse section attachment vessels extending from the mesenteries are evident within the tissues of the planula. These attachments appear as hollow vessels surrounded by columnar cells and may either extend through the endoderm of the planula or may be continuous with the ectodermal layer (Fig. 2d). In longitudinal section these attachments (Fig. 2e) extend from the base of the polyp or from the lateral edges of the mesenteries. Such structures have been previously described, and their function is unclear, although they may be involved in the transfer of nutrients. As the planula grows, zooxanthellae become more numerous, the mesenterium enlarges and differentiates. Spermatocysts become clearly visible in the ectoderm. In the final stages of development, the planula occupies most of the space in the gastrovascular cavity of the polyp, and the attachments are finally lost (Fig. 2f).

Planula behavior

If newly settled planulae were removed and transferred to fresh seawater, the planulae would reattach with no apparent detrimental effects. This phenomenon was first observed by Richmond (1965) in larvae of Pocillopora damicornis.

Frequency of planulae

Preliminary observations on the release of planulae showed a marked asynchrony within and between colonies (Table 1). Some colonies produced pulses of planulae, while others appeared to generate larvae almost continuously. Certain colonies did not produce any planulae throughout the sampling period. There was no relationship between the number of planulae produced and colony size. No lunar phase could be detected in the timing of planula release, which is in contrast to previous observations by Stimson (1976) who found a peak in planulae release. The maximum number of planulae released from an individual colony of C. ocellata (10 cm diameter) was 350. Ideally, planulae should be collected from individual colonies in the field, since maintenance of colonies in aquaria is likely to disturb the genetic and planulation rhythms of corals. The possible cues for planula release. However, this was not feasible for this study.

Discussion

Cyclostrea ocellata is a hermaphroditic species of massive coral. Its gonad structure resembles that of other species in which ovaries and testes develop intermingled on the same mesenteries, such as Pocillopora damicornis (Marshall and Stephenson, 1931), Pocillopora aspera (F. & C. B.), Pocillopora aspera and Euphyllia divisa (Kojis and Quiñon, 1961). C. ocellata exhibits simultaneous hermaphroditism, which allows the opportunity for self-fertilization. It has been suggested (Purcell, 1956) that self-fertilization is a mechanism to reduce reproductive wastage, and may be of prime importance in areas of recolonization in which population densities are low. However, this mode of reproduction is also found in common species such as Acropora formosa and Pocillopora damicornis on the Great Barrier Reef (Pichon, unpublished).

In C. ocellata, gonads are present throughout breeding colonies, irrespective of their position, as observed in other massive species of coral (Kojis and Quiñon, 1961), whereas in branching species gonads are absent from the actively growing tips. This has been observed in Pocillopora damicornis (Harrigan, 1973)
**Fig. 2.** *Cyprestes ocellata* planula development. Scale bars = 50 microns. Abbreviations: AV = Attachment Vessels; E Ectoderm; S = Spermatids; P = Planula; u = Planula mesentery. *Cyprestes ocellata* planula: Transverse section of planula and mature gonads in adjacent mesenteries.

**Fig. 2b.** Longitudinal section of developing *Cyprestes ocellata* planula.
Fig. 2c. Oblique section of developing *Cyclospicaria ocellata* planula with lateral attachment structures.

Fig. 2d. Transverse section of *Cyclospicaria ocellata* planula with adult polyp showing attachment vessels.
Fig. 2c. Longitudinal section of mature planula.

Fig. 2f. Scanning Electron Micrograph of a settled *Euphasia pacifica* planula.
Table 1. Daily production of planula larvae in 15 individual colonies of Cladophora gracilis between 6 June 1983 and 10 July 1983.

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</tbody>
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It has been proposed by Sinkevich and Loya (1979a,b) that morphological constraints of polyp size predispose coral species to certain forms of reproduction. They suggested that branching, small polyp species in which gonads develop in the body cavity, exhibit brooding, while large polyp or massive species (in which gonads develop on the mesenteries) broadcast gametes. The present study conflicts with this hypothesis, together with observations by other workers. C. ocellata is a massive species in which the gonads develop on the mesenteries, but in contrast to the theory, it broods its planulae. Smart-Preelisch et al. (1989) concluded that there was “no universal rule” to the relationship between polyp size, egg size and developmental mode. Bothwell (1981) found Acropora species with small polyps that broadcast eggs. This is opposite to the suggestion that brooding generally occurs in small polyp species. Fadallah and Pease (1982) have shown that large polyp solitary corals may exhibit brooding or broadcast spawning.

Nevertheless, it is obvious that there will be a limit to the number of planulae or eggs developed simultaneously, imposed by the space within individual polyps available for brooding embryos to an advanced stage of development. The brooding of planulae was not an energetic cost to the adult polyp. The presence of a planula filling the gastrovascular cavity is likely to impair its feeding capabilities. The importance of energy transfer between polyps of a colony is not known. Perhaps only a small percentage of polyps are reproductively active at any one time, due to energetic constraints.

It is likely that there is a physiological minimum amount of energy required for metamorphosis, which sets a lower limit to the size of planulae depending upon how the energy is packaged. Energy rich lipids are often found in larvae and serve as a concentrated energy source, thereby minimizing the size of planulae. However, planulae contain zooanthellae, and it is not known what contribution they make to the energy requirements of planulae.

Released planulae vary considerably in shape from a contracted sphere to an extended pear-shape. Characteristically, small “pearly vesicles” are scattered throughout the planula tissues of C. ocellata. (first described by Edmondson, 1946) become twisting larvae move by ciliary action and undergo frequent changes in shape. When viewed under ultra-violet light, the planulae exhibit a general green fluorescence, with the zooanthellae appearing as bright spheres. It has been suggested that this green fluorescent pigment, originally observed in the planulae of *Stylophora pistillata* (Sinkevich and Loya, 1979a) is capable of converting short wave radiation into light which may be utilized by the zooanthellae in photosynthesis (Kawaguti, 1973).

The planulae of *C. ocellata* move slowly throughout the water column, and show no obvious phototactic responses. Most of the forms of movement described by Karlson (1972) and Sinkevich and Loya (1979a,b) were also observed in the larvae of *C. ocellata*. Close observation of the oral pore revealed the movement of particulate material into and out of the planula. However, it is not clear whether material incorporated into the larva in this fashion can be utilized at this stage.

Laboratory observations of settlement activity in planulae showed that the period between release and settlement is highly variable, which may reflect the range of developmental stages released from colonies. Planulae from some colonies settled in the collecting cups whereas others showed a more protracted settlement period. The temporal aspects of settlement may be modified by not only differential stages at release, but also environmental regime, substrate availability or a combination thereof. It is not known if the time period to settle-
ment is progressed to time of release, or whether a particular stage of development must be attained before settlement is possible.

A few planulae were observed to settle on glass slides and deposit skeletal material. Under stress (for example, if colonies were left in stagnant water) such planulae would withdraw their living tissue from the attached skeleton or detach completely.

Egg number per gonad may be indicative of reproductive mode (Connell, 1973; Blaskevich and Loza, 1979a,b) although its predictive value requires further substantiation. Although male gonad structures have been recorded (Fussner, 1902; Gardiner, 1905; Marshall and Stephenson, 1931; Blaskevich and Loza, 1979a,b; Padillah and Pearse, 1982) spermatogenesis in corals has rarely been described (Blaskevich and Loza 1979b). Perhaps this is because it is not readily quantifiable, since measurements of spermatogenic dimensions do not reflect developmental stage. In _G. occellica_ mature sperm can be observed directly adjacent to mature eggs. Different stages of development may be seen within lobes of the same testes. The interaction of sperm and egg remains poorly documented.

A number of studies have described the existence of planula brooding and considerable differences have been observed in the stages at which planulae are released (Byman, 1940; Edmondson, 1946; Atoda, 1953; Harrigan, 1972; Padillah, 1973, 1979a). However, the development of planulae from the mesenteries in which attachment vessels encase the planula within the polyp, as seen in _G. occellica_, has not been previously described. The unusual hollow vessels which pass through the inner tissues of the planula may have some nutrient transfer function. The brooding of planulae in this unique fashion might facilitate the development of the planula to reach an advanced stage before release. This could be an adaptation for rapid settlement and establishment of new colonies.

Considerable interest has been focused on the seasonality and timing of planulation (Marshall and Stephenson, 1931; Atoda, 1947; Harrigan, 1972; Blaskevich and Loza, 1979a,b). Observations by Edmondson (1946) and later, Stimson (1976) revealed that _G. occellica_ was capable of releasing planulae throughout the year. Stimson (1978) also suggested that the release of planulae in _G. occellica_ was related to the lunar phase. The present study failed to detect any such periodicity, but a marked asynchrony was observed between colonies, which is consistent with the observations of other workers (Jokiel, unpublished). The time period between planula release and settlement also showed considerable variability. The underlying cues for larval release, and the adaptive significance of synchronous or asynchronous release of planulae is unknown. A consequence of the asynchronous gametogenesis and planulation in _G. occellica_ is the perennial availability of propagules for the colonization of new substrates.

The numbers of planulae released from individual colonies of _G. occellica_, a massive, slow growing coral, are low in comparison with _Pocillopora damicornis_ (Harrigan, 1972) which is a rapid growing branching species. This difference could be attributed to either the number of polyps per unit surface area available for development of planulae or perhaps due to differential energy accumulation and reproductive energy budgets. Alternatively, the differences in planulation may result from the differential time schedules involved in the asexual production of planulae in _P. damicornis_ and the sexual reproduction which gives rise to planulae in _G. occellica_.

Attempts to decipher possible trends in coral reproductive patterns have failed to adequately encompass the observed complexity. The theoretical r-K continuum, developed by Pianka (1970) has been invoked to rationalize coral reproduction. Loza (1976) discusses the reproductive characteristics of _Sergastrea pistillata_ in terms of r-K selection theory. However, the criteria often used to categorize species have not been consistent, and a number of deviations from this theoretical framework are known (Renge, 1975; Grassle and Grassle, 1976). Padillah and Pearse (1962) suggested that solitary corals may be selected to reproduce at opposite extremes of various modes of sexual reproduction. Stimson (1970) endeavoured to explain coral reproductive patterns in terms of habitat. He suggested that shallow water species (including _G. occellica_) produce planulae, whereas deeper water species adopt modes of broadcast spawning. Furthermore, it was proposed that shallow water species reproduce in a fashion which favours the retention of reproductive propagules within the parental habitat. However, with the influx of new data, the validity of such generalizations is now questionable.
It is apparent from the foregoing discussion, that no profound trends or generalizations can be made to explain the observed patterns of reproduction in corals. Numerous combinations of sexual characteristics including gonochoric and hermaphroditic species, brooding and broadcast spawning have been described in both solitary and colonial corals. Superimposed upon these reproductive mechanisms are a range of gametogenic and planktonic schedules which compound the problems in rationalizing such phenomena. Reproduction is a vital process to which the life history of each species is geared. A particular environment presents a set of environmental contingencies which must be met in order for a species to survive. It is evident that coral species have solved their ecological problems by their mere existence, but each may have employed a different combination of life history characteristics. Perhaps certain combinations of life history traits may lead to particular forms of propagation. It may therefore be essential to view reproductive patterns together with growth characteristics in the context of further ecological dimensions in order to decipher any meaningful trends in coral reproduction and life histories.

Literature Cited


Gametogenesis and origin of planulae in the hermaphroditic coral *Porites australis*

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Abstract

In order to describe the gametogenesis of *Porites australis* and relate this process to the origin of planulae in this monthly planulater species, three colonies were tagged on a fringing reef in Kameha Bay, Oahu, Hawaii, and sampled every 2 to 3 weeks during the summer of 1983, and prepared for histological study. Gametogenesis in *P. australis* is similar to that reported for other scleractinians, but differs in the final stages in that no consumption of spermogonia takes place. Gametogenesis takes approximately 5 weeks. Larvae develop within 2 weeks. The planulae appear to originate from ovulated oocytes by partenogenesis with eventual production of asexual planulae. The ability of single colonies and single polyps to produce larvae over a period of two consecutive months cycles is described.

Introduction

Planulation in corals is well documented (Marshall and Stephenson, 1933; Connell, 1973; Stimson, 1978; Feige and Quinn, 1954; van Hoek, 1983; Fadell, 1983) and has been assumed to be the mechanism of sexual reproduction in scleractinians (Nyama, 1940). Very little is known about the transition from gonad to planulae in the corals that breed larvae (Pinkovich and Loya, 1979; Szant-Tregilich et al., 1982; Fadell, 1983). Recently, it has been proposed by Stoddart (1983) that the planulae are asexually produced in the widely distributed hermaphroditic coral *Porites australis*. This hypothesis is supported by electrophoretic evidence of genetic identity between the planulae and the parent colony, raising the question about the possibility of asexual origin of the coral larvae. *P. australis* is a very common inhabitant of the reef flats of Kameha Bay, Hawaii (Narog, 1972), with a fairly constant lunar periodicity in planulation throughout the year (Marshall, 1933; Stimson, 1978; Richmond and Jokiel, 1984). Despite the fact that many people have studied the reproductive and larval biology of this species (Edmondson, 1946; Atoda, 1967; Harrigan, 1972; Stimson, 1978; Jokiel and Quinn, 1978; Richmond, 1983; Stoddart, 1985; Richmond and Jokiel, 1983), the temporal development of gonads remains undocumented. The present study describes the gametogenic cycle of *P. australis* in Hawaiian waters and discusses the relationship between this process and the uncertain origin of the planulae.

Materials and Methods

In order to follow the development of the gonads within the same colony throughout a planulation cycle, three large (>20 cm diameter) and healthy colonies of *Porites australis* type "a" (Richmond and Jokiel, 1983) were tagged on the reef flat of the Coconut Island fringing reef in Kameha Bay, Hawaii. The field collection of samples for histological examination was done every 2 to 3 weeks during the months of June and July, 1983, following the same procedure used by Pinkovich and Loya (1979), and assuming synchronization in breeding between different branches within the same colony (Harrigan, 1972). The branch tips were immediately fixed in 10% formalin in seawater for 24 h; rinsed in the water and partially decalcified in a 2% formic acid - 5% formalin solution for 3 to 5 d. Once decalcified, small pieces of tissue were peeled from the middle portion of the branches. This area has the highest proportion of polyps with brooding of the branches. This area was then positioned in 10% formalin solution, dehydrated for 6 to 8 microns thick and stained with either Watson's hematoxylin and eosin or Mallory-Fontainein (Nyarick, 1984). Better results were obtained with the former stain.
Since P. dasycrinus in an hermaphroditic coral (Harrigan, 1972; Grigg and Boucher, unpublished manuscript; Stoddart, personal communication), the gametogenic cycle of male and female gametes was followed in the same 3 tagged colonies. For the qualification of spermary state, an arbitrary system of 5 stages was used, based on a visual assessment of their maturity (Table 1). Female gonads were difficult to separate on an arbitrary basis. Therefore, size was used as a relative index of maturity of oocytes (Giese and Pearse, 1974), and was estimated as the mean value of the maximum diameter of oocytes and the perpendicular diameter of this maximum length. Several polyps per branch for each colony were examined until 10 spermaries and 5 oocytes were measured with a calibrated ocular micrometer. Photomicrographs were taken with a light phase Zeiss microscope.

Table 1. Arbitrary developmental stages of spermaries in Pocillopora dasycrinus as seen in histological sections of the mesenteries.

<table>
<thead>
<tr>
<th>Stage No.</th>
<th>Spermary Condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Bulging of spermaries from mesenteries</td>
</tr>
<tr>
<td>II</td>
<td>Oval shaped, filled with spermatocytes</td>
</tr>
<tr>
<td>III</td>
<td>Beginning of lumen formation</td>
</tr>
<tr>
<td>IV</td>
<td>Conspicuous lumen, and bouquet-like arrangements of spermatocytes</td>
</tr>
<tr>
<td>V</td>
<td>Presumably in resorption</td>
</tr>
</tbody>
</table>

The frequency of oocytes and planulae per polyp was estimated by observing and counting a large number of polyps (>30) from each of several different colonies.

Results

The three colonies showed a similar temporal pattern of development of gonads and planulae (Figs. 1-6). As expected, all 3 showed a simultaneous hermaphroditic condition; a single polyp has male and female gonads but never on the same mesentery. In general, a mesentery bearing spermaries faced mesenteries bearing ovaries.

The gonads develop from the mesenteries as in other anthozoans (Radbillah, 1983) and while growing, fill the gastric cavity of the polyp. These polyps often contain twelve fertile mesenteries, upon which the gonads are attached by stalks derived from the endoderm. Both male and female gonads are enclosed by two layers of endodermal tissue and mesoglea.

An individual colony planulates at least for two consecutive months (Figs. 1-3) and even though very few polyps of the colony produce planulae at the same time (Harrigan, 1972), most of the mid-branch polyps are fertile (Table 2).

Table 2. Relative distribution of polyps with mature oocytes and/or planulae. Values shown in table are numbers of polyps examined followed by percent frequency in parentheses.

<table>
<thead>
<tr>
<th>Number of Planulae per Polyp</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oocytes</td>
<td>5 (9%)</td>
<td>40 (70%)</td>
<td>12 (22%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td>Planulae</td>
<td>5 (10%)</td>
<td>29 (61%)</td>
<td>12 (25%)</td>
<td>2 (4%)</td>
</tr>
</tbody>
</table>

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Fig. 1. Gamete and planula growth in *Porilla* *denticornis* colony No. 1. Arrows indicate where embryo-like structures began to appear. Bars represent one standard deviation.
Fig. 2. Oocyte and planula growth in *Pocillopora damicornis* colony No. 2. Arrows indicate where embryo-like structures began to appear. Bars represent one standard deviation.
Fig. 3. Oocyte and planula growth in Pocillopora damicornis colony No. 3. Arrows indicate where embryo-like structures began to appear. Bars represent one standard deviation.
Fig. 9. Percentage of male gonads at arbitrary stages of development (see text) for colonies No. 1, No. 2 and No. 3.
Fig. 5. Resorptive stage of erysaries. Scale bar in microns.

Fig. 6. Longitudinal section of a polyp with male gonads located in the lower part of the westerleys. Erysaries at early stages of development. Scale bar in microns.
Fig. 7. Spermary starting to develop a lumen. Scale bar in microns.

Fig. 8. Early stages of development of female gonad (c), nucleus (n) and nucleolus (nl). Scale bar in microns.

Fig. 9. Two mesenteries (m) of the same polyp, one bearing a spermary (s) and the other an oocyte (o) with prominent nucleus (n) and nucleolus (nl). Scale bar in microns.
Fig. 10. Mature oocyte with zooxanthella (zx) in the surrounding endoderm. Note the prominent yolk vesicles, nucleus (n) and nucleolus (nl). Scale bar in microns.

Fig. 11. Early stage in the formation of a planulae (p) still attached to the mesentery by a stalk (st). Scale bar in microns.
Fig. 12. Transverse section of a polyp completely filled with a mature planula (p) with fully developed mesenteries (m). Scale bar in microns.
The planulae (and ovaries and testes) present in a given colony at any particular time were all at about the same stage of development. This was also observed by Barrigan (1972).

Discussion

The gametogenic cycle of P. damicornis is similar to those reported for other species of anthozoans (Fadallah, 1983), but differs in the final stages because spermatogenesis is rarely completed and oocytes not commonly fertilized.

If fertilization of female gametes is not the rule, the origin of planulae must be explained by other means for this species. Stoddart (1983) postulated the asexual origin of planulae and gave two possible explanations: formation of larvae occurs independently of gametes, by budding for example, or in relation with female gametes, by parthenogenesis. Results from this study negate the first possibility and support the second. No evidence of budding planulae or similar modes of reproduction were observed in more than one hundred histological sections prepared. On the contrary, several facts support the genetic origin of larvae in P. damicornis. Figs. 1 to 3 clearly show the relation between oocytes and the first appearance of small planulae, without participation of spermatogonia. This could mean that oocytes developed parthenogenetically in planulae. Results from Table 2 also show a clear relationship between oocytes and planulae; the distribution of both in the polyps is similar.

This inferred asexual process has not been previously described. The possible adaptive advantages of this reproductive pattern in a colonizer species of highly perturbed environments are discussed by Stoddart (1983). He also mentions that genetic variability between adjacent populations is not expected in obligately asexual organisms. The eventual observation of mature sperms enables possible self or cross fertilization, assuring asexual recombination during the infrequent production of sexual planulae.

Even though it is well known that the population of P. damicornis of Kaneohe Bay planulae in a lunar cycle throughout the year (Barrigan, 1972; Stimson, 1978; Richmond and Jokiel, 1984), it is not clear if a single colony could produce planulae at least for two consecutive months, and also suggests that a single polyp has this capability because of the coexistence of planulae and female gametes in the same polyp.

Literature Cited


Preliminary observations on the abundance and distribution of planktonic coral larvae in Kaneohe Bay, Oahu, Hawaii.

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Abstract

Little quantitative information is available concerning the abundance and distribution of coral planulae following their release from parent colonies. A planktonic sampling technique was designed for the capture of coral planulae. It was based on surface tows using a small, fine-mesh net. More than 250 tows were made along five transects established near the southeast fringing reef of Coconut Island. Time between collection and sorting was minimized, and low temperature storage was employed in lieu of chemical fixatives to prevent decomposition of the planulae prior to identification.

More than 100,000 ciliated larvae, most of which were scleractinian planulae, were collected and sorted. Twelve different types of ciliated larvae were differentiated. Two appear to be the zoanthellae larvae of the zoanthid Polypodium erectus and Zoanthus pacificus. Six were identified as the planulae of the corals Acropora palmata, Acropora compressa, Montipora trevoorum, M. dianthus, Merulina aculeata, and Cylindrophyllum sp. Planulae generally occurred 3 - 7 days after the onset of spawning or fertilization. Limited data on the vertical distribution of 3 species of coral planulae indicate that they may undertake a diurnal migration similar to that of other demersal planulae. The potential for the export of large numbers of coral planulae from Kaneohe Bay is considered high, but whether this export is significant to recruitment on reefs outside the bay remains to be seen.

Introduction

An increasing amount of work has focused on the subject of coral reproduction and recruitment. These studies have documented the timing and mode of reproduction, the recruitment of juveniles to artificial and natural substrates and the behavior of coral planulae in the laboratory (see citations in chapter introduction). Recent attention has shifted to the question of planula dispersal. The caloricometric work of RFEM and B. (1984) has demonstrated that the century-old assumption that coral planulae are capable of dispersing over long distances is at least energetically justified in certain species. Despite these advances, and the enticing biogeographic possibilities they suggest, little effort has been made to measure the abundance and distribution of coral planulae in the field.

Planktonic sampling with nets first came into vogue in the early 1900's (Frazer, 1979). Since then dozens of reports have been published concerning tropical plankton in the open ocean and near shore (Table 1). However, not many have recorded larval ciliates (Gibbs, 1965). Although several of these studies were devoted to a description of the zooplankton found living near coral reefs, surprisingly few have reported coral planulae.

Vaughan (1916) claimed that "hexacorallian planulae" were frequently obtained in the plankton tows off the Dry Tortugas, but provided no supporting data. In contrast, nearly every researcher since then who has tried to obtain coral planulae using nets has remarked on their scarcity.

The most recent concerted effort to net coral planulae appears to be that of Yasunagi (1972) who searched through 60 plankton hauls made in Palau and recovered only a single specimen. We wrote, "The paucity of coral planulae in the plankton samples has been recorded by previous workers who tried to find them. The present survey agrees well with those results." Perhaps more surprising is the complete lack of planulae caught by the specialized demersal plankton traps of Porter and Porter (1977), Porter et al. (1977), Aldridge and King (1977), Birkeland and Smalley (1981) and Walter et al. (1981). These traps were placed directly over the reef substrate. In contrast, Kitalong (this volume) reports that hundreds of coral planulae were routinely caught in her demersal traps.
Table 7. Selected tropical plankton studies. This list includes tropical plankton studies in which cnidarian larvae might have been recovered given the sampling methods employed. Note that cnidarian larvae have rarely been reported, and coral planulae only 7 times. CP = coral planulae, CL = cnidarian larvae.

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Larvae reported</th>
</tr>
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<tbody>
<tr>
<td>Balachandran (1973)</td>
<td>Indian Ocean</td>
<td>CL</td>
</tr>
<tr>
<td>Birkeland et al. (1976)</td>
<td>Palau Islands</td>
<td></td>
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<tr>
<td>Bogoror (1967)</td>
<td>Pacific</td>
<td></td>
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<tr>
<td>Chacko (1950)</td>
<td>India</td>
<td></td>
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<tr>
<td>Clayshulte et al. (1978)</td>
<td>Truk Islands</td>
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<tr>
<td>Clutter (1973)</td>
<td>Hawaii (Kaneohe Bay)</td>
<td>CP</td>
</tr>
<tr>
<td>Edmundson (1929)</td>
<td>Hawaii</td>
<td></td>
</tr>
<tr>
<td>Emery (1968)</td>
<td>Florida</td>
<td></td>
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<tr>
<td>George (1953)</td>
<td>India</td>
<td></td>
</tr>
<tr>
<td>Gilmartin (1958)</td>
<td>Eniwetok</td>
<td>CL</td>
</tr>
<tr>
<td>Glyn (1973)</td>
<td>Caribbean</td>
<td>CL</td>
</tr>
<tr>
<td>Harrigan (1972)</td>
<td>Hawaii (Kaneohe Bay)</td>
<td>CP</td>
</tr>
<tr>
<td>Hirota and Smyser (1976)</td>
<td>Eniwetok</td>
<td></td>
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<tr>
<td>Hobson and Chess (1978)</td>
<td>Marshall Islands</td>
<td></td>
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<tr>
<td>Johanss (1954)</td>
<td>Palau Islands</td>
<td>CP</td>
</tr>
<tr>
<td>Kawaguti (1940)</td>
<td>Central Pacific</td>
<td></td>
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<tr>
<td>King and Beach (1953)</td>
<td>Yap Islands</td>
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</tr>
<tr>
<td>Lansbury (1978)</td>
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<td>Le Borgne (1977)</td>
<td>Bermuda</td>
<td></td>
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<tr>
<td>Moore (1949)</td>
<td>Cuba</td>
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<tr>
<td>Morijakova and Sampos (1966)</td>
<td>Eniwetok</td>
<td></td>
</tr>
<tr>
<td>Olus and Olus (1955)</td>
<td>Hawaii (Kaneohe Bay)</td>
<td></td>
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<tr>
<td>Peterson (1975)</td>
<td>Hong Kong</td>
<td>CL</td>
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<tr>
<td>Pakesanampala (1975)</td>
<td>Caribbean</td>
<td>CL</td>
</tr>
<tr>
<td>Qing-choo (1980)</td>
<td>Gr. Barrier Reef</td>
<td>CP</td>
</tr>
<tr>
<td>Riley (1938)</td>
<td>Gr. Barrier Reef</td>
<td>CP</td>
</tr>
<tr>
<td>Russell and Colman (1934)</td>
<td>India</td>
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<tr>
<td>Sale et al. (1976)</td>
<td>Florida</td>
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<td>Sambukmaeki and Saravathy (1981)</td>
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<td>Smith et al. (1950)</td>
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<tr>
<td>Stephens (1933)</td>
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<tr>
<td>Suarez-Cabero et al. (1965)</td>
<td>Dry Tortugas</td>
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<td>Tanner and George (1969)</td>
<td>Singapore</td>
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<td>Vaughan (1910)</td>
<td>Kenya</td>
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<tr>
<td>Wacke (1958)</td>
<td>Burma</td>
<td>CL</td>
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<tr>
<td>Black (1961)</td>
<td>Florida</td>
<td>CP</td>
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<tr>
<td>Black (1961)</td>
<td>Palau Islands</td>
<td>CP</td>
</tr>
<tr>
<td>Elizur (1952)</td>
<td>Kyushu, Japan</td>
<td></td>
</tr>
<tr>
<td>Ziemann (1970)</td>
<td>Hawaii (Kaneohe Bay)</td>
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</table>
Information gathered during the present study points to numerous technical and biological factors which may account for the low catches of coral planulae previously reported. This reconciles the low reported catch rate with the high fecundity of corals measured in the laboratory (Stimson, 1978).

The purpose of the present paper is to identify and quantify species of coral planulae found near coral reefs in Hawaii. Information on the residence time of planulae on the reef front, their horizontal distribution near corals in the plankton after release, and their abundance in the study area is also presented. To the writer's knowledge, no previous quantitative work has been attempted in this area.

Materials and methods

Plankton Tows

In many cases the number of planulae per m² was very low. In order to avoid the use of small fractions of planulae, all values in this study will be normalized to 100 m² of seawater filtered.

The primary study area was located at the southeast fringing reef of Coconut Island, Kanehewa, Hawaii (Fig. 1). This portion of reef was chosen because of the abundance of Porites lobata colonies. This species is known to produce abundant planulae following a lunar cycle (Richmond and Jokiel, 1984).

Three plankton tow transects were initially established parallel to the reef edge. The reef flat transect (No. 1) was located between the zone of active coral growth on the outer reef flat and the sandy inner reef flat. This clear ecological break was generally 10 m from the seaward reef edge. Transect No. 2 was established along the seaward edge of the reef front and parallel to it. Transect No. 3 was established until halfway into the study period. Transect No. 5 was located in an outflow channel of the Kaneohe Bay, southeast basin. The beginning and end points of the transects were marked relative to pilings along the reef edge. Due to the current strength, the outer two transects (No. 3 and No. 5) were slightly further seaward of the reef, the outer two transects (No. 3 and No. 5) were slightly further seaward than the 200 m long seaward reef edge transect (No. 2). Plankton samples were taken in various other locations within and outside the bay.

All plankton tows were made using a 30 cm diameter, 100 micron mesh nylon net fitted with a 75 cm flow meter. To enable sampling over the reef flat, the net was towed behind a skiff at an average speed of 2 to 3 knots for all tows except when the water was insufficient over the reef flat. At these times the net was towed by hand while walking over the reef flat along the transect. Separate calibrations were made for the 75 cm flow meter at the boat and the walking speeds. A sample run consisted of one pass along a given transect. This would usually take 3 to 4 minutes and filtered 17.5 m³ of water. At the end of a sample run the net was washed down and the plankton collected in a 6 ounce (177 ml) cod end bottle. Clogging was occasionally observed during test runs therefore the net was handwashed in seawater after each tow.

Generally, sampling was conducted every other day between 22 June through 2 August. An exception was the seaward 20 m transect which was not established until mid-July. During June, sampling was carried out primarily just after low tides, because preliminary results of a related study (Holloran, this volume) indicated that the diurnal rhythm of Porites lobata planulae distribution showed a peak abundance during low tide. After June, samples were taken at a variety of times and tidal stages.

One 24 hour and one 12 hour continuous sample series were also carried out. For the 24 hour series (29 - 30 June), 4 sample runs were taken every 4 hours along the
Fig. 1. Map of study reef off Coconut Island with the 5 plankton sampling transects.
Fig. 2. Basic current patterns in Kamehameha Bay, incoming tide (from Ratna, 1968).
seaward reef edge transect. The sampling regime of the 12 h series entailed 3
double sample runs (up and back) along the seaward reef edge every 2 h from
noon to midnight (29 July). The 24 h study was designed to clarify the diurnal pat-
ttern of abundance of *P. damicornis* planulae, whereas the purpose of the 12 h
study was mainly to estimate sampling error, taking use of the great abundance
of *Purpurpereus compressum* planulae present at that time.

Two short experiments were conducted in order to describe the vertical dis-
tribution of planulae in the water column. For the first test a hand-operated,
3.1 l/min diaphragm pump (Diapram Corporation, Diaphragm pump model 1174) was used to
sample the plankton abundance at three depths: 10 cm and 200 cm below the surface.
Both samples were taken at one location 3 to 4 m seaward of the central, study
reef edge, between 1200 h and 1300 h on 30 July. Each sample was obtained by
pumping 1.74 m³ from the specified depth via a hose into the plankton net used
for the plankton tow.

The second test of the vertical distribution of planulae was performed using
the previously described plankton net with the floats removed. Four hauls were
taken along the transect 10 m seaward, at 3 depths; surface, 1 m, and 5 to 6 m.
The water depth at this location is approximately 13 m. This test was performed
before and after 1600 h on 5 Aug. The water transparency on the day of the
test was such that the net disappeared from view below a measured 5 m depth. To
accomplish the 5 to 6 m depth tow, the net was maintained at the level where it
was just visible by adjusting the tow speed and towline length.

On three occasions, the sea was calm enough to allow plankton tows to be made
outside the "barrier" reef of Kaneho Bay using a skiff. These surface tows
were made within 100 m of the seaward reef front and parallel to it.

**Processing Samples**

In the field, all plankton samples were decanted from the cod end bottle into
279 ml glass bottles and stored in a 20 l insulated plastic container. The sam-
ple vials were cooled with seawater and ice chips. All samples were counted with the
aid of a dissecting microscope within 1 h of collection. No formalin or other
fixatives were added. All planulae were counted individually in a sorting dish
and removed for settling experiments unless their abundance was greater than
200. In this case, subsampling was carried out for the abundant species, with
the less abundant species counted individually from the total sample.

**Results**

**Weather and Water Circulation**

During the study period, the water temperature off the reef edge was 26.4 °C
(79.5 °F). The normal northeast tradewinds for this period blew at an average
velocity of 9.7 ± 5.9 mph. The average direction was from 58° east of north with
a range of 10° (National Weather Service). The strength of the wind has a pro-
found effect upon the water circulation in the bay as noted by Bateman (1968).
This effect is especially marked in shallow areas such as the reef flats. There
the wind can create strong currents which may run in opposite directions to
the tidal currents.

Although the general water circulation patterns in Kaneho Bay have been
characterized by Bateman (1968), additional drogue and fluorescein dye release
experiments were performed to provide a more detailed picture of the water cir-
culation around Coconut Island, and especially the study reef. Figs. 2 and 3
show the general circulation patterns in the bay as determined by Bateman (1968).
Figs. 4 and 5 provide the more detailed results of the present study. A 10 mph
wind generated a current over the study reef along the reef flat transect (No 1)
ranging between 7 and 10 cm sec⁻¹ when the water depth was 70 cm. It is impor-
tant to note the presence of a gyre near the south end of the study reef which
exists during an incoming tide (Fig. 4). Another significant feature of the loc-
al circulation is that during an outgoing tide, dye and drogues released at the
surface near the north end of the patch reef located just over 100 m east of the
study reef, were swept directly onto the study reef within 1 to 2 h (Fig. 5).
They crossed the study reef in 2.5 h and were then swept into the outflow
channel south of the island. Kaneho Bay has a modified semi-diurnal tidal cy-
cle which had a range of 1 m during the study period.
Fig. 2. Basic current patterns in Kaneohe Bay, outgoing tide (from Bateman, 1968).
Fig. 4. Current patterns near study reef, incoming tide.
Fig. 5. Current patterns near study reef, outgoing tide
Types and abundance of Planulae

Well over 100,000 ctenarian planulae were collected and counted over the course of the study; the majority of these were scleractinian planulae. Twelve types of larvae were differentiated, of which two were tentatively identified as Zoanthids and six were positively identified to the species level as coral planulae. The six were: Pocillopora damicornis, Porites compressa, Montipora verrucosa, Cyphastrea ocellata, and Pocillopora scutaria. These identifications were confirmed via laboratory settling experiments. The remaining types of planulae remain unidentified.

The planulae larvae of P. damicornis have been described in detail by Harrigan (1972) and Vandermeers (1974). The average daily number of P. damicornis planulae collected per 3 tows along each transect is plotted in Fig. 6. Although the planulae of P. damicornis, Type B (Richmond and Jokiel, 1984) may be smaller on the average than those of Type Y, there is no way to positively assign a given individual planula taken in a plankton tow to its proper type because of the large overlap in their size ranges. Therefore all P. damicornis planulae are lumped into one group for the present analysis. The major peak in the catch occurred between 27 June and 28 June, reaching over 100 planulae per 100 m². There were 3 smaller peaks around 23 June, 6 July and 18 July, with the last peak subsiding slowly through August when the study ended.

Porites compressa colonies were observed spawning eggs in the field and in the laboratory at approximately two week intervals (at new and full moon) beginning on 26 June. The water surface of the channel at the mouth end of Compton Island (Fig. 1) was covered with beige Porites compressa eggs and planulae during each one to two day spawning period. A sample of 10 P. compressa planulae (age 2 days) had the average dimensions 278 ± 25 microns x 227 ± 27 microns (Fig. 7).

The average daily catch of P. compressa planulae per 3 tows along each transect is plotted in Fig. 8 using the natural logarithm of the quantity x-1, where x-average catch. There are 3 main peaks of abundance at about 2 week intervals. At peak abundance, the number of P. compressa planulae recovered reached 1000 per 100 m².

Montipora verrucosa colonies spawned the majority of their egg-spore packets in the field and in the laboratory and in the field between July 10 and 12 (full moon) at approximately 2100 h (Fig. 9a). Small numbers of remaining egg-spore packets were released on the following 3 nights. A complete description of the spawning of this species is given by Herdendorf (this volume). Egg-spore packets, eggs and later planulae, were collected in the plankton tows between 10 July and 22 July, with a peak on 18 July which reached 16,000 planulae per 100 m². The natural logarithm of the quantity x-1, where x-average catch, is plotted in Fig. 10.

Montipora dimitata colonies were observed to begin spawning in the laboratory and in the field on 26 July. Eggs and planulae were subsequently recovered in numbers reaching 100 planulae per 100 m² on the final two days of the study, 1 Aug and 3 Aug (Fig. 10).

The distinct planulae of Cyphastrea ocellata, originally described by Edmundson (1929), were caught sporadically from all transects throughout the study period (Table 2). A maximum of 6 planulae per 100 m² was recovered; too few to detect any peaks in abundance during the study.

The planulae of Pocillopora scutaria are small (90 - 120 microns), but can usually be distinguished by their unique, rapid swimming pattern described by Krupp (1983). Pocillopora larvae were sporadically taken from all transects just after their June spawning and prior to their next spawning in July, as assessed by observations of colonies in the laboratory. Because of their small size, it is reasonable to assume that most Pocillopora larvae slipped through the 104 micron mesh net.

A number of specialized, fast moving planulae which appear to belong to the sea anemone Corallimorph sp., were caught sporadically from all transects except the channel (Table 2). These distinct larvae have been described by Carlgren (1906). The present types ranged in color from tan to brilliant orange, usually with a darker band around their white, oral end (Fig. 11). Their entire surface
Fig. 6. Average number of *P. fasciculus* Planulæ collected per 100 m²

Fig. 7. Three to 4 day old *P. compressa* Planula (fixed)
Fig. 8. Average number of *P. compressa* planulae collected per 100 m³.

Fig. 9. *Montipora verrucosa*: 1) freshly spawned egg-sperm packet (backlit). Sperm is contained in the center of the ball. Maternally derived zooxanthellae appear as dark specks within each egg. Packets break up into individual eggs within 0.5 h after they are spawned. Diameter = 1300 microns. B) Planula (3 d old, fixed). In life, shape is more elongate. Size = 330 x 260 microns.
Fig. 10. Average number of *H. verrucosa* planulae collected per 100 m³.

Fig. 11. Swimming *Corianthus* sp. larva (lateral view)
except the flattened oral end is covered with slightly longer cilia which propel them through the water at 5 to 8 mm sec⁻¹, faster than most of the other planulae observed. Since settlement experiments with these larvae failed, their identity has not been confirmed. In fact, it is pertinent to note that Nagayas (1941) description and figure of the planulae of Euphylia glabrescens, an Indo-Pacific coral not found in Hawaii, resembles the present Cerianthus-like planulae in all respects except size. With a diameter of 0.7 mm, the Euphylia planulae are about double the size of those recovered from Kaneohe Bay.

Table 2. Abundance of L. ocellina, P. scutaria and Cerianthus sp. larvae. Each number is the combined total from 3 tows along the specified transect. A blank indicates no larvae recovered. Reef, 10 m, 20 m, Channel indicate areas sampled moving seaward (deeper) from reef edge to channel. Ce = Cerianthus sp., Cy = Cerianthus ocellina, Tu = Tintia scutaria

<table>
<thead>
<tr>
<th>Date</th>
<th>Reef Flat</th>
<th>Reef Edge 10 m</th>
<th>Reef Edge 20 m</th>
<th>Channel</th>
</tr>
</thead>
<tbody>
<tr>
<td>6-22</td>
<td></td>
<td>10ce</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-29</td>
<td>3Cy</td>
<td>2Cy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-10</td>
<td>1ce</td>
<td></td>
<td></td>
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<tr>
<td>7-14</td>
<td>6ce</td>
<td>2ce</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-18</td>
<td>2Cy</td>
<td>2Cy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-20</td>
<td>3Cy</td>
<td>2Cy, Ce</td>
<td>3Cy</td>
<td></td>
</tr>
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<td>3Cy</td>
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<td>7-28</td>
<td>2Cy, 4Ce</td>
<td>2Cy</td>
<td></td>
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<tr>
<td>7-29</td>
<td>1Cy</td>
<td></td>
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<td></td>
</tr>
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</table>

Two types of what appear to be the larvae of zoanthids were obtained from tows along all transects in large numbers. These unique larvae correspond to the "zoanthina" type discovered by Sespe (1867) and described in detail by Van Beneden (1890, 1896), Conklin (1908) and Cary (1911). They are essentially polypina, but have a lateral constriction located between their equator and oral end (Fig. 7). Branching from this circular groove is a ring of long (100 micron) cilia which beat with a jerky motion in an anterior-posterior direction. The remainder of the larval surface is covered with the normal, short (20 micron) cilia found on most planulae. Type 1 Sespe's larvae are colored greenish-brown by the numerous zoanthallae they contain. As they grow larger, they become more darkly colored. Sespe's larvae type 2 are longer, thinner and a lighter shade of brown without the greenish tint.

Type 1 Sespe's larvae were caught consistently throughout the study period but showed abundance peaks around 6 July (400 planulae per 100 m²) (Figure 13). Unfortunately none of the larvae of either Type 1 or 2 were induced to settle in the laboratory. But because of their abundance, these larvae are assumed to be derived from Palythoa vestita and Zoanthus pacificus, the two most common zoanthids in the bay. Spawning of these species has not yet been observed directly (Cooke, 1983).

An unidentified cnidarian planula was quite abundant in July with a peak just prior to the full moon of about 200 planulae per 100 m². These planulae are small (220 x 340 micron), rod-shaped and transparent except for a bright red-orange center at the oral end (Fig. 14). Unfortunately none of these larvae were induced to metamorphose in the laboratory, although several settled temporarily. Because of their abundance, it is suspected that they may be the larvae of one of the common sea anemones, e.g. Anthopleura nigrescens (Dunn, 1974).
Fig. 12. Type 1 Semper's larva (fixed)
   a. Lateral view, oral end to right
   b. Silhouette of same
   c. Circular groove and long cilia
   d. High magnification of long cilia

Fig. 13. Average abundance of Semper's larvae collected per 100 m²
Fig. 14. Planula of *Anthopleura Madison* (?)

Fig. 15. Average abundance of *P. damicornis*
Diurnal Cycles

The changes in abundance of *Pocillopora damicornis* planulae over a 24 h period (29 - 30 June) and of both *P. damicornis* and *Porites compressa* planulae over a 12 h sampling period (29 July), along the seaward reef edge transect are shown in Figs. 15 and 16. There were significantly more *P. damicornis* planulae recovered from the night tows than from the day tows over the 24 h period (*p < 0.001*) and the 12 h period (*p < 0.025*). Although the total abundance of *P. compressa* planulae captured during the night is nearly 1.5 times higher than the number caught during the day (12 h study), this difference is not significant.

Horizontal Distribution

More *P. damicornis* planulae were usually recovered along the transect 10 m seaward than from each of the other transects (Fig. 6). Although fairly consistent, this difference is not statistically significant using a Sidak's t-test to compare all main effects means (SAS Inst., 1982). The distribution of the catch of the other types of planulae among the 5 transects shows only a few consistent trends. One trend is that the planulae of *P. verrucosa* were caught in greater numbers from the transect 20 m seaward than from the other transects. In contrast, the *Sesperm's larvae tended to be more common along the reef flat and seaward reef edge transects than from the tow made 10 and 20 m away from the reef.

The results of the tows made outside the "barrier" reef are presented in Table 3. Only *Pachyphyte* *P. verrucosa* larvae and an unidentified ciliarian larva were collected.

**Table 3. Abundance of planulae from tows taken outside the “barrier” reef off Kaneohe Bay. Tows were made within 100 m of the reef front and parallel to it.**

<table>
<thead>
<tr>
<th>Date</th>
<th>Time</th>
<th>Larvae recovered</th>
<th>Water filtered (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6-28</td>
<td>0630 h</td>
<td>unknown 1, Sesperm's 1</td>
<td>203</td>
</tr>
<tr>
<td>7-12</td>
<td>1255 h</td>
<td><em>P. compressa</em> 22, Sesperm's 4</td>
<td>54</td>
</tr>
<tr>
<td>7-18</td>
<td>1930 h</td>
<td>none</td>
<td>89</td>
</tr>
</tbody>
</table>

Vertical Distribution

The results of the pumping experiment (1200 to 1300 h on 30 July) were 7,000 planulae per 100 m³ recovered just below the surface versus 56,854 per 100 m³ at 2 m depth. The series of tows at 3 depths on 4 August are presented in Table 4. Together these results suggest that during these 2 daytime sampling periods, more *P. dillihens* and *P. compressa* planulae were found below one meter than at the surface. They further suggest that there may be an increase in abundance with increasing depth from below 1 m to 6 m. These differences are not statistically significant (Sidak's t-test).

Discussion

Problems With Traditional Procedures

This study suggests several reasons why coral planulae have rarely been reported in tropical plankton studies. Perhaps the most common reason is that many of the previous studies (Table 1) had a different focus. Coral planulae were simply overlooked or ignored. At best, they may have been relegated to a "miscellaneous" category. However, this obvious explanation cannot be applied to the studies wherein planulae were actively sought, but were found to be exceedingly rare or unobtainable (Yamaguchi, 1972).
Table 4. Differences in the abundance of calcareous larvae at 3 depths. Each number is an average abundance from 4 plankton tows normalized to the number per 100 3's of filtered seawater. Tows were made between 1440 h and 1610 h on 4 August along the seaward 10 m transect. Water depth there is approximately 12 m.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Montipora</th>
<th>Serpula Type A</th>
<th>Type B</th>
<th>Porites</th>
<th>Pocillopora</th>
<th>Paracanina</th>
<th>P. scutaria</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface</td>
<td>103</td>
<td>8</td>
<td>34</td>
<td>27</td>
<td>0</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>1 - 6</td>
<td>183</td>
<td>6</td>
<td>9</td>
<td>54</td>
<td>5</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>5 - 6</td>
<td>200</td>
<td>10</td>
<td>6</td>
<td>63</td>
<td>0</td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>

The results of the present study indicate that the procedure may be linked to the traditional procedure of adding buffered formalin to the plankton hauls "as soon as possible" (SWESCO, 1979) after they are brought in. The formalin kills the plankton which then settle to the bottom of the container. It has the secondary effect of rapidly bleaching any planulae white, and was also observed to disrupt the structural integrity of the delicate outer membrane of one and two day old P. compressa and P. tenuicorona planulae. Following routine handling (e.g. transfer of the samples into permanent storage jars) it was noted that many of these planulae had subsequently fragmented. This makes identification difficult if not impossible. Formalin does not appear to damage the larger forms such as P. tenuicorona planulae in this manner.

An alternative procedure which worked well in the present study is to allow the freshly caught plankton to settle in a bottle without adding a fixative or preservative. The most important benefit of this procedure is that most of the living coral planulae will orient towards the surface. Within a few minutes, the majority of the planulae will be found at the surface or just below the surface. Those that can be observed with the naked eye are those that swim about in the clear water. From there it is a simple procedure to collect them with a pipette for settling experiments. The remaining plankton can then be examined to find the injured or dead planulae which generally sink to the bottom (usually about one third of the total number). Few planulae will be found in the middle layers of clear water above the settled mass of plankton. Only Serpula's Type 1 and the red, sea anemone larvae were found more commonly on the bottom with the settled samples than at the surface.

The above discussion can adequately explain why coral planulae have been reported so infrequently. Additional problems which may have historically prevented the capture of planulae are: net mesh size too large, sampling at times when few corals were spawning or planulating, difficulties with identification, and as Yasui (1979) suggested, insufficient amount of water filtered.

When deciding what net-mesh size to use to trap planulae of a given size, one must bear in mind that the plankton netting will stretch under the pressure of incoming water. During a tow, this will effectively increase the mesh size. The combination of net stretch and the plastic body form of the planulae will most likely allow individuals of perhaps twice the dimensions of the mesh width (unstretched) or more to slip through.

Although several coral species have been reported to planulate or spawn during every month of the year in various parts of the world, many species appear to concentrate their reproductive activities during the summer months (Stimson, 1979; Harriott, 1983; Fadallah, 1983). Therefore plankton tows taken outside of this period would presumably be less likely to contain planulae.
Distribution of Planulae

Planulae share a common feature with most plankton in that they exhibit a highly patchy horizontal distribution (Balachandran, 1973). Standard deviations were often as large as the mean in each set of 3 to 4 surface tows along a single transect, therefore they were not included in Figs. 6, 8, 10 and 13. Tows taken minutes apart along the same transect showed a disparity of thousands of planulae per 0.0 m³ of filtered seawater. The most obvious cause of a patchy distribution of planulae is the differential timing and location of release between colonies as suggested by laboratory observations on spawning and planulae. Numerous other potential biological and physical causes of plankton patchiness have been reviewed by Kline and Tenore (1980).

Despite this patchiness, several general spatial patterns of abundance are apparent. Overall, the lowest abundances of planulae were recorded from the reef flat and the channel transects. P. damicornis planulae were consistently more abundant along the seaward reef edge and 10 m seaward transects than along the others. Both P. compressa and P. verrucosa show an increasing abundance from the seaward reef edge to the 10 and 20 m seaward transects.

The interpretation of these data is complicated by the pattern of water circulation within the southeast basin which may tend to concentrate planulae in the waters adjacent to the study reef. Bathe et al. (1988) has described the large counterclockwise eddy centered in the basin and the overlying southwestward wind drift of the 0 to 2 m surface layer. During the study period, both of these currents were apparent. The counterclockwise eddy could be expected to carry planktonic larvae located below 2 m depth away from the study area. These planulae might be dispersed to any location in the path of the eddy in the southeast basin. Perhaps some planulae would be carried back around to their point of origin. At the same time, the southwestward wind drift would tend to transport near-surface planulae across the basin, where they might be concentrated along northeast facing shores such as those of Coconut Island.

An additional complication precluding the simple interpretation of the data, is the presence of a submerged [3 - 5 m deep] patch reef (about 250 m long x 150 m wide), located 125 m east of the study reef. Short qualitative surveys of this patch reef revealed the presence of numerous colonies of P. verrucosa and P. compressa, but P. damicornis colonies were very rare. An attempt was made to determine the potential of the patch reef as a source of planulae by comparing the planulae abundance upstream with that downstream of the patch reef. On 20 July, during the spawning period of P. verrucosa, planulae tows were taken upwind of the patch reef in addition to sampling along the normal (downwind) 5 transects. On the other hand, verrucosa planulae and eggs were recovered from the downwind tows (seaward 10 m and 20 m transects) than from those taken upwind, suggesting that the patch reef may be a large potential source of both P. compressa and P. verrucosa planulae. In this area, living coral is restricted to the upper 10 m depth range. The sandy lagoon floor is devoid of corals. There are no other possible sources of planulae in the vicinity.

The drogue and dye release experiments indicate that some of the planulae released from the north end of the patch reef would be carried directly over the study reef by the westward wind drift within about 3 h. If large numbers of P. verrucosa and P. compressa planulae are originating at the patch reef and being carried by the southwest wind drift towards the study reef, this provides a plausible explanation for the observed trend of increasing abundance of these planulae recovered from the seaward reef edge to the 20 m seaward transect. It may also clarify why the P. damicornis planula abundance distribution does not follow this trend, but in contrast, shows a peak abundance along the seaward reef edge and seaward 10 m transects. The majority of the P. damicornis larvae presumably originate from the study reef itself where this species covers almost 3% of the outer reef flat.

In addition, the small gyre (noted previously) which exists during conditions of an incoming tide and northerly trade winds (Fig. 4) could also increase the concentration of planulae off the study reef. The dye and drogue studies indicate that under these conditions the trade winds push the water over the study reef in a southerly direction until it reaches the reef edge. At this point it is redirected out into the channel and then back up to the north by the incoming tidal currents.
Vertical Distribution

Although no attempt was made to systematically determine the diurnal vertical distribution of the various species of larvae in the water column, the results of the two short sampling experiments at different depths raised interesting questions. The limited data on vertical distribution suggest that _P. compressa_ and _M. verrucosa_ planulae are at greater abundance at 6 m depth than at the surface during the day. The results of sampling at the surface over 12 h and 24 h periods indicate that more _P. compressa_ and _P. compressa_ planulae are present at night than during the day (Figs. 15 and 16).

Taken together, this information could suggest a nighttime spawning and planula peak, and/or the possibility that some species of planulae undertake a diurnal vertical migration. In 24 h laboratory tests Holobat, (this volume) found that _M. jagorii_ colonies may reach their peak planulae at various times during the day or night. The timing of _P. compressa_ spawning was also variable. In contrast, I observed _M. verrucosa_ and _M. dilatata_ colonies to spawn only at night, usually several hours after sunset (also see Heyward, this volume).

Kawaguti (1940a), documented vertical migration of coral planulae in Iwayama Bay. Planulae were abundant at the surface at night, but absent from the surface during the day. During the daytime, however, large numbers of planulae were netted from 5 m below the surface. Another study which has noted diurnal migration is that of Palachandran (1973) who found that in the Indian Ocean, anthozoan larvae were present in 61% of nighttime plankton hauls to various depths in the sea in only 50% of daytime hauls. He concluded that night "seems to influence the upward movement of the larvae." Although a full account of research has been devoted to the investigation of planula behavior of several species, it is difficult to extrapolate from studies of small containers to the potential behavior of planulae in the field. However, these studies at least show that planulae respond to irradiance (Duerden, 1942; Edmondson, 1972; Ame, 1947; Kawaguti, 1941; Harrigan, 1972; Lewis, 1974), gravity and currents (Kawaguti, 1941), and, because of their gregarious settling behavior, chemical and tactile stimuli (Duerden, 1942; Edmondson, 1972; Kawaguti, 1941, Harrigan, 1972, Lewis, 1974). Planulae appear to have the ability to carry out a diurnal vertical migration. The swimming rates of several species of planulae were measured by Harrigan (1972) and Hodos (1955). They are too slow (2 to 3 cm sec⁻¹) to allow a planula to make headway against the more rapid horizontal currents encountered over the study reef or in the bay (5 to 15 cm sec⁻¹). However, this swimming speed would allow for substantial vertical migrations of up to 11 m h⁻¹.

An additional piece of evidence which appears to support the idea that some coral planulae undertake a daily vertical migration comes from the work of Hidalgo (this volume). Prior to sunset on 15 July, she placed a desmatal plankton trap over a _M. compressa_ colony located on the same study reef used in the present work. The next morning the desmatal trap was retrieved and the sample counted. Over 700 _M. verrucosa_ planulae were recovered in this haul. One possible interpretation of this finding is that these planulae were seeking shelter or an appropriate settlement under the Porites head next during the day. After sunset, they may have detached from their temporary mucus strand attachments and were then caught in the plankton trap as they swam upwards.

Two coral species whose planulae have been intensively studied are _Favia_ sparsa (Lewis, 1974) and _F. jagorii_ (Harrigan, 1972). The behavior of both _F. sparsa_ and _F. jagorii_ planulae includes periods of crawling, temporary attachment, and preferential settlement in "dark" crevices. I observed _F. verrucosa_ planulae to behave in a similar fashion when held in aquaria. More detailed study will be necessary to ascertain if these planulae regularly aggregate under coral colonies of various species during the day, and then return to the surface at night.

Export of Coral Planulae from Kaneohe Bay

If large numbers of planulae are being released into Kaneohe Bay, it is possible that some of these may be exported out of the bay. In addition, if the numbers of planulae exported from the bay are large in comparison to local planula production at this time, for example, the reefs just outside of the bay entrance, the rate of coral recruitment on these reefs might be substantially increased by the "extra" Kaneohe Bay planulae.
In order to estimate the number of coral planulae which may be exported from the southeast basin, it is necessary to know the average density of the planulae in the water going out of the bay with the tide, and the daily gross outflow of water. According to Bathen's study (1968), most incoming tidal water is separated from the outflow. Since the density of planulae spawned outside the bay would presumably be greatly reduced by dilution from the ocean, the probability of these planulae being carried back into the bay is assumed to be negligible.

The average abundance of all types of coral planulae from all transects combined per day during the study was 328 planulae per 100 m$^2$. Several factors might affect the accuracy of applying this estimate to the entire southeast basin. The proximity of the plankton tow transects to potential sources of planulae, and their location in an area of probable planulae concentration due to the action of wind and currents might indicate that this is an over estimate of the true planulae density if applied to the entire southeast basin. However, if most planulae are undergoing a migration away from the surface during the day, the above estimate which is derived from daytime surface tow could be a considerable underestimate of their true abundance in the basin. To what extent the above factors counteract each other is not known. A conservative estimate of planulae density for the upper 5 m of the southeast basin during the study, is considered to be on the order of 1 planula per 100 m$^2$.

The average daily gross outflow (daily exchange transport) of water from the southeast basin has been calculated to be approximately 18 x 10$^6$ m$^3$ (Bathen, 1968). The majority of this water exits directly to the sea without passing via the north bay. About half of the gross outflow might not be expected to contain planulae if most planulae are concentrated above the 5 m depth range as indicated by Ravault's work (1960) in Pailo. Given the conservative estimate of planulae density of 1 planula per 100 m$^2$, and a gross outflow of planula-containing water of 9 x 10$^6$ m$^3$ d$^{-1}$, the average net export of planulae (assuming zero import) would be 90,000 planula per day. Over the 44 d study period this totals 4 x 10$^7$ planulae. Whether this number of exported planulae has a significant effect on recruitment at reefs outside the bay, or even farther away, remains to be seen.

Despite the huge dilution factors involved, planulae may be expected to be recovered up to several miles from a reef. Russell and Colgan (1934) netted several thousand coral planulae 3 miles east of the nearest reef (Low Isles, Great Barrier Reef, Australia) during the last two weeks of December, 1928. They made oblique, 30 minute tows to a depth of 23 m, using fine mesh (23 and 77 strands cm$^{-1}$), 0.5 m diameter nets. They probably filtered about 150 m$^3$ of water per tow.

Unfortunately, during the present study, rough seas during the periods of peak planulae abundances prevented plankton sampling outside the "tercier" reef except on 3 days (Table 3). Only on 18 July were significant numbers of planulae (F. terricosta) recovered. According to Bathen (1968), as water leaves the bay during an outgoing tide it sinks due to its higher density. He reports that three-fourths of the water leaving the bay exits below 3 m depth. This information suggests that future studies on the export of planulae from similar areas such as Kaneohe Bay, could concentrate their sampling at night and from the water column below the 3 m level outside the reef, as opposed to the daytime surface samples used in the present study.

**Planktonic Lifespan of Planulae**

It is tempting to infer a planktonic life span from the number of consecutive days a given planula type was recovered in plankton basis. However the average residence time of the water in the southeast basin has been estimated to be 5 d (Bathen, 1968) and 4.5 d (Steinbicker, 1970). Theoretically, this means that every planula released on Day 1, and not settled by Day 5 will be exported out of the southeast basin.

Most F. compressa and F. damicornis planulae were recovered in plankton tows within 5 days after the last day of each spawning period. Possible explanations for these results are: 1) that the majority of planulae have been washed out of the study area as predicted by the average residence time estimates, 2) they are settling, 3) they are residing in the sub-surface layers, or 4) their numbers have been reduced by predation. However, F. terricosta planulae were recovered up to 8 d after the last spawning observed in the field and laboratory.
This might indicate that certain groups of *Z. verrucosa* colonies spawn slightly out of phase and later than the colonies I was observing, or that the planulae are being retained in the bay beyond the theoretical 5-4 residence time. Several factors which might explain the latter hypothesis are abiotic effects such as gyres in the water circulation pattern which might retain planulae, or biotic effects such as temporary settlement of planulae followed by their reentry into the plankton.

Several studies of the settling behavior of a wide variety of species of coral planulae indicate that provided a proper substrate most species of planulae can settle within a few days. When deprived of a suitable settling site, e.g., improper substrate or insufficient irradiance, the majority of planulae tested can survive several weeks without settling, and then successively settle when a substrate is provided (Holz, 1957; Edmundson, 1979; Vaughan, 1980, 1981). I observed that *Z. verrucosa* and *P. compressa* planulae were able to settle on various substrates provided in indoor aquaria by Day 7, but some individuals existed for two weeks in the free-swimming stage.

Considering the numerous potential factors affecting the number and success rates of species of planulae, it is clear that the present data cannot be used to judge the planktonic lifespan of these coral planulae.

**Summary**

1) A planktonic sampling technique was designed to net coral planulae. The method is based on surface tows using a small, fine-mesh net, cooling the sample, and minimizing the time between collection and sorting. A list of using fixatives.

2) Over 100,000 ciliarian larvae were collected and sorted from a total filtered volume of approximately 5,300 m³. Most of these were scleractinian planulae. Twelve types of ciliarian larvae were differentiated. Two have been tentatively identified as the *Spongosorites* larvae of the zoanthids *Palythoa vestiti* and *Solenostoma pacificus*. Six have been positively identified as the planulae of the scleractinian corals *Pocillopora damicornis*, *Porites compressa*, *Montipora verrucosa*, *Montipora foliata*, *Orbicella caribbaea*, and *Fungia scutaria*. The remaining planulae remain unidentified.

3) The horizontal distribution of *Z. damicornis*, *P. compressa*, and *Z. verrucosa* planulae among 3 plankton tow transects was studied. *P. damicornis* planulae were more commonly recovered directly along the study reef front, further away from the study reef.

4) The spawning and planulation patterns of *Z. damicornis*, *P. compressa*, and *M. verrucosa* were followed by observing colonies held in the laboratory and in natural field populations. The peak recovery of the planulae in the plankton tows generally occurred 3-4 days after the onset of spawning or planulation.

5) The planktonic lifespan of each planula species cannot be deduced from the plankton tow data due to various confounding biotic and abiotic factors.

6) Limited data suggest that some coral planulae may undertake a diurnal migration, spending the day at several meters depth and then migrating to near the surface at night.

7) The potential for the export of coral planulae from Kaneohe Bay is considered to be good, but whether this export is important to recruitment on reefs outside the bay remains to be seen.

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Literature Cited


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