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The reproductive biology of *Parazoanthus parasiticus* (Hexacorallia: Zoanthidea) in Bermuda★

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Abstract

The zooxanthellate macrocnemic zoanthid *Parazoanthus parasiticus* lives at densities of 3–10 cm^{-2} in the chimney sponge *Callyspongia vaginalis* in Bermuda. It is gonochoric and oviparous. Small oocytes appear in the mesenteries in February–March, grow slowly at first, then increase volume rapidly as seawater temperature passes 27 °C in July. In 1993, oocytes were found to have been shed over 2–3 days around the full moon on 1 September, with inferred small spawnings over the preceding and following full moons. Reproduction had finished by November. In 1999, spawning of azooxanthellate eggs ~250 μm diameter took place on 28 August, two nights after full moon. Spawnings therefore precede those known for four oviparous scleractinians and one gorgonian in Bermudian waters by about a week. The eggs are not shed in bundles and lack zooxanthellae. The unknown embryonic development and larval type in macrocnemic zoanthids is discussed and remains to be resolved by further study with *P. parasiticus*.

Introduction

Parazoanthus parasiticus (Duchassaing & Michelotti) is one of five zooxanthellate sponge-dwelling zoanthid species known from the Caribbean region (West, 1979) but the only one present in Bermudian waters (Sterrer, 1986). In Bermuda, its principal host is *Callyspongia vaginalis* (Lamarck), which forms clumps of clustered cylindrical oscula some 200 mm in height. *P. parasiticus* is a shallow water representative of the Macrocnemina (one of two zoanthid suborders). Unlike Brachycnemina, Macrocnemina are distributed worldwide but most often in deep water: they are difficult to obtain live and have been little studied. The abundance of the sponge containing *P. parasiticus* close to the Bermuda Biological Station (BBSR) provided the opportunity to study the reproduction and spawning periodicity.

Zoanthids, with the known exception only of *Isozoanthus giganteus*, are oviparous, with eggs externally fertilized in the water column (Ryland, 1997). Development in Brachycnemina proceeds to a pelagic, modified planula (Semper's larva), either a zoanthina (family Zoanthidae) or a zoanthella (Sphenopidae), but embryonic development in Macrocnemina is unknown (Ryland et al., 2000). Oviparous hexacorals tend to have annual reproductive cycles with a relatively short spawning period (Harrison & Wallace, 1990; Ryland, 1997; Ryland, 2000). Spawning occurs after nightfall and is often synchronized to the lunar cycle, although water temperature and possibly other ultimate factors are involved. For example, many coral species in the Great Barrier Reef (GBR) spawn in October or November (Babcock et al., 1986), but

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in tropical western Australia the same species spawn in March or April (Simpson, 1991). In the western Atlantic, coral spawning also occurs in relation to moon phase (Szmant, 1991; Wyers et al., 1991). Such regulation of the spawning cycle in marine invertebrates is widespread. One common intertidal zoanthid in the GBR, *Protopalythoa heliodiscus* (Ryland & Lancaster, 2003), spawns almost simultaneously with scleractinian corals ~5 d after the October or November full moon (Ryland & Babcock, 1991). Both the process of spawning and the subsequent development of the zoanthella larva of this species have been described (Babcock & Ryland, 1990), while the incorporation of zooxanthellae into late oocytes ensures vertical transmission of these symbionts (Ryland & Babcock, 1991).

Initially, we studied gametogenesis in *P. parasiticus* to establish the periodicity of the reproductive cycle, the seasonality of spawning, and whether zooxanthellae were vertically transmitted. With spawning clearly linked to moon phase by the histological study, it was then necessary to confirm the predicted spawning *in situ*. Also, given the abundance of *P. parasiticus* in the enclosed Bermudian waters, the longevity of Semper's larvae (Scheltema, 1971), and that the circulation patterns around the Bermuda Rise tend to conserve lagoon plankton at all times of year (Boden, 1951; Boden & Kampa, 1953), it was decided also to search for larvae using plankton nets.

Methods

Samples ~50 mm in length of *Callyspongia vaginalis* containing *Parazoanthus parasiticus* were cut from six marked clumps (A–F) near Castle Cut in Castle Harbour in 5 m depth (Fig. 1). Monthly collections were made from March to August in both 1992 and 1993, but at 2-day intervals from late August through September 1993. One collection was used to determine the density of *P. parasiticus* in the sponge. The samples were fixed in Bouin's fluid, washed, and stored in 70% ethanol. Pieces 5×5 mm were then immersed in 20% hydrofluoric acid for 24 h to remove the siliceous spicules (Langenbruch, 1988) and subsequently dehydrated, cleared in Histoclear, wax embedded, sectioned at 8 μm, and stained in Mallory's Triple

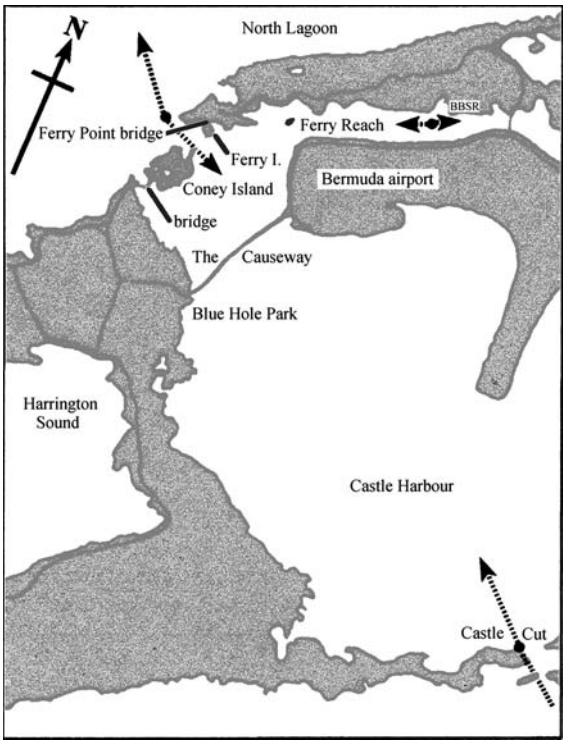

Figure 1. Map of Castle Harbour – Ferry Reach study area in Bermuda, with the direction and strength of ebb/flow tidal currents (from Morris et al., 1977) indicated by arrows.

to display the oocytes and nucleoli. The longest and shortest axes in each of 100 oocytes were measured, using video image analysis, in sections which passed through the germinal vesicle and nucleolus. The former marks the animal pole and the latter (diameter of 8–10 μm) ensured that only one, median section per oocyte was used. The two dimensions were then averaged. Descriptive statistics were performed in Excel and the measurements sorted into classes of 20 μm to construct size frequency histograms. Means of 100 averaged diameters per sample were also converted to volumes to provide a better index of the rate of vitellogenesis. In addition, toward predicted spawning time, a 'gravidity index' was defined which compensated for variations in zooid length: the number of oocytes (nucleoli) present per mm (125 sections) of column. Sea temperatures were not then systematically recorded at BBSR but annual curves have been published (Stephenson & Stephenson, 1972; Morris et al., 1977). A number of spot values were also available from the Bermuda Inshore Water Investigation run by BBSR.

In late summer 1999, direct evidence for spawning was sought in two ways. Two days before full moon, sufficient pieces of *Callyspongia* 'chimney' were collected from large clumps to represent at least three separate male and female *Parazoanthus* clones (safeguarding a possible incompatibility). 'Chimneys' were bagged underwater and then placed over plastic pegs (to anchor them) in running water aquaria at BBSR. At dusk the water flow was reduced, the outflow covered with fine mesh plankton cloth, and the tanks covered with black plastic to exclude extraneous light. This standard method was used by Babcock & Ryland (1990) in the zoanthid *Protopalythoa heliodiscus*. As an alternative, since all zoanthid eggs then known had been buoyant, a *Callyspongia* clump containing female *Parazoanthus*, adjacent to Ferry I. bridge (Fig. 1), was covered during the day by a heavily weighted, 0.5 m mouth diameter plankton net, the bucket of which was buoyed with a float. Male *Parazoanthus* were present below the bridge, about 3 m distant. The net was recovered from the bridge the same night (2200–2300 h), after any spawning would have occurred. As the net had often twisted in the changeable current, the contents were well washed into the bucket which was immediately examined for eggs.

Finally, a 1 m mouth diameter plankton net, 200 μm mesh, was streamed in the cuts north of Castle Harbour to try to capture embryonic or developed larvae from the abundant *P. parasiticus* in the surrounding waters. With tidal amplitude only 0.6–1.0 m, tidal velocities in the channels are much influenced by wind. Published data (Morris et al., 1977) nevertheless suggested that flow under the Coney I. and Ferry I. bridges (Fig. 1) would be sufficient to stream a plankton net. In fact flow did not follow the predicted pattern and had first to be investigated. At times of steady flow around high water, a net weighted with 1–2 kg lead, 5 m overall length, 200 μm mesh, with the bucket buoyed with a float, was deployed for 1 h from both of the bridges (a shorter net would have been more manageable but was not available). The fast flow necessitated firm anchorage for the rope.

Results

Oocyte growth

At the patch reef near Castle Cut (as throughout Castle Harbour) *Callyspongia vaginalis* was the commonest sponge. All the clumps investigated contained *Parazoanthus parasiticus*. The densities of *P. parasiticus* were estimated in each of the marked clumps A–F (Table 1). On histological sectioning it was ascertained that three of the sponges contained exclusively male zoanthids and three exclusively female (gonochorism is usual in Macrocnemina [Ryland, 1997]), suggesting that each was inhabited by a single clone. It is, however, possible that any sponge clump may contain more than one zoanthid clone: this must have been the case in clump D (see below).

Table 1. Description of materials, Castle Harbour, 25 August 1993. Abundances of *Parazoanthus* are based on 10 counts per clump using an area of 1.767 cm^2

Callyspongia vaginalis				*Parazoanthus parasiticus*	
Cluster	Number of tubes	Tube length (range, cm)	Tube diameter (range, cm)	Sex	Mean number (cm^{-2}) ± SD
A	24	15.0–42.0	1.3–3.0	F	5.32 ± 2.76
B	11	2.0–24.5	2.0–2.5	F	6.56 ± 2.34
C	33	4.5–31.0	0.5–2.4	M	9.62 ± 2.46
D	16	4.0–15.0	0.8–2.4	F[a]	2.89 ± 1.29
E	25	1.4–24.0	0.5–2.2	M	5.32 ± 2.12
F	17	6.5–23.5	1.1–2.1	M	7.98 ± 2.07

The densities differ significantly between clumps (ANOVA, $p < 0.001$) but not within them.
[a] There was more than one zoanthid clone in clump D since samples taken after April 1993 were male.

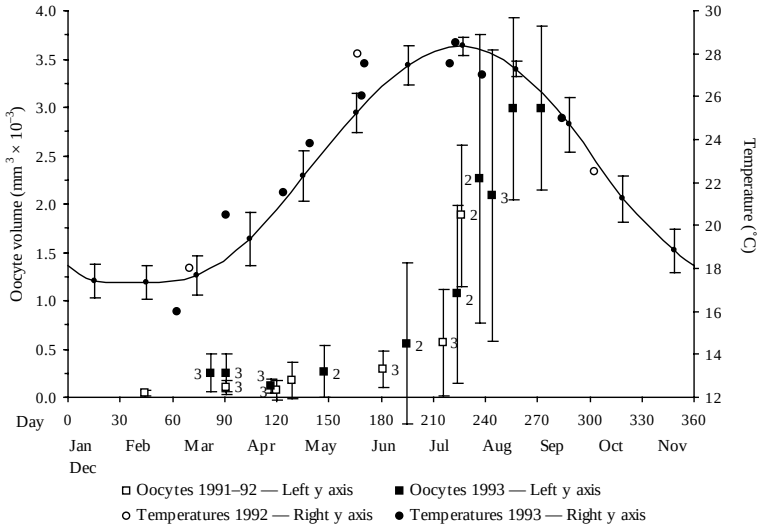

Figure 2. Sample mean oocyte volumes for 1991–1992 (the single point from 1991 indicated) and 1993 (left *y* axis): error bars represent ± 1 SD. When samples have been combined, the number is indicated in the label; $n = 100$ (except for the second sample on day 227, 1991, in which $n = 65$). Sea temperature monthly means (right *y* axis) and ranges (heavy lines) redrawn from Morris et al. (1977) and individual data points, 1992–1993 (provided by Bermuda Inshore Water Investigation).

Oocyte mean volumes have been compared with sea surface temperature (Fig. 2). With no continuous monitoring in 1991–1993, mean sea surface temperatures and ranges have been read from Fig. 6.5 in Morris et al. (1977), though there is no indication to which years they refer. An earlier line, for 1950–1951 (Fig. 5.2 in Stephenson & Stephenson, 1972), matches almost exactly. A few spot points confirm that actual temperatures will have been reasonably close to the means, although the two points for June are 2–3 °C higher. Summer temperatures above the long-term mean were then becoming commoner (Cook et al., 1990). The correlation between oocyte volume (and vitellogenesis) and temperature is striking. Volume remained low from March until June but increased rapidly from July when temperatures would have reached about 27 °C. The breeding cycle is completed at the time of highest temperature. By fortuitous comparison we have one additional value, 0.72×10^{-3} mm^3, in a sample from near Marathon, Florida Keys, 8 March 1993, where temperatures would have been some 7 °C higher than in Bermuda (Fig. 5.2 in Stephenson & Stephenson, 1972).

The error bars in Figure 2 indicate increasing variances as the season progressed, but the means are poor descriptors owing to the frequent non-normality of the sample measurements. More instructive are size frequency distributions, shown sample by sample in Figure 3, remembering that fixation and histological processing cause up to 20% shrinkage. This diagram spans the period from 15 March 1992 until 31 October 1993, and no samples were collected during the 1992–1993 winter period. Oocytes were actually already present in February (Fig. 2) but grew little early in the year. Either few oocytes in any cohort grew or new oocytes were continuously being formed from oogonia (or both): thus towards August, and even in early September, the size range spreads but there is no clear mode, perhaps a reflection of the huge increase in volume required for the egg to mature (Fig. 2). The diagrams for clone A (Fig. 3A) show no clear indication of spawning, as the last three samples show only the disappearance of small oocytes: possibly the shedding of a proportion of the largest oocytes would not be apparent (sampling dates were arbitrary, and not necessarily well timed – the exact relationship with the lunar cycle was, of course, not known). Clone B (Fig. 3B and D), on the other hand, shows a marked reduction in the percentage of large oocytes (>160 μm diam) between the samples of 25 August and 1 September 1993, evidence that spawning occurred during this period, though it

was clearly not complete in the sectioned polyp of 2 September. Only at the very end of the season is there a total absence of small oocytes (Fig. 3A and B). Samples from sponge clump D were originally female (Fig. 3C) but those collected after 23 March 1993 were male.

When it became apparent, from the size of the oocytes, that spawning was imminent, the

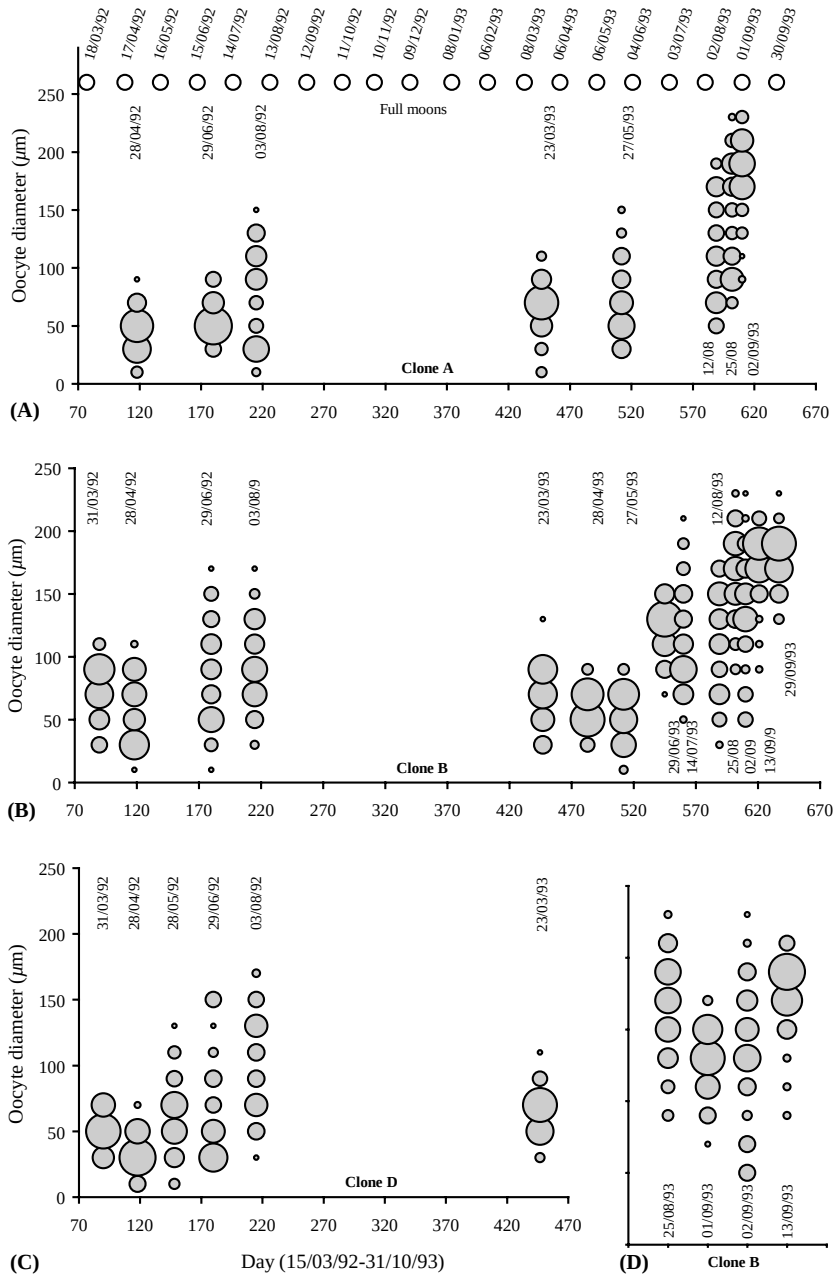

Figure 3. Oogenesis in *Parazoanthus parasiticus*. Bubble histograms of oocyte diameter in samples ($n = 100$) from Castle Harbour, Bermuda, 1992–1993; class intervals are 20 μm and bubbles are centred on the class midpoint; bubble area indicates percentage. Days (abscissae) start from 1 January 1992; day 70 = 15 March. (A) Clone A. (B) Clone B (the sample from 1 September is omitted). (C) Clone D. (D) Clone B, four samples taken over the full moon (1 September 1993) period of spawning; ordinate as C, abscissa intervals arbitrary. Full moons are shown at the top of the figure.

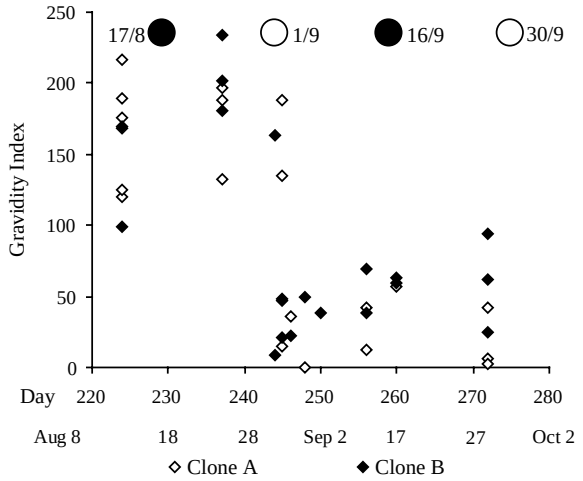

Figure 4. Evidence for spawning in *Parazoanthus parasiticus*. The data plotted are "gravidity index," the number of oocytes per mm zooid column length, in samples of two clones from Castle Harbour, Bermuda, between 8 August and 2 October 1993. Moon phases (new and full) are shown at the top of the figure, the critical full moon falling on 1 September. The sharp fall in gravidity between 1 and 3 September shows that 100–150 eggs per mm column length were spawned over those dates.

frequency of sampling was increased and the 'gravidity index' calculated (Fig. 4). These data show that the gravidity index was high ($\geq$100 mm^{-1}) in polyps of both clones on 12 August and 25 August 1993; on 1 and 2 September 1993 polyps of both clones had some polyps with a high index but in others it was low ($\leq$50 mm^{-1}); and on 3, 5 and 7 September all polyps had a low index (Fig. 4). Full moon was 1 September, so that spawning occurred on two or more nights just before and over full moon. Comparison of the oocyte size distributions in clone B for 14 July and 12 August 1993 (Fig. 3B) shows both a loss of the rather few large oocytes (>150 μm) and the presence of a new cohort of small ones. Together, these suggest that a small spawning took place at or close to the full moon on 2 August. No comparable observations can be made for 1992 since the last samples were taken on 3 August, well before the full moon on 13 August. A few oocytes remained after the 1–2 September 1993 spawning (Fig. 4) and the smaller oocytes grew, resulting in a modal diameter 170–200 μm by 13 September (Fig. 3D) and still apparent on 29 September (Fig. 3B). Unfortunately 29 September was the last sample and the full moon fell on 30th, so spawning at that time can only be inferred. No oocytes were present in November samples (26 November 1992, 19 November 1993).

Observed spawning

BBSR was visited again in 1999 to cover the full moons falling on 28 July and 26 August over which, the 1993 observations demonstrated, spawning of *P. parasiticus* would occur. However, freshly collected *Parazoanthus* in running water aquaria did not spawn on any night, although numerous *Callyspongia* parenchymulae appeared. In one of the tanks, on full moon + 1 day, the water was mixed with an extract of sperm but the zooids are so small that the extract was heavily contaminated with zooxanthellae and sponge cells – this did not initiate spawning. In a different approach, one clump near the Ferry I. bridge was covered with a plankton net each evening, from shortly before sunset to about 2200 h. On 28 August (2 days after full moon), when there was still no spawning, a previously sampled female colony well away from the bridge was checked: it had not spawned. Abundant spawning of *P. parasiticus* eggs ~250 μm diameter into the net then occurred that night. That confirmed the date of spawning in relation to the full moon. The collected eggs were not buoyant when placed in an aquarium and none cleaved; it was assumed that they had not been fertilized. They did not contain zooxanthellae.

Plankton samples

Throughout August numerous hour-long plankton samples were collected by deploying the net from the Coney I. and Ferry I. bridges. Flow, quite unlike the pattern described by Morris et al. (1977), was found to be southerly and maximal around high water (HW), and strong for about 2 h on each side of it. Flow was moderate and northerly around low water (LW), but reduced by a west, northwest or north wind. The high tide period was better, owing to the greater depth of water. Flow was then strong and the net streamed well. Although clogging with scyphomedusae, mangrove leaves, and *Syringodium* was a problem, coral planulae and sponge parenchymulae were obtained but no Semper's larva was ever caught. Occasional zoanthinae, probably of *Zoanthus*

sociatus, and numerous other planulae were found in plankton tows made in the North Lagoon. Thus no larvae possibly attributable to *Parazoanthus parasiticus* have ever been recognized.

Discussion

The oocytes develop at an increasing rate during summer (Fig. 2), leading possibly to three spawnings at monthly intervals between late July/early August and late September/early October, with that in late August/early September the largest. Information on the reproductive periods of other broadcasting Anthozoans in Bermuda is limited to four scleractinian species, *Diploria strigosa*, *D. labyrinthiformis*, *Montastrea cavernosa*, and *M. annularis* (Wyers et al., 1991) and one gorgonian, *Pseudoplexaura porosa* (de Putron, 2003), all of which are reported to undergo one or two spawnings per year over July to September. Spawning of scleractinian species in the Caribbean is similarly restricted to one or two months at the time of and just after maximum seawater temperature, which occurs in August and September at most locations (de Putron, 2003). The reproductive season of the gorgonian *P. porosa* is slightly longer (3–4 months) in the lower Caribbean (Kapela & Lasker, 1999) compared to Bermuda, and such a lengthening of the reproductive season with decreasing latitude also occurs for some scleractinians that reproduce via a brooding reproductive mode (de Putron, 2003).

While the spawning time of *P. parasiticus* approximates to full moon, the actual night(s) range from full −2 days to full +2 days, with some variation between clones (Fig. 4, data for 1 September). This is closer to the full moon than found by Wyers et al. (1991), who recorded synchronous broadcast spawning by *D. strigosa* and the *Montastrea* species 6–8 days after the full moon (within 1 day of the third quarter moon phase). The gorgonian *P. porosa* has also been observed to spawn over these days (de Putron, 2003). Multi-species spawning of a few scleractinian and gorgonian species over the third-quarter moon phase has been observed in Bonaire (de Graaf et al., 1999), and in Panama several gorgonian species mass spawn over the same nights (Brazeau & Lasker, 1989). These are less concentrated events than the spawning of numerous unrelated species over 1–2 nights observed in the GBR (Babcock et al., 1986; Alino & Coll, 1989), where *Protopalythoa heliodiscus* precedes most corals by about 2 days (Ryland & Babcock, 1991). There seems no obvious explanation for *P. parasiticus* spawning several days earlier than the Bermudian corals and gorgonian.

Aspects of reproduction and spawning in *P. parasiticus* are markedly different from those in the only other fully studied zoanthid, the brachycnemic *Protopalythoa heliodiscus*. Apart from being hermaphroditic (a character of the suborder), *Pr. heliodiscus* mature oocytes already contain zooxanthellae and are spawned as egg or egg/sperm bundles (Babcock & Ryland, 1990; Ryland & Babcock, 1991). It is difficult to explain why *Parazoanthus* did not spawn in tanks (though there is a similar problem with soft corals, Y. Benayahu, personal communication). Two possible explanations are: (1) that cutting the *Callyspongia* 'chimneys' releases toxins or other inhibitory chemicals, or (2) that there is some environmental cue missing in a tank. This might be a stimulus from another species or the pressure change of a rising tide (hence linkage to a specific moon phase: on full moon +2 days LW was at 1620 and HW at 2240) – though this would imply a surprising degree of sensitivity since, even on this spring tide, the amplitude was only 0.9 m.

While the failure to obtain fertilized eggs was disappointing, the demonstration of late summer spawning in *Parazoanthus parasiticus* paves the way for additional study. Establishing the pattern of development is an important goal. When Ryland et al. (2000) published their review of the probable development of macrocnemic zoanthids, based on the established restriction of zoanthina larvae to low latitudes (water >18 °C) compared with the ocean-wide distribution of macrocnemic adults, they overlooked the reported occurrence of zoanthinae over the Patagonian shelf (Zamponi, 1982) in water only 10 °C. These outlying occurrences are so far removed from any others that they require some explanation. Although Zamponi (1982) sectioned a larva, he unfortunately chose one with an anomalous pattern of septation, such as is occasionally observed (Ryland et al., 2000): it therefore remains unestablished whether these subantarctic occurrences are of a brachycnemic species of *Zoanthus* or *Isaurus* (which would be

remarkable), or whether they are actually macrocnemic larvae.

Brachycnemic zoanthids are zooxanthellate and have an essentially warm-water distribution comparable to that of scleractinian corals. The most southerly occurring brachycneme is *Zoanthus robustus*, distributed around the southern coasts of Australia (latitudes down to about 39° S) (Shepherd & Thomas, 1982). The approximate temperature ranges along these coasts are: August, 12–15 °C; November, 14–16 °C; February, 16–18 °C; May, 15–17 °C (Tchernia, 1980). These are low enough to suggest that a study of the reproductive biology of *Z. robustus* would be instructive, but still far above the 5–10 °C range over the Patagonian Shelf. It would be remarkable to discover a species of *Isaurus* or *Zoanthus* at such temperatures. The other possibilities are that the larvae are passive immigrants or that they come from indigenous macrocnemes (*Epizoanthus* or *Parazoanthus*). The main ocean current in this region is the cold, north-flowing Falkland Current, but there is an intermittent, south-flowing coastal current conveying water from the warm region off Uruguay and the Rio de la Plata (Arkhipkin, 2001). Given the known longevity of zoanthinae (Scheltema, 1971; Ryland et al., 2000), this origin seems not impossible but, if so, their ability to survive after reaching much colder water was unsuspected.

There seem to be three possible developmental strategies in Macrocnemina: a zoanthina (though the numerous zoanthinae sectioned in the past have never been macrocnemic), a rather undifferentiated (and therefore unrecognized) planktonic planula, or some kind of larva-less development close to the sea bed, as envisaged by Pax & Müller (1962). Sectioning any remaining larvae from Zamponi's collection might resolve the zoanthina possibility but, following the present study, the only realistic way forward is to pursue attempts to obtain and rear eggs of an accessible macrocnemic species, such as *Parazoanthus parasiticus*, in the way that Babcock & Ryland (1990) did for *Protopalythoa heliodiscus*.

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