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Histological Analysis of Reproductive Trends of Three *Porites* Species from Kāne'ohe Bay, Hawai'i[1]

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ABSTRACT: Gonad development and synchrony among *Porites compressa, P. lobata,* and *P. evermanni* colonies, collected in Kāne'ohe Bay during the summer of 1997, were histologically examined and compared. All three species are gonochoric broadcast spawners, releasing gametes predominantly around the time of full moon during the breeding season. Histological sections of fertile polyps confirmed the maturity of gonads and presence of zooxanthellae surrounding the oocytes and moving into the ooplasm of the mature eggs before spawning.

IT HAS BEEN DEMONSTRATED that mode and timing of reproduction, gametogenesis, and early development are variable among scleractinian corals (Connell 1973, Campbell 1974, Szmant-Froelich et al. 1985, Szmant 1986, Babcock et al. 1986, Richmond and Hunter 1990). Regardless of the mode of reproduction most coral species show a periodicity in larval or gamete release. Temperature variation, lunar and tidal cycles, variations in nocturnal illumination, and the diel light-dark cycle appear to influence the release of larvae and gametes (Kojis and Quinn 1981, Jokiel et al. 1985, Hunter 1989).

Variations in reproductive strategies among *Porites* species have been described (Stimson 1978, Kojis and Quinn 1981, Tomascik and Sander 1987, Richmond and Hunter 1990, Glynn et al. 1994). *Porites astreoides* is a hermaphroditic brooder (Chornesky and Peters 1987); *P. murrayensis* and *P. panamensis* are gonochoric brooders (Richmond and Hunter 1990, Glynn et al. 1994). *Porites lobata, P. compressa, P. evermanni, P. australensis,* and *P. lutea* are gonochoric broadcast spawners (Stimson 1978, Kojis and Quinn 1981, Szmant 1986, Richmond and Hunter 1990, Glynn et al. 1994).

Contributing to the knowledge of *Porites* species, the most common and widespread genus of hermatypic corals in Hawai'i and in many other tropical regions (Maragos 1977), this study provides detailed histological information on reproductive trends of *P. compressa, P. lobata,* and *P. evermanni* collected in Kāne'ohe Bay (O'ahu, Hawai'i).

MATERIALS AND METHODS

Colonies were collected in Kāne'ohe Bay from shallow reef flats around Coconut Island, Kekepa, and Ahuolaka at approximately fortnightly intervals in June and July 1997. Branches of *P. compressa* and small fragments of *P. lobata* and *P. evermanni* were sampled haphazardly at 2 to 5 m depth.

Previous studies suggested that spawning in *Porites* species in 1997 in Kāne'ohe Bay would occur in June, July, and August, during the full moon and new moon. Therefore, to assess the gamete developmental stage before first spawning, samples of each colony were collected on 18–19 June, 2 days before full moon. During the full moon, on 20–21 June, two colonies of *P. lobata* and one colony each of *P. evermanni* and *P. compressa* were sampled. On 4–6 July, during the new moon, three colonies of *P. lobata* and two colonies each of *P. evermanni* and *P. compressa* were collected. Fragments of three colonies each of *P. evermanni* and *P. com-*

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pressa and two colonies of *P. lobata* were collected at the full moon on 19–20 July.

Specimens were fixed in 10% formalin for 24–48 hr and decalcified in a solution of 4% formic acid and 2% Formalin. Polyps were dehydrated in ethanol series and cleared in xylene for routine paraffin embedding. Serial transversal sections cut from paraplast blocks at 6.0 to 7.0 μm were placed on glass slides, deparaffinized in xylene, rehydrated through graded ethanols to water, and stained with Mallory's triple stain. Longitudinal sections were prepared for colonies of *P. evermanni* considered unfertile.

Histological sections of fertile polyps were examined to determine sexuality, pattern of gonad arrangement, maturity of gonads before spawning, and mode of reproduction. Oocyte and spermary developmental stages were classified according to the criteria adopted by Glynn et al. (1994).

RESULTS

Porites compressa

Porites compressa is gonochoric and releases gametes that are fertilized externally. Lunar periodicity of gamete shedding was observed when colonies held in shallow outdoor tanks spawned during full moon periods on 21–24 June and 20–21 July (summer 1997) (Table 1).

Gonads formed between retractor muscles and septal filaments within complete mesenteries. Gametes of various sizes were characterized in stages III and IV. Stained mature oocyte color varied from dark pink to purplish. Numerous zooxanthellae were observed within ovarian membranes surrounding oocytes (stage III) or inside ooplasm (stage IV). Late stage of egg development was characterized by the migration of zooxanthellae into the ooplasm and movement of the nucleus toward the periphery of the cell (Glynn et al. 1994). Not all oocytes were shed in June or July during the full moon spawning events. Oocytes that were unspawned were generally smaller and appeared to be less mature. It is likely that they were reabsorbed by maternal tissue after a short period of degeneration. Colorless lipid vesicles imparted a frothy appearance to the ooplasm. Mature, prespawning oocytes had zooxanthellae centrally concentrated in the ooplasm (late stage IV).

Sperm clusters were distinguishable from oocytes primarily by the absence of germinal vesicles. Mature spermaries had a lumen, and spermatozoa were arranged with the pink transparent tails projecting toward the lumen and the dark condensed heads located peripherally. Gonads containing partially and completely spawned spermaries appeared as irregular pouches or spaces with a few residual, mature spermatozoa.

Porites lobata

Mode of reproduction, gonad structure, and stage of gamete development of *P. lobata* were similar to those in *P. compressa.*

Early spermatogenic cells and immature testicular cysts were found throughout the sampling period. The former were characterized as small groups of blue-staining cells aggregated in the gastrodermis of mesenteries adjacent to the mesoglea, and the latter were composed of a peripheral layer of spermatogonia and an inner layer containing spermatids. Immature cysts had a centrally located lumen.

Male and female colonies were observed releasing gametes in June, during the first spawning event. As in *P. compressa*, *P. lobata* showed increased egg development toward July full moon. However, during the second spawning event, only female colonies were observed releasing gametes (Table 1).

Porites evermanni

This study confirmed that *P. evermanni* is a gonochoric species with broadcast spawning, because the reproductive colonies had either sperm or eggs, without brooded larvae. Although gonads were found in four sampled colonies, three male and one female, no spawning event was observed during the summer of 1997. Mature eggs appeared on complete and incomplete mesenteries. Com-

TABLE 1

NUMBER OF FERTILE COLONIES FOUND ON DIFFERENT SAMPLING DATES (PARENTHESES REPRESENT TOTAL NUMBER OF COLONIES COLLECTED IN EACH PERIOD)

DATE	*Porites compressa*	*Porites lobata*	*Porites evermanni*
18–19 June[a]	2 (3)	1 (1)	0 (1)
20–21 June[b]	1 (1)	1 (2)	0 (1)
4–6 July[c]	2 (2)	2 (3)	2 (2)
19–20 July	2 (3)	2 (2)	2 (3)

[a] Two days before full moon.
[b] During full moon.
[c] During new moon.

plete mesenteries contained at least 10 eggs, and incomplete mesenteries had less than 3 eggs (Figure 1). Histological analysis of mature eggs showed the presence of lipid droplets and zooxanthellae. Zooxanthellae were initially abundant in the gastroderm surrounding the oocytes and were incorporated into the cytoplasm and became centrally concentrated later in development (stage IV) (Figure 2). Resorption of oocytes was inferred through loss of integrity and colorless aspect, which was verified in stage III and IV oocytes. Most resorbing oocytes in *P. evermanni* were surrounded by and contained zooxanthellae.

Most spermaries were immature, without spermatozoa, and commonly had one or two holotrichous nematocysts. Unfertile colonies had brownish, swollen mesenteries with clusters of early reproductive cells.

DISCUSSION

Despite the small sample size, this study confirmed some important aspects of the reproductive biology of three species of Poritidae from the central Pacific region. Although histology has disadvantages, which include possible inaccuracies in oocyte size measurements due to shrinkage of tissues (Harriott 1983) and underestimating oocyte

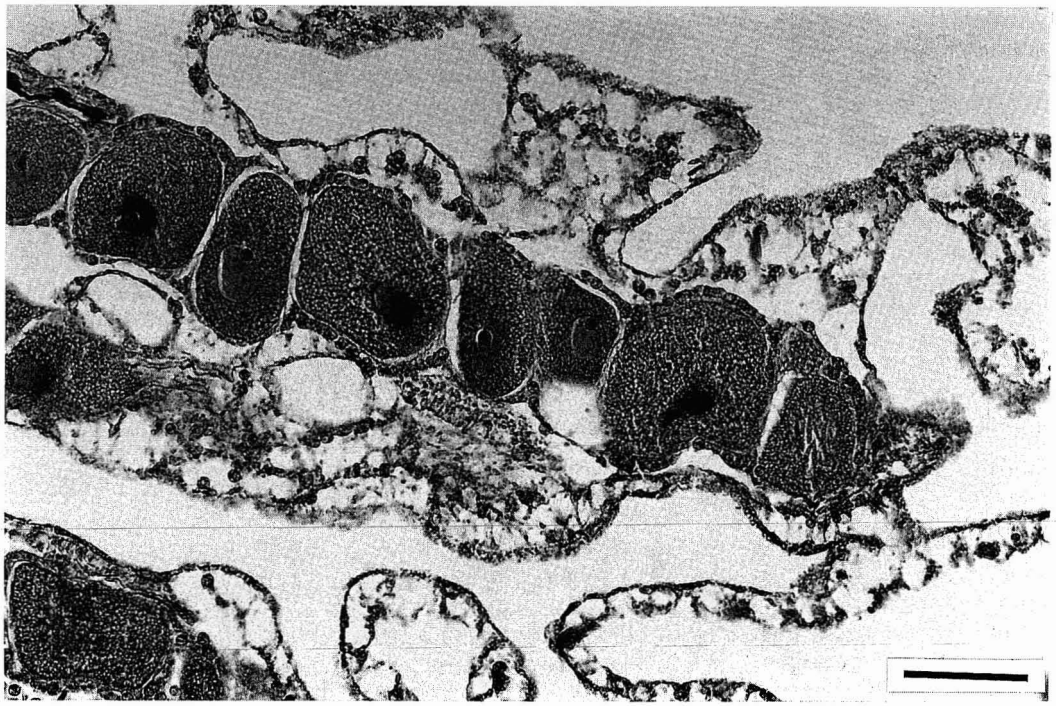

FIGURE 1. *Porites evermanni.* Fertile mesentery with stage III oocytes. Scale bar = 100 μm.

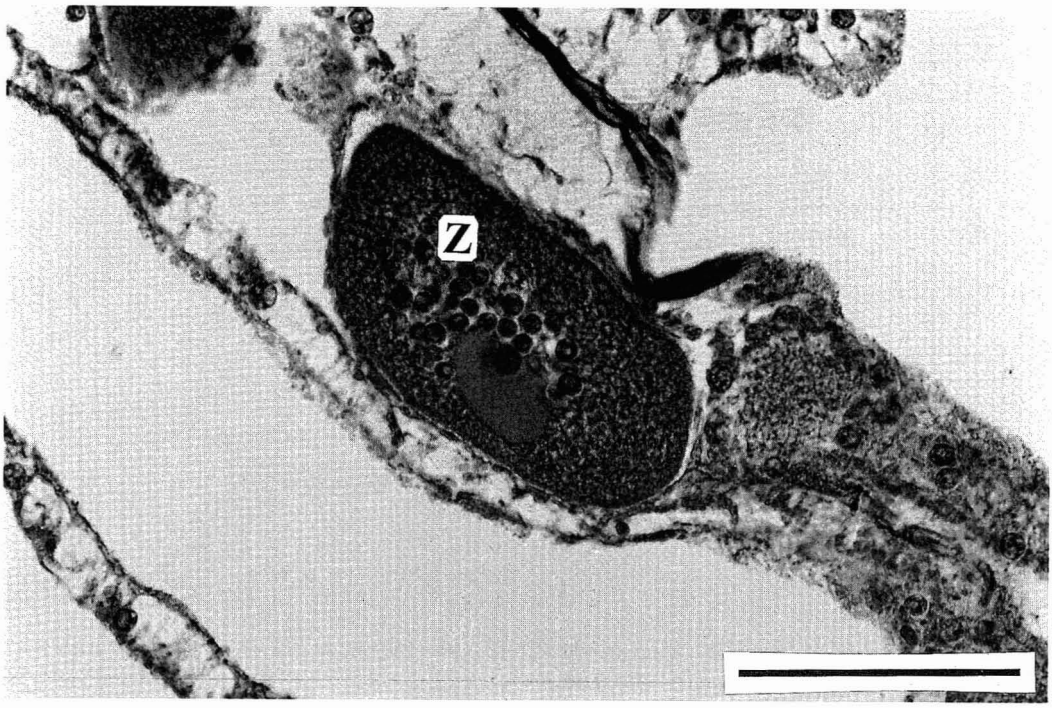

FIGURE 2. *Porites evermanni.* Stage IV oocyte (Z, zooxanthellae). Scale bar = 100 μm.

numbers by failing to section whole gonads or polyps (Harrison and Wallace 1990), it is essential for analysis of the stages of gonadal development and as a means to determine sexual patterns among corals.

This study indicated that *P. compressa, P. lobata,* and *P. evermanni* exhibited similar patterns of sexual reproduction. All of them were gonochoric and released gametes for external fertilization and development. As previously recorded by Stimson (1978) and Hunter (1988), *P. compressa* and *P. lobata* spawned during the full moon in the summer.

Stage III and IV oocytes were found on the same mesenteries in all fertile colonies. After complete maturation gametes seemed to be released into the gastrovascular cavity. Oocytes had an intact nucleus with a single nucleolus, indicating that final divisions occurred after spawning and/or fertilization. Although Harrison and Wallace (1990) suggested that oocytes of most corals lack algal symbionts, zooxanthellae were present in mature eggs of all studied species, mainly during late stage IV when they became centrally concentrated in the ooplasm. According to Beneyahu et al. (1992) acquisition of algal symbionts in mature oocytes only could indicate a seasonal trend. Studies dealing with timing and mechanisms of acquisition are needed, because the presence of zooxanthellae is considered essential for some coral planulae to achieve competence (Richmond 1987).

Resorption of stage III and IV oocytes was apparent in all three species. Despite morphological degeneration, some oocytes were relatively large, with zooxanthellae and lipid vesicles in the ooplasm. Previous studies have mentioned partial reproductive failure by resorption or phagocytosis of unspawned oocytes (Rinkevich and Loya 1979, Szmant-Froelich et al. 1980, Kojis and Quinn 1981, Harriott 1983, Kojis 1986). Rinkevich and Loya (1979) suggested that successful oocytes might absorb nutrients through phagocytosis of other oocytes. However, to date there is no consistent evidence concerning the mecha-

nisms of oocyte degeneration. Further studies are needed to assess the oosorption phenomenon by corals as a way to provide successful oocytes with nutrients as well as to elucidate the presumed participation of phagocytes.

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