

Reproduction in the Giant Clams *Tridacna gigas* and *T. derasa* In Situ on the North-Central Great Barrier Reef, Australia, and Papua New Guinea

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Abstract. Small groups of *T. gigas* and a single individual of *T. derasa* have been observed to spawn sperm in nature during the austral summer on the Great Barrier Reef. In *T. gigas* diel periodicity to the spawning generally coincided with incoming tides near second (full), third and fourth (new) quarters of the moon phase. Intense spawning ranged from 30 min to 2½ h, with spawning contractions occurring every 2–3 min. Eggs were never observed being spawned in nature. A new technique, an egg catching device, was used for sampling eggs of *T. gigas* which were observed spawning sperm. Results indicated that the egg phase of spawning did not follow spawning of sperm. Some clams which do not respond to a spawning neighbour may be reproductively inactive. In 70% of observations of nearest spawning neighbours the clams were within 9 m of one another. A hypodermic extraction technique was used for clam gonadal material. Examination of tissue suggested a potential early to mid-austral summer spawning for *T. gigas*, and to a lesser degree for *T. derasa*.

Introduction

The rapid decline of giant clam (Fam. Tridacnidae) populations from overharvesting for food has been reported in the Pacific region (Hester and Jones 1974; Bryan and McConnel 1976; Pearson 1977; Hirschberger 1980). Thus, research has increasingly become focused upon reproduction and mariculture potential (Stepenson 1934; Wada 1954; La Barbera 1975; Jameson 1976; Yamaguchi 1977; Beckvar 1981; Fitt und Trench 1981; Gwyther and Munro 1981; Munro et al. 1983; Munro and Heslinga 1982; Heslinga et al. 1984; Fitt et al. 1984). Giant clams are sequential simultaneous hermaphrodites. The role that this sexual pattern and the natural spawning cycles play in the reproductive success of tridacnids must be understood to develop mariculture technology directed toward mass culture of giant clams.

Local spatial distribution and broad scale geographic distribution of the largest two tridacnids, *Tridacna gigas* and *T. derasa*, on the Great Barrier Reef of Australia have been studied with reference to reproductive pattern, strategy and recruitment (Braley, in preparation). Results of nearest neighbour analysis (Clark and Evans 1954), on high density natural populations at an outer shelf barrier reef have shown clumping by species on some substrates. In localities with low density populations of these clams it has been suggested that the collection and placing of mature clams in close proximity to each other will assure greater success in fertilisation (Beckvar 1981; Gwyther and Munro 1981) and that mature clams may require chemical signals from other clams in the population to achieve full spawning synchrony (Munro et al. 1983). Thus, spatial patterns of distribution and density may affect spawning patterns in giant clams. The timing and intensity of spawning in clam specimens which have been transported to running seawater systems for spawning induction or spontaneous spawning may be altered under these conditions. Heslinga et al. (1984) have demonstrated lunar and diel periodicity in spontaneous spawnings of *T. gigas* brood stock held in a running seawater system for 7 months in Palau, and have suggested that future workers attempt to refute the hypothesis that reproduction in giant clams is aseasonal. It is fortuitous for the mariculture potential of giant clams if holding of brood stock in running seawater systems triggers a regular pattern of spawning activity as demonstrated in Palau.

This report addresses the question of whether spawning is likely to be seasonal or aseasonal, in natural populations of clams on the Great Barrier Reef and in Papua New Guinea, and the timing and duration of natural spawning with reference to possible spawning cues.

Methods and Materials

Natural Spawning

Daily morning and afternoon observations were made on populations of the giant clams *T. gigas* and *T. derasa* at northern Escape Reef (15°50' S,

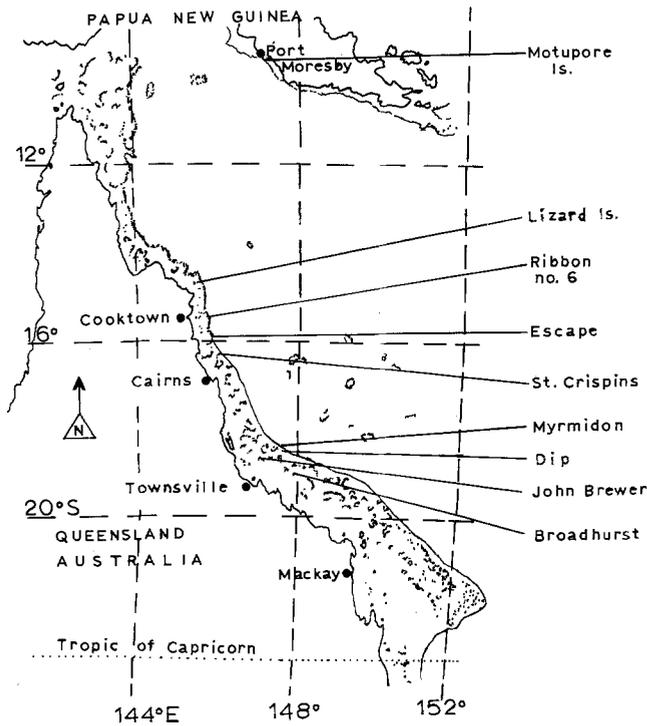


Fig. 1. Map of reefs' localities in text

145°50' E) in December 1981 and December 1982, and at Lizard Island (14°41' S, 145°27' E) in late November-early December 1983. Each time period was for two weeks. Similar observations on these two clam species were made at a study site at Myrmidon Reef (18°15' S, 147°27' E) for 5 days in early October 1983, 6 days in January 1984, and in June 1982 at Motupore Island Research Centre, near Port Moresby, Papua New Guinea (see Fig. 1). Some of the *T. gigas* specimens observed at Motupore Island had been gathered into an offshore fenced enclosure by previous researchers. Also observed were newly and previously gathered *T. gigas* held in tanks. Casual observations were made for spawning activity of *T. gigas* and *T. derasa* during a Great Barrier Reef Marine Park Authority Coral Trout Survey covering 57 reefs from the Whitsunday Islands area (20°11' S) to outer shelf reefs just northeast of Lizard Island (14°27' S), a distance of approximately 817 km along the reef.

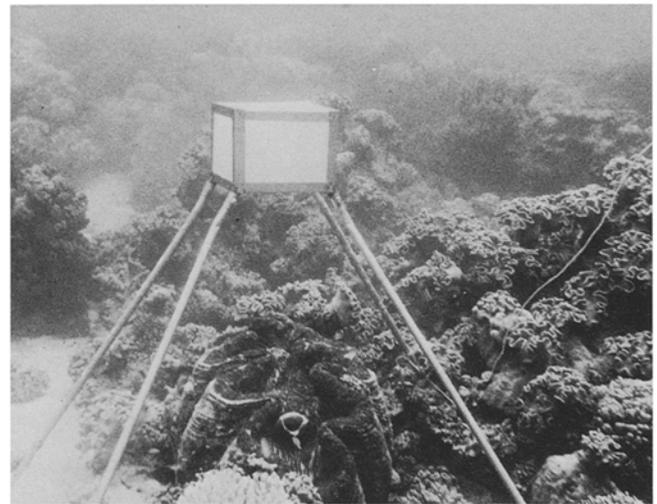


Fig. 2. Egg catching device in position over excurrent siphon of *T. gigas*

An egg catching device (Fig. 2), having aluminium legs and stainless steel box frame (25 cm × 25 cm × 20 cm) with 80 µm nylon silk around the sides and plexiglass angled upward around the bottom opening, was used as a new technique for catching eggs of clams which were observed to be spawning sperm naturally at the Lizard Island sites. A different spawning clam was chosen for 3 of 4 late afternoons in which spawning was occurring. The device was positioned directly over the excurrent siphon of a spawning *T. gigas* so that the plume of sperm forced out of the excurrent siphon entered directly into the opening of the box. The following morning a sample of material caught in the trough of plexiglass was removed by pipette, preserved in 2% formalin, and examined microscopically.

Gonad Samples

Gonad biopsy samples were collected from clams at Escape Reef in December of 1981 and 1982, at Motupore Island and nearby reefs in June 1982, at 5 other reefs on the Great Barrier Reef in February 1982 and March, May 1983, Myrmidon Reef in May and October 1983, and Lizard Island in November-December 1983 (Fig. 1). The hypodermic extraction technique was suggested by Gwyther and Munro (1982) for use

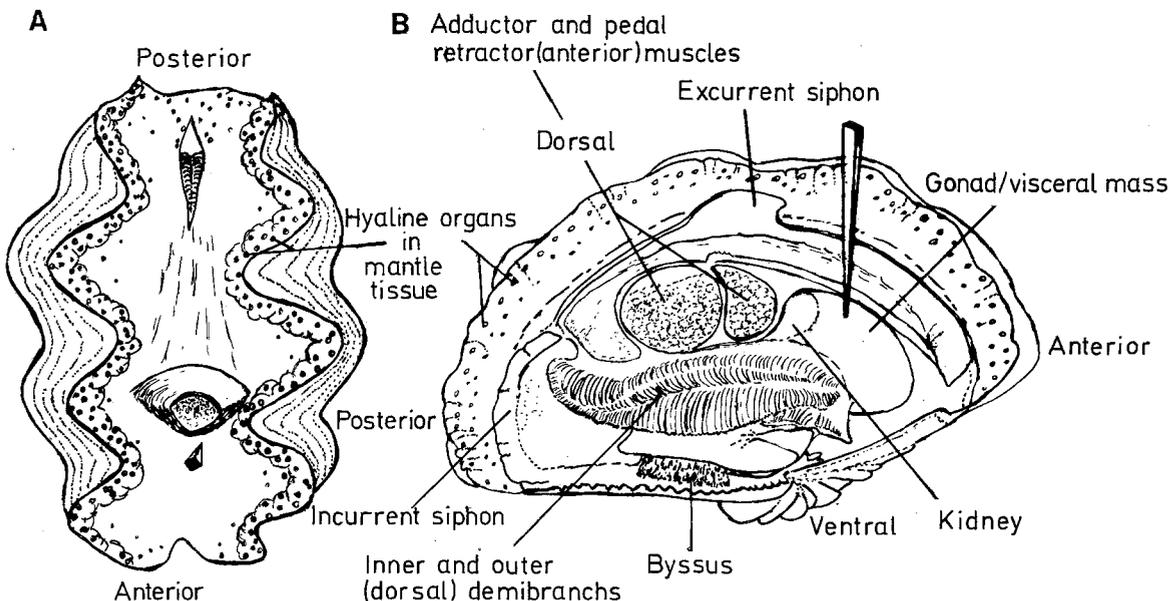


Fig. 3 A, B. Diagrammatic sketches of A *T. gigas* from dorsal view, and B *T. derasa* looking from the removed right side (modified after Stasek 1962). Pointers show area and angles from which biopsies of gonadal tissue were taken

on tridacnids. This technique was also used by Kenchington during surveys of *Acanthaster* on the Great Barrier Reef (R. Kenchington, personal communication, 1984). Using a 10 cm hypodermic needle and a 20 cc plastic plunger syringe generally allowed for extractions of a small amount of gonadal tissue to be obtained. Careful practice was required for repeated success at extractions (see Fig. 3). The material was preserved in 2% buffered formalin and egg-size determinations were made from means of 15 randomly chosen eggs using an ocular lens vernier on a compound microscope. Sperm, when present, was noted. Stages of gonad condition for eggs were:

Developing: Eggs up to 110 μm , generally various sizes in a progressive state;

Ripe: Eggs from 110 μm and larger, vitellogenesis complete (ova cytoplasm filled with yolk), easily ruptured;

Regressive: (post-spawning) eggs any size but degenerative;

Resting: Lack of eggs in sample (all "resting" samples involved several extraction attempts by hypodermic to be certain of the lack of eggs).

In Palau, 110 μm and $106 \pm 1 \mu\text{m}$ were found to be the mean size of eggs which developed to metamorphosed larvae after fertilisation (N. Beckvar, personal communication, 1979 and Heslinga et al. 1984,

respectively). All gonad samples were taken from *T. gigas* and *T. derasa* on the Great Barrier Reef, but only *T. gigas* was sampled in Papua New Guinea (no *T. derasa* present in the Port Moresby area).

Results

Natural Spawning

Observations of in situ natural spawning on *T. gigas* were made during December 1981 at Escape Reef, late November – early December 1983 at Lizard Island and late January 1984 at Myrmidon Reef (Table 1, Fig. 4A–C). The only observation of in situ natural spawning on *T. derasa* was by a single individual on 5 October 1983 at Myrmidon Reef at low tide, on the day of the full moon at 1300 h. Clams at the Escape Reef East Bommie site spawned later in the afternoon just after full moon phase than did clams which spawned before the new moon phase at both sites (Table 1). This coincides with incom-

Table 1. Observations on natural spawning of sperm by *Tridacna gigas* at Escape Reef, Lizard Island and Myrmidon Reef. Dates of observations: Escape Reef, 12–22 December, 1981; Lizard Island, 26 November–6 December 1983; Myrmidon Reef, 25–30 January 1984; +, after times, indicate spawning continued after observations

Site	Clam no.	Shell length (cm)	Spawning times (h)	Day from full moon (tide, m)	Day from new moon tide, m)	Distance between clams (clam no., m)
Escape (East Bommie)	3	77	1700–1730 +	+1 (low 1611, 0.8)		(3 and 4, 3.7)
			1700–1730 +	+2 (low 1711, 0.9)		
	4	93	1700–1730 +	+1		
			1700–1730	+2		
	5	101	1700 + 1730 +	+1		(5 and 4, 2.8)
(North Reef-A)	9	104	1500–1545		–3 (low 1324, 1.9)	(9 and 5, 8.0)
			1700–1730 +	+1		
			1500–1545		–3	
	58	112	1515–1615		–3	(58 and 2, 21)
	48d	101	1430–1540		–3	(48d and 2, 12)
	2	94	1500–1620		–3	
Lizard Island (Palfrey South)	15	84	1651–1700	+6 (high 1707, 2.5)		(15 and 14, 1.2)
	18	84	1657	+6		(15 and 20, 15)
	19	54	1615–1701 +	+6		(18 and 19, 3.2)
			1638–1900 +	+7 (high 1750, 2.5)		
	20	73	1619–1657 +	+6		(20 and 19, 1.4)
			1630–1640	+7		
	14	83	1646–1650	+7		
28	78	1649–1910 +	+7		(28 and 15, 30)	
(Watson Bay)	7	83	1707–1704 +		–5 (high 1905, 2.4)	no other spawners observed
	60	89	1646–1652 +		–6 (high 1828, 2.5)	
	62	92	1654–1658 +		–6	(62 and 60, 14)
	83	93	1736–1800		–6	(83 and 62, 2.0)
Myrmidon	1	94	1625–1645 +		–3	(1 and 2 or 3, 1.5)
	2	88	1627–1632		–3	(2 and 3, 0.7)
	3	76	1640–1647 +		–3	
	5	101	1628–1648 +		–3	(3 and 5, 5.2)
	9	96	1553–1556		–3	(9 and 5, 14)
	17	89	1601–1622 +		–3	(17 and 3, 20)
	33	62	1608–1616 +		–6	(33 and 35, 4.5)
	35	65	1629–1640 +		–6 (high 1803, 2.4)	(33 and 35, 4.5)
			1717–1723		–3 (low 1524, 0.9)	
	36	91	1635–1731 +		–6	(35 and 36, 5.4)
	38	57	1652–1710 +		–6	(38 and 39, 0.8)
	39	62	1652–1710 +		–6	
	42	76	1551–1715 +		–6	(42 and 72, 9)
72	103	1703–1735 +		–6	(72 and 39, 8.2)	

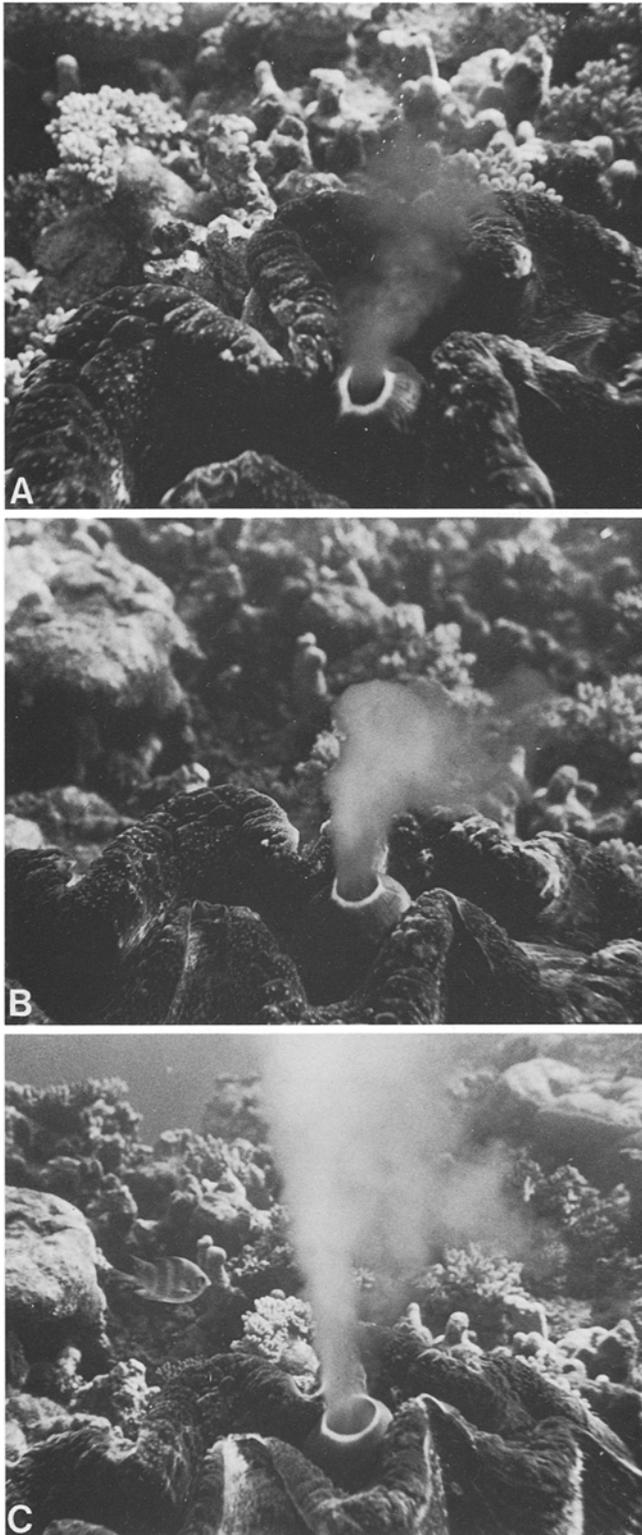


Fig. 4A–C. Natural spawning of sperm by a *T. gigas* individual (110 cm shell length) on East Bommie, Escape Reef, Great Barrier Reef (12 December 1981, 1700 h)

ing tides at both new and full moon phases while no spawning was noticed at any other time on the daily morning and afternoon surveys. At Lizard Island spawning was generally on incoming tides but continued beyond high tide in some cases and took place around

Table 2. Spawning (sperm) intervals for *T. gigas* in situ from Lizard Island, late November–early December 1983

Site	Clam no.	Shell length (cm)	Number of expulsions observed	Mean interval min–s ± SD	Amount of sperm expelled + little; ++ copious
Palfrey-South	7	83	5	1–47 ± 0–37	++ and +
	14	83	2	1–40 ± 0–00	++
	15	84	3	2–07 ± 0–09	++
	18	84	1		+
	19	54	20	2–02 ± 0–54	++ and +
			15	3–03 ± 1–36	++ and +
	20	73	11	2–29 ± 0–54	++
Watson Bay			3	1–42 ± 0–17	+
	28	78	17	1–27 ± 0–15	
	60	89	3	2–44 ± 0–32	+
	62	92	2	4–00 ± 0–00	+
	83	93	4	5–52 ± 2–53	+

Table 3. Gonad condition in natural spawning clams after spawning and results of egg catching device on naturally spawning clams. Lizard Island, December 1983; Site A, Watson Bay; Site B, Palfrey-South

Site	Clam no.	Shell length (cm)	Debris in egg catching device-analysis	Gonad biopsy several days after spawning
A	83	93	No clam eggs; other invertebrate eggs, some granular material (yolky)	
B	7	83	No clam eggs; varied invertebrate eggs, diatoms dinoflagellates	
B	28	78	No clam eggs; other invertebrate eggs	Eggs ripe, abundant; sperm now sparse
B	19	54	Device not used	Eggs developing, abundant; sperm now sparse
B	20	73	Device not used	Eggs developing abundant; sperm now sparse
B	14	83	Device not used	Eggs ripe, abundant; sperm now sparse

third quarter moon phase or +6 to 9 days from full moon (Table 1).

The photographs of Fig. 4A–C show a progression of closing valves as the sperm is being forced out of the ex-current siphon of *T. gigas*. Spawning behaviour was similar to the description given by Wada (1954). The expulsion of sperm occurred at intervals of about two minutes for *T. gigas* which spawned copious amounts of sperm, but generally longer intervals for individuals spawning small amounts of sperm (Table 2). One minute intervals were noted for the single *T. derasa* observed at Myrmidon Reef. The spawning process continued in some copious spawners from 30 min to more than 2½ h (Table 1). At no time were eggs observed being spawned. Likewise, no clam eggs were found in the egg catching device (Table 3).

Table 4. Observations on spawning-type contraction of 7 *T. gigas* living in 2700-l fibreglass tanks for about 2 years at M.I.R. C., Papua New Guinea. The number of contractions are shown over a 9-day period. All of these excurrent siphon contractions noticed in the late afternoon (beginning about 1700 h). The moon was at the end of the first quarter on 30 May and full on 6 June 1982. Time of high tide shown below date

Tank no/ clam no	Shell length	Number of spawning-type contractions								
		29 (1622)	30 (1730)	31 (1820)	1	2	3	4	5	6 (2135)
1/1	37.6									
1/2	21.2									
1/3	71.8	16	1	2				1	1	
1/4	71.5		19	2	5			3	7	
3/5	82.4		1	1					1	
5/6	65.4		4	2				1	3	
5/7	38.5									

Several clams which were observed spawning sperm in situ, including some on which the egg catching device was employed, were biopsied for gonad condition several days after the spawning observations. In all cases abundant eggs were present in the sample, *developing* or *ripe*, but sperm was noticeably sparse (Table 3), indicating that the egg phase of spawning did not follow spawning of sperm.

The distances between spawning clams and their nearest spawning neighbours give an indication of the effective distance of the chemical signals to elicit the spawning response (Table 1). Fifty percent of nearest spawning neighbours were within 5 m of one another, 70% were within 9 m, while 13% were between 20–30 m of one another. Although not indicated in Table 1, many clams were closer to a spawning individual than nearest spawning neighbour, but these showed no response. No spawning activity was observed in the group of 25 *Tridacna gigas* held in the fenced enclosure offshore of Motupore Island, Papua New Guinea, during the month of June 1982. Although no spawning activity was noted in the 7 *T. gigas* observed in the three 2700-l tanks at Motupore Island Research Centre, numerous spawning-type contractions (excurrent siphon expulsions; conversely, incurrent siphon contraction-expulsions of water occur occasionally, but not with induced or natural spawning activity) were recorded, mainly in the late afternoon (Table 4). Contractions repeatedly occurred within 2–3 min of each other. The moon was in its first and second quarters and the timing may have been associated with incoming or high tides (Table 4).

Gonad Samples

T. gigas (Fig. 5). At Escape Reef, the percentage of clams found in *developing* and *ripe* stages of gonad condition in December 1981 and December 1982 were 60% and 33.4%, respectively. Clams sampled in late November–early December 1983 at Lizard Island which were in similar gonad condition represented 54.6% of

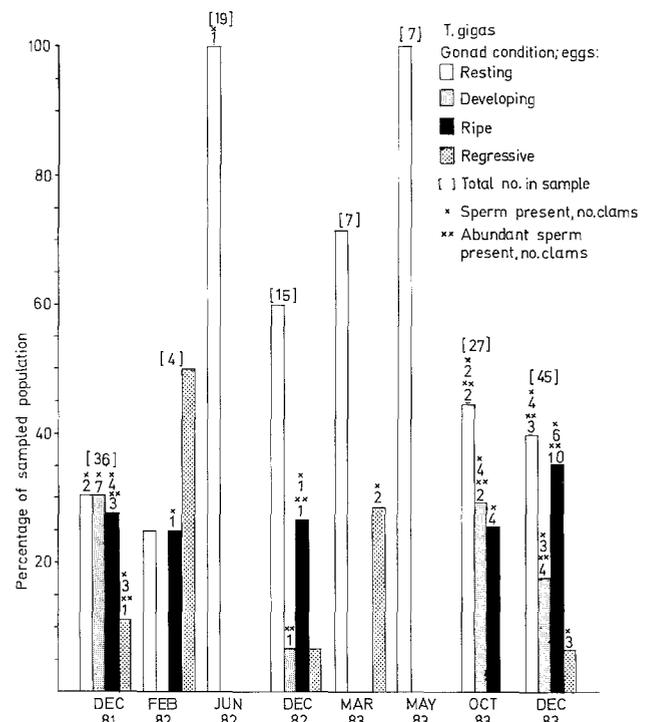


Fig. 5. Histogram of gonad condition in *T. gigas* based on mean egg size and showing sperm abundance; Great Barrier Reef. *Reefs*: December 1981, 1982, Escape; February 1982, John Brewer and Broadhurst; June 1982, Port Moresby, Papua New Guinea; March 1983, St. Crispins and Ribbon no. 6; May and October 1983, Myrmidon; December 1983, Lizard Island

those sampled. No *developing* stages of gonad condition were found after the December samplings until the October sampling at Myrmidon Reef. Austral winter samplings in June 1982 and May 1983 resulted in 100% of sampled clams in the *resting* stage. Sperm was present in some clams which showed a *resting* stage for the eggs, but this was common only on approaching the austral summer. The R × C test of independence using the G-test (Sokal and Rohlf 1969) was significant at $P < 0.005$ rejecting the null hypothesis that reproduction is aseasonal.

2. *T. derasa* (Fig. 6). The percentage of clams found in *developing* and *ripe* stages of gonad condition in December 1982 at Escape Reef was 13.4%, and those sampled in late November – early December 1983 at Lizard Island and nearby outer shelf reefs showed 100% *resting* stage for gonad (egg) condition. No sperm was found in any clams sampled at this time. The February 1982 and March 1983 samples show most clams to be in a *regressive* (post-spawning) stage. A May 1983 sample at Myrmidon Reef showed 100% of the sampled clams were in the *resting* stage. In October 1983 at this same reef all stages were represented, with 17.4% of the clams in *developing* and *ripe* stages. Fewer cases of sperm and eggs present together were found for *T. derasa* than for *T. gigas*. Although the percentage of *T. derasa* in *resting* stages was very high at all samplings, the R × C test of significance using the G-test (Sokal and Rohlf 1969) was significant at $P < 0.01$ rejecting the null hypothesis that reproduction is aseasonal.

Although these data were collected from different localities on the Great Barrier Reef (and Papua New Guinea only for June 1982) they suggest a potential austral early-mid-summer spawning for *T. gigas* and an austral late spring to early summer spawning for *T. derasa*. The natural spawning of *T. gigas* was observed in December 1981, late November – early December 1983, late January 1984, and in early October 1983 for *T. derasa*. *T. gigas* dissected by Gwyther and Munro (1981) in October and November in Papua New Guinea had very ripe gonads, but these authors also stated that eggs could be extracted from the gonads of large *T. gigas* throughout the year. All 22 *T. gigas* specimens which I sampled in Papua New

Guinea in June 1982 were in a *resting* stage. However, my data does indicate that the percentage of the populations of *T. gigas* and *T. derasa* in the *resting* stage may vary considerably during the same season of different years. These data also indicate that all clams in the sampled population are not functional hermaphrodites, since sperm and eggs were not found together in all samples.

Discussion

Spawning

The spontaneous spawning regularity ($N = 14$) exhibited by brood stock of *T. gigas* held in tanks in Palau during 6 out of 7 months of observations suggest an aseasonality of spawning (Heslinga et al. 1984). However, of 11–18 specimens present over this period, 5 of the 14 spawnings were due to a single individual, 2 spawnings to 2 other clams, and 7 spawnings to groups of 2–7 clams. Heslinga et al. (1984) have suggested that many of the clams were reproductively inactive in comparison with a few potentially heavy spawners. This may be true in natural populations as well, since the *resting* stage in the present report was high even in the period of peak potential spawning for both *T. gigas* and *T. derasa*. A higher percentage of the population of *T. derasa* sampled were in the *resting* stage than for *T. gigas* sampled. Local environmental conditions (Fitt and Trench 1981) and possible population density (Beckvar 1981; Gwyther and Munro 1981; Braley, in preparation) may affect the overall reproductive success of the clam and the actual timing of reproduction as well as the percentage of the population actively involved in the reproductive effort for that season. The natural spawning observations on *T. gigas* also suggest that there may be reproductively inactive clams in close proximity to the observed spawners or those non-responding clams may require a greater combination of environmental cues to trigger spawning. The maximum distance which will still elicit the spawning response needs further quantification, which may be accomplished by spawning induction in situ.

A lunar periodicity to spawning of *T. gigas*, *T. derasa* and *Hippopus hippopus* was first suggested by Beckvar (1981). In this study 5 of 8 observed spawnings were on or near the day of new moon, late afternoon on a rising tide. She reported on a single observation of in situ spawning made by G. Heslinga in 1979, –1 day from new moon in the late afternoon. In my study natural spawnings at Escape Reef occurred in the mid to late afternoon near both new and full moon phases on rising tides, and at Myrmidon Reef late afternoon on –3 and –6 days from the new moon. The diel periodicity is the same in observations by Heslinga et al. (1984) in outdoor raceways, but in Palau the lunar phases of peak spawning activity began +7 to 13 days from new moon and a less intense period +7 to 13 days from full moon. This is in agreement with natural spawning of *T. gigas* from +6 to 9 days from full moon at Lizard Island. Therefore, lunar

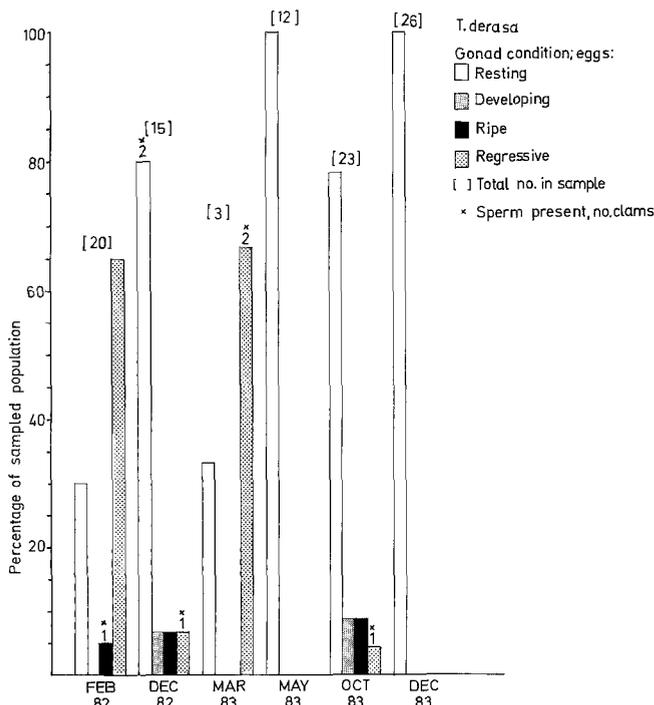


Fig. 6. Histogram of gonad condition in *T. derasa* based on mean egg size and showing sperm abundance; Great Barrier Reef. (For reef see legend of Fig. 5)

periodicity in spawning may vary with locality within the reproductive season on the Great Barrier Reef.

The spawning-like contractions observed at Motupore Island Research Centre were also diel and lunar. The significant diel periodicity in spawning of *T. gigas* is of primary concern since it is evident in Palau and on the Great Barrier Reef. From fertilisation the developing embryos hatch into actively swimming trochophore larvae by 16 h (Jameson 1976, *T. maxima*; Beckvar 1981, *T. gigas*). A late afternoon spawning would allow the developing embryos relative protection overnight from the myriads of planktivorous fish on the coral reef. However, research on the feeding of the reef building corals *Montastrea cavernosa* and *Porites lobata* (Porter 1974; Johannes and Tepley 1974) has shown peak feeding activity at both dusk and dawn. Therefore, complete protection is not afforded by this spawning strategy.

Few high density (> 30 clams ha^{-1}) reefs were found on a broad scale geographic distribution of *Tridacna gigas* and *T. derasa* on the Great Barrier Reef (Braley, in preparation). These reefs may have a sufficient critical number of clams to assure reproductive success and even act as "reproductive centres" for much larger areas of the reef (Braley, in preparation). Recruitment of *T. gigas* and *T. derasa* is extremely low (Yamaguchi 1977; Pearson 1977; Munro and Heslinga 1982). Juvenile clams (< 14 cm) at Escape Reef comprised 1.3% and 1.5% of the populations of *T. gigas* and *T. derasa*, respectively, while an annual mortality rate of adults from 1981 to 1982 was 2.7% and 1.1% for *T. gigas* and *T. derasa* (Braley, in preparation). Sporadic and low rates of recruitment may be associated with high mortality due to predation but ultimately it relates to the reproductive patterns of the adults. My field observations on natural spawning and results from the egg-catching device indicate sperm may be spawned more readily than eggs. Likewise for clams in captivity sperm is spawned more readily than eggs (Heslinga et al. 1984). Local environmental cues in nature, varying from place to place, may trigger gonad maturation and spawning (Fitt and Trench 1981). Birkeland (1982) suggests that if high rainfall affects phytoplankton blooms as a result of the increased nutrients from terrestrial runoff, then there would also tend to be a seasonality in spawning of tropical marine invertebrates as there is in temperate regions. It is reasonable that such environmental conditions may occur in certain years only, thus resulting in sporadic spawnings and low recruitment rates observed in nature.

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Note added in proof. Results from egg-catching device at Lizard Island in October–November 1984 support previous observations and one group natural spawning (*T. gigas*) occurred +3 to 7 days from new moon in late October.