

Spatial distribution and population parameters of *Tridacna gigas* and *T. derasa*.

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Abstract— Highly significant differences were shown in substratum preference by undisturbed populations of *T. gigas* and *T. derasa* at four sites on the Great Barrier Reef. They favored branching *Acropora* spp. coral.

Significant aggregated distributions were found on two substrata for pairs of *T. gigas* (Tg-Tg) and one substratum for *T. derasa* (Td-Td). A significant uniform distribution was found for Tg-Tg in the highly preferred branching *Acropora* spp. Aggregation in clams was also supported by an experiment at Lizard Is. Research Station which directly tested substratum preference and spatial distribution on two month old *H. hippopus* juveniles.

Annual natural mortality rates of populations of giant clams at 4 reef localities between 18°15'S and 14°41'S averaged $1.65 \pm 0.54\%$ for *T. gigas* and $2.07 \pm 2.59\%$ for *T. derasa*.

Introduction

Many papers describe the demise of the giant clams, *Tridacna gigas* (Linnaeus) and *T. derasa* (Roeding) as a result of poaching and over-harvesting in the Indo-West Pacific region (Hester and Jones, 1974; Bryan and McConnell, 1976; Pearson, 1977; Hirschberger, 1980; McKoy, 1980; IUCN, 1983), but a paucity of knowledge exists on the ecology of natural populations. Relatively undisturbed populations of these two species on the GBR of Australia make it an ideal region for 'baseline' ecological studies. Yamaguchi (1977) suggested that giant clams are similar to 'K-strategists' like whales or forest trees and may be managed like forests. In addition to reproductive studies of tridacnids (Wada, 1954; LaBarbera, 1975; Jameson, 1976; Beckvar, 1981; Fitt and Trench, 1981; Gwyther and Munro, 1981; Munro *et al.*, 1983; Munro and Heslinga, 1983; Heslinga *et al.*, 1984; Fitt *et al.*, 1984; Braley, 1984; Braley, 1985), management programs require information on their natural habitat, spatial distribution, and population biology.

Only one study (Hamner, 1978) has statistically examined the natural spatial distribution of adult *T. crocea*. This paper reports on (1) the spatial distribution of *T. gigas* and *T. derasa* at four study sites, and a study of substratum preference at one of these sites, (2) mortality, and (3) an experimental design to test spatial distribution and substratum preference of laboratory-reared juvenile clams.

Materials and Methods

A study site was established in December 1981 on northern Escape reef (Figs. 1 and 2), an outer continental shelf reef and further studied over a two weeks in December 1982 (Fig. 1, inset). The southern end of the reef provides an excellent anchorage surrounded by patch reefs and smaller 'bommies' which rise from a lagoon floor of 7–10 m depth to

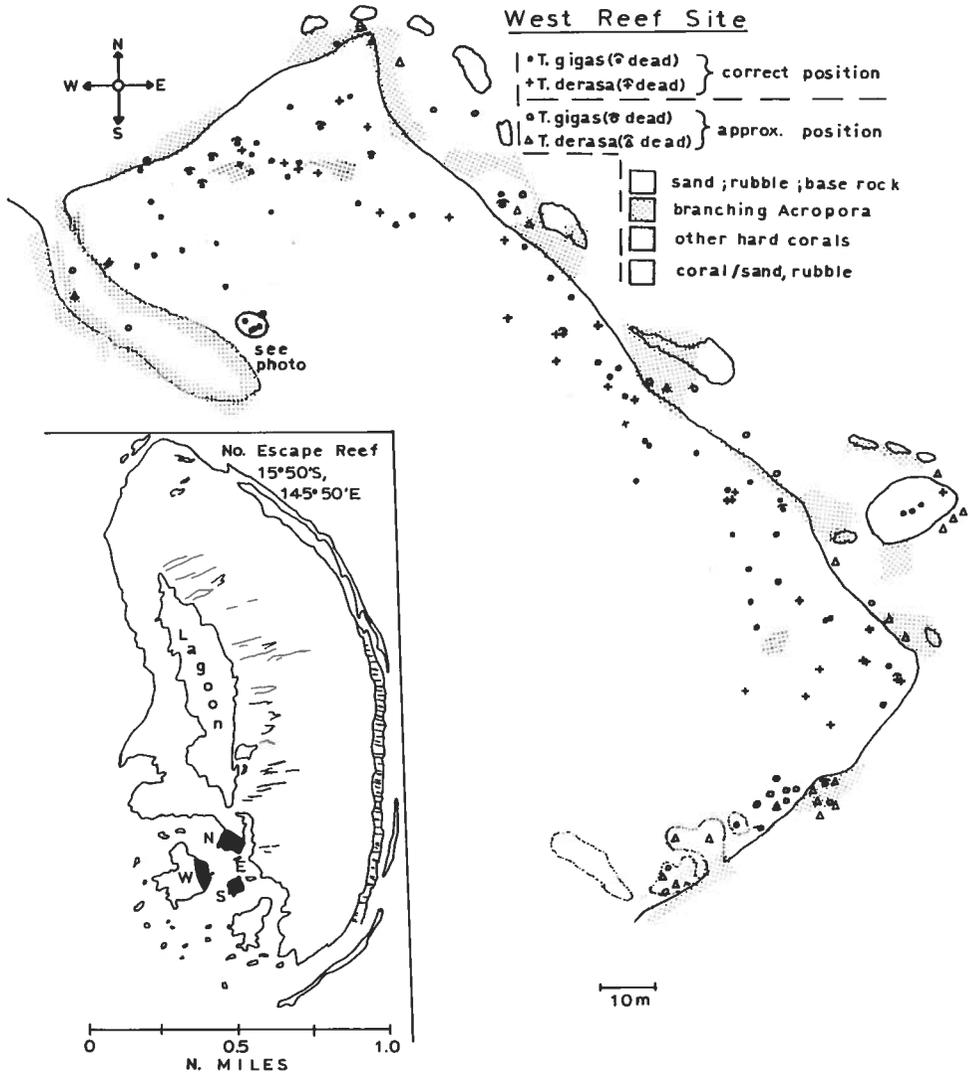


Fig. 1. Map of west reef site, northern Escape reef, showing spatial distribution of the *Tridacna gigas* and *T. derasa*. Inset map of northern Escape reef showing study sites of west-reef (W), north-reef (N), east-bommie (E), and south-reef (S). Four basic substrata types are shown in approximate locations.

less than 1-m below the surface at low tide. Scleractinian corals are abundant in a band along their edges, along with *T. gigas* and *T. derasa*. Both clams are scattered over the lagoon floor, with greater aggregations found on top of the patch reefs and bommies. In 1981 transect tapes were used to map the location of clams. Shell length was measured with large calipers, and water depth and substratum type were recorded. Four substratum types surrounding the clams were recognised and will be here referred to by their assigned

numbers: (1) sand, rubble, base rock; (2) branching *Acropora* spp. coral; (3) other hard coral and soft coral; (4) coral interspersed with sand, rubble patches.

The null hypotheses to be tested here are: (1) clams occur in equal densities on each substratum, and (2) within each substratum clams are randomly distributed.

In 1982 a portion of the 1981 clam population was remapped by measuring exact distances between the centers of each clam and those of its neighbors. At north reef polygonal areas A and B (designated by solid lines) show exact locales of distance mapping (Fig. 2).

The G-test (Sokal and Rohlf, 1969) was employed to test if clams occur in equal density on each substratum. *Tridacna gigas* and *T. derasa* were tested separately and combined. The G-test is similar to the chi-square test but it has theoretical advantages and is simpler for tests of independence.

The Clark and Evans' (1954) nearest neighbor distance (R-test) and its appropriate test of significance (the C-test: Mather, 1947; Clark and Evans', 1954) were used to analyze the spatial distribution within substrata. The 1982 position measurements were used. In the R-test, the ratio of observed mean distance between clams (\bar{r}_A) to the expected mean distance (\bar{r}_E) measures the departure from randomness in a given area, where $R = \bar{r}_A/\bar{r}_E$. R ranges from zero, indicating maximum clumping, through 1, for random distribution, to 2.1491, indicating perfect uniformity. Simberloff (1979) has shown that a circle method is more accurate for determining R than the Clark and Evans' (1954) classical point method for cases where the diameter of the large circle is $\geq 1/2$ of the expected mean nearest neighbor distance. Here the diameter of the large circle was always less than $1/2$ of the expected mean nearest neighbor distance. Thus, the classical point method was sufficiently accurate. The possible nearest neighbor (n.n.) pair combinations of *T. gigas* (Tg) and *T. derasa* (Td) which were analysed by the R-test within substrata will be referred to by the following letters in this report: (A) Tg-Tg; (B) Td-Td; (C) Tg-Td; (D) All pair combinations.

In addition to spatial distribution, population parameters relevant to such distributions were collected. These included size-frequency distributions of both live and dead clam shells from various sites at Escape reef.

Lizard Island—Two sites at Lizard Is. (Fig. 3) were established in late 1983 and mapped for exact inter-clam distances as at Escape reef. The Watson's Bay site comprised 0.55-ha and had 165 live *T. gigas* and *T. derasa*. The Palfrey-South Is. channel site was about 0.73-ha with 100 live clams mapped. Lizard Is. is in the mid-shelf reef zone. Both sites were protected from the prevailing southeasterly winds.

Here, substrata included mainly type (3) at Watson's Bay site and types (2) and (3) at the Palfrey-South Is. channel, but these were not analyzed for spatial patterns as at Escape reef. All n.n. pair combinations were tested during the R-test except (D) (all pair combinations).

The null hypothesis here was that clams were randomly distributed within the study site areas.

Myrmidon Reef—Two study sites were established in January 1984 (see Fig. 4). The area of site 1 was 0.25 ha with 51 live *T. gigas* and *T. derasa*, and site 2 was 0.17 ha with 47

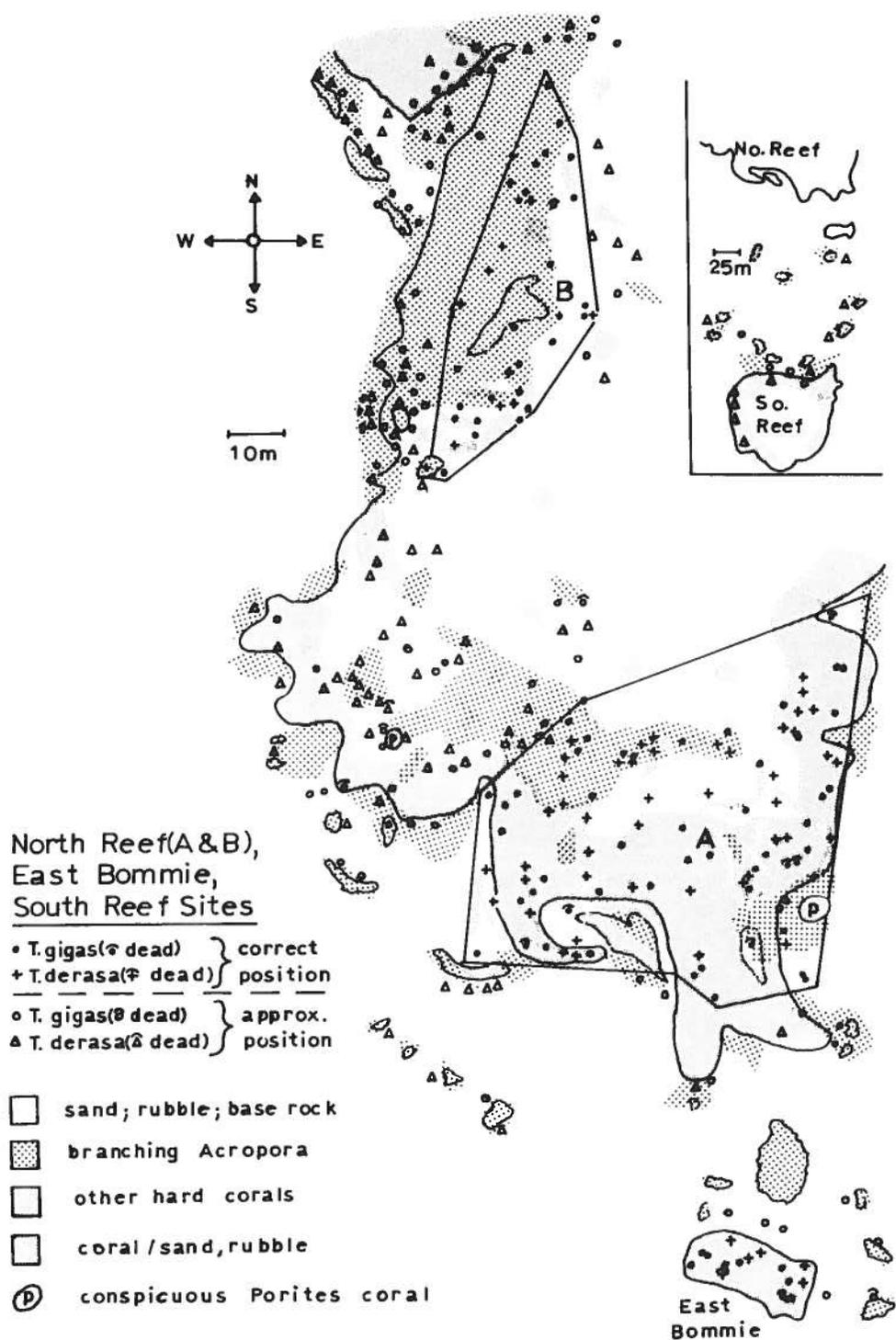


Fig. 2. Map of north-reef site (exact distance measurements at A and B, designated by solid lines), east-bommie site and south-reef site, at northern Escape reef, showing spatial distribution of the *Tridacna gigas* and *T. derasa*. Four basic substrata types are shown in approximate locations.

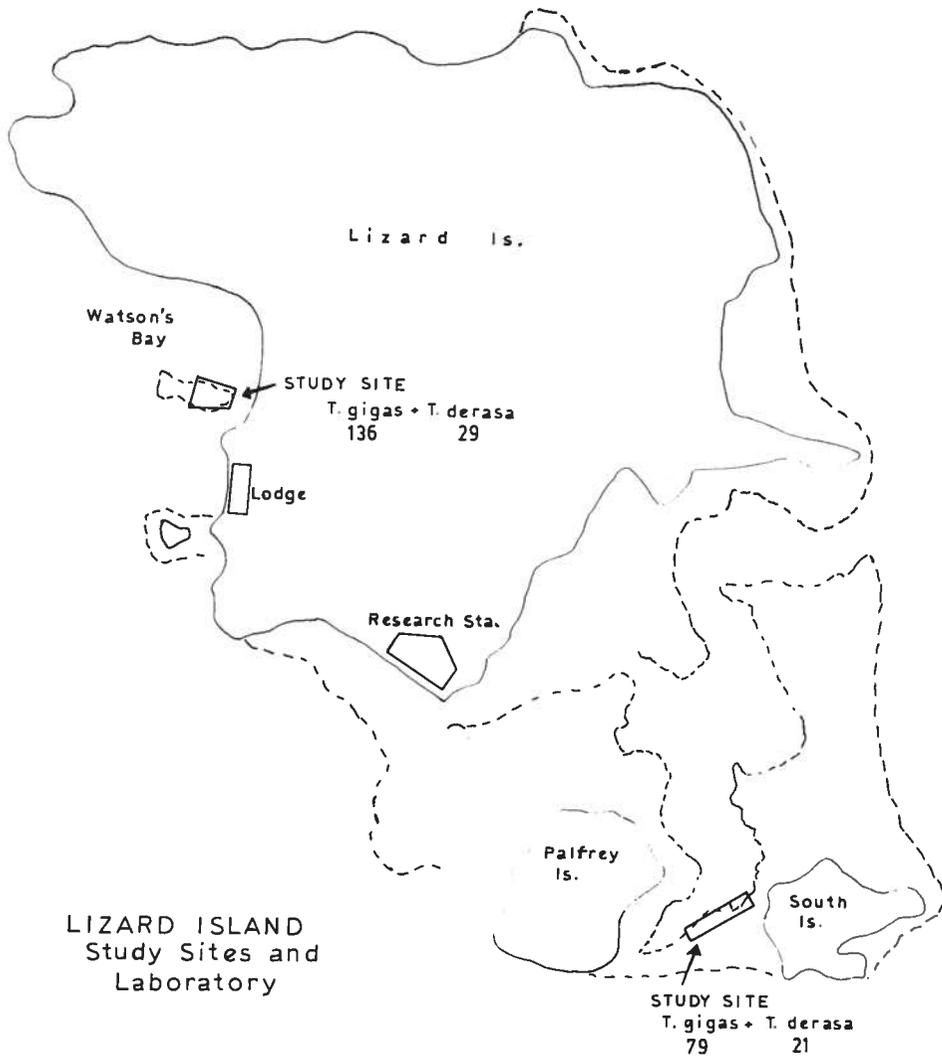


Fig. 3. Map of Lizard Island and lagoon, including two study sites.

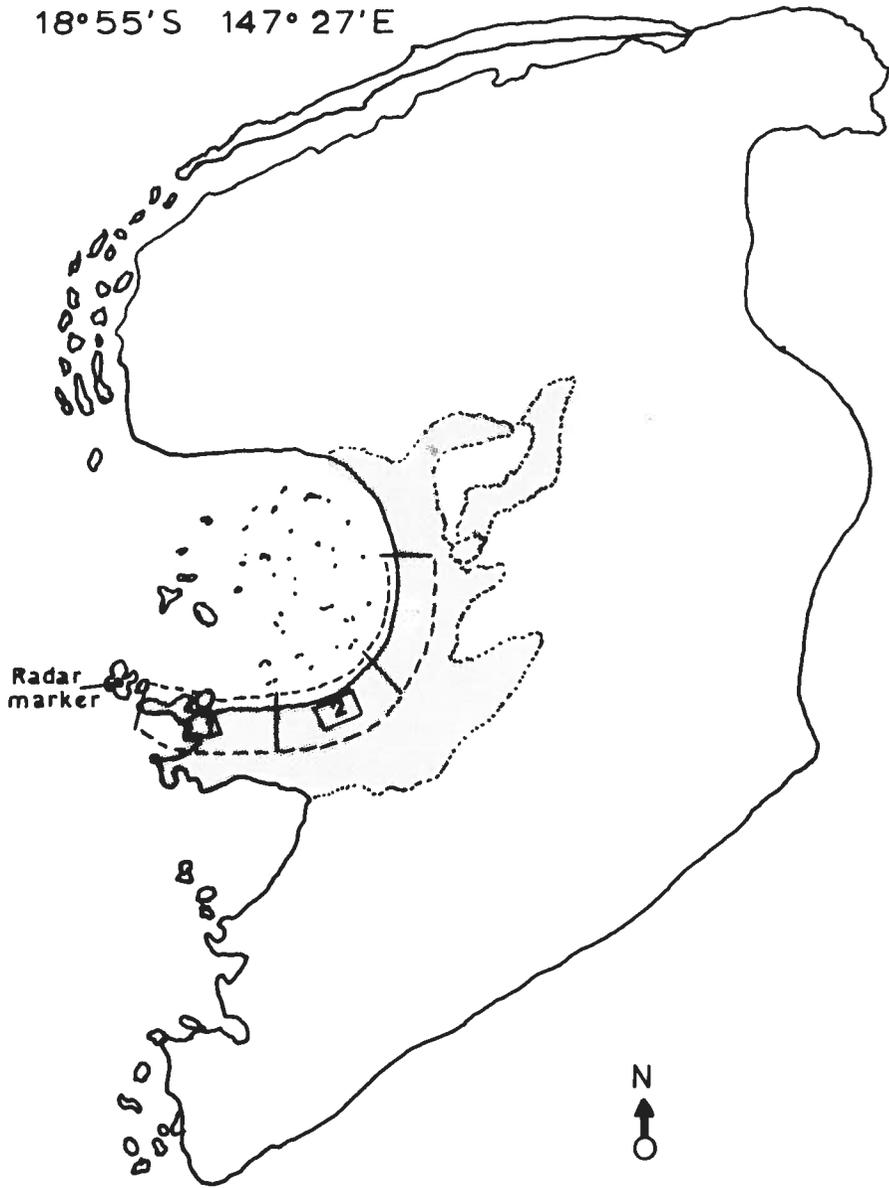
live clams. This outer-shelf reef has oceanic conditions. It was the most southerly reef with large aggregations of *T. gigas* in the survey of 57 reefs (Braley, this issue). Sites 1 and 2 border the 10-m deep lagoon and are mainly in the lee of the prevailing south-easterly winds. Conditions here resemble Escape reef.

Substrata were types (2), (3), and a little of (4) but were not mapped with clams for analysis. All n.n. pair combinations were tested using the R-test.

The null hypothesis was that clams were randomly distributed within the study site areas.

Michaelmas Cay Reef—The small study site (Figs. 5 and 6) established in January 1984 was 0.12-ha with 92 live clams. It borders the sand spit at the SW end of the Cay and was

QUARTERLY STUDY SITE -
MYRMIDON REEF
18°55'S 147° 27'E



□ Reef flat(coral cover)

- 1 Area: 35 T.gigas(Tg), 16 T.derasa(Td)
- 2 Area: 41 Tg, 6 Td

Fig. 4. General map of Myrmidon reef showing area where sites are located.

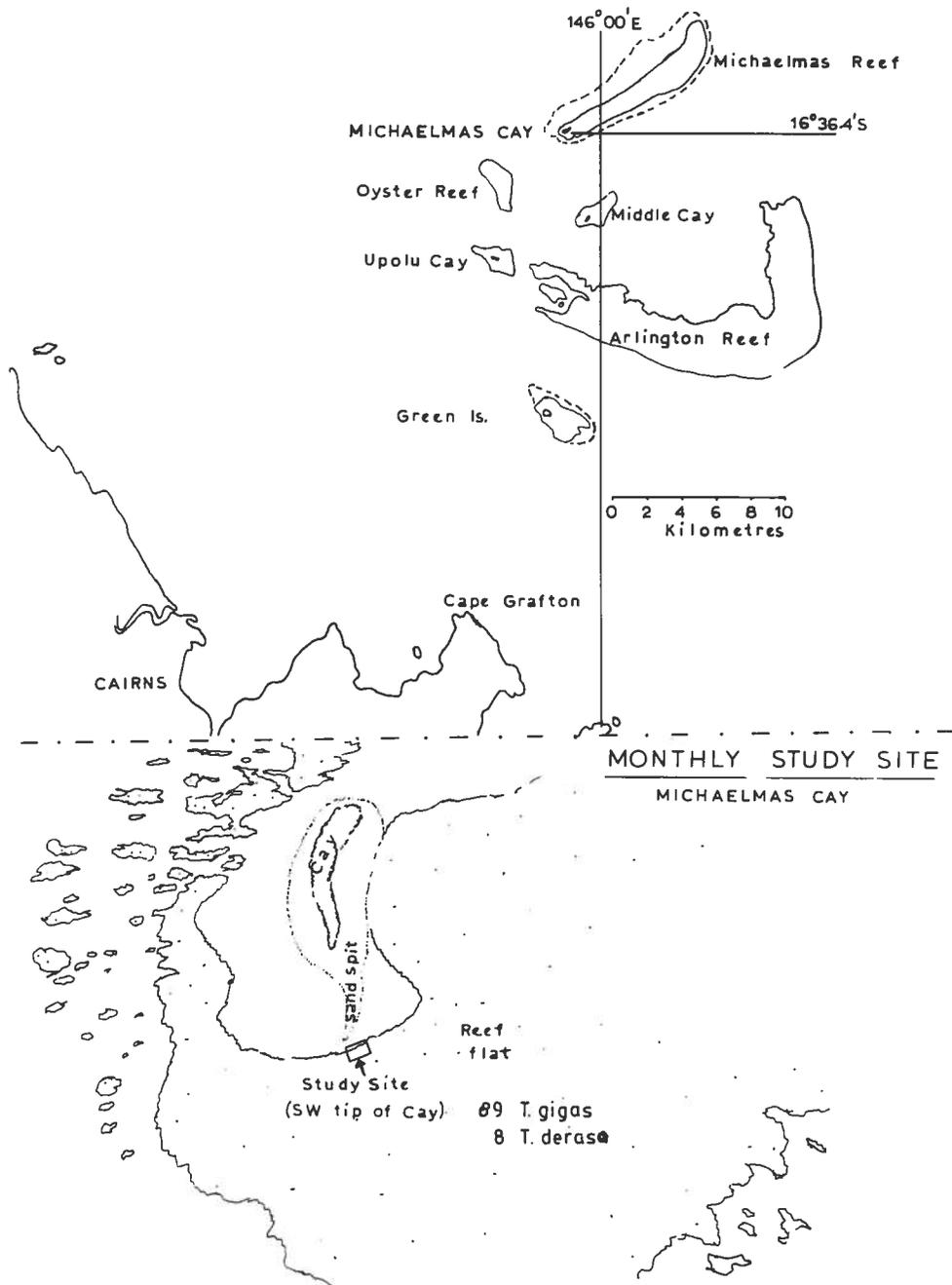


Fig. 5. General map of location of Michaelmas Cay reef.

1000-m from the large clam site of Queensland Fisheries (R. Pearson) established in the mid-1970s to follow growth, mortality and recruitment. During this study the sand spit invaded the area of live coral and clams, burying some of this coral and killing or stressing clams. This is a most dynamic zone.

The substratum here was mostly type (3) with some type (4) but clams were not analysed with substrate. All n.n. pair combinations were analysed by the R-test.

Again, the null hypothesis was that clams were randomly distributed within the study site area.

SUBSTRATUM PREFERENCE AND SPATIAL DISTRIBUTION

Juvenile *Hippopus hippopus* from a late October 1985 spawning at Lizard Is. Research Station (LIRS) were used in an experimental design to support data on substratum preference and spatial distribution of giant clams *in situ*. A grid 10-cm \times 10-cm, marked at 1-cm intervals, was drawn onto the bottom side of a rigid clear plastic surface; on the top side broken pieces of branching *Acropora* sp. and white granite were glued (Aquatapoxy) to the intersection of lines in a uniform distribution (ie, granite, *Acropora*, granite, etc.) (see Fig. 7). Juvenile *H. hippopus* were then set into the centers of each 1-cm \times 1-cm square and left in a pool with flow-through seawater. Positions of clams were recorded on average every 3 days. Four trials were run between 19.12.85 and 29.1.86. The null hypothesis was that juvenile clams showed no preference for any particular substratum. The Chi-square test was used for analysis of distribution.

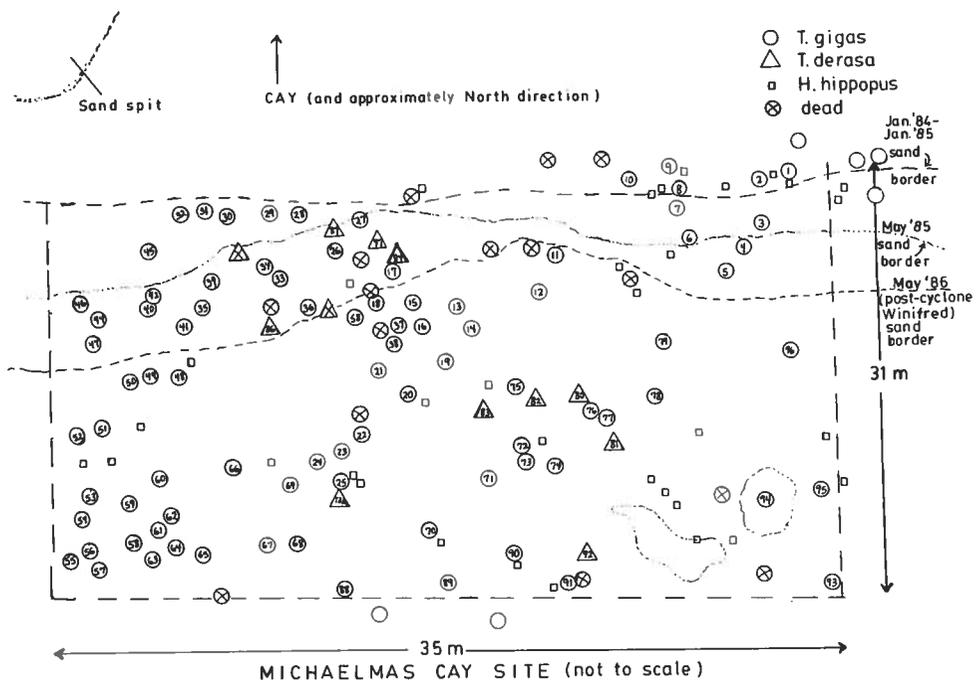


Fig. 6. Map of clams at Michaelmas Cay reef site.

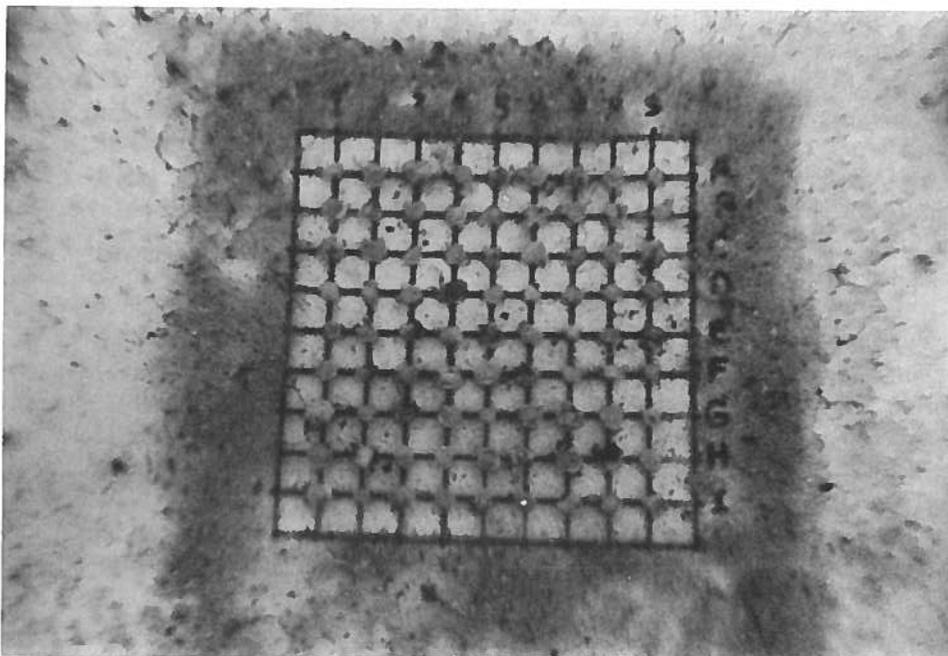


Fig. 7. Photograph of experimental design for testing spatial distribution and substratum preference on *H. hippopus* juveniles. Grid is marked at 1-cm intervals on clear rigid plastic, granite and branching *Acropora* sp. pieces are glued to intersections in a uniform pattern. Here, juveniles can be seen clumped onto some *Acropora* pieces.

Results

SPATIAL DISTRIBUTION

Escape Reef—Maps of the patch reef sites at northern Escape reef show the local-scale spatial distribution of *T. gigas* and *T. derasa* (Figs. 1 and 2). The centers of west-reef and south-reef platforms are slightly higher than the north-reef site and lacked live coral and clams except on their periphery. Maps of clams were produced by direct measurements made underwater, but the 4 substratum types were mapped underwater by eye. Substratum areas were further expressed as percentages of reef sites, shown with numbers of clams on each substratum (Table 1). Most of the combined study site areas were comprised of hard coral (other than branching *Acropora* sp.) and soft coral, followed by a combination of coral interspersed with sand and rubble patches. Branching *Acropora* sp. coral comprised a very small portion at the periphery of west-reef.

The density of clams (combined species) varied significantly from the expected equal density of clams over each substratum ($G=30.49$, $p<0.005$) as did the populations of *T. gigas* and *T. derasa* taken separately ($G=17.98$, $p<0.005$ and $G=45.43$, $p<0.005$, respectively). Densities of clams on substratum (St) 2, branching *Acropora* sp., were consistently higher than expected, showing that this substratum was favored by both species of giant clam (Table 2). The null hypothesis (1), that clams occur on each substratum equally, was rejected.

Table 3 shows the results of the possible n.n. pair combinations of *T. gigas* and *T. derasa* which were analyzed by the R-test within the 4 substrata. Combination (A) was significantly aggregated on St 1 ($p < 0.01$) and St 3 ($p < 0.001$), slightly clumped on St 4 and significantly uniform on St 2 ($p < 0.001$). Combination (B) was slightly aggregated on St 1, decidedly clumped on St 1, decidedly clumped on St 3 and St 4, and slightly uniform on St 2. Combination (C) was clumped on St 1, and very close to random on St 2, 3, and 4. Finally, combination (D) was slightly aggregated on St 1, decidedly uniform on St 2 and close to random for St 3 and 4. Only n.n. pairs of *T. gigas* (A) showed significant aggregation ($p < 0.001$).

For comparison, results of the R-test and C-test of significance by patch reef areas, without regard to substratum type, are shown in Table 4. Combination (A), Tg-Tg, was significantly clumped at 3 of 4 study areas ($p < 0.05$ – $p < 0.001$), while combination (B), Td-Td was significantly clumped at only one area ($p < 0.001$). The significance of distributions other than random for (A), in particular, support the results shown in Table 3 for pooled data at all study sites (see also Table 1 for percentage of various substrata at patch reef areas).

At Escape reef, the low density of clams on St 1 could magnify apparent aggregation but aggregation was found clearly on St 3. Substratum 2, which was highly preferred

Table 1. Approximate percentage of site area shown for each of 4 substrata types, and observed numbers of *Tridacna gigas* (Tg) and *T. derasa* (Td) on each substratum. Four sites and the combined areas of these sites at Escape reef are shown. Substratum types are: (1) sand, rubble, base rock; (2) branching *Acropora* sp.; (3) other hard and soft coral; (4) combination of coral interspersed with sand, rubble patches. Observed numbers of Tg,Td shown below percentages. Density [no. Tg/ha, no. Td/ha].

Sites	Percent site area in Substratum Type			
	(1) (Tg,Td)	(2) (Tg,Td)	(3) (Tg,Td)	(4) (Tg,Td)
W. reef 0.561 ha	13.0% (4,2)	0.9% (6,1)	69.7% (39,21)	16.5% (12,6)
N. reef-A 0.360 ha	21.8% (2,5)	14.2% (11,13)	35.9% (24,26)	28.1% (8,6)
N. reef-B 0.108 ha	9.9% (3,1)	56.2% (11,6)	8.3% (1,0)	25.7% (11,3)
E. bommie 0.022 ha	0	0	100.0% (9,6)	0
Combined sites 1.051 ha	15.4% (9,8) 0.162 ha	11.1% (28,20) 0.117 ha	52.4% (73,53) 0.55 ha	21.0% (31,15) 0.221 ha
Density [no./ha]	[55.6,49.4]	[239.4,170.9]	[132.7,96.4]	[140.3,67.9]

Table 2. The percentage difference from the expected equal density of clams on 4 substrata for *Tridacna gigas*, *T. derasa* and total clams (combined species) at Escape reef. The percentages were derived from G-test results.

Substratum	Percentage difference from expected density of clams		
	<i>T. gigas</i>	<i>T. derasa</i>	<i>T. gigas</i> + <i>T. derasa</i>
1	-58.5	-45.9	-53.4
2	+79.5	+88.7	+82.5
3	-1.2	+5.4	+1.4
4	+4.7	-25.7	-7.6

Table 3. Test for random spatial distribution of *Tridacna gigas* (Tg) and *T. derasa* (Td) on four substratum types (pooled from 3 patch reefs) using Clark-Evans' R on nearest neighbor (n.n.) distance (Clark and Evans, 1954) at Escape reef. N = number nearest neighbor measurements, C = standard variate of normal curve. There is perfect uniformity at R = 2.1491, uniform for R > 1, random when R = 1, clumped or aggregated when R < 1. Combinations of possible nearest neighbor pairs are (A) Tg-Tg; (B) Td-Td; (C) Tg-Td; (D) All pair combinations. For description of substrata 1-4 see Table 1.

Significance levels are: ns- $p > 0.05$, *- $p < 0.05$, **- $p < 0.01$, ***- $p < 0.001$.

Substrata	Combina- tions n.n.	Area (m ²)	N	R	C	Probability of greater difference between expected and observed mean distances to n.n.	Significance level
1	(A)	1622	8	0.544	2.467	0.014	**
	(B)	1622	4	0.807	0.737	0.461	ns
	(C)	1622	5	0.641	1.536	0.124	ns
	(D)	1622	17	0.817	1.441	0.149	ns
2	(A)	1171	19	1.405	3.374	0.0008	***
	(B)	1171	9	1.129	0.738	0.460	ns
	(C)	1171	19	0.996	0.031	0.971	ns
	(D)	1171	47	1.481	6.309	0.000002	***
3	(A)	5505	50	0.684	4.277	0.00002	***
	(B)	5505	24	0.559	4.136	0.0004	***
	(C)	5505	54	1.016	0.224	0.823	ns
	(D)	5505	126	0.967	0.712	0.483	ns
4	(A)	2213	16	0.876	0.949	0.343	ns
	(B)	2213	7	0.621	1.918	0.056	ns
	(C)	2213	20	0.989	0.091	0.278	ns
	(D)	2213	43	1.034	0.429	0.667	ns

(Table 2), showed no clumping by any n.n. combination of clam pairs. A clump of 4 *T. gigas* which were circled in Fig. 1 ('see photo' label) is shown in Fig. 8. Other small aggregations such as this are discernible on the maps (Figs. 1 and 2) but are not typical on less densely populated reefs. The null hypothesis (2), that within each substratum, clams are randomly distributed, is rejected for 3 of 4 substrata for Tg-Tg but for only 1 of 4 substrata for Td-Td. *T. gigas* shows a distribution other than random more often than *T. derasa*.

Lizard Island—Results of the R-test and C-test of significance, without regard to substratum type, are shown in Table 5. Combinations (A), (B), and (C) were highly significantly aggregated for both Watson's Bay and Palfrey-South Is. channel sites ($p < 0.001$). The main concentrations of clams was along the channel edge at the Palfrey-South site. The study area included reef flat which had few clams, thus affecting the analysis of spatial distribution. If the Palfrey-South area were reduced by 50% in the analysis, the distri-

Table 4. Test for random spatial distribution of *Tridacna gigas* (Tg) and *T. derasa* (Td) at 4 patch reef areas on Escape reef, using Clark and Evans (1954) R on nearest neighbor (n.n.) distance.

N = number of nearest neighbor measurements, C = standard variate of the normal curve.

Distribution is uniform for $R > 1$, random for $R = 1$, clumped for $R < 1$.

Significance levels are: ns- $p > 0.05$, *- $p < 0.05$, **- $p < 0.01$, ***- $p < 0.001$.

Combinations A-D as per Table 3.

Site	Combinations	Area (m ²)	N	R	C	Probability of greater difference between expected and observed mean distances to n.n.	Significance level
West reef	(A)	4542	42	0.841	2.168	0.030	*
	(B)	4542	13	0.744	0.518	0.604	ns
	(C)	4542	36	1.016	0.185	0.045	*
	(D)	4542	91	1.048	0.872	0.936	ns
North reef-A	(A)	3600	27	0.636	3.619	0.000	***
	(B)	3600	25	0.651	4.479	0.000	***
	(C)	3600	43	0.978	0.280	0.779	ns
	(D)	3600	95	0.969	0.572	0.567	ns
North reef-B	(A)	1080	21	1.144	1.266	0.206	ns
	(B)	1080	4	1.201	0.769	0.442	ns
	(C)	1080	12	0.753	1.639	0.110	ns
	(D)	1080	37	1.329	3.831	0.000	***
East bommie	(A)	220	7	0.535	2.356	0.018	*
	(B)	220	2	0.776	0.605	0.545	ns
	(C)	220	6	1.236	1.106	0.269	ns
	(D)	220	15	1.068	0.258	0.796	ns

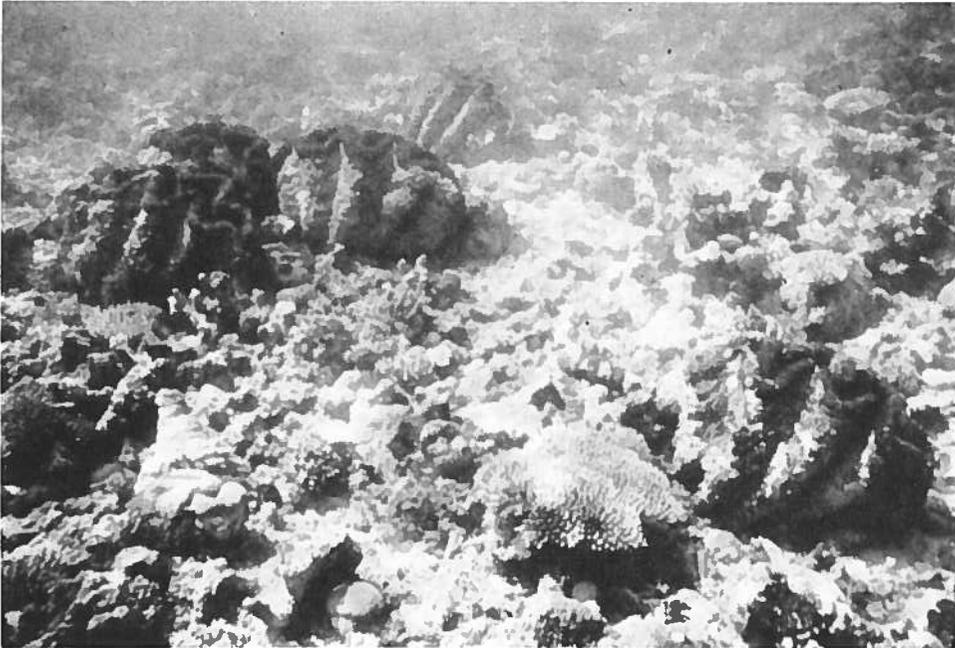


Fig. 8. A clump of 5 *Tridacna gigas* indicated on the map of west reef (as 'see photo,' Fig. 1). Each clam is about 1-m shell length.

bution would still be clumped but at a lower level of significance (ie., combination (A), $R=0.8549a$, $p<0.05$). The Watson's Bay site does not have this inherent problem because it includes much of a whole patch reef.

Myrmidon Reef—Without regard to substratum type, results of the R-test and C-test of significance are shown in Table 6. A clumping distribution was highly significant only for combination (A) Tg-Tg, and only at site 1 ($p<0.001$). Combination (B) at both sites was aggregated but was not significant, and (D) was also clumped at site 1. At site 2 combination (A) was nearly random while (C) and (D) were random to slightly uniform. The highly significant clumping of Tg-Tg at site 1 may have been influenced by bottom topography. While site 2 was coral covered reef flat, site 1 has ridges of coral limestone meandering through low flat areas covered in branching *Acropora* sp., other corals and some sand.

Michaelmas Cay Reef—Results of the R-test and C-test of significance, without regard to substratum type, are shown in Table 7. Clumping was significant ($p<0.05$) in combination (A), Tg-Tg. No Td-Td pairs were nearest neighbors, while combination (C), Tg-Td, was highly significantly uniform ($p<0.001$), and (D) was nearly random but not significant. The aggregation of Tg-Tg was somewhat expected as 84 of the 92 live clams were *T. gigas*.

Table 5. Test for random spatial distribution of *Tridacna gigas* and *T. derasa* at two sites surrounding Lizard Is., using Clark and Evans (1954) R on nearest neighbor (n.n.) distance.

N = number of n. n. measurements, C = standard variate of the normal curve.

Distribution is uniform for $R > 1$, random for $R = 1$, clumped for $R < 1$.

Significance levels are: ns- $p > 0.05$, *- $p < 0.05$, **- $p < 0.01$, ***- $p < 0.001$.

Combinations A-C as per Table 3.

Site	Combinations	Area (m ²)	N	R	C	Probability of greater difference between expected and observed mean distances to n.n.	Significance level
Watson Bay	(A)	5540	132	0.748	5.534	0.000	***
	(B)	5540	9	0.246	4.329	0.00002	***
	(C)	5540	23	0.219	7.167	0.000	***
Palfrey-South	(A)	7300	78	0.604	6.684	0.000	***
	(B)	7300	6	0.270	3.422	0.0006	***
	(C)	7300	14	0.073	6.650	0.000	***

Table 6. Test for random spatial distribution of *Tridacna gigas* and *T. derasa* at two sites on Myrmidon reef, using Clark and Evans (1954) R on nearest neighbor (n.n.) distance. N = number of n.n. measurements,

C = standard variate of the normal curve.

Distribution is uniform for $R > 1$, random for $R = 1$, clumped for $R < 1$.

Significance levels are: ns- $p > 0.05$, *- $p < 0.05$, **- $p < 0.01$, ***- $p < 0.001$.

Combinations A-D as per Table 3.

Site	Combinations	Area (m ²)	N	R	C	Probability of greater difference between expected and observed mean distances to n.n.	Significance level
1	(A)	2500	33	0.566	4.796	0.000002	***
	(B)	2500	7	0.637	1.834	0.067	ns
	(C)	2500	11	1.119	0.755	0.449	ns
	(D)	2500	53	0.882	1.647	0.099	ns
2	(A)	1728	36	1.091	1.046	0.296	ns
	(B)	1728	3	0.416	1.934	0.053	ns
	(C)	1728	8	1.220	1.193	0.233	ns
	(D)	1728	47	1.177	2.320	0.020	*

Table 7. Test for random spatial distribution of *Tridacna gigas* and *T. derasa* at Michaelmas Cay reef, using Clark and Evans (1954) R on nearest neighbor (n.n.) distance. N = number of n.n. measurements,

C = standard variate of the normal curve.

Distribution is uniform for $R > 1$, random for $R = 1$, clumped for $R < 1$.

Significance levels are: ns- $p > 0.05$, *- $p < 0.05$, **- $p < 0.01$, ***- $p < 0.001$.

Combinations A–C as per Table 3, but D here includes all dead/live Tg-Td.

Combinations	Area (m ²)	N	R	C	Probability of greater difference between expected and observed mean distances to n.n.	Significance level
(A)	1200	84	0.859	2.467	0.017	*
(B)	1200	0	—	—	—	—
(C)	1200	9	1.818	4.696	0.000002	***
(D)	1200	97	0.996	0.077	0.939	ns

POPULATION PARAMETERS

A census of the giant clam populations was taken for each of the patch reef studies at northern Escape reef (Table 8). In the total population, 7.9% of *T. gigas* and 1.9% of *T. derasa* were dead (empty shell). The size-frequency distributions of 53 dead *T. gigas* and 20 dead *T. derasa* found at Escape reef sites and adjacent areas (Fig. 9) were similar to the distributions of live clams (Fig. 10), although the largest size classes of *T. derasa* appear to be under-represented among dead individuals.

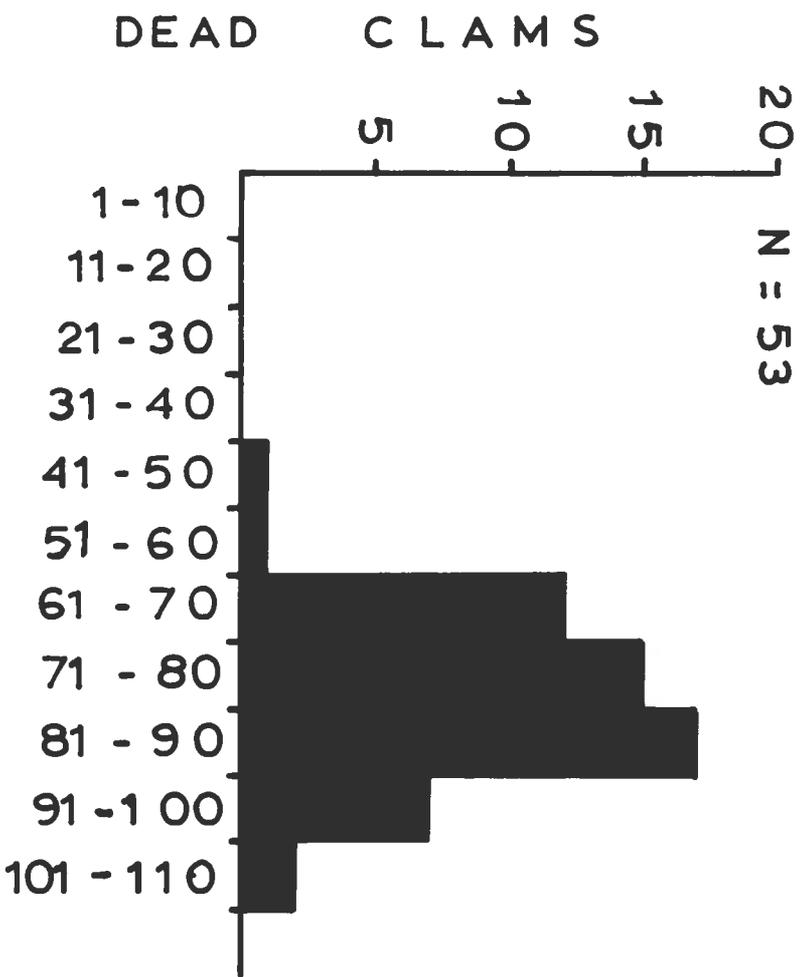
Mortality rates of clams at all study sites are shown in Table 9. The mean mortality of clams at combined sites was $1.65 \pm 0.54\%$ (s.d.) for *T. gigas* and $2.07 \pm 2.59\%$ for *T. derasa*: these represent natural mortality. Other clams died after biopsy sampling and there was a mass mortality at Lizard Is. in mid-1985: these were not included (see Table 9). At Escape reef, there were 7 nearest neighbor pairs of which both members were dead *T. gigas*. The shell lengths of the two individuals in each of these pairs were very similar (within $7.3 \pm 2.7\%$ of one another).

SUBSTRATUM PREFERENCE, SPATIAL DISTRIBUTION

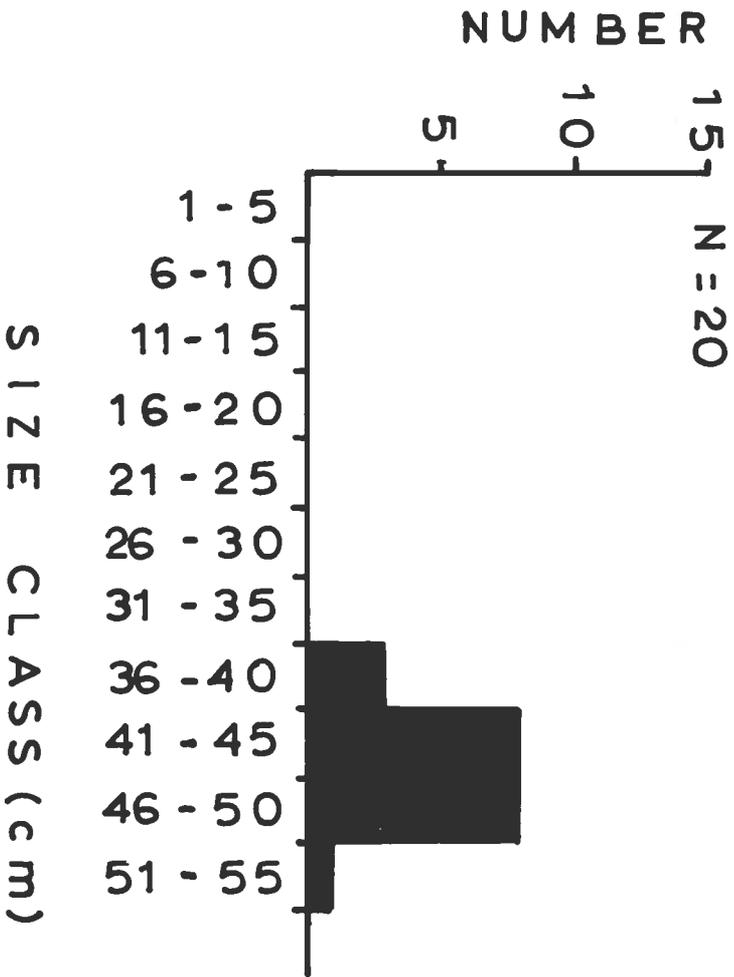
Results of the 5 trials and individual measurement dates are shown in Table 10 and Fig. 11. Chi-square values for all measurement dates were highly significant ($p < 0.005$), thus rejecting the null hypothesis that juvenile clams showed no preference for any particular substratum when offered granite, branching *Acropora* sp., or clear rigid plastic with sparse sand grains. Although areas of each substratum were not equal (ie., granite—11.5%; branching *Acropora* sp.—11.5%, plastic + sparse sand—77%) the expected equal numbers of clams selecting the 3 substrata was rejected. Had expected numbers of clams been set as proportional to the areas of substrata, the chi-square values would have been higher but the significance the same.

In the initial trial, almost 70% of *H. hippopus* juveniles moved both onto the plastic

A *Tridacna gigas*



B *Tridacna derasa*



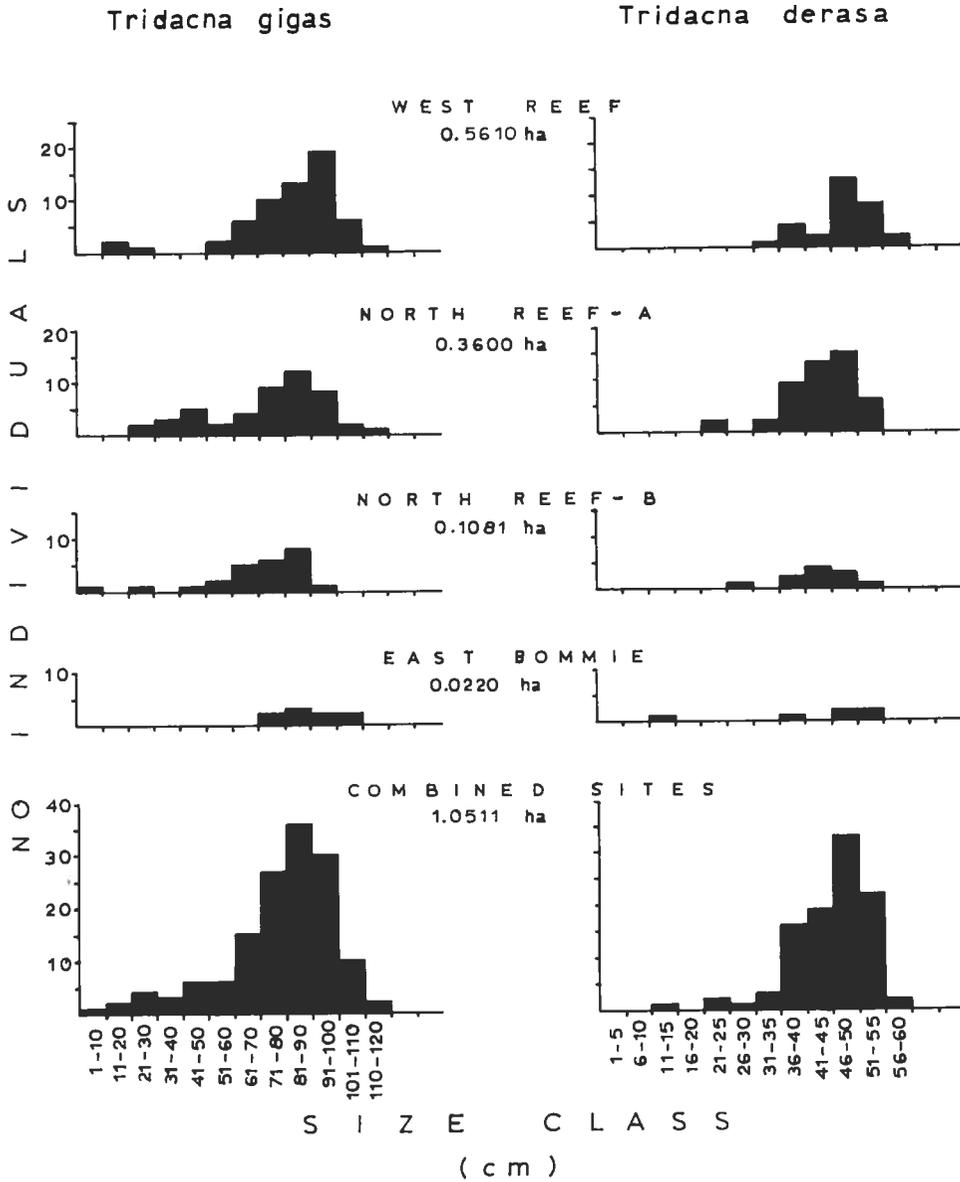


Fig. 9. Size-frequency distributions of A: dead *Tridacna gigas*, and B: dead *T. derasa*, both at northern Escape reef.

Fig. 10. Size-frequency distributions of the *Tridacna gigas* and *T. derasa* at study site area northern Escape reef.

Table 8. Census of *Tridacna gigas* and *T. derasa* populations at Escape reef sites. Total clam populations were censused in 1981, while in 1982 exact distance measurements were made on a subset of the 1981 population.

1981: Site	<i>T. gigas</i>			<i>T. derasa</i>		
	live	dead	% dead	live	dead	% dead
West reef 1.62 ha	87	9	9.4	55	2	3.5
North reef 1.2 ha	148	9	5.7	138	1	0.7
East bommie 0.042 ha	16	4	20.0	6	1	14.3
South reef 0.51 ha	3	0	0	6	0	0
Total	254	22	7.9	205	4	1.9
1982: (subset of 1981)						
West reef 0.561 ha	61	7	11.5	30	2	6.2
North reef-A 0.36 ha	45	5	10.0	50	0	0
North reef-B 0.108 ha	26	1	3.7	11	0	0
East bommie 0.022 ha	9	3	25.0	6	1	14.3
Total	141	16	10.2	97	3	3.0

and outside of the grid area, while about 30% of juveniles settled onto 45% of the available *Acropora* pieces and a rare few juveniles on granite (Fig. 11). From trial 2 through trial 4 granite was selected as a settlement substratum by about 15–20% of clam juveniles, *Acropora* was selected by 55–80% of the clam juveniles, and plastic was selected by 2–25% of clam juveniles. The percentages of total *Acropora* and granite pieces on which clams were settled are listed above each measurement date on Fig. 11.

These juvenile *H. hippopus* were clumped throughout the period of the trials according to the coefficient of dispersion (Table 11). However, the chi-square values were significant ($p < 0.005$) between 21.12.85 to 29.1.86, while the first 3 dates of measurement (21.12–30.12.85) were not significantly different from the Poisson distribution.

Table 9. Mortality rates of *T. gigas* (Tg) and *T. derasa* (Td) at study sites.

Site	Total live clams at start	Percent annual mortality	Comments
Escape	254 Tg	2.0	
	205 Td	1.4	
Lizard Is. Watson Bay	136 Tg	0.84	All pre-1985 mass mortalities 1.97% with biopsy deaths
	29 Td	0.0	
Palfrey-South	79 Tg	1.44	5.44% with biopsy deaths
	22 Td	0.0	
Myrmidon	76 Tg	1.5	2.25% with biopsy deaths 5.1% with biopsy deaths
	22 Td	0.0	
Michaelmas	89 Tg	2.25	18.8% with biopsy death + missing clam
	8 Td	6.25	

Table 10. Results of chi-square test on substratum preference of *H. hippopus* juveniles (from October 1985 spawning, LIRS). Null hypothesis: juvenile clams show no preference for any particular substratum when offered granite, branching *Acropora* spp. pieces or plastic with sparse sand grains. Expected juvenile settlement on each substratum = 33.3%. Actual total area of each substratum: granite—11.5%, *Acropora*—11.5%, plastic + sparse sand—77%. Mean shell length and weights of juvenile *H. hippopus* on 17.12.85 were 1.233 ± 0.22 mm and 0.00075 ± 0.00081 g.

Date	Trial #	Chi-square value	Probability	R (reject) or A (accept) null hypothesis
21.12.85	1	43.63	$p < 0.005$	R
27.12.85	1	71.73	$p < 0.005$	R
30.12.85	2	60.6	$p < 0.005$	R
2.01.86	2	51.6	$p < 0.005$	R
5.01.86	2	19.48	$p < 0.005$	R
8.01.86	3	33.0	$p < 0.005$	R
11.01.86	3	68.31	$p < 0.005$	R
14.01.86	3	95.97	$p < 0.005$	R
17.01.86	4	41.68	$p < 0.005$	R
20.01.86	4	78.86	$p < 0.005$	R
23.01.86	4	86.1	$p < 0.005$	R
26.01.86	4	44.45	$p < 0.005$	R
29.01.86	4	57.42	$p < 0.005$	R

Conclusion: *H. hippopus* juveniles actively seek a particular substratum.

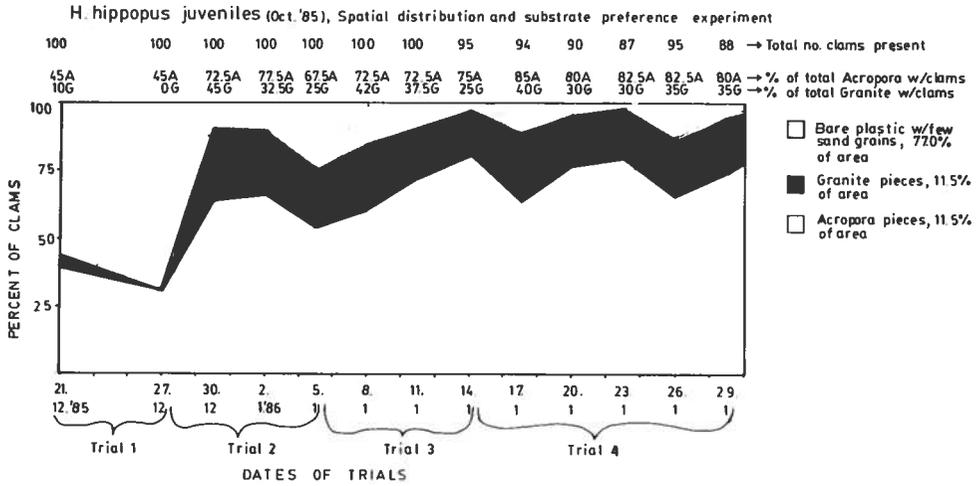


Fig. 11. Results of spatial distribution and substratum preference experiment on juvenile *H. hippopus* at LIRS. Three substrata show the proportion of clams that settled on them at different measurement dates. The percentage of available pieces of *Acropora* and granite which have clams on them at each measurement are shown above the graph.

Table 11. Results of chi-square test on number of *H. hippopus* juveniles found on single pieces of branching *Acropora* spp. substratum. Null hypothesis: Distribution of juvenile *H. hippopus* on a given substratum does not differ significantly from a Poisson distribution. The coefficient of dispersion ($CD = s^2/Y$) is near to 1 for Poisson distributions, >1 for clumped, and <1 for repulsed distributions (Sokal and Rohlf, 1969).

Date	Chi-square value	CD value/distribution	Probability	R (reject) or A (accept) null hypothesis
21.12.85	4.845	8.13/clumped	$p > 0.05$	A
27.12.85	1.6	8.29/clumped	$p > 0.05$	A
30.12.85	6.484	20.15/clumped	$p > 0.05$	A
21.12.85-29.01.86	37.57	168.5/clumped	$p < 0.005$	R

Discussion

Tridacna gigas and *T. derasa* occurred preferentially amongst branching *Acropora* spp. (substratum 2, St 2) and other hard corals (St 3). The extreme aggregation pattern of *T. crocea* ($>100/m^2$) on the surface of coral heads (Hamner, 1978) suggests a gregarious settling response or extreme larval abundance with preferential survival. The exhalant seawater of adult clams may stimulate competent larvae to settle or perhaps larvae actively settle near adult pseudofaeces.

Clumps of *T. gigas* or *T. derasa* were found occasionally on sand, coral rubble or bare base rock, generally close to beds of branching *Acropora* spp. Skeletal growth rates

of the branching *Acropora formosa* have been found to be 8 cm/yr at shallow depth (5-m) and 12 cm/yr at mid-depth (10-m), with greater branch thickness at shallow depth (Oliver *et al.*, 1983). *Acropora* spp. beds can be damaged heavily by storm waves, and new beds may grow quickly from fragmented branches (Highsmith, 1982) upon substrata which would be otherwise unsuitable for the survival of post-larval and juvenile tridacnids. Likewise, branching *Acropora* spp. beds containing clams may be destroyed, thus leaving surviving groups of clams on sand, coral rubble or base rock. This dynamic process would continually provide new preferred substrata or at least substrata with a high survival potential (branching *Acropora* sp.) on which competent clam larvae could settle. Movement of the sand spit over a portion of the study site at Michaelmas Cay (Fig. 6) is a good example of the changes that can occur on a reef where giant clams are located.

At all study sites *T. gigas* and *T. derasa* clumped with individuals of their own species. The level of significance and this tendency was more pronounced for *T. gigas* than *T. derasa*. This may have been a result of the larger population of *T. gigas* at all sites than *T. derasa*.

Predation and Mortality

Fish eat small tridacnid clams (Heslinga *et al.*, 1984), and I have observed an estimated 15% of shells of dead *T. gigas* and *T. derasa* up to 20-cm in length with characteristic adjacent double 'bite' marks on one edge of one valve. Balistids or tetrodontids are implicated (W. Starck, pers. comm., 1983). Therefore, this close clam/coral association (also noted by Hardy and Hardy, 1969; Hester and Jones, 1974) may serve as a refuge.

The dead clam nearest neighbor pairs were of similar size (hence, age), perhaps part of a cohort that died together, or diseases may have killed nearest neighbors rather than more distant individuals.

In nature clams prefer certain habitats and they are gregarious: these experiments on substratum preference behaviour are consistent with this. The juvenile clams in this experiment were less than two months old and observably mobile within a small grid. Branching *Acropora* sp. pieces were preferred over granite pieces and clumping of up to 7 juveniles on a single piece of *Acropora* occurred.

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