

# Spatial pattern in the abundance and structure of mollusc populations in the soft sediments of a coral reef lagoon

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**ABSTRACT:** A hierarchical sampling programme, carried out during October 1985, encompassed 4 spatial scales: broad habitat zones of different depth and sediment composition; random 1 ha locations within zones; random 25 m<sup>2</sup> sites within locations; and random 0.01 m<sup>2</sup> air-lifted cores from each site. Of 69 species collected, we describe the patterns of distribution of the 10 most common. Spatial differences in their abundances were observed at all scales, but most of the variation (50 to 85 %) occurred at the broadest scale – between zones. Zones of peak abundance differed among species, some being most abundant in deep, fine-sediment habitats, e.g. *Tellina* cf. *myaformis*; some in deep, intermediate-sediment habitats, e.g. *Exotica* cf. *virgulata* and *Pupa nitidula*; others in shallow, coarse-sediments to the north, e.g. *Tellina obtusalis*, *Umboonium guamensis*; and still others in the shallow sediments to the south, e.g. *Rhinoclavis aspera*. In terms of population structure, tellinid bivalves reached greatest sizes in the coarse shallow zones. At the broadest scale, zones did not appear to represent homogeneous assemblages, due largely to a variable response of species to the environment at a location scale. Overall, species richness tended to increase from fine to coarse sediment, except at the very shallow coarse sediments in the southern zone, where low numbers of species were found.

## INTRODUCTION

A focus upon organisms either attached to, or moving over, hard substrata forms the basis of most of the ideas about the factors affecting abundance and diversity on coral reefs (see reviews by Sale 1980, Connell & Keough 1985, Huston 1985, Doherty & Williams 1988). However, lagoons and back-reef regions can be predominantly made up of carbonate sands and gravel (Thomassin 1978). A cursory comparison between reefs and these uniform and superficially barren habitats might suggest that they are an unimportant part of the reef system. On the contrary, recent investigations into the biota of tropical soft sediments indicate abundant and diverse assemblages, including molluscs, crustaceans, echinoderms, polychaetes and nematodes (e.g.

Fishelson 1971, Taylor 1971, McWilliam et al. 1981, Jones 1984, Suchanek & Colin 1986, Jacoby & Greenwood 1988). These invertebrates fall prey to a variety of teleost and elasmobranch fishes which forage over the sand (Alheit 1981, Alheit & Scheibel 1982, Suchanek & Colin 1986, St John et al. 1989). These trophic interactions and the role played by soft sediments in coral reef systems are potentially important, yet poorly understood.

General descriptions of species-habitat relationships in tropical soft sediments, and data on the abundances of broad and arbitrary categories, such as macrofauna or meiofauna, are readily available (e.g. Fishelson 1971, Thomassin et al. 1976, Thomassin 1978, Alheit 1981, Alheit & Scheibel 1982, Thomassin et al. 1982, Colin 1986, Grelet et al. 1987). However, a quantitative description of pattern is a necessary basis for assessing the importance of ecological processes which limit populations and structure assemblages (Choat 1982, Andrew & Mapstone 1987). A quantitative approach has only recently been applied to tropical soft sediment communities (Hughes & Gamble 1977, Faubel 1984, Jones 1984, Suchanek & Colin 1986, Jacoby & Greenwood 1988, Riddle 1988). Molluscs may be the most

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important group of invertebrates in these habitats, both in terms of biomass and as a source of food for teleosts. In contrast to the wealth of information on the distribution and abundance of molluscs inhabiting soft-sediments in temperate waters (see Gray 1974, 1981), there are few such studies on equivalent tropical species (but see Taylor 1971). Investigations into the ecological role played by molluscs must be founded upon fundamental information on the species present, their distribution and abundance and the relationship between abundance and features of the habitat.

The main aim of this investigation was to describe spatial patterns in the distribution, abundance and structure of mollusc populations inhabiting the soft sediments of One Tree Lagoon, Great Barrier Reef, Australia. Further, we wished to identify the spatial scales at which these populations respond to the lagoon environment as a preliminary step toward examining the impact of fish predation. The effects of changing the scale of focus, when describing patterns or identifying causal processes, is a major issue in contemporary ecology (see Ogden & Ebersole 1981, Dayton & Tegner 1984, Andrew & Mapstone 1987 for discussions relating to marine systems). An arbitrary decision to focus on any one scale could lead to a complete failure to detect the patterns of most importance to the majority of the species. Given no prior information on these mollusc assemblages, we chose 4 scales, from a broad scale (10 km<sup>2</sup>) encompassing the major habitat zones within the lagoon, down to a fine scale (0.1 m<sup>2</sup>), represented by replicate cores. Quantifying the variance explained by each level in this hierarchy enabled us to identify the scales of most importance, in terms of the magnitude of changes in density and the size-structure of populations.

Spatial patterns in the structure of soft sediment assemblages in temperate regions have primarily been correlated with changes in depth and sediment characteristics (reviewed by Gray 1974, 1981, Whitlatch 1981). Recent studies in tropical systems have detected the same sorts of trends (Jones 1984, Grelet et al. 1987). In view of this, sampling at the largest spatial scale was structured in relation to broad zones, distinguished on the basis of depth and sediment characteristics. In addition, measurements of depth and sediment grain size-frequency distributions were made at all sites sampled, to examine the numerical responses of individual species to these environmental factors at each scale.

## METHODS

This study was carried out during October 1985 in the main lagoon of One Tree Reef, near the southern limit of the Great Barrier Reef (23° 30' S, 152° 06' E). This lagoon is ca 10 km<sup>2</sup> in area, and reaches a depth of 7 m. The

lagoon floor primarily consists of carbonate sediments, with the remainder being made up of isolated patch-reefs and reticulated reef structures. Sediments of differing coarseness occur in almost concentric bands within the lagoon, with the coarse sand found in shallow water near the perimeter and the finest sediment in the deepest, central region (Davies et al. 1976, Johnstone et al. 1988). For the purposes of sampling, the lagoon was stratified into 5 zones, which could be distinguished on the basis of geographic location, depth and sediment characteristics (Fig. 1). The North Shallow zone (NS) was characterized by relatively coarse sediments (> 250 µm) and reached a mean depth of 2.3 m. South Shallow (SS) had similar sediment composition, but only reached a mean depth of 0.6 m. The Central zone (CN), with an average depth of 3.5 m, was made up of relatively fine sediments (< 125 µm). North Deep (ND) and South Deep (SD) zones consisted of sediments of intermediate coarseness, the average depths being 2.8 m at South Deep and 4.2 m at North Deep.

A pilot survey was conducted at 2 locations in the North deep zone to ascertain to what depth sediment cores needed to be taken to sample molluscs. We wished to determine the appropriate sample unit size necessary to obtain a level of precision of 0.15 given 4 replicate cores. This was obtained following the procedures suggested by Andrew & Mapstone (1988). The abundances of common molluscs were compared by means of circular cores taken at depths of 5 and 10 cm. We found no significant differences in estimates of mean density for any of the common species, therefore the 5 cm depth was considered adequate to sample these sub-surface dwelling species. In the shallow zones, the 5 cm layer of sediment was often the full extent of soft substratum above a compacted rubble layer. Two core sizes were examined, 0.03 and 0.06 m<sup>2</sup>. The data suggested that a core size slightly larger than 0.06 m<sup>2</sup> was necessary to achieve the desired precision for the more abundant species. A core size of 0.1 m<sup>2</sup> allowed us to obtain this precision but we recognized that this may have been too small to get meaningful estimates for rarer species. A comparison of the proportions of molluscs collected in nested 3, 2 and 1 mm sieves, indicated that the finest sieve was necessary to retain the smallest size classes. This mesh should retain more than the 1.4 mm mesh recommended by Thomas-sin (1978) for tropical soft sediments.

A hierarchical sampling design was employed to describe spatial patterns in abundance at 4 scales (Fig. 2). We compared differences between: (1) Broad habitat zones, together encompassing most of a 10 km<sup>2</sup> lagoon (see Fig. 1). (2) Random 10 000 m<sup>2</sup> locations within zones, 100 to 1000 m apart. (3) Random 25 m<sup>2</sup> sites within locations. (4) Random 0.1 m<sup>2</sup> cores within sites. A second pilot survey was conducted to deter-

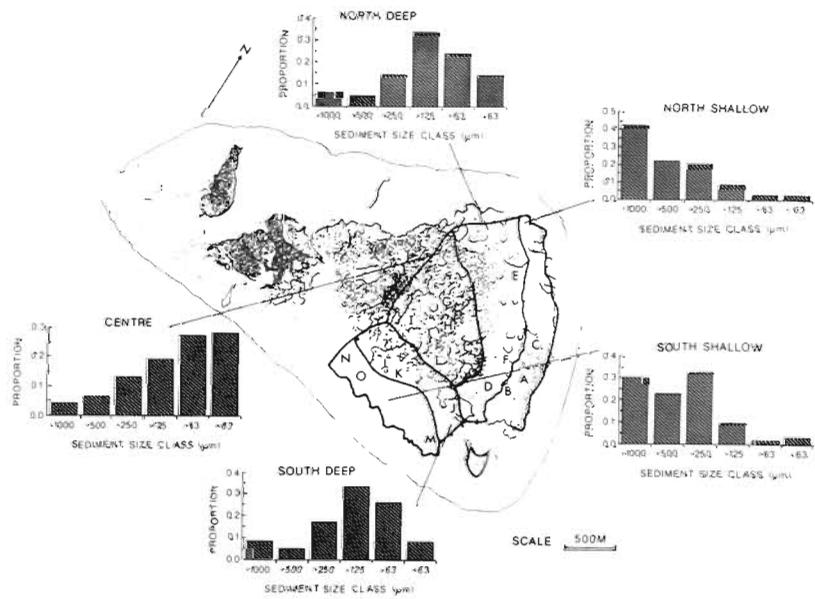


Fig. 1. Map showing the 5 lagoon zones and locations (A to O). Surrounding graphs show the mean sediment grain size composition for the 5 zones. Proportions are based on weight in each of the 1  $\phi$  classes

mine both the total number of samples which could be collected and sorted within a 2 wk period, and the best way to allocate this effort among sites and locations. During May 1985, we sampled 2 zones, 2 locations, and 3 sites, with 4 replicates from each. This indicated that we could process ca 120 cores in the time available. It also showed that zones explained much more of the variance present than the lower levels. By sampling 3 locations and 2 sites within each location, the 120 replicates were distributed in such a way as to put maximum effort into the levels where most of the variation occurred, while maximizing the power of the test for differences among zones (procedures recommended by Underwood 1981) (Fig. 2).

The 4 replicate 0.1 m<sup>2</sup> cores from each site were collected using a diver-operated air lift attached to a SCUBA cylinder (Thomassin 1978). The sediment was deposited in nylon bags with a 1 mm mesh diameter. All living macrofauna were fixed in formaldehyde and simultaneously stained with Beibrich scarlet, to enhance visibility for sorting. All molluscs were extracted from the sediment, identified to species level and counted. Selected abundant species were also measured: bivalves – *Tellina robusta*, *T. cf. myaformis*, *Exotica rhomboides*, *E. cf. virgulata*, *Fragum fragum* and *Fragum sp.*; gastropods – *Umbonium guamensis*, *Rhinoclavis aspera* and *Pupa nitidula*. A complete check-list of molluscan fauna from this sampling programme appears in Table 1.

At each site, depth was measured at low tide and two

50 ml jars of sediment were collected from random positions. These samples were processed to quantify structure following the methods outlined by Folk (1974) for carbonate sediments. Samples, which were stored in ethanol, were first dried to a constant weight (ca 7 d at 60°C) and then wet-sieved through a 63  $\mu$ m screen to remove the silt fraction. The collected sand sample was dried, re-weighed and separated into fractions with 1  $\phi$  intervals by shaking for 10 min on a geological sieve shaker. Each fraction was then weighed separately to measure the proportion of sediment in 6 size categories.

## RESULTS

### Taxonomic composition

The mollusc assemblage on One Tree Lagoon was found to be rich in species, with a total of 69 species distributed among 27 families recorded in the pilot and main surveys (Table 1). The most speciose families were the bivalve family Tellinidae (8 species), and the gastropod families Cerithiidae (7 species) and Naticidae (7 species).

In terms of the numbers of individuals, the assemblage was dominated by 5 tellinid bivalves, including *Tellina robusta*, *T. obtusalis*, *T. cf. myaformis*, *Exotica rhomboides* and *E. cf. virgulata*, the cardiid *Fragum sp.*, and 4 gastropods in separate families – *Pupa nitidula* (Actaeonidae), *Rhinoclavis aspera* (Cerithiidae), *Umbonium guamensis* (Trochidae) and *Alys cylindricus*

Fig. 2. Hierarchical sampling programme showing the main sampling levels and relationships between them. Four replicate cores were taken at each site

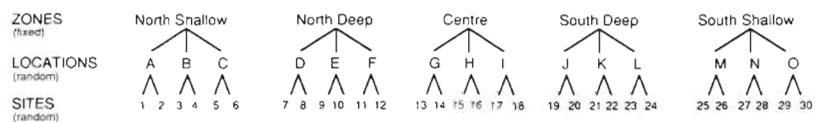


Table 1. Molluscs found in sediments of One Tree Lagoon, Great Barrier Reef

<b>GASTROPODA</b>	<b>ENTOMOTAENIATA</b>
<b>ARCHAEOGASTROPODA</b>	<b>Pyramidellidae</b>
<b>Trochidae</b>	<i>Pyramidella acus</i> (Gmelin, 1791)
<i>Chrysostoma paradoxum</i> (Born, 1780)	<b>CEPHALASPIDEA</b>
<i>Mesoclanculus</i> sp.	<b>Acteonidae</b>
<i>Umbonium guamensis</i> (Quoy & Gaimard, 1834)	<i>Pupa alveola</i> (Souverbie, 1863)
<b>Neritidae</b>	<i>Pupa nitidula</i> (Lamarck, 1916)
<i>Nerita</i> sp.	<i>Pupa solidula</i> (Linné, 1758)
<b>MESOGASTROPODA</b>	<i>Pupa sulcata</i> (Gmelin, 1791)
<b>Cerithiidae</b>	<b>Scaphandridae</b>
<i>Cerithium alveolus</i> Hombron & Jacquinot, 1854	<i>Tornatina sandwichensis</i> Pease, 1860
<i>Cerithium columna</i> Sowerby, 1834	<i>Tornatina</i> sp.
<i>Cerithium</i> sp.	<b>Atyidae</b>
<i>Clypeomorus zonatus</i> Wood, 1828	<i>Atys cylindricus</i> (Helbing, 1779)
<i>Rhinoclavis aspera</i> (Linné, 1758)	<b>BASOMMATOPHORA</b>
<i>Rhinoclavis fasciata</i> (Brugierè, 1792)	<b>Ellobiidae</b>
<i>Rhinoclavis vertagus</i> Linné, 1758	<i>Allochroa layardi</i> (H. & A. Adams, 1855)
<b>Eulimidae</b>	<b>BIVALVIA</b>
<i>Eulima</i> sp.	<b>SOLEMYOIDA</b>
<b>Strombidae</b>	<b>Solemyidae</b>
<i>Strombus gibberulus</i> (Linné, 1758)	<i>Solemya</i> sp.
<i>Strombus luhuanus</i> Linné, 1758	<b>MYTILOIDA</b>
<i>Terebellum terebellum</i> (Linné, 1758)	<b>Limidae</b>
<b>Naticidae</b>	<i>Limidae</i> sp.
<i>Natica bougei</i> Sowerby, 1908	<b>VENEROIDA</b>
<i>Natica gualteriana</i> Recluz, 1844	<b>Lucinidae</b>
<i>Natica onca</i> (Röding, 1798)	<i>Anodontia (Cavatidens) omissa</i> (Iredale, 1930)
<i>Natica</i> sp. 1	Unidentified sp. 1
<i>Natica</i> sp. 2	<b>Kelliidae</b>
<i>Polinices flemingiana</i> (Recluz, 1844)	<i>Kellia</i> sp.
<i>Polinices tumidus</i> (Swainson, 1840)	<b>Cardiidae</b>
<b>NEOGASTROPODA</b>	<i>Fragum fragum</i> (Linné, 1758)
<b>Pyrenidae</b>	<i>Fragum</i> sp.
<i>Mitrella ligula</i> (Duclos, 1840)	<i>Fulvia radiata</i>
<b>Nassariidae</b>	<b>Mesodesmatidae</b>
<i>Nassarius albescens</i> (Dunker, 1846)	<i>Ervillea</i> sp.
<i>Nassarius ecstilbus</i> (Melvill & Standen, 1896)	<b>Tellinidae</b>
<i>Nassarius shackelfordi</i> (Melvill & Standen, 1896)	<i>Exotica (Loxoglypta) rhomboides</i> (Quoy & Gaimard, 1834)
<i>Nassarius spendidulus</i> (Dunker, 1846)	<i>Exotica c.f. virgulata</i> (Hanley, 1845)
<b>Olividae</b>	<i>Tellina robusta</i> (Hanley, 1844)
<i>Amalda</i> cf. <i>edithae</i> (Pritchard & Gatliff, 1899)	<i>Tellina (Cadella) obtusalis</i> Destayes, 1845
<i>Olivella</i> sp.	<i>Tellina (Abranda) cf. myaformis</i> Sowerby, 1868
<b>Volutidae</b>	<i>Tellina (Scissulina) dispar</i> (Conrad, 1837)
<i>Amoria maculata</i> Swainson, 1822	<i>Tellina (Quadrans) parvitas</i> (Iredale, 1937)
<i>Cymbiolacca pulchra</i> Sowerby, 1825	<i>Tellina (Cadella) semen</i> (Hanley, 1844)
<b>Marginellidae</b>	<b>Semelidae</b>
<i>Granula</i> sp.	<i>Semele</i> sp.
<b>Turridae</b>	<b>Veneridae</b>
<i>Clavus leforestieri</i> (Hervier, 1896)	<i>Dosinia extranea</i> (Iredale, 1937)
<i>Eucithara delacouriana</i> (Crosse, 1896)	<i>Lioconcha ornata</i> (Lamarck, 1817)
<i>Eucithara funiculata</i> (Reeve, 1846)	<i>Timocla (Glycydonta) marica</i> (Linnaeus, 1758)
<i>Lophiotoma acuta</i> (Perry, 1811)	<i>Callista (Callista) semisulcata</i> (Sowerby, 1857)
<b>Conidae</b>	<i>Circe</i> cf. <i>scripta</i> (Linné, 1758)
<i>Conus spectrum</i> (Linné, 1738)	

(Atyidae). Together, these 10 species comprised 76 % of the individuals collected.

**Population abundance and structure**

Detailed descriptions were made of spatial pattern in the distribution and abundance of the 10 most common species. No species was cosmopolitan in its dis-

tribution. Differences in density were observed at all spatial scales examined (Fig. 3, Table 2). Nine of the 10 species exhibited significant differences among zones; 6 of the 10, significant differences among locations; and 7 of the 10, significant differences among sites (Table 2). These spatial scales were not, however, equally important in terms of the magnitude of the variation observed. Zones explained between 50 and

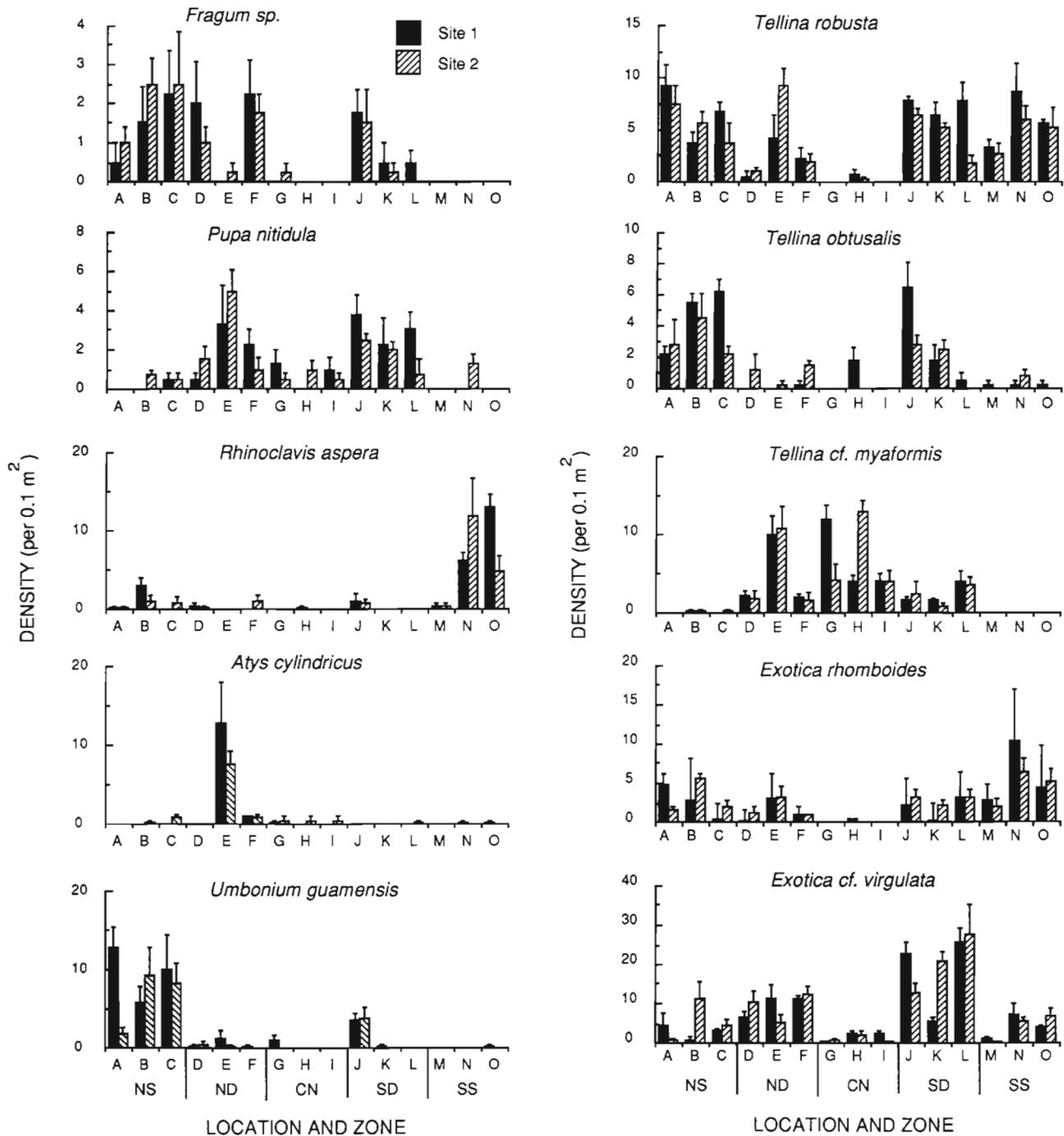


Fig. 3. Mean densities (per 0.1 m<sup>2</sup> ± SE) of 10 common molluscs within each zone, location (A to O) and site. For clarity, the 2 random sites within each location are represented by solid and cross-hatched histograms

85 % of the variation in numbers for all species except *Alys cylindricus*. *A. cylindricus* exhibited a location effect only, and locations explained 72 % of the variance observed (Table 2). Excluding *A. cylindricus*, locations explained an average of 16% of the variance, sites 7 % and replicates 15 %. Hence, the varia-

tion in numbers declines fairly dramatically with decreasing scales of focus between zones and sites.

There were substantial differences among species in their distributions among zones (Fig. 3). The 5 common tellinids each showed a unique pattern. *Tellina robusta* was the most widespread, being abundant in

Table 2. Analyses of variance of abundance for 10 species of mollusc in One Tree Reef lagoon. All data were transformed  $\sqrt{x+1}$  for F-ratios but untransformed data were used for calculation of percent variance explained at each level. Cochran's value denoting significant heterogeneity of variances for these samples = 0.16. Degrees of freedom for each F-ratio shown in parentheses. \*p < 0.05. Percentage variance explained, calculated as described by Underwood (1981)

Species	Cochran's value	F-ratio			Percent variance explained			
		Zone (4, 10)	Loc. (10, 15)	Site (15, 90)	Zone	Loc.	Site	Rep.
<i>Tellina robusta</i>	0.11	6.78*	2.79*	2.17*	0.60	0.17	0.07	0.15
<i>T. obtusalis</i>	0.20	5.83*	2.08	3.61*	0.65	0.12	0.11	0.11
<i>T. cf. myaformis</i>	0.12	6.26*	3.26*	2.84*	0.58	0.20	0.13	0.09
<i>Exotica rhomboides</i>	0.18	5.03*	3.11*	1.96*	0.55	0.25	0.06	0.15
<i>E. cf. virgulata</i>	0.16	13.1*	1.48	3.19*	0.79	0.04	0.08	0.08
<i>Fragum</i> sp.	0.16	3.90*	8.61*	0.41	0.51	0.28	0	0.31
<i>Pupa nitidula</i>	0.22	6.40*	1.78	1.64	0.59	0.15	0.03	0.23
<i>Alys cylindricus</i>	0.57	1.35	25.3*	0.93	0.09	0.72	0	0.20
<i>Rhinoclavis aspera</i>	0.47	4.14*	4.60*	2.14*	0.60	0.20	0.10	0.10
<i>Umboonium guamensis</i>	0.24	19.1*	1.07	3.00*	0.85	0	0.09	0.12

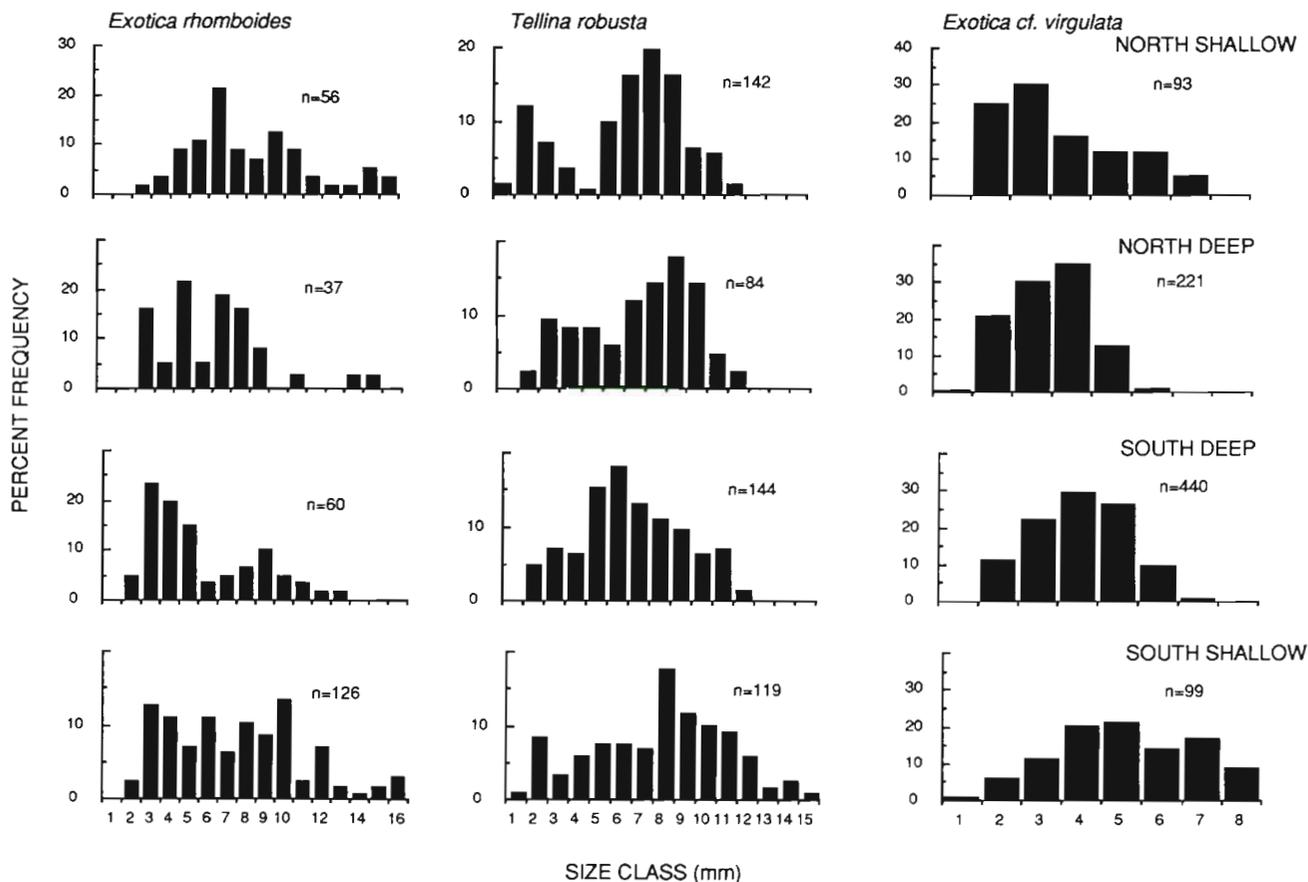


Fig. 4. Percent frequency of individuals, in 1 mm size classes, for 3 tellinid bivalve species collected from 4 zones – North Shallow, North Deep, South Deep and South Shallow. Low numbers of these species in the Centre zone precludes any comparison

all zones except the centre, where *T. cf. myaformis* dominated. *T. obtusalis* was most common in NS and *Exotica rhomboides* at SS, with *E. cf. virgulata* reaching peak abundances in the deeper channels of ND and SD. Of the other species examined, *Fragum* sp. and *Umbonium guamensis* were most abundant at NS, *Rhinoclavis aspera* at SS, and *Pupa nitidula* at ND and SD. Nearly all the *Atys cylindricus* at counted were confined to one location in the ND channel.

There were also consistent patterns among species in population size-structure (Fig. 4). The tellinid bivalves common to the shallow and deep zones of the northern and southern halves of the lagoon, all reached larger sizes in the south shallow zone. The other species were too restricted in their distributions to detect such patterns, although location and site differences in population structure appeared to be common.

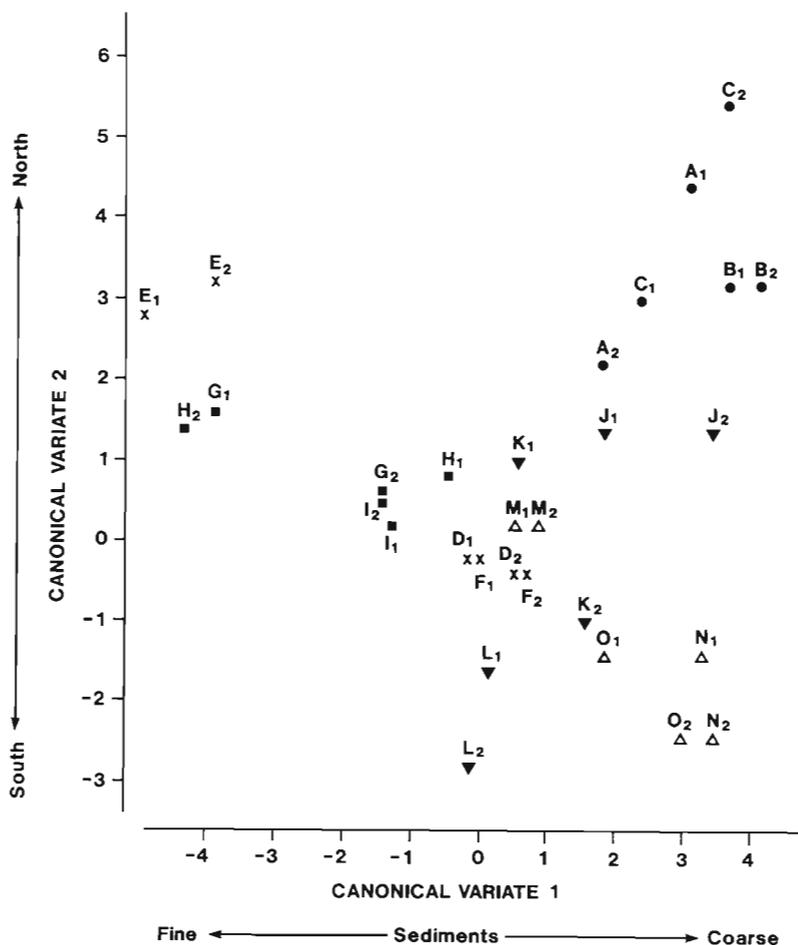


Fig. 5. Canonical discriminant analysis for maximal separation of sampling locations (A to O) and sites (1, 2) based on the abundances of the 10 common molluscs plotted in Fig. 3. Canonical variate 1 (x-axis) vs canonical variate 2 (y-axis) (see Williams 1983). North Shallow (●); North Deep (x); Centre (■); South Deep (▼); South Shallow (Δ)

Table 3. Pearson's correlation matrix between pairs of species, in terms of mean abundance for the 30 sites. Species were: (*T. r.*) *Tellina robusta*; (*T. o.*) *T. obtusalis*; (*T. m.*) *T. cf. myaformis*; (*E. r.*) *Exotica rhomboides*; (*E. v.*) *E. cf. virgulata*; (*F. sp.*) *Fragum* sp.; (*P. n.*) *Pupa nitidula*; (*A. c.*) *Atys cylindricus*; (*R. a.*) *Rhinoclavis aspera*; and (*U. g.*) *Umbonium guamensis*. Correlations shown in boldface are significant at  $p = 0.05$  level for single paired comparisons

Species	<i>T. r.</i>	<i>T. o.</i>	<i>T. m.</i>	<i>E. r.</i>	<i>E. v.</i>	<i>F. sp.</i>	<i>P. n.</i>	<i>A. c.</i>	<i>R. a.</i>
<i>T. o.</i>	<b>+0.40</b>								
<i>T. m.</i>	-0.31	<b>-0.38</b>							
<i>E. r.</i>	<b>+0.63</b>	0	-0.35						
<i>E. v.</i>	0.25	0.15	-0.06	0.21					
<i>F. sp.</i>	0.11	<b>+0.63</b>	-0.35	-0.14	0.15				
<i>P. n.</i>	0.31	0.06	<b>+0.46</b>	-0.08	<b>+0.50</b>	0.07			
<i>A. c.</i>	0.13	-0.21	<b>+0.54</b>	0.05	0.04	-0.16	<b>+0.55</b>		
<i>R. a.</i>	0.27	-0.1	-0.33	<b>+0.61</b>	-0.12	-0.22	-0.25	-0.13	
<i>U. g.</i>	<b>+0.39</b>	<b>+0.68</b>	-0.30	0.14	-0.08	<b>+0.57</b>	-0.16	-0.09	-0.13

### Species associations and richness

The Pearson's correlation matrix for these 10 species, based upon the means for each site, indicated various positive and negative associations among species (Table 3). *Tellina cf. myaformis*, *Atys cylindricus* and *Pupa nitidula* are all positively associated, being common to the ND, CN and SD zones. *Rhinoclavis aspera* and *Exotica rhomboides*, which are both abundant at SS, are positively correlated. Several species common to NS, including *T. robusta*, *T. obtusalis*, *E. rhomboides*, *Fragum* sp. and *Umbonium guamensis* also tend to be positively correlated in occurrence.

A canonical discriminant analysis (CDA) was carried out to assess, objectively, whether zones represent discrete homogeneous assemblages, and describe any trends in the overall change in species composition across the lagoon (Fig. 5). CDA is commonly used in ecology to explore pattern in multivari-

ate data, by reducing it to 1 or 2 dimensions (canonical variates). Canonical variates are linear combinations of the measurement variables (abundances), which maximize discrimination among groups (sites) (Williams 1983). The CDA displayed trends in the data which were not immediately obvious from the observations on individual species (Fig. 5). The first canonical variate (x-axis) explained 34% of the total variation and appeared to separate sites along a gradient from the very fine sediments of CN, and location E within ND (dominated by *Tellina cf. myaformis* and *Atys cylindricus*) to the coarse sediments of NS and SS (characterized by *T. obtusalis*, *Exotica rhomboides* and others). The second canonical variate (y-axis), which explained 22% of the variation, appears to identify a trend from our northern to our southern zones. Large positive values represent the NS assemblage dominated by *T. obtusalis* and *Umbonium guamensis*, and large negative values, sites

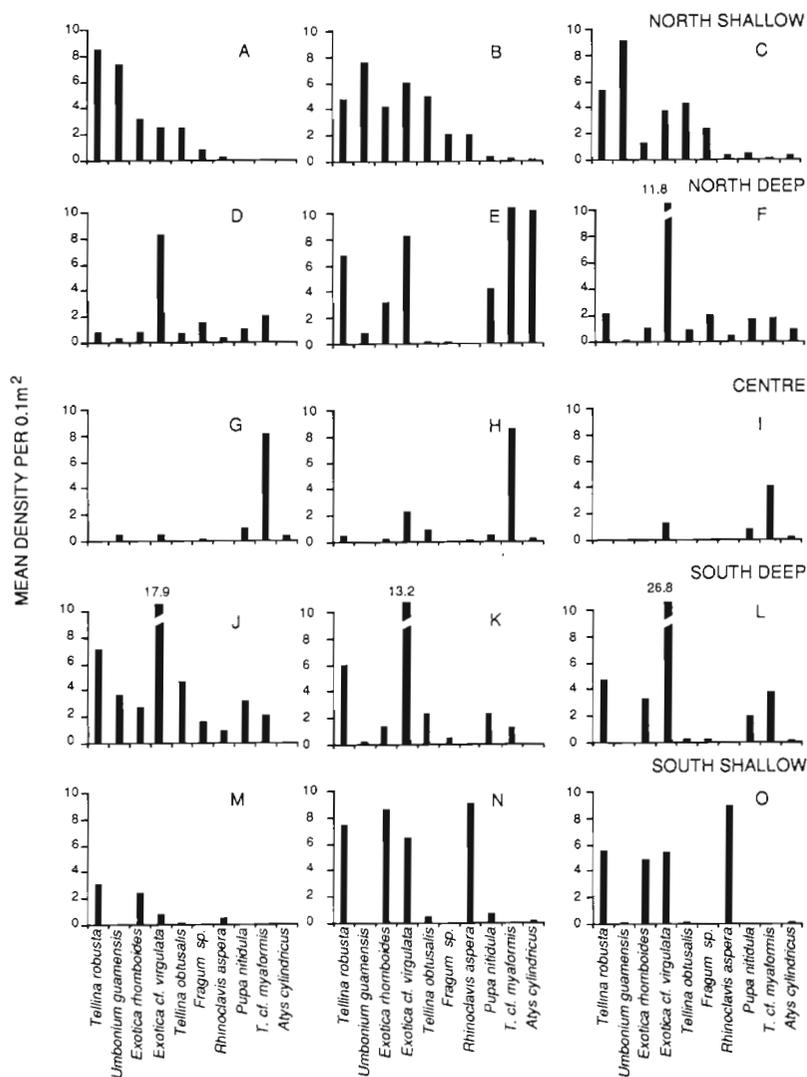


Fig. 6. Species identity vs mean density curves for pooled sites within each location (A to O), within each of the 5 lagoon zones. Species are ranked in order of decreasing abundance for North Shallow, Location A.

dominated by *E. cf. virgulata* in SD and *Rhinoclavis aspera* at SS.

On the basis of these 2 trends, detected by the CDA, zones were separated in terms of their composition, and sites within locations were very similar (Fig. 5). The degree of separation of locations was variable, but somewhat intermediate between zones and sites. Only the NS and CN zones appeared to represent homogeneous assemblages. All locations at NS were dominated by a diverse assemblage including *Tellina robusta*, *T. obtusalis*, *Exotica rhomboides*, *E. cf. virgulata*, *Fragum* sp. and the gastropod *Umbonium guamensis* (Fig. 6). A single species, *Tellina cf. myaformis*, dominated all locations at the Centre (Fig. 6).

For the other 3 zones, locations did not fall into well defined groupings (Fig. 5). The precise differences upon which locations were separated, are best viewed by examining species versus abundance plots for each location in these zones (Fig. 6). In ND, for example, location E differed substantially from D and F due to the presence of high densities of *Tellina cf. myaformis* and *Atys cylindricus*. *Exotica rhomboides* was the only species abundant at all locations. In SS, 2 nearby locations, N and O, were nearly identical, being dominated by the gastropod *Rhinoclavis aspera* and the 3 tellinids *T. robusta*, *E. rhomboides* and *E. cf. virgulata*. The other location, M, was extremely depauperate by comparison. The reasons for these location differences are not clear, but they may represent long-shore trends in species composition. Location E was quite distant from the other 2 in the ND zone, and was the only area covered in a thin mat of algae.

There were apparent differences in species richness among zones (Fig. 7). Greatest species richness was observed in the NS zone and the lowest at the CN zone. Species richness was also relatively low at SS, but tended to be intermediate in the deep channels.

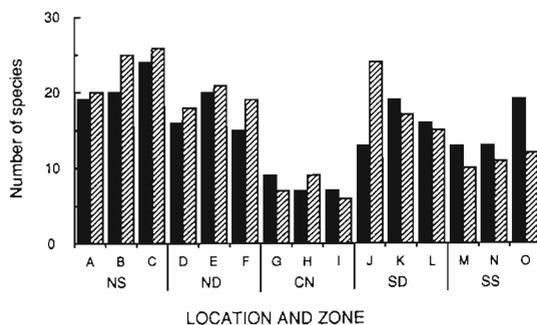


Fig. 7. Total number of species recorded within each zone, location (A to O) and site. For clarity, the 2 random sites within each location are represented by solid and cross-hatched histograms

Table 4. Correlations between physical parameters (A), and between physical parameters and abundance (B) for 10 species (see legend of Table 3 for species codes). Correlations significant at  $p = 0.05$  for single paired comparisons in boldface

A			
Mean grain size vs sand-silt ratio			$r = +0.52$
Mean grain size vs depth			$r = -0.53$
Sand-silt ratio vs depth			$r = -0.72$
B			
Species	Mean grain size	Sand-silt ratio	Depth
<i>T. r.</i>	<b>+0.38</b>	0.33	-0.33
<i>T. o.</i>	<b>+0.44</b>	0.14	-0.10
<i>T. m.</i>	<b>-0.56</b>	<b>-0.50</b>	<b>+0.60</b>
<i>E. r.</i>	0.24	<b>+0.48</b>	<b>-0.61</b>
<i>E. v.</i>	-0.35	-0.23	0.15
<i>F. sp.</i>	0.32	0	0.18
<i>P. n.</i>	<b>-0.49</b>	<b>-0.44</b>	<b>+0.55</b>
<i>A. c.</i>	-0.21	-0.20	<b>+0.47</b>
<i>R. a.</i>	0.14	<b>+0.73</b>	<b>+0.62</b>
<i>U. g.</i>	<b>+0.40</b>	0.22	-0.08

#### Associations with depth and sediment characteristics

Changes in species composition, abundance and population-structure among zones were clearly associated with changes in water depth and sediment characteristics (Fig. 1). However, there were also subtle differences in these parameters among locations and sites. The closeness of correlations between abundances, depth and 2 commonly used measures of sediment coarseness (mean grain size and the sand/silt ratio) were examined for each of the 10 common species (Table 4). As expected, the measures of sediment coarseness were positively correlated, and they were both negatively correlated with depth. Five species were significantly correlated with at least one of the measurements of increasing sediment coarseness, including *Tellina robusta*, *T. obtusalis*, *Exotica rhomboides*, *Rhinoclavis aspera*, and *Umbonium guamensis* – all species common in at least one of the two shallow zones. Negative correlations for *Pupa nitidula* and *T. cf. myaformis* indicated an association with finer sediments. *R. aspera* and *E. rhomboides*, which characterized SS, were negatively correlated with depth. The abundance of *T. cf. myaformis*, *Atys cylindrica* and *P. nitidula* increased with depth.

#### DISCUSSION

The mollusc assemblage within the soft sediments of the lagoon at One Tree Reef proved to be rich in species (69), with a number of these reaching very high densities (up to  $250 \text{ m}^{-2}$ ). These values appear to be comparable to other tropical reef sediments for which

numerical data have been published (Taylor 1971, Salvat 1972). Unfortunately, since the review by Thomassin (1978), little quantitative work has been done on these assemblages.

The abundances of marine organisms are characteristically variable at a number of spatial scales (Andrew & Mapstone 1987). Frequently, quantitative sampling programmes are inadequate to distinguish one scale of variability from another (Hurlbert 1984). Such confusion can lead to incorrect conclusions about processes structuring communities, and cause avoidable debate over issues which are scale dependent (e.g. Ogden & Ebersole 1981, Sale & Douglas 1984). The hierarchical survey employed in this study provided a clear method of distinguishing variability among strata at progressively larger scales from the variation within these strata at each level (Underwood 1981, Andrew & Mapstone 1987). Such nested designs have been used effectively in detecting the scale at which species respond to their environment in a number of ecological surveys (e.g. Caffey 1985, Choat & Bellwood 1985, Phillips & Fleeger 1985).

In terms of changes in abundance and species composition, the most dramatic changes occurred at the largest scale examined (between habitat zones). This scale accounted for between 50 and 85 % of the variation in abundance, for all but one species examined. There was moderate variation on an intermediate scale (among broadly spaced 1 ha locations within zones), and considerably less variation within locations (among sites within locations). This suggests that the most important factors affecting the distribution and abundance of this fauna operate on a relatively broad spatial scale in this lagoon.

It was not possible to directly attribute the large scale variation of features of the habitat (habitats were not replicated). Depth and sediment type are clearly associated with abundance patterns in this system, however any causal effects on species distributions would have to be assessed experimentally. This is a recurring feature of mollusc communities, whether arctic (e.g. Carey et al. 1984), temperate (e.g. Richter & Sarnthein 1977, Oliver et al. 1980) or tropical (e.g. Taylor 1971, Thomassin et al. 1982, Grelet et al. 1987). Although not necessarily causative factors in themselves, depth and sediment are clearly correlated with the factors responsible for determining species distributions. Species-specific settlement preferences, either for different sediment types, for different depths or other unknown but correlated factors, are an obvious potential mechanism causing the observed distributions (Gray 1974). Experimental sediment transplants, such as that carried out by Richter & Sarnthein (1977) in the Wadden Sea, may be the only way to separate these factors, in terms of their relative importance.

Changes in depth and sediment composition usually relate to changes in a host of other physical factors (e.g. water movement, oxygen supply, nutrients) (Richter & Sarnthein 1977, Johnstone et al. 1988). These in turn may affect a range of biological factors, such as the accumulation of detritus, productivity and microbial activity; physical factors may mediate disturbance or predator effects, whether by epibenthic organisms (e.g. Commito 1982, Arnold 1984) or fish (Van Blaricom 1982, Jones et al. 1988). The scales at which all these potentially important variables operate need to be considered before meaningful experiments can be designed to examine their impact. Those factors exhibiting recognizable patterns in their intensity at larger scales would be primary targets for future research.

This study was conceived primarily as a basis for a future assessment of the role soft-sediment molluscs play in coral-reef food-chains. Although potential epibenthic predators, such as crabs and naticid gastropods, were frequently encountered in samples, numbers were too low to get a clear idea of their patterns of distribution. It has been suggested that naticids play an important role as predators in other tropical soft sediment areas (Berry 1982). Spatial variation in the abundance and feeding intensity of teleosts known to consume soft sediment molluscs have been investigated at One Tree Reef (Jones et al. 1988, unpubl.). These studies showed that there was considerable variation in teleost feeding pressure, on both zone and location scales, but little evidence of a major impact of teleosts on prey numbers, either in shallow or deep regions of the lagoon.

Species-specific patterns of change in abundance at progressively larger scales, lead to fairly predictable species groupings in some zones. However, zones do not appear to be homogeneous assemblages in terms of their biotic structure. Considerable variability in species composition was apparent, from location to location, due to the patterns exhibited by some species (e.g. *Atys cylindricus* was common at one location only). Trends in species richness across the lagoon may also reflect responses of individual species. Increasing species richness in relation to increasing sediment coarseness is a recurring pattern in soft sediment communities (see Gray 1974). Our finding of low diversity in the fine sediments of the centre of the lagoon, and high diversity in the coarse sediments of the northern periphery, is consistent with this. However, low species numbers in the coarse, shallow sediments to the south would not be expected on the basis of this generalization.

This paper presents a static picture of the abundance and structure of mollusc populations in One Tree Lagoon. The obvious extension of this study, an exami-

nation of whether the patterns present at each scale remain coherent over time, is currently under way (Jones et al. unpubl.). However, the large-scale trends in species and sediment composition across the lagoon are sufficient to suggest a number of testable hypotheses about processes important in tropical soft sediment systems. This is a first step in an understanding of the relationship between these poorly known communities and the adjacent coral reefs.

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