Larger Foraminifera from the Spermonde Archipelago (Sulawesi, Indonesia)

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A systematic description of the distributional patterns of larger symbiont-bearing benthic Foraminifera from the Spermonde Archipelago (Sulawesi, Indonesia) and their relation with local coral reef growth is presented. The larger Foraminiferal assemblages and diversity indices correspond with the diversity of Scleractinia and marine plants on the Spermonde platform. Our results indicate that the group is an excellent biomonitor for the health condition of recent coral reefs and a valuable tool for paleo-environmental reconstructions.

Contents

Introduction

Symbiont-bearing benthic Foraminifera ('larger Foraminifera') are characteristic inhabitants of warm, shallow and oligotrophic tropical seas, often associated with reefs and reefal environments. They do not constitute a taxonomically coherent group but are distinguished by their large size (3-300 mm^3), complex internal @structures and their association with symbionts such as naked diatoms, dinoflagellates, Rhodophycea and Chlorophycea (Ross, 1974; Reiss & Hottinger, 1984; Hallock et al., 1991). They are thus well adapted for survival and growth in this environment by internal recycling of N, P, CO_2, O_2 and organic compounds (Ross, 1974; Röttger, 1976; Muller, 1977; Lee et al., 1979; Hottinger, 1982; ter Kuile & Erez, 1987; Lee and Anderson, 1991).

Field studies have shown that the larger Foraminifera are prolific carbonate producers (Hallock et al., 1991) playing an important role in the world's CO_2/CO_3^{2-} budget (Lee & Anderson, 1991). Maxwell (1968) estimated that 10-15% of the accumulated sediment of the Australian Great Barrier Reef and adjacent shelf consists of foraminiferal shell debris. Sakai & Nishihira (1981) estimated a production of 6.10^2 g $CaCO_3.m^{-2}.y^{-1}$ solely by *Baculogypsina sphaerulata*, a calcarinid larger foraminifer, living on the Okinawa reef, Japan. From the geological past the widespread lower Tertiary nummulitic limestones are indicative of their potential as rock forming organisms.

In recent years the understanding of the functional morphology (Hallock et al., 1991) and ecological aspects of larger Foraminifera has grown. However, little is known about the relationship between physical, chemical and biological factors, the distribution and population dynamics of the group (Murray, 1991). Better understanding of the ecological parameters that influence distribution of living Foraminifera will lead to a more accurate interpretation of facies relationships and depositional histories of ancient reefs. This study is a first attempt to consider some of these parameters in a tropical region where larger Foraminifera thrived for millions of years.

The study concentrates on two topics:

1) Distribution patterns of larger Foraminifera in a variety of reefal environments on the Indonesian Spermonde Shelf and their relation to environmental (a)biotic parameters and

2) If such a relationship exists, to see whether larger Foraminifera can be used as a biomonitoring tool for the health condition of the reefal eco-system.

The Spermonde Archipelago is situated in the southern Makassar Strait off the SW peninsula of Sulawesi (Fig. 1a) The area is in the center of a zone with highest reef-organism diversity, extending from the Philippines to Irian Barat. The topography of the platform is largely a Pleistocene relict, with reef-growth following the most recent sea-level rise.

Previous research in the Spermonde Archipelago concerned the distribution of Scleractinia (Moll, 1983), fungiid corals (Hoeksema, 1989), seagrasses (Erftemeijer, 1993) and marine plants (Verhey, 1993). These studies provided the quantitative information used on abiotic parameters for the area. Parameters include offshore distance of surveyed islands, water energy (wave action and current velocity), transparency, salinity, carbonate content of the sediment, water temperature and water quality (particulate organic carbon and nitrogen, chlorophyll a, phosphate, ammonium and nitrite-nitrate nitrogen concentration). The data are summarized in the present study and used to quantify relationships between these parameters and larger foraminiferal distribution patterns.

The Spermonde Archipelago

On the basis of geography, geomorphology and distance to the shore, the Spermonde Archipelago can be subdivided into four strips perpendicular to the coast and each encompassing a number of islands (van Vuuren, 1920, Fig. 1b). Previous research has shown that these strips differ essentially in biotic and abiotic parameters (de Klerk, 1983; Mol ,1983; Hoeksema, 1989; Erftemeijer, 1993; Verhey, 1993). An east-west gradient of environmental components on the shelf is present. Strong winds

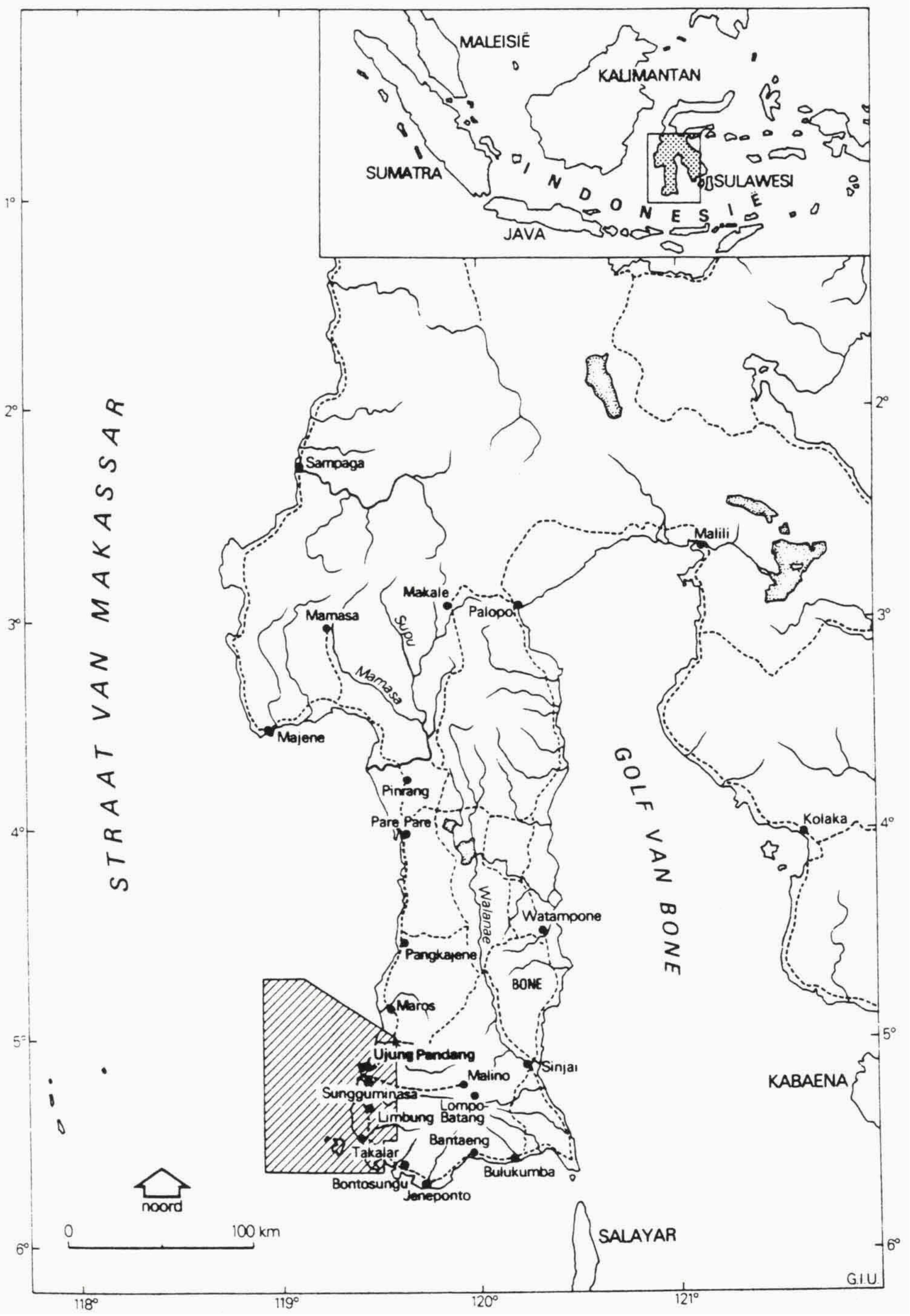


Fig. 1a. Location of the Spermonde Archipelago.

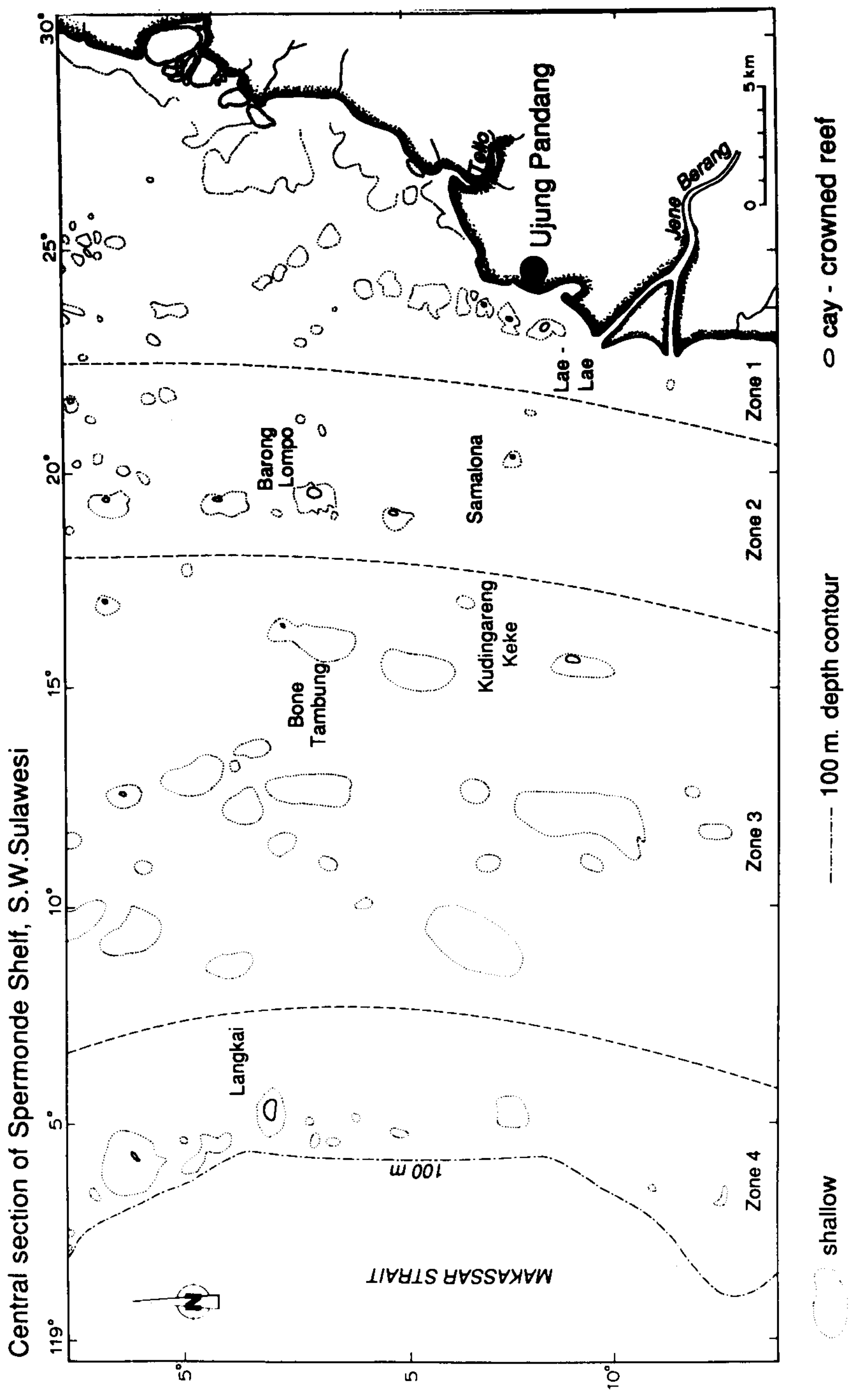


Fig. 1b. The Spermonde Archipelago and its coral islands, arranged in strips parallel to the shore as determined by van Vuuren (1920), after de Klerk (1983).

occur during the northwest monsoon while the southeastern monsoonal winds are weakened by the mainland mountains. Consequently the exposed western reefs are well developed while the sheltered eastern reefs suffer more sedimentation stress, have a different coral fauna which may even be absent (Moll, 1983).

Fluvial discharge of rivers, such as the Jene Berang near the city of Ujung Pandang, causes fresh water inflow and the input of terrigenous sand and silt, particularly during the northwestern 'wet' monsoon. Ujung Pandang with its population of nearly one million people may itself have a polluting effect.

The southeast monsoon causes upwelling along the outer shelf rim in the West and consequently a decrease in water temperature and dissolved oxygen and an increase in salinity and nitrate-nitrogen (Hoeksema, 1989). In addition to the east-west gradient, locally important disturbances occur. All over the Spermonde Archipelago, but predominantly around near-shore islands, the coral reefs are heavily fished for reef fishes, shrimps, molluscs, tripang (edible holothurians) and algae. Coral rock is extracted from reefs for construction purposes. Reefs around inhabited islands have to deal with organic and inorganic effluents. These disturbances alter the natural composition of the coral reef complexes. The surveyed islands in the present research are positioned at an increasing distance offshore, thus according to a specific set of interrelated environmental factors.

Environmental components

The environmental parameters related to offshore distance in the Spermonde Archipelago are reviewed in Table 1. In the wet season salinity values of the surface layer (0-0.5 m) may drop to $20^{0}/_{00}$ due to rainfall and river discharge. Below 0.5 m salinity for a given time-interval is generally constant and varies during the year between 30 and $35^{0}/_{00}$ (Storm 1989).

Temperature of the surface water varies during the year between 26.5 and 32.5°C (Erftemijer 1993).

Based on the environmental parameters listed in Table 1 the four strips of islands as recognized by van Vuuren (1920; Fig. 1b) can be characterized as follows:

Strip 1 (near shore; Island Lae Lae) — Transparency of the water is low during both wet and dry seasons due to river sediment load. Carbonate content of the reefal sediment is consequently low. Water quality is poor due to the high concentrations of organic and inorganic nutrients, resulting in eutrophication. Water energy is low.

Strip 2 (mid-platform; Islands Samalona and Barang Lompo) and Strip 3 (mid-platform; Islands Kudingareng Keke and Bone Tambung) — Transparency of the water is intermediate. During the wet season the Jene Berang river-plume reaches Samalona (Storm, 1989) resulting in a poor transparency. Water energy is moderate around the islands during the dry season but significantly higher during the wet season on the exposed northern and western edges (Verhey, 1993).

Strip 4 (outer platform rim; Islands Langkai and Kapoposang) — Transparent oligotrophic waters, especially phosphate and nitrate concentrations are extremely low compared to the other strips. The expected upwelling effects near the shelf rim during the dry season (Hoeksema, 1989) are not confirmed by the present data. Water energy is high, especially during the wet season.

Table 1. Surveyed islands in the Spermonde Archipelago and environmental parameters related to distance offshore.

Surveyed reefs	Offshore distance (km)	Population	Reef exploitation	Water movement[1] (DF) (yearly)	Transparency[1] (secchi depth m) (wet)	(dry)	Carbonate content (% of sediment)
Lae Lae	1.5	dense	severe	3.9	0.5-2.5	2.5-5	5-30
Samalona	6	moderate	severe		1-2.5	5-12.5	75-85
Barang Lompo	10	dense	moderate/high		2.5-5	10-17.5	75-85
Kudingareng Keke	12	none	moderate/high		5-7.5	12.5-17.5	75-85
Langkai	40	moderate	moderate		17.5-22.5	27.5-22.5	85-95
Kapoposang	60	low	moderate	8.7	20-22.5	30-32.5	85-95

Surveyed reefs	POC[2] (mg/l) (dry)	PON[2] (mg/l) (dry)	Chl a[2] (µg/l) (dry)	PO4[2] (µm) (dry)	(yearly)	NH4[2] (µm) (dry)	(yearly)	NO3 + NO2[2] (µm) (dry)	(yearly)
Lae Lae	0.54 ± 0.12*	0.08 ± 0.01*	2.9 ± 1.5*	1.7 ± 0.1*	1.4 ± 0.6*	1.4 ± 0.4	3.2 ± 2.8	0.6 ± 0.5*	1.4 ± 1.3*
Samalona									
Barang Lompo	0.19 ± 0.01	0.03 ± 0.01*	0.5 ± 0.2*	0.8 ± 0.4	0.8 ± 0.4	1.4 ± 0.6	2.2 ± 1.9	0.9 ± 0.1	0.9 ± 0.6
Kudingareng Keke	0.16 ± 0.04*	0.03 ± 0.01	1.0 ± 0.1						
Langkai	0.16 ± 0.02	0.02 ± 0.01	0.7 ± 0.1	0.2 ± 0.1		(below detection)		0.5 ± 0.2	
Kapoposang									

[1] (Verheij 1993)

[2] (Erftemeyer 1993)

* Value not from surveyed reef but from site positioned at comparable distance offshore

(DF) Diffusion factor; plaster-of Paris clod method according to Doty (1971) and Jokiel & Morrissey (1993); (wet) wet monsonal period (November-April); (dry) dry monsonal period (April-November).

Material and methods

Monitoring of larger Foraminifera.

The material for this study was collected during two field surveys. During October-November 1989, a reconnaissance inventory was made for the different reef zones (reef-flat, edge, slope and base) on different substrate types (algae, seagrasses, coral rubble, soft coral, stable/instable sediment) on the four wind sides of the coral islands Kudingareng Keke, Barang Lompo, Bone Tambung and Langkai.

During October-November 1992 a systematic inventory was made of foraminiferal distribution across the shelf, on leaward (East) and windward (West) sides of the coral islands, all on coral rubble at comparable depths in the various reef zones to allow comparison between the various islands. Systematically monitored reefs were Lae Lae West and East, Samalona West and East, Barang Lompo western slope, Kudingareng Keke West and East and Kapoposang northern reef-flat and drop-off reef. The position of the surveyed islands in the Spermonde Archipelago is shown in Fig. 1.

Collection and handling of samples

Samples were taken by SCUBA-diving, collecting a substratum area (algae, seagrasses, coral rubble, sediment) of 25 x 25 cm. During the systematic inventory coral rubble samples were taken at depth intervals of 3 m on reef slope and reef base while on the reef-flat samples were taken at 10, 20 and 50 m away from the reef crest coinciding with depths of approximately 2, 1.5 and 1 m respectively. On most reefs the crest coincides with the 3 m depth isobath.

Each sample was transported in a plastic bag to the laboratory and subsequently submerged in fresh water. The Foraminifera were detached from the substratum with a soft brush and a pair of tweezers, washed over a 0.6 mm sieve and sun-dried. With a stereo-microscope the Foraminifera (>0.6 mm) were subsequently sorted out, identified and counted. Only well-preserved specimens were registered, many of them still showing their characteristic symbiontic color.

Distribution patterns, assemblages and diversity indices

To allow quantitative comparison between the various sites, the proportional species abundance for each sample was calculated. The distribution of the species was visualized by mapping the proportional species abundances of the samples across shelf, around islands (windward-leaward sides) and related to depth. Assemblages were mapped in the same way, whereby an assemblage is defined as an 'aggregate of symbiont-bearing benthic Foraminifera found in a sample station'. The species richness, i.e. the number of species, and Shannon's index of diversity was calculated for each sample. For the calculations only samples with more than 100 individuals were considered.

Discussion and results

In this chapter distributional patterns and assemblage characteristics will be discussed. In a separate section detailed information on individual species will be given.

Fig. 2 shows the composition of the larger foraminiferal assemblages along an east-west transect with increasing distance to the shore. From each strip one island has been selected.The assemblages are the average of the samples taken from the reef-flat, upper reef slope, lower reef slope and reef base on exposed (western) and sheltered (eastern) sides of the islands. All samples were taken from hard substrate (coral rubble). Only species which make up more than 5% of the total assemblages are included.

The upper part of the figure shows the characteristics of the transect such as a generalized bottom profile, sample position and fluvial/oceanic influence. Human occupational density and vegetation of the various islands are also schematically indicated. The lower part of the figure shows the faunal composition for each sample unit.

The environmental niche preference of the larger symbiont-bearing benthic Foraminifera from the Spermonde Archipelago displays distinct distributional pat-

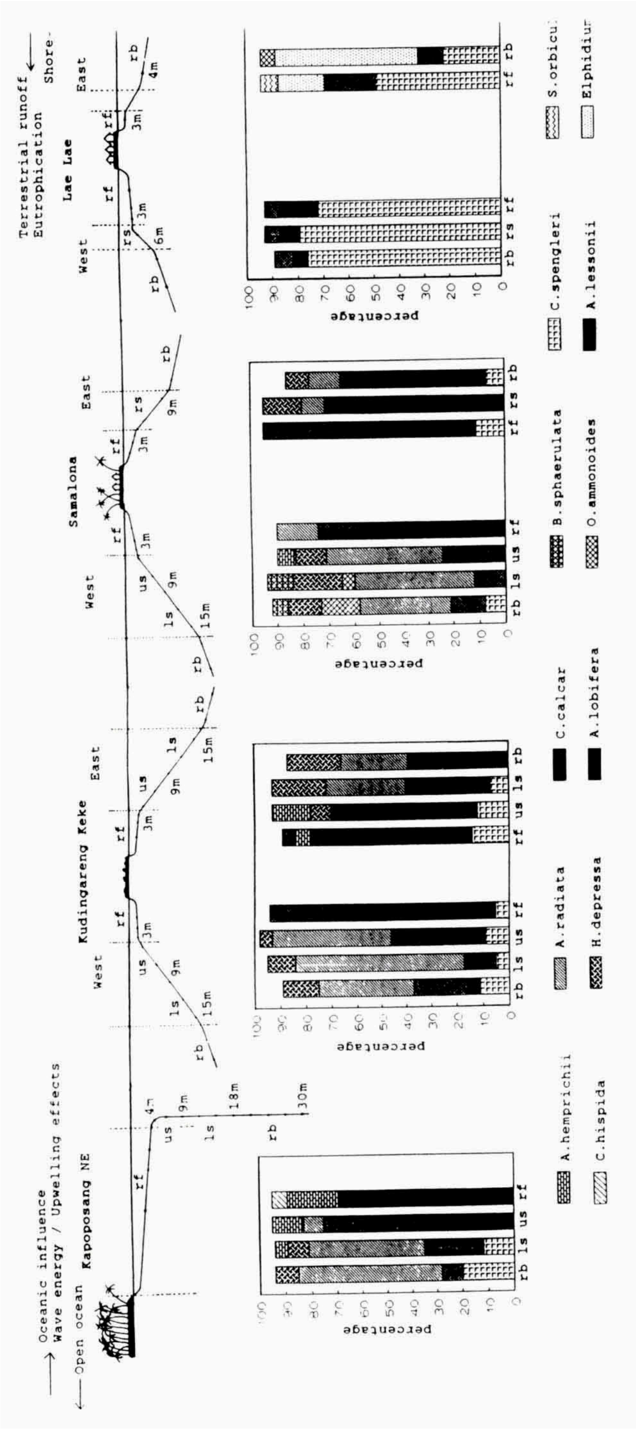


Fig. 2. Schematic cross-section of the Spermonde Platform with four coral islands positioned at increasing distance offshore (see also Fig. 1) The various reef zones are indicated and corresponding larger foraminiferal assemblages are shown. Note high frequencies of *Calcarina spengleri* and *Elphidium* around near-shore island Lae Lae, indicating eutrophication. rr = reefflat; us = upper reefslope; rs = reefslope; ls = lower reefslope; rb = reefbase.

terns related to environmental conditions in an offshore gradient. The patterns of individual species and assemblages show that the near shore eutrophic reefs are dominated by a few species only (*Calcarina spengleri* and *Elphidium* spp.) which are replaced by species such as *Heterostegina depressa* and *Amphistegina radiata* on mid-shelf reefs reflecting more stable 'predictable' environmental conditions. At the outer platform reefs, with more unstable 'unpredictable' open ocean influence a shift towards species such as *Amphisorus hemprichii* and high abundancies of *Amphistegina lessonii* takes place. Slobodkin & Sanders (1969) state that in such an unpredictable environment the variance of ecological properties around their mean value are relatively high and unpredictable both spatially and temporally.

This trend is also reflected by the statistical characterization of the assemblages. Applying Shannon's diversity index to each sample (n>100) results in the recognition of a relatively high species richness and diversity at midshelf reefs compared to outer rim and near shore reefs. A relatively low species richness and diversity around the reef crest (about 3 m depth) compared to other reef zones is also noted (Fig. 3). This is in accordance with the theory, reviewed by Gray (1989), that 'changes in community structure occur in response to stressors what leads to reduction in diversity and retrogression to dominance by opportunistic species'. Main stressors in the Spermonde Area on a horizontal scale are increasing water energy and decreasing eutrophication in an offshore gradient. Water energy (surf break) as stressor also explains the relatively low species richness and diversity on the reef crest of all surveyed reefs.

The distribution patterns and assemblages make clear that several species are nowhere prominent (>5% in assemblage). Amoung these are the rhodophyte (Peneroplidae) and chlorophyte (Archaiadae) symbiont-bearing species. These species are thus significantly less succesfull compared to the dinoflagellate (Soritidae) and diatom (Amphisteginidae, Calcarinidae and Nummulitidae) symbiont-bearing species in the Spermonde Area. This may in part be due to a sampling artifact, because *Peneroplis* and *Archaias* show a strong preference for a sea-grass substrate. According to Reiss & Hottinger (1984) *P. pertusus* frequently dominates lagoonal associations in the Persian Gulf, while *A. angulatus* is extremely abundant in shallow waters of the Florida Keys in the microhabitat of *Thallassia testudinum* stems (Lee et al., 1974).

Biomonitor potential of larger Foraminifera.

The larger Foraminifera encoutered in the Spermonde Area clearly show specific habitat preferences characterized by a specific set of environmental parameters. The optimum preferences for each species are summarized in Table 2. This does not imply that a given species habitat is hostile to all other species. The natural yearly variation of the parameters allows the co-occurence of various species. However, if one or more parameters exceed the boundery conditions for a particular species, it will result in the decline or eventually the disappearence of this form.

A quantitative presence/absence study of individual larger foraminiferal species with known habitat boundariy conditions can thus be used to monitor a given location on a short-term (1-3 months) basis.

The diversity indices of the larger foraminiferal assemblages across the Spermonde Platform show strong similarities with the coral reef development in that

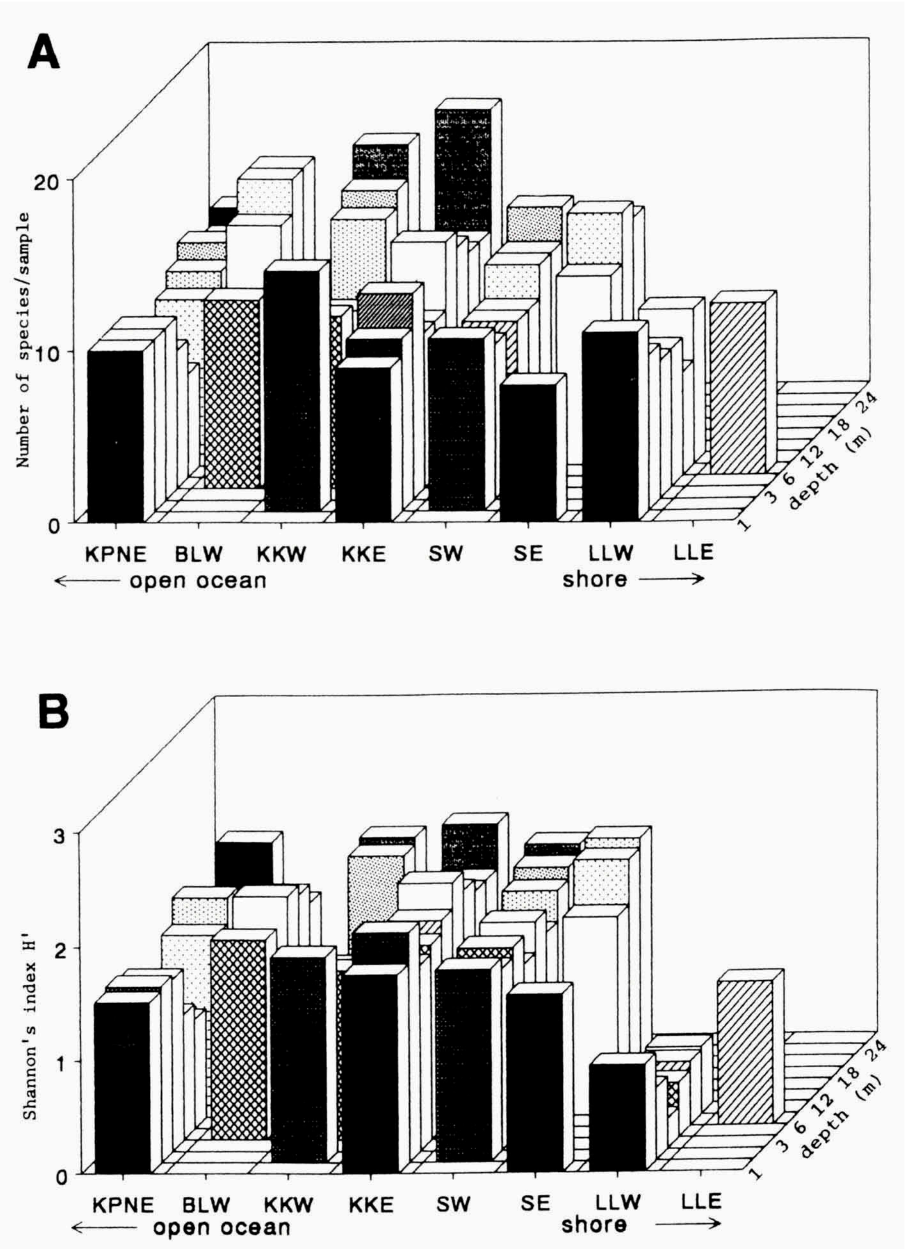


Fig. 3. Statistical characterization of larger foraminiferal samples taken on reefflat and 3 m depth intervals on exposed (West) and sheltered (East) sides of coral islands positioned at increasing distance offshore (LL = Lae Lae; S = Samalona; KK = Kudingareng Keke; BL = Barong Lampo; KP = Kapoposang; see also Fig. 1).

3A. Species richness = number of species per sample.

3B. Shannon diversity index: $H' = -\Sigma p_i \ln pi$.

Table 2. Habitat preferences of larger symbiont bearing benthic Foraminifera in the Spermonde Archipelago. 1 = present; 2 = preference. Larger Foraminifera from the Spermonde Archipelago (Sulawesi, Indonesia).

	light intensity high medium low					substrate soft hard			water energy			eutrophication		
species	reefflat	upper slope	slope	lower slope	base	sediment	algae/seagrass	coral rubble	high	medium	low	high	medium	low
A. lobifera	2	1					1	1	1	2			1	2
A. lessonii	2	2	1	1			1	1	1	1			1	2
A. radiata		1	2	2	1		1	2		1	2			1
H. depressa		1	1	2	2	1	1	2		1	2			1
O. ammonoides				1	2	2	1				1		1	2
A. hemprichii	2	2	1	1			1	1	2	1				1
S. orbiculus	1	1					2			1			1	2
S. marginalis				1	1	1					1			1
A. angulatus	1	1				1		1		1	1			1
P. pertusus	1	1	1	1	1		1	1		1	1			1
P. planatus	1	1	1	1	1		1	1		1	1			1
C. calcar	2	1					2	1		1			1	2
C. hispida	2	1					2	1	2	1				1
C. spengleri	1	1	1	1	1	1	1	2		1	1	2	1	1
C. gaudichaudii	2						1			1				1
B. sphaerulata			1	2			1	2		1	1			1
E. craticulatum			1	1	1	1					1	2		
E. crispum			1	1	1	1					1	2		
A. quoii					1	1					1			1

they differentiate the platform into three strips rather than the four published by van Vuuren (1920). Moll (1983) found this subdivision (1, 2-3 and 4), based on the coverage percentage of hermatypic corals while Verhey (1993), using present/absent data of marine plants, came to a similar conclusion. Hoeksema (1989) on the other hand described a classical subdivision into four strips using present/absent data of fungiid coral species.

Except for the fungiid coral species, these findings thus point to an environmental control which affect Scleractinea, sea-grasses and larger Foraminifera in the same way. Important environmental factors for these three different groups are primarily water-energy and -transparency. One can only speculate on the fine interactions between the organisms, their symbionts and nutrients. Of these groups the larger Foraminifera have the shortest life-span. Changing environmental conditions will thus be detected first in this group, as the suppressed reproductive behaviour will quickly lead to the absence of living individuals. The high frequencies of *Elphidium* spp. at Lae-Lae near the mouth of the polluting river Jene Berang may be indicative of such changing environmental conditions. *Elphidium* spp. show low frequencies at the other, oligotrophic, sites.

Notes on species distribution

In this section short notes on the distribution and environmental characteristics of the larger foraminiferal species encountered in the Spermonde Archipelago will be given and a comparison is made with their occurrence elsewhere. As these species are generally well-known no systematic description is given. For frequency data reference is made to Fig. 4. To avoid unnecessary repetitions, positions of the different islands are only listed here:

Strip 1	The near-shore island Lae-Lae.
Strips 2 and 3	The mid-platform islands Samalona, Kudingarang Keke and Barong Lompo.
Strip 4	The outer-platform islands Kapoposang and Lankai.

Amphistegina lobifera Rosenkrands, 1976
Fig. 4A

Symbiont type — Diatom. B2-type (Reiss & Hottinger, 1984); *Nitzschia frustulum* var. *symbiotica* and other species (Leutenegger, 1977, 1984; Lee et al., 1989).

Areal distribution and additional observations — The frequency distribution of *A. lobifera* around the investigated islands is given in Fig. 4a. It is also abundant as epiphyte on algae and seagrasses on the reef-flats of Barang Lompo, Kudingareng Keke, Bone Tambung and Langkai.

Comments — *A. lobifera* is a characteristic shallow-water species living both on hard substrate and as epiphyte on algae and seagrasses. It thrives on the reef-flats of the mid-platform islands. The lower frequencies on the flats of Lae Lae and Kapoposang are probably related to the poor water transparency around the first and the high water energy around the second island. The latter factor is considered responsible for its more prominent occurrence on the upper slopes of the sheltered eastern reefs compared to the exposed western reefs of the midshelf islands. Its high light requirement is confirmed by Hallock (1981) who found that *A. lobifera* reproduces in culture asexually only at the highest light levels.

Amphistegina lessonii d'Orbigny, 1826
Fig. 4B

Symbiont type — Diatom. B2-type (Reiss & Hottinger, 1984) *Nitzschia frustulum* var. *symbiotica* and other species (Leutenegger, 1984; Lee et al., 1989).

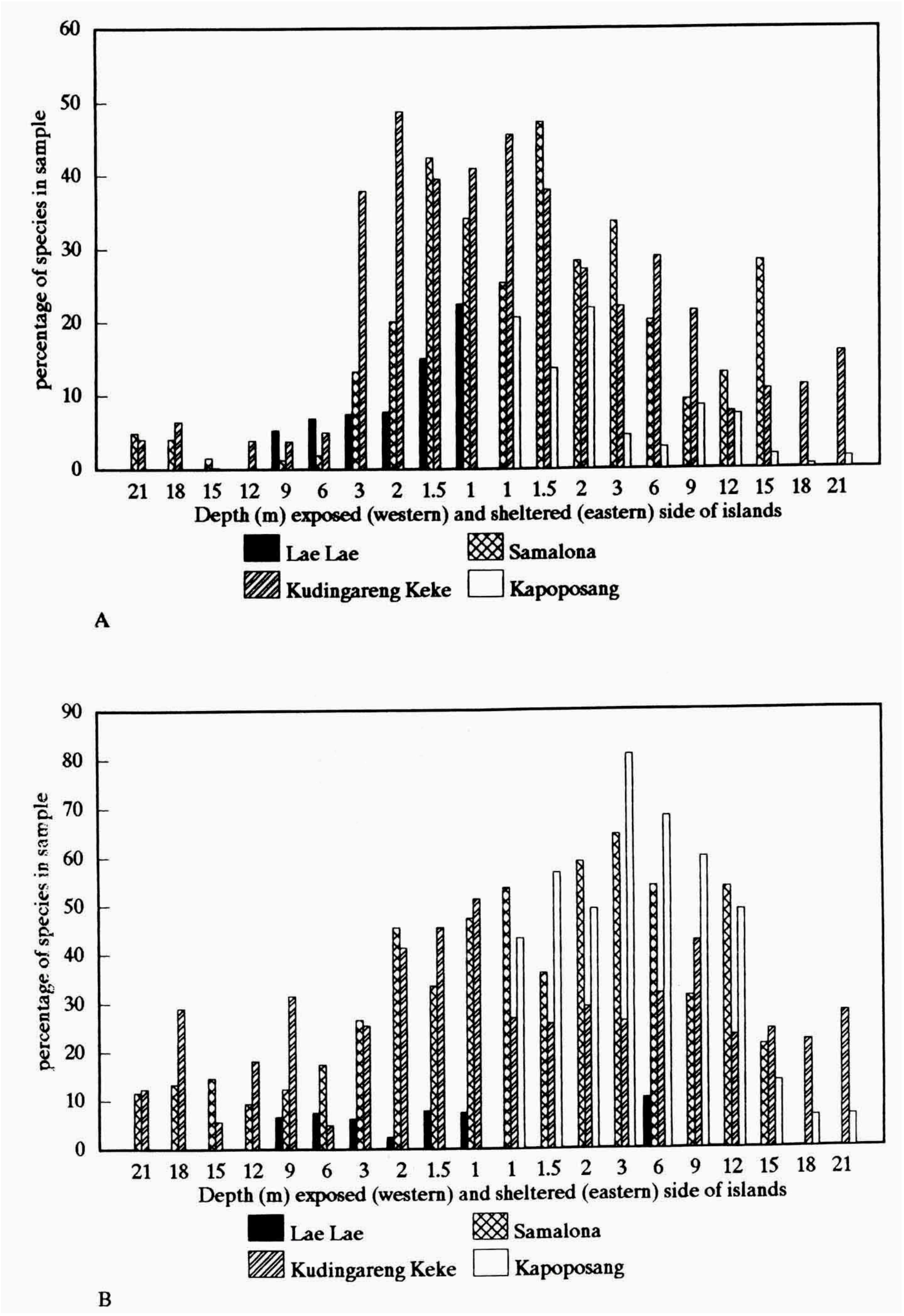


Fig. 4A-B. Frequency distribution of individual species with depth on the exposed (western, left) and sheltered (eastern, right) sides of the surveyed islands; A. *Amphistegina lobifera*; B. *A. lessonii*. For comments see text.

Areal distribution and additional observations — Fig. 4b shows the frequency distribution of *A. lessonii* along the sample transects. Further it is seen as epiphytic species on algae and seagrasses of the reef-flats and -slopes, particularly on Langkai.

Comments — *A. lessonii* is a shallow-water species living on hard substrate and as epiphyte on algae and seagrasses. It thrives on the reef-flats of both the mid- and outer-platform islands. Relatively poor occurrences at Lae Lae are thought to be related to poor light conditions. Although a typically shallow-water species its depth distribution is less limited than *A. lobifera* indicating an adaptation to lower light intensities. This is confirmed by Hallock (1981) who found that in cultures *A. lessonii* reproduces asexually at all available light levels and *A. lobifera* only at the highest. In contrast to the Gulf of Aqaba, where *A.lessonii* dominates the faunas of quieter lagoons or channels (Reiss & Hottinger 1984), on the Spermonde Platform it dominates high energy sites like the reef-flat and upper steep reefs of Kapoposang and Langkai. Reiss & Hottinger (1984) also found *A. lessonii* on hard bottoms and as epiphytes on *Halophila* and other plants.

Amphistegina radiata (Fichtel & Moll, 1798)
Fig. 4C

Symbiont type — Diatom. B4-type (Reiss & Hottinger, 1984).

Areal distribution and additional observations — The distribution of this species along the transects is given in Fig. 4C. It is also present in low frequecies on algae and seagrasses nea Kudingareng Keke, Bone Tambung and Barang Lompo.

Comments — This is a typical deeper-water species. It occurs on hard substrate and although not abundant also epiphytic on algae and seagrasses. It is common on the lower western reef-slope and -base of the mid-platform islands and the steep reef of the outer rim island. Lower frequencies are found on the leaward sides of the mid-platform islands supposedly due to the absence of hard substrates, because the coral rubble here is covered with a layer of fine-grained sediment. The species is virtually absent from the reefs around Lae Lae. The poor illumination of these reefs does not explain the absence of *A. radiata* because the deeper-water distribution on the mid-platform reefs shows its adaptation to low light intensities. A plausible explanation could be the high sedimentation rates around this island, covering the hard substrates with a layer of fine terrigenous sediment resulting in a low $CaCO_3$ content. The absence of *A. radiata* from the Gulf of Aquaba is explained by a possible lack of B4-type of diatoms in the bottom flora which provide symbionts to *A. radiata* after sexual reproduction (Reiss & Hottinger, 1984). The deeper-water distribution of *A.radiata* on the Spermonde Shelf is in agreement with the findings of Muller (1977) who stated that in the Western Pacific *A. radiata* begins to replace *A. lessonii* at depths of 10-20 m depending upon water clarity.

Heterostegina depressa d'Orbigny, 1826
Fig. 4D

Symbiont type — Diatom. B3d-type (Reiss & Hottinger 1984), *Nitzschia panduriformis* var. *continua* and other species (Leutenegger, 1984; Lee et al., 1989).

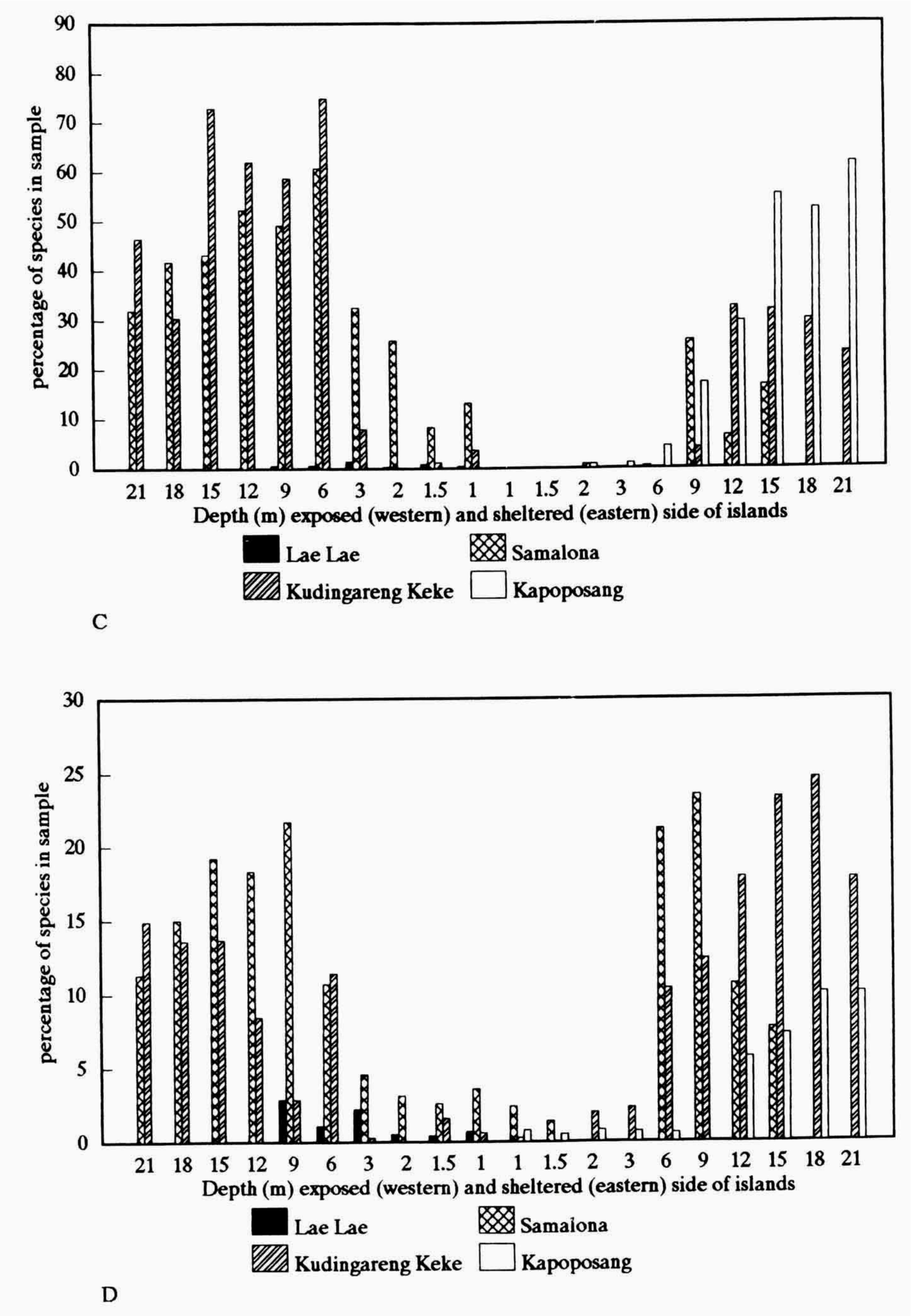


Fig. 4C-D. Frequency distribution of individual species with depth on the exposed (western, left) and sheltered (eastern, right) sides of the surveyed islands; C. *Amphistegina radiata*; D. *Heterostegina depressa*. For comments see text.

Areal distribution and additional observations — For the frequency distribution of this species along the transects see Fig. 4D. It is also found as a minor element at Kudingareng Keke, Bone Tambung, Langkai and Barang Lompo on hard substrates overgrown with algae and in shady shallow-water sites.

Comments — *H. depressa* is typically a deeper-water species on hard substrates and algae. Its almost absence on the reefs around Lae Lae is probably related to lack of hard substrates caused by the high sedimentation rates.It occurs deeper on Kudingareng Keke compared to Samalona, which is related to the higher water transparency on the former island. The relative low frequencies of the species on Kapoposan cannot easily be explained, exept in terms of water energy. The depth distribution in the Spermonde Area is in agreement with observations from the Gulf of Aquaba. Reiss & Hottinger (1984) determined the depth distribution of *H. depressa* from 20-130 m on hard bottoms and shallower in shaded areas in. Röttger et al. (1980) experimentally determined an optimum growth rate at lower light intensities (12-16 $Em^{-2}s^{-1}$) which is reflected in the field by a deeper water distribution. Feeding experiments proved that *H. depressa* does not engulf food, but that it lives entirely on its symbionts (Röttger et al., 1980). Schmaljohann (1980) concluded that *H. depressa* can thrive without food, while it is able to absorb all the nutrients it needs from sea water. These findings indicate that *H. depressa* is a truely oligotophic species reflected in its poor occurence on the eutrophic reefs of the Spermonde Archipelago.

Operculina ammonoides (Gronovius, 1781)
Fig. 4E

Symbiont type: Diatom. *Achnanthes maceneryae* and *Nitzschia laevis* and other species (Lee et al., 1989).

Areal distribution and additional observations — Fig. 4E shows the frequency distribution of this form along the transects. It is further found on algae at Kudingareng Keke, Bone Tambung and Barang Lompo but is conspicuously absent near Langkai and Kapoposang.

Comments — This is typically a deeper-water species, mainly on soft bottoms and on algae. The depth distribution in the Spermonde Area is similar to that of *H. depressa*. They also have the same diatom symbionts (Reiss & Hottinger, 1984) The lower frequencies of *O.ammonoides* compared to *H. depressa* in the Spermonde Area are a sampling artifact as systematically only coral rubble substrates were collected. As *O. ammonoides* prefers soft substrates, it is clearly underrepresented in this study.

The depth distribution in the study area is in agreement with findings from the Gulf of Aqaba where *O. ammonoides* is found from 20-130 m on soft sediments, sometimes even a few millimeters below the surface (Reiss & Hottinger, 1984). Although *O. ammonoides* prefers low light intensities and soft substrates, its occurrence on the eutrophic reefs of Lae Lae is poor. According to ter Kuile et al. (1987) feeding rates of *O. ammonoides*, like *H. depressa*, are low, marking it as a truely oligotrophic form. Its total absence from the outer rim reefs of Kapoposang and Langkai is possibly related to the prevailing high water energy regime.

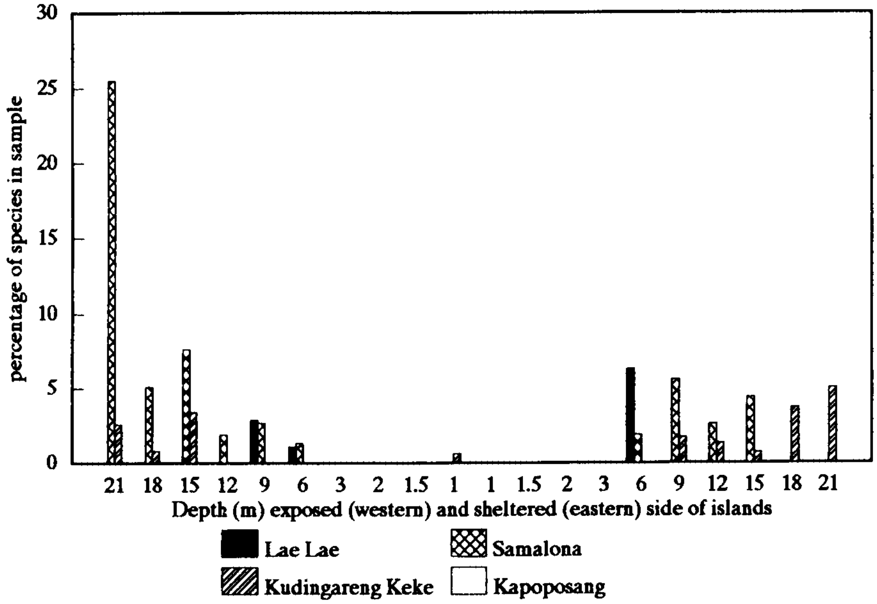


Fig. 4E. Frequency distribution of *Operculina ammonoides* with depth on the exposed (western, left) and sheltered (eastern, right) sides of the surveyed islands. For comments see text.

Amphisorus hemprichii Ehrenberg, 1839
Fig .4F

Symbiont type — Dinoflagellate. *Symbiodinium* sp. (Ross, 1974; McEnery & Lee, 1981; Lee and Lawrence, 1990).

Areal distribution and additional observations — See Fig. 4F for the frequency distribution of *A. hemprichii* along the transects. It further occurs on algae at Kudingareng Keke, Bone Tambung, Langkai and Barang Lompo; also in deeper water (down to 25 m). It has high densities at Langkai where aberrant forms with a second plane perpendicular to the first containing two embryos and severely folded species resembling flowers were also observed. *A. hemprichii* is very abundant on hard substrates of the reef-flat of Kapoposang. The tests strongly adhere to the substrate and are difficult to remove.

Comments — Although *A. hemprichii* shows a wide depth distribution, it is most abundant on hard substrates and algae in shallow waters near reef-crests where water-energy is high. Compared to other species this form can withstand high wave-energy which explains its high frequencies near Langkai and Kapoposang. The aberrant forms encountered here were also noted by Reiss & Hottinger (1984) in the Gulf of Aqaba. They explained this phenomenon as caused by short-time adverse conditions such as extreme temperature and salinity changes as may be expected in these shallow environments. High water-energy is thus an additional factor.

Feeding experiments demonstrate that Soritids are primarily dependent upon active feeding (Lee & Bock, 1976; ter Kuile et al., 1987) but do not survive in the dark when fed. Their growth thus depends on food and light (Faber & Lee, 1991). Reiss & Hottinger (1984) state that growth of *A. hemprichii* under natural conditions is correlated to some extent with the availability of food, in particular diatoms. It reacts quickly to the amount of nutrients in the sea- water.

Sorites orbiculus Ehrenberg, 1839
Fig. 4G

Symbiont type — Dinoflagellate. *Symbiodinium* sp. (Leutenegger, 1977).

Areal distribution and additional observations — Frequencies of this form along the transects are given in Fig. 4G. The species was further found on algae and seagrasses at Kudingareng Keke, Bone Tambung, Langkai and Barang Lompo at various depths (0.5-20 m). Barang Lompo seagrass samples from reef-flat show 25-65% epiphytic *S. orbiculus.*

Comments — In the Spermonde Archipelago this form lives epiphytic on algae and seagrasses, with highest frequencies on reef-flats. Locally it is the dominant species on seagrass-leaves.It has insignificant occurrences on hard substrates. In the Gulf of Aqaba *S. orbiculus* is limited by the 35 m isobath and is frequent in very shallow *Diplanthera* meadows (Reiss & Hottinger, 1984).

Sorites marginalis (Carpenter, 1856)

Symbiont type — Dinoflagellate. *Symbiodinium* sp. (Müller-Merz & Lee 1976).

Areal distribution — this species has minor occurrences on midshelf reefs.

Additional observations — Regular discoid-shaped forms with a distinct green color are found free on the sediments.

Comments — In the Spermonde Archipelago this species is found iin low numbers around the deeper midshelf reefs. According to Müller-Merz & Lee (1976) this species is an active algal eater.

Archaias angulatus (Fichtel and Moll 1798)
Fig. 4H

Symbiont type — Chlorophyte *Chlamydomonas hedleyi* (Lee et al., 1974).

Areal distribution — The frequency distrbution of this form is shown in Fig. 4H.

Comments — Only scarce shallow-water occurrences of this species were encountered in the Spermonde Area. Lee et al. (1974) report high frequencies of this species in the shallow water of Florida Keys associated with the micro-habitat of *Thallassia testudinum* stems. In the Spermonde Area *A. angulatus* is probably an unsuccesfull competitor in the environments studied.

Feeding experiments demonstrate that this species requires food and can not grow solely on organic compounds produced by its endosymbionts (Faber & Lee, 1991).

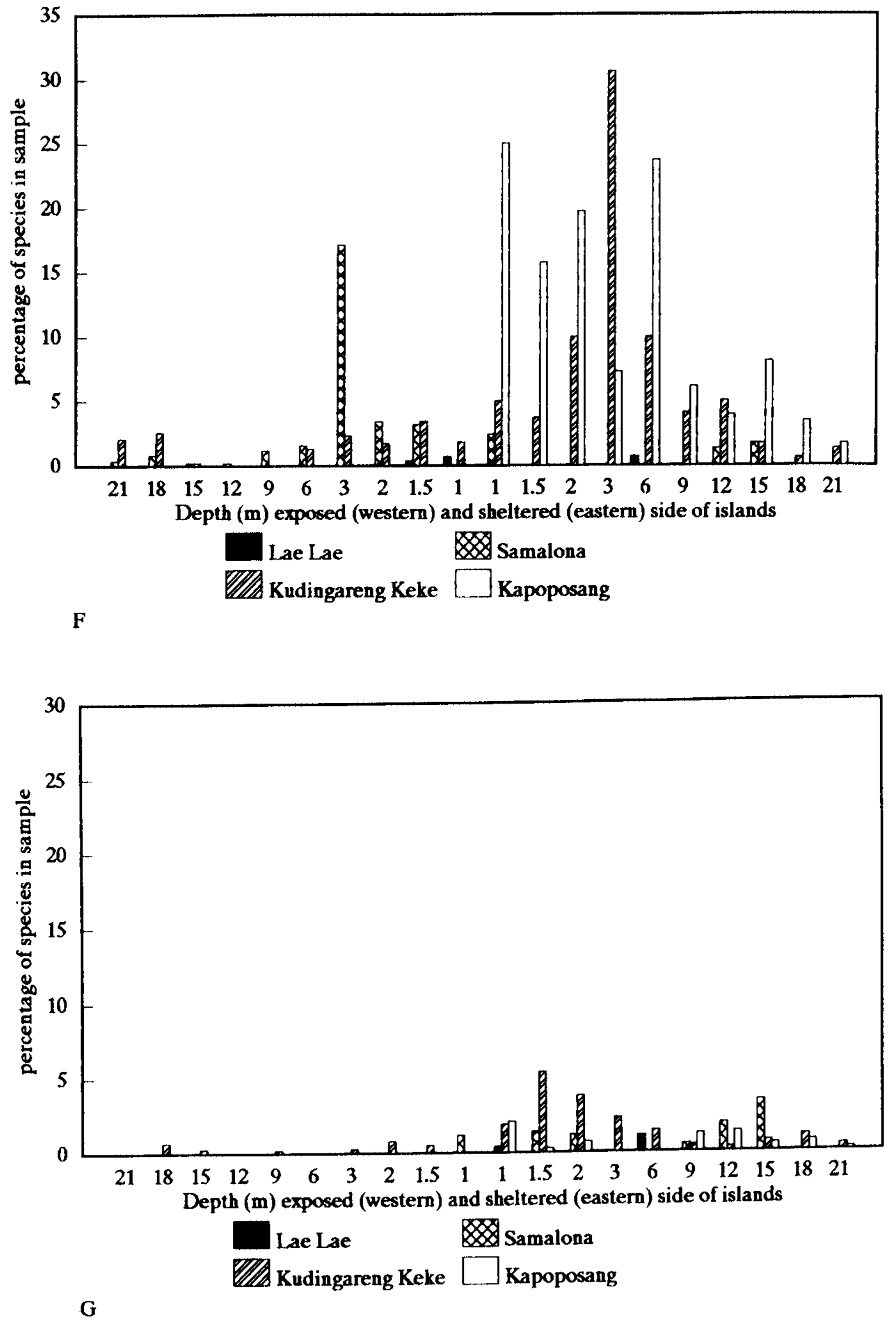


Fig. 4F-G. Frequency distribution of individual species with depth on the exposed (western, left) and sheltered (eastern, right) sides of the surveyed islands; F. *Amphisorus hemprichii*; G. *Sorites orbiculus*. For comments see text.

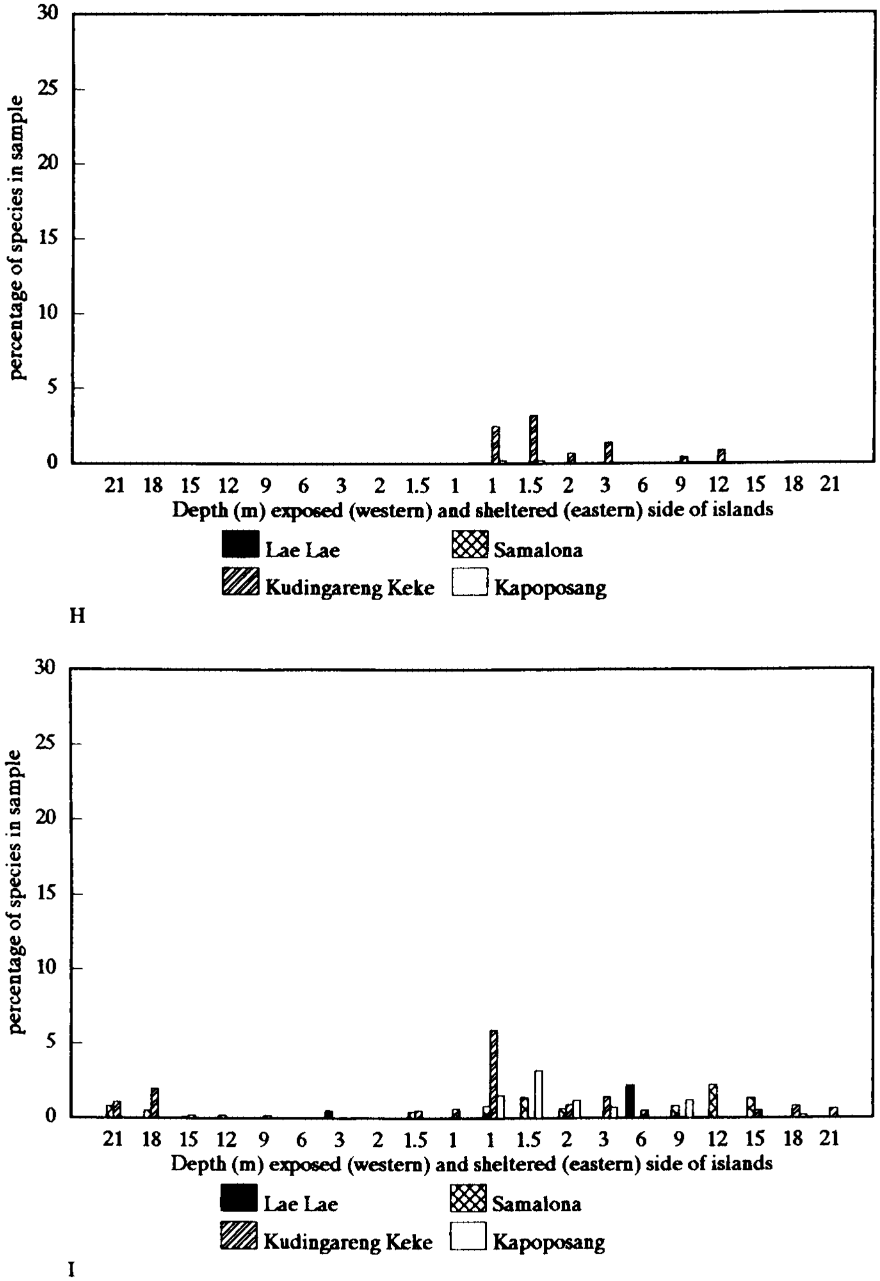


Fig. 4H-I. Frequency distribution of individual species with depth on the exposed (western, left) and sheltered (eastern, right) sides of the surveyed islands; H. *Achaias angulatus*; I. *Peneroplis* spp. For comments see text.

Peneroplis pertusus Forskål, 1775 and *P. planatus* (Fichtel & Moll, 1798)
Fig. 4I

Symbiont type — Rhodophyte. *Porphyridium purpureum* (Leutenegger, 1984; Lee, 1990).

Areal distribution and additional observations — In Fig. 4I the frequency distrbution of the genus *Peneroplis* along the transects is given. Both species are present on seagrasses and algae at Kudingareng Keke, Bone Tambung, Barang Lompo and Langkai at various depths (0.5-15 m). They can withstand exposure during low tides on the reef-flats.

Comments — In the study area the peneroplids show a widespread distribution pattern, but they are never dominant. Feeding experiments indicated that *P. planatus* needs both light and food for growth and survival (Faber & Lee, 1991).

Calcarina calcar (d'Orbigny, 1839)
Fig. 4J

Symbiont type — Diatom. *Nitzschia frustulum* var. *symbiotica* and other species (Hottinger & Leutenegger, 1980; Lee et al., 1989).

Areal distribution and additional observations — Fig. 4J shows the distribution of *C. calcar* along the sampled transects It further occurs abundantly on the reef-flats of Kudingareng Keke, Bone Tambung, Barang Lompo and Langkai as epiphyte on algae and sea-grasses. It is also present on algae in deeper water (down to 22 m) but not abundant. During low tide it can withstand exposure.

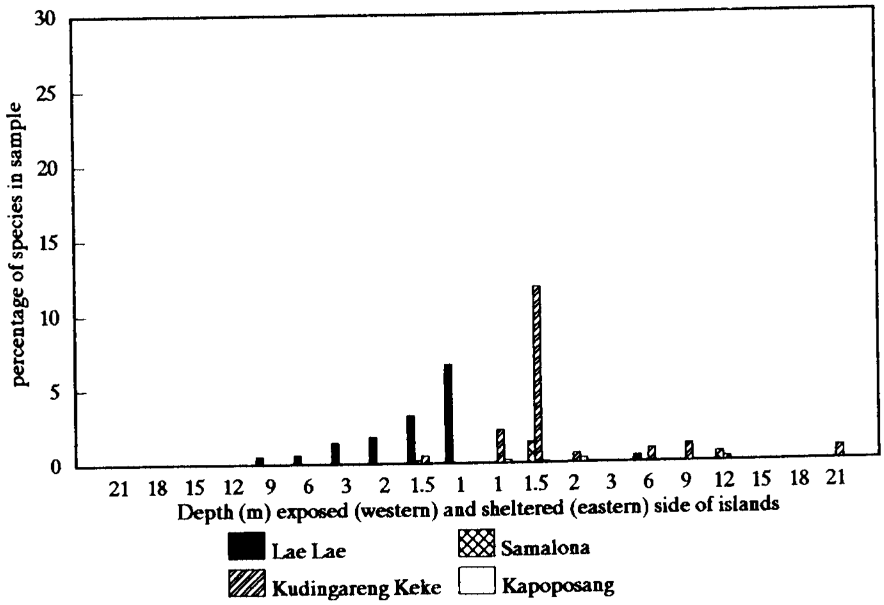


Fig. 4J. Frequency distribution of *Calcarina calcar* with depth on the exposed (western, left) and sheltered (eastern, right) sides of the surveyed islands. For comments see text.

Comments — *C. calcar* is a shallow water species which lives epiphytic on seagrasses and algae around all surveyed reefs in the Spermonde Archipelago. It is less abundant on hard substates. The species shows is common on the western reef of Lae Lae and thus has a tolerance to eutrophic conditions.

Calcarina hispida Carter, 1880
Fig. 4K

Symbiont type — Diatom. *Nitzschia frustulum* var. *symbiotica* (Lee & Anderson, 1991).

Areal distribution and additional observations — See Fig. 4K for the frequency distribution of this species. It is rare to abundant as an epiphyte on seagrasses and algae from Kudingareng Keke, Bone Tambung, Barang Lompo and Langkai (0.5-22 m). It tolerates exposure during low tide.

Comments — *C. hispida* occurs abundantly as an epiphyte on algae and seagrasses in a wide depth range around the islands of the three outer strips. Rare occurrences are noted on the reefs from Lae Lae, probably related to the prevailing eutrophic conditions. The species is prominent at the outer rim reefs of Langkai and Kapoposang, suggesting its tolerance to high water movement. Röttger & Krüger (1990) found this species as epiphytes on clumps of *Cladophyora* covering the sandy sea floor of seagrass meadows.

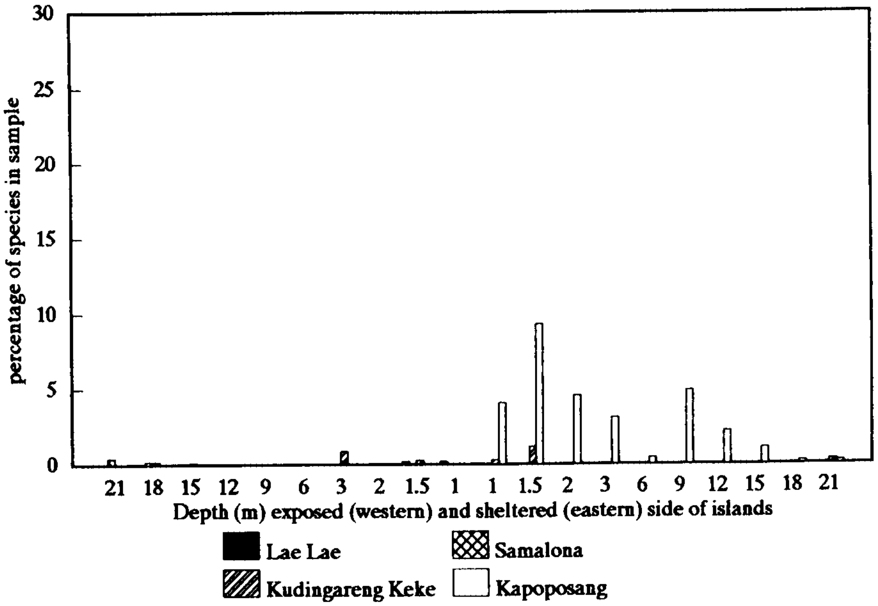
Calcarina spengleri (Gmelin, 1791)
Fig. 4L

Symbiont type — Diatom. *Nitzschia frustulum* var. *symbiotica* (Lee & Anderson, 1991).

Areal distribution and additional observations — The distribution of this species along the studied transects is given in Fig. 4L. It is also present on algae in deeper water at Kudingareng Keke, Bone Tambung, Barang Lompo and Langkai (3-22 m).

Comments — *C. spengleri* is found in all reef zones of the reefs surveyed in the Spermonde Archipelago both on on algae and hard substrates. It is a dominant species on the eutrophic reefs of Lae Lae, indicating adaptation to low light intensities and high sedimentation rates. This species might be an active eater, independent of its endosymbionts when particulate organic compounds are available. On the other oligotrophic reefs of the Spermonde Platform, *C. spengleri* is not dominant but conspicuously present, thus able to compete succesfully with more specialized oligotrophic species. At the outer rim island Kapoposang it is only found in deeper water exhibiting a flattened test in contrast to shallow-water spheroid tests.

The distribution patterns of *C. spengleri* in the Spermonde Archipelago show it to be an opportunistic species which flourishes in eutrophic environments but can also compete succesfully with other species in an oligotrophic situation. According to Röttger & Krüger (1990) the calcarinid family is restricted to shallow water considering their thick walls which provide protection from high insolation and energetic wave action. This restriction is not reflected by the depth distribution of the flat-shelled *C. spengleri* occurring in the deeper reef parts (15-30 m) of Kapoposang.



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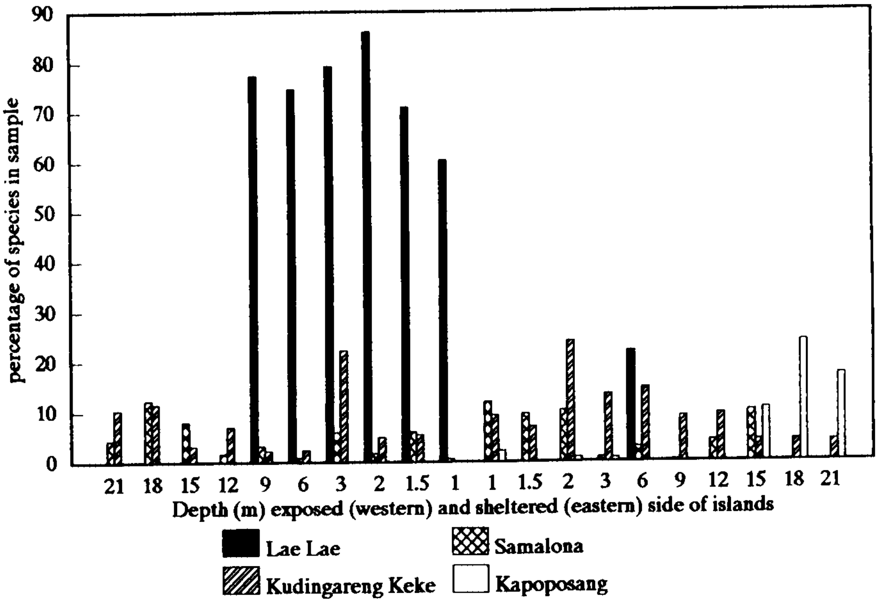


L

Fig. 4K-L. Frequency distribution of individual species with depth on the exposed (western, left) and sheltered (eastern, right) sides of the surveyed islands; K. *C. hispida*; L. *C. spengleri*. For comments see text.

Calcarina gaudichaudii d'Orbigny, 1840

Symbiont type — Diatom (Röttger & Krüger, 1990).

Areal distribution and additional observation — This species is relatively rare in the study area. It was not found on hard substrates but only incidentally in high numbers as epiphyte on algae in shallow waters of the mid-shelf islands reef-flats.

Comments — Around Belau Röttger and Krüger (1990) encountered this species in shallow water (1 m).

Baculogypsina sphaerulata (Parker & Jones, 1860)

Fig. 4M

Symbiont type — Diatom. *Nitzschia frustulum* var. *symbiotica* (Lee & Anderson, 1991).

Areal distribution and additional observations — Fig. 4M shows the frequencies of this form along the transects. Besides it is common on lower western reef-slope of Barang Lompo. During the reconnaissance inventory it was encountered on algae at the western reef-base of Bone Tambung, the eastern reef-base of Langkai and the western reef-slope of Barang Lompo.

Comments — *B. sphaerulata* has a patchy distribution. Locally it can be a prominent species, found predominantly in deeper water at the western sides of islands both on hard substrates and on algae. The relationship between its distribution and environmental parameters is not clear. This species might be competitive preferring specific algal substrates or other micro-habitats. It is confined to oligotrophic reefs. Leutenegger (1983) and Sokai & Nishira (1981) considered *B. sphaerulata* a shallow water species confined to the reef-flat. This is not in accordance with its distribution in the Spermonde Archipelago where it is encountered only in the deeper parts of the reefal environments.

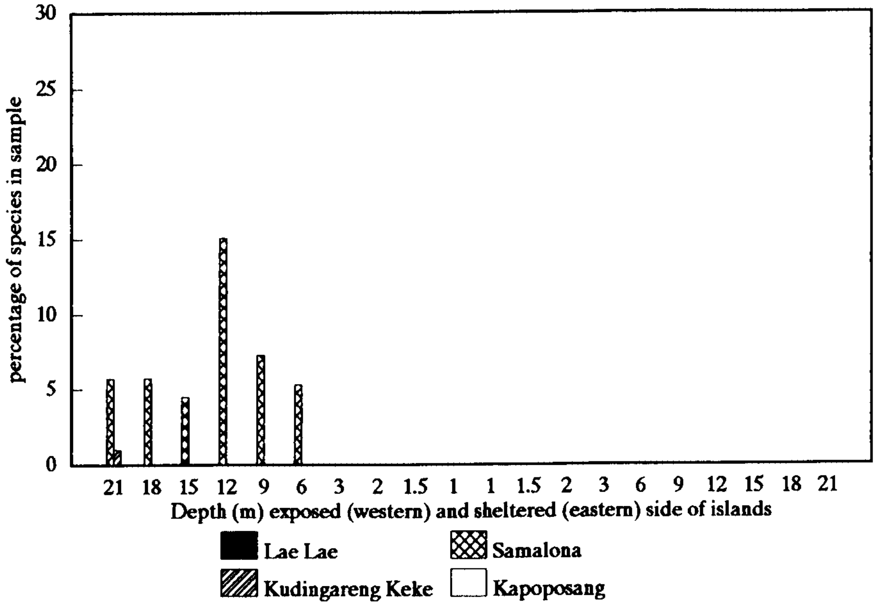
Elphidium craticulatum (Fichtel & Moll 1798) and *E. crispum* (Linné, 1758)

Fig. 4N

Symbiont type — Chloroplast husbandry of diatom origin (Lopez, 1979; Reiss & Hottinger, 1984; Lee & Anderson 1991).

Areal distribution and additional observations — See Fig. 4N for the frequency distribution of *Elphidium* spp. along the transects. The specimens near Lae Lae are green-colored, either as result of feeding or a sign of chloroplast husbandry.

Comments — In the Spermonde Area these species flourish only in the most eastern part of the Lae Lae reefs which are characterized by a very poor water transparency, high sedimentation rate and low carbonate content of the sediment (Table 1). Salinities are variable due to river runoff, especially in the wet season In this environment *Elphidium* spp. are highly competitive with the symbiont-bearing species in contrast to the oligotrophic sites in the Spermonde Archipegalo.



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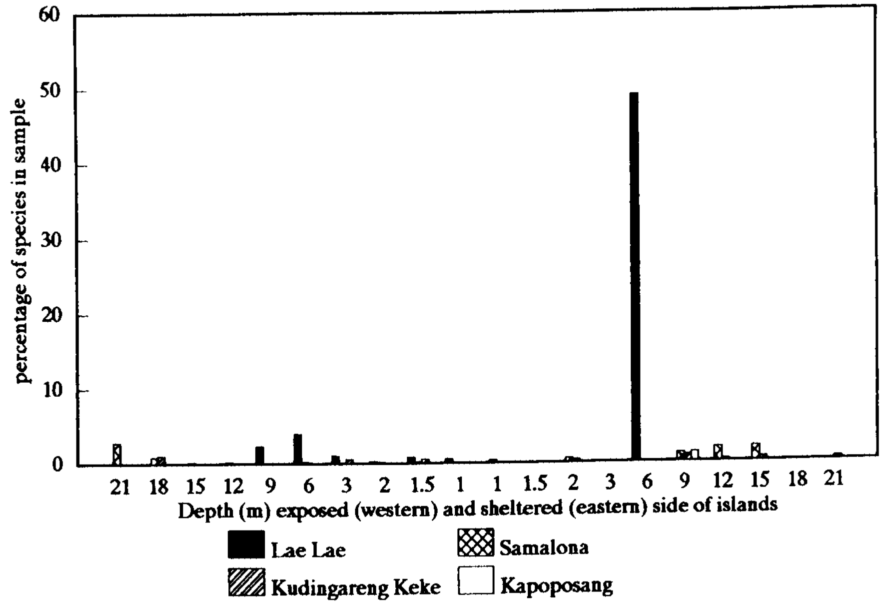

N

Fig. 4M-N. Frequency distribution of individual species with depth on the exposed (western, left) and sheltered (eastern, right) sides of the surveyed islands; M. *Baculogypsina sphaerulata*; N. *Elpidium* spp. For comments see text.

Alveolinella quoii (d'Orbigny)

Symbiont type — Diatom. *Fragilaria shiloi* and other species (Leutenegger, 1984; Lee et al., 1989).

Areal distribution and additional observations — This species was found only on the sandy reef-base (20-30 m) of the mid-shelf islands half buried in the surface sediments. It is characterized by a striking red color.

Comments — *A. quoii* is confined to the sandy reef base of the coral islands. They occur in low numbers. Lipps (1991) found this species living epifaunally on stable sand-slopes at the inside of the reef lagoons.

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