The Effect of Crustaceans on the Taphonomy of Reefs in Phuket, South Thailand

by

Clare Bradshaw

Submitted for the degree
of Doctor of Philosophy

University of Edinburgh
May 1997

DECLARATION

This thesis was researched and written by myself, except where specifically stated.

ABSTRACT

This study investigates the role of present day crustacean bioerosion and bioturbation in the development and taphonomy of a muddy coral reef environment (Phuket, South Thailand). At the main locality, a 200m wide, 400m long, intertidal fringing reef flat drops 3m on to a muddy sea bed where fine surface sediments comprise 80% terrigenous clays. Adjacent intertidal sand waves and tidal pools are composed of gravel- to sand-size sediments. *In situ* experimentation involved transect and quadrat surveys, resin casting and airlift excavation of burrows, coring, measurement of sediment turnover rates and direct observation of sediment mixing using tracer sediment. Grain size analysis, carbonate content determination and microscopy studies of sediments, borers and coral growth patterns were carried out in the laboratory.

Crustacean bioerosion, especially the 'passive' boring by hapalocarcinid crabs, pyrgomatid barnacles and alpheid shrimps, alters coral colony morphology which in turn affects reef development. Reef progradation relies on the continued growth of large coral boulders that have fractured along large upogebiid and alpheid boreholes and then toppled from the reef front on to the fore-reef slope. Bioerosion also results in the production of calcareous sediment. Active erosion by upogebiid and alpheid shrimps directly produces grains in the gravel to silt size range. Coral colonies weakened by boring are prone to physical disintegration into boulder- to silt-sized fragments.

Crustacean bioturbation, mainly by callianassid and alpheid shrimps and *Dotilla* crabs, is abundant in both intertidal and subtidal reef sediments. The subtidal sediment slope shows an offshore zonation of crustacean burrowers. Simple, sloping burrows of near-reef alpheids give way to deep, spiral off-reef alpheid burrows and then to complex *Thalassinoides*-type burrow networks of callianassids offshore. Burrow distribution seems to be related to the grain size and sediment thickness of the slope. Tiered burrows, in densities of up to $350/m^2$, were measured subtidally. Depths of turnover of up to 25cm (subtidal callianassid and alpheid shrimps) and turnover rates of up to $0.4m^3/m^2$/year ($550kg/m^2$/year; *Dotilla* crabs) were calculated. Subtidal bioturbation rates are three times the rate of sediment accumulation on the fore-reef slope. Biogenic sorting of sediment occurs, with subtidal callianassids burying coarse grains in shelly pockets at depths of >25cm, thereby maintaining a relatively gravel-free surface layer. In contrast, intertidal and near-reef alpheids

sort grains to produce a heterogeneous distribution of gravel patches exposed at the sediment surface.

In off-reef, subtidal areas dominated by alpheids, the gravel fractions showed higher levels of degradation (abrasion and microbioerosion) when compared to that of the callianassid area. This is attributed to the continual re-exposure to surface processes of these grains by alpheids during their burrowing activity, whereas callianassids bury coarse grains well below the sediment/water interface. In contrast, the incorporation of bioeroded grains into mud linings by the shrimp *Upogebia* may increase the preservation potential of these skeletal fragments.

The abundant and diverse epifaunal traces are unlikely to be preserved due to continual reworking by waves and tides. At one locality, a storm in 1985 destroyed the reef and completely altered the intertidal and subtidal sediments. Eight years after the storm the sedimentary record, as revealed by coring and airlift excavation, is dominated by this single event. However, biogenic overprinting by deep tier burrowers (alpheids and callianassids) is visible.

Bioturbation features, such as burrow linings and faecal remains, were not found lithified in this relatively low salinity environment. This decreases their preservation potential. It is likely that burrows will be compacted on burial and their former existence reflected ultimately as nodules, lenses and layers of coarse skeletal grains in fine-grained, terrigenous-rich sediments.

Under steady state conditions of slow sediment accretion the reefs will gradually prograde seawards, resulting in a shallowing-upwards sequence in the geological record, from off-reef sediments through near-reef sediments through reefal deposits to back-reef muds, sandy beach deposits and ultimately soils.

CONTENTS

APPENDIX A - REEF & CORAL DATA

B - SEDIMENT CHARACTERISTICS

3. Breakdown of coarse (>5mm) fraction by components - details and summary for all cores
4. Extent of degradation of >5mm diameter infaunal bivalve fragments in alpheid and callianassid areas
5. Carbonate content for cores
6. Weight: volume relationships of intertidal and subtidal sediments.
7. Sediment water content (subtidal callianassid and off-reef alpheid areas).
8. Substrate analysis of intertidal sand waves and tidal pools in Tang Khen Bay

C - SPECIFIC BIOGENIC SEDIMENT DATA

1. *Dotilla* burrow measurements and densities
2. Feeding and excavation pellet data *(Dotilla)*
3. Grain size distributions for profiles through the intertidal *Dotilla* area
4. Intertidal callianassid burrow measurements
5. Intertidal alpheid burrow measurements and shovelling frequency
6. Grain size of intertidal callianassid mounds, burrow measurements of subtidal callianassids and grain size of intertidal sipunculid casts.
7. Total burrow densities for the subtidal sediments

D - BIOEROSION DATA

1. Barnacle hole measurements
2. Hapalocarcinid and *Upogebia* hole measurements
3. Catalogue of hapalocarcinid samples
4. Sexual dimorphism of hapalocarcinids and their boreholes
5. Bioerosion by *Lithophaga*
6. *Lithophaga* borehole measurements

E - PUBLISHED PAPER

Bradshaw C (1997 in press) Bioturbation of Reefal Sediments in Phuket, Thailand. Proceedings of the 8th International Coral Reef Symposium, Panama 1996.

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

LIST OF PLATES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

CHAPTER 1

INTRODUCTION

This chapter first outlines the objectives of this research (1.1). The work is then put in context by describing the study area, both on a broad scale (1.2) and at the site level (1.3), and summarising the current state of knowledge about the area (1.4). Section 1.5 provides details on the methods used to obtain the data in this project, both in the field and in the laboratory, and the chapter ends with sections 1.6 (important terminology) and 1.7 (thesis layout).

1.1 OBJECTIVES

The main aim of this study was to investigate how the taphonomy of reefs is influenced by crustaceans. Taphonomy is the entire post-mortem history of skeletal grains, including all the processes leading to fossilisation (Scoffin 1992, Clarkson 1993). This study concentrates on two main aspects of early taphonomy, bioerosion and bioturbation. By examining processes occurring in a modern reef system in Phuket, Thailand, it was hoped that some wider-ranging questions could be answered regarding the preservation of reefs and their sediments.

Reef sediments are composed (partly or solely) of the skeletons of reef organisms such as corals, bryozoans, calcareous algae, bivalves, barnacles, bryozoans and echinoids. The initial transformation of coral reef to calcareous debris in the reef sediment is brought about not only by physical breakdown but by bioerosion. Reef framework is either actively removed or weakened by biological erosion. On the reefs of Laem Panwa (Fig. 1.1), the study site in this work, four crustacean bioeroders are common, alpheid and upogebiid shrimps, hapalocarcinid crabs and pyrgomatid barnacles. The gross and fine morphologies of their boreholes were investigated in order to address the following questions:

- How do these crustaceans affect reef breakdown and sediment production?
- Will their activities be recorded in the fossil record and, if so, how will we recognise them and what will they tell us about the origins of reef structure?

Once a skeletal grain has reached the sediment, it still has some way to go before it reaches its final position of preservation. During a grain's time in the sediment it may be exposed to a combination of further physical reworking, chemical microenvironments and biological reworking, all of which affect its preservation. Bioturbation, the disturbance of sediment by animal activity, is a powerful agent of sediment processing in the intertidal and subtidal sediments of Phuket, the main bioturbators being three types of crustaceans, soldier crabs (*Dotilla myctiroides*), alpheid and callianassid shrimps. The preservation of individual grains and features within the sediment, especially biogenic traces, were studied using a wide range of techniques both above and below water. The following questions were considered:

- What effect do the crustacean burrowers have on the sediment, in terms of grain mixing or sorting and burrow formation?
- Will their activities be recorded in the fossil record and, if so, how will we recognise them and what will they tell us about the origins of reef structure?

Although a lot of work has been done on tropical carbonate sediments, little has been done on sediments such as these, which are rich in terrigenous clays.

1.2 THE STUDY AREA

1.2.1 Location (see Fig. 1.1a and b)

Ko Phuket (Phuket island) is the largest island in Thailand (50km long by 20km wide) and lies off the SW coast of the Thai Peninsula at 8°00'N and 98°20'E. To the west is the Andaman Sea (East Indian Ocean), and to the north-east are the relatively sheltered waters of the vast (1500km^2) Ao Phangnga (Phangnga Bay). Run-off from the large catchment area of Ao Phangnga results in turbid, muddy water and the coast there is fringed with mangroves. The topography of Phuket is generally hilly ('Phuket' is from the Malay 'Bukit' meaning 'hill') and covered in tropical vegetation, be it rubber or coconut plantations, or forest.

1.2.2 Climate

The island has a monsoonal climate. During the NE monsoon from October to May, light northeasterlies bring dry (50mm rain/month) and increasingly hot (up to 37°C) weather from mainland Asia. From May to October, the SW monsoon results in high rainfall (300mm/month), stronger winds, and relatively cool temperatures (down to 24°C during the

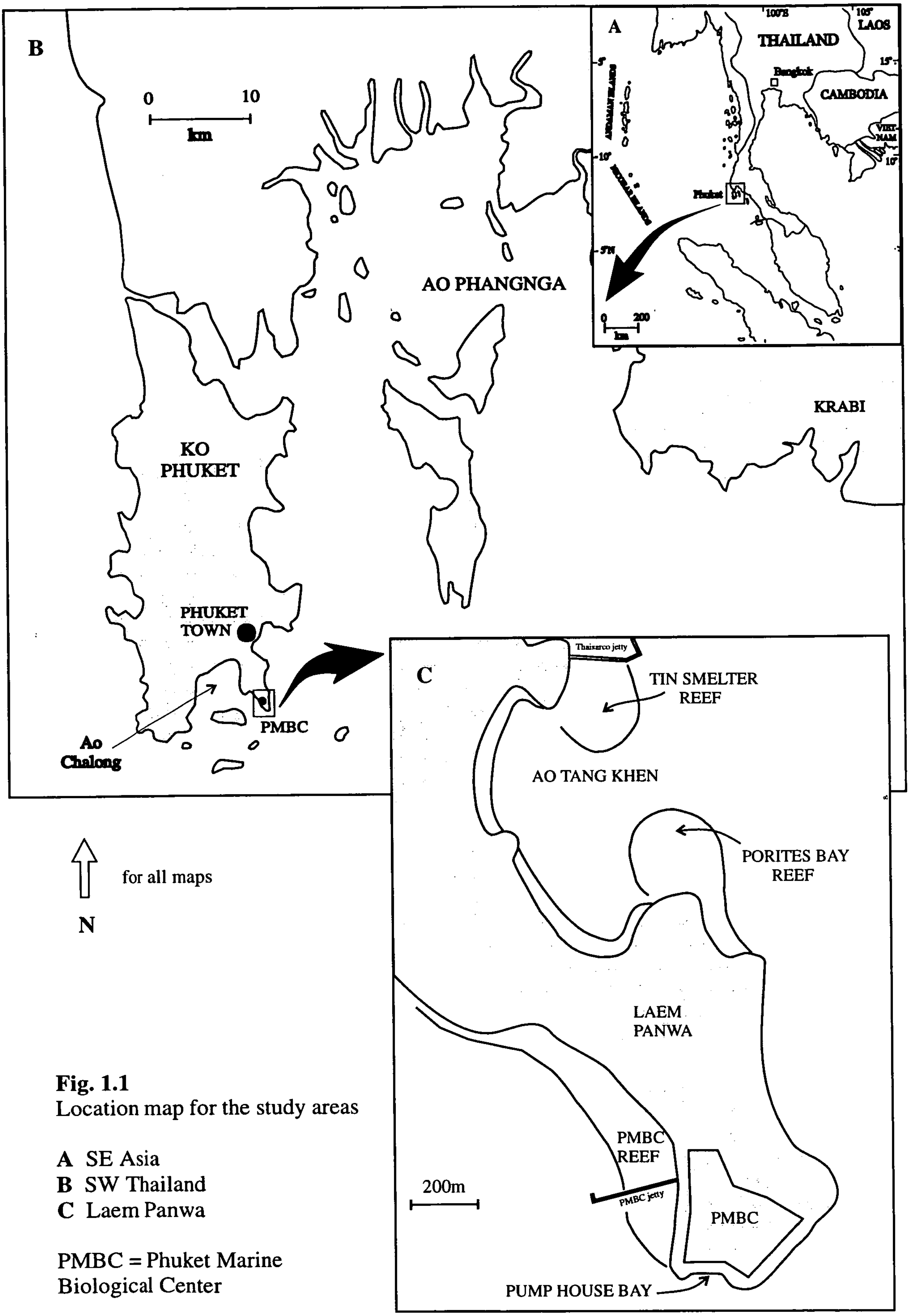


Fig. 1.1
Location map for the study areas

A SE Asia
B SW Thailand
C Laem Panwa

PMBC = Phuket Marine Biological Center

day). The island is not in the hurricane belt, though the weather may be stormy during the SW monsoon.

1.2.3 Sea conditions

A combination of this monsoonal climate and the presence of the turbid water body to the NE of the island strongly influences the shoreline characteristics and reef development (Brown and Holley 1984). On the east coast sedimentation rates are high year round as the sea is generally calm during both monsoons, due to the sheltering effect of the mainland. Reefs are almost totally absent from the east coast, probably due mainly to the large quantities of fine sediment from Ao Phangnga; large stands of mangrove and muddy bays are common on further north on this coast. Scoffin et al (1997) measured turbidity on the reef flat of Tin Smelter Reef as 20mg/l, though this may be greater than 47mg/l during the SW monsoon (Limpsaichol 1981).

The west coast consists of a series of sandy bays and rocky headlands, but despite less muddy input than the east coast, reefs are fairly poorly developed, perhaps due to the rough seas during the SW monsoon. In the Phuket area, the reefs with highest coral diversity and live coral cover are found on some of the offshore islands where the water is clearer and deeper (e.g. Ko Phi Phi, Ko Dok Mai, Ko Mai Thon, Ko Racha). However, the south-east corner of Phuket, Laem Panwa (Cape Panwa), has the most extensive reef flats in Phuket, at PMBC (Phuket Marine Biological Center) Reef, Porites Bay Reef and Tin Smelter Reef in Ao Tang Khen. It was the latter that was the reef study site (Figures 1.1c and 1.3).

The area has semidiurnal tides with a range of up to 2.8m during spring tides, and as little as 0.4m during neaps. Tidal currents can be very strong, especially on spring tides. Channelling of water between the main island and smaller islands in Ao Chalong (see Fig. 1.1a) can result in unidirectional currents around this area (Limpsaichol 1981). At Pump House Bay it is almost impossible to predict when slack water will occur although it is generally within an hour either side of high or low water; this may also be due to channelling. Slack water is very short, ranging from half an hour to a few minutes (pers. obs. diving on neap tides only). Sea surface temperatures range from 26-31°C (Limpsaichol 1981).

The high fresh water input from terrigenous run-off in this area may be responsible for the relatively low levels of carbonate saturation in the sea water. As a result, beachrock and other marine cements are rare.

1.2.4 Geology

Ao Phangnga (especially in the north) is characterised by its spectacular limestone karst landscape, with vertically-sided, mangrove-fringed islands rising out of the green water. This tower karst is part of the Permian Rat Buri formation (Carr 1992).

Phuket itself has many tin-rich granite and pegmatite outcrops of Cretaceous age, especially in the south and west, and Quaternary weathering of these rocks has resulted in the accumulation of thick marine deposits (Garson et al 1975, Carr 1992). These onshore rocks are mined and the offshore sediments dredged for their tin. Tin production is a major source of income for the region. Some tin is smelted in the immediate vicinity of one of the study areas, Ao Tang Khen (Fig. 1.2). The immediate area around PMBC (Phuket Marine Biological Center) has phyllite beds which are well exposed on the coast (see Plate 1.3).

The marine sediments around Laem Panwa are a mixture of land-derived sediments and reef-derived carbonates. The terrigenous material originates from the weathering of granites and sedimentary rocks to produce kaolinite and illite clay minerals and quartz silt and sand (Carr et al 1991). The majority of this terrigenous sediment is transported by currents and tides from Ao Phangnga to the north-east. The percentage mix of reef- and land-derived sediment varies with proximity to reefs, distance off shore (Carr et al 1991) and depth within the sediment (sections 3.3, 3.4, 4.6.3).

1.3 SITE DESCRIPTIONS

1.3.1 Ao Tang Khen and Tin Smelter Reef

In the SE of Phuket is Laem (Cape) Panwa, which comprises a series of rocky headlands and bays. On the eastern side of Laem Panwa lies Ao Tang Khen (Fig. 1.2, Plate 1.1), a shallow bay of about $0.5km^2$, which at spring tides is exposed for 4-5 hours every low tide to reveal a series of sand waves (wavelength 40m, height 0.4m), interspersed with shallow (max. 0.2m deep) sandy/rocky pools. These features run more or less parallel to the shore. Ao Tang Khen sand flats were the study site for intertidal burrowers. The north and south ends of the bay are slightly more sheltered than the central sand wave area and are the exits

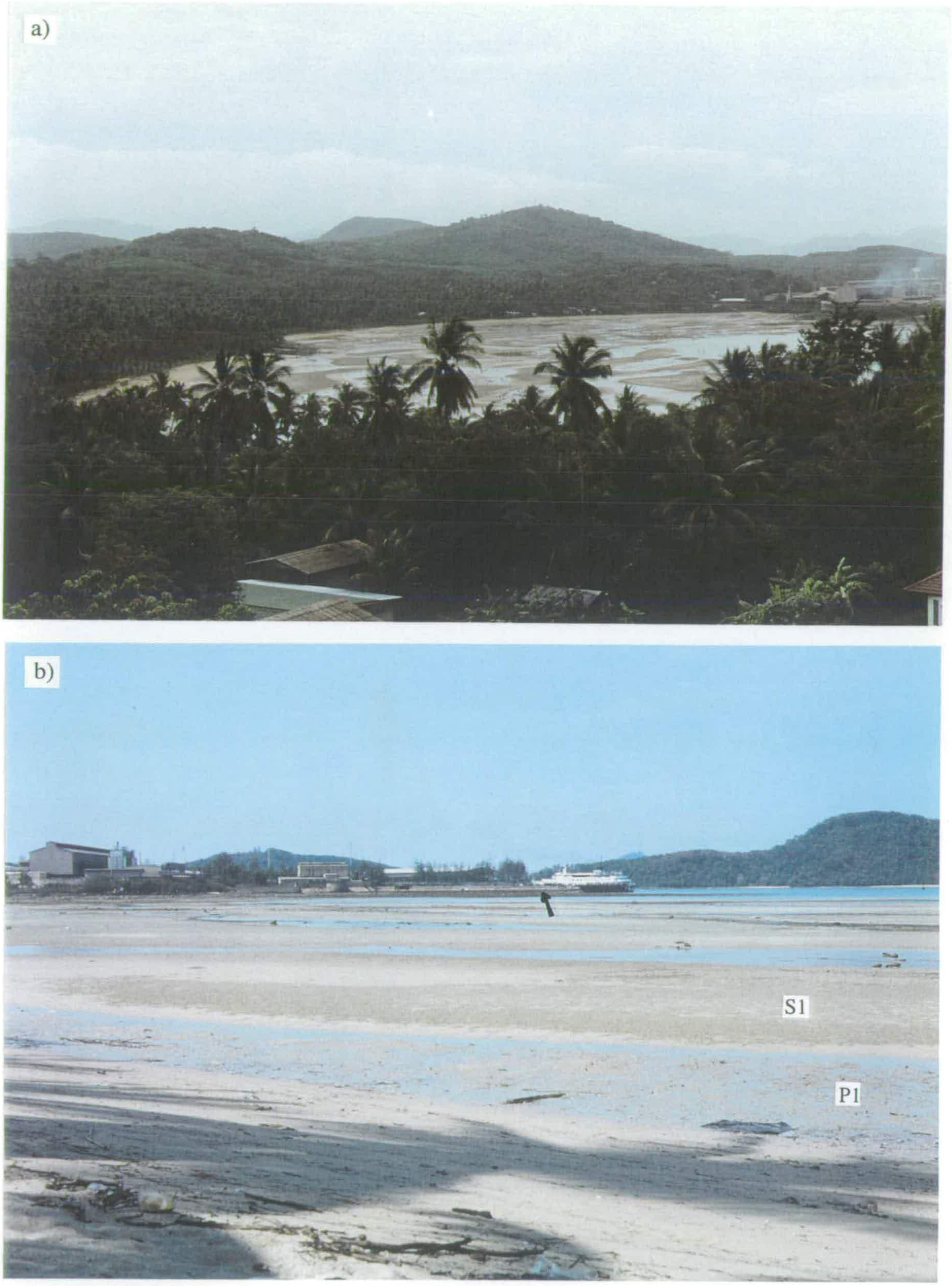


Plate 1.1 Tang Khen Bay. **a)** View from Panwa Hill looking NW across the bay at low water springs; note the alternating sand waves and pools. **b)** View from the beach looking NE. In the foreground is the beach and Pool 1 (P1); note how shallow this pool is. Behind Pool 1 on Sand wave 1 (S1) the darker area is covered in pellets from *Dotilla* activity. The dark brown streak near the jetty in the background is Tin Smelter Reef (arrow).

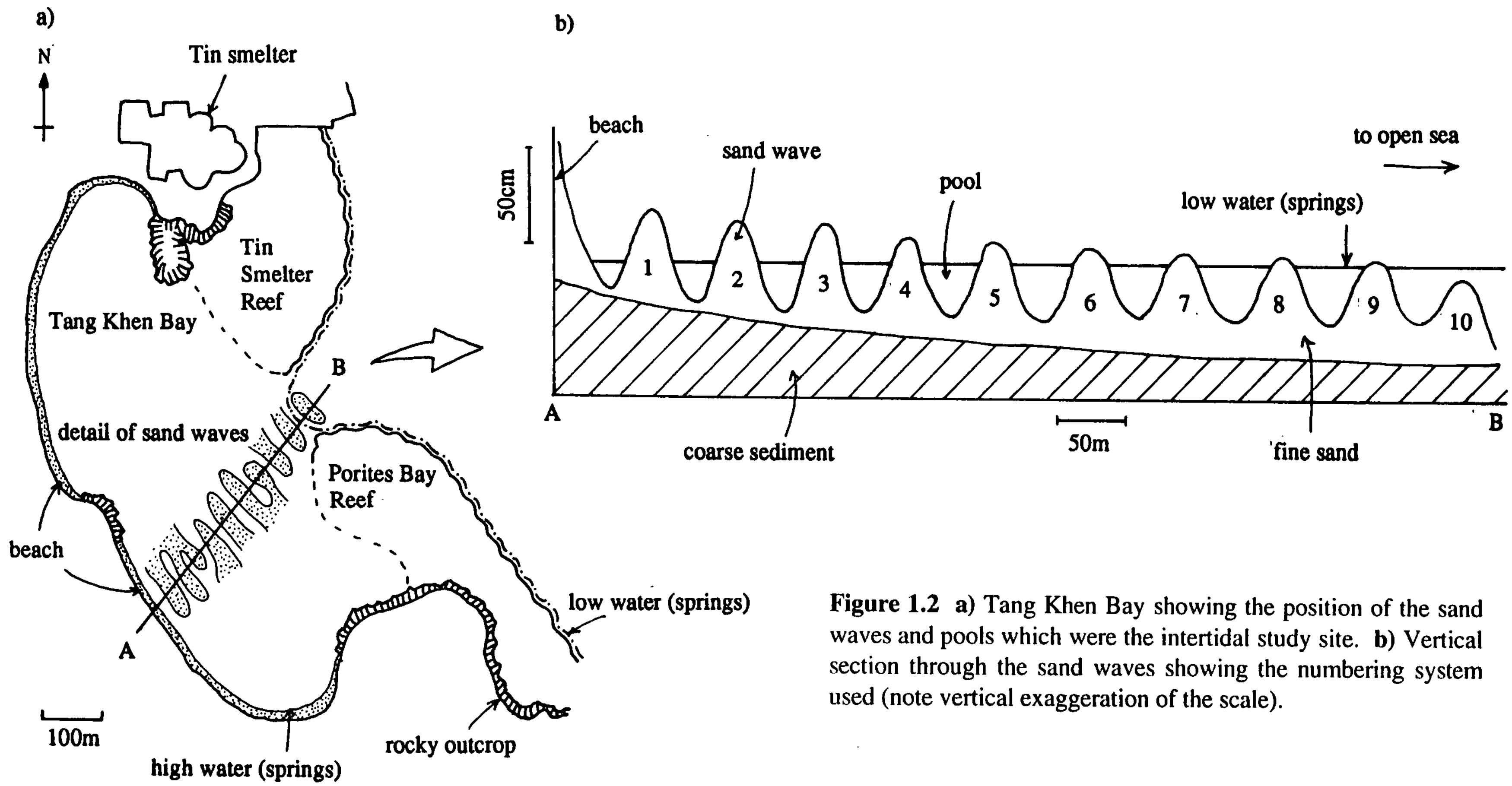


Figure 1.2 **a)** Tang Khen Bay showing the position of the sand waves and pools which were the intertidal study site. **b)** Vertical section through the sand waves showing the numbering system used (note vertical exaggeration of the scale).

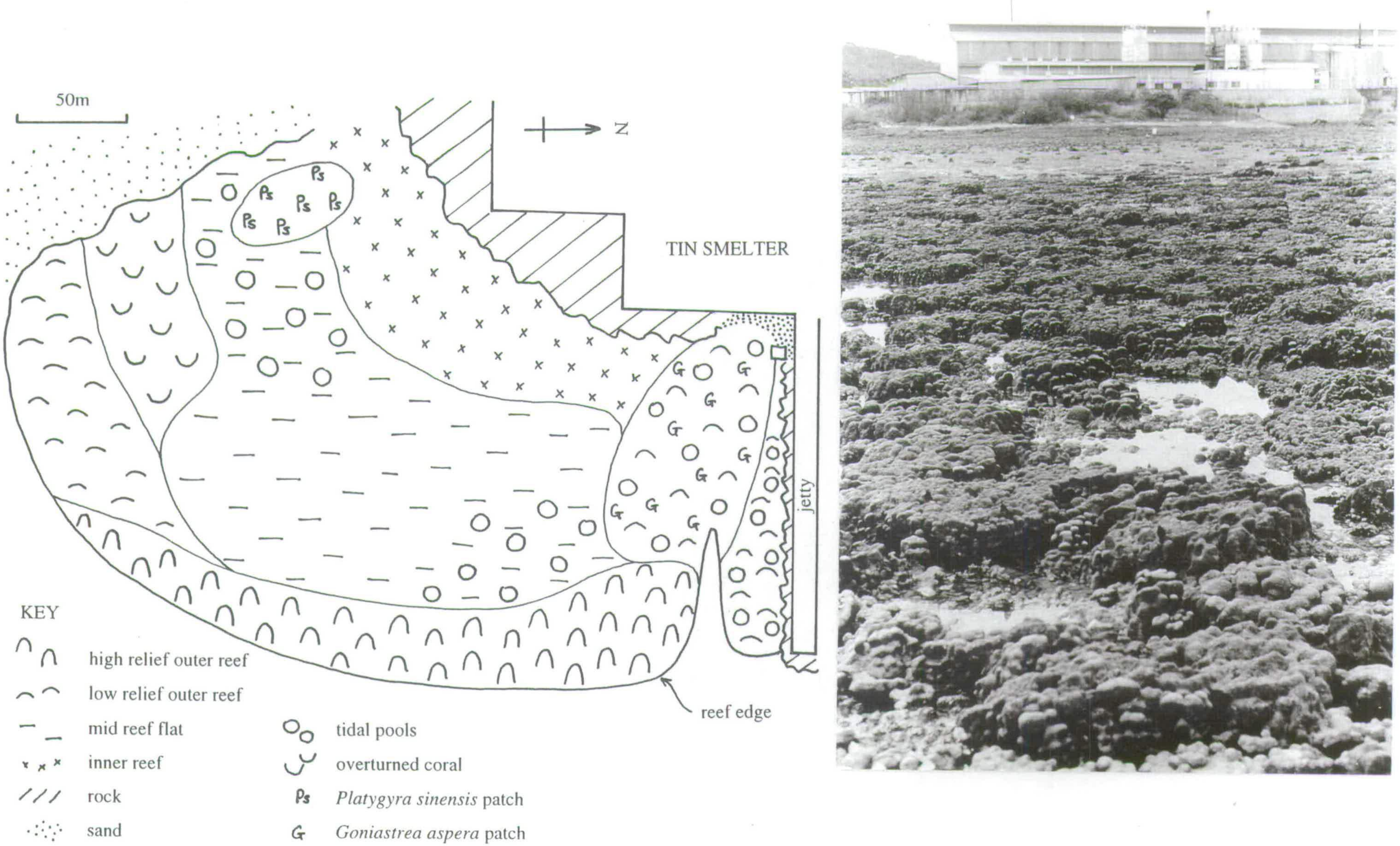


Figure 1.3 Zonation of Tin Smelter Reef; photo shows a view NW across the high relief outer reef area (foreground) to the mid reef flat, inner reef flat and tin smelter (background).

Plate 1.2 Mid-reef area of Tin Smelter Reef. **a)** Looking SE across the flat mid-reef pavement (foreground) to the higher relief reef edge; pale coral in foreground is c.40cm diameter. [Pale corals are the result of a bleaching event, May 1995]. **b)** Detail of mid reef pavement showing mud-covered horizontal surfaces, abundant algae (*Padina*) and low live coral cover. Links of the chain transect across the centre are 1cm long.

for two small streams into the bay. Thus, these areas are more muddy in consistency than the central region, with mangroves colonising the south side.

At each end of the bay is a small fringing reef; at the south end "Porites Bay Reef" (Fig. 1.2) and to the north "Tin Smelter Reef" (Fig. 1.2, 1.3, Plate 1.2). This latter reef was the site for the bioerosion aspect of this study. It has a 200m wide reef flat which backs on to a rocky shoreline next to the large tin smelter on the shore and is 440m long along its seaward edge. Tin Smelter Reef has a small (3-4m) drop-off along most of its length (on to a muddy sea bed), though the south edge grades into the sandy channel in the centre of Tang Khen Bay. The reef exists in extreme conditions, being surrounded by very turbid water (commonly up to 20mg/l; Scoffin et al 1997, but up to 47mg/l; Limpsaichol 1981), and being exposed at low tide (for periods of up to 3 hours at low water springs).

The reef can be divided into three main parts; inner, mid and outer. The inner reef has little live coral (14.7% areal coverage) and is coated with large amounts of fine mud. The mid reef, though also muddy, has about 26.1% live coral cover, *Porites lutea* being the most abundant species. This mid-reef area is pavement-like with small pools forming in between the coral colonies at low tide. The outer reef has a higher relief (actual to plan surface area ratio of 1.51 compared to 1.17 in the mid reef; see Appendix A) and a higher percentage of live coral cover (37.7% of the substrate). The dominant coral is *Goniastrea retiformis* whose growth form is columnar and provides most of the relief in this outer zone. This data was collected using the transect method described below in section 1.5.2.1. Fig. 1.3 and 1.4 and Plate 1.2 show the relative amounts of live and dead substrate in the three areas and raw data is provided in Appendix A.

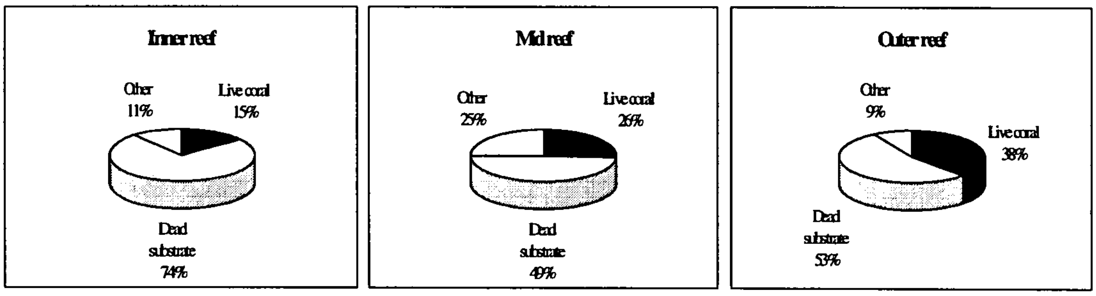


Figure 1.4 Relative cover of live and dead coral for the three reef areas of Tin Smelter Reef.

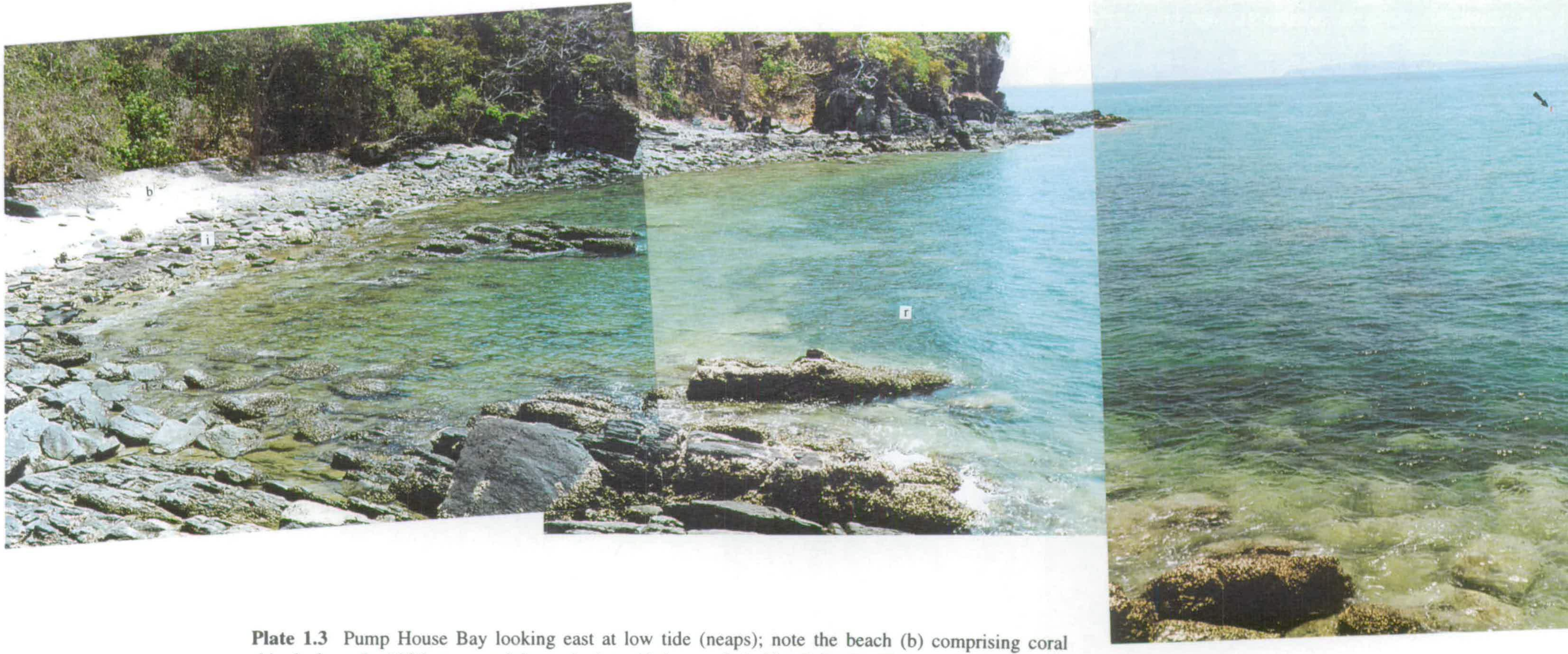


Plate 1.3 Pump House Bay looking east at low tide (neaps); note the beach (b) comprising coral shingle from the 1986 storm and the rocky intertidal area of phyllite slabs (i). The patchy dark area in the right hand half of the picture is the subtidal reef (r). The red buoy (arrow) at the far right marks the junction between transect lines 2 and 3 (see Fig. 1.5)

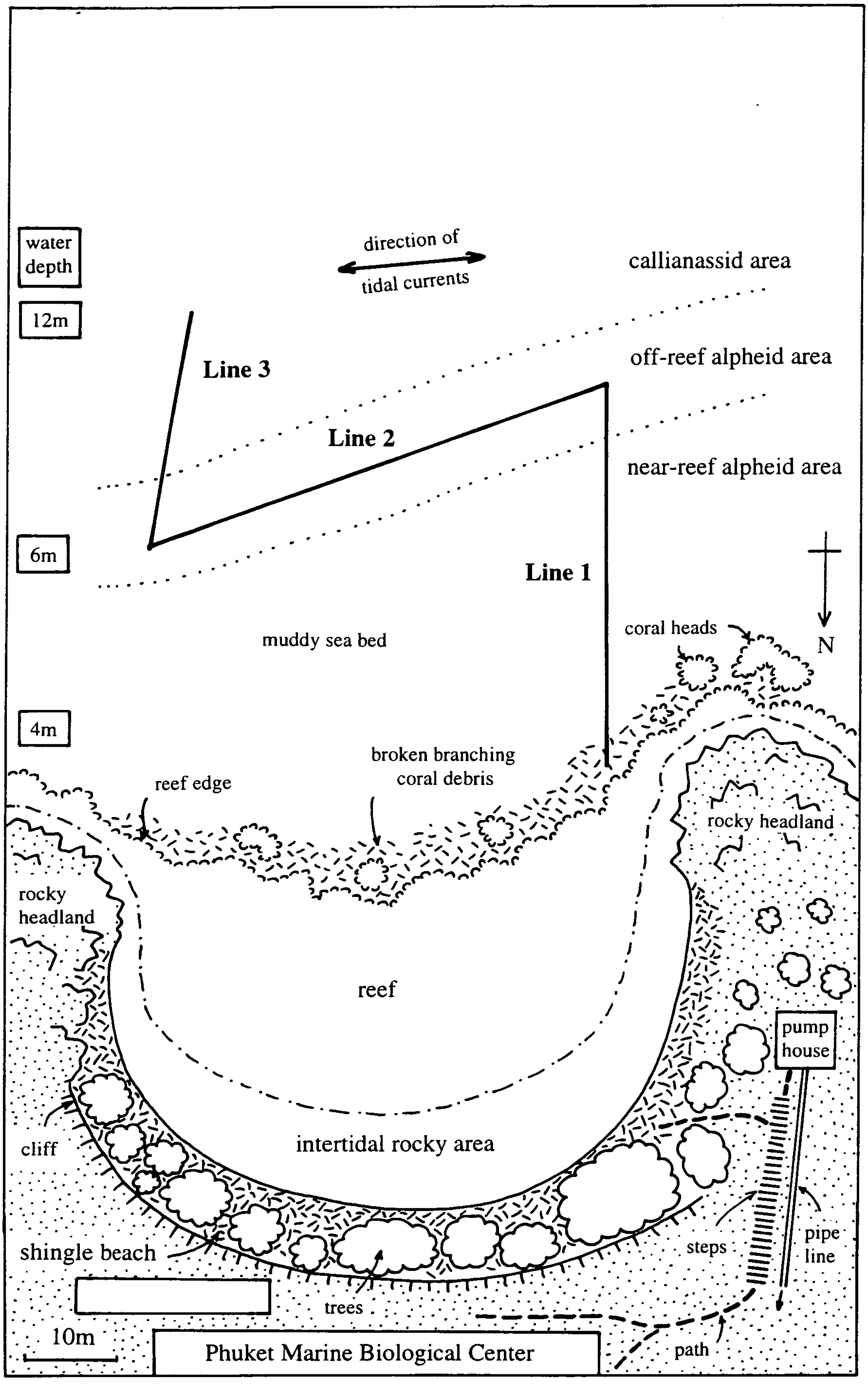


Figure 1.5 Map of Pump House Bay and the positions of the three offshore transect lines used in the subtidal part of this study.

1.3.2 Pump House Bay

At the tip of Laem Panwa is Pump House Bay, a tiny bay (150m long) which contains a coral shingle beach and a small reef (Fig. 1.5, Plate 1.3). The reef comprises mainly the massive corals *Porites* sp., *Goniastrea* sp. and *Diploastrea* sp. and stands of various species of branching *Acropora*. Immediately seawards of the reef edge (at about 4m water depth) is a 2-5m wide band of dead branching coral debris beyond which are fine muddy sediments such as those in Ao Tang Khen. Isolated coral colonies of species such as *Turbinaria* are found on this mud near the reef. This was the subtidal study site, chosen for its abundance of burrowing fauna and ease of access from the Phuket Marine Biological Center (PMBC). Due to its position at the end of the point and the proximity of several small islands which channel water flow, this site suffered from strong currents, especially during spring tides. Diving during spring tides was therefore nearly impossible and potentially dangerous and this, combined with zero visibility, forced all dives to be carried out during the 9 day period spanning neap tides. Over this period strong currents were still experienced, though never too strong to swim against, and visibility remained very poor (0-2m horizontally), especially when involving work that stirred up the fine sea bed.

1.4 PREVIOUS WORK DONE IN PHUKET

Previous authors have noted the muddiness of the sediments in the area (e.g. Carr et al 1991, Scoffin 1997, Scoffin et al 1992, 1997) and the fore-reef sediment's bioturbated nature (Scoffin et al 1992, Tudhope and Scoffin 1994). Other work has described the burrowing infauna of Phuket, but concentrated mainly on the distribution and ecology of various animal groups (e.g. Frith et al 1976, Tantanasiriwong 1978, Chatananthewej and Bussawarit 1987).

Limpsaichol (1981) measured some of the environmental variables near PMBC, including sea surface salinity, sea surface temperature and suspended solids (these results are summarised in Table 1.1). He also looked at current flow around the area of Laem Panwa and how it varies with season (mainly due to the effect of wind).

Table 1.1 Selected sea water measurements from Limpsaichol (1981).

	PMBC Pier 1971 (average value for year)	E Coast May-Oct (SW monsoon)1978	E Coast Nov-Apr (NE monsoon)1978
Surface salinity (ppt)	30.5-31.5 (Range:0.5 - 34.9)	31.8	32.2
Surface temperature (°C)	25-30	27.5	28.9
Total suspended solids (mg/l)	17.7±1.8	30.4-47.1	17.9-20.0

The research at PMBC falls into five main subject groups; a) taxonomy, b) reef and mangrove ecology, c) marine biological productivity, d) marine environment and pollution and e) life history and behaviour. Their findings are generally published in the centre's own journal, the Phuket Marine Biological Center Research Bulletin.

A substantial amount of work has been carried out on the reefs around Laem Panwa. Brown (and others) from Newcastle University and Scoffin from Edinburgh University have monitored Tin Smelter Reef since 1979 and studied the effects of solar bleaching (e.g. Brown et al 1994), coral growth (e.g. Scoffin 1997, Scoffin et al 1992, 1997, Tudhope and Scoffin 1994) and coral assemblages (Brown and Holley 1984, Brown et al 1986).

Danish scientists have long had close ties with PMBC and have published a variety of papers in the fields of biology and zoology. Papers relevant to this work include those on bioerosion (especially *Lithophaga* (Nielsen 1976), *Gastrochaena* (Nielsen 1986) and sipunculids (Hylleberg 1994)), coral taxonomy and zonation (Ditlev 1978).

Other work specifically relevant to this thesis is mentioned in the main text.

1.5 METHODS

1.5.1 Investigation of burrows and sediments

1.5.1.1 Transects

Due to the featureless bottom topography and extremely poor visibility in the subtidal area, a permanent set of transect lines were laid down to enable the relocation of experiments. Three main transects were emplaced; one leading from the shore out to sea across the reef and through the area of near-reef alpheids, joining a second which ran parallel to the shore at about 6m water depth through the area of off-reef alpheids, leading to a third which ran down the slope to about 12m water depth through the callianassid area (see Fig. 1.5).

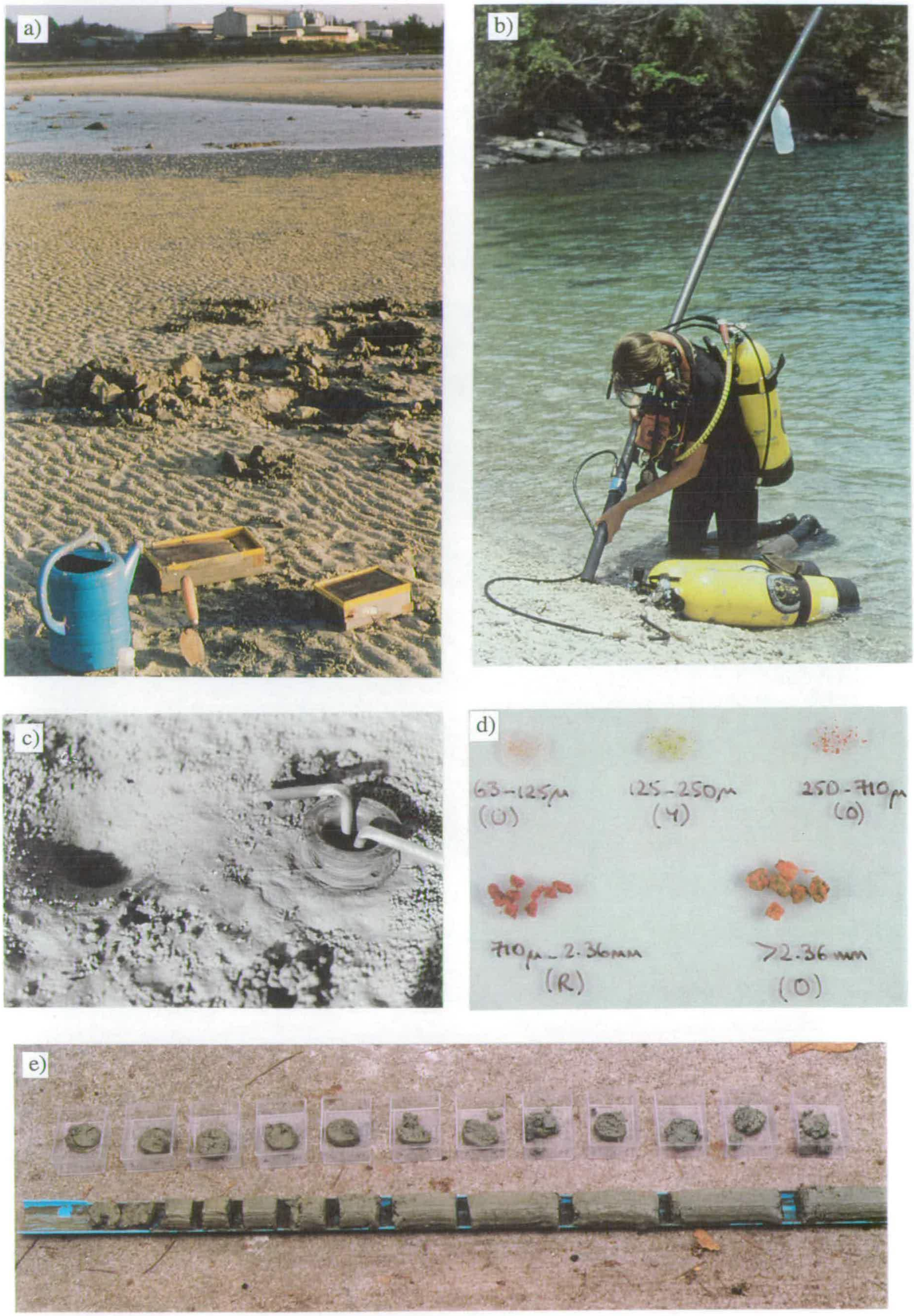


Plate 1.4 Methods. **a)** Resin casting, box coring and resin peeling; box cores are taken as described Fig. 1.7, pre-catalysed resin is poured from the watering can on to the prepared box cores (foreground) or into a burrow entrance. **b)** Subtidal airlift (see section 1.5.1.2); the photo was set up on the beach as underwater visibility was too poor for photography. **c)** Callianassid trap; a weighted line from the free moving reel (right) is fed into the callianassid crater (left). See section 1.5.1.10. Reel diameter is 15cm. **d)** Tracer sediment (actual size) see section 1.5.1.6. **e)** Tube coring and subsampling. Internal diameter of corer is 4.2 cm; the core is from the subtidal callianassid area.

The transects consisted of tough 7mm line attached to the soft substrate by means of 1m long aluminium stakes. The stakes were driven into the sediment so that 30cm projected above the sediment surface and the four 'corner' stakes were 150cm long for added strength. The top of each stake had a small hole made in the metal through which a wire loop was threaded; the ends of this wire were twisted tightly around the transect line to hold it in place. Where the line crossed the reef, it was secured by winding it around dead coral heads. Once the lines had been placed, they were tagged every 5m with a bright yellow distance marker.

These transects were able to withstand the strong currents in the area, but lines 2 and 3 were uprooted and disappeared towards the end of the study period. This can only have been due to a boat passing overhead trailing an object such as fishing gear or an anchor which snagged the line.

1.5.1.2 Airlifting (Plate 1.4b)

The airlift is a tough plastic tube of diameter 5cm and is used underwater to remove sediment from the sea bed. It is made of interconnecting 30cm long sections of tubing, thus enabling the total length to be varied (up to a maximum of 2m) according to water depth. Air enters the tube from a standard 12l SCUBA cylinder via a valve 25cm from the bottom of the airlift. The expansion of the air as it rises up the tube creates suction which enables sediment to be lifted off the sea bed. Varying the airflow affects the power of suction. Sediment removed in this way is also carried up the tube, leaving the water around the site of excavation clear from suspended sediment. The airlift is best operated in a slight current so that excavated sediment falls downstream of the excavated area.

An attempt was made to filter off the coarse fraction (>5mm) and any large animals that were sucked up through the airlift. A 5mm mesh box was made and secured to the upper end of the airlift to allow the finer grains through and retain the coarse fraction. However, the sediment is very clay-rich and comes out of the seabed in lumps rather than in a continuous stream. These lumps are 4-8cm in diameter and therefore would not pass through the mesh but collected in a mass and weighed down the end to such an extent that it was hard to keep the airlift upright.

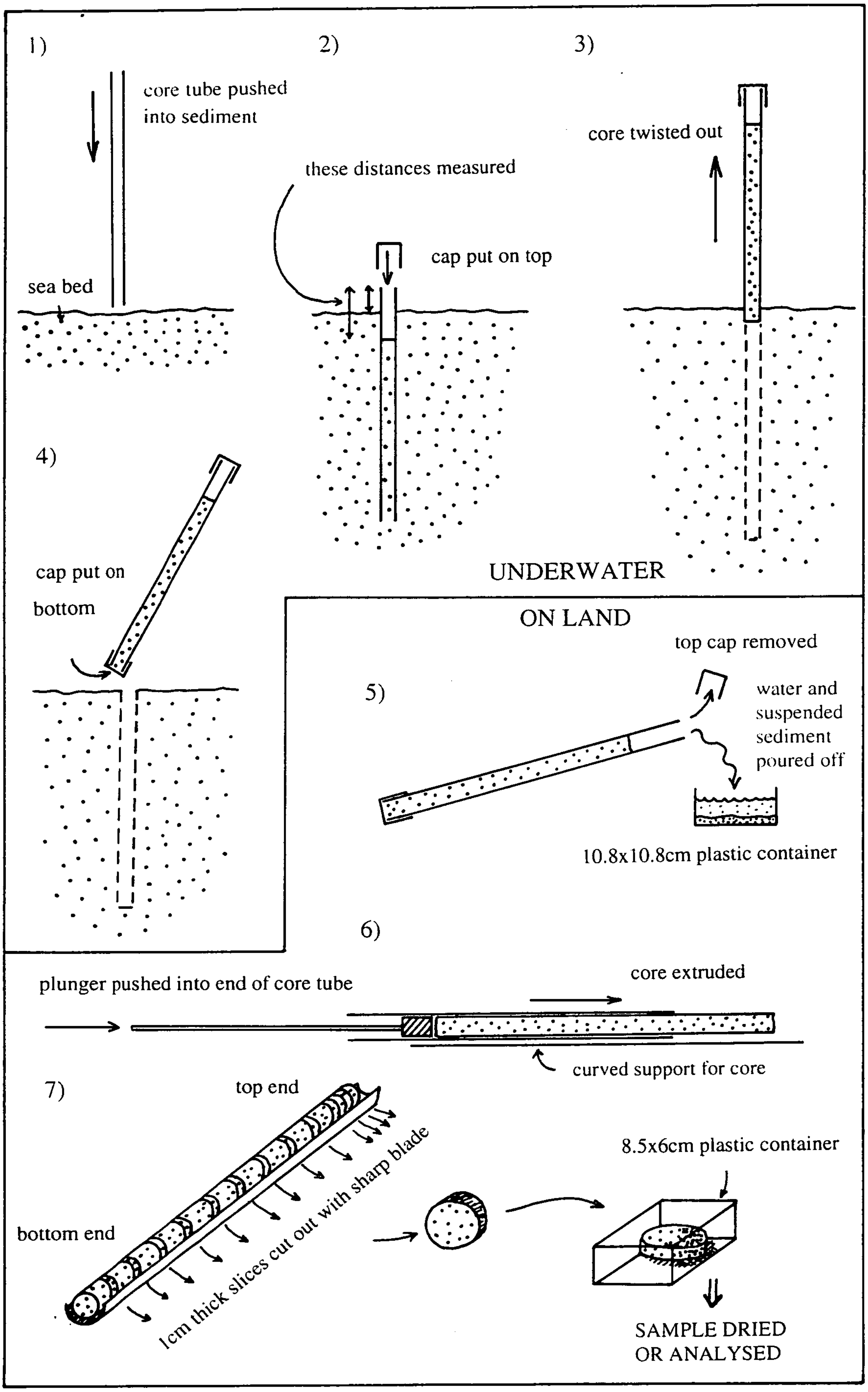


Figure 1.6 Subtidal tube coring and core processing methods used in this study.

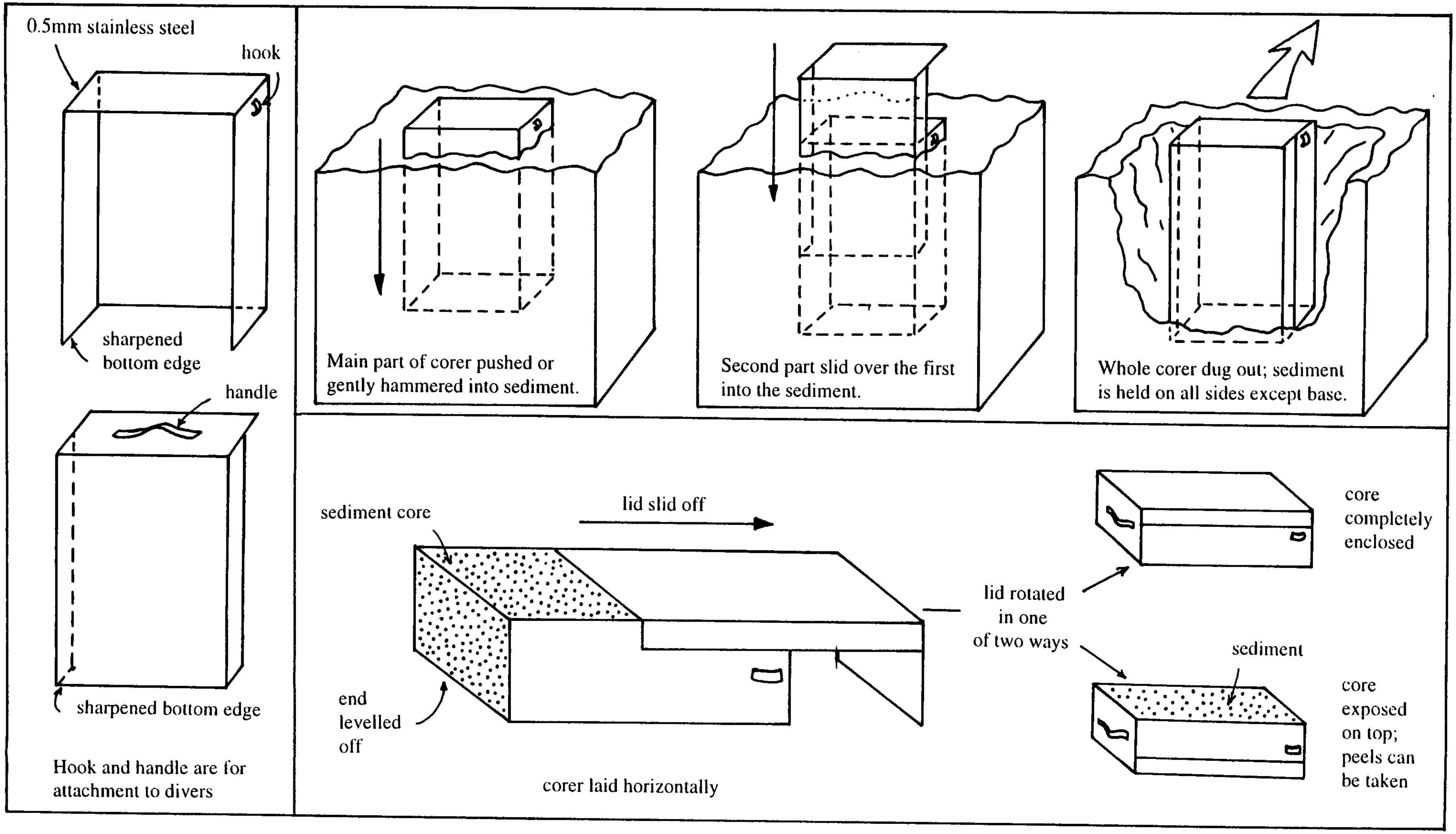


Figure 1.7 Box coring. **a)** The two halves of the box corer. **bi)** to **biii)** Taking a box core. **c)** Preparing the core for analysis.

1.5.1.3 Coring

Tube corers

Tube corers were used to sample the subsurface sediment profile to a maximum depth of 120cm in the subtidal site. Cores were subsequently analysed for grain size and carbonate content (see 1.5.1.4 and 1.5.1.5).

Sampling method (Fig. 1.6)

The cores were 133cm lengths of plastic piping (internal diameter 4.2cm, plastic thickness 1mm). One end of the tube was sharpened using a file to aid its penetration of the sediment and two plastic end pieces fitted closely over each end to seal off the core tube. The corers were used to take samples in the subtidal sediments and were more successful further offshore where the fine sediment was thicker; very coarse material impeded the coring by jamming in the end of the tube.

The sharpened end of the tube was placed gently on the sediment surface and then pushed in to the sea bed by hand as far as was possible. A small mallet was then used to tap the corer in as far as it would go. Care was taken to ensure the corer entered the sediment at right angles to the surface, one diver guiding the other. The amount of compression undergone by the core was measured by lowering a ruler into the upper end of the corer while it was still in the sediment and measuring the distance from the corer end to the top of the core. The length of corer that was still above the sediment surface was also measured. A plastic cap was put on to the exposed end of the corer and the corer then pulled from the sediment with a twisting motion. A second cap was put on the other end of the corer as soon as it emerged from the sediment. The full corers were taken up to the surface, taking care not to move them too suddenly and thus disturb the contents. The cores were processed as soon as possible after they were brought up to prevent settling or decomposition.

Processing (Fig. 1.6 and Plate 1.4e)

A 150cm length of plastic tubing of an identical type to the tube corers was sawn in half lengthways to make a core holding tray. A plunger was also constructed to push the cores out of the corers; a 5cm length of core tube was placed vertically with a 150cm length of metal pole standing upright in the centre. Polyester resin was then poured into the core tube and allowed to set around the metal pole, thus making a tight-fitting plunger which was used to extrude the cores.

The core tube was laid horizontally in the holding tray and the cap from the blunt (top) end removed. All the water and loose, soft sediment from the top of the core was poured off into a plastic box and the sediment allowed to settle out. The cap from the sharpened end was then removed and the plunger was inserted and used to extrude the core. A general description of the appearance of the core was made, noting features such as changes in sediment texture and colour, possible burrows and large pieces of coral (see Fig. 3.24). The length of the core was also measured to check for any evidence of further compression of the core during extrusion. Slices of sediment were then cut off using a sharp blade. One centimetre slices were usually taken; these were closely spaced at the top of the core where the sediment appearance changed over short distances but further down the core they were usually taken every 5cm. Large pieces of coral debris were avoided but their presence noted. If tracer counts (section 1.5.1.6) were to be done on the slices, each one was placed in a small plastic box ready for analysis. If the slices were to be dried for transport back to Britain, they were put straight into snapseal bags ready for oven drying. In some cases, the 5cm pieces of core left between the 1cm slices were kept and washed through a 5mm mesh for analysis of the components of the coarse fraction of the sediments. Individual pieces were scored as one of twelve categories; bivalve, gastropod, mollusc (indet.), coral, barnacle, sand dollar, other echinoid, crustacean, calcareous worm tube, wood, inorganic, unidentifiable (see Appendix B).

The sediment suspension from the top of the core was allowed to settle out for six hours in a transparent plastic box (base dimensions 10.8 x 10.8cm; area 116.64cm^2). The thickness of the settled sediment was then measured through the side of the box to the nearest 0.5mm using a ruler. This was repeated three times on each side of the box and a mean of the twelve measurements taken to represent the thickness of sediment. The volume was calculated by multiplying the thickness of sediment by 116.64cm^2. The volume could be converted to an equivalent core length by dividing the volume by 13.85cm^2, the cross-sectional area of the core whose diameter was 4.2cm ($\pi r^2 = 3.14 \times (4.2/2)^2 = 13.85$).

Box cores

Senckenberg boxes are used to take cores in which the internal structures of the sediment are undisturbed, and are therefore ideal for taking samples of burrow structures and their surrounding sediments. They are also useful in the preparation of sediment peels using polyester resin.

The Senckenberg box (Bouma 1969) consists of two parts (see Fig. 1.7) which slide together to enclose the sediment core within. Two sizes were used in this study, both 20x10cm wide, one 25cm and the other 35cm long. Both were made from 0.5mm thick stainless steel to prevent corrosion, and the bottom edges of both parts were sharpened to prevent excessive disturbance of the sediment as the core was pushed in. The design described by Bouma (1969) was modified slightly to make the carrying of the corers easier underwater. Small metal rings were welded to the upper parts of both parts of the corer so that they could be clipped to the diver when not in use. The corer was deployed as illustrated in Fig. 1.7.

If resin peels were to be made from the core, the edges of the two halves of the corer were taped with tough packing tape before the core was taken to prevent the resin sticking to the metal. After the core had been taken in the normal way, the lid was turned through 180° and slid underneath the other half to expose one of the vertical surfaces of the core (Fig. 1.7). This surface was then smoothed off using a small spatula to remove any disturbed sediment from the coring process. The two halves of the corer were then taped together and a thin layer (3-4mm) of pre-mixed polyester resin poured on to the prepared core surface (Plate 1.4a) and allowed to soak into the sediment core and semi-solidify (30-45 minutes). A sharp blade was then run along the edges of the peel to separate it from the core box, and the resin lifted off and laid flat to harden completely. Once the resin was completely set, the sediment laden surface was washed gently with water to remove loose grains.

The Senckenberg box was not so successful underwater, mainly due to the nature of the subtidal sediment; because of the large amount of clay-size fraction, the cores smeared easily when the lid was slid on and off. Any attempt to remove this smeared layer to see the undisturbed central sediment just resulted in further smearing. The clayey sediment also prevented the resin from soaking in.

Other corers

Small pocket corers were also used to take quick sediment samples either above or below the water, for instance whilst airlifting burrows. They comprised plastic photographic film canisters which were pushed into the sediment, twisted out and the lid snapped on. This method was quick and cheap and the canisters were easy to come by in large numbers. The sediment samples could also be transported easily back to the lab for drying in the samplers.

1.5.1.4 Grain size analysis

Sieving

Samples were dry sieved through a 500µm mesh sieve and the >500µm fraction separated further through nested sieves of mesh size 1mm, 2mm and 4mm. The <500µm fraction was analysed using a Coulter LS100 Particle Size Analyser.

Coulter Counter

This machine uses diffraction to size sediment grains from 0.4-800µm diameter. Sediment grains are suspended in water and flow through a diffraction sample cell, a sheet-like, 3mm wide chamber. A collimated laser beam (750nm) hits this chamber at right angles, falls on the sediment particles and is diffracted by varying amounts depending on the grain size. Two Fourier lenses focus the diffracted light on to three sets of photodiode detectors. Samples containing various particle sizes, such as the ones in this study, produce a complex diffraction pattern determined by the particle sizes and number of particles present. The speed and position of the particle are not important. A computer uses the information from the detectors to generate the best-fit size distribution from a Fraunhöfer light diffraction pattern (Coulter Operator's Guide 1990).

The samples analysed as part of this work were the <500µm sieved fraction. Each sample was run in triplicate. Sample size varied according to particle size; it is recommended by the manufacturers that an obscuration value of 10-12% is the optimum for obtaining good results in the 1-800µm range, and this was achieved with 5-7g of coarse intertidal sediment (e.g. intertidal callianassid mounds, sipunculid worm casts, *Dotilla* pellets), 0.5g of surface subtidal sediments and 0.75-1.25g of subsurface subtidal sediments. Distilled water was run through the Coulter Counter for 10 minutes before each batch of samples was run to ensure that there were no impurities in the system. Samples were soaked and gently stirred in distilled water for 10 minutes before pouring them into the machine where they were subjected to 30 seconds pre-run sonication to disaggregate clumped grains. Any longer than this was thought to increase the risk of actually breaking up the more fragile skeletal grains in the sample (Ian Alexander pers. comm. 1994). Sodium hexametaphosphate is often used as an anti-flocculating agent, but during control runs was found to have little effect on the final particle size distribution and so was not added to the samples.

1.5.1.5 Carbonate Content

To calculate the weight percent of calcium carbonate in the sediment samples, a titration method was used in which the sample was digested with HCl and then excess acid titrated with NaOH, using bromophenol blue as an indicator.

Standards were run before each day's titrating and every time a new solution of hydrochloric acid or NaOH was made up. A standard of 0.5g pure, dry $CaCO_3$ was reacted with excess 0.5N HCl (25ml). When the reaction was complete, i.e. there were no signs of effervescence, 0.35N NaOH was used to titrate the excess HCl using 4 drops of bromophenol blue to indicate the endpoint (a colour change of yellow to blue). NaOH was also titrated directly against 25ml of HCl using the same indicator.

The following equation was used to calculate the amount of carbonate consumed by 1ml HCl:

volume HCl consumed by $CaCO_3$ standard (x) = $v - (v_1 \times v_2/v_3)$ (i)

therefore 1ml HCl consumes w/x g of $CaCO_3$ (ii)

where
w = weight of $CaCO_3$ standard (g)
v = volume of 0.5N HCl in standard reaction (ml)
v_1 = volume 0.35N NaOH needed to neutralise the excess HCl (ml)
v_2 = volume of 0.5N HCl in NaOH titration (ml)
v_3 = volume of 0.35N NaOH in NaOH titration (ml)

Samples of the <500μm sieved fractions were then run. If grains larger than this were included they caused too much variation between repeats. Larger samples (e.g. 1g) were impractical due to the large amounts of NaOH and HCl that would have been required. Each sample was run in triplicate and great care was taken to ensure that the procedure was identical for all samples.

The following equation was used to calculate the weight percent of carbonate in the sample:

volume HCl consumed by CO_3 in sample = $v_{HCl} - (v_{NaOH} - v2/v3)$ (iii)

% CO_3 = volume HCl consumed by CO_3 in sample x (w/x)/sample weight x 100 (iv)

where
v_{HCl} = volume HCl used in sample run (ml)
v_{NaOH} = volume NaOH used in sample run (ml)
other abbreviations as in equations (i) and (ii)

$CaCO_3$ standard and sediment samples were weighed to the nearest 0.0001g on a Mettler H20T five-figure balance, HCl volumes measured with a Gilson pipette, and NaOH volumes measured from the burette.

It is assumed in calculations (iii) and (iv) that all the carbonate present in the sample was present as $CaCO_3$. Given the nature of the carbonate grains (reef- and infauna-derived skeletal remains) this is thought to be a reasonable assumption.

1.5.1.6 Tracer Sediment

Preparation

Garden sand was dry sieved through nested sieves of 63μm, 125μm, 250μm, 710μm and 2.36mm mesh sizes. Each size fraction was then mixed with enough fluorescent paint to coat the grains, the mixture spread out into a thin layer and oven dried at 60°C. Three different colours of paint were used, yellow, orange and red, and each grain size fraction was made into two colours of tracer. Once the paint and sediment had dried, a rolling pin was used to crush the layer and separate the grains. Due to the paint coating, the grain sizes had changed and so the sediment was re-sieved to obtain a exact size fractions (Plate 1.4d).

In the field, some >5mm fraction was also made up using local beach sediment sieved through a plastic mesh and prepared in the same manner, though with non-fluorescent paint in pale blue and yellow.

Analysis

Sediment samples containing tracer grains were washed to remove the bulk of the <63μm particles which otherwise coat the tracer grains and obscure the colour. This was done by simply shaking the sediment with water, allowing the sediment to settle for one minute and pouring off the water and suspended fine particles. Although not precise, this is a quick and effective method for removing most of the fines. The discarded washings of a sample were oven-dried and examined for any evidence of tracer which might have been removed by this process, and only tiny amounts of the 63-125μm fraction were found.

To count the grains, the sediment was spread out into a thin (2-3mm maximum) layer over the bottom of a small transparent plastic container (base 6 x 8.5cm; area $51cm^2$), by shaking it gently to and fro in a small amount of water. Grains were searched for under UV light (using a small hand held lamp) in a darkened room. Both the sediment surface and the sediment visible through the base of the box were examined, as smaller grains settled out at the bottom and larger ones above. If no grains could be seen on the initial examination, the box was gently shaken again to redistribute the grains. Three shakes were tried, but if there were still no grains visible, a score of zero was then recorded. If grains of the same size were visible from both above and below, the largest count was taken. A sum of the counts was not used as there was the possibility of the same grain being visible from both sides. The two largest size fractions were only counted from above. If tracer grains were abundant, as was often the case with the 63-125µm and 125-250µm fractions, the surface was divided into quarters by eye, and the number in one quarter multiplied by four to obtain a comparable figure. If the tracer grains were too abundant even for this method, the average counts from three square centimetres was multiplied by 51 to obtain a value for the whole box (6 x 8.5cm). In some cases, simple presence/absence criteria were used, or a rank scale of rare, occasional, common, abundant, superabundant. The amount of sediment examined was standardised when cores were being analysed as 1cm slices of a standard core diameter (4.2cm) were use in the analysis.

Tracer control experiments for core sampling

As a tube corer (section 1.5.1.3) is driven into the sediment it can take with it sediment from upper layers and carry it down to lower layers, thus ‘smudging’ the outside of the core. Similarly, when the core is extruded, mixing of grains from different levels in the core can occur, transporting grains either up or down the core. Tracer is no different from other sediment in this respect. Some of the tracer experiments carried out in this study were to investigate the vertical transport of grains by the burrowers concerned. The possibility of tracer grains being pulled down to biologically artificial depths by the coring process therefore needed to be assessed. Four control experiments (A-D) were carried out, A and D using a standard 20g tracer dose (2g of 63-125µm, 2g of 125-250µm, 2g of 250-710µm, 2g of 720µm-2.36mm, 2g of >2.36mm, 10g of >5mm) and B and C using a 10g dose (half of all the above quantities). In experiments A-C the tracer was placed in a fairly concentrated layer, approximately 5 x 8cm in area, on the seabed and a core taken immediately through the tracer patch. In experiment D, the first attempt at coring failed due to hitting a large piece of coral below the surface, so a second attempt was made through the sparse trail of tracer that had spread along the seabed in the current. The cores were then analysed in the normal way, i.e.

extruded and sliced and the slices analysed for tracer as described above. Results are shown in Tables 1.2a to d and Fig. 1.8.

The results showed that tracer could be carried a considerable distance vertically down the core by the coring process itself. There is a correlation (correlation coefficient = 0.61) between the number of tracer grains at the surface and the maximum depth at which the tracer is found in the core (see Fig. 1.8). If surface tracer concentrations are high, significant quantities (especially of the 63-710μm fraction) are visible up to depths of 15-20cm, with a few grains getting as far as 30-40cm down the core. Larger tracer grains (710μm - >5mm) were not found as far down the core, only reaching 5-10cm below the surface.

Where lower tracer concentrations are present on the surface, only a few grains get carried down the core by the process. If a peak in tracer concentration is observed at depth in the core and there is a low surface tracer concentration, it can therefore be assumed that this is a genuine indication of a concentration of tracer at depth, though this will presumably be smeared out along the core as well.

Subtleties in tracer distributions as a result of biogenic activity will therefore be obscured by the artefacts caused by the coring process. Only large concentrations of tracer can be considered to be 'real' signals and their position in the core relative to other tracer should be carefully considered. Any fewer than about 10-15 tracer grains (of the 63-710μm fractions) in a core section cannot be interpreted as anything other than background noise. The movement of tracer was therefore usually analysed in combination with airlift excavation of burrows in a non-quantitative way.

Tables 1.2a-d. Tracer sediment distribution through control cores.

Table 1.2a

Control A	Tracer sediment grain size fraction					
Depth in core (cm)	63-125μm	125-250μm	250-710μm	710μm - 2.36mm	>2.36mm	>5mm
0-5.4	SA	~970	~360	~110	23	3
5.4-6.4	~150	~220	~50	6	0	0
6.4-7.4	~400	~185	~50	1	0	0
7.4-8.4	~200	~200	~40	3	0	0
8.4- 9.4	~100	~150	26	1	0	0
11.4-12.4	~80	~150	28	2	0	0
15.4-16.4	~65	31	16	0	0	0
19.4- 20.4	5	7	0	0	0	0
27.4-28.4	8	7	4	0	0	0
35.4-36.4	0	1	0	0	0	0
45.4-46.4	0	2	0	0	0	0
55.4-56.4	0	0	0	0	0	0
65.4-66.4	0	0	0	0	0	0

Table 1.2b

Control B	Tracer sediment grain size fraction					
Depth in core (cm)	63-125μm	125-250μm	250-710μm	710μm - 2.36mm	>2.36mm	>5mm
0-2.5	SA	SA	SA	125	33	11
2.5-3.5	SA	~1275	~561	22	5	1
3.5-4.5	SA	~240	~120	8	1	1
4.5-5.5	SA	~200	61	4	0	0
5.5-6.5	SA	~90	42	0	0	0
9.5-10.5	~130	~70	27	0	0	0
16.5-17.5	no data available - core section damaged					
27.5-28.5	5	7	0	0	0	0
37.5-38.5	1	3	1	0	0	0
47.5-48.5	0	0	0	0	0	0
57.5-58.5	0	0	0	0	0	0
67.5-68.5	0	0	0	0	0	0

SA = superabundant (uncountable)

Table 1.2c

Control C	Tracer sediment grain size fraction					
Depth in core (cm)	63-125μm	125-250μm	250-710μm	710μm - 2.36mm	>2.36mm	>5mm
0-6.2	SA	~1380	SA	~140	24	8
6.2-7.2	SA	SA	~200	4	1	1
7.2-8.2	SA	~250	~100	2	2	1
8.2-9.2	SA	~180	~80	4	0	0
9.2-10.2	SA	~150	46	3	0	0
12.2-13.2	~75	79	27	0	0	0
18.2-19.2	11	18	2	0	0	0
25.2-26.2	14	24	4	0	0	0
32.2-33.2	8	5	0	0	0	0
42.2-43.2	0	0	0	0	0	0
52.2-53.2	0	0	0	0	0	0
62.2-63.2	0	1	1	0	0	0
72.2-73.2	0	0	0	0	0	0

Table 1.2d

Control D	Tracer sediment grain size fraction					
Depth in core (cm)	63-125μm	125-250μm	250-710μm	710μm - 2.36mm	>2.36mm	>5mm
0-1.9	0	0	0	1	0	0
1.9-2.9	1	1	0	0	0	0
2.9-3.9	1	2	0	0	0	0
3.9-4.9	0	2	0	0	0	0
4.9-5.9	0	1	0	0	0	0
7.9-8.9	1	0	0	0	0	0
12.9-13.9	0	0	0	0	0	0
19.9-20.9	0	0	0	0	0	0
27.9-28.9	0	0	0	0	0	0
37.9-38.9	0	1	0	0	0	0
46.9-47.9	0	0	0	0	0	0
58.9-59.9	0	0	0	0	0	0
79.9-80.9	0	0	0	0	0	0

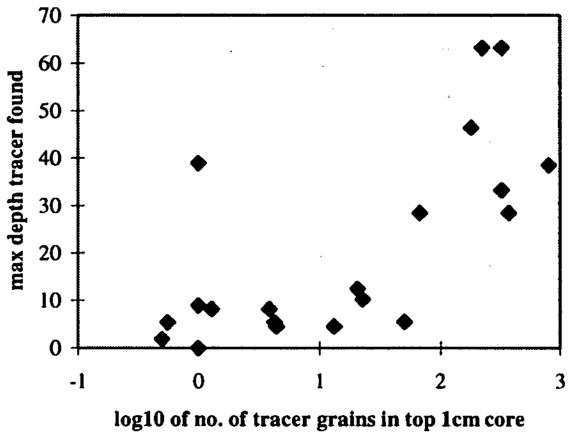


Figure 1.8 Correlation between the number of tracer grains at the sediment surface and the depth of penetration of tracer during coring.

1.5.1.7 Resin casting

Polyester resin was mixed with catalyst in the ratio 200:1 to give a setting time of between 30-45 minutes (depending on temperature). It was poured into the burrows from a watering can, the position of the burrow labelled with a marker, and the cast dug up by hand or airlift 24hrs later (see Atkinson and Chapman 1984, Plate 3.5).

A styrene thinner has been used by some workers (Bouma 1969, Atkinson pers comm 1994) to make the resin more fluid and therefore increase its ability to penetrate burrow structures and box core samples. However, it was not available at the boatyard in Phuket where the resin was bought. More successful resin peels and casts of finer structures would have been obtained had the resin been thinner.

1.5.1.8 Burrow density estimates

In order to obtain estimates of the rate of sediment turnover by various burrowers it is necessary to measure the densities of those animals' burrows. The methods used varied with the type of animal under investigation, due to greatly varying densities and the different conditions under which the measurements were made (e.g. subtidal vs. intertidal). Details are given in the relevant sections in Chapter 3.

1.5.1.9 Aquarium

One of the original aims in the field was to collect live specimens of the burrowing crustaceans and keep them in sediment-filled aquaria to observe their modes of sediment manipulation at close range and to perform tracer sediment experiments in the laboratory.

A large mud sample (approximately $2500cm^3$) was collected from the off-reef alpheid area and kept in an aquarium (20x60cm base by 40cm high) which had a continuous through-flow of running sea water. The sediment was allowed to settle out and the fauna it contained started to burrow. Unfortunately, no study crustaceans were caught (see section 1.5.1.10), but the aquarium was still useful for examining the sedimentary effects of some of the other smaller infauna. (Plate 3.10).

1.5.1.10 Catching crustacean burrowers

Attempts were made to catch callianassid and alpheid shrimps and the alpheids' commensal gobies in order to identify them and to keep the in an aquarium (section 1.5.1.9) to observe their burrowing at close range. It was therefore necessary that some animals be captured alive, and various methods were employed to achieve this.

Callianassid shrimps

a) the method of de Vaugelas (1985)

A 4m length of thin fishing line was weighted at one end with eight 0.5g weights, four spaced at 15cm intervals and four closely spaced at the end. The other end of the line was attached to a plastic reel which was able to rotate freely around a metal stake which was driven into the sand next to a burrow opening. The weighted end was then lowered into the burrow opening as far as it would go without disturbing the loose sediment of the crater walls (Plate 1.4c) . The line was left for two or three days and checked at every low tide by pulling gently on the line to ascertain whether there was a shrimp entangled below. Shrimp paste was also smeared on the weighted end of the line to encourage the crustacean to investigate the line.

b) yabby pump (Dexter 1996, pers comm) (intertidal only).

Neither of these methods was successful in catching the animals. When using de Vaugelas' method in Tang Khen Bay, the shrimps were sometimes felt pulling firmly on the line, and on one occasion the head and large chela of one individual was glimpsed when the line was gently pulled out of the burrow as it was being tugged from below. Evidently the shrimps were investigating the line but not becoming entangled and so were not being caught. At no stage was the animal felt pulling on the line, or showing any other sign of interest in the case of subtidal callianassids. Due to the very narrow passageway at the bottom of the vertical inhalent shaft, the fine weighted line could not be positioned far enough into the burrow. Furthermore, the presence of the line even seemed to block the shaft to some degree, with the craters often becoming infilled with sediment and new craters forming elsewhere. The yabby pump method probably did not work due to the large volume of the intertidal burrows.

Alpheids/gobies

a) Traps were made out of plastic mesh (hole size 5mm). These had a 10x5cm base and were 5cm high. The base had a 1.5cm hole leading into an internal flared collar reaching almost to the top of the inside of the trap. This was to act as a one-way (no return) entrance tube for the animal. The trap was placed over the burrow entrance so that the hole in the base of the trap coincided with the burrow entrance. This method failed to catch any animals.

b) Small, home-made, elastic-powered spear guns with a four-pronged end were used to catch both fish and shrimps. Some practice was needed in order to anticipate the rapid retreat of both animals as the gun was fired and only three animals were caught (two fish, one shrimp). These were given to Ukkrit Satapoomin at PMBC for identification.

Dotilla

These crabs were collected simply by picking them up by hand from the sand surface.

1.5.2 Investigation of bioerosion and corals

1.5.2.1 Reef substrate analysis

The reef flat of Tin Smelter Reef is clearly made up of different amounts of live and dead coral, different species of coral and different amounts of relief in different areas; an attempt was made to quantify this. After extensive visual surveying of the reef flat whilst walking over it at low tide, a sketch was made of the most obvious zones (see Fig. 1.3). The three most areally extensive of these were selected for further quantification of substrate type and were also the areas in which the bioerosion studies were carried out. The linear point intercept method was used to obtain values for percentage cover of different substrate types. Five metre long, chain transects were laid randomly across the reef flat, each being placed so that it followed the relief of the corals (Plate 1.2b). The nature of the substrate underneath every 10th link of the chain was identified as one of the following categories:

- Corals; *Goniastrea retiformis*, *Goniastrea aspera*, *Coeloseris mayeri*, *Porites lutea*, *Platygyra* sp., *Favites* sp., *Favia* sp., other coral species
- Other substrate; algae, unidentified dead coral or mud, borehole, sand, rubble, reef cavity, and other substrate.

It was also noted whether coral species were live or dead and whether they were oriented horizontally (approx. 0-10° from the horizontal) , vertically (approx. 80°-90° from the horizontal) or at an angle (approx. 10°-80° from the horizontal). The randomness of the transects within each area was achieved by walking a random number of paces in a random direction between each count. Sixteen transects were done in the outer-reef area, fourteen in the mid-reef area and four in the inner-reef area.

Percentage cover of each category was determined by dividing the number of points of each category by the total number of points on each line; data are presented in Appendix A.

1.5.2.2 Borer density estimates

Belt transects were used to estimate borer densities at low tide when the reef flat was exposed. Different area transects were used for different boreholes due to the differing densities of the borers and the nature of the substrate in which they bore. The areas used for density estimates were chosen as being the reef zones where the borers were most common. Randomness within these areas was achieved by taking a random distance and direction between transects.

Upogebiid shrimps

Nineteen 10 x 100cm band transects were done randomly in the mid-reef area and the number of boreholes visible in these bands counted. The transects consisted of a 100cm length of chain laid on the reef surface with a 10cm ruler used to provide the width. Thus, a total of 19000cm^2 was covered.

Hapalocarcinid crabs

Sixteen small band transects were done on the live surfaces of *Goniastrea retiformis* in the outer-reef area. Due to the patchy nature of the live and dead coral and the variable coral colony size on the outer reef, the transects were variable in length, ranging from 19cm to 66cm, but the width was kept at 2cm. Transects were delineated with a tape measure and a ruler and were done on randomly selected coral heads within the outer-reef area; the number of hapalocarcinid borehole entrances within each transect and its diameter (in millimeters) was recorded. A total of 1224cm^2 was surveyed in this manner.

Alpheid shrimps and barnacles

No density estimates were obtained for these borers

1.5.2.3 Coral Sampling

Specimens were collected from the reef flat using a hammer and a wide-ended chisel (7-8cm wide). Most corals were collected from the outer reef as borers were often present in higher densities and it was easier to remove the higher relief corals than to excavate pieces of reef pavement from the mid reef. Photos and sketches of the corals were taken before removal and the coral's orientation relative to North noted. Photos taken of freshly split surfaces with their exposed boreholes were also taken for reference once the corals were dried and dead and broken into pieces.

Coral blocks up to about 30x30x30cm size were removed and broken up in a more controlled manner in the lab. As the corals were split, careful notes were taken to ensure every fragment could be traced back to its position on the original coral. Some corals were split straight away, while still fresh, others after having been bleached or frozen. Most corals were immersed in a bleach solution immediately after collection in order to kill the coral tissue (and all other organisms) and thus prevent rotting. They were left in bleach for 1-2 days and then dead coral tissue blasted off using a jet of water. Specimens were then either dried in the sun for a week and transported back to Britain, or further analysed in the field. A few corals were frozen for two weeks, after which the coral tissue came off easily with a water jet and the borers were fairly well preserved. As well as taking photos of *in situ* and sampled boreholes, detailed drawings and measurements were made.

Back in Britain the finer structures of the boreholes were examined using light and scanning electron microscopes; photos were taken using 1:1 and x10 macro lens set ups. Thin sections were made of the borehole linings. (See section 1.5.2.5)

1.5.2.4 Silicone casting

Casts were made of some of the larger boreholes using silicone sealant of the type used in bathroom tiling. The silicone was injected into the borehole opening from the silicone gun until excess began to come back out of the hole. The casts were left for a day to solidify and then extracted by breaking the coral and peeling the casts from the coral. This method was not entirely successful, rarely filling the boreholes completely. Further attempts were made on boreholes that had already been split in two; the two halves of the borehole were filled with silicone and then reassembled and held together with two or three strong elastic bands until the casts had solidified. When the elastic bands were removed, the two halves of coral could easily be separated and the casts removed. This method was more successful as it allowed more complete casts, and also allowed any animals inside the holes to be removed before casting.

1.5.2.5 Microscopy and photography

Coral samples were embedded in Araldite MY778 (with HY951 hardener) prior to thin sectioning to a thickness of 30-50μm. The slides had permanent coverslips mounted.

Two set-ups were used to take photos of slides; a) Wild Makroskop M420 with Wild/Leica MPS 48/52 camera attachment and b) Wild Photomakroskop M400 with Photoautomat MPS 55 attachment.

Close up, black and white photos of whole specimens were taken with a Leitz Aristophot modified for use with an automatic Pentax with 1:1.56/120 lens and a Pentax P30 with 1:1 lens.

A Cambridge Stereoscan 250 was used for scanning electron microscopy; coral samples were cut to a maximum size of 0.5cm^3, mounted on 12.5mm stubs, carbon dagged and gold sputter-coated (gold thickness approx. 20nm).

1.6 TERMINOLOGY

Throughout this thesis, the terms ‘burrow’ and ‘burrower’ imply the excavation of a hole in an *unconsolidated* substrate, i.e. in sediment. In contrast, ‘boring’, ‘borehole’, and ‘borer’ refer to the holes made animals in *hard* substrate, i.e. coral.

1.7 LAYOUT OF THESIS

Chapters 2, 3 and 4 present the results of this research. Each chapter starts with a review of the literature pertinent to the chapter’s subject, then goes on to present and discuss the data obtained and ends with a summary of the main findings. Chapter 2 considers the bioerosion part of this work, Chapter 3 bioturbation and Chapter 4 the geological implications of bioturbation. A synthesis of the role of crustaceans in the development and taphonomy of the Phuket reefs is presented in Chapter 5. Chapter 6 is a summary of the main conclusions reached as a result of this work. Appendices A-D scontain all the raw data referred to in the main body of the thesis.

CHAPTER 2

BIOEROSION

The chapter begins (2.1) with a general introduction to the subject of bioerosion and specifies the areas that are considered further in this study (2.2). Section 2.3 describes in detail the borehole morphology of four crustacean bioeroders on Tin Smelter Reef, Phuket; pyrgomatid barnacles (2.3.1), hapalocarcinid crabs (2.3.2), upogebiid (2.3.3) and alpheid shrimps (2.3.4). The fine structure of these holes is used to reconstruct their method of production and the implications for coral and reef growth are discussed in section 2.4. Finally, section 2.5 summarises the main points raised by this work.

2.1 INTRODUCTION TO BIOEROSION

2.1.1 Definitions

Bioerosion is the breakdown of a solid substrate or grains of that substrate by biological activity. This chapter will only refer to coral reef substrates. Grazing and microbioerosion affect only the surface of the substrate. In contrast, macroborers create boreholes centimetres deep into the substrate which are used as a home and as a shelter from which to feed; this study concentrates on these macrobioeroders.

Bioerosion is either passive or active. Passive boring occurs when an organism settles and allows the coral to grow up around it. As the coral and borer grow upward together a hole is created. Active boring occurs when the organism physically removes coral. It is achieved by mechanical (McLean 1967, Scott 1985) or chemical (Lazar and Loya 1991) means, or a combination of the two (Yonge 1963, Soliman 1969). Products of active erosion (solution products or grains) then become a potentially important component of reef sediments.

2.1.2 Distribution

Most coral borers attack only the dead parts of corals (Scoffin & Garrett 1974, Patton 1976) or are most active in dead areas (Scoffin 1972). It is also common to find the greatest densities at the bases of or beneath coral colonies (Scoffin 1972, Hein & Risk 1975). Some species can colonise live corals (Goreau et al 1972, Patton 1976).

The densities, size and shape of borings vary greatly with substrate and conditions (McLean 1974, Warme 1977). Since bioeroders are limited by environmental conditions, their traces can be used in palaeoenvironmental reconstruction, especially with respect to degree of sedimentation (Scoffin 1972, Warme 1977, Bromley and Asgaard 1993a) and water depth (Warme 1977, Ekdale et al 1984, Bromley and d'Alessandro 1990). Hutchings (1986) notes the importance in the variation in recruitment of juvenile borers to suitable substrates with time and space, and its subsequent effect on the variation in the extent of boring.

2.1.3 Effects and significance of bioerosion

Like soft-bottom fauna (see Chapter 3), trace fossils of borers are often the only sign of their soft-bodied makers. (Ekdale et al 1984). They are also evidence of animal behaviour, though most are domichnia (dwelling traces) that the animals have bored for protection, especially from predation (Warme 1977, Bromley 1994). Some bioeroders bore to obtain food in the form of epi- and endolithic organisms, especially algae.

Widespread boring of reef corals developed during the Mesozoic and Cenozoic and was important in the evolution of reefs, reef ecology and reef biota due to the resultant increase in diversity of endo- and cryptolithic fauna (Warme 1977, Brett 1988).

As this study concentrates on the taphonomic implications of **macroborers** in **coral**, the literature discussed below only focuses on this aspect of bioerosion. There is a huge volume of literature on grazing bioeroders, on microbioeroders and eroders of shells and other non-reef substrates. The reader is directed to a review by Hutchings (1986) for information on coral reef grazers and microbioeroders.

2.1.3.1 Reef growth and structure

Bioerosion (both active and passive) comprises one of the main processes in the growth-encrustation-erosion-sedimentation-cementation cycle that forms reef framework The relative rate of these processes determines the development of internal structures (Scoffin and Garrett 1974, Scoffin et al 1980). This has important implications for the ability of a reef to cope with changing sea level (the "keep-up, catch-up or give-up" theory; Neumann and Macintyre (1985). A few attempts have been made to quantify these processes in order to produce a carbonate budget for reef systems (Chave et al 1972, Hein & Risk 1975, Stearn et al 1977, Scoffin et al 1980, Bak et al 1984, Kiene 1985, 1988). For summary tables of rates of bioerosion for individual groups or species of animals see Trudgill (1983) and Scoffin (1987).

Due to borers' activities, much of the original framework can be lost and replaced with multiple generations of encrusting organisms and infills, though there may be no loss in overall size or mass of the reef (Ginsburg et al 1971, Scoffin 1972, Schroeder and Zankl 1974, Scoffin and Garrett 1974, Warme 1977, Zankl and Multer 1977). The sequence of events leading to a particular 'lithoturbate texture' or 'bioerosion fabric' can be traced using cross-cutting relationships of the various tiers of bioeroders and their relationship to encrusting layers and cements (Ginsburg and Schroeder 1973, Warme 1977). Reconstruction of reef surface morphology from its internal structures is also possible (Scoffin and Garrett 1974, Scoffin et al 1980).

Boreholes increase the surface area available for colonisation by further bioeroders and also by cryptic species (e.g. Scoffin and Garrett 1974, Jones & Pemberton 1988a). The weakening and subsequent breakage of reef substrate also periodically opens up fresh colonisation surfaces. Alteration of coral growth patterns by passive borers can also influence both the fine and gross morphology of corals.

2.1.3.2 Carbonate removal and sediment production

Sediment can be produced a) by active borers by the direct removal of substrate or b) indirectly by substrate weakening and subsequent physical erosion, which results from both active and passive boring (Jehu 1918, Otter 1937, Hein & Risk 1975, Warme 1977, Jones & Pemberton 1988a, Scott and Risk 1988). Dead corals are especially susceptible to weakening by borers

(Scoffin 1972, Warme 1977) and successive generations and composite borings can cause the reef skeleton to erode away along an advancing 'front' of boring (Scoffin 1972).

Active boring removes carbonate and produces solution products such as carbon dioxide, mucus and carbonate muds and grains. A wide range of grain sizes can be produced (McLean 1974, Fig. 6.1 in Scoffin 1987, Jones & Pemberton 1988a), from fine carbonate 'dust' (Ahr and Stanton 1973, Kleeman 1973, Le Campion-Alsumard et al 1993) to coarse silt (e.g. sponge chips; Fütterer 1974) to cobble- or boulder-sized reef debris that has been physically eroded from the borer-weakened substrate. The particles formed can be highly characteristic of their producer, for example the chips of carbonate formed by the boring sponge *Cliona* sp. (Fütterer 1974), or have a characteristic size range, depending on their method of production (Scoffin 1992). The nature of the substrate is also important in determining the nature of the eroded product. For example, bioerosion of massive corals produces mainly fine sediments whereas branching corals produce mainly rubble and sand (Scoffin et al 1980).

The sediment produced can be a) preserved *in situ* as coral boulders or internal sediments in crevices and cavities, b) become part of the wider reef sediment, or c) be exported from the system by water currents. The preservation of freshly eroded grains is determined by the degree of physical and biological reworking that occurs before burial (see Chapter 3).

2.2 AIMS OF THIS STUDY

The field of bioerosion is a large and complex one, so for this study it was decided to limit investigations to one of the less well known groups of bioeroders, the (intertidal) crustaceans. As can be seen from the paragraphs below, little work has been done on crustacean borers in the past, and although they are fairly inconspicuous and are not the most abundant borers, they are common on the reefs of Phuket.

As most of these boreholes have not, to the author's knowledge, been described in the literature, the first aim was simply to provide a detailed illustrated description of the borehole morphologies and, where possible, the boring product. By carefully examining borehole structure and coral growth patterns from the macro to the micro scale it was hoped that the mechanism of bioerosion could be deduced. Special attention was paid to any possibility of active bioerosion and the removal of coral skeleton and the resulting importance of the boring to the reef carbonate budget. The usefulness of these four crustaceans' borings in interpreting the origin of fossil reef structure is also considered.

2.3 CRUSTACEAN BIOERODERS

All work was carried out on Tin Smelter Reef (see section 1.3.1 for site description and 1.5.2 for methods). Whole specimens, thin sections and scanning electron micrographs formed the basis of this morphological study. Evidence for passive or active nature of boring was extracted from the borehole structure and the patterns of coral growth relative to the boreholes.

Boreholes in reef flat corals from Tin Smelter Reef (*Coeloseris mayeri*, *Goniastrea aspera*, *Goniastrea retiformis*, *Platygyra daedelea*, *Platygyra sinensis* and *Porites lutea*) were found to contain four types of crustaceans; alpheid shrimps, upogebiid shrimps, hapalocarcinid crabs and pyrgomatid barnacles.

In the following descriptions, the term 'distal' is used to indicate the end of the hole at the coral surface, and 'proximal' for the end furthest from the coral surface.

2.3.1 Pyrgomatid barnacles

2.3.1.1 Classification

Subclass Cirripedia, Superorder Thoracica, Order Sessilia, Superfamily Balanoidea, Subfamily Pyrgomatinae (Anderson 1994). The species may be *Savignium crenatum*, judging by the structure of the wall plate and opercular plate (adductor plates on the scutae and a bare area on the underside of the wall plate)(Darwin 1854, Anderson 1992).

The most well-known coral boring barnacles are the those in the Order Pedunculata, for example *Lithotrya*. It is thought that these barnacles use mechanical means to remove the coral skeleton, which might be chemically pre-softened by glandular secretions (Anderson 1994). The pyrgomatids have become much more highly specialised than the pedunculates to adapt to their coral-dwelling way of life, both in their calcareous plate and soft tissue morphology. In this

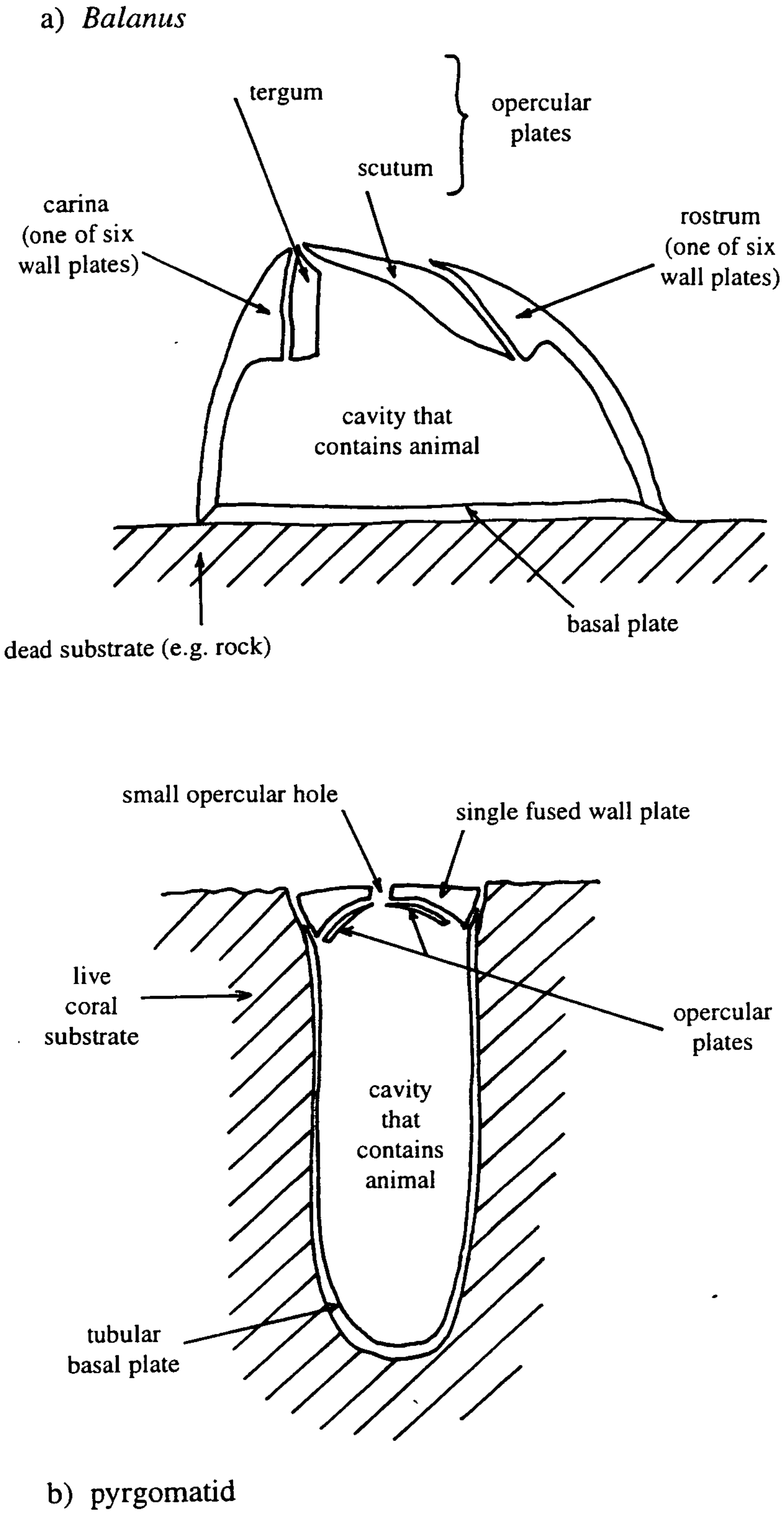


Figure 2.1 Schematic cross sections to compare the morphology of **a)** a typical sessile balanoid barnacle *Balanus* with **b)** a boring pyrgomatid barnacle.

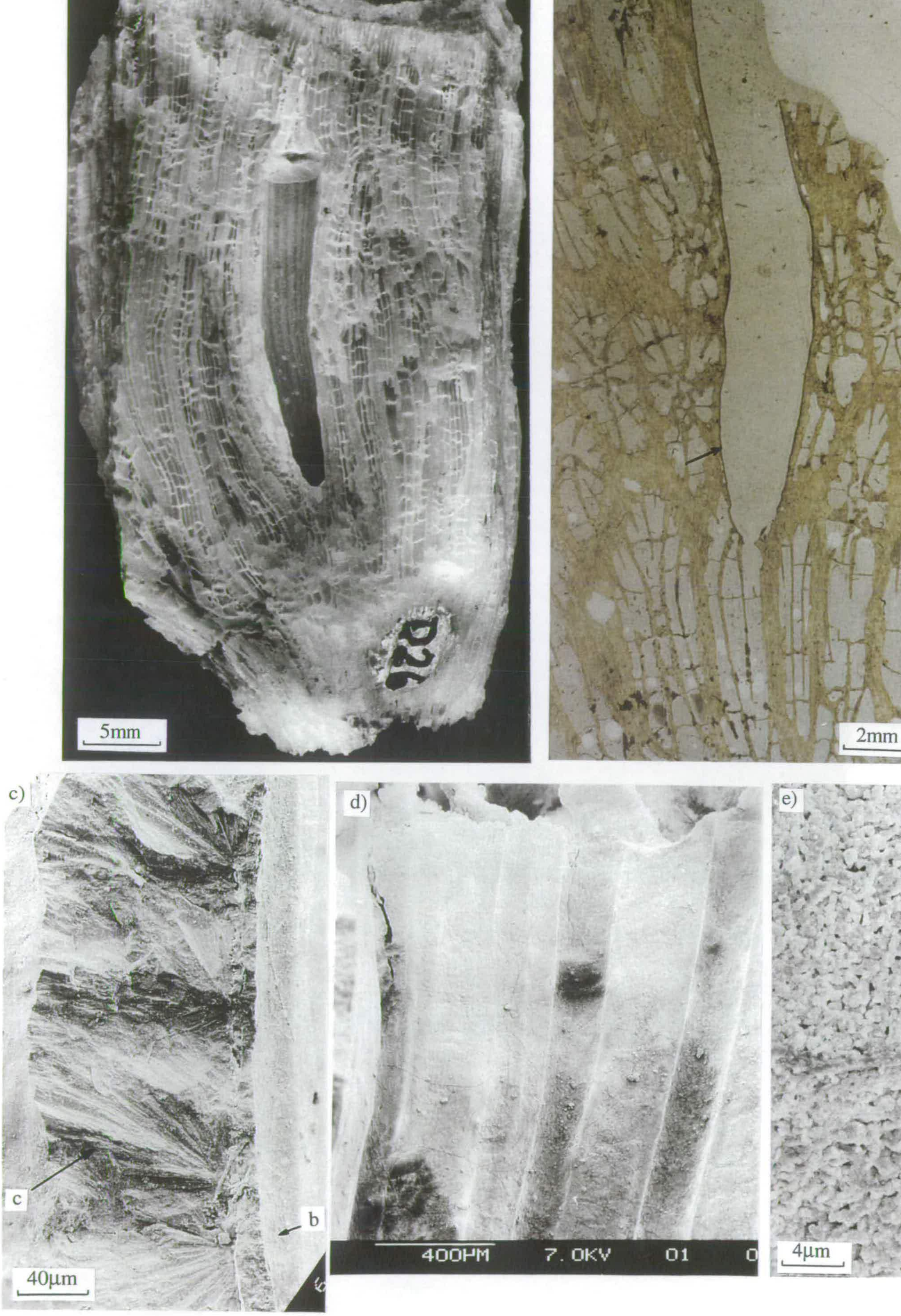


Plate 2.1 Longitudinal sections through pyrgomatid barnacle boreholes. **a)** Overgrown borehole in *Goniastrea retiformis*; note the corrugated basal plate tube and the coral growth pattern around the borehole. **b)** Thin section of a borehole; thin basal plate (arrow) and altered coral growth visible. **c)** SEM showing coral aragonite bundles (c) growing off the barnacle plate (b). **d)** Detail of corrugated distal end of the corrugated basal tube. **e)** High magnification view of basal plate surface

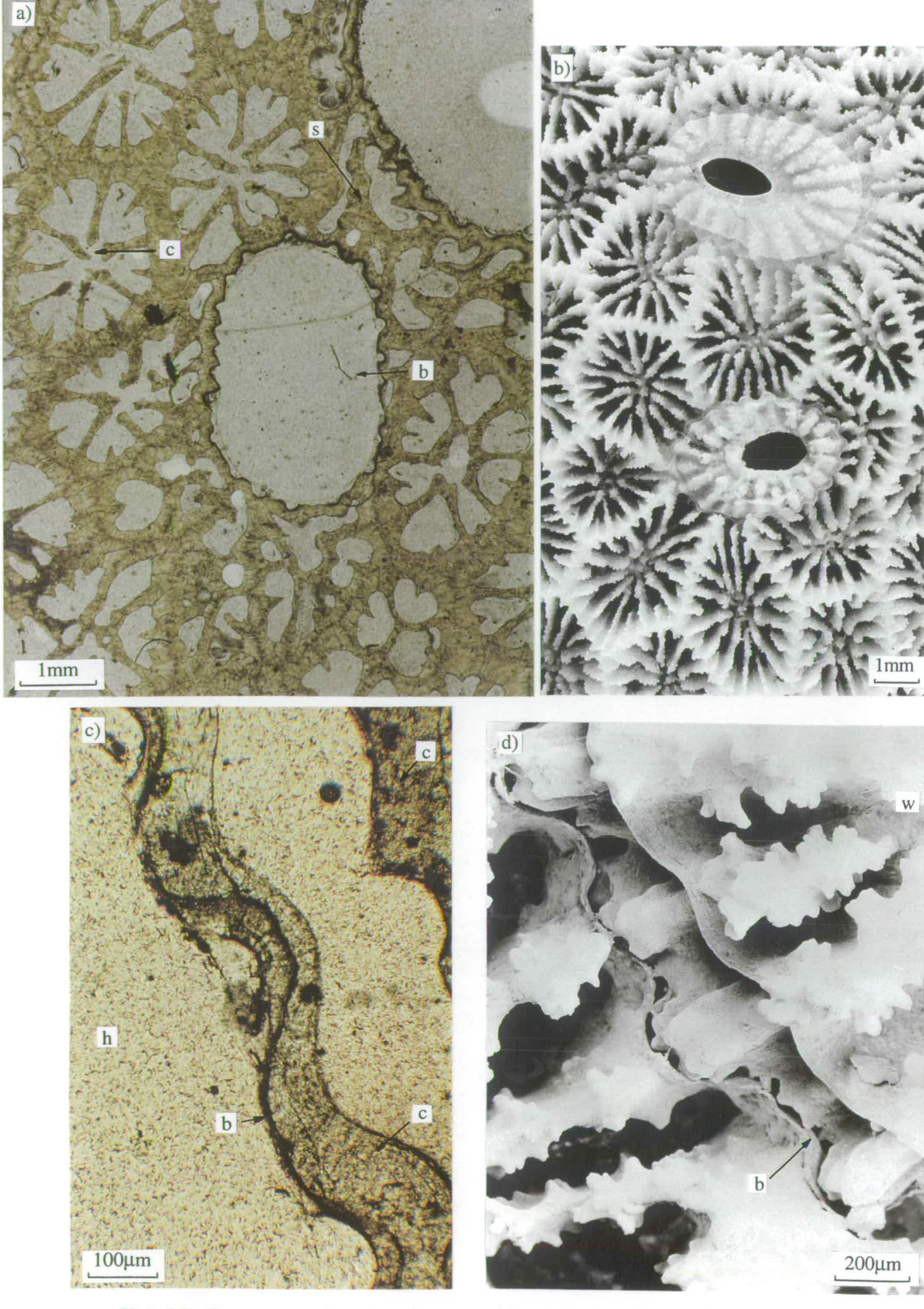


Plate 2.2 Transverse sections through pyrgomatid barnacle boreholes. **a)** Thin section through two boreholes (b). Coral skeletal 'scar tissue' visible (s); compare with normal corallite growth (c). **b)** Surface appearance of two barnacles. **c)** Thin section detail of crenellated basal tube (b). 'c' = corallite, 'h' = borehole. **d)** SEM of junction of surface wall plate (w) and basal tube (b).

study, the soft parts did not preserve well but the boreholes and plate structures were used as the basis of a detailed structural study. Fig. 2.1 shows the structure of a pyrgomatid with a better-known balanoid, the seashore barnacle *Balanus*, for comparison. From this figure it can be seen that in the pyrgomatid barnacles the wall plates are fused together to form a disc at the coral surface, with marginal processes anchoring the edges of this plate to the apical margin of the tube-shaped basal plate (basis) which penetrates deep into the coral skeleton (Darwin 1854, Anderson 1992, 1994). All barnacle parts are made of low-Mg calcite (X-ray diffraction analysis).

2.3.1.2 Borehole morphology

The borehole is a long, narrow hole with an oval cross-section, widest and more or less parallel-sided at the distal end but tapering, at first gradually and then suddenly, downwards to form a pointed proximal end (Plate 2.1a and b). The hole is perpendicular to the coral surface and tends to be parallel to the direction of corallite growth. Live barnacles are only found in live coral; the few holes found in dead coral did not contain animals and were starting to be overgrown with encrusters. Boreholes are quickly overgrown with coral after the barnacles' death and it was common to find holes hidden well beneath the live coral surface when corals were split open (Plate 2.1a). Mean borehole length was 14.3mm (st. dev. = 8.12, n = 79; Appendix D). There is only a weak correlation between hole width (at the surface) and length (correlation coefficient = 0.38, n = 78 pairs of data).

Wall plate structure

At the coral surface is the wall plate which is about the same size as a coral polyp (in *Goniastrea retiformis*) oval in shape and less than twice as long as it is wide (Plate 2.2b). Mean plate length was measured as 4.2mm (st. dev. = 0.86, n = 83) and mean plate width as 2.65mm (st. dev. = 0.64, n = 68; Appendix D). The plate has a smaller oval opercular hole offset to one end surrounded by a radial array of ornamented ridges. The distance of these ridges from the opercular hole decreases with increasing overall size (=age?), i.e. the smaller the plate, the larger the smooth, bare area around the hole. Larger plates also have heavier ornamentation and thicker radial ridges. The radial ridges are oriented so that they align with projections on the wavy edge of the plate and also with the septa or interpolyp walls of the neighbouring coral polyps which are physically attached to the projections of the frilled basal tube edge (Plate 2.2a and d). The appearance of the ornamentation of the coral septa and the radial ridges are almost identical (Plate 2.2b). In some specimens, surrounding polyps have thickened and more heavily ornamented septa on the side that adjoins the barnacle. Usually the neighbouring polyps abut the barnacle so that the corallite wall coincides with the barnacle edge but one or two polyps of the six or seven that surround a barnacle appear to have been cut through or modified by the barnacle (Plate 2.2d).

The thick edge of the wall plate has longitudinal ridges all the way round which align with the processes of the top surface and are similarly ornamented like coral septa. These vertical ridges also correspond exactly with the corrugations of the basal plate and are a point of attachment for the wall and basal plates (Plate 2.2d). This attachment is not very solid, as the wall plate is fairly easy to detach undamaged from the borehole. This is probably because it is this junction that is the area of growth for both plates and is not a permanent join.

The underside of the plate is an upwardly curving dome, smooth but with very fine concentric rings around the opercular hole. It is to this smooth area that the soft tissue of the animal attaches, holding the opercular plates in position in the central hole at the coral surface.

Tubular basal plate and altered coral growth

The sides of the borehole are lined with the calcareous tubular basal plate or basis. The basis is grooved parallel to the borehole sides with 20-30 grooves which themselves have very fine longitudinal grooves on their surfaces (Plate 2.1a and d).

The tubular basis is visible in SEM images as a thin (8-12μm), wavy edge disappearing into the coral and is also clear as a crenellated oval outline in transverse thin section (e.g. Plate 2.2a and d). The basal plate has a variable thickness, ranging from 15-85μm and averaging around 40μm (29 measurements taken from thin sections and scanning electron micrographs). The thinner parts of the plate are those that protrude into the borehole lumen, whereas the grooves that fold back into the coral are thicker and show a radiating crystal structure in transverse section (Plate 2.2c).

Immediately behind and adjoining the basal tube is a thicker undulating layer (min 45μm, max. = 300μm, average c.200μm from 24 measurements from SEM photos and thin sections; Plate 2.2a and c). This is abnormal coral skeleton which seems to be laid down in response to the barnacle's presence. The junction of this layer and the main coral skeleton is not always distinct.

2.3.1.3 Borehole formation

Corallite growth patterns immediately surrounding the borehole are disrupted and corallite lumens with irregular shapes, abnormal septae and thick expanses of dense coral matrix can be seen in this area (Plate 2.2a), as if the coral is producing a skeletal 'scar tissue' in response to the barnacle. The barnacle basal tube is evidently laid down before the coral skeleton, as tabulae are visible in Plate 2.1c growing off the barnacle plate into the coral structure. Barnacle plate growth at the distal end of the basal plate and the outer edge of the wall plate enable the barnacle to keep pace with coral growth while increasing in width (Anderson 1994). Thus, borehole growth is controlled entirely by the barnacle which alters the host coral's growth pattern.

There is still the question of how the settling barnacle larva overcomes the coral defence mechanisms and establishes the initial stages of the hole. Most of the holes sectioned in thin sections and in whole samples are centred on a single polyp (e.g. Plate 2.1b), with some evidence to suggest initial attachment is on a septum. At this proximal end the barnacle tube is narrow and smooth, commonly with an irregularly folded form producing a convoluted structure. In most thin sections the fragile basal plate has been damaged at its base, but whole specimens show the plate covering the bottom of the hole. The hole quickly widens and becomes regularly corrugated and remains more or less parallel sided for the rest of its length. The corallite in which the barnacle hole started continues to grow upwards for a short distance but as the barnacle becomes wider the corallite tapers to a thin layer of amorphous skeleton along the basal plate (e.g. Plate 2.1b). General coral growth direction is around the proximal end and up the sides of the barnacle hole (Plate 2.1b).

Pyrgomatids are unique in their mechanism of restraining coral growth. Modified tergo-scutal flaps form a glandular fold, the aperture frill, which expands over the rim of the orifice when the cirri are active and extended. This fold appears to produce a secretion which chemically inhibits coral overgrowth (Anderson 1994).

Anderson (1992) suggested that pores in the basal plate of *Creusia spinulosa* and *Newmania elongatum* and the uncalcified ribbed structure of *Pyrgoma cancellata* could enable these barnacles to feed by uptake of dissolved nutrients from the surrounding polyps. No such pores are visible in this species, though it does have a ribbed basis. The basal tube is well calcified and it is more likely that they feed through the operculum at the surface with their cirri, which are long and well developed.

2.3.1.4 Rate of erosion

Pyrgomatid boreholes are formed by purely passive growth caused by alteration of coral growth by the barnacle. The length of the borehole is therefore a direct measurement of its age if the growth rate of the coral host is known. The linear extension rate of *G. retiformis* on Tin Smelter Reef has been measured at 1.85±0.18cm/year on the top surface of corals and 0.48±0.03cm/year on the sides of colonies (Scoffin 1997). Barnacle hole lengths ranged from 3mm to 33mm; 3mm is equivalent to an age of 2 months at the coral top and 7.5 months on the side, 33mm is equivalent to 1.78 or 6.88 years for the top and side respectively. The holes found overgrown inside the coral skeleton ranged in length from 7 to 33mm, indicating a minimum age at death of 4.5 months to 1.46 years (coral top and side respectively) and a maximum of 1.78 to 6.88 years (top, side).

2.3.2 Hapalocarcinids

The Hapalocarcinidae are a highly modified family of crabs which are found exclusively in cavities in corals and are commonly known as gall crabs due to their ability to cause corals to form growths around them. Most species are found in the Indo-Pacific and the structure of their galls varies with coral and crab species and how the animal is oriented relative to the direction of coral growth (Patton 1976). Galls are commonly small protrusions or growths on the coral surface (Patton 1976, Shaw and Hopkins 1977), but tubular holes extending deep into the coral are also found (Shaw and Hopkins 1977, this study). Patton (1976) stated that cavity formation is initiated by the crab remaining in one place until the underlying coral tissue is killed and Shaw and Hopkins (1977) added that the tunnel length and width are increased by the continued growth and movement of the crab. A degree of chemical interference with coral growth is also proposed to account for the strange growth patterns and the fact that coral gall tissue lacks zooxanthellae but is still alive (Patton 1976).

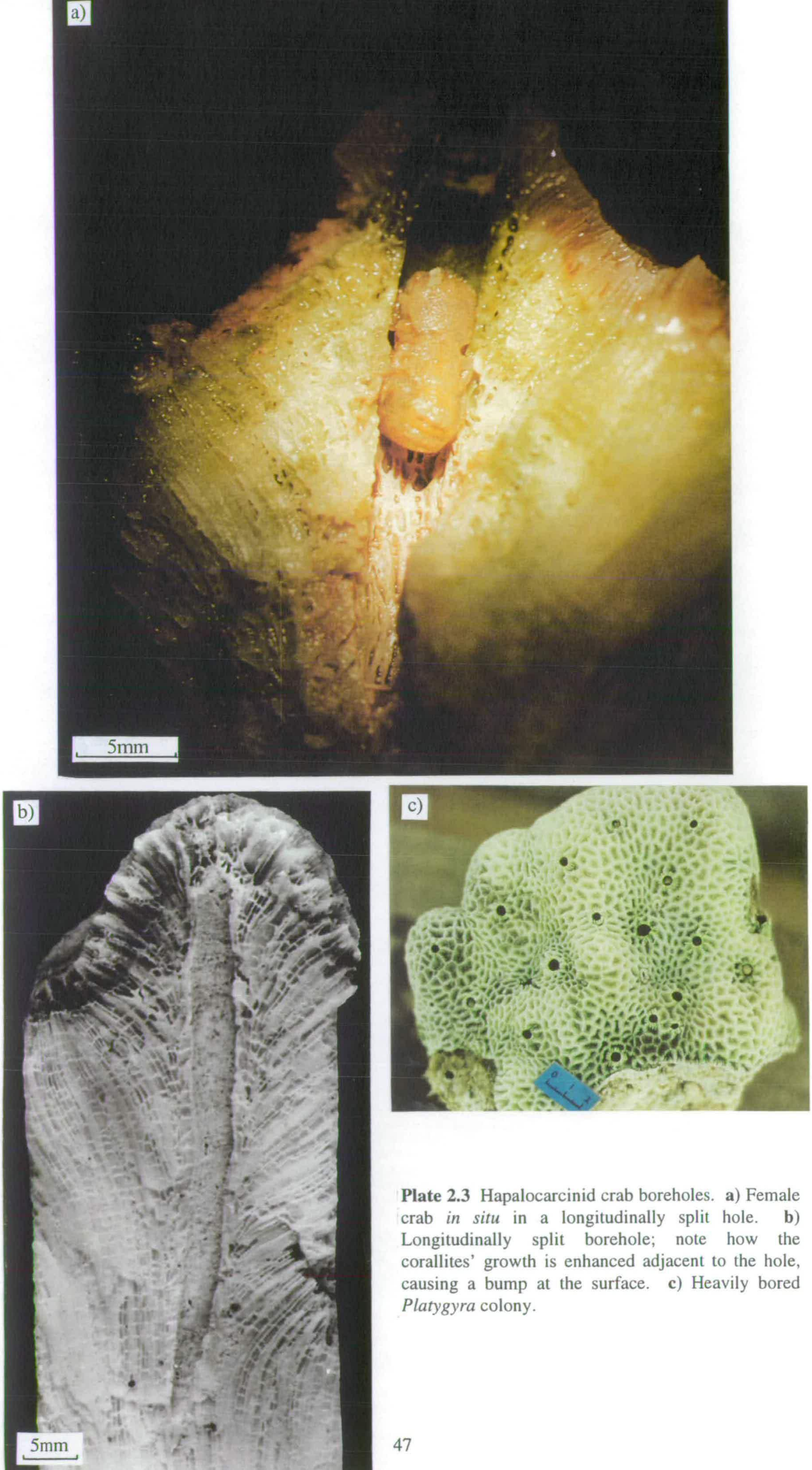


Plate 2.3 Hapalocarcinid crab boreholes. **a**) Female crab *in situ* in a longitudinally split hole. **b**) Longitudinally split borehole; note how the corallites' growth is enhanced adjacent to the hole, causing a bump at the surface. **c**) Heavily bored *Platygyra* colony.

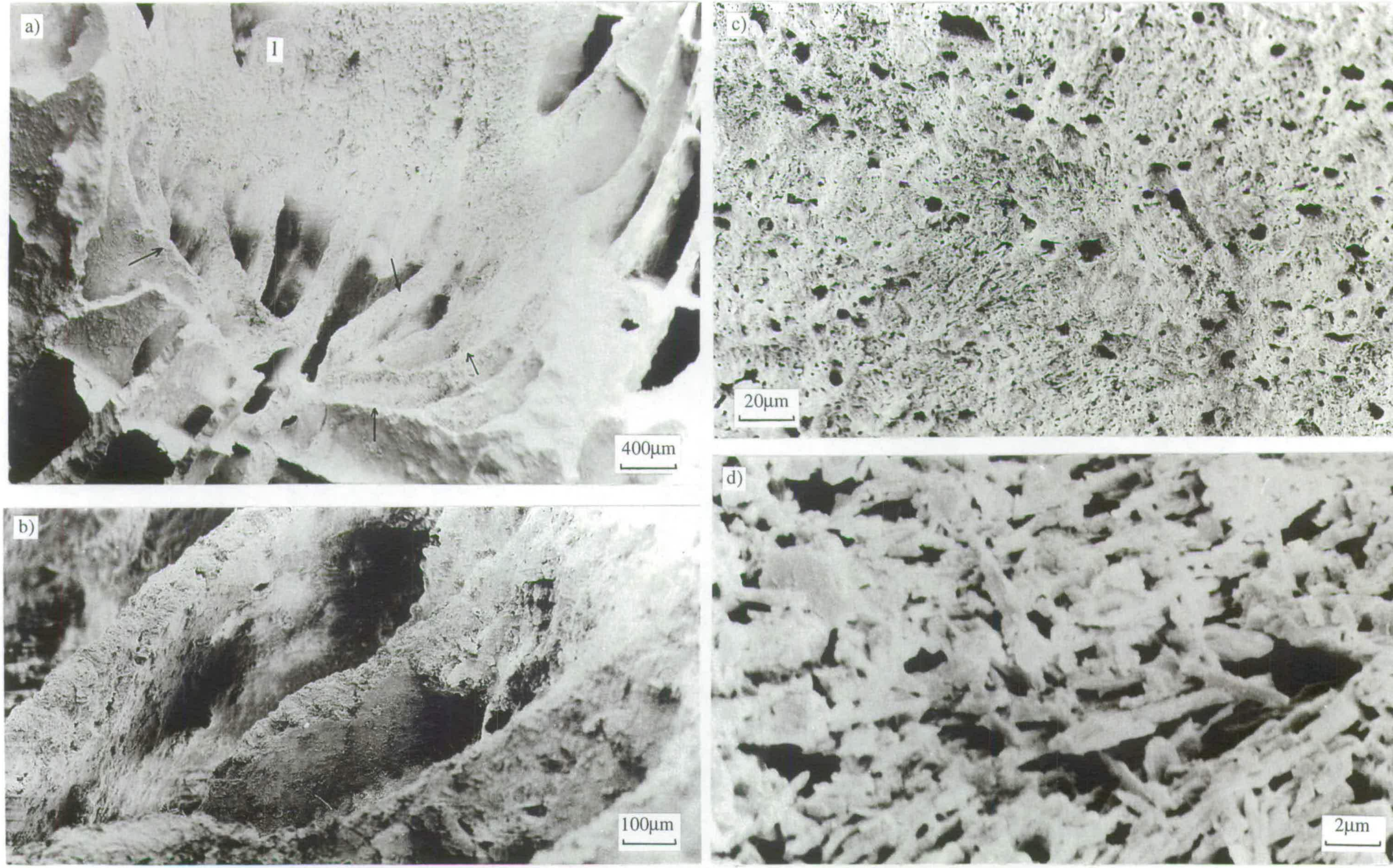


Plate 2.4 Hapalocarcinid crab boreholes. **a)** Smoothly eroded coral septae (arrows) and chalky lining (l) of proximal end of hole. **b)** Detail of eroded septae. **c)** Chalky lining of borehole sides are heavily infested with microborers. **d)** Detail of chalky lining showing etched appearance of coral.

2.3.2.1 Distribution

Boreholes in Phuket were only found in live coral, and mainly in *Goniastrea retiformis* and *Platygyra sinensis* on the outer reef. They had a clustered distribution, with some corals sheltering huge numbers (e.g. Plate 2.3c) and others none, but in all cases the crabs were most abundant on the vertical sides of the corals. Their presence on the outer reef and on vertical surfaces suggests that they prefer conditions where sedimentation is low.

2.3.2.2 Burrow morphology

The borehole is a narrow, cylindrical hole perpendicular to the coral surface and more-or-less straight or slightly curved (in the same direction as coral growth)(Plate 2.3a and b). The holes are perfectly circular in cross section. Hole diameters at the coral surface ranged from 2 to 5mm diameter and lengths from 4 to 61mm (n = 58; Appendix D). Occupied holes are sealed at the entrance by an operculum formed by the crab itself which has a modified carapace front and front legs which close off the borehole (Plate 2.3a). The crab fits exactly (widthways) into this hole, although its body is generally far shorter than the hole length, enabling it to move up and down within the hole (Plate 2.3a). The rounded borehole base closely fits the abdomen and tail of the crabs. This is especially evident in the case of the females whose abdomens are extended into egg-carrying structures. Sexual dimorphism was observed in both crab and borehole morphology (see Appendix D).

Chalky deposit/lining

The borehole surface is partly covered with a chalky looking deposit, especially at the distal end (e.g. Plate 2.4). In thin section, this layer is seen to be highly irregular in thickness, from completely absent to about 450μm thick (18 measurements from thin sections). In places it is up to 750μm thick, although it is often difficult to see where the lining ends and the coral skeleton begins. The chalky appearance of the lining (compared, for instance, to a shiny barnacle tube) is reflected in its appearance in thin section; the edge bordering the hole lumen, although flat, is not sharply defined but looks almost flocculent due to the loosely packed material on the surface. The junction between this lining and the coral looks irregular and lumpy and is sometimes separated from the coral matrix by a thin line, though it is more often indistinct. This chalky material is always more abundant at the distal end of the hole, completely coating the surface. An intermediate area in the central region, where large holes are visible in the lining, gives way to the proximal end where chalky material is restricted to a fine dusting over the smoothed coral septae (Plate 2.4b).

From thin sections and SEM images it is seen that shallow holes in the underlying coral structure get filled in with this calcareous deposit but deeper ones do not, hence the patchy appearance of the lining. Deep holes contain no deposit in their deeper reaches where the smooth and slightly ornamented texture of the coral septae is visible. This implies that the crabs are able to concentrate the deposit in areas that they choose, perhaps to best use the available carbonate to smooth the interior of their holes.

Microbioerosion is extremely abundant in the chalky lining and adjacent coral (Plate 2.4c), and partly contributes to the porous appearance of the hole surface. In freshly split corals the endolithic algal layer is very dense around the hole entrances and appears as a thick green band just below the live coral tissue. In thin section the skeleton and lining are part of a band that looks dark due to the high density of microbioerosion. The presence of the crabs might enhance the microborers' growth due to organic secretions and the hapalocarcinids could actually use these microborers as a source of food. Their delicate pointed chelae suggest that they feed in a grazing manner, either on these microborers or on coral tissue.

2.3.2.3 Borehole formation

The features described in section 2.3.2.2 indicate that hapalocarcinid boreholes are formed by a combination of passive and active erosion. See Fig 2.2 for a summary.

Evidence for passive erosion and coral growth alteration

1. The borehole tends to parallel the direction of coral growth.
2. The coral surface is often swollen into a bump around the hole entrance and corallites often fan outwards from the hole, suggesting stimulation of coral growth next to the hapalocarcinid hole (Plate 2.3b).
3. The proximal end of the hole always centres on a single corallite and the initiation of the boring process could be by inhibition of a single polyp's growth

Evidence for active erosion

1. The surface of the coral, where it forms the curved borehole wall appeared chemically etched (Tudhope pers. comm; Plate 2.4e).
2. The borehole cuts through previously formed coral polyps in places, especially at the proximal end of the borehole where the lining is often absent (e.g. Plate 2.4a and b). The septae in this area appear to be eroded as they are flat edged rather than showing the tapered cross-section and slight ornamentation that normal septae do. The coral surface exposed in the borehole is smooth, though full of holes where the open corallite structure has been exposed. This suggests *active* boring.
3. The perfect fit of the crab in the hole, combined with the smoothness of the walls suggest that chemical boring is occurring. Scott et al (1988) postulated that upogebiid shrimps could chemically soften the coral surface by the application of their tails to the coral surface and secretion from glands. Hapalocarcinids could employ a similar method to erode their boreholes. It is unlikely that purely mechanical erosion occurs as the crabs have small and delicate chelae which are not well suited to removing a hard substrate (unless that substrate is pre-softened by chemical breakdown). Since all sizes of crabs fit their holes so snugly and must grow in width during their lifespan they must enlarge the diameter of the borehole with time.
4. The chalky deposit seen on the borehole surface may be a solution product of chemical erosion.

It is concluded that the crab settles on one polyp and inhibits its growth, ultimately killing it. Surrounding corallite growth is also affected by the crab so that it grows up and around it, forming a cylindrical hole by **passive** erosion. Any widening of the hole is achieved by **active** chemical erosion and is accompanied by the laying down of a chalky lining which is likely to be a by-product of this erosion. See Fig. 2.2.

2.3.2.4 Rate of bioerosion

Since the extension of hole length is achieved by coral growth, the length of the hole is a direct measurement of its age, as is the case with barnacles (section 2.3.1.4). Ages range from about 4 months to 5 years (see Table 2.1), given that *G. retiformis* and *P. sinensis* have average linear extension rates of 11.45mm/year and 14.5mm/year respectively (Scoffin 1997).

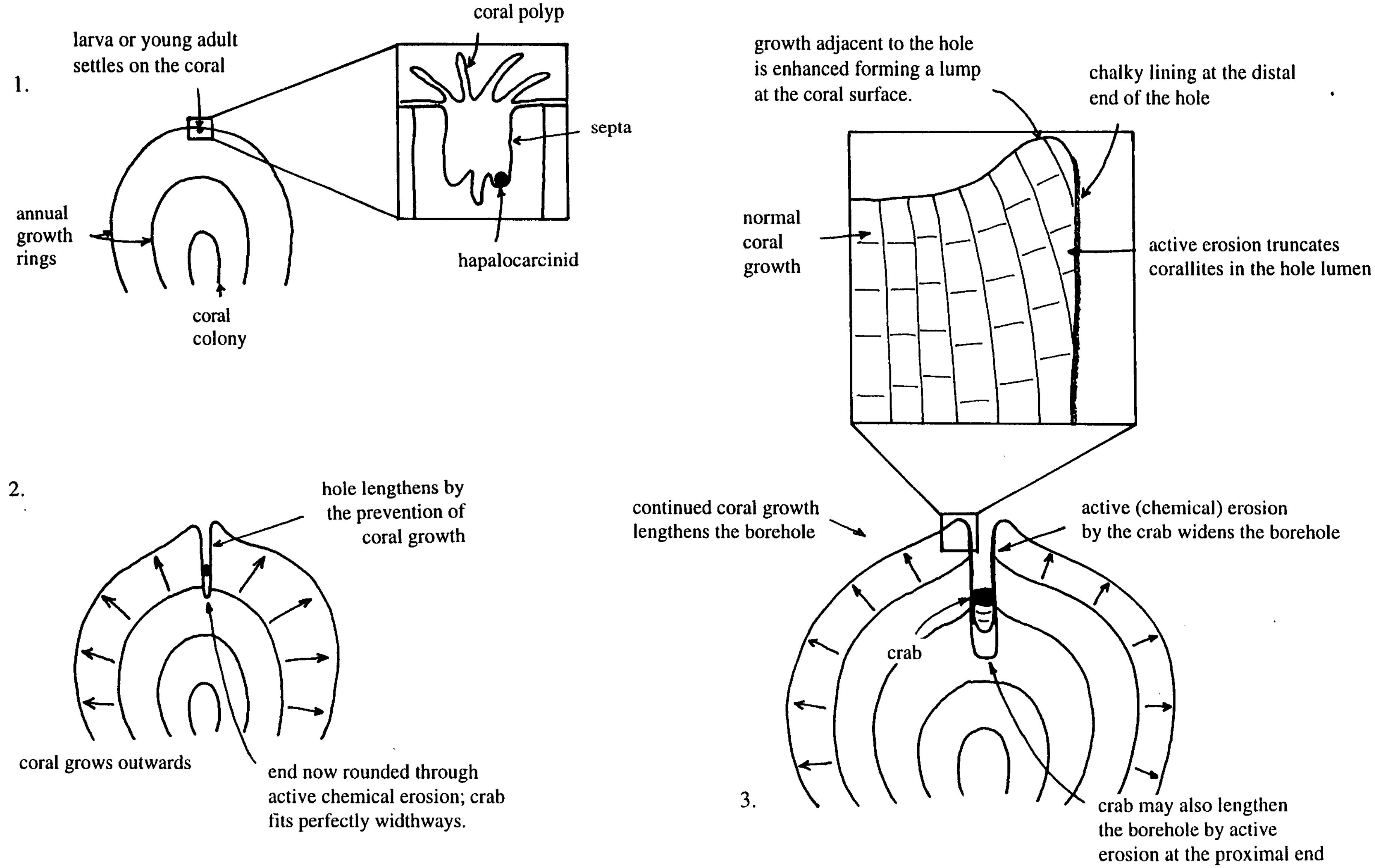


Figure 2.2 Proposed mechanism for the formation of hapalocarcinid boreholes

Table 2.1 Summary of the age range of hapalocarcinid holes.

Coral species	**Hapalocarcinid hole length (mm)**		**Age of hapalocarcinid hole**	
	minimum	maximum	minimum	maximum
G. retiformis	4	61	4.2 months	5.3 years
P. sinensis	5	60	4.1 months	4.1 years

Densities of hapalocarcinids were measured on the outer reef in live *Goniastrea retiformis* using random small band transects as described in section 1.5.2.2; the mean density was 334/m^2 (n = 16 transects, st. dev. = 307; Appendix D). The average volume of the boreholes was worked out from the measurements taken in *G. retiformis* (n = 26) and came to 134mm^3 (st. dev. = 161.0). This represents 44.8cm^3/m^2 live *G. retiformis* absent due to hapalocarcinids. As far as the whole reef budget is concerned this is probably a negligible amount, especially since much of this volume represents passive boring as opposed to active removal of the substrate. No population density measurements were taken on *P. sinensis* colonies, but hole volumes tended to be greater in that species (mean volume 319.8mm^3, st dev. = 268.6, n = 24).

2.3.3 Upogebiids

2.3.3.1 Classification

Order Decapoda, Superfamily Thalassinoidea Latreille 1831, Family Upogebiidae Borradaile 1903. The species is thought to be *Upogebia darwinii* (Miers) from Chatanantawej (1986).

2.3.3.2 Borehole morphology

The only visible sign of the borehole at the coral surface are two or three (usually three) small holes of about 5mm diameter, usually in shallow rounded depressions (Plate 2.5b). These widen quickly into one centimetre diameter holes with a round cross-section leading straight down into the coral or reef. These tubular holes are usually about 5cm long (Plate 2.5a), though occasionally larger (10-15cm long) examples were seen (Plate 2.5d), and join at the bottom to form a three-pronged borehole which carries on down a short way as a single tube with a rounded blind end. Each borehole system is home to a pair of shrimps.

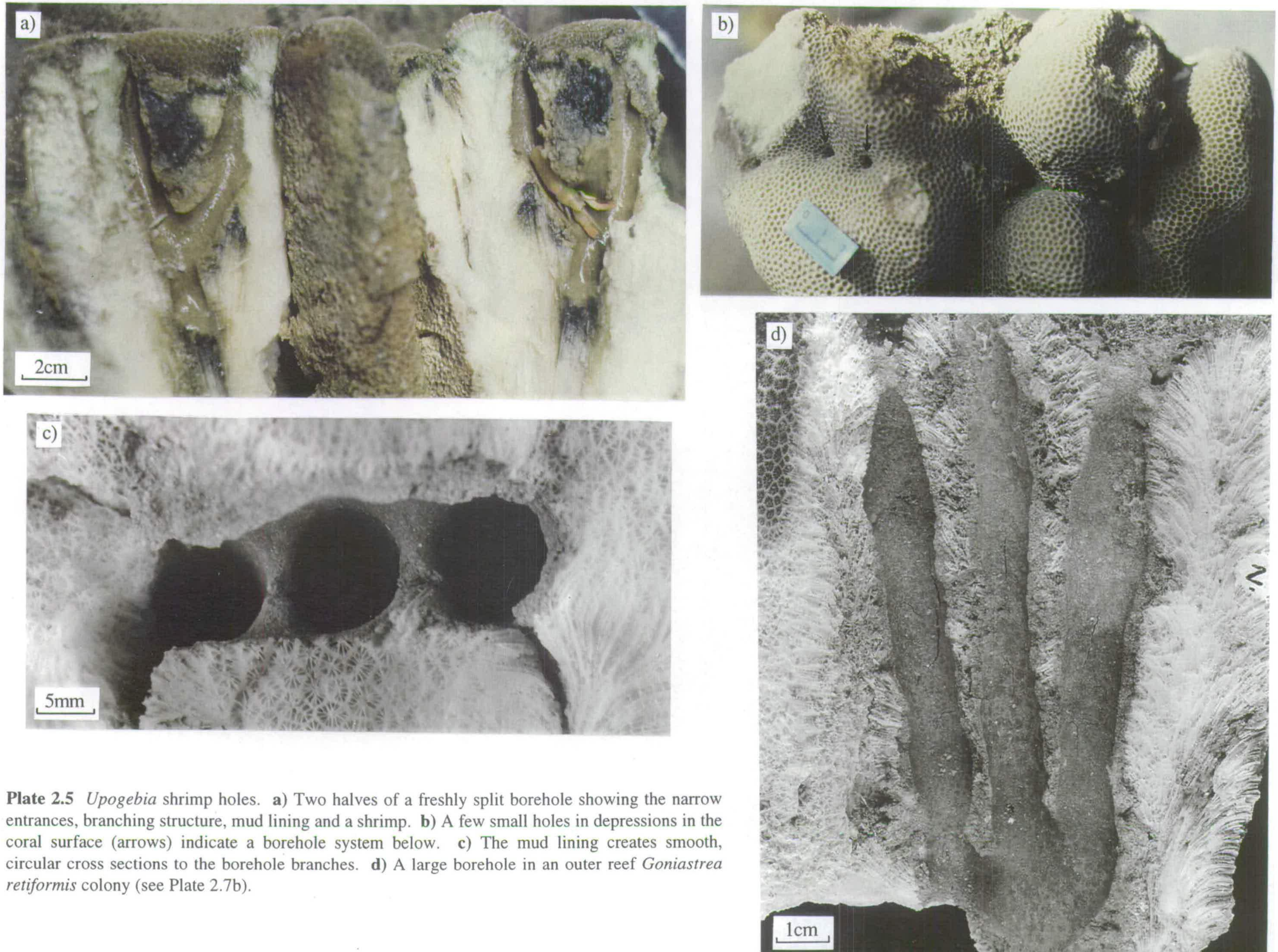


Plate 2.5 *Upogebia* shrimp holes. **a)** Two halves of a freshly split borehole showing the narrow entrances, branching structure, mud lining and a shrimp. **b)** A few small holes in depressions in the coral surface (arrows) indicate a borehole system below. **c)** The mud lining creates smooth, circular cross sections to the borehole branches. **d)** A large borehole in an outer reef *Goniastrea retiformis* colony (see Plate 2.7b).

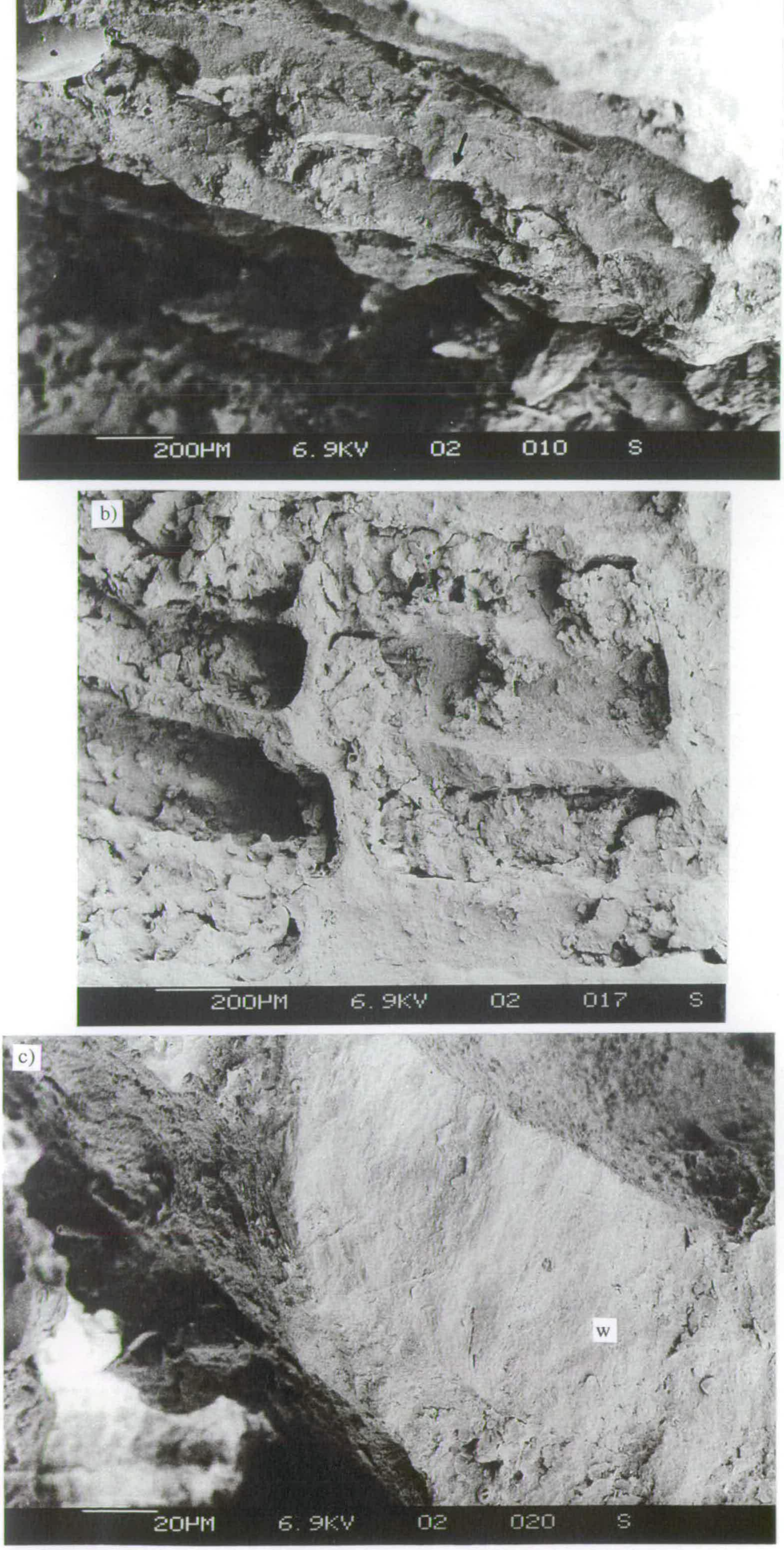


Plate 2.6 Eroded corallite structure beneath the mud lining of a *Upogebia* borehole; most of the mud has been cleaned away. **a)** Scalloped edge (arrow) where the shrimp has mechanically removed coral skeleton. **b)** Plan view of eroded corallites. **c)** Detail of the eroded corallite wall (w).

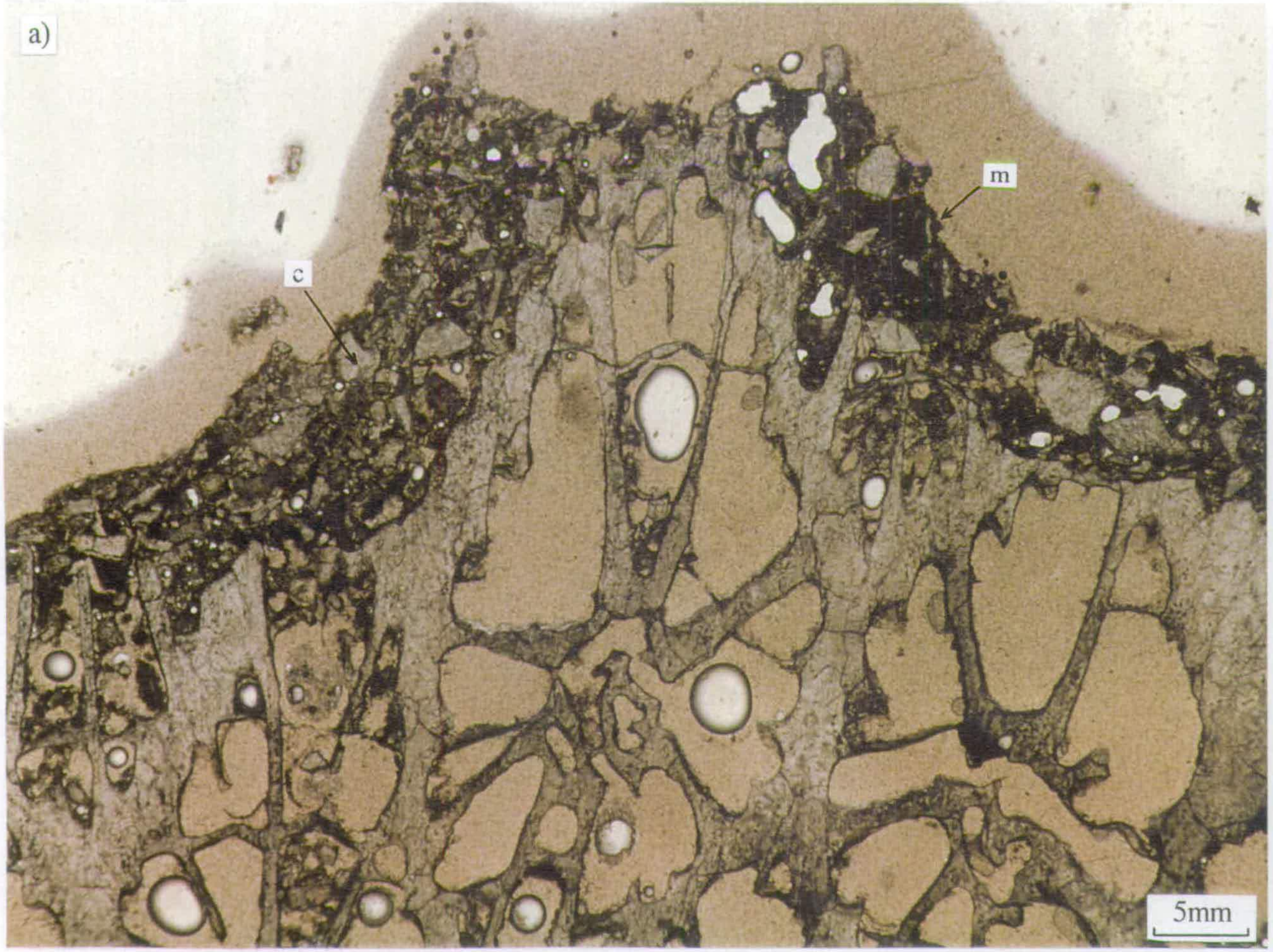


Plate 2.7 Mud lining of a *Upogebia* borehole. **a)** Thin (transverse) section through two branches of a burrow; the rough edges of the eroded corallites have been smoothed over with the application of mud. The lining shows coral fragments (c) embedded in an organic-rich mud matrix (m). **b)** Detail of Plate 2.5d showing how the mud lining fills the irregularities in the eroded coral to produce a smooth borehole lumen.

Mud lining

The entire structure is lined with a mixture of coral fragments and fine mud. This lining gives the interior of the borehole a smooth circular cross-section (Plate 2.5c), although the excavated hole is much more irregular in shape. The thickness of the lining is highly variable(Plate 2.7), from a few small grains (i.e. 0.1mm) thick to about 5mm thick, with some patches up to 1cm thick. The average thickness is about 0.5-1mm. The mud fills in the hollows in the coral structures below to provide a smooth inner surface to the borehole, filling any corallite that is open to the borehole and occasionally corallites below that have been broken into. Sediment found any deeper into the coral than this in thin section is likely to have been moved there during slide preparation (sawing, embedding, sectioning), as freshly fractured boreholes show the limit of sediment encroachment into the coral to be limited to one or two corallites. The extremely thick mud patches occur where a pre-existing cavity in the coral has been exposed by the excavation of the borehole, and in order to keep the shape of the hole, the entire cavity has been filled in with sediment until it reaches the same level as the rest of the lining. Thicker areas are also common at the borehole entrances where they are used to constrict the entrance to a narrow (0.5mm diameter) hole (Plate 2.5a and d).

The smoothness of the mud surface is due to it comprising mainly silt-sized grains and, when fresh, also a mucus layer which is not visible in dried and sectioned samples. Forty-one grains were measured from SEM photographs and ranged in size from 10 to 120µm in diameter, though most fell within the 16-63µm size range (medium to coarse silt). However, due to clumping of clay particles into platy aggregates, this probably underestimates the importance of finer silts and clays.

Cross-sections through the sediment lining show the range of grain sizes and grain types which make up this mud layer (thin sections, e.g. Plate 2.7a):

- A fine-grained, dark brown, blotchy matrix with no clearly definable characteristics.
- Coarser-grained, jagged-edged coral fragments embedded in the mud matrix. These are a variety of sizes, ranging from <0.05mm to 2mm diameter. Their shape is also variable, though from loose sediment samples long, thin grains seem particularly abundant among the larger size fraction.

In some thin sections the lining is slightly layered suggesting it has been added to at different times during the hole's creation. Long, thin grains tend to be oriented parallel to the walls; this must be the most effective way for the shrimp to obtain a smooth lining without using huge quantities of mud.

2.3.3.3 Borehole formation

Active erosion

All the evidence described above points to an active (mechanical) erosional mechanism for *Upogebia* borehole formation:

1. The corallites bordering the mud lining show abruptly truncated corallites structures (Plate 2.6). The edge are eroded back close to the corallite wall, so that only narrow strips of septae protrude in to the mud lining (Plates 2.6b and 2.7a). This presumably means that the shrimp has to use less sediment in order to build up a smooth lining to the hole. The eroded coral edges are sharp but their surface is uneven which implies that mechanical, erosion has occurred. (However, chemical pre-softening as suggested by Scott et al (1988) cannot be ruled out). In some areas (Plate 2.6a) there are signs of a scalloped edge, perhaps where the shrimp's chelae have nipped out small pieces of coral.
2. The bulk of the coral fragments in the lining are probably derived from the erosional activity of *Upogebia*. Some pieces have evidently been removed from very close by, as they can be matched with the adjacent eroded coral skeleton. The highly variable shapes and sizes of these coral grains either reflect a particular method of erosion by the shrimp or simply the normal appearance of broken down corallite structure. It is also uncertain what percentage of the coral fragments in the lining are due to shrimp erosion and what percent is composed of coral grains from external sedimentation. It is likely that most sand-sized grains are a product of the shrimp's activities as these grains would generally be too coarse to be carried in suspension in sea water and be deposited on the reef top. If they had been carried across the reef they would also be expected to be more rounded than those seen in the lining

Origin and formation of the mud lining

The shrimp uses carbonate sediment derived from its own erosional activity combined with reefal sediment (of skeletal and terrigenous origins) from outside the borehole to line its burrow. External sediment may be actively sucked into the borehole or passively settle out through the entrance. Evidence for the dual origins of the lining comes mainly from X-ray diffraction analysis.

X-ray diffraction of the fine fraction of the mud lining showed the presence of abundant kaolinite and quartz and some muscovite. These three minerals are part of the terrigenous fraction of the reef sediments, all being products of granite weathering. The presence of these minerals in *Upogebia* borehole linings indicates that reef sediment is being incorporated into the boring, either from sediment cleared from the narrow entrance or from grains filtered out of the water during feeding.

X-ray diffraction of bulk samples of the lining was compared with similar samples from the top 0-5cm section of a sediment core taken just off Tin Smelter Reef and both samples contained aragonite and high-Mg calcite (as well as quartz and kaolinite). The *Upogebia* lining contained more calcite than the core sample. As crustaceans must moult periodically in order to grow, some of the shed exoskeleton (which partly comprises high-Mg calcite) may be incorporated into the lining, thus making it more calcite-rich.

The smooth lining creates a borehole that is water tight and circular in cross section. This will enable the shrimp to generate an efficient respiratory and feeding current. Although present in *Goniastrea retiformis* in the outer reef, the boreholes are most common in the mid-reef area, in live and dead colonies of all coral species. The water meniscus in these holes can be seen to pulse regularly for periods of a few minutes. This is probably caused by a rhythmic pumping action by the shrimp below as it pumps water through the burrow. A little jet of water also frequently spurts from the entrance; this probably removes settling sediment from the entrance, changes the water in the hole for fresh oxygenated water, and possibly acts as an anti-predator device. Mud placed in the hole was blown clear seconds later and a small crab was also seen to be forcibly propelled from the entrance in the same manner!

2.3.3.4 Rate of bioerosion

An estimate was obtained of the amount of reef carbonate removed as a result of *Upogebia* boring. The volume of an average sized borehole was calculated by dividing it into 4 cylinders; one for the single shaft at the base and one for each of the three branches which reach the coral surface. An average diameter of 10mm was taken for all four cylinders and lengths of

5cm and 2.5cm were used for the three arms and bottom shaft respectively. These figures were estimated from measurements taken of samples from the mid reef and outer reef. Using the formula for the volume of a cylinder ($V = \pi r^2 l$, where r is the radius and l is the length), a whole borehole volume was calculated as 13.75cm^3.

Densities of upogebiid holes were measured on the mid-reef pavement (see section 1.5.2.2). In the area sampled there was a mean of 75.3 holes per m^2 (plan surface area). As three holes represents one boring, this is 25 borings/m^2. If each borehole has an average volume of 13.75cm^3 this is equivalent to 344cm^3 carbonate removed per m^2 of mid-reef pavement.

To estimate a time scale for this erosion, the growth rate of the dominant mid-reef coral (*Porites lutea*) was used. If *P. lutea* grows at 1.04cm/year (Scoffin 1997) an average size borehole of 7.5cm length is a maximum of 7.2 years old.

344cm^3/m^2/7.2 years is equivalent to 47.8cm^3/m^2/year or 52.1g/m^2(plan area)/year (density of *Porites* is 1.09g/cm^3; Scoffin 1997).

2.3.4 Alpheids

2.3.4.1 Borehole morphology

The surface morphology of these boreholes is a deep, horizontally-branching crack in the coral surface (especially in *Goniastrea retiformis* and *Coeloseris mayeri* and to a lesser extent in *G. aspera* and *Playgyra sinensis*; Plate 2.9). These cracks reach 5-10cm into the coral, are approximately 5mm in width and are lined at the top with a fringe of tufty green and red algae. Each branch extends up to about 5cm across the coral surface. At the base of the cracks, especially in holes from the taller corals (e.g. *G. retiformis*), is an uneven-walled tunnel or lobed hole in which the shrimp can rest safely (Plate 2.8b). However, not all cracks have these excavated features at their bases; where cracks lead into the shallow reef pavement they often simply join up to the network of crevices and holes within the reef. In these cases the shrimps must shelter in natural recesses in the reef structure. Some mud is sometimes present on the hole walls, but not in a coherent lining like in upogbiid boreholes (section 2.3.3).

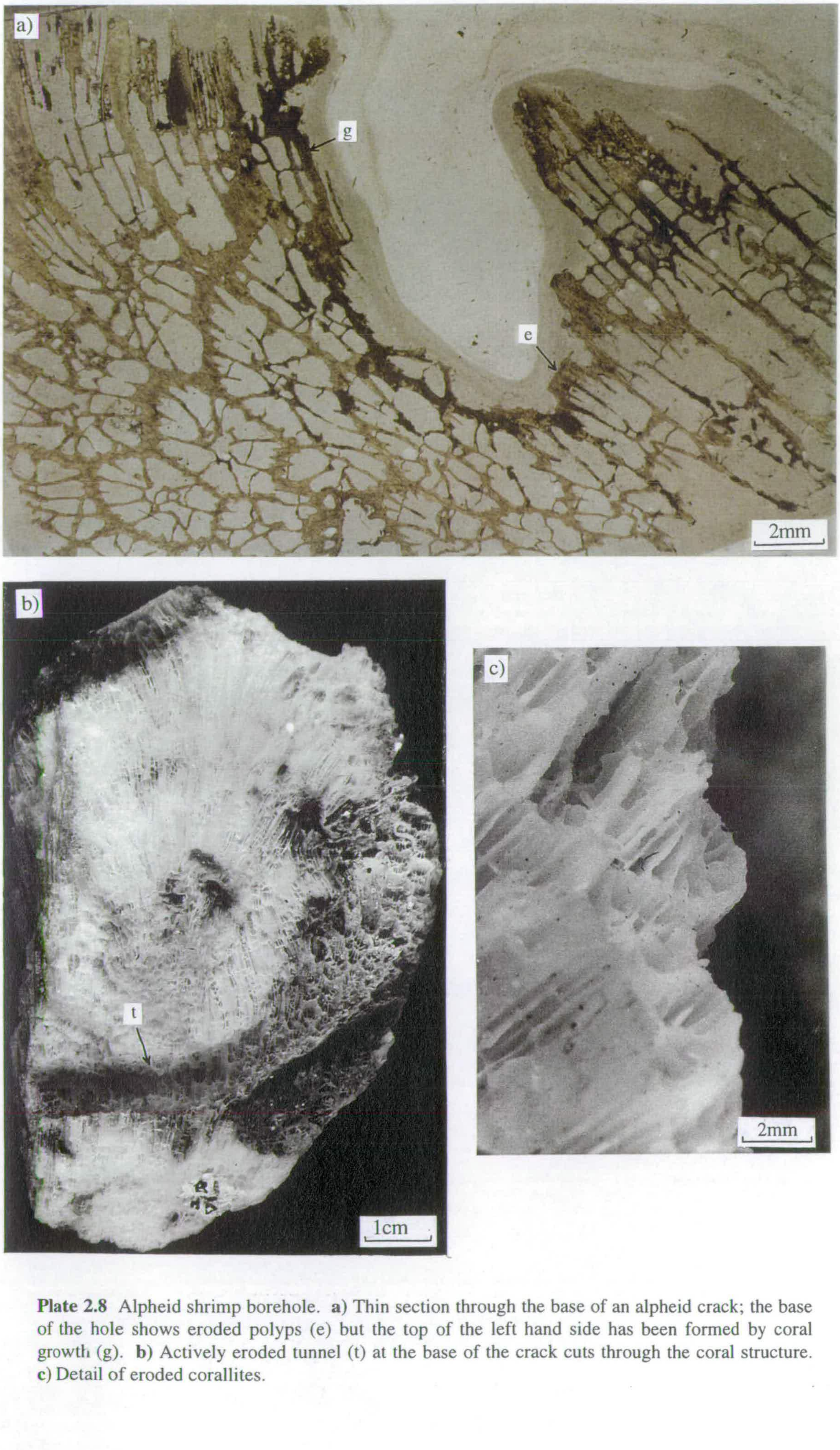


Plate 2.8 Alpheid shrimp borehole. **a)** Thin section through the base of an alpheid crack; the base of the hole shows eroded polyps (e) but the top of the left hand side has been formed by coral growth (g). **b)** Actively eroded tunnel (t) at the base of the crack cuts through the coral structure. **c)** Detail of eroded corallites.

2.3.4.2 Borehole formation

Passive erosion and coral growth patterns

The walls of this crack have a characteristic appearance (Plate 2.9e). Close inspection of the corallites that border the crack shows that they are all whole corallites whose polyps have died, rather than an actively eroded surface. This is shown by the fact that the corallite walls project up around the inner structures (septae and corallum) as they do in life. The coral's constant attempts to close over the crack results in a distorted growth pattern with corallites curving towards the cracks. As a result, all areas of the crack appear the same with respect to the aspect of the corallite visible at the surface. Successive failed attempts by the coral to grow into and over the crack sometimes results in a series of small ridges protruding a few millimetres into the crack. The death of the coral polyps bordering the crack is probably due to the lack of light due to the surrounding coral growing higher. The shrimp must inhibit coral growth by some means to stop the crack being grown over. The dead coral surface is encrusted with a mat of epifauna and flora, such as calcareous and non-calcareous algae, sponges, foraminifera, bryozoans and calcareous worm tubes, and is commonly covered with a thin layer of fine mud which has settled out from the water above. It is possible that the shrimp feeds on this growth, even sustainably harvesting it.

Active erosion

At the base of the crack, actively eroded areas can be seen where tunnel-like or lobed structures have been excavated through the coral (Plate 2.8a and b). The active removal of coral is shown by the uneven surfaces of the corallites bordering these tunnels that have been eroded from the side, from above and from below, revealing all internal corallite structures (Plate 2.8c). The surrounding corallite growth pattern shows no disruption as it was laid down before the hole was made; in fact, the continuation of individual corallites on the other side of the excavated hole can often be traced (Plate 2.8b).

In transverse and longitudinal thin sections, active erosion can be seen on some borehole edges as cut away corallite structure. For example, in Plate 2.8a corallite walls, septae or dissepiments border the hole lumen. Due to the absence of any kind of lining, the dissected corallites are therefore open to the lumen. In places, flat-edged surfaces suggest an active removal of coral rather than a coral growth pattern or haphazard breakage (e.g. base and right side of hole in Plate 2.8a)). At the top of the holes seen in thin section, the successful growth of the coral in a lobe over one side of the crack can be seen; corallite growth in that region is parallel to the crack surface (left side of hole in Plate 2.8a).

Summary: proposed mechanism for the formation of alpheid holes (see Fig. 2.3, Plate 2.9)

Younger colonies of *G. retiformis*, *Playgyra* sp. and *Coeloseris mayeri* are more or less hemispherical, but the gross morphology of older colonies which are contain alpheid cracks are severely affected, causing it to have a greater relief.

On the surface of some corals and leading off from small shrimp cracks, strips of mud can occasionally be seen. I hypothesise that the young shrimp actively excavates a small hole, large enough for it to shelter in, and from that hole then lays out thin strip of mud across the live coral surface. This eventually kills off the coral directly underneath by suffocation and the blocking out of light. The coral grows up around this dead area, thus growing to form an ever-deepening groove and constantly trying (and failing) to grow over the crack. The shrimp prevents this overgrowth either by constant movement or active removal or inhibition of the coral tissue. Meanwhile the shrimp actively excavates (mechanically) its initial burrow which is now at the bottom of the crack, forming the tunnel-like or lobed structure described above. Both active and passive boring processes are therefore used by this crustacean.

The only similar structure to these cracks to have been described is by Bruce (1979). He found 'deeply channelled corals' at Eniwetok Atoll which he attributed to the pontoniine shrimp *Ctenopontonia cyphastreophila,* despite finding only one pair of this species and commonly finding *Alpheus obesomanus* in these cracks. The evidence he presents, combined with the findings in this thesis, suggests to me that the cracks are more likely to have been produced by the *Alpheus*, not the *Ctenopontonia*. Cortes (1985) also studied bioeroding alpheids (*Alpheus simus*) in the Caribbean, but these shrimps excavated cylindrical chambers roofed over by a sieve-like plate, a very different structure to that described here.

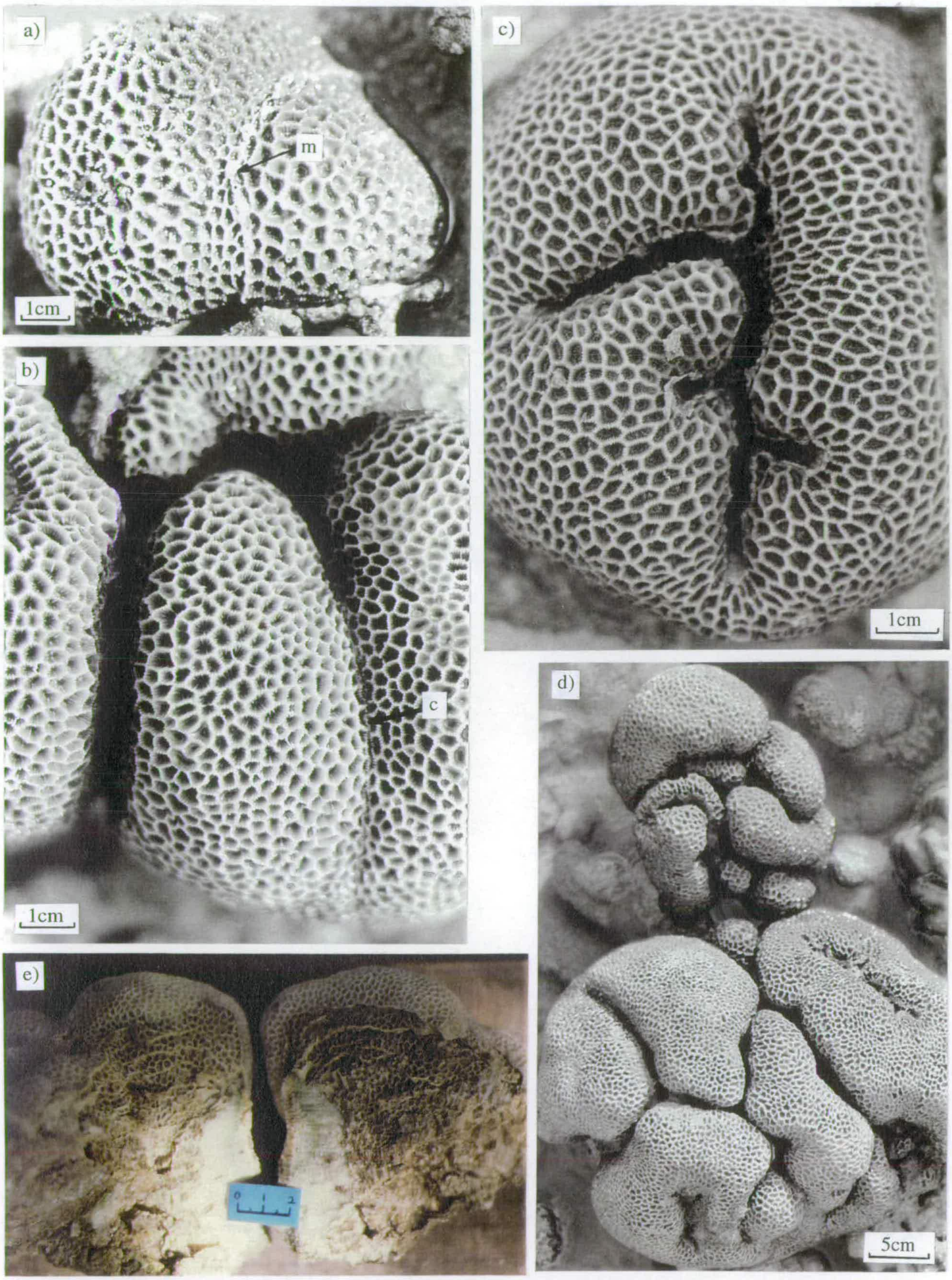


Plate 2.9 The proposed formation of alpheid shrimp cracks in *Platygyra daedalea*. **a)** A strip of mud is laid on the coral surface preventing coral growth (m). **b)** A 'young' crack (c). **c)** The crack deepens due to the death of the coral bordering the crack. **d)** The coral becomes dissected with deep grooves. **e)** The inside of an alpheid crack as revealed on two halves of a split coral. An actively eroded chamber is visible at the base (arrow).

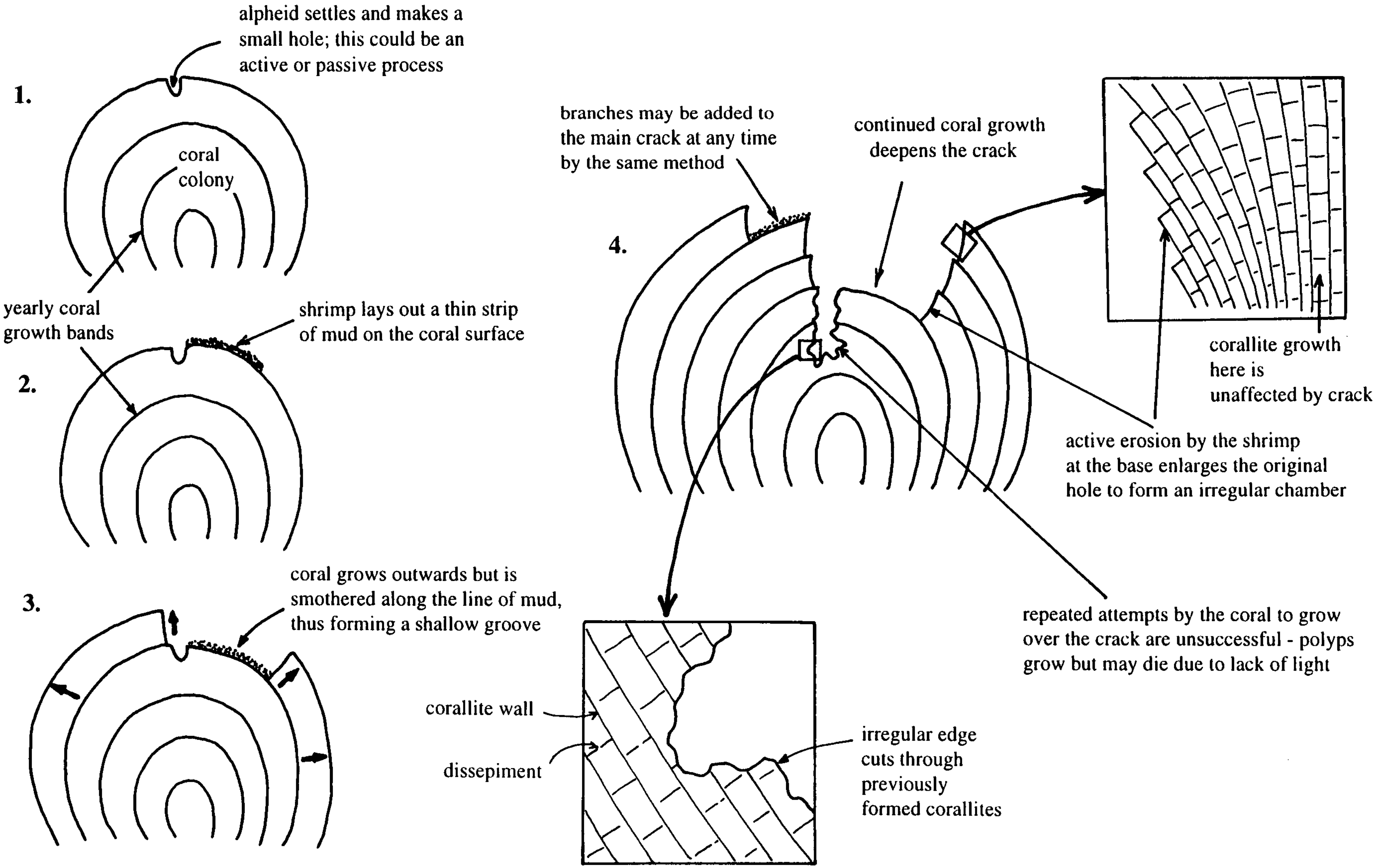


Figure 2.3 Proposed mechanism for the formation of alpheid cracks by a combination of passive and active means.

2.3.5 Other coral-dwellers seen in Phuket

2.3.5.1 Borers

Apart from the crustacean borers described in the preceding sections, certain other macroboring groups are also well represented on Tin Smelter Reef. Of these, the bivalves are the most noticeable, with large areas of dead coral being completely infested with various *Lithophaga* species. During the course of collecting data on the crustacean borers, some measurements were also taken of *Lithophaga* hole sizes and densities. These are presented in Appendix D. To summarise, densities of the characteristic dumbbell-shaped borehole entrances were estimated at nearly $800/m^2$ on dead *G. retiformis* on the outer reef and a bioerosion rate of $1365cm^3/m^2$/year (actual area) or $1570g/m^2$ (actual)/year or $2370g/m^2$(plan)/year was calculated. *Lithophaga* species that bored live coral were also seen.

A few boring *Gastrochaena* and abundant nestling and encrusting species, such as *Malleus* (the hammer oyster) and other bivalves (e.g. *Pinna*, *Isognomon*, *Saccostrea*), were seen on the Tin Smelter Reef flat. Nielsen (1976) provides a useful illustrated guide to the bivalve species of the reef flats of Laem Panwa, including representatives of these borers.

Other common macroborers were polychaete and sipunculid worms which produce long thin holes through the coral. From their relationship to coral growth patterns it would seem that different types of worm use different mechanisms to produce their holes (i.e. both active and passive means). Soft, brown, mud tubes (c. 5mm diameter) were common leading into holes in the coral and these were seen to contain fan worms. These animals and their erosional effects were not investigated further, but for information on worm borings the reader is directed to the review by Hutchings (1986) and references therein.

2.3.5.2 Grazers

Grazing by echinoids (McLean 1967, Hunter 1977, Ogden 1977, Glynn et al 1979, Bak et al 1984) parrotfish (Bardach 1961, Gygi 1975, Ogden 1977, Frydl and Stearn 1978) and to a lesser extent gastropods (Trudgill 1983) has been shown to be of major erosional importance on many reefs. In Phuket, neither parrotfish nor echinoids are abundant on the reef and are therefore unlikely to play a major role in the carbonate budget. However, at low tide there are enormous numbers of grazing crabs on the reef flat of Tin Smelter Reef; densities of $30/m^2$ were estimated.

Examination of areas where the crabs had been grazing did not show any obvious scrape marks, such as those seen where parrotfish have grazed, so it is thought that no carbonate is removed during grazing.

2.4 DISCUSSION

2.4.1 Distribution of macroborers

Each type of macroborer seen in this study shows a clear preference for a particular type of substrate, be it a coral species, live or dead coral, a particular area of the reef or orientation of coral surface. Passive borers such as the hapalocarcinids and barnacles require a live coral substrate in order to construct their holes and live passive borers are thus found in greater abundance on the outer reef where live coral cover is highest (see section 1.3.1 and Appendices A and D). Borers which can only use dead substrate (e.g. some *Lithophaga* species) are also more abundant in the outer reef, despite plentiful dead coral in inner areas. This is probably due to the high sedimentation rates in the inner reef which would easily clog the boreholes. It is probably for this reason that some borers (e.g. hapalocarcinids and barnacles) are more abundant on the vertical sides of corals rather than horizontal surfaces where sediment settles out. Upogebiids flourish in the mid-reef area, despite its fairly high sediment loading, perhaps due to their ability to flush sediment out of their holes by squirting water at high pressure through the borehole entrance. The shrimps may actually require a certain amount of mud in order to line their burrows. The inner reef contains very few borers, probably due to the large amounts of fine sediment and perhaps to the long periods of exposure at low tide during which this area will become a highly stressful environment with high temperatures and no water exchange.

The species of coral is also important to live coral borers; species with smaller polyps are generally less aggressive (Scott 1987) and are therefore an easier substrate for a larva to settle on and begin making a hole.

In some cases there may be negative feedback involved; boreholes that severely weaken coral structure (e.g. alpheid cracks and branching upogebiid holes) are more likely to survive for a substantial amount of time away from the reef edge in the more stable low relief coral pavement

(Hylleberg 1994). A balance between higher sedimentation rates but greater stability on lower relief corals and lower sedimentation but greater instability on higher relief corals must be achieved.

It was noted that larger (older) corals have disproportionately more boreholes than smaller (younger) ones of the same species and within a zone. In the case of live coral borers, older colonies have more vertical surfaces and are raised further off the reef than younger colonies, both of which factors provide surfaces with lesser amounts of sediment and a more attractive colonisation surface. Older colonies also have larger dead areas in their centres and quickly become infested with dead-coral borers such as *Lithophaga*. Younger corals may also simply contain younger boreholes which cannot be seen due to their small size.

West-facing sides of corals often have high levels of *Lithophaga* boring due to more dead substrate on these surfaces. Repeated solar lesions on the west-facing surfaces of Tin Smelter Reef corals leads to asymmetric growth and mortality (Brown et al 1994, Scoffin et al 1997), with the West faces of many corals being dead. A common shape is ring-like, with a dead centre surrounded by live lobes of coral, often shorter on the west side than the east (Plate 2.10). In tall, outer-reef *G. retiformis* colonies this outer ring is pillar-like (Fig. 1.3). The tops of these pillars (vertical as well as horizontal surfaces) are often dead, presumably due to excessive periods of exposure, and have an algal covering. On a single coral colony of this sort there is therefore a common pattern of borer colonisation. The largely live eastern side and a thin band of live coral around the entire colony are home to barnacles, hapalocarcinid crabs, various worm holes and occasional *Lithophaga*, with fan worms restricted mainly to the base of the live part of the colony where they remain underwater at all states of the tide. Alpheid cracks are often present between the ‘pillars’ and probably cause this growth form (see section 2.4.2, Plate 2.10).

Similar coral shapes and borer distributions can be seen in other colonies in the mid reef. In this area, a few *G. retiformis* and *Platygyra daedalea* colonies protrude above the coral pavement (mainly *Porites lutea*). *G. retiformis* shows a far less columnar, lower relief morphology with larger, dead, mud-filled centres and completely dead west faces. *Lithophaga* is still the dominant borer in the dead centres, though it is not so abundant. Encrusting and nestling bivalves (e.g. *Malleus*) are very common, as is the brown alga *Padina*.

To give an indication of the types, numbers and distribution of the boring community on a single coral, all the borers on a typical outer-reef and mid-reef *G. retiformis* colony of similar size are described below in Table 2.2.

Table 2.2 Comparison of the distribution and abundance of macroborers in *Goniastrea retiformis* in the outer and mid areas of Tin Smelter Reef.

	Outer reef		Mid reef	
Size of coral (cm):				
Height	34		18	
	E-W direction	**N-S direction**	**E-W direction**	**N-S direction**
Plan diameter	46	48	60	65
Actual diameter	94 (of which 40.4% is live)	92 (of which 51.1% is live)	80 (of which 41.3% is live)	83 (of which 33.7% is live)
Relief (ratio actual:plan)	2.04	1.92	1.33	1.28
Borers	**Dead coral**	**Live coral**	**Dead coral**	**Live coral**
Lithophaga	72	4	6	0
hapalocarcinids	0	9	0	0
barnacles	0	15	0	0
fan worm tubes (hard)	0	5	10	0
fan worm tubes (soft)	0	17	0	0
tiny holes or tubes (mostly worms?)	0	88*	100's	100's**
other unidentified holes	0	0	7	0

*these holes tend to cluster in groups of 10-15 and open at a raised point between polyps. They are found near the water level at low tide.

**all holes at or below water level at low tide

2.4.2 Effects of bioerosion on reef morphology and carbonate budget

2.4.2.1 Individual colony morphology

On the reef flat of Tin Smelter Reef five factors modify coral colony morphology: coral growth, sea level, solar bleaching, bioerosion and sedimentation. In turn, coral morphology affects these latter three factors which all influence each other through their effects on coral morphology as illustrated in Fig. 2.4 (arrows indicate a direct effect).

With equal growth on all sides, a coral colony would achieve a perfectly hemispherical growth form. The three factors mentioned above prevent this growth; die-back and regrowth are controlled by a combination of sedimentation, solar damage and bioerosion events which can be traced in the morphology of a coral (Scoffin et al 1997).

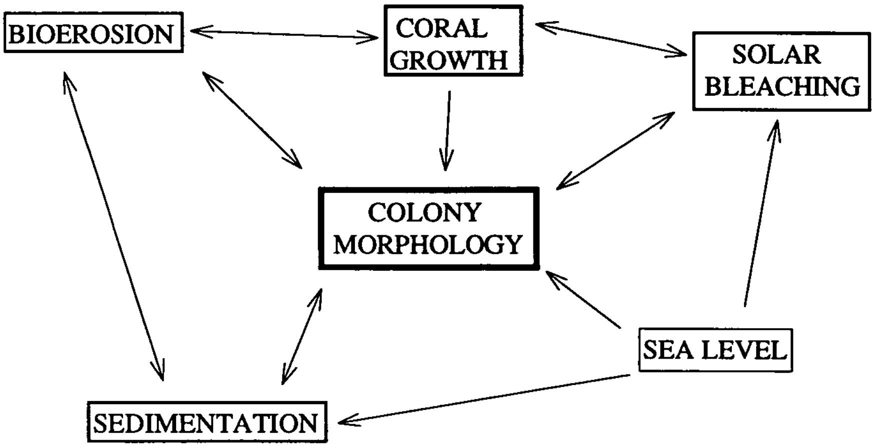


Figure 2.4 Influences on coral colony morphology on Tin Smelter Reef.

Direct alteration of growth form by bioerosion

Coral morphology and growth patterns are strongly affected by animal activity, as described in detail for the four crustaceans in section 2.3. On the small scale, a few corallites show distorted growth in the immediate vicinity of a barnacle hole while on a larger scale, whole colony morphology is shaped by an alpheid shrimp forming a branching crack. As well as the requirement of either a live or a dead coral substrate, the orientation of the surface is important to borers in muddy environments such as Tin Smelter Reef, as described in section 2.4.1. The increase in relief caused by alpheids provides a more heterogeneous substrate for colonisation by a wide range of borers and encrusters and thus helps maintain biodiversity on the reef.

Physical breakage due to pre-weakening by borers

Indirect effects of bioerosion are equally as important as direct ones; infested areas are weakened and are more likely to sustain physical damage, increasing the dead area and/or exposing fresh substrates for encruster and borer colonisation. A succession of borers from initial microbioeroders through sponges to macroborers will ensue (e.g. Davies and Hutchings 1983, Kiene 1988, Peyrot-Clausade et al 1992) and this cycle of erosion will continue until the coral is completely broken down. Alpheid cracks and *Upogebia* holes, especially in the tall, outer-reef corals, will cause planes of weakness; it is relatively simple to break off one of the columnar growths of a *G. retiformis* colony as the colony naturally splits along the borehole. Corals in the

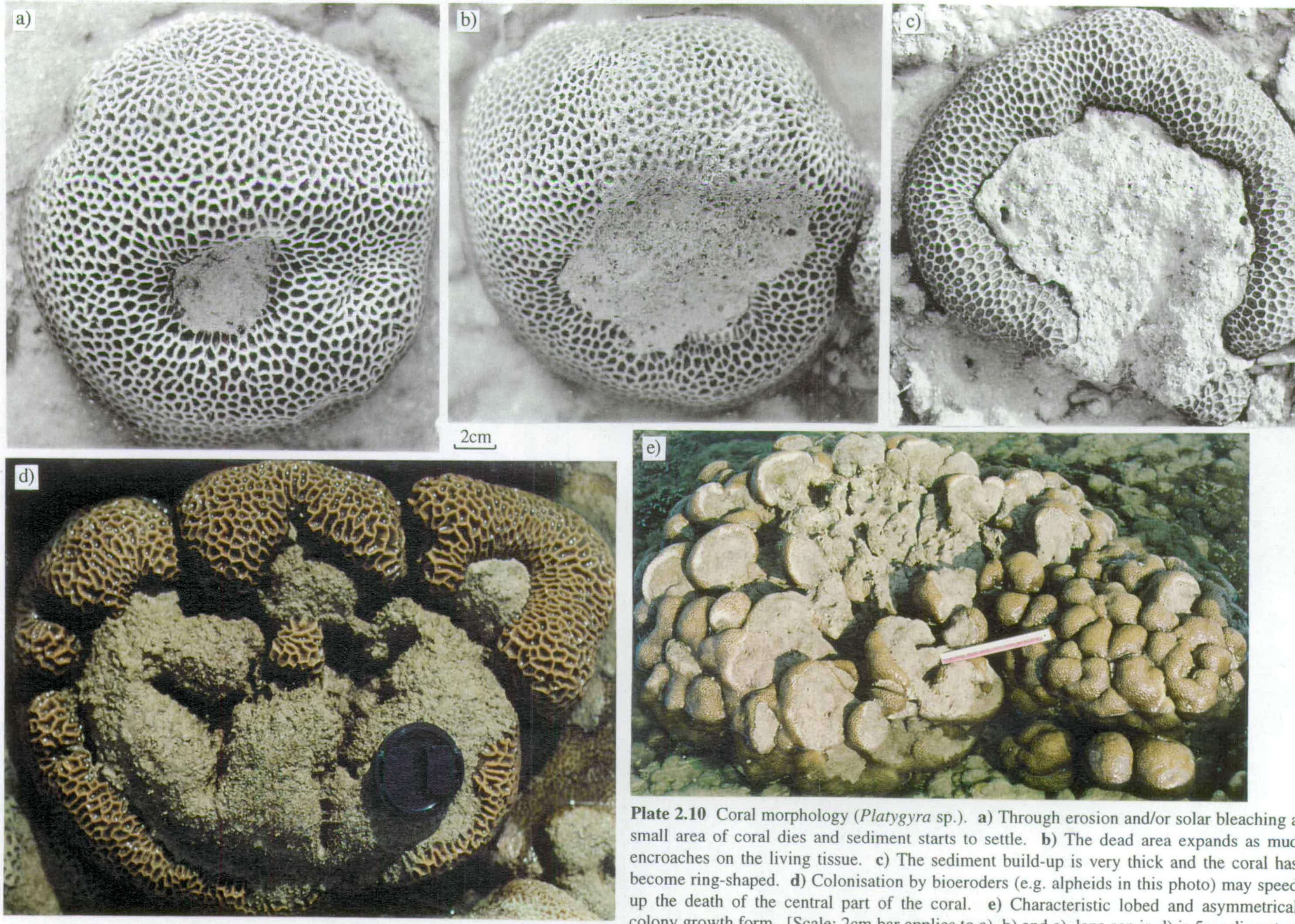


Plate 2.10 Coral morphology (*Platygyra* sp.). **a)** Through erosion and/or solar bleaching a small area of coral dies and sediment starts to settle. **b)** The dead area expands as mud encroaches on the living tissue. **c)** The sediment build-up is very thick and the coral has become ring-shaped. **d)** Colonisation by bioeroders (e.g. alpheids in this photo) may speed up the death of the central part of the coral. **e)** Characteristic lobed and asymmetrical colony growth form. [Scale: 2cm bar applies to a), b) and c), lens cap in d) is 5cm diameter, ruler in e) is 22cm long].

mid reef are less prone to breakage and even if broken are unlikely to move far as they are held fast within the reef pavement. However, continual slight movement and erosion (biological and physical) could widen these gaps enough for the surrounding *Porites* to grow over the surface. In the mid and inner reef the majority of live coral is found on vertical surfaces between colonies. Shrimp erosion and subsequent coral fracturing may help the continued growth of *Porites* colonies. Colonies at the edge of mid-reef pools or those that have been excavated underneath by burrowers and borers break easily; on several occasions pressure from walking on a coral on the reef flat caused the cleavage of the *Porites* along a *Upogebia* borehole, and where this occurred at a pool edge, the piece of coral fell into the pool. No cleaved surfaces like this were seen naturally; it must take higher than average energy conditions (i.e. storms) to break these corals, and the fractured surfaces are presumably quickly colonised with algae, encrusters and other borers and therefore become unrecognisable.

Bioerosion and sedimentation

The reefs around SE Phuket are perhaps more prone to the effects of sedimentation than many other reefs that have been studied. The high levels of suspended fine terrigenous sediment will quickly smother a coral if allowed to settle. Live corals can cope with the sedimentation rate, at least in the mid- to outer-area of the reef, but any area in which sediment can settle is likely to enlarge and begin to smother neighbouring live coral tissue. Sites of bioerosion provide just such centres for sediment accumulation. Although occupied boreholes are usually kept clear of mud by their inhabitants they quickly fill up when the animal dies. Sediment can then begin to spread and kill surrounding coral. This is especially the case in large features such as alpheid cracks and in areas of high density colonisation such as *Lithophaga* clusters and areas of high sediment loading (mid to inner reef)(Plate 2.10).

Bioerosion and bleaching

In Phuket, solar bleaching events are a further factor to consider in this cycle. Areas of coral killed by solar irradiation expand due to the settlement of sediment and/or borers. Not only do solar lesions provide an area for bioerosion, but some bioeroders may in turn increase the likelihood of a coral bleaching. Alpheid shrimps (and to a lesser extent upogebiids) increase the relief of the colonies they inhabit and therefore increase the areas of west-facing coral surfaces that are prone to bleaching.

In this way, the interaction of bleaching, bioerosion and sedimentation gradually destroy the corals. Without the influence of bioerosion, the destruction of corals by this cycle of events would be slowed. Coral colony morphology would also be very different in the absence of bioeroders, particularly in the tall, outer-reef corals and higher relief, mid-reef corals where alpheids and upogebiids cause a lobed growth form. The growth and destruction of individual coral colonies has implications for whole reef morphology; this is the focus of the next section of this discussion.

2.4.2.2 Whole reef morphology

The preceding discussion might seem to imply that corals are caught in a downward spiralling cycle of destruction but it is the reef-wide, *relative* rates of coral growth, erosion and sedimentation that will ultimately decide the fate of the reef. The continued growth of a reef relies on reef accretion (growth of corals and encrusting calcareous organisms and calcification) exceeding carbonate removal (physical erosion and active bioerosion); Fig. 2.5.

Bioerosion weakens the reef

Although passive bioerosion creates holes in the reef framework, no removal of carbonate is involved. The importance of passive bioerosion in the carbonate budget is thus due to its role in creating sites of weakness for subsequent physical erosion. This is especially the case for large boreholes such as those made by alpheid shrimps. Active erosion, for example by *Upogebia*, also has this result.

This feature of bioerosion has an important *positive* role in the development of Tin Smelter Reef. Breakage and toppling of corals from the reef front is essential for reef progradation on this reef, as some parts of the fallen corals continue growing and other corals colonise their fractured surfaces until the reef once again reaches sea level (Tudhope and Scoffin 1994). Bioerosion, especially by upogebiids and alpheids, create planes of weakness which enable large portions of colonies to break away, and infestation of dead coral in the centres of and from beneath living colonies also weakens the reef structure. Strengthening of the coral structure by lithification and cementation is not an important factor in this area, thus relatively increasing the effect of bioerosion.

Weakening of the substrate in this way is also important in the production of carbonate sediment. As well as the formation of coral boulders, smaller particles will also be produced due to subsequent biological and physical breakdown.

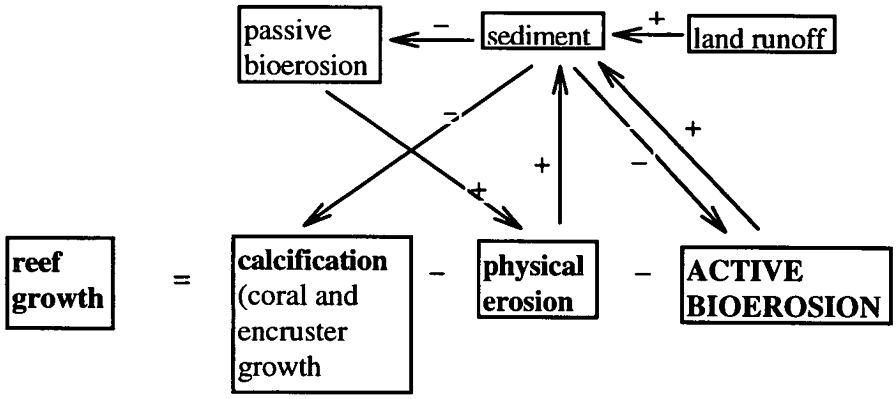


Figure 2.5 Summary of the processes involved in reef growth and development; '+' indicates a positive effect, '-' a negative effect. For coral growth rates see Scoffin (1997), for sedimentation rates see Tudhope and Scoffin (1994) and Scoffin et al (1997).

Bioerosion affects reef zonation

As discussed in section 2.4.2.1, bioerosion is at least partially responsible for the morphology of coral colonies and therefore must also be a factor in determining the general appearance of the inner-, mid- and outer-reef zones. Alpheid and upogebiid shrimps contribute to the high relief, columnar growth forms in corals such as *G. retiformis* on the outer reef flat. The higher diversity of coral species in the outer reef may be due partly to the abundance of dead and freshly broken surfaces available for colonisation as a result of breakage of borer-weakened corals, although low sedimentation rates, short exposure times and greater water movement will also play a part.

As the reef progrades seawards, corals that were in the outer reef will either break away and form the basis of the new reef front or will become part of the mid reef and eventually the inner reef. As a coral effectively moves away from the reef edge, it experiences shallower water and becomes exposed even at high tide, resulting in the death of its top surface. Rapid bioerosion of these dead surfaces will soon reduce the relief of the reef and level out the reef surface as it undergoes the transition from outer to mid to inner reef. Coral species unable to cope with the increased sediment levels and exposure times will not survive long and will also be bioeroded and overgrown or replaced with better adapted species such as *Porites lutea* which dominates the mid-reef pavement. In a similar way, most mid-reef corals 'moving' into the inner reef will die, mainly due to excessive sediment smothering. This environment is also hostile to boring infauna, of which there are relatively few in the inner reef.

Active bioerosion removes reef substrate and produces carbonate sediment

Implications for the carbonate budget and reef growth

Upogebia removes 61g of reef carbonate/m^2/year (see Table 2.3 and section 2.3.3.4) through bioerosion, which is equivalent to 2% of the overall $CaCO_3$ production for Tin Smelter Reef. (Total $CaCO_3$ production is 3000g/m^2(plan area)/year; Scoffin 1997). However, the relative importance of this bioerosion will be greater in the mid reef (where *Upogebia* is commonest) because $CaCO_3$ production will be less in that area; most coral growth is on the outer reef.

Table 2.3 Summary of calculated rates of active erosion for *Upogebia* in the mid reef.

Units	actual surface area	plan surface area
cm^3/m^2/year	47.8	55.9
g/m^2/year	52.1	61.0

(see section 2.3.3.4 and Appendix D for details and constraints of methods)

Implications for sediment production

Of the four crustaceans mentioned in section 2.3, two are known to actively remove calcium carbonate (*Upogebia* and alpheids) and one (hapalocarcinid crabs) does to some degree. The products of *Upogebia*'s activities are obvious in the form of coral fragments ranging in size from <0.05-2mm embedded in the mud lining of the borehole (Plate 2.7, sections 2.3.3.2 and 2.3.3.3). The fragments show a range of uneven shapes, though long, thin grains in the larger size fraction may reflect coral microstructure. Grains eroded by *Upogebia* could not be distinguished from other coral grains in the reef sediment by the methods used in this study.

Upogebia removes 55.9cm^3 $CaCO_3$/m^2(plan area)/year. The mud lining occupies c.30% of the borehole lumen (given an average internal diameter of 10mm and a 1mm thick mud layer).

The lining comprises approximately 2/3 coral fragments and 1/3 terrigenous mud (from thin sections). Therefore, c.20% of the coral removed during borehole excavation (i.e. 11.2cm^3/m^2/year) remains in the borehole and the remaining 80% (44.7cm^3/m^2/year) is flushed out. If it is assumed that 1/3 of this 44.7cm^3 settles elsewhere on the reef, 1/3 settles in the fore-reef slope and 1/3 is exported from the reef, a further 14.9cm^3/m^2/year is added to the reef flat by the shrimps, giving a total amount settling of 26.1cm^3/m^2/year. This is equivalent to a 0.03mm thick layer, or 3% of the total increase in reef flat height each year (the reef flat increases in height by c. 1mm every year; Scoffin 1997). This sediment is likely to comprise the coarser components of the bioeroded sediment; finer sediment will remain in the water column for longer and is more likely to settle on the fore-reef slope or even be exported in suspension.

14.9cm^3/m^2/year is added to the fore-reef slope. This is a total of 730100cm^3 from the reef as a whole, or 0.8% of the total sediment added to the fore-reef slope each year (88x10^6 cm^3 is added each year; Scoffin 1997).

Alpheids do not retain any of their erosional products in the borehole, so it is uncertain what size and shape coral grains are produced in the excavation of the lower portion of their boreholes. By the size of the shrimp and the structure it produces and the rough hewn appearance of the hole walls, it is likely that grains up to several millimetres big are produced. Chemical erosion of substrate by hapalocarcinids and *Lithophaga* bivalves is more likely to produce only fine grains in the silt to clay size range and dissolved carbonate. Boreholes produced by passive means, such as the upper crack-like part of the alpheid hole and the tubular barnacle cavities, are not a source of carbonate sediment of any size.

The different fates of bioeroded sediments have implications for the preservation of those sediments; this is discussed section 2.4.3.2.

2.4.3 Geological implications

2.4.3.1 Trace fossils and palaeoreconstructions

Boreholes may be preserved as trace fossils or lithoturbate textures (see sections 2.1.3.2 and 2.1.3.4) in the fossil record. Their preservation depends on whether they are found in live or dead coral and the rapidity of preservation after their formation. Small passive borers (e.g. hapalocarcinids and barnacles) are likely to get overgrown or rebored if empty. Samples from Tin Smelter Reef frequently reveal concealed barnacle borings whose wall plates had evidently been rapidly overgrown by the surrounding coral host (Plate 2.1a). If the coral is then preserved soon after death, these barnacles will be well preserved and show all the features visible in a modern example. If the coral dies and is then rebored by other bioeroders, these enclosed borings will be cross cut as shown in other specimens collected from Tin Smelter Reef where *Lithophaga* cuts through previously bored barnacle holes. Alpheid cracks and *Upogebia* holes are less likely to be preserved whole if they are sites of coral breakage and will not therefore be protected by the surrounding coral. If they are preserved enclosed in the coral they will become sites of sediment accumulation and due to their large size will be able to hold large amounts of up to gravel-size sediment. Settling of sediment into these holes could result in fining upwards sequences due to coarse particles sinking to the bottom first, though reworking of these sediments may occur as lithification is slow in this area. Mud-filled *Lithophaga* holes from Tin Smelter Reef were occasionally seen to contain small spiral burrows within the mud infill.

If the death and preservation of the reef and its borers are slow, there will be time for substantial modification to abandoned boreholes before they are completely infilled with sediment. Not only will the boreholes be extensively microbioeroded (a process that begins while the hole is still occupied), resulting in a lack of definition to the walls, but empty holes often become home to other (non-boring) species such as nestling bivalves, fish and crabs.

Thus, the nature of preservation of boring traces relies on a fine balance of timing. If preservation is rapid (e.g. by rapid sedimentation or drop in relative sea level), whole borings will be well preserved but if slow, different tiers of borings will destroy the previous ones resulting in a lithoturbate texture.

Unlike burrow traces, compression will not occur in a hard substrate, so boreholes will be preserved whole unless cross-cut by more borings. Like burrow traces, the deepest tiers of macrobioeroders will be the best preserved and will cut through the upper tiers of microbioeroders, although microeroders are quick to colonise surfaces provided by macroborings, even while these large holes are still in use (see section 2.3 and Plates 2.2c and 2.4c). Detailed examination of coral growth patterns around boreholes (as described in section 2.3 of this study) and cross-cutting relationships of boreholes can be used to reconstruct the sequence of events (coral growth and death, bioerosion, sedimentation) that resulted in a particular texture within a fossil reef.

The most likely cause of death and preservation of Tin Smelter Reef and its bioeroding community is a gradual silting up. In this case, the outer reef is unlikely to be preserved in its present form; with a slow increase in sediment load this zone will get progressively narrower and become more like the mid or inner reef is today. The coral species diversity will decrease and more sediment tolerant species will survive until they too are overcome. Associated with this change in species composition and increase in dead coral area, the bioeroder community will also change. Live coral borers, such as barnacles, hapalocarcinids and alpheids will die out and be replaced with dead coral borers (*Upogebia* and *Lithophaga*) whose boreholes cross-cut those of the preceding live borers. Eventually these borers will also be killed by the sediment load. This succession of borer species is likely to produce lithoturbate textures rather than whole borings. All reef areas will eventually become so smothered in sediment that the reef will become a calcareous shelf covered with a layer of sediment which, if sediment levels are high enough, will start to dry out and become supratidal sediment, or remain as shallow subtidal sediment. The amount of erosion, both biological and physical, that occurred before burial will determine the depth of the carbonate basement under the sediment layer. In Tang Khen Bay, up to 1-2m of sediment overlie a solid reef pavement dated as being between 3000-5000 years old (Tudhope and Scoffin 1994). These authors also thought that these ancient reefs were killed by gradual sediment smothering. On the reef flat of Tin Smelter Reef large dead corals have been interpreted as former reef-edge corals (Tudhope and Scoffin 1994) and it is likely that the majority of the reef flat is made up of former outer-reef corals that have been grown over by a veneer of later mid- and inner-reef corals; some of these corals may be partially preserved within the reef.

Tin Smelter Reef exists only in the top 4m of sea water and its reef flat is exposed to some degree at most low tides. As a result, any slight drop in sea level would have a catastrophic effect, killing the entire reef flat and leaving only a thin live edge.

Boring traces have been used to indicate various depth zones in the fossil record (e.g. Bromley 1994), but as Tin Smelter Reef only extends to 4m water depth this will not be a particularly useful feature in this site. Distinct zones are visible on this reef (inner, mid and outer zones) and might be recognisable at least in part from their boring traces. Some of these traces would be more useful in small-scale interpretations of colonies rather than larger reef-wide interpretations. For instance, hapalocarcinid and barnacle borings are good indicators of live vertical coral surfaces and could be used to deduce the original orientation of colonies. Geopetal structures within boreholes will also indicate the orientation of the holes at the time of sediment infill, if cemented, and the combination of these two lines of evidence with that of coral growth patterns could aid in the interpretation of the history of a mobile coral boulder, such as the large slabs that fall off the reef front on Tin Smelter Reef. Other borers are less useful in this respect; for example, *Lithophaga* can be found on all surfaces of a coral colony and in live or dead coral. Although in a present reef it can be seen that different species of *Lithophaga* species occupy these different surfaces (e.g. on Tin Smelter Reef *Lithophaga teres* is restricted to overhanging surfaces), the boreholes of these species are indistinguishable from each other.

As passive borers require live coral, they are most common in the reef top corals of the outer reef where live coral cover is highest. These reef-top corals (and their passive boreholes) have a low preservation potential as they die and are obliterated by subsequent generations of active bioeroders as they pass into the mid-reef zone (see section 5.1.4).

Ichnospecies names for trace borings are fairly all-encompassing, so that '*Trypanites*' describes any cylindrical macro boreholes with a single entrance (Bromley 1994). The broad nature of this species both in morphology and time scale (*Trypanites* was abundant throughout the Phanerozoic) means that it must include holes made in different ways by numerous different animals (e.g. hapalocarcinids and barnacles as well as sipunculids) and therefore is not a particularly useful palaeoindicator. Slightly more specific is the ichnospecies *Gastrochaenolites* which is the fossil equivalent of the flask-shaped bivalve holes made by *Lithophaga* and other bivalves. No trace fossil equivalents of alpheid or *Upogebia* holes have been described.

Tin Smelter Reef lacks carbonate-scraping grazers when compared to other bioerosion studies (e.g. Scoffin et al 1980). Although parrot fish, gastropods and echinoids are present, they are not abundant and there is no obvious sign of their grazing activities (e.g. parrot fish scrape marks). The only possible bioeroding grazers on the reef are the large number of crabs which graze on the reef flat at low tide. However, it is uncertain whether they actually remove the underlying coral substrate during feeding. Scraping noises can be heard as they feed, but close inspection of their feeding sites does not show any direct evidence of erosion.

2.4.3.2 Sediment preservation

From this study, it does not seem that any of the active bioeroders produce recognisable sediment grains as a result of their bioerosion activities on Tin Smelter Reef. Unlike the distinctive sponge chips much quoted in the literature, most bioeroders probably produce grains whose shape is determined mainly by the skeletal structure of the eroded substrate and are therefore indistinguishable from physically eroded grains.

Following on from the last point of section 2.4.2, I will consider the preservational implications of each of the four possible fates of reef-derived sediment.

1. *Incorporated into the mud lining of a Upogebia borehole.* Fragments of coral that are removed in the excavation of a *Upogebia* borehole may be plastered to the walls in a mud matrix almost immediately. If the borehole is preserved within the coral, these grains will experience no deterioration from physical processes and are likely to stay the same size and shape as when they were embedded. However, the constant flushing of the burrow with sea water and the high concentrations of organic matter in the mud walls must provide an ideal environment for microborers and other bacteria. From SEM photos and thin sections, microboring seems to be rife in the walls of these boreholes, and grains in the mud matrix do not escape this attack. Pristine preservation is therefore unlikely. As described in a section above, corals preferentially split along planes of weakness caused by *Upogebia* boreholes. In this case, the mud lining with its carbonate constituent will be exposed to the sea and will probably be washed off within days, unless the fractured coral falls into the fore-reef sediment.
2. *Washed into a cavity in the reef.* Various lengths of time can elapse between a fragment of coral being eroded and it settling into a cavity within the reef. During this time it will be subject to differing degrees of physical, chemical and biological degradation, so that the sediment that ultimately collects in a such a void will comprise a mixture of rounded, angular, fresh and degraded grains. Particles settling out into a sheltered cavity might show grain sorting (increasingly fine grains moving upwards) and geopetal surfaces. (Scoffin (1997) found that 80% of the internal sediment of Tin Smelter Reef was skeletal carbonate, finer terrigenous particles being winnowed or removed by continual flushing with seawater.
3. *Remaining in suspension or solution in sea water.* Dissolved bicarbonate is an important constituent in the sea water around reefs as it is required by many animals (e.g. corals,

molluscs, crustaceans, echinoderms, bryozoans) and plants (calcareous algae) in order to make their calcareous shells or skeletons. Borers thus play a vital role in replenishing the bicarbonate levels in the water by releasing fine grained or dissolved $CaCO_3$ into the water.

4. *Transported off the reef on to the seabed.* Once in the reef sediment grains are subject to a variety of further disturbances and destruction before they finally work their way into a permanent resting place deep within the sediment. This is the subject of Chapter 3.

2.5 CHAPTER SUMMARY

1. The examination of borehole morphology and its relationship to coral growth patterns was successfully used to interpret the mechanisms of borehole formation for four crustacean bioeroders. The analysis of coral samples of all sizes, from both fresh and preserved whole coral specimens to thin sections and SEM preparations, was essential in gleaning information at all scales. This little used approach is useful as it does not require the presence of the animal (though this is helpful) and can therefore be used on modern or fossil reef substrates, enabling direct comparisons.
2. Pyrgomatid barnacles and hapalocarcinid crabs passively bore small, more-or-less cylindrical holes by modifying coral growth. Barnacles lay down a corrugated calcareous plate which lines the hole and a highly ornamented wall plate at the coral surface. The exact fit of the hapalocarcinids in their holes and the smooth inner surface of the borehole indicate that the crabs use active chemical erosion to widen their boreholes. A chalky deposit on the hole walls may be a by-product of this chemical erosion.
3. Upogebiids mechanically excavate branching boreholes in coral which they line with a thick mud layer comprising sediment from the reef flat and from their own erosive activity. 30% of the coral removed during excavation is incorporated into this lining.
4. Alpheids use a combination of active and passive erosion to form their holes; the branching crack seen at the coral surface is created by the prevention of coral growth but the irregular chambers at the base are actively (mechanically) excavated.
5. Bioerosion on Tin Smelter Reef strongly affects coral morphology. Together with the effects of sedimentation and die-back from exposure and solar bleaching, bioerosion by alpheids and

upogebiids influences individual colony growth form. Shrimp boreholes cause the lobed columnar structure of outer-reef *Goniastrea retiformis*. The common, ring-shaped colonies with dead centres seen in *G. retiformis* and *Platygyra sinensis* may be enhanced by the initial settlement of sediment in abandoned shrimp cracks and by subsequent intensive bioerosion by *Lithophaga*.

6. Reef morphology is dependent on bioerosion as Tin Smelter Reef progrades seawards by the repeated toppling of corals off the reef front on to the sea bed, a process speeded by the weakening of reef front corals by bioerosion. As the reef moves seawards, back-reef areas become progressively more silted up and levelled by the combined effects of death and bioerosion. Thus, reef-top corals from the reef edge have a low preservation potential. This has implications for the preservation of passively and actively formed boreholes. Passive borers need live coral and are therefore most common in the outer reef top corals. These corals die and are subsequently rebored by active borers, obliterating earlier passive boreholes. *Upogebia* causes planes of weakness along which the reef pavement fractures. This may have a number of outcomes. This might either a) allow colonisation of the fresh vertical surfaces by bioeroders such as sponges,. thus increasing coral breakdown, or b) enable *Porites* to spread on to relatively sediment-free surfaces, thus maintaining live coral cover in the mid and inner reef. Water currents from the shrimps' borehole entrances may also help to prevent smothering of nearby corals with mud.
7. Sediment plays an extremely important part in the development of this reef. The large quantities of fine sediment on the reef flat and in waters surrounding the reef continually threaten to smother the reef. Bioeroders have a central role in the sediment pathways, not only producing sediment (either directly or indirectly) but also forming centres for sediment accumulation when holes are abandoned, thus raising the reef relative to sea level. The activities of *Upogebia* alone are responsible for 3% of this reef flat elevation and for 0.8% of the sediment input to the prograding fore-reef slope.

CHAPTER 3

BIOTURBATION

This chapter first provides an overview of the published literature on bioturbation, starting with the more general principles and effects of animal-sediment interactions (sections 3.1 and 3.2). Included in these sections are the physical, chemical and biological implications of bioturbation. Sections 3.3 and 3.4 describe the findings of this study, dealing first with intertidal (3.3) then subtidal (3.4) bioturbation. Each of these two sections contains a discussion of the results and the chapter ends with a summary (3.5) of the main conclusions reached as a result of this research.

Reef sediments have two principal origins, terrigenous and reefal, which occur in varying proportions depending on the surrounding geography and local currents and tides. Those of reefal origin are derived from the biological and physical breakdown of reef organisms (including reef sediment infauna), such as corals and molluscs. They are subject to various interlinked processes (Orme 1977, Rhoads and Boyer 1982):

- physical - currents, tides and larger-scale storms and hurricanes
- chemical - dissolution, cementation, redox variations
- biological - bioturbation

Bioturbation is the movement of sediment as a result of the activity of living organisms. Through ingestion, defaecation, manipulation, and displacement during their daily activities, organisms alter the texture of sediments in which or on which they live (e.g. Rhoads 1967, Myers 1977, Bromley 1990). The relative intensity of bioturbatory processes depends on the faunal composition and the sedimentary environment, which in turn are interrelated in a highly complex way.

Biogenic effects vary both temporally (tidally, diurnally, seasonally or over longer cycles) and spatially (within one habitat, or between geographical areas), so that a single species produces different results in different places or at different times of the year (Rhoads & Boyer 1982, Bromley 1990). It is the relative importance of physical and biological influences that affects the ultimate appearance of the sediments (Rhoads & Stanley 1965, Aller & Dodge 1974, Grant 1983).

3.1 THE EFFECT OF THE PHYSICAL ENVIRONMENT ON SEDIMENT INFAUNA

Variations in the physical environment (for example, bathymetry, geography, and hydrogeography) affect the substrate stability and composition (especially grain size) which in turn controls the distribution, density, type and rate of reworking of organisms that affect the sediment (Ginsburg 1956, Purdy 1964, Clifton and Hunter 1973, Swift 1993). Organisms may have flexible burrowing and feeding habits to cope with varying conditions (Dworschak 1987a, Nickell and Atkinson 1995). Grain size is one of the most important factors due to its influence on

- Quantity and quality of food; e.g. de Vaugelas et al (1986)
- Burying ability of the animal; e.g. Pinn and Ansell (1993)
- Particle size selective feeding; e.g. Rhoads and Stanley (1965), Bakus (1973), Nowell et al (1981), Vogel (1984).

3.2 THE EFFECT OF ORGANISMS ON THE SEDIMENT

3.2.1 Physical effects

Benthic organisms modify the physical conditions of a sediment by

- altering individual particle characteristics and their vertical and horizontal distribution and sorting,
- changing the bulk characteristics of sediment, such as permeability, compaction, water content, bulk density and cohesiveness and
- varying boundary properties of flow by altering surface roughness, critical entrainment velocities and shear strength.

(Purdy 1964, Nowell et al 1981, Rhoads and Boyer 1982, Scoffin 1987, Bromley 1990, Meadows and Meadows 1991).

The resultant physical modification depends on the method of feeding, the level of bioturbation relative to the sediment-water interface, the degree of mobility of the organism, organism size and population density (Rhoads and Boyer 1982). The organic or nutrient content of the sediment determines how long an animal stays in one burrow, how often they expand the existing burrow or leave and start a new one and if they change or mix feeding methods (Bromley 1990). The sphere of influence of a burrow may be very localised or extend far into the sediment in all dimensions (Ginsburg and Lowenstam 1958, Rhoads and Boyer 1982).

3.2.1.1. Decrease in water content (compaction or stabilisation)

Stabilisation of a sediment is a result of increasing its shear strength. This is achieved by mucus production (Nowell et al 1981), tube formation (Rhoads and Young 1970, Featherstone & Risk 1977, Rhoads & Boyer 1982) or pelletisation (Scoffin 1987). Sedentary suspension and deposit feeders tend to tighten fabrics (Rhoads 1967, Aller 1978, Bromley 1990).

3.2.1.2. Increase in water content (loosening or destabilisation)

Destabilisation usually occurs through frequent disturbance by mobile deposit and detritus feeders at the sediment surface (e.g. Young & Rhoads 1971, Aller 1978, Bromley 1990, Davis 1993). Particle advection and burrow excavation dilates or "fluffs" the sediment, decreasing shear strength and critical shear velocity (Rhoads and Boyer 1982). Tracks and trails can double boundary roughness and decrease the critical entrainment velocity by as much as 20% (Nowell et al 1981). Destabilisation of surface layers in turn increases the likelihood of resuspension (Aller and Dodge 1974) and lateral transport of fines may be high, especially when combined with rough weather (Roberts et al 1981, Davis 1993). Particles can also be directly resuspended by infaunal activities such as feeding, locomotion and burrow development (Davis 1993).

3.2.1.3. Formation of structures in or on the sediment

Surface structures

Evidence for bioturbation is often most evident from surface structures such as excavation mounds or hollows, faecal pellets or mounds, feeding pellets or tracks, trails and resting traces formed by motile fauna (Myers 1977).

Open structures in the sediment

Open structures include void spaces created by head-down deposit feeders (Rhoads and Boyer 1982) or burrows, which make take a variety of forms (Table 3.1). They may be lined or unlined, permanent or temporary, or shallow or deep within the sediment.

Structures vary widely both within and between species and with varying environmental conditions (e.g. Dworschak 1983, Suchanek 1985, Bromley 1990).

Table 3.1: Examples of the most common crustacean burrow morphologies and their inhabitants with references from the literature.

Burrow type	Example of organism responsible	Author
Single shaft or spiral, sloping or vertical	amphipods	Bromley 1990
	Cardisoma, *Uca*, (crabs)	Shinn 1968
U-shaped	crabs, including *Goneplax rhomboides*	Rice and Chapman 1971 Atkinson 1974
	Maera loveni *Corophium volutator* (amphipods)	Atkinson et al 1982 Bromley 1990
	lobsters, mantis shrimps	Myers 1977
	upogebiid shrimps	Dworschak 1983 Curran 1996
	Nephrops norvegicus (prawn), and *Calocaris macandreae* (thalassinid shrimp)	Chapman and Rice 1971
	Ocypode spp (ghost crab)	Farrow 1971
J-shaped	fiddler and ghost crabs	Braithewaite and Talbot 1972 Farrow 1971
Y-shaped	*Upogebia* spp (shrimps)	Swinbanks and Luternauer 1987 Swinbanks and Murray 1981 Dworschak 1983
	alpheid shrimps	Shinn 1968 Farrow 1971
	Nephrops (prawn) and *Goneplax* (crab)	Rice and Chapman 1971
Complex branching structures (i.e. mazes, boxworks, dentritic structures	thalassinid shrimps	Dworschak 1983 Shinn 1968 de Vaugelas 1990

Rearrangement or sorting of grains

- *grain size change*

Overall grain size can be increased and sorting improved by selective feeding processes (e.g. Rhoads 1967), binding or pelletisation (Swinbanks 1981, Rhoads and Boyer 1982, Bromley 1990). Winnowing of fines that have been moved to the surface leaves an overall coarser sediment (Swinbanks 1981, Tudhope and Scoffin 1984, Scoffin 1987, de Vaugelas et al 1986).

- *fine fraction buried at depth*

Filter or suspension feeders filter fine grains from suspension and emplace them into the substrate as burrow linings, faecal pellets or pseudofaeces (Myers 1977, Bromley 1990).

- *coarse fraction buried at depth*

Callianassid shrimps have commonly been observed to bury coarse particles in deep chambers in their burrows, and to eject fines at the surface. The cut-off point of grain size varies; for example, de Vaugelas et al (1986) found it to be 200μm, but Tudhope and Scoffin

(1984) found it to be at around 1-2mm. The latter also found some evidence of preferential arrangement (concave-up) of shell particles in the deep burrow chambers. Other examples include condensed shell beds formed by the "injection" of coarse particles into the sediment by shrimps and polychaetes (Meldahl 1987) and passive burial by undermining (Clifton and Hunter 1973).

- *coarse grains brought to the surface*

Studies on alpheid shrimps (e.g. Karplus 1987) have shown that the shrimps stack coarse particles at the entrances of their burrows to provide strength to the sloping entrance. McCave (1988) postulated that burrowing organisms can move gravel (grains >2mm) upwards by pushing aside particles that are too big to be eaten.

- *biogenic graded bedding and biogenic stratification*

(Rhoads and Stanley 1965, Warme 1967, Meldahl 1987)

3.2.1.4 Mixing or homogenisation

Primary sedimentary structures (i.e. those made by physical processes such as waves and currents) can be disrupted or completely homogenised by bioturbation (Thomassin 1974, Byers 1982, Miller 1984, Scoffin 1987, Bromley 1990, Tedesco & Wanless 1991). The rate and depth of homogenisation depends on the density of the infauna, the coarseness of the sediment and the physical conditions (Clifton and Hunter 1973).

3.2.2 Chemical effects

This subject is outside the scope of this thesis. For a review see Aller (1982)

3.2.3 Biological effects

Bioturbation changes the physical and chemical properties of the environment, as described above, thus altering the quality of habitat so that the community structure is modified. This creates conditions that have a negative or positive effect on other organisms and/or their activities (Rhoads & Young 1970, Aller and Dodge 1974, Myers 1977, Suchanek 1983, 1985, Bromley 1990).

3.2.3.1 Trophic group amensalism

Trophic group amensalism is "the modification of the benthic environment by deposit feeders, resulting in the exclusion of many suspension feeders and sessile epifauna" (Rhoads and Young 1970, Aller and Dodge 1974, Myers 1977). It is attributed mainly to deposit feeders causing the instability of the fluid, faecal-rich surface sediment which then clogs the feeding apparatus of the suspension feeders, buries, or at least discourages, larval settlement and inhibits adult attachment (Young and Rhoads 1971, Brenchley 1981).

3.2.3.2 Enhancement of populations of other organisms

Microbial distributions, diversity and abundances are often enhanced in the vicinity of burrows due to the elevated levels of oxygen and organic carbon (Aller 1982, Yingst and Aller 1982, Nickell 1992, Ziebis et al 1996). Suspension feeders that are able to stabilise the sediment create a habitat which can support abundant epifauna (e.g. Young and Rhoads (1971).

3.2.4 Geological effects

Traces of bioturbation can pass into the geological record where they are preserved as trace fossils or bioturbate textures. The results of animal activity in the sediment affect preservational conditions and hence the ultimate appearance of bioturbation in the fossil record. A full discussion of this topic is found in Chapter 4.

3.3 INTERTIDAL BIOTURBATION

The intertidal study site was Ao Tang Khen which has a large (0.5km^2) intertidal sand flat made up of sand waves (height 0.4m, wavelength 40m) alternating with shallow sandy/rocky pools. This was the intertidal study site for the work reported here. See section 1.3.1 for a detailed site description. Fig. 3.1 shows the distribution of the study animals in the sand waves and pools.

3.3.1 *Dotilla myctiroides* (soldier crabs)

The crabs were identified as *Dotilla myctiroides* (Crustacea, Brachyura, Ocypodidae, Scopimerinae; Satapoomin pers. comm. 1995, Dexter pers. comm. 1997).

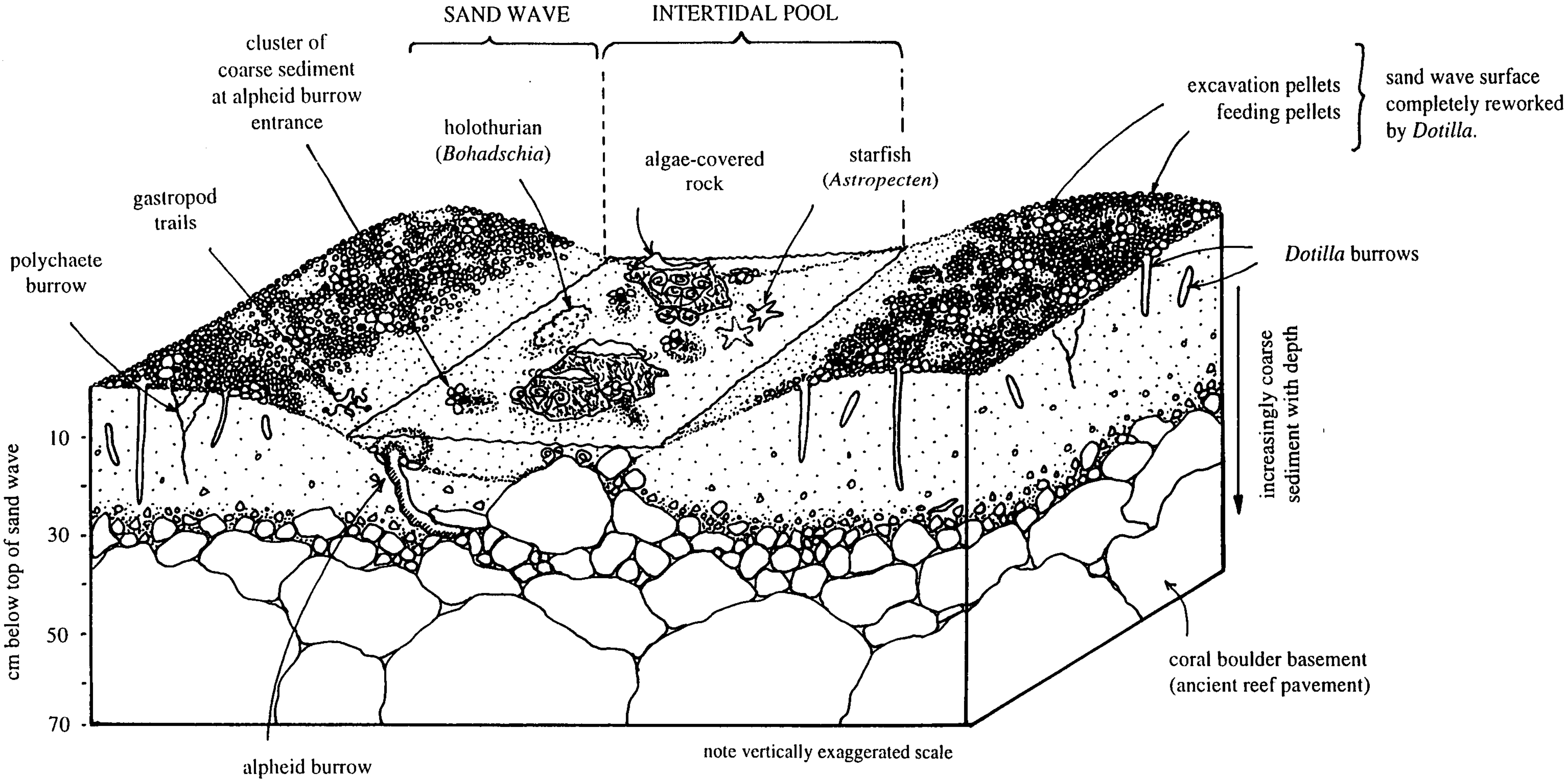


Figure 3.1 Bioturbators in intertidal sediments; sand waves and intertidal pools as they appear at low spring tide (see also Plates 3.7-3.9)

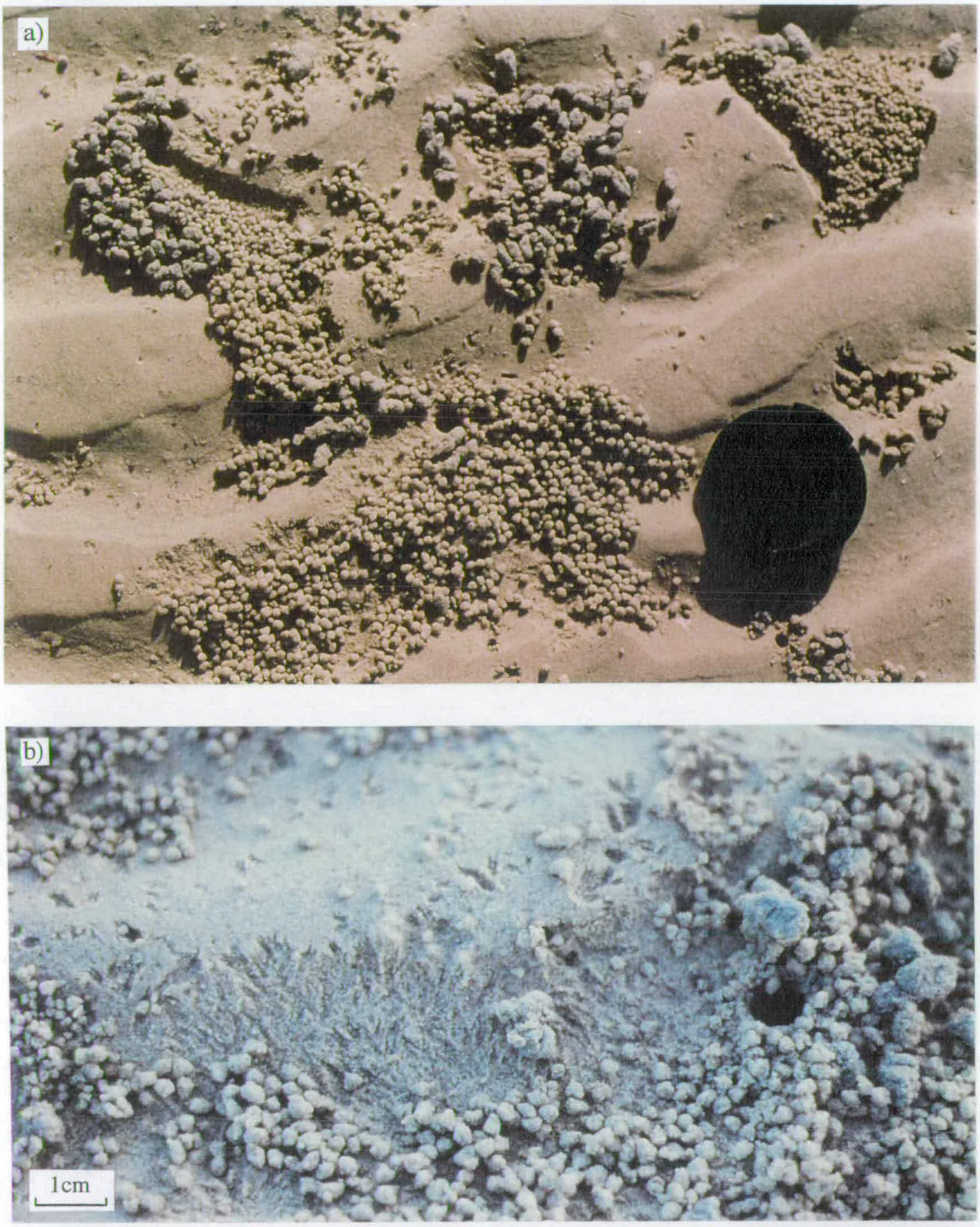


Plate 3.1 Intertidal bioturbation by soldier crabs (*Dotilla myctiroides*) in Tang Khen Bay. **a**) Four burrows showing large grey excavation pellets and smaller grey feeding pellets. Feeding has taken place along distinct lines leading from the burrow entrances. **b**) Detail of one burrow showing the two pellet types and the feeding groove 'scratched' by the crab's feeding activity. **c**) escape 'chimneys' made by quick spiralling burial. **d**) and **e**) *Dotilla* crabs. e) also shows a fiddler crab (*Uca*).

They have an almost spherical body of between 5-10mm diameter and are1 a pale blue/grey colour with fine dark stripes and pale orange legs and eyes (Plate 3.1d and e).

Most of the work on *Dotilla* was done on sand waves 4 and 5 (see Fig. 1.2) as these waves were thought to show average conditions with respect to exposure time due to their central position between low and high water marks.

3.3.1.1 Burrow structure and formation

Burrow dimensions were measured to the nearest millimetre with a ruler when exposed at low tide. The diameter of the entrance could be measured easily without disturbance but to measure depth the burrow was dug away from one side using a small trowel, until the bottom of the hole was reached. Burrows were selected for measurement on a random basis to obtain representative mean values for diameter and depth.

The burrows are simple cylindrical tubes, which are more or less vertical in the sediment, and penetrate to an average depth of 81mm (st. dev. = 28.7, n = 27), with an average width of 7.8mm (st. dev. = 3.0, n = 30; see Appendix C)

During daylight, burrowing occurs just after the sand waves become exposed as the tide falls. Within the first 10-15 minutes after the tide has fallen low enough, the crabs emerge from the sediment where they have been buried during high tide and in doing so produce 5-20 large excavation pellets (up to 1cm diameter). This slight lag between wave exposure and emergence of the crabs might allow the drainage of water to produce a better burrowing consistency, or ensure the simultaneous emergence of many crabs, which would be an effective anti-predator strategy.

Five quadrats were laid out on the crest of sand wave 5 on two days (once in the morning, once in the afternoon/evening) before the crabs had emerged. Photographs were taken of each of the quadrats at regular intervals to monitor the emergence of the crabs and their excavation and feeding activity throughout the tidal exposure (Plate 3.2).

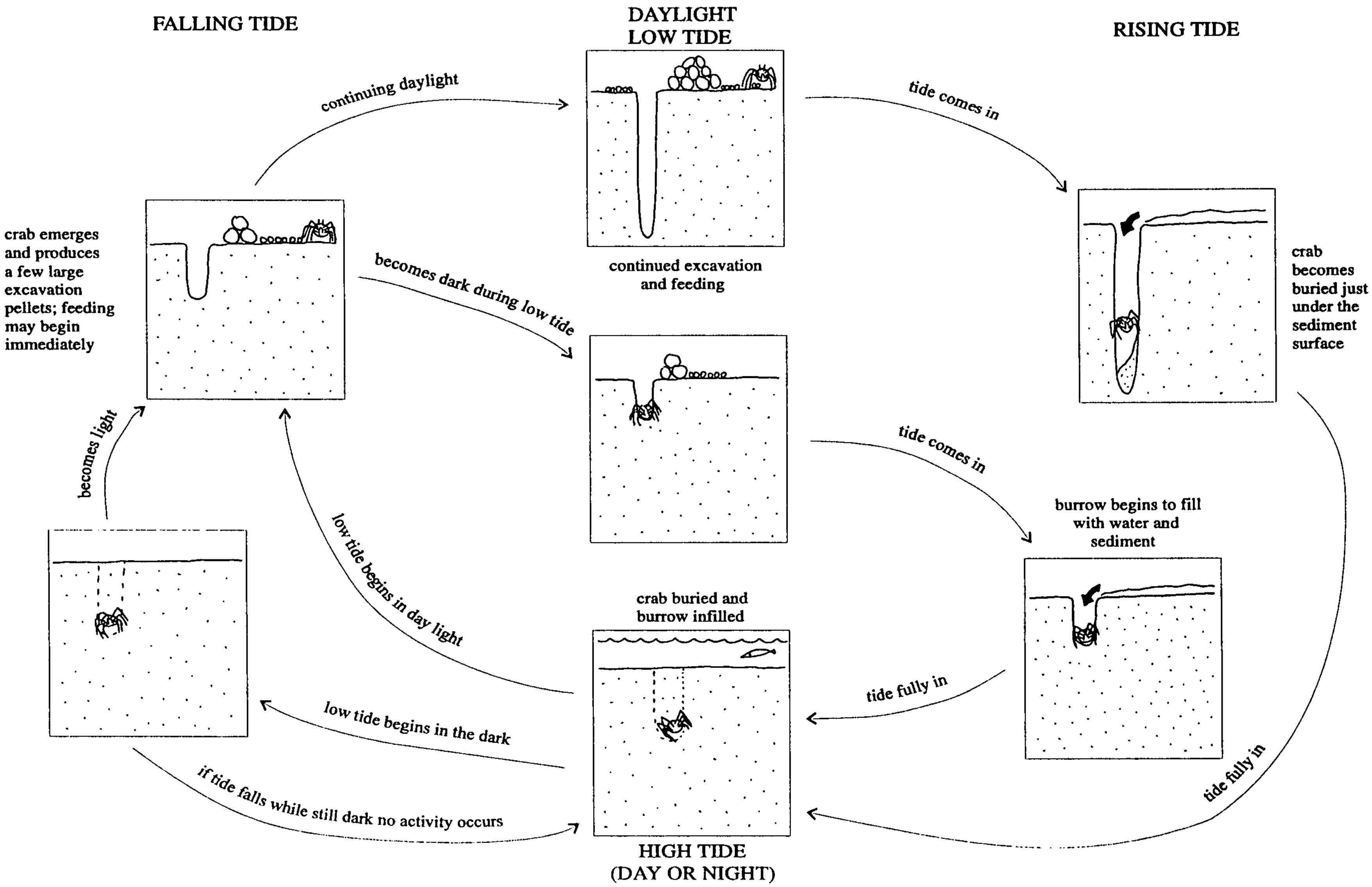


Figure 3.2 Diagram showing how the activity of soldier crabs (*Dotilla* sp.) depends on the relative timing of the tides and daylight.

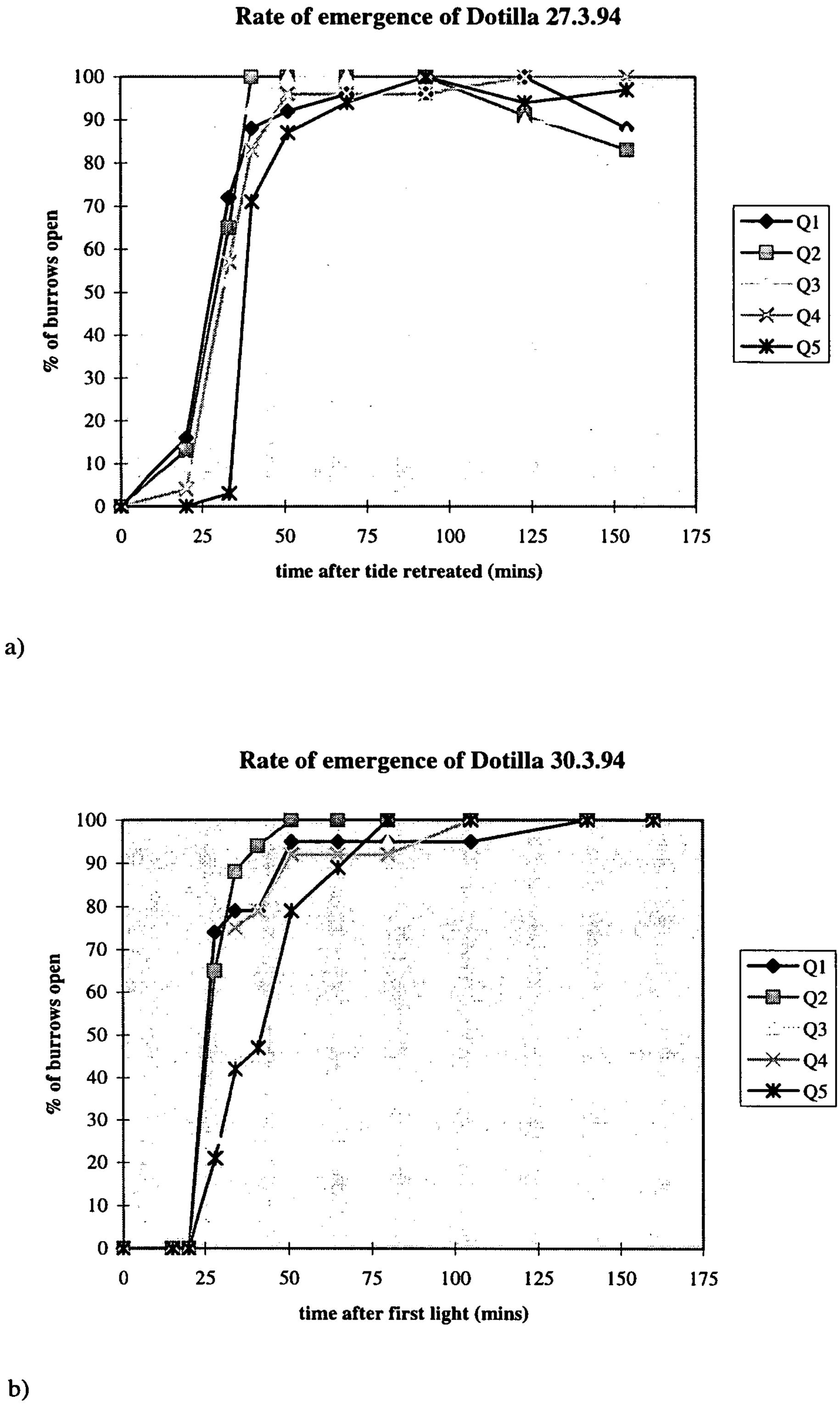


Figure 3.3 The timing of crab emergence (i.e. burrow formation) for the five quadrats (Q1-5) placed at a) an afternoon low tide and b) a dawn low tide.

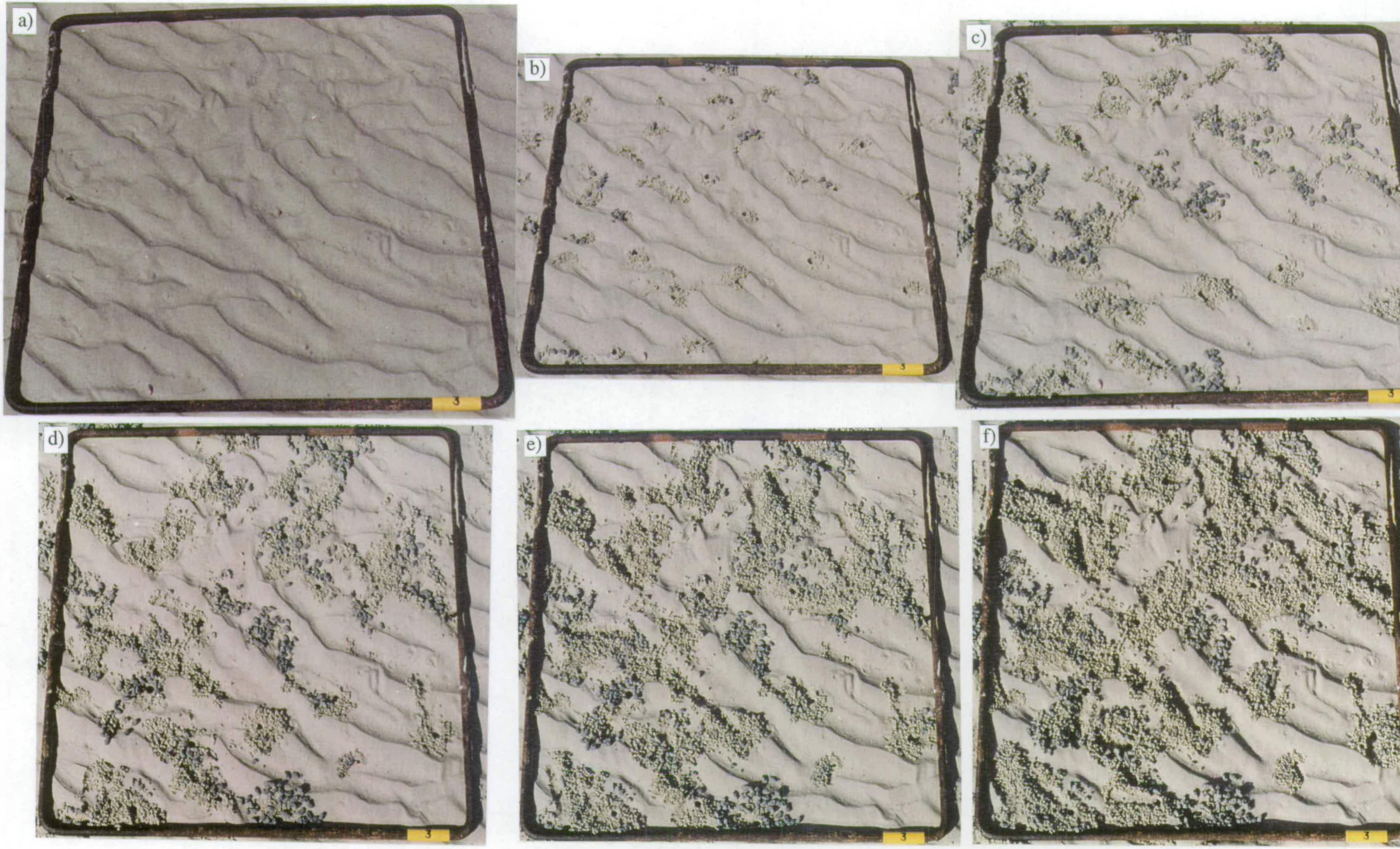


Plate 3.2 Time series of soldier crab (*Dotilla*) emergence at 20, 40, 51, 69, 93 and 123 minutes (photos **a)** to **f)**) after exposure of the sand on an afternoon low tide. The

The crabs only emerge during daylight hours; during otherwise ideal low tides at night, no crabs are seen on the sand. When the sun rises half way through a low tide, the crabs only emerge once it is light (there is a lag of 15-20 minutes after first light); during the dark part of the low tide they remain buried in the sediment. Likewise, when dusk falls during a low tide, the crabs retreat down their burrows as the light fades and no feeding is carried out in the dark, despite long periods of surface exposure.

The slight drop in numbers of burrows seen towards the end of the observation period is probably due a) burrow entrances being hidden by the large quantities of pellets which crowd the surface after intensive feeding and b) some crabs sealing themselves in, in preparation for the incoming tide.

During the exposure of the sand waves the soldier crabs graze almost continually on the surficial sediments, covering the surface with tiny feeding pellets (diameter 1-2mm), often arranged in lines radiating from the burrow entrance. They also deepen their burrows, resulting in a further 10 to 30 excavation pellets (Plate 3.1). The reason for this is unclear. Not all crabs seem to need a deep burrow; many burrows are only a few centimetres deep. The purpose of the burrow must be for protection from predators, but may also be necessary for the crabs to cool off during the heat of the day, and to keep their gills moist. A deeper burrow would take the crab down to where the air is humid due to the damp sediment.

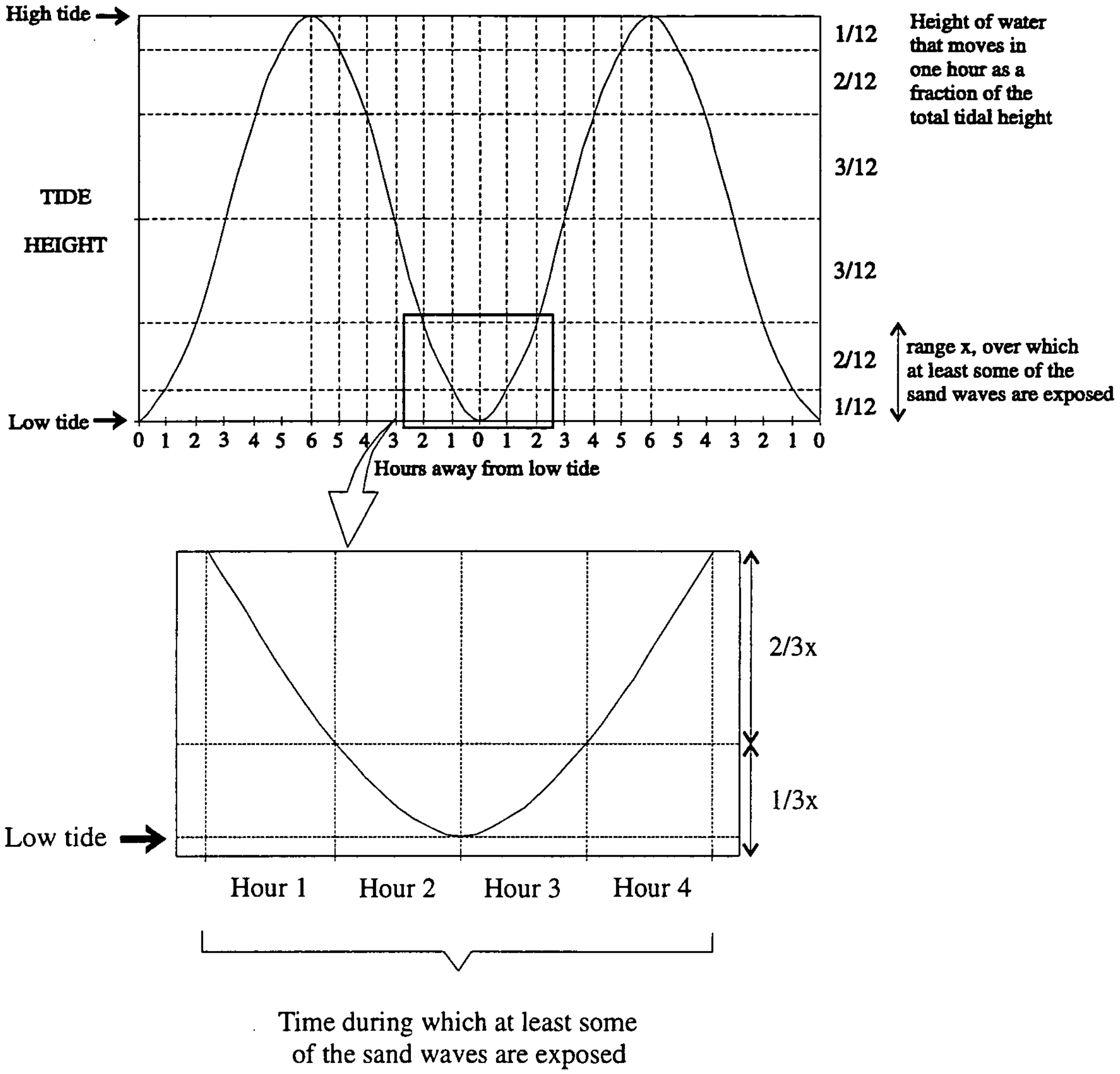
As the tide comes in, the crabs retreat down their burrows, which are then filled in with sediment as the water covers them. Most of this sediment will be the loose feeding and excavation pellets produced by the crabs at low tide, thus mixing the surface layers into the sediment. It is thought that the burrows are not completely filled with sediment; the crabs probably maintain an air pocket beneath the surface during high tide (Takeda et al 1996). The crabs are quite near the surface when the tide falls, as only a few pellets are excavated as the crabs emerge at the next low tide. The crabs' proximity to the surface could be achieved in two ways; a) by the crabs burrowing upwards through the sediment by displacement (i.e. sediment from in front is moved to the rear as they move upwards) or b) by allowing sediment washing in to the burrow on the rising tide to flow past them and fill in the lower reaches of the burrow before burying the crabs themselves. Fig. 3.2 summarises this sequence of events.

Another, less common, surface feature is produced when the crabs are alarmed. Usually, the crabs dart into their burrows but if they are a long distance away from their holes they will burrow rapidly into the sediment in a spiral manner, creating a small chimney-like structure on the sediment surface (Plate 3.1c). This is especially common in areas where there are no burrow entrances and the sediment is waterlogged (e.g. near the pool edges). It is easier for the crabs to bury themselves quickly in wet sand, which occurs frequently when the crabs are "droving" on the sand waves. This is when up to several hundred crabs move in a crowd across the sand waves and along the pool edges. Ens et al (1993) described this activity in fiddler crabs (*Uca* sp.), suggesting that it was only seen in the larger crabs which have higher energy requirements than smaller ones and must therefore cover a larger area to search for food. By moving in a large group they reduce the risk of predation. Takeda et al (1996) studied the function of the chimney structures, which are often roofed over to form what they call 'igloos'. They proposed that these igloos enabled the construction of a subsurface air chamber in sediment that is too fluid for normal burrow construction.

3.3.1.2 Distribution of the crabs on the sand waves

The sea level obviously has a strong effect on the burrowing activity of *Dotilla*, controlling when they emerge from the sediment. Therefore, it might be expected that the height of exposure of a sand wave (i.e. the depth of the water table beneath the burrowed area) would also strongly influence their distribution. To investigate this hypothesis, the depth of the water table beneath the edge of the burrowed area on a sand wave was measured by digging a small hole (about 10cm diameter) with a trowel and allowing it to fill with water (Fig. 3.5). The distance from sediment surface to water level was then measured. This was done between three and five times on the landward and the seaward side of each sand wave, and on a series of sand waves from close inshore to offshore (see Fig. 3.5). The time at which the measurement was taken was recorded to the nearest minute so that the values could be standardised to a particular time to account for changes in sea level. This was done by consulting tide tables for the area and working out the change in water height over the period the measurements were taken. A tidal prediction software package (Tidal Prediction by the Simple Harmonic Method, Ministry of Defence Hydrographic Office, Crown Copyright 1989-1991) was also used for this purpose.

Results indicate that there was no absolute minimum depth of water table below which the crabs would not burrow or feed; values ranged from 0.9 to10.5cm (Fig. 3.5). It would seem that the depth of dry sediment is not an important factor in burrow distribution on a sand wave; burrows on the crest of an inner sand wave could be at least 30cm above the



For the four hour period above:

- During Hour 1, the tide drops 2/3 of the range x, thus exposing 2/3 of the sand waves (waves 1 to 6); ie. one wave is exposed every 10 minutes
- During Hour 2, the tide drops the last 1/3 of x, exposing the last 1/3 of the sand waves (waves 7 to 9); ie. one wave exposed every 20 minutes
- During Hour 3, the tide rises by 1/3x, submerging waves 9 to 7
- During Hour 4, the tide rises by 2/3x, submerging the last six waves (6 to 1)

Figure 3.4 Explanation of the method used to obtain exposure times for the intertidal sandwaves in Tang Khen Bay.

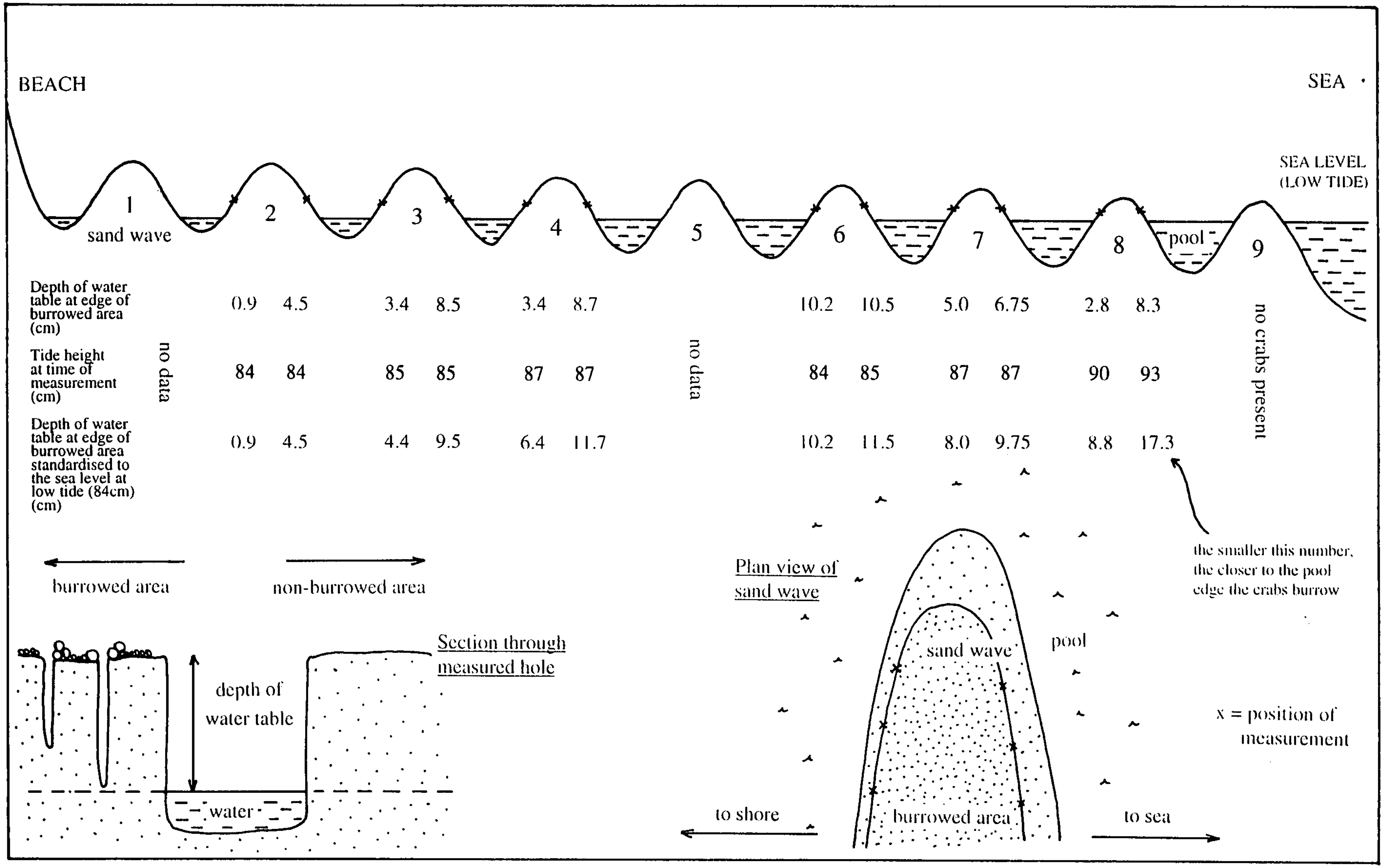


Figure 3.5 Experiment to determine the effect of sand wave exposure on *Dotilla* distribution and activity. **a)** Measurements of water table depth taken at various tidal heights (see section 3.3.1.2). **b)** Method for measuring water table depth. **c)** Plan sketch showing position of measurements.

water table, and therefore not reach the water at all. In contrast, the bottoms of pool edge burrows will extend under water a short distance from the burrow entrance.

Exposure rates for the ten sand waves from inshore to offshore were calculated for a maximum spring tide. The innermost (1st) sand wave becomes exposed two hours before low tide and is resubmerged two hours after low tide, and is thus exposed for four hours on a maximum spring tide. The outermost (10th) sand wave is never exposed. In the hour preceding low tide, the tide falls at half the speed of the hour before, and likewise rises at half the speed of the second hour after low tide (Rule of Twelfths; see Fig. 3.4). In calculating the time sequence of wave exposure and total time exposed, it was assumed that the sand waves were equally spaced and of equal widths, on a constant slope and parallel to the sea, and that the sea level was the same as the water level measured in the pits dug (Table 3.2 and Fig. 3.5). Although there is some variation in the dimensions of the sand waves, it was thought that, for the purposes of this model, the simplification was valid.

Table 3.2: Calculated exposure times of the ten intertidal sand waves for an average spring tide.

Sand wave number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Exposure time (min)	240	220	200	180	160	140	120	80	40	0

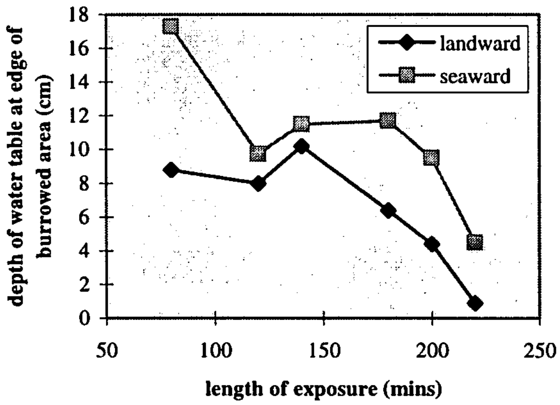


Figure 3.6 - The relationship between the exposure time of the sand wave and the extent of burrowing by *Dotilla myctiroides* (represented by depth of water table at the edge of the burrowed area).

There is a relationship between the water table depth at the edge of the burrowed area (i.e. extent of burrowing) and the exposure time of the sand wave (Fig. 3.6); the shorter the time of exposure, the less close the crabs burrow to the sand wave edge. This is not because of the depth of the water table beneath the sand wave; from the innermost sand waves it is seen that crabs can burrow as little as 0.9cm above the water table. Therefore, the extent of burrowing must be due to the time of exposure; with only 40 minutes exposure (maximum) to feed on the outermost wave, the crabs have no time to exploit the whole sediment surface. Crab densities (as indicated by number of burrow entrances) are also lower on the outer dunes (personal observation; no numerical data) so there is less competition for feeding space than there is on the crowded inner waves. These low densities are presumably related to the suboptimal conditions of low exposure time on the outer waves; at least the outer wave is not exposed at all during neap tides, so the crabs must remain buried underwater all this time. Klaassen and Ens (1993) measured a range of microclimatological conditions in a *Uca*-burrowed area and also came to the conclusion that these crabs preferred the higher zone because they could dig deeper burrows there due to the longer time available for digging.

There is also a general trend for the landward side of all sand waves to be burrowed closer to the pool edge than the seaward. This is not because of exposure times or water table depth, as these will be more or less identical across a single wave. A subtle change in surface grain size across a sand wave, due to physical grain sorting in the formation of a sand wave by wave action, could result in a more favourable feeding surface (finer particles and/or higher organic content?) on the landward side than the seaward.

3.3.1.3 Sediment texture

In the *Dotilla* area, sediment sampling on the tops of the sand waves to depths of 30cm (at which point the sediment was impenetrable by manual coring due to large quantities of reef debris) showed an increase in mean grain size with depth. Sorting decreased steadily with depth, from moderately well sorted in the top 8cm to very poorly sorted at 30cm (Fig. 3.11).

Dotilla feed selectively on certain grain sizes (Vogel 1984), and this combined with their small size (and thus their inability to shift grains larger than a particular size) will result in "passive segregation" of the sediment; that is, coarse grains will become buried by the continual burrowing and feeding activity on smaller grains by the crabs.

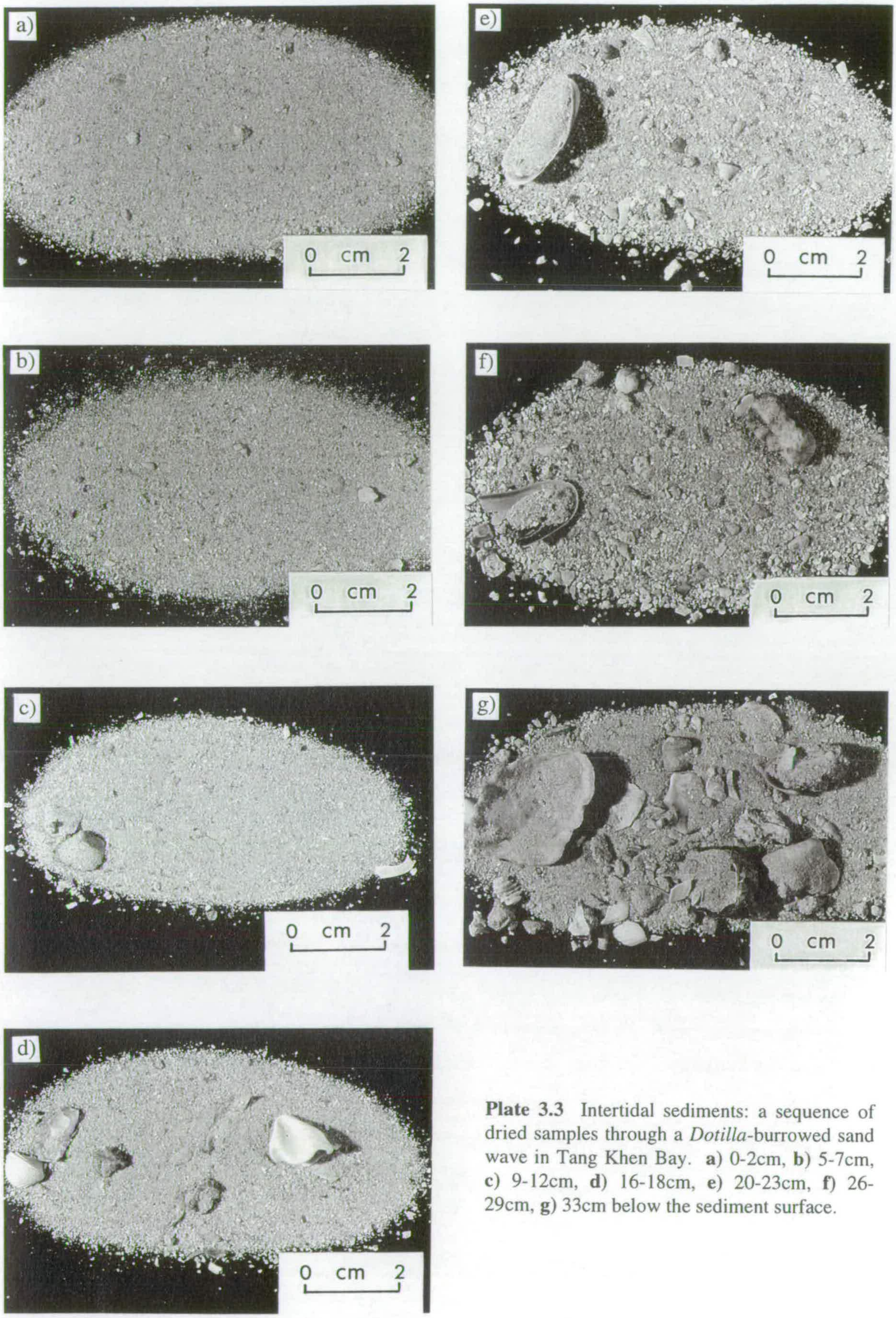


Plate 3.3 Intertidal sediments: a sequence of dried samples through a *Dotilla*-burrowed sand wave in Tang Khen Bay. **a)** 0-2cm, **b)** 5-7cm, **c)** 9-12cm, **d)** 16-18cm, **e)** 20-23cm, **f)** 26-29cm, **g)** 33cm below the sediment surface.

Cores showed an increase in mean grain size and a decrease in sorting with depth, but the effect of tides and waves in the intertidal zone will also have a major sorting effect. Tracer sediment placed on the sediment surface moved several metres horizontally in a single tide. It is not known what proportion of the sorting is due to physical and biological causes, but wave and tide action probably acts with the biogenic activity to increase sorting in at least the upper few centimetres of sediment..

3.3.1.4 Rates

Two methods were used to calculate the sediment turnover rates of the crabs. The methods give more or less identical figures:

a) Squares were defined using 25cm x 25cm quadrats as soon as the tide exposed sand wave 5. All the pellets that were produced during the entire low tide were collected, keeping feeding pellets separate from excavation pellets. The pellets were dried and weighed. This was done on 2 different occasions (once in the morning and once in the afternoon/evening), and 5 quadrats were laid on the crest of the sand wave each time. The tides were chosen to represent an average exposure time for a spring tide.

An average of 1.5kg pellets/m^2 (st. dev. = 0.66, n = 10) was produced over one tidal exposure, of which feeding pellets accounted for 67.4% and excavation pellets 32.6% (Appendix C). Spring low tides in this area always fall in the early morning (usually starting before dawn) and in the afternoon (often ending after dark). Therefore, it is uncommon for an entire exposure to occur in daylight. Assuming two suitable exposures every day during spring tides (a half tide in the morning and a half tide in the afternoon) and none during neaps (i.e. an average of one exposure a day over the whole year), the total turnover rate is 548.5kg (dry weight)/m^2/year, which is equivalent to 0.42m^3/m^2/year (sediment density is 1.3g/cm^3; Appendix B).

The total turnover rate can be split into burrowing rate (179kg (dry weight)/m^2/year or 0.14m^3/m^2/year) and feeding rate (370kg (dry weight)/m^2/year or 0.28m^3/m^2/year) according to the ratio of feeding to burrowing pellets.

b) Measurements of burrow depth and diameter were taken of random burrows on the sand flat, and an average of 89.8mm depth and 7.5mm width found. The burrows were assumed to be cylindrical, and the formula $V = \pi r^2 l$ used to calculate the average burrow volume. The average density of burrows was $91/m^2$ (st. dev. = 18.2, n = 31 quadrats), so using this method the burrowing rate is $0.13m^3/m^2$/year or $170.5kg$(dry weight)$/m^2$/year. Burrowing accounts for 32.6% of the total turnover rate, so by extrapolation the total burrowing rate is $0.4m^3/m^2$/year (or 523kg (dry weight)$/m^2$/year) and the feeding rate is $0.27m^3/m^2$/year or 353kg (dry weight)$/m^2$/year. These figures are equivalent to the top 9 cm of sediment being completely reworked 5 times every year.

3.3.2 Callianassid shrimps

Classification: Phylum Crustacea, Order Decapoda, Infraorder Thalassinidea Latreille 1831, Superfamily Thalassinoidea Latreille 1831, Family Callianassidae Dana 1852

The identification of these animals as callianassids is based solely on burrow morphology, as the shrimps were never caught. Two methods were used to attempt to catch them (section 1.5.1.10), but neither was successful.

On the mid to outer sand waves, especially in the central region of Tang Khen Bay, mounds of sediment and crater-shaped burrow entrances are abundant in the pools and on the sand waves. These structures have been described frequently in the literature (e.g. Shinn 1968, Tudhope and Scoffin 1984, Dworschak 1985, de Vaugelas 1990). In this central region of the bay the sediment is thick, with the gravelly layer only being reached about 30-50cm below the surface of the sand wave (deepest towards the top of the sand wave). Callianassid burrows are only found in this deep sediment. This could be for reasons of predator avoidance, sediment stability, or to ensure that there is enough depth of sediment for the several layers of galleries.

3.3.2.1 Burrow structure and formation (see Fig. 3.7, Plates 3.4 and 3.5)

The shape and dimensions of the burrow mounds vary depending on the mound location; those in intertidal pools form cones whose tops are truncated by the water level, and those which are exposed at low tide are spread out and flat due to the ripple action of the receding tide (Plate 3.4b). Thirty random sediment mounds (both in and out of pools at low tide) were measured using a ruler; two diameters were taken at right angles to each other, and height of the mound was also noted. The mean height was 3.10cm (st. dev. 0.98, n = 30) and the diameter ranged from 8cm to 40cm with a mean of 22.6cm (st. dev. 8.03, n =

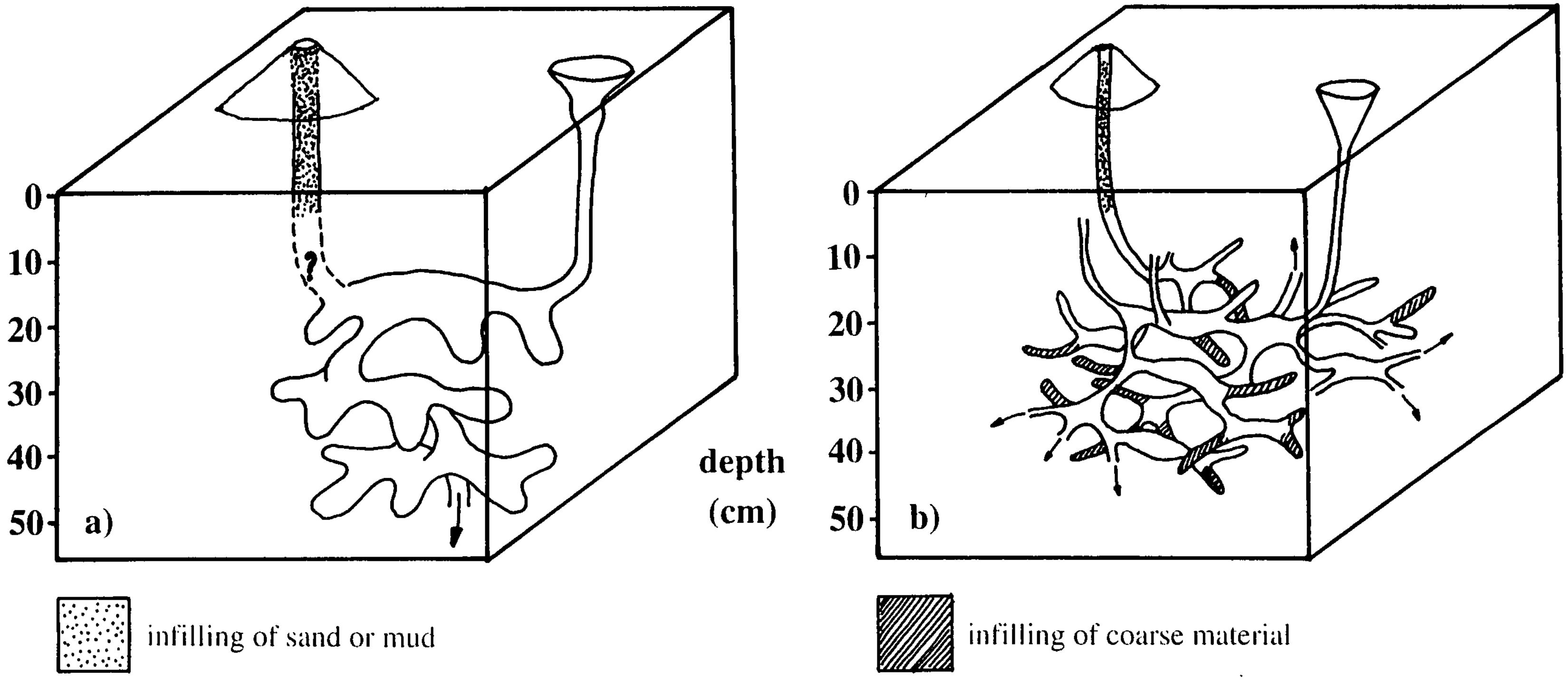


Figure 3.7 Comparision of the morphology of **a)** intertidal and **b)** subtidal callianassid burrows. The intertidal burrows have much wider chambers and distinct layers, whereas the subtidal burrows are more a fine branching boxwork of tunnels and blind-ended tubes.

Plate 3.4 Intertidal callianassid shrimp bioturbation. **a**) Fine sediment mound ejected at the surface - note dark anoxic sediment streaming from the top of the mound. **b**) Two pairs of mounds and craters; ruler is 22cm long. [Concentric rings on the mounds are due to erosion by falling tide]. **c**) General view of centre of Tang Khen Bay (looking N) to show scattered, sparse distribution of callianassid burrows. Darker areas are seagrass.

Plate 3.5 Resin casts of callianassid burrows. a) to d are intertidal, e) is subtidal. **a) and b**) Side and obliqu views, respectively, of the same cast, showing thre layers of chambers. **c**) Cast of the upper region of burrow with the characteristic crater-shaped entrance **d**) View of a three-layered cast from above. **e**) Firs layer of the narrow branching structure of a subtida burrow; compare with the larger chambered structure o the intertidal type. (NB cast in e) shows underside of th burrow). [Scale: a) to c) - lens cap is 5cm diameter, d ruler is 22cm long].

30). The entrance craters of these 30 burrows were also measured and found to have a mean diameter of 14.9cm (st. dev. = 5.15), and mean depth of 4.7cm (st. dev. = 1.56, n = 17).

Resin casting was carried out at low tide; polyester resin, pre-mixed with catalyst, was poured slowly into the burrow entrance, taking care not to allow resin to touch and loosen the sand at the top of the crater. The resin level was continually topped up until no more resin sank down into the burrow. Casts revealed a complex subsurface burrow (Plate 3.5a to d), despite all casts being incomplete. A permanently open vertical shaft (average diameter 3.2cm; st. dev. = 0.75, n = 30) of circular cross-section leads down from the crater to a depth of 25-30cm, where it turns sharply through 90° to run horizontally and expands into a wide (c. 5cm) chamber with blind-ended side chambers leading off roughly horizontally at right angles to the main burrow. These chambers are up to 6cm wide in all dimensions and smooth inside like the rest of the burrow system. This layer of chambers is the first of at least three layers reaching at least 50cm into the sediment, each connected to the ones above and below by a short vertical passageway. These chambers are similar in appearance to those described by Tudhope and Scoffin (1984) for an undescribed *Callianassa* species in the Great Barrier Reef and by Braithewaite and Talbot (1972) for '*Callianassa* sp. 2' in the Seychelles.

An open exhalent shaft leading to the surface mound was never found, as it seems to be loosely blocked with sediment, preventing resin casting but not the ejection of sediment from below, which can occur at any state of the tide. Careful excavation of the mounds from the surface showed that they had a central core with a coarser texture than the bulk of the mound. This core was a few centimetres in diameter, and must allow the passage of water and suspended sediment from below, as apparently blocked mounds were seen to eject watery sediment. A similar feature was noted by Nickell and Atkinson (1995). A few mounds had a very narrow (1mm) open shaft running through the middle of the core.

There was no evidence for shelly pockets leading off the chamber as found in the subtidal burrows in this study; the burrow walls were smooth to the touch, despite the coarse gravelly nature of the surrounding sediment at the level of the chambers. The burrows must therefore be lined with finer grains and presumably mucus. Other specific secretions such as 'collophanite' (Weimar and Hoyt 1964) may also be present. Coarse grains would be impossible for the shrimp to eject on to the sediment mound; they must therefore be disposed of at the level of the chambers. Since the chambers seemed to be empty and smooth-walled this coarse material must be buried outside the chambers and sealed off behind the burrow wall. There was no evidence for a 'knobby' exterior to the burrow wall

(Weimar and Hoyt 1964, Swinbanks and Luternauer 1987) which is diagnostic of the trace fossil *Ophiomorpha* (section 5.6.2).

3.3.2.2 Movement of mounds and craters

To investigate the permanence of the surface features of the callianassid burrows, ten burrows were marked with metal stakes, and the size and positions of the crater and mound relative to the marker stake noted daily during a series of spring low tides. Individual burrows were chosen on the basis that they were far enough away from neighbouring burrows to avoid confusion between surface features of different burrow systems. Tracer sediment placed down the crater and subsequently appearing in the associated mound (see section 3.3.2.3) also reinforced which surface features belonged to a common burrow. Due to the disappearance of some of the stakes, it was not possible to follow six of these burrows, but the results from the remaining four are shown below (Fig. 3.8). The mounds continually shift position by a few centimetres as sediment is ejected from them. The craters remain stationary. These observations do not allow an accurate assessment of the quantity of sediment ejected from the burrows, but together with observations of sediment flowing from the mounds and from tracer sediment experiments it is thought that the equivalent of a new mound was formed about every two days.

3.3.2.3 Sediment texture

The callianassid burrows were found both in the pools and on the sand waves in the central region of the bay. As already mentioned, the surface sand layer in this area is thick, even in the pools, the coarse gravelly layer not appearing until between 30-50cm below the surface. The top 30cm comprise fairly well-sorted, fine sand which grades into a coarser gravelly layer at the level of the callianassid chambers (Fig. 3.11). This texture may be due to the activities of the shrimps, as has been described by Tudhope and Scoffin (1984), but callianassids are not present in high densities and energy levels are high due to wave action and tidal draining in this shallow intertidal area. This sediment profile is also seen elsewhere in the bay where callianassids are absent. Therefore, it is more likely that this is a physically-produced texture, and that callianassids happen to form their chambers at the level where the sediment becomes coarse. This may be due to higher concentrations of food at that level.

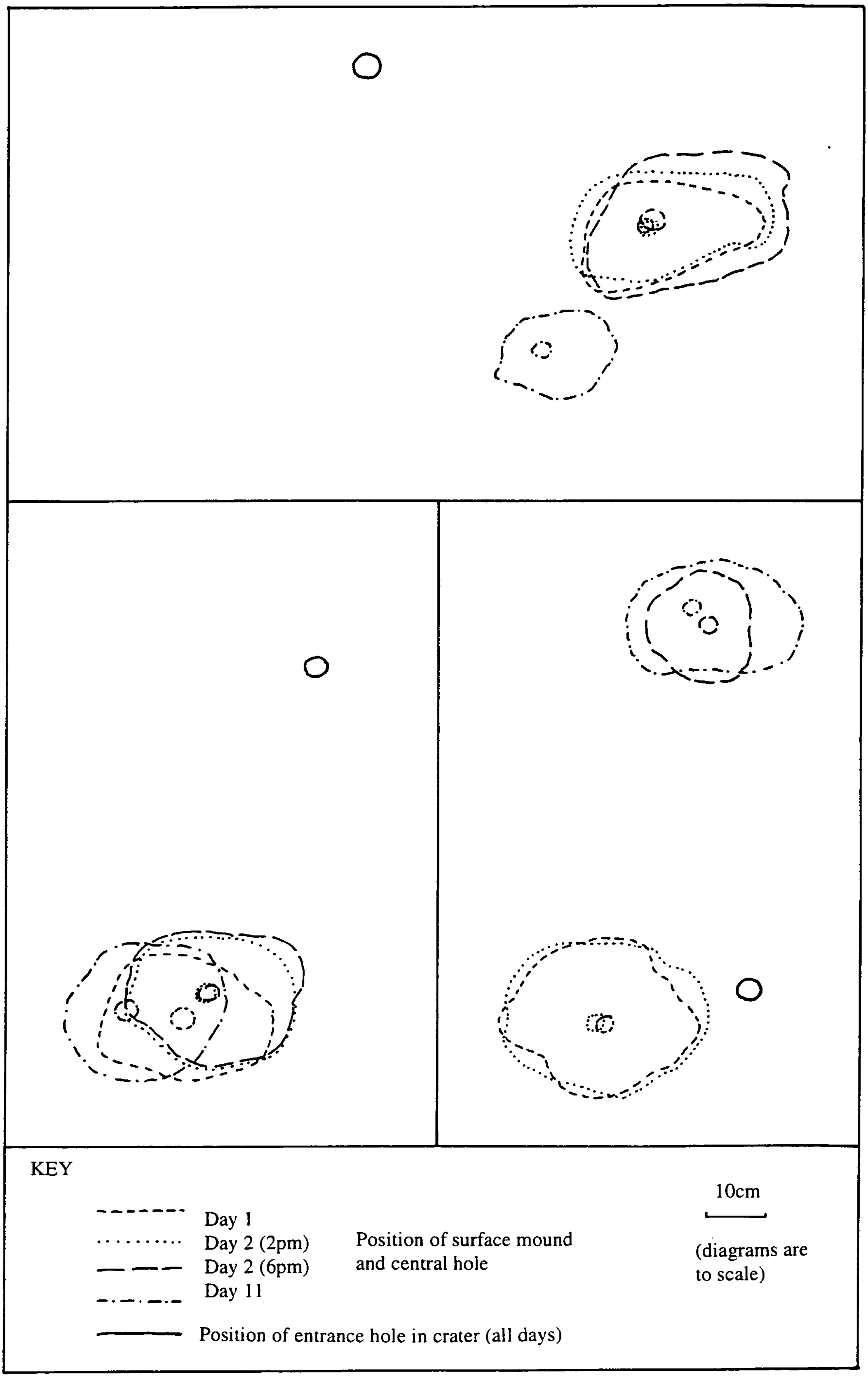


Figure 3.8 The movement of the surface mounds and craters of three subtidal callianassid burrows over an eleven day period.

Tracer sediment experiments were carried out to see how fast an influx of sediment to the inhalent shaft could be cleared, and if any grain sorting was carried out in the process. See section 1.5.1.6 for details of tracer preparation. Twenty grams of tracer, comprising 2g each of the 63-125µm, 125-250µm, 250-710µm, 710µm-2.36mm, and >2.36mm fractions and 10g of >5mm fraction, were poured into the shafts of four burrows at low tide, taking care that most of the tracer fell straight down the shaft and did not stick to the sides of the crater. Within an hour some tracer was visible in two of the mounds, though samples were not taken at this time. The mounds of these burrows were sampled 23-25 hours later using a pocket tube corer (diameter 3cm, length 4.5cm). Tracer was obvious on the mound surface and samples were taken through the centre and the edges of the mound, even where tracer was not evident. Inspection of the samples in a dark room, with a handheld UV lamp, revealed that a range of grain sizes from 63-710µm, and occasionally grains up to 2.36mm were ejected from the burrows on to the mounds (see Table 3.2 below). The mounds were re-examined ten days later and fresh ejecta of sediment seen to contain substantial quantities of tracer. The coarser fractions remained below and never appeared at the sediment surface.

Table 3.2: Summary of the results of the intertidal tracer sediment experiments on callianassid shrimp burrows.

Callia-nassid burrow	**Time after tracer applied (hours)**	**Area of burrow sampled**	**Tracer sediment grain size categories**					
			63-125µm	**125-250µm**	**250-710µm**	**710µm-2.4mm**	**>2.4mm**	**>5mm**
a	23	mound opening	O	O	O	O	O	O
a	23	new ejecta	O	O	O	O	O	O
a	23	old ejecta	O	O	O	O	O	O
a	23	shaft lining	X	X	O	O	O	O
b	23	mound opening	O	O	O	O	O	O
c	23	mound top	XXX	XXX	X	O	O	O
c	23	mound side	XXX	XXX	O	O	O	O
c	23	top 1cm of mound side	XXX	XXX	O	O	O	O
c	23	2cm within mound	O	X	X	O	O	O
c	23	shaft lining	O	X	X	O	O	O
a	25	mound opening	XXX	XXX	XXX	X	O	O
a	25	new ejecta	XXX	XXX	XXX	O	O	O
a	25	old ejecta	XXX	XXX	XXX	O	O	O
c	25	mound top	XXX	XXX	XXX	O	O	O
c	25	mound side	XXX	XXX	XXX	O	O	O

KEY: O - no tracer, X - few grains of tracer, XXX - abundant tracer.

Ten further un-tracered mounds were sampled in the same manner and particle size analysis of a subsample of each mound carried out in the using an LS100 Coulter Counter for the <500μm fraction and sieving for the >500μm fraction (section 1.5.1.4). This revealed that the bulk of the mound comprises fine sand in the range 125-250μm, with a mean of 218μm (see Appendix C).

3.3.2.4 Turnover rates

Callianassids were found in densities of $37/100m^2$, as counted in a 10x10m grid measured out on the sand flat at low tide. Both mounds and craters were counted; only those that seemed to be in use were included. Active burrows were distinct as the craters were open and not infilled in any way and the mounds had distinct boundaries and did not blend in with the surrounding substrate as disused, wave-damaged ones do. Thirty-seven craters and forty-two mounds were counted. The number of craters was taken to be an accurate reflection of the number of burrows. From resin casts, it is evident that each burrow has only one crater, but the number of mounds per burrow can not be ascertained from casts as the mound shaft never cast due to it being blocked by sediment. From observations on the sand flats it seems that the vast majority of burrow systems have only one mound (i.e. a ratio of 1 crater: 1 mound for each burrow), but disused mounds persist for several days before being completely flattened by waves. The excess number of mounds counted in the 10m x 10m grid was probably due to the most recently abandoned mounds being difficult to distinguish from those in use.

As described above, (section 3.3.2.2), marked burrows were observed and new mounds were seen to appear about every two days. Rates of sediment turnover were calculated on the basis of an average-sized mound being produced every other day. Taking the mounds to be cones, with a volume of $\frac{1}{2}\pi r^2h$, where r is the radius and h is the height, the average diameters were halved to obtain a radius, and volumes were calculated for the thirty cones (see section 3.3.2.1 and Appendix C). The volumes calculated averaged $787cm^3$ (st. dev. = 757, n = 30). This is equivalent to 1023g dry weight ($1cm^3$ = 1.3g dry weight).

A turnover rate of $0.05m^3/m^2$/year (69kg (dry weight)/m^2/year) was calculated which is equivalent to a sediment thickness of 25cm being completely turned over in 4.7 years. This is almost certainly an underestimate as some sediment ejected from the burrow on to the mound will undoubtedly be removed by wave action in this shallow intertidal area.

3.3.3 Alpheids

Of the three types of alpheids studied, only one is intertidal. It is a small (4cm long) species, found in intertidal pools on the sand flats of Tang Khen Bay, commensal with a non-burrowing gobiid fish (Plate 3.6d). Neither animal has been identified, as neither could be caught despite efforts with a small, four-pronged, elastic-powered spear and attempts to quickly cut off the burrow retreat with a spade. Usually there is one shrimp to one fish, but it is not uncommon to find two shrimps in one burrow, both of which are active burrowers. All work on these shrimps was carried out in pools 4, 5 and 6 (see Fig. 1.2).

The commensal relationship between alpheid and goby has been the subject of a few biological and behavioural studies which suggests that the goby acts as a burrow guard while the shrimp is the burrow excavator and sometimes also cleans the fish. Karplus (1987) provides a thorough review of previous work on this association.

3.3.3.1 Burrow structure and formation

All average measurements mentioned below were taken at low tide in tidal pools 4, 5 and 6. A ruler was used to measure hole diameter, sediment pile length, width and depth, and the dimensions of the area of the coarse debris pile (see Appendix C).

There is usually one entrance to the burrow, which either enters the sediment at an angle, with a pile of excavated sediment at the surface in line with the burrow direction, or is more vertical with a ring of sediment piled around it. Mean burrow entrance diameter is 2.3cm (n = 17, st. dev. = 0.4). Very occasionally there are two entrances which join in a Y shape at depths of about 10-15cm, as seen in resin casts formed from polyester resin poured into the two burrow entrances. These observations of the upper burrow parts are very similar to those of Shinn (1968), Farrow (1971) and Karplus et al (1974), although double entrances were not so common in this study. The lower burrow parts seem more highly variable, with Shinn (1968) finding extremely complex and deep structures and Farrow (1971) describing a highly regular branching pattern. In this study, the irregular

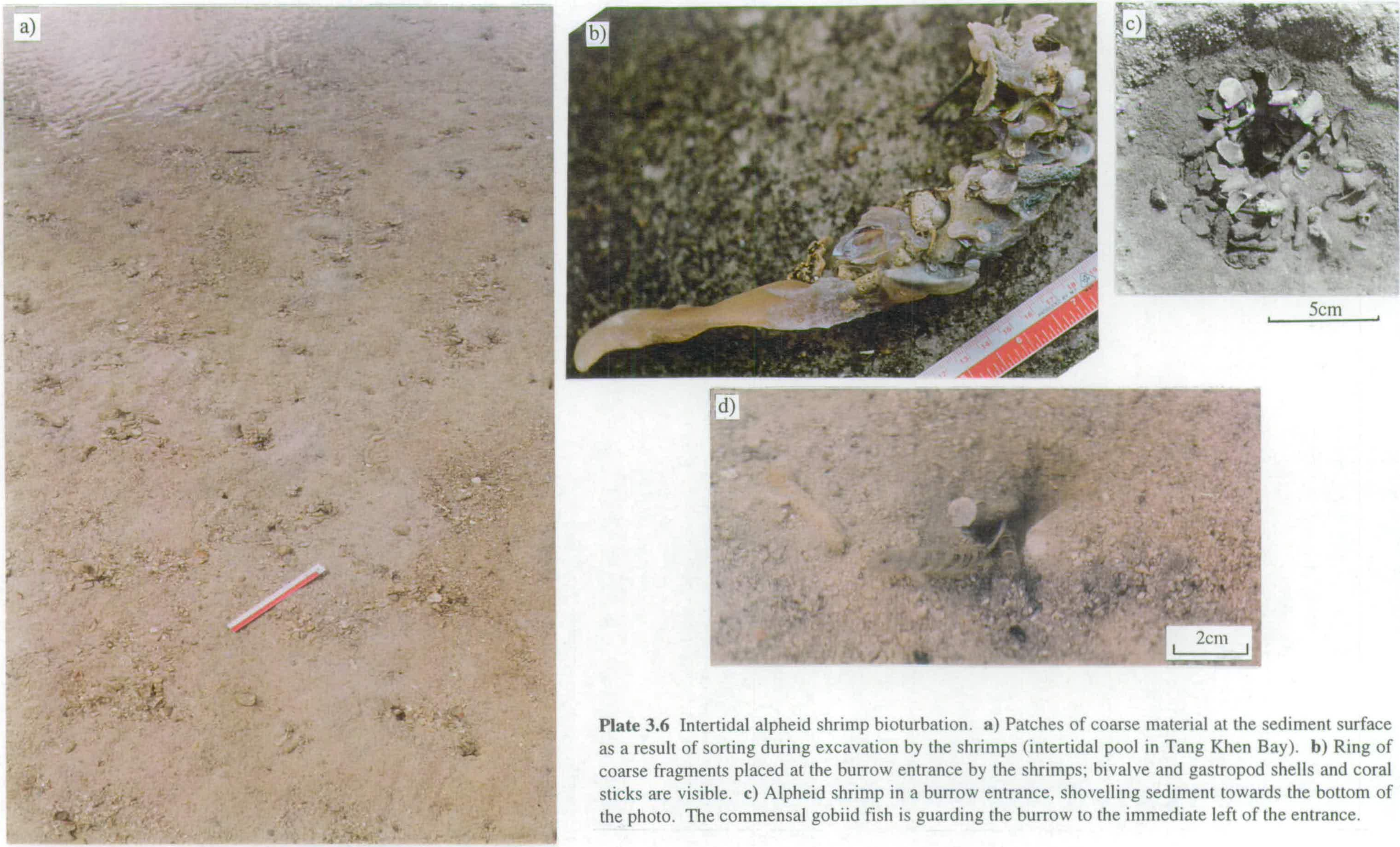


Plate 3.6 Intertidal alpheid shrimp bioturbation. **a)** Patches of coarse material at the sediment surface as a result of sorting during excavation by the shrimps (intertidal pool in Tang Khen Bay). **b)** Ring of coarse fragments placed at the burrow entrance by the shrimps; bivalve and gastropod shells and coral sticks are visible. **c)** Alpheid shrimp in a burrow entrance, shovelling sediment towards the bottom of the photo. The commensal gobiid fish is guarding the burrow to the immediate left of the entrance.

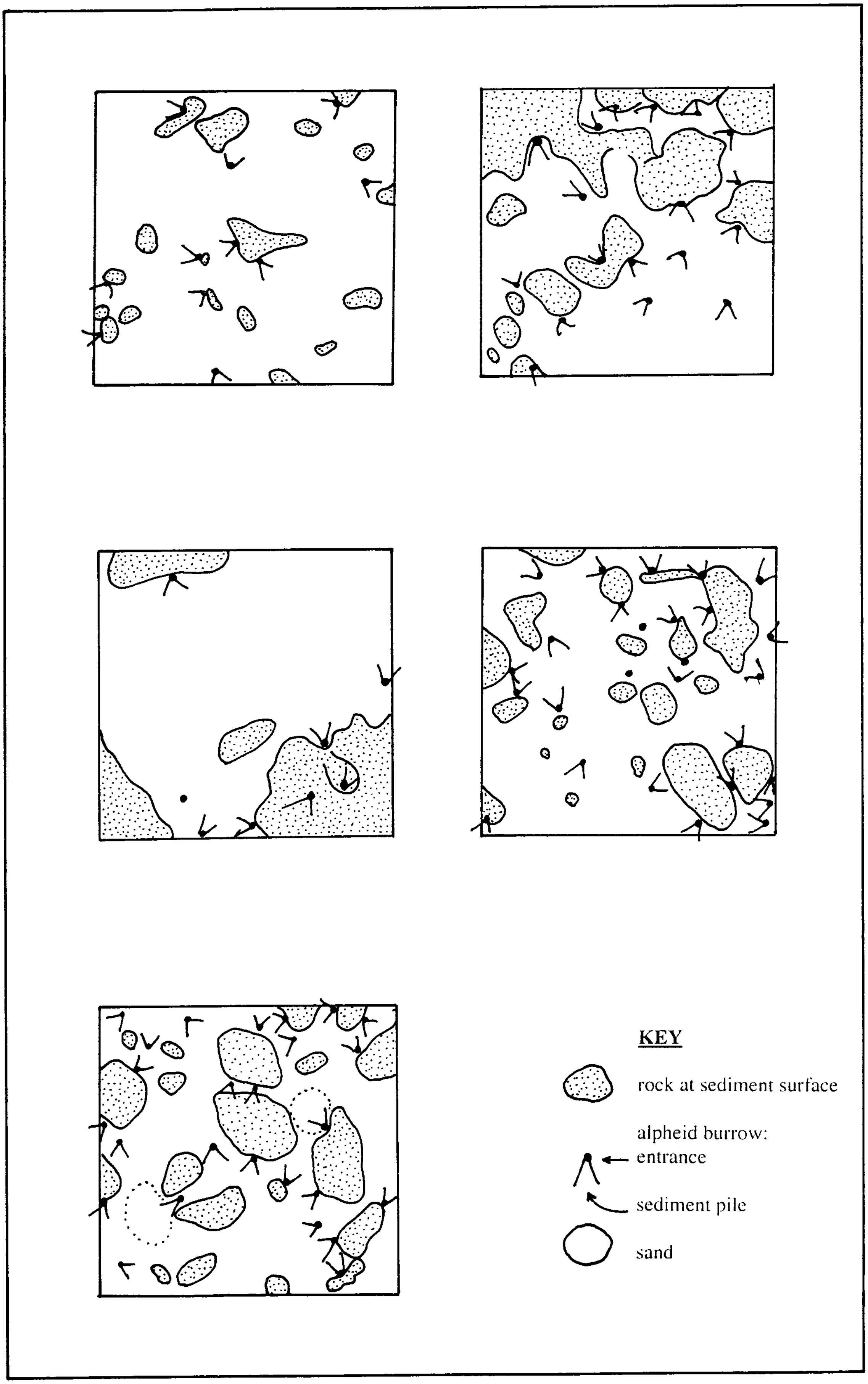


Figure 3.9 Distribution of intertidal alpheid burrows in the central rocky area of tidal pools; alpheids usually burrow underneath the rocky boulders . Each square represents a 50cm x 50cm quadrat.

nature of the subterranean structure and the determination of its morphology by buried reef debris is more similar to that of Karplus et al (1974).

Coarse material which is brought to the surface is separated out from the finer sediment and placed around the burrow entrance, forming a shelly 'collar' around the more vertical burrows and a shelly 'roof' to the sloping ones (Plate 3.6b and c). It seems that the pieces of shell and coral provide support to the upper reaches of the burrow and can be seen from resin casts to surround the burrow wall in the top 5-10 cm of burrow (Plate 3.6b). These upper reaches of the burrow therefore have a highly uneven surface with fragments projecting into the lumen, whereas the lower portions have a smoother interior. Some casts show evidence of a smooth floor and a rougher ceiling, as found by Karplus et al (1974). Where rocks are present in the intertidal pools, burrow entrances often slope underneath them so that the rock itself is the ceiling of the burrow. The distribution of burrows in some of these rocky pools was mapped and is shown in Fig. 3.9.

The burrows with sloping entrances are more common and slope downwards at an angle of 30-45° to the horizontal to depths of 20-30cm, the level at which most of the sediment comprises cobble to boulder size reefal fragments. The irregular burrow morphology seems to be determined by the presence of large pieces of reef debris, which are abundant in the sediments they inhabit.

The gravelly nature of the sediment made resin casting impossible in the centre of the pools, as the resin was not constrained by the burrow but drained away into the surrounding sediment. Where burrows extended underneath coral boulders, they could not be extracted from the sediment. As a result, all resin casts obtained were from the pool edges where the sediment was more sandy.

The alpheids were observed to be active only in the daytime, and the intertidal type also became inactive whenever low tides fell between about 10am and 4pm, presumably due to the heat. Snorkelling over the sand flat confirmed that the shrimps are also active during daytime high tides, but are never active at night, whatever the state of the tide.

The shrimps remove piles of fine sediment by using their front appendages to shovel the sediment in front of them (as seen in Plate 3.6d). This activity forms roughly circular piles either surrounding or to one side of the burrow entrance; on average these piles are 17.5cm in diameter (n = 34, st. dev. = 4.1; Appendix C). Larger pieces of coral and shell are picked up individually and placed around the burrow entrance. Presumably the cut-off size between coarse and fine sediment depends strongly on the size of the individual shrimp and its ability to physically lift large grains. Attempts to quantify this cut-off point using the placing of tracer sediment in the burrow entrance were unsuccessful either due to the complete blocking of the entrance or the sudden inactivity of the shrimp during the observation period. However, shrimps were observed to pick up coral sticks longer than their own body length. Up to 50 pieces of coarse debris were counted around a single burrow, with an average of 14.5 fragments (st. dev. = 10.7, n = 17). These figures only include those pieces that are visible at the surface; resin casts revealed fragments incorporated into the burrow walls to depths of 10-15cm.

Sediment shovelling rates were measured in the intertidal pools during morning and evening low tides; burrows were watched for up to 50 minutes and every time a shrimp emerged with a load of sediment the time to nearest second was noted. This was repeated for six different burrows. The general pattern was one of frequent shovelling (e.g. about once every 5-15 seconds) for periods of several minutes, punctuated by long periods (up to 10 minutes) where no activity was seen. These pauses were sometimes attributable to disturbance at the surface, but at other times must have had other causes. It is not known whether the shrimps rest during these pauses, or are engaged in some other activity below the surface, such as feeding, burrow maintenance or the digging of new passageways at depth. The pauses were not followed by any measurable burst of activity such as might follow after subterranean digging to clear the burrow, so it seems likely that the shrimp is simply resting.

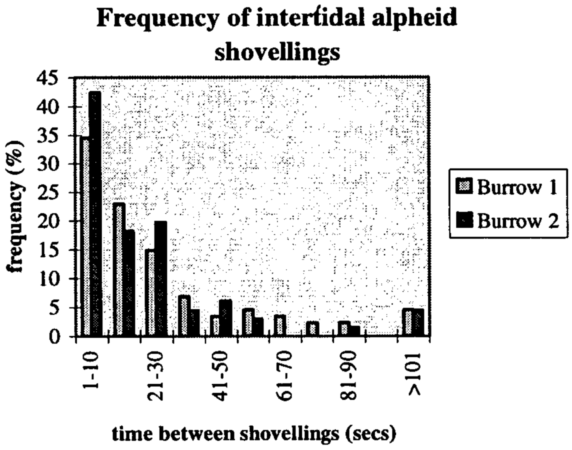


Figure 3.10 Shovelling frequency of intertidal alpheids in two different burrows

Excavation of the sediment surrounding burrows was extremely difficult due to the coarse, unstable nature of the sediment, but there was some evidence for remnants of old, infilled burrow branches leading off the open burrow at depths of about 6-8cm in the sediment. Resin casts of multiple-entranced burrows also showed the burrow to branch at about 7cm below the sediment surface. This evidence, combined with observations made on subtidal alpheid burrows in similarly coarse sediment (section 3.4.2.1) suggests that the lower portion of the burrow is fairly permanent, whereas the top portion changes position. Burrows with two entrances may simply be a half-way stage between the changing of a single burrow entrance. This changing of entrance may be to do with the alpheid's feeding strategy; it is a deposit feeder and needs to process fresh sediment to obtain nutrition. By changing the upper part of the burrow on a regular basis, it can maintain a safe retreat while working through large volumes of sediment.

3.3.3.2 Sediment texture

Sediment coring was not possible in the intertidal pools due to the large amount of coarse debris and coral rock present. Excavation with a small trowel showed that coarse material was abundant throughout the depth of sediment but increased with depth until solid coral rock was reached only 10-20cm below the surface; this also often protruded above the sediment surface.

The result of sediment sorting by the alpheids in the intertidal pools (as described in section 3.3.3.1) is that groups of shells from both current and disused burrow entrances create a patchy texture in the top few centimetres of sediment. This is clearly visible on the surface of the sediment as shown in Plate 3.6a. From resin cast evidence and subtidal near reef excavation (where the sediment is of a similar nature - see section 3.4.2.2) this texture presumably extends some centimetres into the sediment.

3.3.3.3 Rates

Burrow densities were calculated from transect data (linear point intercept method) collected while mapping the sand waves. In this method, a 5m long tape measure was leapfrogged over itself to give total of 166m of transect in the intertidal pools, and the substrate every 20cm along the tape was noted. 19.7% of the substrate was identified as being part of an occupied alpheid burrow (i.e. actual entrance, or associated sediment pile; Appendix B). Occupied burrows were fairly easy to distinguish from unused ones as the entrances were open and the sediment piles appeared freshly excavated, often with the characteristic dark grey colour of the deoxidised sediment from below. Burrow measurements gave an average sediment pile diameter of 17.5cm (st. dev. = 3.1, n = 34; see Appendix C). From these measurements and from observations at low tide it can be seen that the pile is more or less circular in shape and the area it occupies can therefore be calculated using the formula for a circle, area = πr^2, where r is the radius. The sediment pile delimits the boundary of the surface features of the burrow, so it can be said that one average burrow system occupies 240cm^2 at the surface ($\pi(17.5/2)^2$). Using this figure and the fact that alpheid burrows occupy 19.7% of the sediment surface area (transect data; Appendix B), this represents a burrow density of $8.2/\text{m}^2$, although densities of up to $25/\text{m}^2$ were recorded in the centre of some pools.

In section 3.3.3.1 the regular movement of the burrow entrance was postulated. No data was obtained regarding the frequency of entrance movement, so for the calculation below, the figure of once a day is used, as obtained for subtidal near-reef alpheids which make similar burrows and inhabit similar sediment. The length of burrow that is dug each day is taken to be 10cm; this is the length of the branches on the forked resin casts obtained. Due to the slope of the burrow, this represents the portion of the burrow in the top 7cm of sediment. From measurements at low tide, a mean burrow diameter of 2.3cm is taken (st. dev. = 0.4, n = 17; Appendix C).

Rates of turnover were calculated by assuming a 10cm length of a 2.3cm diameter cylindrical burrow to be excavated daily. A turnover rate of $0.12\text{m}^3/\text{m}^2/\text{year}$ was thus calculated for the top 7cm of sediment. This is equivalent to $158\text{kg/m}^2/\text{year}$ (sediment density is 1.3g/cm^3) or to the top 7cm being turned over 1.7 times every year.

3.3.4 Other bioturbators

(See Plates 3.7, 3.8 and 3.9 for photos of some of these traces.)

Immediately above high water mark, at the junction between the beach and the grass, is a patch of exposed orange clayey earth which is heavily burrowed by land crabs. Large burrow entrances (up to 7-8cm diameter) are surrounded by mounds of earth which appear to have solidified (sun dried or plastered together by the crabs?), giving a hummocky appearance to the area.

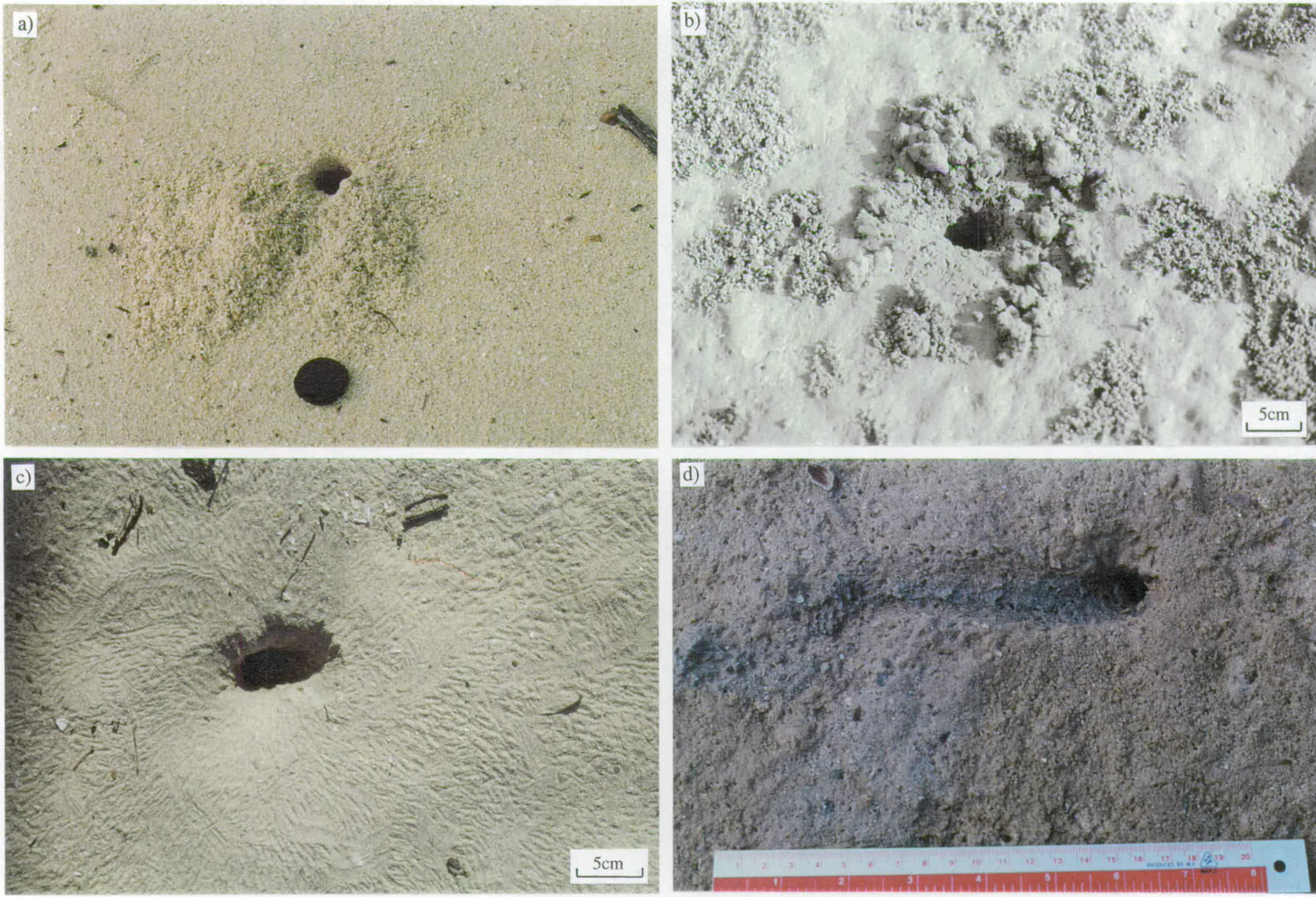


Plate 3.7 Surface intertidal bioturbation in Tang Khen Bay. **a)** Ghost crab burrow in beach sediment; sand has been thrown from the entrance into a loose irregular pile. **b)** Nocturnal ghost crab burrow on an intertidal sand wave; large excavation pellets visible and also note surrounding *Dotilla* burrows. **c)** Ghost crab burrow in dry

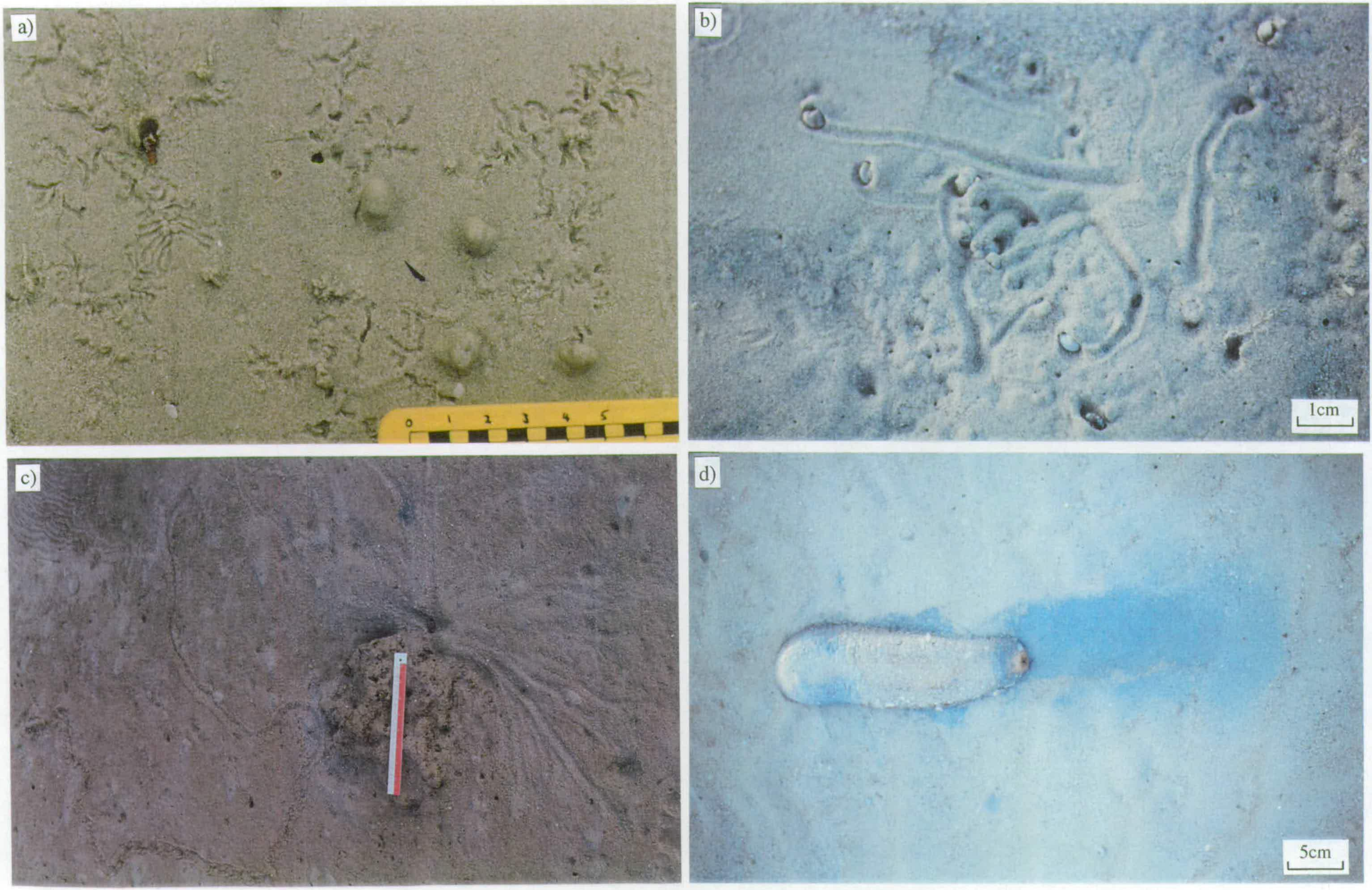


Plate 3.8 Surface intertidal bioturbation in Tang Khen Bay. **a)** Traces made by tiny hermit crabs inhabiting *Bathylaria* shells (top left). **b)** Trails left by unidentified gastropods. **c)** Radial feeding traces of a crab and a large meandering trail of a moon shell (*Polinices* sp.). **d)** Holothurian (*Bohadschia* sp.) feeding to the left has left a

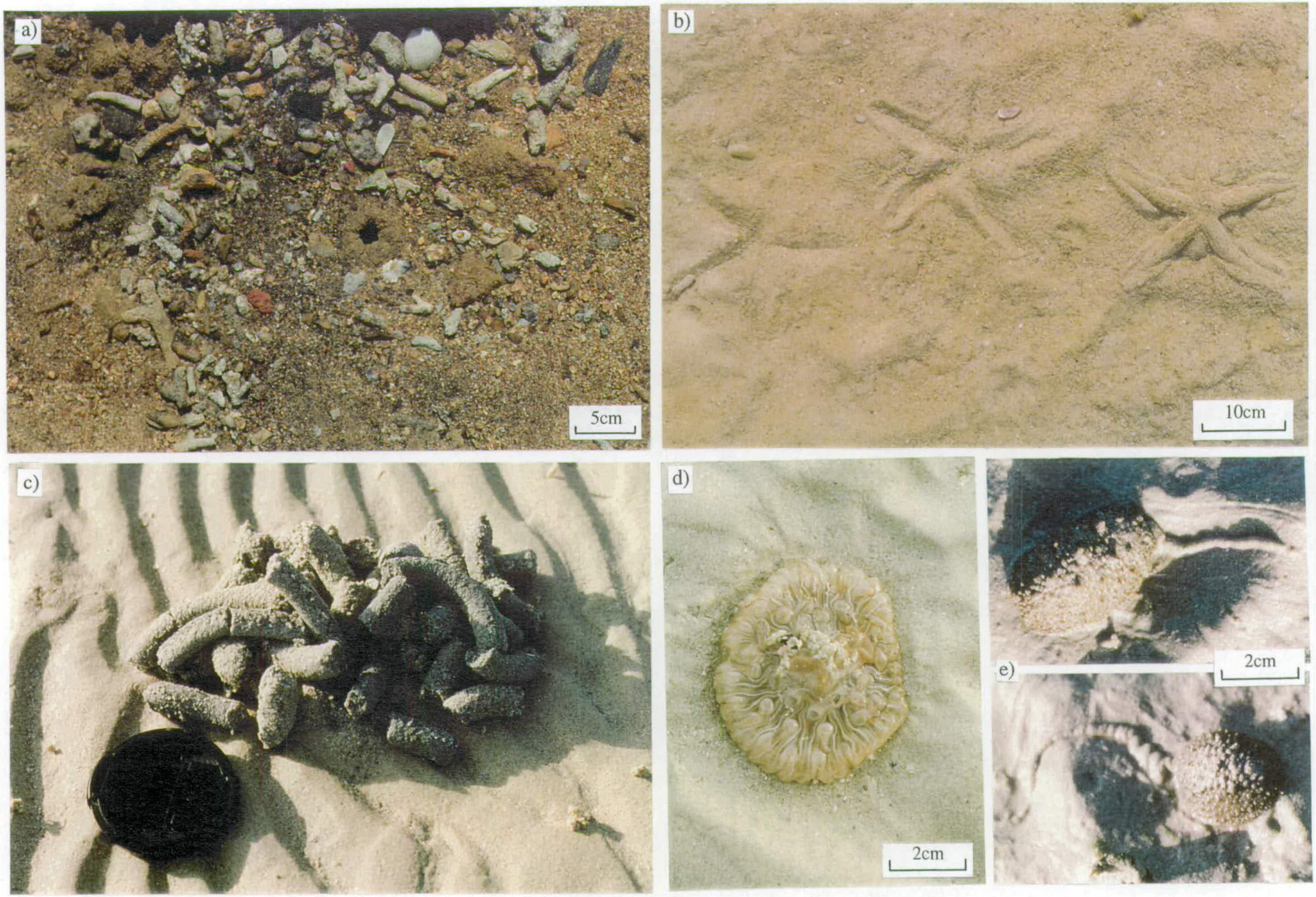


Plate 3.9 Surface intertidal bioturbation in Tang Khen Bay. **a)** stomatopod shrimp burrow - note central hole ringed with a paler 'flap' and excavated debris about 10-15cm away. **b)** Starfish (*Astropecten* sp.) has moved left to right leaving resting traces. **c)** Sipunculid worm cast - anoxic sediment from below the sediment surface is ejected at the surface. **d)** Burrowing anemone - note faint radial traces surrounding it. **e)** *Onchidium*, a pulmonate gastropod, leaving faecal trails.

On the beach itself, ghost crab (*Ocypode* sp(p).) burrows spiral down at the top of the beach, through loose, dry surface sand into the damp and more compacted sand below (Plate 3.7c). These burrows have a very restricted vertical distribution in the bay; the beach itself is only a few metres wide, and large ghost crabs are found only at the top of the beach, i.e. at around the spring high water mark. Smaller ghost crabs are seen burrowing and running around the lower areas of the beach at low tide and their tracks can be seen as a series of scratchy trails criss-crossing the sand. Both large and small ghost crabs leave radial scratch marks around their burrow entrances (Plate 3.7c), made while shovelling sand out of the burrow entrance. Loose excavated sand is flicked by the crab to a distance of up to 30-40cm away from the burrow entrance.

Small cockle-type bivalves inhabit the lower reaches of the beach; local villagers harvest these at low tide by digging in the sand to a depth of about 10cm with a small tool or spoon. The bioturbatory effect of these molluscs is unknown, and no obvious surface traces are visible.

Numerous other animals use the sediment in Tang Khen Bay. In the pools between the sand waves at low tide, small crabs make trails that radiate out from a central burrow (Plate 3.8c), the starfish *Astropecten* forms star-shaped resting traces (Plate 3.9b), sea cucumbers (synaptids, and juvenile *Bohadschia* sp.) feed on the surface sediments while feeding and tiny anemones are visible in the sediment around half-buried rocks. Swimming crabs rapidly bury themselves in the sediment when startled and tiny hermit crabs (occupying *Bathylaria* shells) are locally abundant (Plate 3.8a).

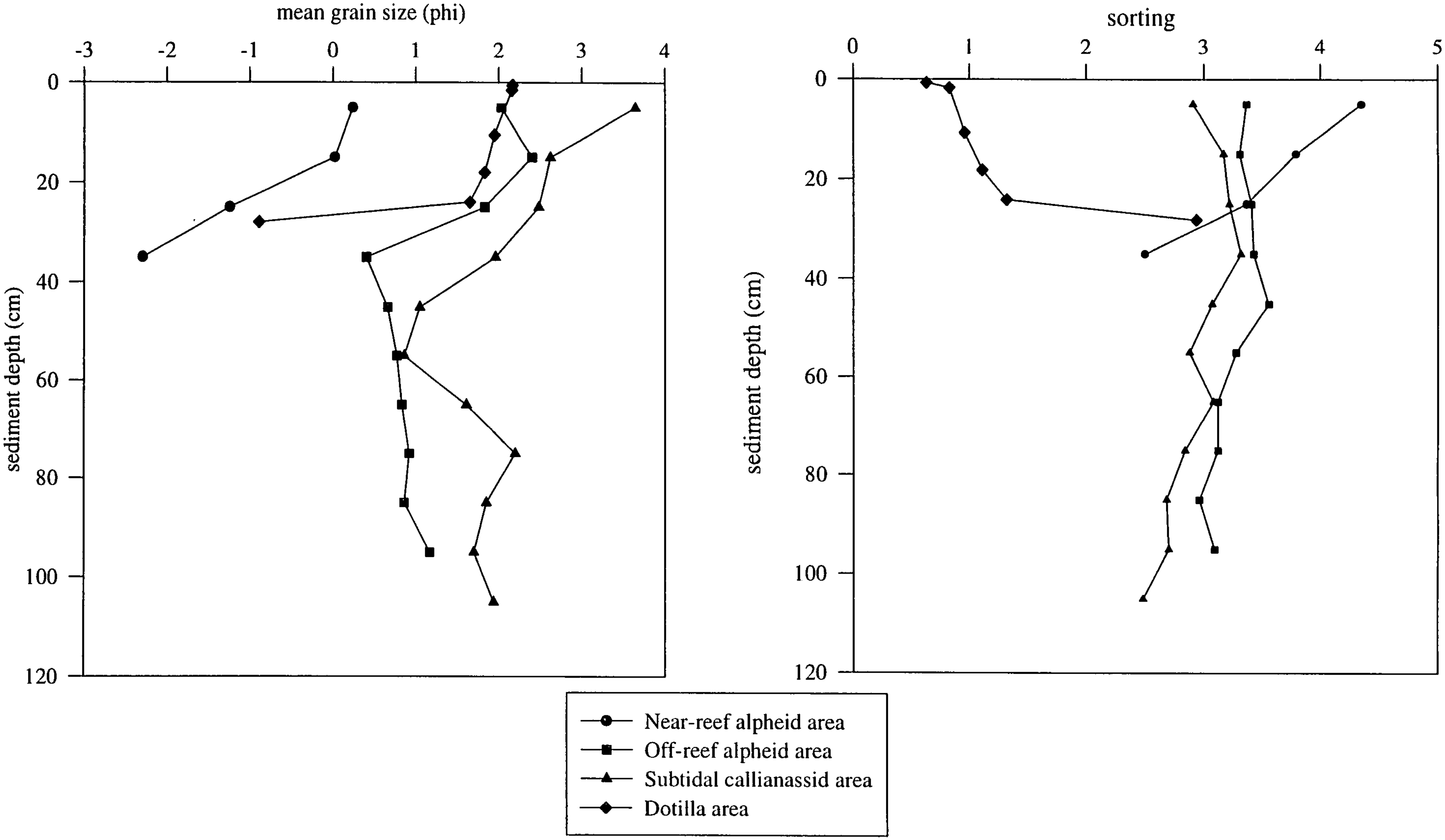
In the wet sediment at the pool edges, two types of gastropod snail make meandering trails in the surface sediment (Plate 3.8b and c) and *Dotilla* chimneys (Plate 3.1c), occasional burrowing anemones (Plate 3.9d) and large stomatopod burrows (5-6cm diameter; Plate 3.9a)) are also seen.

In the sand waves themselves, thin red polychaete worms are common in smooth-walled branching burrows, and at the low tide mark, adult *Bohadschia* sp. lie half buried in the sediment (Plate 3.8d), and occasional burrowing sea pens are seen. Large ghost crabs live on the inner sand waves, only emerging at night; big excavation pellets are formed as they dig their burrows which are wide curved tubes (Plate 3.7b). The outer sand waves contain abundant sipunculid worms that create thick casts on the surface (Plate 3.9c). These worms are used as fish bait by the locals. These worms are head-down deposit feeders, forming centimetre-thick mucus-lined burrows to at least 50cm within the sediment. At these depths in the sediment the grains have a wide size range and there is a high proportion of coarse material. However, the casts at the surface comprise mainly 125-250µm size fraction (Appendix C); the worms must be feeding selectively on this size fraction.

At high tide, the whole bay is submerged and fish come in to feed. These include rays (up to a body diameter of 30cm were seen), which can create large depressions in the sediment during feeding (visually estimated as being up to about 15cm deep by 40cm wide) and also partially bury themselves while at rest, which would stir up the top ?5-10cm), goatfish (especially *Upeneus tragula* which feeds on the sediment surface using its barbels to stir up the top few cm), mullet (which feed in shoals on the sediment surface, creating small depressions, a few cm diameter by 1cm deep, as they dart at the seabed), mojarras (which also make small individual feeding depressions), and occasional small morays and flatfish.

In the muddy sediments at each end of the bay, *Dotilla* is absent and abundant fiddler crabs (*Uca* sp.?) are seen making simple oblique burrows into the wet mud (Plate 3.7d). *Onchidium*, a pulmonate mollusc is also patchily common, and leaves cylindrical trails of faecal material on the sediment surface (Plate 3.9e).

Figure 3.11 Trends in mean grain size and sorting in intertidal and subtidal sediments.



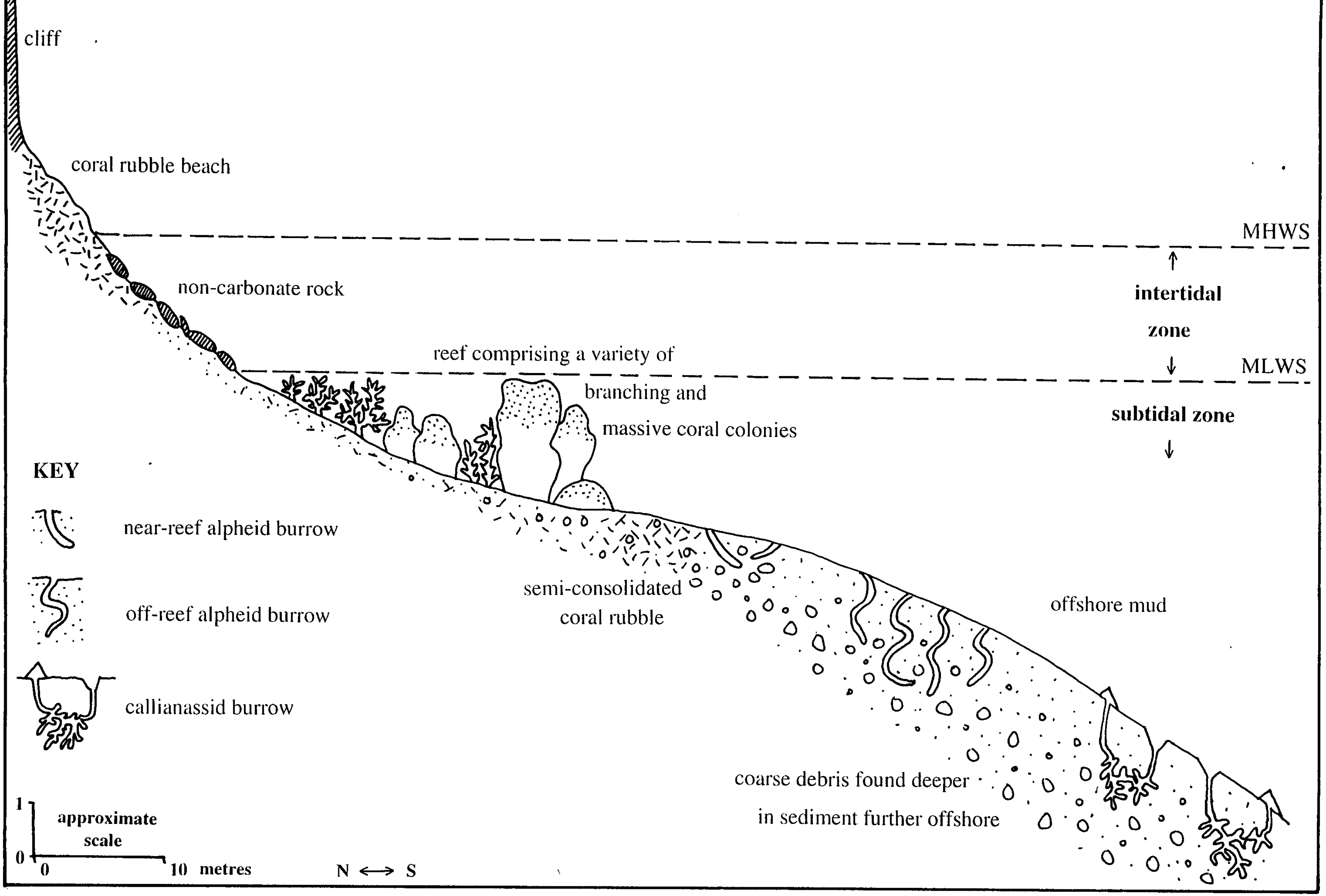


Figure 3.12 Schematic vertical section through Pump House Bay to illustrate the zonation of burrowers.

3.4 SUBTIDAL BIOTURBATION

The study site, Pump House Bay, is described in section 1.3.2. An illustration of the distribution of burrowers is given in Fig. 3.12.

3.4.1 Callianassids

Classification: Phylum Crustacea, Order Decapoda, Infraorder Thalassinidea Latreille 1831, Superfamily Thalassinoidea Latreille 1831, Family Callianassidae Dana 1852.

The method of de Vaugelas (1985), as described in section 1.5.1.10, was used to try and capture the shrimps for identification and for observation in sediment-filled aquaria. However, no animals were caught; the identification of the animals was therefore impossible, and they can only be assumed to be callianassids by their burrow structure.

3.4.1.1 Burrow structure and formation

As in intertidal callianassids, the surface features of the burrow are a crater (or craters) and a mound. In order to find out which burrow openings were connected below the sediment surface, a concentrated solution of red food colouring was injected into the burrow at the base of the inhalent shaft via a plastic tube attachment to the syringe. The appearance of red colouring at other entrances in the vicinity was expected but failed to happen, although subsequent excavation revealed the interconnection of entrances in the area. The burrow volumes may have been large enough to effectively 'absorb' the marker liquid, despite large quantities (up to 50ml) of fairly concentrated solution being used. Underwater visibility was also so poor, due to suspended fines in the water, that it is possible that the diluted marker fluid exiting the burrow elsewhere may not have been seen.

This methodology was not investigated further as it was usually obvious which burrow entrances were part of the same burrow system, due to the low density of burrows.

Resin casting and excavation showed that subtidal callianassids have a complex subsurface network of passages linked to a single surface crater and single mound (Fig. 3.7, 3.13. 3.14. 3.15 and Plate 3.5e). The vertical shaft leading down from the crater is permanently open and takes the form of an inverted, elongated cone of approximately 6cm diameter at the surface, tapering to about 1.5cm diameter by a depth of 25cm where it curves to meet the chambered section of the burrows. The vertical shaft below the mound is

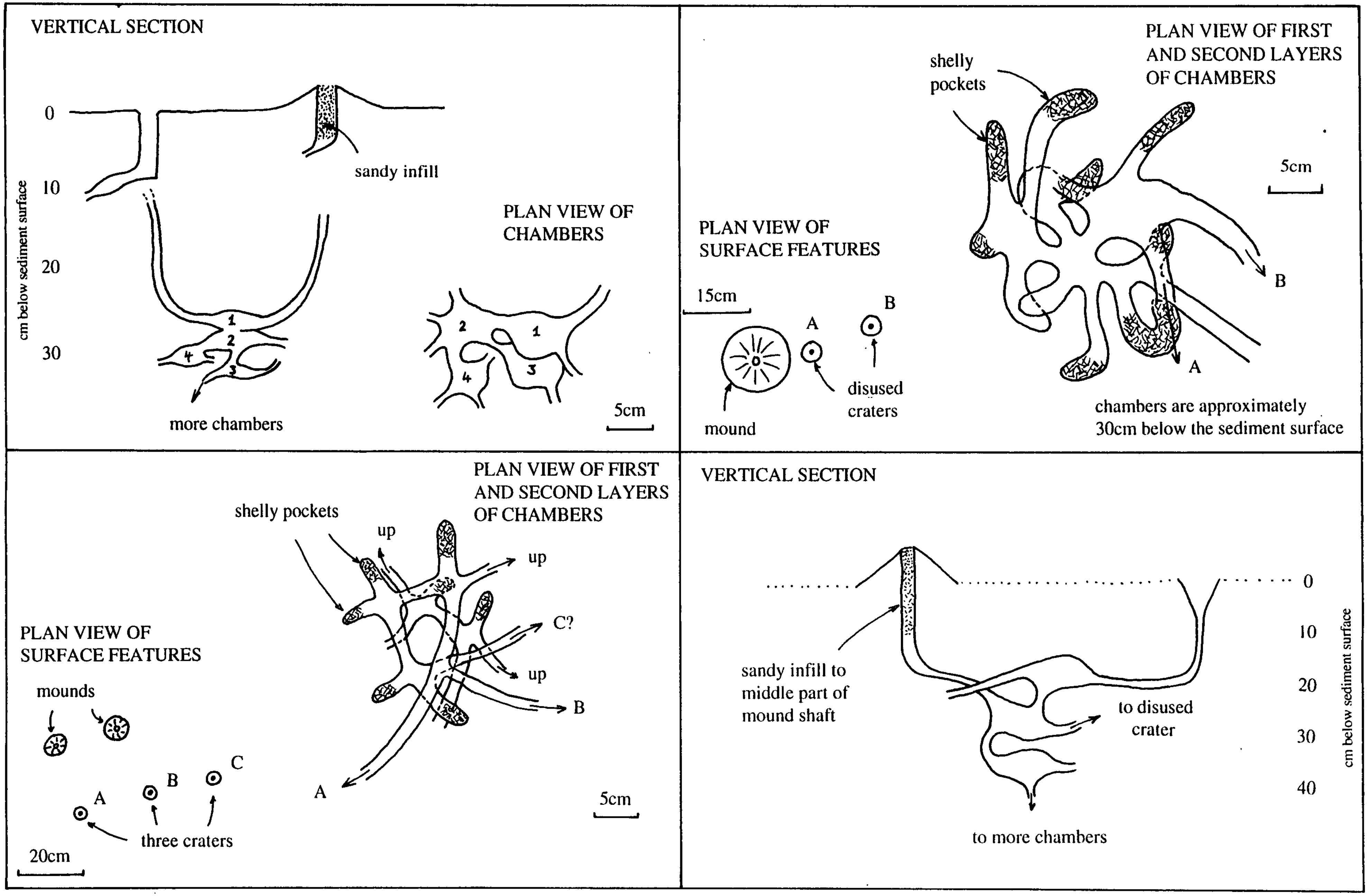


Figure 3.13 Structure of four subtidal callianassid burrows, as revealed by airlift excavation and resin casting.

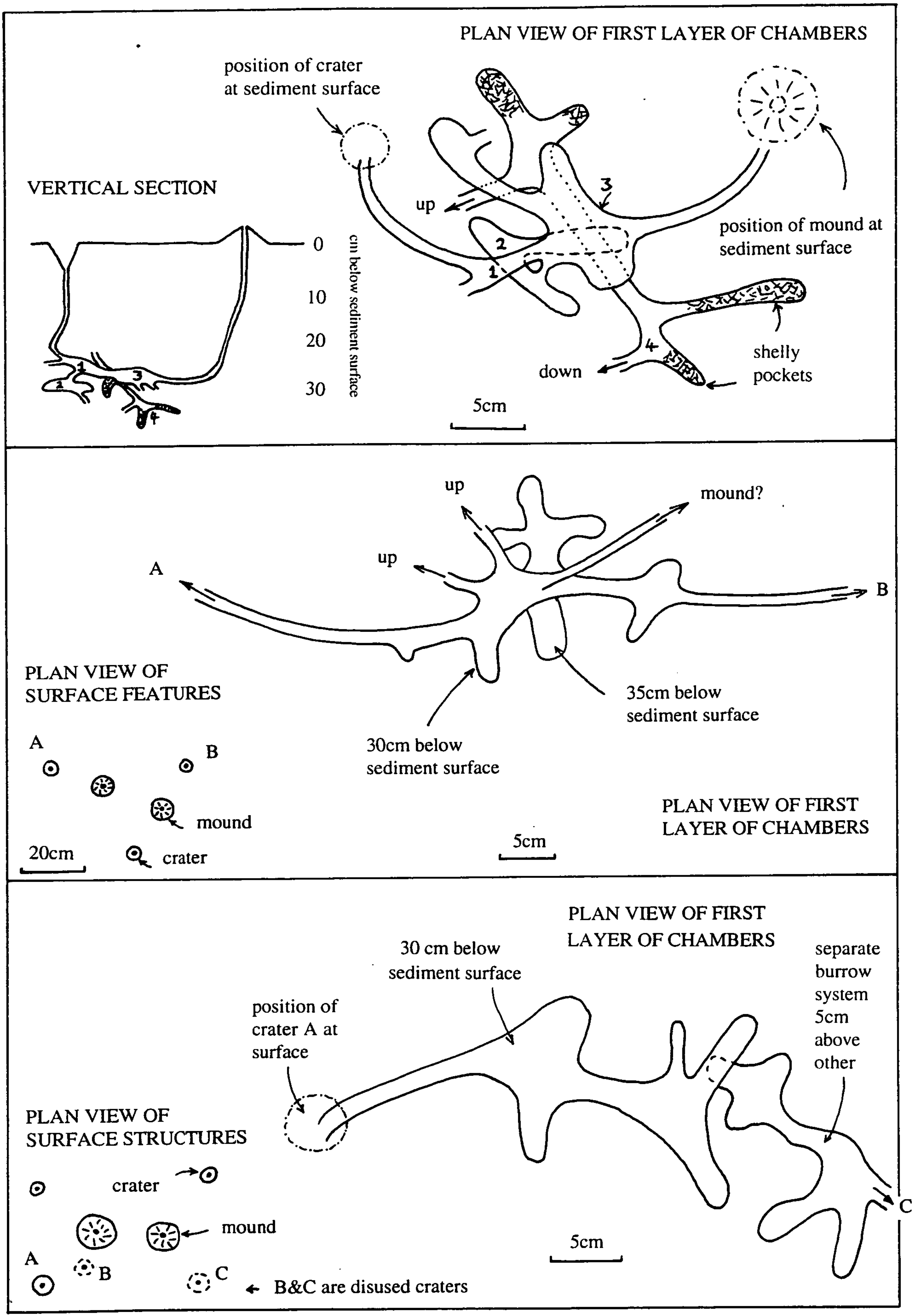


Figure 3.14 Structure of three subtidal callianassid burrows, as revealed by airlift excavation and resin casting.

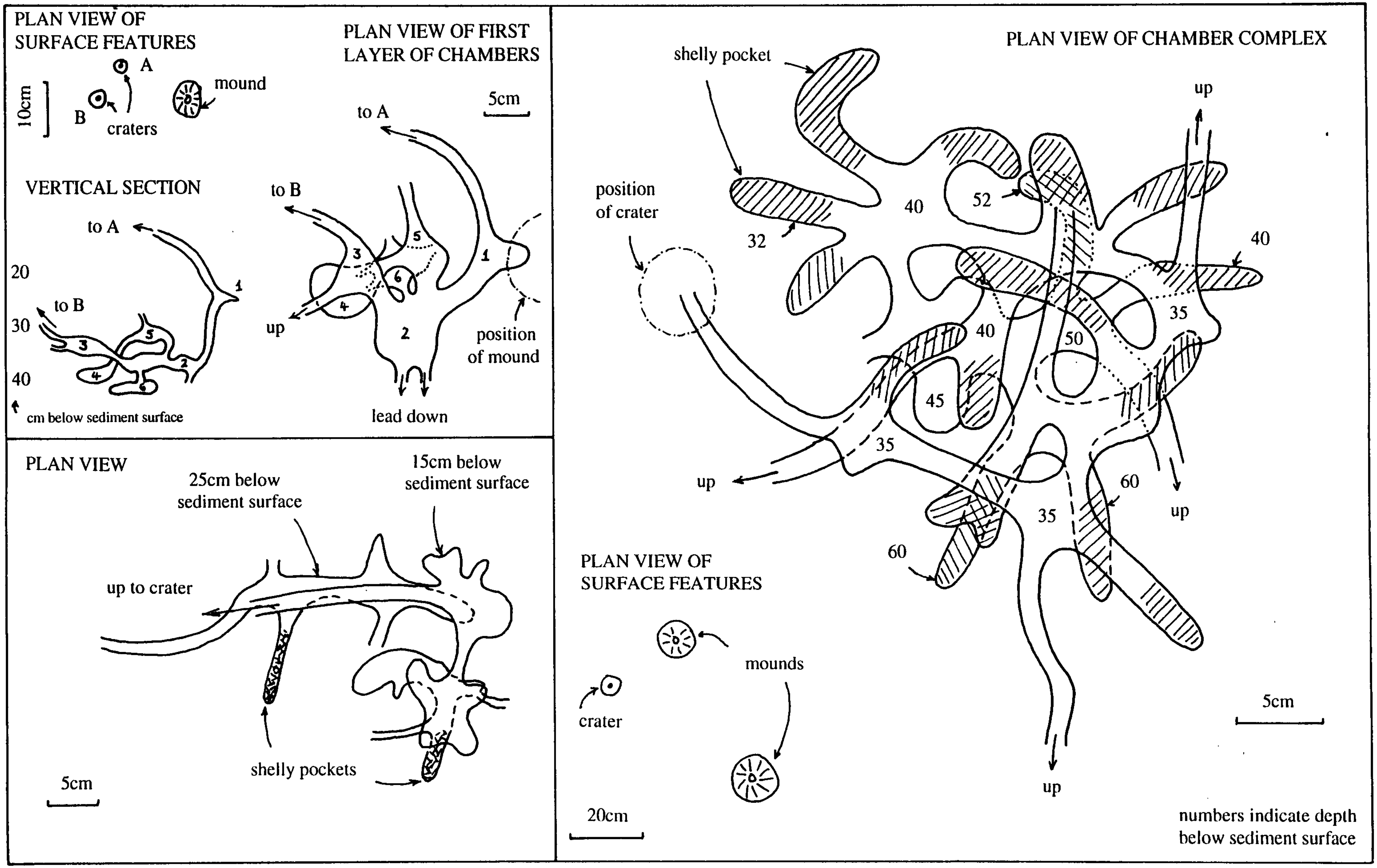


Figure 3.15 Structure of three subtidal callianassid burrows, as revealed by airlift excavation and resin casting.

blocked at the surface, opening out at about 10cm sediment depth to form a narrow (0.5cm) hole. Many craters had other small (<1cm diameter) burrows leading off horizontally at the top of the crater. Alpheid shrimps were occasionally seen at the mouths of these burrows, but it is probable that a range of animals could make burrows in this well-ventilated but sheltered environment.. It has been suggested that burrow linings are only necessary in unstable sediments such as carbonate sands. However, their presence in these muddy Phuket sediments suggests that this is not so. It is more likely that animals such as callianassids that feed and respire by creating a water current through their burrow require smooth walls in order to create an efficient flow.

The subtidal burrows are smaller than the intertidal callianassids, with a mean mound diameter of 11.3cm (st. dev. = 3.4, n = 23), mean height of 2.5cm (st. dev. = 1.34, n = 15) and shaft diameter of 1.5cm (see Appendix C). The burrow complex of the subtidal shrimps also has a different structure, being more a branching network of smooth-walled tunnels and blind endings rather than having large chambers. This structure is similar to that described by Shinn (1968) in Florida and the Bahamas and by Nickell and Atkinson (1995) in the Clyde, Scotland.

Subtidal tracer sediment experiments were used to investigate the fate of sediment that falls into the crater. Twenty grams of tracer were poured into six separate craters (2g of 63-125µm, 2g of 125-250µm, 2g of 250-710µm, 2g of 710µm-2.36mm, 2g of >2.36mm, 10g of >5mm, of various fluorescent colours). The burrows chosen were at least 5m apart to

Table 3.3: Sampling schedule for the tracer sediment experiments on subtidal callianassid burrows

Day	Burrow 1	Burrow 2	Burrow 3	Burrow 4	Burrow 5	Burrow 6
1	20g tracer applied to all burrow craters					
2			4 cores taken			
3	extra 20g tracer	extra 20g tracer		extra 20g tracer	airlifted	
4	mound sampled	mound sampled		mound sampled		
5						8 cores taken
6		airlifted, 3 samples				
17	airlifted, 1 sample					
19				airlifted, 3 samples		

avoid any possible mixing of tracer from separate experiments. Three of the burrows had a second, 20g dose of tracer added two days later to give a stronger signal. Two burrows were sampled by taking tube cores through the burrow area (through the mound, next to the crater, between the mound and crater) and the other four were airlift-excavated and careful notes taken of where tracer was seen within the burrow. Some samples were also taken during the airlifting using a pocket corer. Mound sediment samples were taken from three of the burrows. Details of the sampling procedure are given in Table 3.3.

Any samples taken were washed to remove the majority of the <63μm fraction, which otherwise coated the tracer grains, making them difficult to see, even under UV light. The samples were then analysed on a simple presence/absence basis for each tracer size fraction, as described in section 1.5.1.6. The results are shown in Table 3.4 below.

Table 3.4: Results of tracer sediment size fraction distribution in samples taken from subtidal callianassid burrows.

Day of sampling	**Sample description**	**Tracer sediment size category**					
		63-125μm	**125-250μm**	**250-710μm**	**710μm-2.4mm**	**>2.4mm**	**>5mm**
4	from mound 1	X	X	X	X	O	O
4	from mound 2	X	X	X	X	O	O
4	from mound 3	X	X	X	X	O	O
6	from shelly patch outwith burrow 2	X	X	X	O	X	O
6	chamber lining from burrow 2	X	X	X	X	X	O
6	chamber lining from burrow 2	X	X	X	O	X	X
17	from shelly pocket of burrow 1	X	X	X	X	X	X
19	from shelly patch outwith burrow 3	X	X	X	X	X	X
19	burrow lining from burrow 3	X	X	O	O	X	O
19	from shelly pocket in burrow 3	X	X	X	X	X	X

KEY: X = present, O = absent

From Table 3.4 it can be seen that a wide range of grain sizes are incorporated into the shelly pockets. These pockets are finger-like projections between 5-10cm long and 1.0-1.5cm wide leading off the main burrow complex. They are packed with randomly orientated grains which appeared *in situ* to comprise a coarse sand- to gravel-based fill, though from these tracer experiments it is clear that all grain sizes are present. Table 3.4 is based only on presence/absence data, not relative abundances of different grain sizes which would have shown the dominance of the coarser fractions. Likewise, the burrow passage and chamber linings also contained a wide range of grain sizes, though they appeared fine-grained and were smooth to the touch. A high concentration of black organic matter was present in some shelly pockets. Whether this is utilised by the shrimp as a food source, as suggested by Suchanek (1985) and Dworschak (1987b) is unknown. Only a few of the pockets contained this organic matter, so it may be that the shrimp does not actively collect organic matter but may stash and use any that happens to fall into the crater.

Tracer counts from cores are not discussed as it was found that downward movement of tracer by the coring process itself obscures any tracer signal from biogenic movement (section 1.5.1.6). The only viable tracer result was from a core taken through the sediment between the mound and crater. Here, there was no tracer on the surface but a strong signal at 17-18cm below the surface, where there was abundant 63-250μm tracer and a few grains up to gravel size. This can only be due to the movement of tracer grains through the burrow system from the crater.

Movement of burrows

Observations on marked burrows showed that craters moved roughly every two days, in contrast to intertidal callianassids whose craters were completely stationary. This movement was not a gradual migration , as seen in the mounds, but an abrupt shift of up to about 15cm, suggesting that an entire new vertical shaft was being dug. However, few burrows were monitored and observations could only be made over a period of 6 consecutive days during neap tides due to diving conditions deteriorating during spring tides. Methods such as time lapse photography during springs were not possible due to the poor water clarity (0.5-1m horizontal visibility). Dives carried out at the earliest opportunity after the worst of the spring tides showed that over the spring tide period the sea bed is smoothed and flattened by the strong currents, infilling burrow craters and flattening the mounds. No open craters were seen, which suggests that no attempt is made to clear the craters during spring tides; this would certainly be a very time- and energy-consuming activity. Ejection of sediment at the surface may still continue, but it would be rapidly transported from the area. The other alternative is that the shrimps cease activity altogether, wait for the strong currents to subside and then reopen their craters and create new mounds. The craters probably only fill down to the bottom of the vertical shaft, as the right-angle bend at that point tends to block quickly and prevent sediment getting further into the burrow (observations from resin casting and airlift excavation).

3.4.1.2 Sediment texture

The active sediment sorting by these shrimps (burying large grains in shelly pockets at depth and ejecting fines at the surface) and passive burial of coarse material by the fine sediment mounds should, in time, result in a well-sorted upper layer with remnants of old vertical shafts to the depth at which the first subsurface chambers and shelly pockets occur, and below this a heavily burrowed coarser layer full of these chambers and pockets. This layering has been described by other workers such as Tudhope and Scoffin (1984).

Old shafts and were seen in the top 10-20cm of sediment around the burrows, characterised by sand-filled, smooth-walled vertical tubes. Shelly pockets were abundant branching off the burrow and patches of coarse debris were also found outside the burrows in the surrounding sediment; these could be relict shelly pockets. This sediment around the complex part of the burrow (deeper than 25-30cm below the sediment surface) thus had a heavily burrowed appearance. A slight increase in mean grain size was seen at a depth of about 40-50cm (Fig. 3.11) which corresponds with the depth of the shelly pockets, but this is more likely to be a storm deposit (see section 4.6). The topmost sediment was not particularly well sorted, suggesting that the shrimps were either not abundant enough or had not inhabited the sediment for long enough to have a major sorting effect. Tiering or storm effects again may have played a role in the appearance of these upper layers (see sections 4.6.3, 4.6.4). General sediment descriptions were made of cores taken throughout the area; see Fig. 3.24.

3.4.1.3 Rates

Rates of sediment turnover were calculated on the basis of an average sized crater being excavated every 2 days. Crater sizes were calculated using the formula "Volume = $\frac{1}{2}\pi r^2 d$", where r is the radius (cone diameter is 6cm at the sediment surface) and d is the depth (25cm) of the inverted cone-shaped crater. The average volume was $353cm^3$.

Callianassids were found in densities of $24/100m^2$ (as counted along a belt transect). A turnover rate of $0.015m^3/m^2$/year (or $24.7kg/m^2$/year; subtidal sediment density = $1.54g/cm^3$; Appendix B) was calculated. This is equivalent to a layer 25cm thick being completely reworked in 16 years. These figures are certainly underestimates as they do not take into account the reworking of sediment that falls into the crater or sediment that is reworked from parts of the burrow other than the crater and associated shaft.

3.4.2 Alpheids

Two types of subtidal alpheid were seen:

i) subtidal near-reef; a small (5cm long) species in the coarse sediments close to the reef front, and

ii) subtidal off-reef; a large (7cm long) species in the sediments approximately 50m from the reef front.

Both were commensal with gobiid fish; see Karplus 1987 for details of this association.

Near-reef gobies were identified by Ukkrit Satapoomin at PMBC as *Ctenogobiops crocineus* Smith 1959, *Cryptocentrus strigilliceps* (Jordan & Seale 1906), *Cryptocentrus leptocephalus* Bleeker 1876 and an undescribed species of *Cryptocentrus*. Off reef gobies include *Mahidolia mystacina* (Valenciennes 1837), *Amblyeleotris fontanesii* (Bleeker 1852), *Amblyeleotris gymnocephalus* (Bleeker 1853) and *Amblyeleotris steinitzi* (Klausewitz 1974).

3.4.2.1 Burrow structure and formation

The near-reef alpheid burrow structure is very similar to the intertidal type; the burrows slope downwards, from a single entrance, at an angle of 30-45° to depths at which most of the sediment comprises cobble- to boulder-size reefal fragments. In the subtidal near-reef environment this occurs at about 15-25cm sediment depth. The irregular burrow morphology also seems to be determined by the presence of large pieces of reef debris, which are abundant in the sediments they inhabit. A roughly spiral form was seen in some of the burrows excavated but others twisted randomly from left to right while others were quite straight (Fig. 3.16). A smooth floor was always present and side walls and ceilings were more uneven. Airlift excavation showed the remnants of side branches leading off the main burrow at sediment depths of 5-10cm. These had not been visible from the surface and are therefore assumed to have been infilled in the top layers of the sediment. These disused shafts stood out against the surrounding clayey surface sediment due to their gritty texture and pale brown oxidised coloration.

Off-reef alpheids living further from the reef in a greater thickness of fine sediment are not limited by buried reefal debris, and form spiral burrows which turn in a

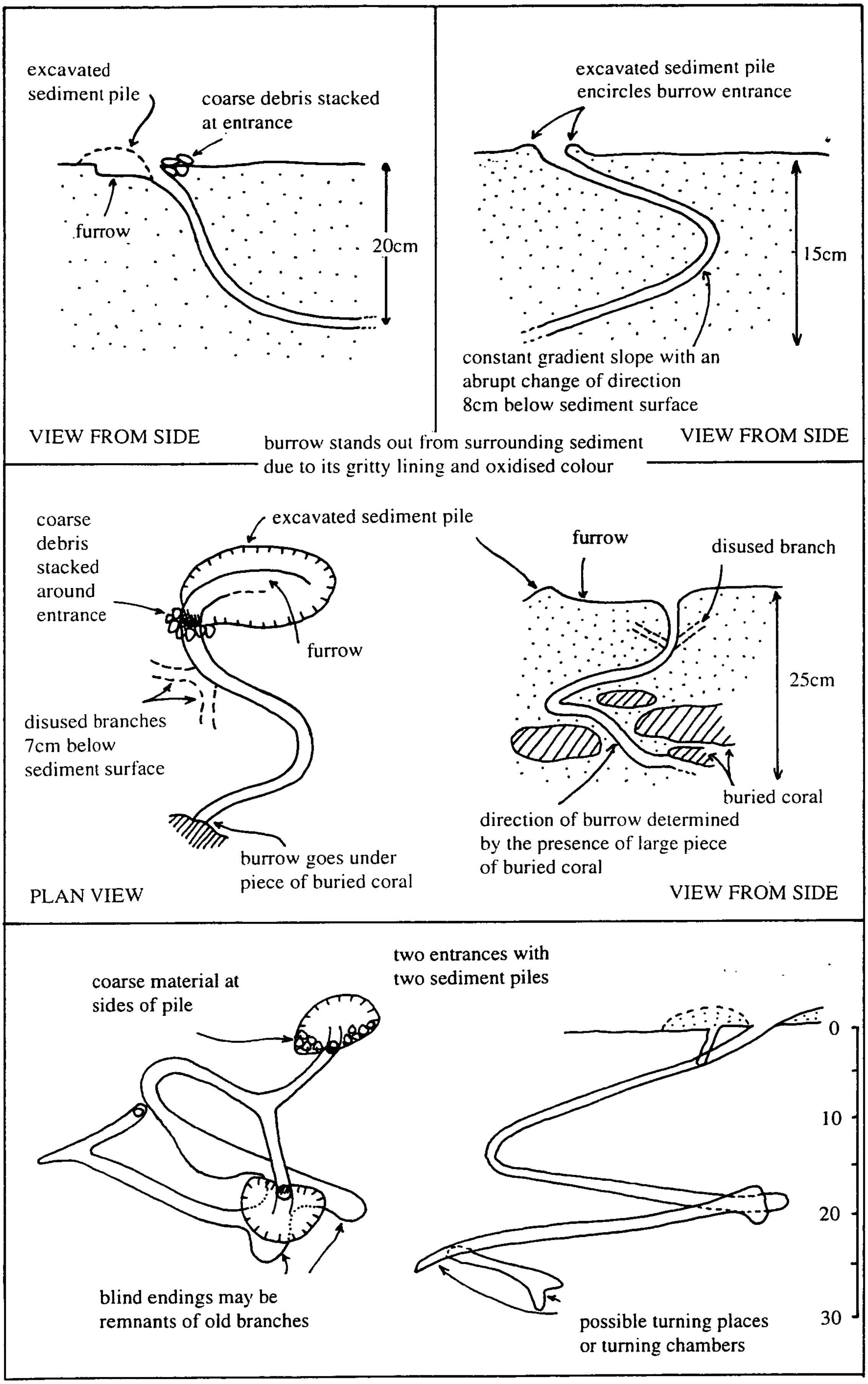


Figure 3.16 Structure of four near-reef alpheid burrows, as revealed by airlift excavation.

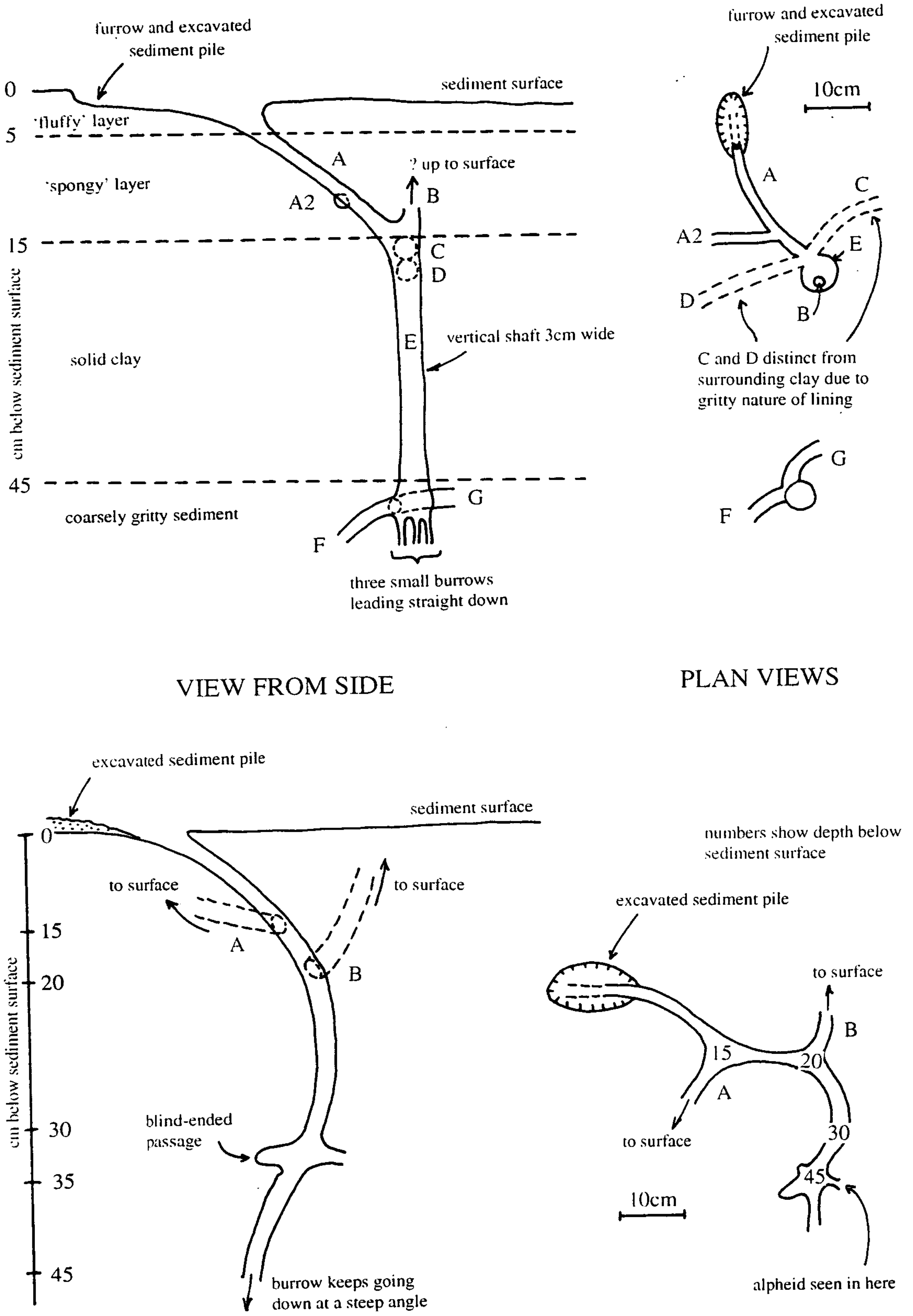


Figure 3.17 Structure of two off-reef alpheid burrows, as revealed by airlift excavation

clockwise or anticlockwise direction and reach depths of at least 50cm (Fig. 3.17) However, variation from this basic form can be substantial, especially deeper in the sediment. Unfortunately, c.50cm was the limit of airlifting, so only two burrows were excavated this deep. One combined airlift and resin casting also reached this depth. The first burrow to be airlifted showed an abrupt right angle bend at 45cm after which the burrow continued down at a shallow angle. Several narrow vertical shafts also lead off the bottom of this bend, but these may have been made by another animal, as they were much too narrow for an alpheid or goby to enter. This burrow also had a wide (3cm) vertical part between 20 and 45cm. The other burrow had three exits leading horizontally off the main burrow at 35 cm sediment depth. Two of these were dead end tubes, and the third (which may also have been a dead end) contained the shrimp itself. This may have been an area in which the shrimp could turn around, although this was not seen in other burrows. It is possible that other burrows contained more subtle turning points, such as slight widenings at old burrow branches. Wide points at angled corners in the spiral may also be used as turning points. See Fig. 3.17 for drawings of these burrows. Like the near-reef burrows, the subtidal burrows had smooth floors and more uneven ceilings and also showed evidence of old tunnels leading upwards to the surface. The disused surface passages branched off from the main burrow at sediment depths of 15-20cm and must have been blocked in the upper parts as they were not visible at the surface. The structures seen in Phuket are unlike those of Shinn (1968), the only study to have described such deep alpheid burrows as these. The burrows he describes are more similar to those of callianassids, with intricate branching networks suggesting mining of the deep sediment for food. In Phuket, it is the repeated digging of branches to the surface which provides food for the shrimp.

The gobies are not involved in burrow excavation, but alpheids shovel sediment from depth to the sediment surface. The near-reef alpheids separate out coarse and fine grains at the surface, stacking coarse debris above the angled burrow entrance and piling fines to one side. Off-reef alpheids do not sort grains, but simply pile sediment to one side of a shallow groove leading from the burrow entrance. Two-entrance burrows are common in off-reef alpheids; the two entrances are in line with the excavated pile and join in a shallow U-shape a few centimetres below the surface.

The sediment in the piles at the surface is mainly from new burrow entrances that are dug upwards from the deeper, more permanent part of the burrow; a proposed mechanism for this is shown in Fig. 4.7. Evidence for this comes from airlift excavation and tracer experiments as described below.

Off-reef alpheids (tracer experiments)

A 20g dose of tracer sediment (2g of 63-125µm, 2g of 125-250µm, 2g of 250-710µm, 2g of 710µm-2.36mm, 2g of >2.36mm, 10g of >5mm) was poured into the entrances of six off-reef alpheid burrows. The burrows were marked with a flag pushed into the sediment exactly 25cm due North of the burrow entrance.

Core samples were taken between 1 and 5 days later (see Table 3.5) through the area of the burrow and tracer grains quantified throughout the cores. The burrow entrance movement and core positions are shown in Fig. 3.18.

Table 3.5 Timetable for the tracer experiments on subtidal off-reef alpheid burrows

Day	Burrow 1	Burrow 2	Burrow 3	Burrow 4	Burrow 5	Burrow 6
0	20g tracer applied to all burrow entrances					
3/4		3 cores taken				
1			4 cores taken			
3	flag seen drifting - experiment abandoned			4 cores taken		
4					4 cores taken	
5						4 cores taken

Note: Day 3/4 = 17 hours after the initial tracer was applied

All cores taken from these alpheid burrows showed greater amounts of tracer at the surface, dropping off with depth down the core and abundance of tracer at the surface was strongly related to the amount seen in the core. These results can not be distinguished from the burial of tracer by sampling (section 1.5.1.6), so are not used in the following discussion. However, it is possible to use the relative abundances of surface tracer along with observations taken underwater regarding the distribution of tracer at the time of coring to make the following points:

1. All grain sizes are shovelled out of the burrow entrance; there is no sorting.
2. Disused burrow entrances (cores 3i, 4i, 5i, 6i) always showed high concentrations of tracer. Tracer is also seen 20-30cm down the cores but this must be assumed to reflect the smearing of tracer by the core process rather than the incorporation of tracer deep into the sediment by the shrimp.
3. Disused excavation piles also show abundant tracer (cores 3ii, 4ii, 5ii, 6ii), usually in even greater amounts than in the disused burrow entrance cores.

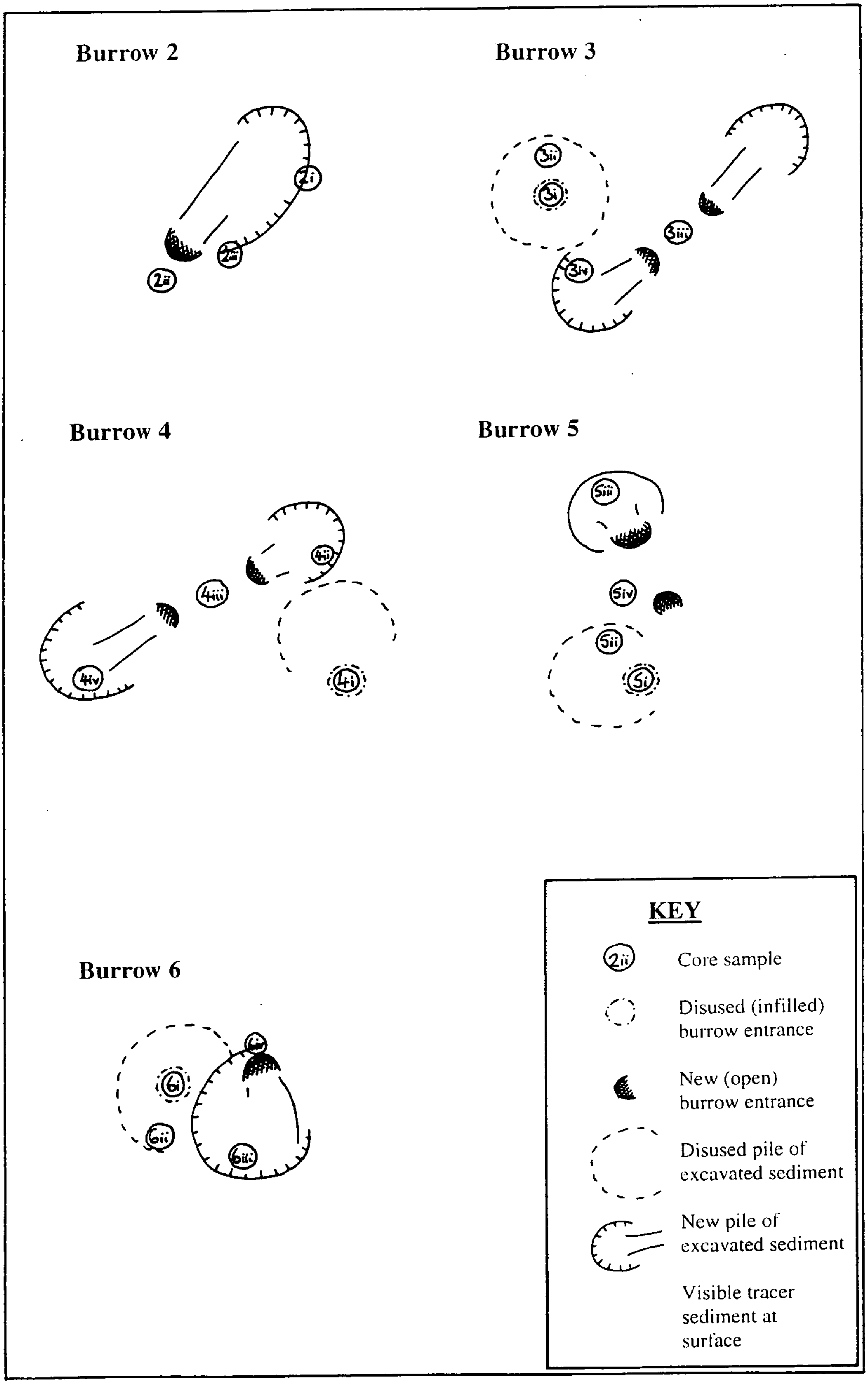


Figure 3.18 Schematic diagrams of the moving surface features of five off-reef alpheid burrows with the positions of cores taken for tracer sediment analysis (see section 3.4.2.1).

4. Newly excavated piles show negligible amounts of tracer (cores 2i, 3iv, 4ii, 4iv, 5iii, 6iii).

5. Newly formed burrow entrances also show negligible amounts of tracer (cores 2ii, 3iii, 4iii, 5iv). Core 6iv is the exception to this, but can probably be explained by the proximity of this core to the disused pile of excavated sediment.

To conclude, tracer sediment that is placed in the entrance of the alpheid burrow is shovelled out on to the sediment pile almost immediately. Thus, high concentrations are seen in the burrow structures present at the time the tracer was laid but low concentrations are seen in the new structures formed after the tracer has been shovelled out of the old burrow entrance.

Near-reef alpheids

Eighteen near-reef alpheid burrow entrances were marked with a flag pushed into the sediment exactly 22cm North of the entrance and sketches drawn of the relative positions of the entrance and excavated pile. One day later the positions of the entrances were measured relative to the flag and pile positions redrawn. Fifteen out of the eighteen burrow entrances (i.e. 83%) had moved (c.f. 75% Karplus et al 1974). The remnants of the old entrances were small, infilled depressions on the sediment surface covered with a fine layer of fine, brown organic matter. One entrance (i.e. 6%) had not moved at all and two (= 12%) had disappeared completely. All the 15 that had moved were recognisable nearby as holes with freshly excavated sediment. Details of the movements of seven of these burrows were mapped and are shown in Fig. 3.19. The maximum distance moved was 20cm, though 10cm was the norm, and there was no directional effect involved in the movement. Entrances were moved in all directions of the compass and factors such as the dominant E-W current in the area had no influence on the positioning of the new entrances.

Off-reef alpheids

Quadrat experiment

Five off-reef alpheid burrows were selected for observation, the selection criteria being that they were visible from the reference transect line and that they were at least one metre away from any other alpheid burrow. A 100x100cm quadrat was placed over each burrow in turn, so that the burrow lay roughly centrally in the square, and the burrow entrance's position noted as a x-y coordinate. The coordinate (0,0) was taken as one of the corners of the quadrat which had been marked with a metal stake. The opposite corner (i.e.

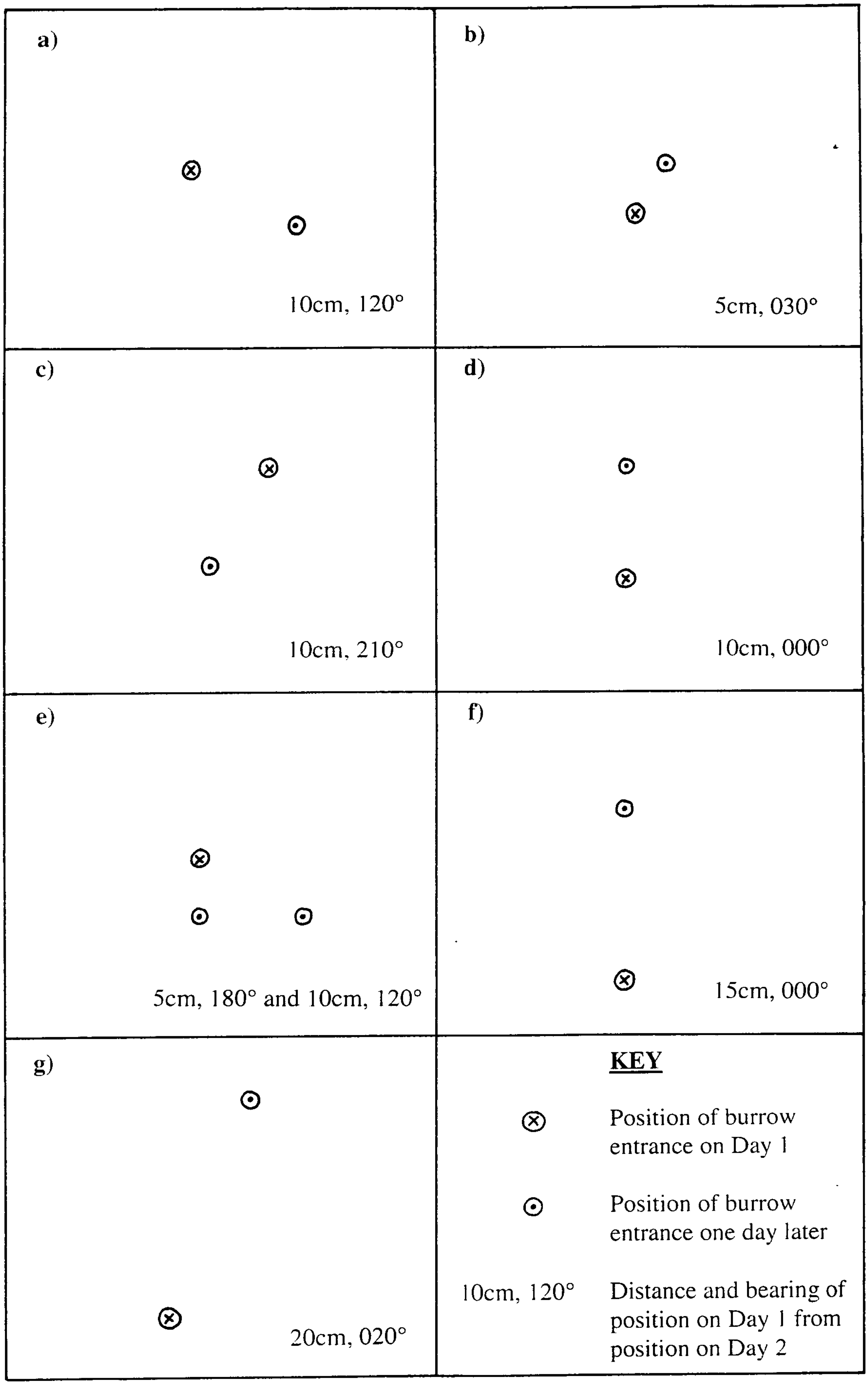


Figure 3.19 Seven examples of the movement of the upper parts of near-reef alpheid burrows, with distance moved (to the nearest 5cm) and direction of movement (to the nearest 10°).

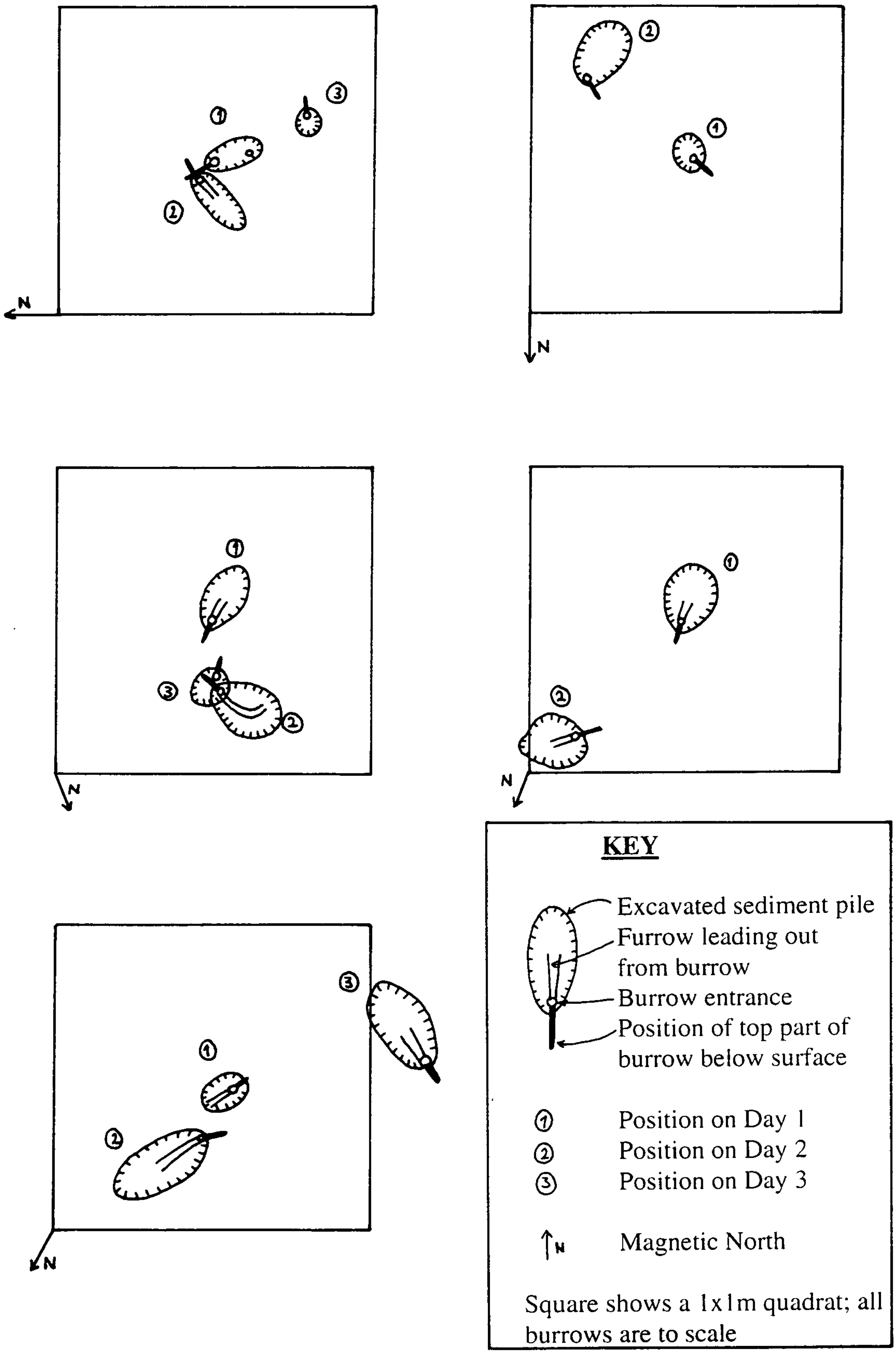


Figure 3.20 Five examples of the movement of the upper parts of off-reef alpheid burrows.

(100,100)) was marked with a second, shorter stake. Sketches were drawn of the relative sizes and positions of the sediment pile and burrow entrance, and the position of the burrow just below the surface estimated from what could be seen through the burrow entrance. A bearing of this burrow relative to North was taken. The burrows were remapped one and two days later in the same way. Results are shown in Fig. 3.20 and in Table 3.6 below

Table 3.6 Coordinates and bearings of off-reef alpheid burrow entrances on successive days.

Quadrat number	**Burrow entrance coordinates on Day 1**	**Distance moved (Day 1 to Day 2)**	**Bearing of position on Day 2 from that of Day 1**	**Burrow entrance coordinates Day 2**	**Distance moved (Day 2 to Day 3)**	**Bearing of position on Day 3 from that of Day 2**	**Burrow entrance coordinates Day 3**	**Distance moved (Day 1 to Day 3**	**Diameter of circle of influence of burrow**
1	(55,45)	17	358°	(47,30)	75	221°	(118,55)	64	75
2	(50,50)	7	315°	(45,45)	39	120°	(79,65)	33	39
3	(52,50)	43	127°	(18,76)	-	-	-	-	43
4	(50,50)	23	353°	(53,27)	4	155°	(50,30)	20	23
5	(49,49)	50	023°	(15,13)	-	-	-	-	50

(All distances to the nearest cm)

From the quadrat data shown in Table 3.6 it is apparent that the burrow entrances move position at least every day. Observations on Day 1 showed that all the burrows had moved position. A day later, two were not found at all and the other three had moved position. The distance between the burrow entrances on consecutive days averages 32.3cm (st. dev. = 24.1, n = 8) and ranges from 4cm to 75cm. From the airlift excavation data described in section 3.4.2.1, the new burrow entrances are shown to be made by creating new branches from the more permanent deeper parts of the burrow. Assuming this deep part stays in the same place, the new entrances would be expected to fall within a circle around the central, permanent burrow section. The minimum diameter of the circle which would enclose the burrow entrances in each quadrat was taken as the maximum distance between burrow entrances during the days of study and is shown in the last column of Table 3.6. The mean diameter of such a circle is 46cm (st. dev. = 19, n = 5). The burrows which were used in the tracer sediment experiment also showed an entrance movement at least daily. Neither the burrows observed in the quadrat experiment nor the tracer experiment showed any directional movement of the entrance.

Double entrances are more common in the off-reef alpheids than the near-reef species; 50% of the burrows described in the tracer and quadrat experiments had two entrances in use simultaneously. They do not reflect old burrow branches that remain open after a new entrance has been made. In all cases these double entrances were close together after a new entrance has been made. In all cases these double entrances were close together and linked only a few centimetres under the sediment surface in a shallow U-shape and seem to be a characteristic feature of many off-reef alpheid burrows. Old burrow branches and their entrances seem to fill in rapidly once abandoned, and are obvious as disused entrances as hollows in the sea bed surrounded by old excavation piles. All abandoned structures quickly become covered in a layer of fine brown organic matter and structures in use, such as fresh excavation piles, are distinct due to the lack of this coating.

From general observations whilst diving in both near-reef and off-reef areas it is evident that new burrow entrances can be made over a matter of hours. Alpheids are not active at night, and burrow entrances fill in to some extent overnight. The first activity of the day must therefore to be to either clear the burrow entrance or to dig a new one.

There must be a good reason for this seemingly energetically costly activity. I suggest that the sediment excavated by the shrimp is used for harvesting food particles, both by the shrimp and the fish. The constant turnover of the upper layers of the sediment must also aerate it and thus enhance the microbial and meiofaunal communities which the alpheid and goby then feed on. The continual moving of the burrow entrance also allows the animals to feed on a wide area of surface sediment without having to stray too far from the safety of the burrow. In this way they are practising shifting cultivation, completely working over one area of surface sediment before turning to another. They also leave a fresh substrate (the excavated sediment) on which a new crop of organisms can grow There is some evidence that the gobies feed mainly on the organisms in these surficial sediments whereas the alpheids feed on the detritus within the excavated sediment (Karplus et al 1974). This method of burrow movement would therefore benefit both animals.

3.4.2.2 Sediment texture.

Airlift excavation of a number of burrows clearly showed disused branches of the burrow leading off at sediment depths of about 15-20cm; the sediment surrounding a burrow was therefore filled with old parts of burrows in various states of preservation (presumably reflecting the length of time they had been neglected). Some of these were infilled with sediment that looked identical to the background sediment and a few were still open, although they did not reach the sediment surface. Where these parts tunnelled through the solid clay layer, their walls stood out as a gritty textured tube through the clay.

Grain size analysis of cores through the off-reef sediments indicated poorly sorted sediments throughout and an increase in mean grain size to a maximum at 35cm and deeper (Fig. 3.11). General sediment descriptions were made for cores taken in the area and the data; see Fig. 3.24.

3.4.2.3 Rates

A turnover rate was calculated for off-reef alpheids on the basis that they dig a new shaft to the surface once a day. The rate of turnover was calculated by estimating the volume of this new burrow created each day, assuming the burrows to be cylindrical. An average diameter of 1.75cm and average length of 25cm were estimated from measurements taken from resin casts and during airlift excavations, giving an average volume of 60cm^3. A density of 1 burrow every 7.5m^2 was obtained from belt transects (equivalent to 13 per 100m^2). This gives a turnover rate of 2920cm^3/m^2/year for the top 20cm of sediment (or 4.5kg/m^2/year; subtidal sediment density = 1.54g/cm^3; Appendix B). This is equivalent the top 20cm being completely reworked every 69 years.

3.4.3 Other bioturbators

Although callianassids and alpheids dominate their particular areas of the sea bed, many other infaunal organisms are present. While working on the soft subtidal sediments it was apparent that the sea floor was riddled with numerous tiny burrows. The total burrow density was quantified by counting their numbers within 50x50cm square quadrats which were subdivided into 25 10x10cm squares. All burrows visible to the naked eye were counted; these were generally no smaller than 1mm in diameter. A mean of 241 burrows/m^2 was found (st. dev. = 59, n = 15), with a maximum of 352/m^2. All counts were done in the daytime during neap tides. Fig. 3.21 shows the relative numbers of different sizes of burrows; raw data are in Appendix C.

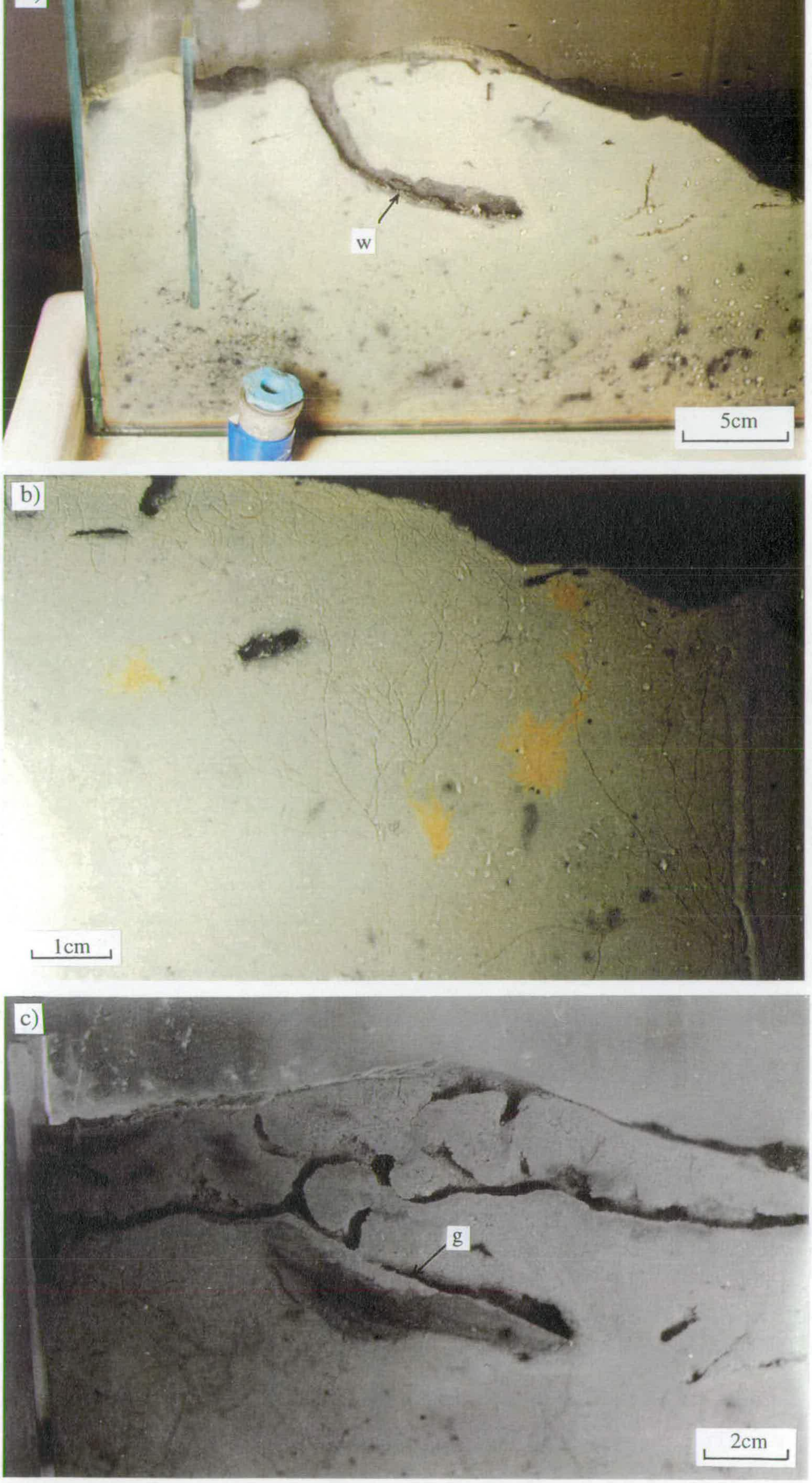


Plate 3.10 Aquarium set up with subtidal sediments. Sediment surface was originally horizontal, but burrowers have disrupted it. **a)** Large burrow (w) is made by an echiuran worm, one of the animals that makes up the '10cm layer'. **b)** Detail of fine meiofaunal traces, probably made by crustaceans (arrow). **c)** After the death of the echiurid, its burrow became infilled. Note the geopetal surface (g) rests at about 30° off the horizontal. A small crab has burrowed into the top 5cm of the area.

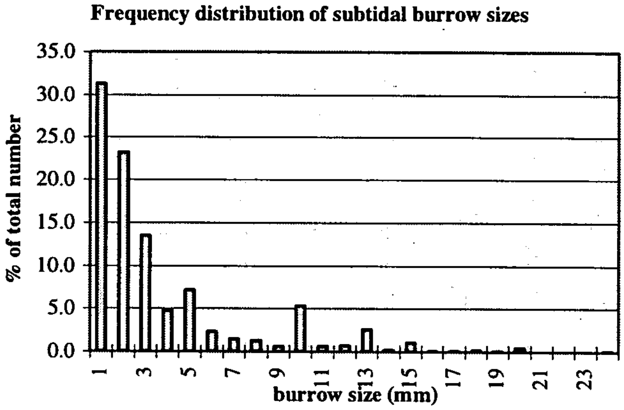


Figure 3.21 Size frequency distribution of subtidal burrows.

Christoph Meyer, then a Masters student at Osnabrück University, and Dr. Robert Higgins from the Smithsonian Institution both looked at samples of the fine upper centimetre of sediment from this area and identified the following meio- and microfauna: kinorhynchs, turbellarians, ciliates, nematodes, sipunculids, crustaceans (harpacticoid copepods, amphipods, ostracods, cumaceans, decapods, tanaids, holocarids) and molluscs (gastropods and bivalves). C. Meyer also found 17 families of polychaetes, most of which are poorly described, and one of which is a new species (*Boguea panwaensis*).

From this diverse fauna, it is most likely that the crustaceans, nematodes and polychaetes are the animals that make the tiny burrows (see Plate 3.10b). Larger burrows were probably larger worms (polychaetes and echiurids), crabs and small alpheids and fish.

Excavation reveals 'tiers' of burrowers (Ausich and Bottjer 1982)(Fig. 3.22); the uppermost tier consists of the rich meiofauna described above which make burrows in the order of 1mm diameter and reaching a maximum depth of 2-3cm. Below this, at about 10cm depth, is a layer of interlinked burrows (approx. 1cm diameter) made by crabs, echiurids, and other unseen animals; some of these were successfully kept in a sediment-filled aquarium for a number of weeks (Plate 3.10a-c). Airlift excavation to remove the sediment above this layer allowed the drawing and casting of portions of this network at 10cm (see Fig. 3.23).

A very distinctive burrow was also cast; the construction is a series of U's with common vertical shafts, thus forming a looping structure with multiple entrances which are obvious at the surface as a cluster of round holes about 1.5cm diameter and 5-10cm apart.

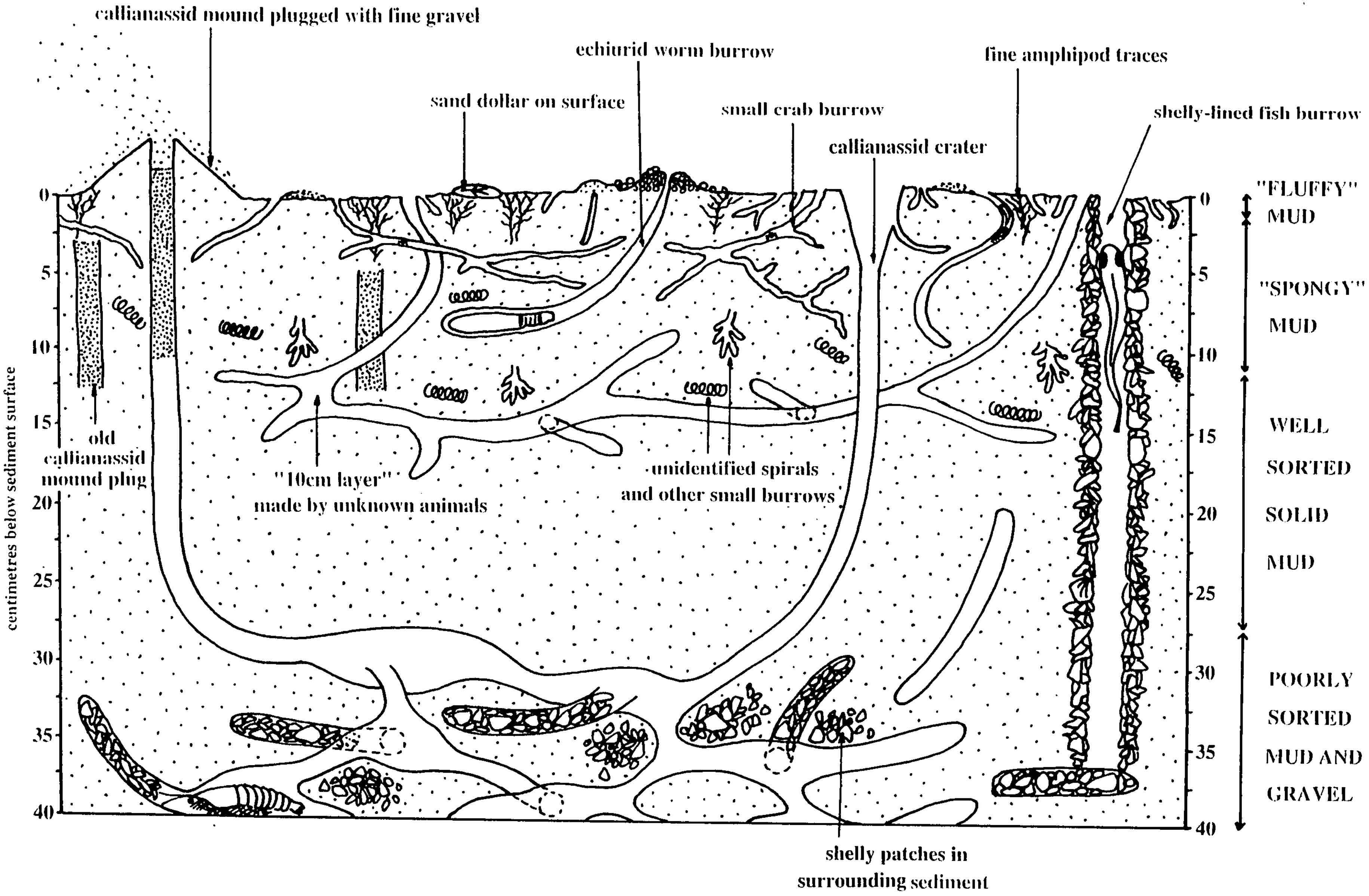


Figure 3.22 Schematic vertical section through the subtidal callianassid area showing tiering.

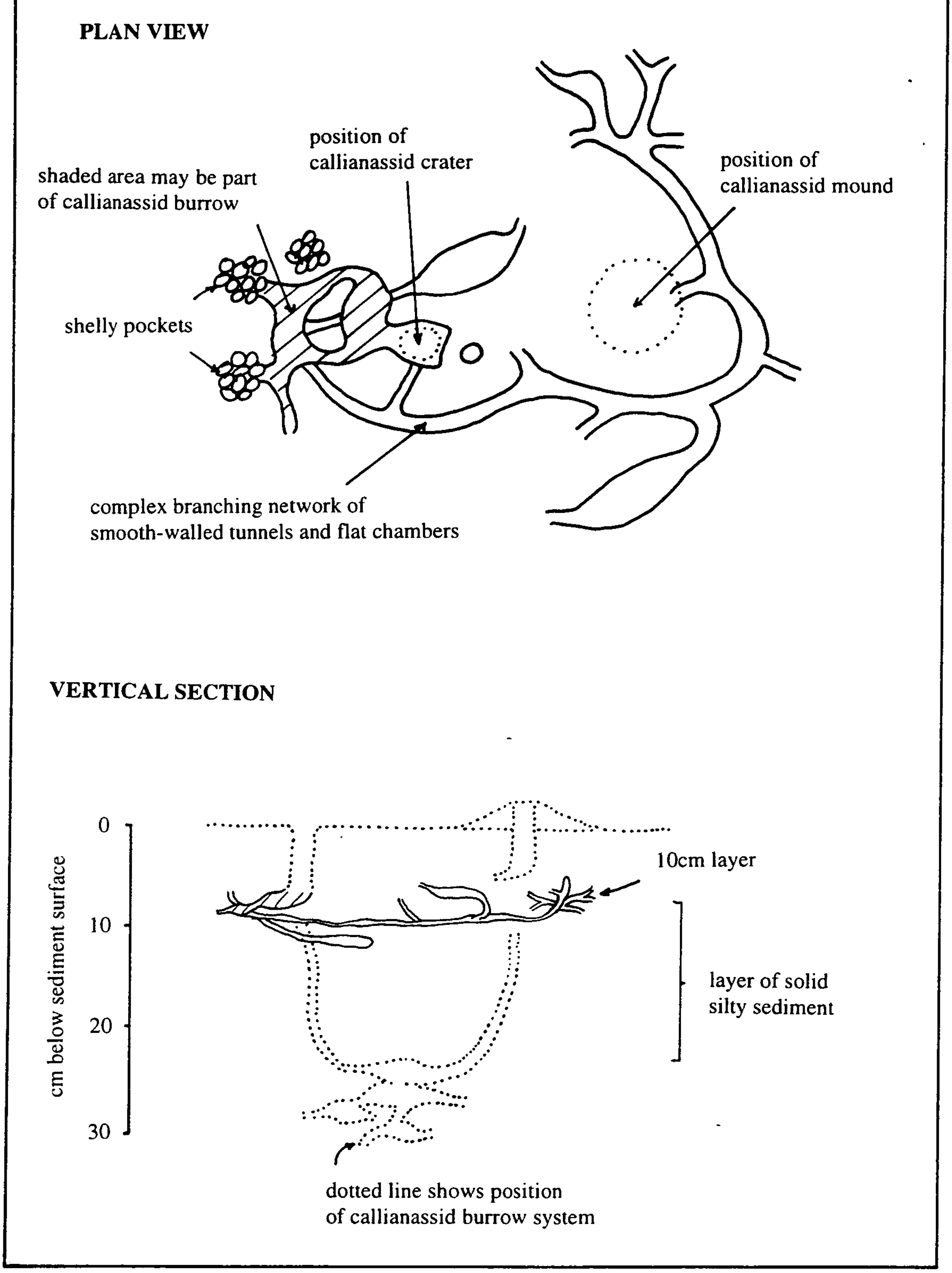


Figure 3.23 An example of part of the '10cm layer' as excavated by airlift. **a)** Plan view of features exposed during excavation. **b)** The position of the 10cm layer in relation to a callianassid burrow.

From the literature (e.g. Suchanek 1985, Dworschak 1987a, de Vaugelas 1990) these are probably upogebiid shrimp burrows.

Cutting through all these are the deepest tiers, the alpheids or callianassids, with burrow structures reaching depths in excess of 60cm. Also reaching into the deepest tiers were the following burrows:

i) occasional vertical burrows with a diameter of between 2-4cm whose walls were constructed of coarse debris such as bivalve and gastropod shells, barnacles, coral and sand dollar fragments, all arranged to give a perfectly circular inner hole, and cemented together in some way (chunks of this coarse lining came away intact during airlifting). This shelly lining extended to at least 30 cm below the sediment surface and two holes were seen on one occasion to join up at a depth of 25cm in a wide U shape which was not encrusted with coarse material. These burrows are inhabited by dartfish (Family Microdesmidae; *Ptereleotris arabica* Randall & Hoese 1985; this is a first record of the species outside the Red Sea and Persian Gulf; Satapoomin pers. comm.). These burrows were not common but were extremely distinctive. One or two different fish burrows were occasionally seen; these seemed to be simple vertical shafts.

ii) stomatopod shrimp burrows, which go straight down vertically into the sediment and have a smooth inner wall. No successful resin casts were obtained and none were airlifted. Distinctive surface features are the burrow entrance which has a mucus bound flap around the perimeter, effectively making the hole smaller than the burrow width, and a ring of debris which has been thrown from the burrow entrance by the shrimp. These were rare; only two were seen in total.

3.5 CHAPTER SUMMARY

The results presented in sections 3.3 and 3.4 clearly show that both the intertidal and subtidal sediments around Laem Panwa in Phuket have an abundant and highly active infauna and epifauna. In the course of their daily activities (feeding, moving, burrowing) these animals leave a variety of traces on and in the sediment. The morphology of these traces is generally diagnostic not only of the animals that made them but also of the type of activity that caused them. The activities that involve sediment turnover and burrow formation were investigated in detail for intertidal soldier crabs (*Dotilla*), alpheid and callianassid shrimps and subtidal alpheids and callianassids. Burrow morphology, the nature of sediment sorting or mixing and rates of turnover were investigated for these crustaceans using airlift excavation, resin casting, tracer sediment experiments and sediment coring.

The crustaceans were found in distinct zones. In the intertidal area, the sand waves were monopolised by *Dotilla* soldier crabs, whereas the sediment of the tidal pools between them were dominated by alpheid shrimps. Intertidal callianassids were found only in the central region of the bay closer to the low tide mark. In the subtidal sediments, an offshore zonation was found, with near-reef alpheids giving way to off-reef alpheids and then callianassids further from the reef.

1. *Dotilla*

These crabs dig vertical, cylindrical burrows every daylight low tide that the intertidal sand waves are exposed by a critical amount; suitable tides occur twice daily during spring tides and not at all during neaps. Within the first 10-15 minutes after the tide has fallen low enough (less than 1.6 metres above lowest low water) or 15-20 minutes after first light at a dawn low tide, the crabs emerge from the sediment where they have been buried during high tide, thus producing 5-20 large pellets. During the exposure of the sand waves the crabs graze almost continually on the surficial sediments, covering the surface with tiny feeding pellets (diameter 1-2mm) and also expand their burrow, resulting in a further 10-30 excavation pellets. Burrowing is limited to times of exposure at low tide and is correlated with the length of time of exposure rather than the depth of the water table beneath the sediment surface. The crabs' activity will result in passive burial of coarse sediment due to their ability to process only small grains.

2. Callianassids

These shrimps excavate complex burrows with a network of layered tunnels and chambers. This network is connected to the surface by an inhalent shaft, leading from a surface crater, and an infilled exhalent shaft from which fine particles are ejected on to a mound. In the intertidal burrows coarse grains are apparently buried outside the burrow chambers and sealed off behind the smooth lined burrow wall. In subtidal burrows coarse material can be seen in shelly pockets leading off the main burrow. The deeper reaches of the burrows occupy a fairly permanent position in the sediment, although individual chambers may be sealed off and new ones dug. However, the surface mound (in the case of intertidal shrimps) and crater (in the case of subtidal shrimps) move position regularly.

Attempts have been made by various authors to classify thalassinid burrows according to their morphology, which in turn usually reflects their method of feeding (Suchanek 1985, Griffis and Suchanek 1991). However these attempts are oversimplistic and it is difficult to assign the two Phuket callianassid burrow types to particular categories. Burrow morphology is much more flexible than supposed by these authors and structures may have more than one function, may vary between individuals or with environmental conditions. Feeding behaviour is also variable, depending on food supply. De Vaugelas (1990) and Nickell and Atkinson (1995) used function rather than form to suggest more flexible models allowing for this variation.

3. Alpheid shrimps

Intertidal and subtidal near-reef species create irregularly shaped burrows which slope down at a shallow angle. The burrow entrance changes position daily and this involves the re-digging of the upper 7-8cm of burrow. In doing so, the shrimps separate out coarse from fine sediment to create a patchy sediment surface with clusters of coarse debris. The burrow morphology below this changing upper part is determined mainly by the presence of large pieces of reefal debris in the sediment, which often form the ceilings of the alpheid burrows. In contrast, subtidal off-reef alpheids dig deep spiral burrows and do not sort grains according to size. However, they also re-excavate the top portions (15-20cm) of their burrows and thus change their entrance positions. This processing of sediment provides the shrimps with a fresh supply of food particles.

Rates of sediment turnover were calculated for each of these burrowers and are summarised in Table 3.7.

Although these crustaceans are some of the most obvious burrowers in the shallow waters around Laem Panwa, many other animals live in or on the sediment and affect it in some way. In the intertidal area, epifauna are common and produce a wide range of tracks and trails on the sediment surface. In the subtidal muds, there is an abundant meiofauna which live in the surficial layers of the sediment. A "10cm layer" of larger burrowers (crabs, worms, fish) is also present and overlies the deepest tier of burrowers, the callianassid or alpheid shrimps.

The different elements of this diverse fauna affect the sediment in different ways. For example, surface feeders such as fish and gastropods simply mix the sediment surface, intertidal alpheid shrimps burrow to depths of 25-30cm and continually excavate sediment from below which they sort at the surface according to grain size, and deep tier callianassids bury coarse material at sediment depths of >25cm and eject fine sediment at the surface. The effects these animals have on the sediment are in turn affected by other burrowers and by physical processes such as wave and current action. The preservation of these biogenic traces in the geological record is the subject of Chapter 4.

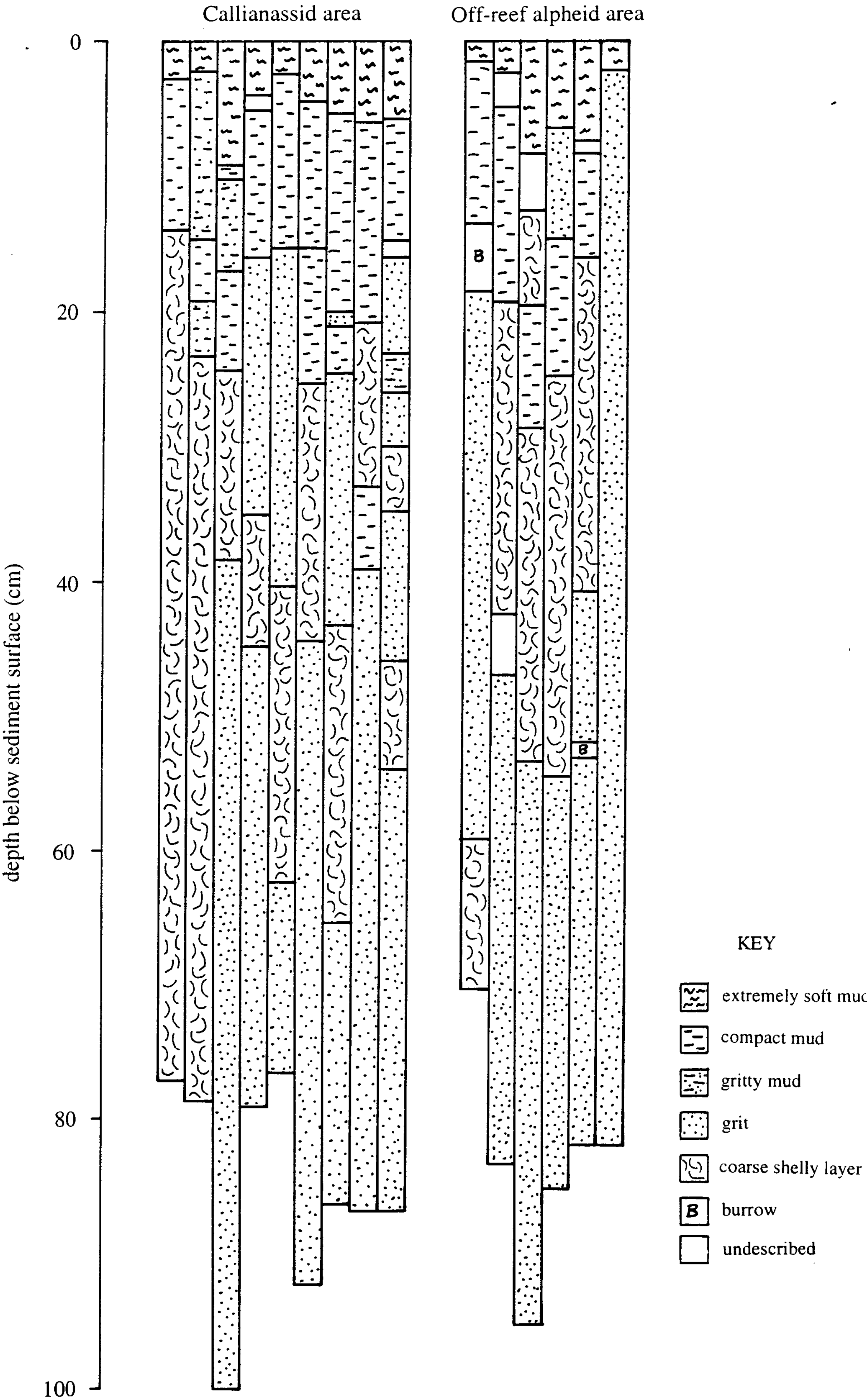


Figure 3.24 Sediment textures down cores taken through subtidal sediments; descriptions are qualitative observations made during core processing.

Table 3.7- Summary of rates of turnover of sediment by *Dotilla*, alpheids and callianassids

Burrowing organism	**Burrow density (number per 100m^2)**	**Turnover rate**				**Max. depth of burrow (cm below sediment surface)**	**Average depth of sediment working (cm below sediment surface) ***	**Turnover rate expressed as the time taken to rework the burrowed layer**
		(m^3/m^2/yr)	(kg/m^2/yr)	(m^3/burrow/yr)	(kg/burrow/yr)			
Dotilla	9100	0.4 - 0.42	523 - 549	0.004 - 0.005	5.8 - 6.1	25	9	top 9cm turned over 5x/year
alpheid - intertidal	820	0.12	158	0.015	19.7	30	7	top 7cm turned over 1.7x/year
alpheid - subtidal off-reef	13	2.9×10^{-3}	4.5	0.022	33.8	>60	20	top 20cm turned over every 69 years
callianassid - intertidal	37	0.05	69	0.14	187	>50	25	top 25cm turned over every 4.7 years
callianassid - subtidal	24	0.015	23.8	0.065	99.33	>60	25	top 25cm turned over every 16 years

* This is taken as the average depth of the side branches in the alpheid burrows and the average depth of the first chamber in the callianassid burrows

CHAPTER 4

BIOTURBATION IN THE ROCK RECORD

This chapter deals with the geological aspects of burrowing organisms and their traces. Section 4.1 gives a background to the subject of ichnofabrics, their preservation and their uses. Sections 4.2 to 4.7 discuss the preservation and geological implications of the bioturbation investigated this study, starting with the effect of intertidal or subtidal environments (4.3). Three possible types of preservation are then discussed; by sudden burial with no erosion (4.4), under conditions of continuous steady sedimentation (4.5) and the effect of storms (4.6). The implications of bioturbation for the preservation of grains and traces are covered in section 4.7 and a summary of the main conclusions (4.8) ends the chapter.

4.1 WHAT IS THE EVIDENCE IN THE ROCK RECORD?

An ichnofabric comprises "all aspects of the texture and internal structure of a sediment that result from bioturbation at all scales" (Ekdale et al 1984, Bromley 1990) and therefore includes everything from discrete burrows to bioturbate textures (Ekdale et al 1991). An ichnofabric is the result of the interaction between physical and biological controls (Droser et al 1994, section 4.1.5.2).

4.1.1 Individual burrows

A wide range of trace fossil morphologies have been described, from simple tubes to branching burrows and networks, and random tracks and trails to highly organised grazing patterns. The full range of forms can be seen in Häntzchel (1975); this treatise provides a catalogue of trace fossils with numerous drawings, photographs and descriptions.

4.1.1.1 Trace fossil classification

Trace fossils are given taxonomic names based on their morphology, following similar rules to modern animal and plant classification, each having an ichnogenus and an ichnospecies name, e.g. *Ophiomorpha nodosa*. Trace fossils can be classified according to the behaviour they represent (ethological classification; Seilacher 1964b, Frey 1973, 1978). Alternatively they may be classified toponomically, i.e. with respect to their mode of preservation and position relative to the casting medium (Seilacher 1964b, Martinsson 1970). Useful summaries of definitions and terminology can be found in Frey (1973), Basan (1978), Frey (1978), Ekdale et al (1984) and Pemberton (1992).

4.1.2 Bioturbate textures

The activities of bioturbating organisms can completely destroy all evidence of the primary (physically produced) fabric such as bedding and create new bioturbate textures. Common examples include biogenically-produced coarse layers (e.g. McCave 1988, Goldring 1995), coarse patches (Tedesco and Wanless 1991) and other "bioretexturing" Pedley (1992).

Bioturbation Indices have been designed to quantify the amount of biological reworking, based on the percentage of primary fabric still visible (Droser and Bottjer 1986, Bottjer and Droser 1991, Taylor and Goldring 1993).

4.1.3 Characteristics of trace fossils:

- A long time range
- A narrow facies range
- No secondary displacement
- Often produced by soft-bodied organisms that are not otherwise preserved
- Often occur in otherwise unfossiliferous rocks
- One species can make different types of traces
- Different animals can make similar traces
- A number of animals can make a joint structure
- Tend to destroy primary depositional features

see Seilacher (1964a, 1964b), Basan (1978), Byers (1982), Ekdale et al (1984), Briggs & Crowther (1990), Pedley (1992), Pemberton (1992) for further details.

4.1.4 Geological history of trace fossils

The oldest unambiguous trace fossils date from about 700Ma BP (Byers 1982, Crimes 1994). At about the Precambrian-Cambrian boundary there was a dramatic increase in abundance, diversity and complexity of trace fossils (Crimes 1987, 1992a, 1992b). This could have been related to

- the increase in diversity of behaviour in the shallow seas (Crimes 1974, Seilacher 1974)
- increasing oxygen levels and sea level changes increasing the area of habitable sea floor, especially the shallow marine zone
- biological factors, such as the development of macropredation (Crimes 1994)

The tiering of benthic, marine, suspension-feeding communities in soft substrata has also varied throughout the Phanerozoic (Ausich and Bottjer 1982).

4.1.5 Preservation and interpretation of ichnofabrics

4.1.5.1 Diagenesis

A modern deposit can be thought of in terms of three layers characterised by their preservational state (Ekdale et al 1984, Goldring 1995). The upper layers are still subject to physical and biological disturbance and are known as the 'mixed layer'. As a sediment passes from the mixed layer through the 'transition layer' it becomes compacted and dewatered and subsequently processes such as cementation and mineralisation produce the 'historical layer'. Unlike many cases of body fossil preservation, diagenesis usually enhances the preservation of burrows (Byers 1982, Bromley 1990). Bioturbation within a sediment can promote the early diagenesis of sediments and grains by increasing their chemical reactivity either by providing conduits for fluid flow and/or concentrating oxygen, organic material and ions (e.g. Fe, Mn, Zn), especially in the burrow wall or fill, or in mucus-rich deposits (Byers 1982, Ekdale et al 1984, Bromley 1990).

The original sediment type is also important in the nature of preservation. For example, carbonate sediments generally lithify quickly, with differential cementation between the burrow wall and fill accentuating trace fossil definition. Alternating sand/clay/sand sequences provide contrasting infills for burrows, whereas uniform sedimentation of one sediment type is less likely to reveal traces. Biogenic structures may be well preserved because of constructional differences in compaction, grain orientation and organic content of fill and walls introduced by the burrower (Bromley 1990). These diagenetic effects are not necessarily restricted to the burrow itself, but may extend into the surrounding sediment, which is also chemically affected by the bioturbation (section 3.2.2).

Bioturbation can affect the preservation of grains (see Brett 1990, Scoffin 1992). High turnover rates expose a greater volume of sediment to surface processes such as carbonate dissolution (Aller 1978) and microboring (Tudhope & Scoffin 1984). Animals may ingest grains and physically or chemically break them down in their guts (Crozier 1918, Bakus 1973).

4.1.5.2 Relative rates of erosion, deposition and bioturbation

The single most important factor which determines the nature of preservation of bioturbation is the relationship between the rates of sediment deposition, sediment erosion and bioturbation. It is not just the relative rates of these three parameters but also whether they are constant or fluctuating (e.g. Goldring 1964, Howard 1975, 1978, Ekdale et al 1984, Pemberton 1992). Areas with strong currents, or intertidal wave washed zones and areas frequently disturbed by storms have a lower preservation potential than sheltered inshore lagoons or subtidal environments. The patterns and inter-relationships of physically and biologically formed sedimentary structures can provide much information about the timing of these sedimentary processes (e.g. Howard 1978, Byers 1982).

4.1.5.3 "Rare" events

Storm events provide a good example of alternating erosional and depositional phases. A storm passing over a sediment will usually initially cause erosion and then deposition. "Rare" events like these are only rare on a human time scale. On a geological time scale they are common and may make up the bulk of the rock record (Seilacher 1982, Dott 1983).

The physical evidence for storms is usually quite distinctive in the sedimentary record. Features such as hummocky cross-stratification and fining-upward sequences are typical of a storm deposit or tempestite (Kreisa 1981, Seilacher 1982, Duke 1985). Trace fossil evidence can also help to identify storm events. Parallel-laminated-to-burrowed cycles record alternations in the rate of deposition as indicated by the increasing degree of bioturbation moving up the sequence (Howard 1975, Byers 1982). Storms also affect the biota of a sediment by redistributing organic matter and causing a net change in grain size (Seilacher 1982).

Unusually strong storm events may completely wipe out the sedimentary record of previous weaker events. However, the relative strength of a storm to fair weather conditions and the length of time between storms have more preservational importance than the storm strength *per se* (Wanless et al 1988, Scoffin 1993). Storm scour can erode the sediment down to a previous coarse layer which will then inhibit further erosion and the coarse material at these condensed horizons may be the product of many storms (Aigner and Reineck 1982). Repeated exposure by erosion may change the erosional behaviour of different layers of sediment. In carbonate sediments, early diagenesis tends to cement layers which become more and more resistant reference horizons during repeated reburial and re-exposure by subsequent events (Seilacher 1982).

4.1.5.4 Tiering and cross-cutting of trace fossils

Tiering is the vertical partitioning of a community within a single habitat in the sediment due to environmental variations with sediment depth (Ausich and Bottjer 1982, Bottjer and Ausich 1986). This leads to the reworking of burrows within a single community and cross-cutting of trace fossils in the resulting ichnocoenosis. A highly bioturbated area is less likely to show clear trace fossils due to extensive reworking, and may even be interpreted as a trace-free sediment. A sediment where little bioturbation has occurred is more likely to show distinct individual trace fossils. For examples in the rock record see Bromley and Ekdale (1986).

The simplest tiered ichnofabric to interpret is a “frozen tiered profile” (Bromley 1990, Droser et al 1994), where the benthic community has been preserved in the fossil record just as it appeared at the time the animals were alive, i.e. it is not been reburrowed by subsequent communities.

As a sediment column migrates upwards with steady accretion, the tiers will also move upwards creating a “composite ichnofabric” (Bromley and Ekdale 1986). The last traces to be made will be the ones that are best preserved (Bromley and Ekdale 1986), and these are often the deepest tiers which cut through, or otherwise disturb, the upper ones (Bottjer and Droser 1994).

Cross-cutting relationships allow the sequence of emplacement of burrows to be reconstructed. The juxtaposition of sharply-defined, relatively little-compacted trace fossils on indistinct, compacted ones indicates tiering and allows tiered trace fossil associations to be distinguished from composite ichnofabrics (Bromley and Ekdale 1986, Frey and Goldring 1992).

4.1.6 Trace fossils as indicators of palaeoenvironment

Trace distribution is directly related to the distribution and density of the animals that made them. The inter-related factors acting on the extent of bioturbation include

- geographical area (e.g. tropical vs. arctic sediments)
- oxygen levels (Savrda and Bottjer 1986, 1987)
- bathymetry (Seilacher 1967)
- sediment consistency (grain size and stability; Byers 1982)
- biological interactions (e.g. predation levels and competition from other organisms for food and space; Kitchell et al 1978, Kitchell 1979)
- turbulence and energy levels in the environment (Moore and Scruton 1957, Allen 1965, Byers 1982, Ekdale et al 1984, Ekdale 1988, Pemberton and Jones 1988, Jones and Pemberton 1989).

Furthermore, different environments have different diagenetic influences acting on them, and differing preservation potentials, so that the eventual trace fossil assemblage seen may differ due to preservational biases (Seilacher 1964, Bromley and Asgaard 1991).

Deep tier traces may be the best preserved, but they are also the traces furthest removed form the sediment-water interface and therefore potentially the least sensitive to environmental conditions. Therefore, palaeoenvironmental reconstructions based only on deep tier fossils may be incomplete and/or misleading. (Bromley and Ekdale 1986).

4.2 THE GEOLOGICAL IMPLICATIONS OF THIS STUDY

Curren (1994) summed up the study of ichnology when he wrote:

> "...a continuing frustration is the overall lack of knowledge about modern trace-maker organisms [in tropical carbonate environments]. Commonly the past is the key to the present in these settings.......a full understanding of the trace fossil record cannot be realised until we know far better what the burrower organisms really are doing beneath the substrate surface."

Modern tropical carbonate sand environments are in fact fairly well studied when compared to tropical muds. This study sets out to look at the less studied, terrigenous clay rich, tropical setting in attempt to solve at least some of the questions posed when looking at

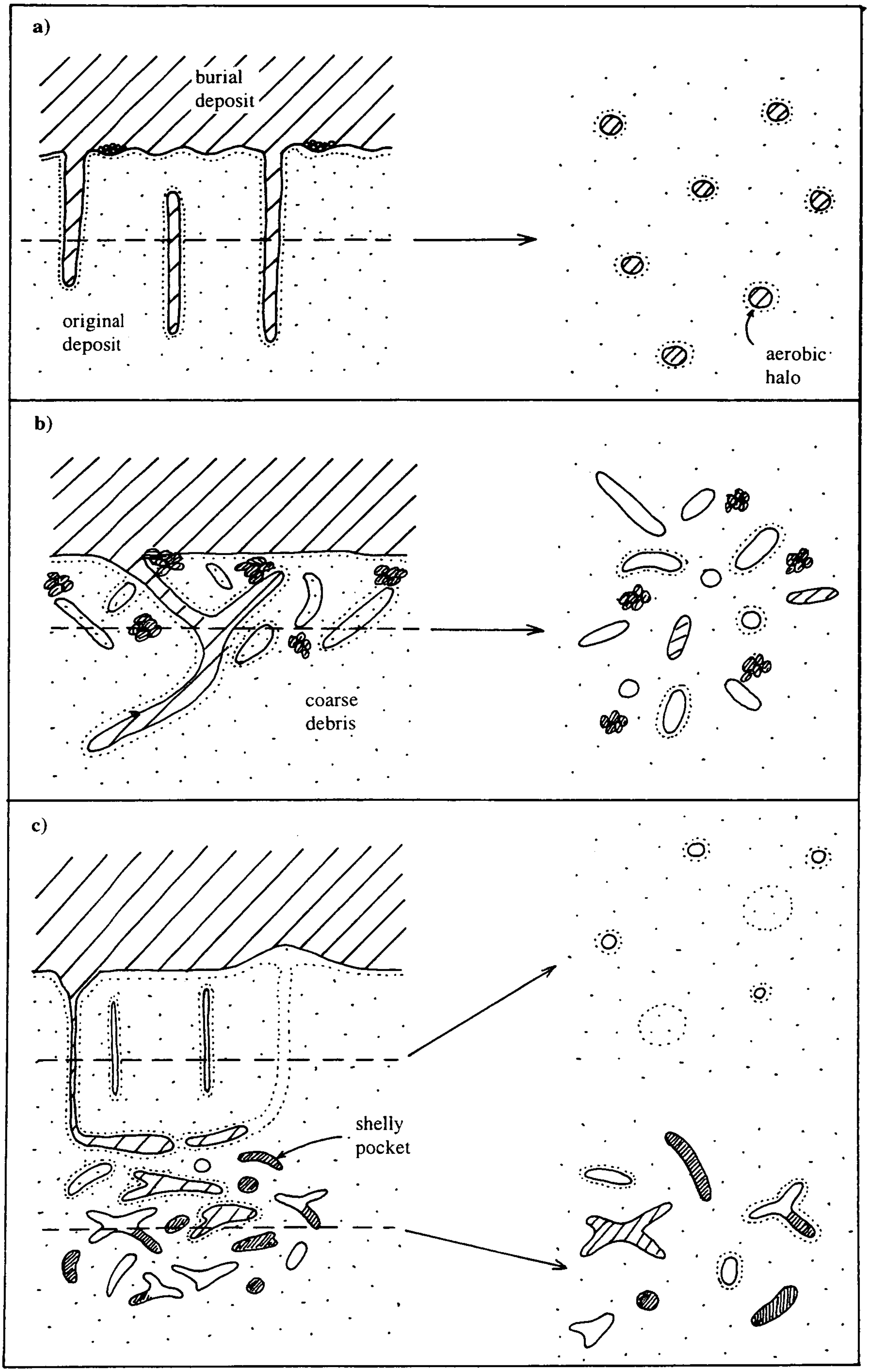


Figure 4.1 The appearance of deposit when exposed as a section perpendicular to the beds (left diagram) or parallel to the bedding plane (right diagram) with **a)** *Dotilla*, **b)** intertidal or near-reef subtidal alpheid and **c)** subtidal callianassid burrows.

both trace fossils and modern traces. In this section the present is used as a key to the future and the following questions are discussed. What will the Phuket sediments look like if they pass into the geological record? Under what conditions would they be preserved, and how will different conditions of preservation affect their appearance? What will their preserved remains tell us about the environment they were created in and the animals that made them?

In predicting the appearance of trace fossils from their present day traces (Fig. 4.1), two processes must be taken into account; those that affect the appearance of the present day sediments (as discussed in detail in Chapter 3) and preservational factors that will alter this appearance as the sediments pass into the geological record, for example, the conditions of deposition and taphonomic alteration.

The conditions of deposition determine what is to be preserved. The relative rates of deposition, erosion and bioturbation vary with the type of event that causes preservation. The time of year at which the sediment is preserved may also affect the appearance of the sedimentary deposit. In Phuket, the changing weather in the two monsoons influences the extent of physical disturbance, especially in shallow water. The animals themselves probably show seasonal variations due to their breeding cycles, thus causing changes in densities of burrowers with the time of year. Very little is known about the life history and ecology of the animals studied, for example whether juveniles create new burrows, which would be smaller than those of the adults, or if they live in part of the adults' burrows, or even take over the adult burrow once the adult has died.

4.3 INTERTIDAL VS. SUBTIDAL PRESERVATION

4.3.1 Intertidal preservation

The sediments of the intertidal environment are strongly affected by tide and wave action and have a low preservation potential due to their exposed nature. Even in calm weather, wave influence is obvious in the form of ripples on the sand surface. Tracer sediment placed on the surface was moved several metres laterally in a single spring tide, although it did not move more than a few millimetres vertically. This surface mobility suggests that biogenic structures in the top few millimetres to centimetres would be obscured by physical processes even under normal conditions. These structures include numerous tracks and trails caused by gastropods and crabs moving across the sand surface, resting traces such as those made by starfish, escape traces such as chimney-like structures made by rapidly burrowing soldier crabs, worm casts, *Dotilla* pellets and burrows, callianassid mounds and craters and alpheid burrow entrances (section 3.3, Plates 3.7, 3.8 and 3.9). Only rapid burial with large quantities of sediment and no erosion would preserve these intertidal burrows and surface traces.

The nature of the traces preserved would also differ depending on the state of the tide at the time of preservation. Many of the traces described above do not exist at high tide, either because wave action destroys them as they are made or because the animals themselves are not active.

4.3.2 Subtidal preservation

The subtidal environment has a higher preservation potential than the intertidal as it is a lower energy zone, but in such shallow water (<15m) the sediments are above rough weather wave base and are also subject to water currents, which can be strong in the area studied. Fine tracer laid on the sea bed travelled 2m within minutes on a neap tide, and a resin cast was buried 10cm beneath the shifting sediment surface over a period of two weeks. Storm conditions will have a major impact at these depths (see section 4.6). As in the intertidal sediments, the time at which preservation occurred could affect what was seen in the preserved deposit. The sediments look very different during spring tides and neap tides due to the varying speed of water currents; callianassid mounds are flattened and craters filled in so that the sea bed looks completely bare. The rough weather during the six month rainy season (SW monsoon) will also affect the bottom topography to a great extent.

4.4 PRESERVATION BY A SUDDEN DEPOSITIONAL EVENT (WITH NO EROSION)

Sudden preservation caused, for example, by sudden burial or sudden uplift (with no erosion) will form a "frozen tiered profile" (section 4.1.5.4 and Fig. 4.2c), a snapshot of the appearance of the sediments as they are today (with only diagenetic alterations to the basic appearance). All the tiers of burrows (section 3.4.3 and Fig. 3.22) and bioturbate textures will be preserved. Each trace described in this study would certainly be characteristic of its maker and a complete burrow made by one of these animals could not be confused with that of another (see descriptions in sections 3.3 and 3.4). In a rock exposure it is more usual for

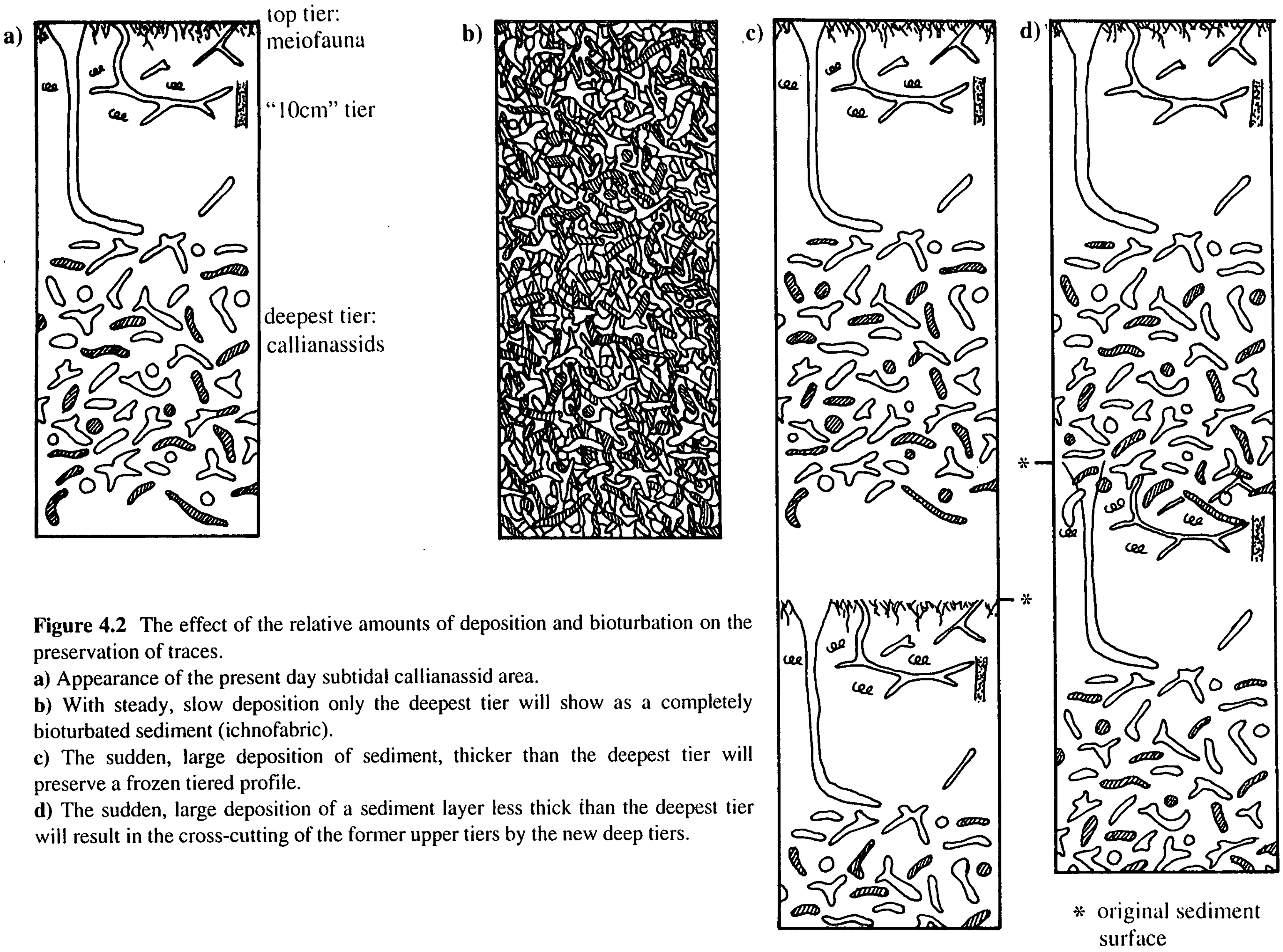


Figure 4.2 The effect of the relative amounts of deposition and bioturbation on the preservation of traces.

a) Appearance of the present day subtidal callianassid area.

b) With steady, slow deposition only the deepest tier will show as a completely bioturbated sediment (ichnofabric).

c) The sudden, large deposition of sediment, thicker than the deepest tier will preserve a frozen tiered profile.

d) The sudden, large deposition of a sediment layer less thick than the deepest tier will result in the cross-cutting of the former upper tiers by the new deep tiers.

parts of a structure to be visible; wall characteristics and the shape of these parts would therefore be more important in burrow recognition (Fig. 4.1). For example, a burrow with chambers could only be a callianassid. Features such as straight tunnels would be more difficult to identify as they are common to several different burrows. The nature of the burrow wall could be very diagnostic; *Dotilla* burrows have no lining or wall, alpheid burrows have a smooth floor (with possible laminations in cross section), a rough ceiling and possibly an oval cross section and callianassids produce a smooth-walled interior.

Aerobic haloes are present in all these burrows as they penetrate into the anoxic zone; differential preservation or diagenesis may accentuate the burrow-sediment interface as a result (e.g. Bromley 1990). The characteristics of the surrounding sediment will also be very important in identifying burrows and environments. Intertidal sediments differ markedly from those of the subtidal area, as do subtidal near-reef from subtidal off-reef sediments (see Chapter 3 and Appendix B).

4.4.1 Subtidal sediments

The subtidal sediment is tiered (section 3.4.3), from the small microfaunal burrows in the upper few centimetres of sediment through the 10cm layer to the deep tier alpheids or callianassids (see Fig. 3.22). With a sudden large deposition of sediment it is likely that the original fauna will be killed and recolonisation of the new sediment surface will take place. The new colonisers will start to burrow down from the new sediment surface into the fresh deposit (Fig. 4.2d). These organisms could be of the same species as the buried fauna or new 'pioneer' species. In this latter case it is likely that the pioneer community will be succeeded by a fauna similar to the buried one.

The depth of the deposit is important in determining the eventual appearance of the sedimentary sequence. If the deposit is thicker than the depth of the deepest tier, the buried traces will be preserved much as they appeared before burial, since the new deep tier animals will not burrow deep enough to rework the buried structures. This is known as a frozen tiered profile (4.1.5.4, Fig. 4.2c). The open burrows will have been filled in with the new deposit, possibly providing a contrasting infill, and there may be signs of attempted escape by the buried fauna as they tried to dig upwards through the new sediment in the form of escape traces (fugichnia). The resulting ichnofabric will show two sets of tiers, one above the other, separated by a layer of unbioturbated sediment (Fig. 4.4d), which might show physical characteristics of the event that caused the sedimentation (e.g. fining upwards textures). In Phuket, the deep tier burrows penetrate at least 50-60cm below the sediment surface, so a deposit of at least this thickness would have to be deposited to create a complete frozen tiered profile.

If the depth of deposit is less than the depth of the deepest tier, the new deep burrows will penetrate through to the buried structures and crosscut them (Fig. 4.2d). Depending on the thickness of the new deposit, the new burrows may only reach down to the upper tiers of the buried sequence or may even rework deeper tiers.

Upper tiers will be more heavily burrowed than lower ones because a) there are more burrows there (all tiers pass through the upper layers) and b) the lower parts of these deep tier burrows appear to change position less than the upper parts so leaving less traces in the surrounding sediments.

The amount of time that elapses between sedimentation events is also important; the longer the interval between physical events the more bioturbation will rework the sediments and cross cut each other leading to less clear individual burrows and more of a bioturbate texture. A short interval will allow little time for reworking and individual burrows are likely to be more distinct.

4.4.2 Intertidal sediments

The depth of deposit is as important in the preservation of intertidal burrows as it is in subtidal ones; it determines the extent of reworking by both biogenic and physical processes. As most *Dotilla* burrows only reach sediment depths of about 8cm, less sediment would be needed to prevent reworking by a post-event *Dotilla* population. Alpheid and callianassid burrows would require more than 60cm of deposit. A thick layer of sediment deposited intertidally potentially raises the sediment surface above the high tide mark where a whole new range of preservational parameters come into play. The effects of wind and fresh water and the possibility of plant growth in the exposed sediments would drastically alter the appearance of the sedimentary deposit.

As mentioned above, the state of the tide at the time of burial will affect which features are preserved. Taking *Dotilla* traces as an example, if the burrows were buried in sediment at low tide they would become infilled with the deposit, possibly producing a contrasting infill, and the pellets at the surface would also be preserved in a layer between the pre- and post-depositional sediments. However, the burrows become infilled with surrounding sediment when the tide is in and the pellets on the surface get washed away. In this case, there would be no obvious structures to be preserved and the positions of burrows might be picked out only by aerobic haloes within the sediment.

The intertidal environment would produce a laterally more heterogeneous sedimentary sequence than the subtidal environment due to the sand waves and pools with their different sediment types and burrowing fauna. Moving along an exposure, patches of well-sorted, sandy deposits with small, vertical trace fossils (*Dotilla*) and occasional large complex trace fossils (callianassids) representing the sand wave habitat would alternate with poorly-sorted coarser patches with clusters of shells, large pieces of reef debris and sloping trace fossils with a variable morphology (alpheids). Surface traces such as pellets, casts, tracks and trails may be preserved at the interface between the pre- and post-depositional deposits, though any slight disturbance during deposition will disrupt these traces.

Any trace that can be attributed to an intertidal organism is a good indicator of sea level at the time of preservation and therefore has important implications for palaeoenvironmental reconstructions. Ghost crabs which inhabit burrows in the beach sediments and land crabs which live just above the high tide mark are further examples of sea level indicators but have not been studied in detail in this work.

4.4.3 Trace fossil equivalents

The similarity in morphology between some ancient trace fossils and modern burrows or traces is quite striking. It should be remembered that more than just the burrow in use at the time of preservation may pass into the geological record. For example, a deposit feeder mining at depth may make numerous forays into the sediment from the base of its burrow, producing multiple burrow branches which may all be preserved as a cumulative structure recording the activity of the animal over a period of time. The trace fossil will therefore look much more complex than a resin cast of the modern burrow. In order to imagine what a trace fossil might look like from its modern counterpart the nature of the burrowing activity over time, as well as the basic morphology, must be considered. A trace fossil is rarely seen in its three-dimensional entirety; usually only sections through the sediment are exposed, either vertically throughout the sequence such as is seen in a cliff side, quarry or road cutting, or along planes of weakness such as bedding planes which will reveal horizontal sections, possibly at the original sediment surface. Fig. 4.1 shows how three of the burrow types discussed here would appear in vertical and horizontal section.

Trace fossil analogues can be found for several of the modern traces described in this study. Of these, perhaps the most studied is that of callianassid burrows whose

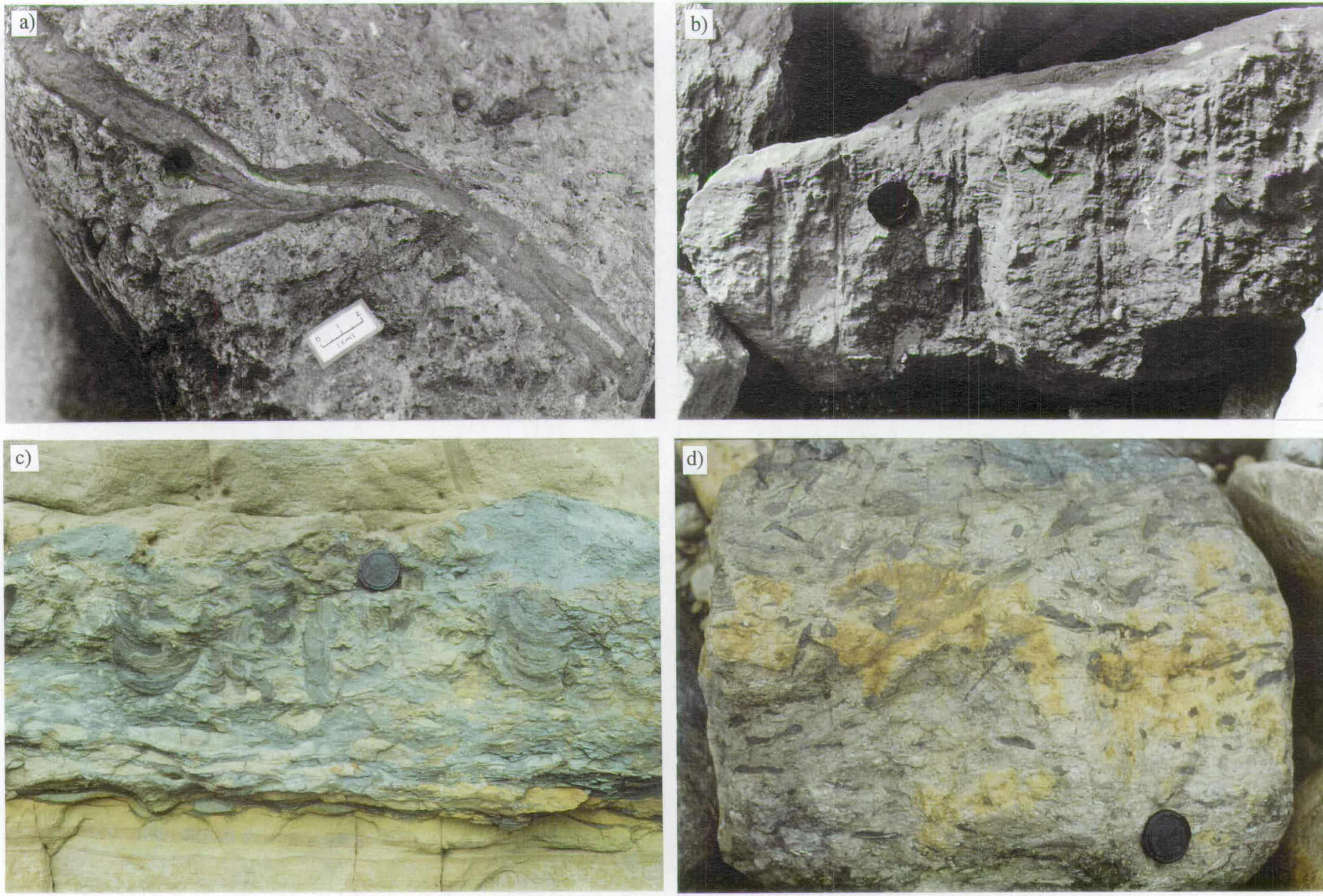


Plate 4.1 Whole burrow preservation: **a)** a potential analogue for alpheid burrows; note the disused side branches (from Pinhay Bay, Lower Jurassic, Dorset). **b)** *Skolithos* an ancient analogue for *Dotilla* burrows (from Bridport Sands, Lower-Mid Jurassic, Dorset) and **c) and d)** Bioturbate textures resulting from the complete biologica reworking of the substrate; few individual burrows are seen - a general mottled texture with lenses and streaks of contrasting lithologies is all that indicates biogenic activit

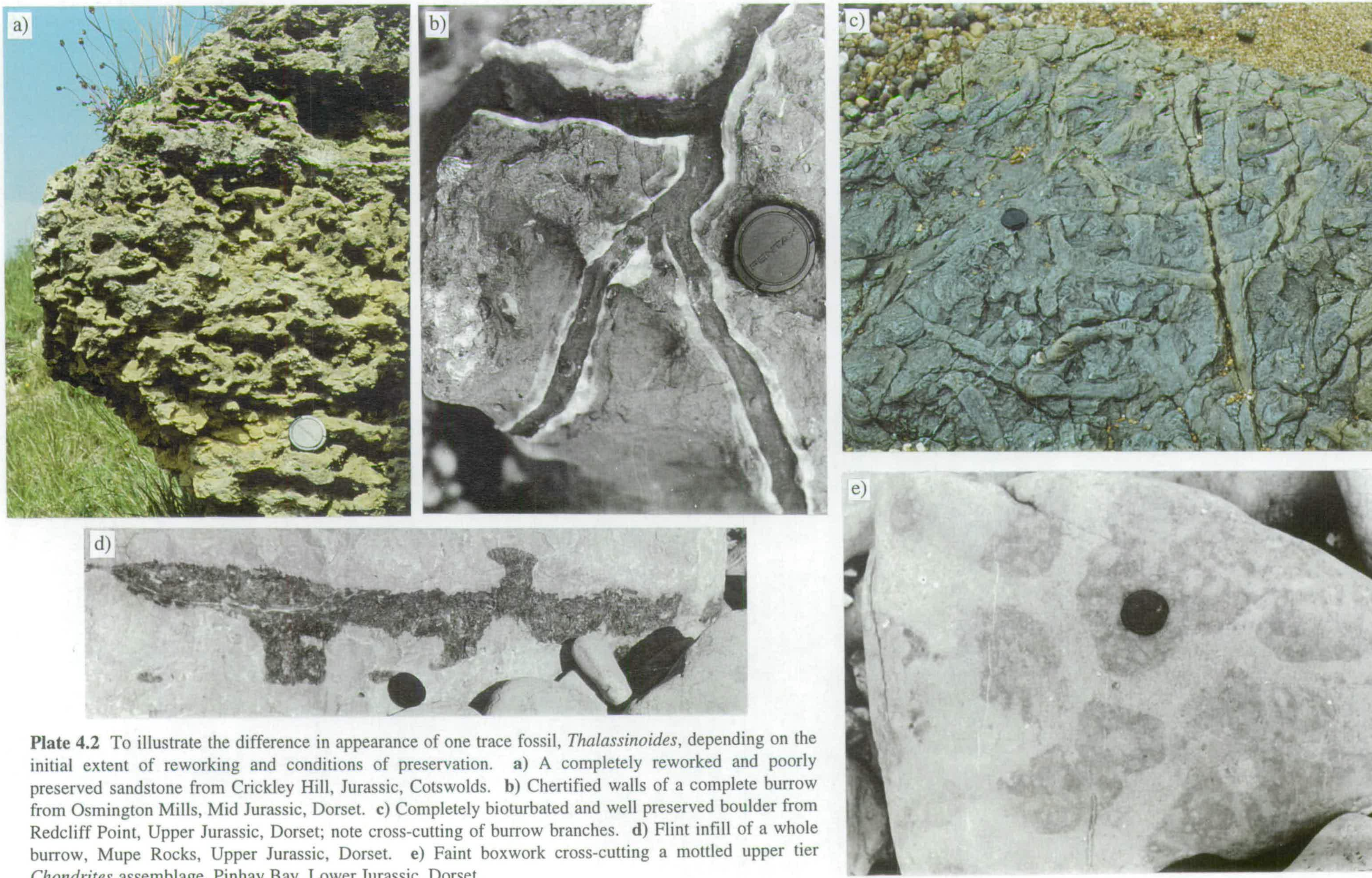


Plate 4.2 To illustrate the difference in appearance of one trace fossil, *Thalassinoides*, depending on the initial extent of reworking and conditions of preservation. **a)** A completely reworked and poorly preserved sandstone from Crickley Hill, Jurassic, Cotswolds. **b)** Chertified walls of a complete burrow from Osmington Mills, Mid Jurassic, Dorset. **c)** Completely bioturbated and well preserved boulder from Redcliff Point, Upper Jurassic, Dorset; note cross-cutting of burrow branches. **d)** Flint infill of a whole burrow, Mupe Rocks, Upper Jurassic, Dorset. **e)** Faint boxwork cross-cutting a mottled upper tier *Chondrites* assemblage, Pinhay Bay, Lower Jurassic, Dorset.

morphology can be almost identical to that of the trace fossils *Thalassinoides* and *Ophiomorpha* (compare Fig. 3.7 and Plate 5 of modern callianassid burrow structure with Plate 4.2, *Thalassinoides*). Häntzschel (1975) describes *Thalassinoides* as:

> "Cylindrical burrows forming 3-dimensional branching systems consisting of horizontal networks connected to surface by more or less vertical shafts; burrows....typically 10-15mm....in diameter; regularly branching, Y-shaped bifurcations;.....typical swellings at points of branching....undoubtedly feeding and dwelling burrows of crustaceans....."

Thalassinoides has a smooth outer as well as inner wall (Plate 4.2), whereas *Ophiomorpha* has a 'knobbly' outer wall due to its pelletoid nature. It was not possible to see the wall structure of the intertidal callianassid burrows in Phuket; the airlift does not operate in such shallow water, and any other form of excavation produces such large amounts of suspended sediment visibility is reduced to zero. Excavation at low tide resulted in a pit, full of a dark grey soup of water and sediment, whose sides frequently subsided inwards; burrow structure was only revealed by resin casts and by tracing the orientation of uncast burrow parts by touch. These methods showed that the interior burrow walls were smooth, but were unable to describe the exterior walls. Subtidal burrows were seen during airlifting to have a smooth interior surface to the walls and there was no evidence for a knobbly exterior. The fossil equivalent is therefore *Thalassinoides* rather than *Ophiomorpha*.

The trace fossils created by *Dotilla* burrows are likely to be of the *Skolithos* type. To quote Häntzschel again, they are:

> "straight tubes or pipes perpendicular to bedding and parallel to each other, subcylindrical, unbranched; 1-15mm in diameter, constant for each tube; few cm up to 30cm long;...tubes commonly closely crowded; frequent on arenaceous sediments."

Although usually attributed to worms, I suggest that crabs such as *Dotilla* are an equally good explanation of the *Skolithos* trace fossil, given their close similarity. Plate 4.1b shows an example of *Skolithos* from the Corallian beds of Dorset; compare with the structure of modern *Dotilla* burrows from Phuket (Fig. 3.1).

The third of the crustaceans studied in detail here, the alpheid shrimp, is the least comparable to any described trace fossil. With its upper parts regularly changing position, it could form a highly complex trace fossil with a sloping lower portion and a radially branching upper part, each branch being oblique to the bedding plane and thus forming an inverted cone of burrows (see Fig. 4.1b). Alternatively, if only the open part of the burrow is preserved, a fossil similar in shape to the resin casts made in this study will result. Plate 4.1a shows the possible appearance of an alpheid trace fossil. A summary of possible ancient analogues for other burrows and traces seen in Phuket is given in Table 4.1.

Table 4.1 Possible trace fossil analogues for modern traces seen in the Phuket sediments.

Modern trace	**Possible trace fossil analogue(s)**
Ghost crab burrows	*Psilonichnus*
Starfish resting trace on the sediment surface (intertidal)	*Asteriacites*
Intertidal sipunculid burrows	?*Dactyloidites* ?*Chondrites* ?*Diplocraterion* ?*Arenicolites*
Intertidal radial trails on the sediment surface	?*Asterosoma* ?*Phoebichnia* ?*Glockeria* ?*Micatuba*
Subtidal 10cm layer	?*Palaeophycus* ?*Planolites*
Intertidal anemones	various radial or medusoid traces (see Häntszschel 1975)
Various tracks and trails (intertidal and subtidal) made by crabs, gastropods, sea urchins,	many repichnia have been described; none quite fit the trails seen here.

The sub-surface burrow structure and the mode of feeding is uncertain for the intertidal sipunculids, hence the variety of possible trace fossil analogues. The only part of the structure that is certain is that the burrow below the surface faecal cast extends vertically down into the sediment for at least 30cm. If the burrow is a J-shape and the bottom part moved as the worm mines the sediment for food, a trace fossil like *Dactyloidites* (Bromley 1990) could be produced. If the worm inhabits the vertical shaft and then makes repeated probings into the surrounding sediment, a *Planolites*-type structure will result. It is less likely that an *Arenicolites* or *Diplocraterion* trace will be produced, as these are both based on a U-shape structure, and there was no evidence for a second entrance in these burrows.

Various biogenic sedimentary structures are also seen on the sediment surface (see Plates 3.1, 3.4, 3.6, 3.7, 3.8, 3.9). These raised structures on the sediment surface may also be preserved in semirelief at the boundary between the buried and burying deposits. The type of substrate that animals move across affect the type of trace that is produced; damp sand and muds allow the formation of individual 'footprints', whether these are crab appendages, gastropod shell grooves or sea urchin spines. In contrast, loose sand will collapse into the trail as the animal moves on, leaving only a simple groove.

4.5 PRESERVATION UNDER CONDITIONS OF CONTINUOUS STEADY SEDIMENTATION

4.5.1 Preservation of tiering

In an environment of continual slow deposition of sediment in Phuket all tiers will keep up with the sediment surface. With time, the deepest tier's structures will be found in the areas that were once the surficial sediments and will therefore cut through these old upper tier structures. Depending on the rate of sedimentation and the thoroughness of the burrowing by the deep tier animals, the original upper tiers may be completely reworked by the newer deep tier structures (Plates 4.2(c and d) and 4.3). The eventual texture will be one comprised solely of the deepest part of the deepest tier (callianassid or alpheid depending on distance from the reef front). For example, in the callianassid area, the texture will be one of branching tubes and finger-like shelly pockets bounded by walls with smooth interiors, with patches of coarse material also found outside the burrow walls (Fig. 4.2b).

4.5.2 Prograding reef sediments (subtidal)

The crustaceans studied in this paper are found in mutually exclusive zones moving seawards. Just off the reef are the near-reef alpheids, giving way to off-reef alpheids a little further offshore and further still the callianassids (Fig. 3.12). Their distributions are probably limited by the nature of the sediment texture and thickness, which varies with distance from the reef front (Appendix B). As distance from the reef increases, the total sediment thickness increases, as does the thickness of the fine-grained upper layer. Thus the abundance of large particles in the upper sediments decreases away from the reef.

In a situation of steady slow reef growth and continuous slow sedimentation on the fore-reef sediment slope the prograding reef and sediment slope will move seaward over time. In this way, the position of the modern day slope will, in time, lie under a future reef and a shallowing upward sequence will be formed. A section through this sequence will show beach sediments overlying coral reef and then sediments characterised by alpheid and

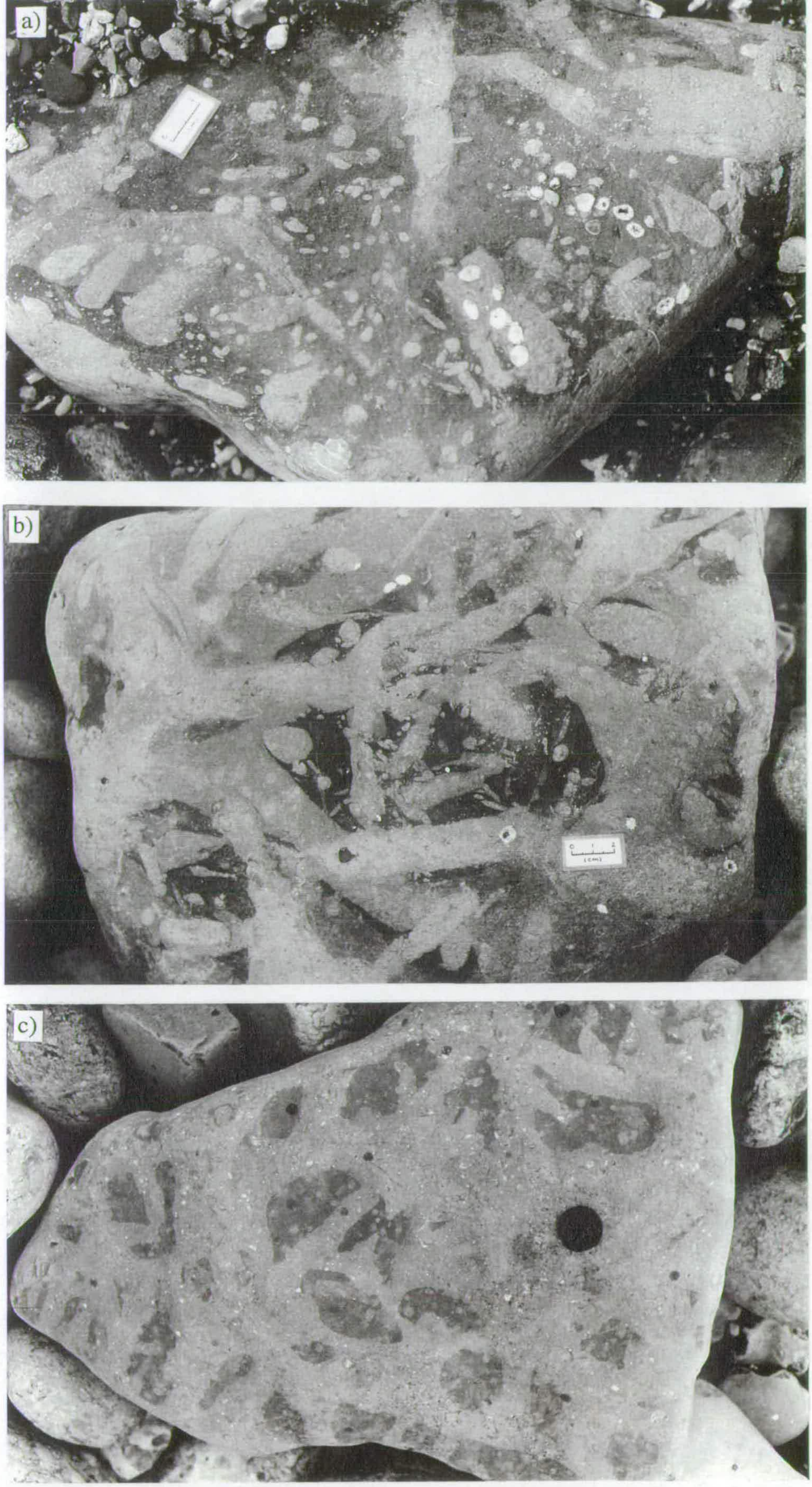


Plate 4.3 Tiering: Deep tier *Thalassinoides* cross-cutting a variety of smaller (shallower tier) *Chondrites*-type trace fossils. Increasingly slower deposition from **a)** to **c)** allowed more thorough reworking so that progressively less of the dark background rock can be seen. All from Pinhay Bay, Lower Jurassic, Dorset.

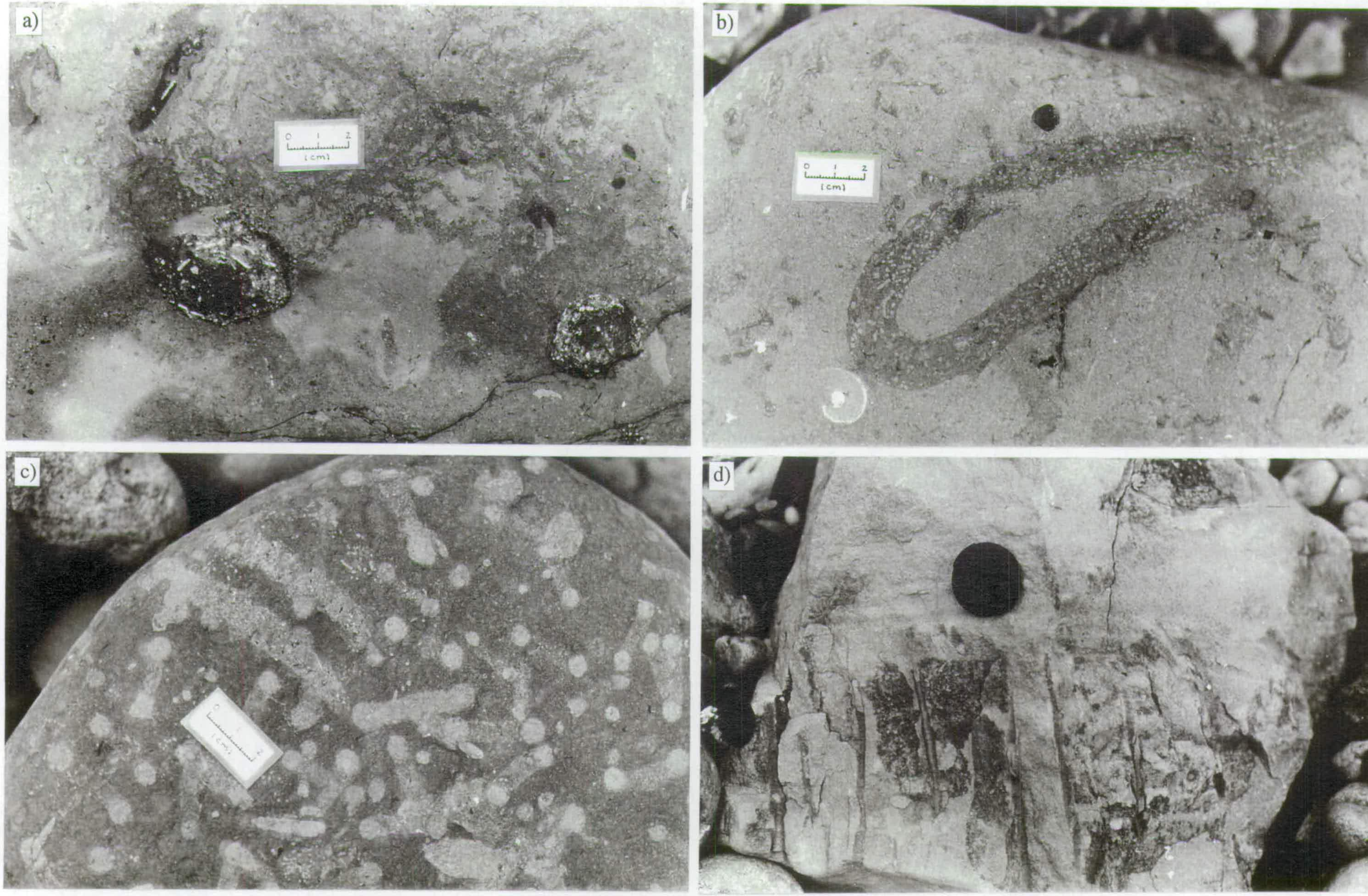


Plate 4.4 **a)** Coarse infill of the two large burrows seems oriented parallel to the edges; this may have been placed there by the animal or could be a tubular tempestite. **b)** Infill of the large U-shaped burrow has been reburrowed by smaller *Chondrites* **c)** Coarse infill in marked burrows is irregularly arranged. **d)** The sudden deposition of a large volume of sediment has buried these vertical *Skolithos* burrows under a deep layer of unburrowed sediment. Photos a) to c) are from Pinhay Bay, Lower Jurassic, Dorset, d) is

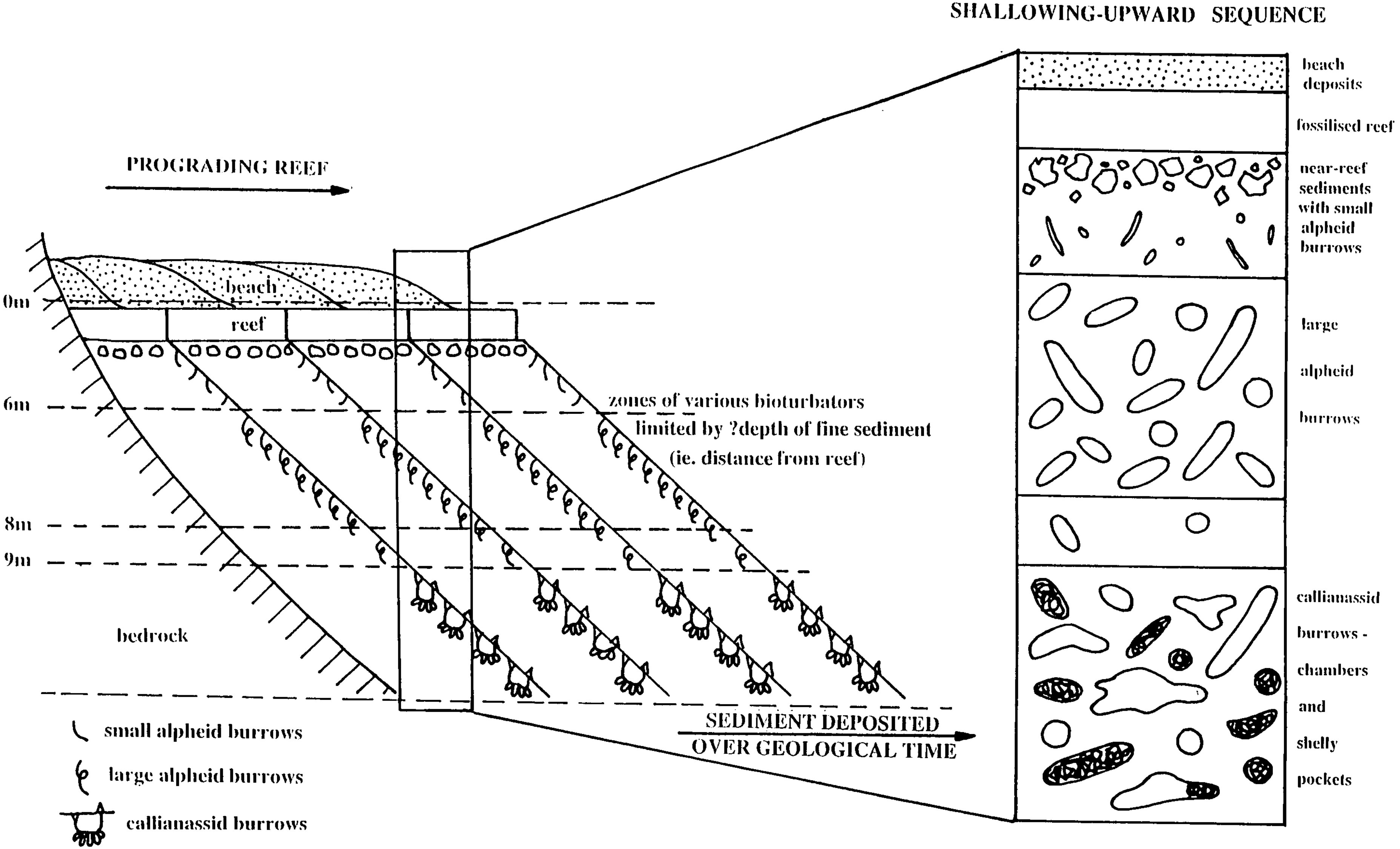


Figure 4.3 The preservation of subtidal sediments under conditions of slow, steady sedimentation and reef growth. The prograding reef and sediment slope will form a shallowing upward sequence, characterised by different trace fossils.

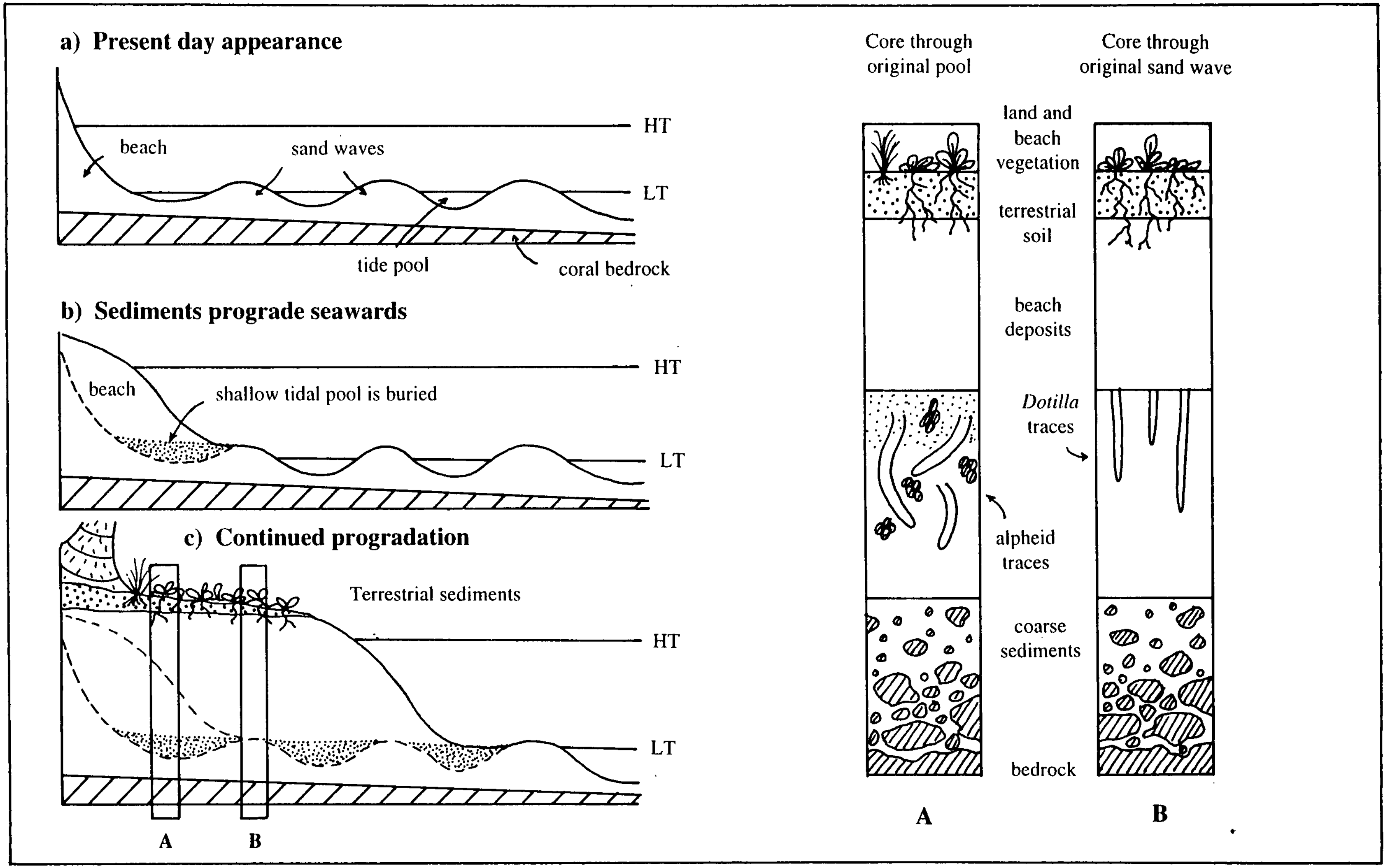


Figure 4.4 The slow progradation of intertidal sediments will result in a shallowing upward sequence which will be laterally heterogeneous due to the different appearance of intertidal sand wave and tidal pools sediments and infauna.

then callianassid traces (Fig. 4.3). These different zones of sediment should be recognisable by the biogenic features of the deep tier burrows as described in section 3.4.

4.5.3 Prograding sediments (intertidal)

Like the subtidal area, the intertidal sand flat environment is also divided into zones of animals, but not in such a clear sequence from inshore to offshore. The burrowers have a more patchy distribution due to the alternating habitats of sand waves and pools. The centre of the bay, which is not sheltered from the sea by reef, is of a coarser sediment type than the more muddy, sheltered corners of the bay and this also affects the animal distributions, though these muddier areas were not studied in detail in this work.

Whereas the subtidal sediments form a slope which will prograde outwards in a relatively predictable manner, the intertidal sediments have a more complex profile of sand waves and intertidal pools. The furthest inshore of these pools are very shallow and silty (Plate 1.1b) , indicating a build up of fine sediments under low energy conditions. The sand waves either move very slowly across the bay or remain stationary for long periods of time (?decades) before moving some distance (Scoffin pers. comm.), so it is likely that sedimentation in Tang Khen Bay occurs by the filling in of the inshore pools and the advancing of the beach sediments over them. As the inshore pools become very shallow they will become less suitable for burrowers as they will be exposed to the heat of the sun for long periods every low tide or may even dry out completely. In the latter stages of an inshore pool there will probably be little activity by alpheids (none were seen there in 1994/5) and their burrows may therefore be poorly preserved. It is unlikely that creatures such as *Dotilla* will start to use the pools for burrowing and feeding as the sediment is probably too fine. Eventually beach crest vegetation, such as the beach vine *Ipomoea* and eventually larger bushes and trees, will colonise the beach sands and a terrestrial soil will form over the sand. Cores taken through the sediments would therefore show a sequence moving down from terrestrial soil through beach sediments through sand wave or pool sediments to the carbonate bedrock below. There may be some cross-cutting of burrows; beach burrowers, such as ghost crabs, form extremely deep burrows (at least 50cm deep) which could cut through old pool sediments and plant roots could similarly penetrate beach sediments or even pool sediments. Fig. 4.4 is a schematic representation of this hypothesis.

4.6 EFFECTS OF STORM EVENTS ON PRESERVATION

Storms have the greatest impact in the shallowest water so the intertidal area would be most affected, especially by erosion but also by deposition. The beach in Pump House Bay was changed from a sandy beach into coral shingle during the 1986 storm. It is likely that most intertidal sediments would be completely reworked by a storm and that few pre-storm features would remain. The only exception to this might be the deeper reaches of the callianassid burrows which might be beyond the reach of a less severe storm and may become infilled with storm debris. The increasingly coarse sediment with depth through the sediments of Tang Khen Bay is most likely to be a concentration of repeated physical disturbance and sorting by physical processes. The following discussion focuses on the more complex picture of the subtidal sediments in Pump House Bay.

Severe storm damage is rare in these study areas; Phuket is not in the hurricane belt and the E (Ao Tang Khen) or SE (Pump House Bay) aspect of the bays usually shelter them from rough weather in the rainy season (SW monsoon). However, in May 1986 a storm from the south hit Pump House Bay, almost completely destroying the reef (live coral cover was reduced to a few corals in the deepest part of the reef; Phongsuwan 1991, Fig. 4.5). A large amount of the destroyed reef was heaped on the beach as piles of branching coral rubble, much of which remains to this day (Plate 1.3). Branching coral debris was also found on the seabed at the seaward edge of the reef in 1995. Such a storm, with force that could destroy a reef to a water depth of 4m, undoubtedly had a major effect on the reef sediments, not only through physical disturbance but through input of reef material (Fig. 4.5).

In August 1988, two years after the storm, Scoffin et al sampled the off-reef sediments at Pump House Bay and described the surface as sandy and rippled, with the <63μm fraction comprising 1% by weight and with few obvious burrows (Tudhope pers. comm. and Scoffin et al 1992; note, their name for Pump House Bay is Shark Point). In contrast, in 1995 the surface sediments consisted of about 40% <63μm fraction (Appendix B) and large numbers of burrowers were present. Cores and airlift excavation of these sediments showed a coarse layer; the mean grain size and percentage gravel (>2mm) fraction peaked at a depth of 30-40cm 40m from the reef front where off-reef alpheids were numerous, and 40-50cm 50m from the reef front where callianassids were abundant (Fig. 3.11). The coarse (>4mm) fraction comprised between 50-75% (by weight) reef-derived

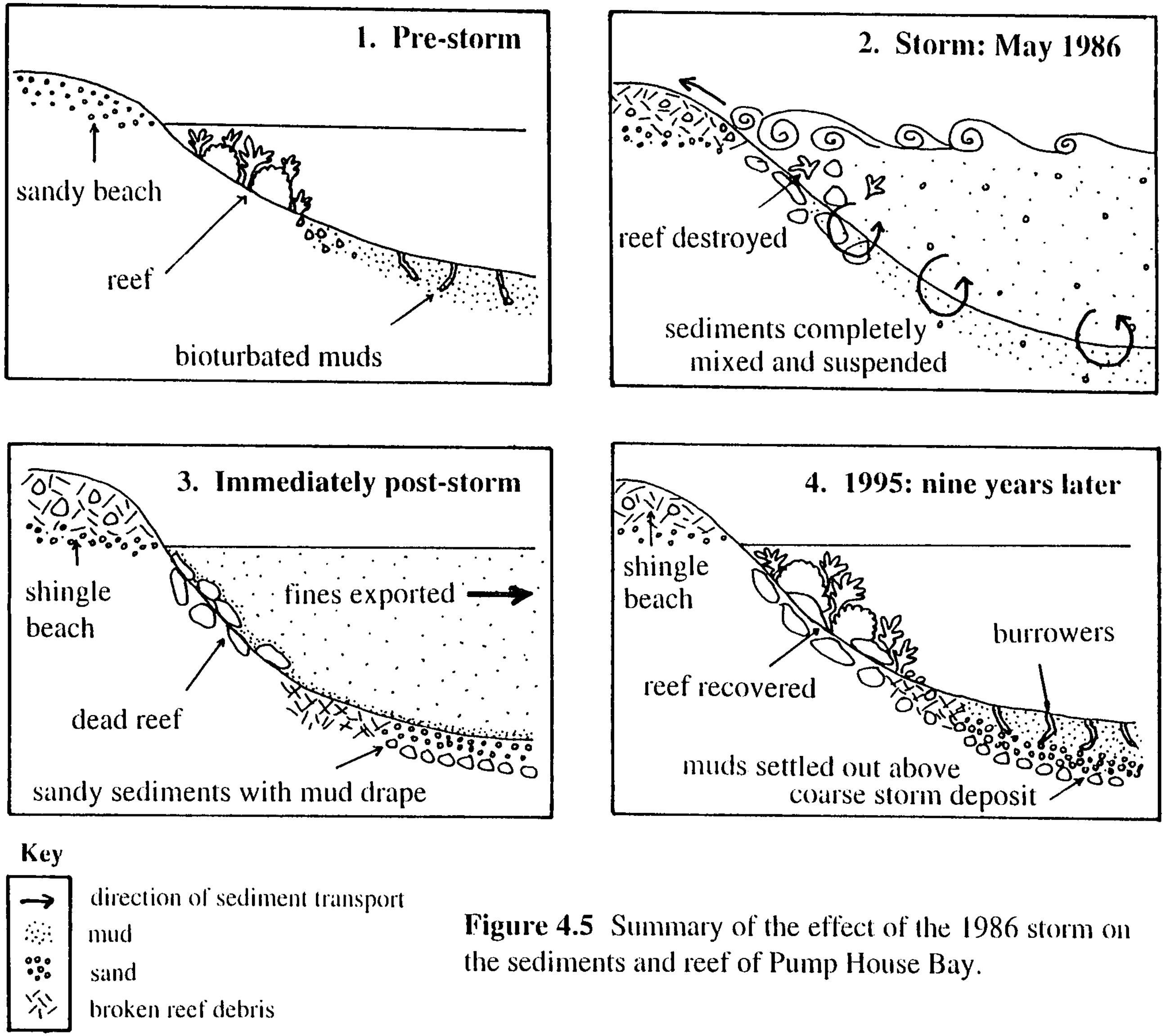


Figure 4.5 Summary of the effect of the 1986 storm on the sediments and reef of Pump House Bay.

remains, such as coral, barnacles and encrusting bivalves, a large part of which was probably laid down during the storm. The rest was infaunal remains such as mollusc shells and echinoderm tests and a tiny fraction of non-carbonate material (Appendix B).

The sediments cored in 1994-5 were sampled in order to determine whether bioturbation effects (burrows or grain sorting patterns) could be discerned in the sediment profile, but it soon became obvious that the situation was much more complex than a simple biogenically sorted sediment. The cores were therefore analysed to see if an explanation could be reached for their grain size distributions, coarse fraction appearance and carbonate content, all of which vary with distance from the reef and distance down the core. In order to decide on the origins of the sedimentary features seen, it is easiest to predict the effects that the different components (physical and biological) will have on the sediment profile (sections 4.6.1, 4.6.2) and then to compare these predictions with what is actually seen (section 4.6.3).

4.6.1 What sedimentary features would be expected in a solely storm-generated sediment sequence?

- A sharp erosional base (possibly with bidirectional tool marks in the sole).
- Base overlain by a coarse lag deposit of reef debris, with shells often convex-up and fragmented. This coarse layer could be the result a single or multiple storms (condensed horizon; Aigner and Reineck 1982).
- A coarse deposit overlain by a fining-upwards sequence from gravel to sands to muds. The thickness will depend on the amount of transport that has occurred during the storm. All levels of the sequence may contain coarse reef material as it continues to come loose from the reef during the depositional phase. There may be other smaller fining upwards sequences above the major one as a results of smaller storms.
- The finer layers may show some evidence of wave-generated structures (parallel or low-angle laminae with internal discordances and deposition from suspension pulses) and also wave-ripple lamination and wave ripples (abating or post-storm bedload movement; Aigner and Reineck 1982)
- In Phuket, it is likely that a net export of fines occurred leading to the overall increase in coarse fraction and lack of muds 2 years after storm.

4.6.2 What features would be expected in a solely biogenically-generated sediment sequence?

The different crustaceans present each have a different effect on the subtidal sediments in which they live (Fig. 4.6). The details of this bioturbatory activity are given in section 3.4, but a brief summary is given below, giving the expected sediment appearance if the burrowing community was quite dense and had thoroughly reworked the biologically occupied sediment depth.

Callianassid area:

- A fine-grained, well-sorted surface layer overlying a patchy, poorly-sorted coarse layer below; the boundary between the two should be quite sharp and lie at about 25-30cm sediment depth. The fine layer might show evidence of old mound tubes as sandy-cored vertical shafts and laminations from the repeated piling of sediment in surface mounds. The coarse layer would contain fine material from burrow linings and the grains would be randomly oriented. Shelly pockets would be visible (Plate 4.4b and c).

Off-reef alpheids

- A thoroughly mixed (very poorly sorted) surface layer, of about 15-20cm thickness, overlying a coarser poorly sorted layer where very large grains are biologically winnowed. There may be laminations from repeated piling of sediments at the surface and traces of burrow tubes may be visible as compacted walls running at angle of about 30-45° to the horizontal. The upper 15-20cm will be much more heavily bioturbated than the layer below.

Near-reef alpheids

- A very coarse basal layer next to the bedrock with a patchy mixture of coarse and fine sediment above; all sediments poorly sorted and traces of burrows running through the entire sediment thickness.

4.6.3 What is ACTUALLY seen in Pump House Bay core sediments?

- The near-reef sediments are less fine at the surface than those of the off-reef alpheid and callianassid areas; for the top 0-10cm sediment, mean grain size was 0.24ϕ (847μm) in the near-reef alpheid area, 2.58ϕ (167μm)in the off-reef alpheid area and 4.19ϕ (55μm) in the callianassid area (Appendix B, Fig. 3.11).

- The surface fine layer increases in thickness moving offshore; see Table 4.2 below for comparisons of amounts of mud (<63μm) and gravel (>2mm) fractions in the three areas cored.
- Sorting is very poor throughout all cores in all areas at all sediment depths (Table 4.3)
- There is a gradual increase in mean grain size moving down all cores in all areas, with a coarse peak at 30-50cm or 40-60cm sediment depth in the off-reef alpheid and callianassid areas respectively (Fig. 3.11).
- The beach is made entirely of coral shingle and behind the present shingle beach is evidence of past storms in the shape of banks of coral debris (Plate 1.3).

Table 4.2 Changing grain size characteristics through the sediment in the three subtidal sediment areas.

	% of sediment that is <63μm fraction			% of sediment that is >2mm fraction		
Depth (cm)	near-reef alpheid area	off-reef alpheid area	callianassid area	near-reef alpheid area	off-reef alpheid area	callianassid area
0-10	28.9	38.59	58.13	30.3	14.95	2.00
10-20	21.4	42.22	42.16	43.23	11.17	7.76
20-30	14.08	34.65	41.23	54.83	13.61	9.61
30-40	7.59	22.9	31.79	70.88	25.54	11.97
40-50		19.08	21.09		25.59	17.61
50-60		21.6	17.19		22.56	16.91
60-70		20.83	25.87		20.83	12.71
70-80		21.11	31.96		19.37	7.18
80-90		19.16	26.43		20.26	7.69
90-100		23.68	24.58		17.49	10.73
100-110			24.95			5.21

Table 4.3 Sediment sorting for the three subtidal sediment areas. (Values 2-4 indicate very poor sorting. >4 indicate extremely poor sorting)

Depth (cm)	**Near-reef alpheid area**	**Off-reef alpheid area**	**Callianassid area**
0-10	4.35	3.37	2.91
10-20	3.79	3.32	3.17
20-30	3.37	3.41	3.22
30-40	2.5	3.43	3.31
40-50		3.56	3.07
50-60		3.28	2.88
60-70		3.12	3.08
70-80		3.12	2.84
80-90		2.96	2.68
90-100		3.09	2.70
100-110			2.48

The question remains; what do the present sediments of Pump House Bay tell us about their depositional history? Are they a) biogenic deposits, b) storm deposits or c) a combination of the two? Table 4.4 summarises the evidence for and against the Pump House Beach sediments being any one of these three categories. The evidence is discussed further below.

Table 4.4 Summary of the evidence for and against the main controls on subtidal sediment appearance at Pump House Bay.

REASON FOR SEDIMENT APPEARANCE	Evidence FOR	Evidence AGAINST	Evidence AMBIGUOUS / ABSENT
Solely BIOGENIC influence	**Patchy appearance of sediment,** especially in coarse layer **Coarse fraction** more degraded in alpheid than callianssid area	**Alpheid- and callianassid-dominated areas show the SAME features,** despite the animals having different sorting effects on the sediment	**Coarse material in the upper sediment layers**; this would be expected from alpheid mixing, but not from callianassid sorting. However, it may be that animals have not been there long enough or in high enough densities to achieve this?
Solely PHYSICAL influence (Storm lag and shallowing upward sequence)	1. **Coarse layer** at 40-60cm sediment depth (callianassid area) and 30-50cm (off-reef alpheid area). 2. **Fining-upwards** from the coarse layer in all three areas cored.	**Patchy nature of coarse layer**	1. **Presence of reef-derived skeletal grains offshore**; some physical force must be required to get the reef debris off the reef and >50m offshore in such large quantities. However, its presence at depth in the sediment could be due to physical or biological processes. 2. **No evidence of laminations or coarse grain orientation.**
Mixture of biogenic and physical storm influence - tubular tempestites	None	1. **Coarse layer is too coarse?** No finer matrix as described in tubular tempestites by Tedesco and Wanless (1991). 2. **Peak in coarseness -** Tedesco and Wanless (1991) describe tubular tempestites as being massively bedded. This can be more easily explained as a storm lag. 3. **No evidence of oriented grains in coarse patches.**	1. **Patchy nature of coarse components** - could result from storm-infilling of burrows or bioturbation of a storm deposit. 2. **Coarse skeletal material has a mixture of origins** - this could result from storm lag, storm infilling of burrows or bioturbation 3. **Broken, abraded and bored skeletal material in burrow infill.** Grains could be repeatedly exposed by numerous storms or biological reworking

4.6.4 Discussion

The sedimentary characteristics described above (surficial fine sediment increasing in thickness and decreasing in grain size moving offshore) are much as would be expected with decreasing energy levels moving offshore. Increasing distance from the reef means decreasing energy levels due to increasing water depth and greater amounts of fine sediment can therefore settle out. Greater proximity to the reef also increases the input of coarse reef debris, therefore increasing the amount of >2mm sediment and consequently mean grain size in near-reef sediments.

The coarse layer is nearer the sediment surface in the near-shore sediments than those offshore, but it is present in *all* sediments, which would not be expected if bioturbation was the sole reworking force. Callianassids and alpheids should produce different looking sediment profiles but this is not the case; the sediments appear identical except for the slightly thicker fine layer in the callianassid area. This strongly suggests that the major factor determining the appearance of the sediments in Pump House Bay is a storm event.

The presence of cobble- to boulder-sized reef debris near to the underlying bedrock (in intertidal and near-reef sediments) is to be expected as storms or rough weather completely reworking the sediment will winnow them downwards. Even if the boulders are too big for the storm to move, surrounding finer sediments can be mixed into the water and later redeposited, coarsest first, around the larger boulders which will effectively have sunk downwards. Burrowers will do the same by avoiding the large immovable pieces and thus passively burying (or biologically winnowing) them downwards.

It is likely that transport of fines occurred in the area during or directly after the 1986 storm; the sediment was described as being coarse and sandy with ripples in August 1988 (Tudhope pers. comm., Scoffin et al 1992). Around Laem Panwa the currents are quite unpredictable (in some places unidirectional, despite tides, or certainly stronger in one direction than another) so it is not impossible that the bulk of the storm-suspended fine sediment could have been transported elsewhere. The direction of transport could have been to Tang Khen Bay or to Ao Chalong depending on the exact direction of the wind and the state of tide (i.e. direction of tidal currents). If the fine layer did not get deposited for at least two years after the storm, the sediment must have originated from background levels of fine material (from terrigenous and reef sources) settling out.

It is likely that weakened reef will continue to 'shed' pieces of weakened coral into the sediment during the depositional phase and possibly for some time after the storm. This may explain the poorly sorted though generally fining-upwards nature of the sediments in Pump House Bay.

There is also evidence that biogenic activity affects also the appearance of the sediments, especially looking at the structures that are plainly visible when casting and airlifting and the results of the tracer sediment experiments. However, biogenic effects are less obvious if cores and particle size distributions are analysed.

Although clearly a result of a mixture of biogenic and physical processes, these sediments do not show tubular tempestites, as described by Wanless et al (1988) and Tedesco and Wanless (1991). At best the evidence is ambiguous; the patchy nature of coarse components and the fact that they derive from a number of sources and are broken, abraded and bored to some degree could mean they are the result of bioturbation of previous storm deposits and not necessarily the product of storm-infilling. None of the features described by Tedesco and Wanless (1991) as being diagnostic of tubular tempestites (e.g. the presence of a fine matrix around the coarse infill resulting from the slurry of material entering the burrow during the storm, massive bedding of the tubular tempestites and grains oriented tangentially to the burrow walls) are seen in these sediments.

4.6.5 Summary of storm discussion:

1. There is no solid evidence that these coarse deposits are tubular tempestites.
2. Most evidence seems to point to the coarse layer being a storm deposit (lag).
3. There may be some overprint of biogenic activity but the animals are not present in high enough densities and have not been there for long enough (only since 1988 at the most) to have really reworked the sediments. Physical influences (waves and tidal currents) are likely to be far more important in this shallow water. Storms will only add to this and the frequency of high energy events will be all important in controlling the amount of biogenic activity recorded in the rock record.

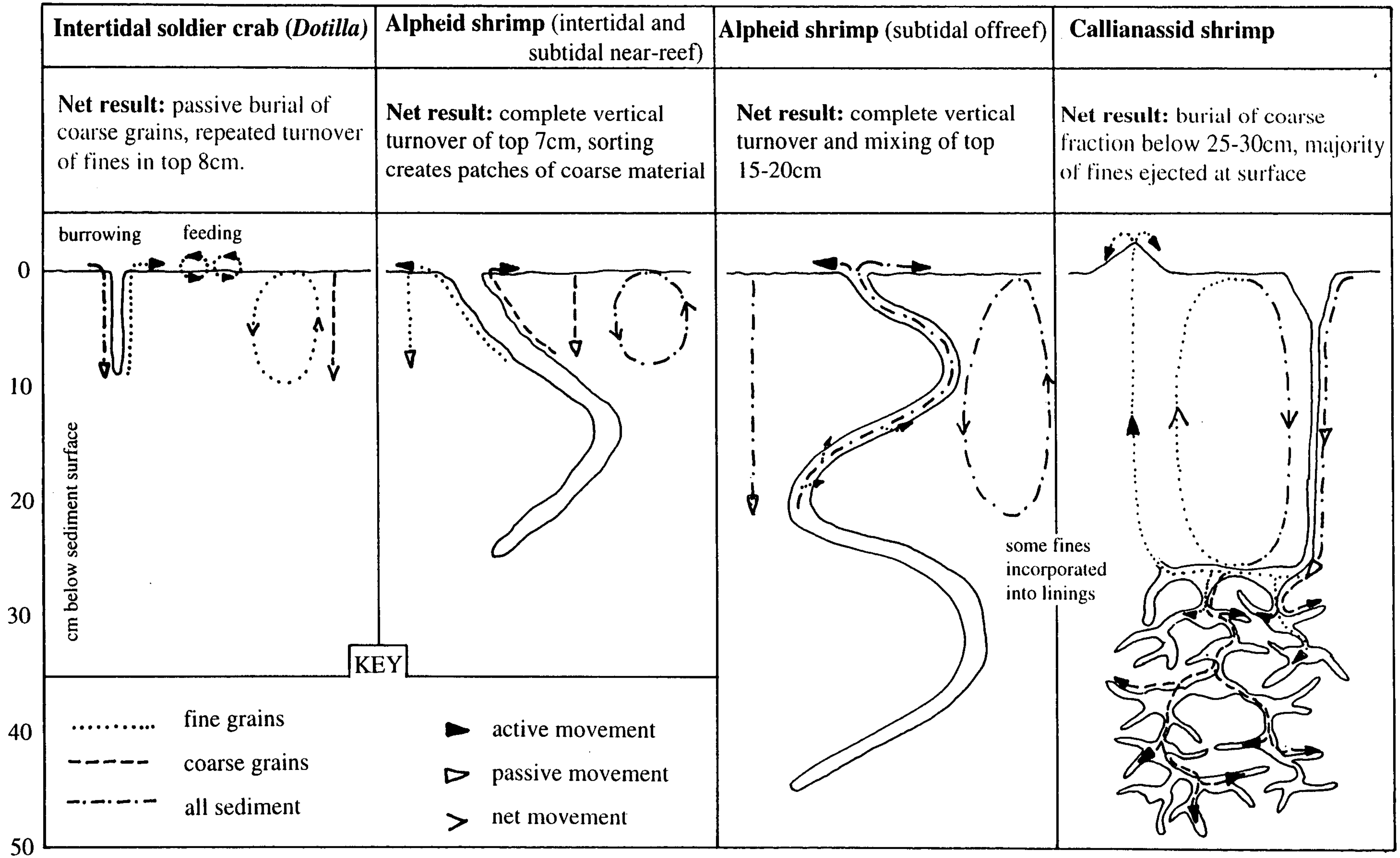


Figure 4.6 A summary of the sorting and/or mixing effects of the main bioturbators in Phuket.

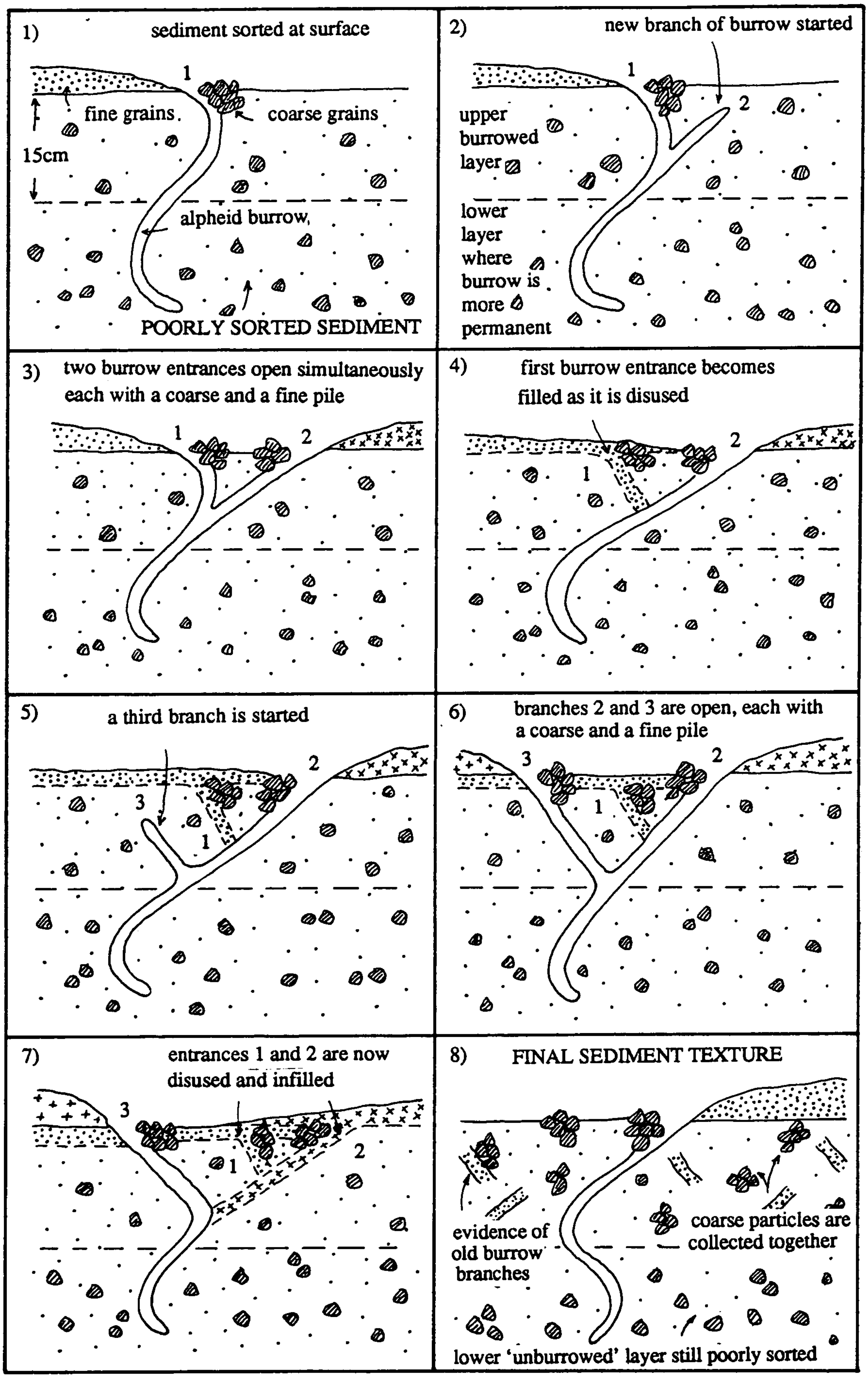


Figure 4.7 Proposed effect of intertidal and near-reef subtidal alpheids on the surrounding sediments

4.7 IMPLICATIONS OF BIOTURBATION FOR THE PRESERVATION OF GRAINS AND TRACES IN PHUKET

4.7.1. Differential preservation due to sediment sorting during bioturbation

The crustaceans in this study continually turn over the upper part of the sediment in which they live. Each kind of crustacean has a different sorting effect (Fig. 4.6, 4.7) which has important implications for the taphonomy of the grains. Grains brought to the surface are likely to suffer erosion, mainly through physical abrasion and microbioerosion. The dominant groups of microborers are filamentous green algae, cyanobacteria and fungi which cause either direct solution and/or structural weakening of the grains. Once grains have been attacked their surface area is greatly increased, which in turn makes them more susceptible to further breakdown. Grains buried at depth (e.g. by passive burial by *Dotilla* or active burial by callianassids) will escape this degradation.

Callianassids preferentially bring only the fine sediment to the sediment surface, burying coarser grains at depth. In contrast, alpheids excavate all grain sizes, up to particles several centimetres in size, bringing them to the surface. It would therefore be expected that shell and coral debris in an alpheid area would show much more evidence of physical abrasion and microbioerosion than those from a callianassid area.

This hypothesis was tested in a semi-quantitative way by examining >5mm infaunal bivalve shell fragments from two cores, Core 42 from the subtidal callianassid area and Core 44 from the off-reef alpheid area. A skeletal grain from an infaunal organism was chosen, as any signs of damage were likely to have occurred due to processes in or on the sediment since the organisms' death. In contrast, reef-derived debris could have spent variable amounts of time on the reef subjected to surface processes before entering the sediment. Bivalves were chosen as they were common throughout both cores. Shells were scored on a relative scale for degree of rounding of the fragment edge and ornamentation and also for the degree of shininess. Extent of microbioerosion and encrustation was also noted. Although not statistically significant, it can be seen from Fig. 4.8 that grains from the alpheid area have more rounded edges, more eroded ornamentation, are duller and more microbioeroded when compared to those from the callianassid area, as hypothesised. This is evidence for a taphonomic bias to preservation; skeletal grains in an alpheid area are less likely to be well preserved than those from a callianassid area.

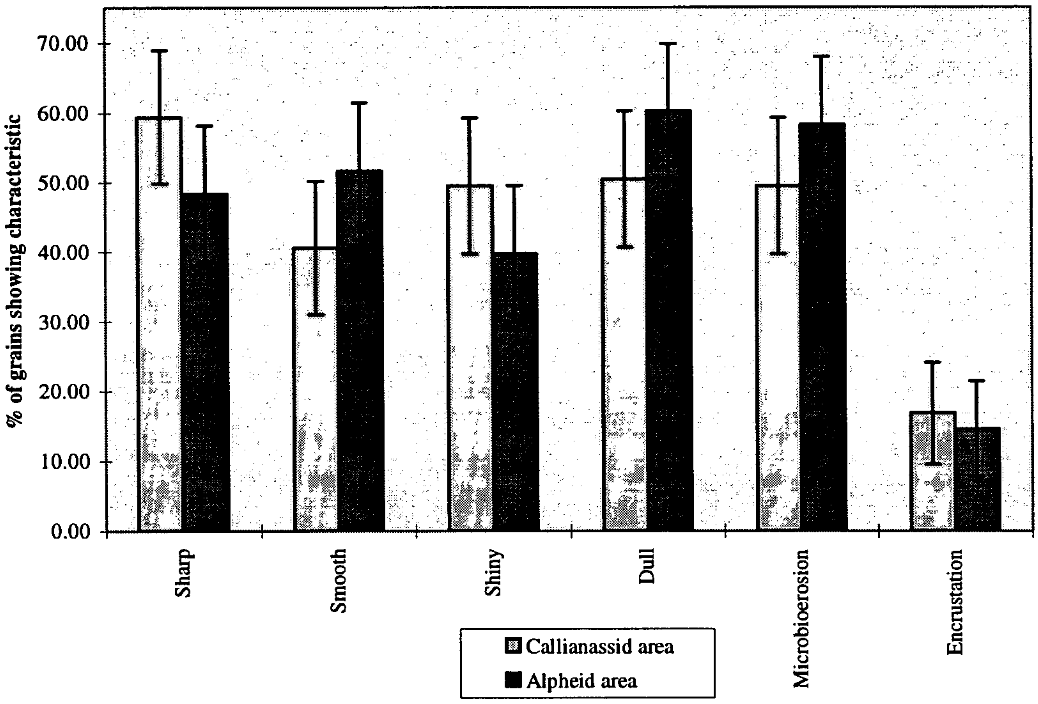


Figure 4.8 A comparison of skeletal grain degradation in off-reef alpheid and subtidal callianassid areas. 'Sharp' and 'smooth' refer to the degree of roundedness of the grain edges and shell ornamentation, 'shiny' and 'dull' to the general freshness of the shell surface. Error bars show 95% confidence limits. Full data in Appendix B.

The patchy distribution of calcareous gravel produced by sorting by intertidal and near-reef alpheids and callianassids will also affect the overall sediment texture in the geological record; see section 4.7.2.4.

4.7.2 Turnover of sediments by bioturbation

4.7.2.1 Time taken to turn over the burrowed layer and to incorporate settling sediments

Turnover rates for each of the animals studied have been calculated; see sections 3.3.1.4, 3.3.2.4, 3.3.3.3, 3.4.1.3 and 3.4.2.3 for details of the calculations and Table 3.7 for a summary of the figures obtained. These figures should be taken only as an indication of rates of turnover, not as absolute values, and should be compared with each other only on a order of magnitude scale. This is because i) different methods were used to obtain the figures for different burrowers and ii) the methods themselves only provide an estimate of rates. For example, intertidal callianassid rates were obtained by calculating mound volumes which probably results in an underestimate of total turnover as it does not account for removal of sediment from the mounds by currents or wave action. In the case of alpheids and callianassids, neither method used takes into account the volume of the more permanent part of the burrow or any subsurface sediment transport within the burrow system (Nickell 1992) as no estimates were obtained regarding the time scales over which these parts are altered.

It is perhaps most useful to think of the turnover rate in terms of the time it takes for the burrowed layer of sediment to be completely reworked (Table 4.5) as this gives some indication of the frequency with which grains are exposed to the surface.

Table 4.5 Turnover rates by crustacean bioturbators given as a thickness of sediment over time

	Turnover rate	
Bioturbator	**cm/year**	**time taken to turn over the depth of bioturbation**
Dotilla	45	top 9cm every 4.7 years
intertidal alpheids	12	top 7cm 1.7x a year
subtidal off-reef alpheids	5.3	top 20cm every 69 years
intertidal callianassids	0.29	top 25cm every 4.7 years
subtidal callianassids	1.55	top 25cm every 16 years

Turnover rates are only useful when compared to the rates of other processes in the area. To put these figures in context, the vertical sedimentation accretion rate on the fore-reef slope is 0.4cm/year (calculated from Scoffin 1997). The relative importance of sediment accretion and bioturbation rate on the fore-reef slope of Tin Smelter Reef were calculated as follows (see also Table 4.6):

1. The area of occupation of each crustacean was calculated using basic trigonometry; the reef edge is 440m long and the fore-reef slope dips at an angle of 5.7° to the horizontal from 3m to 8m water depth over a horizontal distance of 50m (Scoffin 1997). Off Tin Smelter Reef the water depth limits of each crustacean are 3-5m, 5-6.5m and 6.5-8m for near-reef alpheids, off-reef alpheids and callianassids, respectively (observations from dives, this study).
2. Turnover rates in $m^3/m^2/year$ were calculated (for details see Chapter 3) for Pump House Bay sediments. Diver observations indicated that burrowers were present in similar densities off Tin Smelter Reef, so the rates were assumed to be the same in both sites. Near-reef alpheids turnover rates were estimated as being similar to intertidal alpheids, although present at density of $1/m^2$ (i.e. 1/8 the density of intertidal alpheids). Therefore, near-reef alpheids were taken to have a turnover rate of 1/8 that of intertidal alpheids.

3. By multiplying the area of occupation of each animal by its rate of sediment turnover and summing the figures obtained, a total turnover volume for the whole fore-reef slope of 251.7m^3 was calculated.

Table 4.6 Total turnover of sediments by crustaceans each year on the fore-reef slope of Tin Smelter Reef.

Bioturbator	**turnover rate (m^3/m^2/year)**	**area of occupation (m^2)**	**total volume turned over in year (m^3)**
near-reef alpheids	0.015	8844	132.7
off-reef alpheids	0.0029	6644	19.3
callianassids	0.015	6644	99.7
TOTAL		22132	**251.7**

The volume added to the fore-reef slope of Tin Smelter Reef each year is 88m^3 (Scoffin 1997). Therefore the total volume turned over by these crustaceans for the same area (251.7m^3) is **2.9** times the sediment accumulation rate. Grains settling on the fore-reef slope will be rapidly worked into the main body of the sediment.

4.7.2.2 Time averaging

Time-averaging is the mixing of skeletal grains from different generations of animals into a single assemblage in a deposit (Kidwell 1991, Kidwell and Bosence 1991). Thus, an environment in which no vertical mixing occurred would produce a simple sequence in which the further the grains were from the sediment surface, the older they would be. With an active population of burrowers that have an impact at least 60cm from the sediment surface, this relationship becomes blurred. Grains at the sediment surface or 60cm below it may be derived from animals that a) died at the same time, b) a matter of days previously or c) a number of years previously. Vertical mixing of grains by bioturbators thus *increases* the average age (i.e. time since initial deposition) of grains at the surface and *decreases* the average age of grains at depth (Jumars et al 1981).

Scoffin (1997) estimated that the fore-reef sediment slope off Tin Smelter Reef prograded seawards by 4cm every year. For a slope that drops vertically by 5m over a distance of 50m, this is equivalent to a vertical sediment accumulation rate of 4mm/year. At this rate of physical accumulation, 60cm of sediment represents 150 years of accumulation. However, recently dead shells can be also found at this depth due to burial by callianassids so any one sediment level time-averages 150 years.

4.7.2.3 Trace preservation

The relative rates of physical sedimentation and bioturbation are important in determining the eventual appearance of the preserved sediment. As described in the section above, the subtidal bioturbation rates exceed the sedimentation rate by three times. Under conditions of slow physical sedimentation rates such as these, bioturbation will completely rework the physically deposited sediment to produce bioturbate textures of deep tier traces rather than distinct trace fossils.

In these sediments, burrow walls and pellets are completely unlithified, beachrock is absent and the reef framework is unconsolidated. This indicates that calcium carbonate saturation is not as high as in areas such as the Great Barrier Reef where burrow walls become indurated while the burrow is still in use and pieces of solid burrow wall are found in the sediment (Tudhope and Scoffin 1984, Davies Reef lagoon).

The lack of early cementation in the Phuket sediments means that burrows will be compacted by the increasing overburden of sediment. Therefore, the burrows will show an oval as opposed to circular cross-section, or may even be completely flattened, appearing in the rock record as a mottled texture or as lenses of mud within the nodular limestone. Examples of this resulting bioturbate texture are shown in Plate 4.1c and d and Plate 4.5c. Burrow linings were observed to be coarser than the surrounding sediment in the upper layers of these muds, so in contrast to the shelly layer, a mudstone containing sandy or carbonate-rich streaks might be preserved.

Slow sediment accretion is likely to be interrupted by events such as storms (see section 4.6). Storms have left a strong signature the Phuket sediments as a coarse carbonate-rich layer overlain by a finer mud layer. Repeated events like these could lead to alternating shelly and mud layers, the possible origins of a limestone-shale alternation in the rock record. The coarse shelly layer would form a nodular limestone containing finer patches and lenses caused by subsequent bioturbation, and the upper fine layers would become compacted into fine mudstones or shales. The intertidal terraces exposed in Dorset at Pinhay Bay provide a good example of bioturbated limestone shale alternations (see Plate 4.5). In these Upper Jurassic (Corallian) rocks limestone beds form intertidal terraces with abundant *Rhizocorallium* interleaved with finer grey muds.

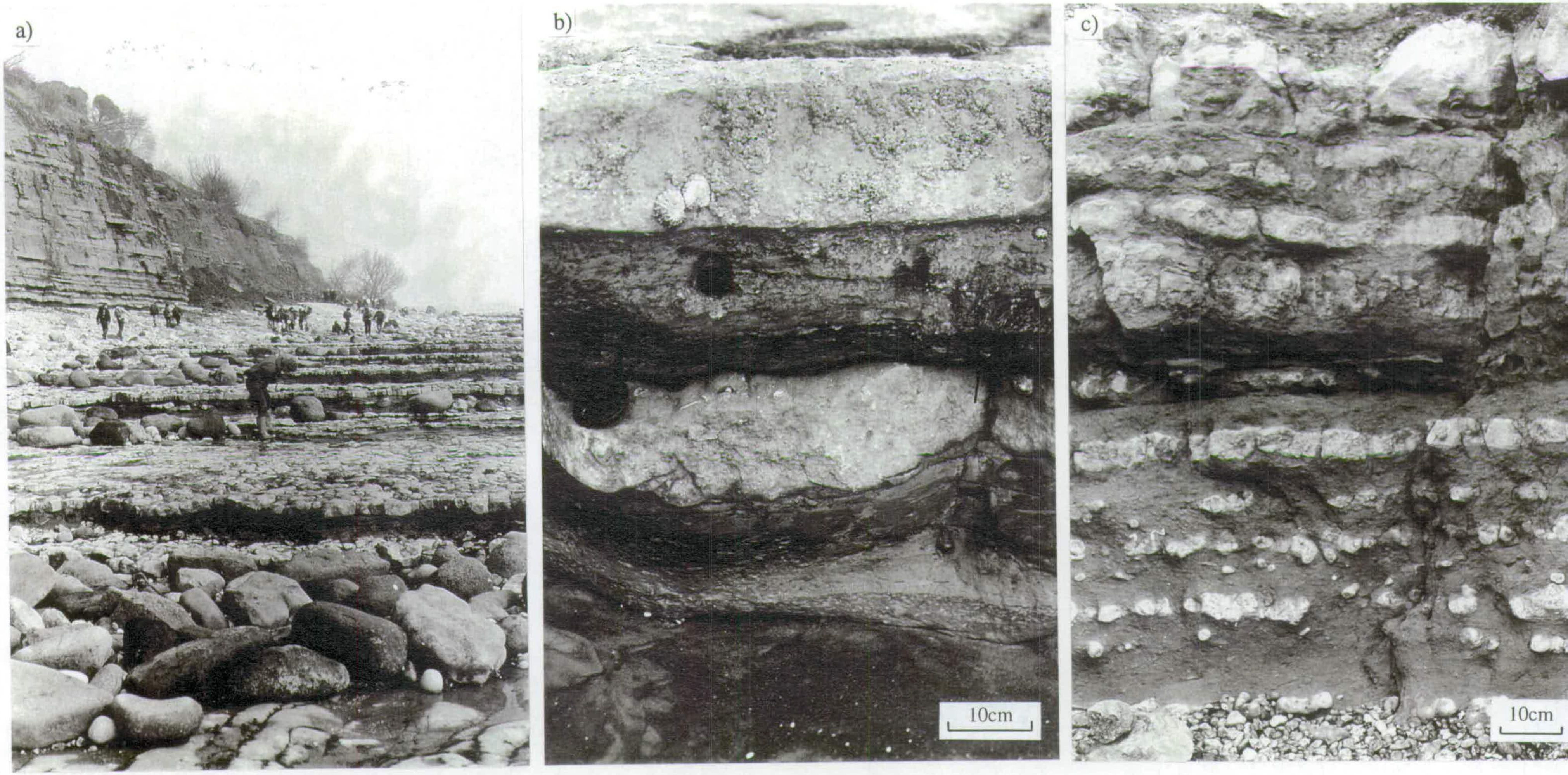


Plate 4.5 Lime-shale alternations. **a)** Hard limestone forms ledges visible in the cliffs and on the shore. **b)** Detail of one of these ledges showing alternating cemented carbonate beds and laminated, organic-rich shales. **c)** *Thalassinoides* forms carbonate nodules in a shale surround. All photos from Pinhay Bay, Lower Jurassic, Dorset.

4.7.2.4 The effect of grain mineralogy on taphonomy in bioturbated areas

In Phuket, the sediments are mineralogically heterogeneous, comprising reef- and infauna-derived skeletal carbonates and non-carbonate material of terrestrial origin. The percentage carbonate is related to the grain size and thus varies with site, proximity to the reef and depth down the core. Plots of mean grain size (from Coulter counter analysis) against dry weight percent carbonate (titrations) for the <500μm fraction of eight sediment cores show a very strong correlation (correlation coefficient 0.95; Fig. 4.9). At the other end of the grain size scale, 50-75% (by weight) of the >4mm fraction and 96.5% (by number) of the >5mm fraction is skeletal carbonate (data is from eight sediment cores; see Appendix B).

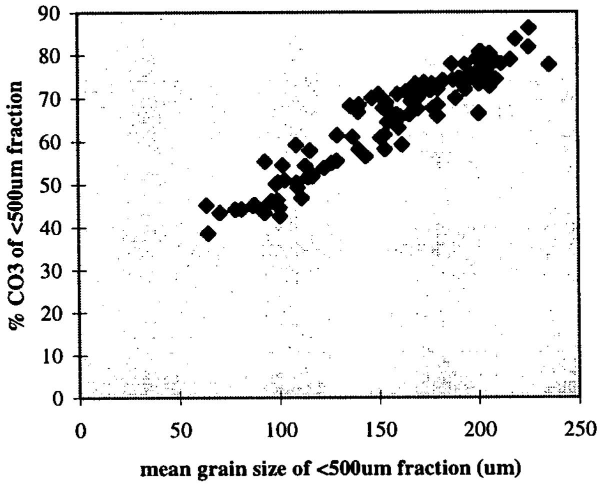


Figure 4.9 The relationship between grain size and carbonate content. (Correlation coefficient = 0.95)

Carbonate-rich patches in the sediment, such as the shelly pockets produced by callianassids, are likely to be preserved as nodular limestones in a mudstone surround or a limestone containing mud patches, depending on the relative amounts of each component. Combined with compacted burrows (4.7.2.3) and possibly storm deposits, the resulting rock will be a mottled, heterogeneous mix of lenses, nodules and layers of limestone and mudstone.

4.8 CHAPTER SUMMARY

1. Burrow traces made by the crustaceans in this study are easily identified from each other by overall structure, wall characteristics and grain sorting patterns. They would be distinct indicators of the zones of sediment they occupied if preserved in a frozen tiered profile. However, at least 60cm of deposit would need to be suddenly deposited for the deep tier callianassids and alpheids to be preserved without reworking from subsequent generations of burrowers.
2. Trace fossil analogues for callianassid burrows and *Dotilla* burrows are *Thalassinoides* and *Skolithos*, respectively. There is no described ancient analogue for alpheid burrows.
3. Under the most likely situation of steady, slow sedimentation, reworking of the sediments by deep tier burrowers will obliterate the upper tiers. In the callianassid area, this will produce a sediment characterised by branching tubes and finger-like shelly pockets bounded by walls with smooth interiors, with patches of coarse material also found outside the burrow walls.
4. Intertidal deposits in the geological record will be horizontally heterogeneous due to the sand waves and pools. Patches of well-sorted, sandy deposits with small, vertical trace fossils (*Dotilla*) and occasional large complex trace fossils (callianassids) representing the sand wave habitat would alternate with poorly-sorted, coarser patches with clusters of shells, large pieces of reef debris and sloping trace fossils with a variable morphology (alpheids).
5. Progradation of the reefs and their sediment slopes will lead to a shallowing upwards sequence, from off-reef sediments, through near-reef sediments, through reefal deposits, to back-reef muds, sandy beach or tidal pool deposits and ultimately soils. Each zone of sediment will be recognisable by the biogenic features of the deep tier burrows.
6. Sand ripples and horizontal tracer movement indicate that intertidal sediments are dominated by physical processes. The abundant tracks, trails, pellets and casts made by gastropods, starfish, crabs and worms on the sediment surface will only be preserved by sudden large-scale burial with no erosion. In the shallow subtidal environment, strong currents can flatten callianassid mounds and wave action during rough weather or storms will severely modify the sediment.
7. Severe storm damage is rare in these study areas. However, in May 1986 a storm from the south hit Pump House Bay, almost completely destroying the reef and changing the sediments from muddy to rippled sand which were still present two years later. Today,

sediments off Pump House Bay have a fine, terrigenous clay rich layer overlying an increasingly coarse (calcareous) layer. The depth of this coarse layer in the sediment increases offshore. Sorting is poor throughout. A sediment profile generated solely by callianassids would be expected to show a coarse layer at depth due to the sorting activity of these shrimps, in contrast to that produced by alpheid activities. However, off Pump House Bay the coarse layer is present in the alpheid as well as callianassid area; the major factor determining the appearance of these sediments is physical not biological. Biogenic overprinting on this physically-generated sediment is seen as abundant burrows and shelly pockets. Either the animals are not dense enough or they have not been working the sediment long enough to produce a purely biogenic deposit.

8. Bivalve fragments showed higher levels of degradation (through abrasion and microbioerosion) in alpheid than callianassid areas, resulting in a taphonomic bias to skeletal grain preservation.
9. The overall rate of bioturbation on the forereef slope was found to exceed the sediment accretion rate by a factor of three. Bioturbation should completely rework the sediment if it is not interrupted by physical events. Grains accumulating on the sea bed will be rapidly worked into the sediment. Time-averaging by callianassid burrowing means that grains 60cm below the sediment surface could be anything between 0-150 years old.
10. A lack of early lithification (as indicated by the absence of indurated pellets and burrow walls, uncemented reef framework and lack of beachrock) means that burrows will be compacted during preservation. Since different grain size fractions comprise different proportions of carbonate, by sorting grains with respect to *size* crustaceans are also indirectly selecting for grain *type*, producing a mineralogically heterogeneous sediment. Compacted burrows and coarse (carbonate-rich) patches and storm layers will lead to a mottled, heterogeneous mix of lenses, nodules and layers of limestone and mudstone in the rock record.

CHAPTER 5

SYNTHESIS OF TAPHONOMY

This section brings together the findings of all the different strands of this thesis, namely, how crustacean bioeroders and bioturbators affect the taphonomy of reefs and sediments in south-east Phuket.

5.1 THE ROLE OF CRUSTACEAN BIOEROSION IN THE FORMATION OF REEFS AND SEDIMENTS

5.1.1 Coral colony morphology

Bioerosion affects coral morphology on all scales (sections 2.3 and 2.4.2.1). Whole colony morphology is altered by upogebiid and alpheid shrimps. Alpheids, and to a lesser extent upogebiids, dissect the coral colonies they inhabit, inducing a lobed growth form. In the outer reef, this contributes to the high-relief, columnar growth form of *Goniastrea retiformis*. In areas of high sediment loading, boreholes act as centres for sediment accumulation which, together with die back from solar bleaching and bioerosion by *Lithophaga* bivalves, causes the dead-centred, ring shape of many mid-reef colonies. At the small end of the scale, boring pyrgomatid barnacles and hapalocarcinid crabs modify coral growth patterns in their immediate vicinity. In the case of hapalocarcinids this commonly creates a knobby growth form.

5.1.2 Sediment production

All crustacean borers, especially upogebiids and alpheids, weaken their host corals. The subsequent disintegration of bored corals by physical processes produces sediment of all grain sizes from silt to boulder size. The sediment produced both indirectly and by active bioerosion contributes to the internal sediments of the reef and to the prograding fore-reef sediment slope. An estimated 0.8% of the sediment input each year to the prograding fore-reef slope is due to direct bioerosion by *Upogebia*.

Upogebia produces carbonate sediment in the clay to gravel size range during the mechanical excavation of its borehole. 30% of this eroded sediment (mainly the coarser component) is incorporated into the lining by the shrimp. Coral actively eroded by *Upogebia* (61g/m^2/year) is equivalent to 2% of the annual $CaCO_3$ production by reef corals.

5.1.3 Whole reef morphology

The activities of boring crustaceans play an important role in reef progradation and the transition from outer to mid to inner reef (section 2.4.2.2). Most important in this respect is the creation of deep boreholes by upogebiid and alpheid shrimps which form planes of weakness along which reef-front corals easily fracture. The resulting boulder-sized fragments topple on to the fore-reef slope. It is the regeneration of the upper surfaces of these toppled corals that enables the reef to prograde forward over the sediment (Tudhope and Scoffin 1994).

As the reef grows seawards, corals that were once at the reef front eventually become part of the mid reef and then the inner reef. Toppled *Porites* form the basis of the reef flat (Tudhope and Scoffin 1994). High relief, reef-top corals (mainly *Goniastrea retiformis* and *Platygyra* sp.) are eroded and levelled or completely disintegrate by the time they reach the mid/inner-reef areas. These back-reef areas become progressively more silted up and levelled by the combined effects of bioerosion, sediment smothering and solar bleaching. Coral breakdown by bioerosion produces skeletal carbonate sediment which, together with terrigenous sediment input, fills in the reef framework, thus raising the reef flat relative to sea level. The sediment produced by *Upogebia* erosion alone makes up 3% of this reef flat elevation.

Upogebia causes planes of weakness along which the mid-reef pavement fractures. This might either a) allow colonisation of the fresh vertical surfaces by bioeroders such as sponges, thus increasing coral breakdown, or b) enable *Porites* to grow on to relatively sediment-free surfaces, thus maintaining live coral cover in the mid and inner reef. Water currents from the shrimps' borehole entrances may also help to prevent smothering of nearby corals with mud.

As the reef progrades seawards, its physical structure influences the hydrodynamic conditions and hence the sedimentary regimes on the reef and surrounding areas. For example, in Tang Khen Bay the sheltered back-reef areas are muddy, whereas the channel between Tin Smelter Reef and Porites Bay Reef contains coarser sand deposits. This in turn affects the nature of bioturbation in those sediments.

5.1.4 Taphonomy of the reef top

Tall, outer-reef colonies on the reef top are eroded from above and below by a range of bioeroders and are dissected by shrimp borings. These outer reef flat corals have a poor preservation potential since they are mainly converted into sediment by bioerosive activity. Outer reef top corals are also unlikely to be preserved by sediment burial as little sediment settles on the reef edge. In contrast, mid- and inner-reef areas have a higher preservation potential due to the lower levels of bioerosion and higher sediment loading. Therefore, the relative importance of bioerosion and sedimentation leads to a taphonomic bias in reef coral preservation (Scoffin 1997). The preferential preservation of inner and mid reef flat corals also means that outer reef boring traces, such as those made by pyrgomatid barnacles and hapalocarcinid crabs, are unlikely to be preserved. Therefore, there is also a preservational bias towards the traces of sediment-tolerant, active boring species, such as *Upogebia*, and against the preservation of passive borers which are most common on the outer reef.

5.1.5 Taphonomy of the sediments

Boreholes, once abandoned, become centres for sediment accumulation. Grains that settle in a borehole will be protected from the worst of physical degradation, enhancing their preservation potential. Grains in *Upogebia* linings are less likely to be preserved in the outer reef, as outer-reef boreholes are likely to be sites of coral fracture. Breakage of corals along *Upogebia* boreholes decreases the likelihood of those holes' preservation as linings will be washed away and the exposed surfaces will be physically and microbiologically eroded. The mud linings of mid-reef boreholes have a greater chance of being well preserved, not only because their host corals are less likely to break up, but also because of the increased chances of being buried by sediment.

Internal sediment in Tin Smelter Reef is 90% skeletal carbonate (Scoffin 1997). This is due to the flushing out of (mainly terrigenous) fines by water filtering through the reef framework and the suspension and export of fines from the reef top. Boreholes are sites of sediment accumulation within the reef framework which will retain these skeletal fragments. Coarse (sandy) calcareous internal reef sediments in a fossil reef that give the

Coarse (sandy) calcareous internal reef sediments in a fossil reef that give the impression of a relatively high energy, mud-free environment may in fact be from a muddy terrigenous environment such as Phuket.

5.2 THE ROLE OF CRUSTACEAN BIOTURBATION IN THE FORMATION OF REEFS AND SEDIMENTS

5.2.1 Effects on the sorting or mixing of sediments

Intertidal and subtidal callianassid shrimps sort the sediment that they process, burying coarse grains in deep chambers and ejecting fine sediment at the surface. This produces a layer of patchy gravel debris >25cm below the sediment surface. In contrast, alpheid shrimps bring grains of all sizes to the sediment surface, though intertidal and near-reef alpheids sort the grains into a coarse and a fine pile on the sea bed.

Passive burial of coarse grains occurs during bioturbation by soldier crabs and alpheid shrimps. Individual grains that are too big for the animals to move become buried by successive layers of finer sediment that *is* turned over by these crustaceans. In this way, coarse grains build up below the depth of sediment turnover. The recognition of these features in the sediment is strongly affected by the density of burrowers present and physical processes that also act on the sediment.

5.2.2 Formation of burrows and trace fossils

The crustaceans studied in this work produce burrows that are characteristic of the animals that made them, the activity that caused them and the environment in which they live. Different areas of the sediment are dominated by one type of crustacean, enabling the identification of zones by their crustacean burrows. For example, intertidal sand waves have a dense population (90 burrows/m^2) of soldier crabs which dig cylindrical burrows to depths of 10-20cm. Intertidal pools are crowded with alpheid shrimp burrows and clusters of gravel. The subtidal sediment slope shows zonation of crustacean burrowers moving offshore from the simple, sloping burrows of near-reef alpheids to deep, spiral burrows of off-reef alpheids to the complex, *Thalassinoides*-type burrow networks of callianassids.

The distribution of these crustaceans appears to be determined mainly by the sediment thickness and grain size, which in turn are related to the hydrodynamic regime of different water depths.

5.2.3 Taphonomy of sediments

A comparison of gravel-sized skeletal grains in subtidal alpheid and callianassid areas showed that the type of bioturbation has an important effect on the taphonomy of those grains. Grains that are repeatedly re-exposed to the sediment surface by the bioturbation of alpheid shrimps are more prone to physical abrasion and microbioerosion, thus decreasing the likelihood of them being preserved as recognisable skeletal grains. In contrast, rapid, deep burial of coarse grains by callianassids favours their pristine preservation by removing them from surface processes.

In Phuket, beachrock and lithified burrow walls are absent (c.f. Tudhope and Scoffin 1984; Great Barrier Reef) and the reef framework is uncemented (Tudhope and Scoffin 1994). This relatively low level of carbonate saturation and resulting lack of early lithification will lead to the compaction of burrow traces during preservation, resulting in bioturbate textures rather than discrete trace fossils in the geological record.

Grain size is related to calcium carbonate content in this environment, with larger size fractions containing higher percentages of skeletal (calcium carbonate) material. Sorting of grains of different sizes by crustaceans and by physical processes leads to mineralogically patchy sediments which could be preserved as nodular limestones in a muddy/shaley background or lenses of mud in a limestone. Biological sorting (into a coarse calcareous layer beneath a terrigenous clay rich layer) may result in the small-scale limestone-shale alterations common in the geological record.

Bioturbation by subtidal crustaceans was estimated to turn over 252m^3/year over the 20100m^2 fore-reef sediment slope (to a water depth of 8m). The total amount of sediment added to the slope each year is 88m^3 (Scoffin 1997), so bioturbation completely turns over this new sediment c.3 times a year. Sediment settling on the fore-reef slope is thus quickly incorporated into the accumulating sediment pile.

5.2.4 Taphonomy of the reef

Burrowing under reef-front corals (e.g. by near-reef alpheids, crabs, fish and holothurians) will undermine, and theus destabilise reef front corals. This has implications for reef progradation and development. However, resuspension of fines around these fallen blocks by burrowers will kill coral polyps that are near the sediment surface and thus discourage regrowth of parts of these toppled corals. Once basal polyps are killed, these areas at the base of reef front and toppled corals are likely to be bioeroded, further adding to the breakdown of corals at the reef front and to the scale of the undermining. Further seawards growth by the surviving parts of the coral will increase the overhang and instability of these corals.

Crustacean bioturbation helps to maintain high sediment levels in the water a) by keeping the surface sediments loose and easily resuspended and b) through the activities of animals (e.g. callianassid shrimps) which preferentially bring fines to the surface. These processes increase fine sediment loading in the back-reef area, inhibiting coral growth and borer colonisation and increasing the likelihood of burial and preservation of back-reef corals.

Some alpheid shrimps maintain large quantities of coarse reef debris at the sediment surface and it is possible that these fragments might have enabled coral larval settlement on an otherwise shifting substrate in tidal pools in Tang Khen Bay.

5.3. RECOGNISING THE EFFECTS OF CRUSTACEANS IN THE ROCK RECORD AND THE EXTENT OF INFORMATION LOSS DURING PRESERVATION

5.3.1 Evidence of crustacean activity in the rock record

Burrow traces and bioturbate traces or ichnofabrics are the most obvious sign of crustacean activity. However, many features seen in the fossil record may be indirectly attributable to bioerosion or bioturbation but may not be recognisable as such, even if clearly preserved. For example;

- fallen reef blocks in the rock record might represent a much lower energy event than expected if the corals had been pre-weakened by borers

- heavily eroded or abraded grains could be associated with repeated exposure through bioturbation
- irregularly shaped reef fragments in the sediment could have been biogenically produced (e.g. by the shrimp *Upogebia*), but do not have a distinctive shape and may be taken as products of physical breakdown
- shelly pockets could be due to storm infill of burrows or active sorting by animals such as callianassid shrimps
- coral growth forms may be biogenically induced by infauna, e.g. alpheid shrimp cracks

5.3.2 Loss of information due to crustacean activities

Burrowing and boring are self-destructive as reworking obliterates previously formed holes. In the case of bioturbation, deep tier burrowers such as the crustacean burrows described in this study will obliterate upper tiers. Reworking will lead to a bioturbate texture with few recognisable burrows visible against a mottled background. Repeated bioerosion will completely destroy the substrate in which the activity is occurring so that the traces will be lost. Since active boring is most common in dead coral substrates and passive boring requires live coral, early passive borings are likely to be eroded by subsequent active eroders after the death of the corals. The relative rates of bioerosion and sedimentation on the reef flat leads to the preferential preservation of inner- and mid- reef corals and their (mainly active) boring traces (see section 5.1.4).

Thus, the widespread and important effects of present day crustaceans described in the preceding chapters may be under- or over-represented in a fossil reef due to taphonomic and preservational biases.

5.3.3 Information loss due to storms

The intensity and frequency of high energy events will be a very important factor in the preservation of these reef sediments. Background physical processes such as waves and currents decrease the preservation potential of traces. For example, traces in intertidal sediments which are continually affected by wave action (e.g. *Dotilla* burrows) are less likely to be preserved than subtidal traces. The effect of storms in this study site merits a special mention. Although the SE corner of Phuket suffers from little severe weather, occasional storms that do reach the shores of Laem Panwa can have a devastating effect.

The storm that hit Pump House Bay in 1986 still dominates the sedimentary record, although a subsequent biogenic overprint is visible. Infauna are not present in high enough densities to produce an entirely biogenic sequence and the physical signatures in the sediment therefore dominate, despite the intensive bioturbation observed. Therefore, the geological record will be biased towards single large scale events at the expense of the lower level continuous activity that may have actually dominated the sediment, thus severely underestimating the importance of these crustaceans in the history of a reef and its sediments.

Although potentially destructive, storms may also be essential in reef formation in this area. Elevated energy levels are required to loosen biologically pre-weakened reef front corals in order for the reef to prograde seawards. In a young reef, a storm may have a completely destructive effect (as in Pump House Bay in 1986), but once a more solid reef flat, built mainly of massive corals, has been established, storms may be of paramount importance in enabling continued reef growth. Large areas of coral rubble may form the basis of new reefs by providing an area that is relatively free of fine sediment for coral spat settlement or by supporting fallen massive coral blocks above the fine sea bed.

At any stage of reef growth, reef sediments will be severely affected by storms as sediment suspension and disruption of infaunal communities will result. The sediment settling out at the end of a storm event will be recolonised by burrowers once normal hydrodynamic conditions returned, albeit possibly a different community to the pre-storm infauna. In contrast, sediment settling on a reef flat may smother corals and their borers. In this way, a storm may destroy burrow traces but preserve boring traces.

5.4 THE MOST LIKELY FATE OF THIS AREA (TANG KHEN BAY, TIN SMELTER REEF AND PUMP HOUSE BAY)

Chapters 2 and 4 proposed various preservational pathways for the present day reefs and sediments of Laem Panwa. Below is a summary of the most likely fate of these environments, approached by hypothesising what the area will look like in 2000 years from now. The preservation of these reefs and their surrounding sediments depends on the relative rates of sedimentation, erosion, reef growth and sea level changes. The scenario below assumes no relative sea level change.

A young reef, as Pump House Bay is today, is very susceptible to destruction by storms. Despite an approximately constant sea level for the last 5-6000 years, no reef has developed in this bay. This suggests that storms might be regular enough to prevent reef flat development on this exposed headland.

On other nearby reefs, such as Tin Smelter Reef and PMBC Reef, storms have been infrequent enough that the original patch reefs and coral heads have expanded and eventually coalesced. Once a more solid reef-flat structure develops, it becomes more resistant to high energy levels and the reef will take hold. Two thousand years from now, Tin Smelter Reef will have prograded out a further 80m (given a rate of 4cm/year; Tudhope and Scoffin 1994), assuming similar conditions of terrigenous sedimentation and coral growth and erosion rates. The resultant wider back-reef area will become completely sediment-covered and the subsidence of the dead reef, caused in part by bioerosion and undermining by burrowers, will enable a layer of fine sediment to accumulate. This area will stay muddy due to its sheltered location and burrowers from the adjacent muddy corners of the bay (e.g. fiddler crabs, *Uca* sp.) will colonise the area.

The fate of the reef depends on the relative rates of sedimentation and reef growth. If sedimentation is greater than reef growth, the sea bed becomes shallower, leaving less vertical space for the reef to grow into (Tudhope and Scoffin 1994). For this reason, it is unlikely that Tin Smelter Reef and Porites Bay Reef will bridge the gap between them. Sedimentation of clastic sediments in the centre of the bay leads to very shallow water at the reef edges, in contrast to the small drop-off at the seaward edges of these reefs. Therefore, the reefs are likely to only prograde seawards.

It is possible that sedimentation may increase due to human activity in the area. Dredging to clear shipping channels only metres from the reef, expansion of the deep sea port immediately north of Tin Smelter Reef, offshore tin dredging and deforestation in the water catchment area of Phangnga Bay will all increase suspended sediment load in the water around Laem Panwa.

Increasing sediment levels from natural or anthropogenic causes will not only smother larger areas of reef but also raise the level of the sea bed, thus 'pinching out' the reef. As the reef became increasingly affected by sediment, other factors such as solar bleaching or increased sea surface temperatures would be more likely to cause coral death of the already stressed corals.

It is probable that these reefs will silt up completely as the water depth decreases due to sediment build-up. Their appearance will then be like Ao Man, the neighbouring bay to the north which is closer to the terrigenous source. There, there is almost no live coral and thick, fine mud covering the old reef flat. The substrate available to burrowers will therefore increase at the expense of that of the borers. With further sedimentation and shallowing, terrestrial species such as land crabs and mangroves may begin to encroach on what was the intertidal area.

CHAPTER 6

SUMMARY AND CONCLUSIONS

6.1 Objectives

- How is the development and preservation of reefs and reefal sediments influenced by crustacean bioeroders and bioturbators?
- Will the activities of these crustaceans be recorded in the fossil record? If so, how will we recognise them and what will they tell us about the origins of fossil reef structure?

6.2 Methods

The following methods were used in the field and in the laboratory to investigate a) crustacean burrow and borehole morphologies and b) the processes involved in their formation:

- Airlifting, coring, grain size analysis, carbonate content titration, tracer sediment, resin casting, silicone casting, quadrats and transects, aquarium, reef substrate analysis, coral sampling, microscopy (light and scanning electron microscope), thin sections, X-ray diffraction.

6.3 Location: a modern, muddy reef system in Phuket, Thailand:

- Reef locality: Tin Smelter Reef, a 200m wide, 440m long, intertidal, fringing reef flat which drops 3m on to a muddy sea bed.
- Intertidal sediment locality: Tang Khen Bay. Alternating sand waves and tidal pools composed of gravel- to sand-size sediments; immediately adjacent to Tin Smelter Reef.
- Subtidal sediment localities: a) Pump House Bay, a muddy sediment slope between 4 and 12m water depth. b) Tin Smelter Reef (see above).

These sites in SE Phuket are affected by large quantities of terrigenous clay, which mostly originate from Phangnga Bay to the NE. The water is turbid (up to 47mg/l) and the reefal sediment surface comprises up to 85% terrigenous clay (kaolinite and muscovite; X-ray diffraction analysis). The water is inferred to have a relatively low saturation of $CaCO_3$ due to this terrigenous input. Currents and wave action are important in this shallow setting.

6.4 Present day crustacean traces

6.4.1 Bioerosion

- Passive borers (hapalocarcinid crabs, pyrgomatid barnacles and alpheid shrimps) require live corals for borehole formation and are therefore found mainly in the outer reef where live coral cover is highest. Upogebiid shrimps bore outer- and mid-reef corals. Relatively few borers are found in the inner reef as fine sediment accumulation is so great.
- Pyrgomatid barnacles and hapalocarcinid crabs passively bore small, more-or-less cylindrical holes by modifying coral growth. Barnacles lay down a corrugated calcareous plate which lines the hole and a highly ornamented wall plate at the coral surface. The etched appearance of the smooth inner surface of the borehole and the exact fit of the hapalocarcinids in their holes indicate that the crabs use active chemical erosion to widen their boreholes. A chalky deposit on the hole walls may be a by-product of this chemical erosion.
- Upogebiids mechanically excavate branching boreholes in coral which they line with a thick mud layer, comprising sediment from the reef flat and from their own erosive activity. 30% of the coral excavated in this way is incorporated into the lining.
- Alpheids use a combination of active and passive erosion to form their holes; the branching crack seen at the coral surface is created by the prevention of coral growth but the irregular chambers at the base are actively (mechanically) excavated.

6.4.2 Bioturbation

- Crustacean bioturbators occupy distinct zones on the sea bed. In the intertidal area, the sand waves are monopolised by soldier crabs *(Dotilla myctiroides)*, whereas the sediment of the tidal pools (which alternate with the sand waves) are dominated by alpheid shrimps. Intertidal callianassids are found only in the thick sediments of the central region of the bay, closer to the low tide mark. In the subtidal sediments, an offshore zonation is found, with near-reef alpheids giving way to off-reef alpheids and then callianassids further from the reef. This distribution seems to be related to grain size and sediment thickness.

- *Dotilla* crabs dig vertical, cylindrical burrows every daylight low tide that the intertidal sand waves are exposed by a critical amount; suitable tides occur twice daily during spring tides and not at all during neaps. The crabs emerge from the sediment within the first 10-15 minutes after the tide has fallen low enough (less than 1.6 metres above lowest low water), or 15-20 minutes after first light at a dawn low tide. This produces 5-20 large excavation pellets. During the exposure of the sand waves the crabs graze almost continually on the surficial sediments, covering the surface with tiny feeding pellets (1-2mm diameter). They also expand their burrow, resulting in a further 10-30 excavation pellets. Burrowing and surface feeding are limited to times of exposure at low tide and are correlated with the duration of exposure rather than the depth of the water table beneath the sediment surface. The crabs' activity will result in passive burial of coarse sediment due to their ability to process only sand-size grains.
- Callianassid shrimps excavate complex, *Thalassinoides*-type burrows with a network of layered tunnels and chambers reaching >25cm below the sediment surface. This network is connected to the surface by an inhalent shaft leading from a surface crater and an infilled exhalent shaft from which fine particles (mainly 125-250µm grains) are ejected on to a mound. Intertidal burrows comprise large chambers leading off a central tunnel, in contrast to the network of narrow tubes made by subtidal shrimps. In the intertidal burrows, coarse grains are apparently buried outside the burrow chambers and sealed off behind the smooth lined burrow wall. In subtidal burrows this gravel is collected in shelly pockets leading off the main burrow. The deeper reaches of the burrows occupy a fairly permanent position in the sediment, although individual chambers may be abandoned and new ones dug. However, the surface mound (in the case of intertidal shrimps) and crater (in the case of subtidal shrimps) move position regularly.
- Subtidal near-reef and intertidal alpheid shrimps create irregularly shaped burrows which slope down at a shallow angle. The burrow entrance changes position daily and this involves the re-digging of the upper 7-8cm of burrow. In doing so, the shrimps separate coarse from fine sediment to create clusters of coarse material at the sediment surface. Burial of these gravel clusters by subsequent excavation creates a patchy upper layer of sediment. The burrow morphology below the transient upper part is determined mainly by the presence of large pieces of reefal debris in the sediment, which often form the ceilings of the alpheid burrows. Subtidal off-reef alpheids dig deep spiral burrows and do not sort grains according to size. However, they also re-excavate the top portions (15-20cm) of their burrows and thus change their entrance positions at least once a day.

- In the intertidal area, epifauna are common and produce a wide range of tracks and trails on the sediment surface. In the subtidal muds, burrowers are tiered; an abundant meiofauna live in the surficial layers of the sediment above a "10cm layer" of larger burrowers (crabs, worms, fish), which overlies the deepest tier of burrowers, the callianassid or alpheid shrimps.

6.5 Taphonomy

6.5.1 Preservation of crustacean traces

- Burrow traces made by the crustaceans in this study are easily identified from each other by overall structure, wall characteristics and grain sorting patterns. They would be distinct indicators of the zones of sediment they occupied if preserved in a frozen tiered profile. However, complete deep tier callianassid and alpheid burrows would require sudden burial under at least 60cm of deposit to prevent their upper reaches being reworked by subsequent generations of burrowers.
- Well-preserved intertidal deposits in the geological record will be horizontally heterogeneous due to the sand waves and pools. Patches of well-sorted, sandy deposits with small, *Skolithos*-type, vertical trace fossils (*Dotilla*) and occasional, large, complex trace fossils (callianassids), representing the sand wave habitat, would alternate with poorly-sorted coarser patches with clusters of shells, large pieces of reef debris and sloping trace fossils with a variable morphology (alpheids).
- Under the most likely situation of steady slow sedimentation, reworking of the sediments by deep tier burrowers will obliterate the upper tiers. In the callianassid area, this will produce a sediment characterised by branching tubes and finger-like shelly pockets bounded by walls with smooth interiors, with patches of coarse material also found outside the burrow walls. Progradation of the reefs and their sediment slopes will lead to a shallowing upwards sequence, from off-reef sediments, through near-reef sediments, through reefal deposits, to back-reef muds, sandy beach or tidal pool deposits and ultimately soils. Each zone of sediment will be recognisable by the biogenic features of the deep tier burrows.
- Sand ripples and horizontal tracer movement indicate that intertidal sediments are dominated by physical processes. The abundant tracks, trails, pellets and casts made by

gastropods, starfish, crabs and worms on the sediment surface will only be preserved by sudden large-scale burial with no erosion. In the shallow subtidal environment, strong currents can flatten callianassid mounds and wave action during rough weather or storms will severely modify the sediment.

- Severe storm damage is rare in these study sites. The sheltered E or SE aspect of the study sites protects them from the worst of the storms during the SW monsoon. However, in May 1986 a storm from the south hit Pump House Bay, almost completely destroying the reef and changing the sediments from bioturbated muds to rippled sands which were still present two years later. Today, the subtidal sediments of Pump House Bay have a fine, terrigenous clay rich layer overlying an increasingly coarse (calcareous) layer. The depth of this coarse layer in the sediment increases offshore. Sorting is poor throughout. A sediment profile generated solely by callianassids would be expected to show a coarse layer at depth due to the sorting activity of these shrimps, in contrast to that produced by alpheid activities. However, off Pump House Bay the coarse layer is present in the alpheid as well as the callianassid area; the major factor determining the appearance of these sediments is physical not biological. Biogenic overprinting on this physically-generated sediment is seen in the form of numerous burrows and shelly pockets. Either the animals are not dense enough or they have not been working the sediment long enough to produce a purely biogenic deposit.
- In contrast to burrow traces, storms can enhance the preservation of boreholes by burying corals with sediment. Corals that have been broken from the reef front and become buried in the fore-reef slope will preserve their boreholes well, although they will not be *in situ*. However, corals that die from temporary sediment smothering will be rebored by dead-coral borers, thus obliterating pre-storm boring traces.
- Passive borers require a live coral substrate and are thus early in the succession of bioeroders in a coral. After the death of a coral, passive borers will be rebored by subsequent dead-coral borers unless they are quickly buried or aerially exposed. The presence of numerous live-coral borers in the rock record would indicate swift preservation after coral death, whereas many cross-cutting dead-coral borers are more likely to indicate a period of stasis.
- On Tin Smelter Reef, passive borers are most common in the reef top corals of the outer reef where live coral cover is highest. These reef-top corals (and their passive boreholes) have a low preservation potential as they die and are obliterated by subsequent generations of active bioeroders as they pass into the mid reef. Under continuing

conditions of slow reef progradation, passive borers are likely to be under-represented in the rock record.

- The fracture of reef-front corals along alpheid and upogebiid boreholes has implications for the boreholes' preservation. The resultant coral boulder will fall on to the fore-reef slope, and boreholes (which are now exposed on the outer surface of these boulders) will either be buried in the sediment, enhancing their preservation, or be exposed to reboring by dead-coral borers.

6.5.2 The effect of crustaceans on reef development and taphonomy

- Alpheids continually bring gravel to the sediment surface, whereas callianassids actively bury it. Consequently, infaunal bivalve fragments showed higher levels of degradation (through abrasion and microbioerosion) in alpheid than callianassid areas, due to the different activities of the two shrimps. This will result in a taphonomic bias to skeletal grain preservation.
- The overall rate of crustacean bioturbation on the fore-reef slope was found to exceed the sediment accretion rate by a factor of three. Grains accumulating on the sea bed will be rapidly worked into the sediment. Bioturbation should completely rework the sediment if it is not interrupted by physical events. The time taken to rework the burrowed depth ranges from 69 years (off-reef alpheids) to 16 years (callianassids). Intertidal rates are substantially faster. Time-averaging by callianassid burrowing means that grains 60cm below the sediment surface could range from 0-150 years old.
- A lack of early lithification (as indicated by the absence of indurated pellets and burrow walls, uncemented reef framework and lack of beachrock) means that burrows will be compacted during preservation. Since different grain size fractions comprise different proportions of carbonate, by sorting grains with respect to *size* crustaceans are also indirectly selecting for grain *type*, producing a mineralogically heterogeneous sediment. Compacted burrows and coarse (carbonate-rich) patches and storm layers will lead to a mottled, heterogeneous mix of lenses, nodules and layers of limestone and mudstone in the rock record.
- Bioerosion on Tin Smelter Reef strongly affects coral morphology. Together with the effects of sedimentation and die back from exposure and solar bleaching, bioerosion by alpheids and upogebiids influences individual colony growth form. Shrimp boreholes contribute to the lobed columnar structure of outer-reef *Goniastrea retiformis*. The

common, ring-shaped colonies with dead centres seen in *G. retiformis* and *Platygyra sinensis* may be enhanced by the initial settlement of sediment in abandoned shrimp cracks and by subsequent intensive bioerosion by *Lithophaga*. Small-scale coral growth pattern alteration is also caused by hapalocarcinid crabs and pyrgomatid barnacles.

- Reef morphology is dependent on bioerosion as Tin Smelter Reef progrades seawards by the repeated toppling of corals off the reef front on to the sea bed, a process speeded by the weakening of reef front corals by bioerosion. Burrowing also undermines reef front corals and keeps suspended sediments high near the sea bed, thus preventing coral growth there and leading to an overhanging growth form. Combined with bioerosion under the overhang, burrowing will increase the instability of the reef front corals, helping progradation.
- As the reef moves seawards, back-reef areas become progressively more silted up and levelled by the combined effects of death, bioerosion and the growth of more sediment-tolerant flat *Porites* colonies. Levelling of the mid reef leads to a preservational bias against mid and outer reef-top corals (and their mainly passive, live-coral borers) because of the changing relative importance of sedimentation and bioerosion across the reef.
- *Upogebia* causes planes of weakness along which the reef pavement fractures. This may have a number of outcomes. This might either a) allow colonisation of the fresh vertical surfaces by bioeroders such as sponges, thus increasing coral breakdown, or b) enable *Porites* to spread on to relatively sediment-free surfaces, thus maintaining live coral cover in the mid and inner reef. Water currents from the shrimps' borehole entrances may also help to prevent smothering of nearby corals with mud.
- Bioeroders have a central role in the sediment pathways, not only producing sediment (either directly or indirectly) but also creating centres for sediment accumulation when holes are abandoned. Accumulating sediment raises the level of the reef base, decreasing the amount of vertical space for the reef to grow into. The gravel to silt-sized sediment actively eroded by *Upogebia* is responsible for 3% of this reef flat elevation and for 0.8% of the sediment input to the prograding fore-reef slope. Indirect erosion produces boulder- to silt-size reef debris.

In conclusion, crustaceans have a vital role in many aspects of reef taphonomy in Phuket. The activities of crustaceans affect coral colony morphology, sediment production, sediment fabric and reef development and preservation.

BIBLIOGRAPHY

Aigner T, Reineck HE (1982) Proximity trends in modern storm sands from the Heligoland Bight (North Sea) and their implications for basin analysis. Senck. Marit. 14:183-215. (quoted in Wanless et al 1988)

Ahr WM, Stanton RJ (1973) Sedimentologic and palaeoecologic significance of *Lithotrya*, a rock-boring barnacle. J. Sed. Pet. 43:20-23

Allen JRL (1965) Late Quaternary Niger Delta and adjacent areas: sedimentary environments and lithofacies. Am. Assoc. Pet. Geol. Bull. 49:547-600

Aller RC (1978) Experimental studies of changes produced by deposit feeders on pore water, sediment and overlying water chemistry. Am. J. Sci. 278:1185-1234

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In McCall PL & Tevesz MJS (eds) Topics in Geobiology vol. 2: Animal-sediment relations. The biogenic alteration of sediments. Plenum Press New York London p 53-102

Aller RC, Dodge RE (1974) Animal-sediment relations in a tropical lagoon, Discovery Bay, Jamaica. J. Mar. Res. 32:209-232

Alpert SP (1977) Trace fossils and the basal Cambrian boundary. In Crimes TP & Harper JC (eds) Trace Fossils 2. Seel House Press Liverpool p 1-8

Anderson DT (1992) Structure, function and phylogeny of coral-inhabiting barnacles (Cirrepedia, Balanoidea). Zool. J. Linn. Soc. London 217:663-682

Anderson DT (1994) Modes of Life: Phylogeny. Chapter 10 in Barnacles. Structure, Function, Development and Evolution. Chapman and Hall London p 287-330.

Atkinson RJA (1974) Spatial distribution of *Nephrops* burrows. Est. Coast. Mar. Sci. 2:171-176

Atkinson RJA, Chapman CJ (1984) Resin casting: a technique of investigating burrows in sublittoral sediments. Progress in Underwater Science 9:15-25.

Atkinson RJA, Moore PG, Morgan PJ (1982) The burrows and burrowing behaviour of *Maera loveni* (Crustacea: Amphipoda) J. Zool. London 198:399-416

Ausich W I, Bottjer D J (1982) Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. Science 216:173-174

Bak RPM, Carpay MJE, de Ruyter van Steveninck E (1984) Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. Mar. Ecol. Prog. Ser. 17:105-108

Bakus GJ (1973) Biology and Ecology of Tropical Holothurians. Chapter 10 in Jones OA & Endean R (eds) Biology and Geology of Coral Reefs Volume II (Biology 1)

Bardach JE (1961) Transport of calcareous fragments by reef fish. Science 133:98-99

Basan PB (1978)(ed) Trace Fossil Concepts. SEPM Short Course 5 Oklahoma 181pp

Bottjer DJ, Ausich WI (1986) Phanerozoic development of tiering in soft strata suspension-feeding communities. Palaeobiology 12:400-420

Bottjer DJ, Droser ML (1991) Ichnofabric and basin analysis. Palaios 6:199-205

Bouma AH (1969) Methods for the study of sedimentary structures. John Wiley and Sons, Inc., 458pp

Brett CE (1990) Destructive taphonomic processes and skeletal durability. In Briggs DEG & Crowther PR (eds) Paleobiology: a synthesis. Blackwell, Oxford p223-226

Braithewaite CJR, Talbot MR (1972) Crustacean burrows in the Seychelles, Indian Ocean. Paleogeog., Paleoclim., Paleoecol. 11(4):265-285

Brenchley GA (1981) Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. J. Mar. Res. 39:797-790

Brett CE (1988) Paleoecology and evolution of marine hard substrate communities: an overview. Palaios 3:374-378

Briggs DEG, Crowther PB (1990) Palaeobiology: a synthesis. Blackwell Scientific Publications Oxford 583pp.

Bromley RG (1990) Trace Fossils; Biology and Taphonomy. Special Topics in Palaeontology 3. Unwin Hyman London 280pp

Bromley RG (1994) The Palaeoecology of Bioerosion. Chapter 5 in Donovan SK The Palaeobiology of Trace Fossils. Wiley & Sons Chichester p 134-154

Bromley RG, Asgaard U (1991) Ichnofacies: a mixture of taphofacies and biofacies. Lethaia 24:153-163.

Bromley RG, Asgaard U (1993a) Endolithic community replacements on a Pliocene rocky coast. Ichnos 2:93-116

Bromley RG, D'Alessandro A (1990) Comparative analysis of bioerosion in deep and shallow water, Pliocene to Recent, Mediterranean Sea. Ichnos 1:43-9

Bromley RG, Ekdale AA (1986) Composite ichnofabrics and tiering of burrows. Geol. Mag. 123(1):59-65

Brown BE, Holley MC (1984) Coral assemblages of intertidal reef flats at Ko Phuket; Thailand. Phuket Marine Biological Center Res. Bull. 30:10pp

Brown BE, Dunne RP, Scoffin TP, Le Tissier MDA (1994) Solar damage in intertidal corals. Marine Ecology Progress Series 105:219-230

Brown BE, Howard LS, le Tissier MD (1986) Variation in the dominance and population structure of intertidal corals around Ko Phuket, Thailand. PMBC Res. Bull. 41:9pp

Bruce AJ (1979) *Ctenopontonia cyphastreophila*, a new genus and species of coral-associated pontoniine shrimp from Eniwetok Atoll. Bull. Mar. Sci. 29(3):423-435

Byers CW (1982) Geological significance of marine biogenic sedimentary structures. In McCall PL & Tevesz MJS (eds) Topics in Geobiology 2: Animal-sediment relations. The biogenic alteration of sediments. Plenum Press New York London p 221-256

Carr DJ (1992) Quaternary sediments of a tropical estuary and bay: Phangnga Bay, South Thailand. Unpublished PhD Thesis, University of Edinburgh, 368pp.

Carr DJ et al (1991) Grain size, calcium carbonate content and accumulation rates of Recent sediments in Phangnga Bay, South Thailand. Phuket Marine Biological Center. Res. Bull. 5:77-96

Chapman CJ, Rice AL (1971) Some direct observations on the ecology and behaviour of the Norway lobster *Nephrops norvegicus*. Mar. Biol. 10:321-329

Chatananthawej B (1986) On the thalassinid genus *Upogebia* (Decapoda, Thalassinidea) from coral reefs of Phuket Island, Andaman Coast of Thailand. Proc. of the 24th Kasetsart Univ. Conference Fisheries Section National Inland Fisheries Institute p 61-73

Chatananthawej B and Bussawarit S (1987) Quantitative survey of the macrobenthic fauna along the west coast of Thailand and the Andaman Sea. Phuket Mar. Biol. Cent. Res. Bull. 47:23pp

Chave KE, Smith SV, Roy KJ (1972) Carbonate production by coral reefs. Marine Geology 12:123-141

Clarkson ENK (1993) Invertebrate Palaeontology and Evolution. Chapman and Hall London 434pp

Clifton HE, Hunter RE (1973) Bioturbational rates and effects in carbonate sand, St. John, US Virgin Islands. J. Geol. 81(3):253-268

Cortes J (1985) Preliminary observations of *Alpheus simus* Guerin-Meneville 1856 (Crustacea: Alpheidae): a little-known Caribbean bioeroder. Proc. 5th Int. Coral Reef Congress, Tahiti 5:351-353

Coulter Operator's Guide. Coulter LS Series (1990) Coulter Electronics Inc., Hialeah, Florida

Crimes TP (1974) Colonisation of the early ocean floor. Nature 248:328-330

Crimes TP (1987) Trace fossils and correlation of late Precambrian and early Cambrian strata. Geological Magazine 124:97-119

Crimes TP (1992a) Changes in the trace fossil biota across the Proterozoic-Phanerozoic boundary. J. Geol. Soc., London 149:637-646

Crimes TP (1992b) The record of trace fossils across the Proterozoic-Cambrian boundary. In Lipps JH and Signoe PW (eds) Origins and Early Evolution of the Metazoa. Plenum New York p 117-202

Crimes TP (1994) The period of early evolutionary failure and the dawn of evolutionary success: the record of biotic changes across the Precambrian-Cambrian boundary. Chapter 4 in Donovan SK (ed) The Palaeobiology of Trace Fossils. John Wiley and Sons Chichester p105-133

Crozier WJ (1918) The amount of bottom material ingested by holothurians (*Stichopus*). J. Exp. Zool. 26:379-389

Curran HA (1994) The palaeobiology of ichnocoenoses in Quaternary, Bahamian-style carbonate environments: the modern to fossil transition. In Donovan SK (ed) The Palaeobiology of Trace Fossils. John Wiley and Sons Chichester p 83-104

Curran HA (1996) Burrowing behaviour of thalassinidean shrimp in a Bahamian intertidal carbonate sand flat. Sixth North American Palaeontological Convention, Washington DC. Palaeontological Society Special Publication No 8 Abstracts Volume p93

Darwin C (1854) A monograph on the Subclass Cirrepedia with figures of all the species. The Balanidae (or Sessile Cirrepedes), the Verrucidae, etc. Ray Society London 684pp, 25 Plates

Davies PJ, Hutchings PA (1983) Initial colonisation, erosion and accretion on coral substrates - experimental results, Lizard Island, Great Barrier Reef. Coral Reefs 2(1):27-35

Davis WR (1993) The role of bioturbation in sediment resuspension and its interaction with physical shearing. J. Expt. Mar. Biol. Ecol. 171(2):187-200

Ditlev H (1978) Zonation of corals (Scleractinia: Coelenterata) on intertidal reef flats at Ko Phuket, Eastern Indian Ocean. Mar. Biol. 47:29-39

Dott RH Jr (1983) 1982 SEPM Presidential address: Episodic sedimentation - How normal is average? How rare is rare? Does it matter? J. Sed. Pet. 53:5-23

Droser ML, Bottjer DJ (1986) A semiquantitative field classification of ichnofabric. J. Sed. Pet. 56:558-559

Droser ML, Hughes NC, Jell PA (1994) Infaunal communities and tiering in Early Palaeozoic nearshore clastic environments: trace-fossil evidence from the Cambro-Ordovician of New South Wales. Lethaia 27:273-283

Duke WL (1985) Hummocky cross-stratification, tropical hurricanes, and intense winter storms. Sedimentology 32:167-194

Dworschak PC (1983) The biology of *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea) I. The burrows. P.S.Z.N.I. Mar. Ecol. 4(1):19-43

Dworschak PC (1987a) The biology of *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea) II. Environments and zonation. P.S.Z.N.I. Mar. Ecol. 8(4):337-358

Dworschak PC (1987b) Feeding behaviour of *Upogebia pusilla* and *Callianassa tyrrhena* (Crustacea, Decapoda, Thalassinidea) Inv. Pesq. 51(1):421-429

Ekdale AA (1988) Pitfalls of palaeobathymetric interpretations based on trace fossil assemblages. Palaios 3:464-472.

Ekdale AA, Bromley RG, Pemberton SG (1984) Chapter16: Shallow Marine Carbonate Environments. In SEPM Short Course No. 15 Ichnology: The Use of Trace Fossils in Sedimentology and Stratigraphy. Tulsa, Oklahoma p 199-213.

Ekdale AA, Bromley RG, Bockelie JF, Droser ML, Bottjer DJ (1991) "Ichnofabric" it is! Palaios 6:100-101.

Ens BJ, Klaassen M, Zwarts L (1993) Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behaviour. Neth J. Sea Res. 31(4):447-494

Farrow GE (1971) Back-reef and lagoonal environments of Aldabra Atoll as distinguished by their crustacean burrows. Symp. Zool. Soc. Lond. 28:455-500

Featherstone RP, Risk MJ (1977) the effects of tube-dwelling polychaetes on intertidal sediments of the Minas Basin, Bay of Fundy. J. Sed. Pet. 47:446-450

Frey RW (1973) Concepts in the study of biogenic sedimentary structures. J. Sed. Pet. 43:6-19

Frey RW (1978) Behavioural and ecological implications of trace fossils. Chapter 3 in Basan PB (ed) Trace fossil concepts. SEPM Short Course No 5, Oklahoma p43-66

Frey RW, Goldring R (1992) Marine event beds and recolonisation surfaces as revealed by trace fossil analysis. Geol. Mag. 129(3):325-335

Frith DW, Tantanasiriwong R and Bhatia O (1976) Zonation of macrofauna on a mangrove shore, Phuket Island. Phuket Mar. Biol. Cent. Res. Bull. 10:37pp

Frydl P, Stearn GW (1978) Rate of bioerosion by parrotfish in Barbados reef environments. J. Sed. Pet. 48:1149-1157

Fütterer DK (1974) Significance of the boring sponge *Cliona* for the origin of fine-grained material of carbonate sediments. J. Sed. Pet. 42:211-226

Garson MS, Mitchell AHG, Young B, Tait BAR (1975) The Geology of the Tin Belt in Peninsula Thailand around Phuket, Phangnga and Takua Pa. I. G. S. Overseas Memoir 1 112pp.

Ginsburg RN (1956) Environmental relationships of grain size and constituent particles in some South Florida carbonate sediments. AAPG Bull. 40:2384-2427

Ginsburg RN, Lowenstam HA (1958) Influence of marine bottom communities on the depositional environment of sediments. J. Geol. 66:310-318

Ginsburg RN, Schroeder JH (1973) Growth and submarine fossilisation of algal cup reefs, Bermuda. Sedimentology 20:575-614

Ginsburg RN, Marszalek DS, Schneidermann N (1971) Ultrastructure of carbonate cements in a Holocene algal reef of Bermuda. J. Sed. Pet. 41:472-482

Glynn PW, Wellington GM, Birkeland C (1979) Coral reef growth in the Galapagos: limitation by sea urchins. Science 203:47-49

Goldring R (1964) Trace fossils and the sedimentary surface in shallow marine sediments. In van Straaten LMJU (ed) Deltaic and shallow marine deposits. Developments in Sedimentology 1:136-143

Goldring R (1995) Organisms and the substrate: response and effect. In Bosence DWJ and Allison PA (eds) Marine palaeoenvironmental analysis from fossils. Geol. Soc. Spec. Publ. 83:151-180

Goreau TF, Goreau NI, Yonge CM (1972) On the mode of boring in *Fungiacava eilatensis* (Bivalvia: Mytilidae) J. Zool. 166:55-60

Grant J (1983) The relative magnitude of biological and physical sediment reworking in an intertidal community. J. Mar. Res. 41:673-689

Griffis RB, Suchanek TH (1991) Model of burrow architecture and trophic modes in thalassinid shrimps. Mar. Ecol. Prog. Ser. 79:171-183

Gygi RA (1975) *Sparisoma viride* (Bonnaterre), the stoplight parrotfish, a major sediment producer on coral reefs of Bermuda. Ecl. Geol. Helvet. 68(2):327-359

Häntzchel W (1975) Trace Fossils and Problematica. Part W, Miscellanea. in Teichert C (ed) Treatise on Invertebrate Palaeontology. Geol. Soc. Amer. and Univ. of Kansas, Lawrence 269pp

Hein FJ, Risk MJ (1975) Bioerosion of coral heads: inner patch reefs, Florida Reef Tract. Bull. Mar. Sci. 25(1):133-138

Howard JD (1975) The sedimentological significance of trace fossils. In Frey RW (ed) The Study of Trace Fossils. Springer Verlag New York p131-146

Howard JD (1978) Sedimentology and trace fossils. In Basan PB (ed) Trace Fossil Concepts. SEPM Short Course 5: 13-47

Hunter IG (1977) Sediment production by *Diadema antillarum* on a Barbados fringing reef. Proc. 3rd Int. Coral Reef Symp., Miami 2:105-109

Hutchings PA (1986) Biological destruction of coral reefs. Coral Reefs 4:239-252.

Hylleberg J (1994) Phylum Sipuncula - Part 2. Cryptic fauna with emphasis on sipunculans in hump coral *Porites lutea*, the Andaman Sea, Thailand. Phuket Marine Biological Center Res. Bull. 59:33-41

Jehu TJ (1918) Rock-boring organisms as agents of coastal erosion. Scot. Geog. Mag. 34:1-11

Jones B, Pemberton SG (1988) Bioerosion of corals by *Lithophaga*: an example from the Pleistocene Ironshore formation of Grand Cayman, BWI. Proc. 6th Int. Coral Reef Symp., Townsville, Australia 3:437-440

Jones B, Pemberton SG (1988) *Lithophaga* borings and their influence on the diagenesis of corals on the Pleistocene Ironshore formation of Grand Cayman Island, BWI. Palaios 3:3-21

Jones B, Pemberton SG (1989) Sedimentology and ichnology of a Pleistocene unconformity-bounded, shallowing-upward carbonate sequence: the Ironshore Formation, Salt Creek, Grand Cayman. Palaios 4:343-355.

Karplus I (1987) The association between gobiid fishes and burrowing alpheids. Oc. Mar. Biol. Ann. Rev. 25:507-562

Karplus I, Szlep R, Tsurnamal M (1974) The burrows of alpheid shrimps associated with gobiids in the Northern Red Sea. Mar. Biol. 24:259-68

Kidwell SM (1991) The stratigraphy of shell concentrations. Chapter 5 in Allison PA and Briggs DEG (eds) Taphomony: releasing the data locked in the fossil record. Vol 9 of topics in Geobiology. Plenum Press New York p212-290

Kidwell and Bosence (1991) Taphonomy and time-averaging of marine shelly faunas. Chapter 4 in Allison PA and Briggs DEG (eds) Taphomony: releasing the data locked in the fossil record. Vol 9 of topics in Geobiology. Plenum Press New York p115-209

Kiene WE (1985) Biological destruction of experimental coral substrates at Lizard Island (Great Barrier Reef, Australia) Proc. 5th Int. Coral Reef Congress, Tahiti 5:339-344

Kiene WE (1988) A model of bioerosion on the Great Barrier Reef. Proc. 6th Int. Coral Reef Symp., Townsville, Australia 3:449-454

Kitchell JA (1979) Deep-sea foraging pathways: An analysis of randomness and resource exploitation. Palaeobiology 5:107-125

Kitchell JA, Kitchell JK, Clark DL, Dangeard L (1978) Deep-sea foraging behaviour: Its bathymetric potential in the fossil record. Science 200:1289-1291

Klaasen M, Ens BJ (1993) Habitat selection and energetics of the fiddler crab (*Uca tangeri*) Netherlands Journal of Sea Research 31(4):495-502

Kleeman KH (1973) Der Gesteinsabbau durch Ätzmuscheln an Kalkküsten. Oecologia (Berlin) 13:377-395.

Kreisa RD (1981) Storm-generated sedimentary structures in subtidal marine facies with examples from the Middle and Upper Ordovician of southwestern Virginia. J. Sed. Pet. 51:823-848

Lazar B, Loya Y (1991) Bioerosion of coral reefs - a chemical approach. Limnol. Oc. 36(2):377-383

Le Campion-Alsumard T, Romano JC, Peyrot-Clausade M, Le Campion J, Paul R (1993) Influence of some coral reef communities on the calcium carbonate budget of Tiahura reef (Moorea, French Polynesia). Mar. Biol. 115(4):685-693

Limpsaichol P (1981) Environmental factors estimated at PMBC. Phuket Marine Biological Center Research Bulletin 28:23-26

McCave IN (1988) Biological pumping upwards of the coarse fraction of deep sea sediments. J. Sed. Pet. 58(2):148-158

McLean RF (1967) Erosion of burrows in beachrock by the tropical sea urchin *Echinometra lucunter.* Can J. Zool. 45:586-588

McLean RF (1974) Geological significance of bioerosion of beachrock. Proc. 2nd Int. Coral Reef Symp., Brisbane 2:401-408

Magwood JPA, Ekdale AA (1994) Computer-aided analysis of visually complex ichnofabrics in deep-sea sediments. Palaios 9(1):102-115

Martinsson A (1970) Toponomy of trace fossils. In Crimes TP & Harper JC (eds) Trace Fossils. Seel House Press, Liverpool. p323-330.

Meadows PS, Meadows A (1991) The geotechnical and geochemical implications of bioturbation in marine sedimentary ecosystems. Symp. Zool. Soc. London 63:157-181

Meldahl K (1987) Sedimentologic and taphonomic implications of biogenic stratification. Palaios 21:350-58

Miller MF (1984) Bioturbation of intertidal quartz-rich sands: a modern example and its sedimentologic and paleoecologic implications. J. Geol. 92:201-16

Moore DG, Scruton PC (1957) Minor internal structures of some Recent unconsolidated sediments. Am. Assoc. Pet. Geol. Bull. 41:2723-2751

Myers AC (1977) Sediment processing in a marine subtidal sandy bottom community I. Physical aspects. II. Biological consequences. J. Mar. Res. 35:609-647

Neumann AC, Macintyre I (1985) Reef response to sea level rise: keep-up, catch-up or give-up. Proc. 5th Int. Coral Reef Symp. 3:105-110

Nickell LA (1992) Deep bioturbation in organically enriched marine sediments. PhD Thesis London University 400pp

Nickell LA, Atkinson RJA (1995) Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. Mar. Ecol. Prog. Ser. 128:181-197.

Nielsen C (1976) An illustrated checklist of bivalves from PMBC Beach with a reef-flat at Phuket, Thailand. Phuket Marine Biological Center Res. Bull. 9:25pp

Nielsen C (1986) Fauna associated with the coral *Porites* from Phuket, Thailand. (Part 1): Bivalves with description of a new species of *Gastrochaena.* Phuket Marine Biological Center Res. Bull. 42:24pp

Nowell ARM, Jumars PA, Eckmann JE (1981) Effects of biological activity on the entrainment of marine sediments. Mar. Geol. 42:133-153

Ogden JC (1977) Carbonate sediment production by parrot fish and sea urchins on Caribbean reefs. In Frost SH, Weiss MP, Saunders JB (eds) AAPG Studies in Geology No.4. AAPG Tulsa Olkahoma USA p 281-288

Orme GR (1977) Aspects of sedimentation in the coral reef environment. Chapter 5 in Jones OA & Endean R (eds) Biology and Geology of Coral Reefs (Vol 4 Geology 2) Academic Press New York.

Otter GW (1937) Rock-destroying organisms in relation to coral reefs. Scientific Report of the Great Barrier Reef Expedition 1928-29 1:323-352

Patton WK (1976) Animal associates of living coral reef corals. In Jones OA & Endean R (eds) Biology and Geology of Coral Reefs Volume III (Biology) Chapter 1. Academic Press New York p 1-36

Pedley M (1992) Bio-retexturing: early diagenetic fabric modifications in outer-ramp settings - a case study from the Oligo-Miocene of the Central Mediterranean. In Sellwood BW (ed) Ramps and Reefs. Sed. Geol. 79:173-188

Pemberton SG (1992) Applications of Ichnology to Petroleum Exploration. SEPM Core Workshop No. 17 429pp

Pemberton SG, Jones B (1988) Ichnology of the Pleistocene Ironshore Formation, Grand Cayman Island, British West Indies. J. Palaeo. 62(4):495-505

Peyrot-Clausade M, Hutchings PA, Richard G (1992) Temporal variations of macroborers in massive *Porites lobata* on Moorea, French Polynesia. Coral Reefs 11(3):161-166

Phongsuwan N (1991) Recolonisation of a coral reef damaged by a storm on Phuket Island, Thailand. Phuket Marine Biological Center Research Bulletin 56:75-83

Pinn EA, Ansell AD (1993) The effect of particle size on the burying ability of the brown shrimp *Crangon crangon*. Journal of the Marine Biological Association 73:365-377

Purdy EG (1964) Sediments as substrates. In Imbrie J & Newell N Approaches to Paleoecology. John Wiley and Sons Inc. New York. p 238-271

Rhoads DC (1967) Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbour and Buzzards Bay, Massachusetts. J. Geol. 75:461-476

Rhoads DC, Boyer LF (1982) The effects of marine benthos on physical properties of sediments. A successional perspective. In McCall PL & Tevesz MJS (eds) Topics in Geobiology 2: Animal-sediment relations. The biogenic alteration of sediments. Plenum Press New York, London p 3-52

Rhoads DC, Stanley DJ (1965) Biogenic graded bedding. J. Sed. Pet. 35:956-963

Rhoads DC, Young DK (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150-178

Rice AL, Chapman CJ (1971) Observations on the burrows and burrowing behaviour of two mud-dwelling decapod crustaceans *Nephrops norvegicus* and *Goneplax rhomboides*. Mar. Biol. 10:330-342

Roberts HH, Wiseman WJ, Suchanek TH (1981) Lagoon sediment transport: the significant effect of *Callianassa* bioturbation. Proc. 4th Int. Coral Reef Symp., Manila 1:459-465

Savrda CE, Bottjer DJ (1986) Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. Geology 14:3-6

Savrda CE, Bottjer DJ (1987) The exaerobic zone, a new oxygen-deficient marine biofacies. Nature 327:54-56

Schroeder JH, Zankl H (1974) Dynamic reef formation: a sedimentological concept based on studies of Recent Bermuda and Bahama reefs. Proc. 2nd Int. Coral Reef Symp., Brisbane. 2:413-428

Scoffin TP (1972) Fossilisation of Bermuda patch reefs. Science 178:1280-1282

Scoffin TP (1987) An introduction to carbonate sediments and rocks. Blackie and Son Ltd. Glasgow London 274pp

Scoffin TP (1992) Taphonomy of coral reefs: a review. Coral Reefs 11:57-77

Scoffin TP (1993) The geological effects of hurricanes on coral reefs and the interpretation of storm deposits. Coral Reefs 12:203-221

Scoffin TP (1997) Preservation and $CaCO_3$ budget of reef-flat corals, Phuket, South Thailand. Proceedings of the Eighth International Coral Reef Symposium, Panama (in press)

Scoffin TP, Garrett P (1974) Processes in the formation and preservation of internal structure in Bermuda patch reefs. Proc. 2nd Int. Coral Reef Symp., Brisbane. 2: 429-448

Scoffin TP, Stearn CW, Boucher D, Frydl P, Hawkins CM, Hunter IG, MacGeachy JK (1980) Calcium carbonate budget of a fringing reef on the West Coast of Barbados. Part II: Erosion, sediments and internal structure. Bull. Mar. Sci. 30(2):475-508

Scoffin TP, Tudhope AW, Brown BE, Chansang H and Cheeney RF (1992) Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. Coral Reefs 11:1-11

Scoffin TP, Brown BE, Dunne RP, Le Tissier MDA (1997) The controls on growth form of intertidal massive corals, Phuket, South Thailand. Palaios (in press)

Scott PJB (1985) Aspects of living coral associates in Jamaica. Proc. 5th Symp. 5:345-350

Scott PJB (1987) Associations between corals and macroinfaunal invertebrates in Jamaica with a list of Caribbean and Atlantic coral assemblages. Bull. Mar. Sci. 40(2):271-286

Scott PJB, Risk MJ (1988) The effect of *Lithophaga* (Bivalvia: Mytilidae) boreholes on the strength of the coral *Porites lobata*. Coral Reefs 7(3):145-151

Seilacher A (1964a) Biogenic sedimentary structures. In Imbrie J & Newell N (eds) Approaches to Paleoecology. John Wiley and Sons New York p 296-316

Seilacher A (1964b) Sedimentological classification and nomenclature of trace fossils. Sedimentology 3:253-256

Seilacher A (1967) Bathymetry of trace fossils. Mar. Geol. 5:413-428

Seilacher A (1969) Paleoecology of boring barnacles. Am. Zool. 9(3):705-719

Seilacher A (1974) Flysch trace fossils: evolution of behavioural diversity in the deep sea. Neues Jahrbuch für Geol und Paläo Monatschefte 1974:233-245

Seilacher A (1982) General Remarks About Event Deposits. In Einsele G & Seilacher A (eds) Cyclic and Event Stratification. Springer-Verlag Berlin Heidelberg New York p161-173

Shaw JK and Hopkins TS (1977) Distribution of the family Hapalocarcinidae (Decapoda, Brachyura) on the Florida Middle Ground with a description of *Pseudocryptochirus hypostegus* (new species). Proc. 3rd Int. Coral Reef Symp., Miami 1:117-183

Shinn EA (1968) Burrowing in the Recent lime sediments of Florida and the Bahamas. J. Palaeo. 42:879-894

Soliman GN (1969) Ecological aspects of some coral-boring gastropods and bivalves of the Northwestern Red Sea. Am. Zool. 9:887-894

Stearn CW, Scoffin TP, Martindale W (1977) Calcium carbonate budget of a fringing reef on the West Coast of Barbados. Part I: Zonation and productivity. Bull. Mar. Sci. 27(3):479-510

Suchanek T (1983) Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea; Thalassinidae) bioturbation. J. Mar. Res. 41:281-292

Suchanek T (1985) Thalassinid shrimp burrows: ecological significance of species-specific architecture. Proc. 5th Int. Coral Reef Congress, Tahiti 5:205-210

Swift DJ (1993) The macrobenthic infauna off Sellafield (North-Eastern Irish Sea) with special reference to bioturbation. Journal of the Marine Biological Association 73:143-162

Swinbanks DD (1981) Sediment reworking and the biogenic formation of clay laminae by *Arenicola pacifica*. J. Sed. Pet. 51:1135-1145

Swinbanks DD, Murray JM (1981) Biosedimentological zonation of Boundary Bay tidal flats, Fraser River Delta, British Columbia. J. Sed. Pet. 28:201-237

Swinbanks DD, Luternauer JL (1987) Burrow distribution of thalassinidean shrimp on a Fraser Delta tidal flat, British Columbia. J. Palaeo. 61:315-332

Takeda S, Matsumasa M, Yong H-S, Murai M (1996) "Igloo" construction by the ocypodid crab, *Dotilla myctiroides* (Milne-Edwards)(Crustacea: Brachyura): The role of an air chamber when burrowing in a saturated sandy substratum. J. Exp. Mar. Biol. Ecol. 198(2):237-247

Tantanasiriwong R (1978) An illustrated checklist of marine shelled Gastropods from Phuket Island, adjacent mainland and offshore islands, western Peninsula Thailand. Phuket Mar. Biol. Cent. Res. Bull. 21:22pp

Taylor AM, Goldring R (1993) Description and analysis of bioturbation and ichnofabric. J. Geol. Soc., London 150:141-148

Tedesco LP, Wanless HR (1991) Generation of sedimentary fabrics and facies by repetitive excavation and storm infilling of burrow networks, Holocene of South Florida and Caicos Platform, B.W.I. Palaios 6:326-343

Thomassin BA (1974) Soft bottom carcinological fauna *sensu lato* on Tuléar coral reef complexes (SW Madagascar): distribution, importance, roles played in trophic food-chains and in bottom deposits. Proc. 2nd Int. Coral Reef Symp, Brisbane 1:297-320

Trudgill ST (1983) Measurement of rates of erosion of reefs and reef limestones. In Barnes DJ (ed) Perspectives on Coral Reefs. AIMS/Clouston, Townsville p 256-262.

Tudhope AW, Scoffin TP (1984) The effects of *Callianassa* bioturbation on the preservation of carbonate grains in Davies Reef Lagoon, Great Barrier Reef, Australia. J. Sed. Pet. 54(4):1091-1096

Tudhope AW, Scoffin TP (1994) Growth and structure of fringing reefs in a muddy environment, South Thailand. J. Sed. Res. A64(4):752-764

Vaugelas JV de (1985) A new technique for collecting large-sized callianassid mud-shrimp (Decapoda, Thalassinidea) Crustaceana 49(1):105-109

Vaugelas JV de (1990) Ecologie des callianasses (Crustacea, Decapoda, Thalassinidea) et milieu recifal Indo-Pacifique. Consequences du remaniement sédimentaire sur la distribution des matieres humiques, des métaux trace et des radionucléides. Memoire présenté a l'Université de Nice, 269pp.

Vaugelas JV de, Delesalle B, Monier C (1986) Aspects of the biology of *Callichirus armatus* (A. Milne-Edwards 1870)(Decapoda, Thalassinidea) from French Polynesia. Crustaceana 50(2):204-216

Vogel F (1984) Comparative and functional morphology of the spoon-tipped setae on the second maxillipeds in *Dotilla* Stimpson, 1958 (Decapoda, Brachyura, Ocypodidae). Crustaceana 47:225-234

Wanless HR, Tedesco LP, Tyrrell KM (1988) Production of subtidal tempestites by Hurricane Kate, Caicos Platform, British West Indies. J. Sed. Pet. 58:739-750

Warme JE (1967) Graded bedding in the Recent sediments of Mugu Lagoon, California. J. Sed. Pet. 37:540-547

Warme JE (1977) Carbonate borers - their role in reef ecology and preservation. In Frost SH, Weiss MP & Saunders JB (eds) AAPG Studies in Geology No.4. AAPG Tulsa Olkahoma USA p 261-279

Weimar RJ, Hoyt JH (1964) Burrows of *Callianassa major*, geological indicators of littoral and shallow neritic environments. J. Palaeo. 38(4):761-767

Yingst JY, Aller RC (1982) Biological activity and associated sedimentary structures in HEBBLE area deposits, western north Atlantic. Mar. Geol. 48:M7-M15

Yonge CM (1963) Rock-boring organisms. In Sognnaes RF (ed) Mechanics of hard tissue destruction. Amer. Assoc. Adv. Sci. Publ. 75:1-24

Young DK, Rhoads DC (1971) Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. II. Reworking by *Molpadia oolitica*. Mar. Biol. 11:242-252

Zankl H, Multer HG (1977) Origin of some internal fabrics in Holocene reef rocks, St. Croix, USVI. Proceedings of the 3rd Int. Coral Reef Symp. 127-133

Ziebis W, Forster S, Huettel M, Jørgensen BB (1996) Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed. Nature 382:619-622

ACKNOWLEDGEMENTS

My supervisors Terry Scoffin and Sandy Tudhope helped me at all stages, from the initial planning and fieldwork, through lab work and data analysis, to discussion and speedy reading of various drafts of this thesis.

In Phuket, all the staff at PMBC made my total of 7 months there really enjoyable and also provided help with accommodation and lab space. Particular mention should go to Hansa, Ukkrit, Niphon and Pitul but also toSomchai, Woody, Anuwat and Suree.

Special thanks go to Jason who was invaluable as my field assistant in 1995. He was remarkably tolerant of an exhausting diving timetable, in often unpleasant and difficult conditions, and was full of good ideas; thank you for everything.

Thanks also to the Danes, Svend, Dorte, Sus and Torben, who became such close friends; the expeditions in the bathtub to Dok Mai, fantastic food at the Yam Yen and trips in to town were all memorable distractions from my fieldwork. And, of course, thanks to Debbie Dexter, who wore us out with her boundless energy but invited us all to swim in her hotel pool to wind down!

Barbara Brown, Martin le Tissier and others from Newcastle University also assisted with the logistics of my first trip to Phuket and helped me find my feet in Phuket.

Back in Edinburgh, numerous people helped me with the lab stage of the project: They are (among others): Ann Mennim (carbonate titrations and Coulter counter), Mike Hall (thin sections), John Findlay (SEM), Yvonne Cooper (photography), Diana Baty (photography, drafting), Alan Pike (who made the box corers), Euan Clarkson and John Craven (microscopes and cameras), Shane and Chis (all things computing), and Geoff Angell (X-ray diffraction).

I have been lucky to be writing up with a crowd of other people who made me feel I wasn't the only one trying to achieve the impossible. My fellow writers were Alan, Sarah, Coleen, Sally, Sniper, Meryl, Janet and the Cambridge crowd. My office mates and other residents of the Mouse House (both past and present) have made my time in the Geology Department most enjoyable. Thank you to Jon for all the coffee breaks and Swann lunches which provided a welcome break.

Last, but not least, thanks go to my family and to my friends and flatmates for support, distractions and for keeping me sane, especially during the latter stages. Particular thanks go to Harriet, Jeremy, Simon and Doug.

This project was supported by NERC, as was my field assistant and my trip to Panama for the Eighth International Coral Reef Symposium.

APPENDIX A - Reef and coral data

	LIVE												DEAD														
Coral species	Horizontal				Vertical				Angled				Horizontal				Vertical				Angled				Total	% coral	% total
Goniastrea retiformis	2	0	3	1	0	0	3	2	1	2	2	0	8	1	4	5	1	0	2	1	2	0	4	0			
	1	0	0	0	1	5	1	2	0	7	2	1	0	10	14	5	0	2	3	2	0	8	14	7			
	3	3	2	2	1	2	3	1	3	4	9	8	0	7	11	2	1	4	9	0	0	6	10	1			
	3	2	0	3	4	6	3	1	5	5	2	3	0	2	0	2	1	1	1	0	0	7	4	1	277	52.7	38.4
Goniastrea aspera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00
Coeloseris mayeri	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0			
	1	0	0	0	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0			
	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	0	1	1	0	0	1	0	0	0	6	1	0	0	4	0	0	0	0	0	0	0	2	0	27	5.13	3.74
Porites lutea	1	1	0	0	0	0	0	2	0	0	0	0	3	6	0	1	0	0	1	0	1	1	0	1			
	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0			
	1	0	0	0	0	1	0	0	4	0	0	0	2	2	0	0	0	0	0	0	2	0	0	0			
	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	40	7.60	5.54
Platygyra sp.	0	2	0	0	0	2	0	1	0	2	0	4	0	1	0	1	0	0	0	0	0	1	0	1			
	0	1	0	1	2	0	0	1	1	0	0	1	3	1	0	0	1	0	0	0	1	0	0	0			
	2	2	0	0	1	1	0	3	9	2	1	4	0	1	0	2	0	1	1	1	0	4	0	3			
	0	1	0	2	0	0	0	1	0	1	1	4	0	1	0	1	0	0	0	0	0	0	0	3	81	15.40	11.22
Favites	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0			
	0	2	0	1	0	0	0	1	0	0	2	1	0	2	1	1	0	0	0	0	0	0	0	0			
	0	1	0	0	0	0	0	1	0	0	0	3	1	2	0	0	0	0	0	0	0	0	0	0			
	3	4	1	4	2	1	0	0	11	5	3	2	5	2	2	3	0	0	0	0	2	1	1	0	77	14.64	10.66
Favia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	0	0	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0			
	1	0	0	0	2	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0			
	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	2.66	1.94
Other spp	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0			
	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1.90	1.39
Total	76				61				135				127				34				93				526		
% of coral	14.4				11.6				25.7				24.1				6.46				17.7				100	100.0	
% of total	10.5				8.45				18.7				17.6				4.71				12.9				72.9		72.9

Substrate	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	total	%
Algae	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	4	0.55
Indet coral/mud	6	3	0	6	8	3	3	13	11	3	3	17	12	10	9	14	121	16.8
Crack	1	3	0	1	0	0	0	0	1	1	0	1	0	0	3	0	11	1.52
Borehole	2	3	3	3	1	0	1	1	0	0	0	1	1	2	1	1	20	2.77
Sand	0	0	0	0	1	2	2	2	1	1	0	0	0	0	0	0	9	1.25
Rubble	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	4	0.55
Hole	0	0	0	0	0	5	3	3	0	1	0	0	0	0	4	0	16	2.22
Others	0	1	0	1	0	1	0	0	3	0	2	1	0	0	0	2	11	1.52
Total number	12	10	3	12	10	13	9	20	17	6	5	20	13	12	17	17	196	27.1

Layout of above table:

A	B	C	D
E	F	G	H
I	J	K	L
M	N	O	P

A-P are repeat transects

Total number of data points = 722

MID REEF TRANSECTS

	LIVE												DEAD														
Coral species	Horizontal				Vertical				Angled				Horizontal				Vertical				Angled				Total	% coral	%total
Goniastrea retiformis	2	0	3	0	0	0	0	0	1	2	4	0	8	1	5	0	1	0	1	0	2	0	0	0			
	0	0	1	0	0	0	0	0	0	0	2	0	0	5	0	0	0	2	0	0	0	4	0	0			
	1	0	3	2	3	1	1	0	1	0	4	2	0	0	1	1	0	0	0	0	0	0	0	0			
	0	1			1	0			0	1			0	1			0	0			1	1			70	17.72	10.22
Goniastrea aspera	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0			
	0	0	3	1	0	0	0	0	0	2	2	0	0	4	3	0	0	1	0	0	0	0	1	0			
	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0			
	0	1			0	0			0	1			2	1			0	0			0	0			29	7.34	4.23
Coeloseris mayeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0			
	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0			
	0	0			0	0			0	0			0	0			0	0			0	0			7	1.77	1.02
Porites lutea	1	1	0	1	0	0	0	0	0	0	2	5	3	6	3	6	0	0	0	1	1	1	0	2			
	0	0	1	1	4	1	2	0	4	0	1	7	13	2	6	11	0	0	0	0	2	0	2	2			
	2	0	0	0	3	0	2	3	7	1	1	0	15	13	6	18	0	3	0	0	4	0	1	3			
	0	2			0	3			2	0			1	6			0	1			2	2			193	48.9	28.18
Platygyra sp.	0	2	2	0	0	2	0	0	0	2	0	1	0	1	0	0	0	0	0	0	0	1	1	0			
	0	0	1	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0	0	0	0	2	0	0			
	0	0	0	0	0	0	0	0	0	0	2	2	0	0	1	0	0	0	0	1	0	0	0	0			
	3	2			0	3			1	1			5	8			0	0			3	3			55	13.92	8.03
Favites	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0			
	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	0			0	0			0	0			1	0			0	0			0	0			10	2.53	1.46
Favia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	4	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	1			0	0			0	0			0	0			0	0			0	0			11	2.78	1.61
Other spp	0	0	3	0	0	0	1	0	0	0	1	3	0	2	0	0	0	0	0	0	0	0	0	0			
	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
	1	1			0	0			0	0			0	0			0	0			0	0			20	5.06	2.92
Total				64				31				84				161				12				43	395		
% of coral				16.2				7.85				21.3				40.8				3.04				10.9	100	100.0	
% of total				9.34				4.53				12.3				23.5				1.75				6.28	57.7		57.66

Substrate	A	B	C	D	E	F	G	H	I	J	K	L	M	N	total	%
Algae	3	0	9	13	12	3	14	21	11	2	11	11	12	6	128	18.7
Indet coral/mu	6	3	16	16	8	6	8	5	3	14	7	10	8	3	113	16.5
Crack	1	3	0	0	4	1	0	0	1	4	1	1	4	0	20	2.92
Borehole	2	3	0	0	0	1	0	1	0	0	2	0	0	1	10	1.46
Sand	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	0.58
Rubble	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.15
Hole	0	0	0	1	0	3	2	1	1	1	0	0	1	2	12	1.75
Others	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0.29
Total number	12	10	25	30	24	14	24	28	16	21	23	22	29	12	290	42.3

Layout of above table:

A	B	C	D
E	F	G	H
I	J	K	L
M	N		

A-N are repeat transects

Total number of data points = 685

INNER REEF TRANSECTS

Coral species	LIVE Hor	LIVE Vert	LIVE Ang	DEAD Hor	DEAD Vert	DEAD Ang	Total	% coral	%total
Goniastrea retiformis	0	0	0	0	0	0			
	0	2	0	0	0	0			
	0	0	1	1	0	0			
	0	0	0	0	0	0	4	5.33	1.97
Goniastrea aspera	0	0	0	0	0	0			
	0	1	1	3	1	2			
	0	0	0	0	0	0			
	0	0	0	0	0	0	8	10.67	3.94
Coeloseris mayeri	0	0	0	0	0	0			
	0	0	0	0	0	0			
	0	0	0	0	0	0			
	0	0	0	0	0	0	0	0.00	0.00
Porites lutea	0	1	1	0	0	0			
	1	0	0	5	0	1			
	0	0	2	11	3	4			
	0	3	2	6	1	3	44	58.67	21.67
Platygyra sp.	0	0	0	0	0	0			
	0	0	0	0	0	0			
	0	0	0	0	0	0			
	0	0	0	0	0	0	0	0.00	0.00
Favites	0	0	0	0	0	0			
	0	0	0	0	0	0			
	0	0	0	0	0	0			
	0	0	0	0	0	0	0	0.00	0.00
Favia	0	0	0	0	0	0			
	0	0	0	0	0	0			
	0	0	0	0	0	0			
	0	0	0	0	0	0	0	0.00	0.00
Other spp	3	1	1	1	0	2			
	2	1	4	1	0	0			
	1	0	0	0	0	0			
	2	0	0	0	0	0	19	25.33	9.36
Total	9	9	12	28	5	12	75		
% of coral	12	12	16	37.3	6.67	16	100	100.0	
% of total	4.43	4.43	5.91	13.8	2.46	5.91	36.9		36.95

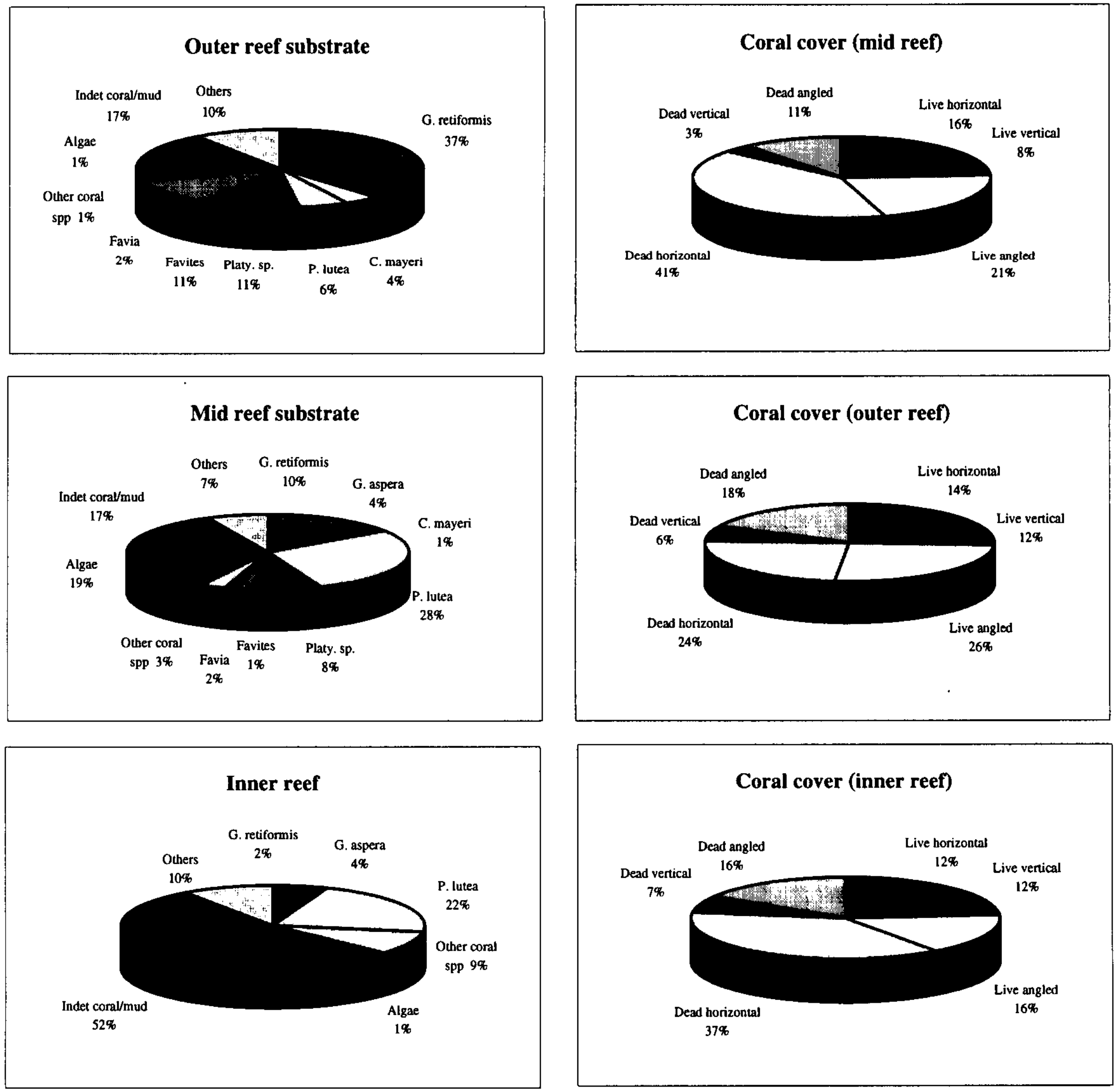
Substrate	A	B	C	D	total	%
Algae	1	1	0	0	2	0.99
Indet coral/mud	36	22	25	23	106	52.2
Crack	0	0	0	0	0	0
Borehole	0	0	1	0	1	0.49
Sand	0	0	0	0	0	0
Rubble	0	0	0	0	0	0
Hole	4	3	1	6	14	6.9
Others	1	0	0	4	5	2.46
Total number	42	26	27	33	128	63.1

Total no. data = 203

Layout of above table:

A
B
C
D

A to D are repeat transects



Summary pie charts of the substrate data in this Appendix

ACTUAL / PLAN AREA RELATIONSHIPS
FOR TIN SMELTER REEF

	Actual (m)	Plan (m)	Ratio (A/P)
Outer reef	3.00	2.20	1.36
	3.00	2.05	1.46
	3.00	2.21	1.36
	5.20	3.14	1.66
	5.20	3.58	1.45
	5.20	3.68	1.41
	5.20	3.29	1.58
	5.20	3.16	1.65
	5.20	3.62	1.44
	5.20	3.71	1.40
	5.20	3.41	1.52
	5.20	3.71	1.40
	5.20	3.30	1.58
	5.20	3.19	1.63
	5.20	3.26	1.60
	5.20	3.14	1.66
		mean	**1.51**
		stdev	0.11
		n	16
Mid reef	3.00	2.59	1.16
	3.00	2.55	1.18
	5.20	4.45	1.17
	5.20	4.57	1.14
	5.20	4.52	1.15
	5.20	4.33	1.20
	5.20	4.58	1.14
	5.20	4.68	1.11
	5.20	4.54	1.15
	5.20	3.92	1.33
	5.20	4.43	1.17
	5.20	4.72	1.10
	5.20	4.39	1.18
	5.20	4.56	1.14
		mean	**1.17**
		stdev	0.05
		n	14
Inner reef	5.20	3.38	1.54
	5.20	3.66	1.42
	5.20	4.09	1.27
	5.20	3.22	1.61
		mean	**1.46**
		stdev	0.15
		n	4

A 3.00m or 5.2m long line was laid so as to contour the reef surface and the horizontal distance it covered was measured to obtain the plan distance.

APPENDIX B - Sediment characteristics

PARTICLE SIZE DISTRIBUTIONS FOR MAIN CORES (Figures are weight percents)

Sediment depth (cm)	Size fraction													
	<4um	4-8um	8-16um	16-31.5um	31.5-63um	63-125um	125-250um	250-500um	0.5-1mm	1-2mm	2-4mm	4-8mm	8-16mm	16-32mm
CORE 38														
1.2-2.2	7.41	5.05	8.48	9.43	12.23	6.84	5.54	3.68	15.40	10.79	12.35	0.78	2.02	0.00
7.2-8.2	7.34	4.54	7.89	10.21	12.83	7.92	6.83	3.33	15.73	10.02	7.28	2.88	3.19	0.00
13.2-14.2	7.15	4.24	7.25	9.24	11.46	7.10	6.88	4.43	18.29	13.34	8.13	1.87	0.62	0.00
19.2-20.2	8.54	5.32	9.08	10.99	11.85	5.89	4.64	2.48	14.87	8.74	5.79	1.43	2.96	7.41
25.2-26.2	4.24	2.53	4.29	5.63	6.97	4.61	5.44	3.44	17.80	14.18	8.87	5.09	11.93	4.97
31.2-32.2	3.43	2.13	3.76	5.00	6.47	5.08	6.87	5.26	15.24	13.96	10.51	4.29	7.59	10.43
37.2-38.2	3.55	2.17	3.83	5.27	6.98	5.50	7.43	4.94	14.57	10.53	6.52	3.78	13.69	11.25
43.2-44.2	2.77	1.73	3.19	4.54	6.33	5.30	9.14	6.35	16.64	12.38	7.21	3.59	11.03	9.79
49.2-50.2	2.69	1.71	3.21	4.58	6.56	6.22	10.41	6.53	16.96	14.23	11.95	3.36	7.69	3.91
55.2-56.2	3.03	1.82	3.32	5.10	8.00	6.79	10.65	7.21	17.78	10.88	5.78	8.63	11.01	0.00
61.2-62.2	3.81	2.33	4.27	6.33	9.49	7.99	12.01	8.02	19.95	10.66	8.27	3.03	3.82	0.00
67.2-68.2	2.70	1.65	3.08	4.64	7.39	6.32	10.11	6.41	15.74	9.32	7.87	6.69	18.08	0.00
73.2-74.2	2.63	1.60	3.02	4.59	7.03	6.07	10.00	8.35	16.48	9.08	6.75	1.77	4.62	18.04
79.2-80.2	3.39	2.13	3.90	5.19	7.40	6.16	9.79	7.32	16.75	12.44	9.37	2.19	13.97	0.00
85.2-86.2	1.99	1.19	2.24	3.47	5.66	5.13	8.44	6.38	13.35	14.53	21.99	4.61	11.02	0.00
91.2-92.2	2.86	1.74	3.30	4.99	7.86	6.80	10.13	6.72	17.72	11.72	12.35	3.66	10.14	0.00
CORE 41														
6.9-7.9	10.40	6.83	12.59	15.40	18.81	8.73	5.89	5.25	9.63	4.18	2.30	0.00	0.00	0.00
12.9-13.9	6.69	4.17	7.22	8.91	10.78	6.47	6.94	7.19	17.62	10.89	7.99	2.17	2.97	0.00
18.9-19.9	3.39	2.20	3.73	4.38	5.93	3.94	8.44	10.24	28.45	19.60	7.77	1.46	0.47	0.00
24.9-25.9	6.88	4.42	7.24	8.01	10.69	6.64	8.34	5.43	16.92	12.63	7.78	2.92	2.12	0.00
30.9-31.9	5.00	3.33	5.38	5.71	7.26	5.74	8.96	8.72	20.19	11.84	7.84	2.79	7.24	0.00
36.9-37.9	3.27	2.02	3.68	5.31	7.62	7.32	12.44	10.49	16.11	9.78	10.43	3.72	7.79	0.00
42.9-43.9	2.81	1.72	3.05	4.17	5.91	5.67	10.28	6.95	18.30	11.93	10.34	1.84	3.26	13.77
48.9-49.9	3.01	1.80	3.26	5.07	8.58	7.76	11.52	7.10	15.00	8.04	5.18	2.68	14.47	6.52
54.9-55.9	2.14	1.34	2.50	3.59	5.33	4.74	10.59	7.90	17.36	14.44	14.92	5.23	9.91	0.00
60.9-61.9	3.21	1.92	3.54	5.42	8.81	8.13	14.42	9.04	18.46	12.40	7.67	2.28	4.70	0.00
66.9-67.9	4.50	3.00	4.93	5.51	7.82	6.89	12.85	7.72	17.07	12.12	10.45	5.14	1.99	0.00
72.9-73.9	4.85	2.91	5.24	7.65	11.23	9.61	15.91	6.98	15.82	10.54	8.13	1.11	0.00	0.00
78.9-79.9	5.48	3.32	5.85	7.88	10.98	9.40	14.30	8.56	14.11	8.86	7.36	0.68	3.21	0.00
84.9-85.9	4.24	2.55	4.68	6.94	10.26	8.95	14.35	9.51	16.20	10.34	5.38	2.46	4.12	0.00
90.9-91.9	3.45	2.06	3.83	6.12	10.12	9.32	16.19	9.98	16.09	10.86	7.48	2.58	1.92	0.00
96.9-97.9	4.18	2.44	4.44	6.96	11.61	10.34	16.51	8.80	14.61	9.31	5.93	4.21	0.67	0.00

Sediment depth (cm)	Size fraction													
	<4um	4-8um	8-16um	16-31.5um	31.5-63um	63-125um	125-250um	250-500um	0.5-1mm	1-2mm	2-4mm	4-8mm	8-16mm	16-32mm
CORE 42														
5.8-6.8	9.22	5.71	9.59	12.02	13.37	8.11	10.75	9.45	12.68	6.81	1.53	0.76	0.00	0.00
11.8-12.8	9.08	5.57	9.44	11.81	13.95	8.76	9.57	8.11	13.76	6.55	2.82	0.56	0.00	0.00
17.8-18.8	6.54	4.04	6.78	8.32	10.00	6.64	10.88	10.48	16.52	8.53	7.34	1.57	2.36	0.00
23.8-24.8	7.30	4.32	7.31	9.62	11.91	7.84	10.33	8.85	16.17	8.73	6.05	1.58	0.00	0.00
29.8-30.8	4.86	2.93	5.06	6.86	9.00	6.52	12.29	11.48	17.67	9.54	6.13	4.17	3.48	0.00
35.8-36.8	5.34	3.25	5.59	7.42	9.45	6.90	14.74	13.71	19.43	9.67	3.91	0.58	0.00	0.00
41.8-42.8	3.18	1.94	3.32	4.36	5.59	4.33	11.64	13.04	20.42	16.91	11.57	2.00	1.68	0.00
47.8-48.8	4.45	2.66	4.50	5.99	7.82	5.75	13.25	15.03	19.60	11.81	7.17	1.41	0.56	0.00
53.8-54.8	3.14	1.95	3.39	4.41	5.82	4.37	15.04	18.20	23.73	11.96	6.26	1.11	0.61	0.00
59.8-60.8	5.97	3.48	5.89	8.04	10.10	7.60	12.40	9.99	16.69	9.24	7.56	3.04	0.00	0.00
65.8-66.8	5.23	3.15	5.41	7.39	10.27	6.46	13.68	12.79	15.99	6.82	3.77	1.23	2.70	5.10
71.8-72.8	6.64	3.94	6.76	9.09	11.59	8.14	13.46	12.72	16.67	6.32	2.40	2.27	0.00	0.00
77.8-78.8	7.08	4.21	7.12	9.57	12.08	8.47	12.23	10.46	17.00	7.99	3.29	0.52	0.00	0.00
83.8-84.8	4.00	2.46	4.39	6.36	9.19	7.40	17.76	16.65	17.36	9.21	4.58	0.64	0.00	0.00
89.8-90.8	2.81	1.73	3.18	4.77	7.38	5.49	16.38	16.30	14.28	8.20	11.89	5.29	2.30	0.00
95.8-96.8	3.15	1.94	3.52	5.31	8.19	6.96	18.64	16.48	16.97	9.52	6.18	2.65	0.48	0.00
101.8-102.8	3.49	2.15	3.83	5.64	8.46	7.09	19.34	20.29	16.87	7.71	3.76	1.37	0.00	0.00
107.8-108.8	3.84	2.35	4.16	6.01	9.38	7.50	19.45	18.03	17.37	6.70	3.67	1.54	0.00	0.00
CORE 43														
5.5-6.5	11.37	6.95	11.77	14.46	15.89	8.25	8.63	6.41	9.72	5.13	1.41	0.00	0.00	0.00
11.5-12.5	11.77	6.93	11.14	13.18	14.66	7.71	8.42	5.95	10.52	6.04	3.67	0.00	0.00	0.00
17.5-18.5	10.76	6.43	10.32	11.81	13.00	6.99	7.65	5.96	13.15	8.49	4.68	0.76	0.00	0.00
23.5-24.5	9.31	5.46	8.84	10.62	11.76	6.33	7.32	6.10	16.64	9.22	6.25	1.05	1.10	0.00
29.5-30.5	8.63	5.16	8.57	10.46	12.01	7.06	9.26	8.13	15.21	9.67	3.95	0.52	1.37	0.00
35.5-36.5	6.95	4.23	7.18	9.05	10.18	6.31	11.65	12.48	16.42	7.64	6.18	0.85	0.85	0.00
41.5-42.5	4.19	2.69	4.63	5.70	6.48	4.45	13.55	17.15	20.91	9.71	5.63	2.09	2.81	0.00
47.5-48.5	3.51	2.23	3.81	4.61	5.49	3.95	11.61	15.54	23.14	13.43	7.63	3.26	1.80	0.00
53.5-54.5	3.00	1.88	3.25	4.19	5.63	4.50	13.52	16.75	21.48	13.12	8.80	1.06	2.83	0.00
59.5-60.5	3.11	1.94	3.40	4.51	5.96	4.66	13.50	17.06	20.73	9.68	7.09	1.42	6.94	0.00
65.5-66.5	3.43	2.07	3.64	5.25	8.33	7.12	18.05	17.73	20.21	8.97	4.27	0.92	0.00	0.00
71.5-72.5	3.41	2.07	3.62	5.19	7.76	6.51	17.02	17.18	18.11	8.93	5.28	1.64	1.31	1.97
77.5-78.5	4.14	2.51	4.37	6.19	9.06	7.35	17.82	18.02	18.68	7.97	3.38	0.51	0.00	0.00
81.5-82.5	3.94	2.40	4.10	5.67	8.09	6.76	16.36	17.57	19.77	9.48	5.42	0.45	0.00	0.00
89.5-90.5	3.87	2.41	4.19	5.87	8.38	6.70	18.36	17.81	16.64	7.88	3.69	2.16	2.03	0.00
95.5-96.5	4.05	2.48	4.28	6.09	8.65	6.72	19.18	19.94	16.97	6.74	3.47	0.85	0.60	0.00
101.5-102.5	3.75	2.31	4.01	5.69	8.26	6.45	19.30	19.67	17.57	8.15	3.53	1.32	0.00	0.00
107.5-108.5	4.29	2.58	4.39	6.21	9.00	7.36	19.41	18.23	14.71	8.12	4.30	1.39	0.00	0.00

Sediment	Size fraction													
depth (cm)	<4um	4-8um	8-16um	16-31.5um	31.5-63um	63-125um	125-250um	250-500um	0.5-1mm	1-2mm	2-4mm	4-8mm	8-16mm	16-32mm
CORE 44														
3.6-4.6	5.39	3.40	5.99	7.48	9.22	5.90	6.89	7.20	19.19	12.32	9.62	5.29	2.10	0.00
9.6-10.6	8.27	5.13	8.70	10.23	11.91	6.62	6.53	6.03	17.41	10.53	4.28	2.71	1.66	0.00
15.6-16.6	9.18	5.45	8.81	10.36	12.08	6.76	6.62	6.19	18.01	11.94	4.59	0.00	0.00	0.00
21.6-22.6	8.53	5.05	8.08	9.34	10.39	6.22	7.57	7.54	18.57	10.73	5.64	1.28	0.00	1.07
27.6-28.6	5.54	3.43	6.00	7.71	8.95	6.11	8.34	9.89	21.08	11.28	6.46	2.99	2.20	0.00
33.6-34.6	5.08	3.09	5.13	6.29	7.18	5.06	8.80	11.59	22.37	13.37	7.30	2.62	2.14	0.00
39.6-40.6	3.76	2.36	4.11	5.21	6.33	4.87	10.07	12.35	24.92	12.97	6.58	1.92	4.56	0.00
45.6-46.6	3.20	2.08	3.70	4.82	6.12	4.90	10.49	13.73	21.76	12.04	7.34	2.18	7.65	0.00
51.6-52.6	5.12	3.13	5.55	7.39	9.01	6.28	9.61	10.60	20.61	11.58	5.66	2.59	2.87	0.00
57.6-58.6	2.55	1.65	3.17	4.37	5.86	4.81	10.98	13.06	19.98	11.46	8.07	4.97	1.82	7.27
63.6-64.6	3.18	2.07	3.94	5.10	7.11	5.94	13.05	14.63	20.36	13.40	6.92	0.86	0.46	2.97
69.6-70.6	2.89	1.88	3.55	4.63	6.39	5.19	11.27	11.67	19.57	12.27	11.67	1.83	5.40	1.79
75.6-76.6	3.07	1.93	3.56	4.82	6.60	5.19	10.60	12.11	20.11	12.23	8.50	3.93	7.37	0.00
81.6-82.6	3.15	2.00	3.73	5.06	7.13	5.93	12.85	13.94	21.39	12.30	5.52	3.68	3.31	0.00
87.6-88.6	3.29	2.06	3.85	5.30	7.38	6.12	13.08	15.03	22.08	11.19	7.31	2.53	0.79	0.00
93.6-94.6	4.10	2.47	4.49	6.34	9.22	7.46	14.26	13.74	19.31	9.77	5.17	0.85	2.81	0.00
CORE 45														
6.5-7.5	6.70	4.04	7.13	8.92	10.65	6.17	5.63	5.76	16.92	13.79	6.94	5.40	1.94	0.00
12.5-13.5	7.72	4.61	8.07	10.07	12.37	7.12	6.42	6.26	17.13	10.98	7.08	2.19	0.00	0.00
18.5-19.5	6.83	4.01	6.88	8.37	9.18	5.29	5.40	5.44	18.96	13.35	8.81	5.98	1.50	0.00
24.5-25.5	7.60	4.59	8.04	10.08	11.56	7.07	7.90	8.20	20.90	10.14	3.42	0.50	0.00	0.00
30.5-31.5	4.57	2.88	4.98	5.86	6.76	4.64	7.47	9.81	21.79	13.22	7.65	4.00	6.39	0.00
36.5-37.5	3.53	2.15	3.78	4.88	5.91	4.23	7.05	8.40	18.33	12.17	10.08	8.10	11.38	0.00
42.5-43.5	2.39	1.57	2.77	3.33	4.25	3.45	7.30	9.28	16.00	10.54	6.49	4.32	3.01	25.29
48.5-49.5	3.27	2.02	3.65	5.09	7.10	5.50	9.42	10.51	17.62	10.21	7.63	6.24	5.01	6.74
54.5-55.5	2.75	1.72	3.13	4.26	5.46	4.14	7.86	9.96	18.08	11.08	11.65	5.78	14.13	0.00
60.5-61.5	3.37	2.06	3.70	5.12	6.97	5.66	10.10	10.43	18.37	12.65	6.20	7.77	7.60	0.00
66.5-67.5	2.21	1.44	2.83	3.81	5.53	4.92	11.81	13.42	19.36	11.10	9.17	5.61	8.80	0.00
72.5-73.5	3.61	2.26	4.20	5.62	7.79	6.33	11.88	13.37	21.90	13.43	5.98	3.39	0.23	0.00
78.5-79.5	3.48	2.15	4.00	5.64	7.71	6.16	11.85	13.54	23.39	12.68	7.46	1.95	0.00	0.00
CORE 47														
4-5	5.29	3.04	4.76	5.51	6.41	3.47	3.27	3.11	13.78	15.72	17.35	3.54	6.51	8.25
10-11	3.44	2.01	3.40	4.31	5.59	3.26	2.47	2.46	11.01	12.27	14.84	15.29	19.67	0.00
16-17	3.08	1.81	3.09	3.94	4.66	2.75	2.10	1.98	9.08	10.66	15.60	14.98	26.27	0.00
22-23	2.38	1.40	2.31	2.76	3.17	1.99	2.40	3.45	10.55	8.69	7.63	5.23	19.66	28.38
CORE 48														
9.1-10.1	5.82	3.84	6.20	7.56	9.34	5.94	4.80	4.18	15.67	11.73	13.13	4.79	3.12	3.90
15.1-16.1	5.61	3.36	5.45	6.42	7.93	5.07	5.42	5.41	18.21	14.06	12.14	5.15	5.78	0.00
21.1-22.1	3.88	2.33	3.65	4.04	4.65	2.72	2.83	3.35	13.88	13.86	15.10	5.19	24.52	0.00
27.1-28.1	2.41	1.47	2.35	2.57	2.88	1.95	2.57	3.87	11.58	9.57	9.53	5.83	36.99	6.43
33.1-34.1	1.38	0.84	1.43	1.82	2.12	1.57	2.08	2.78	8.38	6.71	7.93	4.70	34.92	23.33

INTERTIDAL SAND WAVE SEDIMENT *(Dotilla* AREA)

Depth (cm)	Mean (phi)	 (um)	Sorting
0.5	2.19	220	0.62
1.5	2.18	221	0.82
5.0	2.02	247	0.73
10.5	1.97	255	0.95
18.0	1.85	277	1.10
24.0	1.67	314	1.31
28.0	-0.87	828	2.93

SUBTIDAL SEDIMENTS

	Near-reef alpheid area			**Off-reef alpheid area**			**Callianassid area**		
Depth (cm)	Mean (phi)	 (um)	Sorting	Mean (phi)	 (um)	Sorting	Mean (phi)	 (um)	Sorting
0-10	0.24	847	4.35	2.03	245	3.37	3.64	80	2.91
10-20	0.02	986	3.79	2.40	190	3.31	2.62	163	3.17
20-30	-1.24	2362	3.37	1.83	281	3.41	2.48	179	3.22
30-40	-2.29	4891	2.50	0.40	758	3.43	1.96	257	3.32
40-50				0.66	633	3.56	1.05	484	3.07
50-60				0.77	586	3.28	0.86	551	2.88
60-70				0.83	563	3.12	1.61	328	3.08
70-80				0.92	529	3.12	2.20	218	2.84
80-90				0.86	551	2.96	1.85	277	2.68
90-100				1.17	444	3.09	1.70	308	2.70
100-110							1.94	261	2.48

Values are calculated from inserting percentages obtained from cumulative curves of grain size into the equations below

Mean = (16% + 50% + 84%)/3
Sorting = (84%-16%)/4 + (95%-5%)/6.6

KEY

<0.35	**very well sorted**
0.35-0.50	**well sorted**
0.50-0.70	**moderately well sorted**
0.70-1.00	**moderately sorted**
1.00-2.00	**poorly sorted**
2.00-4.00	**very poorly sorted**
>4.00	**extremely poorly sorted**

(McManus 1989, Folk and Ward 1957)

BREAKDOWN OF COARSE (>5mm) FRACTION BY COMPONENTS

(data in table is number of grains)

Core 38 depth (cm)	0- 1.2	2.2- 7.2	8.2- 13.2	14.2- 19.2	20.2- 25.2	26.2- 31.2	32.2- 37.2	38.2- 43.2	44.2- 49.2	50.2- 55.2	56.2- 61.2	62.2- 67.2	68.2- 73.2	74.2- 79.2	80.2- 85.2	86.2- 91.2	Total no.	% of total
coral	3	5	10	5	19	22	18	26	15	20	21	13	18	17	7	16	235	46.9
gastropod	0	1	1	0	0	0	1	2	2	4	1	0	1	1	1	0	15	3.0
bivalve	2	6	6	1	5	19	5	28	15	10	9	9	2	9	3	8	137	27.3
mollusc indet.	0	2	3	5	2	0	5	4	9	6	7	10	5	5	3	1	67	13.4
sand dollar	0	0	0	0	0	0	0	7	0	0	0	0	0	1	0	0	8	1.6
echinoid	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
crustacean	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0.4
barnacle	0	1	1	0	0	0	0	0	1	1	1	0	2	0	0	2	9	1.8
worm tube	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
inorganic	1	0	0	0	0	0	1	1	1	0	1	1	1	0	2	0	9	1.8
wood	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
indet	3	0	0	3	1	0	1	2	1	0	2	0	0	1	2	2	18	3.6
total number	9	15	22	15	27	41	31	70	44	41	42	34	29	34	18	29	501	100
% of total	1.8	3.0	4.4	3.0	5.4	8.2	6.2	14.0	8.8	8.2	8.4	6.8	5.8	6.8	3.6	5.8	100	

94.61% = skeletal material

Core 39 depth (cm)	0- 5.1	6.1- 11.1	12.1- 17.1	18.1- 23.1	24.1- 29.1	30.1- 35.1	36.1- 41.1	42.1- 47.1	48.1- 53.1	54.1- 59.1	60.1- 65.1	66.1- 71.1	72.1- 79.1	80.1- 85.1	86.1- 91.1	Total no.	% of total
coral	3	0	3	13	21	18	22	9	15	12	17	14	17	12	22	198	45.0
gastropod	0	0	1	2	0	3	0	1	2	1	2	1	2	0	0	15	3.4
bivalve	1	3	6	7	4	17	12	5	3	5	5	14	5	10	14	111	25.2
mollusc indet.	1	1	5	8	3	9	10	7	4	3	4	0	3	5	5	68	15.5
sand dollar	0	0	0	0	0	7	0	0	0	0	0	0	1	0	0	8	1.8
echinoid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
crustacean	0	0	0	0	1	1	0	1	0	0	1	0	1	1	0	6	1.4
barnacle	0	1	0	0	0	1	2	1	0	0	0	0	2	2	0	9	2.0
worm tube	0	0	1	0	1	0	2	0	0	0	0	0	0	0	1	5	1.1
inorganic	0	2	1	0	0	1	0	1	0	1	1	1	1	1	0	10	2.3
wood	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
indet	0	0	1	0	1	3	0	2	0	1	0	0	2	0	0	10	2.3
total	5	7	18	30	31	60	48	27	24	23	30	30	34	31	42	440	100
% of total	1.1	1.6	4.1	6.8	7.0	13.6	10.9	6.1	5.5	5.2	6.8	6.8	7.7	7.0	9.5	100	

95.45% = skeletal material

Core 40 depth (cm)	0- 9.1	10.1- 15.1	16.1- 21.1	22.1- 27.1	28.1- 33.1	34.1- 39.1	40.1- 45.1	46.1- 51.1	52.1- 57.1	58.1- 63.1	64.1- 69.1	70.1- 75.1	76.1- 81.1	Total no.	% of total
coral	0	2	8	12	13	15	9	5	13	11	4	7	5	104	39
gastropod	0	0	2	0	1	1	0	0	1	0	1	4	0	10	3.75
bivalve	1	2	4	7	7	9	8	10	10	7	6	4	3	78	29.2
mollusc indet.	1	2	4	3	6	12	5	4	4	6	5	3	3	58	21.7
sand dollar	0	0	0	0	0	0	1	0	0	2	0	0	0	3	1.12
echinoid	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0.37
crustacean	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.37
barnacle	0	0	0	0	1	0	1	0	1	0	0	0	1	4	1.5
worm tube	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
norganic	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.37
wood	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ndet	0	1	0	0	0	0	0	1	2	1	2	0	0	7	2.62
otal	2	7	18	22	28	37	24	20	31	28	19	18	13	267	100
% of total	0.7	2.6	6.7	8.2	10.5	13.9	9.0	7.5	11.6	10.5	7.1	6.7	4.9	100	

97.0% = skeletal material

Core 41 depth (cm)	0- 6.9	7.9- 12.9	13.9- 18.9	19.9- 24.9	25.9- 30.9	31.9- 36.9	37.9- 42.9	43.9- 48.9	49.9- 54.9	55.9- 60.9	61.9- 66.9	67.9- 72.9	73.9- 78.9	79.9- 84.9	85.9- 90.9	91.9- 96.9	97.9- 102.9	total no.	% of total
coral	1	3	2	8	7	15	7	9	18	10	4	8	8	3	8	5	9	125	30.3
gastropod	1	0	0	0	0	0	1	0	0	2	1	4	0	0	2	1	1	13	3.2
bivalve	2	1	2	5	8	9	4	12	52	7	9	17	5	5	17	4	6	165	40.0
mollusc indet.	2	1	1	2	9	6	3	10	5	7	9	10	5	4	5	5	2	86	20.9
sand dollar	0	0	0	0	0	0	0	0	0	0	1	1	1	0	2	0	0	5	1.2
echinoid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0.2
crustacean	0	2	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	6	1.5
barnacle	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0.5
worm tube	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
norganic	0	1	0	0	0	2	0	1	0	0	1	1	0	0	0	0	1	7	1.7
wood	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
ndet	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0.5
otal	6	9	5	15	24	32	15	32	76	27	26	42	19	12	34	16	22	412	100
% of total	6.0	9.0	5.0	15.0	24.0	32.0	15.0	32.0	76.0	27.0	26.0	42.0	19.0	12.0	34.0	16.0	22.0	100	

NB 38 of the 52 bivalves in 43-48 are flakes off one mother of pearl shell

97.82% = skeletal material

Core 42 depth (cm)	0-5.8	6.8-11.8	12.8-17.8	18.8-23.8	24.8-29.8	30.8-35.8	36.8-41.8	42.8-47.8	48.8-53.8	54.8-59.8	60.8-65.8	66.8-71.8	72.8-77.8	78.8-83.8	84.8-89.8	90.8-95.8	96.8-101.8	102.8 107.8	total no.	% of total
coral	0	0	0	2	4	5	4	9	8	4	0	2	1	0	12	4	3	2	60	24.7
gastropod	0	0	0	1	0	0	0	0	1	0	0	0	1	0	2	2	0	0	7	2.9
bivalve	0	1	2	3	3	17	2	6	11	3	3	10	2	6	24	7	3	9	112	46.1
mollusc indet.	0	1	0	3	0	3	0	2	1	3	1	3	0	1	4	4	5	1	32	13.2
sand dollar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0.4
echinoid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0.8
crustacean	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0.8
barnacle	0	1	0	0	1	1	3	2	1	0	4	5	0	0	0	1	0	0	19	7.8
worm tube	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	0.8
inorganic	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
wood	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.4
indet	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	2	5	2.1
total	0	3	2	9	8	28	9	20	23	12	8	21	4	7	45	18	11	15	243	100
% of total	0.0	1.2	0.8	3.7	3.3	11.5	3.7	8.2	9.5	4.9	3.3	8.6	1.6	2.9	18.5	7.4	4.5	6.2	100	

97.53% = skeletal materia

Core 43 depth (cm)	0-5.5	6.5-11.5	12.5-17.5	18.5-23.5	24.5-29.5	30.5-35.5	36.5-41.5	42.5-47.5	48.5-53.5	54.5-59.5	60.5-65.5	66.5-71.5	72.5-77.5	78.5-83.5	84.5-89.5	90.5-95.5	96.5-101.5	102.5 107.5	total no.	% of total
coral	0	1	0	0	3	2	8	1	3	2	3	4	6	0	3	1	1	0	38	18.0
gastropod	0	0	1	0	0	0	3	2	0	2	1	0	2	1	3	2	1	1	19	9.0
bivalve	0	1	1	0	1	3	10	6	7	9	4	6	1	4	8	9	23	6	99	46.9
mollusc indet.	0	0	0	2	0	2	4	3	3	3	1	1	3	0	2	2	4	0	30	14.2
sand dollar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3	1.4
echinoid	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.5
crustacean	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0	5	2.4
barnacle	0	0	0	0	0	0	0	3	2	1	1	0	0	0	1	0	0	0	8	3.8
worm tube	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
inorganic	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
wood	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.5
indet	0	1	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	7	3.3
total	0	3	3	2	6	7	27	16	16	19	10	11	13	7	17	17	30	7	211	100
% of total	0.0	1.4	1.4	0.9	2.8	3.3	12.8	7.6	7.6	9.0	4.7	5.2	6.2	3.3	8.1	8.1	14.2	3.3	100	

96.21% = skeletal materia

Core 44 depth (cm)	0-3.6	4.6-9.6	10.6-15.6	16.6-21.6	22.6-27.6	28.6-33.6	34.6-39.6	40.6-45.6	46.6-51.6	52.6-57.6	58.6-63.6	64.6-69.6	70.6-75.6	76.6 81.6	82.6-87.6	88.6-93.6	total no.	% of total
coral	2	4	4	2	3	5	6	9	23	7	6	5	11	3	5	2	97	26.8
gastropod	0	0	0	0	0	2	0	1	2	0	1	0	1	0	1	0	8	2.21
bivalve	7	8	3	4	11	6	5	16	19	9	12	11	19	11	5	6	152	42
mollusc indet.	4	0	0	1	0	3	2	5	2	1	5	2	8	0	3	2	38	10.5
sand dollar	0	1	0	0	0	0	1	0	1	5	0	0	2	1	6	5	22	6.08
echinoid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0.28
crustacean	0	0	0	1	1	0	0	0	1	0	2	0	0	0	0	0	5	1.38
barnacle	0	0	1	1	1	3	3	6	2	2	0	1	0	0	0	1	21	5.8
worm tube	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0.83
inorganic	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0.55
wood	0	0	0	0	0	0	1	3	1	0	0	0	0	0	0	0	5	1.38
indet	1	1	0	1	1	0	1	0	0	0	1	1	1	0	0	0	8	2.21
total	14	14	8	10	17	19	21	40	51	24	27	20	42	18	20	17	362	100
% of total	3.9	3.9	2.2	2.8	4.7	5.2	5.8	11.0	14.1	6.6	7.5	5.5	11.6	5.0	5.5	4.7	100	

95.86% = skeletal material

Core 45 depth (cm)	0-6.5	7.5-12.5	13.5-18.5	19.5-24.5	25.5-30.5	31.5-36.5	37.5-42.5	43.5-48.5	49.5-54.5	55.5-60.5	61.5-66.5	67.5-72.5	73.5-78.5	total no.	% of total
coral	1	5	5	4	7	10	15	12	15	8	9	14	7	112	29.8
gastropod	0	1	0	0	1	1	3	0	0	2	1	1	0	10	2.7
bivalve	1	8	10	6	4	14	20	13	9	14	13	14	6	132	35.1
mollusc indet.	1	3	5	1	4	8	12	5	4	2	6	4	3	58	15.4
sand dollar	0	1	0	0	0	0	0	0	0	0	1	0	2	4	1.1
echinoid	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.3
crustacean	0	2	0	0	0	1	0	4	1	3	0	2	0	13	3.5
barnacle	1	1	2	1	2	5	8	4	2	6	0	2	0	34	9.0
worm tube	0	0	0	0	0	0	0	1	0	3	0	0	0	4	1.1
inorganic	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
wood	0	0	0	0	0	0	0	4	0	1	0	0	0	5	1.3
indet	0	0	0	1	1	0	0	0	0	0	0	0	1	3	0.8
total	4	21	23	13	19	39	58	43	31	39	30	37	19	376	100
% of total	1.1	5.6	6.1	3.5	5.1	10.4	15.4	11.4	8.2	10.4	8.0	9.8	5.1	100	

97.87% = skeletal material

Core 46 depth (cm)	0- 7.5	8.5- 13.5	14.5- 19.5	20.5- 25.5	26.5- 31.5	32.5- 37.5	38.5- 43.5	44.5- 49.5	50.5- 55.5	56.5- 61.5	62.5- 67.5	68.5- 73.5	74.5- 79.5	80.5- 85.5	86.5- 91.5	92.5- 97.5	total no.	% of total
coral	1	2	6	1	4	6	10	10	6	7	14	11	27	20	22	9	156	35.6
gastropod	0	0	0	0	0	0	0	2	2	0	1	2	1	0	1	2	11	2.51
bivalve	1	1	4	2	10	8	9	9	13	6	14	12	34	25	22	23	193	44.1
mollusc indet.	0	3	0	0	0	0	0	0	2	0	1	4	0	1	8	0	19	4.34
sand dollar	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	4	0.91
echinoid	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.23
crustacean	0	1	0	0	2	0	0	0	1	1	0	0	4	0	0	0	9	2.05
barnacle	0	0	0	0	2	1	3	1	2	2	1	0	0	9	0	2	23	5.25
worm tube	0	0	0	0	0	0	0	0	2	0	1	0	0	2	0	0	5	1.14
inorganic	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
wood	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.23
indet	0	0	0	3	1	0	0	2	2	0	1	1	4	1	0	1	16	3.65
total	2	7	10	6	19	16	22	24	30	16	34	30	72	59	53	38	438	100
% of total	0.5	1.6	2.3	1.4	4.3	3.7	5.0	5.5	6.8	3.7	7.8	6.8	16.4	13.5	12.1	8.7	100	

96.12% = skeletal material

Core 47 depth (cm)	0- 4	5- 10	11- 16	17- 22	23- 28	total no	% of total
coral	14	32	55	33	43	177	52.4
gastropod	0	0	1	3	1	5	1.48
bivalve	12	26	23	25	23	109	32.2
mollusc indet.	0	5	0	3	3	11	3.25
sand dollar	0	0	0	0	0	0	0
echinoid	0	0	0	0	0	0	0
crustacean	0	0	3	0	0	3	0.89
barnacle	0	3	1	2	1	7	2.07
worm tube	0	0	1	0	0	1	0.3
inorganic	0	0	0	0	1	1	0.3
wood	0	0	0	0	0	0	0
indet	2	4	9	7	2	24	7.1
total	28	70	93	73	74	338	100
% of total	8.3	20.7	27.5	21.6	21.9	100	

92.60% = skeletal material

Core 48 depth (cm)	0- 9.1	10.1- 15.1	16.1- 21.1	22.1- 27.1	28.1- 33.1	34.1- 39.1	total no.	% of total
coral	7	8	37	26	59	44	181	55
gastropod	0	1	3	0	2	4	10	3.04
bivalve	6	8	26	16	33	12	101	30.7
mollusc indet.	0	2	3	3	0	0	8	2.43
sand dollar	0	0	0	0	0	0	0	0
echinoid	0	0	0	0	0	0	0	0
crustacean	1	2	0	0	3	1	7	2.13
barnacle	0	0	1	1	1	0	3	0.91
worm tube	1	0	0	2	2	0	5	1.52
inorganic	0	0	0	0	0	0	0	0
wood	0	0	0	0	0	0	0	0
indet	3	0	2	3	0	6	14	4.26
total	18	21	72	51	100	67	329	100
% of total	5.5	6.4	21.9	15.5	30.4	20.4	100	

94.22% = skeletal material

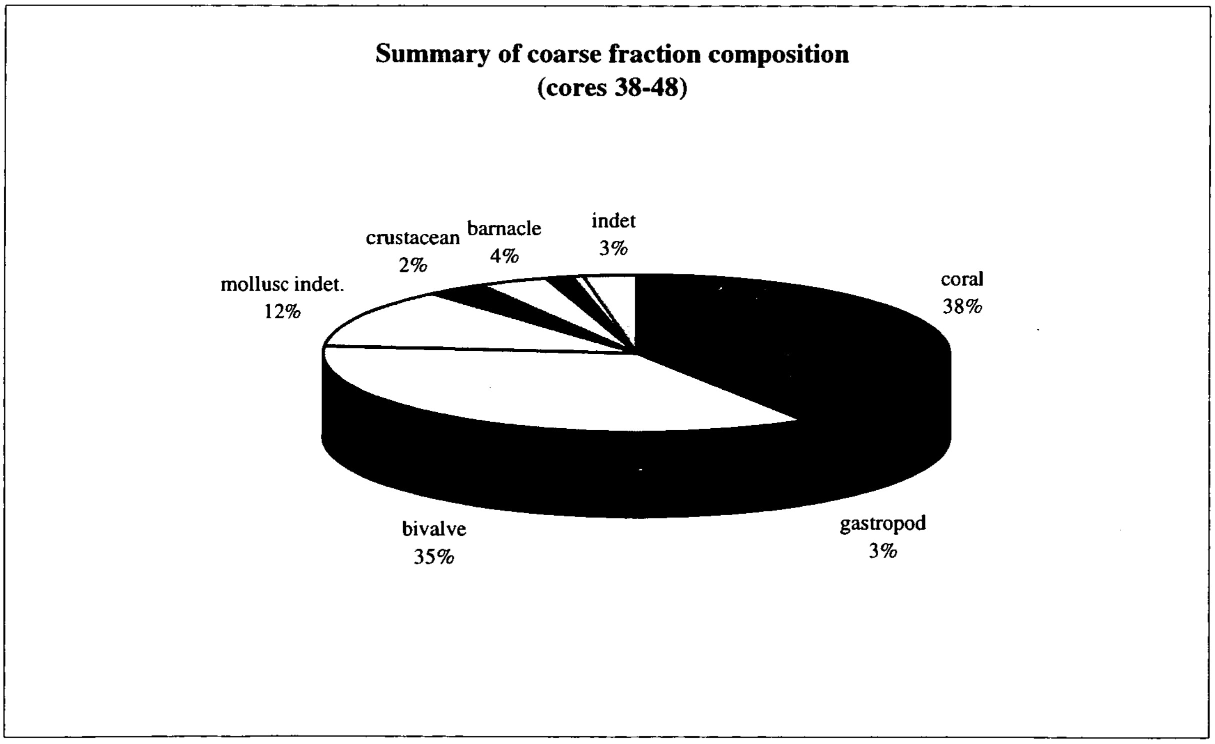
SUMMARY OF COARSE FRACTION (>5mm) COMPOSITION

Number of grains

Core No	38	39	40	41	42	43	44	45	46	47	48	total
coral	235	198	104	125	60	38	97	112	156	177	181	1483
gastropod	15	15	10	13	7	19	8	10	11	5	10	123
bivalve	137	111	78	165	112	99	152	132	193	109	101	1389
mollusc indet.	67	68	58	86	32	30	38	58	19	11	8	475
sand dollar	8	8	3	5	1	3	22	4	4	0	0	58
echinoid	1	0	1	1	2	1	1	1	1	0	0	9
crustacean	2	6	1	6	2	5	5	13	9	3	7	59
barnacle	9	9	4	2	19	8	21	34	23	7	3	139
worm tube	0	5	0	0	2	0	3	4	5	1	5	25
inorganic	9	10	1	7	0	0	2	0	0	1	0	30
wood	0	0	0	0	1	1	5	5	1	0	0	13
indet	18	10	7	2	5	7	8	3	16	24	14	114
total	501	440	267	412	243	211	362	376	438	338	329	3917

% of grains (based on number)

Core No	38	39	40	41	42	43	44	45	46	47	48	total%
coral	46.91	45	38.95	30.34	24.69	18.01	26.8	29.79	35.62	52.37	55.02	37.9
gastropod	2.99	3.41	3.75	3.16	2.88	9.00	2.21	2.66	2.51	1.48	3.04	3.1
bivalve	27.35	25.23	29.21	40.05	46.09	46.92	41.99	35.11	44.06	32.25	30.7	35.5
mollusc indet.	13.37	15.45	21.72	20.87	13.17	14.22	10.5	15.43	4.338	3.254	2.432	12.1
sand dollar	1.60	1.82	1.12	1.21	0.41	1.42	6.08	1.06	0.91	0.00	0.00	1.5
echinoid	0.20	0.00	0.37	0.24	0.82	0.47	0.28	0.27	0.23	0.00	0.00	0.2
crustacean	0.40	1.36	0.37	1.46	0.82	2.37	1.38	3.46	2.05	0.89	2.13	1.5
barnacle	1.80	2.05	1.50	0.49	7.82	3.79	5.80	9.04	5.25	2.07	0.91	3.5
worm tube	0.00	1.14	0.00	0.00	0.82	0.00	0.83	1.06	1.14	0.30	1.52	0.6
inorganic	1.80	2.27	0.37	1.70	0.00	0.00	0.55	0.00	0.00	0.30	0.00	0.8
wood	0.00	0.00	0.00	0.00	0.41	0.47	1.38	1.33	0.23	0.00	0.00	0.3
indet	3.59	2.27	2.62	0.49	2.06	3.32	2.21	0.80	3.65	7.10	4.26	2.9


Summary of coarse fraction composition
(cores 38-48)

EXTENT OF DEGRADATION OF GRAINS AS INDICATED BY >5mm DIAMETER INFAUNAL BIVALVES

Core 42			**Grain edge/ornamentation**				**Shell surface**				**Microbioerosion**		**Encrustation**	
Depth (cm)		No. of grains	Very sharp	Quite sharp	Quite rounded	Very rounded	Very shiny	Quite shiny	Quite dull	Very dull	Slight	Extensive	Slight	Extensive
0-5.8	Whole	1	1				1							
	Fragment	1		1					1				1	
6.8-11.8	Whole													
	Fragment													
12.8-17.8	Whole	0												
	Fragment	2		1	1		1		1					
18.8-23.8	Whole	1	1					1						
	Fragment	4	1	2	1		1	1	1	1	1	1	1	
24.8-29.8	Whole	1				1				1		1	1	
	Fragment	2		1	1			1	1		2			
30.8-35.8	Whole	3	1		2		1		2		2		1	
	Fragment	10	2	4		4	2	4		4	2	3	1	
36.8-41.8	Whole	1				1				1		1	1	
	Fragment	2				2				2		1		
42.8-47.8	Whole	2			2					2		2	2	
	Fragment	5		2	2	1	1	1	1	2		2	1	
48.8-53.8	Whole	1	1				1							
	Fragment	8		1	7			1	2	5	3	4	2	
54.8-59.8	Whole	0												
	Fragment	5		3	2			2	3		5		1	
60.8-65.8	Whole	1			1				1		1			
	Fragment	2	1	1				2			1			
66.8-71.8	Whole	1			1				1		1		1	
	Fragment	4	1	2	1		1	2		1		1	1	
72.8-77.8	Whole	0												
	Fragment	1	1				1							
78.8-83.8	Whole	1			1					1		1		
	Fragment	2	1	1			1	1					1	
84.8-89.8	Whole	1		1				1						
	Fragment	21	6	7	5	3	6	5	4	6	5	5	2	
90.8-95.8	Whole	0												
	Fragment	7	4	3			4	2	1		1		1	
96.8-101.8	Whole	1		1				1						
	Fragment	7	2	3	1	1	3	1	2	1	2	1	1	
102.8-107.8	Whole	3		3				2		1				
	Fragment	7		2	1	4			2	5	1	4		1
	Totals	108	23	39	29	17	24	28	23	33	27	27	19	1
	%s	100	21.30	36.11	26.85	15.74	22.22	25.93	21.30	30.56	25.00	25.00	17.59	0.93

Note: Core 42 is from the subtidal callianassid area.

Core 44 Depth (cm)		No. of grains	Grain edge/ornamentation Very sharp	Quite sharp	Quite rounded	Very rounded	Shell surface Very shiny	Quite shiny	Quite dull	Very dull	Microbioerosion Slight	Extensive	Encrustation Slight	Extensive
0-3.6	Whole	1				1				1		1		
	Fragment	8		3		5		1	1	6	2	6	3	
4.6-9.6	Whole	3		2	1			2		1		1	1	
	Fragment	3				3				3		3		
10.6-15.6	Whole	0												
	Fragment	2			2			1	1		1	1		
16.6-21.6	Whole	2		1	1			1	1		1			
	Fragment	2				2				2		2		
22.6-27.6	Whole	1			1					1		1		
	Fragment	7		2		5		1		6		6	1	
28.6-33.6	Whole	0												
	Fragment	6	2	2		2	1	2	1	2	2	2		
34.6-39.6	Whole	1			1				1			1	1	
	Fragment	6		1		5		1		5		5	2	
40.6-45.6	Whole	4		2	2		2		2					
	Fragment	6	1		1	4	1		1	4		4		
46.6-51.6	Whole	0												
	Fragment	18	1	9	3	5		6	3	9	2	9	3	
52.6-57.6	Whole	0												
	Fragment	10	7	1	1	1	6	2		2		2	1	
58.6-63.6	Whole	2	2				1	1						
	Fragment	18	8	2	3	5	4	1	8	5	4	5	3	
64.6-69.6	Whole	3	2			1		2		1		1		
	Fragment	9	1	2	2	4	1	3		5	2	5	2	
70.6-75.6	Whole	2		1	1			1	1					
	Fragment	14	5	1	5	3	5	1	5	3	6	3	2	1
76.6-81.6	Whole	0												
	Fragment	7	4			3	3	1		3		3	1	
82.6-87.6	Whole	2		2				1	1					
	Fragment	6	4	1		1	3	2		1		1		
88.6-93.6	Whole	0												
	Fragment	8		4	3	1		3		5	1	5	1	
	totals	151	37	36	27	51	27	33	26	65	21	67	21	1
	%s	100	24.50	23.84	17.88	33.77	17.88	21.85	17.22	43.05	13.91	44.37	13.91	0.66

Note: Core 44 is from the subtidal off-reef alpheid area

Sediment depth (cm)	CO3 % repeats			Average CO3 %
	a	b	c	
Core 38				
1.2-2.2	42.40	42.90	42.44	42.58
7.2-8.2	44.33	45.65	45.37	45.12
13.2-14.2	44.16	44.61	44.94	44.57
19.2-20.2	38.35	38.49	39.02	38.62
25.2-26.2	54.51	53.17	53.73	53.80
31.2-32.2	61.53	61.78	59.69	61.00
37.2-38.2	60.94	60.90	62.31	61.38
43.2-44.2	67.80	67.52		67.66
49.2-50.2	68.52	69.10	68.16	68.59
55.2-56.2	72.63	70.96	71.26	71.62
61.2-62.2	68.15	68.33	67.11	67.86
67.2-68.2	70.17	71.36	69.37	70.30
73.2-74.2	71.77	72.02	71.38	71.72
79.2-80.2	71.66	70.23	72.64	71.51
85.2-86.2	71.98	74.22	73.67	73.29
91.2-92.2	71.29	71.80	71.43	71.51
Core 41				
6.9-7.9	34.80	33.61	34.61	34.34
12.9-13.9	43.24	42.82	44.08	43.38
18.9-19.9	67.00	66.66	65.83	66.50
24.9-25.9	48.97	49.61	49.13	49.24
30.9-31.9	59.08	59.41	59.11	59.20
36.9-37.9	65.62	66.77	66.23	66.21
42.9-43.9	69.73	69.46	69.49	69.56
48.9-49.9	66.89	66.03	66.75	66.56
54.9-55.9	73.56	74.75	72.39	73.57
60.9-61.9	69.38	69.35	68.98	69.24
66.9-67.9	68.53	69.19	69.19	68.97
72.9-73.9	68.32	68.32	67.80	68.15
78.9-79.9	66.75	66.70	67.04	66.83
84.9-85.9	70.43	71.62	70.71	70.92
90.9-91.9	70.97	70.77		70.87
96.9-97.9	68.15	68.30	69.17	68.54
Core 42				
5.8-6.8	50.05	50.73	50.49	50.42
11.8-12.8	46.59	46.90	46.94	46.81
17.8-18.8	57.00	55.39	57.10	56.50
23.8-24.8	51.88	51.78	53.50	52.39
29.8-30.8	65.16	64.51	65.70	65.12
35.8-36.8	66.99	67.96	67.71	67.55
41.8-42.8	73.15	72.89	72.21	72.75
47.8-48.8	68.10	68.49	68.63	68.41
53.8-54.8	77.51	78.58	76.99	77.69
59.8-60.8	58.10	56.86	59.25	58.07
65.8-66.8	64.12	64.28	64.82	64.41
71.8-72.8	60.45	61.84	62.21	61.50
77.8-78.8	54.37	56.64	55.41	55.47
83.8-84.8	72.60	75.21	74.67	74.16
89.8-90.8	76.38	76.66	76.40	76.48
95.8-96.8		75.24	74.10	74.67
101.8-102.8	74.29	74.82	74.18	74.43
107.8-108.8	74.46	74.50	74.46	74.47

CO3 % values obtained by reaction with HCl and titration with NaOH; three or four subsamples of the <500um fraction were used and a mean value calculated.
See section 1.5.1.5 for details

Sediment depth (cm)	CO3 % repeats				Average CO3 %
	a	b	c		
Core 43					
5.5-6.5	46.00	45.20	44.65		45.28
11.5-12.5	44.08	43.66	44.60		44.11
17.5-18.5	43.73	44.46	44.34		44.18
23.5-24.5	55.86	55.14	54.97		55.32
29.5-30.5	59.13	59.18	59.20		59.17
35.5-36.5	68.85	71.62	69.43		69.97
41.5-42.5	80.77	81.04	79.22		80.34
47.5-48.5	83.34	83.33	84.45		83.71
53.5-54.5	84.99	89.33	84.37		86.23
59.5-60.5	81.30	82.58	81.51		81.80
65.5-66.5	80.99	80.87	80.32		80.73
71.5-72.5	80.66	81.24	80.29		80.73
77.5-78.5	72.90	73.74	73.61		73.42
81.5-82.5	73.63	72.84	73.29		73.25
89.5-90.5	74.00	74.69	75.54		74.74
95.5-96.5	79.11	79.08	79.17		79.12
101.5-102.5	79.01	78.43	78.58		78.67
107.5-108.5	77.33	77.45	79.08		77.95
Core 44					
3.6-4.6	55.12	55.09	54.66		54.96
9.6-10.6	45.71	47.43	45.73		46.29
15.6-16.6	47.09	47.54	46.84		47.16
21.6-22.6	53.67	54.55	54.82		54.35
27.6-28.6	61.23	59.72	61.39		60.78
33.6-34.6	67.11	66.04	64.47		65.87
39.6-40.6	71.41	72.93	71.69		72.01
45.6-46.6	79.37	79.85	79.37		79.53
51.6-52.6	65.32	65.57	67.96		66.28
57.6-58.6	77.70	77.64	78.70		78.01
63.6-64.6	77.00	77.72	79.61		78.11
69.6-70.6	75.35	77.84	80.28		77.82
75.6-76.6	75.90	75.27	74.18		75.12
81.6-82.6	76.63	76.66	76.95		76.75
87.6-88.6	77.19	77.01	77.42		77.21
93.6-94.6	74.80	74.12	73.14		74.02
Core 45					
6.5-7.5	51.69	50.94	50.29		50.97
12.5-13.5	50.95	49.90	50.58		50.48
18.5-19.5	54.11	53.76	55.43		54.43
24.5-25.5	57.55	58.29	57.81		57.88
30.5-31.5	67.28	69.06	66.57		67.64
36.5-37.5	69.68.	70.80	69.97		70.15
42.5-43.5	74.89	74.99	75.39		75.09
48.5-49.5	71.99	71.80	72.46		72.08
54.5-55.5	72.60	74.57	74.78		73.98
60.5-61.5	73.47	73.43	72.97		73.29
66.5-67.5	78.92	79.06	78.82		78.93
72.5-73.5	74.76	73.00	75.50		74.42
78.5-79.5	75.07	74.72	75.34		75.04
Core 47					
4-5	46.49	46.83	43.28	43.22	44.96
10-11	45.88	46.13	45.95	46.74	46.18
16-17	42.82	43.75	43.13	43.63	43.33
22-23	57.43	59.17	58.43	57.58	58.15
Core 48					
9.1-10.1	45.33	44.87	45.23		45.14
15.1-16.1	52.24	51.62	51.76		51.87
21.1-22.1	52.56	51.38	50.92		51.62
27.1-28.1	63.89	63.13	62.32		63.11
33.1-34.1	65.85	65.74	65.58		65.72

INTERTIDAL SEDIMENTS

	dry wt (g)	volume (cm^3)	wt>vol: x by	vol>wt: x by
Sipunculid casts				
1	180	140	0.778	1.286
2	630	476	0.756	1.324
3	190	136	0.716	1.397
4	548	428	0.781	1.280
Dotilla quadrats (50x50cm)				
A1	545	430	0.789	1.267
A2	491	390	0.794	1.259
A3	610	492	0.807	1.240
A4	398	310	0.779	1.284
A5	609	484	0.795	1.258
B1	432	330	0.764	1.309
B2	399	304	0.762	1.313
B3	247	180	0.729	1.372
B4	367	280	0.763	1.311
B5	259	194	0.749	1.335
Mean conversion factors:			**0.77**	**1.30**

(Volumes measured to the nearest 2cm^3 with a 250ml measuring cylinder

SUBTIDAL SEDIMENTS

Core no.	Depth (cm)	Dry wt (g)
Core 38	1.2-2.2	23.69
	19.2-20.2	16.69
	25.2-26.2	23.76
	31.2-32.2	20.76
	37.2-38.2	25.07
	43.2-44.2	20.72
	49.2-50.2	24.57
	55.2-56.2	20.28
	61.2-62.2	22.41
	67.2-68.2	21.58
	79.2-80.2	25.69
	85.2-86.2	20.89
	91.2-92.2	23.8
Core 39	5.1-6.1	16.42
	11.1-12.1	20.97
	17.1-18.1	19.48
	23.1-24.1	18.52
	35.1-36.1	16.54
	41.1-42.1	20.1
	47.1-48.1	22.3
	53.1-54.1	25.3
	59.1-60.1	25.03
	65.1-66.1	25.88
	71.1-72.1	25.61
	83.1-84.1	20.86
Core 40	15.1-16.1	16.97
	27.1-28.1	21.44
	33.1-34.1	22.15
	39.1-40.1	19.95
	45.1-46.1	19.87
	51.1-52.1	19.24
	57.1-58.1	22.29
	63.1-64.1	24.08
	69.1-70.1	22.14
	75.1-76.1	21.26
Core 41	54.9-55.9	20.78
	66.9-67.9	26.49
	72.9-73.9	20.4
	84.9-85.9	23.53

Core no.	Depth (cm)	Dry wt (g)
Core 42	5.8-6.8	14.35
	11.8-12.8	17.6
	17.8-18.8	19.24
	23.8-24.8	18.82
	29.8-30.8	21.59
	35.8-36.8	22.13
	41.8-42.8	22.3
	47.8-48.8	21.67
	53.8-54.8	23.1
	59.8-60.8	15.45
	65.8-66.8	16.72
	71.8-72.8	15.73
	77.8-78.8	15.56
	83.8-84.8	23.32
	89.8-90.8	23
	95.8-96.8	23.93
	101.8-102.8	25.5
	107.8-108.8	23.39
Core 43	5.5-6.5	17.58
	11.5-12.5	17.55
	17.5-18.5	18.18
	23.5-24.5	23.04
	29.5-30.5	16.78
	35.5-36.5	19.76
	41.5-42.5	21.73
	47.5-48.5	21.27
	53.5-54.5	23.6
	59.5-60.5	23.53
	65.5-66.5	20.56
	71.5-72.5	22.45
	77.5-78.5	23.21
	83.5-84.5	22.03
Core 44	15.6-16.6	21.61
Core 45	6.5-7.5	19.99
	12.5-13.5	23.25
	18.5-19.5	20.99
	24.5-25.5	22.07
Core 46	7.5-8.5	17.11
	13.5-14.5	18.64
	19.5-20.5	21.48
	25.5-26.5	19.53
	31.5-32.5	26.62
	37.5-38.5	25.17
	43.5-44.5	24.8
	49.5-50.5	27.14
	55.5-56.5	21.42
	61.5-62.5	26.11
	67.5-68.5	20.99

INTERTIDAL SEDIMENTS

To convert from cm^3 to g, x by 1.30

To convert form g to cm^3, x by 0.77

SUBTIDAL SEDIMENTS

Average weight of
a core section = **21.37g**
(st dev = 3.12, n = 87)
Core sections are 13.85cm^3 in volume
Therefore:

To convert from g to cm^3, x 0.65

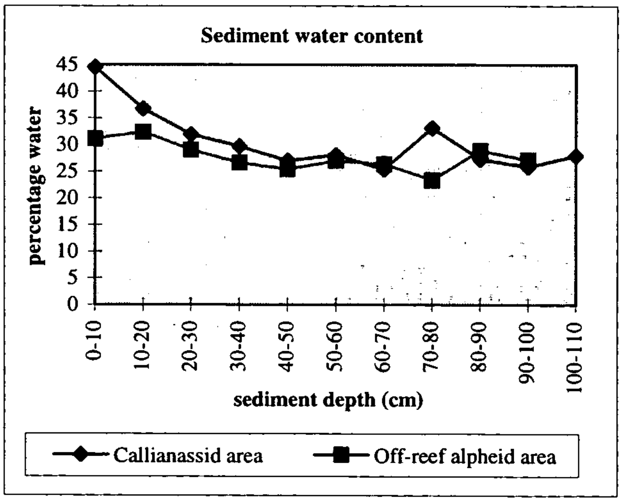
To convert from cm^3 to g, x 1.54

Sediment water content

Core no.	Depth (cm)	Wet wt (g)	Dry wt (g)	% water
Core 38	1.2-2.2	32.31	23.69	26.68
	7.2-8.2	26.81		
	13.2-14.2	25.03		
	19.2-20.2	27.63	16.69	39.59
	25.2-26.2	33.12	23.76	28.26
	31.2-32.2	27.8	20.76	25.32
	37.2-38.2	34.48	25.07	27.29
	43.2-44.2	28.42	20.72	27.09
	49.2-50.2	32.38	24.57	24.12
	55.2-56.2	28.9	20.28	29.83
	61.2-62.2	31.54	22.41	28.95
	67.2-68.2	29.97	21.58	27.99
	73.2-74.2	41.52		
	79.2-80.2	33.56	25.69	23.45
	85.2-86.2	29.39	20.89	28.92
	91.2-92.2	32.69	23.8	27.19
Core 39	5.1-6.1	26.15	16.42	37.21
	11.1-12.1	31.03	20.97	32.42
	17.1-18.1	26.24	19.48	25.76
	23.1-24.1	26.24	18.52	29.42
	29.1-30.1	30.63		
	35.1-36.1	22.63	16.54	26.91
	41.1-42.1	28.59	20.1	29.70
	47.1-48.1	30.6	22.3	27.12
	53.1-54.1	34.11	25.3	25.83
	59.1-60.1	35.64	25.03	29.77
	65.1-66.1	32.37	25.88	20.05
	71.1-72.1	34.41	25.61	25.57
	77.1-78.1	25.52		
	83.1-84.1	29.42	20.86	29.10
	89.1-90.1	31.52		
Core 40	9.1-10.1	31.41		
	15.1-16.1	25.37	16.97	33.11
	21.1-22.1	29.34		
	27.1-28.1	29.52	21.44	27.37
	33.1-34.1	29.91	22.15	25.94
	39.1-40.1	28.64	19.95	30.34
	45.1-46.1	27.66	19.87	28.16
	51.1-52.1	27.89	19.24	31.01
	57.1-58.1	31.44	22.29	29.10
	63.1-64.1	30.09	24.08	19.97
	69.1-70.1	27.97	22.14	20.84
	75.1-76.1	30.26	21.26	29.74
	81.1-82.1	26.69		
Core 41	6.9-7.9	29.16		
	12.9-13.9	27.99		
	18.9-19.9	23.82		
	24.9-25.9	29.34		
	30.9-31.9	33.84		
	36.9-37.9	29.07		
	42.9-43.9	33.16		
	48.9-49.9	30.84		
	54.9-55.9	28.06	20.78	25.94
	60.9-61.9	27.63		
	66.9-67.9	30.98	26.49	14.49
	72.9-73.9	29.11	20.4	29.92
	78.9-79.9	31.3		
	84.9-85.9	31.51	23.53	25.33
	90.9-91.9	31.2		

Core no.	Depth (cm)	Wet wt (g)	Dry wt (g)	% water
Core 42	5.8-6.8	26.8	14.35	46.46
	11.8-12.8	28.72	17.6	38.72
	17.8-18.8	28.9	19.24	33.43
	23.8-24.8	28.99	18.82	35.08
	29.8-30.8	29.75	21.59	27.43
	35.8-36.8	30.69	22.13	27.89
	41.8-42.8	30.5	22.3	26.89
	47.8-48.8	29.77	21.67	27.21
	53.8-54.8	31.13	23.1	25.80
	59.8-60.8	25	15.45	38.20
	65.8-66.8	25	16.72	33.12
	71.8-72.8	26.41	15.73	40.44
	77.8-78.8	26.62	15.56	41.55
	83.8-84.8	33.31	23.32	29.99
	89.8-90.8	30.88	23	25.52
	95.8-96.8	32.29	23.93	25.89
	101.8-102.8	35.32	25.5	27.80
	107.8-108.8	32.53	23.39	28.10
Core 43	5.5-6.5	30.65	17.58	42.64
	11.5-12.5	27.79	17.55	36.85
	17.5-18.5	29.27	18.18	37.89
	23.5-24.5	33.95	23.04	32.14
	29.5-30.5	25.08	16.78	33.09
	35.5-36.5	28.85	19.76	31.51
	41.5-42.5	30.04	21.73	27.66
	47.5-48.5	28.83	21.27	26.22
	53.5-54.5	31.9	23.6	26.02
	59.5-60.5	31.08	23.53	24.29
	65.5-66.5	28.81	20.56	28.64
	71.5-72.5	29.92	22.45	24.97
	77.5-78.5	32.53	23.21	28.65
	83.5-84.5	30.71	22.03	28.26
Core 44	15.6-16.6	32.39	21.61	33.28
Core 45	6.5-7.5	28.34	19.99	29.46
	12.5-13.5	32.39	23.25	28.22
	18.5-19.5	29.07	20.99	27.79
	24.5-25.5	30.72	22.07	28.16
Core 46	7.5-8.5	27.28	17.11	37.28
	13.5-14.5	29.13	18.64	36.01
	19.5-20.5	30.28	21.48	29.06
	25.5-26.5	28.15	19.53	30.62
	31.5-32.5	36.11	26.62	26.28
	37.5-38.5	34.74	25.17	27.55
	43.5-44.5	33.38	24.8	25.70
	49.5-50.5	36.11	27.14	24.84
	55.5-56.5	28.25	21.42	24.18
	61.5-62.5	34.38	26.11	24.05
	67.5-68.5	27.86	20.99	24.66

Depth (cm)	Callia-nassid area	Off-reef alpheid area
0-10	44.55	31.14
10-20	36.72	32.33
20-30	31.93	29.01
30-40	29.70	26.61
40-50	26.99	25.44
50-60	28.05	27.00
60-70	25.42	26.41



Note: Cores 41,42, 43 are from the callianassid area, cores 38, 44, 45, 46 are from the off-reef alpheid area

SUBSTRATE ANALYSIS (USING LINEAR POINT INTERCEPT METHOD) OF INTERTIDAL SAND WAVES AND TIDAL POOLS IN TANG KHEN BAY

A1		A2		A3		A4		A5		A6		A7	
Dist	Subst	Dist	Subst	Dist	Subst	Dist	Subst	Dist	Subst	Dist	Subst	Dist	Subst
20	sp	**20**	**as**	**20**	**ms**	20	mi	20	mi	**20**	**r**	**20**	**ms**
40	sp	**40**	**ms**	40	mi	40	mi	40	mi	**40**	**r**	**40**	**ms**
60	mi	**60**	**ms**	60	mi	60	lp	60	mi	**60**	**r**	60	mi
80	mi	**80**	**as**	80	mi	80	mi	80	mi	**80**	**ms**	80	mi
100	sh	**100**	**r**	100	mi	100	sp	100	mi	**100**	**as**	100	mi
120	mi	**120**	**r**	120	mi	120	mi	120	mi	**120**	**ah**	120	sp
140	mi	**140**	**ms**	140	sp	140	sp	140	mi	**140**	**ms**	140	lp
160	sp	**160**	**as**	160	sp	160	mi	160	t	**160**	**ms**	160	lp
180	sp	**180**	**as**	180	sp	180	lp	180	t	**180**	**ms**	180	sp
200	mi	**200**	**r**	200	mi	200	lp	200	r	**200**	**as**	200	sp
220	sp	**220**	**ms**	220	mi	220	sp	220	mi	**220**	**r**	220	sp
240	mi	**240**	**ms**	240	sp	240	sp	240	mi	**240**	**ms**	240	sp
260	sp	**260**	**as**	260	sp	260	mi	260	as	**260**	**a**	260	sp
280	mi	**280**	**ms**	280	sp	280	mi	280	mi	**280**	**r**	280	sp
300	mi	**300**	**ms**	300	mi	300	mi	300	mi	**300**	**a**	300	lp
320	mi	**320**	**as**	320	sp	320	mi	320	mi	**320**	**ms**	320	sp
340	mi	**340**	**ms**	340	mi	340	sp	**340**	**ms**	**340**	**r**	340	mi
360	t	**360**	**ms**	360	lp	360	sp	**360**	**ms**	**360**	**r**	360	sp
380	mi	**380**	**ms**	380	mi	380	sp	**380**	**ms**	**380**	**r**	380	sp
400	mi	**400**	**sh**	400	sp	400	sp	**400**	**ms**	**400**	**r**	400	mi
420	mi	**420**	**as**	420	mi	420	sp	**420**	**ms**	**420**	**ms**	420	mi
440	mi	**440**	**ms**	440	mi	440	sp	**440**	**sh**	**440**	**as**	440	mi
460	mi	**460**	**ms**	460	sp	460	dh	**460**	**r**	**460**	**r**	460	mi
480	mi	**480**	**ms**	480	lp	480	sp	**480**	**r**	**480**	**r**	480	sp
500	mi	**500**	**ms**	500	sp	500	sp	**500**	**r**	**500**	**r**	500	mi
520	mi	**520**	**r**	520	sp	520	mi	**520**	**as**	**520**	**as**	520	dh
540	mi	**540**	**ms**	540	mi	540	sp	**540**	**r**	**540**	**ms**	540	mi
560	**ms**	**560**	**r**	560	mi	560	sp	**560**	**r**	**560**	**as**	560	sp
580	**mi**	**580**	**r**	580	sp	580	mi	**580**	**sh**	**580**	**as**	580	sp
600	**ms**	**600**	**as**	600	sp	600	mi	**600**	**sh**	**600**	**as**	600	mi
620	**ms**	**620**	**ms**	620	sp	620	sp	**620**	**r**	**620**	**ms**	620	sp
640	**ms**	**640**	**ms**	640	mi	640	sp	**640**	**r**	**640**	**ms**	640	mi
660	**ms**	**660**	**ms**	660	mi	660	mi	**660**	**as**	**660**	**r**	660	sp
680	**ms**	**680**	**ms**	680	mi	680	sp	**680**	**ms**	**680**	**ms**	680	sp
700	**ms**	**700**	**as**	700	mi	700	mi	**700**	**ms**	**700**	**ms**	700	sp
720	**ms**	**720**	**ms**	720	mi	720	mi	**720**	**as**	**720**	**ms**	720	lp
740	**ms**	**740**	**ms**	740	mi	740	sp	**740**	**a**	**740**	**ms**	740	sp
760	**as**	**760**	**r**	760	mi	760	mi	**760**	**ms**	**760**	**ms**	760	lp
780	**ms**	**780**	**r**	780	lp	780	mi	**780**	**r**	**780**	**as**	780	mi
800	**ms**	**800**	**ms**	800	sp	800	mi	**800**	**as**	**800**	**ms**	800	sp
820	**as**	**820**	**ms**	820	mi	820	sp	**820**	**ms**	**820**	**ms**	820	mi
840	**ms**	**840**	**ms**	840	lp	840	mi	**840**	**ms**	**840**	**ms**	840	sp
860	**ms**	**860**	**ms**	860	dh	860	mi	**860**	**sh**	**860**	**ms**	860	mi
880	**ms**	**880**	**ms**	880	lp	880	mi	**880**	**ms**	**880**	**a**	880	mi
900	**as**	**900**	**ms**	900	mi	900	mi	**900**	**r**	**900**	**r**	900	sp
920	**as**	**920**	**ms**	920	mi	920	mi	**920**	**as**	**920**	**a**	920	sp
940	**ms**	**940**	**ms**	940	mi	940	mi	**940**	**as**	**940**	**ms**	940	mi
960	**as**	**960**	**ms**	960	mi	960	mi	**960**	**r**	**960**	**r**	960	mi
980	**r**	**980**	**ms**	980	sp	980	mi	**980**	**r**	**980**	**ms**	980	sp
1000	**r**	**1000**	**ms**	1000	mi	1000	mi	**1000**	**r**	**1000**	**ms**	1000	mi

KEY

dh = dotilla hole
lp = large pellet
sp = small pellet
mi = unburrowed mud (above pool surface)
ms = unburrowed mud (below pool surface)
a = algae
ah = alpheid hole
as = alpheid shovelling
r = rock
t = track/trail
c = sea cucumber
sh = shell

NOTES:

All transects done shore to sea direction on 28.3.95, starting with A1 at 2pm

Transect 1 starts half way between top of wave 4 and pool edge and 7 ends just over the top of wave 6

Transect A1 continues as A2, then A3, A4 etc.

Bold font indicates transect points in pool; non-bold are sand wave

Summary of substrate type (for complete sand waves or pools only)

	Pool 1		**Pool 2**			**Sandwave**	
Type	No.	%	No.	%	Type	no	%
ms	48	64.9	35	40.7	mi	66	57.4
mi	1	1.4	0	0.0	sp	35	30.4
as	14	18.9	14	16.3	lp	8	7.0
r	10	13.5	27	31.4	dh	2	1.7
sh	1	1.4	4	4.7	t	2	1.7
ah	0	0.0	1	1.2	r	1	0.9
a	0	0.0	5	5.8	as	1	0.9

SUBSTRATE ANALYSIS OF INTERTIDAL AREA CONTINUED.....

B1		B2		B3		C1		C2		C3	
Dist	Subst	Dist	Subst	Dist	Subst	Dist	Subst	Dist	Subst	Dist	Subst
20	sp	**20**	**ms**	20	mi	**20**	**sp**	**20**	**as**	**20**	**ms**
40	sp	**40**	**ms**	40	lp	**40**	**sp**	**40**	**r**	40	mi
60	sp	**60**	**ms**	60	sp	**60**	**sp**	**60**	**r**	60	mi
80	sp	**80**	**ms**	80	sp	**80**	**sp**	**80**	**ah**	80	sp
100	sp	**100**	**ms**	100	sp	**100**	**sp**	**100**	**as**	100	sp
120	sp	**120**	**ms**	120	sp	**120**	**sp**	**120**	**sh**	120	sp
140	sp	**140**	**r**	140	sp	**140**	**sp**	**140**	**sh**	140	sp
160	sp	**160**	**as**	160	dh	**160**	**sp**	**160**	**ms**	160	sp
180	spp	**180**	**ms**	180	sp	**180**	**sp**	**180**	**ms**	180	sp
200	mi	**200**	**ms**	200	sp	**200**	**lp**	**200**	**as**	200	sp
220	sp	**220**	**ms**	220	sp	**220**	**sp**	**220**	**r**	220	sp
240	mi	**240**	**ms**	240	sp	**240**	**sp**	**240**	**r**	240	sp
260	sp	**260**	**ms**	260	mi	**260**	**sp**	**260**	**ms**	260	sp
280	mi	**280**	**ms**	280	sp	**280**	**sp**	**280**	**r**	280	sp
300	mi	**300**	**ms**	300	mi	**300**	**lp**	**300**	**r**	300	sp
320	sp	**320**	**as**	320	sp	**320**	**sp**	**320**	**ms**	320	sp
340	sp	**340**	**as**	340	sp	**340**	**sp**	**340**	**as**	340	sp
360	mi	**360**	**ah**	360	mi	**360**	**sp**	**360**	**ms**	360	lp
380	mi	**380**	**ms**	380	mi	**380**	**sp**	**380**	**r**	380	lp
400	sp	**400**	**ms**	400	sp	**400**	**sp**	**400**	**r**	400	sp
420	mi	**420**	**ms**	420	lp	**420**	**sp**	**420**	**ms**	420	mi
440	sp	**440**	**ms**	440	sp	**440**	**mi**	**440**	**r**	440	sp
460	mi	**460**	**ms**	460	sp	**460**	**mi**	**460**	**ms**	460	sp
480	mi	**480**	**ms**	480	sp	**480**	**sp**	**480**	**ms**	480	sp
500	mi	**500**	**as**	500	mi	**500**	**mi**	**500**	**ms**	500	sp
520	mi	**520**	**as**	520	sp	**520**	**dh**	**520**	**t**	520	sp
540	mi	**540**	**ah**	540	sp	**540**	**mi**	**540**	**ms**	540	sp
560	mi	**560**	**ms**	560	sp	**560**	**sp**	**560**	**as**	560	mi
580	sp	**580**	**r**	580	lp	**580**	**sp**	**580**	**ms**	580	sp
600	mi	**600**	**r**	600	sp	**600**	**mi**	**600**	**r**	600	sp
620	mi	**620**	**as**	620	mi	**620**	**mi**	**620**	**as**	620	mi
640	mi	**640**	**r**	640	mi	**640**	**lp**	**640**	**r**	640	sp
660	mi	**660**	**ms**	660	mi	**660**	**sp**	**660**	**as**	660	mi
680	mi	**680**	**ms**	680	mi	**680**	**mi**	**680**	**as**	680	sp
700	mi	**700**	**ms**	700	mi	**700**	**mi**	**700**	**ms**	700	sp
720	mi	**720**	**as**	720	sp	**720**	**mi**	**720**	**r**	720	mi
740	**ms**	**740**	**ms**	740	mi	**740**	**sp**	**740**	**r**	740	sp
760	**ms**	**760**	**ms**	760	sp	**760**	**mi**	**760**	**r**	760	sp
780	**ms**	**780**	**r**	780	mi	**780**	**r**	**780**	**r**	780	sp
800	**ms**	**800**	**ms**	800	sp	**800**	**mi**	**800**	**r**	800	sp
820	**ms**	**820**	**as**	820	mi	**820**	**r**	**820**	**sh**	820	sp
840	**ms**	**840**	**ms**	840	mi	**840**	**r**	**840**	**r**	840	mi
860	**ms**	**860**	**ms**	860	sp	**860**	**mi**	**860**	**as**	860	sp
880	**mi**	**880**	**ms**	880	mi	**880**	**r**	**880**	**as**	880	sp
900	**mi**	**900**	**ms**	900	mi	**900**	**as**	**900**	**r**	900	lp
920	**mi**	**920**	**ms**	920	mi	**920**	**ms**	**920**	**t**	920	mi
940	**mi**	**940**	**ms**	940	mi	**940**	**ms**	**940**	**ms**	940	sp
960	**mi**	**960**	**ms**	960	mi	**960**	**as**	**960**	**ms**	960	mi
980	**mi**	**980**	**ms**	980	mi	**980**	**as**	**980**	**ms**	980	sp
1000	**mi**	**1000**	**ms**	1000	mi	**1000**	**ms**	**1000**	**ms**	1000	sp

NOTES: Transects done on 28.3.95, starting with B1 at 4pm
Transect B is about 4m North of A, C is 6m South of A, all parallel to each other
Bold font indicates transect points in pool; non-bold are sand wave

Summary of substrate type (for complete sand waves or pools only)

	Pool 1		**Pool 2**			**Sandwave**	
Type	No.	%	No.	%	Type	no	%
ms	42	65.6	20	35.7	mi	34	35.8
mi	7	10.9	0	0.0	sp	48	50.5
as	8	12.5	12	21.4	lp	6	6.3
r	5	7.8	18	32.1	dh	2	2.1
sh	0	0.0	3	5.4	t	0	0.0
ah	2	3.1	1	1.8	r	4	4.2
a	0	0.0	0	0.0	as	1	1.1
t	0	0.0	2	3.6			

SUBSTRATE ANALYSIS OF INTERTIDAL STUDY SITE

(Transects A and B start at the shoreward edge of wave 5 and runs to the seaward edge of wave 6, B is about 10m South of a. Transects run in series, eg A1-A2-A3 etc from shore to sea. Done 29.3.95, started 14.25)

A1 (14.25)		A2		A3		A4		A5		A6		A1 (15.25)	
20	*mi*	20	dh	*20*	*t*	**20**	**a**	20	mi	20	sp	*20*	*mi*
40	*mi*	40	mi	*40*	*t*	**40**	**ms**	40	mi	40	lp	*40*	*mi*
60	*mi*	60	sp	*60*	*mi*	**60**	**ms**	60	mi	60	sp	*60*	*sp*
80	*sp*	80	mi	*80*	*mi*	**80**	**as**	80	mi	80	mi	*80*	*sp*
100	*mi*	100	sp	*100*	*sh*	**100**	**r**	100	mi	100	sp	*100*	*sp*
120	mi	120	mi	*120*	*r*	**120**	**r**	120	sp	120	lp	120	mi
140	sp	140	sp	*140*	*t*	**140**	**ms**	140	mi	140	mi	140	sp
160	sp	160	sp	***160***	***ms***	**160**	**r**	160	mi	160	lp	160	sp
180	sp	180	sp	***180***	***r***	**180**	**a**	180	sp	180	sp	180	sp
200	mi	200	mi	***200***	***ms***	**200**	**as**	200	sp	200	sp	200	dh
220	sp	220	mi	***220***	***ms***	**220**	**sh**	220	lp	220	sp	220	sp
240	mi	240	sp	***240***	***ms***	**240**	**as**	240	mi	240	sp	240	sp
260	sp	260	sp	***260***	***ms***	**260**	**as**	260	sp	260	sp	260	sp
280	mi	280	sp	**280**	**ms**	**280**	**a**	280	mi	280	lp	280	sp
300	sp	300	sp	**300**	**ms**	**300**	**ms**	300	sp	300	mi	300	sp
320	mi	320	sp	**320**	**ms**	**320**	**r**	320	sp	320	mi	320	lp
340	mi	340	dh	**340**	**as**	**340**	**as**	340	sp	340	sp	340	sp
360	mi	360	lp	**360**	**as**	**360**	**ms**	360	mi	360	sp	360	sp
380	sp	380	sp	**380**	**ms**	**380**	**sh**	380	lp	380	sp	380	sp
400	mi	400	sp	**400**	**as**	**400**	**ms**	400	sp	400	sp	400	sp
420	lp	420	mi	**420**	**ms**	**420**	**ms**	420	lp	420	mi	420	sp
440	sp	440	mi	**440**	**r**	**440**	**ms**	440	sp	440	sp	440	mi
460	mi	460	mi	**460**	**as**	**460**	**ms**	460	lp	460	mi	460	lp
480	mi	480	sp	**480**	**r**	**480**	**as**	480	mi	480	mi	480	sp
500	mi	500	mi	**500**	**ms**	**500**	**ms**	500	mi	500	sp	500	sp
520	sp	520	mi	**520**	**as**	**520**	**sh**	520	lp	520	lp	520	mi
540	mi	540	sp	**540**	**a**	**540**	**r**	540	sp	540	sp	540	mi
560	mi	560	mi	**560**	**r**	**560**	**a**	560	mi	560	sp	560	mi
580	mi	580	mi	**580**	**ms**	**580**	**ms**	580	mi	580	sp	580	sp
600	mi	600	sp	**600**	**ms**	**600**	**ms**	600	mi	600	sp	600	mi
620	mi	620	sp	**620**	**ms**	**620**	**ms**	620	mi	620	mi	620	mi
640	sp	640	mi	**640**	**r**	**640**	**ms**	640	dh	640	sp	640	sp
660	mi	*660*	*mi*	**660**	**r**	***660***	***ms***	660	sp	660	sp	660	mi
680	mi	*680*	*lp*	**680**	**as**	***680***	***ms***	680	mi	680	mi	680	mi
700	mi	*700*	*mi*	**700**	**as**	***700***	***ms***	700	sp	700	sp	700	mi
720	mi	*720*	*mi*	**720**	**a**	***720***	***ms***	720	sp	720	mi	720	sp
740	sp	*740*	*mi*	**740**	**r**	***740***	***ms***	740	sp	740	mi	740	mi
760	mi	*760*	*r*	**760**	**r**	***760***	***ms***	760	mi	760	lp	760	sp
780	lp	*780*	*r*	**780**	**r**	***780***	***ms***	780	sp	780	mi	780	mi
800	sp	*800*	*r*	**800**	**r**	***800***	***ms***	800	lp	800	sp	800	sp
820	mi	*820*	*r*	**820**	**r**	***820***	***ms***	820	sp	820	sp	820	sp
840	mi	*840*	*r*	**840**	**as**	***840***	***ms***	840	sp	840	mi	840	sp
860	sp	*860*	*r*	**860**	**as**	***860***	***ms***	860	lp	860	sp	860	mi
880	sp	*880*	*r*	**880**	**r**	*880*	*mi*	880	sp	880	sp	880	dh
900	sp	*900*	*sh*	**900**	**as**	*900*	*mi*	900	sp	900	mi	900	sp
920	mi	*920*	*as*	**920**	**as**	*920*	*mi*	920	sp	*920*	*mi*	920	mi
940	sp	*940*	*dh*	**940**	**ms**	*940*	*mi*	940	sp	*940*	*mi*	940	mi
960	mi	*960*	*mi*	**960**	**ms**	*960*	*mi*	960	lp	*960*	*mi*	960	sp
980	mi	*980*	*mi*	**980**	**ms**	980	mi	980	sp	*980*	*t*	980	sp
1000	mi	*1000*	*mi*	**1000**	**r**	1000	sp	1000	lp	*1000*	*mi*	1000	sp
										1020	*mi*		
										1040	*mi*		
										1060	*mi*		
										1080	*mi*		
										1100	*mi*		
										1120	*mi*		
										1140	*mi*		
										1160	*mi*		
										1180	*mi*		
										1200	*mi*		
										1220	*mi*		
										1240	*mi*		
										1260	*mi*		
										1280	*mi*		
										1300	*mi*		
										1320	*mi*		
										1340	*mi*		

NOTE

normal type = sand wave
bold type = pool
italics = unburrowed edge of each zone (sand wave or pool)

SUMMARY OF SUBSTRATE TYPES (%)

Type	Wave edge (14:25)	Wave	Wave edge	Wave edge	Wave	Wave edge	Wave edge (15:25)	Wave
mi	80	51.95	36	100	34	95.45	40	33.33
sp	20	41.56	0	0	49.5	0	60	57.78
lp	0	3.896	4	0	15.5	0	0	4.4
dh	0	2.597	4	0	1.03	0	0	4.4
t	0	0	0	0	0	4.5	0	0
r	0	0	0	0	0	0	0	0
as	0	0	4	0	0	0	0	0
sh	0	0	8	0	0	0	0	0
r	0	0	32	0	0	0	0	0
t	0	0	12	0	0	0	0	0

Type	Pool edge	Pool	Pool edge
ms	83.33	37.7	100
mi	0	0	0
as	0	24.6	0
r	16.67	24.6	0
sh	0	4.35	0
ah	0	0	0
a	0	8.7	0
t	0	0	0

SUBSTRATE ANALYSIS OF INTERTIDAL STUDY SITE CONTINUED....

B1	wave edge	B1/ B2	wave	B3	wave edge	B3	pool edge	B3/ B4	pool	B4	pool edge
20	*t*	20	lp	*20*	*mi*	**20**	**ms**	*20*	*mi*	20	lp
40	*mi*	40	sp	*40*	*sp*	**40**	**ms**	*40*	*mi*	40	sp
60	*mi*	60	mi	*60*	*sp*	**60**	**ms**	60	sp	60	sp
80	*mi*	80	mi	*80*	*mi*	**80**	**ms**	80	sp	80	sp
100	*sp*	100	mi	*100*	*mi*	**100**	**as**	100	sp	100	sp
120	*sp*	120	mi	*120*	*mi*	**120**	**r**	120	sp	120	lp
140	sp	140	mi	*140*	*mi*	**140**	**r**	140	sp	140	lp
160	sp	160	lp	*160*	*mi*	**160**	**a**	160	sp	160	sp
180	mi	180	lp	*180*	*mi*	**180**	**as**	180	sp	180	sp
200	sp	200	mi	*200*	*mi*	**200**	**ms**	200	sp	200	sp
220	mi	220	sp	*220*	*mi*	**220**	**r**	220	sp	220	mi
240	sp	240	mi	*240*	*mi*	**240**	**r**	240	sp	240	sp
260	mi	260	sp	*260*	*mi*	**260**	**r**	260	lp	260	sp
280	mi	280	sp	*280*	*sp*	**280**	**r**	280	sp	280	sp
300	sp	300	mi	***300***	***r***	**300**	**as**	300	sp	300	lp
320	sp	320	sp	***320***	***as***	**320**	**as**	320	mi	320	sp
340	mi	340	mi	***340***	***t***	**340**	**r**	340	mi	340	sp
360	lp	360	sp	***360***	***r***	**360**	**r**	360	sp	360	sp
380	sp	380	mi	***380***	***r***	**380**	**r**	380	sp	380	sp
400	lp	400	mi	***400***	***r***	**400**	**as**	400	mi	400	sp
420	lp	420	mi	***420***	***r***	**420**	**as**	420	mi	420	sp
440	mi	440	mi	***440***	***mi***	**440**	**as**	440	sp	440	sp
460	sp	460	sp	**460**	**ms**	**460**	**as**	460	sp	460	sp
480	mi	480	mi	**480**	**ms**	**480**	**ah**	480	sp	480	sp
500	sp	500	mi	**500**	**ms**	**500**	**ms**	500	mi	500	mi
520	mi	520	sp	**520**	**ms**	**520**	**r**	520	lp	520	sp
540	lp	540	sp	**540**	**ms**	**540**	**as**	540	sp	540	lp
560	mi	560	lp	**560**	**a**	**560**	**as**	560	mi	560	sp
580	mi	580	sp	**580**	**ah**	**580**	**as**	580	lp	580	mi
600	mi	600	sp	**600**	**a**	**600**	**as**	600	mi	600	sp
620	mi	620	sp	**620**	**ms**	**620**	**r**	620	sp	620	sp
640	mi	640	mi	**640**	**ms**	**640**	**ms**	640	sp	640	sp
660	sp	660	sp	**660**	**ms**	**660**	**ms**	660	mi	660	sp
680	mi	680	sp	**680**	**ms**	**680**	**ms**	680	sp	680	sp
700	mi	700	sp	**700**	**ms**	**700**	**ms**	700	sp	700	sp
720	sp	720	mi	**720**	**ms**	**720**	**ms**	720	sp	720	sp
740	lp	740	sp	**740**	**as**	**740**	**ms**	740	mi	740	mi
760	mi	760	sp	**760**	**ms**	**760**	**ms**	760	sp	760	sp
780	sp	780	sp	**780**	**as**	**780**	**ms**	780	sp	780	mi
800	mi	800	sp	**800**	**r**	**800**	**ms**	800	mi	800	sp
820	mi	820	sp	**820**	**r**	**820**	**ms**	820	sp	820	sp
840	sp	840	sp	**840**	**ms**	***840***	***ms***	840	sp	840	dh
860	mi	860	sp	**860**	**r**	***860***	***ms***	860	lp	860	sp
880	sp	880	mi	**880**	**ms**	***880***	***ms***	880	lp	880	sp
900	mi	900	sp	**900**	**ms**	***900***	***ms***	900	mi	900	lp
920	sp	920	mi	**920**	**ms**	***920***	***ms***	920	sp	920	lp
940	mi	940	mi	**940**	**ms**	***940***	***ms***	940	sp	940	sp
960	sp	960	sp	**960**	**ms**	***960***	***ms***	960	sp	960	sp
980	sp	980	sp	**980**	**ms**	*980*	*mi*	980	lp	980	lp
1000	mi	1000	sp	**1000**	**as**	*1000*	*mi*	1000	sp	1000	sp
										1020	mi
										1040	mi
										1060	lp
										1080	*mi*
										1100	*sp*
										1120	*sp*
										1140	*sp*
										1160	*mi*
										1180	*sp*
										1200	*sp*
										1220	*mi*
										1240	*mi*
										1260	*mi*

NOTE

normal type = sand wave
bold type = pool
italics = unburrowed edge of each zone (sand wave or pool)

SUMMARY OF SUBSTRATE TYPES (%)

Type	Wave edge	Wave	Wave edge	Wave edge	Wave	Wave edge
mi	50	44.7	78.57	100	17.82	50
sp	33.33	45.7	21.43	0	66.34	50
lp	0	9.57	0	0	14.85	0
dh	0	0	0	0	0.99	0
t	0	0	0	0	0	0
r	0	0	0	0	0	0
as	0	0	0	0	0	0
sh	0	0	0	0	0	0
r	0	0	0	0	0	0
t	1	0	0	0	0	0

Type	Pool edge	Pool	Pool edge
ms	0	35	7
mi	1	0	0
as	1	15	0
r	5	14	0
sh	0	0	0
ah	0	2	0
a	0	3	0
t	1	0	0

APPENDIX C - Specific biogenic sediment data

Dotilla BURROW MEASUREMENTS

Date	Burrow diameter (mm)	Burrow depth (mm)	Burrow volume (mm3)
31.3.94	9	90	5726
	8	107	5378
	7	77	2963
	7	80	3079
	9	114	7252
	6	89	2516
	12	127	14363
	7	90	3464
	7	53	2040
	12	78	8822
	5	23	452
	4	18	226
	11	115	10929
	8	89	4474
	11	83	7888
8.4.94	13	86	11415
	5	57	1119
	6	73	2064
	7.5	90	3976
	6	73	2064
	16	54	10857
	7	57	2194
	6	67	1894
	11.5	125	12984
	6.5	85	2821
	8	58	2915
	7	62	2386
	7	60	2309
	7	64	2463
	9	70	4453
	6.5	58	1925
	5.5	30	713
	7	80	3079
	10	84	6597
	7	115	4426
	6	98	2771
	8	175	8796
	9	113	7189
8.4.94	13	107	14202
	4.5	90	1431
	6	84	2375
	5	55	1080
15.2.95	8	95	4775
	7	63	2425
	5	27	530
	15	123	21736
	7	67	2578
	5	68	1335
	8	157	7892
	9	100	6362
	4	21	264
	11	95	9028
	12	89	10066
	13	98	13008
	5	65	1276
	4	40	503
	4	30	377
	9	137	8716
	8	64	3217
	6	65	1838
	4	33	415
	6	60	1696
	8	59	2966
	11	102	9693
	12	89	10066
	10	96	7540
	12	88	9953
	16	91	18297
	8	108	5429

Average volume = 4463 mm^3 (st dev = 3875, n = 27);
Average width = 7.5mm (st dev = 3.5)
Average length = 89.8mm (st dev = 22.8)
Data from 8.4.94 only as this was collected randomly.

Date	Burrow densities				
30.3.94	21	29	21	16	24
	22	26	19	25	27
	30	19	20	21	20
	20	15	16	26	26
27.3.94	25	23	30	23	31
31.3.94	18	17	19	24	19
	30				

mean density = 22.6 per 50x50cm quadrat
this is equivalent to 90.58 / m^2 (st dev = 18.23, n = 31)

Figures in Table are counts from random 50x50cm quadrats

FEEDING AND EXCAVATION PELLET DATA

Date	Burrow diam (mm)	Burrow depth (mm)	Excavated pellet dry wt (g)	Feeding pellet dry wt (g)	Burrow volume (mm3)	% of pellets that are excavated	% of pellets that are feeding
30.3.94	9	90	3.28	6.16	5726	34.75	65.25
	8	107	2.6	12.25	5378	17.51	82.49
	7	77	1.88	5.98	2963	23.92	76.08
	7	80	1.6	6.59	3079	19.54	80.46
	9	114	7.44	15.84	7252	31.96	68.04
	6	89	3.52	1.67	2516	67.82	32.18
	12	127	7.56	22.19	14363	25.41	74.59
	7	90	1.25	7.22	3464	14.76	85.24
	7	53	6.11	4.41	2040	58.08	41.92
15.2.95	8	59	26.88	-	2966	**32.64**	**67.36**
	11	102	9.19	-	9693	Mean percents	
	12	89	24.69	-	10066		
	10	96	17.92	-	7540		
	12	88	21.2	-	9953		
	16	91	32.21	-	18297		
	8	108	15.8	-	5429		

Pellets collected from individual burrows

Date	Quadrats (1/4m2)	Dry weight (all pellets) (g)	No. of burrows	Weight per burrow (g)	Equivalent per m2 (g)
27.3.94	1	545	25	21.80	2180
	2	491	23	21.35	1964
	3	610	30	20.33	2440
	4	398	23	17.30	1592
	5	609	31	19.65	2436
30.3.94	1	432	18	24.00	1728
	2	399	17	23.47	1596
	3	247	19	13.00	988
	4	367	24	15.29	1468
	5	259	19	13.63	1036
					1743

st dev = 516. n = 10

GRAIN SIZE DISTRIBUTIONS FOR PROFILES THROUGH THE INTERTIDAL DOTILLA AREA

A	**Grain size**									
Depth (cm	<63um	63-125um	125-250um	250-500um	0.5-1mm	1-2mm	2-4mm	4-8mm	8-16mm	16-32mm
0-1	1.96	26.50	61.24	7.32	0.90	0.70	0.59	0.91	0.00	0.00
1--2	1.51	27.14	59.00	5.46	3.00	2.00	1.70	0.20	0.00	0.00
3--7	2.14	17.79	62.68	11.21	1.30	1.00	3.47	0.33	0.00	0.00
8.5-12.5	1.98	19.53	61.44	10.27	1.50	1.10	2.41	0.68	1.00	0.00
16-20	1.92	14.84	57.47	17.21	2.30	1.20	1.37	1.73	2.11	0.00
22-26	3.83	17.94	41.00	21.12	8.60	2.50	1.47	0.87	0.36	2.40
28	3.01	9.10	19.13	11.16	7.50	8.30	10.88	4.47	11.70	14.85

B	**Grain size**							
Depth (cm	<63um	63-125um	125-250um	250-500um	0.5-1mm	1-2mm	2-4mm	>4mm
0-1	0.30	32.40	60.80	3.90	1.40	1.10	0.30	0
1-3	0.30	34.50	56.30	3.60	1.30	1.10	0.90	2
4-8	0.30	22.40	65.10	6.30	1.80	1.10	1.00	2
10-14	0.30	21.10	61.80	8.20	2.10	1.80	1.30	3.3
16-20	0.90	18.40	40.60	24.00	10.10	3.50	1.60	0.9
23-27	1.00	28.10	40.30	13.00	8.30	4.00	1.70	3.6
29-33	1.60	20.00	27.90	11.80	8.90	8.10	6.60	15.60
>33	1.10	15.00	23.80	11.20	9.60	7.60	6.70	25.00

C	**Grain size**						
Depth (cm	<125um	125-250um	250-500um	0.5-1mm	1-2mm	2-4mm	>4mm
0-2	42.60	47.90	3.20	2.00	1.80	1.90	0.60
5-7	30.80	58.00	5.30	2.00	1.5	1.50	0.90
9-12	23.80	59.70	7.00	2.40	1.8	2.80	2.60
16-18	20.40	52.60	7.00	2.40	1.7	1.10	13.90
20-23	14.80	43.40	16.50	9.50	7.1	4.30	4.30
26-29	9.00	33.40	21.20	12.10	7.1	5.30	11.90
33.00	23.70	32.30	7.90	5.20	4.4	6.00	20.50

All data based on weight percents as obtained through dry sieving

INTERTIDAL CALLIANASSID DATA

Date	Hole diam (cm)	Crater depth(cm)	Crater diameter (cm)			Mound height(cm)	Mound diameter (cm)			Mound vol (cm3)
			a	b	mean		a	b	mean	
15.2.95	2.3		8.3		8.3	2	13.5	14.3	13.9	152
	2.7		11	10.3	10.65	2.8	18.5	13.5	16	281
	3.4		15.1	13.2	14.15	2.4	19	14.5	16.75	264
	2.4		15	16	15.5	3.1	24.5	23.5	24	701
	1.3		11	9.5	10.25	2.1	21	15.5	18.25	275
	4		10	9	9.5	2.1	24.5	15.5	20	330
	2.2		9.5	9	9.25	1.9	10	12.5	11.25	94
	3		11	10	10.5	2.6	12	17	14.5	215
	4		13.5	12.5	13	2.4	19	15.5	17.25	280
	3.4		12	12	12	2.7	20	19	19.5	403
	3.2		12	12.5	12.25	2.1	19	20	19.5	313
	2.3		15	14	14.5	2.1	28	25	26.5	579
	3.5		22	22	22	4	40	48	44	3040
17.2.95	2.5	5.8	18	19	18.5	5.2	25	20	22.5	1033
	4	7.5	23	22	22.5	4.1	29	28	28.5	1307
	4	4.8	20	20	20	3.8	20	22	21	658
	4.3	2.8	17	15	16	3.7	22	23	22.5	735
	3.7	5.5	17	16	16.5	3	31	29	30	1060
	4.2	5.2	20	18	19	4.3	24	27	25.5	1097
	3.3	7.6	30	30	30	4.9	40	40	40	3077
	2.3	3.5	14	12	13	3.2	15	14	14.5	264
	3.3	3.3	12	12	12	3.3	14	14	14	254
	3	4	13	12	12.5	2.3	21	22	21.5	417
	3.8	3.5	12	11	11.5	1.7	27	20	23.5	368
	3.8	3.3	12	11	11.5	3.8	27	24	25.5	970
	4	5.1	18	18	18	3.9	30	32	31	1471
	3.5	5.7	20	20	20	3.7	31	33	32	1487
	3.3	6.6	22	24	23	4.2	30	29	29.5	1435
18.2.95	2.5	3.4	10	10	10	3.9	27	24	25.5	995
	4	2.9	10	10	10	1.7	8.5	8	8.25	45
n	30	17	30	29	30	30	30	30	30	30
mean	3.24	4.74			14.86	3.10			22.56	786.71
stdev	0.75	1.56			5.15	0.98			8.03	756.69

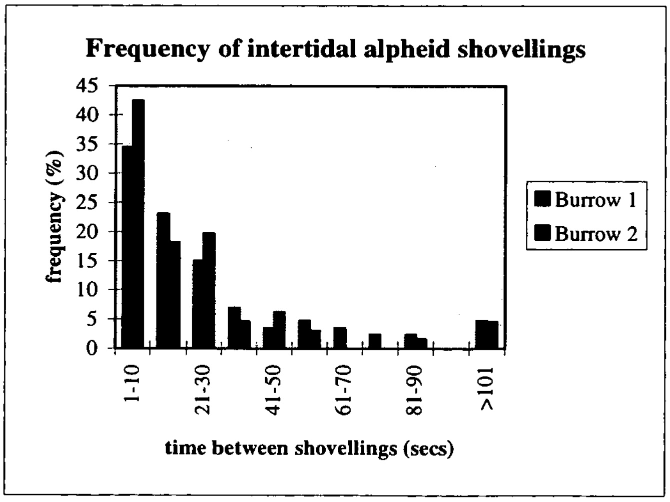
Mound volume calculated from width and height measurements, assuming mounds are conical

MEASUREMENTS OF INTERTIDAL ALPHEID BURROWS

	Hole diameter (cm)	Heap length (cm)	Heap width (cm)	Heap length (cm)	Length of coarse area	Width of coarse area	No. of visible coarse grains
	2.5	20	20	2.9	7	3	20
	2.5	20	20	2.2	6	2	10
	2.75	23	20	3	5	2	5
	2.5	12.5	12.5	1.5	5.5	2.5	18
	2	18	23	2.2	4.5	2	13
	2.5	23	15	1.5	0	0	none
	3	12	19	1.8	8	4	20
	2.5	20	15	2.1	10	5	50
	2	17	17	1.4	4	4	12
	2	16	15	1.6	6	3	12
	2	13	13	1.9	5	2	22
	2	11	15	1.7	4	2	9
	2	17	25	2.6	3	2	8
	2	14	17	2.5	5.5	2	12
	2.5	15	29	2.6	4	2	9
	2.5	15	19	2.8	5	2	11
	1.5	15	18	1.4	4	2	16
average	2.28	16.56	18.38	2.10	5.41	2.59	15.44
st dev	0.37	3.67	4.33	0.55	2.15	1.12	10.40

FREQUENCY OF ALPHEID SHOVELLINGS FROM TWO INTERTIDAL BURROWS

Time between shovellings (secs)	Number of occurrences		Occurrences as %	
	Burrow 1	Burrow2	Burrow 1	Burrow 2
1-10	30	28	34.5	42.4
11-20	20	12	23	18.2
21-30	13	13	14.9	19.7
31-40	6	3	6.9	4.5
41-50	3	4	3.4	6.1
51-60	4	2	4.6	3
61-70	3	0	3.4	0
71-80	2	0	2.3	0
81-90	2	1	2.3	1.5
91-100	0	0	0	0
>101	4	3	4.6	4.5



Intertidal callinassid mounds - grain size

Sample number	Grain size <63um	63-125um	125-250um	250-500um	500um-1mm	1-2mm	2-4mm	>4mm	Mean (um)
1	2.97	17.73	71.13	6.57	0.80	0.60	0.20	0.00	196.63
2	3.64	19.80	62.22	10.21	1.94	1.40	0.80	0.00	234.22
3	3.77	15.63	65.35	11.80	2.22	1.14	0.00	0.00	216.46
4	2.65	6.31	65.83	23.36	1.32	0.53	0.00	0.00	235.71
5	2.75	4.53	62.02	28.58	1.81	0.32	0.00	0.00	246.95
6	3.15	7.10	62.51	23.96	2.32	0.96	0.00	0.00	246.52
7	4.04	18.20	68.82	8.15	0.60	0.20	0.00	0.00	185.51
8	3.78	12.49	68.79	12.67	1.39	0.44	0.44	0.00	219.66
9	4.16	12.38	69.81	12.56	0.88	0.20	0.00	0.00	200.56
10	3.99	16.43	68.02	9.97	0.69	0.91	0.00	0.00	200.48
Mean	3.49	13.06	66.45	14.78	1.40	0.67	0.14	0.00	218.27

BURROW MEASUREMENTS - SUBTIDAL CALLIANASSIDS

	Mound height(cm)	Mound diameter (cm) a	b	mean	Mound vol (cm3)
	5	15			442
	5	17	17	17	567
	2	10	9	9.5	71
	3	15	15	15	265
	3	10	12	11	142
	3	12	14	13	199
	4	14	14	14	308
	2	6	7	6.5	33
	2	8	8	8	50
	1.5	8			38
	2	12			113
	1	11			47
	1.7	12			96
	0.5	6			7
	1.7	8			43
n	15			23	15
mean	2.49			11.30	161.41
stdev	1.34			3.42	166.22

Mound volume calculated from width and height measurements, assuming mounds are conical

WEIGHT PERCENT GRAIN SIZE FRACTIONS FOR FIVE INTERTIDAL SIPUNCULID CASTS

Sample no	% Grain size (dry weight) <31.5um	31.5-63um	63-125um	125-250um	250-500um	0.5-1mm	1-2mm	2-4mm	4-8mm	8-16mm
1	4.06	0.65	5.05	38.99	36.11	8.78	3.15	3.21	0.00	0.00
2	4.08	1.43	13.08	63.62	15.83	1.04	0.57	0.35	0.00	0.00
3	3.78	1.09	8.75	67.69	16.82	0.65	0.43	0.27	0.52	0.00
4	2.62	0.96	9.43	67.77	17.15	1.04	0.61	0.42	0.00	0.00
5	2.11	0.76	9.36	70.35	14.65	1.98	0.50	0.28	0.00	0.00

Note: All figures are the average of three subsamples of each cast
<500um fraction determined using Coulter Counter, >500um fraction by dry sieving.

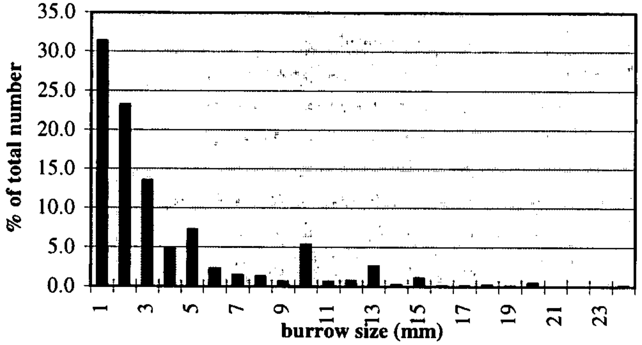
TOTAL BURROW NUMBERS IN SUBTIDAL SEDIMENTS AS COUNTED IN RANDOM QUADRATS

Date	17.2.95	17.2.95	24.2.95	25.2.95	25.2.95	26.2.95	26.2.95	28.2.95	28.2.95	4.3.95	4.3.95	8.3.95	11.3.95	13.3.95	22.3.95	Total no. (total area = 5.09sqm)	Total as %
Area (sqm)	1	1	0.24	0.25	0.25	0.25	0.25	0.25	0.24	0.25	0.25	0.2	0.17	0.24	0.25		
Position	A	A	C	C	C	C	C	C	C	B	B	C	C	C	C		
Burrow diam (mm)	Number of burrows																
<2	34															34	3.0
1	22	0	24	39	20	29	19	19	20	36	32	12	18	13	50	353	31.3
2	42	35	15	9	16	18	5	17	10	23	17	25	10	9	11	262	23.2
3	14	47	10	10	4	8	1	1	8	11	6	19	3	6	4	152	13.5
4	10	1	3	6	0	3	2	0	2	7	6	2	2	6	4	54	4.8
5	12	34	8	2	0	3	3	0	5	5	3	2	2	2	0	81	7.2
6	13	1	1	1	3	0	0	0	1	2	1	0	1	0	2	26	2.3
7	1	6	0	2	1	0	0	0	1	2	1	0	0	1	1	16	1.4
8	1	1	0	1	2	1	2	1	0	1	0	1	0	2	1	14	1.2
9	1	0	1	3	1	0	0	0	1	0	0	0	0	0	0	7	0.6
10	9	34	5	1	3	1	1	0	2	1	0	0	1	2	0	60	5.3
11	2	0	0	1	0	0	1	0	0	0	0	0	0	3	0	7	0.6
12	0	4	0	1	0	0	1	1	0	0	0	0	0	1	0	8	0.7
13	0	20	0	0	1	1	2	1	1	0	0	0	1	2	0	29	2.6
14	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0.2
15	4	0	0	0	1	0	3	1	1	0	0	0	0	2	0	12	1.1
16	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0.1
17	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0.1
18	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0.2
19	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.1
20	0	3	1	1	0	0	0	0	0	0	0	0	0	0	0	5	0.4
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
24	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.1
Total	165	186	68	78	53	64	43	42	52	88	66	61	38	51	73	1128	100.0
number/m2	165	186	283	312	212	256	172	168	217	352	264	305	224	213	292	mean = 241 / m2 st dev = 58.53	

NOTE:

A = near-reef alpheid area,
B = off-reef alpheid area,
C = callianassid area

Frequency distribution of subtidal burrow sizes



APPENDIX D - Bioerosion data

BARNACLE MEASUREMENTS

Date	Ref. No.	Coral species	Plate length (mm)	Plate width (mm)	Hole Length (mm)	Surface/ Hidden (*)
9.3.95	B16	?G.retiformis	4.5	2.5	13	S
	B17	?G.retiformis	4	2.5	16	S
	B18	?G.retiformis	4.5	3	12	S
	B19	?G.retiformis	4	2.5		S
	B20	?G.retiformis	2.5	1.5		S
	B21	?G.retiformis	1.5	1		S
19.3.95	B40	?G.retiformis	4.5	2.5	9.5	S
	B42	?G.retiformis	4	2.5	5	S
29.3.95	D13	G. retiformis	3		36	S
	D17	G. retiformis	3		10	H (~30)
	D20	G. retiformis	4.5		14	H
	D21	G. retiformis	3		7.5	S
	D22	G. retiformis	3.5		9	S
	D26	G. retiformis	3.5		25	H (10.5)
1.4.95	I2	G. retiformis	3		13	S
	M6	G. retiformis	5		24	H (20)
	N1	G. retiformis	5	3	8	S
	N10	G. retiformis	5	3	20	S
	N11	G. retiformis	4	2	8	S
	N12	G. retiformis	3.5	2	11	S
	N13	G. retiformis	4	2.5	12	S
	N14	G. retiformis	5.5	3.5	20.5	S
	N15	G. retiformis	4	2.5	10	S
	N16	G. retiformis	3	1.5	3	S
	N17	G. retiformis	4	2.5	8	S
	N18	G. retiformis	4	2	4	S
	N19	G. retiformis	3.5	2.5	7	S
	N20	G. retiformis	6	4	22	S
	N21	G. retiformis	5	3	13	S
	N22	G. retiformis	4.5	2.5	10	S
	N24	G. retiformis	4	2	9.5	S
	N25	G. retiformis	5	3.5	34	S
	N26	G. retiformis	4.5	2.5	16	S
	N27	G. retiformis	2.5	1.5	4	S
	N28	G. retiformis	3.5		20	H (6)
	N29	G. retiformis	5	3	18	S
	N2a	G. retiformis	4	2.5	12	H (3)
	N2b	G. retiformis	4	3	16	H (9)
	N3	G. retiformis	2.5		6.5	S
	N30	G. retiformis	5	2	16	H (4)
	N31	G. retiformis	5	3	13	S
	N32	G. retiformis	4.5	2.5	19	S
	N33	G. retiformis	3.5	2.5	6	S
	N34	G. retiformis	4.5	3	14	S
	N35	G. retiformis	3.5	2	7	S
1.4.95	N36	G. retiformis	5.5	4	33	S
	N37	G. retiformis	4	2	11	S
	N38	G. retiformis	4	2.5	10	S
	N39	G. retiformis	5	3.5	34	S
	N4	G. retiformis	2.5		7	S
	N40	G. retiformis	3.5	2	6	S
	N42	G. retiformis	4.5	2.5	10	S
	N43	G. retiformis	5	3	14	S
	N44	G. retiformis	5	4	24	S
	N45	G. retiformis	4	2.5	10	S
	N46	G. retiformis	5	3	30	S
	N47	G. retiformis	4	2	29	H (7)
	N48	G. retiformis	5	3	15	S
	N49	G. retiformis	5	3.5	20	S
	N5	G. retiformis	5	3	18	S
	N50	G. retiformis	5	3	14	S
	N52	G. retiformis	5	3.5	11	S
	N53	G. retiformis	4	2	7	H (10)
	N54	G. retiformis	4	2	8	S
	N55	G. retiformis	4	2.5	12	S
	N56	G. retiformis	4	2.5	11.5	H (8)
	N59	G. retiformis	5	3.5	30	S
	N6	G. retiformis	4		33	H (13)
	N62	G. retiformis	?	2	7	S
	N63	G. retiformis	4.5	2.5	9	S
	N64	G. retiformis	4	2.5	12	S
	N65	G. retiformis	5	3	10	S
	N66	G. retiformis	4.5	3	15	S
	N67	G. retiformis	5	3.5	20	S
	N68	G. retiformis	4	2.5	13	S
	N7	G. retiformis	4.5	2.5	9	S
	N8	G. retiformis	4	2	6	S
	N9	G. retiformis	4	2.5	7	S
	Q10a	G. retiformis	3.5		9	H (38)
	Q10b	G. retiformis	4		31	H (17.5)
	Q10c	G. retiformis	4		28+	H (14)
	Q20	G. retiformis	5.5			H (15)
	R22	Platygyra	5.5	3	9	S
	R24	Platygyra	6.5	4	14	S
		mean>	4.000	2.500	13.369	
		st dev>	0.905	0.618	7.379	
		n>	45	35	42	

* = distance below surface

Hapalocarcinid crab data - borehole measurements and densities

Hole width (mm)	Hole length males (mm)	Hole length females (mm)
1.5	2.5	
2	5.5	
2	4	
2	6	
2	4	
2	6	
2.3	6	
2.5		6
2.5		10.5
3	12	
3	20	
3		9.5
3		10
3		19
3.5	12.5	
4	9	
4	9	
4		15
4		34
4		17
4		14
4.5		27
4.5		24
4.5		25
5		25
5		60
mean>	8.04	21.143
stdev>	4.89	13.757

Area sampled (cm2)	No. of holes	No. per sq. m	Hole diameters (mm)							
56	1	179	3							
64	1	156	4							
38	0	0								
62	3	484	4	3	2					
84	2	238	2	4						
96	3	313	4	4	3					
68	7	1029	3	2	3	3	4	2	4	
50	2	400	4	2						
132	5	379	3	3	3	4	4			
60	1	167	3							
118	8	678	3	3	4	4	4	3	5	4
132	4	303	3	4	4	5				
45	4	889	4	4	2	3				
25	0	0								
32	0	0								
162	2	123	5	4						

Notes:

Total of 1224cm2 surveyed; 43 boreholes counted. This is equivalent to 351 boreholes / m2

Mean number of boreholes / m2 = 334 (st dev = 306.8, n = 16)

Mean diameter of boreholes = 3.75 (st dev = 0.89, n = 43)

Upogebia borehole densities

No. of holes per 1000cm^2
5
4
6
6
18
7
10
8
11
7
6
6
10
9
6
4
7
4
9

Note: Counts done in 10x100cm band transects
on mid-reef pavement
Three surface holes = one subsurface boring system
so this represents 75.3 holes/m^2 or 25.1 borings/m^2

mean density = 7.53 per 1000cm^2
(st. dev. = 3.29, n = 19)

Date	Ref. No.	Hole diam. (mm)	Hole Length (mm)	Animal Length (mm)	Notes on animal	Lining?	Raised lump at surface?	Coral species	Estimated volume (Pi r2 L)
3.3.95	A3	2.3	6	~4.5	male**	?Y	N	Goniastrea retiformis	25
	A4**	2	6		male**	?	Y	Goniastrea retiformis	19
	A5**	4	14		no animal	Y(top)	Y	Goniastrea retiformis	176
	A6**	2.5		3.5	male**		N	Goniastrea retiformis	
	A7**	2.5	6	5	female**			Goniastrea retiformis	29
	A8**	2.5	12		no animal	Y	Y	Goniastrea retiformis	59
	A9**	4	15	9	gravid female (?**)	Y(top)	Y	Goniastrea retiformis	188
	A10	2	4		male**			Goniastrea retiformis	13
	A11	4	13		no animal	Y(top)	N	Goniastrea retiformis	163
	A12**	4	34	10	gravid female **	Y(top)	Y	Goniastrea retiformis	427
	A13	3	20	4.5	male		Y	Goniastrea retiformis	141
	A14**	4	17	10	gravid female (?**)	Y	Y	Goniastrea retiformis	214
4.3.95	A15	~3	~9.5	6.5	female**		Y	Goniastrea retiformis	
	A16	~2	~6		male**		N	Goniastrea retiformis	
	A17	2	5		no animal		N	Goniastrea retiformis	16
	A19	3	10	9	gravid female**		Y	Goniastrea retiformis	71
	A24**	2	4	4	male**	Y(top)		Goniastrea retiformis	13
	A28	1.5	2.5	2.5	male		Y	Goniastrea retiformis	4
8.3.96	B5**	3.5	27		damaged**	Y	Y		260
	B8**	3.5	12.5	5	male**				120
1.4.95	G1	5	25		gravid female	?		Platygyra sinensis	491
	G4	2.5			male			Platygyra sinensis	
	I1	3	19	7	female	Y	Y	Goniastrea retiformis	134
4.4.95	M5	2.5	10.5		gravid female			Goniastrea aspera	52
8.4.95	Q9	3.5	61		female	Y		Goniastrea retiformis	587
	Q11	4	31		no animal			Goniastrea retiformis	389
10.4.95	R7	5	60	13	female	?N		Platygyra sinensis	1178
	R11	4.5	27	~10	female	?N		Platygyra sinensis	429
	R6	4.5	24	~11.5	female	?N		Platygyra sinensis	382
	R5	4.5	22		no animal	?N		Platygyra sinensis	350
	R4	4.5	25	~10	female	?N		Platygyra sinensis	397
	R3	2.5	5		no animal	?N		Platygyra sinensis	25
	R1	3	10		no animal	?N		Platygyra sinensis	71
	R2	3.5	13		no animal	?N		Platygyra sinensis	125
	R8	4.5	32		no animal	?N		Platygyra sinensis	509
	R17	4	14	9	female	?N		Platygyra sinensis	176
	R15	5	32			?N		Platygyra sinensis	628
	R16	4	9	6.5	male	?N		Platygyra sinensis	113
	R9	4.5	14		no animal	?N		Platygyra sinensis	223
	R10	3.5	10.5		no animal	?N		Platygyra sinensis	101
	R26	4	10.5		no animal	?N		Platygyra sinensis	132
	R18	3.75	9		no animal	?N		Platygyra sinensis	99
	R27	4	9	6	male	?N		Platygyra sinensis	113
	R20	4.5	21		no animal	?N		Platygyra sinensis	334
	R19	4.5	23.5	~9	damaged	?N		Platygyra sinensis	374
	R21	5	24	carap 5	damaged	?N		Platygyra sinensis	471
	R13	5	38		no animal	?N		Platygyra sinensis	746
	R12	4	13		no animal	?N		Platygyra sinensis	163
	R14	2.75	8		no animal	?N		Platygyra sinensis	47
12.4.95	N3	2.5	6.5	?	**			Goniastrea retiformis	32
	N4	2.5	7		no animal			Goniastrea retiformis	34
	N69	2.5	21				Y	Goniastrea retiformis	103
	N41	2	7		no animal		N	Goniastrea retiformis	22
	N51	3	>19		no animal			Goniastrea retiformis	
	N57	4	38		no animal		Y	Goniastrea retiformis	477
	N58	3	12	4	male			Goniastrea retiformis	85
	N60	2	5.5	3	male			Goniastrea retiformis	17
	N61	2.75	9		no animal	Y		Goniastrea retiformis	53
n = 58	mean>	3.43	17.25		33/58 occupied			mean>	219
	stdev>	0.98	12.78		14 males			stdev>	231.1
					15 females (of which 6 gravid)			n>	53
					4 unsure (damaged)				

Notes:

* all borings had entrances in live coral, except Q9 (emerged into a live patch but there was a small dead halo just around the entrance (this also seen in A3, A11,B8)

* all coral samples from outer reef zone

* holes seem to be from all orientations (NSEW) but mainly on vertical surfaces

*algal layer in coral often intense around borehole entrance

** = collected

SEXUAL DIMORPHISM OF HAPALOCARCINIDS AND THEIR BOREHOLES

The hapalocarcinid crabs seen in Phuket corals show distinct sexual dimorphism. The smaller males are squat, about as long as they are wide with quite large back legs. The females are similar but have smaller back legs and a much longer abdomen which is almost as long as the carapace when curled under the body. The females were often seen carrying an egg mass in their curled abdomen (Plate 2.3a). There is only ever one animal per hole, the females generally living in longer holes than the males (Fig. A). Occupancy is about 57% in the holes studied; 33 out of 58 contained crabs. Of these four were too damaged to identify, 14 were males and 15 were females; six of these females were carrying eggs. Females' boreholes were generally longer and wider than those of the males (Fig. A, Appendix D). This would imply either that females live longer or that they pass their holes on more often than males.

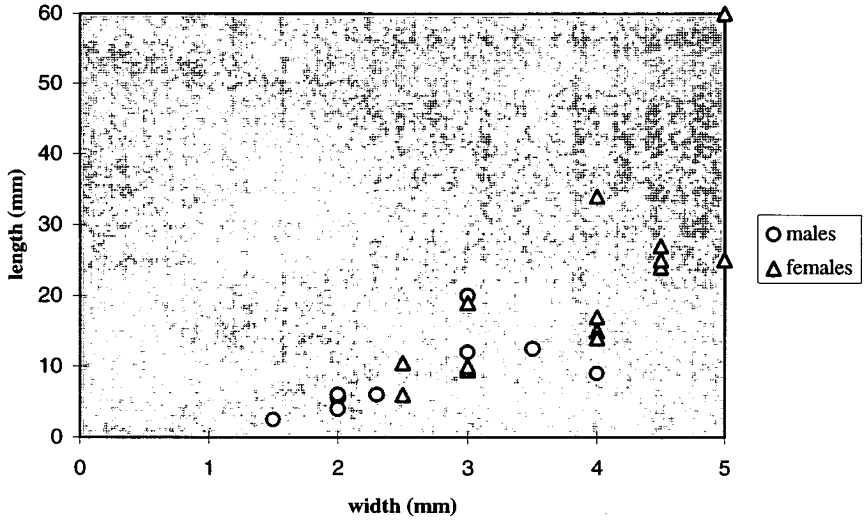


Figure A Dimorphism in borehole structure between male and female hapalocarcinid boreholes

Many questions are raised about the biology of these crabs. At what stage of its life cycle (larva, subadult, adult) does the crab settle and form a new hole? Does a hole get passed from one generation to the next when the occupant dies? The female carries eggs, but what life stage hatches from them and how long do they remain in the hole with the female? Does the crab ever emerge form its hole? All these fascinating questions are outside the remit if this study but will hopefully be answered by future biological investigations.

Bioerosion by *Lithophaga*

In the course of this fieldwork, measurements were taken of another, non-crustacean, bioeroder on Tin Smelter Reef. *Lithophaga* bivalves (various species) are very common, especially in the central dead areas of coral colonies in the outer and mid reef. Densities of the characteristic dumbbell-shaped borehole entrances were estimated at nearly 800/m^2 on dead *G. retiformis* on the outer reef (250 boreholes counted in the 3130cm^2 surveyed; see Table below). *Lithophaga* species that bored live coral were also seen. The length of the borehole entrance ranged from 1.5mm to 20mm and the width from 1.5 to 9mm. Of the *Lithophaga* boreholes measured from split coral samples, the borehole length ranged from 8mm to 108mm and width from 2.5mm to 20mm. These measurements do not distinguish between different *Lithophaga* species. The amount of carbonate removed as a result of *Lithophaga* activity was calculated by estimating the average volume of a borehole and multiplying this figure by the density of 800/m^2. Raw data are in the Table below.

Calculation:

- from density counts, mean entrance length = 9.7mm
- from size measurements, mean ratio of borehole length to entrance length = 5.89
  - so mean borehole length is 57.13mm
  mean ratio of borehole length to width = 4.3
  - so mean borehole width is 13.3mm
- taking the mean volume of a borehole to approximate 2/3 of a cylinder, using a length of 57.13mm and a radius of 6.65mm, the average borehole volume is 5291mm^3.
- at a density of 800/m^2 this represents 4233cm^3 carbonate removed per m^2 of dead substrate
- The average length of a *Lithophaga* boring the top of a dead *G. retiformis* coral on the outer reef is 5.71cm (Table below). As *G. retiformis* grows upwards at a rate of 1.85cm/year, holes of this size are a maximum of 3.1 years old.
- 4233cm^3/m^2 (actual area) dead *G. retiformis* are removed by this bivalve over this 3.1 year period, giving a rate of 1365cm^3/m^2/year (actual area) or 2061cm^3/m^2/year (plan area)(actual: plan = 1.51 for the outer reef; Appendix A). These figures are equivalent to 1570g/m^2 (actual)/year or 2370g/m^2(plan)/year, using the coral density value of 1.15g/cm^3 for *G. retiformis*.

Tin Smelter Reef progrades seawards at a rate of 4cm a year (Tudhope and Scoffin 1994); the outer metre of reef therefore represents 25 years of growth. Given that the reef front is approximately 400m long and that dead *G. retiformis* makes up 35.2% of the substrate, this means that in the outer 1m band there is 212.6m^2 dead *G. retiformis*. If *Lithophaga* removes 2061cm^3/m^2(plan)/year, over 25 years approximately 11m^3 of substrate will be removed from the reef edge by these bivalves' activities over this time.

LITHOPHAGA BOREHOLE MEASUREMENTS

Sample ref. no.	Shell width (mm)	Shell length (mm)	Width of entrance hole (mm)	Length of entrance hole (mm)	Borehole width (mm)	Borehole length (mm)	Dead or Live coral	Coral species	Ratio of hole L: entrance L	Ratio of hole L: hole width
A1	8	31	2.5	10	9	42	D	*G. retiformis*	4.20	4.67
A27	12	42	5	11	13	~72	L	*G. retiformis*		
C2				7.5	11	~40	D	*G. retiformis*	5.33	3.64
C4	8	28	2.5	4	9	33	D	*G. retiformis*	8.25	3.67
B2	9.5	39		6 to 18		?58	D	*G. retiformis*		
B10					6	26	D	*G. retiformis*		4.33
B11	10	34			10	48+	D	*G. retiformis*		
B12					16	~65	D	*G. retiformis*		4.06
B22	9	34		~10	9	56	D	*G. retiformis*	5.60	6.22
B24	7	28	2.5	6	8	43	D	*G. retiformis*	7.17	5.38
B29	?7	18			?4.5	30	?D	*G. retiformis*		6.67
B30	5.5	~20	2.5	5		32	D	*G. retiformis*	6.40	
B31	9	33	5	5	9.5	44	D	*G. retiformis*	8.80	4.63
B34	4.2	12			4.2	16	?D	*G. retiformis*		3.81
B37	4	14	1.5	2	5	18	L	*G. retiformis*		
B39	5.5	16		~3	6	21	D	*G. retiformis*	7.00	3.50
B41	7	20	3.5	4.5	8	27	D	*G. retiformis*	6.00	3.38
D2	9.5	25			11	43	D	*G. retiformis*		3.91
D3	11				11.5	54+	D	*G. retiformis*		
D4					11.5	45	D	*G. retiformis*		3.91
D5					15	62+	D	*G. retiformis*		
D9					12	52	D	*G. retiformis*		4.33
D16	5	23	3	9	6	34	D	*G. retiformis*	3.78	5.67
D18	15	49	5	14	15	67	D	*G. retiformis*	4.79	4.47
D23	~5		3	4	5	16	D	*G. retiformis*	4.00	3.20
D24	5	18	2	4	5.5	18	D	*G. retiformis*	4.50	3.27
D25	4	13	2.5	3	4.5	15	D	*G. retiformis*	5.00	3.33
D27	9	28.5	3	8	9	38	D	*G. retiformis*	4.75	4.22
D28	6	19		3.5	6	29	D	*G. retiformis*	8.29	4.83
D29	12	41.5	3.5	10.5	12.5	54.5	D	*G. retiformis*	5.19	4.36
D30	8.5	29			8.5	36	D	*G. retiformis*		4.24
D31	8	25	2	5.5	~8	34	D	*G. retiformis*	6.18	4.25
D14	11	37.5	5	10		51+	D	*G. retiformis*		
D35	13.5	35.5	6	14	15	68	D	*G. retiformis*	4.86	4.53
D36	12	45	5.5	13	13	61	D	*G. retiformis*	4.69	4.69
D37	9	28.5	3.5	7	9.5	40	D	*G. retiformis*	5.71	4.21
D32	13	43	5.5	12	13	60	D	*G. retiformis*	5.00	4.62
D33			4	9	8.5	31	D	*G. retiformis*	3.44	3.65
D34			9	11	11	33	D	*G. retiformis*	3.00	3.00
Dx					8	28		*G. retiformis*		
D38	10	10	3.5	8	10.5	38.5+	?D	*G. retiformis*		
D39					15	59	?D	*G. retiformis*		3.93
D41					14	52	D	*G. retiformis*		3.71
E2	10	36			10.5	50	D	*G. retiformis*		4.76
E3	5	19.5	3	4	6.5	?23	D	*G. retiformis*	5.75	3.54
E4	9.5	38			10.5	49	D	*G. retiformis*		4.67
E5	7	26	2.5	4.5	7	36.5	D	*G. retiformis*	8.11	5.21
E6	7	29	2.5	6	7.5	42	D	*G. retiformis*	7.00	5.60
E7	9	32	3	6	9	47.5	D	*G. retiformis*	7.92	5.28
E8			5	9	13	54	D	*G. retiformis*	6.00	4.15
E9					10.5	53		*G. retiformis*		
E10	?9.5	34	3	7.5	?8.5	49	D	*G. retiformis*	6.53	5.76
E11	12	41			13	55	D	*G. retiformis*		4.23
F1	11.5	37.5	4	9	12	52	D	*G. retiformis*	5.78	4.33
F2	11	33.5	3.5	7.5	12.5	~48	D	*G. retiformis*	6.40	3.84
F3	11	33	3.5	8	12	45	D	*G. retiformis*		
G2	14	43	5.5	10	15	55	L	*Platygyra sp.*		
G3	?5.5	18	2	2.5	?5	28	?L	*Platygyra sp.*		
H1	16	52	5	12	17.5	65+	L	*G. retiformis*		
H2	6	20			6.5	~23		*G. retiformis*		
H3	7.5	24	2	4	8.5	30	D	*G. retiformis*	7.50	3.53
J2			3	7	10	45	D	*G. retiformis*	6.43	4.50
J3	9	33			9	61	D	*G. retiformis*		6.78
J4					6	20	D	*G. retiformis*		3.33
J5	12	43					D	*G. retiformis*		
J6	8	33	2	4	9	42	D	*G. retiformis*	10.50	4.67
J7	2.5	6.5		1.5	2.5	8	D	*G. retiformis*	5.33	3.20

Table of *Lithophaga* borehole measurements continued...

Sample ref. no.	Shell width (mm)	Shell length (mm)	Width of entrance hole (mm)	Length of entrance hole (mm)	Borehole width (mm)	Borehole length (mm)	Dead or Live coral	Coral species	Ratio of hole L: entrance L	Ratio of hole L: hole width
J8	11	33			11.5	48	D	*G. retiformis*		4.17
J9	8.5	22	3	8.5	9.5	40	D	*G. retiformis*	4.71	4.21
J11	10.5	33	3	8.5	11	44	L	*G. retiformis*		
J12	13	39	4	9	13	65	D	*G. retiformis*	7.22	5.00
J13	12	34	4	8	13	48	D	*G. retiformis*	6.00	3.69
J14	?8.5	22.5	2.5	4	?8	32	D	*G. retiformis*	8.00	4.00
J15	11	32	4	7	12	44	D	*G. retiformis*	6.29	3.67
J16	12	41	3.5	8	13.5	55	D	*G. retiformis*	6.88	4.07
J17	11	36			11.5	45+	?	*G. retiformis*		
J18	10	31			10.5	41+	?	*G. retiformis*		
K1	9.5	29.5	3.5	9	10.5	52 (+12?)	L	*G. aspera*		
K2	10	29.5	3	8.5	10.5	38	L	*G. aspera*	4.47	3.62
K3			4	4.5	7	23	D	*G. aspera*	5.11	3.29
K5					10.5	34.5	D	*G. aspera*		3.29
L1	10	~29	4	9	12.5	35	L	*G. aspera*		
L2	11	30	4	7	11	45	?L	*G. aspera*		
M1	9	27.5	3.5	8	10	36 (+8)	L	*G. aspera*		
M2	10	30	3.5	8	11.5	41 (+9)	L	*G. aspera*		
M3	10	30	2.5	7	10.5	37 (+10)	L	*G. aspera*		
M4	9.5	28	2.5	6.5	10	36 (+9)	L	*G. aspera*	6.92	4.50
Q3	16.5	66	?	15	17.5	108	D	*G. retiformis*	7.20	6.17
Q2	15	51	5	13	16.5	~44	D	*G. retiformis*	3.38	2.67
Q1	12	37	4	8.5	12	52	D	*G. retiformis*	6.12	4.33
Q4	16	49	5	15	17.5	77	D	*G. retiformis*	5.13	4.40
Q5	15	50.5	5.5	15.5	15.5	77	D	*G. retiformis*	4.97	4.97
Q6	14.5	45	5	10	15	72.5	D	*G. retiformis*	7.25	4.83
Q7	14.5	48	6	17.5	15.5	79	D	*G. retiformis*	4.51	5.10
Q8	12.5	39	5.5	?	?13.5	?50	D	*G. retiformis*		3.70
Qx	11.5	31	4	10	11.5	~53.5	D	*G. retiformis*	5.35	4.65
Q0			4.5	15	16	77	D	*G. retiformis*	5.13	4.81
Q12	17.5	59	6	~11	20	86	D	*G. retiformis*	7.82	4.30
Q13	11.5	39	4	9	12.5	54	D	*G. retiformis*	6.00	4.32
Q15	13.5	41	4	11	14	68	D	*G. retiformis*	6.18	4.86
Q16			6	7	9	32	D	*G. retiformis*	4.57	3.56
Q17	16.5	55	6	16	17	78.5	D	*G. retiformis*	4.91	4.62
Q18	13.5	40.5	5	13	15	58	D	*G. retiformis*	4.46	3.87
Q21	15	45	4.5	11	15.5	63	D	*G. retiformis*	5.73	4.06
Q22	12	39	5	12	13.5	58.5	D	*G. retiformis*	4.88	4.33
Q23	14	46	5.5	14	14.5	72	D	*G. retiformis*	5.14	4.97
Q24	12	38	3.5	9	13	51	D	*G. retiformis*	5.67	3.92
Q25	10	27			11.5	40	D	*G. retiformis*		3.48
Q26	9	33			10	40	D	*G. retiformis*		4.00
Q27	9	31.5			10	36	D	*G. retiformis*		3.60
Q28	9.5	39	~3	~7	10.5	53	D	*G. retiformis*	7.57	5.05
								mean	5.89	4.30
								st dev	1.44	0.80
								n	65.00	85.00
			9	17.5	20	108		**<maximum>**	10.50	6.78
			1.5	1.5	2.5	8		**<minimum>**	3.00	2.67

APPENDIX E Published paper

BIOTURBATION OF REEFAL SEDIMENTS BY CRUSTACEANS IN PHUKET, THAILAND

C. Bradshaw

Dept.of Geology and Geophysics, Edinburgh University, Edinburgh, EH9 3JW, UK. email: bradshaw@glg.ed.ac.uk

ABSTRACT

Tracer sediment, resin casting, airlift excavation and coring were used to investigate the nature and rates of bioturbation in muddy fringing reef sediments. Intertidal soldier crabs, burrowing cylindrical burrows, passively segregate the sediment to an average depth of 8cm at each daylight low tide; the turnover rate is 0.5 m^3/m^2/year, of which 29% is due to excavation and 71% due to feeding. Alpheid and callianassid shrimps form large burrows, to depths of 30 and >50cm respectively, with rates of turnover of 0.13 and 0.05m^3/m^2/year. Subtidally, there is tiering of the infauna with alpheids and callianassids comprising the deepest (>60cm) and most extensive tier. Turnover rates of 2.9×10^{-4} and 7.1×10^{-3} m^3/m^2/year were estimated for alpheids and callianassids respectively. The latter also sort the sediment during the course of feeding and/or excavating, burying coarse material in shelly pockets at depths of >30cm and expelling the <1mm fraction at the sediment surface. Prograding forereef sediments containing burrowing organisms in zones related to water depth will result in a shallowing upward succession of traces, with only the deepest tiers being represented. Storm deposits may show as coarse layers in the sediment depending on the frequency of storms and the density of burrowers.

INTRODUCTION

Through ingestion, defaecation, manipulation and displacement, organisms alter the sediments in which or on which they live. This bioturbation may be highly conspicuous in modern day reef settings as features such as burrow entrances and pellets on the sediment surface.

This study attempts to describe the biogenic features present not just at the sediment surface, but in the sediment itself, to characterise the infauna by their sedimentary traces and to ask three questions: a) would these traces be preserved in a fossil reef setting? If so, b) what would they look like? and c) what could they tell us about the original environment and the processes occurring at the time of preservation?

Infaunal animals produce various sedimentary effects which have been extensively studied in both tropical and temperate seas. Apart from the more obvious burrows and pellets, animals may either sort or mix grain sizes, stabilise or loosen the sediment (Bromley 1990) and through their bioturbation affect the preservation of grains in a variety of ways (see Scoffin 1992 for a review).

Of the bioturbators investigated in this paper, callianassid shrimps have received the most attention to date. Three common observations are i) the presence of mounds of fine sediment that has been ejected from the burrow, ii) underground networks of passageways and chambers, and iii) coarse material at the depth of the chambers burrow (eg. Shinn 1968, de Vaugelas 1984, Tudhope and Scoffin 1984). Suchanek (1985) categorised different species of thalassinids into three ecological groups based on their burrow structure which reflects their feeding method, and Griffis and Suchanek (1991) updated this classification to six major burrow groups. Nickell and Atkinson (1995) presented an alternative classification based on individual components of burrow morphology rather than the complete burrow.

Alpheid shrimps and their burrowing and sediment sorting effects have been studied by Shinn (1968) and Karplus et al (1974), and reviewed by Karplus (1987).

The island of Phuket (8°00'N 98°20'E) lies off the SW coast of peninsula Thailand, separated from the mainland by a large (1500km^2) and shallow muddy bay, Ao Phangnga. The climate of the area is monsoonal, with strong winds and rain (300mm/month) from the SW from May to October, and calm, dry weather from the NE for the other half of the year. The combination of monsoon direction and the presence of the turbid water body to the NE results in reefs on the east coast of Phuket being subjected to high sedimentation rates year round; reef growth is limited and the reef sediments are muddy. These muddy sediments are home to an abundant and diverse burrowing infauna, including crabs, shrimps, worms, fish, anemones and holothurians. Of these, the most conspicuous and active bioturbators are the crustaceans, especially alpheid and callianassid shrimps and soldier crabs (*Dotilla* sp).

Previous authors have noted the muddiness of the sediments in the area (eg. Carr et al 1991) and the forereef sediment's bioturbated nature (Tudhope and Scoffin 1994, Scoffin et al 1992). Other work has described the burrowing infauna of Phuket, but concentrated mainly on the distribution and ecology of various animal groups (eg. Chatananthewej and Bussawarit 1987, Frith et al 1976, Tantanasiriwong 1978).

In the SE of Phuket is Laem (Cape) Panwa which comprises a series of rocky headlands and bays. These bays contain sandy beaches, fringing reefs in various states of health and muddy subtidal sediments. One large bay (Ao Tang Khen) also has a large (0.5km^2) intertidal sand flat made up of sand waves (height 0.2 wavelength 40m) alternating with shallow sandy/rocky pools. This was the intertid study site for this work. Subtidal work was carried out at the tip of Laem Panwa, Pump House Bay. This tiny bay (150m long) contains a small reef which is n developed into a reef flat like those of Ao Tang Khen.

The area is tidal with the range of spring tides being up to 2.8m, and of neap tides little as 0.4m. Due to the shape of the coastline and the presence of nearby islan strong currents may develop around Pump House Bay, especially during spring tide

MATERIALS AND METHODS

All methods except airlifting were used both intertidally and subtidally.

The subtidal airlift is an adjustable length (up to approx. 2m) tough plastic tube diameter 5cm. Suction is achieved by air entering at the bottom from a standard 1 SCUBA cylinder expanding up the tube. Varying the airflow affects the power suction.

Polyester resin was mixed with catalyst in the ratio 200:1 to give a setting time between 30-45 minutes (depending on temperature). It was poured into the burro from a watering can, the position of the burrow labelled with a marker, and the c dug up by hand or airlift 24hrs later.

Two types of corer were used: stainless steel box cores (15x10x10cm) to descri bioturbated textures, and simple plastic core tubes (internal diameter 4.2cm, leng 135cm) with sharpened ends and fitted endpieces to collect sediments for grain si and carbonate analysis.

Tracer sediment was made by mixing six grain size fractions (63-125μm, 12 250μm, 250-710μm, 710m-2.36mm, >2.36mm, >5mm) with various colours fluorescent paint, oven drying and resieving them. Known amounts of a range fractions were placed on the sea bed or down burrows and their movement over few days traced using coring and airlifting and samples scanned with a hand held U light in a darkened room to estimate tracer abundance.

Observations and timings of animal activities were also done, including the marki of burrow entrances to time rates of movement.

Standard quadrat and transect methods were used to estimate animal abundances. Grain size analysis involved dry sieving the >500μm fraction and using a Coult LS100 Particle Size Analyser for the <500μm fraction.

RESULTS

1. Soldier crabs (*Dotilla* sp.)

Soldier crabs make vertical, cylindrical burrows on intertidal sand waves eve daylight low tide that the sand waves are exposed by a critical amount; suitable tid occur twice daily during spring tides and not at all during neaps. Within the first minutes after the tide has fallen low enough (less than 1.6 metres above lowest lo water), the crabs emerge from the sediment where they have been buried during hig tide, thus producing 5-20 large pellets (up to 1cm diameter). Crabs were found to present at densities which averaged 91/m^2 (st dev = 18.2, n = 31).

During the exposure of the sand waves the soldier crabs graze almost continually the surficial sediments, covering the surface with tiny feeding pellets (diameter 2mm), often arranged in lines radiating from the burrow entrance. They also enlarg their burrows (to an average depth of 81mm, st dev = 28.7, n = 27, and average wid 7.8mm, st dev = 3.0, n = 30), resulting a further 10 to 30 excavation pellets (Fig. An average of 1.74kg/m^2 (st dev = 0.52, n = 10) of pellets was produced over o tidal exposure (this figure is the total of feeding and excavation pellets). This equivalent to 1.4×10^{-3} m^3/m^2/tidal exposure. As the tide comes in, the crabs retre down their burrows, which are then filled in with sediment as the water covers them.

Using the above data, it was possible to calculate the total turnover rate 600kg/m^2/year or 0.5m^3/m^2/year (of which 29% is due to excavation, and 71% due feeding).

In the *Dotilla* area, sand wave sediment sampling to depths of 30cm (at which poi the sediment was impenetrable by manual coring due to large quantities of re debris) showed an increase in mean grain size with depth (Fig. 2a). Sortin decreased steadily with depth, from moderately well sorted in the top 8cm to ve poorly sorted at 30cm (Fig 2b).

2. Alpheid shrimps

Three species of alpheid shrimps were encountered:

i) intertidal: a small (4cm long) species, found in intertidal pools on the sand flats of Tang Khen Bay.

ii) subtidal near-reef: a small (5cm long) species in the coarse sediments close to the reef front, and

iii) subtidal off-reef: a large (7cm long) species in the sediments approximately 50m from the reef front.

All were commensal with gobiid fish. Collected shrimp and fish species are currently being identified.

The gobies are not involved in burrow excavation, but alpheids shovel sediment from depth to the sediment surface. From airlift excavation and tracer experiments this sediment appears to be mainly from new burrow entrances that are dug upwards from the deeper, more permanent part of the burrow. A new entrance is formed approximately every day, and the old one becomes disused and infilled. The alpheids were observed to be active only in the daytime, and the intertidal type also became inactive whenever low tides fell between about 10am and 4pm, presumably due to the heat.

The irregular burrow morphology of intertidal and near-reef alpheids seems to be determined by the presence of large pieces of reef debris, which are abundant in the sediments they inhabit. These burrows slope downwards at an angle of 30-45° to depths of 20-30cm, the level at which most of the sediment comprises cobble to boulder size reefal fragments. The alpheids also separate out coarse and fine grains at the surface, stacking coarse debris above the angled burrow entrance and piling fines to one side. The cut-off between coarse and fine grains is limited by the size of the shrimp. In contrast, off-reef alpheids living further from the reef in thicker sediments are not limited by buried reefal debris, and form spiral burrows reaching depths of at least 50cm. They do not sort grains, but simply pile sediment to one side of a shallow groove leading from the burrow entrance.

Burrow densities of 830/100m^2 and 13/100m^2 were found for intertidal and off-reef alpheids respectively.

Rates of turnover were calculated by estimating the volume of burrow moved each day (assuming the burrows to be cylindrical and have an average diameter of 2.3cm (st dev = 0.4, n = 19) for intertidal alpheids, and 1.75cm for off-reef alpheids); figures for these rates are given in Table 1.

In the intertidal pools, groups of shells from old alpheid burrow entrances create a patchy texture in the top few cm of sediment (Fig 3). The sediment in these pools is a maximum of about 20cm deep overlying solid coral rock, and this obviously limits burrowing depth. Excavation of subtidal areas showed old disused burrow branches leading off the open burrow. These were usually blocked off from the main burrow and filled with loose sediment from the surface. Grain size analysis indicated poorly sorted sediments throughout the cores taken in the area (Fig. 2b) and an increase in mean grain size to a maximum at 35cm and deeper (Fig 2a).

3. Callianassids

Callianassids feed on organic matter coating sediment grains (see Nickell and Atkinson 1995 for details of feeding mechanisms). These grains may fall into the burrow's crater-like entrance at the sediment surface or be excavated at depth during burrow construction. After feeding, fine grains (<2mm in the subtidal type, and <1mm in the intertidal type) are ejected by means of a water current produced by the shrimp, creating a mound at the surface.

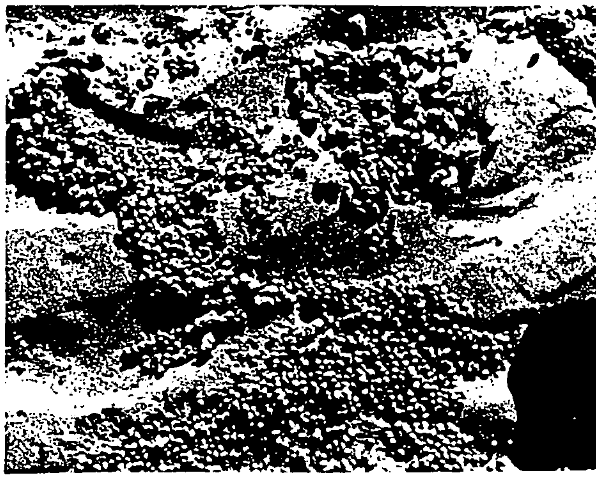


Fig. 1. *Dotilla* surface traces; burrow entrance and two types of pellets, larg excavation pellets and smaller and more numerous feeding pellets.

Resin casting and excavation showed that both intertidal and subtidal callian have a complex subsurface network of chambers and passages, linked to the s crater and mound. The vertical shaft leading down from the crater is perma open, whereas that below the mound is blocked when not in use. However, th several differences in structure (Fig. 1): this could be due to the shrimps different species (identification was not possible, due to a lack of success in ca the animals), or to differences in sediment type or in the nature of the interti subtidal habitat.

Intertidal callianassids create much larger burrows (eg. vertical shaft 4cm dia than subtidal ones (vertical shaft 1.5cm diameter), and their sediment mounc tend to be bigger (average mound diameter 23cm (st dev = 8.0, n = 30) compa average mound diameter 11.4cm (st dev= 3.2, n = 18) for intertidal calliana Distinct layers of smoothly lined chambers are found from sediment depths 30cm in the intertidal burrows. In contrast, the burrow complex of the s shrimps is more a branching network of smooth-walled tunnels and blind e Subtidal tracer sediment experiments indicated that grains >1mm in size are below in shelly pockets. These pockets are finger-like projections between 5 long and 1.0-1.5cm wide leading off the main burrow complex. They are with randomly orientated grains, and sometimes a high concentration of organic matter. A range of grain sizes (all sizes up to 1mm) is also incorporat the smooth lining of the burrow walls.

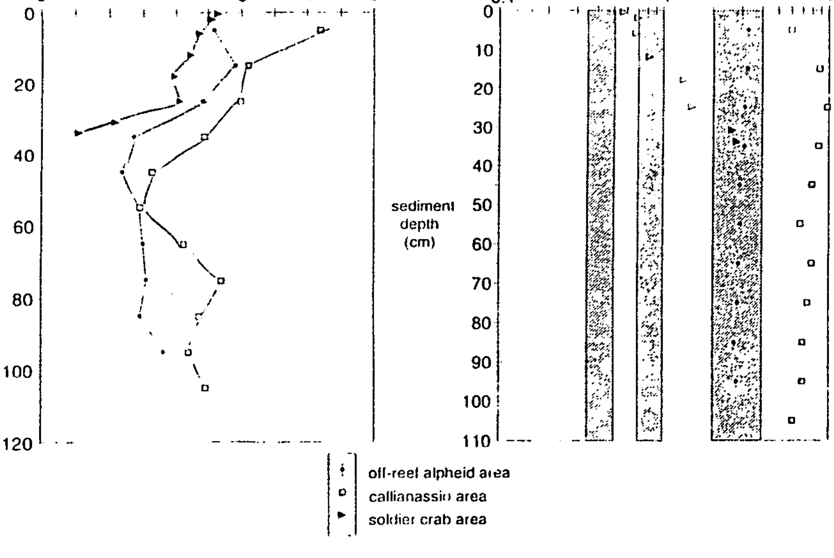


Fig. 2. Graphs of core data showing changes with depth in a grain size and b) sorting (for subtidal off-reef alpheid, s callianassid and *Dotilla* areas. The peak in mean grain siz subtidal areas is most probably a storm deposit from th storm. Poor sorting in the subtidal sediments indicates bioturbators have not had time and are not found in high densities to have completely reworked the sediment. In c on the intertidal sand waves, intensive burrowing by high d of soldier crabs acts together with wave action to s sediments.

Rates of sediment turnover were calculated on the basis of an average sized mound being produced every 2 days. Mound sizes were calculated using the formula "Volume = $\frac{1}{3}\pi r^2 h$", where r is the radius and h is the height, and averaged 786cm^3 (st dev = 758, n = 30) for intertidal mounds and 162cm^3 (st dev = 166, n = 15) for subtidal mounds. Callianassids were found in densities of 37/100m^2 (intertidal) and 24/100m^2 (subtidal). Rates of turnover are given in Table 1.

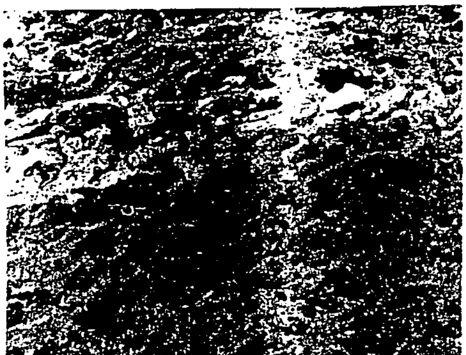


Fig. 3. Photo of surface texture produced by alpheid reworking (intertidal pool, Ao Tang Khen): note the clusters of shelly debris marking the entrances of current and disused burrows

In the subtidal callianassid area, old shafts were seen, shelly pockets were abundant branching off the burrow, and patches of coarse debris were also found outside the burrows in the surrounding sediment; these could be relict shelly pockets. A slight increase in mean grain size was seen at a depth of about 40-50cm (Fig. 2a) which corresponds with the depth of the shelly pockets, which may also be linked to a storm event (see discussion). The topmost sediment was not particularly well sorted, suggesting that the shrimps were either not abundant enough or had not inhabited the sediment for long enough to have a major sorting effect.

Tiering

Although callianassids and alpheids dominate their particular areas of the sea bed, many other infaunal organisms are present; total burrow densities of up to 350/m^2 were measured. Excavation reveals 'tiers' of burrowers (Ausich and Bottjer 1982): the uppermost tier consists of a rich meiofauna (mainly polychaetes and crustaceans; C. Meyer pers. comm. 1996) which make burrows in the order of 1mm diameter and reaching a maximum depth of 2-3cm. Below this, at about 10cm depth, is a layer of interlinked burrows (approx. 1cm diameter) made by crabs, upogebiid shrimps, echiurids, and other unseen animals. Cutting through all these are the deepest tiers, the alpheids or callianassids, with burrow structures reaching depths in excess of 60cm.

DISCUSSION

From the above observations of biogenic sediment sorting and burrow structure,it is possible to hypothesise on the appearance of the sediment fabrics, and to compare this with the actual fabrics found and described above. Explaining any discrepancies between the observed and expected appearances provides some insight into sedimentary processes occurring in the area. The relative importance of physical and biogenic processes in the preservation of trace fossils is also discussed, especially with reference to storm events.

Two processes must be taken into consideration; those that effect the appearance of present day sediments, and preservational effects that will alter this appearance as the sediments pass into the geological record.

Intertidal sand waves (*Dotilla* area):

Dotilla feed selectively on certain grain sizes (Vogel 1984), and this combined with their small size (and thus their inability to shift grains larger than a certain size) will result in "passive segregation" of the sediment; that is, coarse grains will become buried by the continual burrowing and feeding activity of the crabs.

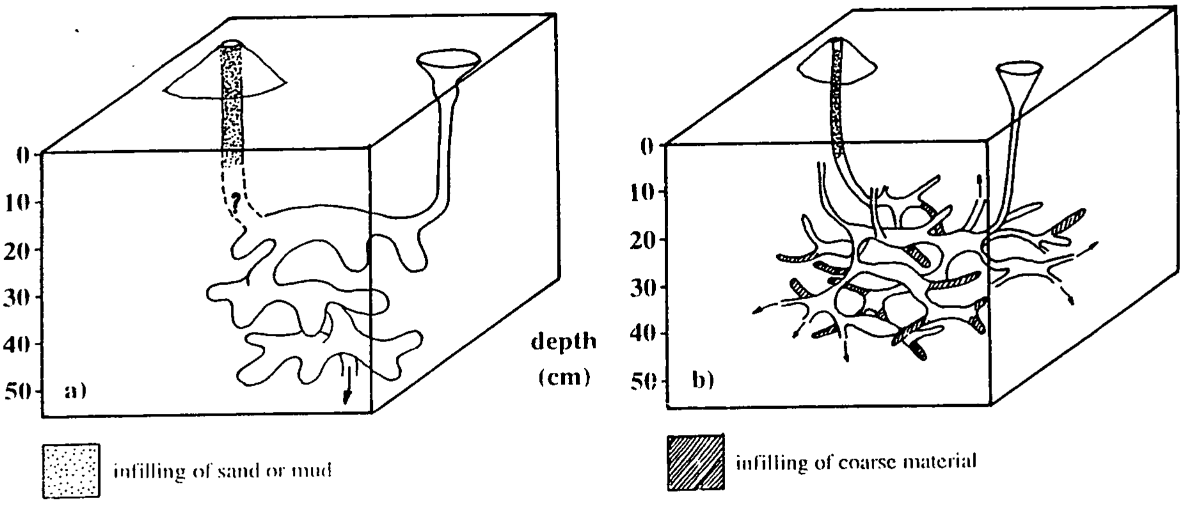


Fig. 4. 3-D block diagram to show the structures of a)intertidal and b)subtidal callianassid burrows. Note the differences in the wideness of burrow passageways, size and shape of chambers and presence of shelly pockets in the subtidal burrows. Both types have a mound and a crater at the sediment surface and reach to similar depths in the sediment

Table 1 Comparison of burrow density, turnover rate and depth of sediment working for *Dotilla*, alpheids and callianassids

Burrowing organism	Burrow density (number per 100m^2)	Turnover rate (m^3/m^2/yr)	(kg/m^2/yr)	Depth of sediment working (cm below sediment surface)
Dotilla	9100	0.5	600	average 8, max. 25
alpheid - intertidal	830	0.13	163	30
alpheid - subtidal off-reef	13	2.9×10^{-3}	0.48	>60
callianassid - intertidal	37	0.05	69	>50
callianassid - subtidal	24	7.1×10^{-3}	1.2	>60

Cores showed an increase in mean grain size and a decrease in sorting with depth (figs 2a and 2b) but the large tidal and wave effect in the intertidal zone will also have a major sorting effect. It is not known what proportion of the sorting is due to physical and biological causes, but wave and tide action probably acts with the biogenic activity to increase sorting in at least the upper few centimetres of sediment.

Alpheid area

In the absence of major physical disturbance, continual alpheid burrowing should produce a patchy, poorly sorted upper sediment layer with remnants of disused burrow branches, and (where intertidal and near-reef alpheids are present) patches of shells and reef debris which had been stacked at the burrow entrance but buried by subsequent digging activity. Below this, a relatively unbioturbated layer would be expected, where the deeper, more permanent parts of the burrow are. This might be characterised by infrequent and therefore distinctive burrows.

These features were observed in the sediments studied, but in addition there was a distinct coarse layer at sediment depths in excess of 35cm. This is probably due to storm deposition (see section below).

Subtidal callianassid area

The active sorting by these shrimps (burying large grains in shelly pockets at depth and ejecting fines at the surface) and passive burial of coarse material by the fine sediment mounds should result in a well-sorted upper layer with remnants of old vertical shafts to the depth at which the first subsurface chambers and shelly pockets occur, and below this a heavily burrowed coarser layer full of these chambers and pockets.

At sediment depths of 25-30cm and deeper, the sediment does have this heavily burrowed appearance, but upper layers are not well sorted. This may be due to tiering or storm effects, as discussed in the following sections.

Whatever the appearance of the modern sediments, preservational effects and rare events such as storms may change their ultimate appearance in the geological record:

Intertidal preservation

The intertidal environment is strongly affected by tide and wave action and has a low preservation potential due to its exposed nature. Even in calm weather, wave influence is obvious in the form of ripples on the sand surface. Tracer sediment placed on the surface was moved several metres laterally in a single spring tide, although it did not move more than a few millimetres vertically. This surface mobility suggests that biogenic structures in the top few millimetres to centimetres would be obscured by physical processes even under normal conditions. These structures include numerous tracks and trails caused by gastropods and crabs moving across the sand surface, resting traces such as those made by starfish, escape traces such as chimney-like structures made by rapidly burrowing soldier crabs, and worm casts, as well as the *Dotilla* pellets described above. Only rapid burial with large quantities of sediment would preserve the *Dotilla* burrows and surface traces and also create a contrasting infill to the burrows which would ease identification in the rock record.

Aerobic haloes are found immediately surrounding the burrows: this might be seen in the deeper reaches of the deepest burrows (which penetrate up to 20cm) as differentially preserved sediments.

Subtidal preservation and the influence of storms

The subtidal environment has a higher preservation potential than the intertidal, but in such shallow water (<10m) wave action during storms has a major effect, and will substantially reduce the likelihood of preservation.

Severe storm damage is rare in these study areas; Phuket is not in the hurricane b and the E (Ao Tang Khen) or SE (Pump House Bay) aspect of the bays usua shelter them from rough weather. However, in May 1986 a storm hit Pump Ho Bay, almost completely destroying the reef (live coral cover was reduced to a corals in the deepest part of the reef (Phongsuwan 1991)). A large amount of the r ended up on the beach as heaped coral rubble, much of which remains to this d Branching coral debris was also found on the seabed at the seaward edge of the r in 1995. Such a storm, with force that could destroy a reef to a water depth of undoubtedly had a major effect on the reef sediments, not only through physi disturbance but through input of reef material (Fig 5).

Two years after the storm, the off-reef sediments at Pump House Bay were samp and the surface found to be sandy and rippled, with the <63μm fraction compris 1% by weight, and with few obvious burrows (Scoffin et al 1992; note, their Sh Point is the same as Pump House Bay in this paper). In contrast, in 1995, the surf sediments consisted of about 40% <63μm fraction and large numbers of burrow were present. Cores and airlift excavation done in these sediments showed a coa layer, most likely the result of the 1986 storm; the mean grain size and percent gravel (>2mm) fraction peaked at a depth of 30-40cm 40m from the reef front wh off-reef alpheids were numerous, and 40-50cm 50m from the reef front wh callianassids were abundant (Fig 3a). The coarse (>4mm) fraction compri between 50-75% reef-derived remains, such as coral, barnacles and encrust bivalves, a large part of which was probably laid down during the storm. The was infaunal remains such as mollusc shells and echinoderm tests.

It would seem that the muddy nature of the sediments seen in 1995 has come ab since August 1988 when they were analysed by Scoffin et al (1992), and represen return to pre-storm conditions due to the redeposition of fine sediment from surrounding muddy water (see Fig 5).

These physical influences on the sediment (the 1986 storm causing a removal of top layer, followed by an increase in fine sediment deposition) may be respons for the appearance of the sediments in 1995, that is, a layer of coarser material increasing depth in the sediment moving offshore) covered with a layer of finer s and mud which increases in thickness with distance from the reef and increa water depth. The patchy coarse fabrics seen at depth in the Phuket sediments represent tubular tempestites, formed by coarse material filling the deeper reache the burrows during the storm (Wanless et al 1988, Tedesco and Wanless 1991). sediment appearance is similar in the alpheid and callianassid areas, despite different biogenic effects these two animals have on the sediment. The densitie the burrowers, and the short time period (6.5 years maximum) they have working the sediment may not be enough to have had a significant effect on the g size distribution. However, even if sediment textures are not characteristic of modern burrowing fauna, the burrow~~s~~ traces themselves are, and these are used in sediment preservation models put forward below.

Preservation of tiering

Differing levels of deposition and erosion in bioturbated areas will result in diffe ichnofabrics, as discussed by many authors including Ekdale et al (1986).

In an environment of continual slow deposition of sediment all tiers will keep up the sediment surface, the deepest tier's structures replacing those of the tiers were above (Bromley 1990). The eventual texture will be one comprised solel the deepest part of the deepest tier (callianassid or alpheid depending on dist from the reef front); upper tiers will be completely reworked. For example, in callianassid area, the texture will be one of branching tubes and finger-like sh pockets bounded by walls with smooth interiors, with patches of coarse material found outside the burrow walls.

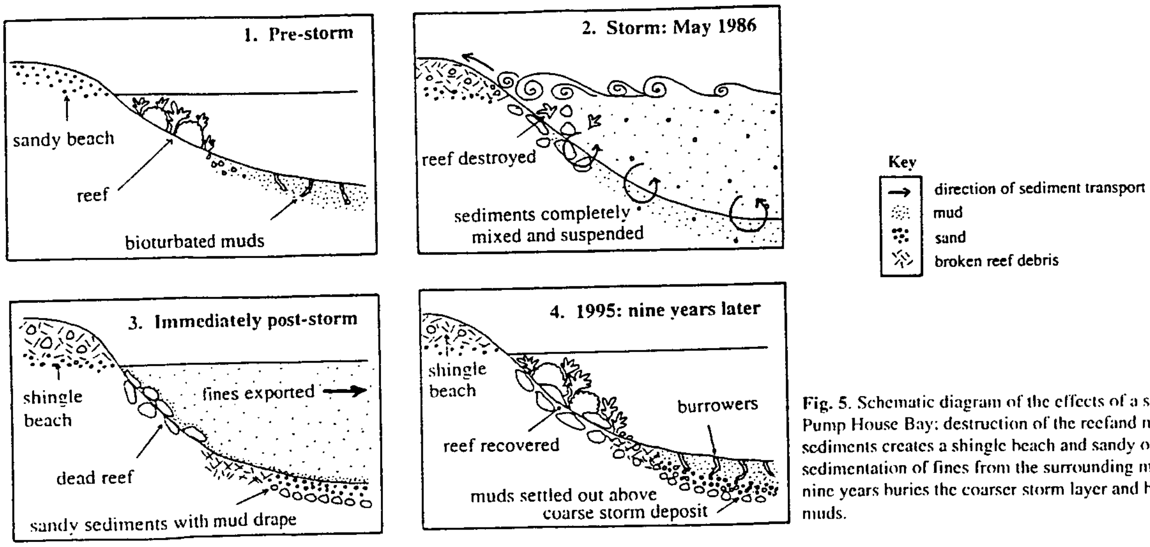


Fig. 5. Schematic diagram of the effects of a storm on the sediments Pump House Bay; destruction of the reefand mixing and removal of sediments creates a shingle beach and sandy off-reef sediments. How sedimentation of fines from the surrounding muddy water over the ne nine years buries the coarser storm layer and burrowers recolonise th muds.

With a sudden large deposition of sediment, thicker than the depth of the callianassid tier, it is likely that the original fauna will be killed and recolonisation of the new sediment surface will take place. Due to the depth of sediment deposited, the new callianassid tier will not penetrate far enough to rework the original upper meiofaunal tier, and all original tiers will therefore be preserved, unless there has been post-depositional erosion. The resulting ichnofabric will show two sets of tiers, one above the other, separated by a layer of unbioturbated sediment, which might show features of the event that caused the sedimentation, for example storm deposits.

Intermediate levels of deposition would result in varying amounts of the upper tiers being preserved, showing as traces cross-cut by the new deep tier. The formation of escape traces to keep up with fast sedimentation is not discussed here; although their formation is likely under certain conditions, subsequent reworking during periods of slower sedimentation will probably obscure them.

Prograding reef sediments

The crustaceans studied in this paper are found in mutually exclusive zones moving seawards (eg. near-reef alpheids, off-reef alpheids, callianassids), and are probably limited in their distribution by the nature of the sediment texture , which varies with distance from the reef front. A prograding reef and sediment slope will lead to the formation of a shallowing upward succession, from beach sediments through coral reef to sediments characterised by alpheid and then callianassid traces (Fig. 6). These different zones of sediment should be recognisable by their biogenic features as described in the section above. Storm events may also be recognised in the sedimentary record by changes in sediment texture (mean grain size and sorting) and by the distribution of trace fossils, assuming enough time elapses between major storm events for the burrowing fauna to reestablish itself and to thoroughly rework the sediment.

Summary of main conclusions

1. Burrows of *Dotilla* soldier crabs, alpheid and callinassid shrimps are characteristic of their makers, and of specific areas of sediment (intertidal sand waves, near-reef and off-reef sediments) in modern reef sediments in Phuket.
2. Over a geological timescale, a prograding reef slope will preserve these deepest tier burrows as a shallowing upward succession of trace fossils.
3. Given high enough densities of animals and adequate time, the sediment texture will also be affected by bioturbation.
4. However, events such as a storm in 1986 have prevented complete reworking and left a storm deposit in the subtidal sediments described.

ACKNOWLEDGEMENTS

I thank Terry Scoffin and Sandy Tudhope for constructive discussion at all stages this project. Phuket Marine Biological Center for enabling me to stay and work Thailand, and Jason Shepherd for invaluable field assistance.This work was fund by the Natural Environment Research Council of Britain.

REFERENCES

Ausich W I, Bottjer D J (1982) Tiering in suspension-feeding communities on sof substrata throughout the Phanerozoic. Science 216:173-174

Bromley RG (1990) Trace Fossils:Biology and Taphonomy. Unwin Hyman London 280pp

Carr D J et al (1991) Grain size, calcium carbonate content and accumulation rates of Recent sediments in Phangnga Bay, South Thailand. Phuket Mar Biol Cent Re Bull 55:77-96

Chatananthawej B and Bussawarit S (1987) Quantitative survey of the macrobenth fauna along the west coast of Thailand and the Andaman Sea. Phuket Mar Biol Cent Res Bull 47:23pp

Frith DW, Tantanasiriwong R and Bhatia O (1976) Zonation of macrofauna on a mangrove shore, Phuket Island. Phuket Mar Biol Cent Res Bull. 10:37pp

Ekdale AA, Bromley RG, Pemberton SG (1986) Chapter 8 Trace fossils as indicators of sedimentologic processes, pp 88-96 in Ichnology: Trace fossils in sedimentology and stratigraphy. SEPM Short Course No. 15 Tulsa Oklahoma.

Griffis RB, Suchanek TH (1991) A model of burrow architecture and trophic mod in thalassinidean shrimp (Decapoda:Thalassinidea). Mar Ecol Prog .Ser 79:171-183

Karplus I, Szlep R, Tsurnamal M (1974) The burrows of alpheid shrimps associate with gobiids in the Northern Red Sea Mar Biol 24:259-68

Karplus I (1987) The association between gobiid fishes and burrowing alpheids. Mar Biol Ann Rev 25:507-562

Nickell LA, Atkinson RJA (1995) Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. Mar Ecol Prog Ser 128:181-197

Phongsuwan N (1991) Recolonization of a coral reef damaged by a storm on Phuk Island, Thailand. Phuket Mar Biol Cent Res Bull 56:75-83

Scoffin TP (1992) Taphonomy of coral reefs: a review. Coral Reefs 11:57-77

Scoffin TP, Tudhope AW, Brown BE, Chansang H and Cheeney RF 1992) Pattern and possible environmental controls of skeletogenesis of *Porites lutea*. South Thailand. Coral Reefs 11:1-11

Shinn EA (1968) Burrowing in the Recent lime sediments of Florida and the Bahamas. J.Palaeo 42:879-894

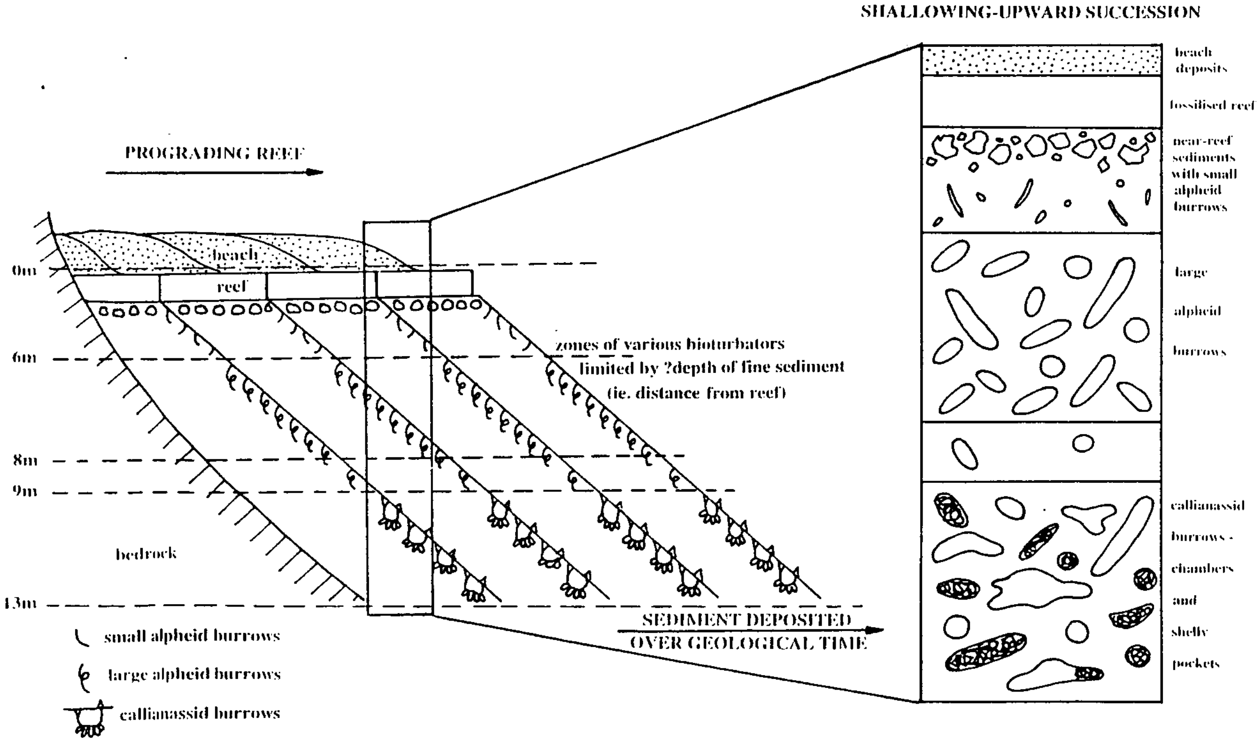


Fig. 6. With time, the reef and its slope will prograde seawards creating a shallowing upwards succession from beach deposits through reef to sediments. The sediments will contain characteristic trace fossils, from near-reef alpheid to off-reef callianassid burrows.

With a sudden large deposition of sediment, thicker than the depth of the callianassid tier, it is likely that the original fauna will be killed and recolonisation of the new sediment surface will take place. Due to the depth of sediment deposited, the new callianassid tier will not penetrate far enough to rework the original upper meiofaunal tier, and all original tiers will therefore be preserved, unless there has been post-depositional erosion. The resulting ichnofabric will show two sets of tiers, one above the other, separated by a layer of unbioturbated sediment, which might show features of the event that caused the sedimentation, for example storm deposits.

Intermediate levels of deposition would result in varying amounts of the upper tiers being preserved, showing as traces cross-cut by the new deep tier. The formation of escape traces to keep up with fast sedimentation is not discussed here; although their formation is likely under certain conditions, subsequent reworking during periods of slower sedimentation will probably obscure them.

Prograding reef sediments

The crustaceans studied in this paper are found in mutually exclusive zones moving seawards (eg. near-reef alpheids, off-reef alpheids, callianassids), and are probably limited in their distribution by the nature of the sediment texture , which varies with distance from the reef front. A prograding reef and sediment slope will lead to the formation of a shallowing upward succession, from beach sediments through coral reef to sediments characterised by alpheid and then callianassid traces (Fig. 6). These different zones of sediment should be recognisable by their biogenic features as described in the section above. Storm events may also be recognised in the sedimentary record by changes in sediment texture (mean grain size and sorting) and by the distribution of trace fossils, assuming enough time elapses between major storm events for the burrowing fauna to reestablish itself and to thoroughly rework the sediment.

Summary of main conclusions

1 Burrows of *Dotilla* soldier crabs, alpheid and callinassid shrimps are characteristic of their makers, and of specific areas of sediment (intertidal sand waves, near-reef and off-reef sediments) in modern reef sediments in Phuket.

2. Over a geological timescale, a prograding reef slope will preserve these deepest tier burrows as a shallowing upward succession of trace fossils.

3. Given high enough densities of animals and adequate time, the sediment texture will also be affected by bioturbation.

4. However, events such as a storm in 1986 have prevented complete reworking and left a storm deposit in the subtidal sediments described.

ACKNOWLEDGEMENTS

I thank Terry Scoffin and Sandy Tudhope for constructive discussion at all sta this project. Phuket Marine Biological Center for enabling me to stay and w Thailand, and Jason Shepherd for invaluable field assistance.This work was f by the Natural Environment Research Council of Britain.

REFERENCES

Ausich W I, Bottjer D J (1982) Tiering in suspension-feeding communities on substrata throughout the Phanerozoic. Science 216:173-174

Bromley RG (1990) Trace Fossils:Biology and Taphonomy. Unwin Hyman London 280pp

Carr D J et al (1991) Grain size, calcium carbonate content and accumulation r of Recent sediments in Phangnga Bay, South Thailand. Phuket Mar Biol Cent Bull 55:77-96

Chatananthawej B and Bussawarit S (1987) Quantitative survey of the macrobe fauna along the west coast of Thailand and the Andaman Sea. Phuket Mar Bi Cent Res Bull 47:23pp

Frith DW, Tantanasiriwong R and Bhatia O (1976) Zonation of macrofauna on mangrove shore, Phuket Island. Phuket Mar Biol Cent Res Bull. 10:37pp

Ekdale AA, Bromley RG, Pemberton SG (1986) Chapter 8 Trace fossils as indicators of sedimentologic processes, pp 88-96 in Ichnology: Trace fossils i sedimentology and stratigraphy. SEPM Short Course No. 15 Tulsa Oklahoma

Griffis RB, Suchanek TH (1991) A model of burrow architecture and trophic m in thalassinidean shrimp (Decapoda:Thalassinidea). Mar Ecol Prog .Ser 79:1 183

Karplus I, Szlep R, Tsurnamal M (1974) The burrows of alpheid shrimps assoc with gobiids in the Northern Red Sea Mar Biol 24:259-68

Karplus I (1987) The association between gobiid fishes and burrowing alpheids Mar Biol Ann Rev 25:507-562

Nickell LA, Atkinson RJA (1995) Functional morphology of burrows and troph modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. Mar Ecol Prog Ser 128:1 197

Phongsuwan N (1991) Recolonization of a coral reef damaged by a storm on P Island, Thailand. Phuket Mar Biol Cent Res Bull 56:75-83

Scoffin TP (1992) Taphonomy of coral reefs: a review. Coral Reefs 11:57-77

Scoffin TP, Tudhope AW, Brown BE, Chansang H and Cheeney RF 1992) Patt and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. Coral Reefs 11:1-11

Shinn EA (1968) Burrowing in the Recent lime sediments of Florida and the Bahamas. J.Palaeo 42:879-894

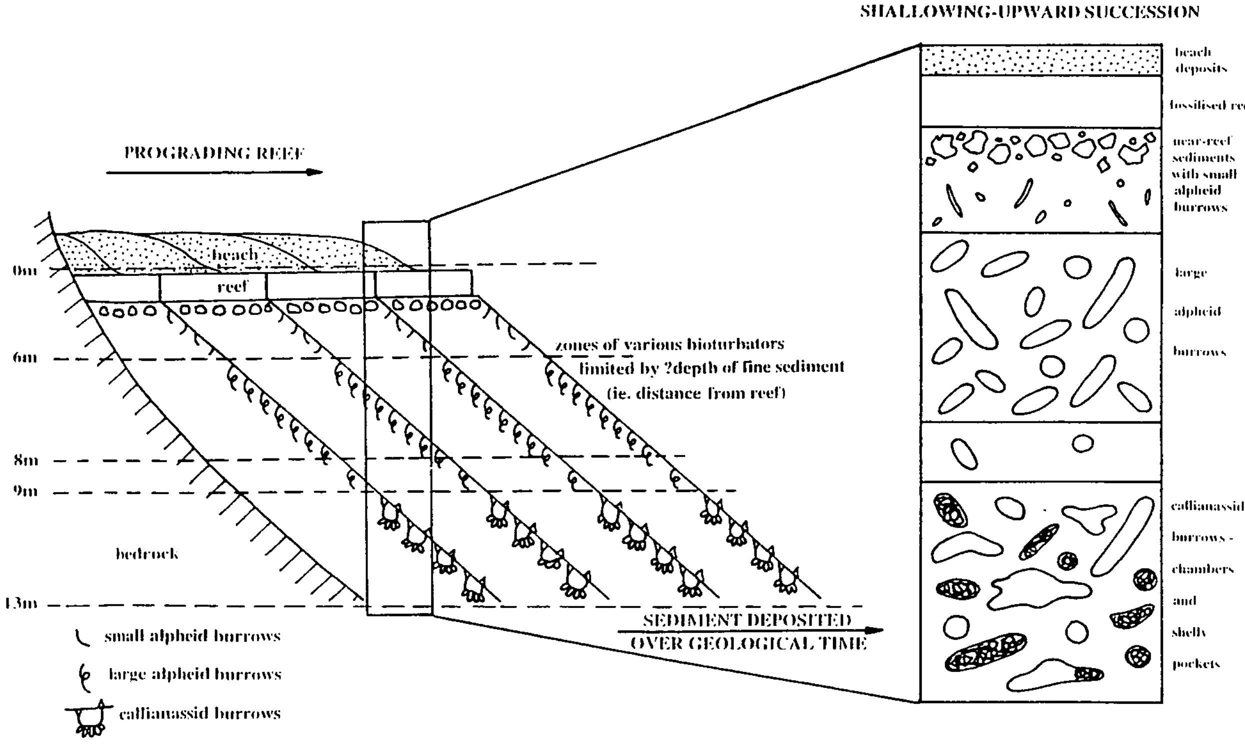


Fig. 6. With time, the reef and its slope will prograde seawards creating a shallowing upwards succession from beach deposits through reef to sediments. The sedimen will contain characteristic trace fossils, from near-reef alpheid to off-reef callianassid burrows.

Suchanek T (1985) Thalassinid shrimp burrows: ecological significance of species-specific architecture. Proc.5th Int Coral Reef Congress. Tahiti 5:205-210

Tantanasiriwong R (1978) An illustrated checklist of marine shelled Gastropods from Phuket Island, adjacent mainland and offshore islands, western Peninsula Thailand. Phuket Mar Biol Cent Res Bull 21:22pp

Tedesco LP. Wanless HR (1991) Generation of sedimentary fabrics and facies by repetitive excavation and storm infilling of burrow networks. Holocene of South Florida and Caicos Platform, BWI. Palaios 6:326-343.

Tudhope AW. Scoffin TP (1984) The effects of *Callianassa* bioturbation on the preservation of carbonate grains in Davies Reef Lagoon, Great Barrier Reef, Australia. J.Sed Pet 54(4):1091-1096

Tudhope AW. Scoffin TP (1994) Growth and structure of fringing reefs in a muddy environment. South Thailand. J Sed Res A64(4):752-764

Vaugelas J de (1984) Preliminary observations on two types of callianassid (Crustacea, Thalassinidea) burrows, Gulf of Aqaba (Red Sea) Proc Symp.Coral Reef Env.Red Sea Jeddah pp 520-539

Vogel F (1984) Comparative and functional morphology of the spoon-tipped setae on the second maxillipeds in *Dotilla* Stimpson, 1958 (Decapoda, Brachyura, Ocypodidae). Crustaceana 47:225-234

Wanless HR.Tedesco LP. Tyrell KM (1988) Production of subtidal tubular and surficial tempestites by Hurricane Kate, Caicos Platform, British West Indies. J Sed Pet.58:739-750