DOCTOR OF PHILOSOPHY

The impact of anthropogenic and natural stresses on the coral reefs of Rodrigues, Western Indian Ocean

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Award date:
2004

Awarding institution:
Bangor University

THE IMPACT OF ANTHROPOGENIC AND NATURAL STRESSES ON THE CORAL REEFS OF RODRIGUES, WESTERN INDIAN OCEAN

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2004

A thesis submitted in accordance with the requirements of the University of Wales, Bangor for the degree of Doctor of Philosophy.

Abstract

This study investigated the interaction between natural and anthropogenic impacts on the reefs of Rodrigues. Rodrigues remains undeveloped, however as a result of deforestation in the 1800s, the reefs are subjected to episodic fluvial inputs following high rainfall, resulting in high sedimentation/turbidity within the lagoon. The island is also affected by natural impacts such as coral bleaching and cyclones. Despite these factors the reefs in Rodrigues are currently in good health. This study assessed whether fluvial inputs are having a sub-lethal effect on coral colonies on the fore reef slopes, by studying coral growth rates, larval settlement and recovery from injury at 3 sites with varying sediment regimes. The severity of a coral bleaching episode, which affected the island in 2002, was also assessed. The results show that at the 2 inshore sites (Totor and Trou Malabar) sediment deposition was well above 'tolerable' levels for coral reefs (up to 96 mg cm^{-2} d^{-1}), suggesting that this threshold is not applicable for these reefs. It is suggested that high turbidity and sediment deposition are related to high rainfall, resulting in land run-off, combined with high wind causing sediment resuspension. This periodic high sedimentation and turbidity appeared to be having a sub-lethal effect on coral colonies, resulting in a decrease in growth rates of *Acropora austera* and *Porites rus*, low coral recruitment and a low ability of *Montipora* spp. to recover from injury. The bleaching event was not widespread and coral mortality was restricted to sites in the north and west of the island. Where bleaching did occur, it was severe, resulting in mortality of up to 75 % of coral colonies at some sites, particularly branching and tabular *Acropora* spp. One year later, dead coral colonies had become heavily eroded and overgrown with turf and macro-algae, although some recovery had occurred.

Acknowledgements

I would like to thank my supervisor, Dr John Turner for his help and advice. I would also like to thank the Ministry of Fisheries, the Mauritius Oceanography Institute and especially Mrs Ruby Moothien Pillay at the MOI for supporting this work. I am grateful to the Mauritius Meteorological Services for providing meteorological data and Rebecca Klaus for providing the AVHRR data.

None of this would have been possible without the staff and volunteers of *Shoals Rodrigues* – so a huge thank you to everyone there. I am very grateful to Tara Lynch and Tom Hooper for providing me with facilities, boats and staff and for their excellent organisational skills. A big thank you to Eric Blais, Thierry Begué, Michael Meunier, Antonio Jolicoeur and Tom Hooper for driving the boats; to Teddy and Ricardo for their excellent welding; and to everyone who acted as surface cover and to all my diving/snorkelling buddies for all their help measuring, cutting, photographing and hammering – Fabio Allas, Alex André, Henri Ally, Thierry Begué, Cathryn Christensen, Tracy Clark, Christopher Felicité, Natacha Felicité, Lorna Fox, Christophe Gontran, Wendy Grancourt, Ricardo Kishtoo, Hansley Leong Lone, Charlie Lindenbaum, Tara Lynch, Sabrina Meunier, Sydney Perrine, Runolph Raffaut, Jovani Raffin, Jonathan Smith and Michelle Taylor. Thank you also to Sabrina for sieving sediment samples and for answering my many questions and to Charlie for PhotoShop and MapInfo help.

Thank you to Charlie Lindenbaum and to my family for all their support and encouragement throughout and to Leonie Salmon for being a good office-mate.

Finally, I would like to thank Dr Chris Richardson and Dr James Scourse for helping with funding problems, the University of Wales, Bangor for providing funding for the fieldwork and the Charles Henry Foyle Trust and the Fox Memorial Trust for providing additional funding for equipment.

Table of Contents

Chapter 1 The island of Rodrigues

Chapter 2 The environmental and biological characteristics of three coral reef sites on the north coast of Rodrigues

Chapter 3 Growth rates of the branching corals *Acropora austera* and *Porites rus* under varying sediment regimes

Chapter 4 Coral settlement and regeneration under varying sediment regimes

Chapter 5 Adaptations of coral colonies to high sediment/low light conditions

Chapter 6 The extent of coral bleaching in Rodrigues

Chapter 7 The human and natural impacts affecting coral reefs in Rodrigues

List of Plates

List of Tables

List of Figures

CHAPTER 1: The island of Rodrigues

The aim of this study is to investigate the interaction between some of the potential factors affecting the health of the coral reefs surrounding Rodrigues; to make predictions about the future of the reefs and to suggest techniques for minimising further damage. The island of Rodrigues remains undeveloped, however as a result of deforestation in the 1800s, the reefs are subjected to episodic fluvial inputs following high rainfall, resulting in high sedimentation/turbidity within the lagoon. The island is also affected by natural impacts such as coral bleaching and cyclones. Despite these factors the reefs in Rodrigues are currently in good health. This study will assess whether fluvial inputs are having a sub-lethal effect on coral colonies on the fore reef slopes, by studying coral growth rates, larval settlement and recovery from injury at sites with varying sediment regimes. The extent and severity of a coral bleaching episode which affected the island in 2002 will also be assessed. This chapter describes the island of Rodrigues, its marine environment and the pressures that are currently being exerted upon the island's coral reefs.

1.1 Rodrigues

Rodrigues is an island state of Mauritius, situated at 19 ° 42' S and 63 ° 25' E, 595 km east of Mauritius. Together with Mauritius and Rèunion it forms part of the Mascarene Archipelago. It is 18 km at its longest and 8 km at its widest with an area of 107.8 km^2, making it the smallest of the three Mascarene Islands. Figure 1.1 shows the island of Rodrigues and the location of places described in this chapter. Rodrigues is of volcanic origin and was formed 1.5 million years ago and rises to a height of 396 m (Turner *et al.*, 2000a). The island is situated on an elliptical submarine platform, with a width of 30 km and a length of 55 km. The platform slopes gently outwards to the 100 m contour, beyond which there is a marked increase in slope, and depths increase rapidly to over 2,000 m (McDougall *et al.*, 1965). Rodrigues is enclosed by a 200 km^2 fringing reef, encompassing a very shallow lagoon extending to 13 km width in the south (Turner *et al.*, 2000a). The reef is relatively young, having grown to within 2 m of present sea level 2-3,000 years ago (Rees *et al.*, in press).

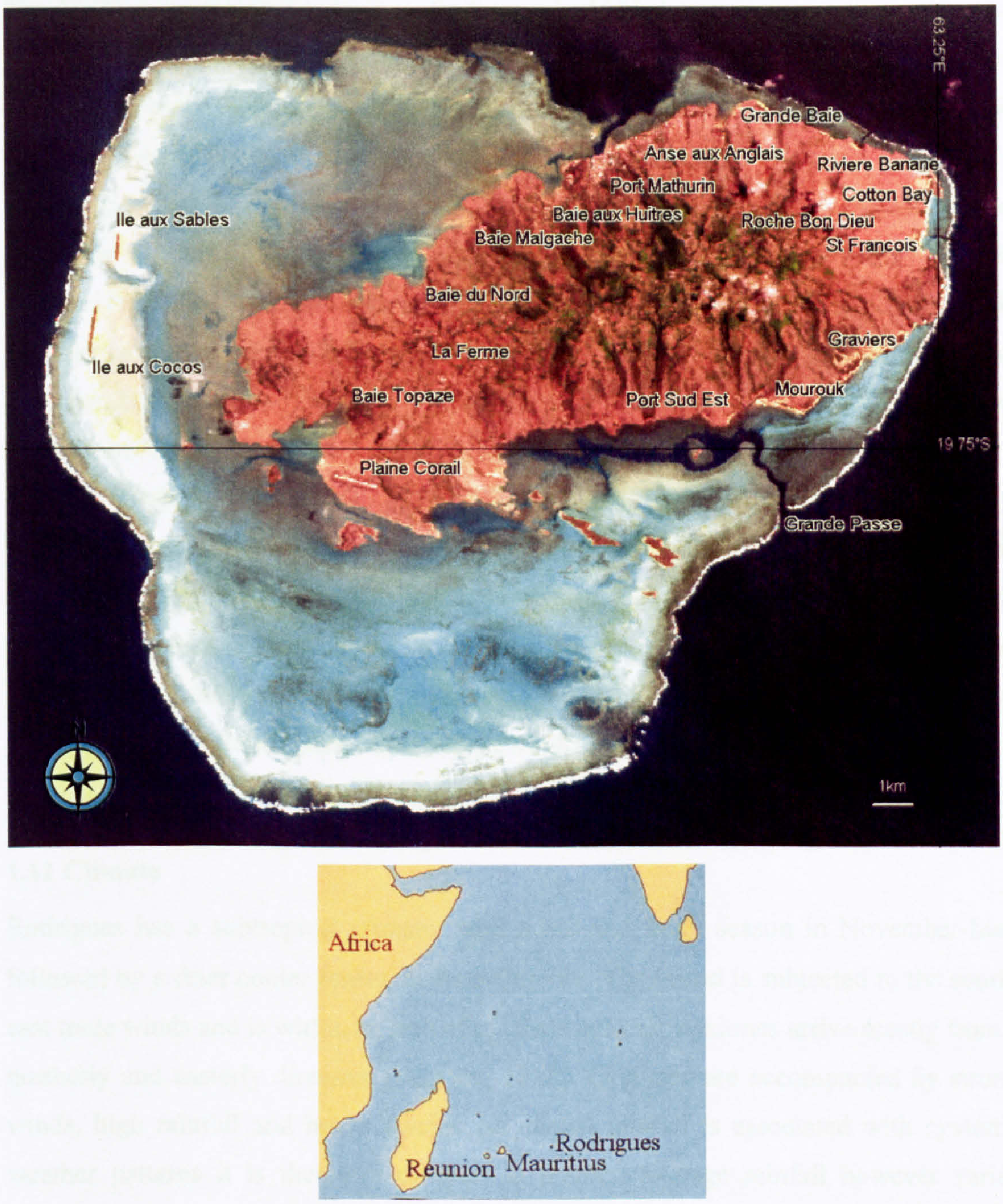


Figure 1.1 The island of Rodrigues (Landsat 7 satellite image processed by B. Chapman) and it's position in the Western Indian Ocean.

The Dutch were the first to land on Rodrigues in 1601, however the earliest settlement was in 1691 when François Leguat visited Rodrigues staying for 2 years, with his crew of 9 men (Gade, 1985; Cheke, 1987). There was no permanent settlement until 1792 when Frenchmen from Mauritius arrived with slaves to cultivate the land. In 1804 the island's population was only 104 and the land was sparsely settled until the abolition of slavery in 1833. By 1851 the population had increased to 495 and was 13,333 by 1952 (Gade, 1985). Rodrigues now has a population of 35,546. The population density is 342 persons km^{-2}, with a growth rate of 0.48 % yr^{-1} (CSO, 2000). The population has however, been stabilised by massive emigration to Mauritius (MEPD, 1995). Rodrigues remains undeveloped and the economy is based mainly on agriculture, livestock and fisheries (Genave, 2000; Turner *et al.*, 2000a). Employment is low at 38.5 % with 34.7 % of employed people working in agriculture and fishing (CSO, 2000). The main centre of urban development is Port Mathurin on the north coast, where 10,000 people live; the remaining population is scattered in 137 hamlets throughout the island (Turner *et al.*, 2000a). Rodriguans are largely African and Malagasy in origin and the majority of the population are Catholic (Gade, 1985; IELS, 1998).

1.11 Climate

Rodrigues has a subtropical climate, with a hot and rainy season in November-May followed by a drier cooler season in June-October. The island is subjected to the south-east trade winds and is within an area of cyclonic activity; cyclones arrive mostly from a northerly and easterly direction (Pearson, 1988). Cyclones are accompanied by strong winds, high rainfall and heavy swells. As annual rainfall is associated with cyclonic weather patterns it is therefore difficult to predict; average rainfall however varies between 1,090 mm in the lowlands to 1,710 mm in the uplands (MEQL, 1991). Mean yearly air temperature is 28.8 °C (Pearson, 1988) however, temperatures often exceed 30 °C (UNEP/IUCN, 1988).

1.12 Oceanography

Rodrigues is influenced by the South Equatorial Current transporting water in a west-north-westerly direction and varying seasonally to a west-south-westerly direction. Current velocities are in the order of 0.5-1.0 knots, although these may be affected by cyclonic weather patterns (Pearson, 1988). Current patterns within the lagoon are wind driven, flowing predominantly in a westerly or north-westerly direction with mean speeds of <0.1 m s^{-1} to 0.5 m s^{-1} (Lynch *et al.*, 2003a). Tidal effects can be detected in certain parts of the lagoon, mainly in the major channels, close to passes and in the sheltered central northern lagoon. Tides are semi-diurnal and range from 0.5 m during neap tides to 1.9 m during spring tides. Sea surface temperatures range from 22-24 °C in winter (May to October) to 26-28 °C in summer (November to April) (Genave, 2000).

1.2 The marine environment

Rodrigues has the "most substantial and best developed reefs in the Mascarenes" (Montaggioni and Faure, 1980). A wide expanse of reef platform extends without a break for 90 km around Rodrigues, most markedly towards the west. The reef flat occurs 1 or 2 km from the land in the east of the island (though sometimes as little as 50 m) and as much as 10 km in the west. Emerging above the level of the reef flat are several small islands, some of which are basaltic, and others such as Ile aux Cocos and Ile aux Sables, are sand cays (UNEP/IUCN, 1988).

When the first settlers arrived in Rodrigues dugongs were abundant in the shallow lagoon, with schools of 30-40 (Gade, 1985; Cheke, 1987) and in the 1730s the dugong (*lamentin*) fishery was reported as being "considerable and a major resource for the Isle of France, while many are transported salted together with turtles" (d'Heguerty, 1754, in Cheke, 1987). Dugongs were scarce by 1761 and the last record is by Marragon in 1795 (in Cheke, 1987). All early visitors to Rodrigues mentioned the abundance of turtles (Hawksbill and Green), however these also suffered heavy exploitation during the 18th century and since the 1950s no longer nest on Rodrigues (Gade, 1985).

Until recently the coral reefs around Rodrigues have received very little study. Comprehensive surveys were however carried out in the mid 1970s to early 1980s by Montaggioni and Faure (Montaggioni, 1974; Faure, 1975; Montaggioni, 1980; Montaggioni and Faure, 1980). The surveys found that the reef flat varies between 50 m and 2 km wide (Montaggioni, 1974) and can be divided into 4 sections (Faure, 1975; Montaggioni, 1980). The compact reef flat ranges from 50-300 m wide in the north-east and south but is poorly developed in the west. It has 20-30 % live coral cover, consisting of massive and digitate coral colonies such as *Platygyra sp.*, *Goniastrea sp.*, *Porites* sp., *Montipora* sp., *Pavona* sp., *Acropora* spp., *Pocillopora* sp. and *Stylophora* sp. (Faure, 1975; Montaggioni and Faure, 1980). Further in towards the lagoon the reef flat breaks up into scattered coral colonies separated by a system of shallow basins and short meandering channels. This is one of the most marked aspects of the reef flat in Rodrigues (Montaggioni and Faure, 1980). It has 20-30 % coral cover, consisting of massives (diverse Faviids, *Porites* sp.), encrusting colonies (*Turbinaria* sp., *Echinopora* sp., *Hydnophora* sp.) and branching corals (*Acropora* sp., *Pocillopora* sp.) (Faure, 1975; Montaggioni and Faure, 1980). This region is followed by a zone of coral-built alignments, 1-5 m wide, running perpendicular to the reef edge and separated by shallow grooves. Coral cover is 80-100 %, however there is a decline in species richness with *Pocillopora* sp., *Stylophora* sp. and *Galaxea* sp. becoming rare (Faure, 1975; Montaggioni and Faure, 1980). Finally, in sheltered sites, there is a region of micro-atolls, formed from massive *Porites* sp. colonies or occasionally by *Goniastrea* sp. and *Platygyra* sp. (Montaggioni, 1974; Faure, 1975; Montaggioni and Faure, 1980).

In exposed sites, such as on the east coast, the reef edge consists of calcareous algae, including *Lithothamnium* sp., *Lithophyllum* sp. and *Porolithon* sp; this does not however, form a true algal crest such as those found around coral islands and atolls in the Pacific Ocean (Faure, 1975; Montaggioni and Faure, 1980). In more sheltered sites the reef edge is colonised by coral colonies (50-60 % cover) including *Acropora* spp., *Pocillopora* spp., *Stylophora* sp., *Platygyra daedalea* and *Goniastrea pectinata* (Faure, 1975; Montaggioni and Faure, 1980). Just beyond the reef edge, the shallow reef slope consists of a compact pavement, interspersed with channels; in the south it is colonised by *Millepora* sp.; in the north it is colonised by branching corals dominated by *Acropora* spp. (Faure, 1975; Montaggioni and Faure, 1980).

The reef slope descends fairly steeply at most points around the island (UNEP/IUCN, 1988). In exposed areas the fore reef comprises steep walls, frequently in spur and groove formations (Montaggioni, 1974; Montaggioni and Faure, 1980; Chapman, 2000). Spur and grooves are poorly developed at the north-western point of Port Mathurin Bay and in sections from Grande Pointe to Passe Sable, but are well developed in western sections from Pointe des Quatre-Vingts Brisants (Montaggioni and Faure, 1980). Spurs vary in width from 6 to 10 m and grooves have a maximum width of 2 m (Montaggioni, 1974).

In the shallows (0 – 4 m) the fore reef tends to be colonised by *Millepora* spp. and branching corals such as *Acropora* spp., *Stylophora pistillata, Pocillopora damicornis* and *P. verrucosa* (Faure, 1975; Montaggioni and Faure, 1980). Below 4 m the slope is characterised by encrusting and massive colonies including *Leptoria phrygia, Platygyra daedalea, Goniastrea pectinata, Favites pentagona, Favia speciosa, F. pallida, Montastrea curta, Leptastrea purpurea, Oxypora lacera* and *Echinopora gemmacea*, as well as the soft corals, *Lobophytum* sp., *Sinularia* sp. and *Sarcophyton* sp. (Faure, 1975; Montaggioni and Faure, 1980*)*. The lower section, down to 20 m, is characterised by massive corals of the genera *Favia, Acanthastrea, Coscinarea, Turbinaria, Hydnophora, Goniopora* and *Astreopora (*Faure, 1975; Montaggioni and Faure, 1980*)*. The grooves consist of biogenic sand containing a community of molluscs (*Terebra babylonia, T. lanceolata, Oliva epsicopalis, Conus* sp. and *Mitra* sp.) and errant polychaetes (Faure, 1975). In more sheltered areas the reef slope is steep, lacking grooves and the walls are dominated by laminar and encrusting species (Chapman, 2000; Montaggioni, 1974). Coral cover on steeper areas commonly exceeds 50-70 % (UNEP/IUCN, 1988).

Passes, creeks and channels break the otherwise continuous reef flat in several places. Some of the larger reef passes are the site of the most prolific coral growth within the lagoon with large coral patches dominated by branching and tabular *Acropora* spp. and occasionally abundant soft corals (Chapman, 2000). One channel, the Grande Passe de Port Sud-Est is 40 m deep and 200 m wide and stretches 2.5 km from land to the outer edge of the reef flat (Faure, 1974; 1975). At its landward end it is connected with a back-reef channel which runs along the coast from east to west. The upper regions of its walls are dominated by small branching corals (*Acropora* sp., *Stylophora* sp., *Pocillopora* sp. and *Millepora* sp.) and soft corals. Between 4 and 10 m the wall is dominated by massive corals (*Favia* sp., *Favites* sp., *Goniastrea* sp., *Platygyra* sp. and *Lobophyllia* sp.) and between 10 and 18 m by encrusting forms (*Echinopora* sp., *Echinophyllia* sp., *Oxypora* sp. and *Mycedium* sp.) and soft corals. Below 20 m the slope is characterised by dead coral rubble, covered with calcareous mud and a very sparse distribution of living corals. The floor of the channel lies at 35 to 40 m depth and is covered by rubble and coarse well-oxidised sediment or outcrops of bare rock (Faure, 1974; 1975; Montaggioni and Faure, 1980). Other passes have a similar zonation. Passe Ile aux Fous in the north is also a rich coral site with high live coral cover and pools and depressions with large coral complexes (Chapman, 2000).

Recent surveys show that the shallow fore reef sites are dominated by *Acropora* spp., particularly branching growth forms (Clark, 2001; Lynch *et al.*, 2002). The most commonly occurring species were found to be *Acropora abrotanoides*, *Acropora austera*, *Acropora cytherea*, *Platygyra daedalea and Montipora* spp. (Clark, 2001). The surveys found that hard coral cover ranged from 35 % to 60 % (Clark, 2001), 44 % to 63 % (Ahmada *et al.*, 2002) and from 40 % to 71 % (Lynch *et al.*, 2002). All surveys found that dead coral cover and macro-algal cover were low (<5 % and <1.5 %, respectively), indicating that the reefs are in good health. Coral cover on the reef flat was however lower ranging from 15 % to 28 % (Ahmada *et al.*, 2002) and 15 % to 53 % (Lynch *et al.*, 2002). Sites on the reef flat were found to be affected by trampling from octopus fishers (Clark, 2001). Corals on the fore reef however, were found to be healthy with little sign of bleaching and no sign of disease (Clark, 2001; Fenner *et al.*, 2004).

Bruggemann (1879) catalogued 49 species of coral from Rodrigues. Faure (1977) recorded 90 species and 41 genera of corals (84 species and 38 genera of scleractinian corals). Chapman (2000) recorded 77 coral species (34 genera), whilst Clark (2001) recorded 88 species of coral (34 genera). A recent survey by Fenner *et al.* (2004) recorded 131 species and 40 genera of hard corals (126 species and 37 genera of zooxanthellate Scleractinia). This brings the total number of reported coral species from all sources to 160, which is close to the 163 species most recently reported from Mauritius (Moothien Pillay *et al.*, 2002a).

1.3 Uses of the coastal zone in Rodrigues

The coastline of Rodrigues is 60.2 km long and is dominated by basaltic rock rubble, however at some locations the shore is formed from aeolian limestone (Faure, 1973). There are only 5 small sand beaches (Turner *et al.*, 2000a) and small cliff walls (2-3 m high), composed of eroded fossil coral reef, occur on the east coast (Coppejans *et al.*, 2004). Most of the island is steeply sloping and thus many activities are either concentrated along the coastal zone or have an impact on it.

1.31 Agriculture

The island was stripped of its vegetation for agriculture during the early 1800s through woodcutting and burning and by 1825 the vegetation was reduced to a savannah with scattered trees (Cheke, 1987). In the 1830s many ex-slaves hacked out plots in the forest to plant crops and when the soil was exhausted after a few years a field was abandoned and a new one created by burning (Gade, 1985). The large numbers of goats and cattle prevented the regeneration of the native forests. An inventory in 1879 showed that cultivated land covered 3 % of the surface, pasture 85 %, uncultivated land 2 % and forest <10 % (De Blic, 1986). In 1955 a programme constructing terraces was started and the Agricultural Services built 3,600 hectares of terraces between 1955 and 1980 however the terraces have been poorly maintained.

Agriculture is now a major economy in Rodrigues and subsistence plots occupy one third of the island (Gade, 1985). Rodrigues, however only provides one third of its own food needs and few crops are sold, apart from onions and garlic that are produced for export. The main crops grown are maize, which occupies 80 % of the cropland, sweet potatoes, manioc, haricot beans and peanuts. Domesticated animals including goats, sheep, cattle and pigs are also a source of cash income. High wind and rainfall which accompany tropical cyclones during November to May can affect agriculture on Rodrigues, killing livestock and destroying crops. In addition, Rodrigues is also affected by droughts and during half of the year, low rainfall limits farming and often causes food shortages between January and March. Under the Agricultural Development Programme initiated in 1983, land and pasture development, construction of access roads and the establishment of agricultural infrastructure facilities were implemented in order to further develop agriculture in Rodrigues (MEPD, 1996).

1.32 Fishing

Artisinal fishing is important in Rodrigues as the lagoon is three times the area of the land. There were 1,999 registered fishers in 1999 and 1,130 registered fishing boats (CSO, 2000), with 1,000 regular unregistered fishers and a further 1,000 who are not registered and fish on a more casual basis (Lynch *et al.*, 2003b). Due to weather conditions and the lack of large boats the majority of the fishing effort is concentrated within the lagoon. Of the 1,999 registered fishers only 187 were recorded as off-lagoon fishers. The total fish caught during the year 1999 was 1,715.50 tonnes. Fish are caught either on the outer reef slope or from the coral communities along the edges of the channels. The most important species in the lagoon fishery is the Rabbitfish, *Siganus sutor* (Lynch *et al.*, 2003b), however other common species caught include mullet, trevally, goatfish, emperors, parrotfish, unicornfish, groupers and snappers (Cross and Judge, 1990). Fishing methods used include seine net, hook and line, trap and harpoon (Genave, 2000). Measures taken to develop outer-lagoon fishing, include the use of fish aggregating devices (FADs) in deeper water (MEPD, 1996; EDF, 1999; Jeetoo and Yung, 1999). The total catch from outer-lagoon fishing however remained insignificant during the trial period and due to poor maintenance the FADs are no longer in place (EDF, 1999).

The seine net fishery is the most important fishery in Rodrigues in terms of size (Lynch *et al.*, 2003b). Fishing is undertaken by teams of fishers using 4 to 8 boats. During 2002, 8 seine net licenses were granted and 96 fishermen were registered. Fishers use a semi-circular net and herd fish into the net by walking towards it beating the water with poles. Trap fishing was undertaken by 834 fishers in 2002. A variety of traps are used, these range in size from 1 to 3 m diameter and are made from traditionally woven bamboo panels or from wire. Traps are baited with algae and/or invertebrates such as molluscs and are left for 2-3 days.

The exploitation of octopus is another major fishery within the lagoon. There are in excess of 2,000 registered octopus fishers and the fishing grounds are located within the lagoon and concentrated on the reef region (Genave, 2000; Lynch *et al.*, 2000). 43 % of octopus fishers have access to boats, thus fishing effort is concentrated during periods of low neap tides when fishers can reach the fishing grounds by foot. Fishing grounds support an average fishing population of 13-94 fishers who fish for 2-8 hours each day. The majority of octopus caught are *Octopus cyanea*; fishers also supplement their catch with fish and other molluscs. Catches ranges from a mean of 0.2 – 3.5 kg per day per fisher, with maximum daily catches ranging from 1 – 14.2 kg per fisher (Lynch *et al.*, 2000). Landings are either air-dried or frozen and beyond subsistence are almost exclusively for an export market in Mauritius (Genave, 2000).

1.33 Habitation

The population is scattered in approximately 137 hamlets, although some concentration occurs in the semi-urbanised zone of Port Mathurin and Baie aux Huitres with around 10,000 persons (Figure 1.1). Water consumption is very low at 47 $l\ d^{-1}$. Most households have pit latrines rather than flushed toilets and the few hotels have cess-pits (Turner *et al.*, 2000a). There are proposals for improvements in domestic water supplies including the use of more effective pumps, construction of dams, desalination instalments (Jeetoo and Yung, 1999) and the installation of water treatment plants (MEPD, 1996), all of which have the potential to impact the marine environment.

1.34 Tourism

Tourism is in its infancy in Rodrigues. In 1994 4,013 tourists visited the island (IELS, 1998; MEPD, 1996), by 1999 this figure had doubled to 8,292 (CSO, 2000). The majority of visitors come from Mauritius (25,638 passengers) or from Réunion (6,299 passengers) and most arrive by plane (39,721 passengers) (CSO, 2000). Rodrigues has 4 3-star hotels in Port Mathurin, Anse aux Anglais, Mourouk and Cotton Bay (Figure 1.1) and the total number of rooms available in 1999 was 200 (EDF, 1999). The Government is now, placing much hope on tourism being able to strengthen the island's economy (Jeetoo and Yung, 1999). The construction of 5 new hotels around the north and east coast has already commenced, a new airport has been built at Plaine Corail and the runway has been extended to allow direct flights from Réunion.

1.35 Industry

There is no real industry in Rodrigues and impact is low (Turner *et al.*, 2000a). Manufacturing activities are confined to indigenous craft traditions (MEQL, 1991) and small-scale businesses producing mainly for the local market (Jeetoo and Yung, 1999) and the export of manufactured goods to Mauritius is negligible (MEPD, 1996). Measures are however, being implemented to boost private sector industry on Rodrigues (Jeetoo and Yung, 1999) and it is also suggested that industrialisation in Mauritius may require the re-location of some labour-intensive industries to Rodrigues (MEQL, 1991). It is hoped that the location of small and medium industries in Rodrigues will increase employment, create wealth and stem migration to Mauritius (MEQL, 1991; Jeetoo and Yung, 1999). An office of the Small and Medium Industries Organisation (SMIDO) was set-up in 1990, providing advice and monitoring for new enterprises (MEPD, 1996).

1.36 Quarrying

Quarrying is an important industry to supply building material for road and building construction. Two major stone-quarrying companies operate in Rodrigues near La Ferme and near Roche Bon Dieu (EDF, 1999) (Figure 1.1). There is a coral stone quarry near Plaine Corail, however quarrying at this location has now been stopped. Coral sand is extracted from licensed areas to the south-west of Ile aux Cocos and on the St Catherine Bank south-west of Baie Topaze (EDF, 1999). The sand is used for construction work. Erosion of sand from Ile aux Cocos and Ile aux Sables during cyclones has been attributed to this sand extraction (Saha, 1993).

1.37 Dredging and land reclamation

The channel at Port Mathurin was first dredged in 1975 to allow the *Mauritius Pride* supply vessel easier access to the port. Material from the operation was used in reclamation of land in the Camp du Roi area of Port Mathurin, Baie Lascars and Baie aux Huitres (Saha, 1993) (Figure 1.1), as well as in the creation of Ile Hollandaise on the reef flat (EDF, 1999). The channel was dredged again in 1990 with much of the material being used for land reclamation in Baie aux Huitres (EDF, 1999). There are proposals to dredge more of the channels and to dispose of dredge spoil for coastal land reclamation (Turner *et al.*, 2000a).

1.4 Impacts to the coastal zone

1.41 Natural impacts to coral reefs

1.311 Cyclones

Rodrigues is situated within an area of cyclonic activity. Cyclones develop from small tropical depressions within the Intertropical Convergence Zone, between 10 and 25 °. Cyclones tend to travel in a westward or north direction and can move at 700-1000 km per day (Météo France La Réunion, 1997). They tend to occur when the sea temperature is above 26.5 °C and thus occur predominantly between December and March. They become known as a tropical cyclone when wind gusts exceed 117 km hr^{-1}, however winds close to the centre may be up to 300 km hr^{-1}. Cyclones are accompanied by high rainfall and heavy swells. In the Western Indian Ocean, approximately 12 tropical depression systems occur on average each year, of which an average of 4 become tropical cyclones. Some of the worst cyclones to affect Rodrigues include Cyclone *Monica* (1968), *Fabienne* (1972), *Jessy* (1973), *Celine* II (1979) and *Bella* (1991) with winds exceeding 200km per hour (Mauritius Meteorological Services). During March 2003 Rodrigues was affected by Cyclone *Kalunde*, which passed 20 km to the east of the island. *Kalunde* produced winds of up to 200 km per hour, causing damage to property, crops and livestock.

Cyclones may cause damage to coral reefs through physical destruction of reef organisms by wave action and movement of coral rubble, increased sedimentation and turbidity and increased run-off after heavy rain (Brown, 1996). There have been no detailed studies of the impact of cyclones on coral reefs of the Mascarenes. In Réunion Naim *et al.* (2000) state that 27 % of reef flat corals are degraded by cyclones, however this figure is only based on the impact of Cyclone *Firinga* in 1989. Naim *et al.* (1997) showed that extremely high sedimentation caused by high rainfall associated with Cyclone *Firinga* caused 99 % mortality to one reef flat area and Letourner *et al.* (1993) studied the impact of this cyclone on fish community structure. The impact of hurricanes has however been studied, particularly in the Caribbean. Cyclones have been shown to cause coral mortality down to depths of 30 m and branching coral species tend to be most vulnerable (Woodley *et al.*, 1981; Rogers *et al.*, 1991; Van Woesik *et al.*, 1991; Bythell *et al.*, 1993). Two of the most recent cyclones to affect Rodrigues, *Evariste* and *Dina* were found to cause very little damage to the reefs and surveys conducted after the cyclones had passed found only very few overturned *Acropora* tables (Clark, 2001; *pers. obs.*). Cyclone *Kalunde*, however does appear to have caused damage to the northern fore reef slopes and recent coral mortality was observed down to depths of 10 to 12 m (*pers. obs.*).

1.412 Coral bleaching

Coral bleaching is a general stress response that may result from a variety of environmental conditions and anthropogenic stresses. A variety of different stresses have been suggested as being potentially responsible for causing coral bleaching. Localised bleaching events have been associated with bacterial and other infections (Kushmaro *et al.*, 1996), chemicals such as cyanide (Jones and Hoegh-Guldberg, 1999), solar radiation (Fisk and Done, 1985; Harriott, 1985a), sea level drops (Glynn, 1976), reduced salinity (Goreau, 1964), increased turbidity (Rogers, 1983) and temperature changes (Coles and Jokiel, 1978). Recent work however, highlights increased sea surface temperatures and solar radiation (including ultraviolet radiation) as the most common factors believed to be responsible for large-scale coral bleaching (e.g. Glynn, 1984; Brown and Suharsono, 1990; Brown *et al.*, 1996; Winter *et al.*, 1998; Quinn and Kojis, 1999; Spencer *et al.*, 2000).

Since 1980, there has been a significant increase in the number of reported large-scale coral bleaching events (Winter *et al.*, 1998). During 1997-1998 coral reefs were subjected to the most geographically widespread and probably most severe bleaching event in recorded history. There was unprecedented bleaching in coral reefs throughout the Indian Ocean, the Middle East, Southeast and East Asia, the Caribbean, the Far West and Far East Pacific and the Atlantic Ocean (Wilkinson *et al.*, 1999). The coral reefs of Mauritius and Rodrigues were however, some of the few reef areas in the Indian Ocean to escape this mass coral bleaching event. A rapid assessment of the status of the coral reefs in Mauritius during April 1999 (Turner *et al.*, 2000b) and a Reef Check survey in Rodrigues during September 1999 (Vogt *et al.*, 1999) showed that the reefs were generally healthy with no large areas of dead standing coral. A study by Moothien Pillay *et al.* (2002b) in Mauritius confirmed that coral bleaching had been mild, affecting <10 % of coral colonies and that the majority of colonies had recovered. Analysis of meteorological data showed that during the period of elevated Sea Surface Temperature (SST), unstable weather associated with Cyclone *Anacelle* caused higher cloud cover, very high rainfall and lower hours of sunshine than normally experienced at that time of year. It was suggested that these unsettled conditions protected the coral reefs from severe bleaching during 1998 (Turner *et al.*, 2000b). Very few signs of coral bleaching were observed on the reefs of Rodrigues during surveys in 2000 (Chapman, 2000; Clark, 2001), however a severe coral bleaching event occurred in the north and west of Rodrigues during 2002 and further coral bleaching was observed on the northern reefs during 2003 (*pers. obs.*). The 2002 coral bleaching event will be described in more detail in chapter 6.

1.413 Disease and predators of coral colonies

Outbreaks of the Crown-of-thorns starfish, *Acanthaster planci* were first documented on the Great Barrier Reef in 1962 (Barnes, 1966); since then outbreaks have occurred in the Red Sea, South Africa, the Maldives, Indonesia, the Cook islands and Fiji (Moran, 1986). Natural densities of starfish range from 1 to 35 individuals per hectare, however during an outbreak numbers may increase to up to >1,500 per hectare (Moran and De'ath, 1992). *A. planci* favours branching and tabular *Acropora* spp and *Montipora* spp, but may eat massive corals during severe outbreaks (Moran, 1986). The starfish can cause considerable damage to coral reefs and during the 1979-1991 outbreak on the Great Barrier Reef, reefs experienced 30->50 % mortality (Moran *et al.*, 1992). There have been serious outbreaks of *A. planci* over the past 20 years in Mauritius, possibly linked to the decline in population of its main predator *Charonia tritonis* (Fagoonee, 1990). However coral reef surveys in Rodrigues have found no evidence of *A. planci* (Vogt *et al.*, 1999; Chapman, 2000; Lynch *et al.*, 2000; Lynch *et al.*, 2002).

Coral diseases such as white-band disease, black-band disease and white plague were first reported from the Caribbean in the 1970s and 1980s (Antonius, 1973; 1977; Peter *et al.*, 1983). Since these times, reports of coral diseases have increased, new diseases have been described and diseases have been reported from a wide geographical area including the Indo-Pacific (Antonius, 1985), the Arabian Gulf (Coles, 1994; Korrübel and Riegl, 1998) and the Great Barrier Reef (Miller, 1996). Coral diseases have been recorded in Mauritius (Antonius, 1993) and in addition a coralline red algae was also observed to be overgrowing and killing a number of coral colonies (Antonius and Afonso-Carillo, 2001). Studies of the corals in Rodrigues have found coral colonies to be healthy with little or no sign of disease (Clark, 2001). Recent surveys however have found evidence of white band disease, although this requires further study (Hooper, *pers. comm.*).

1.42 Human impacts to coral reefs

1.421 Pollution

The increase in human population in coastal areas and rapid urbanization has resulted in increased pollution on coral reefs. One of the major forms of pollution to affect coral reefs is eutrophication caused by sewage and agricultural run-off, although pollution also occurs from heavy metals and oil (Roberts, 1993; Brown, 1996; Dubinsky and Stambler, 1996). Marine pollution in the Mascarene region can be considered to be relatively low, however pollution 'hot spots' occur close to coastal towns (Turner *et al.*, 2000a). In Mauritius the discharge of both treated and untreated domestic and industrial waste occurs in shallow water, causing increased turbidity and eutrophication. Water pollution arises from sugar industry wastes such as flyash and alkaline waste water, effluent from dye houses, printing, tanning and paint manufacture and heavy metals from chemical works (Fagoonee and Daby, 1993). In addition, agricultural practices result in nutrient enrichment and pesticide contamination within the lagoons (Daby, 1999). In contrast, marine pollution is minimal in Rodrigues. There is no real industry and surveys of water quality found that nutrient levels were very low and appeared unconnected to land use (Lynch *et al.*, 2002).

1.422 Overfishing and destructive fishing practices

Reef fish communities have been exploited by coastal communities throughout history, however, increasing human population, more effective fishing methods and increased access to reefs has resulted in increased fishing pressure on reef fish stocks around the world (Spalding *et al.*, 2001). In Rodrigues, fishing activities within the lagoon impacts heavily on fish stocks and in addition fishing causes damage to coral colonies through anchor damage, deployment of basket traps, trampling and the deliberate breaking and overturning of corals in the search for octopus (Pearson, 1988). The annual artisanal fisheries fell from 1,900 tonnes in 1991 to 840 tonnes in 1994, indicative of a serious decline in the fishery (IELS, 1998). During 1997 a net buy-back scheme was introduced to reduce pressure on the lagoon. In addition, the seine net fishery has a number of management measures in place, including a closed season (30th September to 1st March), 5 closed areas where seine net fishing is permanently prohibited, a minimum mesh size of 9 cm and minimum catch sizes for different fish species (Lynch *et al.*, 2003b).

These legal restrictions are however not enforced in any of the closed areas and illegal seine net fishing takes place all year round, all over the lagoon (EDF, 1999; Lynch *et al.*, 2003b). Despite this, recent work shows that the reduction in fishing effort since 1997 has been sufficient to create a sustainable fishery as the catch weight and effort were found to be at about 75 % of the maximum sustainable yield (Lynch *et al.*, 2003b). There is however evidence that growth and recruitment overfishing of the Rabbitfish is still occurring. Furthermore, a change in the composition of fish catches is taking place with herbivorous and omnivorous fish, such as Rabbitfish and Goatfish, becoming more important than predatory species, such as Emperors and Trevallys, indicating a degraded ecosystem.

The octopus fishery is also being exploited beyond its sustainable level. Fishers report that catches have declined and that octopus sizes have decreased over the past decade (Lynch *et al.*, 2000). Reports from exporters suggest that the volume of catch had decreased by 50% during the 30 years before the FAO report (Pearson, 1988) and there has been a steady decrease in octopus catches from 732.2 tons in 1995 to 476 tons in 1999 (Genave, 2000). A recent study by Genave (2000) found that densities of *Octopus cyanea* were low in areas close to dense population centres despite the fact that suitable habitats were available. Octopus densities ranged from 0.0 to 0.3 individuals 500 m^{-2} at sites close to population centres compared to 10.0 individuals 500 m^{-2} at sites further away from human habitation, suggesting that octopus fishing in Rodrigues has exceeded sustainable levels in many areas of lagoon.

The propulsion of boats in shallow areas is carried out by poles which fracture and damage coral surfaces and the use of stone anchors cause damage as the stone drags over the bottom. Basket traps are placed in close proximity to or on coral surfaces causing damage during the deployment or recovery or though movement while the traps are *in situ*. Large coral heads are used to anchor traps in place and are also used to erect V-shaped walls to drive fish into the traps. Reef walking for line and octopus fishing results in the destruction of coral colonies. Line fishing causes substantial damage to corals as a result of line entanglement and the seine net is reported to cause damage though the practice of herding reef fish into the net by striking corals (Pearson, 1988). Genave (2000) found a negative correlation between octopus abundance and the amount of coral damage. Octopus fishers were observed to overturn coral in the search for octopus and in some areas up to 57 % of corals were damaged probably by a combination of boat anchoring, trampling and bad fishing practices. Chapman (2000) also observed several destructive fishing practices in the lagoon including the use of poles for propulsion across areas of high coral cover, fishing lines entwined around coral branches, damage from basket traps, construction of Y-shaped walls from coral heads and reef trampling by octopus fishers at low tide. She comments that numerous survey sites showed evidence of coral damage particularly in the form of broken branching corals and large overturned tabular corals, which may have resulted from damage from basket traps or from deliberate overturning in the search for octopus.

1.423 Sedimentation

Soil erosion is a serious problem in Rodrigues and siltation derived from terrestrial sources is the principal visible impact to the marine environment (TROMES, 1995). For some time after its discovery, Rodrigues remained well wooded and early reports describe the island as having a stratified evergreen forest 15-20 m high, which covered most of the island (Leguat, 1708, in Gade, 1985). As late as the end of the 18th century, the forests were still "thick and difficult to penetrate" over much of the island. Two centuries of human habitation have however greatly changed the native vegetation, which now only exists in scattered places (De Blic, 1986). Corby (1845, in Cheke, 1987) describes an island largely deforested with pockets of woodland here and there and Higgin (1849) comments that there is "no great number of trees nor any approach to forest growth". In 1879 Balfour (in Cheke, 1987) wrote that the island was " now... a bare parched volcanic pile with deep stream courses for the most part dry, in place of the verdant well-watered island of 200 years ago".

Extensive deforestation on the island had an effect on water availability as early as 1825, leading to the loss of most of the biologically active soil and causing all but a few of the 150 original springs to dry up (Cross and Judge, 1990). Since 1970 Rodrigues' stream courses only flow after heavy rains (Gade, 1985). The natural vegetation was also destroyed by goats, cattle and pigs which ran wild in the woods until this century (Gade, 1985). Poor maintenance of the terraces, overgrazing and damage to the terraces by cattle has caused further loss of soil, silting rivers, lagoon channels and areas of lagoon (EDF, 1999; Turner *et al.*, 2000a). Soil loss was mentioned in most colonial reports on the island in the mid 19th century. It has now been estimated that soil erosion affects 95 % of the total surface area of the island, facilitated by the clay texture of the soil, the sloping terrain and intense rainfall associated with tropical cyclones (Gade, 1985).

All bays to the east of Port Mathurin are subject to heavy siltation and in 1988 Pearson estimated that the bathymetry of these embayments had been reduced by 80 cm since 1978. Turbidity is constantly high in some inshore areas such as Baie du Nord and Baie Topaze despite sediment traps which have been constructed in many of the main river outlets (EDF, 1999; Chapman, 2000). Field surveys found that in Baie du Nord and Baie Topaze a silt layer up to 2 m thick covers the seabed (EDF, 1999). This silt consists of particles of <16 μm, which is easily resuspended. Chapman (2000) also comments that sediment is readily re-suspended in many areas of the lagoon, particularly in the windy conditions which prevail over the island. Coastal channels around the island were found to have considerable terrigenous content (typically approximately 50 %) (Cross and Judge, 1990). A recent study of sediment distribution patterns confirmed that suspended sediment is deposited in northern and western areas of the lagoon in areas where currents are weakest (Lynch *et al.*, 2003a). Sediment entering the lagoon was found to be derived from both marine and terrestrial sources however the input of terrestrial material to the lagoon was shown to be episodic, occurring when heavy rain during January – March, may carry 55-412mg l^{-1} of eroded soil into the lagoon.

Sediment can affect coral colonies by physical damage through abrasion (Tomascik, 1991), smothering by the sediment (Wittenberg and Hunte, 1992) and by reducing coral recruitment as larvae are unable to successfully establish themselves in shifting sediments (Rogers, 1990). Extensive sedimentation may result in coral bleaching and tissue death (Marshall and Orr, 1931; Rogers, 1983; Peters and Pilson, 1985; Riegl, 1995; Nemeth and Sladek-Nowlis, 2001). In addition, suspended or overlying sediment can disturb a coral's energy budget by reducing the amount of light available which reduces zooxanthellar photosynthesis (Rogers, 1979; Suresh and Mathew, 1995), by interfering with the capacity to capture food and by increasing the energy demand for active sediment rejection (Kendall *et al.*, 1985; Stafford-Smith and Ormond, 1992; Riegl and Branch, 1995). Rogers (1990) quotes tolerable rates of sedimentation for coral reefs as being up to 10 mg cm^{-2} d^{-1}. Pastorok and Bilyard (1985) and Rogers (1990) predict that on reefs with high sedimentation rates (>10 mg cm^{-2} d^{-1}) species diversity will be low; live coral cover will be low; there will a greater abundance of resistant forms and species and there will be an upward shift in depth zonation. There will also be decreased growth rates, reduced recruitment and the predominance of altered growth forms (Pastorok and Bilyard, 1985).

Field studies have confirmed that coral reefs in high sediment sites are characterised by a decrease in coral species richness and a decrease in live coral cover (Squires, 1962; Roy and Smith, 1971; Loya, 1976; Cortés and Risk, 1985; Supriharyono, 1986; Acevedo *et al.*, 1989; Brown *et al*, 1990; Edinger *et al.*, 2000; Crabbe and Smith, 2002), an increase in the proportion of injured corals (van Katwijk *et al.*, 1993) and bleached corals (Nemeth and Sladek-Nowlis, 2001) and an increase in bare substrate (van Katwijk *et al.*, 1993; Crabbe and Smith, 2002). Van Woesik *et al.* (1999) and West and Van Woesik (2001) showed that coral cover decreased with increasing proximity to river mouths, due to increased suspended matter. Increased sedimentation as a result of heavy rainfall has also been shown to cause coral mortality. In Mexico increased soil erosion during periods of high rainfall resulted in coral mortality due to burial (Ochoa-Lopez *et al.*, 1998). Rainfall associated with Cyclone *Joy* on the Great Barrier Reef caused extensive flooding and this resulted in high coral mortality due to a combination of low salinity, sedimentation, sand blasting and decreases in ambient light (Van Woesik *et al.*, 1995). Furthermore, increased sedimentation associated with Hurricane *Firinga* resulted in 99 % mortality of coral colonies on a reef flat community in Réunion (Naim *et al.*, 1997).

In contrast, other studies have found that increased sedimentation and turbidity have had little impact on coral community composition (e.g. Sheppard, 1980; Dollar and Grigg, 1981; Perry, 2003; Schleyer and Celliers, 2003). Leão de Mara *et al.* (1999) found rich and diverse coral reefs close to the mouth of the River Amazon and there are healthy coral reefs in the Lakshadweep Islands, despite sedimentation rates of 125 mg cm^{-2} d^{-1} during the monsoon (Suresh and Mathew, 1993). The inner Great Barrier Reef is characterised by coral reefs, which have developed despite a long-term history of high terrigenous sediment input and high turbidity (e.g. Kleypass, 1996; Smithers and Larcombe, 2003). McClanahan and Obura (1997) found that on reefs under high siltation conditions, coral cover and diversity was comparable to healthy reefs. The high siltation reefs did however tend to be dominated by sediment tolerant corals such as *Porites* sp., *Echinopora* sp., *Galaxea* sp., *Hydnophora* sp., *Millepora* sp. and *Platygyra* sp., with a very low abundance of sediment intolerant corals such as *Favia* sp., *Montipora* sp. and *Pocillopora* sp.. Dodge and Vaisnys (1977) also found a change in species composition with increased sedimentation, from a reef dominated by *Diploria strigosa* to a reef dominated by *Diploria labyrinthiformis*. Van Woesik and Done (1997) also show that although there was no difference in coral cover on reefs in turbid and non-turbid regions, reefs in turbid areas tended to be predominately composed of encrusting and foliaceous coral colonies.

Suspended or overlying sediment may also disturb a corals energy budget, resulting in a number of sub-lethal impacts. Field studies have demonstrated a reduction in growth rates with increasing levels of sedimentation (Aller and Dodge, 1974; Dodge *et al.*, 1974; Dodge and Vaiŝnys, 1977; Tomascik and Sander, 1985; Tomascik, 1990). Experimental manipulations have also shown a negative correlation between growth rates and sedimentation, however shading, mimicking high turbidity, has been shown to have a greater effect than the direct addition of sediment (Rogers, 1979; Kendall *et al.*, 1985; Anthony, 1999; Te, 2001). Other studies have shown a reduction in reproductive activity (Tomascik and Sander, 1987), an inhibition of fertilisation (Gilmour, 1999) and a decrease in larval settlement (Hodgson, 1990; Babcock *et al.*, 2000) in areas of high sedimentation. High sedimentation has also been shown to affect a coral's ability to regenerate injuries (Meesters *et al.*, 1992).

As described in section 1.1, Rodrigues is situated on a large shallow shelf (McDougall *et al.*, 1965) and it is likely that throughout geological history the reefs have been subjected to constant resuspension of sediments on the this shallow shelf and thus may have developed in a naturally turbid environment. In addition, deforestation in the early 1800s appears to have resulted in heavy siltation within the shallow lagoon (Pearson, 1988; TROMES, 1995; EDF, 1999). This sediment is resuspended by wind-driven currents resulting in constant high turbidity within inshore areas. Sediment is transported onto the fore reef slopes by tidal currents, where it settles on the sea bed in sheltered areas (Lynch *et al.*, 2003). Furthermore, during periods of heavy rainfall, which tend to occur between January and March, there may be episodic influxes of terrestrially-derived sediment of up to 412mg l^{-1} carried by the rivers in to the lagoon.

Despite this high sediment/high turbidity environment, coral reefs in Rodrigues appear healthy with high coral cover and high species diversity, in contrast to many studies described above (e.g. Squires, 1962; Roy and Smith, 1971; Loya, 1976; Cortés and Risk, 1985; Supriharyono, 1986; Acevedo *et al.*, 1989; Brown *et al*, 1990; Edinger *et al.*, 2000; Crabbe and Smith, 2002), suggesting that coral reefs may have become adapted to these conditions. However, high sedimentation can also result in sub-lethal impacts to coral colonies due to disruptions to the energy budget and it is therefore possible that during periods of high rainfall the periodic increase in sediment input to the marine environment may have an effect on coral colonies on the fore reef slopes. This study will therefore concentrate on investigating whether this increased sediment load is having an impact on coral health, by assessing biological processes which are likely to be affected by changes in the energy budget as a result of high turbidity and sedimentation (coral growth, recruitment and regeneration from injury). The study will also determine whether coral colonies show any adaptations to the high sediment/turbidity conditions which are likely to have persisted for at least 200 years.

1.5 Coastal zone management in Rodrigues

Ile aux Cocos and Ile aux Sables were established as Nature Reserves for their plants and seabird colonies in 1981 (Cross and Judge, 1990). The two lagoon islands support important nesting sea bird colonies and original vegetation. Ile aux Cocos has large colonies of Brown *Anous stolidus* and Lesser Noddies *A. tenuirostris* (4000-7000 of each) and about 400 white terns *Gygis alba.* Ile aux Sables has smaller colonies of the same 3 species. Birds on these islands have been seriously disturbed by egg collectors.

At present the only marine protected areas are the 5 closed areas where seine net fishing is prohibited. These Fisheries Reserves were declared under the Fisheries Act 75 of 1984 and occur in the shallow inshore areas from Pointe Venus – Pointe la Gueule, Pointe la Gueule – Pointe Manioc, Baie Topaze, Anse Quitor and the outer section of Grande Passe (Figure 1.2). These areas are highly sedimented and unproductive and therefore Pearson (1984) recommended that further reserve areas be declared. These recommendations were never acted upon, however, the Non-Governmental Organisation, *Shoals Rodrigues,* has recently put forward 4 new reserves which have been approved by the Rodrigues Regional Assembly. The reserves will be at Rivière Banane, Anse aux Anglais, Grand Basin and Passe Démie. In addition, a UNDP-GEF project is planning to establish an integrated marine and terrestrial protected area at Mourouk (Figure 1.3).

1.6 Aims and objectives

Anthropogenic impacts tend to be chronic disturbances causing sub-lethal affects such as a reduction in reproduction and recruitment of coral colonies (Richmond, 1993). In Rodrigues, the major human impact to the marine environment is sedimentation, as a result of deforestation, with high turbidity occurring within the lagoon, however despite these conditions the reefs around Rodrigues appear healthy with high coral cover and high species diversity. However, as described in section 1.423 sediment may also disrupt a coral colony's energy budget, resulting in sub-lethal effects. The major focus of this work was therefore to assess the sub-lethal impacts of sedimentation on coral colonies on fore reef slopes in the north of Rodrigues by comparing coral growth rates, larval settlement and recovery from injury. The methods that coral colonies use to adapt to sedimentation were also investigated by studying changes in colony morphology and zooxanthellae densities.

The impact of sedimentation on coral colonies was addressed by:

- A quantification of sedimentation values and other environmental parameters at 3 study sites at increasing distance from the shore in the north of Rodrigues (Chapter 2).

The following chapters will investigate the sub-lethal impacts of sedimentation on coral colonies at these study sites by:

- An assessment of coral growth rates (Chapter 3)
- A determination of coral recruitment rates and regeneration from injury (Chapter 4).
- An investigation of coral colonies morphological and physiological adaptations to sedimentation (Chapter 5).

In contrast to anthropogenic impacts, natural disturbances are critical to the maintenance of diversity on reefs (Connell, 1973), however can be exacerbated by human impacts (Richmond, 1993). Coral reefs in Rodrigues are affected by two major natural impacts: cyclones and coral bleaching. During March 2003 coral bleaching was observed on the shallow reef flat in the north of the island. A study was therefore initiated to assess the extent of coral bleaching around the island, the degree of coral mortality and the impacts of the bleaching event to reef structure.

The impact of coral bleaching on the coral reefs of Rodrigues will be investigated by:

- An assessment of the extent of coral bleaching around the island, including vulnerable species.
- An investigation into impacts of the bleaching event on coral reef structure 1 year later (Chapter 6).

The results of the previous chapters will be summarised and discussed in relation to the future of coral reefs around in Rodrigues in Chapter 7.

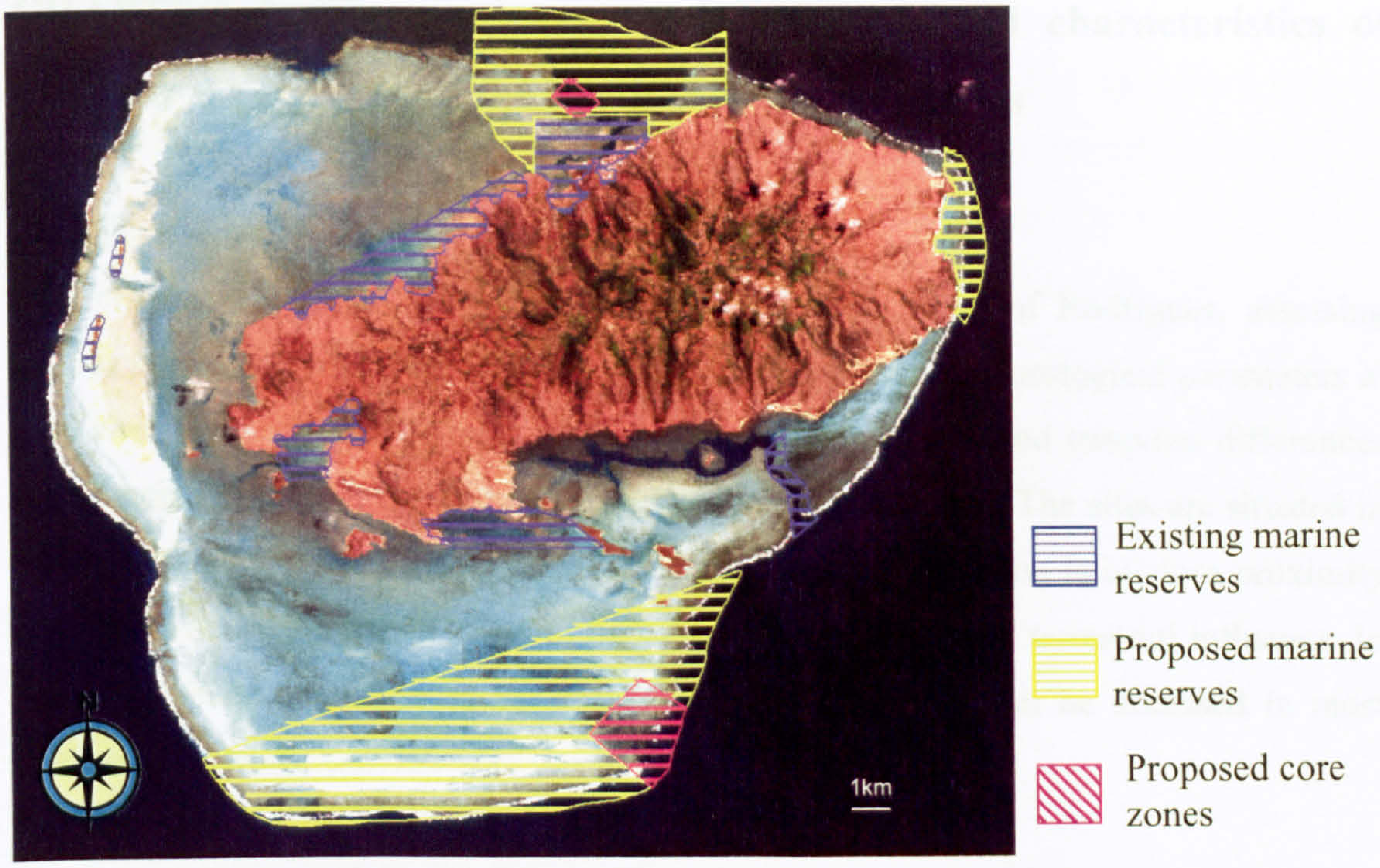


Figure 1.2. The existing and proposed reserve areas as identified by Pearson (1988). Adapted from Chapman and Turner (2001).

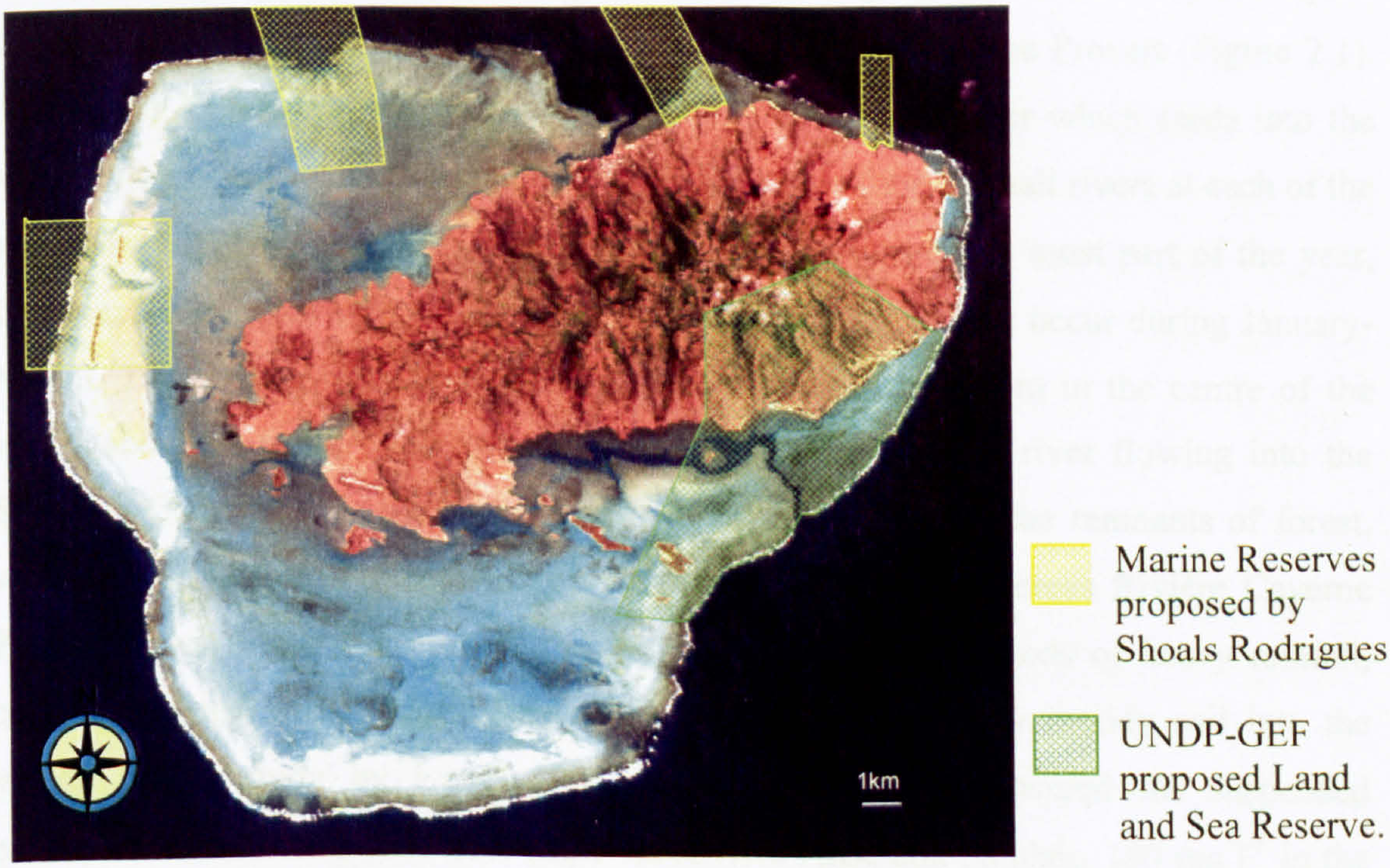


Figure 1.3 An estimation of the boundaries of the 4 marine reserves proposed by Shoals Rodrigues in the north of the island and the UNDP-GEF marine and terrestrial reserve at Mourouk. Landsat 7 satellite image processed by B. Chapman.

CHAPTER 2: The environmental and biological characteristics of three coral reef sites on the north coast of Rodrigues

2.1 INTRODUCTION

This chapter describes the 3 study sites on the north coast of Rodrigues, assessing species composition and diversity and environmental and meteorological parameters at each site. The chapter will particularly concentrate on spatial and temporal differences in sediment deposition and sediment composition at the 3 sites. The sites are situated in Port Mathurin Bay on the north coast of Rodrigues, as this region is in close proximity to the land and is therefore likely to be subjected to the greatest terrestrial influence. In addition, the area is close to the research station and sites can be accessed in most weather conditions.

2.11 Port Mathurin Bay

Port Mathurin Bay is situated in the north-east of Rodrigues. It is bordered by the capital Port Mathurin and the villages of Anse aux Anglais and Caverne Provert (Figure 2.1). The bay is linked to the terrestrial environment by a small river which feeds into the main shipping channel into Port Mathurin harbour and further small rivers at each of the two villages. These rivers tend to be dry or stagnant during the most part of the year, however flow following periods of heavy rainfall, which usually occur during January-March. The rivers originate in the high land around Mont Lubin in the centre of the island and tend to be overgrown with grasses and reeds. The river flowing into the Shipping Channel and Rivère Anse aux Anglais flow through the remnants of forest, which occur in the northern valleys, into developed areas, whereas Rivière Caverne Provert flows through pasture and cultivated land. During periods of heavy rainfall, often associated with cyclones, the rivers can be seen to carry muddy soil into the lagoon and a study by Lynch (2003a) in March 2002 measured the suspended particulate matter load to be 69.5 mg l^{-1} in Rivière Anse aux Anglais, 160 mg l^{-1} in the harbour at Pointe Monier and 202.7 mg l^{-1} in Rivière Caverne Provert. This sediment input, which is likely to have occurred episodically over the past 200 years since deforestation first took place, is carried into the shallow lagoon and can be seen flowing over the reef edge of the northern fore reefs close to the shore.

Lynch *et al.* (2003a) show that within the lagoon, sediment depths commonly exceed 4m, indicating significant infilling of the lagoon, however sand is the most important component of this sediment. The fine grained silt and clay particles are kept in suspension by wind-driven currents resulting in high turbidity (up to 40-50mg l^{-1}) throughout the lagoon. In areas close to passes and at the reef edge these particles are then transported from the lagoon by tidal currents to slightly deeper, sheltered areas offshore. Port Mathurin Bay is sheltered from the prevailing winds, which tend to come from the south-east and east, although outer reefs are exposed to the north-easterly winds. The reefs in the centre of the bay and on the eastern side are therefore sheltered from wave action, whilst reefs towards the edge of the bay and on the western side are exposed to ocean swell. The bay area tends to have high turbidity, particularly at the sheltered sites close to the shore.

In the centre of the bay, the reef slope consists of steep walls and spur and groove formations are poorly developed. Towards the edge of the bay however, the reef consists of more gradual spur and groove formations. All reefs within the bay tend to be shallow, rarely exceeding 20 m, where they meet a gently sloping sand/silt plain extending to at least 30 m. Pearson (1988) surveyed 2 sites within Port Mathurin Bay. He described the reef at the inner site (Totor) as a steep slope and commented that corals were in poor condition but diversity was relatively high, with diversity and condition improving above 10 m depth. The reef towards the edge of the bay (Chaland) is described as a spur and groove formation, dominated by platy corals down to approximately 20 m depth, where there is a sand/silt plain sloping to great depths. Pearson (1988) commented that the corals are in excellent condition.

Chapman (2000) places the inner reefs within biotope CR14, which is described as "steep reef slopes with diverse corals, dominated by laminar *Montipora* on the steep lower slopes, and branching and table *Acropora* on the shallow slopes". These sites tend to have low visibility of between 8 – 15 m, and are sheltered from wave action, with very little current. Coral cover is high ranging from 51 – 75 % with between 44 and 55 invertebrate and macro-algae species at these sites. Reefs towards the edge of the bay are placed within biotope CR15, which is described as "irregular spur and groove formation, spurs dominated by *Acropora abrotanoides* on tops, and massives and submassives on sides". These sites have visibility ranging from 12 – 15 m, are more exposed to wave action, but also have very little current. Coral cover at these sites is between 51 – 100 % and 45 – 53 invertebrate and macro-algae species were recorded. Fenner *et al.* (2004) reports between 24 and 43 coral species from reefs within Port Mathurin bay.

Pearson (1988) commented that corals at the inner ref site are in poor condition and stated that this is due to high sedimentation at the site. He also noted that the reef crest at this site was destroyed by octopus fishers trampling on the reef at low tide. Recent surveys confirm this observation and Clark (2001) reports that coral cover on the reef crest at Totor is now only 2-5 % due to trampling by octopus fishers. In contrast, Pearson (1988) noted that corals at the outer reef site were in excellent health, however he did state that corals on the reef crest were also damaged by fishermen and that handline fishing took place on the reef slope. Lynch *et al.* (2000; 2002) report approximately 40 % cover of living hard corals at a site close to the one surveyed by Pearson (1988), with 88 % of all corals alive. In 2002 surveys (Lynch *et al.*, 2002) noted low levels of anchor damage to coral at this site and discarded ropes.

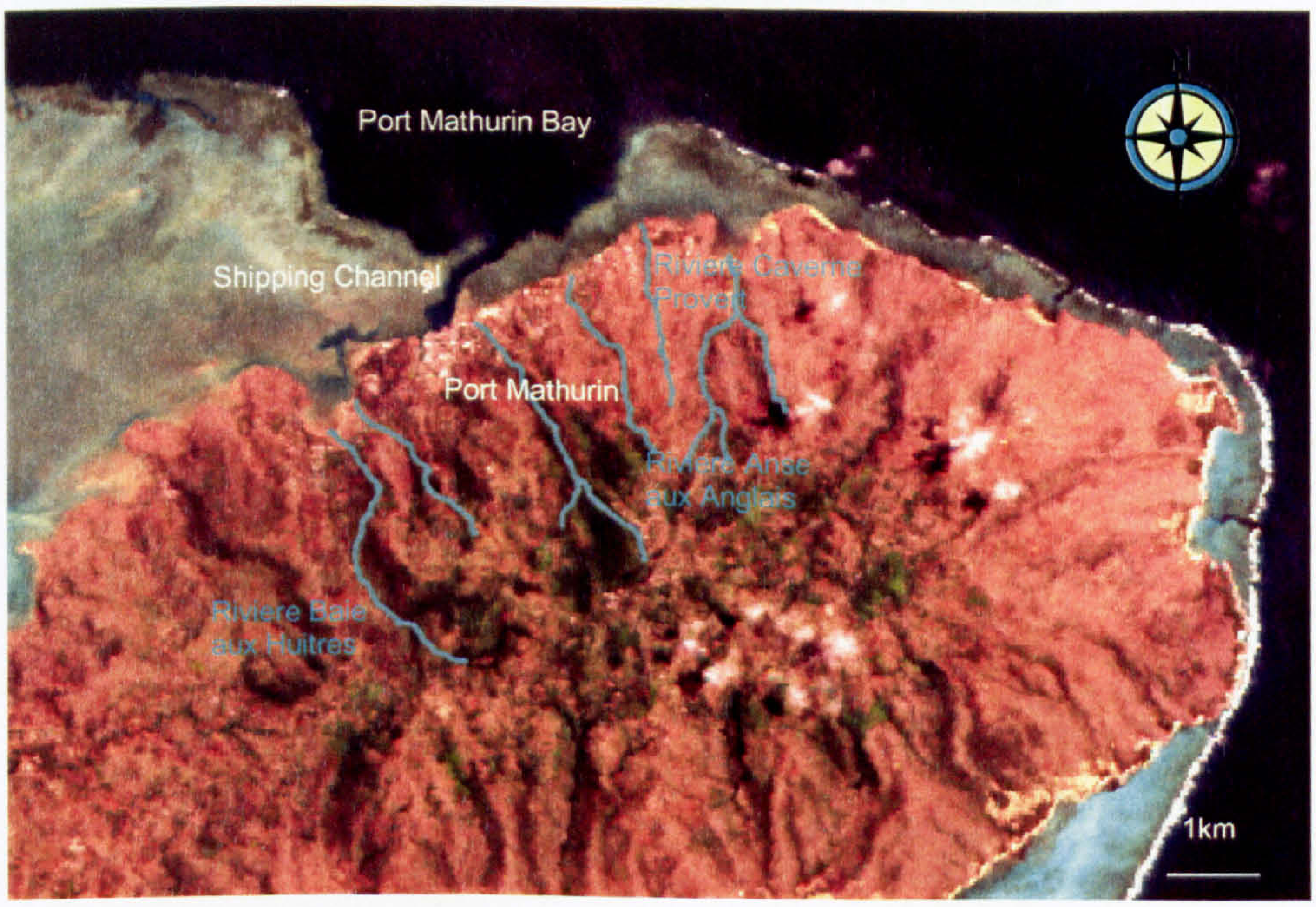


Figure 2.1 Port Mathurin Bay in the north-east of Rodrigues, indicating the rivers flowing into the northern lagoon.

2.12 Aims and objectives

The aims of this chapter are to identify three survey sites on the north coast of Rodrigues, which are similar in structure and easy to access on a regular basis, and to describe the biological, physical and meteorological parameters at each site. These objectives will be met by:

- Assessment of the benthic composition of each of the 3 reef sites, including hard and soft coral species diversity, using rapid assessment techniques.
- Determination of temporal changes in environmental parameters (temperature, salinity, visibility and light attenutation) at the 3 survey sites over two 4-month periods in 2002 and 2003.
- Quantification of variations in sediment deposition at each of the 3 survey sites over two 4-month periods during 2002 and 2003.
- Assessment of changes in sediment composition (particle size and organic content) at the 3 survey sites over two 4-month periods during 2002 and 2003.
- Investigation of changes in meteorological conditions by studying temperature, sunshine, rainfall, cloud cover and wind speed data provided by the Mauritius Meteorological Services during the 2 survey periods.

2.2 METHODS

2.21 Site selection

Exploratory dives were carried out at a number of sites around Port Mathurin Bay and from these dives, 3 comparable study sites at Totor, Trou Malabar and Chaland were selected. In order to assess whether coral reefs are affected by sediment from episodic fluvial inputs the 3 sites were located at increasing distances from the shore (and sources of riverine inputs), were accessible during most weather conditions and were within 20 minutes boat journey from the laboratory (Table 2.1, Figures 2.2, 2.3). Each site was marked using a hand-held GPS (Global Positioning System, Magellan 320) and a sub-surface marker buoy (plastic bucket tied to the substrate) on the reef. All diving was carried out according to the University of Wales Bangor/Shoals Rodrigues diving regulations and the relevant permits were provided by the Mauritius Ministry of Fisheries.

Table 2.1 The position and basic description of the 3 survey sites on the north coast of Rodrigues.

Site Name	Latitude	Longitude	Description
Totor	19° 40.189 S	63° 25.748 E	Sheltered site close to mouth of shipping channel, 700m offshore.
Trou Malabar	19° 40.254 S	63° 25.017 E	Sheltered site to the north of the shipping channel, 1.1km offshore.
Chaland	19° 39.956 S	63° 24.577 E	Moderately exposed site approximately 1km from the mouth of the shipping channel, 1.8km offshore.

At each of the 3 sites a rapid assessment was made of the reef structure and biological composition. Timed surveys of 60 minutes duration were carried out over a 100 x 100 m area during February 2002. Two levels of visual survey were made (Devantier *et al.*, 1998, Turner *et al.*, 1999). Broad scale physical and biological features of the reef were first recorded using a 6-point semi-quantitative scale (0 = 0 %; 1 = <1 %, 2 = 1-10 %, 3 = 11-30 %, 4 = 31-50 %, 5 = 51-75 % and 6 = 76-100 %). Substratum categories used were live hard coral, dead standing coral, soft coral, turf algae, macro-algae, coralline algae, sponges or other, unconsolidated rubble, hard substrate, sand and silt. A second level description of the species composition of the reef was also made, in which the biodiversity of hard and soft coral species and other invertebrates was assessed at each of the 3 sites. All hard and soft coral species encountered were recorded in an underwater notebook. Hard corals were identified to species where possible using Veron

(2000) (except for genus *Acropora*, when Wallace (1999) was used). Soft corals were identified using Fabricius & Alderslade (2001) and other species using Richmond (1997). In addition, photographs were taken of coral species on a dive during April 2003 using an Olympus C5050z 5.0 Mega pixel digital camera in an underwater housing (Olympus PT-15).

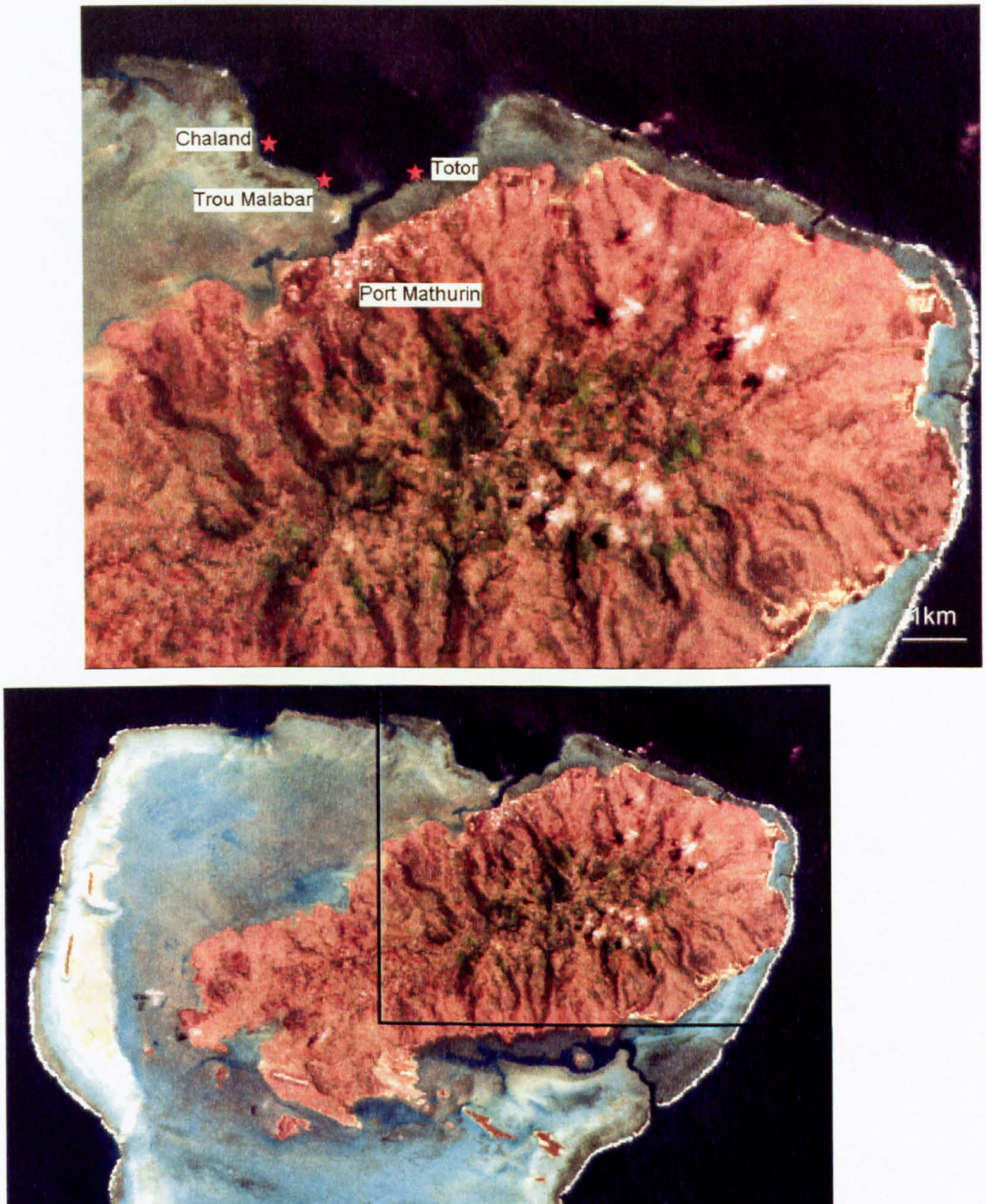


Figure 2.2 The position of the 3 survey sites on the north coast of Rodrigues. Landsat 7 satellite image processed by B. Chapman.

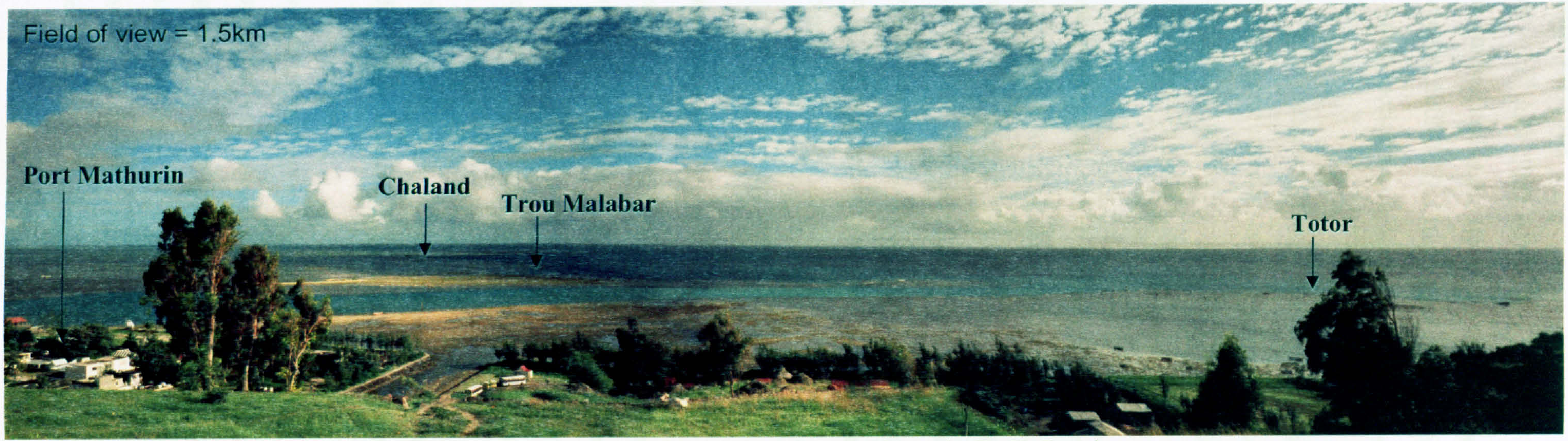


Figure 2.3 The 3 survey sites around Port Mathurin Bay, taken from Pointe Canon. Photos by Dr K. Dernie.

2.23 Environmental variables

Between 3rd April – 21st June 2002 and 7th April and 19th June 2003 water temperature and salinity at the surface and at the survey depth were recorded before each dive using a CTD probe (Valeport 600MKII). Due to equipment failure, water temperature at other times during the survey period was measured using a dive computer (Suunto Spyder).

Vertical visibility was measured using a Secchi disc at each site before each dive (approximately 4 times per month) during February – June 2002 and April – August 2003. Horizontal visibility at the study depth (10-12 m) was also measured using a Secchi disc between April – August 2003.

Downwelling photosynthetically active radiation (PAR) was measured at 1 m intervals at depths ranging from 0 m to the seabed (13-18 m depth) at 2 of the sites (Totor and Chaland) between 3rd June and 4th July 2002 using a PAR underwater quantum sensor (LI COR LI-192 SA). The sensor was deployed from a boat at noon, where possible, and data were logged using a data logger (underwater model LI1000). Measurements were made as the sensor was both lowered to the seabed and raised to the surface and the mean value found.

2.24 Sediment deposition

Three sediment trap stands (galvanised stakes), each containing 3 sediment traps (plastic 0.4 litre containers) were hammered into the substrate at the base of the reef slope at a depth of 10-13 m (Plate 2.1). Sediment traps had a height of 13 cm and a width of 7 cm and were set 20 cm above the sea bed. Four baffles were inserted into the mouth of each trap to reduce the formation of eddies in the water column above. Traps were collected and replaced in the stands every 4 weeks. Sediment collected was oven dried at 110 °C for 48 hours and dry weight determined using a Status SP300 balance (±0.01 g).

The sediment was then ground up with a pestle and mortar and grain size analysis was carried out. The sediment was placed in a Retsch AS200 sieve shaker for 10 minutes and shaken through a series of 6 graduated sieves at 60 amplitudes. Each of the size fractions was then weighed using an electric balance. In order to assess organic content samples were returned to the UK and weighed using a Sartorius BP-3105 balance (±0.001 g). Samples were then placed in a muffle furnace for 6 hours at 550 °C and then re-weighed to determine the ash free dry weight. During 2002 organic content of sediment was only determined for 1 month (April-May), however during 2003 organic content was determined for sediment from the whole 4 month period.

Plate 2.1 A sediment trap stand containing 3 sediment traps on the reef at Trou Malabar.

2.25 Meteorological data

Meteorological data for Rodrigues were obtained from the Mauritius Meteorological Services. Data were obtained for monthly air temperature (minimum and maximum, °C), sunshine (total hours of sunshine per month) and rainfall (total monthly rainfall, mm) for January 1997 – September 2003 (data from May – December 1999 are missing). Data were also obtained for cloud cover (number of observations of 0, 1-2, 3-5, 6-7 and 8 oktas per month, based on 7 observations per day) and mean wind speed (km/hr, based on 4 observations per day) for January 2000 to September 2003 and for wind direction (based on 4 observations per day) for January to September 2003.

2.3 RESULTS

2.31 Site description

Reef structure at the 3 sites is similar, however as the reef becomes more exposed to wave action it changes from a steep wall to a spur and groove structure. All sites have high hard coral cover ranging from 51-75 % at Totor and Trou Malabar to 31-50 % at Chaland (Figure 2.4). Dead standing coral is low, <10 % at Totor and Trou Malabar and 1-10 % at Chaland and turf and macro-algae cover is low (1-10 % and <1 % at all sites, respectively), indicating that the reefs are healthy. The percentage cover of silt decreases from Totor (11-30 %), to Trou Malabar (1-10 %) to Chaland (<10 %) and the percentage cover of sand increases.

Biodiversity of hard coral species was highest at Chaland (59) and lowest at Trou Malabar (49) (Table 2.2). The number of coral genera and coral families was however higher at Chaland than at Totor and Trou Malabar. Acroporidae diversity was high at all 3 sites, however at Totor it consisted of more branching *Acropora* species, whereas at Chaland the family was composed of more encrusting *Montipora* species. Chaland also had a higher diversity of Faviids than Totor and Trou Malabar (Table 2.3). Cluster analysis confirmed that the sites had similar species composition with 84.22 % similarity based on number of species in each genus (Figure 2.5). Based on the number of species within each genus Chaland and Trou Malabar were found to be more similar to each other, than to Totor.

Table 2.2 The number of Scleractinian species, genera and families at each of the 3 survey sites.

	Totor	Trou Malabar	Chaland
Species	55	49	59
Genera	26	25	29
Families	11	11	12

Species diversity of soft corals and other invertebrates was low. Only 3 genera of soft coral were recorded at Totor and Trou Malabar and 4 genera were recorded at Chaland. Only 5 species of other invertebrates were recorded: 3 species of echinoderm (*Echinometra mathaei, Diadema setosum* and *Stichopus chloronatus*), 1 species of mollusc (*Tridacna* sp.) and 1 species of crustacean (*Panulirus* sp). At Totor 2 species of echinoderm, 1 mollusc and 1 crustacean were recorded; all 5 invertebrate species were observed at Trou Malabar, where as at Chaland only 2 species of echinoderm were recorded.

Table 2.3 The number of species within each Scleractinian family at each of the 3 survey sites.

Family	Totor	Trou Malabar	Chaland
Pocilloporidae	2	1	3
Acroporidae	14	14	13
Poritidae	5	4	5
Siderastreidae	1	0	3
Agariciidae	5	4	2
Fungiidae	1	1	1
Oculinidae	1	1	1
Pectiniidae	6	4	5
Mussidae	5	3	6
Merulinidae	0	1	1
Faviidae	12	15	18
Dendrophyllidae	2	1	1

A description of each site is given below.

Totor

The site at Totor is a fore reef slope situated at the southern entrance to the main shipping channel, 700 m offshore. The site is sheltered and visibility is always poor (<10m). The reef consists of a steep wall rising from a fine silt seabed at 12 m depth up to 3 m. Below 12 m the seabed is a gentle silty slope with occasional hard coral colonies down to 18 m+. The base of the wall at 12 m is colonised by large laminar colonies, >0.5m in diameter, such as *Montipora aequituberculata, Pachyseris speciosa, Mycedium* sp., *Oxypora* spp. and *Echinophyllia* sp. as well as small massives (*Favia* spp. *Favites* spp., *Platygyra* spp.) and soft corals (*Sarcophyton* sp. and *Sinularia* sp.). At 8 m the wall is colonised by laminar *M. aequituberculata*, branching, tabular and corymbose *Acropora* spp., *Porites rus* and small massives (*Goniastrea* spp., *Favia* spp., *Platygyra* spp.). The top of the wall at 3-6 m is colonised by branching and tabular *Acropora* spp. with diverse massive and sub-massive species (Plate 2.2). Very few invertebrates were observed, *Tridacna* sp. and *Diadema* sp. were occasional on the reef slope, although *Echinometra mathaei* were abundant at 3-4 m depth.

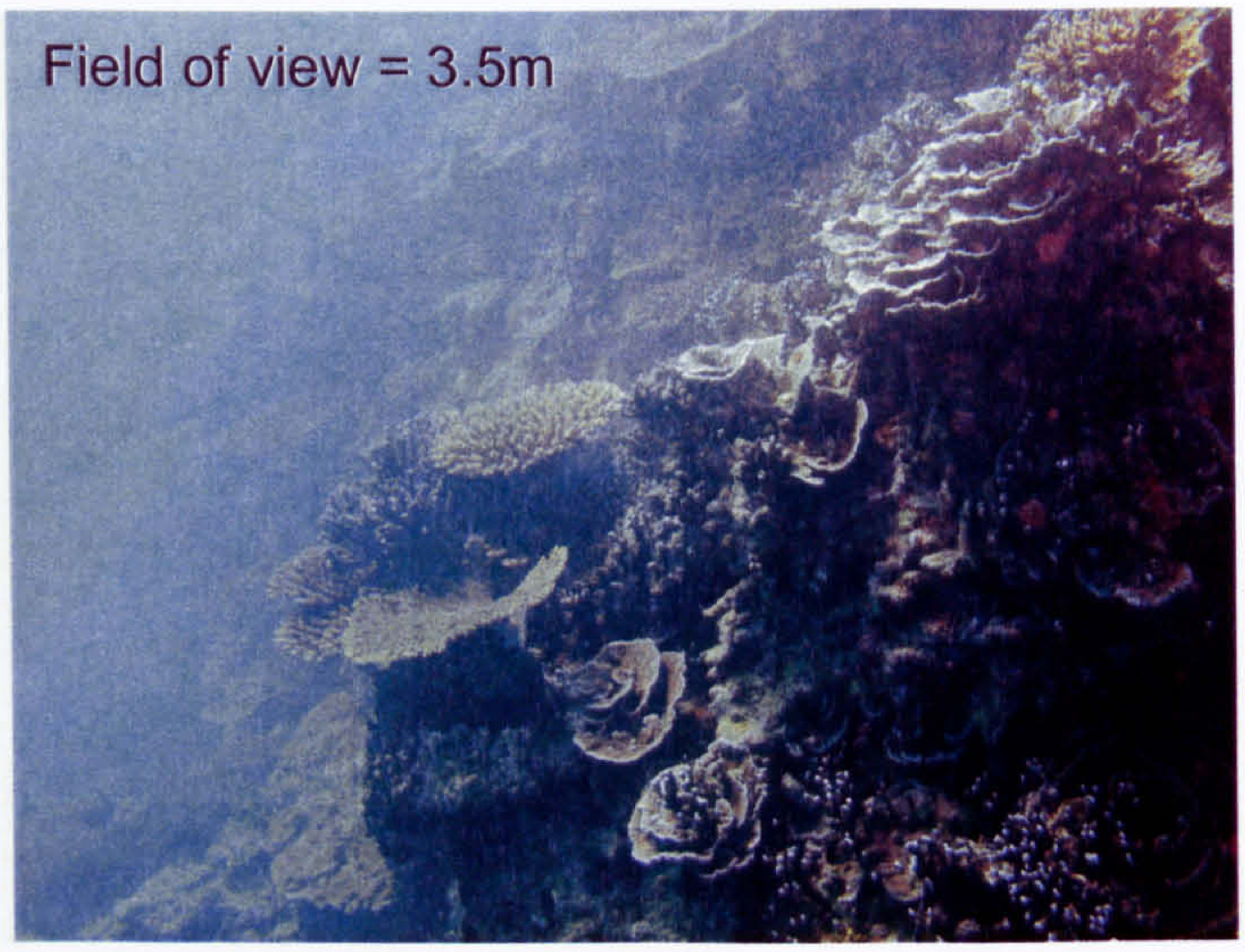
Trou Malabar

The site at Trou Malabar is a fore reef slope situated to the north of the shipping channel, close to Ile Hollandaise, approximately 1 km west of Totor and 1.1 km offshore. The site is sheltered from the prevailing winds but is exposed to north-easterly winds; visibility can be poor (<12m). The reef consists of a steep wall rising from a coarse silt and rubble seabed at 10 m depth up to 2 m. Below 12 m the seabed is a gentle slope with occasional hard coral colonies down to 18 m+. The reef has a slightly spurred structure with some deep gullies. The base of the wall has low coral cover (<30% cover) and is colonised by large laminar species, >0.5m in diameter, such as *Pachyseris speciosa, Mycedium* sp., *Oxypora* spp. and *Echinophyllia* sp. as well as small massives (*Favia* spp. *Favites* spp.) and soft corals (*Sarcophyton* sp. and *Sinularia* sp.). The wall between 6 and 10 m is colonised by *Montipora aequituberculata,* which forms tiered monospecific stands, *Porites rus,* branching and tabular *Acropora* spp., and diverse massives *(Faviids, Porites)*. The top of the wall is colonised by branching and tabular *Acropora* spp. with diverse massive and sub-massive species (Plate 2.3). *Tridacna* sp., *Diadema* sp. and *Echinometra mathaei* were occasional, however *Stichopus chloronatus* were abundant in the rubble at the base of the wall. Corals at the site suffered mortality between June 2002 and April 2003 and there were large areas of dead standing corals covered with a thin layer of silt.

Chaland

The site at Chaland is a fore reef slope situated on the western side of Port Mathurin Bay approximately 1 km north of Trou Malabar and 1.8 km offshore. The reef is exposed to easterly and north easterly winds and visibility tends to be good (10-15m). The reef consists of irregular spurs and grooves; spurs are approximately 50 m wide and grooves up to 15 m wide. The spurs rise steeply from a coarse silt and rubble base at 22 m depth up to 7 m, where they slope more gently up to 4 m. The lower spurs, below 15 m, have 50-75% coral cover and are colonised by small laminar and encrusting species, <0.5m in diameter, such as *Pachyseris speciosa, Echinophyllia* spp., *Oxypora* spp., *Mycedium* sp., *Turbinaria* sp. and soft corals (*Sarcophyton* sp. and *Sinularia* sp.). The spurs are colonised by laminar and encrusting *Montipora* spp., *Porites rus*, diverse massive (Faviids), branching and tabular *Acropora* spp. and large colonies of *Lobophyllia corymbosa.* The upper spurs have a higher cover of dead coralline substrate and are colonised by branching and tabular *Acropora* spp., with diverse massive and sub-massive species (Plate 2.4). Very few invertebrates were observed and *Diadema* sp.

and *Echinometra mathaei* were occasional. Corals at the site suffered fairly severe mortality between June 2002 and April 2003 and most branching *Acropora* and many *Lobophyllia* colonies were damaged.



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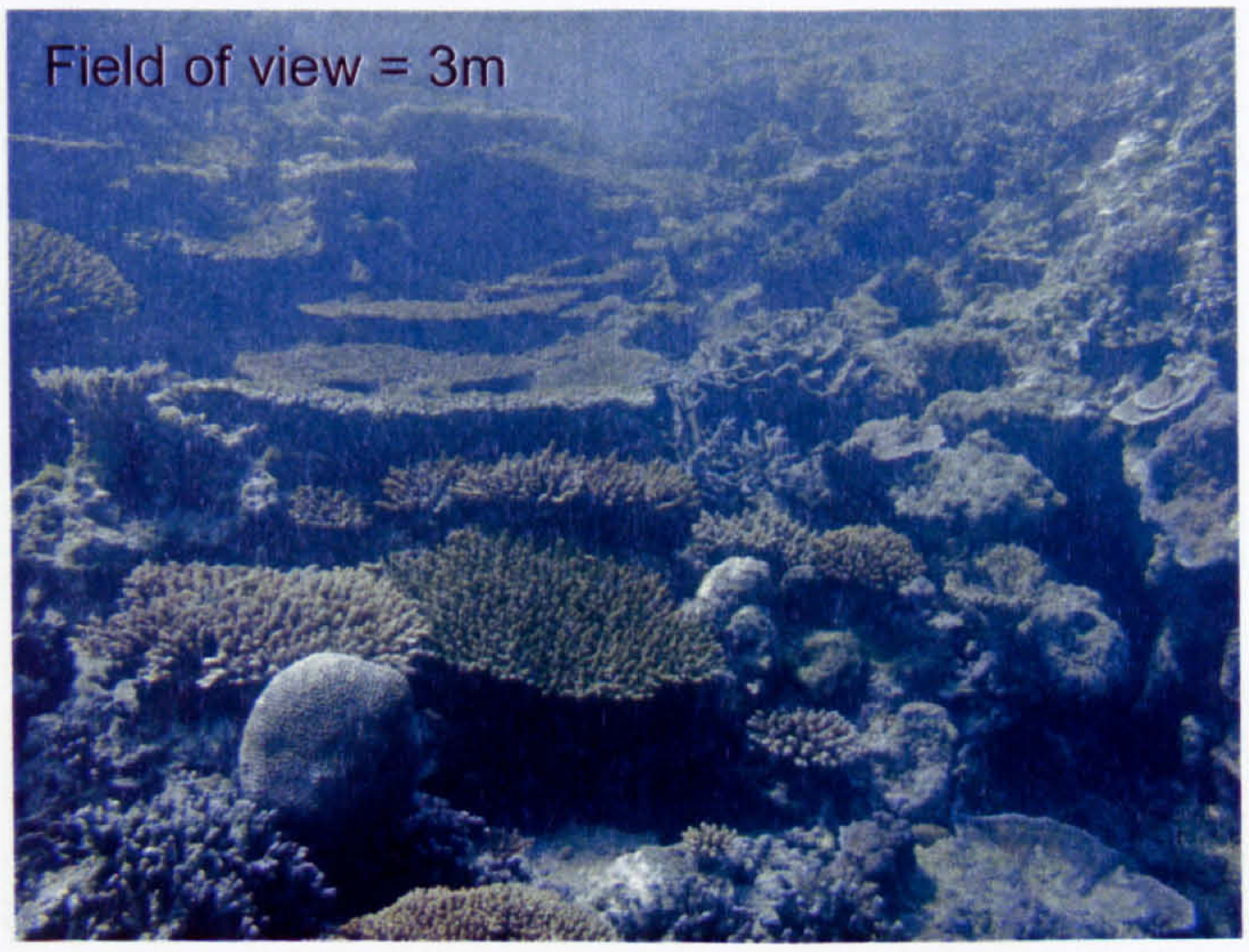

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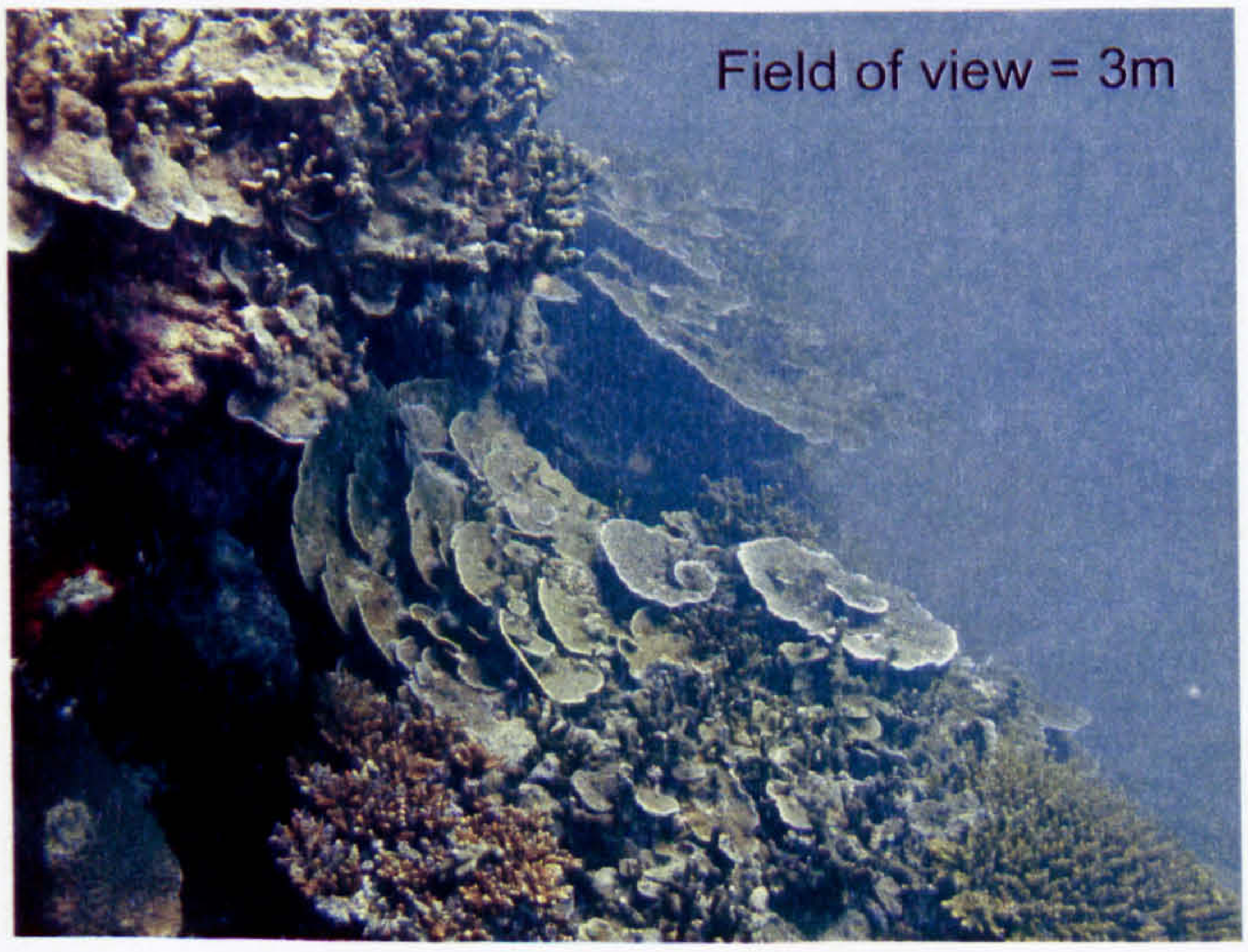
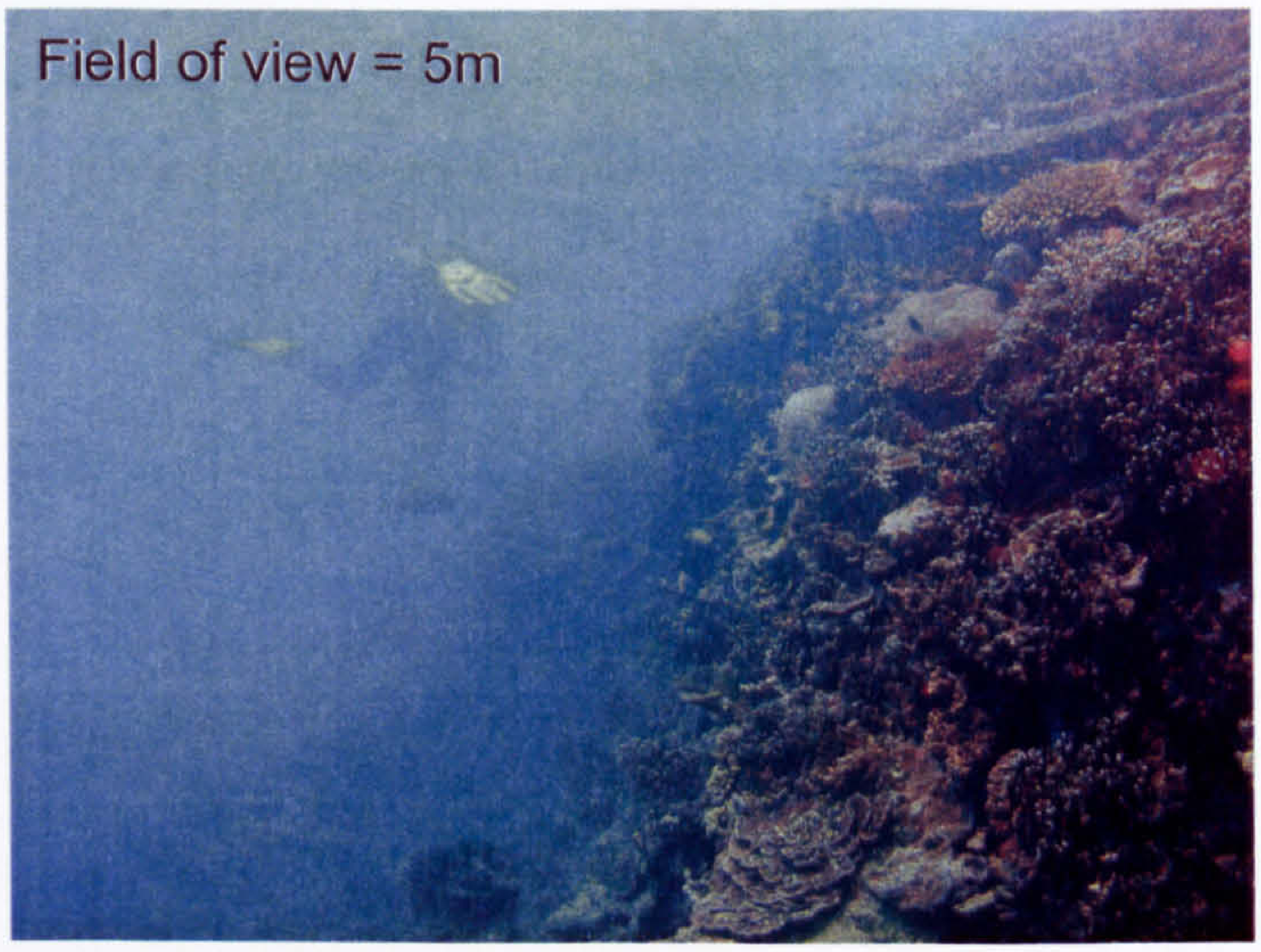


c)

Plate 2.2 The reef at Totor, (a) general reef structure (b) the reef at 5-6m depth, with branching and tabular *Acropora* spp. with diverse massives and submassives, (c) the reef at 10m depth, with laminar *Montipora*, branching *Acropora* and *Porites rus*.



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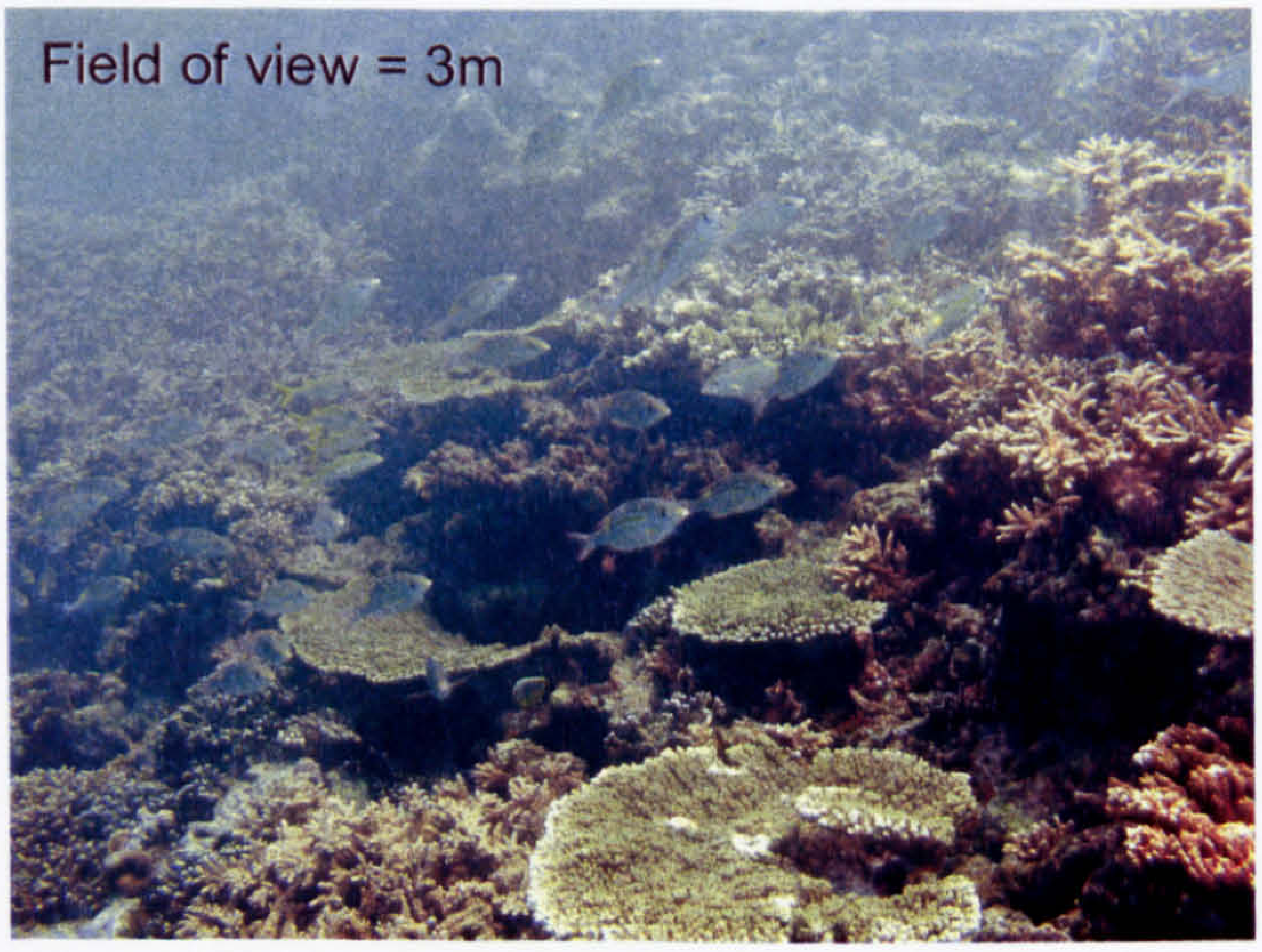

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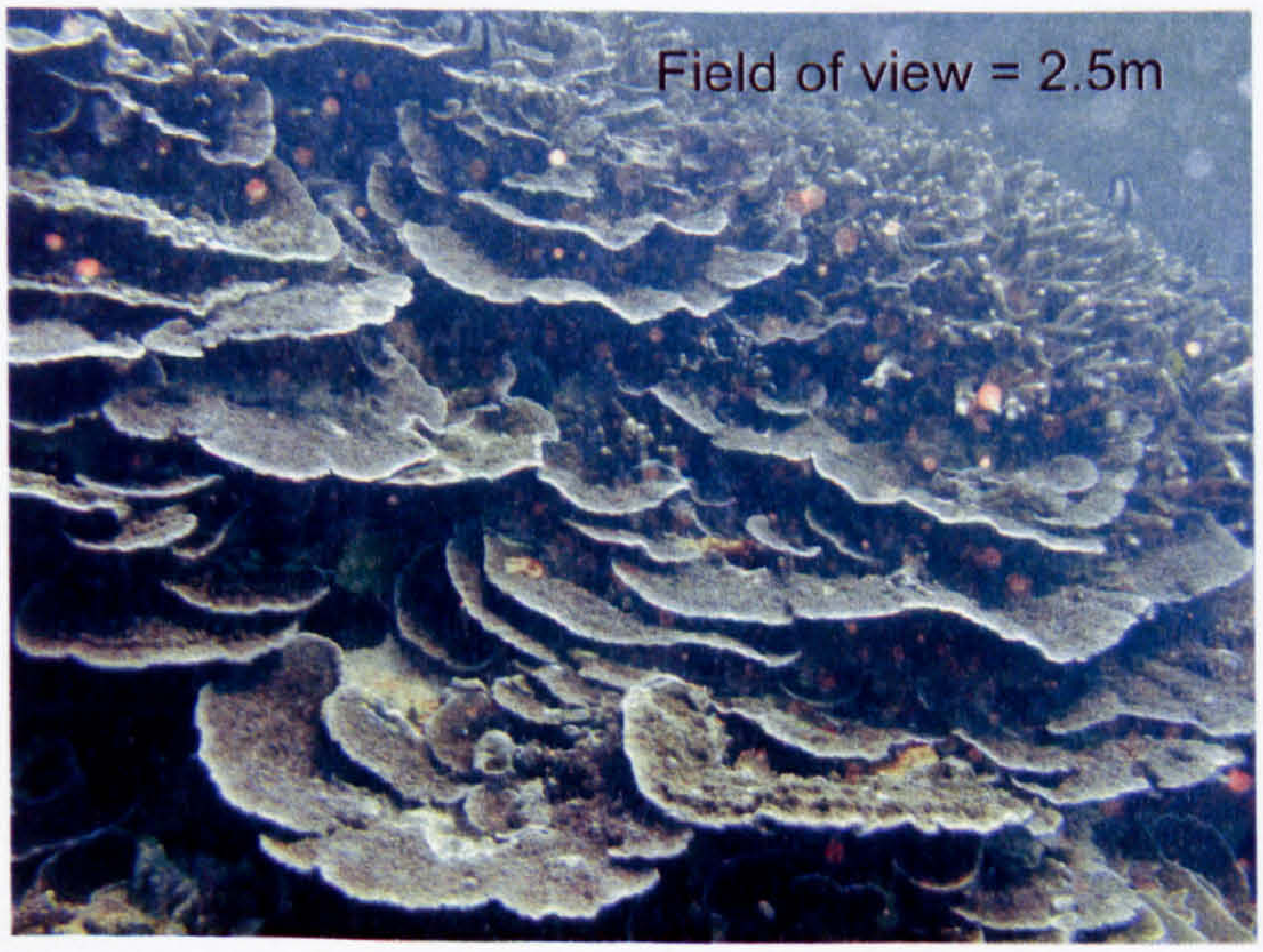
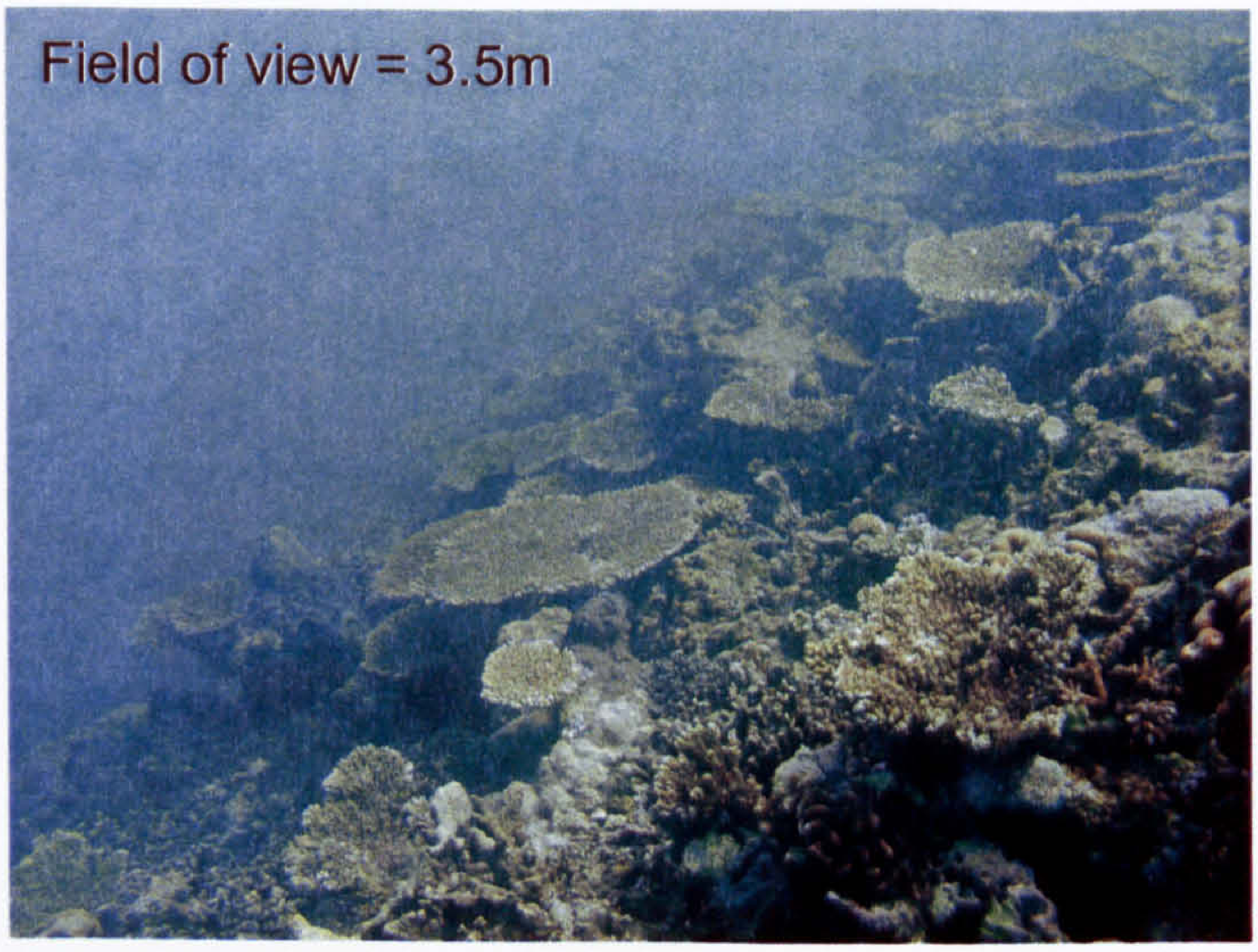


c)

Plate 2.3 The reef at Trou Malabar, (a) general reef structure, (b) the reef at 5-6m depth, with branching and tabular *Acropora* spp. (c) the reef at 10m depth, dominated by *Montipora aequituberculata* with branching *Acropora* spp.



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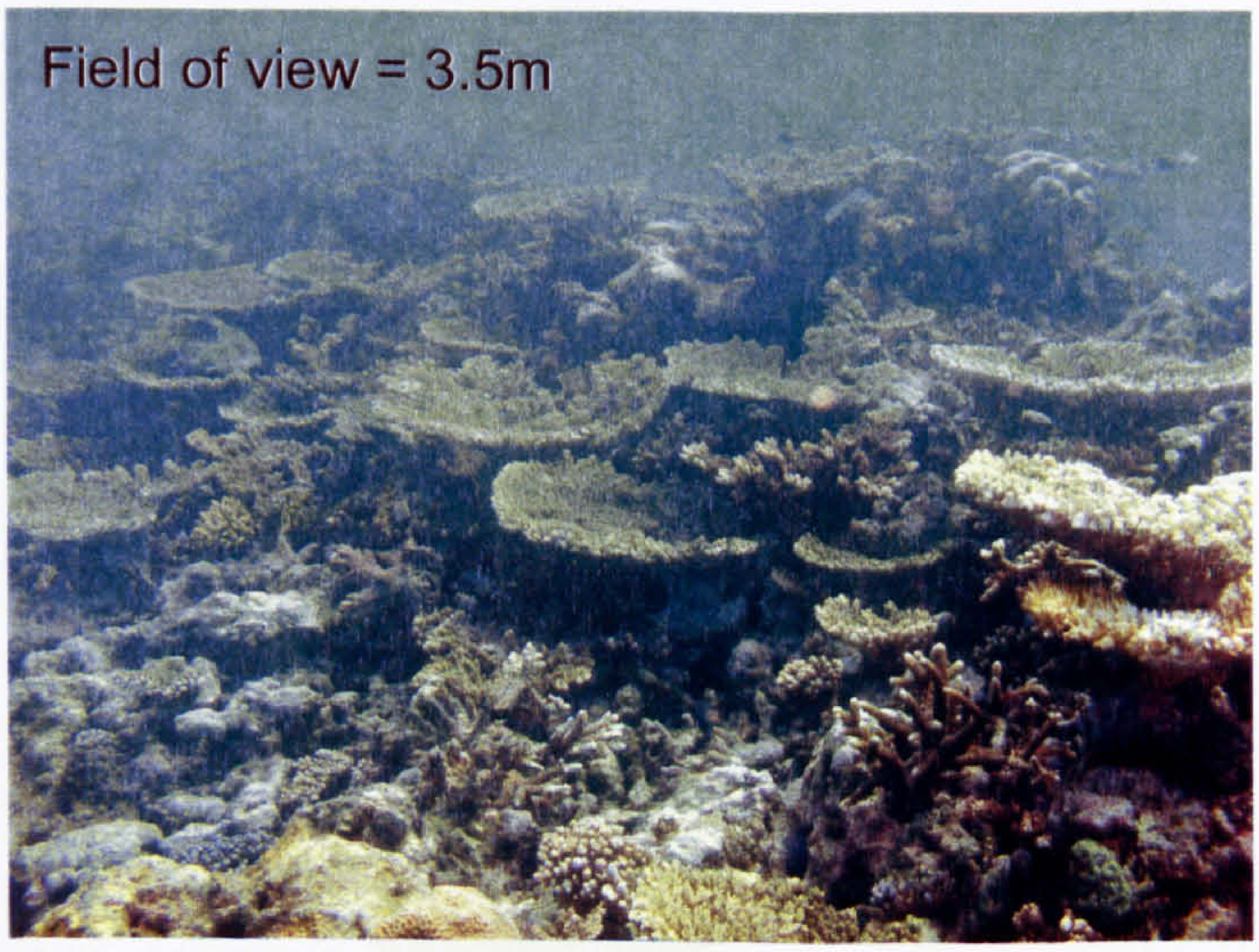

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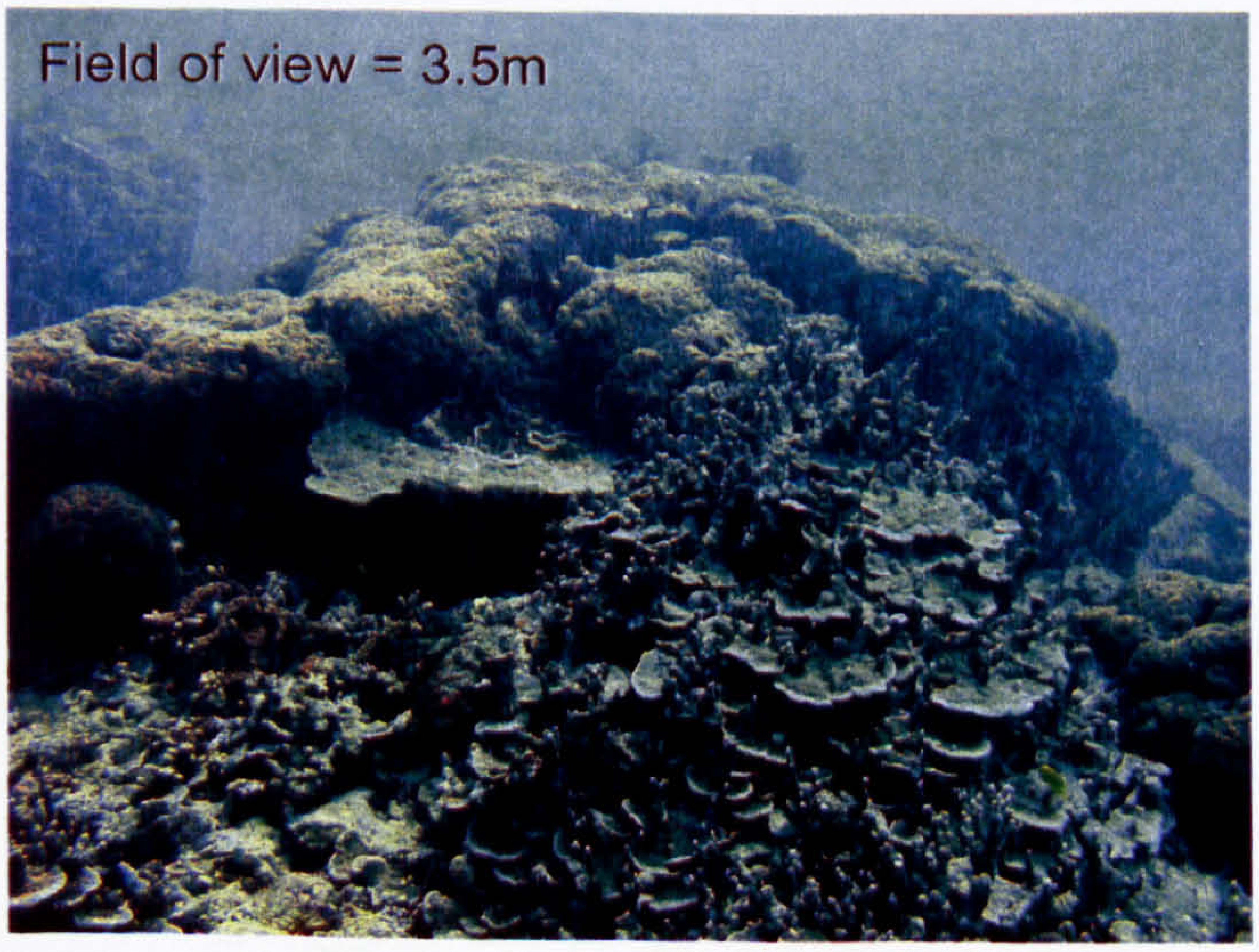


c)

Plate 2.4 The reef at Chaland, (a) general reef structure, (b) the reef at 5-6m depth, with branching and tabular *Acropora* spp. with diverse massives and submassives, (c) the reef at 12m depth, with *Lobophyllia corymbosa* and *Porites rus*.

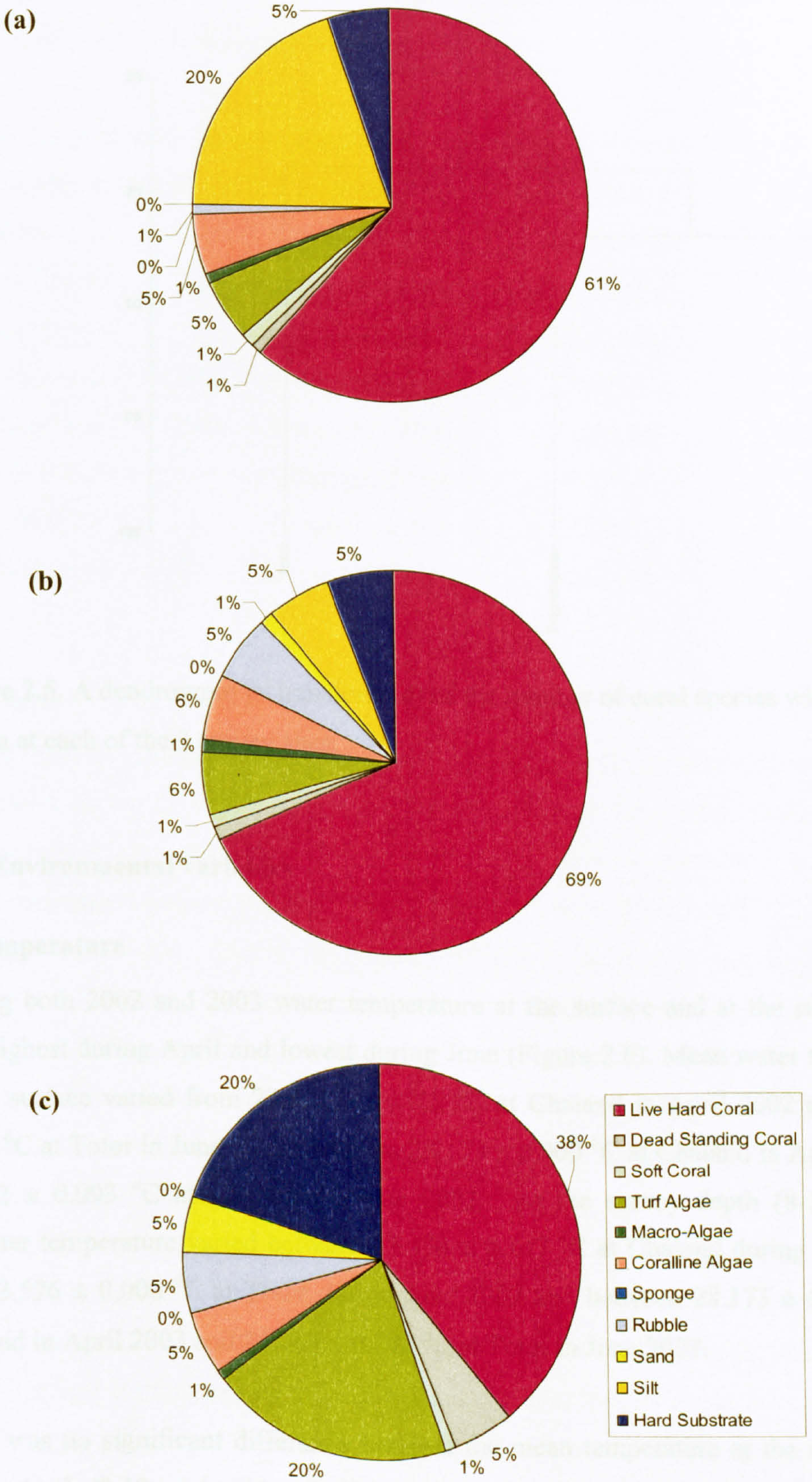


Figure 2.4 The percent cover of benthic substrate types (based on the mid-point of each percent cover category) at (a) Totor, (b) Trou Malabar and (c) Chaland, based on a rapid assessment survey.

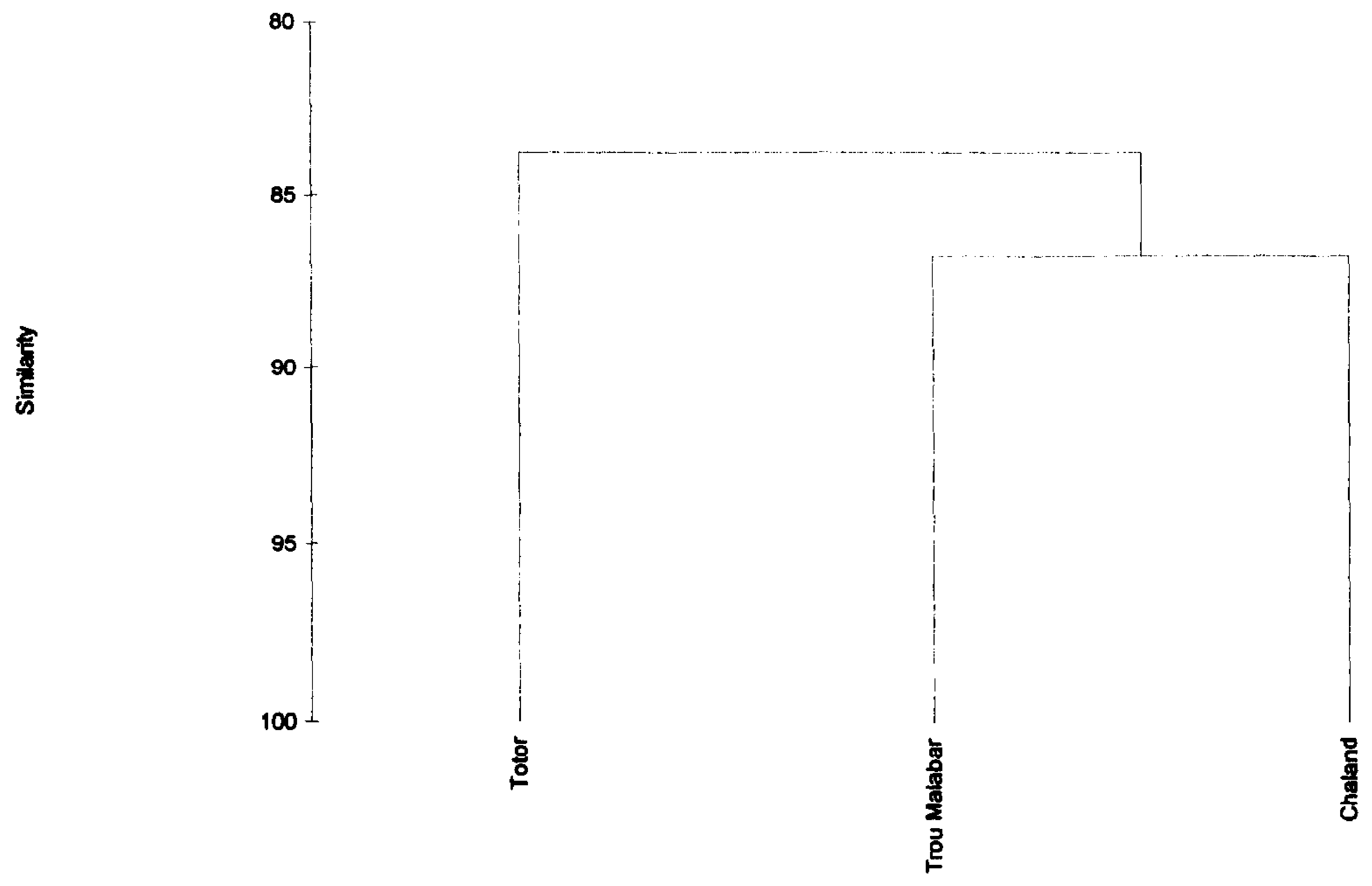


Figure 2.5. A dendrogram (√ transformed) of the number of coral species within each genera at each of the 3 survey sites.

2.32 Environmental variables

a) Temperature

During both 2002 and 2003 water temperature at the surface and at the survey depth was highest during April and lowest during June (Figure 2.6). Mean water temperature at the surface varied from 27.822 ± 0.1722 °C at Chaland in April 2002 to 23.615 ± 0.000 °C at Totor in June 2002 and from 28.173 ± 0.000 °C at Chaland in April 2003 to 25.172 ± 0.093 °C at Chaland in June 2003. At the survey depth (8-12m) mean seawater temperature varied between 27.454 ± 0.147 °C at Chaland during April 2002 and 23.576 ± 0.000 °C at Totor during June 2002 and between 28.173 ± 0.000 °C at Chaland in April 2003 and 25.103 ± 0.272 °C at Totor in June 2003.

There was no significant difference between the mean temperature at the surface and survey depth (8-12 m) in either 2002 or 2003 at the 3 survey sites (Table 2.4). During both 2002 and 2003 the mean temperature was significantly higher in April than in May or June and significantly higher in May than in June (Figure 2.6; Table 2.4). There was no significant difference in mean temperature during April 2002 and April 2003 nor between May 2002 and May 2003. Mean temperature during June 2002 was however, significantly lower than during June 2003.

Table 2.4 Statistical analysis results for temperature data measured at all sites during April – May 2002 and 2003. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	p
Surface*Depth	2002	1-way ANOVA	0.74 (F)	1	>0.05
Surface*Depth	2003	1-way ANOVA	0.02 (F)	1	>0.05
Apr*May*Jun	2002	1-way ANOVA	174.97 9F)	2	<0.05*
Apr*May*Jun	2003	1-way ANOVA	52.03 9F)	2	<0.05*
Apr 2002*2003	-	2-sample T-test	0.20 (T)		>0.05
May 2002*2003	-	2-sample T-test	2.65 (T)		>0.05
Jun 2002*2003	-	2-sample T-test	4.68 (T)		<0.05*

b) Salinity

During 2002 salinity at both the surface and at the survey depth was highest during May and lowest during June. During 2003 salinity at both the surface and survey depth was highest during May and lowest during April (Figure 2.7). Mean salinity at the surface varied between 35.423 ± 0.009 at Trou Malabar in May 2002 and 34.935 ± 0.071 at Chaland in June 2002. During 2003 mean salinity at the surface was lowest at Totor (34.491 ± 0.107) and Trou Malabar (34.553 ± 0.000) during April and highest at Totor (35.025 ± 0.155) during May. At the survey depth mean salinity varied between 35.325 ± 0.023 at Trou Malabar during May 2002 and 34.880 ± 0.127 at Chaland during June 2002 and between 34.962 ± 0.053 at Totor during May 2003 and 34.542 ± 0.000 at Trou Malabar during April 2003.

There was no significant difference between the mean salinity at the surface and survey depth in either 2002 or 2003 at the 3 survey sites (Table 2.5). During 2002 the mean salinity at both depths was significantly higher in May than in April and June (Figure 2.7; Table 2.5). During 2003 the mean salinity was significantly higher during May and June than during April. Mean salinity was significantly higher during April 2002 than during April 2003 and significantly higher during May 2002 than during May 2003. There was no significant difference in mean salinity during June 2002 and June 2003.

Table 2.5 Statistical analysis results for salinity data measured at all sites during April – May 2002 and 2003. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	p
Surface*Depth	2002	1-way ANOVA	0.15 (F)	1	>0.05
Surface*Depth	2003	1-way ANOVA	0.05 (F)	1	>0.05
Apr*May*Jun	2002	1-way ANOVA	15.29 (F)	2	<0.05*
Apr*May*Jun	2003	1-way ANOVA	6.52 (F)	2	<0.05*
Apr 2002*2003	-	2-sample T-test	-6.23 (F)		<0.05*
May 2002*2003	-	2-sample T-test	-5.29 (F)		<0.05*
Jun 2002*2003	-	2-sample T-test	-0.44 (F)		>0.05

c) Visibility

Mean vertical visibility was lowest at Totor during both 2002 and 2003 (Figure 2.8). During 2002 mean vertical visibility varied from 6.3 ± 0.5 m at Totor to 6.6 ± 0.3 m at Chaland and 6.6 ± 0.4 m at Trou Malabar. During 2003 mean vertical visibility varied from 5.7 ± 0.4 m at Totor to 8.4 ± 0.8 m at Trou Malabar. There was however no significant difference between mean vertical visibility during 2002 (Table 2.6). During 2003 mean vertical visibility was significantly higher at Trou Malabar than at Totor. There was no significant difference in mean vertical visibility during 2002 and 2003 at Chaland or Totor. Mean vertical visibility at Trou Malabar was however, significantly higher during 2003 than during 2002.

During 2002, mean monthly vertical visibility was lowest during March at Totor (5.0 ± 0.7 m) and Chaland (5.4 ± 0.5 m) and was highest at Chaland in April (7.9 ± 0.6 m), at Trou Malabar in May (7.9 ± 0.5 m) and at Totor in June (9.3 ± 0.0 m). During 2003, mean monthly vertical visibility was lowest at all 3 sites during April (Totor: 3.3 ± 0.2 m, Trou Malabar: 4.0 ± 0.1 m, Chaland: 3.6 ± 0.5 m) and was highest at Trou Malabar during May (11.3 ± 0.7 m) and June (10.9 ± 0.0 m) and at Chaland during August (8.9 ± 0.8 m). A 1-way ANOVA confirms that for all sites mean vertical visibility during April 2003 and March 2002 was significantly lower than during the remaining 8 months (Table 2.6).

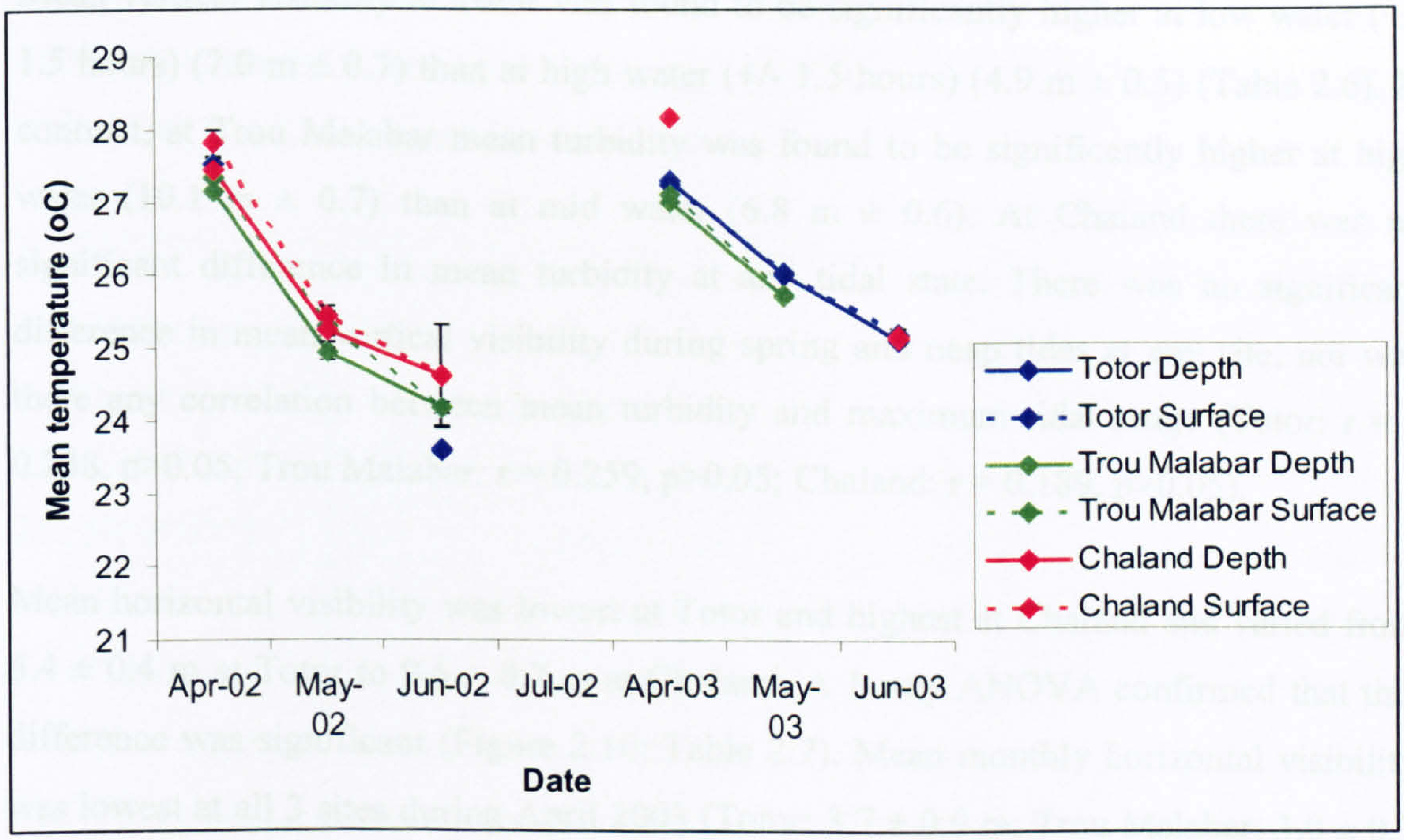


Figure 2.6 The mean temperature (°C) ± SE measured at the surface and survey depth (10-12m) at Totor, Trou Malabar and Chaland.

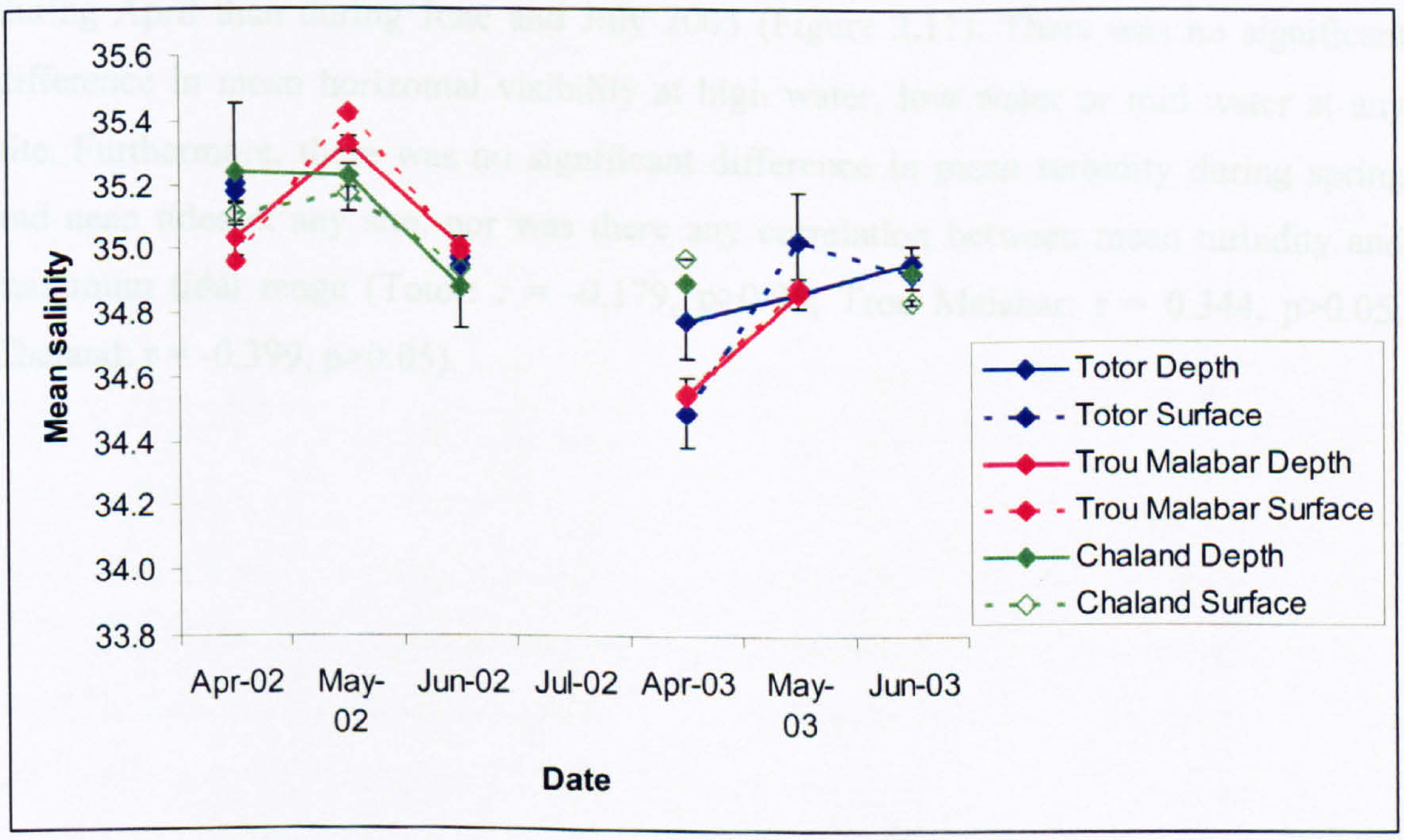


Figure 2.7 The mean salinity ± SE measured at the surface and survey depth (10-12m) at Totor, Trou Malabar and Chaland.

Mean vertical visibility at Totor was found to be significantly higher at low water (+/- 1.5 hours) (7.0 m ± 0.7) than at high water (+/- 1.5 hours) (4.9 m ± 0.5) (Table 2.6). In contrast, at Trou Malabar mean turbidity was found to be significantly higher at high water (10.1 m ± 0.7) than at mid water (6.8 m ± 0.6). At Chaland there was no significant difference in mean turbidity at any tidal state. There was no significant difference in mean vertical visibility during spring and neap tides at any site, nor was there any correlation between mean turbidity and maximum tidal range (Totor: $r = -0.238$, $p>0.05$; Trou Malabar: $r = 0.259$, $p>0.05$; Chaland: $r = 0.189$, $p>0.05$).

Mean horizontal visibility was lowest at Totor and highest at Chaland and varied from 5.4 ± 0.4 m at Totor to 9.6 ± 0.7 m at Chaland. A 1-way ANOVA confirmed that this difference was significant (Figure 2.10; Table 2.7). Mean monthly horizontal visibility was lowest at all 3 sites during April 2003 (Totor: 3.7 ± 0.9 m, Trou Malabar: 3.0 ± 0.3 m, Chaland: 4.6 ± 0.5 m) and was highest at Trou Malabar (12.8 ± 0.9 m) and Chaland (10.7 ± 1.1 m) during June 2003. If the data for all 3 sites are combined into mean monthly values it can be seen that mean horizontal visibility was significantly lower during April than during June and July 2003 (Figure 2.11). There was no significant difference in mean horizontal visibility at high water, low water or mid water at any site. Furthermore, there was no significant difference in mean turbidity during spring and neap tides at any site, nor was there any correlation between mean turbidity and maximum tidal range (Totor: $r = -0.179$, $p>0.05$; Trou Malabar: $r = 0.344$, $p>0.05$; Chaland: $r = -0.399$, $p>0.05$).

Table 2.6 Statistical analysis results for vertical visibility data measured during February – June 2002 and April – August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	p
Tot*TM*Chal	2002	1-way ANOVA	0.15 (F)	2	>0.05
Tot*TM*Chal*	2003	1-way ANOVA	7.14 (F)	2	<0.05*
Tot 2002*2003	-	2-sample T-test	-1.03 (T)		>0.05
Chal 2002*2003	-	2-sample T-test	0.24 (T)		>0.05
TM 2002*2003	-	2-sample T-test	2.09 (T)		0.05*
All Months	-	1-way ANOVA (√)	5.96 (F)	9	<0.05*
Tot*Tidal height	-	1-way ANOVA	4.87 (F)	2	<0.05*
TM*Tidal height	-	1-way ANOVA	5.05 (F)	2	<0.05*
Chal*Tidal height	-	1-way ANOVA	0.49 (F)	2	>0.05
Tot*Tidal range	-	2-sample T-test	1.94 (T)	33	>0.05
TM*Tidal range	-	2-sample T-test	-1.03 (T)	24	>0.05
Chal*Tidal range	-	2-sample T-test	0.05 (T)	23	>0.05

Table 2.7 Statistical analysis results for horizontal visibility data measured during April - August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Test	Test statistic	df	p
Tot*TM*Chal*	1-way ANOVA	12.05 (F)	2	<0.05*
Apr*May*Jun	1-way ANOVA	3.79 (F)	4	<0.05*
Tot*Tidal height	1-way ANOVA	0.53 (F)	2	>0.05
TM*Tidal height	1-way ANOVA	2.86 (F)	2	>0.05
Chal*Tidal height	1-way ANOVA	0.96 (F)	2	>0.05
Tot*Tidal range	2-sample T-test	0.16 (T)	23	>0.05
TM*Tidal range	2-sample T-test	-1.52 (T)	15	>0.05
Chal*Tidal range	2-sample T-test	1.67 (T)	17	>0.05

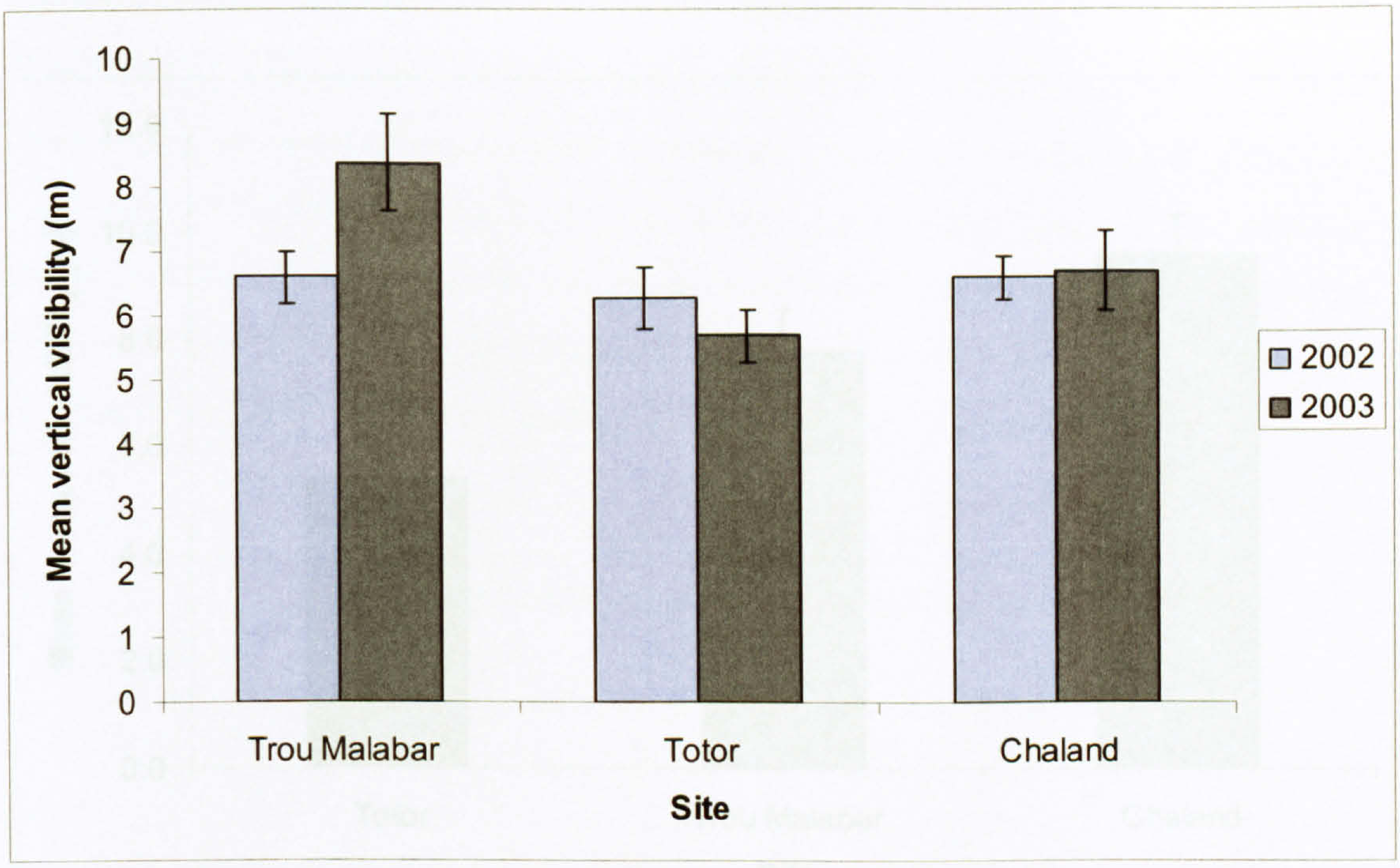


Figure 2.8 The mean vertical visibility (m) ±SE, based on secchi disc extinction rate, measured at the 3 survey sites between February and June 2002 and April and August 2003.

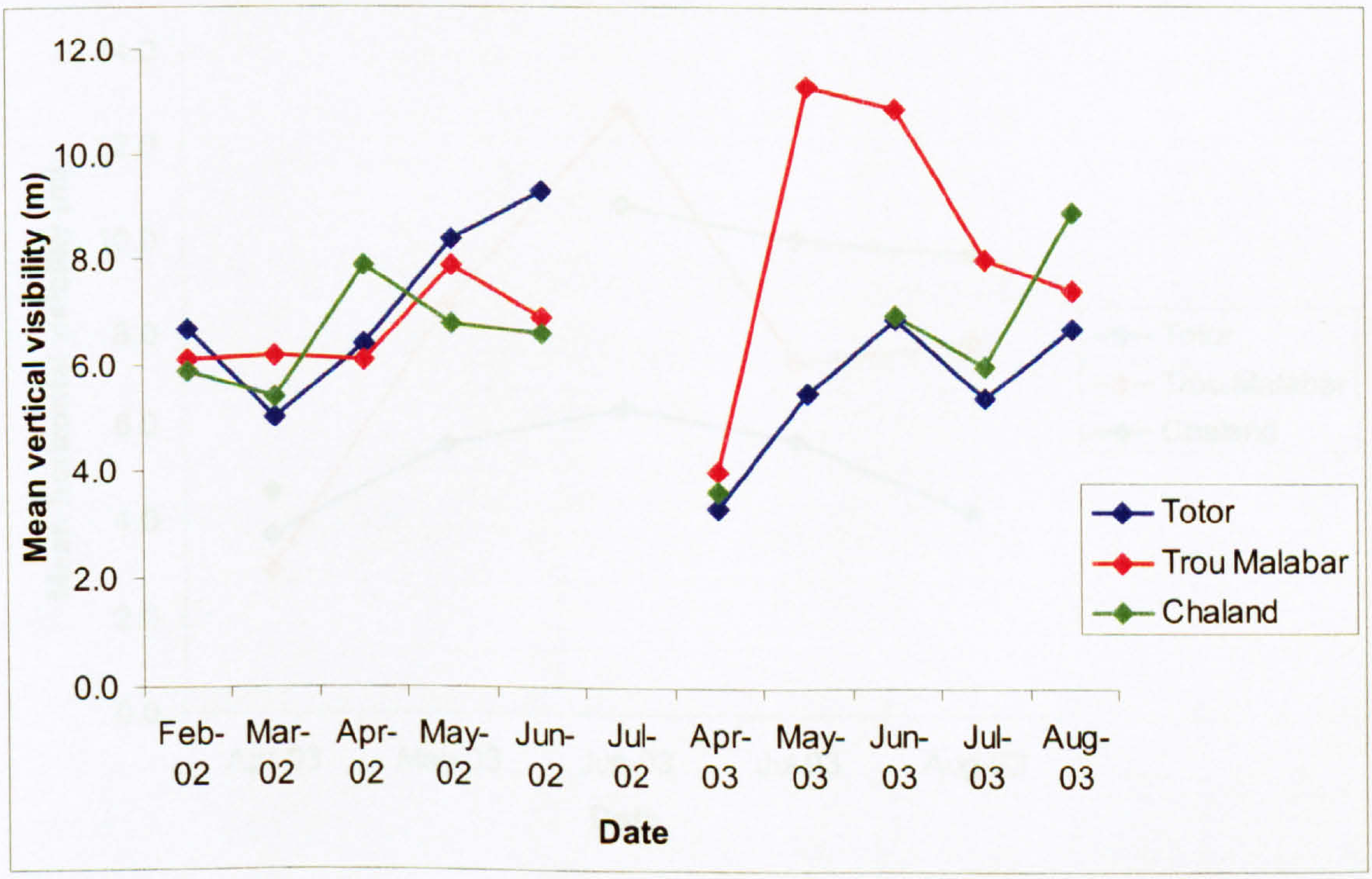


Figure 2.9 The change in mean vertical visibility (m) ±SE at the 3 survey sites, based on secchi disc extinction rate, between February and June 2002 and April and August 2003.

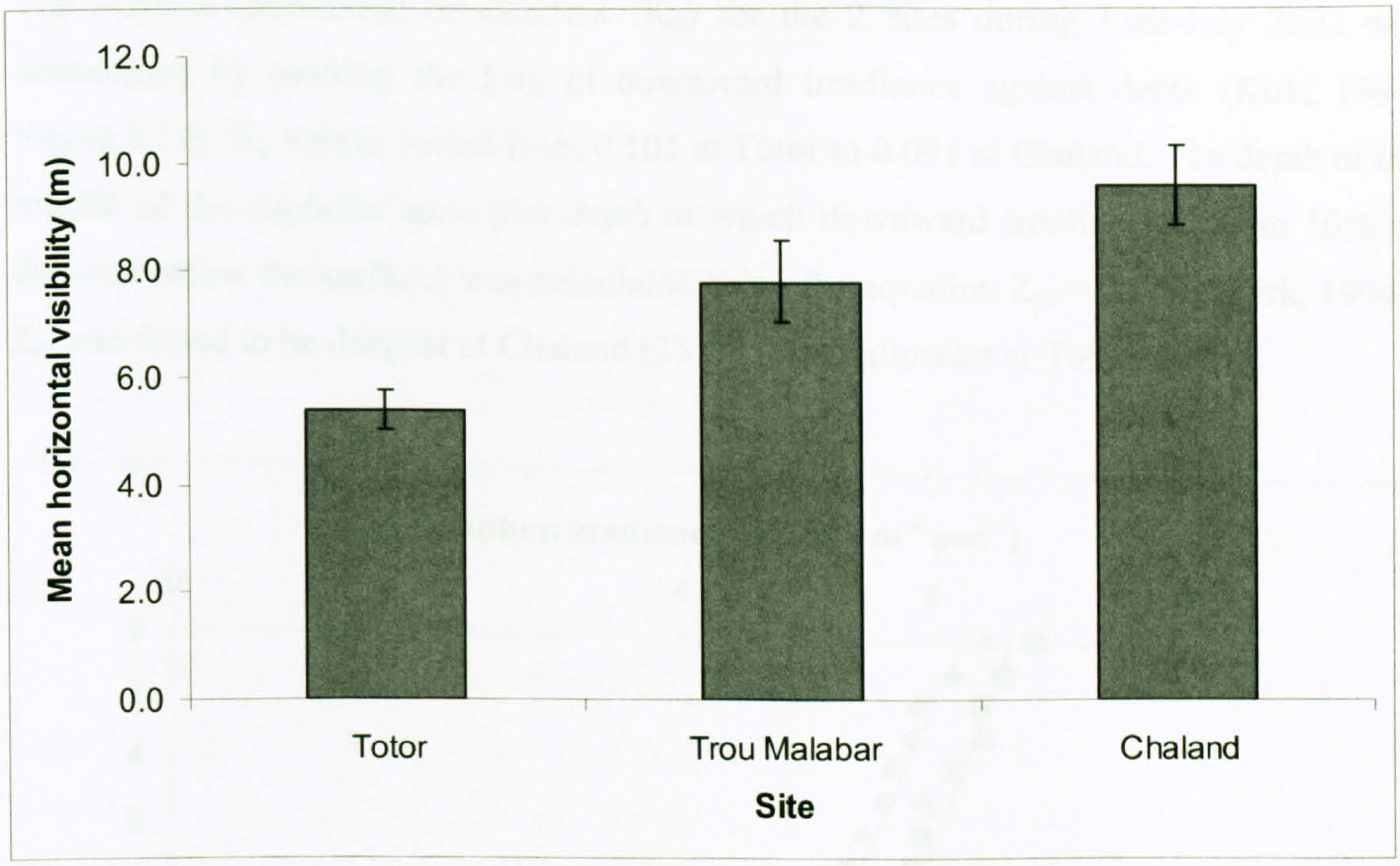


Figure 2.10 The mean horizontal visibility (m) ±SE, based on secchi disc extinction rate, measured at the 3 survey sites between April and August 2003.

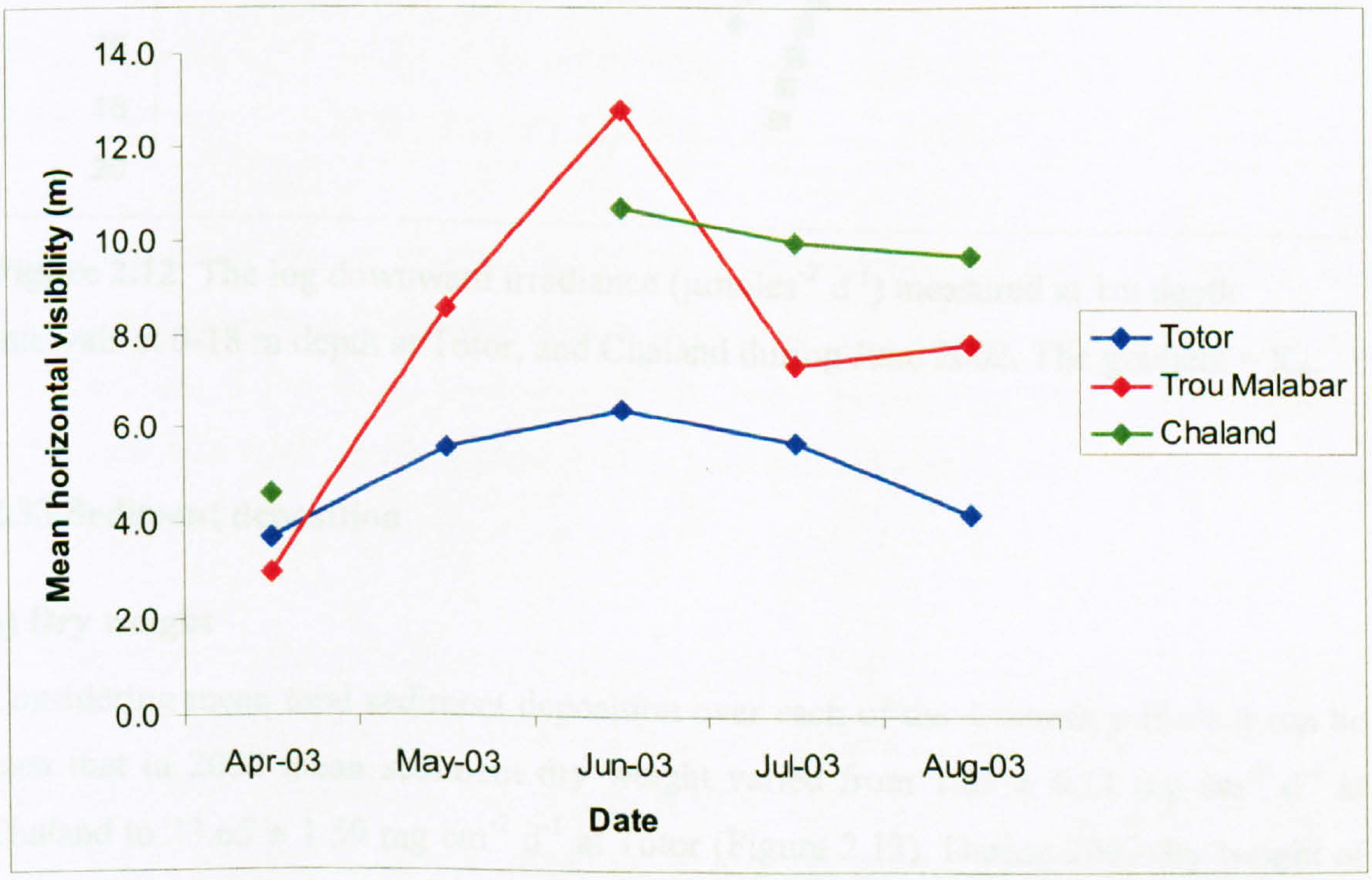


Figure 2.11 The change in mean horizontal visibility (m) ±SE at the 3 survey sites, based on secchi disc extinction rate, between April and August 2003.

d) Downwelling photosynthetically active radiation (PAR)

The vertical attenuation co-efficient (K_d) for the 2 sites during June-July 2002 was determined by plotting the Log of downward irradiance against depth (Kirk, 1994; Figure 2.12). K_d values varied from 0.105 at Totor to 0.091 at Chaland. The depth of the middle of the euphotic zone (the depth at which downward irradiance falls to 10% of that just below the surface) was calculated using the equation $Z_m = 2.3/K_d$ (Kirk, 1994). Z_m was found to be deepest at Chaland (25 m) and shallowest at Totor (22 m).

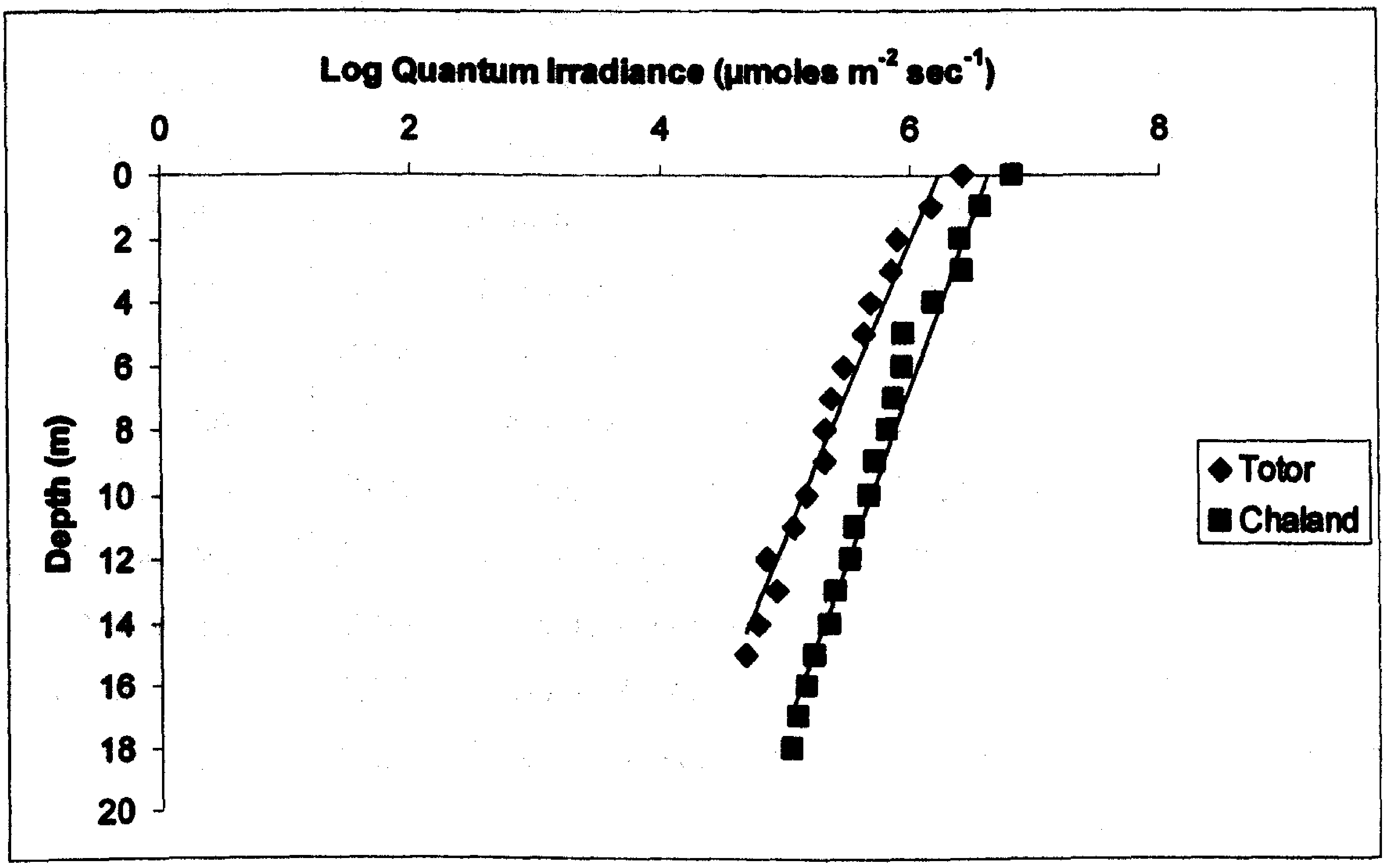


Figure 2.12. The log downward irradiance (µmoles^{-2} d^{-1}) measured at 1m depth intervals at 0-18 m depth at Totor, and Chaland during June 2002. The gradient = K_d.

2.33 Sediment deposition

a) Dry weight

Considering mean total sediment deposition over each of the 4-month periods it can be seen that in 2002 mean sediment dry weight varied from 1.68 ± 0.11 mg cm^{-2} d^{-1} at Chaland to 23.65 ± 1.59 mg cm^{-2} d^{-1} at Totor (Figure 2.13). During 2003 dry weight of sediment varied from 4.66 ± 0.43 mg cm^{-2} d^{-1} at Chaland to 47.04 ± 5.40 mg cm^{-2} d^{-1} at Trou Malabar. Mean sediment deposition during 2002 was significantly higher at Totor than at Trou Malabar and significantly higher at Trou Malabar than at Chaland (Figure 2.13; Table 2.8). During 2003 total sediment deposition was significantly higher at

Totor and Trou Malabar than at Chaland. Mean total sediment deposition was found to increase significantly between 2002 and 2003 at all three sites.

Table 2.8 Statistical analysis results for total sediment deposition data measured during February – June 2002 and April – August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	P
Tot*TM*Chal	2002	Kruskall-Wallis (Log)	67.04 (H)	2	<0.05*
Tot*TM*Chal*	2003	Kruskall-Wallis (Log)	85.84 (F)	2	<0.05*
Tot 2002*2003	-	2-sample T-test (Log)	-2.15 (T)	49	<0.05*
TM 2002*2003	-	Mood's Median	62.23 (X^2)	2	<0.05*
Chal 2002*2003	-	2-sample T-test (Log)	-6.88 (T)	39	<0.05*
Sites*Feb-Mar	2002	1-way ANOVA (√)	459.01 (F)	2	<0.05*
Sites*Mar-Apr	2002	1-way ANOVA (√)	1034.27 (F)	2	<0.05*
Sites*Apr-May	2002	Kruskall-Wallis	23.14 (H)	2	<0.05*
Sites*May-Jun	2002	Kruskall-Wallis	23.15 (H)	2	<0.05*
Sites*Apr-May	2003	1-way ANOVA (√)	242.31	2	<0.05*
Sites*May-Jun	2003	1-way ANOVA	47.50	2	<0.05*
Sites*Jun-Jul	2003	1-way ANOVA	146.05	2	<0.05*
Sites*Jul-Aug	2003	1-way ANOVA (√)	425.93	2	<0.05*

During each of the 4 months in 2002 mean monthly sediment deposition was significantly higher at Totor and significantly lower at Chaland than at Trou Malabar (Figure 2.14; Table 2.9). During each of the 4 months in 2003 mean sediment deposition was significantly higher at Trou Malabar and significantly lower at Chaland than at Totor.

At Totor mean monthly sediment deposition during 2002 varied from 14.87 ± 0.64 mg cm^{-2} d^{-1} during May-June to 34.86 ± 1.13 mg cm^{-2} d^{-1} during March-April; in 2003 mean monthly sediment deposition varied from 8.87 ± 0.36 mg cm^{-2} d^{-1} during May-June to 64.17 ± 2.01 mg cm^{-2} d^{-1} in April-May. Mean monthly sediment deposition during 2002 was significantly higher during March-April and April-May than during February-March and May-June (Table 2.9). During 2003 mean sediment deposition was significantly higher during April-May and significantly lower during May-June than the remaining months. Mean sediment deposition increased significantly between April-

May 2002 and April-May 2003 (2-fold) and between May-June 2002 and May-June 2003 (1.5-fold).

At Trou Malabar mean monthly sediment deposition during 2002 varied from 1.83 ± 0.16 mg cm^{-2} d^{-1} during February-March to 6.19 ± 0.41 mg cm^{-2} d^{-1} during April-May; in 2003 mean monthly sediment deposition varied from 11.10 ± 1.01 mg cm^{-2} d^{-1} during May-June to 95.98 ± 6.21 mg cm^{-2} d^{-1} in April-May. Mean monthly sediment deposition during 2002 was significantly higher during April-May and significantly lower during February-March than the remaining months (Table 2.9). During 2003 mean sediment deposition was significantly higher during April-May and significantly lower during May-June than the remaining months. Mean sediment deposition increased significantly between April-May 2002 and April-May 2003 (16-fold) and between May-June 2002 and May-June 2003 (2-fold).

At Chaland mean monthly sediment deposition during 2002 varied between 1.02 ± 0.13 mg cm^{-2} d^{-1} during February-March to 2.02 ± 0.22 mg cm^{-2} d^{-1} during May-June; in 2003 mean monthly sediment deposition varied from 2.68 ± 0.21 mg cm^{-2} d^{-1} during May-June to 6.68 ± 0.72 mg cm^{-2} d^{-1} during June-July. Mean monthly sediment deposition during 2002 was significantly lower during February-March than during the remaining months (Table 2.9). During 2003 mean sediment deposition was significantly higher during April-May and June-July than the remaining months. Mean sediment deposition increased significantly by 3-fold between April-May 2002 and April-May 2003 (3-fold) and between May-June 2002 and May-June 2003 (1.5-fold).

Table 2.9 Statistical analysis results for monthly sediment deposition data measured during February – June 2002 and April – August. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	p
Sites*Feb-Mar	2002	1-way ANOVA (√)	459.01 (F)	2	<0.05*
Sites*Mar-Apr	2002	1-way ANOVA (√)	1034.27 (F)	2	<0.05*
Sites*Apr-May	2002	Kruskall-Wallis	23.14 (H)	2	<0.05*
Sites*May-Jun	2002	Kruskall-Wallis	23.15 (H)	2	<0.05*
Sites*Apr-May	2003	1-way ANOVA (√)	242.31 (F)	2	<0.05*
Sites*May-Jun	2003	1-way ANOVA	47.50 (F)	2	<0.05*
Sites*Jun-Jul	2003	1-way ANOVA	146.05 (F)	2	<0.05*
Sites*Jul-Aug	2003	1-way ANOVA (√)	425.93 (F)	2	<0.05*
Tot*Months	2002	1-way ANOVA	99.77 (F)	3	<0.05*
Tot*Months	2003	1-way ANOVA	320.51 (F)	3	<0.05*
Tot Apr 02*03	-	2-sample T-test	13.79 (T)		<0.05
Tot May 02*03	-	2-sample T-test	-8.20 (T)		<0.05
TM*Months	2002	1-way ANOVA	50.96 (F)	3	<0.05*
TM*Months	2003	1-way ANOVA (√)	154.54 (F)	3	<0.05*
TM Apr 02*03	-	2-sample T-test	14.43 (T)		<0.05*
TM May 02*03	-	Mann-Whitney	118.0 (W)		<0.05*
Chal*Months	2002	1-way ANOVA (√)	8.51 (F)	3	<0.05*
Chal*Months	2003	1-way ANOVA	6.29	3	<0.05*
Chal Apr 02*03	-	2-sample T-test	-3.35 (T)		<0.05*
Chal May 02*03	-	2-sample T-test	-2.18 (T)		<0.05*

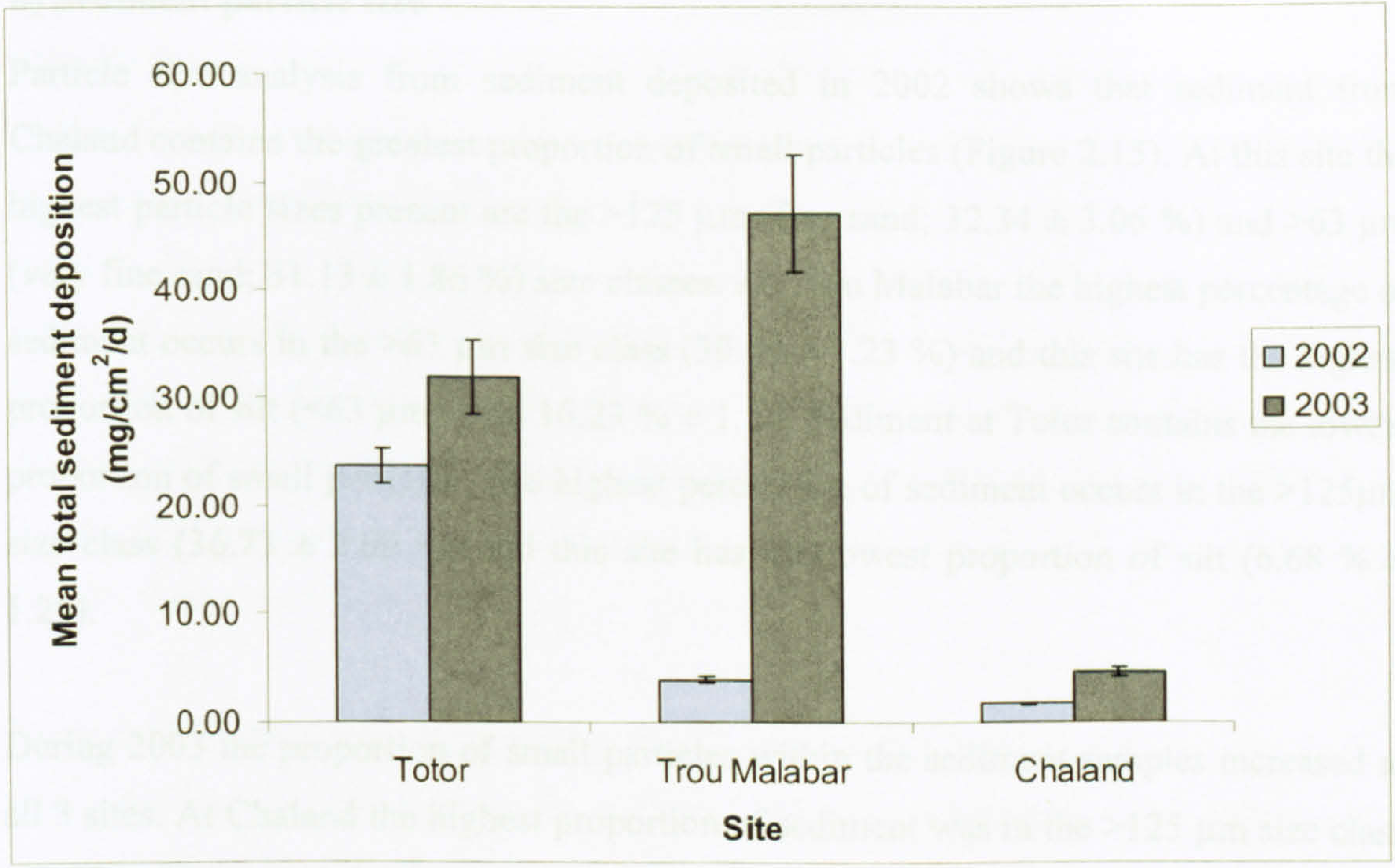


Figure 2.13 The mean total sediment deposition (mg cm^{-2} d^{-1}) ± SE measured at the 3 survey sites between February and June 2002 and April and August 2003.

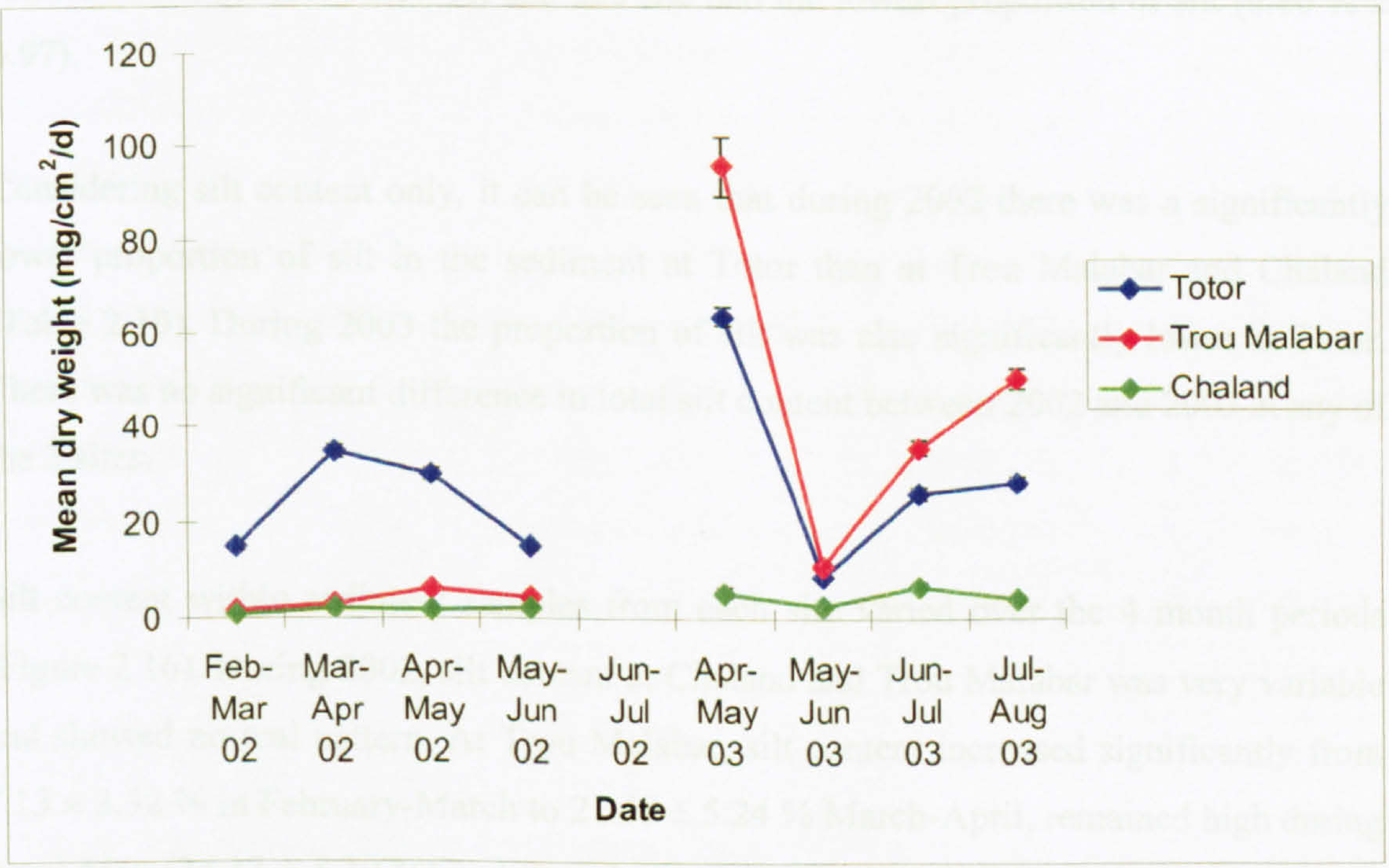


Figure 2.14 The mean monthly sediment deposition (mg cm^{-2} d^{-1}) ± SE measured at the 3 survey sites between February and June 2002 and April and August 2003.

b) Sediment particle size

Particle size analysis from sediment deposited in 2002 shows that sediment from Chaland contains the greatest proportion of small particles (Figure 2.15). At this site the highest particle sizes present are the >125 μm (fine sand; 32.34 ± 3.06 %) and >63 μm (very fine sand; 31.13 ± 1.86 %) size classes. At Trou Malabar the highest percentage of sediment occurs in the >63 μm size class (30.60 ± 1.23 %) and this site has the highest proportion of silt (<63 μm) with 16.23 % ± 1.50. Sediment at Totor contains the lowest proportion of small particles. The highest percentage of sediment occurs in the >125μm size class (36.73 ± 2.09 %) and this site has the lowest proportion of silt (6.68 % ± 1.25).

During 2003 the proportion of small particles within the sediment samples increased at all 3 sites. At Chaland the highest proportion of sediment was in the >125 μm size class (45.78 ± 3.21 %) and this site had the highest proportion of silt (19.36% ± 2.16). At Trou Malabar the highest particle sizes present are the >125 μm (40.87 ± 2.68 %) and >63 μm (45.01 ± 1.49 %). At Totor the highest proportion of sediment was in the >125 μm size class (61.44 ± 2.19 %) and this site had the lowest proportion of silt (6.80 % ± 0.97).

Considering silt content only, it can be seen that during 2002 there was a significantly lower proportion of silt in the sediment at Totor than at Trou Malabar and Chaland (Table 2.10). During 2003 the proportion of silt was also significantly lower at Totor. There was no significant difference in total silt content between 2002 and 2003 at any of the 3 sites.

Silt content within sediment samples from each site varied over the 4 month periods (Figure 2.16). During 2002, silt content at Chaland and Trou Malabar was very variable and showed no real pattern. At Trou Malabar, silt content increased significantly from 7.13 ± 3.32 % in February-March to 21.59 ± 5.24 % March-April, remained high during April-May (24.17 ± 5.30 %) and then decreased to 11.99 ± 7.99 % in May-June (Table 2.10). At Chaland, silt content decreased significantly from 25.15 ± 8.8 % in February-March to 8.53 ± 3.32 % in March-May. At Totor, silt content remained low during the first 3 months (February-May; 3.41 – 4.37 %) and then increased significantly to 15.2 ± 8.72 % during May-June.

Silt content within sediment samples from Trou Malabar and Chaland was again very variable during 2003 however the 2 sites showed a very similar pattern. At both sites silt content was low in April-May (Trou Malabar: 6.59 ± 2.01 %, Chaland: 16.59 ± 4.09 %), rose in May-June (Trou Malabar: 26.10 ± 3.02 %, Chaland: 28.31 ± 3.87 %), decreased again in June-July (Trou Malabar: 3.48 ± 1.19 %, Chaland: 4.97 ± 1.09 %) and then increased again in July-August (Trou Malabar: 16.99 ± 1.38 %, Chaland: 27.57 ± 1.93 %) (Table 2.10). Variation in silt content at Totor however showed a different pattern and was very low during April-May (1.91 ± 0.34 %), rose during May-June (7.56 ± 2.26 %) and then remained at this level during June-August (June-July: 9.24 ± 1.97 %, July-August: 8.80 ± 1.78 %).

Table 2.10 Statistical analysis results for silt content data measured during February – June 2002 and April – August. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	P
Tot*TM*Chal	2002	1-way ANOVA (Arcsin)	14.86 (F)	2	<0.05*
Tot*TM*Chal	2003	Mood's Median	11.78 (X^2)	2	<0.05*
Tot 2002*2003	-	Mann-Whitney	1192.0 (W)		>0.05
TM 2002*2003	-	Mann-Whitney	1102.0 (W)		>0.05
Chal 2002*2003	-	2-sample T-test	1.68 (T)		>0.05
TM*Months	2002	1-way ANOVA	16.52 (F)	3	<0.05*
Chal*Months	2002	1-way ANOVA (Arcsin)	16.12 (F)	2	<0.05*
Tot*Months	2002	1-way ANOVA	8.65 (F)	3	<0.05*
TM*Months	2003	1-way ANOVA	29.43 (F)	3	<0.05*
Chal*Months	2003	1-way ANOVA	13.20 (F)	3	<0.05*
Tot*Months	2003	Mood's Median	12.50 (X^2)	3	<0.05*

c) Organic content

Mean organic content during 2002 ranged from 11.90 ± 0.46 % at Trou Malabar to 13.10 ± 0.55 % at Chaland. There was however no significant difference in organic content at the 3 sites (Table 2.11). During 2003 mean total organic content was again lowest at Trou Malabar during every month. During 2003 organic content was measured each month over the 4 month period. During April-May mean organic content was significantly higher at Totor than at Trou Malabar and Chaland (Table 2.11); during

May-August mean organic content was significantly higher at Totor and Chaland than at Trou Malabar. Although no statistical comparisons can be made organic content is similar during 2002 and 2003 at Totor and Chaland, however is 1.5 times lower during 2003 than 2002 at Trou Malabar.

Mean organic content of the sediment varied over time and followed a similar pattern at all 3 sites with high organic content during May-June (Figure 2.17). At Totor, mean organic content of the sediment was significantly higher during May-June (12.68 ± 0.04 %) than during the remaining 3 months (10.73-11.16 %) (Table 2.11). At Trou Malabar, mean organic content was significantly higher during May-June (8.88 ± 0.30 %) and June-July (7.92 ± 0.53 %) than during April-May (6.07 ± 0.35 %) and July-August (7.63 ± 0.25 %). At Chaland, mean organic content was significantly higher during May-June (11.41 ± 0.46 %) and July-August (12.31 ± 0.06 %) than during April-May (9.17 ± 0.46 %) and June-July (9.86 ± 0.44 %).

Table 2.11 Statistical analysis results for organic content data measured during April - May 2002 and April – August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	p
Tot*TM*Chal	2002	1-way ANOVA	0.69 (F)	2	>0.05
Apr Tot*TM*Chal	2003	1-way ANOVA	59.46 (F)	2	<0.05*
May Tot*TM*Chal	2003	Mood's Median	6.30 (X^2)	2	<0.05*
Jun Tot*TM*Chal	2003	Mood's Median	6.30 (X^2)	2	<0.05*
Jul Tot*TM*Chal	2003	1-way ANOVA	40.88 (F)	2	<0.05*
Tot*Months	2003	1-way ANOVA	8.14 (F)	3	<0.05*
TM*Months	2003	1-way ANOVA	9.73 (F)	3	<0.05*
Chal*Months	2003	1-way ANOVA	8.50 (F)	3	<0.05*

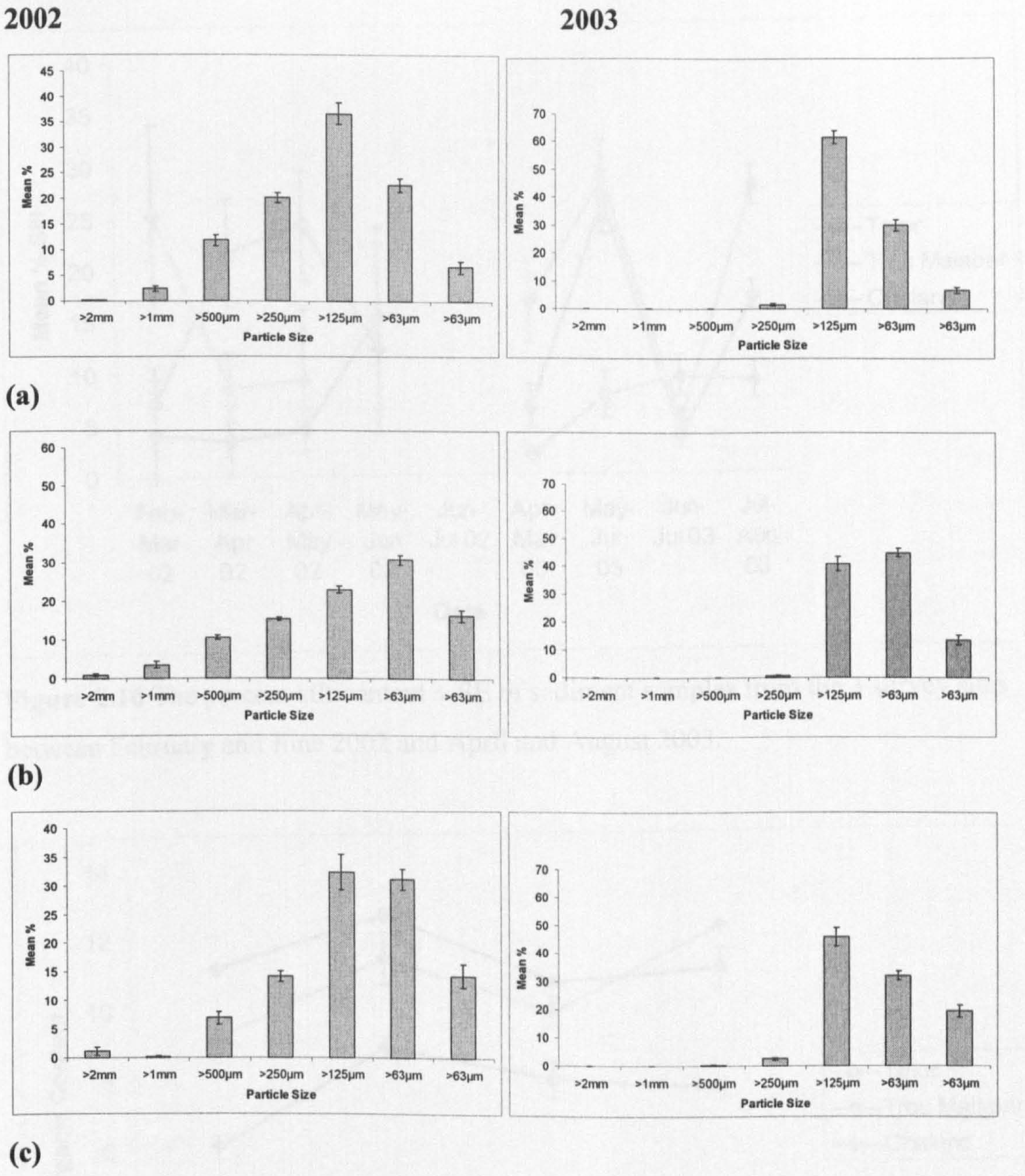


Figure 2.15 The particle size distribution (mean % particle size) ± SE of sediment samples collected during February to June 200 and April to August 2003 at (a) Totor, (b) Trou Malabar and (c) Chaland.

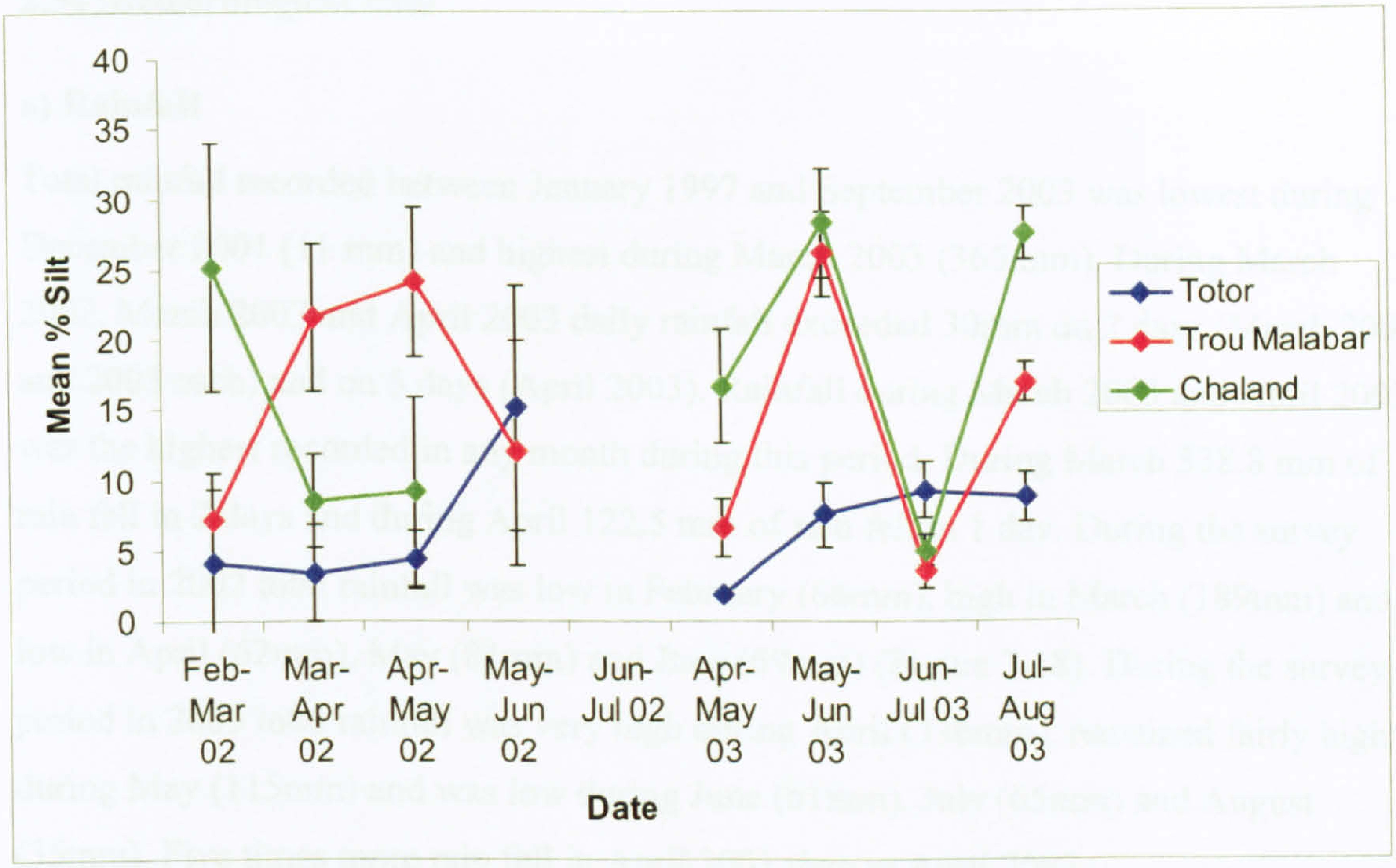


Figure 2.16 The percent silt content ± SE of sediment samples from the 3 survey sites between February and June 2002 and April and August 2003.

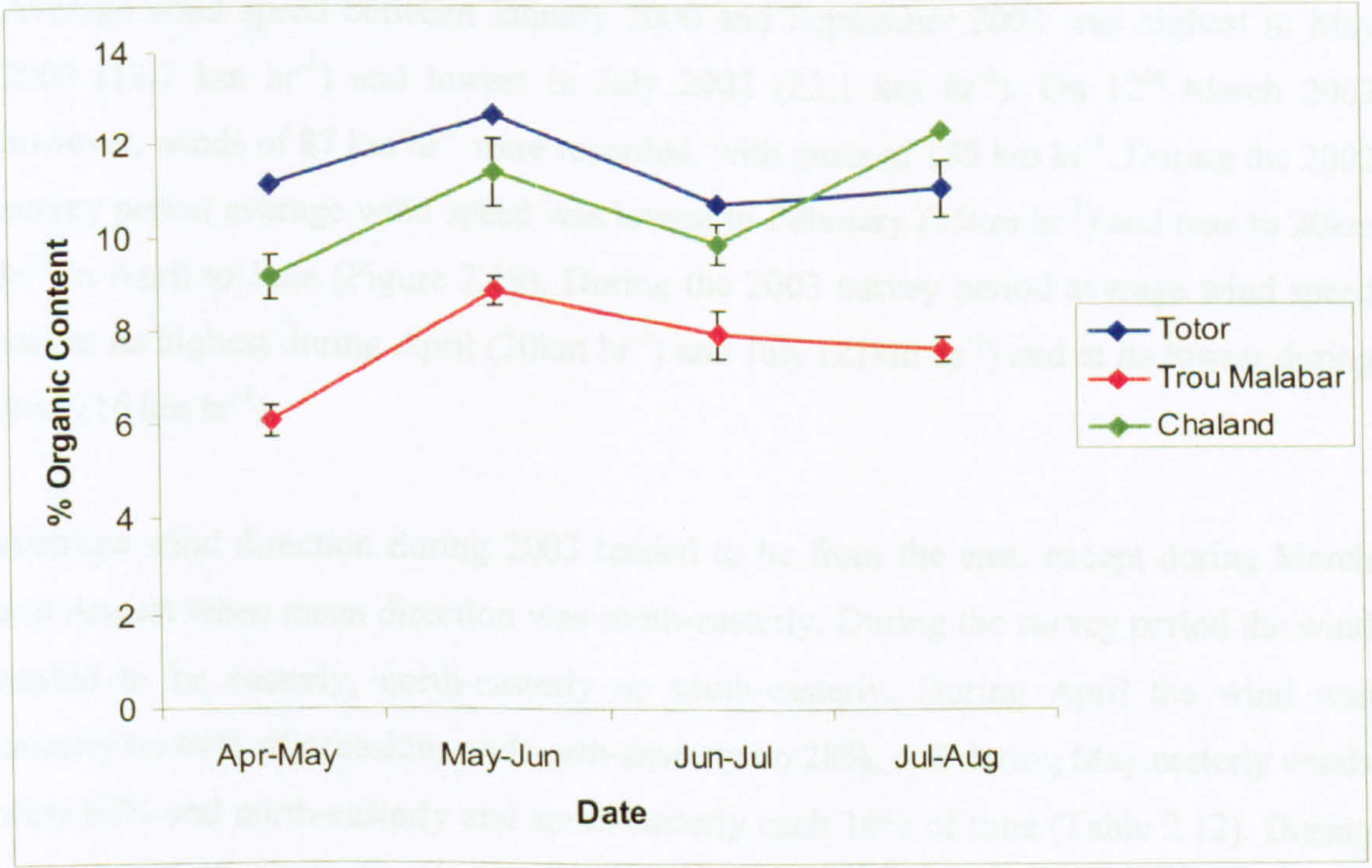


Figure 2.17 The mean monthly percent organic content of sediment ± SE measured at the 3 survey sites between April and August 2003.

2.34 Meteorological data

a) Rainfall

Total rainfall recorded between January 1997 and September 2003 was lowest during December 2001 (11 mm) and highest during March 2003 (365 mm). During March 2002, March 2003 and April 2003 daily rainfall exceeded 30mm on 2 days (March 2002 and 2003 each) and on 5 days (April 2003). Rainfall during March 2003 and April 2003 was the highest recorded in any month during this period. During March 338.8 mm of rain fell in 2 days and during April 122.5 mm of rain fell in 1 day. During the survey period in 2002 total rainfall was low in February (66mm), high in March (189mm) and low in April (62mm), May (81mm) and June (69mm) (Figure 2.18). During the survey period in 2003 total rainfall was very high during April (336mm), remained fairly high during May (115mm) and was low during June (61mm), July (65mm) and August (35mm). Five times more rain fell in April 2003 than in April 2002.

b) Wind speed

Average wind speed between January 2000 and September 2003 was highest in May 2000 (13.7 km hr^{-1}) and lowest in July 2002 (23.1 km hr^{-1}). On 12th March 2003 however, winds of 87 km hr^{-1} were recorded, with gusts of 185 km hr^{-1}. During the 2002 survey period average wind speed was lowest in February (15km hr^{-1}) and rose to 20km hr^{-1} in April to June (Figure 2.19). During the 2003 survey period average wind speed was at its highest during April (20km hr^{-1}) and July (21km hr^{-1}) and at its lowest during June (16 km hr^{-1}).

Average wind direction during 2003 tended to be from the east, except during March and August when mean direction was south-easterly. During the survey period the wind tended to be easterly, north-easterly or south-easterly. During April the wind was easterly on 64% of occasions and north-easterly on 28%, and during May easterly winds were 62% and north-easterly and south-easterly each 16% of time (Table 2.12). During both months the majority of high wind ($\geq$30 km hr^{-1}) came from the east. During June wind came from the east on 46% of occasions and from the south-east 31% of time. Wind speed was low throughout the month and wind speeds of 30km hr^{-1} were only recorded on 2 occasions. During July wind came from the east (56%) and south-east (29%) and during August the majority of wind came from the south-east (49%) and the east (34%).

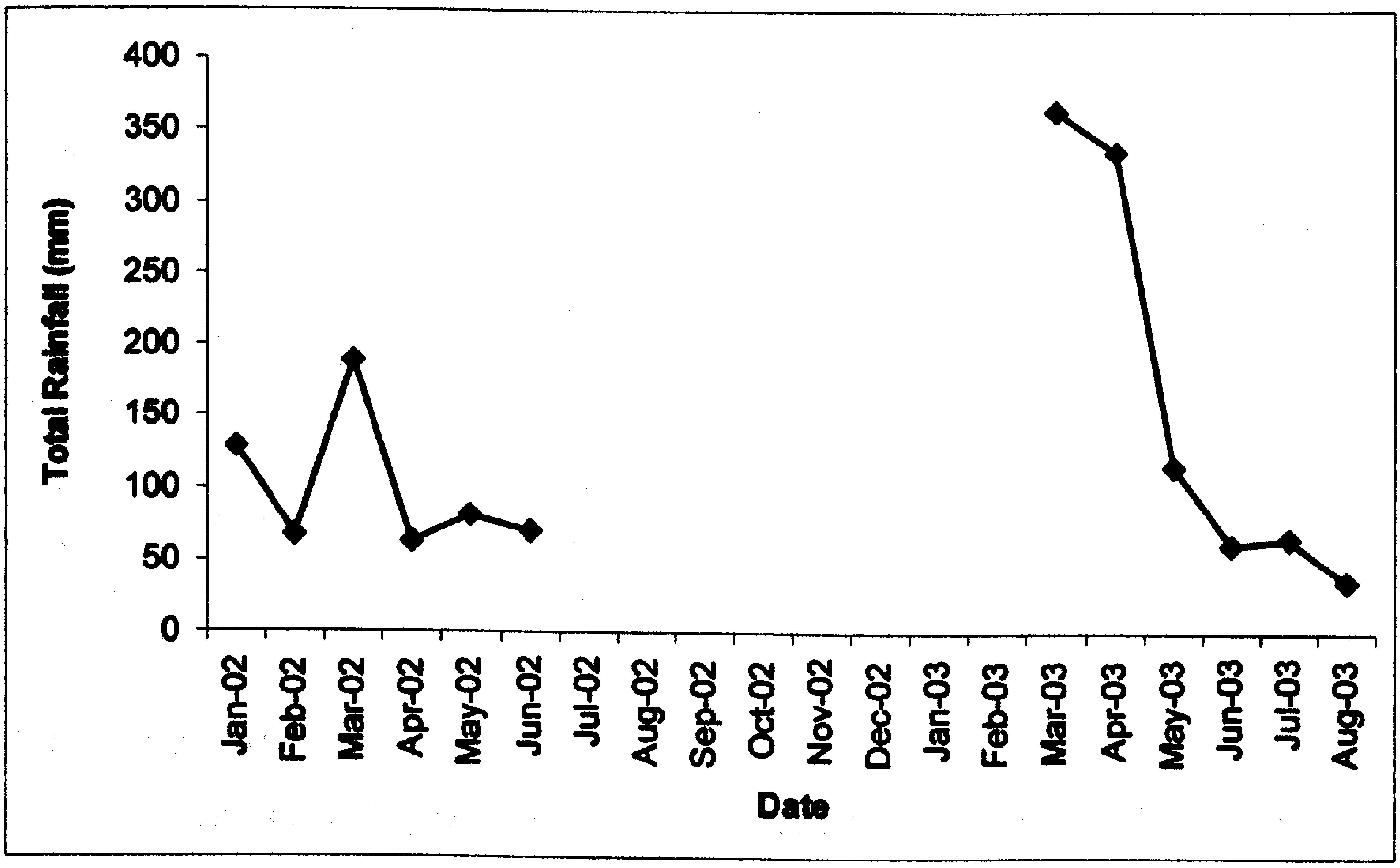


Figure 2.18 The total monthly rainfall (mm) measured at Pointe Canon, during the survey period (February – June 2002 and April – August 2003). Data provided by the Mauritius Meteorological Service.

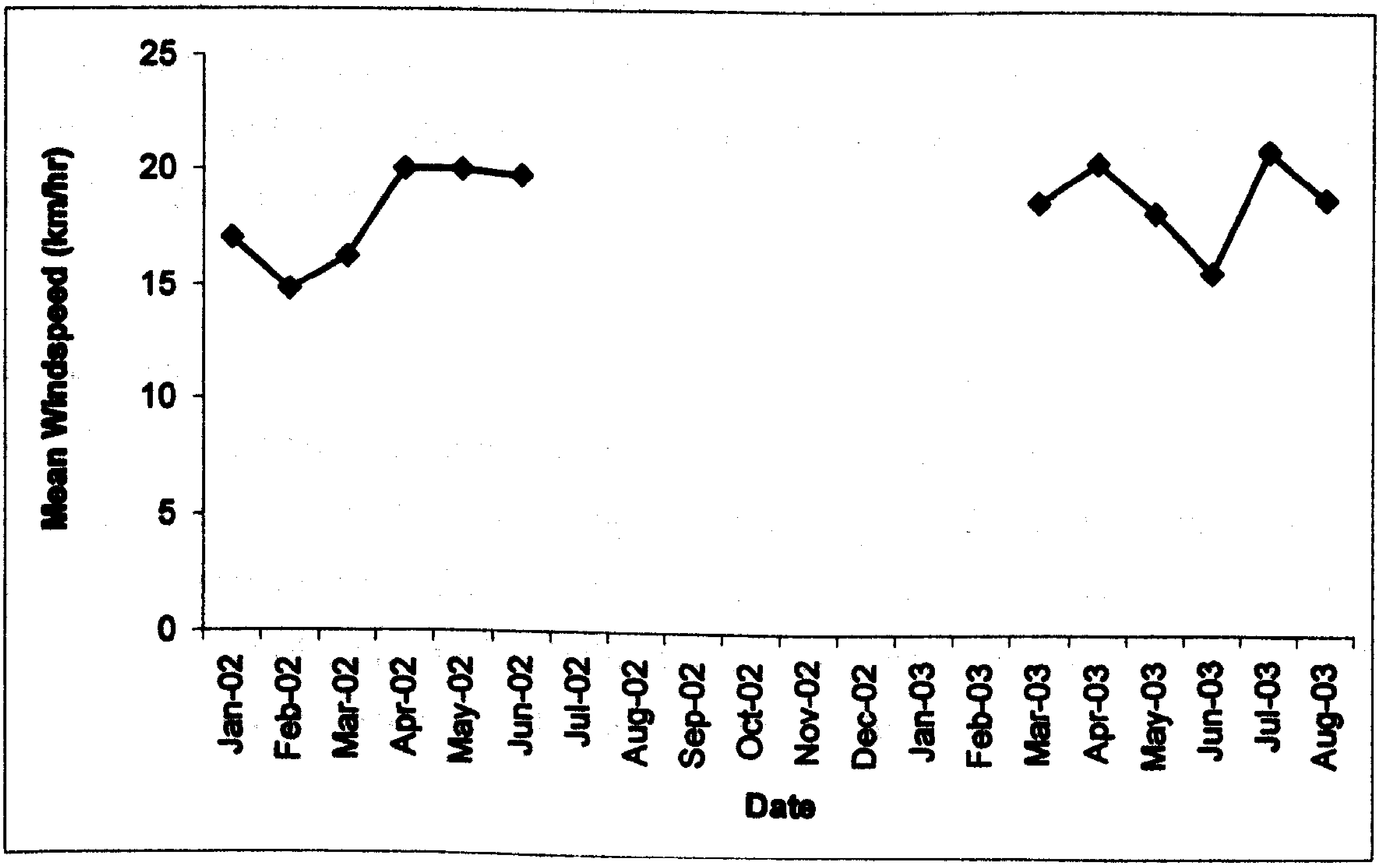


Figure 2.19 The mean windspeed (km hr^{-1}) measured at Pointe Canon, during the survey period (February – June 2002 and April – August 2003). Data provided by the Mauritius Meteorological Service.

Table 2.12 The percentage of observations of wind from each direction during the survey period April – August 2003. Data provided by the Mauritius Meteorological Service.

	April	May	June	July	August
North	0	5	3	0	2
North-East	28	16	6	10	8
East	64	62	46	56	34
South-East	7	16	31	29	49
South	1	1	9	2	7
South-West	0	0	3	2	0
West	0	0	3	1	0
North-West	0	0	0	1	0

c) Air temperature

Air temperature in Rodrigues tends to be highest during January – March and lowest during July – August. Maximum air temperature between January 1997 and September 2003 varied between 24.4°C recorded in August 2002 to 31.2°C in February 2002. The maximum and minimum air temperature fell gradually during both survey periods. During 2002 maximum air temperature fell 5 °C, from 31 °C in February and March to 26 °C in June, whilst minimum air temperature fell from 23 °C in February to 19 °C in June (Figure 2.20). During 2003 maximum air temperature fell 4 °C, from 29 °C in April to 25 °C in July and August and minimum air temperature fell from 23 °C in April to 20 °C in June to August.

d) Sunshine

Total hours of sunshine recorded between January 1997 and September 2003 varied from 187.8 hours to 320.8 hours. During the survey period in 2002 total sunshine fell gradually over the 5-month period from 264.5 hours in February to 191.0 hours in June (Figure 2.21). Sunshine hours during the 2003 survey period remained low during April to July (203.2 – 225.4 hours) and then rose to 248.8 hours in August.

e) Cloud Cover

During the 2002 survey period the cloudiest month was April (60% observations of >5 oktas) and the clearest month was May (30% observations of <3 oktas) (Figure 2.22). During the 2003 survey period the cloudiest months were April (60% observations of

>5 oktas) and July (50%), whereas the clearest month was June (25% observation of <3 oktas).

2.35 Physical and meteorological links

There was found to be a high negative correlation, although not significant, between salinity and rainfall during 2002 and 2003 (Table 2.13). There was no correlation between mean vertical visibility and mean wind speed, however mean vertical visibility and total rainfall were found to be significantly correlated. In addition, there was no correlation between mean horizontal visibility and mean wind speed, however there was a significant correlation between mean horizontal visibility and total rainfall.

There was a significant correlation between sediment deposition and rainfall at Totor over the whole survey period and a high correlation between sediment deposition at Trou Malabar and rainfall during 2003, although this was not significant (Table 2.13). There was a high correlation between sediment deposition and wind speed at Chaland during 2003 and at Trou Malabar during 2002, although neither were significant.

Table 2.13 Pearson correlation co-efficients (r) for physical and environmental data. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	r	p
Salinity*Rainfall	2002	-0.751	>0.05
Salinity*Rainfall	2003	-0.982	>0.05
Vertical visibility*Wind speed	-	-0.085	>0.05
Vertical visibility*Rainfall	-	-0.863	<0.05*
Horizontal visibility*Wind speed	-	-0.628	>0.05
Horizontal visibility*Rainfall	-	-0.930	<0.05*
Tot Sediment*Rainfall	-	0.821	<0.05*
TM Sediment*Rainfall	-	0.796	>0.05
Chal Sediment*Rainfall	-	0.298	>0.05
Tot Sediment*Wind speed	-	0.208	>0.05
TM Sediment*Wind speed	-	0.900	>0.05
Chal Sediment*Wind speed	-	0.888	>0.05

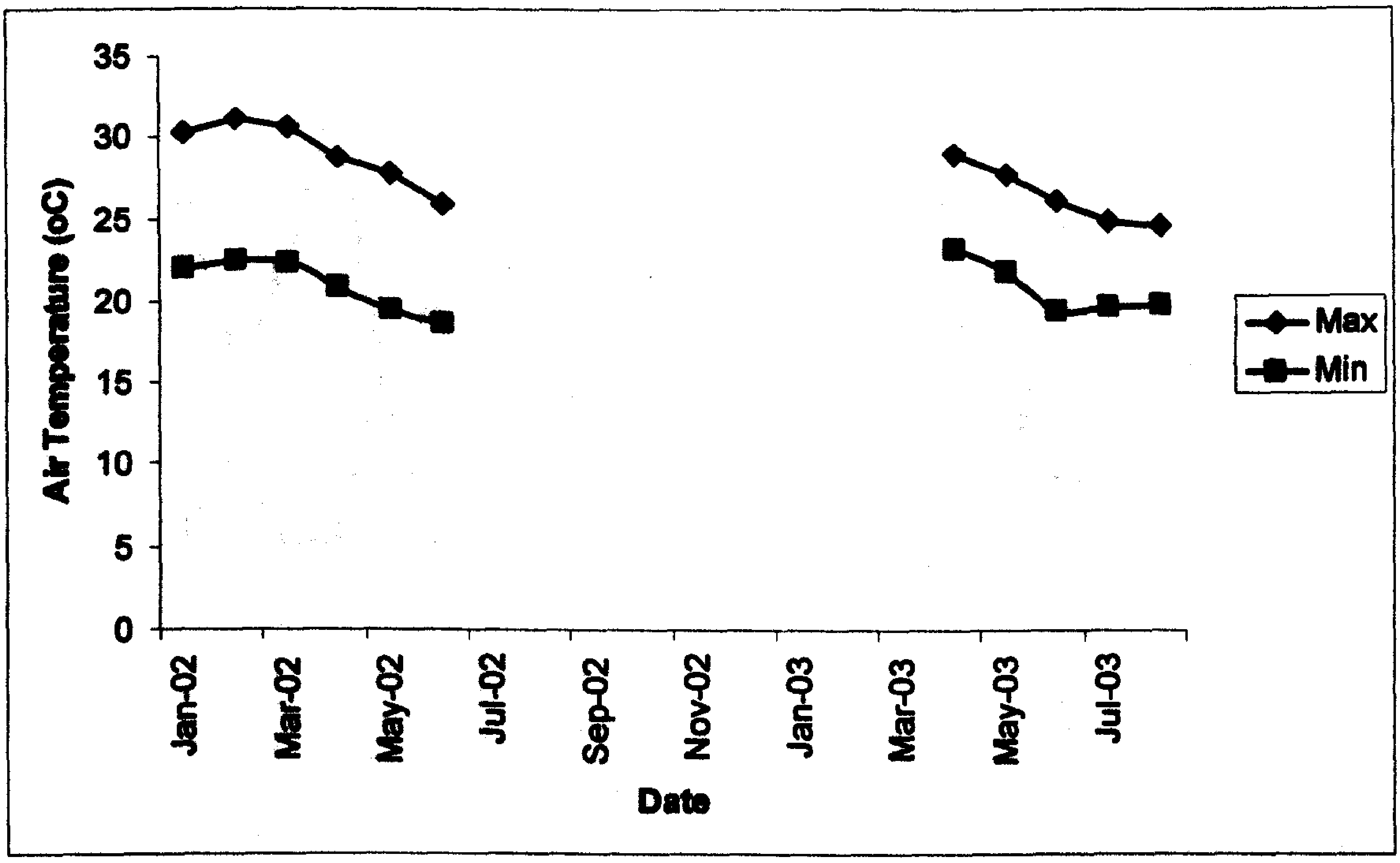


Figure 2.20 The maximum and minimum air temperature (°C) measured at Pointe Canon, during the survey period (February – June 2002 and April – August 2003). Data provided by the Mauritius Meteorological Service.

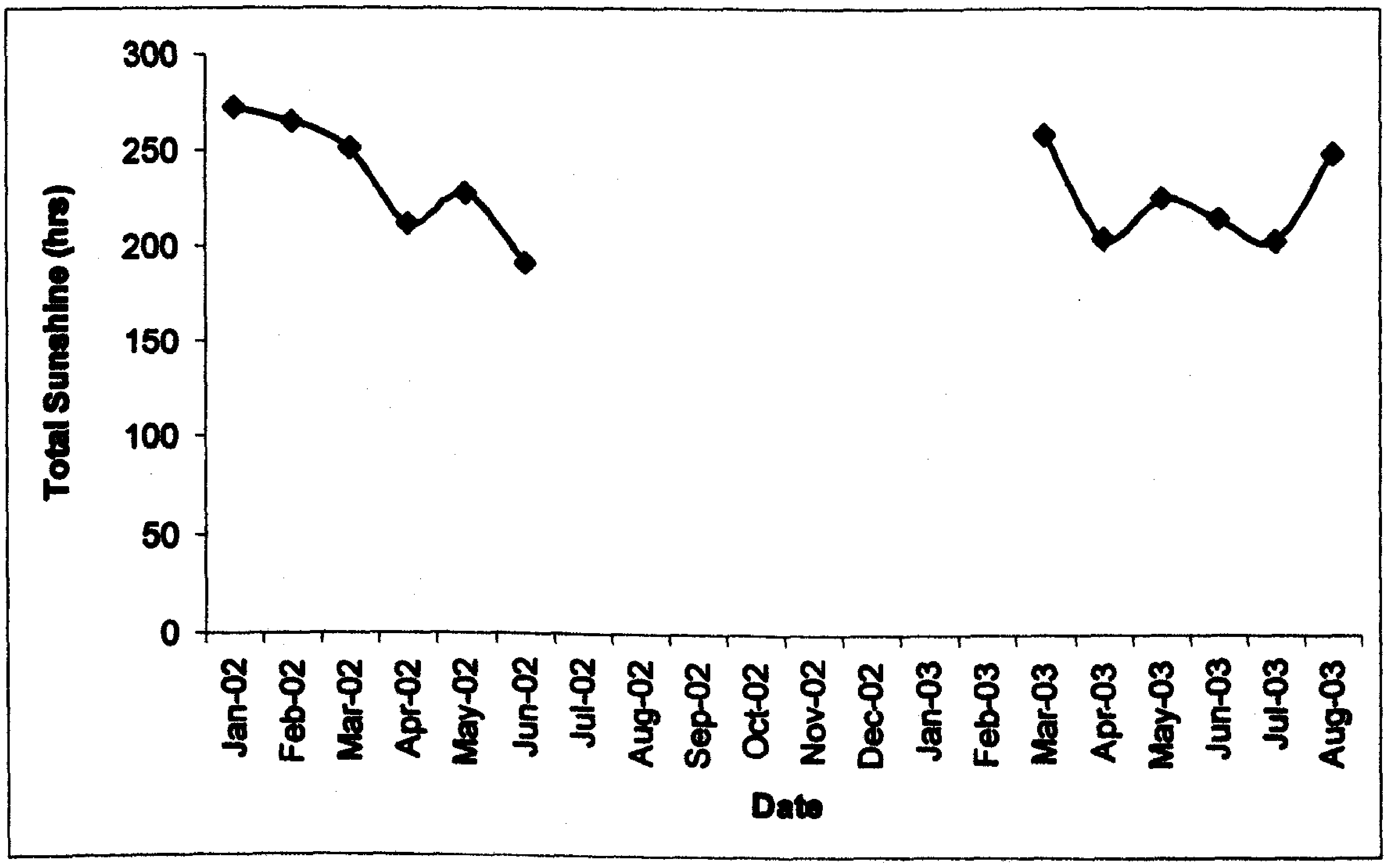


Figure 2.21 The total monthly sunshine (hr) measured at Pointe Canon, during the survey period (February – June 2002 and April – August 2003). Data provided by the Mauritius Meteorological Service.

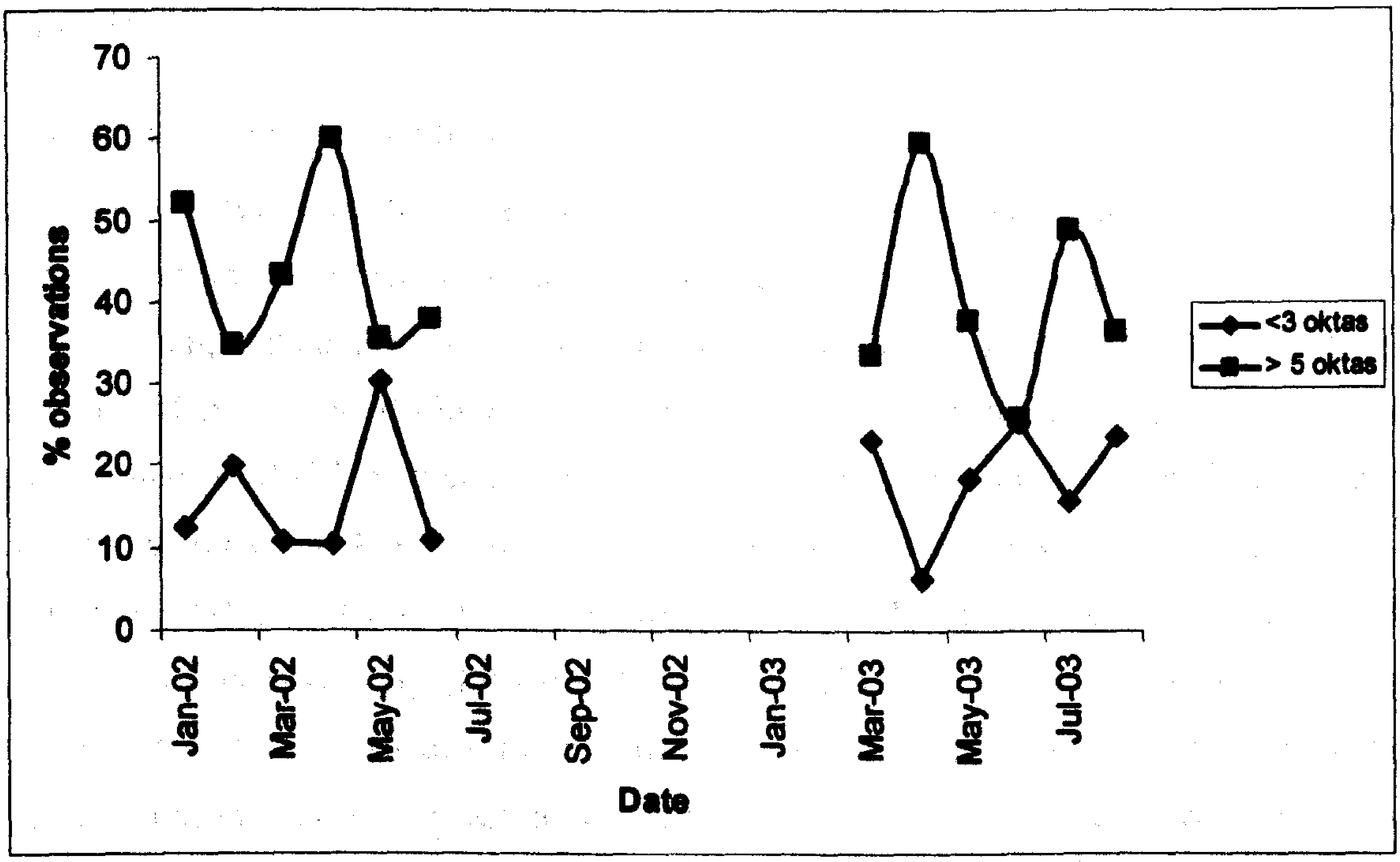


Figure 2.22 The % of observations of <3 oktas and >5 oktas during the survey period (February – June 2002 and April – August 2003), based on 7 observations per day. Data provided by the Mauritius Meteorological Service.

2.4 DISCUSSION

2.41 Environmental variables

Seawater temperatures decreased over time, which is consistent with a decrease in air temperature and a reduction in hours of sunshine, due to the change from the warm, rainy season, which occurs in November-May to the drier, cooler season in June-October. There was no difference in mean seawater temperature or mean salinity at the surface and at 10-12 m depth, suggesting that there is no stratification in the water column. Salinity was low during April 2003, particularly in the surface waters at Totor and Trou Malabar and at the survey depth at Trou Malabar, and there was a high correlation (although not significant) between rainfall and salinity. This suggests that the high rainfall experienced during April 2003 caused a large input of freshwater to the marine environment, which had a significant affect on salinity even down to 10-12 m depth. Other studies have observed low salinity as a result of high rainfall associated with cyclones and it has been proposed that this has resulted in coral bleaching and mortality (Goreau, 1964; van Woesik *et al.*, 1995; Perry, 2003), however this was not observed at these sites.

2.42Visibility and sedimentation

Horizontal and vertical visibility and levels of Photosynthetically Active Radiation (PAR) were all lower at Totor than at Chaland. Vertical visibility was low during March 2002 and horizontal and vertical visibility were both very low during April 2003 at all 3 sites. Mean vertical visibility during April 2003 was 3.6 m, with a minimum of 3 m recorded at Totor; mean horizontal visibility was 3.7 m, with a minimum of 2.5 m recorded at Totor. The vertical attenuation co-efficient (K_d) at Totor was 0.11, which is comparable to measurements made at St Croix (0.10-0.16; Gleason, 1998), but lower than measurements at Fanning Island, central Pacific Ocean (0.13 – 0.28; Roy and Smith, 1971), Gulf of Panama (0.18; Glyn and Stewart, 1973), Castle Harbour, Bermuda (0.28; Dryer and Logan, 1978) and Indonesia (0.18 – 0.37; Edinger *et al.*, 2000). Doyle (2002) found that mean turbidity was also significantly higher at Totor than at Chaland, however the turbidity levels recorded were not high compared to other studies in the literature (e.g. Rogers, 1983; Tomascik and Sander, 1985; Riegl, 1995; Kleypass, 1996) and were well within 'typical' concentrations on reefs, which tend to be less than 10 mg l^{-1} (Rogers, 1990).

Tolerable sedimentation rates for coral reefs are quoted as being 10 mg cm^{-2} d^{-1} or less (Rogers, 1990). Sedimentation levels recorded at Totor during 7 out of the 8 months and at Trou Malabar during all 4 month of 2003 were greater than 10 mg cm^{-2} d^{-1} suggesting that coral colonies are capable of surviving sedimentation levels greater than this threshold. Other studies have shown healthy coral reefs to occur in areas of high sedimentation (e.g. Sheppard, 1980; Dollar and Grigg, 1981; Leão de Mara, 1999; Perry, 2003; Schleyer and Celliers, 2003; Smithers and Larcome, 2003), indicating that this value may not be applicable for many coral reef regions and thus may need revising. The use of sediment traps to measure sedimentation may result in an overestimation of values (Ogston *et al.*, 2004) however sedimentation levels recorded at Totor and Trou Malabar are also greater than those recorded using sediment traps at other 'turbid' sites such as Jamaica (Dodge *et al.*, 1974; Mallela, 2002), Puerto Rico (Rogers, 1983), the Sabaki River, Kenya (McClanahan and Obura, 1997), the US Virgin Islands (Gleason, 1998) and Indonesia (Edinger *et al.*, 2000) and are comparable with those recorded in Barbados (Tomascik and Sander, 1985) (Table 2.14).

Table 2.14 A comparison of sedimentation rates (mg cm^{-2} d^{-1}) measured at Rodrigues compared with other reef sites.

Site	Sedimentation rate (mg cm^{-2} d^{-1})	Reference
Rodrigues	**1.02 – 95.98**	**This study**
India	2.30 – 124.50	Suresh and Mathew (1993)
Kenya	0.89 – 4.25	McClanahan and Obura (1997)
Tanzania	18.90 – 77.10	Nzali *et al.* (1998)
South Africa	16.80 – 43.2	Schleyer and Celliers (2003)
Indonesia	0.07 – 38.50	Edinger *et al.* (2000)
Jamaica	0.50 – 1.10	Dodge *et al.* (1974)
Jamaica	3.10 – 10.60	Mallela (2002)
Dominican Republic	0.33 – 37.15	Torres *et al.* (2001)
St Lucia	0.30 – 64.00	Nugues and Roberts (2003a)
St Croix, USVI	1.30 – 9.00	Gleason (1998)
Puerto Rico	9.60	Rogers (1983)
Barbados	2.33 – 88.52	Tomascik and Sander (1985)

A significant negative correlation was found between rainfall and both horizontal and vertical visibility in 2002 and 2003. Furthermore a significant correlation was found between rainfall and sediment deposition at Totor during the survey period. A high correlation (although not significant) was also found between rainfall and sediment deposition at Trou Malabar during 2003. This suggests that the low visibility and high sediment deposition at Totor and at Trou Malabar during 2003 may be linked to land run-off caused by the high rainfall. Other studies have observed increased turbidity after high rainfall, often associated with hurricanes and cyclones. In the U.S. Virgin Islands, increased rainfall associated with Hurricane *Hugo* caused increased turbidity and suspension of reef sediments (Rogers *et al.*, 1991); in Mexico Hurricane *Keith* resulted in significantly higher resuspended sediments within the lagoon (Beltran-Torres *et al.*, 2003); Cyclone *Joy* caused increased flooding resulting in high sedimentation and turbidity on inshore reefs on the Great Barrier Reef (Van Woesik *et al.*, 1995) and in the Dominican Republic high sedimentation rates were recorded following the passage of Hurricane *Hortense* (Torres *et al.*, 2001).

In Rodrigues, increased Suspended Particulate Matter (SPM) concentrations due to land run-off have been found to be detectable only following daily rainfall of at least 30 mm and SPM only become significant if this magnitude of rainfall occurred repeatedly within a period of a few days (Lynch *et al.*, 2003a). Rainfall of 30 mm or more occurred on 2 occasions during March 2002, 2 occasions during March 2003 and 5 occasions during April 2003. During March 2002 89.4 mm of rain fell in 2 days, whilst during March 2003, 338.8 mm of rain fell in 2 days and during April 162 mm of rain fell in 3 days. During this time it is therefore likely that there was significant land run-off into the lagoon. As described in section 2.11 there are 3 sources of terrestrial material, affecting the survey sites: the harbour at Port Mathurin, Rivière Anse aux Anglais and Rivière Caverne Provert; the latter are usually dry, however flow following heavy rain. During the heavy rainfall in March 2002, Rivière Anse aux Anglais was found to carry 69.5 mg l^{-1} suspended particulate matter, whilst the harbour at Pointe Monier carried 160 mg l^{-1} and Rivière Caverne Provert carried 202.7 mg l^{-1} (Lynch *et al.*, 2003a). River sediment loads exceeding 50 mg l^{-1} are considered to indicate significant particle transport events (Walling and Leeks, 2001). Fine material from river discharge does not accumulate within the shallow lagoon due to wind/wave action and it is kept in suspension where it becomes concentrated in the slightly deeper, more sheltered channels, just offshore (Lynch *et al.*, 2003a). It is therefore likely that sediment from land run-off was deposited at Totor and Trou Malabar, both sheltered sites, accounting for the very high sediment deposition and low visibility recorded at Totor during March-April 2002 and at Totor and Trou Malabar during April-May 2003.

Sediment deposition remained high at Totor and Trou Malabar during 2003 despite low rainfall during May – August. Land run-off is not therefore the only source of sediment to these sites and resuspension of bottom sediments is also likely to be important. Larcombe *et al.* (1995) found that at shallow reef sites, resuspension of sediments occurred primarily due to locally produced waves and thus conditions were heavily influenced by the wind regime. In Rodrigues, short term studies have demonstrated a relationship between sediment deposition and wind. Martin (2002) found a positive correlation between turbidity within the lagoon and wind speed and showed that during periods of transitional/shallow waves, waves are having a direct effect on resuspension of sediment. In addition, Thompson (2003) found that higher sedimentation rates on the fore reef at Totor and Chaland corresponded to periods of high wind speed. Within the lagoon winds of 16 knots (30 km hr^{-1}) or more have been shown to increase the resuspension of bed sediments, including heavier sand sediments (Lynch *et al.*, 2003a).

Wind speeds were high during May-June 2002 and April-May and July-August 2003. Totor and Trou Malabar are both shallow sites (<15 m depth) and therefore resuspension caused by wind is likely to be significant. Chaland, is a deeper site (>20 m depth) and thus, this site may be subjected to resuspended sediment from the lagoon, spilling over the reef edge. During 2002 wind speed was however low during March-April, when sediment deposition was high. It seems therefore that the very high sediment deposition at Totor in March-April 2002 and at Totor and Trou Malabar during April-May 2003 was caused by high rainfall and increased sediment loading of rivers. During April-May 2002 and June-August 2003, wind speed was high resulting in high sediment deposition due to resuspension of sediments by wind.

2.43 Sediment composition

Silt content of the sediment samples at the 3 sites was very variable, ranging from 2 – 28 %. Silt content was however always lower at Totor than at Trou Malabar and Chaland, indicating that sediment at this site consisted mostly of coarse grains. This was surprising, as wave action is lowest at Totor and one would therefore predict more fine grained sediments to settle out. Fine sediment grains are however more easily moved than coarser grains and so will tend to travel further, thus sediment size will decrease with increasing distance from the source (Dyer, 1986). During 2003 silt content at Trou Malabar and Chaland displayed a similar pattern, suggesting that these sites are influenced by similar processes; during 2002 however the sites showed contrasting patterns in silt content. Silt content at Totor however, appears to increase throughout the year with low silt content during February to April and then an increase in silt content during May to August. These variations in silt content could suggest different sources of sediment to the 3 sites and a change in sediment source between 2002 and 2003 at Trou Malabar. At all sites, silt content was relatively low during April-May, when sediment deposition was high, and consisted of a high percentage of coarse grained material with a low organic content.

Organic content of the sediment was similar to that measured in other studies of reef sediments (e.g.; Glynn and Stewart, 1973 (1.7–11.5 %); Tomascik and Sander, 1985 (2.3-10.9 %); Gleason, 1998 (9-15 %); Bastidas *et al.*, 1999 (12 %)). Some studies have observed an increase in the organic content of sediment with increasing proximity to river mouths (van Woesik *et al.*, 1999; Nugues and Roberts, 2003a); however this study did not show any correlation between organic content and proximity to the land, with high organic content recorded at both Totor and Chaland. Furthermore, organic content of the sediment was low during April-May when sediment deposition was high due to run-off caused by heavy rain and was highest during May-June when sediment deposition was low. As a result of high soil erosion Rodrigues has very nutrient poor soil (Gade, 1985) and this may explain why organic content of the sediment during April-May was relatively low. Studies within the lagoon have however, shown that the majority of organic material in suspension is relatively degraded, but that samples collected after a period of high rainfall contained relatively fresh organic material (Lynch *et al.*, 2003a). Further analysis of the sediment would be required in order to determine the source of the organic matter.

2.44 Biological variables

Despite the high sedimentation levels at Totor and Trou Malabar the reefs are still healthy with 51-75 % live coral cover, 50-58 hard coral species observed and little evidence of coral bleaching. This is in contrast to a number of other studies, which have reported low coral species richness and a decrease in live coral cover on reefs in high sediment sites (Squires, 1962; Roy and Smith, 1971; Loya, 1976; Randall and Birkeland, 1978; Cortés and Risk, 1985; Supriharyono, 1986; Acevedo *et al.*, 1989; Brown et al., 1990; Edinger *et al.*, 2000; Crabbe and Smith, 2002). Some studies have however reported healthy coral reefs in areas of high sedimentation and turbidity (e.g. Sheppard, 1980; Dollar and Grigg, 1981; Suresh and Mathew, 1993; McClanahan and

Obura, 1997; Leão de Mara *et al.*, 1999; Perry, 2003; Schleyer and Celliers, 2003), suggesting that coral colonies are capable of withstanding high sediment conditions.

Although all 3 sites were fairly diverse with high live coral cover, there did appear to be a shift in species composition with a higher number of species of *Acropora* at Totor than at Chaland and a higher number of species of Faviids at Chaland compared to Totor. Brown *et al.* (1990) found that massive species, in particular Faviids, showed a marked decline in abundance after increased sedimentation due to dredging, whereas *Acropora* spp did not appear to be adversely affected. Other studies have however found that high sediment sites were dominated by massive species such as Faviids (Van Woesik *et al.*, 1999; West and Van Woesik, 2001; Schleyer and Celliers, 2003), with low abundance of Acroporids (Cortés and Risk, 1985; Rice and Hunter, 1992; Van Woesik and Done, 1997; Van Woesik *et al.*, 1999; Torres and Morelock, 2002). Chaland is a more exposed site than Trou Malabar and Totor and this change in species composition may be due to an increase in exposure, rather the sedimentation, which tends to result in coral colonies becoming more massive and encrusting (Chappell, 1980). Laminar corals were also abundant at Totor and Trou Malabar and this is also concurrent with Chappell (1980), who showed that coral colonies become more branching and foliose with increasing sediment influx. Changes in coral colony orientation and morphology will be discussed further in chapter 5.

2.45 Summary

The main findings of this study are that:

- Sea temperature decreased by 3 °C between April and June of both 2002 and 2003. Salinity was low during April 2003, when rainfall was very high.
- Mean vertical visibility was lowest during March 2002 and April 2003. Mean horizontal visibility was lowest during April 2003. There were significant correlations between rainfall and both vertical and horizontal visibility. Horizontal visibility was lower at Totor than Trou Malabar and Chaland.
- Mean sediment deposition was highest at Totor in 2002 and Totor and Trou Malabar in 2003. Total sediment deposition at all sites was higher in 2003 than in 2002.

- Mean monthly sediment deposition in 2002 was highest during March-May at Totor (approximately 30 mg cm^{-2} d^{-1}). In 2003, mean monthly sediment deposition was highest at Totor and Trou Malabar during April-May (>60 mg cm^{-2} d^{-1}). Sediment deposition at Totor was significantly correlated with rainfall.
- High sediment deposition appears to be related to high rainfall (March 2002 and April 2003) resulting in land run-off, combined with high wind speed causing resuspension of sediments.
- Despite high levels of sediment deposition coral reefs at the 3 study sites are healthy with high coral cover and high species diversity.

2.46 Conclusions

The results show that coral colonies at Totor and Trou Malabar are subjected to sedimentation levels above the threshold set by Rogers (1990) of 10 mg cm^{-2} d^{-1}, suggesting that this value is not applicable for the reefs of Rodrigues and may require revision. The reef at Totor has rates of sedimentation constantly above 10 mg cm^{-2} d^{-1} whereas at Trou Malabar, sedimentation rates tend to be low, but periodically may be increased after heavy rainfall and high winds. It is likely that this periodic high sedimentation has been affecting these inshore reefs since deforestation first took place in the 1800s. In contrast, although Chaland suffers from low visibility, sedimentation rates are low (< 7 mg cm^{-2} d^{-1}). Despite the high sediment deposition, coral reefs at all 3 sites appear healthy with high coral cover and high coral diversity. Sedimentation can however, have a number of sub-lethal impacts, such as a decrease in growth rate (e.g. Dodge *et al.*, 1974; Dodge and Vaišnys, 1977; Tomascik and Sander, 1985), a decrease in larval recruitment (Tomascik and Sander, 1987; Gilmour, 1999) or a decrease in recovery from injury (Meesters *et al.*, 1992). The impact of sediment on these 3 processes at Totor, Trou Malabar and Chaland will be described in the following chapters.

CHAPTER 3: Growth rates of the branching corals *Acropora austera* and *Porites rus* under varying sediment regimes

3.1 INTRODUCTION

The previous chapter has described the 3 survey sites on the north coast of Rodrigues and has shown that the reefs, particularly the inshore reefs at Totor and Trou Malabar are subjected to high sedimentation and high turbidity. In contrast, sediment deposition was constantly low at Chaland. Despite this high sedimentation coral cover at all three sites was high, with high species diversity. High sediment may cause a disturbance to a coral's energy budget, by reducing the amount of light available which reduces zooxanthellar photosynthesis (Rogers, 1979; Suresh and Mathew, 1995), by interfering with the capacity to capture food and by increasing the energy demand for active sediment rejection (Kendall *et al.*, 1985; Riegl and Branch, 1995; Stafford-Smith and Ormond, 1992). This may have a number of sub-lethal impacts on the coral colony including a decrease in growth rate or reduced recruitment. This chapter will investigate whether high sedimentation at sites in the north of Rodrigues is causing a decrease in coral growth rates, by measuring growth under the varying sediment regimes.

3.11 Coral growth

Colonial organisms such as corals grow by asexual reproduction by a process of budding, which forms new polyps, and by the deposition of new skeletal material. Corals require high light intensities, clear and shallow water, temperatures of between 25-30 °C and salinities of 32-35 ‰ and although corals can survive in less than optimal conditions, growth rates will be greatest in the most favourable conditions (Stephenson and Stephenson, 1940). Coral species exhibit a range of different growth forms which can often be attributed to the environment in which they grow. In general, colonies become less robust, more slender or flattened with increasing depth (Barnes, 1973; Chappell, 1980), more globose or encrusting with increasing wave stress, more branching and foliose with increasing sediment influx and more encrusting as aerial exposure increases (Chappell, 1980).

3.12 Environmental factors affecting coral growth rates

Coral growth rates are variable on all time scales; there are differences between species and growth forms of the same species (Stephenson and Stephenson, 1940), differences with age or size (Stephenson and Stephenson, 1940; Bak, 1976; Hughes and Jackson, 1985; Chornesky and Peters, 1987; Chadwick and Loya, 1990) and differences on diurnal (Barnes and Crossland, 1980) and seasonal bases (Yap and Gomez, 1984; Miller, 1995; Vago *et al.*, 1997). Environmental variables such as depth (Baker and Weber, 1975; Dustan, 1975; Highsmith, 1979; Highsmith *et al.*, 1983; Hughes and Jackson, 1985; Huston, 1985; Logan *et al.*, 1994), temperature (Clausen and Roth, 1975; Glynn, 1977; Dodge and Lang, 1983; Miller, 1995; Vago *et al.*, 1997a), turbidity (Dodge *et al.*, 1974), light levels (Goreau, 1959; Bak, 1974) and exposure (Glynn, 1994) also account for some of the observed differences in coral growth rates. Coral colonies at higher latitude sites also tend to have lower growth rates than the same species at lower latitude sites (Harriott, 1998).

3.121 Water temperature

Glynn and Stewart (1973) found that temperature and coral growth showed a highly significant positive correlation; coral growth rate was found to decline rapidly at and below 21 °C, with the highest growth rate occurring at 29 °C. Glynn (1977) demonstrated that water temperature was significantly correlated with coral growth in an area of seasonal upwelling (Gulf of Panama) and coral growth declined markedly during the upwelling. There was also a significant negative correlation between coral growth and cloud cover at the non-upwelling site (Gulf of Chiriquí) year round and in the Gulf of Panama during the upwelling season. Dodge and Lang (1983) also found a good correlation between coral growth rates and sea temperature in the Northwest Gulf of Mexico; in general coral growth was found to be higher in years of warmer water temperature. In the U.S. Virgin Islands growth rates of *Acropora palmata* and *A. prolifera* were found to be significantly higher in the warm autumn months than in the cooler spring months (Gladfelter *et al.*, 1978).

Lough and Barnes (2000) demonstrated that the growth rate of *Porites* sp was significantly related to the annual average sea surface temperature (SST). They showed that for each 1 °C rise in SST, the average growth rate increased by 3.1 mm yr^{-1}. Vago *et al* (1997a) also found that variations in coral growth rate closely tracked the seasonal changes in sea temperature, although with a 2 month delay. Loya (1985) demonstrated that in *Stylophora pistillata* small immature colonies exhibited significantly faster growth rates during the summer than during the winter. The author also found significant positive correlations between growth rates and total sun-hours per month and also between growth rates and mean seawater temperatures. Larger mature colonies showed no such relationships. It is suggested that during the summer, warmer water temperatures and longer periods of sun induce faster growth rates since most energy is allocated for growth. In mature colonies energy is channelled into both growth and reproduction during the summer months, resulting in a slow-down in growth rates during this time.

In contrast, growth rates of *Acropora pulchra* in the Philippines were found to decrease significantly with the onset of warmer months and remained at a constant low for the duration of the summer; the onset of the cooler, rainy months was accompanied by a significant increase in growth rates (Yap and Gomez, 1984). The authors suggest that during the summer months temperatures may be approaching the upper limits for coral growth and survival causing stress to the coral colonies and resulting in decreased growth rates. Jokiel and Coles (1977) demonstrated that coral growth rates were optimal at temperatures of approximately 26 °C. Coral growth rates declined if temperatures were decreased to 21-22 °C or increased to 28 °C.

3.122 Light

Bak (1974) concluded that the number of sun hours appeared to be the main influence on coral growth rates in Curaçao; he found a significant positive correlation between the number of sun hours and growth rates for *Madracis mirabilis, Agaricia agaricites* and *Montastrea annularis*. Buddemeier (1974) found a positive correlation between rainfall and skeletal density in *Porites lobata* and suggests that this is due to seasonal changes in light intensity. Guzmán and Cortés (1989) found that in Costa Rica, *P. lobata* and *Pocillopora damicornis* had significantly higher growth rates during the dry season than during the rainy season. The authors conclude that this is due to more hours of sunlight combined with lower turbidity, as a result of less river run-off. Sea surface temperature was found to vary little during the year indicating that it did not influence seasonal growth rates.

Other studies have demonstrated that coral growth rates decrease with increasing water depth, due to reduced availability of light (e.g. Baker and Weber, 1975; Dustan, 1975; Highsmith, 1979; Highsmith *et al.*, 1983; Hubbard and Scaturo, 1985; Hughes and Jackson, Huston, 1985; Logan *et al.*, 1994). Dustan (1975) demonstrated that growth rates of *Montastrea annularis* are correlated with water depth and that growth decreases exponentially with water depth. Growth rates of *Favia pallida, Goniastrea retiformis* and *Porites lutea* were found to decrease with depth; the highest growth rates for all species were among colonies collected in <5 m of water (Highsmith, 1979). Growth rates of *M. cavernosa* were found to decrease significantly with increasing depth and the highest growth rates for *M. cavernosa, M. annularis* and *P. asteroides* all occurred in colonies from <10 m depth (Highsmith *et al.*, 1983). Hubbard and Scaturo (1985) found that there was a decrease in the growth rate of *M. annularis* between 12 and 18 m and the authors suggest this may reflect a light threshold below which photosynthesis and calcification are inhibited.

3.13 The impact of sediment on coral growth

Sediment can inhibit coral growth by reducing the amount of available light which reduces zooxanthellar photosynthesis (Rogers, 1979) and from the metabolic costs associated with sediment removal (Kendall *et al.*, 1985; Riegl and Branch, 1995). Extensive sedimentation may result in coral bleaching and tissue death as a result of smothering (Marshall and Orr, 1931; Rogers, 1983; Peters and Pilson, 1985; Riegl, 1995).

Rogers (1979) found that experimental shading, mimicking extreme turbidity, resulted in a significant decline in growth rates of *Acropora cervicornis* compared to control colonies. In contrast, daily application of 200 mg cm^{-2} of sediment had no affect on growth rate. The author concluded that the main affect of suspended matter in the water column is to reduce light penetration by absorption and scattering, decreasing net primary production and respiration. Kendall *et al.* (1985) found that the addition of 100 ppm kaolin to colonies of *A. cervicornis* caused a significant reduction in calcification rate. The authors show that turbidity not only produced a decrease in light availability but also significantly increased the use of stored organic molecules for mucus production and sediment removal. In the laboratory the growth rates of both *Porites cylindrica* and *Goniastrea retiformis* were found to be affected by sediment load (Anthony, 1999a). Shading, as a result of high suspended particulate matter (SPM), resulted in significantly reduced growth rates in both species. An increase in particle load however increased the growth rate of *G. retiformis* and the author concludes that this species supplements its nutrition, using SPM as a food source. Te (2001) found that in the field, sediment loading levels of between <1 and >300 mg cm^{-2} d^{-1} had no significant effect on coral growth rates. In the laboratory there was again no significant difference in the growth rates of corals at different sedimentation rate levels, however coral growth was noticeably affected by a reduction in light caused by increased turbidity. There were significant differences between the growth rates of coral colonies at different light levels, and colonies in high light environments had faster growth rates than colonies in low light environments.

In Bermuda, sedimentation from extensive dredging resulted in a marked decline in coral growth which lasted for many years and eventually resulted in coral death (Dodge and Vaišnys, 1977). Aller and Dodge (1974) and Dodge *et al.* (1974) found that in Jamaica, high resuspension of sediments also caused a decline in coral growth; sedimentation also decreased the variability in growth rates, suggesting that the ability of corals to respond to other less limiting environmental variables was reduced. The application of 100 ppm drilling mud over a 48 day period in the laboratory was also found to significantly depress the growth rate of *Montastrea annularis* (Dodge, 1982). In Barbados, growth rates of *M. annularis* were found to increase with distance from a source of land-based pollution; growth rates were lowest at the sites nearest the pollution source and highest at the furthest sites (Tomascik and Sander, 1985; Tomascik, 1990). Suspended particulate matter (SPM) appeared to be the main environmental variable affecting the growth rates of *M. annularis*. The authors also suggest that SPM may act as an energy source for corals, increasing growth up to a certain maximum concentration; after this reduction of growth occurs due to smothering, reduced light levels and reduced zooxanthellae photosynthesis.

In contrast, Torres and Morelock (2002) found that the linear extension rates of 3 coral species were not significantly affected by increased sediment. Similarly, Edinger *et al* (2000) could find no significant correlation between growth rates of *Porites lobata* and pollution in Indonesia. Coral extension rates at sites severely polluted from land-based sources were found to be similar to those at offshore unpolluted reefs. The construction of an open-cut gold mine in Papua New Guinea caused ten-fold increases in sedimentation on adjacent fringing reefs. Although average annual skeletal density, annual extension and annual calcification of *Porites* sp all tended to be less in the period after mining operations began compared with pre-construction levels, these general declines could not be linked to the increased sedimentation (Barnes and Lough, 1999). Furthermore, although dredging at Ko Phuket in Thailand caused increased sedimentation on the reef flat, Brown *et al* (1990) could find no significant differences in the growth rate of *P. lutea* before, during and after the dredging operation. They suggest however, that this may be because they used X-radiographic techniques to measure annual growth rates and therefore that short-term decreases in growth rate may not be picked up.

3.14 Methods of measuring coral growth rates

A variety of different methods have been used to assess growth rates of coral colonies; these have been reviewed by Buddemeier and Kinzie (1976) and Brown and Howard (1985). Techniques employed have included using photography to record changes in colony size over time (Barnes and Crossland, 1980; Van Moorsel, 1985; Maida *et al.*, 1994; Vago *et al.*, 1994; Tanner, 1995), the use of a fixed base-line from which to measure growth (Rogers, 1979; Goreau and Macfarlane, 1990), radiometric dating methods (Moore and Krishnaswami, 1972; 1974) and ^{45}Ca and ^{14}C incorporation rates (Clausen and Roth, 1975). Vago *et al.* (1997b) developed an underwater laser, which they used to measure growth rates over a timescale of minutes to hours and could detect growth rates of as little as 10 μm. Other techniques include X-radiographic techniques, Alizarin staining and buoyant weight techniques and these will be discussed further below.

3.141 X-Radiography

This method of ageing coral colonies was first initiated by Knutson *et al.* (1972) who found that coral samples from Enewetak Atoll showed distinct and fairly regular alternating dark and light bands, reflecting a cyclic variation in the density of the deposited skeletal material. This density banding was found to be annual with pairs of consecutive dark (high density) and light (low density) bands reflecting one years growth. These density patterns are easily detected by X-radiographic techniques. This method has since been extensively used to measure long-term growth rates and growth histories retrospectively (Buddemeier, 1974; Buddemeier *et al.*, 1974; Highsmith, 1979; Highsmith *et al.*, 1983; Klein and Loya, 1991; Logan *et al.*, 1994) and to relate annual growth patterns to past environmental conditions and pollution incidences (Dodge *et al.*, 1974; Dodge and Vaišnys, 1977; Dodge and Lang, 1983; Tomascik, 1990; Barnes and Lough, 1999).

The advantages of X-radiography are that it is capable of measuring long-term growth rates and as discussed above, can be used to investigate the impact of environmental conditions on growth rates. The disadvantages are that it cannot accurately measure time increments of less than 1 year (Brown *et al.*, 1990), it requires technical skills and equipment for sample preparation and band measurement and only really applies to the study of massive coral species (Buddemeier and Kinzie, 1976).

3.142 Alizarin staining

Sodium alizarinesulphonate (Alizarin Red S) is a dye used to stain bone and has also been used as a textile dye. Corals subjected to Alizarin Red dissolved in seawater incorporate the dye into their skeleton. The colour remains as a permanent stain indicating where calcification has occurred during the experiment (Lamberts, 1974; 1978). Barnes (1970) developed the use of Alizarin Red staining techniques to investigate coral growth rates, observing that the dye left a permanent mark from which growth over time could be measured. The method usually involves placing a clear polythene bag around the coral colony, injecting Alizarin Red at a concentration of 10-20 mg l^{-1} and leaving it to incubate for a number of hours, depending on the colony size. Growth rates over a number of months can then be assessed by measuring the distance between the stain and the new apical polyp (Dustan, 1975; Glynn, 1977; Dodge, 1982; Wellington, 1982; Heyward and Collins, 1985; Hughes and Jackson, 1985; Ward, 1995; Harriott, 1998).

The advantages of Alizarin Red are that it is inexpensive and does not require special equipment; growth may be measured in any direction and as with all measurements of length, the greater amount of linear growth data in the literature means that comparisons can be made with other studies. The disadvantages of the technique are that initial manipulation of the colony may cause damage and that it requires the sacrifice of the colony at the end of the experiment and therefore cannot be used to make repeated measurements (Lamberts, 1974; Buddemeier and Kinzie, 1976).

3.143 Buoyant Weight Technique

This technique involves weighing living coral while it is suspended in a medium of seawater and predicting from this weight the weight of the skeleton. The method was first used by Franzisket (1964), Bak (1973; 1976) and Jokiel *et al.* (1978). Bak (1973) designed an underwater weighing apparatus, allowing frequent accurate measurement of changes in coral weight over long periods of time to be determined. This technique was modified by Jokiel *et al.* (1978), who described the theoretical basis of the technique and the relationship between buoyant weight and dry skeleton weight. They used the method in both field and laboratory studies for the accurate measurement of changes in coral skeletal weight over both long and short time intervals. The method was then further adapted by Davies (1989) who increased the accuracy of the technique, allowing growth rates to be determined in the laboratory over intervals of less than 24 hours.

The advantages of the buoyant weight technique are that it is very accurate, simple, and inexpensive; as the technique is non-destructive it provides repeatable measures of growth. The technique can also be used to measure changes in growth over very short time periods (24 hours) (Bak, 1973; Buddemeier and Kinzie, 1976; Jokiel *et al.*, 1978; Davies, 1989). The main disadvantage of the technique is the initial specimen manipulation, which may cause damage to the coral colony. Due to the accuracy of growth measurements over a short period of time and the use of simple equipment this technique was chosen to measure coral growth rates in Rodrigues.

3.15 Aims and objectives

The aims of this study are to assess whether high levels of sedimentation on the reefs of Rodrigues are having a sub-lethal impact on coral colonies, by investigating coral growth rates at sites with different levels of sedimentation. This will be achieved by:

- Quantification of coral growth rates at the 3 survey sites over two 4-month periods in 2002 and 2003 using the buoyant weight technique and *in situ* measurements.
- A comparison of changes in coral growth rates with variations in sediment deposition and other environmental parameters at the 3 sites described in Chapter 2.
- Transplantation of corals from high sediment sites to low sediments, in order to assess whether any differences in growth rate were due to environmental conditions at the site or to genetic differences in the corals from each site.

3.2 METHODS

3.21 Buoyant Weight

Coral growth rates were assessed at the 3 study sites (Totor, Trou Malabar and Chaland) between February - June 2002 and April – August 2003 using the buoyant weight technique.

Acropora austera and *Porites rus* were chosen as the study species as they are both commonly occurring species in Rodrigues (Fenner *et al.*, 2004) and occur at the base of reef slopes at a depth down to approximately 15 metres. During 2002 however, only growth rates of *A. austera* were measured. At each of the 3 study sites 15 *A. austera* and 15 *P. rus* colonies were identified at depths between 7 and 14 m and were tagged using a cable-tie and label. One branch tip (approximately 5 cm in length) was taken from each coral colony using pliers, placed in a plastic sample bag and returned to the laboratory, where it was placed in a shaded, aerated aquarium maintained at ambient temperature. Branch tips were then attached to ceramic bathroom tiles (10 cm x 10 cm), using epoxy putty (Starbrite) to form nubbins (Plate 3.1). The corals could then be handled by the tile, thus minimising any damage to the tissue.

Buoyant weighings were made using a Status SP300 Balance (± 0.01 g), positioned above the aquarium. A weighing platform was constructed from 4 plastic rods suspended below the balance by monofilament nylon fishing line; this allowed the coral to be suspended 16 cm below the water surface. During weighing the air pump in the tank was switched off to exclude water movement. Any bubbles adhering to the coral and any sediment that had settled on the tile were removed using a fine paintbrush prior to weighing. Care was also taken not to wet the aerial portion of the suspending wires.

The density of seawater was determined from temperature and salinity measurements (Grasshoff *et al.*, 1999) immediately before weighing the coral nubbins. The air weight of each coral skeleton was then determined using equation (1).

(1) Weight of object in air = weight in water/(1 - D_{water}/D_{object})

The density of the skeleton was determined by placing 15 *Acropora austera* and 15 *Porites rus* branch tips in domestic bleach (3.6 %) for 7 days, buoyant weighing the tips in seawater, washing them in distilled water, drying the tips to constant weight at 70 °C and then weighing the dried skeleton.

After weighing, the coral nubbins were transported back to the reef, while immersed in seawater and shaded from the sun. The coral nubbins were then attached to 2 wire-mesh racks (1 rack per species; 50cm x 80cm) on the boat using wire ties; nubbins were sprayed gently with seawater throughout this process to reduce stress due to aerial exposure. The rack was taken underwater and attached to the substratum using 4 metal pegs hammered into the substrate at each corner. At sites where the substrate was coralline rock, the rack was tied to the substrate using nylon fishing line. Racks were placed either at the bottom of the reef slope on silt/sand or on the reef slope on coralline rock at a depth of 10-12 m close to the original colonies. The rack allowed coral nubbins to be raised 14 cm above the substrate (Plate 3.2).

The growth rate was determined each month using the buoyant weighing technique over a 4 month period. Each month the rack of coral nubbins was collected from the site and transported to the laboratory while immersed in seawater and shaded from the sun. The nubbins were placed in the aquarium over night and then their weight was determined using the buoyant weight technique. After weighing, the corals were re-attached to the metal rack and returned to the reef.

At the end of the growth rate experiment the coral nubbins were removed from the tiles and any remaining skeletal material was dissolved in 5 % Hydrochloric Acid. The tile and glue were buoyant weighed and then were dried and weighed in the air. The buoyant weight of the tile and glue at each weighing was then determined using equation (2). This figure was subtracted from the total buoyant weight to give the buoyant weight of the coral nubbin. The density of the tile was determined using equation (3).

(2) Weight of object in water = weight in air (wt in air/D_{object} * D_{water})

(3) Density of object = weight in air * $Density_{water}$/weight in air – weight in water

Plate 3.1 An *Acropora austera* coral nubbin.

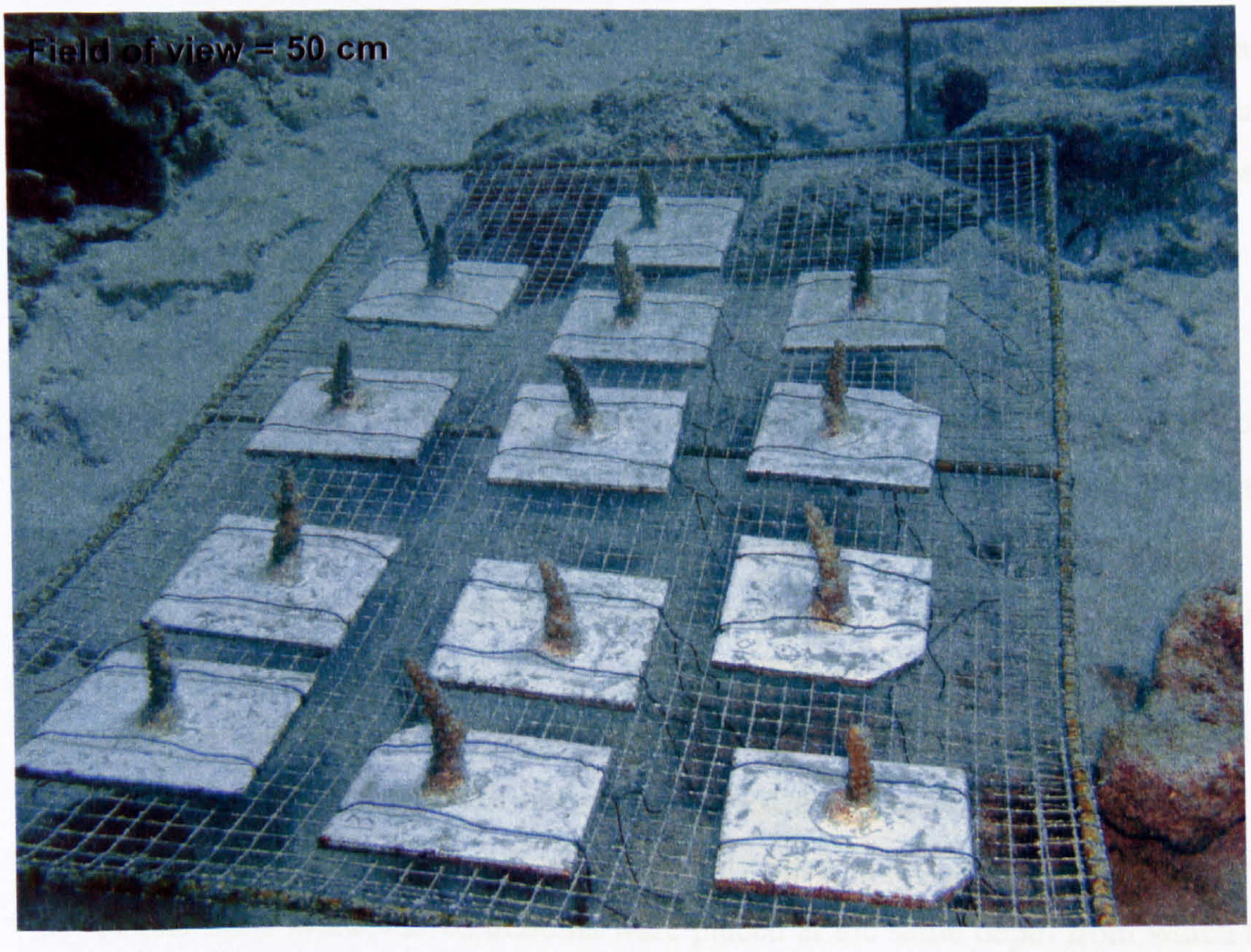


Plate 3.2 A rack of *Acropora austera* nubbins on the reef at Trou Malabar.

3.22 In situ Growth

In order to verify measurements made using the buoyant weight technique, *in situ* growth rates were also measured using 2 techniques. At each site 15 *Acropora austera* and 15 *Porites rus* colonies were identified and 1 branch was tagged using a fine cable-tie, fixed tightly, approximately 5 cm from the tip. The cable-ties were used as a fixed baseline and the length of the branch, from the baseline to the tip, was then measured using vernier callipers. This was repeated over a 3 month period during March – June 2002 and May – August 2003.

In addition, the tagged branches were photographed using a digital camera (Olympus c5050z, 5.0 Mega pixels) in an underwater housing (Olympus PT-15). A laminated grid of 20 cm x 20 cm divided into 1 cm squares was held immediately behind the coral colony in each of the photographs to act as a reference. The photographs were registered as a Non-Earth image in MapInfo Professional (version 6.0) using intersections on the grid as control points. The coral branch was then digitised using the polygon tool. The length, surface area and perimeter of the branch tip could then be calculated. The coral branches were photographed once every month over a 3 month period during May – August 2003; growth could not be measured during April-May due to unavailability of the camera. Care was taken to photograph the branch from the same angle and distance. This allowed changes in coral branch length and perimeter to be calculated and images could be overlaid on each other to assess where these changes had occurred (Figures 3.1 and 3.2).

3.23 Transplantation

A transplantation experiment was carried out during April – June 2002. Due to rough weather this experiment could not be repeated during 2003. In addition to the 3 study sites, 3 'control' sites were identified outside of the Port Mathurin Bay (Figure 3.3; Table 3.1). These sites had similar reef structure to the 3 study sites, however were exposed to wave action and had higher visibility. Fifteen *Acropora austera* branch tips (approximately 5 cm in length) were collected from each of the 6 sites and returned to the laboratory, where they were buoyant weighed as described in section 3.21. The nubbins were then transplanted from the 3 study sites to the 3 control sites and vice versa (Table 3.2). Transplanted nubbins were placed at the same depth from which they had been collected. An additional 15 *A. austera* branch tips were collected from each site and replaced back at the site from which they were collected to act as controls.

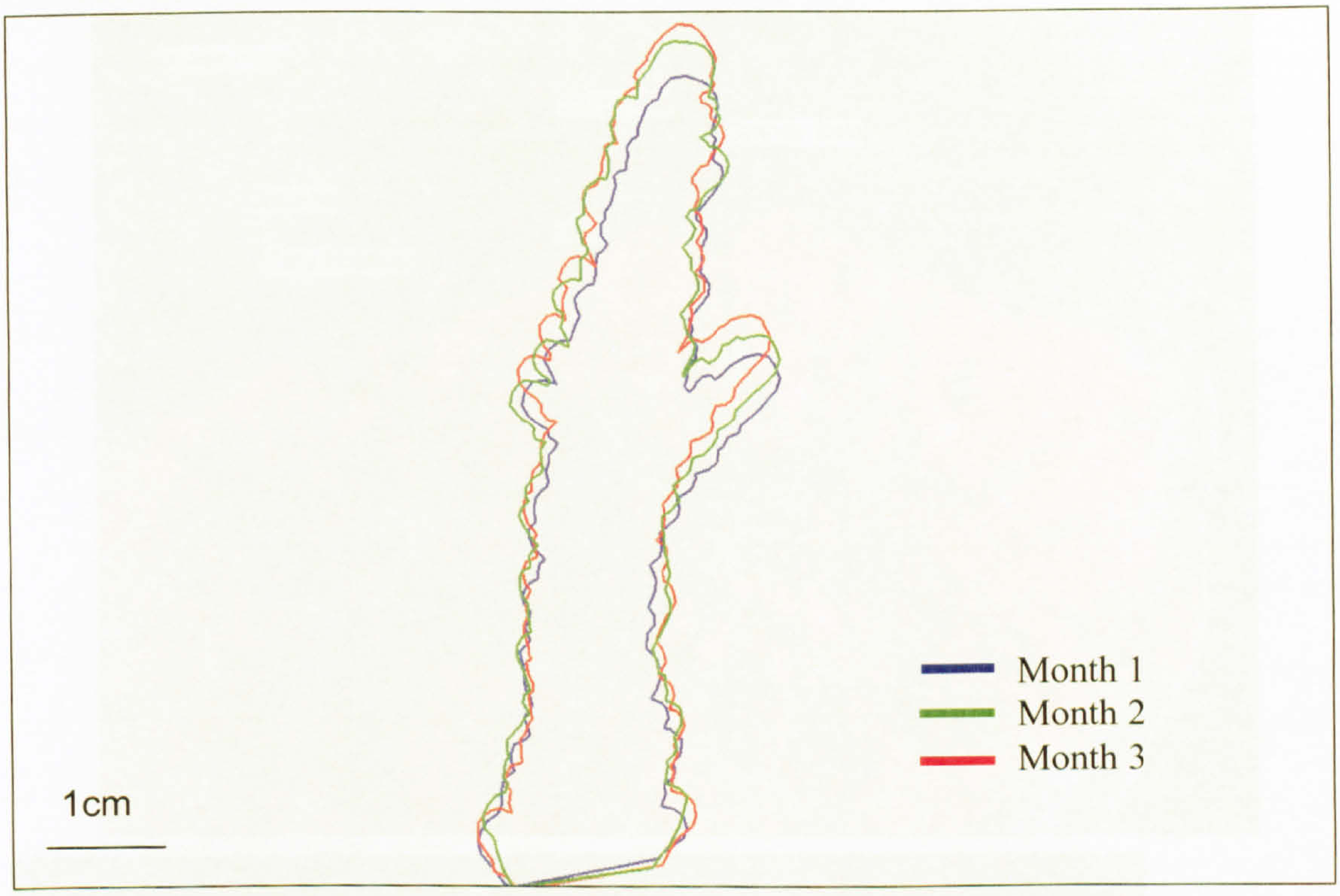


Figure 3.1 Digitised *Acropora austera* branches overlaid on one another to show growth rate over a 3 month period.

Figure 3.2 Digitised *Porites rus* branches overlaid on one another to show growth rate over a 3 month period.

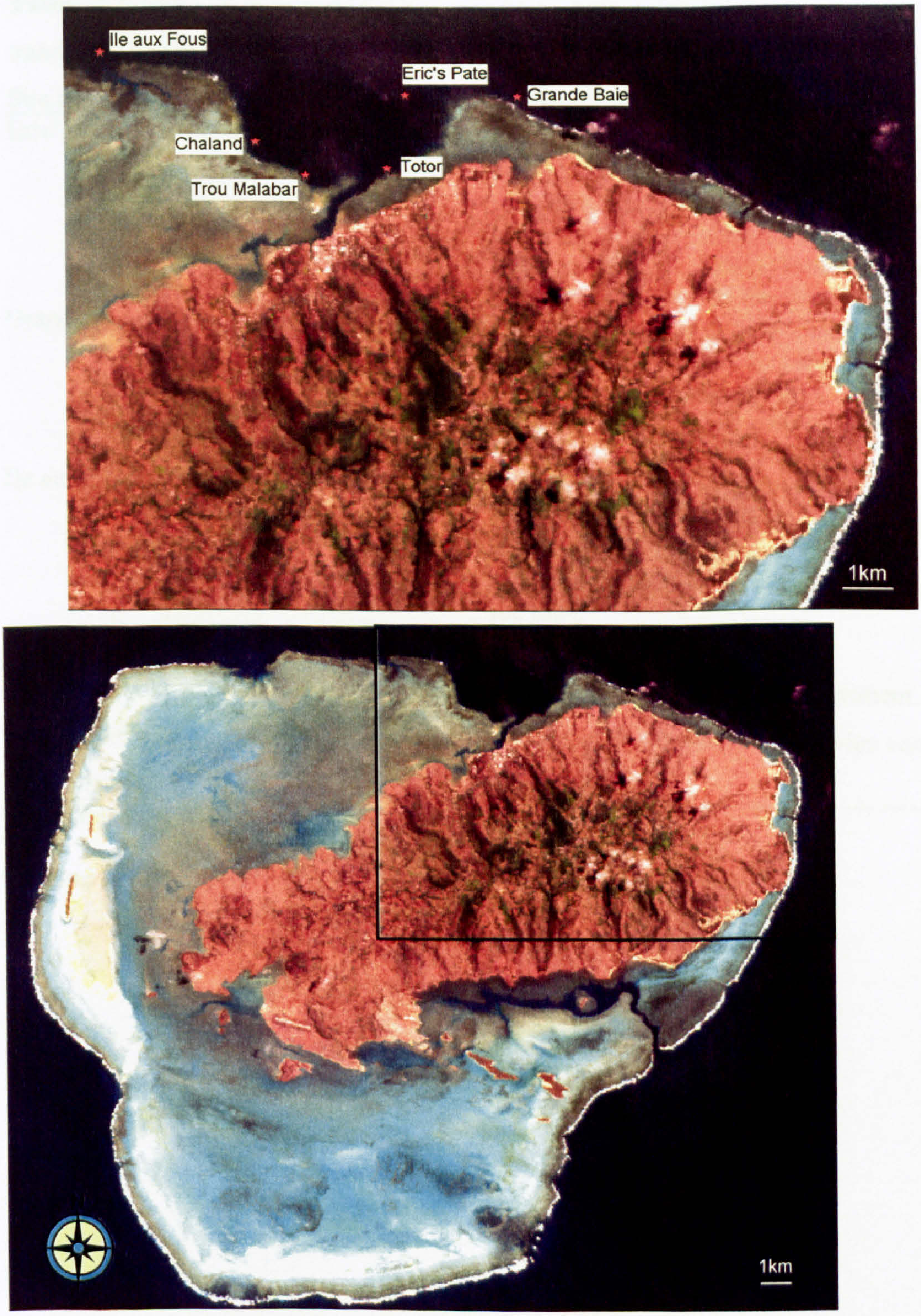


Figure 3.3 The position of the 3 non-turbid sites (Eric's Paté, Grande Baie and Ile aux Fous) and the 3 turbid sites (Totor, Trou Malabar and Chaland) on the north coast of Rodrigues. Landsat 7 satellite image processed by B. Chapman.

Table 3.1. The 3 non-turbid sites outside of Port Mathurin Bay used in the transplantation experiment.

Site Name	Latitude	Longitude	Description
Eric's Paté	19° 39.526	63° 25.916	Gentle slope rising from a sand and rubble sea-bed at 17m depth up to 10m at the base of a steep-sided coral outcrop rising to 6m. Diverse corals on sides of outcrop. A lot of coral rubble and newly broken branching *Acropora* colonies on the slope.
Grande Baie	19° 39.520	63° 26.923	Irregular spur and groove rising from sand base. Spurs from 6m to 13m depth. Spurs with diverse massive and sub-massive corals; branching and tabular *Acropora* on the tops.
Ile aux Fous	19° 39.121	63° 23.178	Irregular spur and groove rising from sand base. Spurs from 8m to 13m. Diverse massive and sub-massive corals on spur sides; branching and tabular *Acropora* on the tops.

Table 3.2. The turbid and non-turbid sites used in the transplantation experiment. Coral nubbins were transplanted from the turbid sites to the non-turbid sites and vice versa.

Turbid sites		Non-turbid sites
Trou Malabar	↔	Ile aux Fous
Totor	↔	Grande Baie
Chaland	↔	Eric's Paté

3.3 RESULTS

3.31 Buoyant Weight

Considering mean total growth over each of the 4-month periods it can be seen that in 2002 mean growth rate of *Acropora austera* varied from 66.63 ± 2.97 mg d^{-1} at Totor to 171.93 ± 9.33 mg d^{-1} at Trou Malabar (Figure 3.4). During 2003 mean growth rate varied from 32.77 ± 2.96 mg d^{-1} at Totor to 80.20 ± 5.99 mg d^{-1} at Chaland. Mean growth rate of *A. austera* was significantly higher at Trou Malabar than at Chaland and significantly higher at Chaland than at Totor during 2002 (Figure 3.4; Table 3.3). During 2003 mean growth rate was significantly higher at Chaland than at Trou Malabar and significantly higher at Trou Malabar than at Totor. Mean total growth rate decreased significantly between 2002 and 2003 at all sites: at Totor growth rate decreased 2-fold from 66.63mg d^{-1} to 32.77mg d^{-1}, at Chaland from 126.59mg d^{-1} to 80.20mg d^{-1} and at Trou Malabar growth rate decreased 3-fold from 171.93 mg d^{-1} to 59.13mg d^{-1}. Mean total growth rate of *Porites rus* varied from 45.98 ± 1.17 mg d^{-1} at Totor to 53.32 ± 2.52 mg d^{-1} at Chaland. There was however no significant difference in mean total growth rate of *P. rus* at the 3 sites during 2003 (Figure 3.5; Table 3.4).

Table 3.3 Statistical analysis results for total growth rate data measured using the buoyant weight technique for *Acropora austera* during February – June 2002 and April – August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	p
Tot*TM*Chal	2002	1-way ANOVA	38.37 (F)	2	<0.05*
Tot*TM*Chal*	2003	1-way ANOVA	43.89 (F)	2	<0.05*
2002*2003	-	1-way ANOVA (√)	111.20 (F)	1	<0.05*
Sites*Feb-Mar	2002	1-way ANOVA	1.85 (F)	2	>0.05
Sites*Mar-Apr	2002	2-sample T-test	0.45 (T)	15	>0.05
Sites*Apr-May	2002	2-sample T-test	3.96 (T)	4	<0.05*
Sites*May-Jun	2002	2-sample T-test	3.51 (T)	4	<0.05*
Sites*Apr-May	2003	1-way ANOVA	3.39 (F)	2	>0.05
Sites*May-Jun	2003	1-way ANOVA (Log)	9.43 (F)	2	<0.05*
Sites*Jun-Jul	2003	1-way ANOVA (Log)	43.09 (F)	2	<0.05*
Sites*Jul-Aug	2003	1-way ANOVA	4.35 (F)	1	>0.05
Tot*Months	2002	1-way ANOVA	159.68 (F)	3	<0.05*
Tot*Months	2003	1-way ANOVA	114.86 (F)	2	<0.05*
TM*Months	2003	1-way ANOVA (√)	91.72 (F)	3	<0.05*
Chal*Months	2002	1-way ANOVA	1.52 (F)	3	>0.05
Chal*Months	2003	1-way ANOVA	17.68 (F)	3	<0.05*

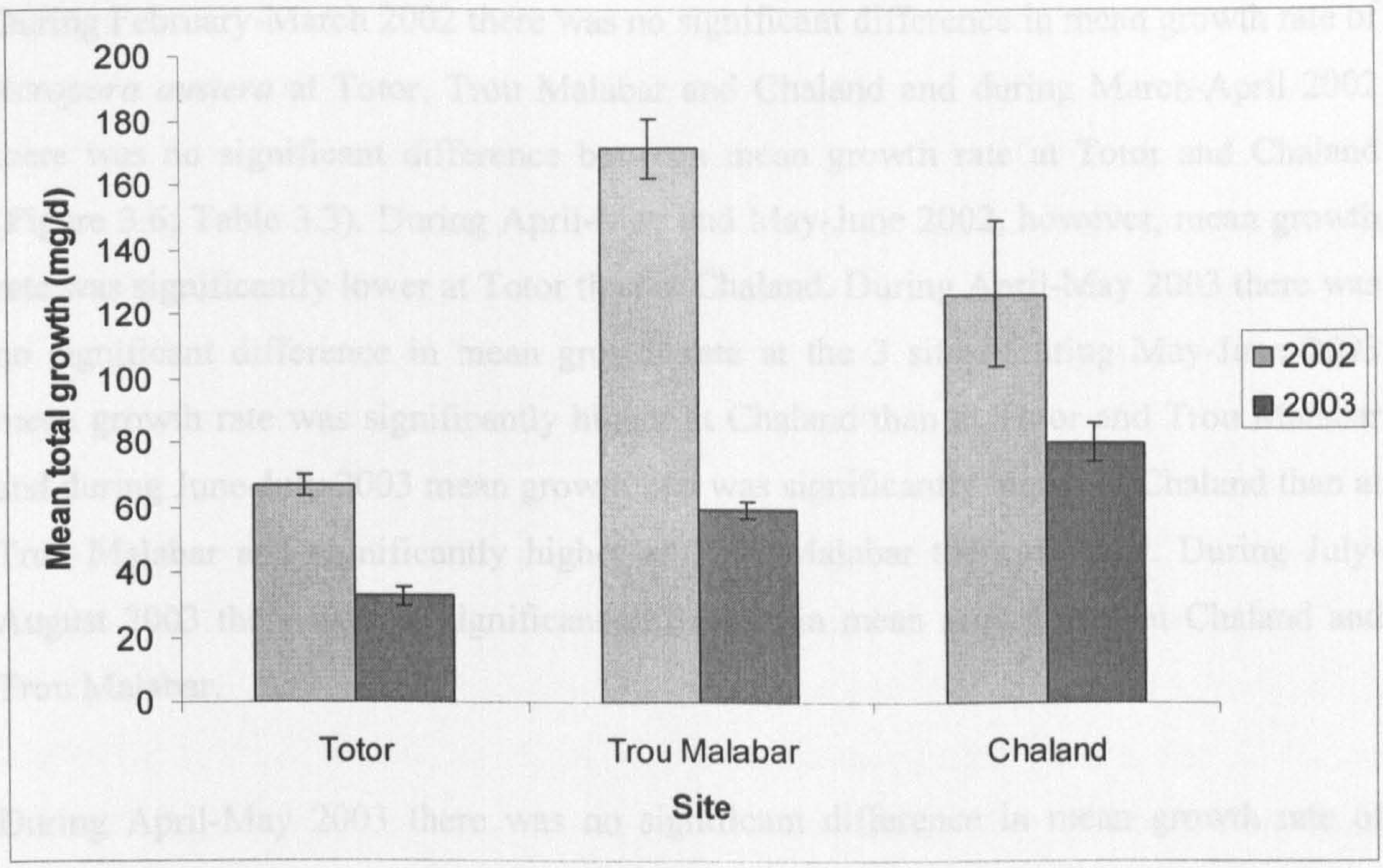


Figure 3.4 The mean total growth rate (mg d^{-1}) ± SE of *Acropora austera* measured using the buoyant weight technique at the 3 survey sites between February and June 2002 and April and August 2003.

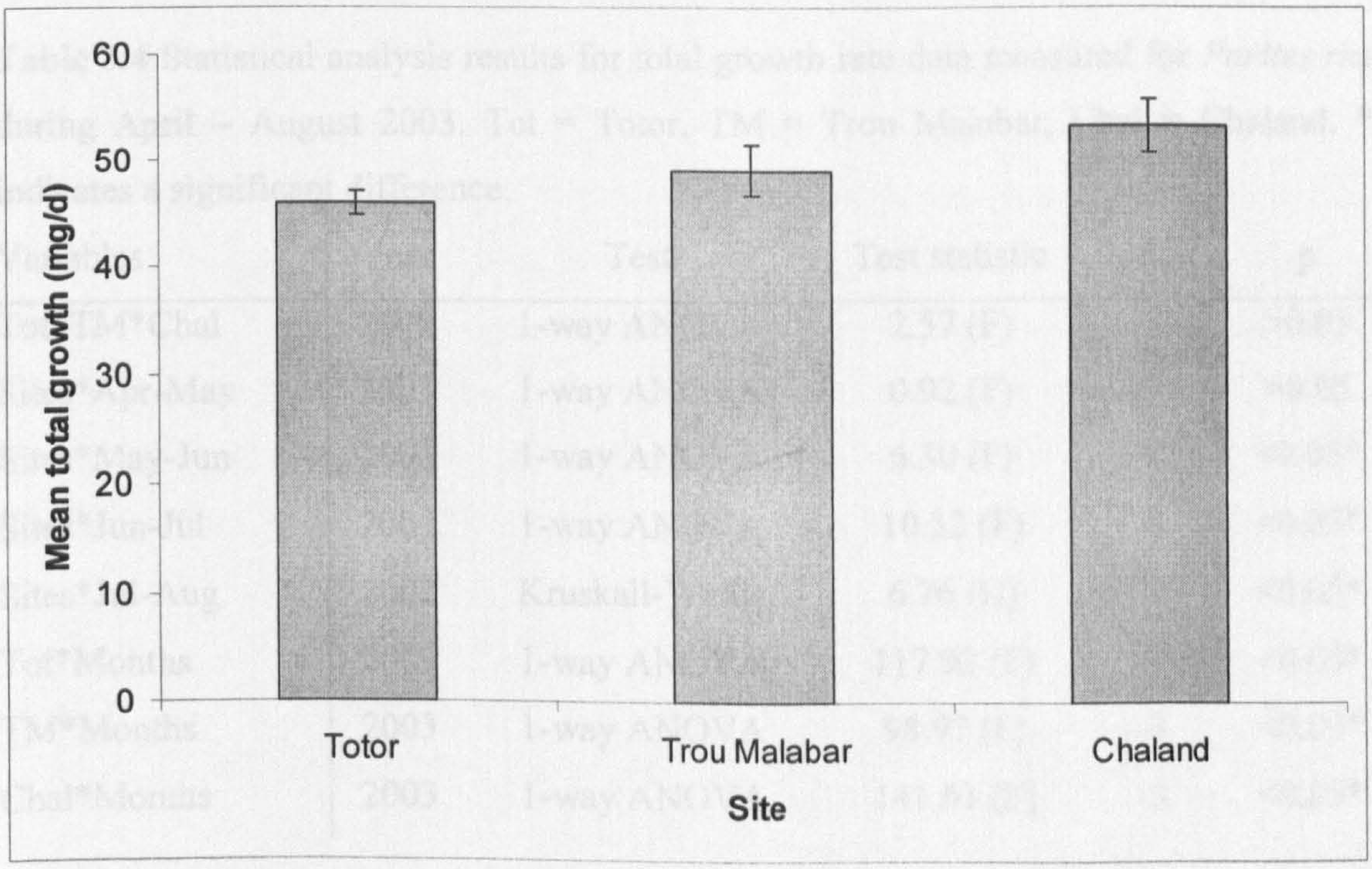


Figure 3.5 The mean total growth rate (mg d^{-1}) ± SE of *Porites rus* measured using the buoyant weight technique at the 3 survey sites between April and August 2003.

During February-March 2002 there was no significant difference in mean growth rate of *Acropora austera* at Totor, Trou Malabar and Chaland and during March-April 2002 there was no significant difference between mean growth rate at Totor and Chaland (Figure 3.6; Table 3.3). During April-May and May-June 2002, however, mean growth rate was significantly lower at Totor than at Chaland. During April-May 2003 there was no significant difference in mean growth rate at the 3 sites. During May-June 2003 mean growth rate was significantly higher at Chaland than at Totor and Trou Malabar and during June-July 2003 mean growth rate was significantly higher at Chaland than at Trou Malabar and significantly higher at Trou Malabar than at Totor. During July-August 2003 there was no significant difference in mean growth rate at Chaland and Trou Malabar.

During April-May 2003 there was no significant difference in mean growth rate of *Porites rus* at Totor, Trou Malabar and Chaland (Figure 3.7; Table 3.4). During May-June mean growth rates were significantly lower at Chaland than at Totor and Trou Malabar. During June-July and July-August mean growth rates were significantly lower at Totor than at Chaland and Trou Malabar.

Table 3.4 Statistical analysis results for total growth rate data measured for *Porites rus* during April – August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	p
Tot*TM*Chal	2003	1-way ANOVA	2.57 (F)	2	>0.05
Sites*Apr-May	2003	1-way ANOVA	0.92 (F)	2	>0.05
Sites*May-Jun	2003	1-way ANOVA	6.30 (F)	2	<0.05*
Sites*Jun-Jul	2003	1-way ANOVA	10.32 (F)	2	<0.05*
Sites*Jul-Aug	2003	Kruskall-Wallis	6.76 (H)	2	<0.05*
Tot*Months	2003	1-way ANOVA	117.92 (F)	3	<0.05*
TM*Months	2003	1-way ANOVA	98.97 (F)	3	<0.05*
Chal*Months	2003	1-way ANOVA	141.61 (F)	3	<0.05*

At Totor, mean monthly growth rate of *Acropora austera* during 2002 was significantly higher during February-April than during April-June (Table 3.3). Mean growth rate varied from 134.19 ± 3.93 mg d^{-1} during February-March to 21.41 ± 4.67 mg d^{-1} during May-June. During 2003 mean monthly growth rate was high during April-May and then declined significantly in May-June, remaining low throughout the study. Mean growth rate varied from 160.72 ± 18.20 mg d^{-1} during April-May to 17.40 ± 1.45 mg d^{-1} during June-July. Mean monthly growth rate of *Porites rus* in 2003 at Totor showed a similar pattern with a high growth rate in April-May and then a significant reduction in growth rate in May-June. Mean growth rate varied from 107.74 ± 3.50 mg d^{-1} in April-May to 2.75 ± 4.02 mg d^{-1} in June-July and was significantly higher in April-May than May-June and significantly higher in May-June than in June-August (Table 3.4).

At Trou Malabar mean monthly growth rate of *Acropora austera* during 2003 was high during April-May and then declined significantly in May-June, remaining low throughout the study (Table 3.3). Mean growth rate varied from 116.42 ± 5.99 mg d^{-1} in April-May to 28.24 ± 3.01 mg d^{-1} in May-June. Mean monthly growth rate of *Porites rus* was also high in April-May, then declined significantly in May-June and remained low until the end of the experiment (Table 3.4). Mean growth rate varied from 100.64 ± 2.37 mg d^{-1} in April-May to 22.78 ± 2.59 mg d^{-1} in July-August.

At Chaland there was no significant difference in mean monthly growth rate of *Acropora austera* during February-June 2002, with growth rates remaining high throughout the experiment (87.26 ± 18.20 – 166.68 ± 36.10 mg d^{-1}) (Table 3.3). During 2003 mean monthly growth rate was high in April-May, then declined significantly in May-June, remaining low in the remaining 2 months. Mean growth rate varied from 122.14 ± 7.67 mg d^{-1} in April-May to 49.20 ± 8.07 mg d^{-1} in May-June. Mean monthly growth rate of *Porites rus* at Chaland showed a similar pattern to *A. austera* with high growth rates during April-May, then a significant decline in growth rate during May-June and growth rates remaining low throughout the study (Table 3.4). Mean growth rate varied from 111.34 ± 5.73 mg d^{-1} in April-May to 11.71 ± 3.30 mg d^{-1} during May-June.

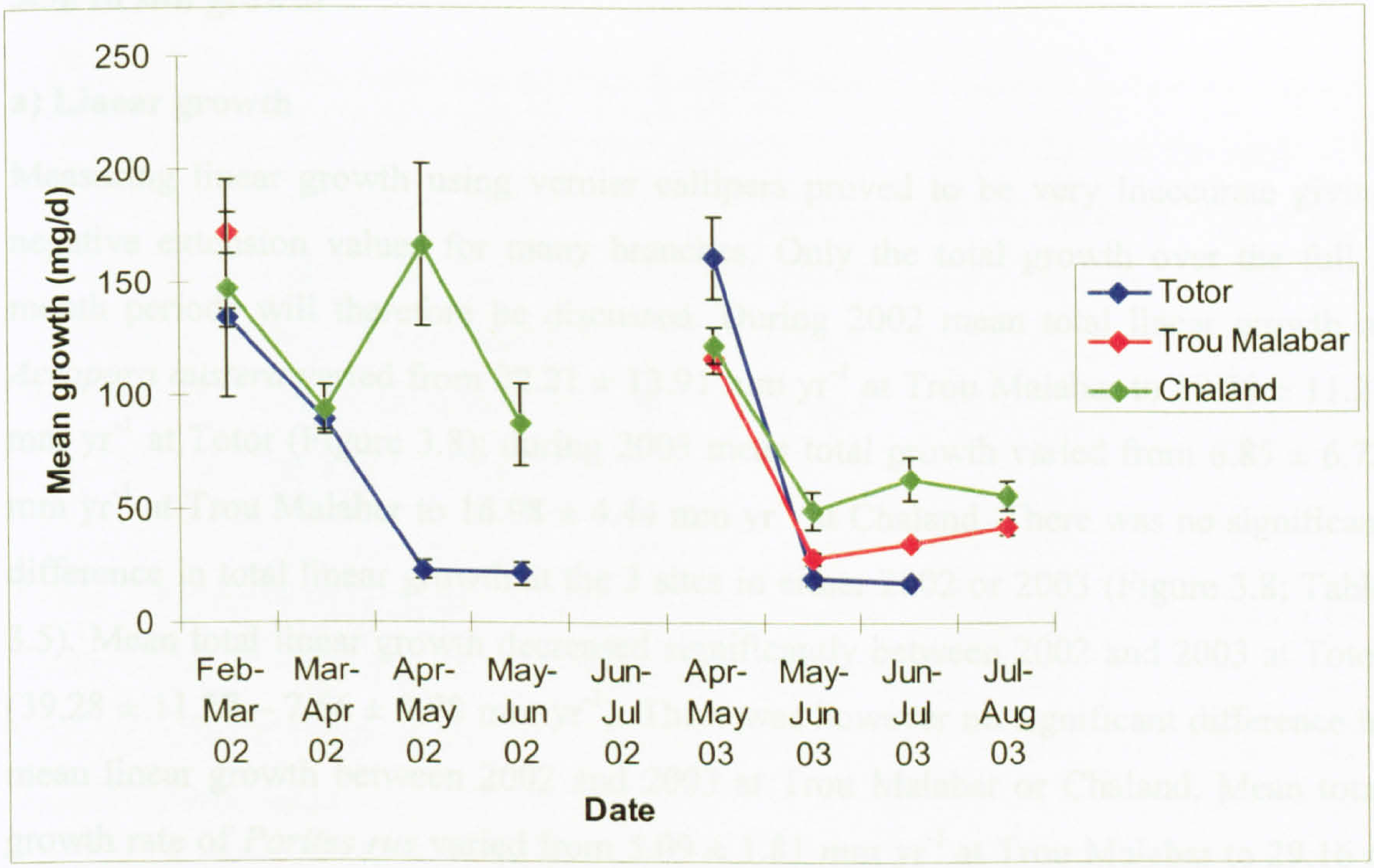


Figure 3.6 The mean monthly growth rate (mg d^{-1}) ± SE of *Acropora austera* measured using the buoyant weight technique at the 3 survey sites between February and June 2002 and April and August 2003.

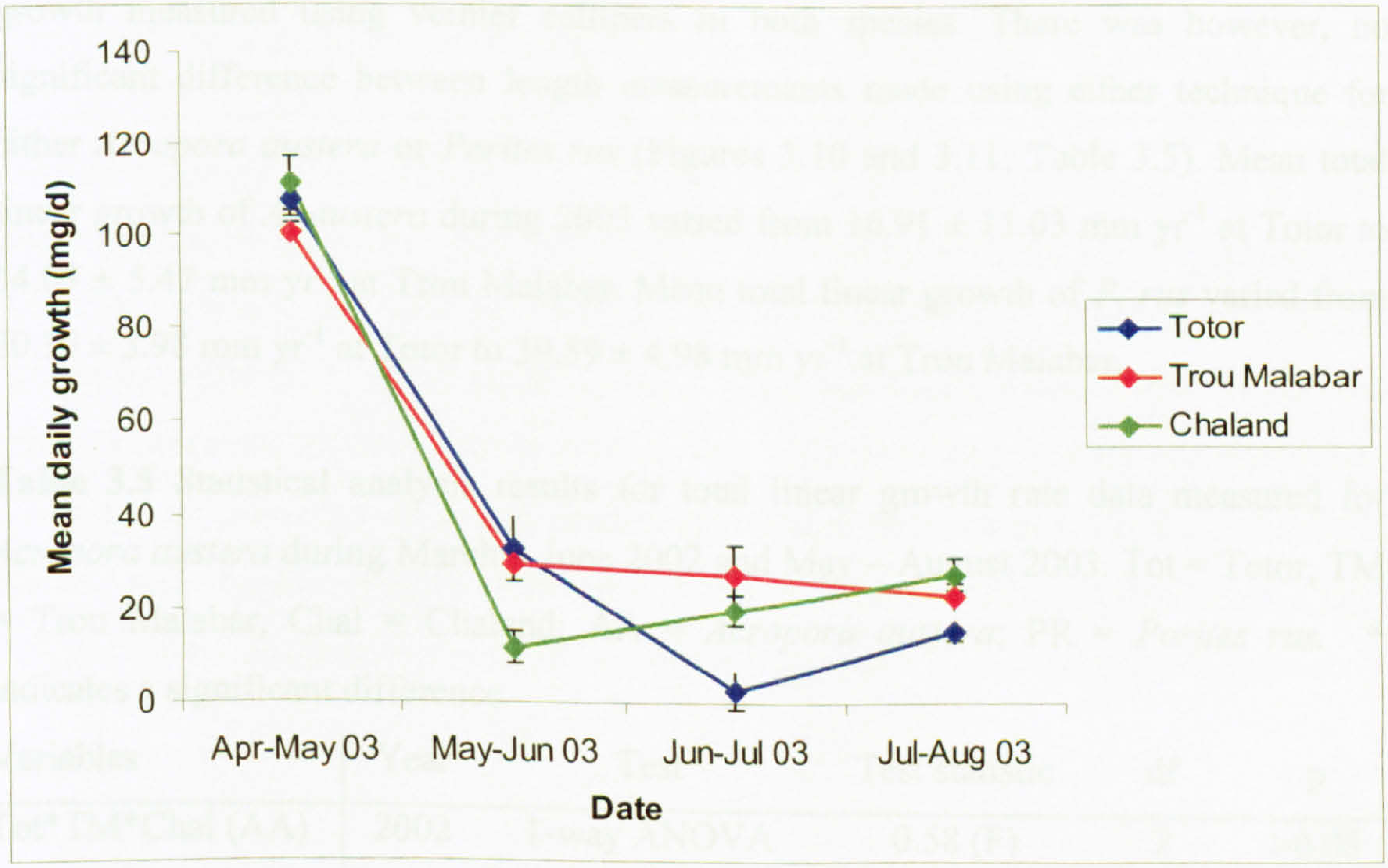


Figure 3.7 The mean monthly growth rate (mg d^{-1}) ± SE of *Porites rus* measured using the buoyant weight technique at the 3 survey sites between April and August 2003.

3.32 In situ growth

a) Linear growth

Measuring linear growth using vernier callipers proved to be very inaccurate giving negative extension values for many branches. Only the total growth over the full 3 month periods will therefore be discussed. During 2002 mean total linear growth of *Acropora austera* varied from 22.21 ± 13.91 mm yr^{-1} at Trou Malabar to 39.38 ± 11.27 mm yr^{-1} at Totor (Figure 3.8); during 2003 mean total growth varied from 6.85 ± 6.72 mm yr^{-1} at Trou Malabar to 16.98 ± 4.44 mm yr^{-1} at Chaland. There was no significant difference in total linear growth at the 3 sites in either 2002 or 2003 (Figure 3.8; Table 3.5). Mean total linear growth decreased significantly between 2002 and 2003 at Totor (39.28 ± 11.27 – 7.56 ± 9.78 mm yr^{-1}). There was however no significant difference in mean linear growth between 2002 and 2003 at Trou Malabar or Chaland. Mean total growth rate of *Porites rus* varied from 5.09 ± 1.81 mm yr^{-1} at Trou Malabar to 29.16 ± 10.96 mm yr^{-1} at Totor. There was no significant difference in mean linear growth rate at the 3 sites (Figure 3.9; Table 3.5).

Linear growth measured using digital photography showed different patterns to linear growth measured using vernier callipers in both species. There was however, no significant difference between length measurements made using either technique for either *Acropora austera* or *Porites rus* (Figures 3.10 and 3.11; Table 3.5). Mean total linear growth of *A. austera* during 2003 varied from 16.91 ± 11.03 mm yr^{-1} at Totor to 34.09 ± 5.47 mm yr^{-1} at Trou Malabar. Mean total linear growth of *P. rus* varied from 20.39 ± 3.98 mm yr^{-1} at Totor to 39.59 ± 4.98 mm yr^{-1} at Trou Malabar.

Table 3.5 Statistical analysis results for total linear growth rate data measured for *Acropora austera* during March – June 2002 and May – August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland; AA = *Acropora austera*; PR = *Porites rus*. * indicates a significant difference.

Variables	Year	Test	Test statistic	df	p
Tot*TM*Chal (AA)	2002	1-way ANOVA	0.58 (F)	2	>0.05
Tot*TM*Chal (AA)	2003	Mood's Median	1.22 (X^2)	2	>0.05
Tot*TM*Chal (PR)	2003	Mood's Median	3.49 (X^2)	2	>0.05
Tot*TM*Chal (AA)	2003	Mann-Whitney	18774.0 (W)		>0.05
Tot*TM*Chal (PR)	2003	Mann-Whitney	5434.0 (W)		>0.05

b) Increase in branch perimeter

As for linear growth, there was no significant difference in increase in branch perimeter of ***Acropora austera*** at any of the sites (Figure 3.12; Table 3.6) and the mean total change in branch perimeter varied from 58.47 ± 28.05 mm yr^{-1} at Totor to 95.93 ± 32.11 mm yr^{-1} at Chaland. For ***Porites rus*** mean total increase in branch perimeter was significantly lower at Totor than at Trou Malabar and Chaland (Figure 3.13; Table 3.6) and mean total change in branch perimeter varied from 56.26 ± 21.64 mm yr^{-1} at Totor to 132.74 ± 8.31 mm yr^{-1} at Trou Malabar

Table 3.6 Statistical analysis results for total increase in branch perimeter rate data measured for ***Acropora austera*** during May – August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland; AA = *Acropora austera*; PR = *Porites rus*. * indicates a significant difference.

Variables	Test	Test statistic	df	p
Tot*TM*Chal (AA)	1-way ANOVA	0.04 (F)	2	>0.05
Tot*TM*Chal (PR)	1-way ANOVA	6.22 (F)	2	<0.05*

3.33 Relationships between growth rate and environmental variables

There were no significant correlations between mean monthly growth rates at the 3 sites and monthly rainfall, sunshine hours, cloud cover, visibility or sediment deposition over the whole survey period (Table 3.7). During 2002 mean monthly growth rate at Totor was significantly correlated with hours of sunshine and maximum air temperature, but not with sediment or visibility. During 2003 there was a high (but not significant) correlation between monthly growth rates at Totor and Chaland and visibility. At Trou Malabar however, monthly growth rates during 2003 were significantly correlated with visibility. All sites showed a high positive correlation between growth rate and rainfall and this was significant at Trou Malabar. Totor and Trou Malabar both showed a high (but not significant) positive correlation between growth rate and sediment deposition.

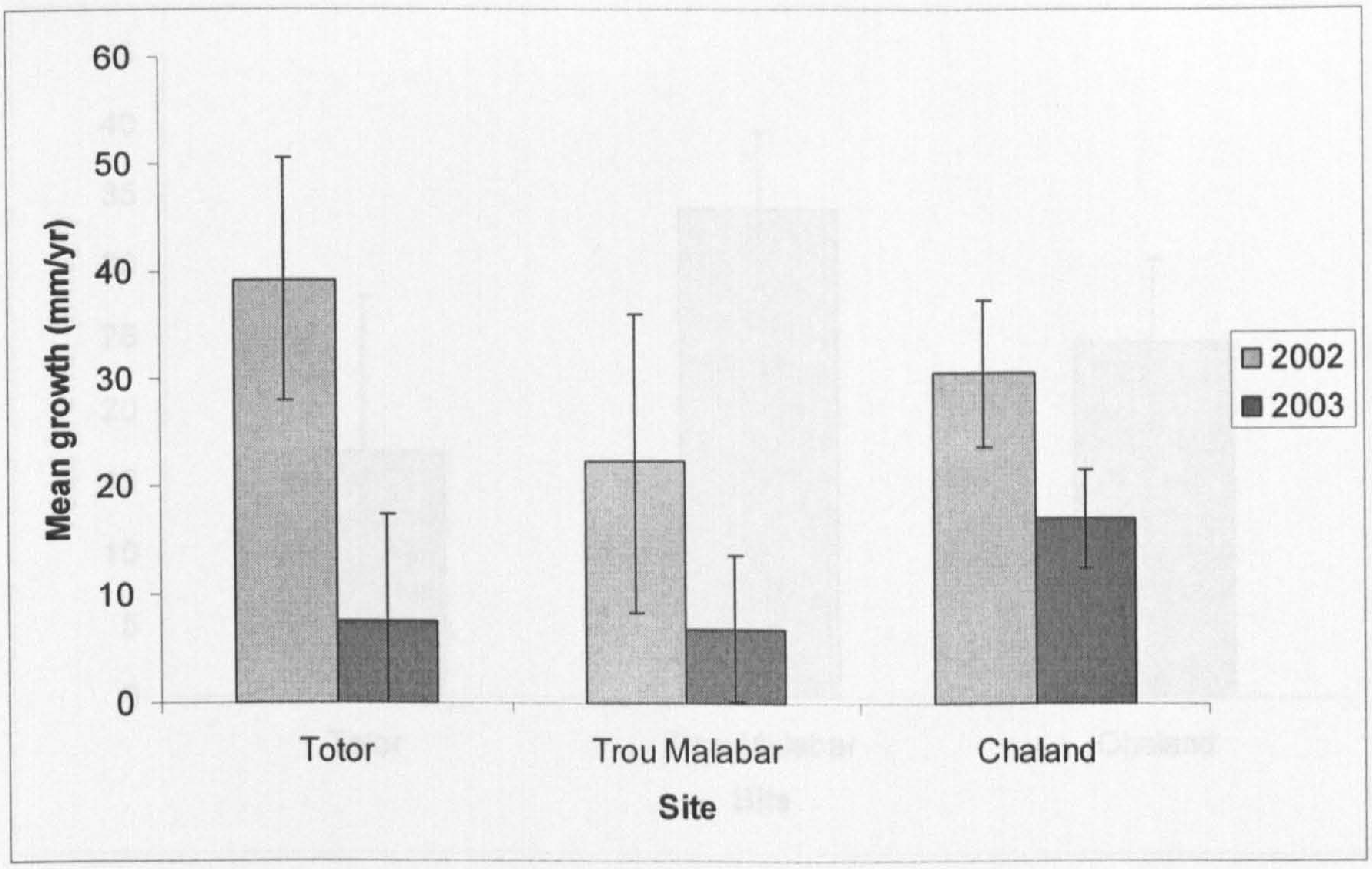


Figure 3.8 The mean total linear extension rate (mm yr^{-1}) ± SE of *Acropora austera* measured using vernier callipers at the 3 survey sites between March and June 2002 and May and August 2003.

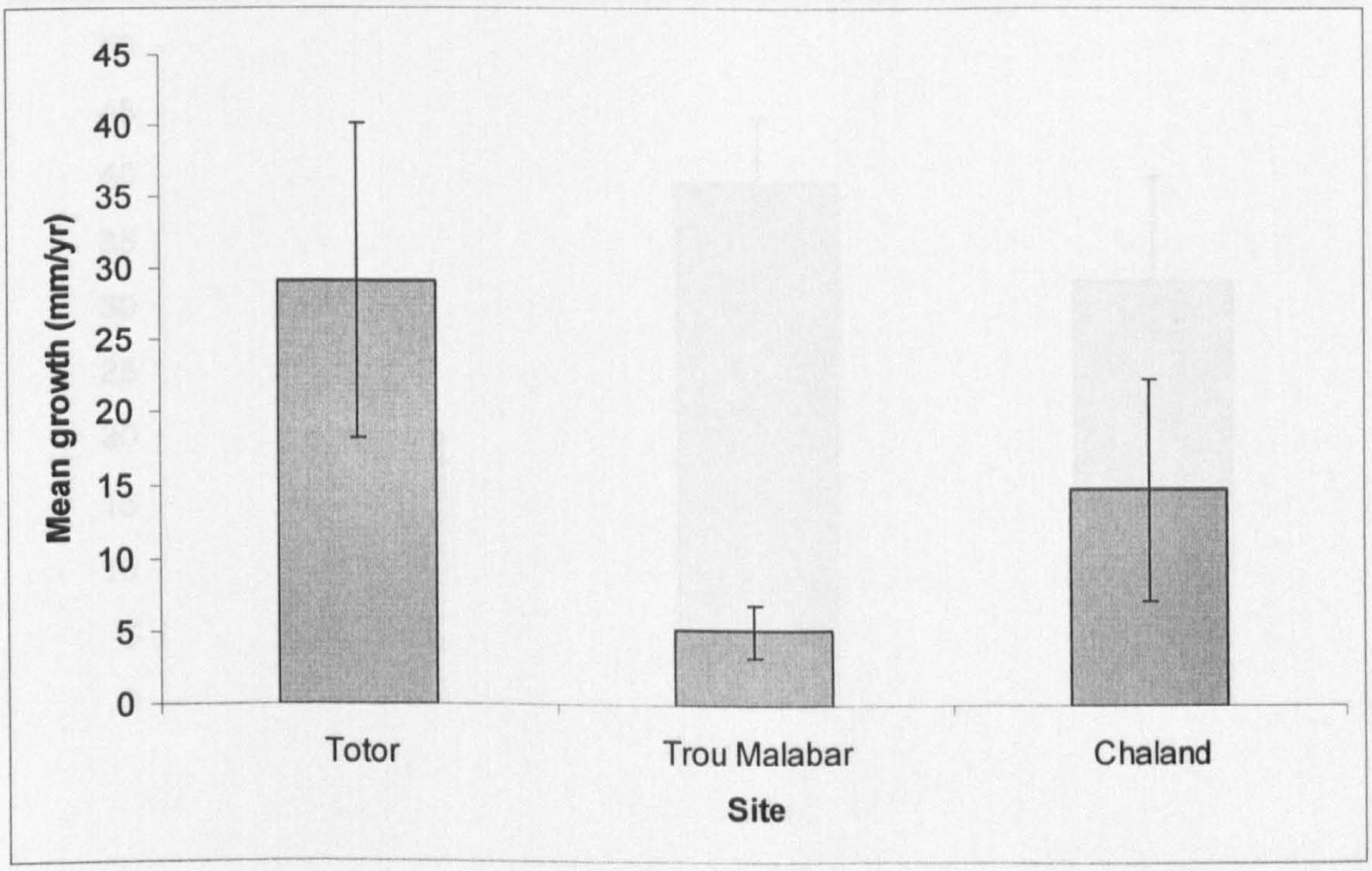


Figure 3.9 The mean total linear extension rate (mm yr^{-1}) ± SE of *Porites rus* measured using vernier callipers at the 3 survey sites between May and August 2003.

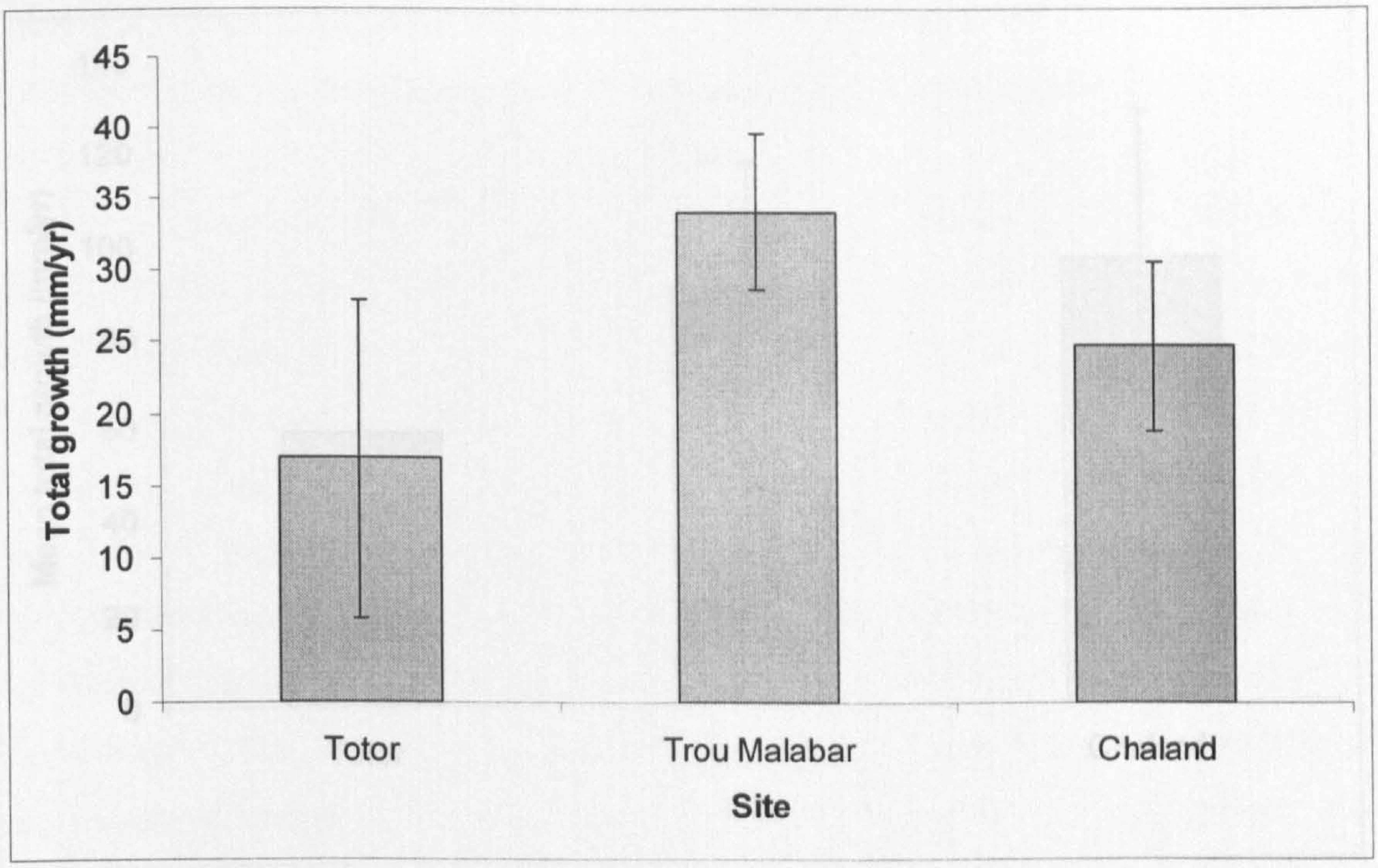


Figure 3.10 The mean total linear extension rate (mm yr^{-1}) ± SE of *Acropora austera* measured using digital photography at the 3 survey sites between May and August 2003.

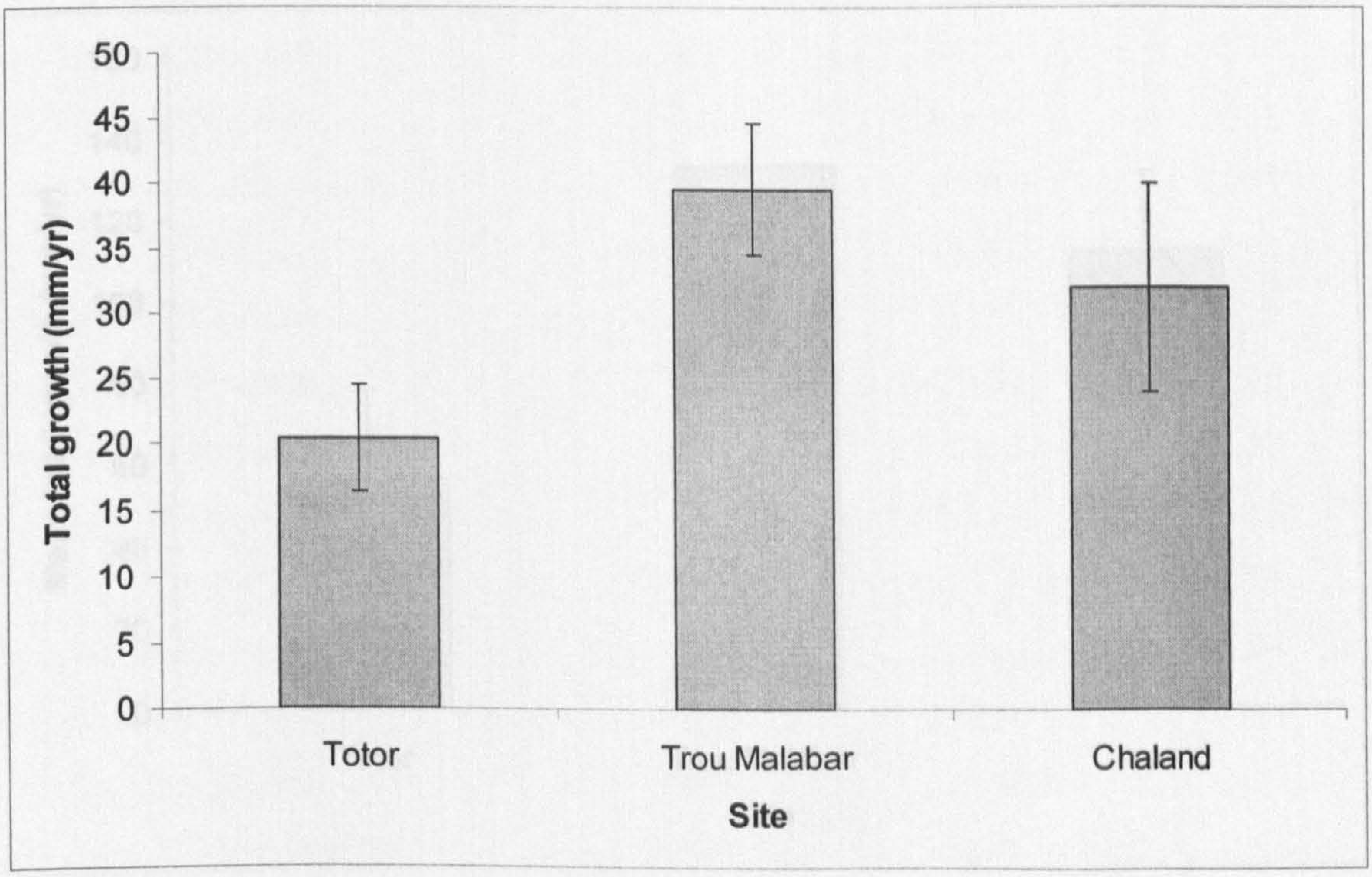


Figure 3.11 The mean total linear extension rate (mm yr^{-1}) ± SE of *Porites rus* measured using digital photography at the 3 survey sites between May and August 2003.

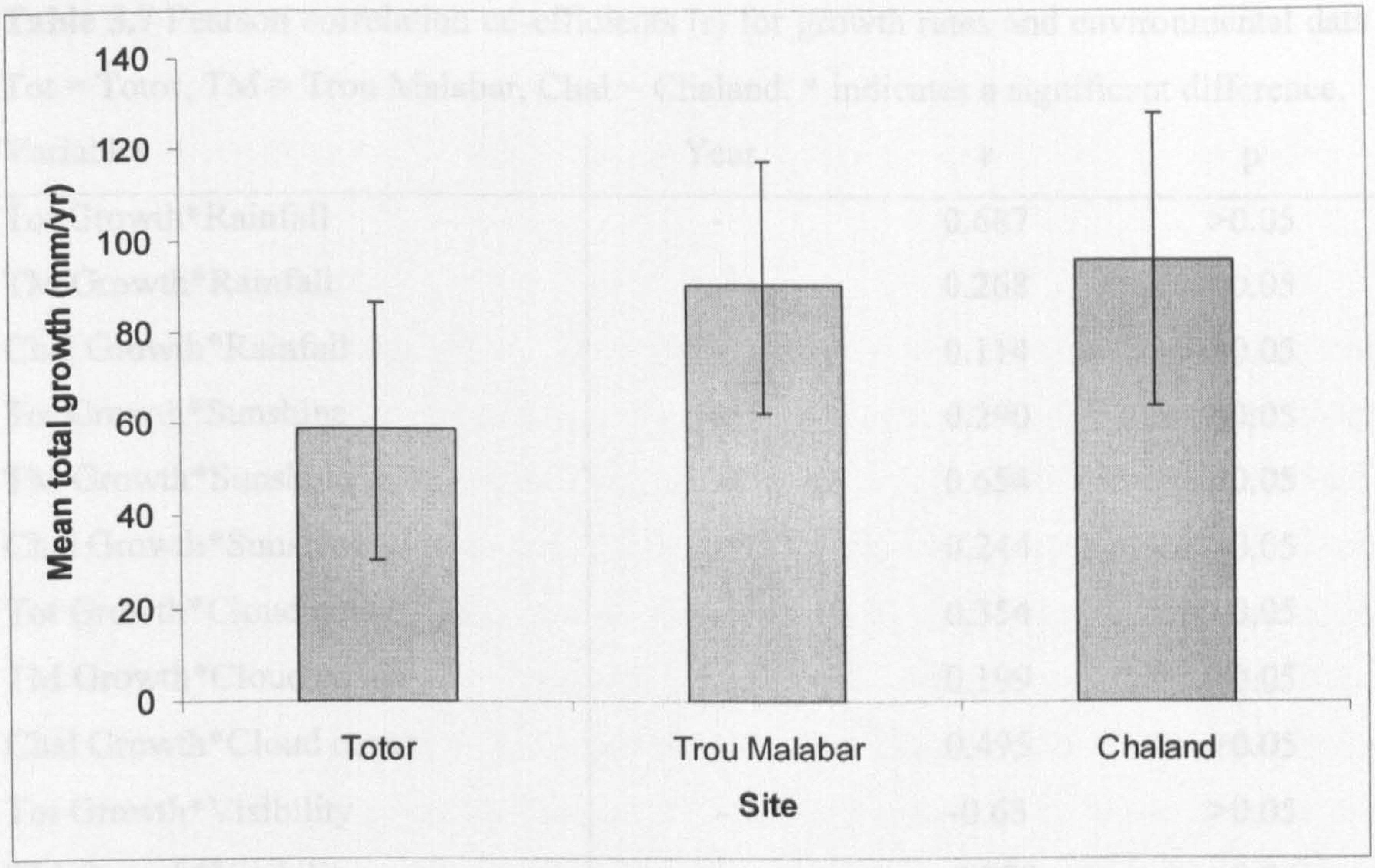


Figure 3.12 The mean total increase in branch perimeter (mm yr^{-1}) ± SE of *Acropora austera* measured using digital photography at the 3 survey sites between May and August 2003.

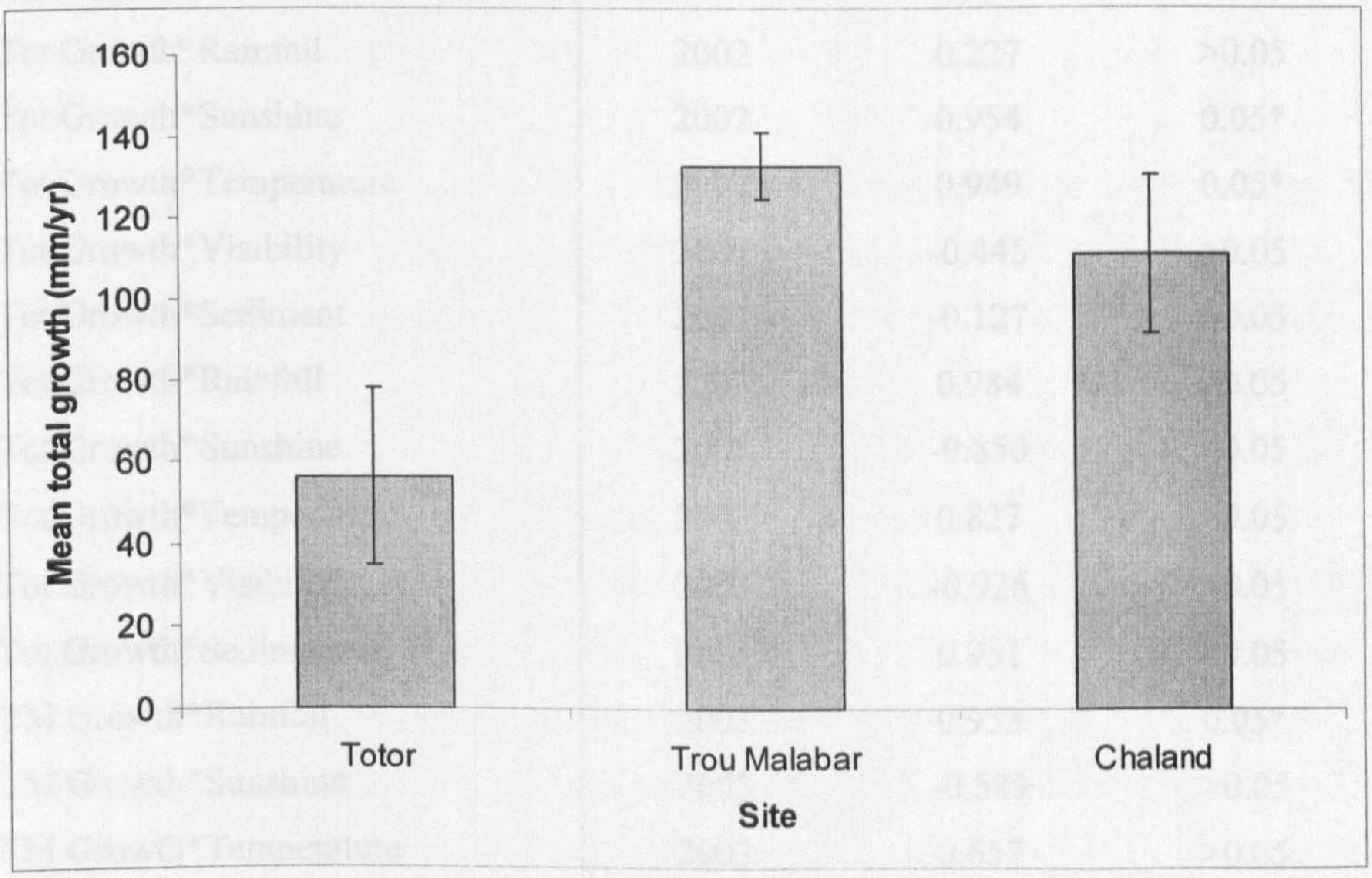


Figure 3.13 The mean total increase in branch perimeter (mm yr^{-1}) ± SE of *Porites rus* measured using digital photography at the 3 survey sites between May and August 2003.

Table 3.7 Pearson correlation co-efficients (r) for growth rates and environmental data. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Year	r	p
Tot Growth*Rainfall	-	0.687	>0.05
TM Growth*Rainfall	-	0.268	>0.05
Chal Growth*Rainfall	-	0.114	>0.05
Tot Growth*Sunshine	-	0.290	>0.05
TM Growth*Sunshine	-	0.654	>0.05
Chal Growth*Sunshine	-	0.244	>0.05
Tot Growth*Cloud cover	-	0.354	>0.05
TM Growth*Cloud cover	-	0.199	>0.05
Chal Growth*Cloud cover	-	0.495	>0.05
Tot Growth*Visibility	-	-0.63	>0.05
TM Growth*Visibility	-	-0.790	>0.05
Chal Growth*Visibility	-	0.100	>0.05
Tot Growth*Sediment	-	0.613	>0.05
TM Growth*Sediment	-	-0.021	>0.05
Chal Growth*Sediment	-	-0.443	>0.05
Tot Growth*Rainfall	2002	0.227	>0.05
Tot Growth*Sunshine	2002	0.954	0.05*
Tot Growth*Temperature	2002	0.949	0.05*
Tot Growth*Visibility	2002	-0.445	>0.05
Tot Growth*Sediment	2002	-0.127	>0.05
Tot Growth*Rainfall	2003	0.984	>0.05
Tot Growth*Sunshine	2003	-0.850	>0.05
Tot Growth*Temperature	2003	0.827	>0.05
Tot Growth*Visibility	2003	-0.926	>0.05
Tot Growth*Sediment	2003	0.951	>0.05
TM Growth*Rainfall	2003	0.953	0.05*
TM Growth*Sunshine	2003	-0.589	>0.05
TM Growth*Temperature	2003	0.657	>0.05
TM Growth*Visibility	2003	-0.946	0.05*
TM Growth*Sediment	2003	0.941	>0.05
Chal Growth*Rainfall	2003	0.941	>0.05
Chal Growth*Sunshine	2003	-0.531	>0.05

Chal Growth*Temperature	2003	0.687	>0.05
Chal Growth*Visibility	2003	-0.922	>0.05
Chal Growth*Sediment	2003	0.432	>0.05

3.34 Transplantation

Coral nubbins transplanted from Totor (turbid site) to Grande Baie (non-turbid site) showed a significant increase in mean growth rate compared to the controls which remained at Totor from 21.41 ± 4.67 mg d^{-1} to 155.03 ± 5.18 mg d^{-1} (Figure 3.14; Table 3.8). Corals transplanted from Grande Baie to Totor, did not however show a significant difference in mean growth rates compared to the controls. Coral nubbins transplanted from Chaland (turbid site) to Eric's Paté (non-turbid site) did not show a significant difference in mean growth rate compared to the controls, whereas corals transplanted from Eric's Paté to Chaland showed a significant increase in mean growth rate compared to the controls from 49.57 ± 4.02 mg d^{-1} to 112.34 ± 7.12 mg d^{-1} . Coral nubbins transplanted from Trou Malabar (turbid site) to Ile aux Fous (non-turbid site) did not show a significant difference in mean growth rates compared to the controls. In contrast, coral nubbins transplanted from Ile aux Fous to Trou Malabar showed a significant decrease in mean growth rate compared to the controls from 136.76 ± 9.87 mg d^{-1} to 58.83 ± 5.86 mg d^{-1}.

Table 3.8 Statistical analysis results for transplantation growth rate data measured for *Acropora austera* during April – June 2002. Tot = Totor, TM = Trou Malabar, Chal = Chaland; GB = Grande Baie; EP = Eric's Paté; IF = Ile aux Fous. * indicates a significant difference.

Variables	Test	Test statistic	Df	p
Tot→GB Transplants*Control	2-sample T-test	-18.30 (T)	17	<0.05*
GB→Tot Transplants*Control	2-sample T-test	-1.46 (T)	19	>0.05
Chal→EP Transplants*Control	Mann-Whitney	39.0 (W)		>0.05
EP→Chal Transplants*Control	2-sample T-test	-7.44 (T)	17	<0.05*
TM→IF Transplants*Control	2-sample T-test	0.95 (T)	21	>0.05
IF→TM Transplants*Control	2-sample T-test	6.53 (T)	26	<0.05*

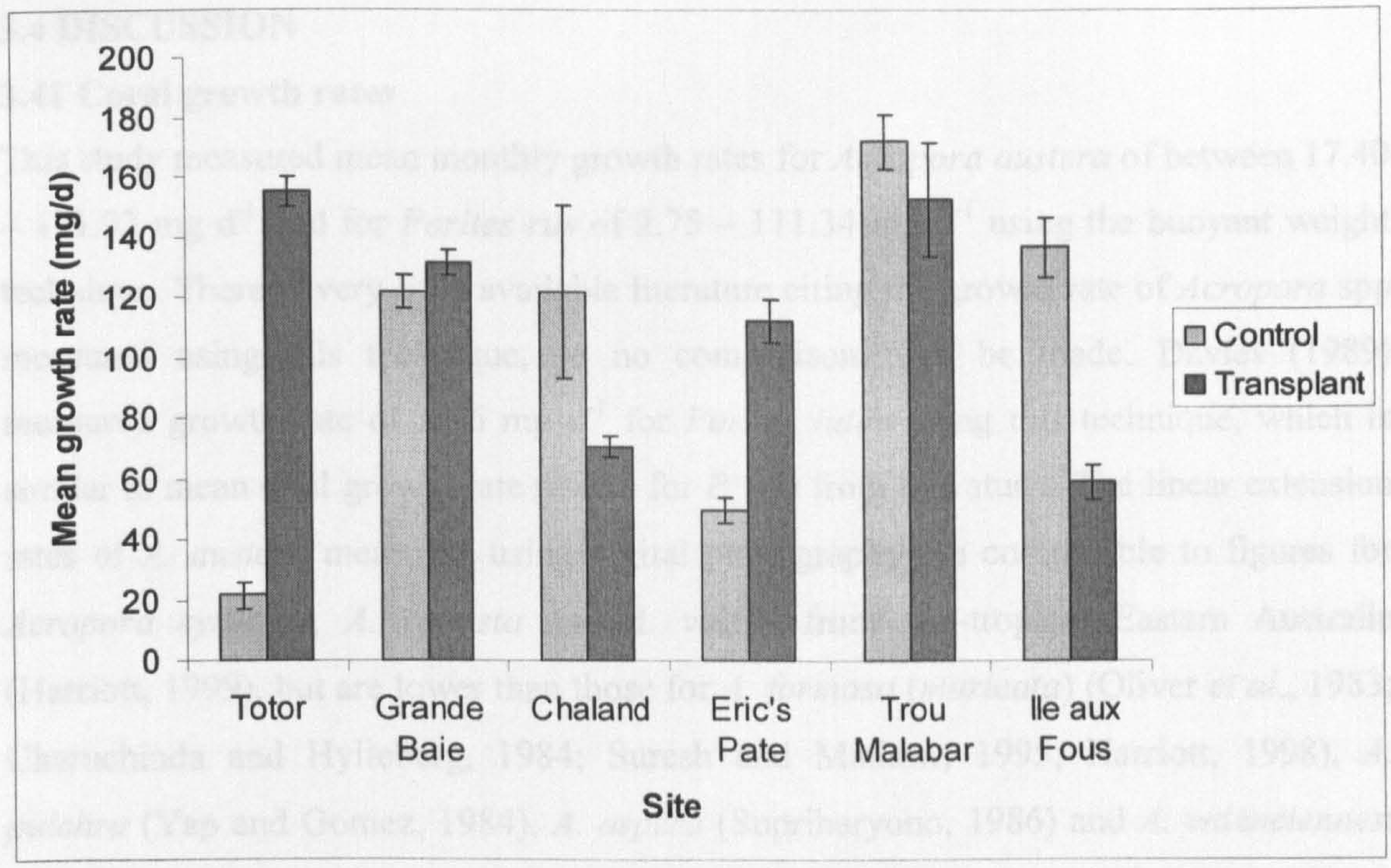


Figure 3.14 The mean total growth rate (mg d^{-1}) ± SE of *Acropora austera* nubbins transplanted from turbid to non-turbid sites and vice versa and the controls which remained at their original site. Growth rates were measured using the buoyant weight technique between April and June 2002. Corals from Totor were transplanted to Grande Baie and vice versa; corals from Chaland were transplanted to Eric's Paté and vice versa and corals from Trou Malabar were transplanted to Ile aux Fous and vice versa.

3.4 DISCUSSION

3.41 Coral growth rates

This study measured mean monthly growth rates for *Acropora austera* of between 17.40 – 171.93 mg d^{-1} and for *Porites rus* of 2.75 – 111.34 mg d^{-1} using the buoyant weight technique. There is very little available literature citing the growth rate of *Acropora* spp measured using this technique, so no comparisons can be made. Davies (1989) measured growth rate of 51.6 mg d^{-1} for *Porites lutea* using this technique, which is similar to mean total growth rate results for *P. rus* from this study. The linear extension rates of *A. austera* measured using digital photography are comparable to figures for *Acropora cytherea, A. robusta* and *A. valida* from sub-tropical Eastern Australia (Harriott, 1999), but are lower than those for *A. formosa* (*muricata*) (Oliver *et al.*, 1983; Charuchinda and Hylleberg, 1984; Suresh and Mathew, 1995; Harriott, 1998), *A. pulchra* (Yap and Gomez, 1984), *A. aspera* (Supriharyono, 1986) and *A. valenciennesi* (Crabbe and Smith, 2002) (Table 3.9). Rodrigues is situated at 19 ° 42'S, which is towards the lower limits of coral reef development. Crossland (1981) and Grigg (1982) both report reduced growth rates of corals with increasing latitude, due to a decrease in seawater temperature, which may explain the lower growth rates. Linear extension rates for *P. rus* are similar to those measured for *P. cylindrica* in Guam but are much higher than values for other *Porites* species, however these species tend to have massive rather than branching growth forms and show very slow rates of linear extension.

At Totor in 2002 and at all 3 sites in 2003, the mean monthly growth rate decreases over time, with high growth rates at the beginning of the study period and very low growth rates towards the end of the study period. Seawater and air temperatures drop throughout the survey period and hours of sunshine also decline over time and thus could be causing this decrease in growth rate. A significant correlation exists between growth rates at Totor during 2002 and maximum monthly temperature and hours of sunshine. Chaland is however subjected to exactly the same meteorological conditions yet in 2002 growth rates at Chaland remained high throughout the study period, whilst those at Totor fell between April and May. Other studies have shown decreases in coral growth rates during winter periods, due to cooler temperatures and lower sunlight (e.g. Glynn and Stewart, 1973; Bak, 1974; Loya, 1985; Supriharyono, 1986; Vago *et al.*, 1997a; Harriott, 1999). Lough and Barnes (2000) showed that between 22 – 29 °C, for every 1 °C rise in sea surface temperature, mean annual extension rates increased by 3.1 mm yr^{-1}. In Rodrigues sea surface temperatures dropped by up to 3 °C over a 3 month period, therefore based on this calculation a 9 mm decrease in growth over the year may be expected.

Although the above studies suggest that temporal changes in growth rate are due to changes in sea temperature and available light, variations in growth rate may also be due to food availability. Studies have shown that zooplankton are an important food source for corals (Sebens *et al.*, 1996) and that coral growth rates and calcification rates are greater in corals fed on *Artemia* naulpii (Houlbreque *et al.*, 2003; 2004) and natural zooplankton (Ferrier-Pagés *et al.*, 2003) than in starved corals. Sebens *et al.* (1998) showed that flow speeds had a significant positive effect on zooplankton capture by *Madracis mirabilis* and *Montastrea cavernosa.* The authors state that flow speeds normally experienced on coral reefs are well below the optimum speeds for particle capture by corals and that periods of high wave action or strong currents may be beneficial for coral growth. Variations in growth rates observed during the present study may therefore be due to changes in wave action and current speed and the resulting variations in ability to capture zooplankton. Chaland is more exposed to wave action than Totor and this may explain the high growth rates at Chaland during 2002. Wind speed during April-May 2003 was high, however this theory does not fully explain the decline in growth rates observed at all sites during May-June 2003.

Sediment deposition values at all sites increased between 2002 and 2003, whilst total growth rates at all sites decreased significantly. The decrease in growth rate was highest at Trou Malabar, where a 3-fold decrease was recorded, and this was the site with the highest increase in sediment deposition. Furthermore, coral growth rates increased in nubbins transplanted from Totor to Grande Baie, a non-turbid site. These factors suggest a possible link between sedimentation rates and growth. In addition, during 2002 sedimentation levels at Totor were high during March-May (>30 mg cm^{-2} d^{-1}), whereas sedimentation remained low at Chaland (2 mg cm^{-2} d^{-1}). During 2003 sedimentation levels were very high (>50 mg cm^{-2} d^{-1}) at both Totor and Trou Malabar during April-May. Tolerable sedimentation rates for coral reefs are quoted as being 10 mg cm^{-2} d^{-1} or less (Rogers, 1990). Pastorok and Bilyard (1985) estimated that at sedimentation rates of 10-50 mg cm^{-2} d^{-1} coral growth rates will be greatly decreased and severe degradation occurs above 50 mg cm^{-2} d^{-1}. High levels of sedimentation have been shown to cause a reduction in coral growth in both the field (Aller and Dodge, 1974; Dodge *et al.*, 1974; Dodge and Vaišnys, 1977; Cortés and Risk, 1985; Tomascik and Sander, 1985;

Tomascik, 1990; Suresh and Mathew, 1993; Torres, 2001; Crabbe and Smith, 2002) and under experimental conditions (Dodge, 1982; Kendall *et al.*, 1985; Anthony, 1999). Dodge *et al* (1974) recorded a decrease in growth rates at sedimentation levels of just 1.1 mg cm^{-2} d^{-1}, whilst Suresh and Mathew (1993) found that coral growth rates declined during the monsoon, when sedimentation rates reached 85 mg cm^{-2} d^{-1}.

Table 3.9. A comparison of coral growth rate (linear extension rate, mm yr^{-1}) for various *Acropora* and *Porites* corals.

Site	Species	Growth (mm yr^{-1})	Reference
Rodrigues	***A. austera***	**16.9 – 34.1**	**This study**
Eastern Australia	*A. cytherea*	20.9	Harriott (1999)
	A. robusta	22.4	Harriott (1999)
	A. valida	23.6	Harriott (1999)
	A. yongei	49.40	Harriott (1999)
Red Sea	*A. eurystoma*	16.7-53.6	Bangiorni *et al.* (2003)
Western Australia	*A. formosa*	50.3-76.0	Harriott (1998)
Great Barrier Reef	*A. formosa*	80.0-120.0	Oliver et al (1983)
Thailand	*A. formosa*	Approx. 80.0	Charuchinda and Hylleberg (1984)
India	*A. formosa*	38.0 – 49.0	Suresh and Mathew (1995)
Philippines	*A. pulchra*	118.0-120.0	Yap and Gomez (1984)
Indonesia	*A. aspera*	20.9-147.7	Supriharyono (1986)
	A. valenciennesi	66.0–120.0	Crabbe and Smith (2002)
Rodrigues	***P. rus***	**20.4 – 39.6**	**This study**
Red Sea	*P. columnaris*	5.7	Klein and Loya (1991)
Eastern Australia	*P. heronensis*	9.0 - 11.8	Harriott (1999)
Marshall Islands	*P. lobata*	5.0 - 11.5	Buddemeier *et al.* (1974)
Guam	*P. cylindrica*	25.0	Neudecker (1981)
Costa Rica	*P. lobata*	6.5 - 14.6	Guzmán and Cortés (1989)
Red Sea	*P. lobata*	7.5	Klein and Loya (1991)
Galápagos Islands	*P. lobata*	8.9	Glynn (1994)
Thailand	*P. lutea*	12.0 – 30.0	Brown *et al.* (1990)
Marshall Islands	*P. lutea*	4.0 - 13.5	Buddemeier *et al.* (1974)
	P. lutea	3.5 - 11.8	Highsmith (1979)

Mean total growth rate of *Acropora austera* at Totor is significantly lower than at the other 2 sites in both 2002 and 2003. It is suggested in chapter 2, that sediment deposition is constantly high at Totor, however that it is only periodically high at Trou Malabar, following periods of high rainfall and high wind. This may explain the lower growth rates observed at Totor. In contrast, there was no significant difference in mean total growth rates of *Porites rus* at the 3 sites. This may indicate that *P. rus* is more resistant to sediment deposition. Stafford-Smith (1993) shows that another branching poritid, *P. cylindrica* is able to remove sediment very efficiently sediment, however there is no data available for *P. rus*.

Sediment inhibits coral growth due to the metabolic costs associated with sediment removal (Dallmeyer *et al*., 1982; Kendall *et al*., 1985; Riegl and Branch, 1995) or by reducing the amount of available light, thus reducing zooxanthellar photosynthesis (Rogers, 1979; Anthony, 1999; Te, 2001). Gravitational loss of sediment has been shown to be the dominant method of sediment clearing for branching corals, so that active rejection is not necessary (Stafford-Smith and Ormond, 1992), and therefore, in the case of *Acropora austera* and *Porites rus*, it is likely that the decrease in growth is due to a reduction in light levels, rather then sediment accumulating on the colony. Although sediment deposition was very high at Totor and Trou Malabar during 2003, sediment deposition at Chaland remained fairly low (<10 mg cm^{-2} d^{-1}). Growth rates at Chaland however showed a similar pattern to the other sites with a decline in May-June, although the decline was not so dramatic and growth rates remained significantly higher than at Totor and Trou Malabar. Chaland is an exposed site with very low sediment deposition values and therefore even a small increase may have been sufficient to cause this decrease in growth rate. Visibility however was low at Totor during March 2002 and was very low at all 3 sites during April 2003. During April, a minimum 2.5 m horizontal visibility was recorded at Totor with 2.7 m and 4.1 m at Trou Malabar and Chaland, respectively. Mean horizontal visibility during the remaining months of 2003 was 6 m at Totor, 9 m at Trou Malabar and 10 m at Chaland, suggesting that high turbidity during April may have caused the observed decline in growth rates.

There were high correlations between coral growth and rainfall during 2003, suggesting that growth is affected by land run-off which causes high sediment deposition and low visibility. Suresh and Mathew (1993) showed that the growth rate of *Acropora formosa* (*muricata*) in India was negatively correlated with rainfall, due to the associated increase in sedimentation and decrease in light intensity. Dodge and Lang (1983) found that coral growth rates in the Gulf of Mexico were correlated with annual river discharge and suggest that this is due to a reduction in ambient light availability during years of high discharge. Miller and Cruise (1995) also showed that in Puerto Rico, growth rates of *Montastrea annularis* were directly influenced by sediment discharged from a nearby river, with the lowest growth rates occurring during periods of increased sediment loading to the bay. Similarly, Nugues and Roberts (2003a) found a decrease in growth rate of *Colophyllia natans* in St Lucia with increasing proximity to a river mouth due to increased sedimentation.

During 2003, growth rates at Totor and Trou Malabar showed high positive correlations with sediment deposition and there were high negative correlations with visibility at all 3 sites. If sediment deposition and/or turbidity are causing a decrease in growth rate, the reverse relationships would be expected. Growth rates at Totor were high during March-April 2002, when sedimentation and turbidity values were high and were also high at all 3 sites during April-May 2003 when sedimentation and turbidity values were very high. Anthony (1999a) found that the growth rates of *Goniastrea retiformis* increased as suspended particulate matter (SPM) increased (between 1-16 mg l^{-1}), suggesting that this species is able to supplement its nutrition with particle feeding. Anthony (2000) also found that *Acropora millepora* and *Pocillopora damicornis* colonies from turbid reefs showed a higher sediment feeding capacity than conspecifics from non-turbid reefs. In addition, *P. damicornis, Montipora digitata, A. millepora* and *Porites cylindrica* all demonstrated a capacity to feed on fine suspended matters (<100 μm) and it is suggested that at high particle concentrations, particle feeding may account for half of the carbon and a third of the nitrogen required for tissue growth (Anthony, 1999b). It is therefore possible that corals are ingesting sediment, resulting in higher growth rates during March and April.

However, not all coral species exhibit this heterotrophic plasticity. In laboratory experiments, Anthony (1999a) showed that *Porites cylindrica* does not supplement its nutrition with particle feeding at high SPM concentration. Furthermore, although *Goniastrea retiformis* showed increased particle feeding with increasing SPM concentrations and in response to shading, *P. cylindrica* showed a lower ability to intake sediment particles, resulting in a loss of tissue mass in shaded and high-SPM treatments (Anthony and Fabricius, 2000). In the current study coral growth rates during both 2002 and 2003 fell significantly during the month following high sediment deposition and low visibility and it seems more likely that this is a stress response to the unfavourable conditions. Vago *et al.* (1997a) showed that coral growth rates in the Red Sea exhibited a 2-month delay in response to changes in seawater temperature and it is possible that in Rodrigues corals may be showing a 1 month delay in their response to increases in sediment deposition and /or increases in turbidity.

It appears therefore that the changes in coral growth rates observed at the 3 sites are caused by a combination of local and large scale environmental variables. The very major decline in growth rate of both *Acropora austera* and *Porites rus* at all sites during May-June 2003 is likely to be caused a synergistic effect of high rainfall and wind, low sunshine, high cloud cover, low salinity, high turbidity and high sediment experienced during April-May, all of which are unfavourable to coral growth. Growth rates remained low during the following months despite low sediment deposition and low turbidity and this may have been due to the cooler temperatures during May-August and the lower hours of sunlight. Similarly, in 2002, high rainfall, high cloud cover, low visibility and high sediment deposition during March-April resulted in a decline in growth rate of *A. austera* at Totor in the following month. Despite lower sedimentation rates and high visibility during the subsequent months, growth rates remained low due to cooler temperatures and lower hours of sunshine.

3.42 Techniques for measuring coral growth rates

There appears to be no relationship between increases in skeletal weight measured using the buoyant weight technique and linear extension measured using *in situ* techniques and digital photography. Measurement of total growth using the buoyant weight technique showed that growth rates at Totor were significantly lower than Chaland and Trou Malabar during both 2002 and 2003. However neither *in situ* measurements nor digital photography found a significant difference in branch extension rate. In the case of *in situ* measurements this may be due to the inaccuracy of the technique however, there is no reason why extension rates and increases in skeletal weight should be related. Buddemeier *et al.* (1974) and Barnes and Crossland (1980) found that calcification rates and extension rates were not directly related. Gladfelter (1984) and Brown *et al.* (1985) showed that calcification rates were more critically controlled by variations in temperature and sunshine hours rather than linear extension rates. Suresh and Mathew (1995) also showed that calcification rate showed a strong association with light level, whereas linear extension was affected by the current regime. It is therefore, important that studies of coral growth rates do not just measure linear extension rates alone.

The least time consuming technique for measuring coral growth rate was found to be *in situ* measurement of linear extension with vernier callipers. For 15 coral colonies this required only an initial 60 minute dive to tag and measure branch tips and then one 30 minute dive per month to re-measure branch tips. There were however, a number of problems with this technique such as difficulties in re-locating coral colonies and damaging coral colonies whilst taking the measurements, particularly for *Porites rus*. The main problem with this technique was inaccuracy in the measurements taken under water. The method produced negative extension values for many branches and the mean values had very high standard errors. As a result this technique was not able to detect differences in growth rates between the 3 sites or over time.

Measurement of coral growth rates using digital photography required the same amount of dive time as *in situ* measurements with an initial 60 minute dive and then one 30 minute dive per month; however this technique also required 3.5 hours laboratory time to edit and process the digital photographs. Problems with this technique included difficulties in re-locating coral colonies, damage to coral colonies whilst taking photographs and ensuring that the photograph was taken from exactly the same angle; this was especially true for *Acropora austera*, due to formation of secondary branches. Using length measurements there was found to be no significant difference in growth rates between sites for either species. Perimeter measurements were however able to detect spatial changes in growth rate for *Porites rus*. Neither technique was able to detect monthly changes in growth rate, however measurements were carried out during May to August when growth rates were very low and tended to show little monthly variation; it is unfortunate that this technique was not used during April-May.

The most time consuming method was found to be the buoyant weight technique, which required an initial 30 minute dive to collect the branch tips and 60 minutes in the laboratory to attach branches to tiles and to weigh nubbins, followed by two 15 minute dives each month to collect and return the racks of nubbins and 45 minutes in the laboratory to weigh the nubbins. Problems with this technique included mortality of the nubbins and the possibility of causing stress to nubbins due to aerial exposure. This technique does however, appear to be the most accurate technique and was able to assess monthly changes in coral growth rate. This method is therefore useful for monitoring the response of coral growth to short-term environmental changes, which annual growth rate measurements may not identify, a problem identified by Brown *et al.* (1990).

The optimal method for monitoring coral growth rates would be a combination of the buoyant weight method and *in situ* measurements. However, for a long-term coral growth monitoring project the digital technique provides the simplest and most accurate method of monitoring coral growth rates over time. It requires only 1 dive per month and is able to measure linear extension as well as changes in branch width and growth of secondary branches using measurements of perimeter.

3.43 Summary

The main findings of this study were:

- Mean total growth rate of *Acropora austera* measured using the buoyant weight technique was significantly lower at Totor than at Trou Malabar and Chaland. There was however no significant difference in mean total growth rate of *Porites rus* at the 3 sites.
- Mean total growth rate of *Acropora austera* measured using the buoyant weight technique decreased significantly between 2002 and 2003 at all sites. In contrast, sediment deposition at the sites increased significantly between 2002 and 2003.
- During 2002 there was no significant difference in mean monthly growth rates of *Acropora austera* at Chaland between February and July. Mean monthly growth rate of *A. austera* at Totor however declined significantly in April-May. During 2003 mean monthly growth rates of *A. austera* and *Porites rus* at all 3 sites declined significantly in May-June. It is suggested that this decline is due to high sediment, high turbidity conditions during March-April 2002 and April-May 2003.
- There was no significant difference in total linear growth rate of *Acropora austera* or *Porites rus* measured using vernier callipers or digital photography or change in mean branch perimeter of *Acropora austera* at the 3 sites.
- Coral nubbins transplanted from Totor to Grande Baie (non-turbid site) showed a significant increase in mean growth rate compared to the controls, suggesting that conditions at Totor are not optimal for growth.

3.44 Conclusions

It is suggested therefore, that the high sediment and high turbidity conditions at Totor may have resulted in low growth rates of *Acropora austera* at this site compared to Trou Malabar and Chaland. *Porites rus* however appears to be more tolerant to the high sediment conditions and there was no difference in growth rate of this species at the 3 sites. In addition, the high sediment and high turbidity conditions experienced at Totor during March-April 2002 and at all sites during April-May 2003, as a result of the high rainfall and wind, in combination with decreasing seawater temperatures and sunlight levels, appear to have resulted in a decrease in growth rates of both *A. austera* and *P. rus*. The study also suggests that future long-term coral growth studies should use the digital photography technique as a simple and accurate method of measuring growth over monthly periods.

CHAPTER 4: Coral settlement and regeneration under varying sediment regimes.

4.1 INTRODUCTION

Chapter 3 described the variations in coral growth rate at the 3 study sites and suggests that high sedimentation and low visibility at Totor and the increase in sediment deposition at all sites between 2002 and 2003, combined with decreasing temperature and light levels, may have resulted in a decrease in coral growth rates. In addition to effects on growth rates, high sedimentation may have a number of other sub-lethal impacts on coral colonies, such as reduced recruitment or regeneration ability. Recovery of coral reefs from impacts depends on recolonisation of the disturbed area by coral planulae settling from the plankton and on the regeneration and continued growth of surviving corals (reviewed by Pearson, 1981). Combined with a decrease in growth rates, decreases in recruitment and regeneration will affect a coral's ability to recover from further impacts. This chapter will therefore investigate whether high sedimentation at sites in the north of Rodrigues is causing a decrease in coral settlement and a decrease in a coral's ability to regenerate after injury.

4.11 Coral settlement and recruitment

4.111 Sexual reproduction in corals

Corals reproduce both sexually and asexually (see Harrison and Wallace, 1990; Richmond, 1997 for reviews). Sexual reproduction involves the process of gametogenesis, spawning and subsequent fertilisation of eggs by sperm. Sexual reproduction results in small, genetically unique, dispersive propagules which may settle, metamorphose and develop into primary polyps. Asexual reproduction occurs through a number of mechanisms including formation of 'polyp balls' (Rosen and Taylor, 1969); polyp bail-out (Sammarco, 1981; 1982a); fragmentation (Bothwell, 1981; Highsmith, 1982); and asexual production of planulae (Stoddart, 1983).

Two distinct modes of development occur among sexually reproducing scleractinian corals: gamete release followed by external fertilisation and development, and brooding of planulae larvae within the polyp. External fertilisation and development has been found to be the dominant mode of development among coral species (Harrison *et al.*, 1984; Babcock *et al.*, 1986). Most corals have distinct breeding seasons and marked periods of spawning or planulae release and the reproductive activities of many coral species are synchronised with lunar phases (Harrison and Wallace, 1990). On the Great Barrier Reef, the majority of coral species spawn together during a few short annual mass-spawning periods (Harrison *et al.*, 1984; Willis *et al.*, 1985; Babcock *et al.*, 1986). In other regions however (e.g. the Caribbean, Central Pacific, Hawaii, Red Sea and southern Japan) coral species show considerable variation in reproductive activity in mode, timing and among species (Shlesinger and Loya, 1985; Richmond and Hunter, 1990; Hayashibara *et al.*, 1993). It is suggested that latitudinal temperature variations may be the ultimate factor in controlling geographical differences in reproductive activity (Oliver *et al.*, 1988).

4.112 Dispersal of larvae

The dispersion and settlement patterns are largely determined by the duration of the planktonic phase, the prevailing hydrological conditions, the competency period of the planulae and their vertical distribution in the water column (Harrison and Wallace, 1990). The long planktonic phase and the highly buoyant nature of most coral embryos and larvae suggest that the majority of externally developed planulae are likely to be dispersed away from their parent reef (Harrison *et al.*, 1984; Babcock *et al.*, 1986). In contrast, other workers suggest that reefs are self-seeded. Sammarco and Andrews (1988) found high concentrations of recruits downstream of the natal reef in areas with low flushing rates and suggest that near-field circulation has an important influence on larval dispersal. Coral recruitment was also found to decline significantly with distance from the reef.

The extent by which reefs are self-seeding or interdependent has important consequences for the recovery potential of coral communities following disturbances. Reefs that are isolated by distance or by a lack of connecting currents may rely on larval retention and self-seeding for population recovery. These reefs will thus recover more slowly from severe disturbances than reefs, which are part of extensive systems where recruits from nearby unaffected reefs could recolonise rapidly (Harrison and Wallace, 1990). Conversely, damage to coral populations supplying recruits to other reefs could adversely affect populations on reefs downcurrent (Williams *et al.*, 1984).

4.113 Settlement

Following larval development and dispersal, coral planulae must settle, metamorphose and grow. Settlement of coral larvae is normally initiated when competent planulae encounter solid substrata, which are deemed suitable for attachment and metamorphosis. Settlement is usually preceded by intensive testing and searching behaviour and extensive exploration of the substratum. This may be followed by settlement, attachment and metamorphosis or temporary attachment (Harrison and Wallace, 1990). Coral larvae have been observed to exhibit a number of behavioural patterns concerned with settlement (Hayashibara *et al.*, 1997): 'touch down', when larvae touch a substratum and stop there momentarily before swimming again; creeping along the surface; spinning, whilst touching their aboral end with the substratum and finally 'anchoring', attaching to the substrata at the aboral end. Early studies suggested that most planulae swim to the bottom and attach within two days after spawning (Connell, 1973), however later studies have shown the duration of the planktonic phase to be more variable (e.g. Harrison *et al.*, 1984; Babcock, 1985; Richmond, 1987; 1988; Hayashibara *et al.*, 1997).

Coral species that are the first to settle in an area affected by disturbance tend to be species characterised by rapid growth rates and small colony size. *Acropora* and *Seriatopora* tend to dominate both as adults and new recruits on the Great Barrier Reef. Conversely in the Caribbean, although *Acropora* is a dominant adult its juveniles are rare and *Agaricia* and *Porites* are the major recruits (Sammarco, 1985). On the Great Barrier Reef, studies using artificial settlement plates confirm that corals from the families Acroporidae and Pocilloporidae dominate early recruiting corals (e.g. Sammarco and Carleton, 1981; Wallace, 1985a, b; Harriott, 1985b; Wallace *et al.*, 1986; Harriott and Fisk, 1987; Mundy, 2000), whilst in the Philippines (Alino *et al.*, 1985) and French Polynesia (Gleason, 1996) *Pocillopora* sp and *Porites* sp were the dominant recruits.

4.114 Factors affecting larval settlement

Many studies have reported large spatial and temporal variability in coral recruitment rates. For example, Connell *et al.* (1997) demonstrated that recruitment rates on the Great Barrier Reef showed considerable temporal variation within sites and that recruitment rates also differed among sites, suggesting that recruitment varied independently from year to year. These spatial and temporal variations in recruitment are caused by a wide range of different factors including variation in the species composition and the reproductive strategies of the coral species present (Harrison and Wallace, 1990), variations in adult coral fecundity (Hughes *et al.* 2000), differences in post-settlement mortality (Bak and Engel, 1979; Fisk and Harriott, 1990; Carlon and Olson, 1993; Dunstan and Johnson, 1998), and changing hydrographic conditions (Sammarco and Andrews, 1988; Black *et al.*, 1991). Connell *et al.* (1997) showed that coral recruitment rate increased with the amount of free space available despite annual variations in unknown factors. This free space was pre-empted by other corals at the exposed sites and macroalgae at the sheltered sites. The authors also demonstrated that variations in the physical suitability of the substrate influenced the spatial and temporal patterns of recruitment but that variations in recruitment rate were not related to the type of larval recruits.

4.115 Post settlement mortality

Newly settled coral recruits suffer a high rate of post-settlement mortality and variations in mortality rates play an important role in the spatial distribution and vertical zonation of coral species (Carlon and Olson, 1993). The rate of mortality tends to be highest in the initial period after settlement and decreases during the subsequent months (Babcock, 1985). Rylaarsdam (1983) and Fitzhardinge (1988) suggest that rapid growth rates of new recruits result in higher survivorship of these colonies, allowing them to escape grazing damage, sediment smothering and overgrowth by algae. They propose that interspecific differences in growth rate result in differential mortality between species and affect juvenile abundance distributions. Mortality of newly settled recruits can occur as a result of high sedimentation (Rogers, 1990; Tomascik, 1991; Wittenberg and Hunte, 1992); grazer damage (Potts, 1977; Wallace *et al.*, 1986; Wittenberg and Hunte, 1992; Reaka-Kudla *et al.*, 1996) and competition with other organisms (Sammarco, 1980; Van Moorsel, 1985; Harriott and Banks, 1995; Maida *et al.*, 1995; Tanner, 1995, 1997).

4.116 The impacts of sediment on coral settlement and recruitment

Sediment accumulating on the substratum is thought to be a factor preventing settlement in some locations (Birkeland, 1977; Bak and Engel, 1979). Direct impacts of high sediments include coral larvae being unable to successfully establish themselves in shifting sediments (Rogers, 1990); physical damage through abrasion (Tomascik, 1991) and smothering by the sediment (Wittenberg and Hunte, 1992). Suspended or overlying sediment can disturb a coral's energy budget by reducing the amount of light available, by interfering with the capacity to capture food and by increasing the energy demand for active sediment rejection (Stafford-Smith and Ormond, 1992). Increased turbidity could also make more cryptic habitats too dark, either increasing mortality rates due to decreased coral growth rate or forcing larvae to settle on more exposed upper surfaces where sediment levels or grazing intensity may be higher (Maida *et al.*, 1994).

Tomascik and Sander (1987) found that colonies of *Porites porites* in turbid areas contained lower numbers of larvae than colonies sampled from a less polluted reef. They suggest that this reduction in reproductive activity is caused by reduced light levels and a reduction of zooxanthellae photosynthesis and/or high suspended particulate matter, which requires additional energy expenditure for cleaning at the expense of reproduction. Gilmour (1999) found suspended sediments to inhibit fertilisation in *Acropora digitifera*. In addition, few larvae survived exposure to high and low sediment concentrations and suspended sediments were associated with significant decreases in larval settlement. His study showed that fertilisation, larval survival and settlement appear to be sensitive to concentrations of sediment of ≈50-100 mg l^{-1}).

The number of juvenile coral species was found to be significantly reduced at sites impacted by sedimentation from river discharge (Schelten, 2000); the percentage of damaged juveniles was found to increase, while the average size of colonies was found to decrease with increasing sediment. Hodgson (1990) found that that sediment coverage of 95 % completely prevented settlement on an artificial substrate. Babcock *et al.* (2000) also found that settlement was approximately 28 % times lower in experimentally manipulated sediment treatments than in control treatments; overall survival over 8 months was 2.5 times higher for juveniles at sites without additional sediment. In contrast, Babcock and Davies (1990) showed that sedimentation rates of up to 325 mg cm^{-2} d^{-1} did not result in a decrease in the total number of settling larvae. They did, however find that less larvae settled on the upper surfaces of settlement plates in the high sediment treatments. Te (1991) also found that settlement of *Pocillopora damicornis* larvae was not influenced by sediment levels of up 1000 mg l^{-1}. Corals did however exhibit reverse metamorphosis, suggesting that conditions were not favourable for continued development.

4.12 Coral regeneration

Coral tissue is continuously being damaged by the action of fish (Bak and Engel, 1979), invertebrates (e.g. crown-of-thorns starfish see Moran, 1986) and microorganisms (Antonius, 1981). Corals also suffer damage from hurricanes (e.g. Bythell *et al.*, 1993; Hughes and Connell, 1999), sedimentation (e.g. Dodge and Vaisnys, 1977; Rogers, 1990), temperature extremes (e.g. Coles and Jokiel, 1978; Glynn, 1984; Brown *et al.*, 1996), competition (Tanner, 1995; 1997) and human activity (Brown and Howard, 1985). The morphology of corals however, allows parts of the colony to die whilst the colony as a whole persists and may subsequently regenerate. The persistence of colonies depends on the recovery exceeding the damage (Ruesink, 1997). Injuries expose the coral skeleton which is soon colonised and overgrown by algae and other organisms; the coral regenerates the injury by overgrowing these invaders (Bak, 1983; Meesters and Bak, 1993; Hall, 1997; van Woesik, 1998; Lirman, 2000). Colonisation by such competitors is a potential threat and thus recovery from injury is an important component of colony survival (Bak and Steward-van Es, 1980). When the living tissue has been damaged the surrounding polyps and coenenchyme respond by regenerating new tissue (Meesters *et al.*, 1997). Regeneration of lesions starts with the formation of a new tissue layer by the surrounding polyps and new polyps start to emerge in this new tissue layer after approximately 1 week (Meesters and Bak, 1993).

4.121 Factors affecting coral regeneration

Initially tissue regeneration is very fast but it slows down exponentially (Bak, 1983; Meesters and Bak, 1993; Oren *et al.*, 1997; van Woesik, 1998; Lirman, 2000) and some studies have shown that healing is often partial and incomplete (Meesters *et al.*, 1994). Corals have varying susceptibilities to damage due to morphological differences and their ability to recover is also variable as species differ in the allocation of resources between regeneration and other demographic processes (Meesters and Bak, 1993; Hall, 1997; Ruesink, 1997). The rate of tissue regeneration is affected by a number of extrinsic parameters including season, ambient water temperature, coral size, lesion size and the coral's reproductive state (van Woesik, 1998; Kramarsky-Winter and Loya, 2000; Lirman, 2000) as well as environmental stresses such as temperature extremes (Lester and Bak, 1985; Meesters and Bak, 1993), wave exposure (Clark, 1997) and sedimentation (Meesters *et al.*, 1992).

Hall (1997) demonstrated that branching species regenerated a greater proportion of their injuries than massive and submassive species within 74 days. Regenerative ability could be ranked according to morphological attributes for the 11 species studied: arborescent > bushy > tabular > massive > submassive. Regenerative ability also differed between the different types of injury for a particular species: repair of superficial tissue and skeleton loss (scraping injury) was greater than recovery of extensive tissue loss, while re-growth of a new branch was the slowest of all. Kramarsky-Winter and Loya (2000) found that in *Fungia granulosa* lesion repair occurred faster at higher water temperatures and that small or immature corals regenerated at a slower rate than larger corals; regeneration was also found to cease during the reproductive period. In contrast, Chadwick and Loya (1990) found that large colonies of *F. granulosa* regenerated much more slowly than small corals, however that survivorship was greater in large colonies. Regeneration of injuries in this species was also found to be dependent on the presence of a mouth and new growth was observed to begin as a fan of septa radiating form the mouth area.

In *Montastrea annularis*, lesion perimeter was found to be the primary factor determining the rate of lesion regeneration (Meesters *et al.*, 1994; 1997). The authors showed that lesions that have a smaller area to perimeter ratio will be regenerated more than lesions that have relatively less perimeter. They predict that a linear lesion will therefore, heal much faster than a circular lesion of the same surface area as there is more tissue bordering the linear lesion. Oren *et al.* (1997) demonstrated that in *Favia favus*, rapid recovery during the first month is regulated mainly by perimeter length of the lesion; during the following months however, recovery is influenced more by the surface area of the lesion and its surface area to perimeter ratio. Lesions with long perimeters were found to have significantly higher recovery rates than lesions with shorter perimeters and those lesions with high perimeter to surface area volumes also exhibited high recovery rates. Van Woesik (1998) also found that in *Porites* spp. lesions with a high perimeter to surface area ratio healed faster than those with a low ratio. These studies suggest that regeneration of lesions is dependent on the amount of healthy tissue surrounding the lesion.

Environmental stresses also affect a coral's ability to regenerate. Meesters and Bak (1993) found that coral bleaching limits the potential of corals to recover from small wounds; bleached colonies were found to regenerate their lesions more slowly than normal colonies. Guzman *et al.* (1994) however, demonstrated that regeneration of coral injuries was significantly faster at sites heavily polluted by oil than at healthy sites; transplantation experiments proved that this rapid recovery was environmentally induced rather than a reflection of some inherent difference.

4.122 Implications of colony regeneration

Regeneration of damaged tissue places an energy cost on the coral colony and thus affects colony growth (Bak, 1983; Chadwick and Loya, 1990; Guzman *et al.*, 1994; Meesters *et al.*, 1994; Ward, 1995), reproduction (Harrison and Wallace, 1990; Van Veghel and Bak, 1994; Ward, 1995), resistance to disease and competitive ability (Bak and Criens, 1981). Meesters *et al.* (1994) demonstrated that growth of *Montastrea annularis* decreased significantly after lesion infliction and that a lesion of only 8.8 % of the total tissue area suppressed growth by approximately 32 % over a 56 day period. Van Veghel and Bak (1994) showed that lesion infliction and regeneration reduce fecundity in *Montastrea annularis*. They found that fecundity and sexual activity were significantly reduced in the coral tissue surrounding lesions compared to tissue from the same colony >20 cm distant from the lesion. They recorded up to a 74 % decrease in fecundity and 54 % decrease in fertility in the coral tissue surrounding lesions. Regeneration rates were also low compared to other data from comparable reefs in the same area and the authors concluded that the reduction in fecundity and low regeneration rates demonstrated the limited amount of energy that is available in coral energy budgets.

Bak (1983) and Meesters *et al.* (1994; 1997) suggest that the resources required for regeneration of lesions are derived only from those polyps directly bordering the lesion area. Oren *et al.* (2001) however suggest that the regeneration of injuries depends upon colony integration. They found that in *Favia favus* the recovery of small lesions was not affected by colony size, indicating that small lesions do not elicit the full regenerative potential. Recovery rates for larger lesions was however found to be positively correlated with colony size suggesting that regeneration of major injuries requires the activation of a greater number of intact polyps. The authors also showed that small lesions only caused a localised reduction in polyp fecundity (up to 1 cm away from lesion) whereas large lesions caused extensive reduction in polyp fecundity, up to 15 cm away from the lesion. They conclude that small lesions induce only a localised energetic involvement for their recovery and that the bordering polyps may be the only ones involved in regeneration; larger lesions on the other hand elicit a much higher level of colony integration.

4.13 Aims and objectives

The aims of this study are to assess whether high levels of sedimentation on the reefs of Rodrigues are having a sub-lethal impact on coral colonies, by investigating coral settlement rates and coral colonies ability to recover from injury at sites with different levels of sedimentation. This will be achieved by:

- Quantification of coral settlement on settlement tiles at the 3 survey sites over a 12 month period.
- Assessment of the ability of coral colonies to recover from artificially-induced lesions over a 5 week period at the 3 survey sites.

4.2 METHODS

4.21 Coral settlement

At each of the 3 survey sites (Totor, Trou Malabar and Chaland), 12 settlement plates were attached in sets of 4 to 3 wire metal racks (Plate 4.1). Settlement plates consisted of unglazed terracotta roof tiles 14 cm x 16 cm, which had been pre-conditioned in seawater for 1 month. The metal racks held the tiles at a 45 ° angle (English *et al.*, 1994), 15 cm above the substrate. The settlement racks were positioned at a depth of 9-13 m and were separated by a distance of approximately 1 m. The settlement plates were put down during May-June 2002 and were collected after 12 months on the reef. Once collected, tiles were washed in freshwater and left to dry in the sun. Tiles were then examined under a dissecting microscope. All coral spat were counted, photographed and identified to family level using Babcock *et al.* (2003) and English *et al.* (1994). The percentage cover of other encrusting organisms was also assessed.

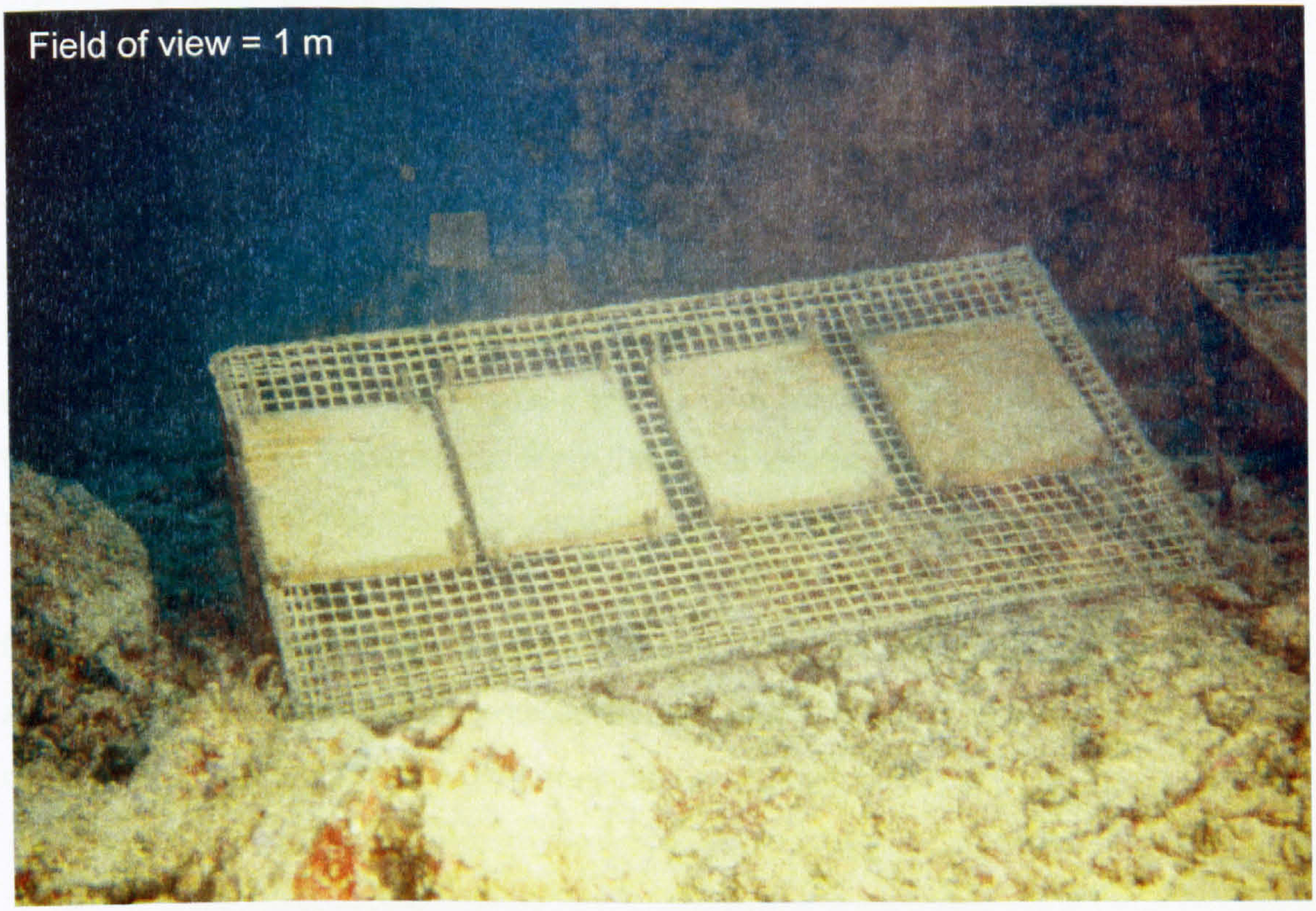


Plate 4.1 A rack of 4 settlement tiles on the reef at Trou Malabar.

4.22 Colony regeneration

At each of the 3 survey sites 10 platy *Montipora* colonies were randomly selected between 9 and 12 m depth and tagged. At Totor and Trou Malabar all colonies were *M. aequituberculata*, however at Chaland *M. tuberculosa, M. grisea* and *M. mollis* were also selected due to a scarcity of *M. aequituberculata*. *Montipora* spp. colonies were used for this study as they are commonly occurring species in Rodrigues (Fenner *et al.*, 2004) and exhibit a platy growth form, which provides an ideal surface for the creation and monitoring of lesions. Coral colonies were photographed using a digital camera (Olympus c5050z, 5.0 Mega pixels) in an underwater housing (Olympus PT-15), with a 50 cm x 50 cm quadrat held in the field of view. The photographs were registered as a Non-Earth image in MapInfo Professional (version 6.0) using the corners of the quadrat as control points. The coral colonies were then digitised using the polygon tool. This allowed the surface area of each colony to be assessed. In addition, any sediment settled on the colony surface was digitised and the percentage of the colony surface area covered in sediment was calculated.

Once the colonies had been photographed three circular lesions were made on the upper surface of each colony. The lesions were approximately 10 cm from the edge of the colony and approximately 20 cm apart. Lesions were made using a blunt-ended metal bolt, which created flat, roughly circular lesions 10 mm in diameter and 2 mm deep. Average lesion surface area was 132 (± 4) mm^2. A photograph was taken of each lesion using the digital camera with a scale bar held in the field of view. The photographs were registered as a Non-Earth image in MapInfo Professional (version 6.0) using intersections on the scale bar as control points. The lesions were then digitised using the polygon tool. This allowed the surface area of each lesion to be calculated. In addition, the diameter of each lesion was measured at 2 points perpendicular to each other using vernier callipers to validate measurements made using photography.

Coral colonies were re-visited after 1 week, 3 weeks and 5 weeks during July and August 2003. Each lesion was re-measured using callipers and re-photographed to allow changes in colony surface area over time to be calculated.

4.3 RESULTS

4.31 Coral settlement

Unfortunately Cyclone *Kalunde*, which hit Rodrigues during March 2003, resulted in the loss of settlement tiles. Only 3 of the 12 tiles were retrieved from Trou Malabar and only 8 were retrieved from Chaland. All 12 settlement plates were recovered from Totor.

After 12 months, settlement tiles at Chaland were heavily encrusted with coralline algae and bryozoans, with high numbers of serpulid worms; other organisms included macro-algae (*Lobophora* sp), and the bivalve *Alectryonella* sp (Table 4.1). Mean cover by encrusting organisms was 90 %. No coral spat were found on the 8 tiles collected from Chaland. At Trou Malabar tiles were also heavily encrusted with coralline algae, *Alectryonella* sp, bryozoans and hydroids with high numbers of serpulid worms; mean cover was 84 %. The lower surfaces had a higher cover of *Alectryonella* sp than the upper surfaces (31 % compared to 3 %), whereas the upper surfaces had a higher cover of coralline algae (54 % compared to 32 %). Coral settlement was very low and only 1 coral spat was recorded on the 3 tiles. The spat was a Poritid and had settled on the lower surface of the tile.

At Totor, the upper surfaces of the settlement tiles were covered in a thick layer of sediment. Once the sediment was washed off, tiles were observed to be colonised by coralline algae, hydroids and serpulid worms, as well as bryozoans and the bivalve *Alectryonella* sp with a total mean cover of 50 %. The lower surfaces had a high cover of the bivalve *Alectryonella* sp with hydroids, coralline algae and bryozoans and a mean total cover of 93 %. The upper surfaces had a higher cover of coralline algae compared to the lower surfaces (28 % compared to 5 %), whereas the lower surfaces had a higher cover of *Alectryonella* sp and hydroids (62 % and 21 % compared to 1 % and 12 %). Thirteen coral spat were however found on the tiles from Totor, which equates to a mean of 1.1 spat per tile or 24 spat m^{-2}. All coral spat were poritids and all were <1 mm in diameter (Plate 4.2). 77 % of the coral recruits had settled on the upper surfaces, whilst only 23 % were on the lower surfaces.

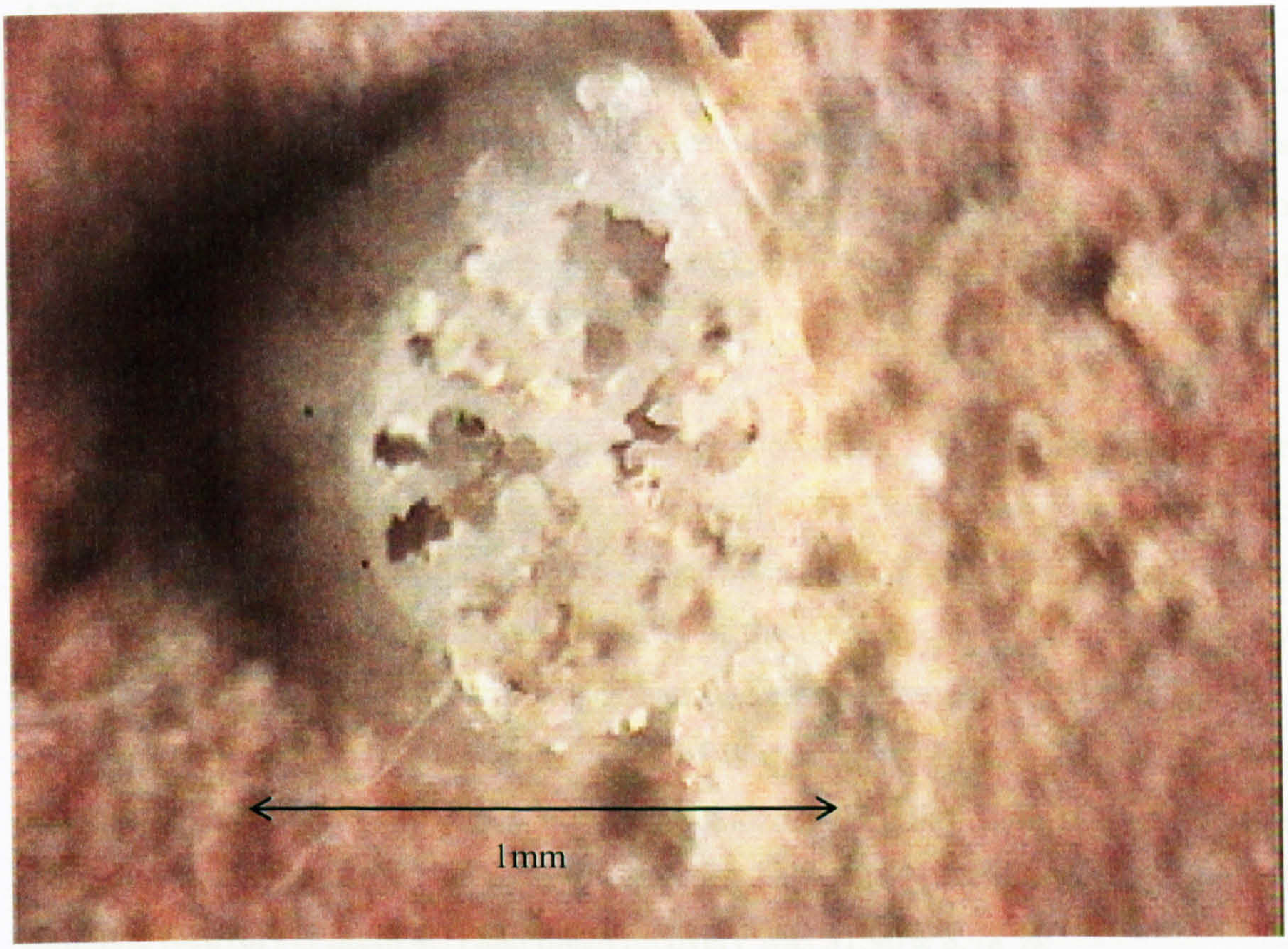


Plate 4.2 A poritid recruit on a settlement tile at Totor.

Table 4.1. The mean percentage cover of encrusting organisms on settlement tiles at the 3 survey sites over a 12-month period.

Site	Coralline Algae	Bryozoans	Macro-Algae	Serpulid Worms	*Alectryonella* sp.	Hydroids
Totor						
Upper	28	5	0	4	1	12
Lower	5	4	0	1	62	21
Trou Malabar						
Upper	54	10	1	7	3	3
Lower	32	13	2	6	31	6
Chaland						
Upper	53	26	6	3	2	0
Lower	34	46	6	3	2	0

4.32 Coral regeneration

Patterns of lesion regeneration varied among sites, colonies and lesions. All sites, however, showed an initial mean increase in lesion size during the first week, as polyps surrounding the lesion also died. During the following 2-week period lesions tended to decrease in size, with a further decrease during the final 2-week period (Figures 4.1 and 4.2).

At Totor, lesions on 80 % of the coral colonies showed an increase in size during the first week and overall lesions increased by a mean of 13.25 ± 5.06 % compared to the original injury. Lesions on 60 % of the colonies became covered in sediment. During the following 2-week period lesions on 90 % of the colonies decreased in size and by day 21, lesions on 80 % of the colonies had decreased relative to their original size. Sediment remained on the lesions of 60% of the colonies. During the final 2-week period lesions on all coral colonies decreased in size and by day 35 lesions on 90 % of the colonies had decreased relative to their original size. 11.5 % of lesions showed complete recovery (Figure 4.3) and mean recovery was 51.90 ± 8.78 %.

At Chaland, lesions on 70 % of the coral colonies decreased in size during the first week, however lesions on the remaining colonies showed large increases in size, giving a mean increase in lesion size of 14.60 ± 10.30 %. Lesions on 50 % of the colonies became covered in sediment, however by day 35 lesions on only 30 % of colonies were covered in sediment. During the following 2-week period lesions on 80 % of the colonies decreased in size and by day 21 lesions on 70 % of the colonies had decreased relative to their original size. During the final 2-week period lesions on 90 % of the coral colonies decreased in size and by day 35 lesions on 70 % of the colonies had decreased relative to their original size. Lesions on 2 colonies had become colonised by green algae, which trapped sediment; lesions on one of these colonies increased in size by 122 %. 8.3 % of lesions showed full recovery (Figure 4.3) and mean recovery was 21.24 ± 17.40 %.

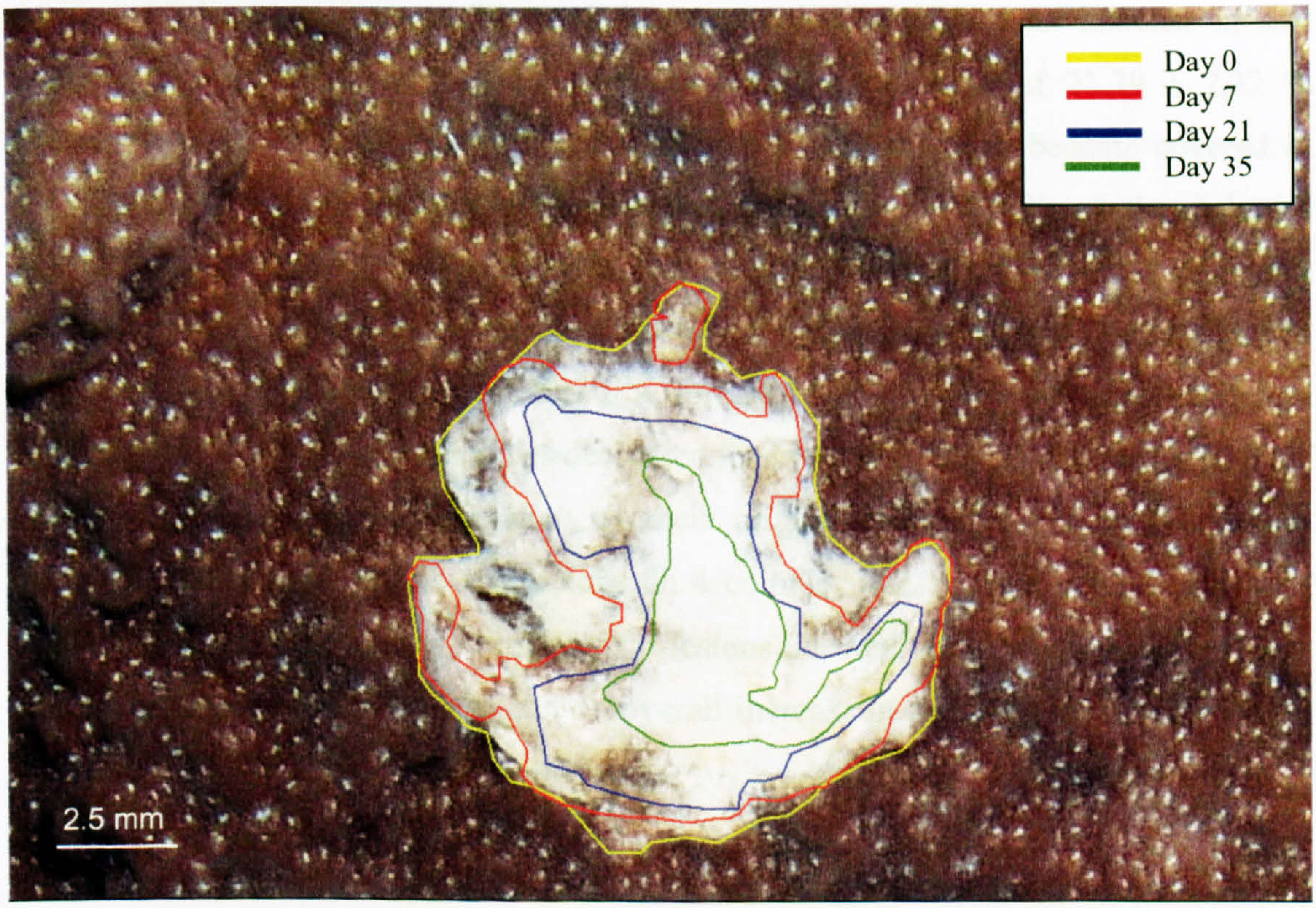


Figure 4.1 Lesion recovery over a 35-day period on a *Montipora mollis* colony at Chaland.

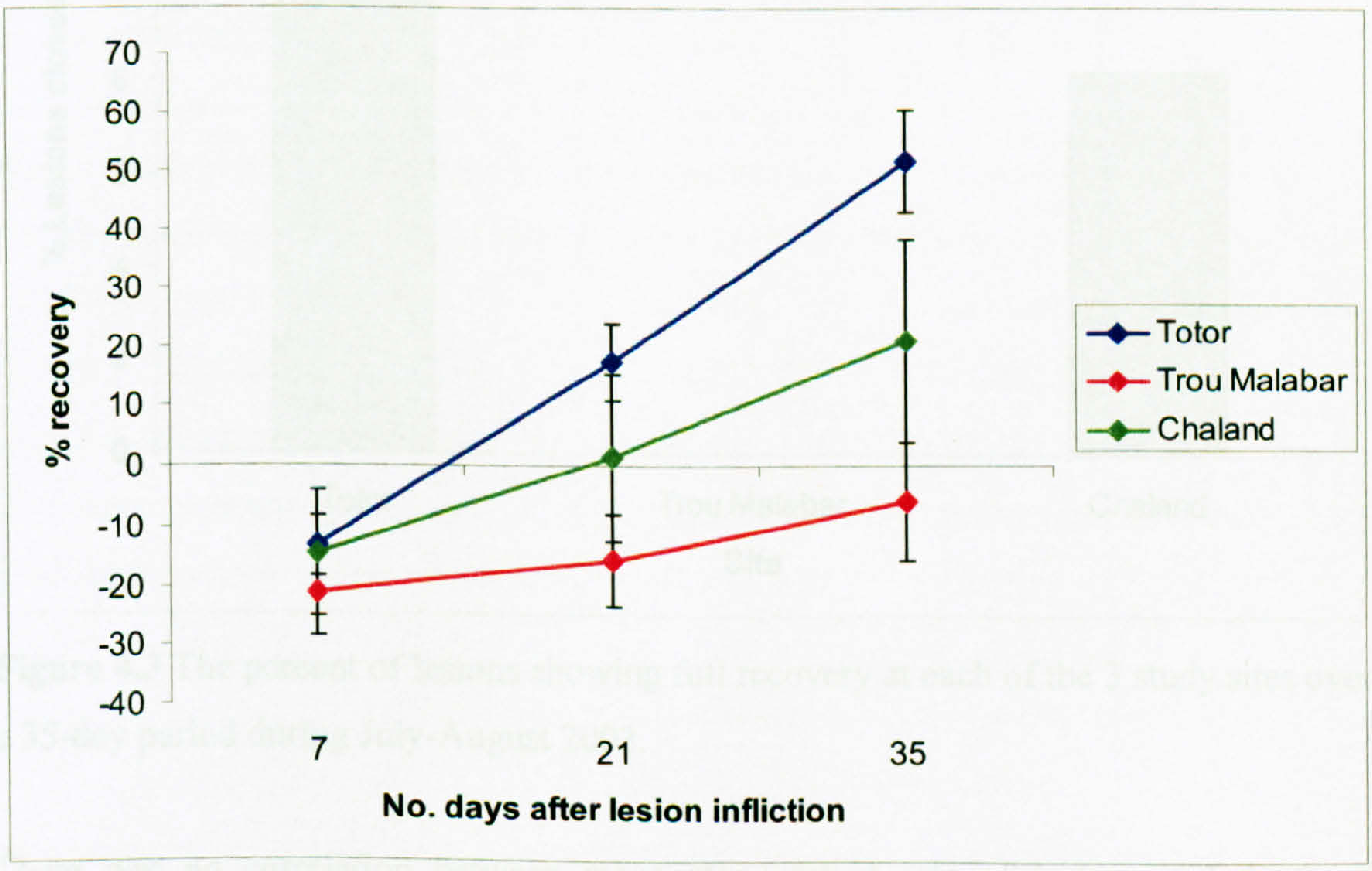


Figure 4.2 The percent recovery compared to original lesion size of lesions on 10 *Montipora* sp coral colonies at each of the 3 study sites over a 35-day period during July-August 2003.

At Trou Malabar, lesions on 80 % of the coral colonies showed an increase in size during the first week and overall lesions increased by a mean of 21.29 ± 7.32 % compared to the original injury. All lesions on all coral colonies became covered in sediment. During the following 2-week period lesions on 80 % of the colonies decreased in size however by day 21 lesions on only 40 % of colonies had decreased relative to their original size. Lesions on 2 colonies continued to increase in size and lesions on 3 colonies became colonised by turf algae. During the final 2-week period lesions on 80 % of the coral colonies decreased in size and by day 35 lesions on 60 % of the colonies had decreased relative to their original size. Lesions on 2 colonies continued to increase in size and lesions on 4 colonies had become colonised by turf algae, which trapped further sediment. No lesions showed complete recovery (Figure 4.3) and after 35 days there was still an overall increase in mean lesion size by 5.83 ± 9.69 %.

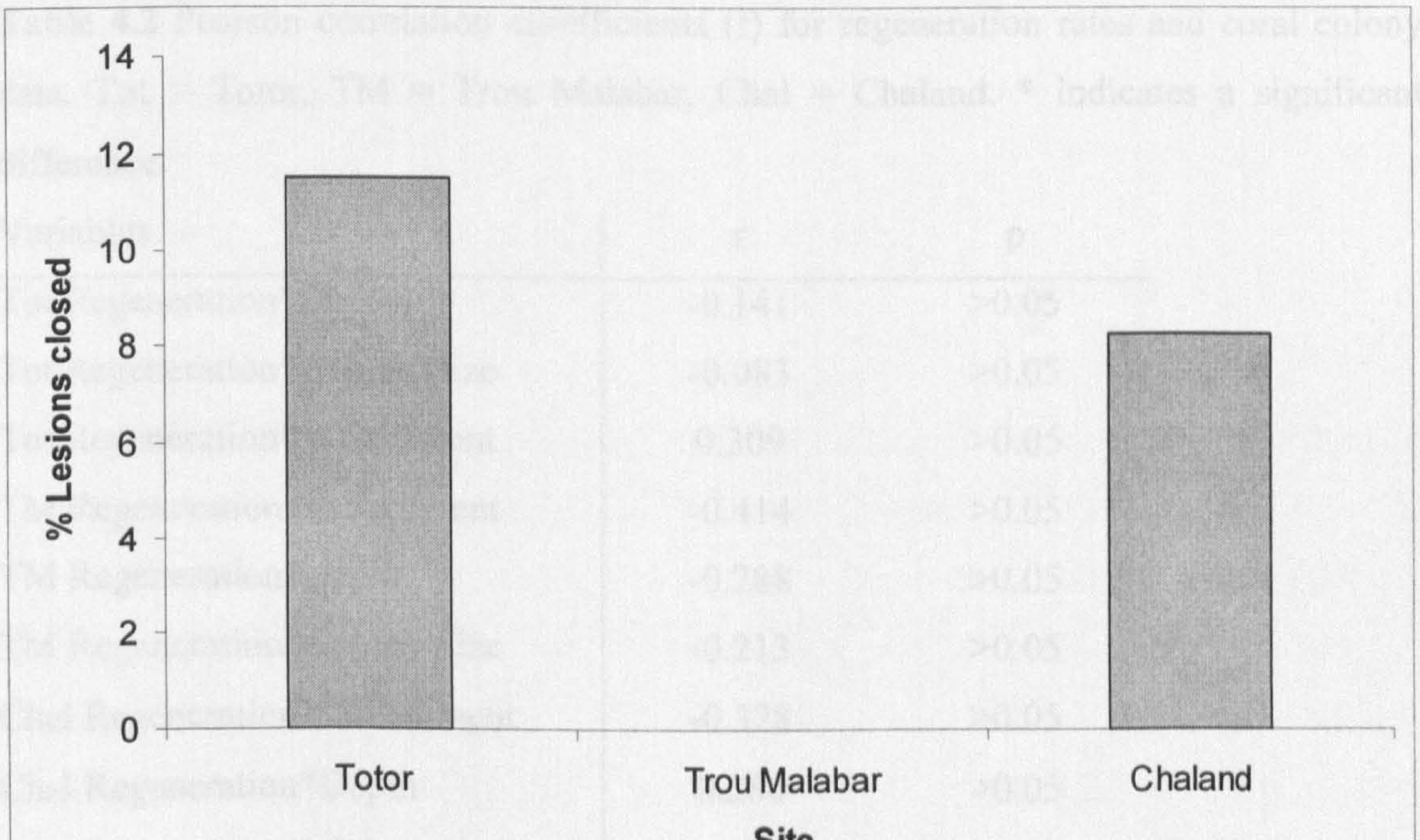


Figure 4.3 The percent of lesions showing full recovery at each of the 3 study sites over a 35-day period during July-August 2003.

There was no correlation between mean regeneration rate of lesions and depth of colony, colony size or the amount of sediment on the colony's surface at either of the 3 survey sites (Table 4.2).

A comparison of the regeneration rate over 5 weeks at each of the 3 sites, showed that mean regeneration after 35 days at Trou Malabar was significantly lower than at Totor and Chaland (Table 4.3). Meteorological conditions and sea temperatures were the same at all three sites, as the study was carried out during the same time period. Total rainfall was low, average windspeed was high, hours of sunshine were high, air temperature was low and seawater temperature was low (Table 4.4). There was no significant difference in mean vertical visibility (secchi disc depth) measured during the experimental period (Table 4.3; 4.5), however mean horizontal visibility was significantly higher at Trou Malabar and Chaland than at Totor. Mean sedimentation deposition during July-August was significantly higher at Trou Malabar than at Totor and Chaland (Table 4.3; 4.5). Coral colonies at Totor had a significantly larger surface area than colonies at Trou Malabar and Chaland (Table 4.3; 4.6) and colonies at Trou Malabar had a significantly higher amount of sediment on their surface than colonies at Totor and Chaland.

Table 4.2 Pearson correlation co-efficients (r) for regeneration rates and coral colony data. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	r	p
Tot Regeneration*Depth	-0.141	>0.05
Tot Regeneration*Colony Size	-0.083	>0.05
Tot Regeneration*% Sediment	0.309	>0.05
TM Regeneration*% Sediment	-0.414	>0.05
TM Regeneration*Depth	-0.288	>0.05
TM Regeneration*Colony Size	-0.213	>0.05
Chal Regeneration*% Sediment	-0.328	>0.05
Chal Regeneration*Depth	0.280	>0.05
Chal Regeneration*Colony Size	0.208	>0.05

Table 4.3 Statistical analysis results for regeneration rate data for *Montipora* spp. and environmental data measured during July – August 2003. Tot = Totor, TM = Trou Malabar, Chal = Chaland. * indicates a significant difference.

Variables	Test	Test statistic	df	p
Tot*TM*Chal	Kruskall-Wallis	19.04 (H)	2	<0.05*
Sites*Vertical visibility	1-way ANOVA	1.11 (F)	2	>0.05
Sites*Horizontal visibility	1-way ANOVA	12.77 (F)	2	<0.05*
Sites*Sediment deposition	1-way ANOVA (√)	425.93	2	<0.05*
Sites*Colony size	1-way ANOVA	15.79 (F)	2	<0.05*
Sites*% Sediment cover	1-way ANOVA (Log)	4.67	2	<0.05*

Table 4.4 Meteorological conditions during the regeneration study period (14th July – 22nd August 2003).

Variable	Observation
Total rainfall (mm)	51.7
Average windspeed (km/hr)	20.2
Total sunshine (hours)	307.2
Mean maximum air temperature (°C)	24.7
Mean seawater temperature (°C)	23.0

Table 4.5 Mean vertical and horizontal visibility and mean sediment deposition (± SE) during the regeneration study period (14th July – 22nd August 2003).

	Totor	Trou Malabar	Chaland
Mean vertical visibility (m)	5.8 ± 0.8	7.4 ± 0.9	7.1 ± 0.7
Mean horizontal visibility (m)	4.9 ± 0.5	7.6 ± 0.7	9.9 ± 1.1
Mean sediment deposition (mg cm^{-2} d^{-1})	28.43 ± 1.27	50.58 ± 2.21	3.98 ± 0.39

Table 4.6 The mean surface area (± SE) of *Montipora* spp colonies used in the regeneration study and the mean % coverage (± SE) of colonies with sediment.

	Totor	Trou Malabar	Chaland
Mean colony surface area (cm^2)	1053.5 ± 96.4	714.6 ± 63.1	474.4 ± 5.31
Mean sediment cover (%)	5.09 ± 1.49	22.08 ± 8.48	2.49 ± 0.99

4.4 DISCUSSION

4.41 Coral recruitment

Settlement of coral spat over the period May 2002 – May 2003 was low at Totor, very low at Trou Malabar and no settlement was observed at Chaland. Spatial variations in coral recruitment have been reported with variability occurring between inshore and offshore habitats (Fisk and Harriott, 1990; Sammarco, 1991; Miller *et al*, 2000) and exposed and protected sites (Tanner *et al.*, 1994). Miller *et al.* (2000) found that juvenile coral mortality was high on offshore reefs and related this to increased physical stresses offshore (e.g. physical abrasion during storms); Sammarco (1991) also related low recruitment rates to abrasion caused by heavy wave surge. It is possible therefore, that coral larvae did not settle at Chaland due to higher wave action at this site compared to Trou Malabar and Totor. Annual recruitment densities are much lower than those recorded on the central Great Barrier Reef (44-242 recruits per tile; Harriott, 1992) and on the northern Great Barrier Reef (16-81 recruits per tile; Fisk and Harriott, 1990), however are similar to densities obtained at high latitude sites in Australia (0.8-6.3 recruits per tile, Banks and Harriott, 1996; 0.3 – 5.4 recruits per tile, Harriott and Simpson, 1997), Taiwan (0.0 – 3.5 recruits per tile, Soong *et al.*, 2003) and the Northern Mariana Islands (0.0 – 7.7 recruits per tile, Quinn and Kojis, 2003).

It is not known at what time of year coral spawning occurs in Rodrigues. On the Great Barrier Reef studies have shown that peak recruitment occurs in the austral spring in October to February (Wallace and Bull, 1981; Harriott, 1985b; Wallace, 1985a; 1985b; Harriott and Fisk, 1988; Fisk and Harriott, 1990), while spawning in the Central Pacific, Hawaii, southern Japan and the Red Sea mostly occurs during summer (Shlesinger and Loya, 1985; Richard and Hunter, 1990; Hayashibara *et al.*, 1993). In Tanzania maximum recruitment occurred during April (Nzali *et al.*, 1998), whilst in Réunion, spawning has been found to occur during December (Rard, Coral-list 2003). Mendes and Woodley (2002) examined coral recruitment patterns at a number of different locations worldwide and concluded that coral spawning is controlled by a combination of temperature and rainfall. They suggest that spawning occurs during the period of highest seawater temperature, prior to the period of heaviest rainfall. In Rodrigues, the period of heaviest rainfall occurs in February (World Climate, 2003); based on this evidence we would therefore expect peak settlement in Rodrigues to occur during December - January.

Recruitment studies undertaken by Shoals Rodrigues staff using settlement tiles placed on the shallow reef flat between August 2003 and January 2004 found coral spat ranging in size from 0.5 mm to 4.0 mm (Clark and Meunier, *pers.* comm.). It is likely that the larger spat had settled some time ago as the diameter of spat at settlement varies between 0.5 mm and 2.5 mm (Babcock *et al.*, 2003) and growth rate of coral recruits tends to be slow during the first 6-8 months (Babcock, 1988). The range in size of recruits suggests that in Rodrigues coral settlement occurs over a number of months or throughout the year. Poritidae and Pocilloporiidae corals have been shown to recruit throughout the year in the Pacific Ocean (Birkeland *et al.*, 1981; Banks and Harriott, 1996; Gleason, 1996) and Rard (Coral-list, 2003) comments that in Réunion recruitment has also been observed throughout the year.

Rainfall and wind speed were high during both March and April 2003, resulting in high sedimentation and high turbidity. It is possible therefore, that unfavourable environmental conditions just after spawning resulted in the observed low rates of larval settlement. Wave action would have been particularly high at the more exposed site of Chaland due to high wind speeds, reducing recruitment due to increased physical stress and abrasion. In addition, Tomascik and Sander (1987) found a reduction in reproductive activity in *Porites porites* in areas of high turbidity. Gilmour (1999) found that suspended sediments inhibited fertilisation in *Acropora digitifera* and were associated with significant decreases in larval settlement. Lam (2000) also found that coral reproduction in Hong Kong was low and attributed this to the fact that coral spawning occurs during the rainy season, when heavy terrestrial run-off causes a decrease in sedimentation and a decrease in salinity, creating unfavourable conditions for reproduction.

At all sites settlement of other encrusting organisms was high, covering up to 90 % of settlement tiles. At Chaland, tiles were colonised by coralline algae and bryozoans and at Trou Malabar by coralline algae, bryozoans and the bivalve *Alectryonella* sp. At Totor cover by encrusting organisms was lower on the upper surfaces, but was high on the lower surfaces where tiles were colonised by *Alectryonella* sp. The amount of available space for settlement on the reef has been observed to affect the rate of coral recruitment. Hughes (1985) showed that there was a significant negative correlation between the mean rates of larval recruitment and the percentage cover of previously established macro-organisms and suggests that lack of available space had a marked inhibitory effect on the net amount of larval recruitment. Gittings *et al.* (1988) and Connell *et al.* (1997) also showed that coral recruitment rate was positively correlated with the amount of free space available. Coral growth and recruitment have also been found to be inhibited by interspecific competition with sessile epifauna and flora such as macro-algae, coralline algae and foraminifers (Bak and Engel, 1979; Sammarco, 1980; Tanner, 1995), polychaetes (Sammarco, 1980), tunicates (Birkeland, 1977; Oren and Benayahu 1997), bryozoans (Birkeland, 1977) and ascidians (Harriott and Banks, 1995; Nzali *et al.*, 1998). Quinn and Kojis (2003) observed that settlement plates at turbid reef sites had a high density of bivalves and fleshy algae settling on them. Dunstan and Johnson (1998) also found that settlement tiles on the Great Barrier Reef had cover of bryozoans and oysters of up to 80 % and suggest that competition reduced coral recruitment. It is therefore likely that coral settlement in Rodrigues is also low due to competition of the coral spat with coralline algae, bryozoans and bivalves.

All coral spat found settled on the tiles were Poritidae; no Acroporidae or Pocilloporidae recruits were observed. This was unexpected as the abundance of adult *Acropora* spp and *Montipora* spp colonies is high at Totor. In addition, Acroporidae and Pocilloporidae tend to dominate new recruits on the Great Barrier Reef (Wallace, 1985a; 1985b; Harriott and Fisk, 1987; Fisk and Harriott, 1990; Banks and Harriott, 1996; Baird and Hughes, 1997; Dunstan and Johnson, 1998), in Western Australia (Harriott and Simpson, 1997), the Philippines (Reyes and Yap, 2001) and Taiwan (Soong *et al.*, 2003). In French Polynesia, recruitment tiles were found to be dominated by pocilloporids in the warm season however, poritids were the dominant recruit during the cool season (Gleason, 1996). The author also comments that although adult colonies of *Acropora* and *Montipora* spp were abundant, the acroporids contributed very little to new recruitment and relates this to the greater resistance of poritids to coral bleaching. It is possible therefore, that coral bleaching on the reef flat, combined with the unfavourable conditions and high sediment deposition resulted in a lack of recruitment in the acroporids, but not in the more resistant poritids.

At Totor, settlement tiles were covered in a thick layer of sediment, smothering the newly settled coral spat. All spat were very small (<1 mm in diameter), indicating that the smothering had occurred soon after settlement. Other studies have shown that in areas of high sedimentation coral larvae either do not settle or undergo early mortality (Fisk and Harriott, 1990; Rogers, 1990; Sammarco, 1991; Tomascik, 1991; Wittenberg and Hunte, 1992). Birkeland *et al.* (1981) suggest that in shallow water coral recruitment is limited by sediment scour, whereas in deeper water smothering by sediment prevents recruitment. Babcock and Davies (1990) suggest that although laboratory experiments showed that coral settlement was not reduced by high sediment levels, in field situations sedimentation could result in reduced levels of settlement due to a lack of suitable surfaces. Hodgson (1990) showed that coral settlement was prevented by high sediment loads and suggests that on reefs affected by chronic sedimentation reproduction may occur asexually by fragmentation, reducing the genetic diversity of such reefs. Furthermore, Te (1991) showed that although initial larval settlement was not affected by high sediment levels, a high number of settled larvae then underwent reversed metamorphosis, indicating that successful recruitment may be limited in high sediment areas.

Coral spat at Totor settled preferentially on the upper surfaces on settlement tiles. A number of different studies have shown settlement orientation of coral recruits to vary with environmental conditions with recruits settling where they can avoid predation by fish or smothering by excessive sediment but still receive adequate light (Birkeland, 1977; Bak and Engel, 1979; Harriott, 1985; Harriott and Fisk, 1988). In contrast to the current study, many studies have found that on horizontal settlement tiles the majority of settlement tends to occur on the lower surface (Birkeland, 1977; Rogers *et al*., 1984; Harriott, 1985; Harriott and Fisk, 1987; 1988; Fisk and Harriott, 1990; Tomascik, 1991; Maida et al., 1994). The Shoals Rodrigues recruitment study carried out on the reef flat also found that the majority of recruits settled on the underside of tiles (Clark and Meunier, *pers*. comm.). It is suggested that spat prefer the lower surfaces habitats due to their susceptibility to fish grazing and sedimentation (Harriott and Fisk, 1988). Babcock and Davies (1990) confirmed this observation and showed that increases in sediment deposition resulted in a reduction in coral larvae settling on the upper surfaces of settlement tiles.

In contrast, Harriott and Banks (1995), Banks and Harriott (1996) and Harriott and Simpson (1997) found that on high latitude reefs, corals settled abundantly on the upper surfaces of settlement plates. They suggest that this preference may be caused by reduced light levels due to reduced day length and light intensity meaning that light on the lower surfaces is too low for coral survival and growth. A number of studies have also shown that coral recruits prefer the lower surfaces of settlement plates in shallower sites but prefer the upper surfaces in deeper water (Wallace and Bull, 1981; Wallace, 1985b). In laboratory experiments five out of six coral species examined exhibited light-dependent settlement (Mundy and Babcock, 1998) and the authors conclude that the orientation of natural recruits on settlement substrata is a consequence of light-dependent settlement behaviour. Furthermore, Mundy and Babcock (2000) state that in transplantation experiments the observed patterns of post-settlement survival suggest that settlement is light-dependent and that planulae are able to detect light quality and/or intensity for locating the optimal settlement substrata. It seems therefore, that the low light levels experienced at Totor, due to increased turbidity, and competition with other organisms, resulted in the coral larvae settling on the upper surfaces of tiles, where they were then smothered by sediment.

The Shoals Rodrigues study found slightly higher settlement rates at Totor than during this study (2.1 recruits per tile in an area affected by coral bleaching and 1.6 recruits per tile in an unaffected area) (Clark and Meunier, *pers. comm.*). This may be due to more favourable environmental conditions during the study period as rainfall tends to be low during August – December and sunlight tends to be high, particularly during December and January. The Shoals Rodrigues study was however carried out on the shallow reef flat at 1-2 m depth, compared to 10-12 m during this study. Wallace (1985b) found that recruitment rates were higher at shallow sites than deep sites (Wallace, 1985b) and Wallace and Bull (1981) also observed the highest recruitment rates on the reef crest. Recruitment rates were however still low and were also low in the southern lagoon with 0.4 recruits per tile in an area affected by bleaching and 1.4 recruits per tile in an unaffected area. In contrast, the study found high recruitment at Ile aux Fous with 7.9 recruits per tile. This highlights the spatial and temporal variations in recruitment patterns around the island and suggests the need for the continued study of coral recruitment patterns.

4.42 Coral regeneration

Regeneration rates were low during this study compared to other experimental results (e.g. Meesters and Bak, 1993; Nagelkerken *et al.*, 1999; Lirman, 2000) and only very few lesions showed complete recovery. Water temperature has been shown to affect lesion regeneration rate (Kramarsky-Winter and Loya, 2000), and the author found that no corals fully recovered during winter when temperatures were as low as 21 °C, whereas complete recovery was observed at temperatures of 26 °C. This experiment was carried out during the period of lowest temperatures in Rodrigues, when sea water temperatures dropped to 23 °C and this may explain the low regeneration rates observed at all sites. Other meteorological conditions were favourable for coral growth with low rainfall and high hours of sunshine. Wind speed was however high during the study period and this may account for the high sediment deposition at Totor and Trou Malabar.

Lesions showed an initial increase in size during the first week. This is in contrast to other studies which found initial tissue regeneration to be very fast (Bak, 1983, Meesters and Bak, 1993; Meesters *et al.*, 1994; 1997; Oren *et al.*, 1997; van Woesik, 1998; Lirman, 2000; Hall, 2001). Van Woesik (1998) did however find that some lesions increased in size during the period of lowest tides and coldest yearly temperatures and Meesters and Bak (1993) observed that some lesions on bleached corals enlarged to many times their initial size. Furthermore, Van Veghel and Bak (1994) found that during the first week following lesion infliction 86 % of the lesions increased in size and they suggest that the regeneration process is slowed down by a delayed allocation of resources. Complete recovery of lesions only occurred in 11.5 % of lesions at Totor and 8.3 % of lesions at Chaland. Nagelkerken *et al.* (1999) also found that most lesions did not completely recover in 49 days and Meesters *et al.* (1994) note that no lesion completely closed during their 55 day study.

The longer lesions remain open there is increased possibility of settlement of alien organisms on the bare skeleton, resulting in further damage (Meesters *et al.*, 1994). At Trou Malabar and Chaland a number of lesions became colonised by turf algae and these lesions continued to increase in size over time. Hall (2001) also found that regeneration was low in corals with high levels of algal settlement. In contrast, other studies have shown that settlement of filamentous algae (Meesters and Bak, 1993; Meesters *et al.*, 1994; Lirman, 2000) and sediment (Van Woesik, 1998) does not slow down regeneration. Meesters *et al.* (1997) however show that although the regenerating tissue can overgrow filamentous algae which settles within the first week, algae that settles later requires more effort and is often not overgrown at all. Settlement of algae on lesions at Trou Malabar and Chaland did not occur until days 7-21 and this may account for the lack of overgrowth by the coral tissue.

Lesion regeneration was significantly slower at Trou Malabar than at Totor and

Chaland. Experimental coral colonies were smaller at Trou Malabar than at Totor and Kramarsky-Winter and Loya (2000) found that in *Fungia granulosa* lesion repair occurred faster in large coral colonies than in small or immature corals. Coral colonies at Trou Malabar were however larger than those at Chaland, yet regeneration rates were faster at Chaland. Coral colonies at Trou Malabar had a significantly higher coverage with sediment than at Totor and Chaland and sediment deposition during the study was also significantly higher. There have been few studies of the effect of sediment on lesion regeneration, however other environmental stresses have been shown to affect a coral's ability to regenerate and Meesters and Bak (1993) and Fine *et al.* (2002) found that corals suffering from bleaching showed reduced recovery of lesions. Clark (1997) showed that high wave exposure resulted in decreased regeneration rates and Nagelkerken *et al.* (1999) showed that lesion recovery was significantly greater in shallow water colonies than deeper water colonies due to lower light levels at depth.

Meesters *et al.* (1993) however did find that regeneration of lesions on *Acropora palmata* and *Montastrea annularis* was slower in high sediment sites. Furthermore, Van Katwijk (1993) found a higher proportion of injured coral colonies at high sediment sites, compared to low sediment sites and relate this to weakened condition of coral colonies in high sediment environments and Nugues and Roberts (2003b) found partial mortality of massive corals to be higher in areas of high sediment deposition, suggesting a lower ability of these corals to regenerate lesions. Sediment rejection requires energy (Kendall *et al.*, 1985; Riegl and Branch, 1995) and regeneration also has high energy requirements and it is therefore possible that due to the energy costs of sediment removal, the coral colonies at Trou Malabar have less available energy for regeneration of lesions.

It has been suggested that there is a trade-off between regeneration and reproduction and a number of studies have found lowered fecundity in damaged corals compared to healthy colonies (Kojis and Quinn, 1985; Guzman and Holst, 1993; Van Veghel and Bak, 1994; Ward, 1995; Kramarsky-Winter and Loya, 2000). This factor may also explain the lack of coral recruitment at Trou Malabar and Chaland. Both of these sites suffered fairly high coral mortality between June 2002 and April 2003, probably as a result of Cyclone *Kalunde*; Totor however was not affected by the cyclone. Reproductive activity at Trou Malabar and Chaland may therefore have been reduced as corals diverted their limited energy supplies towards recovery from this damage.

4.43 Summary

The main findings of this study were:

- Coral settlement during 2002-2003 was very low at all 3 sites, but was highest at Totor. This may be due to high rainfall, high wind, high sediment deposition and low turbidity at the time of spawning or to competition with other encrusting organisms.
- All coral spat were poritids and at Totor most had settled on the upper surfaces of tiles, where they were smothered with sediment.
- Regeneration rates of *Montipora* spp colonies were low and only a few lesions showed complete recovery.
- Lesion regeneration was significantly slower at Trou Malabar than at Totor and Chaland. Coral colonies at Trou Malabar had a significantly higher coverage of sediment than at Totor and Chaland and sediment deposition at this site was also significantly higher.

4.44 Conclusions

The results suggest that during 2003, the 3 survey sites had limited capacity to recover from any damage. All 3 sites showed low sexual recruitment during 2003, with low densities of recruits at Totor and Trou Malabar and no recruits observed at Chaland. Lesion regeneration at all 3 sites was low, and was particularly low at Trou Malabar, where no lesions showed full recovery over the 35 day study. The results suggest that this lack of recruitment and regeneration ability may be linked to high sediment deposition and high turbidity. Although conditions during 2003 are likely to be unusual, this suggests that in years of high rainfall and wind, reefs may be more vulnerable to future impacts due to a reduced potential for recovery.

CHAPTER 5: Adaptations of coral colonies to high sediment/low light conditions.

5.1 INTRODUCTION

The previous chapters have shown that high sedimentation at Totor and the very high sediment deposition recorded in 2003 may be causing a reduction in coral colonies growth, settlement and regeneration rates. Soil erosion has however been taking place on Rodrigues since the early 1800s and it is therefore likely that coral colonies at inshore sites have suffered high sediment conditions for over 200 years. As described in chapter 2 the reefs at these sites are healthy and this chapter will investigate what adaptation techniques coral colonies have developed in order to survive at these high sediment/high turbidity sites.

Corals show great ability to adapt to changing environmental conditions. Adaptation to environmental stress consists of a genetic and non-genetic or phenotypic component (Brown, 1997a). Whereas genetic adaptations occur over thousands of years, phenotypic adaptations usually involve changes in the performance of an individual during it's life-time. Corals are able to adapt to the changing reef environment by a range of phenotypic responses at the organism, cellular and molecular levels and coral colonies show both morphological and physiological responses in relation to different stresses. Morphological adaptation may involve changes in colony growth form, whereas physiological adaptations tend to involve changes in the photosynthetic apparatus of the zooxanthellae. Light is a major factor affecting the distribution of corals; light may vary on a daily or seasonal basis and there are also variations in light levels with increasing depth. The ability to adapt to changing light conditions through morphological and physiological adaptations allows corals to colonise a wide range of different habitats and this will be discussed below.

5.11 Physiological adaptations

Long-term studies of zooxanthellae densities have found considerable variation over time. In Mauritius zooxanthellae density tended to be lowest in the summer (September – March) and was approximately 3 times higher during autumn and winter (Fagoonee *et al.*, 1999). Stimson (1997) and Fitt *et al* (2000) also found that zooxanthellae densities were highest during winter/spring and lowest in late summer/early autumn. Fagoonee *et* *al.* (1999) found positive correlations between zooxanthellae density and nitrate concentration and Stimson (1997) also showed that zooxanthellae densities were positively correlated with dissolved nitrate and negatively correlated with irradiance. Brown *et al.* (1999) found that the lowest zooxanthellae densities occurred at the end of the dry season, when sea temperatures were at their maximum. They suggest that variations in zooxanthellae density are caused by the combined effect of increased photosynthetically active radiation (PAR) and sea surface temperatures resulting in a reduction of zooxanthellae.

Studies of zooxanthellae densities under varying light regimes have found contradictory results, with some studies finding an increase in zooxanthellae density with decreasing light, some finding a decrease and some finding no change. In the hydroid, *Myrionema amboinenese*, shaded polyps were found to contain about half of the zooxanthellae of unshaded polyps (Fitt and Cook, 2001), whereas Muller-Parker (1987) found that anemones (*Aiptasia pulchella*) from a shaded environment had a higher density of zooxanthellae than anemones from a sun environment. In contrast, Muller-Parker (1984) found no significant difference in zooxanthellae density with decreasing irradiance for *A. pulchella* and Harland and Davies (1994) found a similar result for the anemone, *Anemonia viridis*. Steele (1976) showed that zooxanthellae density in *Aiptasia tagetes* initially decreased with decreasing light intensity and then increased at the lowest light intensity.

In corals, Fitt *et al.* (2000) found no significant difference in zooxanthellae densities with increasing depth and Falkowski and Dubinsky (1981) and Porter *et al.* (1984) found no significant difference in zooxanthellae densities of shade and sun adapted corals. Vareschi and Fricke (1986), Kaiser *et al.* (1993) and Masuda *et al.* (1993) found a decrease in the density of zooxanthellae with increasing depth. McCloskey and Muscatine (1984) also found a decrease in zooxanthellae concentration at 35 m depth compared to 3 m however, they state that the decrease in zooxanthellae density did not occur until depths greater than 10 m. Drew (1972) showed that zooxanthellae densities were lowest at 3-5 m depth, increased at 10-20 m depth and then decreased again at 42 m depth. Similarly, Titlyanov *et al.* (2000) found an increase in zooxanthellae density between 88 % Photosynthetically Active Radiation (PAR) and 12 % PAR, but a decrease in zooxanthellae densities as light levels fell from 12 % PAR to <5 % PAR. It has been suggested that fewer algae may reduce shelf-shading therefore increasing the light-capturing efficiency of the algae (McCloskey and Muscatine, 1984; Kaiser *et al.*, 1993) or that hosts in low light conditions may have lower tissue biomass per unit surface area (Fitt *et al.*, 2000; Fitt and Cook, 2001).

The zooxanthellae themselves may adapt to changing light conditions by either changing the size of their photosynthetic unit or by changing the number of photosynthetic units (Chang *et al.*, 1983). Changing the size of the photosynthetic unit involves a change in the amount of photosynthetic pigment within each zooxanthellae cell. Shaded or low-light adapted symbiotic hydroids and anemones and corals have been shown to have increased chlorophyll levels compared to unshaded or high light adapted organisms (Falkowski and Dubinsky, 1981; Dubinsky *et al.*, 1984; Muller-Parker, 1984; 1987; Porter *et al.*, 1984; Harland and Davies, 1994; Fitt and Cook, 2001). Dustan (1982), McCloskey and Musctine (1984) and Fitt *et al* (2000) also found an increase in chlorophyll per zooxanthellae with increasing depth. Dubinsky *et al.* (1984) showed that in shade-adapted corals, chloroplasts and thylakoids were much more densely packed, allowing for the increase in cellular chlorophyll.

Changing the number of photosynthetic units involves a change in the ratio of photosynthetic pigments. In corals, Kaiser *et al.* (1993) found a decrease in the chlorophyll$_a$: chlorophyll$_{c2}$ ratio with increasing depth, whereas Helmuth *et al.* (1997) found higher chlorophyll$_a$: chlorophyll$_{c2}$ in low light environments and Dustan (1982) and Vareschi and Fricke (1986) found no change in the ratio. Chang *et al.* (1983) found that zooxanthellae from the giant clam, *Tridacna maxima* adapt to changing light intensity by altering the size of their photosynthetic units, whereas zooxanthellae from *Aiptasia pulchella* adapt by changing the number of photosynthetic units. Iglesias-Prieto and Trench (1994) found that zooxanthellae adapt to low light environments by simultaneously increasing both the number and size of their photosynthetic units, however they also showed that different species of zooxanthellae show different patterns of photoacclimation.

5.12 Morphological adaptations

Coral species exhibit a wide range of different growth forms, which can be attributed to the environment in which they live. Chappell (1980) predicted that coral colonies would become more branching and foliose with increasing sediment and more globose and ramose with decreasing light. Barnes (1973) stated that in general coral colonies become less robust, more slender or flattened with increasing depth. He related this to reduced light levels at depth as the flattened growth form provides an increased surface area, thus optimising the use of available light at low light intensities. This trend for flattened growth forms with increasing depth and/or decreased light availability has been observed by a number of other studies. Platy coral assemblages occur throughout most of the geological record of Scleractinia (Rosen *et al.*, 2003). Insalaco (1996) describes Upper Jurassic reefs characterised by a coral community of relatively low diversity dominated by the Microsolenidae family with predominantly platy morphologies. He suggests that the main control on the development of these reefs was low light intensities and that the corals adapted to these conditions by a strongly platy growth form and a reduction in growth rates. Rosen *et al.* (2003) examined fossil coral assemblages from the Upper Jurassic (160 million years ago) to the Mid Miocene (15 million years ago) and suggest that in general platy coral assemblages occur in relatively deep water with low light, calm conditions and very slow sedimentation rates. Based on this evidence they predict that where there are turbidity gradients on both a spatial and temporal scale, coral colonies will tend to become more platy as turbidity increases, as long as sediment deposition remains minimal.

On modern coral reefs, Goreau (1959) described the flattened plate-like growth form of *Montastrea annularis* and *Porites asteroides* in Jamaica. Macdonald (2003) also observed that platy corals were common on a turbid inshore reef in Jamaica and notes that *M. annularis* and *Siderastrea siderea*, which typically exhibit massive colony morphologies, were found to display closely tiered platy morphologies. In Costa Rica, *P. asteroides, M. annularis* and *Diploria strigosa* exhibited platy morphologies, even in shallow water due to high turbidity (Cortés and Risk, 1985) and in Puerto Rico platy corals were dominant below 15m depth (Acevedo *et al.*, 1989). On the Great Barrier Reef, turbid inshore reefs were found to be composed of encrusting and foliaceous growth forms with a high abundance of plating *Turbinara* spp (Kleypass, 1996; Van Woesik and Done, 1997).

In shallow water, the characteristic growth form of *Montastrea annularis* was found to be hemispherical; this changed to a peaked or columnar growth form at intermediate depths and became plate-like at the greatest depths (Graus and MacIntyre, 1976). Fricke and Schumacher (1983) showed that branched *Acropora* and *Stylophora* became flatter by branches growing predominantly horizontally with depth. Lobate forms changed to encrusting or platy morphologies and globose or hemispherical forms became cup like and flat. Fricke and Meischner (1985) also found that near-spheroid and hemispherical colonies became flat morphs with increased depth, whilst globular or massive irregular morphs became cup-like and finally flat or creeping crustose morphs. The authors also commented that corals in shaded shallow-water habitats were similar to those in deep water. Using computer simulations, Graus and MacIntyre (1976) showed that light intensity was the major ecological control of coral colony morphology.

Dustan (1975) noted that growth switches from upward growth to outward growth with increasing depth, resulting in flattened colonies at deeper depths. Porter (1976) observed that the maximum surface area: volume ratios resulted from branching or plating morphologies and that these are optimally suited for light interception; in addition small polyps further increases the photosynthetic surface area. The author showed that for Caribbean corals, species with a high SA/V ratio generally have small polyps and are therefore, more adapted to light-capturing. Hughes (1987) also found that there was an increase in surface area: weight ratio with depth, indicating that deeper colonies were thinner and flatter than corals at shallower depths. The author also commented that relatively robust species were more common in shallow water and these were replaced by thinner, more delicate species at depth. Anthony and Hoegh-Guldberg (2003) showed that in low light environments coral colonies had thinner tissue layer and thinner skeletal plates than corals in a high light environment, maximising the surface area for light capture.

Dustan (1975) found that colonies of *Montastrea annularis* transplanted to different depths did not survive as well as control colonies and concluded this was due to genetic differences in the zooxanthellae populations at shallow and deep sites. Other transplantation experiments have however shown that some coral species are capable of considerable phenotypic plasticity. Changes from massive to plating forms were observed on transplantation of *Turbinaria mesenterina* from shallow water to deep water (Willis, 1985), however no changes were observed for *Pavona cactus*. Furthermore, transplanted colonies of *M. annularis* and *Siderastrea siderea* changed their skeletal morphology from that most common in the population at their original habitat to that most common in the population at the environment to which they were moved (Foster, 1979). Plasticity was however found to be greater in *M. annularis* than *S. siderea*.

In high sediment environments advantageous growth forms would intercept the smallest proportion of settling sediment per unit surface area (Chappell, 1980). Horizontal, plate-like colonies have a large surface area to intercept and retain sediment particles, whereas vertical plates and upright branches are less likely to retain sediment (Pastorok and Bilyard, 1985). It has therefore been predicted that there will be a greater abundance of branching growth forms in high sediment environments, due to a greater efficiency at rejecting sediments (Rogers, 1990). Rosen *et al.* (2003) also suggest that platy coral assemblages will only occur in regions subject to low sedimentation as flat colonies are very susceptible to sediment deposition.

Following dredging activities plating corals of *Porites asteroides* were found to be unable to reject sediment and showed partial or total mortality (Bak, 1978). In Thailand, Brown *et al.*, (1990) observed that branching *Acropora* spp were not affected by dredging activities, whilst massive corals, especially Faviids showed a marked decline in abundance. Roy and Smith (1971) found that reefs at a high sediment site were composed mainly of ramose corals, whereas clear-water reefs consisted primarily of encrusting and massive corals. In contrast, in South Africa, high sediment sites were found to consist of mainly massive colonies and encrusting *Montipora* spp (Schelyer and Celliers, 2003). Branching corals have also been shown to exhibit changes in morphology with increased sediment. At a high sediment site in Costa Rica, *Agaricia agaricites* and *Acropora palmata* both occurred in vertical plates and branches (Cortés and Risk, 1985), whereas in Indonesia *Acropora valenciennesi* showed a tabulate growth form at a low sediment site, but growth was found to be more vertical at a high sediment site (Crabbe and Smith, 2002).

Sediment rejection experiments have shown that hemispherical colonies are better at rejecting sediment than horizontal plating colonies (Bak and Elgershuizen, 1976; Riegl, 1995). In addition, colonies of *Montastrea cavernosa* with steep polyp walls or with a steep colony surface were found to show efficient passive rejection of sediment (Lasker, 1980). Rogers (1983) found that the cylindrical branches of *Acropora cervicornis* and the almost spherical morphology of *Diploria strigosa* were better adaptations to high sediment loads, whereas sediment accumulated on the flattened portions of *Acropora* *palmata*. Branching corals species were found to exhibit faster sediment clearing rates than non-branching species (Stafford-Smith, 1993) and gravitational loss of sediment was found to be of such great significance to finely branched species and species with strongly inclined plates that active sediment rejection mechanisms were not required (Stafford-Smith and Ormond, 1992).

5.13 Aims and objectives

The aims of this study are to assess whether coral colonies have developed adaptation techniques in order to survive the high sedimentation/high turbidity found in the sheltered inner reef sites of Rodrigues. Physiological responses will be investigated by examining whether zooxanthellae densities vary with increases in turbidity. In addition, coral colony morphology will be studied to examine whether the greatest control on coral colonies is high turbidity or high sediment deposition. This will be achieved by:

- Quantification of zooxanthellae density of *Acropora austera* at the 3 survey sites over a 3 month period during 2003 to assess physiological adaptation.
- Assessment of variations in platy *Montipora* spp colony morphology at the 3 survey sites to include colony width, height, thickness, orientation and number of tiers.

5.2 METHODS

5.21 Zooxanthellae densities

At each of the 3 study sites, Totor, Trou Malabar and Chaland, 3 coral branch tips (approximately 3 cm in length) were collected randomly from 3 coral colonies at 8 m-12 m depth. Branch tips were collected using pliers and were placed in labelled sample bags. On return to the surface branch tips were immediately placed in 10 % formalin for 48 hours in order to fix the coral tissue. The branch tips were then cut to approximately 2 cm in length so that the 1 cm growing tip was removed and the branch surface area was determined using the aluminium foil technique (Marsh, 1970). The branch was wrapped in a piece of aluminium foil and moulded so that the foil exactly fitted the depressions and projections of the branch. The foil was then weighed on an electric balance (Denver Instrument, Xe, ±0.0001 g). Surface area was determined by weighing a series of pieces of aluminium foil of known surface area and using this factor to calculate surface area of the samples.

Zooxanthellae were extracted from the branch tips using Drew's Technique (Drew, 1972). The branch tips were decalcificed by placing them in 5 % hydrochloric acid for 72 hours. Corals were then homogensied in filtered seawater in a glass tissue grinder. Aliquots of homogenous extracts were counted on a haemocytometer (Fuch's Rosenthal) under a light microscope (x 80). The numbers of zooxanthellae were determined from 5 replicate haemocytometer counts and counts were normalized to coral surface area. This process was repeated once a month during June to August 2003. Zooxanthellae size could not be measured due to the low power of the available microscope.

5.22 Coral morphology

At each of the 3 study sites 15 platy *Montipora* colonies were randomly selected between 7 and 13 m depth. At Totor and Trou Malabar all colonies were *M. aequituberculata*, however at Chaland *M. tuberculosa, M. grisea* and *M. mollis* were also selected due to a scarcity of *M. aequituberculata*. A number of different measurements were made of colony morphology. Maximum width of the colony (cm) was measured using a flexible tape, height of the colony (cm) was measured using a ruler, thickness of the colony (mm) was measured using vernier callipers and orientation of the colony relative to the horizontal was measured using a weighted protractor

(Figure 5.1). The width and height measurements were used to calculate the width: height ratio. Notes were made on the exact depth of the colony and the number and type of tiering. In addition, coral colonies were photographed using a digital camera (Olympus c5050z, 5.0 Mega pixels) in an underwater housing (Olympus PT-15), with a 50 cm x 50 cm quadrat held in the field of view. Coral colonies at Totor and Chaland were photographed during June 2003, whereas colonies at Trou Malabar were photographed during July. The photographs were registered as a Non-Earth image in MapInfo Professional (version 6.0) using the corners of the quadrat as control points. The coral colonies were then digitised using the polygon tool. This allowed the surface area of each colony to be assessed. In addition, any sediment settled on the colony surface was digitised and the percentage of the colony surface area covered in sediment was calculated.

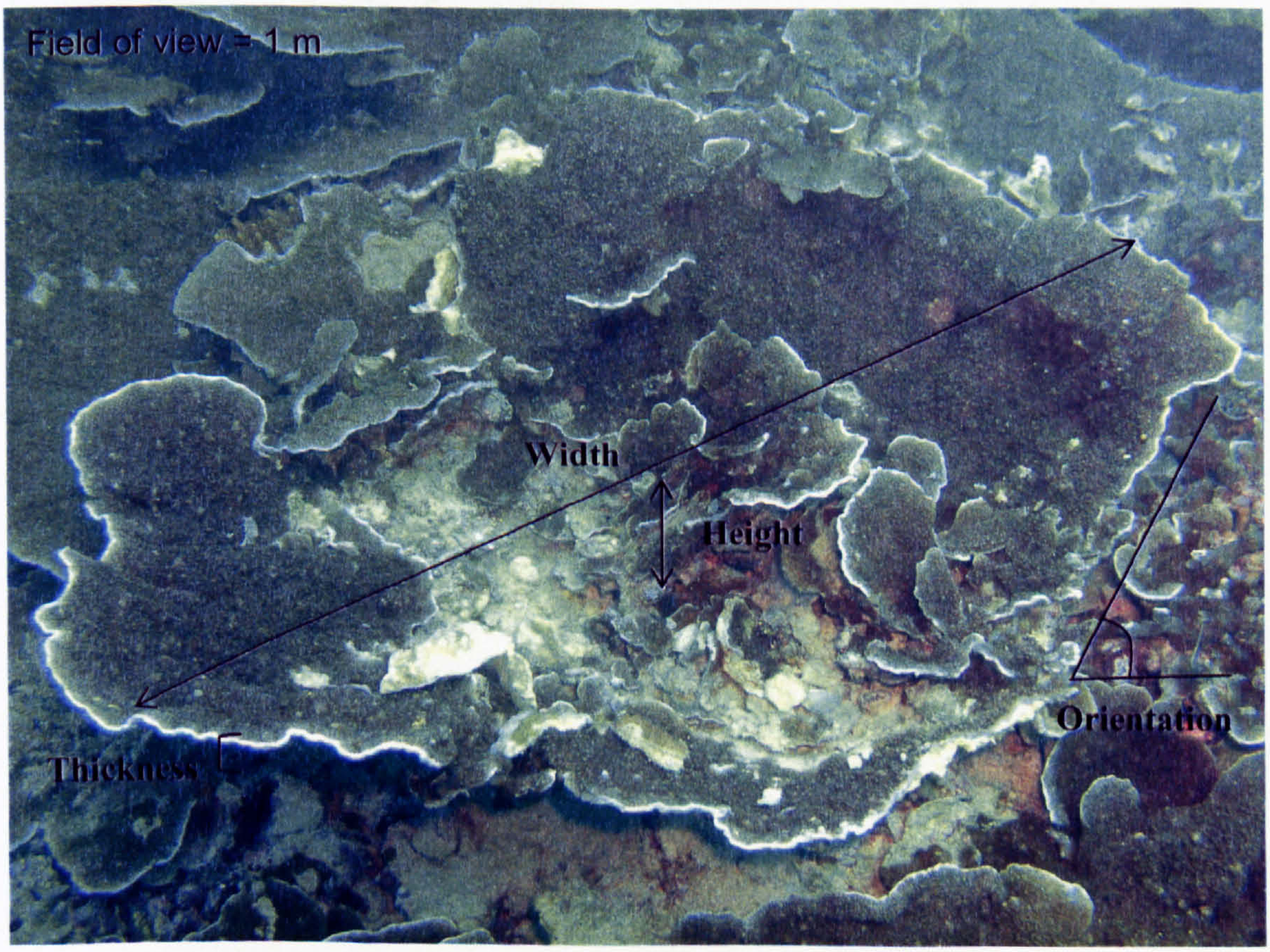


Figure 5.1 The morphological measurements of thickness, width, height and orientation made for each platy coral colony.

5.3 RESULTS

5.31 Zooxanthellae densities

Zooxanthellae densities were very variable at Totor, where the mean density ranged from 0.72 x 10^6 ± 0.02 cells cm^{-2} during July 2003 to 1.14 x 10^6 ± 0.05 cells cm^{-2} during June 2003. Mean zooxanthellae density was significantly higher during June and significantly lower during August 2003 (Table 5.1). At Trou Malabar there was no significant difference in mean zooxanthellae density over the 3-month period with densities remaining at a mean of approximately 0.70 x 10^6 ± 0.02 cells cm^{-2} during all 3 months. Problems arose with the samples collected from Chaland and zooxanthellae densities could only be assessed during July 2003, when the mean density was 0.76 x 10^6 ± 0.04 cells cm^{-2} (Figure 5.2). During June and August 2003 mean zooxanthellae density was significantly higher at Totor than at Trou Malabar (Table 5.1). During July however there was no significant difference in mean zooxanthellae density at Totor, Trou Malabar and Chaland.

Table 5.1 Statistical analysis results for zooxanthellae density data for *Acropora austera* measured during June – August 2003. Tot = Totor; TM = Trou Malabar; Chal = Chaland. * indicates a significant difference.

Variables	Test	Test statistic	df	p
Tot Jun*Jul*Aug	1-way ANOVA (Log)	48.19 (F)	2	<0.05*
TM Jun*Jul*Aug	Kruskall-Wallis	1.46 (H)	2	>0.05
June Tot*TM	2-sample T-test	5.62 (T)	2	<0.05*
July Tot*TM*Chal	Mood's Median	2.77 (X^2)	2	>0.05
Aug Tot*TM	2-sample T-test	-5.60 (T)	87	<0.05*

There was no significant difference in mean vertical visibility nor mean horizontal visibility at Totor during the 3-month study period (Table 5.2). During July mean vertical visibility was significantly lower at Totor than at Trou Malabar, however there was no significant difference during August (Figure 5.3). There are not enough data to calculate significant differences for either horizontal or vertical visibility during June 2003. There was no significant difference in mean horizontal visibility at Totor and Trou Malabar during July or August (Figure 5.4). At Totor, mean sediment deposition was significantly lower during June than during July and August (Figure 5.5). Mean sediment deposition was however significantly higher at Trou Malabar than at Totor during all 3 months. Total hours of sunshine were lowest during July 2003 and highest during August. July also had the highest number of observations of high cloud, with 49% of observations of >5 oktas, compared to 26 % in June and 36 % in August (Table 5.3).

Table 5.2 Statistical analysis results for environmental variables measured at the survey sites during June – August 2003. Tot = Totor; TM = Trou Malabar; Chal = Chaland. * indicates a significant difference.

Variables	Test	Test statistic	df	p
Tot Vertical visibility*Months	1-way ANOVA	0.93 (F)	2	>0.05
Tot Horizontal visibility*Months	1-way ANOVA	1.77 (F)	2	>0.05
July Vertical visibility Tot*TM	2-sample T-test	2.25 (T)	8	0.05*
Aug Vertical visibility Tot*TM	2-sample T-test	0.35 (T)	4	>0.05
July Horizontal visibility Tot*TM	2-sample T-test	-1.50 (T)	10	>0.05
Aug Horizontal visibility Tot*TM	2-sample T-test	0.36 (T)	8	>0.05
Tot Sediment Jun*July*Aug	1-way ANOVA	184.38	2	<0.05*
June Sediment Tot*TM	Mann-Whitney	57.0 (W)	-	<0.05*
July Sediment Tot*TM	2-sample T-test	-4.99 (T)	16	<0.05*
Aug Sediment Tot*TM	2-sample T-test	8.70 (T)	16	<0.05*

Table 5.3 Meteorological variables during the 3-month study period from June – August 2003. Sunshine, cloud and air temperature data provided by the Mauritius Meteorological Service.

	June	July	August
Total sunshine (hours)	214.6	203.2	248.8
% observations >5 oktas	25.7	48.8	36.4
Maximum air temperature (oC)	26.2	24.9	24.7
Seawater temperature (oC)	25	24	23

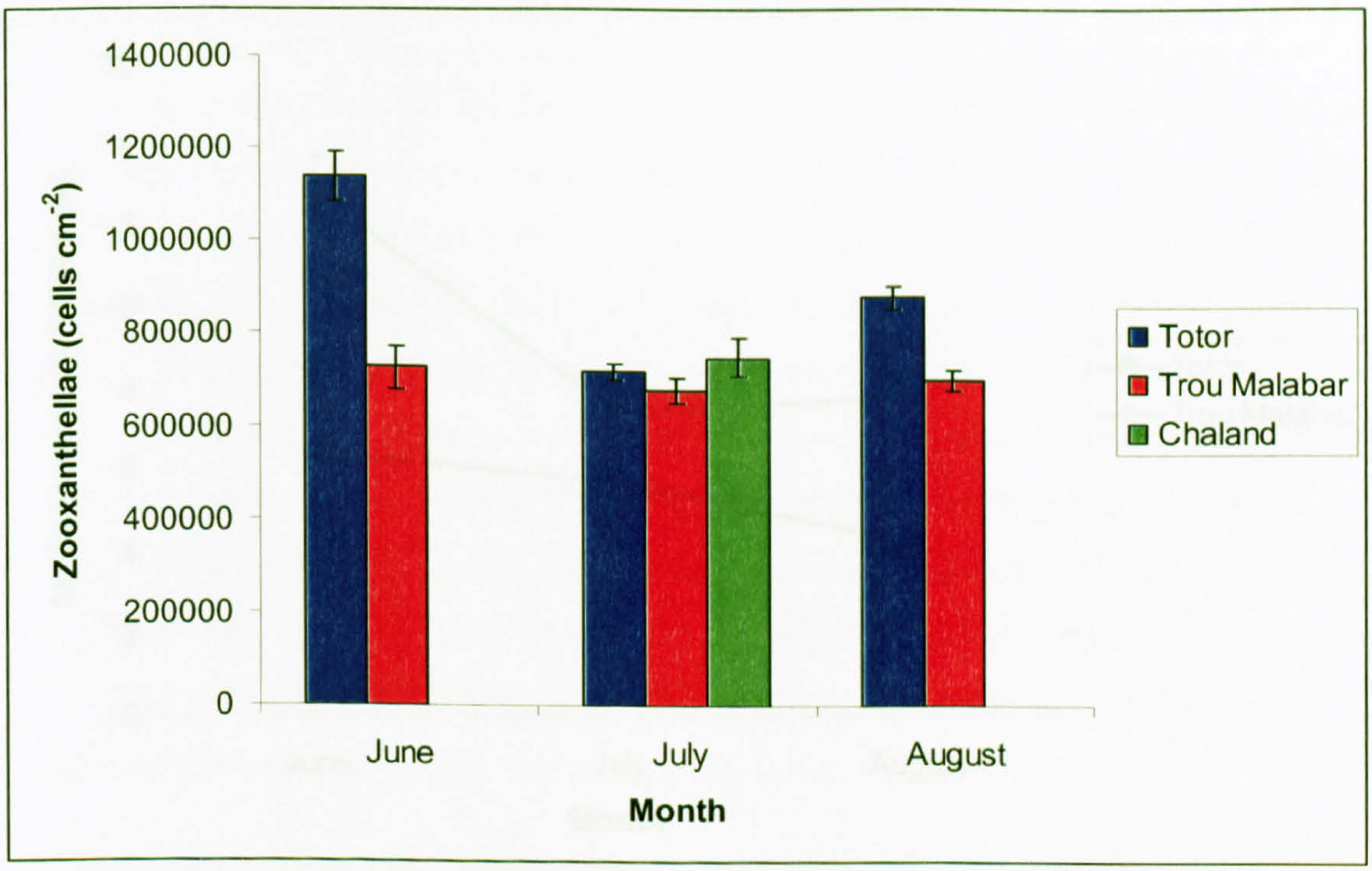


Figure 5.2 The mean density of zooxanthellae (cells cm^{-2}) (± SE) at each of the 3 study sites, measured between June and August 2003.

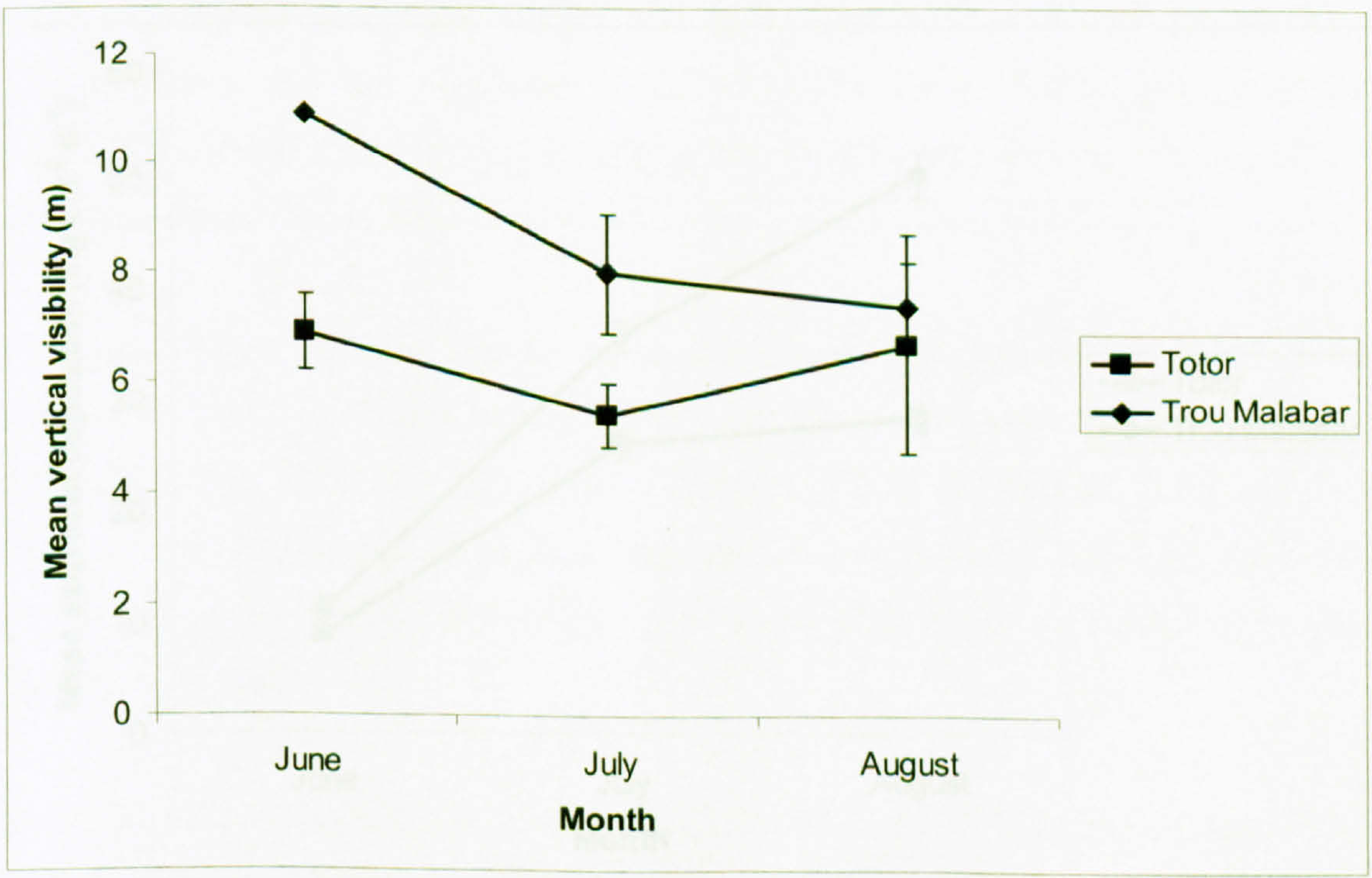


Figure 5.3 The mean vertical visibility (m) (± SE) at Totor and Trou Malabar during June-August 2003.

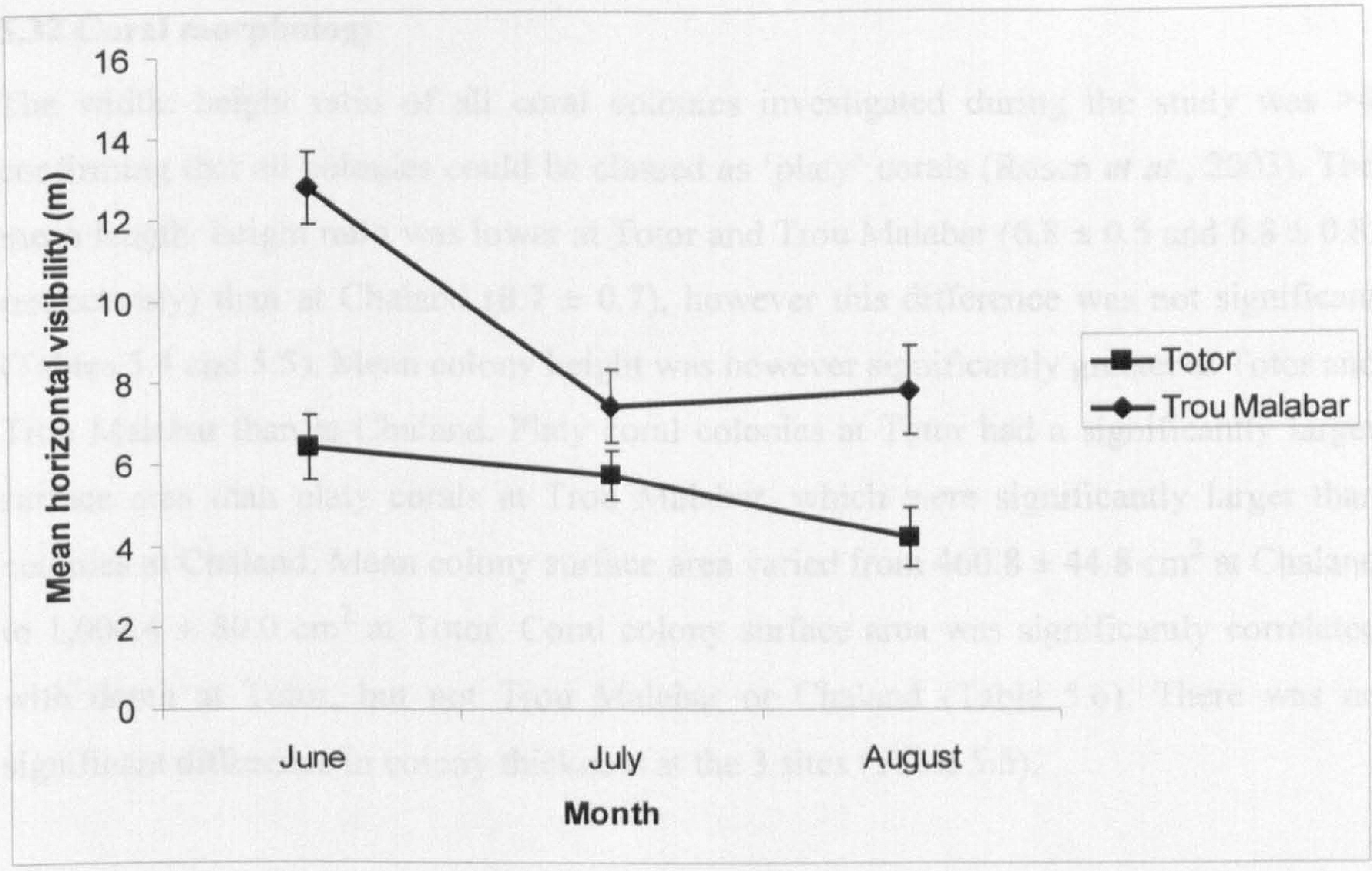


Figure 5.4 The mean horizontal visibility (m) (± SE) at Totor and Trou Malabar during June-August 2003.

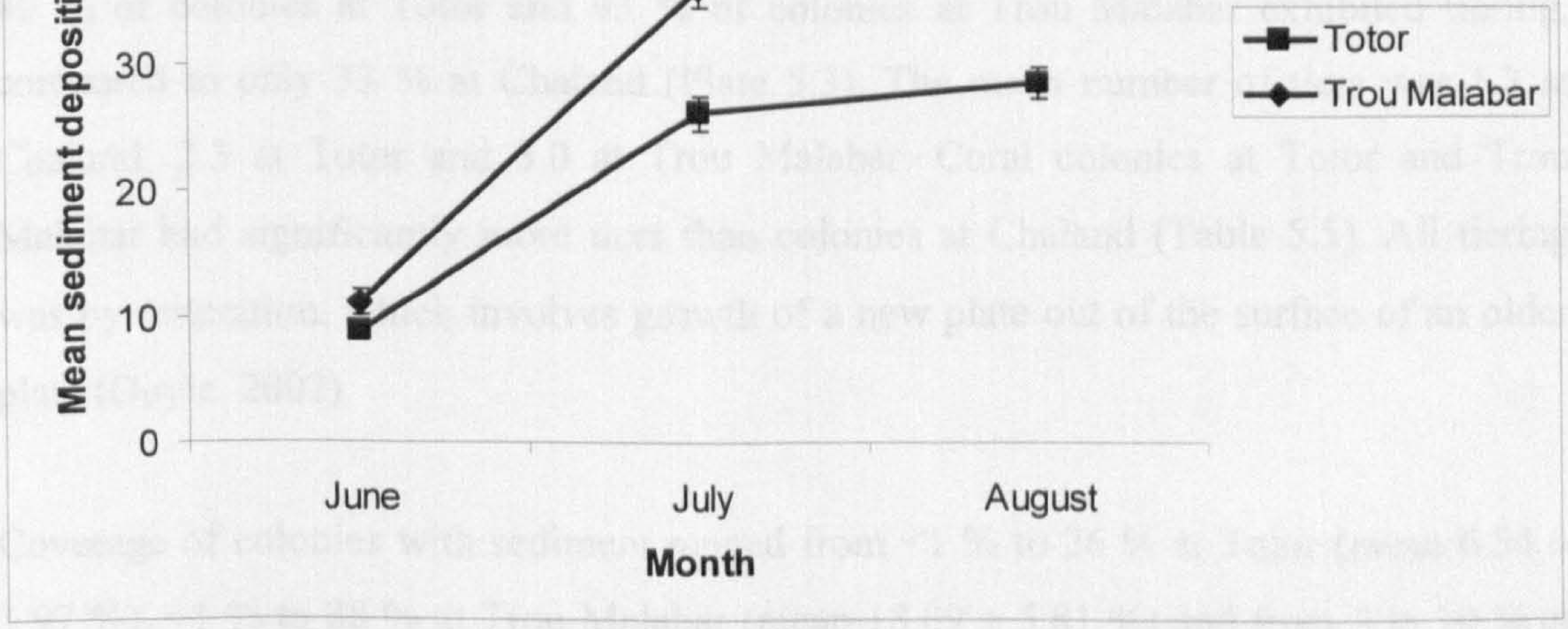


Figure 5.5 The mean sediment deposition (mg cm-2 d-1) (± SE) at Totor and Trou Malabar during June-August 2003.

5.32 Coral morphology

The width: height ratio of all coral colonies investigated during the study was >4 confirming that all colonies could be classed as 'platy' corals (Rosen *et al.*, 2003). The mean length: height ratio was lower at Totor and Trou Malabar (6.8 ± 0.5 and 6.8 ± 0.8, respectively) than at Chaland (8.7 ± 0.7), however this difference was not significant (Tables 5.4 and 5.5). Mean colony height was however significantly greater at Totor and Trou Malabar than at Chaland. Platy coral colonies at Totor had a significantly larger surface area than platy corals at Trou Malabar, which were significantly larger than colonies at Chaland. Mean colony surface area varied from 460.8 ± 44.8 cm^2 at Chaland to 1,004.4 ± 80.0 cm^2 at Totor. Coral colony surface area was significantly correlated with depth at Totor, but not Trou Malabar or Chaland (Table 5.6). There was no significant difference in colony thickness at the 3 sites (Table 5.5).

67 % of colonies at Trou Malabar and 60 % of colonies at Totor were at an angle of >45 ° to the horizontal, compared to only 40 % of colonies at Chaland (Plates 5.1 and 5.2). The mean orientation of coral colonies was highest at Trou Malabar, with a mean angle of 55 ° to the horizontal, compared to 48 ° at Chaland and 45 ° at Totor. However, this difference was not significant (Table 5.5). At Totor, colony orientation was negatively correlated with depth, indicating that colonies become more horizontal with increasing depth (Table 5.6).

80 % of colonies at Totor and 93 % of colonies at Trou Malabar exhibited tiering, compared to only 33 % at Chaland (Plate 5.3). The mean number of tiers was 1.3 at Chaland, 2.3 at Totor and 3.0 at Trou Malabar. Coral colonies at Totor and Trou Malabar had significantly more tiers than colonies at Chaland (Table 5.5). All tiering was by reiteration, which involves growth of a new plate out of the surface of an older plate (Doyle, 2002).

Coverage of colonies with sediment ranged from <1 % to 26 % at Totor (mean 6.54 ± 1.97 %), <1 % to 88 % at Trou Malabar (mean 18.09 ± 5.81 %) and from 0 to 10 % at Chaland (Mean 2.23 ± 0.80 %) (Figures 5.6 and 5.7). Sediment coverage on colonies at Trou Malabar was significantly greater than at Totor and Chaland (Table 5.5). There was no correlation between percentage sediment and length: height ratio or colony orientation at Totor, Trou Malabar or Chaland. At Trou Malabar percentage sediment was significantly correlated with depth of the coral colony (Table 5.6).

Table 5.4 Coral colony morphology measurements (± SE) of 15 *Montipora* spp at each of the 3 study sites. Totor; Tot = TM = Trou Malabar; Chal = Chaland.

	Width: height	Height (cm)	Surface Area (cm^2)	Thickness (cm)	Orientation (°)	No. tiers	% sediment cover
Tot	6.8 ± 0.5	6.4 ± 0.6	1004.4 ± 80.0	0.29 ± 0.03	44 ± 6	2.3 ± 0.3	6.54 ± 1.97
TM	6.8 ± 0.8	6.2 ± 0.7	750.1 ± 66.2	0.46 ± 0.06	55 ± 6	3.1 ± 0.3	18.09 ± 5.81
Chal	8.7 ± 0.7	3.7 ± 0.4	460.8 ± 44.8	0.29 ± 0.06	48 ± 6	1.3 ± 0.1	2.33 ± 0.80

Table 5.5 Statistical analysis results for regeneration rate data for *Montipora* spp. and environmental data measured during July – August 2003. Tot = Totor; TM = Trou Malabar; Chal = Chaland. * indicates a significant difference.

Variables	Test	Test statistic	df	p
Width: height Tot*TM*Chal	1-way ANOVA	2.28 (F)	2	>0.05
Height Tot*TM*Chal	Kruskall-Wallis	12.90 (H)	2	<0.05*
Surface Area Tot*TM*Chal	1-way ANOVA	15.97 (F)	2	<0.05*
Thickness Tot*TM*Chal	Mood's Median	4.34 (X^2)	2	>0.05
Orientation Tot*TM*Chal	1-way ANOVA	0.94 (F)	2	>0.05
Tiers Tot*TM*Chal	Kruskall-Wallis	18.16 (H)	2	<0.05*
Sediment Tot*TM*Chal	1-way ANOVA (Log)	9.73 (F)	2	<0.05*

Table 5.6 Pearson correlation co-efficients (r) for regeneration rates and coral colony data. Tot = Totor; TM = Trou Malabar; Chal = Chaland. * indicates a significant difference.

Variables	r	p
Tot Surface Area*Depth	0.813	<0.05*
TM Surface Area*Depth	0.070	>0.05
Chal Surface Area*Depth	-0.198	>0.05
Tot Orientation*Depth	-0.714	<0.05*
TM Orientation*Depth	0.107	>0.05
Chal Orientation*Depth	-0.156	>0.05
Tot Width: height*Sediment	0.385	>0.05
TM Width: height*Sediment	-0.290	>0.05
Chal Width: height*Sediment	0.195	>0.05
Tot Orientation*Sediment	-0.135	>0.05
TM Orientation*Sediment	-0.075	>0.05
Chal Orientation*Sediment	-0.037	>0.05
Tot Depth*Sediment	0.469	>0.05
TM Depth*Sediment	0.556	<0.05*
Chal Depth*Sediment	-0.368	>0.05

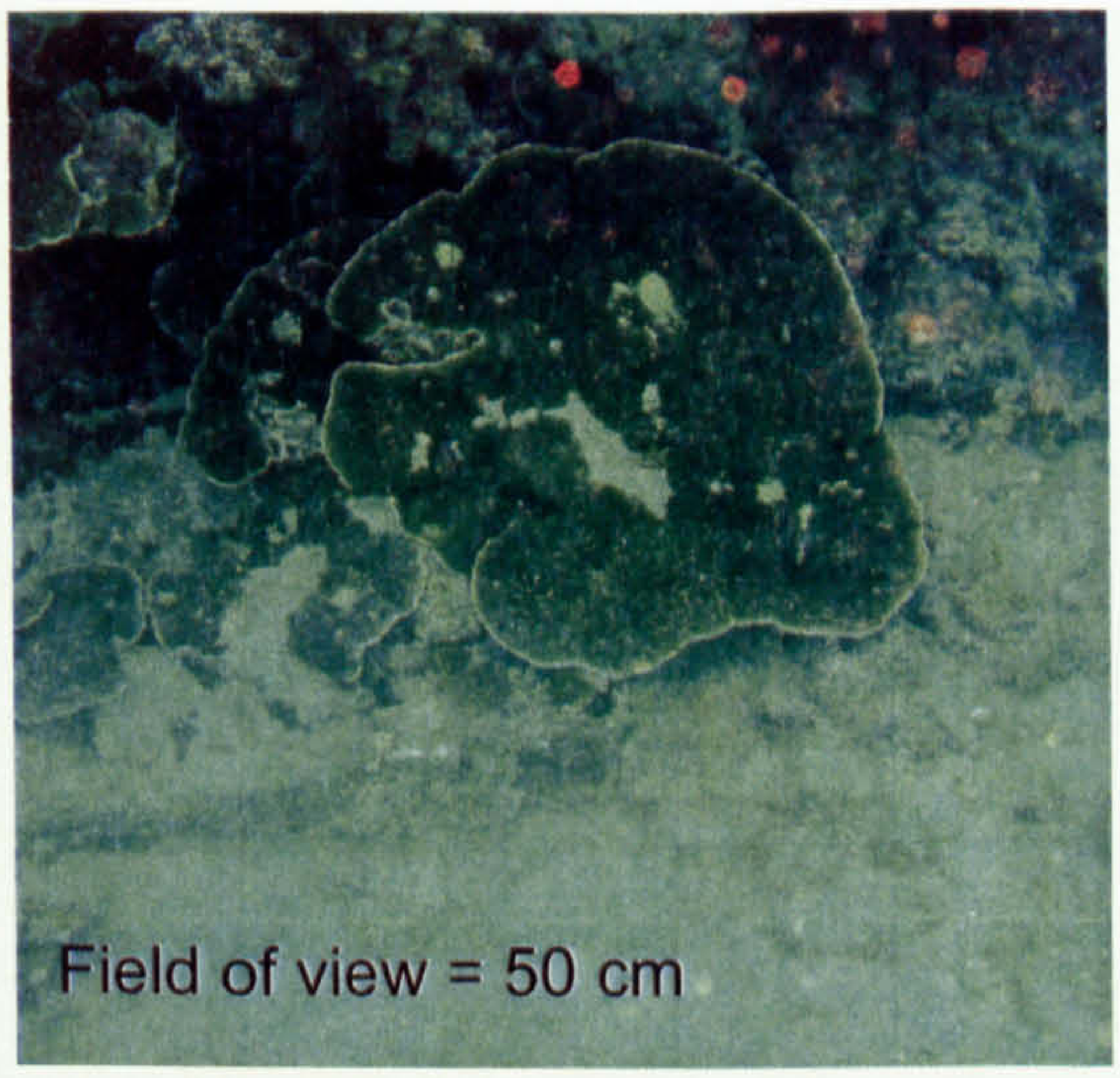


Plate 5.1 A *Montipora aequituberculata* colony at an orientation of 90° to the substrate at Trou Malabar.

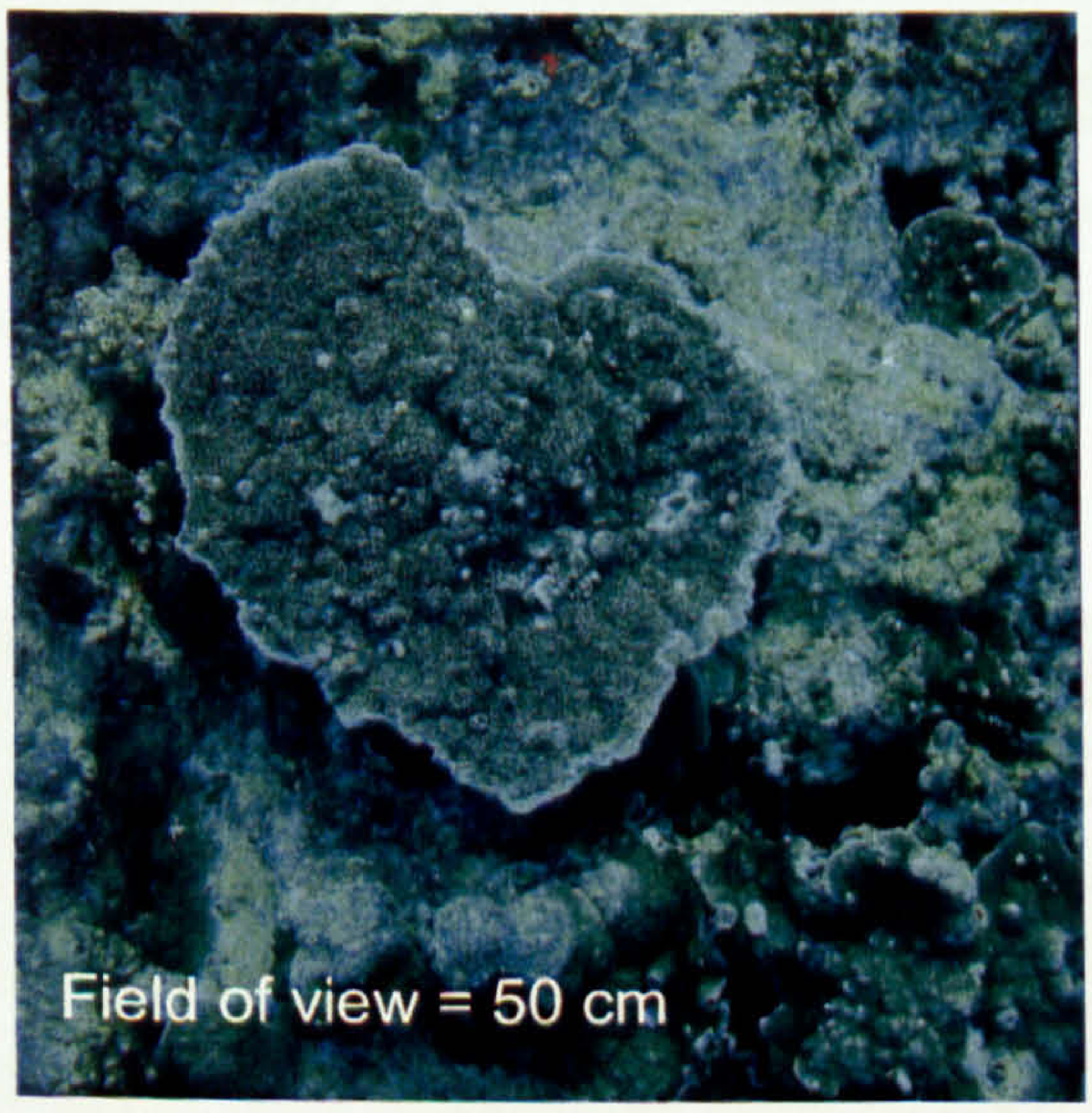


Plate 5.2 A *Montipora aequituberculata* colony at an orientation of 0° to the substrate at Chaland.

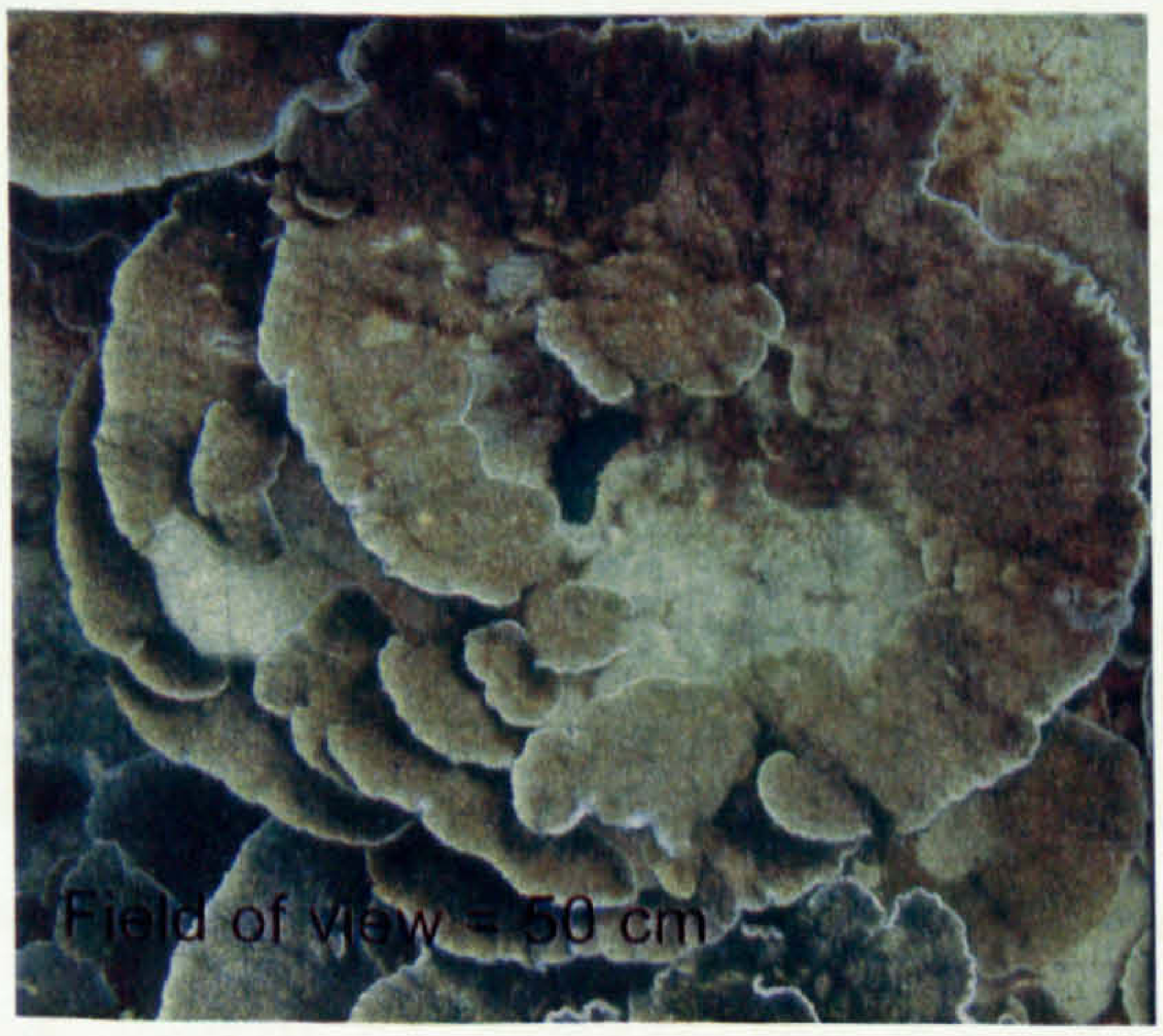


Plate 5.3 A highly tiered *Montipora aequituberculata* colony at Trou Malabar.

Figure 5.6 A platy *Montipora aequituberculata* colony at Totor. The colony has been digitised and the areas of the colony covered in sediment are shown in yellow. This colony has a sediment coverage of 6% its surface area.

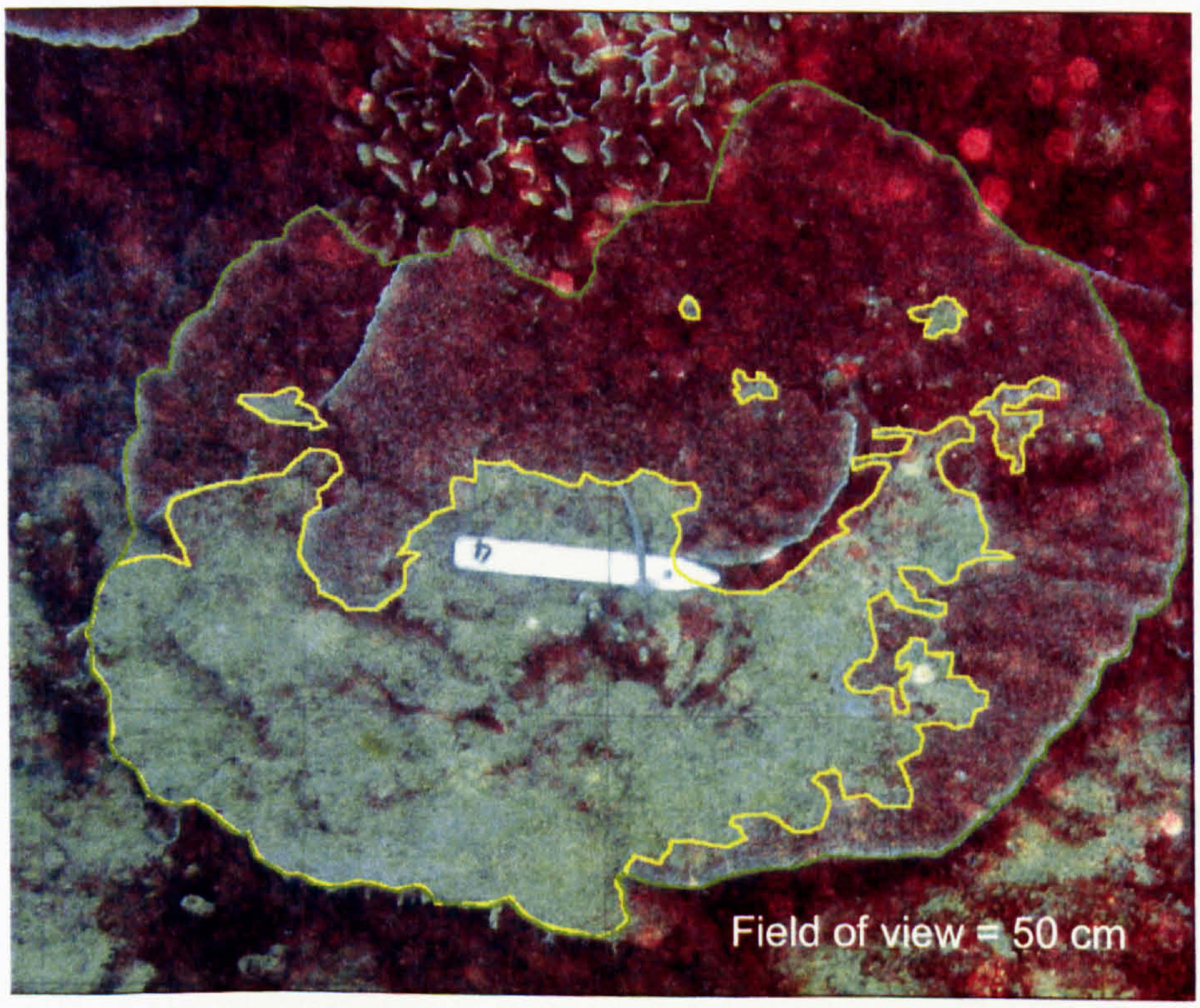


Figure 5.7 A platy *Montipora aequituberculata* colony at Trou Malabar. The colony has been digitised and the areas of the colony covered in sediment are shown in yellow. This colony has a sediment coverage of 45% its surface area.

5.4 DISCUSSION

5.41 Zooxanthellae densities

Zooxanthellae densities measured during this study were considerably lower than mean values measured during June-August in Mauritius (Fagoonee *et al.*, 1999), however the authors do comment that low winter densities were recorded between July and September 1993. Studies have shown the density of zooxanthellae within coral tissues do vary according to illumination (Drew, 1972; McCloskey and Muscatine, 1984; Vareschi and Fricke, 1986; Kaiser *et al.*, 1993; Masuda *et al.*, 1993), sea surface temperatures (Glynn and D'Croz, 1990; Lesser *et al.*, 1990; Jones *et al.*, 2000) and nutrient availability (Hoegh-Guldberg and Smith, 1989a; Muscatine *et al.*, 1989; Stimson and Kinzie, 1991; Stimson, 1997). Sea surface temperatures during this survey period were low (25-23 °C). In addition, rainfall was low during this period, indicating no terrestrial run-off and measurements of nitrate concentrations around Rodrigues have found levels to be low (Lynch *et al.*, 2002). It is therefore, unlikely that zooxanthellae densities were affected by either temperature or nutrients. Hours of sunshine tend to be highest during December-January and lowest during June-July, therefore low illumination at the time of the study may have caused the low densities of zooxanthellae observed.

Underwater visibility was lower at Totor than Trou Malabar during the 3–month study period, suggesting lower light levels at this site. Zooxanthellae densities were higher at Totor than at Trou Malabar during June and August 2003, however were not significantly different during July. Most studies have found a decrease in zooxanthellae density with decreasing light levels (e.g. McCloskey and Muscatine, 1984; Vareschi and Fricke, 1986; Kaiser *et al.*, 1993; Masuda *et al.*, 1993) and this is thought to be because fewer algae reduce shelf-shading therefore increasing the light-capturing efficiency of the algae (McCloskey and Muscatine, 1984; Kaiser *et al.*, 1993). In contrast, Titlyanov *et al.* (2000) showed that *Stylophora pistillata* adapts to low light environments (from 88-12 % surface incident photosynthetically active radiation) by increasing zooxanthellae densities. Data from 2002 indicates that at the survey depth, irradiance was 20-30 % surface values, thus coral colonies at Totor could be adapting to the lower light environment by increasing their zooxanthellae densities.

Zooxanthellae densities at Totor varied over time, with the highest density occurring during June and the lowest density during July. Mean horizontal and vertical visibility did not vary significantly over the study period. It is possible that zooxanthellae are reacting to variations in ambient sunlight as zooxanthellae density at Totor was lowest during July, which had the highest cloud cover and lowest hours of sunshine during the survey period. The decrease in sunshine, combined with the high turbidity at Totor, may have resulted in the observed decrease in zooxanthellae density during July. Measurements of photosynthetically active radiation (PAR) at each of the sites would however be required in order to corroborate this observation.

Sediment deposition was significantly higher at Trou Malabar than at Totor during the study period and this may have resulted in decreased zooxanthellae densities at Trou Malabar. Experimental sediment addition has been shown to cause loss of zooxanthellae in a number of studies. Addition of peat to *Montastrea annularis* resulted in a 22 % reduction in the chlorophyll content of corals, indicating a loss of zooxanthellae (Dallmeyer *et al.*, 1982). Addition of 200 mg cm^{-2} sand to *Astrangia danae* resulted in an initial increase in zooxanthellae densities during the first 4 weeks of the experiment, followed by a decrease in zooxanthellae densities with increasing sediment load (Peters and Pilson, 1985). Fragments of *Montipora peltiformis* covered in sediment showed a continuous decline in numbers of zooxanthellae with time and severe bleaching and necrosis occurred within 24-36 hours of sediment exposure, indicating expulsion of zooxanthellae (Philipp and Fabricius, 2003). Furthermore, sediment deposition at Totor was significantly lower during June when zooxanthellae densities were highest and was high during July, when zooxanthellae densities were at their lowest.

5.42 Coral morphology

Platy corals have been shown to be a common growth form on the reefs in Rodrigues. Doyle (2002) found that platy corals were the most abundant morphology at both Totor and Chaland and Thompson (2003) found that at Totor 83% of *Montipora aequituberculata* colonies were platy compared to 22% at Chaland. This study found that *Montipora* spp. colonies at Totor and Trou Malabar had lower width: height ratios than colonies at Chaland, however this difference was not significant. Doyle (2002), however did find that the mean width: height ratio was significantly lower at Totor than at Chaland and this study found that colony height was significantly greater at Totor and

Trou Malabar than at Chaland. The lower width: height ratio observed by Doyle (2002) at Totor and the greater colony height observed in this study at Totor and Trou Malabar suggests that corals at these sites have steeper colony sides and are tending to become more foliose than colonies at Chaland. Lasker (1980) showed that colonies of *Montastrea cavernosa* with a steep colony surface exhibited efficient passive rejection of sediment and Stafford-Smith and Ormond (1992) also found that gravitational loss of sediment was high in species with strongly inclined plates.

Colonies at Totor were found to have a significantly larger surface area than corals at Trou Malabar, which had a significantly higher surface area than colonies at Chaland. Doyle (2002) also found that colony width was greater at Totor than at Chaland. Porter (1976) concluded that a high surface area: volume ratio provided the optimal colony morphology for light interception therefore, the larger surface area of colonies at Totor is likely to be an adaptation to the low light environment. In addition, colonies at Totor showed a significant correlation between surface area and depth, indicating that surface area increased with increasing depth and thus decreasing illumination. Hughes (1987) also showed that there was an increase in surface area: weight ratio with depth, indicating that deeper colonies were thinner and flatter than corals at shallower depths. There was no significant difference in colony thickness, which is in contrast to Anthony and Hoegh-Guldberg (2003) who showed that platy coral colonies in low light environments are significantly thinner than those in high light environments.

More colonies at Totor and Trou Malabar showed an orientation >45 ° and many were almost vertical to the substrate; at Chaland the majority of colonies were aligned horizontally to the substrate with an orientation <45 °. There was, however found to be no significant difference in mean colony orientation at the 3 sites. Doyle (2002) also found that 77 % of colonies were aligned horizontally (0 °) at Chaland, compared to 36 % at Totor; in contrast 33 % of colonies at Totor were vertical to the substrate (90 °), compared to only 5 % at Chaland. Totor and Trou Malabar had higher sediment deposition than Chaland, and Stafford-Smith and Ormond (1992) noted that on vertical surfaces passive sediment rejection will be aided by gravitational force. Colony orientation was significantly correlated with depth at Totor, indicating that coral colonies became more horizontal with depth. A horizontal orientation provides a greater surface area for light capture and suggests that corals are adapting to lower illumination at depth, by changing their orientation.

Most coral colonies at Trou Malabar and Totor exhibited tiering, compared to only one third of colonies at Chaland and mean number of tiers was significantly greater at Totor and Trou Malabar than at Chaland. Doyle (2002) also found that 76 % of corals at Totor displayed tiering and the number of tiers was significantly greater at Totor than at Chaland. Tiering has been described as a method used by colonies to reduce the effects of sedimentation, by enabling the colony to rise above the sediment accreting at its base (Rosen *et al.*, 2003). Totor and Trou Malabar both had significantly higher sediment deposition than Chaland and so this result supports the theory of Rosen *et al.* (2003). Doyle (2002) however questions this observation as the author found that at Chaland the number of tiers was higher in deeper water, despite low levels of sediment deposition.

Sediment coverage of *Montipora* spp colonies was significantly higher at Trou Malabar than at Totor and Chaland. Trou Malabar also had the highest sediment deposition throughout the 2003 study period. There were no correlations between sediment coverage and colony orientation or width: height ratios suggesting that active sediment mechanisms are also important. Thompson (2003) found that most *Montipora aequituberculata* colonies had low sediment coverage (1-10 %) and that there was no difference in sediment coverage at Totor and Chaland, despite higher sediment deposition at Totor. The author also concludes that for *M. aequituberculata* colony morphology and orientation do not play a significant role in sediment removal, rather that behavioural responses are more important. *M. aequituberculata* has been shown to exhibit poor sediment clearance, and moderate sediment tolerance displaying bleaching after 6 days of sediment coverage of >100 mg cm^{-2} (Stafford-Smith, 1993). It appears therefore, that *M. aequituberculata* colonies at Totor were able to actively remove sediment particles, whereas sediment deposition at Trou Malabar was too high for colonies to efficiently remove all of the settling sediment.

Lasker (1980) demonstrated that fine sediment particles act like a dense liquid and flow off colony surfaces, whereas larger particles are more likely to remain on the colony surface and require active sediment rejection. Hubbard and Pocock (1972) also showed that while most species effectively remove fine sediment (62-500 μm), removal of coarse sediment (500 μm-2 mm) can be less efficient. Furthermore, Stafford-Smith (1993) observed that fine sediments (63-250 μm) are rejected more efficiently than coarse sediments (500 μm-1 mm) and Stafford-Smith and Ormond (1992) found that there was a decline in the ability of corals to clear sediment with cilia as article size increased. This may account for the limited ability of coral colonies at Trou Malabar to remove sediment, however during the survey period sediment at Trou Malabar consisted of a high silt content (17 %) and a low content of coarse particles (31 % >125 μm). Stafford-Smith (1993) and Stafford-Smith and Ormond (1992) however note that, particularly in still water, mucous secretion in response to fine-grained sands and silt may result in a decrease in oxygen diffusion causing anoxia and death of the underlying tissue.

5.43 Summary

The main findings of this study were:

- Zooxanthellae density was significantly higher at Totor than Trou Malabar during June and August. This may be an adaptation to the lower light environment at Totor or corals at Trou Malabar may have experienced loss of zooxanthellae due to sediment stress.
- At Totor, zooxanthellae density was significantly higher during June, possibly due to changes in ambient sunlight. There was however no significant difference in zooxanthellae density over time at Trou Malabar.
- Mean colony height was significantly higher at Totor and Trou Malabar than Chaland. Coral colonies at Totor had a significantly larger surface area than colonies at Trou Malabar and Chaland.
- A greater proportion of coral colonies at Totor and Trou Malabar demonstrated a vertical orientation compared to colonies at Chaland and had significantly more tiers than colonies at Chaland.
- Sediment coverage on coral colonies was significantly greater on corals at Trou Malabar than Totor and Chaland.

5.44 Conclusions

Corals at Totor and Trou Malabar appear to be showing some morphological adaptations to the high sediment/low light conditions, with colonies exhibiting large surface areas to capture maximum light, steeper colony sides to increase passive sediment removal and tiering to increase colony height, thus reducing burial by sediment. At Totor, the *Montipora* colonies appear to be capable of efficiently removing the sediment from their surfaces despite high sediment deposition at the site. In contrast, at Trou Malabar sediment deposition was too high for colonies to effectively remove all of the sediment, resulting in partial mortality of some of the colonies. This suggests that sediment deposition at Trou Malabar during 2003 was higher than usually experienced.

The data do not however indicate any obvious physiological adaptations in terms of changes in zooxanthellae density and it is not clear if zooxanthellae densities are higher at Totor due to lower light levels or if densities are lower at Trou Malabar due to high sediment deposition. Further studies would however be required in order to assess photosynthetic pigment and photosynthetic efficiency at the sites and the study would need to be carried out over a longer time period with more accurate measurements of irradiance and turbidity. Brown *et al.* (1999) state that the greatest correlation of irradiance and zooxanthellae density was at the scale of the day of sampling and therefore mean hours of sunshine are unlikely to show any relationship.

CHAPTER 6. The extent of coral bleaching in Rodrigues

6.1 INTRODUCTION

The previous chapters have assessed the impact of sediment on coral colonies. This chapter will examine the impact of a coral bleaching event, which affected the island during early 2002. The study will assess the geographical extent of the bleaching event, vulnerable species and the impact to the reefs one year later.

Since extensive coral bleaching across the Pacific Ocean was first described by Glynn in 1984 there has been an increasing incidence of reports of coral bleaching throughout the tropics. Repeated coral bleaching has occurred in the Caribbean, Indian and Pacific Oceans on a regular basis (Brown, 1997b), with severe world-wide bleaching events occurring in 1982-83 (Glynn, 1984; Harriott, 1985a; Oliver, 1985; Glynn and Colgan, 1992), 1986-88 (Williams and Bunkley-Williams. 1990) and 1997-98 (Wilkinson, 1998; Hoegh-Guldberg, 1999; Wilkinson *et al.*, 1999; Wilkinson, 2000a; Goreau *et al.*, 2000). Coral bleaching originally referred to the loss of brown pigment by corals (Yonge and Nichols, 1931). More recently, research has shown that coral bleaching may result through either loss of zooxanthellae by corals (Hoegh-Guldberg and Smith, 1989b; Glynn and D'Croz, 1990; Lesser *et al.*, 1990; Le Tissier and Brown, 1996) and/or the loss of photosynthetic pigment per zooxanthella (Hoegh-Guldberg and Smith, 1989b; Lesser *et al.*, 1990; Jones *et al.*, 2000). Bleaching causes corals to turn white or pale because the low concentration of pigments allows the limestone skeleton to become visible through the transparent tissue (Goreau and Hayes, 1994). Bleaching is not limited to scleractinian corals, but also occurs in hydrocorals, soft corals, sea anemones (Williams and Bunkley-Williams, 1990), bivalve molluscs (Addessi, 2001) and sponges that host photosynthetic cyanobacteria (Vicente, 1990).

6.11 Causes of coral bleaching

Coral bleaching is a general stress response that may result from a variety of environmental conditions and anthropogenic stresses. It has been suggested that coral bleaching is a seasonal phenomenon occurring at certain times of the year when seawater temperatures or sunlight are maximal (Oliver, 1985). Fagoonne *et al.* (1999) showed that in a lagoon in Mauritius there is a large seasonal variability in the zooxanthellae population of *Acropora formosa* (*muricata*) with regular episodes of low densities occurring in the spring and summer. Fitt *et al.* (2000) also found seasonal cycles in the densities of zooxanthellae in corals in the Bahamas. All colonies sampled experienced loss of zooxanthellae during the summer period and they suggest that corals worldwide exhibit similar seasonal cycles. These seasonal changes are probably gradual and depend on changes in the physical variables of the near environment (Hoegh-Guldberg, 1999). In such cases where only partial bleaching occurs, zooxanthellae remaining within the live tissues re-grow when conditions change, allowing the coral to recover (Quinn and Kojis, 1999). However, under certain conditions a sudden reduction in the density of zooxanthellae may result in greater rates of loss from the symbiotic hosts (Hoegh-Guldberg and Smith, 1989b). A variety of different stresses have been suggested as being potentially responsible for causing coral bleaching. Localised bleaching events have been associated with bacterial and other infections (Kushmaro *et al.*, 1996), chemicals such as cyanide (Jones and Hoegh-Guldberg, 1999), solar radiation (Fisk and Done, 1985; Harriott, 1985a), sea level drops (Glynn, 1976), reduced salinity (Goreau, 1964), increased turbidity (Rogers, 1983) and temperature changes (Coles and Jokiel, 1978). In most cases the key environmental variables remain poorly defined. Recent work however, highlights increased sea surface temperatures and solar radiation (including ultraviolet radiation) as the most common factors believed to be responsible for large-scale coral bleaching (e.g. Glynn, 1984; Brown and Suharsono, 1990; Brown *et al.*, 1996; Winter *et al.*, 1998; Quinn and Kojis, 1999; Spencer *et al.*, 2000).

6.12 Increased sea surface temperatures

The majority of large-scale bleaching events over that last 2 decades have been linked to increased Sea Surface Temperatures (SST) (e.g. Glynn, 1984; Brown and Suharsono, 1990; Brown *et al.*, 1996; Winter *et al.*, 1998; Quinn and Kojis, 1999; Spencer *et al.*, 2000) and in particular to 'HotSpots', areas where SSTs exceed long-term averages by more than 1 °C during the warmest months (Goreau and Hayes, 1994). Large-scale correlative field studies and analysis of historical SST data provide further evidence that elevated sea temperature is the primary factor triggering coral bleaching. *In situ* observations combined with the US National Oceanographic and Atmospheric Administration (NOAA) satellite-derived sea surface temperature records show that at 7 sites in the Caribbean, mass bleaching events took place when the monthly mean temperature was approximately 1 °C above average during the warmest months (Goreau and Hayes, 1994). Analysis of NOAA's Multi-Channel Sea Surface Temperature data for Bermuda indicates that severe coral bleaching during 1988 occurred when SSTs reached 28.5 °C and remained above 28.1 °C for 6 weeks (Montgomery and Strong, 1994). Moderate bleaching events also occurred in 1990 and 1991 when SSTs reached 28.1 °C and 28.3 °C respectively, causing the authors to conclude that bleaching events occur when SSTs cross a local temperature threshold. In the Andaman Sea, analysis of SST data revealed that the two incidences of extensive coral bleaching occurred in years when the highest seasonal temperatures were recorded, again suggesting that bleaching occurs when average temperature rises above a local threshold (Brown *et al.*, 1996). Analysis of monthly mean Sea Surface Temperature (SST) records from Puerto Rico for the thirty year period 1966-1995 also indicates that severe bleaching occurred when temperatures exceeded the long term mean during the period of maximum annual temperature (Winter *et al.*, 1998).

Analyses have also shown that the mass bleaching episodes appear to be associated with disturbances to the El Niño-Southern Oscillation (ENSO), which causes warm water pools to form in the eastern Pacific (Glynn, 1984; Brown and Suharsono, 1990; Glynn and Colgan, 1992; Fagerstrom and Rougerie, 1994; Goreau and Hayes, 1994; Podestá and Glynn, 1997; McClanahan, 2000). Williams and Bunkley-Williams (1990) suggest that coral bleaching is in fact a cyclic phenomenon occurring every 3-4 years, depending on ENSO activity. Coral bleaching events occurred in 1982/83, 1986/87 and 1991/92; all three years were El Niño years (Goreau and Hayes, 1994). Coral bleaching in French Polynesia occurred in 1991 and 1994, both of which were related to an ENSO anomaly (Fagerstrom and Rougerie, 1994). SST records from 1970-1994 in Panamá and 1073-1994 in the Galápagos Islands indicate that in both areas all bleaching events were associated with El Niño warming events (Podestá and Glynn, 1997).

Moreover, Lough (2000) demonstrated that the average maximum SST was significantly correlated with the average annual ENSO index between 1903-1999. In the severe mass bleaching event of 1997-1998 most incidents of bleaching were associated with the highest tropical SSTs and the strongest ENSO disturbance on record (Hoegh-Guldberg, 1999; Wilkinson *et al.*, 1999; Goreau *et al.*, 2000; Spencer *et al.*, 2000; Wilkinson, 2000b). Although the patterns of coral bleaching do appear to be strongly influenced by El Niño, coral bleaching episodes have also occurred in non-El Niño years suggesting that other factors may be involved. Using a simple oceanographic-ecological model Huppert and Stone (1998) showed that in many cases the 3-7 year ENSO cycle is the ultimate source of mass coral bleaching but that short time-scale weather fluctuations can introduce noise perturbations into the system triggering local bleaching events in non-El Niño years. Other recent work shows that the 1982/83 and 1997/98 El Niños may have been so severe due to Pacific climatic oscillations of warming and cooling over 10-20 years, combined with global warming. These oscillations are not always in phase with El Niño events but coincided with them in these years, boosting their intensity (Kerr, 1999; McPhaden, 1999). In the Indian Ocean, studies show that SST may be more influenced by internally generated climatic oscillations than by ENSO activity (Saji *et al.*, 1999; Webster *et al.*, 1999). These authors argue that the Indian Ocean exhibits strong coupled ocean-atmosphere-land interactions, which are capable of producing a change in the longitudinal SST gradient. Saji *et al.* (1999) show that there is little relationship between this oscillation and El Niño events but that it coincided with them in 1998.

Coral bleaching events are however not simply triggered by high SSTs and tend to coincide with periods of low wind velocity, calm seas and low turbidity when conditions favour heating of shallow waters and high solar penetration. (e.g. Brown and Suharsono, 1990; Williams and Bunkley-Williams, 1990; Glynn, 1991; Goreau and Hayes, 1994). Oliver (1985) suggests that bleaching on the Great Barrier Reef occurs every summer due to a synergistic effect between high summer seawater temperatures and high light levels. Berkelmans and Oliver (1999) conclude that bleaching on reefs on the Great Barrier Reef during 1998 was also caused by a combination of elevated sea temperature and high solar radiation, and on the inshore reefs by lowered seawater salinity. Drollet *et al.* (1994, 1995) suggest that severe bleaching events occur when high total solar irradiance coincides with elevated seawater temperature. They also propose that bleaching is a synergistic interaction between temperature and UV-B radiation, possibly associated with total solar irradiance. Furthermore, Jones *et al.* (1998) demonstrate that light intensifies the extent of damage caused by thermal stress. They show that although temperature has to be higher than normal for a mass bleaching event to occur, light will cause damage even at normal intensities when water temperature is elevated above a critical maximum. Thus the extent of damage during bleaching will be directly correlated with the intensity of the light and elevated temperature will have a reduced effect if corals are shaded from normal sunlight (Hoegh-Guldberg, 1999; Hoegh-Guldberg and Jones, 1999).

6.13 The impacts of coral bleaching on coral reefs

The immediate effects of bleaching on the host are a decline in zooxanthellae density, loss of chlorophyll pigments, an increase in respiration rate and a decline in coral protein, lipid and carbohydrate (Coles and Jokiel, 1977; Glynn *et al.*, 1985; Hoegh-Guldberg and Smith, 1989b; Glynn and D'Croz, 1990; Goreau and Macfarlane, 1990; Jokiel and Coles, 1990; Szmant and Gassman, 1990). In addition, there are a number of non-lethal responses, which may have long-term effects. These include a decrease in coral growth and calcification (Goreau and Macfarlane, 1990), impairment of reproduction (Szmant and Gassman, 1990), and tissue necrosis (Glynn and D'Croz, 1990). Sub-lethal stress caused by coral bleaching may also make corals more susceptible to infection by a variety of pathogens resulting in disease outbreaks and subsequent mortality (Kushmaro *et al.*, 1996; Goreau, 1998). Long-term effects can lead to reduced cover of important reef-building species and to an increased abundance of species that erode reef frameworks (Glynn, 1993).

Reduced growth of bleached corals decreases the capacity of corals to compete favourably for space with other reef benthos such as algal turf, coralline algae, macroalgae, sponges, bryozoans and tunicates (Glynn, 1993). If the intensity of the bleaching event is not great then many corals will recover after a few weeks. An intense episode can, however, cause massive bleaching and the death of corals and other reef organisms (Glynn, 1985). Many of the faster growing branching coral species with high metabolic rates are more susceptible to bleaching and these species may be replaced by the less susceptible slower growing species (Brown and Suharsono, 1990; Jokiel and Coles, 1990; Williams and Bunkley-Williams, 1990; Edwards *et al.*, 2001). When bleached corals die, space becomes available and is often colonised by non reef-building organisms such as macro-algae (Shulman and Robertson, 1996; Ostrander *et al.*, 2000), green or brown fast-growing filamentous algae (Yap and Gomez, 1988; Lindén, 1998), and colonies of blue-green algae (Porter and Meier, 1992; Smith, 1988). These algae are grazed by many different organisms and the reef community is likely to go through a relatively rapid succession, with different species of opportunistic organisms such as sponges, bryozoans and tunicates dominating the reef (Lindén, 1998; Nzali *et al.*, 1998). Studies conducted 1-2 years after the 1998 mass bleaching event report reefs dominated by turf, macro- and coralline algae (Goreau, 1998; Arthur *et al.*, 2000; Bigot *et al.*, 2000; Obura *et al.*, 2000; Turner *et al.*, 2000c; Wilkinson, 2000b; McClanahan *et al.*, 2001), with other benthic organisms such as corallimorpharian anemones (Kuguru and Muhando, 2000; Obura, 2000; Turner *et al.*, 2000c; Wilhelmsson, 2000), zoanthids, soft corals (Turner *et al.*, 2000c) and tunicates (Wilhelmsson, 2000) dominating other reefs. McClanahan (2000) found benthic cover in the Maldives in April-May 1999 to be dominated by coralline and benthic algae (68 % of total cover). Comparison with past data suggests that hard coral cover had decreased from ~60 % in 1958 to just 8 % of the substrate in 1998.

The dead reef framework also provides shelter and grazing surfaces for many potentially destructive organisms such as boring sponges and mussels, sea urchins and fishes which weaken the calcium skeleton, resulting in severe bioerosion of the reef (Schumacher, 1977; Scott *et al.*, 1988; Glynn, 1991; Lindén, 1998). If consolidation by coralline algae does not take place then the coral framework will eventually collapse and degenerate into rubble. Reaka-Kudla *et al.* (1996) found that on reefs in the Galapagos Islands affected by the 1982/1983 coral bleaching event, bioerosion of the reefs by the sea urchin *Eucidaris thouarsii* was causing rapid destruction of the reef framework. They observed that this bioerosion was removing more coral skeleton than was being produced and recorded rapid changes in the topography of the reef. By 1993 Glynn (1994) reported that most of the reef structures had eroded and fallen apart, accelerated by the continued abundance of *E. thouarsii*. Many reefs in the Indian Ocean severely affected by the 1997/98 coral bleaching event have already been reduced to unconsolidated coral rubble (Turner, 1999; Bigot *et al.*, 2000; Turner *et al.*, 2000c; Wilkinson, 2000b).

6.14 The 1997-1998 bleaching event

During 1997-1998 coral reefs were subjected to the most geographically widespread and probably most severe bleaching event in recorded history. Bleaching occurred on coral reefs throughout the Indian Ocean, the Middle East, Southeast and East Asia, the Caribbean, the Far West and Far East Pacific and the Atlantic Ocean (Wilkinson *et al.*, 1999). Many reefs previously regarded as pristine were seriously affected. The global mean surface temperature in 1998 was the highest on record, with sea surface temperatures reaching up to 40 °C in some areas (Wilkinson, 1998). There appears to be some correlation between this bleaching event and one of the strongest El Niño events of the century. In many areas sea surface temperatures rose 2 °-3 °C above the normal seasonal maximum and in some locations 4 °-6 °C increases were recorded. Warm surface waters were first observed in the Indian Ocean in satellite images from the US

National Oceanographic and Atmospheric Administration (NOAA) in January 1998. The first bleaching was reported off the east coast of Africa and Madagascar one month later (Wilkinson *et al.*, 1999). This warm pool of water increased in size and moved northwards during the first six months of 1998, causing bleaching throughout the Indian Ocean. The start of bleaching in the Indian Ocean in February 1998 coincided with a large El Niño event. Bleaching then started in Southeast and East Asia as the South China Sea and Pacific Ocean started to heat up, coinciding with a strong La Niña in June (Wilkinson, 1998).

The most severe bleaching ever reported in the Indian Ocean occurred around the islands of the Maldives, the Seychelles and Sri Lanka and on the coasts and islands of India, Kenya and Tanzania, where up to 95 % of corals bleached and subsequently died (Wilkinson *et al.*, 1999). Bleaching was most pronounced in shallow water, less than 15 metres deep and particularly affected fast-growing species with branching morphologies; researchers reported that virtually all species in the genera *Acropora, Seriatopora, Stylophora, Millepora* and *Pocillopora* were killed over large regions (Goreau *et al.*, 2000). Slower growing species such as *Porites* also bleached, however, many recovered within 1 to 2 months (Wilkinson *et al.*, 1999). Soft corals, anemones, tridacnid clams and some sponges were also affected. By 1999, 80 to 90 % of the bleached corals in the more severely affected areas had died, including previously resistant species and many of the remaining corals were still bleached or had reduced colour. In 1999 it was predicted that this bleaching event had reduced the percentage of live coral across the whole Indian Ocean from 80 % in 1997 to 64 % (Wilkinson *et al.*, 1999). More recent estimates suggest that 27 % of the world's coral reefs have been "effectively lost", with problems being most severe in the wider Indian Ocean where there has been 59 % loss. It is predicted that recovery from the bleaching event may take 2-50 years for reefs to recover and will depend on few or no repeats of this extreme event (Wilkinson, 2000a).

In Kenya and Tanzania bleaching started in March 1998 and continued during April. Bleaching was most extreme in shallow water (90-100 %) but was also 50 % or more at 20 m. Coral mortality was high; reefs have been reduced to between 10 to 50 % of previous levels and algal cover has increased up to 200 % (Lindén and Sporrong, 1999). The Maldives experienced relatively severe, rapid bleaching between late April to May 1998. 80 % of corals were totally or partially bleached in shallow water and 30-45 % at depths of between 10 and 30 metres. Reports indicate that 95 % of mostly *Acropora* communities were dead and soft corals, anemones and giant clams were partially bleached (Wilkinson *et al.*, 1999). On Chagos, live coral cover was reduced to 12 %, and 50 % of the dead corals had turned into loose rubble by early 1999; most *Acropora* colonies were dead and soft corals were almost totally eliminated (Sheppard, in Wilkinson, 2000b). In the Comoros there was 40-50 % coral bleaching, with *Acropora* species again being the worst affected (Bigot *et al.*, 2000). Bleaching in Sri Lanka started in mid April and by late April 80 % of species on the reef flat were bleached. Some recovery was seen in June, but most branching and tabulate *Acropora* and *Pocillopora* colonies were dead (Wilkinson, 1998). In India there was 90 % mortality of corals on the outer-atoll seaward slopes of the Lakshadweep Islands and in the Andaman Islands more than 90 % of massive corals and more than 75 % of branched corals were bleached (Ravindram *et al.*, 1999). In Socotra corals bleached in May and by November all shallow tabular and branching corals were dead and coral rubble was washed ashore (Turner, 1999). Many of these reefs, for example in the Maldives and Kenya, are now showing encouraging signs of recovery, however, reefs in Chagos, Sri Lanka, India and parts of Kenya have not yet recovered (Wilkinson, 2000b).

6.15 Coral bleaching in Mauritius and Rodrigues

The coral reefs of Mauritius and Rodrigues were some of the few reef areas in the Indian Ocean to escape the mass coral bleaching event of 1997-1998 (Turner *et al.*, 2000b). Sea Surface Temperature (SST) anomaly charts produced by NOAA suggested that bleaching may have occurred on reefs surrounding these islands. A rapid assessment of the status of the coral reefs in Mauritius during April 1999 (Turner *et al.*, 2000b) and a Reef Check survey in Rodrigues during September 1999 (Vogt *et al.*, 1999) however showed that the reefs were generally healthy with no large areas of dead standing coral. A study by Moothien Pillay *et al.* (2002b) in Mauritius confirmed that coral bleaching had been mild, affecting <10 % of coral colonies and that the majority of colonies had recovered. Analysis of meteorological data showed that during the period of elevated SST, unstable weather associated with Cyclone *Anacelle* caused high cloud cover, very high rainfall and lower hours of sunshine than normally experienced at that time of year. It is suggested that these unsettled conditions mitigated against severe bleaching during 1998 (Turner *et al.*, 2000b).

During the last 2 weeks of February 2002, Rodrigues experienced very warm temperatures, clear skies and calm seas. *In situ* sea surface temperatures were high and reached up to 32 °C in the shallow lagoon (*pers obs.*). Anecdotal evidence of coral bleaching in Mauritius and Réunion was reported on the Coral-list listserver during March. Moothien Pillay (Coral-list, 2002) reported that at one site on the east coast of Mauritius, most of the tabular corals had bleached and completely died. She also commented that most adult eels, holothurians, juvenile fish and crustaceans had also died and were either floating to the surface or lying on the seabed. Rard (Coral-list, 2002) reported that coral bleaching had also occurred at two sites around Réunion. Quod (Coral-list, 2002) added that Réunion had been experiencing a mass fish kill event since February.

In Rodrigues, a mass fish kill was reported by local fishermen on 24th February; dead fish and eels were observed floating on the surface of the water on 25th February. On 5th March 2002 extensive coral mortality was observed on the shallow reef flat at Trou Malabar (Turner, *pers comm.*). Coral mortality was observed from the shallow reef crest to a depth of about 2 m. All tabulate and branching *Acropora* colonies were dead and had been very recently overgrown with algae. An even and short layer of filamentous algae covered all of the dead corals, indicating that death had probably occurred just days before the observations were made. Some corals, especially *Pocillopora eydouxi, Pocillopora verrucosa* and *Pocillopora damicornis* were white with no algal growth and some had pink and purple colour remaining at the ends of the branches (Plates 6.1-6.6).

6.16 Aims and objectives

This study will investigate the severity of the coral bleaching event in Rodrigues considering geographical and species-specific variations in vulnerability to bleaching, in order to make predictions about the future of the coral reefs in Rodrigues. This will be achieved by:

- Assessment of the geographical extent of the coral bleaching event around Rodrigues using rapid assessment techniques.
- Determination of the coral species which are most vulnerable to coral bleaching.
- Examination of changes in reef structure one year after the bleaching event.
- Quantification of the degree of bioerosion occurring one year after the bleaching event.

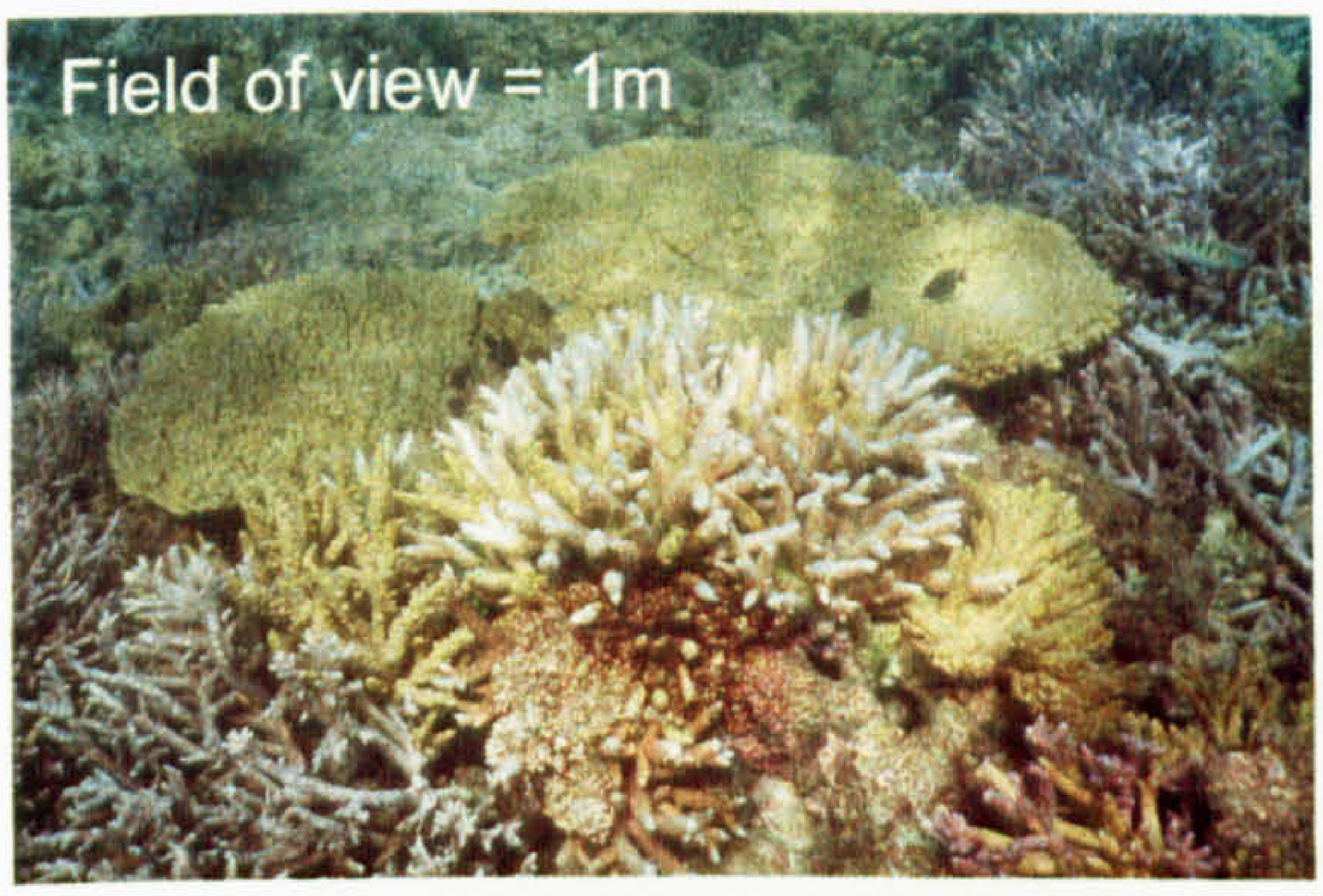


Plate 6.1. A branching *Acropora* colony exhibiting partial bleaching with tabular *Acropora* colonies exhibiting total mortality. Photo by Dr. J. Turner.

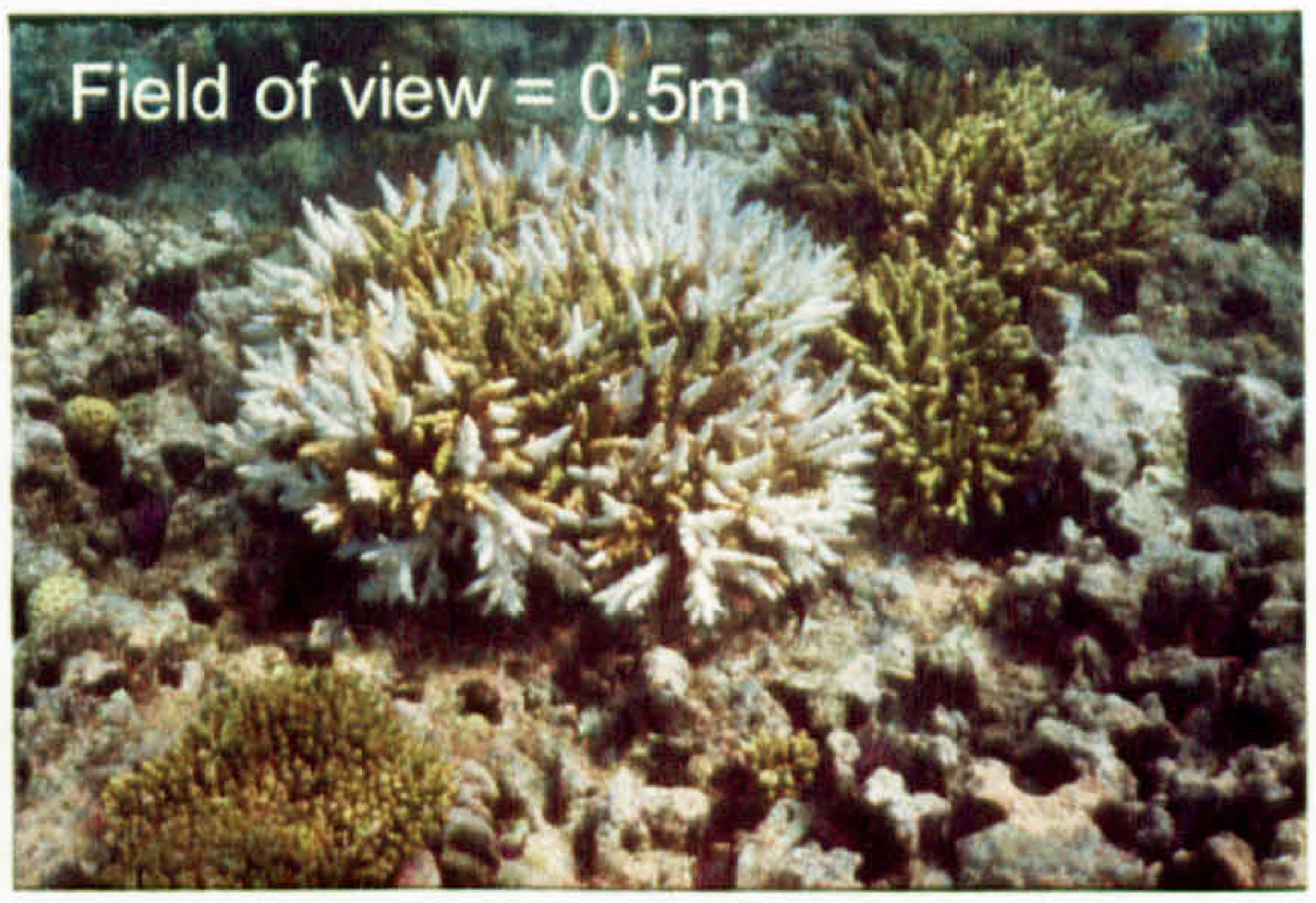


Plate 6.2. A completely bleached *Acropora* colony with partial mortality of lower parts. Photo by Dr. J. Turner.

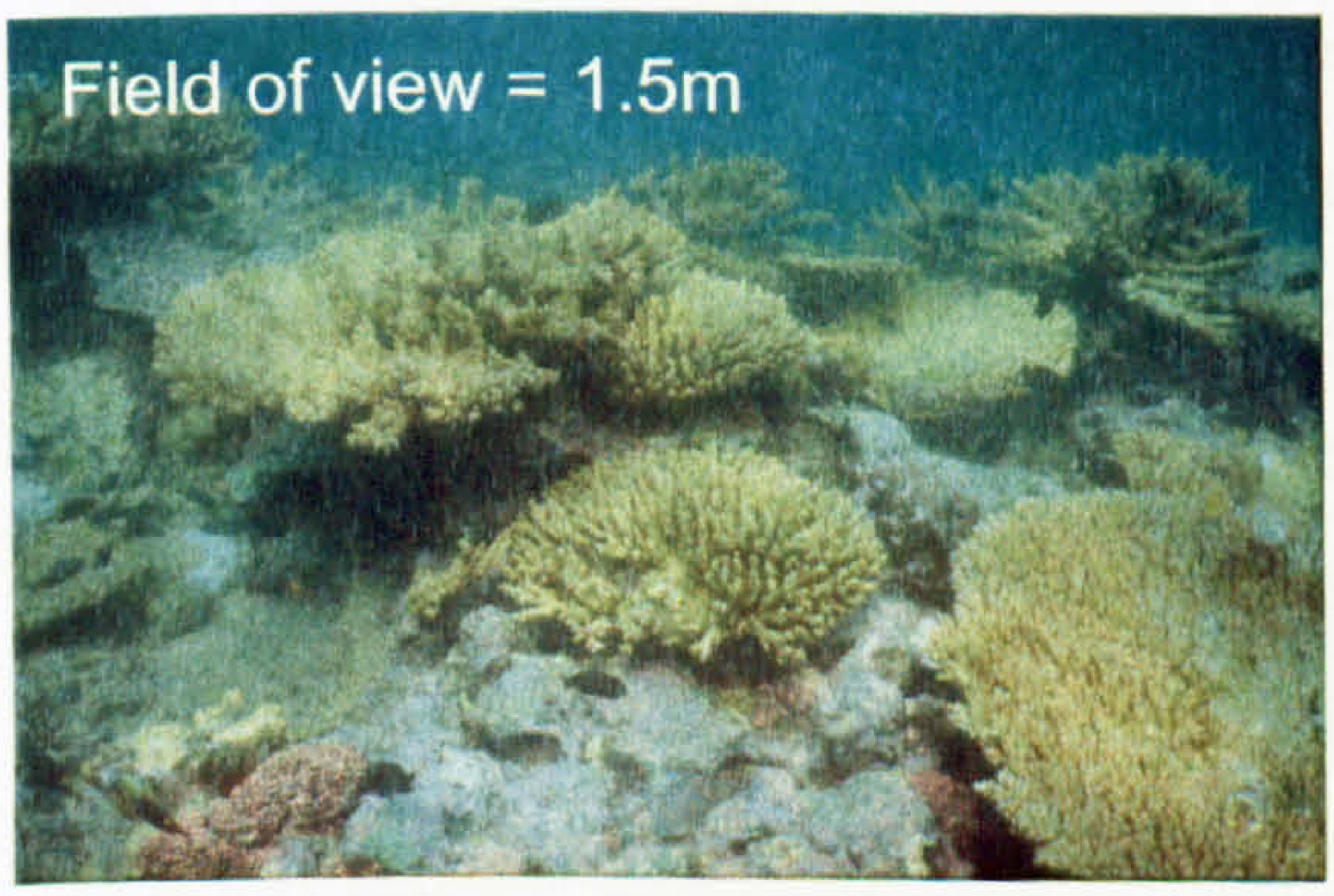


Plate 6.3. Complete mortality of branching and tabular *Acropora* colonies. Photo by Dr. J. Turner.

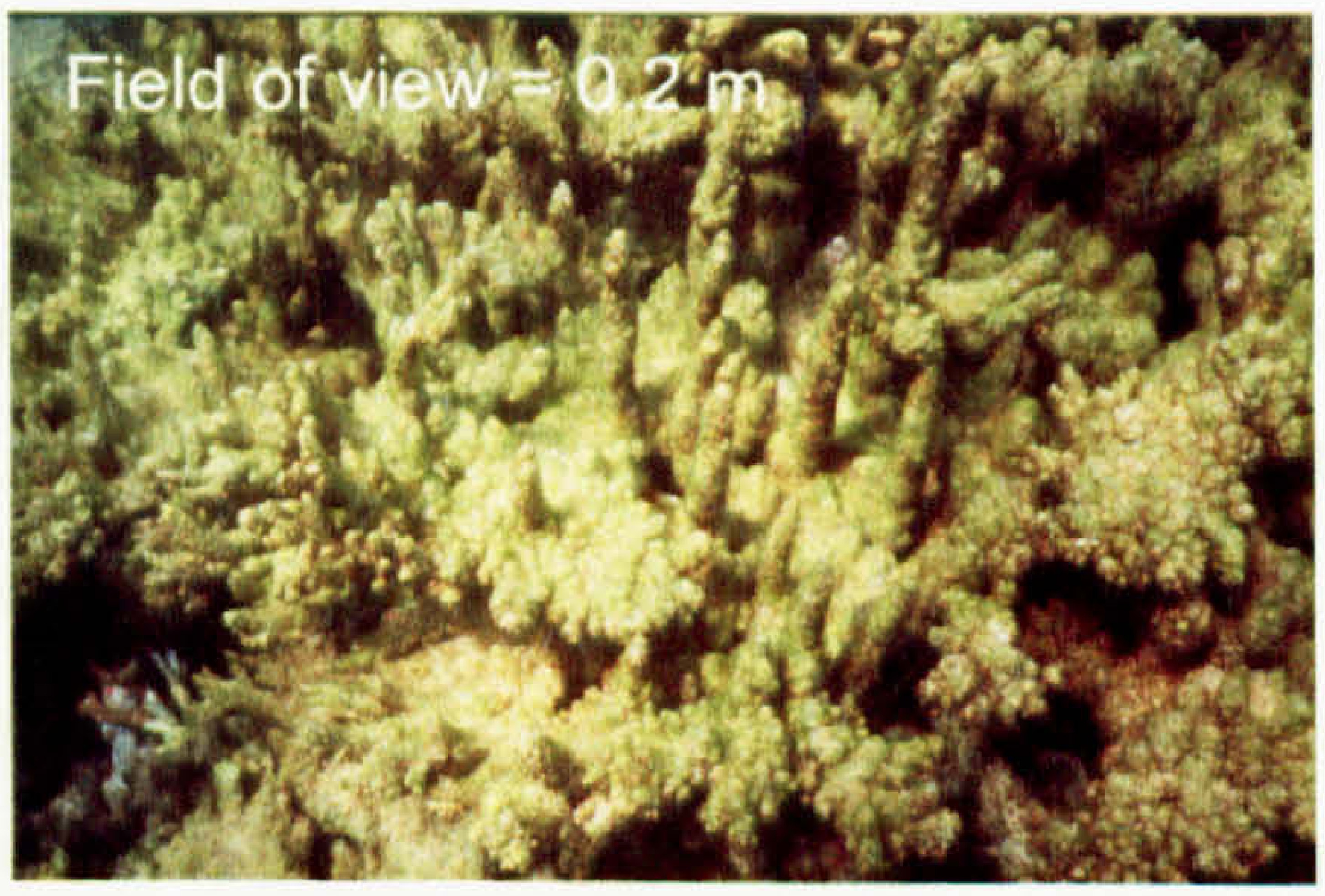


Plate 6.4. A close-up of an *Acropora abrotanoides* colony showing the filamentous algae covering the dead coral. Photo by Dr. J. Turner.

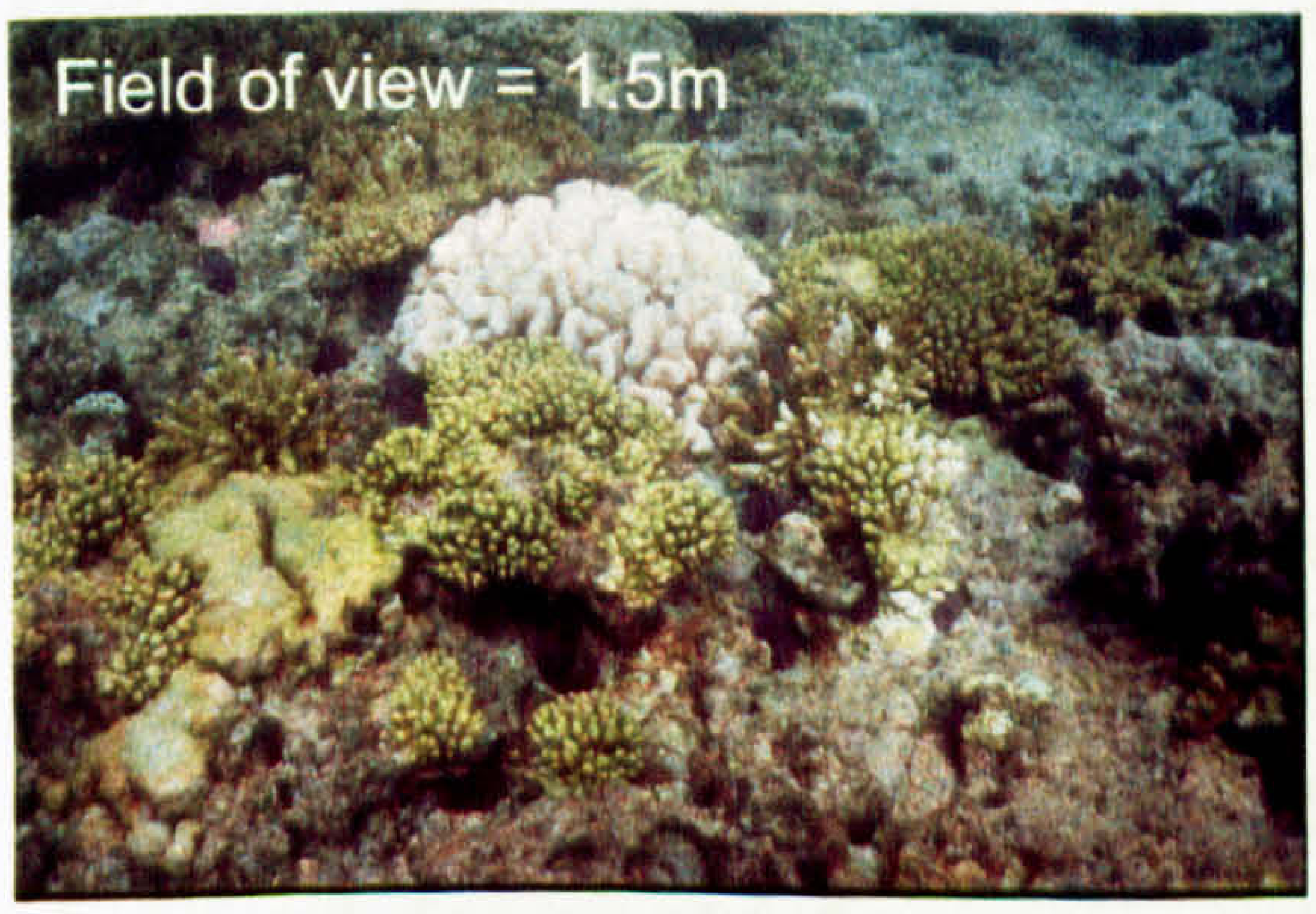


Plate 6.5. A completely bleached *Pocillopora* colony. Photo by Dr. J. Turner.

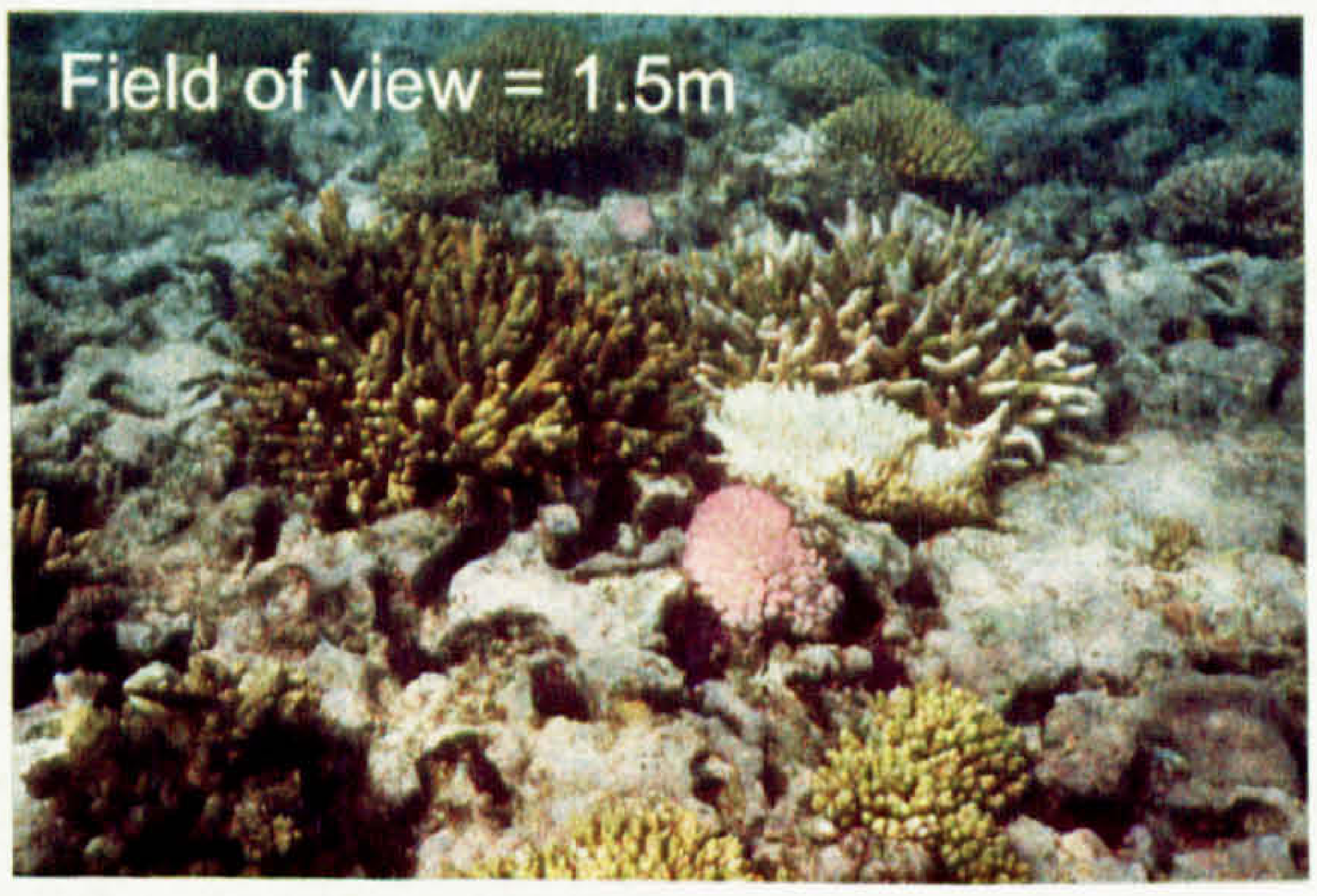


Plate 6.6. A partially bleached *Pocillopora* colony with pink colour remaining at the tips of the branches. Photo by Dr. J. Turner.

6.2 METHODS

6.21 Initial assessment

In order to make an estimate of the extent of coral bleaching and coral mortality around the whole of Rodrigues, rapid assessment surveys were carried out at 22 sites around the island between 6th and 15th March 2002 (Figure 6.1). Sites were identified on the reef flat, reef front and on the patch reefs within the lagoon. The location of the site was obtained using a hand-held Global Positioning System (GPS) (Magellan GPS 315, datum set to WGS-84) and weather conditions, exposure and tidal height were recorded. Surface water temperature was also recorded using an Aquatemp Waterproof Thermometer (0.1 °C).

Timed surveys of between 30 and 60 minutes were carried out using snorkelling techniques. Surveys were carried out by a team of 4 personnel, including staff and volunteers from the local NGO, Shoals Rodrigues. Surveyors swam across the reef area in a zigzag pattern assessing reef composition and health over a 100 x 100 m area. Surveys on the reef flat were carried out at high tide so that surveyors could swim into the lagoon over the reef front and thus access bleaching on the reef front down to a depth of 6-8 m. Two levels of visual survey were made (Devantier *et al.*, 1998, Turner *et al.*, 1999). Broad scale physical and biological features of the reef were first recorded using a 6-point semi-quantitative scale (0 = 0 %; 1 = <1 %, 2 = 1-10 %, 3 = 11-30 %, 4 = 31-50 %, 5 = 51-75 % and 6 = 76-100 %). Substratum categories used were continuous pavement, substratum in blocks >1 m, substratum in blocks <1m, unconsolidated rubble, sand and silt. Live cover was categorised as hard substrate, live hard coral, dead standing coral, soft coral, turf algae, macro-algae, coralline algae, sponges or other. A second level description of the species composition of the reef was also made, in which all hard and soft corals were identified to genus or species level, where possible using Wallace (1999) and Veron (2000). The abundance of each species was recorded using the same semi-quantitative six-point scale. For each species of coral and soft coral, the percentage of that species which was recently dead (still standing, but covered in a thin layer of turf algae) totally bleached, partially bleached and alive was also recorded on a scale of 0-6. At the end of the timed swim the results of all observers were combined onto a single survey form.

Sea surface temperature (SST) data for Rodrigues (63 °E-64 °E, 19 °S-20 °S) between 1st February 2000 and 31st August 2002 was obtained from the Advanced High Resolution

Radiometer Global Area Coverage (GAC) 50km dataset (NOAA, 2002). Meteorological data (air temperature, rainfall, wind speed and hours of sunshine) were also obtained from the Mauritius Meteorological Services.

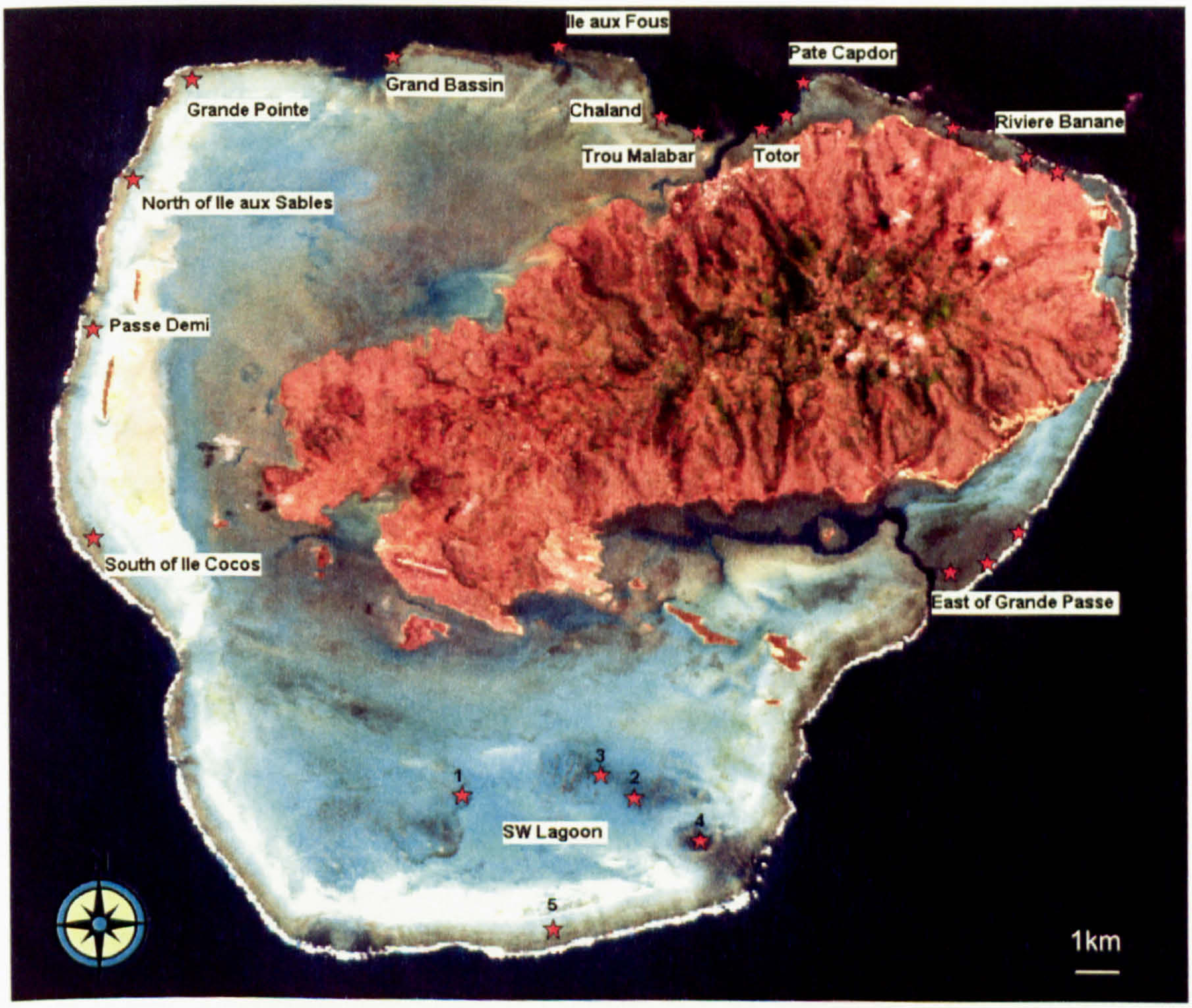


Figure 6.1. The 22 survey sites around the coast of Rodrigues. (Landsat 7 ETM$^+$ image processed by B. Chapman).

6.22 Changes in reef structure

The 2 most severely affected sites were identified in order to set-up permanent transect lines to monitor the recovery of the reefs over time. Permanent transect lines were set-up at Trou Malabar and Ile aux Fous on the reef flat at 1-2 m depth on 11th May 2002 (Trou Malabar) and 12th June 2002 (Ile aux Fous). At each site three 20 m transect lines were laid in a continuous line running parallel to the reef front, where possible, with a 5 m space between the end of one and the start of the next. The beginning, end and mid-point of each line were marked with a metal peg hammered through a plastic bottle. The 3 transect lines were recorded using a digital video camera (Canon MV1) placed in an Amphibico housing. The video camera was held at 45 ° to the substratum and the operator snorkelled slowly along the transect line. The sites were re-visited on 24th July 2003 (Ile aux Fous) and 25th August 2003 (Trou Malabar), 13-15 months later, when transects lines were identified and re-recorded.

The digital video footage was analysed using the random point sampling technique (Foster *et al.*, 1991). Still-images were downloaded from the video tapes onto the computer via a Firewire (IEE394 port) using the software Pinnacle Studio (version 8.6). Screen grabs were then sampled approximately every 5 seconds, depending on the length of the recording. A total of 50 still images were grabbed per 20 m transect (150 still images per site). Ten 10 x 10 grids were created in Adobe Photoshop (version 6.0) each with 10 randomly positioned circles. These grids were overlain on the images and the composition of the benthos under the centre of each circle was recorded. The total number of points for each benthic cover category was summed. Percent cover was calculated by dividing the sum of points per benthic cover category by the total number of points recorded per transect (10 points per screen grab x 50 screen grabs = 500 points per transect). The mean percent cover for each benthic cover category was then calculated.

6.23 Bioerosion

At Trou Malabar and Ile aux Fous, 10 sections of dead branching coral, approximately 10 cm in length, were collected using pliers during July (Ile aux Fous) and August (Trou Malabar) 2003. The coral samples were then placed in 10 % formalin for a minimum of 2 days. Five random cuts were made along the long axis of each piece of dead coral with a saw (Holmes *et al.*, 2000). The rubble pieces were assessed under a binocular microscope and bioerosion was estimated on a 3-point scale (<33 %, 33-66 %, >66 %), based on the percentage surface area of each rubble piece affected by bore-holes (Sheppard *et al.*, 2002).

6.3 RESULTS

6.31 Initial assessment

Sea temperatures around Rodrigues typically peak in late March/April and do not normally exceed 28 °C (Figure 6.2). The 50 km Advanced Very High Resolution Radiometer (AVHRR) data showed that SST reached a maximum of 29.3 °C in late March 2002 (23rd March 2002) which is >1 °C above the long term mean maximum SST. This is confirmed by meteorological data, which show that the mean maximum air temperature during the month of February 2002 was the highest recorded in 6 years (31.2 °C). Rainfall during February was low (66 mm), sunshine levels were high (total of 264.5 hours) and mean wind speed was also low (15 km hr^{-1}). Water temperatures recorded during the survey period ranged from 28.0 °C at sites east of Grande Passe to 30.2 °C on the shallow reef flat in the south lagoon. The mean temperature during the 2-week survey period was 29.1 °C.

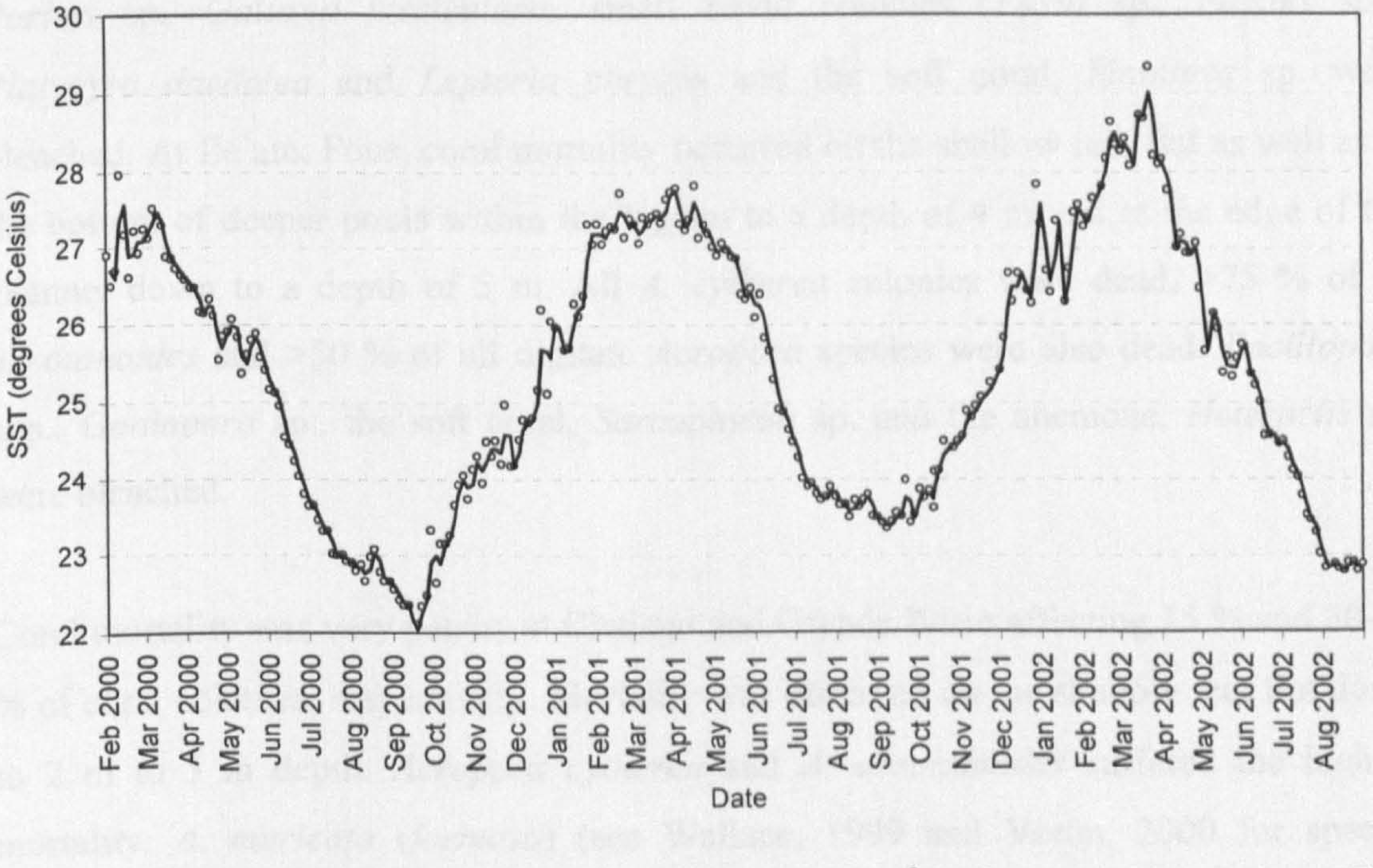


Figure 6.2. Figure 2. Sea Surface Temperature (SST) (°C) from Advanced Very High Resolution Radiometer Global Area Coverage (GAC) 50km dataset (NOAA) for Rodrigues (63°E-64°E and 19°S-20°S) between 1st February 2000 and 31st August 2002 (open circles). Also shown 2 point moving average during this period. Graph produced by R. Klaus.

Recent coral mortality was recorded at 6 of the 22 sites surveyed around the coast of Rodrigues. Coral colonies were still standing and had been very recently overgrown with turf algae. Sites were concentrated in the north and west of the island at Trou Malabar, Chaland, Totor, Ile aux Fous, Grande Bassin and north of Ile aux Sables. The percentage cover of dead standing coral at the sites ranged from 1-10 % at Chaland to 51-75 % at Trou Malabar and Ile aux Fous, while live coral was reduced to 1-10 % at Trou Malabar, Ile aux Fous and Ile aux Sables. Considering the coral colonies only, the percentage of coral colonies that had died ranged from 11-30 % at Chaland to 51-75 % at Trou Malabar, Ile aux Fous and Ile aux Sables (Figure 6.3).

At Trou Malabar live coral cover was reduced to <10 % with dead standing coral constituting 51-75 % cover. Coral mortality occurred from the shallow reef crest to a depth of 2.5 metres. All *Acropora cytherea*, *Acropora abrotanoides* and digitate *Acropora* colonies were dead. *Pocillopora damicornis, P. eydouxi, P. verrucosa, Porites* sp., *Galaxea fascicularis*, small Favid colonies (*Favia* sp., *Favites* sp.), *Platygyra daedalea* and *Leptoria phrygia* and the soft coral, *Sinularia* sp. were bleached. At Ile aux Fous, coral mortality occurred on the shallow reef flat as well as at the bottom of deeper pools within the lagoon to a depth of 4 m and at the edge of the channel down to a depth of 5 m. All *A. cytherea* colonies were dead, >75 % of *A. abrotanoides* and >50 % of all digitate *Acropora* species were also dead. *Pocillopora* spp., *Goniopora* sp., the soft coral, *Sarcophyton* sp. and the anemone, *Heteractis* sp. were bleached.

Coral mortality was very patchy at Chaland and Grande Basin affecting 15 % and 30-40 % of coral colonies, respectively. Mortality was observed on the shallow reef flat down to 2 m to 3 m depth. *Acropora cytherea* and *A. abrotanoides* suffered the highest mortality; *A. muricata* (*formosa*) (see Wallace, 1999 and Veron, 2000 for species discussion) and digitate Acroporids were also affected. At Chaland approximately 50 % of *A. muricata* species were bleached; digitate *Acropora* species, *Pocillopora* spp., *Hydnophora microconos, Galaxea fascicularis* and *Millepora* sp. were also bleached. At Totor, coral mortality was low, affecting <10 % of *A. cytherea* colonies; *P. damicornis* and *G. fascicularis* were bleached. Mortality north of Ile aux Sables was approximately 75 %. 90 % of *A. cytherea* colonies were dead and 50 % of *A. digitata* colonies were also dead. Turbidity at this site was very high and underwater visibility was reduced to 50 cm and <20 cm in places.

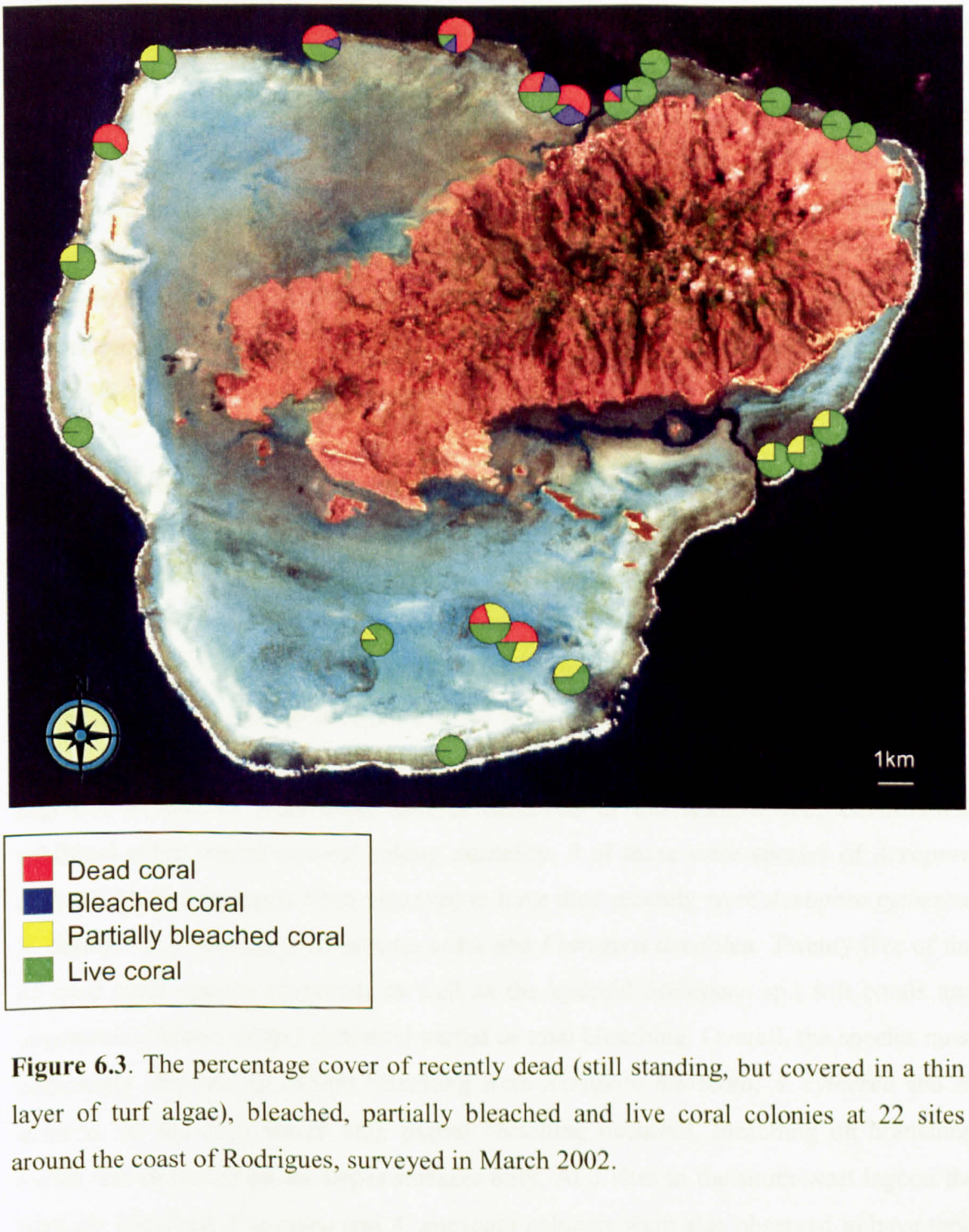


Figure 6.3. The percentage cover of recently dead (still standing, but covered in a thin layer of turf algae), bleached, partially bleached and live coral colonies at 22 sites around the coast of Rodrigues, surveyed in March 2002.

Coral mortality also occurred at 2 sites in the south west lagoon (SW lagoon 2 and 3) and also at a site in the pass at Ile aux Fous. At these 3 sites however, mortality appeared to have occurred earlier, as corals were covered in a thick layer of turf and macro-algae and were heavily eroded. Mortality was particularly severe at SW Lagoon 2, where over 75 % of *Acropora cytherea* colonies were dead. This site was surveyed in August 2000 by Chapman and was recorded as having 60 % live coral cover, suggesting that mortality occurred in 2001. The site in the pass at Ile aux Fous was not surveyed but personal observations found that all foliose *Montipora* and branching and tabular *Acropora* colonies down to 6 m depth were dead and heavily eroded.

Partially bleached coral colonies were recorded at 7 sites on the patch reefs in the south lagoon and at 2 sites on the west coast. The percentage of coral colonies with partial bleaching varied from <1 % to 11-30 %. The remaining 7 sites were healthy with no coral mortality or coral bleaching. Live coral cover varied from 1-10% at the exposed sites in the north east at Rivière Banane to 51-76 % at Paté Capdor. Dead standing coral was <10 % and was not observed at 4 of the sites surveyed.

Eighteen of the 45 hard coral species observed in the shallow reef environment exhibited either partial or total colony mortality; 9 of these were species of *Acropora* (Table 6.1). Species most often observed to have died recently were *Acropora cytherea, A. digitifera, A. muricata, A. abrotanoides* and *Platygyra daedalea.* Twenty five of the 45 hard coral species observed, as well as the hydroid *Millepora* sp., soft corals and anemones (*Heteractis* sp.) exhibited partial or total bleaching. Overall, the species most commonly observed to exhibit bleaching were *Acropora muricata, A. cytherea* and *A. austera.* At the sites where only partial bleaching occurred, bleaching on branching corals was observed on the upper surfaces only. At 3 sites in the south-west lagoon the partially bleached *A. austera* and *A. muricata* colonies were also observed to have their tentacles extended.

Comparisons with data collected in 2000 (Chapman, 2000) highlight changes in benthic composition over time. Comparisons could not be made at Trou Malabar or Grand Basin as these sites were not surveyed during 2000. At Chaland, hard coral cover decreased from abundance score 4 (31-50 %) in 2000 to 3 (11-30 %) in 2002, dead coral cover increased from abundance score 1 (<1 %) to 2 (1-10 %) and turf algae also increased from 1 to 2 (Figures 6.4 & 6.5). At Totor, hard coral cover decreased from abundance score 4 to 2. At Ile aux Fous, hard coral cover decreased from 4 to 2, dead coral increased from 1 to 5 (51-75 %) and turf algae increased from 0 (0 %) to 5. At North of Ile aux Sables, hard coral cover decreased from 4 to 2, dead coral increased from 1 to 4 and turf algae increased from 2 to 4. At SW Lagoon 2, hard coral cover decreased from 5 to 2, dead coral decreased from 1 to 5, turf algae increased from 2 to 4 and macro-algae increased from 1 to 4. Overall, however there was no significant difference in median percent hard coral cover at the 20 sites between 2000 and 2002 (Mann-Whitney Test, W = 466.5.0, p>0.05), nor was there any significant difference in median percent dead coral cover at the 20 sites (Mann-Whitney Test, W = 375.0, p>0.05).

6.32 Changes in reef structure

By May 2002 all bleached coral colonies at Trou Malabar had died and become colonised by turf algae, ascidians and sponges. The substrate consisted of a coralline platform with turf algae (59 %), with little rubble (4 %). The percentage cover of dead standing coral was 31 % and living hard coral was only 6 %. Considering hard corals only, 84 % had recently died and only 16 % were still alive. Dead coral colonies consisted mainly of the branching *Acropora* species, *A. muricata, A. nobilis* and *A. abrotanoides* (48 % of coral colonies), the digitate *Acropora* species, *A. digitifera, A. humilis*, and *A. valida* (19 % of coral colonies) and *A. cytherea* (14 % of coral colonies) (Figure 6.6). Live coral colonies consisted of *A. muricata* (5 % of coral colonies), digitate *Acropora* spp (4 %), *Porites* spp (massive and branching) (2 %) and Faviidae (*Platygyra daedalea, Leptoria phrygia, Goniastrea retiformis*) (3 %) (Figure 6.6).

By August 2003, 17 months after the bleaching event, coral colonies at Trou Malabar had become heavily eroded and many of the branching corals had become unrecognisable (Plates 6.7-6.9). Dead coral colonies were colonised by turf algae, green and brown macro-algae, and coralline algae. However, many branching *Acropora* colonies had re-growing tips; there were also live massive coral species and a number of new *Acropora* sp recruits (Figure 6.7). There was very little rubble (3 %) and the majority of the substrate was coralline platform (57 %). The percentage of dead standing coral had decreased from 31 % in May 2002 to 23 % and the percentage of living hard coral had increased from just 6 % to 16 % (Figure 6.8). Considering hard corals only the percentage of live corals had increased from 16 % in 2002 to 41 % in August 2003. The increase in live coral was mostly due to the re-growth of the branching *Acropora* spp, *A. muricata, A. nobilis* and *A. abrotanoides*, which increased from 5 % in 2002 to 18 % in 2003; digitate *Acropora* spp (*A. digitifera, A. humilis* and *A. valida*) which increased from 4 % to 9 %; *Pocillopora* spp (*P. damicornis, P. verrucosa* and *P. eydouxi*), which increased from 0.8 % to 2 % and the hydrocoral *Millepora* sp which increased from 0 % to 6 %.

By June 2002 all bleached coral colonies at Ile aux Fous had also died and become colonised by turf algae, ascidians and sponges. The substrate consisted of a coralline platform (11 %), with little rubble (9 %). The percentage cover of dead standing corals was 65 % and living hard corals was 16 %. Considering hard corals only, 80 % had recently died and only 20 % were still alive. Dead coral colonies consisted mainly of *Acropora cytherea* (56 % of coral colonies), and *A. muricata* (24 % of coral colonies) (Figure 6.6). Live coral colonies consisted of *Montipora* spp (*M. aequituberculata* and *M. spumosa*) (11 % of coral colonies), *A. muricata* (4 %) and *Fungia* spp (3 %).

By July 2003, 16 months after the bleaching event, coral colonies at Ile aux Fous had become colonised by turf algae, green and brown macro-algae, coralline algae and sponges (Plates 6.10-6.12). Branching *Acropora muricata* colonies were heavily eroded and many *A. cytherea* tables were overturned due to storm damage. Some *A. muricata* colonies had re-growing tips and there were a number of new *Acropora* sp recruits. There were a number of live massive coral species; live *Fungia* sp and *Pavona* spp *(P. decussata* and *P. frondifera*) were also common. The abundance of rubble had increased from 9 % in June 2002 to 35 % in July 2003 (Figure 6.9). Dead standing coral had decreased from 65 % to 32 % and live coral remained low at 13 %. Considering hard corals only, the percentage of live coral had increased from 20 % in 2002 to 29 % in 2003. The increase in live coral was mostly due to *A. muricata*, which increased from 4 % in 2002 to 5 % in 2003; the Faviidae (*Platygyra daedalea, P. crosslandi*, and *Favites sp*), which increased from 0.2 % to 1 %, *Pavona* spp (*P. decussata* and *P. frondifera*), which increased from just 0.3 % to 7 % and *Fungia* spp, which increased from 3 % to 9 %.

Table 6.1. The mean percentage mortality and bleaching for each of the hard and soft coral species recorded at the 22 shallow reef sites and the % of sites at which that species was dead or bleached.

Species	Mortality		Bleaching	
	Mean %	% Sites	Mean %	% Sites
Pocillopora damicornis	0	0	<1	18
Pocillopora eydouxi	<1	14	<1	18
Pocillopora verrucosa	0	0	<1	14
Stylophora pistillata	0	0	0	0
Montipora sp.	<1	9	<1	9
Montipora aequituberculata	<1	5	<1	5
Montipora digitata	0	0	<1	5
Montipora tuberculosa	0	0	<1	5
Acropora sp.	0	0	0	0
Acropora abrotanoides	1-10	18	<1	5
Acropora austera	<1	5	1-10	23
Acropora clathrata	<1	5	0	0
Acropora cytherea	1-10	36	<1	27
Acropora digitifera	<1	23	<1	18
Acropora horrida	0	0	0	0
Acropora humilis	<1	14	<1	9
Acropora muricata (formosa)	<1	23	<1	41
Acropora nasuta	0	0	0	0
Acropora nobilis	0	0	1-10	5
Acropora pinguis	<1	9	<1	5
Acropora tenuis	0	0	0	0
Acropora valida	<1	14	<1	9
Porites sp.	<1	5	<1	9
Goniopora sp.	0	0	1-10	5
Pavona cactus	0	0	0	0
Pavona decussata	0	0	0	0
Fungia sp.	0	0	0	0
Galaxea fascicularis	0	0	1-10	14
Hydnophora sp.	0	0	11-30	5
Hydnophora microconos	0	0	0	0
Favia sp.	<1	5	1-10	9
Favia stelligera	<1	9	<1	5
Favites sp.	<1	9	<1	9
Favites abdita	0	0	0	0
Goniastrea sp.	<1	5	0	0
Goniastrea pectinata	0	0	0	0
Goniastrea retiformis	0	0	0	0
Platygyra daedalea	<1	18	<1	18
Platygyra lamellina	0	0	0	0
Leptoria phrygia	0	0	<1	9
Cyphastrea microphtalma	0	0	0	0
Echinopora sp.	0	0	0	0
Echinopora forskaliana	0	0	0	0
Turbinaria sp.	0	0	0	0

Turbinaria mesenterina	0	0	0	0
Millepora sp.	0	0	<1	5
Sarcophyton sp.	0	0	76-100	9
Sinularia sp.	0	0	0	0
Lobophyton sp.	0	0	0	0
Xenia sp.	0	0	0	0
Palythoa sp.	0	0	0	0
Heteractis sp.	0	0	0	0

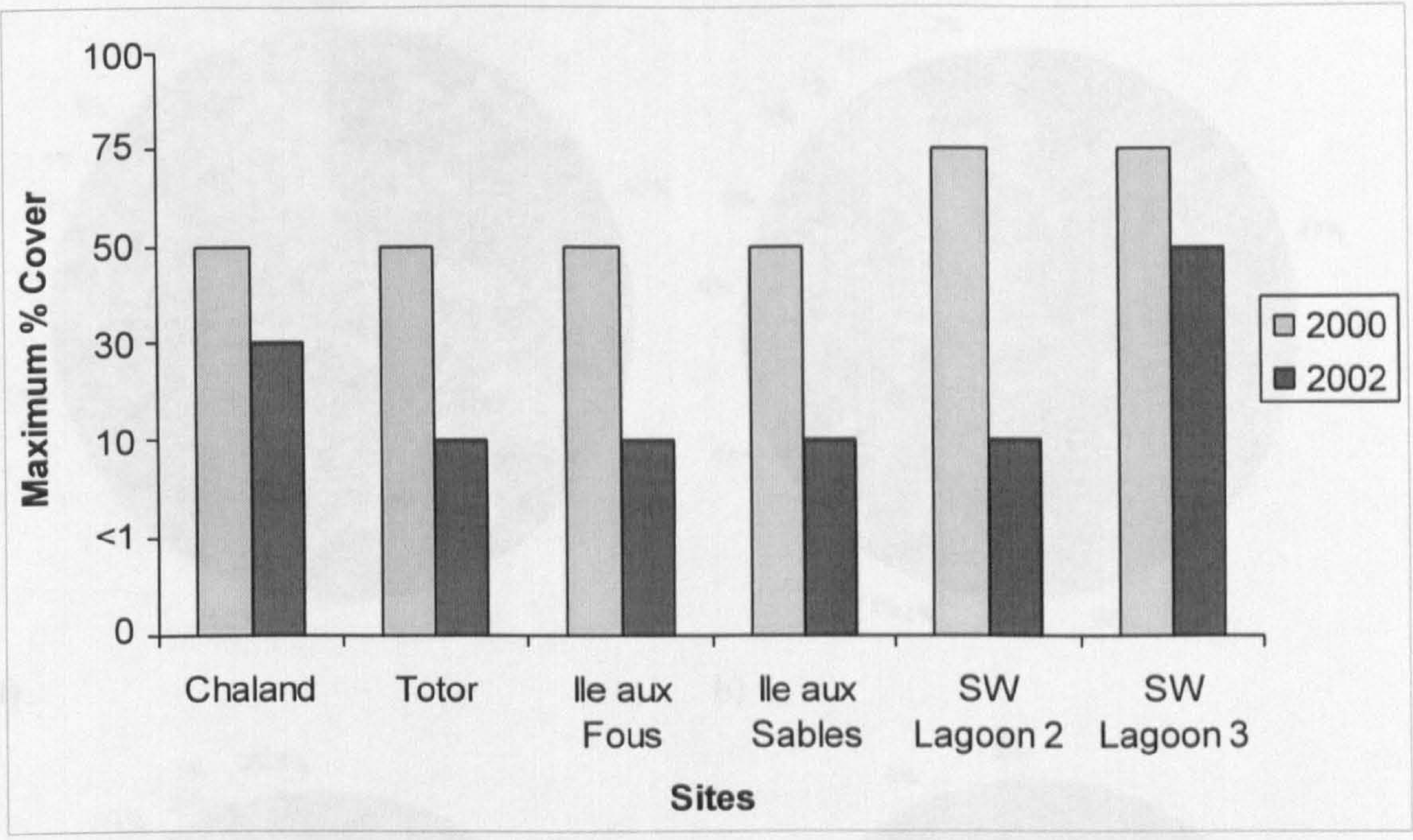


Figure 6.4 The difference in maximum percent cover of living hard coral between 2000 (recorded by Chapman) and 2002 at the 6 most severely affected sites.

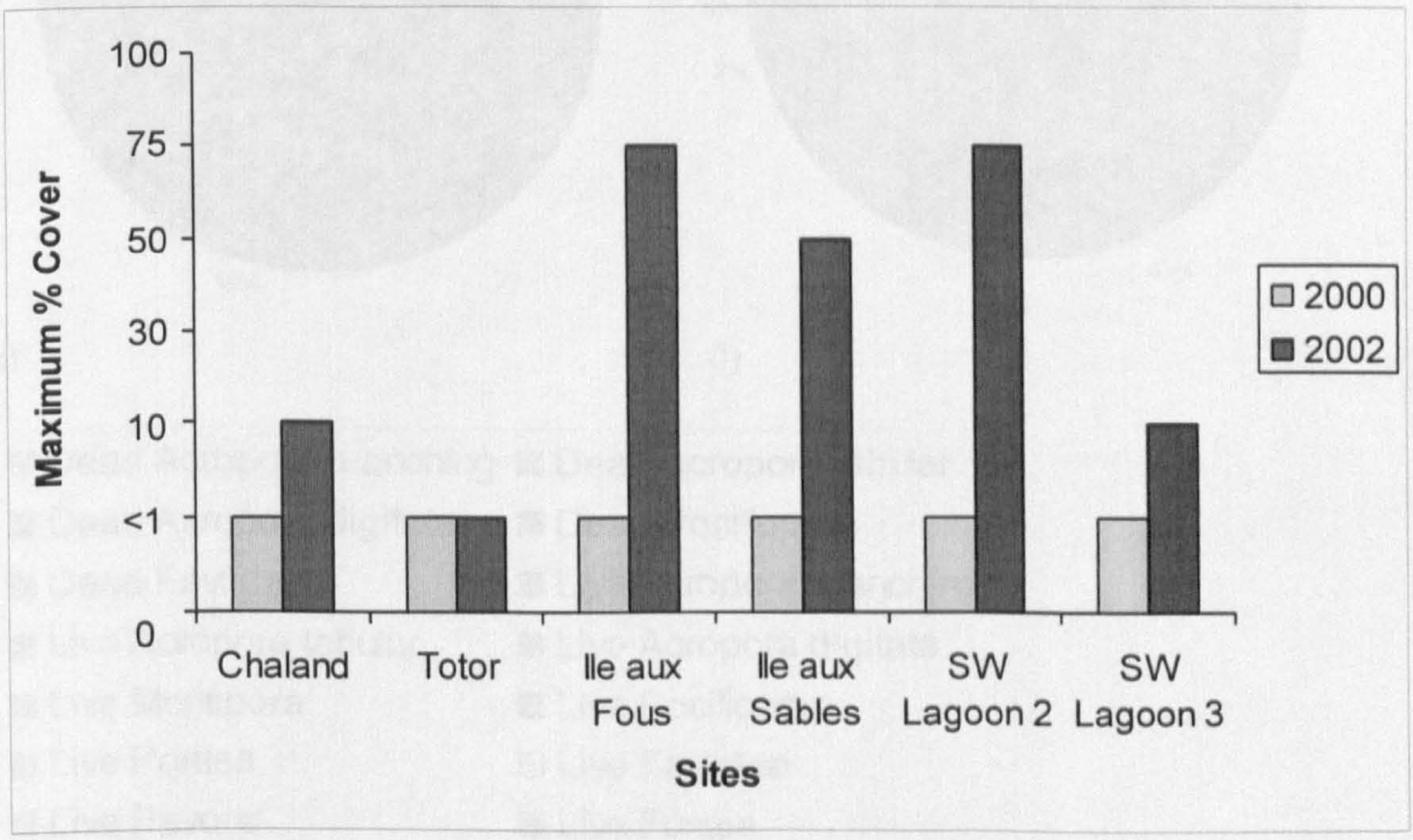


Figure 6.5. The difference in maximum percent cover of dead standing coral between 2000 (recorded by Chapman) and 2002 at the 6 most severely affected sites.

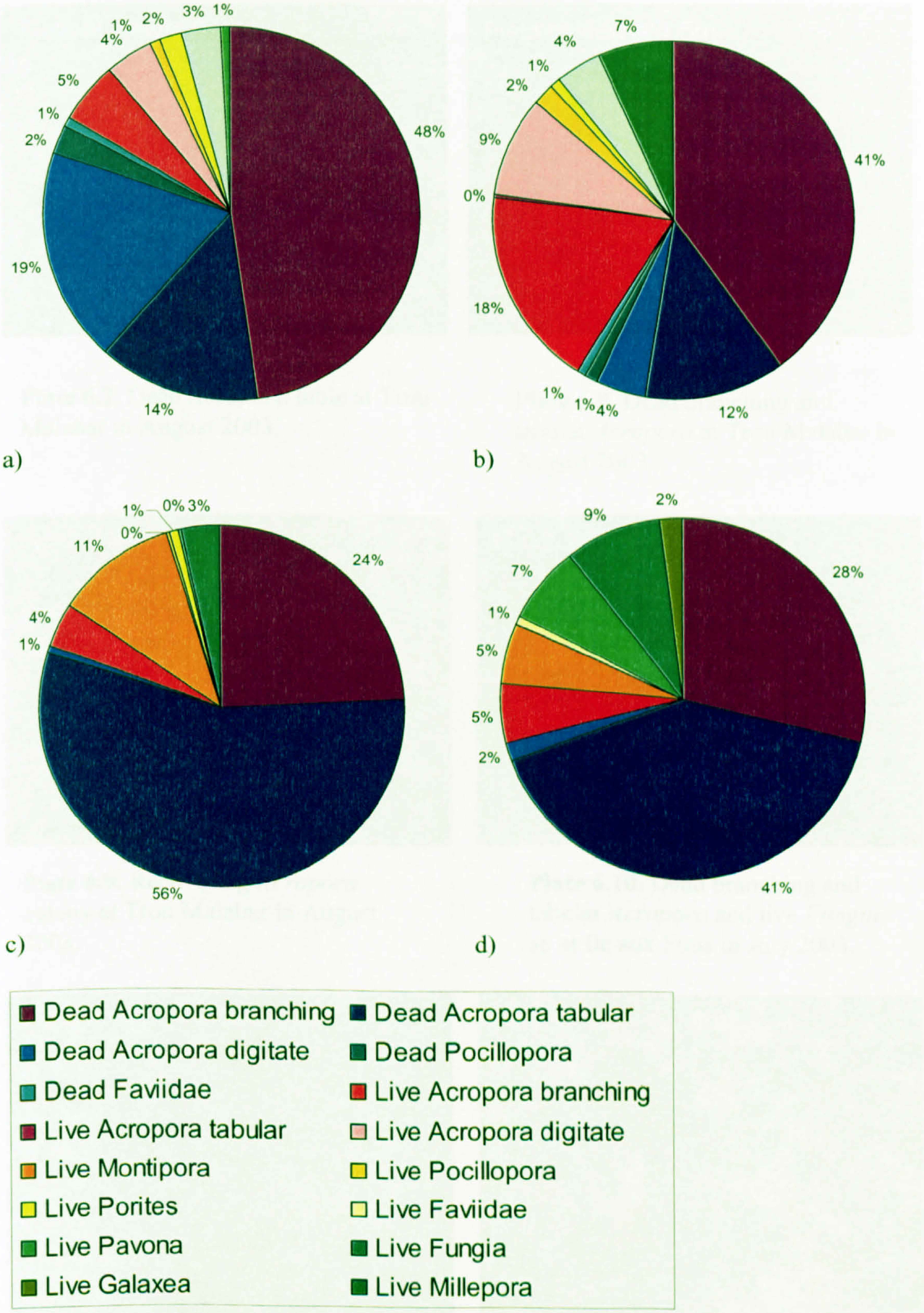


Figure 6.6 The composition of dead coral (purple and blue) and live coral (red, orange, yellow and green) at Trou Malabar in a) May 2002 and b) August 2003 and at Ile aux Fous in c) June 2002 and d) July 2003.

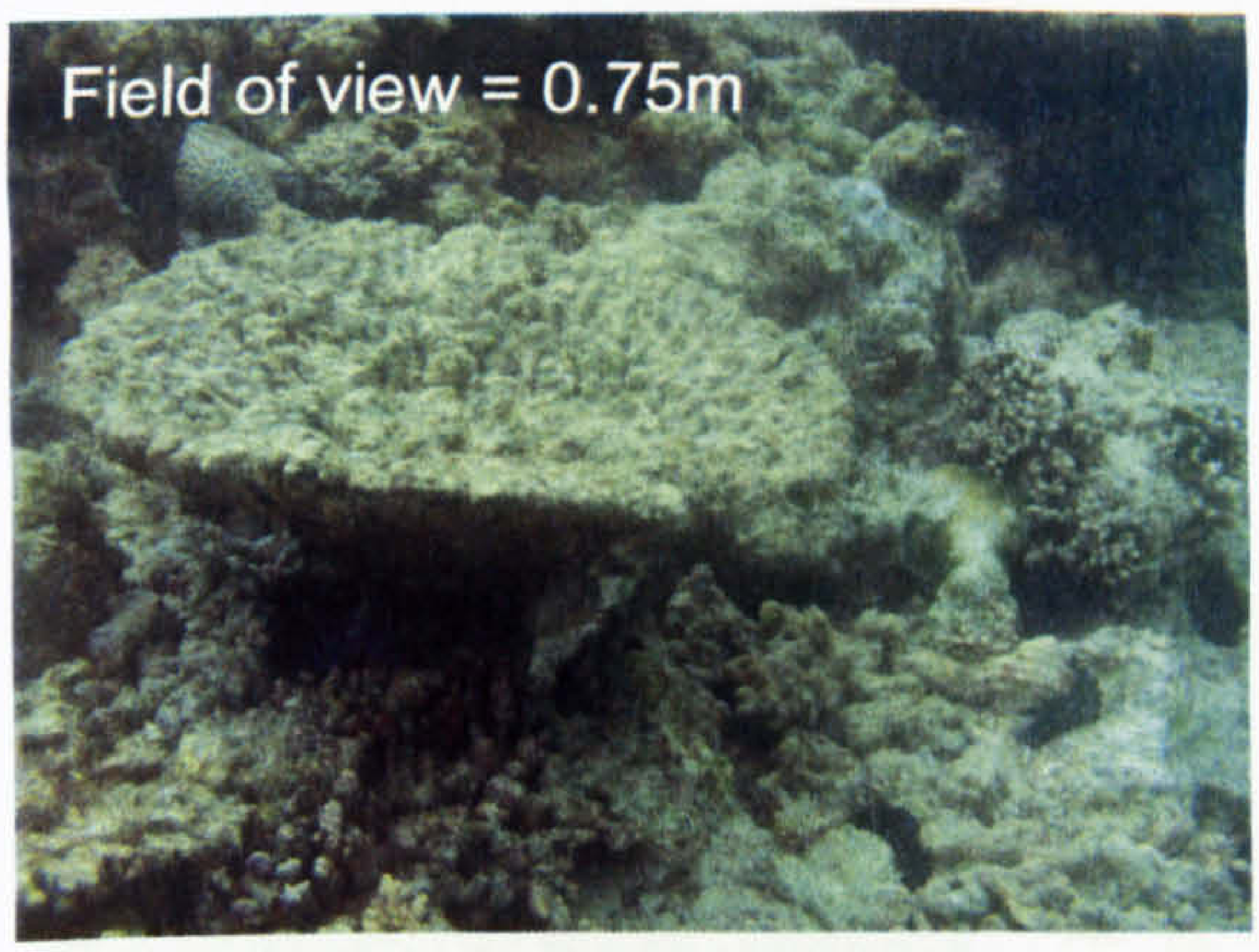


Plate 6.7. Dead *Acropora* table at Trou Malabar in August 2003.

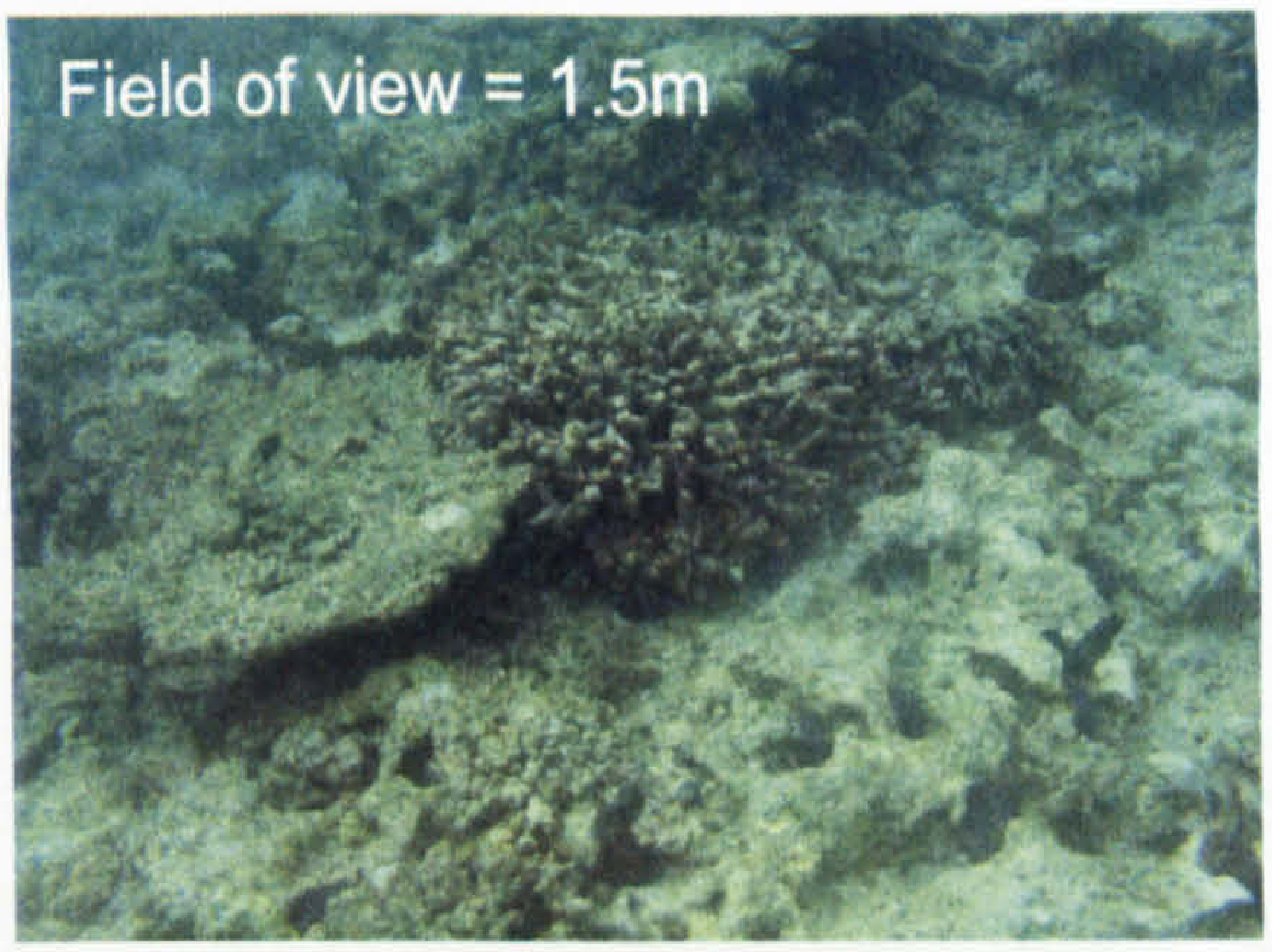


Plate 6.8. Dead branching and tabular *Acropora* at Trou Malabar in August 2003.

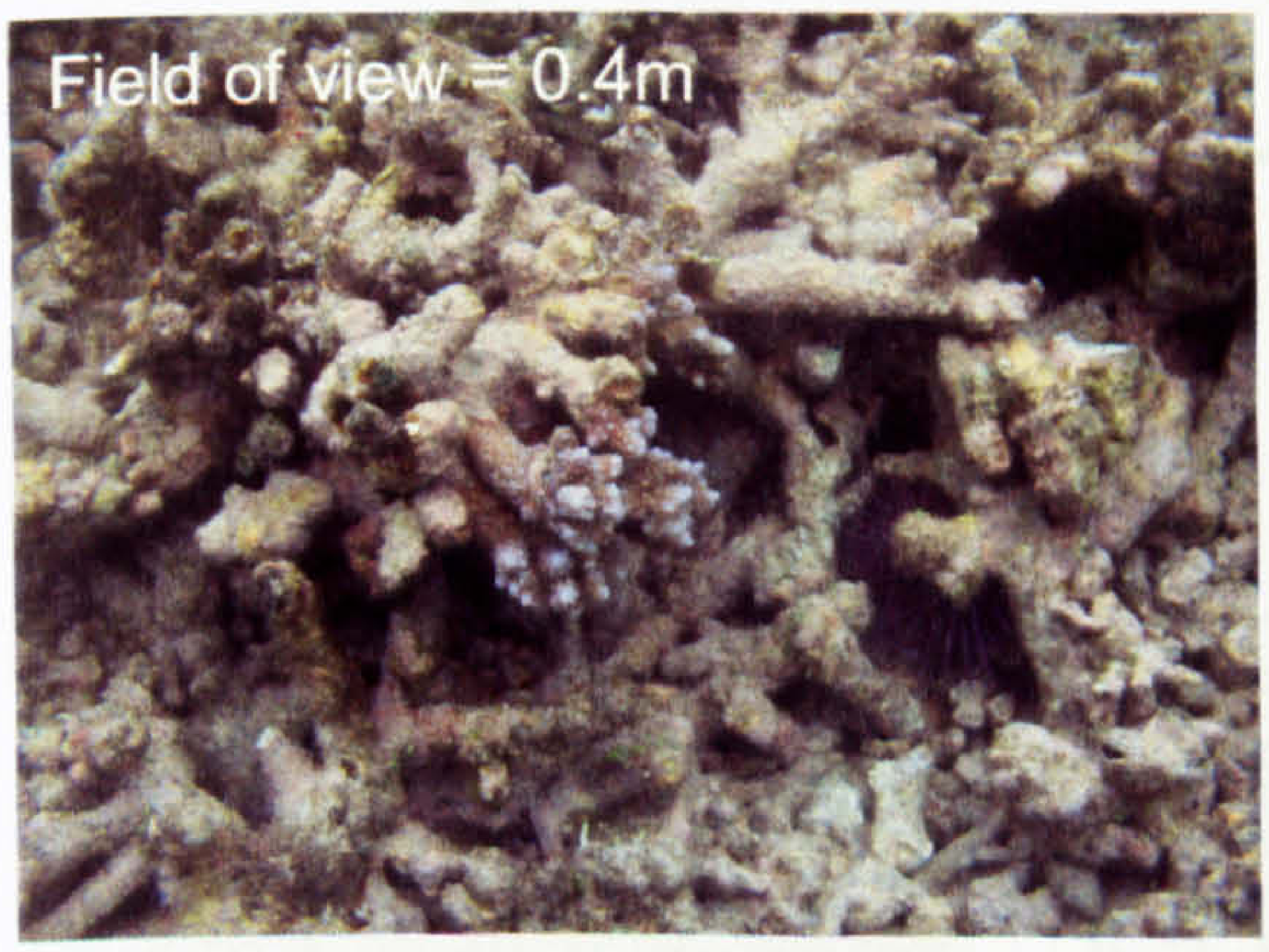


Plate 6.9. Recovering *Acropora* colony at Trou Malabar in August 2003.

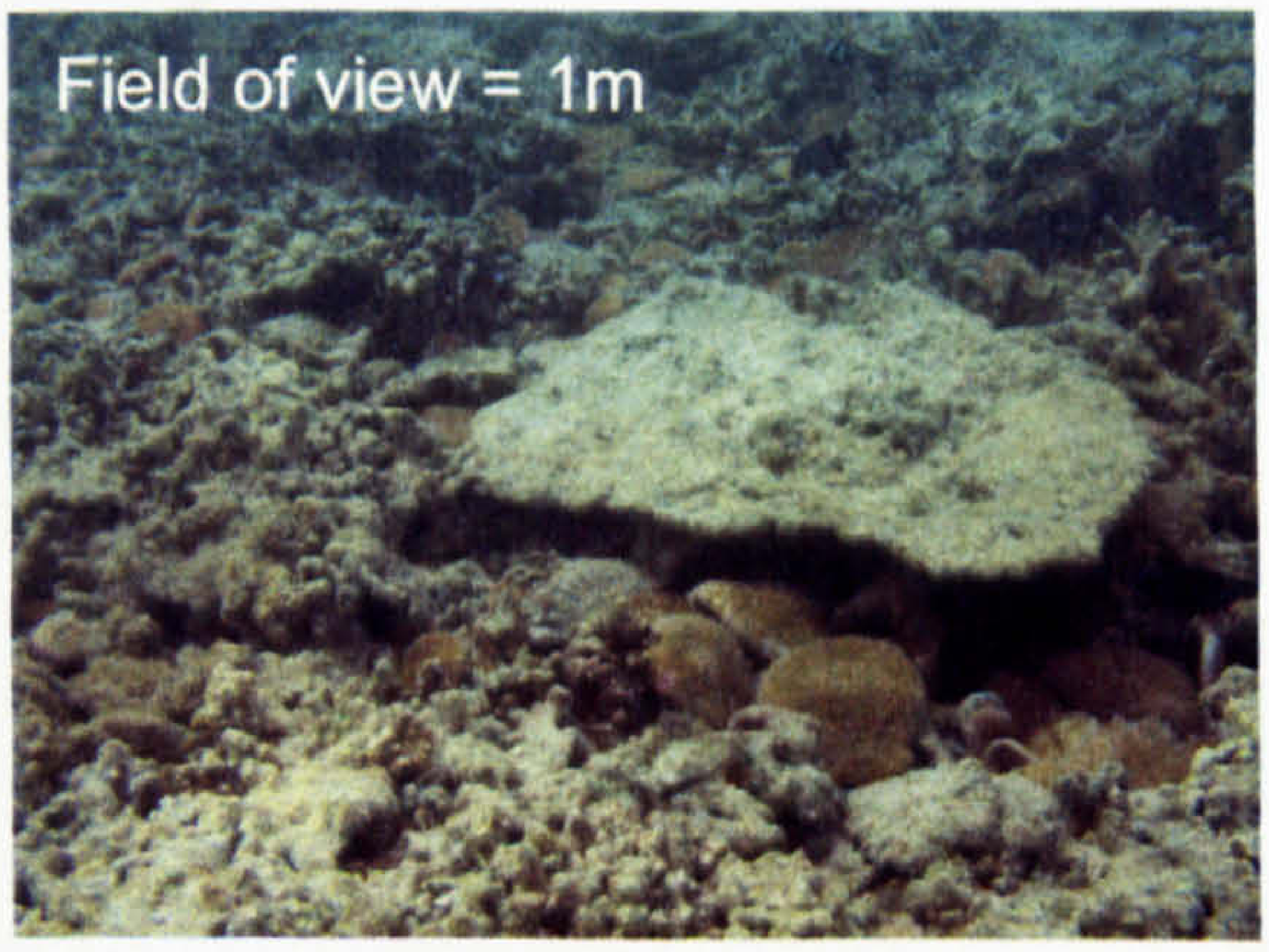


Plate 6.10. Dead branching and tabular *Acropora* and live *Fungia* sp at Ile aux Fous in July 2003.

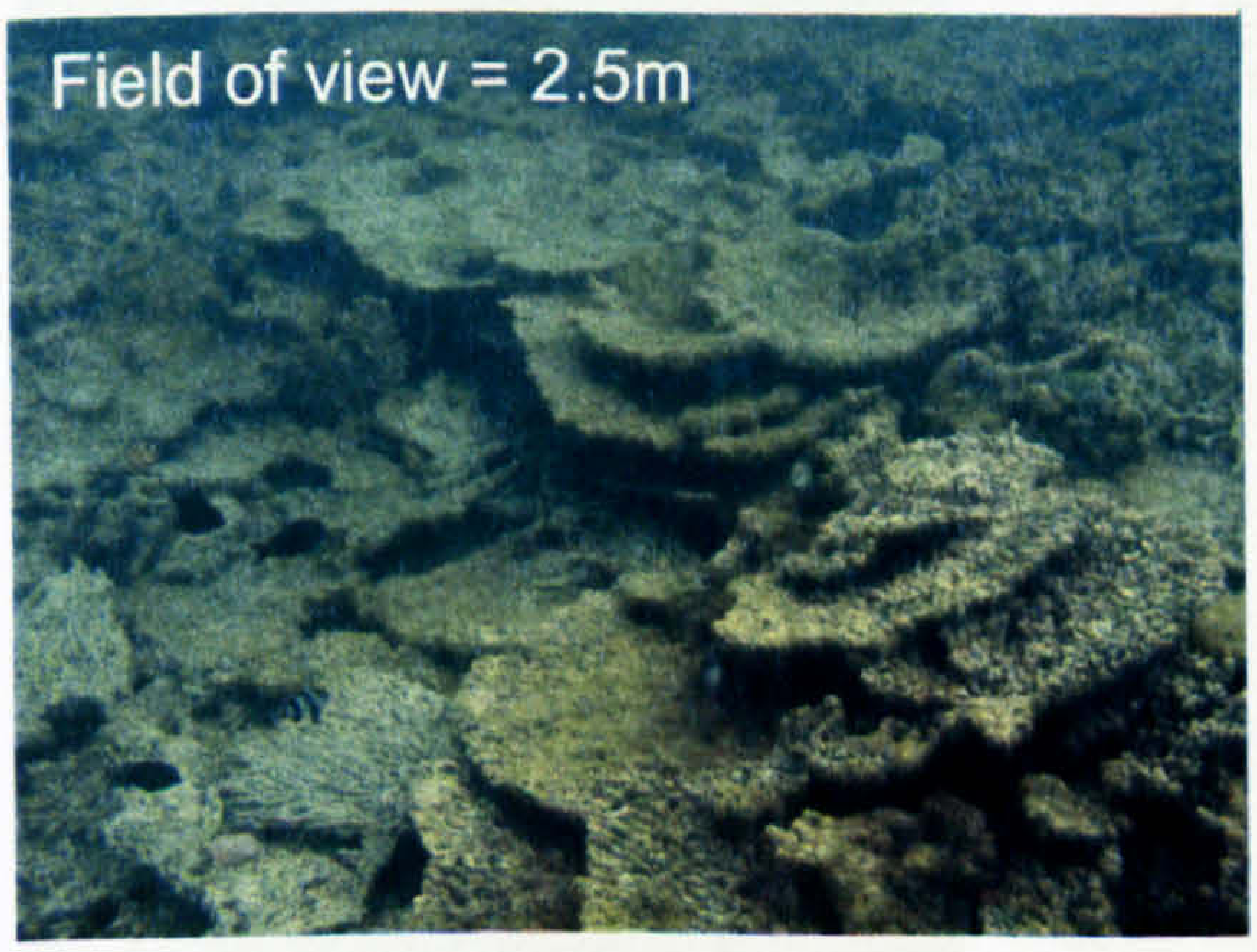
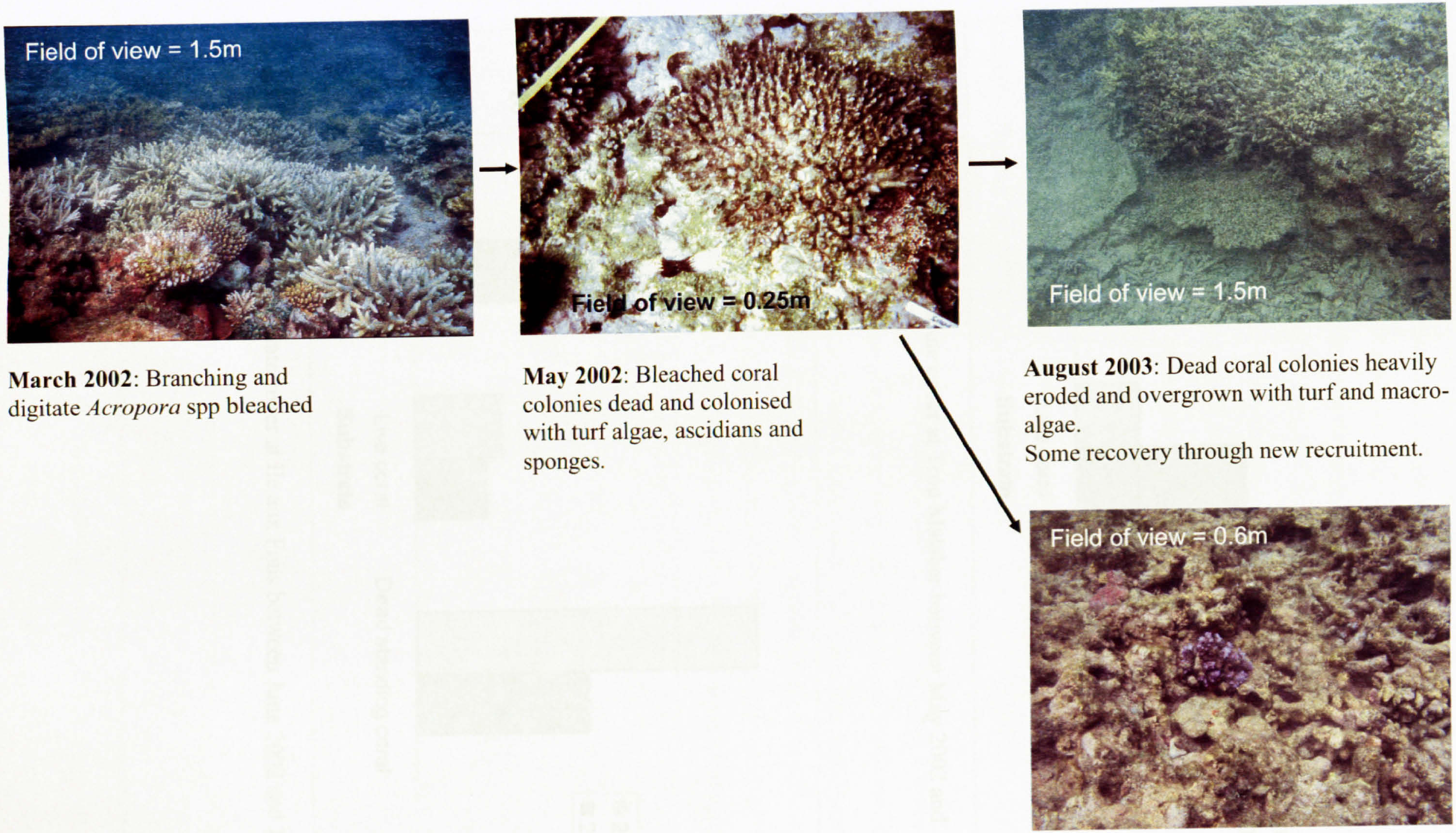


Plate 6.11. Dead tabular *Acropora* colonies at Ile aux Fous in July 2003.

Plate 6.12. Recovering *Pavona* sp colonies at Ile aux Fous in July 2003.



March 2002: Branching and digitate *Acropora* spp bleached

May 2002: Bleached coral colonies dead and colonised with turf algae, ascidians and sponges.

August 2003: Dead coral colonies heavily eroded and overgrown with turf and macroalgae.
Some recovery through new recruitment.

Figure 6.7 The change in reef structure at Trou Malabar, over a 17-month period, following the coral bleaching in March 2002.

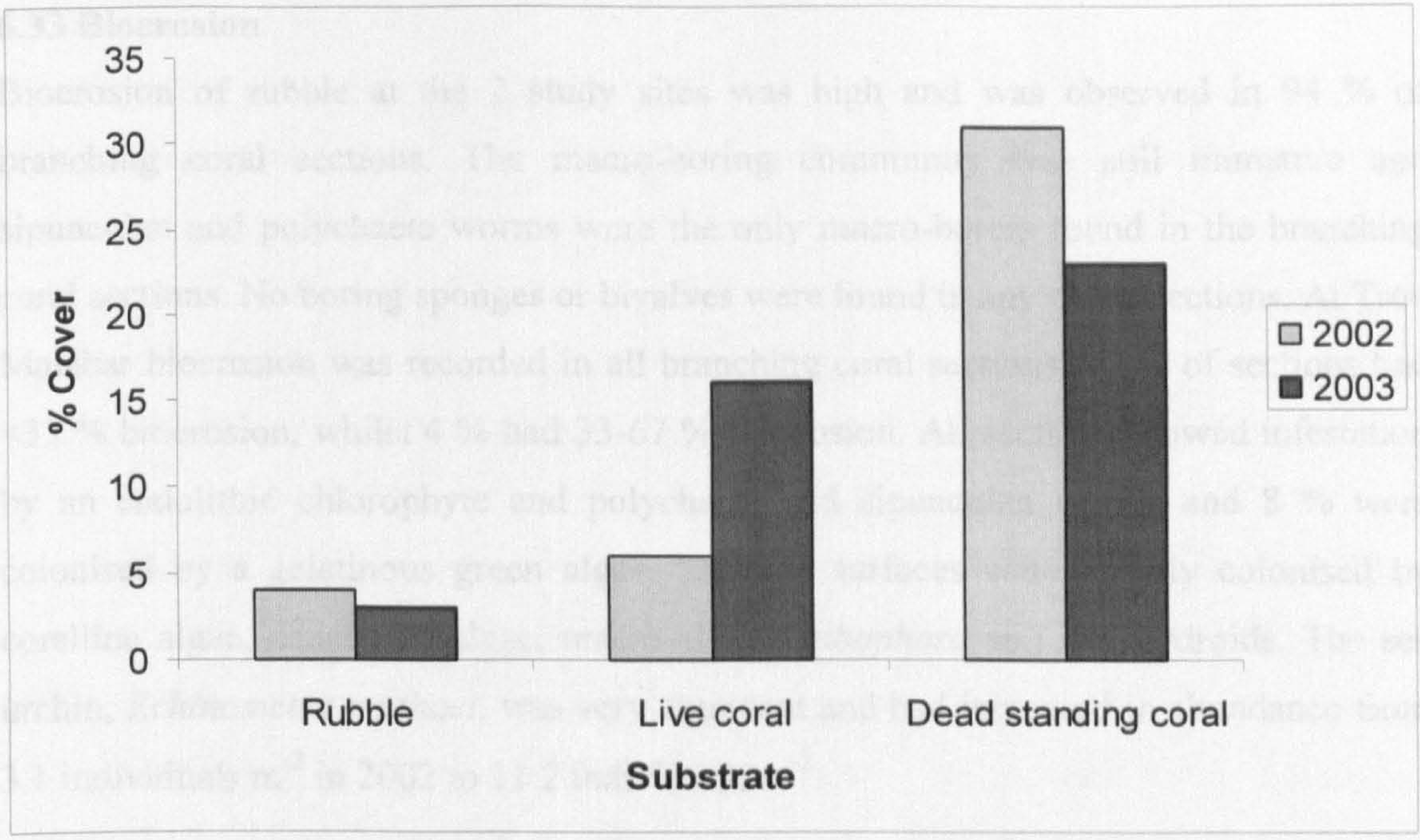


Figure 6.8 The change in substrate cover at Trou Malabar between May 2002 and August 2003.

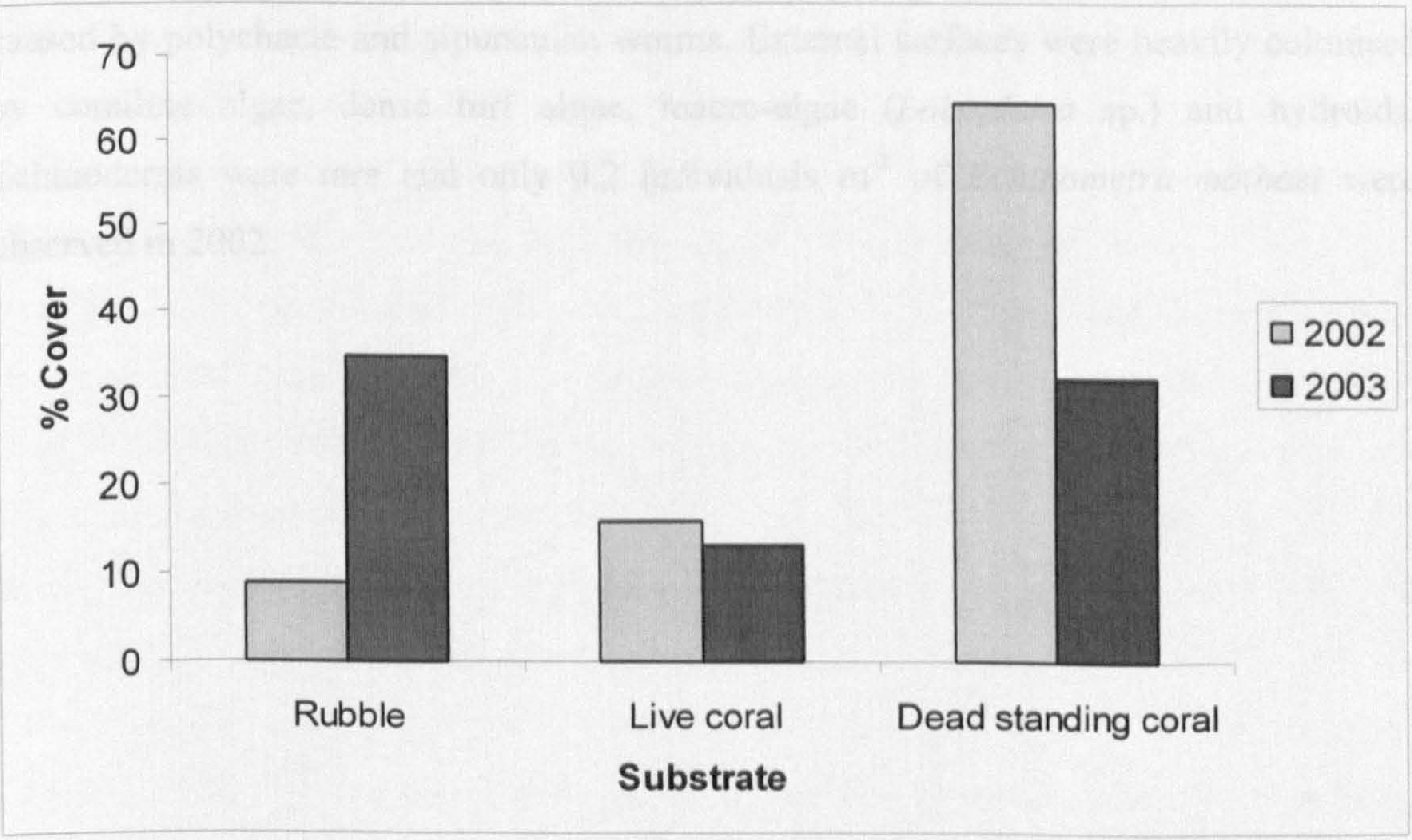


Figure 6.9 The change in substrate cover at Ile aux Fous between June 2002 and July 2003.

6.33 Bioerosion

Bioerosion of rubble at the 2 study sites was high and was observed in 94 % of branching coral sections. The macro-boring community was still immature and sipunculan and polychaete worms were the only macro-borers found in the branching coral sections. No boring sponges or bivalves were found in any of the sections. At Trou Malabar bioerosion was recorded in all branching coral sections. 96 % of sections had <33 % bioerosion, whilst 4 % had 33-67 % bioerosion. All sections showed infestation by an endolithic chlorophyte and polychaete and sipunculan worms and 8 % were colonised by a gelatinous green algae. External surfaces were heavily colonised by coralline algae, dense turf algae, macro-algae (*Lobophora* sp.) and hydroids. The sea urchin, *Echinometra mathaei*, was very abundant and had increased in abundance from 3.1 individuals m^{-2} in 2002 to 11.2 individuals m^{-2}.

At Ile aux Fous, the occurrence of bioerosion was less than at Trou Malabar and bioerosion was only observed in 88 % of branching coral sections. 68 % of sections had <33 % bioerosion, whilst 20 % had 33-67 % bioerosion. All bioerosion was found to be caused by polychaete and sipunculan worms. External surfaces were heavily colonised by coralline algae, dense turf algae, macro-algae (*Lobophora* sp.) and hydroids. Echinoderms were rare and only 0.2 individuals m^{-2} of *Echinometra mathaei* were observed in 2002.

6.4 DISCUSSION

6.41 Extent of coral bleaching

The results show that the bleaching event in Rodrigues was not widespread. The bleaching event occurred at less than one third of the sites surveyed and mortality was restricted to sites in the north and west of the island. Furthermore, the bleaching event did not result in a significant decline in live coral cover at 20 of the sites surveyed between 2000 and 2002. Where bleaching-induced mortality did occur, however it was severe affecting up to 75 % of corals at some sites. Live coral cover was found to have decreased at the sites where coral mortality was observed between 2000 and 2003, particularly at Ile aux Fous, Ile aux Sables and SW Lagoon 2. Bleaching events were also recorded at other locations in the Indo-Pacific region during 2002 including Mauritius (Moothien Pillay, 2002), Réunion (Quod *et al.*, 2002), the Seychelles (Ahamada *et al.*, 2002), Fiji (Sulu *et al.*, 2002), India (Rajasuriya *et al.*, 2002) and the Great Barrier Reef (GBRMPA, 2002; Sweatman *et al.*, 2002). Where details are given, these events do not appear to be severe, affecting only corals in the shallower depths.

Advanced Very High Resolution Radiometer (AVHRR) data shows that the mean sea surface temperature in Rodrigues during February 2002 was over 1 °C above the normal monthly mean. During February 2002, there were high levels of solar radiation, low cloud cover, low rainfall and low wind, promoting heating of shallow water and increased solar penetration. Climatic conditions such as these have been shown to coincide with coral bleaching in past bleaching events (e.g. Brown and Suharsono, 1990). Coral mortality occurred on the shallow reef flats, mostly at depths less than 2m. These corals are exposed at low tide, which occurred during the middle of the day during the period of highest temperatures, suggesting a combination of high sea temperatures, high solar illumination and exposure as the causal factors.

Fish kills were also associated with the coral mortality events in Mauritius (Moothien Pillay, 2002) and Réunion (Quod, 2002). It is possible that the fish kills and coral mortality were linked, possibly due to a harmful algal bloom. Qualitative observations in Rodrigues indicate that there was a build up of phytoplankton in the lagoon during the latter part of February 2002 (Lynch, *pers. comm.*) and harmful algal blooms occurred concurrently along the northern coast of East Africa and in the Gulf of Aden (Obura, 2002). The blooms resulted in mortality of fish species as well as nudibranchs, gastropods, bivalves and crustaceans. There is very little evidence in the literature of a link between harmful algal blooms and coral bleaching, however Guzmán *et al.* (1990) report a severe dinoflagellate bloom in Costa Rica with an associated fish kill and the mortality of shallow water corals. The authors suggest that the coral mortality may have been caused by toxicity of the dinoflagellates, depletion of dissolved oxygen or smothering by mucus from the algae. In Réunion the high fish mortality was found to be caused by the *Streptococcus* bacterial pathogen found in the spleen of fish (Ahamada *et al.*, 2002). It has, however also been suggested that dead or stressed corals and sponges may produce phenols and secondary metabolites that may be toxic to associated fish species, resulting in the fish kills (Cervino, Coral-list, 2002).

Coral mortality was most severe at sites to the north and west of the island. These areas are sheltered from the prevailing south-easterly winds and very light winds during February 2002 may have resulted in decreased water movement, allowing further heating of the shallow water at these sites. In contrast, sites at Rivière Banane, Grande Passe and the southern lagoon are more exposed to the prevailing winds and oceanic swell and greater water movement may have prevented seawater warming in these areas. The site north of Ile aux Sables had very high turbidity at this time, with visibility as low as 20 cm in places. Coral bleaching may be caused by high turbidity (e.g. Rogers, 1983) and Quod *et al.* (2002) suggest that the bleaching in Réunion was caused by high sedimentation as a result of increased rainfall associated with Cyclone Dina, which affected the region during January 2002. In Rodrigues, high winds during this cyclone may have caused resuspension of sediments at shallow lagoon sites, resulting in the high turbidity observed at Ile aux Sables. It is possible therefore, that the bleaching and mortality observed in Rodrigues may have been caused by a combination of factors which caused stress to the coral colonies.

Coral species most affected by the mortality were the tabular Acroporid *Acropora cytherea*, the branching species *A. abrotanoides*, *A. muricata* and the digitate species *A. digitifera* and *A. valida*. Previous studies have shown that the fast growing Acroporids are most susceptible to coral bleaching and subsequent mortality (e.g. Brown and Suharsono, 1990, Gleason, 1993, Edwards *et al.*, 2001). The loss of fast growing branching and tabular species may result in a change in species composition of the reefs with the faster growing species being replaced by the less susceptible slower growing species (Brown and Suharsono, 1990, McClanahan, 2000, Edwards *et al.*, 2001). Partial bleaching also occurred at shallow sites in the southwest lagoon and on the west coast.

At these sites bleaching affected only the Acroporids, *A. austera, A. cytherea* and *A. muricata* and occurred on the upper surfaces only. Many other studies have commented on the patchy spatial distribution of coral bleaching: the extent of bleaching can differ between coral genera (Oliver, 1985; Gates, 1990; Gleason, 1993; Hoegh-Guldberg and Salvat, 1995) and between coral colonies of the same species at the same site (Brown and Suharsono, 1990; Williams and Bunkley-Williams, 1990; Gleason, 1993; Spencer *et al.*, 2000). Some studies suggest that this inter- and intraspecific variability in coral bleaching is due to variations in the concentration of UV-absorbing mycosporinelike amino acids (Gleason, 1993), xanthopylls (Brown *et al.,* 1999) or the concentration of fluorescent pigments (Salih *et al.*, 2000) within coral tissues. Other studies conclude that this patchiness occurs because corals act as hosts to multi-species communities of zooxanthellae which exhibit different tolerances to light and temperature (Rowan *et al.*, 1997; Trench, 1997). Genetic analysis has identified 4 groups of zooxanthellae: A, B, C and D (Rowan and Powers, 1991; Baker, 2001). Recent work suggests that coral colonies living in high temperatures have a higher prevalence of zooxanthellae in group D, indicating that this group may be more tolerant to higher temperatures (Baker, 2004; Berkelmans and Van Oppen, 2004).

Bleaching only occurred on the upper surfaces of horizontal branches suggesting that bleaching may have been caused by solar irradiance (Harriott, 1985b). A number of laboratory studies have shown that high solar irradiance can cause bleaching of coral colonies, irrespective of water temperature (Hoegh-Guldberg and Smith, 1989b; Kinzie, 1993; Jones and Hoegh-Guldberg, 2001). Jones *et al.* (1998) and Jones and Hoegh-Guldberg (2000) suggest that observations in which the most sunlit sides of coral colonies bleach first can be explained by the theory that damage to the dark reactions of zooxanthellae photosynthesis causes increased sensitivity to photoinhibition. They propose that this increased sensitivity makes the extent of damage during stress light-sensitive and explains why surfaces which are exposed to higher irradiance levels exhibit a higher frequency of bleaching.

The coral mortality in Rodrigues appears to have been caused by a combination of causal factors including high sea surface temperatures, increased solar illumination and low wind, increased turbidity and possibly a harmful algal bloom. The presence of areas of dead coral that appear to have died previously suggests that Rodrigues may experience small-scale, but severe bleaching events on a fairly regular basis. Rodrigues did however, escape the mass coral bleaching event of 1997-1998, which caused severe damage at other sites in the Western Indian Ocean; this is thought to be due to Cyclone *Anacelle*, which produced high cloud cover and low solar radiation during the period of high seawater temperatures. The most severe bleaching ever reported occurred around the islands of the Maldives, Chagos, and the Seychelles and on the coasts and islands of India, Kenya and Tanzania, where up to 95% of corals bleached and subsequently died (Wilkinson *et al.*, 1999). Recent surveys suggest that in the Maldives, Seychelles and Chagos, live coral cover is still low (Edwards *et al.*, 2001; Ahamada *et al.*, 2002; Loch *et al.*, 2002; Sheppard *et al.*, 2002) and many reefs in the region have already been reduced to unconsolidated rubble (Bigot *et al.*, 2000; Sheppard *et al.*, 2002). At some sites recovery is occurring slowly, for example in the Maldives (Edwards *et al.*, 2001; Loch *et al.*, 2002), Kenya and Tanzania (Obura *et al*, 2002), Chagos (Sheppard *et al.*, 2002) and remote areas of Comoros (Ahamada *et al.*, 2002), however new recruitment is still low in the Seychelles (Ahamada *et al.*, 2002).

6.42 Changes in reef structure

In Rodrigues, 1 year after the bleaching event dead coral colonies had become heavily eroded and colonised by turf, macro- and coralline algae. A number of studies have shown that coral larvae will settle preferentially on surfaces which are colonised by coralline algae, which induces settlement through chemical stimuli (Morse *et al*, 1988; Carlon and Olson, 1993; Morse and Morse, 1996). At Trou Malabar there is a great deal of available space for new coral recruits to settle as approximately 60 % of the substrate is coralline platform. At Ile aux Fous, larval settlement was found to be high (Clark and Meunier, *pers. comm.*) however the high abundance of unconsolidated rubble does not provide a stable surface, leaving new recruits vulnerable to abrasion and removal during storms. Some recovery has occurred at both sites however, recovery was greatest at Trou Malabar where 41 % of coral colonies were alive, compared to only 29 % at Ile aux Fous. At both sites branching *Acropora* colonies had re-growing tips and there were a number of new *Acropora* spp recruits. At Trou Malabar digitate *Acropora* species and *Pocillopora* spp. also showed some recovery and the hydrocoral, *Millepora* rapidly increased in abundance. At Ile aux Fous, the coralline platform and rubble were colonised by small *Pavona* spp. colonies and many live *Fungia* sp. colonies had accumulated amongst the rubble.

Surveys carried out by Shoals Rodrigues staff in May and June 2003 highlight further variations in recovery potential (Clark and Meunier, *pers. comm.*). The survey found that corals at Totor had been affected by a further bleaching event in February/March 2003. Tabular *Acropora* colonies were most affected by the bleaching, with approximately 50 % of colonies suffering mortality. Branching and digitate *Acropora* spp. and *Pocillopora* spp. were also affected. Overall, 25 % of coral colonies exhibited partial or total mortality. At the site east of Grande Passe corals also appeared to have suffered further mortality and 80 % of branching *Acropora* colonies were dead and 50 % of the digitate and tabular *Acropora* spp. had also died. Overall, 60 % of coral colonies exhibited mortality. At Grande Basin, the reef had been completely reduced to rubble, which had been colonised by the brown macro-algae, *Turbinaria* sp., *Sargassum* sp. and *Padina* sp. and live coral colonies were very rare. At the site north of Ile aux Sables some recovery had however occurred and the percentage of live coral colonies had increased to 40 %. Recovery had occurred through the re-growth of tabular *Acropora* colonies and recolonisation by small massive corals and digitate *Acropora* colonies.

Studies from the 1982-83 bleaching event suggest that recovery from coral bleaching is likely to be slow and is unlikely to occur over the next 10 years. In the Thousand Islands, Java Sea, 5 years after a mass bleaching event in 1983, recovery was not complete and coral cover was still 50 % of its former level (Brown and Suharsono, 1990; Warwick *et al.*, 1990). Coral cover finally attained pre-bleaching levels in 1990 at one site and 1994 at the other site (Brown, 1997b). In the Galápagos Islands, the 1982-1983 El Niño event resulted in 95-99 % coral mortality and Glynn (1994) reports a slow recovery of the coral communities over the following decade. Modest recruitment of Pocilloporid populations was observed 4 years after the bleaching event however most of the reef structures had eroded and fallen apart. The sea urchin *Eucidaris thouarsii* remained abundant throughout the El Niño event and accelerated the erosion of the coral framework. Reaka-Kudla *et al.* (1996) also found that bioerosion of the reefs by *E. thouarsii* was causing rapid destruction of the reef framework

6.43 Bioerosion

The sea urchin, *Echinometra mathaei* appears to be the main bioeroding invertebrate and densities were high at Trou Malabar and at Totor (Clark and Meunier, *pers. comm.*). Densities were not, however, as high as those recorded in Réunion, where densities of up to 28.2 individuals m^{-2} were recorded (Chazottes *et al.*, 2002) or Moorea where densities reached 38.4 individuals m^{-2} on dead coral colonies (Bak, 1990). *E. mathaei* has been shown to be a modest bioeroder, with rates of bioerosion of 0.11 - 0.14 g $urchin^{-1}$ day^{-1} (Bak, 1990; Russo, 1980). In addition to erosion of the substrate echinoderms also have both positive and negative effects on coral recruitment. A number of studies have shown that corals tend to settle more rapidly when grazing by urchins is rapid enough to prevent filamentous non-coralline algae from monopolising available space (Birkeland and Randall, 1981; Dart, 1972; McClanahan *et al.*, 1996). However, if urchins are particularly abundant they may decrease coral recruitment through direct consumption of coral recruits (Reaka-Kudla *et al.*, 1996; Sammarco, 1982b; Wittenberg and Hunte, 1992).

The macro-boring communities at Trou Malabar and Ile aux Fous were still immature, consisting mainly of sipunculan and polychaete worms and no boring sponges or bivalves were observed. This community is similar to that observed in dead *Acropora formosa* branches in Réunion (Zubia and Peyrot-Clausade, 2001) and on experimental blocks after 1 year of exposure in Réunion, (Chazottes *et al.*, 2002) and on the Great Barrier Reef (Tribollet *et al.*, 2002) and in Moorea after 2 years of exposure (Chazottes *et al.*, 1995). Polychaete and sipunculans have been shown to be the dominant type of macro-borers to colonise newly dead substrates (Chazottes *et al.*, 1995; Hutchings and Peyrot-Clausade, 2002). Polychaete worms are the initial agents of macro-boring appearing after 2 months, whilst sipunculans tend to colonise after 6 months of exposure (Chazottes *et al.*, 1995). Boring sponges and bivalves are the most important agents of internal bioerosion, however these macroborers do not settle for a number of years (Kiene and Hutchings, 1994; Hutchings and Peyrot-Clausade, 2002; Pari *et al.*, 1998; Pari *et al.*, 2002). Bioeroding organisms weaken the coral colonies, increasing their susceptibility to physical damage and as bioerosion continues, the reef framework will be reduced to rubble (Tunnicliffe, 1981), resulting in loss of coastal protection.

6.44 Summary

The results of this study suggest that:

- The bleaching event of 2002 was not widespread, affecting only 27% of sites surveyed. The most severe bleaching occurred at sites in the north and west of the island, which are protected from the prevailing winds.
- Where bleaching did occur, it was severe, resulting in mortality of up to 75% of coral colonies at some sites; coral species most affected by the bleaching and subsequent mortality where tabular, branching and digitate *Acropora* species.
- One year after the bleaching event dead coral colonies had become heavily eroded and overgrown with turf and macro-algae.
- Moderately sheltered sites in the north and west of the island showed some recovery after one year with an increase in live coral cover due to the re-growth of branching *Acropora* colonies, surviving massive colonies and new *Acropora* recruits.
- More exposed sites had a high percentage of unconsolidated rubble, although there was some recovery due to re-growth and new recruitment.

6.45 Conclusions

Although Rodrigues escaped the bleaching event of 1998, it already appears to be affected by regular minor bleaching events, with limited but severe mortality occurring in 2002 and 2003 and possibly 2001. After one year, recovery of the affected sites showed a high degree of spatial variability. Moderately sheltered sites showed an increase in coral cover due to the re-growth of branching *Acropora* colonies, surviving massive colonies and new *Acropora* recruits. More exposed sites however, had a high percentage of unconsolidated rubble, which does not provide a stable substrate for new recruits. Bioerosion of the dead corals has already begun, weakening the corals and increasing their susceptibility to physical damage from fishers and cyclones. The possible increased frequency of coral bleaching events means that there is a shorter time period for recovery to occur and this may result in changes to coral community structure or a phase shift, with a possible eventual breakdown of the reef crest structure. The implications of this for the future of the coral reefs in Rodrigues will be discussed in the following chapter.

CHAPTER 7: The human and natural impacts affecting coral reefs in Rodrigues

7.1 INTRODUCTION

This chapter will summarise the results described in the preceding chapters and will discuss these results in relation to the future of the coral reefs in Rodrigues. At present the reefs in Rodrigues appear healthy, however throughout the world, coral reefs are subjected to a number of anthropogenic and natural impacts and it has been estimated that 30% are already severely damaged (Wilkinson, 2002). In addition to greater anthropogenic impacts due to increased coastal development, reefs may also be subjected to an increased frequency of natural impacts such as coral bleaching and cyclones due to Global Warming. It is therefore important that reefs are provided with adequate protection in order to maximise their chances of surviving potential future changes in global climate.

7.2 THE IMPACTS OF SEDIMENTATION ON CORAL REEFS

Sedimentation is one of the major anthropogenic impacts to coral reefs, affecting reefs close to fluvial inputs and areas of urbanisation across the world. Recent studies have shown increased sedimentation as a result of land-clearing for agriculture, increased construction and development projects, road construction, dredging and land reclamation projects, to be affecting areas of coral reef in a number of countries including Egypt (Pilcher and Abou Zaid, 2000), French Polynesia (Salvat *et al.*, 2000), Indonesia (Hopley and Suharsono, 2000), Malaysia (Pilcher and Cabanban, 2000), Japan (Dai *et al.*, 2002), Micronesia (Richmond *et al.*, 2002) and Papua New Guinea (Huber and Opu, 2000). In the US Virgin Islands, shoreline development and construction of roads was found to increase sedimentation during heavy rainfall, causing coral bleaching and a decrease in coral cover (Nemeth and Sladek-Nowlis, 2001). Deforestation and overgrazing by sheep has caused significant soil erosion in Mexico during the rainy season, resulting in a loss of coral cover, change in coral species composition and an increase in algal density (Ochoa-Lopez *et al.*, 1998). Furthermore, in Costa Rica, land clearing for banana plantations since the 1960s is thought to have caused high sediment deposition, resulting in low coral growth rates and low coral cover and species diversity (Cortés and Risk, 1985).

In Rodrigues, terrestrial run-off is likely to have been a problem since the early 1800s with the onset of deforestation to clear land for agricultural purposes (Gade, 1985). Greater coastal development, dredging operations and road construction in more recent years are likely to have increased terrestrial run-off, which occurs episodically during periods of high rainfall. The current study has shown that the sheltered reef at Totor has high sediment deposition (>10 mg cm^{-2} d^{-1} for 7 out of the 8 months studied) and low visibility. Data from 2002 and 2003 suggest that Trou Malabar, 1 km offshore, usually has low sediment deposition, but that periodic high wind and rain associated with cyclones can result in very high sediment deposition (up to 96 mg cm^{-2} d^{-1}) and low visibility at this site. Chaland, which is approximately 2 km offshore, can be classed as a low sediment site with sediment deposition rates always below 10 mg cm^{-2} d^{-1}. High rainfall and wind can however result in low visibility at this site.

Significant land run-off occurs in Rodrigues following daily rainfall of at least 30 mm and only becomes significant if this magnitude of rainfall occurs repeatedly within a short time period of a few days (Lynch *et al.*, 2003a). High rainfall has been recorded in Rodrigues every year since 1997, except for during 2001, and tends to occur during the cyclone season between January and April. No wind data are available for 1997-1999, however in 2000-2003 high windspeed was also recorded during the periods of highest rainfall. This suggests that high sediment/low visibility conditions occur every year at the sheltered inshore sites. Cyclone *Kalunde* hit Rodrigues during March 2003 and rainfall during March and April of this year was the highest recorded during the period January 1997 – September 2003. Rainfall during 2003 was also over double the mean monthly rainfall for March-April based on data between 1951-1989 (World Climate, 2003), indicating that conditions experienced during 2003 were unusual.

Construction work was taking place on the main road from Port Mathurin to Mont Lubin during 2003. Work involved re-surfacing and widening the original road which remained unpaved for a number of months during early 2003. Construction of a new hotel was also taking place at Pointe Venus, opposite the site at Totor. It is possible that run-off from these operations may have further contributed to the high sediment deposition during 2003. Nemeth and Sladek-Nowlis (2001) showed that the magnitude of terrestrial sediment run-off corresponded with the construction schedule of a coastal development in the US Virgin Islands. The authors comment that high rainfall on unpaved roads promoted suspension of fine particles and further increased erosion. It would be interesting to use massive coral cores at the 3 sites to investigate how frequently corals in Rodrigues are exposed to terrestrial run-off. On the Great Barrier Reef Lough *et al.* (2002) showed that luminescent lines in massive *Porites* correlated with annual river flow and distance from the mainland and they suggest this technique provides a good record of terrestrial influence on coral reefs.

In addition to sediment deposition originating from the terrestrial environment, fore reef corals in Rodrigues are also subjected to naturally high sediment deposition of a marine origin. Unlike the other Mascarene Islands which slope steeply to depths of over 2,000 m, Rodrigues is situated on a large shallow submarine platform of 950 km^2 (McDougall *et al.*, 1965). It is likely that throughout geological history, marine sediments have been constantly deposited on this platform, and resuspended during periods of high wind and wave action. Coral colonies in Rodrigues are therefore likely to have originated in a naturally turbid environment and are adapted to these conditions. Increases in terrestrially-derived sediment, as a result of deforestation and coastal development, do however, appear to be having sub-lethal effects on corals during periods of very high rainfall and wind.

Despite the high sediment conditions at Totor and Trou Malabar, both reefs appear healthy with high coral cover and high species diversity. Rogers (1990) suggests that sediment deposition values of 10 mg cm^{-2} d^{-1} can be used as a threshold for healthy coral reef growth; however both sites had sediment deposition values considerably higher than 10 mg cm^{-2} d^{-1} and reaching up to 96 mg cm^{-2} d^{-1}. High sediment deposition at Trou Malabar is likely to be periodic and associated with high rain and wind, as values were low during 2002, however sediment deposition at Totor is likely to be continuously high and has probably been high for the past 100-200 years. Other studies have shown evidence for coral reefs surviving sedimentation values much higher than 10 mg cm^{-2} d^{-1}. For example, Schleyer and Celliers (2003) found no difference in percent cover of hard corals despite sediment deposition values of up to 43 mg cm^{-2} d^{-1} in South Africa. Leão de Mara *et al.*, (1999) found rich and diverse coral reefs near the mouth of the River Amazon and there are healthy coral reefs in the Indian Lakshadweep Islands, despite sedimentation values of 85 mg cm^{-2} d^{-1} during the monsoon (Suresh and Mathew, 1993). Furthermore, many reefs in the inner Great Barrier Reef have also developed despite a long-term history of high sediment input and high turbidity (e.g. Kleypass, 1966; Smithers and Larcombe, 2003).

These studies suggest that corals are capable of surviving in high sediment conditions and that Rogers (1990) value of 10 mg cm^{-2} d^{-1} for tolerable levels of sediment deposition should be revised. Based on previous literature Thomas and Ridd (in press) suggest a threshold of 150 mg cm^{-2} d^{-1} for total coral species and percentage coral cover. This value seems more applicable to the reefs in Rodrigues, where coral cover and species diversity was high. The high variability in coral responses to sediment deposition described in the literature however suggest that it may not be possible (or useful) to establish a global threshold value for sediment tolerance. The response of coral colonies to sediment deposition is likely to depend on a number of site-specific factors such as the frequency and duration of sediment input, hydrodynamics and tidal regime, sediment grain size and composition, biological life history traits and other levels of disturbance on the reef.

Corals at Totor and Trou Malabar do appear to be adapted to the low light/high sediment environment with a high colony surface area, increased sloping of colony sides, greater tiering and a greater percentage of colonies with a vertical orientation. Corals at Trou Malabar however, appear to be less well adapted and less able to remove sediment than corals at Totor. This again suggests that corals at Totor have been subjected to constant high sediment and low visibility conditions over a long time period and have become adapted to this environment. In contrast, at Trou Malabar the 14-fold difference in sediment deposition between 2002 and 2003 caused significant stress to coral colonies during 2003, suggesting that these conditions are not usual and that coral colonies are unable to cope with them. This resulted in a lack of ability of *Montipora aequituberculata* colonies to clear sediment and to recover from injury and the possible loss of zooxanthellae from *Acropora austera*.

Despite the high coral cover and species diversity, high sediment and low visibility does appear to have resulted in a decrease in coral growth rates at Totor during 2002 and at Totor, Trou Malabar and Chaland during 2003; with a decrease in total growth rate at all 3 sites between 2002 and 2003. Recruitment rates at all sites were very low and no recruitment was recorded at Chaland. It is possible that unfavourable conditions, caused by high rainfall and wind following the spawning season resulted in the low recruitment. Recruitment was recorded at Totor, however all recruits settled on the upper surface of the settlement tiles, where they were smothered by a thick layer of sediment. Regeneration rates were found to be low at all sites with no lesions showing full recovery at Trou Malabar. It seems therefore, that the high sediment and low visibility conditions experienced during April 2003 have resulted in low coral growth rates, low recruitment and low regeneration during this year.

7.3 THE IMPACTS OF CORAL BLEACHING ON CORAL REEFS

Coral reefs are becoming increasingly affected by coral bleaching events and there has been a significant increase in the number of reported large-scale coral bleaching events since the 1980s (Winter *et al.*, 1998). Rodrigues escaped the 1998 coral bleaching event due to high cloud cover and low sunlight conditions at the time of the seawater warming. The island does however, appear to have been affected by a number of minor bleaching events in 2002, 2003 and possibly 2001, causing locally severe coral mortality. The shallow reef flat coral colonies which are exposed at low tide, appear to be most vulnerable, particularly those situated in the more sheltered northern and western areas. As in other observed studies, the fast growing branching and tabular Acroporids were most susceptible to coral bleaching and subsequent mortality (e.g. Brown and Suharsono, 1990; Gleason, 1993; Edwards *et al.*, 2001).

It has been predicted that coral bleaching events will occur annually by 2030-2050 (Hoegh-Guldberg, 1999) and Sheppard (2003) estimates that reefs in the Indian Ocean located at 10-15 °S will be affected every 5 years by 2010-2025. These predictions are however based purely on climatic models, suggesting that coral bleaching will occur when temperatures exceed a certain threshold, and do not take biological aspects into account. Klaus and Turner (in submission) suggest that sea surface temperature anomalies occurring in the year prior to bleaching, when zooxanthellae populations are recovering, contribute significantly towards the severity of coral bleaching related mortality. In addition, these predictions do not take into account variability in coral colony recovery rates and assume that coral colonies will not be able to adapt or acclimatise to increasing temperatures. However, since 1980 there has been a significant increase in the number of reported large-scale coral bleaching events (Winter *et al.*, 1998). The 1997-1998 bleaching event was the most geographically widespread and most severe event in recorded history and reefs in the Maldives, the Seychelles, Sri Lanka and on the coasts and islands of India, Kenya and Tanzania, were some of the worst affected areas (Wilkinson *et al.*, 1999). Coral bleaching was reported at a number of Indo-Pacific locations during 2002 (Ahamada *et al.*, 2002; GBRMPA, 2002;

Moothien Pillay, 2002; Quod *et al.*, 2002; Rajasuriya *et al.*, 2002; Sulu *et al.*, 2002; Sweatman *et al.*, 2002) and during 2003 in Kenya (McClanahan, Coral-list 2003; Obura, Coral-list 2003), Tanzania (Obura, Coral-list 2003; Verheij, Coral-list 2003) and the Maldives (Zahir, 2003), however these events did not appear to be as severe.

One year after the 2002 coral bleaching episode, some recovery had occurred at the affected sites; there were a number of new *Acropora* spp recruits and branching *Acropora* colonies had re-growing tips, however more exposed sites had a high percent cover of unconsolidated rubble. The recovery process is complex and is affected by a number of different factors. In a 30 year study on the Great Barrier Reef, Connell *et al.* (1997) found that the rate of recovery of corals after cyclone damage differed among study areas and among cyclones. The authors demonstrate that much of this variation was due to the type, intensity and spatial scale of the disturbance and to some aspects of past history (e.g. alterations in the physical structure of the reef and the amount of initial damage). Done *et al.* (1991) investigated spatial variations in coral recovery between reefs on the Great Barrier Reef and Moorea, French Polynesia. Corals on reefs at both places had been severely depleted by large populations of *Acanthaster planci* in the early 1980s; the reefs had also been affected by cyclones, earlier starfish outbreaks and sea-level anomalies. The authors conclude that differences in reef recovery patterns are governed by localised processes, such as water circulation, depth and abundance of urchins and macro-algae, rather than by large-scale regional processes.

Rodrigues is influenced by the South Equatorial Current, which flows in a westerly direction. This suggests that there is a very limited larval supply to Rodrigues, as the nearest land mass is the west coast of Australia. It is therefore, likely that reefs in Rodrigues rely on larval retention and self-seeding for population recovery. This suggests that the reefs may be more vulnerable to impacts and may recover more slowly from severe disturbances than reefs which are part of extensive systems, where recruits from nearby unaffected reefs could recolonise rapidly (Harrison and Wallace, 1990). In addition, this has implications for the reefs to the west of Rodrigues, such as around Mauritius and Réunion. Rodrigues may act as a larval supply to these reefs and therefore damage to coral colonies in Rodrigues would also affect the recovery of reefs around neighbouring islands.

Bioerosion is already starting to take place on the shallow reef flat at Trou Malabar and Ile aux Fous and lack of reef structure may result in loss of the coastal protection function of the reef (Wilkinson *et al.*, 1999), resulting in increased erosion, coastal flooding and loss of coastal property and habitats. In addition, coral rubble provides very limited hiding places for fish; as a result fish productivity may fall slowly and remain low until there is reasonable recovery of reef structure (Wilkinson *et al.*, 1999). Abeysirigunawardana and Ekaratne (2000) found that in Sri Lanka, fish densities decreased from 310 individuals 250 sq km^{-1} in 1998 (before the mass coral bleaching event) to 197 individuals 250 sq km^{-1} 2 years later. In addition, corallivore abundance became reduced by 78 % and that of herbivores increased by 31 %. Chabanet (2002) and Spalding and Jarvis (2002) also observed a decrease in the abundance of Chaetodontids following the 1998 bleaching event in Mayotte and the Seychelles. Riegl (2002) observed both a decrease in the number of fish species and a decrease in invertivores following the 1996 bleaching event in the Arabian Gulf. Similar changes in fish communities in Rodrigues have potential impacts to the already degraded fishing industry and to the newly developing tourism industry.

7.4 THE FUTURE OF CORAL REEFS IN RODRIGUES

Sea Surface Temperature in Rodrigues may increase over the next 20-50 years resulting in increased coral bleaching and subsequent mortality of coral colonies. Evidence suggests that coral reefs are unable to acclimatise or adapt fast enough to keep up with the rapidly warming oceans (Hoegh-Guldberg, 1999). Done (1999) suggests a number of scenarios which may occur as a result of increased coral bleaching events. A change in age structure may take place, with reefs dominated by younger, smaller coral colonies or a change in coral colony composition may occur with the community composed of more tolerant species. In the Maldives and the Arabian Gulf, coral bleaching events have already resulted in a shift from an acroporid community to one dominated by poritids and faviids (Edwards *et al.*, 2001; Riegl, 2002). In the most extreme cases there may be a phase shift to a community dominated by another group of organisms such as macro-algae (Hughes, 1994; Shulman and Robertson, 1996; Naim *et al.*, 1997). In contrast, a recent study by Baker *et al.* (2004) found that on reefs severely affected by the 1998 bleaching event, corals containing the thermally-tolerant *Symbiodinium* zooxanthellae in clade D were more abundant than on reefs unaffected by the bleaching. They showed that in Kenya 15-65 % of coral colonies contained clade D, compared with only 3 % of colonies in Mauritius and suggest that these affected reefs could become more resistant to thermal stress in the future, allowing reefs to survive longer than other reports suggest.

Cyclones occur in the Indian Ocean when temperatures exceed 26.5 °C. In addition to increased coral bleaching events, rises in sea surface temperatures may therefore also result in a higher frequency of cyclones. IPCC (2001) states that no significant trends in storm intensity and frequency are yet evident, however the report suggests a possible increase of approximately 10-20 % in the intensity of tropical cyclones. Rodrigues was hit by 7 major cyclones between 1962 and 1979; it was then not affected by another major cyclone until *Bella* in 1991, *Hansella* in 1996 and *Kalunde* in 2003. No reports are available of the impacts of previous cyclones on the coral reef, however Cyclone *Kalunde* appeared to cause coral mortality on exposed reefs down to 10-12 m depth. The interaction of coral bleaching and cyclone activity is complex, especially as the climatic conditions causing bleaching are also likely to result in an increase in cyclone activity. Rodrigues appears to have been "saved" from the 1998 bleaching event by Cyclone *Anacelle*, due to the associated cloudy conditions, and therefore despite increasing sea surface temperatures, Rodrigues may be protected from future mass bleaching by cyclones. However, a higher frequency of cyclones will increase the likelihood of Rodrigues actually being hit by a cyclone and an increase in cyclone intensity will cause greater coral mortality, a reduction in recovery time and will speed up the breakdown of the reef structure.

In addition, IPCC (2001) states that between 1990 and 2100 global sea level will rise by 5 mm yr^{-1} with a range of 2 – 9 mm yr^{-1}. In the past, the most rapid rise in sea level occurred between 15,000 and 6,000 years ago, with an average of 10 mm yr^{-1}, however over the past 3,000 years sea level has only risen at a rate of 0.1 – 0.2 mm yr^{-1} (IPCC, 2001). Maximum reef accretion rates in the Indian Ocean appear to have occurred around 7,000 years ago, when sea level was 20 m below the present levels (Stoddart, 1971). Accretion rates reached 2.55 mm yr^{-1} in Réunion and 4.73 mm yr^{-1} in Mauritius, however average accretion rates over the Holocene ranged from 1.75 mm yr^{-1} in Réunion to 2.00 mm yr^{-1} in Mauritius (Camion *et al.*, 1997). Rees *et al.* (in press) state that in the Western Indian Ocean reef accretion rates are on average 2.65 mm yr^{-1}. Historical evidence therefore suggests that reefs in Rodrigues could keep up with sea level rise. The shallow reef corals will play an important role in the ability of the reef to keep up with sea level rise, however these corals are the most vulnerable to coral bleaching as they are exposed during low tides. The reef flat area of Rodrigues, particularly in the north, is however the most degraded part of the coral reef due to trampling damage by octopus fishers, with only 2 – 5 % coral cover recorded at Totor. This suggests that only a very small proportion of the reef would actually be able to keep up with the rising sea level.

Healthy reefs are able to recover after natural disturbances such as cyclones (Connell *et al.*, 1997), however the addition of human stresses means that reefs increasingly fail to recover from natural impacts and this may result in a phase shift (Hughes, 1994; Shulman and Robertson, 1996; Naim *et al.*, 1997). Although corals in Rodrigues appear healthy, sheltered inshore reefs do appear to be affected by high sedimentation. In the Seychelles, corals in turbid environments were found to be less susceptible to coral bleaching (Turner *et al.*, 2000c) and it has been suggested that these environments act as refugia during times of thermal stress (Meesters *et al.*, 2002). The current study however suggests that high sedimentation and turbidity, caused by high rainfall and wind associated with cyclones, causes stress to coral colonies as discussed in section 7.2. This will reduce the ability of coral colonies to recover from further impacts. Although it is suggested that conditions during 2003 were unusual, an increase in cyclone frequency could result in these conditions occurring on a more frequent basis, further reducing recovery potential.

Furthermore, Rodrigues is currently undergoing rapid economic development and the Rodrigues Regional Assembly is particularly keen to develop the tourism industry. The airport runway has already been extended to allow direct flights from Réunion, the construction of 5 new hotels has already commenced and Mauritian property developers are buying much of the coastal land for further developments. An increase in tourism will have a very dramatic effect on the island and in particular on the coastal zone. In the future, hotel developments may include the construction of artificial beaches, groynes and jetties, causing local erosion; lagoon channels may be deepened in order to increase access to offshore islands such as Ile aux Cocos and seagrass beds may also be cleared to increase the area for water sports. These modifications will all have an effect on the hydrodynamics of lagoon system and the transport of sediment. Greater diving and snorkelling activity may cause physical damage to reefs and higher boat activity will cause further damage due to anchoring and pollution. An increase in tourist numbers will result in greater urbanisation with more shops and businesses in Port Mathurin and the expansion of other villages around the new tourist zones; increases in vehicles and the need for the construction of more tarmac roads will also result. An expansion in the population of the island will also result in a rise in the amount of marine pollution, land run-off and sewage and may eventually require the construction of a sewage pipeline; greater water consumption is likely to require a desalination plant. Many of these impacts have already been observed on Mauritius, where the tourist industry is well developed (Turner *et al.*, 2000a). This future development is likely to impact on the health of the coral reef, particularly the shallow reef flat, causing physical damage and weakening coral colonies, leaving them more vulnerable to natural impacts.

If minor coral bleaching events continue to occur on an annual basis as has already occurred in 2002, 2003 and possibly 2001, then this will affect the integrity of the reef structure, causing breaks in the reef's protective barrier, leaving these areas vulnerable to wave action. At present the most exposed reefs in the east of the island are protected from human impacts, due to the lack of habitation and the inaccessibility of the reefs meaning little diving or fishing takes place in these regions, suggesting that these areas are less vulnerable than more accessible reefs in the north. However, the majority of hotel developments are planned for this stretch of coastline, placing increasing pressure on these reefs. Furthermore, if a major bleaching event occurred, as in 1997/1998 the whole reef could be affected. Combined with increases in cyclone intensity and with reefs already weakened by sedimentation and other human impacts, mortality is likely be severe and recovery very slow. Rodrigues is a very isolated island exposed to high winds, particularly during the cyclone season, and large oceanic swells and, the loss of the protective barrier would result in increased costal flooding and storm damage with loss of coastal habitats and significant damage to coastal properties.

7.5 MANAGEMENT OF CORAL REEFS IN RODRIGUES

Attempts are being made to prevent the eroded soil reaching the lagoon in Rodrigues. Mangroves have been planted in several bays including Baie aux Huitres, Baie Diamont, Baie Malgache, Baie Topaze and Grande Baie (EDF, 1999; Chapman, 2000). In 1999 a 4 year anti-erosion project was commenced by the European Development Fund in collaboration with the Government of Mauritius. The project aims to rehabilitate 1,000 ha of terraces and drains, maintain filtration dykes, develop over 100 ha of new areas of forestry and pasture land, initiate reforestation of 200 ha of land owned by villagers and plant a further 40 ha of mangroves as well as organising awareness campaigns and training (EDF, 1999). At present however there is little evidence to suggest that the mangroves are reducing sediment transport to the lagoon (Lynch, *pers. comm.*). A more direct approach was investigated in a study by the European Development Fund (EDF) in 1999, assessing the feasibility of dredging the lagoon in order to remove sediment. This proposal has never been followed-up and it seems that management measures protecting the coral reef and preventing further sediment transport are likely to be more successful.

The decrease in coral growth, recruitment and regeneration as a result of high sediment/low visibility conditions, combined with increases in coastal development and possible increases in coral bleaching events and cyclones, highlights the importance of protecting these environments. West and Salm (2003) state that in order to minimise the impacts of further mass coral bleaching events Marine Protected Areas should be designed to include reefs areas where communities show natural resistance to bleaching. This would include areas of cold upwelling, fast water movement, shaded or turbid areas and communities with diverse populations with high fertilization success. At present the only marine protected areas in Rodrigues are the 5 fishing reserves, which all protect shallow inshore areas, which are now highly sedimented and contain very little coral. Shoals Rodrigues has proposed a further 4 marine reserves, which do include Totor, a site of possible resistance to bleaching due to a history of high turbidity.

The impact of land run-off on the fore reefs of Rodrigues highlights the importance of managing the land and marine environment together. The proposed UNDP/GEF protected area does combine the land and marine environment and together with the 4 Shoals reserves these would protect almost 30 % of the shallow marine environment

(Chapman and Turner, 2004). The 4 marine reserves however have a very small area and although they may be important in increasing reef fish populations, they are unlikely to play any significant role in protecting the reef as a whole from future impacts. In order to protect the integrity of the reef system from impacts such as sea level rise, coral bleaching and cyclone damage, the entire reef area requires some level of protection from future developments on the island. One solution could be to establish a Marine Zoning Plan, protecting the island and its marine resources out to the 12 nautical mile limit. This technique has already been initiated in the Socotra Archipelago, Yemen (Klaus *et al.*, 2003). The Marine Zoning Plan could include areas such as General Resource Use zones where commercial activity is able to continue, as well as National Parks, where only sustainable non-damaging activities are able to take place and Natural Sanctuaries, which receive full protection. These would be designated depending on the conservation importance and vulnerability of habitats, in full consultation with all local stakeholders.

In order to prevent this degradation of reef structure it is therefore important that management measurements are put in place in order to minimise the impact of these developments on the coral reefs. From the results of this study a number of recommendations can be proposed:

- The development of a Marine Zoning Plan, providing some level of protection for the whole coral reef system.
- Where possible coastal development work should be undertaken during the dry season, thus minimising the effect of terrestrial run-off.
- Any coastal construction work should make use of silt curtains and bunds to prevent transport of sediment to the fore reef environment.
- Future developments should have full Environmental Impact Assessments, including the setting of thresholds for parameters such as photosynthetically active radiation, dissolved oxygen and suspended sediment and feedback monitoring throughout the construction process (see Turner *et al.*, in press).

7.6 FUTURE WORK

Recent work suggests that coral bleaching events are likely to increase in the future and this may be combined with an increase in cyclone activity and sea level rise. In addition, greater developments, particularly along the coast have been proposed, possibly causing further impact to coral reef communities from sedimentation. Future work should therefore concentrate on the ability of coral reefs around Rodrigues to survive and recover from these future impacts. This could include:

- Assessment of massive coral cores to determine terrestrial influence on the inshore coral reefs.
- Determination of current patterns and sediment dynamics within Port Mathurin Bay, including sediment resuspension on the shallow submarine platform.
- Assessment of annual coral recruitment/settlement around the island, including the determination of the timing of peak coral spawning and larval dispersal patterns.
- Long-term monitoring of changes in reef structure and recovery at sites affected by the 2002 coral bleaching event.
- Quantification of the impacts of cyclones on coral reef health around Rodrigues, in terms of increased sedimentation related to high rainfall and additional physical damage to coral colonies.

7.7 CONCLUSIONS

Sediment deposition at inshore fore reef sites in Rodrigues is high and can be well above tolerable levels for coral reefs (10mg cm^{-2} d^{-1}; Rogers, 1990), suggesting that this threshold is not applicable to these reefs. Sediment deposition at these sites is likely to have been constantly high over long periods of time due to extensive deforestation in the 19th century and resuspension of marine sediments on the shallow bank. Corals at Totor and Trou Malabar do appear to be showing some morphological adaptations to the high sediment/low light conditions, with colonies exhibiting large surface areas to capture maximum light, steeper colony sides to increase passive sediment removal and tiering to increase colony height, thus reducing burial by sediment. However, during periods of high rainfall and wind, associated with cyclones, sediment deposition and turbidity increase significantly due to land run-off and sediment resuspension. Although coral reefs at all 3 sites appear healthy this increased sedimentation appears to be having a sub-lethal affect on coral colonies, causing a decrease in growth rate of branching corals, low coral recruitment and a low ability to recover from injury.

In addition to impacts from sedimentation, coral reefs in Rodrigues were affected by coral bleaching during 2002. This bleaching event was not widespread and coral mortality was restricted to sheltered sites in the north and west of the island. Where bleaching did occur however, it was severe, resulting in mortality of up to 75 % of coral colonies at some sites. One year later dead coral colonies had become heavily eroded and overgrown with turf and macro-algae. Some recovery had occurred through the re-growth of branching *Acropora* colonies and recolonisation by other species. Predicted increases in coral bleaching and cyclone activity may result in increased coral mortality and breakdown of the reef structure. The loss of the protective reef barrier will leave Rodrigues vulnerable to sea level rise and increased wave action, resulting in erosion, storm damage and coastal flooding. In addition, economic development will result in greater human impacts such as sedimentation and pollution, further weakening the reef structure. It is therefore suggested that management measures, such as the development of a Marine Zoning Plan, are put in place in order to protect the coral reef from future impacts.

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Appendix 1 Biological, Environmental and Meteorological Data

Table A1.1 Invertebrate species list for each of the 3 survey sites.

Family	Genus	Species	Totor	Trou Malabar	Chaland
Pocilloporidae	*Pocillopora*	*damicornis*	+		+
Pocilloporidae	*Pocillopora*	*eydouxi*			+
Pocilloporidae	*Pocillopora*	*verrucosa*	+	+	+
Acroporidae	*Montipora*	*sp*	+		
Acroporidae	*Montipora*	*aequituberculata*	+	+	+
Acroporidae	*Montipora*	*danae*		+	+
Acroporidae	*Montipora*	*grisea*			+
Acroporidae	*Montipora*	*mollis*			+
Acroporidae	*Montipora*	*turgescens*		+	+
Acroporidae	*Montipora*	*undata*		+	
Acroporidae	*Acropora*	*sp*	+		
Acroporidae	*Acropora*	*abrotanoides*	+	+	+
Acroporidae	*Acropora*	*austera*	+	+	+
Acroporidae	*Acropora*	*clathrata*	+	+	+
Acroporidae	*Acropora*	*cytherea*	+	+	+
Acroporidae	*Acropora*	*digitifera*			+
Acroporidae	*Acropora*	*granulosa*	+	+	
Acroporidae	*Acropora*	*hemprichii*	+	+	
Acroporidae	*Acropora*	*cf latistella*	+		
Acroporidae	*Acropora*	*nasuta*	+		
Acroporidae	*Acropora*	*nobilis*	+	+	+
Acroporidae	*Acropora*	*palmerae/pinguis*		+	
Acroporidae	*Acropora*	*samoensis*	+	+	
Acroporidae	*Acropora*	*seriata*			+
Acroporidae	*Acropora*	*valida*	+	+	+
Acroporidae	*Astreopora*	*myriophthalma*	+		
Poritidae	*Porites*	massive	+	+	+
Poritidae	*Porites*	*rus*	+	+	+
Poritidae	*Alveopora*	*allingi*		+	
Poritidae	*Alveopora*	*fenestrata*			+
Poritidae	*Alveopora*	*verrilliana*	+		+
Poritidae	*Goniopora*	*sp*	+		
Poritidae	*Goniopora*	*djiboutiensis*			+
Poritidae	*Goniopora*	*planulata*	+		
Poritidae	*Goniopora*	*stokesi*		+	
Siderastreidae	*Psammocora*	*contigua*	+		+
Siderastreidae	*Psammocora*	*profundacella*			+
Siderastreidae	*Coscinarea*	*monile*			+
Agariciidae	*Pavona*	*cactus*	+		
Agariciidae	*Pavona*	*decussata*	+		
Agariciidae	*Pavona*	*duerdeni*	+	+	
Agariciidae	*Pavona*	*frondifera*		+	
Agariciidae	*Pavona*	*varians*	+	+	+
Agariciidae	*Pachyseris*	*speciosa*	+	+	+
Fungiidae	*Fungia*	*sp*	+	+	+
Oculinidae	*Galaxea*	*fascicularis*	+	+	+
Pectiniidae	*Echinophyllia*	*aspera*	+	+	+

Pectiniidae	*Echinophyllia*	*echinata*	+	+	+
Pectiniidae	*Oxypora*	*crassispinosa*	+		+
Pectiniidae	*Oxypora*	*lacera*	+	+	+
Pectiniidae	*Mycedium*	*elephantotus*	+	+	+
Pectiniidae	*Mycedium*	*robokaki*	+		
Mussidae	*Acanthastrea*	*brevis*			+
Mussidae	*Acanthastrea*	*echinata*	+	+	+
Mussidae	*Lobophyllia*	*corymbosa*	+	+	+
Mussidae	*Lobophyllia*	*hataii*	+		+
Mussidae	*Lobophyllia*	*hemprichii*	+		+
Mussidae	*Symphyllia*	*recta*	+	+	+
Merulinidae	*Hydnophora*	*microconos*		+	+
Faviidae	*Favia*	*favus*	+		
Faviidae	*Favia*	*matthaii*	+	+	+
Faviidae	*Favia*	*maxima*			+
Faviidae	*Favia*	*speciosa*			+
Faviidae	*Favia*	*stelligera*	+	+	+
Faviidae	*Favites*	*chinensis*			+
Faviidae	*Favites*	*flexuosa*		+	
Faviidae	*Favites*	*paraflexuosa*	+	+	+
Faviidae	*Favites*	*pentagona*	+	+	+
Faviidae	*Goniastrea*	*aspera*		+	+
Faviidae	*Goniastrea*	*favulus*	+		
Faviidae	*Goniastrea*	*pectinata*	+	+	+
Faviidae	*Goniastrea*	*peresi*		+	
Faviidae	*Platygyra*	*c.f. carnosus*			+
Faviidae	*Platygyra*	*crosslandi*	+	+	+
Faviidae	*Platygyra*	*daedalea*	+	+	+
Faviidae	*Leptoria*	*phrygia*			+
Faviidae	*Oulophyllia*	*crispa*	+	+	+
Faviidae	*Oulophyllia*	*levis*		+	
Faviidae	*Leptastrea*	*pruinosa*			+
Faviidae	*Cyphastrea*	*microphthalma*		+	+
Faviidae	*Echinopora*	*forskaliana*	+	+	+
Faviidae	*Echinopora*	*gemmacea*	+	+	+
Dendrophyllidae	*Turbinaria*	*stellulata*	+	+	+
Dendrophyllidae	*Tubastrea*	*coccinea*	+		
	Millepora	*sp*	+	+	
	Sarcophyton	sp.	+	+	+
	Sinularia	sp.	+	+	+
	Xenia	sp.	+	+	+
	Soft coral				+
	Echinometra	*matthaei*	+	+	+
	Diadema	*setosum*	+	+	+
	Stichopus	*chloronatus*		+	
	Tridacna	sp.	+	+	
	Panulirus	*longipes longipes*	+	+	

Table A1.2 Survey data obtained during February – June 2002. Temperature (°C) measured using a dive computer; vertical visibility (m) measured using a Secchi disc and tidal state from data provided by the Mauritius Meteorological Services.

Name	Date	Temp	Visibility (m)	Tide	
Trou Malabar	06/02/2002	27	7.3	HW +2.5	Neap
Trou Malabar	07/02/2002	27	4.3	HW +2	Neap
Totor	11/02/2002	27	4.8	HW +1	Spring
Totor	12/02/2002	27	5.9	LW +2	Spring
Trou Malabar	13/02/2002	27	6.8	HW +2	Spring
Chaland	14/02/2002	27	6.4	HW +1	Spring
Chaland	15/02/2002	28	6.6	LW +2	Spring
Totor	18/02/2002	27	8.1	LW +2.5	Neap
Totor	18/02/2002	29	7.9	HW +0.75	Neap
Chaland	20/02/2002	27	4.6	LW +3	Neap
Totor	01/03/2002	28	5	HW +3	Spring
Totor	02/03/2002	28	3.3	HW -1	Spring
Trou Malabar	04/03/2002	28	5.4	LW +3	Neap
Trou Malabar	05/03/2002	28	4.4	LW + 2.33	Neap
Trou Malabar	12/03/2002	28	6.5		Spring
Trou Malabar	13/03/2002	28	8.6	LW +3	Spring
Totor	18/03/2002	28	7.3	LW +2.5	Neap
Totor	19/03/2002	28	4.5	LW +1	Neap
Chaland	26/03/2002	28	5.8	LW -2	Spring
Chaland	27/03/2002	27	4.9	HW +3	Spring
Totor	28/03/2002	27	4.9	HW -1.67	Spring
Totor	29/03/2002	28		LW +3	Spring
Chaland	02/04/2002	27	7.2	LW +2.5	Neap
Trou Malabar	11/04/2002	27	6.9	HW +2	Spring
Trou Malabar	12/04/2002	27	5.2	LW +2	Spring
Totor	19/04/2002	27	7.7	HW -2.67	Neap
Totor	20/04/2002	27	6.4	HW +2.75	Neap
Trou Malabar	23/04/2002	27		LW -0.75	Neap
Chaland	26/04/2002	27	9.0	HW +2	Spring
Chaland	27/04/2002	27	7.4	LW -2	Spring
Totor	30/04/2002	26	5.1	HW -2.5	Spring
Chaland	07/05/2002	26	7.7	LW –2	Neap
Chaland	08/05/2002	26	7.3	LW -1	Spring
Trou Malabar	20/05/2002	25	7.6	LW +1	Neap
Trou Malabar	21/05/2002	25	9.0	LW +0.33	Neap
Trou Malabar	22/05/2002	25	7.2	LW -0.33	Neap
Totor	23/05/2002	25	8.4	LW -1	Spring
Totor	24/05/2002	25		LW -2.5	Spring
Chaland	27/05/2002	25	6.0	LW +0.33	Spring
Chaland	28/05/2002	25	6.0	LW	Spring
Chaland	04/06/2002	25	6.6	HW +1.5	Neap
Chaland	05/06/2002	25		HW	Neap
Totor	17/06/2002	24	9.3	LW	Neap
Chaland	18/06/2002	24		LW +2.67	Neap
Trou Malabar	19/06/2002	24	6.9	LW +1	Neap
Trou Malabar	20/06/2002	24		LW -1	Neap

Table A1.3 Survey data obtained during April – August 2003. Temperature (°C) measured using a dive computer; vertical (V) and horizontal (H) visibility (metres) measured using a Secchi disc, tidal state from data provided by the Mauritius Meteorological Services and weather observations.

Site	Date	Temp	Visibility (m)		Tide		Weather
		(°C)	(V)	(H)			
Totor	07/04/2003	27	3.3	5.5	HW	Neap	Cloudy
Totor	08/04/2003	27	3.6	3.1	HW -1.5	Neap	Cloudy
Totor	09/04/2003	27	3.0	2.5	LW +2.33	Neap	Cloudy
Trou Malabar	10/04/2003	27	4.0	3.2	LW -1.5	Neap	Cloudy
Trou Malabar	11/04/2003	27	3.9	2.7	LW -2.33	Neap	Sunny
Chaland	14/04/2003	28	4.1	5.0	HW +2	Spring	Sunny
Chaland	16/04/2003	28	3.1	4.1	LW +3	Spring	Sunny
Totor	19/05/2003	26	5.0	4.1	LW +1	Spring	Cloudy, Windy
Totor	20/05/2003	26	5.3	4.3	LW	Neap	Cloudy
Totor	21/05/2003	26	5.9	6.1	LW	Neap	Cloudy
Trou Malabar	22/05/2003	26	12.4	6.8	LW - 1.5	Neap	Sunny
Trou Malabar	23/05/2003	26	10.0	11.3	LW - 2.5	Neap	Sunny, Windy
Trou Malabar	26/05/2003	27	11.5	7.7	HW	Neap	Sunny, Calm
Totor	27/05/2003	26	5.6	7.7	HW - 0.5	Neap	Cloudy, Calm
Totor	02/06/2003	25	6.4	5.9	LW - 1.67	Spring	Sunny, Windy
Chaland	03/06/2003	25	6.0	9.8	HW +1.67	Spring	Sunny, Windy
Chaland	04/06/2003	25	6.0	6.2	LW + 1.75	Spring	Sunny, Windy
Chaland	05/06/2003	25	6.0	12.3	LW + 1.25	Neap	Cloudy, Windy
Totor	09/06/2003	25	7.6	3.7	LW - 1	Neap	Sunny, Calm
Totor	10/06/2003	25	9.2	6.1	HW +3	Neap	Sunny, Calm
Totor	11/06/2003	25		10.6	HW - 1	Spring	Sunny, Calm
Chaland	12/06/2003	25	7.5	9.6	LW - 2.67	Spring	Sunny
Chaland	13/06/2003	25	9.6	13.0	HW - 1	Spring	Sunny, Windy
Totor	17/06/2003	25		7.8	LW +2.5	Spring	Sunny, Windy
Totor	18/06/2003	25	5.2	5.1	HW - 1	Neap	Sunny, Windy
Totor	19/06/2003	25	6.3	5.4	LW	Neap	Sunny, Windy
Chaland	20/06/2003	25		13.4	LW +1.33	Neap	Sunny, Windy
Trou Malabar	25/06/2003	24	10.9	13.7	HW	Neap	Sunny, Windy

Trou Malabar	26/06/2003	24	10.9	11.9	HW	Spring	Sunny, Windy
Chaland	02/07/2003	24		11.7	LW +2.24	Spring	Sunny, Windy
Chaland	03/07/2003	24		15.3	LW +2	Spring	Sunny, Windy
Chaland	04/07/2003	24		10.1	LW +1.5	Neap	Sunny
Totor	07/07/2003	24	6.1	7.5	LW - 1.33	Neap	Raining
Trou Malabar	10/07/2003	24		3.6	HW +3	Neap	Sunny, Windy
Trou Malabar	11/07/2003	24	7.8	7.5	HW	Spring	Sunny
Totor	14/07/2003	23	5.6	5.0	HW - 3	Spring	Cloudy, Windy
Chaland	15/07/2003	23	5.5	7.6	HW - 3	Spring	Cloudy
Totor	15/07/2003	24	5.9	5.6	HW +1	Spring	Cloudy
Totor	16/07/2003	23	4.2	3.8	HW -0.33	Spring	Cloudy, Windy
Totor	17/07/2003	23	3.5	4.1	HW -0.33	Spring	Cloudy, Windy
Trou Malabar	18/07/2003	23			LW -0.5	Neap	Sunny, Windy
Trou Malabar	21/07/2003	24		6.3	LW -1.5	Neap	Sunny
Chaland	22/07/2003	23	6.4	8.2	LW - 3	Neap	Sunny
Totor	22/07/2003	24	7.3	8.2	LW +1.5	Neap	Sunny
Totor	23/07/2003	23		5.4	LW - 3	Neap	Sunny
Trou Malabar	25/07/2003	23	4.9	9.6	HW -2	Neap	Cloudy
Trou Malabar	28/07/2003	24	9.4	9.6	HW +1	Spring	Cloudy
Trou Malabar	29/07/2003	23	9.7	7.8	HW - 2.5	Spring	Sunny
Chaland	31/07/2003	23		7.2	HW -0.5	Spring	Sunny
Chaland	01/08/2003	23	8.0	12.1	LW +2	Spring	Sunny
Totor	04/08/2003	23	10.3	5.9	LW	Neap	Sunny, Windy
Chaland	05/08/2003	23	8.3	13.4	LW +1.67	Neap	Cloudy, Windy
Trou Malabar	08/08/2003	23	6.4	7.0	HW +3	Neap	Sunny, Windy
Totor	14/08/2003	23		3.1	LW +2	Spring	Sunny, Windy
Totor	15/08/2003	23	3.6	2.9	LW+2.5	Spring	Sunny, Windy
Totor	18/08/2003	23	6.2	4.8	HW -2.33	Neap	Sunny
Chaland	19/08/2003	23		10.6	LW +2.5	Neap	Sunny, Windy
Trou Malabar	22/08/2003	23	6.8	5.1	LW - 1.67	Neap	Sunny
Trou Malabar	25/08/2003	23	9.1	8.6	HW +2.5	Spring	Cloudy, Calm
Trou Malabar	27/08/2003	23		10.4	LW +2	Spring	Sunny
Chaland	28/08/2003	23	10.4	6.7	LW +2	Spring	Sunny, Calm
Chaland	28/08/2003	23		5.9	HW - 0.5	Spring	Sunny, Calm

Table A1.4 Temperature measurements (°C) at the survey depth (10-12m) during April-June 2002 and 2003.

2002			2003		
April	**May**	**June**	**April**	**May**	**June**
27.761	26.590	25.338	27.560	25.936	25.057
27.238	25.490	23.576	27.059	25.924	25.225
27.181	25.754	23.922	27.010	25.749	25.871
27.347	25.476	24.265	28.173	25.703	25.644
27.352	25.087	24.105		26.471	25.540
27.155	24.824				24.780
27.099	25.056				24.500
26.974	24.677				24.281
27.536					
27.307					
27.600					

Table A1.5 Temperature measurements (°C) at the surface during April-June 2002 and 2003.

2002			2003		
April	**May**	**June**	**April**	**May**	**June**
27.761	26.588	25.331	27.444	25.943	25.079
27.340	25.566	23.615	27.046	25.913	25.265
27.510	25.752	23.933	27.129	25.745	26.101
27.539	25.525	24.263	28.173	25.729	25.843
27.152	25.473	24.109		26.556	25.569
27.011	25.438				24.772
27.084	25.175				24.518
28.000	25.132				24.266
27.650	25.277				
27.994					

Table A1.6 Salinity measurements at the survey depth (10-12m) during April-June 2002 and 2003.

2002			2003		
April	**May**	**June**	**April**	**May**	**June**
35.056	35.107	34.752	34.892	34.887	34.879
35.067	35.303	34.972	34.660	34.910	34.983
34.975	35.240	35.007	34.542	34.928	34.835
35.204	35.244	34.971	34.895	34.861	34.888
35.147	35.348	35.041		34.727	34.859
35.159	35.301				35.027
35.084	35.127				34.979
34.974	35.232				35.182
34.994					
35.453					
35.023					

Table A1.7 Salinity measurements at the surface during April-June 2002 and 2003.

	2002			**2003**	
April	**May**	**June**	**April**	**May**	**June**
35.129	35.13	34.864	34.384	35.477	34.849
34.959	35.218	34.95	34.597	34.882	34.831
35.187	35.277	35.005	34.553	34.957	34.744
35.223	35.339	34.972	34.972	34.879	34.871
34.591	35.414	35.003		34.782	34.924
34.938	35.432				34.956
35.048	35.135				35.040
35.141	35.051				34.994
35.076					

Table A1.8 Photosynthetically active radiation (PAR) measured at Totor between 3rd June and 3rd July 2002.

Depth	**03/06/02**	**05/06/02**	**13/06/02**	**17/06/02**	**19/06/02**
0	144.75	1349.50	769.35	581.15	529.70
1	117.35	967.40	548.40	450.80	452.50
2	107.79	688.90	436.50	374.65	355.10
3	107.04	421.05	373.30	347.95	332.55
4	105.78	364.60	250.80	301.40	323.00
5	103.12	437.05	214.40	276.05	323.35
6	94.87	357.40	220.60	255.05	297.05
7	86.25	410.35	178.15	235.60	264.70
8	79.98	404.55	182.30	209.90	255.80
9	70.43	348.30	150.15	193.35	237.05
10	64.56	317.00	130.05	164.15	218.55
11	56.48	280.25	117.85	152.40	189.40
12	48.46	160.60	101.84	139.70	176.95
13			83.50	109.50	159.25
14			66.07	91.13	130.25
15			51.03	73.11	127.65

Depth	**21/06/02**	**01/07/02**	**02/07/02**	**03/07/02**
0	162.75	1269.30	430.20	271.60
1	119.64	1131.50	253.55	291.25
2	96.93	825.20	207.60	228.30
3	90.63	1095.95	199.80	193.40
4	90.71	820.25	215.00	181.25
5	79.02	696.65	203.05	176.00
6	76.89	504.00	178.95	155.90
7	71.15	547.00	182.15	142.00
8	64.77	442.80	159.35	126.20
9	59.99	496.55	153.80	118.80
10	45.17	395.60	137.15	111.09
11	40.57	355.80	133.40	99.68
12	34.39	290.85	114.50	86.17
13		295.05	108.05	82.42
14		258.30	102.85	66.17
15		231.75	99.98	63.86

Table A1.9 Photosynthetically active radiation (PAR) measured at Chaland between 4th June and 4th July 2002.

Depth	04/06/02	05/06/02	05/06/02	11/06/02	18/06/02
0	328.35	592.50	1432.00	1216.50	1123.50
1	440.64	519.50	881.65	893.25	811.50
2	332.70	222.25	819.90	580.00	626.20
3	351.29	375.45	662.15	552.30	416.15
4	338.85	296.75	462.25	498.40	371.60
5	220.60	282.90	319.50	455.05	282.05
6	308.95	270.60	379.50	371.95	228.80
7	261.75	185.15	317.40	361.95	237.30
8	213.00	156.45	365.10	343.90	165.85
9	223.20	137.15	324.15	327.65	172.35
10	198.65	161.00	260.95	227.95	190.40
11	181.50	137.00	265.95	247.00	190.00
12	124.87	122.20	216.55	261.05	170.80
13	87.08	113.70	208.45	216.05	171.85
14	82.51	82.35	179.25	195.95	172.15
15	83.24	52.20	170.55	178.15	163.25
16	46.63	49.39	147.10	181.95	134.55
17	35.87	76.75	137.60	158.45	139.10
18	30.76		118.78	146.60	123.85

Depth	27/06/02	01/07/02	02/07/02	03/07/02	04/07/02
0	1457.00	1055.90	212.95	547.60	1188.40
1	764.50	1315.00	211.55	439.00	889.90
2	1061.65	932.30	494.80	227.00	745.55
3	482.80	2164.50	331.30	210.30	590.80
4	595.90	897.95	489.05	211.05	696.65
5	402.15	679.30	476.90	177.90	549.70
6	371.80	567.15	630.50	184.65	446.00
7	418.80	632.30	508.00	204.20	403.05
8	404.25	543.75	551.55	251.70	364.40
9	353.85	456.15	516.20	203.65	338.05
10	286.40	561.05	486.00	203.35	322.05
11	261.90	424.80	395.70	177.80	279.70
12	266.00	413.25	453.50	180.90	261.55
13	238.10	383.90	360.15	193.65	224.60
14	264.70	387.85	335.25	192.50	210.45
15	211.85	357.30	312.05	172.70	179.90
16	217.55	317.95	319.55	166.00	161.90
17	200.40	303.60	283.45	159.50	146.60
18	165.80	273.05	265.55	137.55	129.95

Table A1.10 Sediment dry weight (g) and sediment deposition rate (mg cm^{-2} d^{-1}) at Totor between February and June 2002.

February-March		March-April		April-May		May-June	
Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})
9.29	12.37	50.58	35.78	44.67	29.74	16.78	15.83
12.02	16.00	51.21	36.22	46.89	31.22	14.05	13.25
9.72	12.94	50.34	35.61	50.72	33.77	16.07	15.16
10.58	14.09	47.75	33.78	45.62	30.37	12.33	11.63
13.82	18.40	41.72	29.51	53.51	35.62	16.97	16.00
12.68	16.88	49.08	34.72	30.08	20.03	13.29	12.53
11.70	15.58	45.71	32.33	47.23	31.44	17.18	16.20
11.32	15.07	47.72	33.75	43.96	29.27	17.21	16.23
9.61	12.80	59.39	42.01	42.31	28.17	18.04	17.01

Table A1.11 Sediment dry weight (g) and sediment deposition rate (mg cm^{-2} d^{-1}) at Totor between April and August 2003.

April-May		May-June		June-July		July-August	
Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})
123.62	69.95	10.33	8.35	26.27	20.50	37.64	31.56
102.00	57.72	9.49	7.67	31.86	24.87	32.96	27.63
103.26	58.43	9.14	7.39	33.43	26.09	33.44	28.03
100.46	56.85	12.00	9.70	34.32	26.79	29.12	24.41
114.48	64.78	13.13	10.61	35.87	28.00	40.82	34.22
132.33	74.88	11.34	9.17	42.09	32.85	29.59	24.81
119.30	67.51	10.13	8.19	31.98	24.96	39.79	33.36
114.30	64.68	12.34	9.98	38.60	30.13	28.87	24.20
110.89	62.75	10.88	8.80	24.75	19.32	32.98	27.65

Table A1.12 Sediment dry weight (g) and sediment deposition rate (mg cm^{-2} d^{-1}) at Trou Malabar between February and June 2002.

February-March		March-April		April-May		May-June	
Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})	Dry Wt (g)	Deposition (mg cm^{-2} d^{-1})
2.73	2.29	3.02	2.28	12.91	7.49	5.14	4.01
1.13	0.95	3.67	2.77	9.25	5.37	5.56	4.34
1.78	1.49	5.28	3.98	7.28	4.23	4.88	3.81
2.06	1.73	4.73	3.57	9.63	5.59	5.34	4.17
2.80	2.35	4.53	3.42	10.65	6.18	4.10	3.20
2.30	1.93	3.48	2.63	14.61	8.48	6.84	5.34
2.11	1.77	3.90	2.94	11.34	6.58	5.73	4.47
2.57	2.15	5.09	3.84	10.56	6.13	5.90	4.61
2.73	2.29	5.45	4.11	9.83	5.71	6.28	4.90

Table A1.13 Sediment dry weight (g) and sediment deposition rate (mg cm^{-2} d^{-1}) at Trou Malabar between April and August 2003.

April-May		**May-June**		**June-July**		**July-August**	
Dry Wt (g)	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**
191.56	103.24	13.84	9.49	45.68	32.31	60.87	51.03
184.00	99.16	20.24	13.88	58.23	41.19	51.96	43.56
199.50	107.52	18.45	12.66	48.86	34.56	69.47	58.24
171.84	92.61	17.52	12.02	48.77	34.50	63.24	53.02
204.06	109.97	18.05	12.38	51.29	36.28	71.28	59.76
211.28	113.87	16.63	11.41	57.99	41.02	56.34	47.23
114.68	61.80	5.31	3.64	41.54	29.38	47.34	39.69
147.75	79.63	18.69	12.82	57.70	40.81	65.13	54.60
		16.85	11.56	47.31	33.46	57.34	48.07

Table A1.14 Sediment dry weight (g) and sediment deposition rate (mg cm^{-2} d^{-1}) at Chaland between February and June 2002.

February-March		**March-April**		**April-May**		**May-June**	
Dry Wt (g)	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**
0.74	0.49	2.70	1.97	1.92	1.40	2.27	2.45
1.46	0.97	2.65	1.93	2.11	1.54	1.96	2.11
2.58	1.72	2.09	1.53	2.07	1.51	2.26	2.44
1.39	0.93	3.49	2.55	2.17	1.58	0.76	0.82
0.87	0.58	4.78	3.49	2.32	1.69	1.96	2.11
1.80	1.20	1.67	1.22	2.66	1.94	1.12	1.21
1.60	1.07	2.41	1.76	1.96	1.43	1.60	1.72
1.21	0.81	2.52	1.84	2.93	2.14	2.69	2.90
2.11	1.40	2.52	1.84	2.39	1.75	2.22	2.39

Table A1.15 Sediment dry weight (g) and sediment deposition rate (mg cm^{-2} d^{-1}) at Chaland between April and August 2003.

April-May		**May-June**		**June-July**		**July-August**	
Dry Wt (g)	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**	**Dry Wt (g)**	**Deposition (mg cm^{-2} d^{-1})**
18.12	8.20	3.90	3.15	9.42	7.62	5.93	4.97
1.12	0.51	3.59	2.90	9.95	8.04	5.18	4.34
2.99	1.35	2.04	1.65	8.98	7.26	4.71	3.95
12.40	5.61	2.33	1.88	4.48	3.62	2.79	2.34
9.25	4.19	3.22	2.60	7.12	5.76	4.57	3.83
22.29	10.09	3.74	3.02	3.50	2.83	4.41	3.70
16.74	7.58	3.76	3.04	9.21	7.45	3.04	2.55
6.72	3.04	2.85	2.30	10.56	8.54	7.28	6.10
17.23	7.80	4.36	3.52	11.20	9.05	3.93	3.29

Table A1.16 Dry weight of sediment (g) within each grain size category at Totor between February and June 2002.

	Sediment dry weight (g)						
	>2mm	**>1mm**	**>500µm**	**>250µm**	**>125um**	**>63um**	**<63um**
February - March	0.00	0.45	1.48	2.85	2.78	0.45	0.00
	0.00	0.49	1.94	2.63	4.21	1.41	0.13
	0.00	0.30	1.35	2.04	3.76	1.02	0.03
	0.00	0.35	1.61	2.08	4.39	0.95	0.00
	0.08	0.70	2.30	3.15	5.00	1.21	0.05
	0.00	0.23	1.47	1.92	3.05	3.27	0.67
	0.00	0.43	1.66	1.81	2.91	3.21	0.63
	0.00	0.65	1.71	1.98	2.17	2.49	1.65
	0.00	0.50	1.39	1.61	1.43	3.22	0.62
March – April	0.00	0.45	1.48	2.85	2.78	0.45	0.00
	0.00	0.49	1.94	2.63	4.21	1.41	0.13
	0.00	0.30	1.35	2.04	3.76	1.02	0.03
	0.00	0.35	1.61	2.08	4.39	0.95	0.00
	0.08	0.70	2.30	3.15	5.00	1.21	0.05
	0.00	0.23	1.47	1.92	3.05	3.27	0.67
	0.00	0.43	1.66	1.81	2.91	3.21	0.63
	0.00	0.65	1.71	1.98	2.17	2.49	1.65
	0.00	0.50	1.39	1.61	1.43	3.22	0.62
April - May	0.00	0.00	0.63	8.28	18.30	8.83	4.17
	0.00	0.00	0.66	10.25	22.96	11.07	3.32
	0.00	0.00	2.17	14.21	21.13	8.18	1.45
	0.00	0.00	0.81	11.52	24.92	9.35	0.71
	0.00	0.00	0.55	10.03	21.81	7.11	0.43
	0.00	0.00	0.47	10.86	21.99	9.48	0.79
	0.00	0.00	0.74	13.87	23.49	5.88	0.53
	0.00	0.00	0.61	15.95	29.02	9.59	0.77
May - June	0.00	0.04	5.00	7.76	22.33	8.50	0.70
	0.00	0.02	6.16	6.87	17.29	13.12	2.54
	0.00	0.06	7.87	8.27	19.23	11.94	3.00
	0.04	0.05	5.51	7.71	18.99	10.43	1.97
	0.00	0.00	2.98	4.77	11.82	8.82	1.15
	0.00	0.00	7.40	7.03	16.67	12.39	2.93
	0.00	0.00	6.01	6.94	18.80	10.42	1.09
	0.00	0.00	4.88	6.96	18.78	9.91	1.23

Table A1.17 Dry weight of sediment (g) within each grain size category at Totor between April and August 2003.

	Sediment dry weight (g)						
	>2mm	>1mm	>500µm	>250µm	>125um	>63um	<63um
April - May	0.00	0.00	0.06	3.51	88.69	30.43	1.65
	0.00	0.00	0.08	2.89	68.99	23.65	2.65
	0.00	0.00	0.08	1.07	74.97	26.22	1.56
	0.00	0.00	0.04	0.52	70.15	23.00	3.79
	0.09	0.00	0.19	8.20	72.16	30.75	2.96
	0.00	0.00	0.14	9.86	90.46	29.98	1.56
	0.00	0.00	0.06	10.25	81.79	25.69	0.91
	0.00	0.00	0.05	6.43	76.52	31.21	2.73
	0.00	0.00	0.08	8.01	75.75	15.23	0.94
May - June	0.00	0.00	0.00	0.04	6.73	1.18	1.42
	0.00	0.00	0.04	0.07	6.77	1.08	0.32
	0.00	0.00	0.00	0.02	5.45	1.90	1.81
	0.00	0.00	0.00	0.03	6.13	4.88	0.71
	0.00	0.00	0.02	0.06	9.01	2.99	0.60
	0.00	0.00	0.02	0.08	9.04	1.65	0.34
	0.00	0.00	0.03	0.04	7.31	1.89	0.16
	0.00	0.00	0.02	0.03	5.73	3.30	0.60
	0.00	0.00	0.00	0.04	6.73	1.18	1.42
June - July	0.00	0.00	0.02	0.07	12.75	9.72	3.33
	0.00	0.00	0.00	0.03	16.99	10.89	3.56
	0.00	0.00	0.00	0.02	21.36	9.33	1.51
	0.00	0.00	0.00	0.04	20.87	9.43	4.78
	0.00	0.00	0.00	0.03	17.43	11.25	6.97
	0.00	0.00	0.02	0.07	32.13	7.58	0.52
	0.00	0.00	0.02	0.08	22.32	7.45	0.63
	0.00	0.00	0.02	0.03	22.27	11.25	3.44
July - August	0.00	0.00	0.03	0.09	15.00	15.69	1.07
	0.00	0.00	0.00	0.06	14.06	16.56	1.86
	0.00	0.00	0.00	0.06	12.74	14.38	1.47
	0.00	0.00	0.03	0.10	21.97	16.39	1.47
	0.00	0.00	0.00	0.09	11.00	13.58	4.24
	0.00	0.00	0.02	0.15	18.46	17.22	3.53
	0.00	0.00	0.00	0.09	12.20	12.38	4.00

Table A1.18 Dry weight of sediment (g) within each grain size category at Trou Malabar between February and June 2002.

	Sediment dry weight (g)						
	>2mm	**>1mm**	**>500µm**	**>250µm**	**>125um**	**>63um**	**<63um**
February - March	0.02	0.07	0.24	0.52	1.11	0.65	0.09
	0.00	0.05	0.12	0.18	0.28	0.29	0.12
	0.00	0.04	0.12	0.20	0.49	0.64	0.07
	0.00	0.04	0.19	0.35	0.40	0.68	0.18
	0.00	0.03	0.24	0.46	0.58	1.02	0.29
	0.00	0.03	0.14	0.32	0.56	0.87	0.13
	0.00	0.04	0.26	0.36	0.55	0.67	0.14
	0.00	0.03	0.18	0.41	0.52	1.04	0.08
	0.02	0.07	0.24	0.52	1.11	0.65	0.09
March – April	0.00	0.00	0.16	0.39	0.62	0.91	0.43
	0.00	0.00	0.18	0.52	0.81	1.41	0.55
	0.00	0.00	0.30	0.75	1.12	1.73	1.11
	0.00	0.00	0.00	0.82	0.73	1.27	0.98
	0.00	0.00	0.23	0.64	0.99	1.84	0.54
	0.00	0.00	0.21	0.50	0.66	1.11	0.74
	0.00	0.00	0.26	0.62	0.75	1.06	1.06
	0.14	0.00	0.44	0.80	0.98	1.19	1.29
	0.00	0.00	0.39	0.80	1.03	1.64	1.29
April - May	0.00	0.00	1.37	1.89	3.02	3.67	2.03
	0.00	0.00	0.93	1.17	1.51	2.91	1.98
	0.00	0.00	0.78	0.99	1.40	1.41	2.08
	0.00	0.03	0.77	1.23	2.04	2.92	2.04
	0.00	0.00	1.36	1.50	1.83	2.47	2.63
	0.25	0.00	1.42	2.02	3.20	4.75	2.20
	0.27	0.00	1.61	1.71	2.17	2.23	2.44
	0.00	0.00	1.17	1.34	1.95	2.54	2.68
May - June	0.05	0.43	0.58	0.65	0.78	1.11	0.89
	0.17	0.58	0.58	0.56	1.06	1.55	0.47
	0.31	0.38	0.60	0.62	0.94	1.16	1.14
	0.00	0.46	0.71	0.66	1.05	1.38	0.48
	0.03	0.32	0.47	0.43	0.72	0.71	0.15
	0.36	0.81	0.83	0.70	0.82	1.28	1.54
	0.00	0.55	0.66	0.76	1.28	1.47	0.47
	0.04	0.77	0.80	0.68	1.04	1.55	0.21

Table A1.19 Dry weight of sediment (g) within each grain size category at Trou Malabar between April and August 2003.

	Sediment dry weight (g)						
	>2mm	**>1mm**	**>500µm**	**>250µm**	**>125um**	**>63um**	**<63um**
April - May	0.00	0.00	0.33	2.94	118.23	66.63	2.26
	0.00	0.06	0.40	1.97	67.78	105.95	10.49
	0.00	0.00	0.10	1.28	113.50	79.32	5.84
	0.00	0.04	0.23	1.09	55.26	83.09	33.21
	0.00	0.06	0.18	1.76	86.49	93.74	19.89
	0.00	0.00	0.02	0.71	120.11	81.77	10.02
	0.00	0.04	0.20	1.22	67.81	42.55	4.02
	0.00	0.00	0.02	0.33	84.16	55.94	8.60
	0.00	0.00	0.33	2.94	118.23	66.63	2.26
May - June	0.00	0.00	0.00	0.15	3.26	5.54	4.42
	0.00	0.00	0.00	0.38	6.89	8.70	3.92
	0.00	0.00	0.00	0.08	4.65	10.32	1.81
	0.00	0.00	0.00	0.14	4.97	6.81	4.15
	0.00	0.00	0.02	0.20	4.10	7.62	5.41
	0.00	0.00	0.06	0.38	4.67	7.65	2.92
	0.00	0.00	0.00	0.05	0.72	2.39	2.21
	0.00	0.00	0.03	0.14	5.24	8.26	4.33
	0.00	0.00	0.00	0.23	4.37	6.39	4.84
June - July	0.00	0.00	0.00	0.07	30.32	15.22	0.53
	0.00	0.00	0.00	0.04	40.08	18.86	0.92
	0.00	0.00	0.00	0.09	39.63	11.21	0.41
	0.00	0.00	0.03	0.09	36.69	12.13	0.77
	0.00	0.00	0.00	0.03	26.00	24.75	0.78
	0.00	0.00	0.00	0.04	27.36	27.59	2.93
	0.00	0.00	0.02	0.05	20.13	19.78	1.63
	0.00	0.00	0.00	0.02	25.77	30.04	2.13
July - August	0.00	0.00	0.00	0.05	19.78	35.42	6.38
	0.00	0.00	0.02	0.15	16.19	26.05	9.31
	0.00	0.03	0.03	0.08	22.98	33.28	12.51
	0.00	0.00	0.00	0.08	19.10	33.44	9.40
	0.00	0.00	0.03	0.11	18.01	31.18	11.78
	0.00	0.02	0.06	0.37	19.87	29.67	5.86
	0.00	0.00	0.00	0.02	13.74	24.01	9.14
	0.00	0.00	0.02	0.08	18.61	32.93	13.02

Table A1.20 Dry weight of sediment (g) within each grain size category at Chaland between February and May 2002.

	Sediment dry weight (g)						
	>2mm	**>1mm**	**>500µm**	**>250µm**	**>125um**	**>63um**	**<63um**
February - March	0.00	0.00	0.02	0.06	0.12	0.26	0.14
	0.06	0.00	0.09	0.19	0.26	0.38	0.33
	0.11	0.06	0.19	0.32	0.38	1.05	0.31
	0.00	0.00	0.06	0.15	0.25	0.40	0.43
	0.02	0.00	0.02	0.08	0.14	0.17	0.28
	0.00	0.00	0.12	0.23	0.31	0.40	0.55
	0.00	0.00	0.05	0.15	0.28	0.67	0.22
	0.00	0.02	0.06	0.12	0.25	0.50	0.23
	0.00	0.00	0.13	0.30	0.40	0.68	0.44
March – April	0.00	0.00	0.03	0.41	1.54	0.43	0.15
	0.00	0.00	0.05	0.26	1.37	0.60	0.28
	0.00	0.00	0.04	0.18	1.08	0.53	0.17
	0.00	0.00	0.04	0.25	2.06	0.78	0.20
	0.00	0.00	0.05	0.36	3.00	1.07	0.18
	0.00	0.00	0.05	0.18	0.80	0.51	0.12
	0.00	0.00	0.07	0.30	0.92	0.72	0.32
	0.00	0.00	0.04	0.23	1.17	0.68	0.31
	0.00	0.00	0.06	0.31	0.97	0.88	0.19
April - May	0.00	0.00	0.25	0.37	0.44	0.57	0.11
	0.00	0.00	0.12	0.29	0.40	1.10	0.11
	0.00	0.00	0.25	0.40	0.43	0.67	0.20
	0.25	0.00	0.20	0.25	0.43	0.19	0.02
	0.00	0.00	0.27	0.42	0.45	0.61	0.35
	0.00	0.00	0.19	0.36	0.43	0.99	0.49
	0.00	0.00	0.30	0.45	0.49	0.40	0.10
	0.00	0.00	0.38	0.50	0.56	0.88	0.41

Table A1.21 Dry weight of sediment (g) within each grain size category at Chaland between April and August 2003.

	Sediment dry weight (g)						
	>2mm	**>1mm**	**>500µm**	**>250µm**	**>125um**	**>63um**	**<63um**
April - May	0.00	0.00	0.05	0.25	9.61	5.72	0.75
	0.00	0.00	0.03	0.02	0.40	0.63	0.60
	0.00	0.00	0.02	0.10	1.09	1.12	1.16
	0.00	0.03	0.10	0.45	5.53	2.60	2.30
	0.00	0.00	0.05	0.21	1.51	5.31	1.96
	0.00	0.00	0.02	0.16	11.23	8.01	1.21
	0.00	0.00	0.04	0.11	10.46	4.01	1.72
	0.00	0.03	0.06	0.20	3.20	1.84	0.94
	0.02	0.00	0.03	0.44	11.42	4.44	0.30
May - June	0.00	0.00	0.02	0.21	1.68	1.29	1.05
	0.00	0.00	0.02	0.15	0.83	1.16	1.04
	0.00	0.00	0.02	0.16	0.57	0.91	0.42
	0.00	0.00	0.02	0.13	0.90	0.95	0.94
	0.00	0.00	0.00	0.20	0.63	0.85	1.11
	0.00	0.00	0.02	0.18	0.68	0.62	0.78
	0.00	0.00	0.00	0.13	1.50	1.07	0.71
	0.00	0.00	0.02	0.06	0.55	0.46	0.87
	0.00	0.00	0.00	0.25	2.21	1.45	0.26
June - July	0.00	0.00	0.03	0.05	7.94	2.04	0.33
	0.00	0.00	0.00	0.05	6.45	2.29	0.82
	0.00	0.00	0.03	0.05	5.84	2.69	0.34
	0.00	0.00	0.02	0.09	6.50	2.96	1.21
	0.00	0.00	0.00	0.04	4.91	1.44	0.50
	0.00	0.00	0.00	0.27	2.37	0.62	0.08
	0.00	0.00	0.02	0.08	6.65	1.29	0.34
	0.00	0.00	0.03	0.11	7.36	2.72	0.21
July - August	0.00	0.00	0.04	0.10	1.92	2.32	1.36
	0.00	0.00	0.00	0.05	1.45	2.32	1.13
	0.00	0.00	0.00	0.03	1.60	2.06	0.88
	0.00	0.00	0.00	0.03	0.86	0.99	0.90
	0.00	0.00	0.00	0.02	1.68	1.31	1.49
	0.00	0.00	0.00	0.06	1.27	1.77	1.18
	0.00	0.00	0.02	0.06	0.86	1.10	0.87
	0.00	0.03	0.00	0.12	2.38	3.07	1.66

Table A1.22 Ash free dry weight (g) and % organic content for sediment samples collected at the 3 survey sites in March 2002.

Site	Dry Wt (g)	Ash free Dry Wt (g)	% Organics
Totor	84.996	73.006	14.11
	350.654	310.764	11.38
	386.373	340.443	11.89
Trou Malabar	30.752	26.952	12.36
	86.237	76.378	11.43
Chaland	22.831	20.026	12.29
	16.622	14.483	12.87
	10.067	8.644	14.14

Table A1.23 Ash free dry weight (g) and % organic content for sediment samples collected at Totor between April and August 2003.

Date	Dry Wt (g)	Ash free Dry Wt (g)	% Organics
April - May	49.308	43.828	11.11
	49.227	43.742	11.14
	48.288	42.862	11.24
May - June	19.011	16.615	12.60
	20.951	18.283	12.73
	19.749	17.239	12.71
June - July	46.778	41.789	10.67
	48.421	43.209	10.76
	48.863	43.603	10.76
July - August	38.911	42.903	12.28
	49.808	44.650	10.36
	47.956	42.870	10.61

Table A1.24 Ash free dry weight (g) and % organic content for sediment samples collected at Trou Malabar between April and August 2003.

Date	Dry Wt (g)	Ash free Dry Wt (g)	% Organics
April - May	48.442	45.161	6.77
	50.121	47.250	5.73
	48.676	45.894	5.72
May - June	19.485	17.869	8.29
	21.889	19.884	9.16
	20.041	18.197	9.20
June - July	47.844	43.963	8.11
	48.422	45.078	6.91
	49.042	44.759	8.73
July - August	50.346	46.347	7.94
	50.048	46.135	7.82
	48.151	44.719	7.13

Table A1.25 Ash free dry weight (g) and % organic content for sediment samples collected at Chaland between April and August 2003.

Date	Dry Wt (g)	Ash free Dry Wt (g)	% Organics
April - May	19.117	17.423	8.86
	19.293	17.638	8.58
	20.425	18.369	10.07
May - June	4.635	4.169	10.05
	4.945	4.373	11.57
	4.677	4.087	12.61
June - July	18.897	16.868	10.74
	19.259	17.431	9.49
	19.381	17.571	9.34
July - August	9.693	8.492	12.39
	9.482	8.326	12.19
	9.524	8.349	12.34

Table A1.26 Total monthly rainfall (mm) measured at Pointe Canon between January 1997 and September 2003 (data from May-December 1999 were not available). Data were provided by the Mauritius Meteorological Services.

	1997	1998	1999	2000	2001	2002	2003
January	262	148	75	178	61	127	91
February	174	217	116	185	72	66	87
March	75	166	85	110	35	189	365
April	118	85	60	42	101	62	336
May	88	40		63	102	81	115
June	64	28		90	103	69	61
July	91	54		56	111	76	65
August	28	49		51	30	154	35
September	19	42		76	132	46	69
October	43	50		40	65	63	
November	73	29		68	61	14	
December	283	20		15	11	50	

Table A1.27 Mean monthly windspeed (km/hr) and direction (°), in brackets (2003 only) measured at Pointe Canon between January 2000 and September 2003. Data were provided by the Mauritius Meteorological Services.

	2000	2001	2002	2003
January	15.0	20.3	17.0	15.7 (95)
February	20.3	16.6	14.8	18.3 (97)
March	21.0	15.0	16.2	18.7 (122)
April	16.6	14.6	20.0	20.4 (76)
May	13.7	17.2	20.0	18.3 (85)
June	15.1	16.6	19.8	15.7 (117)
July	22.2	19.8	23.1	20.9 (106)
August	20.3	21.8	20.7	18.9 (111)
September	22.2	20.3	19.4	22.2 (78)
October	22.2	16.7	20.0	
November	20.3	16.7	20.0	
December	18.5	14.5	17.4	

Table A1.28 Maximum monthly temperature (°C) between January 1997 and September 2003 (data from May-December 1999 were not available). Data were provided by the Mauritius Meteorological Services.

	1997	1998	1999	2000	2001	2002	2003
January	29.4	30.3	29.1	29.8	30.5	30.3	31.0
February	28.9	30.4	28.7	29.3	30.7	31.2	30.0
March	29.3	30.4	29.6	28.7	31.0	30.7	29.7
April	28.7	28.9	29.6	28.7	30.0	28.8	29.0
May	27.3	27.9		27.8	28.9	27.8	27.8
June	25.7	26.9		25.8	25.9	25.9	26.2
July	24.9	25.6		24.9	25.4	25.0	24.9
August	25.2	25.3		25.0	25.9	24.4	24.7
September	26.0	25.8		25.5	26.3	25.0	25.5
October	26.6	26.3		27.0	26.9	26.3	
November	28.7	27.5		27.6	28.1	28.4	
December	29.7	28.3		29.1	29.7	30.1	

Table A1.29 Total monthly sunshine (hours) between January 1997 and September 2003 (data from May-December 1999 were not available). Data were provided by the Mauritius Meteorological Services.

	1997	1998	1999	2000	2001	2002	2003
January	267.9	291.8	304.7	285.2	284.1	272.2	289.0
February	271.3	189.7	270.5	243.7	246.0	264.5	214.4
March	289.0	238.4	274.9	278.3	224.9	250.6	258.3
April	247.3	224.4	257.4	262.8	230.7	211.2	204.6
May	239.4	227.3		248.7	250.0	227.3	225.4
June	223.8	219.0		187.8	191.6	191.0	214.6
July	228.1	220.8		216.2	212.2	231.5	203.2
August	235.4	212.7		224.9	264.4	241.7	248.8
September	237.4	242.0		215.5	241.7	238.3	231.0
October	248.4	277.7		293.8	279.0	243.3	
November	252.4	275.6		257.7	290.7	273.0	
December	263.5	320.8		319.6	307.0	216.9	

Table A1.30 Monthly cloud cover data for January 2000 to September 2003. The number of observations of 0, 1-2, 3-5 and 8 oktas per month, based on 7 observations per day. Data were provided by the Mauritius Meteorological Services.

			2000					**2001**		
	0	**1-2**	**3-5**	**6-7**	**8**	**0**	**1-2**	**3-5**	**6-7**	**8**
January	0	33	88	85	11	0	20	84	107	6
February	0	17	85	85	16	1	24	98	72	1
March	0	25	123	66	3	0	38	124	54	1
April	0	50	93	64	3	0	33	95	67	15
May	0	74	99	43	1	0	37	120	59	1
June	0	32	104	67	7	0	32	87	81	10
July	0	42	76	99	0	0	38	100	71	8
August	0	37	91	78	11	0	25	126	67	0
September	0	25	91	91	3	0	39	96	64	11
October	0	26	129	61	1	0	37	108	68	4
November	0	27	99	75	9	0	38	118	54	0
December	0	51	128	43	0	0	66	111	40	0

			2002					**2003**		
	0	**1-2**	**3-5**	**6-7**	**8**	**0**	**1-2**	**3-5**	**6-7**	**8**
January	0	27	77	93	20	0	35	101	81	0
February	0	39	89	65	3	0	17	73	101	5
March	0	23	100	87	7	0	50	94	53	20
April	0	22	62	109	17	0	13	72	107	18
May	0	66	74	62	15	0	40	95	65	17
June	0	23	107	76	4	0	53	103	54	0
July	0	36	108	73	5	0	34	77	101	5
August	0	34	87	72	24	0	51	87	71	8
September	0	42	89	73	6	0	33	92	84	1
October	0	20	85	100	12					
November	0	44	80	81	5					
December	0	21	66	125	5					

Appendix 2 Coral Growth Rate Data

Density of skeleton = weight in air * Density$_{\text{seawater}}$/weight in air – weight in water

Table A2.1 Data for the determination of the skeletal density of *Acropora austera*.

Buoyant weight (g)	Dry weight (g)	Density of seawater	Density of skeleton
3.03	5.41	1.02432	2.32839
2.02	3.24	1.02432	2.72033
3.00	5.12	1.02432	2.47383
2.97	4.87	1.02432	2.62549
1.49	2.42	1.02432	2.66543
2.52	4.12	1.02432	2.63762
2.65	4.68	1.02432	2.36149
1.81	3.07	1.02432	2.49576
1.44	2.57	1.02432	2.32965
1.74	2.92	1.02432	2.53476
2.09	3.50	1.02432	2.54264
2.52	4.09	1.02432	2.66845
1.71	2.79	1.02432	2.64616
		Mean	**2.54077**

Table A2.2 Data for the determination of the skeletal density of *Porites rus*.

Buoyant weight (g)	Dry weight (g)	Density of seawater	Density of skeleton
1.67	2.87	1.02743	2.45727
1.97	3.77	1.02743	2.15190
1.45	2.52	1.02743	2.41974
1.76	3.04	1.02743	2.44015
3.04	5.50	1.02743	2.29710
0.79	1.38	1.02743	2.40314
1.57	3.08	1.02743	2.09569
1.44	2.47	1.02743	2.46384
0.96	1.68	1.02743	2.39734
1.30	2.44	1.02743	2.19906
1.10	1.94	1.02743	2.37287
1.20	2.09	1.02743	2.41273
1.86	3.19	1.02743	2.46429
0.66	1.16	1.02743	2.38364
0.71	1.27	1.02743	2.33006
		Mean	**2.35259**

Table A2.3 Buoyant weight data for *Acropora austera* nubbins from Totor during February-March 2002 (28 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
84.58	82.24	1.02432	2.34	3.92	140.02
83.76	81.42	1.02432	2.34	3.92	140.02
85.38	83.00	1.02432	2.38	3.99	142.42
84.47	82.03	1.02432	2.44	4.09	146.01
83.87	81.99	1.02432	1.88	3.15	112.50
84.84	82.66	1.02432	2.18	3.65	130.45
81.70	79.22	1.02432	2.48	4.16	148.40
83.92	82.03	1.02432	1.89	3.17	113.09
80.72	78.73	1.02432	1.99	3.33	119.07
84.51	82.26	1.02432	2.25	3.77	134.64
82.00	79.83	1.02432	2.17	3.64	129.85
82.15	79.58	1.02432	2.57	4.31	153.78

Table A2.4 Buoyant weight data for *Acropora austera* nubbins from Totor during March-April 2002 (32 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
86.31	82.24	1.02432	4.07	5.65	90.58
85.32	81.42	1.02432	3.90	5.48	81.68
87.52	83.00	1.02432	4.52	6.13	112.05
86.71	82.03	1.02432	4.68	6.33	117.28
85.57	81.99	1.02432	3.58	4.85	89.01
86.55	82.66	1.02432	3.89	5.36	89.53
82.90	79.22	1.02432	3.68	5.36	62.83
85.70	82.03	1.02432	3.67	4.95	93.20
82.12	78.73	1.02432	3.39	4.73	73.30
86.50	82.26	1.02432	4.24	5.76	104.19
83.59	79.83	1.02432	3.76	5.23	83.25
83.59	79.58	1.02432	4.01	5.75	75.40

Table A2.5 Buoyant weight data for *Acropora austera* nubbins from Totor during April-May 2002 (35 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
86.89	82.82	1.02432	4.65	6.23	27.76
85.52	81.62	1.02432	4.10	5.68	9.57
87.94	83.42	1.02432	4.94	6.55	20.11
87.50	82.82	1.02432	5.47	7.12	37.82
85.84	82.26	1.02432	3.85	5.12	12.93
86.80	82.91	1.02432	4.14	5.61	11.97
83.04	79.36	1.02432	3.82	5.50	6.70
86.17	82.50	1.02432	4.14	5.42	22.50
82.26	78.87	1.02432	3.53	4.87	6.70
87.60	83.36	1.02432	5.34	6.86	52.66
84.20	80.44	1.02432	4.37	5.84	29.20
84.34	80.33	1.02432	4.76	6.50	35.90

Table A2.6 Buoyant weight data for *Acropora austera* nubbins from Totor during May-June 2002 (24 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
87.01	82.82	1.02432	4.77	6.35	8.38
85.79	81.62	1.02432	4.37	5.95	18.85
88.84	83.42	1.02432	5.84	7.45	62.83
88.01	82.82	1.02432	5.98	7.63	35.60
85.98	82.26	1.02432	3.99	5.26	9.77
86.92	82.91	1.02432	4.26	5.73	8.38
83.39	79.36	1.02432	4.17	5.85	24.43
86.52	82.50	1.02432	4.49	5.77	24.43
82.58	78.87	1.02432	3.85	5.19	22.34
87.99	83.36	1.02432	5.73	7.25	27.23
84.36	80.44	1.02432	4.53	6	11.17
84.39	80.33	1.02432	4.81	6.55	3.49

Table A2.5 Initial buoyant weight data for *Acropora austera* nubbins from Totor during 2003.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
141.38	2.43202	83.04	81.67	1.02713	1.37	2.30
144.33	2.43625	85.83	83.48	1.02713	2.35	3.94
139.73	2.48049	84.33	81.87	1.02713	2.46	4.13
141.84	2.42337	85.81	81.72	1.02713	4.09	6.86
143.68	2.44862	85.33	83.41	1.02713	1.92	3.22
136.32	2.56291	82.54	81.69	1.02713	0.85	1.43
145.13	2.43973	85.07	84.03	1.02713	1.04	1.07
137.68	2.53925	84.36	81.99	1.02713	2.37	3.98
134.98	2.43702	80.31	78.09	1.02713	2.22	3.73
148.85	2.39449	85.72	85.00	1.02713	0.72	1.21
141.90	2.55028	86.15	84.75	1.02713	1.40	1.67

Table A2.6 Weight data for *Acropora austera* coral nubbins from Totor during April-May 2003 (28 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
84.69	81.70	1.02668	2.99	5.02	179.43
86.47	83.51	1.02668	2.96	4.97	177.60
85.01	81.90	1.02668	3.11	5.23	186.66
86.65	81.75	1.02668	4.90	8.23	293.76
86.17	83.44	1.02668	2.73	4.59	163.83
83.83	81.71	1.02668	2.12	3.56	126.98
87.13	84.06	1.02668	3.07	4.48	124.25
85.21	82.01	1.02668	3.20	5.37	191.62
80.87	78.11	1.02668	2.76	4.62	165.12
86.66	85.03	1.02668	1.63	2.74	97.81
86.79	84.77	1.02668	2.02	2.70	60.86

Table A2.7 Weight data for *Acropora austera* coral nubbins from Totor during May-June 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
85.15	81.71	1.02637	3.44	5.76	25.53
86.88	83.53	1.02637	3.35	5.63	22.62
85.31	81.91	1.02637	3.40	5.70	16.31
86.89	81.77	1.02637	5.12	8.60	12.78
86.52	83.45	1.02637	3.07	5.14	19.16
84.06	81.73	1.02637	2.33	3.91	12.33
86.47	84.08	1.02637	2.39	4.02	18.58
85.60	82.03	1.02637	3.57	5.99	21.55
81.27	78.13	1.02637	3.14	5.26	22.12
86.78	85.05	1.02637	1.73	2.91	5.81
86.34	84.79	1.02637	1.55	2.60	30.81

Table A2.8 Weight data for *Acropora austera* coral nubbins from Totor during June-July 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
85.34	81.67	1.02713	3.67	6.16	13.65
87.28	83.48	1.02713	3.80	6.38	25.86
85.62	81.87	1.02713	3.75	6.29	20.52
87.16	81.72	1.02713	5.44	9.13	18.35
86.77	83.41	1.02713	3.36	5.64	17.14
84.45	81.69	1.02713	2.76	4.64	24.98
86.68	84.03	1.02713	2.65	4.45	14.84
85.83	81.99	1.02713	3.84	6.45	15.80
81.52	78.09	1.02713	3.43	5.76	17.00
86.93	85.00	1.02713	1.93	3.24	11.47
86.50	84.75	1.02713	1.75	2.94	11.75

Table A2.9 Initial buoyant weight data for *Porites rus* nubbins from Totor during 2003.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
137.05	2.31556	80.62	76.45	1.02390	4.17	7.39
147.86	2.41949	86.36	85.29	1.02390	1.07	1.89
141.91	2.43746	84.01	82.30	1.02390	1.71	3.02
148.00	2.39880	85.13	84.83	1.02390	0.30	0.54
145.72	2.44165	85.79	84.61	1.02390	1.18	2.09
144.86	2.46250	84.93	84.63	1.02390	0.30	0.54
150.74	2.43099	87.42	87.25	1.02390	0.17	0.30

Table A2.10 Weight data for *Porites rus* coral nubbins from Totor during April-May 2003 (41 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
83.20	76.26	1.02713	6.94	12.32	120.41
86.57	85.09	1.02713	1.48	2.63	110.17
84.56	82.11	1.02713	2.45	2.80	93.24
87.55	84.63	1.02713	2.92	5.19	113.42
86.50	84.42	1.02713	2.08	2.92	97.83
87.28	84.44	1.02713	2.84	5.04	109.99
89.40	87.05	1.02713	2.35	4.17	109.09

Table A2.11 Weight data for *Porites rus* coral nubbins from Totor during May-June 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
83.57	76.28	1.02668	7.29	12.93	20.86
87.37	85.12	1.02668	2.25	4.00	47.23
84.83	82.14	1.02668	2.69	3.23	14.91
87.84	84.66	1.02668	3.18	5.65	15.98
86.96	84.45	1.02668	2.51	3.68	26.48
88.27	84.46	1.02668	3.81	6.75	58.89
90.16	87.08	1.02668	3.08	5.47	44.74

Table A2.12 Weight data for *Porites rus* coral nubbins from Totor during June-July 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
83.61	76.30	1.02637	7.31	12.96	1.22
87.22	85.14	1.02637	2.08	3.70	-10.37
84.70	82.15	1.02637	2.55	2.97	-9.07
88.00	84.68	1.02637	3.32	5.90	8.57
86.27	84.47	1.02637	2.80	4.20	17.81
88.27	84.48	1.02637	3.79	6.72	-1.17
90.38	87.10	1.02637	3.28	5.82	12.24

Table A2.13 Weight data for *Porites rus* coral nubbins from Totor during July-August 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
83.73	76.26	1.02713	7.47	13.26	10.35
87.53	85.09	1.02713	2.44	4.33	21.89
84.85	82.11	1.02713	2.74	3.31	11.91
88.13	84.63	1.02713	3.50	6.21	10.94
87.43	84.42	1.02713	3.01	4.57	12.63
88.50	84.44	1.02713	4.06	7.21	16.95
90.68	87.05	1.02713	3.63	6.44	21.36

Table A2.14 Initial buoyant weight data for *Acropora austera* nubbins from Trou Malabar during 2002.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
146.47	2.34939	85.08	82.61	1.02432	2.47	4.14
145.68	2.36449	84.37	82.57	1.02432	1.80	3.02
139.96	2.38463	80.71	79.84	1.02432	0.87	1.46
149.08	2.34068	83.42	83.00	1.02432	0.42	0.70
139.28	2.40181	80.60	79.88	1.02432	0.72	1.21
142.59	2.43999	85.28	82.73	1.02432	2.55	4.27
146.01	2.38230	83.09	82.95	1.02432	0.14	0.23
136.58	2.41460	80.48	78.64	1.02432	1.84	3.08
139.36	2.39996	80.25	79.88	1.02432	0.37	0.62
144.61	2.42235	85.13	83.46	1.02432	1.67	2.80
138.20	2.29882	81.52	76.62	1.02432	4.90	8.21
140.88	2.30153	81.86	78.18	1.02432	3.68	6.17

Table A2.15 Buoyant weight data for *Acropora austera* nubbins from Trou Malabar during February-March 2002 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
88.20	82.61	1.02432	5.59	9.37	180.26
87.17	82.57	1.02432	4.60	7.71	161.77
83.89	79.84	1.02432	4.05	6.79	183.72
87.37	83.84	1.02432	3.53	5.91	228.21
83.99	79.88	1.02432	4.11	6.89	195.86
87.42	82.73	1.02432	4.69	7.86	123.64
86.09	83.23	1.02432	2.86	4.79	173.32
83.05	78.64	1.02432	4.41	7.39	148.48
83.99	79.88	1.02432	4.11	6.89	216.08
87.24	83.46	1.02432	3.78	6.33	121.91
84.38	76.62	1.02432	7.76	13.00	165.24
84.71	78.18	1.02432	6.53	10.94	164.66

Table A2.16 Initial buoyant weight data for *Acropora austera* nubbins from Trou Malabar during 2003.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
149.94	2.44496	86.16	85.17	1.02390	0.99	1.66
142.97	2.43813	82.68	82.43	1.02390	0.25	0.42
146.21	2.42455	85.32	84.46	1.02390	0.86	1.43
138.58	2.41951	81.25	79.94	1.02390	1.31	2.20
136.58	2.46028	79.89	79.74	1.02390	0.15	0.25
141.49	2.32929	83.31	79.29	1.02390	4.02	6.73
142.45	2.41205	82.33	81.98	1.02390	0.35	0.58
141.55	2.44312	82.86	82.23	1.02390	0.63	1.06
135.09	2.36651	80.49	76.64	1.02390	3.85	6.45
139.45	2.43428	81.46	80.80	1.02390	0.66	1.11

Table A2.17 Buoyant weight data for *Acropora austera* nubbins from Trou Malabar during April-May 2003 (41 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
88.83	86.97	1.02681	1.86	3.12	116.52
85.27	82.76	1.02681	2.51	4.21	112.98
87.81	84.29	1.02681	3.52	5.91	109.17
84.67	79.77	1.02681	4.90	8.23	146.91
81.93	79.58	1.02681	2.35	3.95	90.13
85.34	79.12	1.02681	6.22	10.44	90.64
85.48	81.81	1.02681	3.67	6.16	136.00
85.59	82.06	1.02681	3.53	5.93	118.70
83.65	76.48	1.02681	7.17	12.04	136.45
83.90	80.63	1.02681	3.27	5.49	106.75

Table A2.18 Buoyant weight data for *Acropora austera* nubbins from Trou Malabar during May-June 2003 (34 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
89.32	87.01	1.02621	2.31	3.88	22.32
86.06	82.79	1.02621	3.27	5.48	37.19
88.47	84.33	1.02621	4.14	6.95	30.71
85.34	79.80	1.02621	5.54	9.29	31.27
82.57	79.61	1.02621	2.96	4.96	29.89
86.14	79.15	1.02621	6.99	11.72	37.55
86.19	81.84	1.02621	4.35	7.29	33.21
85.95	82.09	1.02621	3.86	6.47	15.98
83.87	76.51	1.02621	7.36	12.35	9.02
84.65	80.66	1.02621	3.99	6.69	35.25

Table A2.19 Buoyant weight data for *Acropora austera* nubbins from Trou Malabar during June-July 2003 (33 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
89.83	86.98	1.02668	2.85	4.79	27.44
86.71	82.77	1.02668	3.94	6.62	34.51
88.97	84.30	1.02668	4.67	7.84	26.93
86.09	79.78	1.02668	6.31	10.60	39.59
83.14	79.58	1.02668	3.56	5.97	30.36
86.92	79.13	1.02668	7.79	13.08	41.23
86.96	81.82	1.02668	5.14	8.63	40.64
86.53	82.07	1.02668	4.46	7.49	30.94
84.51	76.48	1.02668	8.03	13.47	34.03
85.41	80.64	1.02668	4.77	8.01	40.08

Table A2.20 Buoyant weight data for *Acropora austera* nubbins from Trou Malabar during July-August 2003 (28 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
90.69	87.00	1.02637	3.69	6.20	50.36
87.70	82.78	1.02637	4.92	8.25	58.18
89.53	84.32	1.02637	5.21	8.75	32.38
86.87	79.79	1.02637	7.08	11.87	45.60
83.60	79.60	1.02637	4.00	6.71	26.49
87.58	79.14	1.02637	8.44	14.15	38.32
87.86	81.83	1.02637	6.03	10.11	52.77
87.05	82.08	1.02637	4.97	8.33	30.03
85.11	76.50	1.02637	8.61	14.44	34.79
86.23	80.65	1.02637	5.58	9.36	48.01

Table A2.21 Initial buoyant weight data for *Porites rus* nubbins from Trou Malabar during 2003.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
139.44	2.38894	80.68	79.68	1.02390	1.00	1.78
141.90	2.54882	83.47	82.04	1.02390	1.43	2.53
133.86	2.40566	78.68	76.89	1.02390	1.79	3.18
127.87	2.52649	74.63	73.21	1.02390	1.42	2.51

Table A2.22 Buoyant weight data for *Porites rus* nubbins from Trou Malabar during April-May 2003 (41 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
82.86	79.51	1.02681	3.35	5.95	101.80
88.55	84.73	1.02681	3.82	6.78	102.96
80.92	76.72	1.02681	4.20	7.44	104.13
79.49	75.90	1.02681	3.59	6.37	93.67

Table A2.23 Buoyant weight data for *Porites rus* nubbins from Trou Malabar during May-June 2003 (34 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
83.46	79.54	1.02621	3.92	6.95	29.39
89.20	84.77	1.02621	4.43	7.86	30.58
81.40	76.76	1.02621	4.64	8.23	23.20
83.50	75.93	1.02621	4.27	7.57	35.44

Table A2.24 Buoyant weight data for *Porites rus* nubbins from Trou Malabar during June-July 2003 (33 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
83.74	79.51	1.02668	4.23	7.50	16.60
89.63	84.74	1.02668	4.89	8.68	24.56
81.81	76.73	1.02668	5.08	9.01	23.54
81.01	75.91	1.02668	5.10	9.05	44.86

Table A2.25 Buoyant weight data for *Porites rus* nubbins from Trou Malabar during July-August 2003 (28 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
84.09	79.53	1.02637	4.56	8.09	20.96
89.96	84.76	1.02637	5.20	9.22	19.78
82.31	76.75	1.02637	5.56	9.86	30.51
81.34	75.92	1.02637	5.42	9.61	19.88

Table A2.26 Buoyant weight data for *Acropora austera* nubbins from Chaland during February-March 2002 (35 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
83.43	79.89	1.02432	3.54	5.93	169.4621
84.71	78.92	1.02432	5.79	9.70	277.171
84.10	81.05	1.02432	3.05	5.11	146.0054
85.23	84.77	1.02432	0.46	0.77	-22.0205
84.19	80.74	1.02432	3.45	5.78	165.1537

Table A2.27 Buoyant weight data for *Acropora austera* nubbins from Chaland during March-April 2002 (31 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
84.99	79.89	1.02432	5.10	8.54	84.31
86.42	78.92	1.02432	7.50	12.57	92.42
86.45	81.05	1.02432	5.40	9.05	127.01
85.47	84.77	1.02432	0.70	1.17	62.70
86.08	80.74	1.02432	5.34	8.95	102.15

Table A2.28 Buoyant weight data for *Acropora austera* nubbins from Chaland during April-May 2002 (31 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
90.58	79.89	1.02432	10.69	17.91	302.13
88.59	78.92	1.02432	9.67	16.20	117.28
89.45	81.05	1.02432	8.40	14.07	162.14
87.23	84.77	1.02432	2.46	4.12	95.12
88.98	80.74	1.02432	8.24	13.81	156.74

Table A2.29 Buoyant weight data for *Acropora austera* nubbins from Chaland during May-June 2002 (24 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
92.18	79.89	1.02432	12.29	20.59	111.70
89.42	78.92	1.02432	10.50	17.59	57.94
91.33	81.05	1.02432	10.28	17.22	131.25
87.7	84.77	1.02432	2.93	4.91	32.81
90.45	80.74	1.02432	9.71	16.27	102.62

Table A2.30 Initial buoyant weight data for *Acropora austera* nubbins from Chaland during 2003.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
144.47	2.55028	90.87	86.42	1.02465	4.45	7.45
141.69	2.40716	84.44	81.38	1.02465	3.06	5.13
146.83	2.53432	87.83	87.47	1.02465	0.36	0.61
135.70	2.55446	82.61	81.27	1.02465	1.34	2.25
145.62	2.56134	88.82	87.37	1.02465	1.45	2.44
143.78	2.44874	83.70	83.62	1.02465	0.08	0.14

Table A2.31 Buoyant weight data for *Acropora austera* nubbins from Chaland during April-May 2003 (50 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
94.06	86.24	1.02788	7.82	13.13	113.61
87.90	81.19	1.02788	6.71	11.27	122.82
92.11	87.28	1.02788	4.83	8.11	150.07
85.34	81.10	1.02788	4.24	7.13	97.56
92.70	87.18	1.02788	5.52	9.27	136.59
86.85	83.43	1.02788	3.42	5.75	112.18

Table A2.32 Buoyant weight data for *Acropora austera* nubbins from Chaland during May-June 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
95.57	86.34	1.02621	9.23	15.49	81.38
88.71	81.29	1.02621	7.42	12.46	40.74
93.32	87.37	1.02621	5.95	9.97	64.09
86.16	81.18	1.02621	4.98	8.35	42.03
93.27	87.28	1.02621	5.99	10.05	27.13
87.64	83.53	1.02621	4.11	6.90	39.81

Table A2.33 Buoyant weight data for *Acropora austera* nubbins from Chaland during June-July 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
97.14	86.33	1.02637	10.81	18.14	91.41
89.79	81.28	1.02637	8.51	14.28	63.07
94.83	87.37	1.02637	7.46	12.52	87.93
87.19	81.18	1.02637	6.01	10.09	60.11
93.79	87.27	1.02637	6.52	10.94	30.65
88.41	83.52	1.02637	4.89	8.21	45.12

Table A2.34 Buoyant weight data for *Acropora austera* nubbins from Chaland during July-August 2003 (28 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
98.01	86.31	1.02668	11.70	19.63	53.33
90.62	81.26	1.02668	9.36	15.71	50.94
96.24	87.35	1.02668	8.89	14.92	85.67
87.97	81.16	1.02668	6.81	11.43	47.81
94.59	87.25	1.02668	7.34	12.32	49.08
89.13	83.50	1.02668	5.63	9.45	44.30

Table A2.35 Initial buoyant weight data for *Porites rus* nubbins from Chaland during 2003.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
140.81	2.41983	81.43	81.19	1.02465	0.24	0.42
135.12	2.56693	81.88	81.18	1.02465	0.70	1.24
136.39	2.56198	82.01	81.84	1.02465	0.17	0.30
142.80	2.53005	85.49	84.97	1.02465	0.52	0.92
141.60	2.37887	81.91	80.61	1.02465	1.30	2.31
147.08	2.41136	84.67	84.58	1.02465	0.09	0.16
138.43	2.44607	80.54	80.44	1.02465	0.10	0.18
137.92	2.44548	80.18	80.13	1.02465	0.05	0.09
139.56	2.42514	81.01	80.59	1.02465	0.42	0.74

Table A2.36 Buoyant weight data for *Porites rus* nubbins from Chaland during April-May 2003 (50 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
84.29	81.01	1.02774	3.28	5.83	124.99
81.87	81.02	1.02774	0.85	1.51	125.95
81.89	81.68	1.02774	0.21	0.38	119.94
84.97	84.79	1.02774	0.18	0.32	82.70
85.48	80.42	1.02774	5.06	8.98	133.43
87.70	84.39	1.02774	3.31	5.87	114.31
83.28	80.27	1.02774	3.01	5.35	110.62
82.81	79.96	1.02774	2.85	5.07	99.60
83.38	80.42	1.02774	2.96	5.26	90.52

Table A2.37 Buoyant weight data for *Porites rus* nubbins from Chaland during May-June 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
84.79	81.09	1.02621	3.70	6.55	24.90
81.99	81.10	1.02621	0.89	1.58	2.35
82.04	81.76	1.02621	0.28	0.50	4.18
82.25	84.88	1.02621	0.37	0.66	10.02
85.58	80.52	1.02621	5.06	8.98	0.19
88.27	84.49	1.02621	3.78	6.71	28.92
83.59	80.35	1.02621	3.24	5.74	13.45
83.01	80.04	1.02621	2.97	5.26	6.75
83.71	80.50	1.02621	3.21	5.69	14.59

Table A2.38 Buoyant weight data for *Porites rus* nubbins from Chaland during June-July 2003 (29 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
85.16	81.09	1.02637	4.07	7.23	23.15
82.31	81.09	1.02637	1.22	2.16	20.07
82.39	81.75	1.02637	0.64	1.13	21.92
85.18	84.87	1.02637	0.31	0.55	18.90
85.75	80.51	1.02637	5.24	9.30	10.91
88.63	84.48	1.02637	4.15	7.36	22.56
84.15	80.34	1.02637	3.81	6.75	34.76
83.26	80.03	1.02637	3.23	5.72	15.80
83.88	80.50	1.02637	3.38	6.00	10.92

Table A2.39 Buoyant weight data for *Porites rus* nubbins from Chaland during July-August 2003 (28 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
85.62	81.09	1.02637	4.53	8.04	29.13
82.86	81.09	1.02637	1.77	3.13	34.83
82.48	81.75	1.02637	0.73	1.29	5.70
85.71	84.87	1.02637	0.84	1.49	33.57
86.26	80.51	1.02637	5.75	10.20	32.30
89.17	84.48	1.02637	4.69	8.32	34.20
84.70	80.34	1.02637	4.36	7.72	34.83
83.55	80.03	1.02637	3.52	6.23	18.37
84.26	80.50	1.02637	3.76	6.68	24.07

Table A2.40 Initial buoyant weight data for *Acropora austera* nubbins from Grande Baie.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
143.14	2.53451	86.09	85.29	1.02432	0.80	1.34
142.27	2.46875	82.55	83.24	1.02432	0.69	1.16
140.89	2.34547	85.33	79.36	1.02432	5.97	10.00
136.92	2.75000	85.61	85.92	1.02432	0.31	0.52
142.47	2.55042	85.40	85.25	1.02432	0.15	0.25
138.29	2.3775	79.07	78.71	1.02432	0.36	0.60
143.56	2.42379	82.01	82.89	1.02432	0.88	1.47
131.49	2.73533	82.30	82.25	1.02432	0.05	0.08

Table A2.41 Buoyant weight data for *Acropora austera* nubbins from Grande Baie (39 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
88.75	85.29	1.0243	3.46	5.80	114.28
85.69	83.24	1.0243	2.45	4.10	134.90
87.84	79.36	1.0243	8.48	14.21	107.83
88.79	85.92	1.0243	2.87	4.81	136.62
88.51	85.25	1.0243	3.26	5.46	133.61
81.33	78.71	1.0243	2.62	4.39	97.09
85.06	82.89	1.0243	2.17	3.64	131.03
85.12	82.25	1.0243	2.87	4.81	121.15

Table A2.42 Initial buoyant weight data for *Acropora austera* nubbins from Ile aux Fous.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
141.59	2.40400	82.7	81.26	1.02432	1.44	2.41
141.59	2.40400	83.20	81.26	1.02432	1.94	3.25
141.59	2.40400	84.85	81.26	1.02432	3.59	6.01
141.59	2.40400	80.20	81.26	1.02432	1.06	1.78
141.59	2.40400	78.29	81.26	1.02432	2.97	4.98
141.59	2.40400	83.86	81.26	1.02432	2.60	4.36
141.59	2.40400	84.07	81.26	1.02432	2.81	4.71
141.59	2.40400	85.18	81.26	1.02432	3.92	6.57
141.59	2.40400	81.01	81.26	1.02432	0.25	0.42
141.59	2.40400	80.74	81.26	1.02432	0.52	0.87
141.59	2.40400	82.24	81.26	1.02432	0.98	1.64
141.59	2.40400	78.38	81.26	1.02432	2.88	4.83
141.59	2.40400	79.85	81.26	1.02432	1.41	2.36
141.59	2.40400	80.18	81.26	1.02432	1.08	1.81
141.59	2.40400	81.02	81.26	1.02432	0.24	0.40

Table A2.43 Buoyant weight data for *Acropora austera* nubbins from Ile aux Fous (34 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
86.54	81.26	1.02432	5.28	8.85	189.23
86.77	81.26	1.02432	5.51	9.23	175.92
88.17	81.26	1.02432	6.91	11.58	163.60
83.47	81.26	1.02432	2.21	3.70	161.14
81.43	81.26	1.02432	6.11	5.26	154.73
86.5	81.26	1.02432	5.24	8.78	130.10
85.21	81.26	1.02432	3.95	6.62	56.18
86.8	81.26	1.02432	5.54	9.28	79.83
83.95	81.26	1.02432	2.69	4.51	144.88
84.34	81.26	1.02432	4.12	6.90	177.40
84.33	81.26	1.02432	3.07	5.14	102.99
80.3	81.26	1.02432	4.80	8.05	94.61
82.8	81.26	1.02432	1.54	2.58	145.37
83.06	81.26	1.02432	1.80	3.02	141.92
83.73	81.26	1.02432	2.47	4.14	133.54

Table A2.44 Initial buoyant weight data for *Acropora austera* nubbins from Eric's Paté.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
135.19	2.47902	79.89	79.33	1.02432	0.56	0.94
142.10	2.37178	79.96	80.73	1.02432	0.77	1.29
143.97	2.3483	85.07	81.17	1.02432	3.90	6.53
135.36	2.54454	81.55	80.87	1.02432	0.68	1.14
139.62	2.43472	83.26	80.88	1.02432	2.38	3.99
137.92	2.42739	84.03	79.72	1.02432	4.31	7.22
136.25	2.46622	81.40	79.66	1.02432	1.74	2.92
135.16	2.38496	85.81	77.11	1.02432	8.70	14.58
145.52	2.35778	83.15	82.30	1.02432	0.85	1.42

Table A2.45 Buoyant weight data for *Acropora austera* nubbins from Eric's Paté (99 days).

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
81.81	79.33	1.02432	2.48	4.16	32.49
82.70	80.73	1.02432	1.97	3.30	46.37
88.69	81.17	1.02432	7.52	12.60	61.26
85.25	80.87	1.02432	4.38	7.34	62.62
85.76	80.88	1.02432	4.88	8.18	42.31
87.39	79.72	1.02432	7.67	12.85	56.86
83.69	79.66	1.02432	4.03	6.75	38.76
89.66	77.11	1.02432	12.55	21.03	65.16
85.53	82.30	1.02432	3.23	5.41	40.28

Table A2.46 Initial buoyant weight data for *Acropora austera* nubbins transplanted from Totor to Grande Baie.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
142.68	2.28466	84.51	78.71	1.02432	5.80	9.72
146.19	2.30024	85.53	81.09	1.02432	4.44	7.44
145.01	2.31944	84.98	80.97	1.02432	4.01	6.72
141.03	2.34932	84.51	79.54	1.02432	4.97	8.33
140.18	2.30295	81.20	77.83	1.02432	3.37	5.65
144.26	2.29347	83.85	79.83	1.02432	4.02	6.74
135.96	2.30459	80.43	75.53	1.02432	4.90	8.21

Table A2.47 Buoyant weight data for *Acropora austera* nubbins transplanted from Totor to Grande Baie (39 days)

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
87.95	78.71	1.02432	9.24	15.48	147.79
89.37	81.09	1.02432	8.28	13.87	164.97
88.32	80.97	1.02432	7.35	12.31	143.49
87.81	79.54	1.02432	8.27	13.86	141.77
84.58	77.83	1.02432	6.75	11.31	145.21
87.70	79.83	1.02432	7.87	13.19	165.40
84.54	75.53	1.02432	9.01	15.10	176.57

Table A2.48 Initial buoyant weight data for *Acropora austera* nubbins transplanted from Grande to Baie Totor.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
143.52	2.37958	81.19	81.74	1.02432	0.55	0.92
141.04	2.38360	80.72	80.43	1.02432	0.29	0.49
145.26	2.38030	82.37	82.75	1.02432	0.38	0.64
145.58	2.38136	84.21	82.96	1.02432	1.25	2.09
141.86	2.38565	81.24	80.95	1.02432	0.29	0.49
138.55	2.39486	79.34	79.29	1.02432	0.05	0.08
144.64	2.39699	83.17	82.83	1.02432	0.34	0.57
144.17	2.36433	80.21	81.71	1.02432	1.50	2.51
147.66	2.43678	85.55	85.59	1.02432	0.04	0.07
146.81	2.34457	81.65	82.67	1.02432	1.02	1.71
141.11	2.39101	81.09	80.66	1.02432	0.43	0.72
150.14	2.38141	84.64	85.56	1.02432	0.92	1.54
144.19	2.41216	81.13	82.96	1.02432	1.83	3.07

Table A2.49 Buoyant weight data for *Acropora austera* nubbins transplanted from Grande Baie to Totor (48 days)

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
85.52	81.74	1.02432	3.78	6.33	151.14
84.14	80.43	1.02432	3.71	6.22	119.38
86.34	82.75	1.02432	3.59	6.01	138.58
88.23	82.96	1.02432	5.27	8.83	140.32
84.84	80.95	1.02432	3.89	6.52	125.66
82.61	79.29	1.02432	3.32	5.56	114.14
86.06	82.83	1.02432	3.23	5.41	100.88
84.48	81.71	1.02432	2.77	4.64	149.05
89.39	85.59	1.02432	3.80	6.37	134.04
85.71	82.67	1.02432	3.04	5.09	141.72
84.48	80.66	1.02432	3.82	6.40	118.33
88.55	85.56	1.02432	2.99	5.01	136.48
85.23	82.96	1.02432	2.27	3.80	143.11

Table A2.50 Initial buoyant weight data for *Acropora austera* nubbins transplanted from Trou Malabar to Ile aux Fous.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
141.59	2.40400	84.47	81.26	1.02432	3.21	5.38
141.59	2.40400	78.92	81.26	1.02432	2.34	3.92
141.59	2.40400	75.18	81.26	1.02432	1.08	1.81
141.59	2.40400	84.4	81.26	1.02432	3.14	5.26
141.59	2.40400	83.8	81.26	1.02432	2.54	4.26
141.59	2.40400	80.46	81.26	1.02432	0.80	1.34
141.59	2.40400	80.85	81.26	1.02432	0.41	0.69
141.59	2.40400	83.5	81.26	1.02432	2.24	3.75
141.59	2.40400	83.22	81.26	1.02432	1.96	3.28
141.59	2.40400	84.34	81.26	1.02432	3.08	5.16
141.59	2.40400	81.87	81.26	1.02432	0.61	1.02

Table A2.51 Buoyant weight data for *Acropora austera* nubbins transplanted from Trou Malabar to Ile aux Fous (35 days)

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
87.30	81.26	1.02432	6.04	10.12	135.47
81.92	81.26	1.02432	5.34	8.95	143.61
82.03	81.26	1.02432	7.93	13.29	327.91
86.87	81.26	1.02432	5.61	9.40	118.24
86.77	81.26	1.02432	5.51	9.23	142.18
83.01	81.26	1.02432	3.35	5.61	122.07
83.96	81.26	1.02432	3.52	5.90	148.88
86.75	81.26	1.02432	5.49	9.20	155.58
86.85	81.26	1.02432	5.59	9.37	173.77
86.82	81.26	1.02432	5.56	9.32	118.72
83.78	81.26	1.02432	2.52	4.22	91.43

Table A2.52 Initial buoyant weight data for *Acropora austera* nubbins transplanted from Ile aux Fous to Trou Malabar.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
139.59	2.38786	83.41	79.71	1.02432	3.70	6.20
145.84	2.38181	86.40	83.12	1.02432	3.28	5.50
135.66	2.50017	83.04	80.08	1.02432	2.96	4.96
147.38	2.42279	86.92	85.07	1.02432	1.85	3.10
142.26	2.42988	84.11	82.29	1.02432	1.82	3.05
136.33	2.51568	83.67	80.82	1.02432	2.85	4.78
137.36	2.41422	81.39	79.08	1.02432	2.31	3.87
140.60	2.38049	82.43	80.10	1.02432	2.33	3.90
131.63	2.46087	79.03	76.84	1.02432	2.19	3.67
134.29	2.38730	78.80	76.67	1.02432	2.13	3.57
140.22	2.43111	83.17	81.14	1.02432	2.03	3.40
140.10	2.43150	84.18	81.08	1.02432	3.10	5.19
142.44	2.43946	85.63	82.63	1.02432	3.00	5.03

Table A2.53 Buoyant weight data for *Acropora austera* nubbins transplanted from Ile aux Fous to Trou Malabar.

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
84.19	79.71	1.02432	4.48	7.51	46.67
86.64	83.12	1.02432	3.52	5.90	14.36
83.72	80.08	1.02432	3.64	6.10	40.69
87.62	85.07	1.02432	2.55	4.27	41.89
85.13	82.29	1.02432	2.84	4.76	61.04
84.82	80.82	1.02432	4.00	6.70	68.81
82.62	79.08	1.02432	3.54	5.93	73.60
83.42	80.10	1.02432	3.32	5.56	59.24
80.19	76.84	1.02432	3.35	5.61	69.41
79.70	76.67	1.02432	3.03	5.08	53.85
84.73	81.14	1.02432	3.59	6.01	93.35
85.06	81.08	1.02432	3.98	6.67	52.66
87.12	82.63	1.02432	4.49	7.52	89.16

Table A2.54 Initial buoyant weight data for *Acropora austera* nubbins transplanted from Chaland to Eric's Paté

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
142.17	2.42915	83.85	82.22	1.02432	1.63	2.73
136.34	2.40413	82.51	78.25	1.02432	4.26	7.14
143.22	2.34387	78.7	80.63	1.02432	1.93	3.23
133.71	2.44139	80.28	77.61	1.02432	2.67	4.47
135.61	2.38388	79.98	77.34	1.02432	2.64	4.42
138.12	2.46909	80.89	80.82	1.02432	0.07	0.12

Table A2.55 Buoyant weight data for *Acropora austera* nubbins transplanted from Chaland to Eric's Paté (99 days)

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
88.19	82.22	1.02432	5.97	10.00	73.45
85.83	78.25	1.02432	7.58	12.70	56.19
82.82	80.63	1.02432	6.05	10.14	69.73
84.77	77.61	1.02432	7.16	12.00	75.99
83.86	77.34	1.02432	6.52	10.92	65.66
85.67	80.82	1.02432	4.85	8.13	80.90

Table A2.56 Initial buoyant weight data for *Acropora austera* nubbins transplanted from Eric's Paté to Chaland.

Tile weight in air (g)	Tile density	Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)
141.42	2.39873	80.14	81.03	1.02432	0.89	1.49
135.49	2.480077	78.92	79.53	1.02432	0.61	1.02
145.08	2.426655	80.57	83.84	1.02432	3.27	5.48
143.57	2.434795	82.51	83.17	1.02432	0.66	1.11
146.23	2.420202	82.03	84.34	1.02432	2.31	3.87
140.72	2.438131	80.48	81.60	1.02432	1.12	1.88
136.44	2.417544	77.45	78.63	1.02432	1.18	1.98
141.6	2.472196	82.41	82.93	1.02432	0.52	0.87
144.35	2.433919	82.24	83.60	1.02432	1.36	2.28
139.59	2.395056	78.04	79.89	1.02432	1.85	3.10

Table A2.57 Buoyant weight data for *Acropora austera* nubbins transplanted from Eric's Paté to Chaland (63 days)

Nubbin weight (g)	Tile weight (g)	Density of seawater	Coral weight in water (g)	Coral weight in air (g)	Growth (mg d^{-1})
84.87	81.03	1.02432	5.62	9.42	125.79
83.18	79.53	1.02432	4.87	8.16	113.29
86.73	83.84	1.02432	9.43	15.80	163.82
85.73	83.17	1.02432	3.88	6.50	85.64
86.4	84.34	1.02432	6.68	11.19	116.22
84.31	81.60	1.02432	4.95	8.29	101.86
81.47	78.63	1.02432	5.2	8.71	106.91
85.53	82.93	1.02432	3.64	6.10	82.98
86.45	83.60	1.02432	5.57	9.33	111.96
82.36	79.89	1.02432	6.17	10.34	114.89

Table A2.58 Length of *Acropora austera* branch tips measured in situ at Totor during March-May 2002 (80 days).

Length (mm)			Total Growth (mm d^{-1})
March	April	May	
47.7	52.9	56.5	0.11
42.5	37.3	43.9	0.02
49.0	43.4	48.3	-0.01
64.0	64.1	70.3	0.08
54.9	55.7	64.5	0.12
54.3	58.6	63.6	0.12
44.0	57.9	67.9	0.30
47.1	51.5	41.9	-0.07
42.5	52.1	58.8	0.20
58.9	60.0	70.3	0.14
57.4	61.5	70.6	0.17

Table A2.59 Length of *Acropora austera* branch tips measured in situ at Totor during May-August 2003 (79 days).

	Length (mm)			Total Growth (mm d^{-1})
May	June	July	August	
57.4	44.0	50.5	51.1	-0.08
53.6	56.1	51.2	54.8	0.02
72.0	78.6	83.7	62.3	-0.12
40.6	40.1	40.0	48.8	0.10
44.9	37.7	63.8	44.4	-0.01
33.8	40.9	20.1	28.9	-0.06
51.2	49.7	45.1	68.2	0.22
49.9	46.6	59.5	62.5	0.16
40.3	39.5	40.0	39.8	-0.01
39.4	33.7	31.2	29.3	-0.13
49.1	48.6	47.9	50.6	0.02
69.0	72.9	70.5	74.2	0.07
46.6	44.4	51.3	49.8	0.04
72.5	79.2	71.8	78.5	0.08

Table A2.60 Length of *Acropora austera* branch tips measured in situ at Trou Malabar during March-May 2002 (40 days). NR indicates no measurement was made.

	Length (mm)		Total Growth (mm d^{-1})
March	April	May	
NR	53.0	48.6	-0.11
NR	54.4	56.5	-0.05
NR	40.0	41.0	0.03
NR	50.6	59.6	0.23
NR	42.8	46.7	0.10
NR	35.6	41.4	0.15
NR	58.1	62.0	0.10
NR	67.6	67.4	-0.05
NR	48.3	55.2	0.17

Table A2.61 Length of *Acropora austera* branch tips measured in situ at Trou Malabar during May-August 2003 (97 days).

	Length (mm)			Total Growth (mm d^{-1})
May	June	July	August	
62.7	66.3	68.1	60.9	-0.02
38.6	31.5	29.2	31.2	-0.08
54.9	62.8	61	64.8	0.10
55.9	63.7	64	62.3	0.07
33.6	31.3	38.1	38.1	0.05
44.3	38.6	37.5	37.9	-0.07
44.7	41.7	49	51.5	0.07
52.2	49.2	57	54.8	0.03
51.6	34.3	53.1	54.6	0.03
30.6	34.3	39	31.2	0.01

Table A2.62 Length of *Acropora austera* branch tips measured in situ at Chaland during March-May 2002 (61 days).

Length (mm)			Total Growth (mm d^{-1})
March	April	May	
55.2	62.2	64.1	0.15
44.3	53.6	51.4	0.13
60.9	64.4	61.1	0.00
57.3	58.9	63.8	0.12
58.1	59.6	62.0	0.06
64.2	65.4	68.1	0.07
54.4	58.5	57.7	0.05

Table A2.63 Length of *Acropora austera* branch tips measured in situ at Chaland during May-August 2003 (97 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
24.8	27.6	29.0	30.5	0.07
31.2	34.2	36.7	35.3	0.05
36.4	38.2	41.3	36.7	0.00
46.1	45.0	40.5	50.4	0.05
40.2	36.4	44.6	42.1	0.02
44.1	51.1	55.0	51.5	0.09

Table A2.64 Length of *Porites rus* branch tips measured in situ at Totor during May-August 2003 (58 days). NR indicates no measurement was made.

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
NR	23.4	25.9	23.0	-0.01
NR	14.9	22.2	25.0	0.17
NR	30.1	64.0	39.0	0.15
NR	22.2	26.3	23.1	0.02
NR	28.6	30.9	31.5	0.05
NR	21.6	37.4	27.0	0.09

Table A2.65 Length of *Porites rus* branch tips measured in situ at Trou Malabar during May-August 2003 (61 days). NR indicates no measurement was made.

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
NR	34.5	32.8	36.0	0.02
NR	25.9	25.1	27.5	0.03
NR	32.5	24.9	33.0	0.01
NR	17.2	12.9	18.5	0.02
NR	31.5	21.7	32.0	0.01
NR	37.3	40.9	37.0	0.00

Table A2.66 Length of *Porites rus* branch tips measured in situ at Chaland during May-August 2003 (84 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
19.1	20.0	23.5	26.1	0.07
20.1	23.1	26.1	25.0	0.02
19.9	21.1	16.2	19.0	-0.03
20.4	20.0	22.0	23.0	0.04
28.3	30.0	33.0	38.0	0.10

Table A2.67 Length of *Acropora austera* branch tips measured using digital photography at Totor during May-August 2003 (79 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
44.4	43.0	39.1	43.5	-0.01
67.1	82.7	68.1	57.4	-0.12
40.4	33.0	39.1	38.4	-0.03
35.2	38.5	36.9	36.9	0.02
51.8	56.0	58.6	60.4	0.11
35.8	36.8	41.9	47.0	0.14
35.3	32.9	34.2	34.8	-0.01
76.4	77.4	82.6	82.0	0.07
42.0	42.1	47.9	47.9	0.07
73.0	75.0	83.1	89.7	0.21

Table A2.68 Length of *Acropora austera* branch tips measured using digital photography at Trou Malabar during May-August 2003 (97 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
57.5	69.5	74.5	73.1	0.16
26.8	30.8	29.5	29.1	0.02
41.7	55.7	50.0	54.9	0.14
64.4	70.6	69.2	75.6	0.12
28.6	32.8	36.8	34.8	0.06
36.5	39.7	40.2	41.5	0.05
46.3	47.9	50.6	52.3	0.06
47.7	59.7	61.3	63.1	0.16
49.9	58.4	58.6	56.5	0.07
47.5	53.7	55.1	56.6	0.09

Table A2.69 Length of *Acropora austera* branch tips measured using digital photography at Chaland during May-August 2003 (85 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
30.5	30.0	30.2	28.8	-0.02
40.7	50.5	45.2	45.7	0.06
38.2	44.4	44.4	46.2	0.09
46.1	53.4	52.9	51.1	0.06
45.1	46.7	49.4	52.9	0.09
47.7	51.2	53.4	55.0	0.08
49.2	50.8	53.4	58.2	0.11

Table A2.70 Length of *Porites rus* branch tips measured using digital photography at Totor during May-August 2003 (58 days). NR indicates no measurements were made.

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
NR	20.3	24.0	21.3	0.02
NR	15.0	18.0	19.1	0.07
NR	29.9	31.4	32.7	0.05
NR	27.6	29.1	31.3	0.06
NR	24.2	26.5	28.8	0.08

Table A2.71 Length of *Porites rus* branch tips measured using digital photography at Trou Malabar during May-August 2003 (61 days). NR indicates no measurements were made.

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
NR	18.2	21.2	24.6	0.10
NR	33.4	35.3	36.7	0.05
NR	25.1	30.0	34.6	0.16
NR	19.4	23.4	26.1	0.11
NR	32.5	36.4	40.2	0.13
NR	43.8	45.2	49.9	0.10

Table A2.72 Length of *Porites rus* branch tips measured using digital photography at Chaland during May-August 2003 (84 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
20.6	23.8	24.7	32.3	0.14
25.0	28.8	33.5	28.7	0.04
21.5	22.5	21.3	26.5	0.06
30.7	34.1	36.6	39.8	0.11

Table A2.73 Perimeter of *Acropora austera* branch tips measured using digital photography at Totor during May-August 2003 (79 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
125.3	117.9	107.2	119.9	-0.07
189.1	235.1	203.2	175.5	-0.17
110.1	91.4	111.0	107.0	-0.04
95.8	109.7	103.9	103.5	0.10
134.1	143.6	158.0	164.5	0.38
106.2	111.2	121.2	130.9	0.31
100.4	99.4	99.9	114.4	0.18
139.5	141.5	167.1	156.5	0.22
185.9	188.7	214.3	228.3	0.54

Table A2.74 Perimeter of *Acropora austera* branch tips measured using digital photography at Trou Malabar during May-August 2003 (97 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
167.7	197.4	214.6	210.1	0.44
91.6	100.5	83.2	80.7	-0.11
135.1	186.3	155.1	173.3	0.39
179.3	205.7	198.6	219.8	0.42
88.3	97.0	108.0	99.2	0.11
100.4	113.4	115.9	112.3	0.12
131.4	136.9	137.6	152.8	0.22
138.0	176.6	185.1	198.0	0.62
165.4	166.9	169.1	156.7	-0.09
134.8	166.6	156.6	168.2	0.34

Table A2.75 Perimeter of *Acropora austera* branch tips measured using digital photography at Chaland during May-August 2003 (85 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
92.4	92.7	91.6	91.5	-0.01
130.5	154.3	219.0	136.1	0.07
102.7	126.5	123.7	127.8	0.30
148.8	181.5	187.9	167.2	0.22
124.6	128.8	137.7	144.9	0.24
171.7	193.1	215.0	233.2	0.72
161.9	160.3	175.1	189.0	0.32

Table A2.76 Perimeter of *Porites rus* branch tips measured using digital photography at Totor during May-August 2003 (58 days). NR indicates no measurements were made.

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
NR	58.5	71.2	58.1	-0.01
NR	62.8	73.5	80.9	0.31
NR	86.0	89.2	91.8	0.10
NR	85.5	95.6	101.1	0.27
NR	72.9	74.4	78.5	0.10

Table A2.77 Perimeter of *Porites rus* branch tips measured using digital photography at Trou Malabar during May-August 2003 (61 days). NR indicates no measurements were made.

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
NR	64.0	70.3	82.7	0.31
NR	95.1	108.5	120.0	0.41
NR	65.7	75.0	83.3	0.29
NR	59.7	73.1	81.9	0.36
NR	80.5	94.1	104.1	0.39
NR	112.2	121.7	138.3	0.43

Table A2.78 Perimeter of *Porites rus* branch tips measured using digital photography at Chaland during May-August 2003 (84 days).

Length (mm)				Total Growth (mm d^{-1})
May	June	July	August	
56.9	66.6	67.5	80.5	0.28
81.6	95.8	110.8	108.3	0.32
60.8	67.2	67.0	75.8	0.18
92.8	109.3	113.2	129.6	0.44

Appendix 3 Coral Recruitment and Regeneration Data

Table A3.1 Percent cover of organisms and number of coral recruits on settlement tiles collected from Totor.

		% Cover						
Tile	Face	Coralline Algae	Bryozoans	Macro-algae	*Alectryonella* sp	Serpulid Worms	Hydroids	Coral recruits (No.)
1	Upper	30	10	0	0	2	1	1
	Lower	6	5	0	52	0	22	2
2	Upper	23	8	0	0	8	4	0
	Lower	5	4	0	65	2	24	0
3	Upper	25	2	0	1	3	12	0
	Lower	5	4	0	52	3	21	1
4	Upper	18	1	0	0	6	13	2
	Lower	4	4	0	53	1	21	0
5	Upper	34	5	0	0	4	9	2
	Lower	4	3	0	63	0	23	0
6	Upper	25	4	0	0	3	14	0
	Lower	3	6	0	64	0	23	0
7	Upper	25	0	0	0	6	11	0
	Lower	2	3	0	65	1	27	0
8	Upper	25	4	0	1	4	11	3
	Lower	2	7	0	55	0	30	0
9	Upper	32	4	0	6	4	18	0
	Lower	8	4	0	75	0	10	0
10	Upper	21	5	0	0	0	30	1
	Lower	3	3	0	65	1	22	0
11	Upper	36	8	0	6	2	16	0
	Lower	13	0	0	73	0	10	0
12	Upper	44	6	0	0	3	7	1
	Lower	5	2	0	64	1	20	0

Table A3.2 Percent cover of organisms and number of coral recruits on settlement tiles collected from Trou Malabar.

		% Cover						
Tile	Face	Coralline Algae	Bryozoans	Macro-algae	*Alectryonella* sp	Serpulid Worms	Hydroids	Coral recruits (No.)
1	Upper	74	18	0	1	6	0	0
	Lower	30	21	5	16	6	7	0
2	Upper	43	13	3	8	10	8	0
	Lower	35	7	0	38	4	12	0
3	Upper	46	0	0	0	6	0	0
	Lower	30	12	0	39	7	0	1

Table A3.3 Percent cover of organisms and number of coral recruits on settlement tiles collected from Chaland.

Tile	Face	% Cover						
		Coralline Algae	Bryozoans	Macro-algae	*Alectryonella* sp	Serpulid Worms	Hydroids	Coral recruits (No.)
1	Upper	40	21	12	0	0	0	0
	Lower	14	57	3	0	8	0	0
2	Upper	56	26	0	5	0	0	0
	Lower	26	59	0	3	5	0	0
3	Upper	38	32	0	10	5	0	0
	Lower	33	52	5	0	1	0	0
4	Upper	48	26	3	0	7	0	0
	Lower	24	52	5	0	4	0	0
5	Upper	67	26	6	0	0	0	0
	Lower	62	7	3	3	3	0	0
6	Upper	81	14	5	0	0	0	0
	Lower	19	79	0	2	0	0	0
7	Upper	69	0	25	6	0	0	0
	Lower	48	36	16	0	0	0	0
8	Upper	47	26	3	0	13	0	0
	Lower	21	62	4	4	0	0	0

Table A3.4 Size of artificially induced lesions on 10 *Montipora aequituberculata* colonies at Totor over a 35 day period. NR indicates no measurement was taken.

		Surface Area (mm^2)			
Coral	Hole	Day 0	Day 7	Day 21	Day 35
1	1	98.96	91.49	54.27	13.94
	2	72.36	143.63	17.79	17.80
	3	114.86	109.14	47.23	23.31
2	1	92.85	96.89	109.17	74.72
	2	80.44	142.77	138.80	136.61
	3	91.39	134.61	120.70	84.04
3	1	174.89	153.11	103.89	0.00
	2	102.71	141.12	94.34	0.00
	3	110.08	114.18	95.55	28.08
4	1	137.32	NR	111.87	78.90
	2	145.11	145.89	172.63	31.52
	3	119.13	113.92	107.84	81.60
5	1	149.34	138.93	131.19	19.69
	2	65.88	74.80	31.60	11.70
	3	76.62	101.95	42.90	8.24
6	1	103.66	86.48	69.57	41.44
	2	150.47	121.31	106.50	146.59
	3	85.23	105.39	115.92	78.51
7	1	79.90	111.86	77.29	39.74
	2	82.80	79.67	65.42	NR
	3	103.91	111.19	98.32	62.24
8	1	128.52	131.86	66.64	18.28
	2	118.67	143.86	40.90	0.00
	3	158.20	160.88	57.66	11.12
9	1	87.22	110.56	114.28	115.58
	2	113.49	123.36	104.45	76.50
	3	114.92	106.35	143.84	46.03
10	1	97.61	102.80	78.47	NR
	2	80.34	101.44	61.82	NR
	3	109.58	106.75	45.59	NR

Table A3.5 Size of artificially induced lesions on 10 *Montipora aequituberculata* colonies at Trou Malabar over a 35 day period. NR indicates no measurement was taken.

		Surface Area (mm^2)			
Coral	Hole	Day 0	Day 7	Day 21	Day 35
1	1	167.54	200.74	163.53	43.98
	2	197.62	164.26	182.85	44.49
	3	119.93	144.67	169.54	61.68
2	1	141.70	NR	NR	NR
	2	151.43	138.43	126.9	47.6
	3	163.38	138.42	112.85	39.61
3	1	190.07	231.74	238.41	51.29
	2	130.32	169.46	186.1	49.56
	3	176.09	182.76	233.86	55.18
4	1	122.47	135.19	157.44	40.33
	2	117.26	171.34	156.34	41.5
	3	152.54	211.64	197.74	58.03
5	1	216.25	246.19	270.9	67.17
	2	154.50	188.94	138.57	46.17
	3	150.90	121.57	116.18	39.07
6	1	112.43	130.6	102.86	37.08
	2	140.75	120.38	127.31	44.95
	3	245.77	246.51	255.7	51.27
7	1	148.90	208.54	198.54	60.33
	2	283.01	383.68	317.15	NR
	3	178.12	163.48	137.48	44.93
8	1	167.91	275.55	222.72	58.62
	2	102.34	213.19	182.43	57.79
	3	117.74	309.64	299.59	67.04
9	1	187.93	234.96	163.54	40.65
	2	261.72	331.04	190.87	43.39
	3	138.94	183.58	145.25	46.79
10	1	155.07	142.25	NR	NR
	2	195.09	140.05	NR	NR
	3	148.46	145.34	NR	NR

Table A3.6 Size of artificially induced lesions on 10 *Montipora spp. (M. aequituberculata, M. grisea, M. tuberculosa* and *M. mollis)* colonies at Chaland over a 35 day period. NR indicates no measurement was taken.

		Surface Area (mm^2)			
Coral	Hole	Day 0	Day 7	Day 21	Day 35
1	1	99.22	79.93	94.06	63.18
	2	98.08	117.08	97.18	66.56
	3	93.14	179.29	191.76	197.6
2	1	99.84	92.41	77.78	59.28
	2	110.27	92.72	68.85	32.23
	3	114.95	108.15	NR	61.45
3	1	127.07	154.43	NR	111.69
	2	118.00	77.17	73.22	25.90
	3	104.44	96.91	47.02	0.00
4	1	116.25	96.39	92.45	63.64
	2	145.36	105.25	67.87	26.51
	3	128.90	103.39	83.68	57.55
5	1	146.00	141.77	115.95	91.03
	2	172.15	141.41	130.83	117.70
	3	115.90	109.53	110.91	240.34
6	1	157.35	178.90	166.24	NR
	2	161.33	122.62	67.33	NR
	3	110.11	114.12	108.70	NR
7	1	102.26	190.23	144.96	122.16
	2	146.56	290.05	346.90	253.09
	3	146.19	391.22	550.41	544.48
8	1	119.65	107.28	52.29	43.49
	2	108.50	77.26	72.85	34.52
	3	98.07	116.57	43.64	0.00
9	1	104.07	125.09	71.48	NR
	2	136.28	127.00	65.32	NR
	3	94.47	276.85	181.40	NR
10	1	138.44	122.99	106.03	63.76
	2	153.87	145.89	98.47	69.10
	3	135.86	97.12	88.58	20.49

Appendix 4 Physiological and Morphological Adaptation Data

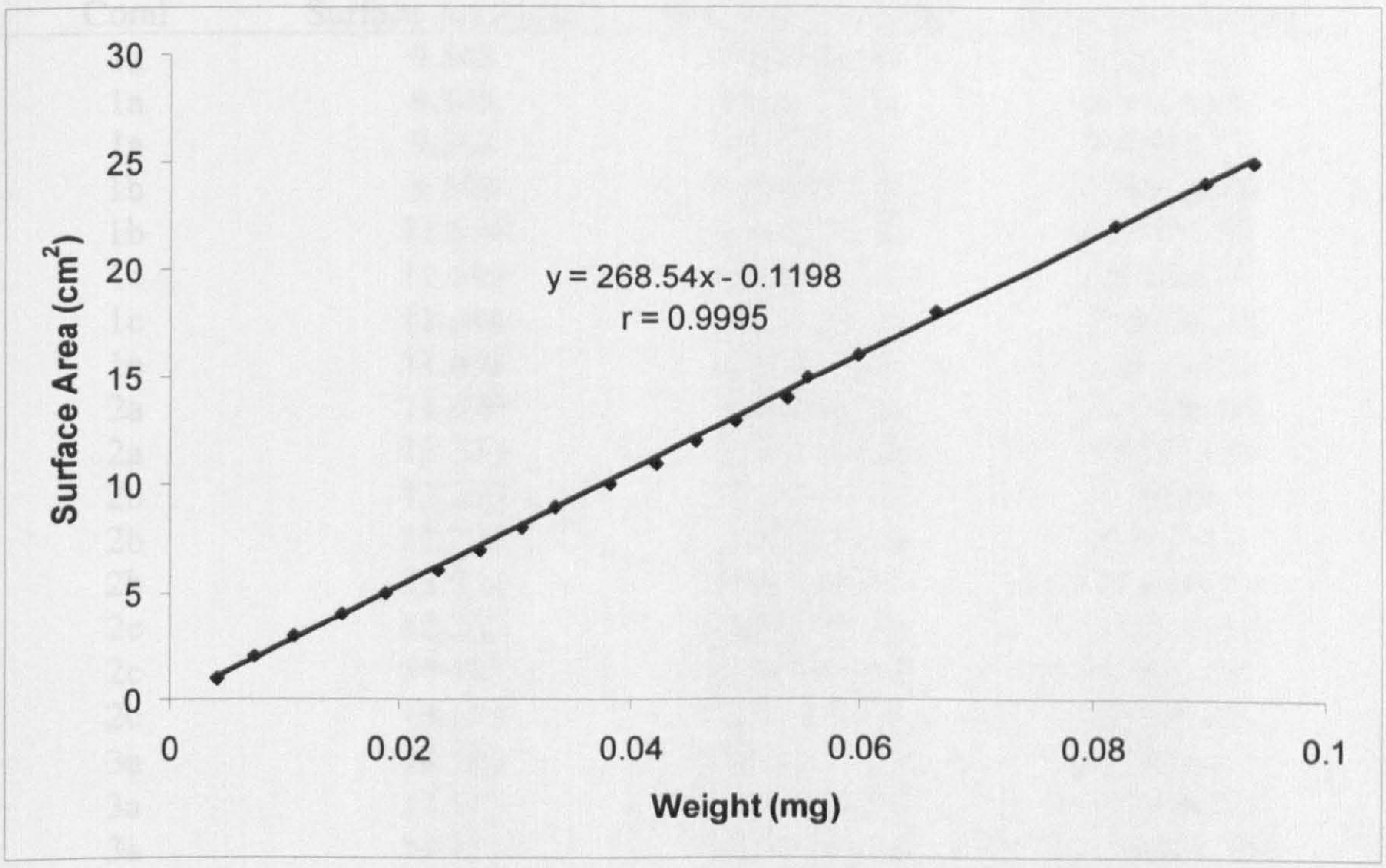

Figure A4.1 Weight/Surface Area conversion based on the aluminium foil technique (Marsh, 1970).

Table A4.1 The density of zooxanthellae in coral branch tips collected from Totor during June 2003.

Coral	Surface Area (cm^2)	No. Zooxanthellae	Zooxanthellae/cm^2
1a	9.548	7968888.89	834613.42
1a	9.548	9351111.11	979379.04
1a	9.548	9471111.11	991947.12
1b	9.548	12115555.56	1268910.30
1b	11.696	16182222.22	1383568.93
1c	11.696	14513333.33	1240880.07
1c	11.696	17133333.33	1464888.28
1c	11.696	13582222.22	1161270.71
2a	11.696	19208888.89	1642346.86
2a	12.233	13572222.22	1109476.19
2b	12.233	14433333.33	1179868.7
2b	12.233	17783333.33	1453718.1
2b	12.233	21266666.67	1738466.99
2c	12.233	14255555.56	1165336.02
2c	14.113	12941666.67	917003.24
2c	14.113	12455555.55	882559.03
3a	14.113	13061111.11	925466.67
3a	14.113	17138888.89	1214404.37
3a	14.113	19255555.56	1364384.30
3b	14.650	11361111.11	775502.46
3b	14.650	14808333.33	1010807.74
3c	14.650	13777777.78	940462.65
3c	14.650	12600000.00	860068.26
3c	14.650	12005555.56	819491.85

Table A4.2 The density of zooxanthellae in coral branch tips collected from Totor during July 2003.

Coral	Surface Area (cm^2)	No. Zooxanthellae	Zooxanthellae/cm^2
1a	7.131	5416666.67	759617.69
1a	7.131	7050000.00	988671.65
1a	7.131	6558333.33	919721.73
1a	7.131	6033333.33	846097.25
1a	7.131	4950000.00	694173.71
1b	10.085	5508333.33	546205.88
1b	10.085	6375000.00	632144.47
1b	10.085	6400000.00	634623.47
1b	10.085	6016666.67	596612.17
1b	10.085	6116666.67	606528.16
1c	12.502	12200000.00	975876.65
1c	12.502	11333333.33	906552.08
1c	12.502	9650000.00	771902.43
1c	12.502	8133333.33	650584.43
1c	12.502	11483333.33	918550.56
2a	8.742	6683333.33	764506.75
2a	8.742	7000000.00	800730.27
2a	8.742	6733333.33	770226.26
2a	8.742	5850000.00	669181.72
2a	8.742	6683333.33	764506.75
2b	7.936	5766666.67	726609.88
2b	7.936	5583333.33	703509.57
2b	7.936	4933333.33	621608.45
2b	7.936	4666666.67	588008.00
2b	7.936	5066666.67	638408.68
2c	8.205	6341666.67	772908.35
2c	8.205	5266666.67	641889.72
2c	8.205	7108333.33	866348.00
2c	8.205	6341666.67	772908.35
2c	8.205	6841666.67	833847.25
3a	7.936	5516666.67	695109.45
3a	7.936	5900000.00	743410.11
3a	7.936	6300000.00	793810.80
3a	7.936	5633333.33	709809.65
3a	7.936	6033333.33	760210.34
3b	10.622	5866666.67	552323.21
3b	10.622	6200000.00	583705.21
3b	10.622	6766666.67	637054.61
3b	10.622	6783333.33	638623.71
3b	10.622	7016666.67	660591.11
3c	10.890	6450000.00	592268.01
3c	10.890	6633333.33	609102.50
3c	10.890	6916666.67	635119.44
3c	10.890	6983333.33	641241.08
3c	10.890	7216666.67	662666.79

Table A4.3 The density of zooxanthellae in coral branch tips collected from Totor during August 2003.

Coral	Surface Area (cm^2)	No. Zooxanthellae	Zooxanthellae/cm^2
1a	10.89	11066666.67	1016222.83
1a	10.89	8100000.00	743801.65
1a	10.89	8083333.33	742271.20
1a	10.89	7150000.00	656565.66
1a	10.89	7683333.33	705540.25
1b	9.011	7416666.67	823068.10
1b	9.011	6833333.33	758332.41
1b	9.011	9266666.67	1028372.73
1b	9.011	8100000.00	898901.34
1b	9.011	8083333.33	897051.75
1c	13.039	9900000.00	759260.68
1c	13.039	8633333.33	662116.22
1c	13.039	11650000.00	893473.43
1c	13.039	13350000.00	1023851.52
1c	13.039	9250000.00	709410.23
2a	6.057	7950000.00	1312530.96
2a	6.057	6833333.33	1128171.26
2a	6.057	7116666.67	1174949.09
2a	6.057	6133333.33	1012602.50
2a	6.057	6466666.67	1067635.24
2b	10.085	6266666.67	621384.90
2b	10.085	6183333.33	613121.80
2b	10.085	6750000.00	669310.86
2b	10.085	6700000.00	664353.00
2b	10.085	7133333.33	707321.10
2c	10.622	9716666.67	914768.09
2c	10.622	7383333.33	695098.22
2c	10.622	9583333.33	902215.53
2c	10.622	10283333.33	968116.49
2c	10.622	8083333.33	760999.18
3a	8.742	7966666.67	911309.39
3a	8.742	7950000.00	909402.88
3a	8.742	8133333.33	930374.44
3a	8.742	7350000.00	840768.70
3a	8.742	8033333.33	918935.41
3b	8.473	9066666.67	1070065.70
3b	8.473	8366666.67	987450.33
3b	8.473	8266666.67	975648.14
3b	8.473	8216666.67	969747.04
3b	8.473	8466666.67	999252.53
3c	7.399	6833333.33	923548.23
3c	7.399	6300000.00	851466.41
3c	7.399	7500000.00	1013650.49
3c	7.399	6350000.00	858224.08
3c	7.399	6633333.33	896517.55

Table A4.4 The density of zooxanthellae in coral branch tips collected from Trou Malabar during June 2003.

Coral	Surface Area (cm^2)	No. Zooxanthellae	Zooxanthellae/cm^2
1a	16.530	9733333.33	588828.39
1a	16.530	9950000.00	601935.87
1a	16.530	12341666.67	746622.30
1b	16.530	12300000.00	744101.63
1b	16.530	11591666.67	701250.25
1c	10.622	7116666.67	669993.10
1c	10.622	7100000.00	668424.03
2a	10.622	7483333.33	704512.65
2a	10.622	8291666.67	780612.57
2b	10.622	8216666.67	773551.75
2b	10.085	8441666.67	837051.73
2c	10.085	8850000.00	877540.90
2c	10.085	12341666.67	1223764.67
3a	10.085	10658333.33	1056850.11
3a	10.085	10741666.67	1065113.20
3a	12.502	5266666.67	421265.93
3b	12.502	5225000.00	417933.13
3b	12.502	6633333.33	530581.77
3c	12.502	7208333.33	576574.41
3c	12.502	6325000.00	505919.05

Table A4.5 The density of zooxanthellae in coral branch tips collected from Trou Malabar during July 2003.

Coral	Surface Area (cm^2)	No. Zooxanthellae	Zooxanthellae/cm^2
1a	8.742	5650000.00	646303.71
1a	8.742	6016666.67	688246.73
1a	8.742	6233333.33	713031.24
1a	8.742	5466666.67	625332.21
1a	8.742	6966666.67	796917.26
1b	12.770	7050000.00	552069.99
1b	12.770	7033333.33	550764.86
1b	12.770	7233333.33	566426.42
1b	12.770	8083333.33	632988.05
1b	12.770	7133333.33	558595.64
1c	6.594	3683333.33	558614.03
1c	6.594	4266666.67	647082.32
1c	6.594	4583333.33	695107.96
1c	6.594	4700000.00	712801.61
1c	6.594	4516666.67	684997.30
2a	8.473	7116666.67	839875.31
2a	8.473	7250000.00	855610.68
2a	8.473	6883333.33	812338.42
2a	8.473	7983333.33	942155.21
2a	8.473	7350000.00	867412.21
2b	8.205	7650000.00	932365.14
2b	8.205	6466666.67	788143.08
2b	8.205	6683333.33	814549.93
2b	8.205	7133333.33	869394.94
2b	8.205	7216666.67	879551.42
2c	8.473	7216666.67	851676.84
2c	8.473	6900000.00	814305.34
2c	8.473	9416666.67	1111310.43
2c	8.473	9850000.00	1162450.37
2c	8.473	7483333.33	883147.58
3a	7.399	3866666.67	522570.54
3a	7.399	3816666.67	515813.16
3a	7.399	4150000.00	560862.35
3a	7.399	4366666.67	590144.32
3a	7.399	3866666.67	522570.54
3b	7.399	3883333.33	524823.00
3b	7.399	3500000.00	473016.44
3b	7.399	3716666.67	502298.41
3b	7.399	3316666.67	448239.39
3b	7.399	3650000.00	493288.57
3c	8.473	3666666.67	432722.64
3c	8.473	3666666.67	432722.64
3c	8.473	4133333.33	487796.43
3c	8.473	4116666.67	485829.51
3c	8.473	3816666.67	450424.93

Table A4.6 The density of zooxanthellae in coral branch tips collected from Trou Malabar during August 2003.

Coral	Surface Area (cm^2)	No. Zooxanthellae	Zooxanthellae/cm^2
1a	7.936	6700000.00	844254.03
1a	7.936	6766666.67	852654.57
1a	7.936	5133333.33	646841.40
1a	7.936	4983333.33	627940.19
1a	7.936	6283333.33	791750.67
1b	10.085	5833333.33	578416.79
1b	10.085	6000000.00	594942.98
1b	10.085	6366666.67	631300.61
1b	10.085	5333333.33	528838.21
1b	10.085	5533333.33	548669.64
1c	8.473	7016666.67	828120.70
1c	8.473	6850000.00	808450.37
1c	8.473	7316666.67	863527.28
1c	8.473	7766666.67	916637.16
1c	8.473	7483333.33	883197.61
2a	9.548	6066666.67	635386.12
2a	9.548	5166666.67	541125.54
2a	9.548	5533333.33	579528.00
2a	9.548	5383333.33	563817.90
2a	9.548	6300000.00	659824.05
2b	7.399	6900000.00	932558.45
2b	7.399	6700000.00	905527.77
2b	7.399	6683333.33	903275.22
2b	7.399	5250000.00	709555.35
2b	7.399	6616666.67	894264.99
2c	8.205	8150000.00	993296.77
2c	8.205	6900000.00	840950.64
2c	8.205	6633333.33	808450.13
2c	8.205	6316666.67	769855.78
2c	8.205	7483333.33	912045.50
3a	14.113	8200000.00	581024.59
3a	14.113	9200000.00	651881.24
3a	14.113	7916666.67	560948.53
3a	14.113	7616666.67	539691.54
3a	14.113	7500000.00	531424.93
3b	10.622	6166666.67	580556.08
3b	10.622	5700000.00	536622.11
3b	10.622	5383333.33	506809.77
3b	10.622	5583333.33	525638.61
3b	10.622	6100000.00	574279.80
3c	9.279	6233333.33	671767.79
3c	9.279	5733333.33	617882.67
3c	9.279	5583333.33	601717.14
3c	9.279	5983333.33	644825.23
3c	9.279	7400000.00	797499.73

Table A4.7 The density of zooxanthellae in coral branch tips collected from Chaland during July 2003.

Coral	Surface Area (cm^2)	No. Zooxanthellae	Zooxanthellae/cm^2
1a	14.113	9983333.33	707385.63
1a	14.113	10566666.67	748718.68
1a	14.113	13183333.33	934126.93
1a	14.113	14466666.67	1025059.64
1a	14.113	11616666.67	823118.17
1b	10.890	5966666.67	547903.28
1b	10.890	5483333.33	503520.05
1b	10.890	6766666.67	621365.17
1b	10.890	6300000.00	578512.40
1b	10.890	6300000.00	578512.40
1c	7.131	7116666.67	997990.00
1c	7.131	6600000.00	925536.39
1c	7.131	5150000.00	722198.85
1c	7.131	5366666.67	752582.62
1c	7.131	5683333.33	796989.67

Table A4.8 Morphological data for 15 *Montipora aequituberculata* colonies from Totor. NR indicates no measurement was taken.

Species	Depth (m)	Width (cm)	Height (cm)	W/H
Montipora aequituberculata	11.3	43.0	4.5	9.6
Montipora aequituberculata	12.5	49.0	6.0	8.2
Montipora aequituberculata	10.7	44.0	4.5	9.8
Montipora aequituberculata	11.4	42.0	9.5	4.4
Montipora aequituberculata	10.2	46.0	9.0	5.1
Montipora aequituberculata	10.3	40.0	4.5	8.9
Montipora aequituberculata	11.2	38.0	7.0	5.4
Montipora aequituberculata	10.5	45.0	10.0	4.5
Montipora aequituberculata	10.0	35.0	5.5	6.4
Montipora aequituberculata	7.8	35.0	4.0	8.8
Montipora aequituberculata	8.6	31.0	3.5	8.9
Montipora aequituberculata	8.5	34.0	4.5	7.6
Montipora aequituberculata	9.0	36.0	7.5	4.8
Montipora aequituberculata	8.6	30.0	5.5	5.5
Montipora aequituberculata	8.7	41.0	10.0	4.1

	Surface Area (cm^2)	Thickness (cm)	Orientation (°)	No. Tiers	% Sediment
Montipora aequituberculata	1090.95	0.30	50	3	26.43
Montipora aequituberculata	1631.03	NR	20	2	11.69
Montipora aequituberculata	1203.56	NR	10	1	3.05
Montipora aequituberculata	1263.00	NR	40	2	0.38
Montipora aequituberculata	1197.68	NR	10	3	2.90
Montipora aequituberculata	1270.69	0.30	50	2	17.08
Montipora aequituberculata	1027.25	0.24	20	2	2.02
Montipora aequituberculata	1213.02	0.22	50	3	14.54
Montipora aequituberculata	789.26	0.23	30	5	6.37
Montipora aequituberculata	775.00	0.28	60	2	0.21
Montipora aequituberculata	592.86	0.37	50	2	1.25
Montipora aequituberculata	806.02	0.49	65	1	5.76
Montipora aequituberculata	628.98	0.25	80	2	4.00
Montipora aequituberculata	520.72	0.15	80	1	1.62
Montipora aequituberculata	1055.52	0.37	60	4	0.82

Table A4.9 Morphological data for 15 *Montipora aequituberculata* colonies from Trou Malabar.

Species	Depth (m)	Width (cm)	Height (cm)	W/H
Montipora aequituberculata	9.3	38.0	5.0	7.6
Montipora aequituberculata	9.5	47.0	6.0	7.8
Montipora aequituberculata	9.5	36.0	6.5	5.5
Montipora aequituberculata	9.6	39.0	7.0	5.6
Montipora aequituberculata	8.8	35.0	6.0	5.8
Montipora aequituberculata	8.7	27.0	11.0	2.5
Montipora aequituberculata	9.0	32.0	2.5	12.8
Montipora aequituberculata	7.9	29.0	10.0	2.9
Montipora aequituberculata	8.1	40.0	5.0	8.0
Montipora aequituberculata	8.8	28.0	7.0	4.0
Montipora aequituberculata	8.1	31.0	6.0	5.2
Montipora aequituberculata	9.0	32.0	4.0	8.0
Montipora aequituberculata	8.6	38.0	3.0	12.7
Montipora aequituberculata	8.3	47.0	10.0	4.7
Montipora aequituberculata	7.4	38.0	4.0	9.5

	Surface Area (cm^2)	Thickness (cm)	Orientation (^{o})	No. Tiers	% Sediment
Montipora aequituberculata	747.23	0.40	90	3	14.24
Montipora aequituberculata	1047.40	0.90	30	3	17.45
Montipora aequituberculata	960.18	0.60	30	2	87.92
Montipora aequituberculata	817.05	0.70	90	2	44.85
Montipora aequituberculata	729.57	0.59	45	2	6.98
Montipora aequituberculata	417.16	0.68	50	3	30.24
Montipora aequituberculata	569.25	0.43	80	2	4.65
Montipora aequituberculata	589.14	0.43	60	6	4.19
Montipora aequituberculata	769.84	0.65	60	3	0.17
Montipora aequituberculata	498.85	0.48	30	1	10.10
Montipora aequituberculata	566.85	0.15	60	4	6.01
Montipora aequituberculata	594.78	0.20	80	3	16.43
Montipora aequituberculata	653.02	0.10	10	3	2.97
Montipora aequituberculata	1436.63	0.25	60	5	15.84
Montipora aequituberculata	853.82	0.20	50	4	9.38

Table A4.10 Morphological data for 15 *Montipora* spp. colonies from Chaland. NR indicates no measurement was taken.

Species	Depth (m)	Width (cm)	Height (cm)	W/H
Montipora aequituberculata	11.3	20.0	2.0	10.0
Montipora aequituberculata	8.8	26.0	4.5	5.8
Montipora aequituberculata	11.6	22.0	2.0	11.0
Montipora aequituberculata	9.7	34.0	2.5	13.6
Montipora aequituberculata	8.4	24.0	3.0	8.0
Montipora mollis	10.1	26.0	2.5	10.4
Montipora aequituberculata	9.8	39.0	7.0	5.6
Montipora grisea	8.3	38.0	3.5	10.9
Montipora aequituberculata	12.2	NR	4.0	NR
Montipora aequituberculata	9.8	32.0	3.5	9.1
Montipora aequituberculata	9.4	31.0	6.0	5.2
Montipora tuberculosa	9.7	29.0	4.0	7.3
Montipora aequituberculata	8.9	20.0	2.0	10.0
Montipora mollis	10.4	33.0	5.5	6.0
Montipora aequituberculata	12.2	NR	3.5	NR

	Surface Area (cm^2)	Thickness (cm)	Orientation (°)	No. Tiers	% Sediment
Montipora aequituberculata	237.21	0.11	40	2	3.59
Montipora aequituberculata	449.19	0.10	30	2	0.68
Montipora aequituberculata	310.24	0.10	30	1	2.45
Montipora aequituberculata	458.87	0.87	30	1	0.48
Montipora aequituberculata	228.31	0.18	30	1	9.89
Montipora mollis	373.36	0.35	50	1	0.79
Montipora aequituberculata	550.80	0.12	90	1	0.00
Montipora grisea	675.31	0.10	90	1	6.30
Montipora aequituberculata	NR	0.23	60	2	NR
Montipora aequituberculata	625.49	0.28	40	1	0.65
Montipora aequituberculata	552.24	0.12	65	2	0.26
Montipora tuberculosa	590.08	0.34	20	1	0.95
Montipora aequituberculata	279.38	0.73	40	1	1.97
Montipora mollis	660.26	0.31	70	2	0.94
Montipora aequituberculata	NR	0.36	30	1	NR

Appendix 5 Coral Bleaching Data

Table A5.1 Site positions and descriptions for the 22 survey sites.

Site	Lat (°S)	Long (°E)	Survey Date	Temp (°C)	Depth (m)
Trou Malabar	19 40.250	63 25.019	06/03/2002	NR	0.5-2.5
Chaland	19 40.069	63 24.586	06/03/2002	NR	0.5-2.0
Totor	19 40.212	63 25.789	06/03/2002	NR	0.5-1.5
Ile aux Fous	19 39.215	63 23.364	07/03/2002	29.2	0.5-5.0
Paté Capdor	19 39.656	63 26.276	07/03/2002	29.2	0.5-3.0
Grande Bassin	19 39.355	63 21.409	08/03/2002	29.2	0.5-3.0
Off English Bay	19 40.052	63 26.082	09/03/2002	29.4	0.5-3.0
SW Lagoon 1	19 48.198	63 22.166	11/03/2002	28.6	0.5-2.5
SW Lagoon 2	19 48.228	63 24.211	11/03/2002	29.1	1.0-2.5
SW Lagoon 3	19 47.947	63 23.815	11/03/2002	29.6	0.5-1.5
SW Lagoon 4	19 48.743	63 24.999	11/03/2002	30.1	0.5-2.5
SW Lagoon 5	19 49.814	63 23.243	11/03/2002	30.2	0.5
Rivière Banane	19 40.197	63 28.053	13/03/2002	29.0	1.0-1.5
Passe Grenade	19 40.554	63 28.925	13/03/2002	29.0	1.0-2.0
East of Passe Grenade	19 40.725	63 29.300	13/03/2002	29.0	1.0-2.5
East of Grande Passe 1	19 45.513	63 28.009	14/03/2002	29.0	1.0-1.2
East of Grande Passe 2	19 45.401	63 28.443	14/03/2002	28.0	1.1-1.3
East of Grande Passe 3	19 45.033	63 28.824	14/03/2002	28.0	1.2-1.3
South of Ile aux Cocos	19 45.120	63 17.800	15/03/2002	28.8	1.0-1.5
Passe Demi	19 42.611	63 17.814	15/03/2002	29.2	1.0-1.5
North of Ile aux Sables	19 40.834	63 18.309	15/03/2002	29.4	1.0-1.5
Grande Pointe	19 39.640	63 19.016	15/03/2002	28.7	1.0-1.5

Table A5.2 Percentage cover of physical attributes for the 22 survey sites, based on a semi-quantitative scale of 0-6, where 0 = 0%, 1= <1%, 2 = 1-10%, 3 = 11-30%, 4 = 31-50%, 5 = 51-75% and 6 = 76-100%. CP = Continuous pavement; LB = Large Blocks (>1m); SB = Small Blocks (<1m); RB = Rubble; SLT = Silt and SD = Sand.

Site	CP	LB	SB	RB	SLT	SD
Trou Malabar	6	0	0	0	0	0
Chaland	6	0	0	2	0	0
Totor	6	0	0	0	0	0
Ile aux Fous	0	0	4	4	0	1
Paté Capdor	0	0	4	4	0	2
Grande Bassin	3	3	3	2	0	0
Off English Bay	4	2	3	2	0	3
SW Lagoon 1	0	5	1	1	0	3
SW Lagoon 2	0	5	2	1	0	3
SW Lagoon 3	0	4	2	1	0	4
SW Lagoon 4	0	5	2	2	0	2
SW Lagoon 5	0	2	3	2	0	4
Rivière Banane	6	0	2	0	0	0
Passe Grenade	4	1	2	2	0	3
East of Passe Grenade	4	1	2	0	0	2
East of Grande Passe 1	0	2	4	2	0	1
East of Grande Passe 2	0	5	2	1	0	2
East of Grande Passe 3	0	2	4	1	0	3
South of Ile aux Cocos	0	4	1	3	0	4
Passe Demi	0	5	2	3	0	3
North of Ile aux Sables	0	5	1	3	0	4
Grande Pointe	0	3	1	3	0	5

Table A5.3 Percentage cover of biological attributes for the 22 survey sites, based on a semi-quantitative scale of 0-6, where 0 = 0%, 1= <1%, 2 = 1-10%, 3 = 11-30%, 4 = 31-50%, 5 = 51-75% and 6 = 76-100%. HS = Hard Substrate; LHC = Living Hard Coral; DSC = Dead Standing Coral; SC = Soft Coral; TA = Turf Algae; MA = Macro-algae; CA = Coralline Algae; SP = Sponge; OT = Other.

Site	HS	LHC	DSC	SC	TA	MA	CA	SP	OT
Trou Malabar	4	2	5	1	5	3	0	0	0
Chaland	5	3	2	1	2	1	3	0	0
Totor	5	2	1	1	1	1	3	0	0
Ile aux Fous	4	2	5	2	5	1	3	0	0
Paté Capdor	3	5	0	0	0	1	3	0	0
Grande Bassin	3	3	3	1	3	1	2	0	0
Off English Bay	4	3	0	1	1	2	4	0	0
SW Lagoon 1	4	3	1	0	3	3	2	0	0
SW Lagoon 2	0	2	5	0	4	4	1	0	0
SW Lagoon 3	0	4	2	0	3	2	1	0	0
SW Lagoon 4	0	5	1	0	3	0	1	1	0
SW Lagoon 5	3	3	1	0	3	3	2	0	0
Rivière Banane	5	2	0	1	3	1	3	0	0
Passe Grenade	5	2	0	1	1	2	1	0	0
East of Passe Grenade	4	2	1	1	2	3	2	0	2
East of Grande Passe 1	4	4	1	2	4	1	1	0	0
East of Grande Passe 2	2	4	1	4	2	1	1	0	0
East of Grande Passe 3	4	4	1	1	2	1	1	0	0
South of Ile aux Cocos	0	4	2	0	2	0	2	0	0
Passe Demi	0	4	1	0	2	0	1	0	0
North of Ile aux Sables	0	2	4	2	4	0	1	0	0
Grande Pointe	0	3	1	0	2	0	1	0	0

Table A5.4 Percentage of coral colonies that are dead, bleached, partially bleached and alive based on a semi-quantitative scale of 0-6, where 0 = 0%, 1= <1%, 2 = 1-10%, 3 = 11-30%, 4 = 31-50%, 5 = 51-75% and 6 = 76-100%

Site	Dead	Bleached	P. Bleached	Live
Trou Malabar	6	3	0	1
Chaland	3	2	0	5
Totor	1	1	0	6
Ile aux Fous	6	1	0	1
Paté Capdor	0	0	0	6
Grande Bassin	4	1	0	4
Off English Bay	0	0	0	6
SW Lagoon 1	0	0	1	6
SW Lagoon 2	5	0	3	2
SW Lagoon 3	2	0	3	5
SW Lagoon 4	0	0	3	5
SW Lagoon 5	0	0	0	6
Rivière Banane	0	0	0	6
Passe Grenade	0	0	0	6
East of Passe Grenade	0	0	0	6
East of Grande Passe 1	0	0	2	6
East of Grande Passe 2	0	0	2	6
East of Grande Passe 3	0	0	2	6
South of Ile aux Cocos	0	0	0	6
Passe Demi	0	0	2	6
North of Ile aux Sables	5	0	0	3
Grande Pointe	0	0	2	6

Table A5.5 The abundance and percentage of each species that are dead, bleached and alive based on a semi-quantitative scale of 0-6, where 0 = 0%, 1= <1%, 2 = 1-10%, 3 = 11-30%, 4 = 31-50%, 5 = 51-75% and 6 = 76-100%.

		Trou Malabar				Chaland				Totor				Ile aux Fous			
			% of species				% of species				% of species				% of species		
Genus	Species	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live
Pocillopora	*damicornis*	1	0	6	1	1	0	2	6	1	0	2	5	1	0	2	5
Pocillopora	*eydouxi*	1	0	6	1	1	2	3	4					1	1	2	4
Pocillopora	*verrucosa*	1	0	6	1	1	0	2	6	1	0	0	6	1	0	2	5
Stylophora	*pistillata*																
Montipora	sp	1	6	0	0	1	2	2	5	1	0	2	5				
Montipora	*aequituberculata*													1	2	3	4
Montipora	*digitata*													1	0	2	6
Montipora	*tuberculosa*																
Acropora	sp																
Acropora	*abrotanoides*	2	6	1	1	3	4	0	3	1	0	0	6	1	6	0	1
Acropora	*austera*																
Acropora	*clathrata*																
Acropora	*cytherea*	3	6	1	1	2	2	0	5	1	2	2	4	4	6	0	0
Acropora	*digitefera*	1	4	3	1	2	1	4	3	1	0	2	5	1	5	0	2
Acropora	*horrida*																
Acropora	*humilis*	1	6	1	1	1	0	3	4					1	5	0	2
Acropora	*muricata*	4	5	1	3	3	1	4	3	1	0	0	6	3	3	0	4
Acropora	*nasuta*																
Acropora	*nobilis*																
Acropora	*pinguis*	1	6	0	0	1	0	6	0								
Acropora	*paniculata*																
Acropora	*tenuis*																

Acropora	*valida*	1	4	3	0	1	0	2	5					1	5	0	2
Porites	sp	1	1	3	4	1	0	0	6	1	0	0	6	1	0	1	6
Goniopora	sp													1	0	6	0
Pavona	*cactus*																
Pavona	*decussata*																
Fungia	sp	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Hydnophora	sp	1	0	0	6	1	0	6	0								
Hydnophora	*microconos*																
Favia	sp	1	1	6	1	1	0	3	5								
Favia	*stelligera*													1	3	0	4
Favites	sp	1	1	6	1	1	2	3	5	1	0	0	6	1	0	0	6
Favites	*abdita*																
Goniastrea	sp																
Goniastrea	*pectinata*													1	0	0	6
Goniastrea	*retiformis*																
Platygyra	*daedalea*	1	1	6	0	1	2	4	4	1	2	0	5	1	0	2	5
Platygyra	*lamellina*																
Leptoria	*phrygia*	1	0	4	4	1	0	0	6	1	0	0	6	1	0	1	6
Cyphastrea	*microphthalma*																
Echinopora	sp																
Echinopora	*forskaliana*									1	0	0	6				
Turbinaria	sp																
Turbinaria	*mesenterina*									1	0	0	6				
Millepora	sp					1	0	3	4					1	2	0	5
Sarcophyton	sp													1	0	6	0
Sinularia	sp	1	0	6	0									2	0	pale	6
Lobophyton	sp																

Xenia	sp																
Palythoa	sp					1	0	pale	6								
Heteractis	sp													1	0	0	6

		Paté Capdor				Grand Bassin				Off English Bay				SW Lagoon 1			
			% of species				% of species				% of species				% of species		
Genus	Species	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live
Pocillopora	*damicornis*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Pocillopora	*eydouxi*					1	1	2	4	1	0	0	6				
Pocillopora	*verrucosa*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Stylophora	*pistillata*													1	0	0	6
Montipora	sp	1	0	0	6	1	0	0	6	1	0	0	6				
Montipora	*aequituberculata*									1	0	0	6				
Montipora	*digitata*	1	0	0	6					1	0	0	6	1	0	0	6
Montipora	*tuberculosa*													1	0	1	6
Acropora	sp																
Acropora	*abrotanoides*	1	0	0	6	3	5	0	2	1	0	0	6	1	0	0	6
Acropora	*austera*	1	0	0	6	1	3	0	4								
Acropora	*clathrata*																
Acropora	*cytherea*	3	0	0	6	1	4	0	4	1	0	0	6	2	0	0	6
Acropora	*digitefera*	1	0	0	6	2	3	0	4	2	0	0	6	1	0	0	6
Acropora	*horrida*																
Acropora	*humilis*	1	0	0	6	1	2	0	5					1	0	0	6
Acropora	*muricata*	2	0	0	6	3	4	0	4					1	0	0	6
Acropora	*nasuta*																
Acropora	*nobilis*																

Acropora	*pinguis*	1	0	0	6	1	3	0	4	1	0	0	6				
Acropora	*paniculata*																
Acropora	*tenuis*	1	0	0	6												
Acropora	*valida*	1	0	0	6	1	2	0	5					1	0	0	6
Porites	sp					1	0	0	6	1	0	0	6				
Goniopora	sp									1	0	0	6				
Pavona	*cactus*																
Pavona	*decussata*					1	0	0	6	1	0	0	6				
Fungia	sp	1	0	0	6	1	0	0	6					1	0	0	6
Hydnophora	sp																
Hydnophora	*microconos*																
Favia	sp													1	0	0	6
Favia	*stelligera*	1	0	0	6	1	2	1	5								
Favites	sp	1	0	0	6	1	0	0	6					1	0	0	6
Favites	*abdita*									1	0	0	6				
Goniastrea	sp					1	2	0	5								
Goniastrea	*pectinata*	1	0	0	6									1	0	0	6
Goniastrea	*retiformis*									1	0	0	6				
Platygyra	*daedalea*	1	0	0	6	1	2	0	5	1	0	0	6	1	0	0	6
Platygyra	*lamellina*													1	0	0	6
Leptoria	*phrygia*	1	0	0	6	1	0	0	6					1	0	0	6
Cyphastrea	*microphthalma*													1	0	0	6
Echinopora	sp																
Echinopora	*forskaliana*	1	0	0	6												
Turbinaria	sp																
Turbinaria	*mesenterina*																
Millepora	sp					1	0	0	6	2	0	0	6				

Sarcophyton	sp					1	0	5	2								
Sinularia	sp					1	0	pale	6	1	0	0	6				
Lobophyton	sp									1	0	0	6				
Xenia	sp																
Palythoa	sp									1	0	0	6				
Heteractis	sp					1	0	0	6								

		SW Lagoon 2				SW Lagoon 3				SW Lagoon 4				SW Lagoon 5			
			% of species				% of species				% of species				% of species		
Genus	Species	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live
Pocillopora	*damicornis*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Pocillopora	*eydouxi*																
Pocillopora	*verrucosa*																
Stylophora	*pistillata*													2	0	0	6
Montipora	sp																
Montipora	*aequituberculata*									1	0	0	6				
Montipora	*digitata*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Montipora	*tuberculosa*	1	0	0	6	1	0	0	6	2	0	0	6				
Acropora	sp																
Acropora	*abrotanoides*													1	0	0	6
Acropora	*austera*	2	0	3	4	2	0	2	6	3	0	2	5				
Acropora	*clathrata*					1	1	0	6								
Acropora	*cytherea*	4	6	2	0	4	2	0	6	4	0	0	6	2	0	0	6
Acropora	*digitefera*													1	0	0	6
Acropora	*horrida*																
Acropora	*humilis*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6

Acropora	*muricata*	3	3	3	3	3	0	3	4	3	0	3	4	1	0	0	6
Acropora	*nasuta*																
Acropora	*nobilis*																
Acropora	*pinguis*																
Acropora	*paniculata*																
Acropora	*tenuis*																
Acropora	*valida*																
Porites	sp																
Goniopora	sp																
Pavona	*cactus*																
Pavona	*decussata*																
Fungia	sp	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Hydnophora	sp																
Hydnophora	*microconos*													1	0	0	6
Favia	sp																
Favia	*stelligera*													1	0	0	6
Favites	sp													1	0	0	6
Favites	*abdita*																
Goniastrea	sp																
Goniastrea	*pectinata*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Goniastrea	*retiformis*					1	0	0	6	1	0	0	6	1	0	0	6
Platygyra	*daedalea*													1	0	0	6
Platygyra	*lamellina*													1	0	0	6
Leptoria	*phrygia*													1	0	0	6
Cyphastrea	*microphthalma*	1	0	0	6	1	0	0	6	1	0	0	6	2	0	0	6
Echinopora	sp									1	0	0	6	1	0	0	6
Echinopora	*forskaliana*																

Turbinaria	sp
Turbinaria	*mesenterina*
Millepora	sp
Sarcophyton	sp
Sinularia	sp
Lobophyton	sp
Xenia	sp
Palythoa	sp
Heteractis	sp

		Rivière Banane				Passe Grenade				E. Passe Grenade				E. Grande Passe 1			
			% of species				% of species				% of species				% of species		
Genus	Species	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live
Pocillopora	*damicornis*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Pocillopora	*eydouxi*	1	0	0	6					1	0	0	6				
Pocillopora	*verrucosa*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Stylophora	*pistillata*																
Montipora	sp	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Montipora	*aequituberculata*																
Montipora	*digitata*	1	0	0	6												
Montipora	*tuberculosa*																
Acropora	sp	1	0	0	6	1	0	0	6								
Acropora	*abrotanoides*	1	0	0	6	1	0	0	6	1	0	0	6				
Acropora	*austera*																
Acropora	*clathrata*																
Acropora	*cytherea*	1	0	0	6	1	0	0	6	1	0	0	6	2	0	3	4

Acropora	*digitefera*	1	0	0	6	1	0	0	6					2	0	0	6
Acropora	*horrida*																
Acropora	*humilis*									1	0	0	6	1	0	0	6
Acropora	*muricata*	1	0	0	6									1	0	2	5
Acropora	*nasuta*																
Acropora	*nobilis*	1	0	2	5												
Acropora	*pinguis*	1	0	0	6	1	0	0	6	1	0	0	6				
Acropora	*paniculata*																
Acropora	*tenuis*	1	0	0	6	1	0	0	6								
Acropora	*valida*	1	0	0	6					1	0	0	6				
Porites	sp	1	0	0	6					1	0	0	6	1	0	0	6
Goniopora	sp													1	0	0	6
Pavona	*cactus*													1	0	0	6
Pavona	*decussata*	1	0	0	6												
Fungia	sp													1	0	0	6
Hydnophora	sp																
Hydnophora	*microconos*	1	0	0	6												
Favia	sp	1	0	0	6					1	0	0	6				
Favia	*stelligera*																
Favites	sp	1	0	0	6									1	0	0	6
Favites	*abdita*																
Goniastrea	sp													1	0	0	6
Goniastrea	*pectinata*																
Goniastrea	*retiformis*																
Platygyra	*daedalea*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	3	4
Platygyra	*lamellina*																
Leptoria	*phrygia*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6

Cyphastrea	*microphthalma*																
Echinopora	sp																
Echinopora	*forskaliana*																
Turbinaria	sp	1	0	0	6					1	0	0	6				
Turbinaria	*mesenterina*																
Millepora	sp	1	0	0	6	1	0	0	6	2	0	0	6	1	0	0	6
Sarcophyton	sp																
Sinularia	sp																
Lobophyton	sp																
Xenia	sp																
Palythoa	sp									2	0	0	6				
Heteractis	sp																

		E. Grande Passe 2				E. Grande Passe 3				S. Ile aux Cocos				Passe Demi			
			% of species				% of species				% of species				% of species		
Genus	Species	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live	abd	dead	bleach	live
Pocillopora	*damicornis*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Pocillopora	*eydouxi*	1	0	0	6	1	0	0	6								
Pocillopora	*verrucosa*	1	0	0	6	1	0	0	6					1	0	0	6
Stylophora	*pistillata*																
Montipora	sp	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Montipora	*aequituberculata*																
Montipora	*digitata*									1	0	0	6				
Montipora	*tuberculosa*																
Acropora	sp																
Acropora	*abrotanoides*	1	0	0	6	1	0	0	6								

Acropora	*austera*	1	0	2	5	2	0	2	5								
Acropora	*clathrata*																
Acropora	*cytherea*	3	0	0	6	3	0	0	6	3	0	0	6	3	0	2	6
Acropora	*digitefera*					1	0	0	6	1	0	0	6	1	0	0	6
Acropora	*horrida*									1	0	0	6				
Acropora	*humilis*	1	0	0	6	1	0	0	6					1	0	0	6
Acropora	*muricata*	2	0	2	5	2	0	3	4	2	0	0	6	2	0	0	6
Acropora	*nasuta*																
Acropora	*nobilis*																
Acropora	*pinguis*																
Acropora	*paniculata*																
Acropora	*tenuis*																
Acropora	*valida*																
Porites	sp	1	0	0	6					1	0	0	6	1	0	0	6
Goniopora	sp	1	0	0	6												
Pavona	*cactus*																
Pavona	*decussata*																
Fungia	sp	1	0	0	6	1	0	0	6	1	0	0	6				
Hydnophora	sp																
Hydnophora	*microconos*	1	0	0	6	1	0	0	6								
Favia	sp					1	0	0	6								
Favia	*stelligera*	1	0	0	6												
Favites	sp									1	0	0	6	1	0	0	6
Favites	*abdita*																
Goniastrea	sp	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Goniastrea	*pectinata*																
Goniastrea	*retiformis*																

Platygyra	*daedalea*	1	0	0	6	1	0	0	6	1	0	0	6	1	0	0	6
Platygyra	*lamellina*																
Leptoria	*phrygia*	1	0	0	6	1	0	0	6								
Cyphastrea	*microphthalma*																
Echinopora	sp																
Echinopora	*forskaliana*																
Turbinaria	sp					1	0	0	6								
Turbinaria	*mesenterina*																
Millepora	sp																
Sarcophyton	sp																
Sinularia	sp																
Lobophyton	sp																
Xenia	sp	4	0	0	6												
Palythoa	sp																
Heteractis	sp																

		N. Ile aux Sables				Grande Pointe			
			% of species				% of species		
Genus	Species	abd	dead	bleach	live	abd	dead	bleach	live
Pocillopora	*damicornis*	1	0	0	6	1	0	0	6
Pocillopora	*eydouxi*								
Pocillopora	*verrucosa*	1	0	0	6				
Stylophora	*pistillata*								
Montipora	sp	1	0	0	6	1	0	0	6
Montipora	*aequituberculata*								
Montipora	*digitata*								

Montipora	*tuberculosa*								
Acropora	sp								
Acropora	*abrotanoides*								
Acropora	*austera*								
Acropora	*clathrata*								
Acropora	*cytherea*	4	6	0	1	3	0	2	5
Acropora	*digitefera*	1	4	0	4	1	0	1	6
Acropora	*horrida*								
Acropora	*humilis*	1	0	0	6	1	0	0	6
Acropora	*muricata*	1	0	0	6	2	0	3	4
Acropora	*nasuta*					1	0	0	6
Acropora	*nobilis*								
Acropora	*pinguis*								
Acropora	*paniculata*								
Acropora	*tenuis*								
Acropora	*valida*					1	0	0	6
Porites	sp	1	0	0	6	1	0	0	6
Goniopora	sp								
Pavona	*cactus*								
Pavona	*decussata*								
Fungia	sp					1	0	0	6
Hydnophora	sp								
Hydnophora	*microconos*								
Favia	sp								
Favia	*stelligera*								
Favites	sp	1	0	0	6	1	0	0	6
Favites	*abdita*								

Goniastrea	sp	1	0	0	6	1	0	0	6
Goniastrea	*pectinata*								
Goniastrea	*retiformis*								
Platygyra	*daedalea*	1	0	0	6	1	0	0	6
Platygyra	*lamellina*								
Leptoria	*phrygia*					1	0	0	6
Cyphastrea	*microphthalma*								
Echinopora	sp								
Echinopora	*forskaliana*								
Turbinaria	sp								
Turbinaria	*mesenterina*								
Millepora	sp	1	0	0	6				
Sarcophyton	sp								
Sinularia	sp								
Lobophyton	sp								
Xenia	sp								
Palythoa	sp								
Heteractis	sp								

Table A5.6 Percentage cover of the substrate at Trou Malabar in 2002 based on video surveys of three 20m transects.

	T1		T2		T3		Total	
	No	%	No	%	No	%	No	%
Coralline platform with turf algae	280	56.0	268	59.6	283	60.2	831	58.5
Rubble	13	2.6	5	1.1	40	8.5	58	4.1
Dead *Acropora abrotanoides*	41	8.2	37	8.2	12	2.6	90	6.3
Dead *Acropora cytherea*	33	6.6	21	4.7	20	4.3	74	5.2
Dead *Acropora digitifera*	44	8.8	33	7.3	18	3.8	95	6.7
Dead *Acropora humilis*	0	0.0	0	0.0	4	0.9	4	0.3
Dead *Acropora muricata*	38	7.6	58	12.9	68	14.5	164	11.5
Dead *Pocillopora eydouxi*	9	1.8	1	0.2	3	0.6	13	0.9
Dead *Goniastrea* sp	4	0.8	0	0.0	0	0.0	4	0.3
Live *Acropora digitifera*	22	4.4	0	0.0	0	0.0	22	1.5
Live *Acropora muricata*	1	0.2	14	3.1	13	2.8	28	2.0
Live *Pocillopora eydouxi*	4	0.8	0	0.0	0	0.0	4	0.3
Live *Porites* sp	1	0.2	0	0.0	0	0.0	1	0.1
Live *Porites rus*	0	0.0	9	2.0	0	0.0	9	0.6
Live *Platygyra daedalea*	1	0.2	1	0.2	0	0.0	2	0.1
Live *Pavona decussata*	2	0.4	3	0.7	0	0.0	5	0.4
Live *Goniastrea sp*	7	1.4	0	0.0	0	0.0	7	0.5
Live *Leptoria phrygia*	0	0.0	0	0.0	9	1.9	9	0.6

Table A5.7 Percentage cover of the substrate at Trou Malabar in 2003 based on video surveys of three 20m transects.

	T1		T2		T3		Total	
	No	%	No	%	No	%	No	%
Coralline platform with turf algae	257	59.8	227	51.6	252	60.0	736	57.1
Rubble	11	2.6	22	5.0	9	2.1	42	3.3
Dead *Acropora abrotanoides*	36	8.4	39	8.9	20	4.8	95	7.4
Dead *Acropora cytherea*	24	5.6	23	5.2	17	4.0	64	5.0
Dead *Acropora digitifera*	8	1.9	8	1.8	7	1.7	23	1.8
Dead *Acropora humilis*	0	0.0	0	0.0	0	0.0	0	0.0
Dead *Acropora muricata*	33	7.7	47	10.7	30	7.1	110	8.5
Dead *Pocillopora eydouxi*	6	1.4	0	0.0	0	0.0	6	0.5
Dead *Goniastrea* sp	0	0.0	4	0.9	0	0.0	4	0.3
Live *Acropora abrotanoides*	2	0.5	2	0.5	7	1.7	11	0.9
Live *Acropora cytherea*	0	0.0	0	0.0	2	0.5	2	0.2
Live *Acropora digitifera*	3	0.7	15	3.4	28	6.7	46	3.6
Live *Acropora muricata*	17	4.0	31	7.0	33	7.9	81	6.3
Live *Pocillopora damicornis*	2	0.5	1	0.2	4	1.0	7	0.5
Live *Pocillopora eydouxi*	3	0.7	0	0.0	0	0.0	3	0.2
Live *Porites* sp	0	0.0	0	0.0	0	0.0	0	0.0
Live *Porites rus*	2	0.5	3	0.7	0	0.0	5	0.4
Live *Platygyra daedalea*	3	0.7	0	0.0	2	0.5	5	0.4
Live *Pavona decussata*	0	0.0	0	0.0	0	0.0	0	0.0
Live *Goniastrea* sp	0	0.0	0	0.0	0	0.0	0	0.0
Live *Favites* sp	2	0.5	2	0.5	2	0.5	6	0.5
Live *Leptoria phrygia*	0	0.0	6	1.4	4	1.0	10	0.8
Live *Millepora* sp	21	4.9	10	2.3	3	0.7	34	2.6

Table A5.8 Percentage cover of the substrate at Ile aux Fous in 2002 based on video surveys of three 20m transects.

	T1		T2		T3		Total	
	No	%	No	%	No	%	No	%
Coralline platform with turf algae	22	4.9	40	9.3	90	18.0	152	11.0
Rubble	56	12.4	15	3.5	50	10.0	121	8.8
Dead *Acropora cytherea*	221	49.1	238	55.3	158	31.6	617	44.7
Dead *Acropora humilis*	0	0.0	6	1.4	0	0.0	6	0.4
Dead *Acropora muricata*	79	17.6	76	17.7	113	22.6	268	19.4
Live *Acropora muricata*	13	2.9	7	1.6	23	4.6	43	3.1
Live *Montipora aequituberculata*	21	4.7	38	8.8	37	7.4	96	7.0
Live *Montipora digitata*	10	2.2	3	0.7	12	2.4	25	1.8
Live *Pocillopora damicornis*	1	0.2	2	0.5	0	0.0	3	0.2
Live *Porites rus*	8	1.8	0	0.0	0	0.0	8	0.6
Live *Platygyra daedalea*	0	0.0	0	0.0	2	0.4	2	0.1
Live *Pavona decussata*	1	0.2	0	0.0	2	0.4	3	0.2
Live *Fungia* sp	18	4.0	5	1.2	13	2.6	36	2.6

Table A5.9 Percentage cover of the substrate at Ile aux Fous in 2003 based on video surveys of three 20m transects.

	T1		T2		T3		Total	
	No	%	No	%	No	%	No	%
Coralline platform with turf algae	46	9.2	127	25.4	95	26.4	268	19.7
Rubble	178	35.6	176	35.2	120	33.3	474	34.9
Dead *Acropora cytherea*	135	27.0	104	20.8	15	4.2	254	18.7
Dead *Acropora humilis*	9	1.8	0	0.0	1	0.3	10	0.7
Dead *Acropora muricata*	87	17.4	23	4.6	66	18.3	176	12.9
Live *Acropora muricata*	21	4.2	8	1.6	3	0.8	32	2.4
Live *Montipora aequituberculata*	5	1.0	14	2.8	1	0.3	20	1.5
Live *Montipora digitata*	3	0.6	4	0.8	5	1.4	12	0.9
Live *Pocillopora damicornis*	0	0.0	0	0.0	0	0.0	0	0.0
Live *Porites rus*	0	0.0	0	0.0	0	0.0	0	0.0
Live *Platygyra daedalea*	1	0.2	0	0.0	0	0.0	1	0.1
Live *Platygyra crosslandi*	0	0.0	2	0.4	0	0.0	2	0.1
Live *Pavona decussata*	0	0.0	27	5.4	16	4.4	43	3.2
Live *Favites* sp	0	0.0	0	0.0	3	0.8	3	0.2
Live *Fungia* sp	13	2.6	15	3.0	25	6.9	53	3.9
Live *Galaxea fascicularis*	2	0.4	0	0.0	10	2.8	12	0.9

Table A5.10 Bioerosion of dead branching coral collected from Trou Malabar during August 2003.

Branch	Section	No.	% Bioerosion				Organisms
		bore holes	0	<33	33-67	>67	
1	1	8		X			Worms (polychaetes/sipunculans)
	2	12		X			Worms
	3	5		X			Worms
	4	14		X			Worms
	5	7		X			Worms
2	1	16		X			Worms
	2	7		X			Worms
	3	4		X			Worms
	4	5		X			Worms
	5	3		X			Worms
3	1	4		X			Worms
	2	15		X			Worms
	3	21		X			Worms
	4	21		X	X		Worms, Green macro-algae
	5	8			X		Worms
4	1	8		X			Worms
	2	4		X			Worms
	3	5		X			Worms
	4	1		X			Worms
	5	4		X			Worms
5	1	3		X			Worms
	2	1		X			Worms
	3	6		X			Worms
	4	10		X			Worms
	5	5		X			Worms
6	1	6		X			Worms, Green macro-algae
	2	3		X			Worms
	3	2		X			Worms
	4	7		X			Worms
	5	9		X			Worms
7	1	5		X			Worms
	2	12		X			Worms
	3	4		X			Worms
	4	6		X			Worms
	5	2		X			Worms
8	1	13		X			Worms
	2	8		X			Worms
	3	6		X			Worms, Green macro-algae
	4	10		X			Worms
	5	7		X			Worms
9	1	11		X			Worms
	2	12		X			Worms, Green macro-algae
	3	14		X			Worms
	4	5		X			Worms, Green macro-algae
	5	2		X			Worms
10	1	3		X			Worms
	2	7		X			Worms

	3	2		X			Worms
	4	4		X			Worms, Green macro-algae
	5	2		X			Worms

Table A5.11 Bioerosion of dead branching coral collected from Ile aux Fous during July 2003.

Branch	Section	No. bore holes	0	<33	33-67	>67	Organisms
1	1	2		X			Worms (polychaetes/sipunculans)
	2	2		X			Worms
	3	3		X			Worms
	4	3			X		Worms
	5	12			X		Worms
2	1	2		X			Worms
	2	10			X		Worms
	3	12		X			Worms
	4	2		X			Worms
	5	5			X		Worms
3	1	3		X			Worms
	2	1		X			Worms
	3	2		X			Worms
	4	3		X			Worms
	5	7			X		Worms
4	1	1		X			Worms
	2	1		X			Worms
	3	1		X			Worms
	4	1		X			Worms
	5	1		X			Worms
5	1	10		X			Worms
	2	1		X			Worms
	3	1		X			Worms
	4	2			X		Worms
	5	3		X			Worms
6	1	2		X			Worms
	2	1		X			Worms
	3	3		X			Worms
	4	0	X				
	5	0	X				
7	1	3		X			Worms
	2	1		X			Worms
	3	5		X			Worms
	4	3		X			Worms
	5	4		X			Worms
8	1	5			X		Worms
	2	4		X			Worms
	3	4			X		Worms
	4	3			X		Worms
	5	2		X			Worms
9	1	2		X			Worms
	2	3		X			Worms

	3	3		X		Worms
	4	4		X		Worms
	5	3			X	Worms
10	1	0	X			
	2	2		X		Worms
	3	0	X			
	4	0	X			
	5	0	X			