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Abundance, Spatial Distribution and Bioerosion of the Sea urchins, *Echinometra* spp. on Nukubuco Reef, Suva, Fiji.

by Subhashni Devi Appana

A thesis submitted in fulfillment of the
requirements for the degree of
Master of Science in Marine Science

Marine Studies Programme
The University of the South Pacific

July, 2001

Declaration

I, Subhashni Appana declare that this thesis is my own work and that, to the best of my knowledge, it contains no material previously published, or substantially overlapping with material submitted for the award of any degree at any institution, except where due acknowledgement is made in the text.

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Acknowledgement

I appreciate the efforts of many people who helped make this study successful and complete, in particular:

- Staff of CSPOD II (Canada-South Pacific Ocean Development Programme) who provided funding for this study
- Dr Robyn Cumming and Dr Veikila Vuki for technical and emotional support
- Liza Koshy, my reef buddy, and a soul whom I could confide in for the tussles faced during the research
- Sidney Malo, Alvin Ram and the field trip crew for field assistance
- Fred Mills, Pene Conway and Steve Narayan for aid with maps and plates
- Pooja Devika and Sandhya Narayan for proofreading assistance
- Posa Skelton for his algal taxonomic skills
- Professor Robin South for his time and photographic expertise
- Rani, my canine friend, who accompanied me late nights during the write up
- And all other people who I have missed and deserve my due respect and gratitude

I dedicate this thesis to my parents, Mrs. Sumintra Appana and late Mr. Balram Appana and husband, Alvin Ram who have provided me with continuous moral support and inspiration during the course of my study. I feel a sense of growth and maturity in my thoughts after the completion of the thesis, which would not have been attained had it not been for all the people mentioned above.

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ABSTRACT

This study has provided ecological distinction between *Echinometra sp.* A and C at all spatial scales (between positions, zones, sites and quadrats) on Nukubuco Reef. The scales of variation were greatest for both species between positions, east and west and zones, crest and flat. *E. sp.* A densities always rated higher than *E. sp.* C. *E. sp.* A had densities of: eastern flat (3.55 ± 0.41), eastern crest (2.16 ± 0.27), western flat (1.24 ± 0.32) and western crest (0.94 ± 0.25). *E. sp.* C, however, had densities of: eastern flat (0.50 ± 0.18 /m^2), eastern crest (1.05 ± 0.25 /m^2), western flat (0.74 ± 0.22 /m^2) and western crest (0.46 ± 0.48 /m^2). Density for a combined species count varied 3-fold among the four habitats: eastern flat (4.08 ± 0.25 /m^2), eastern crest (3.25 ± 0.13 /m^2), western flat (2.20 ± 0.21 /m^2) and western crest (1.64 ± 0.14 /m^2).

Echinometra sp. A was more abundant on all locations compared with *E. sp.* C with difference shown in size-class distribution. However, *E. sp.* C preferred the high-energy crest zones while *E. sp.* A was more readily found on the calmer flats. The difference was attributed to variation in the ecological survivorship of the two species. Nonetheless, the availability of food (turf algae) and large coral rock framework incurred higher numbers of both species on the east compared to the west. Generally, *E. sp.* A (types 1 (black-white-tip), 2 (green-white-tip), 3 (brown-white-tip), 4 (beige-white-tip) appeared to be more adapted and robust to Nukubuco Reef conditions than *E. sp.* C (types 5 (fully green), 6 (fully brown). The possible new species (type 4/fully maroon) was the least abundant presumably due to not being well adapted to the environment.

Size-specific behaviour showed small and medium urchin dominance on the crests engaged chiefly in burrowing and feeding behaviour while the flats demonstrated variable response from all representative size-classes. This difference was a reflection of difference in environments. The crest being an exposed habitat offers limited refuge from surf intensity hence small and medium urchins will mostly be seen in the process of making their way into a crevice or if well fixed in one will be observed filtering for

detrital algae. On the other hand, the flats make a wider area of the reef and with variable topographic complexity and greater rugosity makes available the micro-spatial preferences for urchins of all sizes engaged in all activities.

Echinometra spp. showed a preference for coral rock substratum due to the brittle framework the former provides to make shelter-burrows and availability of turf algae infested on the dead coral for food. Live coral was the second choice because of the compact and intact nature of live colonies and their defense system to repel intruders. The other substratum types showed numbers too low to justify significant patterns.

The low but consistent numbers of *Echinometra* spp. showed net bioerosion after calculation of the erosion-accretion balance on Nukubuco Reef. The bioerosion rates (kg $CaCO_3$/urchin/d) using gut analyses were 0.39 x 10^{-3} reef crest, 0.20 x 10^{-3} reef flat and pooled rate for Nukubuco Reef of 0.21 x 10^{-3}. Cage experiments reported higher bioerosion rates (kg $CaCO_3/m^2$/ urchin/d) of 35-37 x 10^{-3} at the reef crest and 30-43 x 10^{-3} at the reef flat. Gut analyses and cage experiments displayed bioerosion rates very similar to other studies, which have raised concern over their urchin densities. Extrapolation method reported the lowest bioerosion rates (kg $CaCO_3/m^2/d$) of 1.45-3.93 x 10^{-7}at the reef crests and 8.24-26.5 x 10^{-7} at the reef flats. However, considering the weaknesses and strengths of the three methods, extrapolation approach appeared to be the best because it encompassed the area factor, density, species and size of urchin when evaluating bioerosion rates.

Both bioaccretion and bioerosion activity seem to be favoured on Nukubuco Reef due to its uniqueness of being heavily disturbed by anthropogenic and natural factors, but the persistent bioeroding impact of low but consistent *Echinometra* spp. density overrides the net reef growth with net reef destruction. Should these consistent numbers of *Echinometra* continue their bioeroding impact on Nukubuco Reef, it will not take long for the reef to shift from a partially destroyed to an irreparable ecosystem.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 The Nukubuco Reef study

Nukubuco Reef, in Fiji is of interest because of the low-medium but consistent numbers of novel species of *Echinometra.* Additionally the natural and anthropogenic disturbances it experiences continuously make it more important to be studied. The coral reef system in Laucala Bay in which Nukubuco Reef is a part, has been stressed by recent bleaching events (South and Skelton 2000; Cumming *et al.* under review) and by overfishing efforts of the adjacent communities. The influx of partly treated sewage from Kinoya Sewage Treatment Plant (Naidu *et al.* 1991) promotes nutrient enrichment to the Laucala waters with coincident *Acanthaster planci* outbreaks (Zann *et al.* 1990). High sediment loads from logging and intensive farming (Hinrichsen 1998) and sand dredging activities (Penn 1983) amplify coral reef decline.

This study aims to provide valuable information and understanding of the ecology of these abundant sea urchins, *Echinometra sp.* A and *E. sp.* C which will be referred to in this thesis as *E. sp.* A and *E. sp.* C hereafter. The study will investigate the role of urchins in changing the coral community structure through grazing and bioerosion. The results from this study will also serve as a baseline for future assessments of the health of Nukubuco Reef.

To achieve the aims of this study, Chapter 1 will present a comprehensive literature review of population and bioerosion studies of *Echinometra.* Chapter 2 will provide general background information on Nukubuco Reef and report on the preliminary study undertaken. Chapter 3 will adopt a multi-scale approach to report the distribution and abundance patterns of *E. sp.* A and *E. sp.* C. The position (east and west) factor will be studied to identify the effects of

(Matsuoka and Hatanaka 1991). Hibino and Van Woesik (2000) did a spatial and seasonal carbonate budget study on the Ryukyu Islands, Japan on the *E. mathaei* types A, B, C, D. The small genetic and morphologic differences among species coupled with their strong reproductive isolation made them a valuable group for studies of marine speciation (Palumbi 1996a).

After further biochemical and genetic scrutiny, Palumbi (1996a) addressed the Pacific distribution of the four closely related species. He investigated the genetic divergence gradients among *Echinometra* species and found that the identity of species can change over surprisingly short geographic scales. For example, *E. mathaei* and *E. oblonga* are found together in Hawaii and on Niue. Fiji, 1300 km to the west of Niue has two new species of *Echinometra, E. sp. nov.* A (white-tipped) and *E. sp. nov.* C (non-white-tipped) but *E. mathaei* and *E. oblonga* do not occur (Palumbi 1996a). However, our understanding of species distributions is bound to change with more detailed surveys. Hence, this study will provide ecological distinction between *E. sp. nov* A and *E. sp. nov* C thereby addressing the incomplete species level taxonomy from the ecological perspective.

Since no ecological studies have been done on these two new species, no information is available for comparison. Hence, keeping in mind the Pacific sea urchin evolutionary model, an equivalent comparison of ecological factors can be made between the *Echinometra* sp. A and *E. sp.* C and *E. mathaei. Echinometra mathaei* is distributed from central Japan to southern Australia; and from Clarion Islands off Mexico to the Gulf of Suez (Mortensen 1943). Throughout its range it occupies a variety of habitats. Along the western shore of the Gulf of Suez, it has been observed mostly in the open on the dead coral blocks and rubble (Pearse 1969). In many other areas, it has been found to live territorially in partially hidden burrows, nestled under coral ledges on the reef or nearly completely hidden under rocks or in deep crevices. The four *Echinometra* species are widespread, as expected of taxa with planktonic larvae that can disperse for 4-8 weeks before settlement. However, because previous workers combined them all

under one (Mortenson 1943) or two names (Edmonson 1935), the ranges of the recently recognized forms are poorly known (Palumbi 1996a).

1.2.2 Spatial patterns in distribution and abundance of *Echinometra* spp.

The highly diverse and dynamic nature of coral reef ecosystems merits critical measure of the scales of natural variation in *Echinometra* and enables management of modern pressures on reefs worldwide (Ginsburg 1993; Richmond 1993; Wilkinson 1992). The temporal and spatial scale of observation has been central to arguments of the significance of recent changes in coral reef community structure. While some reefs may appear to be more susceptible to disturbances and unpredictable on a temporal scale of decades (Liddell and Ohlhorst 1992), others could persist over millennia (Jackson 1992). Similarly, although patterns and processes may appear patchy on coral reefs (Grassle 1973; Edmunds and Witman 1991), 'ecological anarchy' over a quadrat scale can be replaced by order upon examination of larger scales (Jackson 1991; Aronson and Precht 1995).

Some factors affecting distribution of organisms are differential recruitment (Birkeland 1982; Ebert 1983), competition (Williams 1981; Hay 1984; Hay and Taylor 1985), disease (Bak *et al.* 1984; Lessios *et al.*, 1984; Miller 1985), water flow, food availability (Russo 1977) and surf intensity (Ebert 1983). The upper limit of distribution could be directed probably by desiccation and lower limit by predation. The four most important factors determining urchin abundance are substratum, wave energy, depth and food availability (Ogden *et al.*1989).

1.2.3 Sea urchin prevalence and levels of natural and anthropogenic reef disturbances

A number of reasons have been attributed to the emergence of out-break populations of sea urchins. Sea urchins become more abundant as a result of intensive fishing (McClanahan 1992), and feature strongly in the majority of documented coral-reef trophic cascades. Kenyan and Caribbean reefs provide a

good example of coral reef communities structured by trophic cascades (Jennings and Kaiser 1998). Comparisons between Marine Protected Areas (MPAs) and unprotected areas have been very important in the development of this axiom (Pinnegar *et al.* 2000).

On Kenyan reefs, both top-down (McClanahan and Muthiga 1989) and competitive (McClanahan *et al.* 1994) controls on the abundance of sea urchins (*Echinometra mathaei*) are indicated by comparisons primarily of MPAs (notably Malindi, Kisite and Watamu Marine National Parks) with areas unprotected from fishing (McClanahan and Shafir 1990). The triggerfish *Balistapus undulatus* is considered the single most important predator of sea urchins in MPAs and other lightly-fished sites, and probably controls populations of some sea urchins (McClanahan and Muthiga 1989; McClanahan 1995a). Where this and other urchin predators are depleted, *E. mathaei* tends to become the principal grazer, filamentous ('turf') algae become more abundant presumably because they get acclimatized to urchin grazing, and hard corals decline in substratum cover (McClanahan and Shafir 1990). Other potential urchin predators, which could be locally more important, include large wrasses (*Coris* spp. and *Cheilinus trilobatus*) (McClanahan 1995a). Further predator reduction lead to *Echinometra* outcompeting *Diadema* and the reef may ultimately approach a new equilibrium community of an *Echinometra* sea urchin barren. Sea urchins are thought likely to outcompete important grazing fishes such as parrotfishes (McClanahan *et al.* 1994), and increases in urchin abundance probably have important consequences for reef bioerosion to which they contribute significantly (McClanahan and Muthiga 1988).

Studies have shown that anthropogenic impacts may cause phase shifts in benthic species composition (Done *et al.* 1996) that could alter the bio-constructional process hence the ultimate function of the reef. The shift from net accretion to net erosion can change the reef topography thereby causing changes in reef-associated organisms (McClanahan 1994; Grigg 1995; Van Woesik *et al.* 1999).

of *E. mathaei* (Muthiga 1996). The reef with the highest population density showed similar recruitment levels to that of a lowly populated reef. However, a positive relationship was observed between recruitment and annual seawater chlorophyll concentration (Muthiga 1996). Hence, it can be speculated that inter-annual variation in water-column productivity could increase the success of larvae and the numbers of benthic recruits.

Echinometra distribution can be patchy, with densities varying from 0.1 to 100 m^{-2} over very short distances. This patchiness is not always easy to explain (Hart and Chia 1990) and tends to increase with the spatial scale of collation, being 50% within reef sites and over 150% between reefs (Hart and Chia 1990). Patchiness of settling larvae could be due to post-settlement environmental factors such as desiccation, food, crevice availability and predation. Variation in urchin behaviour and interaction (aggregation or agonistic) could also play a role in directing their distribution (McClanahan and Kurtis 1991). "Settlement of small recruits (<15 mm) on shallow coral reefs in Kenya occurs largely on coral rubble and can vary between 0.4 and 42 recruits m^{-2} $year^{-1}$ (Muthiga 1996). Low recruitment densities of around 1 m^{-2} $year^{-1}$ are typical, as the distribution of these data is leptokurtic rather than normal, with high recruit levels being rare events" (McClanahan and Muthiga 2001).

Predation levels have strongly been suggested a reason for spatial variability in population densities of *Echinometra mathaei* on the Kenyan coral reefs (McClanahan 1998). In contrast, studies on the intertidal rocky shore of Hawaii suggest that water movement and the availability of algal drift positively influence the density of *Echinometra* as well as the ratio of *E. mathaei* to *E. oblonga* (Russo 1977). Water temperatures greater than 40 ^{o}C tend to be lethal to *E. mathaei* though this suggestion might change with the local temperature environment (Tsuchiya *et al.* 1987). It inhabits depths ranging from the intertidal to approximately 10-15m below MLW. Though this species occupies deeper

habitats, especially in Hawaii, it tends to be rare in waters below 15m (Kelso 1970).

Echinometra mathaei is consistently the top competitor for crevice space. Furthermore there would appear to be species succession in the ownership of territories, but because *E. mathaei* experiences high predation rates outside burrows, coexistence is mediated by predation on the competitive-dominant (McClanahan 1988). Since competition is for limited space and larger bodies limit the number of available crevices that an individual can utilize, it may be better to be small, strong and aggressive in acquiring crevices on coral reefs. This appears to be the case for territorial pomacentrids (among coral reef fish) and for *Echinometra* (Grunbaum *et al.* 1978).

Echinometra mathaei do not seem to home at all, and their positions in the habitat seem to be the result of chance (Khamala 1971). The attraction for crevices would be selectively advantageous since it serves to hide them from predators, reduce light intensity and desiccation and provide protection against turbulent waves. Boring into rocks and other hard material by echinoids is well established (Reese 1966), and it is likely that some of the outer reef burrows and crevices in which *E. mathaei* specimens are found are made by the urchins themselves.

The fact that species behaviour changes as a function of environment makes it difficult to generalize about behaviour based on species only (McClanahan and Kurtis 1991). Nonetheless, the agonistic types show more uniform distributions than less agonistic types, which can even form aggregations (Tsuchiya and Nishihira 1985). The agonistic behaviour demonstrated is primarily in defense of predator-free space rather than for food resources and changes with predator abundance (McClanahan and Kurtis 1991). Territorial species show slower recolonization compared with the non-territorial (Tsuchiya and Nishihira 1986). Hence, both genes and the environment

simultaneously operate to influence behaviour thus the distribution and dispersion patterns of *Echinometra*.

The higher latitudes could cause restricted spawning periods as opposed to the tropics where stable temperatures prevail and cause continuous spawning Pearse (1969). Although *Echinometra mathaei* eggs can be fertilized at 28 – 36 °C, normal development only occurs at temperatures below 34°C (Rupp, 1973). Studies on the Kenyan coast have shown seawater temperature and light that are influenced by monsoons to affect the seasonal reproductive pattern of *E. mathaei* (McClanahan 1988). In contrast, populations of *E. mathaei* at Rottnest Is, Western Australia, spawn continuously throughout the year in seawater temperatures that are cooler than on the Kenyan coast (McClanahan and Muthiga 2001). Hence, other confounding factors apart from temperature may be controlling spawning in *E. mathaei*. Alternatively, since *E. mathaei* spawning in Kenya occurs prior to peak in phytoplankton concentrations, availability of food for larvae may be important in controlling spawning.

Two basic feeding modes are adapted by both juvenile and adult *Echinometra* and these vary with species and environment: 1) catching algal drift, and 2) benthic grazing. Individuals of all species likely use both modes. Since guts always show a messy blotch of masticated algae and sediment grains, it is not always easy to discern the source of food for *Echinometra*. Feeders of drift algae may show less sediment in the gut, but may be eating abundant fleshy algae in areas with low sedimentation. The filtering mode is common in shallow waters along shorelines, but also occurs in areas with currents such as reef channels, or shallow tops of patch reefs or reef flats (McClanahan and Muthiga 2001).

Foraging activity is related to body size (Hart and Chia 1990): medium-sized *Echinometra mathaei* are more inclined to feed than the small and large sized. In

an experiment the small-sized urchins showed a low rate of feeding while large-sized initially demonstrated a low foraging rate, which increased throughout the experiment (Hart and Chia 1990). Growth in *Echinometra* is highly dependent on food availability (Muthiga 1996). There are a number of factors that might be related to noted feeding difference among size classes. These include differing nutrient requirements, susceptibility to predation and intraspecific competition for space.

1.2.5 Grazing and bioerosion

Echinometra is a generalized herbivore, feeding on a variety of macrophytes, including seagrass, occasionally consuming benthic organisms such as sponges, corals and algae (McClanahan and Muthiga 2001). Calcium carbonate sediments are usually the largest fraction of the gut content of *Echinometra*, being between 65 and 95% (Black *et al.* 1984; Downing and El-Zahr 1987; McClanahan and Kurtis 1991). These measurements support the inference that grazing of benthic epi- and endolithic algae is the major source of food for *Echinometra* (Odum and Odum 1955). These are largely small, fast growing, filamentous, turf-forming green and blue-green algae that grow in and on the surfaces of coral rock. Though herbivorous urchins may feed on animals if given a chance, *Echinometra* has a lesser preference for animal food (McClintock *et al.* 1982).

Net reef growth is a product of accretional, sedimentological and erosional processes (Hibino and Van Woesik 2000). Accretion can be of three types: biological, through coral framework and calcareous organisms, physical or microbial through mineralization of existing framework and geological through sediment accumulation and in-filling (Smith and Kinsey 1976; Glynn 1997). Reefs may erode from urchin activity (Bak 1990, 1994; Mokady *et al.* 1996), herbivorous fishes (Bellwood 1995), endolithic sponges, bivalve molluscs and polychaetes (Davies and Hutchings 1983; Hutchings 1986; Scoffin 1992 and Glynn 1997). Erosion of carbonates also occurs through physico-chemical

processes from physical abrasion by wave action or suspended sediment (Ball *et al.* 1967), or by geochemical shifts, due to acid shift upon addition of carbon dioxide in the water chemistry, enhancing calcium carbonate dissolution (Gattuso *et al.* 1998; Kleypas *et al.* 1999).

Bioerosion estimates are common for coral reefs (Trudgill 1983; Bak 1990; Kiene and Hutchings 1992 and Eakin 1996), although emphasis has recently shifted to variability within and between locations (Glynn 1988; Kiene and Hutchings 1994 and Peyrot-Clausade *et al.* 1995). Echinoids can affect reef geology in two ways (Russo 1980). Firstly, grazing echinoids, in feeding on calcareous and non-calcareous algae, inhibit the build up of extensive algae mats, especially on shallow lagoon floors. Algae cementation is one of the most important lithification processes in shallow water limestone production (Chilingar *et al.* 1967). Without echinoid grazing, reef growth through algae cementation may increase substantially. Secondly, in the process of echinoid feeding and burrowing, reef limestone is broken down. This material is then added to the pool of unconsolidated sediment, some of which eventually undergoes submarine lithification and diagenesis (Seibold *et al.* 1973). These processes of diagenesis and cementation when measured and compared to bioerosion can, in part, lead to an assessment of long-term net growth or destruction of a reef.

Echinometra spp. both graze the coral and erode the surface to form a shallow depression, a "home cavity". They use their Aristotle's lantern (a complex of articulated plates surrounding the mouth), and perhaps their spines, to scrape away the coral substratum. There are no reports of dissolution of $CaCO_3$ in urchin gut, however, they may obtain nutrients from the algae attached to the coral substratum or from the living coral tissue (Hutchings 1986). Some erosion by *Echinometra* is new while some of the sediments in their gut are from already eroded sediments. The ratio of new to previously eroded sediments has been a problem in estimating the actual or new erosion rates (McClanahan and Muthiga 2001).

Bioerosion has a complex impact on coral reefs. It creates a large number of reef habitats; each characterized by its own community, which are integral parts of a coral reef (Connell 1978). The colonizing cryptofaunal community (Hutchings 1983) may play a major role in nutrient recycling on the reef. Sammarco (1980) suggests limited grazing of algae creates the necessary space for successful coral settlement. However, at higher levels of grazing, recruitment of coral spat is low. Bioerosion may facilitate cementation. Many boring species create fine sediment, which may be trapped within the burrows and subsequently becomes cemented (Davies and Hutchings 1983).

Bioerosion also has long-term significance on coral reefs. Areas of active reef growth where high coral cover occurs (such as reef fronts) do not experience rapid rates of erosion. Davies and Hutchings (1983) detected maximum rates of erosion, at least of initial erosion, on the reef flats where moderate rates of calcification occur (Smith 1973; Kinsey 1983). During the evolution of a reef, areas of a dominant reef growth may gradually evolve to areas of low growth and high rates of erosion (Davies 1983). Obviously more information is needed to fully document oscillations between rapid growth and rapid destruction. These data can only be obtained from present reefs by measuring rates of growth and erosion in a wide variety of habitats on reefs at different stages of evolutionary development (Davies 1983). Thus, rates of bioerosion should provide a sensitive indicator as to the stage of development a particular reef has reached. Finally, bioerosion as already suggested may be very important in maintaining the high diversity of coral reefs by small-scale local disturbances (Connell 1978). This will be extremely important in areas of low physical disturbance; such as on protected leeward reefs. Bioerosion is thus a very crucial agent determining the shape and form of coral reefs.

Areas with low densities (0-12 urchins/m^2) of *Echinometra* have shown low rates (0.1-0.4 g/urchin/day) (Bak 1990) of bioerosion of coral rock. Downing and El-Zahr (1987) have reported values as high as 1.4 g/urchin/day. Consequently,

Echinometra may erode up to 10kg $CaCO_3$ /m^2/year at some high population densities (12-100 urchins/m^2). Typical calcium carbonate deposition rates for coral reefs are 1-4 kg/m^2/year (Smith 1983). Hutchings (1986) has reported bioerosion as an important process since the inception of reefs. It increases the complexity of reef environment, but it may be greatly reduced when erosion exceeds accretion. Consequently, *Echinometra* can play a vital role in the erosional modification of reefs worldwide.

CHAPTER 2

STUDY AREA AND PRELIMINARY STUDY

2.1 Physical setting

The Fiji Island lies in the area of 15 ^{0} S to 23 ^{0} S and 177 ^{0} E to 178 ^{0} W (Figure 2.1) and comprises of 844 islands of which Viti Levu is the largest, covering 10,000km^2 (Penn 1983). The study area, Nukubuco Reef, is located on the south-east coast of Suva Harbour (18^{0}10'S 178^{0}28'E) (Figure 2.2) with an outer reef length of 22km. It is part of the Viti Levu south-eastern reef chain and encloses Suva Peninsula and Laucala Bay. Nukubuco Reef is a barrier reef and lies between one and five km off the coast of Suva. A narrow lagoon of about 10m deep separates the reef from the city of Suva. Suva has a population of approximately 160,000 (1986 census).

Several narrow deep passages through the reef give access to the ocean: Nukulau and Nukubuco Passages in Laucala Bay, the main Suva Passage and Namuka Passages. At its SW corner, Laucala Bay is connected to Suva Harbour by a narrow channel 10-12m deep. It is also connected by a passage of similar depth to Laucala Point and Nukulau Island. To the east of Nukubuco lies the Rewa River delta, of which two tributaries, the Vunivadra Channel and Vunidawa River, enter the NE corner of Laucala Bay.

2.2 Climatology

The Fiji group is influenced by the northerly monsoon system characterized by a general drop in wind strength and the occasional occurrence of cyclones. Nukubuco Reef experiences the East and SouthEast trade winds persistently from July to December. The western edge is sheltered while the eastern edge is more exposed to wind-driven swells and waves. The geographic pattern of rainfall throughout the Fiji Group is highly variable due to the mountainous nature of the

main islands. The southeastern part of Viti Levu Island generally has a high annual rainfall with occasional years of very high summer rainfall. The annual rainfall gets evenly distributed due to rain shadows caused by mountains.

High rainfalls associated with tropical cyclones often lead to severe floods, land erosion and high sediment loads in rivers and coastal waters. Rainfall is seasonal with distinct dry (May-October) and wet (November-April) seasons. About 67% of annual rainfall in Suva has been reported to occur in the wet season (Dickie *et al.* 1991).

Rewa River is the paramount river entering the Suva lagoon and estimates a mean annual discharge equivalent to 160 x 10^6 m^3. Discharge exceeding 10,000 x 10^6 m^3 were experienced in 1972, 1973 and 1986. However, the largest flood record was 17,000-19,000 x 10^6 m^3 in 1931 (Vuki 1994). Several smaller rivers exit along the SE coast of Viti Levu and directly affect the Nukulau to Namuka area. The Laucala Bay accommodates river discharges from Vunidawa, Samabula and Vatuwaqa rivers along the NW shore while Tamavua River empties into the head of Suva Harbour (Figure 2.2).

The mean monthly temperatures range from 23 ^{0}C in July and August to 27 ^{0}C in January. Average temperature changes only 3-4 ^{0}C between the coldest part of the year (July-August) and the warmest (February) (Penn 1983).

2.3 Oceanography

Southeasterly swells predominate through the year with significant easterlies occurring from July to December. The wave and swell records in Laucala Bay show positive correlation with wind data (Dickie *et al.* 1991). Tidal range is very small with an annual mean range of 1.1m. Neap tides record a mean range of 0.9m and springs of 1.30m (Ryland 1981). Semi-diurnal tides predominate in the Suva area with the lower low water springs falling during the night in summer but during the day in winter. Nukubuco reef experienced a lowest neap tide of 0m

and a highest spring tide of 1.8m during the course of the study, year 2000 (Tidal Prediction For Suva Harbour, 2000).

The annual sea surface temperatures in Laucala Bay vary from 24 ^{0}C to 31 ^{0}C, with an average annual variation of 6 ^{0}C. Salinity values are normally 35 ppt but may drop to 10-15ppt after heavy rainfall (Zann *et al.* 1987). Large discharges of terrestrial sediments get transported to the sea during heavy rainfall (Ryland *et al.* 1984) hence causing mortality of marine organisms in Laucala Bay and Nukubuco Reef.

2.4 Description of Nukubuco Reef

The Nukubuco reef is distinctly marked with multispecific strands of seagrasses in the backreef and an algal ridge followed by a rocky platform on the crest. However, an indiscriminate zonation pattern is displayed as follows: (1) seagrass beds in the backreef (2) algal assemblages, sand and rubble zone (3) submassive *Porites* spp., *Acropora* spp. coral zone with soft corals (4) massive *Porites* spp. corals (5) algal turf ridge and (6) the rocky platform at the reef crest.

The back reef, which is not relevant to this study, contains seagrass from genera *Halophila, Syringodium,* and *Halodule.* The reef-flat is a continuous construction of corals and encrusting algae. It has 90% coverage by massive *Porites* spp. with alternating bands of *Acropora cylindrica* and *A. formosa* chiefly at the outer reef flat most of, which are dead, and brittle frameworks. The outer reef flats also consist of deep tide pools, which harbour colourful alcyoniid soft corals from the genera *Sinularia, Lobophytum* and *Sarcophyton.* A patchy distribution of the fleshy macroalgae on the reef includes the phaeophyte genera *Sargassum, Padina* and *Turbinaria.* The reef front consists of various species of live coral from the genera *Acropora, Porites, Montipora* and *Pocillopora.* Rubble and sand together with algal turf are the major components of the reef substrata on the reef flat.

The reef profile is almost a steady platform of flora and fauna with a mosaic distribution of deep tide pools in the outer reef flat and shallow tide pools in the inner reef flat. These areas are continuously covered with water 50 to 200cm deep, depending on tidal conditions

There is vigorous water movement at the outer reef site due to constant wave action while the inner reef flat mostly experiences calm conditions. *Echinometra* spp. inhabits both reef sites colonizing heads of dead *Porites* boulders on the reef platform and crevices of the reef crest.

The eastern Nukubuco Reef (near Nukulau and Makaluva Islands) continuously experiences sewage effluent from Kinoya Sewage Plant, river run-off from Nausori highlands via Rewa, Vunidawa, Vatuwaqa, and Samabula Rivers and sand dredging activities. On the other hand, the western Nukubuco Reef continuously experiences oceanic flushes from proximate Nukubuco Passage. The reef is heavily exploited for finfish and shellfish.

2.5 Pilot study

Data was collected for a pilot study from the separate positions of Nukubuco Reef in March 2000. A 2-level Cost Benefit Analysis (Underwood 1997) helped to develop an efficient experimental design. In particular, the Cost-Benefit Analysis was done to optimize the number of quadrats per site and the number of sites per zone, given that 320 quadrats had to be sampled in total (refer to Appendix 1 for further details). Variable quadrat size used helped to obtain the optimum quadrat size. Quadrat sizes were not subjected to the Cost-Benefit Analysis. Rather, it aided to see how much substrata and urchins could be covered on the reef using either sizes, optimally.

Randomized $1m^2$ and $0.25m^2$ quadrats were sampled alternately in three sites (N = 32, 40, 46 for $1m^2$ quadrats) and (N = 7, 17, 15 for $0.25m^2$ quadrats); sites were 100m x 100m in the west. Similar procedure was repeated for the eastern position where samples were (N = 67, 75, 58) and (N = 20, 18, 26), respectively. An analysis of variance helped to prove the significance of the Cost-Benefit Analysis.

Table 2.1 Analysis of variance for 2-Level Cost Benefit Analysis. Sites were nested in positions. MS=mean square, SS=sum of square, F test=F value, P=significance of results, df=degrees of freedom, s = significant, n.s = not significant

Source	df	SS	MS	F	P
Position	1	1.296	1.296	27.406	0.035 (s)
Position (site)	2	0.009459	0.004730	0.679	0.510 (n.s)
Error	76	5.295	0.006967		

Time (cost) was set as the limiting factor, not precision. The Cost Benefit Analysis took into account the fact that the total time available for sampling was 120 hours or 7200 minutes (C_T), the time to sample per quadrat was 9-12minutes ~ 10minutes (C_Q) and the time available to sample per site was 30 minutes (C_S).

Hence, this aided to determine how much time could be allocated to the sampling of each site. The optimum number of replicate quadrats was calculated to be 14. However, the main study had already been started before the Cost-Benefit Analysis was completed and 20 replicates of quadrats were sampled per site. So 20 quadrats were consistently sampled though 14 were needed. The fact that there was enough time may be attributed to becoming practised with time and help provided by field assistants.

CHAPTER 3

POPULATION STUDY OF *ECHINOMETRA* SPP.

3.1 Introduction

Coral reefs are highly diverse and productive biogenic structures, which form banks, atolls, islands and substantial masses like the Great Barrier Reef. They play an irreplaceable and crucial role in sand formation, as wave buffers, fisheries support, tourist attraction, providing recreational opportunities, and the diversity of natural products that they afford (Richmond 1993). McAllister (1988), estimated fisheries losses due to reef degradation at over $80 million per year, impacting 127 000 jobs and 637 000 family members in the Philippines.

Fragile coral reefs are under continued modern pressures from anthropogenic stresses, sedimentation (Wilkinson 1992; McClanahan 1997a), *Acanthaster planci* predator outbreaks (Zann *et al.* 1990; Keesing 1992), sea urchin infestations (Keesing 1992), overfishing on reefs (McClanahan 1995b, 1997a) and impending global climate change (Wilkinson 1992). This delicate balance with nature makes coral reefs both diverse and dynamic. Rigorous monitoring of the communities within this ecosystem both spatially and temporarily provide means of identifying and ameliorating the disturbances, hence making well-informed management decisions (Grigg and Dollar 1990; Wells 1995). The description of variation among different scales in research helps to provide a true picture of heterogeneity on the reef.

The omnivorous sea urchin, *Echinometra* are best known as major bioeroders of coral reef substrata in the Indo-Pacific and the Caribbean (Ogden 1977; Glynn *et al.* 1979; Scoffin *et al.* 1980; Hutchings 1986; Downing and El-Zahr 1987; Birkeland 1989). Consequently, *Echinometra* are perceived as a serious

destructive force, like the crown-of-thorns starfish (Birkeland and Lucas 1990) and ecological research has focussed on high-density populations of *E. mathaei* (Keesing 1992). *Echinometra*, the rock-boring sea urchin, colonizes extensive areas of coral rock and feeds by removing a large proportion of coral ($CaCO_3$) in addition to the algae (Downing and El-Zahr 1987) and encrusting coralline algae growing on it (Hutchings 1986). In the process they etch a home scar or cavity to which they return after foraging to give them protection from dislodgment by predators or wave action (Hutchings 1986). They scrape food and 'home' using a set of complex articulated plates surrounding the mouth, Aristotle's lantern, and their spines (Hutchings 1986).

High-density populations of *Echinometra* have been implicated in reef damage particularly in Kenya (McClanahan 1988), the Marshall Islands (Russo 1980); Persian Gulf (Shinn (in Hughes and Keij 1973); Hawaii (Russo 1977, 1980), in Japan (Keesing 1992); Kuwait (Downing and El-Zahr 1987) and Jamaica (Sammarco 1982). *Echinometra* is the top competitor among the echinoids (Khamala 1971; McClanahan and Muthiga 1988; McClanahan and Kurtis 1991) and this predominance requires investigation into its effects on reef-building corals, which provide the main structural framework of the reef.

At lower densities, these urchins potentially affect the dynamics of whole coral reef communities. The scales and magnitudes of variation in *Echinometra* density in these "normal" non-outbreak populations have not been addressed. They however are the basis for identifying the ecological processes important for the dynamics of *Echinometra* populations, for developing sampling and monitoring programs to distinguish normal from outbreak populations and for quantifying the impact of *Echinometra* on Nukubuco Reef.

Uehara and Shingaki (1984, 1985) have reported *Echinometra sp.* A, B, C, and D on the Okinawan reef flats in Japan. They are white-tipped or entirely white, entirely brown, dark-brown or green and uniformly black, respectively. On

Nukubuco Reef, *E. sp.* A and *E. sp.* C coexist despite their slight morphological and genetic differences but strong reproductive isolation (Palumbi 1996 a, b). This study addresses the within-reef distribution and abundance patterns of *E. sp.* A and C at a number of spatial scales. Furthermore, the study reports on size-specific behaviour of *Echinometra* in general and how their numbers compare with changing reef substrata coverage.

The following questions need to be addressed to fulfil the aims of this study:

1. **Multi-scale distribution and abundance patterns of *Echinometra* spp.**
   How does the distribution and abundance patterns of *E. sp.* A and C vary between reef habitats?
   The answer to this question will report on the multi-spatial scale distribution and abundance patterns of *E. sp.* A and C. Hence, it will provide a measure of the different factors (anthropogenic and natural disturbances) and their effects on Nukubuco Reef.

2. **Size-frequency patterns of *Echinometra* spp.**
   Is there a difference in size-class distribution of *E. sp.* A and C on the different habitats of Nukubuco Reef?
   With the knowledge of size-class distribution, it is possible to monitor urchin activity and their impact on the reef. Urchin sizes can also reflect prevalence of substratum type and complexity of the different environments.

3. **Size-frequency and dispersion patterns of *Echinometra* colour morphs**
   How do the colour morphs of *E. sp.* A and C interact?
   The answer to this question will report on the dispersion patterns of *Echinometra* types; *E. sp.* A – types 1,2,3,4 and *E. sp.* C – types 5,6 and possible new species – type 7.

4. **Size-specific behaviour**

   Do *Echinometra* spp. show size-specific behaviour?

   The answer to this question will provide understanding on the patterns of size-specific activity. Review of the behaviour patterns could reflect the variation in environment and the influences on the different habitats of Nukubuco Reef

5. **Urchin density in relation to substrata coverage**

   Does urchin density change with different substrata (live coral, coral rock, rock, macroalgae, coralline algae, turf algae, sand, rubble) coverage?

   The answer to this question will provide an indirect measure of the most preferred substratum type and with knowledge of size-specific behaviour, the urchin impacts on those substratum types could be assessed.

3.2 Methodology

3.2.1 Survey sampling design

Optimization technique such as cost-benefit analysis was used to develop an efficient experimental design (refer to 2.5 for Cost-Benefit Analysis details).

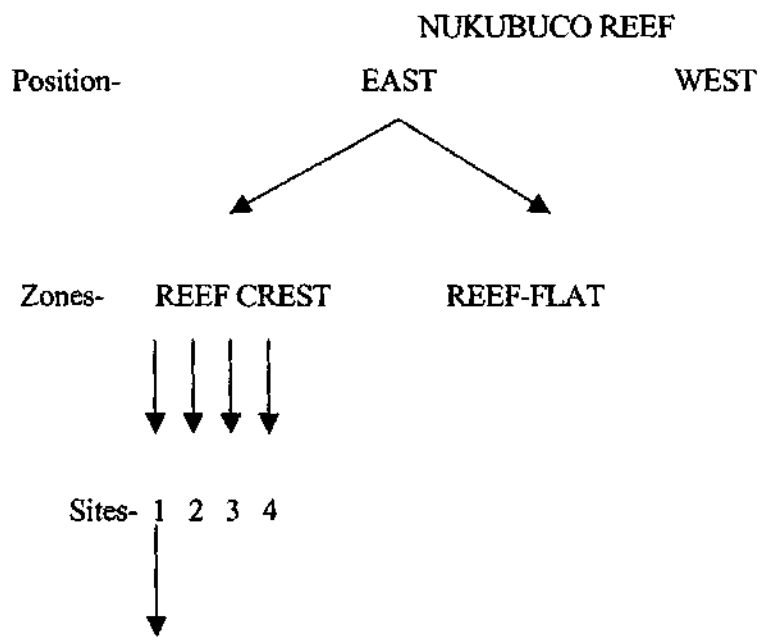
The survey was conducted from April to September 2000 by quadrat sampling.
A three-factor, hierarchical mixed-model nested sampling design was used (Figure 3.1: sample design). The factors were:

1. Positions. Sites were established at the east (near Nukulau and Makuluva Islands) and west positions (near Nukubuco Passage) of Nukubuco reef (Figure 2.2 and 2.3). The eastern and western positions had been adopted for sampling to assess the possible impacts anthropogenic influences such as sewage influx, sand-dredging activity and high sediment loads from river run-offs may be having on the distribution and abundance of urchins on the east. The western position being close to Nukubuco Passage experienced continuous oceanic flushing.

2. Zones. Each position was divided into reef crest and reef flat (Figure 2.3) (the back reef was not delineated as a separate zone since it had extremely low densities of *Echinometra* spp).

3. Sites. Four sites were sampled at each zone, eight at each position; 16 sites were sampled in total. Four sites composed a habitat.

Figure 3.1 Three-Factor, Hierarchical Mixed-Model Nested Sampling Design



Each site was 1 x 10^4 m^2 plot of continuous reef, measuring 100m x 100m. The next site was selected at a horizontal distance of 100m hence keeping the 100m factor constant. Within each site, twenty 1m x 1m gridded quadrats were positioned randomly by the aid of a metre tape and buoys. All sampling took place at low or falling tides. A Lowrance GPS portable meter © was used to record sampling locations (refer to Appendix 2 for further details).

3.2.2 Multi-scale distribution, abundance and size-frequency patterns of *Echinometra* spp.

This section was carried out to report on the distribution, abundance and size-frequency patterns of *Echinometra sp.* A and C. *Echinometra* spp. density counts were done for each quadrat, and distribution and abundance patterns noted. Test diameter was recorded for each urchin using a vernier caliper. These data were compared between habitats (position x zone x site) with a three-way ANOVA

using quadrats as replicates. χ^2 tests were performed to highlight between-site and between-habitat differences.

A depth profile was also carried out on both positions to assess the degree of exposure experienced by *Echinometra* spp. The transect was laid haphazardly keeping in mind that it was around the sampling sites. This selection strategy was acceptable since the derived analysis was more qualitative. At each position two transects were run 100m apart (the 100m distance between transects is kept constant with regards to the site dimensions taken initially) from the edge of the crest until the landward edge of the reef-flat. The degree of change of substratum type was noted. Although tidepools are not considered as substratum, their presence along a transect was noted since water depth is important to exposure and distribution.

3.2.3 Size-frequency and dispersion patterns of *Echinometra* types

Once the distribution of *Echinometra* spp. would be revealed, it would be important to report on the size-frequency and dispersion patterns of the different types that compose the *E. sp.* A and C.

The white-tipped urchins were classified as *Echinometra sp.* A and mono-coloured, non-white-tipped urchins were *E. sp.* C. The two species were further categorized into colour types to distinguish populations. *E. sp.* A comprised of Type 1 = black-white-tipped, Type 2 = green-white-tipped, Type 3 = brown-white-tipped, Type 4 =beige-white-tipped. *E. sp.* C consisted of Type 5 = fully green and Type 6 = fully brown. Type 7 = fully maroon and was possibly a new species. It is important to note that the types encountered in each were not analyzed separately, as they were not abundant enough for statistical tests on their own. Rather a pooled analyses for *E. sp* A and *E. sp.* C was done. However, it is important to note that different morphs may have affected the pooled results. χ^2 tests were performed to distinguish between-morph and between-habitat

differences with specific reference to colour. The Poisson Analysis was adopted to compare within habitat data i.e variation between quadrats. Yates' Correction for continuity was applied to situations where degrees of freedom were 1. Variance mean ratio test was done to distinguish aggregation from uniform distribution for non-Poisson outcomes.

To record representative populations, photographs were taken. Additionally, close-up photographs of different colour morphs of *Echinometra sp.* A and C were also taken, both in and out-doors using a Nikon F1A camera with 55mm micro-NIKKOR lens. Film types used were Kodak Gold and Konica, 100ASA.

3.2.4 Size-specific behaviour

It is important to study the behaviour of bioeroding populations. Knowledge on size-specific behaviour would enable monitoring of *Echinometra* impact where burrowing and grazing behaviour may seem to be harmful to the maintenance of coral reef framework.

Size-specific activity frequency was recorded via observations of feeding, burrowing and scouring for each urchin. When urchin spines were observed boring or resting tightly onto the walls of the burrow, it was classified as 'burrowing'; when the spines were seen propelling at the sight of sinking particles, it was termed 'feeding' and if they were seen to be stationary, 'scouring' was checked. Activity was coded as 1=feeding, 2=burrowing and 3=scouring. The sizes were categorized into 3 size classes: 1-39mm = small; 40-60mm = medium and 61-110mm = large.

3.2.5 Urchin Density in relation to substrata coverage

It is further important to investigate how urchin density changes with substrata coverage in order to know the preferred substratum type and the potential impact consistent densities of *Echinometra* may be having on the coral reefs. Combined

knowledge of size-specific behaviour and substratum type coverage could enable monitoring of coral reef degradation.

The substratum type coverage beneath each urchin was noted. The gridded quadrat (each grid covered 4% of the total quadrat area) aided in calculating percent cover of the substratum. Most dominant substratum types were live coral and coral rock. Other substratum types included sand, rubble, macroalgae, coralline algae, turf algae and rock. To facilitate analyses, percentage cover estimates were coded as 0=0% cover, 1=1-20%, 2=21-40%, 3=41-60%, 4=61-80% and 5=81-100%. Once a quadrat was randomely placed on a surface that had urchins, note was taken on how many squares occupied each type of substratum within the $1m^2$ quadrat. The numbers allocated to each percentage range was arbitrarily chosen for analyses purpose.

3.3 Results

3.3.1 Multi-scale distribution and abundance patterns of *Echinometra* spp.

It is important to report on distribution and abundance patterns of two different and novel species of *Echinometra, E. sp.* A and *E. sp.* C.

The pattern of distribution and abundance found for *Echinometra sp.* A and *E. sp.* C were completely different. *E. sp.* A numbers were shown to differ between east and west positions, crest and flat and the four sites. A highly significant difference was observed (Table 3.1a) between positions ($P < 0.01$) (east and west), zones ($P = 0.014$) (crest and flat) and position x zone (site) ($P=0.052$). There was no significant difference between the position x zone ($P = 0.127$). Contrarily, guilds of *E. sp.* C on east and west, crest and flat and the different sites will show quite uniform distribution and not distinct variations in numbers as *E. sp.* A. *E. sp.* C only showed (Table 3.1b) significant difference between position x zone ($P<0.05$) with the rest of the factors not differing significantly.

Table 3.1 Three-factor, mixed-model analysis of variance on (a) *E. sp.* A and (b) *E. sp.* C density on Nukubuco Reef. Sites were nested in zones, which were nested in positions (see methodology). Data were log (x + 1) transformed to homogenize the variances.

(a)

Source	df	SS	MS	F	P
Position	1	6.737	6.737	76.790	0.000 (s)
Zone	1	0.723	0.723	8.242	0.014 (s)
Position x Zone	1	0.236	0.236	2.690	0.127 (ns)
Site (Position x Zone)	12	1.053	0.08774	1.770	0.052 (s)
Residual	304	15.071	0.04958		
Total	319				

(b)

Source	df	SS	MS	F	P
Position	1	0.140	0.140	2.575	0.135 (ns)
Zone	1	0.08310	0.08310	1.524	0.241 (ns)
Position x Zone	1	0.672	0.672	12.329	0.004 (s)
Site (Position x Zone)	12	0.654	0.05452	1.224	0.265 (ns)
Residual	304	13.543	0.04455		
Total	319				

Density varied greatly between *Echinometra sp.* A and *E. sp.* C on all locations of Nukubuco Reef. *E. sp.* A showed almost a 3-fold increase in abundance on the eastern position compared to *E. sp.* C. However, both *Echinometra* spp. preferred the eastern position. *Echinometra sp.* A showed a preference for the flat while *E. sp.* C occurred in fair numbers on both zones. Densities of 2.9 ± 0.14 urchins/m^2 and 1.1 ± 0.11 urchins/m^2 were shown by *E. sp.* A on the east and west positions respectively (Figure 3.2a). The same species showed 1.6 ± 0.11 urchins/m^2 on the crest and 2.4 ± 0.17 urchins/m^2 on the flat (Figure 3.2b). *E. sp.* C showed densities of 0.8 ± 0.08 urchins/m^2 and 0.6 ± 0.08 urchins/m^2 for positions and zones (Figure 3.2 a and b). All sites 1-16 showed higher densities of *E. sp.* A at all sites compared with *E. sp.* C (Figure 3.2c).

A depth profile was performed to assess the exposure factor for investigating the preference for eastern position. Refer to Appendix 3a, b for further details.

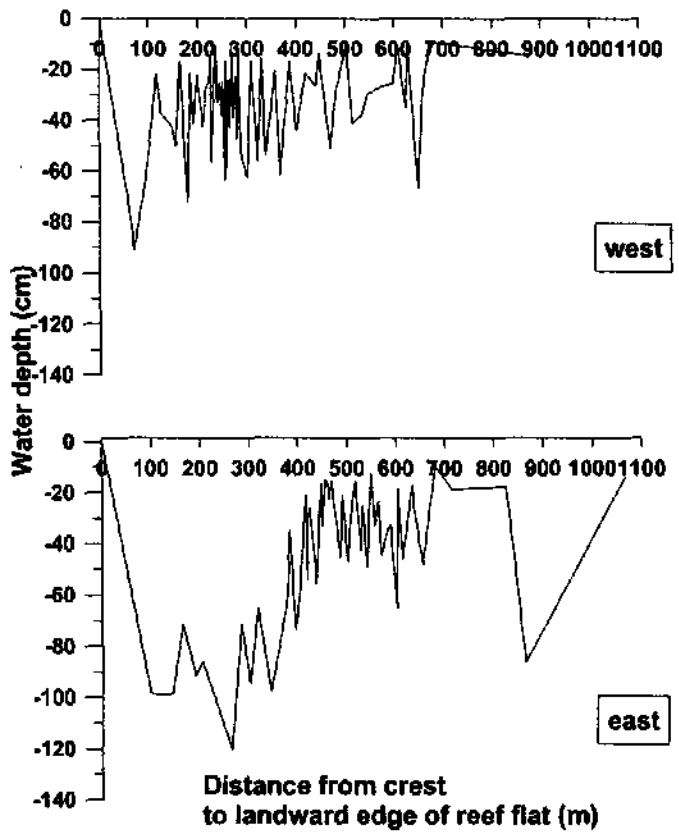


Figure 3.3 Average depth profiles of the western and eastern reef positions. Negative marks indicate water depth below surface.

Greater accumulative distances in the eastern transects showed (Figure 3.3) greater water collections when compared with western transects. This is reflected in the greater number of tidepools that were observed. West transects were narrower (900m) than east transects (1100m). Deeper water pools were seen in the east. More fluctuating water depth values were witnessed for western than eastern position.

3.3.2 Size-frequency patterns of *Echinometra* spp.

With the knowledge of distribution and abundance patterns of *Echinometra* spp., size-frequency of each species would further enhance understanding on distribution patterns.

A total of 893 *Echinometra* spp. were collected from 80 quadrats. The differences between sites in *Echinometra* spp. distribution were verified by the χ^2 test. After knowing the distribution and abundance patterns of *Echinometra* spp. (3.3.1), size-frequency of each species further enhanced knowledge on distribution patterns.

Small *Echinometra* (1-39mm) dominate the crests with a low number of medium (40-60mm) sized urchins as well (Figure 3.4). The crests were completely void of large urchins (61-100mm). Small urchins were mostly observed in the tiny coral grooves and crevices.

Echinometra spp. showed very similar size-frequency distributions on the eastern crest (Figure 3.4a, b) where higher numbers of urchins were observed from the upper limit of small size-class and lower limit of medium size-class of urchins. The four sites on the eastern crest had very similar numbers and size distribution of *E. sp.* A ($P = 0.219$) (Table 3.2a) and *E. sp.* C ($P = 0.537$) (Table 3.3a). The four sites in the western crest had different numbers of *E. sp.* A from different size classes ($P = 0.035$) (Table 3.2b). Similar to the eastern crest, the western crest demonstrated no significant difference in urchin size class distribution between the four sites for *E. sp.* C ($P = 0.263$) (Table 3.3b). However, significant difference ($P<0.05$) was observed in the distribution of *E. sp.* A and C on both the eastern and western crest (Table 3.4a,b). This dissimilarity might have resulted due to lower numbers recorded for the western crest. This demonstrates that the four sites sampled on the crests could have been very uniform in substrata complexity.

The eastern crest showed a greater variety of size-classes than the western crest for *Echinometra sp.* A (P = 0.024) (Figure 3.4a,c) (Table 3.5a). On the contrary, *E. sp.* C seemed to appear very similarly on both crests (P = 0.310) (Figure 3.4 b, d) (Table 3.5b).

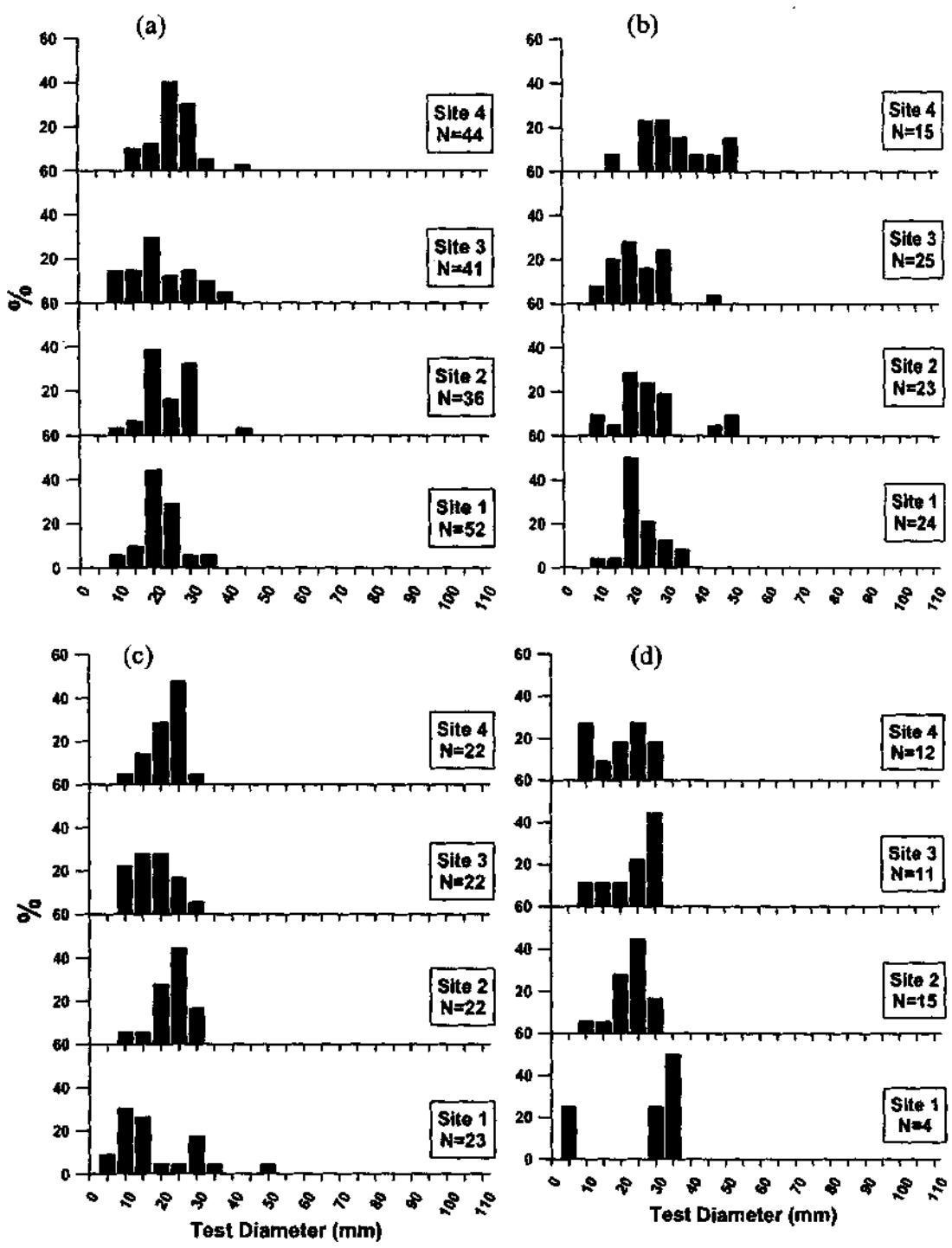


Figure 3.4 Size-frequency distribution on the eastern crest for (a) *E. sp.* A, (b) *E. sp.* C western crest for (c) *E. sp.* A, (d) *E. sp.* C Labels on the category axis are the upper limit of each test diameter category.

Table 3.2 χ^2 analysis of *E. sp.* A at (a) eastern crest and (b) western crest sites 1-4

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	11.892	9	.219
Likelihood Ratio	11.375	9	.251
Linear-by-Linear Association	.491	1	.483
N of Valid Cases	164		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 2.08.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	22.204	12	.035
Likelihood Ratio	22.637	12	.031
Linear-by-Linear Association	1.181	1	.277
N of Valid Cases	80		

8 cells (40.0%) have expected count less than 1. The minimum expected count is 0.23.

Table 3.3 χ^2 analysis of *E. sp.* C at (a) eastern crest and (b) western crest sites 1-4

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	10.905	12	.537
Likelihood Ratio	12.871	12	.379
Linear-by-Linear Association	1.380	1	.240
N of Valid Cases	83		

3 cells (15.0%) have expected count less than 1. The minimum expected count is 0.78.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	3.990	3	.263
Likelihood Ratio	4.103	3	.251
Linear-by-Linear Association	.002	1	.965
N of Valid Cases	37		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.95.

Table 3.4 χ^2 analysis of *E. sp.* A and C at (a) eastern crest and (b) western crest

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	10.801	4	.029
Likelihood Ratio	11.840	4	.019
Linear-by-Linear Association	3.725	1	.054
N of Valid Cases	247		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.68.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	57.486	4	.000
Likelihood Ratio	70.831	4	.000
Linear-by-Linear Association	14.350	1	.000
N of Valid Cases	117		

2 cells (20.0%) have expected count less than 1. The minimum expected count is .32.

Table 3.5 χ^2 analysis of (a) *E. sp.* A and (b) *E. sp.* C for eastern and western crests

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	11.218	4	.024
Likelihood Ratio	11.945	4	.018
Linear-by-Linear Association	1.777	1	.182
N of Valid Cases	244		

2 cells (20.0%) have expected count less than 1. The minimum expected count is 0.33.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	2.341	2	.310
Likelihood Ratio	3.797	2	.150
Linear-by-Linear Association	.223	1	.637
N of Valid Cases	120		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.54.

The eastern flat had a greater variety of size classes of *Echinometra sp.* A in most of its sites compared with the western flat ($P<0.01$) (Figure 3.5 a, c) (Table 3.6a, b). Similarly *E. sp.* C also showed urchins from small, medium and large size classes on the western flat ($P = 0.016$) (Figure 3.5 b, d) (Table 3.7b). However, it showed no significant difference ($P = 0.207$) between sites on the eastern flat (Table 3.7a). Size-class distribution of *Echinometra sp.* A and *E. sp.* C appeared similar on ($P = 0.910$) the eastern flat (Figure 3.5a,b) (Table 3.8a). In contrast, significant difference ($P<0.01$) was observed on the western flat between both species (Figure 3.5c,d) (Table 3.8b).

Echinometra sp. A showed a significant difference between eastern and western flats ($P<0.01$) (Figure 3.5a,c) (Table 3.9a). It demonstrated all size-class distributions and higher abundance compared with *E. sp.* C. Distribution of *E. sp.* C also differed significantly for both flats ($P<0.01$) where small and medium sized urchins were mostly observed (Table 3.9b). This could be due to higher sample size for *E. sp.* A (N=397) compared with *E. sp.* C (N=106). Additionally, the differences in environment of eastern and western flats and the behaviour of species could explain the variation in size-class distributions, *E. sp.* C being more cryptic. Generally, small (1-39mm) and medium *Echinometra* spp. dominated the western flat (Figure 3.5c,d) while the eastern flat (Figure 3.5a,b) comprised of all size classes at almost all sites.

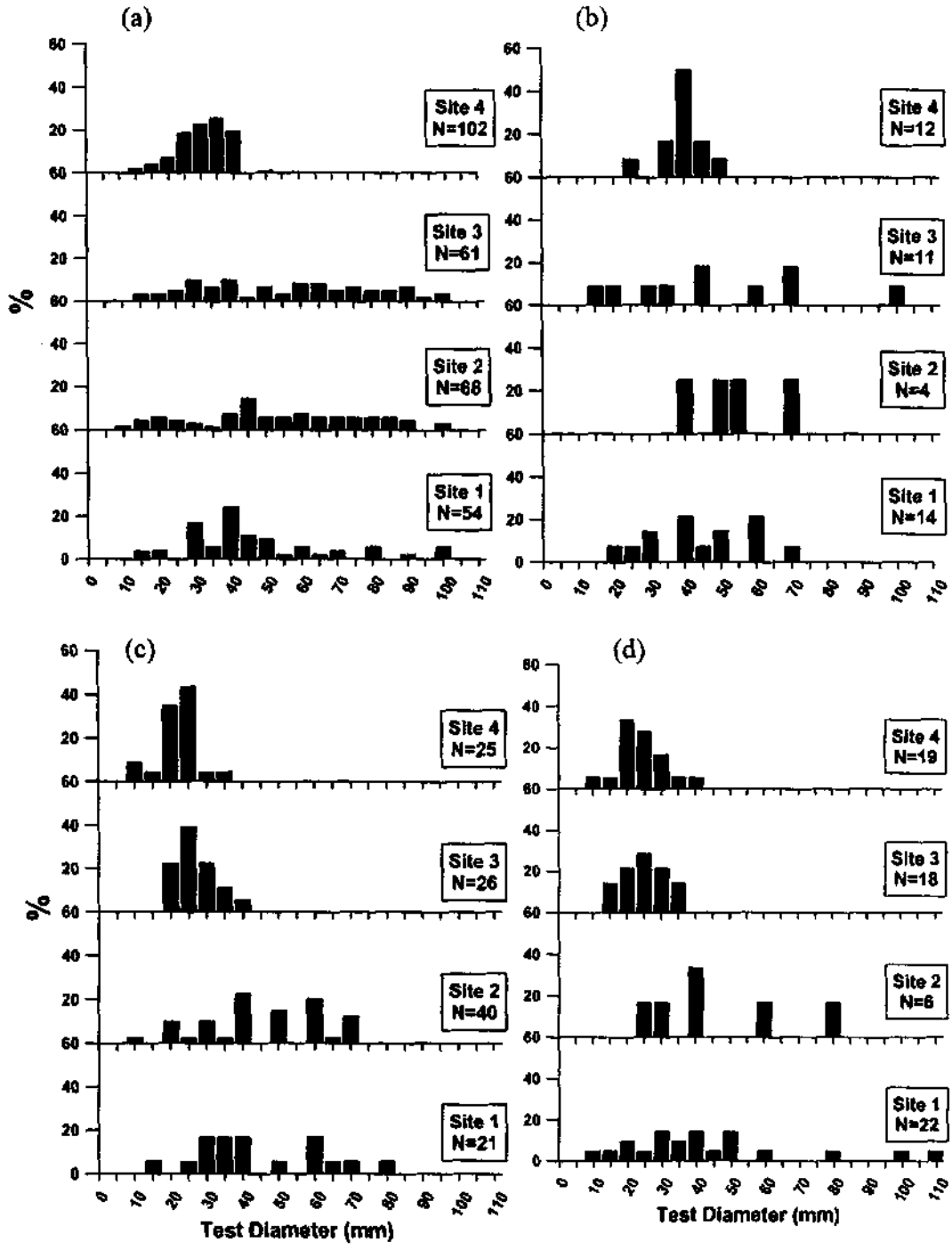


Figure 3.5 Size-frequency distribution on the eastern flat for (a) *E. sp.* A, (b) *E. sp.* C western flat for (c) *E. sp.* A, (d) *E. sp.* C Labels on the category axis are the upper limit of each test diameter category.

Table 3.6 χ^2 analysis of *E. sp.* A at (a) eastern flat and (b) western flat sites 1-4

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	92.608	18	.000
Likelihood Ratio	116.043	18	.000
Linear-by-Linear Association	19.972	1	.000
N of Valid Cases	286		

4 cells (14.0%) have expected count less than 1. The minimum expected count is 0.20.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	50.066	15	.000
Likelihood Ratio	60.166	15	.000
Linear-by-Linear Association	22.845	1	.000
N of Valid Cases	99		

3 cells (12.5 %) have expected count less than 1. The minimum expected count is .55.

Table 3.7 χ^2 analysis of *E. sp.* C at (a) eastern flat and (b) western flat sites
1-4

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	19.154	15	.207
Likelihood Ratio	21.690	15	.116
Linear-by-Linear Association	.212	1	.645
N of Valid Cases	40		

7 cells (29.2%) have expected count less than 1. The minimum expected count is 0.30.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	20.406	9	.016
Likelihood Ratio	24.755	9	.003
Linear-by-Linear Association	8.892	1	.003
N of Valid Cases	59		

3 cells (18.8%) have expected count less than 1. The minimum expected count is 0.41.

Table 3.8 χ^2 analysis of *E. sp.* A and C at (a) eastern flat and (b) western flat

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	1.529	5	.910
Likelihood Ratio	1.659	5	.894
Linear-by-Linear Association	.127	1	.722
N of Valid Cases	326		

2 cells (17.0%) have expected count less than 1. The minimum expected count is .12.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	37.427	5	.000
Likelihood Ratio	48.501	5	.000
Linear-by-Linear Association	1.064	1	.302
N of Valid Cases	158		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.12.

Table 3.9 χ^2 analysis of (a) *E. sp.* A and (b) *E. sp.* C for eastern and western flats

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	35.349	6	.000
Likelihood Ratio	39.134	6	.000
Linear-by-Linear Association	4.964	1	.026
N of Valid Cases	385		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.03.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	16.321	3	.001
Likelihood Ratio	17.096	3	.001
Linear-by-Linear Association	4.881	1	.027
N of Valid Cases	99		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 4.44.

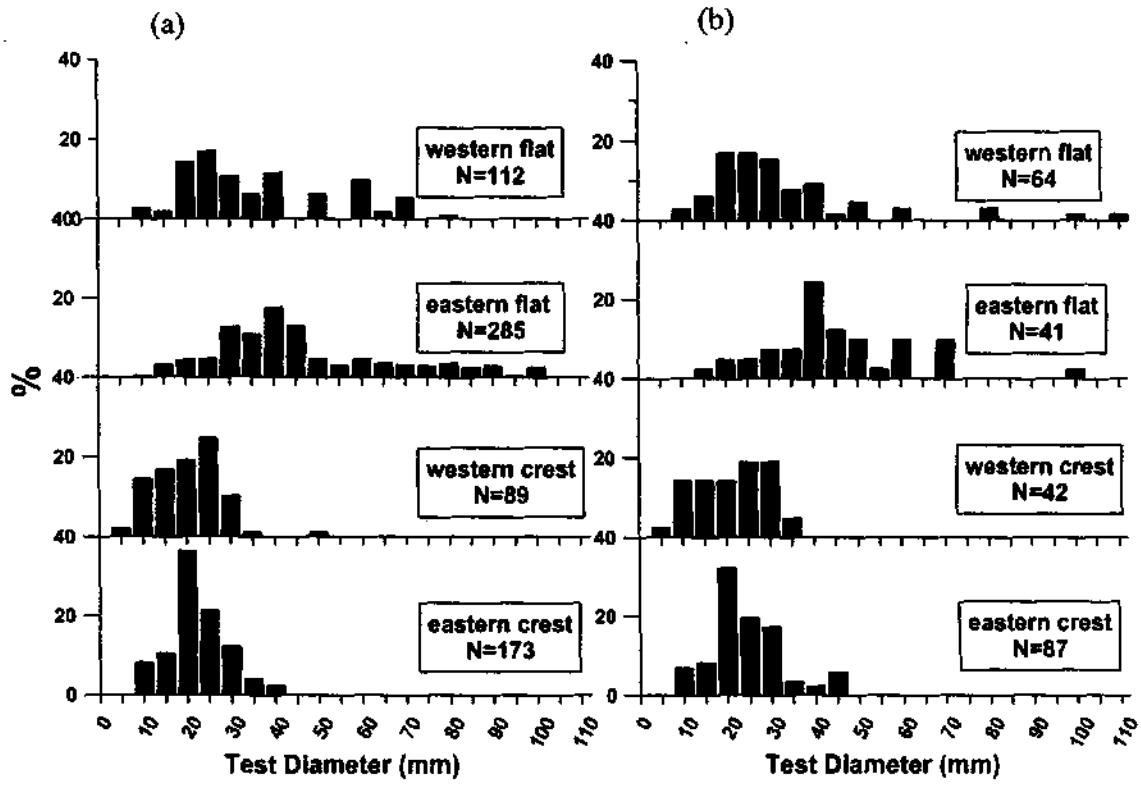


Figure 3.6 Size-frequency distribution of (a) *E. sp.* A and (b) *E. sp.* C on Nukubuco Reef. Labels on the category axis are the upper limit of each test diameter

Table 3.10 χ^2 analysis of *E. sp.* A and *E. sp.* C for (a) eastern and (b) western crest

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	10.801	4	.029
Likelihood Ratio	11.840	4	.019
Linear-by-Linear Association	3.725	1	.054
N of Valid Cases	247		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.68.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	57.486	4	.000
Likelihood Ratio	70.831	4	.000
Linear-by-Linear Association	14.350	1	.000
N of Valid Cases	117		

2 cells (20.0%) have expected count less than 1. The minimum expected count is 0.32.

Table 3.11 χ^2 analysis of *E. sp.* A and *E. sp.* C for (a) eastern and (b) western flat

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	1.529	5	.910
Likelihood Ratio	1.659	5	.894
Linear-by-Linear Association	.127	1	.722
N of Valid Cases	326		

2 cells (16.67%) have expected count less than 1. The minimum expected count is 0.12.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	37.427	5	.000
Likelihood Ratio	48.501	5	.000
Linear-by-Linear Association	1.064	1	.302
N of Valid Cases	158		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.12.

Table 3.12 χ^2 analysis of (a) *E. sp.* A and (b) *E. sp.* C for all habitats

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	304.373	15	.000
Likelihood Ratio	363.124	15	.000
Linear-by-Linear Association	8.430	1	.004
N of Valid Cases	629		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 4.20.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	134.117	15	.000
Likelihood Ratio	157.096	15	.000
Linear-by-Linear Association	8.800	1	.003
N of Valid Cases	219		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.01.

3.3.3 Size-frequency and dispersion patterns of *Echinometra* types

Results from this section would provide understanding on the composition of each *Echinometra* spp. and their dispersion patterns. It would provide information on the size class distribution of each type (colour morphs) in *E. sp.* A and *E. sp.* C and how they interact with each other.

Adult and juvenile *Echinometra sp.* A and C were identified to species using spine colour pattern. The white-tipped urchins were classified species A and the mono-coloured, non-white individuals were classified species C (Palumbi 1996a). A colour code system was developed to further distinguish the urchin populations (Figure 3.7).

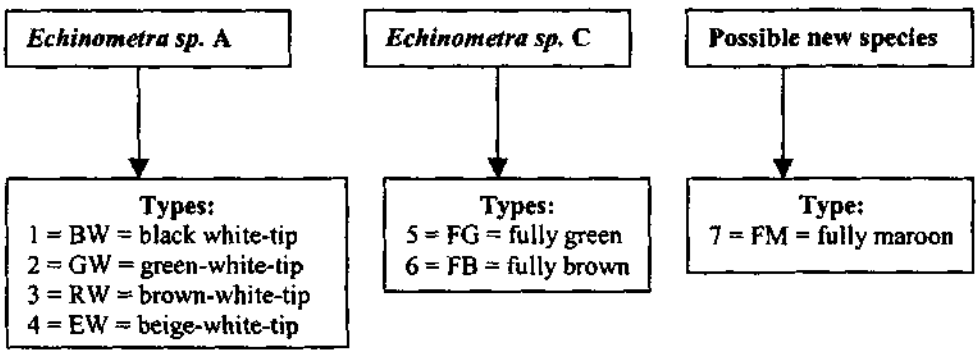


Figure 3.7 Colour Code System

Fully maroon (type 7) urchins co-existed with other *Echinometra* species. The fully maroon urchins have not been previously reported in the literature but are included in the results and should not be confused with *E. sp.* nov A and *E. sp. nov* C.

Fully maroon (type 7) was absent from both crests and brown-white-tip (type 3) was absent from the western crest. Small (1-39mm) *Echinometra* appear in abundance on both crests (Figure 3.8a,b) with very few of medium (40-60mm) size-classes. Large urchins were entirely absent. Type 2 (green-white-tip) and 6 (fully brown) were the most dominant and Type 5 (fully green) were the least on both crests. The eastern crest (Figure 3.8a) had more types (Types 1,2,3,4,5,6) present than western crest (Figure 3.8b) (1,2,4,5,6). Additionally, east crest (P = 0.440) and the west crest (P = 0.734) did not show significant difference between the colour morph distribution (Table 3.13a,b). Thus, both crests showed very similar trends of size-class distribution and urchin type occurrence.

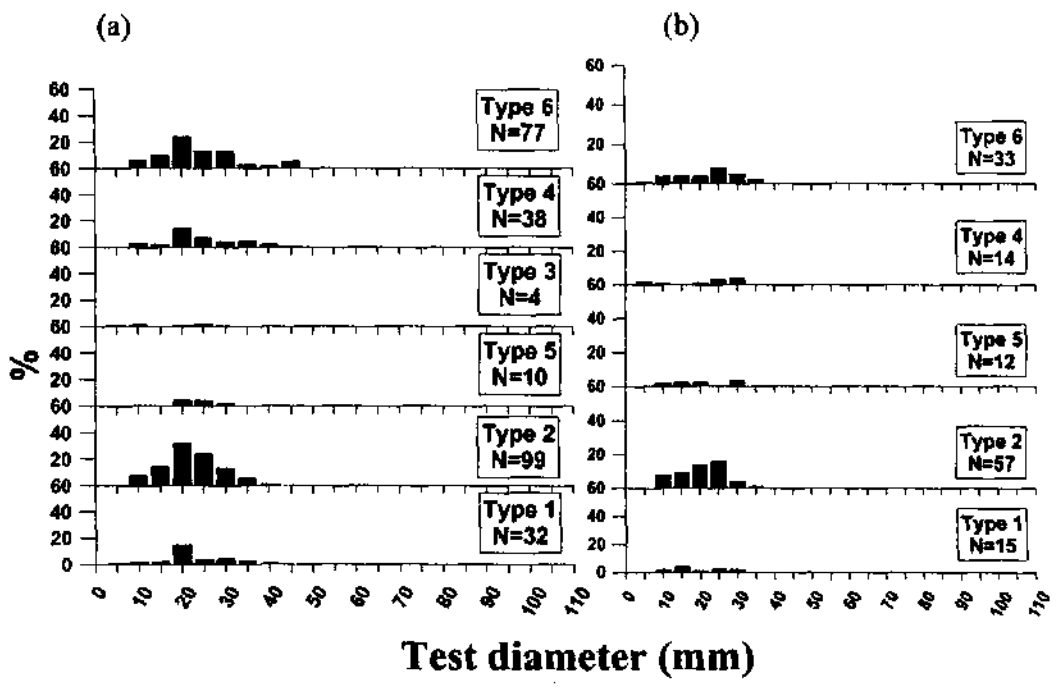


Figure 3.8 Size-frequency distribution of *Echinometra* types on the (a) eastern crest sites 1-4 and (b) western crest sites 1-4. Labels on the category axis are the upper limit of each test diameter category.

Table 3.13 χ^2 analysis of urchin types at (a) eastern and (b) western crest sites 1-4

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	12.068	12	.440
Likelihood Ratio	12.987	12	.370
Linear-by-Linear Association	1.063	1	.302
N of Valid Cases	180		

3 cells (15.0%) have expected count less than 1. The minimum expected count is 0.31.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	8.637	12	.734
Likelihood Ratio	10.264	12	.593
Linear-by-Linear Association	.967	1	.325
N of Valid Cases	112		

3 cells (15.0%) have expected count less than 1. The minimum expected count is 0.32.

Unlike the crests, there is variability in patterns of distribution for *Echinometra* types on the flats (Figure 3.9a,b). Seven morphs were present at the eastern flat (Figure 3.9a) while six existed at the western flat (Figure 3.9b). Type 3 was unique to the eastern flat. Type 7 was also unique to the flats. A mixture of *Echinometra* spp. was observed on the flats. Additionally, the western flat shows distribution very similar to the crests with mostly the small and medium urchins and no large ones while the eastern flat accommodates all size-classes.

The *Echinometra* spp. on the eastern flat showed significant difference ($P<0.01$) between types, where a variable pattern of distribution was observed (Table 3.14a). Conversely, the western flat shows no significant difference ($P = 0.289$) between colour morphs (Table 3.14b). This is shown by similar distribution patterns observed for types. There more type 1, 2, 4 and 6 urchins observed on the eastern flat compared with the western flat.

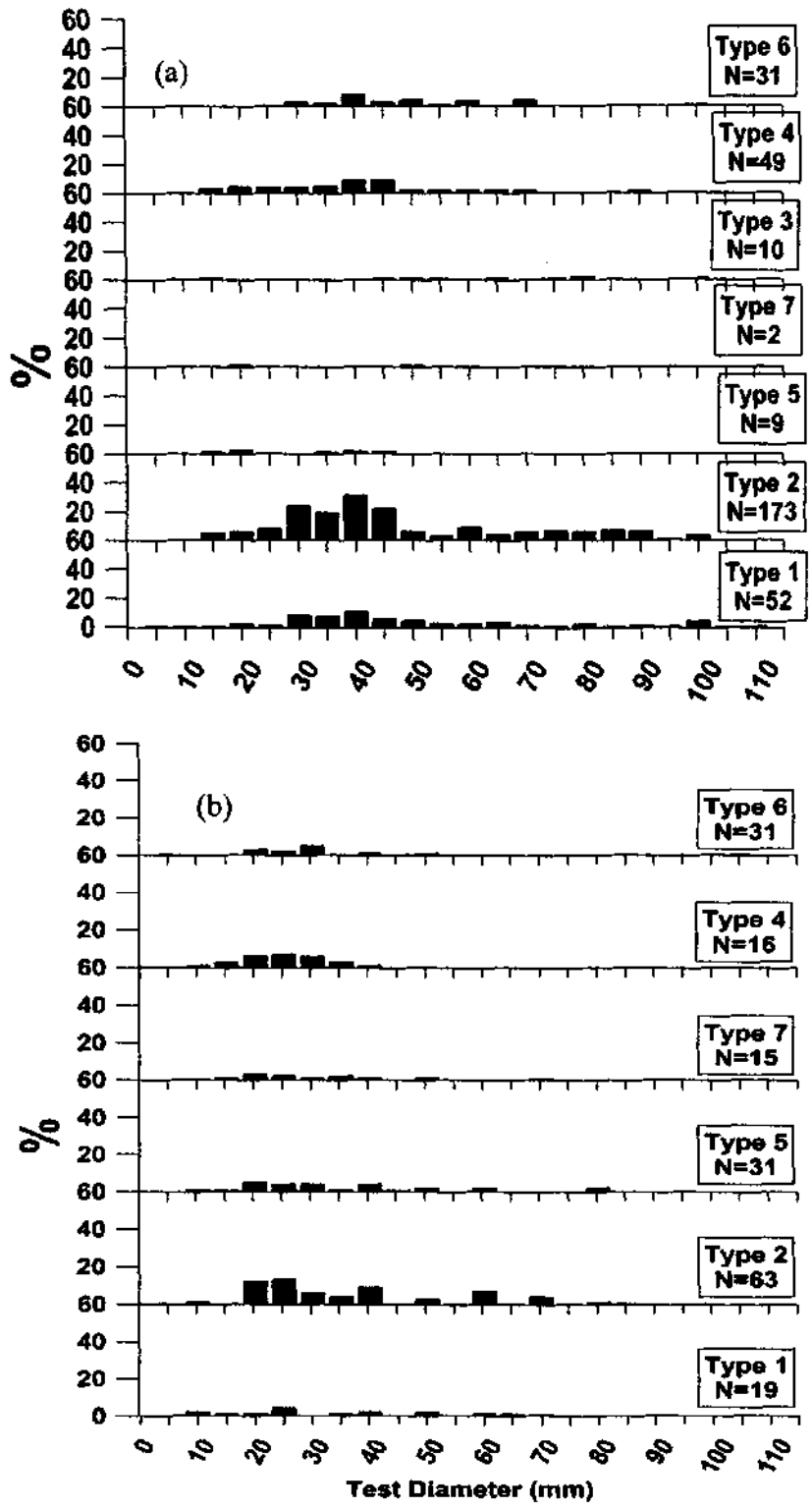


Figure 3.9 Size-frequency distribution of *Echinometra* types on (a) eastern flat sites 1-4 and (b) western flat sites 1-4. Labels on the category axis are the upper limit of each test diameter category.

Table 3.14 χ^2 analysis of urchin types at (a) eastern and (b) western flats sites 1-4

(a)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	87.284	24	.000
Likelihood Ratio	45.151	24	.006
Linear-by-Linear Association	.038	1	.846
N of Valid Cases	327		

12 cells (40.0%) have expected count less than 1. The minimum expected count is 0.01.

(b)

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	22.999	20	.289
Likelihood Ratio	27.116	20	.132
Linear-by-Linear Association	10.877	1	.001
N of Valid Cases	152		

5 cells (17.0%) have expected count less than 1. The minimum expected count is 0.33.

Type 2 (green-white-tip/*Echinometra sp.* A) dominate all habitats on Nukubuco Reef. Type 1 (black-white-tip/*E. sp.* A) and 6 (fully brown/*E. sp.* C) were the second most dominant. These three types show quite similar patterns of abundance in all habitats. Type 7 (fully maroon/possible new species) is absent from both crests but was present in high numbers on the western flat and low numbers in eastern flat. This could be an indicator of specific necessities of a niche or vulnerability to predation in some habitats and not the other. Type 3 (brown-white-tip/*E. sp.* A) was absent from the western position possibly due to less micro-spatial preference availability, more predators, and less available refuge. Fully green urchins (type 5/*E. sp.* C) were in lower numbers at all habitats. This could be due to inter-specific competition and high predation rates on this type. The four habitats showed significant difference ($P < 0.01$) in *Echinometra* types (Table 3.15) (Figure 3.10).

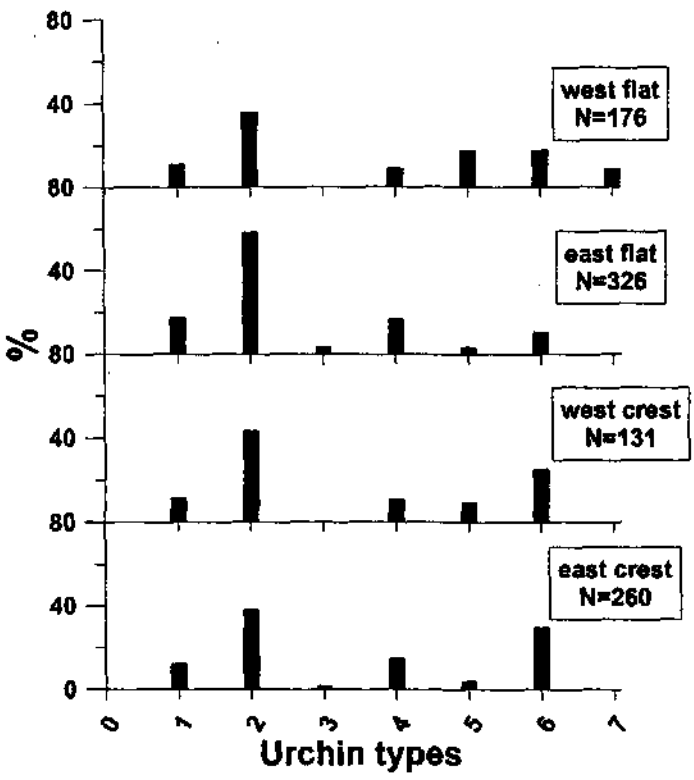


Figure 3.10 Percentage distribution of *Echinometra* colour morphs on Nukubuco Reef. Urchin types were coded as 1= black-white-tip, 2= green-white-tip, 3= brown-white-tip, 4= beige-white-tip, 5= fully green, 6= fully brown and 7= fully maroon.

Table 3.15 χ^2 analysis of urchin types on all habitats

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	75.387	18	.000
Likelihood Ratio	73.850	18	.000
Linear-by-Linear Association	1.504	1	.220
N of Valid Cases	402		

0 cells (0.0%) have expected count less than 1. The minimum expected count is 1.49.

Type 2 (green-white-tip/*Echinometra sp.* A) dominated both zones indicating optimum conditions (low predation rates, high reproduction rates, and low mortality rates) of survival for this type on Nukubuco Reef. Also, this species may

be more adaptable to different habitats and is more robust. Type 2 (green-white-tip/*E. sp.* A) and 6 ((fully brown/*E. sp.* C) dominated the crest zone. These morphs are possibly adapted to high-energy wave action and are robust and/or may be reliant on detrital feeding. Type 7 (fully maroon/possible new species) urchins were only observed on the flats. These urchins could be more adapted to calmer conditions. Type 1 (black-white-tip/*E. sp.* A) and 4 (beige-white-tip/*E. sp.* A) showed similar abundance and distribution patterns since they were both colour morphs of *E. sp.* A. Type 3 (brown-white-tip/*E. sp.* A) was the least abundant in both zones. This type could be the least competitive and most vulnerable to predation. Hence, *E. sp.* A (Types 1, 2, 3, 4) showed higher abundance on Nukubuco Reef compared to *E. sp.* C (Types 5, 6). The possibly new species (Type 7) were also present in low numbers (Figure 3.11).

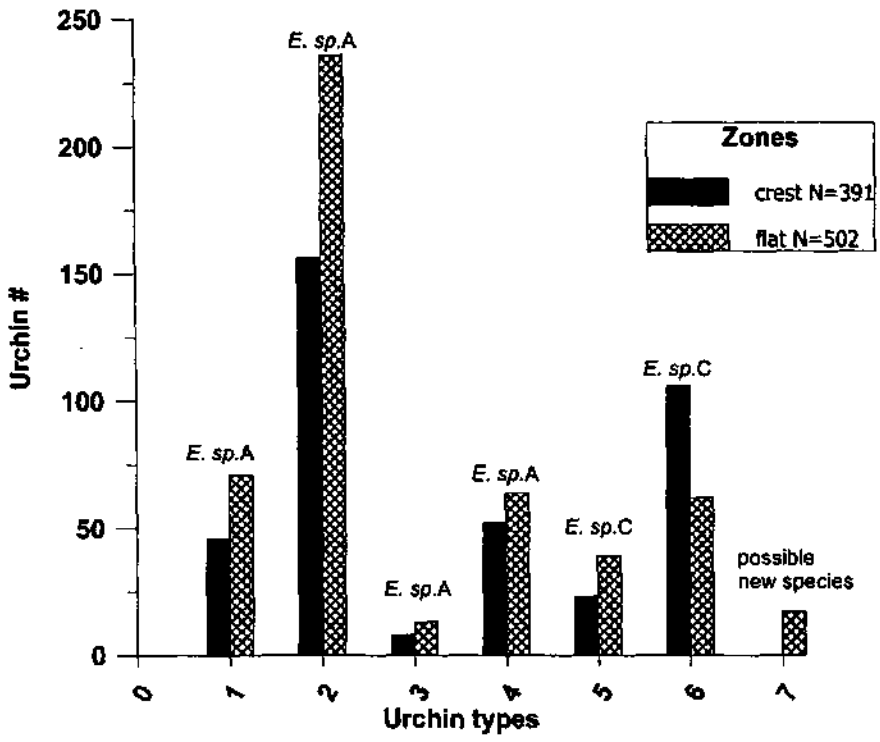


Figure 3.11 Population abundance patterns of *E. sp.* A and C on the flats and crests of Nukubuco Reef.

Aggregation Patterns of *Echinometra sp.* A and *E. sp.* C

The distribution of white-tipped (Types 1-4) *Echinometra* (*E. sp.* A) in all four habitats demonstrated slightly greater than 50% Poisson distribution and 45% non-Poisson or aggregated distribution (Table 3.16). Type 3 (brown-white-tipped) densities were too low to produce significant results for Poisson analysis. The non-white-tipped (Types 5-6) *Echinometra* (*E. sp.* C) deviated significantly from a Poisson distribution (Table 3.16). This may illustrate their tendency to form clusters. Variance Mean Ratio (VMR) was calculated to confirm aggregated (VMR > 1) from uniform (VMR < 1) distribution in the non-Poisson outcomes. VMR is calculating variance from grouped data where the variance is divided by the mean to give a value less than, greater than or equal to one. The grouped

colour morph Poisson distribution (Table 3.17), which had much greater sample size (893), showed completely highly significant aggregations in all the habitats.

Table 3.16 Poisson Distribution By Colour Morphs. Not more than 20% of expected value <1. Data are from 1m x 1m (N = 80 quadrats). Colour coding was as follows: BW = black white-tip; GW = green white-tip; EW = beige white-tip; FB = fully brown; FG = fully green; FM = fully maroon. s = significant, n.s = not significant. * significant, **highly significant, ***very highly significant

Colour Morph	Zone	Distribution Pattern (VMR)	Calculated χ^2	P value	# Urchins Sampled
E. sp. A BW	East Crest	Aggregated (1.6)	12.16	P < 0.001 (s) ***	32
	West Crest	Not aggregated	8.07	0.005 > P > 0.001 (n.s)	15
	West Flat	Not aggregated	2.07	0.95 > P > 0.10 (n.s)	19
	East Flat	Aggregated (1.06)	7.45	0.025 > P > 0.01 (s) **	52
GW	East Crest	Not aggregated	5.26	0.10 > P > 0.05 (n.s)	99
	West Crest	Aggregated (1.95)	7.35	0.05 > P > 0.025 (s) *	57
	West Flat	Aggregated (2.02)	15.51	P < 0.001 (s) ***	64
	East Flat	Not aggregated	8.26	0.95 > P > 0.10 (n.s)	173
EW	East Crest	Not aggregated	2.38	0.95 < P < 2.706 (n.s)	38
	West Flat	Not aggregated	2.68	0.95 > P > 0.10 (n.s)	16
	East Flat	Aggregated (2.17)	21.31	P < 0.001 (s) ***	49
E. sp. C FB	East Crest	Aggregated (1.14)	10.83	0.025 > P > 0.01 (s) **	77
	West Crest	Aggregated (1.6)	17.11	P < 0.001 (s) ***	33
	West Flat	Aggregated (1.33)	4.92	0.05 > P > 0.025 (s) *	31
	East Flat	Aggregated (1.67)	9.49	0.005 > P > 0.001 (s) ***	31
FG	West Flat	Aggregated (2.19)	12.05	P < 0.001 (s) ***	31
Possible new species FM	West Flat	Not aggregated	8.25	0.005 > P > 0.001 (s) ***	15

Table 3.17 Poisson Distribution By Grouped Colour Morphs. Not more than 20% of expected value <1. Data are from 1m x 1m (N = 560 quadrats).

Zone	Distribution Pattern (VMR)	Calculated χ^2	P value	# Urchins sampled
East Crest	Aggregated (5.57)	116.22	P < 0.001 (s) ***	260
West Crest	Aggregated (2.24)	134.43	P < 0.001 (s) ***	131
West Flat	Aggregated (2.07)	122.55	P < 0.001 (s) ***	176
East Flat	Aggregated (2.16)	88.36	P < 0.001 (s) ***	326

Echinometra spp. were observed together in guilds except the possible new species, fully maroon (type 7), which was always seen isolated. Though *Echinometra* types and/or species demonstrated variable aggregating patterns (Table 3.16), an overall aggregated distribution (Table 3.17) was shown statistically. In Okinawa, Japan *E. sp.* A appear in aggregations while *E. sp.* C appear non-aggregated (Tsuchiya and Nishihira 1985). Contrarily, this study shows aggregation for both *E. sp.* A and C. Crown-of-thorns starfish (COTS) was frequently observed on live *Acropora* and semi-live branched corals. *Echinometra* spp. aggregations were seen both on branched corals and mostly on massive and submassive *Porites* since they are suitable habitats. Hence, it could be said that the urchins were a secondary effect of COTS (Keesing 1992).

3.3.4 Size-specific behaviour

The urchins were not distinguished into separate species to study size-specific behaviour as numbers were too low for each species separately to have given distinct trends. It was also beyond the scope of this study. Additionally, the main focus of this section was to investigate the dominant behaviour for different size classes of urchins. Knowledge on such size-specific behaviour would enable monitoring hazardous impact such as burrowing by urchin populations.

Echinometra spp. typically formed small, cryptic guilds on the dead branches of live coral colonies, in substratum crevices, under coral ledges or on dead coral skeleton. They formed immobile guilds near burrows or beside coral knolls, both dead and alive, during the day. The urchins on partly dead corals clustered around the white scars left from grazing activity, which were vividly visible. Urchins of all sizes were commonly seen nestled around massive and submassive *Porites* and smaller ones burrowed in crevices on *Porites* heads.

The eastern (Figure 3.12a) and western (Figure 3.12b) crests displayed very close behavioural trends. Both habitats showed highest burrowing activity followed by feeding then scouring. Only small (1-39mm) and medium (40-60mm) urchins were observed. Small sized *Echinometra* spp. were predominant on the crests, mostly observed very tightly welded to the crevices. Both flats (Figure 3.13 a, b) show all classes of activity by all size classes of *Echinometra* spp. The large ones did not show burrowing behaviour at the western flat. In contrast to the western flat, a higher percentage of feeding compared with burrowing was recorded for the eastern flat. The huge burrowing response observed in the western flat was specific to small sized urchins. This could probably indicate that small urchins principally strive to build a secured habitat.

3.3.5 Urchin Density in relation to substrata coverage

The chief aim of this section was to investigate the pattern between urchin density and substrata coverage. Knowledge of these trends would enable interpretation of destructive impacts by bioeroding populations of urchins on Nukubuco Reef. *Echinometra* were once more not separated into different species due to low numbers not showing distinct trends.

Large numbers of *Echinometra* spp. were observed nestled under *Porites* boulders and tightly burrowed onto crevices of *Porites* heads on Nukubuco reef flats. The landward edge of the crests had high numbers of urchins colonizing the partly bleached *Porites cylindrica* microatolls. Reef flats had sturdier forms while the crests showed more digitate and plate forms of corals. Coral rock masses had high numbers of *Echinometra* spp. with frequent observations of *A. planci* associations. Urchins were mostly evident on semi-live corals and coral rock compared with live coral colonies.

The eastern crest (Figure 3.14a) shows a strong association ($r = 0.767$) between live coral coverage and *Echinometra* density whereby the coral coverage explained 58.3% (adjusted $r^2 = .583$) of the variation in number of urchins at the eastern crest. The regression ANOVA showed a highly significant linear relationship ($F = 110.239$, $P < 0.01$) (Table 3.18a) between the live coral and urchins. Urchin density increased with increasing coverage of live coral. *Echinometra* spp. were closely affiliated with live coral at the crest. Since mostly the small and medium sized urchins were observed at the crest, it could probably have been new recruits of a cohort as the oceanic waters disperse pelagic larvae.

On the other hand, the western crest (Figure 3.14b) showed a weak association ($r = 0.394$) between live coral and urchin density whereby live coral coverage explained only 14.4% (adjusted $r^2 = .144$) of the variation in number of urchins at the western crest. Quite a random scatter was observed between live coral and urchin density but the regression ANOVA showed a highly significant linear

relationship ($F = 14.341$, $P < 0.01$) (Table 318b) between the two variables. Since the mean population density of the western crest (1.64 or 2 urchins/m^2) was less than that of the eastern crest (3.25 or 3 urchins/m^2), the portrayed association could be falsified by a lower population size. Alternatively, though small urchins are confined to the crests (Ebert 1968), the western crest may have experienced variation in recruitment patterns of *Echinometra* spp.

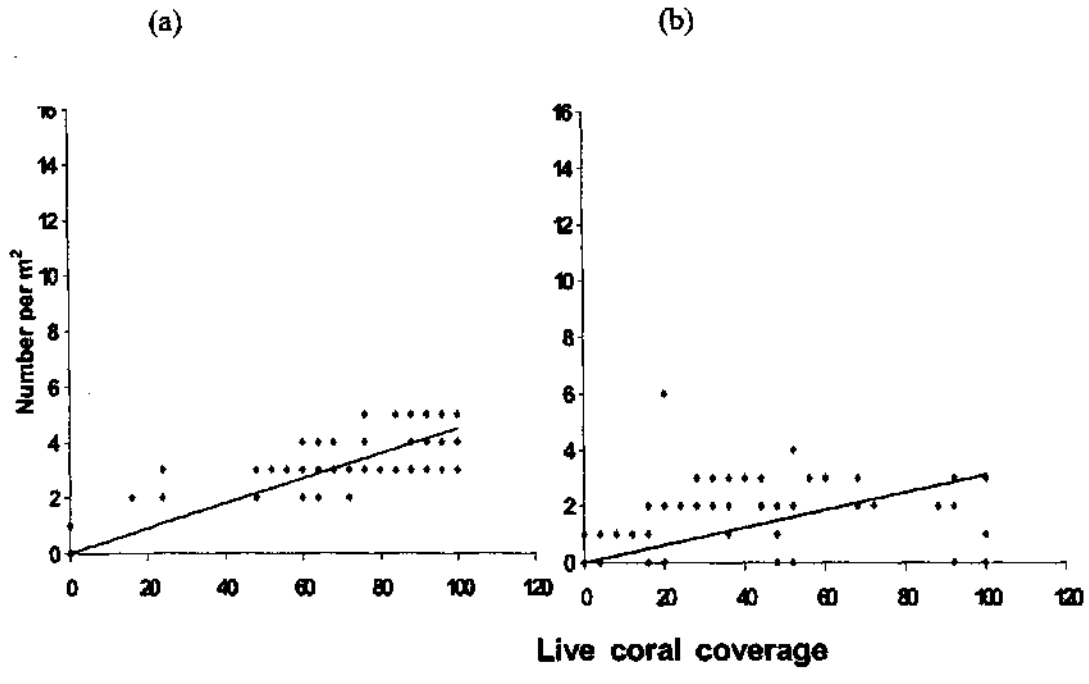


Figure 3.14 *Echinometra* density for varying live coral % coverage for 4 sites of (a) eastern crest and (b) western crest. Data were log (x + 1) transformed to homogenize the variances.

Table 3.18 Regression analysis of variance for urchin density vs live coral coverage on the (a) eastern crest. and (b) western crest.

(a)

Model		SS	df	MS	F	Sig
1	Regression	0.915	1	0.915	110.239	0.000
	Residual	0.639	77	8.302E-03		
	Total	1.555	78			

(b)

Model		SS	df	MS	F	Sig
1	Regression	0.738	1	0.738	14.341	0.000
	Residual	4.014	78	5.146E-02		
	Total	4.752	79			

The western flat recorded *Echinometra* spp. inhabiting live coral and coral rock in a very similar fashion but the former recorded lower numbers than the latter. The coral rock association with urchin density (Figure 3.15a) showed very weak association ($r = 0.127$) whereby it explained 1.0% (adjusted $r^2 = -0.010$) of the variation in number of urchins and the regression ANOVA also showed an insignificant linear relationship ($F = 0.608$, $P = 0.441$) (Table 3.19a) between the two variables. The insignificance could be an indication of sampling sites that had very similar patterns of urchin colonization.

Live coral association with *Echinometra* spp. (Figure 3.15b) showed a good correlation ($r = 0.597$) whereby it explained 33.3% (adjusted $r^2 = .333$) of the variation in number of urchins. The regression ANOVA showed a very highly significant linear relationship ($F = 15.484$, $P < 0.01$) (Table 3.19b) between the two variables. This association was very similar to the scenario observed at the crests.

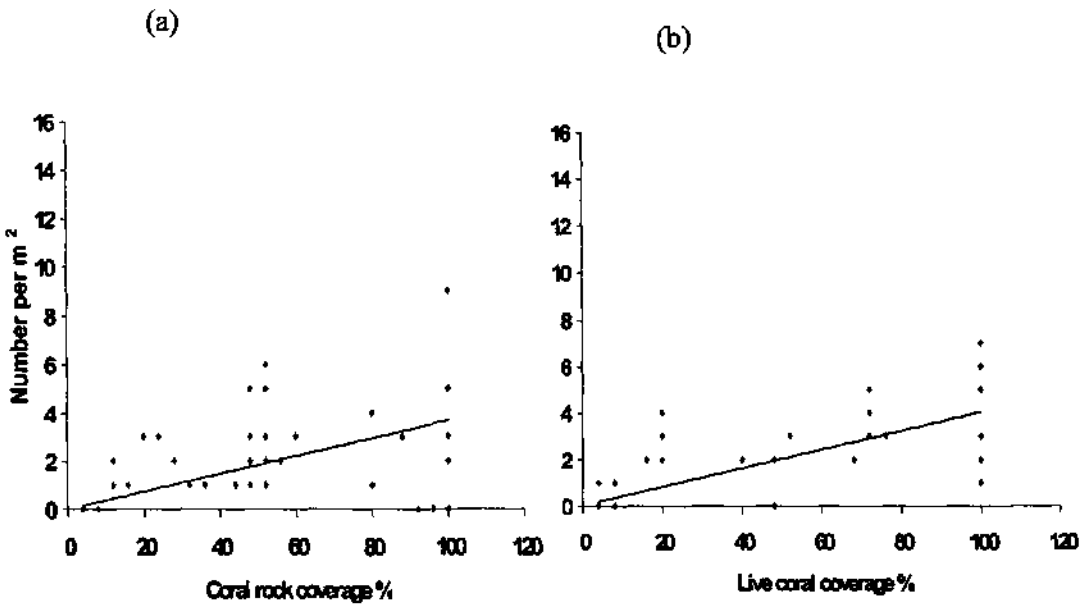


Figure 3.15 *Echinometra* density for varying (a) coral rock % and (b) live coral % coverage for 4 sites of western flat. Data were log (x + 1) transformed to homogenize the variances.

Table 3.19 Regression analysis of variance for urchin density vs (a) coral rock and (b) live coral coverage on the western flat.

(a)

Model		SS	df	MS	F	Sig.
1	Regression	4.372E-02	1	4.732E-02	0.608	0.441
	Residual	2.661	37	7.192E-02		
	Total	2.705	38			

(b)

Model		SS	df	MS	F	Sig.
1	Regression	0.625	1	0.625	15.484	0.001
	Residual	1.130	28	4.035E-02		
	Total	1.754	29			

The eastern flat showed (Figure 3.16a) a moderately good correlation (r = 0.463) whereby coral rock coverage explained 20.0% (adjusted r^2 = .200) of the variation in the number of urchins and the regression ANOVA showed a significant linear relationship (F = 15.786, P < 0.01) (Table 3.20a) between the two variables. Large numbers of *Echinometra* spp. (mean population density = 4 urchins/m^2) were on coral rock at the eastern flat.

Although the eastern flat had lower colonizations of *Echinometra* spp. on live coral (Figure3.16b), a strong correlation (r = 0.793) existed; live coral coverage explained 60.7% (adjusted r^2 = .607) of the variation in number of urchins at the eastern flat. The regression ANOVA showed a significant linear relationship (F = 30.403, P < 0.01) (Table 3.20b) between the two variables. Hence, live coral increase showed a relative decline compared with coral rock, in *Echinometra* densities at the eastern flat. It is possible that an increase in niche sources could result in an increase in urchins.

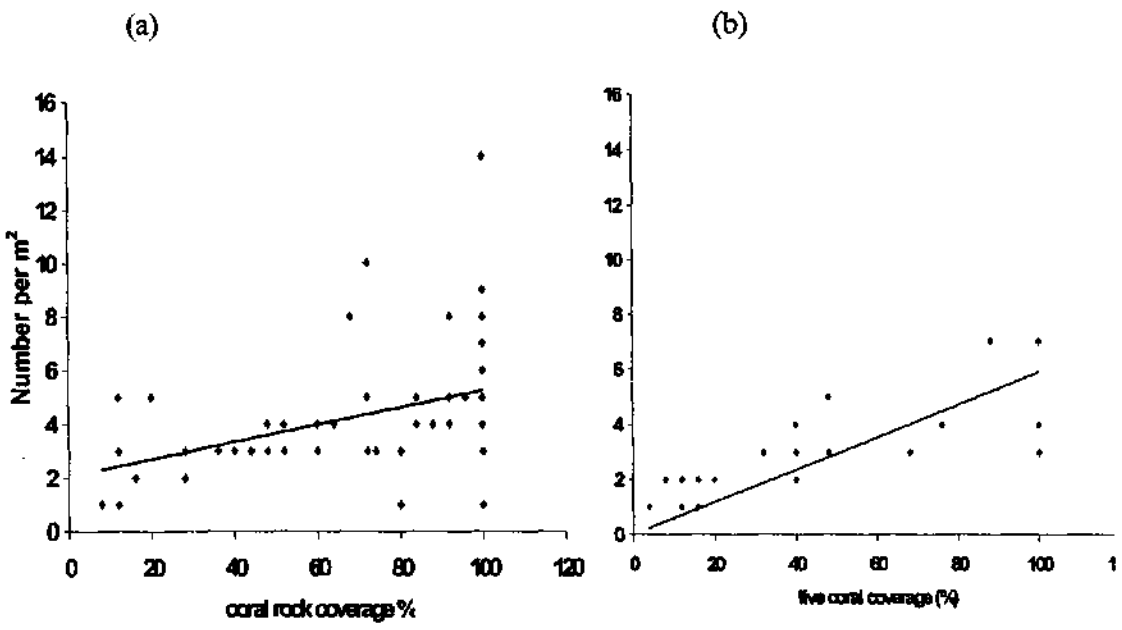


Figure 3.16 *Echinometra* density for varying (a) coral rock % and (b) live coral coverage for 4 sites of eastern flat. Data were log (x + 1) transformed to homogenize the variances.

Table 3.20 Regression analysis of variance for urchin density vs (a) coral rock and (b) live coral coverage on the eastern flat.

(a)

Model		SS	df	MS	F	Sig.
1	Regression	0.656	1	0.656	15.786	0.000
	Residual	2.410	58	4.156E-02		
	Total	3.066	59			

(b)

Model		SS	df	MS	F	Sig.
	Regression	0.370	1	0.370	30.403	0.000
	Residual	0.219	18	1.217E-02		
	Total	0.589	19			

3.4 Discussion

3.4.1 Multi-scale distribution, abundance and size-frequency patterns of *Echinometra* spp.

This study reports a new *Echinometra* spp.' ecology which has resulted from slight gene divergence of *E. mathaei* (Palumbi 1996a). Since no literature is available on it, the findings will be compared with *E. mathaei* ecology, an equitably very close relative.

This study demonstrated similar distribution trends for both species on the eastern and western crests. However, *Echinometra sp.* A and C showed variation in size-class distribution and abundance patterns on both flats. These distinct patterns of between-habitat distribution are likely due to variations in the larger-scale ecological processes of habitat-specific recruitment and mortality, though adult movement could also influence them (Cumming 1999).

Small size classes (1-39mm) of *Echinometra* spp. dominated the reef crests in low urchin numbers with complete absence of large ones (61-110mm) while flats showed variable patterns in urchin size classes. Patchy distribution of *Echinometra* spp. was observed on the reef crest as compared to the more readily found urchins on the flat. Muthiga and McClanahan (1987) reported a similar distribution pattern in Kenya. They explained this by the variable predation within these locations, which in turn may be affected by surf and current activity. Lewis and Storey (1984) disclosed that surf may act as a stress on large *E. mathaei,* but wave action may also reduce predation and therefore be beneficial. Less violent waves could also allow the larvae to settle more easily on the inner reef than on the outer. The sublittoral nature of the inner reef would also reduce dangers of exposure to the sun and air (Clark and Bowen 1949).

The variation in population distribution and abundance of *Echinometra sp.* A and C amongst zones and positions may also be in part due to variations in depth, exposure to wind, community structure and the rates of sedimentation experienced at each locality (Hutchings *et al.* 1992). Some of the variations in colonization between locales may be explained by variation in pelagic dispersal and hence, recruitment. Previously settled urchins who inhibit or modify the rates of residence may also affect the colonization of new recruits (Keesing 1992).

The occurrence of smaller urchins on the high-energy crests and larger ones on the calmer flats indicate that large urchins cannot afford the risk of spine breakage from turbulent waves (Ebert 1968). Ebert (1968) discovered similar size-class and inhabitation patterns for *Strongylocentrotus purpuratus*. He attributed this to the breakage of more spines by turbulent waves on the crests and hence more energy expended for repairs than on the flats, where energy was directed into test growth. The mean test diameter is greater on the calmer coral knoll environment, suggesting a positive inverse relationship between density and growth (Russo 1980).

Alternatively, they may not be able to survive there for very long due to hostile conditions and exposure to predators. Urchins of variable sizes are observed on the flats as it provides ideal habitats for protection, food and refuge when compared with the crests. It can be speculated that the established and hostile nature of large urchins on the reef flats may be posing a threat to the juvenile recruits, hence they colonize the rarely liked crests. On the flats, the chance of robbing the burrow by small urchins would be very small unless the large host dies or gets removed for some other reason (Tsuchiya and Nishihira 1985). Additionally, urchins recruit at the crest and it is here that these small urchins are provided with a constant supply of detrital food in the excessive water flow, as they stay welded to the crevices (Russo 1977)

More depressions were observed on the flats than crests, which had more complete and intact coral knolls and that may explain the high colonization of urchins on the flats. In contrast, Russo (1977) reported that sea urchins increased rapidly from the landward to the seaward edge of the reef, as did water flow and detrital deposition. He noted that echinoids take up residence in the already formed pits and grooves in the substrata (Otter 1932), and that there are more of these on the seaward edge due to reef erosion from constant wave action. Khamala (1971) also found smaller specimens of *Echinometra mathaei* on the sheltered inner reefs and larger ones on the exposed outer reef. The contrast could be explained by the prevalence of massive and submassive *Porites* on the flats of Nukubuco Reef, which could be providing an ideal environment for urchin colonization compared with the exposed crests.

The eastern position showed higher mean densities of *Echinometra* spp. than the western position. The small differences in the length of exposure time between two areas can produce a great difference in the distribution of inshore marine organisms (Khamala 1971). During both LWN and LWS tides, the western position of Nukubuco Reef is exposed for a longer time than the eastern position (personal observation at 0m-tide level). The depth profile demonstrated greater fluctuating depths in the west than the east of Nukubuco. Greater accumulative distances with higher water carrying capacity were witnessed on the eastern reef than on the western position. This was confirmed by greater numbers of tidepools observed in the east (30) than on the west (11). Presumably this is one of the reasons for the significant differences in the mean population densities of *Echinometra* observed between the eastern and western positions of the reef. Khamala (1971) noted similar differences in distribution between the northern and southern sections of the outer reef in Kenya.

Another probable reason for higher urchin densities on the eastern position could be anthropogenic influence such as sewage influx and high sediment input from Kinoya Sewage Plant and Nausori highlands, respectively. These could be

providing good conditions for growth for both *Echinometra* spp. larvae and adults. Birkeland (1989) suggested that terrigenous inputs of nutrients might enhance phytoplankton production leading in turn to higher survivorship in planktotrophic echinoderm larvae. On the other hand, the western position has more live corals and less anthropogenic inputs, restricting sea urchin survival. There is potential for manipulative studies on nutrient level effects on *Echinometra* spp.

Moreover, *Acanthaster planci* were frequently observed on live and semi-live corals on the east of Nukubuco. Keesing (1992) has reported *Echinometra* outbreaks as a secondary effect of sub-infested densities of *A. planci*. Birkeland (1981) and Glynn (1988) have stated that increase in algal abundance following *A. planci* outbreaks or other disturbances may have caused a numerical response from grazing urchins through facilitating higher recruitment. Experimental studies are needed to examine the demographic consequences of *A. planci* in relation to *Echinometra* ecology.

The recent consistent urchin numbers on Nukubuco could also be explained by overfishing of predatory fish such as triggerfish on the reef (Hay 1984; McClanahan and Muthiga 1988, 1989). Urchins such as *Echinometra* and *Diadema* have often been dominant herbivores on unprotected (heavily fished) coral reefs while herbivorous fishes such as parrot and surgeonfishes dominate (little or unfished) protected reefs (Hay 1984; McClanahan and Shafir 1990). Detailed evaluation of fishing pressure evaluations based on the methods developed by McClanahan (1995a) and McClanahan *et al.* (1999) could improve our understanding of the impact of overfishing on urchin abundance and distribution.

3.4.2 Size-frequency and dispersion patterns of *Echinometra* types

Large-scale analysis of pooled colour morphs (sites 1-4) showed significant differences in zones. The *Echinometra sp.* A consisted of black white-tip

(13.2%), green white-tip (44%), brown white-tip (1.6%), and beige white-tip (13.1%). *E. sp.* C comprised of fully green (6.9%) and fully brown (19.3%). And the fully maroon (1.9%), a possible new species was the least abundant on Nukubuco Reef. It was also observed that the fully maroon type was being exceptionally isolated. It is possible that the fully maroon type may not be an *E. sp.* A or *E. sp.* C as there is no report of this type in the literature (Tsuchiya and Nishihira 1984, 1985, 1986; Uehara and Shingaki 1984, 1985; Palumbi 1996 a, b).

Type 2 (green-white-tip/*Echinometra sp.* A) and 6 (fully brown/*E. sp.* C) were the most dominant types of the two different *Echinometra. spp.* These types may have the best adaptation in survivorship (less susceptibility to predation, highly competitive, high reproduction rates, etc.) compared with other types. Type 3 (brown-white-tip/*E. sp. A*) only existed in low numbers at the eastern zones. This may indicate micro-spatial preference or low predation rates in this zone compared to the west. Type 7 (fully maroon/possible new species) was only present on the flats. This is probably because it prefers a calmer environment and adapts to a grazer mode rather than the detrital mode of feeding. Also, it might be more vulnerable to predators and less competitive with other types on the reef crest. Additionally, differences in community structure (microhabitat preferences) along with recruitment patterns in each habitat may be attributable to variations in morph distribution.

Poisson analysis indicated variation in *Echinometra* spp. colour morph abundance at smaller scales (between quadrats), which was most likely due to behavioural responses of adults to their local environment, their 'prey corals' and with each other. The *E. sp.* A (types 1, 2, 3, 4) displayed 45% aggregation and 55% Poisson distribution. The *E. sp.* C (types 5, 6) showed a tendency to form clusters. Upon pooling the colour morphs, all zones showed aggregated distribution.

In contrast to this study, Tsuchiya and Nishihira (1984, 1985, and 1986) state that white-tipped *Echinometra* on the Okinawan reef flat in Japan possess a high tendency to form aggregations while the non-white-tipped did not. This difference might be explained by the dominance of *Porites* microatolls and *Acanthaster planci* on Nukubuco Reef. Previous studies have not mentioned the patterns of aggregation in relation to coral forms or presence of COTS (Tsuchiya and Nishihira 1985).

McClanahan (1998) reported variation in sea urchin diversity and the number of species, with increase in reef rugosity. At the highest levels of predation, however, reef rugosity would have little effect in sustaining sea urchin populations and their diversity. Hence, fishing intensity assessments would make predation intensity of fish on urchins clearer on Nukubuco Reef.

3.4.3 Size-specific behaviour

In general, *Echinometra* spp. were more engaged in burrowing, followed by feeding then scouring activity. The small (1-39mm) and medium (40-60mm) urchins preferred a combination of burrowing and feeding. The large (61-110mm) ones were rarely seen burrowing. Both crests and flats revealed a similar picture. The dominance of burrowing behaviour may be explained by Forster's (1959) and Kelso's (1970) suggestion that ingestion of detrital algae washed into burrows is the main feeding strategy of *Echinometra*. It is conceivable that this feeding behaviour may have been misinterpreted as a burrowing response as the urchins would tend to stay welded to their burrows, not changing their positions and feeding on detrital algae.

Small urchins (1-39mm) dominated the crest and showed highest intensity of burrowing. Medium size-classes (40-60mm) participated in all three activities, while the large ones (61-110mm) were absent from both crests. It can be suggested that the prime intention of juvenile urchins is to feed, grow, achieve

reproductive success and establish a protected refuge. This is reflected by the increased intensity of feeding and burrowing by small and medium sized urchins. On the other hand, the large urchins may mostly be concerned about reproductive success and daily food requirements as they are mostly observed scouring in their well-protected burrows.

All size categories of urchins existed on both flats and demonstrated all behavioural reponses. The flats comprise of a bigger area as compared with the crests hence would have a high variability in substrata and topographic complexity. This increases options for micro-spatial preferences of *Echinometra* spp. (Russo 1980). Moreover, the flats provide ample opportunities for feeding, either using grazing or detrital mode and huge coral rock structures are available for burrowing and escaping predation. Since coral rock presents an 'easy-to work-with' substratum compared with live coral, burrowing activity should have been dominant on the flats than crests. A simulated recruitment study on different *Echinometra* size classes would reveal a more comprehensive picture.

3.4.4 Urchin Density in relation to substrata coverage

Abundant populations of *Echinometra* spp. were found on coral rocks rather than live corals. Benthic epi- and endolithic algae are a major source of food for *E. mathaei* (Odum and Odum 1955) and unlike live coral, coral rock usually has high turf algae cover. Also, coral rock is unresponsive while live coral is defensive and impedes 'easy' colonization by *Echinometra* spp. Unlike live coral, the brittle framework of coral rock allows easier burrowing by urchins. Thus, the flats demonstrated higher numbers of *Echinometra* spp. compared with crests. More so, surf intensity at the crest can easily dislodge the 'homeless' urchins, which are homeless (no crevices), while the flats experience calmer conditions appropriate for cryptic urchins (Ebert 1983). Furthermore, the complex reef rugosity at the flats offers greater niche opportunities for urchins (McClanahan 1998).

Echinometra spp. abundance on Nukubuco reef is associated with vast colonies of submassive and massive *Porites* and sparse colonies of *Montipora* and *Acropora*. McClanahan and Mutere (1994) suggested that coral cover, species richness and diversity are negatively associated with sea urchin abundance to the point where *Porites* compose >90% of the coral cover at the sites of sea urchin dominance. This study supported their findings where a strong association between *Echinometra* abundance and *Porites* assemblage was found on the Nukubuco Reef. McClanahan and Mutere (1994) gave two general explanations: (1) sea urchins directly affect abundance, size and species composition of corals through their feeding and spine abrasion activities (Sammarco 1980, 1982; Carpenter 1981; McClanahan and Shafir 1990), and/or (2) environmental or human impacts simultaneously affect both sea urchins and hard corals.

McClanahan *et al.* (1996) stated that the effects of sea urchins on coral abundance and diversity could be more indirect and complicated. Field and computer simulation studies indicate that reefs dominated by sea urchins can maintain coral cover by reducing the abundance of algae that potentially compete with coral for light and space (Sammarco 1982; Hughes *et al.* 1987; Carpenter 1990; McClanahan 1995b). On the other hand, sea urchin grazing, which is more intense than fish grazing (Birkeland 1989; McClanahan 1992), can damage corals and reduce their recruitment (Bak 1994; Sammarco 1980; McClanahan and Mutere 1994). Hence, the higher numbers of *Echinometra* spp. on coral coverage imply the potential harm they can cause to the longevity of Nukubuco Reef.

CHAPTER 4

COMPARISON OF GUT, CAGE AND EXTRAPOLATION METHODS OF BIOEROSION ASSESSMENT

4.1 Introduction

Ecological processes control the community structure of ecosystems (Carpenter 1988; Duggins *et al.* 1989). Hard corals typically deposit >90% of a coral reef's calcium carbonate (Scoffin *et al.* 1980; Borowitzka 1983; Chalker 1983). This calcium carbonate deposition is the basis of the reef's complex topographic structure (McClanahan and Shafir 1990), which provides shelter and substratum for many coral reef-associated species (Bell and Galzin 1984; McClanahan 1995a). Consequently, impacts on the hard coral assemblage can affect many aspects of a coral reef's ecology.

Bioerosion is a major factor influencing reef construction and morphology. The structure and form of ancient and modern coral reefs is the result of the interaction between reef growth and reef destruction (Hutchings 1986). Reef growth has received much attention, particularly in terms of physical characteristics and patterns of coral zonation. Reef destruction by comparison has received scant attention yet boulder tracts, eroded reef flats and sediments are visible reminders that destructive processes are continually operative and substantially affect reef growth (Davies, 1983). Estimates of rates of destruction are therefore fundamental parameters in understanding overall growth.

High-density populations (12-100 urchins/m^2) of *Echinometra* spp. have been implicated in reef damage at various locations: Panama (Glynn 1988), Okinawa (Keesing 1992), Hawaii (Russo 1980), Kuwait (Downing and El-Zahr 1987), Virgin Islands (Ogden 1977), Barbados (McLean 1967) Bermuda (Hunt 1969), Enewetak (Russo 1977, 1980) and Kenya (McClanahan and Muthiga 1988). On

most other reefs, *Echinometra* occur in low to medium densities (0-12 urchins/m^2) (Ogden 1977; Russo 1980) depending upon the abundance of its predators and competitors (McClanahan and Shafir 1990).

Sea urchins are the coral reef's major substratum eroders (Hutchings 1986; Birkeland 1989) and calcium carbonate balance of coral reefs may therefore reflect the abundance of sea urchins. The omnivorous urchins, *Echinometra* spp. are known as "rock-borers" and agents of large-scale bioerosion, particularly in the Caribbean, Eastern Pacific (Hutchings 1986) and Western Indian Ocean (Conand *et al.* 1997). They burrow into coral rocks for protection from predators (McClanahan 1995b), excessive wave and current action, and to some extent against desiccation at low tide (Otter 1932). Burrows of echinoids are thimble-shaped and circular in diameter, though varying in depth (Otter 1932).

Echinometra burrow exclusively into coral rocks using a screw-like rotatory motion using both the spines and teeth. Once the burrow has been modified for inhabitation, the oral spines perform deepening (Otter 1932). Cases of complete fresh burrows are rare as boring enlarges a pre-existing burrow on the growth of the animal. *Echinometra* creates its own burrow through feeding and spine abrasion and burrows often appear to fit individual requirements avoiding competitive displacement (McClanahan 1988).

Echinoids do not feed on the bored rocks (Hesse 1867; John 1889). Instead they graze on live or dead coral substratum, encrusting coralline algae, tufted or filamentous algae growing on hard reef substrata in search of food. They rasp off the $CaCO_3$ in the process of grazing, however, in some cases algae may be grazed without the loss of $CaCO_3$. Burrow inhabitants seem to remain sedentary as long as food supply is sufficient (Kelso 1970; Russo 1977) and they feed by filtering drift algae at the mouth of burrows.

The interaction of grazing and boring is fundamental in determining the rate of destruction of reef surface (Kiene and Hutchings 1992). Borers create a porous structure in the periphery of substratum that may facilitate the erosion due to grazing. Extensive work has been done highlighting the variability in rates of bioerosion both over space and time (Hutchings 1986; Kiene 1985, 1988).

Two methods have been used to study bioerosion rates by sea urchins: analysis of gut contents and field experiments. Gut analysis studies, specific to urchins from the wild, have been conducted using a number of methods to evaluate bioerosion. These include: subtracting refractory organic matter from the ashed weight (Conand *et al.* 1997), early morning gut content taken as equivalent of daily consumption (Russo 1980; Bak 1990, 1994; Conand *et al.* 1997), and gut filling and evacuation rates (Downing and El-Zahr 1987). Gut analysis method is a good indicator of preferred food items of urchins.

An assessment of the state of reef development may be made not through an assessment of live coral dynamics but through an experimental evaluation of net carbonate changes via experimental carbonate slabs (Hibino and Woesik 2000). Coral reefs in 1997 supported on average only 33% live coral cover (Hodgson 1999) with the majority of the reef being carbonate and unconsolidated sediment. Field experiments have been carried out to determine carbonate substrata erosion by grazers and borers (Bak 1990, 1994; Kiene and Hutchings 1992; Conand *et al.* 1997). This method allows assessment of bioerosion specific to urchins, demonstrates variability of bioerosion on the reef as well as shows the importance of the echinoid activity in modifying dead coral substratum. However, limitations of each method are inevitable.

Documentation of the severe consequences of high-density populations of sea urchins has altered the thought that sea urchins can maintain coral cover by reducing abundance of algae that potentially compete with coral for light and space (Sammarco 1982; Hughes *et al.*, 1987; Carpenter 1990; McClanahan

1995b). Rather, the more intense grazing of urchins compared with fish (Birkeland 1989; McClanahan 1992) can damage corals and reduce coral recruitment (Bak 1994; Sammarco 1980; McClanahan and Mutere 1994). In extreme cases they can change the reef complexity from urchin-dominated to a coral-barren-sand-dominated locale (McClanahan 1988).

At lower densities, sea urchins have bioerosion rates at least an order of magnitude greater than those of finfish grazers such as parrotfish (Birkeland 1989). Consequently, *Echinometra* potentially still affects the carbonate budget of coral reef communities even at lower densities (Ogden 1977; Russo 1977, 1980; Conand *et al.* 1997).

To know how the erosion-accretion balance changes in reef environments as they evolve is fundamental to understanding the ultimate contribution of reef frameworks to reef growth. This study addresses the rates of bioerosion and bioaccretion from gut analysis and cage experiments. It also compares the erosion rates from a new method, extrapolated bioerosion, with the other two conventional methods at different locations on the Nukubuco Reef. It will also report on "low-density-urchin-impact" which will serve as a basis for identifying chronic consequences of *Echinometra* on Nukubuco Reef.

The following questions need to be addressed to fulfil the aims of this study:

1. Gut analysis

Does $CaCO_3$ consumption rate change with an increase in *Echinometra* test diameter?

The answer to this question will enable prediction of $CaCO_3$ in the gut of urchins of any size. It will also report on and allow comparison of bioerosion rates on Nukubuco Reef by *Echinometra* spp. using the gut analysis method.

2. **Cage experiments**

Do bioerosion rates exceed rates of bioaccretion between reef habitats of Nukubuco?

The answer to this question will indicate if the low but consistent densities of *Echinometra* spp. are a threat to Nukubuco Reef. It will also allow comparison of the bioerosion rates with the gut analysis, extrapolation method and other reefs of the world.

3. **Extrapolation bioerosion**

Are the rates of bioerosion from extrapolated method different from gut and cage methods and more representative of the *Echinometra* population?

The answer to this question will show how beneficial or flawed this new method of bioerosion assessment is in comparison to gut analysis and cage experiments. It will also allow deduction of exact bioerosion caused by a population of urchins on separate environments of Nukubuco Reef.

4.2 Methodology

4.2.1 Gut analyses

This experiment was performed to allow quantification of $CaCO_3$ erosion on Nukubuco Reef, not specific to habitats but zones. This method reported bioerosion rates by the conventional gut analyses, specific to urchins (Russo 1980; Bak 1990, 1994; Conand *et al.* 1997).

Fifty urchins (25 from the reef-flat and 25 from the reef crest) of *Echinometra sp.* A - mainly green-white-tipped were brought into the laboratory (17/05-18/05) during the early morning (7.00 am) and dissected for gut analyses. Though Palumbi (1996a) had classified *E. sp.* A (white-tipped) and C (non-white-tipped) in Fiji, *E. sp.* A with mainly the green-white-tipped were collected due to their dominance on the reef.

Standing at the different zones and throwing a stone achieved randomization. Each time the stone fell near a white-tipped urchin, it was picked. This was done a number of times at each zone on the eastern Nukubuco Reef. The east was sampled because urchins were more readily available here than in the west.

The urchins were collected early in the morning to consider their full gut content as a measure of their daily consumption (the assumption being that they feed during the night and that the gut is emptied during the day; Ogden 1977; Russo 1980; Bak 1990, 1994). Downing and El-Zahr (1987) have proved via experiments that gut-filling rates equal gut evacuation rates.

Initially, test diameter was measured using a vernier caliper. Each step was photographed to record observations.

distilled water and returned for drying in the oven (Plate 4.4: Step 4) for 12-15 hours. After cooling in a desiccator, a second constant weight (Plate 4.5: Step 5) was taken (W_1) and the weight difference was calculated to find the amount of calcium carbonate present in the gut of *Echinometra* spp. (refer to Appendix 4 for further details on gut analysis data).

Treatment corrections were carried out on the recorded mass taken to account for a 2% loss in weight in the filter paper during drying and a 2.6% loss on treatment with HCl. These corrections were made in accordance with the analysis carried out by Downing and El-Zahr (1987).

Identification of algae in the gut content and later on the experimental slabs of cage experiments followed standard phycological procedures (Tsuda and Abbott 1985). Larger specimens (>5mm) were identified under an Olympus S7-PT stereomicroscope. Specimens <5mm were mounted on slides after staining with 1% acidified aniline blue and mounted in 60% corn syrup. Then these were identified using an Olympus BH2 photomicroscope. Phycological references from Professor Robin South's library were used to aid in species identification. Every effort was made to identify algal specimen to species level but since reproductive stages were often difficult to ascertain, identification could only be done to generic level.

This activity enabled identification of gut content. It gave a fair estimate of the $CaCO_3$ content in the gut of urchins from reef crest and reef flat. Scatter plots demonstrated the correlation patterns between test diameter of urchins and the respective $CaCO_3$ content in their gut.

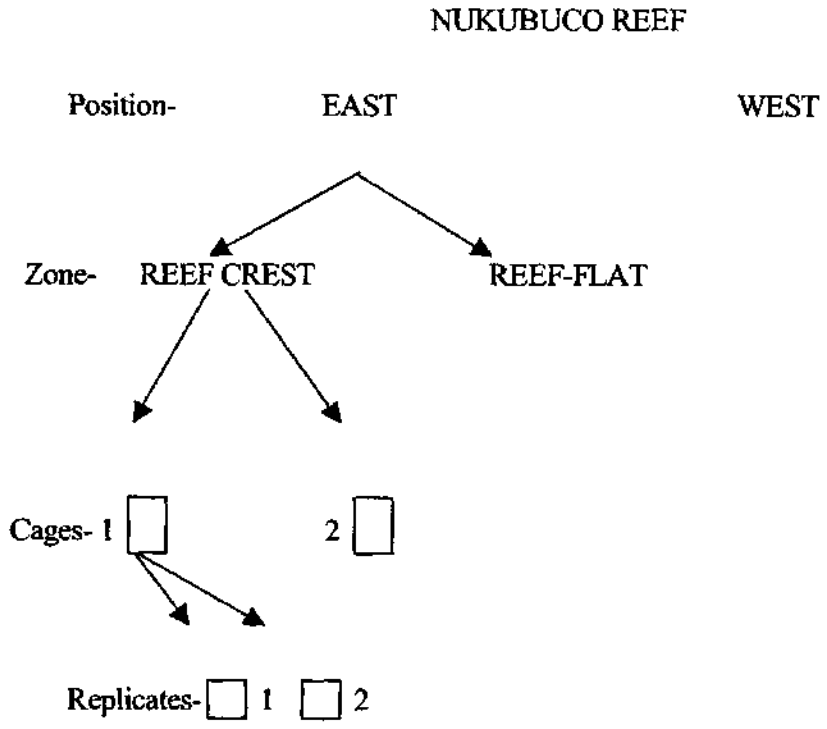
4.2.2 Cage experimental design

The experiment was conducted from May to October 2000. A two-factor sampling design was used (Figure 4.1: sample design). The factors were:

1. Position. Two positions were compared: the east (near Nukulau and Makuluva Islands) and the west (near Nukubuco Passage) of Nukubuco reef (Figure 2.2-2.3). The sample cages were placed in positions in the vicinity of those in the population study of *Echinometra* spp. (Chapter 3). The eastern and western positions were adopted to monitor if the difference in environments had any effect on the grazing effect of urchins in cages.

2. Zone. Each position was divided into reef crest and reef flat (Figure 2.3). The study attempted to unveil differences in the way urchins' bioeroded the different zones. Flats were wider in area, greater in rugosity, comprised mostly of coral rock and calmer environments. Reef crests, on the other hand was narrower, had lower rugosity, mostly had live coral colonies and experienced high-energy environment.

Figure 4.1 Sampling design for the cage-experiment



The cage experiments were performed to enable quantification of bioerosion rates that resulted from the eroding processes of *Echinometra sp.* A on different habitats of Nukubuco Reef. This method reported bioerosion rates using experimental substrata, specific to grazers and borers (Kiene 1985, 1988; Kiene and Hutchings 1992).

To avoid destructive coral harvesting on Nukubuco Reef the coral rock, *Porites lutea,* were bought from those already harvested by the Suvavou villagers from the adjacent Suva Reef and cut into standard sizes (0.1m x0.1m x 0.01m) at the Mineral Resources Department using a core-cutter mounted in a drill press. Any blocks with signs of boring were discarded. The slabs were soaked in freshwater for an hour to remove salt, dried to constant weight and measured. A hole drilled through the center of the blocks allowed them to be attached to the cage by a screw. A galvanized washer was placed under the top screw to protect a small area from erosion and provide a reference as to the original upper surface of the slab (modified from Kiene and Hutchings 1992).

Eight urchin cages were used in total where both cages and slabs were replicated. Each cage was 6-sided and had dimensions 0.2m x 0.1m x 0.1m. The cage was made of galvanized mesh grid with only the top end able to be opened. Initially, a mesh grid size of 2 square inches was used. Later this was changed to 0.01m x 0.01m mesh size due to the fact that urchins escaped through the other size by lowering their spines as they went through the mesh. A partition in the middle of the cage prevented the interaction of urchins from the two replicate slabs (Plate 4.6, 4.7). At each zone, there were 2 cages and in each cage there were 2 slabs and for each slab 1 urchin was introduced. The cages allocated for the crest were actually screwed 100m from the upper crest limit as the high wave intensity would have made sampling difficult and the cages may not have lasted three months. The bottom of the cage had couch screws tapped perpendicular to the cage onto which the coral slabs were bolted. All the construction elements of the cage were coated with red rust guard and then white marine paint to prevent rust

and ensure longevity of the cages. Positions of cages were recorded by using the Lowrance GPS portable meter (refer to Appendix 5 for further details).

The experimental slabs were initially left at the experimental sites for a month to allow infestation of turf-algae before introducing urchins. Urchins' Aristotle's lantern was measured using vernier calipers before placing in the cages (Table 4.1). These cages were placed in the field from 03/08/00 – 16/09/00 for the first set of slabs and 16/09/00 to 30/10/00 for the second set.

Table 4.1 Aristotle's lantern diameter

Zone	Cage	Slab # / Replicate #	Aristotle's lantern diameter (mm)
East crest	1	5 / 1	35
		6 / 2	39
	2	7 / 1	42
		8 / 2	40
West crest	1	13 / 1	42
		15 / 2	40
	2	14 / 1	38
		16 / 2	39
East flat	1	1 /1	37
		4 / 2	39
	2	2 / 1	41
		3 / 2	37
West flat	1	10 / 1	41
		12 / 2	37
	2	9 / 1	41
		11 / 2	39

Cages were colour coded using tags to help in identification. Colour coding was as follows: East crest - red, east flat - green, west crest - yellow and west flat - blue. Since there were two sets of replicates, each slab was tagged to distinguish between set 1 and set 2. Small white tags identified slab 1 and large white tag identified slab 2. One replicate from each cage was brought in after 6 weeks starting from the date of urchin placement, for observations, treatment and analyses.

4.2.2.1 Slab treatment after exposure

Samples were thawed for half an hour (Plate 4.8). All observations were done under a binocular microscope. Samples were bleached using 30ml of household bleach detergent (Janola) and all accretions removed by gentle motion of a toothbrush. All surfaces were washed with distilled water and slabs were then placed in an oven at 60^0C for 48 hours (Plate 4.9). After cooling the slabs were placed in a desiccator and constant weights by difference were recorded.

4.2.2.2 Point-count analysis

Tests were performed for image analysis using Labworks Image Analysis software. The test slab was treated with $3mgl^{-1}$ Alzarin Red S dye to extenuate the cavities made by urchin activity. However, equal staining of the slab obscured details. This prevented usage of the software package since the original view (whole slab) maximized on screen lacked sufficient resolution to highlight the cavities. Also, setting up the right contrast and texture for each square on a slab took excessive time. Fortunately, point-counting using a binocular dissecting microscope was sufficient in terms of time and effort.

The point count analysis was carried out on the second set of slabs, as the first set had not shown sufficient urchin activity for the analysis. The assumption was that urchins grazed randomly.

Each (0.1m x 0.1m x 0.01m) slab was divided into 25 equal squares and numbered using a pencil. The division helped in assessing the slab in detail without missing a profile or repeating it. Looking through a dissecting microscope at magnification 6.7X assessed grazing scars of each square. A transparent grid was overlaid on the slab and the number of points hitting the grazed scar divided by the total number of reference points (361) gave an area fraction percentage. A tally counter was used for counting (refer to Appendix 6 for further details on slab results).

The Aristotle's lantern sizes (Table 4.1) were used to categorize the cavities observed into grazed scars by experimental urchins. Bioerosion only due to grazing activity of urchins was assessed as other boring organisms such as sponges, sipunculids and polychaetes could have made the bored holes as well. The percentage of substratum removed was assumed to be due to urchin activity alone;

i.e. (% grazed) original weight = weight of eroded substratum

4.2.3 Bioaccretion

Samples were observed under a dissecting microscope and all organisms noted before carrying out erosion analysis. Bioaccretion rates were calculated using erosion rates from the point count analysis. The weight of erosion subtracted from the original dry weight of the slab gives a value x, which when subtracted from the dry weight of the slab after collection gives the weight of accretion (Kiene 1988).

i.e. Original dry weight of the slab – the weight of erosion = x
Dry weight of the slab after collection from reef – x = weight of accretion.

4.2.4 Erosion-accretion balance

Rates of bioerosion and bioaccretion were calculated by averaging the slab calcium carbonate eroded / slab encrustation on each of the two replicates at each location divided by 3 months or 92days. These data were compared between habitats (position x zone x sites) using a two-way ANOVA. The net carbonate accumulation was evaluated by subtracting the accretion rates from erosion rates.

4.2.5 Extrapolated bioerosion

This method reported bioerosion rates using extrapolation. It is the third and novel method that this study has used to report on bioerosion rates on Nukubuco Reef. It also allows for comparisons with the other two methods of assessing bioerosion.

Abundance data from the population studies (Chapter 3) and $CaCO_3$ consumption rates from gut analysis were used to extrapolate bioerosion rates for the total number of urchins from different sizes in each habitat. Since the gut analyses was

performed on *Echinometra sp.* A, the assumption is that the extrapolated bioerosion rates are more representative of the dominant species, *E. sp.* A on Nukubuco Reef and not both species although the population study abundance data comprised of both *E. sp.* A and C. These rates allowed comparison of bioerosion in the natural system in contrast to the cage system.

4.3 Results

4.3.1 Gut analyses

Initial observation of the gut contents was a messy blotch of masticated algae and sandy grains. The acid treatment digested the $CaCO_3$ grains and the algae were identified (Table 4.2).

Table 4.2 Algae in the guts of *Echinometra sp.* A

ALGAE Genus (description)
Polyphysa (umbrella)
Hypnea (red)
Chlorodesmis (turf)
Hormothamnion (green hair-like)
Hildenbrandia (red/pink encrust)-non- calcified
Lithothamnion (calcified)

Other interesting observations were colourful tinsels on the filter paper after the first drying. The colours: yellow, orange and green were noted in the vials during preservation. This may be a result of dissolution since shades of these colours were observed on the urchin spines.

The urchin results were specific to the dominant species, *Echinometra sp.* A. and not *E. sp.* C. Hence, results are conclusive for *E. sp.* A only (refer to Appendix 4 (a) for further details on gut analysis).

Regression analysis was performed using linear, power and exponential functions to obtain the best function that fit the trends of the raw data. Linear function appeared most significant for the crest data (Table 4.3a) $p<0.01$ and had a high r^2 value = 0.419. The power and exponential functions gave significant results as well (P = 0.005 and 0.004) but lower r^2 values = 0.269 and 0.292, respectively (Refer to Appendix 4 (b) for further details on regression analysis). Hence, the crest data showed a linear correlation between $CaCO_3$ consumption and urchin

test diameter. The flat data fitted well as a power function (Table 4.3b) with high significance P = 0.006 and r^2 = 0.253. Linear analysis showed no significance (P = 0.076) for the flat data while the exponential function showed P = 0.016 and r^2 = 0.202. Thus, the urchins on the flat ate more with an increase in size and volume. An analysis on the pooled data demonstrated power function as the best fit (P<0.01, r^2 = 0.287) (Table 4.3c) compared to exponential and linear functions which were significant (P<0.01) but had lower or same r^2 = 0.257 (refer to Appendix 4 (b) for further details on regression analysis).

Table 4.3 Regression analysis of variance for $CaCO_3$ consumption (g) vs test diameter on the (a) reef crest, (b) reef flat and (c) pooled data

(a)

Model		SS	df	MS	F	Sig
1	Regression	0.443	1	0.443	18.296	0.000
	Residual	0.557	23	0.02421		
	Total	1.000	24			

(b)

Model		SS	df	MS	F	Sig
1	Regression	5.288	1	5.288	9.119	0.006
	Residual	13.337	23	0.580		
	Total	18.624	24			

(c)

Model		SS	df	MS	F	Sig
1	Regression	7.977	1	7.977	20.752	0.000
	Residual	18.452	48	0.384		
	Total	26.430	49			

The crest (Figure 4.2) had urchin sizes specifically from 30-50mm, which reflects the sizes available at the crest. The flats (Figure 4.3) on the other hand displayed urchins ≥20mm and <80mm. Smaller urchins were too cryptic to be taken out and very large urchins were not encountered in the random sampling. Scatterplots for

crest and flat (Figure 4.2 and 4.3) showed different patterns while the pooled data (Figure 4.4) showed a similar trend to the flat.

The crest demonstrated a linear correlation between $CaCO_3$ consumption and test diameter for *Echinometra* spp. Using equation $y = 0.0187x - 0.532$, bioerosion rates on the reef crest (Figure 4.2) was reported to be 0.39×10^{-3} kg $CaCO_3$ /urchin/d for mean urchin size 41.9mm. The flat reported lower bioerosion rates, 0.20×10^{-3} kg $CaCO_3$ /urchin/d for mean urchin size 40.6mm using $y = 0.0000726x^{2.142}$. This difference is due to different functions allocated for the crest and flat. More data would have presumably masked the effect of difference in bioerosion rates resulting from usage of different functions.

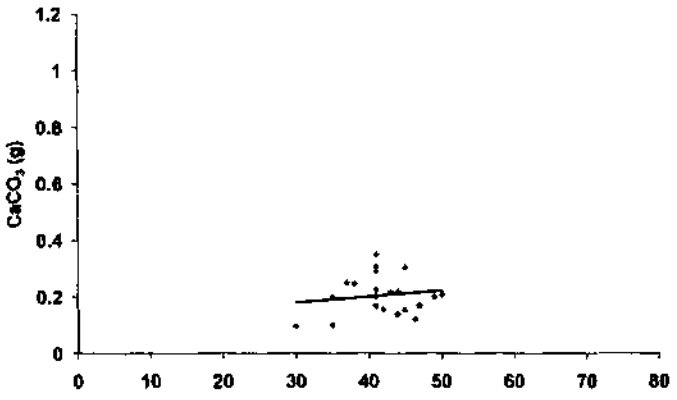


Figure 4.2 Size-specific $CaCO_3$ consumption rates for *E. sp.* A on the reef crest of Nukubuco. Labels on the x-axis are the upper limit of each test diameter size (Total N = 25).
$y = 0.0187x - 0.532$
$p < 0.01$
$r^2 = 0.419$

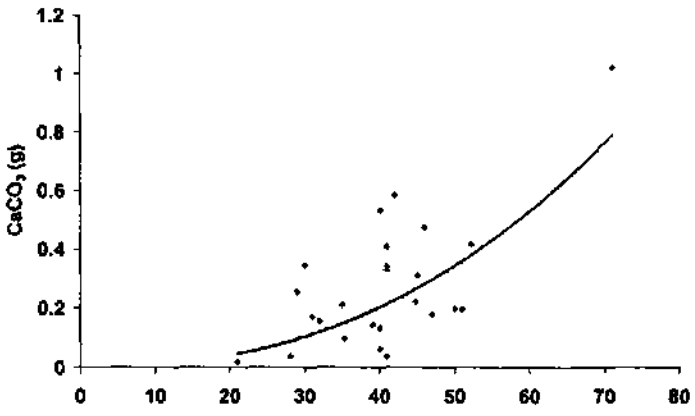


Figure 4.3 Size-specific $CaCO_3$ consumption rates for *E. sp.* A on the reef flat of Nukubuco. (Total N = 25).
$y = 0.0000726x^{2.142}$
$p = 0.006$
$r^2 = 0.253$

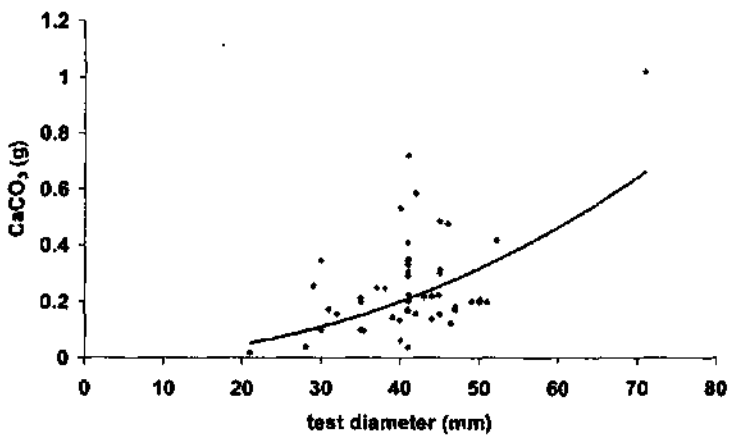


Figure 4.4 Size-specific $CaCO_3$ consumption rates for *E. sp.* A on Nukubuco Reef. (Total N = 50).
$y = 0.0000838x^{2.107}$
$p < 0.01$
$r^2 = 0.287$

4.3.2 Cage experiments

The first set of slabs after six weeks showed insufficient urchin activity for point-count procedures and erosion analysis hence, the second set (after 12 weeks) was used to deduce the bioactivity rates. The grazed scars from urchins were identified using the Aristotle lantern sizes (Table 4.1). These rates were specific to white-tipped or *Echinometra sp.* A.

Bioaccretion and bioerosion rates of replicate slabs (Figure 4.5) show similar trends i.e. with an increase/decrease in replicate 1 of both bioactivities, replicate 2 also increases/decreases in value. However, the eastern flat recorded an exceptionally higher replicate 1 reading compared with replicate 2. Bioerosion rates exceeded bioaccretion rates (Figure 4.6). The mean rates of bioerosion and bioaccretion show similar trends in all habitats. The highest mean bioactivity rate was recorded for the eastern flat as 43 x 10^{-3} kg $CaCO_3$ /m^2/urchin/day (urchin size = 38mm). Then eastern crest recorded 35 x 10^{-3} kg $CaCO_3$ /m^2/urchin/day (urchin size = 37mm). The western flat recorded the lowest rate of 30 x 10^{-3} kg $CaCO_3$ /m^2/urchin/day (urchin size = 39mm) while the western crest rate was 37 x 10^{-3} kg $CaCO_3$ /m^2/urchin/day (urchin size = 41mm). The bioaccretion rates were (40, 34, 29 and 36) x 10^{-3} kg $CaCO_3$ /m^2/d, respectively. The differences in urchin sizes did not seem to cause a difference in the rate of grazing since a mixed response was observed. However, the grazing activity seemed to be habitat specific where the eastern flat especially showed high bioactivity rates. Slabs from the eastern flat showed higher bioactivity rates than western flat. The 2-factor ANOVA (Table 4.4) confirms that no significant difference exists between positions (P = 0.619), zones (P = 0.946) and position x zone (P = 0.487).

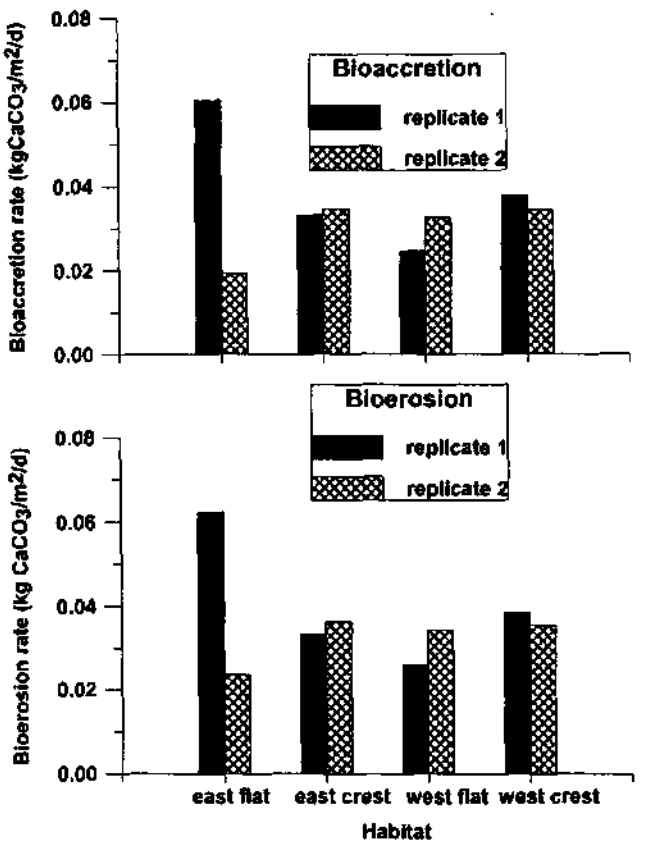


Figure 4.5 Replicates of bioaccretion and bioerosion rates for *E. sp.* A on Nukubuco Reef.

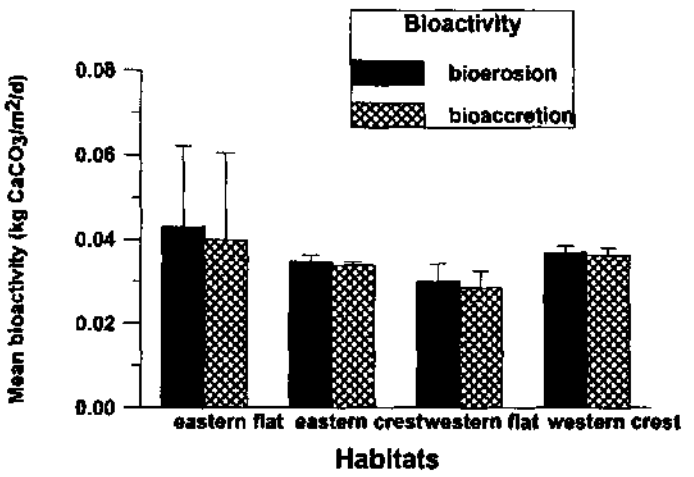


Figure 4.6 Mean rates of bioaccretion and bioerosion for *E. sp.* A on Nukubuco Reef. Vertical bars represent standard error.

Table 4.4 Two-factor, analysis of variance on *Echinometra. sp.* A mean bioerosion rates on different habitats of Nukubuco Reef. (Refer to Appendix 6 (a) for further details on bioerosion data and Appendix 7 for bioerosion analysis)

Source	df	SS	MS	F	P
Position	1	0.0000577	0.00005778	0.290	0.619
Zone	1	0.000001051	0.000001051	0.005	0.946
Position x Zone	1	0.0001163	0.0001163	0.584	0.487
Error	4	0.0007967	0.0001992		

4.3.3 Bioaccretion

Encrusting coralline algae (Table 4.5) were similar to those found in the urchin gut analysis (Table 4.1). These encrustations were on the sides and underneath the slabs. Slabs from the crest however, showed some coralline algae on the top surfaces. It is logical not to have found them on top surface as *Echinometra* graze on them. The encrusting animals were quite small and were also found on the same surfaces as the algae. These animals may have also been in the gut content but in calcareous sediment form.

Table 4.5 Encrusting organisms

ANIMAL	ALGAE Genus (description)
Univalves	Polyphysa (umbrella)
Sea stars	Hypnea (red)
Sea snail spores	Chlorodesmis (turf)
Polychaetes	Hormothamnion (green hair-like)
	Hildenbrandia (red/pink encrust)-non- calcified
	Lithothamnion (calcified)

The two-factor ANOVA on the bioaccretion rates (Table 4.6) also showed no significant difference between positions (P = 0.684), zones (P = 0.943) and position x zone (P = 0.556).

Table 4.6 Two-factor, analysis of variance on mean bioaccretion rates on different habitats of Nukubuco Reef. (Refer to Appendix 8 for further details on bioaccretion analysis)

Source	df	SS	MS	F	P
Position	1	0.00004232	0.00004232	0.192	0.684
Zone	1	0.00000128	0.000001280	0.006	0.943
Position x Zone	1	0.00009113	0.00009113	0.412	0.556
Error	4	0.0008837	0.0002209		

4.3.4 Erosion-accretion balance

The balance between the rates of bioerosion and bioaccretion is an important indication of the impact these processes have on the slab samples and the general Nukubuco Reef. Figure 4.7 shows this balance where the average rates of bioerosion were subtracted from average accretion rates to give an erosion-accretion balance (refer to Appendix 9 for further details on net accumulation analysis). There is no net bioaccretion on Nukubuco Reef. Net destruction is more prominent on the eastern flat followed by the western flat while both the crests show equal rates of net accumulation.

The erosion-accretion balance shows a similar pattern of urchin activity to the population study (Chapter 3) where *Echinometra* spp. dominated the flats compared to the crests hence higher net erosion was observed on the flats than the crests.

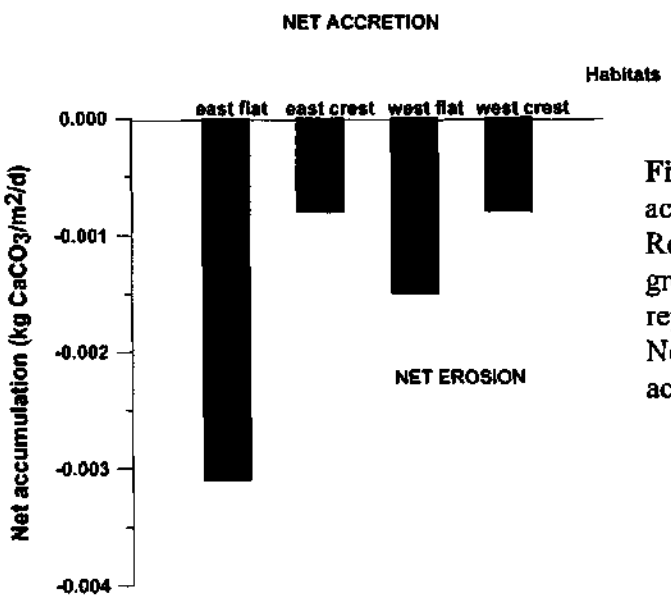


Figure 4.7 Net carbonate accumulations on Nukubuco Reef. Accretion represents growth and erosion represents destruction. Net accumulation = erosion-accretion balance.

4.3.5 Extrapolated bioerosion

This is the third and novel method of assessing bioerosion, which uses extrapolation. Bioerosion rates for coral reef grazers and borers have been reported in the literature based on gut analyses of urchins (Russo 1980; Downing and El-Zahr 1987; Bak 1990, 1994, Conand *et al.* 1997) and experimental coral substrata (Kiene 1985; Kiene 1988; Kiene and Hutchings 1992).

This method made use of the test diameter from population abundance data in Chapter 3 and the $CaCO_3$ consumption rates from gut analysis to deduce the rate of bioerosion from those urchins that were actually sampled on the separate habitats in the population study.

Table 4.7 Extrapolated bioerosion rates

Zones	***Echinometra* Density (no. / m^2)**	**Bioerosion rates (kg $CaCO_3/m^2/d$)**
East flat	4.08 ± 0.25	26.5×10^{-7}
West flat	2.20 ± 0.21	8.24×10^{-7}
East crest	3.25 ± 0.13	3.93×10^{-7}
West crest	1.64 ± 0.14	1.45×10^{-7}

Similar to the cage experiments, this method also showed exceptionally higher bioerosion rates for flats compared to the crests (Table 4.7). This trend is a function of urchin abundance in each habitat. The eastern flat had the highest *Echinometra* spp. density and a similar high bioerosion rate while the western crest had the least urchin density hence the least bioerosion rate. A slight discrepancy was shown for eastern crest and western flat where the density trends did not coincide with the erosion rates.

4.4 Discussion

4.4.1 Gut analyses

Despite a small population (50 urchins), this study has shown size-specific $CaCO_3$ consumption rates, which is consistent with other studies (Conand *et al.*, 1997). Though larger urchins were recorded for flat and frequent grazing activity was observed, flats (0.20×10^{-3} kg $CaCO_3$/urchin/d) demonstrated lower bioerosion rates compared with the crest (0.39×10^{-3} kg $CaCO_3$/urchin/d). It is reasonable to assume that larger urchins will eat more than smaller ones due to energy demands. However, differences may have arisen from the differences in size-classes at each zone. The crests had urchins 30-55mm while the flats had urchins ≥20mm but <80mm. Additionally, use of different functions (power and linear) to calculate bioerosion rates may have contributed to this discrepancy.

The flats offer more coral rock substratum to urchins for grazing on turf algae and burrowing and thus reflect a larger content of $CaCO_3$ in the guts of urchins from this habitat. Contrarily, the generally live coral colonies on the crest do not allow much grazing since they are more defensive compared to dead coral substratum and leaving crevices to graze could dislodge urchins by high wave action. Thus the urchins on the crest may be more adapted to feeding by filtering than grazing (McClanahan and Muthiga 2001). Downing and El-Zahr (1987) suggested that differences in erosion rates are better explained by difference in modes of feeding than difference in urchin sizes.

Moreover, the environment on the Nukubuco Reef is extremely variable in terms of anthropogenic influence on either position. The east position experiences sewage influxes and high sedimentation rates, which might cause variability in algal cover (Birkeland 1982). This may affect the pattern of feeding in *Echinometra* spp. and the ratio of $CaCO_3$ to algal content in the

gut. In contrast, the west position might have a consistent environment. Hence, the erosion rates deduced from gut analysis cannot be applied to the entire reef until further experimentation on feeding rhythms is performed.

As suggested by other workers (Downing and El-Zahr 1987; Conand *et al.*, 1997), size-distribution data allow in depth interpretation of bioerosion rates. The pooled population from the two zones gave a bioerosion rate of 0.21 x 10^{-3} kg $CaCO_3$/urchin/d for mean urchin size 41.3mm using the power equation $y = 0.0000838x^{2.107}$. The bioerosion rate calculated using gut analyses appears similar to rates reported from other studies. Downing and El-Zahr (1987) reported bioerosion rates for *Echinometra mathaei* as 0.9-1.4 x 10^{-3} $kgCaCO_3$/d (mean urchin size = 37.1mm) in Kuwait; Russo (1980) presented rates for *E. mathaei* and *E. aciculatus* as 0.1-0.2 x 10^{-3} $kgCaCO_3$/urchin/d (mean urchin size = 19.5-22mm) in the Marshall Islands; and Ogden (1977) reported rates for *E. lucunter* as 0.12 x 10^{-3} $kgCaCO_3$/urchin/d in the Caribbean.

These reported bioerosion rates from the literature account for bioerosion caused by a variety of borers and grazers such as sipunculids, molluscs, polychaetes, finfish, limpets etc., from different locations on the reef. They lay a basis for comparison only and drawing conclusions on how degraded a reef is on these rates, should be avoided. All reefs differ in developmental stage, reef status, influence of other bioeroders and anthropogenic effects.

This study on Nukubuco Reef investigated the bioerosion rates resulting from *Echinometra* spp. only and the fact that its impacted by sewage effluent, high sedimentation rates (Hinrichsen 1998) and *Acanthaster planci* outbreaks (Zann *et al.* 1990) gives it a wider comparative ground with reefs worldwide.

4.4.2 Bioerosion-bioaccretion cage experiments

The eastern flat recorded exceptionally higher bioactivity rates for replicate 1 or very low rates for replicate 2. This may be possibly due to the non-homogenous nature of the slabs since all slabs were not from one whole coral. It was impossible to have such a large coral colony to adequately cater for the required number of boreless slabs. Since details of algal cover were not known and may be the first replicate slab on eastern flat might have had the most preferred species of algae, excessive grazing might have resulted. In contrast, reduced grazing may have occurred on replicate 2 due to stress on urchins, which may have resulted from exposure or cage effects. It could be assumed that this urchin might have been in a vulnerable state.

Bioerosion rates exceeded bioaccretion rates for both replicates as well as when averaged for all habitats. Urchin size did not seem to cause a significant difference in bioactivities but habitats did. The flats showed higher erosion rates than the crests. It is possible that conditions are calmer at the flats since they do not experience the stress caused by high-energy wave action as the crests do. This stress might cause an alteration in the normal feeding cycle of urchins at the crest from grazing to filter feeding. Also, since flats get exposed more often during low tide, urchins would probably prefer grazing as opposed to filtering detritus from the water column as their principal mode of feeding.

The average bioerosion rates did not differ significantly for the different habitats, suggesting that urchins will graze at the same rate anywhere on Nukubuco Reef. This conclusion could be a function of the cage experiments where identical set-ups had to be used. An open system would have given a different result, which would not have been specific to urchins. Higher densities of *Echinometra* spp. (from population study – Chapter 3) were present on the eastern section of the reef [east flat = (4.08 ± 0.25 /m^2) and east

crest = (3.25 ± 0.13 /m^2) compared to the western section [west flat = (2.20 ± 0.21 /$m^2$and west crest = (1.64 ± 0.14 /m^2)] and would have reflected similar trends of bioerosion rates as to their densities. The flats also showed higher bioerosion rates than the crests. One can speculate that the east may have flourishing conditions for urchins when compared with the west. Alternatively, a low sample size may be the reason for the lack of statistical significance in much of the analyses of these data. Perhaps, an increase in the time frame of the experiment would provide a higher sample size and more discrete conclusions.

A study similar (Hibino and Woesik 2000) to this study was done on Ryukyu Islands, Japan where seasonal changes of net carbonate accumulation were investigated by using carbonate blocks, which were exposed to urchin activity for 3 months. They found higher bioerosion rates from *Echinometra mathaei* type A on softer *Porites* than hard *Acropora* and Pleistocene tiles hence they interpreted that reef erosion rates vary in accordance with not only the community that currently inhabits the reef but also the age of the substratum.

In the natural, non-cage system, the flats would show more erosion due to higher availability of coral rock structures to erode during grazing and burrowing activities. A higher number of cryptic urchins was frequently observed on the dead heads of *Porites* burrowed in small crevices. The crests however, do not have such brittle substrata to work upon. Nonetheless, bioaccretion in the wild would occur as carbonate infilling of vacated borings and growth of encrusting organisms (Kiene 1988) in patterns specific to the rugosity of reef structure.

Nukubuco Reef reports separate bioerosion rates from the cage experiments (Results 4.3.2) for different habitats in the cage experiments. Eastern flat reported the highest, 43 x 10^{-3} $kgCaCO_3/m^2/d$ followed by the western crest 37 x 10^{-3} $kgCaCO_3/m^2/d$, then the eastern crest 35 x 10^{-3} $kgCaCO_3/m^2/d$ and

least the western flat 30 x 10^{-3} kg$CaCO_3/m^2/d$. Thus, the cage experiments reports higher bioerosion rates compared with the gut analysis. The area factor considered in the cage experiments as opposed to the gut analysis may be the reason for this difference.

Despite using different methods of assessing bioerosion, Conand *et al.* (1997) report bioerosion rates similar to those obtained in this study; reef slope = 22.8 x 10^{-3} kg$CaCO_3/m^2/d$; reef flat = 7.8 x 10^{-3} kg$CaCO_3/m^2/d$ and overall calcification rates 8.3 kg$CaCO_3/m^2/d$. Conand *et al.* (1997) used gut analysis while this study used experimental coral substratum. In contrast, she reported higher bioerosion rates on the crests than the flats which could be due to the fact that at Reunion Island, *Echinometra mathaei* density is higher at the crest (45 m^{-2}) compared with the flat (19 m^{-2}). Thus, gut analysis and cage experiments methods could be reliable in reporting bioerosion rates. The calcification rates in Conand *et al.* (1997) study appeared extremely high. This could have resulted from the use of a very precise flow respirometry and alkalinity anomaly technique (Smith and Kinsey 1978). Absence of such a facility restricted the use of the method in this study.

For comparison, *Echinometra* bioerosion accounts for 3.8 kg$CaCO_3/m^2/d$ (14.2 urchins /m^2 on the inner reef and 1.7 urchins /m^2 on the outer reef) in Kenya (McClanahan and Muthiga 1988), 3.9 kg$CaCO_3/m^2/d$ (9-100 urchins /m^2) in the Virgin Islands (Ogden 1977) and 0.4 kg$CaCO_3/m^2/d$ (7.4 urchins /m^2) in French Polynesia (Le Campion-Alsumard 1993). Hence, in comparison to other studies, Conand *et al.* (1997) and this study report lower bioerosion rates. This may be due to similar densities of urchins encountered in the study. Conand *et al.* (1997) reported 3-4 urchins /m^2 in some of her transects while this study reported 2 - 4 urchins /m^2. The study on Ryukyu Islands, Japan, which was very similar to this study because of the 3 month duration, carbonate blocks and *E. mathaei* type A being used reported quite low mean net carbonate change of -1.92 – 1.92 x 10^{-3} kg $CaCO_3/m^2/d$ for an

average density of 10 urchin/m^2. This may be a function of a short-term study or the fact that the Islands support a population of 1.3 million people and human activity, which may be having an influence on the net reef growth in the Ryukyu Islands (Hibino and Woesik 2000).

This study reported bioaccretion rates for different habitats; eastern flat 40 x 10^{-3} $kgCaCO_3$ /m^2/d, western flat 29 x 10^{-3} $kgCaCO_3$ /m^2/d, eastern crest 34 x 10^{-3} $kgCaCO_3$ /m^2/d and western crest 36 x 10^{-3} $kgCaCO_3$ /m^2/d. Bioaccretion rates followed a similar trend to bioerosion rates for the different habitats. Though bioaccretion rates appeared less than those of bioerosion, it is important to note that the cages were closed systems and seasonality patterns exist in recruitment rates of encrusting organisms such as bryozoa, oysters, coralline algae, vermetid gastropods and serpulids in the wild (Kiene 1988). Additionally, the study was only three months long and slabs might not have been exposed long enough to show mature colonies of experimental encrustations. Davies and Hutchings (1983) report that sponges and sipunculans play no part in initial bioerosion of newly available coral substratum, however, within 2-3 years of coral substrata becoming available, they become abundant (Hutchings 1983; Hutchings and Bamber 1985; Kiene 1985). Conversely, polychaetes are the initial colonizers of newly available coral substrata (Hutchings 1986) and were observed on the slabs. Hence, the fresh slab would have taken more time to show significant experimental encrustations.

Bioaccretion rates on three reefs of the southern Great Barrier Reef (GBR) where echinoids were not classed important grazers, were (Llewellyn Reef) reef slope 30 x 10^{-3} $kgCaCO_3$ /m^2/d and reef flat 4.7 x 10^{-3} $kgCaCO_3$ /m^2/d; (One Tree Reef) 3.3 x 10^{-3} $kgCaCO_3$ /m^2/d and reef flat 1.9 x 10^{-3} $kgCaCO_3$ /m^2/d; and (Wreck Reef) reef slope 9.4 x 10^{-3} $kgCaCO_3$ /m^2/d and reef flat 4.6 x 10^{-3} $kgCaCO_3$ /m^2/d (Kiene 1988). Thus, higher encrustation rates were observed on Nukubuco Reef compared to GBR despite the fact that this study

was 3 months old and Kiene's (1988) study lasted 24 months. This could mean that Nukubuco has conditions favourable for encrustation as well as bioerosion.

The cage experiments, in contrast to the gut analysis provides bioactivity rates specific to habitats (area factor) thereby taking into account the variability in reef environments. However there was no significance in between-habitat difference in the cage experiments. Consequently, either of the bioerosion rates could be true for the Nukubuco Reef. In order to overcome this problem which might have been coincidental, or due to cage effects or low sample size, this study designed an extrapolated bioerosion assessment method (discussed in 4.4.4), which presents a more empirical image of the reef environments.

4.4.3 Erosion-accretion balance

The experiments demonstrate that both bioerosion and bioaccretion are major processes that affect dead coral substrata on Nukubuco Reef. It is the balance between the rates of bioerosion and bioaccretion that directs changes in reef environments as they evolve and provide fundamental understanding on the ultimate contribution of reef frameworks to reef growth and sustenance. Erosion exceeds accretion on all habitats with no net accretion on Nukubuco Reef.

Nukubuco reef portrays dominance of grazing over encrustation. This means that dead coral substrata are being converted to sediment by the bioeroding processes (burrowing and grazing) of urchins at a faster rate than contributing to reef building. In order to protect surfaces from grazing and allow framework to accumulate, coral colonies must grow large or overgrow each other (Kiene 1988). This is difficult for Nukubuco Reef because of the

chronic persistence of *Acanthaster planci* populations predating corals (Zann *et al.* 1990).

This erosion-accretion balance estimate may present a virtual picture due to a number of reasons. There is significant biological destruction from grazers (acanthurids and scarids, echinoids, grazing gastropods, limpets), etchers (bacteria, fungi, algae) and borers (sponges, bivalve molluscs, sipunculans, polychaetes) (Hutchings 1986). Due to the cage-experiment, this study has reported rates completely void of other macroscopic bioerosion agents. Since Nukubuco Reef is overfished, finfish, edible gastropods and bivalves would contribute very little to the erosion processes. However, other agents such as polycheates and sponges may still alter the total bioerosion rates.

Variation in reef environments both over space and time could also give inconsistent bioactivity rates. This could result from variability across the reef in larval recruitment of some agents of bioerosion and bioaccretion (Hutchings 1985; Hutchings and Bamber 1985) due to selectivity in preference for differing substrata complexity (Risk and McGeachy 1978). The reef development status would also allow varying extents of erosion depending on the vulnerability of the reef, for example, after a plague of *Acanthaster planci* where virtually all coral is killed, rates of bioerosion may increase drastically. Boring communities are therefore not stable over time. These changes in the composition of the boring community may modify rates of bioerosion. Hutchings and Bamber (1985) report that despite larval sipunculans and sponges being available for recruitment, newly laid coral substrata are not bored by these until 9-12 months of polychaete boring has occurred. This suggests that potential modification of coral rock may enhance the rate of bioactivity.

Superimposed on all these factors are seasonal growth patterns of the boring agents, which may be determined by the seasonality of food supply and other

factors. Tropical reefs have distinct seasonality (Hutchings 1986). Strong currents may also influence the rate of solution of substratum and the removal of eroded sediment or alternatively it may force sediment into eroded substrata and encourage cementation and reduce the net rate of bioerosion.

4.4.4 Extrapolated bioerosion

Generally, the extrapolated bioerosion rates increased as a function of density in different habitats of Nukubuco Reef. However, the slight discrepancy noted could be due to the fact that though this method assumed that all urchins were feeding randomly within each habitat, they may not be so. Factors such as predation, competition, wave stress, recruitment, mortality and alternative food sources may continually influence *Echinometra* populations giving fluctuations in bioerosion rates. Since *E. sp.* A was dissected for $CaCO_3$ consumption rates due to its dominance and availability (see gut analysis methodology), the gut rates were size-specific but not species-specific and extrapolation was based upon the assumption that *E. sp.* A have similar feeding rhythms to *E. sp.* C. A better characterization of species in the gut analyses may help solve this problem.

Eastern flat reported 26.5 x 10^{-7} kg $CaCO_3/m^2/d$ (4.08 ± 0.25 urchins/m^2) while western crest showed the least bioerosion 1.45 x 10^{-7} kg $CaCO_3/m^2/d$ (1.64 ± 0.25 urchins/m^2). These data on bioerosion were far less than literature values by 10^4 order of magnitude.

The three methods of bioerosion, gut analysis, cage experiments and extrapolation method cannot be directly compared, as each comprises different assumptions and conditions. Gut analysis and cage experiments show more weaknesses compared to the extrapolated bioerosion method.

Gut analysis makes use of the assumption that early morning gut content is equivalent to the daily consumption (Russo 1980; Bak 1990, 1994). Hence,

erosion rates are a function of time. A single value is extrapolated for the entire reef without taking into account the density factor, despite the within reef variations (Kiene 1985). But this method has still been used consistently. Nonetheless, this method may well reflect seasonality in preferred food items of urchins. Despite the shortcoming of this method, this study reported bioerosion rates very similar to other studies (Odgen 1977; Russo 1980; Conand *et al.* 1997).

The cage experiments may pose cage effects on an urchin altering its normal cycle of living and hence producing falsified bioerosion rates. The data are size-specific and restrict ability to extrapolate bioerosion rates of other urchin sizes unless extra costs are accommodated on numerous cage set-ups. This method measures erosion on the cut blocks of dead coral and may not describe erosion on living or other reef substrata (Kiene and Hutchings 1992). Calculating rates of erosion by grazing on the upper surfaces of samples only allows comparison of the rates between the samples. Extrapolating these rates to reef surfaces should be avoided (Kiene 1985). This may be suggested due to the fact that reef rugosity is 3-dimensional and assessing bioerosion rates just on sample surfaces would only give an estimate of one-dimensional erosion.

Nevertheless, this method allows assessment of bioerosion exclusively by echinoids inhibiting interaction by acanthurids and scarids (though Nukubuco reef has no contribution from these). Also, it shows variability of bioerosion on reefs and demonstrates the relative importance of the echinoid bioerosion processes in modifying dead coral substratum. Despite its weaknesses, this study gave very similar rates of bioerosion to those obtained by Conand *et al.* (1997) though she used gut analyses and this study used cage experiments.

The new extrapolated bioerosion method (Figure 4.8) may conceal seasonality patterns of grazing and urchin larvae recruitment. Unlike the cage

experiments, it is difficult to report on bioaccretion rates from extrapolations. Hence, in each habitat, the same rate of accretion as erosion would neutralize the degrading effect on Nukubuco Reef. The advantages of this method however, are inevitable. The extrapolation method gave similar trends of bioerosion for zones as gut analysis and cage experiments but should the feeding rhythms of *Echinometra sp.* A and C differ, this method will require further research on gut analysis of *E. sp.* C to designate extrapolated bioerosion rates specific to *E. sp.* A and *E. sp.* C.

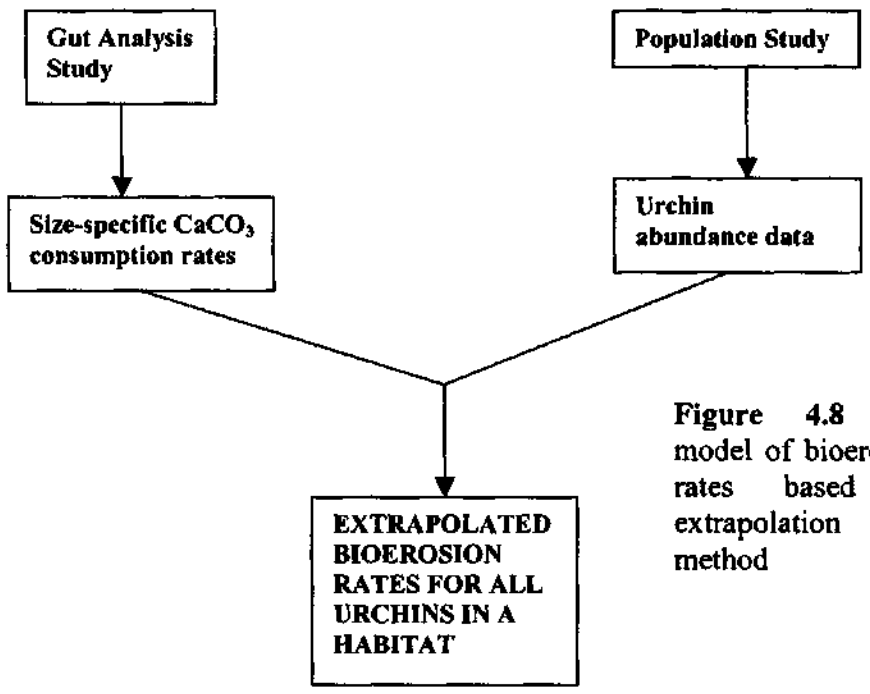


Figure 4.8 The model of bioerosion rates based on extrapolation method

More so, this method makes use of $CaCO_3$ consumption rates from the gut analysis and size-distribution data from the population study to calculate bioerosion rates for all urchins in the sampled habitats. This is a more valid assessment compared with gut analysis or cage experiments as it accommodates the within reef environment variations such as substrata complexity, urchin species, urchin density and size. Russo (1980) and Bak (1990, 1994) strongly suggest reporting bioerosion rates in the framework of

urchin species, density and size. Bioerosion rates using this method would certainly reflect the true developmental stages of reefs, hence avail reef management practices.

CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

5.1 General Discussion

5.1.1 Spatial patterns in distribution and abundance of *Echinometra* spp.

This study has elucidated the ecological aspects of two species of *Echinometra* in Fiji, *Echinometra. sp. nov.* A and *E. sp. nov.* C, which demonstrate slight morphological and genetic variation and strong reproductive isolation (Palumbi 1996a) but co-exist. Apart from the existence of the divergent species of *E. mathaei* (Palumbi 1996a), natural and anthropogenic disturbances affect Nukubuco Reef. It is important to describe these disturbances because it is the interwoven effects of these that help to explain the low but consistent densities and impact of *Echinometra* spp.

Nukubuco Reef, which is a part of the coral reef system in Laucala Bay, has experienced recent bleaching events (South and Skelton 2000; Cumming *et al.* under review) and *A. planci* outbreaks (Zann *et al.* 1990). The continuous influx of sewage from the Kinoya Sewage Treatment Plant (Naidu *et al.* 1991) promotes nutrient enrichment to the Laucala waters further providing food for coral predators. Thus, the high fishing pressures, eutrophic waters and *A. planci* predation, provide flourishing conditions for *Echinometra* spp. Furthermore, high sediment loads from logging and highland farming (Hinrichsen 1998) could also contribute to coral decline.

Echinometra sp. A and *E. sp.* C showed significant differences in distribution and abundance patterns at all scales of spatial analysis. The higher density of *E. sp.* A could mean that this species is very well adapted to high nutrient levels released

from Kinoya Sewage Plant and high sedimentations rates from highland river runoffs and logging activities. The lower density of *E. sp.* C presumably demonstrate its lower resistance to pollution levels or it's less competitive nature with *E. sp.* A. Alternatively, the cryptic behaviour of *E. sp.* C and/or higher susceptibility to predation could have caused lower density of this species. Different substratum requirements could also explain differences in *Echinometra* spp. densities observed.

Echinometra sp. A had higher density on the reef flat while *E. sp.* C showed a preference for the reef crest. Variations in size, micro-spatial preferences (Russo 1980) and behavioural adaptations may explain the contrast. *E. sp.* C is more adapted to high-energy environments and may have a detrital mode of feeding, compared with *E. sp.* A, which prefers calmer flats and grazing (Russo 1977). *Echinometra sp.* A may be more selective in the way they occupy habitats depending on their micro-spatial preference (Russo 1980). Also, since the white-tipped (*E. sp.* A) have shown aggregation on the Okinawan flats (Tsuchiya and Nishihira 1985), the difference in guild patterns may strongly affect the distribution trends. On the other hand, *E. sp.* C may not be as selective and since they do not aggregate, may have shown very similar or uniform distributions on both crests. *E. sp.* A were significantly larger than *E. sp.* C in all habitats of Nukubuco Reef except the eastern flat. This could be a function of variation in rates of predation, reproduction, competition, mortality, recruitment and feeding habits. Furthermore, the differences in size-class distribution shows how efficiently particular size-classes adapt to resources around them.

Echinometra sp. A and *E. sp.* C disclosed a mixed response in their dispersion patterns being both aggregated and non-aggregated. However, pooled species in habitats showed overall aggregation for *Echinometra* spp. Nonetheless, type 4, may be a new species, as it has not been documented in the literature and always appeared solitarily. These aggregation patterns of *Echinometra* spp. found in this study do not agree with the literature. Tsuchiya and Nishihira (1985) reported

aggregated patterns of dispersion for *E. sp.* A and non-aggregated for *E. sp.* C. Aggregation patterns was based on introduction of intruder urchins into burrows and noting responses from host urchins. Nukubuco Reef contains an abundance of massive and submassive *Porites*, which has probably resulted from *A. planci* predation, bleaching events and trampling of branched corals from subsistence fishing. Observations of *Echinometra* spp. guilds nestled around large *Porites* boulders with smaller ones burrowed on the dead heads could probably be the reason for the difference in dispersion patterns. Thus instead of inhabiting single burrows as in the Okinawan study, urchins frequently occurred in large guilds on Nukubuco Reef and this may have been the reason for showing a complete aggregated pattern of dispersion.

Echinometra sp. A (type 2/green-white-tipped) was the most well adapted type as it occurred in higher numbers on crest and flat. It appears the best adapted and robust compared to the other types. Type 2 and *E. sp.* C (type 6/fully brown) appeared in higher densities on the crests. This may be because they were more adapted to the environment probably being detrital feeders and robust to the excessive wave action. The possible new species (type 4/fully maroon) was only seen on the flats presumably due to being adapted to calmer environments. Type 1 (black-white-tipped) and type 4 (beige-white-tipped) shared very similar abundance and distribution patterns since both were *E. sp.* A. Type 3 (brown-white-tipped) appeared to be the least adapted and most vulnerable species as it was the least abundant in both zones. Hence, *E. sp.* A appeared to be more acclimatized to Nukubuco Reef environment than *E. sp.* C.

Knowledge of size-specific activity on the different environments of Nukubuco Reef provided an indirect assessment of the potential impact of *Echinometra* spp. A major difference was noted in the behaviour of *Echinometra* spp. at the crest and flat. Small (1-39mm) and medium (40-60mm) urchins dominated the crests showing high percentages of burrowing and feeding behaviour. The high surf

intensity at the crests urge urchins to seek refuge or create one (Russo 1980) and feed by catching detrital algae from the water column.

Ebert (1968) did a study on *Strongylocentrotus purpuratus* and found that the high-energy crest environment poses a threat to larger urchins' spines and provides grooves and crevices adequately sized for smaller urchins to seek refuge. This could prove true in case of *Echinometra* spp. as small urchins were mostly observed in the tiny coral grooves and the wave action also enhances the possibility of dislodgment on the crests for larger urchins. Contrarily, the flats displayed feeding, burrowing and scouring by all sizes of urchins. This may be a function of higher numbers observed at the flats. Alternatively, the availability of a variety of niches due to variable topographic complexity and high rugosity may accommodate all urchin sizes and activity.

Some general conclusions can also be made for both *Echinometra sp.* A and C. Higher urchin numbers occur on the flats because of the availability of a reef framework of dead coral rock substrata. These brittle structures provide *Echinometra* spp. with an 'easy-to-burrow' substratum for refuge from predation and desiccation (McClanahan and Kurtis 1991). *Echinometra* burrows are a common feature of the upper margin of rocky intertidal and reef flat zones where they form a distinct zone at mean low water (Schoppe and Werding 1996). The reef crest, on the other hand, offers high predation levels with very limited crevice availability.

Increasing cover of turf algae on coral rock provides a major food source for *Echinometra* (Odum and Odum 1955; Keesing 1992) as opposed to the crests, which show high cover of coralline algae a major finfish diet (Conand *et al.* 1997) hence restricting feeding to the catching of algal drift mode. The calmer flats also escape wave stress securing dispersal of pelagic larvae (Khamala 1971) and urchins experience reduced spine breakage and dislodgment problems from high-energy wave action (Ebert 1968). The limited crevice availability and

energy direction into growth rather than test damage repair is also responsible for the smaller size-class distribution of *Echinometra* spp. on the crests compared to the flats (Ebert 1968). Finally, the variable topographic complexity and higher rugosity of the flats offers a wider choice for micro-spatial preferences (in terms of habitat, food, refuge, competition and reproduction) for *Echinometra* spp. than the crests (McClanahan and Kurtis 1991).

Considering the fact that this study aimed to investigate 'if significant differences existed between sites' and not the 'the causes of those differences', clearly there was sufficient site replication in this study. This is further supported by the fact that significant differences were found between sites. It is important to note that if additional processes were to be studied, it would require additional experimental work, which was outside the scope of this study. In future, continued measurements of reef components and environmental variables could be attempted in conjunction with experimentation.

With further genetic studies on the 7 species or morphs of *Echinometra sp.* A and *E. sp.* C and the possibly new species, subtle differences between them could be rectified which could subsequently be used to enhance our knowledge on their ecological distinctions shown in this study. The genetic study would also facilitate the incomplete species-level taxonomy of *Echinometra*. Also, a rigorous investigation on the colour changes of the morphs with age and/or environmental variation may come in handy for in depth understanding on morphometric characterization of *Echinometra* spp.

5.1.2 Sea urchin prevalence and levels of natural and anthropogenic reef disturbances

The uniqueness of eastern Nukubuco Reef reflected a highly significant difference in distribution and abundance patterns of *Echinometra* spp. compared to the western position. The western position being adjacent to Suva Reef

experiences constant flushing from Nukubuco Passage compared to the east, which withstands influence from the Kinoya Sewage Treatment Plant (Naidu *et al.* 1991) and high sediment inputs from Vatuwaqa, Samabula, Vunidawa and Rewa river run-offs (Hinrichsen 1998).

The high levels of terrigenous inputs of nutrients into the bay enhance phytoplankton production leading in turn to higher survivorship in planktotrophic echinoderm larvae (Birkeland 1989). Birkeland (1981) and Glynn (1988) have stated that an increase in algal abundance following *Acanthaster planci* outbreaks or other disturbances may elicit a numerical response from grazing urchins through facilitating higher recruitment. Thus *Echinometra* spp. are believed to be a secondary effect of *A. planci* outbreaks (Keesing 1992). Furthermore, the increased sedimentation from river run-offs suffocates corals and leads to death (Birkeland 1989). Collectively, these effects provide a suitable substratum for *Echinometra* dominance on the east of Nukubuco Reef. A detailed collated demographic study on *A. planci-Echinometra* could be useful in enhancing understanding on their relationship.

Echinometra spp. emergence could also be explained by overfishing of predatory finfish such as triggerfish on the reef (Hay 1984; McClanahan and Muthiga 1988, 1989). Absence of parrotfishes and surgeonfishes on the reef supplement this inference. Urchins such as *Echinometra* and *Diadema* have often been dominant herbivores on unprotected (heavily fished) coral reefs while herbivorous fishes such as parrot and surgeonfishes dominate (little or unfished) protected reefs (Hay 1984; McClanahan and Shafir 1990). Detailed evaluation of fishing pressure assessments based on the methods developed by McClanahan (1995a) and McClanahan *et al.* (1999) could improve our understanding of the impact of overfishing on coral community structure.

5.1.3 Comparison of gut, cage and extrapolation methods of bioerosion assessment

An investigation on the ecological facets of an emerging species would not have been complete without experiments on how its grazing and boring activities have an impact on Nukubuco Reef. Bioerosion rates and their impact were determined via three methods, gut analyses, cage experiments and extrapolation method. The former two methods have consistently been used by other bioerosion scientists for urchins specifically, and grazer and borer communities, respectively. The third method is new in that it makes use of population study from Chapter 3 and the gut analyses to report bioerosion rates of *Echinometra* spp.

The gut analyses demonstrated a lower bioerosion rate on the flats 0.20 x 10^{-3} kg $CaCO_3$ /urchin/d, compared to the crests, 0.39 x 10^{-3} kg $CaCO_3$ /urchin/d. The rates could have been falsely reported since two different functions, power and linear were used to report rates on the different zones. This was only done as those functions demonstrated the best fit of data in those zones. On the reef the population study reported more urchins on the flats due to availability of coral rock substratum for food, refuge, protection from wave stress, desiccation and predators. Hence, the urchins from the flat should show higher bioerosion rates. The small colonies of *Echinometra* spp. on the crests, which are usually dominant feeders of algal drift rather than grazers of turf algae (Ebert 1968) would show lower $CaCO_3$ in their gut. Hence, substratum type could actually act as an indicator of bioerosion rates. Furthermore, reported rates of bioerosion may change according to the function used to report it.

Since reefs are variable in substrata and topographic complexity and in all associated ecological processes (McClanahan and Muthiga 2001), it is difficult to report bioerosion rates using gut analyses which is a function of time [early morning gut content is a measure of daily consumption (Ogden 1977; Russo 1980; Bak 1990, 1994]. Though it helps in the identification of preferred food

items in the gut content, gut analyses disregard the density factor (x g $CaCO_3$ /urchin/d as opposed to x g $CaCO_3$ /urchin/m^2/d) despite the within reef variations. Future work on gut analyses procedures could improve by including a better characterization of morphs in relation to test diameter and $CaCO_3$ content in the urchin gut. This would unveil potential trends of $CaCO_3$ consumption rates subjected by different morphs or species.

The cage experiments also demonstrated high rates of bioerosion on the flats (eastern = 43 x 10^{-3}; western = 30 x 10^{-3} (kg $CaCO_3$/m^2/urchin/d, than the crests (eastern = 35 x 10^{-3}; western = 37 x 10^{-3} (kg $CaCO_3$/m^2/urchin/d). Since the cages were closed systems, reasons for high rates from gut analyses cannot be allocated to the cage experiments. Surf intensity on slabs from the crest may have stressed the urchins hence altering their mode of feeding from grazing to filtering algal drift. Alternatively, the crest environment may have triggered sporadic episodes of grazing from the normal filter feeding. This result is true in the wild as higher densities of *Echinometra* spp. were reported on the flats than the crests in the population study. Nonetheless, the cage experiment reported higher bioerosion rates compared with the gut analysis presumably due to the fact that the area factor was considered in the cage experiment. Hence, a meter square of reef substrata could harbour a variable number of urchins as opposed to the gut analysis, which reports only bioerosion rate per urchin. Further studies on feeding rhythms would enable us to make concrete decisions on changes in modes of feeding relative to influences. An increase in cage replicates, number of sites and time frame would improve understanding on bioerosion trends on Nukubuco Reef.

Bioerosion rates exceeded bioaccretion rates on Nukubuco Reef. It is important to note that despite being exposed for only 3 months, the slabs showed higher encrustation rates compared to Kiene's (1988) study on the Great Barrier Reef, which was 24 months long. Nukubuco Reef does not reflect these high

bioaccretion rates in the wild system presumably due to the bioeroding impact from populations of *Echinometra* spp.

The cage experiment restricts measurement of bioerosion to slabs and conclusions based on these might not accommodate the high variability in reef environments. But this method demonstrates the relative importance of the echinoid bioerosion processes in modifying the reef framework. Both gut analyses and the cage experiments gave bioerosion rates very similar to those of other workers (Downing and El-Zahr 1987; Conand *et al.* 1997) hence justifying their current use.

The extrapolation method is an attempt to produce a more empirical value of bioerosion. It makes use of population distribution and abundance patterns in conjunction with the $CaCO_3$ consumption rates from gut analyses to give an estimate of bioerosion by specific numbers of urchins in an area. This method reports bioerosion assessments of larger areas as opposed to the slabs hence justifying the extrapolation. Though it obscures grazing and recruitment patterns, it accommodates the within reef variability (in terms of substrata rugosity and topographic complexity, urchin sizes, urchin densities, urchin species) when reporting bioerosion rates.

This study has reported distribution and abundance patterns of *Echinometra* spp. populations and their bioeroding rates using three methods. A global comparison of bioerosion rates categorizes Nukubuco Reef with many other reefs, which are moderately bioeroded. Should the low but consistent densities of *Echinometra* spp. continue bioeroding the reef, it will not take long for the deleterious and combined impacts of overfishing, municipal and industrial pollution, high sediment loads, coral bleaching, impending global climate change and *A. planci* to change Nukubuco Reef complexity from the current urchin-dominated to a coral-barren-sand-dominated locale.

CHAPTER 6

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Appendices

Appendix 1

2-Level Cost Benefit Analysis

Formulae for 2-level Cost-Benefit Analysis

1. nesting of quadrat within sites
2. nesting of sites within zones

Cost-Benefit Analysis Table for Quadrats and Replicates

Source	MS Estimates	Estimated Variances
Sites (top level)	$MS_S = \sigma^2_Q + r\sigma^2_S$	$\sigma^2_S = MS_S - MS_Q$
Quadrats (bottom level)	$MS_Q = \sigma^2_Q$	$\sigma^2_Q = MS_Q$

R = Q = quadrats per site

Q = S = sites per zone

MS_S = MS among sites = $\sigma^2_Q + r\sigma^2_S$

MS_Q = MS among quadrats = σ^2_Q

$$\text{Variance among sites} = \frac{MS_S}{r} - \frac{MS_Q}{r} = \sigma^2_Q + r\sigma^2_S - \sigma^2_Q = \sigma^2_S$$

Variance among quadrats = $MS_Q = \sigma^2_Q$

When Cost is Limiting

- Time
- Finance
- Expertise

Optimal no. of quadrats per site (1)

$q_{opt} = sqr\ (C_S S^2_Q / C_Q S^2_S)$

Optimal no. of sites per habitat (2)

$C_r = qC_S + rqC_Q$ = the total cost (in time) per site

Thus,

$$s_{opt} = \frac{C_r}{C_S + r_{opt}\, C_Q}$$

From pilot study

C_T = 120 hours = 7200 minutes = time available

C_Q = 9-12 minutes per quadrat = 10 minutes

C_S = 30 minutes = time available to sample per site

Variance among quadrats $S^2_Q = MS_Q = 0.06967$

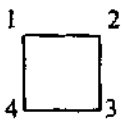
Variance among sites $S^2_S = \frac{MS_S - MS_Q}{r} = \frac{0.0473 - 0.06967}{20} = -0.0011185$

Optimal # quadrats/site

$q_{opt} = sqr\ (C_S S^2_Q / C_Q S^2_S) = sqr\ \{30\ (0.06967) / 10\ (0.0011185)\} = 13.6699 = 14$ quadrats/site. However, 20 quadrats were sampled per site.

Appendix 2

GPS Locations for Population study of *Echinometra* spp.

Position	Zone	Site	GPS
East	Crest 	1	(1)178° 30' 20.909"E 18° 10' 47.294"S (2)178° 30' 20.909"E 18° 10' 43.806"S (3)178° 30' 17.593"E 18° 10' 43.806"S (4)178° 30' 17.593"E 18° 10' 47.294"S
East	Crest	2	(1)178° 30' 27.457E 18° 10' 48.824"S (2)178° 30' 27.457E 18° 10' 45.336"S (3)178° 30' 24.145"E 18° 10' 45.336"S (4)178° 30' 24.145"E 18° 10' 48.824"S
East	Crest	3	(1)178° 30' 14.000E 18° 10' 50.333"S (2)178° 30' 14.000E 18° 10' 46.844"S (3)178° 30' 10.685"E 18° 10' 46.844"S (4)178° 30' 10.685"E 18° 10' 50.333"S
East	Crest	4	(1)178° 30' 06.210"E 18° 10' 48.122"S (2)178° 30' 06.210"E 18° 10' 44.634"S (3)178° 30' 02.898"E 18° 10' 44.634"S (4)178° 30' 02.898"E

			18° 10' 48.122"S
East	Flat	1	(1)178° 30' 24.584"E 18° 11' 18.787"S (2)178° 30' 24.584"E 18° 11' 15.299"S (3)178° 30' 21.269"E 18° 11' 15.299"S (4)178° 30' 21.269"E 18° 11' 18.787"S
		2	(1)178° 30' 30.780"E 18° 11' 20.998"S (2)178° 30' 30.780"E 18° 11' 17.506"S (3)178° 30' 27.464"E 18° 11' 17.506"S (4)178° 30' 27.464"E 18° 11' 20.998"S
		3	(1)178° 30' 17.147"E 18° 11' 18.100"S (2)178° 30' 17.147"E 18° 11' 14.611"S (3)178° 30' 13.835"E 18° 11' 14.611"S (4)178° 30' 13.835"E 18° 11' 18.100"S
		4	(1)178° 30' 09.889"E 18° 11' 16.566"S (2)178° 30' 09.889"E 18° 11' 13.078"S (3)178° 30' 06.577"E 18° 11' 13.078"S (4)178° 30' 06.577"E 18° 11' 16.566"S
West	Crest	1	(1)178° 28' 53.789"E 18° 10' 47.687"S (2)178° 28' 53.789"E 18° 10' 44.195"S

			(3)178° 28' 50.473"E 18° 10' 44.195"S (4)178° 28' 50.473"E 18° 10' 47.687"S
West	Crest	2	(1)178° 29' 00.341"E 18° 10' 46.340"S (2)178° 29' 00.341"E 18° 10' 42.852"S (3)178° 28' 57.029"E 18° 10' 42.852"S (4)178° 28' 57.029"E 18° 10' 46.340"S
West	Crest	3	(1)178° 28' 47.060"E 18° 10' 45.646"S (2)178° 28' 47.060"E 18° 10' 42.154"S (3)178° 28' 43.748"E 18° 10' 42.154"S (4)178° 28' 43.748"E 18° 10' 45.646"S
West	Crest	4	(1)178° 28' 40.508"E 18° 10' 47.158"S (2)178° 28' 40.508"E 18° 10' 43.669"S (3)178° 28' 37.193"E 18° 10' 43.669"S (4)178° 28' 37.193"E 18° 10' 47.158"S
West	Flat	1	178° 28' 52.691"E 18° 11' 09.524"S 178° 28' 52.691"E 18° 11' 06.032"S 178° 28' 49.379"E 18° 11' 06.032"S 178° 28' 49.379"E 18° 11' 09.524"S
West	Flat	2	178° 28' 58.886"E

			18° 11' 11.562"S 178° 28' 58.886"E 18° 11' 08.074"S 178° 28' 55.574"E 18° 11' 08.074"S 178° 28' 55.574"E 18° 11' 11.562"S
West	Flat	3	178° 28' 45.962"E 18° 11' 11.206"S 178° 28' 45.962"E 18° 11' 07.717"S 178° 28' 42.647"E 18° 11' 07.717"S 178° 28' 42.647"E 18° 11' 11.206"S
West	Flat	4	178° 28' 38.172"E 18° 11' 10.349"S 178° 28' 38.172"E 18° 11' 06.860"S 178° 28' 34.856"E 18° 11' 06.860"S 178° 28' 34.856"E 18° 11' 10.349"S

Appendix 3

Depth Profile Details

(a)Transect details

Position	Transect	GPS
West	1	Start- 178° 30' 23.123"E 18° 10' 29.042"S End- 178° 30' 20.023"E 18° 11' 22.499"S
West	2	Start- 178° 30' 17.942"E 18° 10' 28.416"S End- 178° 30' 15.491"E 18° 11' 22.286"S
East	1	Start- 178° 28' 55.024"E 18° 10' 37.801"S End- 178° 28' 54.754"E 18° 11' 12.066"S
East	2	Start- 178° 28' 51.568"E 18° 10' 37.175"S End- 178° 28' 50.650"E 18° 11' 12.883"S

(b) Depth Profile Data

Date: 26/09/00 **Tide: 0.1m** **Transect 1:East**

CODE: (1)LC=live coral; (2)TP=tide pool; (3)SC=soft coral; (4)CR=coral rock; (5)R=rubble; (6)S=sand; (7)MA=macro algae; (8) S+R+MA; (9) S+R; (10)LC+CR

Meter Mark	Description	Water depth	Description code
0	LC FLAT	0	1
90	TP	87	2
130	LC	90	1
160	TP	101	2
200	TP	86	2
220	LC	120	1
300	TP	129	2
310	LC	115	1
317	TP	90	2
343	TP	112	2
357	LC	120	1
368	TP	92	2
389	TP	97	2
393	R	47	5
399	S+R	45	9
405	TP	85	2
411	LC	16	1
412	S+R+MA	66	8
413	LC	30	1
416	R	34	5
419	CR	12	4
425	S+R+MA	41	8
422	SC	11	3
427	R+S	48	9
429	CR	16	4
435	LC	9	1
439	S+R+MA	28	8
443	CR	10	4

448	LC	12	1
451	CR	12	4
457	TP	72	2
468	R+S+MA	39	8
470	LC	27	1
476	CR	18	4
496	TP	71	2
498	R+S	38	9
499	LC	10	1
502	R+S	31	9
505	CR	6	4
511	R+S	52	9
516	LC	23	1
525	TP	69	2
540	R+S	43	9
548	CR	51	4
556	TP	63	2
558	CR	12	4
568	TP	76	2
596	R+S+MA	16	8
600	TP	41	2
620	R+S+MA	27	8
638	CR	7	4
701	R+S+MA	30	8
721	CR	24	4
782	TP	100	2
1033	S+R+MA	18	8

Date: 26/09/00 **Tide: 0.1m** **Transect 2:East**

Meter Mark	**Description**	**Water depth**	**Description code**
0	LC	0	1
110	TP	110	2
157	TP	107	2
168	LC	42	1
182	TP	97	2

189	LC	52	1
229	TP	112	2
259	LC	28	1
286	TP	99	2
293	LC	18	1
332	TP	75	2
343	TP	82	2
368	LC	25	1
373	CR	22	4
392	TP	101	2
400	LC	37	1
421	R+S	25	9
425	LC	42	1
427	SC	29	3
433	R+S+MA	18	8
458	TP	100	2
462	R+S	22	9
470	SC	21	3
472	CR	18	4
480	R+S	14	9
483	LC	22	1
487	R+S+MA	18	8
493	LC	21	1
525	TP	79	2
530	LC	30	1
546	R+S	22	9
548	LC	20	1
555	R+S	16	9
557	LC	12	1
561	CR	14	4
565	LC	12	1
585	TP	88	2
592	R+S	10	9
595	LC	18	1
603	R+S+MA	14	8
612	CR	23	4

617	LC	20	1
627	R+S	26	9
630	LC	14	1
647	TP	67	2
652	LC	25	1
659	CR	16	4
671	R+S+MA	18	8
675	CR	10	4
689	TP	69	2
725	R+S+MA	12	8
729	LC	8	1
929	R+S+MA	11	8
947	TP	72	2
1100	R+S+MA	10	8

Date: 28/09/00 **Tide: 0.1m** **Transect 1:West**

CODE: (1)LC=live coral; (2)TP=tide pool; (3)SC=soft coral; (4)CR=coral rock; (5)R=rubble; (6)S=sand; (7)MA=macro algae; (8) S+R+MA; (9) S+R; (10)LC+CR

Meter Mark	Description	Water depth	Description code
0	LC FLAT	0	1
68	TP	88	2
72	S	67	6
88	TP	99	2
120	LC	20	1
132	S+R	49	9
169	LC	17	1
175	S+R	35	9
178	LC	13	1
189	S+R	43	9
192	LC	11	1
199	S+R	41	9
201	CR	13	4
214	S+R	43	9
217	CR	13	4

222	S+R	37	9
224	LC+CR	13	10
225	CR	14	4
229	R+S	42	9
236	CR+LC	9	10
238	R+S	36	9
242	CR+LC	23	10
245	R+S	50	9
247	CR	18	4
252	S+R	55	9
253	CR	19	4
254	S+R	63	9
259	CR+LC	19	10
264	S+R	54	9
270	CR	10	4
272	S	46	6
274	CR+LC	18	10
278	S+R	50	9
280	LC	12	1
286	S+R	57	9
311	TP	63	2
316	CR	12	4
332	S+R	69	9
333	CR	9	4
335	S+R	69	9
350	CR	14	4
361	R+S	46	9
367	CR	19	4
382	TP	76	2
412	CR	22	4
445	R+S+MA	42	8
449	CR	14	4
471	TP	80	2
489	R+S	42	9
529	LC+CR	6	10
533	S+R	55	9

558	LC+CR	9	10
568	R+S	42	9
613	LC+CR	43	10
651	R+S	37	9
655	CR	12	4
679	S+R	59	9
682	CR	10	4
711	TP	123	2
723	S+R	40	9
733	CR	10	4
937	S+R+MA	17	8

Date: 28/09/00 **Tide: 0.1m** **Transect 2:West**

Meter Mark	Description	Water depth	Description code
0	LC FLAT	0	1
52	R+S	62	9
67	TP	115	2
102	LC	25	1
112	LC+CR	23	10
117	CR	25	4
127	R+S	68	9
135	S	66	6
149	LC	21	1
169	TP	101	2
178	LC	32	1
183	R+S	42	9
197	LC	31	1
208	R+S	42	9
218	SC	41	3
232	CR	11	4
245	LC	17	1
257	TP	99	2
289	LC	19	1
301	CR	21	4

312	R+S	43	9
327	LC+CR	22	10
342	R+S	38	9
367	LC+CR	27	10
374	TP	77	2
408	CR	14	4
420	LC+CR	12	10
428	R+S	21	9
437	LC+CR	11	10
444	CR	13	4
469	R+S	22	9
472	R+S+MA	18	8
478	LC+CR	13	10
497	R+S	27	9
510	TP	67	2
527	R+S+MA	17	8
539	CR	10	4
547	R+S	14	9
562	CR	9	4
569	LC+CR	11	10
575	R+S	12	9
589	CR	10	4
595	R+S	18	9
615	CR	8	4
820	R+S+MA	12	8

Appendix 4

(a) $CaCO_3$ consumption rates for *Echinometra sp.* A using gut analysis

Urchins from eastern reef crest 17/05/00-18/05/00						
urchin	**test diameter**	**w_2-w_1**	**gut + paper**	**Gut +paper after**	**wet gut**	**filter paper**
	(mm)	**$CaCO_3$ in gut**	**wt. (w_2) (g)**	**HCL(w_1)**	**wt. (g)**	**wt. (g) (f_1)**
1	35.35	0.0961	0.8384	0.7423	1.6927	0.646
2	40.98	0.4094	1.7334	1.324	5.1491	0.6366
3	47.02	0.1799	1.2014	1.0215	4.0977	0.6301
4	52.25	0.419	1.7301	1.3111	5.2469	0.6696
5	40.05	0.5325	1.9825	1.45	6.7306	0.636
6	40.01	0.1329	1.4757	1.3428	5.1283	0.644
7	44.85	0.2228	1.4685	1.2457	6.5957	0.6389
8	39.05	0.143	1.0365	0.8935	3.1022	0.6741
9	42.02	0.5861	2.4261	1.84	8.2501	0.6498
10	50.09	0.1989	1.279	1.0801	3.5434	0.6382
11	31.04	0.1713	1.1287	0.9574	2.6502	0.6358
12	41.01	0.3315	1.8378	1.5063	6.0834	0.6514
13	41.02	0.3446	1.464	1.1194	5.0587	0.6446
14	46.02	0.4751	1.755	1.2799	5.335	0.6425
15	40.04	0.0619	0.9023	0.8404	2.4403	0.6412
16	49.05	0.1998	3.7769	2.758	10.4278	0.6514
17	51.03	0.1978	1.5164	1.3186	6.1024	0.6616
18	41.02	0.0374	0.7712	0.7338	1.5267	0.6307
19	29.01	0.2559	1.3608	1.1049	2.788	0.6395
20	30.01	0.3453	1.5359	1.1906	4.7848	0.6829
21	28.04	0.0368	0.9062	0.8694	1.7552	0.6569
22	21.01	0.0182	0.7448	0.7266	0.7084	0.644
23	32.01	0.1566	1.209	1.0524	5.2001	0.6406
24	35.01	0.2117	1.1772	0.9655	3.098	0.6586
25	45.06	0.3124	1.8715	1.5591	7.2216	0.6587
Urchins from eastern reef-flat 17/05/00-18/05/00						
1	41.01	0.1669	1.3076	1.1407	6.5984	0.6489
2	35.05	0.0992	1.2135	1.1143	4.9356	0.6497
3	45.01	0.1537	1.3472	1.1935	4.9154	0.6469
4	50.09	0.2069	1.7161	1.5092	5.5269	0.6858
5	41.09	0.3499	1.7371	1.3872	11.2252	0.682
6	41.05	0.3066	1.9356	1.629	7.4945	0.6495
7	45.05	0.3023	1.8026	1.5003	9.0939	0.6417
8	35.05	0.198	1.321	1.123	6.6648	0.6437
9	41.01	0.2015	2.1198	1.9183	8.6903	0.6737
10	47.03	0.1692	1.3495	1.1803	6.7672	0.6593

11	44.01	0.1375	1.22	1.0825	6.0195	0.6313
12	44.01	0.2185	1.4137	1.1952	5.0519	0.637
13	41.01	0.17	1.6632	1.4932	6.5319	0.6785
14	42.02	0.1558	1.2431	1.0873	6.0976	0.6416
15	41.01	0.2909	1.3783	1.0874	6.3103	0.6307
16	71.06	1.0189	1.1187	0.9189	5.9701	0.6449
17	38.03	0.2469	1.8221	1.5752	7.5394	0.6913
18	41.04	0.7194	1.9363	1.2169	5.6739	0.6481
19	43.05	0.2165	1.607	1.3905	5.6739	0.6383
20	41.01	0.2249	1.5772	1.3523	7.7217	0.6772
21	45.01	0.4863	1.9612	1.4749	5.4634	0.6779
22	46.45	0.1216	1.3345	1.2129	5.2855	0.6551
23	44.03	0.22	1.5334	1.3134	7.0789	0.6354
24	37.03	0.2483	1.5239	1.2756	5.5554	0.6338
25	30.05	0.0964	1.0429	0.9465	2.9371	0.6676

(b) Regression ANOVA for gut analysis using exponential, power and linear functions

Crest

Exponential

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	2.302	1	2.302	10.499	0.004
	Residual	4.823	22	0.219		
	Total	7.125	23			

Power

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	2.176	1	2.176	9.82	0.005
	Residual	5.095	23	0.222		
	Total	7.271	24			

Flat

Power

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	5.288	1	5.288	9.119	0.006
	Residual	13.337	23	0.58		
	Total	18.624	24			

Linear

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	7.59E-02	1	7.59E-02	3.442	0.076
	Residual	0.507	23	2.21E-02		
	Total	0.583	24			

Nukubuco

Power

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	7.977	1	7.977	20.752	0.000
	Residual	18.452	48	0.384		
	Total	26.43	49			

Linear

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	0.432	1	0.432	17.909	0.000
	Residual	1.159	48	2.42E-02		
	Total	1.592	49			

Appendix 5

GPS Locations for cage experiment

Position	Zone	Cage	GPS
East	Crest	1	178° 30' 11.660"E 18° 10' 43.270"S
East	Crest	2	178° 30' 13.381"E 18° 10' 45.541"S
East	Flat	1	178° 30' 26.730"E 18° 11' 14.251"S
East	Flat	2	178° 30' 26.726"E 18° 11' 16.523"S
West	Crest	1	178° 28' 42.488"E 18° 10' 45.628"S
West	Crest	2	178° 28' 43.133"E 18° 10' 48.104"S
West	Flat	1	178° 28' 40.948"E 18° 11' 05.233"S
West	Flat	2	178° 28' 40.724"E 18° 11' 08.329"S

Appendix 6

Slab Results for Point-Count Analysis

Location	Slab #	Square #	# pts. grazed	Area fraction grazed
Eastern flat	1	1	0	0
		2	0	0
		3	5	16.7
		4	9	30
		5	2	6.7
		6	5	16.7
		7	0	0
		8	10	33.3
		9	7	23.3
		10	3	10
		11	6	20
		12	6	20
		13	0	0
		14	4	13.3
		15	7	23.3
		16	6	20
		17	7	23.3
		18	8	36.7
		19	4	13.3
		20	9	30
		21	8	26.7
		22	1	3.3
		23	7	23.3
		24	3	10
		25	6	20
			123	**34.07**
Eastern flat	4	1	0	0
		2	1	3.3
		3	2	6.7
		4	6	20

		5	1	3.3
		6	4	13.3
		7	0	0
		8	0	0
		9	7	23.3
		10	2	6.7
		11	3	10
		12	2	6.7
		13	0	0
		14	1	3.3
		15	5	16.7
		16	3	10
		17	1	3.3
		18	0	0
		19	0	0
		20	6	20
		21	5	16.7
		22	2	6.7
		23	5	16.7
		24	1	3.3
		25	0	0
			57	**15.79**
Eastern crest	5	1	8	26.7
		2	0	0
		3	0	0
		4	2	6.7
		5	2	6.7
		6	3	10
		7	2	6.7
		8	4	13.3
		9	1	3.3
		10	3	10
		11	3	10
		12	2	6.7
		13	0	0
		14	0	0

		15	4	13.3
		16	2	6.7
		17	0	0
		18	0	0
		19	2	6.7
		20	7	23.3
		21	3	10
		22	2	6.7
		23	1	3.3
		24	7	23.3
		25	4	13.3
			62	**17.17**
Eastern crest	6	1	0	0
		2	1	3.3
		3	1	3.3
		4	4	13.3
		5	2	6.7
		6	5	16.7
		7	6	20
		8	5	16.7
		9	8	26.7
		10	4	13.3
		11	0	0
		12	0	0
		13	0	0
		14	5	16.7
		15	1	3.3
		16	2	6.7
		17	5	16.7
		18	0	0
		19	0	0
		20	2	6.7
		21	0	0
		22	0	0
		23	0	0
		24	2	6.7

		25	1	3.3
			54	**14.96**
Western flat	10	1	0	0
		2	0	0
		3	3	10
		4	4	13.3
		5	2	6.7
		6	1	13.3
		7	6	20
		8	1	13.3
		9	2	6.7
		10	3	10
		11	1	13.3
		12	0	0
		13	5	6.7
		14	7	23.3
		15	1	3.3
		16	2	6.7
		17	7	23.3
		18	7	23.3
		19	0	0
		20	3	10
		21	4	13.3
		22	0	0
		23	0	0
		24	0	0
		25	2	6.7
			61	**16.90**
Western flat	12	1	0	0
		2	7	23.3
		3	8	26.7
		4	0	0
		5	3	10
		6	6	20
		7	0	0
		8	0	0

		9	4	13.3
		10	3	10
		11	5	16.7
		12	6	20
		13	5	16.7
		14	4	13.3
		15	6	20
		16	0	0
		17	1	3.3
		18	2	6.7
		19	0	0
		20	3	10
		21	1	3.3
		22	0	0
		23	0	0
		24	0	0
		25	7	23.3
			71	**19.67**
Western crest	13	1	4	13.3
		2	3	10
		3	3	10
		4	5	6.7
		5	0	0
		6	4	13.3
		7	4	13.3
		8	3	10
		9	9	30
		10	3	10
		11	2	6.7
		12	0	0
		13	0	0
		14	0	0
		15	6	20
		16	1	3.3
		17	2	6.7

		18	2	6.7
		19	0	0
		20	8	26.7
		21	5	16.7
		22	3	10
		23	3	10
		24	7	23.3
		25	4	13.3
			81	**22.44**
Western crest	15	1	5	16.7
		2	7	23.3
		3	4	13.3
		4	3	10
		5	2	6.7
		6	2	6.7
		7	6	20
		8	4	13.3
		9	4	13.3
		10	4	13.3
		11	7	23.3
		12	0	0
		13	0	0
		14	0	0
		15	0	0
		16	1	3.3
		17	4	13.3
		18	5	16.7
		19	2	6.7
		20	6	20
		21	5	16.7
		22	2	6.7
		23	7	23.3
		24	3	10
		25	2	6.7
			85	**23.55**

Appendix 7

Bioerosion Rates from Cage Experiment

1. Average bioerosion weight

$$\frac{\{[\text{Slab replicate 1} + \text{slab replicate 2}]\}}{2} \; 1000 = x \text{ kg}$$

2. Bioerosion rate (kg $CaCO_3/m^2/day$)

Slab area = 0.1m x 0.1m = $0.01m^2$

Time of exposure = 92 days

Bioerosion rate = x kg $CaCO_3$ per $0.01m^2$ in 92 days

Thus,

$$\{X \text{ kg} / 0.01m^2\} / 92 \text{ days} = Y \text{ kg } CaCO_3/m^2/d$$

Bioerosion rates

Location	Slab #	% grazed	Wt. Grazed (g)	Bioerosion rate (kg $CaCO_3/m^2/d$)
East flat	1	34.07	57.45	0.0624
	4	15.79	21.70	0.0236
East crest	5	17.17	30.55	0.0332
	6	14.96	33.18	0.0361
West flat	10	16.9	23.69	0.0258
	12	19.67	31.44	0.0342
West crest	15	23.55	35.32	0.0384
	13	22.44	32.57	0.0354

Appendix 8

Bioaccretion rates

Weights of accretion

Original dry weight of slab – weight of bioerosion = x

Hence, total dry weight of slab after collection from reef – x = y = weight of accretion

Location	Slab #	X (g)	Y kg $CaCO_3/m^2/d$
East flat	1	111.166	0.0604
	4	115.748	0.0193
East crest	5	147.368	0.0332
	6	188.641	0.0346
West flat	10	116.509	0.0245
	12	128.381	0.0325
West crest	15	114.670	0.0378
	13	112.563	0.0343

Appendix 9

Rates of Net Accumulation on Nukubuco Reef

Location	Slab #	Mean wt. grazed	Mean bioerosion rate	Mean accretion wt.	Mean bioaccretion rate
East flat	1,4	39.575	0.0430	36.65	0.0399
East crest	5,6	31.865	0.0347	31.14	0.0339
West flat	10,12	27.565	0.0300	26.18	0.0285
West crest	15,13	33.945	0.0369	33.15	0.0361