

Distribution and abundance of regular sea urchins on two coral reefs in Fiji

S. E. COPPARD AND A. C. CAMPBELL

*School of Biological Sciences
Queen Mary, University of London
Mile End Road, London E1 4NS, UK.
E-mail: simon@diadema.fsnet.co.uk
E-mail: a.c.campbell@qmul.ac.uk*

Abstract—The distribution and abundance of thirteen species of regular sea urchin were assessed on Sosoikula and Nukubuco reefs, Fiji. Their morphology and behavior were contrasted relative to wave activity, water depth, substratum composition, food, and predation through all the reefs zones. Densities and relative densities of species in each zone were determined and their significance tested relative to the species distribution. Results indicated species associations with different reef areas, thus habitat preferences, which reflected species' competitive abilities and resource partitioning. *Echinometra mathaei* was the most prolific and adaptable species, having the greatest densities in all zones. Peak mean densities occurred in the mid back reef area on the echinoderm flat (2.64 ind. m⁻²), comprising 93.6% of all echinoids found. *Diadema savignyi* and *Diadema setosum* were found at maximum densities in the boulder zone, utilizing the narrow elevated crevice space. Both these species of *Diadema* showed an increase in test diameters and spine lengths from the reef crest to the hard coral bommies, proportional to the increase in observed crevice size. *Echinothrix diadema* and *Echinothrix calamaris* (brown color morph) demonstrated a similar trend, but with continued growth-related migration to the *Porites* and soft coral zone. The white color morph of *E. calamaris* showed no apparent association between size distribution and crevice space. This was due to behavioral adaptations, where both juveniles and adults aggregated together in the few very large crevices found. Algal and seagrass species distributions appeared to have only a moderate influence on echinoid species distributions, as most species diets appeared broad within habitat. Predation pressure was assessed to be relatively low, with greatest predator densities on the fore reef (0.24 ind. m⁻²). Refuge quality and availability, moderated by predation, combined with different echinoid morphologies and behaviors, determined species distributions through the reefs varied habitats.

Introduction

Recent research has indicated that echinoids play an important role in the ecology of coral reefs (Hughes 1994, Lirman 2001, Williams & Polunin 2001). Grazing by sea urchins alters the distribution, relative abundance, and species composition of marine plants, which in turn affects animal populations by influencing the number of available niches. Algal grazing by echinoids is recognised as being crucial in restoring and maintaining coral re-colonisation, as it protects corals from competition (Glynn et al. 1979, Hughes 1994, Lirman 2001, Williams & Polunin 2001).

Distribution and abundance of echinoids on coral reefs has been attributed to a variety of biotic and abiotic factors (Lawrence 1975, Ebert 1982, Dotan 1990). Wave activity, water depth, substratum composition, food, predation, and behavior have been reported to contribute to the distribution of echinoid species on coral reefs (Dart 1972, Herring 1972, Ebert 1982, Regis & Thomassin 1982, Lawrence 1983, Tegner & Levin, 1983, Denny et al. 1985, McClanahan 1988, Ogden et al. 1989, Dotan 1990).

Echinoid species have evolved and adapted to utilise all areas of the coral reef, thus permitting coexistence among potential competitors. Partitioning of limiting resources, such as food and space (Gladfelter & Johnson 1983, Carpenter 1986, Ogden et al. 1989), selective predation on dominant species (Paine 1966, 1974, Dayton 1971) or non-selective disturbances, keep communities in non-equilibrium states (Levine & Paine 1974, Connell 1978, Sousa 1984). Differing body morphologies and behavior allow spatial resource partitioning of the reefs variable topography (McClanahan 1988), allowing ecologically similar species to coexist (Ogden et al. 1989). McClanahan (1988) demonstrated how differing morphologies allowed different species to utilise different sized crevices, competition for crevice space being frequently won by the largest individual, regardless of species (McClanahan 1988).

This investigation aimed to establish the distribution and abundance of echinoid species, contrasting their morphology and behavior relative to wave activity, water depth, substratum composition, food, and predation through all the reefs zones. This work had a particular focus on diadematid echinoids, which have been shown to be the most widespread and ecologically important shallow water genera of tropical sea urchins (Lawrence & Sammarco 1982, Lessios 1988, Birkeland 1989, Carpenter 1997). The size distributions (horizontal test diameter and spine lengths) of diadematid echinoids were assessed to compare how closely related genera were distributed relative to crevice space to avoid predation.

DESCRIPTION OF STUDY SITE

Suva Peninsula and Laucala Bay are enclosed by Sosoikula Reef and Nukubu Reef (Fig. 1), part of the southeastern reef chain of Viti Levu (Morton & Raj 1980). The reefs form a crescent protecting Suva Harbor to the southeast and skirting the tip of the peninsula at about a 1 km distance (Morton & Raj

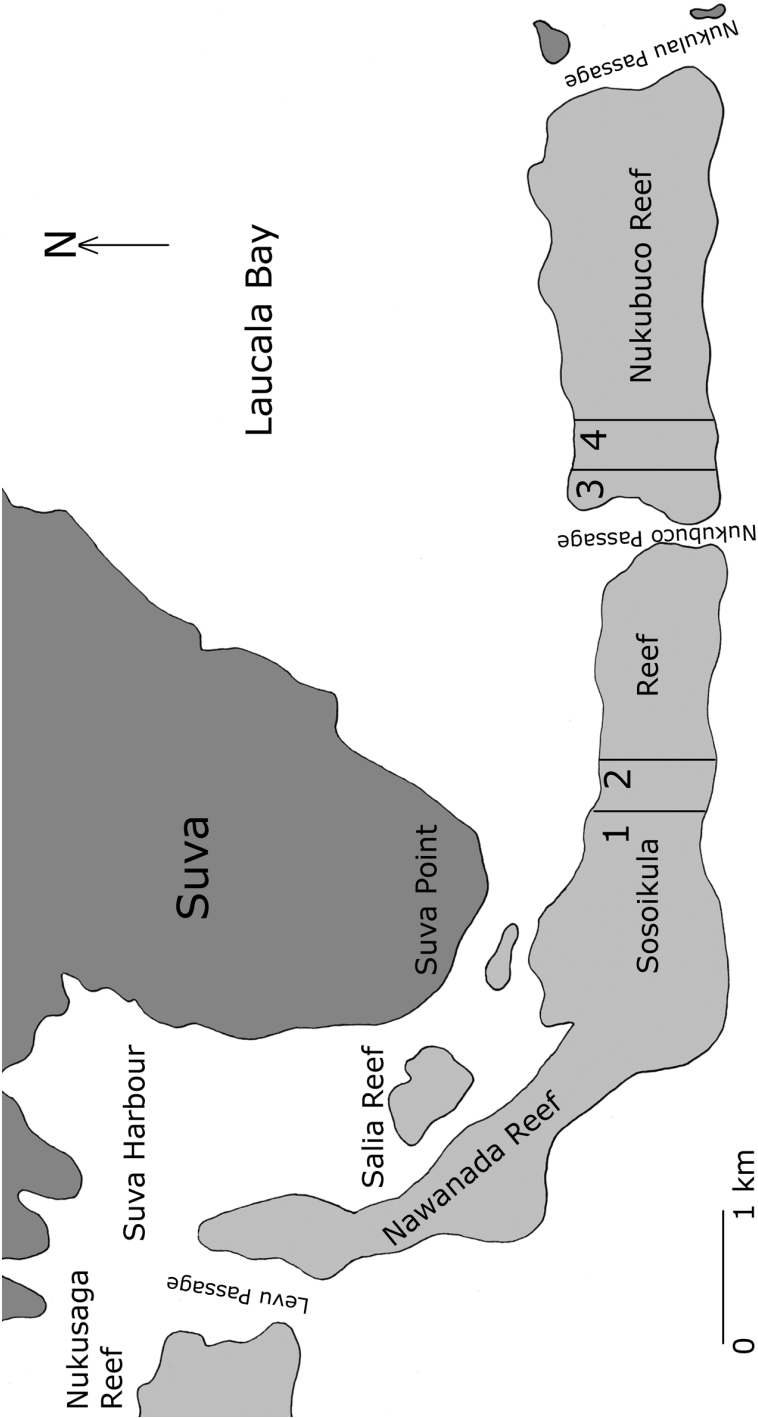


Figure 1. Map of Suva Peninsula.

1980). Sosoikula Reef and Nukubuco Reef enclose Laucala Bay, broken midway by Nukubuco Passage and to the East by Nukulau Passage with its associated sand cay islands of Nukulau and Makaluva. The transverse zonation of Sosoikula and Nukubuco reefs (see Fig. 2) comprised of the fore reef, reef crest, boulder zone, small hard coral bommies, echinoderm flat, *Porites* and soft coral zone, and the seagrass bed. The term 'echinoderm flat' was used by Morton & Raj (1980), and seemed the most appropriate and descriptive of this area.

Methods

Two 2 m x 400 m transects of Sosoikula Reef and two 2 m x 400 m transect of Nukubuco Reef were conducted in October 1998 (see Fig. 1). A 400 m transect line was flagged every meter from the fore reef to the seagrass bed. One-meter quadrats were then recorded each side of the transect, measuring the percentage cover of hard and soft corals, distribution of rock and sand in each quadrat, and the diversity of algal and seagrass species. The abundance, distribution, and diversity of echinoids and predatory fish species were then recorded. Irregular echinoids, well adapted for burrowing and deposit feeding, were not recorded in this investigation due to logistical difficulties in accurately assessing their abundance. The spine lengths and horizontal test diameters of diadematid echinoids were measured using callipers and recorded in relation to the size of available crevice space. To ascertain the species and number of echinoids within each quadrat, particularly those that were cryptic, rocks had to be turned over (replaced as found after looking for the presence of echinoids). The underside of coral heads were viewed with a snorkel and mask or viewing mirror, and specimens were removed from their crevices with a small hand rake where necessary. This information was recorded graphically, so that by using a detailed key their orientation and distribution could be easily referred to later. The abundance, distribution, and diversity of regular echinoids and predatory fish species were then recorded. Irregular echinoids, well adapted for burrowing and deposit feeding, were not recorded in this investigation due to logistical difficulties in accurately assessing their abundance. The spine lengths and horizontal test diameters of diadematid echinoids were measured using callipers and recorded in relation to the size of available crevice space.

Since the work of Staneck (1983), coral reef researchers have failed to agree on a single, reliable method for quantifying the activity of herbivores. The small transect width method minimises the underestimate of true fish population densities inherent in the transect method (Sale & Sharp 1983), and allows an accurate assessment of regular echinoid distribution if carefully surveyed (Aronson et al. 1994). It was not logistically possible to census echinoids at night, so only diurnal data were collected. Many authors believe that an echinoid day census may underestimate their abundance (Carpenter 1981, 1986). However, each quadrat was thoroughly examined to the extent that it can be stated with a high degree of confidence that no regular echinoids were missed.

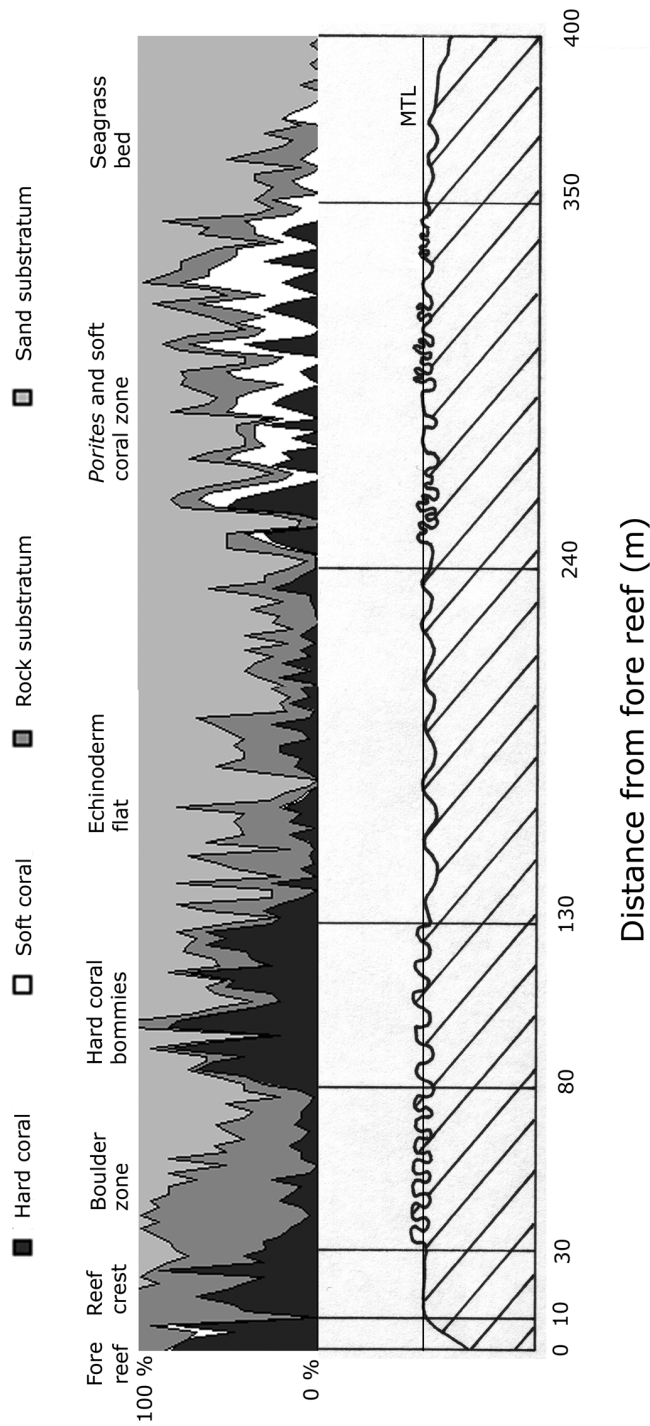


Figure 2. Substratum composition and distribution.

The number of transects replicated in this census was limited to 4 (2 m x 400 m) covering the entire width of the reef (fore reef–back reef), with 3200 1 m quadrats surveyed. This was the maximum number possible in the time frame, and should provide an accurate assessment of echinoid speciation and distribution.

Results

Substratum composition throughout the coral reefs is shown in Figure 2. Echinoid distributions and locations of species peak abundances are shown in Table 1. Species densities, standard deviations, and relative densities of sea urchins were calculated for the different zones and are shown in Table 2. Significance of species densities in each zone was assessed with a T-test, comparing mean species densities for each zone in relation to mean population density (Table 3). Results indicated species associations with different reef areas, thus habitat preferences, which reflected species' competitive abilities and resource partitioning.

Algal and seagrass species were identified using N'Yeurt et al. (1996) and revised using South & Skelton (2004). Species distributions are recorded in Table 4. This shows the number of Rhodophyta, Chlorophyta, Phaeophyta and seagrass

Table 1. Echinoid species distribution.

Fore reef	Reef crest	Boulder zone	Hard coral bommies	Echinoderm flat	<i>Porites</i> and soft coral zone	Seagrass bed
<i>Eu. met</i>	—	<i>Eu. met</i>	—	—	—	—
<i>P. imp</i>	—	<i>P. imp</i>	—	—	—	—
<i>D. sav</i>	—	<i>D. sav</i>	<i>D. sav</i>	<i>D. sav</i>	<i>D. sav</i>	—
<i>D. set</i>	—	<i>D. set</i>	<i>D. set</i>	<i>D. set</i>	—	—
<i>Ech. c</i> (b)	—	<i>Ech. c</i> (b)	<i>Ech. c</i> (b)	<i>Ech. c</i> (b)	<i>Ech. c</i> (b)	<i>Ech. c</i> (b)
—	—	<i>Ech. c</i> (w)	<i>Ech. c</i> (w)	<i>Ech. c</i> (w)	<i>Ech. c</i> (w)	—
<i>Ech. di</i>	—	<i>Ech. di</i>	<i>Ech. di</i>	<i>Ech. di</i>	<i>Ech. di</i>	<i>Ech. di</i>
—	—	—	<i>T. pil</i>	<i>T. pil</i>	—	—
—	—	<i>Tr. gr</i>	<i>Tr. gr</i>	<i>Tr. gr</i>	<i>Tr. gr</i>	—
<i>E. math</i>	<i>E. math</i>	<i>E. math</i>	<i>E. math</i>	<i>E. math</i>	<i>E. math</i>	<i>E. math</i>
—	—	<i>Ec. ac</i>	<i>Ec. ac</i>	<i>Ec. ac</i>	—	—
<i>H. mam</i>	<i>H. mam</i>	<i>H. mam</i>	<i>H. mam</i>	<i>H. mam</i>	—	—
—	<i>H. tri</i>	—	—	—	—	—

Bold type = Species peak abundance (see Table 2)

— = Species absent

Species Key

Eu. met=*Eucidaris metularia*

P. imp=*Phyllacanthus imperialis*

D. sav=*Diadema savignyi*

iD. set=*Diadema setosum*

Ech. c (b)=*Echinothrix calamaris* (brown colour morph)

Ech. c (w)=*Echinothrix calamaris* (white colour morph)

Ech. di=*Echinothrix diadema*

T. pil=*Toxopneustes pileolus*

Tr. gr=*Tripneustes gratilla*

E. math=*Echinometra mathaei*

Ec. ac=*Echinostrephus aciculatus*

H. mam=*Heterocentrotus mammillatus*

H. tri=*Heterocentrotus trigonarius*

Table 2. Densities (individuals m⁻² ± SD) and relative densities (in parenthesis) of sea urchins in the different zones on Sosoikula and Nukubu reefs, Fiji, 1998.

Species	FR	RC	BZ	HCB	EF	PSCZ	SGB
<i>Eucidaris metularia</i>	0.16 ± 0 (9.8 %)	0 (0 %)	0.02 ± 0.03 (0.7 %)	0 (0 %)	0 (0 %)	0 (0 %)	0 (0 %)
<i>Phyllacanthus imperialis</i>	0.06 ± 0 (3.7 %)	0 (0 %)	0.007 ± 0.02 (0.3 %)	0 (0 %)	0 (0 %)	0 (0 %)	0 (0 %)
<i>Diadema savignyi</i>	0.26 ± 0 (16.0 %)	0 (0 %)	0.46 ± 0.23 (16.9 %)	0.24 ± 0.21 (7.8 %)	0.04 ± 0.06 (1.4 %)	0.01 ± 0.03 (1.1 %)	0 (0 %)
<i>Diadema setosum</i>	0.06 ± 0 (3.7 %)	0 (0 %)	0.07 ± 0.04 (2.6 %)	0.03 ± 0.02 (1.0 %)	0.003 ± 0.01 (0.1 %)	0 (0 %)	0 (0 %)
<i>Echinothrix diadema</i>	0.10 ± 0 (6.1 %)	0 (0 %)	0.23 ± 0.18 (8.4 %)	0.21 ± 0.16 (6.9 %)	0.07 ± 0.09 (2.5 %)	0.08 ± 0.07 (8.5 %)	0.03 ± 0.07 (41.1 %)
<i>Echinothrix calamaris</i> (w)	0 (0 %)	0 (0 %)	0.03 ± 0.03 (1.1 %)	0.02 ± 0.04 (0.7 %)	0.003 ± 0.02 (0.1 %)	0.06 ± 0.08 (6.3 %)	0 (0 %)
<i>Echinothrix calamaris</i> (b)	0.06 ± 0 (3.7 %)	0 (0 %)	0.06 ± 0.04 (2.2 %)	0.05 ± 0.04 (1.6 %)	0.006 ± 0.01 (0.2 %)	0.09 ± 0.08 (9.5 %)	0.003 ± 0.04 (4.1 %)
<i>Tripleneustes gratilla</i>	0 (0 %)	0 (0 %)	0.02 ± 0.03 (0.7 %)	0.02 ± 0.02 (0.7 %)	0.01 ± 0.02 (0.4 %)	0.006 ± 0.02 (0.6 %)	0 (0 %)
<i>Toxopneustes pileolus</i>	0 (0 %)	0 (0 %)	0 (0 %)	0.007 ± 0.02 (0.2 %)	0.007 ± 0.01 (0.3 %)	0 (0 %)	0 (0 %)
<i>Echinometra mathaei</i>	0.80 ± 0 (49.0 %)	0.40 ± 0.14 (88.9 %)	1.80 ± 0.46 (66.0 %)	2.42 ± 0.60 (79.3 %)	2.64 ± 1.02 (93.6 %)	0.70 ± 0.60 (74.0 %)	0.04 ± 0.05 (54.8 %)
<i>Echinostrephus aciculatus</i>	0 (0 %)	0 (0 %)	0.02 ± 0.03 (0.7 %)	0.05 ± 0.04 (1.6 %)	0.04 ± 0.12 (1.4 %)	0 (0 %)	0 (0 %)
<i>Heterocentrotus mammillatus</i>	0.13 ± 0 (8.0 %)	0.03 ± 0.05 (6.7 %)	0.01 ± 0.04 (0.4 %)	0.007 ± 0.02 (0.2 %)	0 (0 %)	0 (0 %)	0 (0 %)
<i>Heterocentrotus trigonarius</i>	0 (0 %)	0.02 ± 0.02 (4.4 %)	0 (0 %)	0 (0 %)	0 (0 %)	0 (0 %)	0 (0 %)
Total (ind. m ⁻²)	1.63	0.45	2.73	3.05	2.82	0.95	0.07
FR=Fore reef	RC = Reef crest		BZ = Boulder zone		HCB = Hard coral bommies		
EF = Echinoderm flat	PSCZ = <i>Porites</i> and soft coral zone		SGB = Seagrass bed				

Table 3. T-test results. Significance of mean species densities (m^{-2}) occurring in the different zones, compared with mean species population densities on Sosoikula and Nukubuco reefs, Fiji, 1998.

Species	FR	RC	BZ	HCB	EF	PSCZ	SGB
<i>Eucidaris metularia</i>	-5.95 *+	1.14	0.25	1.14	1.14	1.14	1.14
<i>Phyllacanthus imperialis</i>	-5.96 *+	1.13	0.30	1.13	1.13	1.13	1.13
<i>Diadema savignyi</i>	-1.69	2.21	-4.71 *+	-1.39	1.61	2.06	2.21
<i>Diadema setosum</i>	-3.10 *+	2.39	-4.01 *+	-0.36	2.11	2.39	2.39
<i>Echinothrix diadema</i>	0.09	3.14 *-	-3.89 *+	-3.27 *+	1.00	0.70	0.33
<i>Echinothrix calamaris</i> (w)	1.89	1.89	-1.62	-0.45	1.54	-5.13 *+	1.89
<i>Echinothrix calamaris</i> (b)	-1.35	0.35	-1.35	-0.50	3.24 *-	-3.90 *+	1.20
<i>Tripneustes gratilla</i>	2.35	2.35	-3.52 *+	-3.52 *+	-0.59	0.59	2.35
<i>Toxopneustes pileolus</i>	1.55	1.55	1.55	-3.88 *+	-3.88 *+	1.55	1.55
<i>Echinometra mathaei</i>	1.18	2.21	1.40	-3.00 *+	-3.57 *+	1.44	3.14*+
<i>Echinostrephus aciculatus</i>	1.93	1.93	-0.53	-4.22 *+	-2.99 *+	1.93	1.93
<i>Heterocentrotus mammillatus</i>	-5.85 *+	-0.26	0.85	1.02	1.41	1.41	1.41
<i>Heterocentrotus trigonarius</i>	0.99	-6.00 *+	0.99	0.99	0.99	0.99	0.99

* Significant $T > 2.44$; others were non-significant ($T < 2.44$) (considering only magnitude, regardless of sign, +/-).

NB. *+ Significant in species presence in relation to population distribution.

*- Significant in species absence in relation to population distribution.

FR = Fore reef RC = Reef crest BZ = Boulder zone HCB = Hard coral bommies,
EF = Echinoderm flat PSCZ = *Porites* and soft coral zone SGB = Seagrass bed.

species in each zone, and the total numbers present on the reefs. Algal species diversity was found to be greatest in the boulder zone, which also had the greatest number of Rhodophyta and Chlorophyta species found on the reefs. Phaeophyta species increased in diversity from the boulder zone to the echinoderm flat, while seagrass species were only present from the hard coral bommies to the seagrass bed.

Mean urchin predator (fish) densities are recorded in Table 5, where each zone is ranked (one being the greatest) in order of predation pressure. Fish species that have been reported as echinoid predators were recorded at their greatest density on the fore reef ($0.248 \text{ ind. m}^{-2}$). From observations on the reefs, numbers of damaged tests, and remains of eaten echinoids, predation pressure was relatively

Table 4. Algal species distribution on Sosoikula and Nukubuco reefs.

Species	FR	RC	BZ	HCB	EF	PSCZ	SGB
<i>Amphiroa anceps</i> (Lamarck) Decaisne	0	1	0	0	0	0	0
<i>Amphiroa foliacea</i> Lamouroux	1	1	1	1	1	0	0
<i>Amphiroa fragillisma</i> (Linnaeus) Lamouroux	1	1	1	1	0	0	0
<i>Galaxaura marginata</i> (Ellis and Solander) Lam.	1	1	1	1	1	0	0
<i>Hypnea cervicornis</i> J. Agardh	0	1	0	0	0	0	0
<i>Jania rubens</i> Lamouroux	1	1	0	0	0	0	0
<i>Laurencia intermedia</i> Yamada	0	1	0	1	0	0	0
<i>Liagora subarticulata</i> Grunow	0	0	1	0	0	0	0
<i>Lithophyllum pustulatum</i> (Lamouroux) Foslie	0	1	1	1	0	0	0
<i>Martensia elegans</i> Hering	0	1	0	0	0	0	0
<i>Neogoniolithon frutescens</i> (Foslie) Setchell and Mason	0	0	1	1	0	0	0
Rhodophyta (No. of species)	4	9	6	6	2	0	0
<i>Bryopsis plumosa</i> (Hudson) J. Agardh	1	1	0	0	0	0	0
<i>Caulerpa racemosa</i> (Forsskål) J. Agardh							
var. <i>occidentalis</i> J. Agardh	1	1	0	0	1	0	0
var. <i>peltata</i> (Lamouroux) Eubank	0	1	0	0	0	0	0
<i>Caulerpa serrulata</i> (Forsskål) J. Agardh	0	1	1	0	1	0	0
<i>Chlorodesmis fastigiata</i> (C. Agardh) Ducker	1	1	1	0	0	1	0
<i>Codium geppiorum</i> Schmidt	0	0	1	1	1	1	0
<i>Dictyosphaeria cavernosa</i> (Forsskål) Børgesen	0	1	0	0	0	0	0
<i>Dictyosphaeria versluisii</i> Weber-Van Bosse	0	1	1	1	0	0	0
<i>Halimeda macroloba</i> Decaisne	0	0	0	0	1	1	1
<i>Halimeda micronesica</i> Yamada	1	1	1	1	1	1	1
<i>Halimeda opuntia</i> (Linnaeus) Lamouroux	0	1	0	0	0	0	0
<i>Ventricaria ventricosa</i> (J. Agardh) Olsen and West	0	1	1	1	1	1	0
Chlorophyta (No. of species)	4	10	6	4	6	5	2
<i>Dictyota cervicornis</i> Kützting	0	0	0	0	1	0	0
<i>Dictyota friabilis</i> Setchell	0	0	0	1	1	0	0
<i>Hydroclatharus clathratus</i> (C. Agardh) Howe	0	0	0	0	1	1	1
<i>Padina pavonica</i> (Linnaeus) Thivy	1	1	1	1	1	1	1
<i>Sargassum cristaefolium</i> C. Agardh	1	1	1	1	1	1	0
<i>Sargassum ilicifolium</i> (Turner) J. Agardh	0	0	0	0	0	1	0
<i>Sargassum obovatum</i> Harvey	0	1	0	0	0	0	0
<i>Turbinaria ornata</i> (Turner) J. Agardh	1	1	1	1	1	1	0
Phaeophyta (No. of species)	3	4	3	4	6	5	2
<i>Halodule uninervis</i> (Forsskål) Ascherson	0	0	0	0	0	1	1
<i>Halophila ovalis</i> (Brown) Hooker	0	0	0	1	1	1	1
<i>Syringodium isoetifolium</i> (Ascherson) Dandy	0	0	0	0	0	1	1
Seagrass (No. of species)	0	0	0	1	1	3	3
Total No. of species	11	23	15	15	15	13	7

Key: 0 = Absent 1 = Present

FR=Fore reef RC = Reef crest BZ = Boulder zone HCB = Hard coral bommies

EF = Echinoderm flat PSCZ = *Porites* and soft coral zone SGB = Seagrass bed

Table 5. Mean urchin predator (fish) densities (individuals m⁻² ± SD).

Species	FR	RC	BZ	HCB	EF	PSCZ	SGB
Serranidae							
<i>Epinephelus areolatus</i> (Forsskål)	0	0	0.003 (± 0.10)	0	0	0.002 (± 0.07)	0
<i>Plectropomus leopardus</i> (Lacépède)	0.033 (± 0.22)	0	0	0	0	0	0
Lethrinidae							
<i>Lethrinus miniatus</i> (Schneider)	0.050 (± 0.37)	0	0	0	0	0	0
<i>Lethrinus obsoletus</i> (Forsskål)	0	0	0	0	0	0	0.013 (± 0.14)
Labridae							
<i>Oxycheilinus digrammus</i> (Lacépède)	0.033 (± 0.22)	0	0	0	0	0	0
<i>Coris gaimard</i> (Quoy and Gaimard)	0.033 (± 0.22)	0	0	0.033 (± 0.31)	0.002 (± 0.07)	0	0
Diodontidae							
<i>Diodon liturosus</i> Shaw	0.033 (± 0.22)	0	0	0	0	0	0
Balistidae							
<i>Abalistes stellatus</i> (Lacépède)	0.033 (± 0.22)	0	0	0	0	0	0
<i>Balistoides conspicillum</i> (Bloch and Schneider)	0.033 (± 0.22)	0	0	0.033 (± 0.31)	0	0	0
<i>Balistoides viridescens</i> (Bloch and Schneider)	0	0	0	0	0	0.002 (± 0.07)	0
Balistidae							
<i>Balistapus undulates</i> (Park)	0	0	0	0.033 (± 0.31)	0.002 (± 0.07)	0	0
<i>Rhinecanthus aculeatus</i> (Linnaeus)	0	0	0.003 (± 0.10)	0	0	0	0
Total No. of fish (individuals m ⁻²)	0.248	0	0.006	0.099	0.004	0.004	0.013
Rank	1	6	4	2	5	5	3

FR=Fore reef

RC = Reef crest

BZ = Boulder zone

HCB = Hard coral bommies

EF = Echinoderm flat

PSCZ = *Porites* and soft coral zone

SGB = Seagrass bed

low. The remains of twelve *Echinometra mathaei* (de Blainville), five *Tripneustes gratilla* (Linnaeus), and two *Diadema savignyi* (Audouin) Michelin, which could be attributed to fish predation, were found on the reef during this study. This was determined by bite marks on the test and remnant spines and the way the semi-denuded tests had been attacked from the mouth region; clearly not forms of natural mortality.

The mean size distributions (horizontal test diameter and spine lengths) of *D. savignyi*, *Diadema setosum* (Leske), *Echinothrix diadema* (Linnaeus), and two color morphs of *Echinothrix calamaris* (Pallas) are illustrated in Figure 3.

Diadema savignyi exhibited a distinct increase in both mean test diameters and mean spine lengths from the reef crest to the hard coral bommies, where measurements reached maximum adult size (Fig. 3). This increase appeared proportional to the increase in crevice size observed on the reef, reflecting a migration (juvenile–adult) in echinoid development. The exception to this was on the fore reef, where specimens were found with larger test diameters than those found on the reef crest. These specimens were clearly adult and again their presence reflected the available crevice size.

Diadema setosum exhibited a similar trend to *D. savignyi*, but with greater spine length to test diameter ratios (Fig. 3). The increase in mean test size and spine length from the reef crest to the hard coral bommies was at a reduced rate relative to *D. savignyi*, but signified the same migration of juvenile to adults from the reef crest to the hard coral bommies, in relation to the increase in crevice size and availability. The size of adults decreased after the hard coral bommies zone. However, this could be circumstantial due to the reduced number of *D. setosum* found after this point. No *D. setosum* were found beyond the echinoderm flat.

Echinothrix diadema showed an increase in mean test diameters and spine lengths from the boulder zone to the seagrass bed, where the largest adults were found. Juveniles (banded spines) occurred predominantly on the front edge of the boulder zone, having greater spine lengths to test diameter ratios than adults. This ratio changed in young adults (solid color spines), with test diameters clearly larger than their spine lengths. Small juvenile specimens were found inhabiting areas where predominantly smaller crevices were found (reef crest and the front edge of boulder zone).

Echinothrix calamaris (white color morph) showed no obvious relationship between mean test diameters and spine lengths in relation to their distribution (Fig. 3). Both adults and juveniles were found throughout the reef, frequently occurring together as aggregations in very large crevices. The exception to this was on the fore reef and the reef crest, where no white color morphs were found. Only large adult specimens were found as individuals, in medium (50–150 mm) to large sized crevices (>150 mm), particularly on the echinoderm flat and among the *Porites* and soft coral zone.

Unlike the white color morph, the brown color morph of *E. calamaris* showed a trend of increased mean test diameters and spine lengths from the reef crest to the boulder zone, where maximum adult size was found (Fig. 3). This

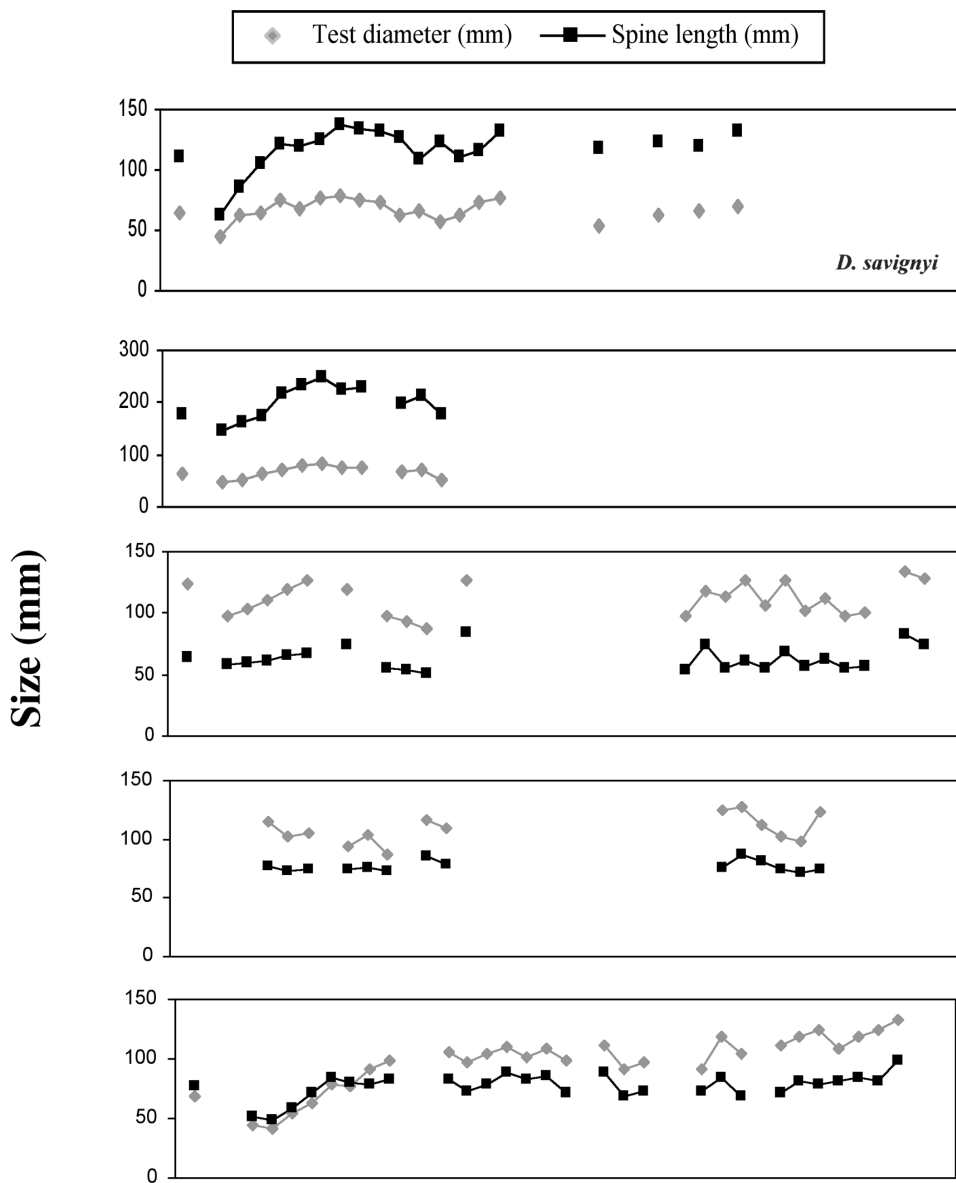


Figure 3. Mean size distribution of diadematid echinoids, based on test diameter and spine length in relation to distribution on Sosoikula and Nukubuco reefs, Fiji.

reflected the increase in crevice size between these zones. Juveniles were predominantly found on the back edge of the reef crest and the boulder zone, to the exclusion of mature adults, and were not seen beyond the hard coral bommies. Young adults, displaying their distinctly different coloration (small test but with

no banding on spines) occurred at their greatest numbers within the boulder zone, ideally suited to the smaller sized crevices (~50 mm). However, they were also found in smaller numbers throughout the rest of the reef, where small crevices were present, resulting in fluctuations in mean test diameters and spine lengths. Large adults were only found on the fore reef and towards the back of the reef among the *Porites* and soft coral, and also aggregated with conspecifics and with *E. diadema* among the few rocky outcrops in the seagrass bed. The distribution of large adults reflected the availability of larger crevices (>150 mm).

Discussion

Echinoid distributions on coral reefs throughout the world are dependent on many factors. The most important of these on Sosoikula Reef and Nukubuco Reef are wave energy, water depth, food, crevice availability, and predation pressure. The low predation pressure recorded is reported to be the result of over fishing in the Laucala Bay area (Jennings & Polunin 1995, 1996a, 1996b, Ledua & Vuki 1998).

Sea urchin assemblages have been reported at their greatest diversity and species richness at intermediate predation rates and low to intermediate sea urchin densities (McClanahan & Shafir 1990). Distributions of echinoids have been shown to be determined by their morphological features and behavior, with an evolutionary and energetic trade off between competitive ability and predator susceptibility (McClanahan 1998). Species morphologies vary in their defensive capabilities from predation, robustness from wave action, and tolerances of environmental stress parameters. Echinoid morphologies vary these features in various proportions so that species exploit different areas of the reef, thus partitioning resources. The species whose morphological features are most adaptable is able to exploit greater areas of the reef. With limited predation pressure this species dominates resources, with their resulting population expanding to the reefs carrying capacity and resulting in intraspecific competition.

On Sosoikula Reef and Nukubuco Reef, as reported on many other reefs (McClanahan 1987, 1998, McClanahan & Shafir 1990), *Echinometra mathaei* demonstrated its adaptability, having the greatest densities in all zones (Table 1). Peak mean densities occurred in the mid back reef area on the echinoderm flat (2.64 ind. m⁻²), typically seen in round-ended galleries excavated by the abrasive force of their robust spines on the coral limestone, with up to 20 ind. m⁻². *Echinometra mathaei* is thought to be the most prolific echinoid species in the world (Morton & Raj 1980), as it is able to live in both sheltered and wave impacted habitats (Khamala 1971, Herring 1972, Lawrence 1973, Ruwa 1984, McClanahan 1988). Its moderate size relative to other reef echinoids, robust spines, ability to bore into rocks, and tolerance of both aerial exposure and high water temperatures make for a very adaptable existence.

At intermediate to low predation rates and high sea urchin densities, *E. mathaei* has been shown to dominate the species composition, particularly when

competing for small crevice spaces (McClanahan & Shafir 1990). Its small size, however, limited its dominance on Sosoikula Reef and Nukubuco Reef, as larger species were able to out compete it for larger crevice space, actively pushing out the smaller species. This resulted in *E. mathaei* forming burrows in the limestone. These provided limited protection, but still exposed this species to increased predation pressure. Such predation was observed on the reef, with *E. mathaei* being the species most commonly fed upon by fish predators. From species distributions, and particularly their maximum mean densities, it can be seen that many species partition resources. Such species have adapted morphologically and physiologically to habitats, which subject them to environmental stresses, such as high water velocity and aerial exposure at low water. Other similar species directly compete for the same habitat.

The fore reef was characterised by the abundant growth of hard corals, with only small pockets of algae. Rhodophyta species were more abundant in more exposed areas, while Chlorophyta and Phaeophyta species occurred in more sheltered protected habitats. The abundance of echinoids on the fore reef was limited by predation and the availability of crevice space in which to find refuge. This was intrinsically influenced by the substratum; with the high abundance of hard coral providing relatively limited suitable refuge. The relatively high predation pressure (ranked 1) observed in this area of the reef allowed for the overlapping of species, due to the reduced overall abundance of competitors.

The reef crest's high wave energy and limited availability of crevices was reflected in the low abundance of echinoids and the presence of specialised species. Algal species were defined by the high diversity of Rhodophyta species (Table 4) and low abundance of Phaeophyta species. *Heterocentrotus trigonarius* (Lamarck) was found at its maximum mean density (0.02 ind. m⁻²) while *Heterocentrotus mammillatus* (Linnaeus) occurred at its second greatest density (0.03 ind. m⁻²). Their robust morphologies, high tenacity in the presence of strong wave action (Dotan, 1990) and their reported dietary preference for crustose coralline algae (Ogden et al. 1989) indicate a specialised existence with this area of the reef. Even though predation pressure was low, the high disturbance from wave action limited the abundance of competitors, allowing for the overlap of species.

The greatest species diversity of echinoids was found in the boulder zone (eleven species), with relatively high echinoid abundance (2.73 ind. m⁻²). The boulder zone had a large abundance of algae, but reduced species diversity (Table 4). Intermediate predation pressure was recorded (ranked 4), while crevice space was observed not to be limiting. Intermediate predation pressure in conjunction with varied refuge availability suited to different echinoid morphologies prevented *E. mathaei* from dominating the habitat.

The hard coral bommies contained a diverse range of crevice sizes, appropriate for a range of sea urchin morphologies. High echinoid species diversity was observed in this zone (ten species), with the maximum mean density of 3.05 ind. m⁻² observed on the reef. Refuge was similar to the previous zone; however, pre-

dation pressure was greater (ranked 2). The hard coral bommies had a reasonable diversity of algal species with an increasing abundance and diversity of Phaeophyta species (Table 4). *Diadema savignyi* and *D. setosum* were ideally suited to this zone, benefiting from the elevated narrow crevices. *Echinostrephus aciculatus* (Agassiz) was found at its maximum mean density (0.05 ind. m⁻²) in this zone, boring into the exposed areas of coral limestone. The larger crevice spaces were ideally suited to the larger diadematid echinoids, with *E. diadema* at significant densities to its overall distribution.

The first 20 m and last 15 m of the echinoderm flat remained immersed at low water, with the majority of this zone typically being exposed, risking its inhabitants to varying degrees of desiccation. This limited the distribution of species through this zone. Predation pressure was low (ranked 5), while the algal assemblage was characterised by the reduction in diversity and abundance of Rhodophyta species from the previous zone. *Echinometra mathaei* was by far the most abundant species. It is able to tolerate limited aerial exposure and high water temperatures (Lawrence 1973), and in this investigation it was seen well above the low water mark on rocks and dead coral where it was exposed to the hot Fijian sun for periods of several hours.

The *Porites* and soft coral zone had a reduced echinoid species diversity and low predation pressure (ranked 5). No Rhodophyta species were found (Table 4), while patches of the seagrass species *Halophila ovalis* (Brown) Hooker and *Syringodium isoetifolium* (Ascherson) Dandy were found in corresponding areas of sandy substratum. The front edge of this zone was emersed on very low tides. However, the back edge always remained immersed thus providing a range of habitats. This zone was characterised by the abundant growth of soft corals, the most common species belonging to the genera *Sarcophyton* and *Sinularia*. *Porites andrewsi* Vaughan was abundant in the deeper stretches of this zone, while *Porites lobata* Dana grew to form micro-atolls over one meter in diameter. Soft coral covered much of the rock present in this zone and in itself provided refuge for echinoids. *Echinometra mathaei* dominated the front edge of this zone where only small crevices occurred with a high risk of desiccation. Larger species such as *E. calamaris* (both white and brown color morphs), *E. diadema*, and *T. gratilla* dominated the latter areas of the zone, where low lying large crevices occurred and refuge was provided under the large colonies of soft corals. Unlike the white color morph, the brown color morph of *E. calamaris* was also found in the open among conspecifics. The differences in interambulacral spine morphologies between the two color morphs of *E. calamaris* (blunt ended in the white color morph, sharp pointed in the brown color morph [Coppard 2002, Coppard & Campbell 2004]) provided them with an added degree of protection from predation. This benefit was maximised when surrounded by conspecifics.

The low abundance of *D. savignyi* (0.01 ind. m⁻²) contradicts many reports (Taylor 1968, Dart 1972, Herring 1972, Benayahu & Loya 1977, Mastaller 1979, Regis & Thomassin 1982), which state that this species prefers sheltered, calm water habitats. Intense competition for large crevice spaces may be the reason

for this. The high abundance of both color morphs of *E. calamaris* and *E. diadema*, which are morphologically more suited to the larger wider but lower crevices found in this zone, would allow them to actively push out smaller species (such as *Diadema*), increasing predation pressure. It is therefore reasonable to assume that *Diadema* did not migrate so far back on the reef, or were out competed.

The seagrass bed remained immersed even on the lowest spring tides, with only the transitional area between the *Porites* and soft coral zone and the seagrass bed ever partially exposed. The substratum composition was almost entirely coarse sand (90 %), with sporadic rock/coral rubble (8 %) strewn throughout and a few small patches of soft coral (2 %). Three species of seagrass were present, *Syringodium isoetifolium* had the greater abundance, while *Halophila ovaes* and *Halodule uninervis* (Forsskål) Ascherson occurred sporadically in patches and isolated areas. *Halimeda macroloba* Decaisne and *Halimeda micronesica* Yamada occurred in small clumps, apparently randomly distributed throughout the seagrass bed, as on most of the reef. The only brown alga seen was *Hydroclathrus clathratus* (C. Agardh) Howe. This typically unattached species was carried around on the reef by water movement, often occurring trapped between the few large rocks present in the seagrass bed and in the small depressions and undulations of the substratum.

The regular urchin population in the seagrass bed appeared to be limited by the lack of crevice space due to the substratum and the raised predation pressure (ranked 3). Food was abundant, with many echinoid species that have been reported to readily feed on seagrass having either a very low abundance or were not present. *Echinometra mathaei* were present, but only in very low numbers, finding refuge by burrowing into the few pieces of coral limestone rock present. Only the very large adult specimens of *E. calamaris* (brown color morph) and *E. diadema* were seen in this zone. Their large size in itself was likely to afford some level of protection from predation, particularly when in aggregations. *Tripneustes gratilla* were not present in any of the transects in this zone. This species has been reported to be typically associated with areas of seagrass (McClanahan 1988, McClanahan & Shafir 1990). Dotan (1990) reported that the ephemeral nature of *Tripneustes gratilla* gives rise to contrasting reports concerning its abundance and ecology. Fielding (1985) also mentioned that in Hawaii this is a wandering species without a home site on the reef. In this investigation it is likely that the abundance and distribution of *Tripneustes gratilla* was greatly affected by the indigenous people who actively search for this species as a food resource.

Where predation and crevice space are not limiting, food availability is reported to govern the reef's carrying capacity of urchin populations (McClanahan 1988). Sea urchin diets are reported to be broad within habitat (McClanahan 1988). Species of *Diadema* are reported to feed extensively on *Thalassia*, *Syringodium* and other brown and green algae (Ogden 1973, Randall et al. 1964, Lewis 1964, Valdez & Villalobos 1978). Species in this genus have

also been reported to feed on foraminiferans, molluscs, polyzoans, crustaceans, corals, boring algae, and diatoms (Mortensen 1940, Taylor 1968, Pearse 1970, Dart 1972, Herring 1972, Atkinson et al. 1973, Williams 1979). From such research it would appear that species of this genus are very adaptable, being able to sustain themselves on a wide variety of food sources. In this study both *D. savignyi* and *D. setosum* were observed feeding on a variety of algal species, particularly *Padina pavonica* (Linnaeus) Thivy and *H. clathratus* when available, but not *Syringodium* as previously reported. For this reason inter- and intra-specific competition for one specific algal species seems unlikely.

Echinometra mathaei has been reported to be dependent on drift algae (Khamala 1971, Campbell et al. 1973, Ogden et al. 1989). This species was observed many times in this area of the reef with small pieces of *P. pavonica* between their spines. Such pieces of algae were observed being moved around to the mouth, whereupon feeding began. However, *E. mathaei* were also observed actively grazing at night. This suggests that although this species of echinoid feeds on drift algae, it is not as dependent on this form of feeding, as some authors have previously believed.

McClanahan et al. (1994) and Seychelles Marine parks expedition 1995 (personal correspondence) reported that *E. diadema* and *E. calamaris* exhibit a preference for sites with areas of seagrass. This, however, was not the finding in this investigation. Only very small populations of *E. diadema* and the brown color morph of *E. calamaris* were found in the seagrass bed, preferring areas with suitable crevice space regardless of algal or seagrass species distribution. The seagrass bed on Sosoikula Reef and Nukubuco Reef was growing predominantly on a sandy substratum, with pockets of rock and coral rubble where regular echinoids aggregated. Earlier studies may have found *E. diadema* in seagrass beds not specifically due to the presence of seagrass, but possibly due to the substratum on which the seagrass was growing providing refuge from predation. This has been shown with *Echinometra mathaei*, which reached high densities within seagrass, only if the seagrass was growing over coral rubble, and avoiding seagrass associated with coral sand (Muthiga & McClanahan 1987).

The findings of this investigation have shown that on Sosoikula and Nukubuco reefs, refuge quality and availability, moderated by predation, combined with different echinoid morphologies and behaviors, determined species distributions through the reefs varied habitats.

Acknowledgements

We would like to thank Peter Newell and Robin South for allowing us to use the facilities at the Marine Studies Programme, University of the South Pacific, Fiji. We are grateful to Shirley Mohammed-Coppard for her assistance with data collection and Posa Skelton for his help with algal species identification.

References

- Aronson, R. B., P. J. Edmunds, W. F. Precht, D. W. Swanson & D. R. Levitan. 1994. Large-scale, long-term monitoring of Caribbean coral reefs: simple, quick, inexpensive techniques. *Atoll Research Bulletin* 421: 1–19.
- Atkinson, C., S. Hopley, L. Mendelson & S. Yacowitz. 1973. Food studies on *Diadema antillarum* on a patch reef, St Croix Virgin Islands. *Special Publications of the West Indies Laboratory, Christiansted* 2: 65–80.
- Benayahu, Y. & Y. Loya. 1977. Seasonal occurrence of benthic algal communities and grazing regulations by sea urchins at the coral reefs of Elat, Red Sea. *Proceedings of the 3rd International Coral Reef Symposium*. Miami, Florida. 1: 383–389.
- Birkeland, C. 1989. The influence of echinoderms on coral-reef communities. 1–79 *In* M. Jangoux & J. M. Lawrence (eds.) *Echinoderm Studies*. A. A. Balkema, Rotterdam, The Netherlands.
- Campbell, A. C., J. K. G. Dart, S. M. Head & R. F. G. Ormond. 1973. The feeding activity of *Echinostrephus molaris* (de Blainville) in the central Red Sea. *Marine Behavior and Physiology* 2: 115–169.
- Carpenter, R. C. 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *Journal of Marine Research* 39: 749–765.
- Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* 56: 345–363.
- Carpenter, R. C. 1997. Invertebrate predators and grazers. 198–248. *In* C. Birkeland (ed.) *Life and Death on Coral Reefs*. Chapman and Hall, New York.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
- Coppard, S. E. 2002. Morphological and ecological differences between species of the genera *Diadema* and *Echinothrix*. Ph.D. thesis, Queen Mary, University of London. 466 pp.
- Coppard, S. E. & A. C. Campbell. 2004. Taxonomic significance of spine morphology in the echinoid genera *Diadema* and *Echinothrix*. *Invertebrate Biology* 123: 357–371.
- Dart, J. K. G. 1972. Echinoids, algal lawns and coral recolonization. *Nature*, London 239: 50–51.
- Dayton, P. K. 1971. Competition, disturbance, and community organisation: the provision and subsequent utilisation of space in a rocky intertidal community. *Ecological Monographs* 41: 351–389.
- Denny, M.W., T. L. Daniel & M. A. R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. *Ecological Monographs* 55: 69–102.
- Dotan, A. 1986. Aspects of the biology and ecology of the sea urchins at the Northern Red Sea, with an emphasis on *Heterocentrotus mammillatus*. Unpublished Ph.D. thesis, Tel. Aviv University, Tel Aviv, Israel.

- Dotan, A. 1990. Distribution of regular sea urchins on coral reefs near the south-eastern tip of the Sinai peninsular, Red Sea. *Israel Journal of Zoology* 37: 15–29.
- Ebert, T. A. 1982. Longevity, life history and relative body wall size in sea urchins. *Ecological Monographs* 52: 353–394.
- Fielding, A. 1985. *Hawaiian Reefs and Tide Pools*. 3rd edition. Island Explorations, Honolulu, HI.
- Gladfelter, W. G. & W. S. Johnson. 1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). *Ecology* 64: 552–563.
- Glynn, P. W., G. M. Wellington & C. Birkeland. 1979. Coral reef growth in the Galapagos: limitation by sea urchins. *Science* 203: 47–49.
- Herring, P. J. 1972. Observations on the distribution and feeding habits of some littoral echinoids from Zanzibar. *Journal of Natural History* 6: 169–175.
- Hughes, T. P. 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551.
- Jennings, S. & N. V. C. Polunin. 1995. Comparative size and composition of yield from six Fijian Reef fisheries. *Journal of Fish Biology* 46: 28–46.
- Jennings, S. & N. V. C. Polunin. 1996a. Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef communities. *Journal of Applied Ecology* 33: 400–412.
- Jennings, S. & N. V. C. Polunin. 1996b. Impacts of fishing on tropical reef ecosystems. *Ambio* 25: 44–49.
- Khamala, C. P. M. 1971. Ecology of *Echinometra mathaei* at Diani Beach, Kenya. *Marine Biology* 11: 167–172.
- Lawrence, J. M. 1973. Temperature tolerance of tropical shallow-water echinoids at Elat (Red Sea). *Israel Journal of Zoology* 22: 143–150.
- Lawrence, J. M. 1975. The relationship between marine plants and sea urchins. *Oceanography and Marine Biology Annual Review* 13: 213–286.
- Lawrence, J. M. 1983. Alternate states of populations of *Echinometra mathaei* (de Blainville) in the Gulf of Suez and the Gulf of Aqaba. *Proceedings of the International Conference of Marine Sciences in the Red Sea, Al Ghardaqa, Egypt*. 141–147.
- Lawrence, J. M. & P. W. Sammarco. 1982. Effects of feeding in the environment: *Echinoidea*. In M. Jangoux & J. M. Lawrence (eds.), *Echinoderm Nutrition*, A.A. Balkema, Rotterdam (1982), 499–519.
- Ledua, E. & V. C. Vuki. 1998. The inshore fisheries resources of Fiji. In *Fisheries and Marine Resources. Papers presented at Symposium 8, VIII Pacific Science Inter-Congress*. The University of the South Pacific.
- Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annual Review of Ecology and Systematics* 19: 371–393.
- Levine, S. A. & R. T. Paine. 1974. Disturbance patch formation and community structure. *Proceedings of the National Academy of Sciences (USA)* 71: 2744–2747.

- Lewis, J. B. 1964. Feeding and digestion in the tropical sea urchin *Diadema antillarum* Philippi. Canadian Journal of Zoology 42: 549–557.
- Lirman, D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19: 392–399.
- Mastaller, M. 1979. Beiträge Faunistik und Ökologie der Mollusken und Echinodermen in der Korallenriffen bei Aquaba, Rotes Meer. Unpublished Ph.D. Dissertation. Ruhr University Bochum.
- McClanahan, T. R. 1987. Over fishing and coral reef degradation: a preliminary report from East Africa. Conservation Biology 1: 97–99.
- McClanahan, T. R. 1988. Coexistence in a sea urchin guild and its implications to coral reef diversity and degradation. Oecologia 77: 210–218.
- McClanahan, T. R. 1998. Predation and the distribution and abundance of tropical sea urchin populations. Journal of Experimental Marine Biology and Ecology 221: 231–255.
- McClanahan, T. R. & S. H. Shafir. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia 83: 362–370.
- McClanahan, T. R., M. Nugues & S. Mwachireya. 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons; the role of reef management. Journal of Experimental Marine Biology and Ecology 184: 237–254.
- Mortensen, T. 1940. Monograph of the Echinoidea. III (1), C.A. Reitzel., Copenhagen. 370.
- Morton, J. & U. Raj, 1980. The Shore Ecology of Suva and South Viti Levu. Institute of Marine Resources, University of the South Pacific, Fiji. 162.
- Muthiga, N. A. & T. R. McClanahan. 1987. Population changes of a sea urchin (*Echinometra mathaei*) on an exploited fringing reef. African Journal of Ecology 25: 1–8.
- N'Yeurt, A. D. R., G. R. South & D. W. Keats. 1996. A revised checklist of the benthic marine algae of Fiji (including the island of Rotuma). Micronesica 29: 49–96.
- Ogden, J. C. 1973. Foraging strategies of the echinoid *Diadema antillarum* Philippi, a coral reef herbivore. Bulletin of the Ecological Society of America 24: 29.
- Ogden, N. B., J. C. Ogden & I. A. Abbott. 1989. Distribution, abundance and food of sea urchins on a Leeward Hawaiian reef. Bulletin of Marine Science 45: 539–549.
- Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100: 65–75.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal competitor. Oecologia 15: 93–120.

- Pearse, J. S. 1970. Reproductive periodicities of Indo-Pacific invertebrates in the Gulf of Suez III. The echinoid *Diadema setosum* (Leske). *Bulletin of Marine Science* 20: 697–720.
- Pearse, J. S. 1998. Distribution of *Diadema savignyi* and *D. setosum* in the tropical Pacific. In *Echinoderms: San Francisco*, R. Mooi & M. Telford (eds.) pp. 777–782.
- Randall, J.E., R. E. Schroeder & W. A. Starck. 1964. Notes on the echinoid *Diadema antillarum*. *Caribbean Journal of Science* 4: 421–433.
- Regis, M. B. & B. A. Thomassin. 1982. Ecologie des échinoides réguliers dans les récifs coralliens de la région de Tulear (S. W. de Madagascar). Adaption de la microstructure des piquants. *Annals de l'Institut Océanographique, Paris.*, 58: 17–158.
- Ruwa, R. K. 1984. Invertebrate faunal zonation on rocky shores around Mombasa, Kenya. *Journal of Science and Technology (B)* 5: 49–65.
- Sale, P. F. & B. J. Sharp. 1983. Correction for bias in visual transect censuses of coral reef fishes. *Coral Reefs* 2: 37–42.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecological Systems* 15: 353–391.
- South, G. R. & P. A. Skelton. 2004. Catalogue of the marine benthic macroalgae of the Fiji Islands, South Pacific. *Australian Systematic Botany* 16: 1–60.
- Staneck, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* 9: 44–61.
- Taylor, J. D. 1968. Coral reef and associated invertebrate community (mainly molluscan) around Mahe, Seychelles. *Philosophic Transactions of the Royal Society, London (B)* 254: 129–206.
- Tegner, M. J. & L. A. Levin. 1983. Spiny lobsters and sea urchins: analysis of a predator prey interaction. *Journal of Experimental Marine Biology and Ecology* 73: 125–150.
- Valdez, M. F. & C. R. Villalobos. 1978. Distribution espacial, correlacion con el substrata y grado de agregacion en *Diadema antillarum* Philippi, (Echinodermata, Echinoidea). *Revista de Biología Tropical* 26: 237–245.
- Williams, A. H. 1979. Interference behavior and ecology of the three spot damselfish; (*Eupomacentrus planifrons*). *Oecologia* 38: 223–230.
- Williams, I. D. & N. V. C. Polunin. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs*, 19: 358–366.