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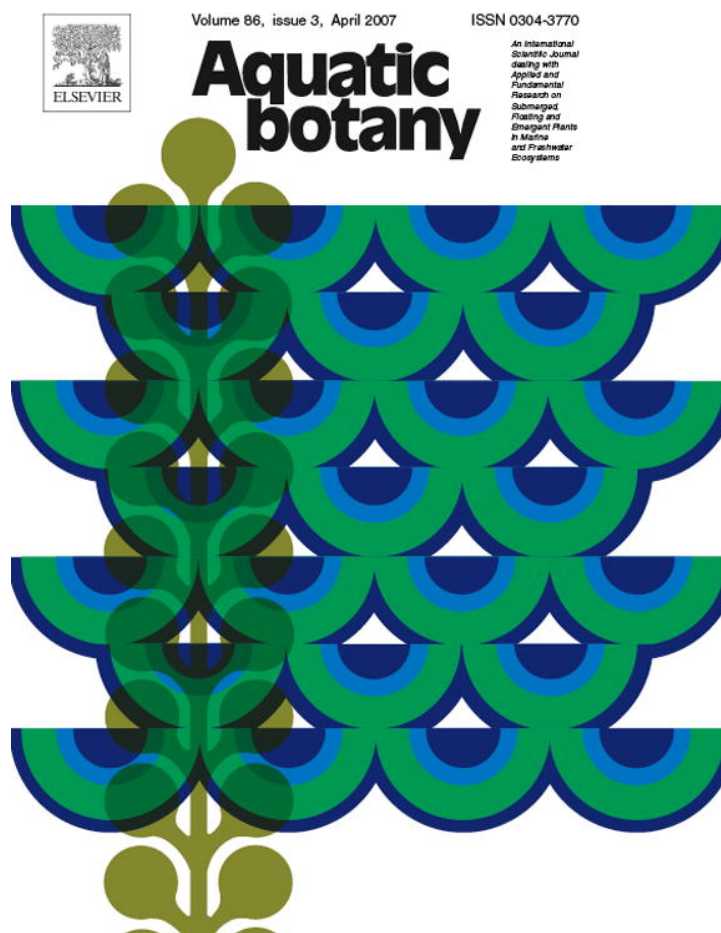


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Grazing preferences of diadematid echinoids in Fiji

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Abstract

Grazing preferences of two species of *Diadema* and two species of *Echinothrix*, including two colour morphs of *Echinothrix calamaris*, were investigated by gut contents analysis, in situ feeding observations, and grazing preferences trials in aquaria. Grazing preferences were compared to the distribution and abundance of diadematid sea urchins and the percentage cover of algal and seagrass species throughout Sosoikula Reef and Nukubuco Reef, Fiji. Results showed that grazing was selective, with distinct preferences between sea urchin genera, species, and colour morphs of *E. calamaris*. Preferred species of algae were non-calcareous, with reportedly low concentrations of tannins, phenols and bioactive compounds. Both *Diadema savignyi* and *D. setosum* selected *Codium geppiorum* as their most preferred species, followed by *Hydroclathrus clathratus*. All *Echinothrix* favoured *Hy. clathratus*, with both colour morphs of *E. calamaris* next selecting *Padina pavonica* and *E. diadema* selecting green filamentous algae. The seagrass species *Syringodium isoetifolium* was only grazed in significant quantities by *E. calamaris* (b) and *E. diadema*. This reflected species distributions in the seagrass bed. Peak abundances of diadematid sea urchins coincided with many of their grazing preferences at their maximum percentage cover. However, only *E. diadema* and *D. savignyi* had significant correlations with preferred algal/seagrass species (*E. diadema* with *Co. geppiorum*, and *D. savignyi* with *G. marginata*) throughout the subhabitats identified on the reefs.

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Keywords: *Diadema*; *Echinothrix*; Algae; Seagrass; Herbivore; Reef

1. Introduction

Coral reef communities hold the greatest marine biodiversity on earth and the Indo-west Pacific in particular has by far the greatest reef ecosystem biodiversity (Schumacher, 1972). Reef systems throughout the world are increasingly under threat from global warming, over fishing, pollution and tourist development (Abelson et al., 1999; Aronson et al., 2002). Evidence of reef degradation is continually being reported, for example the Caribbean (e.g. Hughes, 1994), and the Maldives (e.g. McClanahan, 2000). Grazing animals, especially sea urchins and fish, are known to play an important role in the ecology of coral reefs (Leighton, 1971; Hughes, 1994; Lirman, 2001; Williams and Polunin, 2001) by altering the distribution, relative abundance and species composition of marine plants. Consequently grazing by sea urchins is thought to be crucial in restoring and maintaining coral re-colonisation, as it protects

corals from competition (Glynn et al., 1979; Hughes, 1994; Lirman, 2001; Williams and Polunin, 2001).

One group of sea urchins in particular, the family Diadematidae Peters, 1855 are thought to have a very important role as reef grazers on account of their size and numbers (Mortensen, 1940). In the Caribbean, major algal growths developed over reefs following the mass mortality of the long spined sea urchin, *Diadema antillarum* Philippi, 1845 caused by a toxic infection (Hughes et al., 1985). Despite increases in the abundance of, and grazing by herbivorous fishes, the algal community was found to increase in percentage cover and biomass, resulting in a 75–95% decrease in coral cover over a 6 year period (Hughes et al., 1987). This revealed that increased grazing by fishes did not compensate for the loss of grazing by *D. antillarum* in controlling algal abundance and community structure (Carpenter, 1990). It has also highlighted the need for research to assess the significance of these urchins on coral reefs in the Indo-Pacific where few reports are known (Lawrence, 1987).

Although many sea urchin species are quite catholic in their tastes, others are more specialised, as evidenced by experiments on grazing preference (Solandt and Campbell, 2001). Herbivore

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food preferences have been shown to interact with plants competitive abilities, life histories and physical tolerances, in determining the impact of a grazer on the plant community (Lawrence, 1975; Lubchenco, 1978). This impact strongly influences distribution and abundances of benthic marine plants (Leighton, 1971). Of all the echinoderms, the regular echinoids consume the largest variation in food (Mortensen, 1928). The masticatory apparatus, the Aristotle's Lantern, is adapted for biting, tearing, rasping and can function also as a 'grab' (Ridder and Lawrence, 1982). Echinoids are well documented feeding on a wide variety of plant and animal material, including foraminiferans, molluscs, bryozoans, crustaceans, corals, algae, seagrass and diatoms (Mortensen, 1940; Taylor, 1968; Pearse, 1970; Dart, 1972; Herring, 1972; Atkinson et al., 1973; Williams, 1979; Campbell et al., 2001; Solandt and Campbell, 2001).

Morphological evidence of niche differentiation is perhaps most likely to be seen in the details of feeding apparatus (Townsend et al., 1990) and in echinoids the masticatory apparatus (Aristotle's Lantern) is a major taxonomic indicator used to distinguish between families. Since the present study is investigating members of one family (Diadematidae), where lantern morphology is uniform (Aulodont), lantern structure is not a factor in niche separation. However, different species within a family may target different food resources available within the reef community (Ogden et al., 1973). *Diadema antillarum* has been reported to feed extensively on *Thalassia*, *Syringodium* and red, brown and green algae (Randall, 1961; Randall et al., 1964; Lewis, 1964; Ogden, 1973; Valdez and Villalobos, 1978). McClanahan et al. (1994) reported that *Echinothrix diadema* (Linnaeus, 1758) exhibited a much higher preference for assays of seagrass (*Thalassodendron* sp.) than other sea urchin species, while *Diadema setosum* (Leske, 1778) and *Diadema savignyi* Michelin, 1845 favoured a *Thalassia* sp. dominant diet.

Niche partitioning between species is not always well defined in the literature (Townsend et al., 1990). Niche differentiation among closely related and co-occurring species has been a subject of debate where field observations did not always appear to support theory (i.e. Diamond, 1975; Fenchel, 1975; Hilleberg, 1975, 1976, 1986; Cherrett, 1987). Exclusion occurs when the realised niche of the superior competitor completely fills those parts of the fundamental niche of the inferior competitor that are provided in the local habitat. Based on the literature above, we hypothesise that the structure of feeding apparatus cannot be instrumental in niche differentiation and we speculate that the presently investigated guild of sea urchins that have a varied diet should differentiate in types of food items taken and in selection of subhabitats across the reefs.

We addressed the following specific questions: (a) what are the major algal/seagrass species consumed and do the five urchin taxa differ in food spectrum? (b) do algal/seagrass species taken in the lab and on the coral reef correspond? (c) does quantity and type of food consumed correspond to abundance of food items in the subhabitats distinguished?

2. Description of study site

Suva Peninsula and Laucala Bay are enclosed by Sosoikula Reef and Nukubuco Reef (Latitude 18°08'S, Longitude 178°26'E), part of the southeastern reef chain of Viti Levu (Morton and Raj, 1980). The reefs form a crescent protecting Suva Harbour to the southeast and skirting the tip of the peninsula at about a 1 km distance (Morton and Raj, 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 comprises of the fore reef, reef crest, boulder zone, hard coral bommies, echinoderm flat, *Porites* and soft coral zone and the seagrass bed. The term 'echinoderm flat' was used by Morton and Raj (1980), and seems the most appropriate and descriptive of this area. The mean sea level along the transects was 1.1 m, with a tidal amplitude from 0.2 to 1.9 m throughout the time of the investigation. At low water the boulder zone, hard coral bommies, *Porites* and soft coral zone and the seagrass bed had pools or large areas that remained immersed even on very low spring tides. However, only the first 20 m and last 15 m of the echinoderm flat remained immersed at mean low water, with the majority of this zone typically being exposed, risking its inhabitants to varying degrees of desiccation.

3. Method

Two 2 m × 400 m transects of Sosoikula Reef and two 2 m × 400 m transect of Nukubuco Reef were recorded from the fore reef to the seagrass bed. One metre quadrats were then recorded each side of the transects. The abundance and distribution of diadematid echinoids and the percentage cover of algal and seagrass species were recorded. Eight specimens each of *D. savignyi*, *D. setosum*, *E. diadema*, and two morphologically different colour morphs (white and brown; possible species/subspecies, sensu Coppard and Campbell, 2004, 2005a,b, 2006a,b) of *E. calamaris* (Pallas, 1774) were collected every fourth day from Sosoikula and Nukubuco reefs for a three-month period (January–March, 1999). At this time of year, sea temperatures were highest (27 °C, Coppard and Campbell, 2005a) and consequentially expected feeding rates should be greatest (Pearse, 1975). Four of each of the eight specimens collected were used for gut contents analysis, and four for laboratory grazing experiments. Any in situ feeding activity on the reef was noted. This included snorkelling at night to observe nocturnal feeding. Early morning specimen collection was essential to ensure the presence of food in the gut from the previous nights feeding, before digestion made identification of material impossible. Live specimens were transported to the laboratory in large, sealed, plastic containers. Upon arrival four specimens of each species were dissected and the gut contents removed and preserved in 70% ethanol for further analysis.

Twelve aquaria were set-up eight weeks prior to the food selection experiment, to allow maturation of bacteria in the

under-gravel filtration beds. In each aquarium a power filter was used to initially mechanically clean the water and then drive the pre-cleaned water through the gravel bed of a reverse flow biological filter at a rate of 840 litres/hour. The aquaria were housed in a room with controlled temperature and lighting. Water temperature was set at 27 °C (mean reef water temperature, Coppard and Campbell, 2005a) and the lighting (using Metal Halide bulbs) set at an intensity of 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on a 12 h on, 12 h off regime. Light intensity settings in aquaria measured the average midday readings recorded on coral reefs at a depth of 5 m (Levy et al., 2004). Sea urchins of each species were placed as conspecific pairs into separate aquaria with the two remaining aquaria set-up as controls.

Fifteen algal species and two seagrass species were collected from Sosoikula and Nukubuco reefs. Algae and seagrass species were identified using N'Yeurt et al. (1996) and revised using South and Skelton (2004). Species selected for this study were collected on the basis that they were observed in surrounding areas of high echinoid abundance. Thirty grams of each alga or seagrass (wet weight) were used. The algal and seagrass species were mixed and tied to a perforated plastic sheet. This sheet was buried under the coral sand, allowing the sea urchins equal opportunity to graze any one species. This assay was then presented to two adult specimens of each urchin species and colour morph, in separate aquaria ($n = 92$ individuals of each species/colour morph over three months). The sea urchins were allowed to graze for a 48 h period, with observations of feeding noted diurnally and nocturnally. After this period the algae and seagrass were removed from the tank, blotted dry and re-weighed to ascertain preferential feeding. Two controls were set, with algae and seagrass but no sea urchins, to test for weight losses or gains due to photosynthesis or respiration. The mean percentages (\pm S.E.) of algae and seagrass species consumed were calculated and ranked in order of highest consumption, thus greatest preference. From this, grazing rates were calculated as grams eaten per echinoid per day. Unlike the experimental procedures of Vadas (1977) and Shunula and Ndibalema (1986), sea urchins were not pre-starved for a 24 h period, as this might alter their grazing preferences and behaviour (Campbell et al., 2001).

After the data were initially checked to assess whether they were normally distributed, a chi-square test using Bonferroni adjustment was used to determine the significance of grazing preferences between sea urchin species. One-way ANOVA, using Tukey's Honestly Significant Difference test (HSD) for pair-wise comparisons was used to test the significance of specific grazing preferences, both within and between each sea urchin species and to compare grazing rates between sea urchin species. Preferred species of algae/seagrass were placed into homogenous groups (no significant difference in preference between species pairs within the group) for each sea urchin species. Mean sea urchin densities and mean algal and seagrass species percentage cover (\pm S.E.) were calculated for the different zones. ANOVA and Tukey's HSD were then used to statistically compare sea urchins and algal and seagrass species distributions in the different zones. Sea urchin, algal and seagrass species distributions were ranked (1 = highest)

according to their abundance throughout the reefs zones. Pearson's correlation coefficient was applied to the ranked data to test whether sea urchin species distributions correlate with their preferred algal species distributions.

4. Results

4.1. Grazing preferences trials in aquaria

Grazing preferences were found to be significantly different between all sea urchin species ($P < 0.05$, see Table 1). However, with Bonferroni adjustment (0.05/10; $P < 0.005$) grazing preferences were not significantly different between *E. calamaris* (b) and *E. diadema* ($P = 0.014$). *Codium geppiorum* Schmidt, 1923 was the most preferred species of algae/seagrass ($P < 0.01$) for both *D. savignyi* and *D. setosum* (ranked 4 for both *E. calamaris* (w) and *E. diadema*; 6 for *E. calamaris* (b); homogenous group (HG) III for both colour morphs of *E. calamaris*, HG IV for *E. diadema*), while *Hydroclathrus clathratus* (C. Agardh) Howe, 1920 was the most preferred species ($P < 0.01$) by all *Echinothrix* (ranked 2, HG II for both species of *Diadema*). *Padina pavonica* (Linnaeus) Thivy in Taylor, 1960 and unidentified green and brown filamentous algae were moderately favoured by all species, while all sea urchins showed sustained avoidance of *Sargassum ilicifolium* (Turner) J. Agardh, 1820, *Amphiroa fragilissima* (Linnaeus) Lamouroux, 1816 and *Turbinaria ornata* (Turner) J. Agardh, 1848. *Galaxaura marginata* (Ellis and Solander) Lamouroux, 1816 and *Amphiroa foliacea* Lamouroux in Quoy and Gaimard, 1824 were eaten by both species of *Diadema* but not by the *Echinothrix*. However, both species of *Diadema* showed no significant difference in grazing preference (HG VI and VII) for *A. foliacea* than for those algal/seagrass species they avoided (*Halimeda micronesica* Yamada, 1941, *Halimeda macroloba* Decaisne, 1841, *Syringodium isoetifolium* (Ascherson) Dandy, 1939, *Sa. cristaeifolium*, *Sa. ilicifolium* and *T. ornata*. Similarly *Hali. micronesica* Yamada, 1941 and *Sy. isoetifolium* (Ascherson) Dandy 1939 were grazed by all species of *Echinothrix* but not by either species of *Diadema*. Of these, only *Sy. isoetifolium*

Table 1

Pair-wise comparisons of grazing preferences (using χ^2 with Bonferroni adjustment: $P < 0.005$ =significant) and grazing rates between sea urchin species (using Tukey's HSD; ANOVA: $F = 57.4$, $P = 3.2\text{E}-39$)

Pair-wise comparisons	Grazing preferences			Grazing rates
	χ^2	d.f.	P	P
<i>D. savignyi</i> / <i>D. setosum</i>	31.69	10	4.5E-4	<0.01
<i>D. savignyi</i> / <i>E. calamaris</i> (b)	111.93	14	2.4E-17	<0.01
<i>D. savignyi</i> / <i>E. calamaris</i> (w)	66.12	13	1.7E-9	<0.01
<i>D. savignyi</i> / <i>E. diadema</i>	97.07	13	6.1E-15	<0.01
<i>D. setosum</i> / <i>E. calamaris</i> (b)	94.16	14	6.2E-14	<0.01
<i>D. setosum</i> / <i>E. calamaris</i> (w)	75.50	12	3.1E-11	<0.01
<i>D. setosum</i> / <i>E. diadema</i>	89.71	13	1.6E-13	<0.01
<i>E. calamaris</i> (b)/ <i>E. calamaris</i> (w)	81.26	13	6.4E-12	<0.05
<i>E. calamaris</i> (b)/ <i>E. diadema</i>	25.19	12	0.014	<0.05
<i>E. calamaris</i> (w)/ <i>E. diadema</i>	75.03	12	3.6E-11	N.S.

Table 2
Mean grazing preferences and feeding rates (g eaten echinoid⁻¹ 24 h⁻¹)

Algae and seagrass species	<i>D. savignyi</i> (%)	Rank	HG	<i>D. setosum</i> (%)	Rank	HG	<i>E. calamaris</i> (b) (%)	Rank	HG	<i>E. calamaris</i> (w) (%)	Rank	HG	<i>E. diadema</i> (%)	Rank	HG
<i>Codium geppiorum</i>	81.2 ± 0.9	1	I	76.3 ± 2.1	1	I	37.4 ± 1.2	6	III	45.9 ± 1.9	4	III	34.7 ± 1.2	4	IV
<i>Hydroclathrus clathratus</i>	69.6 ± 1.6	2	II	57.7 ± 2.0	2	II	100 ± 0	1	I	88.6 ± 1.4	1	I	100 ± 0	1	I
<i>Padina pavonica</i>	53.7 ± 2.0	3	III	34.6 ± 1.4	4	IV	57.1 ± 2.1	2	II	86.1 ± 2.2	2	I	43.3 ± 1.4	3	III
Brown filamentous	38.2 ± 1.2	4	IV	17.5 ± 1.0	6	VI	42.1 ± 0.8	5	III	36.6 ± 1.0	5	IV	31.8 ± 0.9	5	IV
Green filamentous	35.5 ± 0.8	5	IV	42.2 ± 1.2	3	III	49.7 ± 1.6	4	II	68.3 ± 2.7	3	II	73.5 ± 2.2	2	II
<i>Caulerpa racemosa</i>	18.6 ± 0.7	6	V	3.2 ± 0.2	8	VII	11.8 ± 0.5	8	IV	3.0 ± 0.2	11	VI	23.8 ± 1.7	7	V
<i>Galaxaura marginata</i>	15.6 ± 0.6	7	V	2.6 ± 0.1	9	VII	0	3	V	25.4 ± 1.2	6	V	0	VI	VI
<i>Halophila ovalis</i>	13.4 ± 0.7	8	V	22.8 ± 0.1	5	V	53.1 ± 1.3	3	II	20.2 ± 0.8	7	V	23.6 ± 1.4	8	V
<i>Chlorodesmis fastigiata</i>	2.3 ± 0.04	9	VI	0	7	VII	9.6 ± 0.3	9	IV	7.8 ± 0.5	9	VI	6.4 ± 0.5	10	VI
<i>Amphiroa foliacea</i>	2.2 ± 0.2	10	VI	4.4 ± 0.3	7	VII	0	10	IV	0	8	V	0	VI	VI
<i>Halimeda micronesica</i>	0		VI	0		VII	9.3 ± 0.3	10	IV	16.6 ± 0.8	8	V	8.7 ± 0.3	9	VI
<i>Syringodium isoetifolium</i>	0		VI	0		VII	35.6 ± 2.4	7	III	6.2 ± 0.5	10	VI	26.2 ± 1.9	6	V
<i>Sargassum cristaefolium</i>	0		VI	0		VII	1.4 ± 0.1	11	V	0	11	VI	2.4 ± 0.3	11	VI
<i>Halimeda macroloba</i>	0		VI	0		VII	0.8 ± 0.2	12	V	0	12	VI	0	VI	VI
Mean grazing rate (g eaten echinoid ⁻¹ 24 h ⁻¹)	24.8 ± 0.6			19.6 ± 0.7			30.4 ± 0.9			33.8 ± 1.0			33.7 ± 0.8		

N.B. *Amphiroa fragilissima*, *Sargassum ilicifolium* and *Turbinaria ornata* were avoided by all sea urchin species and are therefore not included in the table. Percentage of algal species and seagrass species consumed in 48 h (g ± S.E.) by two sea urchins of each species, ranked in order of greatest consumption. Results amended using control data on changes in weight due to photosynthesis and respiration (HG: Homogenous Group based on Tukey's HSD).

grazed by *E. calamaris* (w) showed no significant difference in preference to those algal/seagrass species not eaten.

Of the significantly grazed algal and seagrass species only *Co. geppiorum* and green filamentous algae were consumed in similar quantities by *D. savignyi* and *D. setosum*. Among the *Echinothrix*, similar quantities of *Halophila ovalis* (Brown) Hooker, 1858 were eaten by *E. calamaris* (w) and *E. diadema*, while similar quantities of *Hali. micronesica* eaten by *E. calamaris* (w) and *E. diadema*.

4.2. Grazing rates

Pair-wise comparisons using Tukey's HSD (see Table 1) reveal that grazing rates (Table 2) were significantly different between all sea urchin species ($P < 0.01$ between species of *Diadema* and between species of *Diadema* and species of *Echinothrix*; $P < 0.05$ between species of *Echinothrix*) except between *E. calamaris* (w) and *E. diadema* ($P = 0.94$). Mean grazing rates (results pooled between species within genera) were found to be greater for the *Echinothrix* (32.6 g eaten echinoid⁻¹ 24 h⁻¹) than for the *Diadema* (22.2 g eaten echinoid⁻¹ 24 h⁻¹). *Echinothrix calamaris* (b) recorded the greatest mean grazing rate of 33.8 g eaten echinoid⁻¹ 24 h⁻¹ (see Table 2) while *D. setosum* recorded the lowest mean grazing rate (19.6 g eaten echinoid⁻¹ 24 h⁻¹).

4.3. In situ feeding observations on Sosoikula and Nukubuco reefs

Observed feeding on the reefs (both day at night) (see Table 3) predominantly corresponded to grazing preferences observed (see Tables 2 and 3). Exceptions to this were the selection of *Ca. racemosa* and *Halo. ovalis* by all species except *D. setosum* and *E. calamaris* (w). No sea urchins were observed feeding on *Ca. racemosa*, while only *E. diadema* was observed feeding on *Halo. ovalis*. A relatively small, yet significant quantity of *Chlorodesmis fastigiata* (C. Agardh) Ducker, 1969 was eaten by *E. calamaris* (b) in the grazing preferences trials, however, no species was observed feeding on this species of algae.

4.4. Gut contents analysis

Inspection of the gut contents (see Table 3) revealed small pellets and pieces of algae. These pellets consisted of a high percentage of sand and sediment, as well as green and brown filamentous algae. *Amphiroa foliacea* was found in very small quantities in the guts of both species of *Diadema*, but not in the guts of *Echinothrix*. Only *D. savignyi* and *D. setosum* sampled very small (not significantly different from algal/seagrass species avoided) quantities of *A. foliacea* in the grazing preferences trials. Similarly *Halimeda micronesica* Yamada, 1941 was not found in the guts of, or grazed upon by either species of *Diadema*, but was present in the guts of both species and colour morphs of *Echinothrix*. One notable absence was *Hy. clathratus* from the gut contents of *Diadema*. This algal species was commonly found in the gut

Table 3

In situ feeding observations and gut contents analysis

	<i>D. savignyi</i>			<i>D. setosum</i>			<i>E. cal. (b)</i>			<i>E. cal. (w)</i>			<i>E. diadema</i>		
	OF	GC	LF	OF	GC	LF	OF	GC	LF	OF	GC	LF	OF	GC	LF
<i>Codium geppiorum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Hydroclathrus clathratus</i>	+	–	+	+	–	+	+	+	+	+	+	+	+	+	+
<i>Padina pavonica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Brown filamentous algae	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Green filamentous algae	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Caulerpa racemosa</i>	–	+	+	–	+	–	–	–	+	–	–	–	–	–	+
<i>Galaxaura marginata</i>	+	+	+	+	+	–	+	–	–	+	–	+	+	–	–
<i>Halophila ovalis</i>	–	–	+	–	–	+	–	+	+	–	–	+	+	+	+
<i>Chlorodesmis fastigiata</i>	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
<i>Amphiroa foliacea</i>	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–
<i>Halimeda micronesica</i>	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+
<i>Sargassum isoetifolium</i>	–	–	–	–	–	–	+	+	+	–	–	–	+	+	+
<i>Sargassum cristaefolium</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Halimeda macroloba</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Amphiroa fragilissima</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sargassum ilicifolium</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Turbinaria ornata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

OF: observed feeding, GC: gut contents, LF: lab feeding (significant), +: present, –: absent.

contents of the *Echinothrix* and was eaten by all species in the grazing preferences trials. This inconsistency is explained by the very limited overlapping distributions of *Diadema* and *Hy. clathratus* on the reefs (see Table 4). Only the brown colour morph of *E. calamaris* and *E.*

diadema were found to have ingested the seagrass species *Halo. ovalis* and *Sy. isoetifolium*. All sea urchin species selected *Halo. ovalis* in the grazing preferences trials, while *Sy. isoetifolium* was only selected by species of *Echinothrix*.

Table 4

Mean diademmatid sea urchin densities (individuals m⁻² ± S.E.) and mean percentage cover of algal and seagrass species (% m⁻² ± S.E.) in each zone on Sosoikula and Nukubuco reefs (n: number of 1 m quadrats surveyed in each zone)

	FR	RC	BZ	HCB	FF	PSCZ	SGB
Sea urchin species	n = 80	n = 160	n = 400	n = 400	n = 880	n = 880	n = 400
<i>Diadema setosum</i>	0.06 ± 0.002	0	0.07 ± 0.002	0.03 ± 0.001	0.003 ± <0.001	0	0
<i>Diadema savignyi</i>	0.26 ± 0.01	0	0.46 ± 0.01	0.46 ± 0.01	0.04 ± 0.002	0.01 ± 0.003	0
<i>Echinothrix diadema</i>	0.10 ± 0.009	0	0.23 ± 0.09	0.21 ± 0.008	0.07 ± 0.003	0.08 ± 0.002	0.03 ± <0.001
<i>Echinothrix calamaris</i> (b)	0.06 ± 0.002	0	0.06 ± 0.002	0.05 ± 0.002	0.006 ± <0.001	0.09 ± 0.003	0.003 ± 0.002
<i>Echinothrix calamaris</i> (w)	0	0	0.03 ± 0.002	0.02 ± 0.002	0.003 ± <0.001	0.06 ± 0.003	0
Algal species	n = 80	n = 160	n = 400	n = 400	n = 880	n = 880	n = 400
<i>Amphiroa fragilissima</i>	2.2 ± 0.2	1.0 ± 0.06	1.5 ± 0.04	0.8 ± 0.03	0	0	0
<i>Sargassum cristaefolium</i>	2.2 ± 0.2	16.8 ± 0.9	4.4 ± 0.2	5.6 ± 0.1	3.5 ± 0.1	8.4 ± 0.3	0
<i>Turbinaria ornata</i>	1.7 ± 0.1	5.4 ± 0.2	2.1 ± 0.04	0.8 ± 0.02	1.3 ± 0.03	0.4 ± 0.01	0
<i>Caulerpa racemosa</i>	0.3 ± 0.02	2.1 ± 0.1	0	0	0.8 ± 0.08	0	0
Green filamentous	1.5 ± 0.1	0.4 ± 0.03	14.6 ± 0.2	2.5 ± 0.04	8.6 ± 0.09	4.5 ± 0.07	2.6 ± 0.07
<i>Codium geppiorum</i>	0	0	5.9 ± 0.1	1.6 ± 0.04	1.4 ± 0.02	0.2 ± 0.003	0
<i>Chlorodesmis fastigiata</i>	1.6 ± 0.1	2.2 ± 0.03	4.7 ± 0.08	0	0	1.2 ± 0.05	0
<i>Galaxaura marginata</i>	1.1 ± 0.1	0.4 ± 0.02	3.8 ± 0.07	1.7 ± 0.07	3.8 ± 0.071	0	0
<i>Amphiroa foliacea</i>	1.2 ± 0.09	1.4 ± 0.1	2.8 ± 0.08	1.2 ± 0.05	0.5 ± 0.02	0	0
<i>Hydroclathrus clathratus</i>	0	0	0	0	8.4 ± 0.09	4.3 ± 0.05	2.7 ± 0.06
<i>Padina pavonica</i>	2.7 ± 0.2	2.8 ± 0.1	4.2 ± 0.07	2.7 ± 0.03	8.4 ± 0.2	3.3 ± 0.06	1.4 ± 0.07
Brown filamentous	3.8 ± 0.3	1.2 ± 0.05	8.8 ± 0.2	2.2 ± 0.07	9.6 ± 0.2	24.3 ± 0.2	4.5 ± 0.1
<i>Sargassum ilicifolium</i>	0	0	0	0	0	22.7 ± 0.09	0
<i>Halimeda macroloba</i>	0	0	0	0	2.6 ± 0.04	7.7 ± 0.1	1.6 ± 0.04
<i>Halimeda micronesica</i>	1.2 ± 0.09	0.6 ± 0.02	1.6 ± 0.04	1.5 ± 0.04	2.3 ± 0.04	5.6 ± 0.01	2.4 ± 0.03
Seagrass species	n = 80	n = 160	n = 400	n = 400	n = 880	n = 880	n = 400
<i>Halophila ovalis</i>	0	0	0	8.3 ± 0.3	16.8 ± 0.2	6.6 ± 0.1	11.1 ± 0.1
<i>Syringodium isoetifolium</i>	0	0	0	0	0	19.6 ± 0.4	65.6 ± 0.9

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

Number of algal/seagrass species preferred by each sea urchin species present in each zone, with those present at their maximum percentage cover in that zone, relative to their overall distribution in parenthesis

Species	FR	RC	BZ	HCB	EF	PSCZ	SGB
<i>D. savignyi</i>	5(0)	5(1)	5(3)	6(0)	8(3)	6(1)	6(1)
<i>D. setosum</i>	3(0)	3(0)	3(2)	6(0)	6(3)	6(1)	6(1)
<i>E. diadema</i>	4(0)	4(1)	4(2)	5(0)	7(3)	7(1)	6(1)
<i>E. calamaris</i> (b)	6(0)	6(1)	6(3)	6(0)	8(3)	9(2)	7(1)
<i>E. calamaris</i> (w)	5(0)	5(0)	6(3)	7(0)	8(3)	7(2)	6(0)

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.

4.5. Sea urchin distributions in relation to their preferred algal and seagrass species

Diadema savignyi, *D. setosum* and *E. diadema* were found at maximum mean densities in the boulder zone, at significant densities of 0.46 ± 0.01 individuals m^{-2} , 0.07 ± 0.002 individuals m^{-2} and 0.23 ± 0.09 individuals m^{-2} (see Table 4). Five of *D. savignyi*'s, three of *D. setosum*'s, and four of *E. diadema*'s statistically significant grazing preferences were present in this zone (see Table 5). Of these, three species were recorded at their maximum mean percentage cover (*Co. geppiorum* $5.9 \pm 0.1\%$ m^{-2} , *G. marginata* $3.8 \pm 0.07\%$ m^{-2} , and green filamentous algae $14.6 \pm 0.2\%$ m^{-2}). The echinoderm flat had the greatest number of preferred grazing preferences at their peak abundance for all three sea urchin species.

Both the brown and the white colour morphs of *E. calamaris* were found at maximum mean densities in the *Porites* and soft coral zone, at densities of 0.09 ± 0.003 individuals m^{-2} and 0.06 ± 0.003 individuals m^{-2} . All maximum mean densities were significantly different ($P < 0.01$) to species abundances in other zones (subhabitats).

Nine of the preferred food items of *E. calamaris* (b) were present in this zone (see Table 5); two at their maximum mean percentage cover (unidentified brown filamentous $24.3 \pm 0.2\%$ individuals m^{-2} , *Hali. micronesica* $5.6 \pm 0.01\%$ individuals m^{-2}). This zone had the maximum number of *E. calamaris* (b)'s preferred algal/seagrass species, but not the greatest number of preferred species at their maximum abundance.

Of *E. calamaris* (w)'s statistically significant grazing preferences, seven were present in the *Porites* and soft coral zone; two species at their maximum mean percentage cover (unidentified brown filamentous $24.3 \pm 0.2\%$ m^{-2} , *Hali. micronesica* $5.6 \pm 0.01\%$ m^{-2}). The boulder zone had the greatest number of preferred species and at their peak abundance.

4.6. Correlations between sea urchin distributions/abundance and their preferred algal/seagrass species distributions/abundance

Pearson's correlation coefficient reveals that *D. savignyi* and *D. setosum* only have a significant ($P < 0.01$) correlation (positive or negative) with *G. marginata*. *Echinothrix diadema* had a significant correlation with *Co. geppiorum* ($P = 0.04$) and *G. marginata* ($P = 0.02$). However, unlike *D. savignyi*, *D.*

setosum and *E. diadema* did not significantly select *G. marginata* in the grazing preferences trials. The two colour morphs of *E. calamaris* did not show a statistically significant correlation to any of their preferred algal/seagrass species.

5. Discussion

The findings of this investigation demonstrate that grazing preferences exist among diadematid echinoids, with preferences expressed at both the sea urchin genus and species level. *Echinothrix calamaris* (b) and *E. diadema* were the only species to show no statistical difference (using Bonferroni adjustment) in their grazing preferences. This may be explained by their distributions on the reefs, with both taxa occurring in the same zones. However, their densities in each zone (subhabitats) were very different, with no significant correlation in their distributions ($R = 0.56$, $P = 0.19$).

Differences in grazing preferences between the brown and white colour morphs of *E. calamaris* suggest that these are separate species. These two colour morphs have been shown to have significantly different spine morphologies (Coppard and Campbell, 2004), with slight differences in test and tridentate pedicellariae structures (Coppard and Campbell, 2006a,b). They also exhibit slightly different behavioural adaptations; the brown colour morph showing size-related migration associated with crevice size throughout Sosoikula and Nukubuco reefs, the white colour morph showing no apparent association, with both juveniles and adults aggregated in the larger crevices (Coppard and Campbell, 2005b). Both colour morphs spawn at the same phase (new moon) of the lunar cycle (Coppard and Campbell, 2005a) but with a very low incidence of hybridization. This indicates gametic incompatibility, which demonstrates that they are in fact separate species.

Preferred species of macro-algae (*Co. geppiorum*, *Hy. clathratus*, *P. pavonica*, *Ca. racemosa*) were relatively soft in texture and low in tannins and phenols (Novaczek, 2001), thus easing consumption and digestion. These preferred macro-algal species are also commonly harvested for human consumption throughout the Pacific Islands (Novaczek, 2001). This corresponds to the findings of Shunula and Ndibalema (1986) who linked grazing preferences of *D. setosum* and *Helicoidaris erythrogramma* Valenciennes, 1846 to the soft texture of the algae selected.

Species of algae generally avoided by the sea urchins in this investigation were the articulated calcareous algae (*A. foliacea*, *A. fragilissima*, *Hali. micronesica*, *Hali. macroloba*), those with

high levels of tannins (phlorotannins) and phenols (halophenolics) (*Sa. cristaeifolium*, *Sa. ilicifolium*, *T. ornata*; Hay and Fenical, 1988) or species which have been shown to have high levels of bioactive compounds such as acetogenins and haloacetagenins (*Ch. fastigiata*, *Halimeda*, *Sargassum*; Hay and Fenical, 1988). Such compounds, including tannins and phenols are believed to act as chemical defence against herbivores (Ogino, 1962; Conover and Sieburt, 1964, 1966; Montgomery et al., 1980; Paul and Hay, 1986; Hay and Fenical, 1988). Shunula and Ndibalema (1986) reported that *D. setosum* and *He. erythrogramma* avoided species of *Sargassum* and *Turbinaria*, while Ogden et al. (1973), Ogden (1976) and Littler et al. (1983) reported similar avoidance of these species of algae by the echinoid *D. antillarum*. Klumpp et al. (1993) found that *Triploneustes gratilla* Linnaeus, 1758 and *Salmacis sphaeroides* (Linnaeus, 1758) avoided *Sa. crassifolium* J. Agardh, 1848 even when it was very abundant in habitats where urchins were found. Both species of *Diadema* in this study exhibited a similar response, while species of *Echinothrix* consumed no *T. ornata* and *Sa. cristaeifolium* in very small quantities (not significantly different from those of species avoided). This is indicative of sampling behaviour. Such a response was also demonstrated by both species of *Diadema* grazing on small quantities of *A. foliacea* and *Ch. fastigiata*.

The seagrass species *Halo. ovalis* which was present from the hard coral bommies to the seagrass bed was grazed by all diadematids, however, the seagrass species *Sy. isoetifolium* was only significantly grazed by *E. calamaris* (b) and *E. diadema*. This corresponds with the distribution data (see Table 4). The seagrass beds were dominated by the seagrass species *Sy. isoetifolium* ($65.6 \pm 0.9\% \text{ m}^{-2}$), with patches of *Halo. ovalis* ($11.1 \pm 0.1\% \text{ m}^{-2}$). Only *E. calamaris* (b) and *E. diadema* were found in the seagrass bed, and at low densities ($0.003 \pm <0.001 \text{ individuals m}^{-2}$, $0.03 \pm 0.002 \text{ individuals m}^{-2}$) which explains why in the gut contents analysis, only these two species were found to have ingested *Sy. isoetifolium*. Lower numbers of diadematids observed in the seagrass bed is in agreement with Klumpp et al. (1993), but contrasts with McClanahan et al. (1994). We speculate that this can be related to different habitat configuration, the use of the seagrass bed as refuge, or specific traits of the predominant seagrass species.

The echinoderm flat had the greatest diversity of preferred algal/seagrass species for all species except *E. calamaris* (b), with the largest number of preferred species at their maximum abundance. Only the first 20 m and last 15 m of the echinoderm flat remained immersed at mean low water, with the majority of this zone typically being exposed. This prevents diadematid echinoids inhabiting this region of the reef in large numbers (a few small pools remain in certain areas), as they are unable to tolerate low to moderate levels of desiccation (Mortensen, 1940).

The high abundances of green filamentous algae in the boulder zone and brown filamentous algae in the *Porites* and soft coral zone is likely to be the result of damsel fish (*Stegastes nigricans* (Lacepède, 1803) territories. Such territories are characterised by dense algal turfs, which the damsel fish tend. Such damselfish have been reported to defend their territories

from other reef grazers, including diadematid echinoids (Morrison, 1988).

Diurnal feeding was rarely observed in either species of *Diadema*. These species, as reported by Morrison (1954), Thornton (1956), Magnus (1963), Randall et al. (1964), Pearse and Arch (1969), Ogden et al. (1973) and Klumpp et al. (1993) were nocturnally active with regard to feeding. This feeding behaviour pattern was also observed for the *Echinothrix*. However, *E. diadema* and the brown colour morph of *E. calamaris* were occasionally observed grazing diurnally on the reefs.

Grazing rates were found to be significantly different between all sea urchin species except between *E. calamaris* (w) and *E. diadema* ($P = 0.94$). Mean grazing rates (results pooled between species within genera) were found to be greater for the *Echinothrix* than for the *Diadema*. Such differences are likely to be due to differences in test size, which in turn reflects bite size. This is due to a proportional increase in the size of the Aristotle's Lantern with test diameter, when comparing such closely related sea urchins (Mortensen, 1940). The brown colour morph of *E. calamaris* was calculated to have the fastest grazing rate ($33.8 \pm 1.0 \text{ g eaten echinoid}^{-1} 24 \text{ h}^{-1}$). This species was recorded to grow to a larger size than other *Echinothrix*, with a maximum horizontal test diameter of 143 mm compared to *E. calamaris* (white colour morph) (118 mm) and *E. diadema* (110 mm).

The distribution of sea urchins on Sosoikula and Nukubucu reefs is primarily determined by refuge from wave energy, water depth to avoid desiccation at low water, substratum composition, and the availability of crevice space to avoid predation (Coppard and Campbell, 2005b). Water depth, wave energy and substratum composition also intrinsically influence the distribution of algal and seagrass species. The results of this investigation show that the peak abundances of diadematid sea urchins coincide with those of many of their grazing preferences. This does not necessarily demonstrate cause and effect, but indicates similar habitat requirements for both algae and sea urchins, and suggests an element of ingestive conditioning as reported in other echinoderms (Sloan and Campbell, 1982). This also demonstrates that grazing by diadematid echinoids is not dramatically reducing the abundance of their preferred algal species, and in effect may be increasing the algal species diversity by preventing the dominance of filamentous algae and fast growing macrophytes.

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