

ECOLOGICAL STUDIES ON THE SEA URCHIN, *LYTECHINUS VARIEGATUS*, AND THE ALGAL—SEAGRASS COMMUNITIES OF THE MISKITO CAYS, NICARAGUA*

R.L. VADAS

Department of Botany and Plant Pathology, University of Maine, Orono, ME 04469 (U.S.A.)

T. FENCHEL

Institute of Ecology and Genetics, University of Aarhus, Aarhus (Denmark)

J.C. OGDEN

West Indies Laboratory, Fairleigh Dickinson University, Christiansted, St. Croix 00820 (U.S. Virgin Islands)

(Accepted for publication 2 February 1982)

ABSTRACT

Vadas, R.L., Fenchel, T. and Ogden, J.C., 1982. Ecological studies on the sea urchin, *Lytechinus variegatus*, and the algal—seagrass communities of the Miskito Cays, Nicaragua. *Aquat. Bot.*, 14: 109–125.

Benthic vegetation patterns and sea urchin abundances, feeding and reproductive activities are described along a gradient from shallow lagoons to depths of 8 m. Shallow waters (1 m) are characterized by dense beds of *Thalassia testudinum* Banks ex König, a depauperate algal flora and moderate urchin densities. Siphonous green algae and sea-grasses typify intermediate depths (2–4 m). Deeper waters are dominated by *Syringodium filiforme* Kütz. and green algae. Intermediate and deeper waters contain fewer urchins and have higher plant diversities. Although highest plant diversities were correlated with intermediate grazer densities, the relationship is not causal. Instead diversity and community structure appear to be controlled more by light and competition than by grazing.

Consumption rates of *Lytechinus variegatus* (Lamarck) on *Thalassia* are higher than previously reported, in the order of 5–6 cm³ day⁻¹ or 0.6 g dry wt. day⁻¹. The diet of these urchins appears to be governed primarily by availability and the palatability of food items. With the exception of *Thalassia* none of the common algae or seagrasses are taken preferentially. Detrital *Thalassia* and sediment are the two major food items in the diet. This feeding strategy minimizes the impact of urchin grazing on the structure and viability of *Thalassia* and the algal—seagrass community.

INTRODUCTION

The roles of sea urchins in structuring benthic marine communities are becoming well known. In particular, temperate-boreal urchins influence plant

*Contribution Number 71 of the West Indies Laboratory, Fairleigh Dickinson University.

depth distributions (Jones and Kain, 1967), seaweed colonization and abundances (North, 1963, 1971; Mann, 1973) algal diversity (Paine and Vadas, 1969) and dominance (Vadas, 1968) patterns. Recognition of similar patterns is emerging from tropical regions as well. Distinct 'halos' around patch reefs on St. Croix are caused by *Diadema antillarum* Philippi (Ogden et al., 1973). Abundance and diversity patterns of tropical benthic algae on patch reefs are also directly related to urchin grazing (Sammarco et al., 1974). In addition, algal and coral recruitment on patch reefs are often governed by *Diadema* (Sammarco, 1980). In general, community structure on coral reefs appears to be strongly influenced by herbivores (Ogden and Lobel, 1978).

Preliminary surveys reveal that *Lytechinus variegatus* (Lamarck) is the dominant sea urchin in the shallow Caribbean waters surrounding the Miskito Cays, Nicaragua. Seagrasses, especially *Thalassia testudinum* Banks ex König, dominate the shallower lagoons whereas algae and other seagrasses dominate deeper waters. Intermediate depths appeared to have transitional vegetation patterns (Phillips et al., 1982). Classically, such patterns (zones in the broadest sense) were attributed to physical factors, especially light attenuation (Zaneveld, 1969). More recently attention has focused on biological mechanisms, especially herbivory, in zonation (Connell, 1972; Chapman, 1973).

Here, we are concerned with the causes of these vegetation patterns, with the possibility that *L. variegatus* is involved in structuring these algal-seagrass communities and with the biology and feeding ecology of *L. variegatus* in the Miskito Cays. Our conclusions, however, are limited by the types of data we were able to collect and the lack of time to experiment. These studies were limited to a four-week period on board the RV Alpha Helix (15 October 1977 to 17 November 1977). Nonetheless, we obtained information on plant availability and on the trophic relations, growth and reproduction of *L. variegatus* in four environments. Gut analyses and laboratory studies provided supporting evidence for field observations and information on food passage and consumption of *Thalassia*.

STUDY SITES AND METHODS

Five sites were selected for quantitative studies, four of which were primary study sites for the seagrass expedition (Ogden and McRoy, 1980). Miskito transect 1 (MT-1) is a shallow lagoon on the southeast edge of Miskito Cay (Fig. 1). It averages 1.0 m in depth, has slightly reduced salinities and dense stands of *Thalassia*. MT-2 was immediately seaward of the lagoon in 1.0–1.5 m of water. This site was characterized by dense *Thalassia* and moderate densities of *L. variegatus*. MT-3 was 1.2 km seaward of MT-2 with depths ranging from 2–4 m. Less dense stands of *Thalassia* and siphonous green algae characterized this area. MT-4 was 2.4 km from shore (MT-2) in depths of 6–8 m. *Syringodium filiforme* Kütz. and a variety of algae characterized this area. In addition, and despite the relatively shallow depth of this station, light attenuation was noticeable at depth due to the turbidity of the overly-

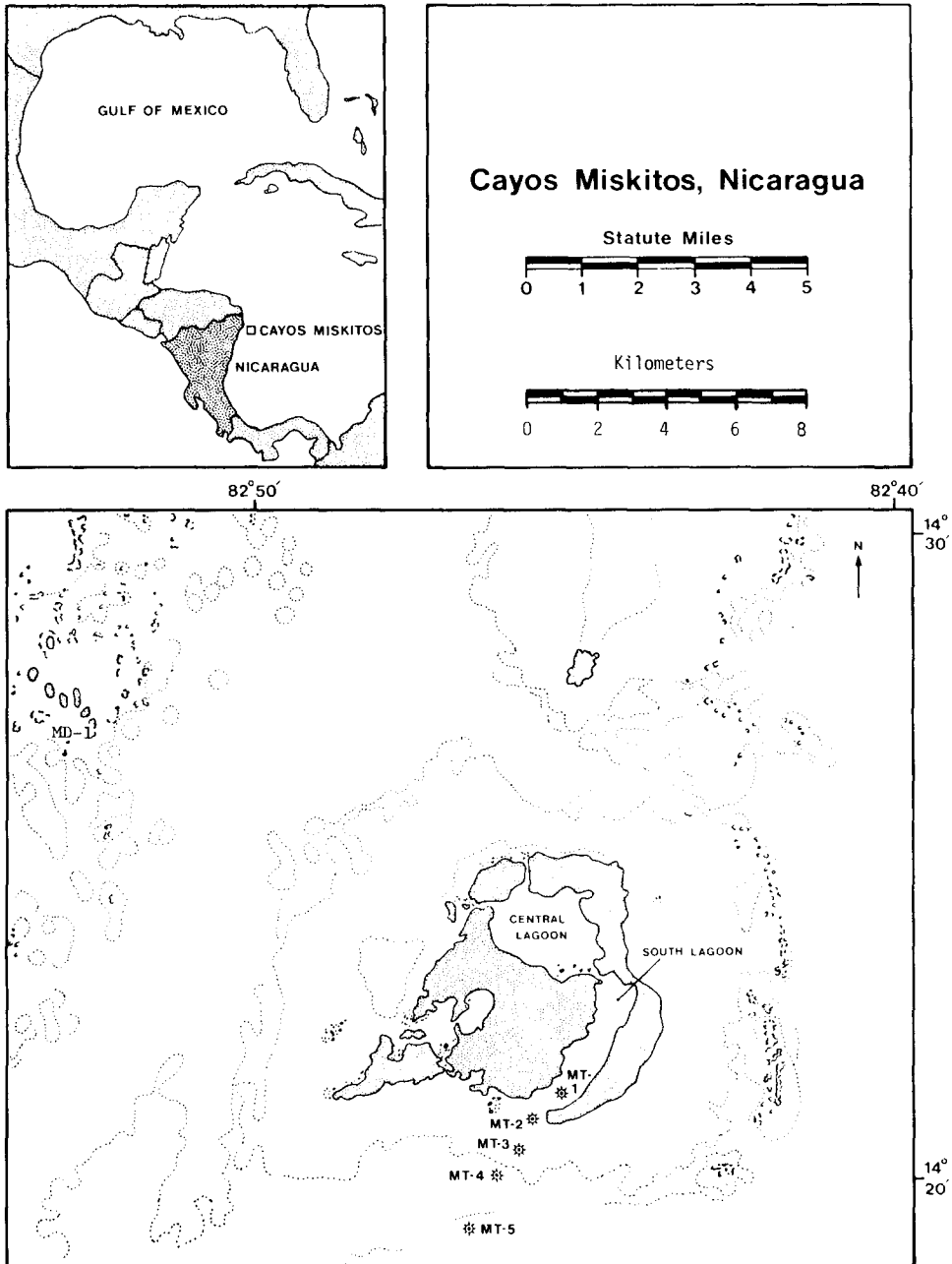


Fig. 1. Study sites in the Miskito and Morrison-Dennis Cays.

ing water (probably caused by runoff from the Cays). MD-1 was located in a shallow (1.0–1.5 m) channel between two islands in the Morrison-Dennis Cays (Fig. 1).

TABLE I

Frequency percentage (FP) and relative abundance (RA)* of algae and seagrasses at sea urchin study sites

Species	MT-1		MT-2		MT-3		MT-4		MD-1	
	FP	RA	FP	RA	FP	RA	FP	RA	FP	RA
Seagrasses										
<i>Syringodium filiforme</i> Kütz.										
<i>Thalassia testudinum</i> Banks ex. König	100	A	100	A	100	P	100	C	67	P
Chlorophyta										
<i>Acetabularia crenulata</i> Lamour.					13	R				
<i>Anadyomene stellata</i> (Wulf.) C. Ag.					47	P	7			R
<i>Avrainvillea nigricans</i> A. & E. S. Gepp					40	P				
<i>Avrainvillea</i> sp.	7	I								
<i>Batophora oerstedii</i> J. Ag.	80	P			7	P	7			
<i>Caulerpa cupressoides</i> (West) C. Ag.	7	P								7
<i>Caulerpa prolifera</i> (Forsskål) Lamour.										P
<i>Dictyosphaeria cavernosa</i> Børg.										
<i>Halimeda incrassata</i> (Ellis) Lamour.			7	R	87	P	100			
<i>Halimeda monile</i> (Ellis & Solander) Lamour.			7	C	40	P				
<i>Halimeda opuntia</i> (L.) Lamour.			27	C	93	P	27			P
<i>Halimeda tuna</i> (Ellis & Solander) Lamour.					93	P	47			P
<i>Penicillus capitatus</i> Lamarck	47	P			7	I	13			I
<i>Penicillus dumetosus</i> (Lamour.) Blainville			27	P	7	I	60			P
<i>Penicillus pyriformis</i> A. & E. S. Gepp					87	P	60			P
<i>Rhipocephalus oblongus</i> (Decaisne) Kütz.			27	C	7	I	33			R
<i>Rhipocephalus phoenix</i> (Ellis & Solander) Kütz.					53	R				P
<i>Udotea flabellum</i> (Ellis & Solander) Lamour.					67	P	7			I
<i>Valonia ventricosa</i> J. Ag.					33	R	7			R
Unknown green (<i>Bryopsis</i> -like)					13	I				
Rhodophyta										
<i>Chondria</i> sp.	13	I	7	R	100	P	13			I

<i>Dasya harveyi</i> Ashmead	33	P											
<i>Laurencia</i> sp.													
Filamentous red													
Red algae (drift)													
Unknown red													
				93		P							13 P
Phaeophyta													
<i>Dictyota dichotoma</i> (Huds.) Lamour.													
<i>Sargassum</i> sp. (drift)													
Brown algae (drift)													
Other													
Brown turf (diatoms)													
Epiphyte on <i>Thalassia</i>													
	100	C	100	C	100	C	100	I	100	R			
Number of attached species	7		6		20		19		5				
Number of epiphytic species	1+		1+		1+		1+		1+				
Number of drift species													3

*A = abundant, C = common, P = present, I = infrequent, R = rare.

Relative abundances of algae and seagrasses were determined in 15 (50 × 50 cm) haphazardly chosen quadrats within each study area (ca. 60 × 60 m) at each site. Species occurrences and their relative abundances were recorded for each quadrat. Densities of *L. variegatus* were estimated from 10–20 (10 × 0.5 m) belt transects taken at irregular intervals. Feeding observations on *L. variegatus* were made throughout the study area and on as many individuals as time permitted. Urchins were turned over quickly and examined closely for signs of feeding following the technique of Vadas (1977). Urchin test diameters were measured with millimeter scales on site and the urchins were then released. Test weights and gonad volumes were determined on 15–20 animals collected per site. Detailed analyses of gut volumes ($n = 11$) and contents ($n = 5$) were made on animals from MT-2. Animals were dissected within 3–15 h of collection. Intestinal pellets (3 mm diameter) were fractionated into four particle sizes and the volumes of each fraction determined with a volumetric cylinder. The qualitative nature of 100–200 particles within each size fraction was determined microscopically. Assuming that all particles within each size fraction had the same volume, frequency percentages (by volume) could be estimated for each prey item. Food passage through the gut was determined on animals (ca. 6 cm in diameter and collected 4 h previously) placed in clean aquaria (28–29°C) with fresh and detrital *Thalassia*. Fecal pellets were collected regularly and their volume determined. Measurement of other gut components included length of the intestine, Eh (with a Pt-electrode) and pH (with indicator paper).

RESULTS

Algae and seagrasses occurring at the five study sites are given in Table I. Abundances of individual species are presented as frequency percentages and relative abundances. Generally the two independently obtained estimates are correlated but not always, e.g., *Batophora oerstedii* J. Ag. at MT-1. This alga occurred in 80% of the quadrats, but was never very abundant in any one quadrat. In addition, these data show that *B. oerstedii* is restricted to shallow water. Conversely, *Thalassia testudinum* occurred at all five sites and generally had a high frequency of occurrence. Its relative abundance, however, varied with depth. It is most abundant at the shallow sites, with the exception of MD-1. Conversely, *Syringodium filiforme*, the other important seagrass, occurs only in the deeper waters (MT-3 and 4). *Penicillus capitatus* Lamarck is the most widely distributed alga. *Halimeda incrassata* (Ellis) Lamour., *H. monile* (Ellis & Solander) Lamour., *P. pyriformis* A. et E.S. Gepp and *Caulerpa prolifera* (Forsskål) Lamour. are the other important components of these grass beds.

Plant diversity patterns are also evident from Table I. Relative abundance estimates reflect dominance patterns among species within sites. The least number of species occurred at the shallowest sites. Five to seven attached species, excluding epiphytes on *Thalassia*, grew at MT-1, MT-2 and MD-1.

Highest plant diversities occurred at MT-3 and 4, the deepest sites.

Sea urchins densities varied throughout the area. *L. variegatus* did not occur in any of the quadrats or belt transects nor in the vicinity of MT-1. Highest densities were recorded at MT-2 and MD-1, 2.16 and 1.20 m⁻² respectively (Table II). Urchin densities at MT-3 and 4 were at least an order of magnitude lower (0.21 and 0.16 m⁻², respectively). Direct observations and high variance to mean ratios at MT-2 and MD-1 (1.6 and 5.5 m⁻²) indicated a high degree of clumping within these populations.

TABLE II

Density, size and reproductive characteristics of *Lytechinus variegatus* in the Miskito Cays : *N* = number of quadrats or searuchins; \bar{X} = mean; *S* = standard deviation

Station	<i>N</i>	\bar{X}	<i>S</i>	Sign (<i>P</i> < 0.05)*
Density**				
MT-2	11	10.8	4.2	a
MT-3	20	1.1	0.8	c
MT-4	20	0.8	1.0	c
MD-1	10	5.9	5.7	b
Test diameter (mm)				
MT-2	26	51.6	6.4	a
MT-3	15	48.7	2.3	a b
MT-4	35	47.5	5.0	b c
MD-1	94	43.2	4.6	c
Test weight (g)				
MT-2	26	63.4	21.7	a
MT-3	15	55.9	6.0	a b
MT-4	15	61.1	8.1	a b
MD-1	15	49.4	7.5	b
Gonad volume (cm ³)				
MT-2	26	1.0	0.5	b
MT-3	15	2.9	1.1	a
MT-4	15	1.6	1.4	b
MD-1	15	0.7	0.4	b

*Means sharing a common letter are not different (ANOVA, DMRT).

**Statistics refer to the (10 × 0.5 m) quadrats.

Diurnal feeding habits were obtained for 379 sea urchins at the four sites containing *L. variegatus* (Table III). Sixty-six percent of the observations were made at MT-2 and MD-1, the sites with the highest urchin densities. All individuals encountered within the study areas at MT-3 and 4 were censused. Over 80% of the urchins were actively feeding and all intestines subsequently examined contained recognizable plant material or sediment. The numbers of prey taken at MT-2, MT-4 and MD-1 ranged from 3–5 whereas at MT-3 11 items were eaten by *L. variegatus*.

Thalassia accounted for 58% of all feeding observations (Table III). Feed-

TABLE III

Diet of *Lytechinus variegatus* in the Miskito Cays

Species	Stations									
	MT-2		MT-3		MT-4		MD-1		Totals	
	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)
Algae										
<i>Acanthophora spicifera</i>							9	7	9	3
<i>Caulerpa prolifera</i>			1	2	1	4			2	1
<i>Chondria/Laurencia</i> spp.			1	2					1	1
Brown turf (benthic diatoms)							10	8	10	3
<i>Dictyosphaeria cavernosa</i>			1	2					1	1
<i>Halimeda incrassata</i>			7	14	1	4			8	3
<i>Halimeda monile</i>			1	2					1	1
<i>Halimeda</i> sp. (plate fragments)							1	1	1	1
<i>Penicillus capitatus</i>	1	1	1	2					2	1
<i>Udotea</i> sp.			3	6					3	1
<i>Sargassum</i> sp. (drift)							6	5	6	2
Seagrasses										
<i>Syringodium filiforme</i>			2	4	1	4	2	2	5	2
<i>Thalassia testudinum</i> (N)*	24	21	2	4	1	4	13	11	40	13
<i>Thalassia testudinum</i> (D)	62	54	14	28	16	64	11	9	103	33
<i>Thalassia testudinum</i> (NE)	9	8	4	8					13	4
<i>Thalassia testudinum</i> (DE)	16	14	5	10	2	8			23	7
<i>Thalassia testudinum</i> total	111	97	25	50	19	76	24	20	179	58
Invertebrates										
Bryozoa					1	4			1	1
Sponge			3	6					3	1
Other										
Sediment	2	2	5	10	2	8	70	57	79	25
Total no. of food items**	3		11		5		5		24	
Total feeding	114	73	50	91	25	69	122	92	311	82
Non-feeding	42	27	5	9	11	31	10	8	68	18
Total (feeding and non-feeding)	156		55		36		132		379	

*N = normal, D = detrital, NE = normal with epiphytes, DE = detrital with epiphytes.

**Excludes the subdivisions of *Thalassia*.

ing counts on *Thalassia* leaves were separated into normal (green and healthy), detrital (brown and decomposing) and epiphytic (normal or detrital) to denote whether or not epiphytes and leaf conditions were important in feeding. On this basis 40% of the diet of *L. variegatus* was detrital *Thalassia*. Detrital *Thalassia* was the major food item at all sites except MD-1, where 57% of the urchins ingested sediment. Other important (> 5%) prey at MD-1 included *Thalassia* (normal and detrital), diatoms and *Acanthophora*. Overall

sediment was the second most important item in the diets of these urchins. Other items of intermediate value (1–5%), in order of importance, included brown turf (primarily diatom films), *Acanthophora*, drift *Sargassum* and *Syringodium*.

Sea urchin test sizes (diameter, height and weight) were largest at MT-2 and smallest at MD-1 (Table II). Differences between these two populations were significant for diameter and weight. Test heights for the four populations ranged from 28.5 mm (MT-3)–31.5 mm (MT-2) but their differences were not significant. Meristic traits for populations of *L. variegatus* at MT-3 and 4 generally were intermediate but not significantly different from those at MT-2 and MD-1. Gonad volumes, however, were 2–4 times larger at MT-3 and 4. Similarly, gonad indices were twice as large at MT-3 and MT-4 (ca. 13%) as indices at MT-2 and MD-1 (ca. 7%; transformed means, significant at $P < 0.05$).

Over 68% of the volume of the gut contents of *L. variegatus* consisted of particle sizes in the 0.5–3.0 mm category (Table IV). The other three smaller

TABLE IV

Relative abundance of different food items and particle size distribution of intestinal contents of *Lytechinus variegatus*

Food in gut	Urchin					Average
	1	2	3	4	5	
	Volume (0/0)					
Brown <i>Thalassia</i> leaves	32.7	64.5	40.9	51.5	56.5	49.2
Green <i>Thalassia</i> leaves	0	8.6	8.8	10.8	1.4	5.9
Bryozoans	17.1	8.8	5.2	8.0	6.9	9.2
Green algae	1.5	0	1.2	0	0	0.5
<i>Polysiphonia</i>	0.6	1.0	3.7	0.3	4.5	2.0
Other red algae	0	0	2.9	0	0.7	0.7
Blue-green algae	0	0	1.0	0	1.4	0.5
Other plant material*	1.6	0.4	0	1.1	9.7	2.6
Unidentified animal tissue	1.3	0	0	0	0	0.3
Detrital conglomerates	46.8	16.7	36.3	28.3	18.9	29.4
	Volume (0/0)					
Particle size (mm)						
0.5 –3.0	51.6	74.6	76.9	63.3	76.0	68.5
0.25 –0.5	29.0	10.2	10.2	24.6	12.0	17.2
0.125–0.25	3.2	1.7	2.6	1.4	4.0	2.6
<0.125	16.1	13.6	10.2	11.6	8.0	11.9

*Possible Mangrove leaves.

size fractions ranged from 2.6–17% of the gut volume. Relative abundance (volume 0/0) of prey in the gut was based on the percentage of each item in the various size fractions. Identifiable items in the two smallest fractions (0.125 mm and 0.125–0.25 mm) were included with detrital conglomerates.

These items included diatom frustules, unicellular green and blue-green algae, crustacean excuviae, sponge spicules and foraminifera. The bulk of the conglomerates, however, were flocculent, unidentifiable organic and CaCO_3 debris. The two most important items, by volume, in the guts of the urchins from MT-2 were detrital *Thalassia* (49%) and detrital conglomerates (29%). Bryozoans and healthy *Thalassia* were the other items accounting for more than 5% of the gut volume.

Intestinal tract measurements ($N = 3$) suggest that intestinal lengths are related to test diameter. Internal pH ranged from 6.0 in the esophagus and mid-stomach to 6.5–7.0 in the mid and lowermost intestinal regions. Eh was difficult to determine because of the difficulty of inserting the probe into various regions of the gut without contaminating it. Eh ranged from +150 mV in the esophagus to +45 in the mid-gut. Higher values were obtained beyond that (lower intestines) and probably were caused by contamination from the coelomic fluid. With the reservation that Eh values may be in error, our readings indicate that there is no fermentative breakdown of carbohydrate in the gut.

The relationships between test weight and test diameter and between test diameter and gut volume are shown in Fig. 2. Correlations for both relationships are strongly positive ($r = 0.91$ and 0.51 , respectively). The average dry weight of the gut contents for the urchins depicted in Fig. 2 was 113 mg cm^{-3} . Of this 68% was CaCO_3 .

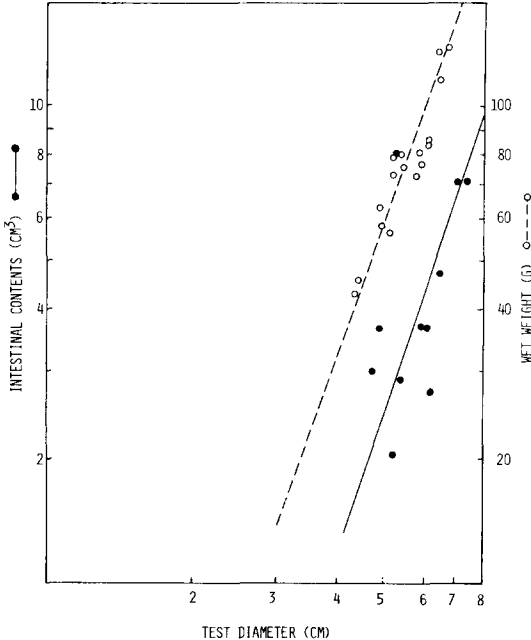


Fig. 2. Relationships between test diameter and test weight and test diameter and gut volume in *Lytechinus variegatus*.

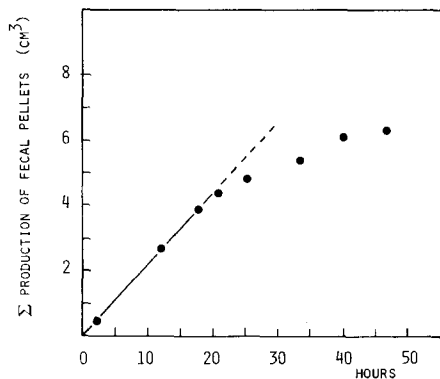


Fig. 3. Rate of fecal pellet production in *Lytechinus variegatus*.

Food-passage times and fecal production are given in Fig. 3. Initial values for food-passage averaged $0.22 \text{ cm}^3 \text{ individual h}^{-1}$ for the first 14.5 h. Values decreased rapidly thereafter and probably were associated with the physiological states of these animals. By 48 h a few animals were inactive and losing spines. Thus the initial rates on healthy animals were used in all calculations.

DISCUSSION

Thalassia testudinum dominated the flora of all of our study sites, especially the lagoons and shallower waters. Reduced abundances of this plant at MD-1 appeared to be related to grazing caused by the moderately high densities of *L. variegatus*. High variance to mean ratios and qualitative observations suggest that sea urchin densities at MD-1 were underestimated by us. Similar aggregations and densities occur with *L. variegatus* in other biogeographical areas (Moore et al., 1963; Rivera, 1979). Considerable areas of MD-1 were sparsely vegetated and resembled the urchin-created 'barrens' of boreal waters (North, 1963; Vadas, 1968; Paine and Vadas, 1969; Pearse et al., 1970; Breen and Mann, 1976). However, benthic substrates (mostly soft bottoms) at MD-1 were covered by fine to coarse carbonate sediments rather than by crustose coralline algae. Paradoxically *Thalassia* was as abundant at MT-2, the site with the highest urchin densities, as it was at MT-1, an area without urchins. Both MT-2 and MT-1 were covered by considerable amounts of dead *Thalassia* leaves and by relatively thick canopies of living material. Despite the shallow depths these leaves reduced the light reaching the understory, which may have been responsible for the reduced abundances of other plants.

Although it is tempting to suggest, based on urchin densities and predation theory, that grazing contributed to the depauperate nature of the flora at MT-2, there is little or no evidence to support such a contention. Urchins were primarily harvesting moribund or dead portions of these plants, a strategy which would have little or no impact on associated species nor on reduc-

ing the competitive ability of *Thalassia*. Furthermore, of the five algae available at MT-2 (Table I) only one was recorded in the diet of *L. variegatus*. The degree of specialization on detrital *Thalassia* lessens the degree to which *L. variegatus* exerts direct control over this community. This feeding behavior allows *Thalassia* to remain abundant and dense enough to shade the understory. Thus, despite the presence of moderate densities of a potentially important herbivore, competitive interactions appear to govern the organization of this community. The absence of *L. variegatus* from MT-1 is unexplained, except perhaps for the shallower depths and other properties associated with the lagoon. Thus plant diversities at MT-1 and MT-2 appear to be the result of physical factors and competition for light, not of predation. Grazing by *L. variegatus* likely determined community structure at MD-1. However, Brian Keller (1981, unpublished Ms., personal communication) has shown that the abundance of *Thalassia* can vary considerably due to factors unrelated to grazing.

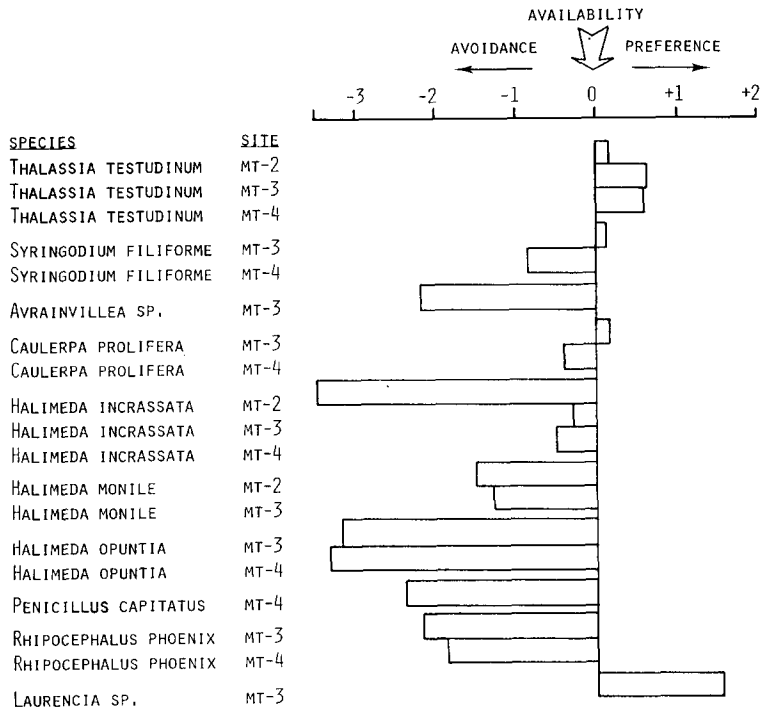
Community structure and seaweed diversity at MT-3 and MT-4 also appear to be strongly controlled by physical factors and competition. Higher plant diversities at both sites are correlated with moderate water depths and low to intermediate sea urchin densities. It is tempting to invoke the predation or herbivore disturbance model (Paine, 1966; Paine and Vadas, 1969; Sammarco et al., 1974; Lubchenco, 1978) in support of a causal role for *L. variegatus*. However, the absence of visible grazing effects at MT-2 (with urchin densities an order of magnitude higher) reduces the likelihood that grazing had an impact on community structure at MT-3 and 4. A simpler and more appealing hypothesis for the Miskito Cays is that depth controls plant diversity. The most likely explanation is that attenuated light reduces the vigor and competitive ability of *Thalassia*, thereby providing space, light or some other requisite for colonization by *Syringodium* and algae. Additionally, the reduced abundance of *Thalassia* at the deeper sites (there is an order of magnitude difference between the biomass of *Thalassia* at MT-2 and MT-4, 18 vs. 185 g/m²; C.P. McRoy, 1981, unpublished) and the presence of high amounts of detrital *Thalassia* in urchin diets at MT-4, suggest that these areas are being enriched by transport from shallower waters. The lack of an inverse relationship between *Thalassia* and *Lytechinus* and the importance of detrital *Thalassia* in the diet of urchins at MT-3 and 4 further question the functional role of *L. variegatus* in structuring these communities. We have not excluded the possibility that other herbivores, such as turtles (Bjorndal, 1980; J.C. Ogden, 1981, unpublished data), may exert some influence on these vegetation patterns (few herbivorous fish were observed in these areas). Alternatively, the degree of grazing on detrital and other forms of *Thalassia* at MT-4 suggests that urchins may be acting in concert with physical factors to stress even further the already reduced populations of *Thalassia* in deeper waters.

Food passage in the gut of *L. variegatus* was estimated to be 0.22 cm³ individual h⁻¹. Since the gut contents of the animals (6 cm in diameter) used in our experiment were 5–6 cm³ (Fig. 2), passage time is of the order of 24 h.

Assuming that these values approximate field conditions, an urchin would consume and pass 5.28 cm^3 of material day^{-1} . This corresponds to 0.60 g dry wt. per 24 h or approximately twice that estimated by Moore et al. (1963). Since the organic fraction comprises only 32% of the ingested material, it means that 0.192 g organic dry wt. is consumed per day. This value is five times higher than values found for slightly smaller urchins (4.8 cm diameter) by Greenway (1976). Returning to our figures, only about 11% of the organic material ingested was fresh *Thalassia* leaves (based on gut contents from MT-2). The estimate for *Thalassia* would be slightly higher (ca. 25%) if field observations from MT-2 were considered. Estimates based on field diets from all sites, however, indicate that healthy *Thalassia*, with or without epiphytes, only accounted for 17% of the diet, which is in good accord with the estimates based on the proportion in the gut contents. Nevertheless, both sets of data indicate that the amount of fresh *Thalassia* consumed by these urchins was quite negligible given the large abundances available.

When feeding is considered on the basis of availability vs. selection it appears that both are involved. A selectivity index (modified from Ivlev, 1961) was calculated for important food items at each site (Fig. 4). Biomass values for seagrasses and algae (C.P. McRoy, 1981 unpublished) were used to estimate availability. Most, but not all, values parallel the abundance estimates given in Table I. At MT-3, for example, *Penicillus capitatus* was not observed in the replicate 0.25 m^2 biomass samples but had a high frequency of occurrence (87%). In such cases the alga or food item in question was not included in the index. These calculations show that of the food available only *Thalassia* was consistently taken on the basis of availability or preference. With the exception of *Laurencia* sp., which may be an anomalous result caused by low numbers, all of the other important components of these communities were avoided or non-preferred, especially the calcareous green algae. The availability of sediment could not be determined in a manner comparable with other foods. Sediment was present at all sites and was consumed in high quantities (MD-1) in the absence of other foods. However, it was also important in the presence of non-preferred foods (MT-3 and 4).

Despite the differences in the flora at the five sites, there was a general convergence in the diets of the four populations of *Lytechinus variegatus* toward *Thalassia*, especially to decaying or detrital material. Lowe and Lawrence (1976) suggested that *L. variegatus* fed preferentially on detrital seagrass material in Florida. Rivera (1979) also observed that *L. variegatus* fed mainly on decaying tips and not on the greener basal segments of *Thalassia* leaves. Detrital portions of *Thalassia* leaves are invariably epiphytized, and are known to have extensive microbial communities associated with them (Fenchel, 1970). These fragments with their microbial populations may be rich nutritional sources for marine herbivores (Fenchel, 1972). In a sense, these urchins are feeding on a predigested and nutritionally rich food source. Similarly Lowe and Lawrence (1976) suggested that *L. variegatus* may be gaining access to a more digestible nutrient and energy source by feeding on



SELECTIVITY INDEX - MODIFIED FROM IVLEV (1961)

$$SI = \text{LOG} \left(\frac{\% \text{ DIET}}{\% \text{ AVAILABLE}} \right)$$

Fig. 4. Selectivity index of *Lytechinus variegatus* in the Miskito Cays. (Sediment was an important component of the diet but could not be included in this analysis.)

detrital seagrass material. It is also possible that the basal (younger) portions of *Thalassia* leaves contain phenols or other noxious chemicals (similar to *Posidonia oceanica* (L.) Delile; Cariello and Zanetti, 1979) which deter sea urchins.

Regardless of these arguments, there are several reasons for questioning the nutritional value of seagrasses (detrital or fresh) to *L. variegatus*. First, although the largest urchins occurred at MT-2, significantly greater amounts of reproductive tissue occurred in urchins at MT-3 and MT-4. The diets at these two sites were quite different. Urchins at MT-4 fed primarily on detrital *Thalassia* (70%) whereas animals at MT-3 fed on a wide variety of algae and seagrasses. Second, there is no indication that urchins were over-harvesting *Thalassia* at MT-2 and therefore the reduced gonadal production cannot be attributed to food limitation per se. Reproductive development in these urchins may depend on a variety of prey. Lowe and Lawrence (1976), al-

though not specifically examining growth or reproductive capacity as a function of diet, indicated that a mixed diet might be nutritionally superior for *L. variegatus*. This possibility is in marked contrast to what is known of boreal urchins; these specialize on prey that provide the greatest gains in growth and reproduction (Vadas, 1977; Larson et al., 1980). Third, the possibility exists that nitrogen fixation (Guerinot et al., 1978; Fong and Mann, 1980) occurs in the guts of these urchins, which further complicates the nutritional picture. Algal preferences by *Strongylocentrotus drobachiensis* Müller in Maine, for example (Larson et al., 1980), were highest for *Laminaria longiciruris* de la Pylaie, the alga inducing the highest rates of N₂ fixation in the studies of Guerinot et al. (1978). Additionally, the relationships between feeding behavior and nutrition in other tropical sea urchins are ill-defined (Ogden et al., 1982). Fourth, despite the fact that populations of *L. variegatus* have the capacity to grow explosively and destroy *Thalassia* beds (Camp et al., 1973), and that such phenomena are evident in localized areas in the Miskito Cays (MD-1), our data and those in the literature indicate that *L. variegatus* does not function as a typical herbivore. In Jamaica *L. variegatus* consumes both *Thalassia* (Greenway, 1976) and considerable quantities of detritus and sediment (Keller, 1976). Similar observations were made in Florida (Lowe and Lawrence, 1976). Rivera (1979) also considered *L. variegatus* to be a generalist consumer. Bach (1979), however, reported that a large population of *L. variegatus* completely grazed the benthic plants (mainly calcareous algae) in Card Sound, Florida and that *Halimeda* recovered within two months once the urchins left the area. Similarly disturbance of a *Thalassia*-dominated climax community in Puerto Rico reverted to an earlier seral stage within the same successional sequence (Margalef, 1963). Presumably recolonization by algae and seagrasses in disturbed or heavily grazed areas is possible only by the reduction or absence of urchins. Fifth, despite the importance of *Thalassia* to the diet of *L. variegatus*, there are few data to support the idea that they feed preferentially on healthy leaves.

Although we lack long-term observations, several aspects of the role of *L. variegatus* in these communities seem worth mentioning. It appears that under normal conditions urchin populations do not exceed densities beyond which *Thalassia* cannot recover. However under those as yet undefined conditions, when population growth becomes explosive or perhaps simply at high densities (ca. 5–10 m⁻², test diameters of 5–6 cm), these urchins reduce the seagrasses and algae to a level where detritus and sediment become important dietary components. These conditions are analogous to the disturbance levels that create instability or disclimax patterns in boreal subtidal algal communities (Vadas, 1968; Breen and Mann, 1976; Foreman, 1977; Vadas et al., 1982). The facultative detrital feeding capabilities of *L. variegatus* permit it to continue to feed and maintain high population levels in disturbed areas, thereby further reducing the likelihood of recolonization by macrophytes. Analogous events and strategies have been noted for boreal urchins as well (Lang and Mann, 1976; Larson et al., 1980). Although this strategy seemingly

would permit these urchins to survive in relatively disturbed environments, it is not clear what normally maintains their population sizes below levels that are disruptive to these seagrass communities.

ACKNOWLEDGMENTS

The authors thank Mike Roblee, Bill Gladfelter and the crew of the Alpha Helix for assistance in the field and for logistical support. Constructive criticism of the Ms by Brian Keller and the editorial reviewers was helpful and greatly appreciated. They acknowledge the support of the Seagrass Ecosystem Studies (SES) program in general and NSF Alpha Helix program. This research was supported by the SES Caribbean Food Web Study, NSF-OCE 7601304 (IDOE seagrass ecosystem study). Support for manuscript preparation was provided by the NOAA Office of Sea Grant, Project No. LRS-53.

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