ECOLOGICAL ENERGETICS OF THE TROPICAL SEA URCHIN DIADEMA ANTILLARUM PHILIPPI IN BARBADOS, WEST INDIES

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ABSTRACT

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The role of Diadema antillarum in energy transfer within a fringing coral reef off Barbados is shown from the urchin population energy budget and the total reef benthic primary production. Approximately 20% of the total net benthic primary production is consumed by Diadema antillarum. Through their abundance and partitioning of available food resources consumed, it is apparent that Diadema antillarum plays a "key" role in processes of energy transfer between benthic primary producers and other levels within the fringing reef community. The most important pathway of energy transfer is through the production of energy rich fecal detrital matter. This energy release amounts to approximately 7% of the total benthic net primary production or 37% of the urchin population caloric intake. Because of their intense grazing pressure on hard reef substrates, the net reef growth is effectively reduced by approximately 24% relative to the measured calcification rate. In this way the Diadema antillarum population influences the calcium carbonate budget of the reef and controls reef morphology.

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## SOMMAIRE

Le rôle de Diadema antillarum dans le transfert d'énergie à l'intérieur d'un récif corallien frangeant à la Barbade est démontré à partir du budget d'énergie de la population d'oursins et de la production benthique primaire totale du récif. Environ 20% de la totalité de la population primaire benthique nette sont absorbés par Diadema antillarum. Sur la base de leur abondance et de la distribution des ressources en nourritures disponibles utilisées, il devient évident que Diadema antillarum joue un rôle essentiel dans le processus de transfert d'énergie entre les producteurs primaires benthiques et les autres niveaux appartenant à la communauté du récif frangeant. Le mode principal de transfert d'énergie s'effectue par l'intermédiaire de matériel détritique fécal riche en réserves énergétiques. L'énergie qu'il contribue correspond à environ 7% de la production benthique primaire nette, soit 37% de l'absorption calorique de la population d'oursins. En raison de leur broutage intense du substrat corallien, la croissance nette du récif est effectivement réduite de 24% par rapport au taux observé de calcification. De cette façon, la population de Diadema antillarum influence le budget de calcaire et la morphologie du récif.

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#### INTRODUCTION

Regular sea urchins are important members of the worldwide benthic marine communities, ranging from the intertidal zone to abyssal depths. In shallow water, they are mainly herbivores which browse upon a variety of algae and vascular plants. As a result of their abundance, food preferences and feeding behavior, urchins are regarded as having a major role in energy transfer within communities as well as in influencing benthic substrate configuration and community structure (Miller and Mann 1973, Ogden et al. 1973a, Sammarco et al. 1974, Foreman 1977, Ogden 1977, Scoffin et al. in press).

The purpose of this study is to investigate the feeding ecology and energetics of a tropical sea urchin in a coral reef community. The role of *Diadema antillarum* Philippi in the transfer of energy within this highly complex and diverse community is examined in detail with attention directed towards the relative importance of the available primary producers as food resources and the concurrent effect that urchin grazing has on hard reef substrates.

Lawrence (1975) has provided an extensive review of sea urchin feeding biology. Some studies have shown that these animals consume a wide spectrum of algal species (Leighton 1966, 1968, Vadas 1968, Himmelman and Steele 1971). However, other investigations have demonstrated that urchins may be highly selective in their choice of food (McPherson 1968, Irvine 1973, Vadas 1977, Ayling 1978). *Diadema antillarum* consumes a wide variety of foods, from macrophytic algae and vascular plants to foraminiferans and even crustaceans. Lewis (1964) found brown, green, coralline and boring algae associated with sand and coral fragments in gut contents of *D. antillarum* from Barbados. In the U.S. Virgin Islands, investigations by Atkinson et al. (1973) showed that the same species feeds upon 32 of the 53 algal species present on patch reefs.

The type of food eaten is apparently important for Leighton (1968) showed that *Strongylocentrotus purpuratus* has higher absorption efficiencies when fed algae of superior nutritional quality (in terms of organic matter) than when fed lower quality foods. Other workers found that absorption efficiencies varied with food type, urchin size and season of the year (Moore and McPherson 1965, Fugi 1967, Himmelman 1969, Boolootian and Lasker 1974, Lowe and Lawrence 1976 and Vadas 1977). These workers examined urchins fed macrophytic algae or sea grasses but only a few studies have investigated the absorption efficiency of urchins feeding on algae present on coral reefs (Lowe 1974, Lilly 1975, Lowe and Lawrence 1976).

Johnston (1969), Dahl (1974) and Benayahu and Loya (1977) have pointed out that fleshy macrophytic algae are uncommon or absent on many coral reefs and thus are not available as food for herbivores. Alternative primary producers available as food resources for *Diadema* in the shallow fringing reef habitat of this study include encrusting coralline, endolithic and epipelic algae. Their importance as primary producers within other coral reef communities has been demonstrated by Marsh (1970), Littler (1973), Wanders (1976) and Sournia (1977).

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Regular urchins can feed on hard substrate surfaces by physically rasping with the five calcaerous teeth of the Aristotle's lantern. Erosion of hard surfaces by echinoids has been investigated by Hunt (1969), Krumbie and Van der Pers (1974), Sammarco et al. (1974), Hunter (1977) and Ogden (1977). Reef geologists have been particularly interested in the contribution of urchins to the erosion of reef primary carbonate framework (corals and coralline algae). Grazer erosion of these surfaces has been shown to be an important component of the overall reef carbonate budget (Scoffin et al. in press). In the Caribbean, Ogden (1977) compared erosion rates of reef parrot fish and sea urchins and found sea urchins to be by far the most important agents of bioerosion. Hunt (1969) determined that Echinometra *lucunter* eroded 7.0 kg m<sup>-2</sup>yr<sup>-1</sup> from reefs in Bermuda, and Hunter (1977) determined that *Diadema antillarum* eroded 5.5 kg m<sup>-2</sup> vr<sup>-1</sup> from a Barbados fringing coral reef.

Some ecologists also have been interested in the effect of urchin grazing on benthic communities. Grazing has been shown by Paine and Vadas (1969a), Sammarco et al. (1974), Mann (1977) and others to alter benthic community structure. Kitching and Ebling (1961) determined that *Paracentrotus lividis* in Loch Ine, Scotland, removed benthic algae as fast as the algae could be replaced by new growth, thereby preventing the establishment of associated fauna. Leighton (1968) reported that *Strongylocentrotus purpuratus* and *S. franciscanus* are capable of denuding vast areas of macrophytic algae in waters off Washington State, U.S.A. Mann (1977) has indicated that entire kelp bed communities in waters

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off Nova Scotia, Canada, have been destroyed by overgrazing by S. droebachiensis. In the Caribbean, Ogden et al. (1973b) have shown that the bare patches (halos) formed around patch reefs resulted from *Diadema antillarum* grazing on sea grass. In the U.S. Virgin Islands, Sammarco et al. (1974) showed that D. antillarum influenced the macrophytic algae abundance and equitability on patch reefs, and recently Bak and Van Eys (1975) reported this species to be a predator of live corals in Curaçao and Bonair (Netherlands Antilles).

While many ecologists have investigated energy flow within marine communities, few studies have dealt specifically with sea urchin population energetics and the importance of sea urchins in energy transfer. Miller and Mann (1973) investigated an Atlantic Canada population of *S. droebachiensis* which grazed on *Laminaria* in a kelp bed community. These authors quantified the food requirements of the urchins from a population energy budget. They also determined that the urchin population utilized one to seven percent of the kelp bed production, with urchins of the smaller size classes accounting for approximately one-half of the population energy flow. Greenway (1976) studied *Lytechinus variegatus* in Jamaican waters and showed that the urchins consumed approximately 48% of the *Thalassia* production from a shallow water sea grass community.

The role of sea urchins in energy transfer within a coral reef community has not been examined. These abundant herbivores are a link in the trophic web from benthic primary producers to other levels within the reef community and thus their

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role would appear vital to the community. The present study quantifies the role of *Diadema antillarum* in energy transfer within a coral reef community by: (1) determining the energy requirements of the population and (2) examining in detail the ways in which *Diadema* partitions energy into various pathways for subsequent utilization by other reef community members.

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#### STUDY SITE DESCRIPTION

All field research was undertaken on a fringing coral reef located on the west coast of Barbados, West Indies. This reef, identified as the North Bellairs Fringing Reef in Figures 1, 2a and 2b, was chosen because it lies near the Bellairs Research Institute of McGill University, is relatively small, and supports a large population of the sea urchin *D. antillarum*. Lewis (1960) has described the physiography and major faunal zones of the reefs along the west coast of Barbados, and Stearn et al. (1977) have described the bathymetry and faunal zones of the North Bellairs Fringing Reef (Figure 3). The relevant zones referred to by Stearn et al. (1977) are as follows:

#### 1. Swash Zone

This zone is located nearest to the shore and extends as a narrow band, 20-30 m wide, parallel to the shore. The depth at low tide is from 0-1 m. The substrate surface consists of approximately 50% sand and 50% dead coral rock; both are generally covered with a thin veneer of filamentous algae.

## 2. Crest Zone

The Crest Zone extends approximately 40 m seaward of the Swash Zone. At extreme low tides it is emerged in places but is normally approximately 1 m below the water surface at low tide. Few living corals are present there and the reef surface is extremely irregular and densely covered with encrusting coralline algae (principally *Porolithon* spp.).

3. Coalesced Spur Zone

This zone lies seaward of the Crest Zone in depths

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Figure 2a Oblique aerial photograph of the North Bellairs Fringing Reef (A) and the South Bellairs Fringing Reef (B).

Figure 2b Overhead aerial photograph of the North Bellairs Fringing Reef (A) and the South Bellairs Fringing Reef (B). Bar scale approximately 60 m.



Figure 3 Faunal zones of the North Bellairs Fringing Reef according to Stearn et al. (1977).

- A Swash Zone
- B Crest Zone
- C Coalesced Spur Zone
- D Spur and Groove Zone
- E Sand



ranging from 1-2 m at low water. Approximately 50% of the total rock surface is uniformly covered by mixed live coral species already noted by Lewis (1960). The remainder of the rock surface is covered with encrusting coralline algae.

## 4. Spur and Groove Zone

The tops of the spurs or ridges range from 1-3 m below the surface at low water. The grooves or valleys are found parallel to the spurs and at right angles to the shore. Depths to the sand floor of the grooves range from approximately 3 m at the landward end to 5 m at the seaward opening. *Montastrea annularis* is the most common coral species covering the sides and seaward fronts of the spurs. Several large massive colonies of *Montastrea*, *Siderastrea* and *Diploria* are found as isolated patches beyond the front of the spurs.

Although *Diadema* occurs further seaward of the Spur and Groove Zone, collections and observations were limited to the four zones described above.

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### MATERIALS AND METHODS

The field and laboratory procedures of this study included: (1) the determination of the physical and chemical characteristics of the reef surface water, (2) the determination of the abundance and productivity of urchin food resources (benthic algae) and (3) the determination of the energy requirements of the *Diadema antillarum* population on the reef. Descriptions of the various experimental methods and materials are presented below.

## I. Physical and Chemical Properties of the Reef Surface Water

Samples of reef surface water were collected in twoliter containers at weekly intervals over a period of one year. Unfiltered samples were analyzed for oxygen with a Beckman Field Oxygen Analyzer connected to a Beckman 39553 0<sub>2</sub> Sensor. The analyzer was calibrated against air-saturated seawater and corrected for salinity and temperature prior to each determination. The remaining seawater samples were HA-Millipore<sup>®</sup> filtered and then, as a matter of convenience, frozen for storage. These samples were analyzed later for reactive nitrate and phosphate following procedures outlined by Strickland and Parsons (1972). Seawater salinity was determined with an inductively coupled salinometer calibrated against standard seawater. Sea surface and air temperatures were measured with a mercury thermometer.

## II. Collection and Preparation of Algal Samples for Primary Productivity Studies

Non-fleshy algae consumed by *Diadema* were classified according to IBP terminology (Round and Hickman 1971) into three types: encrusting coralline algae, endolithic algae and epipelic algae (Figures 4-6). These three types were collected and prepared in the following manner before being offered as food or tested for their rates of primary production.

### A. Encrusting Coralline Algae

Encrusting coralline algae coats reef rock surfaces and is abundant in the Crest Zone and Coalesced Spur Zone. Samples were collected from fragments of reef rock chipped free from the substrate. Only samples which showed no external evidence of fleshy algae or boring organisms when inspected with a dissecting microscope were retained. These samples were maintained in running seawater of ambient temperature for up to one day.

#### B. Endolithic Algae

This algal type is common in all faunal zones of the fringing reef. It occurs as a coating on coral rubble and as a thin veneer on dead heads of reef building corals such as *Montastrea* and *Siderastrea*. The algal veneer was collected *in situ* by chipping large irregular fragments from a coral dead head. Slabs containing only the veneer were cut free from the fragments with a diamond-blade circular rock saw. Coral rubble harbouring endolithic algae was not treated in any special way after field collection. Both sources of endolithic algae were held in the laboratory water table for up to one day. Figures 4a-c Underwater photographs showing *Diadema antillarum* grazing upon endolithic algae growing on exposed coral skeletal framework.

Live coral tissue (A).

Exposed coral skeletal framework harbouring endolithic algae (B).

4a - bar scale 0.5 m. 4b - bar scale 0.5 m. 4c - bar scale 10 mm.

Figure 4d Underwater photograph showing *Diadema antillarum* grazing upon endolithic algae growing on coral rubble fragments.

Bar scale 0.5 m.



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Figures 5a & b Underwater photographs showing Diadema antillarum grazing upon reef substrate coated with encrusting coralline algae. 5a - bar scale 0.5 m.

5b - bar scale 50 mm.

Figures 6a & b Underwater photographs of *Diadema antillarum* grazing upon epipelic algae growing in the shallow surface layers of the sediment.

6a - bar scale 0.2 m. 6b - bar scale 50 mm.



## C. Epipelic Algae

This algal type is generally restricted to the Swash Zone and Spur and Groove Zone. It occurs as a thin veneer of algal filaments living on or within the shallow surface layers of sediment. Samples were collected by inverting the bottom of a glass petri dish on the sediment surface in such a way as to enclose an area of algal turf. The dish was gently pushed into the substrate until the bottom was flush with the algal turf surface. A thin glass plate was then forced under the dish so as to cut the subsurface sediment. The petri dish and glass plate were then lifted together, inverted, the plate removed and the dish covered with its top. Samples were brought to the laboratory and placed in the seawater table where the original algal turf surface was exposed to running seawater.

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## III. Methods of Assessing Reef Primary Productivity

Rates of primary production of ten specimens of each algal type were determined within 24 hours of field collection. Rates were measured at various intervals throughout the day (0600-1800 h) by the light and dark bottle method.

Dark incubation containers were prepared by covering transparent glass jars and their polyethylene caps with several layers of black vinyl tape. All caps were then coated with clear varnish to prevent gas transfer across cap surfaces. Preliminary tests showed that gas exchange across cap surfaces or from poor seals was negligible when treated in this way (Appendix Table 1).

Light and dark containers with algal specimens were sealed while submerged in Whatman<sup>®</sup> GF/C filtered seawater, then tranferred to an open top water bath to incubate in direct sunlight for two hours (Figures 7a, b, c and d). Identical containers without specimens served as controls. Tap water was circulated through the water bath to maintain the temperature at approximately 27<sup>°</sup>C (ambient seawater temperature).

Concentrations of dissolved oxygen were measured at the beginning and end of incubations with the Beckman instruments previously described. Light intensity was recorded in footcandles from hourly readings with a Gossen Panlux Electronic Luxmeter. After incubation, the surface area of living algae was determined by fitting aluminum foil over a specimen, then molding and trimming the foil to conform to the contours, depressions and boundaries of the specimen (Marsh 1970). A value was calculated for conversion of foil weight to surface area from weights of foil

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Figures 7a-c Incubation containers employed for primary productivity studies.

- 7a container with encrusting coralline algae. Bar scale 50 mm.
- 7b container with endolithic algae on coral skeletal framework. Bar scale 50 mm.
- 7c container with epipelic algae on sediment. Bar scale 25 mm.

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Photograph showing experimental apparatus for primary productivity studies.

- (A) waterbath with light and dark containers
- (B) light meter

Bar scale 10 cm.



samples of known surface area.

In order to determine the relative contribution by the benthic algae (excluding the symbiotic algae in live corals) to total reef primary production, the total areas covered by each of the three algal types on the reef were calculated. Stearn et al. (1977) presented data on the rock surface area covered by the major faunistic and floristic components of the North Bellairs Fringing Reef. Their data were converted to express the area covered by each of the three algal types as a percentage of total reef surface area (Appendix Table 2).

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# IV. Urchin Population Density and Size Frequency Distribution

Diadema population density was determined from monthly counts along a meter wide transect across the reef (Figures 8a and b). For each month from July 1975 to June 1976 (excluding December 1975), a nylon line was laid over a different area of reef so as to conform to reef surface irregularities. A scuba diver carrying a digital counter and a "T" bar, one meter wide, followed the line and counted the number of *Diadema* (Figures 9a and b). Population density was expressed as the number of individuals per square meter of reef surface, calculated from the known length of the transect line (110-220 m) and the total number of individuals counted. In addition, three transects laid perpendicular to shore and extending out onto the reef were examined to determine differences in urchin size frequency distribution with increasing distance from shore.

Specimens of *Diadema* were collected for frequency distribution analysis and size measurement on the day following each census. At 10 m intervals along the same transect that counts were made, all *Diadema* enclosed by a meter square quadrat were removed and deposited in a separate numbered bag (Figures 10a and b). In the laboratory, urchins from each bag were sorted according to their maximum test diameter (MTD) into 5 mm groups ranging from 15-60 mm. A record was kept of the number of individuals of each size group and of their quadrat position.

Urchins were measured by several methods for comparison with other size data presented in the literature. Maximum test diameters (MTD) were determined with calipers and volumes by Figure 8a Aerial photograph of the North Bellairs Fringing Reef. Bar scale 100 m.

Figure 8b Locations of transects taken across the North Bellairs Fringing Reef.



Figures 9a & b Underwater photographs showing diver counting Diadema antillarum along a 1 m wide transect. Arrow indicates a hand-held digital counter.

Figures	10a & b	& b	b	Unde	erwater j Diadema	photographs antillarum	show: from	ing a	dive 1 m <sup>2</sup>	er collect- quadrat.
			(A)	A) collection bag.						
				Arro	ow point	s to tongs.				



displacement in seawater. Dry weights were measured with a Mettler H-16 balance after drying whole specimens to a constant weight at  $60^{\circ}$ C.

## V. Sea Urchin Energetics

The energy requirements and food consumption rates were calculated for *Diadema* ranging in size from 15-60 mm MTD. From these data and those on size frequency distribution and abundance, the mean energy requirements and food consumption rate of the total urchin population were calculated on a square meter basis. Energy budgets were determined according to IBP methods (Crisp 1971) and expressed in calories in equations of the form C = P +R + G + U + F where C = consumption, P = production, R = respiration, G = reproductive output, U = excreta, and F = egesta.

#### A. Consumption

In a preliminary attempt to study food consumption in Diadema antillarum, fragments of reef rock or rubble were offered to urchins in separate vessels in the laboratory. However, it was not possible to measure directly the amount of food scraped from the rock surface by Diadema because the amounts of algae removed were insignificant in comparison to the total weight of the fragment. For this reason consumption rates could not be measured from the amount of food ingested per unit time in laboratory experiments nor was it possible to quantify the amount of food eaten in field trials. Consequently, daily consumption rates were estimated from available data in the literature.

In an earlier study, Lewis (1964) provided information on the feeding activity of *Diadema antillarum* in Barbados. Although precise estimates of consumption rates are difficult to extract from his study, Lewis' results give the only data available on feeding rhythm and feeding rates of this species in Barbados.

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Bearing this in mind, daily rates of food consumption were established on the following basis. Lewis showed from laboratory experiments that continuously feeding urchins passed algal food through the digestive tract in 8-12 hours (Appendix Table 3). Because feeding activity in the field was not continuous but rhythmic (most intense in the afternoon and early evening, Lewis 1964, Appendix Table 4), it could only be assumed that the amount of material in the gut at any one time was equal to or, more probably, less than the amount devoured in 24 hours. In other words, the gut content dry weight is thus a measure of the minimum consumption rate over a 24-hour period.

From July 1975 to May 1976 mean gut content dry weights were determined for randomly collected urchins of each size group ranging from 15-60 mm maximum test diameter (MTD) at 5 mm intervals. A minimum of 16 urchins of each size group was collected by sealing each individual in a separate plastic bag. At the laboratory, gut contents of each urchin were dissected free and the compacted food pellets which constitute the gut contents were removed. These were pooled with any pellets released into the plastic bag during collection and transportation. Samples were dried to a constant weight at 60°C and a mean calculated for gut content dry weight of urchins of each size group.

Estimates of the ingested quantities of each of the three food types were then calculated for each urchin size group with the aid of a geological embedding technique. Food pellets pooled from five freshly collected *Diadema* of similar size were dried and embedded in epoxy resin. Petrographic thin sections

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were then prepared according to the methods of Rogers and Kerr (1942). Approximately four hundred to over 1000 pellets were examined from each urchin size group. Each pellet was classified according to the most abundant food type present. Natural food types were identified by comparison with thin sections of food pellets from urchins fed in the laboratory on known reef materials such as encrusting coralline algae, corals and sand (Figures 11-15). In addition, descriptions by Ginsburg (1956), Bathurst (1971) and personal communications with Mr. Ian Hunter of the Geology Department, McGill University proved helpful for identification. After pellets were classified the number of pellets of each food type was expressed as a percentage of the total counted (Appendix Table 5).

The dry weight of each food type comprising the natural mixed diet can be calculated with the assumption that all food pellets contained within the gut contents of similar sized urchins are of similar size (Figure 16) and have similar dry weights. This is supported with data shown in Appendix Table 6. Therefore, irrespective of their origin (hence their composition) the dry weights of any food pellets from the gut contents of an urchin can be considered equal to the dry weights of any food pellets from other urchins of the same size group. Consequently, the percentage of each food type can be used to determine the weight of each food type in an urchin's mixed diet. This was calculated by simply multiplying the mean gut content dry weight times the percentage of each food type in the diet. Figure 11 Petrographic thin section of a food pellet from Diadema antillarum which has fed upon encrusting coralline algae.

Bar scale 0.25 mm.

Figure 12 Petrographic thin section of a food pellet from Diadema antillarum which has fed upon epipelic algae on surface sediments.

Bar scale 0.25 mm.

Figure 13 Petrographic thin section of a food pellet from Diadema antillarum which has fed upon endolithic algae on coral. Bar scale 0.25 mm.

. Figure 14 Grazing marks left by Diadema antillarum on encrusting coralline algae. Bar scale 0.25 mm.



Figure 15 Holding apparatus for maintaining Diadema antillarum studied in laboratory experiments. (A) Seawater filters.

Figure 16 Typical food pellets of *Diadema antillarum*. Bar scale 1.0 mm.

Figure 17 Underwater photograph of a diver inspecting cage which was used for retaining *Diadema antillarum* for growth studies.



Caloric intake per day was then estimated from the proportion of each food type in the mixed diet and the caloric content per gram dry weight of each food type. The latter was determined from freshly collected, dried, powdered samples by the wet oxidation method of Hughes (1969). Values for the weight of each food type in an urchin's diet were multiplied by their respective unit caloric equivalents and summed over all food types to estimate the minimum daily caloric intake per urchin of each size group (Appendix Table 7). To estimate monthly caloric intake, daily rates were multiplied by 30.

To calculate the minimum daily caloric intake for urchins per  $m^2$  of reef surface, the mean daily caloric intake per urchin of each size group was multiplied by their mean number per  $m^2$ and totals were summed over all urchin size groups. The daily rate of caloric intake of urchins per  $m^2$  of reef surface was multiplied by 30 to obtain a value for monthly caloric intake.

## B. Production

Several methods were tried to obtain individual growth rates for different sizes of *Diadema*. Although a number of urchins were tagged with a variety of plastic markers, none were retained by the urchins and the tagging experiments were discontinued. Secondly, urchins of known size were confined in cages attached to the reef surface (Figure 17); this was also unsuccessful because cages were destroyed by wave action. In a third attempt, population size frequency distributions were plotted to determine growth rates. This method of analysis combines various mathematical expressions described by Taylor (1965) and Grossman and Turner (1974) to calculate a set of component normal curves from size frequency data. A set of component normal curves was constructed and modal values were estimated for each component curve. The shift in the mode over successive bimonthly periods was taken to represent the increase in urchin test diameter due to growth.

A growth increment in weight was calculated per mm of test diameter from a relationship established between whole urchin dry weight and maximum test diameter. Growth was expressed in calories by multiplying the mean caloric content of whole urchins times the weight increment. The caloric content of entire urchins (including gonads) was determined by the wet oxidation method previously noted.

## C. Reproduction

Urchins were collected each month throughout one year to obtain samples of reproductive tissue. All gametic tissue was dissected free from two urchins of each five millimeter size group but no attempt was made to determine sex or stage of gametogenesis. The volume of two intact gonads from each individual was determined by displacement in seawater prior to calculation of a gonad index (G.I.) according to the equation G.I. =  $GV/(MTD)^3$ , where GV = total gonad volume and MTD = urchin maximum test diameter (Moore and McPherson 1965, Lewis 1966). The total sample of gametic tissue from each urchin was then dried to a constant

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weight at 60<sup>°</sup>C, ground to a powder and stored in a desiccator for future caloric determination. Caloric content was measured in triplicate with a Philipson Microbomb Calorimeter calibrated against benzoic acid (Parr Instrument Company 1960). No correction was made for acid production or burning of fuse wire as they are considered negligible by Paine (1964, 1971).

# D. Respiration

Respiration in *Diadema antillarum* was previously studied by Lewis (1968a), who expressed rates of oxygen consumption as a function of urchin test volume. It was not considered necessary to repeat his studies, but Lewis' results have been converted to express oxygen consumption as a function of maximum test diameter. The resultant values for oxygen consumption have been converted to calories by the oxy-caloric coefficient,  $1 \text{ mgO}_2 =$ 3.34 calories (Ivlev 1934).

#### E. Excretion and Egestion

Ammonia is the major nitrogenous excretory product of Diadema antillarum (Lewis 1967). Ammonia excretion was measured from freshly collected specimens that were held in the laboratory for one day without food. Urchins of known MTD were sealed in containers filled with seawater and incubated for one hour, after which a 50 ml aliquot was withdrawn for immediate analysis according to methods of Strickland and Parsons (1972). An identical container without a specimen served as a control. Excretion rates were expressed as a function of body size (MTD) and subsequently converted to calories by the relationship, 1 µg at  $NH_3 - N = 4.88 \times 10^{-3}$  calories (Brafield and Solomon 1972,

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Lilly 1975).

Feces for caloric determination were obtained from freshly collected urchins of known MTD held in separate glass vessels. Fecal pellets were siphoned from holding vessels, nonfecal material removed, and the sample washed with distilled water. Feces were pooled from urchins of similar size, then dried to a constant weight at 60°C. Caloric content of feces was determined by the wet oxidation method of Hughes (1969).

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Daily egestion rates were determined for randomly collected urchins of each size group. Collections were made through the year and mainly during the months of August 1975 through February 1976 during the same period in which specimens were collected for gut content (feeding) data. Each urchin was sealed in a plastic bag at the site of collection, and was later transferred to a separate holding vessel in the laboratory water table. Any fecal pellets egested into the collecting bag were pooled with pellets egested over a subsequent 24-hour period. (Data from laboratory feeding experiments showed that the weight of feces produced during a 24-hour period of starvation differed by less than one percent from those of individuals feeding continuously in the laboratory (Appendix Table 16)). These samples were then dried to a constant weight at 60°C and a mean weight calculated for urchins of each size group. The mean weight of feces egested per 24 hours was considered a measure of the daily egestion rate (Glynn et al. 1979). Daily egestion rates were expressed in calories by multiplying the mean weight of feces egested per 24 hours times the mean caloric content per gram dry weight of feces.

## VI. Absorption Efficiency

The efficiency of food absorption by Diadema antillarum was determined by the indirect method of Conover (1966). This method requires neither the quantitative recovery of feces nor the determination of the amount of food eaten if only the percentage absorption is required. The method depends upon the assumption that only the organic component of the food is significantly affected by the animal's digestive processes; ... "it is necessary only to obtain the ratio of ash free dry weight to dry weight (fraction of organic matter) for a sample of food and feces to calculate the percentage assimilation." Conover (1966).

Diadema here grazes on algae growing on sand and hard reef rock surfaces and ingests substantial amounts of inorganic material (Lewis 1964, Hawkins 1977, Hunter 1977, Ogden 1977). To obtain samples of the food eaten by Diadema, fine scrapings (filings) were taken from the upper-most surface layer of reef substrate containing algae. The scrapings thus included inorganic reef rock and organic algal material. This method has been used by other workers to quantify algal biomass growing on reef surfaces (Bakus 1967, Wanders 1976).

The depths to which fine scrapings were made did not exceed 1 mm, which appears to approximate the thickness removed by urchins (McLean 1967a, Hunter 1977). McLean reported that urchins graze hard substrates to a depth of approximately 0.25 mm and, although Hunter (1977) did not measure directly the depths to which *Diadema* grazes, he showed that fecal pellets were composed predominantly of particles ranging in size from 0.25-1.00 mm, even

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though larger particles were frequently found in the feces.

In Barbados, endolithic algae penetrate into coral substrates to depths exceeding one millimeter. Bands found within some corals may reach 2-3 mm in thickness (Odum and Odum 1955). Epipelic algae, which grows as a thin veneer of filaments, penetrate the upper-most surface layers of reef sediment in Barbados to approximately 1 mm. Bathurst (1967) recorded depths in excess of 2.5 mm for algal mats in the Bahamas. Thus epipelic algae also are found within the 1 mm scraped layer.

It was difficult to estimate the depths of 'living surface' of encrusting coralline algae, but Odum and Odum (1955) have estimated that the surface pink layer is 0.5 mm thick. To verify whether scrapings of encrusting coralline algae were representative of food ingested by *Diadema*, the proportions of organic and inorganic material were compared to samples of encrusting coralline algae examined by Paine and Vadas (1969b). They determined that 83% of the dry weight of a powdered sample of the encrusting coralline algae *Lithothamnion* was attributed to inorganic material. Scrapings of encrusting coralline algae from the North Bellairs Fringing Reef contained approximately 80% inorganic matter on a dry weight basis (Appendix Table 8).

The scraping method was thus considered as an acceptable way to obtain representative samples of the three food types ingested by *Diadema antillarum*. Consequently, powdered scrapings were employed for the determination of the ash free dry weight to dry weight ratio (fraction of organic matter) in food ingested.

Absorption efficiencies were determined for various sizes of *Diadema* fed each of the three food types. A single food

type was offered to an urchin held in a separate 10 1 container for a period of eight consecutive days. Fresh food was provided daily in excess and aerated seawater that flowed into the container was filtered through surgical cotton enveloped by glass wool. Prior to initial feeding, each urchin was starved for two days to allow evacuation of the alimentary tract and to ensure that feces originated from the food type provided, only pellets collected from the fifth day onward were analyzed for their organic and inorganic fractions. These feces were siphoned from the containers at the end of each day, dried to a constant weight at  $60^{\circ}$ C and stored under desiccation.

Prior to ashing, fecal pellets and scrapings of each food type were powdered and dried at  $100^{\circ}$ C. These samples were then weighed, ashed at  $450^{\circ}$ C for four hours (Paine 1964, Lilly 1975 and Yingst 1976), and reweighed after cooling in a desiccator. Ash free dry weights of each food were expressed as a percentage of the original sample dry weights, and a mean was calculated for each food type to represent the F' factor (fraction of organic matter in food) required in the equation developed by Conover (Absorption Efficiency = (F'-E')/(1-E')(F') x 100). A mean value for the E' factor (fraction of organic matter in feces) was similarly calculated.

Lilly (1975) regarded the loss of  $CO_2$  resulting from  $CaCO_3$  decomposition during ashing at 450°C to be negligible. However, Crisp (1971) and others have indicated that loss of  $CO_2$  at ashing temperatures above 500°C may be appreciable. Therefore, it was thought advisable to test Lilly's findings by determining

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the percentage weight loss as a result of  $CaCO_3$  decomposition in the food supplied to *Diadema*. Twelve samples of scrapings of encrusting coralline algae and 12 samples of reef substrate harbouring endolithic algae were powdered and prepared for ashing as described above. These samples were then treated to remove all organic matter according to the methods described by Crisp (1971). Reagent grade  $CaCO_3$  also was treated in a similar fashion for comparative purposes. After removal of organic materials, the samples were dried, weighed, ashed at  $450^{\circ}C$  and  $500^{\circ}C$ , then reweighed after cooling. The differences between these weights, before and after ashing, showed that approximately 2% loss in weight occurs, presumably as a result of  $CaCO_3$  breakdown and the evolution of  $CO_2$  (Appendix Table 9). This evidence thus confirms Lilly's findings that loss of  $CO_2$  by this method is negligible.

The absorption efficiencies of urchins having a mixed diet were calculated in terms of calories and organic matter. Methods for determining caloric content of food and feces have been described in a previous section. Organic matter in both food and feces was determined according to the following procedure.

Firstly, the mean organic content per gram dry weight of feces was measured for each of the urchin size groups examined. Feces were obtained from freshly collected urchins held in separate glass vessels in the laboratory. Fecal pellets from an individual of known MTD were siphoned from the holding vessel, non-fecal material removed, and the sample washed with a little distilled water. These samples were dried at 60<sup>°</sup>C to a constant weight.

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The weight of organic material was subsequently determined by ashing samples at 450°C for four hours. The weight of organic material removed was expressed as a percentage of the original sample weight. Total weight of organic matter egested was determined by multiplying the percentage of organic material in feces times the mean dry weight of feces egested per 24 hours.

Secondly, the mean organic content per gram dry weight of the mixed diet was calculated from the percentage of each food type comprising the diet and from the mean organic content per gram dry weight of each food type. The proportions of each food type in diets were determined for urchins of each size group with the aid of the geological embedding technique previously described on page 24. The mean organic content of each food type was determined by ashing powdered samples of foods as previously described. The mean organic content per gram dry weight of the mixed diet was calculated by multiplying the percentage of each food type in the diet by their respective organic content per gram dry weight. The total organic content per gram dry weight of the mixed diet was obtained by summing the organic weight contributions over all food types (Appendix Table 10). Total organic content of food ingested was determined by multiplying the organic content per gram dry weight of the mixed diet times the mean gut content dry weight.

Based upon the above calculations, the difference between the total organic content of food and feces can be determined. This in effect yields an estimate of the weight of absorbed organic matter during transit of food through the digestive tract. Efficiency of organic matter absorption was then calculated

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according to the equation  $C-E/C \ge 100$ , where C = the organic content in food and E = the organic content in feces (Welsh 1968).

# VII. Calcium Carbonate Sediment Production and Erosion of Reef Carbonate Framework

Rates of reef calcium carbonate (CaCO<sub>3</sub>) sediment production were calculated from egestion rates and the mean percentage by weight of calcium carbonate in urchin feces. The percentage of CaCO<sub>3</sub> in feces was determined by dissolving dried, preweighed samples of fecal pellets in dilute (ca. 10%) hydrochloric acid, then weighing the dry residue on a preweighed glass fiber filter. The weight of CaCO<sub>3</sub> dissolved was calculated as a percentage of the original sample dry weight. Rates of total CaCO<sub>3</sub> sediment production were then estimated by multiplying egestion rates times the mean percentage of CaCO<sub>3</sub> in feces.

Rates of erosion of specific carbonate framework builders (corals and coralline algae) also were calculated from the proportions of each in natural mixed diets (Appendix Table 5) multiplied by egestion rates and the mean percentage of  $CaCO_3$  in feces.

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#### RESULTS

# I. Physical and Chemical Properties of the Reef Surface Water

Physical and chemical properties of the reef surface water showed little seasonal variation with the exception of concentrations of reactive nitrate. Reactive nitrate levels were variable throughout the year, ranging between  $0.05-12.3 \mu g$  at N 1<sup>-1</sup>. Concentrations were higher during the latter part of September and through mid-November to early December 1975 than during the rest of the sampling period (Figure 18).

No evident seasonal variation was detected for concentrations of reactive phosphate. Concentrations were consistantly less than 0.10 µg at P  $1^{-1}$  and frequently fell below the limits of detection of the analytical method (0.03 µg at P  $1^{-1}$ , Appendix Table 11). In general, nutrient concentrations in surface water were within the ranges previously reported by Sander (1971).

Dissolved oxygen concentrations in reef surface water showed no regular seasonal variation but levels ranged from  $4.06-6.74 \text{ mgO}_2 \text{ 1}^{-1}$  (Figure 19).

Salinity of surface water ranged from 33.30-35.82% during the sampling period. High salinities were recorded during the months of November 1975 through January 1976 and again in April 1976 (Figure 20). All salinity values were within the range already reported by Lewis et al. (1968).

Sea surface water temperatures varied from 24.0-29.0°C and air temperatures between 24.0 and 29.5°C (Figure 21). In both cases, temperatures were lower from mid-December 1975 to March 1976 than during the remaining sampling period.

Figure 18 Seasonal variation in surface water nitrate concentrations over the North Bellairs Fringing Reef. (Drawn from data in Appendix Table 11).



Figure 19 Seasonal variation in surface dissolved oxygen concentrations over the North Bellairs Fringing Reef.

(Drawn from data in Appendix Table 12).



Figure 20 Seasonal variation in surface water salinity over the North Bellairs Fringing Reef. (Drawn from data in Appendix Table 11).



Figure 21 Seasonal variation in surface water temperature (----) and air temperature (----) over the North Bellairs Fringing Reef.

(Drawn from data in Appendix Table 12).


#### II. Primary Production on the North Bellairs Fringing Reef

Diurnal cycles of primary production of the three algal types are presented in Figures 22 to 24 for data collected in June through August, 1976. Figure 22 illustrates the diurnal pattern of net and gross primary productivity of the encrusting coralline algae. Highest rates of primary production occurred during times of reduced light intensity. The lowest production rates occurred during the midday (1000-1500 h), when light intensity was highest. Low production rates at midday may have been the result of photosynthetic inhibition at high light intensities (Steemann-Nielsen 1975).

The diurnal patterns of net and gross primary productivity of the endolithic algal type are illustrated in Figure 23. Rates of production increased with rising light intensity during the morning (0600-1100 h) and decreased during the midday (1100-1300 h) when there was also a temporary decline in light intensity. During the afternoon, rates continued to increase until 1600 h despite a sharp decrease in light intensity at 1500 h.

The diurnal pattern of net and gross productivity of epipelic algae is shown in Figure 24. Production rates were low during periods of reduced light intensity (0600-0900 h, 1500-1700 h) and high during times of increased light intensity (1000-1400 h).

Mean hourly rates of primary production of each algal type are shown in Table 1. Mean daily rates of primary production shown in Table 2 were calculated by summing mean hourly productivity values (Table 1) over a 12-hour daylight period and assuming constant rates of respiration at night (Brown 1953, Sournia 1976a).

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Figure 22 Daily patterns of light intensity and net and gross primary productivity of encrusting coralline algae. (Drawn from data provided in Appendix Table 13).



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Figure 23 Daily patterns of light intensity and net and gross primary productivity of endolithic algae on coral dead heads.

(Drawn from data provided in Appendix Table 13).



Figure 24 Daily patterns of light intensity and net and gross primary productivity of epipelic algae on surface sediments.

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(Drawn from data provided in Appendix Table 13).



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Mean hourly rates of primary production  $m^{-2}$  of algal surface.

Algal Type	Net Productivity	Respiration	<u>Gross</u> Productivity
	$mgO_2 m^{-2} h^{-1}$	$mgO_2 m^{-1} h^{-1}$	$mgO_2 m^{-2} h^{-1}$
encrusting coralline	$0.38 \times 10^{3}_{3}$ (0.08 x 10 <sup>3</sup> )*	$0.22 \times 10^{3}$ (0.03 x 10 <sup>3</sup> )	$0.60 \times 10^{3}$ (0.09 x 10 <sup>3</sup> )
endolithic	$0.70 \times 10^{3}_{3}$ (0.19 x 10 <sup>3</sup> )	$0.28 \times 10^{3}_{3}$ (0.06 x 10 <sup>3</sup> )	$\begin{array}{c} 0.98 \times 10^{3} \\ (0.24 \times 10^{3}) \end{array}$
epipelic	$0.73 \times 10^{3}$ (0.13 x 10 <sup>3</sup> )	$0.09 \times 10^{3}$ (0.02 x 10 <sup>3</sup> )	$0.82 \times 10^{3}$ (0.14 x 10 <sup>3</sup> )

\* values in parentheses are the ± 95% confidence limits

- 4	9	-
- 4	9	-

Mean daily (24 hours) net and gross primary production  $m^{-2}$  of algal surface.

# 1. Net Productivity

Algal Type	$mgO_2 m^{-2} day^{-1}$	cal m <sup>-2</sup> day <sup>-1*</sup>	gC m <sup>-2</sup> day <sup>-1**</sup>
encrusting coralline	$1.92 \times 10^3$	6.41 x $10^3$	0.72
endolithic	5.04 x $10^3$	16.83 x 10 <sup>3</sup>	1.89
epipelic	7.68 x 10 <sup>3</sup>	$25.65 \times 10^3$	2.88

# 2. Gross Productivity

Algal Type	$mgO_2 m^{-2} day^{-1}$	cal m <sup>-2</sup> day <sup>-1</sup>	gC m <sup>-2</sup> day <sup>-1</sup>
encrusting coralline	$7.20 \times 10^3$	$24.05 \times 10^3$	2.70
endolithic	11.76 x $10^3$	$39.28 \times 10^3$	4.41
epipelic	9.84 x $10^3$	$32.87 \times 10^3$	3.69

\* 1.0 mgO<sub>2</sub> = 3.34 calories Ivlev (1934)
\*\* 1.0 gO<sub>2</sub> = 0.375 gC Westlake (1963)

In Table 2, productivity is expressed in mgO<sub>2</sub> per square meter of algal surface per day and, to allow comparisons with other rates of primary production in the literature, equivalent rates in gC and calories are also included.

The epipelic algae exhibited the highest rates of net production and the endolithic algae the highest rates of gross production. The encrusting coralline algae had the lowest rates of net and gross production of all three algal types. Table 3 shows the mean daily, monthly and yearly rates of primary production per square meter of reef surface in mgO<sub>2</sub>, gC and calories. Productivity per square meter of reef surface by each algal type was determined by multiplying the mean daily production rate in mgO<sub>2</sub> per square meter of algal surface times the percent coverage by each algal type on the whole reef (Appendix Table 2). The mean daily rate of net production per square meter of reef surface was 3.52 gO<sub>2</sub>, equivalent to 1.32 gC and 11.76 kcal.

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Mean daily, monthly and yearly rates of net and gross primary production  ${\rm m}^{-2}$  of reef surface.

1. Net Productivity

Period	$mgO_2 m^{-2}$	cal $m^{-2*}$	gC m <sup>-2**</sup>
day <sup>-1</sup>	$3.52 \times 10^3$	11.76 x $10^3$	1.32
mo <sup>-1</sup>	105.60 x 10 <sup>3</sup>	353.70 x 10 <sup>3</sup>	39.60
yr <sup>-1</sup>	$1284.80 \times 10^3$	4291.23 x 10 <sup>3</sup>	481.80

# 2. Gross Productivity

Period	$mgO_2 m^{-2}$	$cal m^{-2*}$	gC m <sup>-2**</sup>
day <sup>-1</sup>	$6.72 \times 10^3$	$22.44 \times 10^3$	2.52
mo <sup>-1</sup>	201.60 x 10 <sup>3</sup>	673.34 x 10 <sup>3</sup>	75.60
yr <sup>-1</sup>	2452.80 x 10 <sup>3</sup>	8192.35 x 10 <sup>3</sup>	919.80

\* 1.0 mgO<sub>2</sub> = 3.34 calories Ivlev (1934)
\*\* 1.0 gO<sub>2</sub> = 0.375 gC Westlake (1963)

#### III. Quality of Food Resources Ingested by Diadema antillarum

There were marked differences in food quality among the algal types consumed by *Diadema*. Table 4 shows that the encrusting coralling algae had the highest caloric and organic content per gram dry weight among the three food types and the endolithic algae on coral dead heads had the lowest. Although the epipelic algae contained a higher caloric content than the endolithic algae on rubble, it had a somewhat lower organic content.

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Caloric content and organic matter expressed as percent (%) dry weight in the algal food types eaten by *Diadema antillarum*.

Algal Food Type	<u>Caloric</u> cal g <sup>-1</sup>	<u>Content</u> dry wt	<u>Organic Matter</u> percent dry wt			
	Mean	95% C.L.*	Mean		±95% C	L.
encrusting coralline	370.30 (8)**	±42.52	20.55	(25)	0.9	3
epipelic	58.09 (5)	± 4.12	4.81	(39)	1.5	8
endolithic on rubble	40.41 (10)	± 6.49	5.60	(36)	1.9	3 .
endolithic veneer on coral dead heads	37.23 (9)	± 7.54	4.44	(26)	1.8	3

\* confidence limits

\*\* values in parentheses represent the number of samples
 examined

# IV. Urchin Population Densities and Size Frequency Distributions

The abundance of *Diadema* along transects across the North Bellairs Fringing Reef is shown in Table 5. Densities ranged from a low of 4.6 to a high of 26.3 urchins per m<sup>2</sup> of reef surface. Low density values reflect low counts from transects over sandy bottom. A mean density of 17.3 urchins per m<sup>2</sup> was calculated over the whole sampling period.

Urchin densities also were determined from monthly quadrat sampling (Table 6). A mean density of 22.6 urchins per  $m^2$  of reef surface was calculated from quadrat sampling. Quadrat sampling was considered a more accurate method of obtaining population density because of the difficulties in counting all urchins along the meter wide transect while swimming over the reef. Therefore, a density of 23 *Diadema* per  $m^2$  of reef surface was considered a more reliable measure.

Figures 25a-c illustrate monthly size frequency distributions for the *Diadema* population. Histograms express the number of individuals in each size group as a percentage of the total collected in the monthly sample. The size range of urchins collected was similar throughout the sampling period with the exception of July 1975. During this month the recruitment of juveniles is shown by the appearance of a size group less than 10 mm MTD.

Considerable monthly variation occurred in the percentage of urchins within each size group. A histogram of pooled size frequency data (approximately 3500 individuals counted and measured) is shown in Figure 25c (bottom). The frequency distribution over the whole size range has the general shape of a normal distribution

Densities of *Diadema antillarum*  $m^{-2}$  of reef surface from transect counts.

Month	No. Counted	m <sup>2</sup> examined	Density $m^{-2}$
July 1975 (1)*	806	150	5.4
August 1975 (2)	687	150	4.6
September 1975 (3)	2389	140	17.1
October 1975 (4)	3200	180	17.8
November 1975 (5)	4307	180	23.9
December 1975 **	-	-	-
Janu <b>a</b> ry 1976 (6)*	* _	-	-
February 1976 (7)	5778	220	26.3
March 1976 (8)**	-	-	-
April 1976 (9)	1997	120	16.6
May 1976 (10)	2694	110	24.5
June 1976 (11)	2337	120	19.5

mean 17.3 95% C.L.\*\*\* ±6.4

 values in parentheses represent transect locations (Figure 8b)

\*\* transect counts could not be made during these months because of poor weather conditions

\*\*\*confidence limits

.

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#### Table 6

Densities of *Diadema antillarum*  $m^{-2}$  of reef surface from quadrat collections.

Month	No. of urchins	No. of quadrats	Density $m^{-2}$
	collected	examined	
July 1975 (1)*	160	15	10.7
August 1975 (2)	161	15	10.7
September 1975 (3)	) 290	14	20.7
October 1975 (4)	431	18	23.9
November 1975 (5)	594	18	33.0
December 1975 **	-	-	-
January 1976 (6)	378	12	31.5
February 1976 (7)	356	20	17.8
March 1976 (8)	209	12	17.4
April 1976 (9)	326	11	29.6
May 1976 (10)	323	12	26.9
June 1976 (11)	312	12	26.0

mean 22.6

95% C.L.\*\*\* ±5.5

 values in parentheses represent transect locations (Figure 8b)

\*\* quadrat collections could not be made during this month because of poor weather conditions

**\*\*\***confidence limits

Figure 25a Size frequency distributions of *Diadema antillarum* collected in the months of July to October 1975.

Frequency is expressed as the percentage of the total number of individuals in each size group.

Values in parentheses represent transect locations (Figure 8b).

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Figure 25b Size frequency distributions of *Diadema antillarum* collected in the months of November 1975 and January to March 1976.

Frequency is expressed as the percentage of the total number of individuals in each size group.

Values in parentheses represent transect locations (Figure 8b).



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Figure 25c Size frequency distributions of *Diadema antillarum* collected in the months of April to June 1976 and a composite size frequency distribution of all monthly collections.

Frequency is expressed as the percentage of the total number of individuals in each size group.

Values in parentheses represent transect locations (Figure 8b).



FREQUENCY IN PERCENT

0

curve.

Table 7 shows the percentages of urchins of each size group in the population. Values were computed from frequency distributions and the number of urchins per square meter based on a mean density of 23 urchins per m<sup>2</sup>. Urchins of the 20 mm MTD size group and smaller comprised approximately 25% of the total population. The largest proportion of the population (ca. 50%) consisted of urchins of size groups ranging from 25-35 mm MTD, and the remaining proportion by urchins 40 mm and larger. A least squares fit relationship between urchin size groups and density (y = 5.30-0.08x, r = -0.83, where y = density m<sup>-2</sup>, x = urchin size group and r = correlation coefficient) effects a constant logarithmic decrease in number. According to Miller and Mann (1973), this is a situation that would occur if annual recruitment and mortality were constant.

Three transects laid perpendicular to the shore were studied in detail to determine differences in the frequency distributions with increasing distance from the shore. Size frequency distributions from quadrats along the three transects were plotted for successive 10 m intervals from the shore. A progressive decrease in mean urchin size was found within the first 60 m from shore (Figure 26).

The mean size of urchins in the first six quadrats sets were significantly different from one another at the P = 0.05level with the exception of the differences between means of quadrat sets 3 and 4, 3 and 5, and 4 and 5 (Table 8). The means of the remaining quadrat sets 7 to 12 were significantly different when compared to each of the first five quadrat sets with the

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# Table 7

Numbers of *Diadema antillarum* of each size group  $m^{-2}$ , based on a mean density of 23 individuals  $m^{-2}$  of reef surface.

Size Interval (mm)	Size Group (mm)	number of indivi- duals in each size group in the total population (%)	No. of urchins m <sup>-2</sup> of reef surface
(0.0-19.5)	15	13.3	3.1
(20.0-24.5)	20	11.3	2.6
(25.0-29.5)	25	18.6	4.3
(30.0-34.5)	30	17.6	4.0
(35.0-39.5)	35	14.9	3.4
(40.0-44.5)	40	10.3	2.4
(45.0-49.5)	45	7.1	1.6
(50.0-54.5)	50	3.9	0.9
(55.0-59.5)	55	2.2	0.5
(≥60.0)	60	0.8	0.2
Total		100.0	23.0

Figure 26 Size frequency distributions of *Diadema antillarum* collected from transects laid perpendicular to the shore.

Mean urchin size in each quadrat set is connected by the dotted line.



METERS FROM SHORE

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0

120

μ

0

Results of the statistical testing of the difference between the mean size of urchins in each quadrat set with increasing distance offshore (P = 0.05)



S - significantly different

N - not significantly different

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exception of differences between the means of quadrat sets 11 versus 3, 4 and 5.

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#### V. Energy Budgets for Diadema antillarum

#### A. Consumption

The composition of food in the gut contents of urchins varied considerably with body size. Figure 27 shows the percentages of different food types found in urchins of each size group (Appendix Table 5). There appears to be a marked change in diet when urchins reach between 30 and 40 mm MTD. The gut contents of urchins of 30 mm MTD and smaller contained a higher percentage of encrusting coralline algal food pellets than either endolithic or epipelic algal food pellets. Gut contents of larger urchins consisted largely of pellets of the epipelic algal food type. Endolithic algal food pellets were not abundant in gut contents of any urchin size group.

No urchins of the 15, 55 and 60 mm MTD size groups were available when analysis was carried out for determination of the percentage of each food type in the natural diets of urchins of each size group. Consequently, urchins of the 15 mm MTD size group were assumed to have gut contents (diets) of similar percentage composition as urchins of the 20 mm MTD size group. Similarly, urchins of the 55 and 60 mm MTD size groups were assumed to have diets of similar percentage composition as urchins of the 50 mm MTD size group.

The weight of food ingested per individual per day (methods page 24) is shown in Table 9. Estimated minimum consumption rates ranged from 0.129 g dry wt day<sup>-1</sup> for urchins of the smallest size group of 15 mm MTD to 2.934 g dry wt day<sup>-1</sup> for the largest size group of urchins, 60 mm MTD.

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Figure 27 Percentages of different food types found in the guts of *Diadema antillarum* of various size groups.



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# Table 9

Estimated minimum daily consumption rates of Diadema antillarum of various size groups, equivalent to mean gut content dry weight.

Urchin	No. Examined	Consumption Rate	±95% Confidence
Size Group (mm)		(g dry wt day-⊥)	Limits
15	16	0.129	0.113
20	18	0.160	0.020
25	23	0.275	0.040
30	20	0.330	0.071
35	16	0.742	0.126
40	16	1.236	0.144
45	16	1.906	0.034
50	16	2.366	0.411
55	16	2.536	0.319
60	16	2.934	0.299

Table 10 lists the weight of food consumed per square meter of reef surface by urchins of each size group. These were determined by first multiplying the dry weight of food consumed per urchin of each size group times the frequency of each size group in a  $m^2$ . The total weight of food consumed per square meter of reef surface was then calculated by summing food consumption over all urchin size groups. As a minimum estimate approximately 15.85 g dry wt day<sup>-1</sup> are consumed by *Diadema* per square meter of reef surface (or 475.50 g dry wt mo<sup>-1</sup>).

The estimated minimum caloric intake per urchin of each size group is shown in Table 11 (for calculation see Appendix Table 7). Urchins of the smallest size group, 15 mm MTD, acquire 38.66 calories per day from food consumed and urchins of the largest size group, 60 mm MTD, 210.09 calories. The estimated minimum caloric intake per square meter of reef surface is shown in Table 12. Urchins obtain 2.38 kcal m<sup>-2</sup> day<sup>-1</sup> or 71.27 kcal m<sup>-2</sup> mo<sup>-1</sup> from the food they consume.

B. Production

Growth rates of *Diadema* feeding on fleshy macrophytes and sea grasses have been measured by Lewis (1966) in Barbados and Bauer (1976) in Florida. Mean growth rates determined from their studies suggests that urchins less than 35 mm MTD grow at a rate of 3.4 mm mo<sup>-1</sup> and larger urchins at a rate of 1.5 mm mo<sup>-1</sup>. However, *Diadema* on the North Bellairs Fringing Reef do not feed on fleshy macrophytes or sea grasses; their food resources are entirely different and contain large amounts of inorganic material. Thus growth rates determined by Lewis and Bauer may not be applicable to the present study.

Polymodal size frequency distributions were analyzed in an attempt to obtain growth rates of *Diadema* on the fringing reef (Figure 28). Bimonthly size frequency distributions (solid line) were divided into their sets of component curves (dotted line) to detect any regular, progressive increase in modal values. An increase in modal values over successive months represents an increase in urchin size. Modal values did indeed increase between July 1975 and May 1976 (Table 13). Thus, a more detailed examination of the polymodal size frequency distributions was undertaken.

Figure 28 clearly shows that there are two prominent peaks at 5 and 17 mm in the July 1975 polymodal size frequency distribution. These modes appear to represent the recruited young from the spring 1975 and fall 1974 spawnings respectively. This interpretation is based upon the data which show that *Diadema* on the North Bellairs Fringing Reef exhibit two periods of spawning (see Figure 20). The third mode of the July size frequency distribution occurs at 24 mm. This mode is assumed to represent the combined individuals then one year of age (spawned in spring 1974 and fall 1973). The fourth mode at 40 mm then may be considered to represent urchins of two years or older.

Based upon the above interpretation of the July 1975 polymodal size frequency distribution, urchins of the July 1975, 5 mm size group grow from a mean of 5 mm (first mode) to 24 mm (mode three) in one year, a monthly growth rate of 1.6 mm. Further inspection of the July 1975 distribution indicates that

Estimated minimum food consumption rates of Diadema antillarum m<sup>-2</sup> day<sup>-1</sup> expressed in g dry weight based upon gut content dry weight.

<u>Urchin</u> Size Group	Food Consumption Rates	No. of urchins <u>m<sup>-2</sup> of reef</u> surface	Contribution to total weight of food consumed m <sup>-2</sup>
(mm)	(g dry wt day <sup>-1</sup> )		$(g dry wt m^{-2} day^{-1})$
15	0.129	3.1	0.40
20	0.160	2.6	0.42
25	0.275	4.3	1.18
30	0.330	4.0	1.32
35	0.742	3.4	2.52
40	1.236	2.4	2.97
45	1.906	1.6	3.05
50	2.366	0.9	2.13
55	2.536	0.5	1.27
60	2.934	0.2	0.59

Urchin food consumption expressed in g dry wt m<sup>-2</sup> day<sup>-1</sup> = 15.85 Urchin food consumption expressed in g dry wt m<sup>-2</sup> mo<sup>-1</sup> = 475.50

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Estimated minimum caloric intake per individual *Diadema antillarum* of each size group expressed on a daily and monthly (30 days) basis.

Urchin Size	Daily Caloric	Monthly Caloric
Group	Intake	Intake
(mm)	(cal day <sup>-1</sup> )	$(cal mo^{-1})$
15 .	38.66	1159.80
20	48.06	1441.80
25	73.38	2201.40
30	101.87	3056.10
35	167.90	5037.00
40	135.74	4072.20
45	141.12	4233.60
50	169.41	5082.30
55	181.53	5445.90
60	210.09	6302.70

- 70 -
## - 71 -Table 12

# Contribution to total minimum caloric intake $m^{-2}$ day-1 by urchins of each size group and total caloric intake $m^{-2}$ of reef surface day and $mo^{-1}$ .

Urchin Size Group (mm)	Caloric intake per urchin of each size group (cal day <sup>-1</sup> )	No. of urchins m <sup>-2</sup> of reef surface	Contribution to total calo- ric intake per <u>m<sup>-2</sup> of reef</u> surface (cal mo <sup>-1</sup> )
15	38.66	3.1	119.85
20	48.06	2.6	124.96
25	73.38	4.3	315.53
30	101.87	4.0	407.48
35	167.90	3.4	570.86
40	135.74	2.4	325.78
45	141.12	1.6	225.79
50	169.41	0.9	152.47
55	181.53	0.5	90.77
60	210.09	0.2	42.02

Urchin consumption expressed in cal  $m^{-2} day^{-1} = 2375.51$ Urchin consumption expressed in cal  $m^{-2} mo^{-1} = 71265.30$  urchins of the 24 mm size group grow to 40 mm (mode four) by their second year, a growth rate of 1.3 mm mo<sup>-1</sup>. Thus, two growth rates can be derived for *Diadema* on the fringing reef, one of 1.6 mm mo<sup>-1</sup> for urchins less than or equal to 24 mm and the other of 1.3 mm mo<sup>-1</sup> for larger urchins.

Further evidence of the accuracy of these growth rates can be found from examination of the polymodal size frequency distributions of later months. If urchins of the July 1975, 5 mm size group grow at the estimated rate of 1.6 mm mo<sup>-1</sup>, they would attain 11 mm by November 1975, and 21 mm by May 1976. The November size frequency distribution shows a modal peak at 12 mm, and there is a modal peak at 20 mm in May, 1976.

Since polymodal size frequency distribution analysis combines size groupings into major component curves (Taylor 1965), it is not unlikely that mode two of the September 1975 size frequency distribution may be interpretated as evidence of the combined frequencies of the July 17 and 24 mm size groups. This is a reasonable assumption since urchins of the July 1975, 17 mm size group initially would grow faster (1.6 mm mo<sup>-1</sup>) than urchin of the 24 mm size group (1.3 mm mo<sup>-1</sup>), and one would expect to find a fusion of these size groups in later months resulting from differential growth rates. Therefore, at a growth rate of 1.6 mm mo<sup>-1</sup>, urchins of the July 1975, 17 mm size group reach 20 mm by September 1975, and at a growth rate of 1.3 mm mo<sup>-1</sup>, urchins of the July 24 mm size group reach approximately 27 mm. The combined mean of these two size groups in September 1975, is 24 mm and the September 1975 size frequency distribution does

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Figure 28 Polymodal size frequency distributions of *Diadema* antillarum collected at bimonthly periods from July 1975 to May 1976.

The solid line (----) shows the measured frequency distribution of the population.

The dotted line (...) shows the calculated component normal curves from the same data.

Values in parentheses represent transect locations (Figure 8b).



FREQUENCY OF INDIVIDUALS

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## Table 13

Modes of polymodal size frequency distributions.

Month	mode 1	mode 2	mode 3	mode 4
July 1975	5 mm	17 mm	24 mm	40 mm
September 1975	12 mm	23 mm	33 mm	-
November 1975	12 mm	25 mm	43 mm	-
January 1976	17 mm	28 mm	43 mm	-
March 1976	20 mm	37 mm	47 mm	-
May 1976	20 mm	35 mm	47 mm	-

show a modal peak at 23 mm. Furthermore, urchins of the July 1975, 17 mm size group reach 23 mm and those of the July 24 mm size group reach 30 mm by November 1975, giving a combined mean of 26 mm. The November distribution shows a modal peak at 25 mm. By January 1976, urchins of these same two July 1975 size groups reach 26 and 32 mm respectively. The mean size of these two size groups is 29 mm, and the January 1976 distribution shows a modal peak at 28 mm. Further application of the two estimated growth rates to the July 1975, 17 and 24 mm size groups indicates that they reach 32 and 37 mm respectively by May 1976, giving a combined mean of approximately 35 mm. The polymodal size frequency distribution for May 1976 does exhibit a modal peak at 35 mm.

Growth of urchins of the July 1975, 40 mm size group is somewhat difficult to interpret from the polymodal size frequency distributions. However, at a growth rate of 1.3 mm mo<sup>-1</sup> urchins of this size group should reach 45 mm by November 1975, and the plotted distribution for that month shows a modal peak at 43 mm.

The above interpretations of the polymodal size frequency distributions do provide supporting evidence for the selection of the two growth rates. Therefore, the two growth rates derived for *Diadema* of the North Bellairs Fringing Reef were considered reasonable and taken as  $1.6 \text{ mm mo}^{-1}$  for urchins less than or equal to 24 mm MTD and  $1.3 \text{ mm mo}^{-1}$  for larger urchins. These monthly growth increments in test diameter were then converted to an equivalent increase in body dry weight from a relationship between whole urchin dry weight and test diameter (Figure 29).

Monthly secondary production was converted to calories by multiplying the monthly body weight increment times the mean caloric content of whole urchins (Table 14). The resulting mean monthly secondary production of *Diadema antillarum* ranged from 72.64 cal for urchins of the 15 mm MTD size group to 942.36 cal for urchins of the largest size group of 60 mm MTD (Table 15).

Monthly secondary production of urchins per square meter of reef surface is shown in Table 16. Based on the above method

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Figure 29 The relationship between total urchin dry weight (g) and urchin size (MTD in mm) in Diadema antillarum.

Equation of the line:

- $y = 0.0002x^{3.0607}$ , r = 0.9917 where:
- y = urchin total dry weight (g)
- x = urchin size (MTD in mm)
- r = correlation coefficient



Urchin Size	No. Tested	Caloric Content*	<u>+95% Confidence</u>
Group (mm)		(cal g <sup>-1</sup> dry wt)	Limits
15	10	210.22	54.53
20	11	256.41	33.96
25	12	269.12	27.75
30	10	250.34	24.17
35	11	244.29	33.89
40	12	254.34	18.54
45	11 .	251.82	19.88
50	12	253.19	19.18
55	7	248.29	31.03
60	4	272.10	142.04
overall mean		251.02	12.66

Mean caloric content of whole *Diadema antillarum* (including gonads) collected during a one-year period.

\* caloric content determined by wet oxidation (Huges 1969)

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Mean monthly secondary production of *Diadema* antillarum of various size groups.

Urchin Size Group (mm)	Monthly Production (cal mo <sup>-1</sup> )
15	72.64
20	127.94
25	199.41
30	231.09
35	315.43
40	413.38
45	524.98
50	650.37
55	789.61
60	942.36

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Secondary productivity of Diadema antillarum expressed in cal  $m^{-2}$  mo<sup>-1</sup>.

Mo	onth		Proc	luct	ivity
			(cal	m <sup>-2</sup>	$mo^{-1})$
July	1975		5	5,228	3
Augus	st 1975		5	5 <b>,</b> 558	3
Septe	ember 19	75	e	5,175	5
Octol	ber 1975		e	5,003	3
Nover	mber 197	5	4	4,620	ט
Decer	mber 197	5		-	
Janua	ary 1976		(	5,884	4
Febru	uary 197	6	4	4,879	Э
Marcl	h 1976			7,10	B
Apri	1 1976			7 <b>,</b> 54'	7
May	1976		(	5 <b>,</b> 694	4
June	1976			7,160	6
		mean month	Ly	6,169	9
		95% C.L.*	:	± 22:	2
Urchin production	n expres c	sed in al m <sup>-2</sup> mo <sup>-1</sup>	**	6,40	9

\* confidence limits

\*\*based upon the number of urchins of each size group in the mean density (Table 7) of determining growth (somatic and reproductive tissue combined), the monthly energy allocated to growth was similar during the year and ranged from 4.62-7.55 kcal m<sup>-2</sup>. The slight differences in production result from the varying proportions of individuals of each size group in the population sampled each month (Figures 25a-c). Mean production per square meter of reef surface was 6.41 kcal mo<sup>-1</sup>.

C. Reproduction

Seasonal variation in the gonad index of *Diadema* is illustrated in Figure 30. The gonad index increased during July to September 1975 and again from October to May 1976, indicating two periods of gonad maturation. The decreases during September to October 1975 and May to June 1976 were interpreted as spawning periods.

There was very little difference in the caloric content per gram of reproductive tissue among urchins of each size group, even though samples were from monthly collections over the entire year (Table 17). The mean caloric value of reproductive tissue irrespective of urchin size or sex was  $5.41 \pm 0.09$  kcal gm<sup>-1</sup> ash free dry weight, equivalent to 0.76 kcal ml<sup>-1</sup> gonad.

From Figure 30 it is evident that there was considerable loss of reproductive material during the two spawning periods. This loss, expressed in calories, is shown in Table 18 and was obtained by multiplying the difference in gonad volumes between the two spawning periods times the caloric content per ml of reproductive tissue. Caloric loss during the September-October 1975 spawning season ranged from 21.24 calories for urchins of 20 mm MTD to 776.60 calories for urchins of 60 mm MTD. During

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Figure 30 Seasonal variation in gonad index of *Diadema* antillarum vertical bars indicate 95% confidence limits.

> Gonad volume (GV) in ml. Urchin size (MTD) in mm.

(Drawn from data in Appendix Table 14).



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Urchin Size	No. of Urchins	Caloric Content*	±95% Confidence
Group	Examined	(kcal g-1 AFDW)	Limits
(Inun)			
15	1	5.368	-
25	18	5.398	0.194
30	15	5.305	0.271
35	31	5.327	0.152
40	27	5.358	0.165
45	29	5.556	0.185
50	18	5.379	0.230
55	12	5.560	0.603
overall mean	í	5.406	0.088

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Caloric content of reproductive tissue of *Diadema* antillarum, collected during a one-year period.

\* caloric content determined by micro-bomb calorimetry AFDW = ash free dry weight

#### - 82 -

## - 83 -Table 18

Caloric loss of reproductive tissue during the two spawning periods of *Diadema antillarum*.

Urchin Size	Spawning	Mean Monthly	
Group (mm)	SeptOct. 1975 (cal urchin <sup>-1</sup> )	May-June 1976 (cal urchin <sup>-1</sup> )	Loss Over the Year (cal urchin <sup>-1</sup> )
20	21.24	48.54	5.82
25	56.12	94.80	12.58
30	97.08	164.57	21.80
35	153.96	261.65	34.63
40	229.80	389.82	51.64
45	327.63	555.15	73.57
50	449.73	765.98	101.31
55	597.62	1013.22	134.24
60	776.60	1315.82	174.37

Urchin reproductive output expressed in  $cal m^{-2} mo^{-1} = 709.33$ 

the May-June 1976 spawning period 48.54 calories were lost as reproductive products by urchins of 20 mm MTD and 1315.82 calories by urchins of 60 mm MTD.

Mean monthly caloric loss ranged from 5.82 calories for urchins of the 20 mm size group to 174.37 calories for urchins of the largest size group (Table 18). The mean monthly caloric loss in reproductive products per square meter of reef surface was 0.71 kilocalories.

#### D. Respiration

Respiration rates and energy required for respiration are presented in Table 19. Urchins 15 mm MTD consume 0.073  $mgO_2 h^{-1}$  or expend 175.55 cal mo<sup>-1</sup> for maintenance. Urchins of the largest size group, 60 mm MTD, consume 1.636 mgO<sub>2</sub> h<sup>-1</sup> or require 3934.25 cal mo<sup>-1</sup> for maintenance. The loss of energy in respiration per square meter of reef surface was 33.45 kcal mo<sup>-1</sup>.

#### E. Excretion and Egestion

Hourly rates of ammonia excretion and equivalent monthly energy loss by *Diadema* examined in the laboratory are presented in Table 20. Hourly excretion rates ranged from 0.30  $\mu$ g at NH<sub>3</sub>-N for urchins 15 mm MTD to 4.33  $\mu$ g at NH<sub>3</sub>-N for urchins 60 mm MTD. Monthly energy loss ranged from 1.05 cal urchin<sup>-1</sup> for individuals of the smallest size group to 15.21 cal urchin<sup>-1</sup> for urchins of the largest size group. The monthly energy loss per square meter of reef surface by urchins was 0.11 kcal.

Daily egestion rates expressed in grams dry weight are presented in Table 21. Rates range from 0.072 g dry wt day<sup>-1</sup> for urchins of the 15 mm MTD size group to 2.251 g dry wt day<sup>-1</sup>

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Oxygen consumption and equivalent energy requirements for maintenance of *Diadema antillarum*.

<u>Urchin Size</u>	Oxygen Consumption*	Energy Requirements**
Group	$(mgO_2 \text{ urchin}^{-1} h^{-1})$	(cal urchin-1 mo-1)
15	0.073	175.55
20	0.247	593.99
25	0.421	1012.42
30	0.594	1428.45
35	0.768	1846.89
40	0.941	2262.92
45	1.115	2681.35
50	1.288	3097.38
55	1.462	3515.82
60	1.636	3934.25

Urchin oxygen consumption expressed in cal  $m^{-2}$  mo<sup>-1</sup> = 33447.38

\* from Lewis (1968a)

\*\* 1.0 mgO<sub>2</sub> = 3.34 calories Ivlev (1934)

Urchin Size Group	No. Tested	Mean Ammonia Excreted	±95% Confidence Limits	Caloric Expenditure*
(mm)		urchin <sup>-1</sup> $h^{-1}$ )		(cal urchin <sup>-</sup> mo <sup>-1</sup> )
15	3	0.30	0.06	1.05
20	11	0.42	0.23	1.48
25	22	0.71	0.16	2.49
30	16	1.10	0.30	3.87
35	21	1.76	0.59	6.18
40	14	2.05	0.50	7.20
45	5	2.11	0.51	7.41
50	11	3.42	0.83	12.02
55	4	4.23	1.05	14.86
60	-	4.33**	-	15.21
			2 1	

Ammonia excretion and equivalent caloric expenditure mo<sup>-1</sup> by *Diadema antillarum*.

Urchin excretion expressed in cal  $m^{-2} mo^{-1} = 105.44$ 

- \* 1.0 µg at NH<sub>3</sub> = 4.88 x  $10^{-3}$  calories Lilly (1975)
- \*\* value determined from regression equation: y = -1.914 + 0.104x, where  $y = \mu g$  at NH<sub>3</sub>, x = urchin MTD in mm, correlation coefficient r = 0.969

- 87 -Table 21

#### Urchin Egestion Rate ±95% Confidence No. Examined Size Group Limits (g dry wt day<sup>-1</sup>) (mm) 15 0.018 13 0.072 20 12 0.143 0.029 25 13 0.220 0.069 30 11 0.238 0.063 0.734 35 11 0.108 1.095 0.189 40 11 45 13 1.710 0.513 1.836 0.387 50 12 55 13 2.071 0.342 60 11 2.251 0.363

# Daily egestion rates of *Diadema antillarum* of various size groups expressed in grams dry weight.

for urchins of the largest size group, 60 mm MTD. On a square meter basis urchins egest 13.50 g dry wt day<sup>-1</sup> or 405.00 g dry wt mo<sup>-1</sup> (Table 22).

The energy content of egested fecal waste from urchins of each size group collected in the field is shown in Table 23. Results indicated that the caloric content of feces was quite variable over the urchin size groups examined. Caloric content ranged from a low of 19.83 cal  $g^{-1}$  dry weight of feces for urchins of 45 mm MTD to a high of 164.33 cal  $g^{-1}$  dry weight of feces for urchins of 35 mm MTD.

Daily egestion rates in calories are shown in Table 24. Rates ranged from a low of 8.17 cal  $\mathrm{urchin}^{-1} \mathrm{day}^{-1}$  for individuals of 15 mm MTD to a high of 197.75 cal  $\mathrm{urchin}^{-1} \mathrm{day}^{-1}$  for urchins of 60 mm MTD. Urchins egested 869.37 cal  $\mathrm{m}^{-2} \mathrm{day}^{-1}$  or 26.08 kcal  $\mathrm{m}^{-2} \mathrm{mo}^{-1}$  (Table 25).

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## - 89 -Table 22

Egestion rates of *Diadema antillarum* m<sup>-2</sup> of reef surface expressed in grams dry weight day<sup>-1</sup>.

.

Urchin Size Group (mm)	Egestion Rate (g dry wt day <sup>-1</sup> )	$\frac{\text{No. of urchins}}{\frac{\text{m}^{-2} \text{ of reef}}{\text{surface}}}$	Contribution to total egestion m <sup>-2</sup> (g dry wt day-1)
15	0.072	3.1	0.22
20	0.143	2.6	0.37
25	0.220	4.3	0.95
30	0.238	4.0	0.95
35	0.734	3.4	2.50
40	1.095	2.4	2.63
45	1.710	1.6	2.74
50	1.836	0.9	1.65
55	2.071	0.5	1.04
60	2.251	0.2	0.45
		-2	-1 12 50

Urchin egestion expressed in g dry wt m<sup>-2</sup> day<sup>-1</sup> = 13.50 Urchin egestion expressed in g dry wt m<sup>-2</sup> mo<sup>-1</sup> = 405.00

Mean caloric content of feces from freshly collected *Diadema antillarum*.

<u>Urchin Size</u>	No. Tested	Mean Caloric Content	<u>±95% Confidence</u>
Group (mm)		(cal g <sup>-1</sup> dry wt)	Limits
20	4	113.44	6.87
25	4	62.20	15.09
30	4	99.19	15.60
35	4	164.33	38.14
40	5	24.27	5.37
45	5	19.83	5.56
50	4	33.96	7.24
55	5	23.93	8.43
60	4	87.85	3.12

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Caloric content of feces egested by *Diadema* antillarum of each size group expressed on a daily and monthly (30 days) basis.

Urchin Size Group (mm)	Daily Caloric* (cal day-1)	Monthly Caloric Loss (cal mo-1)
15	8.17	245.10
20	16.22	486.60
25	13.68	410.40
30	23.61	708.30
35	120.62	3618.60
40	26.58	797.40
45	33.91	1017.30
50	62.35	1870.50
55	49.56	1486.80
60	197.75	5932.50

\* values for daily caloric loss were obtained by multiplying daily egestion rates (Table 21, column 3) times the mean caloric content of feces (Table 23, column 3).

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Contribution to total caloric loss in feces  $m^{-2}$  day<sup>-1</sup> by urchins of each size group and total caloric loss in feces  $m^{-2}$  of reef surface day<sup>-1</sup> and  $mo^{-1}$ .

Urchin Size Group (mm)	Caloric loss urchin-1 of each size group day-1 (cal)	No. of urchins m-2 of reef surface	Contribution to total caloric loss of m-2 reef surface (cal)
15	8.17	3.1	25.33
20	16.22	2.6	42.17
25	13.68	4.3	58.82
30	23.61	4.0	94.44
35	120.62	3.4	410.11
40	26.58	2.4	63.79
45	33.91	1.6	54.26
50	62.35	0.9	56.12
55	49.56	0.5	24.78
60	197.75	0.2	39.55

Urchin egestion expressed in cal  $m^{-2} day^{-1} = 869.37$ Urchin egestion expressed in cal  $m^{-2} mo^{-1} = 26081.10$ 

#### VI. Summary of Energy Budgets

Table 26 summarizes monthly energy budgets for *Diadema* antillarum of each size group and per square meter of reef surface. Urchins of the 15, 20, 25, 30, 40 and 45 mm MTD size groups can satisfy their energy budget requirements from the food energy obtained at the estimated minimum consumption rates. Urchins of the other size groups show deficits in their energy budgets which range from 0.362-4.522 kcal mo<sup>-1</sup>. This indicates that their budget requirements cannot be met at the estimated minimum consumption rates.

On a square meter basis, the population energy budget shows a surplus of 5.22 kcal mo<sup>-1</sup>.



#### <u>Table 26</u>

Summary of Energy Budgets of  $\it Diadema$  antillarum of various size groups expressed in kcal m^2 mo^1

Urchin Size Group	Consumption	Production	Respiration	Excretion	Egestion	Total	Surplus
(mm)	(C)	(P)	(R)	(0)	(F)	(P+R+U+F)	or deficit
15	1.160	0.073	0.176	0.001	0.245	0.495	0.665
20	1.442	0.128	0.594	0.001	0.487	1.210	0.232
25	2.201	0.199	1.012	0.002	0.410	1.623	0.578
30	3.056	0.231	1.428	0.004	0.708	2.371	0.685
35	5.037	0.315	1.847	0.006	3.619	5.787	-0.750
40	4.072	0.413	2.263	0.007	0.797	3.480	0.592
45	4.234	0.525	2.681	0.007	1.017	4.230	0.004
50	5.082	0.650	3.097	0.012	1.871	5.630	-0.548
55	5.446	0.790	3.516	0.015	1.487	5.808	-0.362
60	6.303	0.943	3.934	0.015	5.933	10.825	-4.522
Urchin Population							
Energy Budget							
$(\text{kcal m}^{-2} \text{ mo}^{-1})$	71.27	6.41	33.45	0.11	26.08	66.05	5.22
(per cent)	(100.00%)	9.00%	(46.93%)	(0.15%)	(36.59%)	(92.68%)	(7.32%)

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#### VII. Absorption Efficiency

Positive efficiencies of organic matter absorption determined by the Conover (1966) method ranged between 2.2 and 72.8% on all foods (Table 27). Absorption efficiencies were higher on encrusting coralline algae than on any other food type and ranged from 26.0% for urchins of 15 mm MTD to 72.8% for urchins of 50 mm MTD. In addition absorption efficiencies varied directly with urchin size for individuals fed encrusting coralline algae (Figure 31).

Absorption efficiencies on the other food types were generally low and showed no direct relationship with urchin size (Table 27). Only urchins of 40 mm MTD and 50 mm MTD had positive absorption efficiencies when fed the endolithic algal veneer (14.2% and 7.1% respectively). *Diadema* of 35 mm MTD and larger showed positive absorption efficiencies ranging from 9.4% to 22.4% when fed the endolithic algae on rubble. Urchins fed the epipelic algae exhibited the lowest positive absorption efficiencies of all examined, 2.2%.

Absorption efficiencies on mixed diets were also determined from the difference between caloric content of food and feces. These efficiencies were calculated using the general equation A.E. =  $(C-F)/C \times 100$ , where A.E. = absorption efficiency, C = caloric content of food and F = caloric content of feces(Miller and Mann 1973, Lawrence 1975). Asborption efficiencies calculated in this way for urchins of each size group are shown in Table 28 (column number 3) and range from 5.9% to 81.4%.

In addition, absorption efficiencies were calculated for urchins with a mixed diet on the basis of organic matter.

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Percent efficiency of organic matter absorption\*\*\* by Diadema antillarum.

## Algal Food Types Tested

Urchin Size Group (mm)	Encrusting Coralline	Endolithic veneer on dead heads	Endolithic on rubble	Epipelic on sand
15	26.0	NE*	NE	NE
25	62.8	**	-	-
30	37.3	-	-	NE
35	38.3	-	11.3	NE
40	46.9	14.2	9.4	2.2
45	60.5	-	22.4	-
50	72.8	7.1	16.9	2.2

- \* NE = not examined
- \*\* negative values were obtained
- \*\*\* absorption efficiency determined by the method of Conover (1966)

where: A.E. =  $\frac{(F'-E')}{(1-E')(F')} \times 100$ ,

- and F' = fraction of organic matter in food
  - E' = fraction of organic matter in feces

Figure 31 Efficiency of absorption of organic matter (in percent) by *Diadema antillarum* which has fed upon encrusting coralline algae.

Equation of the regression line:

- y = 10.65 + 1.10x, r = .72 where:
- y = absorption efficiency in percent
- x = urchin size (MTD) in mm
- r = correlation coefficient



Comparisons of absorption efficiencies calculated by several methods for *Diadema antillarum* of various size groups having a mixed diet. Values are in percent (%).

<u>Urchin Size</u>	Absorption	Absorption	Absorption
Group	Efficiency	Efficiency	Efficiency
(mm)	(1)	(2)	(3)
15	73.5	57.5	78.5
20	31.6	27.1	67.5
25	46.7	37.0	81.4
30	53.3	40.0	76.8
35	43.5	43.7	28.2
40	44.6	39.5	80.3
45	neg.	neg.	75.9
50	neg.	neg.	63.2
55	neg.	neg.	72.7
60	neg.	neg.	5.9

according to Welch (1968) in terms of organic matter
according to Conover (1966) in terms of organic matter
according to Miller and Mann (1973) in terms of calories

Positive efficiencies shown in Table 28 range from a low of 27.1% to a high of 73.5%. The highest value was calculated for urchins of 15 mm MTD and the lowest for urchins of 20 mm MTD. Table 28 also demonstrates that there is little agreement among the absorption efficiencies determined by the three methods. The absorption efficiencies calculated in terms of calories are all higher (except for urchins of 35 mm MTD) than those determined on the basis of organic matter. Irrespective of the methods there appears to be no direct relationship between urchin size and absorption efficiency when urchins feed on a mixed diet.

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#### VIII. Calcium Carbonate Sediment Production and Erosion of Reef Carbonate Framework by Diadema antillarum

Table 29 lists the mean percentage by weight of calcium carbonate (CaCO<sub>3</sub>) in feces from various sizes of *Diadema antillarum*. Calcium carbonate content ranges between a low of 84.44% in feces of urchins of 55 mm MTD and a high of 94.85% from urchins of 40 mm MTD. An overall mean of 89.79% was calculated from pooled values.

Total monthly  $CaCO_3$  sediment production and erosion by urchins is shown in Table 30. Urchins of 15 mm MTD produce 1.98 grams of sediment per month and approximately 83% of this quantity can be attributed to the production of fresh sediment i.e. erosion. Urchins of 60 mm MTD, the largest examined, produce 60.64 grams of  $CaCO_3$  sediment per month but only 29.7% of this quantity can be attributed to erosion. Total monthly sediment production per square meter of reef surface is 368.82 grams. Erosion accounts for 48.9% of the total sediment production (Table 30).

Mean percentage of inorganic matter (CaCO<sub>3</sub>) and organic matter in feces of *Diadema antillarum* of various size groups based on dry weight.

Urchin Size Group (mm)	No. Examined	Mean Percent Inorganic Matter (%)	±95% Confidence Limits	Mean Percent Organic Matter (by difference) (%)
15	4	91.80	9.25	8.20
20	6	87.10	10.80	12.90
25	11	89.73	4.71	10.27
30	14	88.74	7.28	11.26
35	6	92.34	3.89	7.66
40	5	94.85	1.93	5.15
45	6	91.24	7.11	8.76
50	10	90.74	3.25	9.26
55	7	84.44	14.46	15.56
60	-	89.79*	<del>-</del> .	10.21*
* mean	69 1	89.79	2.03	10.21

## - 102 -Table 30

## Monthly calcium carbonate sediment production and erosion by *Diadema antillarum*.

Urchin Size Group (mm)	Total Sediment Production* (gCaCO <sub>3</sub> urchin <sup>-1</sup> mo <sup>-1</sup> ) <sup>3</sup>	Percentage of Primary Reef Framework in the mixed diet**	Fraction of Total Sediment Production Attributed to Erosion*** (gCaCO <sub>3</sub> urchin <sup>-1</sup> mo <sup>-1</sup> ) <sup>3</sup>
15	1.98	83.0	1.64
20	3.74	83.0	3.10
25	5.92	76.3	4.52
30	6.34	88.7	5.62
35	20.33	68.0	13.82
40	31.16	44.3	13.80
45	46.18	27.3	12.78
50	49.98	29.7	14.84
55	52.46	29.7	15.58
60	60.64	29.7	18.01

Urchin sediment production expressed in  $gCaCO_3 m^{-2} mo^{-1} = 368.82$ Urchin bioerosion expressed in  $gCaCO_3 m^{-2} mo^{-1} = 180.37$ Bioerosion expressed as a percentage of sediment production = 48.9%

\* Column 2 obtained by multiplying daily egestion rates in grams (Table 21) times 30 days and the resultant times the mean percentage of CaCO<sub>3</sub> in feces (Table 29).

\*\* Column 3 obtained from the percentage of each food type in gut contents (Figure 29).

\*\*\*Column 4 obtained by multiplying column 2 times column 3.
#### DISCUSSION

#### I. Primary Production on the North Bellairs Fringing Reef

Two important points emerge from the study of productivity of benthic algae from the North Bellairs Fringing Reef. Firstly, rates of primary production per square centimeter of algal surface are as high or higher than rates determined on reefs elsewhere in the Caribbean and Pacific. Secondly, total benthic primary productivity per square meter of fringing reef surface (excluding coral symbiotic algal productivity) is lower than rates of primary production per square meter of reef surface reported for several other coral reefs.

A comparison of rates of production of benthic algae on various reefs is shown in Table 31. Hourly rates of production per square centimeter of algal surface of encrusting coralline algae are in close agreement to those determined by workers in Hawaii and Curaçao while rates of endolithic and epipelic algal production are higher than those measured elsewhere.

Rates of production of fringing reef benthic algae are compared with rates of phytoplankton productivity in oceanic and neritic waters in the vicinity of Barbados in Table 32. Based upon a 10-hour photoperiod and a euphotic zone depth of 100 m, Steven (1971) determined the net production of phytoplankton in oceanic waters to be approximately 1.24 kcal m<sup>-2</sup> day<sup>-1</sup>. Over a similar photoperiod and a euphotic zone depth of 10 m, data of Sander (1971) and Sander and Steven (1971) show a net phytoplankton productivity of approximately 0.97 kcal m<sup>-2</sup> day<sup>-1</sup> in neritic waters adjacent to the North Bellairs Fringing Reef. Rates of

# Table 31

# Primary productivity of several reef associated algae from various locations.

Algal Type	$(cm^{-2}\frac{Ne^{2}}{o})$	t Producti f algal su	vity rface h <sup>-1</sup> )	$(cm^{-2} \frac{Gi}{o})$	ross Produ f algal su	uctivity_1)	Location	Source
	mg02	mgC	calories	mg02	mgC	calories		
encrusting	0.036	0.014	0.120	0.048	0.018	0.160	Hawaii	Marsh (1970)
coralline				0.025- 0.062	0.009- 0.023	0.084- 0.207	Hawaii	Littler (1973)
	0.024- 0.026	0.009- 0.010	0.080- 0.087				Hawaii	Littler and Doty (1975)
	0.015- 0.034	0.006- 0.013	0.050- 0.114	0.023- 0.043	0.009- 0.016	0.077- 0.144	Curacao	۲ Wanders (1976) ہے 4
	0.038	0.014	0.127	0.060	0.023	0.200	Barbados	This Study I
endolithic	0.006	0.002	0.020	0.012	0.005	0.040	Moorea	Sournia (1976a)
	0.12- 0.035	0.005- 0.013	0.040- 0.117				Tuamotu Island	Sournia (1976b)
	0.015- 0.034	0.006- 0.013	0.050- 0.144	0.023- 0.043	0.009- 0.016	0.077- 0.144	Curacao	Wanders (1976)
	0.070	0.026	0.234	0.098	0.037	0.327	Barbados	This Study
epipelic	0.015- 0.034	0.006- 0.013	0.050- 0.144	0.023- 0.043	0.009- 0.016	0.077- 0.144	Curacao	Wanders (1976)
	0.073	0.027	0.244	0.082	0.031	0.274	Barbados	This Study
								•

1.0 mgO<sub>2</sub> = 3.34 calories Ivlev (1934) 1.0 gO<sub>2</sub> = 0.375 g C Westlake (1963)

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# Table 32

#### Daily net primary production of fringing reef benthic algae and phytoplankton in oceanic and neritic waters near Barbados.

Algal Type	(gQ_)	aily Net Productiv	vity (calories)	Location	Source
encrusting coralline	0.56 m <sup>-2</sup> of reef surface	0.21 m <sup>-2</sup> of reef surface	0870.40 m <sup>-2</sup> of reef surface	Fringing reef	This Study
algae	1.92 m <sup>-2</sup> of algal surface	0.72 m <sup>-2</sup> of algal surface	6412.80 m <sup>-2</sup> of algal surface		
endolithic algae	$0.80 \text{ m}^{-2}$ of reef surface $5.04 \text{ m}^{-2}$ of algal surface	$0.30 \text{ m}^{-2}$ of reef surface $1.89 \text{ m}^{-2}$ of algal surface	2672.00 $m^{-2}$ of reef surface 16833.60 $m^{-2}$ of algal surface	Fringing reef	This Study , 105
epipelic	2.16 m <sup>-2</sup> of reef surface 7.68 m <sup>-2</sup> of algal surface	$0.81 \text{ m}^{-2}$ of reef surface 2.88 m <sup>-2</sup> of algal surface	7214.40 m <sup>-2</sup> of reef surface 25651.20 m <sup>-2</sup> of algal surface	Fringing reef	This Study
Total	3.52 m <sup>-2</sup> of reef surface	1.32 m <sup>-2</sup> of reef surface	11756.80 m <sup>-2</sup> of reef surface	Fringing reef	This Study
oc <b>e</b> anic phytoplankton	0.37 m <sup>-2</sup> of water surface	0.14 m <sup>-2</sup> of water surface	1235.80 m <sup>-2</sup> of water surface	Off the west coast of	Steven (1971)*
neritic phytoplankton	0.29 m <sup>-2</sup> of water surface	0.ll m <sup>-2</sup> of water surface	968.60 m <sup>-2</sup> of water surface	Barbados Waters adjacent the fringing	Sander (1971)*

\* their values have been corrected according to Borstad (1978)

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1.0 mgO<sub>2</sub> = 3.34 calories Ivlev (1934)
1.0 gO<sub>2</sub> = .375 gC Westlake (1963)
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net production per square meter of reef surface by each of the three algal types are greater than the rates of net phytoplankton production in oceanic and neritic waters. Productivity of encrusting coralline algae per square meter of reef surface exceeds oceanic phytoplankton productivity per square meter of water surface by a factor of 1.5 and exceeds phytoplankton productivity in waters adjacent to the fringing reef by a factor of 1.9. Net productivities of endolithic and epipelic algae per square meter of reef surface exceed oceanic phytoplankton productivity by factors of 2.2 and 5.8 respectively and neritic water phytoplankton productivity per square meter of water surface by factors of 2.8 and 7.5 respectively. Total benthic algal net productivity per square meter of reef surface exceeds oceanic phytoplankton productivity by a factor of 9.5 and neritic water phytoplankton

It is also of interest to compare rates of total benthic algal production to reef primary productivity elsewhere. Table 33 lists daily rates of non-coral primary production per square meter of reef surface for several coral reefs. The contribution of total reef primary production ranges from a low of 1.78 kcal  $m^{-2} day^{-1}$  to a high of 50.77 kcal  $m^{-2} day^{-1}$ . Wanders (1976) reports that daily net production of benthic algae on a fringing coral reef in Curaçao is in the order of 20.04 kcal  $m^{-2}$  of reef surface which is in close agreement with 17.81 kcal  $m^{-2}$  of reef surface day<sup>-1</sup> measured by Sournia (1976a) in Moorea. In Barbados, daily net productivity by benthic algae is 11.76 kcal  $m^{-2}$  of reef surface.

# Table 33

#### Net productivity by benthic algae\* from several coral reefs

	Contribution to reef productivity by benthic algae			Location	Source	
$(gO_2 m^{-2})$	day <sup>-1</sup> ) (gC	$m^{-2} day^{-1}$ ) (c	al $m^{-2}$ day <sup>-1</sup> )			
15	5.20	5.70	50768.00	Hawaii	Littler (1973)	
0 1	<b>.</b> 53-	0.20- 0.50	1780.22- 4452.22	Hawaii	Littler and Doty (1975)	
5	5.33	2.00	17812.22	Moorea	Sournia (1976a)	
6	5.00	2.25	20040.00	Curacao	Wanders (1976)	
3	.52	1.32	11756.80	Barbados	This Study	

1.0 mgO<sub>2</sub> = 3.34 calories Ivlev (1934) 1.0 gO<sub>2</sub> = .375 gC Westlake (1963)

\* productivity contribution by symbiotic algae in corals not included.

Although hourly rates of benthic algal production per square centimeter of algal surface on the North Bellairs Fringing Reef are similar or higher than those reported elsewhere, the percentage area covered by each of the three algal types on the fringing reef (Appendix Table 2) determines the total benthic productivity per square meter of reef surface (Table 3). Because reef surface topography is highly irregular, it is extremely difficult to quantify the exact surface area occupied by algal covered surfaces (Dahl 1973, 1974). Therefore, the total surface area covered by each algal type may have been underestimated. This would then partly account for a lower overall figure for calculated primary productivity per square meter of reef surface.

Rates of coral reef benthic algal net production are compared with rates of macrophytic algae and sea grass net production in Table 34. Rates of coral reef benthic algal production (excluding the contribution of symbiotic algae in living coral tissue) are generally lower than those reported for several marine benthic plant communities. In Barbados, the rate of benthic algal net production is lower than those reported for the marine plant and other coral reef communities. This result may be considered a function of the area covered by each algal type within a square meter of reef surface, since rates of reef benthic algal production per unit area of algal surface are similar to those reported for marine macrophytes and sea grasses (Luning 1971, 1973, Johnston et al. 1977, Drew 1978).

Nevertheless, the above comparisons between reef benthic algal productivity and oceanic and neritic phytoplankton productivity provide supporting evidence for the generalization that

# - 109 -Table 34

# Net primary productivity of several marine plant communities and coral reefs\*.

Plant		Source		
Community	$(g0_2 m^{-2} mo^{-1})$	$(gC m^{-2} mo^{-1})$	$(kcal m^{-2} mo^{-1})$	)
Fucus	1821.36	683.01	6083.33	Kanwisher
Ascophylum	229.54	86.08	766.67	MacFarlane
Laminaria	436.63	163.74	1458.33	Mann (1972)
Thalassia	1160.18	435.07	3875.00	Odum H.T.
Thalassia	523.95	196.48	1750.00	Qasim and Bhattashiri (1971)
Coral Reef				
Hawaii	456.00	171.00	1523.04	Littler (1973)
Hawaii	15.99- 39.90	6.00- 14.96	53.41- 133.27	Littler and Doty (1975)
Moorea (lagoon)	159.90	59.96	534.07	Sournia (1976a)
Curacao	180.00	67.50	601.20	Wanders (1976)
Barbados	105.60	39.60	353.70	This study

\* as cited in Crisp (1975), Lewis (1977) and others
1.0 mgO<sub>2</sub> = 3.34 calories Ivlev (1934)
1.0 gO<sub>2</sub> = 0.375 gC Westlake (1963)

coral reef communities have higher rates of organic production than their surrounding waters (Sargent and Austin 1949, 1954, Odum and Odum 1955, Kohn and Helfrich 1957, Lewis 1977 and others).

Although measurements of primary production were taken only during a three month period, June through August 1976, the rates were considered a reasonable estimate of primary production occurring throughout the entire year. This assumption was made for several reasons. Firstly, the means of the physical and chemical values (light intensity, nitrates, phosphates, salinity and temperature) taken over the same period as primary production measurements, were not significantly different (P = 0.05) from the annual means (Appendix Table 17). These results are consistant with those of Steven et al. (1970), Sander (1971), Steven (1971) and Sander and Steven (1971) at Barbados who found that variations of physical and chemical values showed no seasonality but values fluctuated randomly around their annual means.

Secondly, Steemann-Nielsen (1971) and Steven (1971) found that the characteristic clarity of waters over tropical regions facilitates the penetration of light to great depths and the radiation in these low latitudes exceeds the saturation level for maximum photosynthesis. In situ light intensities measured over a year at the nearby island of Curacao  $(12^{\circ}01' \text{ N})$ ,  $68^{\circ}44' \text{ W}$ ) were considerably higher than those required at the compensation levels of the benthic algae in the shallow reef waters (Wanders 1976). Since the North Bellairs Fringing Reef extends over a similar depth range as the reef in Curacao, light intensities reaching the benthic primary producers would be similar and thus sufficient for maximum photosynthesis in the shallow Barbados reef waters. Therefore, *in situ* light intensities were never considered to be a limiting factor for photosynthesis on the North Bellairs Fringing Reef.

Wanders (1976) also showed that on-shore values of primary production were similar to those made in situ. This supports data of other workers who have used on-shore measurements of primary production to estimate rates of production in the field (Marsh 1970, Littler 1973, Littler and Doty 1975). On-shore or laboratory rates of production measured by these workers and those of the present study are similar to rates of production measured in the field by Wanders (1976). In addition, Wanders (1976) found little evidence of seasonality in year long studies of benthic primary production of a shallow reef in Curacao. Therefore, on the bases that, 1) physical and chemical values measured over the same period as primary production measurements did not significantly differ from their annual means, 2) that on-shore rates of benthic algal production are similar to in situ rates and 3) that Wanders found little evidence of seasonality of benthic algal rates of production, the on-shore measurements of primary production obtained here during a three month period were considered to be reasonable estimates of rates of production throughout the year.

The lack of seasonality in rates of primary production in this area of the Caribbean has been shown by other workers. Steven et al. (1970), Sander (1971), Steven (1971) and Sander and Steven (1971) found no clear evidence of seasonality in studies of phytoplankton production at Barbados.

# II. Energy Partitioning and Utilization by Diadema antillarum

The net productivity of benthic algae on the North Bellairs Fringing Reef is sufficient to supply the nutritional requirements (in terms of calories) of the *Diadema* population. It is of interest to compare the utilization and partitioning of this production by *Diadema* (Figure 32) with that of other sea urchins. A comparison is shown in Table 35 in which the population energy budget of *Diadema* is compared with similar energy budgets for a temperate water species, *Strongylocentrotus droebachiensis*, and another tropical species, *Lytechinus variegatus*.

Miller and Mann (1973) studied Strongylocentrotus in a marine bay off Nova Scotia, Canada, where the urchins occured at densities of approximately 37 m<sup>-2</sup> in Laminaria (kelp) beds. The population energy budget was based upon separate energy budgets determined for urchins of six age classes ranging in size from approximately 6-45 mm MTD. In Jamaica, the Lytechinus population studied by Greenway (1976) occurred in a Thalassia (sea grass) bed at densities of 20 m<sup>-2</sup>. Greenway determined an energy budget for the population based only upon a 48 mm MTD size class. The population energy budget calculated here for Diadema was based upon separate energy budgets determined for 10 size groups ranging from 15-60 mm MTD (Table 26) and a mean density of 23 m<sup>-2</sup> (Table 7).

From population energy budgets shown in Table 35, it is clear that the monthly caloric intake of 96.02 kcal  $m^{-2}$  by *Strongylocentrotus* and 260 kcal  $m^{-2}$  by *Lytechinus* is sufficient to cover their respective energy budget requirements. The energy acquired by *Diadema* at the estimated consumption rate (71.27 kcal

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Figure 32 Partitioning of energy intake by Diadema antillarum. All values are expressed in terms of kcal m<sup>-2</sup> mo<sup>-1</sup>.



#### Table 35

Monthly energy budgets of three populations of sea urchins expressed in kcal  $m^{-2}$  mo<sup>-1</sup> and as a percentage of net primary production and consumption.

Location	<u>Canada - kelp bed</u>	Jamaica - sea grass bed	Barbados - fringing coral reef
Urchin species	Strongylocentrosus droebachiensis	Lytechinus variegatus	Diadema antillarum
Density	$37 m^{-2}$	$20 m^{-2}$	$23 m^{-2}$
Net Primary	Laminaria	Thalassia	Mixed benthic algae
Production	1458.33	546	353.70
Consumption	96.02	260	71.27
-	(6.58%)	(478)	(20.15%)
Urchin	4.15	120*	6.41
Production	(0.28%)	(22%)	(1.81%)
	((4.32%))	((46%))	((9.00%))
Respiration	14.88	50	33.45
	(1.02%)	(98)	(9.46%)
	((15.50%))	((19%))	((46.93%))
Egestion	36.63	90	26.19**
-	(2.51%)	(16%)	(7.40%)
	((38.15%))	((35%))	((36.74%))
Surplus	40.35	-	5.22
-	(2.77%)	-	(1.48%)
	((42.02%))	-	((7.32%))
Source	Miller and Mann (197	73) Greenway (1976)	This Study

( ) enclosed value is the percentage of net primary production
 (( )) enclosed value is the percentage of consumption

\* determined by difference in this table \*\* includes excretion

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 $m^{-2} mo^{-1}$ ), is sufficient to cover its population energy budget demands, with a surplus of 5.22 kcal  $m^{-2} mo^{-1}$ . Furthermore, Table 35 shows that approximately 20% of the monthly net primary production of the fringing coral reef is consumed by *Diadema*. This percentage is considerably larger than the 7% reported for the consumption of benthic algal production by *Strongylocentrotus* feeding in kelp beds but is lower than the 47% value for consumption of *Thalassia* by *Lytechinus*.

Although the population energy budget of *Diadema* shows a net surplus of 5.22 kcal  $m^{-2} mo^{-1}$ , individual energy budgets of urchins of some size groups have deficits in their energy budgets. Table 26 indicates that four of the ten size groups have deficits in their energy budgets. This may indicate that consumption rates have been underestimated, or that there are alternative ways by which food can be obtained.

While other investigators (Fugi 1967, Miller and Mann 1973, Greenway 1976 and others) have been able to quantify rates of ingestion of fleshy macrophytes and sea grasses, numerous attempts to measure directly the feeding rates of *Diadema* on encrusting coralline, endolithic and epipelic algae failed (see methods page 23). Consequently, consumption rates have been determined indirectly from gut contents and probably have been underestimated. In regards to alternative means of nutrition, Pequignat (1966, 1972) has shown that sea urchins can acquire energy through the absorption of organic molecules across external epithelial tissues.

. Urchin secondary production as growth and reproduction ranges from a high of 120 kcal  $m^{-2}$  mo<sup>-1</sup> for Lytechinus to a

low of 4.15 kcal m<sup>-2</sup> mo<sup>-1</sup> for *Strongylocentrotus*. It may be noted that the very high production figure for *Lytechinus* was not measured independently but was calculated by difference from the terms of its energy budget (Table 35). The monthly production of 6.41 kcal m<sup>-2</sup> of *Diadema* is higher than the monthly production of *Strongylocentrotus* and this is consistent with the findings of Ebert (1975), who has already shown that the majority of tropical urchins grow much faster than boreal ones.

The measured production of *Diadema* can be compared to a predicted value determined from a relationship between respiration and production (Miller and Mann 1973). The equation relating these two variables is of the form of  $P = 0.6440 \ R^{0.8517}$ , where P is production expressed in terms of kcal m<sup>-2</sup> mo<sup>-1</sup> and R, respiration, expressed in the same units. By this equation, the predicted secondary production of *Diadema* is 12.80 kcal m<sup>-2</sup> mo<sup>-1</sup>.

This high secondary production of *Diadema* is of considerable interest since production of *Strongylocentrotus* reported by Miller and Mann (1973) was regarded as being very high. The high production of *Diadema* may be due in part of its high net and gross growth efficiencies. Table 36 shows that gross growth efficiencies (production/consumption x 100, Kozlovsky 1968, Welch 1968) of *Diadema* are all higher than for *Strongylocentrotus* of similar size. In addition, a comparison of net growth efficiencies (production/absorption x 100, Kozlovsky 1968, Welch 1968) shows similar differences. Thus, it is apparent that *Diadema* is more efficient at converting its algal food resources into urchin biomass than is *Strongylocentrotus* of similar size. This ability

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#### Table 36

Net and gross efficiencies of Diadema antillarum and Strongylocentrotus droebachiensis of similar size.

Gross	Growth	Efficiency	( <u>P</u> )	=	(production	kcal	urchin <sup>-1</sup>	mo )	х	100
			( <u></u>		(consumption	kcal	urchin-1	1	)	

Diadema antillarum		Strongylocentrotus droebachiensis					
Urchin Size	P	Age Group	Approx. Size	P			
(mm)	( %)	(yr)	(mm)	(%)			
15	6.3	1	14	4.8			
25	9.0	2	23	4.5			
30	7.6	3	32	4.1			
40	10.1	4	40	3.6			
45	12.4	5	45	3.8			

Range overall size groups (15-60 mm) of Diadema 6.3-15.0%

# - 117 -Table 36 (cont'd)

Net	Growth	Efficiency	(P)	=	(production kcal urchin-1 mo-1) x 100
			$(\overline{A})$		(assimilation kcal urchin-1 mo-1)

<u>Diadema antil</u>	larum	Strongylocentrotus droebachiensis					
Urchin Size Group (mm)	$\frac{P}{\overline{A}}$	Age Group	Approx. Size Group (mm)	<u>P</u> Ā (ዓ)			
15	8.0	1	14	7.8			
25	11.1	2	23	7.2			
30	9.8	3	32	6.7			
40	12.6	4	40	5.8			
45	16.3	5	45	6.0			

Range overall size groups (15-60 mm) of Diadema 8.0-254.9%

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to convert food into urchin biomass more efficiently would lead to faster growth and possibly a reduction in time to reach reproductive maturity.

Ecological efficiencies of *Diadema* and *Strongylocentrotus* are shown in Table 37. Results demonstrate that *Diadema* has an ecological efficiency of 9.0% and *Strongylocentrotus* 4.3%. The efficiency value for *Diadema* is within the predicted range of 5-15% by Slobodkin (1960, 1961), and the value calculated for *Strongylocentrotus* is slightly lower.

Respiration accounts for a substantial proportion of energy budgets in all three urchin species (Table 35). Respired energy loss per square meter in both the tropical species is greater than in *Strongylocentrotus*. It may be noted that Lewis (1968b) and Webster (1975) have reported that tropical urchins respire at higher rates than temperate species.

A high percentage of the caloric intake is also lost through egestion in all three urchin species (Table 35). The energy loss in feces is equal to 38.15% of the caloric intake of *Strongylocentrotus* and 35% of the caloric intake of *Lytechinus*. Although in *Diadema* the energy loss attributed to nitrogenous waste in the form of ammonia is only a very small fraction of the caloric intake (0.15%, Table 26), the energy loss to excretion and egestion combined is 36.74% of the caloric intake (Table 35) Thus it appears that *Diadema* releases as much energy to the benthos in the form of fecal pellet detritus as do the other two urchin species. The significance of this is discussed in Section IV.

#### Table 37

Ecological effiencies\* of the Diadema antillarum and Strongylocentrotus droebachiensis populations.

Urchin Species	Ecological Efficiency**
Diadema antillarum 23m-2	9.0%
Strongylocentrotus droebachiensis 37m <sup>-2</sup>	4.3%
Range for aquatic consumers according to Slobodkin (1960, 1961)	5-15%

- \* Ecological efficiencies calculated according to Slobodkin (1960, 1961) and based upon budget terms shown in Table 35.
- \*\* Ecological =  $(population production kcal m^{-2} mo^{-1})$ Efficiency  $(population consumption kcal m^{-2} mo^{-1}) \times 100$

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#### III. Absorption Efficiency

All positive values of absorption efficiency of Diadema antillarum which fed upon each of the three algal types fall within the ranges reported by Lawrence (1975, 1976). Although these efficiency values varied widely with urchin size and food type, urchins of all size groups absorbed encrusting coralline algae more efficiently than any of the other food types. In addition, absorption efficiencies of Diadema fed only encrusting coralline algae were found to very directly with size. Similarly, Himmelman (1969) found that for Strongylocentrotus droebachiensis fed Laminaria, the efficiency of organic matter absorption ranged between 9.0 and 42.3% for urchins of 40.9-7.3 mm test diameter. However, reports by Miller and Mann (1973) on the same species and Fugi (1967) on S. intermedius do not corroborate Himmelman's findings. The latter authors report little variation in the absorption efficiency with urchin size. Reasons for these conflicting results may be attributed to differences in previous nutritional history (Lawrence 1975) or possibly to the different experimental methods. Clearly, more research is needed to determine the relationship between urchin body size and absorption efficiency.

There are few studies of the absorption efficiency of sea urchins fed coralline algae. Leighton (1968), following the Conover method, determined the efficiency of organic matter absorption by *Strongylocentrotus purpuratus* on the two coralline algae *Bossiella* sp. and *Corallina officialis* to be 29.2% and 16.5% respectively. Because of these low efficiencies, Lawrence (1975) suggested that coralline algae as a group may be poorly

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absorbed. In contrast, the efficiencies determined for *Diadema* of 25 mm MTD and larger are all higher than any value determined by Leighton. In addition, Lowe and Lawrence (1976) found the absorption efficiency of *Lytechinus variegatus* which fed upon the heavily calcified articulate coralline algae *Halimeda incrassata* to be relatively high (43%). These results and those presented for *Diadema* indicate that some heavily calcified algae and encrusting coralline algae are absorbed to a higher degree than previously suspected.

In the absence of fleshy macrophytes, coralline algae may serve as an important food resource for echinoids. In waters off Nova Scotia, Canada, Lang and Mann (1976) found that a dense population of S. droebachiensis remained in an area after kelps had been destroyed by sea urchin grazing. It appeared that the urchin population was consuming 'encrusting algae' and detrital material entering the area from nearby kelp beds. In fact, more recent studies have shown that S. droebachiensis feeds upon encrusting coralline algae in these areas devoid of macrophytes (T. Hackney 1978, personal communication by Dr. K.H. Mann). In waters off the USA west coast, Leighton et al. (1966) and North and Pearse (1970) have reported that S. purpuratus decimates kelp beds to such an extent that only encrusting coralline algae remains and Ebert (1968) has shown that this urchin species consumes encrusting coralline algae in other areas of the USA west coast.

Efficiencies of organic matter absorption by *Diadema* were lower on endolithic and epipelic algae than on encrusting coralline algae, and negative values were obtained in some instances

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(Appendix Table 15). Lowe and Lawrence (1976) propose several reasons for negative absorption efficiencies obtained in studies of Lytechinus, among which include the absorption of significant amounts of ash from foods or loss from feces, enrichment of feces after egestion by bacteria or other microfauna, and the enrichment of ingested food by secretions of mucus from the urchin's digestive tract to coat food and prevent abrasion or the gut lining. In any case, the negative efficiencies determined for *Diadema* fed endolithic and epipelic algae indicate that *Diadema* is not capable of absorbing these food types as well as encrusting coralline algae.

The preceding discussion has dealt specifically with urchins which were fed a single food type. However, urchins ingest a wide variety of algae and other foods. The absorption efficiency of urchins having a mixed diet has not been determined in other species. Table 28 shows that there is no apparent relationship between urchin size and absorption efficiency when *Diadema* feeds on a mixed diet. This is presumably the result of the mix of food and the different nutritional value of each food type (Boyd and Goodyear 1971).

Absorption efficiencies calculated on the basis of the difference between the total organic content in food and feces are quite different from those determined upon a caloric basis (Table 28). In all but one instance, the efficiency value calculated on the basis of calories is higher than on the basis of organic matter. This may be explained in part by the organic method not differentiating between the proportions of the protein, carbohydrate and lipid fractions comprising the total organic

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content of the food and feces. Inherent in the caloric method is some quantification of the proportions of these food components. This is the result of each of the food components having a different calorific equivalent (protein 5.56 kcal  $g^{-1}$  ash free dry weight, carbohydrate 4.10 kcal  $g^{-1}$  ash free dry weight and lipid 9.45 kcal  $g^{-1}$  ash free dry weight, Brody 1945). Therefore, in the same food the ratio of protein to carbohydrate to lipid, when expressed in terms of organic matter, will be quite different than when the same ratio is expressed in terms of calories (Salonen et al. 1976). Thus, when absorption efficiencies are determined by the organic method one would not expect to obtain equivalent results to those obtained on a caloric basis. Care must be exercised when comparing absorption efficiencies among animals and in evaluating the nutritional quality of foods when absorption efficiencies are determined by different methods.

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#### IV. The Role of *Diadema antillarum* in Energy Transfer within the Coral Reef Community

The role and importance of sea urchins on reefs has been examined in terms of sediment production and control of species diversity (Sammarco et al. 1974, Hunter 1977, Ogden 1977), but their role in energy transfer to other members of the reef community has not been considered previously.

The population energy budget for *Diadema* shows clearly the importance of these urchins as energy transformers on a fringing coral reef. A considerable amount of energy is made available to the reef community through the production of energy rich fecal detrital matter. Table 38 shows that fecal detritus produced by Diadema contains approximately 10 times the caloric content of the surface sediments to the north and south of the North Bellairs Fringing Reef and approximately 1.7 times the caloric content of sediments within the fringing reef. Table 26 shows that *Diadema* fecal detritus contributes 26.08 kcal m<sup>-2</sup> mo<sup>-1</sup> to the benthic community. This is equal to 7.4% of the monthly net primary production of benthic algae and 36.6% of the caloric intake of the urchin population. In comparison with Strongylocentrotus and Lytechinus (Table 35), it is evident that Diadema contributes a similar proportion of its caloric intake to the benthos in the form of fecal detritus.

Besides providing this direct source of energy to benthic fauna which feed on large particles, their fecal deposits supply a physical substrate for meiofauna and bacteria to colonize. Sorokin (1971a, 1971b, 1973a, 1973b and 1974) has emphasized the role of bacteria in transformation of detrital organic matter

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# Table 38

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Percentage of organic matter in surface sediments and fecal pellets of *Diadema antillarum*, expressed in terms of dry weight.

Sample Type	Location	Mean percent organic matter (% dry wt)	±95% Confidence Limits	Source
Fecal pellets from Diadema	North Bellairs Fringing Reef	10.20	2.28	This Study
Reef surface sediment	North Bellairs Fringing Reef	6.13	0.28	This Study
Surface sediments	Speightstown Miramar Paynes Bay (all Barbado west coast)	. <1.0 s	-	Macintyre (1967)

into living biomass.

Sediment surface layers are readily resuspended into the water column by wave action and tidal currents. In this way, energy in the form of fecal detrital matter is made available to serve as food for suspension, filter and tentacular feeders. Lewis and Price (1975, 1976) have shown that some Atlantic reef corals behave as suspension feeders and employ mucus nets and strands to capture a wide assortment of particulate matter. Fitzsimons (1965) has shown that the brachial crown of the tropical worm Sabellastarte magnifica acts as a filter feeding device for trapping particulate matter, and Reiswig (1971, 1974) has demonstrated that sponges capture small particulate organic matter from the surrounding seawater. In addition, reef zooplankton have been reported to feed on particulate organic matter of detrital origin (Gerber and Marshall 1974). Although direct quantitative measure of the importance of fecal detrital material as a food resource for benthic coral reef organisms is lacking (Lewis 1977), its potential on the North Bellairs Fringing Reef is clearly apparent.

Urchin production in biomass is another source of energy eventually available to members of the reef community. In *Diadema*, this amounts to 6.41 kcal m<sup>-2</sup> mo<sup>-1</sup> or approximately 1.8% of the monthly net primary production, or 9.0% of the minimum caloric intake of the urchin population. In *Strongylocentrotus*, urchin secondary production is 4.15 kcal m<sup>-2</sup> mo<sup>-1</sup> which is equivalent to 0.3% of the monthly net primary production of *Laminaria* or 4.3% of the caloric intake of the population (Table 35). Urchin production may be channeled to predators (fish, gastropods and

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crustaceans, Randall 1963, Randall et al. 1964, Fricke 1971, 1974, Hughes and Hughes (1971), or liberated as gametes or released to the sediments through mortality. In Barbados, the gastropod *Cassis tuberosa* may prey upon *Diadema* (Hughes and Hughes 1971) but none were observed during the present study.

From the above examples, a flow diagram may be constructed which illustrates, in part, the fates of urchin biomass production and of the particulate organic matter in *Diadema* fecal deposits (Figure 33). This figure clearly illustrates that the production of urchin fecal detritus is the major pathway through which *Diadema* makes the energy from biomass of the benthic primary producers available to other members of the reef community.

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Figure 33 Simplified schematic diagram illustrating pathways of energy transfer directed to other members of the reef community by *Diadema antillarum*. Values are expressed in kcal m<sup>-2</sup> of reef surface mo<sup>-1</sup>.



# V. Sediment Production and Erosion by Diadema antillarum

It is apparent that *Diadema antillarum* is a major bioerosional agent of the North Bellairs Fringing Reef in Barbados. This is shown in Table 39 in which rates of total sediment production and erosion by a number of reef organisms are compared. Monthly rates of total sediment production per square meter of reef surface by *Diadema* are markedly higher than those of other reef grazers.

In Barbados, Hunter (1977) has shown that Diadema produces approximately 0.81 kg CaCO<sub>3</sub> sediment m<sup>-2</sup> mo<sup>-1</sup> with the production of new or fresh sediment (i.e. erosion) accounting for 57% of the total sediment production. His calculations were based upon a density of 23 urchins m<sup>-2</sup> and a mean sediment production rate of 2.07 g CaCO<sub>3</sub> urchin<sup>-1</sup> day<sup>-1</sup> (Lewis 1964). In the present study, however, sediment production rates ranged from 0.06-2.02 g CaCO<sub>3</sub> urchin<sup>-1</sup> day<sup>-1</sup> depending upon urchin size and measured egestion rates. On this basis, total sediment production by *Diadema* is 0.37 kg CaCO<sub>3</sub> m<sup>-2</sup> mo<sup>-1</sup> with erosion accounting for approximately 48.9% of the total sediment production. This is somewhat lower than the 57% figure calculated by Hunter.

It should be noted here that rates of  $CaCO_3$  sediment production are not equivalent to rates of  $CaCO_3$  consumption as estimated in this present study. This is because consumption and egestion were estimated by separate methods.

Stearn et al. (1977) have estimated the rate of calcification on the North Bellairs Fringing Reef at approximately 0.75 kg  $CaCO_3 m^{-2} mo^{-1}$ . This calcification rate may be compared to

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Rates of calcium carbonate sediment production and erosion by various reef associated animals.

Species	Location	Density or Biomass	Sediment Pro Total (kg CaCO, m	duction Erosion 2 mo <sup>-1</sup> )	Substrate	Source
FISH		-	(	•		
Scarus croicensis	Panama Caribbean Coast	47 kg ha <sup>-1</sup>	0.082	0.041	coral reef	Ogden (1977)
Grazers and browsers	Bermuda	55 kg ha <sup>-1</sup>	0.019	0.009	coral reef	Bardach (1961)
Sparisoma virdide	Barbados	4.5 kg ha <sup>-1</sup>	0.005	0.003	fringing coral reef	Frydl (1977) <sub>I</sub>
URCHINS						• 0
Echinometra lucunter	Bermuda	$25 m^{-2}$	<b></b>	0.583	eolianite	Hunt (1969)
Diadema antillarum	Virgin Is.	9 m <sup>-2</sup>	0.758	0.383	coral reef	Ogden (1977)
Diadema antillarum	Barbados	$23 m^{-2}$	0.808	0.461	fringing coral reef	Hunter (1977)
Diadema antillarum	Barbados	23 m <sup>-2</sup>	0.369	0.180	fringing coral reef	This Study

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Rates of calcium carbonate sediment production and erosion by various reef associated animals.

1990 1990

Species	Location	Density or Biomass	Sediment Total	$\frac{\text{Production}}{\text{Erosion}}$	Substrate	Source
MOLLUSCS			(kg CaCO	3 <sup>m</sup> mo)		
Nerita tesselata	Barbados	$220 m^{-2}$	-	0.013	beachrock	McLean (1967b)
SPONGES						
Cliona	Barbados	-	-	0.114	coral reef	Stearn and Scoffin (1977)
Cliona	Curacao	-	-	0.275	coral reef	Bak (1976)
HOLOTHURIANS						131
Holothuria atra	Enewetak	-	0.554	-	sediment reworked	Webb et al. (1977)
Holothuria dificilis	Enewetak	-	0.083	-	sediment reworked	Bakus (1968)

the rate of erosion of primary reef framework by Diadema. The data in the present study indicate that 24% of the calcification is eroded and reduced to sediment. Thus, Diadema can have a significant effect on this reef's carbonate budget and concurrently on the reef's morphology (Scoffin et al. in press). Recently, Stearn and Scoffin (1977) have shown that calcium carbonate bioerosion from all major sources on the North Bellairs Fringing Reef exceeds production by 26 metric tons per year. According to their study, Diadema accounts for approximately 86% of all bioerosion. The contribution to total bioerosion by Diadema was considered by Stearn and Scoffin to be a maximum estimate since they assumed that all urchins completely emptied their gut contents 2.5 times per day. On this basis their estimates of daily egestion rates over all urchin size groups are approximately 2.5-4.5 times higher than estimates obtained in the present study. Consequently, the rates of erosion presented in the present study may be considered minimum estimates and those of Stearn and Scoffin maximum estimates. Although all factors of their carbonate budget have not been assessed, their data indicate that the fringing reef is being eroded faster than it is growing.

In addition, *Diadema* also influences the sediment composition on the North Bellairs Fringing Reef. Hunter (1977) compared the composition of sediments from several coral reefs in the Caribbean and found that the percentage of coral fragments in the surface sediments from the North Bellairs Fringing Reef was higher than on any other coral reef examined. However, he was unable to explain this difference. It now appears likely that this high percentage results from the grazing of *Diadema* on

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endolithic algae associated with the exposed skeletal framework of reef building corals and coral rubble fragments.

The effect on fringing reef morphology by *Diadema* grazing is visually evident and confirmed by the results of Stearn and Scoffin (1977). The grazing marks shown in Figure 14 indicate the intensity of grazing. The rate of erosion (24% of the calcification) and the net loss of CaCO<sub>3</sub> from the fringing reef (Stearn and Scoffin 1977) clearly illustrate that *Diadema* is a major bioerosional agent which influences coral reef carbonate budgets and controls coral reef morphology.

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#### VI. Conclusion

Benthic primary production per square meter of reef surface on the North Bellairs Fringing Reef is low when compared to other coral reefs. Nevertheless, net primary productivity of 353.70 kcal  $m^{-2}$  mo<sup>-1</sup> is sufficient to cover the monthly energy requirements of the Diadema population. Approximately 20% (71.27 kcal) of the monthly net primary production is consumed by the urchin population. The most important pathway of energy transfer to other members of the reef community is through the production of energy rich fecal detritus. This amounts to 7.4% (26.08 kcal) of the monthly net primary production or 36.6% of the monthly caloric intake of the urchin population. Secondary production of urchins is also important in terms of energy transfer. Energy directed through this pathway is approximately 1.8% of the benthic algal net productivity or 9.0% of the urchin population caloric intake.

Diadema antillarum is the major bioerosional agent of the North Bellairs Fringing Reef. Calcium carbonate sediment production by Diadema is markedly higher than by other bioerosional agents. The erosion of primary reef framework constitutes 48.9% of the total sediment production. Furthermore, calcium carbonate deposition on this reef is substantially reduced by grazing urchins. Approximately 24% of the CaCO<sub>3</sub> deposited by reef framework builders is reduced to sediment by Diadema.

It is apparent then, that *Diadema antillarum* on the North Bellairs Fringing Reef may be regarded as a "key species" in two important processes. Firstly, in processes of energy transfer, they are the most important herbivore on the fringing reef which direct a large proportion of the energy accumulated at the primary level to other levels within the reef community. Secondly, they are the most important bioerosional agent of the fringing reef and thus exert control over reef constructional processes and thereby influence reef morphology.
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#### SUMMARY

- Hourly rates of primary production per square centimeter of algal surface of the encrusting coralline, endolithic, and epipelic algae on the North Bellairs Fringing Reef are as high or higher than those reported elsewhere.
- 2. The net benthic primary productivity of 353.70 kcal m<sup>-2</sup> of reef surface mo<sup>-1</sup> on the North Bellairs Fringing Reef is low when compared to primary productivity on other coral reefs. Nevertheless, this productivity exceeds monthly net phytoplankton productivity in oceanic and neritic waters off the west coast of Barbados by factors of 9.5 and 12.1 respectively.
- 3. The net primary production on the fringing reef is sufficient to supply the nutritional requirements (in terms of calories) of the urchin population (23 m<sup>-2</sup>). Approximately 20% of this benthic algal production is consumed by the urchins.
- 4. Monthly energy budgets for urchins of various size groups balance within approximately one kilocalorie at the minimum consumption rates, except for urchins of the largest size groups where there is a larger energy deficit.
- 5. A population energy budget based upon 23 urchins of mixed sizes per square meter of reef surface has a surplus of 5.22 kcal mo<sup>-1</sup>. Consumption accounts for 71.27 kcal mo<sup>-1</sup>, production for 6.41 kcal mo<sup>-1</sup>, respiration for 33.45 kcal mo<sup>-1</sup> and excretion and egestion combined for 26.19 kcal mo<sup>-1</sup>.
- 6. The urchin productivity of 6.41 kcal  $m^{-2} mo^{-1}$  is somewhat higher than any reported for other urchin populations.

- 7. Net production efficiencies on the mixed diet of available food resources ranged from 8.0-22.3% over all urchin size groups with the exception of urchins of the 60 mm MTD size group.
- 8. The egestion of energy rich fecal detrital material by Diadema antillarum (36.6% of the monthly caloric intake of the population) is the most important pathway by which energy fixed as biomass by the primary producers is made available to other members of the reef community.
- 9. Algal food resources consumed by *Diadema antillarum* vary in quality and in proportions comprising the mixed diet. Encrusting coralline algae contains the highest caloric and organic content per gram dry weight of all food types and was most abundant in the mixed diets of urchins less than 35 mm MTD.
- 10. Absorption efficiencies were found to vary directly with size of urchins which were fed only encrusting coralline algae.
- 11. Absorption efficiencies calculated for urchins have a mixed diet show no direct relationship with urchin size. In addition, absorption efficiencies calculated on the basis of percentage of organic matter in the food and feces of urchins having a mixed diet were all lower than when efficiencies were calculated on the basis of calories, with the exception of the 35 mm MTD size group.
- 12. Diadema antillarum is the most important bioerosional agent on the North Bellairs Fringing Reef. Calcium carbonate sediment production is markedly higher than by other reef bioerosional agents.

13. Approximately 48.9% of the total carbonate sediment production is the result of erosion of primary reef framework. This is equivalent to 24% of the calcium carbonate deposited on the fringing reef.

#### LITERATURE CITED

- Atkinson, C., S. Hopley, L. Mendelsohn, & S. Yacowitz, 1973. Food studies on *Diadema antillarum* on a patch reef, St. Croix, U.S. Virgin Islands. In, Spec. Publ. No. 2, West Indies Lab., edited by J.C. Ogden, D.P. Abbott, and I. Abbott, West Indies Laboratory, St. Croix, pp. 65-80.
- Ayling, A.L., 1978. The relation of food availability and food preferences to the field diet of an echinoid Evenechinus choroticus (Valenciennes). J. exp. mar. Biol. Ecol., Vol. 33, pp. 223-235.
- Bak, R.P.M. & G. vanEys, 1975. Predation of the sea urchin Diadema antillarum Philippi on living coral. Oecologia (Ber.), Vol. 20, pp. 111-115.
- Bak, R.P.M., 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Neth. J. Sea Res., Vol. 10, pp. 285-337.
- Bakus, G.J., 1967. The feeding habits of fishes and primary production at Enewetok Marshall Islands. Micronesica Vol. 3, pp. 135-149.
- Bakus, G.J., 1968. Defence mechanisms and ecology of marine tropical holothurians. Mar. Biol., Vol. 2, pp. 23-32.

Bardach, J.E., 1961. Transport of calcaerous fragments by reef fishes. Science, N.Y., Vol. 133, pp. 98-99.

- Bathurst, R.G.C., 1967. Sub-tidal gelatinous mat, sand stablizer and food. Great Bahama Bank. J. of Geol., Vol. 75, pp. 736-738.
- Bathurst, R.C., 1971. Carbonate sediments and their diagensis. Elsevier, Amsterdam. 620 pp.

- Bauer, J.C., 1976. Growth, aggregation and maturation in the echinoid Diadema antillarum. Bull. mar. Sci., Vol. 26, pp. 273-277.
- Benayahu, Y. & Y. Loya, 1977. Space partitioning by stony corals, soft corals and benthic algae on the coral reefs of the northern Gulf of Elat (Red Sea). Helogolander wiss Meeresunters, Bd 30, pp. 362-382.
- Boolootian, R.A. & R. Lasker, 1964. Digestion of brown algae and the distribution of nutrients in the purple sea urchin *Strongylocentrotus purpuratus*. Comp. Biochem. Physiol., Vol. 11, pp. 273-289.
- Borstad, G., 1978. Some aspects of the occurrence and biology of *Trichodesmum* (Cyanophyta) in the western tropical Atlantic near Barbados, West Indies. Ph. D. Thesis, McGill University, Montreal, Quebec, Canada, 234 pp.
- Boyd, C.E. & C.P. Goodyear, 1971. Nutritive quality of food in ecological systems. Arch. Hydrobiol., Vol. 69, pp. 257-270.
- Brafield, A.E. & D.J. Soloman, 1972. Oxy-calorific coefficients for animals respiring nitrogenous substrates. Comp. Biochem. Physiol., Vol. 43A, pp. 837-841.
- Brody, S., 1945. Bioenergetics and growth. Hafner Publishing Company, Inc., New York. 1023 pp.
- Brown, A.H., 1953. The effects of light on respiration using isotopically enriched oxygen. Am. J. Bot., Vol. 40, pp. 719-729.
- Camp, D.K., S.P. Cobb & J.F. van Breedveld, 1973. Overgrazing of sea grasses by a regular urchin Lytechinus variegatus. BioScience, Vol. 23, pp. 37-38.

- Conover, R.J., 1966. Assimilation of organic matter by zooplankton. Limnol. Oceanogr., Vol. 11, pp. 338-345.
- Crisp, D.J., 1971. Energy flow measurements. pp. 197-280. In, Methods for the study of marine benthos, edited by N.A. Holme and A.D. McIntyre International Biological Program Handbook No. 16. Blackwell Scientific Publication, Oxford and Edinburgh, 334 pp.
- Crisp, D.J., 1975. Secondary productivity in the sea. pp. 71-89. In, Proceedings of a Symposium on Productivity of World Ecosystems, Seattle, Washington, edited by D.E. Reichle, J.E. Franklin and D.W. Goodall. National Academy of Sciences, Washington U.S.A., 160 pp.
- Dahl, A.L., 1973. Surface area in ecological analysis: Quantification of benthic coral reef algae. Mar. Biol., Vol. 23, pp. 239-249.
- Dahl, A.L., 1974. The structure and dynamics of benthic algae in the coral reef ecosystem. In, Proceedings of the Second International Symposium on Coral Reefs, edited by A.M. Cameron, B.M. Campbel, A.B. Cribb, R. Endean, J.S. Jell, O.A. Jones, P. Mather and E.H. Talbot, Vol.1, pp. 21-25. The Great Barrier Reef Committee, Brisbane.
- Drew, E.A., 1978. Factors affecting photosynthesis and its seasonal variation in the sea grass Cymodocea nodosa (Ucria) Aschers, and Posidonia oceanica (L.) Delile in the Mediterranean. J. exp. mar. Biol. Ecol., Vol. 31, pp. 173-194.
- Ebert, T.A., 1968. Growth rates of the sea urchin Strongylocentrotus purpuratus related to food availability and spine abrasion. Ecology, Vol. 49, pp. 1075-1091.
- Ebert, T.A., 1975. Growth and Mortality of post-larval echinoids. Am. Zool., Vol. 15, pp. 755-775.

- Fitzsimons, G., 1965. Feeding and tube-building in Sabellastarte
  magnifica (Shaw)(Sabellidae: Polychaeta). Bull. mar.
  Sci., Vol. 15, pp. 642-671.
- Foreman, R.E., 1977. Benthic community modification and recovery
  following intensive grazing by Strongylocentrotus
  droebachiensis. Helogolander wiss Meeresunters., Bd 30,
  pp. 468-484.
- Fricke, H.W., 1971. Fish as enemies of tropical sea urchins. Mar. Biol., Vol. 9, pp. 328-338.
- Fricke, H.W., 1974. Possible influence of predators on the behavior of *Diadema* sea urchins. Mar. Biol., Vol. 27, pp. 59-62.
  - Frydl, P., 1977. The geological effect of grazing by parrotfish (Scaridae) on a Barbados coral reef. MSc. Thesis, McGill University, Montreal, Quebec, Canada, 136 pp.
- Fugi, A., 1967. Ecological studies on the growth and food consumption of Japanese common littoral sea urchin, Strongylocentrotus intermedius (A. Agassiz). Mem. Fac. Fish. Hokkaido Univ., Vol. 15, pp. 83-160.
- Gerber, R.P. & N. Marshall, 1974. Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll. Limnol. Oceanogr., Vol. 19, pp. 815-824.
- Ginsburg, R.N. 1956. Environmental relationships of grain size and constituent particles in some south Florida carbonate sediments. Am. Assoc. Petrol. Geol. Bull., Vol. 40, pp. 2384-2472.
- Glynn, P.W., G.M. Wellington & C. Birkland, 1979. Coral reef growth in the Galapagos: Limitation by sea urchins. Science, N.Y., Vol. 203, pp. 47-48.

Greenway, M., 1976. The grazing of Thalassia testudinum in Kingston harbour, Jamaica. Aquatic Botany, Vol. 2, pp. 117-126.

Grossman, S.I. & J.E. Turner, 1974. Mathematics for the Biological Sciences. MacMillan, New York, 512 pp.

Hawkins, C.M., 1977. The effect of size and food type on the absorption efficiencies of the echinoid Diadema antillarum Philippi. Am. Zool., Vol. 17, pp. 870.

Himmelman, J.H., 1969. Some aspects of the ecology of Strongylocentrotus droebachiensis in Eastern Newfoundland. MSc. Thesis Memorial University of Newfoundland, St. John's Newfoundland, Canada, 159 pp.

Himmelman, J.H. & D.H. Steele, 1971. Foods and predators of the green sea urchin Strongylocentrotus droebachiensis in Newfoundland waters. Mar. Biol., Vol. 9, pp. 315-322.

Hughes, R.N., 1969. Appraisal of the iodate-sulphuric acid wet oxidation procedure for the estimation of the caloric content of marine sediments. J. Fish. Res. Bd Can., Vol. 26, pp. 1959-1964.

Hughes, R.N. & H.P.I. Hughes, 1971. A study of the gastropod Cassis tuberosa (L.) preying upon sea urchins. J. exp. mar. Biol. Ecol., Vol. 7, pp. 305-314.

Hunt, M., 1969. A preliminary investigation of the habits and habitat of the rock boring urchin *Ecinometra lucunter* near Dovenshire Bay Bermuda. In Seminar on organism-sediment interrelationships: Bermuda Biol. Stat. Spec. Pub. 2 eds. R.N. Ginsberg and P. Garrett, 153 p., pp. 35-40.

Hunter, I.G., 1977. Sediment production by Diadema antillarum on a Barbados fringing reef. In, Proceedings of the Third International Coral Reef Symposium, edited by D.L. Taylor, Miami, Florida, Vol. 2, pp. 105-110.

- Irving, G.V., 1973. The effect of selective feeding by two species of sea urchins on the structuring of algal communities. Am. Zool., Vol. 13, p. 1315.
- Ivlev, V.S., 1934. Eine mikromethode zur bestimming des kaloriengehalts von nahrstoffen. Biochem. Z., Vol. 275, pp. 49-55.
- Johnston, C.S., 1969. The ecological distribution and primary production of macrophytic marine algae in the Eastern Canaries. Int. Rev. dergesamten Hydrobiologie, Vol. 54, pp. 473-490.
- Johnston, C.S., R.J. Jones & R.D. Hunt, 1977. A seasonal carbonate budget for a laminaria population in a Scottish sea-loch. Helgolander wiss Meeresunters, Bd 30, pp. 527-545.
- Kainwisher, J.W., 1966. Photosynthesis and respiration in some seaweeds. In, Some contemporary studies in marine science, edited by H. Barnes. Allen and Urwin, London, pp. 407-420.
- Kitching, J.A. & F.J. Ebling, 1961. The ecology of Loch Ine XI, the control of algae by Paracentrotus lividus (Echinoidea). J. Anim. Ecol., Vol. 30, pp. 373-383.
- Kohn, A.J. & P. Helfrich, 1957. Primary organic productivity of a Hawaiian coral reef. Limnol. Oceanogr., Vol. 2, pp. 241-251.
- Kozlovsky, D.G., 1968. A critical evaluation of the trophic level concept. 1. Ecological efficiencies. Ecology, Vol. 49, pp. 48-60.

Krumbien, W.E. & J.N.C. Van Der Pers, 1974. Diving investigations on biodeterioration by sea urchins in the rocky sublittoral of Helgoland. Helogolander wiss Meeresunters, Bd 26, pp. 1-17.

- Lang, C. & K.H. Mann, 1976. Changes in sea urchin populations after the destruction of kelp beds. Mar. Biol., Vol. 36, pp. 321-326.
- Lawrence, J.M., 1975. On the relationship between marine plants and sea urchins. Oceanogr. Mar. Biol. Ann. Rev., Vol. 13, pp. 213-286.
- Lawrence, J.M. 1976. Absorption efficiencies of four species of tropical echinoids fed *Thalassia testudinum*. Thalassia jugosl., Vol. 12, pp. 201-205.
- Leighton, D.L., 1966. Studies of food preference in algivorous invertebrates of southern California kelp beds. Pacif. Sci., Vol. 20, pp. 104-113.
- Leighton, D.L., 1968. A comparative study of food selection and nutrition in the abalone, *Haliotis rufescens* Swainson, and the sea urchin, *Strongylocentrotus purpuratus* (Stimpson). Ph.D. Thesis, University of California, San Diego, California, U.S.A., 197 pp.
- Leighton, D.L., L.G. Jones & W.J. North, 1966. Ecological relationships between giant kelp and sea urchins in Southern California. In, Proc. 5th Int. Seaweed Symp., Halifax, Canada, Pergammon Press, London, pp. 141-153.
- Lewis, J.B., 1960. The coral reefs and coral communities of Barbados West Indies. Can. J. Zool., Vol. 38, pp. 1135-1145.
- Lewis, J.B., 1964. Feeding and digestion in the tropical sea urchin Diadema antillarum Philippi. Can. J. Zool., Vol. 42, pp. 549-557.

- Lewis, J.B., 1966. Growth and breeding in the tropical echinoid Diadema antillarum. Bull. mar. Sci., Vol. 16, pp. 151-158.
- Lewis, J.B., 1967. Nitrogenous excretion in the tropical sea urchin *Diadema antillarum* Philippi. Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 132, pp. 34-37.
- Lewis, J.B., 1968a. Respiration in the tropical sea urchin Diadema antillarum Philippi. Physiol. Zool., Vol. 41, pp. 476-480.
- Lewis, J.B., 1968b. Comparative respiration of tropical echinoids. Comp. Biochem. Physiol., Vol. 24A, pp. 649-652.
- Lewis, J.B., 1977. Processes of organic production on coral reefs. Biol. Rev., Vol. 52, pp. 305-347.
- Lewis, J.B., F. Axelsen, I. Goodbody, C. Page & G. Chislett, 1968. Comparative growth rates of some reef corals in the Caribbean. Marine Sciences Manuscript Rept. 10, McGill University, Montreal, Quebec, Canada, 26 pp.
- Lewis, J.B. & W.S. Price, 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. J. Zool. Lond., Vol. 179, pp. 527-544.
- Lewis, J.B. & W.S. Price, 1976. Patterns of ciliary currents in Atlantic reef corals and their functional significance. J. Zool. Lond., Vol. 178, pp. 77-89.
- Lilly, G.R., 1975. The influence of diet on the growth and bioenergetics of the tropical sea urchin *Tripneustes ventricosus* (Lamark). Ph.D. Thesis University of British Columbia, Vancouver, British Columbia, Canada, 216 pp.
- Littler, M.M., 1973. The productivity of Hawaiian fringing-reef crustose corallinaceae and experimental evaluation of production methodology. Limnol. Oceanogr., Vol. 18, pp. 946-952.

- bution, communities and productivity of *Porolithon*. J. Ecol., Vol. 63, pp. 117-129.
- Lowe, E.F., 1974. Absorption efficiencies, feeding rates and food preferences of Lytechinus variegatus (Echinodermata: Echinoidea) for selected marine plants. M.Sc. Thesis University of South Florida, Tampa, Florida, U.S.A., 97 pp.
- Lowe, E.F. & J.M. Lawrence, 1976. Absorption efficiencies of Lytechinus variegatus (Lamark) (Echinodermata: Echinoidea) for selected marine plants. J. exp. mar. Biol. Ecol., Vol. 21, pp. 223-234.
- Luning, K., 1971. Seasonal growth of Laminaria hyperborea under recorded underwater light conditions near Helgolander. In, Proceedings of the 4th European Symposium on Marine Biology, edited by D.J. Crisp, Cambridge University Press, Cambridge, pp. 347-361.
- Luning, K., 1973. CO<sub>2</sub> fixation and translocation in Benthic marine algae. III Rates and ecological significance of translocation in Laminaria hyperborea and Laminaria saccharina. Mar. Biol., Vol. 23, pp. 275-281.
- MacFarlane, C., 1952. A survey of certain seaweeds of commercial importance in Southwest Nova Scotia. J. Fish. Res. Bd Can., Vol. 30, pp. 78-97.
- Macintyre, I.G., 1967. Recent sediments off the west coast of Barbados West Indies. Ph.D. Thesis, McGill University, Montreal, Quebec, Canada, 169 pp.
- Mann, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. Mar. Biol. Vol. 12, pp. 1-10.

- Mann, K.H., 1977. Destruction of kelp-beds by sea urchins: A cyclical phenomenon or irreversible degradation. Helogolander wiss Meeresunters, Bd 30, pp. 455-467.
- Marsh, J.A. Jr., 1970. Primary productivity of reef building calcareous red algae. Ecology, Vol. 51, pp. 255-263.
- McLean, R.F., 1967a. Erosion of Burrows in beachrock by the tropical sea urchin *Echinometra lucunter*. Can. J. Zool., Vol. 42, pp. 586-588.
- McLean, R.F., 1967b. Measurements of beachrock erosion by some tropical marine gastropods. Bull. mar. Sci., Vol. 17, pp. 551-561.
- McPherson, B.F., 1968. The ecology of the tropical sea urchin Eucidaris tribuloides. Ph.D. Thesis University of Miami, Miami, Florida, U.S.A., 147 pp.
- Miller, R.J. & K.H. Mann, 1973. Ecological energetics of the seaweed zone in a marine bay on the Atlantic Coast of Canada. III. Energy transformations by sea urchins. Mar. Biol., Vol. 18, pp. 99-114.
- Moore, H.B. & B.F. McPherson, 1965. A contribution to the biology of *Tripneustes esculentus* and *Lytechinus variegatus*. Bull. mar. Sci., Vol. 15, pp. 855-871.
- North, E.J. & J.S. Pearse, 1970. Sea urchin population explosion in California coastal waters, Science, N.Y., Vol. 167, pp. 209.
- Odum, H.T., 1956. Primary productivity in flowing waters. Limnol. Oceanogr., Vol. 1, pp. 102-117.
- Odum, H.T. & E.P. Odum, 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr., Vol. 25, pp. 291-320.

- Ogden, J.C., 1977. Carbonate sediment production by parrot fish and sea urchins on Caribbean reefs. In, Reefs and related carbonates-ecology and sedimentology. eds. S.H. Frost, M.P. Weiss, and J.B. Saunders, 421 pp. Am. Assoc. Petrol. Geol. Stud. in Geology, Vol. 4, pp. 281-288.
- Ogden, J.C., D.P. Abbott & I. Abbott, 1973a. Studies on the activity and food of the echinoid *Diadema antillarum* Philippi on a West Indian patch reef. In, Spec. Publ. No. 2, West Indies Laboratory, St. Croix, pp. 81-85.
- Ogden, J.C., R.A. Brown & N. Salesky, 1973b. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. Science, N.Y., Vol. 182, pp. 715-717.
- Paine, R.T., 1964. Ash and caloric determinations of sponge and opistobranch tissues. Ecology, Vol. 45, pp. 384-387.
- Paine, R.T., 1971. The measurement and application of the calorie to ecological problems. Ann. Rev. Ecol. Systemat., Vol. 2, pp. 145-164.
- Paine, R.T. & R.L. Vadas, 1969a. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnol. Oceanogr., Vol. 14, pp. 710-719.
- Paine, R.T. & R.L. Vadas, 1969b. Caloric values and benthic marine algae and their postulated relation to invertebrate food preference. Mar. Biol., Vol. 4, pp. 79-86.
- Parr Instrument Co., 1960. Oxygen bomb calorimetry and oxygen bomb combustion methods. Manual No. 130, Parr Instrument Co., 430 Moline Illinois, 56 pp.
- Pequignat, E., 1966. Skin digestion and epidermal absorption in regular and irregular sea urchins. Nature, Lond., Vol. 210, pp. 397-399.

- Pequignat, E., 1972. Some new data on skin-digestion and absorption in urchins and sea stars (Asterias and Henricia). Mar. Biol., Vol. 12, pp. 28-41.
- Quasim, S.M. & P.M.A. Bhattashiri, 1971. Primary production of a sea grass bed on Kavaratti Atoll (Laccadives). Hydrobiologia, Vol. 38, pp. 29-38.
- Randall, J.E., 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci., Vol. 3, pp. 31-46.
- Randall, J.E., R.E. Schroeder & W.A. Stark II, 1964. Notes on the biology of the echinoid Diadema antillarum, Caribb. J. Sci., Vol. 4, pp. 421-433.
- Reiswig, H.M., 1971. Particle feeding in natural populations of three marine Demospongiae. Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 141, pp. 568-591.
- Reiswig, H.M., 1974. Water transport, respiration and energetics
   of three tropical marine sponges. J. exp. mar. Biol.
   Ecol., Vol. 14, pp. 231-249.
- Rogers, A.F. & P.F. Kerr, 1942. Optical minerology. 2nd ed., McGraw-Hill Book Co. Ltd., New York, London, 390 pp.
- Round, F.E. & M. Hickman, 1971. Phytobenthos sampling and estimation of primary production, pp. 169-196. In, Methods for the study of marine benthos. International Biological . Program Handbook, No. 16, edited by N.A. Holme and A.D. McIntyre, Blackwell Scientific Publications, Oxford and Edinburgh, 334 pp.
- Salonen, K., J. Sarvala, I. Hakala & M.L. Vijaner, 1976. The relation of energy and organic carbon in aquatic invertebrates. Limnol. Oceanogr., Vol. 21, pp. 724-730.

Sammarco, P.W., J,S. Livinton & J.C. Ogden, 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. J. mar. Res., Vol. 32, pp. 47-53.

- Sander, F., 1971. Organic productivity of inshore waters of Barbados. A study of the island mass effect and its causes. Ph.D. Thesis Marine Sciences Center, McGill University, Montreal, Quebec, Canada, 151 pp.
- Sander, F. & D.M. Steven, 1971. Organic productivity of inshore and offshore waters of Barbados: A study of the island mass effect. Bull. mar. Sci., Vol. 23, pp. 771-792.
- Sargent, M.C. & T.S. Austin, 1949. Organic productivity of an atoll. Amer. Geophys. Union Trans., Vol. 30, pp. 245-249.
- Sargent, M.C. & T.S. Austin, 1954. Biologic economy of coral reefs. Bikini and nearby atolls, Part 2 Oceanography (biologic). U.S. Geol. Serv. Prof. Paper 260-E, pp. 293-300.
- Scoffin, T.P., C.W. Stearn, D. Boucher, P. Frydl, C.M. Hawkins, I.G. Hunter & J.K. MacGeachy (in press). Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part II Erosion, sediments and internal structure. Bull. mar. Sci.
- Slobodkin, L.B., 1960. Ecological energy relationships at the population level. Am. Nat., Vol. 94, pp. 213-236.
- Slobodkin, L.B., 1961. Growth and regulation of animal populations. Holt, Rinehart and Winston, New York, Toronto, London, 184 pp.
- Sorokin, Y.I., 1971a. On the role of bacteria in the productivity of tropical ocean waters. Int. Revue. ges. Hydrobiol. Hydrogr., Vol. 56, pp. 1-48.

Sorokin, Y.I., 1971b. Bacterial populations as components of oceanic ecosystems. Mar. Biol., Vol. 11, pp. 101-105.

- Sorokin, Y.I. 1973a. On the feeding of some scleractinian corals with bacteria and dissolved organic matter. Limnol. Oceanogr., Vol. 18, pp. 380-385.
- Sorokin, Y.I., 1973b. Tropic role of bacteria in the ecosystem of the coral reef. Nature, Lond., Vol. 242, pp. 415-417.
- Sorokin, Y.I., 1974. Bacteria as a component of the coral reef community. In, Proceedings of the Second International Coral Reef Symposium, edited by A.M. Cameron and the Great Barrier Reef Committee, Brisbane, pp. 3-10.
- Sournia, A., 1976a. Oxygen metabolism of a fringing reef in French Polynesia. Helogolander wiss Meeresunters, Bd 28, pp. 401-410.
- Sournia, A., 1976b. Primary production of sands in the lagoon of an atoll and the role of foraminiferan symbionts. Mar. Biol., Vol. 37, pp. 29-32.
- Sournia, A., 1977. Analyse et bilan de la production primarie dans les récifs coralliens. Ann. Inst. Oceanogr., Paris, Vol., 53, pp. 47-74.
- Stearn, C.W. & T.P. Scoffin, 1977. Carbonate budget of a fringing reef, Barbados. In, Proceedings of the Third International Coral Reef Symposium, edited by D.L. Taylor, I.G. Macintyre F.R. Fosberg, E.A. Shinn and J.I. Tracy Jr., Miami, Florida, pp. 471-476.
- Stearn, C.W., T.P. Scoffin & W. Martindale, 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part I Zonation and Productivity. Bull. mar. Sci., Vol. 27, pp. 479-510.

Steemann-Nielsen, E., 1975. Marine photosynthesis, with special emphasis on the ecological aspects. Elsevier Oceanographic Series 13, Elsevier, New York, 141 pp.

- Steven, D.M., A.L. Brooks & E.A. Moore, 1970. Primary and secondary production in the tropical Atlantic. Bermuda Biological Sation Final Report 124 pp.
- Steven, D.M., 1971. Primary productivity of the tropical western Atlantic Ocean near Barbados. Mar. Biol., Vol. 10, pp. 261-264.
- Strickland, J.D.H. & T.R. Parsons, 1972. A practical handbook
   of seawater analysis, 2nd ed. Fish Res. Bd Canada, Bull.
   No. 167, 310 pp.
- Taylor, B.J.R., 1965. The analysis of polymodal frequency distributions. J. Anim. Ecol., Vol. 34, pp. 445-452.
- Vadas, R.L., 1968. The ecology of Agarum and the kelp bed community. Ph.D. Thesis University of Washington, Seattle, Washington, U.S.A., 280 pp.
- Vadas, R.L., 1977. Preferential feeding: An optimization strategy in sea urchins. Ecol. Monogr., Vol. 47, pp. 337-371.
- Wanders, J.B.W., 1976. The role of benthic algae in the shallow reef of Curacao (Netherlands, Antilles) 1: Primary Production in the coral reef. Aquatic Botany, Vol. 2, pp. 235-270.
- Webb, K.L., C.F. D'Elia & W.D. Dupaul, 1977. Biomass and nutrient flux measurements on *Holothuria atra* populations on windward reef flats at Enewetak, Marshall Islands. In, Proceedings of the Third International Coral Reef Symposium, edited by D.L. Taylor, Miami, Florida, Vol. 1, pp. 409-415.

- Webster, S.K., 1975. Oxygen consumption in echinoderms from several geographic locations with particular reference to the echiniodea. Biol. Bull. mar. biol. Lab., Woods Hole, Vol. 148, pp. 157-164.
- Welch, H.E., 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology, Vol. 49, pp. 755-759.
- Westlake, D.F., 1963. Comparisons of plant productivity. Biol. Rev., Vol. 38, pp. 385-425.
- Yingst, J., 1976. The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. J. exp. mar. Biol. Ecol., Vol. 23, pp. 55-69.

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## Appendix Table 1-

Results of tests for oxygen leakage from glass jars used for incubation containers in primary productivity experiments.

Duration of tests - 2 hours

	Oxygen Co	ncentration	$(mgO_{2} 1^{-1})$
Light Bottle	Initial	Final	Change
1	2.35	2.25	-0.10
2	2.35	2.35	0.00
3	2.35	2.35	0.00
4	2.35	2.40	+0.05
Dark Bottle			
1	2.35	2.40	+0.05
2	2.35	2.50	+0.15
3	2.35	2.40	+0.05
4	2.35	2.50	+0.15
Control			
Glass Stoppered Bottle	2.35	2.40	+0.05

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Calculations of total reef surface area covered by each of the three algal types examined in this study (from Stearn et al. 1977).

- 1. Reef planimetric rock area 10800  $m^2 = 60\%$  of total reef planimetric surface area of 18000  $m^2$ .
- Remainder a mixture of sand and rubbble substrates
   i.e. 40% of total reef planimetric surface area = 7200 m<sup>2</sup>.
- 3. Macro relief factor of 1.7 applied to the total planimetric reef rock area

i.e.  $1.7 \times 10800 \text{ m}^2 = 18360 \text{ m}^2$  of reef rock surface

4. Total reef surface area 18360 m<sup>2</sup> of reef rock surface  $\frac{7200}{25560}$  m<sup>2</sup> sand and rubble

5. Total rock surface area = 18360  $m^2$ , of which

- encrusting coralline algae makes up 41% or 7528  $\ensuremath{\mathtt{m}^2}$
- dead coral (assumed harbouring endolithic algae) makes up 22% or 4039 m<sup>2</sup>

- live coral makes up 37% or 6793 m<sup>2</sup>

- Total non-rock surface area (assumed harbouring epipelic algae) = 7200 m<sup>2</sup>
- Percentage of total reef surface area covered by each algae type:
  - area covered by encrusting coralline algae =  $7528 \text{ m}^2$  or 29% of total reef surface area (25560 m<sup>2</sup>)
  - area covered by endolithic algae =  $4039 \text{ m}^2$  or 16% of total reef surface area (25560 m<sup>2</sup>)
  - area covered by epipelic algae =  $7200 \text{ m}^2$  or 28% of the total reef surface area (25560 m<sup>2</sup>).

Feeding rates of Diadema antillarum, from Lewis (1964).

Hours of continuous feeding	No. with food in first half of foregut	No. with food in second half of foregut	No. with food in first half of hindgut	No. with food in second half of hindgut	No. with food in rectum	Total No. of specimens examined
1	5 (50%)*	5 (50%)				10 (100%)
2	5 (45%)	6 (55%)				11 (100%)
4		13 (65%)	5 (25%)	2 (10%)		20 (100%) I
8		3 (20%)	4 (27%)	6 (27%)	2 (33%)	15 (100%) H
10				3 (17%)	15 (83%)	18 (100%) I
12				1 (8%)	12 (92%)	13 (100%)
24					10 (100%)	10 (100%)

\* values in parentheses are percentages of the total number of specimens examined.

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## Appendix Table 4

Number of specimens of *Diadema antillarum* collected at hourly intervals with food in the digestive tract, from Lewis (1964).

Time (hours)	Oesophagus	Caecum	First loop foregut	Balance foregut	Hindgut	No. of specimens examined
0100	2	4	25	25	25	25
0200	2	2	18	25	25	25
0300	0	0	16	20	25	25
0400	4	2	16	24	25	25
0500	2	5	16	21	25	25
0600	2	5	13	15	25	25
0700	4	3	16	20	25	25
0800	0	4	16	20	25	25
0900	2	3	18	25	25	25
1000	3	2	14	21	25	25 H
1100	2	6	25	20	25	25 G
1200	3	9	19	21	25	25
1300	4	10	25	25	25	25
1400	6	10	25	25	25	25
1500	3	12	25	25	25	25
1600	4	9	25	25	25	25
1700	7	7	21	25	25	25
1800	5	9	23	25	25	25
1900	6	6	25	25	25	25
2000	0	5	19	25	25	25
2100	7	7	22	25	25	25
2200	8	8	20	25	25	25
2300	8	6	19	24	25	25
2400	4	2	19	25	25	25

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## Appendix Table 5

# Calculation of the percentage of algal food types in the mixed diets of *Diadema antillarum* of various size groups.

Number of Pellets of Each Algal Food Type

Urchin Size Group (mm)	Sample	Total Number of food pel- lets counted	Epipelic	Endolithic	Encrusting Coralline	Unidentified
20	1 2	225 300	23 24	6 <u>14</u>	181 236	15 26
	Total	525	47	20	417	41
	percent	100.0	9.0	3.8	79.4	7.8
25	1 2 3	300 300 410	53 61 68	11. 23 51	220 198 272	16 18 19
	Total	1010	182	85	690	53
	per cent	100.0	18.0	8,4	68.3	5.3
30	l 2 3 Total per cent	$     300 \\     361 \\     400 \\     1061 \\     100.0 $	22 48 <u>26</u> 96 9.1	24 24 <u>30</u> 78 7.4	246 289 <u>325</u> 860 81.1	8 0 <u>19</u> 27 2.5
35	1 2 3	201 257 <u>121</u>	64 58 <u>44</u>	30 24 20	100 170 <u>57</u>	7 5 0
	Total	579	166	74	327	12
	per cent	100.0	28.7	12.8	56.5	2.1

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## Appendix Table 5 (con't)

			Num	per of Pellets of	of Each Algal Fo	bod Type
Urchin Size Group (mm)	Sample	Total number of food pel- lets counted	Epipelic	Endolithic	Encrusting Coralline	Unidentified
40	l 2 3 Total percent	162 207 <u>197</u> 566 100.0	84 119 <u>102</u> 305 53.9	52 49 <u>45</u> 146 25.8	$     25 \\     36 \\     44 \\     105 \\     18.6 $	1 3 <u>6</u> 10 1.8
45	l 2 3 Total percent	107 192 <u>152</u> 451 100.0	75 129 <u>121</u> 325 72.1	23 47 <u>26</u> 96 21.3	8 16 <u>5</u> 29 6.4	1 0 0 1 0.2
50	l 2 3 Total percent	139 141 <u>125</u> 405 100.0	103 85 <u>85</u> 273 67.4	21 39 <u>33</u> 93 22.4	10 12 <u>5</u> 27 6.5	5 5 2 12 2.9

\* for urchins of 15 mm MTD the percentage of each food type in the natural diet was assumed to be similar to urchins of 20 mm MTD since no data were available for the percentage of each food type in their natural diet.

\*\* similarly urchins of 55 and 60 mm MTD were assumed to have a diet similar to urchins of 50 mm MTD.

Mean food pellet size and dry weight from *Diadema antillarum* of various size groups.

## 1. Food Pellet Size

Urchin Size Group (mm)	No. of Pellets Measured	<u>Mean Pellet Size</u> (Diameter in mm)	<sup>±</sup> 95% Confidence Limits
20	80	0.94	0.04
25	80	1.10	0.04
30	80	1.23	0.05
35	80	1.32	0.07
40	80	1.61	0.09
45	80	1.85	0.08
50	80	1.85	0.08

## 2. Food Pellet Dry Weight

Urchin Size Group (mm)	Quantity Measured	<u>Mean dry weight</u> <u>per group</u> (g)	±95% Confidence Limits	Mean dry weight of one pellet (g)
20	10 groups of 100 pellets	0.032	0.009	$3.24 \times 10^{-4}$
25	10 groups of 100 pellets	0.033	0.007	3.31 x 10 <sup>4</sup>
30	10 groups of 100 pellets	0.340	0.006	$3.40 \times 10^{-4}$
35	10 groups of 100 pellets	0.350	0.004	$3.50 \times 10^{-4}$
40	10 groups of 50 pellets	0.361	0.002	$7.22 \times 10^{-4}$
50	10 groups of 25 pellets	0.967	0.008	$3.87 \times 10^{-3}$

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Estimated minimum daily caloric intake of *Diadema antillarum* of various size groups feeding on a mixed diet.

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Urchin Size Group	<u>Mean gut</u> content dry weight	Food type	Percentage of of each food type in the mixed diet	Weight of each food type in the mean gut content	Caloric content of each food type	Caloric of each total c	contribution food type to caloric intake	
( mm )	(g)		(%)	(g)	(cal g dry wt <sup>-1</sup> )		(cal)	
15	0.129	encrusting coralline algae	e 79.4	0.102	370.30		37.77	
		epipelic algae	9.0	0.012	58.09		.70	
		endolithic algae	3.8	0.005	37.23		.19	<u> </u>
						total	38.66	62 -
20	0.160	encrusting coralline	e 79.4	0.127	370.30		47.03	
		epipelic algae	9.0	0.014	58.09		.81	
		endolithic algae	3.8	0.006	37.23		.22	
						total	48.06	
25	0.275	encrusting coralline	e 68.3	0.188	370.30		69.62	
		epipelic algae	18.0	0.050	58.09		2.90	
		endolithic algae	8.4	0.023	37.23		.86	
						total	73.38	

## Appendix Table 7 (Con't)

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<u>Urchin Size Group</u>	Mean gut content dry weight	Food Type	Percentage of of each food type in the mixed diet	Weight of each food type in the mean gut	Caloric content of each food type	Calo of e tota	ric contribution ach food type to 1 caloric intake
( mm )	(g)		(%)	(g)	(cal g dry wt <sup>-1</sup> )		(cal)
30	0.330	encrusting coralline algae	e 81.1	0.268	370.30		99.24
		epipelic algae	9.1	0.030	58.09		1.74
		endolithic algae	7.4	0.024	37.23		.89
						total	101.87
35	0.742	encrusting coralline	e 56.5	0.419	370.30		155.16
		epipelic algae	28.7	0.213	58.09		12.37
		endolithic algae	12.8	0.010	37.23		.37
						total	167.90
40	1.236	encrusting coralline	e 18.6	0.230	370.30		85.17
		epipelic algae	53.9	0.666	58.09		38.69
		endolithic algae	25.8	0.319	37.23		11.88
	`					total	135.74
45	1.906	encrusting coralline	e 6.4	0.122	370.30		45.18
		epipelic algae	72.1	1.374	58.09		79.82
		endolithic algae	21.3	0.406	37.23		15.12
						total	141.12

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#### Appendix Table 7 (Con't)

Urchin Size Group	Mean gut content dry weight	Food Type	Percentage of of each food type in the mixed diet	Weight of each food type in the mean gut content	<u>Caloric content</u> of each food <u>type</u>	Caloric contribution of each food type to total caloric intake
( mm )	(g)		(8)	(g)	(cal g dry wt <sup>-1</sup> )	(cal)
50	2.366	encrusting coralline algae	6.5	0.154	370.30	57.03
		epipelic algae	67.4	1.595	58.09	92.65
		endolithic algae	22.4	0.530	37.23	19.73
					t	total 169.41
55	2.536	encrusting coralline	6.5	0.165	370.30	61.10
		epipelic algae	67.4	1.709	58.09	99.28
		endolithic algae	22.4	0.568	37.23	21.15
					t	total 181.53
60	2.934	encrusting coralline	6.5	0.191	370.30	70.73
		epipelic algae	67.4	1.978	58.09	114.90
		endolithic algae	22.4	0.657	37.23	24.26
					t	total 210.09

\* for urchins 15 mm MTD the percentage of each food type in the natural diet was assumed to be similar to urchins 20 mm MTD since no data were available for the percentage of each food type in their natural diet.

\*\* similarly urchins 55 and 60 mm MTD were assumed to have a diet similar to urchins 50 mm MTD.

Sample	Inorganic Matter
	(% dry weight)
1	76.14
2	82.05
3	80.42
4	80.49
5	80.31
6	79.35
7	81.48
8	81.19
9.	81.14
10	81.19
11	81.34
12	82.00
13	81.53
14	81.15
15	81.01
16	81.06
mean	80.74
95% confidence	+0.77

Inorganic matter expressed as percent (%) dry weight in scrapings of encrusting coralline algae.

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Weight loss of calcium carbonate (CaCO<sub>3</sub>) substrates incinerated at  $450^{\circ}$ C and  $500^{\circ}$ C for four hours expressed as a percentage of the original sample dry weight after treatment to remove organic matter.

#### 1. BLEACH TREATED

Temperature	e	<u>450</u> °	c	<u>500<sup>0</sup>C</u>				
Sample	No. tested	Mean Percent Weight Loss	±95% Confidence Limits	No. tested	Mean Percent Weight Loss	±95% Confidence Limits		
encrusting coralline algae	12	2.51	0.09	12	3.50	0.09		
coral skeleton	12	2.15	0.55	12	2.28	0.59	י רו	
reagent grade CaCO <sub>3</sub>	9	0.26	0.28	9	0.39	0.43	.66 -	
2. <u>NaOH TREAT</u>	ED							
encrusting coralline algae	12	2.66	0.13	12	2.98	0.07		
coral skeleton	12	2.06	0.09	12	2.06	0.09		
reagent grade CaCO <sub>3</sub>	9	0.08	0.17	9	0.21	0.29		

Calculation of organic weight ingested by Diadema antillarum of various size groups having a mixed diet.

Urchin Size Group (mm)	Food Type	Organic content per gram dry weight of each food type (g)	Percentage of each food type in the <u>mixed diet</u> (%)	Contribution of organic matter by each food type (g)	Organic Matter Ingested per gram dry weight ingested (g)
15	encrusting coralline algae	0.193	79.4	0.153	
	endolithic algaé	0.035	3.8	0.001	0.159
	epipelic algae	0.051	9.0	0.005	
20	encrusting coralline algae	0.193	79.4	0.153	     
	endolithic algae	0.035	3.8	0.001	0.159
	epipelic algae	0.051	9.0	0.005	. 1
25	encrusting coralline algae	0.193	68.3	0.132	
	endolithic algae	0.035	8.4	0.003	0.144
	epipelic algae	0.51	18.0	0.009	
30	encrusting coralline algae	0.193	81.1	0.157	
	endolithic algae	0.035	7.4	0.003	0.165
	epipelic algae	0.051	9.1	0.005	

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#### Appendix Table 10 (Con't)

<u>Urc</u>	<u>hin Size</u> Group	Food Type	Organic content per gram dry weight of each food type	Percentage of each food type in the mixed diet	Contribution of organic matter by each food type	Organic Matter ingested per gram dry weight ingested
	(mm)	·	· (g)	· (%)	· (g)	· (g)
	35	encrusting coralline algae	0.193	56.5	0.109	
		endolithic algae	0.035	12.8	0.004	0.128
		epipelic algae	0.051	28.7	0.015	
	40	encrusting coralline algae	0.193	18.6	0.036	
		endolithic algae	0.035	25.8	0.009	0.072
		epipelic algae	0.051	53.9	0.027	α Ι
	45	encrusting coralline algae	0.193	6.4	0.012	
		coralline algae	0.035	21.3	0.007	0.057
		epipelic algae	0.051	72.1	0.038	
	50	encrusting coralline algae	0.193	6.5	0.013	
		endolithic algae	0.035	22.4	0.008	0.055
		epipelic algae	0.051	67.4	0.034	•

\* urchins 55 and 60 mm MTD were assumed to have the same proportions of each food type in their natural diet as urchins 50 mm MTD hence same organic content per gram dry weight of food ingested.

\*\* similarly urchins 15 mm MTD were assumed to have the same proportions of each food type in their
natural diet as urchins of 20 mm MTD hence the same organic content per gram dry weight of food
ingested.

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## Appendix Table 11

Phosphates Salinity Nitrates Date  $(uq at P 1^{-1})$  $(uq at N 1^{-1})$ (<sup>0</sup>/00) 2/9/75 7.144 .085 33.880 8/9/75 4.702 .034 33.302 15/9/75 4.795 33.669 .130 4.763 22/9/75 .009 33.613 6/10/75 2.041 .100 34.502 13/10/75 3.006 .100 34.620 20/10/75 2.385 34.750 .100 27/10/75 34.890 3.267 .100 3/11/75 4.061 .100 34.910 10/11/75 8.112 34.900 .100 17/11/75 8.621 .100 35.280 24/11/75 10.336 .100 35.560 1/12/75 12.305 .100 35.820 8/12/75 2.260 .100 35.510 15/12/75 .050 .100 35.290 22/12/75 .480 .100 35.010 29/12/75 1.710 .100 35.750 5/1/76 2.290 .100 35.730 12/1/76 .295 35.410 .100 19/1/76 .160 .100 35.470 26/1/76 .050 .100 35.695 2/2/76 .205 34.840 .030 9/2/76 .070 34.884 .035 16/2/76 .360 .030 34.976 23/2/76 .760 34.995 .030 1/3/76 1.710 .030 35.243 8/3/76 1.665 .030 34.690 15/3/76 .510 .054 34.878

Salinity, nitrate and phosphate concentrations measured in reef surface waters during one year.

Appendix Table 11 (cont.)

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Date	Nitrates	Phosphates	Salinity
	$(\mu g at N 1^{-1})$	$(\mu g at P 1^{-1})$	( <sup>0</sup> /00)
22/3/76	.415	.044	34.771
29/3/76	.410	.030	34.179
5/4/76	1.545	.040	35.743
12/4/76	2.670	.030	34.911
19/4/76	1.240	.030	34.974
26/4/76	3.580	.030	35.136
3/5/76	2.220	.030	33.839
10/5/76	2.680	.030	33.801
17/5/76	3.750	.030	33.758
24/5/76	3.730	.030	33.721
31/5/76	3.580	.030	33.634
7/6/76	5.300	.030	33.726
14/6/76	2.460	.030	33.881
21/6/76	2.900	.032	33.966
28/6/76	1.590	.030	34.501
5/7/76			33.976
12/7/76			33.934
19/7/76			33.609
26/7/76			34.547
2/8/76			34.217
9/8/76			33.823
16/8/76			33.877
23/8/76			33.674
30/8/76			33.652
6/9/76			33.705

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Oxygen concentrations in surface seawater and air and sea temperatures measured over a period of one year.

Date	Date Temperature C		Dissolved Oxygen	
	Air	Sea	$(mgO_2 1^{-1})$	
2/9/75	28.0	28.0	5.74	
8/9/75	27.0	27.5	6.30	
15/9/75	26.5	28.0	4.85	
22/9/75	29.0	27.0	5.78	
29/9/75	29.0	29.0	4.85	
6/10/75	28.5	29.0	5.25	
13/10/75	24.5	29.0	5.35	
20/10/75	29.5	29.0	5.28	
27/10/75	28.5	28.0	5.20	
3/11/75	28.0	29.0	6.10	
10/11/75	27.5	27.5	4.06	
17/11/75	27.0	27.5	6.51	
24/11/75	28.0	28.5	-	
1/12/75	27.5	27.5	6.20	
8/12/75	27.5	27.5	-	
15/12/75	24.0	27.5	-	
22/12/75	24.0	26.5	-	
29/12/75	24.0	26.5	-	
5/1/76	25.0	25.0	6.74	
12/1/76	24.0	24.5	6.40	
19/1/76	24.5	25.0	5.95	
26/1/76	24.0	24.5	6.30	
2/2/76	25.5	25.0	6.50	
9/2/76	24.0	25.0	4.95	
16/2/76	25.0	24.0	5.25	
23/2/76	24.5	25.0	6.10	
1/3/76	25.0	24.5	6.50	
8/3/76	24.5	24.5	5.90	

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# Appendix Table 12 (cont.)

Date	Temperat	ure <sup>O</sup> C	Dissolved Oxygen
	Air	Sea	(mgO <sub>2</sub> 1 <sup>-1</sup> )
15/3/76	24.5	24.5	5.95
22/3/76	25.5	24.5	6.55
29/3/76	26.5	26.0	6.25
5/4/76	26.5	26.0	6.05
12/4/76	27.0	25.5	6.03
19/4/76	26.0	25.5	5.95
26/4/76	27.0	25.5	6.00
3/5/76	25.5	25.5	5.80
10/5/76	28.0	26.5	6.20
17/5/76	25.0	26.5	5.45
24/5/76	26.0	25.5	5.60
31/5/76	28.0	26.5	6.30
7/6/76	24.5	25.5	6.20
14/6/76	27.5	26.5	5.30
21/6/76	25.0	26.0	4.90
28/6/76	27.5	26.0	6.02
5/7/76	27.5	26.0	5.70
12/7/76	27.0	26.5	5.45
19/7/76	27.0	26.0	6.05
26/7/76	27.0	26.5	6.25
2/8/76	25.5	26.5	6.35
9/8/76	27.0	27.0	6.20
16/8/76	27.0	28.5	5.90
23/8/76	27.5	28.0	5.95
30/8/76	26.5	27.5	5.85
6/9/76	28.0	27.5	5.60

#### Appendix Table 13

Mean hourly rates of primary production of encrusting coralline, endolithic and epipelic algae expressed in  $mgO_2$  cm<sup>-2</sup> of algal surface  $h^{-1}$ .

Algae	Time	Net Pr	oductivity	Resp	piration	Gross I	roductivity
	(h)	mean *	±95% C.L.**	mean	±95% C.L.	mean	±95% C.L.
encrusting	0600-0800	0.058	0.014	0.024	0.003	0.081	0.013
coralline	0800-1000	0.038	0.003	0.031	0.005	0.069	0.017
	1000-1200	0.030	0.008	0.020	0.004	0.050	0.009
	1200-1400	0.031	0.011	0.022	0.005	0.053	0.013
	1400-1600	0.033	0.008	0.018	0.003	0.051	0.009
	1600-1800	0.041	0.005	0.019	0.003	0.060	0.007
	mean hourly	0.038	0.008	0.022	0.003	0.600	0.009
endolithic	0600-0800	0.027	0.008	0.022	0.005	0.049	0.009
	0800-1000	0.086	0.017	0.026	0.004	0.112	0.018
	1000-1200	0.098	0.028	0.042	0.007	0.140	0.029
	1200-1400	0.058	0.019	0.019	0.005	0.077	0.017
	1400-1600	0.068	0.008	0.030	0.006	0.098	0.010
	1600-1800	0.083	0.016	0.033	0.008	0.116	0.017
	mean hourly	0.070	0.019	0.028	0.006	0.098	0.024

\* mean of 10 samples at each time interval

\*\* C.L. = confidence limits

Algae	Time	Net Pr	oductivity	Resp	piration	Gross P	roductivity
	(h)	mean *	±95% C.L.**	mean	±95% C.L.	mean	±95% C.L.
epipelic	0600-0800	0.056	0.007	0.004	0.002	0.060	0.008
	0800-1000	0.078	0.006	0.014	0.002	0.092	0.007
	1000-1200	0.094	0.006	0.008	0.002	0.102	0.005
	1200-1400	0.082	0.011	0.010	0.002	0.092	0.011
	1400-1600	0.082	0.009	0.010	0.004	0.092	0.009
	1600-1800	0.048	0.006	0.010	0.002	0.058	0.007
	mean hourly	0.073	0.013	0.009	0.002	0.082	0.014

Appendix Table 13 (Con't)

\* mean of 10 samples at each time interval
\*\* C.L. = confidence limits

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### Appendix Table 14

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Mean Gonad Index\* for urchins sampled each month over a period of one year.

Month	No. of urchins	Mean Gonad	± 95% Confidence
	sampred	$(\frac{11dex}{x \ 10^{-4}})$	Limit's
July 1975	19	1.292	0.300
Aug. 1975	16	1.398	0.500
Sept. 1975	14	1.519	0.263
Oct. 1975	12	1.045	0.376
Nov. 1975	14	1.185	0.068
Dec. 1975	14	1.254	0.340
Jan. 1976	12	1.330	0.273
Feb. 1976	10	1.502	0.371
March 1976	14	1.795	0.429
April 1976	13	1.999	0.473
May 1976	12	2.056	0.763
June 1976	14	1.253	0.339

\* Gonad Index = (10GV)(MTD)<sup>3</sup> x 100 where: GV = gonad volume in ml. MTD = urchin size in mm.

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### Appendix Table 15

Absorption efficiencies exhibited by *Diadema antillarum* on several food types which occur in their mixed diet.

Urchin Size Group	Food Type	Ash free dry weight to dry	Ash free dry weight to dry	Percent Absorption Efficiency % A.E. = (F'-E') = 100	, -
(mm)		in food	in feces	(1-E')(F') X 100	
15	encrusting	0.206	0.161	26.0	
20	coralline algae		NE		
25			0.088	62.8	
30			0.140	37.3	ı
35		"	0.138	38.3	Ц
40			0.121	46.9	76
45			0.093	60.5	1
50		u	0.066	72.8	
15	endolithic algae	0.044	NE	- -	
20	on coral dead	11	NE	. <b>–</b>	
25	heads	**	0.088	-109.7	
30		u	0.065	- 51.1	
35			0.120	-196.3	
40			0.038	14.2	
45		н	0.091	-117.5	
50		n	0.041	7.1	

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Urchin Size Group	Food Type	Ash free dry weight to dry	Ash free dry weight to dry	Percent Absorption Efficience	<u>y</u>
(mm)		weight ratio in food	weight ratio in feces	* A.E. = $\frac{(F'-E')}{(1-E')(F')} \times 100$	
15	endolithic	0.056	NE	· _	
20	algae on rubble	n	NE	-	
25		11	0.072	-30.8	
30		u	0.073	-32.8	
35		u	0.050	11.3	
40		н	0.051	9.4	ł
45		u	0.044	22.4	17
50		H .	0.047	16.9	7 -
15	epipelic algae	0.048	NE	_	
20		11	NE	-	
25		<b>` н</b>	NE	-	
30		u	NE	-	
35		n	NE	-	
40			0.047	2.2	
45		n	0.050	-4.4	
50		"	0.047	2.2	

NE = not examined

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### Appendix Table 16

Proportion (P) of feces produced by starved urchins (F) relative to continuous feeding urchins ( $F_{f}^{s}$ ).

P –	$(\mathbf{F}_{f} - \mathbf{F}_{s})$
F =	F <sub>f</sub>
0.047	0.110
-0.687	-0.504
-0.028	-0.200
0.062	-0.182
-0.020	0.281
-0.200	-0.059
0.079	0.005
0.454	0.206
-0.151	0.189
0.150	0.021
0.069	0.287
0.145	0.380
0.223	-0.380
0.483	-0.087
0.049	0.258
0.085	0.203
-0.298	0.193
0.164	0.210
-0.088	-0.019
-0.542	-0.048
-0.133	-0.086
-0.018	-0.125
-0.170	0.276
-0.180	-0.387
-0.419	

Mean 0.001 (n = 49) from Arc-sine transformation

#### Appendix Table 17

Means of chemical and physical values recorded during primary production studies compared to annual means.

Factor	June - Au	igust 1975	Annual		
	<u>mean</u> *	( <u>s.d.)</u>	mean	( <u>s.d.</u> )	
Irradiance** (cal cm <sup>-2</sup> day <sup>-1</sup> )	450	(31)	420	(65)	
Nitrates <sup>V</sup> (ug at N l <sup>-1</sup> )	3.06	(1.59)	3.08	(2.94)	
Phosphates <sup>▽</sup> (ug at P 1 <sup>-1</sup> )	0.06	(0.04)	0.03	(0.01)	
Air Temperature ( <sup>O</sup> C)	26.65	(1.00)	26.21	(1.08)	
Sea Temperature ( <sup>o</sup> C)	26.65	(0.86)	26.56	(1.40)	
Salinity ( <sup>0</sup> / <sub>00</sub> )	33.93	(0.30)	34.53	(0.76)	

- \* means for June through August 1976 not significantly different (P = 0.05) from annual means.
- \*\* source, Husbands Meteorological Station, Barbados.
- ✓ June 1976 only (samples for July and August lost). (s.d.) = standard deviation.