ELSEVIER

Journal of Experimental Marine Biology and Ecology
254 (2000) 71–84

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.nl/locate/jembe

Ingestion and transformation of algal turf by *Echinometra mathaei* on Tiahura fringing reef (French Polynesia)

Suzanne C. Mills[a,b,*], Mireille Peyrot-Clausade[a,c], Marie France Fontaine[a]

[a]*Université de la Méditerranée, Centre d' Océanologie de Marseille, CNRS UMR 6540, Station Marine d'Endoume, 13007 Marseille, France*
[b]*School of Biological Sciences, University of East Anglia, Norwich, NR2 7TJ, UK*
[c]*Centre de Recherches Insulaires et Observatoire de l'Environnement, B.P. 1013 Moorea, French Polynesia*

Received 12 August 1999; received in revised form 7 April 2000; accepted 17 July 2000

Abstract

The sea urchin *Echinometra mathaei* is the most abundant herbivore on many tropical reefs. We studied the ingestion and digestion diel rhythms, transformation of algal turf and bioerosion attributable to this species on the Tiahura fringing reef in French Polynesia. Ingestion rates showed a circadian rhythm with most feeding taking place during the night. Absorption of food occurred throughout the day with urchins digesting food outside of the feeding period. A total of 73% of the faecal pellets consisted of $CaCO_3$ eroded from the reef, 20% consisted of organic matter and 7% the refractory organic matter. Of the organic matter, lipids, carbohydrates and chlorophyll were digested and absorbed and proteins were expelled in the faecal pellets. An average individual bioerosion of 0.32 g day^{-1} was estimated for *E. mathaei* from approximately a 35-mm test diameter on the Tiahura fringing reef. We further estimated that *E. mathaei* release 70.5 g m^2 y^{-1} of carbohydrates, 43.8 g m^2 y^{-1} of lipid, 23.3 g m^2 y^{-1} of protein and 2.0 g m^2 y^{-1} of total chlorophyll pigments.

Keywords: Sea urchins; Bioerosion; Grazing; Ingestion; Coral reef

1. Introduction

Benthic algae are the main primary producers on tropical reefs where herbivorous fishes and sea urchins consume the majority of their primary production (Hawkins, 1981; Hawkins and Lewis, 1982; Polunin, 1988; Harmelin-Vivien et al., 1992). The role

*Corresponding author. Tel.: +33-1603-456-161; fax: +33-1603-592-250.
E-mail address: s.c.mills@uea.ac.uk (S.C. Mills).

0022-0981/00/$ – see front matter
PII: S0022-0981(00)00264-1

of herbivorous fish in the reef food web is becoming clearer (e.g., Polunin et al., 1995). However, relatively less is known of the ingestion and digestion of algae by grazing sea urchins and their role in the cycling and transfer of material and energy in coral reef food webs (Farmanfarmaian and Phillips, 1962; Khamala, 1971; Downing and El-Zahr, 1987).

Grazing sea urchins cause erosion to the carbonate reef substrata due to the scraping action of their Aristotle's lantern (Bak, 1994). Rates of bioerosion by echinoids, established from gut contents, range from 0.07 to 0.26 kg of $CaCO_3$ m^2 y^{-1} (*E. mathaei* on Enewetak Atoll; Russo, 1980) to 8.32 kg of $CaCO_3$ m^2 y^{-1} (*E. mathaei* on La Réunion reefs; Conand et al., 1998). Although fish species also erode reef substrata while feeding, even low population densities of sea urchins cause substantially more erosion than fish. At high densities sea urchins cause destruction of the reef with loss of the reef framework (Hubbard et al., 1990; Glynn, 1997). Such destruction is particularly apparent on some heavily fished reefs, such as those on the Kenyan coast, where populations of herbivorous fish and urchin predators are dramatically reduced in numbers by fishing. On these reefs, echinoids become the key herbivorous grazers and destructive bioerosion occurs (McClanahan and Muthuga, 1988; Bak, 1994; McClanahan et al., 1994; McClanahan, 1995; Reaka-Kulda et al., 1996; Peyrot-Clausade et al., 2000).

On the fringing reefs of La Réunion, and Tiahura in French Polynesia, the dominant echinoid grazer is *E. mathaei* (Conand et al., 1998), which ingests algal turf growing on the surface of dead coral. In this study we quantify the role of *E. mathaei* in the reef food web by investigating its ingestion, gut turnover and biochemical transformation of algal turf. The results are used to make preliminary estimates of bioerosion rates on the Tiahura fringing reef by *E. mathaei* and to determine its role in the transformation of primary production into matter that may be used by other species.

2. Materials and methods

2.1. Study sites and species

The investigation was conducted in December 1993 on Moorea island (17°S, 149°W) which is a high island in French Polynesia, Central Pacific Ocean, surrounded by both fringing and barrier reefs (Fig. 1). The study site, the Tiahura fringing reef (1.5–2.5 m depth, Galzin and Pointier, 1985) was dominated by isolated colonies of massive *Porites* and *Montipora*.

Echinometra spp. is a complex of closely related species, presently described as types A, B, C, D (Nishihira et al., 1991; Palumbi and Metz, 1991). On the Tiahura fringing reef, the sea urchins considered were *Echinometra* type A, which were the only type present (Conand et al., 1998).

2.2. Diel ingestion and digestion rhythms

Diel rhythms of ingestion and digestion of *E. mathaei* were investigated during

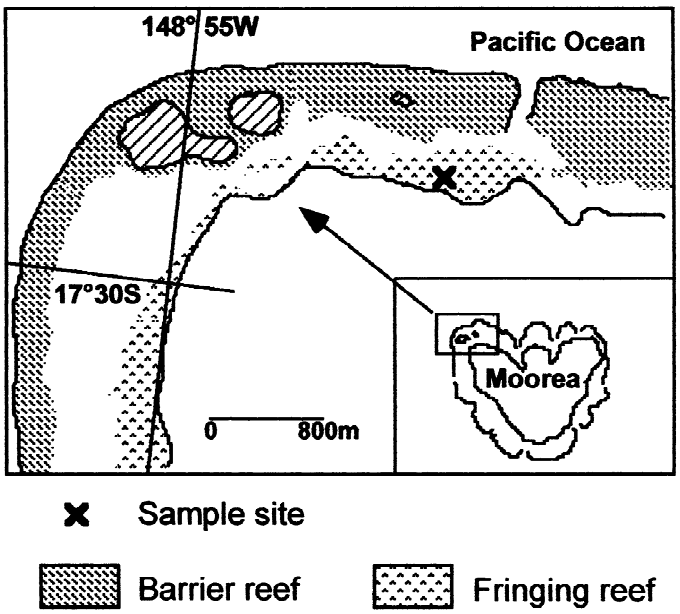

Fig. 1. Location of the Tiahura fringing reef on Moorea. Cross shows position of sample site.

October 1994. Ten specimens were collected from the reef at 0500 h and a further ten from the same reef at 1700 h on the same day. All specimens were of approximately a 35-mm test diameter. The guts were dissected and separated into five sections: oesophagus, stomach, upper and lower intestine and rectum (Fig. 2). Gut contents were stored frozen at -20°C before being freeze-dried and weighed (Metler AE240 10^{-5} g precision). All further analyses were conducted using the freeze-dried samples.

The diel variation in ingestion and digestion of *E. mathaei* was also assessed. Thirty-six sea urchins (35–40 mm test diameter) were collected from the fringing reef at 1700 h and were held without food in six aquaria (45 l) for 23 h at densities of six urchins per aquarium. At 1600 h the following day, pieces of dead coral covered with algal turf were added to the aquaria allowing the urchins to feed. Three sea urchins were removed at random every 2 h over a 24-h period beginning at 1800 h. The contents of the stomach, intestine and rectum of each urchin were removed, freeze-dried and weighed.

2.3. Biochemical composition of gut contents along the digestive tube

To assess the composition of the gut contents, a further 20 *E. mathaei* (of mean test diameter 40 mm) were collected from the reef, ten at 0500 h and ten at 1700 h. The guts were dissected into oesophagus, stomach, upper and lower intestine and rectum and the contents removed from each section for analysis by biochemical assay. $CaCO_3$, protein, lipid, carbohydrate and chlorophyll pigments were all assessed as follows.

The quantity of $CaCO_3$ in each section of the gut was measured after the contents had

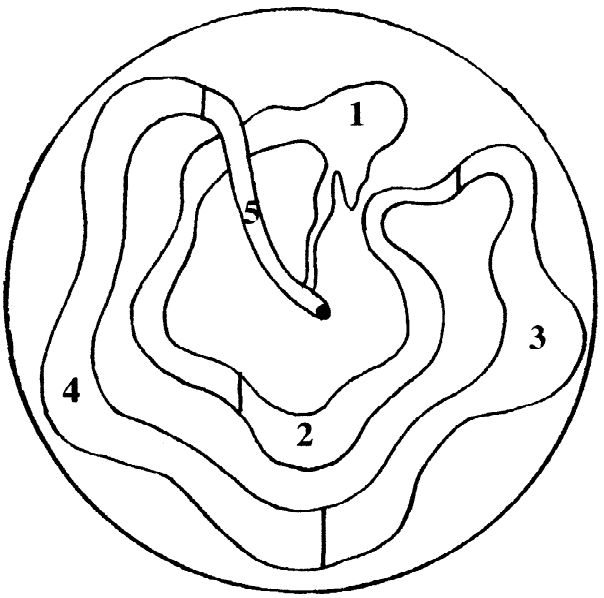

Fig. 2. Diagram of the digestive tube of a sea urchin. The numbers refer to the sections into which the digestive tube of *E. mathaei* was dissected: (1) oesophagus; (2) stomach; (3) upper intestine; (4) lower intestine; (5) rectum.

been heated at 450°C for 5 h. This vaporised all components except the refractory organic and mineral matter. Twenty milligrams of the furnace residue was dissolved in 1.7 ml of 4.5 N HCl, and the $CaCO_3$ content was determined by full titration of the partially carbonate neutralised acid with NaOH using *N*-phenyl-1-naphthylamine as the pH indicator. The mass of refractory organic and other inorganic matter was calculated as the difference between the mass of the furnace residue and that of $CaCO_3$.

Protein content was determined following the method of Lowry et al. (1951). Twenty milligrams of the gut contents were added to 5 ml of 50 mM Tris–Cl pH 8.7, 500 mM NaCl and 5 mM EDTA buffer solution and stored in the fridge for 24 h. After centrifuging, 1 ml was taken and added to 5 ml of a 100-ml solution of 2% Na_2CO_3 in 0.1 N NaOH with the addition of 1 ml of 0.5% $CuSO_4 \cdot 5H_2O$ and 1 ml of 1% sodium potassium tartarate. After 10–45 min, 0.5 ml of Folin reagent (Merck) was added. After 2 h the samples had reached their maximum optical absorbances and were centrifuged. Optical absorbances were measured in a Uvikon 810 twin beam spectrophotometer at 700 nm. The protein content was estimated from a BSA standard curve.

Lipids were extracted from the gut contents using the Blight and Dyer (1959) method. Twenty milligrams of gut contents were oxidised by the addition of 2 ml of conc. H_2SO_4 and the quantity of lipids was measured at 360 nm against a standard curve made with glycerol tripalmate.

To extract the soluble from the insoluble carbohydrates, 20 mg of gut contents were dissolved in 5 ml of water and heated in a water bath for 2 h. The solution was

centrifuged for 15 min and 1 ml of the supernatant was removed and added to 1 ml of 5% phenol and 5 ml of conc. H_2SO_4. After homogenisation, the samples were placed in the dark for 2 h. The soluble carbohydrates were then quantified by measuring their absorbance at 492 nm against a glucose calibration curve. The insoluble carbohydrates were measured using the solid residue collected by centrifuging as described above. The solid residue was dried at 45°C overnight, after which 1 ml of distilled water, 1 ml of 5% phenol and 5 ml of conc. H_2SO_4 were added. After 2 h in the dark and following centrifuging, the supernatant was collected and the insoluble carbohydrates were measured by their absorbance at 492 nm (Dubois et al., 1956). The ratio of insoluble:soluble carbohydrates provides an index of the polymerisation of the carbohydrate material, with the insoluble portion representing the refractory or mechanically degraded material and the soluble part representing the raw material (Handa et al., 1972).

The composition of photosynthetic pigments and degradation products (chlorophyllides, pheophorbides and pheophytins) was determined following de La Giraudière et al. (1989). A 2-ml aliquort of 90% acetone was added to 20 mg of the gut contents and agitated at 5°C for 2 h. The suspension was centrifuged and the pigment composition of the supernatant determined using high-pressure liquid chromatography with a Beckam Ultra-Sphere ODS-C_{18} column of 3-μm silica beads with a spectrofluorimeter measuring fluorescence intensity at 450 nm and under excitation at 430 nm.

2.4. Statistical analysis

The univariate data display (box plots) developed by Tukey (Frigge et al., 1989) was used. Each sample is represented as a box, divided at the median, and two whiskers; the box length is the interquartile range and the whisker ends correspond to the first and the last decile. All observations beyond these limits are plotted individually.

Analyses of variance were performed on log transformed data to reduce the skewed distribution of the original data and the variance homogeneity was checked by Cochran's test (Underwood, 1981). A series of one-way ANOVA fixed models (Model III) were carried out to investigate the difference between the dried gut contents of the urchins collected at 0500 h and 1700 h and the variation of the biochemical components along the digestive tube. Multiple comparisons of means according to Student–Newman–Keul's (SNK) tests (Zar, 1984) were used to determine which of these means were significantly different from each other. All analyses were performed using Statview 5.1 (1998) and Super Anova 1.11 (1991).

3. Results

3.1. Diel ingestion and digestion rhythms

Freeze-dried masses of the contents of the intestine, stomach and total gut contents are given in Table 1. In each case, gut content masses of *E. mathaei* collected at 0500 h were significantly greater than those of *E. mathaei* collected at 1700 h. Nine of the ten

Table 1
Temporal variation in freeze-dried mean mass (g)±S.D. of the gut contents of *E. mathaei*[a]

Gut section	0500 h	1700 h	$F_{2, 18}$	*P*
Stomach	0.10±0.40	0.002±0.007	47.10	***
Intestine	0.33±0.18	0.110±0.070	12.80	**
Total gut	0.45±0.21	0.120±0.090	19.42	**

[a] NS = Not significant; *significant ($P < 0.05$); **highly significant ($P < 0.01$); ***very highly significant ($P < 0.001$).

urchins collected at 1700 h had empty stomachs and their intestines contained on average four times less matter than at 0500 h (Fig. 3).

Analysis of the gut contents of *E. mathaei* fed algal turf over 24 h in aquaria shows a similar pattern of foraging. The gut contents total dry weight increased from 1800 h to 0200 h and then decreased from 0200 h to 1600 h (Fig. 4). The stomach contents reached a maximum dry weight at the beginning of the night between 1800 h and 0000 h. The upper and lower intestines were filled to a maximum at 0200 h, and the rectum was empty twice during the 24-h period at 0200 h and 1400 h.

3.2. Temporal variation in biochemical composition of gut contents

The proportions of $CaCO_3$ and assimilated and refractory organic matter in sections of the gut contents are given in Table 2. The proportion of assimilated organic matter in the intestinal contents of urchins collected at 0500 h was significantly higher than at 1700 h.

The concentrations of proteins, lipids, carbohydrates and chlorophyll in the gut contents are given in Table 2. The lipid concentration in the rectum from urchins collected at 0500 h was significantly lower than that from the urchins collected at 1700 h. Concentrations of both the insoluble and soluble carbohydrates collected at 0500 h were significantly greater than those of *E. mathaei* collected at 1700 h.

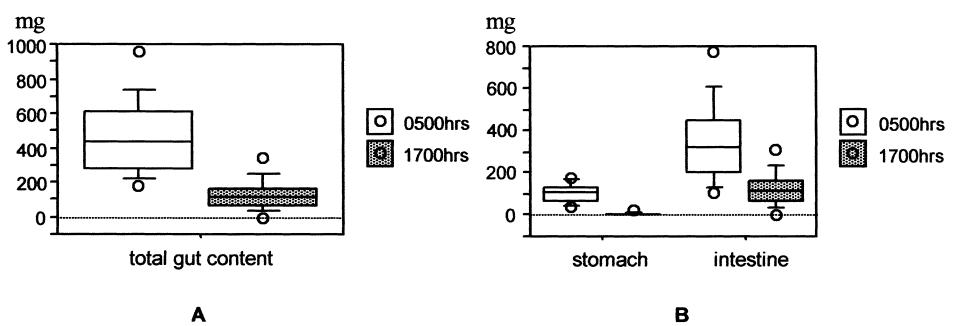

Fig. 3. Temporal decrease in dry gut content weights (mg) from 0500 h to 1700 h in *E. mathaei* removed from *Porites*: (A) shows the dry weights of the total gut contents and (B) shows the dry weights of the stomach and of the intestine separately. $N = 10$ in all cases.

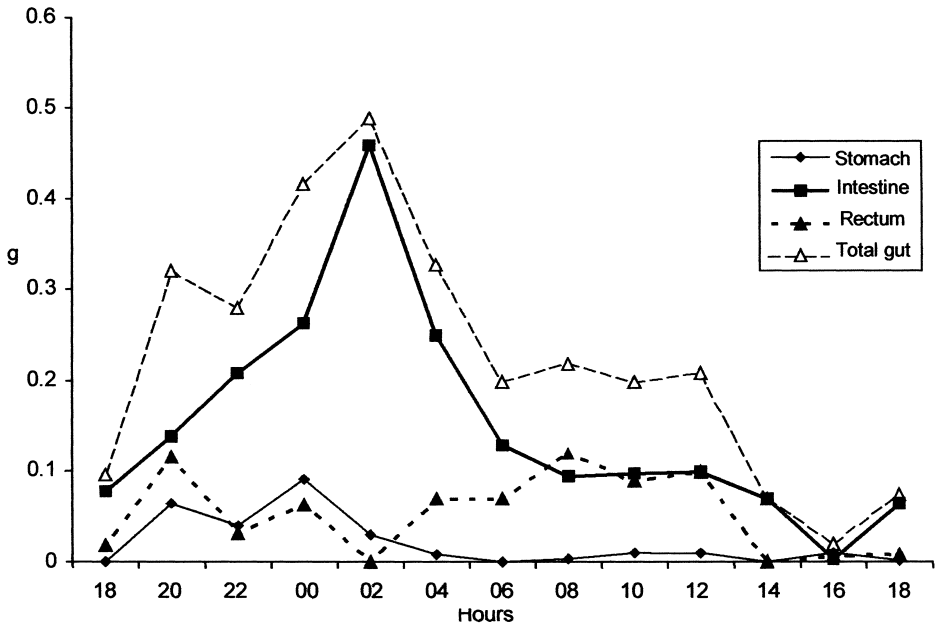

Fig. 4. Temporal variation in the mean dry weight (g) (±S.D.) of the total gut contents and of individual gut sections in *E. mathaei* removed every 2 h over a 24-h period whilst feeding on algal turf in experimental conditions (for visual clarity the error bars are not drawn).

There was a higher density of degraded chlorophyll forms such as chlorophyllides, pheophorbides and pheophytins in the rectum contents of urchins with a very low density of native chlorophyll forms (Table 2). The density of degraded chlorophyll

Table 2
Temporal variation in biochemical composition (±S.D.) of the gut contents of *E. mathaei*[a]

Component	Gut section	0500 h	1700 h	$F_{2,18}$	*P*
$CaCO_3$ (%)	Total gut	73.00±10.00	72.00±26.00	0.02	NS
Assimilated organic matter (%)	Intestine	19.60±5.20	13.00±6.70	4.94	*
Refractory organic matter (%)	Intestine	6.70±6.10	5.80±3.40	0.42	NS
Protein concentration ($\mu g\ mg^{-1}$)	Rectum	38.90±8.40	29.60±7.10	0.49	NS
Lipid concentration ($\mu g\ mg^{-1}$)	Rectum	6.50±0.85	11.01±2.40	22.06	**
Insoluble carbohydrates ($\mu g\ mg^{-1}$)	Rectum	78.37±58.86	30.39±25.11	5.37	*
Soluble carbohydrates ($\mu g\ mg^{-1}$)	Rectum	14.37±9.93	7.20±2.67	5.61	*
Native chlorophyll ($ng\ mg^{-1}$)	Rectum	0.02±0.03	0.033±0.013	3.95	NS
Degraded chlorophyll ($ng\ mg^{-1}$)	Rectum	111.59±7.31	0.381±0.129	13.01	**
Degraded chlorophyll (%)	Total gut	86.00±2.10	92.00±2.00	29.63	***

[a] NS = Not significant; *significant ($P < 0.05$); **highly significant ($P < 0.01$); ***very highly significant ($P < 0.001$).

forms was significantly greater in the rectum of urchins collected at 0500 h than at 1700 h, however, the percentage of degraded forms was higher in the gut contents of urchins collected at 1700 h than in those collected at 0500 h.

3.3. Biochemical composition of gut contents along the digestive tube

The proportions of easily assimilated organic matter, with the mineral and refractory organic matter in each section of the gut are shown in Fig. 5. There was little variation in the percentage of $CaCO_3$ along the digestive tube.

The concentrations of protein, lipid, soluble and insoluble carbohydrates in each section of the gut from *E. mathaei* collected at 0500 h are given in Fig. 6. Protein concentration increased significantly along the digestive tube ($F_{4,6} = 5.15$, $P = 0.0051$). Lipid concentration decreased significantly from the stomach to the rectum ($F_{3,7} = 6.56$, $P = 0.0048$). The lipid concentration was not measured in the oesophagus, as there was not enough organic matter available. The concentration of insoluble carbohydrates was

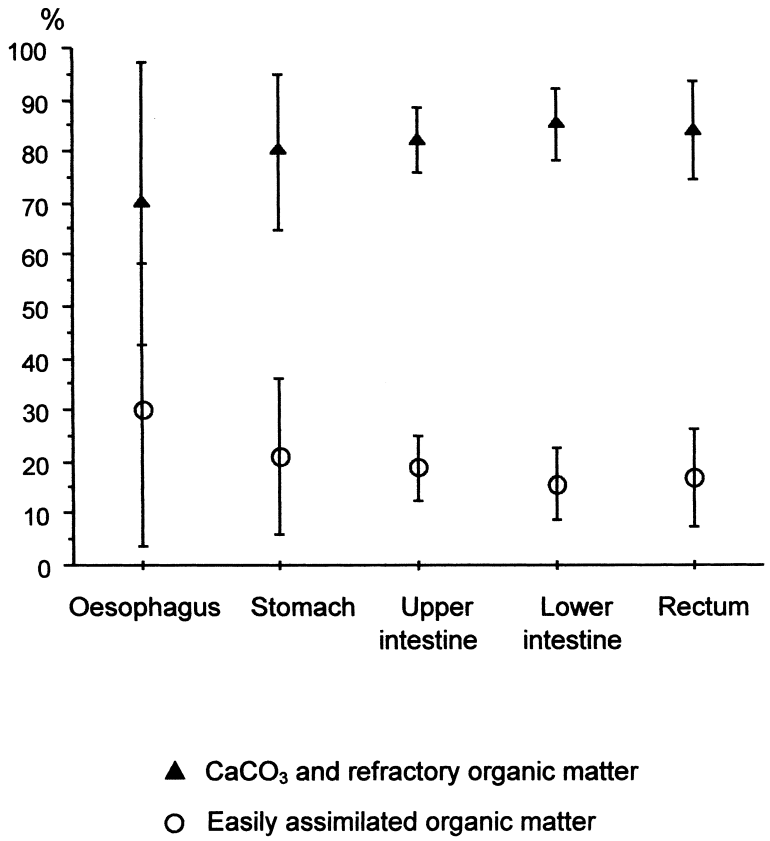

Fig. 5. Variation in mineral and refractory organic matter and of easily assimilated organic matter as a percentage of the total organic matter along the digestive tube of *E. mathaei* removed from *Porites*. $N = 20$.

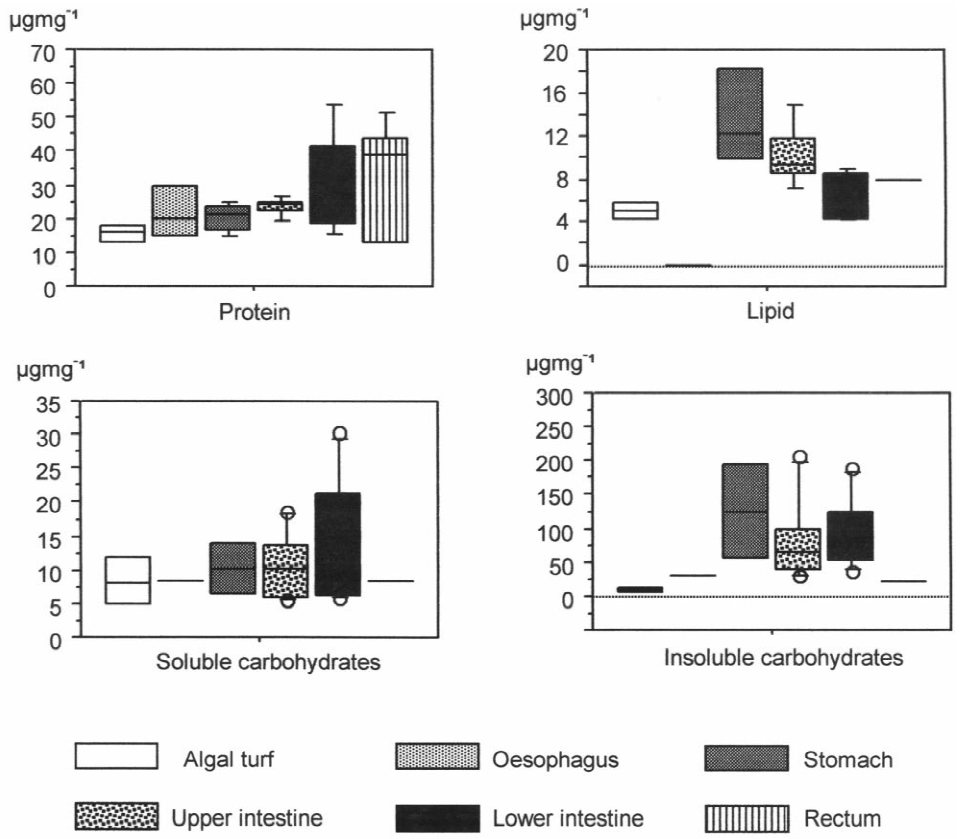

Fig. 6. Box plots showing the biochemical composition of the five parts along the digestive tube of *E. mathaei* and of the algal turf grazed by these urchins. $N = 10$.

considerably greater than that of soluble carbohydrates throughout the gut (Fig. 6). However, when the two types of carbohydrate were analysed together, there was no significant difference in their concentration along the digestive tube ($F = 0.97$, $P = 0.46$).

The concentration of total photosynthetic pigments increased from the stomach (93.4 ng mg^{-1}) to the intestine (328.9 ng mg^{-1}) and then decreased in the rectum (113.3 ng mg^{-1}). The native chlorophyll pigment concentration was low both in the stomach (13.7%) and the rectum (13.9%); but the degraded forms (chlorophyllides, pheophorbides and pheophytins) were present at high concentrations all along the digestive tube with a mean of 86%.

3.4. Comparison between the gut contents and algal turf

The concentrations of protein, lipid, soluble and insoluble carbohydrates in the algal turf collected at 0500 h are also given in Fig. 6. The protein and soluble carbohydrate

concentrations in the stomach contents of *E. mathaei* were not significantly different from their respective concentrations in algal turf (protein: $F = 1.73$, $P = 0.24$; soluble carbohydrates: $F = 1.02$, $P = 0.40$). The lipid and insoluble carbohydrates concentrations of the stomach contents were significantly greater than that of algal turf (lipid: $F = 19.5$, $P = 0.0045$; insoluble carbohydrates: $F = 22.8$, $P = 0.0088$).

Fresh algal turf is composed of 93% chlorophyll in its native forms, in contrast, only 13% of the total pigment composition in the gut contents of *E. mathaei* were chlorophyll native forms.

4. Discussion

This study strongly suggests that *E. mathaei* is mainly a nocturnal grazer, since the weight of organic and inorganic matter in the gut was highest at dawn. Other urchins such as *Diadema antillarum* (Lewis, 1964), *D. setosum* (Lawrence and Hughes-Games, 1972) and *Heterocentrotus mammilatus* (Dart, 1972) found on tropical reefs, also show predominately nocturnal feeding activity.

The easily assimilated organic matter in the gut contents is digested and absorbed as it transits along the digestive tube, there is not, however, a large variation in the amount of $CaCO_3$ along the digestive tube. The $CaCO_3$ gut content in urchins of approximately 35-mm test diameter, indicates an average individual bioerosion of 0.32 g day^{-1}, an estimate of a similar order to that found by McClanahan and Kurtis (1991) on the Kenyan Coast (0.42 g day^{-1}). Given that the mean quantity of $CaCO_3$ eroded by *E. mathaei* on the Moorea fringing reef flat is 0.5 kg m^2 y^{-1} (Peyrot-Clausade et al., 2000) can use the results from urchins collected at dawn to make preliminary estimates of the mean weight of organic matter released. Since the percentage of $CaCO_3$ in the last part of the gut contents is 73%, the total amount of matter released is 0.685 kg m^2 y^{-1}. Of this we can calculate that 0.137 kg m^2 y^{-1} is easily assimilated organic matter (20%) and 0.048 kg m^2 y^{-1} is refractory organic matter (7%). Black et al. (1984) found a similar proportion of inorganic matter (73%) and organic matter (27%) in the gut contents of large *Echinometra* spp. collected at Rottnest Island, Western Australia. If the total carbohydrate fraction in the last part of the digestive tube is 10.3% of the total contents, this suggests that *E. mathaei* release 70.54 g m^2 of carbohydrates per year. Using the same approach, the mean lipid fraction released (6.4% of the total matter) is 43.83 g m^2 y^{-1}, protein (3.4%) is 23.28 g m^2 y^{-1} and total chlorophyll pigments (0.3%) represent 2.04 g m^2 y^{-1}.

The present study shows proteins being expelled from the echinoderm gut, yet this may not reflect the absence of protein digestion and absorption. Although there have been no attempts to study proteases in the gut of *E. mathaei,* protease activity has been observed in the guts of other urchins (e.g., *Strongylocentrotus purpuratus*: Lasker and Giese, 1954; Boolootian and Lasker, 1964; *D. antillarum*: Lewis, 1964; *Echinocardium cordatum*: Kozlovskaya and Vaskovsky, 1970; *Echinus esculentus* and *E. acutus*: Liemans and Dandrifosse, 1972). Therefore, it is reasonable to assume that proteins are broken down by proteolytic activity either secreted by the urchin into the gut or from

bacteria present in the gut. The method used to quantify proteins in this study does not take into account the origin of the protein and thus there may be protein enrichment from mucous secreted by the echinoderm digestive tube. Mucous is secreted that encloses food in large amounts of mucopolysaccharides to prevent abrasion of the gut lining from the calcareous coral that is ingested with the algal turf (Hyman, 1955; Buchanan, 1969; Holland and Ghiselin, 1970). The amount of protein in the digestive tube is the sum of that which is degraded and absorbed from food and that which is secreted as mucous. Further analyses may be required to measure the amino acid content of the gut contents to determine if the protein in algal turf is being degraded to amino acids. Additionally, an assay which involves feeding the urchins radio-labelled algal turf should reveal if the radio-activity is present in the tissues of sea urchins and confirm protease activity and absorption.

The decrease in lipid along the digestive tube is expected because esterases, lipases and phospholipases, that in each case hydrolyse lipid, are known to occur in the digestive tube of echinoids (Vaskovsky and Suppes, 1972). Lawrence (1967) found a high level of lipid in the gut of *Echinometra lucunter* indicating the presence of nutrient reserves in the organ.

The insoluble carbohydrates are not broken down immediately by mastication, as the Aristotle's Lantern causes little mechanical degradation of the organic matter at ingestion, so the sea urchins have to rely upon chemical reactions to break them down (Harmelin-Vivien et al., 1992). The pH of the intestine was shown by Lewis (1964) to be 5.0–6.8. This environment helps decomposition by breaking down algal cell walls rendering the algal turf more available for chemical decomposition. Evidence for further degradation of the organic matter can be shown from the decreasing ratio of insoluble:soluble carbohydrates in the rectum during the day.

The highest concentration of degraded chlorophyll pigments is found in the intestine, suggesting that the decomposition and absorption of these pigments takes place largely in the intestinal section of the alimentary canal. The high concentration of degraded pigments in the digestive tube suggests that the organic matter released by *E. mathaei* contains little non-degraded material.

In addition to enzymes produced in the gut of *E. mathaei*, some digestion might result from the activity of intestinal bacteria. The presence of intestinal bacteria has been demonstrated in other Echinoids (e.g., Prim and Lawrence, 1975; Unkles, 1977) and evidence for the potential involvement of these in digestion is compelling (Lasker and Giese, 1954; Castro, 1969). However, no work has yet been done on the digestive capabilities of bacteria in the gut of *Echinometra* spp.

The protein- and carbohydrate-rich faeces of sea urchins provide a good supply of food for coprophagous fish (Bailey and Robertson, 1982). The faeces also provide a physical substrate for bacteria and fungi to colonise, and once resuspended in the water column the faeces may serve as food for suspension and filter feeders (Hawkins and Lewis, 1982). The bacteria decomposing the plant residue are consumed by flagellates and ciliates, whilst the fungi may be eaten by nematodes (Fenchel, 1970), thus, outlining the importance of *Echinometra* in the cycling of food to the benthic macrofauna, microflora and fauna. Even though *E. mathaei* causes considerable bioerosion by ingesting hard substrate whilst feeding, the sediments produced may accumulate in

cavities promoting internal cementation and strengthening of the reef (Glynn, 1997), and this bioerosion renders new substrates available on the reef that in turn may be colonised by diverse sedentary species.

Acknowledgements

This work was funded by the French National Programme on Coral Reef (PNRCO-INSU). We thank Jenny Gill, Simon Jennings, Phil Stephens and Dan White and two anonymous reviewers for their critical reviews of the manuscript and many helpful suggestions. [SS]

References

Bailey, T.G., Robertson, D.R., 1982. Organic and caloric levels of fish faeces relative to its consumption by coprophagous reef fishes. Mar. Biol. 69, 45–50.

Bak, R.P.M., 1994. Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. Coral Reefs 13, 99–103.

Black, R., Codd, C., Hebbert, D., Vink, S., Burt, J., 1984. The functional significance of the relative size of Aristotle's lantern in the sea urchin *Echinometra mathaei* (de Blanville). J. Exp. Mar. Biol. Ecol. 77, 81–97.

Blight, E.G., Dyer, W.J., 1959. A rapid method of total lipids extraction and purification. Can. J. Biochem. Physiol. 37, 911–917.

Boolootian, R.A., Lasker, R., 1964. Digestion of brown algae and the distribution of nutrients in the purple sea urchin *Stronglyocentrotus purparatus*. Comp. Biochem. Physiol. 11, 273–289.

Buchanan, J.E., 1969. Feeding and the control of volume within the tests of regular sea urchins. J. Zool., London 159, 51–64.

Castro, P., 1969. In: Jangoux, M., Lawrence, J.M. (Eds.), 1982. Echinoderm Nutrition. A.A. Balkema, Rotterdam, Cited therein.

Conand, C., Heeb, M., Peyrot-Clausade, M., Fontaine, M.-F., 1998. Bioerosion by the sea urchin *Echinometra* on La Réunion reefs (Indian Ocean) and comparison with Tiahura reefs (French Polynesia). In: Mooi, R., Telford, M. (Eds.), Echinoderms: San Francisco. A.A. Balkema, Rotterdam, pp. 609–615.

Dart, J.K.G., 1972. Echinoids, algal lawn and coral recolonization. Nature 239, 50–51.

Downing, N., El-Zahr, C.R., 1987. Gut evacuation and filling rates in the rock-boring sea urchin, *Echinometra mathaei*. Bull. Mar. Sci. 41, 579–584.

Dubois, M., Gilles, K.A., Hamilton, J.K., Rebes, P.A., Smith, F., 1956. Colorimetric method for determination of sugar and related substances. Anal. Chem. 28, 350–356.

Farmanfarmaian, A., Phillips, J.H., 1962. Digestion, storage, and translocation of nutrients in the purple sea urchin (*Strongylocentrotus purpuratus*). Biol. Bull. Mar. Biol. Lab. (Woods Hole) 123, 105–120.

Fenchel, T., 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. Limnol. Oceanogr. 15, 14–20.

Frigge, M., Hoaglin, D.C., Iglewicz, B., 1989. Some implementations of Boxplot. The American Statistician 43, 50–54.

Galzin, R., Pointier, J.P., 1985. Moorea Island, Society Archipelago. Proc. 5th Int. Coral Reef Symp. 1, 73–101.

Glynn, P.W., 1997. Bioerosion and coral reef growth: a dynamic balance. In: Birkeland, C. (Ed.), Life and Death of Coral Reefs. Chapman and Hall, New York, pp. 68–95.

Handa, N., Yanagi, K., Matsunaga, K., 1972. Distribution of detrital materials in the Western Pacific Ocean and their biochemical nature. Mem. Instit. Ital. Idrobiolo. 29, 53–71.

Harmelin-Vivien, M., Peyrot-Clausade, M., Romano, J.-C., 1992. Transformation of algal turf by echinoids and scarid fishes on French Polynesian coral reefs. Coral Reefs 11, 45–50.

Hawkins, C.M., 1981. Efficiency of organic matter absorption by the tropical echinoid *Diadema antillarum* Phillipi fed non-macrophytic algae. J. Exp. Mar. Biol. Ecol. 49, 245–253.

Hawkins, C.M., Lewis, J.B., 1982. Ecological energetics of the tropical sea urchin *Diadema antillarum* Phillipi in Barbados. West Indies Estuar. Coast. Shelf Sci. 15, 645–669.

Holland, N.D., Ghiselin, M.T., 1970. A comparative study of the mucous cells in thirty-seven species of the class Echinoidea (Echinodermata). Biol. Bull. Mar. Biol. Lab. (Woods Hole) 138, 286–305.

Hubbard, D.K., Miller, A.I., Scaturo, D., 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, US Virgin Islands): applications to the nature of reef systems in the fossil record. J. Sedim. Petrol. 60 (3), 335–360.

Hyman, L., 1955. The Invertebrates. Echinodermata, Vol. IV. McGraw-Hill, New York.

Khamala, C.P.M., 1971. Ecology of *Echinometra mathaei* (Echinoidea: Echinodermata) at Diani Beach. Kenya Mar. Biol. 11, 167–172.

Kozlovskaya, E.P., Vaskovsky, V.E., 1970. A comparative study of proteinases of marine invertebrates. Comp. Biochem. Physiol. 34, 137–142.

de La Giraudière, I., Laborde, P., Romano, J.C., 1989. HPLC determination of chlorophylls and breakdown-products in surface microlayers. Chem. 26, 189–204, March.

Lasker, R., Giese, A.C., 1954. Nutrition of the sea urchin *Strongylocentrotus purpuratus*. Biol. Bull. 106, 328–340.

Lawrence, J.M., 1967. Lipid reserves in the gut of three species of tropical urchins. Carib. J. Sci. 7, 65–68.

Lawrence, J.M., Hughes-Games, L., 1972. The diurnal rhythm of feeding and passage of food through the gut of *Diadema setosum* (Echinodermata: Echinoidea). Israel J. Zool. 21, 13–16.

Lewis, J.B., 1964. Feeding and digestion in the tropical sea urchin *Diadema antillarum* Phillipi. Can. J. Zool. 42, 549–557.

Liemans, M., Dandrifosse, G., 1972. Equipement digestif enzymatique de quelques échinodermes. Arch. Intern. Physiol. Bioch. 80, 847–851.

Lowry, O., Rosebrough, N.M., Fan, A.L., Randall, R.J., 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. 193, 265–275.

McClanahan, T.R., 1995. A coral reef ecosystem–fisheries model: impacts of fishing intensity and catch selection on reef structure processes. Ecol. Model. 80, 1–19.

McClanahan, T.R., Muthuga, N.A., 1988. Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiol. 166, 269–276.

McClanahan, T.R., Kurtis, J.D., 1991. Population regulation of the rock-boring sea urchin *Echinometra mathaei* (de Blainville). J. Exp. Mar. Biol. Ecol. 147, 121–146.

McClanahan, T.R., Nugues, M., Mwachireya, S., 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. J. Exp. Mar. Biol. Ecol. 184, 237–254.

Nishihira, M.Y., Sato, Y., Arakaki, Y., Tsuchiya, M., 1991. In: Ecological Distribution and Habitat Preference of the Sea Urchin *Echinometra mathaei* on the Okinawan Coral Reefs. Biology of Echinodermata. Balkema, Rotterdam, pp. 91–104.

Palumbi, S.R., Metz, E.C., 1991. Strong reproductive isolation between closely related tropical sea urchins (genus *Echinometra*). Mol. Biol. Evol. 8, 227–239.

Peyrot-Clausade, M., Chabanet, P., Conand, C., Fontaine, M.F., Letourneur, Y., Harmelin-Vivien, M., 2000. Sea urchin and fish bioerosion in la Réunion and Moorea reefs. Bull. Mar. Sci. 66 (2), 477–485.

Polunin, N.V.C., 1988. Efficient uptake of algal production by a single resident herbivorous fish on the reef. J. Exp. Mar. Biol. Ecol. 123, 61–76.

Polunin, N.V.C., Harmelin-Vivien, M., Galzin, R., 1995. Contrasts in algal food processing among five herbivorous coral-reef fishes. J. Fish Biol. 47, 455–465.

Prim, P., Lawrence, J.M., 1975. Utilization of marine plants and their constituents by bacteria isolated from the gut of echinoids (*Echinodermata*). Mar. Biol. 33, 167–173.

Reaka-Kudla, M., Feingold, J.S., Glynn, W., 1996. Experimental studies of rapid bioerosion of coral reefs in the Galapagos. Coral Reefs 15, 101–107.

Russo, A.R., 1980. Bioerosion by two rock boring echinoids (*Echinometra mathaei* and *Echinostrephus aciculatus*) on Enewetak Atoll, Marshall Islands. J. Mar. Res. 38, 99–110.

Statview 5.1, 1998. Manuel utilisateur. Abacus Concepts, Inc., Berkeley, CA.
Super Anova 1.11, 1991. Manuel utilisateur. Abacus Concepts, Inc., Berkeley, CA.
Underwood, A.J., 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 19, 513–605.
Unkles, S.E., 1977. Bacterial flora of the sea urchin *Echinus esculentus*. Appl. Env. Microbiol. 34, 347–350.
Vaskovsky, V.E., Suppes, Z.S., 1972. Phospholipases of marine invertebrates. I. Distribution of phosphoplipase A. Comp. Biochem. Physiol. 43, 601–609.
Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall, New York.