

Detritus as food for grazing fishes on coral reefs

David J. Crossman

School of Biological Sciences, University of Auckland, Private Bag 90219, Auckland, New Zealand

J. Howard Choat

Department of Marine Biology, James Cook University, Townsville, Queensland 4811, Australia

Kendall D. Clements

School of Biological Sciences, University of Auckland, Private Bag 90219, Auckland, New Zealand

Tom Hardy and Jason McConochie

School of Engineering, James Cook University, Townsville, Queensland 4811, Australia

Abstract

Algal turf assemblages of the northern Great Barrier Reef, Australia, were sampled to determine the nutritional value of detritus and algae. Samples were collected with a suction apparatus across an exposure gradient from (1) the reef crest at highly exposed outer barrier reefs, (2) the reef crest of moderately exposed midshelf reefs, and (3) the reef slope of sheltered midshelf reefs. The biomass of algae and detritus decreased from sheltered midshelf reefs to moderately exposed midshelf reefs to highly exposed outer barrier reefs. This decrease was significant only for detritus ($P < 0.005$). Wave energies were calculated across the exposure gradient with the wave model WAMGBR. Detrital mass was inversely correlated with predicted wave energies and fitted a polynomial relationship ($P < 0.001$) and explained 52.8% of the variation. A similar relationship was also found between algal mass and wave energy ($P < 0.001$) but only explained 30.0% of the variation. The nutritional value of samples in protein amino acids and starch was assessed. The amino acid composition of detritus and algae was similar and not considered nutritionally different, whereas the concentration of protein amino acids was significantly ($P < 0.001$) higher in detritus ($21.2 \pm 2.0 \text{ mg g}^{-1}$) than in algae ($11.8 \pm 1.0 \text{ mg g}^{-1}$). Starch content was significantly ($P < 0.05$) higher in algae ($7.7 \pm 0.9 \text{ mg g}^{-1}$) than in detritus ($6.0 \pm 1.0 \text{ mg g}^{-1}$). These results demonstrate that detritus is a potentially valuable food source to grazing fishes on coral reefs.

Two predominant views of coral reef trophic biology are that shallow-water epilithic algal communities (EAC) are the major sites of primary production and that grazing fish and invertebrates are the predominant consumers of this resource (Hatcher 1997). Grazing fish are classified as herbivores and are assumed to derive the significant component of their nutrition through consumption, digestion, and assimilation of living turf algae (Hatcher 1983a, 1988, 1997; Horn 1989; Polunin and Klumpp 1992b; Polunin 1996; Hixon 1997). This paradigm is largely based on feeding observations and the negative impacts grazing fishes have on algal assemblages, with only filamentous and coralline algae being able to tolerate the constant grazing pressure (Steneck 1988; Horn 1989).

EAC are a complex assemblage that consists of (1) a turf of filamentous and crustose algae and (2) detrital material including dead organic matter (e.g., algae, fish feces, and

coral mucus), inorganic material, microbes, microalgae (diatoms, dinoflagellates, and cyanobacteria), and associated meiofauna (Hatcher 1983b, Moriarty et al. 1985; Alongi 1988; Steneck 1988; Ducklow 1990; Choat 1991; Sorokin 1995). This is a complex food resource with many potential food items. It is possible that components of this food resource other than turf algae contribute to the nutrition of grazing fish.

The dominant elements of the herbivorous fish fauna on the Great Barrier Reef (GBR), Australia, are surgeonfishes (Acanthuridae) and parrotfishes (Scaridae) (Russ 1984a,b; Steneck 1988; Horn 1989). Some species do target turf algae, as identified from gut content analysis (Robertson and Gaines 1986). However, the most abundant members of the grazing fauna are usually surgeonfishes of the genus *Ctenochaetus* and parrotfishes of the genus *Scarus* (Choat and Bellwood 1985; Meekan and Choat 1997). For these taxa, the largest component of their diet is calcareous sediments and nondescript organic material with very little evidence of algal consumption (Robertson and Gaines 1986; Nelson and Wilkins 1988; Bellwood 1996). Choat and Clements (1998) have suggested that detritus may be high in protein and be of significant food value to grazing fishes. This view is reinforced by the specialized dentition that enables detritus feeding that is seen in abundant grazing fishes such as *Ctenochaetus striatus* (Purcell and Bellwood 1993).

Acknowledgments

We wish to thank Will Robbins for invaluable field assistance, Will Robbins and Steve Purcell for construction of the sediment sampling apparatus, Garth Cooper for use of his amino acid analyser and biochemical expertise, and Fleur Weaver for laboratory assistance. The Australian Museum made critical resources available through the Lizard Island Research Station. Support was provided by the Australian Research Council through a grant awarded to J.H.C.

Samples of detritus and algae from the EAC were collected from the northern GBR to address two main hypotheses: (1) detritus is potentially of significant nutritional value for grazing fishes, because it contains higher concentration of protein amino acids than algae; and (2) the abundance of detrital and algal food resources is negatively correlated with exposure. To test these hypotheses, samples were collected from the crests of reefs across an energy gradient that extended from exposure to open oceanic swells to sheltered sites on reefs lying within the GBR lagoon. The significance of this exposure gradient is reflected in a number of distributional and demographic features of grazing fishes (Gust et al. 2001). Wave data as a measure of exposure in or near the reef matrix of the GBR are almost nonexistent. A computer wave-generation model was used to numerically predict specific wave energies across the gradient sampled (Hardy et al. 2000). The sampling design also included a biological element with samples from inside and outside the territories of the surgeonfish *Acanthurus lineatus*, which is one of the most abundant herbivorous fish on the reef.

The nutritional quality of the detrital and algal elements from the EAC is poorly known (Alongi 1988; Choat and Clements 1998). Generally, estimates of total nitrogen and carbon are used as indicators of food quality without due consideration of the molecular form of these elements (e.g., Horn 1989; Galetto and Bellwood 1994; Wilson and Bellwood 1997). Much of this nitrogen and carbon may be in a form unavailable to fish (Clements 1997; Choat and Clements 1998; Crossman et al. 2000). In the present study, the measurement of total extractable amino acids (TAA) and starch were used to estimate the nutritional value of samples. Vertebrates, including fishes, have the necessary enzymes to digest and assimilate proteins and starches (Stevens and Hume 1995). Therefore, these parameters allow the estimation of nitrogen and carbohydrate potentially available to consumers via endogenous means. The estimation of TAA (which will include proteins, peptides, and free amino acids) was of particular interest, because nitrogen is often argued to be a limiting nutrient (Horn 1989; Choat 1991; White 1993).

Material and Methods

Sample design, collection, and processing—Detritus by definition is dead organic matter but is rarely found without attached or embedded microorganisms (Bowen 1987). A broad definition of the term is used in this work to include dead organic matter, inorganic material, microorganisms, microalgae, and associated meiofauna. These components would be difficult to separate out and quantify individually.

Samples of epilithic algae and associated detritus were collected across an exposure gradient driven by a prevailing southeasterly winds at south latitude 14°14' on the GBR (Fig. 1), from 14 to 24 December 1996. The sampling gradient consisted of outer shelf (exposed) reef crests, midshelf (partially exposed) reefs, and leeward (sheltered) shallow reef slopes. A wave-generation model was used to predict the creation, growth, dissipation, and propagation of surface waves. This model is based on WAM (WAVE Model), which

has a demonstrated capacity to accurately model waves in a wide variety of conditions (Komen et al 1994). The output of the model is a directional wave spectrum, information that can be condensed into significant wave height (H_s), peak period (T_p), and mean direction (θ_m). The significant wave height is used as a parameter of the wave energy of the wave field and is approximately equal to the average of the largest third of the waves. To increase both the extent and the resolution of the wave predictions a system of three nested grids with resolutions of 20, 4, and 0.8 min of arc was used. The outer grid extended over most of the Coral Sea (the oceanic boundary to the GBR) and used a coarse resolution to provide boundary conditions for the intermediate grid with smaller extent but better resolution. This intermediate grid in turn provided boundary conditions for the inner grid, with the smallest extent but the best resolution. Output is available on this inner grid at a resolution of ~1,500 m.

Significant alterations and additions have been incorporated to adapt WAM for use in the complex GBR region. The most important addition is the reef parameterization scheme, which is a technique to include the dissipative effects of features such as coral reefs that are too small to be adequately resolved in the numerical grid. Model outputs may thus contain the effects of features much smaller than grid resolution. The new model WAMGBR is presented in Hardy et al (2000).

The standing crop of epilithic algae on reef crests is enhanced by the territorial behavior of the herbivorous surgeonfish *A. lineatus* (Choat 1991; Polunin and Klumpp 1992a). Most grazing fishes occur on reef crests, including the surgeonfish *A. lineatus* (Choat 1991; Polunin and Klumpp 1992a). This species enhances the algal standing crop in reef crest habitats by excluding other grazing fishes from its extensive feeding territories (Choat and Bellwood 1985). Partitioning of sampling between the insides and outsides *A. lineatus* territories allowed us to determine the relationship between *A. lineatus* territories and algal standing crop and the influence of increased algal crop on detrital load on reef substrata. Samples were taken from *A. lineatus* territories and adjacent nonterritorial areas at Day Reef north pass and No-Name Reef north pass on outer reefs and at North Reef, South Island, and Washing Machine on midshelf reefs. Additional samples were taken outside *A. lineatus* territories on Day Reef Front (outer barrier) and North Direction Island (midshelf) and inside *A. lineatus* territories at Day Reef north corner (Table 1). Sheltered reef sites (Granite Bluffs and Watson's Bay) contain no territory designation, because *A. lineatus* is not found at these locations. The program provided a total of 19 samples from outer barrier sites (8 outside territories and 11 inside), 24 from midshelf sites (15 outside and 9 inside), and 10 from sheltered sites (Fig. 1, Table 1). All sites had a depth of <5 m mean high water. The analytical program (dry weight, ash, TAA, and starch) is shown in Table 1. A complete set of measurements was not possible for all samples because of small amounts of material collected at some outer barrier sites.

Detrital and algal samples were collected from within a PVC ring with internal area of 100 cm² that was arbitrarily placed and pinned to the substratum. Detritus was collected by use of the electronic sampler and methodology described

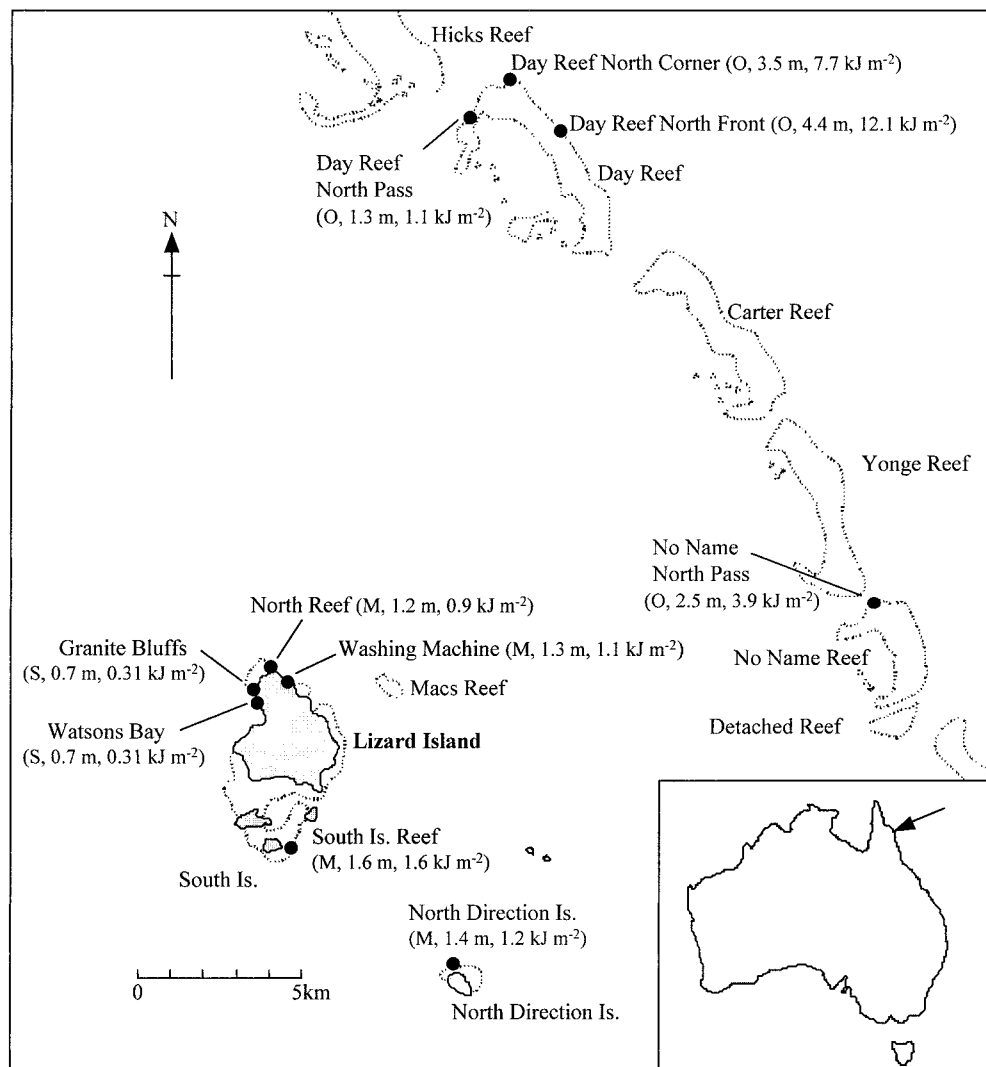


Fig. 1. Map of Lizard Island and surrounding reefs indicating location of sampling sites. O, outer barrier reef; M, moderately exposed midshelf reef; S, sheltered midshelf reef. Numbers within brackets are the mean wave heights and wave energy predicted at the sites by the computer model WAMGBR. Arrow on the insert indicates the location of Lizard Island off the Australian coast.

by Purcell (1996). A sampling period of 60 s was used to brush and vacuum the sampling ring clean of EAC-bound sedimentary material without removal of the attached algae. This sedimentary material was collected in a prefilter that trapped coarse particles and a plastic bag that collected fine particles. Algal samples were collected by immediately scraping the same area to a depth of 2 mm (approximated visually) for 60 s with an angled steel tube fitted to the intake hose of the electronic sampler. The detached algae were vacuumed and retained in a simple filter that contained a 220- μm mesh screen fitted between the terminus and the pump.

Upon return to the field station detritus samples (prefilter + plastic bag) were poured into settlement cylinders (50 cm high and 15 cm diameter) fitted with 63- μm screens that allowed water to pass through but retained the detrital sample. All invertebrates distinguishable to the naked eye (>3

mm) were removed. The sample was then rinsed briefly with distilled water and transferred to sample vials and frozen. The macroalgae in each collection filter was rinsed briefly with distilled water and transferred to vials and frozen. The mean dry weight and range of detritus and algae collected for outer barrier outside territories (OBO) detritus were 0.069 and 0.019–0.175 g, those for OBO algae were 0.451 and 0.104–1.171 g, those for outer barrier inside territories (OBI) detritus were 0.2 and 0.007–0.735 g, those for OBI algae were 1.62 and 0.594–2.875 g, for midshelf outside territories (MSO) detritus was 0.466 and 0.077–1.319 g, those for MSO algae were 1.866 and 0.364–3.547 g, those for midshelf inside territories (MSI) detritus were 0.897 and 0.078–2.727 g, those for MSI algae were 2.589 and 1.165–4.353 g, those for sheltered midshelf (S) detritus were 2.649 and 0.768–4.26 g, and those for S algae were 4.608 and 0.456–15.733 g.

Table 1. Number of samples collected from each site and analysed for nutrients.

Resource territory	Dry Weight				Ash				TAA				Starch			
	Detritus		Algae		Detritus		Algae		Detritus		Algae		Detritus		Algae	
	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In
Outer Barrier sites																
Day Reef north pass	2	3	2	3	2	1	1	3	2	2	2	3			1	3
Day Reef front	3		3		2		2		3		2		1		2	
Day Reef north corner		5		5		5		5		5		5	4			5
No-name reef north pass	3	3	3	3		2	2	3	2	2	2	3	3	1	2	3
Total	8	11	8	11	4	8	5	11	7	9	6	11	4	5	5	11
Midshelf sites																
North Direction Island	6		6		6		6		6		6		6		6	
North Reef	3	2	3	3	3	2	3	3	3	2	3	3	3	2	3	3
South Island	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Washing Machine	3	3	3	3	2	2	3	3	3	3	3	3	2	3	3	3
Total	15	8	15	9	14	7	15	9	15	8	15	9	14	8	15	9
Sheltered sites*																
Granite Bluffs	5		5		5		5		5		5		5		5	
Watson's Bay	5		5		5		5		5		5		5		5	
Total	10		10		10		10		10		10		10		10	

* Note sheltered sites do not contain *Acanthurus lineatus* territories. TAA, total-extractable amino acids; Out, outside *A. lineatus* territories; In, inside *A. lineatus* territories.

Sample preparation—Frozen substratum samples were dried to a constant weight with a Dura-Dry freeze drier. The dried material was then ground to a fine powder in a ball mill (Retsch mixer mill MM2) and stored desiccated in a freezer. Proteins were extracted by weighing accurately ~20 mg of the ground sample into Eppendorf tubes and adding 0.6 ml of 1 M NaOH. Tubes were then mixed by vortexing and placed on a rocker for 12 h. After the extraction period tubes were centrifuged for 5 min at 12,000 × g to pellet particulate material and the supernatant removed for amino acid analysis. For ash and starch analysis, ground samples were used without further treatment.

Analytical methods—Amino acid analysis was performed as described in detail elsewhere (Crossman et al. 2000).

Briefly, acidified protein extracts were loaded into hydrolysis tubes dried under vacuum and hydrolyzed in 6 M HCl and 1% phenol at 150°C for 60 min under nitrogen by use of a PICO-TAG Work Station (Waters). Hydrolyzed samples were derivatized with phenylisothiocyanate and quantified by reverse-phase high-performance liquid chromatography (HPLC) that used a 421 amino acid analyzer coupled to a 172 microbore HPLC (Applied Biosystems). Ash content of the dried samples was determined by combusting 50 mg samples at 500°C in a Kotter kiln for 16 h. Starch content was measured by use of the dimethyl sulfoxide starch assay from Megazyme, as described in Crossman et al. (2000).

Literature amino acid values—Literature values for protein amino acids presented in the discussion are expressed

Table 2. Nutritional analysis of epilithic algal communities.

		OB O	OB I	MS O	MS I	S
Ash % (SE)						
Detritus	\bar{X}	84.3 (5.7)	80.2 (1.8)	79.5 (2.5)	80.7 (2.2)	82.5 (2.4)
Algae	\bar{X}	78.8 (1.8)	80.5 (1.6)	85.7 (2.6)	86.5 (1.3)	80.9 (2.4)
TAA mg g ⁻¹ (SE)						
Detritus	\bar{X}	24.8 (4.5)	17.8 (2.9)	21.4 (4.6)	22.6 (6.0)	19.1 (3.5)
Algae	\bar{X}	12.0 (2.8)	13.9 (1.0)	11.2 (2.5)	11.3 (1.6)	8.9 (0.9)
Starch mg g ⁻¹ (SE)						
Detritus	\bar{X}	4.8 (1.3)	6.1 (1.3)	9.1 (2.7)	6.0 (1.5)	2.9 (0.4)
Algae	\bar{X}	10.8 (2.1)	8.7 (2.4)	5.0 (1.5)	5.1 (1.0)	11.3 (2.1)

OB O, outer barrier outside territories; OB I, outer barrier inside territories; MS O, midshelf outside territories; MS I, midshelf inside territories; S, Sheltered; TAA, total extractable amino acids; \bar{X} , mean; SE, standard error.

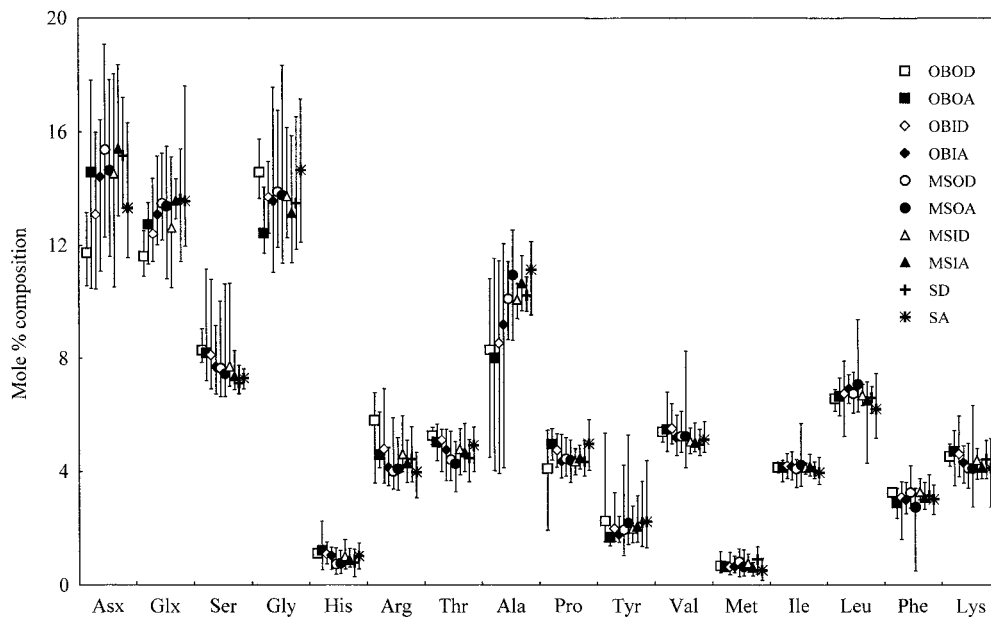


Fig. 2. Means and ranges for mole percent amino acid compositions of detritus and algae from different locations. Abbreviations: OBOD, outer barrier outside detritus; OBOA, outer barrier outside algae; OBID, outer barrier inside detritus; OBIA, outer barrier inside algae; MSOD, midshelf outside detritus; MSOA midshelf outside algae; MSID midshelf inside detritus; MSIA midshelf inside algae; SD, sheltered detritus; SA, sheltered algae; Asx, aspartic acid and asparagine; Glx, glutamic acid and glutamine; Ser, serine; Gly, glycine; His, histidine; Arg, arginine; Thr, threonine; Ala, alanine; Pro, proline; Tyr, tyrosine; Val, valine; Met, methionine; Ile, Isoleucine; Leu, leucine; Phe, phenylalanine; and Lys, lysine.

per dry weight and required modification from the original sources. Crustacean and fish values were calculated from Silva and Chamul (2000) and are based on crude protein measurements of the most edible portions. It is assumed that crude protein values are equivalent to total protein amino acids. Values from Cowie and Hedges (1992) were calculated by multiplying amino acid nitrogen data by the protein conversion factor of 6.25.

Statistical analysis—Two a priori hypotheses were tested: (1) detritus contains a higher concentration of protein amino acids than algae and (2) abundance of detrital and algal food resource is negatively correlated with the wave exposure of the location (e.g. sheltered > midshelf > outer barrier).

Hypothesis (1): A two-way analysis of variance (ANOVA) was used to test for differences in the concentration of amino acids between resource (algae and detritus) and location (OBO, OBI, MSO, MSI, and S). Planned comparisons were used to test for differences in the amino acid concentrations in detritus and algae at the different locations.

Hypothesis (2): ANOVA was used to test for differences among the locations (OBO, OBI, MSO, MSI, and S) for detritus dry weight (g m^{-2}), total detritus amino acids (mg m^{-2}), total detritus starch (mg m^{-2}), algal dry weight (g m^{-2}), total algal amino acids (mg m^{-2}), and total algal starch (mg m^{-2}). Where significant differences were found, planned comparisons were employed to examine where the effect occurred. Nonlinear regression was also performed on the dry weight of detritus and algae against the wave energy of

the sites by use of a first-order inverse polynomial of the form $y = y_o + a/x$, where y is the dry weight of either detritus or algae and x is the wave energy found at the sites.

A two-way ANOVA was employed to test for differences in starch concentration between resource (detritus and algae) and location (OBO, OBI, MSO, MSI, and S). ANOVA was used to test for differences among the locations (OBO, OBI, MSO, MSI, and S) for detritus amino acid concentration (mg g^{-1}), detritus starch concentrations (mg g^{-1}), detrital ash (%), algal amino acid concentration (mg g^{-1}), algal starch concentrations (mg g^{-1}), and algal ash (%). Where significant differences were found, Tukey's HSD for unequal N was used to examine where the effect occurred, because there was no a priori prediction about these tests.

All statistical analysis was carried out on the computer package Statistica version 5.0 (Statsoft). Where data did not meet the assumptions of normalcy or homogeneity of variances the data were (\log_{10}) transformed.

Results

The ash, amino acid, and starch concentrations in detritus and algae from the EAC are presented in Table 2. The percentage of ash is fairly uniform among the samples, with no significant difference between detritus and algae (2-way ANOVA $F_{1,77} = 0.635$, $P = 0.428$). There was also no significant difference between locations for detrital (ANOVA $F_{4,32} = 0.670$, $P = 0.618$) or algal ash (ANOVA $F_{4,45} = 2.00$, P

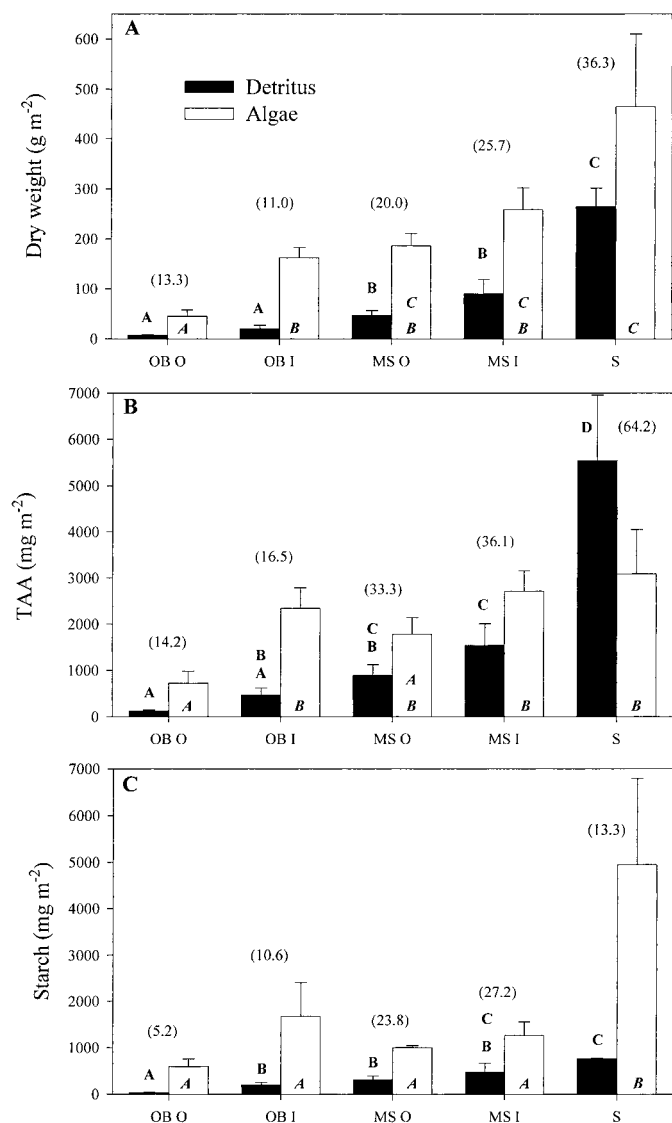


Fig. 3. (A) Dry weight of detritus and algae mass found per unit area (g m^{-2}) at each location. ANOVA showed detritus varied significantly between locations (ANOVA $F_{4,47} = 21.8, P < 0.001$); capital letters above detritus bars show statistical groupings with bars having different letters significantly different (planned comparisons $P < 0.005$); bars with the same letter are not significantly different ($P > 0.05$). ANOVA showed algae varied significantly between locations (ANOVA $F_{4,48} = 11.3, P < 0.001$); italicized capital letters within algal bars show statistical groupings with bars having different letters significantly different (planned comparisons $P < 0.05$). (B) Total extractable amino acids found per unit area (mg m^{-2}) in detritus and algae for each location. ANOVA showed that total detritus amino acids varied significantly between locations (ANOVA $F_{4,44} = 14.2, P < 0.001$); capital letters above detritus bars show statistical groupings with bars having different letters significantly different (planned comparisons $P < 0.05$). ANOVA showed total algal amino acids varied significantly between locations (ANOVA $F_{4,46} = 2.66, P = 0.044$); italicized capital letters within algal bars show statistical groupings with bars having different letters significantly different (planned comparisons $P < 0.05$). (C) Total starch found per unit area (mg m^{-2}) in detritus and algae for each location. ANOVA showed that total detritus starch varied significantly between locations (ANOVA $F_{4,36} = 9.37, P < 0.001$); capital letters above detritus bars show statistical groupings with

$= 0.111$). The concentration of amino acids was, on average, about two times higher in the detritus ($21.2 \pm 2.0 \text{ mg g}^{-1}$) compared with the algae ($11.8 \pm 1.0 \text{ mg g}^{-1}$). This was found to be highly significant (2-way ANOVA $F_{1,90} = 17.8, P < 0.001$). Planned comparisons showed that detritus was significantly higher in amino acids than algae at the following locations: OBO ($P = 0.036$), MSO ($P = 0.004$), and S ($P = 0.029$) but not at MSI ($P = 0.076$) and OBI ($P = 0.567$). No significant difference was found in the amino acid concentration between the locations for detritus (ANOVA $F_{4,44} = 0.377, P = 0.824$) or algae (ANOVA $F_{4,46} = 0.338, P = 0.851$). The mole percentage of specific amino acids found in the detritus and algae at different locations are very similar (see Fig. 2), and observed differences are not considered biologically significant. Starch concentration was found to be significantly higher (see Table 2, two-way ANOVA $F_{1,81} = 4.83, P = 0.031$) in the algae ($7.7 \pm 0.9 \text{ mg g}^{-1}$) compared with the detritus ($6.0 \pm 1.0 \text{ mg g}^{-1}$), but this depended on location, as shown by significant interaction effect (two-way ANOVA $F_{4,81} = 4.14, P = 0.004$) and was only significant at sheltered locations (Tukey's HSD $P = 0.014$). There was no significant difference between locations for detrital starch concentrations (ANOVA $F_{4,36} = 1.43, P = 0.244$). However, there was a significant difference in algal starch concentration between locations (ANOVA $F_{4,45} = 3.80, P = 0.010$), but this was only significantly different between S and MSO (Tukey's HSD $P = 0.045$).

Detrital mass varied across the continental shelf and was in inverse proportion to the wave exposure of the locations (Fig. 3). Most detritus was found in sheltered midshelf sites, with moderate levels at moderately exposed midshelf sites and lowest levels at outer barrier sites. This trend was highly significant ($P < 0.005$, Fig. 3A). The food value of the detritus as measured in TAA per unit area (mg m^{-2}) followed a similar trend and was also significant ($P < 0.05$, see Fig. 3B). The total amounts of starch found per unit area (mg m^{-2}) seem to also follow a similar trend, but this was not as clear statistically (see Fig. 3C).

Algal mass also appears to vary across the continental shelf inversely in proportion to the wave exposure of the locations. Most algal mass was found in sheltered midshelf sites, with moderate levels at moderately exposed midshelf sites and lowest levels at outer barrier sites; however, this trend was not significant at the 0.05% level (Fig. 3A). Algal food quantity parameters total algal amino acids per unit area (mg m^{-2}) and total starch per unit area (mg m^{-2}) did not follow any clear trend (see Fig. 3B,C). However, there was significantly more algal material per unit area and total algal

←

bars having different letters significantly different (planned comparisons $P < 0.01$); bars with the same letter are not significantly different ($P > 0.05$). ANOVA showed that total algal starch varied significantly between locations (ANOVA $F_{4,45} = 5.56, P = 0.001$); italicized capital letters within algal bars show statistical groupings with bars having different letters significantly different (planned comparisons $P < 0.05$). The numbers in brackets are the percent detritus makes up of the total. Error bars represent standard error of the mean. Abbreviations as described in Table 2.

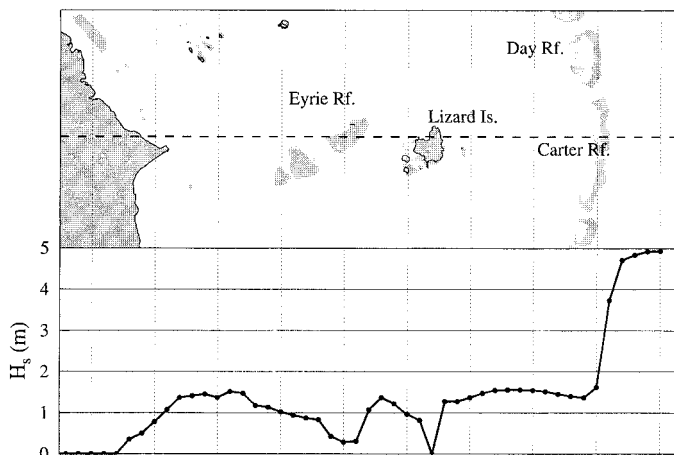


Fig. 4. Significant wave heights on a transect through the study area.

amino acids per unit area inside *A. lineatus* territories than outside at the outer barrier.

Wave exposure of collection sites—The eastern face of the GBR is subject to trade wind conditions from the directional quadrant between east and south for 8 months of the year (March–November). Several times each year, wind speeds are between 25 and 33 knots (~ 12.5 – 16.5 m s^{-1}). A steady and uniform wind speed of 15 m s^{-1} was used to force the numerical wave model to simulate wave conditions in the section of the GBR surrounding Lizard Island that includes the sampling sites. The modeling results are presented in Figs. 1 and 4. Figure 4 contains a plot of significant wave height along a transect from outside the GBR to the mainland coast crossing Lizard Island. Seaward of the GBR, the wave height is almost 5 m. Wave height diminishes abruptly in crossing Carter Reef, reducing to ~ 1.5 m. This energy loss is primarily caused by waves breaking on shallow reef crests and flats and corresponds to findings from field measurements on the GBR that wave height reduces to less than half the water depth during wave breaking (Hardy and Young 1996). There was an increasing trend of wave energy from sheltered midshelf sites (0.31 – 0.4 kJ m^{-2}) to moderately exposed midshelf sites (0.9 – 1.6 kJ m^{-2}) to highest wave exposure at outer barrier reefs (1.1 – 12.1 kJ m^{-2}). Outer barrier sites cover a wide range of wave energies. At the outer barrier, the two pass sites (Day Reef North Pass and No Name North Pass) were lower in wave energy (1.1 and 3.9 kJ m^{-2} , respectively) compared with the two reef front sites (Day Reef North Corner and Day Reef North Front, 7.7 and 12.1 kJ m^{-2}). However, pass sites would also be subjected to substantial directional currents.

A significant inverse polynomial relationship was observed between detritus dry weight and wave energy ($F_{1, 50} = 57.9$, $P < 0.001$) that explained 52.8% of the variation in the data (adjusted R^2 , Fig. 5). A similar relationship was also found between algal dry weight and wave energy ($F_{1, 51} = 23.4$, $P < 0.001$), but this only explained 30.0% of the variation in the data (adjusted R^2 , Fig. 5).

Discussion

The major conclusion from this study is that detritus from shallow water hard substratum surfaces constitutes a potentially important nutritional component of the EAC. First, detritus was significantly richer in TAA and similar in starch concentration to algae. Second, although detritus is less abundant than algae, it still constitutes a significant proportion of the EAC. Detritus ranges from 11% to 36.3% of the dry weight of the EAC, depending on the location. It also contains a substantial portion of the total protein amino acids (14.2%–64.2%) and total starch (5.2%–27.2%). This represents a substantial food resource potentially available to grazing fishes such as the highly abundant grazers of the genera *Ctenochaetus* and *Scarus* (e.g., Choat and Bellwood 1985; Meekan and Choat 1997). The substantial quantities of detritus in *A. lineatus* territories may explain enhanced local densities of the specialized detritus feeder *C. striatus*, which is found in these areas.

Across shelf differences in the amount of detrital matter was a second major element of our findings. This correlated with exposure to wave dynamics (inverse polynomial), with low detrital loads at sites with high wave energies. This is consistent with the findings of Purcell (2000), who found lower sediment loads on the reef crest compared to zones of lower hydrodynamic forces (reef base, fore reef, and reef flat) on a windward reef at Lizard Island. Strong wave energies over shallow surfaces will suspend and transport particulate matter and inhibit the accumulation of detrital material at sites exposed to strong wave action. This is reflected in the data on detrital distribution. However, the wide range of detrital loads at sites of equivalent wave energy suggests that other factors play an important role in determining detrital loads. The interaction between detrital quantity, its renewal and consumption rates, and the action of the physical environment is likely to be complex. For example, grazing fish density is higher on outer as opposed to midshelf reefs, although the mean fish size is smaller (Gust et al. 2001). An important next step in this work will be to examine the dynamics of particulate matter deposition and its accumulation under different regimes of wave activity. Given the uniform nature of the prevailing southeasterly trade winds, modeling of wave dynamics offers an opportunity to examine the interaction between biological and physical processes in this context.

Territorial defense by *A. lineatus* has been viewed as protection of food resource (Choat 1991; Polunin and Klumpp 1992a). The results from this study show a greater amount of algae inside territories only at the outer barrier sites. The food value of this resource is also greater in total amino acids (mg m^{-2}) inside territories at the outer barrier. A larger sample size may have been able to resolve the effect of territory. However, in our sampling design, we harvested total algae from the EAC. This included large amounts of calcareous algae, as shown by the high ash content of samples. The diet of *A. lineatus* would constitute a subset of the sampled algae; this fish feeds predominantly on fleshy non-calcareous filamentous turf algae (e.g., Robertson and Gaines 1986). An estimation of abundance and food value

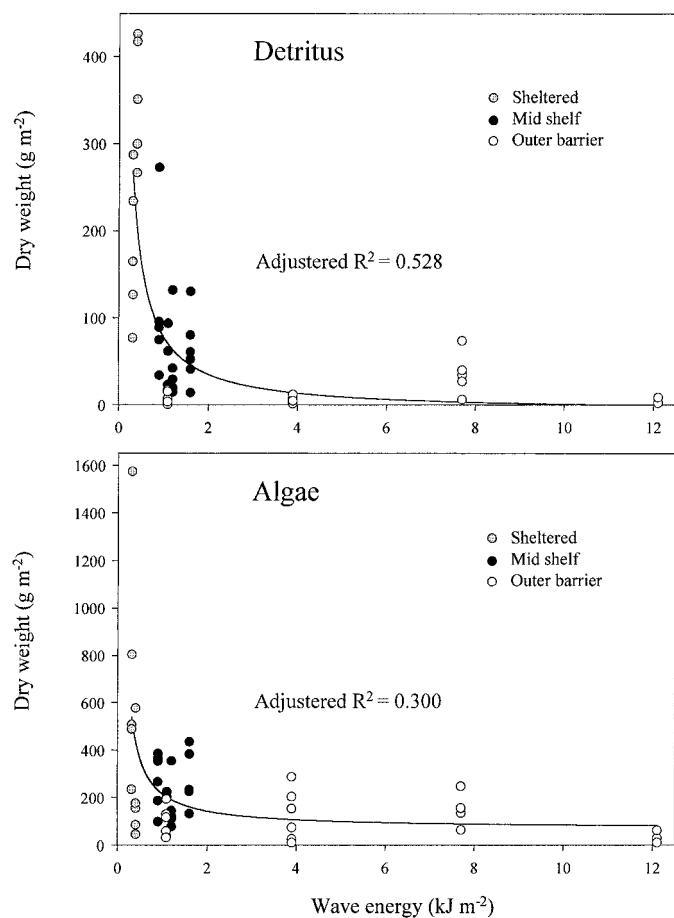


Fig. 5. The relationship between detrital or algal mass and the wave energy of collection sites. Regression line is a first-order inverse polynomial.

of dietary algae would need to be done to test the effect of territory on food resource available to this herbivore.

Amino acid quality—The mole percentage composition of the protein amino acids in the detritus and algae is very similar, with no distinct differences between locations or territories. Of the 20 protein amino acids, 10 are considered to be essential in the diet of fish and most other vertebrates. These are arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine (De-Silva and Anderson 1995). The method of amino acid analysis used in this study measured 16 of the 20 protein amino acids, including 9 of the essential amino acids. The four that were not measured are tryptophan and cysteine, which are partially destroyed during acid hydrolysis, and asparagine and glutamine, which are converted to aspartic acid and glutamic acid, respectively (Kellner et al. 1994). Despite these limitations, the method gives a good measure of amino acid composition. Our results suggest that detritus and algae in qualitative terms provide a very similar source of essential and nonessential amino acids.

The amino acid composition can vary in different sources of dietary protein (Friedman 1996). Fish feeding trials on aquaculture species have revealed that diets low in essential

amino acids give poor growth. These fish may also vary in their requirements for essential amino acids (De-Silva and Anderson 1995). It is possible that the diets of nominal herbivorous fish are poor in essential amino acids relative to the diets of carnivorous fish, especially given that plant proteins are often deficient in essential amino acids (e.g., Friedman 1996). However, a study on amino acid composition in a variety of sources (vascular plants, macrophytes, phytoplankton, zooplankton, bacteria, and fungi) failed to find any significant difference between these categories, although there was substantial variation within the groups (Cowie and Hedges 1992). However, the total concentration of protein amino acids does vary between diet categories with crustaceans (79%–97%) \geq fish (46%–93%) \geq bacteria (31%–55%) \geq zooplankton (14%–44%) \geq fungi (19%) \geq phytoplankton (3%–30%) $>$ macrophytes (8%) $>$ vascular plants (0.3%–7%) (values expressed per dry weight and are calculated from Neidhardt 1987; Cowie and Hedges 1992; Silva and Chamul 2000; see Materials and Methods for explanation). Thus the variation amongst the diet categories in total amino acid concentration is probably more important nutritionally than any qualitative difference in amino acid composition.

Trophic relations—Trophodynamic models of fisheries production on coral reefs have highlighted (1) the importance of detritus based food webs and (2) the lack of information on fluxes and fates of detritus. However, this production is assumed to be largely supported through invertebrate consumption of detritus and subsequent consumption of invertebrates by fish (Polunin and Klumpp 1992b; Polunin 1996). The potential consumption of detritus directly by grazing fishes has not been examined. In freshwater systems, detritus is an important food source to a large assemblage of fishes (Bowen 1980, 1983). In the marine setting, Wilson and Bellwood (1997) have demonstrated that detritus was the most important nutritional constituent of the territories and diet of three tropical damselfish previously thought to feed on turf algae. Bacteria are thought to be important in the diet of the detritivorous mullet *Mugil cephalus* (Moriarty 1976). Microorganisms are abundant in coral reef sediments (Sorokin 1993) and may provide an important nutritional resource to grazing acanthurid and scarid fishes (Choat and Clements 1998). The significant quantities of protein amino acids measured in detritus in this study reinforce this view.

Conclusions—Detritus from the EAC is of potential food value, especially in protein amino acids. Many grazing fish appear to ingest this food resource. This suggests that a significant portion of the fish biomass on coral reefs may be directly supported by the detrital food web. Detritus is of complex composition that includes dead organic matter, inorganic material, microorganisms, microalgae, and associated meiofauna. At present, we know very little about the dynamics of this community and its importance to other components of the food web.

References

- ALONGI, D. M. 1988. Detritus in coral reef ecosystems: Fluxes and fates, p. 29–36. In J. H. Choat et al [eds.], Proceedings of the sixth international coral reef symposium, Townsville, Australia, Vol 1. Executive committee.
- BELLWOOD, D. R. 1996. Production and reworking of sediment by parrotfishes (family Scaridae) on the Great Barrier Reef, Australia. *Mar. Biol.* **125**: 795–800.
- BOWEN, S. H. 1980. Detrital nonprotein amino acids are the key to rapid growth of *Tilapia* in Lake Valencia, Venezuela. *Science*. **207**: 1216–1218.
- . 1983. Detritivory in neotropical fish communities. *Environ. Biol. Fish.* **9**: 137–144.
- . 1987. Composition and nutritional value of detritus, p. 192–211. In D. J. W. Moriarty and R. S. V. Pullin [eds.], Detritus and microbial ecology in aquaculture. International Centre for Living Aquatic Resources Management.
- CHOAT, J. H. 1991. The biology of herbivorous fishes on coral reefs, p. 120–155. In P. F. Sale, [ed.], The ecology of fishes on coral reefs. Academic.
- , AND D. R. BELLWOOD. 1985. Interactions amongst herbivorous fishes on a coral reef: Influence of spatial variation. *Mar. Biol.* **89**: 221–234.
- , AND K. D. CLEMENTS. 1998. Vertebrate herbivores in marine and terrestrial environments: A nutritional ecology perspective. *Annu. Rev. Ecol. Syst.* **29**: 375–403.
- CLEMENTS, K. D. 1997. Fermentation and gastrointestinal microorganisms in fishes, p. 156–198. In R. I. Mackie and B. A. White [eds.], Ecology and physiology of gastrointestinal microbes. Chapman and Hall.
- COWIE, G. L., AND J. I. HEDGES. 1992. Sources and reactivities of amino acids in a coastal marine environment. *Limnol. Oceanogr.* **37**: 703–724.
- CROSSMAN, D. J., K. D. CLEMENTS, AND G. J. S. COOPER. 2000. Determination of protein for studies of marine herbivory: A comparison of methods. *J. Exp. Mar. Biol. Ecol.* **244**: 45–65.
- DE-SILVA, S. S., AND T. A. ANDERSON. 1995. Fish nutrition in aquaculture, 1st ed. Chapman and Hall.
- DUCKLOW, H. W. 1990. The biomass, production and fate of bacteria in coral reefs, p. 265–289. In Z. Dubinsky, [ed.], Ecosystems of the world 25. Elsevier.
- FRIEDMAN, M. 1996. Nutritional value of proteins from different food sources. A review. *J. Agric. Food Chem.* **44**: 6–29.
- GALETTO, M. G., AND D. R. BELLWOOD. 1994. Digestion of algae by *Stegastes nigricans* and *Amphiprion akindynos* (Pisces: Pomacentridae), with an evaluation of methods used in digestibility studies. *J. Fish Biol.* **44**: 415–428.
- GUST, N., J. H. CHOAT, AND M. I. MCCORMICK. 2001. Spatial variability in reef fish distribution, abundance, size and biomass: A multiscale analysis. *Mar. Ecol. Prog. Ser.* **214**: 237–251.
- HARDY, T. A., L. B. MASON, AND J. D. MCCONOCHE. 2000. A wave model for the Great Barrier Reef. *Ocean Engineering*. **28**: 45–70.
- , AND I. R. YOUNG. 1996. Field study of wave attenuation on an offshore coral reef. *J. Geophys. Res.* **101**: 14311–14326.
- HATCHER, B. G. 1983a. Grazing in coral reef ecosystems, p. 164–179. In D. J. Barnes [ed.], Perspectives on coral reefs. Australian Institute of Marine Science.
- . 1983b. The role of detritus in the metabolism and secondary production of coral reef ecosystems, p. 317–325. In J. T. Baker, R. M. Carter, P. W. Sammarco, and K. P. Stark [eds.], Proceedings, inaugural Great Barrier Reef conference. James Cook University Press, Townsville.
- . 1988. Coral reef primary productivity: A beggar's banquet. *Trends Ecol. Evol.* **3**: 106–111.
- . 1997. Organic production and decomposition, p. 140–174. In C. Birkeland [ed.], Life and death of coral reefs. Chapman and Hall.
- HORN, M. H. 1989. Biology of marine herbivorous fishes. *Oceanogr. Mar. Biol. Annu. Rev.* **27**: 167–272.
- HIXON, M. A. 1997. Effects of reef fish on corals and algae, p. 230–248. In C. Birkeland [ed.], Life and death of coral reefs. Chapman and Hall.
- KELLNER, R., H. E. MEYER, AND F. LOTTSPEICH. 1994. Amino acid analysis, p. 93–113. In R. Kellner, H. F. Lottspeich, and E. Meyer [eds.], Microcharacterization of proteins. VCH.
- KOMEN, G. J., L. CAVALERI, M. DONELAN, H. HASSELMANN, S. HASSELMANN, AND P. JANSSEN. 1994. Dynamics and modeling of ocean waves. Cambridge Univ. Press.
- MEEKAN, M. G., AND J. H. CHOAT. 1997. Latitudinal variation in abundance of herbivorous fishes: A comparison of temperate and tropical reefs. *Mar. Biol.* **128**: 373–383.
- MORIARTY, D. J. W. 1976. Quantitative studies on bacteria and algae in the food of the mullet *Mugil cephalus* L. and the prawn *Metapenaeus bennettiae* (Racek and Dall). *J. Exp. Mar. Biol. Ecol.* **22**: 131–143.
- , P. C. POLLARD, D. M. ALONGI, C. R. WILKINSON, AND J. S. GRAY. 1985. Bacterial productivity and trophic relationships with consumers on a coral reef (MECOR I), p. 457–462. In C. Gabrie, J. L. Toffart, and B. Savart [eds.], Proceedings of the fifth international coral reef congress, Tahiti, Vol. 3. Antenne Museum-EPHE.
- NEIDHARDT, F. C. 1987. Chemical composition of *Escherichia coli*, p. 3–6. In F. C. Neidhardt [ed.], *Escherichia coli* and *Salmonella typhimurium*. Cellular and molecular biology. American Society of Microbiologists.
- NELSON, S. G., AND S. D. WILKINS. 1988. Sediment processing by the surgeonfish *Ctenochaetus striatus* at Moorea, French Polynesia. *J. Fish Biol.* **32**: 817–824.
- POLUNIN, N. V. C. 1996. Trophodynamics of reef fisheries productivity, p. 113–135. In N. V. C. Polunin and C. M. Roberts [eds.], Reef fisheries. Chapman and Hall.
- , AND D. W. KLUMPP. 1992a. Algal food supply and grazer demand in a very productive coral-reef zone. *J. Exp. Mar. Biol. Ecol.* **164**: 1–15.
- , AND ———. 1992b. A trophodynamic model of fish production on a windward reef tract, p. 213–233. In D. M. John, S. J. Hawkins, and J. H. Price [eds.], Plant-animal interactions in the marine benthos, systematics association special volume no. 46. Clarendon.
- PURCELL, S. W. 1996. A direct method for assessing sediment load in epilithic algal communities. *Coral Reefs*. **15**: 211–213.
- . 2000. Association of epilithic algae with sediment distribution on a windward reef in the Northern Great Barrier Reef, Australia. *Bull. Mar. Sci.* **66**: 199–214.
- , AND D. R. BELLWOOD. 1993. A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Environ. Biol. Fishes*. **37**: 139–159.
- ROBERTSON, D. R., AND S. D. GAINES. 1986. Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology*. **67**: 1372–1383.
- RUSS, G. 1984a. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* **20**: 23–34.
- . 1984b. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of midshelf and outershelf reefs. *Mar. Ecol. Prog. Ser.* **20**: 35–44.
- SILVA, J. L., AND R. S. CHAMUL. 2000. Composition of marine and

- freshwater finfish and shellfish species and their products, p. 31–45. *In* R. E. Martin, E. Paine Carter, G. J. Flick, Jr., and L. M. Davis [eds.], *Marine and freshwater products handbook*. Technomic.
- SOROKIN, Y. I. 1995. *Coral reef ecology*. Springer-Verlag.
- STENECK, R. S. 1988. Herbivory on coral reefs: A synthesis, p. 37–49. *In* J. H. Choat, D. Barnes, M. A. Borowitzka, J. C. Coll, P. J. Davies, P. Flood, B. G. Hatcher, and D. Hopley [eds.], *Proceedings of the sixth international coral reef symposium, Townsville, Australia, Vol 1*. Executive committee.
- STEVENS, C. E., AND I. D. HUME. 1995. Comparative physiology of the vertebrate digestive system, 2nd ed. Cambridge Univ. Press.
- WHITE, T. C. R. 1993. *The inadequate environment: Nitrogen and the abundance of animals*, 1st ed. Springer.
- WILSON, S., AND D. R. BELLWOOD. 1997. Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidei). *Mar. Ecol. Prog. Ser.* **153**: 299–310.

Received: 5 March 2001

Accepted: 12 July 2001

Amended: 27 July 2001