

Energetics of food selection by the herbivorous parrotfish *Sparisoma radians*: roles of assimilation efficiency, gut evacuation rate, and algal secondary metabolites

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ABSTRACT: Experiments were conducted to investigate the effect of plant energy content and the presence of secondary metabolites on the assimilation efficiency, alimentary tract evacuation rate, and feeding rate of the bucktooth parrotfish *Sparisoma radians*. Alimentary tract evacuation rate was significantly greater (ca 2.5×) when the fish fed on the relatively energy-poor calcareous green alga *Halimeda incrassata* than on the seagrass *Thalassia testudinum*. The greater evacuation rate of *H. incrassata* provided the fish the capacity to increase consumption rate to compensate for low food energy content. However, due to unpalatable secondary chemical metabolites present in *H. incrassata*, actual biomass consumed per unit time was less than for *T. testudinum*. Experiments using *T. testudinum* blades coated with *H. incrassata* organic crude extract showed that the secondary metabolites had no effect on the fish's assimilation efficiency or gut evacuation rate. The increased rate of *H. incrassata* evacuation is more than sufficient to allow compensation for lower gross energy content. *S. radians* can increase evacuation rate sufficiently to allow compensation for differences in available energy over the normal range for most plants consumed in nature. Studies of herbivorous fish foraging and feeding energetics must consider differences in alimentary tract evacuation rate and feeding rate, and the effects of secondary metabolites, in addition to the assimilation efficiency, structural defense and relative plant abundance factors usually considered.

INTRODUCTION

Studies of feeding selectivity in herbivorous fishes and the relative energy and nutrient value of their plant food have provided insight into factors involved in food choice by herbivorous fishes in tropical marine waters (Montgomery 1980, Montgomery & Gerking 1980, Lobel 1981, Lobel & Ogden 1981, Hay 1984) and in temperate seas (Edwards & Horn 1982, Horn et al. 1982, 1985, Horn 1983, Horn & Neighbors 1984). Diet choice should reflect selective feeding to maximize the rate of net energy gain (Pyke et al. 1977, Pyke 1979, Hughes 1980, Horn 1983). Energy value of the plant, assimilation efficiency of the fish for the plant, and nutrient content (in particular N or protein) are the factors generally considered when assessing food value relative to diet choice (Montgomery & Gerking 1980,

Edwards & Horn 1982, Horn et al. 1982, Horn 1983). In addition, secondary metabolites (Paul & Hay 1986, Targett et al. 1986, Paul 1987, Wylie & Paul 1988) and relative availability (Horn 1983, Horn & Neighbors 1984) have been shown to influence food selection by herbivorous fishes. Thallus toughness may also restrict feeding by fishes with mouth structures incapable of effectively removing plant material (Littler et al. 1983, Paul & Hay 1986).

The primary factors included in assessments of plant quality for herbivorous fishes have been those which influence assimilation per unit of plant material. Variation in consumption rate, made possible by differences in alimentary tract evacuation rate from one plant species to another, has not been previously considered. Since the rate of net energy gain is assumed to be the currency to be optimized, any factor causing changes

in evacuation rate and consumption rate would affect the rate of energy gain.

Experiments with trout, marine flatfish, and other fishes fed artificial diets have shown increased evacuation rates when fed on diets low in energy (Rozin & Mayer 1961, Grove et al. 1978, Flowerdew & Grove 1979, Jobling 1980, 1981a, 1986, 1987, Jobling & Wandsvik 1983). Since appetite is related to stomach or foregut fullness, feeding rate is strongly influenced by gastric or foregut emptying rate (Grove et al. 1978, Fänge & Grove 1979, Grove & Crawford 1980, Holmgren et al. 1983, Knights 1985, Horn 1989). More rapid evacuation results in a more rapid increase in appetite. This provides fish with the capacity to increase feeding intensity and food intake rate when feeding on energy-poor diets, and can result in maintenance of a relatively constant level of energy intake (Grove et al. 1978, Brett & Groves 1979, Jobling 1980, 1983, Jobling & Wandsvik 1983, Weatherley & Gill 1987). The mechanisms by which gastric emptying rate is controlled and thereby linked to food intake have not been thoroughly examined, but it has been speculated that receptors in the anterior intestine respond to components in the chyme and in turn affect patterns of alimentary tract muscular contraction (see Jobling & Wandsvik 1983, Jobling 1986, 1987).

Herbivorous fishes would therefore be expected to increase feeding rate on energy-poor plant material, and thus be able to maintain a relatively stable rate of energy intake across a range of plant quality. However, changes in evacuation rates and consumption rates with changes in plant energy content (and fish assimilation efficiency) have not been considered in fishes feeding on natural foods. Demonstration of such a relationship would alter the assessment of food value (rate of net energy gain) based primarily on energy or nutrient content and assimilation efficiency factors, and would also influence interpretation of patterns of food selection by herbivorous fishes.

Parrotfish (Scaridae) are common residents of tropical coral reefs and seagrass beds. The bucktooth parrotfish, *Sparisoma radians*, is an abundant herbivorous fish in Caribbean seagrass beds (Weinstein & Heck 1979, Lobel & Ogden 1981, Robblee & Zieman 1984). This parrotfish is a browser which feeds on turtlegrass *Thalassia testudinum*, other seagrasses, and several macroalgal species including the calcareous green alga *Halimeda incrassata* (Lobel & Ogden 1981). Previous laboratory and field studies have shown that *S. radians* feeds continuously, with nearly constant feeding intensity, during daylight (Lobel & Ogden 1981). *S. radians* is typical of parrotfishes in that it has no true stomach, alkaline conditions (pH ca 8.4) in the anterior intestine, and a pharyngeal mill with which food is finely ground (Lobel 1981).

Sparisoma radians feeds on plant types varying in energy content and digests them with a range of organic matter assimilation efficiencies (Lobel & Ogden 1981). Laboratory and field studies (Lobel & Ogden 1981, Targett et al. 1986) have established that *S. radians* prefers *Thalassia testudinum*, epiphytized and non-epiphytized, over algal species such as *Halimeda incrassata*. Lobel & Ogden (1981) speculated that the large amount of structural CaCO_3 in *H. incrassata* lowered the energy content and biomass obtained per bite, thus decreasing preference by the fish. A role of CaCO_3 in structural defense against herbivores has been suggested previously for *Halimeda* as well as other macroalgae (Paul & Fenical 1983, Paul & Hay 1986). However, Targett et al. (1986) demonstrated the importance of secondary metabolites produced by *H. incrassata* in influencing *S. radians* feeding preferences.

Sparisoma radians and its natural prey provide an opportunity to investigate the potential that evacuation rate and feeding rate may change with energy content of plant species and assimilation efficiency of the fish. Increased alimentary tract evacuation rate in *S. radians* when consuming energy-poor food such as *Halimeda incrassata* compared to *Thalassia testudinum* would demonstrate the capacity to compensate for low energy food by increasing consumption rate. In the absence of structural or chemical feeding deterrents the fish could increase feeding rate and at least partially compensate, in terms of energy assimilation rate, for low assimilation efficiency. Faster evacuation rate without a comparable increase in feeding rate could imply the role of feeding deterrents such as secondary metabolites. Secondary metabolites may simply be unpalatable, or it is possible that they also affect physiological processes such as assimilation efficiency or alimentary tract evacuation rate. Metabolites such as phenolic compounds have been speculated to inhibit digestive processes (Steinberg 1984, 1986, Horn et al. 1985, see also discussion in Lobel 1981), as have other compounds (Benitez & Tiro 1982).

A series of experiments was conducted to investigate the relationship between plant energy content and the presence of secondary metabolites on *Sparisoma radians* assimilation efficiency, gut clearance rate, and feeding rate. The experiments were designed (1) to determine the energy content of *Thalassia testudinum* and *Halimeda incrassata*, and also the total, energy, and organic assimilation efficiency values for *S. radians* feeding on these plants; (2) to determine if evacuation rate is faster for energy-poor food such as *H. incrassata* than for *T. testudinum*, and if so, to determine if *S. radians* feeding rate increases comparably; and (3) to examine the effect of secondary metabolites in *H. incrassata* on assimilation efficiency and evacuation rate.

MATERIALS AND METHODS

Specimen collection and preparation. *Sparisoma radians* were collected with a seine from seagrass beds along the east end of St. Croix, US Virgin Islands. They were held in flow-through aquaria and fed *Thalassia testudinum* prior to experiments. Three macrophyte food types were used in feeding experiments. The macroalga *Halimeda incrassata* and the seagrass *T. testudinum* (without epiphytes) were collected just prior to feeding the fish. The third food type was epiphyte-free *T. testudinum* blades coated with *H. incrassata* organic crude extract (ethyl acetate residue) at its naturally occurring concentration of ca 7.0 mg g⁻¹ (see Targett et al. 1986). This food type was used to test the effects of *H. incrassata* secondary chemistry on digestive energetics. Extracts of *H. incrassata* were prepared from plants collected in the Florida Keys. Processing, extraction, and coating of the extract on *Thalassia* blades are described in Targett et al. (1986).

Feeding experiments. Two series of experiments were conducted. The first determined the energy content of the 3 food types and the assimilation efficiency for *Sparisoma radians* feeding on each. The second measured feeding rate and behavior of *S. radians* on each plant type separately and determined *S. radians* alimentary tract evacuation rate on each plant type.

Assimilation efficiency and food value: Prior to feeding, *Sparisoma radians* were held for ca 20 h in a flow-through aquarium without food to clear their alimentary tracts. A group of *S. radians* was then fed one plant type by clipping freshly collected plants together with weighted wooden clips and placing them in the aquarium. The fish were allowed to feed for up to 4 h and were then all placed in a clean aquarium with non-flowing aerated seawater. Fecal pellets were siphoned from the bottom of the aquarium at < 1 h intervals for ca 6 h. Excess water was removed from the accumulated fecal pellets by pipette and the material dried at 60°C. A subsample of fresh plant material was weighed to the nearest mg wet weight, dried at 60°C, reweighed, and the percentage water determined. Feeding was conducted on a different day for each food type with 4 to 9 fish per group. Water temperature throughout the experiments was 27°C.

Dried macrophytes and fecal material were homogenized to a powder in a Wig L Bug homogenizer and energy content determined using a Phillipson microbomb calorimeter. The proportion of ash and organic matter in the macrophytes and fecal material was determined by heating at 450°C for 24 h.

Assimilation efficiencies were calculated according to the method described by Montgomery & Gerking (1980), which compares organic and ash contents of the food with the corresponding fecal material, using ash

as a non-absorbed reference marker. The following equations were used:

Total Assimilation Efficiency (%) =

$$\left[1 - \left(\frac{\% \text{ ash in food}}{\% \text{ ash in feces}} \right) \right] \times 100 \% \quad (1)$$

'Nutrient' Assimilation Efficiency (%) =

$$\left[1 - \left(\frac{\% \text{ ash in food}}{\% \text{ ash in feces}} \right) \times \left(\frac{\% \text{ nutrient in feces}}{\% \text{ nutrient in food}} \right) \right] \times 100 \% \quad (2)$$

Assimilation efficiencies for energy and organic matter were calculated from Eq. (2) using J mg⁻¹ dry weight and percentage organic matter in the macrophytes and corresponding fecal material. This method assumes that ash is not significantly absorbed during the short experimental period. Any small absorption of minerals is considered negligible compared to the high percentage of ash in the plant material. Total assimilation efficiencies were also expressed in terms of wet weight after conversion using percentage water.

Feeding rate and alimentary tract evacuation rate:

The feeding rate and feeding behavior of *Sparisoma radians* grazing on epiphyte-free *Thalassia testudinum* blades, *Halimeda incrassata* plants, and *T. testudinum* coated with *H. incrassata* organic crude extract was determined in a separate experiment for each food type. Fish were unfed for 18 to 20 h prior to each experiment. Experiments were conducted in a 75 l flow-through aquarium at 26°C. In each experiment a group of 4 *S. radians* (52 to 70 mm total length) was allowed to feed for 4 h (ca 08:30 to 12:30 h). Separate measurements of feeding rate were acquired sequentially during this period, as the fish browsed continuously. Freshly collected plants were blotted dry, weighed, and clipped together with a weighted wooden clip. A clip of one plant type was placed on the bottom of the aquarium and the 4 fish were allowed to feed. Each hour the clip was replaced with a new clip of the same plant type. During the experiments, fish were observed continuously from behind black plastic blinds. Fecal material began to appear 1 to 2 h after feeding began and all feces produced during the 4 h was siphoned from the tank, dried at 60°C, and weighed. The total number of bites taken during each 5 min interval of the 4 h feeding period was recorded and the percentage of bites subsequently rejected was estimated. At the end of the feeding period, macrophyte material remaining in each clip was blotted dry and weighed.

Each fish was then placed into an individual clean aquarium with non-flowing aerated seawater to determine alimentary tract evacuation rate. Fecal pellets were siphoned from each aquarium every 0.5 h for 6 h

and again 12 h later. Preliminary results demonstrated that fecal production was complete by this time. Excess water was removed, and the feces from each time interval was dried separately at 60°C and weighed. This procedure was conducted on a different day for each food type.

Data analysis. Three methods were used to quantify feeding rates during the 4 h feeding period and to compare rates among foods. In the first method, the number of bites taken during each 5 min interval of the 4 h feeding period was compared among food types. The data for each food type were square-root transformed to achieve normality (determined by Kolmogorov-Smirnov tests using the Lilliefors option). Due to heteroscedasticity (determined using Bartlett's test) the transformed data were then analyzed using the Games and Howell method for making multiple comparison tests among pairs of means when variances are heterogeneous (Sokal & Rohlf 1981). The other 2 methods assessed macrophyte biomass removed and consumed during the feeding period. Total wet weight of bites removed from plants during each 1 h interval was determined by subtracting the wet weight of plant material in each of the 4 clips after feeding from the initial wet weights. The data for each food type were normally distributed and homoscedastic. Data were analyzed by ANOVA and significant differences in wet biomass removed by the fish among food types determined using least significant difference (LSD) multiple comparison intervals. A significance level of $p < 0.05$ was established a priori for these tests.

Because of difficulty determining precise wet weights for blotted plants, one other method was used for comparison. In this method, dry weight consumed was determined from dry weight of fecal material produced over the 22 h following initiation of feeding. The dry biomass of each macrophyte consumed was calculated according to the equation:

$$W_C = (W_F \cdot \emptyset_F) / \emptyset_C \quad (3)$$

where W_C = dry weight in grams of food consumed during 4 h; W_F = dry weight in grams of the feces produced; and \emptyset_F and \emptyset_C = the proportion of ash in feces and food, respectively (from Crisp 1984). This method assumes that ash is non-digestible and is not significantly absorbed during the short experimental period.

Alimentary tract evacuation rates were calculated separately for each of the 4 fish, for each food type. Fecal material recovered after each 30 min interval, for 6 h after transfer to food-free aquaria, was weighed and these values summed with the weight recovered 12 h later. All weights were then converted to a percentage of the total recovered from each fish. Percentage food remaining (y) vs time (x) over the 6 h period

was a curvilinear function in all cases and 2 volume-dependent emptying models were applied (Jobling 1981b, 1986, 1987). Transforming the percentage values by either square root or natural logarithm both provided good linear fits to the data. The negative exponential (natural logarithm) model ($y = ae^{-bx}$) was chosen because it has been shown to best describe the emptying curve for fishes feeding on relatively low energy diets and ingesting small particles (Jobling 1986, 1987) and for other species of stomachless fishes (Grove & Crawford 1980, Persson 1982, Beyer et al. 1988). Thus, alimentary tract evacuation rate was calculated for each fish from the linear regression equation:

$$\ln W_T = \ln W_0 - bT \quad (4)$$

where W_T = percentage food remaining in the gut + 1 at time T after feeding ceased; W_0 = the y intercept; $-b$ = the instantaneous rate of evacuation (slope); and T = time (h) (see Jobling 1981b). Adding 1 to the percentage food remaining values allowed inclusion of 0 values (empty alimentary tracts at the end of the 6 h period). The exponential model assumes that a constant proportion of the food material is evacuated per unit time and thus the time necessary for complete evacuation does not depend upon meal size (Jobling 1981b). Subsequent regression analysis of the predicted times for complete evacuation (T when $\ln W_T = 0$, for each fish for a particular food type) vs the amount of feces produced in the food-free aquarium (meal size) showed no relationship, providing additional support for use of the exponential model for the determination of evacuation rate. Evacuation rate data for each food type were normally distributed and homoscedastic and rates were compared among food types with ANOVA and LSD multiple comparison intervals ($p < 0.05$).

RESULTS

The organic content and energy content of *Thalassia testudinum* were much higher than for *Halimeda incrassata* (Table 1). The differences in food quality were reflected in much higher assimilation efficiency values for *Sparisoma radians* feeding on *T. testudinum* than on *H. incrassata* in terms of percentage total weight, organic matter, and energy (Table 1). The high ash content (primarily structural CaCO_3) in *H. incrassata* greatly reduced the organic and energy content, and total dry weight assimilation efficiency was only 3%.

The alimentary tract evacuation rate of *Sparisoma radians* was significantly greater for *Halimeda incrassata* than for *Thalassia testudinum* (Table 2). Mean instantaneous evacuation rate (slope of \log_e -transformed data) was -0.5382 for *H. incrassata* compared

Table 1. Organic and energy content of macrophytes with associated assimilation efficiency by *Sparisoma radians*

Macrophyte	% Water	Organic matter		Energy content (J mg ⁻¹)		Assimilation efficiency (%)			
		% wet wt	% dry wt	Wet wt	Dry wt	Total		Organic	Energy
						Wet	Dry		
<i>Thalassia testudinum</i>	83	12	71	2.2	12.7	7	39	56	64
<i>Halimeda incrassata</i>	76	5	19	1.2	4.9	1	3	19	10
<i>T. testudinum</i> coated with <i>Halimeda</i> organic extract	77	18	77	3.5	15.2	10	46	59	- ^a

^a Too little fecal material available for analysis

Table 2. *Sparisoma radians*. Mean instantaneous evacuation rates, γ intercepts, and times for complete evacuation (\pm SE) of macrophytes from the alimentary tract

Macrophyte	Instantaneous evacuation rate ^a	γ -intercept ^a	Time for complete evacuation (h)
<i>Thalassia testudinum</i>	-0.2166 ± 0.0307^b	96.35 ± 4.12^b	22.4 ± 3.2^b
<i>Halimeda incrassata</i>	-0.5382 ± 0.1286^c	134.63 ± 19.02^b	11.5 ± 3.7^c
<i>T. testudinum</i> coated with <i>Halimeda</i> organic extract	-0.2730 ± 0.0460^b	111.48 ± 8.68^b	$18.3 \pm 2.2^{b,c}$

^a Instantaneous evacuation rate is the mean slope ($-b$), and γ intercept is the mean value of W_0 , from the equation $\ln W_T = \ln W_0 - bT$, over all 4 fish. W_T is percentage food remaining in the gut + 1 at time T after feeding ceased and T is time (h)

^{b,c} Means having the same superscript within a column are not significantly different by ANOVA at $p < 0.05$

with -0.2166 for *T. testudinum*. Thus, evacuation rate for energetically poorer *H. incrassata* was ca $2.5\times$ greater than for *T. testudinum*, providing *S. radians* the capacity to increase consumption rate to allow compensation for low plant energy content.

Feeding rate was quantified in 3 ways (Table 3). Although the higher number of bites taken by *Sparisoma radians* per unit time from *Halimeda incrassata* was not statistically different than the number taken from *Thalassia testudinum* (Table 3), ca 40 % of the bites taken from *H. incrassata* were rejected immediately, compared with $< 1\%$ from *T. testudinum*. This lowered the actual consumption rate of bites from

H. incrassata to a level significantly lower than from *T. testudinum* (Table 3). Although 15 % more bites were taken, ca 31 % fewer bites of *H. incrassata* were actually consumed, relative to *T. testudinum* plants.

The 2 other methods of assessing feeding rate were more quantitative and showed analogous results. Wet weight of macrophyte removed during 1 h intervals over the 4 h feeding experiment did not differ statistically between *Thalassia testudinum* and *Halimeda incrassata*, but when adjusted for percentage *H. incrassata* bites rejected, actual consumption of *H. incrassata* was significantly less (28 % lower) than for *T. testudinum* (Table 3). Dry weight of macrophyte con-

Table 3. *Sparisoma radians*. Feeding rates of fish on macrophytes during 4 h tests when given no plant choice

Macrophyte	Mean number of bites removed (A) and consumed (B) 5 min ⁻¹		Mean biomass of bites removed (A) and consumed (B) h ⁻¹ (g wet wt)		Biomass of macrophyte consumed in 4 h (g dry wt)	Percentage rejections ^b
	A	B ^a	A	B ^a		
<i>Thalassia testudinum</i>	36.42 ^c	36.42 ^c	0.2426 ^c	0.2426 ^c	0.3827	< 1
<i>Halimeda incrassata</i>	41.96 ^{c,d}	25.12 ^d	0.2924 ^c	0.1754 ^d	0.2390	40
<i>T. testudinum</i> coated with <i>Halimeda</i> organic extract	28.71 ^d	28.71 ^d	0.1508 ^d	0.1508 ^d	0.2476	< 5

^a Adjusted for percentage *H. incrassata* bites rejected

^b Observational estimate

^{c,d} Means having the same superscript within a column are not significantly different at $p < 0.05$

sumed, based on dry weight of fecal material produced (adjusted for assimilation efficiency), was also less (38% lower) for *H. incrassata* than for *T. testudinum*.

Although the greater evacuation rate provides *Sparisoma radians* with the capacity to increase feeding rate on energy-poor *Halimeda incrassata*, actual biomass consumed was less than from *Thalassia testudinum* due to rejections. When feeding on *H. incrassata*, *S. radians* was observed to take most bites from the highly calcified bases of the plants. Nearly all of the bites taken from *H. incrassata* plant tips were rejected.

Experiments using *Thalassia testudinum* blades coated with *Halimeda incrassata* organic crude extract provided insight into the potential influence of unpalatable secondary metabolites on *Sparisoma radians* assimilation efficiency, alimentary tract evacuation rate, and feeding rate and behavior. Coating the organic extract on *T. testudinum* blades removed water and added organic matter and energy, compared with uncoated blades (Table 1). Assimilation efficiency was not decreased, and in fact was slightly higher for blades coated with extract on both wet and dry weight bases. Alimentary tract evacuation rate of coated blades was not significantly different from uncoated blades (Table 2). Feeding rate, however, was significantly altered by presence of the organic crude extract. Fewer bites were taken and consumed from coated blades than from uncoated blades (Table 3). Rejection rate was estimated to be <5% compared with <1% for uncoated blades. However, the number of bites taken and consumed from coated blades was not significantly different than the number taken from *H. incrassata* plants. Wet biomass of macrophyte removed and consumed was also significantly less for coated than for uncoated *T. testudinum* blades. Dry weight analysis also showed 35% less consumption of coated than uncoated blades.

Compared with *Halimeda incrassata* plants, less biomass was removed from coated *Thalassia testudinum* blades; but due to high rejection rates for *H. incrassata*, biomass actually consumed was the same in both the wet and dry weight analyses (Table 3). Coating *T. testudinum* blades with *H. incrassata* organic crude extract at naturally occurring concentrations reduced actual consumption rate to a level not significantly different than that on whole *H. incrassata* plants.

DISCUSSION

Sparisoma radians has a significantly faster (ca 2.5×) instantaneous rate of alimentary tract evacuation when feeding on *Halimeda incrassata* than when consuming *Thalassia testudinum*. Since more rapid evacuation leads to a more rapid increase in appetite in fishes

(Grove et al. 1978, Fange & Grove 1979, Grove & Crawford 1980, Holmgren et al. 1983, Knights 1985, Horn 1989), *S. radians* has the capacity to increase consumption rate to compensate for low food energy and low assimilation efficiency. However, consumption of *H. incrassata* plants does not increase, and in fact feeding rate is reduced relative to the rate on *T. testudinum* blades. Furthermore, although *H. incrassata* organic crude extract reduces consumption of *T. testudinum* blades, the compounds do not alter *S. radians* digestive efficiency or rate. The secondary metabolites, which include 1,4-diacetoxy-1,3-butadiene terpenes, are unpalatable and alter feeding rate and food preference (Targett et al. 1986) but do not appear to affect *S. radians* digestive energetics.

The conclusion has often been made that calcareous algae, or other plants of low energy value, are or should be avoided as food by herbivorous fishes because of reduction in rate of net energy gain by the fish (Montgomery & Gerking 1980, Lobel & Ogden 1981, Horn et al. 1982). The relationship between energy content and rate of evacuation by *Sparisoma radians* demonstrates that increased evacuation rate, and thus the capacity to increase feeding rate on energy-poor food, must be considered in assessments of relative plant value and food preferences in herbivorous fishes. As long as chemical or structural defense mechanisms in the plant do not limit the fishes' feeding rate and ability to maintain a full gut, then compensation for low energy level food is possible. Low energy content would, therefore, be a significant factor affecting the net rate of energy intake only (1) when low enough to more than offset the capacity of increased evacuation rate to sufficiently increase intake rate, or (2) if the time necessary to forage for the increased food intake placed constraints on the fish.

Gastric evacuation and food consumption rates in fishes are generally found to change in proportion to digestible (net) food energy rather than total (gross) energy content (see Jobling 1983, Jobling & Wandsvik 1983), although some data have suggested a better relationship to total energy (see Jobling 1981a). The increased rate of evacuation of *Halimeda incrassata* compared with *Thalassia testudinum* by *Sparisoma radians* is more than sufficient to allow compensation for lower gross energy content of *H. incrassata* on a wet weight basis, but not sufficient to fully compensate for the lower energy assimilation efficiency found (net energy content). Restraints imposed by alimentary tract muscular contraction rates may limit evacuation rates and cause increases to be inadequate to maintain a constant rate of energy intake for fishes feeding on food of very low energy value (Jobling 1980). Such a limitation on intake rate was speculated to be the cause of the inability of rainbow trout *Salmo gairdneri* to

increase evacuation and food intake rate to compensate for more than 30% cellulose filler added to fish meal artificial diets (Bromley & Adkins 1984). On the other hand, if the low energy assimilation efficiency (10%) found in the present study for *H. incrassata* is actually higher (Lobel & Ogden [1981] reported 81% assimilation efficiency for dry organic matter), then the increased evacuation rate demonstrated could also compensate for lower net (digestible) energy content.

The relative roles of structural and chemical defense mechanisms in marine macroalgae as deterrents to herbivory by fishes has been examined by Paul & Hay (1986). They concluded that morphological defenses alone do not appear to be adequate to defend most algal species and noted the general occurrence of biologically active secondary metabolites in calcareous algae. Herbivorous parrotfish, such as *Sparisoma radians*, are well adapted for the consumption of heavily calcified prey. The specialized teeth, strong jaws, and pharyngeal mill typical of parrotfishes enable other species in this group to ingest hard corals (Hiatt & Strasburg 1960, Randall 1967). Therefore, whereas thallus calcification may function to reduce herbivory by fishes such as damselfishes and angelfishes (see discussion by Hay 1984) which have small, weak mouths, algal thallus calcification is unlikely to be a physical deterrent to herbivory by fishes such as parrotfishes. In addition, the reduction in algal energy content which accompanies calcification does not function as a deterrent to the rate of net energy intake either, if evacuation rates and consumption rates increase and compensate for low energy content. These factors are consistent with the commonly observed occurrence of multiple defenses in calcified macroalgae (see Paul & Hay 1986).

Sparisoma radians has been demonstrated to increase evacuation rate sufficiently to allow compensation for differences in available energy over the normal range for most plants consumed in nature (see values in Lobel & Ogden 1981). We speculate that the increased evacuation rate would result in greater removal and consumption rate of *Halimeda incrassata* if it were not for the presence of secondary metabolite feeding deterrents (see Targett et al. 1986). In the natural environment, the fish's demonstrated avoidance of *H. incrassata* would manifest itself in the choice of other plant species (Lobel & Ogden 1981, Targett et al. 1986). Furthermore, although *S. radians* appears to not have the capacity to fully compensate for low energy assimilation efficiency (net energy content), *Halimeda* could still be consumed without energetic detriment as part of a mixed diet including other more energy rich macrophytes. The secondary metabolite feeding deterrents in *Halimeda* may serve as a second line of defense against herbivores such as parrotfishes,

which have strong jaws and pharyngeal mills. The mixed diets often consumed by herbivorous fishes (see Horn et al. 1982, Horn 1983) may provide a better balance of nutrients than a single plant diet, and greater alimentary tract evacuation rate with an associated increase in feeding rate may allow compensation for the energy dilution associated with inclusion of lower energy value plants.

Sparisoma radians feeding on *Thalassia testudinum* in the present study had an assimilation efficiency of 56% of dry organic matter. This is greater than the value of only 7% reported by Lobel & Ogden (1981). However, 7% is lower than would be expected based on organic and energy content despite the occurrence of indigestible cellulose (see Thayer et al. 1984). Organic assimilation efficiency of herbivorous sea urchins feeding on *T. testudinum* has been reported to range from 19% in *Lytechinus variegatus* (Lowe & Lawrence 1976) to 37% in *Echinometra lucunter* (Lawrence 1976). Greenway (1976) reported 65% assimilation efficiency for total dry weight in *L. variegatus* feeding on *T. testudinum*. Furthermore, the southern Australian half-beak *Hyporhamphus melanochir* like *S. radians* has a pharyngeal mill, no true stomach, and a near-neutral gut pH (6.5 to 7.0). This fish has an organic matter assimilation efficiency of 38% feeding on the seagrass *Heterozostera tasmanica* (Klumpp & Nichols 1983). These data, therefore, agree with the higher assimilation efficiency found in the present study for *S. radians* feeding on *T. testudinum*.

In their calculations of plant energy value, Lobel & Ogden (1981) multiplied dry organic matter assimilation efficiency by caloric content and 'biteability' (the plant biomass obtained per bite). They concluded from these calculations that *Halimeda incrassata* had the lowest net food value of the plants tested, including *Thalassia testudinum* and that this was the basis for the demonstrated avoidance of *H. incrassata* by *Sparisoma radians*. However, the 'biteability' term was an order of magnitude lower for *H. incrassata* than for *T. testudinum* and accounts for the majority of the difference in calculated food value. *S. radians* was shown in the present study to remove similar biomass per unit time when feeding on these 2 plants, and thus is not deterred from filling its gut by plant structural toughness. The 'biteability' term, therefore, should have little influence on actual net energy value. Based on the present results and those reported by Targett et al. (1986), the avoidance of *H. incrassata* appears to be due largely to the presence of secondary metabolites.

In summary, *Sparisoma radians* feeding on natural prey does, as predicted, increase alimentary tract evacuation rate when feeding on energy-poor plants, and has the potential to increase feeding rate to compensate for low food value. Differences in assimilation

rate can therefore overlie assimilation efficiency considerations, and the rate of net energy gain cannot be determined simply by multiplying plant energy content by assimilation efficiency and calculating net energy content. Furthermore, high plant ash content may be a feeding deterrent for *S. radians* only because assimilation efficiency of energy (net plant energy content) is apparently so low. The avoidance of *Halimeda incrasata* by *S. radians* is due largely to unpalatable *Halimeda* secondary chemistry. Studies of herbivorous fishes' feeding energetics and plant choice must consider differences in alimentary tract evacuation rate and feeding rate, and the effects of secondary metabolites, as well as the assimilation efficiency, structural defense, and relative plant abundance factors usually considered.

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