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Marine macroalgae as foods for fishes: an evaluation of potential food quality

W. Linn Montgomery* & Shelby D. Gerking

Department of Zoology, Arizona State University, Tempe, Arizona 85281, U.S.A.

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Synopsis

A revitalized view of feeding by herbivorous marine fishes is sought through two questions. First, What characteristics of major taxa of algae identify them as predictably high or low quality foods? Second, are marine algae valuable foods for fishes which do not mechanically disrupt cell walls and do not harbor specialized enzymes or microbes capable of lysing cell walls? Energy, ash and nutrient content of 16 species of marine algae were employed to assess food quality of fleshy red, green, brown and calcareous red algae. On the basis of ash, calories, total protein and total lipid content, fleshy algae should be superior to calcareous algae as foods for fishes; in addition, green algae should be superior to brown algae and brown algae superior to red algae. When the probable digestibility of storage and extracellular carbohydrates is considered, green and red algae are predicted superior to brown algae as food. Two species of damselfishes (Pomacentridae) from the Gulf of California, *Eupomacentrus rectifraenum* and *Microspathodon dorsalis*, eat red and green algae and ignore brown and calcareous algae. They feed, therefore, in a fashion consistent with predictions based only on algal chemistry. These fishes absorb at least 20–24% of the biomass, 57–67% of the protein, 46–56% of the lipid and 37–44% of the carbohydrate contained in algae eaten in the wild. Since these damselfishes do not masticate their food, it appears that herbivorous fishes can digest major fractions of algal nutrients without mechanical destruction of algal cells.

Introduction

Plant-eating fishes dominate tropical reef faunas throughout the world (Bakus 1969, Ogden & Lobel 1978), yet they are perhaps the least understood feeding guild of fishes. Analysis of feeding behavior and gut contents demonstrates conclusively the herbivorous diet of many fishes and that they use algae as their principal source of food. On the other hand, some authors working with temperate marine fishes have suggested that algae are ingested incidentally with animal material and are not important sources of nutrients and energy (Williams & Williams 1955, Quast 1968). This belief is bolstered by two observations: i. the lack of endogenous cellulase thought necessary for successful digestion of plants (Stickney & Shumway 1974), and ii. the lack of a consistent intestinal microflora which furnishes enzymes that degrade complex algal polysaccharides (ZoBell 1946, Trust & Sparrow 1974, Sera et al. 1974). According to this view, cell wall materials of plants resist digestion, and herbivorous fishes must rely on mechanical destruction of cell walls to obtain nutrients sequestered within the cells (Lagler et al. 1962). These opposing viewpoints require reexamination in view of their important implications for both understanding of reef ecology and aquaculture of marine herbivores.

We address two primary hypotheses about algae-fish relationships. First, we postulate that certain major taxa or growth forms of marine algae are better foods for fishes than other taxa or forms of algae. From comparisons of energy and chemical content of fleshy green, red and brown algae and of several heavily calcified red algae, we initially predict that fleshy algae should be eaten in preference to calcified algae and that green and brown algae should be eaten in preference to red algae.

We then assume (1) that herbivorous fishes lack cellulase or similar specialized enzymes capable of degrading resistant cell wall carbohydrates and (2) that these fishes generally lack a consistent gut flora capable of degrading those same carbohydrates. A dis-

* Present address: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, U.S.A.

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cussion of the chemistry of algal carbohydrates in light of these assumptions leads to a modification of earlier predictions: green and red algae should be eaten in preference to brown algae (previously acceptable) due to low levels of digestible carbohydrate in brown algae. Herbivorous rabbitfishes, damselfishes and blennioids tend to feed in a manner consistent with this prediction by eating green and red fleshy algae in preference to brown or calcified algae (Tsuda & Bryan 1973, von Westernhagen 1974, Montgomery 1977, 1978).

Our second hypothesis is that significant proportions of organic nutrients contained in marine algae may be digested by fishes which do not masticate their food. To test this hypothesis we estimated nutrient-specific absorption efficiencies for two damselfishes from the Gulf of California, Mexico, using a technique that can be applied to samples of foods and feces collected in the field. The technique measures the assimilation of organic nutrients relative to a substance (ash) which experiences slight or no assimilation (Maynard 1951, Nagy 1977). The damselfishes, which do not masticate their food, assimilate large proportions of the biomass, protein, lipid and carbohydrate contained in algae. Thus, relatively large fractions of algae may be digested by fishes without mechanical disruption of cells.

Materials and methods

Site and fishes studied

Field studies were conducted while skin and scuba diving along the south face of Los Frailes Mountain, Baja California Sur, Mexico, in the lower Gulf of California. At depths below 1 m, granitic boulder surfaces are covered by a mat of intertwined algae 0.5 to 1 m thick composed of over 30 species of small filamentous and leafy algae. This algal mat is selectively grazed by the cortez damselfish, *Eupomacentrus rectifraenum*, a small (110–120 mm standard length) territorial fish which ingests leafy green and filamentous red algae in preference to brown and calcareous red algae. Territories of adult giant blue damselfish, *Microspathodon dorsalis*, are on the upper surfaces of large boulders which rise above the surrounding cobble substratum. These large fish (200–220 mm SL) feed nonselectively on algal assemblages within territories that are dominated by red algae belonging to the genus *Polysiphonia* (Montgomery 1978).

Initial treatment of samples

Sixteen species of red (Rhodophyta), green (Chlorophyta) and brown (Phaeophyta) algae were analyzed. Red algae were subdivided into two categories: (1) calcareous algae, with brittle thalli and cell walls heavily encrusted with carbonates (Dawson 1966), and (2) fleshy algae, with flexible thalli and without noticeable carbonate deposits.

Air-dried samples of these algae were rinsed lightly in distilled water, and undamaged tissues with less than about five percent of the surface covered by a light growth of epifauna were selected for analysis. Analyses were performed on samples dried to constant weight at 80° C for at least 6 hours and ground in a Wiley mill until they would pass through a 60 mesh-per-inch screen.

Stomach samples were removed from cortez and giant blue damselfish which were shot with a hand spear and dissected on shore within an hour. Other cortez damselfish were anesthetized with quinaldine (Kodak; 1 part quinaldine: 8 parts isopropanol, by volume) by squirting the chemical into their crevices with squeeze bottles. These fish were transported to the beach, placed in styrofoam coolers filled with fresh sea water and left covered and undisturbed for 3–4 hours. Feces were filtered from the water with a fine-mesh aquarium net and air-dried before returning to the laboratory. Because giant blue damselfish could not be anesthetized, they were captured by spear. Fecal samples were dissected from the posterior 20 cm of the intestine (approximately 20% of intestine length).

Loss of soluble substances from cortez damselfish feces to the water could elevate measured assimilation efficiencies, but this error is probably small. Feces did not disintegrate upon release but instead remained compact, and fecal packages appeared to have a delicate mucus cover. Diffusion was probably reduced by this arrangement. Further, most dissolved organic nutrients (proteins, lipids, carbohydrates) are absorbed through the mucosa in the anterior portions of the intestine (Fange & Grove 1979). Nutrients exiting with the feces are probably undigested food materials or components of bacteria.

Chemical and energy analyses

Energy

Caloric content was measured by combusting pellets of algae in a Parr 1241 Automatic Adiabatic Calori-

meter. Benzoic acid was used as a standard. Pellets were composed of finely-ground sample mixed with benzoic acid (usually 2:1. sample: acid, by weight) to insure complete combustion. Samples were weighed to the nearest 0.1 mg and ignited in a bomb charged with 25 atmospheres of oxygen. Final temperature readings were made 9 minutes after ignition, when bomb temperature had stabilized. A correction for endothermy (Paine 1966, 1971) was not applied. If all algal ash were $CaCO_3$, the correction for our samples with highest ash content would only amount to about 2% of the measured calories g^{-1} and would not affect our predictions.

Ash

Ash was determined by placing powdered samples of algae or gut contents (usually 0.5–1.0 g) in open crucibles in a Thermolyne Model 2000 muffle furnace heated to 550° C for at least 6 hours. This time was sufficient to bake samples to constant weight. Weights of initial samples and ash were determined to 0.1 mg on a Mettler Model H 43 balance.

Protein

A modification of the method of Lowry et al. (1951) was used to analyze the samples for protein. Powdered samples were weighed to 0.1 mg and digested for at least 12 hours at room temperature in 1 N NaOH with occasional stirring. After centrifuging samples at 500 rpm for 5 minutes to remove particulate matter, 0.2 ml aliquots were transferred to sterile borosilicate culture tubes to which was added 2.0 ml cupric sulfate in potassium-sodium tartrate solution. The solution was mixed and allowed to stand for 15 minutes, after which 0.2 ml 1 N Folin-Ciocalteu phenol reagent (Sigma Chemical Co.) was added. After 40 minutes the concentration of protein was estimated by a Baush and Lomb Spectronic 20 at 750 nm relative to a bovine serum albumin standard curve.

Lipid

Total lipid was determined gravimetrically after extraction according to a modified form of the method of Folch et al. (1957). Ground samples (20–30 mg, weighed to 0.1 mg) were homogenized for 30 seconds with 0.5 ml methanol in a 12 ml ground glass tissue homogenizer. This was followed, in sequence, by: 2 ml methanol (10 seconds grinding) and 4 ml chloroform (30 seconds grinding). The sample was filtered through a scintered glass filter and 0.88 percent aqueous KCl solution was added equal to one-quarter of the filtrate volume. After centrifuging 10 minutes at 1500 rpm, the upper phase of the biphasic solution was aspirated off and discarded. This procedure was repeated using the lower phase containing the lipid. The remaining solution was dried under vacuum at 35° C in a rotary evaporator. Dried lipid was redissolved in chloroform and pipetted into a pre-weighed vial for final drying under vacuum in a stream of natural gas. The vial with sample was then weighed.

Carbohydrates

Stomach contents and feces of the giant blue damselfish (50 mg) were extracted for 20 hours in 5 ml Schweizer's reagent (tetraaminocopper dihydroxide; Windholz 1976), a standard reagent for determination of cellulose and other substances soluble only in strong alkali. The supernatant was recovered after centrifugation, acidified to pH 5 by dropwise addition of glacial acetic acid, and the precipitated cellulose collected by further centrifugation. The pellet was wahed with 1 N acetic acid and water and then incubated for one hour in 2 N KOH. The insoluble material that remained was washed with water, 1 N acetic acid, and water before transfer to a weighed vial for drying and weighing (Lin et al. 1976).

Only cellulose was determined quantitatively. Crude carbohydrate was estimated, however, by subtracting percent ash, percent protein, and percent lipid from 100%.

Calculations

Quantities of food ingested were not measured directly. As a result, assimilation efficiencies were estimated by comparing a nutrient in the food and feces against a component assumed not to be digested or absorbed. Nutrient fractions in feces are thereby adjusted for materials absorbed in the digestive tract. Use of non-absorbed marker substances is common in animal physiology (e.g., manganese, lignin, chromium oxide, Maynard 1951, Nagy 1977). Cellulose was not a practical marker because algal cellulose content is low (often less then 1%). Instead, ash was chosen because it was a major constituent of the algae and

clearly increased in proportion from stomach to feces while proportions of organic nutrients decreased. Ash is generally considered to be nondigestible (Windell 1978, p. 163). Calculations from Buddington's (1978) data on *Tilapia zillii* indicate a total assimilation efficiency of 29.3% based on cellulose as a marker compared to 35% when ash is used as a marker. True assimilation efficiencies may be underestimated if some ash is absorbed, but will not be overestimated. This type of potential error is acceptable for our purposes.

The first step in calculating assimilation efficiencies is a correction of fecal nutrient values. We assume ingested ash equals egested ash, but due to absorption of organic nutrients the amount of ash per gram feces will be greater than ash per gram ingested food. We ease calculations of assimilation efficiencies by adjusting fecal nutrient values so they are expressed as g nutrient remaining per g algae ingested: If A = ash, N = nutrient, F_i = ingested food, F_e = egested feces, and $A_i = A_e$, then

$$\text{Corrected Fecal Nutrient } (N_e F_i^{-1}) = \frac{A_i F_i^{-1}}{A_i F_e^{-1}} \times N_e F_e^{-1}.$$

To facilitate computation with our data we used the percentage form of the equation (see Maynard 1951, p. 254):

Corrected Fecal Nutrient (%) =

$$\frac{\%\text{ ash in food}}{\%\text{ ash in feces}} \times \%\text{ nutrient in feces.}$$

The proportion of the total food that was absorbed is the Total Assimilation Efficiency, and the proportion of a given nutrient assimilated is the Nutrient Assimilation Efficiency:

Total Assimilation Efficiency (%) =

$$\left[1.0 - \frac{\%\text{ ash in stomach contents}}{\%\text{ ash in feces}}\right] \times 100\%,$$

Nutrient Assimilation Efficiency (%) =

$$\left[1.0 - \frac{\text{corrected fecal nutrient (\%)}}{\%\text{ nutrient in stomach contents}}\right] \times 100\%.$$

Table 1. Composition of marine algae. Values are mean ± standard error relative to total dry weight. Collection sites: B-Bahia de los Angeles, Baja California, Mexico; CC-Crescent City, California; Fr-Los Frailes, Baja California; Gu-Guaymas, Sonora, Mexico; RP-Rocky Point (Puerto Peñasco), Sonora, Carbohydrate was calculated by subtracting percent ash, percent lipid and percent protein from 100%.

Taxon	Kcal G^{-1}			Ash (%)			Lipid (%)			Protein (%)			Carbohydrate (%)
	$\bar{X}$	*SE*	*N*	$\bar{X}$	*SE*	*N*	$\bar{X}$	*SE*	*N*	$\bar{X}$	*SE*	*N*	$\bar{X}$
Brown algae													
Dictyota sp.	3.50	0.02	3	27.8	0.3	3	11.6	0.7	4	6.4	0.1	3	54.2
Padina sp. (B)	1.62	0.04	3	54.8	0.7	3	4.7	...	1	8.8	0.2	3	31.8
Padina sp. (Gu)	3.55	0.04	4	16.2	0.2	7	3.3	...	1	8.5	0.2	3	72.1
Sargassum sp. (Fr)	2.58	0.02	3	32.8	0.9	3	2.8	...	1	9.4	0.1	3	55.1
Sargassum sp. (RP)	2.73	0.04	2	24.7	0.2	3	1.8	...	1	8.3	0.1	3	65.2
Green algae													
Ulva sp. (Gu)	3.22	0.02	4	24.2	0.4	5	2.4	...	1	7.2	0.1	3	66.2
Ulva sp. (CC)	3.38	0.04	3	26.6	0.1	3	6.6	...	1	13.2	0.2	3	53.6
Fleshy red algae													
Ahnfeltia concinna	2.87	0.02	3	20.7	0.1	3	1.2	...	1	6.8	0.1	3	71.3
Eucheuma denticulatum	2.31	0.12	3	29.2	0.4	3	1.0	...	1	2.8	0.1	3	67.0
E. nudum	2.60	0.04	3	41.5	1.2	8	2.5	...	1	8.8	0.1	3	47.3
E. striatum	2.09	0.04	3	50.3	0.5	7	1.9	0.2	4	4.0	0.1	3	43.1
Gigartina exasperata	3.00	0.02	3	30.6	0.2	2	1.0	...	1	11.7	0.2	3	56.8
Polysiphonia June1976	2.08	0.01	2	45.9	0.5	2	3.6	...	1	7.5	0.1	3	43.0
sp. Aug. 1977	2.49	0.18	2	36.5	0.5	2	3.1	...	1	11.8	0.2	3	48.6
Jan. 1978	....	....		51.5	0.4	2	2.1	...	1	8.2	0.2	3	38.2
Calcareous red algae													
Jania sp.	....	....		81.2	1.0	2	1.4	...	1	0.8	0.1	3	16.6
Amphiroa sp.	....	....		81.9	2.0	2	1.6	...	1	1.0	0.1	3	15.5
Lithophyllum sp.	....	....		81.8	0.5	2	2.1	...	1	1.7	0.1	3	14.4

Results

Chemical composition of marine algae

Fleshy algae vary greatly in chemical composition within taxonomic divisions and within genera (Table 1). For fleshy red algae the range for ash content was from 20.7 to 51.5% of dry weight, for lipid 1.0 to 3.6%, for protein 2.8 to 11.8%, and for energy from 2.08 to 3.00 kcal g^{-1}. Fleshy brown algae exhibited a range for ash from 16.2 to 54.8% of dry weight, for lipid 1.8 to 11.6%, for protein 6.4 to 9.4% and for energy from 1.62 to 3.55 kcal g^{-1}. Broad variation also exists within genera. For example, *Padina* spp. contained from 16.2 to 54.8% ash and from 1.62 to 3.55 kcal g^{-1} dry weight; *Eucheuma* spp. varied from 29.2 to 50.3% ash and from 2.8 to 8.8% protein. Even specimens of *Polysiphonia* collected five months apart from the same site (Los Frailes) varied from 36.5 to 51.5% ash and from 8.2 to 11.8% protein on a dry weight basis. Composition of algae may vary with species, individual, reproductive condition, age of tissue, and season (Percival & McDowell 1967, Paine & Vadas 1969, Dawes et al. 1974). In view of such variation, we focus on mean values from the different algal divisions which might give clues to major patterns in food value of algae.

Fleshy algae from all three divisions contain approximately 3% lipid, 8% protein, 54% carbohydrate, 34% ash and 3 kcal g^{-1} dry weight (Table 2). Green algae have a higher caloric content than either brown or red algae (3.30 kcal g^{-1} compared with 2.80 and 2.49, respectively), and their ash content (25.4%) is lower than either brown (31.3) or red (38.3) algae. Green algal protein (10.2% is higher than that of brown (8.3%) or red (7.7%), and their lipid (4.5%) is intermediate between that of brown (4.8%) and red (2.1%). Carbohydrate content is high in all three divisions: green algae 59.5%, brown algae 55.7%, and red algae 51.9%.

Calcareous red algae differ in several respects from the fleshy types (Table 2). Calcareous algae average 82% ash compared to 34% for fleshy algae. Calcareous forms contain only 1.2% protein on a dry weight basis, while fleshy algae average 8.2%. Lipid and carbohydrates are also low in calcareous algae (1.7 and 15.5% of dry weight, respectively) relative to fleshy algae (3.3 and 54.2%). Caloric determinations for the three species of calcareous algae were too few and too variable to be reliable. However, the average caloric content of 5 species of calcareous algae examined by Paine & Vadas (1969) was 0.8 kcal g^{-1}, much lower than either their values or mine for fleshy algae (2.7–3.3 kcal g^{-1}).

Comparisons of the average caloric content and chemical composition of the three algal divisions indicate that green algae are superior to brown and red algae as potential foods. Green algae rank higher than the other two divisions in calories, protein and carbohydrates, are intermediate in lipid content, and are

Table 2. Summary of the chemical composition of algae listed in Table 1. Except for caloric content, figures are means and standard errors of percent of algal dry weight.

	Green algae	Brown algae	Red algae	All fleshy algae	Calcareous red algae
Kcal G^{-1}	3.30	2.80	2.49	2.72	0.78*
SE	0.08	0.35	0.14	0.15	0.07
N	2	5	7	14	5
Ash (%)	25.4	31.3	38.3	34.2	81.6
SE	1.2	6.5	3.9	3.1	0.2
N	2	5	8	15	3
Lipid (%)	4.5	4.8	2.1	3.3	1.7
SE	2.1	1.8	0.3	0.7	0.2
N	2	5	8	15	3
Protein (%)	10.2	8.3	7.7	8.2	1.2
SE	3.0	0.5	1.1	0.7	0.3
N	2	5	8	15	3
Carbohydrate (%)	59.9	55.7	51.9	54.2	15.5
SE	6.3	6.8	4.2	3.2	0.6
N	2	5	8	15	3

* value taken from Paine & Valdas (1969).

Table 3. Summary of analyses of the algal mat (available food resource) and stomach contents of cortez damselfish. Data for fish are from Table 4. Except for caloric content, values are means for percent dry weight. Carbohydrate in algal mat was calculated by subtracting percent ash, percent lipid and percent protein from 100%.

	Algal mat	Stomach contents
Kcal G^{-1}	0.40	(2.70)*
N	3	...
Ash (%)	81.6	50.2
N	3	8
Protein (%)	1.7	26.1
N	3	8
Lipid (%)	2.1	3.6
N	1	7
Carbohydrate (%)	14.6	21.4
N	...	7

* Based on data in Table 1

Table 4. Composition of stomach contents and feces of cortez damselfish, *Eupomacentrus rectifraenum*, taken August 1977 at Los Frailes, Mexico. Values are in percent of total dry weight; fecal values are corrected for absorption during digestion. Carbohydrate was calculated by subtracting percent ash, percent lipid and percent protein from 100%.

Stomach sample	% Ash	% Protein	% Lipid	% Carbohydrate
1	60.7	9.6	2.5	27.2
2	60.9	17.9	1.9	19.3
3	45.7	23.6	4.0	26.8
4	61.1	24.6	19.5*	−5.23*
5	50.0	36.3	2.7	11.0
6	29.5	44.8	4.6	21.1
7	64.7	23.7	4.6	6.9
8	29.0	28.5	4.9	37.7
Mean	50.2	26.1	3.6	21.4
SE	5.1	3.8	0.5	3.9
N	8	8	7	7
Fecal sample (adjusted for absorption)				
1	37.9	2.6	2.4	32.9
2	50.2	2.0	1.4	22.2
3	58.5	3.6	1.5	26.4
4	54.7	3.4	0.9	16.9
5	63.8	4.6	1.6	5.9
Mean	50.2	3.2	1.6	20.9
SE	4.4	0.4	0.3	4.6
N	5	5	5	5

* values discarded from calculations of means and standard errors

lowest in ash. Red algae are lowest of the three divisions in calories, lipid, and protein and carbohydrate, and have the highest ash content.

Digestion of algae by fishes

Eupomacentrus rectifraenum

Analyses of the algal mat and of cortez damselfish stomach contents demonstrate the impact of selective feeding (Table 3). The algal mat has a lower concentration of organic nutrients than do the stomach contents. The caloric content of stomach contents was not measured, but is estimated to be 2.7 kcal g^{-1} from analyses of various fleshy red, brown and green algae (Table 2). This is a 6.8-fold difference over the algal mat (0.4 kcal g^{-1}). The ratio of stomach content to algal mat protein is 16 (stomach 26.1 percent, mat 1.7), lipid is 1.7 (stomach 3.6 percent, mat 2.1), and carbohydrate is 1.5 (stomach 21.4 percent, mat 14.6). The high ash content of the mat (81.6%) relative to stomach contents (50.2%) and various fleshy algae (34%; Table 2) is due to a large fraction of calcareous algae in the mat (about 16% of all biological material in the mat) and to sand and shell fragments trapped in the mat. Evidently the fish select the most nutritious foods from the array that is available.

Composition of stomach contents differs substantially from that of feces, as would be expected (Table 4). Because specimens used for collection of stomach contents were not those used for collection of feces, only the means of the two sources are compared. On a dry weight basis (Table 4) stomach contents contain 50.2% ash, 26.1% protein, 3.6% lipid and 31.4% carbohydrate. Adjusted nutrient levels in the feces were 3.2% protein, 1.6% lipid and 20.9% carbohydrate. Thus the fish absorbed approximately 88% of the available protein, 56% of the available lipid and 2% of the available carbohydrate.

Microspathodon dorsalis

The territorial giant blue damselfish feeds non-selectively on an algal turf that is composed almost exclusively of a species of the red algal genus *Polysiphonia*. Analyses of the algal mat outside territory boundaries, *Polysiphonia* from within the territory, and stomach contents of giant blue damselfish demonstrate the advantage of feeding within the territory

(Table 5). *Polysiphonia* is clearly richer than the algal mat in calories, protein, lipid and carbohydrate on a dry weight basis. Even with the relatively high ash content of stomach samples, the *Polysiphonia* is superior to the algal mat in all fractions except ash.

On the average, stomach contents of the giant blue damselfish were 61.4% ash, 14.0% protein, 4.6% lipid and 19.9% carbohydrate (Table 6). Adjusted nutrients in the feces average 4.8% protein, 2.3% lipid and 13.6% carbohydrate. The fish absorbed 57% of the algal protein, 47% of the lipid and 37% of the carbohydrate. Ash content of stomach samples is higher by 25% and carbohydrate lower by 29% than expected, based on analyses of *Polysiphonia* sampled during the same period. The difference may be explained by the fact that fishes collected for stomach and posterior intestine (fecal) samples were taken at some distance from the area where ecological studies were conducted. The food of fish collected for stomach and fecal analyses contained a larger proportion of algae with high ash content than food of fish from territories where *Polysiphonia* was collected for chemical analysis.

Table 5. Summary of composition of algal mat, food *(Polysiphonia)* and stomach contents of giant blue damselfish, *Microspathodon dorsalis*. Values are relative to dry weight. Stomach content composition taken from Table 6. Values are means and standard errors for percent of dry weight.

	Algal mat	Polysiphonia	Stomach
Kcal G^{-1}	0.40	2.49	(2.49)*
SE	0.02	0.18	...
N	3	2	...
Ash (%)	81.6	36.5	61.4
SE	0.6	0.5	4.4
N	3	2	9
Lipid (%)	2.1	3.1	4.6
SE	...	...	0.6
N	1	1	9
Protein (%)	1.7	11.8	14.0
SE	0.1	0.2	1.9
N	3	3	9
Carbohydrate (%)	14.6	48.6	19.9
SE	...	...	2.2
N	...	...	9

* Based on data in Table 1

Assimilation efficiencies

Total and lipid assimilation efficiencies for the cortez damselfish (24.2 and 56.4%, respectively) are similar to those for the giant blue damselfish (20.1 and 46.3%; Table 7) In contrast, protein assimilation efficiency for the cortez damselfish (87.7%) was much higher than that for the giant blue damselfish (57.4%), and the cortez damselfish appeared to digest only 2.3% of the crude carbohydrate compared to the 37.1% digested by the giant blue damselfish. Since both species of fishes eat similar foods (delicate red or green algae) and do not masticate, similar assimilation values are expected; the dissimilar values for protein and carbohydrate deserve attention.

Table 6. Composition of stomach and posterior intestine contents of nine giant blue damselfish, *Microspathodon dorsalis*, collected August 1977 at Los Frailes, Baja California Sur, Mexico. Values are percent of total dry weight. Fecal values (except ash) adjusted for absorption. S = stomach, I = intestine (feces), A = assimilation efficiency.

	% Ash			% Protein			% Lipid			% Carbohydrate		
Specimen	*S*	*I*	*A*	*S*	*I*	*A*	*S*	*I*	*A*	*S*	*I*	*A*
1	60.5	69.5	–	12.3	4.5	63.5	4.6	3.0	35.0	22.6	19.1	15.7
2	69.2	72.7	–	7.6	4.9	35.6	4.4	3.5	21.3	18.9	17.5	7.0
3	43.8	77.1	–	21.7	2.8	87.2	7.3	1.6	78.6	27.3	8.7	68.2
4	52.2	72.3	–	16.8	4.3	74.6	3.9	1.8	53.8	27.1	13.9	48.8
5	49.7	70.3	–	20.3	5.0	75.2	6.2	2.2	64.1	23.9	13.9	41.9
6	55.8	64.0	–	15.7	8.9	43.4	5.2	3.6	31.5	23.3	18.9	19.1
7	76.8	77.0	–	7.8	6.7	14.8	2.4	2.8	-16.5*	13.0	13.5	-3.8*
8	59.9	85.6	–	18.1	2.5	86.1	6.3	1.2	80.5	15.8	6.4	59.7
9	84.8	84.5	–	6.2	3.9	36.4	1.5	1.4	8.5	7.5	10.2	-36.2*
Mean	61.4	74.6	–	14.0	4.8	57.4	4.6	2.3	46.6	19.9	13.6	37.2
SE	4.4	2.1	–	1.9	0.7	8.6	0.6	0.3	9.4	2.2	1.5	8.9

* Values not used in calculations of means and standard errors

Table 7. Assimilation efficiencies for cortez damselfish, *Eupomacentrus rectifraenum*, and giant blue damselfish, *Microspathodon dorsalis*, fed on marine algae. Efficiencies in parentheses are adjusted to correct for inflated protein values in stomach contents of cortez damselfish.

Species	Average assimilation efficiencies (%)*			
	Total	Protein	Lipid	Carbohydrate
Cortez	24.2	87.7 (67)	56.4	2.3 (44)
Giant blue	20.1	57.4	46.3	37.1

* All negative efficiencies excluded from calculations of means

Discussion

Algae as food for fishes

Differences in chemical composition and energy content between algal taxa may indicate differences in their value as foods to fishes. We define a food of high value as one that is readily digested, and which provides a relatively large proportion of required energy and nutrients to the fish per unit weight of food. On the basis of caloric and proximate chemical analyses of algae from three taxonomic divisions, green algae appear superior to both brown and red algae as potential foods. Green algae are highest, red algae lowest and brown algae intermediate in caloric content. Conversely, ash content is lowest in green algae, highest in red algae, and again intermediate in brown algae. Paine & Vadas (1969), in an extensive survey of temperate zone marine algae, also found green algae to be highest in calories and lowest in ash of the three divisions, but their red algae had higher caloric content than did brown algae.

Total lipid is low in all three algal divisions. Lipid levels from our studies and others (Russell-Wells 1932, Black & Cornhill 1951, Idler & Wiseman 1970, Jensen 1972, Dawes et al. 1974, Hayashi et al. 1974) exceeded 5% of dry weight in only 4 of 49 specimens. Algae are also low in protein, a component critical to growth (Gerking 1952, Phillips 1969, Prosser 1973, Cowey 1975). Green algae exceed red and brown algae in protein content. Our values for protein content on a dry weight basis (3–13%) are consistent with the 2–10% in other red and brown algae (Jensen 1972, Madgwick & Ralph 1972, Dawes et al. 1974).

Although they are not notably deficient in any particular nutrient class, calcareous algae are selectively excluded from the diets of several herbivorous fishes (Tsuda & Bryan 1973, von Westernhagen 1974, Montgomery 1977, 1978). Those fishes frequently ingesting calcareous algae tend to be large, highly specialized, non-selective feeders such as surgeonfishes and parrotfishes (Randall 1967). The strong inverse correlations between ash and energy content (correlation coefficient = –0.83 for this study) and ash and organic nutrient content suggest that exclusion of calcareous algae from the diet could have selective advantage.

Algal carbohydrates and digestion by fishes

The major problems in algal digestion reside with hydrolysis of polysaccharides, which are a greater energy reservoir than proteins or lipids. The ease of hydrolysis depends heavily on the bonds which link monosaccharide subunits of the polysaccharides. Alpha (α) linked polysaccharides, such as starch, are more susceptible to amylases than are beta (β) linked polymers. Amylase has high activity in the guts of herbivorous fishes (Barrington 1957, Kapoor et al. 1975, Fange & Grove 1979) Enzymes capable of degrading β-linked polymers such as cellulose and its analogs are rare (Kenyon 1925, Ishida 1936, Al-Hussaini 1947, Barrington 1957, Kapoor et al. 1975) and often may be traced to the transient presence of microorganisms in the gut (Sera et al. 1974, Stickney & Shumway 1974, Trust & Sparrow 1974).

If the alleged inability of fishes to digest β-linked polymers proves to be true it will have definite consequences for potential food value of the algal divisions. The brown algae are characterized by storage compounds and extracellular substances that are β-linked polymers of glucose and various uronic acids (Percival & McDowell 1967, Craigie 1974, Mackie & Preston 1974). In contrast, green algae store starch, an α-linked polymer of glucose, but cell walls contain highly resistant polymers of glucose, mannose of xylose (Craigie 1974, Mackie & Preston 1974). Thus, the bulk of extracellular carbohydrates of green algae are probably not digestible. Red algae store Floridean starch (Craigie 1974), an α-linked glucose polymer, and their extracellular compounds are dominated by diverse polysaccharides composed of galactose and substituted galactose monomers joined by alternate α and β linkages. The variable composition of the extracellular polysaccharides, the acid-labile α bonds (Percival & McDowell 1967), and the broad substrate specificity of many glucosidases (see Larner 1960) may combine to make extracellular carbohydrates of ma-

rine red algae more susceptible to digestion than are those of the green or brown algae.

In this discussion we largely ignore the roles of low gut pH of fishes and secondary defensive compounds of algae. Low gut pH in some fishes may affect algae, but the compounds dissolved or digested are not identified (Ogden & Lobel 1978, P. Lobel, personal communication). Conditions required for partial or complete hydrolysis of algal polysaccharides prior to chemical analysis (Percival & McDowell 1967) suggest that conditions of temperature, pH and residence time in the fish stomach would be insufficient to allow significant digestion. Small amounts of acid hydrolysis would not affect predictions, as the more acid-labile α bonds are also more likely to be broken by unspecialized vertebrate hydrolases (Percival & McDowell 1967). The role of secondary compounds is impossible to assess. Certain fishes ignore algae known to contain high concentrations of noxious compounds (P. Lobel, personal communication), but there is little knowledge of how such compounds at lower concentrations might influence palatability or digestibility of algae.

On the basis of nutrient and energy content, green algae are superior to brown algae, and both are superior to red algae as potential foods. When digestibility of carbohydrates is considered, however, green and red algae should be superior foods for fishes by virtue of their moderate to high levels of protein and lipid and the availability of certain carbohydrates for digestion. Fishes would increase caloric and nutrient intake by ignoring algae with high ash content. Finally, brown algae should have low food value because of their lack of digestible carbohydrates.

Feeding and digestion by fishes

Selective feeding

The feeding tactics of both fishes used in this study fulfill predictions about algal food quality based on nutrient and energy content of algae as well as the digestibility of cell wall and storage carbohydrates. Both species exclude calcareous and brown algae from their diet, either by choice (cortez damselfish) or by feeding from an algal assemblage in which those types of algae are absent (giant blue damselfish). Further, such feeding strongly influences the composition of ingested foods compared with available foods. There is more ash in the algal mat than in ingested food for the cortez damselfish, with a concomitant rise in ingested lipid, protein and carbohydrate. For the giant blue damselfish, there is lower ash and higher lipid, carbohydrate and protein in the stomach and in *Polysiphonia* (from territories) than in the surrounding algal mat.

Many herbivorous marine fishes feed selectively on fleshy red and green algae. Rabbitfishes (Siganidae) reject calcareous and tough brown algae in favor of delicate green algae, such as *Enteromorpha*, and filamentous red algae, such as *Gracilaria* (von Westernhagen 1974). The damselfish *Hemiglyphidodon plagiometopon* removes brown and calcareous algae and deposits them outside territory boundaries, leaving small fleshy algae within the boundaries of the feeding territory (Dennis Lassuy, personal communication). *Cebidichthys violaceus*, a temperate blennioid fish, prefers the leafy green alga *Ulva*, takes several species of red algae, and ignores several species of brown and calcareous red algae (Montgomery 1977).

Assimilation efficiences

Total assimilation efficiencies for natural foods are similar for both Gulf of California damselfishes: 24.2% for the cortez damselfish, 20.1% for the giant blue damselfish. These values are in accord with those determined for *Siganus spinus* fed red algae (6–39%, mean 16%; Bryan 1975), *Tilapia zillii* fed *Najas* (29.3%; Buddington 1978), and the grass carp *Ctenopharyngodon idella* fed various aquatic plants (10–20%; Fischer 1970, Stanley & Jones 1976, Venkatesh & Shetty 1978).

Lipid assimilation efficiencies were also similar for the cortez and giant blue damselfishes – 56% and 46%, respectively, but those for protein differ widely, 88% as opposed to 57%. Protein levels in stomach contents of the cortez damselfish appear to be inflated over expected values. The average level of protein in stomach contents is two times the highest protein value we recorded from 15 species of fleshy algae and three times the average value for fleshy algae. Inflated protein values for stomach contents of cortez damselfish most likely result from the secretion of mucus by cells lining the buccal cavity, esophagus or stomach (Barrington 1957) or from cell debris from the gut lining. These artifacts would be indistinguishable from the true ingested material and would increase the protein levels of the stomach contents. Mucus was clearly present on fresh stomach samples from cortez damselfish and no attempts were made to remove it. In contrast, no mucus was noted in stom-

ach samples from giant blue damselfish, which had stomach protein levels (14%) only slightly higher than values predicted from uneaten fleshy algae (about 9%).

Protein content of red and green algae in cortez damselfish stomach contents should be about 9% of total dry weight. Protein assimilation efficiency based on this predicted value is 67% instead of the measured 26%, close to the value for the giant blue damselfish (57%). Protein absorption efficiencies for plant foods (40–80%) tend to fall below those for animal foods (± 95%; Gerking 1952, 1955, Menzel 1960).

The large differences in apparent carbohydrate absorption efficiency between the cortez damselfish (2.3%) and the giant blue damselfish (37.1%) is probably another artifact of the inflated protein values of stomach contents of the cortez damselfish. The high protein value would suppress the calculated carbohydrate level. Substituting an adjusted protein value of 9% (see above) for the measured 26% leads to a revised carbohydrate absorption efficiency of 43.8%, similar to the value for the giant blue damselfish. Calculations from Buddington's data (1978) for *Tilapia zillii* indicate a non-cellulosic carbohydrate absorption efficiency of 39.9%.

In summary, the major stumbling block to understanding digestion by herbivorous marine fishes is the paucity of information on hydrolysis of beta-linked polysaccharides (cellulose and its analogues). Here we assume, supported by a sparse literature, that fishes are incapable of degrading such polymers with either endogenous enzymes or with a cultured gut flora. Although these assumptions await a rigorous test, herbivorous marine fishes feed in a manner consistent with predictions based only on algal biochemistry (Lewin 1962, Percival & McDowell 1967, Stewart 1974) and the behavior of enzymes common among fishes (Barrington 1957, Kapoor et al. 1975). Thus, the fishes themselves suggest that studies on the digestive abilities of piscine herbivores in relation to the biochemistry of their algal resources will yield more powerful generalizations about herbivory than a search for highly specialized enzymes or cultured microbes.

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