AN ABSTRACT OF THE THESIS OF HERLING R. SANGER for Master of Science in Biology presented June 19, 1989.

Title: Assimilation of epiphytized and nonepiphytized blades of the seagrass *Halodule uninervis* by the herbivorous rabbitfish *Siganus argenteus* (Quoy & Gaimard)

Approved: ______________________________

Stephen G. Nelson, Thesis Committee Chairman

The utilization of epiphytized and nonepiphytized forms of the seagrass *Halodule uninervis* as a nutrient source by the rabbitfish *Siganus argenteus* was investigated. *Siganus argenteus* did not show a preference for either type of seagrass blades. *Siganus argenteus* assimilated proteins from epiphytized seagrass (90.7%) at a significantly higher efficiency than from nonepiphytized seagrass (50.5%). The caloric assimilation efficiencies for epiphytized blades (24.7%) was also significantly higher than nonepiphytized blades (17.1%). No difference was detected in efficiencies of assimilation of either organic matter (19.1%, nonepiphytized and 22.6%, epiphytized) or nitrogen

(42.3%; 23.4%) between nonepiphytized and epiphytized blades. Seagrasses may constitute a more important direct trophic link to herbivorous reef fishes than formerly thought.

TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Herling R. Sanger presented June 19, 1989.

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ASSIMILATION OF EPIPHYTIZED AND NONEPIPHYTIZED BLADES OF THE SEAGRASS *Halodule uninervis* BY THE HERBIVOROUS RABBITFISH *Siganus argenteus* (Quoy & Gaymard)

by

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LIST OF TABLES

INTRODUCTION

Seagrass has not been viewed as an important nutrient source for herbivorous fishes (Lagler *et al.*, 1972). Birkeland & Grosenbaugh (1985) hypothesized that while that there has been enough evolutionary time for herbivorous fishes to adapt to digesting marine algae, this is not so for the marine anthophytes. Angiosperms are relatively recent invaders of the marine environment, and their major grazers, dugongs, turtles, and birds, are those vertebrates which evolved from terrestrial ancestors. Also, as in other vertebrates, fishes lack intrinsic cellulase to break down the structural polysaccharides of plants (Barnard, 1973). The absence of cellulase in the digestive tracts of fishes is supported by the findings of, among others, Stickney & Shumway (1974), Prejs & Blaszczyk (1977), Lindsay & Harris (1980), Montgomery & Gerking (1980), Moerland (1985), and Klumpp & Nichols (1985). Therefore, the observed ingestion of seagrass blades by fishes has been dismissed as incidental to the fishes' presumed target of the epiphytic growth on the blades (Kikuchi, 1974; Van Montfrans *et al.*, 1984; Tribble, 1981).

The digestion of marine algae by herbivorous fishes has been adequately demonstrated (Horn *et al.*, 1986; Montgomery & Gerking, 1980; Gerking, 1984; Anderson, 1987). Fishes can utilize nutrients from algae despite the absence of cellulase in their digestive tracts because they have other adaptations to break down the tough cell wall. Parrotfish, for example, have a pharyngeal mill which masticates the food (Ogden & Lobel, 1978). Low stomach pH, which in effect lyses the cell wall, can be found in many herbivorous fishes (Payne, 1978; Lobel, 1981). Other such adaptations include long digestive tracts, muscular stomachs, longer foraging times, and longer digestion times (Horn *et al*., 1986; Pandian & Vivenkanandan, 1985).

Few studies, however, have focussed on the nutritive importance of seagrass to herbivorous fishes, and most of these studies have been based on stomach content analysis (Kikuchi, 1980; Van Montfrans *et al*., 1984; Ogden, 1980; see also Randall, 1965; 1967). In most of these studies researchers have concluded that seagrasses are not digested by herbivorous fishes. For example, field observations by Kikuchi (1980) led him to conclude that the ingestion of seagrasses by herbivorous fishes is an artifact of the fishes' feeding on the epiphytic growth on the seagrass blades. Also, Bell *et al*. (1978) observed that the leatherjackets *Monacanthus chinensis*, *Meuschenia freycineti*, and *M*. *trachylepis* feed only on the epiphytic growth and not on the seagrasses. Likewise, Ogden (1980) suggested that herbivorous fishes in the Caribbean digest only the epiphytes on the seagrass blade, not the seagrass blade itself. However, when Lobel & Ogden (1981) observed that the diet of the parrotfish *Sparisoma radians* consisted of epiphytized seagrass as well as nonepiphytized seagrass and algae, they concluded that the parrotfish is maximizing its nutrient intake by feeding on a more diverse diet.

A physiological approach to the issue was taken by Klumpp & Nichols (1985) who quantified the efficiencies of assimilation by the omnivorous halfbeak *Hyporhamphus melanochir* feeding on the seagrass *Heterozostera tasmanica*. The efficiencies of assimilation were 38%, 28%, 50%, and 76% for organic matter, energy, protein, and lipids, respectively. However, after calculating the energetic requirements of the fish, they concluded that other nutrition sources, such as crustaceans, are needed for the fish to have a complete diet.

The only other evidence of the digestion of angiosperms by herbivorous fishes comes from research on freshwater fishes. Van Dyke & Sutton (1977) reported assimilation efficiencies of 72%, 61%, and 80% for total organic matter, gross energy, and protein, respectively, for the grass carp *Ctenopharyngodon idella* feeding on the duckweed *Lemna* sp. Buddington (1979) reported that the total organic matter and protein assimilation efficiencies of *Tilapia zillii* feeding on *Najas* sp. were

29% and 75%, respectively. Similar direct assessments are lacking for herbivorous marine fishes.

This study addresses the issues of the digestibility of the seagrass *Halodule uninervis* and the importance of epiphytic growth on its blades to the herbivorous fish *Siganus argenteus*, a common and economically important herbivore (Tobias, 1976) often found in seagrass beds throughout the Indo-Pacific (Woodland, 1983). Siganids have also been reported to be consumers of seagrasses (Lundberg & Lipkin, 1979; Von Westernhagen, 1973). The seagrass *Halodule uninervis* is particularly abundant in Cocos Lagoon, Guam (Tsuda *et al*., 1977).

Three specific questions were asked in this study:

- To what degree can the seagrass *Halodule uninervis* be assimilated by the rabbitfish *Siganus argenteus*?
- Does *Siganus argenteus* better assimilate nonepiphytized or epiphytized seagrass?
- Does *Siganus argenteus* exhibit a preference for either nonepiphytized or epiphytized seagrass?

MATERIALS AND METHODS

COLLECTION

Both nonepiphytized and epiphytized seagrass blades were collected from Cocos Lagoon, on the southern coast of Guam (13°28'N, 144°44'E°). Epiphytic growth on *Halodule uninervis* blades was determined to be mainly filamentous Cyanobacteria and red algae, calcareous red algae, and diatoms. The seagrass was maintained in a flow-through seawater tank for at most one week at the University of Guam Marine Laboratory until it was used in the feeding trials.

The fish used in the feeding preference and assimilation efficiency determinations were selected from approximately 400 *Siganus argenteus*, caught in the May to June 1988 recruitment run. Prior to the experiments, the fish, each about 7 months old and approximately 17 cm in total length, were maintained on a diet of both pelleted feed and the siphonous green alga *Enteromorpha clathrata*.

DESIGN

Four *Siganus argenteus* were placed into each of eight different cages submerged in a cement raceway. The dimensions of the cages and the raceway were 35 cm X 50 cm X 69 cm and 114 cm X 440 cm X 60 cm, respectively. The cages were designed to prevent reingestion of fecal material by the rabbitfish, with each cage consisting of a top level where the fish were kept, and a bottom level where the fish's fecal material accumulated. The removable bottom level was constructed of plastic sheets and was secured to the top level with clothespins.

NUTRIENT ASSIMILATION EFFICIENCIES

FEEDING REGIME

The fish were fed on nonepiphytized *Halodule uninervis* for one week and then starved for 24 h. They were then again fed nonepiphytized seagrass, and the fecal material was collected by siphoning the bottom level of the cage into a 65-um nylon screen mesh at 3-h intervals for two consecutive days. Collections were made only during the day when the fish are normally active and feeding. This procedure was then repeated with epiphytized *Halodule uninervis*. Studies with the closely related *Siganus spinus* have shown that the food retention time of the fish is between two to three hours (Bryan, 1975).

The leaching of water soluble nutrients from fecal material was assumed to be negligible. However, there is a possibility that it is not, which could result in an overestimate in assimilation efficiencies. Montgomery & Gerking (1980) reported that for *Eupomacentrus rectifraenum* and *Microspathodon dorsalis* soluble nutrients are quickly absorbed in the anterior portions of the gut and that the feces consist mostly of undigested, insoluble material.

COMPOSITIONAL ANALYSES

Ash was used as an inert marker to estimate the assimilation efficiencies of total organic matter, protein, calories, and nitrogen of nonepiphytized and epiphytized Halodule uninervis by Siganus argenteus. Ash has been used as an inert marker in several studies of assimilation efficiency of herbivorous fishes (Gerking, 1984; Horn & Neighbors, 1984; Horn et al., 1986). The major assumption of the method is that ash is not appreciably digested by the fish.

The determination of assimilation efficiencies involved the analysis of both the food Halodule uninervis and the fecal material. The food, either nonepiphytized or epiphytized blades of Halodule uninervis, and fecal materials were dried at 60°C to constant weight in a drying oven and then separately homogenized with mortar and pestle. The homogenized samples were then redried at 60°C and stored in a desiccator until ready for analyses. Two subsamples were taken from each sample and processed to determine the ash, protein, calorie, and nitrogen contents.

The organic matter contents of the seagrass and feces were estimated by igniting them at 500°C for 4 h, and then reweighing the samples after they had cooled in a desiccator to room temperature. The weight loss on ignition estimates the total organic matter content of the sample. Total nitrogen content was measured with a Carlo Erba Strumentazione NA 1500 NCS Analyzer. PABA (para-aminobenzoic acid) was used as a standard for calibration. Protein content was measured spectrophotometrically with a Sigma Lowry kit. Bovine serum albumin (BSA) was used as a standard. Caloric contents of dry samples were measured with a Phillipson microbomb calorimeter (Phillipson, 1964; Paine, 1971), using benzoic acid, which contains 6318 calories per mg dry weight, as a standard for calibration.

CALCULATIONS

The total organic matter assimilation efficiency was calculated as follows (from Conover, 1966):

$$U = [(F - E) / ((1 - E)(F))] \times 100$$

U = Total organic matter assimilation efficiency
F = Ash free dry weight/dry weight ratio of food
E = Ash free dry weight/dry weight ratio of feces

Nutrient assimilation efficiency was calculated by the method of Condrey *et al.*, (1972):

$$NAE = F\ [r_i - r_e\ (1 - U/100)]$$

NAE = Total Nutrient Assimilation Efficiency
F = Ratio of organic weight to dry weight of food
r_i = Ratio of nutrient to total organic matter in food
r_e = Ratio of nutrient to total organic matter in feces
U = Total organic matter assimilation efficiency

FEEDING PREFERENCE

Feeding preference of Siganus argenteus for either nonepiphytized or epiphytized Halodule uninervis was determined by offering nonepiphytized and epiphytized blades to the fish on feeding racks constructed of PVC pipe and polypropylene rope. In order to avoid possible complications resulting from depth preference, the two seagrass strands, braided into the ropes, were at the same level in the water when offered to the fish. Two blades, approximately 65 mg, one of each seagrass, were used per feeding trial. Each blade was blotted, pressed, and weighed to the nearest mg, then offered to the fish as described above. When about half of either was eaten, the rack was removed from the cage, and the remaining pieces of seagrass were retrieved, repressed, reblotted, and reweighed. The amount of Halodule uninervis eaten was then determined as the difference between the weight of individual blades prior to and after the feeding period.

STATISTICAL ANALYSIS

The data on efficiencies of assimilation were normalized by performing an arc-sine transformation. Parametric paired t-tests were used for the feeding preference and the assimilation efficiency determination because the data were homoscedastic. In detecting differences in moiety concentrations between nonepiphytized and epiphytized Halodule uninervis, a parametric two sample t-test was used for sets of data that were homoscedastic, and a nonparametric Wilcoxon Rank sum test was used for data that were heteroscedastic. The statistical program BMDP 3D (available from the University of California at Los Angeles BMDP Statistical Software, 1964 Westwood Blvd., Los Angeles, CA 90025) was used in computing the t-values and the exact probabilities for both tests.

RESULTS

Siganus argenteus showed no significant preference for either nonepiphytized or epiphytized blades of *Halodule uninervis* (paired t-test, two-tailed $p = 0.123$, $n = 8$). The fish consumed an average of 55.3% (± 9.66 S.E.M) of the nonepiphytized blades, and 40.7% (± 10.30) of the epiphytized ones.

While epiphytic growth on seagrass blades influenced the efficiencies of assimilation of proteins and calories, it did not have an effect on assimilation of total organic matter or nitrogen (Tables 1). Protein from epiphytized seagrass was assimilated with 90.74% efficiency, which is significantly higher than assimilation efficiency from nonepiphytized blades, 50.54% (paired t-test, $p = 0.000$, $n = 8$). Also, caloric assimilation efficiency was higher in epiphytized blades, 24.66%, than nonepiphytized seagrass, 17.10% (paired t-test, $p = 0.0315$, $n = 8$).

Differences between nonepiphytized and epiphytized blades in nitrogen and caloric concentrations were not significant (t-test, two-tailed $p > 0.05$, Table 2). The percentage of total organic matter was significantly higher in the nonepiphytized *Halodule uninervis* (t-test, two-tailed $p = 0.0017$, Table 2). Although no difference was detected in protein concentrations between nonepiphytized and epiphytized blades of *Halodule* *uninervis* (Wilcoxon Rank-sum test, $p = 0.0688$, Table 2), a type II error, failure to reject a false null hypothesis, could have resulted from the small sample size.

Table 1. Efficiencies of assimilation of different organic moieties in the seagrass *Halodule uninervis* by the rabbitfish *Siganus argenteus*. The sample size in all cases was 8. The data were normalized with an arc-sine transformation, and paired t-tests were used in the statistical analysis.

	Assimilation Efficiency (%) ± S.D.		
Moiety	Nonepiphytized	Epiphytized	p-value
Total organic matter	19.10 ± 2.62	22.55 ± 2.72	0.245
Nitrogen	42.32 ± 6.89	23.35 ± 3.57	0.255
Protein	50.54 ± 4.45	90.74 ± 1.35	0.000
Calories	17.10 ± 3.73	24.66 ± 2.95	0.032

Table 2. Protein, nitrogen, calories, and total organic matter content of the fecal material of the rabbitfish *Siganus argenteus* feeding on either nonepiphytized or epiphytized seagrass *Halodule univervis*. All measurements are on dry weight basis. LOI (Loss on ignition) estimates percentage of organic matter in the sample. The sample size for the fecal material nutrient content analysis is 8. The sample size for the food nutrient content analysis is given in parenthesis.

	Nonepiphytized		Epiphytized	
	Mean ± SEM	Range (n)	Mean ± SEM	Range (n)
FECES (n=8)				
LOI (%)	62.56 ± 1.73	56.12 - 71.24	44.44 + 0.92	39.34 - 47.43
Nitrogen (%)	2.05 ± 0.09	1.77 - 2.61	1.89 ± 0.05	1.70 - 2.12
Protein (%)	9.47 ± 0.86	6.50 - 13.76	4.25 ± 0.64	2.36 - 7.69
Calories (Kcal/mg)	2.31 ± 0.11	1.59 - 2.62	1.70 ± 0.05	1.43 - 1.86
FOOD				
LOI (%)	72.87 ± 1.66	67.38 - 76.19 (4)	51.37 ± 0.01	51.36 - 51.39 (2)
Nitrogen (%)	2.09 ± 0.04	2.04 - 2.15 (2)	1.94 ± 0.07	1.84 - 2.04 (2)
protein (%)	1.48 ± 0.08	1.30 - 1.63 (3)	4.09 ± 0.25	3.73 - 4.44 (2)
Calories (kcal mg^{-1})	2.62 ± 0.10	2.48 - 2.76 (2)	2.02 ± 0.01	2.00 - 2.03 (2)

DISCUSSION

The results of this study indicated that the herbivorous fish Siganus argenteus can digest seagrass, thus providing an example counter to the hypothesis that seagrasses are not readily digested by fishes (Lagler et al., 1972; Pandian & Vivenkanandan, 1985; Ogden, 1980). Thus, seagrass can potentially be an important food source for herbivorous reef fishes. However, the importance of Halodule uninervis epiphytes in determining their food value to Siganus argenteus cannot be entirely discounted, as proteins and calories were both more effectively assimilated from epiphytized blades than from nonepiphytized blades (Table 1). The proteins derived from epiphytes of Halodule uninervis apparently enhance the food value of the seagrass, which has a protein content within the lower range of those reported for marine algae (Birch, 1973; Montgomery & Gerking, 1980). In spite of this, the fish did not prefer either the nonepiphytized or epiphytized seagrass. Thus, they do not appear to recognize the difference in nutrient values of the two seagrass types.

Overall, Siganus argenteus was more efficient at assimilating proteins than it was at assimilating nitrogen, organic matter, or calories. Others have reached similar conclusions with their studies. For example, Sarpa salpa (Gerking, 1984), Cebidichthys violaceus, and Xiphister mucosus (Horn et al, 1986; Horn & Neighbors, 1984) were found to have maximized protein intake, rather than nitrogen, energy, or total organic material. The significance of high protein assimilation efficiency may be that herbivorous fishes need to maximize protein intake.

Klumpp & Nichols (1985) found similar assimilation efficiencies in their investigation of the digestion of the seagrass Heterozostera tasmanica by the halfbeak Hyporhamphus melanochir. They calculated assimilation efficiency rates of 38%, 28%, 50%, and 76% for organic matter, energy, protein, and lipids, respectively (Table 3). Furthermore, although the nutrient contents of angiosperms are comparable to those of marine algae (Birch, 1973; Montgomery & Gerking, 1980; Buddington, 1979; Table 2), herbivorous fishes assimilate these nutrients with efficiencies (17 to 56%) similar to those reported for marine algae (36 to 79%) (Table 3).

In summary, this study showed that the seagrass Halodule uninervis, a marine angiosperm, can be directly used as a source of nutrition by the herbivorous Siganus argenteus. The ability to digest and assimilate seagrass is likely to be a feature shared with other herbivorous marine fishes, and thus, the role of herbivory by fishes in the direct energetic pathway in seagrass beds may be more important than previously thought.

Table 3. Reported efficiencies of assimilation for herbivorous fishes feeding on aquatic plants. * = angiosperm.

		ASSIMILATION EFFICIENCY (%)				
Fish species	Food	Protein	Energy	Organic	Nitrogen	Source
Siganus argenteus	_Halodule uninervis_*					This study
	nonepiphytized	50.5	17.1	19.1	42.3	
	epiphytized	90.7	24.7	22.6	23.3	
Hyporhamphus melanochir	_Heterozostera tasmanica_*	50	28	38		Klumpp & Nichols (1985)
Tilapia	_Najas_*	75		55.7		Buddington (1979)
Sarpa salpa	_Ulva_	81	65	59		Gerking (1984)
Cebidichthys violaceus	Various algae	77-95			72-83	Horn & Neighbors (1984)
Xiphister mucosus	Various algae	69-98				Horn _et al_. (1986)
Eupomacentrus rectifraenum and _Microspathodon dorsalis_	Various algae	57-67				Montgomery & Gerking (1980)
Ctenopharyngodon idella	_Lemna_	80	61	72		Van Dyke & Sutton (1977)
Stegastes lividus	Red algae			36-79	29-72	Lassuy (1984)

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