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Food Habits, Functional Digestive Morphology, and Assimilation Efficiency of the Rabbitfish *Siganus spinus* (Pisces, Siganidae) on Guam[1]

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ABSTRACT: Analyses of stomach contents of *Siganus spinus* showed that algal availability and size and behavior characteristics of the fish determine what kinds of algae are ingested in the field. Sixty-two algal species were tested during multiple-choice food preference trials in the laboratory. Elimination trials and observation tests showed a ranked order of algal preference: (1) *Enteromorpha compressa*, (2) *Murrayella periclados*, (3) *Chondria repens*, (4) *Boodlea composita*, (5) *Cladophoropsis membranacea*, (6) *Acanthophora spicifera*, and (7) *Centroceras clavulatum*. An examination of the morphology of the digestive system showed that the fish are well-adapted herbivores, especially toward the filamentous algae. The assimilation values for the adults ranged from 6 to 39 percent; those for the juveniles ranged from 9 to 60 percent.

AMONG THE FISHES inhabiting Guam waters, members of the family Siganidae constitute one of the more important food resources for local consumption. In Guam, the family is represented by five species (Kami, Ikehara, and DeLeon 1968), of which *Siganus spinus* (Linnaeus) is the most abundant. Siganids are also the focus of considerable maricultural interest (unpublished data from the Siganid Mariculture Implementation Conference, Hawaii Institute of Marine Biology, 1–5 November 1972).

Each year during the months of April and May, and occasionally during June and October, schools of juvenile *S. spinus* swarm on the reef flats of Guam (Tsuda and Bryan 1973) where they spend several months foraging on benthic algae. On Guam adults are usually found in shallow water along the reef front and often venture onto the reef flats to browse on benthic plants. Both adults and juveniles are primarily diurnal feeders, feeding almost continuously during the daytime. These fish are often found in schools but may browse individually or in pairs, sometimes accompanying other siganids, scarids, and acanthurids.

This study deals with the herbivorous nature of *S. spinus*: types of benthic plants ingested and preferred, description of the morphological and functional aspects of the digestive mechanisms as related to ingestion and digestion, and the assimilation efficiency of the most preferred alga ingested.

A food preference study by Tsuda and Bryan (1973) on juvenile *S. spinus* and *S. argenteus* (= *S. rostratus*) indicated a selective feeding habit for filamentous algae and smaller fleshy algae. Jones (unpublished) reported on the stomach contents of 11 specimens of *S. spinus* and offered some insight into the food habits of this species. Descriptions of the digestive tract are available for *Siganus fuscescens* (Suyehiro 1942, Tominaga 1969) and for *S. argenteus* (Hiatt and Strasburg 1960). There are no values available on the assimilation efficiency for any member of this family.

Specimens used for all facets of this study were captured by spearing, throw net, or at night by hand with the aid of flashlights. Those fish captured alive at night were transferred to

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the laboratory. Benthic plants used in experiments were collected from various localities around Guam.

STOMACH CONTENTS

To estimate floral species common to each area, I made algal collections from those areas where the fish were collected. Stomach contents of *S. spinus* were preserved in individual vials with 10-percent formalin prior to examination. Food items found in the stomachs were treated as relative abundance (percentage composition by species) and relative frequency (percentage of occurance; that is, how often a species was found) with a modified version of the point method of Jones (1968*b*) being used. Whereas Jones used 17 points per grid, I used 81 points per grid in this study. The importance values (IV) were obtained by summing relative abundances (RA) and relative frequencies (RF).

Results of stomach content analyses are shown in Table 1. Everything found in the stomachs was identifiable. The four algae representing the highest importance values obtained in this study were *Gelidiopsis intricata* (27 IV), *Boodlea composita* (26 IV), *Sphacelaria tribuloides* (25 IV), and *Centroceras clavulatum* (24 IV). Crustaceans were few (2.1 IV). The pooled stomach contents of 53 young juveniles (30–50 mm fork length [FL]) also were examined. Only four food items were found: *Gelidium pusillum* (64 RA), *Centroceras clavulatum* (35 RA), *Ceramium* sp. (0.8 RA), and one annelid worm (0.2 RA).

TABLE 1

FOOD ITEMS, LISTED IN ORDER OF IMPORTANCE VALUE, PRESENT IN STOMACH CONTENTS OF *Siganus spinus*

CONTENTS	RA	RF	IV
Gelidiopsis intricata	15.0	12.0	27.0
Boodlea composita	18.0	8.0	26.0
Sphacelaria tribuloides	11.0	14.0	25.0
Centroceras clavulatum	15.0	9.0	24.0
Feldmannia indica	8.0	10.0	18.0
Gelidium pusillum	10.0	3.0	13.0
Sargassum polycystum	7.0	5.0	12.0
Calothrix pilosa	5.0	6.0	11.0
Enteromorpha compressa	2.0	5.0	7.0
Cladophoropsis membranacea	1.0	5.0	6.0
Hypnea pannosa	2.0	3.0	5.0
Jania capillacea	1.0	3.0	4.0
Ceramium sp.	0.7	3.0	3.7
Polysiphonia sp.	0.1	2.0	2.1
Crustaceans	0.1	2.0	2.1
Tolypiocladia glomerulata	1.0	1.0	2.0
Padina tenuis	0.5	1.0	1.5
Desmia hornemanni	1.0	0.3	1.3
Cladophora sp.	0.3	1.0	1.3
Dictyota bartayresii	0.2	1.0	1.2
Diatoms (epiphytes)	0.2	1.0	1.2
Champia parvula	0.1	1.0	1.1
Padina sp. (vaughaniella)	<0.1	1.0	1.0
Hormothamnion enteromorphoides	<0.1	1.0	1.0
Rhodymenia sp.	0.6	0.3	0.9
Caulerpa racemosa	0.3	0.3	0.6
Neomeris annulata	0.1	0.3	0.4
Microcoleus lyngbyaceus	<0.1	0.3	0.3

NOTE: *Siganus spinus* specimens measured from 65 to 200 mm fork length; $N = 70$. They were taken from six localities on Guam. RA, relative abundance; RF, relative frequency; and IV, importance value.

FOOD PREFERENCE

Multiple-Choice Trials

Multiple-choice feeding trials were conducted to find out which species of benthic plants were preferred by the fish. Three groups of fish (nine fish in each group, 130–200 mm FL) were held in wooden holding tanks (145 × 85 × 28 cm) with running seawater. The fish were starved for 2 days before tests were begun. Equal quantities of 5 to 15 freshly collected algal species were fastened by clothespins and suspended for 30 to 60 minutes in each tank. The number of algal samples used per trial varied because it was not always possible to collect equal numbers of species and because many of the algae deteriorated quickly when held in holding tanks at the laboratory. Each species of alga was tested at least three times with each fish group (total of nine times); the positions of the algae were alternated for each new test. Sixty-two species (54 genera) of benthic plants were tested.

The results were similar to those found by Tsuda and Bryan (1973) for the juveniles. In that paper, 56 plant species were tested on the juveniles and only 12 were always completely consumed (by both *Siganus spinus* and *S. argenteus*). Of these, nine were filamentous and three were fleshy. The tests on adults revealed that, out of 62 species tested, only nine were always completely ingested; six of the algae were filamentous (*Boodlea composita*, *Cladophoropsis membranacea*, *Enteromorpha compressa*, *Centroceras clavulatum*, *Ceramium* sp., and *Murrayella periclados*) and three were fleshy (*Acanthophora spicifera*, *Chondria repens*, and *Gelidiopsis intricata*). Only 12 species were never consumed by the adults whereas 26 were rejected by the juveniles.

Elimination Trials

Two new tanks of fish (nine fish per tank, 150–200 mm FL) were used to run elimination trials among the seven preferred algal species, as determined from the above experiments, to obtain an indication of rank. (*Ceramium* sp. and *Gelidiopsis intricata* were not available at this time in quantities large enough for further tests.) Three 5-g blotted wet-weight samples of each of the seven preferred species were hung submerged by clothespins in alternating positions from boards placed across the tops of the two tanks. The algae were checked at intervals because the feeding rates of the fish varied. The number of samples of each species consumed was recorded. The algal species with all three samples consumed was eliminated from the next trial. For example, if all three samples of *Enteromorpha compressa* were consumed during the first trial, then that species was eliminated from the rest of the trials, and so on, until all the species were eliminated. If two or more species had all three of their samples consumed during a trial, then that trial was repeated with fresh algal samples. The test fishes were fed less-preferred algae between tests so that partiality among the fish toward those seven algae being tested would be avoided. The preferred algal species were then ranked in order of preference by the fishes. By order of consumption, they are *Enteromorpha compressa*, *Murrayella periclados*, *Chondria repens*, *Boodlea composita*, *Cladophoropsis membranacea*, *Acanthophora spicifera*, and *Centroceras clavulatum*.

Definitive Observation Trials

To test the hypothesis that a ranked order of algal preference existed, I ran six more tests, using new fish for each test. Tests were run in a 150-liter plastic tank containing two fish (140–170 mm FL) that had been starved for the preceding 24 hours. Two fish per experiment were used because solitary fish would not feed properly under experimental conditions. A solitary fish usually occupied its time swimming along the sides of the tank or hiding. However, two fish usually behaved more normally, one fish establishing dominance. Both fish spent most of their time feeding rather than seeking ways to escape from the container or hiding.

One 3-g blotted wet-weight sample of each of the ranked algal species was hung submerged by clothespins near the bottom of the tank. The placement order of the samples was alternated for each new test. A plywood blind was used to observe and record the order in which the algal samples were consumed. Those species that were consumed in the same order as that established by the previous elimination trials were rated 1. The species that were not consumed in the same order as in the elimination trials were rated zero. Even though the fish often fed alternately on several of the algae, the frequency of visits to a particular sample and the length of stay usually correlated nicely with the order of consumption of that alga. However, I strengthened the test statistically by recording two or more species as zero if they could not be distinguished as to their consumed order. The data were entered in a two-way table and the Cochran's test for related observations (Conover 1971) was used to test statistically the hypothesis that a ranked order of algal preference existed.

$$T = c(c-1)\left[\sum_{j=1}^{c}\left(C_j - \frac{N}{c}\right)^2\right] \Big/ \left[\sum_{i=1}^{r} R_i(c-R_i)\right]$$

where R_i = row totals, C_j = column totals, r = number of blocks, c = number of treatments, and N = total number of 1's. T is expected to follow the χ^2 distribution with $c-1$ degrees of freedom.

Based on a 95-percent degree of confidence, the results of these trials led to the rejection of the null hypothesis that no definite order of preference exists ($P \leqslant 0.05$) according to Cochran's test as seen in Table 2. Therefore, the alternate hypothesis that a ranked order of

TABLE 2

RESULTS OF DEFINITIVE FEEDING TRIALS OF *Siganus spinus*

r	*c*								
(FISH PAIRS)	*Enteromorpha compressa*	*Murrayella periclados*	*Chondria repens*	*Boodlea composita*	*Cladophoropsis membranacea*	*Acanthophora spicifera*	*Centroceras clavulatum*	R_i	$R_i(c-R_i)$
1	1	1	1	1	1	1	1	7	0
2	1	1	1	1	0	0	1	5	10
3	1	1	1	1	1	1	1	7	0
4	1	1	1	1	0	0	0	4	12
5	1	1	1	0	0	1	1	5	10
6	1	1	1	1	0	0	0	4	12
C_j	6	6	6	5	2	3	4	32	44

NOTE: Trials tested the order of preference among the seven most preferred algal species and the data used for computation of the Cochran's test for related observations (Conover 1971). *c*, number of treatments; *r*, number of blocks; R_i, row totals; C_j, column totals.

preference exists was accepted: (1) *Enteromorpha compressa*, (2) *Murrayella periclados*, (3) *Chondria repens*, (4) *Boodlea composita*, (5) *Cladophoropsis membranacea*, (6) *Acanthophora spicifera*, and (7) *Centroceras clavulatum*. Randall (1961) also found that *Enteromorpha* was one of the two most preferred algae of the convict tang *Acanthurus triostegus sandvicensis* in Hawaii.

DIGESTIVE MORPHOLOGY

Teeth, gill rakers, and pharyngeal structures were examined with the aid of a dissecting scope. Lengths of the gastrointestinal tracts were obtained by unwinding the gut and measuring from esophagus to anus.

Dentition

The upper jaw of *Siganus spinus* overlaps the lower jaw upon closing. The upper teeth are more pointed than the lowers, the lowers being somewhat rounded. Both the upper and the lower teeth are characterized by having a distinct notch and cusp protruding to one side (Figure 1*A*). The number of teeth present in the upper jaw (150–165 mm FL) is about 32; the number in the lower jaw, about 36. Feeding observations both in the laboratory and in the field revealed that the fish takes short quick bites, often biting, then backing away, pulling and cutting the algae as it does so. Sometimes it will make quick lateral jerks with its head as it bites.

Gill Arches and Pharyngeal Teeth

Siganus spinus has four distinct gill arches, the fifth being modified into pharyngeal tooth plates (Figure 1*C*). The gill rakers of the first and second arches are long and pointed, the central axis having lateral processes which may, in turn, branch in the second arch. The rakers of the third and fourth arches become progressively broader and have serrate upper margins. The lower pharyngeal elements of the fifth arch contain numerous fine spinelike projections oriented in a posterior manner on plates. The upper pharyngeals contain thicker thornlike spines (Figure 1*B*).

Gastrointestinal Tract

The stomach typically lies on the left side of the body and may be divided into the cardiac and pyloric regions. The wall of the cardiac stomach is about 0.5 mm thick in most adult specimens, thickening to about 1.0 mm as it constricts and merges into the pyloric region. Both regions are lined interiorly with thin longitudinal folds. The pyloric region constricts near the pyloric ceca, of which there are always five. The large lobe of the liver lies on the left side of the body, the smaller lobe on the right side. The gall bladder lies on the left side along the upper intestinal regions.

The intestinal wall is rather thick (about 0.8 mm), becoming thinner in the lower regions. The interior is lined with numerous tiny papillae. The complex winding nature of the

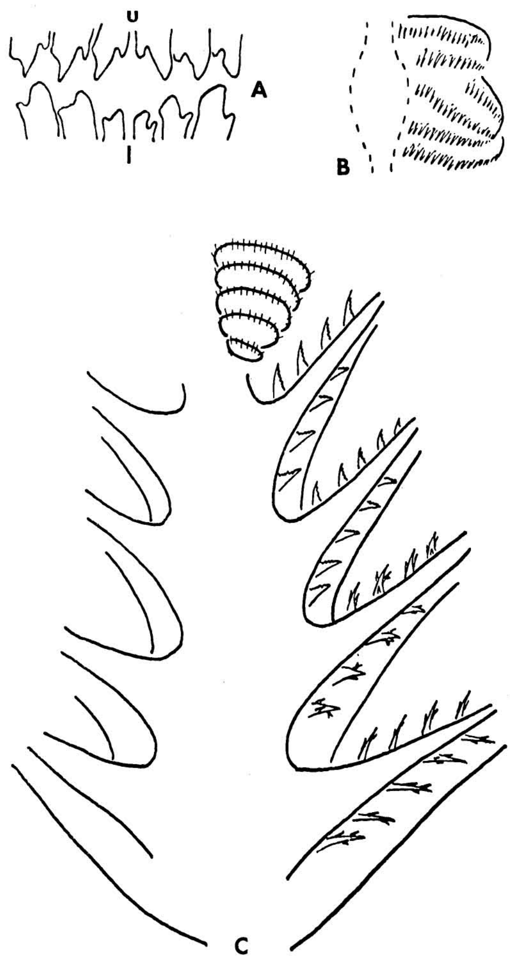

FIGURE 1. *Siganus spinus*. *A*, upper (u) and lower (l) median teeth; *B*, upper pharyngeals; *C*, pharyngeal apparatus showing gill arches 1–4 and the lower pharyngeal bones.

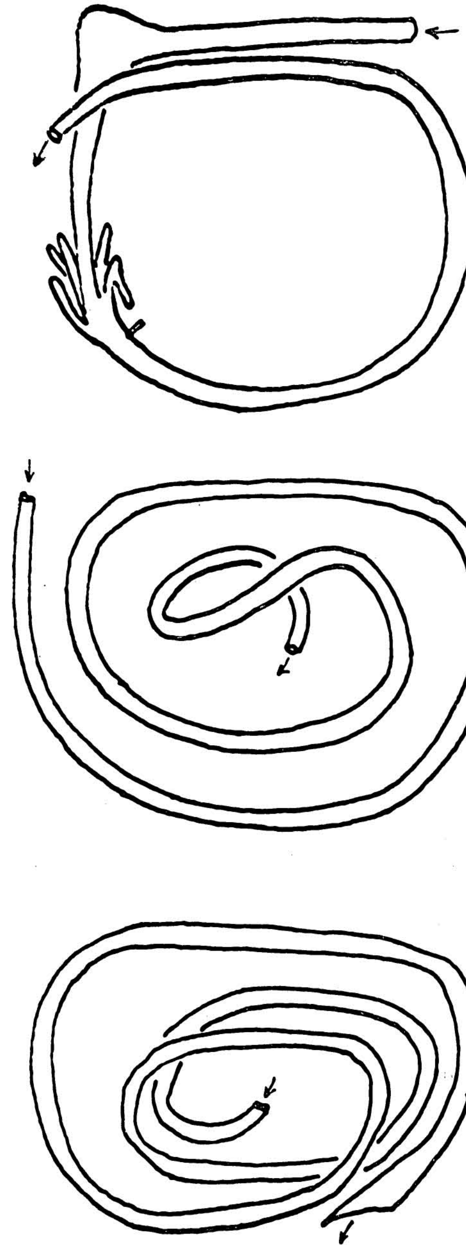

FIGURE 2. Diagrammatic drawing showing the complex coiling of the gastrointestinal tract of *Siganus spinus*.

gastrointestinal tract can be seen in Figure 2 and very nearly duplicates the intestinal winding of that described for *S. fuscescens* by Suyehiro (1942). The length of the gastrointestinal tract of *S. spinus* (102–155 mm FL) is 3.5 to 4.0 times the fork length of the body ($N = 5$).

The amount of time required for food to pass through the gut from the time of ingestion to the time of defecation was determined by feeding *Cladophoropsis membranacea* and *Enteromorpha compressa* to starved fish in a 150-liter tank and then by recording the time of appearance of the first feces. This time may be as short as 1.5 hours in the juveniles, although it usually takes 2 hours or as many as 3 hours in the adults. Because the fish were starved, these results may be biased.

TABLE 3

GROSS ^{14}C ASSIMILATED (%) BY ADULT AND JUVENILE *Siganus spinus* AFTER INGESTING LABELLED *Enteromorpha compressa*

STAGE OF DEVELOPMENT	TRIALS	$\bar{x}$ FORK LENGTH (mm)	GROSS ^{14}C ASSIMILATED (%)
Adults	1	107	20
(N = 2 per	2	114	11
trial)	3	119	7
	4	123	39
	5	131	6
	6	132	8
	7	140	24
Juveniles	1	51	47
(N = 5 per	2	52	60
trial)	3	54	27
	4	59	9

ASSIMILATION EFFICIENCY

A highly desirable method of determining assimilation rates in animals is that of using ^{14}C (Bakus 1969). For each experiment a 12-g blotted wet-weight sample of the most preferred alga, *Enteromorpha compressa*, was allowed to incorporate ^{14}C through photosynthesis. Incubation was made in 250 ml of seawater containing 2 μCi of [^{14}C]$NaHCO_3$ between the hours of 1000 and 1400 in a shaded outdoor area (500–1000 ft-c). The alga was then dipped in a saltwater solution of 0.001 N HCl and rinsed in running seawater for 3 minutes to remove any adsorptive ^{14}C. A subsample was retained and the remainder was fed to either one set of adults (two fish) or one set of juveniles (five fish). In all cases, the fish were previously starved and held in a 150-liter plastic tank with running seawater. Seven trials on adults and four trials on juveniles were run. As they appeared, feces were siphoned onto a paper towel for a period of 1 hour. Samples of the incubated alga at the time of feeding and feces were dried in an oven at 60° C. Equal subsamples of each were weighed to the nearest milligram, ground into a near-powder form, and placed in scintillation vials along with 15 ml of scintillation fluid. The samples were allowed to stabilize in darkness for at least 24 hours before being counted in a Beckman liquid scintillation counter. Percentage of carbon uptake was derived from the formula (fecal cpm/algal cpm) $\times 100 - 100\% =$ gross (%) carbon assimilated.

The results (Table 3) showed that the amount of carbon assimilated by adults ranged from 6 to 39 percent ($\bar{x}$ = 16 percent). Results of tests on juveniles also varied considerably, ranging from 9 to 60 percent ($\bar{x}$ = 36 percent). These values represent gross assimilation as respiration was not accounted for in the experiments. The extreme nervousness of this fish made any accurate measurements of respiration impossible. In addition, Sorokin (1966), basing his conclusion on experiments by Monakov and Sorokin (1961) with *Daphnia*, decided that ^{14}C losses due to respiration are unimportant in short-term experiments (3–6 hours).

DISCUSSION

A comparison of food habit vs. food preference data would seem to be pointless, as it would be expected that most of the preferred kinds of algae would make up a significant portion of the stomach contents. However, the most preferred alga, *Enteromorpha compressa*, grows only in abundance along the intertidal zone of two beach areas on the leeward side of Guam (Tumon and, to a lesser extent, Agana). Similarly, the second ranked alga, *Murrayella periclados*, is relatively rare on Guam, growing mostly intertidally on the basal portions of shaded limestone rocks. The third ranked alga, *Chondria repens*, is often found in inner reef flats. None of the above three algal species were found in the stomach contents of 11 specimens examined from Tumon Bay. Yet, all three algae were available to the fish in large quantities if the fish chose to move close to shore. The nervous behavior of *Siganus spinus* restricts the exploitation of these algae since the postjuvenile fish rarely venture close to the intertidal zones to feed.

Avoidance of blue-green algae by herbivorous acanthurids has been observed by Randall (1961) and by Jones (1968*a*), and for juvenile *S. spinus* and *S. argenteus* by Tsuda and Bryan (1973). Of the four blue-greens tested in food preference studies, only the genus *Schizothrix* was never ingested. This genus was not found in any of the stomach contents, even though it was available to the fish. However, *Calothrix pilosa* rated 5-percent abundance in those fish taken from one area in Pago Bay on the windward coast. These fish were collected in beds of *Sargassum polycystum* where *Sphacelaria tribuloides*, *Calothrix pilosa*, *Hormothamnion enteromorphoides*, *Schizothrix calcicola*, and *Jania capillacea* were growing luxuriantly as epiphytes on the *Sargassum*. *Sphacelaria tribuloides* was most abundant in the stomachs of these fishes. Of the 12 algal species which were never ingested in the food preference multiple-choice trials, only *Jania capillacea* (4 IV) was found in the stomach contents. *Jania capillacea* often grows intermixed with other epiphytic types such as *Sphacelaria tribuloides* and *Calothrix pilosa.*

From stomach samples taken from fish in another area of Pago Bay, *Gelidium pusillum* made up almost 90 percent of those algae found, and *Sphacelaria tribuloides* made up about 5 percent. *Gelidium pusillum*, *Sphacelaria tribuloides*, and *Padina tenuis* were the dominant species of algae found in this area at the time of collection. Similarly, *Boodlea composita*, representing the highest relative abundance (18 percent) and second highest importance value (26) was found almost exclusively in stomach samples taken from the Gun Beach reef flat on the northern end of Tumon Bay on the leeward side of Guam. *Boodlea composita*, *Gelidiopsis intricata*, and *Padina tenuis* were dominant in this area. *Gelidiopsis intricata* represents 15-percent relative abundance and the highest importance value (27) in the food habit data.

Only three species of algae and one annelid worm were found in the pooled stomach contents of 53 juveniles (30–50 mm FL) collected from Pago Bay in May, whereas eight species were found in 13 adults (150–200 mm FL) taken from the same area in March. The algal flora was essentially the same during these months. This suggests that the fish, as it matures, ingests a wider variety of algal types, including such species as *Sargassum polycystum* and *Mastophora macrocarpa*, a lightly calcified alga.

In the food preference tests, over twice as many species of algae were rejected by the juveniles (Tsuda and Bryan 1973) than by the adults. Adults are able physically to bite and ingest the larger, tougher algal species. This factor was probably significant for the high mortalities of starving juveniles recorded by Tsuda and Bryan (1973). They reported on the obvious absence of filamentous algae on the reefs of Guam shortly after the invasion by an extremely numerous run of juvenile *Siganus spinus* and *S. argenteus*. Although both juveniles and adult *S. spinus* prefer the filamentous algae, the young juveniles are probably dependent upon them for survival.

The occurrence of microcrustaceans (2.1 IV) and one annelid worm in the stomach contents is probably due to accidental consumption but may represent a significant supplementary dietary feature in the food of *S. spinus*. In a 42.8-g blotted wet-weight sample of *Centroceras clavulatum* and a 62.3-g sample of *Hypnea pannosa* taken from the outer reef flat of Pago Bay, Larson (1974) found 8,338 microcrustaceans and polychaetes. *Centroceras clavulatum* made up 71 percent of the food found in 13 stomach samples in fish taken from the outer reef flat of Pago Bay where *Centroceras clavulatum* was plentiful. Yet, microcrustaceans and polychaetes were almost absent in the stomach contents.

It is obvious that stomach contents of *Siganus spinus* are indicative only of the particular area where the fish has been feeding prior to capture. The algae must be available to the fish in order to be ingested. Algal availability is dependent on seasonality, zonation, and movement of the fish. Furthermore, preferred algal types will be selected for if they are available. Although a significant food preference exists among these fish, their size and behavior characteristics, combined with algal availability, determine the types of algae ingested by them in the field.

The incising nature of the teeth of *S. spinus* make them well adapted to browsing on benthic plants, particularly the filamentous types. The long coiling gastrointestinal tract increases time for digestion and allows for the almost constant feeding behavior of these fishes. Various similarities exist between the gastrointestinal tract of *S. spinus* and those of other herbivorous fishes, particularly the acanthurids studied by Al-Hussaini (1947, 1949), Randall (1961), and Jones (1968*a*).

Nutritional studies of aquatic animals in which radioisotopic tracers are used are not new, although most of these studies have dealt with zooplankters (Marshall and Orr 1955, 1956; Lasker 1960; Monakov and Sorokin 1960; Berner 1962; Sorokin 1966). Others (Sorokin and Panov 1966) have investigated the nutritional factors of fish larvae by feeding them ^{14}C-labelled zooplankton. Reports of the use of ^{14}C as a tracer element to obtain an index of assimilation efficiency from the carbon uptake by marine herbivorous fishes are virtually nonexistent in the literature.

Although the assimilation efficiency of juveniles appears to be higher than that of the larger fishes, the wide ranges of assimilation values obtained were probably due to several factors such as individual variation among the fish, stress of the fish under experimental conditions, and variations in particle sizes of the ground-up algal and fecal samples used in counting. The figures for average assimilation (16 percent) of *Enteromorpha compressa* by the adult specimens of *Siganus spinus* obtained in this study are not surprising. Johannes and Satomi (1966) determined that the average efficiency of converting food to feces by marine herbivores was about 20 percent. A compilation of literature by Welch (1968) showed that animals with low assimilation efficiencies tend to be plant or detritus feeders. Welch also hinted that animals with low assimilation efficiencies compensate by having high ingestion rates in order to supply enough energy for growth and maintenance. In the case of *Siganus spinus*, which feeds almost continuously, it seems reasonable that the constant ingestion rate would easily compensate for low assimilation.

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LITERATURE CITED

AL-HUSSAINI, A. H. 1947. The feeding habits and morphology of the alimentary tract of some teleosts living in the neighborhood of the Marine Biological Station, Ghardaqa, Red Sea. Publ. Mar. Biol. Stn. Ghardaqa, Red Sea 5: 1–61.

———. 1949. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: anatomy and histology. Quart. J. Microscopical Sci. 90(2): 109–141.

BAKUS, G. J. 1969. Energetics and feeding in shallow marine waters. Vol. 4, pages 275–369 *in* W. J. L. Felts and R. J. Harrison, eds. International review of general and experimental zoology. Academic Press, New York. ix + 392 pp.

BERNER, A. 1962. Feeding and respiration in the copepod *Temora longicornis* (Müller). J. Mar. Biol. Assoc. U.K. 42: 625–640.

CONOVER, W. J. 1971. Practical nonparametric statistics. John Wiley & Sons, New York. x + 462 pp.

HIATT, R. W., and D. W. STRASBURG. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30(1): 65–127.

JOHANNES, R. E., and M. SATOMI. 1966. Composition and nutritive value of fecal pellets of a marine crustacean. Limnol. Oceanogr. 11(2): 191–197.

JONES, R. S. 1968*a*. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). Micronesica (J. Univ. Guam) 4(2): 309–361.

———. 1968*b*. A suggested method for quantifying gut contents in herbivorous fishes. Micronesica (J. Univ. Guam) 4(2): 369–371.

KAMI, H. T., I. I. IKEHARA, and F. P. DELEON. 1968. Check-list of Guam fishes. Micronesica (J. Univ. Guam) 4(1): 95–131.

LARSON, H. K. 1974. Notes on the biology and comparative behavior of *Eviota zonura* and *Eviota smaragdus* (Pisces: Gobiidae). M.S. Thesis. University of Guam, Agana.

LASKER, R. 1960. Utilization of organic carbon by a marine crustacean: analysis with carbon-14. Science 131: 1098–1100.

MARSHALL, S. M., and A. P. ORR. 1955. On the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation and excretion in adult and stage V *Calanus*. J. Mar. Biol. Assoc. U.K. 34: 495–529.

———. 1956. Experimental feeding of the copepod *Calanus finmarchicus* (Gunner) on phytoplankton cultures labelled with radioactive carbon (^{14}C). Pages 110–114 *in* Papers in marine biology and oceanography, deep-sea research, suppl to vol. 3. Pergamon Press, London and New York. xx+498 pp.

MONAKOV, A. W., and JU. I. SOROKIN. 1960. Experimental study of the nutrition of *Daphnia* using ^{14}C. Dokl. Akad. Nauk SSSR 135(6): 1516–1518.

———. 1961. The quantitative data on the nutrition of *Daphnia*. Tr. Inst. Biol. Vodokhran., Akad. Nauk SSSR 4(7): 251.

RANDALL, J. E. 1961. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. Pac. Sci. 15(2): 215–272.

SOROKIN, JU. I. 1966. Carbon-14 method in the study of the nutrition of aquatic animals. Int. Rev. Gesamten Hydrobiol. Hydrogr. 51(2): 209–224.

SOROKIN, JU. I., and D. A. PANOV. 1966. The use of C^{14} for the quantitative study of the nutrition of fish larvae. Int. Rev. Gesamten Hydrobiol. Hydrogr. 51: 743–756.

SUYEHIRO, Y. 1942. A study of the digestive system and feeding habits of fish. Jpn. J. Zool. 10(1): 1–303.

TOMINAGA, S. 1969. Anatomical sketches of 500 fishes. College of Engineering Press, Tokyo. 3 vols., supplement.

TSUDA, R. T., and P. G. BRYAN. 1973. Food preference of juvenile *Siganus rostratus* and *S. spinus* in Guam. Copeia (3): 604–606.

WELCH, H. E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology 49(4): 755–759.