

FOOD HABITS, FUNCTIONAL DIGESTIVE MORPHOLOGY,
AND ASSIMILATION EFFICIENCY OF THE RABBITFISH
SIGANUS SPINUS (PISCES: SIGANIDAE) ON GUAM

by

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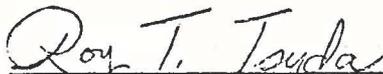
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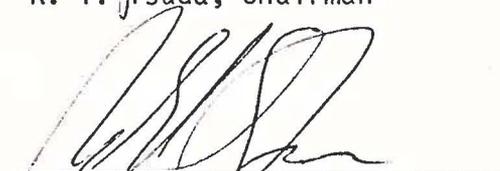
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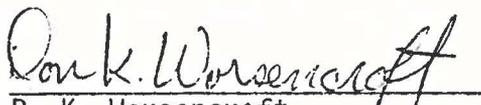
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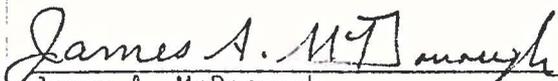

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AN ABSTRACT OF THE THESIS OF Patrick G. Bryan for the Master of Science Degree in Biology presented February 1, 1974.

Title: Food Habits, Functional Digestive Morphology, and Assimilation Efficiency of the Rabbitfish Siganus spinus (Pisces: Siganidae) on Guam

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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 pericladus, 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%; those for the juveniles ranged from 9 to 60%.

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INTRODUCTION

Among the fishes inhabiting Guam waters, members of the family Siganidae comprise one of the more important food resources for local consumption. In Guam, the family is represented by five species (Kami et al., 1968) of which Siganus spinus (Linnaeus) is the most abundant. Siganids are also the focus of considerable maricultural interest (Siganid Mariculture Group, 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 for benthic algae. Adults are usually found in shallow water along the reef front and often venture onto the reef flats to browse on benthic plants. They 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) indicates a selective feeding habit for filamentous algae and smaller fleshy algae. Jones (1968a) reports on the stomach contents of 11 specimens of S. spinus

and offers some insight into the food habits of this species. Descriptions of the digestive tract are available for S. 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 the laboratory. Benthic plants used in experiments were collected fresh from various localities around Guam.

STOMACH CONTENTS

Algal collections were made from those areas where the fish were collected to estimate floral species common to each area. Stomach contents of S. spinus were preserved in individual vials with 10% formalin prior to examination. Food items found in the stomachs were treated as relative (%) abundance and frequency using a modified version of the point method of Jones (1968c). While Jones used 17 points per grid, 81 points per grid were used in this study. The importance values (IV) were obtained by summing relative abundances (RA) and frequencies (RF).

Results of stomach content analyses are shown in Table 1. The four algae representing the highest importance values obtained in this study were Gelidiopsis intricata (27), Boodlea composita (26), Sphacelaria tribuloides (25), and Centroceras clavulatum (24). Crustaceans were few (2.1 IV). The pooled stomach contents of 53 young juveniles (30-50 mm FL) were also 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).

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 x 85 x 28 cm) with running seawater. The fish were

Table 1. Relative abundance (RA), relative frequency (RF), and importance value (IV) of food items present in stomach contents of S. spinus (65-200 mm FL, n=70) taken from six localities on Guam. Species listed in order of IV.

| Contents | RA | RF | IV |
|-----------------------------------|------|------|------|
| <u>Gelidiopsis intricata</u> | 15.0 | 12.0 | 27.0 |
| <u>Boodlea composita</u> | 18.0 | 8.0 | 26.0 |
| <u>Sphacelaria tribuloides</u> | 11.0 | 14.0 | 25.0 |
| <u>Centroceras clavulatum</u> | 15.0 | 9.0 | 24.0 |
| <u>Feldmannia indica</u> | 8.0 | 10.0 | 18.0 |
| <u>Gelidium pusillum</u> | 10.0 | 3.0 | 13.0 |
| <u>Sargassum polycystum</u> | 7.0 | 5.0 | 12.0 |
| <u>Calothrix pilosa</u> | 5.0 | 6.0 | 11.0 |
| <u>Enteromorpha compressa</u> | 2.0 | 5.0 | 7.0 |
| <u>Cladophoropsis membranacea</u> | 1.0 | 5.0 | 6.0 |
| <u>Hypnea pannosa</u> | 2.0 | 3.0 | 5.0 |
| <u>Jania capillacea</u> | 1.0 | 3.0 | 4.0 |
| <u>Ceramium</u> sp. | 0.7 | 3.0 | 3.7 |
| <u>Polysiphonia</u> sp. | 0.1 | 2.0 | 2.1 |
| Crustaceans | 0.1 | 2.0 | 2.1 |
| <u>Tolypocladia glomerulata</u> | 1.0 | 1.0 | 2.0 |
| <u>Padina tenuis</u> | 0.5 | 1.0 | 1.5 |
| <u>Desmia hornemanni</u> | 1.0 | 0.3 | 1.3 |
| <u>Cladophora</u> sp. | 0.3 | 1.0 | 1.3 |
| <u>Dictyota bartayresii</u> | 0.2 | 1.0 | 1.2 |

Table 1. (continued)

| <u>Contents</u> | <u>RA</u> | <u>RF</u> | <u>IV</u> |
|---------------------------------------|-----------|-----------|-----------|
| Diatoms (epiphytes) | 0.2 | 1.0 | 1.2 |
| <u>Champia parvula</u> | 0.1 | 1.0 | 1.1 |
| <u>Padina</u> sp. (vaughaniella) | <0.1 | 1.0 | 1.0 |
| <u>Hormothamnion enteromorphoides</u> | <0.1 | 1.0 | 1.0 |
| <u>Rhodomenia</u> sp. | 0.6 | 0.3 | 0.9 |
| <u>Caulerpa racemosa</u> | 0.3 | 0.3 | 0.6 |
| <u>Neomeris annulata</u> | 0.1 | 0.3 | 0.4 |
| <u>Microcoleus lyngbyaceus</u> | <0.1 | 0.3 | 0.3 |

starved for two days before tests began. 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 many of the algae deteriorated quickly when held in holding tanks at the laboratory. Each species of algae 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 and rated as follows: 0 rejected, - partially ingested, + completely ingested.

The results (Table 2) were similar to those found for the juveniles by Tsuda and Bryan (1973). In that paper, 56 plant species were tested on the juveniles and only 12 were always completely consumed (by both S. 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 and three were fleshy. Only 12 species were never consumed by the adults while 26 were rejected by the juveniles.

Elimination Trials

Two new groups of fish (nine fish per group, 150-200 mm FL) were used to run elimination trials among the seven (Ceramium sp. and Gelidiopsis intricata were not available at this time in quantities large enough for further tests) preferred algal species, determined from the above experiments, to obtain an indication of rank. Three

Table 2. General results of multiple choice feeding experiments (0 rejected, - partially ingested, + completely ingested) on adult populations of S. spinus.

| Species | FILAMENTOUS | Results |
|---------------------------------------|-------------|---------|
| Cyanophyta | | |
| <u>Microcoleus lyngbyaceus</u> | | - |
| <u>Hormothamnion enteromorphoides</u> | | - |
| <u>Schizothrix calcicola</u> | | 0 |
| <u>S. mexicana</u> | | 0 |
| Chlorophyta | | |
| <u>Boodlea composita</u> | | + |
| <u>Bryopsis pennata</u> | | 0 |
| <u>Chlorodesmis fastigiata</u> | | - |
| <u>Cladophoropsis membranacea</u> | | + |
| <u>Enteromorpha compressa</u> | | + |
| <u>Pseudochlorodesmis furcellata</u> | | 0 |
| Phaeophyta | | |
| <u>Feldmannia indica</u> | | - |
| <u>Sphacelaria tribuloides</u> | | - |

Table 2. (continued)

| Species | Results |
|---------------------------------|---------|
| Rhodophyta | |
| <u>Asparagopsis taxiformis</u> | 0 |
| <u>Centroceras clavulatum</u> | + |
| <u>Ceramium</u> sp. | + |
| <u>Murrayella periclados</u> | + |
| <u>Spyridia filamentosa</u> | - |
| <u>Tolypocladia glomerulata</u> | - |
| NONCALCAREOUS FLESHY | |
| Chlorophyta | |
| <u>Avrainvillea obscura</u> | - |
| <u>Boergesenia forbesii</u> | - |
| <u>Caulerpa racemosa</u> | - |
| <u>Codium edule</u> | 0 |
| <u>Valonia fastigiata</u> | - |
| <u>V. ventricosa</u> | - |
| Phaeophyta | |
| <u>Chnoospora minima</u> | - |
| <u>Dictyota bartayresii</u> | - |
| <u>Hydroclathrus clathratus</u> | - |
| <u>Lobophora variegata</u> | - |
| <u>Sargassum polycystum</u> | - |
| <u>S. cristaefolium</u> | 0 |
| <u>Turbinaria ornata</u> | 0 |

Table 2. (continued)

| <u>Species</u> | <u>Results</u> |
|-------------------------------|----------------|
| Rhodophyta | |
| <u>Acanthophora spicifera</u> | + |
| <u>Chondria repens</u> | + |
| <u>Dasyphila plumarioides</u> | - |
| <u>Desmia hornemanni</u> | - |
| <u>Galaxaura filamentosa</u> | - |
| <u>G. marginata</u> | - |
| <u>G. oblongata</u> | - |
| <u>Gelidiopsis intricata</u> | + |
| <u>Gelidiella acerosa</u> | - |
| <u>Gelidium pusillum</u> | - |
| <u>Gracilaria lichenoides</u> | - |
| <u>G. salicornia</u> | - |
| <u>Halymenia durvillaei</u> | - |
| <u>Hypnea pannosa</u> | - |
| <u>Laurencia sp.</u> | - |
| <u>Liagora sp.</u> | - |
| <u>Rhodymenia sp.</u> | - |
| Seagrasses | |
| <u>Enhalus acoroides</u> | - |
| <u>Halophila ovata</u> | - |

Table 2. (continued)

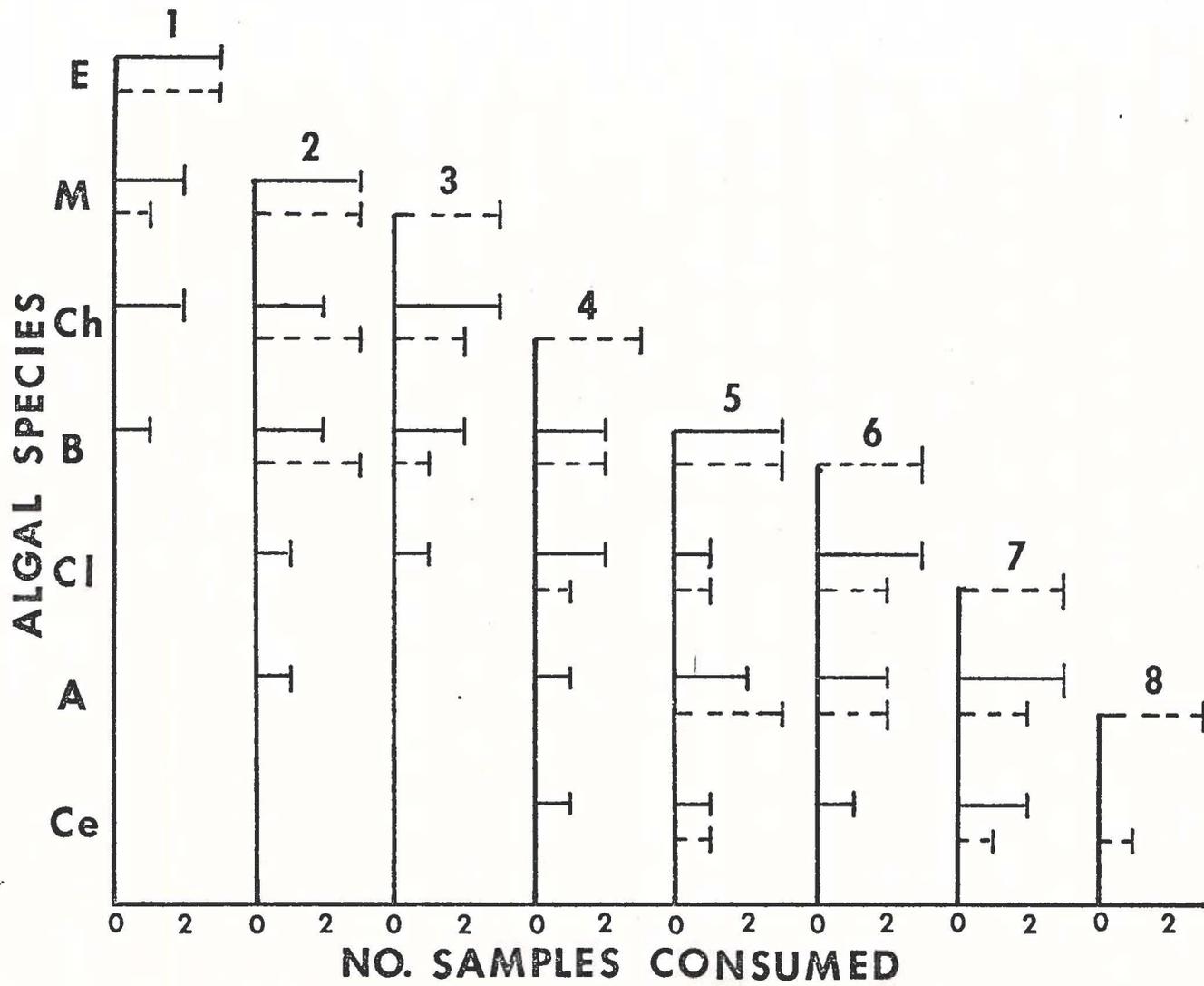
| Species | CALCAREOUS | Results |
|---------------------------------------|------------|---------|
| Chlorophyta | | |
| <u>Halimeda</u> <u>incrassata</u> | | - |
| <u>H.</u> <u>macroloba</u> | | - |
| <u>H.</u> <u>opuntia</u> | | - |
| <u>Neomeris</u> <u>annulata</u> | | - |
| <u>Tydemannia</u> <u>expeditionis</u> | | 0 |
| <u>Udotea</u> <u>argentea</u> | | - |
| Phaeophyta | | |
| <u>Padina</u> <u>tenuis</u> | | - |
| Rhodophyta | | |
| <u>Amphiroa</u> <u>fragilissima</u> | | 0 |
| <u>Actinotrichia</u> <u>rigida</u> | | - |
| <u>Jania</u> <u>capillacea</u> | | 0 |
| <u>Mastophora</u> <u>macrocarpa</u> | | - |
| <u>Neogoniolithon</u> sp. | | 0 |

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 top of the tanks. The algae were checked at intervals since the feeding rates of the fish varied. The number of samples consumed of each species 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 it 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 using fresh algal samples. The test fishes were fed less preferred algae between tests to avoid partiality among the fish toward those seven algae being tested. The preferred algal species were thus ranked in order of preference according to the order of consumption by the fishes (Fig. 1).

Definitive Observation Trials

To test the hypothesis that a ranked order of algal preference existed, six more tests were run using new fish for each test. Tests were run in a 150 l plastic tank containing two fish (140-170 mm FL) previously starved for 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 in hiding. However, two fish usually behaved more normally, one fish establishing dominance. The dominant fish would often chase the other. Both fish spent most of their time feeding, rather than seeking ways to escape from the container or

Figure 1. Results of elimination trials testing the seven most preferred algal species on two groups (Group I——, Group II----) of fish. E = Enteromorpha compressa, M = Murrayella pericladus, Ch = Chondria repens, B = Boodleia composita, Cl = Cladophoropsis membranacea, A = Acanthophora spicifera, Ce = Centroceras clavulatum.



in 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 from a board partially covering 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 which were consumed in the same order as was established by the previous elimination trials were rated 1. The species which were not consumed in the same order as the elimination trials were rated 0. 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 algae. However, to strengthen the test statistically, if two or more species could not be distinguished as to their consumed order, they were recorded as 0. The data were entered in a two-way table and the Cochran's Test for related observations (Conover, 1971) was used to statistically test the hypothesis.

$$T = c(c-1) \frac{\sum_{j=1}^c (C_j - \frac{N}{c})^2}{\sum_{i=1}^r R_i(c-R_i)}$$

R_i = row totals, C_j = column totals, r = number of blocks, c = number of treatments, X_{ij} = 0 or 1, and N = total number of 1's. T is expected to follow the chi-square distribution with $c-1$ degrees of freedom.

Based on a 95% degree of confidence, the results of these trials rejected the null hypothesis that no definite order of preference exists ($P \leq 0.05$) according to the Cochran's Test as seen in Table 3. Therefore, the alternate hypothesis was accepted - 1. Enteromorpha compressa, 2. Murrayella pericladus, 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 sandvicencis 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 S. 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 (Fig. 2A). The number of teeth present in the upper jaw (150-165 mm FL) is about 32 ± 2 , the number in the lower jaw being about 36 ± 2 . Feeding observations both in the laboratory and in the field revealed that the fish take short quick bites, often biting, then backing away, pulling and cutting the algae as they do so. Sometimes they will make quick lateral jerks with the head as they bite.

Table 3. Two-way table showing results of definitive feeding trials testing the order of preference among the seven most preferred algal species and data used for computation of the Cochran's Test for related observations (Conover, 1971).

| | | c | | | | | | | R_j | $R_j(C-R_j)$ |
|-------------------|---|--------------------|---|----|---|----|---|----|-------|--------------|
| | | treatments (algae) | | | | | | | | |
| r (fish pairs) | | E | M | Ch | B | Cl | A | Ce | 7 | 0 |
| | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | |
| 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 7 | 0 |
| 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 4 | 12 |
| 4 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 5 | 10 |
| 5 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 4 | 12 |
| 6 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 32 | 44 |
| C_j | | 6 | 6 | 6 | 5 | 2 | 3 | 4 | | |

Gill Arches and Pharyngeal Teeth

Siganus spinus has four distinct gill arches, the fifth being modified into pharyngeal tooth plates (Fig. 2C). 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 spine-like projections oriented in a posterior manner on plates. The upper pharyngeals contain thicker thorn-like spines (Fig. 2B).

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 caecae, 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 gastrointestinal tract can be seen in Fig. 3 and very nearly duplicates the intestinal winding of that described for S. fuscescens by Suyehiro (1942). The

Figure 2. 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.

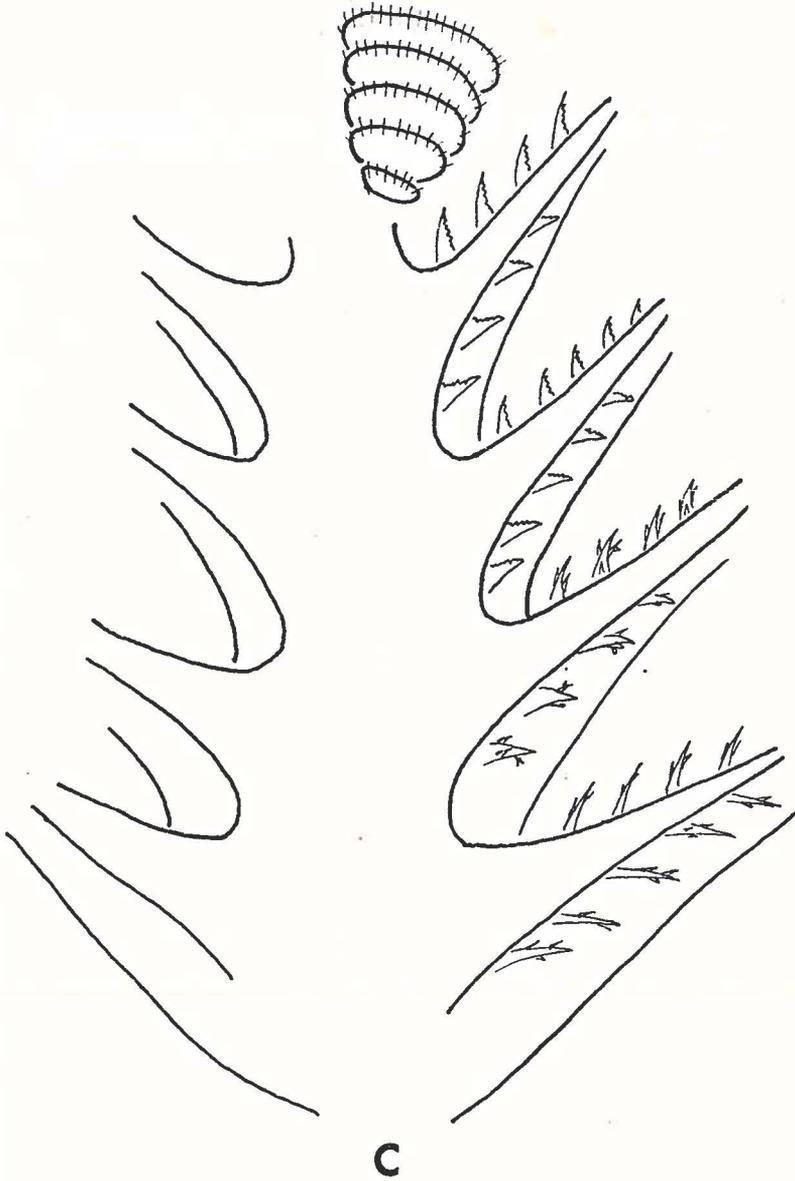
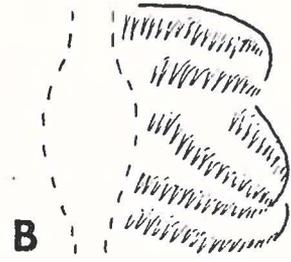
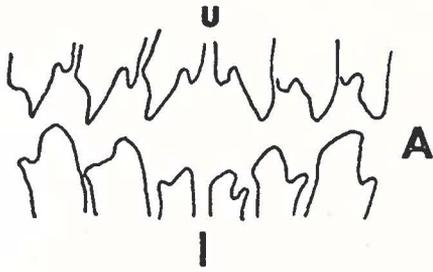
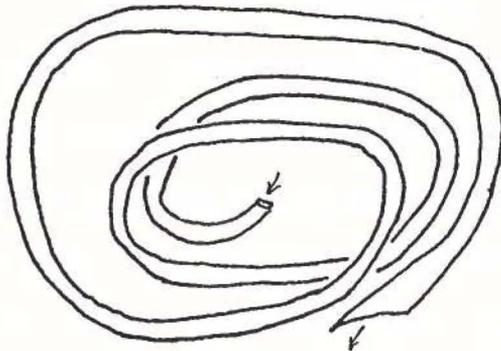
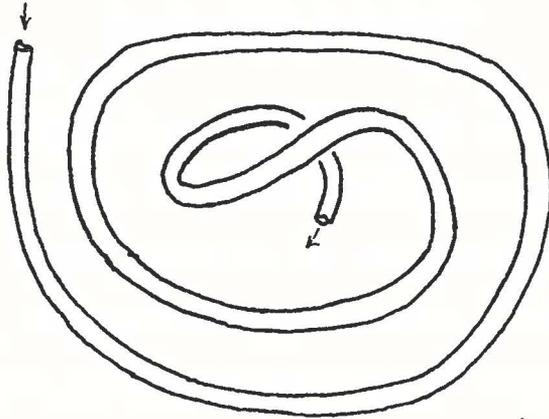
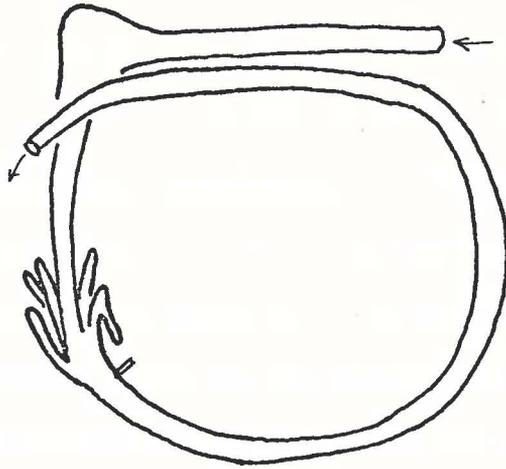


Figure 3. Diagrammatic drawing showing the complex coiling of the gastrointestinal tract of S. spinus.



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 for food to pass through the gut from the time of ingestion to the time of defecation was determined by feeding starved fish Cladophoropsis membranacea and Enteromorpha compressa in a 150 l tank and recording the time of appearance of the first feces. This may be as short as 1.5 hours in the juveniles, although it usually takes two hours or as much as three hours in the adults. Because the fish were starved, these results may be somewhat biased.

ASSIMILATION EFFICIENCY

A highly desirable method of determining assimilation rates in animals is that of using C^{14} (Bakus, 1969). For each experiment a 12 g blotted wet weight sample of the most preferred alga, Enteromorpha compressa, was allowed to incorporate C^{14} through photosynthesis. Incubation was made in 250 ml of sea water containing 2 μ cu of $NaHC^{14}O_3$ between the hours of 1000 and 1400 in a shaded outdoor area (500-1000 ft-c). The alga was then dipped in a salt water solution of 0.001 N HCl and rinsed in running sea water for three minutes to remove any adsorptive C^{14} . A subsample was retained and the remainder 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 l plastic tank with running seawater. Seven trials on adults and four trials on juveniles were run. Feces were siphoned onto a paper towel as they appeared. 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 counting in a Beckman liquid scintillation counter. Percent carbon uptake was derived from the formula, fecal cpm/algal cpm x 100 - 100% = gross (%) carbon assimilated.

The results (Table 4) showed that the amount of carbon assimilated by adults ranged from 6 to 39% (\bar{x} = 16%). Results of tests on juveniles also varied considerably, ranging from 9 to 60% (\bar{x} = 36%). These values represent gross assimilation since 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), based on experiments done with Daphnia by Monakov and Sorokin (1961), concluded that C¹⁴ losses due to respiration were unimportant in short term experiments (3-6 hours).

DISCUSSION

A comparison of food habit data and food preference results at first seems unrealistic since 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 pericladus, is relatively rare on Guam, growing mostly intertidally on the basal

Table 4. Gross C¹⁴ assimilated (%) by adult and juvenile S. spinus after ingesting labelled Enteromorpha compressa.

| | Trials | \bar{x} FL (mm) | Gross C ¹⁴ Assimilated (%) |
|-----------|--------|----------------------|--|
| Adults | 1 | 107 | 20 |
| | 2 | 114 | 11 |
| | 3 | 119 | 7 |
| | 4 | 123 | 39 |
| | 5 | 131 | 6 |
| | 6 | 132 | 8 |
| | 7 | 140 | 24 |
| Juveniles | 1 | 51 | 47 |
| | 2 | 52 | 60 |
| | 3 | 54 | 27 |
| | 4 | 59 | 9 |

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 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 S. spinus restricts the exploitation of these algae since the post-juvenile 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 (1968b), 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% 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% of those algae found and Sphacelaria tribuloides made up about 5%. 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%) and second highest importance value (26) was found almost exclusively in stomach samples taken from the Gun Beach reef flat on the leeward side of Guam. Boodlea composita, Gelidiopsis intricata, and Padina tenuis were dominant in this area. Gelidiopsis intricata represents 15% 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 while 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 the feeding tendency toward a wider variety of algal types as the fish matures, 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 to physically 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 S. spinus and S. argenteus. Although both juveniles and adult S. spinus prefer the filamentous algae, the young juveniles are probably dependent on 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 (1973) found, respectively, 2,855 and 5,483 microcrustaceans and polychaetes. Centroceras clavulatum made up 71% 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 S. spinus are indicative only of that particular area where the fish have 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 if they are available. Although a significant food preference exists among these fish, their size and behavior characteristics combined with algal availability determines 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 numerous highly developed gill rakers efficiently trap

the plant material channeling it back through the well developed pharyngeal apparatus where it is further shredded and directed back into the esophagus. Longitudinal folds in the interior of the stomach regions and the papillae of the intestine enhance absorption while the long length of the 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 (1968b).

Nutritional studies of aquatic animals using radioisotopic tracers is 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 C^{14} labelled zooplankton. The use of C^{14} as a tracer element to obtain an index of assimilation efficiency from the carbon uptake by marine herbivorous fishes is virtually non-existent in the literature.

Although the assimilation efficiency of juveniles appears to be higher than the larger fishes, the wide ranges of assimilation values obtained were probably due to several factors, i.e., 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 average assimilation (16%) of Enteromorpha compressa by the adult specimens of S. spinus

obtained in this study is not surprising. Johannes and Satomi (1966) determined that the average efficiency of converting food to feces by marine herbivores was about 20%. 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 to supply enough energy for growth and maintenance. In the case of S. spinus, which feeds almost continuously, it seems reasonable that the constant ingestion rate would easily compensate for low assimilation.

In conclusion, the herbivorous feeding habit of S. spinus and the availability of juveniles every year may make this fish highly desirable for mariculture endeavors in the tropical Pacific.

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