AN ABSTRACT OF THE THESIS OF Dennis Raymond Lassuy for the Master of Science in Biology presented September 4, 1979.

Title: The Relation of Diet, Intestinal Morphology and Nitrogen Assimilation in the Damselfish *Eupomacentrus lividus*.

Approved: ______________________________
Steven S. Amesbury, Chairman, Thesis Committee

The feeding habits, intestinal morphology and nutritional biology of juvenile and adult *Eupomacentrus lividus* were investigated on Guam. Analysis of stomach contents revealed a shift from omnivory in juveniles to herbivory in adults. Red algae, primarily *Polysiphonia spp.*, *Gelidiopsis intricata* and *Ceramium spp.*, formed the bulk of the diet in all size classes. Foraminifera and small crustaceans were of particular importance in the diets of juveniles. Net nitrogen assimilation efficiency of field-fed *E. lividus* was approximately 60% and did not vary with fish size. The net assimilation efficiencies of fish fed on *Enteromorpha* in the laboratory ranged from 36-79% for nitrogen and from 29-72% for total organic material and increased from juveniles to adults. Juveniles, then, apparently compensate for a relative inability to assimilate plant food by including a higher percentage of animal material in their natural diets. The ratios of intestine length to standard length (IL/SL) and to intestine diameter (IL/ID) increased rapidly in juveniles and leveled off in adults. The retention time for ingested food items may

only be about one-half as long in juveniles as in adults. The combination of observed IL/ID ratios and estimated retention times proved most valuable in the interpretation of ontogenetic changes in feeding habits and assimilation efficiency.

TO THE GRADUATE SCHOOL:

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THE RELATION OF DIET, INTESTINAL MORPHOLOGY AND NITROGEN ASSIMILATION IN THE DAMSELFISH *EUPOMACENTRUS LIVIDUS*

by

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INTRODUCTION

Damselfishes (Pomacentridae) are important contributors to the biomass and diversity of coral reef herbivores (Bakus, 1964; Ogden & Lobel, 1978). Members of the genus *Eupomacentrus* are particularly conspicuous among herbivorous damselfishes and are well-known for their aggressive territorial behavior (Clarke, 1971; Low, 1971; Myrberg & Thresher, 1974; Thresher, 1976). A primary function of this territoriality is the protection of a viable food source (Belk, 1975; Ebersole, 1977; Low, 1971) in the form of an algal "farm." The algal species composition within the territories of several pomacentrids has been studied (Belk, 1975; Brawley & Adey, 1977; Foster, 1972; Lassuy, in press). Brawley & Adey (1977) also found that territorial behavior in damselfishes may increase the algal biomass and productivity of reef systems.

A common territorial herbivorous damselfish on Guam, *Eupomacentrus lividus* (Bloch & Schneider), maintains a crop of filamentous and fine parenchymous algae by the selective removal of high-ash-content algae, e.g., species of *Halimeda*, *Galaxaura*, and *Padina* (Lassuy, in press). The algal component of the diet of adult *E. lividus* has been investigated by Belk (1975) and Lassuy (in press) and the latter briefly mentions some general characteristics of gut morphology. An overall study of the diet and intestinal morphology of the species, both juveniles and adults, is lacking and no information exists on the nutritional biology of this or any other species of herbivorous damselfish.

Investigations of the food and feeding habits of a wide variety of Pacific fishes have been done (Hiatt & Strasburg, 1960; Hobson, 1974). Extensive surveys by Suyehiro (1941) and Al-Hussaini (1947, 1949) provide information on the gut morphologies of numerous Pacific and Red Sea fishes. Studies relating gut morphology and diet of particular groups of fishes, e.g., labrids and scarids (Gohar & Latif, 1959) and acanthurids (Jones, 1968) have also been carried out. Others have demonstrated the relation of diet to morphological variation within a single species (Alevizon, 1975; Klust, 1939, cited in Barrington, 1957). Only a few papers, however, have dealt with the nutritional biology of coral reef herbivores (Bryan, 1975; Menzel, 1959; Pfeffer, 1963). Of these, Menzel (1959) and Pfeffer (1963) address the subject of nitrogen assimilation. None, to my knowledge, has combined studies of the diet, gut morphology and nitrogen assimilation of the juveniles and adults of a single species. Nitrogen retention in the form of protein accumulation is considered a good indicator of animal growth (Brody, 1945; Maynard & Loosli, 1962). Information on the assimilation of nitrogen, therefore, is essential to understanding nutrition in the species under investigation.

Preliminary studies of *E. lividus* revealed a possible dietary shift between young and adults of the species. This provided the opportunity to combine investigations of the feeding habits, intestinal morphology and nutritional biology of a single species in order to better understand the morphological or physiological basis of such ontogenetic changes. The objectives of this study, therefore, have been: 1) to describe the diets of both juvenile and adult *E. lividus* and to note any possible change in feeding strategy; 2) to investigate the general characteristics of intestinal morphology and their patterns of change from juveniles to adults; and 3) to determine the relation of feeding ecology and intestinal morphology to the nutritional biology of the species, particularly with respect to nitrogen assimilation. It was additionally hoped to provide a simple index, or combination of easily measured morphological characteristics, to aid in understanding the observed patterns of assimilation efficiency, particularly in herbivorous fishes.

MATERIALS AND METHODS

Fish for the study were collected with hand nets from Agana and Tumon Bays and Western Shoals, Apra Harbor, Guam. Fish were either put on ice immediately after capture or kept alive until return to the laboratory where they were then weighed, measured and frozen for later analysis. Freezing was necessary in order to handle large numbers of specimens and to maintain the nature of the gut contents.

Upon thawing, the gut was removed and its mesentery severed to allow straight line measurement of the intestine from pylorus to anus. Coiling pattern of the intestine was noted for several specimens during this step. An index of gut cavity volume was calculated by treating the cavity as a box, measuring its maximum length, width and depth posterior to the gill region. Mucosal surface area and intestinal volume were estimated by assuming the intestine to represent a smooth cylinder and making appropriate calculations from the length and mean diameter of the intestine. The method is very similar to that used by Montgomery (1977) and is not intended as an accurate determination but an approximation of sufficient reliability to detect qualitative trends in gut morphometrics.

The contents of the stomach and the terminal one centimeter of the rectum were then removed and analyzed according to the method of Christensen (1978) for diet composition. A variety of methods have been used in the study of the food habits of fishes and detailed reviews of these methods are given by Hynes (1950) and Ricker (1968). The method of Christensen (1978) combines the utility of point systems (Hynes, 1950) and ranking indices (Hobson & Chess, 1973) and accounts for gut fullness and the relative volume and frequency of each food type. Briefly, the stomach, or rectum, contents are subjectively assigned a value from 0 to 30 points as an index of gut fullness. Relative volume of the various food items is estimated and the fullness points are correspondingly subdivided amongst them. This procedure is repeated for several fish and a mean point value per fish of each food item is calculated. This is then "multiplied by the percentage of the total sample of fishes that contained that item" (% occurrence) to yield a "comparative feeding index" (CFI). These values can be scaled down to a percentage to give diet composition. A less subjective replacement of the assigning of gut fullness points in the method of Christensen (1978) might be *"L'indice de réplétion"* of Hureau (1969, cited in Berg, 1979), which is based on actual biomass measurement. This modification was not used, however, in the present study as it was felt that the tiny amounts of gut content material available would not allow adequate precision. A more detailed description of the method and a more comprehensive discussion of its relative merit are given by Christensen (1978). Samples of the contents of both stomach and rectum were taken in order to detect any apparent differences in the relative rates of disappearance of various food items.

Each sample was then dried to constant weight at 50^oC and used in the determination of net organic and net nitrogen assimilation efficiencies of field-fed animals. Net organic assimilation efficiency was determined according to the method of Conover (1966). Conover (1966) defines the "percentage of utilization," i.e., net assimilation efficiency, of total organic material as

$$U' = \left[\frac{(F' - E')}{(1-E')(F')} \right] \times 100,$$

"where F' is the ash-free dry weight:dry weight ratio (fraction of organic matter) in the ingested food, and E' is the same ratio in a representative sample of feces." Net nitrogen assimilation efficiency was determined by a modification of this same method for specific organic moieties (Condrey et al., 1972). Both methods are based on the assumption that digestion acts only upon the organic fraction of food items, and ash is utilized as an inert marker of the amount of food ingested. Total nitrogen was determined by the microKjeldahl technique with a methyl-red color development. Ash content was determined by burning at 500°C for three hours and weighing the residue to the nearest .001 mg on a Cahn Model 4400 Electrobalance.

A group of fish of varying sizes from 1.45 to 21.0 g wet weight were held in the laboratory in 10-*l* aquaria and fed *ad libitum* on the green alga *Enteromorpha clathrata*. Aquaria were provided with a short section of PVC tubing to serve as a shelter. Aquaria were separated from each other by opaque walls to reduce stress in these highly territorial fish. *Enteromorpha* has been used in laboratory experiments on digestive and assimilation efficiencies of *Siganus spinus* (Bryan, 1975) and *Acanthurus sandvicensis* (Pfeffer, 1963). It has also been shown to be a preferred food of various coral reef herbivores (Bryan, 1975; Randall, 1961; Tsuda & Bryan, 1973). The total organic and nitrogen contents of *Enteromorpha* were determined. Feces were collected within one hour of defecation and were analyzed as described above. Net organic and net nitrogen assimilation efficiencies were calculated.

The egestion rate of a small group of juvenile and adult *Eupomacentrus lividus* were determined by placing field-fed animals in 10-*l* aquaria for 16 hours and allowing them to defecate. Feces were collected every two hours and dried. The total accumulation after 16 hours was extrapolated to a daily rate. With information on assimilation efficiency, these values were then used to approximate daily food intake.

RESULTS

Dietary Change

Analysis of stomach contents revealed a shift from omnivory in juveniles to herbivory in adults. The composition of the diet, expressed as comparative feeding index (CFI) and occurrence, is presented in Table 1 for a range of sizes. CFI values are also illustrated in Fig. 1.

Foraminifera (most commonly *Quinqueloculina* sp., *Triloculina* sp., and *Baculogypsina sphaerulata*), small crustaceans (primarily copepods and ostracods), and an array of small benthic invertebrates contributed to the diet of the juveniles. Animal material constituted a mean of 36.5% of the diet of the smallest fish, those less than 30 mm in standard length (SL). The relative contribution of animal material decreased rapidly and a correspondingly sharp rise in plant material occurred with increasing size of the fish. This change was most pronounced between 50 and 60 mm SL, after which size animal material leveled off at a low value of 1-3%. This small but fairly consistent portion of animal material may be of some nutritional importance to adult fish (Mathavan et al., 1976; Menzel, 1959), but it is likely that it is only incidentally captured.

Species of red algae (Rhodophyta) form the bulk of the plant material in all size categories analyzed. *Polysiphonia* spp., *Gelidiopsis intricata* and *Ceramium* spp. were most frequent. Among the Chlorophyta ingested, *Enteromorpha clathrata* and a species of *Cladophora* were most common. *Enteromorpha clathrata* has not been found to be particularly

Table 1. Stomach contents of *Eupomacentrus lividus* expressed as comparative feeding index (CFI, after Christensen, 1978) and percent occurrence. Size classes are in mm standard length.

	Size Class											
Food Item	<30		30-40		40-50		50-60		60-80		>80	
	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Rhodophyta	22.4	85.7	43.5	81.8	49.1	90.0	63.8	100.0	75.8	100.0	72.4	100.0
Chlorophyta	6.9	42.9	14.2	72.7	18.9	80.0	11.5	66.7	5.0	71.4	22.0	73.7
Phaeophyta	11.7	57.1	3.1	27.3	3.5	50.0	17.4	66.7	8.7	71.4	1.7	47.4
Cyanophyta	19.0	57.1	11.7	63.6	13.9	70.0	3.8	83.3	5.8	85.7	2.3	42.1
Bacillariophyta	0.7	14.3	--	--	<0.1	10.0	--	--	--	--	--	--
Unknown plant	--	--	0.5	18.2	0.1	10.0	--	--	1.1	28.6	0.4	26.3
Dinoflagellates	2.8	28.6	7.7	45.5	0.4	30.0	0.9	33.3	--	--	--	--
Crustaceans	8.7	71.4	5.6	54.5	9.5	60.0	0.6	50.0	1.8	57.1	0.8	26.3
Foraminifera	14.6	71.4	2.2	45.5	3.0	70.0	1.4	50.0	1.7	57.1	0.4	42.1
Other Animal*	12.2	57.1	11.5	54.5	1.6	50.0	0.6	50.0	0.1	14.3	<0.1	10.5
	(7)		(11)		(10)		(6)		(7)		(19)	

*includes coral, bivalves, gastropods, sponge, heteropods, polychaetes and unknown animal material.

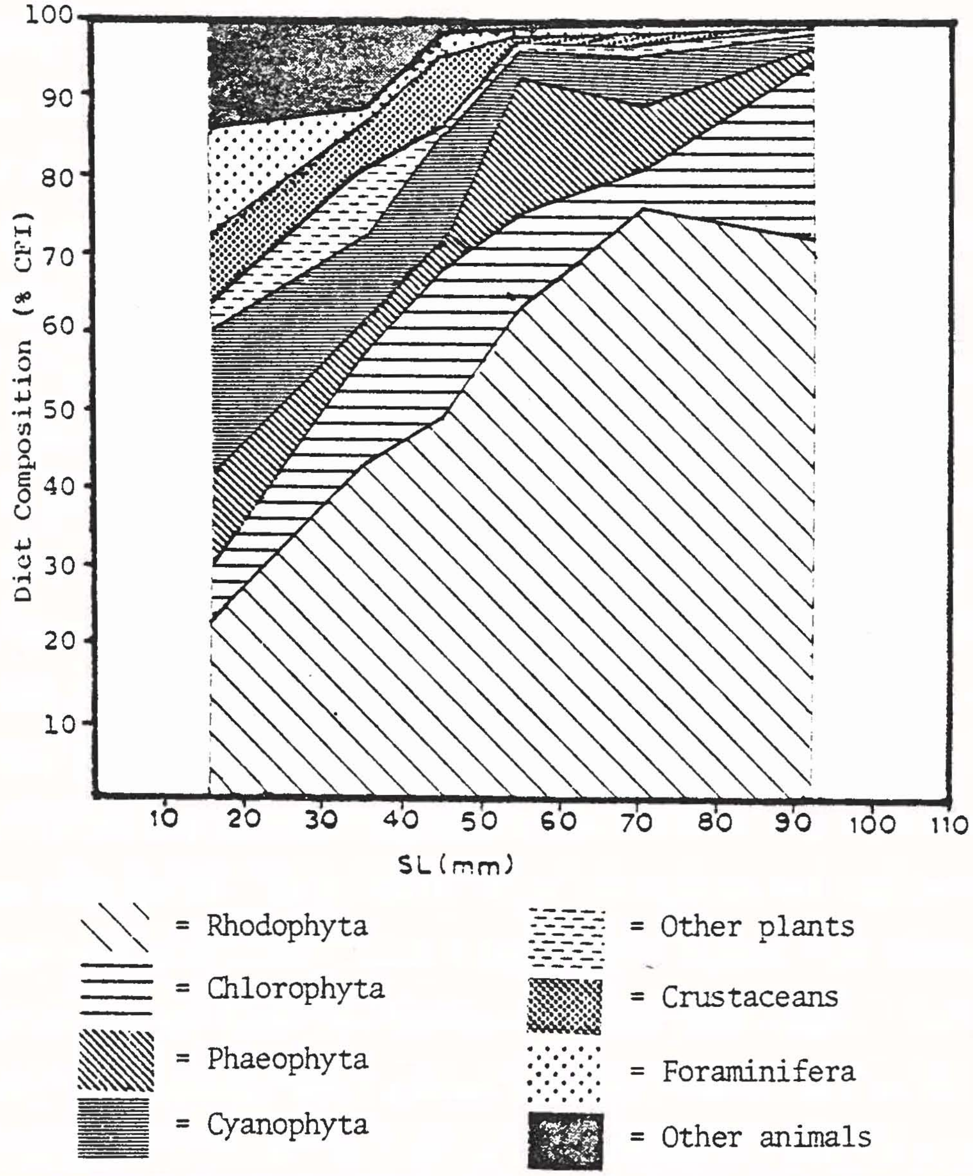

Fig. 1. Changes in diet composition with length in *E. lividus* based on data presented in Table 1. Other animals include corals, bivalves, gastropods, heteropods, sponges, polychaetes and unknown animal material. Other plants include diatoms, dinoflagellates and unknown plant material.

abundant within the territories of *E. lividus* (Lassuy, in press) but was occasionally observed to form the bulk of the stomach contents of adult fish in the present study. This alga, however, can be extremely abundant along the shores of Tumon and Agana Bays (Fitzgerald, 1978), and clumps are often seen floating freely in the water column. The sporadic nature of its appearance in *E. lividus* stomachs, then, is probably a result of feeding on these loose clumps and might suggest some preference for this alga when it becomes available.

Ingested blue-green algae (Cyanophyta) consisted primarily of *Microcoleus lyngbyaceus* with *Calothrix crustacea* as an occasional contributor. The greater contribution of blue-green algae in smaller size classes (Table 1) may be related to the relative ability of juveniles to defend a territory. Juvenile *E. lividus* are commonly found among small, isolated heads of *Acropora* in shallow, relatively quiescent sub-tidal waters. These juveniles do exhibit some degree of territoriality but are usually only effective at repelling fairly small fishes, e.g., juvenile scarids and acanthurids. As a result, their territories are regularly browsed by many reef herbivores. Tsuda & Kami (1973) suggest that browsing by herbivores may favor the dominance of blue-green algae. This may, in part then, explain their greater apparent contribution to the diet of juvenile *E. lividus*. *Ectocarpus breviarticulatus* was the most common brown algae (Phaeophyta) in juvenile stomachs but occurred only occasionally in fish longer than 60 mm SL, while in adults *Sphacelaria* spp. were the dominant brown algae.

Juvenile and adult fish both fed primarily as browsers within their respective territories. Juveniles, however, were occasionally observed to nip at small pieces of rubble or to "sift" the sand beneath the coral head they were occupying. This latter habit resulted in proportionately more sand in the guts of juveniles. Additional analyses of the algal component of the territories and diets of adult *E. lividus* are found in Belk (1975) and Lassuy (in press).

Windell (1967) used the rate of disappearance from the stomach of various food organisms as an indicator of digestibility. By repeating the same analytical method on rectum samples as was used for stomach contents, I was able to provide a similar indicator of relative disappearance which suggests differential digestibilities of the food items. A decrease in a particular food item's CFI from stomach contents to rectum contents suggests digestion has occurred, while an increase suggests that the food item is relatively less digestible than other diet components. CFI and occurrence values for rectum content samples are shown in Table 2. Since these data represent the means of several field-fed fish, they reflect a greater variability than tests with a controlled diet composition, e.g., Windell (1967).

The Rhodophyta showed a consistent pattern of decrease from stomach to rectum while the Cyanophyta always increased. Chlorophyta and Phaeophyta showed mixed results with green algae tending to decrease and brown algae to increase. This would predict an order of digestibility from highest to lowest of Rhodophyta, Chlorophyta, Phaeophyta, Cyanophyta. Some evidence exists on the relative difficulty of digestion of blue-green algae (Payne, 1978; Pfeffer, 1963). For adult fish, i.e., those over 60 mm SL, rectum content CFI values for Chlorophyta are equal to or slightly less than those of the stomach contents. This is not indicative of the apparent highly digestible nature of green algae, as will be discussed later in relation to *Enteromorpha*. This method, then, can only

Table 2. Comparative feeding indices (CFI, after Christensen, 1978) and percent occurrence of food items in the rectum of *E. lividus*. Size classes are in mm standard length.

Food Item	Size Class <30		30-40		40-50		50-60		60-80		>80	
	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Rhodophyta	16.0	57.1	29.3	100.0	23.3	81.8	54.2	100.0	64.1	100.0	69.1	100.0
Chlorophyta	26.3	85.7	11.8	71.4	17.0	90.9	12.8	85.7	5.0	88.9	15.5	75.0
Phaeophyta	9.5	42.9	4.6	57.1	19.1	81.8	5.5	57.1	7.8	55.6	3.2	60.0
Cyanophyta	23.8	71.4	44.4	85.7	33.8	90.9	24.3	85.7	18.7	100.0	4.7	65.0
Bacillariophyta	8.0	42.9	--	--	--	--	--	--	--	--	--	--
Unknown plant	2.8	28.6	0.5	28.6	0.3	18.2	--	--	2.1	33.3	4.1	40.0
Dinoflagellates	2.2	28.6	2.1	28.6	--	--	0.4	28.6	--	--	--	--
Crustaceans	2.7	28.6	2.1	42.9	5.4	63.6	0.7	28.6	0.1	11.1	0.9	45.0
Foraminifera	5.3	71.4	2.8	71.4	0.9	45.5	2.1	71.4	2.1	71.4	2.3	60.0
Other animal*	1.0	28.6	0.9	21.4	<0.1	9.1	--	--	0.1	22.2	0.1	10.0
Unknown matter	2.4	28.6	1.5	21.4	0.2	9.1	--	--	--	--	0.1	5.0
(n)	(7)		(14)		(11)		(7)		(9)		(20)	

*includes coral, bivalves, gastropods, sponge, heteropods, polychaetes and unknown animal material.

suggest a pattern of relative digestibilities and is not meant as substantial evidence.

Assimilation Efficiency

Net organic (U') and net nitrogen (U_n') assimilation efficiencies for field- and laboratory-fed animals are illustrated in Figs. 2 and 3, respectively. Nitrogen assimilation efficiency for *E. lividus* fed on the green alga *Enteromorpha clathrata* ranged from a low of 36.2% for a 1.4-g (wet wt) fish to a high of 79.0% for a fish of 15 g. Values for nitrogen assimilation were consistently higher than the assimilation of total organics which ranged from a low of 29.2% to a high of 71.8% for 1.4- and 15-g fish, respectively. Pandian (1967) observed a similar pattern in two carnivorous fishes with protein assimilation (97%) consistently higher than total food assimilation (91%) but found no appreciable difference among individuals of different body weights. He also stated that of the major organic moieties, "protein is most easily digested and absorbed." Net nitrogen assimilation efficiencies in field-fed animals were consistent for all sizes, varying around the 60% level, while assimilation of organics followed much the same pattern as in laboratory animals.

Recent studies of assimilation efficiency in fishes have dealt primarily with caloric efficiency and, for the most part, have been restricted to freshwater or marine carnivorous fishes (Mathavan et al., 1976; Menzel, 1960; Targett, 1979). Mann (1966) reports protein (Kjeldahl-nitrogen X 6.25) assimilation efficiencies of 42% and 57% with a mean of 53% for *Tilapia melanopleura* fed on *Spirodella* and *Elodea*. Bondi et al. (1957, cited in Hickling, 1971) found much higher values

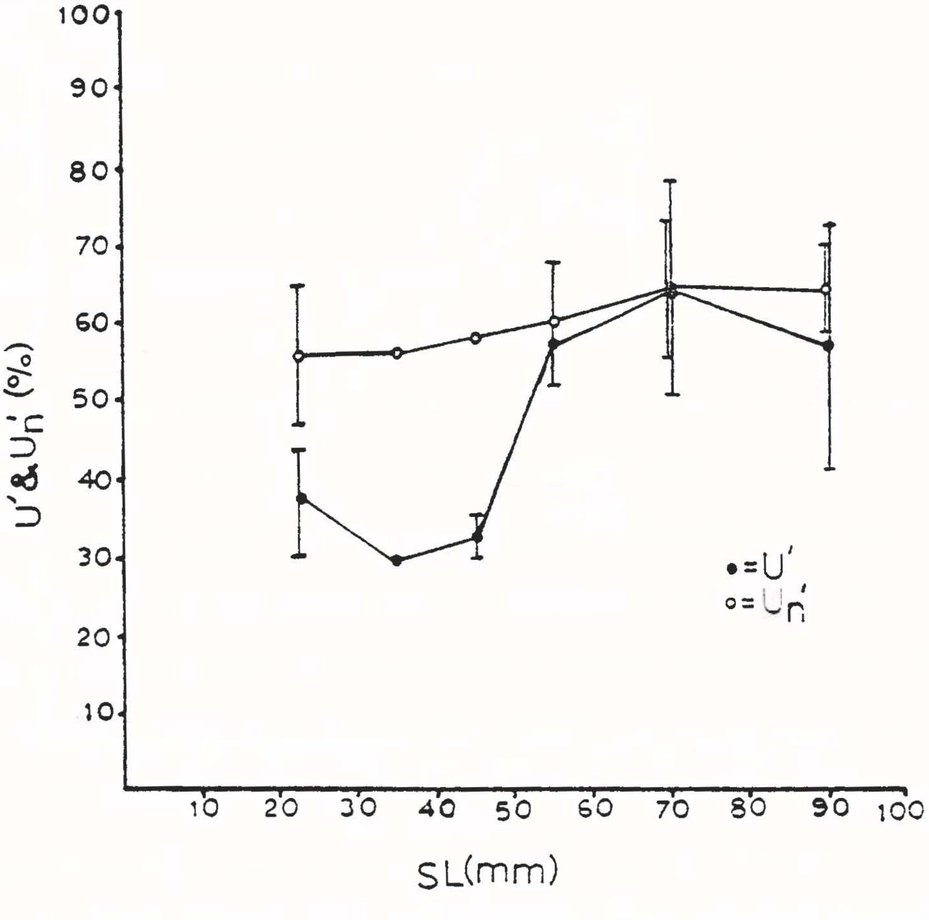

Fig. 2. Mean organic (U') and nitrogen (U_n') net assimilation efficiencies for field-fed *E. lividus* (with standard errors shown).

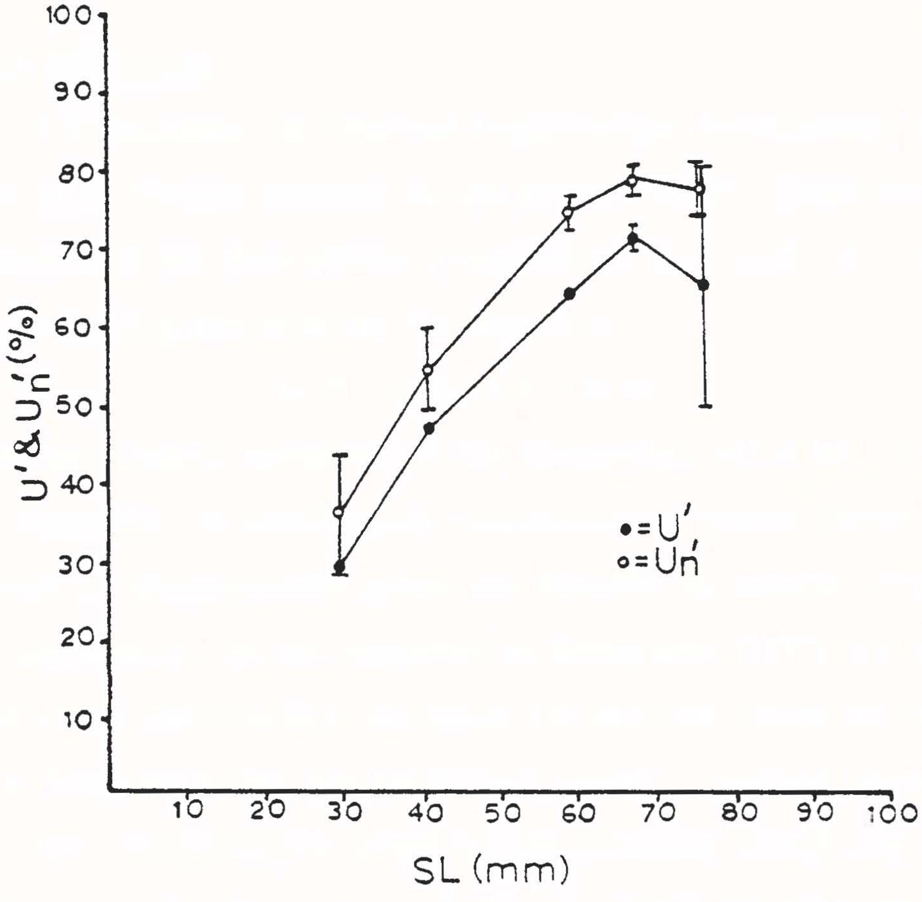

Fig. 3. Mean organic (U') and nitrogen (U_n') net assimilation efficiencies for *E. lividus* fed on *Enteromorpha* (with standard errors shown).

of 78% to 97% for the grass carp, *Ctenopharyngodon idella*, fed on a variety of vegetable diets. The latter, however, were primarily in the form of ground grain meals which essentially eliminated the need for trituration. Published protein assimilation efficiencies for carnivores are consistently high, e.g., 92% to 99% for centrarchids (Gerking, 1952) and 98% for the serranid *Epinephelus guttatus* (Menzel, 1960).

Intestinal Morphology

Fig. 4 illustrates the observed length-weight relationship of 95 specimens of *E. lividus* examined in the present study. Logarithmic transformation of the data yields a significant ($r = 0.997$, $P < 0.001$) linear relationship described by the equation:

$$ln\ W = 2.95\ ln\ L - 9.65.$$

This slope very nearly approximates the theoretical value of 3.0 which typifies isometric, or continuously proportionate, growth (Royce, 1972). This pattern of proportionate growth was observed in several of the measured characters. As was suggested by Montgomery (1977) for the stichaeid blenny *Cebidichthys violaceus* the relative volume of the gut cavity, a "limiting factor for intestinal growth," remained constant (see Fig. 10). The relative volume of the intestine itself also showed no correlation with body size ($r = 0.032$, $P < 0.05$) and remained fairly constant with a mean of just over 0.05 cm^3 per g fish (wet wt).

The observed slope of 5.00 ($r = 0.926$, $P < 0.001$) for the linear relationship of intestine length (IL) to standard length (SL) (Fig. 5) in *E. lividus* is similar to that found by Emery (1973) for *Microspathodon chrysurus* (5.46) and somewhat higher than for *Eupomacentrus planifrons* (3.34). *E. planifrons* is a Carribean damselfish with territorial (Thresher, 1976) and "farming" behavior (Brawley & Adey, 1977; Ogden,

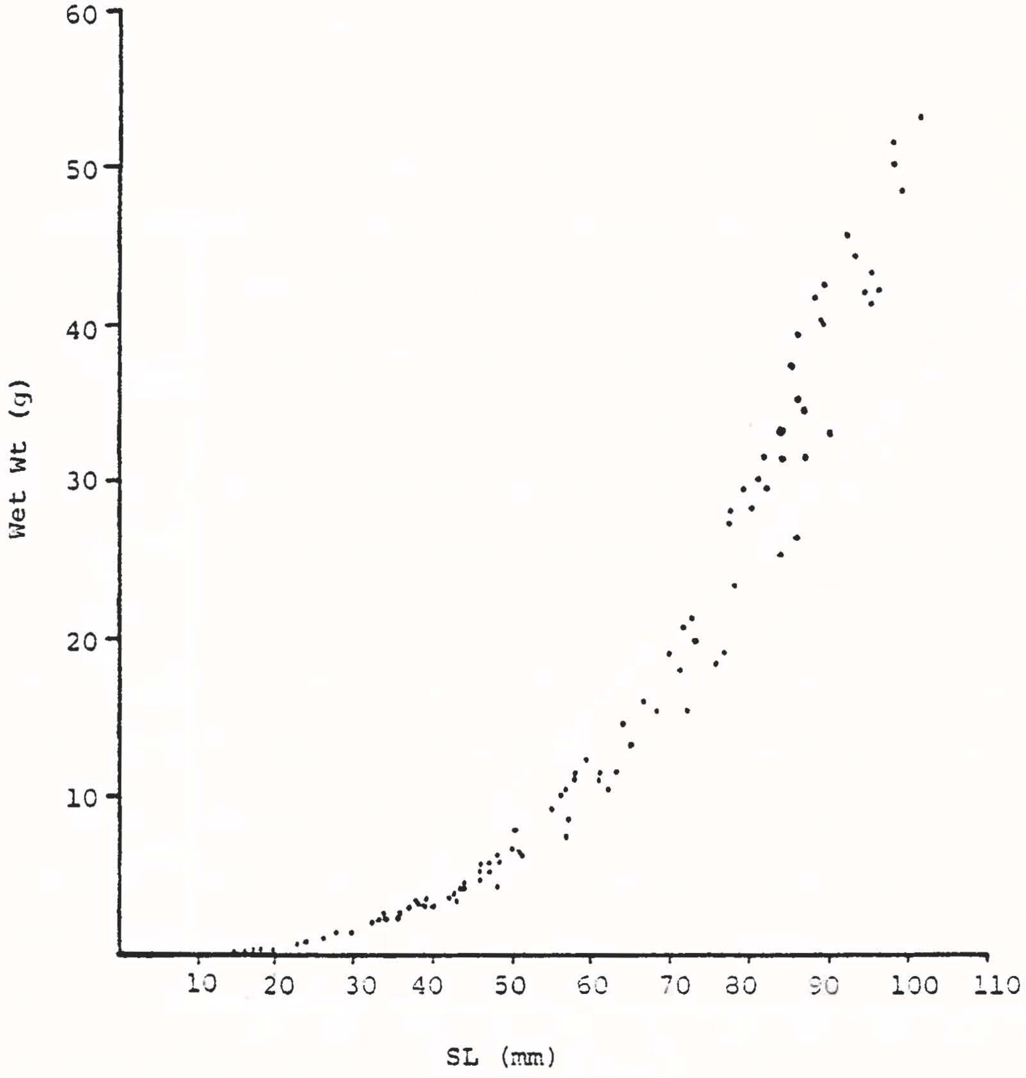

Fig. 4. The relation of wet weight to standard length (SL) in *E. lividus* from Guam.

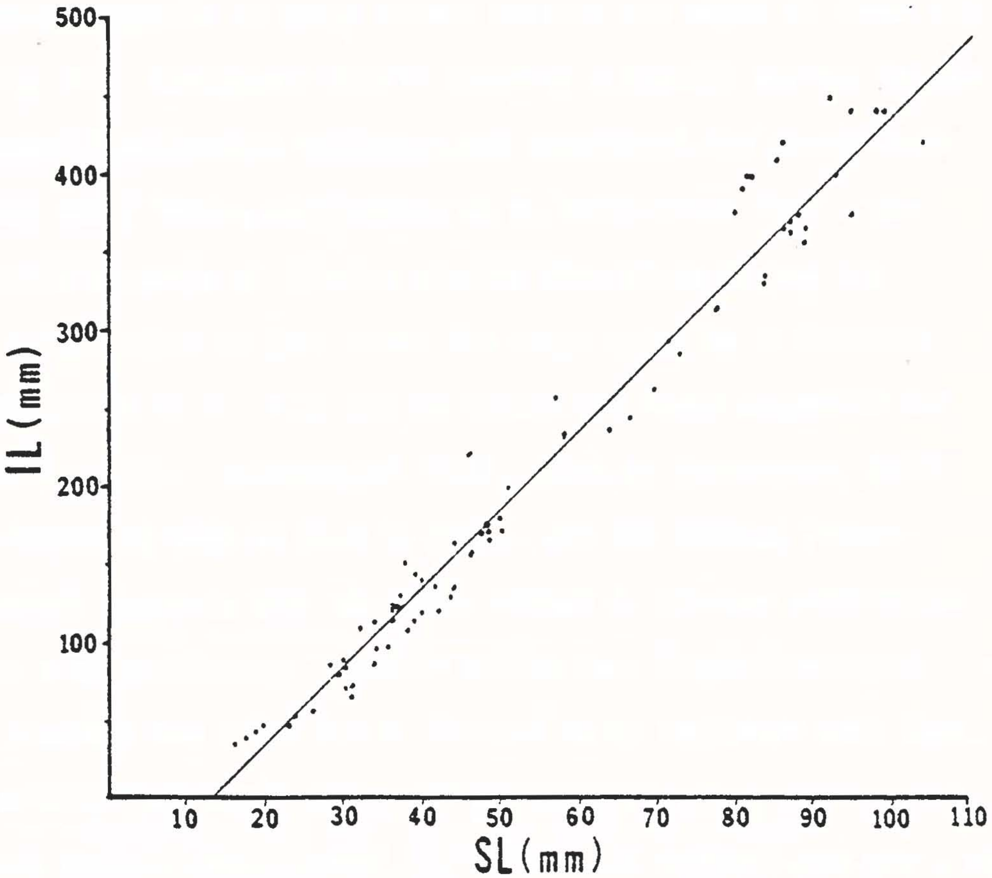

Fig. 5. The relation of intestine length (IL) to standard length (SL) in *E. lividus* from Guam. (IL = 5.00SL - 65.50)

pers. comm., 1978) similar to that of *E. lividus*. Emery (1973) designed a "digestive index" (IL^2/SL^3) for the purpose of relating gut morphology to metabolic activity, but found it revealed no apparent pattern among *M. chrysurus* or *E. planifrons* of varying sizes. Digestive index (DI) in *E. lividus* (Fig. 6) showed a slight but significant decrease from juvenile to adult fishes ($r = -0.316$, $P < 0.01$).

The ratio of intestine length to standard length (IL/SL) in *E. lividus* increased rapidly in early growth periods and began to level out in adults (Fig. 7). Montgomery (1977) observed a similar pattern in the stichaeid blenny *Cebidichthys violaceus* and associated the change with an ontogenetic shift from a carnivorous to an herbivorous diet. The mean IL/SL ratio in adult *E. lividus* greater than 80 mm SL was 4.4 ($\sigma = 0.4$, $n = 21$). This is just above the range given by Al-Hussaini (1947) for omnivores (1.3 - 4.2) but is within the range suggested for herbivores (3.7 - 6.0). Jacobshagen (1913, cited in Barrington, 1957) found IL/SL ratios as high as 15.0 in plant- and mud-feeding fishes. Lassuy (in press) suggests that the algae within *E. lividus* territories may represent a selected crop, "weeded" of the less digestible algal forms. The somewhat low value for *E. lividus* as an herbivore may, then, be related to this "selected" nature of its algal crop.

Estimated mucosal coefficients (cm^2 of mucosal surface area per g of fish, after Al-Hussaini, 1949) and intestinal surface/volume ratios are illustrated in Figs. 8 and 9, respectively. Logarithmic transformation of the data yields negative linear relationships for both mucosal coefficient ($r = -0.929$, $P < 0.001$, slope $= -0.255$) and intestinal surface/volume ratio ($r = -0.960$, $P < 0.001$, slope $= -0.284$). The observed relationship between mucosal coefficients and fish size and between

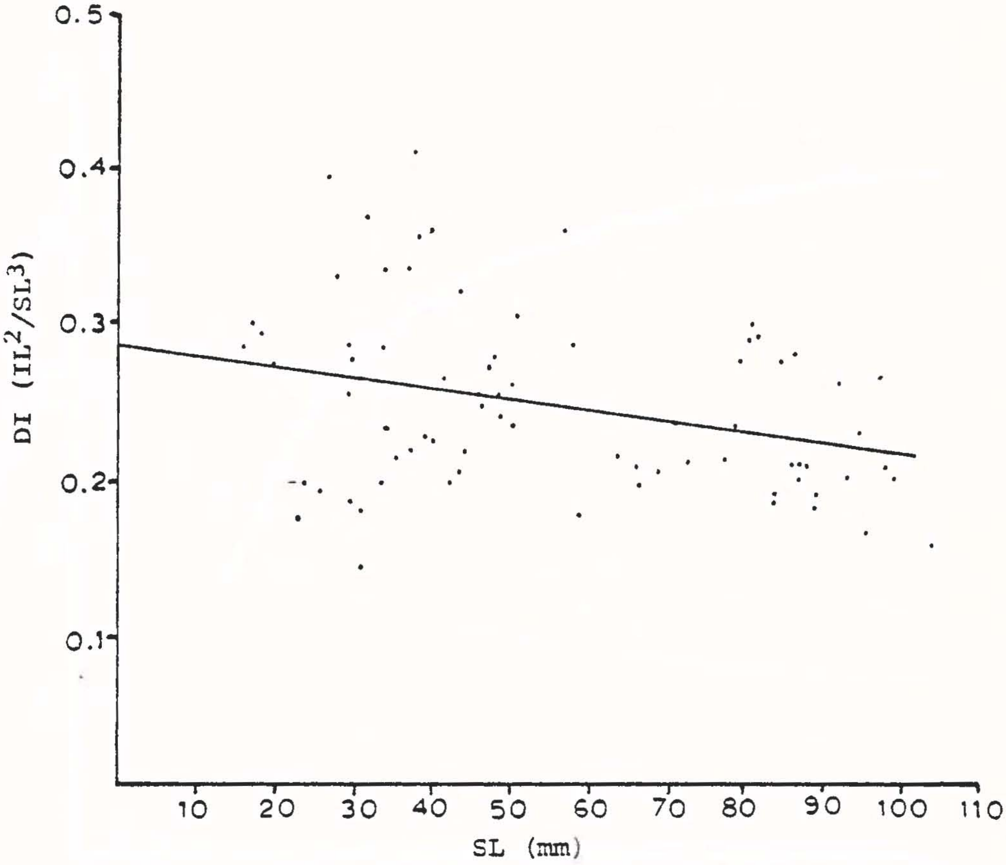

Fig. 6. The relation of digestive index (DI, after Emery, 1973) to standard length (SL) for *E. lividus* from Guam.

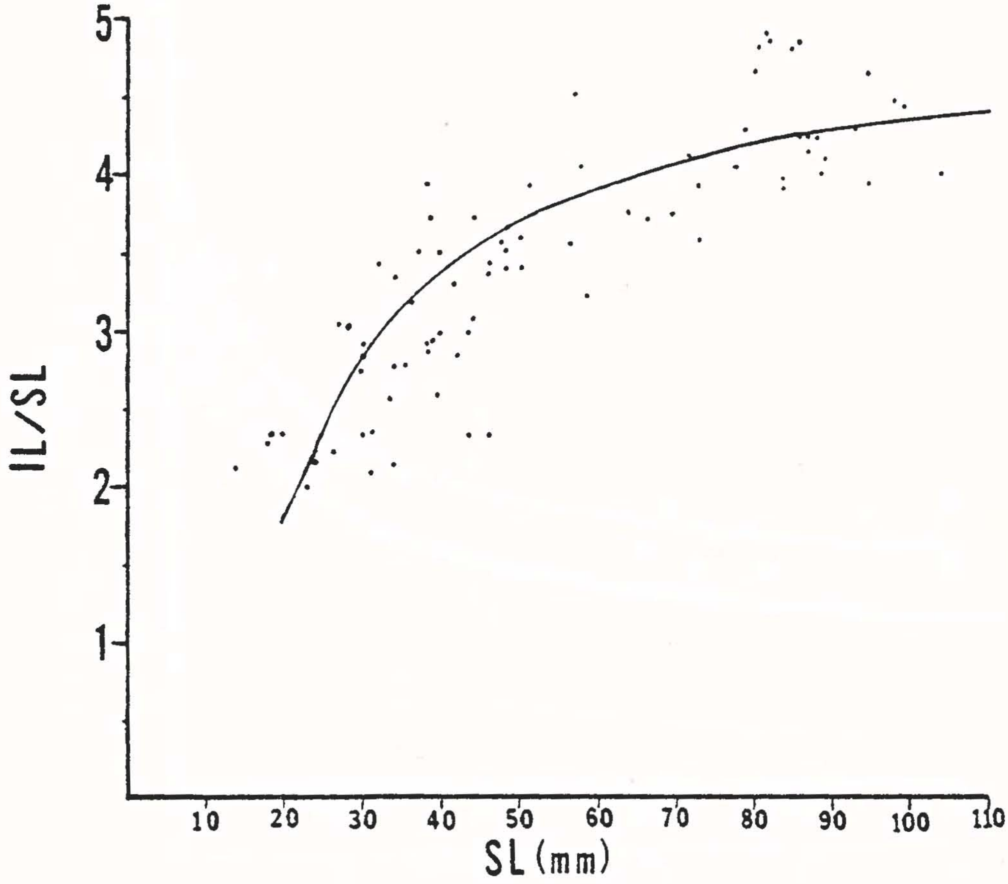

Fig. 7. The relative intestine length (IL/SL) as a function of standard length for *E. lividus* from Guam.

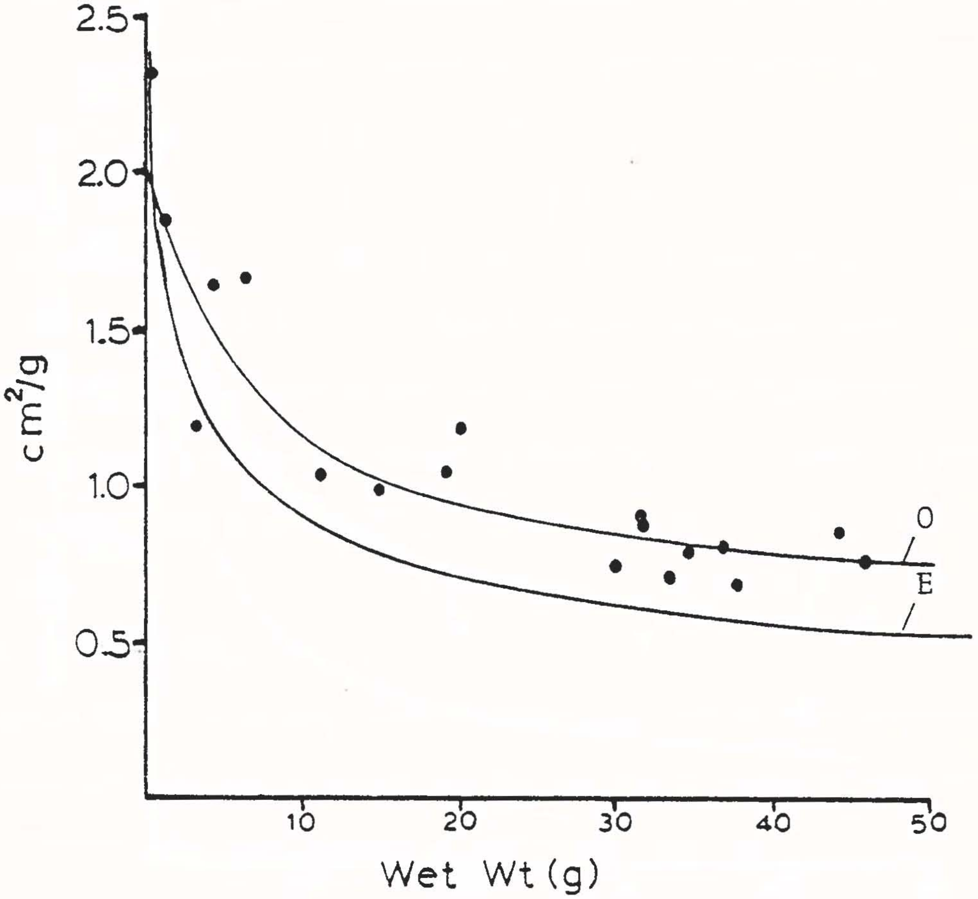

Fig. 8. The relation of mucosal coefficient (cm^2 of mucosal surface area per g of fish, after Al-Hussaini, 1949) to body weight. Curves represent the observed relation (O) and the relation expected had intestinal growth been isometric (E).

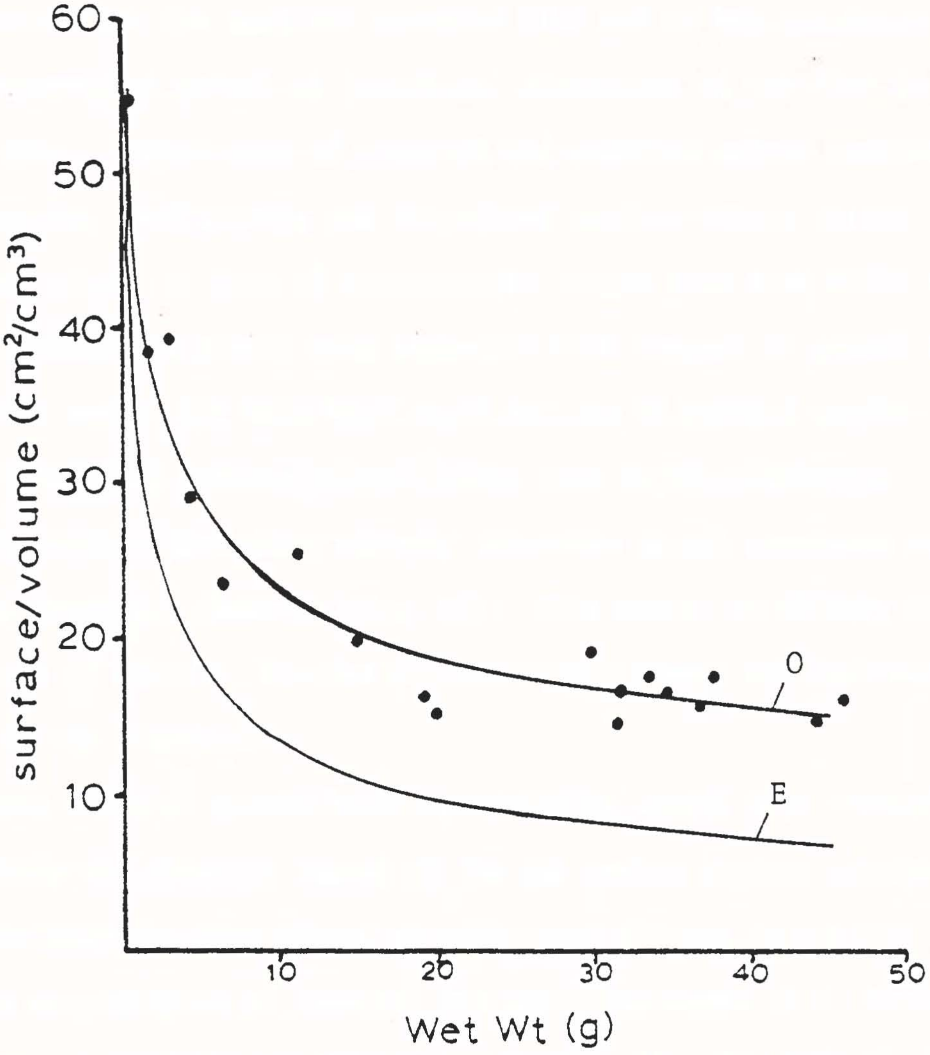

Fig. 9. The relation of intestinal surface/volume ratio to body weight for *E. lividus* from Guam. Curves represent the observed relation (O) and the expected relation had intestinal growth been isometric (E).

intestinal surface/volume ratios and fish size can be compared with the relationships which would occur if the growth of the intestinal dimensions was isometric with respect to growth of the fish. The hypothetical "expected" curves (Figs. 8 & 9) were calculated on the basis of the predicted values for the smallest measured fish and on the assumption of constant proportional growth of intestinal dimensions as the fish increased in size. Comparisons of observed and expected curves indicate that both mucosal coefficients and intestinal surface/volume ratios decrease more slowly in fish of increasingly larger size than would be the case if intestinal growth were isometric with respect to growth of the fish. The reason for this less rapid decline in mucosal coefficients and intestinal surface/volume ratios lies in the allometric growth of intestinal dimensions whereby intestine length increases more rapidly than intestine diameter (Fig. 10). This means, in effect, that the intestines of adult *E. lividus* are relatively longer and narrower than those of the juveniles.

Disparate rates of growth favoring intestine length over intestine diameter, while the relative volume of the gut cavity remains constant, should necessitate the development of additional folding or coiling. The observed morphologies of juvenile and adult specimens of *E. lividus* fit this expected pattern, as illustrated in Fig. 11. The intestinal folding pattern of adult *E. lividus* is similar in appearance to that of *Cyprinus carpio* (Al-Hussaini, 1949) with a "loop" forming over the first limb, but is quite dissimilar from the observed patterns of several species of *Siganus* (Bryan, 1975; Suyehiro, 1941).

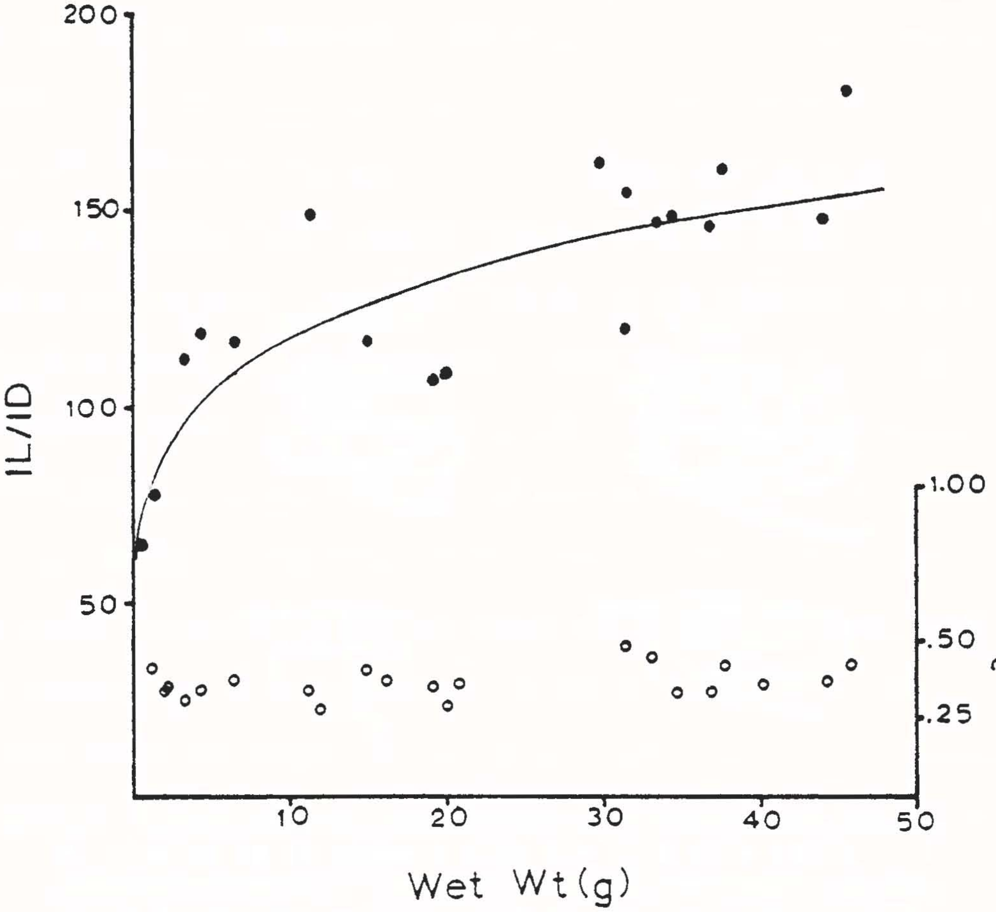

Fig. 10. The relation of intestine length (IL) to intestine diameter (ID) for *E. lividus* from Guam.

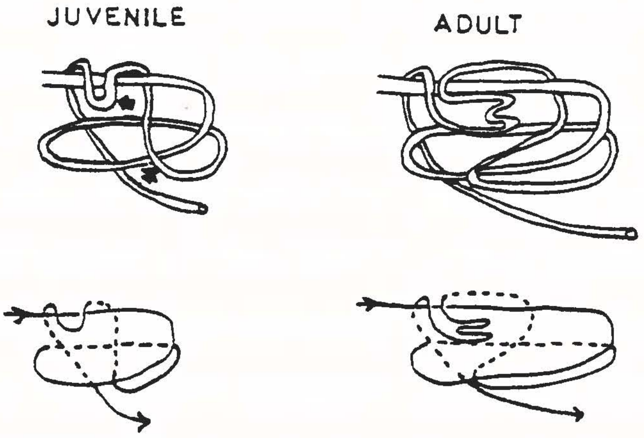

Fig. 11. Intestinal coiling pattern of juvenile and adult *E. lividus* as it appears from the left side (with schematics below). Notice increased complexity of the adult intestine, particularly at the indicated points.

DISCUSSION

The significance of ontogenetic changes in diet must be viewed in relation to parallel changes in the feeding morphology and nutritional biology of the species. Ontogenetic change in diet, as in *Eupomacentrus lividus*, from carnivory or omnivory to herbivory is common in fishes (Ciardelli, 1967; Christensen, 1978; Mitchell, 1953; & others) and is a widespread pattern among other animals with herbivorous adults (Clark & Gibbons, 1969; Pough, 1973). Previous studies of the relation between diet and feeding morphology in fishes have dealt primarily with comparisons of the adults of various carnivorous, omnivorous and herbivorous species. Attention has often been focused on the relation of intestine length to body length (Al-Hussaini, 1949; Suyehiro, 1941), apparently relating a longer intestine to greater retention time (Barrington, 1957). This is not necessarily an appropriate assumption, as in the present study relative intestine volume did not change appreciably with increased intestine length. This means, in effect, that equivalent relative feeding rates in juveniles and adults, regardless of IL/SL ratio, would result in the same retention time for ingested food. A higher feeding rate, however, would correspondingly reduce the retention time and may be expected to reduce absorptive efficiency, particularly when the fish is feeding on plant material.

The relation of intestine length to intestine diameter may be an important consideration in the prediction or interpretation of assimilation efficiencies. By way of explanation, consider the simplified view of the intestine as a cylinder. Digestion, whether by gastric or intestinal enzymes or by endocommensal bacteria, may occur away from the gut walls. However, absorption, or assimilation, occurs only upon contact with the gut lining. The assimilation rate is thus dependent upon the surface/volume ratio of this "cylinder." For a given flow rate (feeding rate) a longer cylinder (intestine) of the same surface/volume ratio can be expected to yield a higher assimilation efficiency. Intestine length (IL), then, needs also to be considered. The surface/volume ratio of a cylinder is calculated as $4/D$, where D is the diameter. An adjustment to include length results in the ratio $4L/D$ or, without the constant, IL/ID (intestine length/mean intestinal diameter). IL/ID, therefore, should be an indicator of assimilation efficiency. In the present study, IL/ID showed a significant correlation with net organic ($r = 0.951$, $P < 0.05$) and net nitrogen ($r = 0.971$, $P < 0.01$) assimilation efficiencies of laboratory fed animals.

As mentioned above, another important factor in the utilization of food, particularly in herbivores, is the length of time that a particular food item is available for digestion and assimilation. Having assumed the intestine to represent a smooth cylinder, I was able to estimate food retention times for juvenile and adult fishes on the basis of estimates of intestinal volume and daily ingestion rates. Retention time can be calculated as:

$$t = V/Q$$

where, V = volume of the cylinder (intestinal volume)
Q = flow rate (ingestion rate).

Estimated daily intake for a 1.4-g (wet wt) juvenile was 0.123 g (dry wt) per day. This individual had an approximate intestinal volume of 0.74 cm^3. If one assumes that the density of food ingested is 1 g per mm^3, the calculated retention time was 14.4 hours. This same value for adult fish of 18.0 g and 45.4 g was 28.5 and 30.6 hours, respectively. Mann (1966) reports direct observations of defecation up to 24-27 hours after ingestion in *Tilapia melanopleura* fed for one hour on plant material. Estimated daily feeding rates (g food/g fish/day) for *E. lividus* were approximately 2.1 times higher in juveniles than in adults. Daily ingestion rates for *E. lividus* are based on the results obtained from a single juvenile and two adult fish and are, therefore, not meant as precise estimations of the population values.

Targett (1979) found that size had no effect on assimilation efficiency for *Fundulus* fed on amphipods and states that "constancy of digestive efficiency [although he describes assimilation efficiency] with changing body size within fish species seems, therefore, to be a general rule." All of his supporting references (Menzel, 1960; Pandian, 1967; & others), however, involve only carnivorous fishes. Constancy of assimilation efficiency was observed for field-fed fish in the present study but not for fish fed on a single item diet of *Enteromorpha.* Juvenile *E. lividus* were less efficient at the removal of plant nitrogen than the adults.

Higher levels of net nitrogen assimilation in field-fed juveniles are attributed to the relatively greater percentage of animal material in their natural diets. The decreased ability of juveniles to assimilate plant food can be explained in terms of their lower ratio of intestine length to intestine diameter (IL/ID) and apparently shorter retention time for ingested food items. Other possible reasons for differential rates of assimilation in juvenile and adult fishes may be the make-up of their respective enzyme compliments or the absence of sufficient populations of endocommensal bacteria. These possibilities were not investigated in the present study, but would make interesting subjects for future research.

In summary, strong correlation has been shown between dietary change, intestinal morphology and nutritional biology in the territorial reef damsel *Eupomacentrus lividus*. Adult *E. lividus* are apparently highly efficient in the assimilation of plant food but may supplement their diets, whether intentionally or incidentally, by the ingestion of a small percentage of animal material. Juveniles compensate for their relative inability to assimilate plant food by ingesting a much higher proportion of animal material. Although overall growth in the species is apparently isometric, disproportionate change in intestinal morphology favors increase in intestine length over intestine diameter and may enhance the ability of the adults to assimilate plant material. The relation of intestine length to intestine diameter (IL/ID), combined with information on retention time of ingested food items, is an important consideration in relating intestinal morphology to assimilation efficiency in herbivorous fishes.

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