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# Relative Intestine Length and Feeding Ecology of Freshwater Fishes

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## RELATIVE INTESTINE LENGTH AND FEEDING ECOLOGY OF FRESHWATER FISHES

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There is a significant relationship between the intestine length ( $Y$ ) and total body length ( $X$ ) for 11 species of freshwater fish ( $Y = 0.08X^{1.42}$ ). Sufficient variation exists about this relationship to indicate important differences among the species' diets. The diets for each species, ranked on a Trophic Index scale determined from literature data, are negatively rank order correlated with the mean relative intestine lengths ( $r_s = -0.67$ ). There is no significant rank order correlation between the Trophic Indices determined from data on stomach contents and the mean relative intestine lengths for fish from a single creek.

INDEX TERMS: Allometric function; diet; fish; intestine length; Trophic Index.

### INTRODUCTION

The pattern of allometric growth is related to the general function of animal's organs. Adaptations arise for organs to efficiently function in varying habitats. For example, the equation for the relation between kidney and body weight is curvilinear in mammals (Brody, 1945), but the structural adaptations of the kidney are reflective of the organism's environment. There is a positive correlation in mammals between the length of the Henle's loops in the kidney and the degree of habitat aridity (Schmidt-Nielsen, 1964).

Assimilation is an important process in the bioenergetics of species. Digestion of different food types is a common problem for species in varying environments. In fish, competition among species and availability of diverse food types has resulted in a wide range of digestive adaptations (Al-Hussaini, 1949; Fänge and Grove, 1979). One of the most obvious of these is the variation in the relative length of the gastrointestinal tract which may be indicative of profound differences in species' food niches.

We achieved two major objectives in this study. First, we tested the degree of correlation between length of intestine and total body length and determined the form of the relationship between these two variables on an intra- and interspecific basis for freshwater fish. Secondly, we described the relationship between the feeding ecology and the mean relative intestine lengths of the same species. Specifically, we tested the hypothesis that the mean relative intestine length is shorter for species feeding at higher trophic levels. Finally, we discussed the general significance of morphological functional

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correlation in relation to fish.

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During October and November 1981, 11 species of freshwater fish were collected with traps and by electrofishing in Steel Creek in Barnwell County, South Carolina, with a minimum of ten fish per species. The species included the American eel—*Anguilla rostrata*, creek chubsucker—*Erimyzonops aliciae*, rock bass—*Ambloplites rupestris*, sunfish—*Lepomis microlophus*, largemouth bass—*Micropterus dolomieu*, northern hog sucker—*Pseudorasbora parva*, redbreast sunfish—*Lepomis gibbosus*, pumpkinseed—*Lepomis gibbosus*, and white sucker—*Catostomus commersoni*. Intestine length as the distance from immediately posterior to anterior was measured for each fish. The diet of each fish was determined by removing the stomach contents and measuring the intestine length as the distance from the mouth to the anus. The fish of family Catostomidae were collected from immediately posterior to anterior material was left in the stomach. The mean relative intestine length for each species was determined by total body length.

The diet of each fish was determined from stomach contents and analyzed for trophic structure. The Trophic Index (TI) was determined for each fish based on its diet. A herbivorous diet, 3 and an insectivorous diet, 4. The proportion of stomach contents consisting of invertebrates, and fish was determined. The TI was then calculated by multiplying the TI value (1, 3, or 5) and a Trophic Index value from a literature source on fish diets (Rohlf, 1981) in a similar manner but as an index of trophic level for the species for which diet data were not available. The Trophic Index was taken from Rohlf (1981) (Table 1).

The parabolic equation  $Y = aX^b$  was used to describe the relationship between intestine length in mm ( $X$ ) and total body length in mm ( $Y$ ). Similarity in the relationship between weight to body weight was tested by analysis with the linear regression method. The coefficient of determination ( $r^2$ ) was determined when compared to the confidence intervals for  $a$  and  $b$  (Rohlf (1981). Statistical

## LENGTH AND FEEDING TROPIC INDEXES OF FRESHWATER FISHES

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(3)

Intestine length ( $Y$ ) and total body length ( $X$ ) were related by the equation  $Y = aX^{1.42}$ . Sufficient variation exists among the species' diets. The Trophic Index scale determined from the mean relative intestine length with the mean relative intestine length order correlation between the contents and the mean relative

Intestine length; Trophic Index.

related to the general function of the digestive organs to efficiently function. The equation for the relationship is linear in mammals (Brody, 1945). The kidney are reflective of a positive correlation in the length of the loops in the kidney and (Nielsen, 1964).

is in the bioenergetics of a common problem for competition among species resulted in a wide range of variation (Fänge and Grove, 1979). The variation in the relative intestine length may be indicative of pro-

his study. First, we tested the relationship between these two variables on a basis for freshwater fish. The relationship between the feeding ecology of the same species. Species were ranked by mean relative intestine length on different trophic levels. Finally, the morphological functional

Department, Colorado State University,

correlation in relation to the evolution and ecology of freshwater fish.

### MATERIALS AND METHODS

During October and November, 1981, fish were collected from Steel Creek in Barnwell County, South Carolina. Fish were collected with traps and by electroshocking. A total of eleven species, with a minimum of ten fish per species, were collected as follows: American eel—*Anguilla rostrata*, redbfin pickerel—*Esox americanus*, creek chubsucker—*Erimyzon oblongus*, lake chubsucker—*Erimyzon sucetta*, northern hog sucker—*Hypentelium nigricans*, yellow bullhead—*Ictalurus natalis*, pirate perch—*Aphredoderus sayanus*, redbreast sunfish—*Lepomis auritus*, spotted sunfish—*Lepomis punctatus*, largemouth bass—*Micropterus salmoides*, and black-banded darter—*Percina nigrofasciata*. Standard and total lengths were measured for each fish. The length of the intestine was determined by removing the gastrointestinal tract and measuring intestine length as the distance from the pylorus to the anus, except for the fish of family Catostomidae where intestine length was measured from immediately posterior of the esophagus to the anus. Fecal material was left in the intestine during measurement. Relative intestine length for each fish was determined by dividing the intestinal length by total body length.

The diet of each fish was ranked on a "Trophic Index" scale based on stomach contents and data on stomach contents from the literature. The Trophic Index varied from 1 to 5, with 1 representing a herbivorous diet, 3 an invertebrate diet, and 5 a piscivorous diet. The proportion of stomach contents that was composed of plants, invertebrates, and fish was estimated visually. The Trophic Index was then calculated by multiplying each proportion by its trophic value (1, 3, or 5) and adding the products. In addition, for each literature source on fish diets, a Trophic Index was determined in a similar manner but as an unweighted mean across studies. For six of the species for which dietary data were lacking, comparable information was taken from the literature for closely related species (Table 1).

The parabolic equation,  $Y = aX^b$ , was used to express the relationship between intestine length in mm ( $Y$ ) and total body length in mm ( $X$ ). Similar use of this function to relate intestine weight to body weight is illustrated by Brody (1945). Preliminary analysis with the linear function ( $Y = a + bX$ ) revealed a lower coefficient of determination ( $r^2$ ) and a relatively large  $Y$  intercept when compared to the results for the curvilinear function. Confidence intervals for  $a$  and  $b$  were determined, as described by Sokal and Rohlf (1981). Statistical significance was indicated by  $P \leq 0.05$ .

## RESULTS

The differences between the curvilinear and linear models in explaining the relationship between intestine length and total body length is illustrated for a single species, *Micropterus salmoides* (Figure 1). The coefficient of determination for the parabolic equation was slightly greater than that of the linear equation for this species ( $r^2 = 0.98$  vs 0.95). Also, the  $Y$ -intercept for the parabolic equation ( $-1.60$ ) was much closer to zero than the  $Y$ -intercept of the linear equation ( $-32.30$ ). An intercept of approximately zero would be expected for allometric relationships similar to the one reported here.

The values defining the allometric function between the intestine length ( $Y$ ) and total body length ( $X$ ) are listed in Table 1. The fit of the data by the allometric function was significant for each species and for all species considered together. The confidence intervals for the  $Y$ -intercepts and slopes overlap for each comparison of species. Although the degree of correlation was generally higher for the single species models as compared to that of the overall species model, the predictability of the latter model was relatively high and within the range of that for the single species models. Furthermore, the confidence intervals for the  $Y$ -intercept ( $a$ ) and slope ( $b$ ) of the overall model overlaps with those of the comparable parameters for the individual species models in every case but two ( $a$ -*Erimyzon*

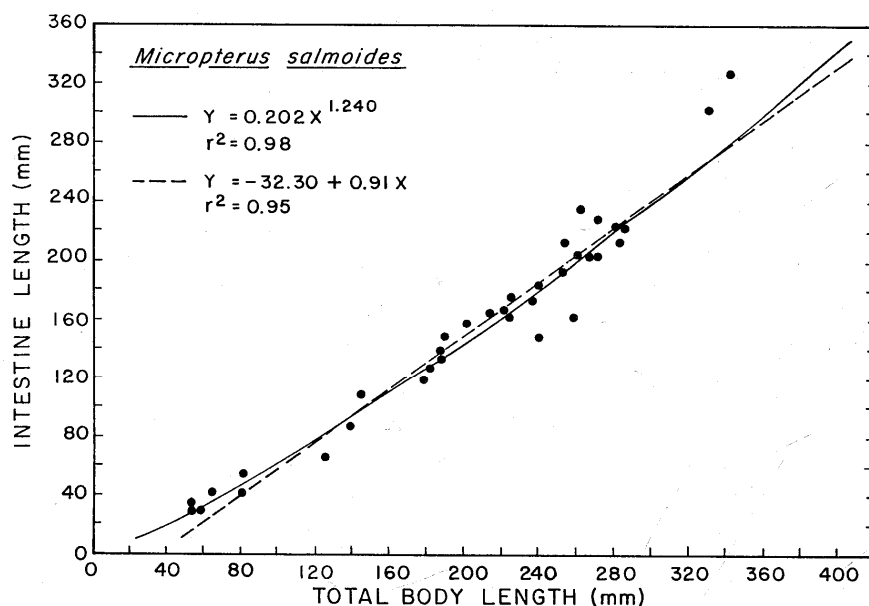


FIGURE 1

The relationship between intestine length and total body length for largemouth bass, *Micropterus salmoides*.

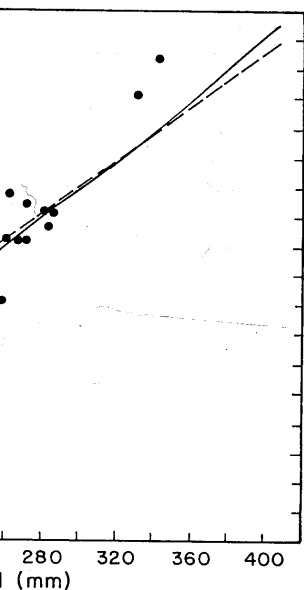
*oblongus*; *b*-*Percina nigricans* species models were all significant and this trend was significant.

The mean relative length was calculated from the stomach contents and the Trophic Index calculated from the Trophic Index (Table 1). The correlation was significant and positive, using a partial correlation. There was either of the trophic index models, except for the overall model was significantly different from the literature ( $r_s = -0.67$ ). The correlation was significantly different from zero related with the Trophic Index. The correlation with the Trophic Index and intestine length was also significant for the individual species models ( $r_s = 0.35$ ; *Erimyzon oblongus*) and was significantly correlated with the slope of the Trophic Index.

There is a significant correlation between intestine length and total body length ( $Y = 0.08X^{1.42}$ ; Table 1) which is greater than those of the other species. This analysis produces a precise estimate of the mean values of the variables. The mean body weight in mammalian species can also be used to estimate the greater relative increase in body length observed in fish. The relationship; the longer the body length, the greater surface area for the intestine. An increase in the diameter of the intestine increases surface area, but in birds the primary mechanism accounts for the increase (Peters, 1962). As fish increase in size, which creates a need for more efficient digestion of the food, the surface area increases as an allometric function (Peters, 1978) and the digestive requirements for this tissue, the surface area, increase as a power function.

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mparable parameters for  
se but two (*a-Erimyzon*



Intestine length for largemouth bass,

*oblongus*; *b-Percina nigrofasciata*). The slopes for the individual species models were all lower than that of the overall species model, and this trend was significant ( $P < 0.01$ ;  $\chi^2$  sign test).

The mean relative length of the intestine, the Trophic Index as calculated from the stomach contents of fish from Steel Creek, and the Trophic Index calculated from literature data are presented in Table 1. The correlation between the two trophic indices was significant and positive, using either least squares or Spearman's rank order correlation. There were no significant correlations between either of the trophic indices and the slope or intercept of the individual species models, except that the intercept of the individual species model was significantly correlated with the Trophic Index from the literature ( $r_s = -0.67$ ). The mean relative intestine length which was significantly different for each species, was significantly correlated with the Trophic Index from the literature ( $r_s = -0.65$ ), but not with the Trophic Index from the stomach contents. The relative intestine length was also correlated with the intercept of the individual species models ( $r_s = 0.65$ ); however, the correlation was not significant with the deletion of the data for one outlying point ( $r_s = 0.35$ ; *Erimyzon oblongus*). The relative intestine length was not correlated with the slope of the individual species models.

#### DISCUSSION

There is a significant relationship between the intestine length ( $Y$ ) and total body length ( $X$ ) for 11 species of fish from seven families ( $Y = 0.08 X^{1.42}$ ; Table 1). The slope of the overall species model was greater than those of the individual species models; the least squares analysis produces a predicted line that lies close to the intraspecific mean values of the variables, thus accounting for the greater slope for the overall model. Stomach and intestine weight is correlated to body weight in mammals and birds, and a similar curvilinear function can also be used to define this relationship (Brody, 1945). The greater relative increase in the intestine length as compared to the body length observed in fish is expected from the surface to volume relationship; the longer-convoluted intestine creates a relatively greater surface area for absorption of food as fish increase in mass. An increase in the diameter of the intestine alone would increase the surface area, but in birds increased length and not diameter is the primary mechanism accounting for increased surface area (Welty, 1962). As fish increase in size, the volume of their food increases, which creates a need to lengthen the intestinal tract to maintain efficient digestion of the food. Since the mass of body tissue increases as an allometric function of linear body growth (Bagenal, 1978) and the digestive tract must provide the nutritional requirements for this tissue, the length of the intestinal tract should also increase as a power function of body length as it does.

Table 1. Parameters of the curvilinear function ( $\bar{Y} = a\bar{X}^b$ ) for the relationship between intestine length ( $\bar{Y}$ ) and total body length ( $\bar{X}$ ) in 11 species of fish. The confidence intervals (CI) and correlation coefficient ( $r$ ) were calculated using the natural logarithmic transformed variables. The mean relative intestine length was calculated by dividing intestine length by total body length. Fish diets were classified on a Trophic Index scale from 1 to 5, with 1 being a plant, 3 an invertebrate, and 5 a fish diet; data were based on observed stomach contents ( $\bar{S}$ ) of fish collected in this study and from the literature ( $\bar{L}$ ).

Family	Species	Sample Size	a (95% CI)	b (95% CI)	r**	Relative Intestine Length $\pm$ 2SE	Trophic Index- $\bar{S} \pm$ 2SE	Trophic Index- $\bar{L}$	Reference*
Anguillidae	<u>Anguilla rostrata</u>	30	0.08(0.03-0.21)	1.24(1.07-1.41)	0.94	0.31 $\pm$ 0.03	3.05 $\pm$ 0.11	3.11	1
Aphredoderidae	<u>Aphredoderus sayanus</u>	27	0.15(0.02-0.96)	1.22(0.79-1.65)	0.75	0.40 $\pm$ 0.02	2.95 $\pm$ 0.11	3.22	2
Catostomidae	<u>Erimyzon oblongus</u>	32	0.59(0.20-1.78)	1.21(1.00-1.42)	0.90	1.81 $\pm$ 0.10	2.79 $\pm$ 0.10	1.78	2
	<u>Erimyzon sucetta</u>	10	0.33(0.01-10.92)	1.31(0.65-1.97)	0.82	1.76 $\pm$ 0.20	2.73 $\pm$ 0.26	1.78	2
	<u>Hypentelium nigricans</u>	12	0.33(0.10-1.11)	1.23(1.00-1.46)	0.93	1.10 $\pm$ 0.18	2.95 $\pm$ 0.10	1.78	1
Centrarchidae	<u>Lepomis auritus</u>	36	0.15(0.10-0.23)	1.28(1.09-1.47)	0.91	0.70 $\pm$ 0.03	2.91 $\pm$ 0.10	2.92	5
	<u>Lepomis punctatus</u>	45	0.16(0.10-0.28)	1.28(1.16-1.40)	0.96	0.59 $\pm$ 0.03	2.73 $\pm$ 0.19	2.92	5
	<u>Micropterus salmoides</u>	35	0.20(0.14-0.29)	1.24(1.17-1.31)	0.99	0.72 $\pm$ 0.04	3.41 $\pm$ 0.31	4.87	6,7,8

Family	Species	Sample Size	a (95% CI)	b (95% CI)	r**	Relative Intestine Length $\pm$ 2SE	Trophic Index- $\bar{S} \pm$ 2SE	Trophic Index- $\bar{L}$	Reference*
Esocidae	<u>Esox americanus</u>	11	0.25(0.02-2.89)	1.16(0.68-1.64)	0.85	0.58 $\pm$ 0.05	4.20 $\pm$ 0.98	3.91	2

Table 1. Continued

Family	Species	Sample Size	a (95% CI)	b (95% CI)	r**	Relative Intestine Length $\pm$ 2SE	Trophic Index-S $\pm$ 2SE	Trophic Index-L	Reference *
Catostomidae									
	<u>Erimyzon oblongus</u>	32	0.59(0.20-1.78)	1.21(1.00-1.42)	0.90	1.81 $\pm$ 0.10	2.79 $\pm$ 0.10	1.78	2
	<u>Erimyzon sucetta</u>	10	0.33(0.01-10.92)	1.31(0.65-1.97)	0.82	1.76 $\pm$ 0.20	2.73 $\pm$ 0.26	1.78	2
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Centrarchidae									
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	<u>Lepomis punctatus</u>	45	0.16(0.10-0.28)	1.28(1.16-1.40)	0.96	0.59 $\pm$ 0.03	2.73 $\pm$ 0.19	2.92	5
	<u>Micropterus salmoides</u>	35	0.20(0.14-0.29)	1.24(1.17-1.31)	0.99	0.72 $\pm$ 0.04	3.41 $\pm$ 0.31	4.87	6,7,8

Table 1. Continued

Family	Species	Sample Size	a (95% CI)	b (95% CI)	r**	Relative Intestine Length $\pm$ 2SE	Trophic Index-S $\pm$ 2SE	Trophic Index-L	Reference *
Esocidae									
	<u>Esox americanus</u>	11	0.25(0.02-2.89)	1.16(0.68-1.64)	0.85	0.58 $\pm$ 0.05	4.20 $\pm$ 0.98	3.91	2
Ictaluridae									
	<u>Ictalurus natalis</u>	11	0.13(0.01-1.49)	1.34(0.86-1.82)	0.88	0.78 $\pm$ 0.16	3.13 $\pm$ 0.25	3.24	2,3,4
Percidae									
	<u>Percina nigrofasciata</u>	28	0.44(0.12-1.57)	0.96(0.66-1.26)	0.78	0.37 $\pm$ 0.01	2.90 $\pm$ 0.09	2.86	2,9
	Overall species	278	0.08(0.04-0.15)	1.42(1.29-1.54)	0.81		3.07 $\pm$ 0.26	2.94 $\pm$ 0.26	

\*References for Trophic Index-L: 1 - Wenner and Musick, 1975; 2 - Flemer and Woolcott, 1966; 3 - Moore, 1972;

4 - Klarberg and Benson, 1975; 5 - Davis, 1972; 6 - Goodson, 1965; 7 - Seaburg and Moyle, 1964; 8 - Chew, 1974; 9 - Karr 1963.

\*\*P < 0.01 for every correlation coefficient.

\*\*\*Species with dietary data lacking and related species which were used to determine the Trophic Index from literature in parenthesis: Erimyzon sucetta, (Erimyzon oblongus); Hypentelium nigricans, (Erimyzon oblongus); Lepomis punctatus, (Lepomis auritus); Esox americanus, (Esox niger); Ictalurus natalis, (Ictalurus nubilosus); and Percina nigrofasciata, (Percina phoxocephala, Percina maculata, Etheostoma nigrum).

The  $Y$ -intercept ( $a$ ) should approximate zero, but the intercepts of each individual species model as well as that of the overall species model were significantly different from zero (Table 1). The discrepancy may be attributed to the lack of data from very small fish. Intercept values higher than zero can be explained by a more rapid intestinal development for the early life history stages than that predicted by the estimated curvilinear functions. Thus, the early intestinal development of a species is related to the relative intestine length of older individuals which is significantly different across species (Table 1). The early intestinal development is probably directly related in part to the diet of the fish (Odum, 1970).

The use of the Trophic Index is an attempt to summarize the diet in one number. Ecologically, it represents a simplification. For example, a fish in category three could occupy quite different trophic positions depending upon the type of invertebrates eaten. A fish that eats a spider might be a tertiary consumer, while one that eats a grasshopper would be a secondary consumer. Despite these difficulties, our crude Trophic Index may still be useful in that it represents an average trophic position for an organism that is an opportunistic feeder (Barrington, 1962). Our Trophic Indices were positively correlated, which indicates that a Trophic Index is at least capable of summarizing general trends in the diets of fish species across their range. In addition, the Trophic Indices of fish from Steel Creek differed significantly across species with largemouth bass and grass pickerel with the highest values, and creek chubsucker and spotted sunfish with the lowest. The range in Trophic Indices across species was less when calculated from stomach contents than from literature data from a variety of geographical locations. Fish from Steel Creek appear to be feeding primarily on invertebrates, rather than utilizing the broader range of food types that their gastrointestinal tracts may have evolved to digest. The Trophic Index calculated from the literature, but not from the stomach data, is negatively correlated with the mean relative intestine length. The limited range of the Trophic Index calculated from stomach contents may be responsible for the lack of significant correlation with the mean relative intestine length.

Other authors have noted that carnivorous fish have relatively shorter intestines than herbivorous fish (Fänge and Grove, 1979; Bond, 1979). In a study of flatfish, De Groot (1971) found that the relative intestine is shortest in Psettididae which eat fish and larger invertebrates, and longest in Soleidae which eat smaller invertebrates. Odum (1970) found an extremely rapid lengthening of the gastrointestinal tract as mullet shifted from primarily an animal diet to a plant diet. These trends and our results suggest that the relative length of the gastrointestinal tract is one of the adaptive features of the feeding ecology of fish.

Features other than the digestive tract. The vary dramatically between these features and the may be relatively co phylogeny of the speci feeding environments. literature and the mean good indicators of pa mathematical equation tionship between the le the body, there is still indicate adaptive trend

We wish to thank A field collections, Dr. W K. Fausch for review presses appreciation to allowance of a semester conducted under the a graduate Research Proj tory, Aiken, South Ca between the Department Institute of Ecology.

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zero, but the intercepts of that of the overall species (Table 1). The discrepancy from very small fish is explained by a more rapid history stages than that functions. Thus, the early led to the relative intestine significantly different across development is probably dish (Odum, 1970).

tempt to summarize the diet into a simplification. For very quite different trophic substrates eaten. A fish that eat, while one that eats a variety. Despite these difficulties it is useful in that it represents a diet that is an opportunistic generalist. Indices were positively correlated and the index is at least capable of comparing fish species across their diets. Fish from Steel Creek and largemouth bass and grass carp, chubsucker and spotted bass. Trophic Indices across species are different than from literature values. Fish from Steel Creek eat invertebrates, rather than utilizing vertebrates. Gastrointestinal tracts may vary and the index calculated from the Trophic Index is negatively correlated. The limited range of the Trophic Index may be responsible for the mean relative intestine

of various fish have relatively similar. Fänge and Grove, 1979; and De Groot (1971) found that the Trophic Index of fish which eat fish and larger fish and fish which eat smaller invertebrates. The rapid lengthening of the intestine is primarily an animal diet and these results suggest that the relative Trophic Index is the adaptive features of

Features other than length are also important to the function of the digestive tract. The anatomy and histological characteristics can vary dramatically between species (Al-Hussaini, 1949; Mok, 1980). These features and the relative length of the gastrointestinal tract may be relatively conservative characters determined by the phylogeny of the species and the selective regime imposed by past feeding environments. The Trophic Index as calculated from the literature and the mean relative length of the intestine may both be good indicators of past feeding environments. Although a single mathematical equation can be used to describe the allometric relationship between the length of the intestine and the total length of the body, there is still sufficient variation about that relationship to indicate adaptive trends for fish with different niches.

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