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Growth, 1983, 47, 292-300

RELATIVE INTESTINE LENGTH AND FEEDING ECOLOGY OF FRESHWATER FISHES

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(Accepted July 1, 1983)

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 -0.67). There is no significant rank order correlation between the lengths $(r_{\rm e} =$ 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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During October and I Steel Creek in Barnwell lected with traps and by with a minimum of ten American eel—Anguilla creek chubsucker-Erim sucetta, northern hog su head-Ictalurus natalis redbreast sunfish-Lepa punctatus, largemouth banded darter-Percina were measured for each mined by removing the tine length as the distan the fish of family Catosto from immediately poste material was left in th intestine length for each nal length by total body

The diet of each fish w on stomach contents and ture. The Trophic Index herbivorous diet, 3 an i The proportion of stoma invertebrates, and fish y was then calculated by value (1, 3, or 5) and a literature source on fish similar manner but as an the species for which di mation was taken from (Table 1).

The parabolic equati relationship between in length in mm (X). Similar weight to body weight analysis with the linear coefficient of determina when compared to the dence intervals for a and and Rohlf (1981). Statist

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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, redfin 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 blackbanded 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, $Y = a X^b$, 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 $P \leq 0.05$.

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testine length (Y) and total body $X^{1,42}$). Sufficient variation exists ences among the species' diets. Index scale determined from with the mean relative intestine torter correlation between the contents and the mean relative

tine length; Trophic Index.

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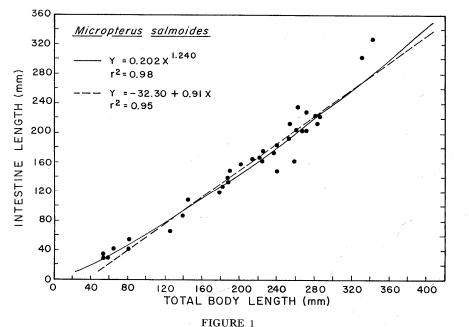
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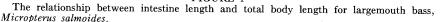
FISH INTESTINE LENGTH

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 $(r^2 = 0.98 \text{ vs } 0.95)$. 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





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oblongus; b-Percina nig species models were all l and this trend was sign

The mean relative le calculated from the stor the Trophic Index calcu Table 1. The correlatio nificant and positive, us order correlation. Ther either of the trophic indi ual species models, exce model was significantly literature ($r_s = -0.67$). was significantly differe lated with the Trophic not with the Trophic Inintestine length was also ual species models (r_s significant with the dele 0.35; Erimyzon oblongi correlated with the slop

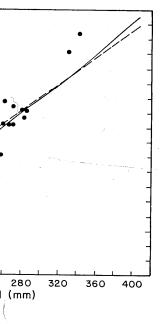
There is a significant and total body length (2 $(Y = 0.08 X^{1.42}; \text{ Table 1})$ greater than those of the analysis produces a premean values of the vari for the overall model. S body weight in mamma tion can also be used to greater relative increase body length observed in relationship; the longe greater surface area for An increase in the diam surface area, but in bir primary mechanism acc 1962). As fish increase which creates a need t efficient digestion of th creases as an allometric 1978) and the digestive ments for this tissue, th increase as a power fui

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ar and linear models in ne length and total body cropterus salmoides (Figor the parabolic equation equation for this species or the parabolic equation *Y*-intercept of the linear eximately zero would be lar to the one reported

too between the intestine and in Table 1. The fit of gnificant for each species e confidence intervals for h comparison of species. generally higher for the at of the overall species l was relatively high and es models. Furthermore, t (a) and slope (b) of the mparable parameters for se but two (a-Erimyzon



ly 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; χ^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 $(Y = 0.08 X^{1.42}; \text{ Table 1})$. 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.

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Parameters of the curvilinear function $(\underline{Y} = \underline{aX}^{b})$ for the relationship between intestine length (\underline{Y}) and total body length an invertebrate, and 5 a fish diet; data were based on observed stomach contents (S) of fish collected in this study and length by total body length. Fish diets were classified on a Trophic Index scale from 1 to 5, with 1 being a plant, 3 (\underline{x}) in 11 species of fish. The confidence intervals (\underline{CI}) and correlation coefficient (\underline{x}) were calculated using the natural logrithmic transformed variables. The mean relative intestine length was calculated by dividing intestine from the literature $(\underline{L})^{\frac{+k+s}{2}}$. Table 1.

Family Species	Sample Size	<u>a</u> (95% <u>CI</u>)	<u>p</u> (95% <u>cr</u>)	** * 11	Relative Intestine Length ± 2 <u>SE</u>	Trophic Index- <u>S</u> ± 2 <u>SE</u>	Trophíc Index- <u>L</u>	Reference
Anguillidae Anguilla rostrata	30	0.08(0.03-0.21)	1.24(1.07-1.41) 0.94	0.94	0.31 ± 0.03	3.05 ± 0.11	3.11	1
Aphredoderidae Aphredoderus sayanus	27	0.15(0.02-0.96)	1.22(0.79-1.65)	0.75	0.40 ± 0.02	2.95 ± 0.11	3.22	7
Catostomidae Erimyzon oblongus	32	0.59(0.20-1.78)	1.21(1.00-1.42)	06.0	1.81 ± 0.10	2.79 ± 0.10	1.78	7
Erimyzon sucetta	10	0.33(0.01-10.92)	1.31(0.65-1.97)	0.82	1.76 ± 0.20	2.73 ± 0.26	1.78	2
Hypentelium nigricans	12	0.33(0.10-1.11)	1.23(1.00-1.46)	0.93	1.10 ± 0.18	2.95 ± 0.10	1.78	1
Centrarchidae Lepomis auritus	36	0.15(0.10-0.23)	1.28(1.09-1.47)	16.0	0.70 ± 0.03	2.91 ± 0.10	2.92	Ω
Lepomis punctatus	45	0.16(0.10-0.28) \ 1.28(1.16-1.40)	1.28(1.16-1.40)	0.96	0.59 ± 0.03	2.73 ± 0.19	2, 92	S
Micropterus salmoides	35	0.20(0.14-0.29)	1.24(1.17-1.31)	0.99	0.72 ± 0.04	3.41 ± 0.31	4.87	6,7,8

Reference 2 Trophic Index-<u>L</u> 3.91 Trophic Index-S ± 2SE 4.20 ± 0.98 Relative Intestine Length ± 2SE 0.58 ± 0.05 ţ 0.25(0.02-2.89) 1.16(0.68-1.64) 0.85 ы <u>b(95% či</u>) <u>a</u>(95% <u>CI</u>) Sample Size Π Table 1. Continued Esox americanus Species Esocidae Family

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Catostomidae									H
<u>Erimyzon oblongus</u>	32	0.59(0.20-1.78)	1.21(1.00-1.42)	0.90	1.81 ± 0.10	2.79 ± 0.10	1.78	2	
Erimyzon sucetta	10	0.33(0.01-10.92)	1.31(0.65-1.97)	0.82	1.76 ± 0.20	2.73 ± 0.26	1.78	5	
Hypentelium nigricans	12	0.33(0.10-1.11)	1.23(1.00-1.46)	0.93	1.10 ± 0.18	2.95 ± 0.10	1.78	T	Ŝ
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Micropterus salmoides	35	0.20(0.14-0.29)	1.24(1.17-1.31)	0.99	0.72 ± 0.04	3.41 ± 0.31	4.87	6,7,8	
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Table 1. Continued							- - -		
Family Species	Size	<u>a</u> (95% <u>CI</u>)	<u>b</u> (95% <u>CI</u>)	* +	Relative Intestine Length ± 2 <u>SE</u>	Trophic Index- <u>S</u> ± 2 <u>SE</u>	Trophíc Index- <u>L</u>	Reference *	D.
Esocidae Esox americanus	11	0.25(0.02-2.89)	1.16(0.68-1.64)	0.85	0.58 ± 0.05	4.20 ± 0.98	3.91	7	AVID O.
Ictaluridae Ictalurus natalis	11	0.13(0.01-1.49)	1.34(0.86-1.82)	0.88	0.78 ± 0.16	3.13 ± 0.25	3.24	2,3,4	. RIBB
Percidae Percina nigrofasciata	28	0.44(0.12-1.57)	0.96(0.66-1.26)	0.78	0.37 ± 0.01	2.90 ± 0.09	2.86	2,9	LE AN
Overall species	278	0.08(0.04-0.15)	1.42(1.29-1.54)	0.81		3.07 ± 0.26	2.94 ± 0.26		ND J
* References for Trophic Index-L:	c Index-	1 - Wenner	and Musick, 1975; 2 -	Flemer a	Flemer and Woolcott, 1966; 3	- Moore, 1972;			псн
4 - Klarberg and Benson, 1975;	ason, 19	975; 5 - Davis, 1972;	; 6 - Goodson, 1965; 7	r	Seaburg and Moyle, 1964; 8 - Chew, 1974; 9	64; 8 - Chew, I	974; 9 - Kar	- Karr 1963.	AEL
$\frac{4\pi}{P} < 0.01$ for every correlation coefficient.	rrelatio	on coefficient.							н.
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**** 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 nubulosus); and Percina nigrofasciata, (Percina phoxocephala, Percina maculata, Etheostoma nigrum).

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Catostomidae Erimyzon oblongus

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The *V*-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 Psettodidae 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. DAVID 0,

Features other than the digestive tract. The vary dramatically betw These features and the may be relatively co phylogeny of the specifeeding environments. literature and the mean good indicators of pas 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 Prog tory, Aiken, South Ca between the Department Institute of Ecology.

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Finge and Grove, 1979; bot (1971) found that the which eat fish and larger nich eat smaller inverterapid lengthening of the primarily an animal diet suggest that the relative 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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AGE AND SEX PROT

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Collagen and noncollagend according to the age and s extracts and the soluble cowhile the insoluble collage sex-differences have been of contents increase with age does not change. In the Elkedly with age, the sialic contents do not vary. Plass change with aging. In the coin the collagen and noncodecrease was observed for hydroxyproline from the the INDEX TERMS: Bone protection

Although the variati have been reported by levede, 1971; Nusgens and Bailey, 1972; Sch 1979), most studies are ous proteins (NCP), he this respect because in collagen makes up ab facilitated since the int method involving ED' tion. Although no clear mineralization process Herring, 1976). Sex di diseases is a well-know quencies according to a bone metabolism and males and females to Raisz, 1978; Cruess an the effect of sex different The present study was of age and sex on co during the first 12 mon dure of bone proteins methods.

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