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SELECTIVE PREDATION WITH RESPECT TO BODY SIZE IN A POPULATION OF THE FISH *XENOMELANIRIS VENEZUELAE* (ATHERINIDAE)¹

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Abstract. The food habits of the planktivorous fish *Xenomelaniris venezuelae* (Atherinidae) in Lake Valencia, Venezuela, were studied in relation to fish size. Mean selection for major prey types and mean breadth of diet were determined for each size class of fish. The smallest fish select the rotifer *Brachionus calyciflorus* while successively larger fish select successively larger prey. Mean length and mean dry mass of the items eaten by the fish are directly related to fish length. Diet breadth, however, is inversely related to fish length, indicating that large fish feed more selectively than small fish. Evidence is presented which suggests that the relationship between *Xenomelaniris* body size and prey selection is due to increased capture efficiency with size, and that the relationship of body size to diet breadth results from growth-related improvements in vision.

Key words: *Atherinidae*; *body size*; *capture efficiency*; *diet breadth*; *planktivorous fish*; *plankton*; *prey detection*; *size-selective predation*; *Venezuela*; *Xenomelaniris*.

INTRODUCTION

Interest in optimal foraging theory and the effects of fish on plankton community structure has led to much study of selective predation by planktivorous fish (Hrbáček 1962, Brooks and Dodson 1965, Werner and Hall 1974, Werner 1977, Zaret 1980a, Werner and Mittelbach 1981). Many studies have been based on artificially simplified fish-prey encounters. Such conditions are useful in isolating important variables, but they carry the risk of oversimplified interpretation. A common type of simplification is the use of several size classes of a single species of prey. Natural plankton prey assemblages usually include several species, which may vary in a number of important properties in addition to size. These include motion (Zaret 1980b), color (Hairston 1979, Byron 1981), luminance contrast (Zaret 1972, Mellors 1975, Zaret and Kerfoot 1975, Eggers 1977, Stenson 1980), vertical migration (Zaret and Suffern 1976, Wright et al. 1980), palatability (Kerfoot et al. 1980, Kerfoot 1982), ease of handling by predators (Werner 1974, Zaret 1980a), and escape ability (Confer and Blades 1975, Drenner et al. 1978, Vinyard 1980). Unfortunately, none of these is as easy to quantify as prey size.

Most studies of selective feeding by planktivorous fish also fail to examine the effects of predator size. This limitation reflects emphasis on the foraging behavior of individual fish rather than fish populations. The effects of planktivory on plankton community structure cannot be properly understood, however, without considering the feeding patterns of fish populations as a whole, and size variation is characteristic of fish populations.

The omission of predator size effects from studies of selective predation by planktivorous fish may also reflect belief that these effects are not very important. Wong and Ward (1972) demonstrated that larval yellow perch selectively preyed on small *Daphnia pulex* during the 1st 3 wk of life and that this selection was explained by the small gape size of the young fry. As the fry grew, they switched to larger prey. These results and others have led to speculation that body size in planktivorous fish has little impact on selection patterns once gape size ceases to be a limiting factor (Zaret 1980a).

In the present study we examine feeding selectivity of a freshwater planktivore, *Xenomelaniris venezuelae* (Eigenmann), in Lake Valencia, Venezuela. The study incorporates information about selective feeding on all prey taxa by all sizes of fish. *X. venezuelae* is well suited to this purpose for several reasons: (1) the species is an exclusively limnetic feeder, so confounding effects of littoral communities are absent; (2) no other fish population inhabits the limnetic zone of Lake Valencia, so confounding effects of interspecific competition and predation are absent; (3) unlike many planktivores that have been studied (Galbraith 1967, Werner and Hall 1977, Hansen and Wahl 1981), *Xenomelaniris* spends its entire life as a planktivore; (4) the population feeds on a wide variety of prey types; and (5) the population breeds throughout the year. This last characteristic results in a population of mixed sizes; it is thus possible to compare feeding patterns of different size classes exposed to a common pool of prey.

Xenomelaniris venezuelae is endemic to Lake Valencia (Eigenmann 1920). Lake Valencia is a large (350 km²), desiccating freshwater lake lying at 10°N latitude. Its current mean depth is ≈ 18 m. The morphology, chemistry, and trophic structure of the lake are summarized by Lewis and Weibezahn (1976).

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TABLE 1. Relative densities of selected prey types of *Xenomelaniris*, expressed as mean numerical proportions of the zooplankton, and mean and maximum ranges among 5 m depth intervals of numerical proportions of these prey types from selected studies in Lake Valencia.

Prey type	Numerical proportion					
	Mean		Mean range		Maximum range	
	Diel	Weekly	Diel	Weekly	Diel	Weekly
<i>Brachionus calyciflorus</i>	0.1261	0.2451	0.0600	0.0625	0.0866	0.1311
<i>Moina micrura</i>	0.0001	0.0000	0.0002	0.0000	0.0003	0.0000
<i>Mesocyclops crassus</i> adult female	0.0043	0.0250	0.0069	0.0217	0.0138	0.0628
<i>Notodiaptomus venezolanus</i> adults	0.0123	0.0180	0.0282	0.0288	0.0540	0.1000
<i>Chaoborus brasiliensis</i> fourth-instar larva	0.0054	0.0076	0.0187	0.0187	0.0746	0.0940

METHODS

Two sets of fish samples were taken: (1) a primary set, taken at frequent intervals over a 24-h period, and (2) a secondary set, taken at weekly intervals over a period of 3 mo. The primary set provided a large number of many different sizes of fish exploiting a common pool of prey, and, because the samples were taken over the entire 24-h period, the data set is inherently corrected for time-related feeding biases. The secondary set provided fish with which to determine the generality of results from the primary set.

The sampling locality for the primary data set was in water 20 m deep, and nearly 4 km from the nearest shore. Previous echo sounding surveys had indicated that the fish were abundant at this site. All fish were collected with a large (2.6 m diameter) hoop net. The bag end of the net used 1.6-mm mesh flat nylon netting, which retained all postlarval sizes of *Xenomelaniris*. The net was drawn through the water vertically, like a plankton townet, so that all depths were equally sampled. Fish were transferred directly from the net to plastic bags containing a 15% solution of formaldehyde. Earlier tests had shown that this technique did not induce regurgitation from the gut.

Fish of the primary set were all taken on 28 and 29 August 1980. Catches were made once every hour except at dawn and dusk when feeding was known to be most intensive. From 0530 to 0930 (dawn) fish were netted every 15 min, and from 1930 to 2230 (dusk) they were taken every 30 min. Mean catch was 122 fish but variance was high (coefficient of variation = 136%). All fish were measured to the nearest millimetre total length with a ruler.

Ten fish from each of the 39 sampling times were randomly selected for gut analysis. Whenever random selection failed to include individuals in each of the three thirds of the total range of fish lengths (16–84 mm), two additional fish from each unrepresented part of the range were analyzed, unless no such fish were present in the catch. Catches from 13 of the sampling periods contained <10 fish. In these cases the gut contents of all fish were examined. The digestive tract of all but the smallest *Xenomelaniris* specimens contains

two sharp bends, creating a natural separation of the gut into three sections. Separate counts of zooplankton prey were compiled for each section. Proportions of the different prey types were the same for each section, so the separate counts were pooled. Gut analyses were made for a total of 559 fish captured during the 24-h study. Zooplankton from the guts were examined with a dissecting microscope. Copepods and *Chaoborus* were classified to instar within species. Rotifers and cladocerans were classified to species. Counts were made for each species and instar using techniques described by Lewis (1979). Mean length, breadth, and dry mass were estimated for each of the major prey types of *Xenomelaniris*: *Brachionus calyciflorus* (Rotifera), *Moina micrura* (Cladocera), *Mesocyclops crassus* (Copepoda) adult females, *Notodiaptomus venezolanus* (Copepoda) adult males and females, and *Chaoborus brasiliensis* (Diptera) fourth instar larvae. Length measurements for all prey types excluded caudal setae or rami. Mean lengths and masses for the copepod species and *Brachionus* were taken from Saunders (1980 and J. F. Saunders III, *personal communication*). For *Moina* and *Chaoborus*, mean masses were estimated from volume approximations of 20 randomly selected animals each. Mean lengths are based on measurements of 40–100 animals for each prey type and mean breadth is the average greatest diameter of 20 animals.

Food selection was quantified by the Strauss (1979) linear food selection index, $L_i = r_i - p_i$, where L_i is the food selection index for prey type i , r_i is the numerical proportion of prey type i in the gut, and p_i is the numerical proportion of prey type i in the plankton samples. This index is superior in several respects to Ivlev's electivity index and other proposed indices of food selection (Strauss 1979). The index can range from -1 to $+1$. Negative values indicate selection against a prey type and positive values indicate selection for a prey type.

Lake zooplankton was collected 2 d before and 2 d after the primary fish sample set. Two replicate 0–20 m integrated samples were taken each day between 0700 and 0800 with an integrating tube sampler. The

TABLE 2. Prey of *Xenomelaniris* in Lake Valencia and mean numerical proportion of each in the diet of fish from the primary data set.

Prey type	Numerical proportion	Prey type	Numerical proportion
<i>Notodiaptomus venezolanus</i> adult female	0.1649	<i>C. brasiliensis</i> larva III	0.0106
<i>Brachionus calyciflorus</i>	0.1584	<i>N. venezolanus</i> nauplius	0.0076
<i>Moina micrura</i>	0.1441	<i>Ceriodaphnia cornuta</i>	0.0060
<i>Mesocyclops crassus</i> adult female	0.1413	<i>N. venezolanus</i> copepodite V	0.0055
<i>N. venezolanus</i> adult male	0.0965	<i>C. brasiliensis</i> instar larva II	0.0031
<i>Chaoborus brasiliensis</i> larva IV	0.0637	<i>N. venezolanus</i> copepodite IV	0.0027
<i>M. crassus</i> adult male	0.0360	<i>M. crassus</i> nauplius	0.0012
<i>C. brasiliensis</i> pupa	0.0358	<i>Brachionus plicatilis</i>	0.0011
<i>M. crassus</i> copepodite IV	0.0278	Ostracod	0.0008
<i>Brachionus havanaensis</i>	0.0220	<i>N. venezolanus</i> copepodite III	0.0005
<i>M. crassus</i> copepodite III	0.0180	<i>Keratella americana</i>	0.0003
<i>M. crassus</i> copepodite V	0.0170	<i>C. brasiliensis</i> larva I	0.0002
<i>M. crassus</i> copepodite I	0.0133	<i>N. venezolanus</i> copepodite II	0.0002
<i>M. crassus</i> copepodite II	0.0119	<i>N. venezolanus</i> copepodite I	0.0001

sampler, which consists of a flexible tube of 7.6 cm diameter, is similar to those designed by Lewis and Saunders (1979) and George and Owen (1978), except that it can sample a much longer column of water. Use of integrated samples may produce biased estimates of plankton densities available to the fish if the vertical distribution of plankton is not uniform. Food selection indices, however, employ estimates of relative prey densities available to the fish, expressed as proportions of the ambient zooplankton density, rather than absolute prey densities (Strauss 1979), so if the major prey types' numerical proportions do not vary substantially with depth, the integrated samples should be suitable for measuring selection.

Two sets of zooplankton samples from previous studies were examined to assess the variability of relative density with depth of *Xenomelaniris*'s major prey. The first set is from a diel study of zooplankton vertical distribution made in mid-September, 1979, and the second set is from a weekly series of early morning collections made from late June through October, 1978. Zooplankton for both studies was sampled with a 5-m integrating tube sampler (Lewis and Saunders 1979). For each 5-m depth interval, each major prey type's numerical proportion of the zooplankton was calculated and the range of proportions was computed over the top 20 m of the water column. Table 1 lists the

mean proportions among all depth intervals and the mean and maximum vertical ranges of the proportions of each major prey type for each of the data sets. The mean and maximum ranges are nearly all <0.1 of the total zooplankton density, so use of the integrated samples should introduce little error in the measurement of prey selection indices. Densities of *Moina* in 1978 and 1979 were too low for reliable estimates, but appeared to be uniform within the upper 20 m.

Differences between the two primary data set plankton sampling dates in mean total zooplankton density and in the mean densities of the major prey items of *Xenomelaniris* were tested by analysis of variance and, except for the rotifer *Brachionus calyciflorus*, were found not to be significant ($P > .05$). Rotifer population densities often change rapidly because rotifers have short generation times. Grand means were used to estimate densities of all prey except *B. calyciflorus*. The larger of the means was used to represent the density of *B. calyciflorus* on the day of fish collecting so that estimates of prey selection on the rotifer would be conservative, though differences in the estimates of prey selection resulting from use of the minimum or average densities would be minor.

Gape size was measured on 57 fish of assorted sizes; maximum gill raker spacing was measured on 20 of these fish. *Xenomelaniris* has a protrusible mouth

TABLE 3. Mean lengths and breadths (± 1 SE) and mean dry mass of major prey of *Xenomelaniris* in Lake Valencia, plus estimated numerical proportions of these prey in the water column and absolute density of all zooplankton for the primary data set.

Prey type	Length (mm)	Breadth (mm)	Dry mass (μ g)	Numerical proportion
<i>B. calyciflorus</i>	0.24 \pm 0.004 ($n = 92$)	0.17 \pm 0.007 ($n = 20$)	0.28	0.1550
<i>M. micrura</i>	0.45 \pm 0.010 ($n = 76$)	0.27 \pm 0.020 ($n = 20$)	0.76	0.0207
<i>M. crassus</i> adult female	0.76 \pm 0.005 ($n = 40$)	0.25 \pm 0.008 ($n = 20$)	1.05	0.0325
<i>N. venezolanus</i> adults	1.23 \pm 0.004 ($n = 60$)	0.41 \pm 0.009 ($n = 20$)	4.88	0.0192
<i>C. brasiliensis</i> fourth-instar larva	6.46 \pm 0.038 ($n = 100$)	0.80 \pm 0.027 ($n = 20$)	129.10	0.0058
All zooplankton; absolute density = 116.0 individuals/L				

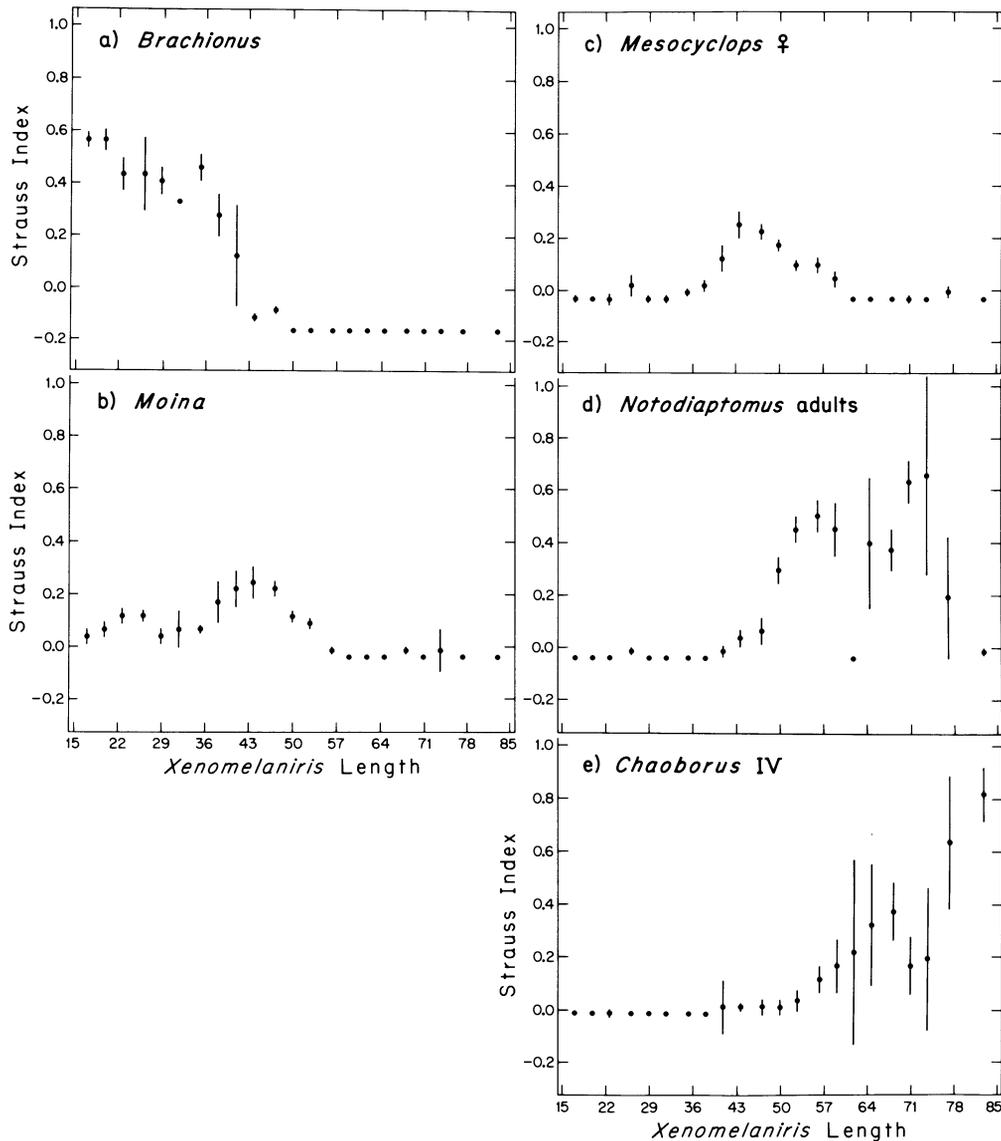


FIG. 1. Strauss index of selection ($\bar{x} \pm 1$ SE) by *Xenomelaniris* on each of its major prey types (primary data set), in relation to fish length.

which opens when the lower lip is gently pulled away from the fish. With the mouth held in this position, the inside gape diameter was measured in the sagittal plane. An ocular micrometer in the eyepiece of a dissecting microscope was used to make the measurements. The gill rakers are long and closely spaced in *Xenomelaniris*, and are supported on the gill arches. The gill arches were removed from the fish and positioned on the stage of a dissecting microscope. Measurements were made of the distances between the bases of adjacent gill rakers. Maximum gill raker spacing was recorded because this measurement was considered to represent best the limit of prey size retention of the rakers.

For the secondary data set, fish were collected from

the deepest part of Lake Valencia (35 m) over a period of 3 mo beginning in December 1979. Two replicate samples were taken once a week with the hoop net from the top 20 m of the water column. The time of sampling was changed from one week to the next according to a sequence: dawn, dusk, midday, midnight. At the same time, two replicate zooplankton samples were collected from the 0–20 m interval with the integrating sampler. Five fish were randomly selected for stomach content analysis from each of the fish samples. Zooplankton from 67 fish stomachs and from the lake were examined according to the procedures already described.

Fish of the primary data set, which ranged in length

TABLE 4. Fish lengths at which selection for various prey types is maximal, as estimated by the "centers of gravity" of the length-prey selection distributions. Center of gravity is defined in the text.

Prey type	Center of gravity (mm)	
	Primary data set	Secondary data set
<i>Brachionus calyciflorus</i>	28	34
<i>Moina micrura</i>	43	44
<i>Mesocyclops crassus</i> adult female	46	57
<i>Notodiaptomus venezolanus</i> adult male and female	61	65
<i>Chaoborus brasiliensis</i> fourth-instar larva	70	64

from 16 to 84 mm, were grouped into length classes of 3 mm, forming a total of 23 length classes. Fish of the secondary set ranged only from 22 to 75 mm. These were grouped into length classes of 2 mm so that the number of length classes created, 27, would be approximately equal to that of the primary set. All count data for each set were pooled by fish length class. Of the fish examined, 7.6% had no food items in the gut (93% of these were fish collected at night) and these fish were excluded from data analyses. Results from the primary data set represent a minimum of 2 and a maximum of 57 fish for a given length class. Results from the secondary set are based on far fewer fish; some length classes are unrepresented or represented by one fish.

RESULTS

Table 2 lists all prey of *Xenomelaniris* in Lake Valencia and the mean proportion of each in the diet of fish of the primary sample set. 77% of the food items consumed by the fish belong to one of five major prey types. These five types are listed in Table 3 along with their mean length, breadth, dry mass, and their estimated numerical proportions of the zooplankton on the day of primary data set sampling. Strauss indices of selection on the major prey for the fish of the primary data set are plotted against fish length in Fig. 1a-e. The graphs demonstrate that the prey selection patterns of the fish are highly length specific. The smallest fish preyed almost exclusively on *Brachionus calyciflorus*, midsized fish selected *Moina micrura* and adult female *Mesocyclops crassus*, larger fish favored adult *Notodiaptomus venezolanus*, and the largest fish fed selectively on fourth-instar *Chaoborus brasiliensis* larvae.

The length-specific patterns of selection on the major prey types of fish from the secondary data set were compared to those of fish from the primary set by means of the centers of gravity of their length-prey selection distributions. The center of gravity of a length-selection distribution estimates the fish length at which

selection for a given prey type is maximal. It is defined as

$$C = \sum s_i(L_i + |L_m|) / \sum (L_i + |L_m|),$$

where C is the center of gravity of the distribution, s_i is the length of size class i , L_i is the corresponding value for the Strauss selection index, and L_m is the minimum value of the Strauss index in the distribution. $|L_m|$ is added to L_i to avoid negative values. The center of gravity was determined for the length-selection distribution of each major prey type for the primary and the secondary data sets (Table 4). The centers of gravity are generally consistent between the two data sets.

Feeding selectivity, as generally understood, encompasses two distinct aspects of feeding behavior: (1) the selective consumption by a predator of a specific prey type, and (2) the breadth of the predator's entire diet. We will refer to the first as "prey selection," and to the second as "breadth of diet." We will continue to use "feeding selectivity" to encompass both aspects. The Strauss index and similar indices estimate prey selection but not breadth of diet. To quantify the diet breadth of *Xenomelaniris*, we used the Petraitis (1979) index of niche breadth:

$$W = q \left(\frac{\sum_{i=1}^q r_i \log_e p_i}{\sum_{i=1}^q r_i \log_e r_i} \right)$$

where W is the Petraitis niche breadth index, q is the total number of prey types available to the predator ($q = 28$ for *Xenomelaniris*), and r_i and p_i are the relative abundances of prey type i in the gut and in the environment. The Petraitis index is well suited for our purpose because, unlike other measures of diet breadth (Colwell and Futuyma 1971, Mac Arthur 1972, Werner and Hall 1974, Charnov 1976, Eggers 1977, Hanski 1978), it incorporates information both about the specificity of the diet and about differences between the

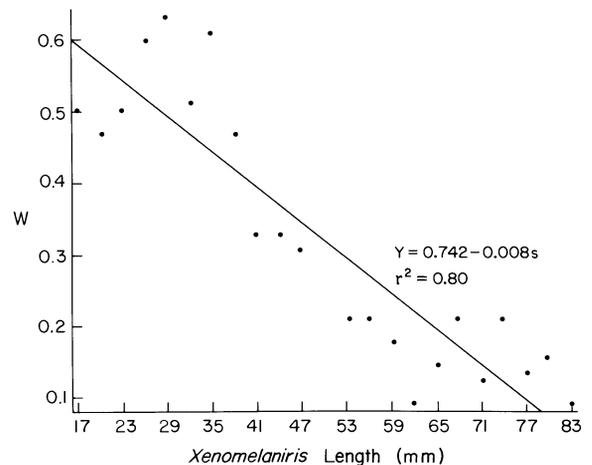


FIG. 2. Regression of diet breadth on length of *Xenomelaniris* (primary data set, $P < .001$).

TABLE 5. Regression statistics for the relationship between *Xenomelaniris* length (mm) and the mean length (mm) or dry mass (μg) of all prey, and of all prey except *Chaoborus*. All regressions are highly significant ($P < .002$).

Data set	All prey			<i>Chaoborus</i> excluded		
	Intercept	Slope	r^2	Intercept	Slope	r^2
Primary, length	-1.32	0.08	0.80	0.10	0.01	0.62
Secondary, length	-1.00	0.05	0.57	0.06	0.01	0.78
Primary, mass	-38.34	1.91	0.73	-0.81	0.06	0.63
Secondary, mass	-35.09	1.21	0.46	-0.65	0.04	0.60

diet and the environment in the relative abundances of prey. The index can range from 0 to 1. Low values indicate a narrow diet; high values indicate a broad diet.

Breadth of diet was computed for each fish and results were pooled by fish length class. To determine if diet breadth in *Xenomelaniris* is a function of the size of the fish, the pooled breadth indices were regressed on fish length (Fig. 2). The relationship is highly significant ($P < .001$) and demonstrates that large fish have a narrower diet than small fish. The coefficient of determination (r^2) indicates that variation in fish length explains 80% of the variation in diet breadth.

Tables 3 and 4 suggest that prey length may be a function of fish length. This relationship was examined critically for both data sets by regression of mean prey length on fish length. The regressions are highly significant for both data sets ($P < .001$) and account for a major amount of variance (Table 5). The regression equations from the two data sets are quite similar. Because *Chaoborus* is so much longer than other prey of *Xenomelaniris*, its presence in the diet may dominate the relationship between fish length and mean prey length. Regression analyses were therefore repeated without *Chaoborus*. Again the regressions are highly significant ($P < .001$) and account for well over half the variance in both data sets (Table 5). Exclusion of *Chaoborus* did not alter the correspondence of the regression equations from the two data sets.

Because of major differences in the shape of prey, regression statistics based on prey lengths may be less reliable than those based on prey mass. This could be particularly important for comparing results of different studies. Pooled mean prey dry mass was regressed on fish length for both data sets; the relationships are highly significant ($P < .002$), with or without *Chaoborus* (Table 5).

Gape size and maximum gill raker spacing are plotted against fish length in Figs. 3 and 4. Both characters are linearly correlated with fish length along the entire range of lengths.

DISCUSSION

A relationship between fish size and feeding selectivity has previously been demonstrated for several planktivorous fishes (Baird and Hopkins 1981, Hansen and Wahl 1981, Hopkins and Baird 1981, Mittelbach

1981, Werner and Mittelbach 1981, Lucas 1982). Mean size of prey or breadth of diet was related to fish size in several of these studies. A variety of factors may explain the changes in prey selection and diet breadth with size in planktivorous fish. These include: (1) morphometric limitations, (2) prey detection, (3) handling time, and (4) capture efficiency. We will consider each of these factors for the Lake Valencia *Xenomelaniris* population. Our data allow us to rule out some of these factors and show the probable importance of others.

Gape size and gill raker spacing are morphometric features that place an upper and lower limit on the size of prey that a fish can consume (Wong and Ward 1972, Werner 1974, Wankowski 1979). Assuming that breadth is the limiting prey dimension, prey size intersects the limits of *Xenomelaniris* gape size and gill raker spacing only at the extremes of fish size and prey size. Figs. 3 and 4 show that gape size prevents fish < 18 mm from eating fourth-instar *Chaoborus* larvae, and that gill raker spacing prevents fish longer than 57 mm from retaining the smallest prey, *Brachionus calyciflorus*. Of the fish whose gut contents were examined, the smallest that had ingested fourth-instar *Chaoborus* was 22 mm long and the largest that had eaten *Brachionus* was 55 mm long. (A substantial number of *Brachionus* were found in one fish 54 mm long.) The correspondence of expected and observed food size extremes based on morphometric limitations is excellent, but should not be taken as evidence that morphometric limitations actually affect diet significantly. Fish < 45 mm fed little on fourth-instar *Chaoborus* and fish > 40 mm rarely ate many *Brachionus*, even though these lengths lie well within the bounds of morphometric limitation. Prey selection and diet breadth of *Xenomelaniris* are not determined to any important extent by gape size and gill raker spacing.

Detection of prey by fish is a function both of various properties of the prey and of the quality of the fish's vision. Visual acuity (Blaxter and Jones 1967, Blaxter 1974, Johns and Easter 1974), luminance contrast discrimination (Hester 1968), and dark vision (Blaxter 1974) all greatly improve as fish grow. Foraging swimming speed also increases with size (Rosenthal and Hempel 1970, Doble and Eggers 1978), so the encounter rate of a fish with a given type of prey should be directly related to fish size. This is in fact

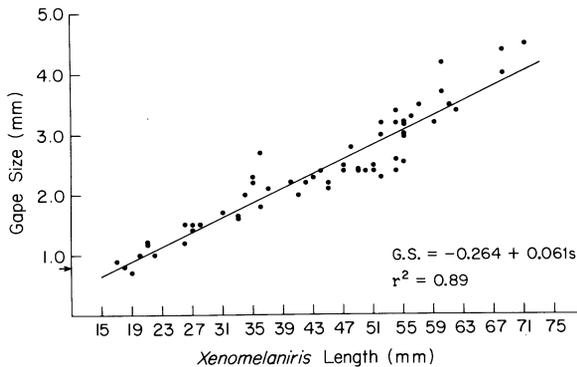


FIG. 3. Gape size (G.S.) as a function of length (s) for *Xenomelaniris*. The arrow on the ordinate indicates the mean breadth of fourth-instar *Chaoborus* larvae.

borne out by the results of Mittelbach (1981:Fig. 3) and Schmidt and O'Brien (cited in O'Brien 1979). Changes in the encounter rate of a fish with its prey may be perceived by the fish as changes in the density of prey (Werner and Hall 1974, Eggers 1977). Predators generally feed more selectively at high prey densities than at low prey densities (MacArthur 1972, Werner and Hall 1974, Charnov 1976, O'Brien et al. 1976, Lewis 1977, Gardner 1981), so a higher encounter rate should lead to a narrower diet. Large *Xenomelaniris* should encounter all prey more frequently than smaller *Xenomelaniris*, and should thus have a narrower diet. Our results (Fig. 2) conform well to this prediction.

Size-related differences in the encounter rates of *Xenomelaniris* with its prey, however, do not appear to explain the observed differences in prey selection of the different sizes of fish. Assuming that improvements in the vision of growing fish affect the detection of all prey types more or less equally, the proportions of encounters of the fish with each prey type should be independent of fish size. On the basis of encounter rates alone, therefore, we would expect, within the morphometric limitations, all sizes of fish to rank prey similarly according to selection value. Our results (Fig. 1a-e) are not consistent with this prediction; large and small *Xenomelaniris* clearly selected different prey. The size of *Xenomelaniris* affects its rate of encounter with prey, which in turn affects its diet breadth, but factors other than encounter rate seem to determine the fish's length-specific patterns of prey selection.

Handling time, the time required to ingest a given prey, can influence the selection of prey by a fish (Werner 1974, Mittelbach 1981). Werner (1974:Fig. 2b) found that for sunfish feeding on *Daphnia magna*, handling time is constant at prey breadths up to $\approx 70\%$ of gape size and increases as an exponential function of prey size thereafter. Handling times for *Xenomelaniris* can be estimated from our gape size and prey size measurements, assuming that Werner's findings

have some general validity. On this basis handling times are constant for all encounters of *Xenomelaniris* with its major prey except for fish shorter than 24 mm feeding on fourth-instar *Chaoborus* larvae. Since 24 mm is well below the length at which *Chaoborus* consumption begins to be important (Fig. 1e), it appears that factors other than handling time limit use of *Chaoborus*. However, our estimates of handling time for *Chaoborus* may be biased. *Chaoborus* larvae are very long and slender; relative to the other prey their breadths greatly underestimate total body size. While breadth is probably the most important prey dimension affecting handling time, length may affect handling time for very elongate prey. Therefore, though handling time is not likely to affect selection by *Xenomelaniris* for most prey, we cannot rule out the possibility that it influences selection of *Chaoborus*.

Capture efficiency, the time or energy spent by a predator pursuing a given type of prey, including unsuccessful pursuits, is a major determinant of prey selection for many predators. Drenner et al. (1978) and Drenner and McComas (1980), using an artificial prey capture device, found that probability of escape was highest for *Chaoborus* and calanoid copepods, intermediate for cyclopod copepods, and lowest for cladocerans. Rotifers were not tested but are very weak swimmers, so their escape probabilities would probably have been lower still. Fortunately, each major prey of *Xenomelaniris* (Table 3) belongs to a different one of these five classes of prey and so can be ranked according to escape ability.

The metabolic value of a prey is affected by its energy content and by the predator's capture efficiency for that prey. Capture efficiency of fish increases enormously with age because young fish are weak swimmers, and possibly also because they lack experience

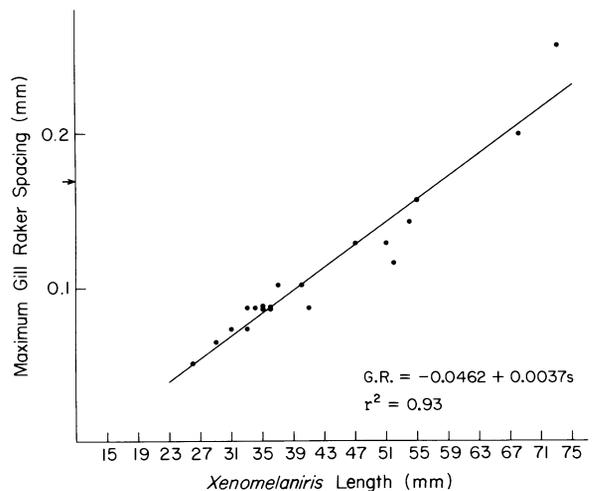


FIG. 4. Maximum gill raker spacing (G.R.) as a function of length (s) of *Xenomelaniris*. The arrow on the ordinate indicates the mean breadth of *Brachionus calyciflorus*.

(Rosenthal and Hempel 1970, Godin 1978). We therefore expect that as a fish grows, differences in the costs of capturing different prey types will be reduced, and thus its choice of prey will be dictated less by differences in the costs of capture and more by differences in the energy content of the different prey. On this basis, and keeping in mind our rankings of prey by escape probability and size, we would predict that small *Xenomelaniris* would select small, easily captured prey, and that successively larger *Xenomelaniris* would favor successively larger prey. Our results (Fig. 1) are entirely consistent with this prediction; the smallest *Xenomelaniris* selected *Brachionus*, a small, slow-swimming prey, while the largest fish selected *Chaoborus*, the largest prey and the best swimmer of the plankton. We believe, therefore, that capture efficiency is a major determinant of prey selection in *Xenomelaniris*.

Optimal foraging theory proposes that diet breadth is a function of prey density, or the encounter rate of predator and prey, while prey selection is determined by the ratio of metabolic costs and benefits of the prey (Mac Arthur 1972, Werner and Hall 1974, Charnov 1976, Werner and Mittelbach 1981). Our analyses of *Xenomelaniris* feeding suggest that the length-specific feeding patterns of the fish are primarily determined by two factors, prey detection and prey capture efficiency. Prey detection determines encounter rate, which in turn affects diet breadth. Large fish see many more prey than small fish and therefore are able to feed more selectively. This results in a narrower diet. At the same time, capture efficiency affects the metabolic cost of feeding. Large fish are more efficient swimmers than small fish and therefore can afford to pursue large, fast-moving prey. Thus for *Xenomelaniris* it appears that prey detection controls diet breadth, while capture efficiency determines prey choice. This conclusion seems to be generally consistent with the predictions of optimal foraging theory, but our results show further that the foraging patterns of a fish are a function of its size as well as of the prey available to it.

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