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## POPULATION ECOLOGY OF A PELAGIC FISH, *XENOMELANIRIS VENEZUELAE* (ATHERINIDAE), IN LAKE VALENCIA, VENEZUELA<sup>1</sup>

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**Abstract.** Trophic bottleneck, which is a common phenomenon in the pelagic food chains of large tropical lakes, was studied in Lake Valencia, a large and eutrophic lake located in Venezuela. Mechanisms of trophic bottleneck in lake Valencia were demonstrated through two years of population studies of *Xenomelaniris venezuelae*, a small planktivorous fish that accounts for most of the zooplankton consumption in open water. Major components of variation in abundance of *Xenomelaniris* included small-scale spatial (0.1–1.0 km, 70%), large-scale spatial (1–10 km, 23%), and temporal (months, seasons, 7%).

The population showed a repeated annual cycle based primarily on a dominant cohort recruited during January and February. Spawning in the littoral zone continued throughout the year, but larvae survived only when rotifer densities exceeded 100 individuals/L, which occurred predictably during late seasonal mixing, but only irregularly thereafter. Steady mortality (15%/mo) of spawning fish occurred through predation. Catastrophic, predictable mortality of all fish occurred through anoxia during early seasonal mixing (57%/mo for two months).

*Xenomelaniris* showed a strong ontogenetic shift in diet from rotifers during early development to copepods and *Chaoborus* during later development. Daily rations ranged from 28% of dry body mass in the smallest fish to 10% in the largest. Although *Xenomelaniris* was the only planktivore and was capable of consuming all major zooplankton taxa, it consumed only 3.6% of zooplankton production because it was never sufficiently abundant to exploit its food resource fully.

Total growth of adult *Xenomelaniris* (somatic plus reproductive) conformed to the same equation as somatic growth of juveniles; growth potential was diverted increasingly to reproduction as the fish aged. Young adult fish showed 66% assimilation efficiency and 11% growth efficiency. Respiration losses decreased during development as the 0.73 power of body mass. The annual ratio of production to biomass was high (4.0), reflecting food sufficiency, a long growing season, and continuous loss of older fish to spawning mortality.

Annual fresh-mass production of *Xenomelaniris* (31 kg/ha) is a small proportion of primary production (<0.03%) and of zooplankton production (3.6%); energy budgets show that actual *Xenomelaniris* production is only one third of potential production given the observed zooplankton production and the measured growth efficiency of *Xenomelaniris*. The explanation of this trophic bottleneck is mortality, which prevents the population from reaching carrying capacity and thus blocks energy flow between zooplankton and pelagic fish. Although there were three significant kinds of mortality, larval mortality—apparently through starvation—was the explanation of the trophic bottleneck because it restricted the reproductive output of *Xenomelaniris*, which could otherwise have brought the population to carrying capacity. The trophic bottleneck may be of significance beyond Lake Valencia, in view of the low diversity and abundance of pelagic planktivores in tropical lakes.

**Key words:** *Atherinidae*; bioenergetics; breeding seasonality; fish production; hydroacoustics; mortality; ontogenetic diet shift; plankton energetics; population regulation; recruitment; reproductive strategy; trophic bottleneck; tropical fish; Venezuela.

### INTRODUCTION

Large tropical lakes often lack fish species capable of exploiting zooplankton production, or show very low diversity of such species (Fernando and Holcik

1982). The absence or low diversity of carnivores capable of consuming zooplankton suggests widespread occurrence of trophic bottleneck at the upper end of the food chain in these lakes. Absence or low diversity of open-water planktivores is of basic importance because it indicates lack of constraint on the plankton community by vertebrate planktivores. There is abundant evidence that plankton communities are strongly affected by vertebrate planktivores, and that the effects

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of vertebrate predation pressure on plankton communities can be transmitted downward along the food chain even to the level of primary producers (Carpenter 1988).

Numerous hypothetical explanations can be given of the trophic bottleneck in the open waters of tropical lakes. However, a resolution of these possibilities requires studies that combine information on dynamics of predator and prey organisms as a means of demonstrating the mechanisms that limit the effectiveness of planktivores in using zooplankton production. This is the purpose of our study, which supports a trophic analysis of *Xenomelaniris venezuelae*, an atherinid fish endemic to Lake Valencia, a large lake located in Venezuela. *Xenomelaniris venezuelae* is the only fish species in Lake Valencia capable of consuming significant proportions of the pelagic zooplankton production; its abundance therefore determines the efficiency of energy transfer from zooplankton to higher trophic levels in Lake Valencia.

Previous studies of zooplankton production in Lake Valencia have shown that predation losses are secondary to inadequate food in controlling zooplankton production (Saunders and Lewis 1988a). This suggests that the transfer of production from zooplankton to *Xenomelaniris* is inefficient. The *Xenomelaniris* study includes an estimate of *Xenomelaniris* production that, when compared to the production of zooplankton, provides a measure of energy-transfer efficiency across trophic levels. Explanations of energy transfer lie in the population dynamics and adaptations of *Xenomelaniris*, which are a second focus of attention for the *Xenomelaniris* study. One possible explanation of inefficiency in energy transfer is low population density of *Xenomelaniris* in relation to the density of zooplankton. For this reason, the study incorporates a detailed treatment of factors that regulate reproductive success and of the amounts of mortality at various stages in the life history of *Xenomelaniris* in Lake Valencia. However, this reveals only part of the connection between zooplankton and *Xenomelaniris*. Also important are quantitative estimates of the rates at which *Xenomelaniris* consumes each of the zooplankton prey, and estimates of *Xenomelaniris* energy allocation that show the efficiency with which consumed zooplankton are converted to somatic and reproductive output. This leads to a determination of the possible role of growth suppression or outright starvation of *Xenomelaniris* by food supplies that are quantitatively or qualitatively inadequate. Simultaneous consideration of all of these factors shows not only the extent of trophic bottleneck but also its causes in Lake Valencia.

#### *Overview of Lake Valencia and its fishes*

Lake Valencia is a large lake (350 km<sup>2</sup>) located in northern Venezuela (10° N, 67° W); it has an elevation of 405 m above sea level, a mean depth of 18 m, and a maximum depth of 39 m (Lewis and Weibezahn

1976). The watershed, which occupies an area of 3000 km<sup>2</sup>, has alternating rainy (May–November) and dry (December–April) seasons. The lake has been desiccating for several centuries (Lewis 1983c) and is becoming increasingly saline (2000 μS/cm, Levine and Lewis 1984). Lake Valencia is highly eutrophic and contains dense populations of blue-green algae (Levine and Lewis 1984, Lewis 1986).

Lake Valencia is warm monomictic. Seasonal mixing extends from November through February or March, and the lake is stratified the rest of the year (Lewis 1983a, b, 1986). During the period of stratification, episodes of incomplete mixing often occur, producing large variations in the thickness of the mixed layer (mean thickness: 12 m). These partial-mixing events strongly affect the phytoplankton community (Lewis 1986). The onset of complete mixing is generally abrupt, and, because the hypolimnion becomes anoxic during the stratification season, the seasonal overturn often produces high mortality of fish and other organisms (Infante et al. 1979). The seasonal mixing of the lake is caused by seasonal changes in air temperature and wind strength.

The fish community of Lake Valencia has changed in recent years, partly in response to introductions of exotic species (Pereira 1979). Two cichlids, *Petenia krausii* and *Sarotherodon mossambicus*, both of which were introduced after 1960, were among the most abundant species in the lake at the time of the *Xenomelaniris* study. Both species inhabit the littoral zone exclusively. Other fish species abundant in the littoral zone were a pimelodid catfish (*Rhamdia* sp.), a characid (*Astyanax bimaculatus*), and an unidentified poeciliid. *Rhamdia* and *A. bimaculatus* were found only occasionally in deep water, where they fed on *Chaoborus* larvae. *Xenomelaniris venezuelae* was the only pelagic species in the lake.

*X. venezuelae* is a small (<95 mm), slender-bodied fish of the family Atherinidae. Atherinids are major components of the fish fauna in aquatic systems throughout the world, although few species have been studied intensively. Most atherinids occupy shallow coastal waters and estuaries, but there are many secondary freshwater species as well (Wheeler 1975, Bond 1979). Atherinids spawn in shallow water; most spawn repeatedly for periods ranging from a few months to a year (e.g., Conover 1984, Middaugh et al. 1984). The lifespan is typically short (1–2 yr). *X. venezuelae* exhibits most of the features that characterize the family.

#### MATERIALS AND METHODS

Fish were sampled primarily with a large (2.6 m diameter), folding, conical lift net (Unger 1985). Hose samplers were used for quantitative zooplankton sampling. Surface-to-bottom samples were obtained with a column-integrating hose sampler (7.6 cm diameter) with a capture efficiency of nearly 100% (Cressa 1985, Unger 1985). A 5-m integrating sampler similar to that

described by Lewis and Saunders (1979) was used in sampling zooplankton at discrete depths.

A quantitative hydroacoustic system was employed to determine biomass and distribution of the *Xenomelaniris* population in Lake Valencia (Unger 1985). The design of this system was based on systems developed at the University of Washington and the University of Wisconsin (Nunnallee 1974, Thorne 1977, Brandt 1978). A 70-kHz echo sounder (Simrad EY-M; Horten, Norway) with accurate gain functions was used for sounding. Echo signals were recorded on chart paper and on analog tape. At frequent intervals a calibration test signal from the echo sounder was also recorded, to monitor variations in receiver gains. The transducer (full beam angle = 11°) was mounted below a depressor-type tow body, and was towed alongside the boat at a depth of ≈ 1 m (velocity: 2 m/s).

The recorded acoustic data were analyzed in the laboratory by means of a custom-built digital analysis system. The system simultaneously performs echo-squared integration and measures peak amplitudes of the echo signals. Biomass estimates were derived from the echo integration measurements. The echo amplitude data were used to distinguish *Xenomelaniris* echoes from those of *Chaoborus*, which is very abundant in Lake Valencia.

Echo integration provides relative estimates of fish abundance. Absolute abundance estimates require knowledge of the mean target strength (acoustic reflectivity) of the fish. The target strengths of *Xenomelaniris* were measured directly in the field. The transducer was supported at the lake surface on a floating wooden frame, and individual live fish were suspended in a harness of acoustically invisible monofilament line ≈ 5 m below the transducer on the acoustic axis. Amplitudes of the fish echoes were measured on an oscilloscope. A ping-pong ball was used as a reference standard (Burczynski and Dawson 1984). Regression analysis indicated that the target strength of a fish was linearly related to the log of its length:

$$TS = 29.6 \log L - 103.2; \quad r^2 = 0.99,$$

where  $TS$  = target strength (in decibels) and  $L$  = total length (in millimetres). The equation provides estimates of target strength for *Xenomelaniris* similar to those derived from the more general empirical equations of Love (1971), McCartney and Stubbs (1971), and Foote (1987).

Every 2 wk throughout the period of study (March 1979–January 1981), temperature and oxygen profiles were measured at an index station over the deepest part of the lake (Fig. 1). At the same time, replicate zooplankton samples were collected with the column-integrating sampler.

Two replicate fish samples were collected weekly at the index station from November 1979 through January 1981 with the lift net. Replicate zooplankton samples were obtained concurrently with the integrating

sampler. Sampling was conducted at dawn, dusk, midday, or midnight. Sequencing of the four sampling times was randomly changed every 4 wk. Prior to November 1979 fish were sampled frequently, but not on a fixed schedule.

Echo-sounding surveys of the *Xenomelaniris* population were carried out once each month from February 1980 through January 1981 along transects covering a total of 55 km and including all of the major regions of Lake Valencia (Fig. 1). Echo sounding was also used at the index station to examine the vertical migration patterns of *Xenomelaniris* and *Chaoborus*.

Diel sampling (typically at 3-h intervals) of *Xenomelaniris* and zooplankton was conducted on three dates as part of a study of the feeding chronology of the fish and vertical migration patterns of the zooplankton.

The spawning behavior of *Xenomelaniris* was studied during January and between May and September 1980. Surveys were carried out for several hours after nightfall (the fish spawn only at night) from a boat along the southeastern shores of the lake. A light was used to locate and observe the spawning fish. Samples of the fish were taken with a dip net.

Fishes of the littoral zone were sampled on three dates in September 1980 with a seine on beaches utilized by spawning *Xenomelaniris*; fishes of the littoral zone do not show large seasonal variations in density and composition (S. Bowen, *personal communication*). Fish were grouped according to species and were weighed. Stomachs of predaceous fish species were removed and preserved in a 10% formalin solution for later analysis of diet.

During the course of the study total lengths of > 18 000 individual *Xenomelaniris* were measured to the nearest millimetre. Wet mass and dry mass were measured for 122 fresh *Xenomelaniris* specimens collected at various times of the year. Stomach content analyses and sex determinations were made for a random subsample of 10 fish from each net sample. Sex and maturity of the fish were determined by inspection of the gonads, and the digestive tract was removed. The digestive tract of all but the smallest *Xenomelaniris* specimens is distinctly partitioned. The anterior portion, which is bulbous, will be referred to as the stomach, although it is not a true stomach (Al-Hussaini 1947). With few exceptions, prey were enumerated only in the stomach because prey in the stomach are more easily identified than prey in the hindgut. Because very small *Xenomelaniris* (< 25 mm total length) have no gut subdivisions, all prey consumed by these fish were counted.

Prey were enumerated for a total of 1158 *Xenomelaniris*. Copepods and *Chaoborus* were classified and counted by instar within species, and rotifers and cladocerans were classified and counted by species. If > about 200 individuals of a species or instar were present in the stomach, abundance of that prey type was estimated by subsampling. Complete counts were



year-class masses were determined from the frequency distributions after conversion of lengths to dry masses.

Energy used by *Xenomelaniris* for egg production was estimated from clutch size and spawning frequency. Counts of ripe eggs were made for 10 gravid females selected from the spawning-survey samples. The eggs from  $\geq 1$  female for each survey date were dried for 24 h at 60° and weighed. The fish were also dried and weighed. The relationship between total fish mass (fish with eggs) and egg number was determined by linear regression.

Estimates were computed for somatic and egg production by 1979 and 1980 year classes in 1980. Somatic production was computed by the discrete increment summation model (Newman and Martin 1983). Egg production for each year class was calculated over 1-mo intervals as the product of dry mass per egg and the mean density, clutch size, and spawning frequency for the month.

## RESULTS

### *Abundance and life history*

During 1980 *Xenomelaniris venezuelae* biomass declined to a minimum over the mixing season (November–February), rose to a maximum over the early stratification season (March–May), and was almost stable for the balance of the stratification season (June–October) (Fig. 2). The seasonal pattern was qualitatively the same in 1979, as shown by net samples (no hydroacoustic data were taken in 1979). During 1980 numerical abundance of the 1980 year class rose during February and March but dropped more-or-less continuously over the remainder of the year. Numerical abundance of the 1979 year class was low throughout 1980. Almost no fish of the 1979 year class were collected after September 1980.

The components of variation in abundance were separated as described by Lewis (1978) so that the relative contributions of spatial and temporal variation could be compared. The effects of location (fixed spatial variation) and of time (temporal variation) and of their

TABLE 1. Components of variance for temporal and spatial variation of *Xenomelaniris venezuelae* abundance (all components can be distinguished at  $P < .05$ ).

Source of variation*	df	Percent of variance
Time of year	8	6.5
Large-scale fixed spatial (among transects)	6	4.7
Large-scale ephemeral spatial (among transects)	42	18.8
Small-scale spatial (within transects)	1750	70.0†

\* For discussion and clarification of this unusual ANOVA presentation, see *Results: Abundance and life history*.

† Includes  $\approx 1\%$  measurement error.

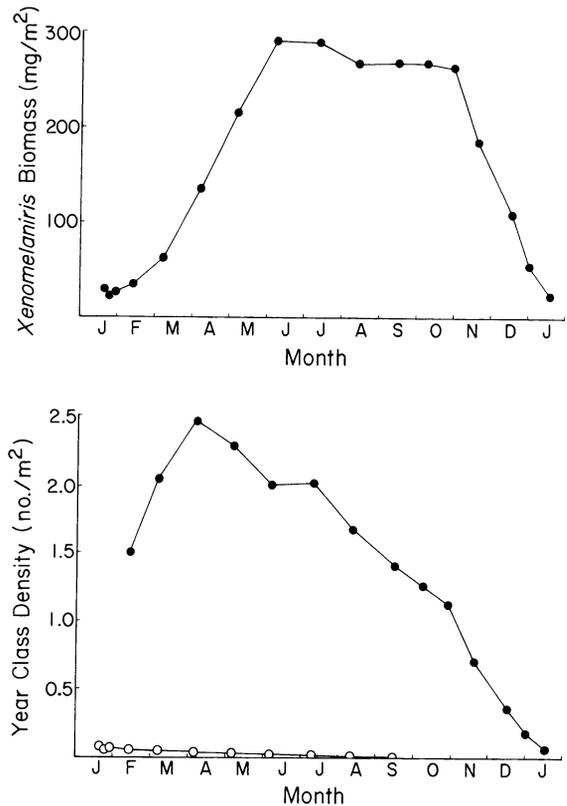


FIG. 2. Estimates of *Xenomelaniris venezuelae* biomass and numerical abundances (O = 1979 year class).

interaction (ephemeral spatial variation) are significant ( $P < .05$ ). The variance components (Table 1) indicate that large-scale fixed spatial variation in abundance (among transects) was smaller than temporal variation, but that large-scale ephemeral spatial variation was much greater than temporal variation.

The relative importance of small-scale patchiness in the spatial distribution of *Xenomelaniris* was estimated from residual variance, following the separation of other variance components, on the basis of 13 randomly selected segments of recorded acoustic data (2 min each). Differences between replicate measurements of the segments never exceeded 1% of the residual component of variance. Therefore, the residual component of variance shown in Table 1, which is very high, is explained mainly by variability in abundance within transects, i.e., small-scale patchiness. Thus the overall comparative magnitudes of abundance variation are: small-scale spatial (0.1–1 km)  $\gg$  large-scale spatial (1–10 km;  $\frac{1}{5}$  fixed,  $\frac{1}{2}$  ephemeral)  $\gg$  temporal (months, seasons).

The fish were observed spawning throughout the year at night in very shallow water over stone and gravel substrates. Larval and juvenile fish were never observed or captured in the littoral zone, nor were any found in stomachs of littoral-zone predators. After

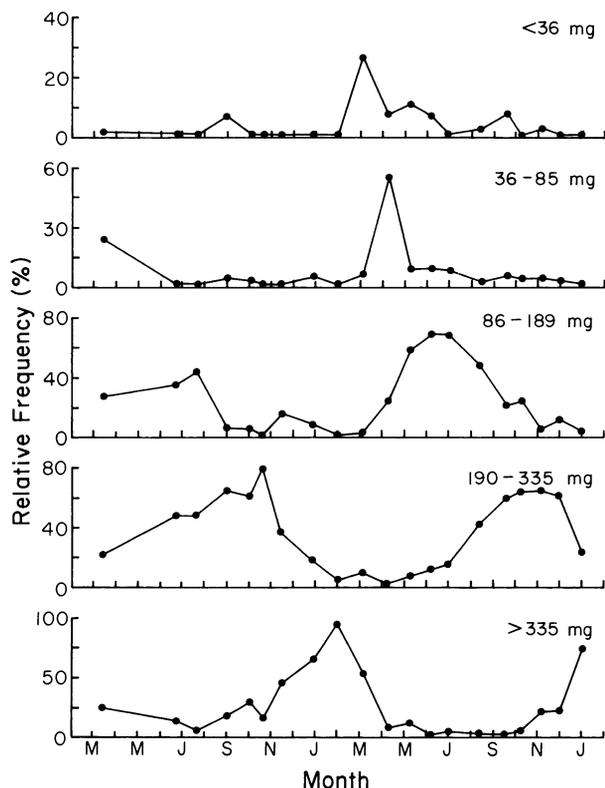


FIG. 3. Relative frequencies of five *Xenomelaniris venezuelae* size classes (March 1979–December 1980): early-stage juvenile (<36 mg dry mass), mid-stage juvenile (36–85 mg), late-stage juvenile (86–189 mg), young-of-the-year adult (190–335 mg), and yearling adult (>335 mg).

hatching, the larval fish apparently moved immediately into the limnetic zone, where they remained until they matured. The larvae were occasionally found in plankton samples from the limnetic zone. Stomach-content analyses of 33 adult *Xenomelaniris* collected from the littoral zone on different dates revealed that the fish fed very little in this habitat: *Xenomelaniris* spawns in the littoral zone, but otherwise is strictly pelagic.

Most of the fish in the littoral zone were males (85%). Females comprised 77% of the adult population in the limnetic zone in 1979 and 78% in 1980.

Although the *Xenomelaniris* population spawned throughout the year, recruitment to the population was largely restricted to the first part of the year both in 1979 and 1980. Fig. 3 shows the relative abundances of five size classes of fish captured over the course of the study. Two major cohorts, corresponding to the 1979 and 1980 year classes, are evident in the figure. Few early-stage juveniles (<36 mg dry mass) were collected in late March and early April 1979 when the study began, indicating that recruitment of essentially all of the 1979 year class occurred before this time. Fish of the 1980 year class were first collected in mid-

March. The mean dry mass of these fish was 19 mg, whereas the mean dry mass per ripe egg was 0.127 mg. The development time of these fish, as estimated from the growth curve (see below) was 57 d. Therefore this year class probably began hatching in January. A few early-stage juveniles were captured throughout 1980, but those present in March formed the principal cohort of the year class (Fig. 3). The low relative frequencies of fish in the yearling (largest) size class following the major periods of recruitment show that a very small percentage of the fish survived >1 yr.

In 1979 and 1980 the majority of the Y-O-Y fish had reached adult size (190 mg dry mass) by September (Fig. 3). However, some Y-O-Y began spawning well before this. Fig. 4 shows the mean dry masses of spawning females collected in the littoral zone on each of the spawning surveys, and the year class growth curves of the 1980 yearling and Y-O-Y female fish. Prior to late June the mean masses of the spawning females corresponded closely to the yearling growth curve, and the standard deviations of mass were relatively small. On 29 June, however, the mean mass of the spawning females dropped to a level intermediate between the growth curves of the yearling and Y-O-Y cohorts, and the standard deviation of mass increased greatly, indicating that Y-O-Y females joined the spawning population at this time. As the year progressed, the mean mass of the spawning adult females moved closer to the Y-O-Y growth curve, reflecting the increasing proportion of Y-O-Y in the population of spawning females.

Feeding

The major prey taxa of *Xenomelaniris* included *Chaoborus*, *Notodiaptomus*, *Mesocyclops*, *Brachionus*, *Moina*, and *Ceriodaphnia*. These taxa made up ≥99%

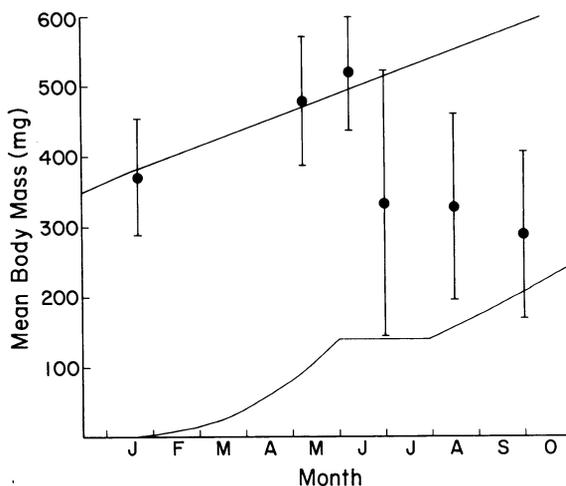


Fig. 4. Mean (●) dry masses per spawning adult female (±1 sd) shown in relation to yearling (upper) and young-of-year (lower) year-class growth curves for females (—).

TABLE 2. The abundances and sizes of *Xenomelaniris venezuelae* prey, and their percentages by mass, in the diets of three size classes of fish.

Prey type	Dry mass ( $\mu\text{g}/\text{indiv}$ )	Abundance ( $\text{mg}/\text{m}^2$ )	Fish dry mass (mg)		
			<85	85-335	>335
Diptera					
<i>Chaoborus brasiliensis</i>					
Pupa	200.00	242	6.3	25.3	24.5
Instar IV	141.30	2353	22.0	42.3	55.0
III	27.22	95	4.1	6.6	5.7
II	6.65	19	5.4	2.3	0.8
I	1.85	3	2.0	0.7	0.0
Copepoda					
<i>Notodiaptomus venezolanus</i>					
Adult female	5.14	706	2.0	11.8	18.4
Adult male	4.62	572	1.4	5.8	10.6
Copepodite V	3.14	326	0.4	0.9	2.0
IV	1.86	150	0.9	0.4	0.4
III	1.11	83	0.3	0.1	0.1
II	0.64	44	0.1	<0.1	<0.1
I	0.35	24	<0.1	0.2	<0.1
Nauplius	0.18	68	0.9	<0.1	<0.1
<i>Mesocyclops decipiens</i>					
Adult female	1.05	68	3.7	5.5	3.5
Adult male	0.40	49	1.8	2.0	0.4
Copepodite V	0.56	49	0.8	1.2	0.2
IV	0.40	49	1.1	0.8	0.3
III	0.28	35	1.6	0.7	0.5
II	0.19	26	1.6	0.5	<0.1
I	0.12	25	2.1	0.3	<0.1
Nauplius	0.04	28	0.1	0.2	0.0
Cladocera					
<i>Moina micrura</i>	1.10	55	12.5	6.4	3.6
<i>Ceriodaphnia cornuta</i>	0.82	160	3.9	2.2	6.0
Rotifera					
<i>Brachionus calyciflorus</i>	0.28	235	24.6	6.4	0.4
<i>Brachionus havanaensis</i>	0.06	41	0.3	<0.1	0.0
<i>Keratella americana</i>	0.01	19	<0.1	<0.1	<0.1

by mass of the diet of fish of all sizes (Table 2). The fish did not eat phytoplankton.

Food consumption by *Xenomelaniris* varied considerably over the course of the day. Fig. 5 shows the mean stomach contents at different times of the diel cycle for the three major size classes of *Xenomelaniris* (pooled for all dates). The means are given in terms of the dry mass of three prey categories: *Chaoborus* larvae, *Chaoborus* pupae, and other zooplankton. For fish of the two larger size classes ( $\geq 85$  mg dry mass), *Chaoborus* pupae resting at the surface of the lake prior to emerging at dawn were especially important food. The smallest fish consumed *Chaoborus*, but were more reliant on larvae than pupae, and fed heavily on other zooplankton during daylight hours. Night feeding was important for all size classes (Fig. 5), though it was limited almost entirely to *Chaoborus*. *Xenomelaniris* is able to detect *Chaoborus* larvae and pupae nonvisually (Unger et al. 1984).

The 24-h zooplankton sampling showed that the small zooplankton prey were typically concentrated in the upper half of the water column at all times of day. This

was especially true when the lower water column was anoxic (May through October). However, *Chaoborus* larvae and, to a smaller extent, *Notodiaptomus* adults migrated a significant amount in the water column on a 24-h cycle. Typically these larger prey were more abundant below a depth of 15 m during the day and above 15 m at night. In 1979 and 1980 the upper mixed layer was between 6 and 18 m thick during most of the stratification season (Lewis 1986).

The vertical migrations of *Xenomelaniris* and of *Chaoborus*, which showed the strongest vertical migration of the prey species and made the largest contribution to the diet of *Xenomelaniris*, were documented with the echo sounder. At night the bulk of the *Chaoborus* population moved toward the surface. The population gradually descended after dawn. On some dates *Chaoborus* eventually moved to the bottom during the day, but on other dates a portion of the population persisted in the middle of the water column all day. *Xenomelaniris* gradually moved toward the surface in the evening and away from the surface in the morning. At night, *Xenomelaniris* were very near

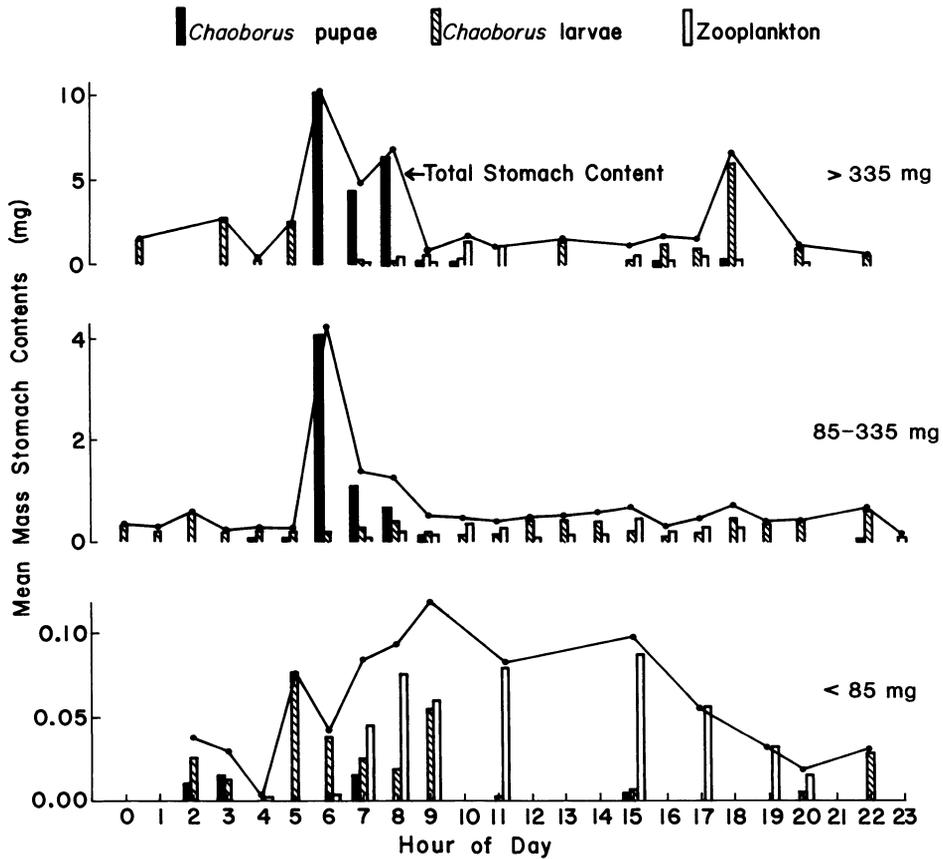


FIG. 5. Mean dry mass of food (mg per fish) in the stomachs of three major size classes of *Xenomelaniris venezuelae* at all times of day. Modified from Unger et al. (1984).

the surface (0–2.5 m). Evening migrations toward the surface have been observed in a number of pelagic tropical fishes (Hopson 1982, Lowe-McConnell 1986).

Daytime depth distributions of *Xenomelaniris* varied greatly over the year. The maximum depth of the fish appears to have been dictated by dissolved-oxygen concentrations (Fig. 6). *Xenomelaniris* was never detected in water with dissolved oxygen <2 mg/L. In February and March of 1980 dissolved-oxygen concentrations exceeded 5 mg/L at all depths, and *Xenomelaniris* was detected in very deep water during the day (Fig. 6).

At all times of the year the bulk of the *Xenomelaniris* population occupied depths <15 m from the surface during the daytime (Fig. 6). During the stratification season, however, the preferred depth of the population gradually shifted from the surface to greater depths. From August through October the population was concentrated just above the thermocline. This shift in daytime habitat was probably related to ontogenetic changes in food preferences (Table 2): the preferred prey of *Xenomelaniris* adults (*Chaoborus* and adult *Notodiaptomus*) was most abundant at greater depths, and most of the fish in the population between August and No-

vember were adults. In November and December most of the fish stayed near the surface, probably reflecting adaptation for use of the surface oxygen source (Lewis 1970) during the period of potential oxygen stress (seasonal mixing).

Table 3 gives estimates of *Xenomelaniris* feeding rates and the mean daily production rate of the prey, as computed from the observed biomass and the mean daily turnover rates (Saunders and Lewis 1988a). The daily consumption of any given prey species by *Xenomelaniris* was almost always <15% of that species' production (Table 3). For 1980, during which measurements are available for all months, the consumption of prey by *Xenomelaniris* was 2.8% of prey production (sum of prey consumed divided by sum of prey production from Table 3); consumption during 1979 was somewhat higher (≈4.5%). Such low cropping rates are not likely to affect zooplankton populations significantly.

*Mortality*

Table 4 shows mortality of juvenile and adult *Xenomelaniris* as calculated from change in population size of Y-O-Y fish following recruitment. There were

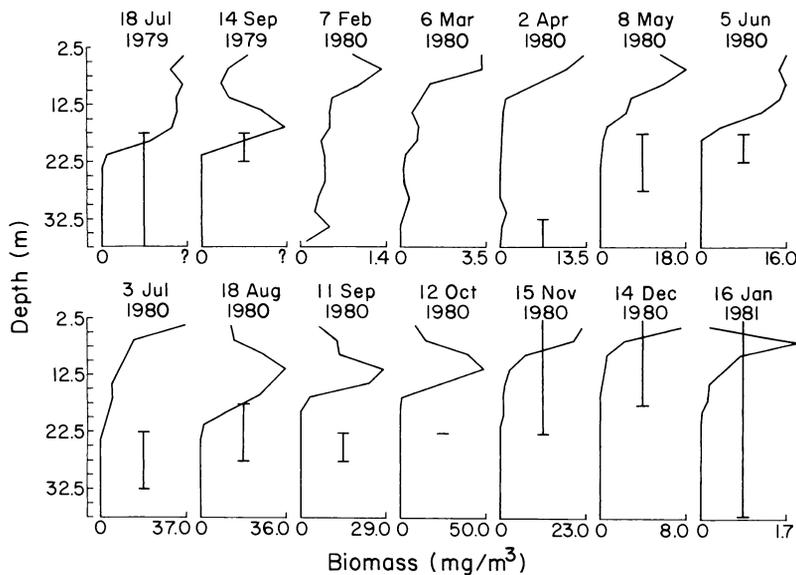


FIG. 6. Daytime depth profiles of *Xenomelaniris venezuelae*. The vertical bars indicate the portion of the water column that falls in the dissolved-oxygen concentration range of 2–5 mg/L.

three stages of mortality: (1) April–June (low); (2) July–October (moderate); (3) November–December (high). The mortality of juveniles and adults is explained by two factors: littoral-zone predation during spawning and catastrophic mortality caused by anoxia. The upward shift in mortality between June and July coincides with increased spawning frequency as the fish mature. The further increase in mortality from October to November occurs at the time of observed mortality caused by seasonal anoxia.

The limnetic zone of Lake Valencia is free of *Xenomelaniris* predators, but the littoral zone is inhabited by several piscivorous species, two of which, the cichlid *Petenia* and the catfish, *Rhamdia*, prey heavily on spawning *Xenomelaniris*. *Xenomelaniris* adults made

up 67% by dry mass of the diets of both fishes, and *Xenomelaniris* eggs comprised 2% of the *Petenia* diet and 11% of the diet of *Rhamdia*. The remainder of the *Petenia* diet consisted primarily of other small fishes and that of *Rhamdia* consisted of chironomids. Infante and LaBar (1977) and Pereira (1979) also found that *Xenomelaniris* eggs and adults were major items in the diets of *Petenia* and *Rhamdia* in Lake Valencia.

The mean dry biomasses of the *Xenomelaniris* predators at the collection sites were 15.2 g/m<sup>2</sup> for *Petenia* and 2.2 g/m<sup>2</sup> for *Rhamdia*. Total dry masses of these two predators at *Xenomelaniris* spawning localities were estimated to be  $93 \times 10^3$  kg for *Petenia* and  $14 \times 10^3$  kg for *Rhamdia*. The mean individual dry masses of the predators were 44.1 g for *Petenia* and 34.8 g for

TABLE 3. The percent of daily dry mass production of each of the major prey types consumed by *Xenomelaniris venezuelae* during 1979 and 1980.

Period	Prey consumption (C) as % of prey production (P)						All taxa		
	<i>Chaoborus</i>	<i>Notodiaptomus</i>	<i>Mesocyclops</i>	<i>Moina</i>	<i>Ceriodaphnia</i>	<i>Brachionus</i>	P (mg/m <sup>2</sup> )	C (mg/m <sup>2</sup> )	%
1979									
Mar–Apr	6.9	4.6	8.9	5.4	...	7.8	311	20	6.4
Aug–Sep	5.5	2.4	2.5	10.2	2.0	3.5	629	31	4.9
Oct–Dec	4.7	2.5	0.8	1.1	2.5	0.0	861	21	2.4
1980									
Jan–Feb	1.4	0.4	0.3	0.1	0.1	0.0	1057	2.5	0.2
Mar–Apr	3.3	1.1	8.9	3.0	0.6	1.3	1012	15	1.5
May–Jun	3.0	3.6	5.3	3.7	3.6	1.9	748	25	3.3
Jul–Aug	26.1	8.1	2.2	3.9	0.6	0.7	482	34	7.1
Sep–Oct	11.5	1.1	3.3	5.5	7.1	0.1	505	32	6.3
Nov–Dec	12.1	0.9	4.7	5.5	2.3	0.1	366	10	2.7
1980 mean	9.6	2.6	4.1	3.6	2.4	0.7	4170*	118*	2.8

\* Sum for 1980.

TABLE 4. Mortality of young-of-year *Xenomelaniris venezuelae* during 1980.

Month	Change in density		Life stage	Cause of mortality*
	(indiv·m <sup>-2</sup> ·mo <sup>-1</sup> )	%/mo		
Apr	-0.06	-2	Juvenile	...
May	-0.26	-11	Juvenile	...
Jun	-0.05	-2	Juvenile	...
Jul	-0.23	-11	Adult	1
Aug	-0.26	-14	Adult	1
Sep	-0.22	-14	Adult	1
Oct	-0.20	-15	Adult	1
Nov	-0.54	-48	Adult, some juvenile	2, 1
Dec	-0.38	-66	Adult, some juvenile	2, 1

\* 1 = predation during spawning, 2 = seasonal anoxia.

*Rhamdia*. No *Petenia* individuals weighing < 34 g (8% of specimens) or *Rhamdia* < 58 g (48%) had consumed *Xenomelaniris* adults. Individuals of all sizes had consumed *Xenomelaniris* eggs.

The daily rations of *Petenia* and *Rhamdia* were estimated from the daily average stomach contents and clearance times. The mean stomach contents of fish captured at various times during the diel cycle were 1.96 mg/g for *Petenia* and 1.54 mg/g for *Rhamdia*. The average clearance times of the fish (5 h) were estimated from values in the literature for piscivorous fish at warm temperatures and in the range of sizes of the *Petenia* and *Rhamdia* specimens that had consumed *Xenomelaniris* adults (Windell 1978, Elliott 1979, Fange and Grove 1979). Jobling (1986) has shown that the clearance rate is generally constant for piscivorous fishes. The estimated daily rations were 9.4 mg/g for *Petenia* and 7.4 mg/g for *Rhamdia*; estimated total consumption of *Xenomelaniris* adults (as dry mass) was 543 kg/d for *Petenia* and 36 kg/d for *Rhamdia*.

Mortality of *Xenomelaniris* for July–October was 0.23 fish·m<sup>-2</sup>·mo<sup>-1</sup> (Table 4), which corresponds to a population loss of dry mass of 500 kg/d. This estimate is close to the total estimated predation mortality (579 kg/d), leading to the conclusion that predation was the major source of mortality of adult *Xenomelaniris*.

Total daily consumption of the eggs was estimated as 17.5 kg of dry mass for *Petenia* and 11.4 kg of dry mass for *Rhamdia*, or 7% of *Xenomelaniris* daily egg production. Larval *Xenomelaniris* were not found in stomachs of littoral-zone predators. Therefore, predators had little influence on eggs or larvae.

The increased mortality of *Xenomelaniris* in November (Table 4) was caused by upwelling of anoxic hypolimnetic water during the initial period of lake mixing. Lewis (1984) estimated that isothermal mixing of the lake in 1980 began within a few days of 15 November. Mortality is explained by a combination of oxygen depletion and hydrogen sulfide poisoning (Infante et al. 1979). Large numbers of *Xenomelaniris*

were piping at the lake surface during the initial mixing periods in both 1979 and 1980, and dead fish were observed at these times. The cumulative effect of predation and anoxia was to reduce the population size drastically: only 3% of the fish present in April 1980 survived until the end of the year.

Food resources of juvenile and adult *Xenomelaniris* were adequate throughout the year, as shown by the consistently positive growth of the fish and the small fraction of the zooplankton consumed during all periods of the year (Table 3). Adequacy of food and good correspondence between observed mortality and expected predation loss indicates that food supply does not regulate juvenile and adult stages.

Larval *Xenomelaniris* appears to be controlled by food supply, given that spawning is continuous and, despite negligible predation, results in recruitment only during two months of the year (January–February). For this reason, relative abundances of larval foods were examined in detail.

Rotifers were the principal prey of the youngest *Xenomelaniris* (Unger and Lewis 1983), and their densities in Lake Valencia varied greatly (Fig. 7; Saunders and Lewis 1988b). Densities were generally high during periods of high survival of *Xenomelaniris* larvae (January and February) and low at other times (March–October). If density of rotifers is an important determinant of larval survival, periods of *Xenomelaniris* recruitment should be related quantitatively to high densities of rotifers. Fish larvae are most vulnerable to starvation shortly after hatching, when they begin autonomous feeding (Hunter 1981). The mean age of the smallest size class of *Xenomelaniris* captured (< 36 mg) was estimated from the growth curve to be 2 mo. Therefore it was hypothesized that abundance of this size class would be positively correlated with density of rotifers ≈ 2 mo prior to the date of collection of the fish. To test this hypothesis, Spearman rank correlation coefficients between mean numbers of young fish per catch and rotifer densities were computed with lag periods of 14 to 365 d. The highest correlation ( $r_s = 0.38$ ;  $P < .05$ ) occurs with a lag period of 72 d. This agrees well with the predicted 2-mo lag, and thus supports the hypothesis that rotifer densities strongly influence survival of *Xenomelaniris* larvae.

Further evidence of the importance of rotifer densities comes from samples collected during 1977 (J. Saunders, *personal communication*), when rotifer densities in late July and early August were exceptionally high. Two months later fish were sampled. Though many juvenile fish were probably lost from the samples because of coarse mesh size, 15% of the fish collected were early-stage juveniles. This is an unusually high percentage of young juveniles for samples collected during the stratification season, and corroborates the hypothesis that survival of *Xenomelaniris* larvae is linked to densities of rotifers.

With respect to seasonal changes in rotifer abun-

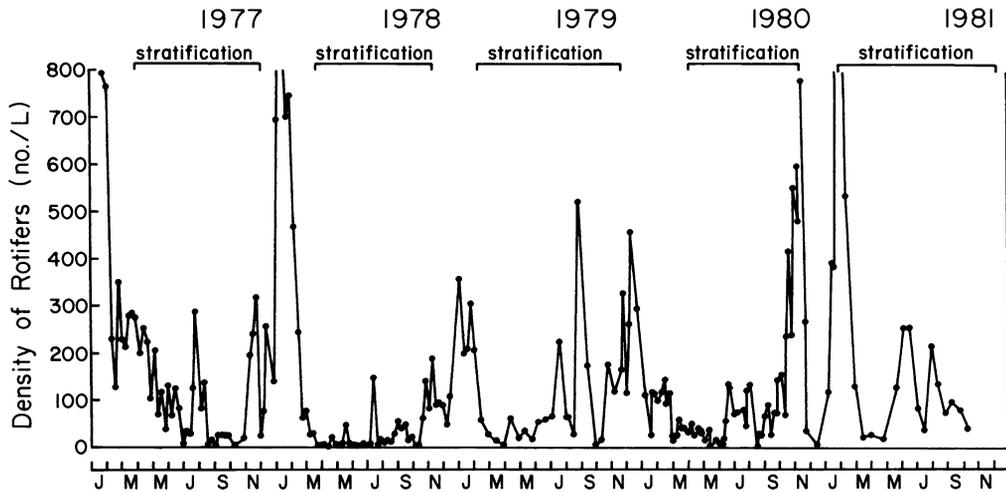


FIG. 7. Five-year record of rotifer density in Lake Valencia. Adapted from Unger et al. (1984).

dance, 1977 was an unusual year. By early March in the years 1978–1981, rotifer densities had dropped well below 100 individuals/L (a common threshold for larval fish: Werner and Blaxter 1980, Hunter 1981, Matthews 1984), but in 1977 rotifers remained abundant until late June (Fig. 7). Such a prolonged period of favorable feeding conditions should lead to reduced seasonality in year-class recruitment and, consequently, to a lower mean size and greater size variability in the year class. Consistent with this prediction, the mean mass per individual in October was much lower in 1977 (152 mg) than in 1979 (288 mg) or 1980 (205 mg), and the coefficient of variation was higher.

The total number of larvae that hatched during the main period of recruitment in 1980 (January and February) can be estimated from the lakewide rates of egg production ( $469 \times 10^6$  eggs/d) and egg mortality ( $228 \times 10^6$  eggs/d): about  $14 \times 10^9$  eggs. The maximum population size of the 1980 year class at the juvenile stage was  $840 \times 10^6$  fish. Therefore,  $\approx 6\%$  of the larvae that hatched during January and February survived, and the mortality rate was  $\approx 4\%/d$  for larvae. Thus even during the period of successful recruitment, larval mortality was substantial.

*Energy intake and energy allocation*

The regression equation describing the relationship between dry mass and total length of *Xenomelaniris* is:

$$M = 0.00045L^{3.29}$$

where  $M$  = dry mass (in milligrams) and  $L$  = total length (in millimetres). Dry mass of *Xenomelaniris* equaled 23% of wet mass.

Growth of the 1979 year class in 1979 was consistently about two months in advance of that of the 1980 year class in 1980, indicating earlier termination of

recruitment in 1979 (Fig. 8). Rates of year-class growth in dry mass varied considerably with the time of year. Three stages of somatic growth are evident for the 1980 year class: (1) from mid-March through May (growth changing smoothly from 0.8 mg/d, or 3.2%/d, to 2.21 mg/d, or 1.6%/d); (2) June and July (no growth); and (3) after July to mid-January (growth changing smoothly from 1.0 mg/d, or 0.72%/d, to 1.4 mg/d, or 0.40%/d). The growth of the 1979 year class changed smoothly from September 1979 (0.94 mg/d, or 0.36%/d) through August 1980 (0.83 mg/d, or 0.15%/d).

Because *Xenomelaniris* adults spawn, their total growth is greater than their somatic growth. In fact, as will be demonstrated below, there is evidence that the total growth of the adult fish conforms to the juvenile growth equation. Growth equations derived from data for juvenile *Xenomelaniris*, therefore, will hereafter be referred to as total growth equations.

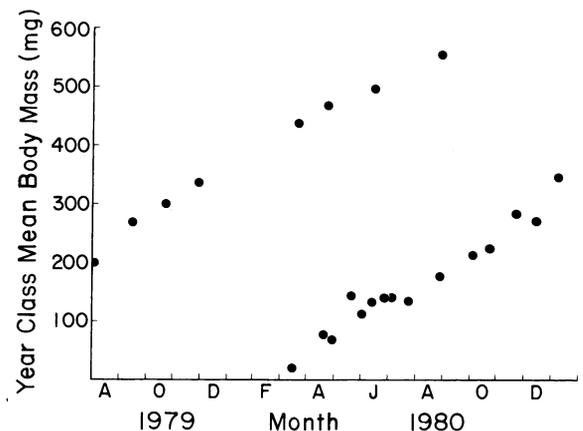


FIG. 8. Mean dry masses per fish of the 1979 (upper) and 1980 (lower) year classes.

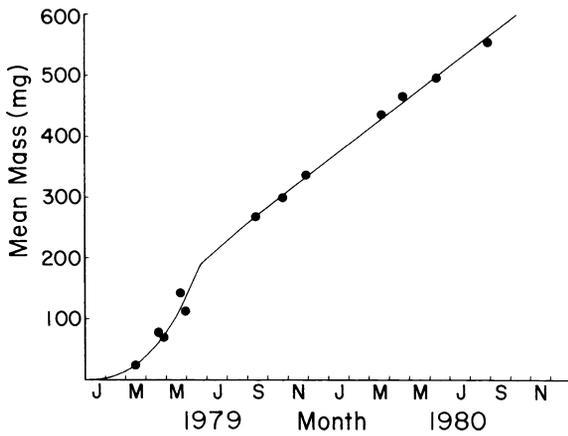


FIG. 9. Mean individual growth curve of *Xenomelaniris venezuelae*.

The specific growth rate (% of body mass per day) of *Xenomelaniris* is:

$$G_t = 12.59M^{-0.42}$$

where  $G_t$  = the total growth rate (% per day) and  $M$  = dry mass of fish (in milligrams per individual). Also:

$$G_s = 215.23M^{-1.16}$$

where  $G_s$  = the somatic growth rate of adult fish (% per day). In both equations, the exponent of mass is negative, reflecting the decline in specific growth rate as the fish grow. Jobling (1983) found that for a variety of fish species the value of the exponent of body mass is  $\approx -0.4$ , which conforms well to the body mass exponent for total growth of *Xenomelaniris* ( $-0.42$ ).

The mean size at maturation of *Xenomelaniris* (mean size at which the fish first become sexually mature) was estimated as the mean of the dry masses of the smallest sexually mature fish and the largest sexually immature fish. Means were computed for all months in which adults and juveniles were available. The estimated size at maturation among all months was  $189 \pm 56$  mg ( $\bar{X} \pm SD$ ).

Growth during the interval between the juvenile and adult stages was estimated by extrapolation of the Y-O-Y juvenile and yearling adult somatic growth curves to the estimated mean dry mass at maturation, 189 mg. The extrapolated curves intersected almost exactly at this mass, so it was not necessary to adjust the intercepts of the curves in order to join them in constructing the composite individual somatic growth curve (Fig. 9).

Adults showed a sexual size dimorphism that increased with age; mean female size reached a maximum of 430 g dry mass, whereas the mean male size peaked at 280 g. A large drop in mean dry mass per individual of adult females beginning in May 1980 (from 430 g to 336 g) marked the entry of fish of the 1980 year class into the adult female population. The

mean dry mass of adult females fell continuously from May until late August (mean: 221 g) as the population of adult females was increasingly dominated by Y-O-Y fish. Most of the males captured in late May were Y-O-Y; the yearling males did not survive as late into the year as the females.

Gut-clearance time was assumed to be related to stomach content according to the square-root model (Jobling 1981):  $K = cS^{0.5}$ , where  $K$  = clearance in milligrams per hour and  $S$  = stomach content in milligrams. The value of  $c$  was determined empirically from an abrupt shift in food type. At dawn, *Xenomelaniris* with lengths  $>40$  mm fed almost exclusively on *Chaoborus* pupae. The availability of pupae ceased abruptly and the fish then switched to larvae; disappearance rate of pupae from the gut thus provided an estimate of  $c$  (Fig. 10). The clearance time of *Xenomelaniris*, as indicated by changes in the mean proportions of *Chaoborus* pupae in the stomach, was 60 min. The mean ( $\pm SD$ ) dry mass of stomach contents during the gut clearance determination was  $2.02 \pm 0.68$  mg. The average clearance rate ( $K$ ), therefore, was 2.02 mg/h, indicating a value of 1.42 for the coefficient  $c$ .

The daily rations, expressed as a percentage of dry body mass, varied from 28% for the smallest size class to 10% for the largest (Table 5). These percentages are within ranges reported for other small fishes (Brett and Groves 1979, Mills and Forney 1981, Peters and Schaaf 1981). Linear regression of daily ration on mean fish dry mass ( $M$ ) using log-transformed data produced the following equation:

$$C = 0.64M^{0.70}; r^2 = 0.997,$$

where  $C$  = daily ration (in milligrams of dry mass).

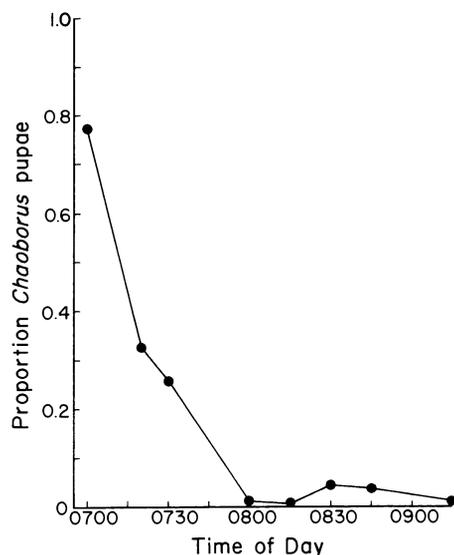


FIG. 10. Mean numerical proportions of *Chaoborus* pupae in stomachs of *Xenomelaniris venezuelae* between 0700 and 0915 on 9 August 1980.

The exponent is close to values determined for Atlantic herring (DeSilva and Balbontin 1974) and trout (Elliott 1979).

Rates of oxygen consumption per unit dry body mass were measured at two levels of stimulation. In the first two experiments the fish were stimulated by movement near the tank, so that they remained active. The oxygen consumption rates under these conditions were 5.6 and 5.7  $\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ . For the other experiments, the fish were isolated from all stimulation; the rates under these conditions ranged from 1.3 to 2.4  $\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ . The first experiments provide an estimate of active metabolic rate (5.6  $\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ ), and the final six experiments approximate standard metabolic rate (1.7  $\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ ; Brett and Groves 1979). The average metabolic rate of the fish in the lake (routine metabolism) is assumed to be intermediate between these rates (3.7  $\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$ ; Beamish 1964).

A  $Q_{10}$  of 2.25 (Duncan and Klekowski 1975) was used to adjust the mean metabolic rate determined in the experiments (24°–25°C) to the average lake temperature (27.5°; Lewis 1984). The corrected metabolic rates were converted to their energy equivalents with a coefficient of 13.6 J/mg  $\text{O}_2$  (Elliott and Davison 1975, Brett and Groves 1979). The corrected mean metabolic rate for a fish of mean dry mass (200 mg) was 301 J/day. The daily metabolic rate determined in this way for *Xenomelaniris* is very close to that predicted by the equation of Mills and Forney (1981) for juvenile yellow perch (*Perca flavescens*).

**SI Units**  
SI unit of energy: joule (J)  
**Conversions**  
1 calorie = 4.1840 J  
1 J = 0.239006 cal.

The daily energy budget (in joules) of *Xenomelaniris* at 200 mg dry mass was:

$$549.4C = 300.4R + 62.3(G_s + G_r) + 187(F + U).$$

Consumption ( $C$ ) and total growth (somatic,  $G_s$ , plus reproductive,  $G_r$ ) were converted to energy equivalents using coefficients of 21 J/mg dry mass for food (Elliott 1976, Vijverberg and Frank 1976, Mills and Forney 1981) and 23 J/mg dry mass for growth (Elliott 1976, Brett and Groves 1979, Flath and Diana 1985). The energy of feces ( $F$ ) plus urine ( $U$ ) was estimated by subtraction of respiration ( $R$ ) and growth ( $G_s + G_r$ ) energies from energy consumed ( $C$ ). The budget indicates that 66% of the energy consumed by the fish was assimilated (respiration plus growth). This value is close to the assimilation efficiency of juvenile yellow perch, which also are planktivorous, as determined by Mills and Forney (1981), and well within the range of

TABLE 5. The mean daily rations of 7 *Xenomelaniris venezuelae* size classes. All mass values are dry masses.

Size-class limits (mg)	n	Mean mass (mg)	Daily ration	
			mg	%
8–30	92	17	4.7	28
31–80	114	61	10.8	18
81–138	153	112	16.7	14
139–180	198	160	21.4	13
181–232	201	206	27.6	13
233–335	207	276	35.4	13
>335	164	506	49.3	10

values reported for a number of other species (Brett and Groves 1979).

Energy budgets for the seven size classes of fish used in the consumption studies are presented in Table 6. Assimilation efficiency was assumed constant (Elliott 1979). Respiration was calculated by subtracting total growth from the assimilated fraction of energy consumed. Therefore, respiration-rate estimates of adult fish included the assumption that total growth of adults conforms to the juvenile growth equation. Linear regression of respiration on body dry mass ( $M$ ) using log-transformed data gave the following equation:

$$R = 6.32M^{0.73}; \quad r^2 = 1.00,$$

where  $R$  = respiration (J/d). The exponent of mass, 0.73, is close to values that have been determined for a wide range of organisms, including fish (Peters 1983, Schmidt-Nielsen 1984, Werner and Gilliam 1984). This similarity and the high  $r^2$  of the equation support the validity of the assumption that total growth of adults follows the juvenile growth equation.

Rates of energy expenditure in the form of egg production per unit of dry body mass ( $G_e = G_r - G_s$ ) differed little among the fish size classes (range = 0.18 to 0.21  $\text{J}\cdot\text{mg}^{-1}\cdot\text{day}^{-1}$ ). This estimate can be independently checked: the number of eggs per unit mass of fish should vary little with fish size if production rates vary little with size. Regression analysis of egg counts for females of various masses indicate that the number of ripe eggs ( $E$ ) is a linear function of female dry mass ( $M$ ):

$$E = 0.304M - 0.442; \quad r^2 = 0.80,$$

The mean dry mass per ripe egg was 0.127 mg and the total dry mass of eggs was  $\approx 3.8\%$  of the fish dry body mass. The mean ( $\pm$ SD) of the daily rates of egg production per milligram of body dry mass for the three adult size classes is  $0.0085 \pm 0.0008$  mg/mg.

The ratio of the mass of eggs carried by the females to the mass of eggs produced each day provides an estimate of the time interval between spawnings. Females probably released all ripe eggs at each spawning (Hubbs 1976). The ratios for the adult size classes in Table 6 indicate that the females produced one clutch of eggs every 4 or 5 d. Frequent spawning (often termed

TABLE 6. Energy budgets for seven *Xenomelaniris venezuelae* size classes. Consumption (*C*), respiration (*R*), somatic growth (*G<sub>s</sub>*), reproductive growth (*G<sub>r</sub>*, females only), and feces plus urine (*F + U*), are expressed as joules per day.

Size class (mm)	Mean dry mass (mg)	<i>C</i>	<i>R</i>	<i>G<sub>s</sub></i>	<i>G<sub>r</sub></i>	<i>F + U</i>
8–30	17	97.9	49.8	15.1	0.0	33.1
31–80	61	237.7	125.5	31.4	0.0	81.2
81–138	112	365.7	196.2	44.4	0.0	124.7
139–180	160	470.3	255.6	54.8	0.0	159.8
181–232	206	560.7	305.9	20.9	43.1	190.8
233–335	276	688.7	378.2	20.1	56.1	234.3
>335	506	1054.4	589.5	18.4	87.9	358.6

fractional or serial spawning) is characteristic of many small fishes of the temperate zone, and of many fishes of all sizes in the neotropics (Lowe-McConnell 1975, Hubbs 1976, 1982, Gale and Gale 1977). Gale and Gale (1977), Gale and Buynak (1978, 1982), Gale (1983, 1986) and Heins and Rabito (1986) determined that the mean spawning intervals for six species of small, non-atherinid (cyprinid) fractional spawners were 5, 7.6, 3.9, 5, 5, and 4.6 d.

The daily energy budget (in joules) for all sizes of *Xenomelaniris* can be described by a single equation:

$$C = R + (G_s + G_r) + (F + U)$$

where  $C = 13.4M^{0.70}$ ,  $R = 6.32M^{0.73}$ ,  $(G_s + G_r) = 2.9M^{0.58}$ ,  $(F + U) = 1.4C$ , and  $M$  = dry body mass of fish (in milligrams per individual).

### Production

Except between 6 June and 10 July, rates of somatic production for the Y-O-Y were greater than those of the yearlings (Table 7). The Y-O-Y rates were highest in May, when most of the year class was in the late juvenile stage (Fig. 3). The low rates of somatic production of adults resulted from the high mortality of adults and the shifting of growth energy into egg production. Annual somatic production of the Y-O-Y plus yearlings in 1980 was 487 mg/m<sup>2</sup> (dry mass) or 21 kg/ha (fresh mass).

Annual dry-mass egg production of the two year classes in 1980 was 224 mg/m<sup>2</sup>. Thus, egg production by the population was ≈50% of somatic production. The total production of *Xenomelaniris* in 1980 was 711 mg/m<sup>2</sup> (dry mass), or 31 kg/ha (fresh mass). The ratio of annual production to mean biomass ( $P/\bar{B}$ ) was 4.0. These may be the only direct estimates for annual production and  $P/\bar{B}$  of a tropical South American fish population.

### DISCUSSION

The ability of the *Xenomelaniris venezuelae* population to exploit zooplankton production in Lake Valencia was shaped by three environmental factors: (1) larval mortality, apparently through starvation, (2) littoral predation on adults, and (3) mortality caused by anoxia. Larval mortality and mortality of other age classes caused by anoxia were seasonal; mortality through littoral predation was not seasonal, and was focused specifically on spawning fish.

Mortality of *Xenomelaniris* larvae was the proximate cause of most of the annual variation in the population. Circumstantial evidence—coincidence of larval survival with rotifer density thresholds, lack of alternate mortality mechanisms, and known sensitivity of larvae in general to food density—links rotifers to larval survival and directs attention to factors that regulate rotifer density. Larval fish have limited searching and prey-capture abilities and may therefore fail to encounter enough suitable food items even when the biomass of food would appear to be sufficient to meet their needs (Rosenthal and Hempel 1970, Hunter 1981). Larval food density is considered by many fish ecologists to be the most important determinant of recruitment success (Lasker 1981). Data presented by Hunter (1981) in a review of larval fish feeding experiments showed that survival rates of larvae of several fish species ranged from 0% to 32% at food densities <100 items/L. Matthews (1984) found that larvae of shad (*Dorosoma* spp.) in Lake Texoma, Oklahoma, starved when mean zooplankton densities fell below 100 individuals/L. Werner and Blaxter (1980) concluded that the prey threshold density for survival of larval herring (*Clupea harengus*) is somewhat above 100 items/L.

TABLE 7. Somatic and egg dry mass production rates of *Xenomelaniris venezuelae*. Y-O-Y = young of year.

Period	Production (mg · m <sup>-2</sup> · d <sup>-1</sup> )			
	Somatic		Egg	
	Yearling	Y-O-Y	Yearling	Y-O-Y
1 Jan–13 Feb	0.05	0.14	0.17	0.00
13 Feb–7 Mar	0.04	0.98	0.16	0.00
7 Mar–6 Apr	0.05	2.03	0.14	0.00
6 Apr–6 May	0.03	3.15	0.11	0.00
6 May–6 Jun	0.02	3.52	0.08	0.17
6 Jun–10 Jul	0.02	0.00	0.06	0.46
10 Jul–12 Aug	0.01	1.03	0.04	0.69
12 Aug–14 Sep	0.01	1.56	0.01	0.92
14 Sep–7 Oct	0.00	1.33	0.00	1.19
7 Oct–28 Oct	0.00	1.34	0.00	1.46
28 Oct–18 Nov	0.00	1.02	0.00	1.28
18 Nov–16 Dec	0.00	0.61	0.00	0.83
16 Dec–1 Jan	0.00	0.31	0.00	0.54
1 Jan–17 Jan	0.00	0.15	0.00	0.27
1980 annual (per year)	6.47	480.30	32.98	190.92

Rotifers in Lake Valencia are regulated by food quality and by *Chaoborus* predation (Saunders and Lewis 1988a). Rotifers are the most highly selected prey of *Chaoborus*. Predation by *Chaoborus* during stratification depresses populations of rotifers, while during the mixing season, when *Chaoborus* abundance is low, the rotifer populations rebound. However, food quality is also important because depression of rotifer populations coincides with sustained, stable layering of the water column even when *Chaoborus* is not the cause of depression. Temporary erosion of the thermocline during stratification restores nutrients to the mixed layer and stimulates rotifer growth, apparently by improving food quality for rotifers.

Degree of breeding seasonality for a population should be related inversely to environmental predictability (Stearns 1976). The principal factors that determine reproductive success of *Xenomelaniris* show elements of both predictability and uncertainty. The initial date of mixing, which controls general mortality by anoxia and leads to conditions favoring recruitment, is highly predictable: it varied by less than a month among the 5 yr of the Lake Valencia study (Lewis 1984). Thus the times of year that are best (late mixing) and worst (early mixing) for reproduction by *Xenomelaniris* are predictable.

Conditions for recruitment during the rest of the year, which corresponds to the stratification season, varied unpredictably. For the most part, larval recruitment was poor during stratification. However, in all years conditions were favorable for recruitment over periods of a week or more during the stratification season. These favorable periods occurred irregularly in relation to meteorological conditions that produced thickening of the mixed layer and increases in rotifer densities. Thus the probability for survival of the larvae during the stratification season varied in an essentially random manner during stratification.

*Xenomelaniris* spawns throughout the year and is therefore able to exploit both the predictable and the unpredictable opportunities for successful breeding. However, the benefits of aseasonal spawning by *Xenomelaniris* appear to be low, whereas the costs are very high. Predation on spawning fish produced an annual mortality rate of  $\approx 60\%$  in 1980. The bioenergetic costs of spawning were also high. A fish that delayed egg production until January would have been able, because of increased size, to produce eggs at about three times the rate of a fish that did not delay egg production.

Oxygen depletion, which causes high fish mortality during the early mixing period, has increased in severity and duration because of recent eutrophication (Lewis and Weibezahn 1976, 1983, Infante et al. 1979). Historically, anoxia in Lake Valencia was more limited than at present, and fish mortality may not have been a consistent feature of the mixing season. Without this

high mortality, continuous spawning by the Y-O-Y would have been more beneficial because more offspring would have survived mixing to reproduce.

The annual fresh-mass production of the *Xenomelaniris* population in 1980 (31 kg/ha) is below the annual yield of many tropical fish populations and is well within the range of production estimates for temperate lake populations (0.43 – 156 kg/ha; Waters 1977, Chapman 1978). The production of *Xenomelaniris* is low in relation to primary production ( $<0.03\%$ ) and zooplankton production (3.6%) (Saunders and Lewis 1988a), given that *Xenomelaniris* is the only pelagic fish in the lake. The time-weighted growth efficiency (ratio of growth to consumption) of *Xenomelaniris* over a year is close to 11%. Thus the trophic bottleneck is  $(11 - 3.6)/11$ , or two-thirds of the zooplankton production.

Melack (1976) and Oglesby (1977), reasoning that primary production should be a reliable index of the food supply for fishes, investigated the relationship between fish yield and primary production for a number of tropical and temperate lakes. They demonstrated, by means of regression analysis, that fish yield increases with primary production. However, there is a great deal of unexplained variation in the relationship, which suggests that primary production does not always reflect the factors that control the growth of fish populations. A disjunction between primary production and fish production is especially likely if, as in the case of the Lake Valencia *Xenomelaniris*, mortality factors suppress fish production below the level that could be sustained by the food supply.

Fernando and Holcik (1982) have shown that, outside of Africa and except where African cichlids have been introduced, fish production in tropical lakes and reservoirs is generally far below the support capacity of trophic resources. They argue that the resident fishes of most tropical lakes are derived from riverine and estuarine stocks and are therefore poorly adapted to lake habitats. According to Fernando and Holcik, one of the most important adaptations for a lacustrine existence is the ability to exploit the plankton resources of the limnetic zone. They note that only a few tropical species are so adapted, and that most of these are endemic to lakes (e.g., *Stolothrissa tanganicae* and *Oreochromis alcalicus*). *Xenomelaniris* is a pelagic planktivore and an endemic lacustrine species, yet it shows low production.

Mortality limits the production of *Xenomelaniris* in Lake Valencia. Of the three types of mortality (predation, larval mortality through non-predation mechanisms, and anoxia), only one (larval mortality) qualifies as a primary cause of disequilibrium between potential production and actual production. Predation on spawning adults is high but could be easily overcome by reproductive potential if steady survival of larvae were possible. Mortality during anoxia is severe

but could be offset by continuous recruitment following anoxia. Thus the true mechanism of population regulation for *Xenomelaniris* in Lake Valencia is a trophic bottleneck involving the requirements of larvae. This mechanism should be studied in other tropical lakes; it is potentially a general explanation for the failure of fishes to exploit limnetic plankton populations in tropical lakes.

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