

Patterns of variation in life history among South American fishes in seasonal environments

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Summary. Ten traits related to life history theory were measured or estimated for 71 freshwater fish species from two locations in the Venezuelan llanos. Multivariate statistics and cluster analysis revealed three basic endpoint patterns bounding a two-dimensional continuum. A suite of attributes associated with parental care and aseasonal reproduction appeared to correspond to an equilibrium strategy. A second group of small fishes was distinguished by traits associated with rapid colonizing ability: early maturation, continuous reproduction, and small clutches. The third basic pattern was associated with synchronized reproduction during the early wet season, high fecundity, absence of parental care, and breeding migrations. A subset of mostly small fishes exhibiting little or no parental care, small clutches, and two to four month reproductive seasons was intermediate between the opportunistic (rapidly colonizing) and seasonal strategies. All ten life history variables showed significant effects of phylogeny. The cluster of species corresponding to the equilibrium group was dominated by siluriform fishes and perciforms of the Cichlidae. The opportunistic cluster was dominated by cyprinodontiform and characiform fishes, whereas the seasonal cluster contained primarily characiform and siluriform fishes. Seven of nine traits were significantly correlated with body length. The three reproductive patterns are interpreted as being adaptive with respect to relative intensity and predictability of temporal and spatial variation in abiotic environmental parameters, food availability, and predation pressure.

Key words: Llanos – Reproduction – Strategies – Tropical fishes – Venezuela

The diversity of methods by which organisms reproduce has long intrigued naturalists. One can argue that traits associated with reproduction should be subject to intense natural selection, as these directly affect the individual's genetic representation within subsequent generations. Alternative modes of reproduction have obvious demographic implications, since all populations experience either gradual or periodic turn-overs. Alternative patterns of reproduction and the degree to which these are successful in different environmental settings have formed the basis for both theoretical and empirical research under the heading life history (Stearns 1976; Southwood 1977; Horn 1978; Sibley and Calow 1986a). In the most basic terms, life history theory involves constraints, or trade-offs, among reproductive and

demographic parameters (Stearns 1983a; Reznick 1985; Pease and Bull 1988). For example, models have incorporated negative correlations between current investment and future investments in reproduction, juvenile survivorship and clutch size, reproductive effort and adult survivorship, and mean generation time and the intrinsic rate of increase. Alternative life history predictions can be tested by evaluating patterns of covariation among reproductive and demographic parameters among heterospecific populations or conspecific demes that have experienced different environmental conditions for long time periods. The present study constitutes one such test, characterizing patterns of reproduction in tropical fishes with a series of dependent variables. The degree of species clustering in multivariate space indicates the likelihood that certain combinations of traits will occur together in nature. Finally, I evaluate species clusters for association with phylogeny and ecological factors.

Tropical freshwater fishes exhibit large diversity in morphological, physiological, and ecological attributes (Lowe-McConnell 1987). Despite few comparative studies of tropical fish reproductive strategies to date (Africa-Welcomme 1969; Central America-Kramer 1978; Asia-DeSilva et al. 1985), these diverse fish assemblages provide excellent systems for evaluation of life history patterns. The great drainage basins of South America harbor the most diverse freshwater fish assemblages on earth (ca. 2400 described species). Rather paradoxically, this ichthyofauna is derived from only a few basic stocks (species belonging to the Characiformes, Siluriformes, and Cichlidae (Perciformes) comprise about 93% of all species, Lowe McConnell 1987). I investigated fish reproductive biology in the llanos of Venezuela during twelve consecutive months in 1984. The region has an average annual temperature of 26.2° C and a highly seasonal pattern of rainfall, with 1189 mm of precipitation occurring from June–November and 178 mm from December–May in 1984. Despite extreme changes in environmental conditions caused by seasonal rainfall, fishes exhibited a wide range of reproductive characteristics in the llanos. This report describes these characteristics for 71 species and interprets the basic patterns within an ecological context.

Methods

Collections

During every month of 1984, fishes were collected from two locations in the state of Portuguesa, Venezuela. The

more faunistically diverse site, Caño Maraca, is a swamp-creek located in the western llanos region (8°52'30" Lat. N; 69°53'30" Long. W). The area studied (termed an "estero") lies within low, flat terrain that experiences extensive sheet flooding during the wettest months (June–August). During this time, the creek's broad floodplain is converted from exposed, sun-baked soil and thorn-scrub habitat into a productive marsh. The aquatic habitat is reduced to a network of pools (average depth ca. 1.0 m) during the driest months (December–May). Dissolved oxygen concentrations are reduced during this time, and many fishes rely on special respiratory adaptations for survival (Winemiller 1988).

The other site, Caño Volcán (8°59'15" Lat. N; 69°53'30" Long. W), is a third order stream in the lowest tier of the Andean Piedmont. This narrow stream flows through deciduous forest and contains both pool and riffle habitats. Caño Volcán differs from C. Maraca in having a slightly steeper gradient, more stable dry season discharge, and a more forested watershed. Caño Volcán experiences frequent but brief flash floods during wet season downpours. Physico-chemical data for each site during the year studied are given in Winemiller (1987).

Fishes were collected by dipnet, seine (3.2 mm mesh/2.5 m length; 12.7 mm/20 m), experimental gillnet, and hook and line. At each site, an attempt was made to sample the entire fish community such that the sample for each species reflected its relative abundance and population size structure during each month. The collecting effort expended each month was approximately equal for each site, consisting of three or four hauls of the 20 m seine in open water habitats, and alternate use of the 2.5 m seine, dipnets, and gillnets for a minimum of 6 h within open water, shoreline, vegetation, and peripheral pool habitats. Sampling was terminated when two hours of collecting yielded no additional rare species. Collections used for comparisons of relative population densities were made during either one or two days between the 11th and 28th of each month. Additional collections were made on other dates in order to supplement the numbers of uncommon species taken in the standard samples. Except for very abundant species (for which a subsample representative of the abundance rank in the collection was retained), all collected individuals were preserved in 15% formalin to assure preservation of viscera and stomach contents. Following examination, preserved specimens were deposited in the Museo de Historia Natural de la Universidad de los Llanos Occidentales Esquiel Zamora, Guanare, Portuguesa and the Natural History Collection of the Texas Memorial Museum, University of Texas, Austin.

During March, June, July, September, and November of 1984, several collections were made at Represa Les Majaguas, a 4250 ha reservoir in western Portuguesa (9°40'00" Lat. N; 69°00'00" Long. W). Fishes were collected from the reservoir by seine (3.2 mm/2.5 m), dipnet, and hook and line. Snorkeling observations provided an additional means for determining the presence of fishes in clear regions of the reservoir. Two regions were sampled: a narrow arm of the lake directly below an inflow canal (from the Río Cojedes), and the main body of the reservoir, both near and offshore. Physico-chemical conditions within the main body of the reservoir are relatively constant, while the former site experiences radial changes associated with seasonal rainfall (e.g. turbidity, depth, and flow rate all increase during the wet season). Voucher specimens were pre-

served in 10% formalin and deposited in the MHN (UNELLEZ) and the TNHC (TMM).

The data

Several attributes related to reproduction and population structure were measured directly and other life history traits were calculated or estimated from these. All preserved specimens were identified and measured for standard length (SL). When available, 30 specimens of each species from each monthly collection at both Caño Maraca and C. Volcán were dissected. The condition of the gonad was coded based in its relative size and color using the following categories: clear (1), translucent (2), opaque (3), small (1), medium/small (2), medium (3), medium/large (4), and large (5). The overall gonad code for each individual was equal to (color code + size code) divided by two, and as a result, values ranged from 1.0 to 4.0. Although the same basic criteria were used in coding male and female gonads, intersexual and interspecific differences in the size, color, and texture of fully mature gonads were taken into account. Undeveloped ovaries were tiny transparent, globular or lamellar structures. Following a gradual transition, fully-developed fish ovaries were large opaque-yellow or orange structures having a grainy appearance due to the presence of mature oocytes. Mature ovaries are cylindrical or lie as sheets along the lateral walls of the abdominal cavity. Immature testes appeared as transparent threadlike or minute lamellar structures in contrast to the smooth, opaque, milky-white appearance of mature testes. Fully-mature testes were either cylindrical, lamellar, or multilobed (the latter condition occurs in catfishes of the Pimelodidae). For several species, gonad codes were regressed against gonadosomatic indices to test their reliability as overall indices of gonadal development (Fig. 1).

Diameters of ten of the largest oocytes in each mature ovary were determined using a dissecting microscope and an ocular micrometer. Oocyte sizes within each examined ovary were classified as extremely uniform, moderately uniform, moderately variable, or extremely variable. The number of separate oocyte size classes present in each mature ovary was recorded whenever these were essentially non-overlapping. The fat content of the body cavity was coded using the following criteria: 1 = none, 1.5 = traces of fat in connective tissue of the coelomic cavity lining, 2 = small amounts around viscera and traces in the connective tissue of the coelomic cavity lining, 2.5 = moderate deposits around the viscera and a thin layer on the coelomic cavity lining, 3 = large deposits around the viscera and coelomic cavity lining, but not filling the coelom, 3.5 = very large deposits filling the coelom, but not producing a visible bulge, and 4 = coelom packed with fat deposits producing a bulge of the belly region. Mean standard lengths, ratio of immature to adult SL's, mean gonad codes, and mean fat codes were plotted for common species by month for estimation of the duration of breeding seasons. Immatures were defined as standard lengths falling below the minimum length for which a fully gravid individual was observed among all collections of a given species.

Ten variables related to life history theory were either measured, coded, or estimated for 59 species from Caño Maraca and 12 species from Caño Volcán.

1) The estimate of annual population density fluctuation was equal to the coefficient of variation (CV) of the popula-

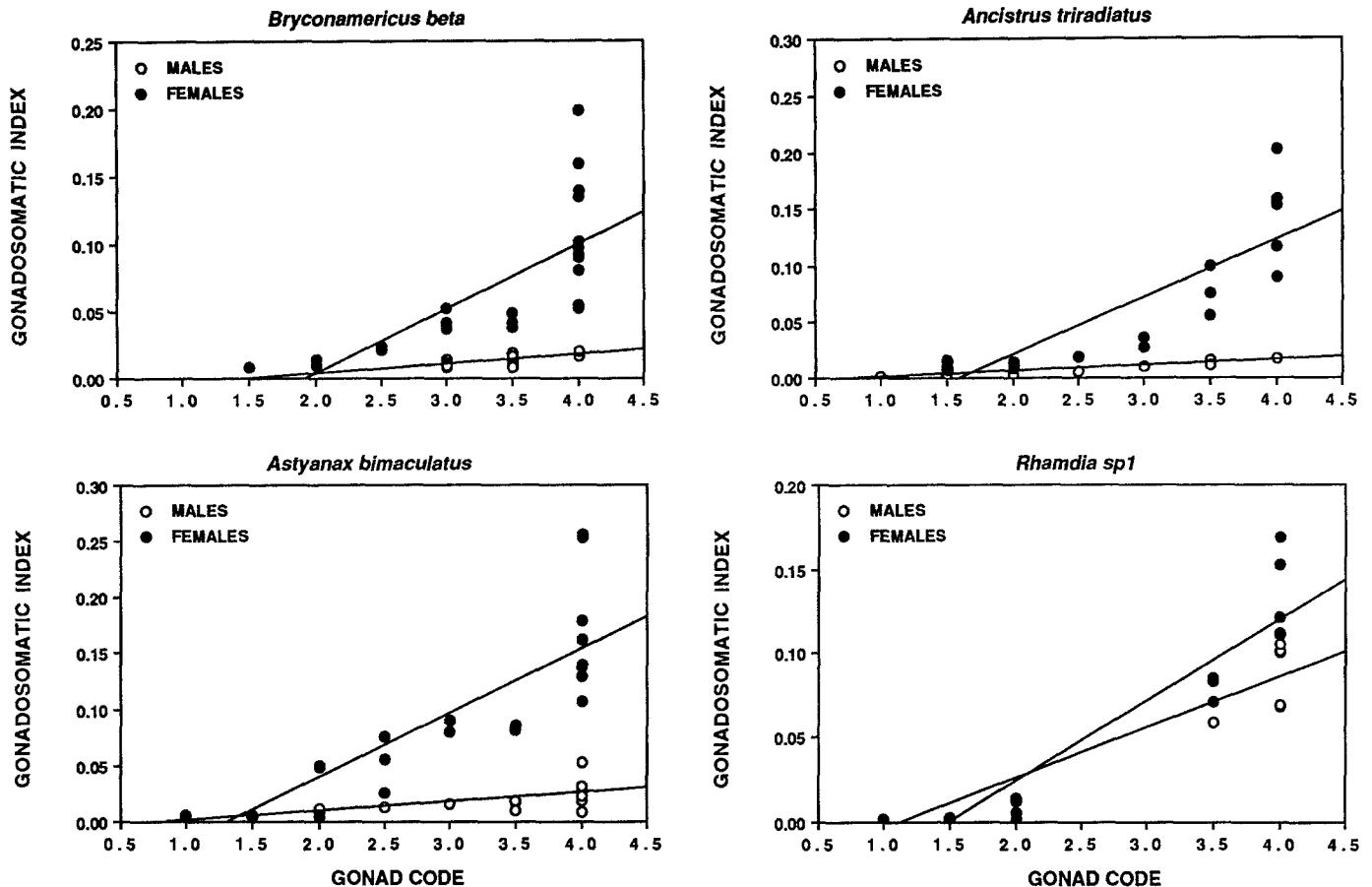


Fig. 1. Linear regressions of gonadosomatic index with gonad code for two tetras and two catfishes from the Venezuelan llanos. Statistics for each regression are as follows: *Bryconamericus beta* (females) $r=0.76$, $F_{23,1}=31.1$, $P<0.0001$; *B. beta* (males) $r=0.60$, $F_{23,1}=13.2$, $P<0.001$; *Astyanax bimaculatus* (females) $r=0.86$, $F_{23,1}=66.3$, $P<0.0001$; *A. bimaculatus* (males) $r=0.80$, $F_{23,1}=41.0$, $P<0.0001$; *Ancistrus triradiatus* (females) $r=0.86$, $F_{18,1}=52.0$, $P<0.0001$; *A. triradiatus* (males) $r=0.97$, $F_{10,1}=145.7$, $P<0.0001$; *Rhamdia sp.1* (females) $r=0.95$, $F_{19,1}=139.9$, $P<0.0001$; *Rhamdia sp.1* (males) $r=0.95$, $F_{10,1}=101.7$, $P<0.0001$

tion sample N's from the 12 standard monthly collections at each site.

2) Mean generation time was estimated as the average number of months from fertilization to the first bout of reproduction by new adults. Estimates were based on the breeding season, monthly size distributions, and minimum size of maturation for each species. For example, mean generation time for *Curimata argentea* was estimated as approximately 12 months, since most reproduction occurred during the first month of the wet season and maturation required a period well in excess of the three months during which offspring were collected (Fig. 2). Average generation times of more continuously breeding species such as *Hoplias malabaricus*, *Roeboides dayi*, and *Aequidens pulcher* (Figs. 2 and 3) were more difficult to estimate based solely on SL frequency histograms, and thus required careful consideration of growth rates.

3) Duration of the breeding season (in months) was estimated from plots of mean gonad codes, visceral fat, SL's, and relative proportions of juveniles to adults by month at each site (Fig. 4).

4) In order to retain as much information as possible for statistical tests, I chose to make a very rough approximation of the number of reproductive bouts per year, rather than code each species in a conservative binary fashion (i.e. single versus multiple brooded). Average reproductive bouts per year per female was estimated from plots of mean gonad

codes by month and records of size distributions of oocytes within mature ovaries. These estimates were very conservative, particularly for species that showed nearly continuous breeding seasons (some of these fishes may even spawn on a daily basis during peak reproductive periods). Bias against the highest values for number of reproductive bouts per year due to conservative estimates would not greatly affect overall ordination of species on the variable (i.e. estimates of bouts per year can be more appropriately viewed as ranks rather than parametric values).

5) Fecundity was recorded as the average number of the largest oocyte size class based on three fully-gravid females. For small species, the total number of oocytes was counted directly. The number of oocytes from large ovaries was estimated by counting and weighing 500 mature oocytes (blotted dry, wet weight to nearest 0.01 g), then weighing the entire ovary, and solving for the total number of oocytes.

6) Maximum oocyte size was equal to the diameter of the largest oocyte in fully developed ovaries (nearest 0.05 mm). Intraspecific variation in diameter of the largest oocyte in mature ovaries was small, ranging from less than 0.05 mm in species with small oocytes to not more than 0.55 mm in species with vary large oocytes (e.g. *Ancistrus triradiatus*). 7) Because tropical fishes exhibit parental care in a variety of forms, it was quantified as the sum of A+B+C+D from the following:

Hoplias malabaricus

Curimata argentea

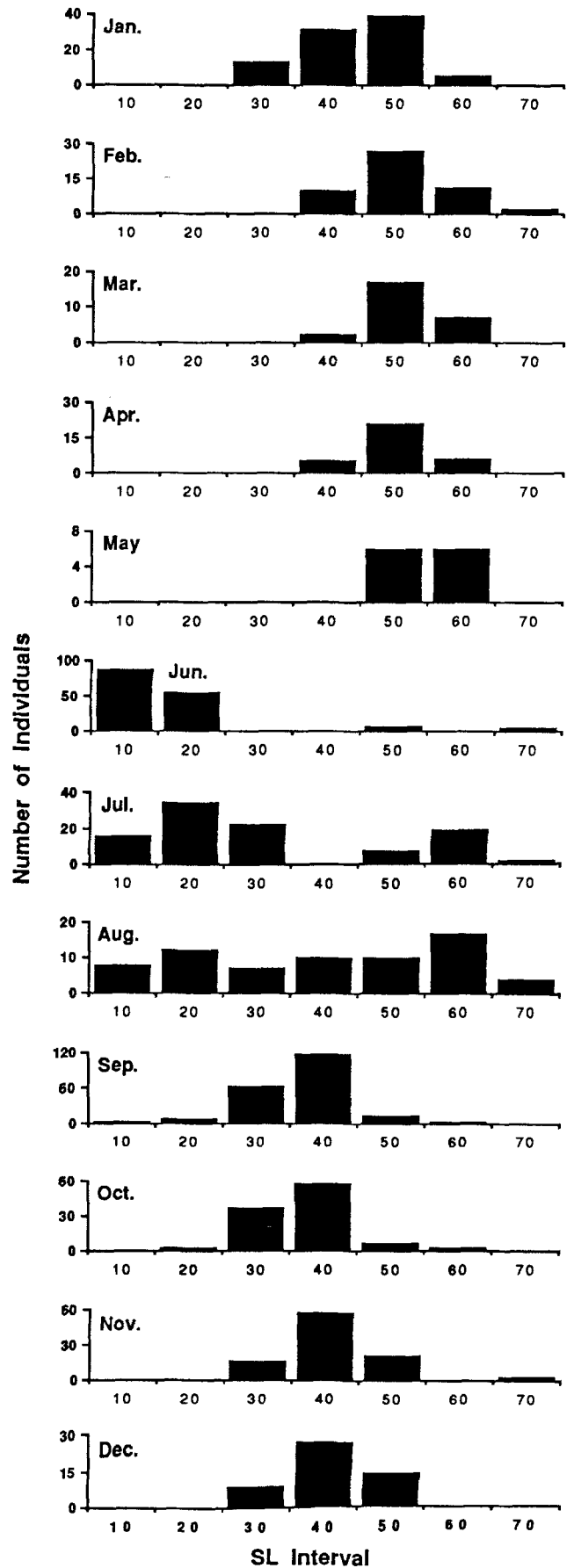
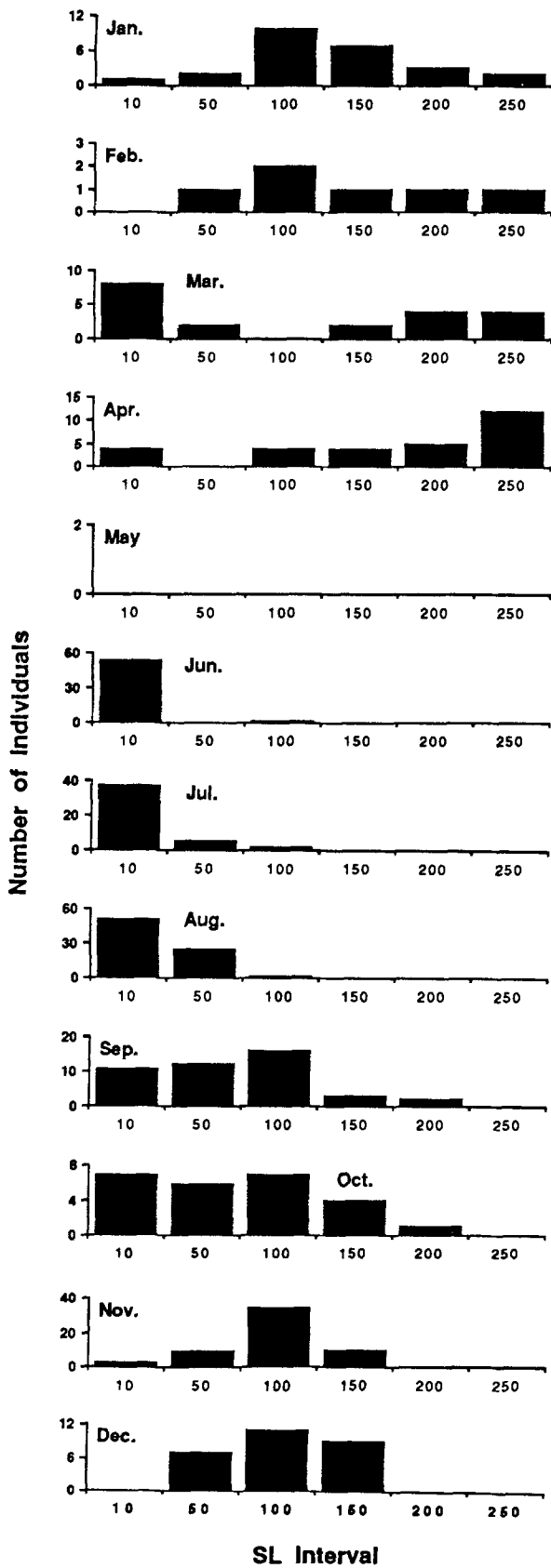


Fig. 2. Standard length frequency histograms during each month for *Hoplias malabaricus* (extended breeder) and *Curimata argentea* (cyclic breeder) at Caño Maraca

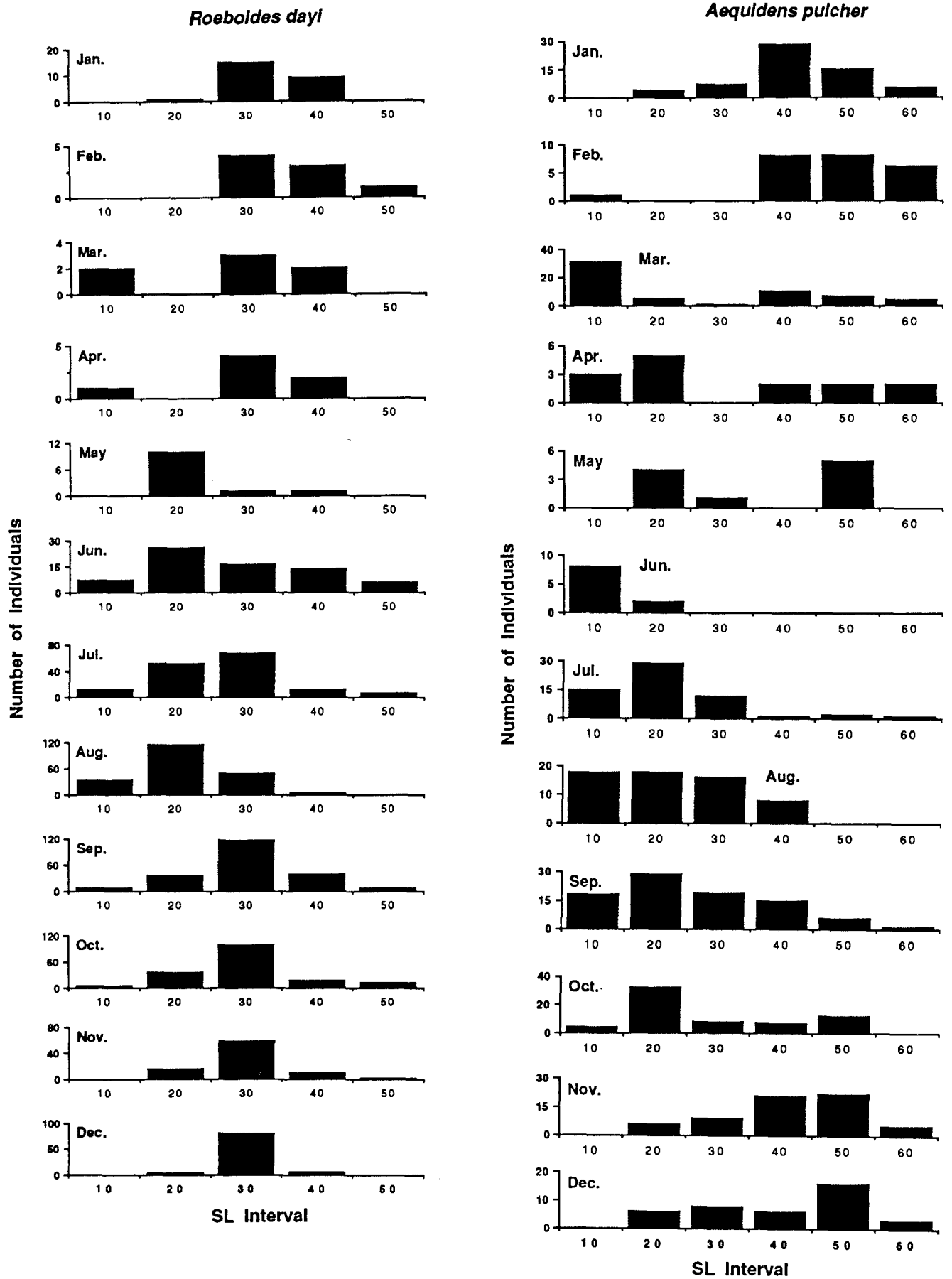


Fig. 3. Standard length frequency histograms during each month for two fishes with extended breeding periods, *Roeboides dayi* and *Aequidens pulcher*, at Caño Maraca

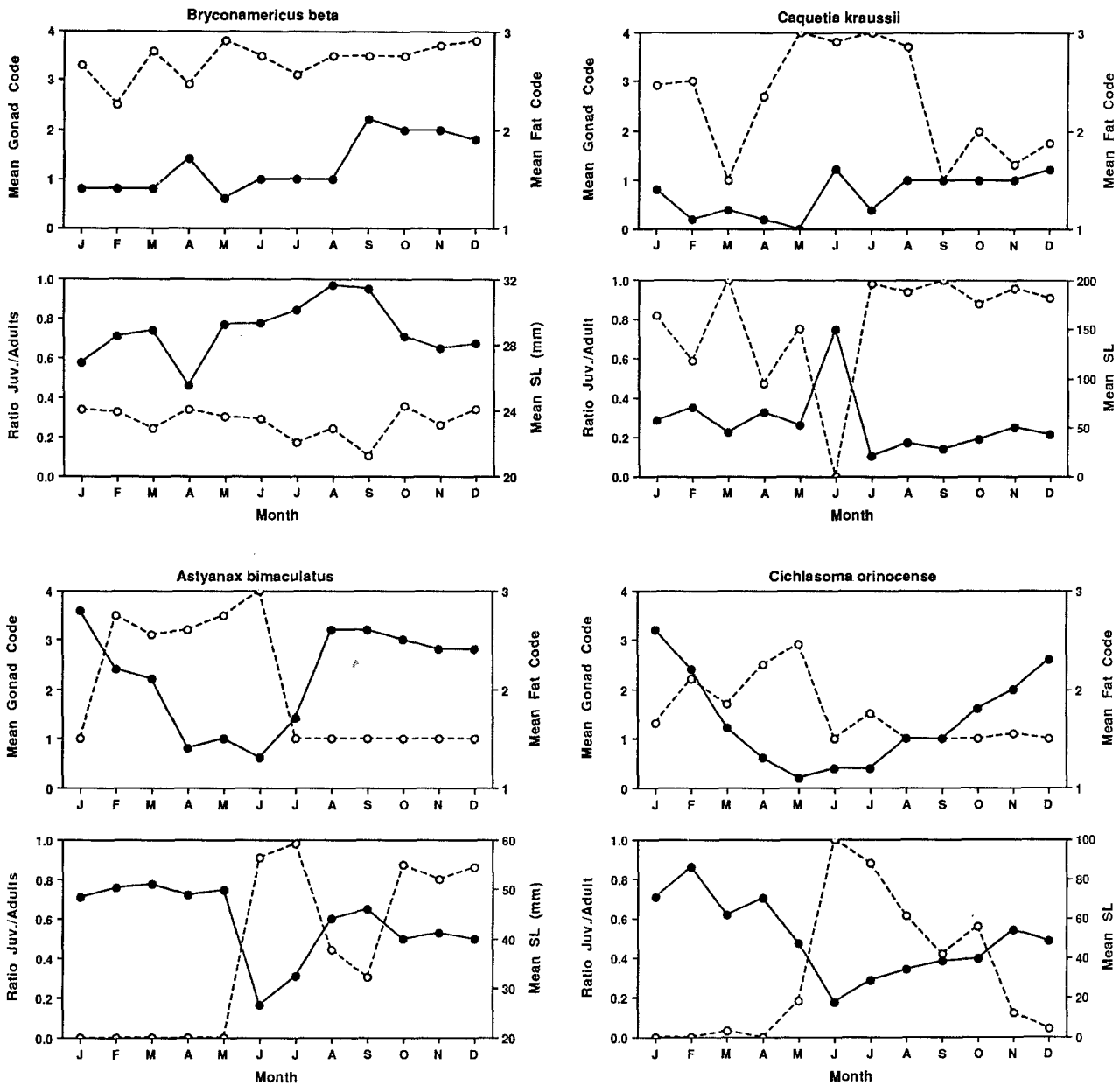


Fig. 4. Comparison of reproductive measures of a multiple-spawning characid (*Bryconamericus beta*) and cichlid (*Caquetia kraussii*) with a seasonally-spawning characid (*Astyanax bimaculatus*) and cichlid (*Cichlasoma orinocense*) from the Venezuelan llanos (closed symbols correspond to mean fat code-top panels, and mean SL-bottom panels; open symbols correspond to mean gonad code-top panels, and ratio of juveniles to adults-bottom panels)

- A= special placement of zygotes (1) or zygotes and larvae (2)
- B= brief period of nutritional contribution to larvae (2), or long period of contribution to larvae or embryos (4)
- C= brief period of parental protection by one sex (1), or both (2), or long period of parental protection by one sex (2), or both (4)
- D= extremely long period of gestation (4) (applied only to *Potamotrygon*)

Parental care codes ranged from 1 to 8 and, with few exceptions, most details of reproductive behavior of a species were documented by field observations of fishes collected at the sites, or the scientific and aquarium literature.

8) Dry season age distribution of each population was coded as either 0–No adults (applied only to two species of annual killifish), 1–Skewed in favor of juvenile and subadult size classes, 2–Approximately even distribution of immature and adult size classes, and 3–Skewed in favor of adult size classes.

9) Wet season age distribution of each population was coded as either 1, 2, or 3 as before.

10) The maximum standard length among all specimens of each species was measured to the nearest 0.1 mm. Maximum length was used in analyses rather than average length of mature adults, since it better reflects genetic potential among fishes exhibiting indeterminate growth.

For ten species that occurred at both sites, data from the site with the highest population density were used in

analyses. Not surprisingly, a few life history variables revealed interregional differences within a species (these provide a basis for comparisons in a future report). The freshwater stingray, *Potamotrygon orbignyi*, was collected from other sites in the llanos (estado Apure) and included in the cluster analysis, since it has very distinctive life history characteristics (e.g. an invariant clutch size of two, viviparity, and a long gestation period). With the exception of *Prochilodus mariae* (both sites) and *Brycon whitei* (C. Volcán), and the freshwater stingray, only species known to be reproducing at the two sites were included in the analysis. Immature yearlings, non-gravid, and gravid adults of *Prochilodus* and *Brycon* were collected, but spawning took place at remote downstream locations. At the beginning of the rainy season, long distance migrations (adults downstream, immatures upstream) are a conspicuous feature of the ecology of these species (Lilyestrom 1983; Lilyestrom and Taphorn 1983). If one or two variables could not be estimated for a species with confidence, the value assigned to its closest phylogenetic relative was used as an estimate of the unknown character (This was performed for only 21 of 720, or about 3% of the observations in the data matrix). Because the reproductive biology of the genus is distinct and well documented (Wourms 1972; L.G. Nico and D.C. Taphorn pers. comm.), the annual killifish, *Pterolebias hoignei*, was included in the data set, even though only two individuals were collected at Caño Maraca during the wet season.

Analyses

A principal components analysis was computed from the correlation matrix derived from 71 fish species and all 10 life history variables in the original data set (Appendix 1). Principal components analysis is an ordination method that allows a multidimensional swarm of correlated data points to be viewed within two or three new orthogonal dimensions. When present, intrinsic patterns within the multidimensional swarm will emerge, generally within a plot of the first two or three components (i.e. independent axes derived from the original dependent variables; Pielou 1984). The strength of each component is reflected by its associated eigenvalue, with values greater than 1.0 being generally accepted as explaining a significant proportion of the variance in the multidimensional data set. Correlations between the first two principal component scores for each species and the original life history variables for each species were computed to provide an index of the relative importance of each variable in the ordination of species into reproductive strategies.

In accordance with recent considerations of the effect of allometry on life history traits (Calder 1984; Dunham and Miles 1985; Gittleman 1986), additional PCA's were computed on modified data matrices with 1) log-transformed SL and fecundity and 2) with nine dependent variables corrected for SL (residuals from log SL linear regression). To test the hypothesis that patterns of interspecific variation among life history traits have a phylogenetic basis (Dunham and Miles 1985), a nested analysis of variance was performed on each of nine life history variables, using family nested within order and log length as a covariate.

A cluster analysis was performed using Euclidean distances based on all 10 attributes among 72 species (stingray included). Each of the ten life history variables was stan-

dardized (mean=0, standard deviation=1) prior to computing Euclidean distances. Clustering was performed by the average linkage method (Sokal and Michener 1958), where the distance between two clusters is the average distance between observations and/or clusters. Canonical discriminant function analyses were performed to explore patterns of within class variation relative to between class variation among life history variables. The type of wet season age distributions (3 states), dry season age distributions (4 states) and parental care (6 states) were used as class variables with the other nine traits as dependent variables. The remaining seven life history variables contained ten or more states, and were thus treated as dependent variables for the purposes of canonical discriminant function analysis.

Results

Univariate statistics

Compared with temperate zone assemblages (Mahon 1984; Wootton 1984), the fishes of both Caño Maraca and C. Volcán exhibited an extremely wide range of life history attributes (Appendix 1). Large interspecific variation in fecundity, body size, and the timing of reproduction was apparent within most orders and families. For example, both aseasonal and seasonally-spawning species were observed in the speciose Characidae as well as the comparatively species-poor Cichlidae (Fig. 4). Diameter of mature oocytes ranged from a low of 0.45 mm in *Curimata argentea* to a high of 4.00 mm in *Ancistrus triradiatus* (i.e., excluding 35.00 mm reported for *Potamotrygon* by Thorson et al. 1983). Forty seven species, including *Curimata argentea*, *Astyanax bimaculatus*, *Brycon whitei*, and *Eigenmannia virescens*, exhibited virtually no parental care following spawning. Cichlids and loricariid catfishes exhibited highest levels of parental care.

Intercorrelations among the ten life history variables appear in Table 1. Significant large positive correlations ($r \geq -0.5$, $P < 0.01$) were obtained for generation time with log SL, log fecundity with log SL, and egg size with parental care. Significant large negative correlations ($r \leq 0.5$, $P < 0.01$) were obtained for generation time with length of breeding season, reproductive bouts per year and wet season age distribution; log fecundity with wet season age distribution; and log SL with wet season age distribution. Twenty six life history variable correlations were negative and 19 were positive or zero. When size was factored out of the analysis using residuals from the log length regression, signs and relative magnitudes of correlations remained essentially unchanged (Table 1).

Multivariate statistics

When all ten variables were included in the data matrix (raw scores for 8 variables plus log fecundity and log SL), the first three principal components reduced variation by 76 percent (Table 2). The result was very similar when SL and fecundity were untransformed (first three PC's modelled 70% of total variation). The first axis was influenced more or less equally by seven variables (population fluctuation, egg size, and parental care excluded). The second axis was derived primarily from egg size, parental care, and log length. Population fluctuation, length of breeding season, dry and wet season size distributions were also significantly correlated with PC2 (Table 3). The third principal compo-

Table 1. Correlation matrix of absolute life history variables for fishes from two sites in the Venezuelan llanos. Values in parentheses are for residuals of regression with log SL

Life history trait	Fluctuation	Generation time	Length breeding season	Bouts per year	Fecundity	Egg size	Parental care	Dry size distr.	Wet size distr.
Fluctuation	×	(-0.09)	(-0.29)**	(0.13)	(-0.01)	(-0.22)**	(-0.36)**	(-0.09)	(-0.09)
Generation time	-0.04	×	(-0.63)**	(-0.53)**	(0.41)**	(-0.16)	(-0.18)	(0.53)**	(-0.30)**
Length breeding season	-0.30**	0.65**	×	(0.39)**	(-0.25)*	(0.27)*	(0.50)**	(-0.45)**	(0.41)
Bouts per Year	0.10	-0.62**	0.44**	×	(-0.49)**	(0.31)**	(0.11)	(-0.75)**	(0.31)**
Fecundity	0.01	0.62**	-0.35**	-0.59**	×	(-0.49)**	(-0.33)**	(0.45)**	(-0.44)**
Egg size	-0.18*	0.15*	0.12	0.08	-0.05	×	(0.62)**	(-0.34)**	(0.27)*
Parental care	-0.34**	-0.01	0.41**	0.00	-0.09	0.65**	×	(-0.38)**	(0.20)*
Dry size distr.	-0.07	0.49**	-0.46**	-0.73**	0.43**	-0.26*	-0.34**	×	(-0.10)
Wet size distr.	-0.10	-0.57**	0.46**	0.46**	-0.67	-0.16	-0.05	-0.15	×
Maximum length	-0.04	-0.57	-0.25*	-0.37**	0.61**	0.47**	0.25*	0.11	-0.70**
Mean value	1.06	10.69	3.78	2.80	5.269	1.39	1.94	2.67	1.46

* $P < 0.05$, ** $P < 0.01$ **Table 2.** Results of the principal component analysis using absolute data (SL and fecundity log-transformed) and length adjusted data for 71 fish species

Absolute data			
	Eigenvalue	Cumulative variance	
PC1	4.01	0.401	
PC2	2.29	0.630	
PC3	1.30	0.760	
Variable	PC1	PC2	PC3
Fluctuation	0.034	-0.244	0.692
Generation time	0.430	0.061	0.692
Length breeding season	-0.345	0.243	-0.051
Bouts per year	-0.396	0.057	0.357
Fecundity	0.410	-0.033	0.003
Egg size	0.023	0.560	0.089
Parental care	-0.060	0.570	-0.166
Dry size distr.	0.315	-0.286	-0.424
Wet size distr.	-0.385	-0.168	-0.275
Maximum length	0.343	0.354	0.230
Length-adjusted data			
	Eigenvalue	Cumulative variance	
PC1	3.71	0.412	
PC2	1.62	0.592	
PC3	1.03	0.707	
Variable	PC1	PC2	PC3
Fluctuation	-0.073	-0.611	0.270
Generation time	-0.364	0.281	0.390
Length breeding season	-0.381	0.127	-0.546
Bouts per year	-0.380	-0.366	0.090
Fecundity	-0.368	0.071	0.090
Egg size	0.325	0.325	0.497
Parental care	0.314	0.472	0.151
Dry size distr.	-0.394	0.243	-0.151
Wet size distr.	0.276	0.061	-0.227

Table 3. Correlations of first two principal component axes with the original life history variables

Life history variable	PC1	PC2
Fluctuation	0.07	-0.37**
Generation time	0.86**	0.09
Length breeding season	-0.69**	0.36**
Bouts per year	-0.79**	0.09
Log fecundity	0.82**	0.05
Egg size	0.05	0.85**
Parental care	-0.12	0.86**
Dry size distr.	0.63**	-0.43*
Wet size distr.	-0.77**	-0.25*
Log length	0.69**	0.54**

* $P < 0.05$, ** $P < 0.005$

ment axis was influenced primarily by population fluctuation, dry season age distribution, and reproductive bouts per year. The fourth axis modelled only 7% of the multidimensional variance and was derived primarily from three variables: length of breeding season (eigenvector = -0.512), log fecundity (-0.527), and egg size (0.450).

A plot of species by their scores on the first two principal components reveals a more or less triangular scatter with apices corresponding to three fairly distinctive suites of characteristics (Fig. 5). Species with intermediate scores on PC1 and high scores on PC2 exhibited the following attributes: well-developed parental care, prolonged breeding seasons, repeated reproduction, evenly distributed size classes throughout the year, long generation times large eggs, and large body size. According to sample CV values, these species tended to exhibit comparatively small-scale fluctuations in local population density over the course of the year. A fourteen species cluster around the first apex was dominated by catfishes (Siluriformes) and cichlids (Fig. 6).

The second apex resulted from low scores on PC1 and intermediate or low scores on PC2 (Fig. 5). This region of two-dimensional component space is characterized by little or no parental care, prolonged breeding seasons, re-

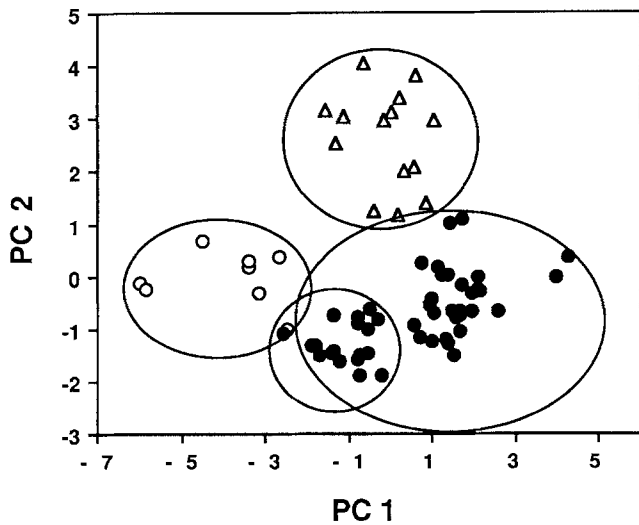


Fig. 5. Plot of Venezuelan fish species scores on the first two principal components (analysis derived from raw life history data with log fecundity and log SL). Symbols group species into three broad categories based on a cluster analysis. Top ellipse bounds an equilibrium strategy, left ellipse bounds an opportunistic strategy, and right ellipse bounds a seasonal reproductive strategy. The small ellipse identifies fishes of small body size that exhibit a strategy intermediate between extreme seasonal reproduction and opportunism ○ Opportunistic; ● Seasonal; △ Equilibrium

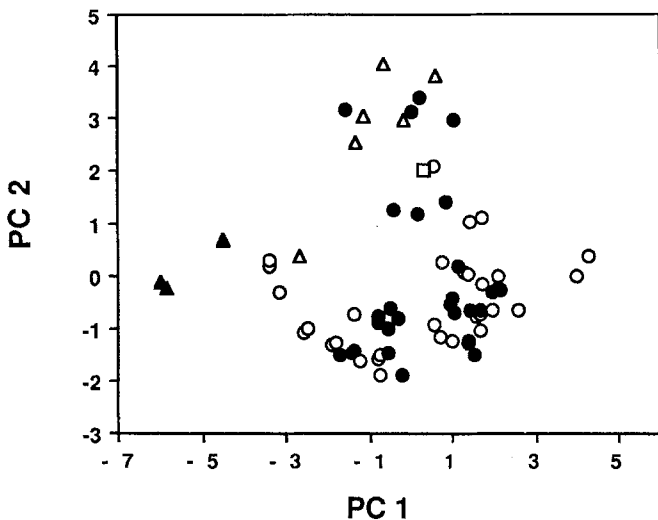


Fig. 6. Plot of tropical fish PCA scores as in Fig. 5, but with symbols identifying species by order. Again, the top apex corresponds to the equilibrium strategy, left apex to opportunism, and right apex to a seasonal reproductive strategy ○ Characiforms; ● Siluriforms; △ Perciforms; ▲ Cyprinodontiforms; □ Synbranchiforms

peated bouts of reproduction, an even size distribution during the wet season (for some species during the dry season as well), short generation time, relatively small clutches, small oocytes, small body size, and intermediate population fluctuations. Characiformes and Cyprinodontiformes were predominant among the nine species grouped near the second apex (Fig. 6).

The third apex was composed of species with high scores on PC1 and intermediate or low scores on PC2 (Fig. 5). Species in this region of principal component two-space were characterized by very little or no parental care, short breeding season, few bouts of reproduction per year, adult-

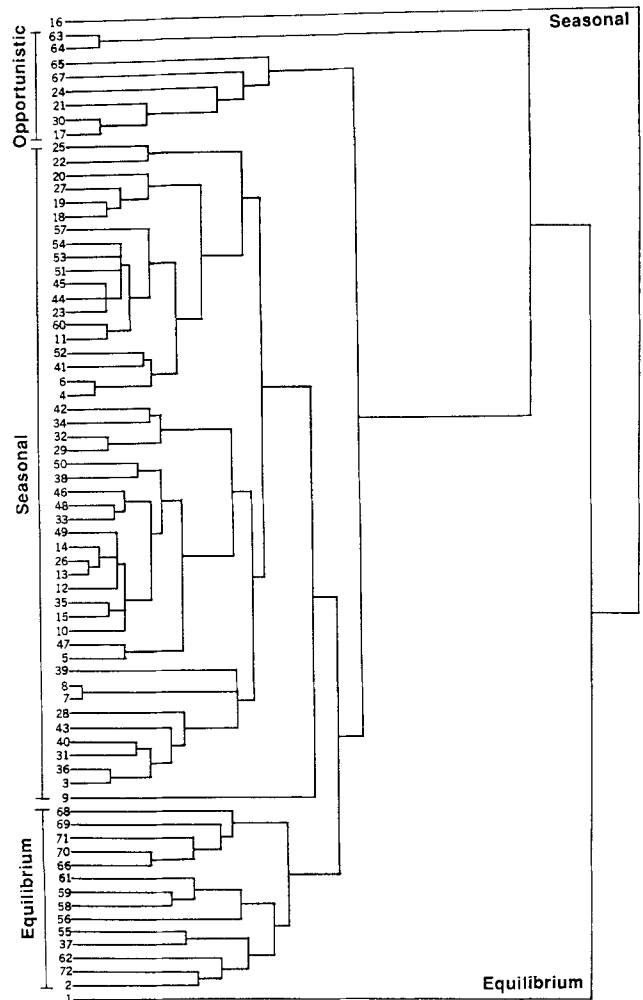


Fig. 7. Cluster diagram of Venezuelan fishes based on Euclidean distances computed from ten standardized life history attributes. Root mean square distances between species is 4.47. Species number codes are given in Appendix 1. Explanation of three patterns appears in text

dominated dry season populations, juvenile-dominated wet season populations, long generation times, intermediate to high fecundities, small oocytes, and intermediate or large body size. For the most part, species located near the third apex exhibited large local population fluctuations. The 48 species located in the region of the third apex belonged to orders Characiformes and Siluriformes exclusively (Fig. 6). Seventeen characiform and siluriform fishes were intermediate between the second and third apices (intermediate and low PC1 and low PC2 scores; Fig. 5). These intermediate fishes were all comparatively small, with prolonged, yet distinctly seasonal reproduction. Egg sizes were small, fecundity intermediate, and parental care absent or weakly developed in this group that included *Corydoras* species, *Ochmacanthus alternus*, and *Odontostilbe pulcher*.

Cluster analysis

Clustering of 72 species based on Euclidean distances resulted in three major groupings plus two single species branches (Fig. 7). The freshwater stingray, *Potamotrygon orbignyi*, was included in this analysis (estimates for several *Potamotrygon* life history parameters were based on the closely related *P. motro* using data from Thorson et al.

1983). The same three basic life history strategies were formed by three large clusters, with *Potamotrygon* and the characid, *Brycon whitei*, representing extreme examples of two of these basic suites of characteristics.

Potamotrygon could be considered an extreme case of the life history strategy that corresponds to long generation time, well-developed parental care, large oocytes, and low fecundity. The same 14 species (5 families, 3 orders) that comprised the first apex from PCA produced this cluster (Figs. 5 and 7). Likewise, *Brycon* represents an extreme case of the strategy exhibited by the 48 species cluster (19 families, 2 orders) characterized by seasonal reproduction, high or intermediate fecundity, no parental care, and generation times from 6 to 48 months. This large cluster of seasonally reproducing fishes contained two subunits that corresponded to 29 large species with high fecundities (e.g. *Prochilodus mariae*, *Rhamdia* spp., and *Rhamphichthys marmoratus*) and 19 small species with much lower fecundities (e.g. *Characidium* spp., *Microglanis iheringi*, and *Ochmacanthus alternus*). An eight species cluster (4 families, 3 orders) corresponded to the short generation time, low fecundity, multiple-brood strategy of the PCA (Figs. 5 and 7).

Creagrutus sp. and *Hemigrammus* sp. were grouped with aseasonally-reproducing, fast-maturing species by PCA, yet placed within the small body size subunit of the seasonally-reproducing group by average clustering (Figs. 5 and 7). *Gephyrocharax valenciae* was placed within the multiple-brood, fast-maturing group by cluster analysis, yet only slightly nearer to small-sized, seasonally-spawning species by the first two principal components. If one examines the original life history variables (Appendix 1), it is clear that all three groups grade into one another as a continuum of reproductive strategies.

Analysis of variance

The composition of the three groups clustered near the apices of Figure 5 is associated to some degree with phylogeny. For example, five of the species in the first apex group (high PC2 scores) are cichlids (Perciformes), seven are catfishes (Siluriformes), one is a characiform (*Hoplias malabaricus*), and one is a synbranchiform eel (*Synbranchus marmoratus*). Likewise, the second group (low PC1 scores) is dominated by characiforms and cyprinodontiforms (two killifishes and one livebearer). The third group (high PC1 scores) is composed entirely of tetras, catfishes, and knife-fishes (Characiformes and Siluriformes). On the other hand, members of the most diverse order, Characiformes, were found in all three groups. Results of nested ANOVA show that order had a significant effect on all ten life history variables when length was not included as a covariate (Type I SS, Table 4). When log length was included as a covariate (Type III SS), the main effect of order on wet season size distribution became marginally insignificant (Table 4). Family significantly affected all life history variables except generation time, length of reproductive season, and log length (Table 4). Length as a covariate did not alter the fraction of family level tests (family nested within order) that attained statistical significance ($P < 0.05$).

Because considerable variation in adult size existed within many families (SL range 28–313 mm for Characidae, 30–230 mm for Cichlidae, 25–216 mm for Callichthyidae, 26–233 mm for Loricariidae, 38–200 mm for Pimelodidae),

Table 4. Results of nested ANOVA for family within order with log length as a covariate

Trait	Class variable	Type I SS		Type III SS		Model r^2
		F	P	F	P	
Population Fluctuation	Order	4.38	0.003	2.79	0.03	0.57
	Family (order)	2.42	0.009	2.36	0.01	
	Log length	0.01	0.974			
Generation time	Order	6.98	0.0001	4.57	0.0018	0.65
	Family (order)	1.53	0.12	1.24	0.27	
	Log length	24.83	0.0001			
Length season	Order	5.50	0.0005	5.96	0.0002	0.50
	Family (order)	0.98	0.49	0.91	0.57	
	Log length	3.49	0.07			
Bouts per year	Order	20.38	0.0001	59.07	0.0001	0.78
	Family (order)	3.54	0.0003	3.51	0.0003	
	Log length	6.13	0.02			
Log fecundity	Order	24.41	0.0001	17.32	0.0001	0.88
	Family (order)	6.38	0.0001	4.01	0.0001	
	Log length	104.31	0.0001			
Egg size	Order	6.68	0.0001	7.98	0.0001	0.77
	Family (order)	4.72	0.0001	4.12	0.0001	
	Log length	48.99	0.0001			
Parental care	Order	72.97	0.0001	67.96	0.0001	0.91
	Family (order)	4.59	0.0001	4.58	0.0001	
	Log length	27.64	0.0001			
Dry season size distribution	Order	18.37	0.0001	11.37	0.0001	0.76
	Family (order)	3.36	0.0005	3.37	0.0005	
	Log length	0.24	0.62			
Wet season size distribution	Order	5.86	0.0003	2.39	0.052	0.74
	Family (order)	2.92	0.002	2.13	0.021	
	Log length	55.78	0.0001			
Log length	Order	4.10	0.0035			
	Family (order)	1.31	0.225			

patterns of covariation among life history variables could have been affected by allometry (Stearns 1983a; Dunham and Miles 1985). Log length was significantly correlated with seven of nine life history variables (Table 1). Again, results from nested ANOVA with log SL as a covariate indicate that length influenced the pattern of variation in only one of 18 tests for phylogenetic effects on life history variables (Table 4). Whereas the potential for a high fecundity might be expected to exhibit an allometric pattern, larger fishes did not always exhibit higher fecundities than smaller fishes (e.g. *Parauchenipterus galeatus*, *Hypostomus argus*, *Loricarichthys typus*, *Pterygoplichthys multiradiatus*, *Crenicichla geayi*).

Canonical discriminant function

Results of the canonical discriminant function analyses indicate that all three of the designated class variables had significant ($P < 0.0001$) ratios of within-class to between-class variance among the remaining nine life history variables. Canonical correlations were 0.88 (wet season size dis-

tribution), 0.84 (dry season size distribution), and 0.84 (parental care). For wet season size distribution, the first canonical eigenvector had high loadings for log fecundity (0.77), egg size (-0.58), length of breeding season (-0.46), and log SL (0.45). Taken together, these data reveal a pattern in which species exhibiting juvenile-dominated wet season populations tend to have high fecundities, large body size, comparatively small oocytes, and a brief reproductive season. Conversely, populations dominated by adults during the wet season were smaller, less fecund, and had larger oocytes and longer reproductive seasons. Reproductive bouts per year (0.91) and log fecundity (-0.43) had the highest loadings for the first canonical eigenvector of dry season size distribution. In one-dimensional space, species ranged between adult-dominated dry season populations exhibiting repeated bouts of reproduction and low fecundities, to juvenile-dominated and uniform populations with relatively fewer bouts of reproduction but larger clutches. The second dry season size distribution canonical vector had a correlation of 0.77 and highest variable loadings corresponding with length of reproductive season (-0.78), parental care (-0.67), and population fluctuation (0.46). The second canonical vector discriminated among dry season distribution classes along a gradient running from short breeding season, little parental care, variable population size, and adult-dominated dry season populations at one end, to prolonged breeding, parental care, more stable population density, and uniform dry season size distributions at the other. Egg size (0.87), length of breeding season (0.42), population fluctuation (-0.39), and log SL (-0.37) had the highest loadings on the first parental care canonical eigenvector. In other words, species exhibiting greater levels of parental care tended to have larger eggs, longer breeding seasons, lower population fluctuations, and smaller body size than fishes with poorly-developed parental care.

Overall, results of canonical discriminant function reinforced findings of PCA and average clustering by Euclidean distances. Patterns of reproduction appear to be particularly consistent when at least two dimensions are incorporated into the model simultaneously. A two-dimensional gradient having three distinct endpoint strategies seems to describe tropical fish life history patterns in the simplest and most parsimonious fashion. Small, multiple-clutching fishes exhibiting small investments in individual offspring correspond to a life history strategy associated with short generation times and rapid population turnover. Larger more fecund, seasonally-spawning fishes also invest little in individual offspring (i.e., small oocytes, no parental care), but much more in total wet season reproductive effort. In contrast to both of these patterns, a group of aseasonally-reproducing fishes had large oocytes, intermediate or small clutches, and parental care of eggs and/or larvae. The last group seems to represent a strategy associated with investing relatively more in individual offspring, leading to higher survivorship and moderation of local population fluctuations.

Discussion

Covariation among life history variables

Even though most of the primary measurements of reproductive and demographic parameters involved thousands of examined specimens (Appendix 1), population fluctua-

tions, average generation times, length of breeding season, and number of reproductive bouts per year should be considered best approximations until new data become available. While limitations of the data should be taken into account, potential life history trade-offs are implicated by 12 significant negative correlations obtained among nine variables (14 using length adjusted values). Egg size and parental care changed from having zero correlations with log fecundity to having significant negative correlations when the data were adjusted for length (Table 1). Because tropical fishes exhibit wide variation in body form (e.g. ranging from the robust *Cichlasoma orinocense* to the snake-like *Synbranchus marmoratus*), length provided only a rough estimate of body size differences. Even though gravimetric or volumetric data could potentially increase the sensitivity of size-adjustments, the seven significant length correlations were consistent with other comparative fish studies (Itô 1978, Mahon 1984; Wootton 1984). For example generation time, fecundity, and egg size were all correlated positively with body length (Table 1). Length of breeding season, bouts of reproduction per year, and the ratio of adults to juveniles during the wet season correlated negatively with length.

Several of the observed negative correlations should have resulted from fundamental physiological constraints. Clutch sizes are bound to be lower in species that exhibit many spawning bouts per year, compared to seasonal spawners that exert total annual reproductive effort during a constricted time period. Likewise, higher total fecundity is achieved by packing less matter and energy into individual oocytes. Many of the positive correlations among variables would be logically anticipated as a consequence of secondary constraints imposed by primary negative constraints (Pease and Bull 1988). The difficult task of assessing which suites of characters might form adaptive life history strategies largely reduces to a problem of critically assessing which attributes constitute key variables responsive to natural selection. Indirect evidence frequently may be required for identification of crucial trade-offs (Pease and Bull 1988). Some variables can be evaluated singularly with regard to a variety of environmental parameters. For example, the timing of reproduction of fishes has been viewed as adaptive with respect to a number of different environmental factors (Kramer 1978; Johannes 1978; Baltz 1984; Keast 1985; and see below).

Basic patterns and ecological correlates

Results of multivariate analyses of tropical fish life history attributes were robust, yielding similar patterns for data sets containing SL as a variable, length log-transformed, data adjusted for length effects, and treating three of the ten attributes as class variables. Moreover, average clustering and PCA produced nearly identical groupings among fishes. At plot of the species on the first two orthogonal axes resulted in a distribution with three apical clusterings, each having fairly homogeneous life history features. One suite of life history traits always contained intermediate or long generation times, large investment in individual offspring, delayed maturation, aseasonal reproduction, and prolonged breeding. To some extent, this association of life history traits agrees with the relative “*K*-strategy” as originally proposed by Pianka (1970). Presumably, the suite of characteristics forming this “equilibrium strategy” is asso-

ciated with higher juvenile survivorship as result of greater parental investment in individual progeny (*Strategies* are used here as *hypotheses* for interpreting observed patterns as adaptive suites of characteristics. Neither teleology nor cognition are implied from the present usage of the term, cf. Chapleau et al. 1988). With the largest oocyte (diameter estimated near 35.0 mm), the smallest clutch (two offspring), long gestation period (19–11 months), and late maturation (ca. 43 months, Thorson et al. 1983), the freshwater stingray, *Potamotrygon*, provides an extreme example of the so called equilibrium strategy. As a group, cichlids tended to exhibit equilibrium strategy characteristics (i.e., comparatively large oocytes, brood protection, and acyclic spawning). Enhanced early survivorship of offspring was indicated by the presence of numerous juvenile size classes of some cichlids throughout the dry season (e.g. *Caquetia kraussii*, Fig. 4). Equilibrium-strategists apparently reproduced with some degree of success, even though predation pressure was intense during the early dry season at Caño Maraca, when fishes were encountered at high densities (Winemiller 1987).

The two remaining associations of life history characteristics appear to divide many of the traits comprising Pianka's (1970) earlier "r-selected" suite of attributes. In an attempt not to introduce new jargon, I will refer to the suite of characteristics composed of short generation time, low fecundity, and minimal investment per offspring as the "opportunistic strategy". The opportunistic strategy was associated with small species (e.g. *Poecilia reticulata*, *Odontostilbe pulcher*) that remained reproductively active despite apparent high juvenile and adult mortality during the harsh conditions and intense predation of the dry season. At Caño Maraca, fishes exhibiting the opportunistic suite of attributes built-up dense local populations from relatively small pools of adult founders over a six month period following the initiation of rains. This population growth was achieved through a combination of multiple bouts of reproduction by older adult survivors with rapid recruitment of new adults via rapid maturation rates.

The third suite of life history attributes clearly constitutes a "seasonal strategy", which is characterized by cyclic (often annual) reproduction, relatively long generation times (usually coinciding with the reproductive cycle), large clutches, and small investment per offspring. Fishes identified as seasonal-strategies exhibited a characteristic burst of reproduction with the early rains, followed by gradual reductions in population size due largely to predation on immatures during the early dry season. *Astyanax bimaculatus* and *Curimata argentea* at Caño Maraca provide good examples of the seasonal strategy, increasing rapidly from relict, adult dry season populations to large juvenile populations in the newly-inundated swamp floodplain. A major fraction of juveniles produced during this "spring bloom" of production never survives to maturity, ultimately falling prey to birds and predaceous fishes during the early dry season. The seasonal strategy seems to exploit both temporal and spatial variation in quality of habitats for enhanced juvenile survival and growth. Eighteen of the species grouped within the seasonal strategy exhibited short-range migrations from the downstream channel into the upper estero for seasonal breeding, whereas only *Hoplias malabaricus*, exhibited comparatively less-pronounced local migrations among the 14 equilibrium-strategists. The large characiforms, *Prochilodus mariae* and *Brycon whitei*, exhibited

long-distance seasonal migrations, with adults moving down from the Andean piedmont to spawn in productive llanos floodplains during the wet season. These adults later return with yearlings to the piedmont, presumably to escape predation and the harsh conditions of the floodplains during the dry season.

Quantitative features of fish habitats were highly variable on a seasonal basis at the sites studied in Venezuela, and interestingly, 48 (20 families, 5 orders) of 71 species were identified as relative seasonal-strategists. These species exhibited gonadal recrudescence during the dry season and a burst of spawning activity following the first heavy rains of the wet season. Several seasonally-spawning species appeared to exhibit no more than one or two bouts of reproduction during the first several weeks following initiation of rains (e.g. *Astyanax bimaculatus*, *Tripottheus* sp.), whereas other local populations exhibited sustained, yet greatly-reduced, levels of spawning for several months after an initial synchronous burst (e.g. *Ctenobrycon spilurus*, *Serrasalmus irritans*). Larval growth and development were particularly rapid and survivorship probably quite high within the newly-expanded aquatic environment. Larval food resources were abundant and adult predatory fishes were at their lowest densities during the early wet season (Winemiller 1987).

During the first three months of the wet season, species classified as seasonal-strategists dominated the fish community at Caño Maraca, both in terms of biomass and density. As the wet season proceeded toward a new dry period, formerly dominant seasonal-strategists gradually gave way to species exhibiting opportunistic and equilibrium strategies. As previously noted, several opportunistic-strategies achieved their highest densities (e.g. *Roeboides dayi*, *Hemigrammus* sp.) during the late-wet/early-dry period of transition (September–December) via continual recruitment of new individuals, this in spite of increasing predation pressure and diminishing food resources. As the dry season gave rise to increasingly harsh conditions (January–May), most local populations were greatly reduced, particularly seasonal-strategists that persisted as adult remnants of the formerly-dominant local populations. Several species of opportunistic- and equilibrium-strategists continued reproduction during periods of extremely harsh dry season conditions, although juvenile mortality was probably quite high. Burt et al. (1988) hypothesized that multiple spawning in the neotropical characid, *Hypessobrycon pulchripinnis*, increases total reproductive output, which could be adaptive at less seasonal, tropical latitudes. Yet many, if not most, tropical ecosystems experience highly cyclic rainfall. Given the theoretical finding that rapid maturation rates maximize the intrinsic rate of population increase more efficiently than increasing either survivorship or fecundity (Lewontin 1965; Sibly and Calow 1986b; and others). I hypothesize that colonizing ability in the face of intense predation or unpredictable variation in quality of aquatic habitats is the major adaptive feature of the opportunistic strategy. Maturing rapidly, producing multiple small clutches, and recolonizing ephemeral habitats each year, the annual killifishes (Cyprinodontidae) provide compelling illustrations of advantages of the opportunistic strategy. Results from Reznick and Endler's (1982) investigation of Trinidadian guppies, *Poecilia reticulata*, further support this interpretation of the opportunistic strategy. Females from environments with greater threats of predation for adult

guppies matured at smaller sizes, had shorter interbrood intervals and allocated larger fractions of tissue to reproduction.

The basic life history strategies displayed by neotropical fishes agree well with the three patterns that emerged from Baltz's (1984) interspecific comparison of temperate surfperches (Embiotocidae). One group of surfperches contained six species having large bodies, moderate to high fecundities, delayed maturation, and long life spans. All of these traits correspond to the relative seasonal strategy derived from the present investigation. Likewise, Baltz's second group of medium-sized surfperches with low fecundity and delayed maturation mirror many characteristics of the equilibrium strategy among neotropical fishes. Moreover, the traits associated with this third group of ten small surfperches (i.e., short-lived, rapidly-maturing, variable clutches) agree well with the suite of traits describing the opportunistic strategy. Baltz (1984) also discussed a trend of higher fecundity in association with more seasonal environments. A general hypothesis of life history evolution in response to environmentally-induced variation in resource availability, predation pressure, and physiological stress emerges from the two independent analyses.

If selection derived from environmental variation is ultimately responsible for the evolution of life history traits (Stearns 1976, 1977; Southwood 1977, 1988), why do all species at a given site not respond in a similar manner? For example, Caño Maraca and C. Volcán are highly seasonal environments, but only 69% of their resident fishes were identified as relative seasonal-strategists, the remainder being either opportunistic- or equilibrium-strategists. Similarly, Kramer (1977) and DeSilva et al. (1985) found both seasonally and continuously-reproducing ostariophysan fishes syntopic in small rainforest streams. The solution probably lies in the relationship between trophic ecology and variation in resource abundance and predation pressure. Most seasonal-strategists at the two sites were omnivorous and insectivorous fishes. The availability of food resources, both aquatic and terrestrially-based, is strongly influenced by seasonal rainfall (Winemiller 1987). Opportunistic-strategists were primarily small fishes with comparatively broad diets and subject to intense predation. *Roeboides dayi*, a facultative scale predator, was a partial exception. *Roeboides* switched from preying primarily upon aquatic insects during the productive rainy season, to a diet comprised mostly of scales during the transition period preceding peak dry conditions. Many of the equilibrium-strategists at both sites were benthic omnivores and piscivores. Relative to other trophic guilds, the density of adult food resources is less variable with season for these species. The period of peak food availability for many adult piscivores (transition season) did not correspond with the period of highest food availability for juveniles (wet season). With adult food resources available for gamete production, equilibrium-strategists probably produced limited numbers of offspring during the dry season via brood protection. Reduction in the overall number of breeding fishes during the dry season might also reduce potential inter-brood competition for limited larval food resources.

Information on fish species distributions within Represa Las Majaguas was used for an additional test of the hypothesis that the seasonal and opportunistic strategies are more adaptive than the equilibrium strategy in periodically-variable environments. The main body of the lake provides

fishes with a stable habitat compared to the shallow coves below the inflow canals that raise the lake's water level during the rainy season. For those species for which I did not have data from Caño Maraca or C. Volcán ($N=15$), a relative life history strategy was assigned based on published information on reproductive behavior of the species and strategies exhibited by closely related species from Appendix 1. For example, all cichlids were assumed to adopt a relative equilibrium strategy, since all are known to exhibit brood protection, relatively large oocytes, et cetera. The life history strategies assigned to each species are presented in Appendix 2. I documented 15 relative equilibrium-strategists, four opportunistic-strategists, and nine seasonal-strategists from the stable lentic region of Las Majaguas. Four equilibrium-, four opportunistic-, and 17 seasonal-strategists were collected from the seasonally-variable canal region of the lake. Caño Maraca, another highly seasonal environment, had 13 equilibrium-, 9 opportunistic-, and 44 seasonal-strategists (Appendix 1). Chi Square analysis indicated a significant association between reproductive strategy and habitat for a 3×3 matrix ($\chi^2 = 16.3$, 4 *df*, $P < 0.001$) and a 3×2 matrix when opportunistic and seasonal strategies were combined ($\chi^2 = 15.6$, 2 *df*, $P < 0.001$). All four of the opportunistic-strategists collected from the lentic body of Las Majaguas were taken from shallow, gently-sloping littoral zones where small, less predictable fluctuations in lake level might be expected to yield relatively large-scale habitat alterations.

Phylogenetic and allometric constraints

Patterns of covariation within the PCA and the hypothesized reproductive strategy affiliations of fishes were influenced by both body length (this being interpreted as an index of size) and phylogeny, particularly at the ordinal level (Table 4). If life history traits represent adaptations, and hence are derived from natural selection, the isolation of a phylogenetic component should not be surprising. Patterns of covariation among life history characters are generally clearer when comparisons are made at higher taxonomic levels (e.g. Itô 1978; Stearns 1983a; Dunham and Miles 1985; Gittleman 1986; Dunham et al. 1987) than at lower levels (e.g. Stearns 1983b). This observation is consistent with the view that life history patterns evolve in response to natural selection, and are not merely phenotypic artifacts correlated with other traits of the organism. Given the appropriate selective regime, members of widely different taxa sometimes exhibit subsequent convergence in life history characters (Tinkle et al. 1970; Stearns 1983a; Dunham et al. 1987). The diverse characiform fishes provide excellent examples of life history character divergence. The order Characiformes exhibits morphological and ecological divergence to a degree that is perhaps unrivalled by any other animal order (Gery 1977). Characiforms spanned the entire spectrum of observed reproductive patterns. Obviously, this phenotypic variation represents evolutionary divergence from an ancestral protocharaciform that exhibited a more limited suite of life history traits. Early protocharaciforms could have been relative equilibrium-strategists, akin to *Hoplias malabaricus* which possesses morphological characters considered primitive for the order. Or perhaps they were seasonal-strategists, as most species of the superorder Ostariophysi appear to be. Either way, given sufficient evolutionary time (estimated to be 100–175 mil-

lion yrs. for characiforms, Fink and Fink 1981), a striking diversity of traits has evolved from what was certainly a more restricted suite of characteristics. If congeners among early protocharaciforms had been compared with one another relative to more distant taxa, phylogenetic design constraints might have been inferred. On a proximate scale, there is every reason to expect that phylogenetic design constraints are real (Harvey and Mace 1982; Dunham and Miles 1985; Gittleman 1986). For precisely this reason, comparisons among distant taxa should serve as more appropriate guides for general theories of life history evolution than intraspecific comparisons. According to Stearns (1983a), "although the comparative method may not be a sharp tool, it can be a strong one with broader scope of application than other methods. It certainly leads to a higher level of generalization, and to a broader perspective on what causes patterns than does the strictly experimental method..."

Body size is both constrained and influenced by evolution of other life history variables. For example, Roff (1984, 1986) explained over 60% of the variation in age of maturation for 30 teleost fishes by incorporating growth functions and a standard assumption for a positive size-fecundity relationship into the model. In the present study, body length was positively correlated with fecundity, both among and within higher fish taxa. Logically, a fish must live long enough and assimilate enough resources in order to achieve a large clutch size. Consequently, a small clutch can be viewed as a logical consequence of small adult body size in many instances (e.g. *Poecilia reticulata*, *Rachovia maculipinnis*, *Creagrutus* sp.). Obviously, larger organisms have greater potential to produce larger clutches (e.g. *Prochilodus mariae*, *Brycon whitei*, *Rhamdia* spp.). Yet based on interspecific comparisons of diverse fishes, high fecundity does not seem to be a necessary consequence of large adult body size (e.g. *Hypostomus argus* and *Potamotrygon orbignyi*, two of the largest fishes in the analysis had average clutches of only 289 and 2 respectively).

Conclusions

Neotropical fishes inhabiting the same highly-seasonal environments exhibit a variety of different life history patterns. Multivariate life history patterns of individual species spanned a two-dimensional continuum bounded by three basic suites of characteristics. A so-called equilibrium strategy was associated with sedentary local populations, relatively stable adult food resources, prolonged breeding seasons, and parental investment in individual offspring, which probably results in enhanced juvenile survivorship and reduced fluctuations in local population density. An opportunistic strategy was characterized by rapid recolonization of disturbed habitats by small, rapidly maturing, multiple spawning fishes. Most fishes in the llanos appeared to be associated with a seasonal life history strategy that exploits an annual expansion of aquatic and community production. In the extreme case, the seasonal strategy was characterized by large adult size, high fecundity, absence of parental care, and long-distance spawning migrations to productive, wet season floodplains.

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Appendix 1. Data matrix of life history attributes for fishes from Caño Maraca and C. Volcan

Species	Fluct.	Dry distr.	Wet distr.	Gen-erat.	Season	Bouts	Fecundity	Egg dia.	Par. care	Length	N	Sites*	Strategy
order Myliobatiformes													
family Potamotrygonidae													
1. <i>Potamotrygon orbignyi</i>	0.46	3	3	43	11	1	2	35.00	8	450	2	4	Equilibrium
order Characiformes													
family Erythrinidae													
2. <i>Hoplias malabaricus</i>	0.63	2	1	12	5–7	4+	2462	2.00	2	352	521	3	Equilibrium
3. <i>Hoplerthrinus umitaeniatus</i>	1.78	3	1	12	2	1+	6024	1.50	2	213	13	1	Seasonal
family Lebiasinidae													
4. <i>Characidium sp.</i>	1.16	3	2	11	4	2	154	0.65	1	28	234	1	Seasonal
5. <i>Lebiasina erythrinoides</i>	0.46	3	1	12	2	2	2688	1.30	1	121	332	2	Seasonal
6. <i>Pyrrhulina lugubris</i>	1.27	3	2	12	3	2	82	1.00	1	35	353	1	Seasonal
family Anostomidae													
7. <i>Leporinus friderici</i>	1.54	3	1	12	1–2	1	28950	1.00	1	252	71	1	Seasonal
8. <i>Schizodon isognathus</i>	1.54	3	1	12	1–2	1	28950	1.00	1	255	91	1	Seasonal
family Prochilodontidae													
9. <i>Prochilodus mariae</i>	0.91	3	1	24	1–2	1	28950	1.00	1	260	363	3	Seasonal
family Curimatidae													
10. <i>Curimata argentea</i>	1.17	3	1	12	2–3	2	3528	0.45	1	92	1671	3	Seasonal
family Characidae													
11. <i>Aphyocharax alburnus</i>	0.90	3	2	11	3	4+	617	0.65	1	37	507	1	Seasonal
12. <i>Astyanax integer</i>	1.00	3	1	12	1	2	8400	1.00	1	92	35	2	Seasonal
13. <i>Astyanax bimaculatus</i>	0.97	3	1	12	2	1+	4287	0.90	1	91	965	3	Seasonal
14. <i>Astyanax metae</i>	0.97	3	1	12	1	1+	9528	1.00	1	106	185	2	Seasonal
15. <i>Astyanax superbus</i>	1.00	3	1	12	1	2	800	0.65	1	64	10	2	Seasonal
16. <i>Brycon whitei</i>	1.00	3	1	24	1	1	171545	1.50	1	313	14	2	Seasonal
17. <i>Bryconamericus beta</i>	0.61	2	2	4	12	6+ **	796	0.95	1	44	1341	3	Opportunistic
18. <i>Bryconamericus deuterodonoides</i>	1.15	3	2	6	6	3	243	0.85	1	39	289	2	Seasonal
19. <i>Charax gibbosus</i>	1.10	3	2	6	6	4	280	1.00	1	101	324	1	Seasonal
20. <i>Cheirodontops geayi</i>	1.39	3	2	12	2	1	1108	0.75	1	28	112	1	Seasonal
21. <i>Corynopoma rüsei</i>	0.80	2	2	4	10	4+ **	135	0.85	1	43	323	2	Opportunistic
22. <i>Creagrutus sp.</i>	0.91	2	2	4	6	2	94	0.80	1	28	754	2	Opport./Seas.
23. <i>Ctenobrycon spilurus</i>	0.69	3	1	11	2–3	3	755	0.75	1	52	1530	1	Seasonal
24. <i>Gephyrocharax valenciae</i>	0.85	3	2	4	5	5+ **	734	0.75	1	37	819	3	Opport./Seas.

Appendix 1 (continued)

Species	Fluct.	Dry distr.	Wet distr.	Gen-erat.	Season	Bouts	Fecundity	Egg dia.	Par. care	Length	N	Sites*	Strategy
25. <i>Hemigrammus sp.</i>	1.23	2	2	4	7-8	4+ **	282	0.75	1	33	170	1	Opport./Seas.
26. <i>Markiana geayi</i>	1.07	3	1	12	2	1	3 398	1.00	1	94	607	1	Seasonal
27. <i>Odontostilbe pulcher</i>	1.06	3	2	4	5	3+ **	1 108	0.75	1	36	2392	1	Seasonal
28. <i>Pygocentrus notatus</i>	1.19	3	1	12	3	2	4 303	2.25	2	248	187	1	Seasonal
29. <i>Roeboides dayi</i>	0.84	2	2	3	7-12	6+ **	280	1.00	1	72	1353	3	Opportunistic
30. <i>Serrasalmus irritans</i>	1.60	3	1	12	3	3	3 048	1.50	2	147	76	1	Seasonal
31. <i>Serrasalmus medini</i>	1.92	2	1	12	3	3	3 048	1.50	2	140	68	1	Seasonal
32. <i>Serrasalmus rhombeus</i>	1.21	3	1	12	3	3	4 303	2.25	2	195	50	1	Seasonal
33. <i>Tetragonopterus argenteus</i>	1.34	3	1	12	1-2	1	3 398	1.00	1	83	169	1	Seasonal
34. <i>Triporthes sp.</i> family Gasteroplecidae	1.35	3	1	12	2	1	3 175	1.80	1	120	560	1	Seasonal
35. <i>Thoracocharax stellatus</i> order Siluriformes suborder Gymnotoidei family Apterodontidae	0.89	3	1	12	2	2	755	0.80	1	42	351	1	Seasonal
36. <i>Adontosternarchus devananzi</i> family Gymnotidae	1.82	3	1	12	2	1	323	1.35	1	185	59	1	Seasonal
37. <i>Gymnotus carapo</i> family Hypopomidae	0.66	3	2	12	5	3	567	2.00	2	297	362	1	Equilibrium
38. <i>Hypopomus sp.</i> family Rhamphichthyidae	0.95	3	1	12	2	3	323	0.75	1	184	68	1	Seasonal
39. <i>Rhamphichthys marmoratus</i> family Sternopygidae	1.56	3	1	12	1	1	1 000	1.35	1	392	23	1	Seasonal
40. <i>Eigenmannia virescens</i> suborder Siluroidei family Auchenipteridae	1.44	3	1	12	2	3	323	1.35	1	172	232	1	Seasonal
41. <i>Entomocorus gameroi</i>	1.60	3	2	12	2	2+	238	0.85	1	42	56	1	Seasonal
42. <i>Parauchenipterus galeatus</i> family Aspredinidae	0.86	3	1	12	2	2	750	1.90	1	115	222	1	Seasonal
43. <i>Bunocephalus sp.</i> family Pimelodidae	0.68	3	2	12	3	4+	178	1.00	1	58	652	1	Seasonal
44. <i>Microglanis iheringi</i>	0.63	3	2	12	3	3+	649	1.10	1	38	292	1	Seasonal
45. <i>Pimelodella sp.1</i>	1.33	3	1	12	1	1	3 150	0.55	1	68	9	1	Seasonal
46. <i>Pimelodella sp.2</i>	1.57	3	1	12	2	2	4 313	0.75	1	80	301	1	Seasonal
47. <i>Pimelodella sp.3</i>	0.63	3	1	12	2	2	1 587	0.85	1	68	208	1	Seasonal
48. <i>Rhamdia sp.1</i>	0.82	3	1	12	2	1	11 200	1.10	1	134	122	1	Seasonal
49. <i>Rhamdia sp.2</i> family Ageneiosidae	0.99	3	1	12	2	1	11 585	1.05	1	200	36	2	Seasonal
50. <i>Ageneiosus vittatus</i> family Trichomycteridae	2.17	3	1	12	1	1	750	1.90	1	130	19	1	Seasonal
51. <i>Ochmacanthus alternus</i> family Callichthyidae	0.83	3	2	12	3	2+	238	0.75	1	38	454	1	Seasonal
52. <i>Corydoras aeneus</i>	1.27	3	2	12	2	1+	152	1.45	2	44	281	1	Seasonal
53. <i>Corydoras septentrionalis</i>	0.93	3	2	12	2	3+	143	1.25	2	56	210	1	Seasonal
54. <i>Corydoras habrosus</i>	0.86	3	2	12	2-4	3+	12	0.70	2	25	477	1	Seasonal
55. <i>Hoplosternum littorale</i> family Loricariidae	0.83	3	2	12	2	2+	2 684	2.00	4	218	138	1	Equilibrium
56. <i>Ancistrus sp.</i>	0.65	2	2	12	4-5	4+	48	4.00	4	68	174	3	Equilibrium
57. <i>Hypoptopoma sp.</i>	1.08	3	2	12	2	4+	52	1.6	1	60	43	1	Seasonal
58. <i>Hypostomus argus</i>	0.40	2	1	12	3-4	3+	289	3.25	4	190	230	3	Equilibrium
59. <i>Loricarichthys typus</i>	0.85	2	1	12	3-4	5+	421	3.05	4	224	233	1	Equilibrium
60. <i>Otocinclus sp.</i>	0.88	2	1	8	4	4	52	0.90	1	26	395	1	Seasonal
61. <i>Pterygoplichthys multiradiatus</i>	0.87	3	2	12	3	3+	763	3.50	4	233	138	1	Equilibrium
62. <i>Rineloricaria caracasensis</i> order Cyprinodontiformes family Cyprinodontidae	0.62	3	1	12	5	3+	255	1.70	2	113	328	1	Equilibrium
63. <i>Pterolebias hoignei</i>	1.97	0	2	1	4-5	12+ **	8	1.30	1	33	2	1	Opportunistic
64. <i>Rachovia maculipinnis</i> family Poeciliidae	1.97	0	2	1	5	12+ **	8	1.35	1	32	126	1	Opportunistic

Appendix 1 (continued)

Species	Fluct.	Dry distr.	Wet distr.	Generat.	Season	Bouts	Fecundity	Egg dia.	Par. care	Length	N	Sites*	Strategy
65. <i>Poecilia reticulata</i> order Perciformes family Cichlidae	0.97	3	3	2	12	4+	19	1.90	4	26	1489	3	Opportunistic
66. <i>Aequidens pulcher</i>	0.55	2	1	8	9–10	3+	871	1.75	6	89	1012	3	Equilibrium
67. <i>Apistogramma hoignei</i>	0.95	2	2	4	6–12	2	59	0.65	4	30	220	1	Opportunistic
68. <i>Astronotus ocellatus</i>	1.04	2	1	14	6	3+	2301	2.40	7	181	106	1	Equilibrium
69. <i>Caquetaia kraussii</i>	0.74	2	1	8	11–12	3+	3702	1.85	6	230	550	1	Equilibrium
70. <i>Cichlasoma orinocense</i>	0.51	2	1	12	6	2+	1287	1.85	6	112	301	1	Equilibrium
71. <i>Crenicichla geayi</i> order Synbranchiformes family Synbranchidae	0.54	2	2	12	6	2+	230	1.80	6	100	106	2	Equilibrium
72. <i>Synbranchus marmoratus</i>	1.08	2	1	12	5	2+	150	1.50	2	330	75	3	Equilibrium

The reproductive strategy assigned to each species for the Chi Square analysis appears in the last column. (* 1=Caño Maraca, 2=C. Volcan, 3=both, 4=collected from other sites in the llanos; ** conservatively estimated from distributions of oocyte size classes and duration of breeding season – actual value is probably many times higher – some species may even spawn daily)

Appendix 2. Reproductive strategies assigned to species inhabiting lentic and lotic habitats at represa Las Majaguas

Species	Lentic	Lotic	Species	Lentic	Lotic
family Potamotrygonidae			<i>Serrasalmus irritans</i>		Seasonal
<i>Potamotrygon orbignyi</i>	Equilibrium	Equilibrium	<i>Serrasalmus rhombeus</i>	Seasonal	Seasonal
family Erythrinidae			family Auchenipteridae		
<i>Hoplias malabaricus</i>	Equilibrium		<i>Parauchenipterus galeatus</i>		Seasonal
family Lebiasinidae			family Pimelodidae		
<i>Pyrrhulina lugubris</i>	Seasonal*	Seasonal	<i>Pseudoplatystoma fasciatum</i>	Seasonal	Seasonal
family Prochilodontidae			family Loricariidae		
<i>Prochilodus mariae</i>	Seasonal	Seasonal	<i>Hypostomus argus</i>	Equilibrium	Equilibrium
family Anostomidae			<i>Loricaria sp.</i>		Equilibrium
<i>Leporinus friderici</i>		Seasonal	<i>Rineloricaria caracasensis</i>		Seasonal
<i>Schizodon isognathus</i>		Seasonal	family Poeciliidae		
family Characidae			<i>Poecilia reticulata</i>	Opportunistic*	Opportunistic
<i>Astyanax bimaculatus</i>	Seasonal*	Seasonal	family Cichlidae		
<i>Astyanax sp.</i>		Seasonal	<i>Aequidens diadema</i>	Equilibrium	
<i>Bryconamericus beta</i>		Opportunistic	<i>Astonotus ocellatus</i>	Equilibrium	
<i>Bryconamericus deuterodontonoides</i>		Seasonal	<i>Caquetaia kraussii</i>	Equilibrium	Equilibrium
<i>Bryconamericus sp.</i>		Seasonal	<i>Cichla ocellaris</i>	Equilibrium	
<i>Colossoma macropomum</i>	Seasonal	Seasonal	<i>Cichla temensis</i>	Equilibrium	
<i>Creagrutus sp. cf. beni</i>		Seasonal	<i>Cichlasoma orinocense</i>	Equilibrium	
<i>Gephyrocharax valenciae</i>		Opportunistic	<i>Cichlasoma psittacum</i>	Equilibrium	
<i>Hemigrammus marginatus</i>	Opportunistic*		<i>Cichlasoma severum</i>	Equilibrium	
<i>Hemigrammus sp.</i>	Opportunistic*		<i>Crenicichla geayi</i>	Equilibrium	
<i>Metynnis sp. cf. orinocense</i>	Seasonal		<i>Crenicichla lugubris</i>	Equilibrium	
<i>Paragoniates alburnus</i>		Seasonal	<i>Geophagus jurupari</i>	Equilibrium	
<i>Pygocentrus notatus</i>	Seasonal		<i>Geophagus surinamensis</i>	Equilibrium	
<i>Roebooides dayi</i>	Opportunistic*	Opportunistic	family Synbranchidae		
			<i>Synbranchus marmoratus</i>	Seasonal	Seasonal

* inhabiting shallow shoreline habitats only