

Microgeographic diversity in the neotropical knife-fish *Eigenmannia macrops* (Gymnotiformes, Sternopygidae)

John G. Lundberg & J. Curt Stager

Department of Zoology, Duke University, Durham, NC 27706, U.S.A.

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Synopsis

Examination of 681 individuals of electric knife-fishes, *Eigenmannia macrops*, from the Orinoco River, Venezuela, revealed a pattern of morphological diversity which covaried with habitat. Fishes from the caños (small stream tributaries) are on average smaller than those from offshore habitats and lagoons. Even at the same body size the tails of caño fishes are relatively shorter, their bodies are deeper, and their heads are relatively wider than those from other habitats. Caño fishes are more different from fishes of the deep channels than from those of the shallow channels, beaches, or lagoons. Several factors are examined for their possible relationship to the origin of the observed diversity including electrophysiology, locomotory adaptation, growth rate and ecology. The problems of genetic versus physiological bases of morphological variation are addressed.

Introduction

Our concepts of evolutionary mechanisms are influenced by known or assumed patterns of diversity at all taxonomic levels (Eldredge & Cracraft 1981, Chernoff 1982). In the course of studying the great diversity of neotropical fishes ichthyologists have focused on interspecific and intergeneric patterns of morphological variation. Because material is often limited, study of microgeographic variation in neotropical fishes has hardly begun. However, it is especially at this level that models of ecophenotypic response, ecotypic divergence and speciation can be developed.

Large collections of fishes were made during two expeditions to the Orinoco River Delta, Venezuela, from the R/V EASTWARD, from smaller craft, and from shore. Use of trawls for sampling in the poorly explored river channels revealed the

unexpected presence of many species of gymnotiform fishes and catfishes. Among many interesting discoveries was the observation of marked variation in size and form in the sternopygid fishes identified as *Eigenmannia macrops* (Boulenger) (Fig. 1).

Despite many taxonomic uncertainties in the gymnotiform fishes, *Eigenmannia macrops* is readily distinguished from its Orinocan congeners, *E. virescens* and *E. limbatus*, by meristic, mensural and coloration characters (Mago Leccia 1978). This diversity within *E. macrops* appeared upon first impression to covary with habitat, and thus to exhibit a clustered pattern. The extent of this variation is, however, much less than that between well established species. In addition the existence of fish with intermediate morphology did not suggest that more than one species was involved. This study describes the patterns of local morphological varia-

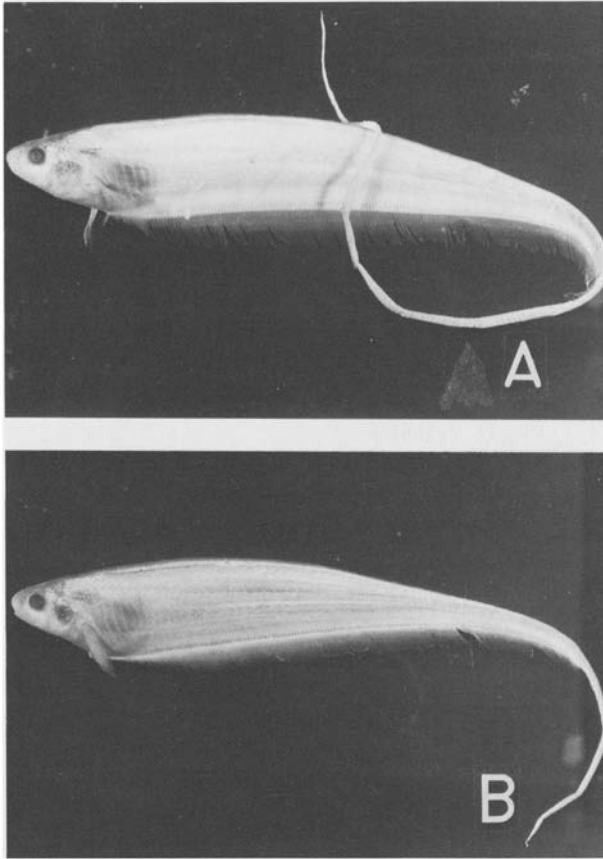


Fig. 1. A-*Eigenmannia macrops*, 123 mm LEA, from 10 m deep river channel of Orinoco River, Venezuela, about 182 nm upstream from sea buoy. B-*E. macrops*, 108 mm LEA, from small caño less than 2 m deep near Curiapo, Venezuela, ~59 nm upstream from Orinoco river sea buoy.

tion in *E. macrops* and discusses the factors that might have led to this diversity.

Materials and methods

All specimens used in this study were collected during the R/V EASTWARD expeditions to the Orinoco River Delta, February 6–27, 1978 and November 3–23, 1979. The Orinoco River oscillates in level and discharge through the annual cycle of wet and dry seasons in northern South America. The 1978 expedition took place during the dry season when the river was relatively low. The 1979

expedition took place at the close of the rainy season when water level was beginning to fall from its seasonal maximum.

Collections were taken from the mouth of the river to well above 200 miles upstream. Offshore stations in the main stem and the larger tributaries were collected from R/V EASTWARD with 3 and 9 m trawls, usually lined with fine mesh seine material or plastic fly screen. Nearshore stations were sampled with seines, ichthyocides and dip nets, and a 3 m trawl towed from a dugout canoe (Lopez et al. 1984).

The material described in this paper is housed in the following museums: National Museum of Natural History, Los Angeles County Museum, Field Museum of Natural History, American Museum of Natural History, University of Michigan Museum of Zoology, Academy of Natural Sciences Philadelphia, California Academy of Sciences, and Universidad Central de Venezuela.

A total of 103 lots of *E. macrops* were collected, consisting of 948 individuals. Each sample was assigned to one of five habitat classes: deep channel (mid-river, 10 to 40 m depth); shallow channel (nearshore, 2 to 10 m depth); beach (along shore, up to 2 m depth); lagoon (bodies of standing water one to several acres in area cut off from or narrowly connected to the river, 1 to 10 m depth); caño (small tributary streams up to 2 m in depth and less than 10 m in width, and which may include adjacent swamps).

Measurements were made on 681 fish from 75 lots. Seven characters were selected for morphometric analysis: length to end of anal fin (LEA), tail length (TAIL), maximum body depth (BODYD), head length (HEADL), interorbital distance (INTORB), eye diameter (EYED), and number of anal fin rays (ARAYS). Because tail damage is common in gymnotiform fishes, presumably due to predation and damage during collection and handling, only specimens judged to have complete tails were used for TAIL measurements. Beyond obvious sharp truncations, partially regenerated tails can be detected externally by abrupt changes in width and often color.

The composite measure $(LEA \times INTORB \times BODYD)^{0.33}$ incorporates variation along the three

major body axes and was used to test (Duncan's multiple range test) for differences in overall body size among fish samples from different habitats. Because LEA scales isometrically with the composite measure, it alone is a reasonable body size measure, and its use in shape analysis allows IN-TORB and BODYD to be examined as separate shape variables. Accordingly, allometries between the metric characters and LEA were determined and, with LEA as the covariate, proportional differences among fish from the five habitats were examined using analyses of covariance followed by significance tests of the adjusted (least squares) character means. Also, we report the results of a principal component analysis performed on the covariance matrix of the log transformed metric characters. Computations were made with the SAS GLM and PRINCOMP procedures (SAS Institute, Inc. 1982).

Results

Eigenmannia macrops was well represented in the

collections from 40 to 200 nautical miles (nm) above the mouth of the river (Table 1). Despite comparable, intensive collecting efforts in the deep channels in both years, *E. macrops* was abundant in the deep channels during the dry season of 1978, but was absent from all but one of the deep channel stations in the high water season of 1979. In 1978 only three shallow channel collections were made; of these, only one contained *E. macrops*. All other shallow channel collections were made in 1979, these yielding 71% of all *E. macrops* taken in that year.

Analysis of variance revealed significant body size differences between the 1978 and 1979 caño habitat samples ($P < 0.025$). Seasonal body size differences within the other habitat types were not significant, although in every case the 1978 (low water) sample means were larger than those of 1979. Among habitats, fishes from the channels were on average the largest and those from the caño were smallest (Table 2) but there is much overlap in size frequency distributions.

Four metric characters have negative allometric relationships with LEA; the slopes (allometric co-

Table 1. Distribution and abundance of *Eigenmannia macrops* in the 1978 and 1979 Orinoco River collections. Counts of individuals are given for different habitats in 20 nautical mile intervals. The rightmost column entitled collecting effort gives the number of collecting stations with *E. macrops* present followed by the total stations for that habitat type and year.

Year	Habitat	Nautical mile \times 10											Collecting effort	
		4	6	8	10	12	14	16	18	20	22	24	Total	
1978	Deep channel	9	8	17	8	10	40	10	37	.	.	.	139	28/111
	Shallow channel	3	.	.	.	3	1/3	
	Lagoon	52	.	1	.	.	.	53	2/8	
	Beach	.	.	2	2	1/26	
	Caño	.	8	.	29	.	2	34	5/20	
												231		
1979	Deep channel	1	.	.	.	2	3	3/88	
	Shallow channel	237	1	4	52	177	.	.	41	.	1	512	18/30	
	Lagoon	4	.	.	.	83	.	87	4/16	
	Beach	1	.	.	6	41	17	.	8	.	.	7	81	9/31
	Caño	20	.	9	.	.	5	34	4/24	
												717		
												Grand total = 948		

efficients) and standard errors of the pooled within group regressions of the log transformed variates are: BODYD .796 \pm .029, HEADL .752 \pm .021, INTORB .530 \pm .028, EYED .513 \pm .030. Also, the number of anal fin rays scales slightly negatively with LEA (allometric coefficient .125 \pm .023). Tail length and LEA have a nearly isometric growth relationship (allometric coefficient 1.022 \pm .088).

The results of the range tests on the adjusted means of each metric character are reported in Table 2. Significant variation among habitats was detected for each character. Four features (ARAYS, TAIL, BODYD and INTORB) have a common pattern in which fishes from the caños are distinct from fishes from other habitats. In three of these features (TAIL, BODYD and INTORB) the caño and deep river channel 'stocks' are the most different from each other, and for all of these comparisons the deep river channel, shallow river channel, lagoon and beach samples are very similar. Thus the caño fishes on average have low anal fin

ray counts, short tails, deep bodies and wide heads. Head length differences are scarcely significant. Relative eye size varies in an unusual pattern, with the caño and deep channel fishes having the largest eyes and those from the beaches having the smallest.

Figure 2 shows the ordination of 142 *E. macrops* on the first two principal components computed from the covariances among the log transformed metric characters. The pattern of differentiation is similar to that inferred from the preceding analysis, i.e., the caño fishes are distinct from all others and most different from the deep channel group. Furthermore many of the fish from the beach and lagoon samples are intermediate in the ordination between the channel samples and the caño samples. This pattern is congruent with the spatial distribution of the habitat types.

Of seven principal components computed, the first two are by far the most important as they explain 70% and 26% of the variance respectively (Table 3). PC1 is overwhelmingly a tail length fac-

Table 2. Patterns of significant differences in size and form characters among populations of *E. macrops* from different habitats: Drc-deep river channels, Src-shallow river channels, Lag-lagoons, Bea-beaches, Cañ-Caños (small streams). For SIZE the means of log (LEA \times INTORB \times BODYD)^{0.33} are reported with lines of significance at the 0.05 level as determined with Duncan's multiple range test. For all other characters least squares adjusted means are reported with lines of significance at the 0.001 level. Means not united beside an unbroken line are significantly different.

Size	Arays		Tail		Bodyd		
Drc	2.588	Lag	2.329	Drc	1.833	Cañ	3.168
Src	2.538	Drc	2.327	Src	1.800	Lag	3.148
Lag	2.523	Bea	2.325	Lag	1.766	Bea	3.144
Bea	2.509	Src	2.323	Bea	1.714	Src	3.142
Cañ	2.503	Cañ	2.303	Cañ	1.459	Drc	3.135
df	251	df	136	df	407	df	257
Intorb	Headl		Eyed				
Cañ	2.555	Cañ	2.999	Cañ	2.444		
Bea	2.525	Src	2.990	Drc	2.428		
Lag	2.522	Bea	2.989	Lag	2.414		
Src	2.519	Drc	2.989	Src	2.413		
Drc	2.512	Lag	2.980	Bea	2.397		
df	257	df	257	df	258		

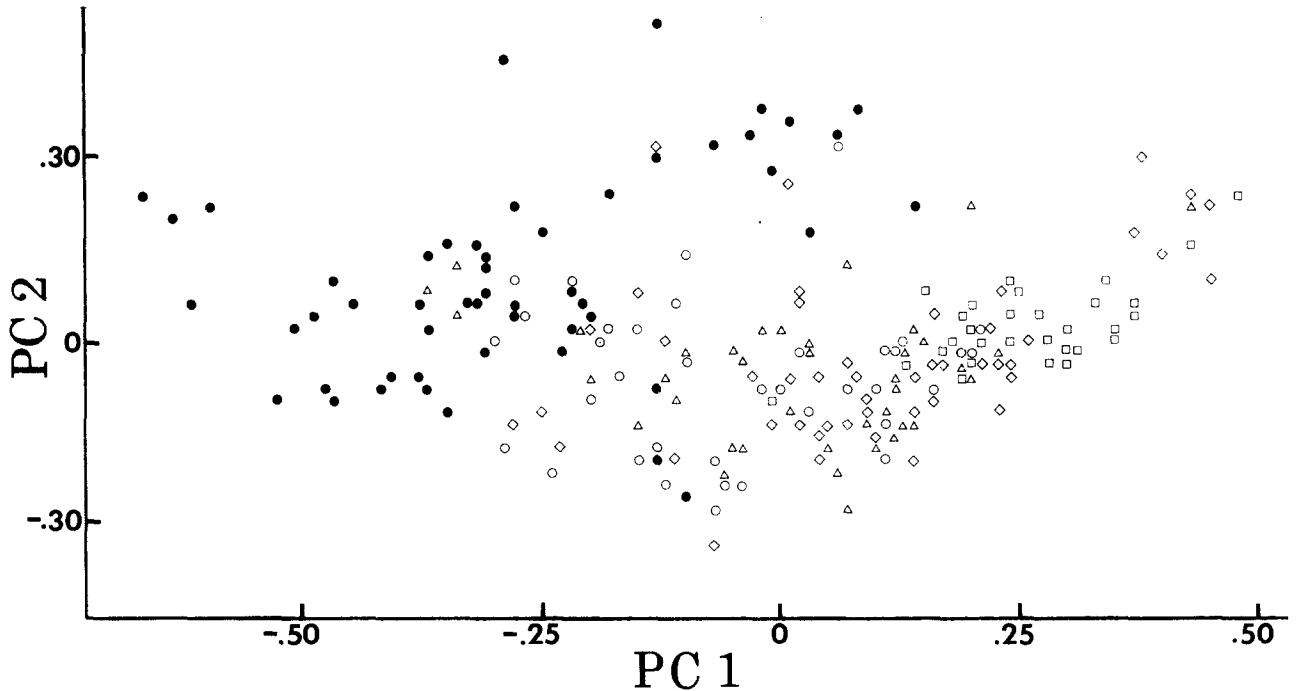


Fig. 2. Ordination of specimens on first two principal components computed from the covariance matrix of log transformed metric data. Individuals are identified by habitat as follows: deep channel = squares, shallow channel = diamonds, beach = circles, lagoon = upright, open triangles, caño = closed circles.

tor and it has low but positive loadings from the other characters (Table 3). PC2 shows the inverse relationship between tail length (with a moderately strong negative loading) and other features, especially BODYD and INTORB (with the highest positive loadings).

A preliminary idea of ration of *E. macrops* was obtained through examination of the stomach con-

tents of ten fish from different habitats, seasons, and daily time of collection. No major differences in quantity of ration were found. Nine fish contained partly digested or undigested benthic insect nymphs (especially trichopterans), ostracods and several types of copepods. One fish from a shallow channel site contained only fine sand in its stomach. There was no obvious correlation between diet and habitat in the individuals examined. The presence of slightly digested invertebrates in the guts of *E. macrops* collected between 0900 and 1500 suggests that the fish are active diurnal feeders, although most workers have found gymnotiforms to be mostly nocturnally active (Steinbach 1970, Lissmann 1961).

Discussion

There is significant microgeographic size and shape variation among adjacent populations of *Eigenmannia macrops* in the lower Orinoco basin. Dif-

Table 3. Loadings of characters on principal components 1 and 2, and variance explained by each component.

Character	Principal component 1	Principal component 2
TAIL	0.92	-0.35
LEA	0.28	0.42
BODYD	0.16	0.49
INTORB	0.03	0.47
HEADL	0.18	0.41
EYED	0.14	0.27
% Variance	70.2%	25.5%

ferences are minor among populations from the freely mixing, open water habitats (channels, beaches, and lagoons), but fish from caños have fewer anal rays, shorter tails, broader heads, deeper bodies and smaller overall size.

The question of causal process underlying the diversity of *E. macrops* remains. Local morphological variation of a species may result from genetic differentiation or from phenotypic growth responses of individuals to different conditions. The mechanisms for, and examples of, genetic differentiation among adjacent or sympatric natural populations are well documented (e.g. Antonovics 1971, Endler 1977). For fishes, factors that have been implicated in promoting such divergence include: predation and sexual selection (Hagen & McPhail 1970, Bell 1976, Endler 1983), selection favoring trophic diversity (Turner & Grosse 1980, Sage & Selander 1975) and reduced gene flow (Avisé & Smith 1974). Also, fish are capable of responding ecophenotypically in growth rates and ultimate size to many factors including temperature, photoperiod, light intensity, ration, competition and parasitism (Barlow 1961, Brett 1979). Shape differences could result from changed growth rates when there are concomitant shifts in the timing of growth curve inflections (Barlow 1961). We cannot determine whether the pattern found in *E. macrops* results from phenotypic response or genetic differentiation. Either hypothesis is plausible based on what is known about population structure and ecology of *E. macrops*.

Habitat selection is a precondition for both ecophenotypic and ecotypic models of differentiation, and for the latter assortative mating is a requirement. For the caño versus open water areas a high level of habitat selection is inferred from the significant morphometric differences, i.e., fish with morphology typical of the caño stocks are rarely found elsewhere, and vice versa. Among open water habitats there may be more movement of individual fish, and in fact it is likely that *E. macrops* move en masse out of the deep river channels in the high water season (Table 1). Migration out of the deep channels is inferred for some species of channel-dwelling knifefishes (Lopez et al. 1984, Mago et al. 1984) whereas others show less movement. As for

assortative mating or possibilities for gene flow among fish from different habitats, almost nothing is known about reproduction in *E. macrops*. We do not know if these fish spawn in their respective habitats or move elsewhere to breed. Examination of several of the larger specimens from both seasons of collection revealed only one fish (a male measuring 210 mm LEA) with well-developed gonads. Despite intensive collecting in various habitats larvae and small juveniles of *E. macrops* were not found. Recent trawl collections in the channels of Rio Apure, a major tributary of the Orinoco in central Venezuela, reveal the presence of reproductively mature gymnotiforms of many species in April and May (F. Provenzano, personal communication).

Temperature, photoperiod and light intensity are positively associated with growth rate in fish (Brett 1979), but these cannot explain diversity in *E. macrops*. The pattern of temperature variation across the habitats occupied by these fishes does not correlate with the pattern of population differentiation. Mean water temperatures in the lower Orinoco are near 28.5°C with seasonal temperature amplitude of only 2°C (William Lewis, Jr., personal communication). Surface warming is significant in open areas and may cause great daily amplitudes in shallow water habitats. Of all habitats the deep and shallow channels should be the most temperature stable. If temperature flux was a significant factor affecting the size and shape of *E. macrops* we would expect to find the lagoon and beach stocks to be more similar to the caño stocks rather than to the channel stocks. In the same way, the patterns of variation of light intensity and photoperiodicity do not correlate with morphological variation of the fish populations. There is very little light penetration into the mainstream of the Orinoco and its adjacent whitewaters from which most of our *E. macrops* come (William Lewis, Jr., personal communication). Thus, fishes inhabiting the channels live in darkness and do not perceive day length changes, but it is from the channels that the largest fishes come.

The amount of food may vary between seasons and habitats, thus causing differences in growth rates, sizes and shapes of fishes. Benthic invertebr-

ates and zooplankton (copepods, cladocera, rotifers) are abundant in shallow water habitats and are at least seasonally abundant in the Orinoco mainstream. The results of our examination of gut contents of fish from different habitats do not suggest any major difference among stocks in quantity or quality of food consumed.

Competition and parasitism are negatively associated with growth of fish. Information on intraspecific competition of *E. macrops* does not exist. Our collections suggest that this is a schooling species like most electric fishes inhabiting the river channels. Because we used different collection methods, each with indeterminate selectivity, relative stock sizes in the different habitats cannot be determined. Despite this and the unexpected rich gymnotiform fauna in the channels, overall fish biomass, numbers and diversity per unit surface area of substrate are greater in caños, beach and lagoon habitats than in the channels. If it exists, competition among generalized carnivores (including many characins, knifefishes, catfishes and cichlids) should be greater in the caños, beaches and lagoons. Direct evidence from their digestive tracts, however, shows that *E. macrops* in all habitats obtain what appear to be substantial rations.

Incidental observations of parasites in and around the viscera of fish used for stomach content analysis suggest that caño fish carry a heavier load of nematodes than channel fish. This might be an important factor in retarding the growth of caño fish, but until more is known of the biology of the parasite and host little more can be offered.

In evolutionary time predation may select for rapid growth and larger size of prey (Heyer et al. 1975; example from tropical frogs). The numbers and taxonomic composition of piscivores vary among the habitats in which *E. macrops* live but the pattern of this variation does not match that of *E. macrops*' morphology. The channel fauna is made up mostly of gymnotiforms and siluriforms with characiforms and cichlids being notably absent. The most likely predators on *E. macrops* in the channels are several species of catfishes. The piscivore assemblage in the caños, lagoons, and along the river banks is much greater in diversity and numbers of individuals. In addition to catfishes

and piscivorous electric fishes, there are predaceous characiforms and cichlids. A high incidence of tail damage in *E. macrops* from the caños and lagoons correlates with the presence of fin-biting characids, especially the piranhas *Serrasalmus* and *Pygocentrus*. This, however, does not explain why undamaged lagoonal fish are more similar morphometrically to channel fish than to caño fish.

Irrespective of the cause of the differences among the stocks of *E. macrops* there are important physiological and hydrodynamic consequences of the size and shape variations. The electric organ of *E. macrops* is longitudinally disposed along the body and throughout the tail. Thus, a number of the characters which differ among stocks are direct or indirect measures of electric organ length: TAIL, LEA, SIZE and ARAYS. The relationships among gymnotiform fish size and shape and electrosensory fields have been studied by Knudsen (1975) and Heiligenberg (1975). These workers have found that larger fish have greater effective fields for electrolocation and electrocommunication. Elongation of the tail expands the range of the electrolocation field posteriorly and deep body form enhances electrolocation. Relating these findings to *E. macrops* we see that fishes from the channels, lagoons and beaches have on average better developed electrosensory systems than caño fishes. The linear relationship between total length of fish and sensory field size determined by Knudsen (1975) is approximately $FIELD = -489 + LENGTH \times 69$. Applying this relation to mean total length to estimate the electrophysiological difference between the fish studied herein we find that relative to the caño stock those from the beach, lagoon, shallow channel and deep channel have larger fields by 1.7, 2.0, 2.1 and 2.9 times respectively. Heiligenberg's (1975) work suggests that the longer tails of channel, lagoon and beach fish further increase their powers of electrolocation. The larger electrosensory fields of *E. macrops* from open water habitats may be related, in an adaptive context, to less closely spaced landmarks (topography, debris) as compared to the caño habitat. Poll (1959a) discovered large numbers of weakly electric mormyrid species in the

channels of the Zaire River. Poll (1959b) also found that the caudal peduncle electric organs of channel mormyrids are relatively longer than those in near shore species. He suggested that this is related to schooling behavior in the channel fish and more solitary existence in the others. As far as our collections indicate, *E. macrops* appear to school in all habitats as do several other gymnotiforms that are found in both channel and marginal habitats. However, conspecifics or groups of conspecifics may be more spread out in the open water habitats, thus placing a premium on enhanced electrocommunication ability.

One of the most impressive physical differences between the channel and caño habitats involves current velocity. Current velocity in the Orinoco main stem is often about 2 m per sec. In the caño current speeds are much lower and pockets of quiet water abound. Exact geometries of current profiles along the channels have not been measured but the flow pattern is surely turbulent and, depending on substrate texture and depth, the velocity gradient over the bed may be very steep (Crickmay 1974). For example, in 30 m of water over a smooth sandy substrate, current velocity just a few centimeters above the bed will be 60% of maximum or about 1.2 m per sec. It is safe to say that channel fishes must sometimes swim faster than beach, lagoon, caño and swamp fishes in order to maintain station.

In knife-fishes such as *E. macrops* the propellor is the anal fin which is undulated to cause forward or backward swimming while the body is held straight. Recently the hydromechanical properties of the gymnotiform mode of swimming have been analyzed by Blake (1983a, b). A major conclusion of Blake's study is that undulatory anal fin propulsion has high hydromechanical efficiency at low swimming speeds. Slow swimming may well be the rule for electric fishes living in quiet, marginal habitats, but now we know that there are dense stocks of many species in river channels. Channel fish almost certainly will on occasion have to attain speeds up to 10 body lengths per second to hold their position in the current. This puts them into the performance class of carangiform-mode fishes in sprint swimming (Webb 1975). *E. macrops* from

the channels have relatively longer anal fins (ARAYS and LEA) than do caño fish, and it is conceivable that this is an adaptive modification in locomotion. It is also possible that elongation of the tail could result in additional drag and a more stable alignment of the head and body with flow lines in the current.

Of the factors we have considered, the electrophysiological and hydromechanical correlates of size and form appeal to us most as likely adaptive factors in this case of local variation. Rigorous demonstration of either is beyond the scope of our data and is perhaps unobtainable. In addition, such demonstration would not tell us if the adaptational mechanism is genetic or physiological. The best evidence to distinguish between the respective roles of environment and genotype would come from controlled breeding and rearing or transplantation experiments, but given the natural history of these fishes such work may be extremely difficult. One possibly fruitful alternative would be to elucidate interstock variation of allozymes. A pattern of allozyme variation that parallels morphological variation would support a hypothesis of genetic differentiation; failure to find such a pattern would be uninformative.

At present we are unable to offer an easy explanation of the microgeographic variation in *E. macrops*. Nevertheless, we believe that the discovery of such variation in electric knife-fishes highlights some significant questions for students of neotropical fishes. How common is localized variation among South American fishes and what are its phenotypic limits? Systematic research on the aquatic fauna at this level is almost non-existent. Recent intensive collecting programs in several areas of the American tropics are yielding better samples which will allow these questions to be addressed. The physiological-ecological versus genetical causes of such variation demand attention. Does the observed pattern of microgeographical variation in *E. macrops* represent the early stages of speciation among adjacent stocks, or simply a response to environmental conditions? If this variation has a genetic basis, it would have important evolutionary and systematic implications in that a parapatric or sympatric differentiation mechanism

might be operating. The mechanisms that produce diversity are of general interest, and a deeper understanding of them would positively influence the development of a more meaningful taxonomic framework for South American fishes at the species level.

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