

## Development of Dermal Lip Protuberances for Aquatic Surface Respiration in South American Characid Fishes

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Thirteen characid and one gasteropelecid fish species from a seasonal swamp-creek of the Venezuelan llanos exhibited dermal protuberances of the lower lip during periods of extreme oxygen depletion. Relative frequencies of protuberances showed large interspecific variation and were independent of fish size within species. Protuberances appeared in three basic forms, the most elaborate of which occurred in two *Triportheus* species. Protuberances only were present in specimens taken from waters with surface dissolved oxygen concentrations less than or equal to 1.4 ppm with corresponding bottom concentrations less than or equal to 0.8 ppm. Environmental correlates of the appearance of lip protuberances agree well with earlier findings for two Amazonian characids. All available evidence strongly suggests that dermal lip protuberances facilitate aquatic surface respiration by reducing mixing between oxygenated surface film and hypoxic water beneath during ventilation. Two other characids, *Roeboides dayi* and *Charax gibbosus*, were common during periods of extreme aquatic hypoxia, yet did not exhibit lip protuberances. Several larger, predatory characid species emigrated downstream to avoid local hypoxic conditions. Both the appearance of lip protuberances under hypoxic conditions and their reabsorption under normoxic conditions are seen as adaptive traits for surface-feeding herbivorous and omnivorous characids.

MANY South American fishes possess respiratory adaptations that permit survival in periodically-hypoxic aquatic habitats (Carter and Beadle, 1931; Kramer et al., 1978; Kramer, 1987). Dickson and Graham (1986) recently demonstrated that the Panamanian erythrinid *Hoplias microlepis* is able to survive for brief time intervals in anoxic water via anaerobic respiration. Physiological acclimation to hypoxic conditions has been demonstrated for a number of fish species, including *Hoplias malabaricus* (Rantin and Johansen, 1984) and *Colossoma macropomum* (Saint-Paul, 1984; Saint-Paul and Soares, 1987). Aerial respiration is performed by many tropical fishes using highly vascularized internal structures for gas exchange. These structures include the swimbladder, branchial chamber and gills, epithelium of the oro-pharyngeal chamber, and the gut (Johansen, 1970).

The majority of fishes living in periodically-hypoxic aquatic habitats generally do not possess adaptations for aerial respiration (Roberts, 1972; Kramer et al., 1978; Junk et al., 1983). For example, Beebe (1945) collected 34 fish species from a pool of liquid mud during the dry season in northeastern Venezuela. Of these, only nine species possessed aerial respiratory

adaptations, yet all were reported to be in good condition at the time of collection. Similarly, only 8 of 20 species collected in the hypoxic waters of the Paraguayan Chaco swamps possessed adaptations for aerial respiration (Carter and Beadle, 1931).

Aquatic surface respiration (ASR) has been suggested to be a means by which many fishes survive during prolonged periods of aquatic hypoxia (Lewis, 1970; Kramer and McClure, 1982). The use of the relatively oxygen-rich surface film under conditions of extreme oxygen depletion may be a widespread phenomenon among tropical freshwater fishes lacking auxiliary respiratory adaptations (Kramer and McClure, 1982; Kramer, 1983, 1987). In 1984, I collected fishes at frequent intervals over a 12 mo period in the Venezuelan llanos. One site in particular was characterized by periodic oxygen depletion in the aquatic environment. This paper presents evidence that 14 South American characiform fishes develop dermal lip protuberances during periods of extreme hypoxia. As has been demonstrated earlier for two Amazonian characids (Braum and Junk, 1982; Braum, 1983a, 1983b), these fleshy protuberances can appear and disappear rapidly and ap-

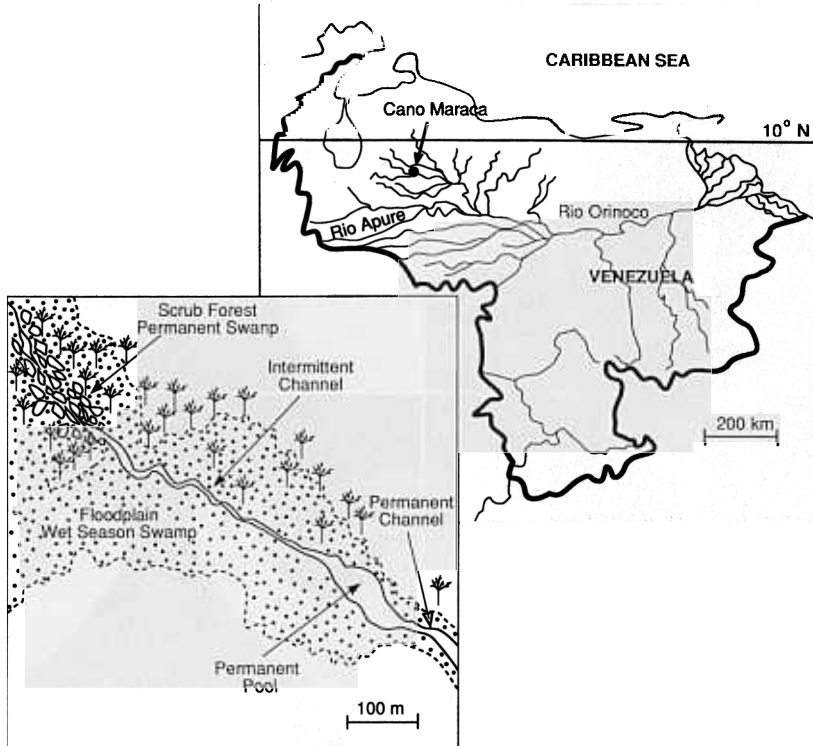


Fig. 1. Map of Venezuela showing the location of Caño Maraca within the Río Apure drainage basin and inset showing study region.

parently function to enhance ASR by shunting more of the oxygenated surface film over the gills. The structures are formed by oedema of the hypodermal skin layer. A survey of 20 other characiform and 44 non-characiform species collected at the same site over the course of a year produced no evidence of mandibular protuberances during periods of aquatic hypoxia.

*Study site.*—The investigation was made at the estero region of Caño Maraca ( $8^{\circ}52'30''\text{N}$ ;  $69^{\circ}27'40''\text{W}$ ), a small, second-order tributary of the Río Apure drainage in the state of Portuguesa, Venezuela (Fig. 1). The site is located within the western llanos, or flatlands, a region characterized by savanna habitat and remnant stands of once-dominant, deciduous forest. The soils of the region are considered the best in Venezuela, due in part to nutrients derived from Andean alluvial deposits. The region receives an average of 1300 mm of rainfall per year, with about 850 mm generally falling between June and Sept. "Esteros" are seasonally-flood-

ed, low-lying areas associated with low order creeks (caños) in the llanos. During the rainy season, esteros are extremely productive and provide important habitat for reproduction and the early life history stages of many llanos fishes (Mago, 1970; Taphorn and Lilyestrom, 1985; Winemiller, 1987a). The estero region of Caño Maraca is gradually reduced to a series of isolated muddy pools during the driest months (e.g., from January to early May). Dry season pools are blanketed by a layer of aquatic macrophytes, in which *Pistia stratiotes*, *Ludwigia helminthorrhiza*, *Salvinia auriculata*, and *S. sprucei* predominate.

#### MATERIALS AND METHODS

Fishes were collected by seine (4.5 m, 3.17 mm mesh and 17.5 m, 12.7 mm mesh), experimental gillnet, and dipnet during every month of 1984. An effort was made to obtain large samples of all species present at the site during each collecting bout (Winemiller, 1987b). I at-

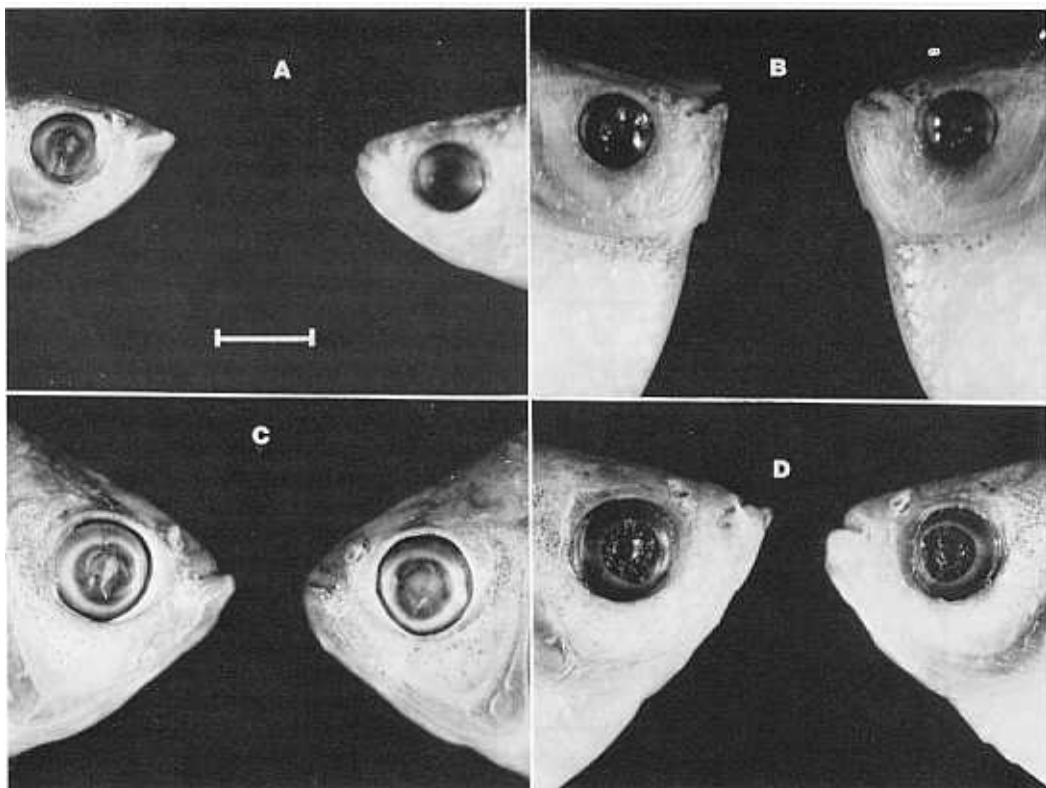


Fig. 2. Photographs of individuals exhibiting the dermal lip protuberance (left) and typical individuals (right): (A) *Gephyrocharax valenciae* (both collected Oct.; scale bar = 1.75 mm), (B) *Thoracocharax stellatus* (both Jan.; scale bar = 3.0 mm), (C) *Astyanax bimaculatus* (both Oct.; scale bar = 3.3 mm), and (D) *Triportheus* sp. (Dec.-left, Jan.-right; scale bar = 6.5 mm).

tempted to capture fishes from all available microhabitats within the estero (depths ranging from 0–1.5 m). Only data pertinent to fish respiration are presented here (for additional physico-chemical data, see Winemiller, 1987b). Fishes were preserved immediately in 15% formalin, transferred to 10% formalin within a period of 1 mo, and transferred to 45% isopropanol within a period of 1 yr. Because our current understanding of the systematics of South American fishes is incomplete, distinct forms had to be designated as “sp.” in some instances (i.e., *Hemigrammus* sp. vs *H. marginatus*). Institutional abbreviations are as listed in Leviton et al., 1985. Voucher specimens were deposited in the MCNG and the TNHC.

Afternoon water temperatures and dissolved oxygen concentrations were measured at the surface and bottom at midpool on 12 principal collection dates, occurring between the 12th and

28th of each month. I measured dissolved oxygen with a YSI oxygen meter (recalibrated several times per month) beginning in March. I determined pH with pH paper (MCB Reagents). Most fishes examined for the present study were taken from the permanent pool area depicted in Figure 1, although a few were also collected from several permanent, vegetation-choked pools of the scrub forest in the upper reaches of the estero, and a narrow channel joining the upper pools to the lower site.

Each specimen was measured for SL (nearest 0.1 mm) and examined for the presence of a dermal lip protuberance. For very small specimens (SL  $\leq$  30 mm), a dissecting microscope aided examination of the mandibular protuberance, which was classified as either typical (no evidence of a protuberance), fully developed (protuberance present in the most complete form characteristic of the species), or in-

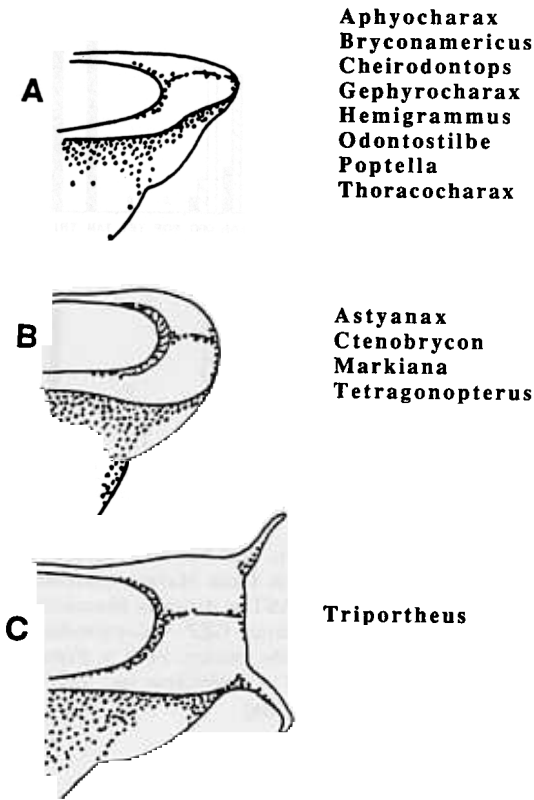


Fig. 3. Morphology of the three characteristic lip protuberances exhibited by the Characidae and Gasteropelecidae of the Venezuelan llanos: (A) corresponds to *Aphyocharax alburnus*, *Bryconamericus beta*, *Cheirodontops geayi*, *Gephyrocharax valenciae*, *Hemigrammus* sp., *Odontostilbe pulcher*, *Poptella orbicularis*, *Thoracocharax stellatus*; (B) corresponds to *Astyanax bimaculatus*, *Ctenobrycon spilurus*, *Markiana geayi*, *Tetragonopterus argenteus*; (C) corresponds to *Triportheus* sp. and *Triportheus angulatus* (see text for descriptions of each form).

intermediate (clear evidence of a protuberance, but the structure was not fully developed). Standard histological methods (Humason, 1979) were used for microscopic examination of the dermal protuberances of three species.

## RESULTS

Thirteen species of Characidae and one species from the characiform family Gasteropelecidae exhibited fleshy lip protuberances on the distal mandibulae (Fig. 2). Morphology of fully-developed lip protuberances varied according to species. The dermal lip protuber-

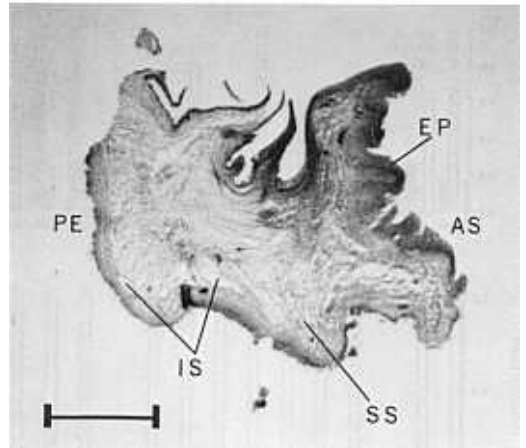


Fig. 4. Parasagittal histological section of the lip protuberance of *Triportheus* sp. (scale bar = 0.7 mm). Extensive oedema of the stratum spongiosum (SS) in the hypodermis is evident from numerous, large intercellular spaces (IS = interstitial spaces, EP = epidermis, PE = posterior edge, AS = anterior surface).

ance of smaller characids and *Thoracocharax* consisted of a soft, fleshy bulge on the distal tip of the lower jaw (Figs. 2A, B, 3A). The snouts of these fishes appear more or less rounded when viewed dorsally. *Astyanax*, *Ctenobrycon*, *Markiana*, and *Tetragonopterus* exhibited lip protuberances that were rectangular when viewed dorsally (Figs. 2C, 3B). The two *Triportheus* species possessed the most elaborate lip protuberances (Figs. 2D, 3C). The *Triportheus* lip protuberance is broadened laterally, and displays a dorso-ventrally flattened barbel on each distolateral tip. In agreement with earlier studies (Braun and Junk, 1982; Braun, 1983a), histological examinations of *Astyanax bimaculatus*, *Markiana geayi*, and *Triportheus* sp. revealed extensive oedema of the hypodermal skin layer within mandibular protuberances (Fig. 4). The absence of any unusual arrangement or density of blood vessels in protuberances supports Braun and Junk's (1982) hypothesis that dermal enlargements perform no extraordinary gas exchange function.

Occurrence of the lip protuberances in these species was limited to three collection dates: 28 Jan., 26 April, and 26 Oct. (Fig. 5). Lip protuberances only were present in fishes collected from water with dissolved oxygen concentrations less than or equal to 1.4 ppm at the surface and 0.8 ppm at the bottom (i.e., Oct.; Fig. 6). Individuals possessing typical, intermediate, and

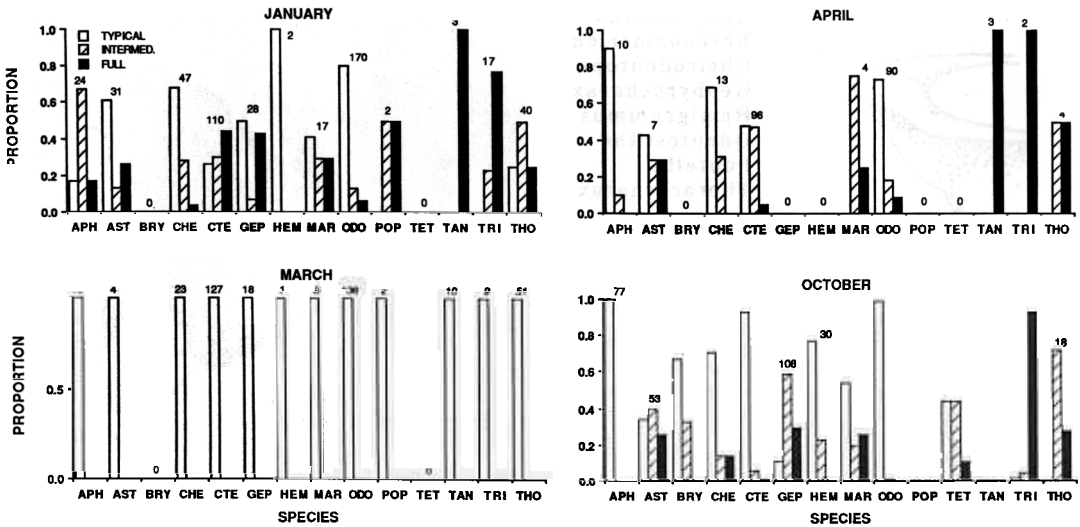


Fig. 5. Proportion of individuals of 14 species showing typical, intermediate, and full development of dermal lip protuberances during the three periods of extreme aquatic hypoxia at Caño Maraca contrasted with the March collection of moderate hypoxia (APH = *Aphyocharax alburnus*, AST = *Astyanax bimaculatus*, BRY = *Bryconamericus beta*, CHE = *Cheirodontops geayi*, CTE = *Ctenobrycon spilurus*, GEP = *Gephyrocharax valenciae*, HEM = *Hemigrammus* sp., MAR = *Markiana geayi*, ODO = *Odontostilbe pulcher*, POP = *Poptella orbicularis*, TET = *Tetragonopterus argenteus*, TAN = *Triportheus angulatus*, TRI = *Triportheus* sp., THO = *Thoracocharax stellatus*, total specimens examined appears above bar for each species).

fully-developed lip protuberances were present in each of three collections from extremely hypoxic waters (Fig. 5). The proportion of specimens exhibiting protuberance development in a sample (all 14 species combined) was inversely related to dissolved oxygen at the surface ( $r = -0.48$ ;  $F = 7.3$ ;  $DF = 1,26$ ;  $P < 0.025$ ) and near the bottom of the water column ( $r = -0.40$ ;  $F = 4.8$ ;  $DF = 1,26$ ;  $P < 0.05$ ). The incidence of lip protuberances was not significantly related to fish length in 11 of 12 within-species tests (ANOVA) containing 10 or more individuals with clear evidence of lip extension development.

No evidence of lip protuberances was observed in three other species of Characidae from the Jan., April, and Oct. collections. *Charax gibbosus* and *Roeboides dayi* were common at the site, whereas *Hemigrammus marginatus* was extremely rare. The following characid species were common in the wet season samples and emigrated downstream during the dry season (Jan.-May): *Pygocentrus notatus*, *Serrasalmus irritans*, *S. rhombeus*, *S. medini*, *Mylossoma duriventris*, and *Xenogoniates bondi*. Four other characids (*Acestrorhynchus microlepis*, *Colossoma macropomum*, *Piaractus brachyopomus*, and *Gymnocorymbus*

*thayeri*) were rare in the estero, and none were taken on the dates of severe aquatic hypoxia.

## DISCUSSION

Dermal lip protuberances in characids are clearly associated with periods of hypoxia at the estero of Caño Maraca (Figs. 5, 6). Extreme aquatic hypoxia during Oct. and probably Jan. appeared to be related to pulses of aquatic macrophyte decomposition, especially of water hyacinths (*Eichhornia diversifolia*). Water depths fell most rapidly during Jan. and Oct. relative to other months. Oxygen deficiencies in the main creek channel were probably influenced primarily by microbial respiration in the draining floodplain during Jan. and Oct. The late April sample coincided with the peak dry season in 1984. Aquatic hypoxia during April was probably derived from respiration by the macrofauna within remaining small bodies of water, in addition to benthic microbial metabolism and possibly nocturnal respiration by submerged tissues of floating macrophytes.

The dermal lip protuberance most likely serves an adaptive function during ASR, channeling the thin surface layer of oxygenated water

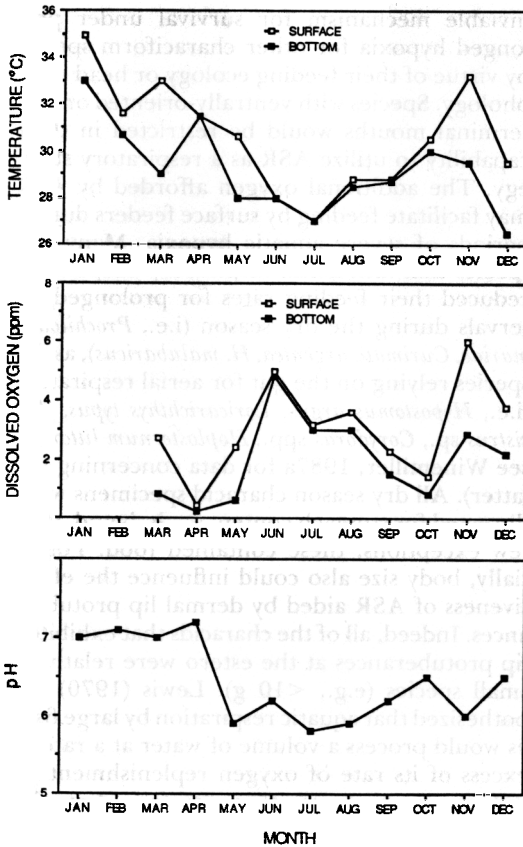


Fig. 6. Monthly temperature, dissolved oxygen, and pH levels at the estero of Caño Maraca during 1984 (all measurements were taken at the same place at approximately 1600 hr).

toward the fish's mouth while minimizing mixing with the hypoxic layer beneath. Small characids were frequently observed swimming just below the surface throughout the dry season, although no clear distinction could be made between feeding and ASR. Braum and Junk (1982) demonstrated a rapid initiation of ASR in response to hypoxia in laboratory-housed *C. macropomum* and *Brycon melanopterus*. They also observed enlargement of lower lip surface area of *Brycon* only 2–3 h following the initiation of ASR. *Colossoma* exhibited a doubling of lip surface area following 5 h of exposure to oxygen concentrations of 0.4–0.5 ppm in the laboratory. After a day of exposure to hypoxia, *Colossoma* lip extensions showed a second two-fold increase in area. Upon the reestablishment of normoxic conditions, *Colossoma* lip protuberances showed a 70% reduction after 90 min.

*Triportheus* sp. from the Venezuelan llanos also show growth and reduction of dermal lip protuberances within 24 h in aquaria (L. Nico, pers. comm.). Taken together, evidence from captive fishes and the correlation between incidence of protuberances and natural aquatic hypoxia strongly support the hypothesis that dermal lip protuberances function to enhance ASR. A similar function was suggested for the mandibular barbels of *Osteoglossum bicirrhosum* (Osteoglossidae) of the Amazon drainage (Kramer et al., 1978). Unlike the lip protuberances of characids, the mandibular barbels of *Osteoglossum* are permanent structures.

Lewis (1970) viewed the flattened heads and dorsally-oriented mouths of cyprinodontoid fishes as adaptive during ASR, noting the prevalence of these forms in many North American swamps where environmental hypoxia is common. Because characiform fishes frequently dominate the species-rich biotas of South American waters, evolutionary convergences toward the cyprinodontiform head morphology to facilitate ASR are likely offset by selective advantages afforded by interspecific morphological diversification in association with specialized feeding behavior (Winemiller, 1987b). Following this view, both the ability to rapidly generate the lip protuberance and its reabsorption would be adaptive for these fishes.

Several common characid species migrated out of the estero region during periods of severe oxygen depletion (e.g., *Pygocentrus notatus*, *Serrasalmus* spp.). Two characid species did not exhibit lip protuberances, even though they were present during one or more episodes of aquatic hypoxia (i.e., numerous *R. dayi* were collected on all three dates). Both species, *R. dayi* and *Charax gibbosus*, are laterally-compressed fishes with very narrow heads. The ratio of body mass to length of these fishes is low, and stealth is their predominant form of feeding behavior. *Roeboides*, in particular, relies upon ambush in order to dislodge scales from fishes using its external snout teeth (Sazima, 1983). A lip protuberance would likely impair this mode of feeding. *Charax* is largely piscivorous in its feeding (Winemiller, 1987b).

*Responses of other fishes to hypoxia.*—Ten additional characiform species, representing five additional families, were collected at the estero. Two of the species, *Leporinus friderici* and *Schizodon isognathus* (Anostomidae), emigrated downstream during the onset of the dry season.

*Hoplias malabaricus*, *Hoplerthrinus unitaeniatus* (Erythrinidae), *Pyrrhulina lugubris*, *Characidium* sp1, *Characidium* sp2 (Lebiasinidae), *Prochilodus mariae* (Prochilodontidae), *Curimata argentea*, and *C. cerasina* (Curimatidae) all were collected during both wet and dry seasons and exhibited no evidence of lip protuberances. The smaller species, such as *Pyrrhulina* and *Characidium* spp., were always captured at the pool margins among vegetation and probably survive in small pockets of more highly oxygenated water. Moreover, *Pyrrhulina* is ecomorphologically convergent with swamp-dwelling cyprinodontiforms discussed by Lewis (1970). Larger species, such as *Hoplias malabaricus* and *Prochilodus mariae*, are presumed to possess physiological adaptations for coping with hypoxia, because these were generally captured during the driest months at midpool, below a continuous layer of floating aquatic vegetation. Evidence of acclimation to hypoxia by *H. malabaricus* and the ability of a congener, *H. microlepis*, to respire for brief time periods anaerobically were mentioned previously (Rantin and Johansen, 1984; Dickson and Graham, 1986). *Hoplerthrinus unitaeniatus* possesses a modified swimbladder used for aerial respiration under hypoxic conditions (Carter and Beadle, 1931; Graham et al., 1978; Kramer, 1978). Immediately prior to and during the 28 Jan. collection, the estero experienced a massive fish die-off comprised of many large *Hoplias malabaricus* and a few large *Astronotus ocellatus* and *Caquetia kraussii* (Cichlidae).

The unusual lip protuberance was not observed in any of the 44 species belonging to 16 non-characiform families collected during the study. Aerial respiratory adaptations have been reported for species belonging to five of these families (Hypopomidae, Aspredinidae, Callichthyidae, Loricariidae, Synbranchidae; Kramer et al., 1978). Three species from two families (Poeciliidae, Cyprinodontidae) possess a morphology which was reported to preadapt members of the order (Cyprinodontiformes) for effective utilization of the thin surface layer of oxygen-rich water (Lewis, 1970; Kramer and Mehegan, 1981). The remaining nine families represented at the site were as follows: Apterontidae (2 spp.), Gymnotidae (1 sp.), Rhamphichthyidae (1 sp.), Sternopygidae (2 spp.), Ageneiosidae (1 sp.), Auchenipteridae (2 spp.), Pimelodidae (7 spp.), Trichomycteridae (1 sp.), and Cichlidae (7 spp.).

*Potential limitations of lip protuberance for ASR.*— Use of lip protuberances for ASR may be an

inviolate mechanism for survival under prolonged hypoxia for other characiform species by virtue of their feeding ecology or head morphology. Species with ventrally-oriented or sub-terminal mouths would be restricted in their capability to utilize ASR as a respiratory strategy. The additional oxygen afforded by ASR may facilitate feeding by surface feeders during periods of severe aquatic hypoxia. Many fish species that lack aerial respiratory adaptations reduced their feeding rates for prolonged intervals during the dry season (i.e., *Prochilodus mariae*, *Curimata argentea*, *H. malabaricus*), as did species relying on the gut for aerial respiration (i.e., *Hypostomus argus*, *Loricarichthys tybus*, *Ancistrus* sp., *Corydoras* spp., *Hoplosternum littorale*, see Winemiller, 1987a for data concerning the latter). All dry season characid specimens were dissected for stomach content analysis and, with few exceptions, these contained food. Potentially, body size also could influence the effectiveness of ASR aided by dermal lip protuberances. Indeed, all of the characids that exhibited lip protuberances at the estero were relatively small species (e.g., <10 g). Lewis (1970) hypothesized that aquatic respiration by large fishes would process a volume of water at a rate in excess of its rate of oxygen replenishment by diffusion at the air/water interface. Yet, the first published reports of dermal lip protuberances deal with two large herbivorous characid species. Machado-Allison (1982) reported dermal lip protuberances in juveniles of the cachama, *Colossoma macropomum* from Venezuela. He suggested that the structures functioned as shunts during midwater plankton feeding and were lost in adult size classes. Yet, as previously noted, investigators working in the central Amazon region presented convincing evidence that dermal lip protuberances in *C. macropomum* and *B. melanopteron* develop in response to aquatic hypoxia and serve to enhance ASR (Braun and Junk, 1982; Braun, 1983a, 1983b). Fish culturists in the Venezuelan llanos have also reported rapid development of lip protuberances in adult *Colossoma* in association with hypoxia in ponds ([C. Olds via] L. Nico, pers. comm.).

Dissolved oxygen measurements are not available for the 28 Jan. samples that exhibited high frequencies of characid lip protuberances. The massive *Hoplias* die-off that occurred on that date was observed at no other time during the year. Consequently, one may infer that dissolved oxygen levels were less than or equal to the lowest values recorded during other months (agro-chemical contamination or excessive hy-

drogen sulfide concentrations were not suspected to be primary factors in this case, and if present, should have affected the smaller characids before the larger *Hoplias* and *Astronotus*. Dead characids were never observed during the course of the study. Given the limited environmental data available, I can only conclude that dissolved oxygen values less than or equal to 1.4 ppm are necessary for the initiation of development of the lip protuberance in the fourteen species studied.

Instances in which all individuals of a species exhibited the protuberance on a given collection date were rare (Fig. 5). This observation raises a number of questions that could be addressed by appropriately designed laboratory experiments. For example, what is the critical level of oxygen depletion required for the development of the protuberance, and is it the same for all species? Is there a synergistic effect of dissolved oxygen with other factors such as temperature, pH, H<sub>2</sub>S, or nutrition levels? Do species exhibit significant geographical variation in expression of the phenotype? What factors account for apparent variation in the responsiveness of individual fish within a population to aquatic hypoxia? The potential role of hormones or other biochemical factors in the development of lip protuberances also remains to be investigated.

With this report, at least 16 South American characiform fishes are now known to exhibit reversible lip protuberances (Braun and Junk, 1982; Braun, 1983a, 1983b). Systematists working with neotropical specimens accompanied by limited ecological data are cautioned against using the lip protuberance or other characters with large potential for showing ecophenotypic variation. For example, Braun (1983b) recently placed *Othonophanes labiatus* (Steindachner 1880) in synonymy with *Brycon cf. melanopterus* (Cope 1871) based on the discovery of the reversible lip protuberance in this species. The broad, fleshy mandibular protuberance is a principal character defining *Poecilia sulphuraria* (Alvarez), a species known only from the Río del Azufre (Sulphur River) in southern Mexico (Alvarez, 1970).

Kramer and McClure (1982) and Kramer (1987) concluded that ASR represents one mechanism by which many tropical fishes live for extended periods under hypoxic conditions. The earlier discovery of mandibular lip protuberances in two large characids and the current findings for 13 characid and one gasteropelecid species support this contention.

Development of dermal lip protuberances in these species represents a form of respiratory adaptation, joining anaerobic respiration and the list of remarkable aerial respiratory adaptations found within diverse fish taxa inhabiting periodically oxygen-deficient habitats.

#### ACKNOWLEDGMENTS

This study would not have been possible without the field assistance of D. Taphorn, L. Nico, A. Barbarino, P. Rodriguez, and N. Greig. D. Urriola was kind enough to offer permission to conduct the investigation on his ranch. F. Mago L., P. Urriola M., R. Schargel, and D. Taphorn are gratefully acknowledged for their assistance in securing visas and permits. The Dirección Administración y Desarrollo Pesquero of the Republic of Venezuela provided a collecting permit. W. G. Reeder and the Texas Memorial Museum provided assistance in the transport of preserved specimens. I am grateful to H. Y. Yan for preparation of the histological sections. I especially thank D. Taphorn for initially identifying the fishes of Caño Maraca, logistical assistance, and hospitality in Guanare. Financial support was provided by National Geographic Society grant #2765-83.

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