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# Feeding and reproductive biology of the currito, *Hoplosternum littorale*, in the Venezuelan llanos with comments on the possible function of the enlarged male pectoral spines

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## Synopsis

For one year, *Hoplosternum littorale* were sampled monthly from Cano Maraca, a seasonal swamp-creek of the western llanos of Venezuela. *H. littorale* exhibited a more or less synchronized burst of reproductive activity that coincided with the onset of the rainy season. Spawning was preceded by gradual gonadal recrudescence and a decline in visceral fat deposits during the 5 month dry season. The species is sexually dimorphic with adult males being of larger average size, attaining a larger maximum size, and possessing elongate, recurved pectoral spines and fat deposits on the pectoral fins just prior to and during the spawning season. Aquarium observations revealed that male *H. littorale* can use the enlarged pectoral spines as weapons during aggressive attacks. This form of aggressive behavior is most likely a component of the brood defense behavior of the species. Both immature and adult *H. littorale* were microphagous scavengers, taking a variety of food items from the soft mud substrate. Aquatic microcrustacea were the major item in the diet of immature fish. During the late wet and dry seasons, 61% of the stomachs sampled were empty and the intestines air- filled, indicating active use of the gut for aerial respiration.

## Introduction

Tropical freshwater habitats harbour the most diverse and productive fish communities on earth, yet relative to temperate systems, scant information is currently available concerning their ecology (for reviews see Roberts 1972, Lowe-McConnell 1975). The reproductive biology of most tropical fish species is not well documented, particularly with respect to phenology (Schwassman 1978, Lowe-McConnell 1979). Most inferences concerning freshwater fish reproductive biology in the tropics are derived from studies of species used in pond culture (e.g. *Tilapia* species, Lowe-McConnell 1959) and species inhabiting African lakes where research facilities operate (e.g. Greenwood 1974). Investigations of fish reproduction in tropical lentic systems have demonstrated breeding periodicity for several species, often in association with seasonal rainfall patterns (see Lowe-McConnell 1975, 1979 for summary). Though rare, long-term studies of reproduction by tropical fish species inhabiting relatively seasonal riverine environments have revealed diverse tactics among sympatric taxa (Welcomme 1969, Kramer 1978, De Silva et al. 1985).

I collected fishes from a seasonal swamp-creek in the Venezuelan llanos over a period of twelve months in 1984 as a part of a comparative investigation of the trophic ecology of neotropical freshwater fish communities. Despite harsh conditions during the driest months (owing primarily to dissolved oxygen depletion), 35 species were common at the site year-round. This report deals with the reproductive biology of the currito, *Hoplosternum littorale,* in a seasonal tropical environment. *H. littorale* is a member of the neotropical armoured catfish family Callichthyidae and serves as a popular food fish in the llanos. In addition to reproductive phenology, the diet, unusual sexual dimorphism of the pectoral fins, seasonal differentiation of the character, and the probable function of the enlarged male pectoral spine are documented herein.

## Methods

### *Study site*

During 1984, fish collections were made at least once per month at several locations of the estero region of Cano Maraca in the state of Portuguesa, Venezuela (8°52′30″Lat.N; 69°27′40″ Long. W). The region averages 1500 m of rainfall per year. Cano Maraca is a second-order stream of the Rio Apure-Rio Orinoco drainage system. The 'estero' region is delimited by low-lying terrain that experiences extensive sheet flooding during the wettest months (June-August). At this time, the estero is converted into a productive marsh with abundant and diverse vegetation, the dominant species being *Eichornia* spp., *Heteranthera reniforuris, Eleochoris interstincta, Paspalum repens,* and *Cyperus* sp. During the dry season (January-May), most of the estero dries up, and isolated bodies of water remain in the scrub forest region of the upper estero and main channel of the lower creek. The dry season pools were generally blanketed by a layer of aquatic vegetation dominated by *Pistia stratiotes, Ludwigia helminthorrhiza, Salvinia* spp., *Hydrocotyl ranunculoides*, and various duckweed species (Lemnaceae). The substrate of the estero and creek channel consisted of a 10–15 cm layer of soft mud and vegetative detritus over a clay foundation.

All of the *Hoplosternum* specimens used for the current report were taken from a large, permanent pool at the lower region of the estero. Figure 1 presents physiochemical data collected at this site. All measurements were made between 1500 and 1700 h between the 22nd and 28th day of each month (except for December when the sample date was the 12th). Dissolved oxygen was determined with a YSI oxygen meter, recalibrated prior to each sampling session. pH was determined with pH paper (MCB Reagents). Dissolved oxygen values are missing for January and February because a functional oxygen probe was not available. All measurements were made at midpool in the deepest region. The measurements obtained from this pool are representative of values from two other locations sampled within the estero.

### *Data collection*

Fishes were collected by seine (3.2, 12.7 mm mesh), and dipnet and preserved immediately in 15% formalin. Within one month, the specimens were transferred to 10% formalin and later to 45% isopropanol. Each *H. littorale* specimen was measured for standard length, dissected, and the entire gut was removed. Contents from the anterior half of the gut were examined under a dissecting microscope, and sorted by functional category. The volume of each category was determined by immersion in graduated cylinders of various sizes. For volumes less than 0.005 ml, a value was estimated by spreading the item on a glass slide and comparing it to a similarly spread substance known to equal 0.005 ml.

The condition of the gonad was coded for each specimen based on size and color, using the following categories; clear = 1, translucent = 2, opaque = 3, small = 1, medium/small = 2, medium = 3, medium/large = 4, large = 5. The gonad code for each individual was equal to (color code + size code) ÷ 2 and values ranged from 1 to 4. The same criteria were used in coding male and female gonads while taking into account intersex differences in the size, color, and texture of the fully mature gonads. The fat content of the body cavity was coded using the following criteria: 1 = none, 1.5 = traces of fat in

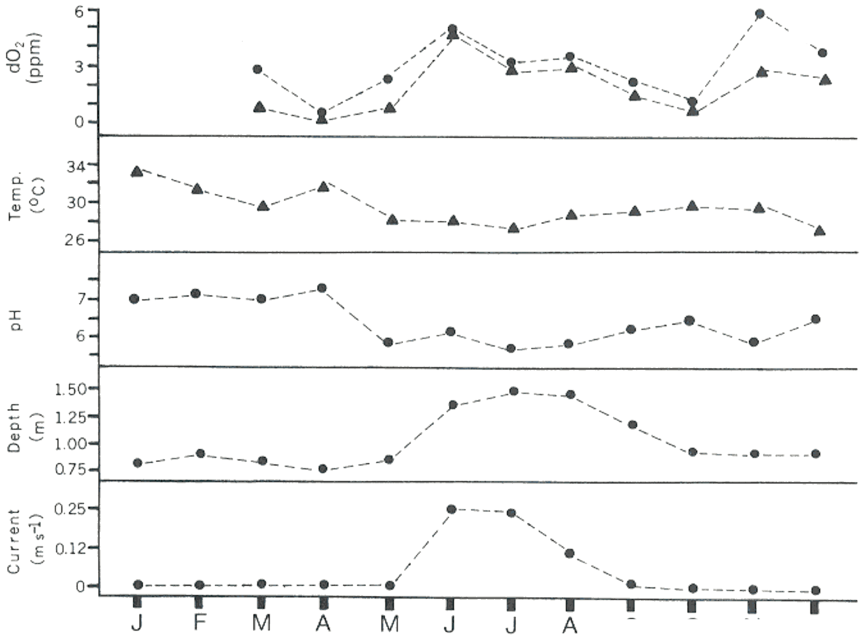


*Fig. 1.* Seasonal trends in dissolved oxygen concentration, water temperature, pH, maximum pool depth, and water current velocity measured at the pool where *Hoplosternum littorale* were collected during 1984 (circles correspond to measurements made at the surface and triangles to measurements made at the pool bottom).

the connective tissue around the viscera, 2 = small amounts around the 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 the coelomic cavity lining, but not filling the coelom, 3.5 = very large deposits filling the coelom, but not producing a visible bulge, and 4 = the coelom packed with fat deposits, producing a visible bulge of the belly region. Fecundity was estimated for 3 gravid females by removing the ovaries from each, counting the number of mature oocytes (defined as yolk-laden oocytes having a diameter within 0.2 mm of that of the largest oocyte in the ovary) in a sample of ovarian tissue, weighing the sample, and weighing the ovary.

For selected specimens, the length of the pectoral spine was measured in a straight line from the juncture of the spine with the outer body surface to its tip. The diameter of the spine was measured at the midpoint of its length (all measurements performed with calipers to the nearest 0.01 mm). No fewer than two *H. littorale* specimens from each monthly collection were deposited in the Natural History Collection of the Texas Memorial Museum, Austin, Texas. Additional voucher specimens were deposited in the Museo de Historia Natural de UNELLEZ, Guanare, Portuguesa.

## Results

### *Breeding phenology and maturation*

*Hoplosternum littorale* were collected every month of the year except September. Most individuals were collected during the dry season (Fig. 2) when the local stock was concentrated at higher densities in drying pools. Adult size classes of *H. littorale* were not collected during the peak wet period (June–Sept., Fig. 2) when the survivors from the dry season pools were widely dispersed at low densities in the flooded estero. The initiation of reproduction by *H. littorale* coincided with the heavy rains that mark the onset of the rainy season in early June. On June 13, several nests were observed in the shallow, flooded estero region among

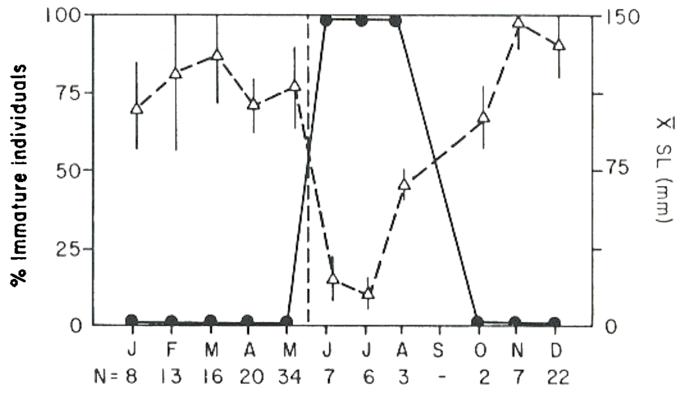


*Fig. 2.* Monthly variation in the percentage of immature to total individuals (●), and the mean standard lengths (△) of *Hoplosternum littorale* at Cano Maraca. The vertical dashed line marks the abrupt onset of the rainy season.

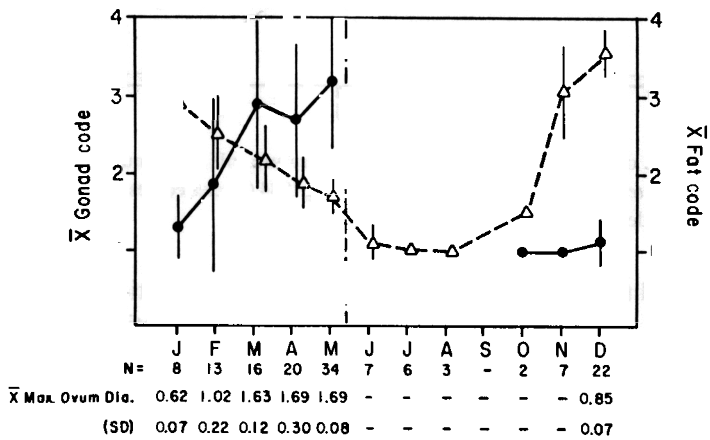


*Fig. 3.* Monthly variation in the mean gonad (●) and fat (△) codes of *Hoplosternum littorale* at Cano Maraca (data for male and female gonads combined). The mean and standard deviation of the maximum ovum diameter of gravid females for each month appear below the graph.

emergent aquatic vegetation, and free-swimming juveniles were collected on June 28. Carter & Beadle (1931) provided a detailed description of the floating mats of vegetation and foam that comprise the nest of *H. littorale*. Juvenile *H. littorale* were always collected in shallow marginal regions of the estero among lush aquatic vegetation where microcrustacea were abundant. On two occasions, the juveniles were taken from small marginal pools that were temporarily isolated from the main body of water.

*H. littorale* exhibits a sexual size dimorphism. The mean standard length of mature males was 119.9 mm (SD = 31.6, N = 54) and 106.3 mm (SD = 25.2, N = 44) for mature females (t = 2.22, p<.03). The minimum length of maturation for males was 86.1 mm SL and 79.5 mm for females. The largest male collected during the study was 218.0 mm SL and the largest female was 167.0 mm.

An inverse relationship between fat deposits and gonad condition was observed (Fig. 3). The heaviest fat deposits occurred during December and January. Relative fat content fell during the dry season coincident with the progression of gonadal recrudescence. The number of mature oocytes removed from three gravid females from the May 28 collection were as follows: 4449 (female 113 mm SL), 1928 (95.2 mm), and 1675 (93.2 mm)

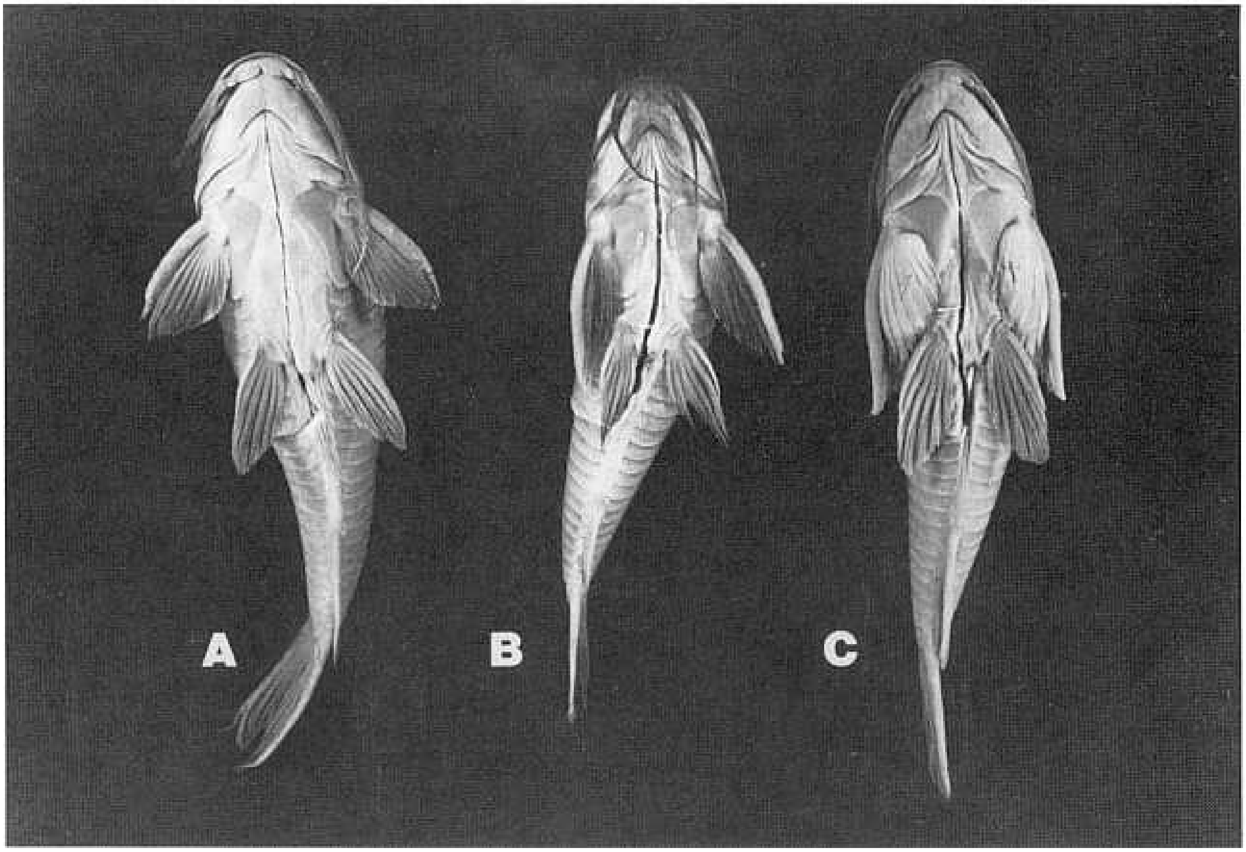


*Fig. 4.* Ventral view of *Hoplosternum littorale*: A- gravid female (SL = 113 mm), B- adult male with intermediate pectoral spine (103 mm), C- adult male with fully developed pectoral spine (111 mm). The mean ratio of pectoral spine length to standard length (measured to the nearest mm) was 0.17 (SD = 0,01, N = 13) for females, 0.19 (SD = 0,02, N = 9) for small-spined males, 0.28 (N = 1) for a medium-spined male, and 0.33 (N = 1) for a large spined male. The mean ratio for spine width to standard length was 0.15 (SD = 0.001, N = 13) for females, 0.016 (SD = 0.002, N = 9) for small-spined males, 0.018 (N = 1) for a medium-spined male, and 0.019 (N = 1) for a large-spined male.

### *Male pectoral spines*

A striking sexual dimorphism exists in the pectoral fins during the reproductive season. Males possess a lengthened and slightly thickened pectoral spine and thick adipose deposits in the soft portion of the fin (Fig. 4). The mature female pectoral fin remained unmodified from the condition present in nonreproductive adults of both sexes. Males with large pectoral spines were not collected during the nonreproductive period (Fig. 5), suggesting that the pectoral spine enlarges during gonadal recrudescence and returns to normal proportions following the reproductive season. Due to their extremely low density, large adult males were not collected during the period immediately following spawning, so it is not known whether or not males with intermediate spines were present at this time. Large adult males collected in November (SL = 115.8, 178.0 mm) and December (SL = 109.7, 132.9, 154.0 mm) had small pectoral spines.

One ripe male and one gravid female *H. littorale* were retained from the April 26 collection and placed in a 75 liter aquarium receiving natural sunlight in the laboratory. Although spawning did not occur during two months of residence in the laboratory, behavioral patterns were observed which were interpreted as components of courtship. The pair frequently hovered in midwater with the male behind the female. While following the female, the

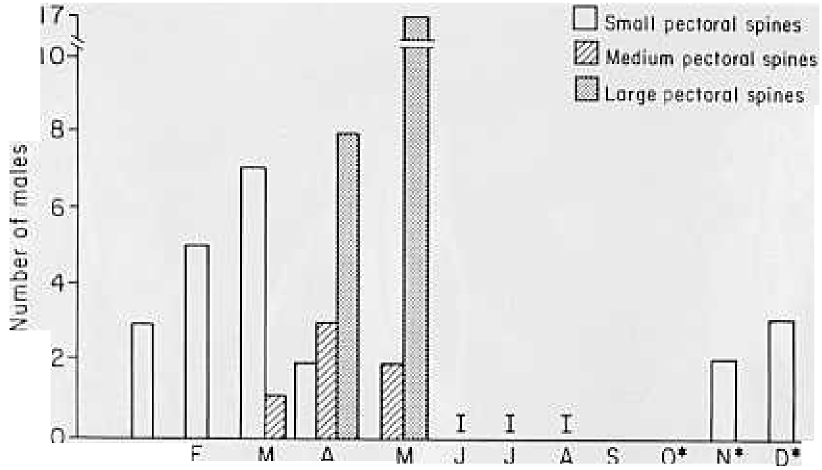


*Fig. 5.* The number of adult male *Hoplosternum littorale* with small, intermediate, and large pectoral spines from each monthly collection (I = only immature fish were collected; * = other fish of adult size were collected but the sex was undetermined).

male's snout frequently made gentle contact with the region of the urogenital pore on the venter of the female. The male frequently circled the female during these hovering bouts.

Throughout this period, which began within one week of placement into the laboratory and ended about one month thereafter, the male was intensely aggressive toward any object placed within the aquarium (hands, aquarium nets, vials, etc.). The aggressive behavior of the male was initiated by a slow approach while hovering in midwater. During the approach, the dorsal and pectoral spines were held erect and the caudal region propelled the fish with an unusually pronounced wagging motion. When in close proximity to the target, the male's attack consisted of a very rapid propulsion of the body forward followed by a sharp lateral turn. This motion resulted in abrupt contact between the erect pectoral spine and the target. Furthermore, this contact and motion caused the rough outer surface of the spine to be dragged across the target, producing significant abrasion. The male was observed to exhibit attack behavior on every occasion in which a large foreign object was moved within the tank. The female was never observed to exhibit aggressive behavior.

*Food habits*

*Hoplosternum littorale* exhibited differences in diet when immatures were compared with adults, and when adults were compared between different seasons. Immatures were defined as standard lengths less than the smallest sexually mature individual documented from the population. Immatures fed primarily on small aquatic crustaceans, especially Cladocera, Ostracoda, Copepoda, and Eubranchipoda. Chironomid larvae were important items in the diets of both juveniles and adults (Table 1). The adult diet was dominated by mixed detritus, terrestrial insects, microcrustaceans, and aquatic beetles during the dry season, and mixed detritus and chironomid larvae during the wet season. The late wet/early dry season transition is marked by a concentration of adult fishes into gradually shrinking bodies of water. At this time, trophic specializations may be employed by fishes as their food resources become diminished and competition relatively more intense (interspecific comparisons will be the subject of a future report). During the peak dry months, oxygen became depleted in the aquatic environment (Fig. 1). During frequent intervals of this period, many *H. littorale* ceased feeding and utilized their intestines for aerial respiration (53 of 91 individuals sampled had empty guts, see Carter 1935, Kramer et al. 1978 for a discussion of the respiratory adaptation). Sixty eight percent of the individuals had empty guts during the late wet season, suggesting that critical dO2 levels for aerial respiration were present during at least a portion of this period as well. In all cases, when empty guts were encountered, the vascularized, thin-walled intestine of the specimen was inflated with air.

## Discussion

*Hoplosternum littorale* exhibits a marked seasonal pattern of reproduction in the llanos. Like many Ostariophysian fishes in seasonal tropical habitats (Lowe-McConnell 1975, 1979), *H. littorale* responds to the flooding produced by the first heavy rains of the wet season with a more or less synchronized burst of spawning activity. Apparently, all spawning activity had ceased at the study site by mid July or earlier, since the last small immatures were collected in late July. Gonadal recrudescence occurred throughout the dry season, with most individuals of both sexes having attained a mature state by April. The early maturation of gonads and their subsequent maintenance permits a rapid response to the first heavy rains during years when these occur early. During years when the rains commence later than average, there may exist an additional physiological cost in association with the maintenance of ripe gonads for periods of one or two months under severely hypoxic conditions. Monthly rainfall averages for the period 1952 to

*Table 1.* Composition of the diet of *Hoplosternum littorale* during three seasons in the llanos (frequency = number of stomachs containing the item).

| Food category | Dry season | | Wet season | | Late wet season | |
|---|---|---|---|---|---|---|
| | % volume | Freq. | % volume | Freq. | % volume | Freq. |
| Fish scales/bones | 6.5 | 3 | 4.5 | 1 | 0.7 | 2 |
| Snails | | | 0.8 | 2 | | |
| Clams | 1.6 | 1 | | | | – |
| Aquatic beetles | 12.2 | 4 | 0.9 | 1 | – | – |
| Chironomid larvae | 5.5 | 10 | 12.9 | 9 | 25.8 | 2 |
| Ephemerptera nymphs | | – | 0.8 | 3 | | |
| Misc. aquatic insects | 0.9 | 4 | | | | |
| Terrestrial insects | 14.6 | 4 | | | | |
| Amphipods | – | – | 1.0 | | | |
| Eubranchiopoda | – | – | 54.5 | 2 | | |
| Other microcrustacea (Cladocera, etc.) | 14.5 | 8 | 23.7 | 13 | 7.5 | |
| Difflugiids (protozoa) | 1.5 | 8 | – | – | | |
| Invertebrate cysts | – | – | 0.1 | 2 | | |
| Nematodes | – | – | 0.1 | 2 | | |
| Filamentous algae | 0.1 | 3 | – | – | 0.7 | |
| Diatoms/desmids | 0.1 | 3 | – | – | 0.1 | |
| Aquatic vegetation | 0.7 | 2 | | | | |
| Terrestrial vegetation | 0.1 | 1 | | | | |
| Seeds/spores | 0.1 | 6 | 0.5 | 1 | 0.1 | |
| *Wolffia* spp. (aq. veq.) | 3.8 | 6 | | | | |
| Vegetative detritus | 6.2 | 11 | | | 0.8 | |
| Fine mixed detritus | 29.0 | 12 | 0. | 1 | 64.1 | |
| Chitin | 0.7 | 7 | | | 0.1 | 1 |
| Empty stomachs | 53 | | 0 | | 21 | |
| N Immatures | 0 | | 16 | | 0 | |
| N Adults | 91 | | 0 | | 31 | |

1980 at nearby Guanare, Portuguesa indicate that the rainy season frequently begins during April and can begin as early as March.

Environmental cues for the initiation of spawning are potentially abundant as many aquatic physico-chemical parameters exhibit sudden changes with the onset of the rainy season (e.g. temperature, dO2, pH, dissolved solids, transparency, and depth). The environmental parameters involved in coordinating hormonal and physiological changes that condition the fish for spawning during the five month dry season are somewhat less apparent. Seasonal changes in photoperiod are small at 8° latitude, yet potentially available as a cue (Schwassman 1971). Data are not currently available on the reproductive biology of *H. littorale* at equatorial latitudes, and no phenological data were provided in a discussion of reproduction in a Paraguayan population (Carter & Beadle 1931). Since *Hoplosternum* generally inhabits shallow aquatic environments experiencing seasonal changes in physico-chemical conditions, the gradual transition to extreme dry season conditions may provide one or more cues sufficiently reliable for the appropriate pituitary responses (Atz 1957, Kirschbaum 1984). Kirschbaum (1975, 1979) experimentally induced the gymnotiform fish, *Eigenmannia virescens*, to experience gonadal recrudescence and spawn by manipulating water level, pH, conductivity, and simulated rain under a constant photoperiod (LD 13:11- criticized by Schwassman (1978) as lying beyond the range experienced by the species in nature). *Eigenmannia virescens* is a cyclically spawning, permanent resident in the estero of Caño Maraca.

*Hoplosternum's* sexually dimorphic pectoral spines were first noted in Hoedeman's (1952) systematic review of the subfamily Callichthyinae. The physiological processes involved in the enlargement and apparent seasonal reduction in the male pectoral spine remain to be investigated. The deposition of fat in the soft tissues of the pectoral fins is analogous to systems described for other fishes (e.g. the nucchal hump in males of many species of Cichlidae). The deposition of fat in conspicuous anatomical regions of the male may be involved in sexual selection, since it would advertise to females success in acquiring food resources during the pre- reproductive season.

The role of fish spines as an antipredator device is well documented (Lowe-McConnell 1975). Brood defense is common within the Siluriformes, with attack behavior consisting of chases and bites. Although nest defense by the male *H. littorale* has been observed previously (Carter & Beadle 1931, Lowe-McConnell 1964 for *H. thoracatum*), the use of enlarged pectoral spines for attacks was not reported. *Hoplosternum* is a microphagous benthic scavenger (Table 1), and its small, ventrally oriented mouth severely limits biting as a viable deterrent against potential brood predators. The rough texture of the epidermal covering of the spine enhances its abrassive properties. The irregular curvature of the enlarged male spine may also enhance its effectiveness in an offensive capacity. Various algivorous and detritivorous species of the armoured loricariid catfishes (*Hypostomus, Pterygoplichthys,* and *Cochliodon* species) exhibit brood protection and possess large, extremely abrassive pectoral spines. Alternatively, the enlarged pectoral spine could be used during the aggression of intrasexual contests if competition for mates is important in the species. Moodie & Power (1982) reported that male *Loricaria uracantha* are able to extend their pectoral spine antero-dorsally much further than females and that this may provide the ability to grasp objects between the spine and opercular bristles. Males of the loricariid *Ancistrus spinosus* were observed to use their erected opercular bristles during intraspecific pushing matches (Power 1984).

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