A Major Food Web Component in the Orinoco River Channel: Evidence from Planktivorous Electric Fishes

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Deep-water sampling of the Orinoco River main channel resulted in the collection of an unexpectedly high abundance and diversity of specialized fishes. Twenty-eight of the more than 60 species collected belong to the Gymnotiformes (New World electric or knife fishes). One of the more numerous of these, a recently described species of the genus *Rhabdolichops*, consumes large numbers of very small planktonic Crustacea and insect larvae. These items are captured in the very swift, turbid, and deep waters of the Orinoco. Although the strong dependence of the river food web on terrestrial and floodplain food sources is well known, the specialized capabilities of *Rhabdolichops* and of other fishes that occur with it indicate a significant extension of the river food web into the main channel.

LARGE TROPICAL RIVERS HAVE VERY diverse fish faunas. For example, it is estimated that some 2500 to 3000 species of fish exist in the Amazon River basin (*1*). The Orinoco River basin, although smaller than the Amazon, probably contains about 1000 fish species. Despite intense regional interest in fisheries and fish culture within the tropics, the diverse faunas of tropical rivers are still poorly known because of difficulties in sampling and taxonomic complexities.

Studies of diverse groups of fishes from large tropical rivers have shown that these fishes are heavily dependent on terrestrial foods of both animal and plant origin (*2*) and that many species rely on floodplain lakes, flooded forest, and backwaters for food and refuge during early development. The waters of the main river channels appear from most studies to contribute principally an access route for migration to smaller tributaries or to floodplains, but to be severely limited in their capacity to support fish because of the apparently low food availabilities and very swift current.

In 1978 and 1979 the R.V. *Eastward* and smaller craft fished intensively with bottom trawls in the lower Orinoco River, Venezuela. Samples from the swiftly running waters of the main channel demonstrated a surprising richness of fishes, and especially of electric fishes (Gymnotiformes) and catfishes (Siluriformes), many of which are undescribed (*3–6*). In subsequent work, zooplankton sampling of the Orinoco River in 1981 and 1982 revealed significant densities (up to 30 per liter) of small crustaceans and Diptera that might serve as fish foods. We report the results of gut content analysis on *Rhabdolichops zareti* (Sternopygidae), one of the more common species of electric fishes from mid-channel and show that these fish consume large numbers of small, suspended organisms.

Observations on related congeneric species indicate similar diets (*6, 7*). This reveals a new dimension in the food web for the Orinoco River and suggests that specialization of fishes for feeding on small planktonic and benthic organisms in the main channels of tropical rivers may be generally significant.

In the 1978–79 collections, electric fishes were especially diverse and abundant in the catch; of 28 species that were collected, ten were undescribed. Up to 17 species and often hundreds of individuals were captured together in short (10- to 15-minute) trawls. The species that compose this surprisingly diverse community in the deep, dark, and swiftly flowing Orinoco channel show a great variety in head shape and feeding morphology. Three of the five Orinocan species of *Rhabdolichops* are planktivores. In contrast to other sternopygids, these species possess a terminal mouth with a relatively large, quadrangular gape, a relatively large eye, and elongate, bony gill rakers. Gill rakers are scarcely developed in other sternopygid genera and in one species of *Rhabdolichops*. The abundant species *Rhabdolichops zareti* is the most highly specialized for planktivorous feeding (*6*) and has additional advanced features of its trophic apparatus (Fig. 1): high number of gill rakers (30 to 35 first arch rakers; congeners have fewer than 20) and fleshy papillae and pads on gill arches and buccopharyngeal roof.

Rhabdolichops zareti is now known to occur widely in the Orinoco basin. The species is most commonly collected with trawls in fast-flowing open river channels. It has not been taken in marginal habitats such as swamps, lagoons, or small streams. In 1978, both shallow stations (2 to 10 m) and deep stations (10 to 40 m) were sampled between 100 and 300 km upstream of Boca Grande, in the Orinoco delta. Fish were not taken in the shallow channel habitat, but were taken in the deep channel. The 1978 collections were made in February, when the river was near its lowest point on the hydrograph. In 1979, the collections were made in November, which is after the annual peak flow but while the water is still 2 to 3 m higher than at low flow. In 1979, numerous fish were taken in shallower portions of the channel, but not in the deeper parts of the channel. Thus it appears that there is a seasonal pattern of movement within the channel. A similar pattern has been inferred for other kinds of electric fishes (*3*).

Fifteen individuals of *Rhabdolichops zareti* were selected for detailed gut-content analysis (Table 1). These specimens, ranging 68

Table 1. Stomach contents of Zaret's *Rhabdolichops* taken from the main channel of the Orinoco River at low water (February) and just after high water (November).

Item	Size per item (micrograms of dry mass)	Mean items per capita: February 1978	Mean items per capita: November 1979
Suspended Crustacea			
Bosmina	0.5	289	1
Bosminopsis	0.4	291	0
Chydoridae	0.5	7	5
Cyclopoid copepods	0.4	402	13
Ostracods	1.0	24	13
Unidentified eggs	0.2	168	15
Other	0.5	6	0
Aquatic insects			
Larvae (mostly Chironomidae)	78.0	51	29
Mouthparts, claws		883	0
Other	1.0	28	29
Total		2150	104

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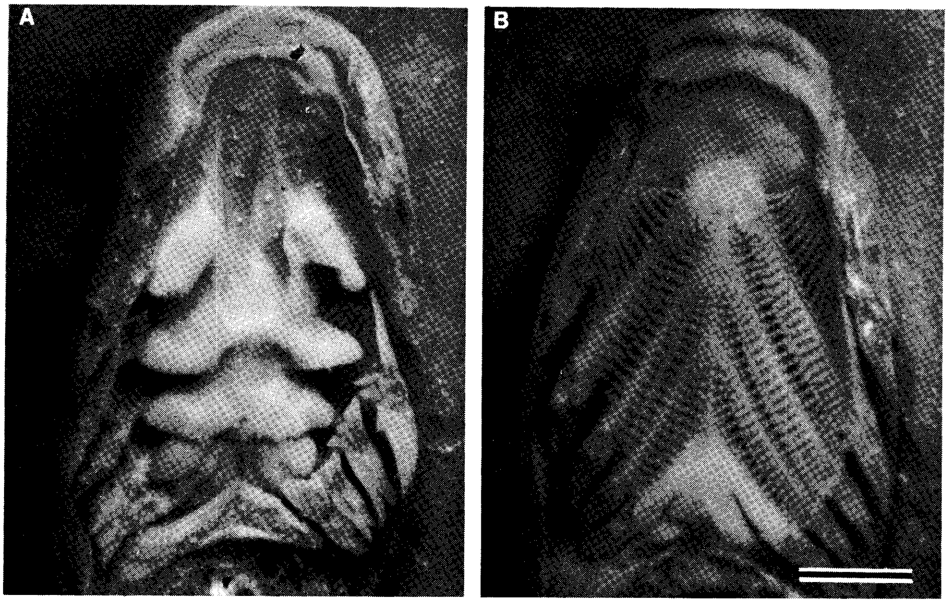

Fig. 1. Specialized pharyngobranchial trophic structures of *Rhabdolichops zareti*. (**A**) Pharyngeal roof bearing four pairs of fleshy, papillate pads. (**B**) Pharyngeal floor with long interdigitating gill rakers especially well developed on the first four branchial arches. Scale bar for both is 5 mm. (Specimen is 240 mm in total length, deposited in the Museo de Biología, Universidad Central de Venezuela, Caracas, catalogue number MBUCV-V-15328.)

to 142 mm in length to base of tail, included fish captured between 1030 to 1330 hours both in the 1978–79 catch. It is evident from the analysis that *Rhabdolichops zareti* feeds almost exclusively on zooplankton and small dipteran larvae (*8*). Qualitative examination of the stomach contents of four sympatric congeners suggests similar zooplanktivorous diets for three species, whereas the fourth species appears to consume a higher proportion of insect larvae (*6*).

Fish collected in February from midchannel contained far greater numbers of food items than fish collected in November in shallower water at the time of faster flow (Table 1). The abundance of zooplankton in the Orinoco River over an annual cycle (Fig. 2) (*9*), helps explain the difference in the abundance of food items in the stomachs on the two different dates. Although the zooplankton data were not taken simultaneously with the fish collections, several years of zooplankton sampling on the Orinoco River main stem have shown that the abundance of planktonic heterotrophs in the river follow a regular seasonal cycle; the abundances of all zooplankton are highest at the time of low water and are strongly reduced when flows are high.

Rhabdolichops zareti must possess extraordinary sensory and locomotory adaptations that allow capture of food items measuring less than 1 mm in complete darkness from water that is flowing at very high velocity. Because of high turbidity and strong dissolved color, the amount of light penetrating to the bottom in water as shallow as a few meters is negligible. Consequently, these zooplanktivorous fishes cannot visually detect their prey in the river channel. Although *Rhabdolichops zareti*, like other electric fishes, is capable of electrolocation through distortion of a self-generated electric field, individual zooplankters are too small to be detected in this way (*10*). Other prey detection systems might include olfaction, mechanoreception through the lateralis system, direct encounters between fish and prey, or electroreception of the direct current field produced by the prey's neuromuscular activity (*10*). Any of these mechanisms operating in the deep river channel habitat would surely require very close proximity between predator and prey, and an extremely rapid response by the fish.

The Orinoco River main stem flows at velocities of up to 2 m per second. The bottom profile in the vicinity of the fish sampling area, and in the lower Orinoco main stem generally, does not contain enough structure to suggest the existence of pockets of water having reduced velocity of flow. Because the river is tens of meters deep over the channels and flow patterns are turbulent, the boundary layer over the substrate will be only several centimeters thick and will have a steep velocity profile (*11*). The gymnotiforms of the deep channels must sometimes experience great flow velocities, especially if they enter the water column for feeding. In order for these fishes to avoid being swept downstream, they may have to swim more than ten body lengths per second (*5*). This is unexpected because previous work on the hydromechanics of gymnotiforms (*12*) suggests that their mode of swimming, involving as it does a long undulating anal fin instead of an undulating whole body, is best designed for low speeds.

Despite the unclear sensory and locomotory mechanisms of *Rhabdolichops zareti*, the advantages of feeding on the zooplankton resource in the deep river channels are clear: the food is delivered to the fish at a very fast rate and cannot be exhausted by any likely rate of feeding.

The zooplanktivorous *Rhabdolichops* are only one group of a number of fishes that make up a dimension of the Orinoco River food web extending into the main channel. The diets of a few other river channel gymnotiforms have been examined and these appear to feed largely on benthic aquatic insects. Marrero (*13*) has found high densities of chironomid larvae in the clayey substrate of the Apure River (an Orinoco tributary) and in coincident gut content samples of *Sternarchorhynchus mormyrus* (Apteronotidae) and *Rhamphichthys reinhardti* (Rhamphichthyidae). In the lower Orinoco, the apteronotid *Adontosternarchus devenanzii* feeds on benthic invertebrates in the deep main channels during the low water season (February samples) and in shallower habitats during high water (November samples) (*4*). Whereas the quieter waters of the flood-

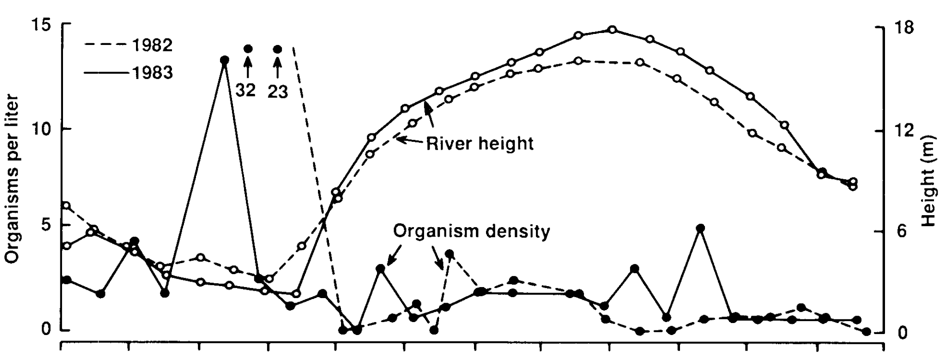

Fig. 2. Annual abundance patterns of small suspended Crustacea in the Orinoco River at Ciudad Bolivar.

plain, side channels, and banks are of undoubted significance to the river fishes of the Orinoco and elsewhere, *Rhabdolichops zareti* illustrates the potential importance of adaptations specifically to the main channel environment.

Araujo-Lima *et al.* (*14*) suggest that characiform fishes in the Amazon receive most of their carbon from food chains that originate with phytoplankton, whereas siluriform fishes in the Amazon receive a significant part of their carbon from other plant sources. Our data show a direct connection of the diets of *Rhabdolichops* with both plankton and benthic food chains. The relative contributions of these two groups to the biomass of fish cannot be resolved quantitatively on the basis of stomach contents, however, because the rates of digestion for foods of different sizes and types may differ substantially. Moreover, certain fish contained exclusively plankton, while others of the same size and species contained a mixture of food types. The zooplankton that are used by *Rhabdolichops zareti* and by other taxa enter the Orinoco River main stem from the floodplain. Alteration in the floodplain leading to significant reduction in its capacity to produce planktonic foods for these main-channel fishes thus can be expected to threaten the basis for the existence of *Rhabdolichops zareti* and other such fishes.

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8. Crustaceans other than chydorids and ostracods are strictly of planktonic origin. Ostracods and chydorids are of littoral origin. The Diptera (which are almost exclusively chironomids) are of benthic origin. However, it is unlikely that any of these organisms are actually resident in the main channel. Because of their small size and weak powers of movement, all the organisms in the open-channel areas where the fish were collected would almost certainly be suspended more or less uniformly through the swiftly moving waters. Concentration of suspended food organisms near the sediment-water interface is unlikely because of the high current velocities, although this is difficult to demonstrate empirically because of the swiftness of the river.
9. The seasonal pattern for abundance expressed as biomass is essentially identical to the seasonal pattern expressed numerically, as shown in Fig. 2. Statistics for biomass abundance of food items are as follows (1982 and 1983, in micrograms dry mass per year): mean 1.57, 0.72; maximum 16.8, 4.89; minimum 0.01, 0.02. Fluxes of food items are as follows (1982 and 1983, as metric tons of carbon per day): mean 1.05, 0.74; maximum 5.43, 2.73; minimum 0.01, 0.01.
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