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OBLIGATE MUCUS-FEEDING IN A SOUTH AMERICAN TRICHOMYCTERID CATFISH (PISCES: OSTARIOPHYSI).—Dietary specializations have been described within most major animal groups. The extreme case can be seen in certain insects that exhibit obligatory feeding on special host plants (oligophagy), frequently in association with secondary chemical compounds (Futuyma, 1983). Trophic specializations among vertebrate species tend to be facultative with diet varying between habitats, seasons, or life stages (Goulding, 1980). Fishes are notable among vertebrates for having comparatively broad and flexible diets (Larkin, 1956; Lowe-McConnell, 1975). For example, many fishes exhibit major diet shifts in association with growth and development (Werner and Gilliam, 1984; Keast, 1985). This report provides evidence of extreme dietary specialization by the tiny South American catfish, *Ochmacanthus alternus* (Trichomycteridae). We postulate that the external mucous slime layer of larger teleost fishes provides the catfish with a rich, continuously renewed resource that is abundant, particularly during periods of high fish densities within seasonally-fluctuating aquatic habitats.

Materials and methods.—Fishes were collected from Caño Maraca, a swamp/creek of the Venezuelan llanos (Portuguesa state), every month during 1984 in order to investigate community trophic ecology (more complete descriptions of the site and methods appear in Winemiller, 1987). During the rainy season, the creek's broad floodplain is a productive marsh. The floodplain dries and the creek is converted into a series of muddy pools blanketed by aquatic vegetation during the period of lowest rainfall (Jan.–May). *Ochmacanthus alternus* were taken during each month of the year and fixed in 15% formalin, yielding a total of 545 specimens. Stomach content analysis was performed on 301 preserved specimens representing all months. Contents from 245 specimens that contained food were identified and sorted under a dissecting microscope, then quantified volumetrically (Winemiller, 1987).

Results.—Mucus comprised over 94% of the catfish's diet by volume during the year. The remainder of stomach contents consisted of silt and detritus (5%), algae (1%), plus a fraction of less than 1% made up of sand grains, nematodes, fish scales, chironomid larvae (Diptera), and water mites (Hydracarina). Virtually no seasonal variation was observed, with mucus comprising 95% of the diet during the wet season (n = 65), 95% during the transition season (Sept.–Dec.; n = 154), and 92% during the dry season (n = 82). We hypothesize that the small non-mucus fraction was ingested by the catfish while burrowing in the substrate, a habit confirmed by aquarium observations. With few exceptions, mucus from the foregut was observed to be rolled into compact bundles of lamellar layers.

The digestive canal of *O. alternus* is a relatively straight tube from the mouth to the anus. The gut wall (less than 30 μm in thickness) contains unusually thin layers of serosa, muscularis and submucosa (Fig. 1). The mucosa layer consists of a single layer of columnar cells with basal nuclei and numerous goblet cells. Histological sections of the foregut containing food were stained using either the colloidal iron method (for acid mucopolysaccharides and mucins; Mowry, 1958) or alcian blue method (for mucosubstances; Luna, 1968). Positive colored histochemical reactions of sections indicated mucous origin of ingested food masses (Fig. 1).

Discussion.—We cannot say with certainty, which of the 88 fish species captured at the site constitute the principal hosts for *O. alternus*. Two of the largest common species, *Hoplias malabaricus* (Erythrinidae) and *Astronotus ocellatus* (Cichlidae) secrete copious amounts of mucus in their protective external slime layers. We have observed aquarium-spawned larvae of *Astronotus* feeding upon the rich, mucous slime of their parents, a well-known phenomenon among other members of the Cichlidae (Goldstein, 1973). Three other large- and medium-sized cichlids at the site (*Caquetia kraussii, Aequidens pulcher,* and *Cichlasoma orinocense*) could also serve as potential sources of mucus for *O. alternus*. We placed three *Aequidens pulcher* (45–70 mm SL) in an aquarium with a single *O. alternus* (30 mm

Fig. 1. Cross section of the foregut of *Ochmacanthus alternus* showing a mass of rolled mucous material (MM) lying within the thin-walled gut (GW). The presence of mucus within the gut was confirmed by green color reaction to Luna's alcian blue staining method (O = ovary; bar indicates 100 μm).

SL) for several weeks. *Ochmacanthus alternus* was observed to emerge from within the gravel substrate at night, and attempt to attach itself to the bodies of the cichlids soon thereafter. Repeated attempts by *O. alternus* to attach itself to the cichlids resulted in behavioral patterns that were easily interpreted as avoidance or a fright response (e.g., erection of medial fins and seemingly undirected swimming bursts of the cichlids), which suggests the presence of a negative impact of mucus-feeding on the host fish.

Based on verbal accounts provided by local fishermen, Roberts (1972) first suggested that a congeneric species, *O. reinhardti*, may feed on the mucus slime layer of *Arapaima gigas* (Osteoglossidae) and other large, scaled fishes in the Amazon basin. The stomachs of all 17 Equadorian specimens of *O. reinhardti* examined by Saul (1975) were empty. Baskin et al. (1980) tentatively classified *O. alternus* from the Venezuelan llanos as a scale-feeder, since scale-feeding has been described for other genera within the subfamily Stegophilinae, and the stomachs of all 22 of their specimens were empty. Since we only found scales in trace amounts in *O. alternus*, it appears likely that scales were removed and ingested incidentally with mucous slime. Feeding specializations have been reported for other species within the family. In addition to scale-feeding specialists (*Apomatoceros alleni, Stegophilus* sp., *Pseudostegophilus nemurus*; Baskin et al., 1980), the Trichomycteridae contains examples of blood-feeding parasites ("candiru" of the subfamily Vandelliinae; Roberts, 1972; Baskin et al., 1980) and numerous generalized, benthic insectivores (subfamily Trichomycterinae; Baskin et al., 1980).

Extreme trophic specializations have been discovered among other tropical fish families, including the Characidae (e.g., fin- and scale-feeding; Sazima, 1983; Machado-Allison and Garcia, 1986), Cichlidae (e.g., scale-feeding, eye-biting, larval-fish predators; Fryer and Illes, 1972; Greenwood, 1981; Ribbink, 1984), and Mochokidae (a brood parasite; Sato, 1986). Unlike scale-, fin-, and eye-biting specialists, *O. alternus* exhibited no evidence of ontogenetic diet shifts across a range of subadult and adult size classes (13–38 mm SL). Furthermore, it is generally agreed that the structure of a fish's alimentary canal is directly related to diet (Fange and Grove, 1979). The unusually thin-walled alimentary canal of *O. alternus* should be adaptive for the specialized mucus diet, since mechanical breakdown of particles would be a minimal requisite. *Ochmacanthus alternus* possesses a leech-like morphology (Fig. 2) that presumably facilitates attachment to the host's body. The broad, ventrally oriented mouth armed with numerous minute teeth may function as a sucker in addition to its primary role as a mucus

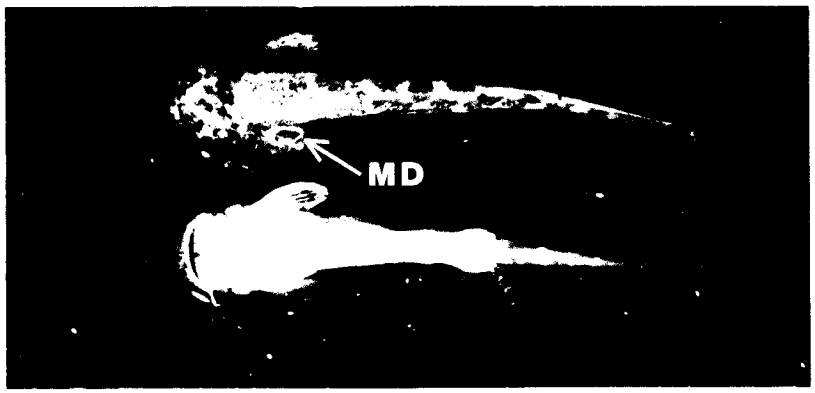

Fig. 2. Photograph of *Ochmacanthus alternus* (32 mm SL) showing elongate morphology and broad ventrally oriented mouth used for mucus feeding and probably attachment to the bodies of larger fishes. The mucus droplet formed near the base of the pectoral fin (MD) may further promote adhesion to the body of the host.

scraper. *Ochmacanthus alternus* also possesses small opercular "teeth" that may be used for attachment to the host, in a fashion similar to the blood-parasites of the related Vandelliinae. In addition, glands located near the base of each pectoral fin secrete mucus that forms large droplets just posterior to each opercle. These droplets may further promote adhesion to the external surface of the host by increasing the fish's ventral surface area with a sticky substance. Freshly caught *O. alternus* frequently stuck to the hands of the collector and required vigorous shaking for removal. We hypothesize that mucus feeding is highly advantageous for the catfish in lowland aquatic habitats where availability of invertebrate prey fluctuates seasonally (Goulding, 1980; Winemiller, 1987). The external mucous slime of fishes provides a rich source of energy and amino acids (Wessler and Werner, 1957; Enomoto et al., 1961; Lewis, 1970) in a form that is harvestable by virtually all catfish size classes. Large, relatively slow-moving, scaled fishes probably provide the primary source of mucus for the catfish. As a consequence, relative availability of mucus may vary to some degree with seasonal changes in fish densities.

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