

Ontogeny of Scale Feeding in the Asian Glassfish, *Chanda nama* (Ambassidae)

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Dietary analysis of a population of the glassfish *Chanda nama* from a wetland in southwestern India revealed facultative scale feeding (lepidophagy). In addition to fish scales, microcrustacea and aquatic insects were consumed by all size classes, with juvenile diets containing larger fractions of invertebrates. More scales were consumed during the wet season, the period when abundance of juvenile fishes was greatest. Aquarium observations revealed how the glassfish uses stealth and ambush tactics. Scales are dislodged by raking the extended lower jaw, distally armed with four curved conical teeth, across the flanks of prey.

SPECIALISED scale feeding, or lepidophagy, is defined as the ingestion of scales without bones or flesh (Sazima, 1983). Lepidophagy has been described for seven Neotropical characid genera (Roberts, 1970; Sazima, 1983; Vari, 1986), three Neotropical trichomycterid genera (Baskin et al., 1980), at least six African cichlid genera (Fryer et al., 1955; Eccles and Lewis, 1976; Liem and Stewart, 1976), an Australian ariid catfish (Roberts, 1978), an Australian teraponid (Whitfield and Blaber, 1978), two carangid genera (Major, 1973; Sazima and Uieda, 1980), and two ambassid genera (Roberts, 1989). Lepidophagous Neotropical characids have morphological and behavioral specializations for removing scales (Sazima, 1977, 1983; Sazima and Machado, 1990). *Catoprion mento* has everted teeth and a long lower jaw that opens to a $> 90^\circ$ angle to rake scales from the flanks of fishes (Sazima, 1983; Nico and Taphorn, 1988). *Exodon paradoxus*, *Roebioxodon guyanensis*, *Serrabrycon magoi*, and *Roeboides* species possess external teeth on the snout that are used to dislodge scales (Roberts, 1970; Sazima, 1983; Vari, 1986). Morphological and behavioral mechanisms for scale feeding are less apparent in most noncharacid fishes (but see Hori, 1993).

In lepidophagous characids (*Catoprion mento* and *Roeboides* spp.), the juvenile diet shifts from microcrustacea to aquatic insects before switching to scales in the adult diet (Sazima and Machado, 1982; Nico and Taphorn, 1988; Peterson and Winemiller, 1997). Frequency of scales in stomachs of *Roeboides dayi* and *Roeboides affinis* in the Venezuelan llanos was greater during the dry season when aquatic insect abundance is lower and fish densities are higher (Peterson and Winemiller, 1997; Peterson and MacIntyre, 1998). Among most marine lepidophagous fishes, scale eating is performed by juveniles and ceases during later ontogeny in association with modification of jaw structure and dentition

(Major, 1973; Sazima and Uieda, 1980; Sazima, 1983).

Roberts (1989) briefly described the dentition of two Asian glassfishes (Ambassidae, Perciformes), *Chanda nama* from India and *Paradoxodacna piratica* from the Malay Peninsula and Western Borneo, presumed to feed on scales. Although the species were described as scale feeders, no assessment of the degree of lepidophagy was provided for either species. Here we report for the first time ontogenetic diet shifts involving scale feeding in *C. nama* from a freshwater wetland in the western Ghats region of India.

MATERIALS AND METHODS

From August 2000 to July 2001, fishes were collected from a natural wetland (approximately 40 ha) at Manavalakurichy ($8^\circ 10' 12''\text{N}$, $77^\circ 18' 24''\text{E}$) in southern region of the western Ghats, Tamil Nadu, India. Annual rainfall in the region is 1.2–1.5 m, with a period of relatively low rainfall from December through March (mean monthly rainfall 35 mm) and high rainfall from April through November (mean rainfall 134 mm). During most years, low rainfall in September (53 mm rainfall during 2000) briefly interrupts the long rainy season. Manipulation of inlet and outlet sluice gates maintains relatively constant water level. Water level increases during unusually wet periods. The wetland contains 28 fish species (ARG, unpubl. data) and lacks exotic carps (e.g., *Catla catla*, *Labeo rohita*, *Chirrhina mrigala*) commonly introduced into surface waters of the country. Fishes were captured with seines (6×2 m, 3 mm mesh), cast nets (3 m radius, 10 mm mesh) and experimental gill nets (150×3 m, with 2, 3.5, 5, 8, and 15 cm mesh). Sampling was conducted from 0600–1400 h. All aquatic habitats were surveyed (i.e., vegetation, open water, edge, and mid-

pool). Specimens were preserved in 15% formalin, then rinsed in freshwater prior to examination in the lab.

Of 3361 *C. nama* captured, 3034 were measured for standard length (SL) to the nearest 0.1 mm, and 382 individuals representing all size classes (grouped by 5 mm intervals), months, and habitats were dissected for stomach contents. Food items in the anterior half of gut were examined under a dissecting microscope and identified to order (invertebrates), species (fishes), or general category (e.g., algae, detritus, scales) yielding a total of 22 prey categories. Food items were blotted dry on paper towel, and their volumes measured by water displacement in graduated cylinders. Resolution for the smallest food items was approximately 1 μ l. To estimate the approximate size of maturation, gonads of dissected specimens were examined under a dissecting microscope, and ovaries were staged as immature (lacking visible oocytes or oocytes within 0.10 mm of the maximum diameter observed for the population) or mature (containing at least some oocytes of the maximum diameter).

RESULTS

Chanda nama were captured during each monthly survey (average sample = 110, range = 15–892). Approximately half of all males and females had mature gonads by 25 mm SL; thus we consider this the size at maturation. In every monthly sample, females > 26.4 mm SL contained ripe ovaries. Ripe ovaries contained multiple oocyte cohorts, and juveniles were present in every sample, which suggests that some segment of the population probably spawns during any given month. March through July (early wet season) samples were dominated by juveniles (10–25 mm SL) and probably reflect peak spawning during this period.

Analysis of volumetric percentages of major diet categories for different size classes of *C. nama* revealed a strong pattern of ontogenetic diet shift (Fig. 1). Juveniles fed heavily on aquatic insects (mostly Ephemeroptera but including Odonata and Coleoptera) and microcrustacea (calanoid copepods, Cladocera, Isopoda, and Amphipoda). Terrestrial insects appeared in the diet at 25 mm SL and remained a minor dietary component (5–17%) for all subsequent size classes. Scale feeding was observed among individuals as small as 15 mm, and the volume of scales in stomachs increased gradually with size until reaching an asymptote at approximately 35 mm (Fig. 1). The correlation between SL and the volume of microcrustacea in the diet

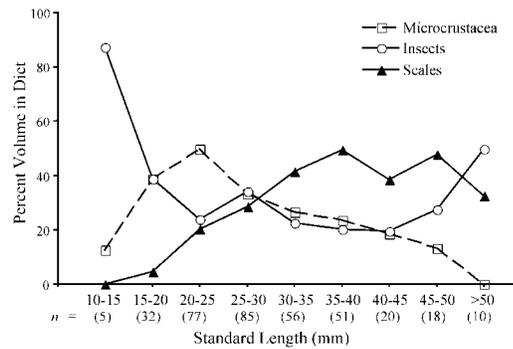


Fig. 1. Volumetric percentages of three major resource categories in diets of size classes of *Chanda nama* (values in parentheses are sample sizes).

was -0.30 (Spearman's rho, $df = 355$, $P < 0.0001$), between SL and the volume of aquatic insects in the diet was -0.26 ($P < 0.0001$), and the correlation between SL and the volume of scales in the diet was 0.86 ($P < 0.0001$). Consumption of scales was facultative, with no size class averaging more than 50% scales in the diet by volume. Nonetheless, scales were the most important diet category for adult size classes (average volumetric percentage = 38%, range among size-class averages = 35–50%). The mean number of scales in individual stomachs was 8.15 for juveniles ($n = 114$) and 13.94 for adults ($n = 242$). The maximum number of scales in individual stomachs was 32 for juveniles and 65 for adults. Only eight juveniles and 17 adults in our sample had empty stomachs.

Diets of both juveniles and adults varied seasonally (Fig. 2). Juveniles (SL < 25 mm) fed predominantly on aquatic insects from late wet to early dry seasons (October to January). Microcrustacea were the most important dietary component for juveniles during other periods, the only exception being July (middle wet season) when scales were the dominant item in juvenile diets. Scales were significant dietary elements for adults throughout the year, comprising from 15–90% of the monthly mean volume of adult stomach contents (Fig. 2). Greatest consumption of scales by adults was during the period April to August (end of dry season–early wet season). Microcrustacea (zooplankton) comprised the greatest percentage of the adult diet during the period November to February (end of wet season–early dry season). Aquatic and terrestrial insects were important diet elements for adults during the late dry season (March to April).

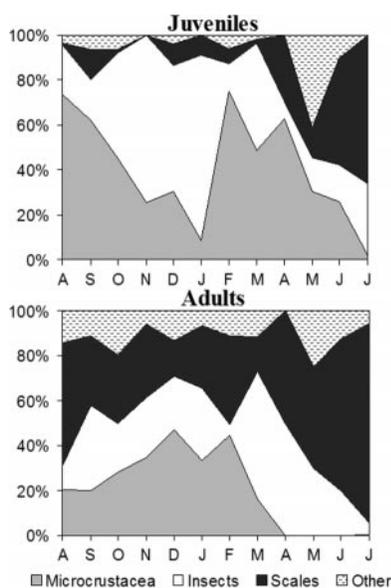


Fig. 2. Volumetric percentages of three major resource categories in diets of juvenile (top graph) and adult (bottom graph) *Chanda nama* at Manavalakurichy wetland during different months (2000–2001).

DISCUSSION

Chanda nama and *P. piratica* are the only freshwater fishes in Asia reported to consume scales (Roberts, 1989). Other freshwater and estuarine ambassid species have been documented to feed on aquatic invertebrates and in a few cases fishes (Nair and Nair, 1981, 1983; Merrick and Schmida, 1984; Martin, 1989). Scales provide lepidophagous consumers an abundant and rapidly renewable resource (Nico and Taphorn, 1988). Fish scales have substantial energy content (van Oosten, 1957; Whitfield and Blaber, 1978; Nico and De Morales, 1994), but their nutritional value has not been investigated extensively. Nico and De Morales (1994) found little variation in energy and protein content of scales from several different Neotropical fish species. The energy content per unit dry mass of fish scales is about two-thirds that of whole fish (Nico and De Morales, 1994). In his study of the cleaner wrasse *Labroides phthiophagus*, Gorlick (1980) suggested the mucus layer associated with ingested scales is an important energy source rich in proteins (Wessler and Werner, 1957) and lipids (Lewis, 1970). Juveniles of several cichlid species (e.g., *Symphysodon* spp.) feed heavily on their parents' mucus, and the Neotropical catfish *Ochmacanthus alternus* (Tichomycteridae) is a specialized mucus feeder (Winemiller and Yan, 1989).

Scale feeding in *C. nama* appears to be fac-

ultative, and adults also consume insects and microcrustacea. In a manner similar to Neotropical characids in the genus *Roeboides*, *C. nama* undergoes an ontogenetic diet shift from feeding primarily on invertebrates as juveniles to scale feeding as adults. *Roeboides dayi* in streams of the Venezuelan llanos fed extensively on seasonally abundant microcrustacea and aquatic insects during the wet season (Peterson and Winemiller, 1997). In contrast, *Roeboides prognathus* from the Cuiabá River in Brazil appears to have a diet largely restricted to scales (Sazima, 1983). Seasonal resource fluctuations could have been associated with temporal variation in the degree of lepidophagy observed in *C. nama* in the Manavalakurichy wetlands. Daily operation of sluice gates maintains a fairly constant water level in this ecosystem. Nonetheless, environmental parameters, such as temperature, pH, DO, turbidity and conductivity, vary in response to seasonal rainfall. During the dry season, temperature, conductivity and turbidity are higher, and DO is lower. Both adults and juveniles consumed relatively large fractions of aquatic insects and microcrustacea during this period. Juveniles that consumed scales did so mostly during the early wet season. Scales were major components of the adult diet throughout the year, but scale consumption was relatively greater during the early wet season. During the early wet season, fish recruitment is high, such that large populations of young fishes yield high availability of scales as a potential food resource.

Chanda nama does not possess external snout teeth as observed in several genera of lepidophagous Neotropical characids. We examined head morphology of three *C. nama* specimens measuring 33.6, 54.2, and 64.1 mm SL. In addition to having numerous rows of tiny conical teeth embedded on both jaws, each specimen possessed two enlarged conical teeth in the anteriolateral region of both mandibular tooth pads (Fig. 3). These teeth are curved anteriorly and presumably are used to dislodge scales. The jaws open to create an approximate 90° angle with the long lower jaw protruding further than the premaxillae. Presumably, *C. nama*, with jaws fully extended, rakes its enlarged mandibular teeth across the flanks of prey to dislodge scales in a manner similar to that used by *Catoprion mento* as described and illustrated by Sazima (1983). Both upper and lower jaws have a degree of bilateral asymmetry (overtly, the anterior projection of lower jaw is skewed either to the right or left side), which suggests populations might have "left-handed" and "right-handed" morphs that attack from only one side, a phenomenon described for a lepidophagous

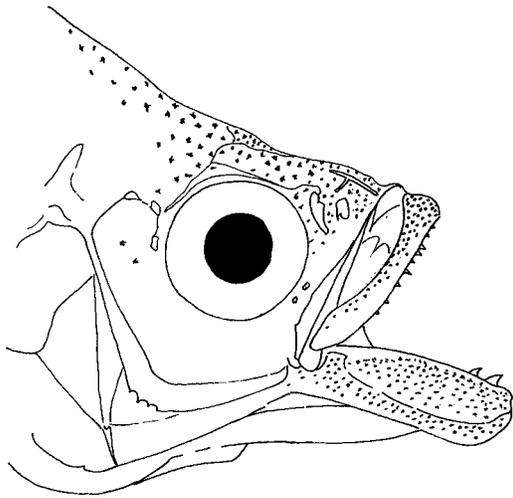


Fig. 3. *Chanda nama* (64.1 mm SL) head morphology showing jaws open to a right angle and curved conical teeth on the mandible.

cichlid from Lake Tanganyika (Hori, 1993). No bilateral asymmetry of dentition was observed in *C. nama*.

To observe scale-feeding behavior directly, we introduced three adult *C. nama*, five adult *Salmostoma bacaila* (Cyprinidae), 10 individuals representing three *Puntius* species (Cyprinidae), and six subadult *Oreochromis mossambicus* (Cichlidae) into a 90-liter aquarium containing aquatic vegetation and rocks. The feeding behavior of *C. nama* was similar to that described for *Catoprion mento* (Characidae) by Sazima (1983). Typically, the attacker hovered near vegetation or rocks then dashed out to attack passing prey. During an attack, the jaws were opened and held agape as the lower jaw was raked across the flank of the prey. Typically, only 1–2 scales were dislodged then consumed as they sank in the water column. *Salmostoma bacaila* and *Puntius* species were attacked more frequently than *O. mossambicus*, the latter preventing many attacks by facing or evading its attacker. The cyprinids were clearly distressed by repeated attacks by *C. nama*, ultimately hovering at the surface in the corner of the aquarium. Sazima (1977) described a similar response by characids attacked by *Probolodus heterostomus* in aquaria, and concluded the behavior was an artifact of confinement. Individual fish seemed to attack consistently from only one side, but we did not attempt to quantify the phenomenon given our small sample size. The question of “handedness” and bilateral asymmetry in *C. nama* warrants further study.

Our aquarium observations were conducted

in clear water, but water of wetlands in southern India frequently has low transparency caused by high densities of phytoplankton. Presumably, stealth tactics of *C. nama* would be enhanced in moderately turbid water. The body of *C. nama* is highly transparent (hence the common name “glassfish”), which undoubtedly reduces its detection by potential prey. The general body plan, body size, and stealth attack behavior of *Roebooides* species, another group of lepidophagous freshwater fishes, are similar to those of *C. nama*, and the two groups (Neotropical characiform and Asian perciform) exemplify convergence in a trophic specialization. Considerable interspecific variation in body transparency and lepidophagy is observed in both groups (Sazima, 1983; Roberts, 1989), but the degree of correlation between these traits is unknown.

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