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Short communication

Grazing of the lambari fish *Deuterodon iguape* is associated with mouth morphology

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ABSTRACT

For a better understanding of fish feeding biology it is desirable to know not only the food items ingested by the species but also the anatomical structures and feeding tactics that enable individuals to access specific food. *Deuterodon iguape* is an omnivorous and small-sized Characidae from coastal Atlantic rainforest. We describe the grazing tactic of *D. iguape* and discuss the associated mouth structures that enable individuals to access algae and debris from bedrocks in Atlantic forest streams. Mouth structures acting together with body inclination of individuals probably confer advantages to the species scraping foraging strategy (herein called hard substrate scraper while laterally inclined) and optimize the food intake. The ability of *D. iguape* to access specific food resources in Atlantic forest streams may confer ecological advantages in relation to other fish species that do not have as much trophic plasticity.

1. Introduction

Studies on feeding biology of fish frequently untangle which food items individuals get access in temporal and spatial scales (Uieda and Pinto, 2011). For a better understanding of fish feeding biology, it is desirable to know not only the items ingested by the species, but also the anatomical structures together with feeding tactics that enable individuals to access the food (Zavala-Camin, 1996). Feeding tactics of fish are necessarily accompanied by some structural adaptations of digestive tract such as size, shape and position of mouth, teeth, and gill rakers (Keenleyside, 1979).

Fish may be carnivorous (e.g., piscivorous or insectivorous), herbivorous or omnivorous, the latter when they feed on plant and animal resources. Especially in the Neotropics, where a variety of feeding resources exists, many omnivorous or generalist species are present (Lowe-McConnell, 1999) and they may change their diet according to the availability of food resources evidencing opportunistic feeding behavior (Uieda and Pinto, 2011). Also, some species change their diet as they grow (Vitule and Aranha, 2002) which may be related to fish morphology since juveniles are anatomically distinct than adults (Dala-Corte et al., 2016). For instance, insectivorous juveniles of *Deuterodon langei* Travassos, 1957 have proportionately smaller intestines than herbivorous adults (Vitule et al., 2008) to increase nutrient absorption since plants are more difficult to digest due their thick cell walls (Gerking, 1994).

Deuterodon Eigenmann (in Eigenmann et al., 1907) is a Characidae genus distributed in aquatic systems of the Atlantic forest. *Deuterodon iguape* Eigenmann et al., 1907 is a small-sized (11.7 cm maximum TL) fish inhabiting the coastal rivers of São Paulo state (southeastern Brazil) that actively explores the full extent of water column during daytime (Oyakawa et al., 2006). It can be found at Paraná and Rio de Janeiro states as well (speciesLink, 2017). *Deuterodon iguape* exhibits trophic plasticity and opportunism, as most *Deuterodon* species (Righi-Cavallaro et al., 2015). The intake of algae, terrestrial insects, leaves and fruits of vascular plants, aquatic insects, arachnids, crustaceans and oligochaetes indicate that *D. iguape* adults are omnivorous and generalist (Sabino and Castro, 1990; Sabino and Silva, 2004; Righi-Cavallaro et al., 2015). Furthermore, it feeds on pieces of leaves and macrophytes (Esteves and Lobón-Cerviá, 2001) and their flattened and multicuspid premaxillary teeth may assist their herbivorous diet (Géry, 1977). Due to its broad food spectrum, *D. iguape* was observed performing several feeding tactics such as drift feeding, picking at relatively small prey, browsing, grazing and surface picking (Sabino and Castro, 1990). Indeed, *D. iguape* individuals were found following substrate clouds resulted from foraging behavior of *Scleromystax barbatus* (Quoy

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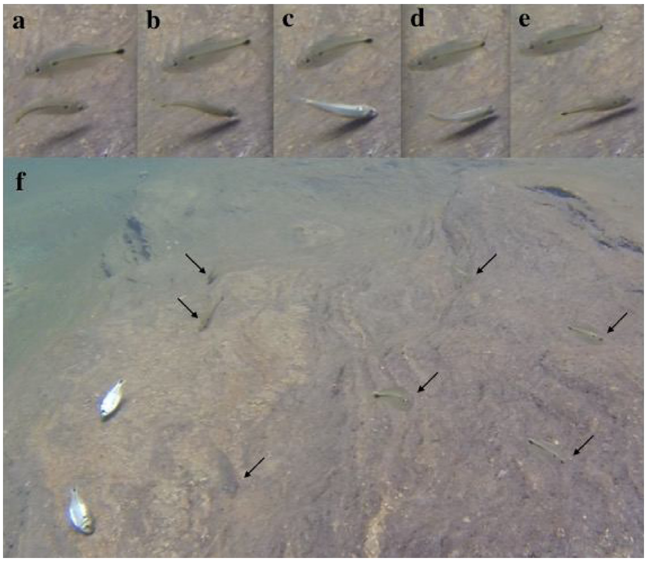

Fig. 1. Sequence of the grazing tactic performed by *Deuterodon iguape*. Foraging movements showing (a) the initial position of one individual close to the pool bottom (b) when it assumes the head-down position with the body tilted laterally up to 45° (c) until the mouth contacts the bedrock laterally and teeth scrape the pool bottom. Then (d-e) fish returns to initial position after performing the grazing tactic. In (f) two foraging fish reflecting the light during body inclination; the other seven non-foraging individuals indicated by arrows are more inconspicuous to human-eyes. Photos: Cristina S. Gonçalves.

and Gaimard, 1824) (Callichthyidae) to pick up the exposed food items (Gonçalves and Cestari, 2013). All these feeding tactics may be an expression of species trophic adaptability since the preferred feeding technique may change on demand (Gerking, 1994).

Grazers fish, including *Deuterodon* species, may forage near the bottom and crop algae by rasping surfaces close to substrate (Keenleyside, 1979; Mazzoni and Rezende, 2003). Sabino and Castro (1990) revealed that *D. iguape* quickly approached the food, tilted the body laterally and snatched the food with one side of the mouth, however, no further details on the context of this behavior was provided. Here, we describe in more details this grazing behavior of *D. iguape* and discuss the associated mouth structures that are probably related with this foraging behavior.

The study was conducted in the clear water stream Córrego da Cachoeira also known as Cachoeira do Guilherme (24°30′28.2″S, 47°15′39.6″W) at Jureia-Itatins Ecological Station, a pristine protected area of Atlantic forest in the São Paulo state, southeastern Brazil. Fish observations were done during daytime on April 19th, 2013 in three lentic pools distanced at least 50 m each other. The pools' bottoms were composed mainly by bedrock and secondarily by boulders, which were covered by biofilm and fine particulate organic matter. Water characteristics of this stream are: pH (6.4–7.3), conductivity (19–20 $\mu S\,cm^{-1}$), dissolved oxygen (8.7–11 $mg L^{-1}$), and temperature (19.9–20.4 °C). Cachoeira do Guilherme has clear water that provides sufficient transparency to observe fish. The focal-animal and the sequence sampling methods (Lehner, 1998) were used to describe the *D. iguape* foraging behavior. Fish were video-taped in order to capture the foraging sequence of movements. Voucher specimens are deposited in the fish collection of Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP, DZSJRP 13243), São José do Rio Preto.

Deuterodon iguape was observed in shoals (16–30 individuals) exploring actively the pools. Grazing individuals swam close to the bottom (Fig. 1a), inclined the body up to 45° to one side assuming a head-down position (Fig. 1b) until the mouth contacted the bedrock laterally (Fig. 1c). The mouth was opened when its side contacted the bottom, then the fish scraped the bedrock with his maxillary and posterior premaxillary teeth, sucked the loosened items and returned to initial position (Fig. 1c–e, Supplementary Video S1). This behavior lasted 1–2 s and fish could repeat it continually to either side. We recorded 75 individuals of *D. iguape* in three distinct shoals that performed the foraging behavior. More than 80% of all fish in each shoal performed the grazing tactic. No other species of lambaris (e.g., *Astyanax* Baird and Girard, 1854) were observed together with *D. iguape*. Additionally, it was observed only in areas covered by bedrock, i.e., fish did not performed this behavior while foraging at other bottom types such as pebble, sand, smaller rocks or plant debris. We propose to name this grazing tactic as hard substrate scraper while laterally inclined. Probably, individuals that performed this foraging behavior can be more easily detected by an observer than those that did not due to the reflection of light on fish bodies when they are inclined and in head-down position (Fig. 1c and f, Supplementary Video S1).

Deuterodon iguape has several mouth structures that jointly with body inclination confer advantages to their scraping foraging strategy and optimize the food items intake. These structures are: (1) the ventral margin of the portion with maxillary teeth arches towards the ventral margin of the premaxillary, forming a continuous axis of teeth in the upper maxilla (Fig. 2), (2) the upper lip with a lateral atrophy that shows a variable number of the posterior premaxillary teeth and maxillary teeth (Lucena and Lucena, 2002), even with closed mouth (Oyakawa et al., 2006) (Fig. 2), (3) the shortened posterior edentulous region of the maxillary (Lucena and Lucena, 2002), (4) the large mouth opening (Gonçalves et al., 2017), and (5) the presence of six to seven cusps in the teeth of the inner row of the premaxillary, maxillary and dentary arranged in the same plane (Lucena and Lucena, 2002). Apparently, the lateral inclination of the body (Fig. 1f) along with the continuous extension of teeth and the wide buccal opening allow the fish to reach larger areas of the substrate to obtain food items at each scrape. It is probably also more advantageous for some characins that are substrate scrapers to have a short edentulous region of the maxillary (and consequently more maxillary teeth), as well as the atrophied upper lip that leaves teeth partially exposed and facilitates the scraping. This lip atrophy is uncommon among Tetragonopterinae (*sensu* Géry, 1977) an old subfamily that several fish, including *Deuterodon*, were placed (Lucena and Lucena, 2002). Furthermore, multicuspid teeth with increased cusp number are shared by few characids (e.g., *Deuterodon*, *Iguanodectes* Cope, 1872, *Jupiaba* Zanata, 1997) with similar plant-based diets (Ohara et al., 2017 and references therein) and it might be advantageous to scrap algae from hard substrate since some freshwater and marine fish evolved convergent teeth to feed primarily on algae (Gibson, 2015).

Among other *Deuterodon* species, we suggest that *D. langei*, *D. stigmaturus*, *D. rosae* and *D. singularis* may perform the same foraging behavior reported herein, given their phylogenetic closeness to *D. iguape* (Pereira, 2010). Barreto and Aranha (2006) observed *Deuterodon langei* swimming close to the bottom searching for algae. Dala-Corte et al. (2016) suggest that the larger area with exposed teeth in adults (compared to juveniles) is an advantage to herbivory. Some studies also evidence the higher consumption of filamentous algae and plant debris by *D. langei* (Vitule et al., 2008), *D. stigmaturus* (Dala-Corte et al., 2016), *D. rosae* and *D. singularis* (Righi-Cavallaro et al., 2015) but detailed observational studies should be conducted to corroborate the occurrence of the grazing tactic as reported.

The hard substrate scraper while laterally inclined foraging behavior probably contributes to the trophic plasticity of *D. iguape* reported by Sabino and Castro (1990), Sabino and Silva (2004) and Righi-Cavallaro et al. (2015) as it facilitates obtaining additional food resources such as algae and debris adhered to bedrock. The ability to take advantage of the wide diversity of food resources available in the aquatic environment confers ecological advantages

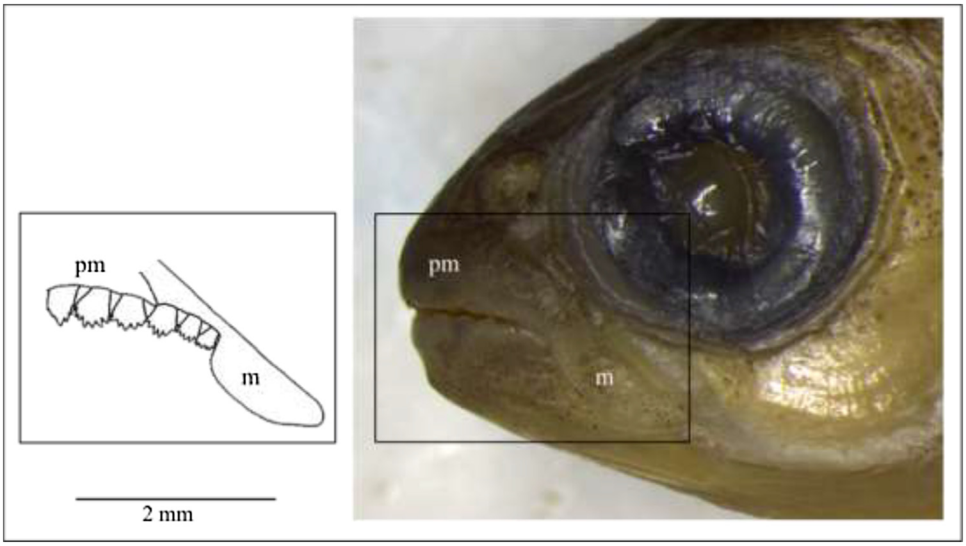

Fig. 2. The mouth of *Deuterodon iguape* (74 mm TL) indicating premaxilla (pm), maxilla (m), three posterior premaxillary teeth and three maxillary multicuspid teeth. Left illustration is modified from Lucena and Lucena (2002). Photo: Fabio Akashi.

to *D. iguape* in relation to other fish species that do not have as much trophic plasticity, especially when a particular food resource is highly available in the environment (Abelha et al., 2001). Despite it, one must consider that hard substrate scraper while laterally inclined foraging behavior may be briefly disadvantageous because it exposes the fish to potential visually oriented predators, such as aquatic birds or piscivorous fish, due to the reflection of the fish scales (Fig. 1f). We hypothesize that benefits from foraging behavior must be higher despite the predation risk, although this should be experimentally tested.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.jcz.2018.01.005.

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