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Short communication

Cannibalism on planktonic eggs by a non-filter feeding fish, *Micropogonias furnieri* (Sciaenidae)☆

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Abstract

Cannibalism by fishes on planktonic eggs is typical of filter-feeding marine planktivores, i.e. fishes that have the ability for filtering large volumes of water and concentrate small food particles. We report an unusual case of cannibalism on planktonic eggs by adults of the non-filter feeding fish *Micropogonias furnieri*, which are opportunistic bottom-feeding carnivores that prey mainly on polychaetes, molluscs and crustaceans. Spawning of *M. furnieri* takes place in the innermost part of the Río de la Plata estuary, near the upstream edge of a salinity wedge. Strong haloclines retain planktonic eggs in a bottom salty layer, thin enough to generate spatial coexistence of the planktonic eggs and the bottom associated adults. Moreover, eggs remain sufficiently concentrated as to be sucked in by fish lacking filtering apparatus. It has been stated that cannibalism appears to be genetically based but controlled or induced by different environmental cues. Our case, however, shows that environmental influence on cannibalism is not restricted to a signal that triggers the cannibalistic behavior: oceanographic processes may also act generating specific scenarios that promote and perhaps regulate the occurrence of cannibalism. © 2001 Published by Elsevier Science B.V.

Keywords: Estuaries; Environmental conditions; Sciaenidae; Croaker; Southwest Atlantic

1. Introduction

Cannibalism is a special form of predation that poses intriguing evolutionary questions, and has been well documented in several animal Phyla (Fox, 1975; Polis, 1981; Dominey and Blumer, 1984; Smith and Reay, 1991; Elgar and Crespi, 1992). Among fishes, intraspecific predation of eggs, larvae and juveniles is very common in nature (Dominey and Blumer, 1984). Cannibalistic behavior on fishes is associated with a wide variety of taxa, habitats and life-history strategies (Smith and Reay, 1991). The majority of identified cases of egg cannibalism by fish are attributed to non-kin intercohort cannibalism. This behavior is typical of filter-feeding marine planktivores as exemplified by anchovies and sardines (Hunter and Kimbrell, 1980; Dominey and Blumer, 1984; Smith and Reay, 1991).

Planktonic eggs are rich in energy and nutrients, and defenseless. They are patchily distributed in the water column, representing a useful food resource for those fish that have the ability for filtering large volumes of water. On the other hand, in fish that cannot efficiently

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concentrate small food particles, cannibalism (if present) mainly occurs on juveniles or adults, being common in piscivores as exemplified by the several species of hake (Alheit and Pitcher, 1995).

The whitemouth croaker (*Micropogonias furnieri*) is a coastal species that makes extensive use of the estuaries located on the Atlantic coast of America, from Yucatán Península in Central America (20°N) to Argentina (41°S) (Isaac, 1988), being common in the Río de la Plata estuary in northern Argentine coast (35°S). Adults are opportunistic bottom-feeding carnivores that mainly prey on polychaetes, molluscs, crustaceans and fish (Sánchez et al., 1991; Vazzoler, 1991; Bremec and Lasta, 1998). In this communication, we report cannibalism on planktonic eggs by adults of *M. furnieri*, and discuss the environmental and biological conditions that promote this unusual behavior in a bottom associated non-filter feeding fish.

2. Material and methods

Samples were taken during a cruise carried out in the Río de la Plata estuary from 13 to 24 November 1995, within the main spawning period of *M. furnieri* (Macchi and Christiansen, 1996). Sampling was performed over a spawning school, covering a 24 h period.

M. furnieri individuals were collected with a bottom trawl at seven stations. Specimens for stomach content analysis ($n = 85$) were randomly selected covering all the 24 h period. Total length (TL) was measured to the nearest centimeter for each individual. Sex and maturity stage (macroscopic examination) was also registered. The stomachs were preserved on 10% formalin for microscopic analysis in laboratory.

Fourteen oceanographic stations were performed with a Sea-bird 19 CTD. Data were processed to achieve a 0.5 m vertical resolution (precision of ±0.03°C in temperature and ±0.05 units in salinity). Salinity is reported as dimensionless values, following the Practical Salinity Scale (Anon., 1981).

Data on planktonic eggs are those presented by Acha et al. (1999). Two plankton tows were performed at six plankton stations, separately sampling the surface and the bottom layers defined by the halocline. Eggs were identified following the descriptions of de Ciechomski (1968) and Weiss (1981).

3. Results

Microscopic examination of the stomach contents was performed on five females (two juveniles and three adults), 78 males (13 juveniles and 65 adults) and two juveniles whose sex was not identified. The specimens ranged between 9 and 52 cm TL

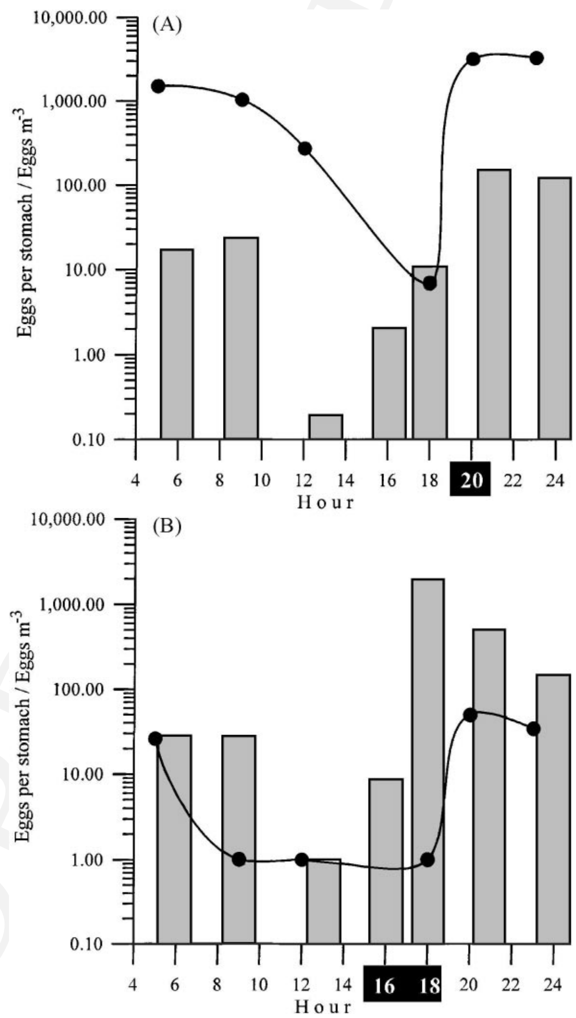

Fig. 1. Planktonic eggs in the stomachs and in the plankton during a 24 h period. (A) Mean values of *M. furnieri* eggs in the stomach contents (line and dots) and in the plankton (bars). (B) Mean values of *B. aurea* eggs in the *M. furnieri* stomachs (line and dots) and in the plankton (bars). Hours within black boxes indicate daily spawning peaks for *M. furnieri* (Macchi and Acha, unpublished data) and *B. aurea* (Acha, 1999).

(mean = 31.21 cm; S.D. = 8.51). All the adult females and 58 males (89.2%) were in reproductive activity (females with hydrated oocytes and males with running sperm).

Stomach analysis revealed that *M. furnieri* and *Brevoortia aurea* eggs were the main item in the contents, in both number and volume. The Brazilian menhaden, *B. aurea*, is an abundant Clupeidae in the Río de la Plata estuary and adjacent coastal waters. The estuary constitutes its main spawning ground in the region (Acha and Macchi, 2000). Eggs of *M. furnieri* were detected in 84 stomachs (98.8%), reaching up to 16,213 eggs per stomach (mean = 2314 eggs per stomach). Eggs of *B. aurea* were present in 54 specimens (63.5%), with a maximum value of 219 eggs per stomach (mean = 29 eggs per stomach). Although a classification of the eggs by developmental stages was not intended, it was evident that most of the eggs were in an early developmental stage. Only about 5% of *B. aurea* eggs and lesser than 1% of *M. furnieri* eggs had reached the point when the embryo becomes conspicuous.

Clams (*Mactra isabelleana* 6–8 mm in length), mysids and remains of other crustaceans were also recognized in the stomach contents, but they were present in very low numbers. A small quantity of plant debris was present in 60 stomachs.

Over a 24 h period, the presence of *M. furnieri* eggs in the stomachs showed highest values during the night (20:00–5:00 h), decreasing in late morning and with minimum values in the afternoon (Fig. 1A). The pattern of *M. furnieri* eggs in the plankton closely resembles that of the cannibalism on eggs. The presence of *B. aurea* eggs, both in the stomachs and in the plankton, also showed the highest values at dusk and during the night. These eggs in the plankton still remain in medium concentrations throughout the morning (Fig. 1B). *B. aurea* eggs showed higher concentrations in the plankton but lower in the stomachs than those of *M. furnieri* (Fig. 1).

Vertical salinity distribution during a 24 h period (Fig. 2) shows a highly stratified water column, with a thicker upper layer (salinity <5) overlying a saltier layer. The halocline fluctuated between 5 and 6.5 m in depth.

4. Discussion

B. aurea and *M. furnieri* have daily spawning cycles in this estuary (Acha, 1999; Macchi and Acha, unpublished data, respectively). The daily cycle of egg ingestion shown in Fig. 1 fits well with those spawning cycles, which peak between 15:00 and 18:00 h (*B. aurea*) and about 20:00 h (*M. furnieri*). Due to the dispersive nature of moving waters (e.g. Sinclair, 1988), egg concentration in the plankton will be highest immediately after the spawning peak. From that moment on, small-scale motions such as turbulence, will increase the inter-egg distance within the patch (Smith, 1973). Coupling of the spawning and egg

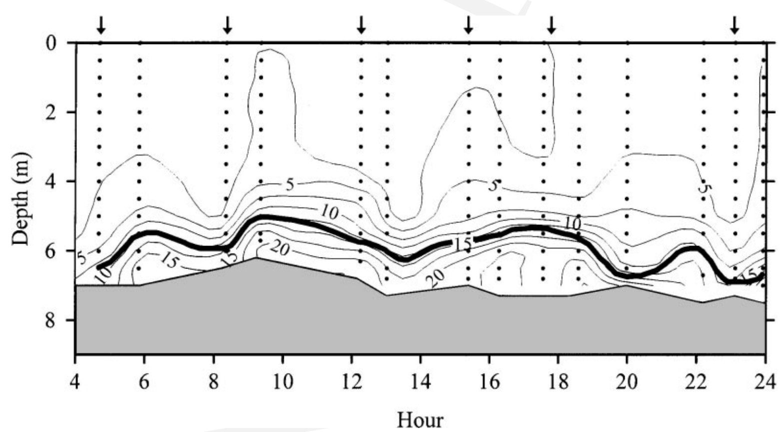

Fig. 2. Vertical salinity distribution during a 24 h period. Isohalines each 2.5 units. Thicker line shows the depth of the maximum vertical salinity gradient. Dots show CTD stations, arrows on the upper axes show plankton stations.

ingestion daily cycles suggests that the availability of eggs may influence the intensity of the cannibalistic behavior (Polis, 1981).

The oceanographic conditions at the spawning scenario seem to facilitate the occurrence of cannibalism by *M. furnieri*. In the Río de la Plata estuary, freshwater flows seaward on the surface, while denser shelf water intrudes along the bottom taking the shape of a salt wedge. The estuary, therefore, becomes a typically two-layer system (Guerrero et al., 1997; Mianzan et al., 2001). *M. furnieri* spawn pelagic eggs 730–1053 μm in diameter (Weiss, 1981) in the inner sector of the estuary, taking advantage of the retention properties at the head of the salt wedge (Acha et al., 1999). Strong haloclines have been measured at the spawning site, with maximum vertical salinity gradients ranging between 0.09 and 21.5 units m^{-1} (Acha et al., 1999). Given that protein (the main substance in most fish eggs) has a considerably higher specific gravity than freshwater (Hempel, 1979), *M. furnieri* eggs would be too dense to float in the lighter freshwater layer above the halocline, thus restricting their vertical distribution to the bottom saline layer. The height of this layer at the spawning site ranged between 0.5 and 3 m (Fig. 2) being thin enough to generate the spatial coexistence of the planktonic eggs and the bottom associated adults.

The reproductive pattern of *M. furnieri* is also shared by *B. aurea* (Acha and Macchi, 2000), and this fact explains the presence of *B. aurea* eggs in the stomach contents of *M. furnieri*. Furthermore, *B. aurea* eggs showed higher concentrations in the plankton but lower in the stomachs than those of *M. furnieri* (Fig. 1). Although the eggs of both species remain in the bottom saltier layer, their buoyancy is probably different. Consequently, the eggs would concentrate at different levels presenting a differential availability to fish, despite the narrow thickness of this bottom water stratum at the head of the salt wedge.

Almost all the specimens sampled were adults. Sex was highly biased with a predominance of males. Previous reports state that spawning schools of this species are numerically dominated by males, in proportions of about 2.5:1–5:1 (Arena and Hertl, 1983; Macchi and Acha, 1998). Females in the partially spent stage are distributed throughout the estuary, but during the oocyte hydration process, they segregate and concentrate at the spawning site and a high proportion of the fish are males (Macchi et al., 1996). Males remain at the spawning site longer than females, retaining their reproductive potential (Macchi et al., 1996). Our data are insufficient to evaluate differential cannibalistic behavior between sexes, but the permanence of the males at the spawning site may impede their visiting other feeding grounds, thus promoting the inclusion of eggs in the diet. However, Mianzan et al. (2001) have shown the presence of dense beds of the bivalve *M. isabelleana*, a genus reported in the diet of *M. furnieri* (Sánchez et al., 1991), near the location of the spawning ground of this species. Main items in the diet of *M. furnieri* are benthic organisms such as molluscs (Pelecypoda and Gastropoda); polychaete worms; crustaceans (Macrura, Natantia and Brachyura); and occasionally small fishes (Sánchez et al., 1991; Vazzoler, 1991; Bremec and Lasta, 1998). Morphological characteristics of *M. furnieri* are typical for a bottom feeder: it has crushing teeth and short gill rakers. The mouth is located in an inferior position, surrounded by well-developed pores of the *acoustico-lateralis* system, and with barbels on the lower jaw (Isaac, 1988). *M. furnieri* also presents protrusible premaxillae, a feature that can be advantageous in getting the mouth close to food that is sucked in from the bottom (Chao and Musick, 1977).

On the other hand, fishes that consume planktonic organisms have typically numerous, close-set, and elongated gill rakers, and non-protrusible jaws (Nikolsky, 1963; Bone et al., 1995). Neither the diet nor the morphological features indicate that *M. furnieri* is adapted to concentrate small food items distributed in the water column. Instead, the planktonic eggs would be relatively concentrated because of the small height of the saline bottom layer at the spawning site (Fig. 2). The estimations of egg concentrations in the plankton reached 159 eggs m^{-3} for *M. furnieri* and 2076 m^{-3} for *B. aurea* (Acha et al., 1999; Acha and Macchi, 2000), but those are mean values for the tows, and patchy distribution generates higher egg densities at smaller spatial scales. This increment in the numerical concentration of the eggs would permit *M. furnieri* to suck in large quantities of them. Low predation by visual feeders at the head of the salt wedge is expected due to high turbidity (Acha et al., 1999), but fishes such as *M. furnieri* that feed not only by sight, but also by olfaction and touch, may nevertheless prey on the eggs, showing that the site of spawning is still chosen in spite of the predation (cannibalism) on the eggs. Probably, the advantages of egg retention in the spawning area are greater than losses from cannibalism: for marine species with complex life histories, the proportion of the total losses from the population due to spatial processes may be much larger than losses due to energetic processes (predation, disease and starvation) (Sinclair and Iles, 1989).

Polis (1981) stated that cannibalism appears to be genetically based, but controlled or induced by different environmental cues. Our case, however, shows that environmental influence on cannibalism is not restricted to a signal that triggers the cannibalistic behavior. The environment, particularly oceanographic processes, may also generate specific scenarios that allow the coexistence of cannibals and their prey. In this mode, the environment promotes and perhaps regulates the occurrence of cannibalism, and although this circumstance may be restricted to species with complex life cycles (i.e. with planktonic stages), it must be noted that this is the case for most marine fishes (Balon, 1984).

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