

***Drift of Colomesus asellus
(Teleostei : Tetraodontidae)
larvae in the Amazon River***

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ABSTRACT

Colomesus asellus is the only Tetraodontidae occurring in the Amazon, which makes identification of the larvae possible, enabling to study its transport in the river. We sampled the mid-channel and the banks of the Amazon River over one year period. The drift occurred mainly during the floods, when the larvae were passively transported to a floodplain lake. The density of larvae near the banks was significantly higher than in midstream, and bank densities were not homogeneous, suggesting that spawning occurs in specific sites by the margins. The spawning strategy of C.asellus differs from that of other amazonian secondary freshwater fishes (sciaenids, engraulids and others) and that of other freshwater tetraodontids; it resembles the strategy of characiforms, siluriforms and of marine tetraodontids.

KEYWORDS : Amazon — Fish — Larvae — Larval development — Larval drift — Reproduction — Tetraodontiformes — *Colomesus*.

RÉSUMÉ

LA DÉRIVE DE LARVES DE *COLOMESUS ASELLUS* (TELEOSTEI : TETRAODONTIDAE) DANS LE FLEUVE AMAZONE

Colomesus asellus est le seul Tetraodontidae du bassin amazonien, ce qui rend possible l'identification des larves et l'étude de leur transport par le fleuve. Durant un an, nous avons échantillonné le cours de l'Amazone et le long des berges. Nous observons une dérive durant la crue, lorsque les larves sont transportées passivement vers les lacs de la plaine inondée. Le long des berges, la densité des larves est significativement plus importante que dans le milieu du fleuve, mais elle n'est pas homogène, ce qui laisse supposer que la ponte se réalise dans des sites spécifiques, près de la berge. La stratégie de reproduction de C.asellus diffère de celle des autres poissons d'eau douce de colonisation secondaire (Sciaenidae, Engraulidae et autres) et des autres tétraodontes d'eau douce, mais elle se rapproche de la stratégie des Characiformes et Siluriformes ainsi que de celle des tétraodontes marins.

MOTS CLÉS : Amazonie — Poisson — Larves — Développement larvaire — Dérive des larves — Reproduction — Tetraodontiformes — *Colomesus*.

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INTRODUCTION

The importance of large rivers channels as habitat for larvae of many important freshwater fishes has been demonstrated for temperate regions, where spawning areas have been identified and larval recruitment estimated (PAVLOV *et al.*, 1979; VAN WINKLE, 1977; HARROW and SCHLESINGER, 1980; HERGENRADER *et al.*, 1982). Large tropical rivers also have been suggested as the spawning areas for many species (WELCOMME, 1985; NAKATANI *et al.*, 1994), but ichthyoplankton data are lacking for the Amazon systems. An unpublished study by ARAUJO-LIMA (1984) reported high densities of characiform larvae drifting in the Amazon river; he did not examine distribution of other groups, but subsequent sorting of his samples revealed the presence of Tetraodontiformes larvae.

The Tetraodontidae (puffers), a predominantly marine and tropical group (LEIS, 1983), is represented in the Central Amazon basin by only one species, *Colomesus asellus* (MÜLLER and TROCHEL, 1848; TYLER, 1964). It is a small sized fish, reaching 11 cm, relatively abundant in the turbid and clearwater rivers of the Central Amazon region, but not found in the Rio Negro (GOULDING *et al.*, 1988). FINK and FINK (1978) and JUNK *et al.* (1983) captured adults of *C. asellus* in floodplain lakes during high and low water-level seasons, but only in sites with high oxygen levels, suggesting that the species is sensitive to low oxygen availability.

The reproductive biology of the freshwater Tetraodontiformes is poorly known (BREDER and ROSEN, 1966; LEIS, 1983). Because only one species from this group occurs in the area, the ease of identification offers a good opportunity to study its early life history. The aim of the present study was to locate *C. asellus*'s spawning sites and to determine the pathways and seasonal dynamics of its larval drift and distribution.

In addition this study also contributes to the understanding of the reproductive strategies used by secondary freshwater fishes (predominantly marine groups) in the Amazon basin.

Study Area

The area of the River Amazon (fig. 1) studied had many islands and side channels. The sections without islands were up to 5 km wide, and the minimum distance between islands and banks was 1.2 km (fig. 1). The water velocities varied from 2 m.s⁻¹ in midstream to 0.3 to 1 m.s⁻¹ near the banks. The banks were steep, and cut by the current even in high parts of the deposition areas (filling banks).

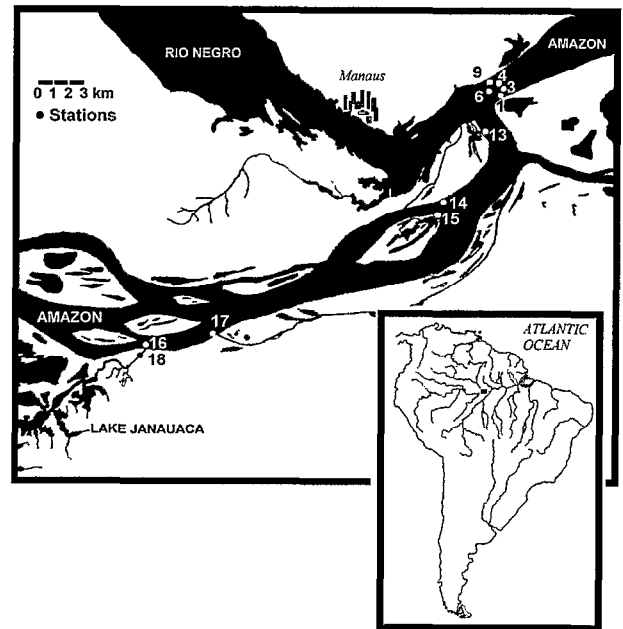


FIG. 1. — Study area and sampling sites.
Zone d'étude et d'échantillonnage.

Floodplains lakes, where most of primary production occurs (FISHER, 1978), were located at the edge of the Amazon and at the interior of islands. They were connected to the main river by channels.

MATERIAL AND METHODS

We sampled fish larvae weekly at six sites along the bank and in midstream of the Amazon (sites 1, 3, 4, 6, 9 and 13; fig. 1) from August 1981 to July 1982 and monthly in five bank sites and one side channel site (sites 14 to 18; fig. 1) from February to July 1982. All samples were taken between 09:00 to 15:00. Sampling failed during three weeks of January 1982 due to technical problems. The bank sites were located at about 5-10 m off margins and islands. Dissolved oxygen and temperature were measured with a YSI-57 probe.

We used a conic-cylinder net with a 0.6 m mouth diameter, 3.25 m length, and 0.4 mm mesh aperture. The net was attached to a rack at the front of a boat. A General Oceanic flowmeter was centrally positioned in the mouth of the net. We pushed the net horizontally for approximately 3 minutes, holding position against the river current, at 0.4 to 1 m deep. This effort filtered near 50 m³ of water. Longer sam-

pling time was unpractised due to the heavy load of sediments.

The larvae were preserved in 10 % formalin and sorted, measured for standard length (sl) and counted using a WILD M8 stereomicroscope. *C. asellus* larvae were distinguished from characiforms and scianids based on its smaller number of myomeres and, relatively larger eyes (WELSH and BREDER, 1924; ARAUJO-LIMA and DONALD, 1988) and from the siluriforms and clupeiforms by the lack of barbels and larger body-height-to-standard-length ratio (FUIMAN, 1983; MCGOWAN and BERRY, 1983). Morphological characterisation of *C. asellus* larvae followed (ARAUJO-LIMA, 1991).

Analysis of variance without replication was used to test for differences in larval density between bank sites (including site 15 and 18). Mean larval densities at sites 1, 9 and 13, grouped as bank, and sites 3, 4 and 6, grouped as midstream, were compared using the Paired Student t-test.

RESULTS AND DISCUSSION

River characteristics

River water temperatures averaged 28.3 °C ($s = 0.25$) with little variation. Dissolved oxygen concentrations were similar at all study sites (avg = 4.63 ppm; $s = 0.40$), except the island site (station 15; fig. 1), where a lower mean concentration (2.86 ppm) was recorded. Differences in the dissolved oxygen concentrations between surface and bottom layers were always smaller than 0.4 ppm, except site 15 at the island and site 18 at the channel that linked the "várzea" lakes to the main river (fig. 1), which occasionally had very low concentrations at the bottom (<1 ppm). The river transports a load of sediments that drastically reduces the light penetration in the water. Secchi disc depth ranges from 0.14 to 0.31 m (FORSBERG *et al.*, 1988).

The main seasonal effect on the study area is the fluctuation of the water level, which varies in average 9.6 m between low water (October-November) and high water season (June-July). The average complete cycle lasts 360 days. The lowest water level during the sampling period was between 11 and 15 November 1981. The flood peaked 29 m (Manaus Harbor gage) on 26 June 1982, the 223rd day after flooding began.

Morphological features

We analysed 50 larvae measuring 2.04 to 2.88 mm standard length. The larvae had large body height

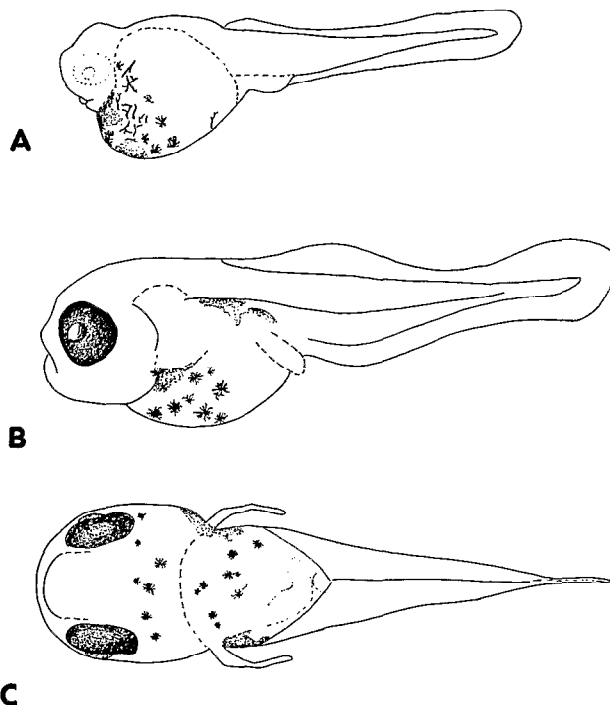


FIG. 2. — Lateral view of *C. asellus* larvae measuring 2.04 mm of SL (A) and of 2.64 mm (B), and ventral view of 2.71 mm larvae (C).

Vues latérales des larves de C. asellus de 2.04 mm LS (A) et 2.64 mm LS (B) et vue ventrale d'une larve de 2.71 mm LS (C).

and eye diameter (fig. 2A, B and C). To reduce the effect of the allometry in the measurements, we divided the data set in two size groups (tab. I). Most of the larvae sampled still possessed their yolk sac. Body pigmentation consisted of 8 to 50 large and ramified melanophores in the ventral part of head and abdomen. The dorsal part of the swimbladder was also pigmented (fig. 2). The myomere number varied from 20 to 22, being 8 to 9 pre-anal ($n = 25$), corresponding to the number found for vertebrae in the adults.

Larval distribution

A total of 145 *C. asellus* larvae were found in 38 of the 255 samples examined. The density of larvae varied from 0 to 25.3 individuals.100 m⁻³, which suggests very low abundance, though of the same order of magnitude as those reported for larvae of species in large temperate rivers, such as the Missouri and Ili Rivers (HERGENRADER *et al.*, 1982; NEZDOLIJ, 1984).

TABLE 1. — Average and range of body proportions relative to standard length (SL) for two size groups (size range in parenthesis) of *C. asellus* larvae. PDL = pre-dorsal length; IOL = inter-orbital distance; PAL = pre-anal length; ED = eye diameter; SNL = snout length; MH = maximum body height

Moyennes et intervalle de variation des proportions du corps, exprimées en pourcentage de la longueur standard (SL), pour deux classes de taille de larves de C. asellus. PDL = longueur pré-dorsale; IOL = distance interorbitale; PAL = longueur pré-anale; ED = diamètre de l'œil; SNL = longueur de museau; MH = hauteur maximum du corps

Larval groups	PDL	IOL	PAL	ED	SNL	MH
2.31 mm group (2.0-2.4)						
Average	29.8 %	25.3 %	52.2 %	9.9 %	7.6 %	25.3 %
Range	21.1 % - 40.0 %	14.0 % - 34.0 %	45.0 % - 64.5 %	6.7 % - 13.5 %	2.3 % - 10.5 %	14.0 % - 34.0 %
N	20	20	20	20	20	20
2.45 mm group (2.41-2.88)						
Average	26.0 %	24.5 %	50.0 %	10.0 %	7.2 %	24.1 %
Range	20.0 % - 36.0 %	18.0 % - 29.0 %	42.0 % - 57.0 %	7.0 % - 14.0 %	3.0 % - 10.0 %	18.0 % - 29.0 %
N	30	30	30	30	30	30

Vertical distribution and night drift could not be determined due to technical difficulties and river current. Vertical stratification seems to be species dependent (PAVLOV *et al.*, 1977; NEZDOLIJ, 1984; CORBETT and POWLES, 1986), and may have influenced our results. PETRY (1989) did not find stratified distribution of characiform larvae, but further analysis is necessary to know if his conclusions can be applied to *C. asellus* larvae. Therefore, the density results should be seen as an index of abundance and not as density estimations. Vertical distribution and day-night variations on the abundance index, however, are unlikely to bias comparison between sampling sites, since the samples were taken at similar depth and within a relatively restricted daytime period.

The largest larvae sampled measured 2.88 mm, suggesting that they may drift in the river up to this length. Larger larvae may escape the current and stay close to the bottom or die of starvation in the river. No larva was found when the water level was lowering and the floodplain lakes were flushing into the Amazon. Larvae started to be caught at the minimum river level (17.24 m) when the water level was changing little (fig. 3). Approximately 97.9 % of the larvae were captured between January and April (fig. 3), constituting a spawning season of four months during 1982. Spawning began 30 days after the beginning of the flood season, suggesting that *C. asellus* spawns mostly in the river, only during the floods, and probably later than many characiform species. The characiforms larval period peaks at the very beginning of the flood (ARAUJO-LIMA, 1984; PETRY, 1989). Comparisons with other groups are limited, since not much is known about the spawning area and season of secondary colonisers (species of predominantly marine groups), such as clupeiforms, scianids and pleuronectiforms; but preliminary data

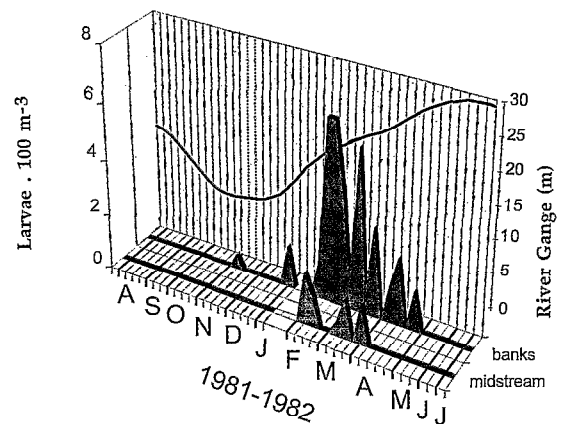


FIG. 3. — Average larval density of bank and midstream sites between August 1981 and July 1982. Only bank sites near the mouth of Rio Negro were averaged.

Moyennes hebdomadaires de la densité en larves dans les stations des berges et de la partie centrale du fleuve entre août 1981 et juillet 1982. Seules sont présentées les moyennes relatives aux stations des berges, près de la confluence avec le Rio Negro.

suggests that the scianids and engraulids spawn during much longer periods (WORTHMANN, 1980; ANNIBAL, 1983; pers. obs.).

We analysed the horizontal distribution of the larvae in two steps using only the data of January to early April, when larval densities were higher. Larval density differed significantly between bank sites (ANOVA; $F = 3.61$; $n = 21$; $d.f. = 6$; $p = 0.02$). Sites 13, 16, 17 and 18, near the mouth of Rio Negro, near side channels and in the channel (fig. 1), seemed to have higher densities than the other sites (fig. 4),

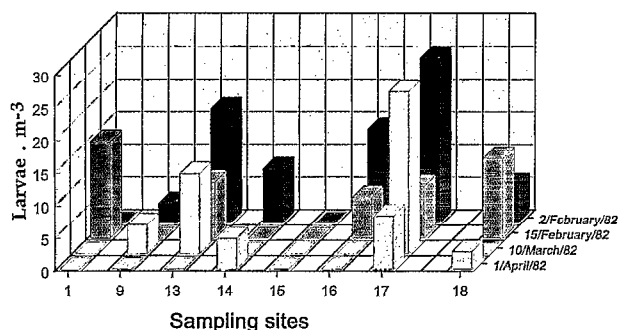


FIG. 4. — Larval density of bank (1 to 17) and Janauaca lake channel sites (18) in four sampling dates.

Densité en larves dans les stations de berges (1-17) et du fleuve du Lac Janauacá (18) sur quatre échantillonnages.

but statistical analysis is still needed to confirm this trend. The channel (site 18) connects the river to a floodplain lake. In this specific site we found larvae of *C. asellus* being transported to a floodplain, if it occurs in other Amazon lakes remains to be checked.

Average larval density varied greatly during the drift season in sites near to the mouth of the Rio Negro (fig. 4). Average larval density in midstream was significantly smaller than at the banks (Paired *t* test; d.f. = 6; *t* = 2.64; *p* = 0.039).

The distribution of *C. asellus* larvae in the Amazon seems to follow the pattern found for the characiforms (ARAUJO-LIMA, 1984), with larval densities being higher near banks and at specific sites, such as mouth of side channels. Drift of larval species near banks have been shown in temperate rivers, as well (PAVLOV *et al.*, 1978; HERGENRADER *et al.*, 1982; STAINES *et al.*, 1983; NEZDOLYI, 1984).

The distribution of *C. asellus* larvae may be influenced by spawning activities, individual-level behavioural responses or river hydrodynamics. Larval behaviour seems of minor importance in a river with strong current and low light penetration such as the Amazon. Meandering rivers have secondary currents, which move the water at speeds higher than 0.3 m.s⁻¹ in a plane normal to the axis of the primary flow (THORNE *et al.*, 1985). In the central part of the channel, helical skew-induced flow produces inward velocities near the bed, which sweep the bedload towards the inner bank (filling bank), and at the outer bank (cutting bank) a small cell of reverse rotation moves towards surface. Owing to secondary cur-

rents, one would expect higher surface concentration of larvae in the filling banks. Sites 9, 16 and 17 were situated on cutting banks and sites 1, 13, 14 and 15 were at filling banks. Therefore, there does not seem to be a good match between larval density and water movements, suggesting that hydrodynamics alone do not explain the pattern of larval distribution.

Spawning activity is probably the main factor leading to larval distribution of *C. asellus*. It may be hypothesised that this species spawns in the river and at banks sites near the mouth of floodplain lakes and tributaries, mostly during floods. Larvae are transported into the floodplain lakes where they can find shelter and food supply. This strategy is similar to the river-spawning characiforms, perhaps because of similar egg characteristics, but quite distinct from the other secondary colonisers, such as sciaenids and tetraodontiforms. The eggs of characiforms and tetraodontiforms sink, whereas those of scianids are buoyant (ARAUJO-LIMA, 1984, 1991; LEIS, 1983; BREDER and ROSEN, 1966). If the eggs of tetraodontiforms were spawned in the lakes, then they would sink to the bottom where dissolved oxygen levels are highly variable, potentially inhibiting their development. Thus oxygen may be a key factor to explain the distribution of young and adults of *C. asellus*.

Spawning in the river is expected to require high fecundity as larvae will be exposed to high mortality rates. The small larval size of *C. asellus* indicate that the species has a small egg size (ARAUJO-LIMA, 1994), as the marine tetraodontids (LEIS, 1983). High fecundity in fish is normally related to spawning migrations, relatively large body size and small eggs (WELCOMME, 1985). A small fish such as *C. asellus* is not adapted to long migrations, but in Central Amazon the spawning migrations could be short, i.e. from the floodplains to the river. The special hydrographic conditions of the basin may not have exerted a selective pressure on *C. asellus* to evolve a reproductive strategy divergent of its marine relatives, such as sedentary life mode and large eggs (and probably low fecundity) such as reported for other freshwater species of this group (LEIS, 1984).

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