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Drift of characin larvae, *Bryconamericus deuterodonoides*, during the dry season from Andean piedmont streams

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Synopsis

The downstream transport of fish larvae is well known from temperate running waters, but there exists remarkably little information for tropical streams. We sampled drift in two Andean piedmont streams during the dry seasons of 1986–1988. *Bryconamericus deuterodonoides* (Characidae) larvae were found to be extremely abundant in some drift collections, with peak drift densities exceeding those of temperate streams by as much as an order of magnitude. Drift of fish larvae displayed pronounced diel periodicity, with more than one-quarter of a million larvae collected during the night compared to two individuals during the day. Fish larvae were more abundant during the latter compared to early part of the dry season, even in years when streams were reduced to small isolated pools by the end of the season. These observations indicate that the dry season represents an important period of reproduction for the characid, *Bryconamericus deuterodonoides*, and possibly other neotropical fish species.

Introduction

Fish larvae are often found drifting downstream in the water column of running waters. Studies from temperate streams show that fish larvae display a pattern of nocturnal peaks in drift densities (e.g. Elliott 1966, Clifford 1972, Gale & Mohr 1978, Naesje et al. 1986). However, there are virtually no published data on drift activity of fish larvae in tropical streams. To our knowledge, the only related tropical study is that of Elouard & Lévêque (1977), who found that small fish displayed diel periodicity in drift collections from an Ivory Coast stream. Here we report on the abundance of larvae of the neotropical characin *Bryconamericus deuterodonoides* in drift collections made during three successive dry seasons from Andean piedmont streams. These observations present new information showing that the abundance of fish larvae in tropical running waters can be much higher than drift values typically reported for temperate streams. Furthermore, a pronounced diel periodicity was observed similar to temperate streams. Finally, fish larvae were abundant during periods when streams were drying up because of drought, which is contrary to the notion that characin reproduction is largely restricted to the rainy season.

Materials and methods

Bryconamericus larvae were collected during the dry season (December–April) from two shallow rocky streams, Rio Las Marias, Portuguesa State and Rio La Yuca, Barinas State, Venezuela. These streams display distinct seasonality, typical of running waters in the Venezuelan Andean piedmont. During the dry season (December–April) piedmont streams are normally transparent with reduced discharge. In contrast, there is often heavy rainfall in the rainy season (May-November), resulting in high discharge, frequent flooding, and high turbidity from large sediment loads.

Rio Las Marias is a stony-bottom stream, 20–30 m wide during the peak of the rainy season, but reduced to a sequence of pools and shallow riffles during the dry season. In two years (1986 and 1988) only small isolated pools remained of the stream by the end of the dry season. At our collection site fish diversity was high (55 species). Drift was sampled during the dry season on five dates between 1986–1988 (3–4 February 1986, 31 December 1986–1 January 1987, 23–24 January 1987, 23–24 December 1987, 21 January 1988). The exact reach changed between years due to shifts in the stream channel that occurred during the previous rainy season floods. Depth at the collecting site ranged from 10–30 cm, and width from 4–8 m.

Rio La Yuca is ca. 20 m wide and flows continuously throughout the year. The stream bed consists of stony riffles and pools, with interspersed sand bars. Fish diversity is lower (we collected 29 species) than at Rio Las Marias, but *B. deuterodonoides* is abundant and the most common fish at the study site. Drift was sampled on three dates during the dry season between 1986–1988 (12–13 March 1986, 25–26 January 1987, 18–19 January 1988). Water depth at the drift site ranged from 10–35 cm. Sampling was conducted on nights during the dark phase of the lunar cycle, because moonlight has been shown for some stream invertebrates to suppress drift activity (Anderson 1966). Drift was collected by suspending two nets (dimensions: mouth opening = 0.32 m × 0.32 m, length = 2 m, mesh = 300 μm) side by side in the water column during regular intervals over a 24 h period. Samples were collected every 4 h at all sites and dates, except 21 January 1988 in Rio Las Marias, when drift was collected from one nighttime (2000–2200 h) and one daytime sampling period (1200–1400 h). Sampling periods lasted for 20 minutes in Rio La Yuca, and ranged from 20–120 minutes in Rio Las Marias, depending on sampling date. Drift was expressed as density per 100 cubic meters, which was calculated by dividing the number of fish larvae collected during the sample period, by the volume of water filtered through the net, and then multiplying the value times 100 (Allan & Russek 1985). The volume of water sampled by the drift nets was measured at the end of each 24 h collection by determining the stream current velocity and water depth at the opening of the nets. Current velocity was measured using a General Oceanics flow meter. In addition, we recorded the water temperature during the times of the drift collections. On some dates dissolved oxygen, pH, and total hardness were measured using LeMotte water chemistry kits.

Fish larvae from a live sample were raised to adults in the laboratory for species identification. We considered fish in our drift collections to be larvae due to the lack of discernible yolk, yet the absence of fully differentiated fins (see Balon 1975).

Results

At both Rio Las Marias and Rio La Yuca, water temperature and dissolved oxygen displayed diel variations. Highest values for both parameters always occurred in the afternoon for all dates and sites (Fig. 1). At Rio Las Marias, water temperature ranged from 22.5 to 32.0° C, depending on date and time of day, whereas dissolved oxygen varied from 5.8 to 8.8 ppm. Rio La Yuca displayed slightly less variation in physical parameters than Rio Las Marias, with water temperature ranging from 24.5 to 29.5° C. Dissolved oxygen was measured only over a single collection date (18–19 January 1988) at Rio La Yuca, with values ranging from 6.7 to 8.8 ppm during the 24 h period (Fig. 1). Finally, at Rio Las Marias the pH varied from 7.6

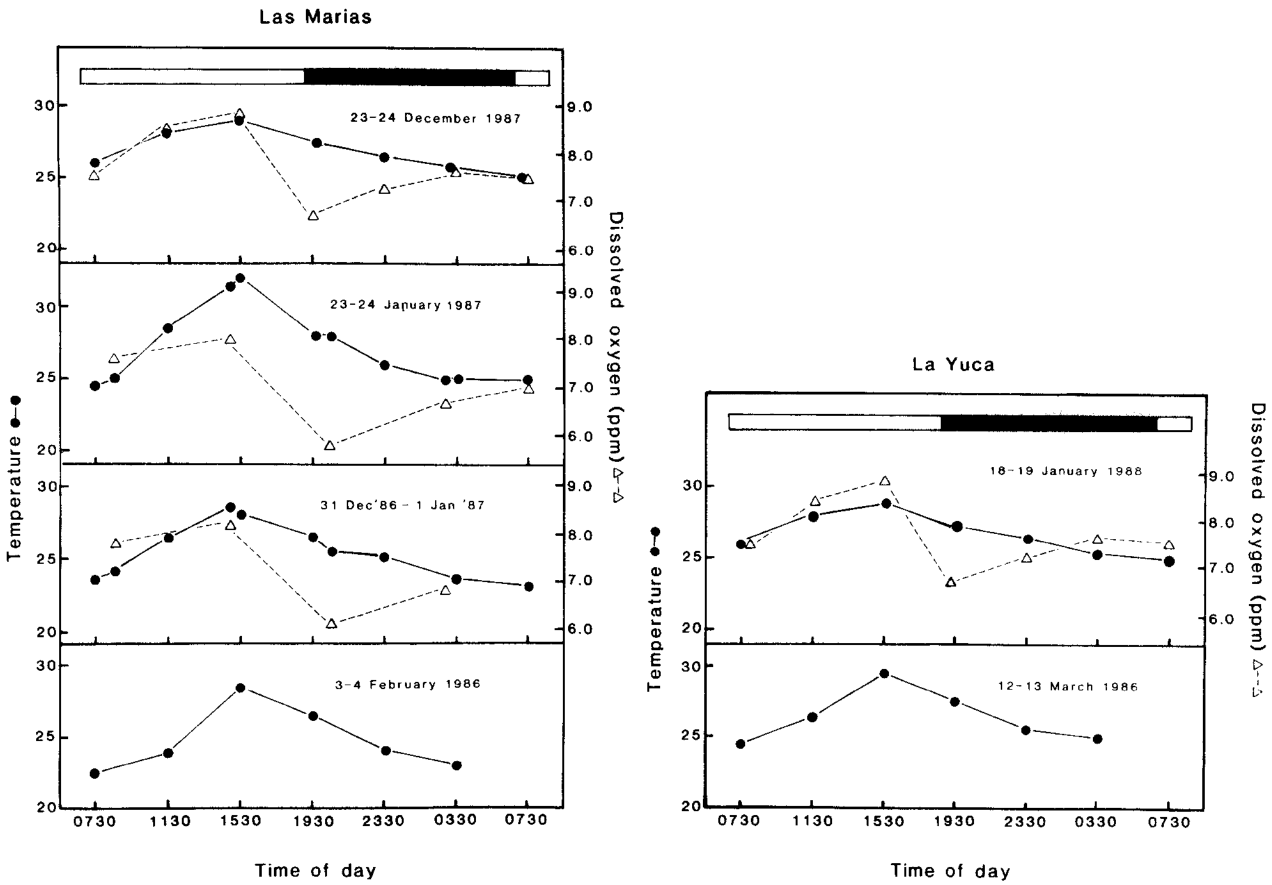

Fig. 1. Diel variation in water temperature (° C) and dissolved oxygen (ppm) in Rio Las Marias and Rio La Yuca during dates of drift collections.

to 8.5 according to date, whereas total hardness ranged from 45 to 70 ppm. At Rio La Yuca the pH varied from 7.9 to 8.0, and hardness exhibited a range of 100 to 120 ppm.

Bryconamericus larvae were found in the drift on all of the eight sampling dates. Drift density varied greatly, depending on both the date and time of the collection (Fig. 2, 3). Drift displayed very pronounced and consistent diel periodicity. We collected more than one-quarter of a million larvae at night (1930 to 0430 h) and only two individuals during the day (0730 to 1630 h). Although on all dates *Bryconamericus* larvae were found in the drift at Rio Las Marias, collections from late in the dry season contained greater numbers of larvae than those made earlier in the season. Peak drift densities always occurred immediately after dark in Rio Las Marias, then steadily declined throughout the night and early morning (Fig. 2). Peak drift densities averages $> 25000 \times 100\,m^{-3}$ on 3 February 1986, $58.0 \times 100\,m^{-3}$ on 31 December 1986, $3383.6 \times 100\,m^{-3}$ on 23 January 1987, $1151.0 \times 100\,m^{-3}$ on 23 December 1987, and $11{,}654.3 \times 100\,m^{-3}$ on 21 January 1988.

Fish larvae were less abundant in the drift at Rio La Yuca compared to Rio Las Marias. *Bryconamericus* larvae were common in Rio La Yuca on 12–13 March 1986, and 18–19 January 1988, however, only a single individual was taken on 25–26 January 1987. Similar to Rio Las Marias, drift of fish larvae was restricted to the nighttime hours at Rio La Yuca (Fig. 3). The peak drift densities seen at this site averaged $457.5 \times 100\,m^{-3}$ on 12 March 1986, and $219.8 \times 100\,m^{-3}$ on 18 January 1988.

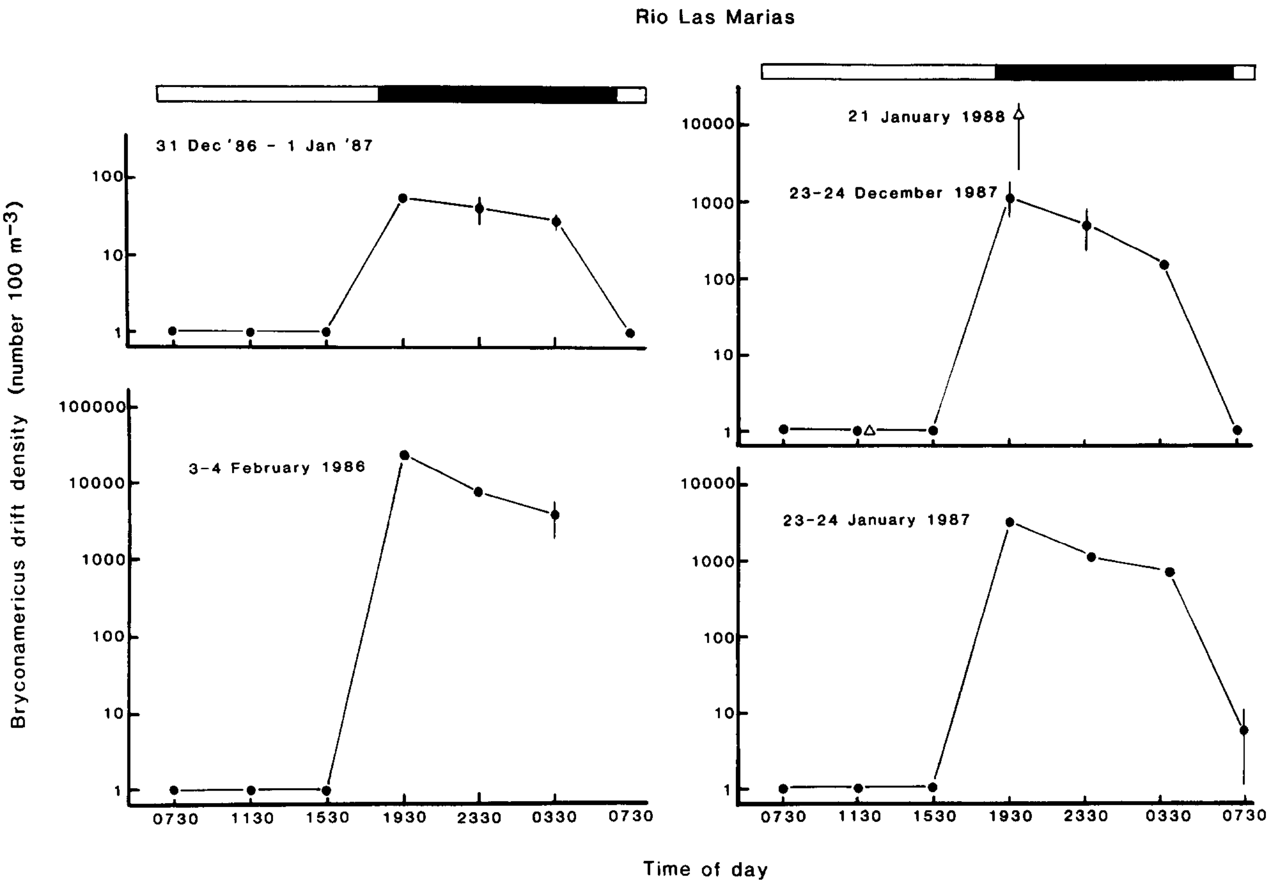

Fig. 2. Drift densities (number $100\,m^{-3}$) of *Bryconamericus* larvae sampled on 5 dates over 24 h periods in Rio Las Marias. Dots represent the mean from 2 replicate drift nets, and vertical bars denote the ranges. Blackened horizontal bar indicates night collections. Collections on 21 January 1988 were made at two time periods only.

Discussion

Little is known about the drift of fish larvae from tropical streams, whereas studies of temperate streams have been conducted on a variety of taxa, from a number of different fish families. We observed much higher peak drift densities for *Bryconamericus* than has been reported for temperate streams from a range of sizes. Representative peak drift densities for freshwater fish larvae and alevins vary from 5–25 × $100\,m^{-3}$ for trout alevins in a small stream in England (Elliott 1966), 2500 × $100\,m^{-3}$ for white sucker in a brown water stream in Alberta, Canada (Clifford 1972), 15–25 × $100\,m^{-3}$ for 18 combined taxa from a mid-size, Arkansas warm-water stream (Brown & Armstrong 1985), 300 × $100\,m^{-3}$ for all taxa in the Mississippi river (Keevin & Thomerson 1985), and 82 × $100\,m^{-3}$ for eight fish species in the upper Colorado River (Carter et al. 1986). The drift density of > 25000 × $100\,m^{-3}$ *Bryconamericus* larvae observed in Rio Las Marias (February 1986) is an order of magnitude greater than the highest reported values for temperate stream fishes (Clifford 1972), and even exceeds the highest drift densities for temperate stream invertebrates (ca. 17000 × $100\,m^{-3}$ for the mayfly *Baetis*, Pearson & Franklin 1968).

Bryconamericus larvae displayed pronounced diel drift periodicity. This is consistent with studies that have been conducted in temperate streams (e.g. Elliott 1966, Gale & Mohr 1978, Brown & Armstrong 1985, Corbett & Powles 1986, Naesje et al. 1986). These other studies, however, showed that at least some larvae typically drifted during the

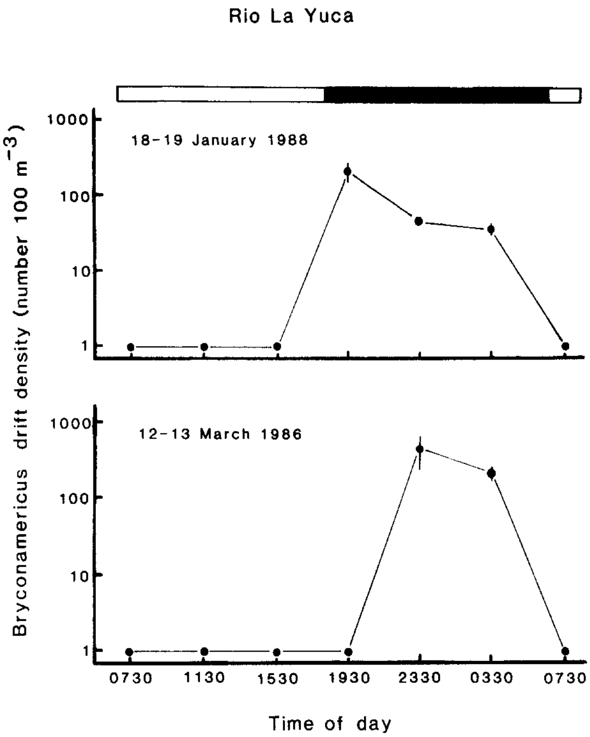

Fig. 3. Drift densities (number $100 m^{-3}$) of *Bryconamericus* larvae sampled on 2 dates over 24 h periods in Rio La Yuca. Dots represent the mean from 2 replicate drift nets, and vertical bars denote the ranges. Blackened horizontal bar indicates night collections.

day, although at lower levels. We found virtually no larvae in the drift during the daytime hours. Armstrong & Brown (1983) also observed catfish alevins to be absent from the drift during the day, because they bury themselves deep in the substrate during the daylight hours.

We speculate that fish larvae drift at night to avoid the numerous diurnal predators common in many running waters. Studies of stream insects also suggest that drift periodicity is an evolutionary response to minimize exposure to day-active, drift-feeding fishes (Allan 1978, personal observation), as the intensity of predation by drift feeders is often greater during the day than by night. Furthermore, diel periodicity is not observed for invertebrate drift from Andean streams that are naturally devoid of drift-feeding fishes (personal observation). Other hypotheses have been proposed to explain diel drift periodicity, including the greater availability of food resulting from increases in invertebrate drift and nocturnal disorientation resulting in accidental dislodgement (Armstrong & Brown 1983). Armstrong & Brown found that although alevins fed predominantly at night, invertebrates common to the drift represented a relatively small percentage of the diet. The possibility of larval disorientation has not been tested for stream fish larvae; however, this does not appear to be important for invertebrate drift (Allan & Feifarek 1989), and is an unlikely explanation for fish larvae.

It is of some ecological significance that fish larvae were so abundant in these two tropical streams midway through the dry season. Our data were unexpected in that tropical stream fishes typically reproduce during periods when rain is abundant and water levels are rising (Lowe-McConnell 1975, Kramer 1978, Welcomme 1979). For example, in the Venezuelan llanos (Taphorn & Lilyestrom 1984) and the lower Orinoco River (Novoa 1982), most species spawn just after the first heavy rains of the wet season. This may allow for protracted larval development in the floodplains, when food may be most abundant and aquatic vegetation provides refugia from predators (Lowe-McConnell 1975). Furthermore, spawning at this time may also ensure that young individuals are not trapped in drying pools, where predators become more concentrated as the dry season progresses and habitats shrink in size.

Although reproduction in tropical fishes has been most commonly reported to occur during the rainy season, there are some notable exceptions. For example, Kramer (1978) found that a number of characoids in a Panamanian stream reproduced during the dry season, and suggested that this was perhaps due to the mild dry season experienced by the local region. His study included the congener *Bryconamericus emperador*, but, unlike *B. deuterodonoides*, this species spawned during the June floods. In southeastern Brasil, several species of characins breed during the dry season. Sazima (1980) observed large spawning congregations of *Apareiodon piracicabae* and *A. ibitiensis* (Parodontidae) in a shallow river, and Uieda (1984) commented that a number of characids (*Bryconamericus* sp., two species of *Astyanax, Hephessobrycon* *anisitsi*, and *Oligosarcus pintoi*) appeared to reproduce during the dry season. Furthermore, Novoa (1982) and Nico & Taphorn (1984) reported that freshwater drum *Plagioscion* sp., and other commercial species spawn year round in Venezuelan waters.

The biology of early life-history stages is virtually unknown for natural populations of tropical stream fishes. This may be in part due to the diurnal habits of biologists studying organisms that are largely nocturnal during their early development. It is clear that *B. deuterodonoides* reproduction occurred in three consecutive dry seasons in our study area. Perhaps more tropical fish species reproduced during the dry season than is commonly believed. It will be difficult to generalize about the life histories of tropical stream fishes until we have a greater understanding of their early life stages.

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