Reproduction, feeding and migration patterns of *Prochilodus nigricans* (Characiformes: Prochilodontidae) in northeastern Ecuador

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The black prochilodus, *Prochilodus nigricans,* is an important food fish distributed throughout aquatic habitats of the Ecuadorian Amazon. We sampled gonad weight, body condition, and feeding of this species to address the question of whether changes in these biological parameters are related to hydrological variation and migration patterns. High frequency of empty stomachs and poor body condition corresponded to migration periods. Gonad condition analysis revealed a single, discrete spawning period in April (end of rising water season). We synthesized our own and published observations on migration patterns of black prochilodus and presumptive factors that influence those movements. Mature individuals make lateral migrations from peripheral flooded habitats to large white water rivers to spawn. Eggs and larvae drift downstream to nurseries at least into Peru and perhaps into Brazil; there do not appear to be nursery habitats in Ecuador. After 6-18 months, they migrate upstream, recruiting to parental stocks. Long-distance migrations of black prochilodus and similar fishes in Neotropical rivers disobey political boundaries. Conservation and management of such migratory fishes, thus, requires international co-operation and integrated conservation efforts.

Keywords: Black prochilodus, Condition factor, Gonadalsomatic index, Life-history, Stomach fullness.

El bocachico, *Prochilodus nigricans*, es una fuente importante de proteínas, distribuido en hábitats acuáticos de las tierras bajas de la Amazonía ecuatoriana. Se muestreo el peso de las gónadas, la condición corporal, y alimentación de esta especie para determinar la relación de estos parámetros biológicos con la variación hidrológica y patrones migratorios. Una frecuencia alta de estómagos vacíos y la pobre condición corporal corresponde a períodos de migración. El análisis del estado de las gónadas reveló un corto periodo de desove en abril (fin de la temporada de aumento del río). Hemos sintetizado nuestras observaciones propias y publicadas sobre migraciones del bocachico, así como los factores que presumiblemente influyen en estos movimientos. Los peces adultos migran lateralmente desde hábitats periféricos inundados hasta ríos de aguas blancas para desovar. Los huevos y larvas flotan aguas abajo hasta llegar a sitios de crianza en Perú y posiblemente en Brasil; no parece haber hábitats de crianza en Ecuador. Después de 6-18 meses, los bocachicos migran aguas arriba, reclutando a las poblaciones parentales. Las migraciones a larga distancia del bocachico y peces similares en ríos Neotropicales desobedecen las fronteras políticas. Una gestión apropiada de este recurso requiere de cooperación internacional y esfuerzos integrados de conservación.

Palabras Clave: Bocachico, Factor de condición, Historia natural, Índice gonadosomático, Llenura del estómago.

Introduction

The black prochilodus, *Prochilodus nigricans* Agassiz,1929, is an important food fish occupying Western and Central Amazonia (Goulding, 1981; Loubens, Panfili, 1995; Castro, Vari, 2004; Batista, Petrere Júnior, 2007). This detritivorous fish (Bowen, 1984) displays a series of movements among habitats in response to varied factors such as hydrological cycles, water chemistry, reproduction, feeding and predation. Researchers throughout the Neotropics have focused on prochilodontids like *P. nigricans* because of their considerable nutritional and economic value. Studies include several on reproductive

behavior and migrations in various areas of the Neotropics (*e.g*., Schwassmann, 1978; Mochek *et al.*,1991; Loubens, Panfili, 1995; Fernandes, 1997; Quizia, Ruffino, 1997; Winemiller, Jepsen, 1998; Stassen *et al*., 2010). Little is known, however, of the life histories and reproductive ecology of black prochilodus and other migratory fishes in eastern Ecuador. Dispersal of a fish species may depend on diverse life stages and the context of geomorphology and habitat heterogeneity in a given river basin (Duque *et al.,* 1998). This analysis complements available information on ecology of *P. nigricans* in eastern Ecuador (Silva, Stewart, 2006), relating their migratory, reproductive and feeding behaviors to seasonal flooding dynamics.

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Migratory fishes with important nutritional and commercial value are highly susceptible to anthropogenic perturbations (*e.g.*, Allen *et al*., 2005). The rapid encroachment of people into the Napo Basin and elsewhere in the Ecuadorian Amazon is causing ecosystem degradations. Oil exploitation over the last four decades, for example, has had negative impacts on terrestrial and freshwater ecosystems (Kimerling, 1993), and evidence of exposure to oil drilling pollution has even been found in otoliths of *P. nigricans* (Hermann *et al*., 2016). Most recently, hydropower projects are rapidly increasing in all Amazon basin countries, where governments are prioritizing new hydroelectric dams as a focus for meeting long-term energy needs (Finer, Jenkins, 2012). Such developments may seriously impact freshwater ecosystems, putting at risk the flow of ecosystem services effected by migratory fishes and associated well-being of local peoples (Castello *et al.*, 2013).

The construction of hydropower facilities in the neotropics may be detrimental to fishes. Dams can cause serious irreversible alterations to the natural hydrological regime of rivers by altering ecosystem quality and the entire biota dynamics (Ponton *et al*., 2000). Hydropower systems may pose a risk to the survival of *P. nigricans*, which concomitantly could affect the functioning of the river ecosystems in the future (*e.g.*, Winemiller, Jepsen, 1998). Furthermore, global climatic changes are presumed to be modifying the rainfall regime of this region, potentially altering the reproductive processes of various fish species.

Pochilodontids are an important ecological component of South American rivers. Annihilation of a fish species from this family may have a large impact on the ecological cycle. *Prochilodus* have been shown to have strong direct and indirect effects on benthic communities, sedimentation and nutrient cycling (Flecker, 1992; 1996). In Amazonian Ecuador as the westernmost part of the large Amazon basin, there is an essential need to understand the biology and migration of the black prochilodus and how it adapts to seasonal hydrological regimes of watercourses to ensure that conservation of is fish population is most effective.

Objectives of this study are: 1. To analyze seasonal dynamics of reproduction, body condition and feeding in a population of black prochilodus from the Ecuadorian Amazon; and 2. To synthesize our own and published observations on migration patterns of black prochilodus in different life stages and consider factors influencing those movements. We anticipate that such a migration model could serve as a foundation for future studies on prochilodontids and other migratory characoids in Ecuador and elsewhere in South America.

Material and Methods

Study area. The Aguarico River is a major tributary within the large Napo River basin (100,500 km^2) in north-eastern Ecuador (Fig. 1a). It arises high in the Andes and cuts down through the eastern cordillera, with rapids and narrow canyons, until it reaches about 300 m altitude near the city of Nueva Loja (or Lago Agrio). Headwater tributaries are typically clear, but

turbidity generally increases after heavy rains. The 400 km long river flows east and then southward to its confluence with the Napo River at the Peruvian border. Between 250-400 m altitude, the Aguarico River begins moderate lateral incisions with meanders, and the water becomes turbid, carrying silt and bottom-load sands that form sandbanks (Sioli, 1984). In the lower reaches, meandering causes lateral erosion of riverbanks and the formation of side-channels, oxbow lakes and pools that connect seasonally to the main river. Lowland tributaries of the Aguarico drain lagoons, swamps and flooded forests, and so are commonly black water rivers with dark, tea color and low pH (Galacatos *et al*., 1996; 2004). During the flood season, muddy waters of the Aguarico River may over-flow into the lowlands, occupying floodplains, connected channels, pools, lakes and lower reaches of most tributaries. During the dry season, many of those habitats revert again to black water conditions.
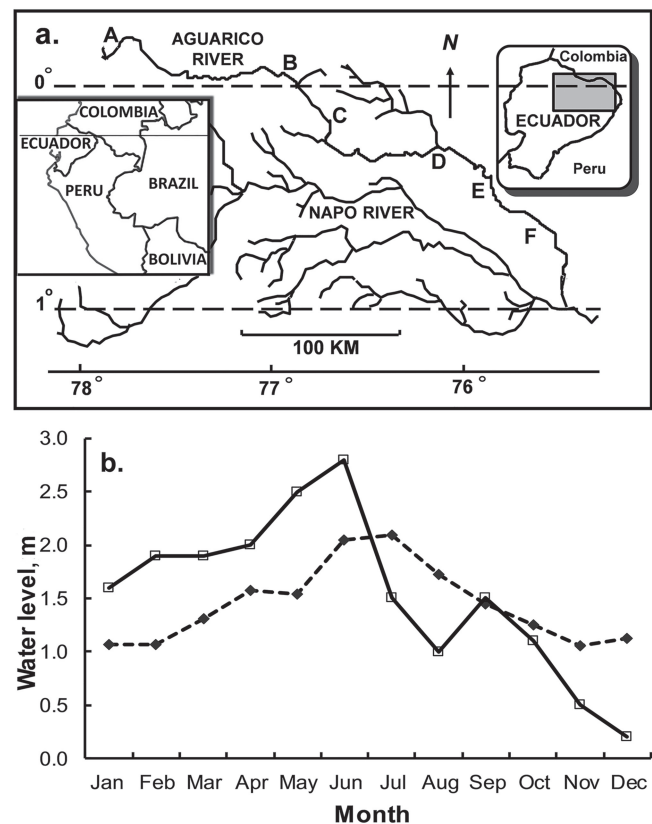

Fig. 1. a. Map of the Napo region in Ecuador and the collecting locations of *Prochilodus nigricans* in the Aguarico River in 1999 (see Tab. 1 for details). A. Due; B. Dureno; C. Chiritza; D. Cuyabeno; E. Sábalo; and F. Yanayacu/Zancudo. Location of our study area within Ecuador is indicated by shaded box in upper-right inset; location of Ecuador relative to neighboring countries in Western Amazon is indicated in inset on center-left. **b.** Mean monthly water level relative to a base level for low flood periods in the Aguarico River. Data for 1999 (solid line) were based on our field observations recorded at Chiritza. Averaged data from 1981-1986 (dashed line) were based on monthly records from near Due provided by Ecuadorian Institute of Meteorology and Hydrology (INAMHI).

The northeastern Ecuadorian Amazon receives high precipitation (2.9 m yr⁻¹) and has a runoff regime characterized by extreme sensitivity to rain events with flash floods (Laraque *et al.*, 2009). A major increase in rainfall occurs between April and July. There is a second, short rainy season in October and November. In December and January, precipitation is typically low. These observations are like those described by Laraque *et al.* (2007) and Saul (1975). Detailed environmental observations and aquatic habitats of the region were thoroughly described in Ibarra, Stewart (1989), Galacatos *et al.* (1996, 2004), Silva, Stewart (2006) and Laraque et al. (2007).

Field samples. During 1999, monthly observations of black prochilodus were made at six stations along the Aguarico River, covering an elevation gradient of 205-465 m, along with various environmental features (Fig. 1a, Tab. 1). Mean monthly fluctuations in water level for 1999 (Fig. 1b) followed a pattern like those previously reported by the Ecuadorian Institute of Meteorology and Hydrology (INAMHI) and Laraque *et al*. (2009), but in 1999, waters rose relatively higher and then declined to lower levels in the dry season. The annual hydrological cycle was divided into four seasons: I - Rising water (1 February to 30 April), II - Flood (1 May to 31 July), III - Falling water (1 August to 31 October); and IV - Low water (1 November to 31 January).

Methods to capture fish depended on the season. In the rising and flood seasons, fishes were taken using multifilament nylon gillnets in shallow areas of the Aguarico River, mouths of tributaries, streams, temporary lagoons, and floodplains. During falling and low water periods, fishes were caught near mouths of tributaries, islands and sandy beaches using cast nets and multifilament nylon gillnets used for seining. Stationary gillnets were set at dusk of each sampling date (20 nights per month, = total for all stations combined) and fishes were removed from the nets every 3 h until dawn. We considered 3 h to be an optimal time to collect fish without notable decay of stomach contents.

Standard length (SL, mm) and weight (g, whole) of each fish were recorded in addition to details of location, date and sex; status of gonads and digestive tract fullness were determined in the field by visual inspection. Developmental stages of gonads were recorded for each sex per morphological appearance employing Nikolsky´s classification (Bagenal, Braum, 1971). Six maturity stages for black prochilodus were as follows: I - virgin; II - maturing virgin or recovering spent; III - developing; IV - mature; V - spawning; and VI - spent. Gonads of juvenile fishes that could not be identified as either testis or ovaries were assigned as undifferentiated. Ovaries of each female fish were removed and weighed (to nearest g) to estimate gonadosomatic index (GSI). The stomach and intestines of each individual were sectioned longitudinally to assess feeding status. The approximate amount of food (fullness) found in the complete digestive tract was recorded using a three-point scale: 0 - empty, 1 - half full and 2 - full.

Data analyses. For all statistical analyses, statistical significance was considered when $p < 0.05$. Length-frequency distributions were constructed for fish caught during each of the four hydrological seasons in 1999. Those seasonal length-frequency distributions were then aggregated and plotted for the entire annual catch, consisting of 20-mm SL classes versus frequency of individuals found in each size class.

The gonadosomatic index (GSI) was used to assess the reproductive cycle of female fishes throughout the year at seasonal intervals. That was calculated as:

$$GSI = 100 * (G/W),$$

where G is gonad weight (g) and W is total fish weight (g), including gonads (King, 1995). Only ovaries were analyzed for GSI because they were larger than male testes, and thus, easier to weigh with better accuracy.

Tab. 1. Environmental condition at collecting sites in the Aguarico River basin of Eastern Ecuador, 1999 (see Fig. 1 for locations). Codes for dominant shoreline vegetation at each site are: T = *Tessaria* sp., G = *Gynerium* sp., C = *Cecropia* sp., Cb = *Ceiba* sp., P = Palmae, I = *Inga* sp. Positions were determined with a hand-held GPS, pH (average of monthly records) was measured with hand-held pH meter (± 0.2), and temperatures are monthly averages made with mercury thermometer. Locations marked with asterisk were in mouths of tributaries.

Location	Altitude, m	Position coordinates	pH	Water temp., °C	Air temp., °C	Current speed, m s⁻¹	River width, m	Water type	Shoreline vegetation
Due (A)	465	0° 00' 25"N 77° 23' 34" W	7.6	20.5	28.1	0.9-2.5	60	clear/white	High Forest T, G, C, P
Dureno (B)	250	0° 05' 09"S 76° 32' 10" W	7.2	22.1	27.5	1.0-2.5	100	turbid/white	High Forest T, G, C, Cb, P
Chiritza (C)	265	0° 05' 08"N 76° 44' 06" W	7.1	22.8	25.7	0.1-0.7	150	turbid/white	High Forest T, G, C, Cb, P
Cuyabeno (D)*	220	0° 15' 30"S 75° 53' 58" W	6.4	24.3	28	0.2-0.8	50	black	High Forest T, I, C, Cb
Sábalo (E)*	210	0° 23' 35"S 75° 40' 05" W	5.4	24.2	27	0.09-0.6	30	black	High Forest I, C, Cb
Yanayacu-Zancudo (F)*	205	0° 34' 55"S 75° 29' 32" W	5.5	24.3	25.3	0.06-0.2	20	black	High Forest T, G, I, C, Cb

The length-weight relation (LW) was estimated for the total number of individuals separately for each sex and each season with the equation (Everhart, Youngs, 1981):

$$\log_{10} W = a + b(\log_{10} L),$$

where a and b are population coefficients calculated with the least square method (using the General Linear Model). To evaluate possible seasonal changes in condition, the LW relationships were compared using analysis of covariance (ANCOVA), where a relatively higher slope and/or intercept could indicate better condition. Residual analyses of the LW relationships were used as a complimentary approach to assessing the condition factor of individual fishes (*e.g.*, Fechhelm *et al.*, 1995). This latter condition factor assessment was done by plotting mean monthly (studentized) residuals against time and observing their positive and negative deviations from the average population predicted value. Positive deviations indicate the fish were in relatively good condition, and negative values indicate poor condition.

Results

Standard lengths (SL) ranging between 80 and 405 mm were obtained from 336 fishes. Proportions of males and females was nearly identical with 47.0 % and 46.7 %, respectively (sex ratio 1:1). The remaining fraction of individuals with undetermined sex because of small virgin gonads was 6.3 % (SL = 80-120 mm). The length frequency histogram indicates the number of black prochilodus in each 20-mm length class collected in the Aguarico River (Fig. 2). The annual length-frequency diagram revealed a clear mode only at age class 0. In fact, most of those age class 0 fish were collected as they migrated upstream in the falling water season, indicating a dominance of immigrant juveniles.
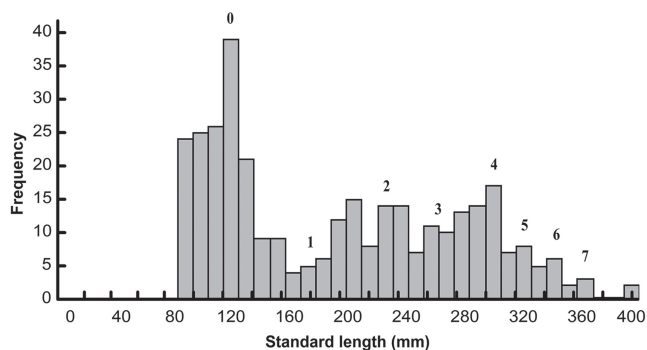

Fig. 2. Annual length frequency distribution of Ecuadorian *Prochilodus nigricans* collected from the Aguarico River in 1999. Numbers above bars indicate average size at each age estimated from otolith data (Silva, Stewart, 2006).

Monthly visual analysis of the gonad development was made for males and females (Fig. 3a). Stages V (spawning) and VI (spent) appeared only in late March and April. These phases correspond to the latter part of the rising water season. Fish

with gonad stages I (virgin) and II (maturing and/or recovering spent) were present in February and from May to December. The abundance of fishes in stage II was high from May to July; all those individuals were adults (SL = 245-405 mm) in the recovering spent phase coinciding with the flood season. In August, at the beginning of the falling water season, fishes with virgin gonads (I) were the most abundant, coinciding with the onset of upstream migration by young-of-year (YOY) fish (< 140 mm). Migrating YOY, yearling, juvenile and adult fish (SL = 92-307 mm) with gonads stages I and II were abundant from September to December, which corresponds to the falling and low water seasons. Fish with gonads at stage III were found in January-February and from October to December. This tendency implies that gonad maturation may start early in the low water season, and it may take up to about six months to reach spawning phases (IV and V).
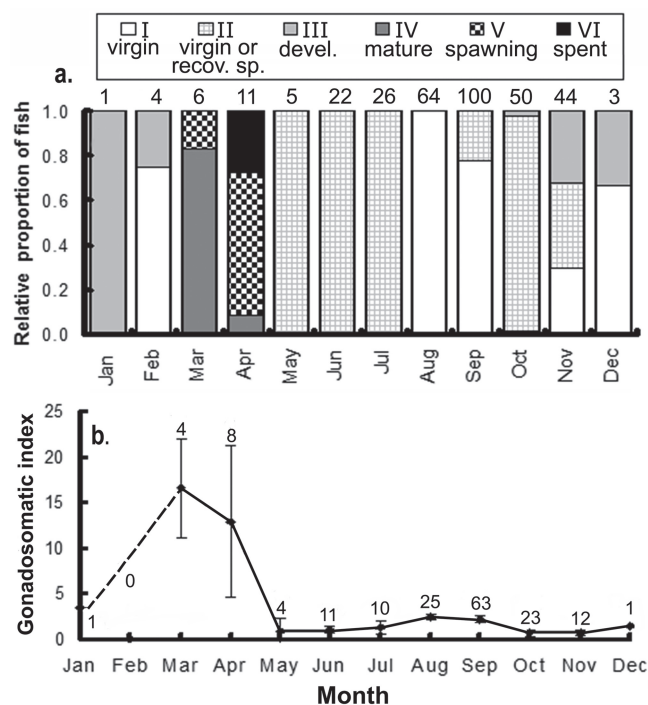

Fig. 3. Monthly gonad condition of *Prochilodus nigricans* in 1999. **a.** Percentage of males and females in six different gonad development stages (sample sizes are above bars). **b.** Monthly mean gonadosomatic indices (GSI) for females; vertical bars are 95% confidence intervals (sample sizes are above bars). recov. Sp. = ?, devel. =?.

Mean monthly GSI calculated for females (Fig. 3b) also reflects the annual reproductive cycle of the fish. Mean monthly GSI remained constantly low from May through December (< 2.5). This extensive series of negative data for ripe gonads provides strong inference that spawning happened before May. The marked increase in March-April corresponded to gonads reaching maturity stages IV and V. The sudden decrease in GSI from April to May could indicate that females reached gonadal stages V and VI just before the peak flood period. This trend suggests that black

prochilodus are total spawners and that the spawning period is short (1 or 2 months). Based on the foregoing results, personal observations and unstructured interviews with local fishermen, we concluded that peak spawning for *P. nigricans* may occur between March and April, coinciding with the water level rising period. The smallest male and female at gonadal stages IV and V during April measured 225 and 283 mm SL, respectively. These sizes correspond to age classes 2 and 3, respectively, as estimated from a von Bertalanffy growth model based on otolith data (Silva, Stewart, 2006). Empirical estimates of mean length at sexual maturity could not be made because of the relatively low number of fish caught in the high-waters of the spawning season.

Tab. 2. Length-weight (LW) regressions $\log_{10}$ W, g = a + b*$\log_{10}$ (SL, mm) for males, females and both sexes of *Prochilodus nigricans* taken in different seasons (1999), with parameter estimates for a (intercept) and b (slope), coefficient of determination (r^2), and sample size, n; SE = standard error. Estimates followed by same letter were not significantly different (based on analysis of covariance, ANCOVA). For definitions of seasons in the flood cycle, see text.

Sex	Seasons	b	± SE	a	± SE	r²	n
Males	All	2.83[u]	0.02	-4.31	0.05	0.992	153
	I-Rising	2.80	0.10	-4.20	0.25	0.990	9
	II-Flood	2.84[f]	0.14	-4.33	0.34	0.943	28
	III-Falling	2.89[f]	0.03	-4.43	0.07	0.990	82
	IV-Low	2.78[f]	0.07	-4.20	0.17	0.978	34
Females	All	2.87[u]	0.04	-4.39	0.05	0.992	162
	I-Rising	3.08	0.44	-4.91	1.11	0.830	12
	II-Flood	2.67[c]	0.18	-3.90	0.45	0.903	25
	III-Falling	2.85[c]	0.03	-4.35	0.07	0.986	111
	IV-Low	2.74[c]	0.06	-4.07	0.15	0.993	14
Combined	All	2.85[d]	0.01	-4.36	0.03	0.992	315
	I-Rising	2.85[d]	0.09	-4.31	0.23	0.980	21
	II-Flood	2.79[e]	0.11	-4.22	0.28	0.924	53
	III-Falling	2.87[d]	0.02	-4.39	0.05	0.988	193
	IV-Low	2.76[e]	0.05	-4.14	0.13	0.983	48

Data for SL and body weight were recorded for 336 fishes. Body weight in females ranged from 16 to 1240 g, whereas in males it ranged from 21 to 940 g. The resulting allometric LW relationship with sexes and seasons combined was: W = 0.00004*SL2.85. Logarithmic expression of this relationship for males, females and both sexes computed for each season and all seasons combined showed highly significant relations in all cases (P < 0.001, Tab. 2). Slopes and intercepts for each sex were not significantly different (Tab. 2, ANCOVA $F_{1,311}$ = 0.79, P > 0.3). Mass-length relationships, however, differed significantly among seasons (Tab. 2, ANCOVA $F_{1,311}$ = 3.16, P < 0.05). The highest and lowest seasonal values of the estimates for females corresponded to the transition between rising water and flood seasons. That condition variation may be explained largely by gonadal weight loss in females during spawning. These hydrological periods coincided with the pre-spawning, spawning and post-spawning stages. Regression

slopes and intercepts for males, females and sexes combined in the low water period were less than those in other seasons. In the falling water period, however, slope estimates were the highest, except in females. These slope values may correspond to fat accumulation in the visceral cavity.

Studentized residuals of the overall LW relationship were used as a condition index for each individual. Indices for males and females were pooled together to obtain mean monthly values that were plotted against time (Fig. 4). There was an increase in the condition factor from February to March (rising water period) associated with gonad development. The condition factor decreased sharply in April and reached lower values by May. This condition factor decline occurred during and after the spawning. The black prochilodus retained similar condition values from June to September (end of flood and a major part of falling water season). The lowest condition index was observed from October to December (end of falling and most of low water seasons).
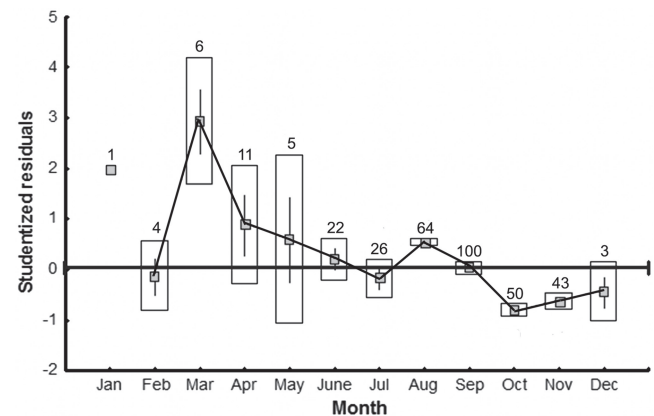

Fig. 4. Residual analysis as an index of condition factor for males, females and unsexed individuals of *Prochilodus nigricans* from the Aguarico River during 1999 (see Fechhelm *et al.*, 1995). Shown are the monthly mean (shaded rectangles), ± standard error (vertical lines) and ± 95% confidence interval (open rectangles); sample sizes are above bars.

Of a total of 335 stomach samples, 214 (64%) were empty. The percentage of individuals with empty stomachs fluctuated from month to month, yet a seasonal trend was not evident (Fig. 5). Two periods with higher percentages of empty stomachs (April and October) coincided with the spawning and upstream migrations, respectively. The high percentage of empty stomachs in July may be related to relocation (lateral) movements in search of food or shelter triggered by rapid declines in water level, which is common at the end of the flood season. There were large proportions of empty stomachs from June to October. As the water level gradually falls from June to December, fishes in early life stages move upwards in the Napo River after leaving downstream floodplains. In September and October (falling water season) juvenile and adult prochilodus were observed migrating upstream. While limitations of the data should be considered, feeding cessation periods appear to correspond to when black prochilodus migrate.
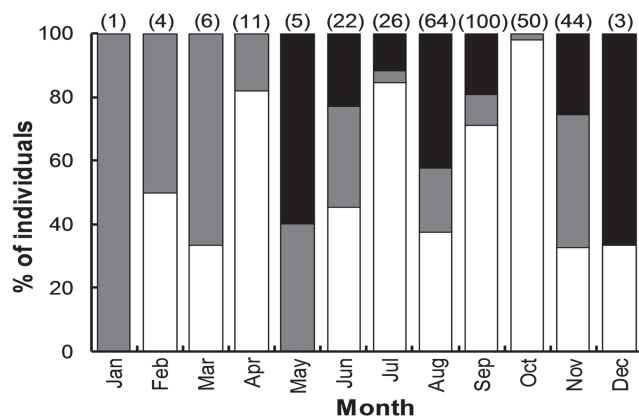
Fig. 5. Monthly percentage of *Prochilodus nigricans* having three different stomach fullness categories: white = empty, grey = half full, black = full (data combined from males, females and undetermined individuals). Numbers above bars are sample sizes.

Discussion

Size-frequency distribution. Size frequency analysis, an alternative method for determining age structure of fish populations, has been widely used in the tropics to provide data on catch composition, production and effort (McManus *et al.,* 1996). We constructed a length-frequency distribution for year 1999 that can be a baseline for monitoring population fluctuations and changes in the population age composition, although in this example, age classes one and older did not show strong abundance modes (Fig. 2). This short-lived fish is a fast-growing species (Silva, Stewart, 2006) with: 1) delayed maturation, 2) moderate to large adult size, 3) high fecundity, 4) short annual spawning season, 5) absence of parental care, and 6) long-distance migrations to productive, wet-season floodplains, all of which ensures rapid replacement of the stock. These traits correspond to a seasonal strategy of neotropical fishes that takes advantage of both temporal and spatial variation in quality of habitats for enhanced juvenile survival and growth (Winemiller, 1989). This adaptive capacity may be in response to uncertainties in environmental fluctuations (*e.g*., delays of the annual and inter-annual flood cycle, drought, El Niño events). The most abundant age class (0) consisted of young fishes migrating upstream during the falling water period. The youngest modal group (120 mm SL) may be the result of a spawning event five-six months earlier (~ April), demonstrating the successful annual addition of YOY fishes to the population of larger juveniles and adults. In other words, recruitment to the local population takes place at a specific time (falling water season, when current velocities are decreasing, and thus, relatively less energy may be needed to swim upstream). Given the discrete size mode for the YOY fishes, it may be feasible to establish a long-term monitoring program focused on applying an annual index of recruitment, which could be useful to determine when harvest rates may be getting excessive and to better understand environmental effects on recruitment (*e.g.*, Stige *et al.,* 2013).

Reproduction. Reproductive behaviors of *Prochilodus* spp. from other regions have been extensively studied (Bayley, 1973; Goulding, 1981; Saldaña, Venables, 1983; Loubens, Aquim, 1986; Lowe-McConnell, 1987; Junk *et al.*, 1997; Mochek, Pavlov, 1998;Schwassmann, 1978; Welcomme, 1979; Winemiller, 1989; Loubens,Panfili, 1995; Ruffino, Issac, 1995; Duque *et al.*, 1998; Stassen *et al.*, 2010; Gurgel *et al.*, 2012). Black prochilodus are total spawners that show no parental care; the eggs are semi-pelagic and the chorion is slightly sticky. There are discrepancies concerning the reported number of eggs produced by black prochilodus. Loubens, Panfili (1995) estimated 200,000 eggs for a 1-kg female, Schwassmann (1978) calculated approximately 300,000 eggs, and Junk *et al*. (1997) estimated about 500,000 eggs in gonads that represented 15% of total body mass. The latter two authors, however, did not report body mass or length of fishes examined. After spawning, eggs and larvae apparently drift downstream several hundreds of kilometers to floodplains where food is abundant and chance of survival may be higher (Araujo-Lima, Oliveira, 1998). Reproduction is highly seasonal and, as in the Aquarico River, it takes place during rising waters just before the flood period (Ruffino, Issac, 1995). Observations of fully developed gonads in various other commercial characin fishes of the Amazon also coincide with onset of the rainy season when water levels begin to rise. This is the time when fishes make their reproductive migrations from floodplains, lagoons and small tributaries to the turbid main rivers with well-oxygenated waters and neutral pH (Lowe-McConnell, 1987; Schwassmann, 1978; personal observations). Turbulence in the larger, white water mainstreams also may help to keep the eggs and early larval stages suspended in the water column. This reproductive strategy during flood season benefits larvae and young fish that need to drift downstream where they can find a diversity of flooded environments for natural protection, as well as excellent conditions for feeding and rapid growth (Montreuil *et al.*, 2001).

The results of this study on the spawning behavior of black prochilodus in Ecuador agree with the general patterns seen for prochilodontids elsewhere. Gonad maturation took place between January and April. The peak reproductive season occurred in April near end of the rising water and onset of the flood season. The hydrological regime thus appears to be a main factor influencing the reproductive cycle of this species. This pattern coincides with observations of reproduction of black prochilodus in the Peruvian Amazon (Montreuil *et al.*, 2001), which concurred with the period of water rising in the Amazon River (December to March). Also, Stassen *et al*. (2010) observed that changes in water chemistry following the onset of rainy season may trigger gonad development and spawning in *P. lineatus* (Valenciennes, 1837) in the Pilcomayo River.

The overall sex ratio for this species was balanced. We found an apparent predominance of females at ages older than six, which may be because females were caught more readily than males. Females were slightly bigger than

males, especially in girth as eggs develop, and thus, more susceptible to size-selective fishing gears (*e.g.*, gillnets). Age at sexual maturity was two for males and three for females. These findings, apparently, are similar with those reported by Loubens, Aquim (1986) and Loubens, Panfili (1995) in the Mamoré River in Bolivia. However, estimated age at sexual maturity for black prochilodus from the Central Amazon was lower, 1.5 years (Ruffino, Issac, 1995).

Seasonality of body condition. In analyses of the LW relation, black prochilodus from the Aguarico River had lower slope values than those reported for this species in other studies (*e.g.*, Loubens, Panfili, 1995; Ruffino, Issac, 1995). Ruffino, Issac (1995) estimated a slope value of 3.18 in Brazil, compared to 2.85 estimated for the Ecuadorian population. However, elsewhere in Brazil (*e.g.*, Araguaia River, Tocantins basin), the slope value was only 2.45 for black prochilodus (Sena-Oliveira *et al.,* 2013). Estimates of the LW relationship in eight floodplain lakes along the middle and lower Solimões River in Brazil ranged from 2.26-2.45 for this same species (Tribuzy-Neto *et al.*, 2015). These differences in LW regression estimates between populations may be influenced by sample size, length range, sexual maturity, food availability, time of sampling, and more generally, the particular ecosystem conditions in each region.

Although males and females had similar LW relationships (Tab. 2), it was evident that females reach larger body mass and length than males. A comparison of the LW relation between seasons indicated notable changes in condition of the fish. Decreases in slope estimates were evident in the rising water and low water seasons. In the first case, fish condition seemed to have been influenced by spawning activities that took place in March-April. In the latter case, the decreasing slope may be correlated with the massive upstream movement and reductions in available food resources (or less feeding opportunities during migrations). Residual analysis used as an index of condition (Fig. 4) showed similar seasonal differences in fish condition. The condition increment during rising water season might be associated with peak reproductive activity. In contrast, the lowest condition during the low water season may be correlated with extensive upstream migrations.

Feeding dynamics. Diet, energy sources and food assimilation of black prochilodus have been widely studied through direct analyses of the stomach contents, fat storage and analyses of stable carbon isotopes by several authors (Goulding, 1981; Junk, 1985; Araujo-Lima *et al.,* Yossa, Araujo-Lima, 1998 Goulding, 1981; Junk, 1985;). Although visual assessment of stomach fullness of black prochilodus in the Aguarico River was qualitative, it showed a decrease in feeding activity during migrations (Fig. 5). Similar findings were reported for *P. lineatus* in the Pilcomayo River (Bayley, 1973; Mochek, Pavlov, 1998). Prochilodontids exhibit morphological and behavioral adaptations to take advantage of detritus food resources. Detritivorous fishes such as *Prochilodus*

often dominate the ecosystem biomass and can have major direct and indirect impacts on benthic community structure (Bowen, 1984; Flecker, 1992, 1996; Taylor *et al.*, 2006). Also, migratory detritivorous fishes influence the function and structure of food webs at different spatiotemporal scales by functioning as linkages of energy and matter flow through ecosystems (Flecker, 1997 ; Winemiller, Jepsen, 1998; Taylor *et al.*, 2006). In the Napo basin, YOY *Prochilodus* apparently transfer energy towards the headwaters by migrating from Peruvian floodplains to rivers and lagoons in Ecuador. Adult fishes may also transfer energy during lateral migrations from lagoons and tributaries to the larger rivers (*e.g.*, Galacatos *et al.*, 2004), where they could be vulnerable to large predators (*e.g.*, *Brachyplatystoma filamentosum* (Lichtenstein, 1819) and other big catfishes).

Migratory patterns: a synthesis. Migrations of adult *Prochilodus* and other characoid fishes have been extensively studied (Welcomme, 1979; Goulding, 1980, 1981; Lopez-Carvalho, Merona, 1986; Payne, 1986; Ribeiro *et al.*, 1995; Fernandes, 1997; Junk *et al.*, 1997; Winemiller, Jepsen, 1998; Carolsfeld *et al.*, 2003; Araujo-Lima, Ruffino, 2004; Stassen *et al.*, 2010). Also, there are various studies on the movement of eggs, larvae and juvenile characin fishes in Neotropical river basins (*e.g.*, Flecker *et al.*, 1991; Araujo-Lima, 1994; Pavlov *et al.*, 1995; Araujo-Lima, Oliveira, 1998; Araujo-Lima *et al.*, 2001; Barthem *et al.*, 2014). Fish movements in tropical freshwater rivers are principally affected by flood pulse dynamics (*e.g.*, Junk *et al.*, 1989). Water level fluctuations produce changes in areas of the floodplain, river discharge, food availability and large variations in the physico-chemical conditions such ion compositions and total dissolved solid concentrations (Stassen *et al.*, 2010 ; Castello *et al.*, 2013). These variations compel fish to have flexibility in feeding habits, habitat requirements, migratory behavior and life history strategies (Welcomme, 1979; Payne, 1986; Junk *et al.,* 1997; Winemiller, Jepsen, 1998).

Based on the foregoing studies on migrations of Neotropical fishes, local traditional knowledge of food fish movements in the Napo basin and our own observations, we present a general hypothesis for black prochilodus migrations in the Napo basin (Fig. 6). Descriptions of black prochilodus migrations provided here represent the best assumptions currently available for the westernmost part of the Amazon basin that lies in the Ecuadorian territory, and hopefully, this framework will be tested and refined through future research. Otolith microchemistry studies (*e.g.*, Hermann *et al.*, 2016), genetic analyses (*e.g.*, Sivasundar *et al.*, 2001; Machado *et al.*, 2016) and radio-tagging (*e.g.*, Núñez-Rodríguez *et al.*, 2015) are other technologies being used increasingly to further our understandings of migrations by Amazonian fishes.

There appears to be four types of migrations by black prochilodus in the Napo basin: 1. A reproductive migration that takes place to and then upstream in some of the main white water rivers; this often involves lateral movements from black water lagoons and tributaries into the larger

rivers; 2. A passive drifting of eggs and larvae in the white water main stream that coincides with beginning of the high water season; 3. A massive upstream migration during dry season associated with recruitment, dispersal and survival of fish in the river system; and 4. Local/lateral movements of fish as a response to changing habitat conditions. Each of these is discussed in more detail below.

1. At the end of the rising water and start of the flood periods, adult black prochilodus leave the flooded habitats located in tributaries, lagoons, and floodplain forest to spawn in the main white water river (Araujo-Lima, Ruffino, 2004). This migration may be a response to factors like rising water level, water chemistry, dissolved solid concentrations, current speed, and internal hormonal cycles (Junk *et al.*, 1997; Stassen *et al.*, 2010). The turbid waters of the main river have a relatively neutral pH (Tab. 1) and, in general, there would be more favorable survival conditions for eggs and larvae (Montreuil *et al.*, 2001). Eggs or larvae suspended in clear or black water systems, for example, would likely be more vulnerable to predation by abundant small characins

that dominate most habitats in the Napo (*e.g.*, Ibarra, Stewart, 1989; Galacatos *et al.*, 1996, 2004;). After spawning, adult black prochilodus return to feeding grounds in the tributaries, lagoons and adjacent flooded forests to recover their condition because breeding requires a large amount of energy (Fig. 6). Burgos *et al.* (2011) described this migration in the upper Napo River as the 'big mijano' or 'chunda mijano' based on interviews with local fishers between the cities of Francisco de Orellana (in piedmont) and Nuevo Rocafuerte (in lowland) situated at the international boundary with Peru. These movements were associated with abundant spawning between February and April. The findings of Burgos *et al.* (2011) coincide with results of this study, as stages V (spawning) and VI (spent) appeared only in late March and April. These phases corresponded to the last part of the rising water season. In Loreto Province of Perú, local communities residing along the Tapiche and Blanco rivers described this movement as 'short mijano' because relatively few species migrate when rivers reach the highest water level from January to March (Tribuzy-Neto *et al.*, 2015).
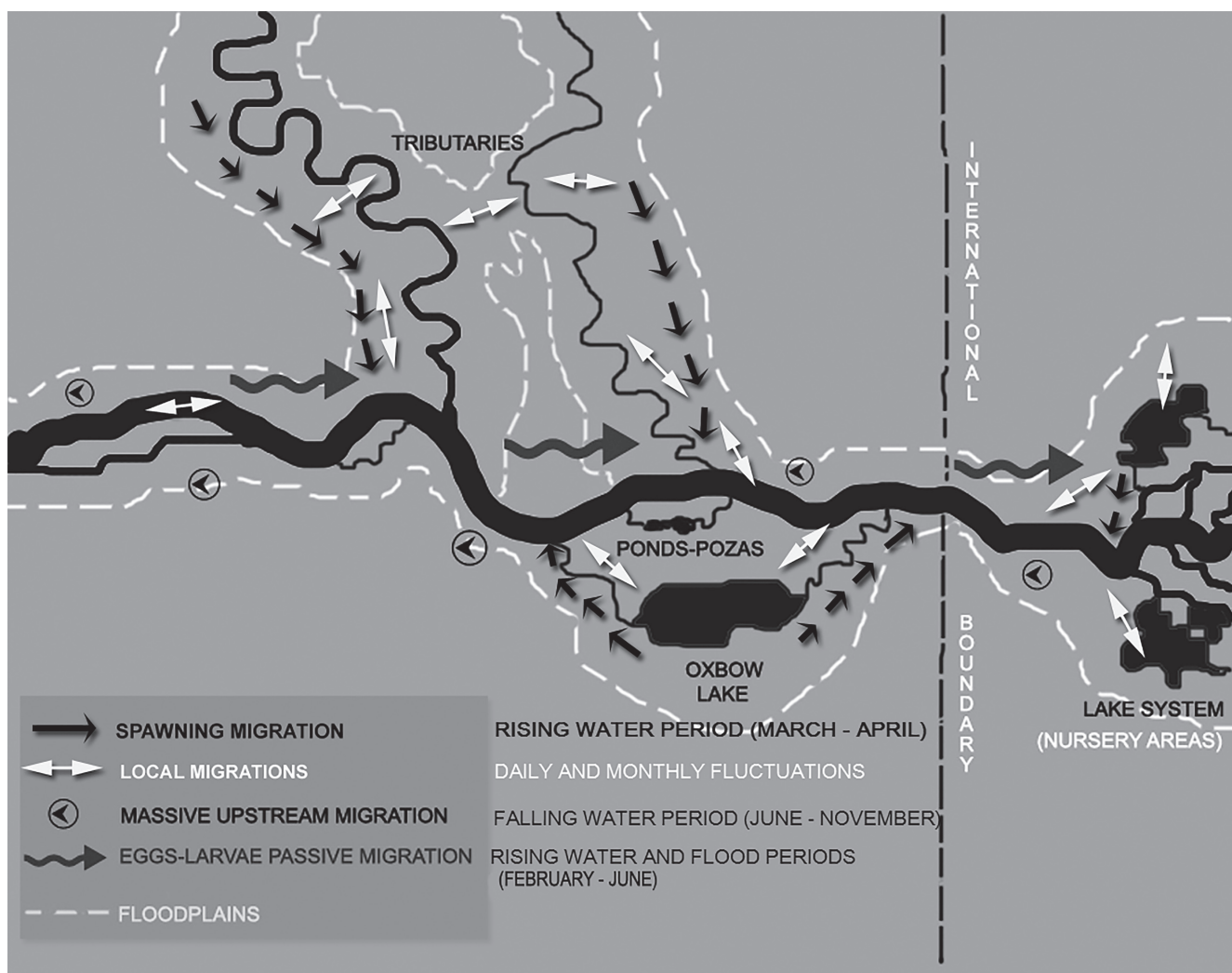

Fig. 6. Proposed graphic model for migration patterns of *Prochilodus nigricans* in the Napo basin, Ecuador, based on a synthesis of our observations, unstructured interviews with local fishers, and published information on the same species from other areas.

2. A large number of eggs and larvae passively drift down-river several hundred kilometers to extensive nursery areas probably located where the Napo River meets the Amazon River (*e.g.*, Napo-Amazon várzea floodplain in Peru; Pinedo-Vasquez, 1999). We estimated the likely travel time from spawning areas to those nursery habitats, considering average current speeds in the midstream and near the banks of the Amazon River: 1.0 ms^{-1} and 0.4 ms^{-1}, respectively (Araujo-Lima, Oliveira, 1998). We observed similar or higher current speeds in the Napo basin (Tab. 1; and DJS observations in Napo mainstream). Araujo-Lima (1994) noted that the time from fertilization to hatching for many characins with small eggs is short (< 16 h). This suggests that most of the passive drifting would occur in the larval stage. These tiny larvae (< 10 mm) can drift about 15 days before dying of starvation (Araujo-Lima, 1994: Araujo-Lima, Oliveira, 1998; Araujo-Lima, Ruffino, 2004). Based on the above information, we hypothesized that eggs of *P. nigricans* should travel about 58 km in the midstream or 23 km near the bank before hatching. Thus, egg hatching would take place within the Aguarico basin because river distance is about 320 km from Due to confluence with the Napo River (Fig. 1a). The larvae, in contrast, could have drifted much farther downstream in the midstream or near the banks before reaching safe nursery habitats. Extensive lateral floodplains, oxbows and temporary lagoons along all white water mainstreams are uncommon in the upper Napo and Aguarico basins because of proximity to the Andean piedmont. For this reason, eggs and larvae may be getting swept directly downstream to occupy vast floodplains in the lower reaches of the Napo River in Peru (about 900 km) or the Amazon River of western Brazil (> 1000 km). Local fishermen from Sabalo, however, collected a few young individuals (SL ~ 50 mm) trapped in inundated backwaters. Sometimes larvae drifting near the river shore could passively drift or actively take refuge along the flooded riverbanks to be carried out later by the falling water (Welcomme, 1985). Nonetheless, extensive samples taken with diverse experimental gears such as fine-mesh seines throughout the Napo basin between 1981 and 1998 yielded no *Prochilodus* smaller than about 80 mm SL (DJS, personal observations), so it seems smaller individuals are rare in the Ecuadorian portion of the basin.

3. A massive upstream migration (called 'mijano' in eastern Ecuador) was observed at the end of the flood season (July), during the falling water period (August-October) and beginning of low water season (November). Such migrations would seem to be necessary to spatially counterbalance the downstream displacement of drifting larvae (Barthem, Goulding, 1997). The mijano involves migration of fishes at various life stages. As the water level gradually declines (July-August), fishes in early life stages (YOY, yearlings) ascend the Napo and Aguarico rivers after leaving their downstream floodplain nurseries. In September and October, mixed schools of juvenile and adult fish were more abundant in the region. Juveniles possibly recruit to migrating schools at one or two years of age (Araujo-Lima, Ruffino, 2004). As

waters recede, both groups of fish leave the floodplains in search of alternative shelter and food resources. In November, the last schools of migratory *Prochilodus* have few juveniles and an abundance of adults. Adult fish may be involved in a longitudinal migration cycle, moving to the next tributary upstream. Welcomme (1985) describes this phase of the seasonal cycle as the 'true piracema', perhaps because it involves primarily fishes of commercial sizes. The sequential movements described above, however, indicate that the mijano should not be associated only with recruitment; it also relates to escaping unfavorable environmental conditions of the flooded forest and floodplains as waters recede (Fig. 6). We saw no evidence of large-scale downstream movements for any post-larval life stage. That suggests an interesting testable hypothesis that, once black prochilodus return to Ecuador from downstream nursery areas, they remain in the region for the rest of their life. If further studies substantiate such behavior, it would have important implications for conservation and management of black prochilodus.

Upriver movements of *P. lineatus* in Argentina have been documented using tagging experiments (Welcomme, 1985). The fish moved upriver at 8.7 km d^{-1}. Using those data to compute a possible upstream migration distance for black prochilodus in the Napo basin, we estimated they could move 518 km in two months and 1300 km in five months. The latter estimation is less likely to occur for YOY individuals because most of them were only about six months old when they were captured in the Aquarico River. This finding supports our inference that some nursery areas might be no farther away than confluence of the Napo and Amazon Rivers. Fishes older than one year could come from farther distances.

The upriver movement is explained as a massive migration of smaller fish between August and October. The indigenous fishers call this migration 'little mijano' or 'chunda mijano', which occurs when river levels are falling or at the lowest stage (Burgos *et al.*, 2011). In this study, we found migrating YOY, yearling, juvenile and adult fish with gonads stages I and II were abundant from September to December, which corresponds to the falling and low water seasons. Alvira Reyes *et al.* (2015) developed an agroecological calendar with local communities in Loreto Province, Perú, illustrating fish migrations from July to October when river waters recede (dry season). This was named by locals 'big mijano' since it involved migrations of many species of fishes.

Using Mn:Ca isotope ratios as potential otolith chemical marker for black water habitats, Hermann *et al.* (2016) observed that the first Mn:Ca peak was not preceded by a visible growth check (no annuli) in black prochilodus collected in Ecuador in 1999. So that mark likely denotes the first migration from downstream white water nursery habitats to upstream black water systems. This finding further suggests that larval and YOY individuals (< 80 mm SL) use white water floodplains as nurseries along the lower Napo or Peruvian Amazon rather than black water lagoons or tributaries with their acidified, perhaps hypoxic conditions. A translucent zone (not an annuli) formation in smaller black

prochilodus (< 170 mm) preceding such Mn:Ca markers could be associated with increased metabolic stress due to very low feeding rates while migrating upstream for the first time. Silva, Stewart (2006) concluded that black prochilodus in Ecuador form annuli on their otoliths, with the first annulus forming at a SL of about 180 mm (Fig. 2), while others have suggested that black prochilodus and various other fishes in the Central Amazon appear to form bi-annuli on their scales (*e.g.*, Oliveira, 1997 ; Arantes *et al.*, 2010). More research is needed to determine the causes and possible regional variations in translucent zone formation in this and related taxa.

4. Black prochilodus undertake local migrations, also known as relocation movements (Welcomme, 1985), among habitats in search of food and shelter. The migratory behaviors, in this case, may be adaptations in response to biotic and abiotic factors in the fluctuating river environment (Mochek, Musatov, 1989). These relocation movements could take place among habitats within the main channel, the floodplains or lagoons (Mochek *et al*., 1991; Loubens, Panfili, 1995;). In the Brazilian Amazon, excluding the Tocantins basin, black prochilodus adults migrate between successive floodplain lakes during the receding water season (~September) according to Araujo-Lima, Ruffino (2004). In lentic systems, they are active in the day, moving between littoral and off-shore areas in search of food. The habitat preferences of this species are apparently flooded forest and areas associated with macrophytes that provide food and shelter (Mochek *et al.,* 1991). There is not much information on behavior of black prochilodus in lotic systems. Flecker (1997) indicated that *P. mariae* Eigenmann, 1922, dominated pools of Andean streams in Venezuela during the dry season. The factors that influenced this sort of behavior were linked to predation pressure, competition and food availability. In larger systems like the Aguarico River, we observed that black prochilodus moved to shallow areas of the river around islands and sandbars at dusk, perhaps to feed and avoid predation during the night. During the day, they moved to the main channel or deeper backwaters. There are also seasonal lateral movements between habitats (Winemiller, Jepsen, 1998). Fishes move out of transitory floodplain habitats to rivers as the water level gradually decreases (Fernandes, 1997). Daily and monthly hydrological fluctuations seemed to be the main factors that influence these relocation movements; getting trapped in a drying pool can be lethal.

Implications for conservation and management. The Napo basin in Ecuador is a primary area for reproduction of black prochilodus and many other seasonal migratory food fishes (*e.g*., Galacatos *et al*., 2004). Unfortunately, this basin is in a region where proliferation of hydroelectric dams and reservoirs could reduce connectivity of these freshwater ecosystems, causing declines in migratory fish populations. Today, the Napo basin is practically a free-flowing ecosystem. The only two existing dams are less than ten megawatts each and do not occur on major tributaries. However, 19 additional dams are planned, including two at

over 1,000 megawatts each in headwaters of the Napo basin (Finer, Jenkins, 2012)**.** The high reproductive potential of black prochilodus may compensate for the effects of natural inter-annual variability, but permanent changes in river flow volume, hydrograph, sediment transport dynamics and/or longitudinal connectivity could compromise persistence of *Prochilodus* and other fishes with similar biology. Migratory detritivorous fishes modulate carbon flow and ecosystem productivity (*e.g.*, Winemiller, Jepsen, 1998). The apparent absence of functional redundancy for black prochilodus in the Napo basin highlights the possible importance of particular species and implies that losing one such species could affect ecosystem functioning, even in species-rich regions such as the Amazon (Taylor *et al.*, 2006).

Long distance migrations of fishes in the Amazon, Paraguay/Paraná and Orinoco basins disobey geopolitical boundaries. Most likely, black prochilodus populations that reproduce in Ecuador use the vast floodplains of Peru and Brazil as nursery areas. Anthropogenic perturbation to freshwater ecosystems that encompass nursery grounds and migration routes may affect or interrupt the different phases of fish life cycles (Winemiller, Jepsen, 1998; Castello *et al.*, 2013). Environmental damage to these diverse riverine ecosystems will significantly affect local communities who directly depend on freshwater ecosystem goods and services (Castello *et al.*, 2013). In addition to stresses posed by local human activities like over-fishing, deforestation and dams, climate change may exacerbate these pressures, leaving Amazonian tributaries and floodplains vulnerable to increasing ecological deterioration. Reducing degradation may require an adaptive management system, which according to Castello *et al.* (2013), needs on-site data monitoring for ecosystem integrity indicators and for causes of degradation. As noted above, an annual index of YOY *Prochilodus* abundance in the mijano could be a useful integrity indicator. Research and periodic monitoring should be done at the local, regional and landscape levels to provide data that can effectively guide the design and implementation of policy and conservation measures (Barthem, Goulding, 1997; Castello *et al.*, 2013). Further international co-operative research and long-term conservation perspectives are needed to safeguard these culturally and economically valuable fishes.

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