


Reproductive allocation by Amazon fishes in relation to feeding strategy and hydrology

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Abstract Seasonal environments favor the evolution of capital breeding, whereby reproduction uses surplus energy from resources acquired during an earlier period. Consequently, reproductive effort in capital breeders is expected to depend on traits associated with energy storage rather than environmental conditions at the time of reproduction. Based on a 15-year dataset, we investigate the effect of phenotype (body size and condition) and environmental conditions (intensity of hydrological seasons, predator density, and density of conspecifics) on

fecundity three capital breeding fish species from the strongly seasonal Amazon River floodplain: *Psectrogaster rutiloides*, *Triporthus angulatus*, and *Acestorhynchus falcistrostris*. Fecundity of all three species was strongly correlated with phenotype and modulated by unfavorable environmental conditions during the period of reproduction, especially high density of conspecifics. Fecundity was negatively affected by the density of conspecifics for small females of *A. falcistrostris*, and for *T. angulatus* females with poor body condition. Fecundity of *P. rutiloides* declined during periods of drought when density of conspecifics was highest. A clear tradeoff between quantity and quality of oocytes was found only for *P. rutiloides*. This study highlights that reproductive allocation of capital breeders in seasonal environments is strongly linked to environmental conditions before and during the reproductive period.

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Introduction

In seasonal environments, organisms face periodic suboptimal or unfavorable conditions for feeding and reproduction, and optimal environmental conditions for these activities often are asynchronous (Jönsson,

1997). This favors evolution of mechanisms that allow the accumulation of surplus energy to support reproduction at a later time (Stearns, 1992; Boyd, 2000; Stephens et al., 2009), in effect reducing constraints caused by asynchronous conditions for adult feeding versus offspring survival (Varpe, 2017). Known as capital breeding, this strategy of energy and reproductive allocation should be especially favored in habitats where food resources fluctuate seasonally in a relatively predictable (tractable) manner, which allows reproduction to occur despite low food availability during the breeding season (Boyd, 2000; Varpe et al., 2009; Varpe, 2017). Thus, the annual energy allocation for reproduction of capital breeders, especially ectotherms, is expected to depend more on the ability to store energy and biomass than the ability to respond rapidly to changes in environmental conditions (Reznick & Yang, 1993; Stephens et al., 2009, 2014; Hamel et al., 2010). For capital breeders, reproductive investment should be linked to the ability to store energy and nutrients provided by reversible somatic growth, such as fat or liver tissue. The capital breeding strategy contrasts with the income breeding strategy that rapidly allocates acquired energy and nutrients to reproduction (Jönsson, 1997; Boyd, 2000). Fitness under this strategy is dependent upon short-term availability of resources rather than the ability to store energy, requiring income breeders to be responsive to rapid environmental change (Stephens et al., 2014).

Life history theory predicts that costs and benefits of breeding vary according to the organism's current phenotype and past, present, and potential future environmental conditions, which includes abiotic factors, resources (e.g., food and shelter), population density, and predation risk. In iteroparous capital breeders, reproductive allocation to one reproductive event may affect future reproductive output when it increases the risk of mortality or has a long-lasting impact on the organism's condition. Under this scenario, there should be a tradeoff between the energy needed for current reproduction and the ability to recover energy deficits for survive and reproduce during subsequent periods (Stearns, 1992). Tradeoffs between costs and benefits of reproduction should be more pronounced under unfavorable environmental conditions (Clutton-Brock et al., 1996). Because reproductive potential and environmental conditions can interact and mask the cost of reproduction (Cam

et al., 2002), both intrinsic (organismal and demographic) and extrinsic (environmental) conditions must be considered together to understand investment strategies.

Seasonal environments (those with large intra-annual variation) also can have significant inter-annual variation among abiotic environmental conditions, food resources, population density, and predation risk. Periodic occurrence of severe conditions affects fitness via parental and/or offspring survival, thereby exerting selection on reproductive traits such as fecundity and spawning frequency (Clutton-Brock et al., 1996; Rideout & Tomkiewicz, 2011). Environmental factors influencing fitness act with different intensities according to different temporal and spatial scales (e.g., Johansson & Rowe, 1999). Consequently, the relative importance of various factors on the cost of reproduction may be most apparent when data are obtained from long-term studies of natural systems (Pinot et al., 2014; Robert et al., 2015).

Most tropical rivers undergo major seasonal fluctuations in hydrology (Lowe-McConnell, 1987), and many fishes have evolved a capital breeding strategy (Junk, 1985; Winemiller, 1989). These species have distinct feeding and reproductive periods that are strongly linked to seasonal fluctuations in food resources and mortality risk from predation or harsh abiotic conditions (Lowe-McConnell, 1987). For example, herbivorous, invertivorous, and omnivorous fishes acquire surplus energy during prolonged flood pulses when they can forage within expanded aquatic habitats in floodplains (Junk, 1985). In contrast, many piscivorous fishes have enhanced foraging opportunities when aquatic habitats shrink and fish densities increase during flood subsidence (Junk, 1985; Neves dos Santos et al., 2010). Although energy and nutrient storage depends to some degree upon feeding strategy, most tropical river fishes allocate surplus energy to reproduction during the rising-water phase of the annual flood pulse (Menezes et al., 1992; Neves dos Santos et al., 2010). The transfer of somatic biomass into gonadal biomass generally takes place during the mid-to-late dry season, a period when environmental conditions in floodplain habitats can become harsh in terms of low water quality (e.g., high temperatures, low dissolved oxygen concentrations, high hydrogen sulfide concentrations), low resource availability, and high predation risk (Lowe-McConnell, 1987; Winemiller, 1989; Winemiller & Jepsen, 1998). Given the

tradeoff between current reproduction and maternal somatic mass (representing potential future reproduction), environmental conditions have strong direct and indirect effects on strategies of reproductive allocation (Depczynski et al., 2007; McBride et al., 2015).

Neotropical freshwater fishes provide an excellent model system for evaluating how environmental variation influences strategies of reproductive allocation. Neotropical freshwater fishes inhabit a vast range of aquatic habitats and encompass diverse life history strategies (Winemiller, 1989). For this study, we selected three characiform fishes from a floodplain area of central Amazon River based on their distinct reproductive strategies and abundance in surveys of the local fish assemblage. *Triportheus angulatus* (Spix and Agassiz, 1829) is an omnivorous bryconid (Claro-Junior et al., 2004; Yamamoto et al., 2004) that can grow to 27 cm standard length (SL) (Prestes et al., 2010). *Psectrogaster rutiloides* (Kner, 1858) is a detritivorous curimatid (Ferreira et al., 1998) that can attain 20 cm in SL. *Triportheus angulatus* and *P. rutiloides* store fat during the annual periods of high and receding water, undergo gonadal maturation 4–6 months later during the late low-water period and early rising-water period, and spawn during the subsequent rising-water phase (García-Vázquez et al., 2015; Fig. 1). *Acestorhynchus falcistrostris* (Cuvier, 1819) is a piscivorous characid that can attain 35 cm SL (Ferreira et al., 1998) and store fat during the receding and low-water periods of the annual flood pulse (Neves dos Santos et al., 2008), with gonadal maturation and spawning presumed to occur 1–3 months later. This species has a long reproductive period that extends from the late low-water period until the peak of the annual flood pulse (Neves dos Santos et al., 2010; Fig. 1). Decoupled periods of fat storage and reproduction suggest that all three species are capital breeders, yet they may vary along a continuum of strategies (McBride et al., 2015). The relatively long reproductive period of *A. falcistrostris* that partially overlaps with the annual period when prey are abundant suggests this species could have a more variable allocation strategy. These species appear to have determinate fecundity (sensu Brown-Peterson et al., 2011), with females spawning once per year (i.e., total or isochronal spawners) by scattering gametes into the water column, often near submerged vegetation, without parental care. Lifespan of all three species is about 5 years (Barthem & Fabr e, 2004;

Prestes et al., 2010). Within the study area, first reproduction occurs at age-1 for *P. rutiloides* (ca. 100 mm SL) and *T. angulatus* (ca. 90 mm SL) and at age-2 for *A. falcistrostris* (ca. 140 mm SL) (R pke et al., 2017). Here we analyze variation in reproductive investment of these species from a lake in the floodplain of the central Amazon River in relation to intra- and inter-annual variation of environmental conditions. Specifically, we evaluated relationships between fecundity, body size and condition, egg size, and environmental variables to assess tradeoffs associated with a capital breeding strategy.

Methods

Study area and fish samples

The study was conducted in Lago Catal o, a floodplain lake in the central Amazon region that has been surveyed for 16 years (R pke et al., 2017), and includes data collected monthly from October 1999 until August 2014. Surveys were conducted using ten gillnets of several mesh sizes (30–140 mm between opposite knots). Gillnets were set at the same site each month and left in the water for 24 h, with fishes removed every 6 h (a map of the study area and further description of survey methods can be found in R pke et al., 2016).

Each specimen was identified to species, and sex was determined based on dissection. The following were recorded for each female specimen: standard length (mm), body weight (g), eviscerated body weight (g), and ovary weight (g). Species sample size for female specimens varied among survey periods in accordance with captures. A total of 195 ripe females of *A. falcistrostris*, 117 of *T. angulatus*, and 278 of *P. rutiloides* were available for this study (supplementary dataset).

Response variables

Mature ovaries (those with oocytes in the final stage of vitellogenesis, Fran a et al., 2010) were removed from the body cavity and weighed, immersed in Gilson's solution and periodically shaken to dissociate oocytes, and preserved in 70% ethanol solution prior to examination. Fecundity was estimated according to the gravimetric method. For each fully mature female,

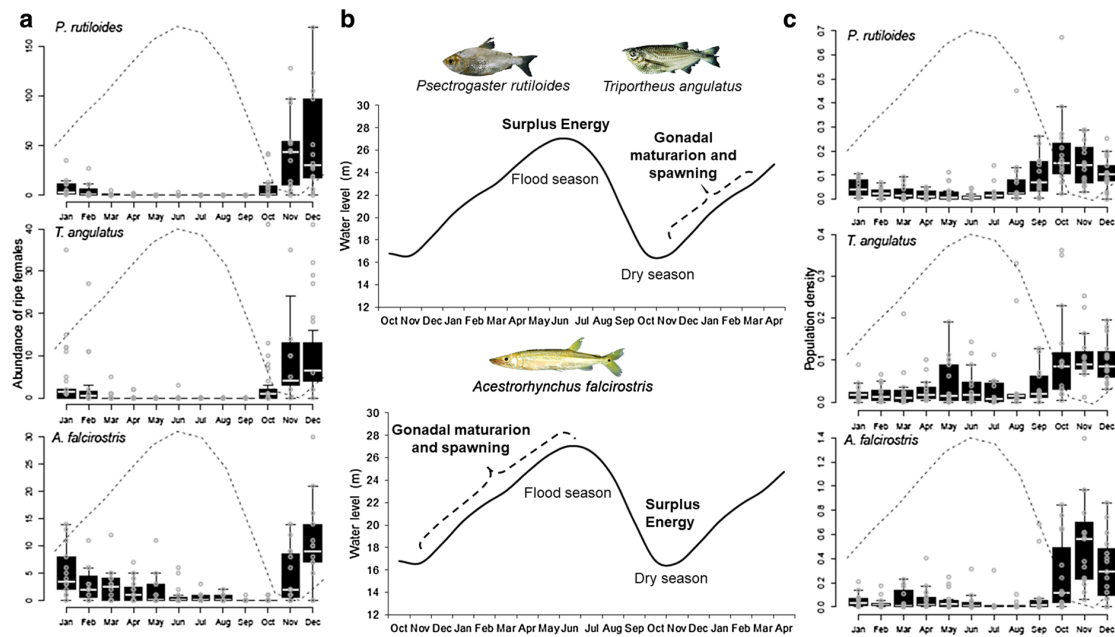


Fig. 1 Periods of reproduction (a, b) and energy/biomass storage (b) of *P. rutiloides*, *T. angulatus*, and *A. falcirostris*. For *P. rutiloides* and *T. angulatus*, surplus energy is stored during the flood season (April–June) and energy is allocated to reproduction during the following dry season (October–January). For *A. falcirostris*, surplus energy is stored during the low-water season and reproduction occurs during the end of low-water season and beginning stages of the annual flood pulse. Box-plots show the frequency of ripe females (a) and density of

conspecifics (c) by month based on data from 1999 to 2014. Densities of resident fish stocks in Lago Catalão are highest when water levels are lowest (August–January), providing greater food availability for piscivores, such as *A. falcirostris*. Food resources are most available for *P. rutiloides* (detritivore) and *T. angulatus* (omnivore) during the annual flood pulse. Months with no data indicate that ripe females were not collected during standardized surveys

Table 1 Variables included in statistical models for fecundity of three fish species

Variable	Type	Modeling role	Levels
Batch fecundity (number of mature oocytes)	Continuous	Response	
Oocyte size (diameter, mm)	Continuous	Explanatory	
Standard length (mm)	Continuous	Explanatory	
Body condition	Continuous	Explanatory	
Monthly density of predators	Continuous	Explanatory	
Monthly density of conspecifics	Continuous	Explanatory	
Season of reproduction (only for <i>Acestrorhynchus falcirostris</i>)	Category—3 levels	Explanatory	1—dry; 2—rising water; 3—flood
Intensity of dry season preceding breeding season	Category—3 levels	Explanatory	1—weak; 2—moderate; 3—strong
Intensity of flood season preceding breeding season	Category—3 levels	Explanatory	1—weak; 2—moderate; 3—strong

oocytes from a subsample of ovarian tissue were counted and measured to the nearest 0.01 mm. Graphical representation of frequency of occurrence by class

size was used to distinguish the minimal diameter of oocytes included to estimate batch fecundity (i.e., vitellogenic oocytes, and see Fig. S1). For estimation

Table 2 Estimates and coefficients from the generalized linear mixed model (GLMM) for the best model relating explanatory variables to fecundity for three fish species from Lago Catalão

Explanatory variable	Coefficient estimates	Std. error	t/z	P
<i>Acestrorhynchus falcistrostris</i>				
Intercept	6.20	0.75	8.12	< 0.001
Standard length	0.01	0.01	4.93	< 0.001
Mean oocyte size	2.18	0.78	2.80	< 0.01
Body condition	0.12	0.03	4.20	< 0.001
Density of conspecifics	– 10.76	3.13	– 3.43	< 0.001
Reproductive season: flood versus dry season	3.93	1.44	2.77	< 0.01
Reproductive season: rising versus dry season	1.11	0.85	1.30	0.30
Reproductive season: flood versus rising season	– 2.82	1.33	– 2.11	0.08
Mean oocyte size × flood season	– 4.15	1.60	– 3.03	< 0.01
Mean oocyte size × rising season	– 1.48	0.99	– 1.52	0.25
Standard length × density of conspecifics	0.03	0.01	2.73	< 0.01
<i>Triportheus angulatus</i>				
Intercept	7.80	0.50	15.75	< 0.001
Standard length	0.02	0.00	8.81	< 0.001
Mean oocyte size	– 0.61	0.48	– 1.27	0.21
Body condition	– 0.98	0.31	– 3.18	< 0.01
Density of conspecifics	– 1.33	0.73	– 1.84	0.07
Strong flood × moderate flood season	– 2.22	0.77	– 2.89	< 0.01
Weak flood × moderate flood season	0.87	1.48	0.59	0.82
Weak flood × strong flood season	3.10	1.63	1.9	0.13
Mean oocyte size × strong flood season	2.36	1.00	2.37	< 0.05
Mean oocyte size × weak flood season	– 0.91	1.97	– 0.46	0.65
Body condition × density of conspecifics	1.10	0.55	2.01	< 0.05
Mean oocyte size × body condition	1.12	0.39	2.89	< 0.001
<i>Psectrogaster rutiloides</i>				
Intercept	9.75	0.51	18.82	< 0.001
Standard length	1.81	0.23	7.72	< 0.001
Mean oocyte size	– 1.74	0.36	– 4.81	< 0.001
Body condition	– 0.04	0.05	– 0.82	0.38
Density of predators	– 0.69	0.59	– 1.14	0.29
Density of conspecifics	– 2.68	0.67	– 3.99	< 0.001
Density of conspecifics—lag 1 month	0.30	0.13	2.25	< 0.05
Weak dry season—strong dry season	0.34	0.12	2.70	< 0.05
Strong dry season—moderate dry season	– 0.20	0.10	– 1.91	0.13
Weak dry season—moderate dry season	0.14	0.11	1.26	0.41
Body condition × density of conspecifics	0.12	0.07	1.66	0.07
Density of predators × density of conspecifics	1.93	1.17	1.64	0.09
Mean oocyte size × density of conspecifics	1.68	0.54	3.13	< 0.01

Months nested in year of captured mature females were set as a random intercept term to account for repeated measurements over time. For *P. rutiloides*, standard length was rescaled as (SL/100). All significant variables are in bold. Values presented for the comparison among categorical variables (reproductive season, hydrologic season) are from Tukey's test. Analysis is based on 195 observations for *Acestrorhynchus falcistrostris*; 117 observations for *Triportheus angulatus*; 278 observations for *Psectrogaster rutiloides*. Model selection can be found in Table S4

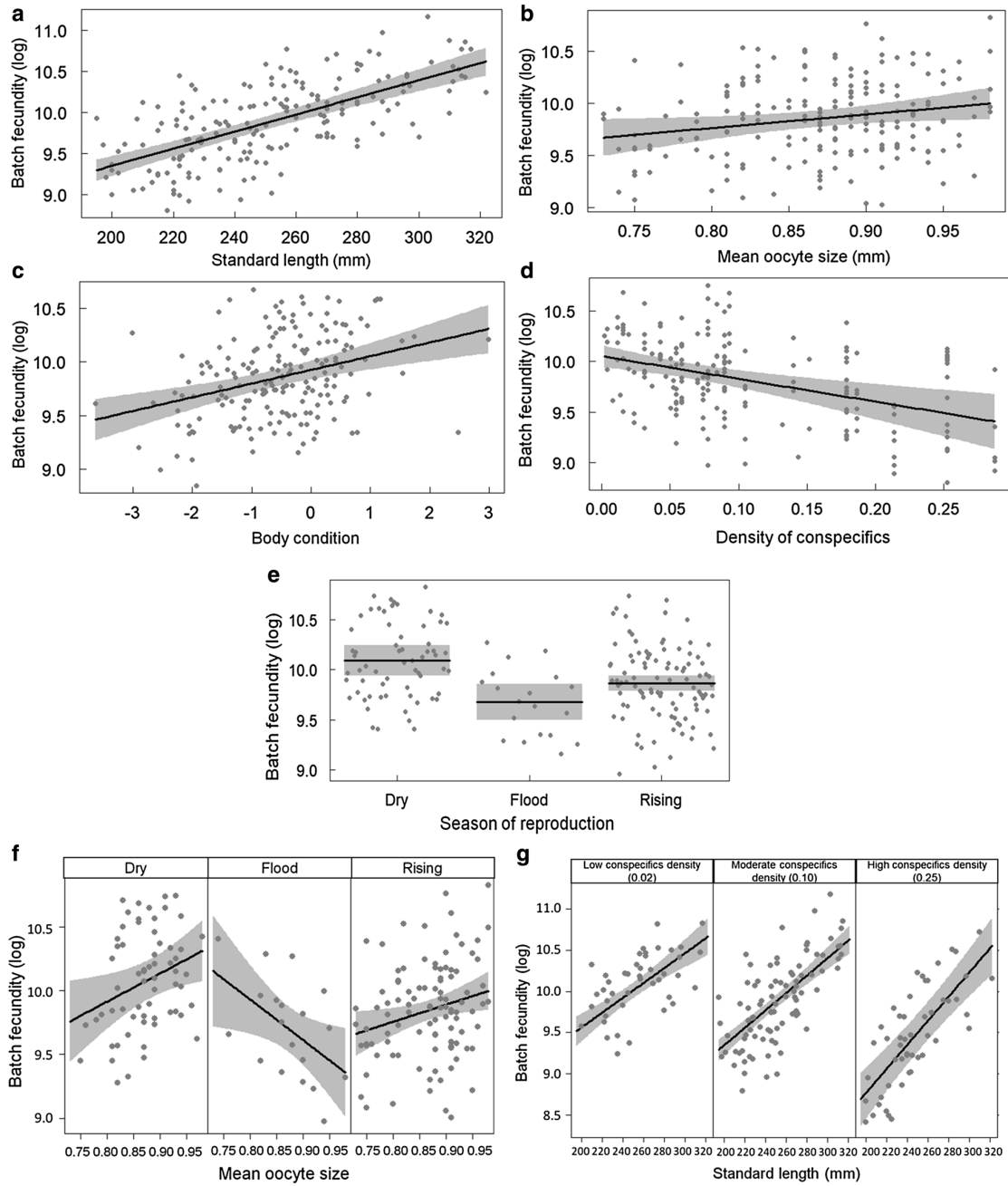


Fig. 2 Plots showing relationships from GLMM modeling of batch fecundity for *A. falcirostris*. Gray bands represent 95% confidence intervals. Analysis is based on 195 observations. **a** relationship between batch fecundity and standard length (SL) of each individual fish. **b** relationship between batch fecundity and oocyte size of each individual (average size from most developed oocytes batch of each individual). **c** Relationship between batch fecundity and body condition, as represented by the residuals from linear regression of $\log(\text{eviscerated weight}) \times \log(\text{standard length})$. **d** Relationship between batch fecundity and density of conspecifics, as recorded by capture-per-unit-effort (individuals/m² of gillnets, a measure of standardized effort per month) **e** Relationship between batch fecundity and reproductive season (hydrological season when ripe females were captured). **f** Relationship between batch fecundity and mean oocyte size for each reproductive season ('dry,' 'flood,' and 'rising' represent the reproductive season). **g** Relationship between batch fecundity and standard length by categories of density of conspecifics. 'low conspecific density' pertains to values < 0.02 indiv./m²; 'moderate conspecific density' pertains to values > 0.01 and < 0.10 indiv./m²; and 'high conspecific density' pertains to values > 0.10 and < 0.25 indiv./m²

of batch fecundity, we counted the largest oocytes in the cohort, which could include oocytes at stages ranging from incomplete to complete vitellogenesis (Murua & Saborido-Rey, 2003; Brown-Peterson et al., 2011; Lowerre-Barbieri et al., 2011). Irrespective of stage, these oocytes were assumed to comprise the batch that would be released during the next reproductive bout (Brown-Peterson et al., 2011). Non-vitellogenic oocytes were considered to contribute to future reproduction and were not considered in fecundity estimates. Oocyte size (diameter in the longest dimension) distributions of the three species were bimodal, although a trimodal distribution was observed for 31 individuals of *A. falcirostris* (Fig. S1). The minimum diameter of mature oocytes varied greatly among individual, from 0.7 to 0.9 mm for *A. falcirostris*, from 0.5 to 0.7 mm for *T. angulatus*, and from 0.6 to 0.9 mm for *P. rutiloides* (Fig. S1). Batch fecundity, the number of mature oocytes shed during a given spawning bout, was estimated as $\text{Fec} = nW/w$, where n is the number of mature oocytes estimated in the subsample; W is the weight of entire ovaries; and w is the weight of the subsample. Batch fecundity ranged from 5,409 to 63,914 for *A. falcirostris*, 2,308 to 50,080 for *T. angulatus*, and 6,549 to 77,775 for *P. rutiloides*.

Explanatory variables

Seven explanatory variables and their interactions were evaluated for potential effects on reproductive

investment: three fish traits (standard length, mean oocyte size, female body condition) and two abiotic environmental factors (water level during the reproductive period, water level during the major feeding period), and two biotic environmental factors (density of conspecifics, density of predators). For *A. falcirostris*, we included the hydrological season when females were mature (dry, rising water, or flood) as an additional variable. Mean oocyte size in the ovary, which can vary in response to body lipid content and other factors (Johnson, 2009), was estimated by the arithmetic mean size of fully mature (vitellogenic) oocytes, and it was strongly correlated with maximum oocyte size (*A. falcirostris* $r = 0.7$, *T. angulatus* $r = 0.8$, *P. rutiloides* $r = 0.7$). Body condition was estimated as the residual of the linear regression (Jakob et al., 1996) of log-transformed standard length and eviscerated fresh weight. Visceral fat weight was not added to eviscerated fresh weight because it was not measured continuously over the study period; also, we noted that females with ripe ovaries frequently did not have visceral fat. All adult females (mature or not) captured between 1999 and 2014 were used in the regression to estimate the body condition of each species (*A. falcirostris* $N = 2,798$ individuals; *T. angulatus* $N = 1,985$; *P. rutiloides* $N = 3,513$).

Conspecific densities of each species and collective density of piscivorous and carnivorous fishes were estimated for each month based on the standardized surveys (recorded as catch-per-unit-effort, CPUE). Densities were estimated for months when ripe females were captured to represent conditions during the spawning period. Density of conspecifics during the month that preceded final egg development (the month preceding capture of the first ripe female) was recorded and analyzed to test whether this could have influenced allocation strategy. The extent of the flood event preceding reproduction and the extent of low-water conditions during the reproductive period were assessed and classified either as weak, moderate, or strong based on frequency distributions of days of duration (sensu Bittencourt & Amadio, 2007) observed at a nearby gage over the past 115 years (Röpke et al., 2017; Fig. S2). This classification of hydrological status reflects variation in environmental conditions as well as connectivity between the floodplain lake and river channel (Junk et al., 1989; Röpke et al., 2016). 'Weak floods' usually had gage water levels < 27.3 m for 100 days or less, 'moderate

floods' had water level from 27.3 to 28.8 m lasting from 100 to 140 days, and 'strong floods' had water level > 28.8 m lasting > 140 days. 'Weak dry seasons' had water level > 17 m lasting 60 days or less, which corresponded to an extensive connection between the lake and the river, 'moderate dry seasons' had water levels between 15 and 17 m for 60–100 days that maintained a small connection between the lake and river, and 'strong dry seasons' had water levels < 15 m for 100 days or more that completely disconnected the lake and river channel. During strong dry seasons, availability of most food resources is reduced, temperature increases, and dissolved oxygen decreases (Rodríguez & Lewis 1994; Winemiller & Jepsen, 1998; Brito et al., 2014). Strong floods increase availability of food resources and shelter for most fishes, and also reduce densities of conspecifics, competitors, and predators within expanded aquatic habitat (Sánchez-Botero & Araújo-Lima, 2001; Claro Jr et al., 2004; Correa & Winemiller, 2014; Röpke et al., 2014, 2016).

Data analysis

Fecundity was modeled based on eight explanatory variables and their potential interactions (Table 1). To avoid collinearity issues, we first performed a cross-correlation analysis for the full set of explanatory variables, using a correlation threshold of 0.5 for inclusion in the model (Tables S1–S3). The initial model to predict fecundity of each species included female SL, mean oocyte size, body condition, monthly density of the conspecifics, density of conspecifics based on a 1-month lag of response, monthly density of predators, categories of flood season and low-water season hydrology, interaction of SL with population density, interaction of SL with hydrology during the spawning season, interaction of body condition with density of population, and interaction of body condition with hydrology during the spawning season (Table S4). To infer a possible tradeoff between the quantity and quality of the eggs produced, mediated by energetic restriction and environmental condition, tests were performed for the interaction of mean oocyte size with body condition, hydrological condition, and densities of conspecifics and predators.

Simple linear models, with a Gaussian error distribution, were performed on log-transformed data of fecundity for *A. falcistrostris* and *T. angulatus*. A

negative binomial error distribution with raw data of fecundity was used for *P. rutiloides*, because log-transformed data violated assumption of normality. This was conducted using the function `glm.nb` and log link function implemented using the MASS package in R (Venables & Ripley, 2002). In order to account for the repeated measures of independent variables associated with time periods and potential temporal correlations, we included month nested within year as a random intercept, thus running generalized linear mixed models (GLMM) for the three species. Mixed models were constructed using the R package `lme4` (Bates et al., 2015). Final variable selection was conducted using the function `stepAIC` from MASS package, and the best model to predict batch fecundity was selected based on the Akaike's Information Criterion (AIC, and Δ AIC) (Table S4). When values of AIC between concurrent models were smaller than 2, the final model was the one with fewest variables and interactions. Due to computational limitations of GLMM (due to scaling of variables), a different procedure was conducted for *P. rutiloides*. For this species the backwards procedure for variable selection started without the random variable (i.e., a GLM was used as the initial model). Addition of the random variable (performing the GLMM) was conducted after the backwards process was carried out on the initial GLM. Standardized residuals were examined for all independent variables, whether they were included in the final model; variables with pattern in the residuals were included in the final model when they increased the prediction power of the complete model (Zurr et al., 2009). Standardized residuals were inspected to identify outliers and to verify the assumption of variance homogeneity (Zurr et al., 2009).

Tukey post hoc tests were performed with the `glht` function in the `multcomp` package in R (Hothorn et al., 2008) to assess fecundity differences among levels of the categorical variables. We used `visreg` package (Breheny & Burchett, 2017) to generate partial regression plots and graphically represent the portion of variance to explain each independent variable while taking into account the importance of other variables in the model. All analyses were done with R 3.3.2 (R Development Core Team, 2016).

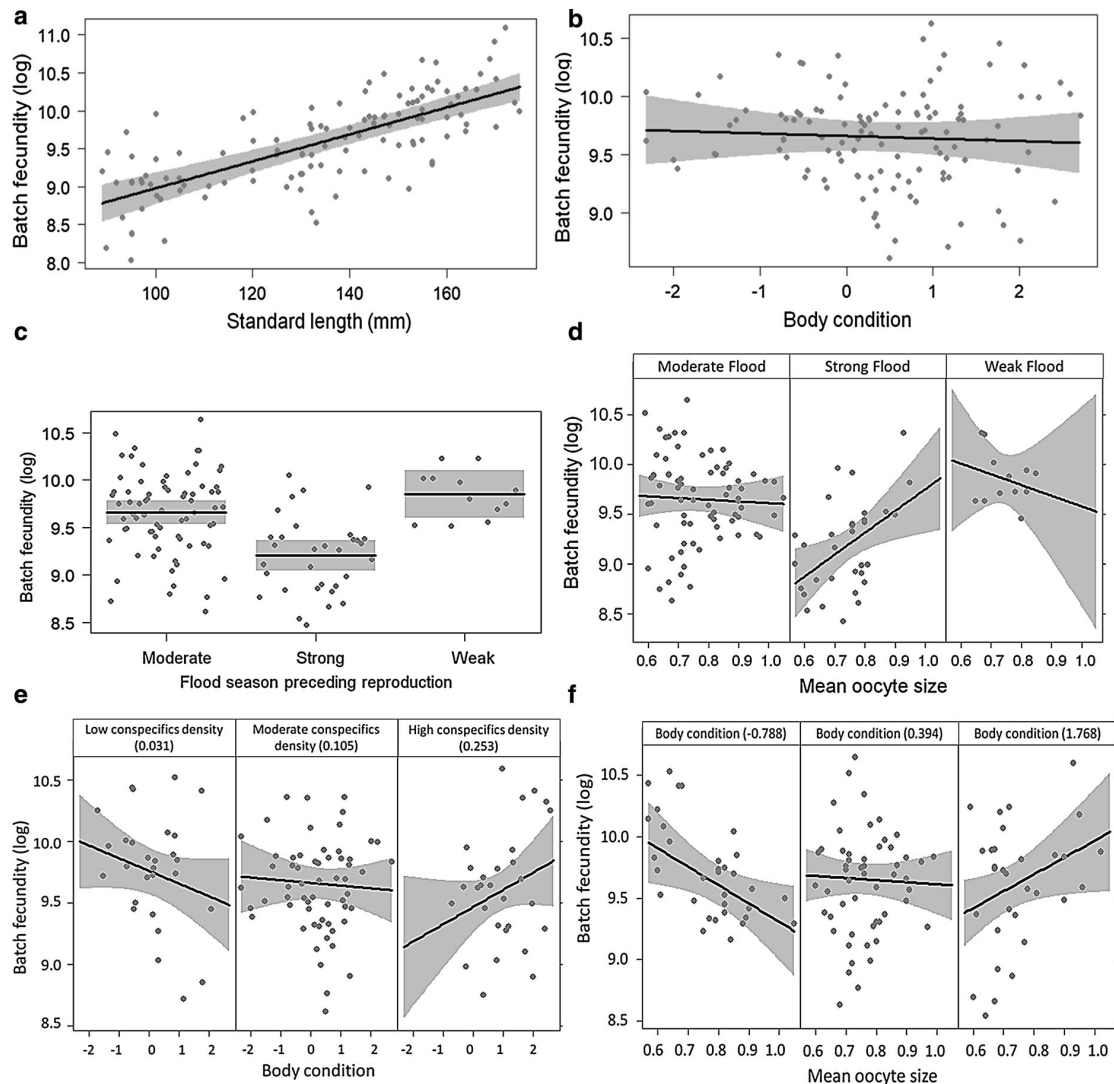


Fig. 3 Plots showing relationships from GLMM modeling of batch fecundity for *T. angulatus*. Gray band represents 95% confidence intervals. Analysis based on 117 observations. **a** Relationship between batch fecundity and standard length (SL) of individual fish. **b** Relationship between batch fecundity and body condition as represented by the residual values from linear regression of $\log(\text{eviscerated weight}) \times \log(\text{standard length})$. **c** Relationship between batch fecundity and intensity of the flood season that preceded reproduction. Intensity was classified as moderate, strong and weak based on maximum water level and number of days of flood. **d** Relationship between batch fecundity and mean oocyte size for the three categories of

flood season. **e** Relationship between batch fecundity and density of conspecifics as recorded from capture-per-unit-effort (individuals/m² of gillnets, a standardized effort per month); ‘low conspecific density’ pertains values < 0.031 indiv./m²; ‘moderate conspecific density’ pertains to values < 0.105 indiv./m²; ‘high conspecific density’ pertains to values < 0.253 indiv./m². **f** Relationship between batch fecundity and mean oocyte size for three categories of body condition; ‘low body condition’ pertains to values < - 0.788; ‘moderate body condition’ pertains to values < 0.394; ‘high body condition’ pertains to values < 1.768

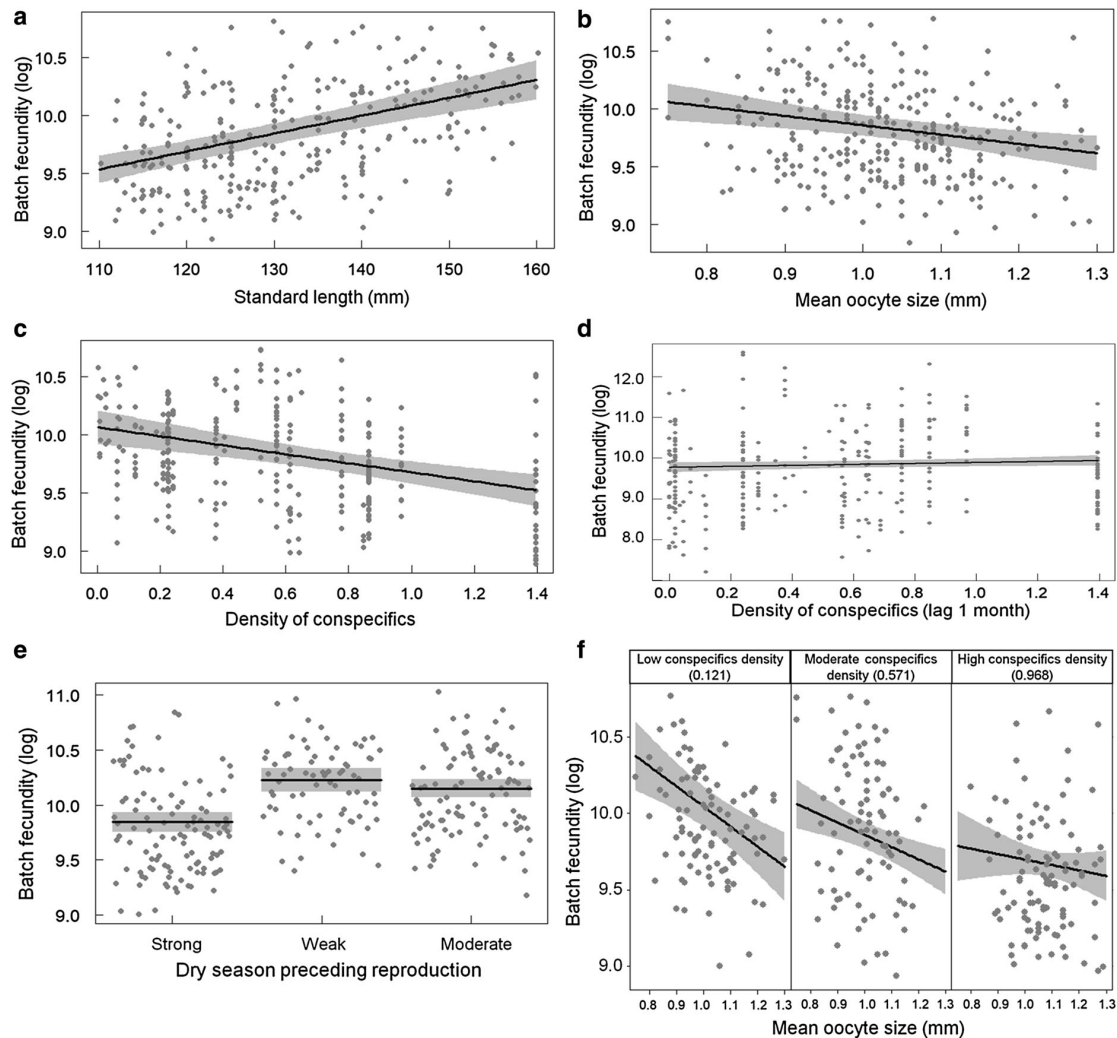


Fig. 4 Plots showing relationships from GLMM modeling of batch fecundity for *P. rutiloides*. Gray band represents 95% confidence intervals. Analysis based on 278 observations. **a** Relationship between batch fecundity and standard length (SL) of each individual fish. **b** Relationship between batch fecundity and mean oocyte size from individual fish. **c** Relationship between batch fecundity and density of conspecifics as presented by unit-by-capture-effort (individuals/m² of gillnets a standardized effort per month). **d** Relationship

between batch fecundity and density of conspecifics one month prior to reproduction. **e** Relationship between batch fecundity and intensity of the dry season, classified based on minimum water level and duration of the dry season. **f** Relationship between batch fecundity and mean oocyte size for three categories of conspecific density; 'low conspecific density' pertains to values < 0.121 indiv./m²; 'moderate conspecific density' pertains to values < 0.571 indiv./m²; 'high conspecific density' pertains to values < 0.968 indiv./m²

Results

Standard length, mean oocyte size, body condition, and density of conspecifics, either alone or interacting with other variables, were important predictors of fecundity for all three species (Table 2, Figs. 2, 3, 4).

The importance of hydrological conditions during or preceding reproduction and interactions depended on species (Table 2). Findings for each species are as follows:

Acestrorhynchus falcirostris

Fecundity was positively correlated with SL ($\beta = 0.01$, Fig. 2a), mean oocyte size ($\beta = 2.18$, Fig. 2b), and body condition ($\beta = 0.12$, Fig. 2c), and was negatively correlated with conspecific density ($\beta = -10.76$, Fig. 2d, Table 2). The season when reproduction occurred was also important ($\beta_{\text{flood season}} = 3.93$, Fig. 2e); females captured during dry or rising-water seasons had higher fecundity compared to the flood season. Fecundity was significantly associated with the interaction between mean oocyte size and period of reproduction ($\beta_{\text{oocyte size} \times \text{flood season}} = -4.15$, Fig. 2f), indicating that changes in fecundity related to tradeoff between egg quantity and quality were only strong for females during the flood season. The interaction between SL and conspecific density indicates that smaller females had lower fecundity when population density was high ($\beta = 0.03$, Fig. 2g). Densities of conspecifics were more likely to be higher during moderate and strong dry seasons (Fig. S3).

Triportheus angulatus

Fecundity increased with SL ($\beta = 0.02$, Fig. 3a) and decreased with body condition ($\beta = -0.98$, Fig. 3b, Table 2). Fecundity depended significantly on the intensity of the flood during the season preceding reproduction (Table 2), being lower in years with larger floods compared to years with moderate floods ($\beta_{\text{strong flood season}} = -2.22$, Fig. 3c). The significant interaction between intensity of the flood season and mean oocyte size ($\beta_{\text{strong flood season}} = 2.36$, Fig. 3d) suggests that large floods allowed females to increase both fecundity and oocyte size. The effect of body condition on fecundity depended on conspecific density ($\beta = 1.10$, Fig. 2e). Under low density, females in better condition invested less in fecundity than those in poorer condition, but under high density, females in better condition invested more in fecundity than those in poorer condition. Body condition also mediated the tradeoff between fecundity and oocyte size (expressed in the model by the interaction of body condition \times mean oocyte size), with females in better condition investing more in egg quality than quantity ($\beta = 1.12$, Fig. 3f).

Psectrogaster rutiloides

Fecundity was positively correlated with SL ($\beta = 1.81$, Fig. 4a) and negatively correlated with mean oocyte size ($\beta = -1.74$, Fig. 4b) and density of conspecifics ($\beta = -2.68$, Fig. 4c, Table 2). Density of conspecifics in the previous month showed a positive effect on fecundity ($\beta = 0.30$, Fig. 4d), but the effect size was smaller than for density of conspecifics during the same month when fish were captured. Intensity of the dry season was negatively correlated with fecundity ($\beta_{\text{weak dry season}} = 0.34$, Fig. 4e). During years with strong dry seasons, females had lower fecundity when compared to years with a weak dry season. During such years, no significant change in oocyte size was observed (the interaction term between dry season class and oocyte diameter was not retained in the final model, Table S4). The interaction between mean oocyte size and conspecific density ($\beta = 1.68$, Fig. 4f) suggests that the tradeoff between egg quantity and quality depended, to some degree, on conspecific density.

Discussion

Body size and body condition, our proxies for investment in future reproduction, were strongly associated with fecundity for two of the fish species, and this was the case whether variables were analyzed alone or with environmental conditions as covariates. In these capital breeders, fecundity varied in relation to an interaction between body size and condition with environmental factors. In iteroparous capital breeders, allocation to current reproduction reduces future reproductive output by way of increased mortality risk and/or reduced body condition (Festa-Bianchet et al., 1998; Wright et al., 2017). Consequently, there should be particularly strong selection to balance investment in current versus future reproduction when current conditions increase the cost of reproduction (Houston & McNamara, 1992). For the study species, this seems to occur when conspecific density is high and/or environmental conditions are unfavorable, which increases demand to maintain basal metabolism.

Body size was the variable most strongly correlated with fecundity for all three species. Somatic growth represents investment in reproductive potential;

investment in tissues and organs that enhance survival represent a long-term investment, whereas nutrient storage in the form of fat and liver tissue represents a short-term investment (Ejmond et al., 2015). These allocation strategies are especially relevant for teleost fishes and other organisms with indeterminate growth, most of which have a positive relationship between fecundity and body size. Thus, investment in current reproduction would reduce the potential for future reproduction to a greater degree in smaller females. This inverse relationship between the cost of reproduction and size was especially evident for *A. falcistrostris*. For this species, smaller females had lower fecundity when conspecific density was high, which suggests that intraspecific competition for food resources (Byström and García-Berthou, 1999; Amundsen et al., 2007) may influence reproductive allocation strategies.

Also evident for *A. falcistrostris* was a tradeoff between fecundity and short-term energy reserves, here indexed by body condition. Female *A. falcistrostris* with poorer body condition had lower fecundity, suggesting a greater dependency on recent acquisition of resources for reproductive allocation (Descamps et al., 2016) when compared to the other two species. In *T. angulatus*, body condition was inversely correlated with fecundity and was not important for *P. rutiloides*. For *Triportheus angulatus*, females with better body condition invested in larger oocytes but did not invest more in fecundity.

Larger floods should create more favorable conditions for foraging by the omnivorous *T. angulatus* and the detritivorous *P. rutiloides*, and therefore should allow for greater reproductive allocation during the next breeding season. However, larger floods had a negative association with fecundity of *T. angulatus* and no effect on either fecundity or egg size of *P. rutiloides*. Strong floods were positively associated with oocyte size of *T. angulatus*, suggesting a possible effect of surplus energy on egg quality. A similar pattern was observed in marine sardines and anchovies in which lipid storage was positively associated with oocyte size but not fecundity (Brosset et al., 2016). Larger floods with greater duration would lead to higher availability of fruits and seeds for this species (Yamamoto et al., 2004). Female of *A. falcistrostris* had lower fecundity during the flood season, suggesting that great expansion of aquatic habitat reduced foraging success that in turn affected its reproductive

allocation. During the ascending phase of the annual flood pulse, aquatic habitat is greatly expanded within the floodplain, and densities of prey are reduced for piscivores such as *A. falcistrostris* (Neves dos Santos et al., 2008). Floods of greater magnitude, therefore, should increase the cost of reproduction for this species.

The costs of reproduction for future survival are greater during periods with harsh environmental conditions (Clutton-Brock et al., 1996). Under harsh environmental conditions, an organism should reduce its reproductive investment, as reported for diverse organisms (Clutton-Brock et al., 1996; Lourdais et al., 2002; Lescroël et al., 2009; Garnier et al., 2016). We expected that all three species to respond to drought conditions; however, only *P. rutiloides* showed a response. Under drought conditions, female *P. rutiloides* apparently adopted a strategy of survival over current reproduction. During drought conditions, many lakes in the Amazon floodplain may lose over 70% of surface water, with some drying completely (Frappart et al., 2012). During drought, lake water temperature and levels of excreted substances (e.g., ammonia) and hydrogen sulfide often increase (Brito et al., 2014) to levels that cause physiological stress for fishes, often accompanied by reduction of energy reserves (Correia et al., 2014). Under such conditions, density of conspecifics often is high (Fig. S3). Reduced fecundity of *P. rutiloides*, but not the other two species, during drought might be associated with the greater gonadal investment of the former (Fig. S4). Life history theory predicts a tradeoff between energy needed for current reproduction and the ability to recover energy deficits to survive and spawn in subsequent years (Dutil, 1989). Depending on this residual reproductive value, elevated standard metabolic rate during a warm period with low food availability should reduce reproductive investment (Wright et al., 2017), somatic growth, and the rate of energetic recovery when environmental conditions improve again.

Fecundity was negatively associated with population density for *A. falcistrostris* and *P. rutiloides*. Population densities of these species were high during droughts and moderate dry periods compared to weak dry periods (Fig. S3). Competition for high-quality food resources is probably the mechanism leading to the associations between fecundity rates and density (Dantzer et al., 2013). The likely effect of competition

on reproduction by *T. angulatus* and *P. rutiloides* is evidenced by lower body condition when conspecific density was high. Under a scenario of high population density, selection should favor production of fewer, larger eggs (Allen et al., 2008; Plaistow & Benton, 2009) that yield larger larvae, and this response should be strongest when high population density affects juveniles more than adults (Sibly & Calow, 1989). This seems to be valid for *P. rutiloides* but not for *T. angulatus* and *A. falcistrostris*. The absence of a relationship between population density and oocyte size suggests that density-dependent processes may have relatively little influence on investment per offspring in these species, and availability of habitat and associated predation threat for early life stages may be more important than intraspecific competition among early life stages (Rollinson & Hutchings, 2013).

Long-term studies provide the most effective means for investigating the influence of environmental variation on strategies of reproductive allocation (Pinot et al., 2014; Robert et al., 2015). Life history variation revealed by capital breeding fishes in an Amazon floodplain lake was linked to phenotypic characteristics associated with energy acquisition and storage as well as environmental conditions associated with seasonal hydrology. The costs of reproduction were most evident under unfavorable hydrological conditions; for *A. falcistrostris*, the piscivorous species, unfavorable conditions apparently occur during strong floods; for the other two species, they occurred during droughts when aquatic habitat was reduced and population densities were high. Our results suggest that intraspecific variation in allocation strategies plays an important role in population resilience to major environmental fluctuations produced by seasonal and inter-annual variation in precipitation and hydrology. These relationships are important to understand because, under recent climate projections for the Amazon, inter-annual variation in precipitation is increasing.

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Author contribution CPR, KW, and SA conceived the idea; CPR, DWF, CPD, and SA obtained the data; CPR and THSP

analyzed the data; CPR, THSP, and KW wrote the manuscript; and all authors provided editorial advice. All authors contributed significantly to the paper and approved the submitted version.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

Ethical approval All applicable institutional guidelines for the care and use of animals were followed, INPA's ethics committee rules (Protocol Number 33/2012). Fish surveys were authorized by IBAMA through license #101932, and followed.

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