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ARTICLE

Life-History traits of *Hollandichthys multifasciatus* (Eigenmann & Norris, 1900) (Characiformes: Characidae) in coastal Atlantic Forest blackwater streams from Southeastern Brazil

Vinicius de Carvalho Cardoso[1] **& Katharina Eichbaum Esteves**[2]

[1] Secretaria da Agricultura e Abastecimento do Estado de São Paulo, Agência Paulista de Tecnologia dos Agronegócios (APTA), Instituto de Pesca. São Paulo, SP, Brasil. ORCID: https://orcid.org/0000-0002-7604-6684. E-mail: viniciusc.cardoso@yahoo.com.br
[2] Secretaria da Agricultura e Abastecimento do Estado de São Paulo, Agência Paulista de Tecnologia dos Agronegócios (APTA), Instituto de Pesca, Centro de Pesquisa em Recursos Hídricos. São Paulo, SP, Brasil. ORCID: https://orcid.org/0000-0001-5123-9669. E-mail: kesteves.ke@gmail.com (corresponding author)

Abstract. Ecological and life history traits have been used to understand the basic ecology of fishes. This study aimed to examine the existence of plasticity in life history traits of populations of *Hollandichthys multifasciatus* in ten blackwater streams. This is an inseminating Characidae, endemic to the Atlantic coastal drainages of Brazil. Different aspects of the life-history of the species, such as mean length, sex ratio, absolute and relative fecundity, gonadosomatic index, condition factor, length-weight relationship and the growth parameter (b) of 185 specimens were studied during the period of low precipitation (June-September). Fish samples were obtained along a 100 m stretch of each stream, and some habitat variables recorded. ANOVA and Kruskal-Wallis tests indicated a similarity in most of the analyzed traits, with exception of the mean length of immatures, Gonadosomatic Index of mature males and condition factor of immatures and mature adults. Also, slope tests of the length-weight relationship were significantly different for immatures. The observed differences were attributed to heterogeneity in food availability and/or other site-specific factors, which may influence growth and/or breeding aspects among the studied localities. The approach used herein may improve understanding of trait plasticity under natural conditions, helping to understand fish-community responses to anthropogenic changes.

Keywords. Length-weight relationship; Condition factor; Humic waters; Baixada Santista.

INTRODUCTION

Variations in life-history traits between and within fish populations have been described for several native populations from tropical (Winemiller, 1989; Grether *et al.*, 2001; Gomes & Monteiro, 2007) and temperate habitats (García & Braña, 1988; Lobón-Cerviá & Rincón, 1998; Craig *et al.*, 2017), with spatial and temporal patchiness of resources resulting in variation in reproductive traits. Resource availability is considered a major driver for selection of various life-history strategies in organisms and can affect population growth and productivity (Begon *et al.*, 2006). However, other factors, such as environmental stability (*e.g.*, hydrology; Lytle & Poff, 2004), light radiance, temperature, and oxygen levels may be related to variations in growth and reproductive strategies (Jobling, 1994), and thus life-history traits of fish populations may vary among habitat types (Blanck & Lamouroux, 2007).

Several studies have shown that organisms in unproductive environments may grow more slowly and allocate their limited energy to growth for a longer time until they become large enough to produce sufficient offspring (Pianka, 1970). Organisms are likely to mature later than those in more productive environments where they can grow faster and get larger quicker (Stearns & Koella, 1986). In this respect, important drivers of freshwater productivity as Dissolved Organic Carbon (DOC) have been shown to affect life-history characteristics of *Lepomis macrochirus* Rafinesque, 1819 in North American lakes such

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that fish in high-DOC lakes reached smaller sizes, but had similar fecundity and egg size, at a given size (Craig *et al.,* 2017).

Since streams exhibit variation in physiographic and physicochemical factors, which are often patchily distributed (Pringle *et al.,* 1988), shifts in resource availability are important in predicting the adaptiveness of traits of species populations. Blackwater Atlantic Forest rivers and streams present some environmental heterogeneity, low pH (Camargo *et al.,* 1997; Gonçalves & Braga, 2012) and varied levels of DOC concentrations (Felisberto, 2020), owing to high humic acid contents (Por, 1992). They are also part of Atlantic Forest coastal drainages, which correspond to a system of isolated streams that originate at different points in a region between marine and coastal environments, draining directly into the Atlantic Ocean. Freshwater fishes in these coastal basins have evolved in isolation with sporadic dispersal with inland basins of Brazil (Ribeiro, 2006). As small and/or non-migratory species with specific habitat requirements may be susceptible to variation in habitat across the landscape, limiting their dispersal between populations (Waters & Burridge, 2016), isolated streams may be good model ecosystems for understanding how intraspecific traits vary in response to different conditions.

Hollandichthys multifasciatus (Eigenmann & Norris, 1900) is an endemic characid to the Atlantic coastal drainages of Brazil, occurring from Rio de Janeiro to Rio Grande do Sul states, and in the upper Tietê river (Lima *et al.,* 2007; Menezes *et al.,* 2007). Despite being one of the most representative species in several coastal stream surveys (Ferreira & Petrere, 2009; Gonçalves & Braga, 2012; Lemos, 2019; Felisberto, 2020), biological aspects of *H. multifasciatus* are still poorly known. It is an inseminating species found in clear and blackwater streams (Sabino & Castro, 1990; Esteves & Lobón-Cerviá, 2001; Esteves *et al.,* 2019) with little running water and a muddy bottom, associated with preserved Atlantic Forest riparian vegetation (Bertaco, 2003). Adults display solitary habits, while juveniles form shoals of three to six individuals (Bertaco & Malabarba, 2013). It is considered an omnivore which consumes few autochthonous items and great proportions of plants and terrestrial insects (Abilhoa *et al.,* 2009; Gonçalves *et al.,* 2018), displaying a surface picking behavior as described for several characin species (Sazima, 1986). *Hollandichthys multifasciatus* is classified as Data Deficient (DD) by the Brazilian federal list of endangered species (ICMBio/MMA, 2018) and as Least Concern (LC) in the regional list of São Paulo State (Oyakawa *et al.,* 2009).

Here we examined the existence of plasticity in life history traits of populations of *H. multifasciatus* from ten preserved blackwater streams, assessing their mean length, absolute and relative fecundity, condition factor, length-weight relationship, type of growth (b), sex ratio and gonadal-somatic index among the streams.

MATERIAL AND METHODS

The present study was carried out in the coastal region of São Paulo State (southeast Brazil) in the municipalities of Bertioga and São Sebastião, comprising ten blackwater streams which belong to the Guaratuba, Itapanhaú, Itaguaré and Una sub-basins (Figs. 1, 2, Table 1). The first three sub-basins are located in the Baixada Santista Hydrographic Basin (Ribeiro, 2018), and the Una sub-basin in the Northern Coast, all of them included in the Ribeira do Iguape Ecoregion *sensu* Abell *et al.* (2008). Sampled streams are independent coastal slow-moving acidic environments with high humic acid content. They have their origins at low altitudes in the alluvial plains, also called Coastal Plain Forest, which represents one of the faces of the Atlantic Forest biome, commonly found in the region of the Serra do Mar hills (Marques *et al.,* 2015). The area consists of Dense Ombrophilous Forest and Pioneer Formations, with emphasis on Restinga vegetation (coastal sand-dune habitats) (Instituto Ekos

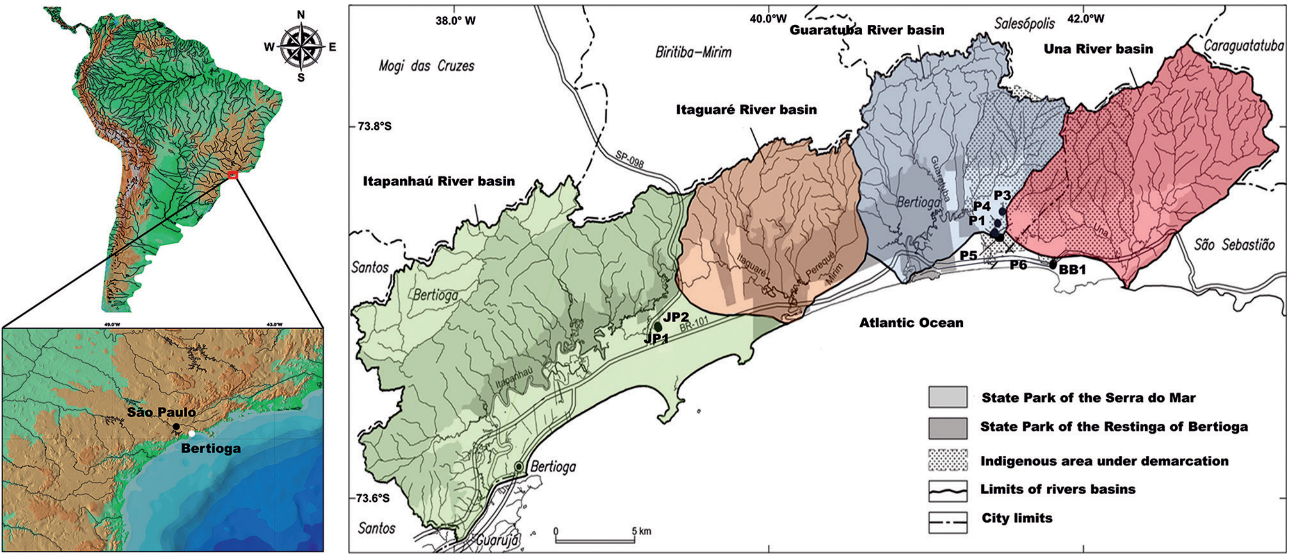

Figure 1. Study area, coastal region of the State of São Paulo. Sampled streams (JP1, JP2 – Itapanhaú); (P1-P6 – Guaratuba); Itaguaré (MP) and Una (BB1 – Una). Adapted from Esteves *et al.* (2019).

Table 1. Characteristics of the sampling sites in the municipalities of Bertioga and São Sebastião, SP. FaR – High dry Restinga Forest; FODT – Lowland Rainforest; FODM – Dense Sub-Montana rainforest (Adapted from Esteves *et al.*, 2019).

Sub-basin	Catchment Area (ha)	Stream	Distance from the sea (km)	Acronym	Dominant vegetation	Coordinates
Guaratuba		Peralta 1**	1.75	P1		S23°44′27.1″ W045°50′28.5″
		Peralta 2**	1.87	P2		S23°44′23.7″ W045°50′24.6″
		Peralta 3**	2.97	P3		S23°43′47.6″ W045°50′07.9″
	11.30	Peralta 4**	2.35	P4	FaR, FODT	S23°44′08.0″ W045°50′18.3″
		Peralta 5**	1.57	P5		S23°44′33.0″ W045°50′16.8″
		Peralta 6**	1.56	P6		S23°44′33.0″ W045°50′11.8″
Itaguaré	9.04	Maneco Pinto	3.1	MP	FaR, FbRb	S 23°46′08.2″ W 46°00′20.4″
Itapanhaú		João Pereira 1*+	3.17	JP1		S23°47′06.6″ W046°03′01.2″
	14.90	João Pereira 2*+	3.29	JP2	FaR	S23°47′03.0″ W046°03′03.6″
Una	12.06	Bora Bora 1+	0.39	BB1	FODT, FODM	S23°45′21.8″ W045°48′14.6″

* sites located within the Parque Estadual Restingas de Bertioga (PERB). ** sites within private properties; + proximity of villages/roads.

Figure 2. View of one of the sampling sites (JP1, Itapanhaú sub-basin), showing block nets at the 100 m sampled stretch.

Brasil, 2008), which range from grasslands and shrublands to forests, with a maximum canopy height of 20 m (Bonilha *et al.*, 2012).

Samplings were performed during the low rainfall season (July-September/2016). The criteria used to select the sampling sites were accessibility, the adequacy for electrofishing, salinity ≤ 0.05 ppm and good conservation status of the streams, for instance, with preserved vegetation and with a minimum of anthropic influences.

Streams were characterized according to its dominant terrestrial vegetation, based on França & Rolim (2000), Instituto Ekos Brasil (2008), Guedes *et al.* (2006) and Pinto-Sobrinho *et al.* (2011). A physical assessment of some habitat variables was conducted along a 100 m stretch of each stream. The following descriptors were considered and scored according to Callisto *et al.* (2014): percentage of high canopy (Diameter at Breast Height > 0.3 m); leaf banks (%); overhanging vegetation (< 1 m from the surface) (%); sand (0.6-2 mm) (%); silt/clay (%). Some water variables as temperature, pH, dissolved oxygen and electrical conductivity were recorded at each stream with a HORIBA multiparameter probe, model U-5000G. Dissolved Organic Carbon (DOC) was analyzed according to APHA/AWWA/WEF (2012).

Each stream was sampled three times along a 100 m stretch isolated with block nets, where electrofishing was performed using a Honda EUi10 Generator (CA, 1000 W). Fish were separated into containers, anesthetized in eugenol solution, fixed in a 10% formalin solution, and transferred to 70% ethanol after 10 days. Specimens were deposited at the ichthyological collection of the Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso" (ZUEC 16629).

Specimens were measured (total length, mm) and weighed (W, g) in the laboratory. Sex was determined through macroscopic analysis of the gonads, which were removed, weighed, and fixed in 70% ethanol. The degree of maturation was determined according to Vazzoler (1996). Specimens were considered immature/juveniles if it was not possible to distinguish sex through gonads or secondary characteristics. The gonadosomatic index (GSI) was calculated for mature females and males according to Santos (1978), following the formula $GSI = 100\ G_W \cdot T_W^{-1}$, where G_W is the gonad weight and T_W is the total weight. Fecundity was estimated by direct counts of fixed mature ovarian subsamples. Oocytes were sub-sampled three times with a Hensel-Stempel pipette, samples counted and measured in a Sedgewick Rafter chamber (Sá-Oliveira & Chelappa, 2002). A minimum of 50 oocytes were measured for each female according to Gomes *et al.* (2011). Absolute fecundity was calculated considering the total of vitellogenic oocytes (Vazzoler, 1981), herein considered those with a diameter ≥ 0.6 mm. To calculate the relative fecundity, the absolute fecundity of each female was divided by its weight (g) (Adebisi, 1987), and then the average relative fecundity per stream was calculated. The sex ratio was determined by the distribution of male and female frequencies in each stream.

The length-weight relationship (LWR) was calculated for mature and immature specimens separately. We calculated the regression for each stream according to the equation $W = a\ L^b$, where W = weight, L = Length, a = intersection with y-axes and b = slope (angular coefficient). After logarithmic transformation of the data we obtained the coefficient A and B by the least squares method for the equation $\log(W) = \log A + \log Bx$, where $a = e^A$ and $b = B$ (Santos, 1978; Braga, 1986). Prior to regression analysis, $\log_{10}$-$\log_{10}$ plots of W and L were used to detect and exclude outliers (Froese, 2006). Initially, to test for significant differences between males and females, we compared the slope (B) of the linearized regressions for grouped streams using PAST 4.05 software. When slopes were statistically similar, males and females were grouped for each stream in the subsequent analysis. Linearized equations of the LWR were performed to compare the slopes (b) obtained for immatures and adults of the different streams, using the PAST 4.08 software (Hammer *et al.,* 2001). The coefficient of determination R^2 was used as a measure of the strength of the straight-line relationship.

The allometric condition factor ($K = W/L^b$) was assessed for comparisons among adults (females and males) and immatures (Le Cren, 1951; Weatherley, 1972) from the different streams, where b is the allometry coefficient related with the form of the individuals' growth calculated from the length-weight relationship. A Student t-test (one-tailed; $p < 0.025$) was performed to test whether the estimated b values differed significantly from a value of 3. The species growth was considered isometric when the value of $b = 3$, and allometric when this value was lower or higher than 3 (Ricker & Carter, 1958).

Data analysis

We performed a Principal Component Analysis (PCA) from the linear correlation matrix of the environmental variables on the PC-ORD v.6.0 software (McCune & Mefford, 2011). Data in percentage were arcsin square-root transformed, and the axes retained for interpretation chosen through the Broken-stick criterion (McCune & Mefford, 2011).

The Shapiro-Wilks test of normality and Levene's test of homoscedasticity were used to determine whether parametric ANOVA or the non-parametric Kruskal-Wallis test should be used to test for differences between mean oocyte diameter, gonadal-somatic index, condition factor and total length of females, males and immatures. When data fit assumptions of normality and/or homogeneity of variance, we employed a one-way ANOVA considering the streams as independent samples. A post hoc Tukey test was used to determine which streams showed significant differences ($p < 0.05$). For non-parametric data, the Kruskal-Wallis ANOVA and Dunn's post-hoc test were employed. A chi-square test ($\alpha = 0.05$) was applied to verify the existence of significant differences between the number of males and females, and a 'two sample' t-test to compare mean lengths between males and females (grouped streams), with significance at the 5% level. All analyses were performed with PAST 4.08 software (Hammer *et al.,* 2001).

RESULTS

Environmental variables presented high variation among sites as shown by Table 2 and Fig. 3. The first PCA axis retained for interpretation (eigenvalue = 2.78) explained 27.9% of total variance, and the second axis (eigenvalue = 2.64) 26.4% (Fig. 3). Axis 1 reflected habitat characteristics related to substrate type, with sand ($r = 0.950$) and silt/clay (-0.834) showing the highest loadings, to which P5 was associated. Sites from the Itaguaré and Itapanhaú sub-basins (MP, JP1, JP2) were associated to high canopy and pH on the positive side of Axis 2, while most of the sites of the Guaratuba sub-basin were related to higher temperature ($r = -0.863$) and leaf banks ($r = -0.698$) on the negative side.

Table 2. Basic environmental characteristics of ten coastal blackwater streams sampled in in the municipalities of Bertioga and São Sebastião, SP, in the low pluviosity season, indicating the range of values, mean and Standard Deviation (SD).

	Maximum	Minimum	Mean	SD
High Canopy (%)	72.5	17.5	36.0	16.2
Leaf Banks (%)	95.0	20.0	63.5	23.9
Overhanging vegetation (%)	50.0	25.0	41.5	9.8
Sand (%)	73.0	12.0	41.0	18.9
Silt/Clay(%)	80.0	8.0	45.6	25.9
Temperature (°C)	20.9	17.0	19.2	1.2
pH	6.1	3.6	4.7	1.0
Conductivity ($\mu S.cm^{-1}$)	125.0	66.0	91.4	17.6
Dissolved Oxygen ($mg.L^{-1}$)	10.1	1.4	5.9	2.7
Dissolved Organic Carbon ($mg.L^{-1}$)	87.1	13.9	41.6	30.1

A total of 185 specimens were analyzed, comprising 82 adults (37 males and 45 females) and 103 immature individuals. Mean length of females and males was similar among streams (Table 3), while for immatures, the Kruskal-Wallis test indicated significant differences among sites. The highest values were observed in streams P2, P3 and MP (Table 4). The two sample t-test on mean length between males and females, showed no significant differences between them ($t = 0.229$; $p = 0.81$).

The sex ratio (male: female) varied among streams, however the values did not depart significantly from the expected 1:1 ratio in the different streams according to the χ^2 test ($p \geq 0.05$). The mean Gonadosomatic Somatic Index (GSI) of the females was similar between stream samples, while significant differences were found between males according to the ANOVA (Table 3). The mean absolute fecundity for 25 females varied between 604 and 708 oocytes (SD = 98.7) and the relative fecundity between 132 and 192 oocytes (SD = 65.3). ANOVA did not show significant differences between these variables among streams (Table 3).

The condition factor of mature adults was significantly different among streams as indicated by the ANOVA, with exception of P4 and P6 from the Guaratuba sub-basin (Table 3). For immatures, the condition factor also differed significantly among streams, as shown by the Kruskal-Wallis test (Table 4), with highest value observed at MP (0.068) and the lowest value at JP2 (1.3×10^{-5}). Dunn's post hoc comparisons showed that P1 and P2 presented similar values.

Fecundity data was obtained from the analysis of 25 mature females which ranged from 58.0 to 99 mm TL. They were obtained at streams P2 (N = 4), P3 (N = 3), P4 (N = 10), P5 (N = 4), P6 (N = 4). Oocyte diameter varied from 0.35 mm to 0.90 mm, showing a more developed group ready to be released, with mode at 0.6 mm observed in all streams (Fig. 4).

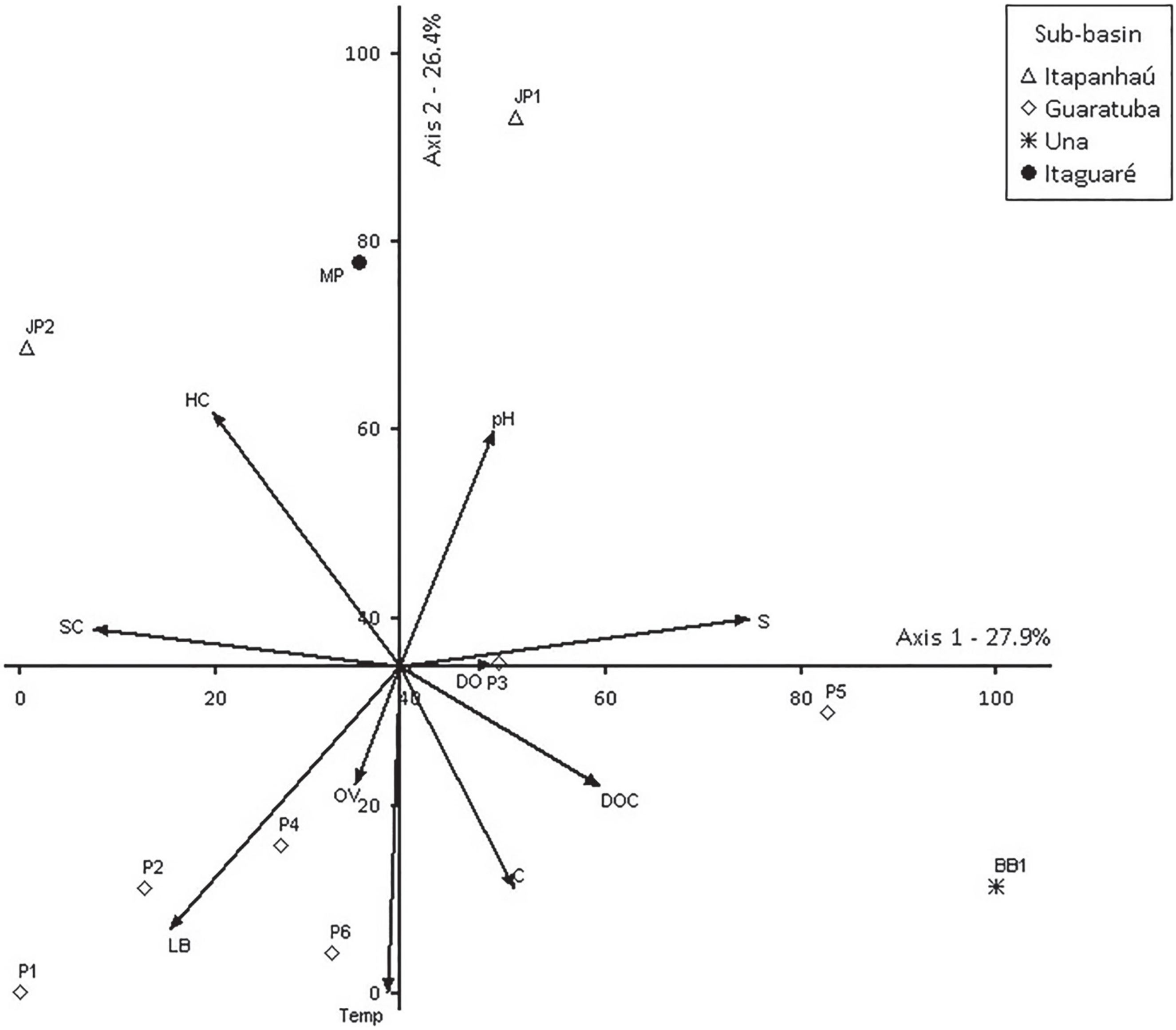

Figure 3. Principal Components Analysis (PCA) plot of environmental variables measured at 10 blackwater streams in the Baixada Santista and Northern Coast Basins, São Paulo state. Environmental variables are indicated by vectors. DOC = Dissolved Organic Carbon; Temp = Temperature; C = Conductivity; DO = Dissolved Oxygen; HC = High Canopy; S = Sand; SC = Silt/Clay; LB = Leaf Banks; OV = Overhanging vegetation. For stream acronyms see Table 1.

Table 3. Intraspecific variation of life-history traits in streams where mature adults of *Hollandichthys multifasciatus* were found, and results of the ANOVA and Chi-Squared test (χ^2). F = Females; M = Males; GSI = Gonado-Somatic Index; RF = Relative Fecundity; AF = Absolute Fecundity. Means with different superscripts were significantly different ($p < 0.05$). For stream acronyms see Table 1.

Site	**P2**	**P4**	**P5**	**P6**	**P3***	**BB1***			
Life history trait							**ANOVA (*F*)**	**p-level**	**χ^2**
Size range (mm)	48-87	42-90	47-107	58-90	51-99	45-84			
Sex ratio (M:F)	1: 1.1	1: 1.2	1: 0.7						$p > 0.05$**
Mean GSI (F)	5.2	6.1	7.4	7.5			1.664	0.200	
Mean GSI (M)	1.96^{ac}	0.77^{bd}	1.35^{cd}			1.57^{cd}	6.014	0.003	
Mean Condition Factor (K)	$3.22 \times 10^{-5,a}$	$9.45 \times 10^{-6,b}$	$4.08 \times 10^{-5,c}$	$7.72 \times 10^{-6,b}$		$1.23 \times 10^{-5,d}$	683.4	0.000	
Mean RF	157.8	192.9	132.6	148.9	154.1		1.066	0.388	
Mean AF	604.1	713.3	679.1	708.2	605.5		1.269	0.314	
Mean length (mm) (F)	59.2	66.8	74.3	70.3	73.2		1.895	0.133	
Mean length (mm) (M)	64.5	67.6	73.7			62.4	0.506	0.645	
N – Females	9	18	6	6	4	2			
N – Males	8	15	9	0	0	5			

* site with low number of specimens not used to calculate all variables.

** values obtained at the different streams.

Table 4. Intraspecific variation of mean length and condition factor (K) in streams where immature specimens of *Hollandichthys multifasciatus* were obtained, and results of the Kruskal-Wallis (H) test. Means with different superscripts were significantly different ($p < 0.05$). For stream acronyms see Table 1.

Site	JP1	JP2	P1	P2	P3*	MP	H	*p*
Life history trait								
Size range (mm)	22-40	23-76	15-35	48-62	48-55	47-96		
Mean Condition Factor (K)	3.55×10^{-5a}	1.31×10^{-5b}	9.38×10^{-5c}	5.78×10^{-5c}		0.068^{d}	90.62	0.000
Mean length (mm)	29.8^{a}	30.3^{a}	24.0^{c}	53.6^{b}	52.6^{b}	60.9^{b}	65.41	0.000
N	25	24	27	11	6	10		

* site with low number of specimens not used to calculate all variables.

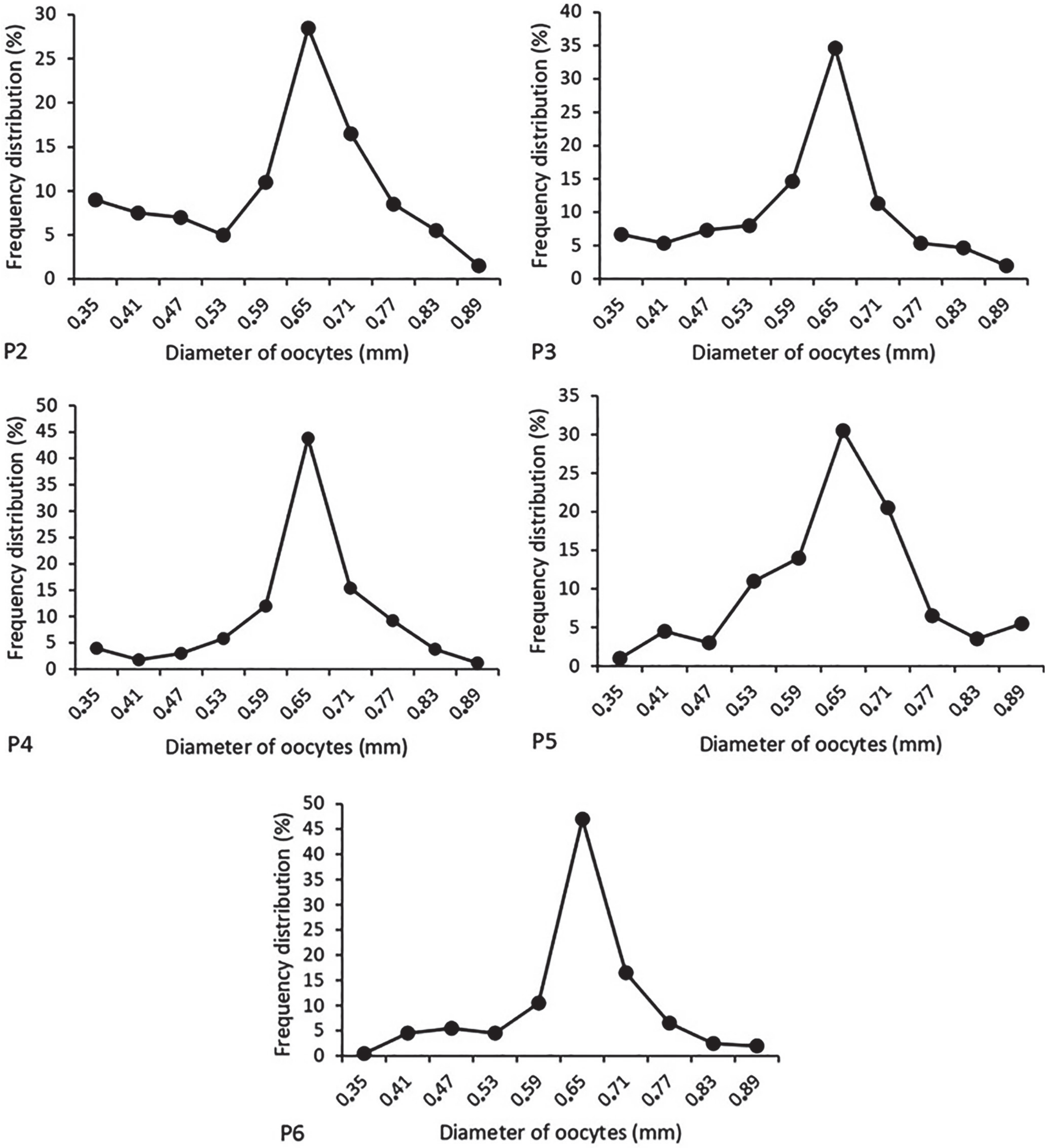

Figure 4. Frequency distribution of oocytes diameter (mm) of mature females of *Hollandichthys multifasciatus* sampled at the different coastal blackwater streams in the Baixada Santista and Northern Coast Basins, São Paulo state. P2 (N = 4); P3 (N = 3); P4 (N = 10); P5 (N = 4); P6 (N = 4).

Table 5. Coefficients of the length-weight regressions of mature adults (females + males) (A) and immatures (B), according to the equation: log (TW) = log (a) + b * log (TL), where "a" is the intercept (coefficient related to condition factor), "b" is the regression coefficient (indicative of growth type), and R^2 is the coefficient of determination, or proportion of variance explained by the model; t = t-test for the results of b values compared to the theoretical value ($b = 3$, $p < 0.025$). For stream acronyms see Table 1.

(A)

Stream/Parameters	N	a	b	R^2	t
P4	28	9.45×10^{-6}	3.04	0.960	0.310
BB1	7	1.23×10^{-5}	2.99	0.996	0.104
P2	15	3.22×10^{-5}	2.79	0.973	1.512
P6	6	7.72×10^{-6}	3.09	0.991	0.950
P5	13	4.08×10^{-5}	2.70	0.980	2.140*
Slope Test (F)	1.354				
p	0.259				

(B)

Stream/Parameters	N	a	b	R^2	t
JP1	25	3.53×10^{-5}	2.70	0.948	2.092*
JP2	24	1.29×10^{-5}	3.01	0.959	0.048
P1	27	9.21×10^{-5}	2.42	0.882	2.720**
P2	11	0.02	2.63	0.924	1.396
MP	10	0.07	1.04	0.961	26.625**
Slope Test (F)	5.47				
p	0.001				

* b is significantly different from 3 ($P = 0.025$).
** b is significantly different from 3 ($P = 0.01$).

The high coefficient of determination values obtained in the assessment of LWRs for adults and immatures at the different streams indicated a good quality of the prediction of the linear regression for ($R^2 > 0.88$) (Table 5). The slope test (b) between the LWR obtained for the different streams indicated no significant differences between adults ($p = 0.259$), but significant differences between immatures ($p = 0.001$). The b coefficient, which is indicative of the type of growth, varied from 2.7 to 3.09 for adults (males and females) and 1.04 to 3.01 for immatures. The growth was predominantly isometric in streams P4, BB1, P2 and P6, and allometric in P5, JP1, P1 and MP.

DISCUSSION

Streams were located in preserved areas with some heterogeneity of environmental conditions, which distinguished streams from the Guaratuba sub-basin from the other sub-basins due to higher values of temperature and leaf banks. Compared to other Atlantic Forest coastal plain rivers (Ferreira *et al.,* 2014), lower values of pH and higher conductivity were observed in our study. For DOC values, no information was found for Atlantic Forest backwater streams, but when they are compared to those observed in blackwaters of the Rio Negro, the major tributary to the Amazon, we obtained higher values than Duarte *et al.* (2016), who recorded concentrations between 8-12 mg C L^{-1}, but up to 35 mg C L^{-1}.

Most of the analyzed life-history traits of *H. multifasciatus* were similar among streams, suggesting that site-specific factors did not influence size of adults, maturation, sex ratio or fecundity. Resource availability seems to play an important role in life-history aspects of different species, being considered theoretically a potent agent of selection on life history traits (Grether *et al.,* 2001). High levels of dissolved organic carbon (DOC) reduce ecosystem productivity and resource availability (Craig *et al.,* 2015), and such relations were observed by Craig *et al.* (2017) for populations of bluegill (*Lepomis macrochirus*). They found a strong negative relationship between maximum size and DOC concentration and lower fecundity in a set of lakes with DOC concentrations ranging from 3 to 24 mg. L^{-1}. Guppies (*Poecilia reticulata* Peters, 1859) from Trinidad streams living in resource-rich streams were able to grow faster, reach larger sizes, and allocate more resources to reproduction (Grether *et al.,* 2001), and in this case, stream differences in canopy cover could translate into stream differences in resource availability. Although these aspects must be further investigated in blackwater streams, the similarity in the several life-history traits of *H. multifasciatus,* suggests that the preserved riparian conditions of the different streams may be more important than the high DOC levels in determining resource availability for this species. This may be explained by the food habits of *H. multifasciatus,* which is considered an omnivorous species that consumes great proportions of plants and terrestrial insects, due to its surface picking behavior (Abilhoa *et al.,* 2009).

We observed that mature females with vitellogenic oocytes displayed a similar spawning pattern among sites during the sampling period, suggesting that mature oocytes are spawned at once within this reproductive event. This agrees with Lemos (2019) who found that *H. multifasciatus* had high frequencies of mature females in the rainy and dry seasons in coastal streams of Bertioga (SP). Frequency distribution of oocyte diameter indicated total spawning, and size was higher than that observed by Oliveira (2019) for this species (0.15-0.7 mm). Nevertheless, fecundity was lower than the mean values recorded by this author in clear and blackwater Atlantic Forest streams (860.2), which may be attributed to a higher size attained by the species in their study, since larger fish have large gonads and consequently can produce more oocytes and more offspring (Wootton, 1992). Observed fecundity values can be considered low when compared to non-inseminating characids, as found by Mazzoni *et al.* (2005) for *Astyanax janeiroensis* Eigenmann, 1908 (3.169-18.714 oocytes) in coastal streams of Rio de Janeiro State. This may be explained by the fact that among small sized species, lower relative fecundity values may be associated with the presence and efficiency of insemination (Azevedo, 2010).

Environmental factors may also regulate variations in either egg size or number between and within populations of freshwater fish, as reported by Lobón-Cerviá *et al.* (1997), who found that trout at sites which were fully covered by canopy spawned fewer, but larger, eggs than fast-growers in unshaded sites. In coastal streams, rainfall regime may be considered an important factor as pointed out by Menezes & Caramaschi (1994). Braga *et al.* (2008) for example, reported that insemination of the Glandulocaudinae *Mimagoniates microlepis* (Steindachner, 1877) seems to occur in the dry season, when the habitat is reduced and encounters between males and females are most probable. As *H. multifasciatus* and *M. microlepis* are both inseminating and related species (Thomaz *et al.,* 2010), it is possible that the low water level during the period of our study may also influence the reproductive behavior of *H. multifasciatus.*

The condition factor of adults, immatures and the mean length of immatures were the only parameters that showed intraspecific variations, which can be related to differences in such factors as temperature and food supply, as condition factor is an index that indicates the "well-being" of the fish (Froese, 2006). The higher condition factor observed for immatures suggests that they are in a rapid growth phase, directing the feeding resources to their growth. This has been observed for other Neotropical species, as several characids in the Upper Paraná River floodplain (Lizama & Ambrósio, 2002) and *Micropogonias furnieri* (Desmarest, 1823), with higher condition independent of the time and distribution area (Costa & Araújo, 2003).

Spatial differences in the condition factor among adults were observed even at nearby streams like P2 and P4, which showed similar environmental conditions, suggesting that site-specific factors other than food availability may have influenced these values. In fact, differences in the condition factor have been interpreted as a measure of several biological events, such as fat reserves, adaptation to the environment and gonadal development (Le Cren, 1951). It is known that fish usually decrease their feeding activity and use their lipid reserves during spawning which results in a decrease in condition (Lizama & Ambrósio, 2002). Thus, it is possible that the observed dissimilarities in condition were related to differences in growth and/or breeding of fish between localities, as confirmed by the difference in slopes of the LWR for immatures. Similar observations were found for trout, by Lobón-Cerviá & Rincón (1998) who observed differences in growth between localities 1-2 km apart.

It can be concluded that *H. multifasciatus* showed few intraspecific variations of the analyzed life-history traits under natural conditions during the low precipitation period, despite variations in some environmental conditions among sub-basins. Although other aspects of the biology of *H. multifasciatus* should be further investigated, the obtained results may help to document natural variations of traits of an endemic fish species, providing foundation for future efforts to examine the biotic and abiotic factors associated with the life histories of imperiled fishes.

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Papéis Avulsos de Zoologia
Museu de Zoologia da Universidade de São Paulo

Erratum

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