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Effects of temperature on prey consumption and growth in mass of juvenile trahira *Hoplias* aff. *malabaricus* (Bloch, 1794)

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The influence of temperature on prey consumption and growth in mass of juvenile trahira *Hoplias* aff. *malabaricus* were investigated. Consumption of small-sized lambari *Astyanax altiparanae* (mean standard length, L_S, 5·43 cm) varied from zero to 65 over a period of 30 days. Temperatures ranged from 14 to 34° C and the size of trahiras ranged from 17·5 to 24·7 cm L_S. Prey consumption differed significantly among temperatures. Trahiras at 18° C consumed significantly less than those at 30° C. A linear multiple regression model including temperature, prey consumption and L_S explained 89·4% of the variability in growth in mass. Some caution is suggested when inferring the impact of *H.* aff. *malabaricus* piscivory on assemblage structures in systems that, despite their location in tropical regions, are subjected to seasonal thermal variations.

Key words: body size; empirical modelling; growth in mass; *Hoplias* aff. *malabaricus*; prey consumption; temperature.

INTRODUCTION

The influences of temperature on prey consumption and growth rate are of fundamental importance in fish ecology. Generally, there is an optimal temperature range for consumption and conversion of food in growth (Brett, 1979; Burel *et al.*, 1996) and a reduction in growth rate as individuals age (von Bertalanffy growth model; Otterlei *et al.*, 1999). Most studies on the influence of temperature on fish consumption and growth have investigated early life stages of commercially valuable species (Larsson & Berglund, 1998; Otterlei *et al.*, 1999), but these relationships are still unknown for most neotropical species.

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Fishes in neotropical floodplains may experience extreme temperatures over the seasons, especially in shallow water bodies, which can alter their metabolism and food consumption. These alterations interfere in resource allocation for growth with consequences on biotic interactions. The trahira *Hoplias* aff. *malabaricus* (Bloch, 1794) exhibits a differential capacity to thrive in harsh environments and its recruitment is usually successful due to morphological (Fernandes *et al.*, 1994), physiological (Rantin *et al.*, 1992, 1993; Rios *et al.*, 2002) and behavioural adaptations (sedentary habit, parental care and tolerance to long periods of starvation) (Azevedo & Gomes, 1942). *Hoplias* aff. *malabaricus* is an ambush predator that preferentially inhabits structured areas in the littoral zone, where several small-sized fish species are abundant under macrophyte stands (Delariva *et al.*, 1994; Súarez *et al.*, 2001). Although several studies have already described the diet of *H.* aff. *malabaricus* (Azevedo & Gomes, 1942; Barbieri *et al.*, 1982; Bistoni *et al.*, 1995; Loureiro & Hahn, 1996; Hahn *et al.*, 2004), little is known about its prey consumption rates.

Prey consumption and growth, for instance, may be influenced by environmental (such as temperature) and intrinsic (such as body size) conditions of the organism that may have implications in relationships among species. According to Brett (1979), temperature is the main factor that influences fish growth. The size of organisms, however, interferes with this relationship (Ostrovsky, 1995; Imsland *et al.*, 1996; García-Berthou, 2001). Based on these considerations, the aims of the present study were to (1) investigate the effects of temperature on prey consumption of juvenile *H.* aff. *malabaricus* from the upper Paraná River floodplain and (2) evaluate the effect of temperature on growth in mass, controlling possible influences of prey consumption and body size.

MATERIALS AND METHODS

EXPERIMENT

Thirty individuals of trahira *H.* aff. *malabaricus* ($17{\cdot}5 <$ standard length, $L_S < 24{\cdot}7$ cm) were captured in marginal lagoons of the upper Paraná River floodplain (22°35′–22°55′ S; 53°10′–53°40′ W) in April 2004. These individuals were kept for 6 days in two 500 l tanks with controlled temperature (23° C), and submitted to treatment with fungicide and bactericide solution to prevent infections. To determine individual prey consumption and to avoid hierarchy dominance effects (Sloman & Armstrong, 2002), fish were transferred to 250 l aquaria (one fish per aquarium), arranged in six rows (five aquaria per row; replicates) and exposed to a 12D:12L light regime. Each row of five aquaria had independent control of temperature. To better acclimate and enable the ambush strategy of trahira, aquaria were structured with rocks and polyethylene ribbons that simulated submerged plants.

The maximum and minimum temperatures recorded in the upper Paraná River floodplain between February 2000 and November 2002 (35·5 and 12·4° C, respectively; A. C. Petry, unpubl. data) were used as the thermal range for the experiment. Six fixed temperatures were assigned (14, 18, 22, 26, 30 and 34° C). These temperatures were reached after an acclimation period of 15 days with elevations or reductions $<1°$ C day^{-1}, to reduce thermal stresses associated with rapid alterations in temperature (Rantin *et al.*, 1985). The period of acclimation was based on the results of a previous study (Rantin *et al.*, 1985) and the aim was to simulate natural temperature fluctuations (14° C conditions rarely last more than seven consecutive days in the region). Water temperature was controlled electronically by submerged sensors located in six water containers feeding the aquaria. At the beginning of the experiment, L_S did not differ significantly among temperatures (ANOVA F-test, d.f. = 5, 24, $P > 0{\cdot}05$).

Small-sized lambari *Astyanax altiparanae* Garutti & Britski, 2000 (mean ± S.D. 5·43 ± 0·05 cm) were used as prey. This species was chosen because (1) its high abundance and wide distribution in the upper Paraná River floodplain and (2) its high occurrence in the stomachs of *H.* aff. *malabaricus* (Loureiro & Hahn, 1996; Hahn *et al.*, 2004). A prey density of 10 prey per aquarium was maintained during the experiment. During the thermal acclimation, all trahiras consumed prey (between two and six, mean of 4·2) with no significant differences among the six aquaria rows (ANOVA F-test, d.f. = 5, 24, $P > 0{\cdot}05$). Seventy-two hours before the beginning of the experiment, non-consumed prey were removed.

The experiment was conducted over 30 days. For each fish, L_S (cm) and mass (M_t; g) were recorded at the beginning and at the end of the experiment. In addition to the daily record of prey consumed, some procedures were performed in order to standardize the conditions inside aquaria: replacement of consumed prey (0700 hours) or dead prey (0700, 1400 and 2200 hours), faeces removal (2000 hours), and adjustments of temperature (<0·5° C) and dissolved oxygen (>6 mg l^{-1}) (0800 hours).

DATA ANALYSIS

Effect of temperature on prey consumption

The choice of six levels of temperature with 4° C intervals was made to improve the statistical power of tests (Gotelli & Ellison, 2004). According to Myers (1990) and Eberhardt & Thomas (1991), this is a valid procedure for manipulative experiments, because it allows the interpolation of results. To address the effects of temperature on prey consumption, a scatterplot was constructed and a multiple regression performed by adding L_S and M_t (alternated between standard length and biomass at the beginning of the experiment; L_{Si} and M_{ti}, respectively), in addition to temperature [T_C (centred variable)], as well as their quadratic terms (L_{Si}^2, M_{ti}^2 and T_C^2). As residual diagnosis did not support the statistical model, treatment means were only compared by ANOVA. The Tukey test was employed to detect significant differences between treatments (Gotelli & Ellison, 2004).

Modelling growth in mass

A multiple linear regression model was adjusted considering growth in mass as the response variable (G) and prey consumption (C), temperature (T_C) and L_{Si} as predictor variables. Growth in mass was calculated based on the equation: $G = \ln(M_{tf} - M_{ti})$, where M_{tf} is the individual mass at the end of the experiment. Natural logarithm (ln) was used in order to meet assumptions of the statistical analysis.

Prey consumption and body size were included in the statistical model to control for their effects and to remove possible parameter biases (Myers, 1990) not controlled by the random assignment of treatments. The need for considering prey consumption and body size in relationships between G and temperature for poikilothermic animals is discussed in more detail in Ostrovsky (1995). Multicollinearity, a problem in any multiple regression model, among predictor variables (C, T_C and L_{Si}) was measured through the variance inflation factor (F_{VI}). According to Myers (1990), values <10 indicate weak influence on parameter variance. The contribution of each predictor variable to the model was inferred by β values and uniqueness index (U). Beta values are the regression coefficients for the standardized variables (mean 0 and 1 S.D.), whereas U represents the percentage of variance explained by each predictor above and beyond the variance accounted for by the other variables in the model (Hatcher & Stepanski, 1994). Relationships between growth in mass and predictor variables were explored through scatterplot of partial residuals (partial regression plots). As a quadratic relationship between temperature and growth in mass was observed, estimation of the temperature in which growth was maximum (the optimal temperature) was done through the partial derivative of G in relation to temperature (Pinto & Morgado, 2004). A series of residual diagnostics (Shapiro–Wilk normality test, Breuch–Pagan homoscedasticity test, Ramsey RESET test for omitted variables) and methods of parameter estimation (truncated and robust regressions, robust S.E. and bootstrap residuals) were performed in order to evaluate the robustness of the results (Myers, 1990; Draper & Smith, 1998).

When necessary, data were transformed in order to meet ANOVA and regression assumptions. Statistical analyses were performed using the softwares Statistica® and Stata®. Since the primary purpose of this paper was to determine relationships, results were inferred considering probability of type I error (α) of 1, 5 and 10% of significance (Manly, 1997).

RESULTS

EFFECT OF TEMPERATURE ON PREY CONSUMPTION

Consumption varied from zero to 65 prey in the range of tested temperatures. Individuals exposed to 14° C did not consume any prey during the experiment. From 18 to 30° C, prey consumption increased gradually and decreased at 34° C. Trahiras exposed to 30° C consumed four times more than those acclimated to 18° C and twice more than those acclimated to 22, 26 and 34° C.

One trahira died on day 20 of the experiment at 30° C and was excluded from all analyses. The temperature of 14° C was also excluded from analyses, due to the lack of feeding of trahiras. A linear model for prey consumption ($\log_{10}$ transformed) as a function of temperature was chosen from multiple regression analyses (Fig. 1). In spite of significant parameters ($P < 0{\cdot}01$), residuals were heteroscedastic, with apparent problems of model specification (Fig. 1). Residuals from ANOVA were homoscedastic and this analysis detected significant differences in prey consumption among temperatures (ANOVA F-test, d.f. = 4,19, $P = 0{\cdot}01$). Trahiras acclimated to 18° C consumed significantly less prey than those kept at 30° C (Tukey; $P < 0{\cdot}05$).

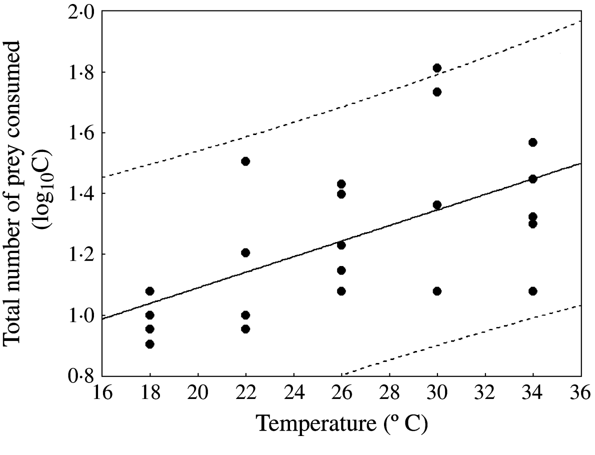

FIG. 1. Relationship between prey consumption and temperature. The curve was fitted by $y = 0{\cdot}578 + 0{\cdot}026\,x$ ($r^2 = 0{\cdot}35$; broken line indicates 95% CI).

MODELLING GROWTH IN MASS

Correlations revealed that only water temperature (T_C:$r = 0{\cdot}46$ and T_C^2:$r = -0{\cdot}32$) and prey consumption (C:$r = 0{\cdot}89$) were significantly related to growth in mass (Table I). Then, a multiple linear regression analysis was performed regressing growth in mass against water temperature, prey consumption and L_{Si}. These variables presented significant coefficients and explained 89·4% of the variability in growth in mass (ANOVA F-test, d.f. = 4, 24, $P < 0{\cdot}01$; r^2 adjusted = 0·88).

Beta values and U were evaluated to determine the relative importance of each predictor variable (Table II). Both presented similar results for the relative importance of each predictor variable. The U demonstrated that prey consumption accounted for 52% of the variability in growth in mass (ANOVA F-test, d.f. = 1, 24, $P < 0{\cdot}05$), whereas L_S accounted for 6%, and T_C for 4% (U for the last two were not significant; $P > 0{\cdot}05$) (Table II). According to partial regression plots (Fig. 2), temperature had a negative quadratic relationship [Fig. 2(a)], while prey consumption (positive) and L_S (negative) were linearly related to growth in mass [Fig. 2(b), (c)]. After correction for C and L_{Si}, the optimal temperature for growth in mass of *H.* aff. *malabaricus* was estimated at 21·4° C.

Diagnosis of the regression analysis indicated the robustness of results. Residuals were normal (Shapiro–Wilk, $P > 0{\cdot}05$) and homoscedastic (Breuch–Pagan, χ^2, $P > 0{\cdot}10$), apparently without omitted variables (Ramsey RESET, F-test, d.f. = 3, 21, $P > 0{\cdot}10$) and $F_{VI} < 10$. In addition, parameters estimated through truncate and robust regressions (without the treatment of 34° C, that presented greater residuals), and with robust S.E. did not differ significantly ($P > 0{\cdot}05$) regarding those presented in Table II.

DISCUSSION

In poikilothermic animals, temperature and body size drive metabolic rates, affecting physiological processes (Brett, 1979; Lovell, 1998; Gilman *et al.*, 2006). These processes involve food consumption, efficiency of food conversion into growth (Burel *et al.*, 1996) and behaviour (Castonguay & Cyr, 1998), with consequences for interspecific interactions (Persson, 1986). Close to tolerable extremes, the influence of temperature is more conspicuous because it promotes the interruption of food consumption and, consequently, leads to a loss of

TABLE I. Mean ± S.D. ($n = 29$) and Pearson correlation coefficient between growth in mass (G) and predictor variables (water temperature T_C and T_C^2, consumption C and standard length (L_{Si}) of juvenile trahira

		r				
	Mean ± S.D.	G	T_C	T_C^2	C	L_{Si}
G	0·10 ± 0·12	1				
T_C	0·00 ± 6·98	0·46†	1			
T_C^2	46·99 ± 41·38	−0·32*	0·08	1		
C	17·17 ± 15·32	0·89‡	0·65‡	−0·16	1	
L_{Si}	20·87 ± 2·00	−0·13	0·14	0·01	0·15	1

*$P < 0{\cdot}10$; $^†P < 0{\cdot}05$; $^‡P < 0{\cdot}01$.

TABLE II. Results of the multiple linear regression ($n = 29$) between growth in mass and water temperature (T_C and T_C^2), consumption (C) and standard length (L_{Si}) of juvenile trahira. Variance inflation factor (F_{IV}), regression coefficient ± S.E., t-test for the adjusted coefficient, coefficients of the standardized multiple regression (β) of predictor variables and uniqueness indexes (U) for each variable

	F_{IV}	Coefficient S.E.	t	β	U
T_C	1·84	−0·002275 ± 0·0015714	−1·45	−0·13	0·04
T_C^2	1·09	−0·000430 ± 0·0002038	−2·11*	−0·15	
C	1·88	0·007838 ± 0·0007240	10·83†	0·996	0·52*
L_{Si}	1·03	−0·015428 ± 0·0040918	−3·77†	−0·25	0·06
Constant		0·304278 ± 0·0864864	3·52†		

*$P < 0·05$; †$P < 0·01$ (significances inferred from t-and Fisher $F(U)$-tests).

body mass (Larsson & Berglund, 1998). In this experiment, lack of feeding and loss of mass were observed in fish exposed to 14° C. These factors suggest that metabolic rates of *H.* aff. *malabaricus* in the upper Paraná River floodplain are reduced at lower temperatures and prey consumption ceases completely at some level between 18 and 14° C. For the pintado *Pseudoplatystoma corruscans* (Agassiz, 1829) from the same region, prey consumption ceased at 17° C (Marques *et al.*, 1992).

The present study indicated that growth in mass of juvenile *H.* aff. *malabaricus* was closely dependent on prey consumption, temperature and body size. Although coefficient values were distinct, the patterns observed between response and predictor variables for trahira are congruent with results presented by other authors that evaluated species from temperate (Brett, 1979; Wurtsbaugh & Cech, 1983; Burel *et al.*, 1996) and tropical (Piana *et al.*, 2003) regions. One exception is the study of Allen & Wootton (1982), which reported a positive linear tendency between growth rate and temperature for the three-spined stickleback *Gasterosteus aculeatus* L. According to Mooij *et al.* (1994), these relationships could vary with trophic category.

The optimal temperature for growth in mass of juvenile *H.* aff. *malabaricus* is situated below the temperature in which prey consumption was maximum, indicating that food conversion of this species decreased at temperatures >21·4° C. Similar tendencies were recorded by Wurtsbaugh & Cech (1983) and Piana *et al.* (2003). These results, however, differ in some way from patterns reported for temperate species. For salmonids such as the Arctic charr *Salvelinus alpinus* (L.) and brown trout *Salmo trutta* L., for example, the level in which energy acquisition (tightly related to consumption) is the maximum was equal or near the optimal temperature for growth in mass (Larsson & Berglund, 1998; Elliott & Hurley, 2000).

Although it is difficult to make generalizations from experimental data (other variables besides temperature should have been measured), experimental studies strongly control some factors (*i.e.* temperature and body size) and reduce system complexity as well. The present study follows a general and growing trend of adopting experimental approaches in fish ecology, which may substantially contribute to highlighting ecological mechanisms of variation in assemblage patterns (Taniguchi *et al.*, 1998; Schlosser *et al.*, 2000). The

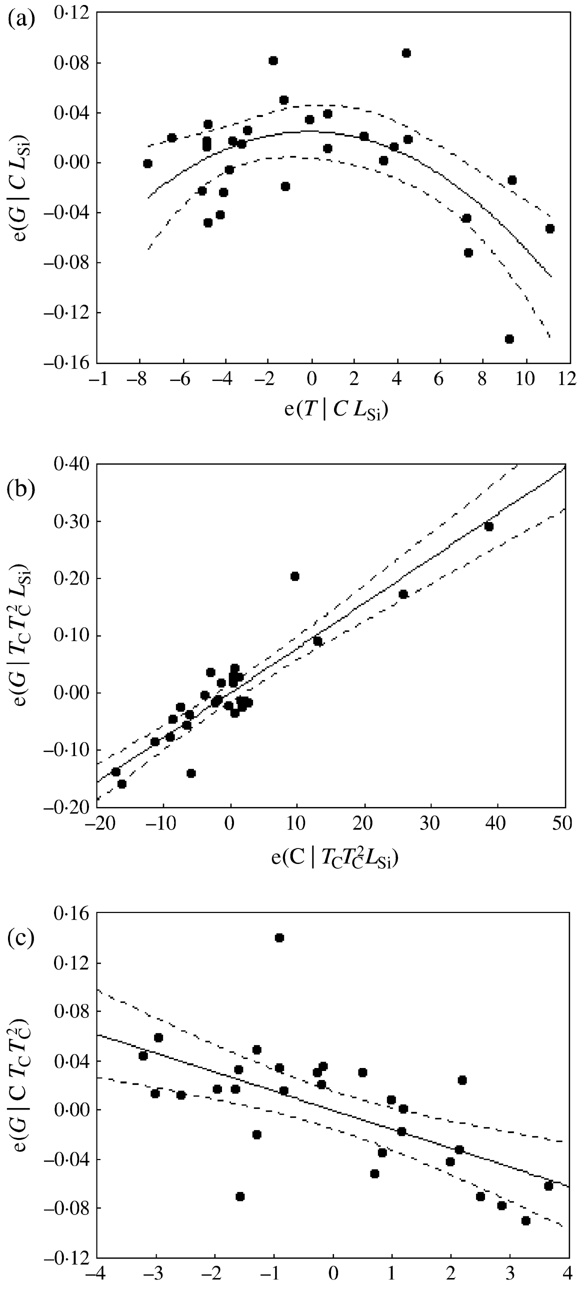

FIG. 2. Partial regressions between growth in mass (G) and (a) water temperature (T) (b) consumption (C) and (c) standard length (L_{Si}) (see Table II; broken line indicates 95% CI). $\mathrm{e}(T_{\mathrm{C}}|CL_{\mathrm{Si}})$, expected value of T_{C} beyond that explained by C and L_{Si}; $\mathrm{e}(G|CL_{\mathrm{Si}})$, expected value of G beyond that explained by C and L_{Si}; $\mathrm{e}(C|T_{\mathrm{C}}T_{\mathrm{C}}^2L_{\mathrm{Si}})$, expected value of C beyond that explained by T_{C}, T_{C}^2 and L_{Si}; $\mathrm{e}(G|T_{\mathrm{C}}T_{\mathrm{C}}^2L_{\mathrm{Si}})$, expected value of G beyond that explained by T_{C}, T_{C}^2 and L_{Si}; $\mathrm{e}(L_{\mathrm{Si}}|CT_{\mathrm{C}}T_{\mathrm{C}}^2)$, expected value of L_{Si} beyond that explained by C, T_{C} and T_{C}^2; $\mathrm{e}(G|CT_{\mathrm{C}}T_{\mathrm{C}}^2)$, expected value of G beyond that explained by CT_{C} and T_{C}^2.

evaluation of how environmental factors act to modulate predator physiological processes is the primary aspect of determining the role of piscivory in fish assemblages. As demonstrated in this study, temperature affected the intensity of interspecific interactions of *H.* aff. *malabaricus*, directly (prey consumption) and indirectly (growth in mass).

From an ecological perspective, the results obtained may contribute to elucidate the role of *H.* aff. *malabaricus* in structuring fish assemblages through predation, especially in isolated ponds, as suggested by Súarez *et al.* (2001) and Okada *et al.* (2003). According to Gilliam & Fraser (2001), *H.* aff. *malabaricus* interfere with fish movement, affecting patterns of spatial distribution. Its effects as a voracious predator, however, are still under evaluation by several authors, based on empirical evidence (Paiva *et al.*, 1994; Bistoni *et al.*, 1995; Pelicice *et al.*, 2005). By providing a quantification of factors affecting prey consumption and growth in mass of juvenile *H.* aff. *malabaricus*, this study suggests that temperature can mediate fish species coexistence.

Water temperature fluctuations can occur naturally or as a result of anthropogenic perturbations (*i.e.* thermal pollution, deforestation and climate change) and influence distribution, behaviour and growth of several aquatic organisms (Gilman *et al.*, 2006), including fishes (Petersen & Kitchell, 2001; Caissie, 2006). In marine systems, water temperature increases of 3° C, such as those recorded at upwelling events, can strongly affect the interaction strength of the keystone starfish *Pisaster ochraceus* on rocky intertidal mussels (as experimentally demonstrated by Sanford, 1999). Thus, caution is especially necessary in generalizations about the impacts of *H.* aff. *malabaricus* piscivory on assemblage structure in systems like the upper Paraná River floodplain that, despite their location in tropical regions, are subjected to seasonal thermal variations.

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