



Condition factor variations over time and trophic position among four species of Characidae from Amazonian floodplain lakes: effects of an anomalous drought

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(With 5 figures)

Abstract

The effects of extreme droughts on freshwater fish remain unknown worldwide. In this paper, we estimated the condition factor, a measure of relative fitness based on the relationship of body weight to length, in four fish species representing two trophic levels (omnivores and piscivores) from Amazonian floodplain lakes for three consecutive years: 2004, 2005 (an anomalous drought year), and 2006. The two omnivores, *Colossoma macropomum* and *Mylossoma duriventre*, exhibited trends consistent with their life cycles in 2004 and 2006: high values during the hydrologic seasons of high water, receding water, and low water, with a drop following reproduction following the onset of rising water. However during the drought year of 2005 the condition factor was much lower than normal during receding and low water seasons, probably as a result of an abnormal reduction in resource availability in a reduced habitat. The two piscivorous piranhas, *Serrasalmus spilopleura* and *S. elongatus*, maintained relatively stable values of condition factor over the hydrologic cycles of all three years, with no apparent effect of the drought, probably because the reduction in habitat is counterbalanced by the resulting increase in relative prey density. We suggest that if predictions of increasing drought in the Amazon are correct, predatory species may benefit, at least in the short run, while omnivores may be negatively affected.

Keywords: fish fitness, environmental effects, *Colossoma macropomum*, *Mylossoma duriventre*, *Serrasalmus spilopleura*, *Serrasalmus elongatus*.

Variações do fator de condição de quatro espécies de Characidae de lagos de várzea da Amazônia como função do tempo e da posição trófica: efeitos de uma seca anômala

Resumo

Os efeitos de secas extremas sobre peixes de água doce ainda é globalmente desconhecido. Neste artigo, nós estimamos o fator de condição, uma medida relativa de bem estar baseada na relação entre o peso do corpo e o comprimento, em quatro espécies de peixes de lagos da Amazônia, pertencentes a dois níveis tróficos (onívoros e carnívoros), capturadas durante três anos consecutivos: 2004, 2005 (quando ocorreu uma seca anômala) e 2006. As duas espécies onívoras, *Colossoma macropomum* e *Mylossoma duriventre* exibiram tendências consistentes com seu ciclo de vida nos anos de 2004 e 2006: valores mais altos na cheia, vazante e seca, seguida por uma queda na enchente que coincide com a estação reprodutiva. No entanto, o fator de condição foi muito menor durante a seca e a enchente em 2005, provavelmente devido a redução anormal na disponibilidade de recursos em um habitat reduzido. As duas espécies piscívoras, as piranhas *Serrasalmus spilopleura* e *S. elongatus*, mantiveram relativa estabilidade nas estimativas do fator de condição, ao longo do ciclo hidrológico dos três anos, sem efeito aparente da seca extrema, provavelmente porque a redução do habitat foi contrabalanceada pelo aumento na densidade de presas. Caso as predições de aumento de frequência de secas extremas venha a se confirmar, acreditamos que espécies predadoras poderão ser beneficiadas, ao menos no curto prazo, enquanto as onívoras serão negativamente afetadas.

Palavras-chave: bem estar, efeitos ambientais, *Colossoma macropomum*, *Mylossoma duriventre*, *Serrasalmus spilopleura*, *Serrasalmus elongatus*.

1. Introduction

The aquatic environment of the Amazonian floodplains in Brazil contains thousands of lakes and associated wetlands that are interconnected to varying degrees, forming a huge and complex drainage network. These environments are highly dynamic, with an annual hydrologic cycle known as the flood pulse (Junk et al., 1989). The flood pulse is the main driving force structuring the aquatic biota of the floodplain ecosystem along the Amazon River (Junk et al., 1989; Sousa and Freitas, 2008; Hurd et al., 2016). In general, the seasonal flood reaches its peak in June and July, and its lowest point in October and November (Bittencourt and Amadio, 2007). This phenomenon promotes dramatic changes in the floodplain landscape, with alternation between terrestrial and aquatic periods of several months duration.

In general, the period of seasonal flooding is advantageous for fish, since there is an expansion of the aquatic environment, improving the accessibility of habitat and food sources (Goulding, 1980). At such time lake fish can enter the adjacent flooded forest and feed on fruits, seeds, insects, and terrestrial invertebrates (Fernandes, 1997; Claro-Junior et al., 2004; Mérona and Rankin-de-Mérona, 2004; Noveras et al., 2010; Correa and Winemiller, 2014). In contrast, lakes diminish in depth and area during the low-water season, with a consequent decline in habitat and food availability.

Over evolutionary time, these strong but predictable changes in the physical environment have promoted a variety of physiological, morphological and behavioral adaptations among fish species (Saint-Paul and Soares, 1987; Almeida-Val and Val, 1990; Val et al., 1998). However, these floodplains are currently under increasing threat from climate change and resultant modifications to the hydrologic cycle (Melack and Coe, 2013). The intra-annual hydrologic cycle caused by the normal flood pulse is exacerbated by the warming sea-surface temperatures in the Tropical Atlantic, as well as by events such as the El Niño-Southern Oscillation phenomenon (Marengo et al., 2013), which in turn can have dramatic impacts on aquatic organisms in the Amazon Basin (Freitas et al., 2013). These relatively recent changes could well be outside the adaptive range of many species. Recent studies indicate that increasing the frequency of extreme events of flood and drought could disrupt the ecological and evolutionary balance of this ecosystem with unpredictable consequences (Freitas et al., 2013). Fish species at risk may include some that are important protein sources for residents of the Amazon Basin, as well as those that may be important to maintaining the ecological integrity of the system.

Two species that are very important constituents of Amazonian fisheries are *Colossoma macropomum* (tambaqui) and *Mylossoma duriventre* (pacú-manteiga). Both of these are omnivorous species (Araújo-Lima and Goulding, 1998; Claro-Junior et al., 2004; Soares et al., 2007). Adults of both species undergo annual migrations during rising water from the lakes to the rivers and then

upriver for breeding (Goulding and Carvalho, 1982; Lima and Araujo-Lima, 2004; Granado-Lorencio et al., 2005). After breeding, they move to floodplain areas for shelter and feeding in the flooded forests (Fernandes, 1997; Saint-Paul et al., 2000; Soares et al., 2007; Noveras et al., 2010). *Colossoma macropomum* is the second largest scaled fish in the Amazon basin, and its populations are already overexploited in some areas (Isaac and Ruffino, 1996; Freitas et al., 2007; Campos et al., 2015). *Mylossoma duriventre* is a smaller-bodied fish that forms large schools during reproductive migrations (Granado-Lorencio et al., 2005). At such times this species is heavily fished with purse seines known locally as *redinha*.

In contrast, two species in the family Serrasalminidae that are not commercially exploited, probably due in part to their large number of intra-muscular bones, are *Serrasalmus spilopleura* and *S. elongatus*. These piranha species occupy a different trophic position than the other two species, being piscivorous, and are both widespread and very abundant in Amazonian floodplain lakes.

Ficke et al. (2007) proposed that environmental changes would first result in detectable effects at the organism level, and next at the population level. Therefore, we measured a component of ecological fitness known as the condition factor, estimated by the body weight-length relationship, as a welfare index for all four of the above-described Characid species over three consecutive years to test two null hypothesis: (1) there were no inter-annual changes in the fish fitness (comparison among years) and (2) there were no intra-annual changes in the fish fitness (comparison among seasons of the hydrologic cycle). Finally, we compared the dynamics of this index between the two trophic positions represented by the four studied species.

2. Material and Methods

2.1. Study area

The study area comprised eight lakes situated along 400km of the floodplain adjacent to the Solimões River: Baixio, Preto, Iauara, Ananá, Maracá, Araçá, Poraquê and Aruã (Figure 1). All these lakes normally remain connected to the main river during most of the year, typical of permanent floodplain lakes. There was an extreme drought in this region during 2005 as a result of combined effects of El Niño Southern Oscillation – ENSO and abnormally elevated sea surface temperatures in the southern area of the North Atlantic (Marengo, 1992; Marengo et al., 2008). This drought affected both terrestrial (Phillips et al., 2009) and aquatic (Freitas et al., 2013) ecosystems in this region. We therefore have data from our fish assemblages immediately before, during, and following the drought.

2.2. Sampling Procedure

We sampled *C. macropomum*, *M. duriventre*, *S. spilopleura* and *S. elongatus* in these lakes in 2004, 2005, and 2006 during the middle of all four seasons of the hydrologic cycle: rising water, high water, receding water, and low water. The fish were collected from each

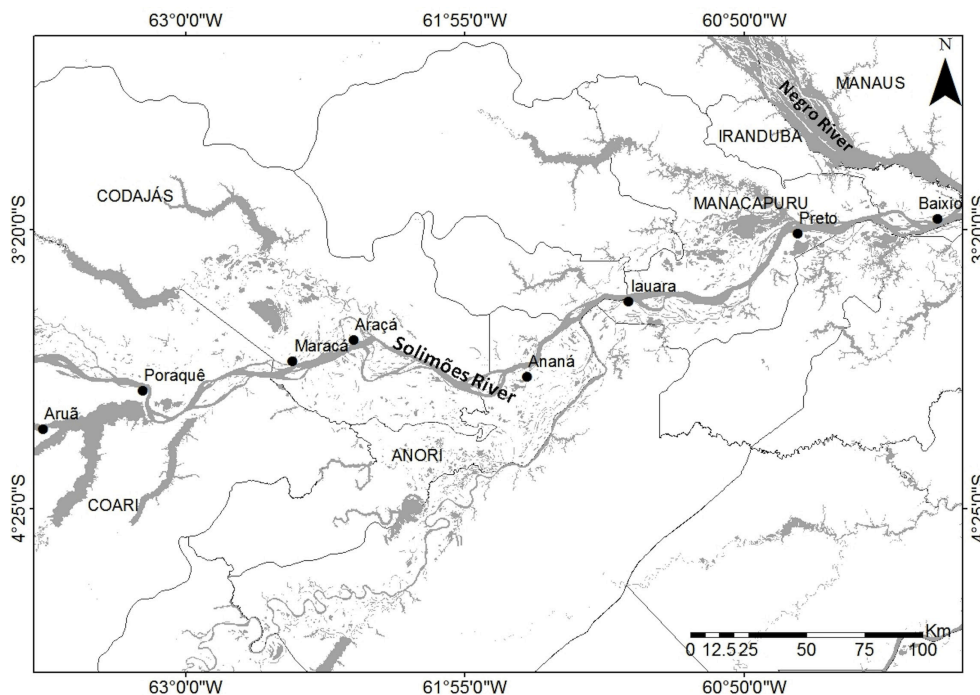


Figure 1. Map of the study area highlighting the Solimões River and the eight floodplain lakes where we sampled fish.

lake with eight gillnets of standardized dimensions (20 m long and 2 m high) and different mesh sizes: 30, 40, 50, 60, 70, 80, 90, and 100 mm between opposite knots. The nets were placed at sunrise, during the hour 5-6am, remained in place for 12 hours, and removed at sundown, between 6-7pm. Collected fish were identified, measured (standard length, cm) and weighed (total body mass, g) immediately after the catch. Any species that were difficult to identify on site were preserved in 10% formalin and transported to the Laboratory of Fishing Ecology at the Federal University of Amazonas (UFAM), where identification was made with expert support.

2.3. Data analysis

The parameters of the weight-length relationship were determined for all four species by non-linear estimation, employing the Levenberg-Marquardt algorithm (Myers, 1990). The relative condition factor (kn) was estimated by the equation $kn = W_{obs}/W_{est}$ (Cren, 1951), where W_{obs} is the measured body mass of each fish and W_{est} is the estimated weight calculated for each length using the estimated weight-length relationship. The log (ln) of the mean of the relative condition factor (kn) was estimated on the grouped data for each hydrological season and year. After a graphic check for violations of the linear conditions, a two-way Analysis of Variance was employed to test the following null hypotheses: H_01 : there were no effects of the year on the condition factor; H_02 : there were no effects of the hydrologic season on the condition factor; and, H_03 : there were no effects of interactions between

year and the hydrological season on the condition factor. A Tukey's *post hoc* test was employed whenever a null hypothesis was rejected. All statistical procedures were performed using the software Statistica 9.0 (Statsoft Inc, 2009) with a confidence level of 0.05.

3. Results

We collected 1,318 fish over the three years of the study. The piranha *S. spilopleura* was more than twice as abundant as each of the other three species (Table 1). The composite data in Table 1 show that *S. spilopleura* was also the smallest bodied fish, while the omnivore *C. macropomum* was the largest. However, the composite data do not show the variations that occurred in the weight-length condition factor index. The estimated weight-length relationship exhibited a good fit for all species (Table 2), besides *C. macropomum* and *M. duriventre* were represented mainly by small individuals.

Both of the omnivorous species and one of the piranhas (*S. spilopleura*) exhibited significant differences in the condition factor by year, by season of the hydrologic cycle and were detected interaction effects of year and season of the hydrologic cycle (Table 3). For *C. macropomum*, this interaction effect can be identified with the anomalous drought of 2005. In general, the relative condition factor of *C. macropomum* was highest during the high and receding water seasons of all three years, showing intermediary values for rising water seasons of 2004 and 2005 and low water seasons of 2004 and 2006. The lowest estimates were observed during the rising water of 2006

Table 1. Number of sampled fish, minimum (*min*), maximum (*max*), mean (\bar{x}) and standard deviation (*sd*) of length and weight of the four characids.

Species	n	Length (cm)		Weight (g)	
		$\bar{x} \pm sd$	min-max	$\bar{x} \pm sd$	min-max
<i>Colossoma macropomum</i>	255	19.5±3.9	10-36	299.6±196.1	40-1560
<i>Mylossoma duriventre</i>	254	13.1±2.6	5.5-22	111.0±73.0	5-470
<i>Serrasalmus spilopleura</i>	557	11.6±3.1	5.5-20	73.9±48.1	8-210
<i>Serrasalmus elongatus</i>	252	15.0±2.8	6.0-28	83.0±41.8	10-295

Table 2. Summary of length-weight relationships for the four floodplain lake characids.

Species	Model	R ²
<i>Colossoma macropomum</i>	$W = 0.0716L^{2.771}$	0.9207
<i>Mylossoma duriventre</i>	$W = 0.0429L^{3.004}$	0.9597
<i>Serrasalmus spilopleura</i>	$W = 0.0698L^{2.802}$	0.9301
<i>Serrasalmus elongatus</i>	$W = 0.0533L^{2.720}$	0.8701

Table 3. Summary of two-way ANOVA results applied to compare the condition factor of *Colossoma macropomum*, *Mylossoma duriventre*, *Serrasalmus spilopleura* and *S. elongatus* by year and season of the hydrological cycle.

Source of Variation	<i>Colossoma macropomum</i>			<i>Mylossoma duriventre</i>			<i>Serrasalmus spilopleura</i>			<i>Serrasalmus elongatus</i>		
	df	F	p	df	F	p	df	F	p	df	F	p
Year	2	13.81	< 0.001	2	48.86	< 0.001	2	13.89	< 0.001	2	0.56	0.569
Season	3	38.74	< 0.001	3	31.75	< 0.001	3	6.54	< 0.001	3	1.92	0.127
Year*Season	6	34.53	< 0.001	6	17.69	< 0.001	6	2.17	< 0.001	6	0.99	0.433
Error	243			242			545			240		

df = degrees of freedom; F = F-statistic; p = p-value; * = interaction.

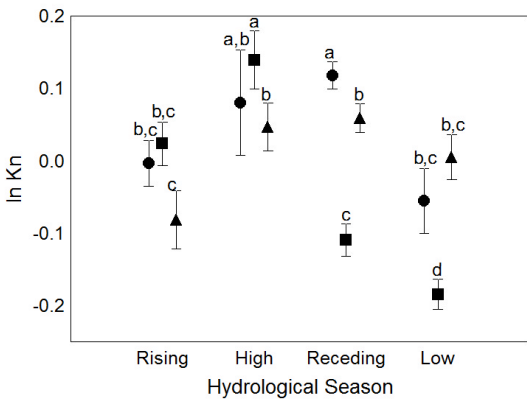


Figure 2. Temporal variation of the condition factor for *Colossoma macropomum* in the four seasons of the hydrologic cycle: rising, high water, receding and low water for the years 2004 (circle), 2005 (square) and 2006 (triangle). (Different letters imply statistically different means).

and receding and low water seasons of 2005, the year of the drought (Figure 2).

The pattern for *M. duriventre* was similar, and even more striking: the lowest values of the condition factor occurred as the lakes were shrinking during the drought of 2005, and there was a sharp recovery in the post-drought year of 2006 during low water (Figure 3). However, the

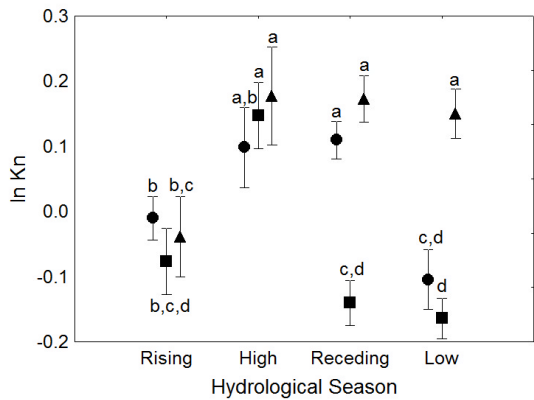


Figure 3. Temporal variation of the condition factor for *Mylossoma duriventre* in the four seasons of the hydrologic cycle: rising, high water, receding and low water for the years 2004 (circle), 2005 (square) and 2006 (triangle). (Different letters imply statistically different means).

condition factor for this species was also low during the low water period of 2004, before the drought.

In contrast to the patterns for the two omnivorous species, the two piranha species maintained similar values for the condition factor during and after the drought (2005 and 2006, Figures 4 and 5). *Serrasalmus spilopleura* exhibited its lowest values, with high variability, during high and

receding water during the pre-drought year of 2004, but showed no changes associated with the drought in 2005 or the subsequent year (Table 3, Figure 4). There were no significant variations in the condition factor for *S. elongatus* among years or seasons of the hydrologic cycle (Figure 5).

Besides, the interaction effects between intra- and inter-annual factors detected for *C. macropomum* and *M. duriventre* exhibited opposite patterns in comparison with *S. spilopleura*. The first two omnivorous species showed a marked reduction of the condition factor during the extreme drought of 2005 (Figures 2 and 3), while the lowest values for *S. spilopleura* were obtained during the pre-drought year of 2004 (Figure 4).

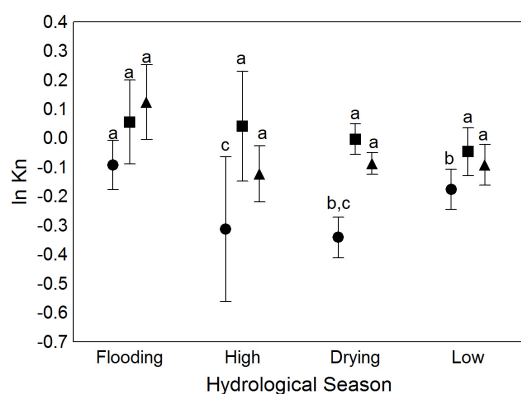


Figure 4. Temporal variation of the condition factor for *Serrasalmus spilopleura* in the four seasons of the hydrologic cycle: rising, high water, receding and low water for the years 2004 (circle), 2005 (square) and 2006 (triangle). (Different letters imply statistically different means).

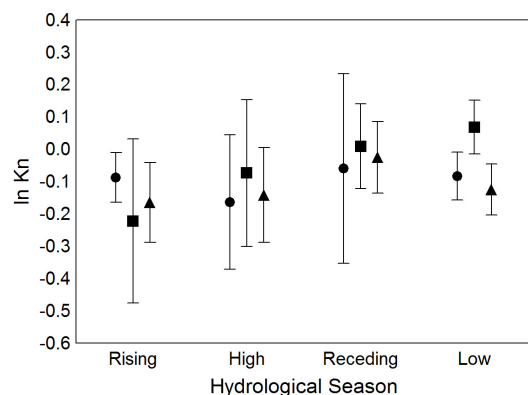


Figure 5. Temporal variation of the condition factor for *S. elongatus* in the four seasons of the hydrologic cycle: rising, high water, receding and low water for the years 2004 (circle), 2005 (square) and 2006 (triangle).

4. Discussion

Our results suggest that the intensity of an anomalous drought can result in perceptible effects on Amazonian fish that are related to their trophic niche. The general pattern of intra-seasonal condition factor for the two omnivores reflects their life histories, particularly their feeding strategies. Both tambaqui and pacú-manteiga normally exhibit ontogenetic and seasonal changes in their feeding preferences (Honda, 1974; Costa et al., 1999; Soares et al., 2007), which are pre-adapted to correlate with a predictable and monomodal hydrologic cycle. These species enter the flooded forest around floodplain lakes after breeding in order to feed and shelter as the water rises each year (Honda, 1974; Fernandes, 1997; Araújo-Lima and Ruffino, 2003). The importance of allochthonous items, as fruits and seeds, originated from the flooded forest in the diet of *C. macropomum* and *M. duriventre* is well-known (Araújo-Lima and Goulding, 1998; Claro-Junior et al., 2004).

Thus, their condition factor is high while they are feeding in the forest and their fat stores may carry them through most of the short low water season, and then they reproduce during rising water (Araújo-Lima and Ruffino, 2003). Both of these fish populations exhibited much lower mean condition factors during the receding and low water seasons during the year of the drought, when the flooded forest would have been available to them for less time than usual. This may be an indication that increasing drought duration and frequency, predicted as a result of global climate change (Malhi et al., 2008; Marengo et al., 2008; Melack and Coe, 2013), fish species with high dependency of flooded habitats could be more affected. Thus, extreme droughts could push them beyond their adaptive limits and thus have negative, and potentially catastrophic, impacts on their population biology.

Serrasalmus spilopleura is predominantly piscivorous, but also has been found to eat insects (Costa et al., 2005) and varies its diet over the course of the year (Raposo and Gurgel, 2003). Whereas the diet of *S. elongatus* is more constant along the year, being composed mainly by fish fins and scales (Nico and Taphorn, 1988). These two piranhas exhibited no changes in condition factors that could be attributed to the extreme drought that happened in 2005. Low water periods, if not extremely long, may favor this trophic level, since as water volume declines the relative density of potential prey increases, which increases the encounter rate between predators and their prey (Winemiller and Jepsen, 1998). This phenomenon acts as a buffer against loss of fitness because unlike the omnivores, their food source is still available to them. On this basis one might predict that predators would fare better, at least in the short run, during climate change. The differences between *S. spilopleura* and *S. elongatus* could be associated with the habitat availability. Sazima and Zamprogno (1985) stated that young *S. spilopleura* use the floating meadows of *Eichornia crassipes* as shelter and foraging place, and larger juveniles also can be found in open water areas of lakes. We suggest that the complete

disappearance of floating meadows during the extreme drought of 2005 was more critical for *S. spilopleura* than for *S. elongatus*.

Obviously, the effects of extreme events of flood and drought would differ among species as well as among trophic levels. Some authors have proposed that the present dominance of omnivorous species within the Amazon Basin may be an evolutionary response to the large diversity of food items and to the seasonality of their abundance and availability (Lowe-McConnell, 1999; Mérona and Rankin-de-Mérona, 2004; Blanchette et al., 2014). An extreme drought could result in a severe deterioration of the water quality, with high temperature and low dissolved oxygen, which would in turn have negative consequences for the quality of their food sources. For instance, it has been suggested that in addition to feeding on abundant C4 autotrophic sources (Martinelli et al., 1994), Amazonian fish would prefer to exploit C3 sources such as phytoplankton, that are easier to absorb (Forsberg et al., 1993; Mortillaro et al., 2015), but these sources have a tendency to become very scarce during extreme droughts. Both the timing and duration of extreme climatic events are therefore likely to have profound effects on life history strategies of floodplain fish (Ficke et al., 2007). Some wild species, such as the bird *Parus major* (Charmantier et al., 2008) have been shown to have enough phenotypic plasticity to withstand a limited degree of climatic change by shifting the timing of their life history events, but the degree that this is true, and for which species, can only be determined after the climate has changed, which may well be too late to preserve them.

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