

DOI: https://doi.org/10.31686/ijier.vol10.iss11.3995

Temporal dynamics of size spectrum of a fish population in neotropical

reservoirs

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Abstract

Studies on the size spectrum allow indirect inferences of how the energy flows from one organism to another. Assuming that the bottom-up is more intense than the top-down mechanism along the cascade of reservoirs, which limits the growth and development of individuals, we investigated the effect of a cascade of reservoirs in a neotropical basin on the stock and distribution of the population of Oligosarcus longirostris, a species at the top of the food chain. Samples were conducted quarterly in five reservoirs, from March 2004 to December 2008. Stock size was estimated by catch per unit effort (CPUE); to establish the size spectra slopes of fish, we used Pareto I model, and data was analyzed using univariate analysis of variance followed by Tukey's test. There was a higher proportion of smaller individuals in the first reservoir of the cascade, with a decline in this proportion along the succession of reservoirs in the cascade. It can be concluded that there is an effect of the reservoir cascade on the abundance and size of individuals of Oligosarcus longirostris. Keywords: Oligosarcus longirostris, bottom-up, top-down, impact, biodiversity, Iguaçu River.

1. Introduction

River impoundments are important agents in reorganizing aquatic communities, with different influences on population structure and causing several direct impacts on the environment. Aside from changes in physical and chemical properties of water (Agostinho et al., 1999; Jinpeng Li et al., 2013; James et al., 2015; Cooper et al., 2016; Fearnside, 2016), disturbances caused by dams lead to changes in the species habitat, altering community composition with negative effects on flora and fauna, including the decline in species richness (Richter et al., 2010; Tonella et al., 2022) and prevent mass migration for reproduction (Fearnside, 2014).

While large dams generate electricity, they bring serious consequences for populations located downstream of dams for hundreds of kilometers (Richter et al., 2010). These environmental and social impacts should be considered during planning and decision making (Fearnside, 2016).

Tools have been developed to elucidate the actual impacts dams have on aquatic populations, including studies associating the abundance of individuals with their body size, called size spectrum. These studies indirectly predict the way the energy flows through organisms, providing information on the dynamics of food webs. The pioneer work of Sheldon et al., (1972) demonstrated the distribution of biomass of bacteria and whales, sparking the theory that biomass could be distributed in logarithmic scales. Studies have been conducted used the size spectrum freshwater (Sprules et al., 1983; Echevarría & Rodríguez, 1994; Asaeda & Rashid, 2012, Tarling et al., 2012), and several other researchers studied the dynamics of marine and aquatic food-webs (Andersen & Pedersen, 2010; Blanchard et al., 2009; Boit et al., 2012; Jennings et al., 2008, Moloney & Field, 1991; Law et al., 2012; Tarling et al., 2012, Watson et al., 2015).

There are several ways of measuring the size of individuals; the most accepted measure is biomass because it efficiently presents the range of weight classes in logarithmic scale, allowing the observation of the integrations between physiological characteristics of organisms and their relationship to ecosystem functioning (Han & Straskraba, 1998; Dickie et al., 1987; Boudreau et al., 1991). Studies of body size allow us to predict predator-prey interactions, reflecting biomass of the trophic structure (Thiebaux & Dickie, 1993).

Also, to predict the patterns of energy transfer, since the biological properties of individuals change with size, which is often a good indicator of trophic level of the species (Jennings & Brander, 2010; Jennings et al., 2001). Understanding the processes that act upon individual success and survival is crucial to understand the population dynamics (Poulos & McCormick, 2015).

The construction of reservoirs in cascade along the course of a single river can generate cumulative impacts throughout the ecosystem, as it changes the relationship between rivers and their basins (Cooper et al., 2016) by retaining nutrients; thus, causing oligotrophication of the river and severe changes in fish fauna. These developments change markedly the local landscape, causing economic, social, and environmental changes, drastically altering the natural dynamics of fisheries (Agostinho et al., 2007; Graeb et al., 2009; Petesse & Petrere Jr, 2011) and are exacerbated by climate change (Guo et al., 2022).

The variation in the biomass spectrum is an efficient method because it indicates human interference and its effects on the energy flow of the ecosystem (Rice & Gislason, 1996). Organisms of the same size are treated

as energetic equivalents regardless of the taxa, attesting the anthropogenic impacts on biological production (Kerr & Dickie, 2001), since it reduces the complexity of the food web into a single quantitative variable.

Piscivorous species are essential for the maintenance and balance of ecosystems, by regulating the abundance of species at the top of the food chain and their prey (Novakowski et al., 2007), controlling the natural fish stocks and increasing the mortality rate among individuals (Link & Garisson, 2002).

The present study sought to identify the effect of the cascade of reservoirs in a neotropical basin (Iguaçu River basin) on the stock and length distribution of the population of the piscivorous *Oligosarcus longirostris* Menezes & Gèry (Osteichthyes, Acestrorhynchinae). The central hypothesis is that the of the stock size is reduced along the reservoirs in the cascade (downwards) due to the retention of nutrients and its effects on the dynamics of the size spectrum of this population.

2. Material and Methods

2.1 Study area

The Iguaçu River basin has an area of 72,000 km2 approximately, of which 79% belongs to Parana State, 19% to the Santa Catarina State and 2% to Argentina. It flows 1,060 km, with an east-west direction from its headwaters on the western slope of the Serra do Mar, near Curitiba, to its mouth on the Parana River (Eletrosul, 1978).

Parana river is located on the third plateau and exhibits a high slope in its watershed, which gives it an enormous potential for hydroelectric power generation. Currently, there are five major power plants in its bed, turning the stretch into a succession of large lakes, which led to a series of changes in the hydrological regime (655 Km²). The studied reservoirs and their coordinates are: Foz do Areia (FA, 26° 0'35.40"S/ 51°39'44.39"W), Salto Segredo (SE, 08°48'04.0" S/6356'59.8"W), Salto Santiago (SS 25°51'19"S /52°31'46"W), Salto Osório (SO, 25°36'33.04"S/52°18' 33.94"W), Salto Caxias (SC 25°32'35" S/ 53°29'43"W).

The reservoirs of these power plants show different degrees of human occupation, different limnological characteristics and include environments with variable depths and areas (Table 1).

2.2 Data collection

Fish were sampled through quarterly collections conducted in the reservoirs, from March 2004 to December 2008. Simple gill nets were used to capture the specimens (meshes from 2.4 cm to 16 cm) and trammel nets (6 cm to 8 cm between opposite knots), which were assembled in three layers (margin, surface, and bottom) and remained exposed for 24 hours with inspection every 8 hours.

After sampling, fish were anesthetized with benzocaine hydrochloride (250 mg/L), as required by the Resolution 714/CFMV from July 20th, 2002, which regulates the procedures and methods of euthanasia in animals (CFMV, 2002); and then fixed in 10% formalin and 70% ethanol (Shibatta & Cheida, 2003).

These individuals were identified to species level, based on identification keys proposed by Eschmeyer (1990), Britski et al., (1999) and Graça & Pavanelli (2007). Each sampled individual was measured (total and standard length, in cm) and weighed (in grams). All species caught have voucher specimens deposited in the Ichthyological Museum of Nupélia/State University of Maringa (NUP 11856).

2.3 Data analysis

The stock size was estimated by catch per unit effort (CPUE), in number of individuals per 1000m2. The net was exposed for 24 hours for each collection month and assessed by univariate analysis of variance followed by Tukey's test for comparison of means to check for possible differences (P < 0.05) between the reservoirs of the cascade.

Size distribution of the population of *O. longirostris* was evaluated by two population parameters: the average size of individuals and the size spectrum of the population. Both parameters were tested by a univariate analysis of variance followed by Tukey's test for comparison of means to check for possible differences (p < 0.05) between the reservoirs. The size spectra for each month of collection in each reservoir was obtained according to Pareto type I model (Vidondo et al., 1997). This model was selected, in a complementary way to the average size of individuals, once it is less sensitive to the presence of missing size classes, i.e, without capture of fish (Benoît & Rochet, 2004).

According to Pareto type I model, the probability of finding an individual of size s superior to a given size S decreases linearly on a logarithmic scale size insofar as the individual size increases, which is represented by the following equation:

 $\log 2 \left[\operatorname{Prob}(s \ge S) \right] = c * \left[\log 2(K) - \log 2(S) \right]$

In this model, $Prob(s \ge S)$ is estimated by the proportion of individuals (s) larger than a certain size taken at random (S). The constant c, or slope of the linear relationship is, in this case, the rate of decrease in the probability of finding larger individuals so far as the individual size increases. In other words, it is a measure that represents the frequency distribution of the body size of fish. Thus, if c is equal to -1, the individual frequency distribution is uniform between fish of different sizes; if c is smaller than -1, the frequency of individuals is greater for smaller sizes; and when c is higher than -1, the frequency of individuals is greater for larger sizes. The constant c was estimated by linear regression between the log2[Prob(s \ge S)] and the log2(S) by the least squares method in Statistica® 7.0 (Stat Soft, 2004).

3. Results and Discussion

The catch per unit effort (CPUE – ind.1000m2net-1.day-1) was different among the reservoirs. The reservoir upstream in the cascade (FA) showed the highest CPUE, while the following reservoirs showed increasingly lower values, according to the succession of reservoirs in the cascade (Fig. 1).



Figure 1. Catch per unit effort – CPUE \pm 95% confidence interval obtained for each reservoir: FA, SE, SS, SO and SC, from January 2004 to October 2008.

As to the size distribution of O. longiostris population, the average size of individuals and the size spectrum of the population showed a significant effect of reservoirs, unlike the result of stock size. Both average weight and the constant c of Pareto type I model indicated a greater proportion of smaller individuals in the first reservoir of the cascade. The second reservoir had a high number of individuals with longer standard length, which has been reduced according to the succession of reservoirs in the cascade (Fig. 2).



Figure 2. Mean values \pm 95% confidence interval for the weight of individuals (A) and constant c of Pareto type I model (B), obtained for each reservoir: FA, SE, SS, SO and SC, from January 2004 to October 2008. Different letters over the bars indicate significant differences by Tukey's test.

These results suggest that the first reservoir (with 41.5% of individuals \leq 32 g) had high levels of recruitment, but only a small proportion achieved larger sizes. This may occur due to death or emigration of large individuals. Reservoirs in the sequence of the cascade (with 21.3% of individuals \leq 32 g), (with 29.8% of individuals \leq 32 g) (with 38.7% of individuals \leq 32 g) exhibited high proportions of larger individuals, indicating a possible downward migration. The last reservoir (with 47.2% of individuals \leq 32 g), in turn, at the end of the sequence, showed a greater proportion of smaller individuals (Fig. 3).



Figure 3. Frequency of weight of individuals caught in the reservoirs of FA, SE, SS, SO and SC, from 2004 to 2008. The first line corresponds the total catch in each reservoir.

The combination of temporal and spatial variables along the river revealed marked changes in the dynamic of the size spectrum of fish population in the five reservoirs. The expected value for the constant c for the assemblage was close to -1, for a population in which a higher value was expected. This was possibly due to high positive asymmetry in fish populations. Most species show a positive symmetry in body size distribution when analyzed on a regional scale, regardless of the ecological or taxonomic group (May, 1986; Brown & Maurer, 1989; Lawton 1991; Knouft, 2004).

Population body size distribution in the first reservoir showed a high proportion of individuals (CPUE) with low biomass (\leq 32 g) compared to other reservoirs. The reduced body condition can make individuals vulnerable, particularly in early stages of the life cycle, when they have lower reserve levels and metabolic rate (Donelson et al., 2009), and affect the fecundity and mortality of the population (Booth & Beretta, 2004).

The proliferation of small fish suggests the presence of favorable conditions of food and shelter. This observation is explained by the Cascading Reservoir Continuum Concept (CRCC), which states reservoirs located at the beginning of a series present higher nutrient availability due to changes in abiotic factors, providing high production at all trophic levels (Barbosa et al., 1999). Additionally, the reservoir receives all the nutrients from a metropolitan urban area generating a high aquatic production (Gubiani et al., 2008).

Along the succession of reservoirs, the proportion of smaller individuals in a large number was replaced gradually for smaller amounts of larger fish. This can provide information on size-based predation dynamics as from predator-prey models (Thiebeaux & Dickie, 1993) and may represent trophic positions (Goyke, 1995).

Body condition affects competitiveness and survival, animals with larger body sizes are more likely to rule the territory (Poulos & McCormick, 2015). Thus, body size can determine the vulnerability of individuals, populations and communities (Rice & Gislason, 1996). The high body size condition, usually acquired with a higher consumption of food, determines the level of aggression and territoriality of organisms with a lower body size condition is more difficult to start fights and have higher rates of mortality and it is the main factor affecting survival (Donelson et al., 2009; Poulos & McCormick, 2015; Nawrocki et al.,2022). Larger individuals tend to be more territorial and competitive reflecting fewer specimens, but with a high body condition, as found in this study.

The high productivity can greatly influence the fish community. In such environments, the pressure generated by competition could determine the size distribution of the stock, since there are high numbers of individuals competing for resources. These competitive interactions directly affect species abundance (Stevens & Willing, 2000). Nevertheless, the high frequency of piscivores can be justified by the proliferation of opportunistic species, which are usually small and common in reservoirs, being an important food resource in this type of environment (Agostinho et al., 2007).

Besides that, the large number of individuals with low biomass may be related to the amount of spatial niche available, which probably resulted in the observed positive skewness (Hutchinson & MacArthur, 1959). These authors suggest that the environment, by failing to provide enough space for large animals, creates more space for the abundance of smaller species. This theory explains the high number of species of smaller size, but it does not elucidate why smaller species are numerous. It is known that body size is related to evolutionary aspects, relative size of the ancestor, and factors associated with regional distribution which must include at least some historical information (Knouft, 2004). Meanwhile, Stanley's (1973) argues that the trends in size are the result of responses of species to environmental conditions and that this response may influence the formation of a frequent distribution; hence, the influences of the particularities of each impoundment on the aquatic community have to be considered (Agostinho et al., 1999).

The reservoirs showed a pattern consistent with the Cascading Reservoir Continuum Concept (CRCC), where there is a longitudinal gradient in the cascade of four reservoirs, with a progressive increase in CPUE along the series. The patterns of size distribution exhibited an inverse pattern of CPUE, with a reduction along the cascade, being observed a relationship between the increasing number of individuals and the decrease in size and biomass of the population. In agreement with Agostinho et al., (1999), over time and depending on the reservoir area, the dammed environments typically show a decline in fish abundance. According to these authors, after the initial phases of the impoundment, when there is a large productivity, a drop in its values is observed, being more pronounced especially with reservoir aging.

The significant change in the structure of size spectra of the studied population size, which shows a large increase in population biomass in the second reservoir compared with the first, may be related to the availability of prey. According to Pelicice et al., (2005), with greater biomass of prey species, it would be possible to maintain greater biomass of piscivorous species. The biomass of piscivorous species is positively correlated with the biomass of prey species (Pelicice et al., 2005).

Nevertheless, the number of species (CPUE) in the second reservoir was smaller than in the first. The

primary productivity in this reservoir is lower, since the organic material possibly settles down in the first reservoir of the cascade, thus reducing the amount of nutrients in the second reservoir, affecting the fertility of the other levels of the chain. Cascading reservoirs commonly have a reduction in the concentration of nutrients throughout the series, which reduces productivity downstream (Miranda et al., 2008).

Thus, the decrease in the number of prey works limiting the growth of predators over the reservoir cascade, pointing to the bottom-up mechanism, since the availability of prey has a direct and vital influence on the population dynamics of the predator (Frederiksen et al., 2006). Piana et al., (2005) investigated the mechanism regulating fish biomass in different reservoirs of Parana State and found that the phytoplankton productivity had a predictor role in fish biomass, occurring discreetly the bottom-up mechanism (abundance determined by resources).

There is a great possibility of, along the longitudinal gradient of the reservoirs, an inversion in the mechanisms regulating the trophic structure of the environment, because the fish biomass keeps decreasing (SS, SO and SC). Aspects related to changes in water level can produce environmental disturbances that alter the biotic interactions and energy dynamics (Tundisi et al., 2003).

The relative effectiveness of the top-down versus bottom-up mechanisms in food webs depends partially on the efficiency of predators in consuming their prey. Reversing mechanisms can occur according to the interaction between consumers, consumers and resources and between less similar trophic levels and thus modify the top-down forces in food webs (Power, 1992; Liu et al., 2018).

5. Conclusion

The results presented herein show changes in *O. longirostris* population structure, regarding the size spectra along the five reservoirs studied. The main mechanism involved in these changes of biomass and number of individuals is possibly related to the effects generated by the productivity of ecosystems, causing changes in the efficiency of energy transfer between the different trophic levels.

6. Acknowledgement Heading Level-1

The research is financed by Group of Research in Fisheries and Limnology- Gerpel and the Graduate Program in Comparative Biology - UEM.

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Appendix

TABLE 1. Summarized information of the five cascading reservoirs in the Iguaçu River.

Source: IAP (2009) and Copel (2009).					
Technical data	Foz do Areia	Segredo	Salto	Salto	Salto Caxias
	(FA)	(SE)	Santiago	Osório	(SC)
			(SS)	(SO)	
Operation	1980	1982	1979	1975	1998
Catchment area	29,800	34,100	43,330	45,800	57,000
(Km ²)					
Reservoir area (Km ²)	139	82,5	208	55	141
Normal maximum	744	607	506	397	325
level (level) (m)					
Mean depth (m)	41.6	36.6	35.0	25.5	25.3
Residence time	102	47	51	16	31
(days)					
Classification (ONS)	Regulation	Run-off-	Regulation	Run-off-	Run-off-river
		river		river	
Length (Km)	+- 80	+-70	+-80	+-70	+-80
Depletion (m)	Up to 20	Up to 5	Up to 25	Up to 2.5	Up to 2.0
Classification	III	III	II	II	II
(IQAR)					
Dam Height (m)	160	145	80	56	67
Dam Length (m)	160	145	80	56	67