



Community attributes reflecting the zooplankton secondary production: using field and experimental approaches

Atributos da comunidade refletindo a produção secundária do zooplâncton: usando abordagens de campo e experimentais

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Cite as: Dias, J.D. et al. Community attributes reflecting the zooplankton secondary production: using field and experimental approaches. *Acta Limnologica Brasiliensia*, 2024, vol. 36, e102. <https://doi.org/10.1590/S2179-975X4624>

Abstract: Aim: We investigated the relationship between ecological attributes of the zooplankton community and its secondary production. **Methods:** Samples were taken from lakes in the floodplain of the Upper Paraná River (Brazil), in low and high-water periods, and in a manipulative experiment realized in mesocosms. **Results:** The highest amount of production was related to the dominance of few species. Secondary production of larger and long-lived organisms, such as copepods, had been most associated with the biomass, whereas smaller ones, such as rotifers, with the abundance. **Conclusions:** These attributes of the zooplankton community (biomass and abundance) can be used as proxies to estimate the zooplankton secondary production in the floodplain, supporting the studies on monitoring and conservation of these ecosystems.

Keywords: ecosystem property; environmental monitoring; proxies; biomass; abundance.

Resumo: Objetivo: Nós investigamos a relação entre atributos ecológicos da comunidade zooplanctônica e a produção secundária. **Métodos:** Amostras foram coletadas em lagos da planície de inundação do Alto Rio Paraná (Brasil), em períodos de águas baixas e altas, e em um experimento manipulativo realizado em mesocosmos. **Resultados:** A maior produção secundária esteve relacionada à dominância de poucas espécies. A produção secundária de organismos de maior tamanho e maior ciclo de vida, como os copépodes, foi mais associada à biomassa, enquanto os menores, como os rotíferos, à abundância. **Conclusões:** Esses atributos da comunidade zooplanctônica (biomassa e densidade) podem ser usados como proxies para estimar a produção secundária de zooplâncton na planície de inundação, subsidiando os estudos de monitoramento e conservação desses ecossistemas.

Palavras-chave: propriedade do ecossistema; monitoramento ambiental; proxies; biomassa; abundância.



1. Introduction

A fraction of the energy amount within ecosystems is represented by the secondary production, which is defined as the biomass accumulated by heterotrophic populations per unit of volume and time (Edmondson & Winberg, 1971; Downing & Rigler, 1984; Melão, 1999). The secondary production represents the energy available in the ecosystem to be assimilated and oxidized by the higher trophic level-organisms, or it can flow through other paths in the ecosystem, since after the death of consumer organisms it may become a potential source of energy for decomposing organisms contributing to the remineralization process (Lindeman, 1942), or enter the energy transfer process through the microbial loop (Pomeroy, 1974; Azam et al., 1983). At this stage, microorganisms are responsible for transforming dissolved organic matter (mainly carbon) into particulate organic matter, which enters the energy flow. In this sense, the secondary production reflects the functional role of heterotrophic organisms in the ecosystem, linking primary producers, consumers and decomposers (Benke, 1993; Lemke & Benke, 2009), by providing an estimate of the energy available for transfer between these trophic levels.

Knowledge of secondary production provides the basis for understanding how different taxa contribute energy to the ecosystem. Despite the importance of studies on the secondary production to understand ecosystem functioning, its quantification is a difficult and laborious process, which requires long periods in the laboratory and in the field, and can be impractical for environmental monitoring proposals. Thus, several issues at the ecosystem functioning level, in the long term, cannot be answered. Issues of greatest interest in secondary production studies, according to Downing & Rigler (1984), include the elucidation of matter and energy transfer, ecosystem service management, understanding of ecosystem functioning, detection of pollution effects and production theory framework. For example, a study demonstrated that the secondary production in fish can be the most sensitive variable to detect environmental impacts related to ecosystem fragmentation (Valentine-Rose et al., 2011). In addition, the secondary production can contribute to better understanding the biodiversity–ecosystem functioning, as well the species functional role (Dolbeth et al., 2012; Setubal et al., 2020a, b). Thus, it is essential to include the secondary production in environmental monitoring studies environmental to assess human impacts on aquatic ecosystems.

The primary method for estimating secondary production of zooplankton in aquatic ecosystems is through population dynamics (Edmondson & Winberg, 1971) and calculations of birth and death rates, and age structure. It also involves the counting of eggs, and assessment of development time in different cohorts and temperature (Edmondson & Winberg, 1971). Another method widely used, mainly for microcrustaceans, is the increase in biomass (Winberg et al., 1965), which includes measurements of weight increase in each developmental stage and requires the knowledge of these variations throughout the life cycle. The methodological difficulties in calculating the secondary production of zooplankton are one of the main reasons for the small number of works focusing on this, especially in environmental monitoring studies.

Some environmental factors, such as physical and chemical variables of water, can control or limit the secondary production of zooplankton in aquatic ecosystems (Lehman, 1988; Shuter & Ing, 1997; Melão, 1999; Casanova et al., 2009; Panarelli et al., 2010; Dias et al., 2014, 2017). Considering this influence, some studies have estimated the secondary production of organisms using physical and chemical variables (Huntley & Lopez, 1992), especially those variables related to the availability of resources, such as phytoplankton (Gomez et al., 2012).

Secondary production is interpreted as the reflection of factors representing the success of populations, which can be described by, for example, the abundance, biomass, fecundity, and body size (Benke, 2010). Biomass has been the most used community attribute to estimate the secondary production (Grosholz & Gallo, 2006; Guevara et al., 2009; Valentine-Rose et al., 2011), but these relationships have not been well elucidated. We aimed to analyze the relationship between ecological attribute of the zooplankton community (richness, abundance, diversity, evenness, and biomass) and the zooplankton secondary production in a neotropical floodplain (field and experimental conditions) and which ones could be used as proxy for secondary production in environmental monitoring. We investigated the hypothesis that the biomass is the most strongly correlated proxy variable to estimate the secondary production of rotifers, cladocerans, and copepods, once it is an instantaneous measure of production. Our study represents an advance in understanding the zooplankton ecology and an important

contribution to the understanding of aquatic food webs and ecosystem ecology.

2. Materials and Methods

2.1. Field and experimental study

Our study was carried out in field and experimental conditions. The combination of field data with experiment in mesocosm to test our hypothesis was chosen because they are complementary approaches and can contribute to better answering our hypothesis. While in field sampling we have greater realism, the mesocosm experiment we have greater control of other variables that may be important for the secondary production of zooplankton (as nutrient concentration and primary production) and other intervening factors can be eliminated or controlled. Furthermore, as zooplankton production is very scarcely estimated as it represents a technical challenge, we used the entire set of data we have on zooplankton secondary production to test our hypothesis.

The field sampling occurred in the Upper Paraná River floodplain, which is in the second largest watershed of South America, in length and drainage area, the La Plata River basin. It occupies an area of about 802,150 km² in Brazilian territory. This floodplain is formed by a wide variety of terrestrial, aquatic and transition environments, such as large rivers, permanent shallow lakes, temporary lakes, side channels and “varzea” (Agostinho et al., 2004) and maintain a high species diversity due to habitat heterogeneity and hydrological temporal variability.

A systematic sampling in two different seasons (low and high-waters) and in two marginal shallow lakes of the floodplain, which differ in their hydrological characteristics: the Pau Vêio Lake (22°44'S; 53°15'W, 233 m altitude, 3ha area, 5 m maximum depth) which is permanently connected to the main river and the Osmar Lake (22°46'S; 53°19'W; 232 m altitude, 0.006 ha area, 3 m maximum depth) which is closed lake on an island, isolated from the river (Figure 1).

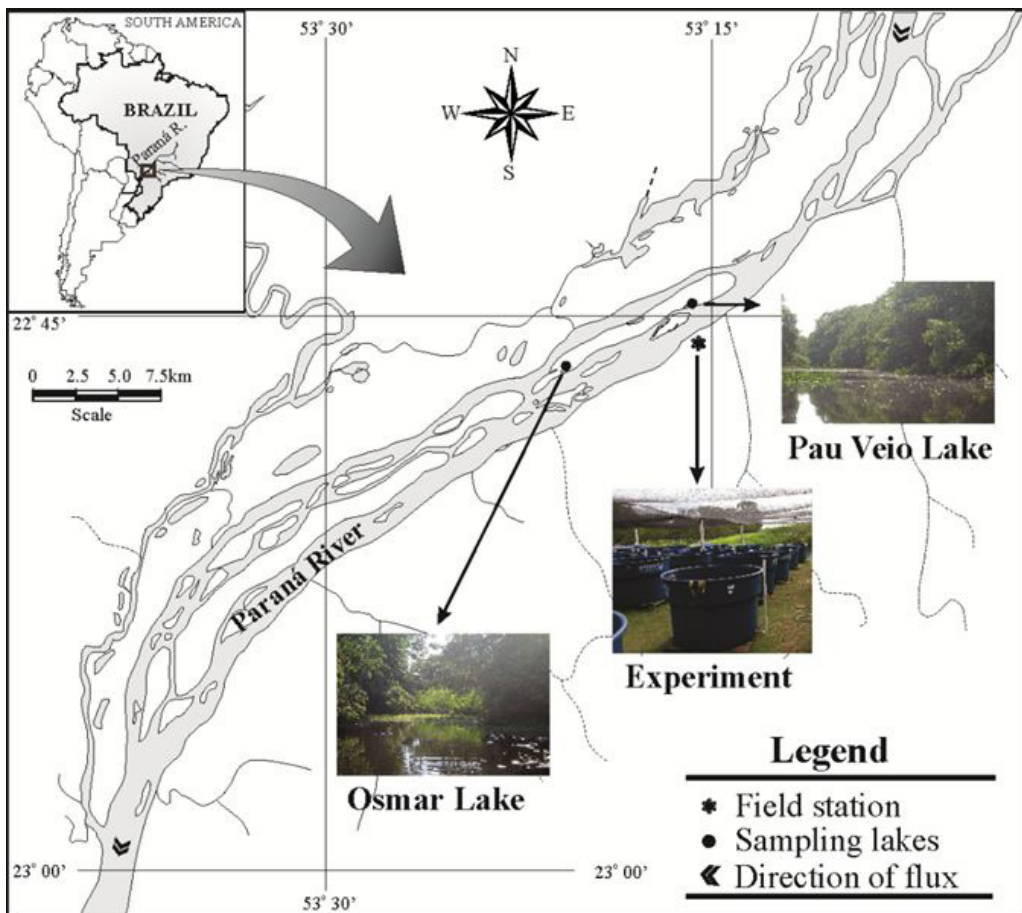


Figure 1. Map of the study area with location of the sampled lakes and the field station where the experiment was conducted in the Upper Paraná River floodplain (Brazil).

The experiment was carried out at the field station (22°45'S; 53°15'W; Figure 1) located in the Upper Paraná River floodplain, very close to the mentioned lakes, was run for 30 days. The experimental units consisted of polyethylene mesocosms (1.0 m high, 1.4 m in diameter, and capacity to 1000 L) filled with 800 L water from the Paraná River. The experimental design was randomized with three levels of nutrients (nitrogen and phosphorus) replicated three times, which were maintained by the addition of a solution composed (80 g NO₃ L⁻¹ and 4 g PO₄ L⁻¹) every three days to prevent depletion over time to have the following three nutrient final concentrations in the mesocosms: N1 = 100 µg NO₃ L⁻¹ and 5 µg PO₄ L⁻¹; N2 = 240 µg NO₃ L⁻¹ and 12 µg PO₄ L⁻¹; and N3 = 360 µg NO₃ L⁻¹ and 18 µg PO₄ L⁻¹. We control the nutrients because this is an important limnological variable that influences the secondary production of zooplankton. We added a mix of phytoplankton and zooplankton species in each mesocosm, collected by filtering water in the same lakes of the field study (Pau Véio Lake and Osmar Lake) and others with similar conditions of the floodplain through a plankton net (20-µm, 45-µm, and 68-µm of the mesh size), concentrated, and homogenized. Invertebrate or vertebrate predators of zooplankton were not included in the experiment. We added to each mesocosm the filtrate of water once, at the beginning of the experiment. This procedure was applied to simulate lakes of the floodplain in the mesocosms, with high species diversity. In a previous study, we analyzed the effects of the nutrient enrichment on primary and secondary productivities and on zooplankton community structure (Melo et al., 2019), but in this study we focused on evaluating the relationship between the ecological attributes of the zooplankton community and its secondary production.

For limnological characterization, we measured several variables (temperature, dissolved oxygen, pH, and conductivity) during both field sampling and the experiment using a HORIBA multiparameter probe. The average temperature was 24.5 (± 2.9) °C in the field and 28.7 (± 2.9) °C in the experiment. The average pH was 6.5 (± 0.4) and 8.8 (± 0.6) in the field and experiment, respectively. The average conductivity was 68 (± 22) µS cm⁻¹ in the field and 75 (± 7.4) µS cm⁻¹ in the experiment. The average dissolved oxygen was 2.7 (± 2.1) mg L⁻¹ and 8.5 (± 1.0) mg L⁻¹ in the field and experiment, respectively.

2.2. Zooplankton sampling and laboratory analysis

In the field, samples of zooplankton organisms were taken in the isolated and connected lakes for

a month in two hydrological periods: the low water period (08 September to 6 October 2009) and the high-water period (February 23 to 23 March 2010). For rotifers, samples were collected daily for the first 15 days (n = 30) and for cladocerans and copepods, every two days throughout the month (n = 30), considering the life cycle of such organisms. Water seasonality and hydrological connectivity were prioritized in the field sampling, once they are considered the major driving forces structuring the zooplankton community in floodplains (Baranyi et al., 2002; Alves et al., 2005; José de Paggi & Paggi, 2008; Simões et al., 2013; Dias et al., 2014, 2017). More details about the field sampling can be found in Dias et al. (2014, 2017). In the experiment, zooplankton samples were taken at the beginning and every five days until the end of the experiment (11 November to 11 December 2013), totaling 63 samples.

Integrated samples of the water column were collected in the limnetic region of the lakes using a motorized pump to filter 500 liters of water per sample through a plankton net (68-µm mesh size), always at the same time of the day to minimize the effect of vertical migration. In mesocosms, the zooplankton was sampled by filtering 10 liters of water through plankton net (45-µm mesh size). The filtered water through plankton net returned to mesocosms to keep the water volume (800 L). Zooplankton samples were narcotized with CO₂ saturation and preserved in a formaldehyde solution (4%) buffered with calcium carbonate with added glucose to prevent the detachment of eggs.

Rotifers, cladocerans, and copepods were identified to the lowest possible taxonomic level with specific literature (see Lansac-Tõha et al., 2009). Species richness per sample was analyzed until the stabilization of the collector curve. The abundance of organisms (ind m⁻³) was estimated by sub-samples taken with a Hensen-Stempel type pipette and counting at least 10% of the concentrated sample in Sedgewick-Rafter chamber (Bottrell et al., 1976). Eggs and number of females with eggs were also quantified. Organisms were measured (30 individuals of each species and nauplii, copepodites, and adults of copepods were measured separately) to calculate the biomass (µg DW m⁻³).

2.3. Secondary production and community attributes

The dry weight of rotifers was estimated from biovolume (Ruttner-Kolisko, 1977) and of cladocerans and copepods from length-weight

regressions (Dumont et al., 1975; Maia-Barbosa & Bozelli, 2005; Azevedo et al., 2012). The species diversity of zooplankton groups was calculated by the Shannon-Wiener index. The evenness was determined by dividing the Shannon diversity by the natural logarithm of species richness.

The secondary production of rotifers was estimated by the recruitment method (Edmondson & Winberg, 1971) for rotifers and by the increase in biomass (Winberg et al., 1965) for cladocerans and copepods. Recruitment was calculated as the product of the finite birth rate ($B = E/De$, where E = number of eggs/female and De = egg development time) and the number of females. Development time was calculated using the formula of Bottrell et al. (1976) ($\ln De = \ln a + b \ln T + c \ln T^2$, where a , b and c = constants determined for the group and T = temperature). Thus, the secondary production of rotifers corresponds to recruitment multiplied by the individual dry weight. In the biomass method is considered the variation in weight, development time and number of individuals of each size class (cladocerans) and stage (nauplii, copepodites, and adults of copepods). The egg weight and the embryonic and post-embryonic development time were obtained from the literature (Espíndola, 1994; Rietzler, 1995; Melão, 1999; Santos-Wisniewski & Rocha, 2007; Santos et al., 2010). Despite to methodology for calculating secondary production varies among rotifers and microcrustaceans, both methods consider the abundance and biomass of organisms in their calculation.

2.4. Data analysis

Repeated measures analyses of variance were employed to test for significant differences in secondary production of rotifers, cladocerans, and copepods between lakes (isolated and connected), hydrological periods (low and high waters). In the experiment, we tested the differences in secondary production between the zooplankton groups through repeated measures analyses of variance. We consider a mean of the experiment data because the main goal was to find the associations of the attributes of the community and the secondary production of the zooplankton groups in the experimental study. In this case, the spatial and temporal variation was used to increase the total data variability.

To assess which attribute of the zooplankton community can be considered a proxy of secondary production of zooplankton groups, data analysis was performed in two steps. First, we tested the

relationship of the attributes of the community with the secondary production of rotifers, cladocerans, and copepods using Spearman correlations (significance of $P < 0.05$), considering the different lakes or hydrological periods in the field study. The purpose of this step was to select which attribute of the community is more associated with the secondary production through the correlation level.

After obtaining the associations between the community attributes and the secondary production of zooplankton groups in the previous step, we evaluated the effect of the community attribute on the secondary production controlling seasonality, hydrological connectivity and/or nutrient concentration through an analysis of covariance (ANCOVA; Gotelli & Ellison 2004), if necessary. This analysis was performed for each zooplankton group separately considering the different lakes or hydrological periods. The response variable used was the secondary production of rotifers, cladocerans, and copepods and the explanatory variables, the ecological attributes significantly related to it, according to the results of Spearman correlations. All statistical analyses were run in R statistical environment (R Core Team, 2014).

3. Results

In the field study, the secondary production of rotifers was significantly higher in the isolated lake in both periods (ANOVA, $F = 65.96$, $P < 0.001$, Figure 2a). For cladocerans, secondary production was higher in the connected lake in the low water period, with significant variation between the lakes (ANOVA, $F = 6.17$, $P = 0.016$, Figure 2b). Copepods also exhibited greater secondary production in both lakes, in the low water period. In general, copepods had greater secondary production when compared to other zooplankton groups, but significant spatial and temporal variations were not observed (ANOVA, $P > 0.05$, Figure 2c). In the experiment, the copepod secondary production continued higher than other zooplankton groups (ANOVA, $F = 227.80$, $P < 0.001$, Figure 2d).

The community attributes were correlated with secondary production (Spearman correlation coefficient) in both field study and experiment (Table 1). In general, the abundance and biomass were the attributes with the highest associations with the secondary production of zooplankton groups. For copepods, biomass was the attribute most associated with secondary production, and for rotifers, the abundance showed the highest association. Secondary production of cladocerans

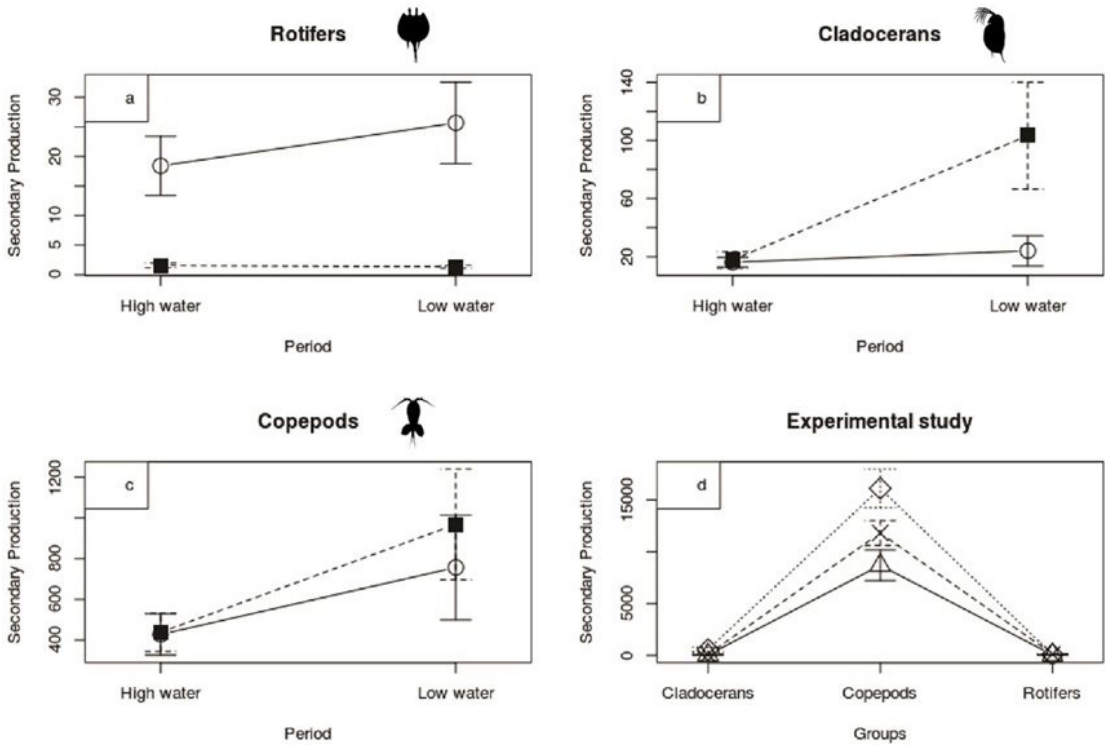


Figure 2. Secondary production of rotifers (a), cladocerans (b) and copepods (c) in the sampled lakes and two hydrological periods. Secondary production of rotifers, cladocerans, and copepods (d) in the mesocosms. In (a), (b) and (c) empty circle and full squared are isolated and connected lakes, respectively. In (d) triangle, “X”, and lozenge are N1, N2, and N3 treatments, respectively. Secondary production was estimated in $\mu\text{g DW m}^{-3} \text{ day}^{-1}$ (symbol = mean; bar = standard error).

Table 1. Spearman correlation coefficient between community structure attributes and secondary production of rotifers, cladocerans, and copepods in the sampled lakes and hydrological periods.

			Richness	Diversity	Evenness	Abundance	Biomass
Rotifers	Connected	LW	0.22	-0.31	-0.39	0.65*	0.69*
		HW	0.48*	-0.54*	-0.79*	0.71*	0.69*
	Isolated	LW	-0.08	-0.71*	-0.71*	0.95*	0.90*
		HW	-0.08	-0.41*	-0.52*	0.90*	0.90*
	Experiment	N1	0.41	-0.02	-0.25	0.69*	0.74*
		N2	0.55*	-0.49*	-0.68*	0.83*	0.48*
N3		0.39	0.23	0.40	0.68*	0.58*	
Cladocerans	Connected	LW	0.76*	0.25	-0.06	0.86*	0.88*
		HW	0.35	0.01	-0.63*	0.89*	0.91*
	Isolated	LW	0.06	-0.64*	-0.87*	0.97*	0.91*
		HW	0.64*	0.63*	0.23	0.58*	0.49
	Experiment	N1	0.43	0.28	0.11	0.52*	0.80*
		N2	0.45*	0.31	0.21	0.83*	0.94*
N3		0.35	0.01	-0.61*	0.87*	0.85	
Copepods	Connected	LW	0.25	0.06	-0.29	0.96*	0.97*
		HW	0.26	0.10	-0.10	0.61*	0.81*
	Isolated	LW	0.48*	0.18	-0.51*	0.76*	0.90*
		HW	0.68*	0.57*	-0.39	0.87*	0.97*
	Experiment	N1	0.31	0.16	0.16	0.55*	0.93*
		N2	0.12	-0.36	-0.23	0.66*	0.94*
N3		0.36	0.18	-0.14	0.69*	0.89*	

LW, low water; HW, high water; N1, N2, and N3, nutrients treatments. *significant results ($P < 0.05$).

showed no clear pattern with the attributes analyzed, correlated with abundance in half of the dataset and with biomass in the other half (Table 1).

Secondary production models of the zooplankton groups showed a high explanation of the total data variability in both the field and experiment studies. Abundance and biomass showed a positive association with the secondary production of zooplankton groups (Tables 2 and 3).

In the field study, the rate of conversion of the abundance of rotifers (ind m^{-3}) in secondary productivity ($\mu g DW m^{-3} day^{-1}$) was 0.001 (Table 2) while in the experimental study that rate was 0.002 (Table 3). It means each 1,000 rotifers, 1 $\mu g DW m^{-3} day^{-1}$ was available in the lakes while 2 $\mu g DW m^{-3} day^{-1}$ was available in the mesocosm (Figure 3a, b).

The effect of biomass on the secondary production of cladocerans depended on the hydrological period (significant interaction $P < 0.001$, results no showed) (Table 2) in the field study. During the low water period, the slope was 0.05, while during the high-water period, the slope was 0.19, indicating that the conversion rate of biomass into secondary production was higher in the second period (Figure 3c). In the experimental study, the conversion rate of cladocerans biomass in secondary production was 0.308 (Table 3), showing each increase in 10 $\mu g DW m^{-3}$ in cladocerans biomass convert into 3.08 $\mu g DW m^{-3} day^{-1}$ in secondary productivity (Figure 3d).

For the copepods in the field study, the effect of the biomass on the secondary production depended on hydrological period (significant interaction $P < 0.001$, results no showed). During high water, the rate conversion was 0.214 while in the low water it was 0.015 (Figure 3e). In the experimental study (Table 3), copepods showed a rate of conversion of biomass into secondary production 0.286 (Figure 3f). There was no difference in the conversion rate of abundance/biomass into secondary production among nutrients treatments for all analyzed zooplankton groups.

4. Discussion

We find a way to estimate the secondary production of zooplankton based on the community attributes, since these attributes directly reflect the response of populations. Our results showed that secondary production of larger and long-lived organisms, such as copepods, had been most associated with the biomass, whereas smaller ones, such as rotifers, with the abundance. Secondary production of the zooplankton in the pelagic compartment is essential for energy transfer in aquatic systems, and therefore for the maintenance of food chains. Several studies have shown the importance of zooplankton secondary production in all aquatic ecosystems (Akbulut, 2000; Melão & Rocha, 2000; Mageed, 2006; Casanova et al., 2009; Kang et al., 2009; Lemke

Table 2. Summary of general linear models showing the effects of the main sources of variation on the secondary production of zooplankton groups in the field study.

Field sampling	Intercept	Abundance effect		Adjusted R ²
Rotifers	7.384	0.001* (0.0001)		0.69
		Biomass effect in HW period	Biomass effect in LW period	Adjusted R ²
Cladocerans	3.780	0.19* (0.04)	0.05* (0.04)	0.76
		Biomass effect in HW period	Biomass effect in LW period	Adjusted R ²
Copepods	43.686	0.217* (0.01)	0.115* (0.01)	0.90

LW, low water period; HW, high water period. *significant results ($P < 0.05$). Standard error in brackets.

Table 3. Summary of general linear models showing the effects of the main sources of variation on the secondary production of zooplankton groups in the experimental study.

	Experimental study				Adjusted R ²
	Intercept (N1)	Abundance effect	N2	N3	
Rotifers	-1.193	0.002* (0.001)	-8.602 (23.07)	-29.10 (22.69)	0.79
		Biomass effect			Adjusted R ²
Cladocerans	-10.85	0.308* (0.017)	-60.497 (71.577)	7.315 (76.770)	0.86
		Biomass effect			Adjusted R ²
Copepods	1220	0.285* (0.01)	-827 (860.34)	108 (921.45)	0.87

N1, N2, and N3, nutrients treatments. *significant results ($P < 0.05$); standard error in brackets.

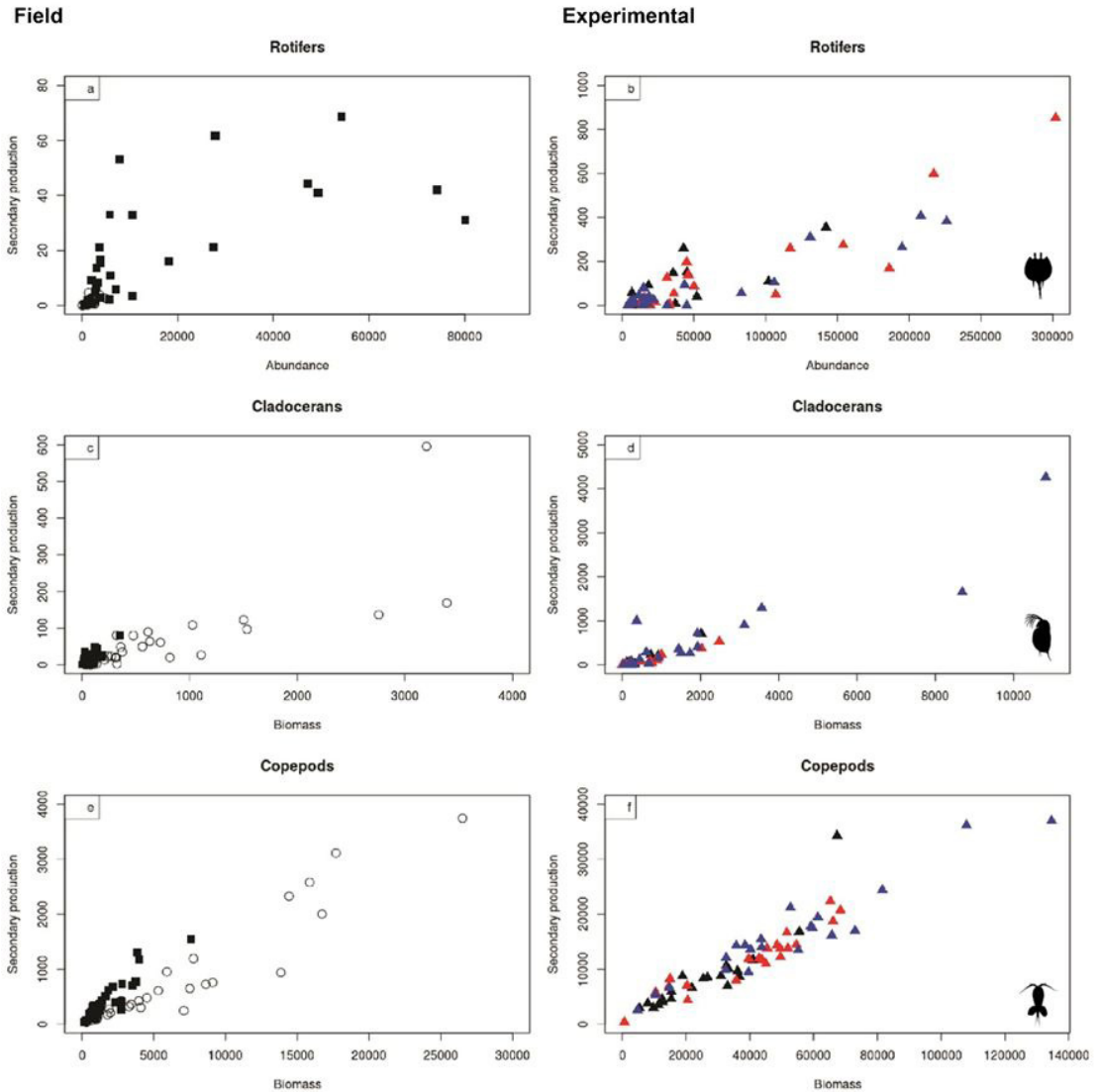


Figure 3. Increasing secondary production of rotifers as a function of abundance in the field and experimental studies. Increasing secondary production of cladocerans and copepods as a function of biomass in the field (left column) and experimental (right column) studies. In (a) empty circle and full squared are connected and isolated lakes, respectively; while in (c) and (e) empty circle and full squared are low and high waters periods, respectively. In (b), (d) and (f) black, red, and blue triangle are N1, N2, and N3 treatments, respectively.

& Benke, 2009; Panarelli et al., 2010; Dias et al., 2014, 2017; Setubal et al., 2020a). However, unlike primary production that is based on a metabolic process (photosynthesis), there is still no such direct measurement to estimate the secondary production. The estimation of zooplankton production in freshwater ecosystems is based on a complex methodology involving continuous sampling and analysis of cohorts (Downing & Rigler, 1984) and also the quantification of individuals and eggs, biomass, age structure, growth and reproductive rates (Edmondson, 1974). Considering the high diversity of zooplankton

species in freshwater ecosystems, it is very difficult to have all the information of autoecology of all species. In addition to the methodological difficulties, there is also a lack of adequate high-cost equipment (i.e. highly accurate micro-analytical balance) and of infrastructure for physiological autoecology studies. For these reasons, it is necessary to find a method that can more easily be applied to estimate the secondary production of zooplankton in these ecosystems, contributing to advances in environmental monitoring studies. Sastri et al. (2013) suggested a method to estimate secondary production of the microcrustacean community

based on an enzyme (chitinase), secreted by these organisms. Taking into account the productivity-diversity relationship, Thackeray (2007) identified the phytoplankton biomass (ecological attribute) as the best proxy for primary production to estimate the production of zooplankton than the concentration of chlorophyll-a and nutrients.

Most studies on the zooplankton community, especially those resulting from environmental monitoring, has estimated some of its ecological attributes, such as density, diversity, and biomass. Our study is the first one relating the secondary production of zooplankton with ecological attributes of the community. Among these attributes, biomass and density promote the secondary production or even maximize it, as in the case of species diversity (Hooper et al., 2005; Loreau et al., 2001). In this context, we found that the abundance and biomass are good estimators of the secondary production of zooplankton, as verified by the high values of the correlation coefficient. This was expected, since these attributes are used to calculate the production of the community (Winberg et al., 1965; Edmondson & Winberg, 1971), and thus are directly proportional. Nevertheless, considering the methodological difficulties to estimate secondary production, the question arises of which attribute of the community is more reliable to make such inferences. Our results demonstrated that the answer to this question depends on the zooplankton group, the type of environment and the water seasonality.

The differences recorded among zooplankton groups can be attributed to variation in mean body size. Body size is known to determine the ecological and physiological characteristics of organisms, promoting differences in mortality by predation, and competitive ability of species (Lampert & Sommer, 2007). Besides that, larger sized animals have a lower metabolism than smaller ones, so they use resources more efficiently and grow more slowly (Woodward et al., 2005a). Still, body size directly influences the metabolism of organisms and therefore has a direct effect on its secondary production (Woodward et al., 2005b). For larger zooplankton organisms, like copepods, biomass may better represent the secondary production, in turn, for smaller organisms, such as rotifers, the abundance may be a better and easier estimator of production. This occurs because individuals with larger body size generally have lower abundances, but higher biomass (Woodward et al., 2005a, b), indicating the greater availability of energy to the next trophic level. In this case, using abundance

to estimate the secondary production of larger organisms, such as copepods that have a series of different sized stages, tends to underestimate it. Likewise, using biomass to estimate the secondary production of eutelic organisms, such as rotifers, can underestimate it. Therewith, using abundance run into the error of underestimating the secondary production of large species, while using biomass, may underestimate the production of small-sized species.

The ecological pattern shows larger sized individuals with greater biomass have lower abundances (Woodward et al., 2005a). This relationship is very well recognized for zooplankton communities in tropical and subtropical lakes because rotifers are often the most abundant organisms (Cardoso & Marques, 2004; Bonecker et al., 2009; Lansac-Tôha et al., 2009; Simões et al., 2012). Due to their small size, contribution of rotifers to total zooplankton biomass is unimportant.

An interesting aspect is that despite the relationship between secondary production and community attributes that differ among zooplankton groups, each group presented similar relationships when conditioned the main sources of environmental variation: connectivity with the river and hydrological periods, which differed in the characterization of environmental conditions. The production of rotifers mainly responded to the connectivity with the river, allowing the use of predictive models regardless of the hydrological period. Unlike rotifers, the main source of variation for microcrustaceans was the hydrological period, suggesting that the secondary production predictive model may be used irrespective of the environment. The models showed a high degree of explanation (above 80%), and highlighted the positive effect of abundance or biomass, as well as the interaction of abundance with the type of environment, for rotifers, and with hydrological period, for cladocerans. In this way, the number of individuals/biomass that can be converted into secondary production may differ under certain environmental conditions. For copepods, this interaction was not significant, suggesting that the conversion rate is similar in different environmental conditions, given by variations of these in the type of environment or hydrological period.

Another interesting finding was the negative association between secondary production of rotifers, cladocerans, and copepods and the evenness of these groups in different periods and lakes, which indicates that, regardless of the

group, the highest production is related to the dominance of a few species. Thus, the increase in secondary production is due to few r-strategist species that exploit the availability of resources more promptly and increase their reproductive effort, prevailing in the community (Allan 1976; Dodson, 1992). Diversity and namely as more even is the species distribution of individuals is smaller when secondary production is higher. However species richness is positively associated with secondary production, this could be related to “overyielding” a concept used to explain the positive relationship between primary production and species richness (Tilman et al., 1996) since a mixture of species increases the likelihood of a productive species being more productive. Resource complementarity may be a mechanism by which a mixture of species, which abundances are unevenly distributed, controls the system production. In any case, higher production is associated with unevenness of the species abundances. We have to consider also that the relationship primary production – biomass is asymptotic; therefore, the ratio primary production/biomass (P/B) decreases with ecosystem succession. Thus, in more mature ecosystems in the sense of (Margalef, 1997) biomass will be relatively much higher than primary production. The asymptotic character of the relationship production vs. biomass in zooplankton is also applicable and it is well shown in Figure 3 that displays this relationship for the different zooplankton groups.

The higher secondary production values observed in the experiment, compared to the field study, can be attributed to zooplankton predation. In the experiment, the lack of fish or invertebrate predators likely contributed to the increased secondary production. Predation is the ultimate factor responsible for structuring zooplankton community (Brooks & Dodson 1965; Iglesias et al., 2011).

5. Conclusions

We relate the zooplankton secondary production with ecological attributes of the community in the search for a simpler method for its estimate. Our hypothesis was partially confirmed, because the abundance is an important predictor of secondary production of the smaller zooplankton (rotifers), while biomass represents better the production of larger individuals (cladocerans and copepods). Therefore, our study contributes to the ecology of plankton and of aquatic ecosystems, since the use of ecological attributes of the community to

estimate its production will provide an important contribution to the understanding of the ecosystem, helping environmental monitoring programs in the implementation of strategies for biodiversity conservation, and give answers to ecological theories related to the production of aquatic communities.

Acknowledgements

The authors are grateful to the LTER (PIAP)/CNPq for financial support and CNPq for postdoctoral (JDD) and research productivity (CCB and NRS) fellowships. JDD also thanks CAPES for the scholarship of interuniversity exchange doctorate (Process number 9144-11-0).

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Received: 14 May 2024

Accepted: 10 September 2024

Associate Editors: Claudia Bonecker, Gilmar Perbiche-Neves, Maria Stela Maioli Castilho Noll.