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PRIMARY RESEARCH PAPER

Effects of nutrient enrichment on primary and secondary productivity in a subtropical floodplain system: an experimental approach

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Abstract In this study, we evaluated the effects of nutrient enrichment on primary and secondary productivity, the relationship between these ecosystem processes, and the relationship between the resources of zooplankton community in response to ecosystem processes, experimentally. The experimental design was randomized, with three levels of nutrient replicated three times, giving a total of nine experimental units, for a period of 30 days (November–December, 2013). We measured primary productivity, secondary productivity, and zooplankton community structure, at the beginning and after every seven days of the experiment. Primary and secondary productivity increased with nutrient enrichment. Secondary productivity was supported by a few dominant species with ecologically selected traits, especially large-bodied zooplankton (copepods and large cladocerans). Nutrient enrichment turned the relationship between primary and secondary productivity from positive to negative and intensified the biotic process of competition because of exploitation by zooplankton populations, favoring an increase in the dominance of large microcrustaceans. This reflects the initial effects of a moderate eutrophication. At a larger temporal scale and at higher nutrient concentrations, effects of higher magnitude are expected, which may disrupt the whole community, resulting in the loss of ecosystem processes.

Keywords Zooplankton · Overyielding · Competition · Ecosystem functioning · Eutrophication

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Introduction

Anthropogenic activities change the ecological integrity of aquatic ecosystems, mostly through nutrient (nitrogen and phosphorus) enrichment, which has caused dramatic changes in aquatic communities and ecosystem functioning (Smith et al., 2006; Elser et al.,

2007). Under natural conditions, primary productivity positively responds to an increase in nutrient concentrations and influences the secondary productivity, a chain reaction driven by bottom up processes through the response of communities (Onandia et al., 2014).

Nutrient enrichment affects phytoplankton density and morphology, increases the population growth rates of a few species, mostly inedible (filaments and colonies), hindering their ingestion and interfering with the structure and dynamics of zooplankton community (Anderson et al., 2002; Gobler et al., 2007; Pan et al., 2014). This causes competitive exclusion by exploitation of nutrients, both in phytoplankton (Tilman, 1977) and zooplankton (Rothhapt, 1988) communities, consequently reducing species richness and increasing dominance of a few species (Rosenzweig, 1971; Abrams, 1995).

Species richness in a community has an important role in primary production processes and ecosystem functioning (Loreau et al., 2001). Ecosystem processes can be maintained by several species with different phenotypic traits that complement each other (niche complementarity), or by a few species with certain ecologically selected traits that dominate the environment (overyielding) (Loreau, 2000). Communities with high species richness are more likely to have higher phenotypic trait diversity (Chapin et al., 1997; Loreau et al., 2001).

Manipulative experiments are important in ecological studies, because they assume that variables act simultaneously, most studies have been investigating the effects of nutrient enrichment by relating it to an increase in primary productivity and/or changes in the attributes of aquatic communities, such as richness, abundance, and biomass (Jeppesen et al., 2000; Cottingham et al., 2004; Donohue et al., 2009; Sorf et al., 2015). It is necessary and important to study the secondary productivity in this context, as it allows estimating the amount of energy incorporated through consumption that is available to higher trophic levels, giving a quali-quantitative meaning to energy transfer processes and representing a functional measure of energy flow through trophic levels (Santos-Wisniewski & Rocha, 2007).

The Upper Paraná River floodplain is located in the subtropical region of South America, and is characterized by intense human occupation, resulting in anthropogenic effects, such as elevated nutrient input from domestic sewage, intense agricultural activity,

intense use of agriculture chemicals, and elimination of riparian vegetation (Agostinho et al., 2007, 2008). In this way, using a manipulative experiment, we evaluated (i) the effects of moderate nutrient enrichment on primary and secondary productivities, (ii) the relationship between these ecosystem processes, and (iii) the relationship between the attributes of zooplankton community in response to moderate nutrient enrichment. We tested the hypothesis that primary and secondary productivity are positively affected by nutrient enrichment because of the higher quantities of resources available to primary producers, and consequently, to consumer organisms. We predicted that nutrient enrichment would influence zooplankton community structure (species richness, density, biomass, dominance, and composition) via bottom up processes, consequently altering the temporal dynamics of secondary productivity.

Methods

Experimental setup

The experiment was performed at the Advanced Research Base of Nupélia (Research Nucleus in Limnology, Ichthyology and Aquaculture), located near the Upper Paraná River floodplain, Porto Rico–PR, Brazil. Mesocosms (polyethylene tanks: 1.0 m high, 1.4 m in diameter) were filled with 800 l of water from the Paraná River on November 08, 2013. On the same day, phytoplankton and zooplankton inocula were collected from the lakes of Upper Paraná River floodplain (environments with high species richness—Lansac-Tôha et al., 2009) using plankton nets of 20 μm (phytoplankton), 45 μm, and 68 μm (zooplankton) mesh size to improve collection efficiency. On November 10, these inocula were homogeneously added to the mesocosms. The first sampling was performed on November 11 and samples were taken after every five days, until December 11, 2013. We chose this period of the year because it is an intermediate period in the Upper Paraná River floodplain, with neither floods nor droughts. Extreme events could influence phytoplankton and zooplankton communities that were added to mesocosms. Fishes and aquatic macrophytes are present in the Upper Paraná River floodplain environments, but we did not include them in the experiment because our objective was to

evaluate the strength of bottom up process with simple two trophic level communities.

The experimental design was randomized with three levels of nutrient, replicated three times, giving a total of nine experimental units. Nutrient concentrations used in different levels were: N1—100 µg NO_3 l^{-1} and 5 µg PO_4 l^{-1}; N2—240 µg NO_3 l^{-1} and 12 µg PO_4 l^{-1}; and N3—360 µg NO_3 l^{-1} and 18 µg PO_4 l^{-1}. These concentrations were maintained by addition of different volumes of a compound solution (80 g NO_3 l^{-1} and 4 g PO_4 l^{-1}) every 3 days, to avoid depletion over time. These concentrations were defined based on previously performed studies at the Upper Paraná River floodplain. Because most habitats in this floodplain are characterized as oligotrophic (Roberto et al., 2009), the concentrations defined in our study are considered to cause moderate eutrophication, compared to similar studies.

Daily measurements of dissolved oxygen (mg l^{-1}), water temperature (°C), conductivity (µS cm^{-1}), pH, and turbidity (NTU) were performed to monitor the experiment. The results were similar between the replicates of each treatment (Supplementary Material).

Net primary productivity (NPP) of phytoplankton

Phytoplankton NPP (mgC m^{-3} h^{-1}) in each mesocosm was estimated at the beginning and after every five days until the end of the experiment, totaling seven measurements over the experimental period (November 11–December 11, 2013). This estimate was obtained by evaluating the changes in water oxygen concentrations per unit of time inside light and dark bottles, a common approach used to measure the aquatic metabolism (Wetzel & Likens, 2000; Simões et al., 2013). In each mesocosm a light and a dark bottle were incubated for 4 h, from 10 to 14 h. Dissolved oxygen concentration was measured at the beginning and at the end of the incubation, using YSI® digital oximeter. In the light bottle, oxygen was produced through photosynthesis and consumed through respiration, whereas in the dark bottle only consumption occurred. Therefore, NPP was estimated as oxygen production minus consumption. The values of net primary productivity were converted to carbon using the relationship of 0.375 mol of carbon to 1 mol of oxygen (Wetzel & Likens, 2000).

Secondary productivity (SP) and zooplankton community structure

Rotifers, cladocerans, and copepods were sampled concomitantly with the measurement of NPP. We filtered 10 l of water from each mesocosm (a sufficient amount to represent the community without affecting zooplankton density) using a plankton net of 45 µm mesh size, and the filtered water was returned to the mesocosm to avoid reduction in the water level. Zooplankton were narcotized by CO_2-saturated water prior to fixation in sugar-saturated formaldehyde solution (4%) buffered with calcium carbonate. This procedure prevents the contraction of individuals and egg detachment, which is important for calculating the secondary productivity.

Species identification was performed using specialized literature (see Lansac-Tôha et al., 2009). Individual dry weight was calculated from the biovolume of rotifers (Ruttner-Kolisco, 1977), and most of the length–weight relationships of microcrustaceans were based on the data reported from the floodplain (Azevedo et al., 2012). The others were from literature, mostly from tropical regions (Dumont et al., 1975; Melão, 1999; Maia-Barbosa & Bozelli, 2005; Santos, 2010). However, we considered the shape and variation of the body size in the choice of equations. Measurements (length, width, and height) of up to 30 individuals of each species of rotifers, cladocerans, and adult and juvenile copepods, were taken in each sample. Secondary productivity (µgDW l^{-1} $days^{-1}$) was estimated for rotifers using recruitment method (Edmondson & Winberg, 1971), through which the finite birth rate (B) and the mean individual dry weights of the organisms were evaluated, and only species with eggs, in the samples, were used. This method is mainly applied to organisms showing small differences in the size of newly hatched and adult individuals (Peláez-Rodrigues & Matsumura-Tundisi, 2002), such as rotifers. For microcrustaceans, we used the method of biomass increment (Winberg et al., 1965), considering the variation in weight, development time, and the number of individuals in each size class (cladocerans) and developmental phase (copepods). Egg development time, egg weight, and embryonic and post-embryonic developmental durations were obtained from the literature, mostly from tropical regions (Espíndola, 1994; Rietzler, 1995; Melão, 1999; Santos-Wisniewski & Rocha, 2007).

Richness corresponds to the number of species registered in the samples. Density of individuals (ind l^{-1}) was obtained through sub-samplings, and at least 10% of the concentrated sample (10 l of water filtered) was counted. Samples with a reduced number of individuals were counted entirely. Biomass (μgDW l^{-1}) was calculated as a product of density and individual dry weight. Dominance was estimated through community equitability (Pielou, 1966).

Statistical analysis

Factorial Analysis of Variance (Factorial ANOVA) was performed to test the effects of nutrient enrichment, time, and their interactions, on NPP, SP, richness, density, biomass, and dominance. Data were log-transformed ($x + 1$), and normality and homoscedasticity assumptions were tested. When results were significant ($P \leq 0.05$), the means of each treatment and the day of sampling were compared using Tukey tests, to verify the significant difference between them ($P \leq 0.05$).

To investigate the dynamics between NPP and SP, and their relationships in different treatments were compared using Analysis of Covariance (ANCOVA) (Gotelli & Ellison, 2004). We tested the hypothesis of parallelism before testing for significant differences in the slope. When significant differences were observed in the slope, a new model with separate slopes was applied. On the other hand, when no significant differences were found in the slope, a traditional ANCOVA was performed.

Non-metric multidimensional scaling (NMDS) (Clarke, 1993) was performed to observe the effects of nutrient enrichment and time on zooplankton composition. For this, we calculated a Jaccard distance matrix, from a presence-absence data matrix. The significance of results ($p \leq 0.05$) was tested through a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2001), with 999 permutations and Jaccard distance.

PERMANOVAs were also used to test if community compositions in the treatments were significantly different on each day of sampling, separately, to verify the moment in which the communities may have differed from one another.

Factorial ANOVA and ANCOVA were performed using the software Statistica version 8.0 (StatSoft Inc., 2007), and the other statistical analyses were performed in software R (R Core Team, 2014) using the packages *vegan* (Oksanen et al., 2014), *BiodiversityR* (Kindt & Coe, 2005) and *MASS* (Ripley et al., 2015).
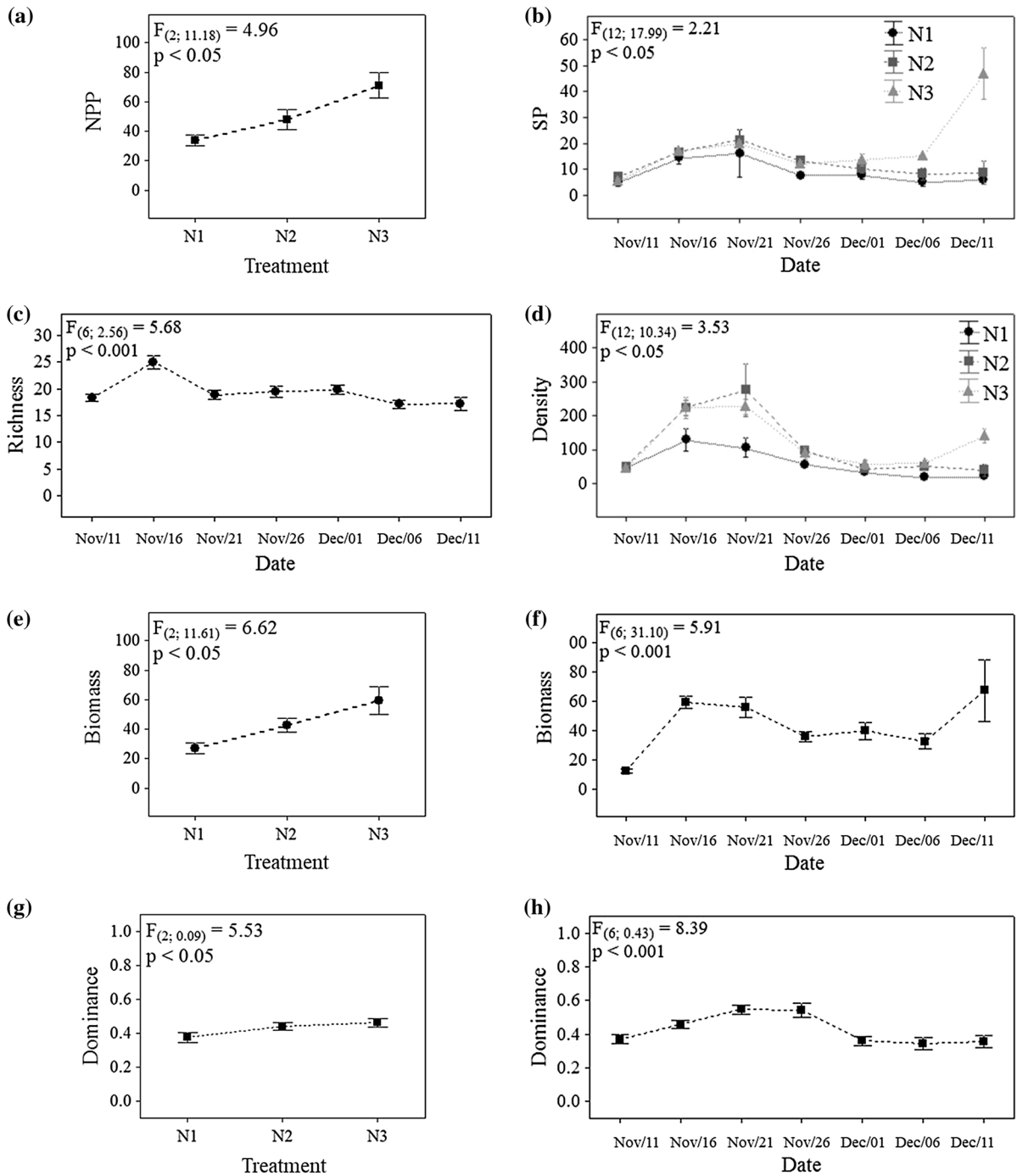
Results

The mean NPP was 34.7 mgC m^{-3} h^{-1} in treatment N1, 47.7 mgC m^{-3} h^{-1} in treatment N2, and 71.4 mgC m^{-3} h^{-1} in treatment N3, with significant differences among treatments ($F_{2;11.18} = 4.96$, $p < 0.05$), in which treatment N1 differed from N3 ($p < 0.01$) (Fig. 1a). No significant differences between days of sampling or interactions were found.

The mean SP of zooplankton was 8.97 μgDW l^{-1} days^{-1} in treatment N1, 12.23 μgDW l^{-1} days^{-1} in treatment N2, and 18.60 μgDW l^{-1} days^{-1} in treatment N3. A significant interaction was found between the treatments and days of sampling ($F_{12;17.99} = 2.21$, $p < 0.05$), showing that from the fifth day to almost the end of the experiment (Dec/01), SP in treatment N3 became higher than that in the other treatments (Fig. 1b).

ANCOVA showed that the relationships between NPP and SP in all treatments were significant (Fig. 2). Positive relationships were found between the primary and secondary productivities in treatments with N1 and N2 nutrient concentrations, whereas a negative relationship was found in the treatment with N3 concentrations. An increase in nutrient concentration modified the relationship between NPP and SP from positive to negative.

Mean zooplankton richness was 14 species in treatment N1, 15 species in treatment N2, and 16 species in treatment N3 (Fig. 1c), with no significant differences between treatments, but only over time ($F_{6;2.56} = 5.68$, $p < 0.001$), with higher values observed on the second day of sampling. Tukey test showed that the mean species richness on this day of sampling was significantly different from the other days, except the fifth day of sampling. No significant interactions between factors were found.

Mean density was 58.82 ind l^{-1} in treatment N1, 110.90 ind l^{-1} in treatment N2, and 119.88 ind l^{-1} in treatment N3 (Fig. 1d). We found significant interactions between factors ($F_{12;10.34} = 3.53$, $p < 0.05$), especially on the second and third days of sampling, in treatments N2 and N3.

Fig. 1 Factorial ANOVA significant results represented in graphs. Net primary productivity (NPP) (mgC m^{-3} h^{-1}) between treatments with different nutrient concentrations (N1, N2, N3) (**a**). Secondary productivity of zooplankton (SP) (µgDW l^{-1} days^{-1}) in treatments and over time (**b**). Species richness over time (**c**). Density (ind l^{-1}) between treatments and over time (**d**). Biomass (µgDW l^{-1}) between treatments (**e**) and over time (**f**). Dominance between treatments (**g**), and over time (**h**). Secondary productivity and density showed significant interaction between factors. Bars represent standard error
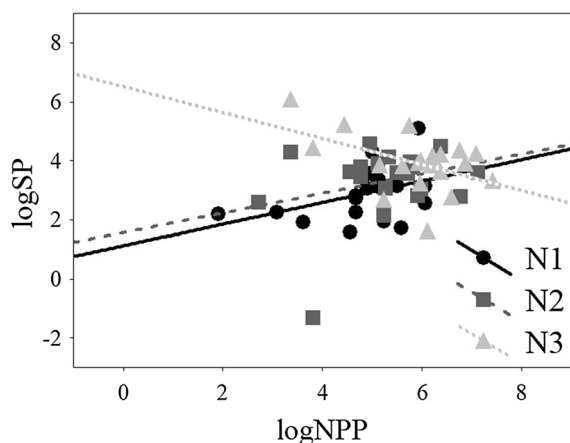
Fig. 2 Relationship between secondary productivity of zoo-plankton (SP) (μgDW l^{-1} days^{-1}) and net primary productivity (NPP) (mgC m^{-3} h^{-1}) in treatments with different nutrient concentrations (N1, N2, N3), βN1 = 0.36; βN2 = 0.33; βN3 = − 0.44. Data were log-transformed

Mean biomass was 27.19 μgDW l^{-1} in treatment N1, 42.53 μgDW l^{-1} in treatment N2, and 59.53 μgDW l^{-1} in treatment N3 (Fig. 1e). Factorial ANOVA showed that the biomass was significantly different between treatments ($F_{2;11.61}$ = 6.62, $p < 0.05$), i.e., N1 was significantly different from N3, and over time ($F_{6;31.10}$ = 5.91, $p < 0.001$), i.e., biomass at the beginning of the experiment was different from that of all the other days, except the sixth day of sampling (Fig. 1f). No significant inter-actions between factors were found.

Mean dominance was 0.37 in treatment N1, 0.44 in N2, and 0.46 in N3 (Fig. 1g), showing significant differences between treatments ($F_{2;0.09}$ = 5.53, $p < 0.05$) and over time ($F_{6;0.43}$ = 8.39, $p < 0.001$). In this case, dominance in treatment N1 was signif-icantly different from N3; the third and fourth days of sampling were similar among them but significantly different from the other days (Fig. 1h). No significant interactions between factors were found.

The zooplankton community was represented by 77 species in all treatments, with 48 rotifers, 14 clado-cerans, and 15 copepods.

Copepod species that contributed the most to secondary production were *Notodiaptomus henseni* (Dahl, 1894) (adult calanoid) and *Thermocyclops decipiens* (Kiefer, 1929) (adult cyclopoid), in addition to juvenile stages (nauplii and copepodites). The high productivity of copepods was responsible for a major

fraction of total secondary productivity (Fig. 3), with a mean value of 12.2 μgDW l^{-1} days^{-1}. Higher values registered on the second and third days of sampling, in all treatments, decreasing on the fourth day (Nov/26), and showed a peak on the last day of sampling in treatment N3 (Fig. 3). This high value was mainly due to an increase in the productivity of calanoid cope-pods. On the other hand, mean secondary productivity of rotifers was the lowest, 0.23 μgDW l^{-1} days^{-1}, with main contributions from *Euchlanis dilatata* Ehrenberg, 1832, *Filinia terminalis* (Plate, 1886), *Hexarthra intermedia* (Wiszniewski, 1929), *H. mira* (Hudson, 1871), *Keratella americana* Carlin, 1943, *K. cochlearis* (Gosse, 1851), and *K. tropica* (Apstein, 1907). In this group, higher SP values were generally found at the beginning of the experiment, especially in treatment N2 (Fig. 3). Mean secondary productivity of cladocerans was 0.85 μgDW l^{-1} days^{-1}, with contri-butions from *Chydorus pubescens* Sars, 1901, *C. parvireticulatus* Frey, 1897, *Daphnia gessneri* (Herbst, 1967), and *Simocephalus serrulatus* (Koch 1841). Contrary to rotifers, these microcrustaceans showed higher SP values in treatment N3 at the end of the experiment, supported mainly by *S. serrulatus* (Fig. 3).

Zooplankton community composition, as shown by the non-metric multidimensional scaling (NMDS), did not show any separation between treatments, but only over time (Fig. 4). This result was confirmed by the PERMANOVA, which was significant only over time (F = 11.51; p = 0.001). However, there seems to be a segregation in the zooplankton composition until the fourth day of sampling, which was not observed on the other days. This was corroborated by PERMANOVAs performed for each point of time separately, which showed that on Nov/11 (F = 0.63; p = 0.57), Nov/16 (F = 0.63; p = 0.56), Nov/21 (F = 0.23; p = 0.78), and Dec/01 (F = 2.42; p = 0.17), the treatments were not significantly different. However, on Nov/26 (F = 8.81; p = 0.03), Dec/06 (F = 9.79; p = 0.02) and Dec/11 (F = 13.09; p = 0.03), the treatments were significantly different.

Discussion

Nutrient enrichment positively affected the ecosystem processes and influenced the community structure of zooplankton over time. However, the relationship
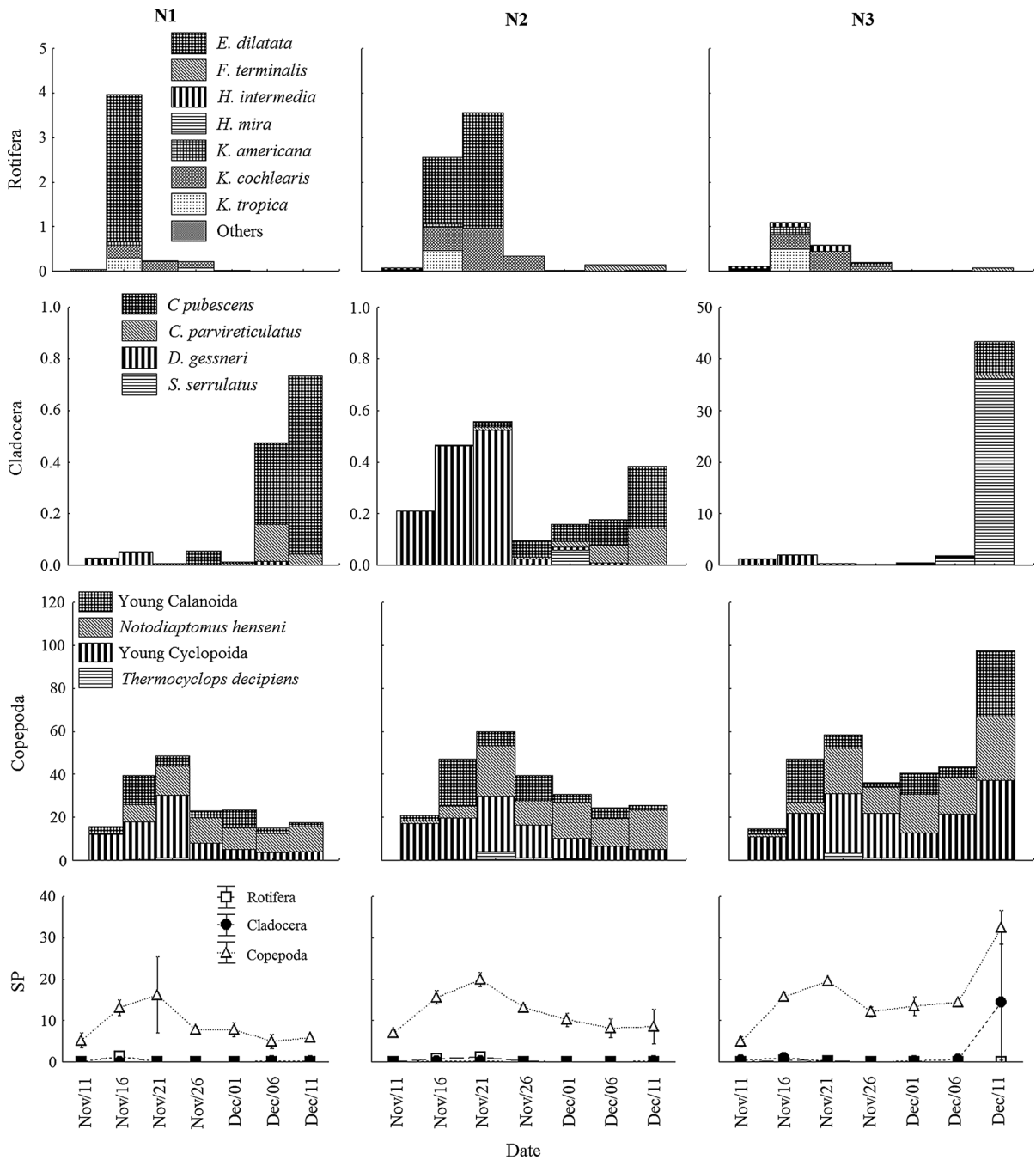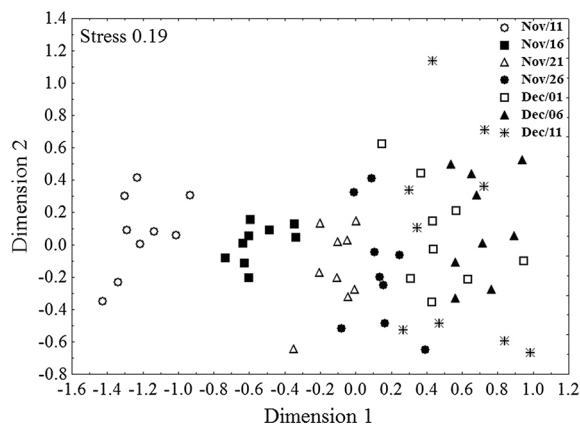
Fig. 3 Secondary productivity of zooplankton (SP) (μgDW l^{-1} days^{-1}) by group, in each treatment: N1, N2, N3, and over time. SP is the sum of the secondary productivities of species represented in each group and bars represent standard errors. Note that graphs have different scales on the y-axis

between NPP and SP was positive in the treatments with lower nutrient concentrations (N1), becoming negative at the higher levels (N2 and N3). At the highest nutrient concentrations, inedible algae were

likely favored, influencing the interactions among zooplankton populations, which was corroborated by PERMANOVAs performed at each point of time and by the higher dominances, and resulting in a negative

Fig. 4 Non-metric multidimensional scaling (NMDS) of zooplankton community separating the times (Nov/11, \Nov/16, Nov/21, Nov/26, Dec/01, Dec/06 and Dec/11)

relationship between primary and secondary productivities. However, the amount of energy available at the lowest nutrient concentration (N1) may have been a limiting factor, resulting in a linear positive response of zooplankton species to the increase in NPP. When nutrients were not limiting, i.e., at the highest concentrations of the experiment, there was sufficient energy and populations did not respond to this increase in NPP.

Nitrogen and phosphorus are known to regulate and significantly increase primary productivity when simultaneously added to the environment, representing higher resource availability for aquatic producers (Smith et al., 2006; Elser et al., 2007). With nutrient enrichment, phytoplankton invest in growth and reproduction (Pan et al., 2014), influencing zooplankton density and biomass (Sorf et al., 2015). As nutrient concentration affects phytoplankton-zooplankton relationships (Perhar et al., 2013; Pan et al., 2014), it is likely that nutrient enrichment competitively selected filamentous and colonial species, mainly species of colonial cyanobacteria such as *Aphanocapsa* spp. and *Radiocystis* sp., which are difficult to ingest (Anderson et al., 2002; Pan et al., 2014), altering the zooplankton community.

Calanoid copepods and the cladoceran, *Simocephalus serrulatus,* were favored by an increase in nutrient concentration, and these species were responsible for the higher SP values found at the end of the experiment, as they are both large-bodied herbivorous microcrustaceans, with high biomass, and good resource competitors, compared to rotifers (Brooks

& Dodson, 1965). Moreover, fish were absent, allowing the occurrence and dominance of medium- and large-bodied species (Iglesias et al., 2011) such as the microcrustacean species previously mentioned. In the absence of fish predation on medium- and large-bodied zooplankton species, rotifers are, in turn, suppressed or even excluded by large-bodied microcrustaceans through competition for the same food resources, in this case phytoplankton, as larger organisms feed more efficiently (Gilbert, 1988; Kirk, 1991; Baranyi et al., 2002). The decrease in large-sized zooplankton abundance and biomass was related to an increase in fish density, in the shallow lakes of the same floodplain (Bonecker et al., 2011). We agree with the importance of predation by the fish, to the zooplankton community structure. However, the objective of our study was to evaluate the effects of nutrient enrichment (bottom up) without the influence of top down effect.

SP was supported by a few dominant species with certain ecologically selected traits. This mechanism, known as overyielding (Loreau, 2000), is important for ecosystem stability. Dominant species, acting as controllers of ecosystem functions, may be resistant to the reduction of ecosystem functions in a short-term, being able to maintain ecosystem processes even with the non-random loss of rare species due to anthropogenic effects (Loreau, 2000; Smith & Knapp, 2003). However, a simultaneous loss of complementary interactions among rare species may contribute, in the long-term, to a higher species loss and cause the loss of ecosystem functions (Smith & Knapp, 2003).

Studies indicate zooplankton species loss and consequent reduction in species richness with nutrient enrichment (Dodson et al., 2000; Jeppesen et al., 2000; Declerck et al, 2007; Sorf et al., 2015); however, this was not found in our study. Although the magnitude of nutrient enrichment used in our experiment was not high, compared to the above-mentioned studies, richness was significantly different over time, with higher values at the beginning of the experiment. This event occurred because of an expressive increase in zooplankton density at the beginning of the experiment, mainly at N2 and N3 concentrations, which enhanced the probability of species being sampled. Moreover, nutrient enrichment increased dominance, with higher values at the middle of the experiment (Nov/21 and Nov/26), likely because of the copepods. As previously mentioned, this group has a competitive

advantage due to efficient consumption of the resources, in the absence of fish (Iglesias et al., 2011), domination of the environment, and supporting secondary productivity. Therefore, nutrients affected the secondary production by influencing the relationships of dominance and competition among zooplankton species. From the beginning until the middle of the experiment (15–20 days after the beginning of the experiment), treatments showed a similarity in zooplankton composition, which was not observed on the other days (corroborated by PERMANOVA results), which may be related to the dominance. This is because dominance increased until the middle of our study, as well as secondary productivity of copepods, which when reduced, also led to a reduction in dominance, as other species, such as some cladocerans, could increase their SP (Figs. 1, 2).

An increase in zooplankton biomass with the increase in nutrient concentrations was expected (Camargo & Alonso, 2006; Sorf et al., 2015) because of the effects of this process on the phytoplankton community and consequent increase in the resources available to the zooplankton (Pan et al., 2014). However, small-bodied organisms such as rotifers, can be favored (Gannon & Stemberger, 1978) because they are opportunists with high fertility rates, direct development, parthenogenetic reproduction, and rapid growth rates (Pourriot et al., 1997), besides, the presence of fish in the ecosystems reduces the density of large-bodied zooplankton, such as copepods (Sorf et al., 2015). In our study, the absence of fish competitively favored large-bodied zooplankton and resulted in a high dominance of these organisms at the end of the experiment. This occurs in environments with low predation pressure by fish, as otherwise medium- and large-bodied zooplankton (copepods and large cladocerans) are consumed, and only small-bodied organisms remain and naturally dominate the environments (Brooks & Dodson, 1965; Iglesias et al., 2011).

Therefore, nutrient enrichment intensified the biotic process of competition due to exploitation by zooplankton populations, favoring an increase in the dominance of large microcrustaceans. Moreover, it transformed the relationship between NPP and SP from positive to negative, indicating the presence of inedible algae, which interfered in the transfer of energy to the zooplankton community, and that the energy was not limiting to the populations that responded independently to the increase in NPP. This reflects the initial effects of a moderate eutrophication. Furthermore, at a larger temporal scale and at higher nutrient concentrations, higher magnitude effects are expected, which may de-structure the whole community, resulting in the loss of ecosystem processes (Donohue et al., 2009; Smith & Schindler, 2009; Braghin et al., 2015).

References

Abrams, P. A., 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology 76: 2019–2027.

Agostinho, A. A., L. C. Gomes & F. M. Pelicice, 2007. Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil. Eduem, Maringá, PR.

Agostinho, A. A., F. M. Pelicice & L. C. Gomes, 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Brazilian Journal of Biology 68: 1119–1132.

Anderson, M. J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46.

Anderson, D. M., P. M. Glibert & J. M. Burkholder, 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuaries 25: 704–726.

Azevedo, F., J. D. Dias, L. Braghin & C. C. Bonecker, 2012. Length–weight regressions of the microcrustacean species from a tropical floodplain. Acta Limnologica Brasiliensia 24: 1–11.

Baranyi, C., T. Hein, C. Holarek, S. Keckeis & F. Schiemer, 2002. Zooplankton biomass and community structure in a Danube River floodplain system effects of hydrology. Freshwater Biology 47: 473–482.

Bonecker, C. C., F. Azevedo & N. R. Simões, 2011. Zooplankton body-size structure and biomass in tropical floodplain lakes: relationship with planktivorous fishes. Acta Limnologica Brasiliensia 23(3): 217–228.

Braghin, L., B. Figueiredo, T. Meurer, T. S. Michelan, N. R. Simões & C. C. Bonecker, 2015. Zooplankton diversity in a dammed river basin is maintained by preserved tributaries in a tropical floodplain. Aquatic Ecology 49(2): 175–187.

Brooks, J. L. & S. I. Dodson, 1965. Predation, body size, and composition of plankton. Science 150: 28–35.

Camargo, J. A. & A. Alonso, 2006. Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: a global assessment. Environment International 32: 831–849.

Chapin III, F. S., B. H. Walker, R. J. Hobbs, D. U. Hopper, J. H. Lawton, O. E. Sala & D. Tilman, 1997. Biotic control over the functioning of ecosystems. Science 277: 500–504.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecology 18(1): 117–143

Cottingham, K. L., S. Glaholt & A. C. Brown, 2004. Zooplankton community structure affects how phytoplankton respond to nutrient pulses. Ecology 85: 158–171.

Declerck, S., A. Vanderstukken, A. Pals, K. Muylaert & L. de Meester, 2007. Plankton biodiversity along a gradient of productivity and its mediation by macrophytes. Ecology 88: 2199–2210.

Dodson, S. I., S. E. Arnott & K. L. Cottingham, 2000. The relationship in lake communities between primary productivity and species richness. Ecology 81: 2662–2679.

Donohue, I., A. L. Jackson, M. T. Pusch & K. Irvine, 2009. Nutrient enrichment homogenizes lake benthic assemblages. Ecology 90: 3470–3477.

Dumont, H. J., I. Van De Velde & S. Dumont, 1975. Dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from plankton, periphyton and benthos of continental waters. Oecologia 1: 75–97.

Edmondson, W. T. & G. C. Winberg, 1971. A manual on methods for the assessment of secondary productivity in freshwaters. Blackwell Scientific Publications, Oxford and Edinburgh.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. Shurin & J. E. Smith, 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10: 1135–1142.

Espíndola, E. L. G., 1994. Dinâmica da associação congenérica das espécies de Notodiaptomus spp. na represa de Barra Bonita, São Paulo. Thesis, Federal University of São Carlos, São Paulo, SP.

Gannon, J. E. & R. S. Stemberger, 1978. Zooplankton (especially crustaceans and rotifers) as indicators of water quality. Transactions of the American Microscopical Society 97: 16–35.

Gilbert, J., 1988. Suppression of rotifer populations by Daphnia: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. Limnology and Oceanography 33: 1286–1303.

Gobler, C. J., T. W. Davis, K. J. Coyne & G. L. Boyer, 2007. Interactive influences of nutrient loading, zooplankton grazing, and microcystin synthetase gene expression on cyanobacterial bloom dynamics in a eutrophic New York lake. Harmful Algae 6: 119–133.

Gotelli, N. J. & A. M. Ellison, 2004. A Primer of Ecological Statistics. Sinauer Associates, Massachusetts.

Iglesias, C., N. Mazzeo, M. Meerhoff, G. Lacerot, J. M. Clemente, F. Scasso, C. Kruk, G. Goyenola, J. García-Alonso, S. L. Amsinck, J. C. Paggi, S. J. Paggi & E. Jeppesen, 2011. High predation is of key importance for dominance of small-bodied zooplankton in warm shallow lakes: evidence from lakes, fish exclosures and surface sediments. Hydrobiologia 677: 133–147.

Incorporation, Statsoft, 2007. Statistica. Statsoft Inc, Tulsa.

Jeppesen, E., J. P. Jensen, M. Sondergaard, T. Lauridsen & F. Landkildehus, 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology 45: 201–218.

Kindt, R. & R. Coe, 2005. Tree Diversity Analysis. A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies. World Agroforestry Centre (ICRAF, Nairobi.

Kirk, K. L., 1991. Particles alter competition in grazing plankton: the role of selective feeding. Ecology 72: 915–923.

Lansac-Tôha, F. A., C. C. Bonecker, L. F. Velho, N. R. Simões, J. D. Dias, G. M. Alves & E. M. Takahashi, 2009. Biodiversity of zooplankton communities in the Upper Paraná River floodplain: interannual variation from long-term studies. Brazilian Journal of Biology 69: 539–549.

Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91: 3–17.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman & D. A. Wardle, 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294: 804–808.

Maia-Barbosa, P. M. & R. L. Bozelli, 2005. Length-weight relationships for five Cladoceran species in an Amazonian lake. Brazilian Archives of Biology and Technology 48: 303–308.

Melão, M. G. G., 1999. Desenvolvimento e aspectos reprodutivos dos cladóceros e copépodos de águas continentais brasileiras. In Pompêo, M. L. M. (ed.), Perspectivas na Limnologia do Brasil (chapter 3). Gráfica e Editora União, São Luís, MA.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs & H. Wagner, 2014. vegan: Community Ecology Package. R package version 2.2-0 [available on internet at http://CRAN.R-project.org/package=vegan].

Onandia, G., M. R. Miracle & E. Vicente, 2014. Primary production under hypertrophic conditions and its relationship with bacterial production. Aquatic Ecololy 48: 447–463.

Pan, Y., Y. Zhang & S. Sun, 2014. Phytoplankton–zooplankton dynamics vary with nutrients: a microcosm study with the cyanobacterium Coleofasciculus chthonoplastes and cladoceran Moina micrura. Journal of Plankton Research 36: 1323–1332.

Peláez-Rodrigues, M. & T. Matsumura-Tundisi, 2002. Rotifer production in a shallow artificial lake (Lobo-Broa Reservoir, SP, Brazil). Brazilian Journal of Biology 63: 509–516.

Perhar, G., G. B. Arhonditsis & M. T. Brett, 2013. Modeling zooplankton growth in Lake Washington: a mechanistic approach to physiology in a eutrophication model. Ecological Modelling 258: 101–121.

Pielou, E. C., 1966. The measurement of diversity in different types of biological collection. Journal of Theoretical Biology 13: 131–144.

Pourriot, R., C. Rougier & A. Miquelis, 1997. Origin and development of river zooplankton: example of the Marne. Hydrobiologia 345: 143–148.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rietzler, A. C., 1995. Alimentação, ciclo de vida e análise da coexistência de espécies de na represa de Barra Bonita, São Paulo. Thesis, University of São Paulo, São Paulo, SP.

Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt & D. Firth, D, 2015. MASS: Support Functions and Datasets for Venables and Ripley's MASS Package. R package version 7.3-37 [available on internet at http://cran.r-project.org/web/packages/MASS/index.html].

Roberto, M. C., N. F. Santana & S. M. Thomaz, 2009. Limnology in the Upper Paraná river floodplain: large-scale spatial and temporal patterns, and the influence of reservoirs. Brazilian Journal of Biology 69: 717–725.

Rosenzweig, M. L., 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171: 385–387.

Rothhapt, K. O., 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. Nature 333: 660–662.

Ruttner-Kolisco, A., 1977. Suggestions for biomass calculations of plankton rotifers. Archive für Hydrobiologie Beiheft Ergebnisse Limnologie 8: 71–76.

Santos, R. M., 2010. Estrutura das comunidades fitoplanctônica e zooplanctônica, com ênfase na produção secundária do zooplâncton, e fatores ambientais relacionados nos reservatórios do Baixo Rio Tietê, SP. Thesis, Federal University of São Carlos, São Paulo, SP.

Santos-Wisniewski, M. J. & O. Rocha, 2007. Spatial distribution and secondary production of Copepoda in a tropical reservoir: Barra Bonita, SP, Brazil. Brazilian Journal of Biology 67: 223–233.

Simões, N. R., M. A. M. Colares, F. A. Lansac-Tôha & C. C. Bonecker, 2013. Zooplankton species richness–productivity relationship: confronting monotonic positive and hump-shaped models from a local perspective. Austral Ecology 38: 952–958.

Smith, M. D. & A. K. Knapp, 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters 6: 509–517.

Smith, V. H. & D. W. Schindler, 2009. Eutrophication science: where do we go from here? Trends in Ecology and Evolution 24: 201–207.

Smith, V. H., S. B. Joye & R. W. Howarth, 2006. Eutrophication of freshwater and marine ecosystem. Limnology and Oceanography 51: 351–355.

Sorf, M., T. A. Davidson, S. Brucet, R. F. Menezes, M. Sondergaard, T. L. Lauridsen, F. Landkildehus, L. Liboriussen & E. Jeppesen, 2015. Zooplankton response to climate warming: a mesocosm experiment at contrasting temperatures and nutrient levels. Hydrobiologia 742: 185–203.

Tilman, D., 1977. Resource competition between plankton algae: an experimental and theoretical approach. Ecology 58: 338–348.

Wetzel, R. G. & G. E. Likens, 2000. Limnological Analyses. Springer, Nova York.

Winberg, G. C., G. A. Pechen & E. A. Shusshkina, 1965. Production of planktonic crustaceans in three lakes of different type. Zoologichesky Zhurnal 44: 676–687.