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Productivity–diversity relationships in reservoir phytoplankton communities in the semi-arid region of northeastern Brazil

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The aims of study were to 1) evaluate the productivity–diversity relationships (PDR) in reservoir phytoplankton communities in the semi-arid of northeastern Brazil on the local and regional scales; 2) determine the association between regional dissimilarity in species composition and regional mean productivity; 3) test the potential of productivity as well as physical and chemical factors of the water as descriptors of phytoplankton diversity using generalized linear models. Nutrient availability (total nitrogen and total phosphorus) and phytoplankton biomass were used as measures of productivity, whereas species richness as measure of diversity. Unimodal PDR was found when total phosphorus and biomass were considered as measure of productivity. Regional dissimilarity diminished with regional mean productivity. This finding may be attributed to the effect of eutrophication on diminishing the differences in the composition of species between compartments within each reservoir, leading to a loss of diversity in these ecosystems. Moreover, the analysis of the models demonstrated evidence that PDR may be influenced by environmental factors, such as electrical conductivity, total dissolved solids and pH in reservoirs located in semiarid regions of northeastern Brazil.

1. Introduction

Arid and semiarid regions are characterized by high temperatures and scarce, unpredictable, disproportionally distributed rainfall. Reservoirs in such regions are subject to reductions in water volume during the dry season, which leads to an increase in the concentration of nutrients and a population explosion of algae, with an increase in biomass productivity that contributes to eutrophication (Bouvy et al., 2003; Câmara et al., 2009). High levels of nitrogen and phosphorus and increased phytoplankton biomass in reservoirs located in semiarid regions are related to the dominance of some species and a reduction in the diversity of the community (Bouvy et al., 2000; Chellappa et al., 2009; Moura et al., 2012). Thus, the climatic conditions of a hydrographic basin in which aquatic ecosystems are found constitute a key element to the characterization of the interaction of nutrient availability, biomass production and diversity.

Nutrient availability and phytoplankton biomass are used as measures of productivity in freshwater ecosystems and are strongly related to species diversity (Ptacnik et al., 2008; Cardinale et al., 2009). Mathematic models of productivity–diversity relationships (PDR) offer evidence that the nutrient availability affects species richness, which, in turn, simultaneously affects productivity (Gross and Cardinale, 2007).

Studies on PDR are motivated mainly by the global decline in biodiversity caused by human actions and seek to clarify factors that influence and are affected by diversity to generate knowledge and arguments for the management and preservation of biodiversity (Mittelbach et al., 2001; Korhonen et al., 2011). Moreover, such studies can contribute to the perception of the importance of the productivity potential in freshwater environments to maintain the pool of biodiversity in hydrographic basins located in semiarid regions.

PDR is classified in five forms: positive linear, "hump-shaped" (unimodal), negative linear, U-shaped and with no describable relationship (non-significant patterns) (Whittaker, 2010). Studies

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have found that the form of PDRis positive linear on regional scales and unimodal on local scales when regional dissimilarity in species composition increases with regional mean productivity (Chase and Leibold, 2002; Chase, 2003; Ptacnik et al., 2010). The effect of the dispersion of organisms has been considered in the study of PDR, since the form of PDR has been found to depend on the spatial scale when species dispersion among local communities is minimal (Chase and Ryberg, 2004).

Studies on phytoplankton have demonstrated variations in the form of PDR on the local scale (Gamfeldt and Gamfeldt, 2011; Korhonen et al., 2011), which suggests that environmental factors exert a local influence on these relationships. Another point to consider is the way that PDR can vary with the type of productivity measure adopted. The concentration of nutrients in water (total nitrogen and phosphorus) (Leibold, 1999) and biomass calculated by phytoplankton volume (Corcoran and Boeing, 2012) have been used as potential descriptors of the richness of phytoplankton species. Besides productivity, other physical and chemical environmental factors may be descriptors of biodiversity in aquatic ecosystems and should be considered in the study of PDR (Dodson et al., 2000; Chase and Leibold, 2002; Korhonen et al., 2011). The spatial variability in these environmental factors reflects heterogeneity, which has been associated with the unimodal form of PDR in aquatic ecosystems (Waide et al., 1999).

Reservoirs are known for longitudinal heterogeneity characterized by the presence of compartments: lotic near tributaries, lentic near the dam and transitional between these sites (Dantas et al., 2008; Costa and Dantas, 2011). In the semi-arid region of northeastern Brazil, these ecosystems are subjected to prolonged droughts, high temperatures, an evaporation rate that exceeds the annual precipitation and the lowers of the water level, which contributes to the process of eutrophication, thereby determines the dynamics of phytoplankton communities (Chellappa et al., 2008a). High water temperature, pH, electrical conductivity and turbidity are characteristics of reservoirs in this region and exert an influence on biomass production and the abundance of phytoplankton species (Câmara et al., 2009; Moura et al., 2012). Thus, the study of PDR can contribute to the clarification of the mechanisms by which nutrient availability and biomass act as determinant forces of phytoplankton diversity in the semi-arid region, with the physical and chemical conditions of these ecosystems considered important aspects of these mechanisms.

The present study was carried out at reservoirs in the semi-arid region of northeastern Brazil with the following aims: 1) analyze the form of the relationships between phytoplankton diversity and both nutrient availability and biomass on the local (compartment) and regional (reservoir) scales; 2) determine the association between regional dissimilarity in species composition and regional mean productivity; and 3) test the potential of productivity as well as physical and chemical factors of water as descriptors of phytoplankton diversity on the two scales.

2. Methods

2.1. Study area

The reservoirs studied are part of the Paraíba River Basin in northeastern Brazil. The basin has an area of 20,071.83 km^2 and is located between latitudes 6°51′31″S and 8°26′21″S and longitudes 34º48′35″W and 37°2′15″W. The areas that compose the entire basin are the sub-basin of the Taperoá River and the upper, middle and lower courses of the Paraíba River itself. According to the Köppen classification, the climate in the region is BSHs' (low latitude, hot, semi-arid). The dry season can last as long as 11 months and mean annual precipitation is 300 mm (Lucena et al., 2011). Table 1 displays the municipalities, rivers of origin, geographic coordinates, maximum capacity and volume of the seven reservoirs selected for the present study.

2.2. Sampling and data collection

In the seven reservoirs (regional scale), 23 sampling sites were established in the pelagic zone, lentic compartment near the dam, lotic compartment near the river/creek, transition compartment between dam and river/creek and littoral compartment (local scale). Sixteen sites were sampled in December 2012 and an additional seven sites were sampled in February 2013. All sampling took place during the dry period of the same seasonal cycle to avoid the temporal changes in environmental conditions.

In the field, the following physical and chemical factors were measured using a multi-purpose meter: water temperature (°C), pH, electrical conductivity (mS cm^{-1}), turbidity (NTU), dissolved oxygen (mg L^{-1}), total dissolved solids (TDS; g L^{-1}) and salinity (‰). Water samples were collected for the determination of nutrient content in the laboratory. Concentrations (μg L^{-1}) of total phosphorus and total nitrogen were obtained based on Standard Methods for the Examination of Water (APHA, AWWA, WPCF, 1992) and Mackereth (1978), respectively.

Phytoplankton was collected at the sub-surface of the water column at the different sampling sites. For estimates of diversity, qualitative samples were obtained from horizontal drags of a plankton net with a 20-μm mesh, stored in 200-mL flasks and preserved in a 3% formalin solution. For estimates of biomass (phytoplankton biovolume), quantitative samples were obtained directly from water using 100-mL plastic flasks with a wide mouth and preserved in Lugol's acetic solution (Dantas et al., 2008).

Phytoplankton diversity was determined based on species richness, with the identification of taxa to the lowest possible hierarchical level using specialized literature. Semi-permanent "n" slides were made for the determination of richness. This procedure was terminated when no new species were found on three consecutive slides. For the determination of phytoplankton biovolume (mm^3 L^{-1}), the density (ind mL^{-1}) of each species was estimated by counts in a sedimentation chamber (Utermöhl, 1958). Density values were multiplied by the mean volume of the cells, considering cell measures of up to 30 individuals of each species whenever possible, based on the methods described by Hillebrand et al. (1999) and Sun and Liu (2003). Biomass (mg L^{-1}) was determined by converting the biovolume and considering a specific gravity of 1 mg mm^{-3} (Wetzel and Linkens, 1991).

2.3. Data treatment

To determine the spatial heterogeneity of the environmental conditions, spatial variability in the environmental factors among the reservoirs was determined using analysis of variance, which is a criterion for datasets.

Three species richness estimates were considered. The first regards the observed values at each sampling site (observed local richness [S]). The second was obtained by extrapolating the observed local richness using the Chao 2 richness estimator (Chao, 1987), based on the presence/absence of taxa on the slides (estimated local richness [Chao2]). The third was obtained considering the total observed richness per reservoir (observed regional richness [S_{reg}]). Richness estimators are useful when studying small organisms with unpredictable distribution of occurrence (Korhonen et al., 2011). The t-test for independent samples was used to determine the statistical significance of the difference between richness estimates(S and Chao2).

Dissimilarity in the species composition of the compartments