Limnology (2024) 25:11–23
https://doi.org/10.1007/s10201-023-00726-5

RESEARCH PAPER

The effects of presence of macrophytes on resource uptake by phytoplankton and zooplankton in a tropical reservoir

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Received: 7 April 2022 / Accepted: 20 June 2023 / Published online: 20 July 2023

Abstract

The understanding of factors affecting resource uptake is important to elucidate community dynamics in aquatic ecosystems. Here, we analyzed nutrient–phytoplankton and phytoplankton–zooplankton interactions in open water areas without macrophytes and in areas with floating and submerged macrophytes in the tropical Cajueiro reservoir, semiarid Brazil. Phytoplankton species were classified into functional groups according to life form and cell size, and zooplankton species were grouped based on functional feeding groups and trophic guilds. Macrophytes favored the effect of nutrients on phytoplankton and the availability of prey for the zooplankton. In open water, unicellular and flagellated phytoplankton were positively influenced by nitrate and inorganic phosphate, while colonial, filamentous, small, medium and large phytoplankton were positively influenced by total phosphorus and nitrite. Colonial phytoplankton, mainly filamentous cyanobacteria, was positively associated with zooplankton in areas with macrophytes, while flagellated phytoplankton was negatively related to zooplankton in open water areas. Our results showed that the presence of floating and submerged macrophytes has different influences on the effect of nutrients on phytoplankton and on the effects of phytoplankton on zooplankton in Cajueiro reservoir, and this should be considered when analyzing these communities' dynamics in similar environments, i.e. tropical reservoirs.

Keywords Colonial cyanobacteria · Filter-feeding zooplankton · Filter-scraper zooplankton · Flagellate · Nitrogen · Phosphorus

Introduction

Trophic interactions have been studied in aquatic ecology for more than five decades (Martin 1970; McQueen et al. 1986; Brett and Goldman 1997; Sommer 2008; Diniz et al. 2019; Severiano et al. 2021). The food chain structure can be strongly regulated by bottom-up effects, that is, when the energy flow in the food chain occurs as a function of available resources (McQueen et al. 1989). In this sense, nutrients are the main factors controlling phytoplankton growth (Carpenter et al. 1985), with nitrogen and phosphorus being the limiting nutrients (Müller and Mitrovic 2015; Paerl et al. 2018; Lewis et al. 2020; Liu et al. 2021).

The effects of nutrients on phytoplankton have been widely demonstrated in several ecosystems (Smith and Lancelot 2004; Jeppesen et al. 2012; Liu et al. 2018). More recently, studies have shown that bottom-up effects are more common in phytoplankton communities than top-down regulation by zooplankton (Li et al. 2020; Frau et al. 2021). For zooplankton, trophic interactions are influenced by functional feeding groups and tropic guilds, species body size, and selectivity and physiological tolerance to ingested toxins (DeMott 1986; Kiørboe et al. 2018; Gomes et al. 2019), and by defense characteristics of the prey (Ger et al. 2014; Lürling 2021). In addition, the strength of bottom-up effects on zooplankton is dependent on the degree of predation pressure by fish as top-down effects (Braun et al. 2021).

Nutrient uptake by phytoplankton is related to the size and structure of organisms, with intermediate-sized

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Handling Editor: Wataru Makino.

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phytoplankton being able to exploit available nutrients more efficiently (Marañón 2015; Mousing et al. 2018). Along with nutrient availability, water turbulences also influence phytoplankton metabolism, since they increase nutrient uptake, especially in larger organisms (Naselli-Flores et al. 2021).

Throughout evolution, phytoplankton developed different and efficient morphological, physiological and behavioral strategies to avoid predation by zooplankton, among which the main morphological strategies are the formation of spines and colonies and the increase in size (Lürling 2021). These strategies can be described as functional traits based on their role in regulating predation by zooplankton (Colina et al. 2016). They are informative in explaining the dynamics and structure of the phytoplankton community and its relationship with environmental factors (Chen et al. 2019; Kruk et al. 2021), such as the climatic, chemical and biological factors of the environment (Reynolds et al. 2002).

In freshwater ecosystems, macrophytes have several effects on nutrient cycling, including a reduction in sediment resuspension through water column stabilization (Nurminen and Horppila 2009). Many of the nutrients taken up by macrophytes return to the environment through the decomposition of plant tissues (Banks and Frost 2017; Xiao et al. 2017), or by the release of nutrients from the reductive sediment through thermal stratification of the water column induced by macrophytes (Vilas et al. 2018), or by fluctuation in water level (Keitel et al. 2016). Although little is known about the effects of macrophytes on the availability of resources for aquatic communities in tropical reservoirs, studies have shown that nutrients released by macrophytes favor phytoplankton growth (Vilas et al. 2018; Wang et al. 2018), and also metaphyton, which consists of large sized algae (e.g. *Oedogonium* sp., *Oscillatoria* sp.) that are associated with the presence of macrophytes (Barrow et al. 2019). In this sense, macrophytes are also important in the interaction between phytoplankton and zooplankton, as they increase the availability of prey for zooplankton (Fischer and Pusch 2001; Kovalenko et al. 2012).

The main question of the present study was: do macrophytes enhance resource uptake by phytoplankton and zooplankton communities? To answer this question, we examined the effects of resource availability on phytoplankton and zooplankton in open water areas without macrophytes and in areas with floating and submerged macrophytes in a tropical reservoir, in semiarid Brazil. For this, we analyzed the potential factors controlling phytoplankton (nutrients) and zooplankton (prey availability) in a field study. We tested the following hypotheses: (i) the interaction between phytoplankton–nutrients and phytoplankton–zooplankton is favored by the presence of macrophytes, by increasing the availability of resources, and (ii) functional groups of phytoplankton and zooplankton respond differently the resource availability in areas with and without the presence of macrophytes.

Materials and methods

Study area and sampling

The study was carried out in Cajueiro reservoir (8°59′21.3″ S and 36°28′19.9″ W), municipality of Garanhuns, state of Pernambuco, Northeastern Brazil (Fig. 1). The regional climate is tropical “As” (Alvares et al. 2013), characterized by dry summers and rainy winters. The dry period is concentrated between September and March, and the rainy period between April and August (APAC 2019). The reservoir is shallow, with an average depth of 5.33 ± 0.88 m, and has multiple uses, such as water supply for the municipality, irrigation, fishing and recreation for the population. The Cajueiro reservoir is eutrophic, and the banks are colonized by extensive banks of floating macrophytes *Nymphoides indica* (L.) Kuntze, *Eichhornia crassipes* (Mart.) Solms, *Salvinia auriculata* Aubl. and *Salvinia oblongifolia* Martius, and banks of submerged macrophytes *Chara* sp., *Egeria densa* (Planch.) Casp. and *Myriophyllum aquaticum* (Vell.) Verdc.

Samples for analysis of abiotic variables, phytoplankton and zooplankton were taken in open water areas (absence of macrophytes, $n = 3$) and in areas with floating macrophyte banks ($n = 3$) and submerged macrophyte banks ($n = 3$), quarterly between November 2018 and August 2019, comprising an annual cycle. The sampling sites were located approximately 400 m equidistant from each other (Fig. 1). Water temperature (°C), dissolved oxygen (mg L^{-1}), pH, electrical conductivity (µS cm^{-1}) and total dissolved solids (mg L^{-1}) were measured using a HANNA multiparameter probe (HI 9829). The Secchi disk was used to estimate the water transparency, in meters, and the light intensity (µmol photons m^{-1} s^{-2}) was measured with a photometer (LI-250A). Reservoir water samples were collected 10 cm below the water surface using graduated buckets with a capacity of 10 L in open water areas and in areas with floating macrophytes, while in areas with submerged macrophytes, water was collected at a depth of 0.86 ± 0.13 m using a van Dorn bottle. The mean depth in the open water sites was 5.33 ± 0.88 m, and 1.06 ± 0.42 m and 0.86 ± 0.12 in the floating and submerged macrophyte banks, respectively.

Water for nutrient analysis was sampled and immediately placed in 300 mL plastic bottles and kept under refrigeration in a Styrofoam box with ice and transported to the laboratory, where samples were frozen until analysis. Samples for phytoplankton counting were taken directly from the water reservoir at the sampling sites and immediately placed in 150 mL amber flasks and fixed with 1% acetic Lugol. For taxonomic analysis of phytoplankton, water was filtered

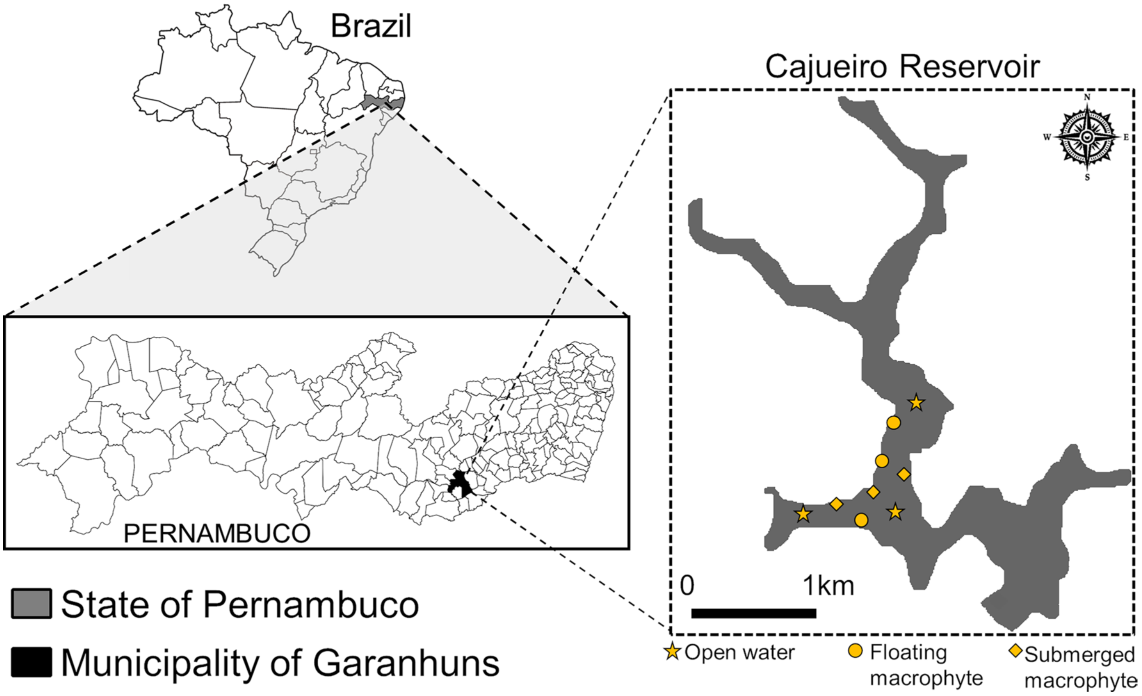

Fig. 1 Location of the Cajueiro reservoir, target of the present study

through a plankton net with 25 µm mesh, placed in 150 mL vials and fixed with 4% formaldehyde. Samples for identification and quantification of zooplankton were collected by filtering 100 L reservoir water from open water areas and areas with floating and submerged macrophytes, following the procedures for collecting water used for phytoplankton analysis, but using a plankton net with 50 µm mesh. Subsequently, samples were placed in 200 mL plastic bottles and fixed with 4% formaldehyde.

Laboratory analysis

The concentration of nutrients (µg L^{-1}), including nitrite (NO_2^-), nitrate (NO_3^-) and ammoniacal nitrogen (NH_4^+) was determined according to Golterman et al. (1978), Mackereth et al. (1978) and Koroleff (1976), respectively. Dissolved inorganic nitrogen (DIN) concentrations were obtained by the sum of concentrations of NO_2^-, NO_3^- and NH_4^+. Orthophosphate (PO_4^{3-}), inorganic phosphate (Pi) and total phosphorus (TP) were quantified according to the A.P.H.A. (2005).

Phytoplankton species were identified under an optical microscope using specific literature (Anagnostidis and Komárek 1988; Komárek and Anagnostidis 1999, 2005; Komárek and Cronberg 2001; Prescott et al. 1982; Krammer and Lange-Bertalot 1991; Popovský and Pfiester 1990; John et al. 2002), and then classified into morphofunctional groups according to life form (unicellular, colonial, filamentous and flagellar) and cell size (small: < 50 µm, medium: 50–100 µm and large: > 100 µm). Phytoplankton density (ind mL^{-1}) was estimated according to Utermöhl (1958) using sedimentation chambers and an inverted microscope (Bioval XDS-1B) at 400 × magnification. Biovolume (mm^3 L^{-1}) was estimated based on the volume of species calculated using geometric models by Hillebrand et al. (1999), and multiplied by the population density for each species. Biovolume (mm^3 L^{-1}) was converted to biomass (mg L^{-1}) according to Wetzel and Likens (2000).

Zooplankton species were identified using specific literature (Koste 1978; Reid 1985; Montú and Goeden 1986; Elmoor-Loureiro 1997; Neumann-Leitão et al. 1989). The density of zooplanktonic species (ind L^{-1}) was calculated by counting the organisms under an optical microscope (Opton TNB 41B) with samples concentrated to 100 mL and counting three sub-samples of 2 mL in a Sedgewick-Rafter chamber. Species-specific biomass of zooplankton (µg DW m^{-3}, where DW is dry weight) was determined through the density and the average length and body weight of the taxa according to the regression equations of Ruttner-Kolisko (1977) for rotifers, and of Dumont et al. (1975) for copepods and cladocerans. Zooplankton species were grouped based on functional feeding groups and trophic guilds: rotifers as microphagous (Obertegger et al. 2011), cladocerans as filter-feeders and filter-scrapers (Barnett et al. 2007), adult Calanoida copepods as herbivorous (Frau et al. 2019) and Copepoda nauplii as microphagous. Only groups that can feed on phytoplankton (herbivorous or omnivorous zooplankton) were considered.

Data analysis

Potential differences in phytoplankton and zooplankton biomass and nutrient concentrations between sampling sites (open waters, with floating macrophytes and with submerged macrophytes) were tested by an Analysis of Variance (one-way ANOVA) followed by a Tukey's post hoc test. Normality of variance was tested by the Kolmogorov–Smirnov test, and homoscedasticity by the Bartlett test. For heteroscedastic variances, we applied the non-parametric Kruskal-Walllis test, followed by the pairwise Mann–Whitney U-test.

Generalized additive models (GAM) were applied to test the effect of nutrients on phytoplankton and effects of phytoplankton on zooplankton in open waters and in sites with floating and submerged macrophytes. The estimated degree of freedom (e.d.f.) was used to evaluate the smoothing of models, and the fit and significance of the model were evaluated using adjusted R^2 and p values. Dissolved inorganic nitrogen and orthophosphate for phytoplankton, and total phytoplankton biomass for zooplankton, were used as the predictor variable, respectively. Data were log-transformed $(x+1)$ before statistical analysis.

Redundancy Analysis (RDA) was used to check the influence of nutrients on phytoplankton groups and the influence of phytoplankton groups on zooplankton groups. For this, the analysis was applied based on the length of the first axis of the Detrended Correspondence Analysis (DCA) (Legendre et al. 2011). Dependent variables were log transformed and explanatory variables were standardized. Only variables with variance inflation factor below 20 and with a significance of $p<0.05$ were considered in the final RDA models through the Ordistep function.

Analyses were performed using the *vegan* (Oksanen et al. 2013) and *mgcv* (Wood 2004, 2011) package in R software (R Development Core Team 2019) with a significance of $p<0.05$.

Results

Nutrients

The limnological variables found in Cajueiro reservoir in areas without macrophytes and areas with floating and submerged macrophytes throughout the study period are provided in the supplementary material (Table S1). High concentrations of nutrients were found in the floating macrophyte banks; however, no statistical variation was observed between areas without macrophytes and areas with macrophytes for nitrate ($F=0.03$, $p=0.962$), nitrite ($F=0.15$, $p=0.857$), ammoniacal nitrogen ($F=0.52$, $p=0.609$), dissolved inorganic nitrogen ($F=0.52$, $p=0.609$), orthophosphate ($F=1.38$, $p=0.298$), inorganic phosphate ($H=0.47$, $p=0.788$) and total phosphorus ($F=1.92$, $p=0.201$) (Fig. 2).

Biomass of phytoplankton and zooplankton

Eighty-four phytoplankton taxa were identified in Cajueiro reservoir, which were grouped into seven functional groups based on cell size and life form (Table S2). The colonial cyanobacteria *Coelomoron tropicale* P.A.C.Senna, A.C.Peres & Komárek and the filamentous cyanobacteria *Raphidiopsis raciborskii* (Wołoszyńska) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno were the dominant species in the phytoplankton community of the reservoir, representing 30.99% and 10.32% of the total biomass of phytoplankton and constituting the colonial and filamentous groups, respectively. In addition to cyanobacteria, the diatom *Cyclotella meneghiniana* Kützing (9.43%) and dinoflagellate *Ceratium furcoides* (Levander) Langhans (8.55%), belonging to the unicellular and flagellate groups, respectively, were dominant in Cajueiro reservoir. The group of algae with flagella was mainly represented by dinoflagellates and cryptophyceans. Large and medium filamentous species represented 15.20% total biomass of phytoplankton, and were composed of the diazotrophic cyanobacteria *Raphidiopsis* and *Dolichospermum*, and the non-diazotrophic cyanobacteria *Anagnostidinema*, *Oscillatoria*, *Phormidium*, *Planktothrix* and *Pseudanabaena*.

In areas with floating and submerged macrophytes, a significant increase was found for the biomass of unicellular ($H=9.78$, $p=0.007$), colonial ($F=3.37$, $p=0.046$), filamentous ($F=7.34$, $p=0.002$), small ($F=7.63$, $p=0.001$) and large ($F=3.76$, $p=0.034$) functional groups, except for medium-sized ($H=4.54$, $p=0.103$) and flagellated phytoplankton ($F=0.73$, $p=0.489$; Fig. 3a–g). The total phytoplankton biomass differed significantly between the open water areas and sites with floating and submerged macrophytes, with higher biomass found in the submerged macrophyte banks (96.52 ± 65.09 mg L^{-1}, $H=9.86$, $p=0.007$; Fig. 3h).

Fifty zooplankton taxa were identified, in addition to the class Bdelloidea and order Calanoida and Copepoda nauplii. Zooplankton taxa were grouped into four functional feeding groups and trophic guilds (Table S3). The herbivorous-microphagous group had the highest biomass during the study; however, it did not differ significantly between sampling sites ($H=5.57$, $p=0.061$, Fig. 4a). Higher total zooplankton biomass was observed in floating macrophyte banks (183.80 ± 146.70 µg DW m^{-3}) and in submerged macrophyte banks (169.12 ± 218.12 µg DW m^{-3}), significantly differing ($H=9.46$, $p=0.008$) from open water areas

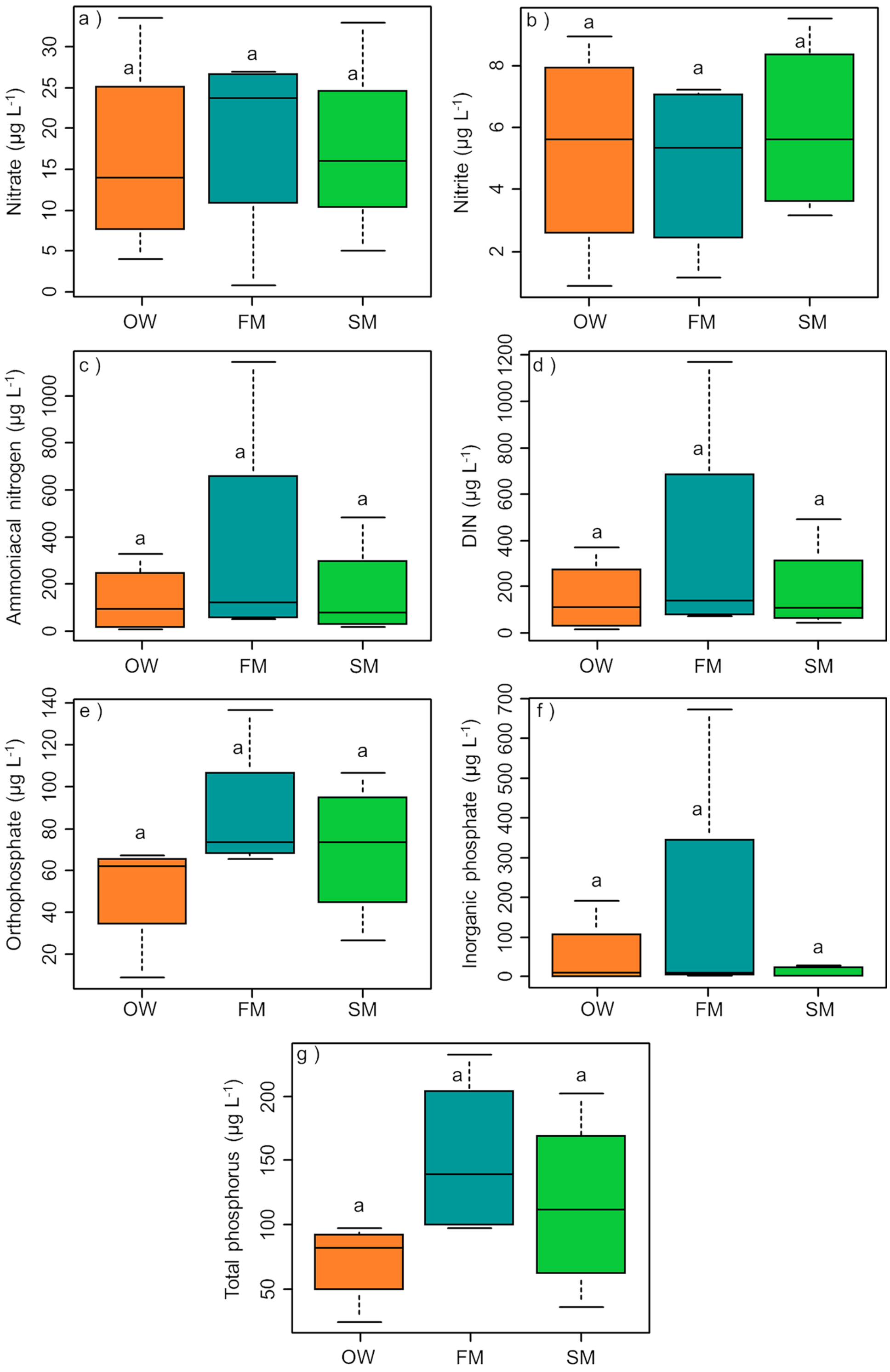

Fig. 2 Variation in concentrations (µg L^{-1}) of nitrate (**a**), nitrite (**b**), ammoniacal nitrogen (**c**), dissolved inorganic nitrogen (DIN, **d**), orthophosphate (**e**), inorganic phosphate (**f**) and total phosphorus (**g**) between open water areas (OW) and areas with floating (FM) and submerged (SM) macrophytes in Cajueiro reservoir, Northeastern Brazil. Lowercase letters represent statistical differences based on the post-hoc test ($p < 0.05$) among sampling sites

(37.88 ± 30.71 µg DW m^{-3}; Fig. 4e). Floating and submerged macrophytes favored the increase in biomass of the filter-scraper functional group ($F = 24.18$, $p < 0.001$), and floating macrophytes favored the increase in filter-feeder biomass ($F = 3.48$, $p = 0.042$; Fig. 4c–d). Microphagous biomass did not differ significantly between sampling sites ($F = 0.58$, $p = 0.565$; Fig. 4b).

Interaction between nutrients–phytoplankton and phytoplankton–zooplankton

Generalized additive models (GAM) showed that total phytoplankton biomass had a marginally significant positive relationship with dissolved inorganic nitrogen in open water areas ($p = 0.054$, Fig. 5a) and a significantly

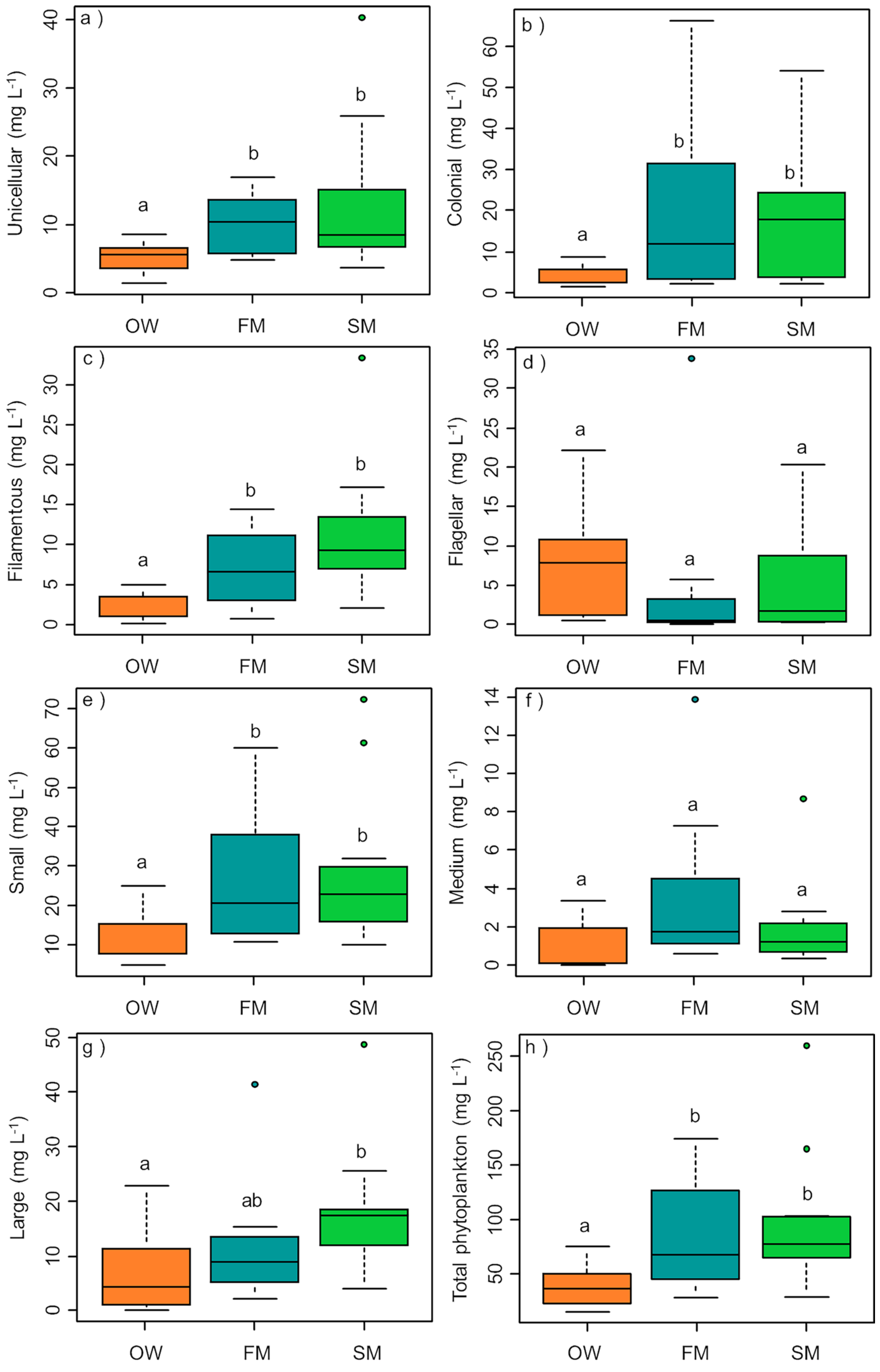

Fig. 3 Variation in concentrations (mg L^{-1}) of unicellular (**a**), colonial (**b**), filamentous (**c**), flagellated (**d**), small (**e**), medium (**f**) and large (**g**) morphofunctional groups of phytoplankton and total phytoplankton biomass (**h**) between open water areas (OW) and areas with floating (FM) and submerged (SM) macrophytes in Cajueiro reservoir, Northeastern Brazil. Lowercase letters represent statistical differences based on the post-hoc test ($p < 0.05$) among sampling sites

negative relationship in sites with floating macrophytes ($p = 0.0003$, Fig. 5b). No significant relationship was observed between dissolved inorganic nitrogen and total phytoplankton biomass in areas with submerged macrophytes ($p = 0.654$, Fig. 5c). A positive relationship was found between orthophosphate and total phytoplankton biomass in open water areas ($p = 0.039$, Fig. 5d) and with submerged macrophytes ($p = 0.022$, Fig. 5f), while in sites with floating macrophytes, no significant relationship was observed ($p = 0.076$, Fig. 5e). Total zooplankton biomass was not significantly related to total phytoplankton biomass (Fig. 5g–i).

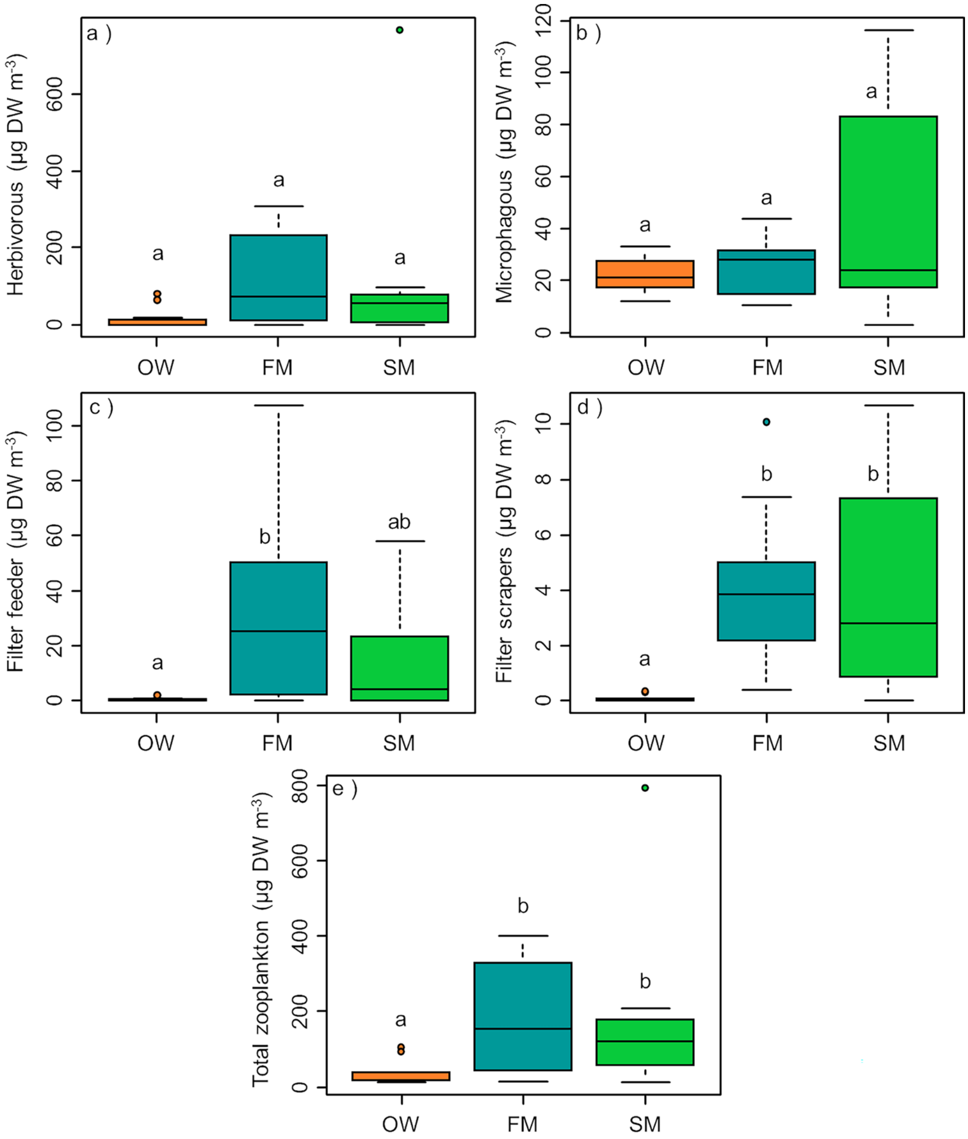

Fig. 4 Variation in concentrations (μg DW m^{-3}) of herbivorous (**a**), microphagous (**b**), filter-feeders (**c**) and filter-scrapers (**d**) functional groups of zooplankton and total zooplankton biomass (**e**) between open water areas (OW) and areas with floating (FM) and submerged (SM) macrophytes in Cajueiro reservoir, Northeastern Brazil. Lowercase letters represent statistical differences based on the post-hoc test ($p < 0.05$) among sampling sites

Redundancy analysis

The RDA model revealed that nutrients explained 59.65% of variation in phytoplankton community compositions ($F = 11.08$, $p = 0.001$). Axis 1 ($F = 24.64$, $p = 0.001$) and axis 2 ($F = 17.62$, $p = 0.001$) were significant for the distribution of explanatory variables, with unicellular phytoplankton influenced by inorganic phosphate (Pi), flagellate phytoplankton by nitrate (NO_3^-), and other groups (colonial, filamentous, small, medium and large) influenced by total phosphorous (TP) and nitrite (NO_2^-). Two groups distinguishing the sites with and without macrophytes were formed on axis 1, with TP and NO_2^- related to functional phytoplankton groups in floating and submerged macrophyte banks and Pi and NO_3^- in sites without macrophytes (Fig. 6a).

For functional feeding groups and trophic guilds of the zooplankton, the RDA indicated that phytoplankton functional groups explained 41.79% of variation in zooplankton community compositions ($F = 11.48$, $p = 0.001$), with only axis 1 ($F = 22.26$, $p = 0.001$) showing the significant distribution of groups. On the axis 1, there was a separation between open water areas and sites with macrophytes, where colonial phytoplankton biomass, positioned to the right of the axis, positively influenced herbivores, filter-feeders and filter-scrapers in floating and submerged macrophyte sites, while flagellate phytoplankton were positively related to sites without macrophytes (Fig. 6b).

Discussion

In the present study, we showed the nutrient-phytoplankton and phytoplankton–zooplankton interactions in areas with and without macrophytes. The unicellular, colonial,

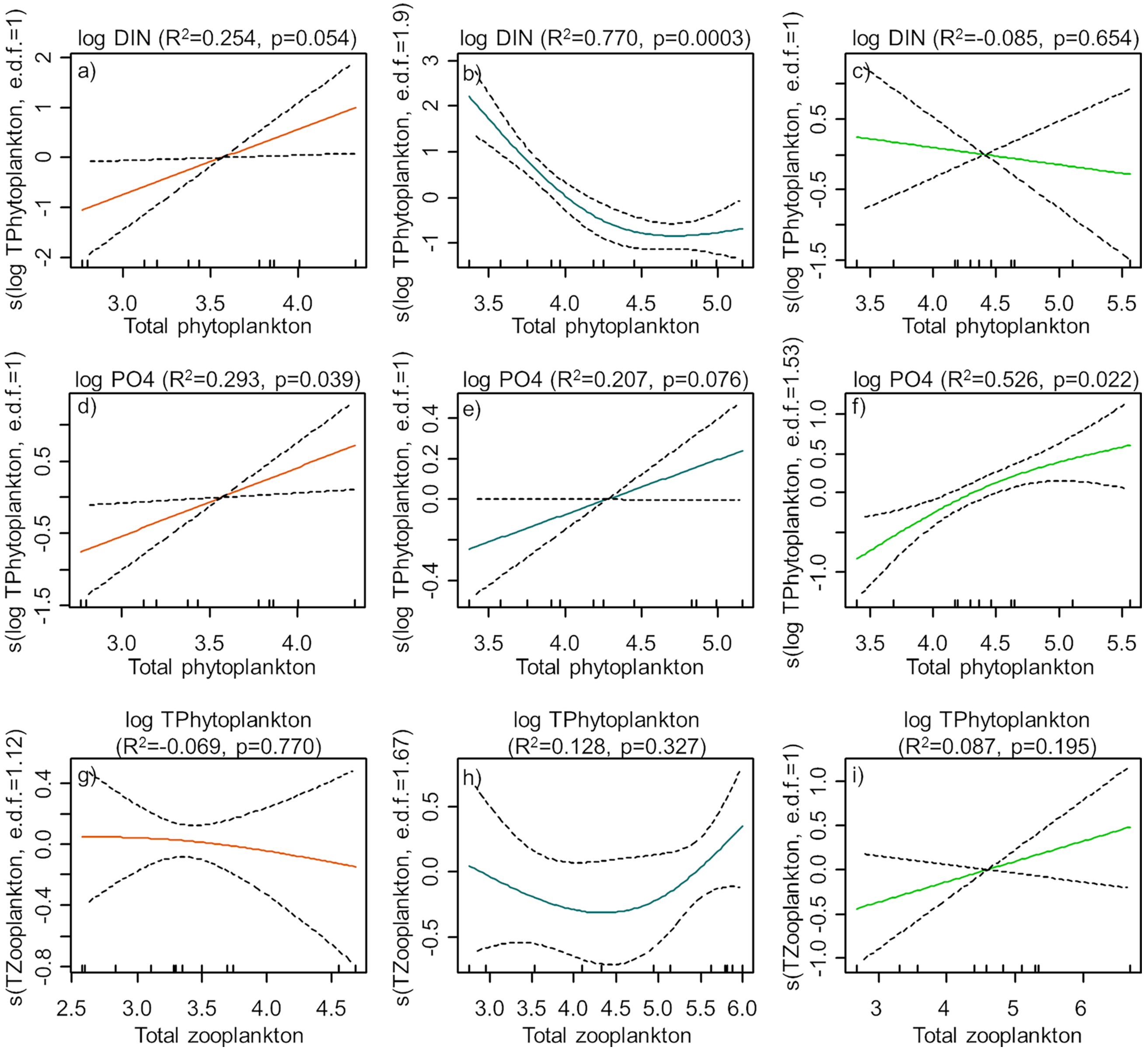

Fig. 5 Generalized additive models (GAM) showing the relationships between nutrients–phytoplankton (**a**– **f**) and phytoplankton–zooplankton (**g**, **h**, **i**) in open water areas (orange line) and areas with floating (blue line) and submerged (green line) macrophytes. The solid line represents the fitted values of the general model. DIN: dissolved inorganic nitrogen, PO_4: orthophosphate, TPhytoplankton: total phytoplankton biomass, TZooplankton: total zooplankton biomass

filamentous, small and partly the large functional phytoplankton groups presented higher values of biomass in floating and submerged macrophyte banks. For zooplankton, only cladocerans (filters and scrapers) presented high biomass in floating and submerged macrophyte banks. Phytoplankton was positively correlated with orthophosphate in sites with submerged macrophytes, and negatively correlated with dissolved inorganic nitrogen in sites with floating macrophytes, while no significant relationship was found between zooplankton and phytoplankton, partially confirming our first hypothesis.

Our results showed that floating and submerged macrophytes promoted changes in the phytoplankton community. Macrophytes are responsible for providing heterogeneous ecological niches that support diverse aquatic communities (Barrow et al. 2019; Stephan et al. 2019). For phytoplankton, macrophytes act as nutrient sources because, through the decomposition of plant tissues, nutrients become bioavailable in water (Wang et al. 2018), in addition to serving as substrate for algal colonization due to structural complexity (Nascimento-Filho et al. 2021). Algarte et al. (2017) showed that both the species richness

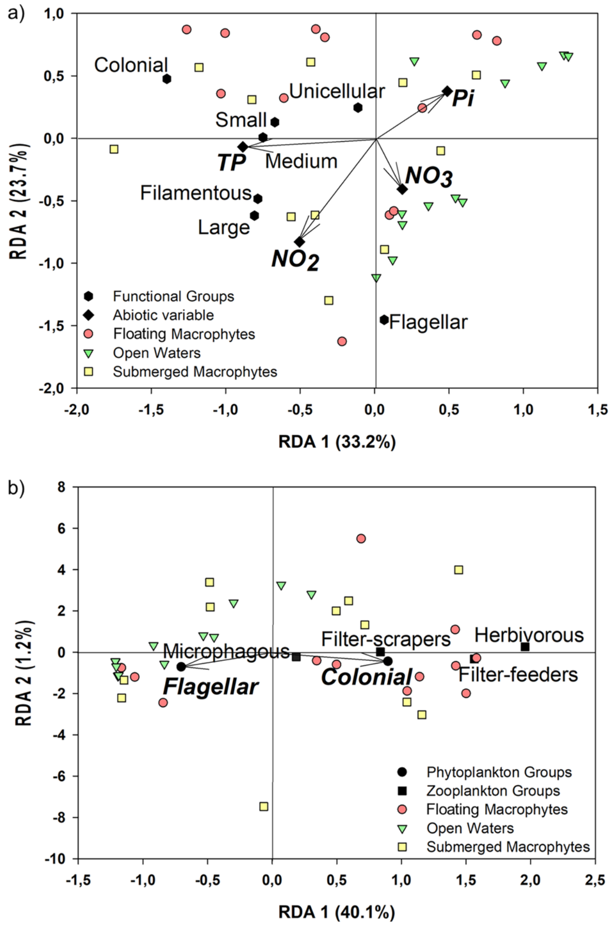

Fig. 6 Redundancy Analysis (RDA) of (**a**) phytoplankton morpho-functional groups and (**b**) zooplankton functional feeding groups and trophic guilds in relation to variables in open water areas and areas with floating and submerged macrophytes. TP: total phosphorus, Pi: inorganic phosphate, NO_2: nitrite, NO_3: nitrate

of small-motile algae and the richness of large species were positively related to the presence of macrophytes, so the presence of macrophyte banks may have facilitated the coexistence of different species of algae.

For zooplankton, macrophytes serve as a refuge against predators (Figueiredo et al. 2018) and a place for colonization and egg laying (Battauz et al. 2017), and they also increase food availability (Rossa and Bonecker 2003; Brito et al. 2020). In this way, different macrophyte species may harbor different zooplankton species (Zeng et al. 2017), and this can have different effects on phytoplankton. In the present study, although floating macrophytes harbored higher biomass of herbivorous filter-feeders and scrapers zooplankton (cladocerans), no negative effect was found on phytoplankton biomass (Fig. 5h). Differently, the negative effect of zooplankton filter-feeders on phytoplankton was evidenced in other studies (Kozak et al. 2015; Gerasimova et al. 2018), and this can be explained by their generalist habit, predominant in several species represented by cladocerans.

Our second hypothesis was partially confirmed, as the RDA analysis showed that unicellular and flagellated phytoplankton were favored by nitrate and inorganic phosphate in open water areas, and nitrite and total phosphorus positively influenced the colonial, filamentous, small, medium and large functional phytoplankton groups in sites with macrophytes. According to Zhang et al. (2020), some macrophyte species can provide suitable substrates for filamentous algal growth. Similar results were observed by Takamura et al. (2003), who showed that phytoplankton species responded differently to the presence of macrophytes, with colonial and filamentous species of medium to large size positively related to lakes with the presence of macrophytes, and flagellated and unicellular species related to both the presence and absence of macrophytes. Our results showed that this relationship can be explained by the effect of nutrients (Fig. 6a). Studies performed in semi-arid regions of Brazil showed that submerged macrophytes play an important role in providing nutrients, especially during the dry season and rewetting, common in these regions due to the reduction in water level (Keitel et al. 2016; Barbosa et al. 2020). Thus, the nutrients available in areas covered by submerged macrophytes have a positive effect on phytoplankton, favoring filamentous, unicellular or colonial species (Monteiro et al. 2021).

During the growth period, macrophytes can accumulate nutrients from water or sediment, and when they decompose, the absorbed phosphorus is returned to the aquatic ecosystem (Wang et al. 2018). The algae attached to these macrophytes absorb 3.4–8.9% phosphorus released by macrophytes (Carignan and Kalff 1982). High phosphorus concentrations favor the development of phytoplankton, especially cyanobacteria (Simić et al. 2017), and non-diazotrophic cyanobacteria due to their inability to fix atmospheric nitrogen. Reservoirs in Northeastern Brazil are susceptible to cyanobacterial blooms (Moura et al. 2018), and eutrophication represents a factor that contributes to the success of these organisms (Amorim and Moura 2021; Macêdo et al. 2021).

In contrast, although no significant difference was observed in the biomass of flagellated species between sampling sites, a positive relationship between flagellated algae and nutrients was observed in the absence of macrophytes (Fig. 6a). This suggests that flagellated algae, predominantly represented by *C. furcoides* in the present study, use resources more efficiently in areas without macrophytes. According to Crossetti et al. (2019), reduction in the relative stability of the water column caused by the absence of macrophytes and the increase in water transparency are decisive for the success of *C. furcoides*. This supports our results, as the flagellated group was related to nitrogen in sites without macrophytes, as shown in the RDA (Fig. 6a).

Colonial phytoplankton was positively related to three functional groups of zooplankton in sites with macrophytes. This result accord with Amorim et al. (2020), which showed a positive correlation between cyanobacteria and zooplankton, such as rotifers and copepod nauplii. This relationship can be explained by ability of zooplankton to coexist with cyanobacteria in eutrophic waters (Amorim et al. 2020), in addition to a poor ability to avoid the ingestion of cyanobacteria (Lürling 2003, 2021; Colina et al. 2016), leading to the exploitation of alternative food sources, such as other algae (Ger et al. 2016). In contrast, a negative relationship was found between flagellated phytoplankton and zooplankton. Herbivorous crustaceans, such as cladocerans and calanoid copepods found in our study, have a feeding preference for medium to large-sized flagellated organisms (Colina et al. 2016; Titocci et al. 2022). Any evidence was found of zooplankton grazing *C. furcoides* (Colina et al. 2016).

Conclusion

This study showed that the macrophytes promoted significant changes in plankton communities, favoring the growth of small and large-sized algae and unicellular, colonial and filamentous species, in addition to increasing the biomass of filter-feeder and filter-scraper zooplankton. Floating and submerged macrophytes favored nutrient-phytoplankton interactions, while phytoplankton–zooplankton interactions occurred both in the presence of submerged macrophytes and in open water sites, partially confirming our first hypothesis. Our second hypothesis was partially confirmed too, as colonial, filamentous, small, medium and large phytoplankton were favored by the presence of macrophytes, and flagellated and colonial phytoplankton, represented by cryptophyceans, *C. furcoides* and colonial cyanobacteria, respectively, significantly influenced zooplankton in sites with macrophytes. Our results highlight the importance of evaluating the effects of floating and submerged macrophytes on the relationship between phytoplankton and zooplanktonic communities in tropical reservoirs.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10201-023-00726-5.

Acknowledgements This work was supported by Fundação de Amparo a Ciência e Tecnologia do Estado de Pernambuco—FACEPE, Brazil (process IBPG-0549-2.03/18) and by Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq, Brazil (process PQ 305829/2019-0).

Author contributions ASD: conceptualization, investigation, data curation, methodology, formal analysis, visualization, writing—original draft preparation, writing—review & editing. WAG: conceptualization, formal analysis, visualization, writing—review & editing. ANM: conceptualization, writing—review & editing, supervision.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author (ariadne_moura@hotmail.com) on reasonable request.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

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