



ECOSYSTEMS

Non-predatory mortality of planktonic microcrustaceans (Cladocera and Copepoda) in neotropical semiarid reservoirs

LEIDIANE P. DINIZ, ELTON J. FRANÇA, CLAUDIA C. BONECKER,
CATARINA R. MARCOLIN & MAURO DE MELO JÚNIOR

Abstract: The accuracy of traditional methods to sample planktonic microcrustaceans depends on two assumptions: that organisms are alive during sampling and that all carcasses can be identified despite their degradation state, but fresh carcasses are not easy to distinguish by traditional methods. Previous studies about mortality have shown that neglecting dead organisms can provide biased ecological information. Thus, our objective was to determine the mortality rate and the proportion of dead microcrustacean in three tropical reservoirs. Sampling was carried out in 12 stations during two periods. The proportion of dead organisms was verified using aniline blue and it varied between 0.6% and 90.6%. The carcass decomposition period varied between 3 to 16 days and microcrustaceans mortality rate varied between 0.005 and 0.314 d⁻¹. Traditional preservation techniques with formalin do not significantly overestimate species abundance. However, these values should not be disregarded, because corrected (disregarding organisms that were dead) and formalin-preserved abundances were correlated with distinct limnological descriptors. Therefore, the traditional formalin preservation technique could provide misleading ecological interpretations. Other studies over larger temporal scales in addition to experiments to evaluate the effects of viruses, parasitism and the toxic effects of cyanobacteria on zooplankton would enlighten mortality rate patterns in freshwater ecosystems.

Key words: Abundance, aniline blue, Caatinga, proportion of dead, zooplankton.

INTRODUCTION

Ecological studies on microcrustaceans and the zooplankton community have been widely performed in the last 40 years (Allan 1976, Bonecker et al. 1996, Folt & Burns 1999). These invertebrates are particularly interesting because they influence the dynamics of other aquatic communities by relationships within the food web (Melão et al. 2005) or by contributing faecal pellets to the particle flux (Shatova et al. 2012). However, most ecological studies do not consider the proportion of dead organisms at the moment samples are taken. Recent studies

have argued that neglecting dead individuals may lead to biased ecological information (Tang et al. 2014, Besiktepe et al. 2015).

Zooplankton mortality is caused by several factors such as senescence, predation, variability in abiotic factors and even parasitism (Dubovskaya 2009, Ersoy et al. 2019). A meta-analysis showed that, apart from predation, these other factors might account for one third of the mortality in copepods (Hirst & Kiørboe 2002). Nevertheless, the cause of death is mostly attributable to predation (Freitas et al. 2007, Serpe et al. 2009). The information on the proportion of dead organisms in aquatic environments

is relevant because it has implications on population dynamics and the energy flow through both pelagic and benthic food webs (Dubovskaya et al. 2003, 2015). Disregarding deceased individuals may lead to biased ecological information (Besiktepe et al. 2015). Even so, studies on the mortality of zooplankton in reservoirs are scarce, and most such studies were performed in Russia (Dubovskaya 1987, Sergeeva et al. 1989, Dubovskaya et al. 2004, Dubovskaya 2005, Tang et al. 2014).

The simplest parameter in plankton studies is species abundance, which is widely used to obtain numerous ecological data such as population growth, biomass and secondary production (Lemke & Benke 2009, Azevedo et al. 2012, Tang & Elliott 2014). However, depending on the decomposition rate, dead and live zooplankton can be identical even many days after their deaths. Therefore, quantifying microcrustacean carcasses in preserved plankton samples can be challenging (Tang et al. 2006a). Consequently, most studies do not distinguish among live and dead individuals (Diniz et al. 2013, Paranhos et al. 2013, Tang et al. 2014, Besiktepe et al. 2015, Diniz & Melo-Júnior 2017); therefore, they assume that all preserved animals were alive during the sampling.

Several methodologies for determining zooplankton mortality have been described (Weikert 1977, Terazaki & Wada 1988), and the most appropriate technique for large numbers of samples is by means of using a biological stain (Crippen & Perrier 1974, Seepersad & Crippen 1978). In 2009, Bickel and colleagues developed a method using aniline blue ($C_{32}H_{27}N_3O_9S_3Na_2$) to distinguish dead (dyed blue) from living (non-dyed) organisms that inhabit continental waters.

Environments under high anthropogenic pressure, with elevated nutrient loads or under eutrophication processes, usually have high proportions of dead zooplankton (Semenova

2010, Bickel et al. 2011, Tang & Elliott 2014). However, some researchers have already found the opposite pattern (more living organisms in eutrophic environments). A possible explanation is that in polluted environments the microbial activity is faster, which accelerates the decomposition of zooplankton, increasing the living-to-dead ratio (Mukhanov & Litvinyuk 2017). On the other hand, in oligotrophic and less-affected environments, the proportion of dead organisms can be high depending on, for instance, the high incidence of solar radiation (Speckmann et al. 2000, Leech et al. 2005, Häder et al. 2007, Al-Aidaros et al. 2014). This pattern is evident in neotropical semiarid regions (Wiegand et al. 2016), where temperatures are high and springs may dry up over the year (Maltchik & Medeiros 2006). It is, therefore, crucial to consider the organisms that are dead at the moment samples are taken to avoid biases in ecological information. To our knowledge, this is the first study that considers the proportion of dead and living microcrustaceans in freshwater ecosystems from the tropical semiarid regions.

The present study investigated the mortality of microcrustaceans (Cladocera and Copepoda) in three, relatively close in location, neotropical reservoirs from the same hydrogeographic basin, but with different usages and environmental statuses. This study allowed us to test two hypotheses: (i) the proportion of dead (%) and the mortality rate (d^{-1}) of microcrustaceans are influenced by physico-chemical characteristics of the reservoirs, and (ii) there is an overestimation of microcrustacean abundances when dead organisms are not considered in the moment of sampling.

MATERIALS AND METHODS

Study area

We sampled three reservoirs in a neotropical semiarid area located in the Pernambuco State, Brazil: Cachoeira II (07° 56' 35" S, 038° 20' 07" W), Saco I (07° 59' 31" S 038° 17' 5" W) and Borborema (07° 58' 41" S, 038° 17' 59" W) (Figure 1). Cachoeira II is an eutrophic reservoir, used for water supply (water-supply reservoir: WSR), Saco I is a hypereutrophic reservoir, used for aquaculture activities (aquaculture-use reservoir: AUR), and Borborema is also a hypereutrophic reservoir used for sewage discharge (sewage-discharge reservoir: SDR) (Diniz & Melo-Júnior 2017).

The reservoirs of the Brazilian semiarid region undergo relevant changes in terms of

limnological descriptors throughout the year (Barbosa et al. 2012). These reservoirs are used for several activities such as recreation, fishing and receiving solid and liquid wastes. In addition, the damming itself is another source of impact. Therefore, there is a great susceptibility to eutrophication in these systems (Bouvy et al. 1999, Eskinazi-Sant'Anna et al. 2013). The climate is dry and hot, and the annual average rainfall is 800 mm. All these characteristics are a source of vulnerability to the biota in these ecosystems (Maltchik & Medeiros 2006), and just a few species, mostly small and opportunistic rotifers (Allan 1976), cladocerans and copepods (Diniz & Melo-Júnior 2017), are adapted to survive in such conditions.

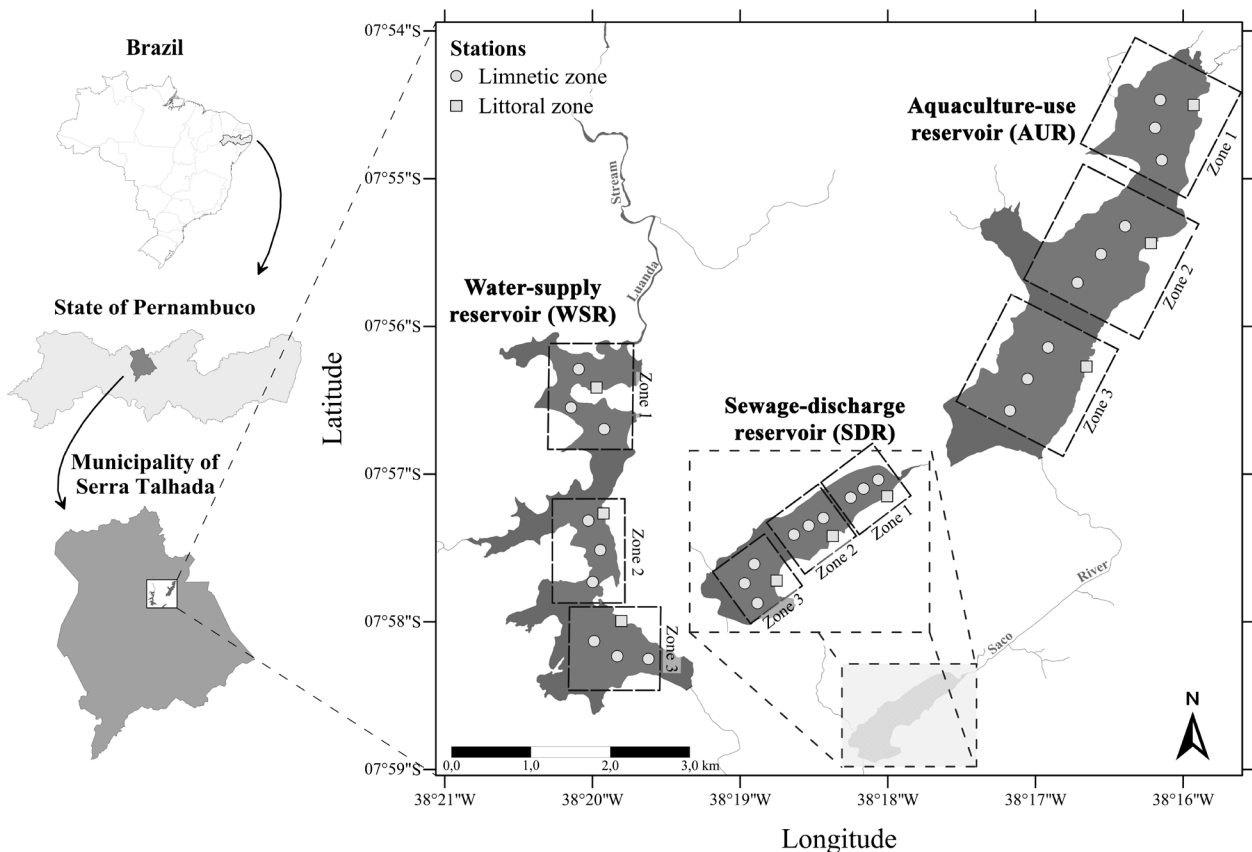


Figure 1. Distribution and location of the sampling stations in three reservoirs in the neotropical semiarid ecosystem (Pernambuco, Brazil): Cachoeira II (water supply reservoir—WSR), Borborema (sewage discharge reservoir—SDR) and Saco I (aquaculture-use reservoir—AUR).

Limnological descriptors

We determined the following limnological descriptors: temperature ($^{\circ}\text{C}$), pH, dissolved oxygen (mg L^{-1}), conductivity (mS cm^{-1}), total solids (g L^{-1}) and turbidity (NTU) using a Horiba U-52 multiparameter probe (Horiba, Japan). Chlorophyll *a* (mg L^{-1}) was determined from subsurface water samples (500 mL), which were filtered through cellulose membrane GF/F filters ($0.45\ \mu\text{m}$ porosity and 47 mm diameter) (Millipore[®], USA). The filters were frozen prior to chlorophyll *a* determination. We followed the methodology described in Chorus & Bartram (1999). Also, subsurface water samples (500 mL) were frozen for nutrient determination: phosphorus ($\mu\text{g L}^{-1}$), nitrite ($\mu\text{g L}^{-1}$), nitrate ($\mu\text{g L}^{-1}$) and ammonia ($\mu\text{g L}^{-1}$); we followed the methods described in Mackereth et al. (1978) for nitrate (NO_3^-) and nitrite (NO_2^-), Strickland & Parsons (1960) for total phosphorus (P) and Koroleff (1976) for ammonia (NH_3).

Sampling design and biological material analysis

We performed two sampling campaigns in each reservoir between August and September 2015 (dry season) and in March 2016 (rainy season), between 09:00 am and 12:30 pm. We selected 12 stations (9 in the limnetic region and 3 in the littoral region) distributed over three zones (river zone: “zone 1”, transition zone: “zone 2” and lacustrine zone: “zone 3”) within each reservoir (Figure 1). These comprised 144 samples, with 72 samples for formalin fixation and 72 samples for aniline blue staining. The stations were chosen at random and covered the entire reservoir.

For each station, we collected 100 L of subsurface water, which were filtered through a 45- μm mesh plankton net. The organisms were preserved with 4% formalin (LABSYNTH Ltda, Brazil). In addition, we filtered 50 L of subsurface water through a 45- μm mesh and concentrated

the sample in an amber bottle to estimate the proportion of dead microcrustaceans from living plankton samples. We added 0.45 M aniline blue (CAAL Ltda, Brazil, 16.7 g of aniline blue and 50.30 mL of deionised water) to these samples, immediately after sampling, to evaluate the mortality ratio (Bickel et al. 2009). The samples were stored in the dark at room temperature. After 15 minutes, the samples were filtered again (pieces of net, 45 μm), placed in Petri dishes, covered with aluminium foil, stored in ice in the field and then transferred to the laboratory, where they were frozen and held for up to two months.

In the laboratory, we took three subsamples (2 mL) of the preserved samples and analysed them using a Sedgwick-Rafter-type chamber (Microscopia Ltda, Brazil). We counted at least 300 individuals per sample. Zooplankton identification was performed under an optical microscope and stereomicroscope (Opton, Brazil), using the relevant literature (e.g. Reid 1985, Matsumura-Tundisi 1986, Elmoor-Loureiro 1997, Perbiche-Neves et al. 2015). Regarding the samples for proportion of dead microcrustacean analysis, each one was slightly acidified with hydrochloric acid (<3%) to differentiate between dead (bright blue colour) and live individuals (natural colour) (Figure 2). We counted at least 100 individuals in each sample to obtain the proportion of dead microcrustaceans. Because of the low number of individuals (< 100) in the SDR, it was not possible to calculate the proportion of dead microcrustaceans in the rainy season, according to Bickel et al. (2009).

In this study, we focused on the microcrustacean species that were dominant in the three reservoirs. These were *Moina micrura* Kurz, 1873, *Ceriodaphnia cornuta* Sars, 1885, *Diaphanosoma spinulosum* Herbst, 1967, *Thermocyclops decipiens* (Kiefer, 1929), *Mesocyclops ellipticus* Kiefer, 1936,

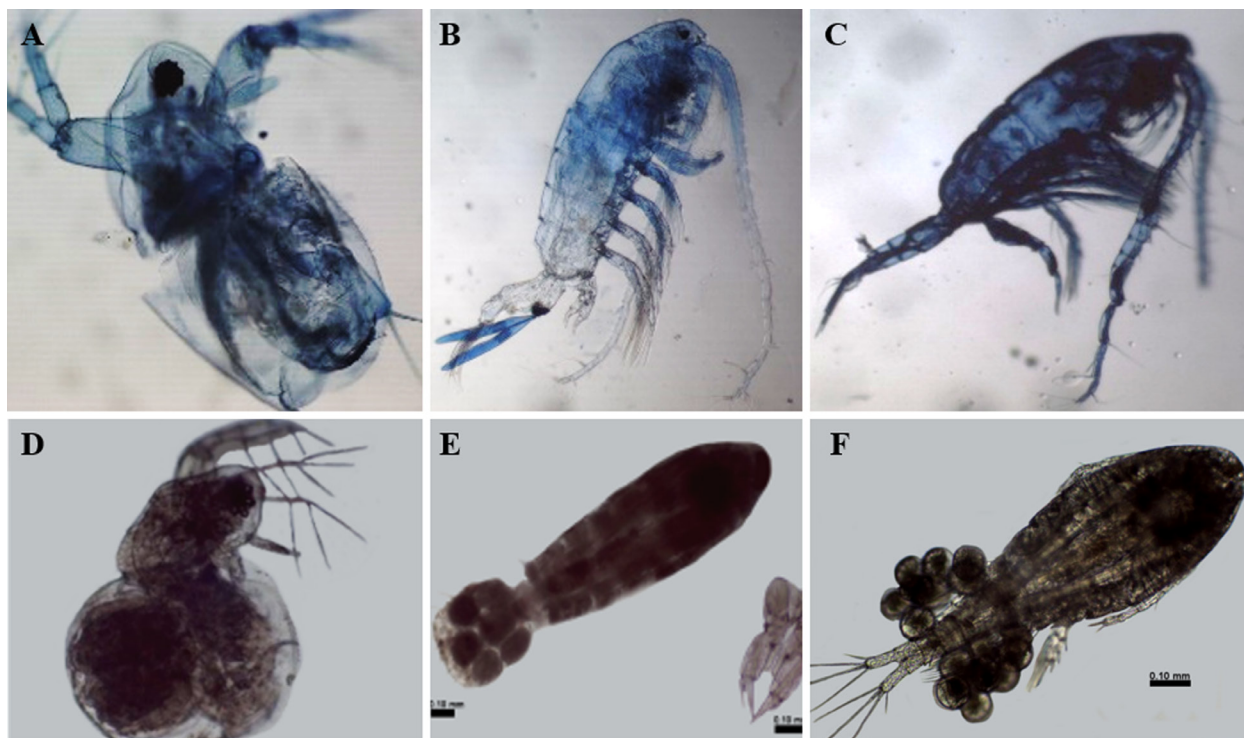


Figure 2. Dead (bright blue colour a–c) and alive (natural colour of the animal d–f) microcrustaceans in three reservoirs in the neotropical semiarid ecosystems (Pernambuco, Brazil). a and d - *Moina micrura* Kurz, 1874; b, c, and e - *Notodiaptomus cearensis* (Wright, 1936); F - *Thermocyclops decipiens* (Kiefer, 1929).

Notodiaptomus iheringi (Wright, 1935) and *N. cearensis* (Wright, 1936).

Microcrustacean carcass decomposition in laboratory

To estimate the mortality ratio from microcrustacean carcasses, we performed laboratory observations to follow the decomposition process. Individuals in the live plankton samples were killed by thermal shock to obtain fresh carcasses. These microcrustaceans were incubated in Petri dishes with filtered water (using a 10- μ m mesh), specific to each of the three reservoirs, at $25 \pm 1.5^\circ\text{C}$ and observed with a stereomicroscope in regular intervals (6h).

Non-predatory mortality rate was estimated as, where D is the proportion of dead microcrustaceans and Y is the time in days to achieve full decomposition of the body at a certain temperature (Tang et al. 2006a).

Data analysis

A principal components analysis (PCA; Pearson 1901; function in R “prcomp”) was applied to describe the variability of limnological descriptors among reservoirs. Only the first axis was used for interpretation, according to the Broken-Stick criterion (Jackson 1993), using Euclidean distance. All variables, except pH, were log-transformed to stabilise the variance. Since the assumptions of normality and homoscedasticity were met, we performed parametric tests. To test for differences between reservoirs in relation to the abiotic variables, one-way ANOVAs were used. If significant effects were detected, post hoc methods (Tukey test) were used to see which reservoir was distinct from the others.

The microcrustacean abundance was reported as (i) formalin-preserved abundance—total abundance obtained from

formalin-preserved samples with no distinction between dead and living organisms and (ii) corrected species abundance—species abundance of the living organisms at the time of collection, excluding the dead ones (methodology using aniline blue). To verify differences between the formalin-preserved abundance and the corrected abundance we applied a *t* test. The data was log-transformed to meet the assumptions of normality and homogeneity of variance. We performed Shapiro-Wilk's test (function in R "shapiro.test") and Levene's test (function in R "leveneTest") to evaluate normality and homogeneity of variance, respectively.

We performed a redundancy analysis (RDA; Legendre & Legendre 1998) to search for relationships between formalin-preserved abundance, corrected species abundance and limnological descriptors. The biotic matrix represented the abundance of microcrustaceans, transformed by Hellinger, since this method is appropriate for matrices that contain many zeros (Legendre & Gallagher 2001). The environmental parameters were log-transformed (except pH). To determine which variables would be selected, we followed the selection process according to Blanchet et al. (2008). This procedure uses permutations to define the variables that should be used in the model. The principal components were tested with ANOVA, and significance was set at $p < 0.05$.

A generalised linear model (GLM) with binomial distribution was applied to test for the effect of limnological descriptors on the proportion of dead microcrustaceans. To remove correlated limnological descriptors, we calculated the variance inflation factor (VIF) and removed variables with $VIF > 3$ (Zuur et al. 2010). The assumptions of the analysis were visually verified, and when necessary, the data was log-transformed (Zuur et al. 2010).

All analyses were performed in the software R 3.0.2 (R Development Core Team 2015), using the following packages: *Vegan* (Oksanen et al. 2018), *ade4* (Chessel et al. 2004), *nlme* (Pinheiro et al. 2019), *nortest* (Juergen & Ligges 2015), *car* (Fox & Weisberg 2019) and *ggplot2* (Wickham 2016).

RESULTS

Limnological descriptors

The reservoir used for water supply (WSR) was different from the hypereutrophic reservoirs (SDR and AUR) ($p < 0.05$) in terms of dissolved oxygen, turbidity, chlorophyll *a* and phosphorus (Table I). Water temperature was always high in all reservoirs ($> 23^{\circ}\text{C}$), and pH varied from neutral to alkaline (7.1–9.2). The water was predominantly well oxygenated, except for a sampling station in the AUR, where it reached a minimum value of 0.4 mg L^{-1} (Table I).

The PCA first canonical axis explained 65.37% of the data and was the only axis selected. The reservoir that is used for sewage discharge (SDR) and the one that is used for aquaculture (AUR) were grouped closer to each other in the PCA, indicating higher homogeneity of the environmental descriptors in the hypereutrophic reservoirs in relation to the eutrophic reservoir used for water supply (WSR). The first axis was positively correlated to chlorophyll *a* and pH. Chlorophyll *a* and pH were more closely associated with SDR and AUR than with the WSR (Figure 3).

Proportion of dead microcrustaceans and carcass decomposition

The proportion of dead microcrustaceans oscillated between low and high values. In the SDR, the proportion of dead animals ranged from 4.4% and 90%. In the AUR, the proportion of dead microcrustaceans varied between 3.2

Table I. Ranges (minimum - maxim), means and standard deviations (SD) of the environmental descriptors in the reservoirs of neotropical semiarid ecosystems (Pernambuco, Brazil).

Environmental descriptors	Water-supply reservoir (WSR)			Sewage-discharge reservoir (SDR)			Aquaculture-use reservoir (AUR)		
	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Water temperature (°C)	25.8-32.1	29.0	1.9	25.5-30.4	28.2	1.5	23.6-33.7	28.6	2.4
pH	7.1-8.8	7.6	0.4	8.1-9.2	8.8	0.2	8.1-8.9	8.5	0.2
Conductivity (mS cm ⁻¹)	-	0.5	-	2.7-4.2	3.4	0.7	3.9-6.6	5.2	1.4
Turbidity (NTU)	20.2-358.0	127.9	128.0	151.0-259.0	202.4	42.2	124.0-246.0	170.5	34.4
Dissolved oxygen (mg L ⁻¹)	5.0-10.8	7.3	1.6	4.1-17.7	12.4	3.5	0.4-17.3	11.5	3.5
Oxygen saturation (%)	66.1-146.6	95.0	20.6	92.1-248.7	157.4	52.9	6.1-236.1	151.7	48.8
Total solids (g/L ⁻¹)	-	0.3	-	1.7-2.7	2.1	0.4	0.8-4.2	3.3	0.9
Chlorophyll <i>a</i> (mg L ⁻¹)	7.4-540.6	61.5	125.8	118.5-1096.0	563.8	318.9	133.3-681.2	439.2	174.3
Phosphor P (µg L ⁻¹)	95.3-273.0	157.5	72.4	327-1158.8	725.3	421.3	278.1-685	478.1	196.9
Ammonia NH ₃ (µg L ⁻¹)	5.1-185.3	55.8	65.9	26.6-347.4	97.9	123.8	17.1-923.1	373.2	398.7
Nitrite NO ₂ ⁻ (µg L ⁻¹)	1.2-25.5	11.6	9.1	2.1-34.2	10.1	12.4	1.2-5.4	3.2	1.4
Nitrate NO ₃ ⁻ (µg L ⁻¹)	12.0-310.8	117.2	128.5	5-21.4	9.9	6.2	4.4-6.7	6.6	1.7

and 57.4%, whereas in the WSR it varied between 0.6 and 67.9% (Figure 4).

The proportion of dead microcrustaceans varied between species. The highest proportion of dead was found for *Moina micrura* (49.4%), whereas *Diaphanosoma spinulosum* had the lowest proportion (0.6%). Cyclopoida and Calanoida adult copepods had a proportion of dead < 40%, whereas copepod nauplii had a proportion of dead of 50.5%. Formalin-preserved abundances did not significantly differ in relation to the corrected abundances (*t* test; *p* > 0.05).

The experiments to determine carcass decomposition did show differences among zooplankton groups (Table II). The necessary time to completely decompose the carcasses was lower for nauplii and the family Daphniidae. Carcasses from the family Chydoridae took the longest to completely decompose. The other groups completely decomposed in less than 10 days (Table II).

The mortality rates of microcrustaceans, considering all reservoirs, was 0.122 d⁻¹. In addition, the non-predatory mortality rate also differed among zooplankton groups. The highest

rate was found for nauplii (0.314 d^{-1}), whereas the lowest rate was found for Cyclopoida copepods (0.005 d^{-1}). The other groups had mortality rates $< 0.05 \text{ d}^{-1}$ (Table II).

Relationship between community attributes and limnological descriptors

We could not detect an influence of the limnological descriptors neither on the proportion of dead microcrustaceans nor on the mortality rates ($p > 0.05$, GLM with binomial distribution). The corrected and the formalin-preserved species abundances were associated with the same variables in the model: conductivity, total solids and phosphorus. However, the chlorophyll *a* was only selected in the formalin-preserved abundance (traditional formalin studies).

The power of the RDA axis was 92% for the formalin-preserved abundance approach; 60% of the variance was explained by the first axis. For the corrected approach (disregarding dead organisms), the power of the axis was slightly

higher (96%), with 59% of the variance explained by the first axis (Figure 5).

DISCUSSION

Our study showed that, even though the proportion of dead microcrustaceans may reach high values the formalin-preserved abundances did not significantly differ from the corrected abundances. Therefore, traditional preservation techniques with formalin do not overestimate species abundance in tropical reservoirs. Nevertheless, these values should not be disregarded, because the corrected and the formalin-preserved abundances were correlated with distinct limnological descriptors. This shows that some environmental variables may be neglected or erroneously associated when formalin-preserved abundances are used. The proportion of dead microcrustaceans and the mortality rate were not related to any of the limnological descriptors of the reservoirs. This indicates that the mortality values in tropical reservoirs may be related to other factors,

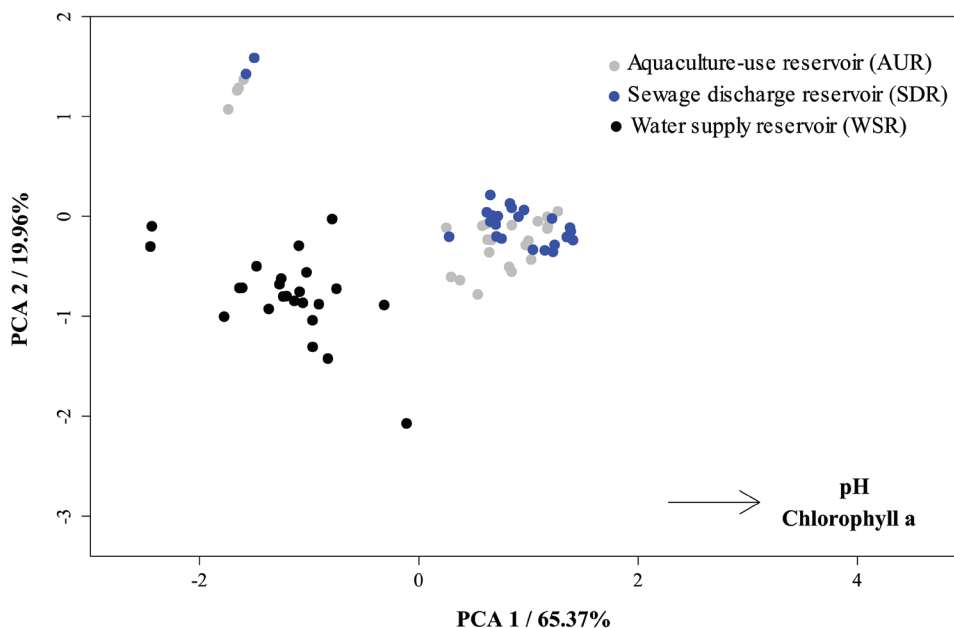


Figure 3. First two canonical axes of the PCA for three reservoirs in the neotropical semi-arid ecosystem (Pernambuco, Brazil). The arrow indicates the variables that most positively influenced axis 1 (chlorophyll *a* and pH). Only scores of the first axis were interpreted, according to the Broken-Stick selection criteria.

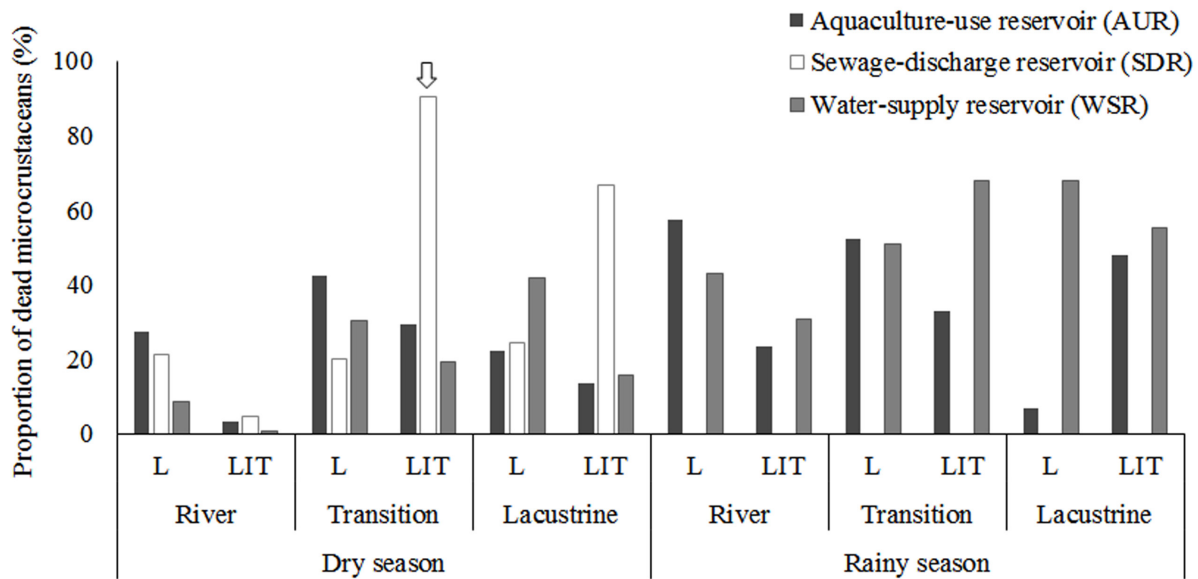


Figure 4. Percentages of microcrustacean mortality in three reservoirs in the neotropical semiarid ecosystems (Pernambuco, Brazil). Because of the reduced number of individuals (< 100 ind.) in the sewage discharge reservoir (SDR, white bars), it was not possible to calculate the proportion of dead microcrustaceans in the rainy season. L–Limnetic, LIT–Littoral. The arrow indicates the highest proportion of dead organisms recorded.

such as parasitism, viruses, toxic effects of cyanobacteria and algal blooms, for example (Comps et al. 1991, Gladyshev et al. 2003, Bickel et al. 2011, Tang et al. 2014, Dubovskaya et al. 2015).

This is the first study in the Neotropical region in continental aquatic environments to consider the proportion of dead microcrustaceans and their mortality rates. All previous mortality studies on zooplankton inhabiting reservoirs using the blue aniline method, were performed in Russia (Dubovskaya 1987, Sergeeva et al. 1989, Dubovskaya et al. 2004, Dubovskaya 2005). The low number of studies could be related to a common opinion among researchers that all animals in the water column are alive during the sampling. According to Elliott & Tang (2011), neglecting such information could result in unrealistic ecological data, and our study supports their argument. Other studies have highlighted the importance of considering dead

organisms. Semenova (2011) found that dead microcrustaceans reached 26% in abundance and 49% in biomass in a lake close to the Baltic Sea under high anthropogenic influence. This reduction in abundance and biomass values should not be ignored in ecological studies, as it may lead to errors, such as overestimating carcass-mediated nutrient and carbon fluxes (Tang et al. 2014).

An important issue is whether dead organisms actually correspond to real carcasses or whether they are dying from the sampling process. It is still unknown how the handling of samples may increase zooplankton mortality (Daase et al. 2014). Bickel et al. (2011) determined that marine copepods may die because of the boat engine turbulence. To avoid mortality caused by handling stress, our samples were taken slowly and by means of filtering a lower volume in relation to the samples collected for formalin preservation, minimising the possible

Table II. Results of laboratory experiments to determine the non-predatory mortality rate of planktonic microcrustaceans in three reservoirs in neotropical semiarid ecosystems (Pernambuco, Brazil).

	Number of individuals	Temperature (°C)	Total decomposition (days)	Mortality rate (d⁻¹)
CLADOCERA				
Daphniidae	5	25 °C	6.0	0.047
Chydoridae	55	25 °C	16.0	0.000
Macrothricidae	29	25 °C	10.0	0.000
COPEPODA				
Nauplii	71	25 °C	3.0	0.314
Calanoida	53	25 °C	9.7	0.035
Cyclopoida	66	25 °C	9.3	0.005

consequences of sampling artefacts. Therefore, we believe that death by sampling stress is negligible in this study.

In our study, the hypothesis of abundance overestimation when dead organisms are not considered was rejected. This shows that if we had considered only the traditional formalin methodology, we would not have overestimated the abundance of zooplankton available for grazing, for example. Even so, the high proportion of dead microcrustaceans found in our study suggests the importance of not neglecting dead zooplankton at the time of collection in aquatic ecological studies. This is because non-predatory mortality affects not only zooplankton population dynamics, but also microbial and benthic food networks (Dubovskaya et al. 2015). There are still few studies in the literature that considered the non-predatory mortality of microcrustaceans worldwide (Giesecke et al. 2017, Krautz et al. 2017). This number is even lower for freshwater ecosystems (Tang et al. 2014). This shows the need for further studies

to improve our comprehension of the mortality patterns for freshwater zooplankton, especially in tropical semiarid areas.

We also found the highest mortality proportion (%) and mortality rates (d⁻¹) in the reservoir that is used for sewage discharge. The higher ratios for microcrustacean mortality are usually associated with polluted areas or ecosystems under high anthropogenic pressure (Semenova 2010, Bickel et al. 2011, Tang et al. 2014). The proportion of dead individuals was also high in the reservoir used for aquaculture. Intensified aquaculture activities may cause a series of negative effects, including the deterioration of water quality and ecological damages for the entire aquatic biota (Zhou et al. 2011, Arruda et al. 2017).

In nature, organisms live in constant trade-offs between surviving, growing and reproducing (Litchman et al. 2013). In our study, the mortality rate was higher for nauplii. Overall, high mortality rates for young stages of copepods are to be expected. The life cycle of copepods is longer

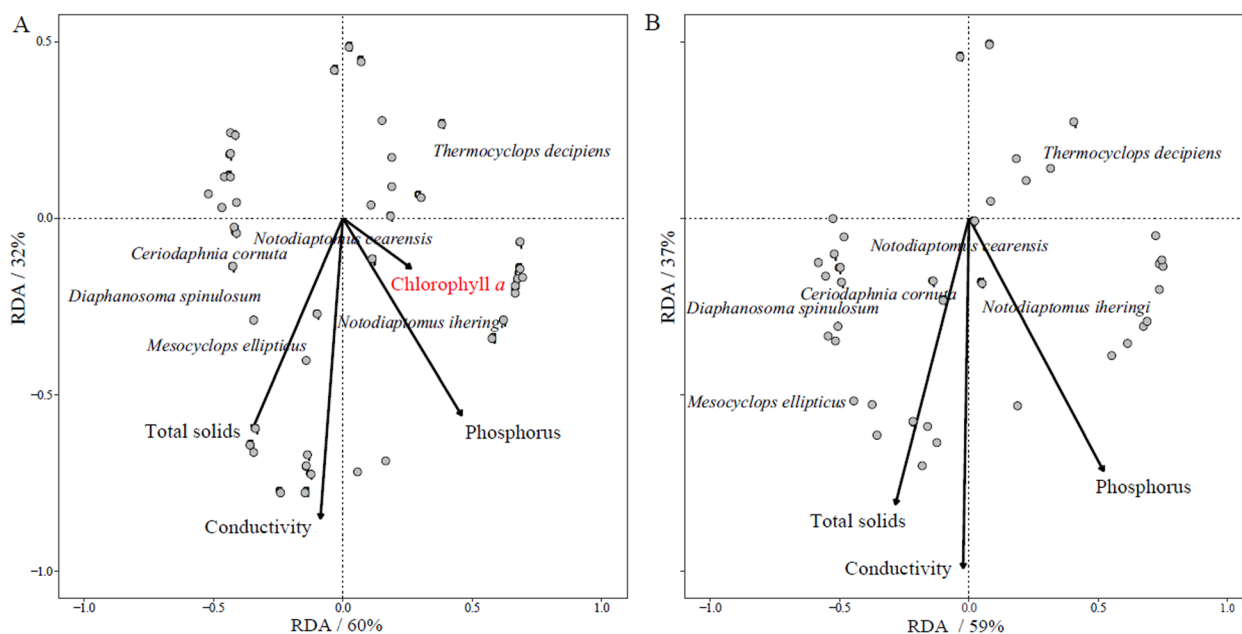


Figure 5. Redundancy Analysis (RDA) of microcrustaceans (Cladocera and Copepoda) and environmental descriptors that were significant in the analysis considering formalin-preserved abundance (a) and corrected abundance values (b) in three reservoirs in neotropical semiarid ecosystems (Pernambuco, Brazil). In red, we highlight the variable that was selected only in the formalin-preserved abundance (traditional studies of formaldehyde). The arrows indicate the influence vectors of each explanatory variable.

compared to other zooplankton groups and may have higher mortality rates before reaching adulthood (Santos et al. 2013). Indeed, the high production of young stages is considered an adaptive strategy to compensate for high mortality rates before reaching adulthood (Espíndola et al. 2000). When the environment suffers constant impacts, as in the case of the reservoirs of this study, a higher mortality of the younger stages is to be expected. Elliott & Tang (2011b), for example, observed a 30% non-predatory mortality for naupliar stages of copepods. In addition, McCauley et al. (2017) observed mortality of all larval forms and higher mortality for small-sized copepods when studying the negative impact of marine seismic survey air gun operations. Furthermore, Futuyama (2002) argues that organisms usually invest energy for their own body development in stressful situations, such as in the presence of predators. This sort of behaviour avoids

wasting resources on an offspring with little or no chance of survival. On the other hand, large-sized zooplankton are better competitors when resources become limiting. This is because they can survive even at lower levels of food and may feed on a wider size range of particles (Gliwicz 1969, Bonecker et al. 2011).

Individuals from the Chydoridae family were the last to have their carcasses decomposed. This could be related to their peculiar features such as being phytophile, with a robust and thick carapace (Fryer 1995, Sousa & Elmoor-Loureiro 2008). On the other hand, family Daphniidae, a typically planktonic family, with finer and delicate carapace, was the first to reach total decomposition. Both carcass decomposition and microcrustacean mortality rates had high variability, and there are virtually no studies that have been performed in similar ecological systems. Zooplankton carcasses are “hot spots” of pelagic microorganism

activity (Tang et al. 2006b, Elliott et al. 2010). Therefore, providing a comprehensive picture on the decomposition of carcasses is crucial for calculating remineralisation rates by the bacterial community and understanding ecosystem dynamics (Kolmakova et al. 2019).

The proportions of dead microcrustaceans and the mortality rates were not related to any of the limnological descriptors in these neotropical semiarid reservoirs. Although other studies found similar results (Besiktepe et al. 2015), there are other variables that could be causing mortality. Predation has a major impact on zooplankton (Ersoy et al. 2019), but for ponds and reservoirs the decline of organisms in the environment is mostly related to non-predatory mortality, leaving carcasses intact for hours or several days (Gries & Güde 1999, Dubovskaya et al. 2003).

Although Tang et al. (2006a) found that temperature is a variable that affects mortality rate, we found no relationship between temperature and the decomposition or mortality rates of planktonic microcrustaceans. In general, resident tropical semiarid species are already adapted to high temperatures (Barbosa et al. 2012), which does not mean that these species can handle temperature increases. Although we did not find a relationship with temperature, it is known that increases in this variable (such as from climate change) could promote changes in the patterns of zooplanktonic organisms and impact energy transfer and nutrient flow along aquatic food webs (Meerhoff et al. 2007, Jeppesen et al. 2014, Tang et al. 2014). Temperature rises may favour a few zooplankton species, promoting increases in abundance (Hall & Burns 2002, Mantovano et al. 2019), but may also affect individual metabolisms, increasing energy expenditure (Regaudie-de-Gioux & Duarte 2012), which could indirectly affect the mortality rate by affecting the individual fitness.

Considering the importance of determine mortality rates, particularly with such a simple and easily applied method (Tang et al. 2006a, Capua & Mazzocchi 2017), we argue that future studies should include this approach to improve the understanding of global patterns in non-predatory mortality, as has already been pointed out by Tang et al. (2014). Therefore, other studies about non-predatory mortality on microcrustaceans in broader temporal and spatial scales must be developed to provide a more accurate estimate of the influence that non-predatory mortality on ecological indexes, particularly in continental aquatic ecosystems.

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LEIDIANE P. DINIZ^{1,3}

<https://orcid.org/0000-0002-7516-6879>

ELTON J. FRANÇA²

<https://orcid.org/0000-0002-6719-4757>

CLAUDIA C. BONECKER³

<https://orcid.org/0000-0003-4338-9012>

CATARINA R. MARCOLIN⁴

<https://orcid.org/0000-0003-3701-3772>

MAURO DE MELO JÚNIOR¹

<https://orcid.org/0000-0002-7963-1205>

¹Universidade Federal Rural de Pernambuco (UFRPE), Departamento de Biologia, Laboratório de Ecologia do Plâncton (LEPLANC), Rua Dom Manoel de Medeiros, s/n, Dois Irmãos, 52171-900 Recife, PE, Brazil

²Universidade Federal Rural de Pernambuco (UFRPE), Unidade Acadêmica de Serra Talhada (UAST), Laboratório de Ecologia e Sistemática de Peixes, Avenida Gregório Ferraz Nogueira, s/n, José Tomé de Souza Ramos, 56909-535 Serra Talhada, PE, Brazil

³Universidade Estadual de Maringá (UEM), Laboratório Zooplâncton, Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura (Nupélia), Av. Colombo, 5790, 87.020-900 Maringá, PR, Brazil

⁴Universidade Federal do Sul da Bahia (UFSB), Centro de Formação em Ciências Ambientais, Campus Sosígenes Costa, Rodovia Porto Seguro - Eunápolis-BA, BR-367, km 10, 45810-000 Porto Seguro, BA, Brazil

Correspondence to: **Leidiane P. Diniz**

E-mail: leidianeediniz@gmail.com

Author contributions

Leidiane Pereira Diniz and Mauro de Melo Júnior - conceived of the presented idea, collected the data, designed the data analysis, and wrote the paper. Elton José França - collected the data and wrote the paper. Claudia Costa Bonecker - designed the data analysis and wrote the paper. Catarina da Rocha Marcolin - designed the data analysis and wrote the paper.

