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Natural history of *Notodiaptomus amazonicus* (Wright, 1935) (Copepoda, Calanoida, Diaptomidae) in a protected urban area lake in Amazonia

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Abstract: The main goal of this work was to characterize the population structure of the copepod *Notodiaptomus amazonicus* present in an urban lake (Lake of Americanos) in a preserved area in Roraima's lavrado, Amazonia. This lake is the only remaining lake from a system of lakes that characterized the lavrado where the city of Boa Vista is located today, in the State of Roraima. Samples were collected six times during drought season in this region (October to March), covering three lake microhabitats: (i) margin with grasses and Cyperaceae, (ii) limnetic portion and (iii) margin without vegetation. Three guiding questions were addressed in this study, all related to the proportions of ontogenetic phases of copepods - adults (males and females), copepodites (juvenile) and nauplii (larvae) - present in the microhabitats. The results indicated three general patterns: i) when the ontogenetic phases were compared within and between the microhabitats, the copepodite and adult densities were higher than those of nauplii, ii) the densities of representative individuals in these ontogenetic phases suffered reductions as the water level fell in the lake, and iii) females with eggs spread themselves homogeneously among the microhabitats when the lake was at its maximum water level and were heterogeneously distributed when the levels dropped.

Keywords: Amazonia´s lake, copepods, population study, population structure.

Resumo. História natural de *Notodiaptomus amazonicus* (Wright, 1935) *(Copepoda, Calanoida, Diaptomidae)* em lago de área urbana protegida no lavrado de Roraima. O objetivo geral deste trabalho foi caracterizar a estrutura populacional do copépode *Notodiaptomus amazonicus* presente em um lago urbano (lago dos Americanos) de área preservada no lavrado de Roraima, Amazônia. Este lago é o único remanescente de um sistema de lagos que caracterizava a área do lavrado onde hoje situa-se a cidade de Boa Vista, no Estado de Roraima. As amostragens foram feitas em seis coletas durante a estiagem na região, abrangendo três microhabitats do lago: (i) margem com vegetação de gramíneas e ciperáceas, (ii) porção limnética e (iii) margem sem vegetação. Foram três perguntas norteadoras do estudo, todas relacionadas às proporções das fases ontogenéticas dos copépodes – adultos (machos e fêmeas), copepoditos (jovens) e náuplius (larvas) presentes nos microhabitats. Os resultados indicaram três situações gerais: i) quando comparadas entre si as fases ontogenéticas, dentro e entre os microhabitat, as densidades de copepoditos e adultos prevaleceram sobre os náuplius, ii) as densidades de indivíduos representantes destas fases ontogenéticas sofreram reduções conforme diminuía o nível de água do lago, iii) fêmeas com ovos se distribuem

homogeneamente entre os microhabitat quando o lago esteve com o nível máximo de água e heterogeneamente distribuídas quando baixam os níveis.

Palavras-Chaves: Lago da Amazônia, copépodes, estudo populacional, estrutura populacional.

Introduction

Copepods are microinvertebrates belonging to the class Copepoda (Dussart and Defaye, 1995) and subphylum Crustacea and are representative of the group of organisms know as zooplankton. They have relevant ecological importance in the environments in which they live, occupying an intermediary position as a "link" between producers and consumers in the trophic chain. Their elevated sensitivity and quick response to changes in the aquatic environment cause constant changes in the structure and dynamics of their populations, influencing the system equilibrium as a whole (Hardy, 1980; Carvalho, 1984; Dussart and Defaye, 1995; Ibanez *et al.*, 2004).

Studies regarding zooplankton and Amazon copepod ecology were first conducted by Braun (1952) and Marlier (1967) resulting in huge advances in limnology for this region. The first investigations regarding population dynamics and density were documented by Brandorff (1977; 1978), contributing to the knowledge of not only the biology of these organisms but also regarding Amazonian ecosystems in general. Other studies on the zooplanktonic fauna have been conducted in the Amazon (Melack and Fisher, 1983; Carvalho, 1983, 1984; Robertson and Hardy, 1984; Hardy, 1980), filling knowledge gaps and being fundamental for the understanding of the natural history of these organisms.

Natural history can be understood as a term that defines the study of the structure and function of a certain aspect of nature, including the ecological aspects of population structure (Pianka, 1994). In the Amazon, several works have investigated the ecological parameters involved in specific features of the natural history of Copepoda, such as their population structure (Waichman *et al.*, 2002; Melo *et al.*, 2006), density (Hardy, 1980), and reproductive aspects (Brandorff and Andrade, 1978; Santos-Silva, 1991), among others.

Such works provide fundamental information allowing us to make inferences about ecosystem structure and operation. Some Amazon regions lack zooplanktonic studies, possibly as a result of poor logistics for research, particularly for copepods, for example, on the edge of the Hiléia morphoclimatic domain (Ab'Saber, 2002) and in the states of Roraima, Acre and Amapá. To the north, toward Venezuela, there are several reports on zooplankton specifically addressing copepods, for example, Infante (1980), Dussart (1984), Twombly (1994) and Ibañez *et al.* (2004).

These are good studies from ecological and geographically distinct regions that can serve as a guide for works in these areas on the edge of the Amazonian domain. However, there is a need for more firm references about what occurs with the zooplankton from reasonably near regions containing other ecosystems, for example, the lakes region in the surroundings of Manaus and the lavrado's lakes in Roraima; there is much information for the former (Brandorff, 1977; Brandorff, 1978; Brandorff and Andrade, 1978; Junk, 1980; Hardy, 1980; Carvalho, 1983; Melack, 1983; Carvalho, 1984; Waichman *et al.*, 2002; Junk and Wantzen, 2004; Robertson and Darwich, 2008; Alves *et al.*, 2013) but almost none for the latter.

It was with this perspective that the present study was conceived. The study of a lake in Roraima's lavrado, a region characteristically composed of lakes, can generate information that supplemental with information from other studies, can provide elements allowing us to understand the tropical ecosystem structure with more accuracy and to interpret the distribution patterns, species composition and zooplanktonic population structure in the Amazon and its many environments. Particularly for copepods little is still known from a limnological point of view regarding Roraima's lavrado, on the north edge of the Amazonian morphoclimatic domain.

Notodiaptomus amazonicus (Wright, 1935) was the only calanoid species present in the environment studied during the collections performed as tests for the development of this study, and during its accomplishment, in this way it was the organism selected for this study. This species is widely distributed in South America, occurring from Venezuela to Argentina (Santos-Silva *et al.*, 2013).

Therefore, the primary goal of this study was to characterize the population structure of the calanoid copepod *N. amazonicus* (Wright, 1935) present in an urban lake in the city of Boa Vista of Roraima's lavrado with the secondary objectives to

investigating the dynamics and proportions of life phases of this organism, sexual ratio, female reproductive aspects, and the influence of variation in the environmental water level on the proportions of this organism's life stages.

Based on several previous studies in the Amazon (Brandorff, 1977; Brandorff, 1978; Brandorff and Andrade, 1978; Hardy, 1980 Carvalho, 1983; Melack, 1983; Carvalho, 1984; Waichman et al., 2002; Alves et al., 2013) we hypothesized that the proportion of males, females, juveniles and larvae of *N. amazonicus* are homogeneous throughout the lake.

Materials and Methods

The Lake of Americanos is situated in the Lavrado region within an urban area protected by a municipal park in Boa Vista, Roraima's capital (approximately 2° 50'N, 60° 40'W), being the only remnant of a group of lakes characteristic of the area that were destroyed in the process of urban expansion (Fig. 1).

The lake has a maximum depth of 1.16 meters in its center, and was recorded as being totally full in December of 2014. The total area was 65.000 m² (6.5 ha) in this full phase of the lake. The lake largest width is 251.33 meters by 296.81 meters, the outline is regular and approximately circular, and there is an elevated density of macrophytes distributed in zonal form along part of its margin. During the low waters (drought) period (September-May), the water level is reduced to less than 1/3 of its total capacity, showing a soil with abundant mud and the presence of few live organisms (Poerschke, 2011). It is a lake with low nutrient content and is defined as oligotrophic (Poerschke, 2011).

Microhabitat and environmental phases: The samplings of *N. amazonicus* were performed during 6 visits (samples) distributed in a total of 30 days, during december of 2014 to January of 2015, which constitutes the drought period in this region (Barbosa, 1997). Three microhabitats in the lake were previously defined: i) margin with vegetation, ii) limnetic portion and iii) margin without vegetation (Fig. 2). These microhabitats were categorized according to the natural environment to create the treatments for the statistical analyses and to evaluate the population behavior in these three heterogeneous microenvironments within the lake.

This heterogeneity results in an independence problem among the samples, where the microhabitats constitute the samples and the observations (replicates) were the collection dates. Below, in the question presentation, samples and observations will be again emphasized.

Phase 1: Maximum water level during the study period - high water level, area of about 65.000 m², maximum depth of 1.16 meters and a minimum of 0.41 meters. This period corresponds to the 1st and 2nd samples.

Phase 2: Water level reduced in relation to the first phase, period characterized as one of transition between the high water level and the low water level in the lake - intermediary**,** area of about 34.440 m², maximum depth of 1.113 meters and minimum of 0.39 meters. This period corresponds to the 3rd and 4th samples.

Figure 1. Study area (aerial picture illustrating the region of the lake) - Lake of Americanos, Boa Vista, Roraima, Amazon. Source: Metric Landscape Laboratory, Geography Department, Federal University of Roraima.

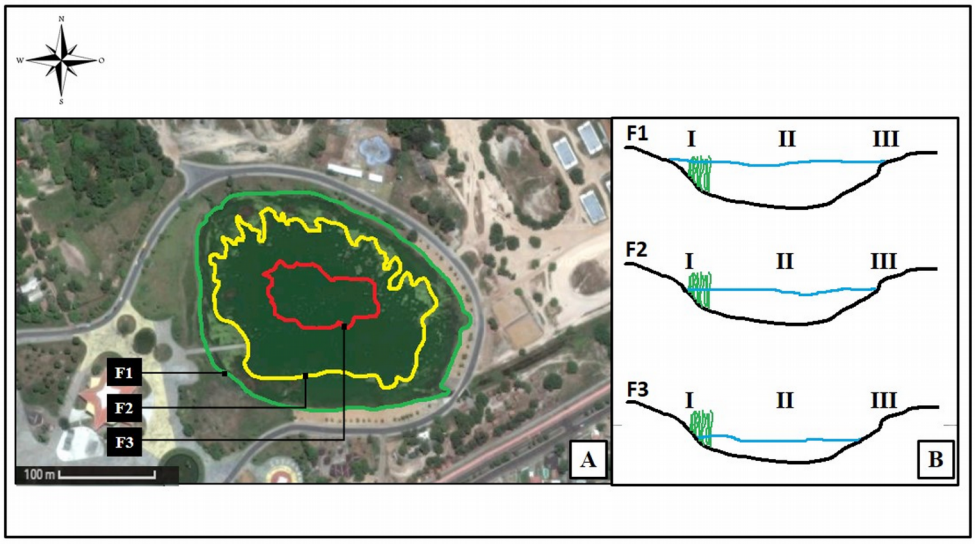

Figure 2. A. Lake of Americanos – area delimitation: Phase 1 - full lake (green line); phase 2 - lake in intermediary period between low water level and high-water level (yellow line); and phase 3 - dry lake (red line). B. Profile of the hydric level phases: F1 - full lake, F2 - lake in intermediary phase, F3 - dry lake and microhabitats: (I) margin with vegetation, (II) limnetic zone and (III) opposite margin without vegetation.

Phase 3: Critical water level in relation to phases 1 and 2, period of smaller area and depth, with an area of about 13.670 m² and maximum and minimum depths of 0.43 and 0.27 meters, respectively - drought. This period corresponds to the 5th and 6th samples.

Species zooplankton of the study: N. amazonicus (Wright, 1935) was the species on which this study was carried out. This is a zooplankton species of the family Diaptomidae, order Calanoida, whose typical locality is Arari lake, situated in the island of Marajó, Pará (Santos-Silva *et al.*, 2011, 2013) and represents one of the twenty-four true species of the genus *Notodiaptomus* occurring in Brazil, the most representative taxonomic genus of the diaptomids of the Neotropical region (Santos-Silva *et al.*, 2013). Individuals of this species reaches about 1580 µm in size. The adult male can be recognized through segment 13 of the right antigen, where the presence of a modified arrow can be observed constituting a spiniform process with rounded apex. The females have the fifth pair of legs with the outer arrow of the base reaching half of the first segment of the exopod, although the endopod is unisected without discontinuity in the cuticle or suture (Santos-Silva *et al.*, 2013).

Zooplankton sampling: Sampling was conducted at 5-day intervals, in a time frame between 17:00 and 18:00 hours, local time, period of marked reduction of sunlight and temperature, with greater activity of the organisms, besides favoring the logistic aspects of this study. For the attainment of the quantitative observations (counts of individuals for the analysis of proportions), a 12-liter Schindler/Patalas collector (© Wildlife Supply Company®, Yulee, Florida-USA) was employed at 4 randomly defined points in each microhabitat, for a total of 48 liters of water filtered through a plankton net with a mesh aperture of 50 µm coupled to the collector. The 4 samples in each microhabitat were pooled as a method to ensure the representativeness and robustness of the samples since the microhabitats were considered homogeneous, and the 4 points were considered as a single sample to avoid the risk of statistical pseudoreplication (Zar, 1994).

A plankton net with a mesh aperture of 68 µm coupled to a PVC collector of 150 ml was utilized for the qualitative observations (presence/absence of species) by performing free horizontal drags. Each sample was concentrated, fixed in 4% formalin, conditioned in a 100 ml polyethylene vial and labeled with the date.

In the laboratory, the material was identified and quantified using a Zeiss stereoscopic microscope with an objective lens of 40× and ocular lens of 1× and a Nikon optic microscope with lenses of 4-100× to screen and score each ontogenetic phase: nauplius, copepodite, and adult, as well as the number of eggs in the females. Santos-Silva *et al.* (2013) and Dussart and Defaye (1995) were used as references for the identification of phases.

Taxonomic identifications were performed in the Plankton Laboratory at the National Institute of Amazon Research (INPA), the material is thoused at the scientific collection of Crustacea – registered under the number INPA 2297.

For the fish catches, successive collections (from center to margin) were carried out for approximately 30 minutes each (Vanzolini and Papavero, 1967). Two manual trawls, 3.5 x 1.7 m and 5 mm mesh size, were used. All the specimens were immediately fixed in 5% formalin, stored in 70% alcohol and taken to the Laboratory of Ichthyology of the Federal University of Roraima (UFRR) for identification. *Data analysis:* Data analysis attempted to answer the general question: How is the copepod population of a Roraima urban lake structured? There were three specific questions, each proceeded in the following sequence: for each of the specific questions, the inquiries pertaining to the whole lake were addressed, followed by analysis regarding each microhabitat individually and among the microhabitats, always with respect to (i) the proportions of individuals in each ontogenetic phase, (ii) the proportion of males and females and (iii) the density of females with eggs. The first question was: **(P1)** how is the population of *N. amazonicus* structured in relation to the proportion of nauplii, copepodites and adult individuals in the lake? The second question was: **(P2)** How is the population structured in relation to the proportion of males and females in the lake? And the third question was? **(P3)** What is the density of females with eggs in the copepod population of the lake during the study period considering the three phases of the lake? Each questioning presented a corresponding hypothesis for homogeneity among and among the proportions analyzed.

The non-parametric chi-square test was used for proportions (Zar, 1994; Vanzolini, 1993) using the variables and categories treated through the model of the analysis of double-entry contingency tables for nominal scales (Vanzolini, 1993). Each question was evaluated using chi-squared tests under the null hypothesis of homogeneity among the proportions analyzed.

For the analysis of the effects of variation in the area and depth of the environment (phases 1, 2 and 3) on fecundity, the fecundity index provided by Santos-Silva (1991) was adopted: Fec = X. A / B. Where "**X**" is the average number of eggs per female ovate, "**A**" is the total number of females with eggs and "**B**" is the total number of adult females (ovate females + females without eggs). The average number of eggs per female was obtained by scoring 10 females with eggs from each microhabitat considered in this study, for a total of 30 analyzed females with eggs in each microhabitat and a total of 90 females carrying eggs in the entire Lake of Americanos.

Stomach contents were analyzed using the Hynes method (1950) and examined under a Zeiss dissecting microscope with a 40x objective lens and a 1x eye lens.

Results

Population characterization - structure and proportions: *N. amazonicus* (Wright, 1935) was the only calanoid copepod species found in Lake of Americanos during the period studied. A total of 16694 specimens were collected (22.43 individuals/liters), with copepodites (juvenile stage) being the most represented in the population composition (34.28 individuals/liters), followed by the adult form (28.89 individuals/liters) and the larval form, the nauplius (4.14 individuals/liters). In microhabitat I (vegetation present) were verified 14.19 individuals/liters, in microhabitat II (the limnetic zone) 29.71 individuals/liters and in microhabitat III (the margin free of vegetation) 22.68 individuals/liters. The initial hypothesis regarding homogeneity (1:1:1) among the life stages of this species was rejected ($\chi^2_{0.05,1}$ = 5695.3906, p<0,05), with copepodites, adults and nauplii occurring at a ratio of 8:7:1, respectively ($\chi^2_{0.05,1}$ = 1.5765, p>0.05).

The statistical analysis for the comparison among the microhabitats indicated a ratio of 4:3:2 corresponding to microhabitats II, III and I, respectively ($\chi^2_{0.05,1}$ = 1.05718, p>0.05), showing that *N. amazonicus* presented a higher frequency of occurrence in the limnetic zone, followed by the frequency found for the opposite margin without vegetation and the margin with macrophytes present.

The analysis of the data collected within each microhabitat confirmed that copepodites stage was predominant in the population structure. In microhabitat I (vegetation present), the hypothesis of homogeneity among the life stages (1:1:1) was rejected ($\chi^2_{0.05,1}$ = 1275.1230, p<0.05), with a prevailing ratio of 8:8:1 ($\chi^2_{0.05,1}$ = 1.6847, p>0.05) for copepodites, adults and nauplii, respectively. Microhabitat II (the limnetic zone) had a ratio of

7:5:1 ($\chi^2_{0.05,1}$ = 1.9389, p>0.05) for copepodites, adults and nauplii, respectively. In microhabitat III (the margin free of vegetation), copepodites, adults, and nauplii occurred at a ratio of 9:8:1 ($\chi^2_{0.05,1}$ = 0.5415, p>0.05), respectively.

When the population structure was analyzed among the microhabitats, nauplii (larval phase) presented a higher frequency of occurrence in the limnetic zone and were present in Lake of Americanos at the ratio of 6:3:2 ($\chi^2_{0.05,1}$ = 4.4523, p>0.05) in microhabitats II, III and I, respectively. For the copepodites (young form), the hypothesis of homogeneous density among the microhabitats (1:1:1) was not supported ($\chi^2_{0.05,1}$ = 902.9655, p<0.05), and the ratio was 14:9:6 ($\chi^2_{0.05,1}$ = 3.9984, p>0.05) for microhabitats II, III and I, respectively. The adult life stage was present in the three microhabitats at the ratio of 8:8:5 ($\chi^2_{0.05,1}$ = 2.9655, p>0.05) in microhabitats II, III and I.

Sex ratio: In the Lake of Americanos, the percentages of adult males and females were approximately 50% when considering all of the microhabitats together. The hypothesis initially formulated for this homogeneity (1:1) was not rejected ($\chi^2_{0.05,\ 1}$ = 0.9506, p>0.05). Although the results show a sexual ratio of 1:1, the same was not found when the microhabitats were analyzed individually. In microhabitat I (the margin with vegetation) females and males were present at a ratio of 9:7 ($\chi^2_{0.05,1}$ = 3.7511, p>0.05), respectively; in microhabitat II (the limnetic zone), females and males presented a ratio of 7:6 ($\chi^2_{0.05,1}$ = 3.2617, p>0.05), while microhabitat III (margin without vegetation) showed homogeneity (1:1) in the sexual ratio ($\chi^2_{0.05,1}$ = 0.5152, p>0.05).

The ratio found for adult males in microhabitat II, microhabitat III and microhabitat I was 6:6:4 ($\chi^2_{0.05,1}$ = 1.8716, p>0.05), respectively. For adult females, the ratio was 7:7:4 ($\chi^2_{0.05,1}$ = 5.3915, p>0.05) for microhabitats II, III and I, respectively. Both ratios show higher densities in the limnetic zone and in the margin without vegetation.

Proportion of females carrying eggs and fecundity: Female *N. amazonicus* with eggs were present in the three hydric level phases considered in this study: phase 1 (full), phase 2 (intermediary), and phase 3 (critical water level). The ratio of females with eggs was 3:3:2 among the phases ($\chi^2_{0.05,1}$ = 4.2420, p>0.05), which was considered relatively homogeneous.

In the high-water phase, phase 1, the females carrying eggs presented a higher absolute frequency in microhabitat III (non-vegetated margin); however, the values were similar, and the homogeneity hypothesis was supported ($\chi^2_{0.05,1}$ = 3.9163, p<0.05). In phase 2, the intermediary phase, the proportions of females carrying eggs were more dissimilar, 8:4:1 ($\chi^2_{0.05(2)1}$ = 2.1037, p>0.05), being observed in the limnetic zone with a higher frequency of occurrence, followed by the margin with vegetation and the margin without vegetation, respectively. In phase 3, critical water level for the lake (drought), the ratio of females among the microhabitats was 3:3:1 ($\chi^2_{0.05,1}$ = 2.1947, p>0.05) for the margin without vegetation, the limnetic zone and the margin with vegetation, respectively.

The hypothesis that the presence of females carrying eggs would be homogeneous among the three phases was rejected in microhabitat I, and the ratio was 3:3:1 ($\chi^2_{0.05,1}$ = 0,1481, p>0.05), corresponding to phases 1, 2 and 3, respectively. In microhabitat II, the ratio was 2:1:1 ($\chi^2_{0.05,1}$ = 1,2157, p>0.05), indicating a superior density corresponding to the high-water period in this environment. For microhabitat III, the margin without vegetation, the ratio was 7:7:1 ($\chi^2_{0.05,1}$ = 1,3347, p>0.05) for the full-lake, intermediary and low-water (drought) phases, respectively.

The fecundity of *N. amazonicus* in Lake of Americanos was considered zero, with an absolute fecundity index of 0.93 eggs/female. The variation among the high-water phase, the intermediary period and the low-level waters (drought) in the environment was considered discrete, with the limnetic zone presenting higher values compared to those of the other microhabitats. The calculated fecundity in microhabitat I, the margin with vegetation, reached its maximum peak at the low-water phase in the environment (phase 3), with 1.21 eggs per female. In the intermediary period, between high waters and low waters, the population presented 0.72 eggs/female, with this index being even more reduced, at 0.31 eggs/female, when the lake was full.

A total of 19 fish specimens were collected from Lake of Americanos: 10 from *Mesonauta insignis* (Heckel, 1840), 7 from *Hoplias malabaricus* (Bloch, 1794) and 2 from *Heros* sp. The analysis of the stomach contents indicated the presence of Copepoda as the predominant food component in 16 of the 19 stomachs examined, with nauplius being the most observed life form of Copepoda.

Discussion

Population structure - ontogenetic stages and microhabitat: In the Lake of Americanos, the estimated relative frequencies show that the copepodite (juvenile stage) is the most representative life form of the *N. amazonicus* population, while the nauplius stage presented low densities. Both observations contradict the population pattern of N. amazonicus for the Amazon (Espíndola et al., 1996; Ibanez et al., 2004; Melo et al., 2006), especially for zone limnetic of the Amazonian lakes, where the population structure present higher density and is generally characterized by higher relative densities at the base of the life cycle (Hardy, 1980; Saunder and Lewis Jr. (1988); Santos-Silva (1991).

The life cycle with larval (nauplius) and juvenile (copepodite) forms appears to be a good explanation for the frequent finding of this pattern in studies of calanoid copepods in South America (Alves *et al.*, 2013), where the short period of time until the following stage (Dussart and Defaye, 1995) requires the constant input of new individuals for the maintenance of populations. Ibanez *et al.* (2004) also suggests size-selective predation as a factor that promotes the high densities of nauplii and copepodites and the low density of adults in the environment, where larger organisms tend to be easier prey for planktophagous and carnivorous predators (Sornes e Aksnes, 2004).

Nauplii, because of their smaller form, are preyed upon predominantly by invertebrate larvae, such as *Chaoborus* and Chironomidae (Diptera) and *Notonela* (Hemiptera), as the high incidence of these predators in the environment seems to serve as an incentive for the development of a survival strategy preventing the formation of a larger number of eggs or diapause phases (Ibanez *et al.*, 2004). The low nauplius density observed in this study seems to be related to the predation exercised by other organisms that live in the Lake of Americanos. To assess this possibility, fishes present in the environment were collected, and the analysis of the stomach contents of these organisms resulted in the observation of larval forms of copepods (nauplii) in sufficient quantity to cause the repletion of the digestive tracts of these fishes.

The taxonomic identification of these predators allocated them to *Mesonauta insignis* (Heckel, 1840), *Hoplias malabaricus* (Bloch, 1794) and *Heros* sp. belonging to the orders Characiformes and Perciformes. The reports in the literature related to these fishes do not clearly indicate whether copepods are a common food item; however, they note the planktivorous behavior of these species in some of their litages (Montag *et al.*, 2008).

Araújo-Lima and Bittencourt (2001), in a study performed with *H. malabaricus* (Characiformes) in the floodplain environments of the Amazon river, verified that, soon after hatching, the larvae of this species actively prey upon microcrustaceans in general. Montag *et al.* (2008), when studying the ichthyofauna in the Pará region, also identified this feeding tendency in species of Perciformes, confirming that these fishes preferentially feed on autochthonous invertebrates in their environments.

Along these lines, although these data are not sufficient to determine with great precision the influence of the ichthyofauna on the copepod population in the Lake of Americanos, the finding of nauplii in the stomachs of these fishes makes it possible to confirm the hypothesis that they might be contributing to the decrease in the number of nauplii of *N. amazonicus* and hence contributing 6to this population structure pattern for Copepoda in this environment in Roraima's lavrado, which has been found to be uncommon in the Amazon.

The analysis of the population structure of *N. amazonicus* in the Lake of Americanos shows heterogeneity in the distribution of these organisms among the verified microhabitats, following the spatial distribution pattern verified in other similar environments in the tropical region, where the limnetic zone appears to shelter a large number of copepods (Carvalho, 1983)

According to Ibanez *et al.* (2004), the presence and distribution of the zooplankton within a given environment are determined by the supply of microhabitats that promote the availability of food and shelter against predation. In the Amazon, the phenomena that occur in these ecosystems, such as high temperatures, force of the winds that move the base of these environments and the changes of water levels (see Junk and Wantze, 2004) seem to stimulate the constant formation of microzones either through the daily deposition of nutrients and oscillation of the water level, which change and determine the trophic state (Junk, 1980; Waichman *et al.*, 2002), or because of the presence of aquatic submerged, coastal and floating vegetation.

For the lake system of Roraima's lavrado region, the depositional process in the lakes (Morais and Carvalho, 2015) possibly contributes to the emergence of microzones or life compartments for diverse types of organisms. In Lake of Americanos, these microzones were distinguished from microhabitats in this study, and they were heterogeneously distinct in three categories, as previous clarified.

In particular, the evaluation performed within microhabitat II (limnetic zone) and microhabitat III (opposite margin without vegetation) align them more clearly with populations formed predominantly by young and adult individuals, confirming what Pennak (1957), Sollberger and Poulson (1991) and Walseng *et al.* (2006) reported with respect to the resemblance between these two environments, which are free of the colonization and influence of aquatic vegetation.

Studies of zooplankton performed in temperate lakes exhibit the same pattern of homogeneity in terms of the distribution of these organisms in the environment in both coastal and limnetic zones (Sollberger and Poulson, 1991). Pennak (1957) and Walseng *et al.* (2006) report that the presence of macrophytes associated with the bottom substrate promote an additional variety of strata and shelter compartments for many species, causing a differential distribution in the environment, which highlights the characteristic indicating that where vegetation is present, there is a higher density of organisms.

The analysis performed individually for each microhabitat corroborated the observations of the population structure of *N. amazonicus* for the total area of Lake of Americanos, in which the nauplius was the life form with the lowest frequency of occurrence within each microzone studied, with the copepod populations represented mainly by copepodites, followed by adults. In general, these results seem to follow the verified patterns for Copepoda in these types of environments (Hardy, 1980; Robertson and Hardy, 1984; Melo *et al.*, 2006).

The population structure of the ontogenetic phases among the microhabitats in Lake of Americanos also confirmed the observed results for the total area of the environment, where the limnetic zone presented higher densities of nauplius, copepodites and adult forms. The observed pattern for the *N. amazonicus* distribution in Lake of Americanos is possibly related to predation pressure, a hypothesis already suggested in terms of the nauplius and copepodite distributions, in accordance with what has also been suggested in other zooplanktonic studies (Maly, 1970; Hairston *et al.*, 1983; Sollbeger and Poulson, 1991; Ordaz *et al.*, 2006; Russo and Hahn, 2006; Lima *et al.*, 2013).

Waichman *et al.* (2002) reported that in different microhabitats of an Amazonian lake, predation is one of the factors that affects the zooplankton distribution in the environment, in which the copepod forms found were more dominant in the open area in comparison to the areas containing macrophytes because of the predation exercised by fishes, among other reasons.

In relation to this subject, Hairston *et al.* (1983) notes the importance of the visual aspect in terms of prey size as a selective factor in predation, explaining that larger prey forms would be the preferential targets within the environments.

An observation from this study becomes relevant in this context: in the Lake of Americanos, it was possible to identify the presence of zooplankton in the stomachs of fishes captured in the macrophyte zone (Perciformes spp. and Characiformes spp.). This relates to the observations made by Waichman *et al.* (2002) and Hairston *et al.* (1983), which support the assumption that in the Lake of Americanos, the adult copepods present in the macrophyte zone (microhabitat I) possibly exhibit superior selective predation potential as a result of their bigger size in relation to other organisms in the local microfauna. Therefore, the higher densities of adult individuals of *N. amazonicus* found in microhabitat II (limnetic zone) and microhabitat III (margin without the presence of macrophytes) could be the result of lower predation pressure.

This hypothesis could be refuted by the fact that copepods have a preferentially planktonic habit (Reid, 1985; Dussart and Defaye, 1995); even so, by chance, differential dispersal and predation could occur. It thus seems reasonable to suppose that the macrophytes function as a shelter, not for copepods but for their predators, working as a microhabitat where the predation pressure is increased because there is a greater concentration of predators.

Proportion of adult males and females: The results regarding the sexual ratio of *N. amazonicus* in Lake of Americanos were similar to those found in a study conducted by Santos-Silva (1991) in an Amazon lake, where equivalence in the sexual ratio of

calanoids was observed, being *N. amazonicus* one of them. These results also corroborate the reports of Hairston *et al.* (1983), which suggest that the mandatory sexual characteristics of Copepoda would be reflected within the population structure, causing the sexual ratio of adult individuals to be equivalent.

In the lake as a whole, when the microhabitats were grouped, the results displayed equivalent sexual ratios; however, the same result was not detected when the microhabitats were analyzed individually. With the exception of microhabitat III (opposite margin without vegetation), the other studied microenvironments exhibited a lack of evenness in the sexual ratio of these organisms, in which there was a difference between the sexes, with the females prevailing over the males in this study.

Hairston *et al.* (1983), in a study about the sex ratios of copepods in 2 lakes, attempted to identify the ecological causes and evolutionary consequences of this phenomenon in the natural history of these organisms. In their study, in lacustrine environments that contain planktivorous fish populations, the copepod females exhibited lower densities compared to the males, while in the absence of these predators, sexual equivalence was predominant.

Nevertheless, this hypothesis could not be used to explain the lack of evenness in the sexual ratio observed for the *N. amazonicus* population within microhabitat I (margin with vegetation) and microhabitat II (limnetic zone) in the Lake of Americanos because in the present study, the adult males were the ones to exhibit a smaller number, providing evidence for the selective predation of this gender in this species.

The explanation offered by Maly (1970) therefore seems to be the one that would best justify the lack of evenness in the sexual ratio in two of the three microhabitats considered in the present study, where the lower density seen in copepod males within a population would be related to the presence of small predators which preferably, based on their feeding strategy, would preferentially prey on males on account of their smaller body size in comparison to females.

For that reason, we can consider the idea for later verification that Lake of Americanos can possibly shelter a predator that preferentially feeds on adult males of *N. amazonicus*.

The individual proportions of males and females among the microhabitats in Lake of Americanos exhibited a similar distribution pattern in relation to their individual densities among the microhabitats. Males were found in larger numbers in the limnetic zone and in the margin without vegetation, and the females had a higher presence in the limnetic zone.

It seems that the hypothesis regarding predation should be faced with more scrutiny in this population dynamics study of *N. amazonicus* in Lake of Americanos based on the results regarding sexual proportions. Ordaz *et al.* (2006) confirmed in Venezuela that copepods are a regular item in the diets of fishes that show higher predation activity in zones with high aquatic plant densities. Russo and Hahn (2006), in a study of small fish diets in three isolated lakes in the Paraná basin, confirmed the results of Ordaz *et al.* (2006), showing that the ichthyofauna present in the macrophyte zones are those that show higher copepod percentages in their food composition.

Another factor possibly related to the results of this study is selective predation, as suggested by Maly (1970), Hairston *et al.* (1983) and Sornes and Aksnes (2004). These authors argued that body size and light availability in the environment influence the presence and distribution of copepods within the habitats. For Lake of Americanos, which is shallow, with a maximum depth of 1.16 meters in the limnetic zone and 0.47 meters at the margins, light is likely an important factor due to the facilitation of visualization of adult copepods as a preferential prey item owing to their superior size in relation to others development forms of these organisms.

Variation in the population of females carrying eggs: The females with eggs of *N. amazonicus* exhibited a decrease in absolute numbers with a reduction in the area and depth of Lake of Americanos. This result is congruent with the report of Santos-Silva (1991), which verified that the low-water period in a lake in the Amazon was more prone to the occurrence of egg-carrying forms of these organisms. He found that the lower depth under the wind action during these periods is a factor that causes suspension of the bottom sediments, offering higher nutrient availability and inducing superior egg production in copepods.

It is possible that the heterogeneous distribution of the proportion of females with eggs during each lake phase and among the microhabitats is related to predation pressure. With the lake in its intermediate state (between low and high waters) it

is assumed that the total area available for predation colonization begins to overlap. This causes copepods with eggs to become progressively susceptible to this overlapping of their niches and thus more exposed and vulnerable to predation in the margins without growth (Pennak, 1957), so they move and colonize the limnetic zone in densities, according to what was verified in this study.

The results obtained for the females with eggs in relation to the environmental phases showed differences in the densities within each microhabitat. The high-water period appeared to present better conditions for the development and production of *N. amazonicus* eggs; in the low-water period, females with eggs were not present at the same densities.

These results are not consistent with those of studies performed in other lakes (Santos-Silva, 1991; Espíndola *et al.*, 1996). Santos-Silva (1991), in a study addressing copepods with eggs in three water phases in an Amazon lake, verified that for *N. amazonicus*, the higher peaks presented in the zones with a high density of macrophytes occurred during the low-water period (drought). Espíndola *et al.* (1996) confirmed this tendency for female copepods with eggs in the low-water period in the Mato Grosso region.

Fecundity: The results found for *N. amazonicus* fecundity reveals discrete numbers within Lake of Americanos. In microhabitat I (margin with vegetation), the population fecundity increased as the area and depth declined until the low-water phase, thus supporting the results found by Santos-Silva (1991), which also confirmed higher fecundity values for this species in the period that corresponds with drought in Lake Calado in the Amazon.

Notwithstanding, within this microenvironment, the frequencies of females with eggs among the lake phases (F1- high waters, F2 - intermediary period and F3 - low waters) followed an inverse pattern in relation to the fecundity indexes also verified among these periods. While the total female fecundity declined as the lakes dried, the fecundity presented an inverse relationship and an increase in terms of the number of eggs per female. The hypothesis related to this phenomenon is that natural predator activity was influential in the disappearance of females with eggs while the lake was drying, as described by Brandorff and Andrade (1978) for Lake Jacaretinga in the Amazon.

This argument suggests that the high number of females with eggs is a strategy for species survival, in which the noticeably smaller eggs produced in higher quantities compared to those observed in the high-water period possibly represent an investment in the success of group permanence in this environment (Odum, 2004) rather than indicating higher recirculation and an increased nutrient supply caused by the physical reduction of the lake, as suggested by other studies (Whitehouse and Lewis, 1973).

In the limnetic zone (microhabitat II), a lower fecundity index of *N. amazonicus* was verified during the high-water phase, followed by an increase and a higher value observed during the ensuing period, between the high and low waters (intermediary phase), again declining when the environment experienced a greater reduction in its depth and area (low-water phase). These results corroborate the conclusions of Santos-Silva (1991) for similar microenvironments within another Amazonian lake and again correspond to the higher frequency of females with eggs during the intermediary period - Phase 2.

In microhabitat III, which is the opposite margin without vegetation, the maximum fecundity was observed during the low-water phase, once more corresponding with the conclusions of Santos-Silva (1991), showing a greater number of eggs/female occurring in the dry period in Lake Calado in the Amazon.

Conclusion

N. amazonicus in the Lake of Americanos showed a population structure distinct from the pattern observed in other large lakes in the Amazon basin. The densities of juveniles (copepodites) and adults, which always occurred in greater proportions in comparison to the larvae, were not consistent with those found in the studies of Hardy (1980), Espíndola *et al.* (1996), Ibanez *et al.* (2004) or Melo *et al.* (2006), which report the nauplius as being the life form showing higher proportions within the populations. Conceivably, the observation of nauplii in the diet composition of small forms of the fishes analyzed supports the hypothesis of the existence natural predators of these organisms within Lake of Americanos, especially in the microenvironment with an elevated density of macrophytes, which, in this study, presented lowest numbers of copepods. In relation to the analyzed patterns of the sexual ratios

and reproductive aspects (females with eggs and fecundity), these continue to be observed in Amazonian lakes in general.

References

Ab'Saber, A. N. 2002. Bases para o estudo dos ecossistemas da Amazônia brasileira. **Estudos Avançados,** 16(45): 7-30.

Alves, B. P. F., Pereira, R. H. G., Barros, A., Dias, D. A., Silva, R. V. & Reis, S. D. 2013. Variação sazonal dos estágios de desenvolvimento de Copepoda (Calanoida: Cyclopoida) da lagoa comprida no município de Aquidauiana, MS. **Revista Eletrônica de Biologia,** 6: 325-338.

Araújo-Lima, C. A. R. M & Bittencourt, M. M. 2001. A reprodução e o início da vida de *Hoplias malabaricus* (Erythrinidae; Characiformes) na Amazônia Central. **Acta Amazonica,** 31: 693-693.

Barbosa, R. I. 1997. Distribuição das chuvas em Roraima. In Barbosa, R. I., Ferreira, E. G. J. & Castellón, E. G. (eds**). Homem, ambiente e ecologia no Estado de Roraima**. Instituto Nacional de Pesquisa da Amazônia, Manaus AM: 325-336.

Bloch, M. E. 1794. Naturgeschichte der ausländischen Fische. **Naturgeschichte der Ausländischen Fische,** Berlin (GER). v. 8: i-iv + 1-174: 361-396.

Brandorff, G-O. 1977. Untersuchung zur Populationsdynamik des Crustaceanplankton im tropischen Lago Castanho (Amazonas Brasilien). **PhD. Thesis**. Cristian-Albrechts-Univ. Kiel, Alemanha. 108 p.

Brandorff, G-O. 1978. Preliminary comparison of the crustacean plankton of a white and a black water lake in Central Amazon. **Verhandlungen des Internationalen Verein Limnologie**, 20: 198-1202.

Brandorff, G-O. & Andrade, E. R. 1978. The relationship between the water level of the Amazon River and the fate of the zooplankton populations in Lago Jacaretinga and varzea lake in Central Amazon. **Studies on Neotropical Fauna and Environment,** 13: 63-90.

Braun, R. 1952. Limnologische Untersuchungen an einigen Sum im Amazonasgebiet. **Schweeiz Z. Hydrobiologia**, 14: 1-128.

Carvalho, M. L. 1983. Efeitos da flutuação do nível da água sobre a densidade e composição do zooplâncton em um lago de várzea da Amazônia, **Brasil. Acta amazonica,** 13:715-724.

Carvalho, M. L. 1984. Influence of predation by fish and water turbity on a *Daphia gessneri* population in an Amazonian floodplain lake, Brazil. **Hydrobiologia,** 13: 243-247.

Dussart, B. H. 1984. Some Crustacea Copepoda from Venezuela. **Hydrobiologia,** 113: 25-67.

Dussart, B. H. & D. Defaye, 1995. **COPEPODA: Introduction to the Copepoda.** SPB Academic Publishing, Amsterdam NED, 277 p.

Espíndola, E. G., Matsumura-Tundisi, T. & Moreno, I. H. 1996. Efeitos da dinâmica hidrológica do sistema patanal matogrossense sobre a extrutura da comunidade de zooplâncton da lagoa Albuquerque. **Acta Limnologica Brasiliensia,** 8: 37-57.

Hairston, N. G. Jr., Walton, W. E. & Li, K. T. 1983. The causes and consequences of sex-specific mortality in a freshwater copepod. **Limnology Oceanography,** 28: 935-947.

Hardy, E. R. 1980. Composição do zooplâncton em cinco lagos da Amazônica Central. **Acta Amazonica,** 10: 577-609.

Heckel, J. 1840. **Johann Natterer's neue Flussfische Brasilien's: nach den beobachtungen und mittheilungen des entdeckers.** Erste Abtheilung, Die Labroiden, Germany (GER). 160p.

Ibañez, C., Paggi, J. C., Molina, C., Pinto, J. & Koste, W. 2004. Zooplancton de las lagunas. In Pouilly, M., Beck, S. G., Moraes, R. M. & Ibañez, C. (eds). **Diversidad biológica en la llanura de inundación del río Mamoré. Importancia ecológica de la dinámica fluvial.** Funadación Simón I. Patiño, Santa Cruz: 272-299.

Infante, A. 1980. Los rotiferos del Lago de Valencia. **Acta Cientifica Venezolana,** Caracas, 31: 30-47.

Junk, W. J. 1980. Áreas inundáveis – Um desafio da Limnologia. **Acta Amazonica,** 10: 775-795.

Junk, W. J. & Wantzen, K. M. 2004. The flood pulse concept: new aspects, approaches and applications - an update. In **Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries.** Bangkok: FAO Regional Office for Asia and the Pacific; RAP Publication: 117-140.

Lima, A. F.; Makrakis, M. C.; Gimenes, M. F.; Makrakis, S.; Silva, P. S. & Assumpção, L. 2013. Mudanças morfológicas no trato digestório e composição da dieta de larvas e juvenis do linguado *Catathyridium jenynsii* no reservatório de Itaipu, rio Paraná, Brasil. **Iheringia,** 103: 214-221.

Maly, E. J. 1970. The influence of predation on the adult sex ratios of two copepod species. **Limnology and Oceanography**, 15: 566-573.

Marlier, G. 1967. Ecological studies of some lakes of Amazon Valley. **Amazoniana,** 1:91-115.

Melack, J. M. & T. R. Fisher, 1983. Diel oxigen variations and their ecological implications in Amazon floodplain lakes. **Archive Hydrobiologie,** 98: 422-442.

Melo, N. F. A. C., Paiva, R. S. & Silva, M. M. T. 2006. Considerações ecológicas sobre o zooplâncton do lago Bolonha, Belém, Pará, Brasil. **Boletim do Museu Paraense Emílio Goeldi,** 1: 115-125.

Montag, L. F. A., Freitas, T. M. S., Wosiaki, W. B. & Barthem, R. B. 2008. Os peixes da Floresta Nacional de Caxiuanã (municípios de Melgaço e Portel, Pará - Brasil). **Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais,** Belém, Pará, 3: 11-34.

Morais, R. P. & Carvalho, T. M. 2015. Aspectos dinâmicos da paisagem do lavrado, nordeste de Roraima. **Geociências,** 34: 55-68.

Odum, E. P. 2004. **Fundamentos de Ecologia.** 6ª ed.: Fundação Calouste Gulbenkian, São Paulo.

Ordaz, M., González, E. & Peñaherrera, C. 2006. Depredación de peces sobre el zooplancton en três embalses neotropicales con distintos estados tróficos. **Interciencia,** 31: 517-524.

Pennak, R. W. 1957. Species composition of Limnetic zooplankton communities. **Limnology and Oceanography,** 2: 222-232.

Pianka, E. R., 1994. **Evolutionary Ecology.** Harper Collins, New York.

Poerschke, N. 2011. Relatório ambiental dos igarapés de Boa Vista – RR. **Graduation Monograph,** Universidade Federal de Roraima, Boa Vista RR, 60 p.

Reid, J. W. 1985. Chave de identificação para as espécies continentais sul-americanas de vida livre da Ordem Cyclopoidea (Crustacea, Copepoda). **Boletim de Zoologia.** Universidade de São Paulo, 9: 17-143.

Robertson, B. A. & Darwich, A. J. 2008. Diel changes in the size structure of a *Moina minuta* Hansen, 1989 population (Anomopoda: Moinidae) in an Amazonian floodplain lake. **Biologia Geral e Experimental**, 8: 21-28.

Robertson, B. A. & Hardy, E. R. 1984. Zooplankton of Amazonian lakes and rivers. Cap. 13. In Sioli, H. (Ed), **The Amazon: limnology and landscape.** The Hague: Dr. W. Junk Publishers, Monographie Biologicae, 56: 337-352.

Russo, M. R. & Hahn, N. S. 2006. Importance of zooplankton in the diet of a small fish in lagoons of the upper Paraná River floodplain, Brazil. **Acta Limnologica Brasiliensia**, 18: 357-366.

Santos-Silva, E. N., 1991. Composição, abundância e reprodução de Calanoida (Copepoda) do lago Calado, Amazônia Central. **Msc. Thesis**, Instituto Nacional de Pesquisas da Amazônia/ Fundação Universidade do Amazonas, Manaus, Amazonas. 143 p.

Santos-Silva, E. N.; Rocha, C. E. F. & Boxshall, G. A. 2013. Revisão das espécies do "complexo *nordestinus*" (Wright, 1935) de *Notodiaptomus* Kiefer, 1936 (Copepoda: Calanoida: Diaptomidae). **Biologia Geral e Experimental**, 13: 1-115.

Saunders, J. F. III & Lewis, W. M. Jr. 1988. Zooplankton abundance in the Caura River, Venezuela. **Biotropica,** 20: 206-214.

Sollberger, P. J. & Poulson, L. J. 1991. Littoral and limnetic zooplankton communities in Lake Mead, Nevada-Arizona, USA. **Hydrobiologia,** 0: 1-11.

Sornes, T. A. & Aksnes, D. L. 2004. Predation efficiency in visual and tactile zooplanktivores. **Limnology and Oceanography**, 49: 69-75.

Twombly, S. 1994. Comparative demography and population dynamics of two coexisting copepods in a Venezuelan floodplain lake**. Limnology and Oceanography** 39: 234-247.

Vanzolini, P. E. & Papavero, N. 1967. **Manual de Coleta e Preparação de Animais Terrestres e de Água doce.** Departamento de zoologia,

Secretaria de Agricultura do Estado de São Paulo, 223p.

Vanzolini, P. E. 1993. *Métodos estatísticos elementares em sistemática zoológica*. Ed. HUCITEC., 130p.

Waichman, A. V., García-Dávila, C. R., Hardy, E. R. & Robertson, B. A. 2002. Composição do zooplâncton em diferentes ambientes do lago Camaleão, na Ilha da Marchantaria, Amazonas, Brasil. **Acta Amazonica,** 32: 339-347.

Walseng, B., Hessen, D. O., Halvorsen, G. & Schartau, A. K. 2006. Major contribution from littoral crustaceans to zooplankton species richness in lakes. **Limnology and Oceanography,** 51: 2600-2606.

Whitehouse, J. W. & Lewis, B. G. 1973. The Effect of Diet and Density on Development, Size and Egg Production in *Cyclops abyssorum* Sars, 1863 (Copepoda, Cyclopoida). **Crustaceana,** 25: 225-36.

Wright, S. 1935. Three new species of Diaptomus from Northeast Brazil. **Anais da Academia Brasileira de Ciências**, 7: 213-233.

Zar, J. H., 1994. *Biostatistical Analysis*. Prentice-Hall, New Jersey. 663p

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