The abundance and biomass of mesozooplankton and ichthyoplankton in the confluence boundary of the Negro and the Amazon Rivers

Ryota Nakajima Corresp., [1] , **Elvis V Rimachi** [2] , **Edinaldo N Santos-Silva** [2] , **Adi Khen** [1] , **Tetsuo Yamane** [3] , **Anthony I Mazeroll** [4,5] , **Jomber C Inuma** [6] , **Erika YK Utumi** [7] , **Akira Tanaka** [7]

[1] Scripps Institution of Oceanography, University of California San Diego, La Jolla, California, United States
[2] National Institute of Amazonian Research (INPA), Manaus, Amazonas, Brazil
[3] Biotechnology Laboratory, Amazonas State University (UEA), Manaus, Amazonas, Brazil
[4] Soka University of America, Aliso Viejo, California, United States
[5] Amazon Research Center for Ornamental Fishes, Iquitos, Peru
[6] Centro de Projetos e Estudos Ambientais do Amazonas (CEPEAM), Manaus, Amazonas, Brazil
[7] Instituto Água Floresta e Vida, Manaus, Amazonas, Brazil

Corresponding Author: Ryota Nakajima
Email address: rnakajima@ucsd.edu

The boundary zone between two different hydrological regimes is often a biologically enriched environment with distinct planktonic communities. In the center of the Amazon River basin, muddy white water of the Amazon River meets with black water of the Negro River, creating a conspicuous visible boundary spanning over 10 km along the Amazon River. Here, we tested the hypothesis that the confluence boundary between the white and black water rivers concentrates prey and is used as a feeding habitat for juvenile fish by investigating the abundance, biomass and distribution of mesozooplankton and ichthyoplankton communities across the two rivers. Our results show that mesozooplankton abundance and biomass were higher in the black-water river compared to the white-water river; however an exceptionally high mesozooplankton abundance was not observed in the confluence boundary. Nonetheless we found the highest abundance of ichthyoplankton in the confluence boundary, being up to 9-fold higher than in adjacent rivers. The confluence boundary between black and white water rivers may function as a boundary layer that offers benefits of both high zooplankton prey concentrations (black-water) and low predation risk (white-water). This forms a plausible explanation for the high abundance of ichthyoplankton in the confluence zone of black and white water rivers.

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[1]Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, USA
[2]National Institute of Amazonian Research (INPA), Manaus, Amazonas, Brazil
[3]Biotechnology Laboratory, Amazonas State University (UEA), Manaus, Amazonas, Brazil
[4]Soka University of America, Aliso Viejo, CA, USA
[5]Amazon Research Center for Ornamental Fishes, Iquitos, Peru
[6]Centro de Projetos e Estudos Ambientais do Amazonas (CEPEAM), Manaus, Amazonas, Brazil
[7]Instituto Água Floresta e Vida, Manaus, Amazonas, Brazil

Correspondence Author: Ryota Nakajima (rnakajima@ucsd.edu)

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Abstract

The boundary zone between two different hydrological regimes is often a biologically enriched environment with distinct planktonic communities. In the center of the Amazon River basin, muddy white water of the Amazon River meets with black water of the Negro River, creating a conspicuous visible boundary spanning over 10 km along the Amazon River. Here, we tested the hypothesis that the confluence boundary between the white and black water rivers concentrates prey and is used as a feeding habitat for juvenile fish by investigating the abundance, biomass and distribution of mesozooplankton and ichthyoplankton communities across the two rivers. Our results show that mesozooplankton abundance and biomass were higher in the black-water river compared to the white-water river; however an exceptionally high mesozooplankton abundance was not observed in the confluence boundary. Nonetheless we found the highest abundance of ichthyoplankton in the confluence boundary, being up to 9-fold higher than in adjacent rivers. The confluence boundary between black and white water rivers may function as a boundary layer that offers benefits of both high zooplankton prey concentrations (black-water) and low predation risk (white-water). This forms a plausible explanation for the high abundance of ichthyoplankton in the confluence zone of black and white water rivers.

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Introduction

The region where two different hydrological regimes meet is characterized by strong physical and biological processes (Walkusz et al. 2010; Bolotov et al. 2012). The boundary zone between two densities of waters is generally enriched in both dissolved and particulate organic matters as a result of their accumulation at this interface (Hill & Wheeler, 2002). The boundary zone is also a biologically enriched environment with distinct planktonic communities (Morgan, De Robertis & Zabel, 2005; Walkusz et al., 2010; Bolotov, Tsvetkov & Krylov, 2012). Extensive research on oceanic fronts between coastal water and river plumes has shown that the boundary zone can lead to increased primary productivity (Franks, 1992), mechanically concentrating zooplankton (Epstein & Beardsley, 2001; Morgan, De Robertis & Zabel, 2005), and attracting tertiary consumers (Grimes & Kingsford, 1996). Thus, the boundary zone is important for local ecosystem functioning.

The Amazon River is well-known for its largest and most dense river network in the world and has the highest level of discharge, contributing ca. 20% of the global continental water discharge into the oceans (Sioli, 1984). In the center of the Amazon basin, muddy white water of the Amazon River (locally named Rio Solimões) meets with black water of the Negro River, one of the largest tributaries, creating a conspicuous visible boundary spanning over 10 km along the Amazon River (Fig. 1). The black water of the Negro River is derived from the high concentration of humic substances, while the white water of the Amazon River is derived from highly suspended inorganic materials (Sioli, 1984; Furch & Junk, 1997; Junk et al., 2015). The

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water properties of the white and black waters are different in terms of many parameters such as flow speed, conductivity, turbidity, pH, water temperature, nutrient concentrations, and dissolved and particulate organic matter concentrations (Laraque et al., 1999; Moreira-Turcq et al., 2003; Leite, Silva & Freitas, 2006; Filizola et al., 2009; Laraque, Guyot & Filizola, 2009; Franzinelli, 2011; Röpke et al., 2016). Due to these differences, the black and white water rivers are not completely mixed until over 100 km beyond the confluence (Laraque, Guyot & Filizola, 2009).

The conspicuous boundary between black and white water rivers may be ecologically important as it may act as a mechanical aggregator of planktonic organisms, and contribute to the subsequent attraction of consumers such as juvenile fish. Although local fishermen have observed that the confluence of black and white water rivers is rich in fish, likely due to higher prey abundance, the abundance and biomass of zooplankton and fish at the confluence remains unclear from a quantitative perspective. To date, most studies on zooplankton and fish in this region have been conducted in the floodplain lakes associated with large rivers (Brandorff, 1978; Robertson & Hardy, 1984; Saint-Paul et al., 2000; Keppeler, 2003; Leite, Silva & Freitas, 2006; Trevisan & Forsberg, 2007; Duncan & Fernandes, 2010; Ghidini & Santos-Silva, 2011; Röpke et al., 2016), but studies from large rivers are scarce (Robertson and Hardy 1984; De Lima and Araujo-Lima 2004). Similarly, previous studies investigated zooplankton and fish in the floodplain lakes of mixed waters from black and white water rivers (Trevisan & Forsberg, 2007; Caraballo, Forsberg & Leite, 2016; Röpke et al., 2016), yet very little is known about the boundary interface between white and black water rivers.

To test the hypothesis that the confluence boundary between white water of the Amazon River and black water of the Negro River concentrates prey and is used as a feeding habitat for juvenile fish, we investigated the abundance, biomass and distribution of mesozooplankton and ichthyoplankton communities of the of the Amazon and the Negro Rivers and compared them with water at the confluence boundary. We were interested in examining (1) How high is the abundance, biomass and composition of mesozooplankton in black and white water rivers? and (2) How much higher is the abundance and biomass of mesozooplankton and ichthyoplankton at the confluence?

Materials & Methods

Study sites

This study was conducted in the center of the Amazon basin where the white water of the Amazon River (locally named Rio Solimões) and the black water of the Negro River (locally named Rio Negro) merge in Manaus, Brazil (Fig. 1). All experiments and preparation of samples were carried out using the facilities of Centro de Projetos e Estudos Ambientais do Amazonas (CEPEAM) on the banks of the Negro River. The sampling of mesozooplankton and ichthyoplankton was conducted at five sites across the rivers: the bank (St. 1) and center (St. 2) of the Amazon River, the confluence (St. 3), and the center (St. 4) and bank (St. 5) of the Negro River (Fig. 1). The bottom of the Amazon River was covered in muddy and sandy sediments, while the river bottom of the Negro River was characterized by hard bedrocks (Junk et al., 2015).

The water depths at the five sites was 11 m (St. 1), 72 m (St. 2), 44 m (St. 3), 62 m (St. 4) and 6 m (St. 5), which were measured by a measuring rope with a 20 kg weight.

Sample collection

We collected mesozooplankton and ichthyoplankton at each sampling site during the day (1200-1400 h) and night (1930-2030 h) during the rising water period in March 2012. In total, 6 samplings were conducted at each sampling site (3 days and 3 nights). Mesozooplankton and ichthyoplankton were sampled by pooling three vertical tows of a plankton net (mesh size, 180-µm; diameter, 30 cm; length, 100 cm) equipped with a flowmeter (Rigo) from 10 m depth to the surface. The plankton net used in this study was not strictly designed for collection of ichthyoplankton (usually a net with a larger mouth and mesh opening is used), thus our net may have misrepresented the number and species richness of fish larvae. Due to a large amount of sand and detrital particles such as plant debris, especially in the white water, the net was washed after every towing in order to reduce net clogging. The pooled samples were immediately brought back to the field laboratory within 30 min, and fixed with buffered formalin to a final concentration of 5% for subsequent microscopic observation.

Prior to the plankton collection, transparency was measured using a Secchi disc and water temperature was measured with a mercury thermometer. The transparency was measured only during the day. In addition, surface water was sampled by a 10 L bucket at three sites (St. 1, 3 and 5) for measurements of chlorophyll-*a* (chl-*a*) and particulate organic carbon (POC) and nitrogen (PON) concentrations. The collected water (10 L) from each site was pre-filtered through a 180-μm mesh screen to remove zooplankton and the water samples were brought back to the laboratory along with the plankton samples. Additional surveys for transparency, water temperature and chl-*a* were conducted monthly over a year from March 2012 to February 2013.

Sample analysis

For chlorophyll analysis, triplicate subsamples (50-100 mL each from bucket) were filtered onto GF/F filters (25 mm, Whatman), then immersed in 90% acetone and stored at 5°C for 24 h. After centrifugation at 3000 rpm for 5 min, the concentrations of chl-*a* were determined using a spectrometer (Shimadzu, UV mini 1240) according to the equation of Ritchie (2006). For POC/N analysis, triplicate subsamples (100-200 mL from bucket) were filtered onto pre-combusted (500°C, 4 h) GF/F filters (25 mm, Whatman), and then dried for 24 h at 60°C and stored in a desiccator until analysis. The POC/N concentration was measured using a CN analyzer (Fisons EA 1108 CHNS/O).

Mesozooplankton and ichthyoplankton were identified to the lowest taxonomic level possible and counted under a dissecting microscope (Leica MZ9.5). Upon observation, large debris (e.g. wood and plant debris) was removed from the samples as much as possible, and then rose bengal was added to facilitate the separation of organisms from suspended matter. Large zooplankton and/or rare species (e.g. larval insects and calanoid copepods) and fish larvae were first counted and sorted out, then the remaining was split (1/2-1/16), from which all zooplankton were characterized and enumerated. At least 300 zooplankton were enumerated in each sample. Copepods and cladocerans were identified to species level and insect and fish larvae to family level

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whenever possible. In the present study, we did not consider rotifers because we used a plankton net with 180 μm mesh, which may have lost a considerable number of rotifers.

The body length of copepods, cladocerans and insect larvae was measured using an eyepiece micrometer. The length measurements of zooplankton individuals were converted to dry weight (*DW*, mg) using previously reported length-weight regression equations (Table 1). The biomass (B, mg m^{-3}) of a given taxonomic group was estimated based on its abundance (A, inds. m^{-3}) and individual dry weight: $B = A \times DW$. Reported length-weight regressions of some species that occur at the sampling site were not available, but we used regressions according to similar genera or shapes. Regressions established in tropical waters were also used when possible.

Statistical analysis

The difference between day and night abundance of mesozooplankton was determined using Student's *t*-test. The difference in the abundance of mesozooplankton and ichthyoplankton between different sites was determined using one-way ANOVA and then differences among means were analyzed using Tukey-Kramer multiple comparison tests. A difference at $P < 0.05$ was considered significant.

Spatial similarities of mesozooplankton assemblage structure were graphically depicted using non-metric multidimensional scaling (MDS) and group average clustering was carried out. The similarity matrix obtained from the abundance values was calculated by the Bray-Curtis index (Bray & Curtis, 1957) with square-root transformed data. To test for spatial variation in community density, analysis of similarities (ANOSIM) was then undertaken (Clarke

& Warwick, 1994). All multivariate analyses were conducted with the software PRIMER v. 6 (Plymouth Marine Laboratory).

Results

Environmental factors

Water temperature, transparency, and chlorophyll concentrations varied among months throughout the year, and these parameters were consistently distinct for white and black water rivers (Fig. 2). The values in the confluence in general were in the middle between black and white water rivers. The surface water temperatures were higher from October to December (Fig. 2a), and the average (mean ± SD) surface water temperature in black water was higher by 1.2 ± 1.0 ºC than that in white water, though the difference was not significant (Table 2; t = -1.86, df = 20, p = 0.078). Transparency (secchi depth) was significantly lower in white water (0.32 ± 0.10 m) than black water (0.95 ± 0.14 m) (Fig. 2b, Table 2). Chl-*a* concentrations in white water river showed higher values during May-September and December-January, while those in black water river were relatively high in May and December-January (Figs. 2c). The chl-*a* concentrations were significantly higher in white water, being 2.2-fold higher than in black water (Table 2). POC and PON concentrations in white water river were also significantly different and 2.8-2.9-folds higher than in black water (Table 2). C/N ratio was comparable between black and white water rivers, but lower in the confluence.

Mesozooplankton abundance and biomass

There was no significant difference in mesozooplankton abundance between day and night at all sites (Student's *t*-test, df = 4, P>0.05 at all sites). The highest abundance (2,817 ± 1,162 inds. m^{-3}, mean ± SD) and biomass (5.14 ± 2.55 mg m^{-3}) of mesozooplankton were observed at the center of the Negro (black water) river (St. 4), while the lowest abundance (577 ± 345 inds. m^{-3}) and biomass (1.30 ± 0.46 mg m^{-3}) were observed at the center (St. 2) of the Amazon (white water) river (Fig. 3a, b). The mesozooplankton abundance and biomass from the center of black water river were significantly different and 4.9-fold and 3.9-fold higher, respectively, than those of white water river (Student's *t*-test; t = -4.5, df = 10, p < 0.005 for abundance; t = -3.6, df = 10, p < 0.005 for biomass). At the confluence (St. 3), the mesozooplankton abundance (2,060 ± 1,269 inds. m^{-3}) and biomass (4.70 ± 3.28 mg C m^{-3}) showed intermediate values between black and white water rivers. The abundance and biomass of mesozooplankton in the confluence showed the highest abundance two times out of a total of 6 sampling times. Cladocerans were the most dominant group in terms of abundance, contributing 66.2%-82.2% of the total mesozooplankton abundance at all sites, followed by copepods (19.7-41.7%) and insect larvae (0.1-0.6%) (Fig. 3a). On the contrary, copepods were the most important in terms of biomass, contributing 64.0-79.1% of the total mesozooplankton biomass, followed by cladocerans (13.4-20.9%) and insect larvae (6.5-17.4%) (Fig. 3b).

In total 26 species of cladocerans were observed (Table 3), among which *Diaphanosoma polyspina* was the most dominant taxa at all sites, contributing 33.4%-65.5% of the total cladoceran abundance and 51.2%-80.3% of the biomass (Fig. 3c,d). Among the dominant cladocerans that comprised 1% or more of total cladoceran abundance at all sites, *Bosmina hagmanni*, *B. longirostris* and *B. deitersi* showed higher abundance and biomass in black water than in white water (Fig. 3c,d). In contrast, those of *Moina minuta* were higher in white water than in black water.

The abundance of copepods was highest in the center (St. 4) of black water river (1,047 ± 508 inds. m^{-3}), followed by the confluence (860 ± 684 inds. m^{-3}) (Fig. 3e). On the other hand, the biomass of copepods in the confluence (St. 3) and the center (St. 4) of black water river were comparable, at 3.71 ± 3.05 mg C m^{-3} and 3.79 ± 2.00 mg C m^{-3}, respectively (Fig. 3f). In total 25 species of copepods were observed (Table 4), among which (excluding copepodites) *Oithona amazonica* was the most dominant taxa in terms of abundance at all sites, contributing 9.0%-40.6% of the total copepod abundance, while *Dactylodiaptomus pearsei* was the most important in terms of biomass (34.6-58.5%) (Fig. 3e,f). The highest abundance of *O. amazonica* was observed at the center (St. 4) of black water river (388 ± 566 inds. m^{-3}), followed by the confluence (349 ± 405 inds. m^{-3}).

The abundance of insect larvae was highest in the bank (St. 5) of black water river, followed by the confluence (St. 3) and the bank (St. 1) of white water river (Fig. 3g). Chaoboridae (diptera larvae) was numerically abundant in the black water river, while chironomidae (diptera) and coleoptera were dominant in the white water river (Fig. 3g). The biomass of insect larvae was the highest in the bank of the black water river (St. 5) decreasing toward the bank (St. 1) of the white water river (Fig. 3h).

Ordination of the mesozooplankton community

The MDS ordination plot and group-average clustering showed that mesozooplankton communities in the black water river were clearly separated from those in the white water river (Fig. 4). The result of ANOSIM test showed that the community structure between black and white water rivers was significantly different (Global R = 0.622, P=0.001). The communities from the confluence were in between black and white water communities.

Ichthyoplankton abundance and composition

The abundance of juvenile fish in the confluence (St. 3) (9.7 ± 2.5 inds m^{-3}) was significantly and 2.1-8.8 times higher than in the other sites (Tukey-Kramer, df = 29, P<0.01) (Fig. 5). Characiformes were the most dominant group in the confluence, contributing 47.2% to the total juvenile fish abundance, followed by Pimelodidae siluriformes (34.5%). The juvenile fish abundance at the bank of white water river (St. 1) was the next abundant (4.6 ± 3.7 inds m^{-3}). Auchenipteridae siluriformes were only sampled at the banks of both white (St. 1) and black water rivers (St. 5), while clupeiformes were only observed in the center of the white water river (St. 2).

Discussion

This study describes the abundance and composition of mesozooplankton and ichthyoplankton across the Negro (black water) and the Amazon (white water) rivers in the center of the Amazon basin to elucidate the distributional differences between the two rivers and their confluence zone, which were not previously well-described quantitatively. The water properties of the two rivers were distinct: surface water temperatures and transparency were always higher in black water rivers, while chlorophyll and particulate organic matter concentrations were always higher in white water rivers. Surface water temperature in black water was higher by 1.2ºC on average than white water throughout the year, which is congruent with previous studies reporting higher temperature by 1ºC in the Negro River (Franzinelli, 2011). The higher water temperature in the Negro River may result from its darker color and slower current speed compared to the Amazon River (0.1-0.3 m s^{-1} vs. 1.0-1.3 m s^{-1}) (Moreira-Turcq et al., 2003; Filizola et al., 2009; Franzinelli, 2011).

The mean concentration of chl-*a* in the white water river (10.5 µg l^{-1}) was higher than that in the black water river (4.8 µg l^{-1}) in this study. Although concentrations are much different between lakes and rivers, a similar pattern was previously reported in floodplain lakes, where surface water chl-*a* concentration was higher in lakes associated with the Amazon (white water) river (50-80 µg l^{-1}) than in lakes adjacent to the Negro (black water) rivers (10-20 µg l^{-1}) (Fisher & Parsley, 1979; Trevisan & Forsberg, 2007). Higher chl-*a* concentration in white water lakes may be the result of higher concentrations of inorganic nutrients derived from the Amazon River (Trevisan & Forsberg, 2007). However, in the Amazon River system, primary production is not likely because of poor light penetration due to high turbidity (euphotic depth: ca. 0.3 m), where the mixing depth was probably always down to the bottom due to turbulence associated with the strong current, making respiration higher than photosynthesis (Fisher & Parsley, 1979).

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Therefore, the presence of chlorophyll in the Amazon River probably results from the input of more productive environments such as the adjacent lakes (Fisher & Parsley, 1979).

That the white river had higher POC concentrations than the black river (1,262 vs. 446 mg m^{-3}) in this study is in agreement with previous studies reporting higher POC in the Amazon River (~1,820 mg m^{-3}) than in the Negro River (720-1,030 mg m^{-3}) during the low water period (Moreira-Turcq et al., 2003). The C/N ratio was similar for white and black waters (3.8 vs. 3.9) in this study, which is congruent with previous studies (Moreira-Turcq et al., 2003). However, the C/N ratios in this study during the rising water period was much lower than those previously observed during low water periods (September, C/N = 9) (Moreira-Turcq et al., 2003). These differences suggest that the composition of particulate organic matter (POM) varies over seasons rather than between black and white waters.

Mesozooplankton difference of black and white water rivers

As the MDS and ANOSIM analyses clearly indicated, the present study revealed that the compositions of mesozooplankton assemblages differ between the white water of the Amazon River and black water of the Negro River. We also found a higher abundance of mesozooplankton communities in black water river compared to white water river. The abundance of zooplankton in tropical large rivers depend largely on the supply from adjacent lentic sources (standing water bodies) connected to the river such as channel and floodplain habitats (Rzoska, 1978; Saunders & Lewis, 1988a, 1989; Basu & Pick, 1996; Reckendorfer et al., 1999; Górski et al., 2013). The zooplankton sampling period in this study corresponds to the rising water period (March), where rising riverine water starts to wash out ambient zooplankton from associated lentic sources into the rivers (Saunders & Lewis, 1988a,b, 1989). Assuming that adjacent lentic areas (e.g., floodplain lakes) are a major source of zooplankton in river systems in this study, there may have been a larger zooplankton transport from stagnant water bodies connected to the Negro (black water) river compared to those of the Amazon (white water) river. However, there are fewer lakes in the Negro River floodplain than in the floodplains of white water rivers because of the lower hydrodynamics (Junk et al., 2015). Previous studies from floodplain lakes in the center of the Amazon basin reported that the abundance of mesozooplankton (cladocerans and copepods) was 2-25 fold higher in black water lakes associated with the Negro River than in white water lakes during rising-high water periods (Feb-June) (Brandorff, 1978; Hardy, 1980), which might explain the higher mesozooplankton abundance in the black water river in this study. However, previous studies conducted during the end of low water periods (November-December) reported higher zooplankton abundance in white water lakes (Brandorff, 1978; Trevisan & Forsberg, 2007), suggesting that growth and mortality processes of lake zooplankton vary over seasons among the different water lakes.

Reproduction of zooplankton in the flowing waters can also increase abundance at a low flow rate (Bertani, Ferrari & Rossetti, 2012). River zooplankton are unable to reproduce in flow speed exceeding 0.4 m s^{-1} (Rzoska, 1978) and thus lower residence time can mean a lower zooplankton density (Basu & Pick, 1996). Considering that the flow speed of the Amazon River (Rio Solimões) exceeds 1.0 m s^{-1} (Filizola et al., 2009), reproduction of zooplankton is likely impossible in this white water river. Large amounts of inorganic suspended particles in white

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water river may also negatively influence zooplankton abundance in this system (McCabe & O'Brien, 1983; Kirk & Gilbert, 1990; Junk & Robertson, 1997). Indeed, zooplankton abundance in the white water river was higher in the bank than at the center, suggesting that adjacent lentic sources are the primary source of zooplankton in this white river system. On the contrary, zooplankton are able to reproduce in the slower current of black water rivers (0.1-0.3 m s^{-1}) (Moreira-Turcq et al., 2003; Franzinelli, 2011). Indeed, our results of mesozooplankton in the Negro River showed higher abundance in the center of the river than in the bank, implying that zooplankton reproduction occurs in this black water river. In summary, the higher supply of zooplankton from adjacent lentic water bodies (such as floodplain lakes) and/or possible reproduction might help to explain why mesozooplankton abundance was higher in the black water river compared to the white water river.

Mesozooplankton and ichthyoplankton in the confluence

As previously examined in oceanic frontal boundaries between river plumes and adjacent marine waters (Morgan, De Robertis & Zabel, 2005; Walkusz et al., 2010), convergent flow at the boundary between distinct water masses functions to concentrate planktonic organisms, including larval fish. In the present study, we found significantly higher abundance of fish larvae in the confluence throughout the study period, supporting the hypothesis that the confluence between white and black water rivers functions as an ecological concentrator of ichthyoplankton. However, an exceptionally high zooplankton number, as often seen in oceanic fronts (Morgan, De Robertis & Zabel, 2005), was not observed in the confluence boundary in this study. The highest average abundance of mesozooplankton was observed in the center of black water river (the Negro River), though there was no difference in terms of zooplankton biomass between the confluence and the center of black water river. Unlike oceanic fronts, where riverine freshwater plumes stand still facing the coastal marine water, which enhances the mechanical concentration of zooplankton (Morgan, De Robertis & Zabel, 2005), the black and white water rivers in the present study flow down together (but without mixing), probably making the zooplankton concentration less distinguished in the boundary zone. However it should be noted that the mesozooplankton abundance in the confluence was far higher than that in white water river, and the abundance and biomass of mesozooplankton in the confluence sometimes exceeded the abundance in the center of the Negro River.

Then the question arises as to why ichthyoplankton abundance was high in the confluence boundary zone. In black water rivers, potentially higher predation risks for larval fish would be expected given that larvae can be more easily seen by predators due to fewer suspended solids (De Lima & Araujo-Lima, 2004). On the contrary, white waters with high suspended solids are considered to be safer places for juvenile fish because of lower transparency and higher turbulence, which may act as refuge from predators (De Lima & Araujo-Lima, 2004). Therefore the confluence zone can be a boundary interface between high and low predation pressures for fish larvae. From the perspective of food availability (at least for zooplanktivorous fish), the confluence between white and black waters is sandwiched by both environments with low and high food concentrations. Fish larvae may find more prey in the center of black water, yet fish larvae abundance was the lowest in the Negro River, suggesting higher predation pressure in black water river even in a food-rich environment. Therefore, the confluence zone between black and white water rivers may function as a boundary layer that has benefits from both low predation risk and high food concentrations for fish larvae. In summary, the combined effects of food availability and predator avoidance form a plausible explanation for the high abundance of ichthyoplankton in the confluence zone of black and white water rivers. The lower C/N ratio of POM found in the confluence (2.8) compared to the adjacent rivers (3.8-3.9) may be the result of higher heterotrophic activity in this boundary zone since the C/N ratio of carnivorous fish feces is generally very low (ca. 3, Smriga et al. (2010)).

Conclusion

We found that mesozooplankton abundance and biomass were higher in the black-water of the Negro River compared to the muddy white-water of the Amazon River, probably due to a higher supply of zooplankton from lentic waters adjacent to the Negro River and/or reproduction. An exceptionally high mesozooplankton abundance was not observed in the confluence boundary between the two rivers; nonetheless we found that the confluence zone acts as an aggregator of ichthyoplankton. The confluence boundary between black and white water rivers may function as a boundary layer that offers benefits of both high food (zooplankton) concentrations and low predation risk. This forms a plausible explanation for the high abundance of ichthyoplankton in the confluence zone. These combined effects may also explain the reason for the larger fish catches in the confluence of black and white water rivers that have been empirically noted by local fishermen.

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Figure 1

Location of the study sites

(A) the Amazon Basin in South America. (B) the Amazon River (locally named Rio Solimões) and the Negro River in the center of the Amazon basin. (C) sampling sites across the two rivers: bank (St. 1) (S03º07'36.35'';W59º53'10.25'') and center (St. 2) (S03º07'29.89'';W59º53'30.92'') of the Amazon River, the confluence (St. 3) (S03º07'29.64'';W59º53'55.10''), and center (St. 4) (S03º07'13.43'';W59º54'05.19'') and bank (St. 5) (S03º06'57.97'';W59º54'17.74'') of the Negro River. (D) the confluence.

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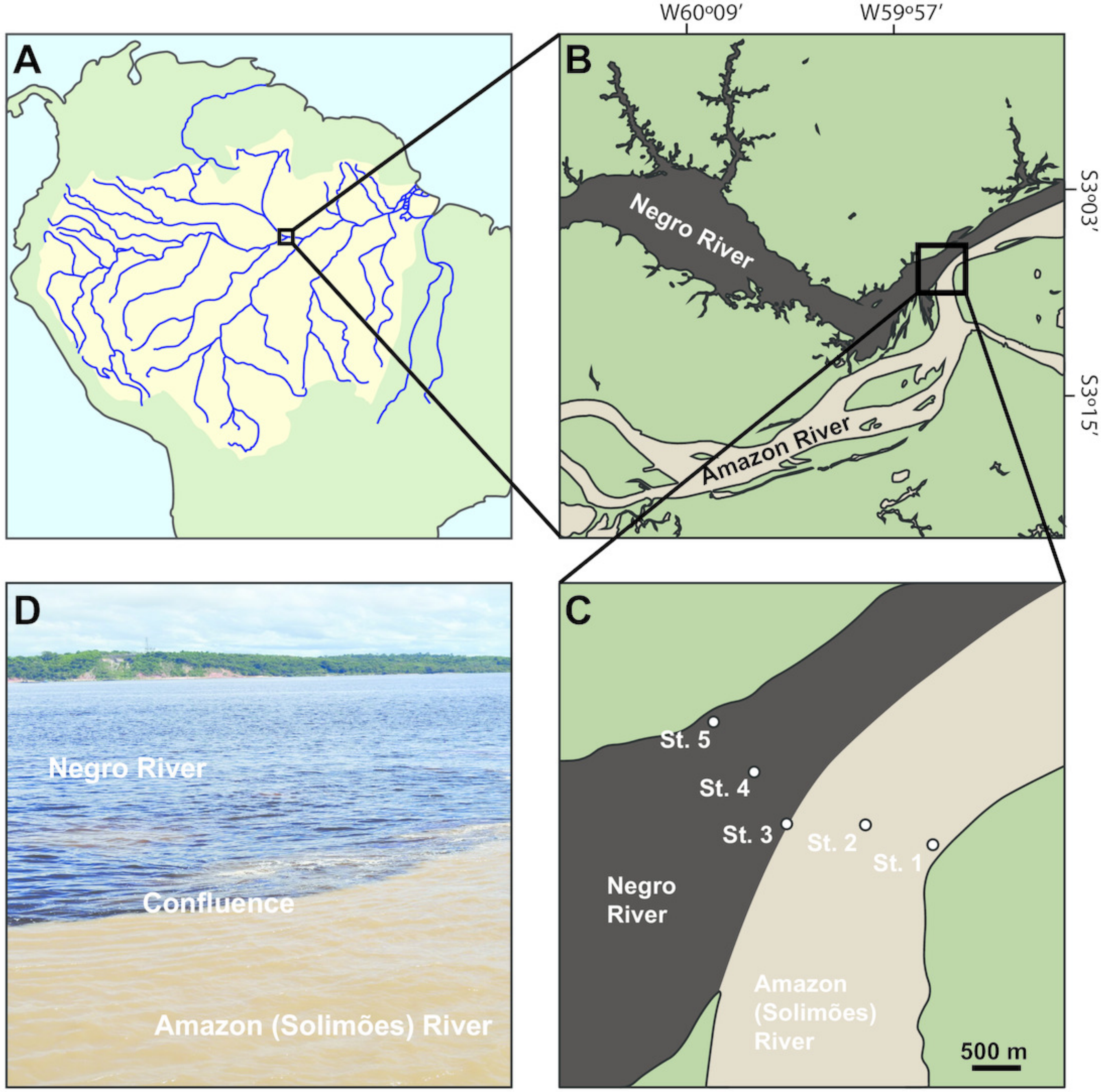
W60º09′
W59º57′
S3º03′
S3º15′
A
B
C
D
Negro River
Amazon River
St. 5
St. 4
St. 3
St. 2
St. 1
Negro River
Amazon (Solimões) River
500 m
Negro River
Confluence
Amazon (Solimões) River

Figure 2

Temporal changes in environmental parameters in the Amazon River (St. 1), the confluence (St. 3) and the Negro River (St. 5)

(A) water temperature, (B) transparency (secchi depth), and (C) chlorophyll-*a* (chl-*a*) concentration. Data were taken from March 2012 to February 2013. Sts. 1, 3 and 5 correspond to those in the map in Fig. 1. Error bars in chl-*a* indicate standard error (SE) of triplicate measurements.

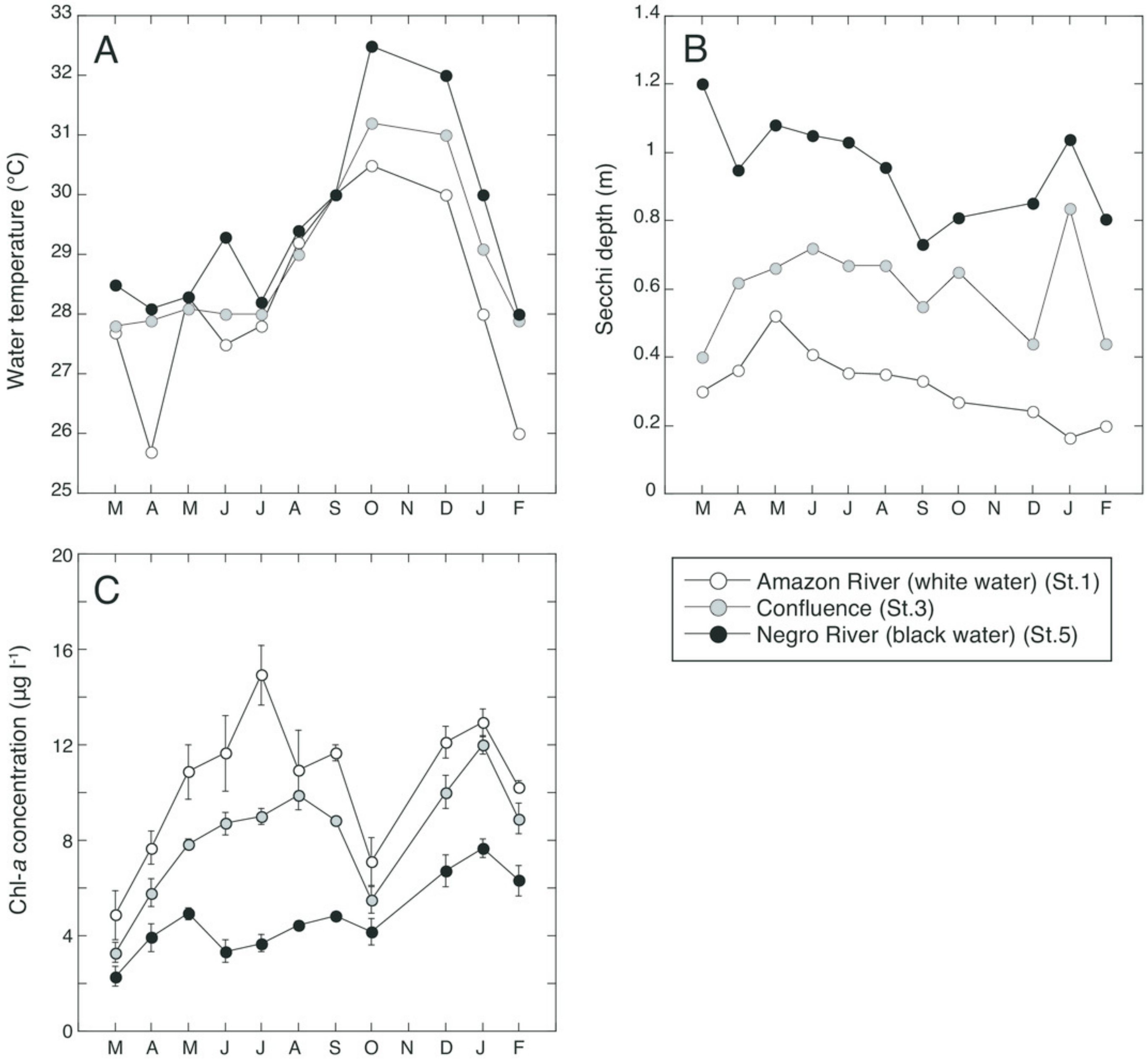
A
B
C
Water temperature (°C)
Secchi depth (m)
Chl-a concentration (µg l⁻¹)
33
32
31
30
29
28
27
26
25
1.4
1.2
1
0.8
0.6
0.4
0.2
0
20
16
12
8
4
0
M A M J J A S O N D J F
Amazon River (white water) (St.1)
Confluence (St.3)
Negro River (black water) (St.5)

Figure 3

Spatial variations in abundance and biomass of mesozooplankton

Abundance and biomass of (A,B) total mesozooplankton, (C,D) cladocerans, (E,F) copepods, and (G,H) insect larvae in the Amazon River (St. 1-2), the confluence (St. 3), and the Negro River (St. 4-5) in the center of the Amazon basin. Sts. 1-5 correspond to those in the map in Fig. 1. Error bars represent standard deviation (SD) of abundance or biomass for 6 replicate measurements.

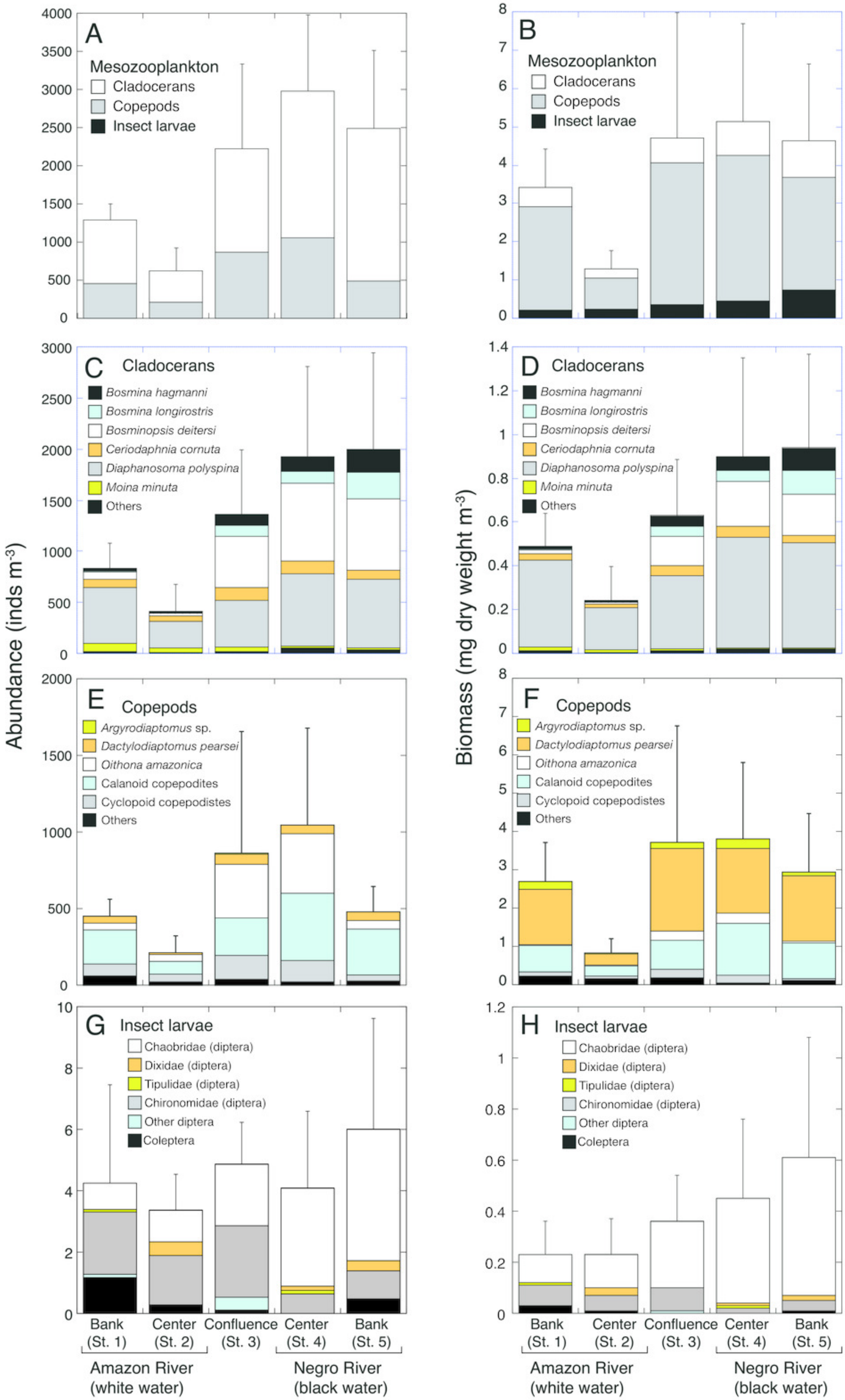
A
Mesozooplankton
Cladocerans
Copepods
Insect larvae
B
Mesozooplankton
Cladocerans
Copepods
Insect larvae
C Cladocerans
Bosmina hagmanni
Bosmina longirostris
Bosminopsis deitersi
Ceriodaphnia cornuta
Diaphanosoma polyspina
Moina minuta
Others
D Cladocerans
Bosmina hagmanni
Bosmina longirostris
Bosminopsis deitersi
Ceriodaphnia cornuta
Diaphanosoma polyspina
Moina minuta
Others
E Copepods
Argyrodiaptomus sp.
Dactylodiaptomus pearsei
Oithona amazonica
Calanoid copepodites
Cyclopoid copepodistes
Others
F Copepods
Argyrodiaptomus sp.
Dactylodiaptomus pearsei
Oithona amazonica
Calanoid copepodites
Cyclopoid copepodistes
Others
G Insect larvae
Chaobridae (diptera)
Dixidae (diptera)
Tipulidae (diptera)
Chironomidae (diptera)
Other diptera
Coleptera
H Insect larvae
Chaobridae (diptera)
Dixidae (diptera)
Tipulidae (diptera)
Chironomidae (diptera)
Other diptera
Coleptera
Abundance (inds m-3)
Biomass (mg dry weight m-3)
Bank (St. 1)
Center (St. 2)
Confluence (St. 3)
Center (St. 4)
Bank (St. 5)
Amazon River (white water)
Negro River (black water)

Figure 4

Non-metric multidimensional scaling (MDS) plots

MDS plots showing similarity of mesozooplankton community in different sites (the Amazon River; the Negro River; the confluence). Bray-Curtis similarities were calculated based on the square-root of abundance. The legends above each symbol indicate site number (st1-5), day (D) or night (N), and date of sampling (8-12 March 2012).

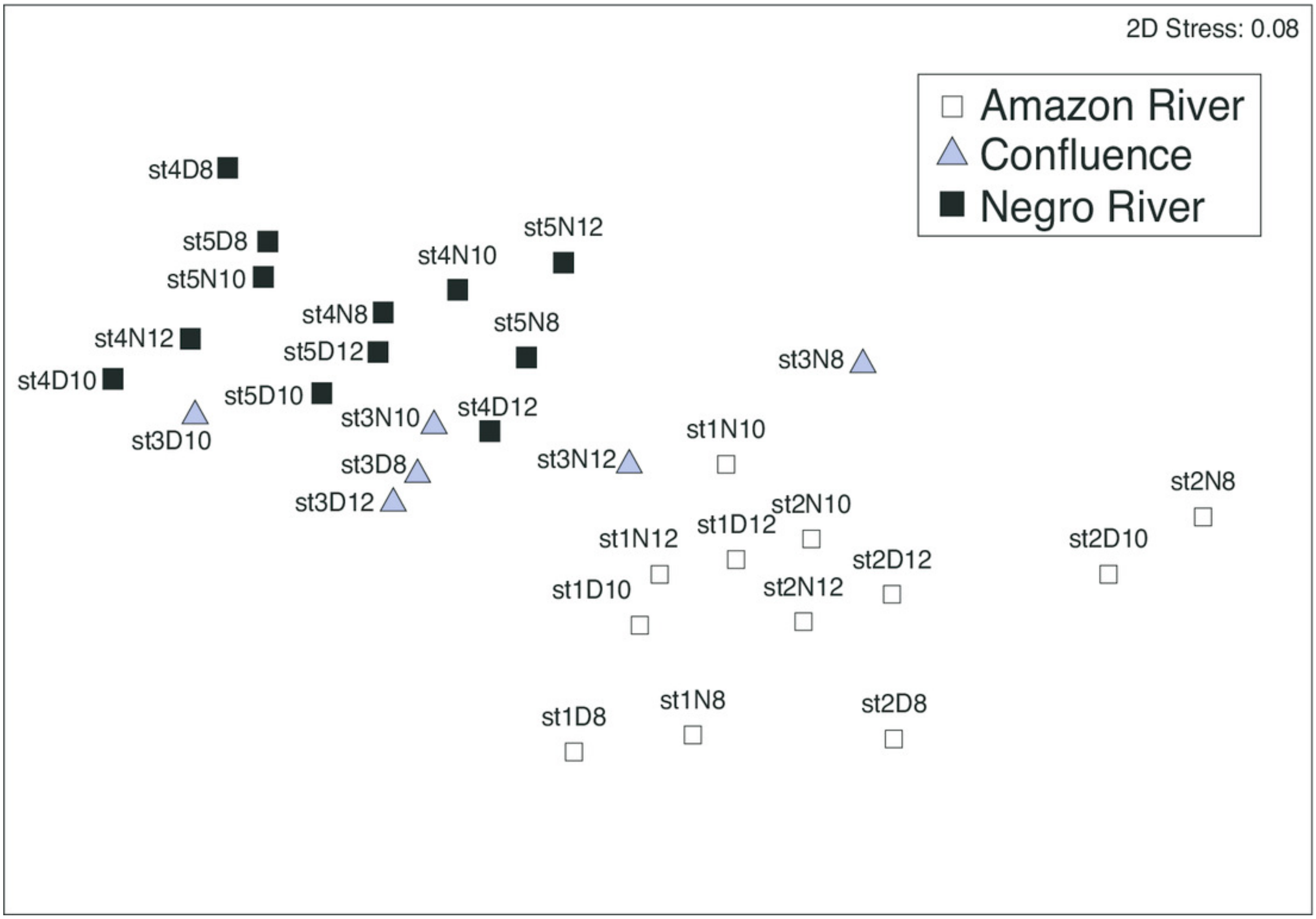

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Figure 5

Spatial variation in abundance of ichthyoplankton

Abundance of ichthyoplankton community in the surface water of the Amazon River (St. 1-2), the confluence (St. 3), and the Negro River (St. 4-5). Error bars represent standard deviation (SD) of ichthyoplankton abundance for 6 replicate measurements.

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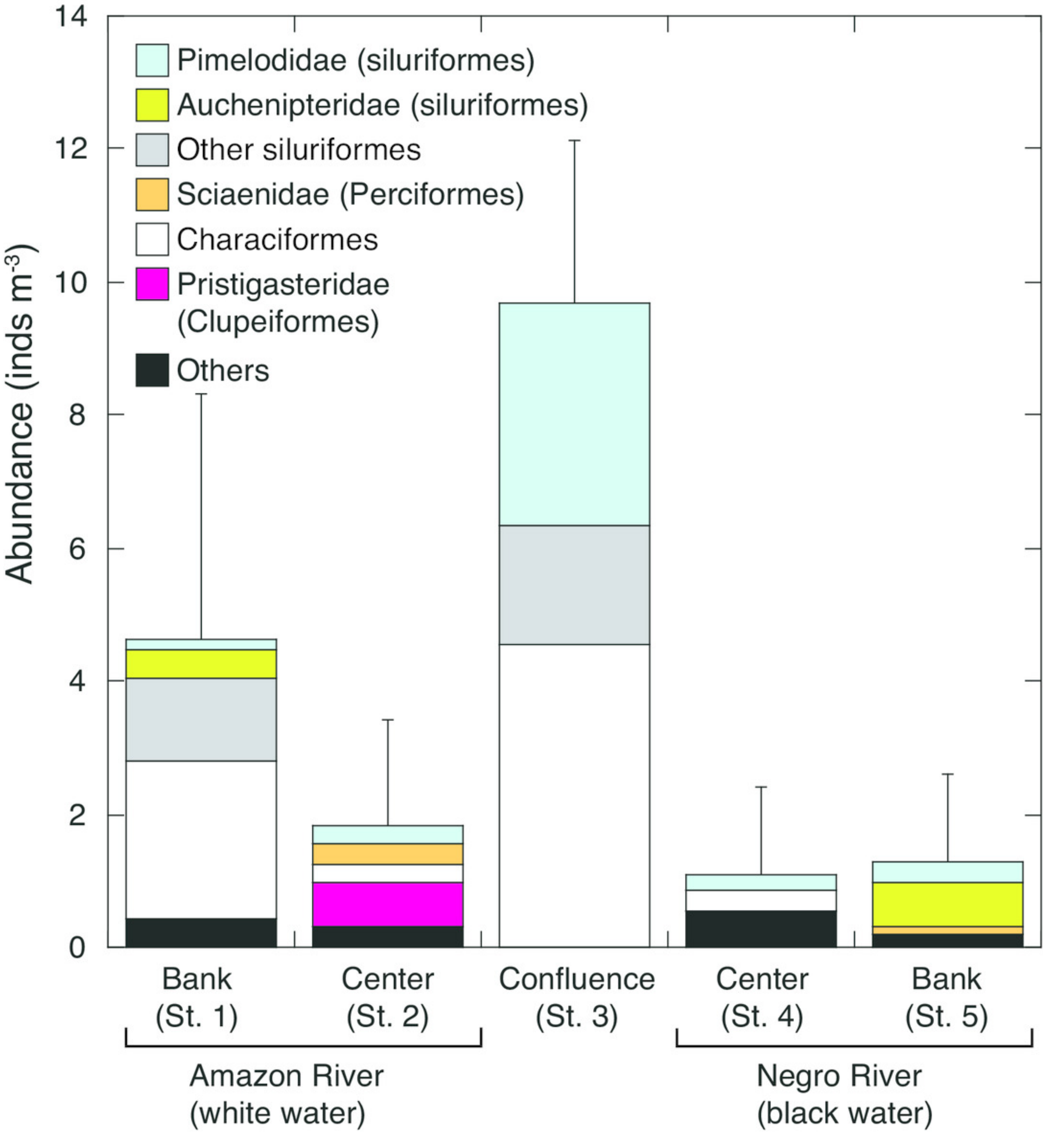

14
12
10
8
6
4
2
0
Abundance (inds m-3)
Pimelodidae (siluriformes)
Auchenipteridae (siluriformes)
Other siluriformes
Sciaenidae (Perciformes)
Characiformes
Pristigasteridae (Clupeiformes)
Others
Bank (St. 1)
Center (St. 2)
Confluence (St. 3)
Center (St. 4)
Bank (St. 5)
Amazon River (white water)
Negro River (black water)

Table 1(on next page)

Length-weight regression equations

Length-weight regression equations used for biomass calculations of different mesozooplankton taxa. DW, dry weight; L, body length; ln, natural logarithm (log_e).

Taxonomic group	Equation	Source
Cladocerans		
Bosmina sp.	ln DW (µg) = 2.68 ln L (mm) + 2.479	Maia-Barbosa & Bozelli (2005)
Bosminopsis sp.	ln DW (µg) = 2.221 ln L (mm) + 1.808	Maia-Barbosa & Bozelli (2005)
Ceriodaphnia cornuta	ln DW (µg) = 1.888 ln L (mm) + 1.442	Maia-Barbosa & Bozelli (2005)
Chydorus sp.	ln DW (µg) = 3.93 ln L (mm) + 4.493	Dumont, Van de Velde & Dumont (1975)
Daphnia gessneri	ln DW (µg) = 3.22 ln L (mm) + 1.169	Azevedo & Dias (2012)
Diaphanosomoa birgei	ln DW (µg) = 1.738 ln L (mm) + 1.653	Maia-Barbosa & Bozelli (2005)
Diaphanosoma sp.	ln DW (µg) = 2.22 ln L (mm) + 1.140	Azevedo & Dias (2012)
Macrothrix sp.	ln DW (µg) = 3.177 ln L (mm) + 2.850	Azevedo & Dias (2012)
Moina sp.	ln DW (µg) = 1.549 ln L (mm) + 0.149	Maia-Barbosa & Bozelli (2005)
Other cladocerans	ln DW (µg) = 2.653 ln L (mm) + 1.751	Bottrell et al. (1976)
Copepods		
Argyrodiaptomus sp.	ln DW (µg) = 2.560 ln L (mm) + 2.440	Azevedo & Dias (2012)
Notodiaptomus sp.	ln DW (µg) = 2.160 ln L (mm) + 2.290	Azevedo & Dias (2012)
Other calanoids	ln DW (µg) = 3.150 ln L (mm) + 2.470	Azevedo & Dias (2012)
Eucyclops sp.	ln DW (µg) = 2.40 ln L (mm) + 1.953	Bottrell et al. (1976)
Mesocyclops sp.	ln DW (µg) = 2.556 ln L (mm) + 1.211	Shumka et al. (2008)
Thermocyclops decipiens	ln DW (µg) = 3.244 ln L (mm) + 1.570	Azevedo & Dias (2012)
Thermocyclops minutus	ln DW (µg) = 2.770 ln L (mm) + 1.340	Azevedo & Dias (2012)
Other cyclopoids	ln DW (µg) = 2.40 ln L (mm) + 1.953	Bottrell et al. (1976)
All nauplii	ln DW (µg) = 2.40 ln L (mm) + 1.953	Bottrell et al. (1976)
Insect larvae		
Chaoboridae (diptera)	ln DW (mg) = 2.692 ln L (mm) -5.992	Benke et al. (1999)
Tipulidae (diptera)	ln DW (mg) = 2.681 ln L (mm) -5.843	Benke et al. (1999)
Chironomidae (diptera)	ln DW (mg) = 2.618 ln L (mm) -6.320	Benke et al. (1999)
Other diptera	ln DW (mg) = 2.692 ln L (mm) -5.992	Benke et al. (1999)
Coleoptera	ln DW (mg) = 2.910 ln L (mm) -4.867	Benke et al. (1999)

1

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Table 2 (on next page)

Environmental factors

Average (mean ± SD) water temperature, transparency (secchi depth), chlorophyll-*a* (chl-*a*), particulate organic carbon (POC) and nitrogen (PON) at the bank of the Amazon River (St. 1), the confluence (St. 3) and the bank of the Negro River (St. 5) between March 2012 and February 2013. Sites 1, 3 and 5 correspond to those in the map in Fig. 1. *P* values indicate the differences in the values between St. 1 and St. 5 tested by Student's *t*-test. POC and PON data were from the zooplankton sampling period only (March 2012).

	Amazon River (St. 1)	Confluence (St. 3)	Negro River (St. 5)	P (St. 1 vs. St. 5)
Water temperature (ºC)	28.2 ± 1.6	28.9 ± 1.3	29.5 ± 1.6	0.0783
Secchi depth (m)	0.32 ± 0.10	0.60 ± 0.14	0.95 ± 0.1	<0.0001
Chl-a (µg L-1)	10.5 ± 2.9	8.2 ± 2.4	4.8 ± 1.6	<0.0001
POC (µg L-1)	1,262 ± 420	881 ± 144	446 ± 62	0.0291
PON (µg L-1)	333 ± 23	316 ± 27	114 ± 3	0.0001
C/N	3.8 ± 1.1	2.8 ± 0.3	3.9 ± 0.6	0.8570

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Table 3 (on next page)

Abundance of cladocerans

Average (mean ± SD) abundance (inds m^{-3}) and relative abundance (%RA) of various cladoceran species at the Amazon (Solimões) and the Negro Rivers, the center of the Amazon basin. Sites 1-5 correspond to those in the map in Fig. 1.

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	Amazon River				Confluence		Negro River			
	Babk (St. 1)	%RA	Center (St. 2)	%RA	(St. 3)	%RA	Center (St. 4)	%RA	Bank (St. 5)	%RA
Alona incredibilis	1.3 ± 3.1	0.2	0.0 ± 0.0	0.0	4.1 ± 6.3	0.3	1.7 ± 4.2	0.1	0.0 ± 0.0	0.0
Biapertura sp.	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	2.8 ± 6.8	0.1
Bosmina hagmanni	28.5 ± 28.1	3.4	15.7 ± 9.8	3.8	109.0 ± 78.8	8.0	137.7 ± 115.3	7.2	227.0 ± 123.2	11.4
Bosmina longirostris	7.8 ± 8.4	0.9	6.1 ± 7.1	1.5	108.7 ± 78.4	8.0	118.7 ± 134.7	6.2	255.7 ± 195.9	12.8
Bosminopsis brandorffi	2.6 ± 6.3	0.3	0.8 ± 2.0	0.2	6.4 ± 6.5	0.5	9.2 ± 11.3	0.5	15.3 ± 18.8	0.8
Bosminopsis deitersi	73.3 ± 37.4	8.8	28.8 ± 25.7	7.0	501.1 ± 315.6	36.8	759.5 ± 309.3	39.5	704.7 ± 424.2	35.2
Bosminopsis negrensis	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	1.1 ± 2.7	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Ceriodaphnia cornuta	79.6 ± 34.2	9.5	47.2 ± 29.0	11.4	122.9 ± 96.0	9.0	131.8 ± 142.8	6.9	90.0 ± 79.9	4.5
Chydorus evrinotus	0.0 ± 0.0	0.0	0.2 ± 0.4	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Chydoros sphaericus	2.2 ± 3.0	0.3	0.4 ± 0.9	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Daphnia gessneri	2.6 ± 6.3	0.3	0.8 ± 1.0	0.2	4.0 ± 6.2	0.3	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Diaphanosomoa birgei	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	1.5 ± 3.8	0.1	0.0 ± 0.0	0.0
Diaphanosoma polyspina	546.4 ± 170.4	65.5	266.0 ± 175.9	64.2	462.0 ± 179.7	33.9	705.0 ± 488.2	36.6	667.2 ± 333.5	33.4
Diaphanosoma spinulosum	0.5 ± 1.2	0.1	0.6 ± 1.5	0.2	0.7 ± 1.8	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Ephemeroporous sp.	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	26.4 ± 18.6	1.4	6.1 ± 8.0	0.3
Evryalona brasiliensis	0.5 ± 1.2	0.1	0.2 ± 0.4	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Holopedium amazonicum	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	2.7 ± 4.6	0.2	5.1 ± 12.5	0.3	2.6 ± 4.1	0.1
Ilyocryptus spinifer	8.1 ± 4.2	1.0	5.7 ± 4.5	1.4	0.8 ± 1.3	0.1	3.9 ± 6.4	0.2	5.5 ± 6.8	0.3
Kurzia latissima	0.0 ± 0.0	0.0	0.4 ± 0.9	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Leydigia cf. *propinqva*	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	4.3 ± 6.8	0.2	0.0 ± 0.0	0.0
Macrothrix laticornis	0.0 ± 0.0	0.0	0.3 ± 0.8	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Macrothrix sp.	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	1.4 ± 3.4	0.1
Moina minuta	78.9 ± 13.7	9.5	40.9 ± 29.3	9.9	37.9 ± 17.0	2.8	19.4 ± 24.6	1.0	17.9 ± 8.0	0.9
Moina reticulata	1.3 ± 3.1	0.2	0.2 ± 0.4	0.0	1.7 ± 2.6	0.1	0.0 ± 0.0	0.0	1.1 ± 2.6	0.1
Moinodaphnia macleayi	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	2.0 ± 3.3	0.1
Plevroxus sp.	0.5 ± 1.2	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0

Table 4 (on next page)

Abundance of copepods

Average (mean ± SD) abundance (inds m^{-3}) and relative abundance (%RA) of various copepod species at the Amazon (Solimões) and the Negro Rivers, the center of the Amazon basin. Sites 1-5 correspond to those in the map in Fig. 1.

	Amazon River				Confluence		Negro River			
	Babk (St. 1)	%RA	Center (St. 2)	%RA	(St. 3)	%RA	Center (St. 4)	%RA	Bank (St. 5)	%RA
Calanoids										
Aspinus acicularis	0.5 ± 1.2	0.1	0.0 ± 0.0	0.0	0.9 ± 2.3	0.1	1.7 ± 4.2	0.2	0.0 ± 0.0	0.0
Argyrodiaptomus sp.	3.5 ± 3.9	0.8	0.6 ± 1.5	0.3	2.6 ± 4.5	0.3	3.9 ± 6.4	0.4	1.6 ± 3.8	0.3
Dasydiaptomus coronatus	1.5 ± 2.5	0.3	3.1 ± 3.6	1.5	4.1 ± 6.2	0.5	0.0 ± 0.0	0.0	3.0 ± 5.3	0.6
Diaptomus ohlei	11.3 ± 14.4	2.5	2.6 ± 3.8	1.2	2.3 ± 3.6	0.3	1.3 ± 3.2	0.1	0.8 ± 2.0	0.2
Dactylodiaptomus pearsei	44.7 ± 25.5	9.9	8.9 ± 4.3	4.2	66.5 ± 64.8	7.7	52.2 ± 43.2	5.0	53.3 ± 38.4	11.1
Notodiaptomus simillimus	1.3 ± 3.1	0.3	1.1 ± 1.5	0.5	1.3 ± 3.1	0.1	0.0 ± 0.0	0.0	0.8 ± 2.0	0.2
Notodiaptomus sp.	1.3 ± 3.1	0.3	2.8 ± 3.9	1.3	2.3 ± 3.8	0.3	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Rhacodiaptomus calatus	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.5 ± 1.3	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Rhacodiaptomus retroflexus	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	2.0 ± 4.9	0.4
Unidentified calanoid copepodites	224.1 ± 123.7	49.5	84.4 ± 61.4	40.2	245.1 ± 223.5	28.5	438.5 ± 316.7	41.9	300.2 ± 157.6	62.7
Cyclopoids										
Ectocyclops sp.	2.9 ± 4.5	0.6	0.3 ± 0.8	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	1.6 ± 4.0	0.3
Eragaselidae	0.5 ± 1.2	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Eucyclops sp.	1.3 ± 3.1	0.3	0.0 ± 0.0	0.0	2.4 ± 3.7	0.3	0.0 ± 0.0	0.0	1.1 ± 2.6	0.2
Mesocyclops longisetus	2.5 ± 4.9	0.6	2.5 ± 4.5	1.2	0.7 ± 1.8	0.1	1.3 ± 3.1	0.1	1.6 ± 4.0	0.3
Mesocyclops meridianus	5.7 ± 4.8	1.3	0.6 ± 1.5	0.3	4.8 ± 7.4	0.6	1.3 ± 3.1	0.1	3.2 ± 5.2	0.7
Metacyclops cf. *brauni*	0.0 ± 0.0	0.0	0.3 ± 0.8	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Microcyclops cf. *alius*	0.5 ± 1.3	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Microcyclops cf. *auceps*	0.5 ± 1.3	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Microcyclops brasilianus	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	1.0 ± 2.5	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Microcyclops ceibaensis	0.0 ± 0.0	0.0	0.3 ± 0.8	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Microcyclops sp.	3.3 ± 3.6	0.7	0.5 ± 1.1	0.2	0.7 ± 1.8	0.1	0.0 ± 0.0	0.0	0.8 ± 2.0	0.2
Oithona amazonica	40.6 ± 24.1	9.0	43.4 ± 26.8	20.7	348.8 ± 405.4	40.6	388.5 ± 556.3	37.1	54.9 ± 53.4	11.5
Thermocyclops decipiens	15.7 ± 12.2	3.5	6.3 ± 4.5	3.0	5.7 ± 7.0	0.7	0.0 ± 0.0	0.0	0.8 ± 2.0	0.2
Thermocyclops cf. *minutus*	5.1 ± 12.5	1.1	1.6 ± 3.9	0.8	2.4 ± 3.7	0.3	0.0 ± 0.0	0.0	1.6 ± 3.8	0.3
Thermocyclops sp.	0.0 ± 0.0	0.0	0.5 ± 0.8	0.2	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Unidentified cyclopoids	0.5 ± 1.2	0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0	0.0 ± 0.0	0.0
Unidentified cyclopod copepodites	78.0 ± 30.8	17.2	49.0 ± 24.4	23.4	157.3 ± 168.3	18.3	143.1 ± 135.4	13.7	42.0 ± 45.6	8.8
Nauplii	7.3 ± 9.7	1.6	1.0 ± 1.8	0.5	10.4 ± 10.5	1.2	15.4 ± 13.7	1.5	9.4 ± 5.7	2.0