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

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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 (blackwater) 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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18	neotropical		
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22 Abstract

23 The boundary zone between two different hydrological regimes is often a biologically enriched 24 environment with distinct planktonic communities. In the center of the Amazon River basin, 25 muddy white water of the Amazon River meets with black water of the Negro River, creating a 26 conspicuous visible boundary spanning over 10 km along the Amazon River. Here, we tested the 27 hypothesis that the confluence boundary between the white and black water rivers concentrates 28 prey and is used as a feeding habitat for juvenile fish by investigating the abundance, biomass 29 and distribution of mesozooplankton and ichthyoplankton communities across the two rivers. 30 Our results show that mesozooplankton abundance and biomass were higher in the black-water 31 river compared to the white-water river; however an exceptionally high mesozooplankton 32 abundance was not observed in the confluence boundary. Nonetheless we found the highest 33 abundance of ichthyoplankton in the confluence boundary, being up to 9-fold higher than in 34 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) 35 36 and low predation risk (white-water). This forms a plausible explanation for the high abundance 37 of ichthyoplankton in the confluence zone of black and white water rivers.

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43 Introduction

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45 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 46 47 between two densities of waters is generally enriched in both dissolved and particulate organic 48 matters as a result of their accumulation at this interface (Hill & Wheeler, 2002). The boundary 49 zone is also a biologically enriched environment with distinct planktonic communities (Morgan, 50 De Robertis & Zabel, 2005; Walkusz et al., 2010; Bolotov, Tsvetkov & Krylov, 2012). Extensive 51 research on oceanic fronts between coastal water and river plumes has shown that the boundary 52 zone can lead to increased primary productivity (Franks, 1992), mechanically concentrating 53 zooplankton (Epstein & Beardsley, 2001; Morgan, De Robertis & Zabel, 2005), and attracting 54 tertiary consumers (Grimes & Kingsford, 1996). Thus, the boundary zone is important for local 55 ecosystem functioning. 56 The Amazon River is well-known for its largest and most dense river network in the 57 world and has the highest level of discharge, contributing ca. 20% of the global continental water 58 discharge into the oceans (Sioli, 1984). In the center of the Amazon basin, muddy white water of

59 the Amazon River (locally named Rio Solimões) meets with black water of the Negro River, one

60 of the largest tributaries, creating a conspicuous visible boundary spanning over 10 km along the

61 Amazon River (Fig. 1). The black water of the Negro River is derived from the high

62 concentration of humic substances, while the white water of the Amazon River is derived from

63 highly suspended inorganic materials (Sioli, 1984; Furch & Junk, 1997; Junk et al., 2015). The

64 water properties of the white and black waters are different in terms of many parameters such as 65 flow speed, conductivity, turbidity, pH, water temperature, nutrient concentrations, and dissolved 66 and particulate organic matter concentrations (Laraque et al., 1999; Moreira-Turcq et al., 2003; 67 Leite, Silva & Freitas, 2006; Filizola et al., 2009; Laraque, Guyot & Filizola, 2009; Franzinelli, 68 2011; Röpke et al., 2016). Due to these differences, the black and white water rivers are not 69 completely mixed until over 100 km beyond the confluence (Laraque, Guyot & Filizola, 2009). 70 The conspicuous boundary between black and white water rivers may be ecologically 71 important as it may act as a mechanical aggregator of planktonic organisms, and contribute to the 72 subsequent attraction of consumers such as juvenile fish. Although local fishermen have 73 observed that the confluence of black and white water rivers is rich in fish, likely due to higher 74 prey abundance, the abundance and biomass of zooplankton and fish at the confluence remains 75 unclear from a quantitative perspective. To date, most studies on zooplankton and fish in this 76 region have been conducted in the floodplain lakes associated with large rivers (Brandorff, 1978; 77 Robertson & Hardy, 1984; Saint-Paul et al., 2000; Keppeler, 2003; Leite, Silva & Freitas, 2006; 78 Trevisan & Forsberg, 2007; Duncan & Fernandes, 2010; Ghidini & Santos-Silva, 2011; Röpke et 79 al., 2016), but studies from large rivers are scarce (Robertson and Hardy 1984; De Lima and 80 Araujo-Lima 2004). Similarly, previous studies investigated zooplankton and fish in the 81 floodplain lakes of mixed waters from black and white water rivers (Trevisan & Forsberg, 2007; 82 Caraballo, Forsberg & Leite, 2016; Röpke et al., 2016), yet very little is known about the 83 boundary interface between white and black water rivers.

84	To test the hypothesis that the confluence boundary between white water of the
85	Amazon River and black water of the Negro River concentrates prey and is used as a feeding
86	habitat for juvenile fish, we investigated the abundance, biomass and distribution of
87	mesozooplankton and ichthyoplankton communities of the of the Amazon and the Negro Rivers
88	and compared them with water at the confluence boundary. We were interested in examining (1)
89	How high is the abundance, biomass and composition of mesozooplankton in black and white
90	water rivers? and (2) How much higher is the abundance and biomass of mesozooplankton and
91	ichthyoplankton at the confluence?
92	

- 93 Materials & Methods
- 94
- 95 Study sites

96 This study was conducted in the center of the Amazon basin where the white water of 97 the Amazon River (locally named Rio Solimões) and the black water of the Negro River (locally 98 named Rio Negro) merge in Manaus, Brazil (Fig. 1). All experiments and preparation of samples 99 were carried out using the facilities of Centro de Projetos e Estudos Ambientais do Amazonas 100 (CEPEAM) on the banks of the Negro River. The sampling of mesozooplankton and 101 ichthyoplankton was conducted at five sites across the rivers: the bank (St. 1) and center (St. 2) 102 of the Amazon River, the confluence (St. 3), and the center (St. 4) and bank (St. 5) of the Negro 103 River (Fig. 1). The bottom of the Amazon River was covered in muddy and sandy sediments, 104 while the river bottom of the Negro River was characterized by hard bedrocks (Junk et al., 2015).

- 105 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
- 106 m (St. 5), which were measured by a measuring rope with a 20 kg weight.
- 107

108 Sample collection

109 We collected mesozooplankton and ichthyoplankton at each sampling site during the 110 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 111 112 and ichthyoplankton were sampled by pooling three vertical tows of a plankton net (mesh size, 113 180-µm; diameter, 30 cm; length, 100 cm) equipped with a flowmeter (Rigo) from 10 m depth to 114 the surface. The plankton net used in this study was not strictly designed for collection of 115 ichthyoplankton (usually a net with a larger mouth and mesh opening is used), thus our net may 116 have misrepresented the number and species richness of fish larvae. Due to a large amount of 117 sand and detrital particles such as plant debris, especially in the white water, the net was washed 118 after every towing in order to reduce net clogging. The pooled samples were immediately 119 brought back to the field laboratory within 30 min, and fixed with buffered formalin to a final 120 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

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126	a 180-µm mesh screen to remove zooplankton and the water samples were brought back to the		
127	laboratory along with the plankton samples. Additional surveys for transparency, water		
128	temperature and chl- <i>a</i> were conducted monthly over a year from March 2012 to February 2013.		
129			
130	Sample analysis		
131	For chlorophyll analysis, triplicate subsamples (50-100 mL each from bucket) were		
132	filtered onto GF/F filters (25 mm, Whatman), then immersed in 90% acetone and stored at 5°C for		
133	24 h. After centrifugation at 3000 rpm for 5 min, the concentrations of chl-a were determined using		
134	a spectrometer (Shimadzu, UV mini 1240) according to the equation of Ritchie (2006). For POC/N		
135	analysis, triplicate subsamples (100-200 mL from bucket) were filtered onto pre-combusted		
136	(500°C, 4 h) GF/F filters (25 mm, Whatman), and then dried for 24 h at 60°C and stored in a		
137	desiccator until analysis. The POC/N concentration was measured using a CN analyzer (Fisons EA		
138	1108 CHNS/O).		
139	Mesozooplankton and ichthyoplankton were identified to the lowest taxonomic level		
140	possible and counted under a dissecting microscope (Leica MZ9.5). Upon observation, large debris		
141	(e.g. wood and plant debris) was removed from the samples as much as possible, and then rose		
142	bengal was added to facilitate the separation of organisms from suspended matter. Large		
143	zooplankton and/or rare species (e.g. larval insects and calanoid copepods) and fish larvae were		
144	first counted and sorted out, then the remaining was split (1/2-1/16), from which all zooplankton		
145	were characterized and enumerated. At least 300 zooplankton were enumerated in each sample.		
146	Copepods and cladocerans were identified to species level and insect and fish larvae to family level		

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147 whenever possible. In the present study, we did not consider rotifers because we used a plankton 148 net with 180 µm mesh, which may have lost a considerable number of rotifers. 149 The body length of copepods, cladocerans and insect larvae was measured using an 150 eyepiece micrometer. The length measurements of zooplankton individuals were converted to dry 151 weight (DW, mg) using previously reported length-weight regression equations (Table 1). The 152 biomass $(B, \text{mg m}^{-3})$ of a given taxonomic group was estimated based on its abundance $(A, \text{inds. m}^{-1})$ ³) and individual dry weight: $B = A \times DW$. Reported length-weight regressions of some species that 153 154 occur at the sampling site were not available, but we used regressions according to similar genera 155 or shapes. Regressions established in tropical waters were also used when possible. 156 157 Statistical analysis 158 The difference between day and night abundance of mesozooplankton was determined 159 using Student's t-test. The difference in the abundance of mesozooplankton and ichthyoplankton 160 between different sites was determined using one-way ANOVA and then differences among 161 means were analyzed using Tukey-Kramer multiple comparison tests. A difference at P < 0.05162 was considered significant. 163 Spatial similarities of mesozooplankton assemblage structure were graphically depicted using non-metric multidimensional scaling (MDS) and group average clustering was 164 165 carried out. The similarity matrix obtained from the abundance values was calculated by the 166 Bray-Curtis index (Bray & Curtis, 1957) with square-root transformed data. To test for spatial 167 variation in community density, analysis of similarities (ANOSIM) was then undertaken (Clarke

- 168 & Warwick, 1994). All multivariate analyses were conducted with the software PRIMER v. 6
- 169 (Plymouth Marine Laboratory).
- 170
- 171 Results
- 172
- 173 Environmental factors

174 Water temperature, transparency, and chlorophyll concentrations varied among months 175 throughout the year, and these parameters were consistently distinct for white and black water 176 rivers (Fig. 2). The values in the confluence in general were in the middle between black and 177 white water rivers. The surface water temperatures were higher from October to December (Fig. 178 2a), and the average (mean \pm SD) surface water temperature in black water was higher by 1.2 \pm 179 1.0 °C than that in white water, though the difference was not significant (Table 2; t = -1.86, df = 180 20, p = 0.078). Transparency (secchi depth) was significantly lower in white water (0.32 ± 0.10 181 m) than black water $(0.95 \pm 0.14 \text{ m})$ (Fig. 2b, Table 2). Chl-a concentrations in white water river 182 showed higher values during May-September and December-January, while those in black water 183 river were relatively high in May and December-January (Figs. 2c). The chl-a concentrations 184 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 2.8-2.9-185 186 folds higher than in black water (Table 2). C/N ratio was comparable between black and white 187 water rivers, but lower in the confluence.

188

189 Mesozooplankton abundance and biomass

190 There was no significant difference in mesozooplankton abundance between day and 191 night at all sites (Student's *t*-test, df = 4, P>0.05 at all sites). The highest abundance (2,817 ± 192 1,162 inds. m⁻³, mean \pm SD) and biomass (5.14 \pm 2.55 mg m⁻³) of mesozooplankton were 193 observed at the center of the Negro (black water) river (St. 4), while the lowest abundance (577 \pm 194 345 inds, m⁻³) and biomass (1.30 \pm 0.46 mg m⁻³) were observed at the center (St. 2) of the 195 Amazon (white water) river (Fig. 3a, b). The mesozooplankton abundance and biomass from the 196 center of black water river were significantly different and 4.9-fold and 3.9-fold higher, 197 respectively, than those of white water river (Student's *t*-test; t = -4.5, df = 10, p < 0.005 for 198 abundance; t = -3.6, df = 10, p < 0.005 for biomass). At the confluence (St. 3), the 199 mesozooplankton abundance $(2,060 \pm 1,269 \text{ inds. m}^3)$ and biomass $(4.70 \pm 3.28 \text{ mg C m}^3)$ 200 showed intermediate values between black and white water rivers. The abundance and biomass 201 of mesozooplankton in the confluence showed the highest abundance two times out of a total of 202 6 sampling times. Cladocerans were the most dominant group in terms of abundance, 203 contributing 66.2%-82.2% of the total mesozooplankton abundance at all sites, followed by 204 copepods (19.7-41.7%) and insect larvae (0.1-0.6%) (Fig. 3a). On the contrary, copepods were 205 the most important in terms of biomass, contributing 64.0-79.1% of the total mesozooplankton 206 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.

214 The abundance of copepods was highest in the center (St. 4) of black water river 215 $(1,047 \pm 508 \text{ inds}, \text{ m}^{-3})$, followed by the confluence $(860 \pm 684 \text{ inds}, \text{ m}^{-3})$ (Fig. 3e). On the other hand, the biomass of copepods in the confluence (St. 3) and the center (St. 4) of black water river 216 217 were comparable, at 3.71 ± 3.05 mg C m⁻³ and 3.79 ± 2.00 mg C m⁻³, respectively (Fig. 3f). In 218 total 25 species of copepods were observed (Table 4), among which (excluding copepodites) 219 Oithona amazonica was the most dominant taxa in terms of abundance at all sites, contributing 220 9.0%-40.6% of the total copepod abundance, while Dactylodiaptomus pearsei was the most 221 important in terms of biomass (34.6-58.5%) (Fig. 3e,f). The highest abundance of O. amazonica 222 was observed at the center (St. 4) of black water river (388 ± 566 inds. m⁻³), followed by the 223 confluence $(349 \pm 405 \text{ inds. m}^{-3})$.

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).

230

231 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.

- 237
- 238 Ichthyoplankton abundance and composition

239 The abundance of juvenile fish in the confluence (St. 3) $(9.7 \pm 2.5 \text{ inds } \text{m}^{-3})$ was 240 significantly and 2.1-8.8 times higher than in the other sites (Tukey-Kramer, df = 29, P<0.01) 241 (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 242 243 fish abundance at the bank of white water river (St. 1) was the next abundant $(4.6 \pm 3.7 \text{ inds m}^{-3})$. Auchenipteridae siluriformes were only sampled at the banks of both white (St. 1) and black 244 245 water rivers (St. 5), while clupeiformes were only observed in the center of the white water river 246 (St. 2).

247

248 Discussion

249

250 This study describes the abundance and composition of mesozooplankton and 251 ichthyoplankton across the Negro (black water) and the Amazon (white water) rivers in the

252 center of the Amazon basin to elucidate the distributional differences between the two rivers and 253 their confluence zone, which were not previously well-described quantitatively. The water 254 properties of the two rivers were distinct: surface water temperatures and transparency were 255 always higher in black water rivers, while chlorophyll and particulate organic matter 256 concentrations were always higher in white water rivers. Surface water temperature in black 257 water was higher by 1.2°C on average than white water throughout the year, which is congruent with previous studies reporting higher temperature by 1°C in the Negro River (Franzinelli, 2011). 258 259 The higher water temperature in the Negro River may result from its darker color and slower 260 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 261 al., 2003; Filizola et al., 2009; Franzinelli, 2011).

262 The mean concentration of chl-a in the white water river (10.5 μ g l⁻¹) was higher than 263 that in the black water river (4.8 μ g l⁻¹) in this study. Although concentrations are much different 264 between lakes and rivers, a similar pattern was previously reported in floodplain lakes, where 265 surface water chl-a concentration was higher in lakes associated with the Amazon (white water) 266 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 267 268 may be the result of higher concentrations of inorganic nutrients derived from the Amazon River 269 (Trevisan & Forsberg, 2007). However, in the Amazon River system, primary production is not 270 likely because of poor light penetration due to high turbidity (euphotic depth: ca. 0.3 m), where 271 the mixing depth was probably always down to the bottom due to turbulence associated with the 272 strong current, making respiration higher than photosynthesis (Fisher & Parsley, 1979).

273	Therefore, the presence of chlorophyll in the Amazon River probably results from the input of	
274	more productive environments such as the adjacent lakes (Fisher & Parsley, 1979).	
275	That the white river had higher POC concentrations than the black river (1,262 vs. 446	
276	mg m ⁻³) in this study is in agreement with previous studies reporting higher POC in the Amazon	
277	River (~1,820 mg m ⁻³) than in the Negro River (720-1,030 mg m ⁻³) during the low water period	
278	(Moreira-Turcq et al., 2003). The C/N ratio was similar for white and black waters (3.8 vs. 3.9)	
279	in this study, which is congruent with previous studies (Moreira-Turcq et al., 2003). However,	
280	the C/N ratios in this study during the rising water period was much lower than those previously	
281	observed during low water periods (September, $C/N = 9$) (Moreira-Turcq et al., 2003). These	
282	differences suggest that the composition of particulate organic matter (POM) varies over seasons	
283	rather than between black and white waters.	
284		
285	Mesozooplankton difference of black and white water rivers	
286	As the MDS and ANOSIM analyses clearly indicated, the present study revealed that	
287	the compositions of mesozooplankton assemblages differ between the white water of the	
288	Amazon River and black water of the Negro River. We also found a higher abundance of	
289	mesozooplankton communities in black water river compared to white water river. The	
290	abundance of zooplankton in tropical large rivers depend largely on the supply from adjacent	
291	lentic sources (standing water bodies) connected to the river such as channel and floodplain	
292	habitats (Rzoska, 1978; Saunders & Lewis, 1988a, 1989; Basu & Pick, 1996; Reckendorfer et al.,	
293	1999; Górski et al., 2013). The zooplankton sampling period in this study corresponds to the	

294 rising water period (March), where rising riverine water starts to wash out ambient zooplankton 295 from associated lentic sources into the rivers (Saunders & Lewis, 1988a,b, 1989). Assuming that 296 adjacent lentic areas (e.g., floodplain lakes) are a major source of zooplankton in river systems in 297 this study, there may have been a larger zooplankton transport from stagnant water bodies 298 connected to the Negro (black water) river compared to those of the Amazon (white water) river. 299 However, there are fewer lakes in the Negro River floodplain than in the floodplains of white 300 water rivers because of the lower hydrodynamics (Junk et al., 2015). Previous studies from 301 floodplain lakes in the center of the Amazon basin reported that the abundance of 302 mesozooplankton (cladocerans and copepods) was 2-25 fold higher in black water lakes 303 associated with the Negro River than in white water lakes during rising-high water periods (Feb-304 June) (Brandorff, 1978; Hardy, 1980), which might explain the higher mesozooplankton 305 abundance in the black water river in this study. However, previous studies conducted during the 306 end of low water periods (November-December) reported higher zooplankton abundance in 307 white water lakes (Brandorff, 1978; Trevisan & Forsberg, 2007), suggesting that growth and 308 mortality processes of lake zooplankton vary over seasons among the different water lakes. 309 Reproduction of zooplankton in the flowing waters can also increase abundance at a 310 low flow rate (Bertani, Ferrari & Rossetti, 2012). River zooplankton are unable to reproduce in 311 flow speed exceeding 0.4 m s⁻¹ (Rzoska, 1978) and thus lower residence time can mean a lower 312 zooplankton density (Basu & Pick, 1996). Considering that the flow speed of the Amazon River 313 (Rio Solimões) exceeds 1.0 m s⁻¹ (Filizola et al., 2009), reproduction of zooplankton is likely 314 impossible in this white water river. Large amounts of inorganic suspended particles in white

315 water river may also negatively influence zooplankton abundance in this system (McCabe & 316 O'Brien, 1983; Kirk & Gilbert, 1990; Junk & Robertson, 1997). Indeed, zooplankton abundance 317 in the white water river was higher in the bank than at the center, suggesting that adjacent lentic 318 sources are the primary source of zooplankton in this white river system. On the contrary, 319 zooplankton are able to reproduce in the slower current of black water rivers $(0.1-0.3 \text{ m s}^{-1})$ 320 (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 321 322 zooplankton reproduction occurs in this black water river. In summary, the higher supply of 323 zooplankton from adjacent lentic water bodies (such as floodplain lakes) and/or possible 324 reproduction might help to explain why mesozooplankton abundance was higher in the black 325 water river compared to the white water river.

326

327 Mesozooplankton and ichthyoplankton in the confluence

328 As previously examined in oceanic frontal boundaries between river plumes and adjacent 329 marine waters (Morgan, De Robertis & Zabel, 2005; Walkusz et al., 2010), convergent flow at the 330 boundary between distinct water masses functions to concentrate planktonic organisms, including 331 larval fish. In the present study, we found significantly higher abundance of fish larvae in the 332 confluence throughout the study period, supporting the hypothesis that the confluence between 333 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 & 334 335 Zabel, 2005), was not observed in the confluence boundary in this study. The highest average

336 abundance of mesozooplankton was observed in the center of black water river (the Negro River), 337 though there was no difference in terms of zooplankton biomass between the confluence and the 338 center of black water river. Unlike oceanic fronts, where riverine freshwater plumes stand still 339 facing the coastal marine water, which enhances the mechanical concentration of zooplankton 340 (Morgan, De Robertis & Zabel, 2005), the black and white water rivers in the present study flow 341 down together (but without mixing), probably making the zooplankton concentration less 342 distinguished in the boundary zone. However it should be noted that the mesozooplankton 343 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 344 345 the Negro River.

346 Then the question arises as to why ichthyoplankton abundance was high in the 347 confluence boundary zone. In black water rivers, potentially higher predation risks for larval fish 348 would be expected given that larvae can be more easily seen by predators due to fewer suspended 349 solids (De Lima & Araujo-Lima, 2004). On the contrary, white waters with high suspended solids 350 are considered to be safer places for juvenile fish because of lower transparency and higher 351 turbulence, which may act as refuge from predators (De Lima & Araujo-Lima, 2004). Therefore 352 the confluence zone can be a boundary interface between high and low predation pressures for fish 353 larvae. From the perspective of food availability (at least for zooplanktivorous fish), the confluence 354 between white and black waters is sandwiched by both environments with low and high food 355 concentrations. Fish larvae may find more prey in the center of black water, yet fish larvae 356 abundance was the lowest in the Negro River, suggesting higher predation pressure in black water

357	river even in a food-rich environment. Therefore, the confluence zone between black and white
358	water rivers may function as a boundary layer that has benefits from both low predation risk and
359	high food concentrations for fish larvae. In summary, the combined effects of food availability and
360	predator avoidance form a plausible explanation for the high abundance of ichthyoplankton in the
361	confluence zone of black and white water rivers. The lower C/N ratio of POM found in the
362	confluence (2.8) compared to the adjacent rivers (3.8-3.9) may be the result of higher heterotrophic
363	activity in this boundary zone since the C/N ratio of carnivorous fish feces is generally very low
364	(ca. 3, Smriga et al. (2010)).
365	
366	Conclusion
367	
368	We found that mesozooplankton abundance and biomass were higher in the black-
369	water of the Negro River compared to the muddy white-water of the Amazon River, probably
370	due to a higher supply of zooplankton from lentic waters adjacent to the Negro River and/or
371	reproduction. An exceptionally high mesozooplankton abundance was not observed in the
372	confluence boundary between the two rivers; nonetheless we found that the confluence zone acts
373	as an aggregator of ichthyoplankton. The confluence boundary between black and white water
374	rivers may function as a boundary layer that offers benefits of both high food (zooplankton)
375	concentrations and low predation risk. This forms a plausible explanation for the high abundance
376	of ichthyoplankton in the confluence zone. These combined effects may also explain the reason

377	for the larger fish catches in the confluence of black and white water rivers that have been		
378	empirically noted by local fishermen.		
379			
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381			
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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) (S03°07'36.35'';W59°53'10.25'') and center (St. 2) (S03°07'29.89'';W59°53'30.92'') of the Amazon River, the confluence (St. 3) (S03°07'29.64'';W59°53'55.10''), and center (St. 4) (S03°07'13.43'';W59°54'05.19'') and bank (St. 5) (S03°06'57.97'';W59°54'17.74'') of the Negro River. (D) the confluence.

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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.



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.



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Bank

(St. 5)

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).



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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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).

1

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

Table 2(on next page)

Environmental factors

Average (mean \pm 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).

1

	Amazon River (St.	1)	Confluence (St. 3)		Negro River (St.	P (St. 1 vs. St. 5)	
Water temperature (°C)	$28.2 \pm$	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	$881 \pm$	144	446	± 62	0.0291
PON (µg L-1)	333 \pm	23	316 ±	27	114	± 3	0.0001
C/N	3.8 ±	1.1	2.8 ±	0.3	3.9	± 0.6	0.8570

Table 3(on next page)

Abundance of cladocerans

Average (mean \pm 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.

	Amazon River					Confluence	Confluence			/er							
	Babk (St	t. 1)		%RA	Center (S	t. 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	$0.0 \pm$	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	$108.7 \pm$	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	$501.1 \pm$	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 ±	.00	0.0	$0.0 \pm$	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 \pm	0.0	0.0	0.0 ±	.00	0.0	$0.0 \pm$	0.0	0.0
Chydoros sphaericus	2.2	±	3.0	0.3	0.4 =	±	0.9	0.1	0.0 \pm	0.0	0.0	0.0 ±	. 0.0	0.0	$0.0 \pm$	0.0	0.0
Daphnia gessneri	2.6	±	6.3	0.3	0.8 =	±	1.0	0.2	4.0 \pm	6.2	0.3	0.0 ±	.00	0.0	$0.0 \pm$	0.0	0.0
Diaphanosomoa birgei	0.0	±	0.0	0.0	0.0 =	±	0.0	0.0	0.0 \pm	0.0	0.0	1.5 ±	3.8	0.1	$0.0 \pm$	0.0	0.0
Diaphanosoma polyspina	546.4	±	170.4	65.5	266.0 :	±	175.9	64.2	$462.0 \pm$	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 \pm	1.8	0.1	0.0 ±	. 0.0	0.0	$0.0 \pm$	0.0	0.0
Ephemeroporous sp.	0.0	±	0.0	0.0	0.0 =	±	0.0	0.0	$0.0 \pm$	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 \pm	0.0	0.0	0.0 ±	: 0.0	0.0	$0.0 \pm$	0.0	0.0
Holopedium amazonicum	0.0	±	0.0	0.0	0.0 =	±	0.0	0.0	$2.7 \pm$	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 \pm	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 \pm	0.0	0.0	0.0 ±	. 0.0	0.0	$0.0 \pm$	0.0	0.0
Leydigia cf. propinqva	0.0	±	0.0	0.0	0.0 =	±	0.0	0.0	$0.0 \pm$	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 \pm	0.0	0.0	0.0 ±	: 0.0	0.0	$0.0 \pm$	0.0	0.0
Macrothrix sp.	0.0	±	0.0	0.0	0.0 =	±	0.0	0.0	$0.0 \pm$	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	$37.9 \pm$	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 \pm	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	$0.0 \pm$	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 \pm 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							nce		Negro Rive	Negro River				
_	Babk (St. 1)		%RA	Center (St. 2)		%RA	(St. 3))	%RA	Center (St. 4	4)	%RA	Bank (St. 5)	%RA
Calanoids															
Aspinus acicularis	$0.5 \pm$	1.2	0.1	$0.0 \pm$	0.0	0.0	0.9 ±	2.3	0.1	1.7 ±	4.2	0.2	$0.0 \pm$	0.0	0.0
Argyrodiaptomus sp.	$3.5 \pm$	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	$0.0 \pm$	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	$0.8 \pm$	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	$0.0 \pm$	0.0	0.0	$0.8 \pm$	2.0	0.2
Notodiaptomus sp.	1.3 ±	3.1	0.3	$2.8 \pm$	3.9	1.3	2.3 ±	3.8	0.3	$0.0 \pm$	0.0	0.0	$0.0 \pm$	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	$438.5 \pm$	316.7	41.9	$300.2 \pm$	157.6	62.7
Cyclopoids															
Ectocyclops sp.	$2.9 \pm$	4.5	0.6	0.3 ±	0.8	0.1	0.0 ±	0.0	0.0	$0.0 \pm$	0.0	0.0	1.6 ±	4.0	0.3
Eragaselidae	$0.5 \pm$	1.2	0.1	$0.0 \pm$	0.0	0.0	0.0 ±	0.0	0.0	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0
Eucyclops sp.	1.3 ±	3.1	0.3	$0.0 \pm$	0.0	0.0	2.4 ±	3.7	0.3	$0.0 \pm$	0.0	0.0	1.1 ±	2.6	0.2
Mesocyclops longisetus	$2.5 \pm$	4.9	0.6	$2.5 \pm$	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	$0.0 \pm$	0.0	0.0	0.3 ±	0.8	0.1	0.0 ±	0.0	0.0	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0
Microcyclops cf. alius	$0.5 \pm$	1.3	0.1	$0.0 \pm$	0.0	0.0	0.0 ±	0.0	0.0	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0
Microcyclops cf. auceps	$0.5 \pm$	1.3	0.1	0.0 ±	0.0	0.0	0.0 ±	0.0	0.0	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0
Microcyclops brasilianus	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0	1.0 ±	2.5	0.1	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0
Microcyclops ceibaensis	$0.0 \pm$	0.0	0.0	0.3 ±	0.8	0.1	0.0 ±	0.0	0.0	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0
Microcyclops sp.	3.3 ±	3.6	0.7	$0.5 \pm$	1.1	0.2	0.7 ±	1.8	0.1	$0.0 \pm$	0.0	0.0	$0.8 \pm$	2.0	0.2
Oithona amazonica	40.6 ±	24.1	9.0	43.4 ±	26.8	20.7	$348.8 \pm$	405.4	40.6	$388.5 \pm$	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	$0.0 \pm$	0.0	0.0	$0.8 \pm$	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	$0.0 \pm$	0.0	0.0	1.6 ±	3.8	0.3
Thermocyclops sp.	$0.0 \pm$	0.0	0.0	0.5 ±	0.8	0.2	0.0 ±	0.0	0.0	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0
Unidentified cyclopoids	0.5 \pm	1.2	0.1	$0.0 \pm$	0.0	0.0	0.0 ±	0.0	0.0	$0.0 \pm$	0.0	0.0	$0.0 \pm$	0.0	0.0
Unidentified cyclopod copepodites	$78.0 \pm$	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

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