Zooplankton diversity of three floodplain lakes of the Dibru-Saikhowa Biosphere reserve, upper Assam, northeast India

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Abstract: Limnological survey (October 2013–September 2015) of Maghuri, Khamti Guali and No.11 floodplain lakes (beels) of the Dibru-Saikhowa Biosphere Reserve (DSBR), upper Assam, northeast India (NEI) revealed 210 (184±4) species of zooplankton, belonging 78 genera and 32 families, with several species of global and regional distribution interest. The biodiverse zooplankton assemblage and interesting taxa are hypothesized to habitat diversity and environmental heterogeneity of these wetlands located in the Assam-gateway - an important biogeographic corridor of India. The monthly richness and community similarities depicted heterogeneity of zooplankton composition of the individual beels. Low abundance is attributed to soft–moderately hard waters with low ionic concentrations. Zooplankton richness and abundance followed no definite pattern of monthly or annual variations; Rotifera > Cladocera influenced overall diversity in the three beels. High species diversity affirmed habitat heterogeneity, while high evenness and low dominance without quantitative importance of any species affirmed ‘generalist nature’ of zooplankton of the different beels. Our results indicated limited influence of individual abiotic factors but CCA registered moderately high cumulative importance of seventeen abiotic factors on zooplankton assemblages of DSBR beels.

Introduction
Zooplankton, an integral component of freshwater metazoans, has been studied from different parts of India since more than one century. The Indian literature depicts proliferation of ‘routine’ reports from varied ecosystems loaded with incomplete species lists and even unidentified species and thus provides limited information for biodiversity and ecology considerations (Sharma and Sharma, 2008). Nevertheless, some detailed works on zooplankton diversity from this country are limited to the floodplain lakes (beels) of Assam (Sharma, 2011a; Sharma and Sharma, 2011a, 2012; Sharma and Hatimuria, 2017) and pats of Manipur (Sharma, 2011b) states of NEI. In addition, Sharma and Sharma (2008, 2017a, b, 2019) emphasized these floodplains to be one of the globally interesting habitats for zooplankton taxocoenosis.

Realizing paucity of meaningful information on freshwater zooplankton diversity of India in general and NEI in particular, we undertook limnological survey of three beels of the upper Brahmaputra river basin, and located in the Assam-gateway and the Indo-Burma biodiversity hot-spot. Our observations deal with monthly variations in richness, species composition, abundance, species diversity, equitability and dominance, and analysis of individual and cumulative influence of abiotic factors on zooplankton and the constituent groups the sampled beels. The salient features of faunal diversity, abundance and ecology noted vide this study are highlighted and discussed vis-a-vis importance for zooplankton diversity of India as well as of the tropical and subtropical floodplain lakes.

Materials and Methods
The observations were undertaken in three floodplain lakes namely Maghuri (altitude: 96.1 m ASL, area:
119 ha), Khamti Guali (altitude: 97.4 m ASL, area: 11 ha) and No. 11 (altitude: 94.7 m ASL, area: 12 ha) beels of the Dibru-Saikhowa Biosphere Reserve (DSBR), Tinsukia district, upper Assam, NEI (Fig. 1). The sampled beels are invariably refereed as ‘DSBR beels’ in this text.

Water samples as well as qualitative and quantitative plankton and semi-plankton samples were collected monthly from the three beels during October 2013-September 2015. Water samples were examined for 17 abiotic parameters. Water temperature was recorded using a centigrade thermometer; pH and specific conductivity were recorded with the field probes; and the rainfall data was obtained from the Citrus Research Station, Tinsukia, Assam. Dissolved oxygen was estimated by the modified Winkler’s method, and other abiotic factors namely free carbon-dioxide, total alkalinity, total hardness, calcium, magnesium, chloride, dissolved organic matter, total dissolved solids, phosphate, nitrate, sulphate and silicate were analyzed following APHA (1992).

The qualitative plankton and semi-plankton samples collected each, by towing nylonolt plankton net (No. #50 µm), were preserved in 5% formalin. These samples were screened with a Wild Stereoscopic Binocular Microscope for isolation of various taxa which were mounted in polyvinyl alcohol–lactophenol mixture. Various zooplankton were observed with Leica (DM 1000) stereoscopic phase contrast microscope fitted with an image analyzer and species were identified following Koste (1978), Michael and Sharma (1988), Korovchinsky (1992), Ranga Reddy (1994, 2001), Segers (1995), Sharma (1998), Sharma and Sharma (1999a, b, 2000, 2008, 2013), Orlova-Bienkowskaja (2001), Jersabek and Leitner (2013), and Sharma et al., (2017). The community similarities were calculated vide Sørensen’s index and the hierarchical cluster analysis.
was consequently done using SPSS (version 20).

Monthly quantitative plankton samples from DSBR beels were obtained by filtering 25 L of water each through nylobolt plankton net and were preserved in 5% formalin. Quantitative enumeration of zooplankton and their constituent groups was done using Sedgewick-Rafter counting cell. The abundance of various taxa was expressed as n/l as well as ranges and means ± S.D. Species diversity (Shannon’s index), dominance (Berger-Parker’s index) and evenness (E1 index) were calculated following Ludwig and Reynolds (1988), and Magurran (1988). Two-way analysis of variance (ANOVA) was applied to ascertain significance of variations of the biotic assemblages. Pearson correlation coefficients for Maghuri, Khamti Guali and No.11 beels (r1, r2 and r3, respectively) were calculated between abiotic and biotic parameters; P-values were calculated vide http://vassarstats.net/tabs.html and their significance were ascertained after applying Bonferroni corrections. The canonical correspondence analysis (XLSTAT 2015) was done to observe cumulative influence of seventeen abiotic parameters namely water temperature, rainfall, pH, specific conductivity, dissolved oxygen, free carbon-dioxide, total alkalinity, total hardness, calcium, magnesium, chloride, dissolved organic matter, total dissolved solids, phosphate, nitrate, sulphate and silicate on zooplankton assemblages of the three beels.

Results

The temporal variations (mean±SD) of the different abiotic parameters of Maghuri, Khamti Guali and No.11 beels, during October 2013-September 2015, are presented in Table 1. Plankton and semi-plankton samples examined from DSBR beels revealed total 210 zooplankton species, spread over 78 genera and 32 families (Table 2), with individual richness of 190 > 182 > 180 species in No.11 > Khamti Guali > Maghuri beels, respectively (Table 3).

The monthly zooplankton richness (Table 4) varied between 34-90, 39-99 and 30-105 species during the study period (Figs. 2-3), and recorded 39.1-71.7, 37.8–73.0 and 37.0-76.2% community similarities...
in Maghuri, Khamti Guali and No.11, respectively (Table 4). Of the important components, Rotifera richness ranged between 16-59, 15-70 and 14-76 species, while Cladocera richness varied between 10-26, 10-31 and 12-31 species Maghuri beel, in Khamti Guali beel and No.11 beel, respectively (Table 4). The hierarchical cluster of zooplankton assemblages of the three beels are indicated in Figures 4-6.

In Maghuri beel (Fig. 4), peak zooplankton similarity was observed between April, 2014 and June, 2014, during the first year and between June, 2015 and July, 2015 in the following year. In all 35, 26, 3 and 2 instances indicated 51-60, 41-50, 61-70, and 31-40% similarities, while 36, 15, 14 and 1 instance indicated between 51-60, 41-50, 61-70, and 71-80% similarities during two years, respectively. In Khamti Guali beel (Fig. 5) peak similarity was observed between October, 2013 and November, 2013 during first year; 36, 16, 11 and 3 instances indicated 51-60, 61-70, 71-80 and 31-40% similarities, respectively. During the second year, peak similarity was observed between October, 2014 and November, 2014 and 27, 25, 10, 2 and 2 instances indicated 51-60, 41-50, 61-70, 71-80 and 31-40% similarities, respectively. Zooplankton similarities of No.11 beel (Fig. 6) recorded peak between April, 2014 and May,
2014 during the first year and 34, 23, 7 and 2 instances indicated similarities between 51-60, 41-50, 61-70, and 31-40%, respectively. Peak similarity was noted between July, 2015 and August, 2015 during second year and 27, 25, 10, 2 and 2 instances indicated similarities between 51-60, 41-50, 61-70, 71-80 and 31-40%, respectively.

Zooplankton density ranged between 139-286, 150-261 and 99-268 n/l in Maghuri, Khamti Guali and No. 11 beels, respectively (Table 5) during the study period (Figs. 7-8); it comprised between 59.0±9.9 to 61.9±10.0% of net plankton abundance. Rotifera recorded abundance between 56-152, 56-155 and 37-152 n/l; Cladocera abundance ranged between 24-101,
41-121 and 37-113 n/l; Rhizopoda recorded density variations of 0-34, 0-34 and 12-37 n/l; and Copepoda density ranged between 10-29, 4-24 and 0-21 n/l; and Ostracoda density ranged between 0-6, 1-6 and 0-4 n/l in Maghuri beel, Khamti Guali beel and No. 11 beel, respectively (Table 4). Lecanidae and Chydoridae recorded quantitative importance; Lepadellidae, Brachionidae, Daphniidae and Macrothricidae
indicated limited role, while no individual zooplankton species indicated importance in the three beels (Table 4). The species diversity, dominance and evenness varied (Table 4) between $3.372-4.206$, $3.401-4.324$ and $3.257-4.454$; $0.041-0.074$, $0.036-0.100$ and $0.027-0.120$; $0.935-0.969$, $0.921-0.963$ and $0.930-0.972$ in Maghuri, Khamti Guali and No. 11 beels, respectively (Table 5).

Zooplankton richness is positively correlated with total dissolved solids ($r_3=0.575$, $P=0.0033$) and Rotifera richness showed positive correlation with rainfall ($r_3=0.692$, $P=0.0002$) only in No. 11. Zooplankton abundance positively correlated with rainfall ($r_2=0.746$, $P=0.0001$) and water temperature ($r = 0.603$, $P=0.0018$); Rotifera abundance showed positive correlation with rainfall ($r_2=0.596$, $P=0.596$).

### Table 5. Quantitative variations of zooplankton of DSBR beels (ranges, mean ± SD) (October 2013- September 2015).

<table>
<thead>
<tr>
<th>Abundance</th>
<th>Maghuri beel</th>
<th>Khamti Guali beel</th>
<th>No.11 beel</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net plankton n/l</td>
<td>214-950</td>
<td>359±150</td>
<td>366±56</td>
</tr>
<tr>
<td>Zooplankton n/l</td>
<td>139-286</td>
<td>198±36</td>
<td>205±31</td>
</tr>
<tr>
<td>% composition</td>
<td>14.6-83.0</td>
<td>60.4±15.8</td>
<td>61.9±10.0</td>
</tr>
<tr>
<td>Species diversity</td>
<td>3.372-4.206</td>
<td>3.827±0.197</td>
<td>3.401-4.324</td>
</tr>
<tr>
<td>Dominance</td>
<td>0.041-0.074</td>
<td>0.058±0.010</td>
<td>0.036-0.100</td>
</tr>
<tr>
<td>Evenness</td>
<td>0.935-0.969</td>
<td>0.955±0.008</td>
<td>0.921-0.963</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Different Groups</th>
<th></th>
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<tbody>
<tr>
<td>Rotifera (n/l)</td>
<td>56-152</td>
<td>99±24</td>
<td>103 ±30</td>
</tr>
<tr>
<td>% composition</td>
<td>35.0-61.7</td>
<td>50.0±6.5</td>
<td>49.6±9.5</td>
</tr>
<tr>
<td>Cladocera</td>
<td>24-101</td>
<td>58±18</td>
<td>66±17</td>
</tr>
<tr>
<td>% composition</td>
<td>14.6-37.9</td>
<td>29.0±5.7</td>
<td>32.9±9.1</td>
</tr>
<tr>
<td>Rhizopoda</td>
<td>0-34</td>
<td>20±8</td>
<td>20±7</td>
</tr>
<tr>
<td>% composition</td>
<td>0.0-19.9</td>
<td>10.2±4.7</td>
<td>9.6±3.8</td>
</tr>
<tr>
<td>Copepoda</td>
<td>10-29</td>
<td>18±5</td>
<td>14±5</td>
</tr>
<tr>
<td>% composition</td>
<td>3.8-15.2</td>
<td>9.2±3.3</td>
<td>7.0±2.2</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>0-6</td>
<td>3±2</td>
<td>2±1</td>
</tr>
<tr>
<td>% composition</td>
<td>0.0-3.5</td>
<td>1.6±0.9</td>
<td>0-1.8</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Important families (n/l)</th>
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<tbody>
<tr>
<td>Lecanidae</td>
<td>32-81</td>
<td>48±12</td>
<td>48±16</td>
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<tr>
<td>Lepadellidae</td>
<td>3-23</td>
<td>10±5</td>
<td>11±7</td>
</tr>
<tr>
<td>Brachionidae</td>
<td>0-26</td>
<td>10±6</td>
<td>12±4</td>
</tr>
<tr>
<td>Chydoridae</td>
<td>15-55</td>
<td>39±13</td>
<td>41±13</td>
</tr>
<tr>
<td>Daphnidae</td>
<td>0-17</td>
<td>7±4</td>
<td>13±5</td>
</tr>
<tr>
<td>Macrothricidae</td>
<td>1-23</td>
<td>9±5</td>
<td>8±4</td>
</tr>
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Figure 7. Monthly variations in zooplankton abundance of DSBR beels (2013-2014).

![Figure 7](image-url)
Lecanidae showed positive correlation with rainfall ($r^2=0.597$, $P=0.0021$); Chydroridae showed positive correlation with rainfall ($r^2=0.575$, $P=0.0023$) in Khamti Guali beel. Zooplankton and its constituent groups showed no significant relationship with any abiotic factor in Maghuri beel. The canonical correspondence analysis (CCA) with 17 abiotic factors (Figs. 9-11) registered cumulative influence.
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Figure 10. CCA coordination biplot of Zooplankton and abiotic factors of Khamti Guali beel.

**Abbreviations:** **Abiotic:** Ca (Calcium), Cl (Chloride), DOM (dissolved organic matter), DO (dissolved oxygen), FCO2 (free carbon dioxide), Rain (rainfall), No3 (nitrate), Po4 (phosphate), Sio2 (silicate), Sc (specific conductivity), So4 (sulphate), TA (total alkalinity), TDS (total dissolved solids), TH (total hardness), pH (hydrogen-ion concentration), Wt (water temperature). **Biotic:** Bra (Brachionidae), Chy (Chydoridae), Cld (Cladocera), CIR (Cladocera richness), Cop (Copepoda), Dap (Daphniidae), Lec (Lecanidae), Lep (Lepadellidae), LB (Lecane bulla), L1 (Lecane leontina), Mac (Macrothricidae), M (Macrothrix triserialis), NP (Net Plankton), Ost (Ostracoda), Rot (Rotifera), RR (Rotifera richness), Rhz (Rhizopoda), Pp (Platiumus patulus), Tri (Trichocercidae), Zoo (Zooplankton), ZR (Zooplankton richness).

Figure 11. CCA coordination biplot of Zooplankton and abiotic factors of No. 11 beel.

**Abbreviations:** **Abiotic:** Ca (Calcium), Cl (Chloride), DOM (dissolved organic matter), DO (dissolved oxygen), FCO2 (free carbon dioxide), Rain (rainfall), No3 (nitrate), Po4 (phosphate), Sio2 (silicate), Sc (specific conductivity), So4 (sulphate), TA (total alkalinity), TDS (total dissolved solids), TH (total hardness), pH (hydrogen-ion concentration), Wt (water temperature). **Biotic:** Bra (Brachionidae), Chy (Chydoridae), Cld (Cladocera), CIR (Cladocera richness), Cop (Copepoda), Cs (Chydorus sphaericus), Dap (Daphniidae), Lec (Lecanidae), Lep (Lepadellidae), L1 (Lecane leontina), Mac (Macrothricidae), M (Macrothrix triserialis), NP (Net Plankton), Ost (Ostracoda), Rot (Rotifera), RR (Rotifera richness), Rhz (Rhizopoda), Pp (Platiumus patulus), Tri (Trichocercidae), Zoo (Zooplankton), ZR (Zooplankton richness).
of 73.65, 61.42 and 63.56% on zooplankton assemblages, along first two axes, in Maghuri, Khamti Guali and No.11 beels, respectively.

Discussions

Low ionic concentrations warranted their inclusion under Class I category of trophic classification vide Talling and Talling (1965), while water temperature concurred with geographical location of the three beels. Besides, other notable attributes included soft to marginally hard, circumneutral-alkaline, and moderately oxygenated calcium poor waters; total alkalinity attributed to bicarbonate ions; and low chloride, lower nutrients and occurrence of free carbon dioxide throughout the study period (Sharma et al., 2017).

Total zooplankton richness (210 species) of DSBR beels compared with the reports of 209 species from 15 beels of Assam (Sharma and Sharma, 2008), and 206 species from 15 pats of Manipur (Sharma, 2005a); it is more biodiverse than 141 species known from three beels (Sharma and Hatimuria, 2017) and is marginally species-rich than 197 species observed from 12 beels (BKS, unpublished) of the Majuli River Island of upper Assam. DSBR beels thus depicted one of the diverse zooplankton assemblages known from India which is hypothesized to habitat diversity and environmental heterogeneity of these low ionic concentration wetlands located in the Assam-gateway, an important biogeographic corridor of India. This generalization supported hypothesis of Sharma and Sharma (2008, 2014, 2019) on biodiversity importance of the floodplains of NEI and that of the tropics and subtropics (Segers et al., 1993).

Individual DSBR beels recorded higher mean richness (184±4 species) with No. 11 > Khamti Guali > Maghuri beels and registered 88.4-90.9% community similarities (vide Sorenson index). The latter affirmed high homogeneity of zooplankton composition due to common occurrence of 157 species (~75%) amongst the three beels. Our results recorded high mean richness individually with lower inter-beel variations as compared with the reports of 109±20 species known from 15 pats of Manipur (Sharma, 2005a), 102-118 species from > 30 beels of the Brahmmaputra river basin of Assam (Sharma and Sharma, 2008), 118±8 species from three beels of the Majuli river island (Sharma and Hatimuria, 2017), and 178±13 species from four beels of lower Assam (BKS, unpublished). Further, zooplankton of individual DSBR beels are distinctly speciose than the reports of 110 species from various Kashmir wetlands (Wanganeo and Wanganeo, 2006); 110 and 103 species from Waithou and Utra pats of Manipur (Sharma, 2011b); 76 species (Khan, 2002) and 89 species (Khan, 2003) from the floodplain lakes of Southeastern West Bengal; 76 species from two floodplain wetlands (Datta, 2011) of north Bengal; and 51 species from two floodplain lakes (Khan, 1987) of Kashmir.

Rotifera > Cladocera mainly contributed to zooplankton richness of the three beels, while Rhizophoda > Copepoda > Ostracoda indicated limited role. Rotifera revealed total 141 species (Sharma et al., 2017) comprising ~34.0 and ~50.0% of species of the phylum known from India and NEI, respectively with one species new to the Oriental region, two new records to the Indian Rotifera, three new to Assam, 21 species (~15.0%) of global biogeographic interest and ~10% species restricted to NEI (Sharma et al., 2017). Rotifera richness of DSBR beels corresponded with 140 species from the floodplains of the Kashmir Himalayas (Sharma and Sharma, 2018). The species predominance of this phylum concurred with the reports of Sharma (2005a, b, 2009a, b, 2011a, b), Sharma and Sharma (2001, 2005, 2012, 2014, 2019) and Sharma et al. (2015, 2016, 2018) from the floodplains of NEI and West Bengal (Khan, 2002, 2003). It also concurred the reports from Rao Tapajos (Koste, 1974), Lago Camaleao (Koste and Robertson, 1983), Lake Guarana (Bonecker et al., 1994) of Brazil, Lake Iyi-Efi and Lake Oguta from Niger delta (Segers et al., 1993), Thale-Noi Lake, Thailand (Segers and Pholpunthin, 1997), Laguana Bufeos, Bolivia (Segers et al., 1998), and the Rio Pilcomayo National park, Argentina (Jose De Paggi, 2001).

Cladocera richness (49, 47±2 species) deserved importance in light of a conservative estimate of
occurrence of up to 60-65 species of the taxon from tropic and subtropics waters of the Indian subcontinent (Sharma and Michael, 1987; Michael and Sharma, 1988; Sharma and Sharma, 2017b). With ~90.0% of the species observed from all DSBR beels and higher community similarities (94.6-98.9% vide Sørensen’s index), our results affirmed high homogeneity in species composition of these microcrustaceans amongst the beels concurrent with the reports from certain floodplains of Assam (Sharma and Sharma, 2008, 2013) and Manipur (Sharma and Sharma, 2009, 2010). The mean richness is marginally higher than the report of 44±3 species from four beels of lower Assam (BKS, unpublished) while it is distinctly higher than 26±6 species known from 12 Majuli beels (Sharma et al., 2015). This group is represented by ~20.0% biogeographically interesting elements, including two Australasian, three Indo-Chinese, three Oriental endemics, the Paleartic Kurzia latissima, and the paleotropical Dunhevedia serrata. Our results depicted the diverse nature of Chydoridae (~63%) and common occurrence of Macrothricidae and thus depicted the littoral periphytic character to the cladoceran assemblages (Sharma and Sharma, 2017b). This study is notable for paucity of the Bosminidae and Moinidae and lack of Daphnia concurrent with the report from the Majuli floodplains, upper Assam (Sharma et al., 2015). DSBR Cladocera recorded ten cosmotropical species and several tropical and sub-tropical taxa and thus depicted a broadly ‘tropical character’ concurrent with the reports on tropical assemblages (Sharma and Michael, 1987; Sharma and Sharma, 2008).

Rhizopoda indicated (11, 10±1 species) importance of species of Lobosea than that of Filosea concurrent with the remark of Sharma and Sharma (2011b). The rhizopod richness is lower than the reports of 21 species from Deepor Beel (Sharma and Sharma, 2011b) but broadly compared with the reports of 12 species from Tripura (Das et al., 2000), 10 species from Melghat Wildlife Sanctuary, Maharashtra (Bindu, 2010); and 13 species from Pench National Park, Maharashtra (Bindu and Das, 2010). Amongst Copepoda species, Mesocyclops aspericornis, M. isabellae and Tropodiaptomus signatus are new records from NEI, while M. varicans and Thermocyclops crassus are new records from Assam. In general, zooplankton of DSBR beels depicted the littoral-periphytic assemblages and a broadly ‘tropical character’ following the remarks on the composition of several tropical zooplankton assemblages vide Fernando (1980), Dussart et al. (1984), and Sharma and Sharma (2008, 2013).

Zooplankton indicated wider monthly richness variations and registered 39.1-71.7, 37.8-73.0 and 37.0-76.2% community similarities in Maghuri, Khamti Guali and No.11 beels, respectively with majority of instances in the similarity matrices indicating lower ranges of 41-60%. The stated features along with the differences in the hierarchical cluster groupings affirmed heterogeneity in monthly composition of zooplankton of the three beels which is hypothesized to habitat heterogeneity. Our results highlight interesting zooplankton consortia per samples of 99 (April, 2015) and 105 (May, 2014) species in Khamti Guali and No. 11 beels, respectively. We categorize these as ‘Zooplankton paradox’ following analogy to the classical ‘paradox of the plankton’ reported by Hutchinson (1961). Such instances are hypothesized to the intriguing possibility of the co-existence of a number of species in the floodplain ecotones due to high amount of niche overlap (MacArthur 1965). Rotifera monthly richness significantly influenced zooplankton richness variations in Maghuri (r₁=0.940, P<0.0001), Khamti Guali (r₂=0.942, P=0.0001) and No.11 (r₃=0.959, P<0.0001) beels, respectively. The report of maximum 76 species per single sample in No. 11 beel is interesting in light of ‘Rotifera paradox’ of 80+ species advanced by Sharma and Sharma (2019) for certain floodplain lakes of NEI. Cladocera contributed significantly to zooplankton richness only in Maghuri beel (r₁=0.773, P<0.0001) although the record richness of 31 species per sample each in Khamti Guali beel and in No.11 beels is noteworthy.

Low zooplankton abundance of reported from Maghuri, Khamti Guali and No. 11 beels, respectively is attributed to low ionic concentrations’ and ‘soft –
moderately hard waters. This generalization concurred with the reports from Loktak Lake (Sharma and Sharma, 2009) and two floodplain lakes (Sharma, 2011a) of Manipur, Ghorajan beel (Sharma and Sharma, 2012) of Assam, and from a reservoir of Mizoram (Sharma and Pachuau, 2013). ANOVA indicated significant monthly density variations amongst the three beels ($F_{23, 71} = 2.5061, P=0.0039$). The zooplankton did not follow any definite pattern of quantitative variations during the study period; peak densities recorded during pre-monsoon (June, 2015), monsoon (July, 2015) and autumn (November, 2014) in Maghuri, Khamti Guali and No. 11 beels, respectively differed from the winter maxima reported by Sharma (2011a, b), and Sharma and Sharma (2011a). This study lacked quantitative importance of any individual zooplankton species and thus suggested their ‘generalist-nature’ (Sharma and Sharma, 2014; Sharma and Hatimuria, 2017) in contrast to importance of certain species reported by Sharma and Sharma (2008, 2011b, 2012).

Rotifera, the dominant component (50.0±6.5, 49.6±9.5 and 44.6±8.6%), significantly contributed to zooplankton density variations in Maghuri, Khamti Guali and No. 11 beels, respectively ($r_1$=0.871, $P<0.0001$; $r_2$=0.818, $P<0.0001$; $r_3$=0.848, $P<0.0001$). The concurrence of peak densities of Rotifera with zooplankton peaks in the three beels re-affirmed this generalization. The stated importance of Rotifera agreed with the reports of Khan (1987), Sanjer and Sharma (1995), Sharma (2005a, b, 2011a, b), and Sharma and Sharma (2001, 2008, 2011a, 2012) while it differed from sub-dominant role of this taxon in Holmari beel (Sharma and Hatimuria, 2017) as well as vide the reports of Yadava et al. (1987), Sharma (2000), Sharma and Hussain (2001) and Khan (2002). The rotifer abundance of DSBR beels concurred with the reports from Loktak Lake (Sharma, 2009a) and two floodplain lakes (Sharma, 2011b) of Manipur, and a reservoir of Mizoram (Sharma and Pachuau, 2013) while it is relatively lower than the reports from Deepor beel (Sharma, 2011a) and from Ghorajan beel of Assam (Sharma and Sharma, 2012). Peak rotifer densities were observed during monsoon (July, 2015) in Maghuri beel, post-monsoon (October, 2014) in Khamti Guali beel and in summer (May, 2014) in No.11 beel. The post-monsoon peak in Khamti Guali beel concurred with the report from the floodplains of the Kashmir valley (Khan, 1987) while summer peak in Holmari beel concurred with the reports of Yadava et al. (1987) and Sanjer and Sharma (1995). The reported maxima differed from winter peaks known from certain floodplain lakes of NEI (Sharma and Hussain, 2001; Sharma, 2009a, 2011a; Sharma and Sharma, 2011a, 2012). Lecanidae > Brachionidae > Lepadellidae influenced the rotifer abundance in Maghuri and Khamti Guali beels, and Lecanidae > Brachionidae recorded importance in No.11 beel. Lecanidae contributed significantly to zooplankton abundance in Maghuri beel ($r_1$=0.605, $P<0.0017$), Khamti Guali ($r_2$=0.750, $P<0.0001$), and No.11 beel ($r_3$=0.798, $P<0.0001$). The importance of these families concurred with the reports from the floodplains of NEI (Sharma and Hussain 2001; Sharma, 2005a, 2009a, b, 2011a; Sharma and Sharma 2001, 2008, 2014) but differed from lack of such trend from West Bengal (Khan, 2002) and Assam (Sharma and Sharma, 2012).

Cladocera comprised between 29.0±5.7, 32.9±9.1 and 36.5±8.2% of zooplankton abundance in the three beels, respectively and contributed significantly to the latter in Maghuri beel ($r_1$=0.836, $P<0.0001$) and No.11 beel ($r_3$=0.636, $P<0.0008$). Cladocera abundance is higher than the results of Khan (1987), Yadava et al. (1987), Sharma and Hussain (2001) and Sharma and Hatimuria (2017) from certain floodplain wetlands of India. The cladocerans recorded peak densities during pre-monsoon (June, 2015) in Maghuri, summer (May, 2015) in Khamti Guali and pre-monsoon (June, 2015) in No.11 beels. This group recorded importance of Chyadoridae in the three beels concurrent with the reports of Sharma (2011a) and, Sharma and Sharma (2008, 2011a, 2012). Rhizopoda formed 10.2±4.7, 9.6±3.8, and 11.6±3.3% of zooplankton abundance in the three beels, respectively. It recorded peak in February and November, 2014 and in July, 2015 in the three beels, respectively. The rhizopod abundance is relatively
lower than the reports of Sharma and Sharma (2008) while it is higher than the results of Sharma and Pachuau (2013) and Sharma and Hatimuria (2017). Copepoda density comprised 9.2±3.3, 7.0±2.2 and 6.4±2.9% of zooplankton in Maghuri, Khamti Guali and No. 11 beels, respectively. ANOVA registered significant monthly variations of copepods density amongst the three beels (F$_{2, 71}$=10.486, $P$=0.0001). The sub-dominance of copepods in DSBR beels concurred with the reports from Deepor beel (Sharma and Sharma, 2011a) and Ghorajan (Sharma and Sharma, 2012) beels of Assam, and from Loktak Lake (Sharma and Sharma, 2009b) and two floodplain lakes (Sharma, 2011b) of Manipur but was lower than the report from Ghorajan beel (Sharma and Sharma, 2012) of Assam. Nauplii recorded throughout the study period showed an active continuous reproductive phase of the cyclopoids concurrent with the reports of Sharma (2011a, b), Sharma and Sharma (2011a) and Sharma and Pachuau (2013). Ostracoda contributed insignificant fraction of zooplankton of the three DSBR beels.

High zooplankton species diversity with H´ values > 4.0 during 3, 9 and 10 months in Maghuri, Khamti Guali and No. 11 beels, respectively, coupled with lower densities of majority of species, is attributed to fine niche portioning in combination with micro- and macro-scale habitat heterogeneity as hypothesized by Segers (2008) and endorsed by Sharma (2011a, b), Sharma and Sharma (2011a, 2012) and, Sharma and Pachuau (2013). The species diversity was directly influenced by richness of zooplankton, Rotifera and Cladocera; and abundance of zooplankton, Rotifera, Cladocera, Lecanidae and Brachionidae in Maghuri beel. It was influenced by richness of zooplankton, and Rotifera; and abundance of rotifers, Lecanidae, Brachionidae and Trichocercidae in Khamti Guali beel. It was influenced richness of zooplankton and Rotifera; and abundance of Rotifera, Lecanidae, Lepadellidae in No. 11 beel. Low zooplankton dominance in Maghuri, Khamti Guali and No. 11 beels and lack of quantitatively important species is hypothesized to the fact that the habitat of the sampled beels has resources for utilization by majority of species and thus providing high amount of niche overlap (MacArthur, 1965). Zooplankton depicted higher evenness in Maghuri, Khamti Guali and No. 11 beels, respectively which affirmed low densities and equitable abundance of various species and thus reiterated that the majority of zooplankton are ‘generalists’ vis-à-vis their general environment. The present results concurred with the reports from the floodplain lakes of NEI (Sharma 2011a, b; Sharma and Sharma, 2008, 2011a, 2012; Sharma and Hatimuria, 2017).

Our study depicted limited significance of individual abiotic parameters on richness and abundance of zooplankton in DSBR beels. The former concurred with the results of Sharma (2005b) and Sharma and Sharma (2012), while the latter corresponded with the reports of Yadava and Dey (1990), Sharma and Hussain (2001), Sharma (2011a), and Sharma and Sharma (2011a). These generalizations are affirmed by the fact that the richness of zooplankton and Rotifera is positively correlated with total dissolved solids and rainfall only in No.11 beel. Abundance of zooplankton and Rotifera is negatively correlated with nitrate and sulphate in Khamti Guali beel; zooplankton abundance is positively correlated with rainfall and water temperature and Rotifera abundance is positively correlated with rainfall in No.11 beel. On the other hand, the Canonical correspondence analysis (CCA) with 17 abiotic factors registered moderate cumulative influence of 73.65, 61.42 and 63.56 zooplankton assemblages, along first two axes, in Maghuri, Khamti Guali and No.11 beels, respectively.

CCA coordination biplot indicated influence of water temperature, dissolved oxygen and chloride and total hardness on zooplankton abundance; water temperature on rotifera richness; rainfall on Rotifera abundance; water temperature on Lecanidae; rainfall on Daphnidae; and dissolved organic matter on Macrothricidae in Maghuri beel. CCA recorded influence of total alkalinity on Macrothricidae and Plationus patulus; rainfall on zooplankton abundance and Brachionidae; dissolved organic matter on zooplankton richness and Lecanidae; chloride on
Rotifer abundance and richness; pH, calcium, total dissolved solids and silicate on Copepoda abundance; and water temperature on *Lecane bulla* in Khamti Guali beel. Zooplankton abundance was influenced by rainfall; magnesium influenced abundance of Cladocera, Daphnidae and *L. leontina*; pH influenced Rhizopoda abundance; Lecanidae was influenced by total dissolved solids; and *P. patulus* was influenced by nitrate in No. 11 beel.

The present study thus indicated limited influence of individual abiotic factors, while CCA registered moderately high cumulative importance of 17 abiotic factors vis-à-vis richness and abundance of zooplankton assemblages of DSBR beels. The former affirmed that zooplankton species are largely ‘generalist’ in terms of individual abiotic factors; the results, hence, suggested the importance of analysis of factors associated with habitat variations in the sampled wetlands.

To sum up, the biodiverse zooplankton with high total richness in the three DSBR beels, new records and various species of biogeographic interest; the littoral-periphytic nature with broadly tropical character; species homogeneity amongst the three beels and heterogeneity in individual beels; and ‘zooplankton paradox’ are hypothesized to habitat diversity and environmental heterogeneity of these floodplain wetlands located in ‘the Assam-gateway’. Low abundance of zooplankton is attributed to ‘soft – moderately hard waters’ with ‘low ionic concentrations’. Our results did not depict any pattern of monthly or annual richness and density variations, while Rotifera > Cladocera influenced diversity in the three beels. Our results are characterized by high species diversity, high evenness, low dominance, and lack of quantitative importance of any individual zooplankton species; the last aspect indicated ‘generalist nature’ of various taxa. This study highlights limited influence of Individual abiotic factors on richness and abundance of zooplankton but CCA registered moderately high cumulative importance of seventeen abiotic factors on zooplankton assemblages of DSBR beels. This study marks an important contribution on diversity of freshwater zooplankton of India in general and that of the floodplain lakes of NEI as well as the tropics and subtropics in particular.

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