



Does Intra-Site Connectivity Influence the Dynamics of Zooplankton Metacommunity in Freshwater Habitats?

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Abstract

The paper reported on a metacommunity analysis of zooplankton in two freshwater wetlands having contrasting ecological features for three seasons over a year. The effects of spatial connectedness, habitat fragmentation, environmental changes mediated by seasonal fluctuations and variability in assemblages of aquatic vegetation on the zooplankton community were compared. A total of 116 zooplankton species were recorded from both the study sites. Few zooplankton showed affinity for Site 1, whereas others were unique to Site 2. Sorensen's similarity index revealed that the two sites were moderately similar with respect to zooplankton composition, but were moderately dissimilar with regard to floral composition. The present study has tested Community Wide Character Displacement (CWCD) hypothesis based on the results which exhibited less similarities in the fragmented local habitats within the same wetland than two major distantly located wetlands in respect of zooplankton species composition. Principal Components Analysis (PCA) and Cluster analysis have revealed that direct connectivity might have played most vital role in shaping community structure especially in case of planktonic organisms, followed by the influence of seasons and macrophytes.

Keywords: Zooplankton diversity, macrophytes, community structure, fragmentation, wetlands, Midnapore.

Introduction

To paraphrase John Donne (1624): No pond is an island, entire of itself. While communities are comprised of all individuals of the resident species that potentially interact within a single patch or local area of habitat, Metacommunity represents a set of local communities that are linked by dispersal of multiple interacting species (Wilson, 1992). Metacommunities can reorganize their relationships at various scales, depending on the environmental context (Leibold and Miller, 2004) (Figure 1). Habitat fragmentation poses an inherent problem for metacommunity dynamics in wetlands, as dispersals among communities are hindered by increasing isolation and loss of patches. Wetlands representing similar system have undergone excessive destruction and fragmentation in recent years (Perrow and Day, 2002). Freshwater zooplankton communities by virtue of their diversity and density have appeared to be an excellent biotic model to study how metacommunity structure is affected by habitat fragmentation. Although freshwater ponds are being considered as isolated and closed systems embedded in the

terrestrial matrix, yet their isolation is not absolute, as individuals have been shown to move between ponds via both direct connections e.g., water channels or floodings (Michels *et al.*, 2001) and overland dispersal (Cáceres and Soluk, 2002; Cohen and Shurin, 2003), thereby connecting populations within the metacommunity (Figure 1).

Local communities can be structured both by local interactions e.g., competition, predation, environmental variables and regional interactions like dispersal of individuals between habitats or spatial configuration (taking into account dispersal pathways) (Cottenie *et al.*, 2003). Metacommunity perspective can strongly modify the ways how communities are regulated and how community structure is related to environmental conditions. Additionally, aquatic vegetation supply nutritional resources, provide protection and shelter against both invertebrate and vertebrate predation and constitute a habitat for epiphytic and littoral organisms (Joniak *et al.*, 2007). Clear water bodies dominated by macrophytes contribute to the maintenance of aquatic invertebrate diversity (Declerck *et al.*, 2011a).

The objective of the present study was to record the density and diversity of zooplankton in selected

sub-sites of two wetlands of Midnapore (West) district, West Bengal, India, having contrasting ecological conditions. An attempt was also made here to compare effects of spatial connectedness, habitat fragmentation, specific environmental changes mediated by seasonal fluctuations, and variability in assemblages of aquatic vegetations on rotiferan community, especially during the lean or flow period, influencing species dispersal. The hypothesis of Community Wide Character Displacement (CWCD) (Leibold *et al.*, 2004) was tested as a part of the study.

Materials and Methods

Physiography of Two Selected Study Sites

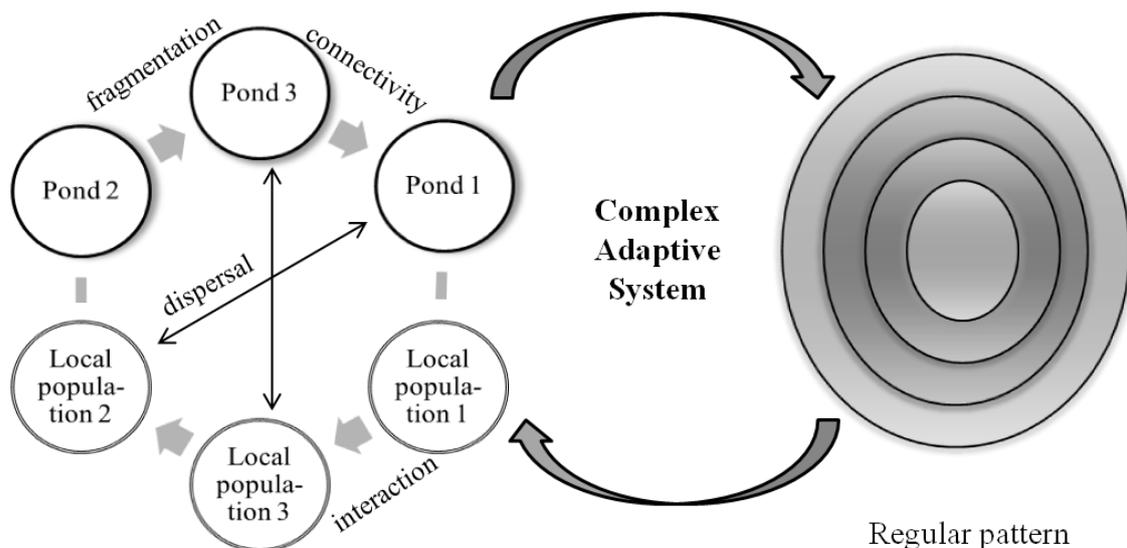
Study Site-1: Gurguripal being an eco-restored, natural and perennial wetland (22.432° N, 87.218° E) located within the lateritic tract endowed with tropical deciduous forest in the Midnapore (West) district, West Bengal, India (Figure 2). This site is split into two water basins (Figure 3): a larger, lesser vegetated part having luxuriant population of *Scirpus* sp., but only with sparse *Nymphoides* sp. Four sub-sites were identified for samplings (G-I, G-II, G-III, G-IV) from this water body. The smaller, densely vegetated part (sub-site: G-PB) enjoys a substantial coverage of *Nymphoides* sp. and *Utricularia* sp. in addition to *Scirpus* sp.

Study Site-2: Sundra (22.58°N, 87.33°E) representing a shallow, temporary, depressed wetland located around 30 kms away from the Site 1 (Figure 2) experiences seasonal inputs from adjoining agricultural runoff. Site 2 also has two basins (Figure 3): a larger water basin (with sub-sites: S-I, S-II and

S-III) supported by more than a dozen macrophytes primarily dominated by *Nymphaea* sp. while a smaller, fragmented water basin (sub-site: S-Bw) devoid of any such vegetation excepting scanty occurrence of *Cyperus* sp.

Collection and Analysis of Samples

Zooplankton samples were collected from the subsurface water using a nylobolt plankton net (25 µm mesh size) at monthly intervals during early morning hours from March 2011 to February 2012. A total of 100 L of water was filtered from each sampling site and the concentrated plankton samples were preserved in 5% buffered formalin in small plastic vials. Zooplankton were identified to the lowest possible taxonomic level, mostly up to species or genera, following standard references (Pontin, 1978; Michael and Sharma, 1988; Sharma, 1998; Segers, 2007; Roy, 1999). Quantitative study of zooplankton was done under a phase contrast microscope (Model no. Zeiss 1000 1098), by taking three replicates of 1 ml from each sub-site into a Sedgewick Rafter counting cell and counting them. Macrophytes were collected from all sampling sites and identified in consultation with Pradhan *et al.* (2005) and Fassett (2006). Physicochemical parameters of water [temperature of surface water (Wtemp-°C), pH, dissolved oxygen (DO-mg/l), biochemical oxygen demand (BOD-ppm), turbidity (Turb-mg/l), total dissolved solids (TDS-ppm), conductivity (Cond-µs/m) and salinity (Sali-ppm)] of the selected study sites were analyzed over the same period with the aid of water analyzer (Water quality checker TOWA 22 A, Japan) either on the spot of



Variable interactions in METACOMMUNITY

Figure 1. Schematic approach indicating dispersal, connectivity and fragmentation as the dynamic contributors of Metacommunity development, finally reorganising into regular pattern of attributes in the form of Complex Adaptive System.

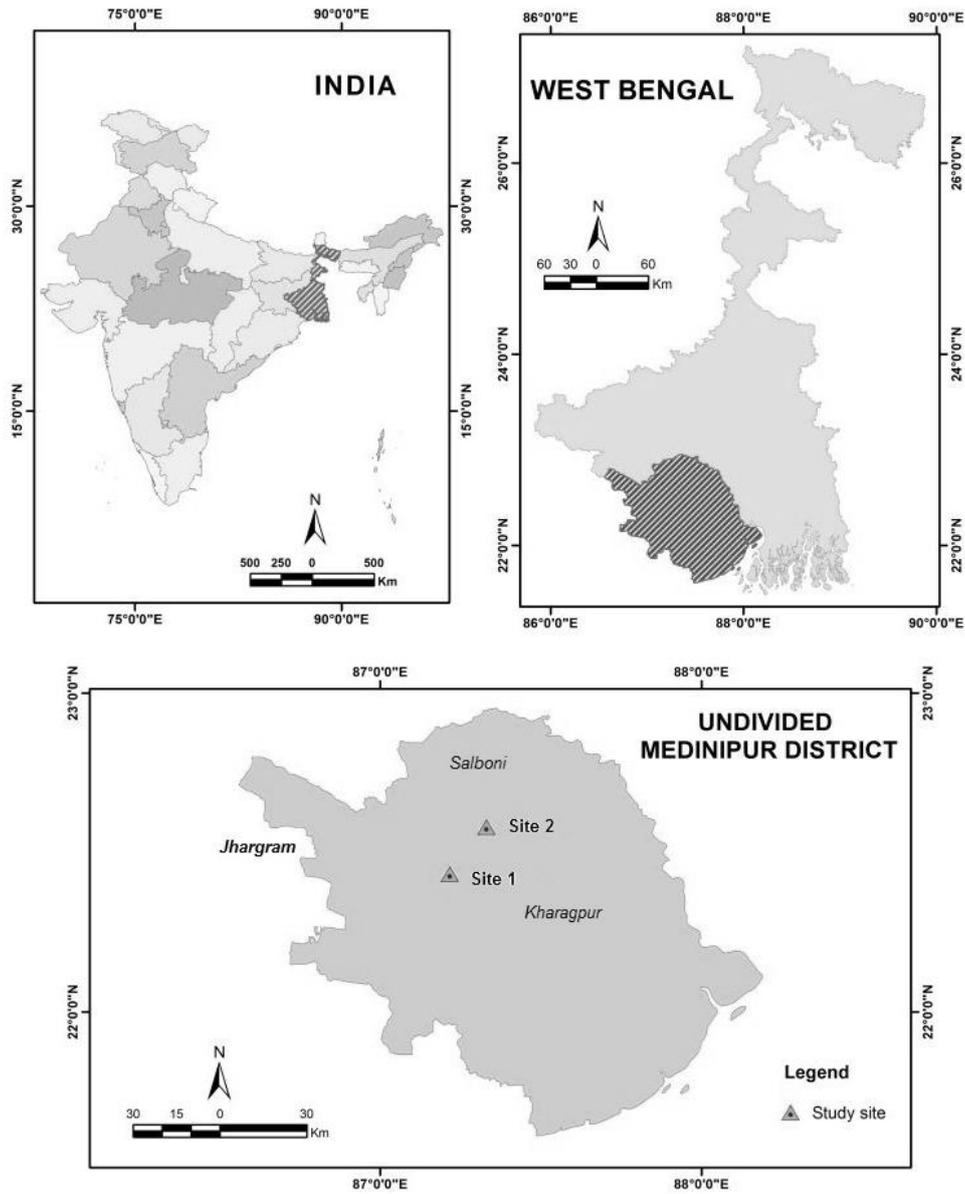


Figure 2. Map of India, West Bengal and Midnapore (West) district, showing the location of two Study Sites- 1: Gurguripal and 2: Sundra; few adjacent local towns are labelled.

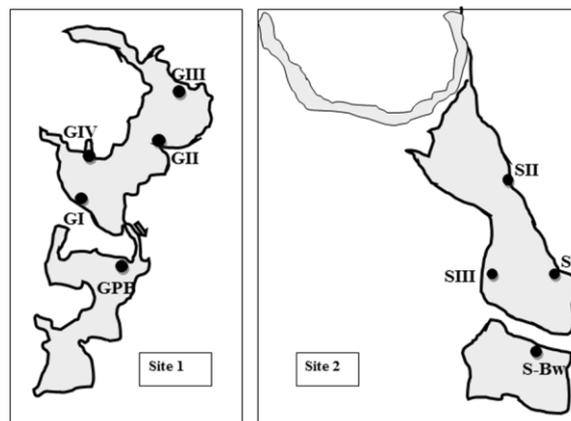


Figure 3. Schematic representation of selected wetlands. Dots represent the respective sub-sites: G-I, G-II, G-III, G-IV belong to higher basin and G-PB lies in the lower basin of Site 1, connected by an overflow channel (indicated by arrow); S-I, S-II, S-III belong to the larger basin and S-Bw lies in the fragmented part of Site 2.

collection or volumes of water were brought back in bottles to the laboratory for further qualitative analysis (APHA, 2005).

Analysis of Data

Analysis of the seasonal change in the community structure was performed for two local sites as well as individual sub-sites. These sites were also considered as pseudoreplicates for metacommunity analysis since the fragmentation and connectivity occurred in natural set-up. Relationships between densities of rotifer, cladocera and copepoda, and major physicochemical factors were computed using MS excel and SPSS software (version 11). Similarities were deduced on the basis of annual occurrence of zooplankton and macrophytes of both study sites, using Sorensen's coefficient (C_S) at regional level and similarity index (C_N) (Bray and Curtis, 1957) at local level, for each season. Additionally, such intra-site and inter-site comparisons have been used to test the *CWCD hypothesis* (Leibold *et al.*, 2004) stating that "Locally coexisting species should be less similar to each other than those that would have been expected by random draws from a larger regional pool", as to establish whether species compositions were more similar at local-habitat or regional-habitat level. Other community indices such as relative abundance (RA), frequency (F) and dominance index (DI) for rotifers, copepods and cladocerans were also calculated to find out the species of importance. Minitab software (version 16) was used to compute the *Principal components analysis* (PCA) in order to predict the response of zooplankton species assemblages to multiple interacting factors; and *Cluster analysis* was used to sort out linked observations.

Results

Species Composition of Macrophytes

The macrophyte communities in the two study sites were found to display distinct pattern of surface coverage depicting features of ecological succession. Site 1 was endowed with 5 aquatic plants viz. *Scirpus*

articulatus, *Nymphoides cristatum*, *Utricularia* sp., *Oryzae sativa* and *Cyanotis* sp.; while Site 2 was found to possess 13 variety of plant species viz. *Alternanthera* sp., *Nelumbium cruciferum*, *Nymphaea tetragona*, *Ipomoea aquatica*, *Jussiaea repens*, *Lemna major*, *Marselia quadrifolia*, *Eichhornia crassipes*, *Utricularia* sp., *Polygonum hydropiper*, *Sagittaria latifolia*, *Oryzae sativa* and *Cyperus* sp. Sorensen's Similarity index for floral community (Table 1) indicates that these sites were moderately dissimilar ($C_S=0.33$).

Species Composition of Zooplankton

A total of 116 zooplankton taxa were recorded in this study which included 74 rotifers, 6 copepods, and 28 cladocerans. A complete list of the species identified with their RA and F values is presented in Table 2. Site 1 possessed 55 rotifers while Site 2 had 54. Some rotifers viz. *Ascomorpha ovalis* (Bergendal, 1892), *Filinia camasecla* Myers, 1938, *Brachionus donneri* Brehm, 1951, *B. forficula* Wierzejski, 1891, *Lecane lunaris* (Ehrenberg, 1832), *L. papuana* (Murray, 1913c), *Monommata* sp. Bartsch, 1870, *Platylas quadricornis* (Ehrenberg, 1838) and *Trichotria tetractis* (Ehrenberg, 1830) exhibited habitat preference towards Site 1; while Site 2 was found to have been inhabited by a unique suite of taxa viz. *Brachionus bidentatus* Anderson, 1889, *B. calyciflorus* Pallas, 1766, *B. diversicornis* (Daday, 1883), *Collotheca campanulata* (Dobie, 1849), *Keratella cochlearis* (Gosse 1851), *Lecane curvicornis* (Murray, 1913), *L. luna* (O.F. Müller, 1776), *Lepadella cristata* (Rousselet, 1893), *Trichocerca longiseta* (Schrank, 1802) and *Mytilina ventralis* (Ehrenberg, 1830). A total of 35 rotifers, 6 copepods and 17 cladocerans were found to be common to both sites. Sorensen's similarity index for zooplankton species (Table 1) indicates that both the sites were moderately similar ($C_S=0.67$). DI for Site 1 (17.84) was lower than that of Site 2 (29.2) (Table 1). RA revealed the dominance of three rotifers at Site 1 i.e. *Keratella cochlearis* (5.86%), *Polyarthra vulgaris* Carlin, 1943 (7.86%), and *Hexarthra mira* (Hudson, 1871) (5.27%). Only one rotifer- *P. vulgaris* was found to be Eudominant (25.58%) at Site 2. One species each belonging to Copepoda - *Heliodiaptomus*

Table 1. Species richness of Zooplankton and Macrophytes in the two study sites

Number of Biota	Site - 1	Site - 2	Common
Total Rotifera	55	54	35
Total Copepoda	6	7	6
Total Cladocera	28	24	17
Total Zooplankton Richness	89	85	58
(Zooplankton) Sorensen's Similarity index		0.67=>Moderately Similar	
Dominance index (DI)	17.8	29.2	
Macrophytes' Species Richness	5	13	3
(Macrophytes) Sorensen's Similarity index		0.33=>Moderately Dissimilar	

Table 2. The annual species diversity, density (numbers/l) and Relative Abundance (RA) with status (Skubala, 1999) of Rotifera, Copepoda and Cladocera at Site 1 and Site 2

Sr. No.	Species Name	SITE-1					SITE-2				
		Range	Mean± SE	RA (%)	Status	Commo	Range	Mean± SE	RA	Status	
1	<i>Anuraeopsis fissa</i> Gosse, 1851	.52-4.60	2.23±.89	2.13	S	+	.40-17.00	6.45±3.18	3.09	S	
2	<i>Ascomorpha</i> sp.	.12-.12	.12±0	0.02	U						
3	<i>Asplanchna priodonta</i> Gosse, 1850	.20-1.75	.85±.33	0.61	U	+	.11-6.80	2.06±1.22	0.82	U	
4	<i>Brachionus angularis</i> Gosse, 1851	.17-.24	.21±.02	0.11	U	+	.60-1.75	1.14±.19	0.45	U	
5	<i>B. bidentatus</i> Anderson, 1889						.25-.50	.38±.13	0.06	U	
6	<i>B. budapestinensis</i> Daday, 1885						6.80-6.80	6.80±0	0.54	U	
7	<i>B. calyciflorus</i> Pallas, 1766						.15-6.80	3.48±3.33	0.56	U	
8	<i>B. caudatus personatus</i> Barrois and Daday, 1894	.13-1.50	.59±.17	2.47	S	+	.50-5.20	2.85±2.35	0.46	U	
9	<i>B. caudatus vulgatus</i> Barrois and Daday, 1894						.13-8.30	3.08±2.62	0.74	U	
10	<i>B. diversicornis</i> (Daday, 1883)						1.10-5.10	3.10±2.00	0.50	U	
11	<i>B. donneri</i> Brehm, 1951	.10-1.22	.46±.14	0.66	U						
12	<i>B. falcatus</i> Zacharias, 1898	.20-.80	.42±.09	0.67	U	+	1.10-7.30	4.20±3.10	0.67	U	
13	<i>B. forficula</i> Wierzejski, 1891	.36-3.60	1.45±.59	1.29	R						
14	<i>B. mirabilis</i> Daday, 1897						.28-17.00	3.61±2.69	1.73	R	
15	<i>Plationus patulus</i> (Müller, 1786)	.20-1.70	.58±.17	0.82	U	+	.10-7.80	1.79±1.04	1.00	U	
16	<i>B. quadridentatus</i> Hermann, 1783	.40-1.80	.89±.46	0.47	U						
17	<i>B. rubens</i> Ehrenberg, 1838	.10-.30	.17±.07	0.09	U	+	1.50-1.50	1.50±0	0.12	U	
18	<i>Brachionus</i> sp.1	.10-.10	.10±0	0.02	U	+	1.50-1.80	1.65±.15	0.26	U	
19	<i>Cephalodella gibba</i> (Ehrenberg, 1830)	.12-.24	.17±.03	0.12	U	+	.37-13.60	6.98±6.62	1.12	R	
20	<i>Collotheca campanulata</i> (Dobie, 1849)						.40-.40	.40±0	0.03	U	
21	<i>Colurella obtusa</i> (Gosse, 1886)	.17-.25	.22±.02	0.15	U	+	.21-.88	.52±.09	0.29	U	
22	<i>C. uncinata uncinata</i> (Muller, 1773)	.10-.77	.35±.11	0.44	U						
23	<i>Conochilus natans</i> (Seligo, 1900)	.05-2.16	.55±.19	0.98	U	+	.16-5.25	3.02±.88	1.45	R	
24	<i>Euchlanis dilatata</i> Ehrenberg, 1832	.05-1.60	.44±.18	0.62	U	+	.13-11.30	1.96±1.56	1.10	R	
25	<i>Filinia longiseta</i> (Ehrenberg, 1834)	.50-5.52	2.41±1.09	1.71	R	+	.22-12.50	4.61±3.95	1.10	R	
26	<i>F. camasecla</i> Myers, 1938	.12-3.57	.97±.41	1.38	R						
27	<i>F. opoliensis</i> (Zacharias, 1898)	.44-.46	.45±.01	0.16	U						
28	<i>F. novaezealandiae</i> Shiel and Sanoamuang, 1993	.24-9.48	1.66±1.12	2.36	S						
29	<i>Gastropus stylifer</i> (Imhof, 1891)	.15-1.50	.75±.21	0.93	U	+	.35-2.08	1.22±.87	0.19	U	
30	<i>Hexarthra mira</i> (Hudson, 1871)	.20-22.80	3.71±2.76	5.27	D	+	.22-3.40	1.11±.77	0.35	U	
31	<i>Keratella cochlearis</i> (Gosse, 1851)	.18-7.47	1.94±.51	5.86	D	+	3.78-5.02	4.40±.36	1.05	U	
32	<i>Keratella tecta</i> (Gosse, 1851)						.14-.50	.32±.18	0.05	U	
33	<i>Keratella tropica</i> (Apstein, 1907)	.10-7.50	2.10±1.06	2.62	S	+	.34-1.50	1.01±.35	0.24	U	
34	<i>Lecane</i> sp. 1	.21-.36	.27±.05	0.14	U	+	.18-.20	.19±.01	0.03	U	
35	<i>L. bulla</i> (Gosse, 1851)	.11-1.34	.46±.11	0.98	U	+	.06-17.00	3.09±1.76	2.71	S	
36	<i>L. clostrocerca</i> (Schmarda, 1859)	.77-1.40	1.09±.32	0.39	U	+	.15-.15	.15±0	0.01	U	
37	<i>L. decipiens</i> (Murray, 1913)	.11-.11	.11±0	0.02	U	+	.17-1.00	.59±.42	0.09	U	
38	<i>L. lunaris</i> (Ehrenberg, 1832)	.10-1.12	.53±.21	0.37	U						
39	<i>L. pyriformis</i> (Daday, 1905)						.26-.46	.36±.10	0.06	U	
40	<i>L. quadridentata</i> (Ehrenberg, 1830)	.10-5.20	1.23±1.00	1.09	R	+	.62-.62	.62±0	0.05	U	
41	<i>L. unguitata</i> (Fadeev, 1925)	.70-.71	.71±.01	0.25	U						
42	<i>L. inopinata</i> Harring and Myers, 1926	.12-1.44	.84±.30	0.59	U	+	.28-.54	.40±.08	0.10	U	
43	<i>L. curvicornis</i> (Murray, 1913)						.49-.49	.49±0	0.04	U	
44	<i>L. hornemanni</i> (Ehrenberg, 1834)	.42-.44	.43±.01	0.15	U						
45	<i>L. leontina</i> (Turner, 1892)	.09-1.12	.49±.32	0.26	U	+	.51-.51	.51±0	0.04	U	
46	<i>L. luna</i> (Müller, 1776)						.20-.20	.20±0	0.02	U	
47	<i>L. papuana</i> (Murray, 1913)	.36-.36	.36±0	0.06	U						
48	<i>L. signifera</i> (Jennings, 1896)						.23-.36	.28±.04	0.07	U	
49	<i>Lecane</i> sp. 2	.10-.90	.59±.17	0.52	U	+	.60-.87	.74±.14	0.12	U	
50	<i>Lecane</i> sp. 3						.18-.90	.54±.36	0.09	U	
51	<i>Lepadella cristata</i> (Rousselet, 1893)						.14-3.40	1.77±1.63	0.28	U	
52	<i>L. ovalis</i> (Müller, 1786)						.16-.16	.16±0	0.01	U	
53	<i>L. patella persimilis</i> De Ridder, 1961	.72-.72	.72±0	0.59	U	+	.40-.53	.47±.07	0.07	U	
54	<i>L. patella</i> (Müller, 1773)	.19-1.26	.55±.18	0.13	U						
55	<i>L. rhomboides rhomboides</i> (Gosse, 1886)						.20-.20	.20±0	0.02	U	
56	<i>Lepadella</i> sp.1	.11-.25	.18±.07	0.06	U						
57	<i>Macrochaetus collinsi</i> (Gosse, 1867)	.09-.78	.36±.11	0.39	U	+	.37-.90	.57±.16	0.14	U	
58	<i>Macrochaetus</i> sp.1	.80-5.60	2.20±1.14	1.57	R						
59	<i>Monommata</i> sp.	.42-1.40	.91±.49	0.32	U						

Table 2. Continued

	SITE-1					SITE-2				
60	<i>Mytilina ventralis</i> (Ehrenberg, 1830)					.30-1.10	.70±.40	0.11	R	
61	<i>Philodina citrina</i> Ehrenberg, 1832	.20-5.81	1.02±.39	2.54	S	+	.20-5.85	1.55±.60	1.11	R
62	<i>Platylas quadricornis quadricornis</i> (Ehrenberg, 1832)	.20-.20	.20±0	0.04	U					
63	<i>Polyarthra vulgaris</i> Carlin, 1943	.22-1.95	1.05±.19	1.87	R	+	.22-297.50	29.12±26.8 6	25.58	E
64	<i>Polyarthra</i> sp.1	.10-20.40	3.40±1.52	7.86	D	+	.18-.26	.22±.04	0.04	U
65	<i>Scardium longicaudum</i> (Müller, 1786)	.05-.19	.12±.07	0.04	U	+	.02-.55	.32±.16	0.08	U
66	<i>Testudinella emarginula</i> (Sternroos, 1898)	.10-.16	.13±.03	0.05	U	+	.13-1.17	.69±.21	0.27	U
67	<i>Trichocerca capucina</i> (Wierzejski and Zacharias, 1893)	.21-.21	.21±0	0.04	U	+	.40-.50	.45±.05	0.07	U
68	<i>T. elongata</i> (Gosse, 1886)	.43-2.80	1.19±.54	0.84	U					
69	<i>T. longiseta</i> (Schrank, 1802)						.10-.10	.10±0	0.01	U
70	<i>T. pusilla</i> (Jennings, 1903)	.05-.50	.28±.07	0.34	U	+	.11-.52	.26±.09	0.08	U
71	<i>T. similis</i> (Wierzejski, 1893)	.20-.80	.41±.06	0.81	U	+	.78-2.80	1.61±.43	0.51	U
72	<i>Trichotria tetractis</i> (Ehrenberg, 1830)	.11-.57	.32±.12	0.23	U					
73	Unidentified sp. 1						1.54-60.55	25.14±18.0 3	6.02	D
74	Unidentified sp. 3	.18-.22	.20±.02	0.07	U					
	Total Rotifera		55			35		54		
75	<i>Eucyclops agilis</i> (Koch, 1838)	.14-3.00	1.28±.44	1.60	R	+	1.03-2.16	1.60±.33	0.38	U
76	<i>Macrocyclops</i> sp.						.12-.40	.22±.09	0.05	U
77	<i>Mesocyclops thermocyclopoidea</i> Harada, 1931	.10-6.33	2.36±.48	6.70	D	+	.41-11.00	3.38±.95	3.24	S
78	<i>Microcyclops varicans</i> (Sars, 1863)	.10-1.20	.65±.55	0.23	U	+	.21-2.20	1.21±1.00	0.19	U
79	<i>Heliodiaptomus viduus</i> (Gurney, 1916)	.10-18.00	6.15±2.47	9.85	D	+	.11-90.00	20.18±10.2 2	14.51	E
80	<i>Neodiaptomus schmackeri</i> (Poppe and Richard, 1892)	.46-7.20	3.07±1.26	2.73	S	+	.15-1.44	.88±.38	0.21	U
81	<i>Phylloidiaptomus annae</i> (Apstein, 1907)	.10-1.00	.40±.30	0.21	U	+	1.00-1.00	1.00±0	0.08	U
	Total Copepoda		6			6		7		
82	<i>Alona costata</i> Sars, 1862	.30-.60	.45±.15	0.16	U	+	.14-1.04	.58±.26	0.14	U
83	<i>A. pulchella</i> King, 1853	.92-2.10	1.51±.59	0.54	U	+	.20-.20	.20±0	0.02	U
84	<i>A. rectangula richardi</i> (Stingelin, 1894)	.20-3.65	1.93±.62	1.72	R	+	.29-.29	.29±0	0.02	U
85	<i>Alona</i> sp.1	.12-.12	.12±0	0.02	U	+	.11-1.40	.61±.21	0.29	U
86	<i>Alonella excisa</i> (Fischer, 1854)	.96-1.25	1.11±.15	0.39	U					
87	<i>Biapertura karua</i> (King, 1853)	2.15-2.15	2.15±0	0.38	U	+	.10-1.95	.75±.60	0.18	U
88	<i>Bosmina longirostris</i> (Muller, 1776)	.16-1.30	.44±.22	0.39	U					
89	<i>Bosminopsis deitersi</i> Richard, 1895	.12-2.34	.65±.30	0.81	U					
90	<i>Ceriodaphnia cornuta</i> Sars, 1885	.12-.50	.29±.09	0.21	U	+	.80-.80	.80±0	0.06	U
91	<i>Ephemeropterus barroisi</i> (Richard, 1894)	.10-12.30	3.75±1.36	7.99	D	+	.18-6.76	2.75±1.25	1.10	R
92	<i>C. eurynotus</i> Sars 1901	.20-.20	.20±0	0.04	U	+	.30-.30	.30±0	0.02	U
93	<i>C. herrmanni</i> Brehm, 1934	.21-.21	.21±0	0.04	U					
94	<i>C. kallipygos</i> Brehm, 1934						1.71-1.71	1.71±0	0.14	U
95	<i>C. parvus</i> Daday, 1898	.14-.43	.29±.15	0.10	U	+	.40-.75	.58±.18	0.09	U
96	<i>C. sphaericus</i> (O.F. Muller, 1776)	.10-1.44	.45±.13	0.71	U	+	.10-.46	.28±.18	0.04	U
97	<i>C. ventricosus</i> Daday, 1898						.04-.15	.11±.04	0.03	U
98	<i>Dadaya macrops</i> (Daday, 1898)	.80-.80	.80±0	0.14	U					
99	<i>Diaphanosoma excisum</i> Sars, 1885	.40-1.50	.87±.33	0.46	U	+	1.09-14.58	8.50±3.95	2.04	R
100	<i>D. sarsi</i> Richard, 1894	.05-12.40	2.72±1.73	3.38	S	+	.20-59.50	20.15±19.6 7	4.83	S
101	<i>Kurzia latissima</i> (Kurz, 1875)	.86-.86	.86±0	0.15	U					
102	<i>Latonopsis australis</i> Sars, 1888	.22-.40	.31±.09	0.11	U					
103	<i>Macrothrix triserialis</i> Brady, 1886	.24-2.15	.78±.29	0.83	U	+	.36-.36	.36±0	0.03	U
104	<i>Macrothrix</i> sp. 1						.30-.78	.51±.12	0.16	U
105	<i>Macrothrix</i> sp. 2						.14-.44	.29±.09	0.07	U
106	<i>M. laticornis</i> (Jurine, 1820)	.32-5.40	2.13±1.64	1.13	R					
107	<i>M. spinosa</i> King, 1853						.25-.48	.37±.12	0.06	U
108	<i>Moina micrura</i> Kurz, 1875	.10-.73	.42±.15	0.30	U	+	.12-100.00	19.57±11.3 2	14.07	E
109	<i>M. brachiata</i> (Jurine, 1820)	.12-11.20	2.24±1.80	2.38	S	+	.28-15.30	4.56±2.74	1.82	R
110	<i>Moina</i> sp.						1.60-1.60	1.60±0	0.13	U
111	<i>Moinodaphnia</i> sp.	.48-.48	.48±0	0.09	U					
112	<i>Picripleuroxus similis</i> (Vavra, 1900)	3.01-3.01	3.01±0	0.54	U					

Table 2. Continued

	SITE-1					SITE-2				
113 <i>Pleuroxus aduncus</i> (Jurine, 1820)	.22-.80	.44±.18	0.23	U	+	.70-.70	.70±0	0.06	U	
114 <i>Pseudosida</i> sp.	.10-1.80	.95±.85	0.34	U	+	.10-.10	.10±0	0.01	U	
115 <i>Simocephalus serrulatus</i> (Koch,1841)						.42-.74	.58±.16	0.09	U	
116 Unidentified cladocera sp.1	.10-.50	.30±.20	0.11	U						
Total Cladocera		28			17		24			
Total Species Richness		89			58		85			

* E= eudominant (>10%), D= dominant (5.1-10%), S= subdominant (2.1-5%), R= recedent (1.1-2%), U= subrecedent (<1%); + indicates species common to both sites.

viduus (Gurney, 1967) and Cladocera - *Moina micrura* Kurz, 1874 also experienced Eudominant status (14.5% and 14% respectively).

The physicochemical parameters recorded from both study sites over one-year duration are plotted in Figure 4. In case of Site 1, it is evident that the water temperature of sub-site G-PB (18.9°C) was substantially lower than the remaining sub-sites during post-monsoon (Figure 4a). This may be due to the extensive coverage of macrophytes in an undisturbed condition in the lower basin, which shielded the water from solar heating during winter. In case of Site 2 (Figure 4b), an exceptional deviation was observed in case of turbidity at sub-site S-III (389 ppm) which exceeded other readings during pre-monsoon. This phenomenon was due to the excessive reduction in water level of the wetland due to extreme summer accompanied with loss of macrophytes, making the soil more soluble in the water.

Seasonal variation in density and diversity of zooplankton community at sub-sites of both sites were found to be irregular (Figure 5), which are supposed to be due to dynamic interactions of populations at functional level, but annually, there were distinct synchronous peaks in population density of constituent biotic groups (rotifers, copepods and cladocerans), highlighting the preponderance of rotifers in most cases. Figure 5a indicated highest rotifer richness (27) as well as abundance (43) at Site 1 during late monsoon, followed by pre-monsoon exhibiting considerably high richness (~20) for all zooplankton groups. Unlike Site 1, Site 2 (Figure 5b) reflected a different picture where species richness and abundance did not vary proportionately over months i.e. few number of species accounted for high species density at specific periods; and pre-monsoon showed uni-modal peak for zooplankton density (~100-150) but tri-modal peaks at each season for zooplankton diversity (8-11). This exceptional abundance of biota during pre-monsoon was supposed to be directly correlated with the enhanced turbidity in the same season at Site 2, but actually was an indirect effect of summer that drastically reduced water level, diversity of macrophytes as well as predator organisms in the wetland, leading to proliferation of zooplankton within a short period.

Community Similarity indices 'C_N' (Bray and Curtis, 1957) and 'j' for mean zooplankton density in selected sub-sites across three major seasons during

the year 2011- 2012 revealed lowest C_N and 'j' of G-PB PoM with remaining 4 sub-sites (C_N=0.087, 0.022, 0.01, 0.038 and j=2, 1, 1, 1 respectively); and highest C_N between G-II PoM – G-I PoM (C_N=0.665), G-III PrM – G-II PrM (C_N=0.553) and G-PB Mo – G-II Mo (C_N=0.582) for Site 1 (Table 3a). Such phenomena indicated that local patches of Site 1 enabled limited dispersal among each other and fragmentation of lower basin was disrupted only during monsoon (Figure 3b). Occurrence of less number of common species between the local patches and low similarity between S-Bw PoM and rest 3 sub-sites (S-I, S-II and S-III with C_N = 0.047, 0.029 and 0.07 respectively) may indicate high fragmentation and low dispersal rates in Site 2, except a single case of similarity (C_N=0.555) between S-Bw PrM and S-II PrM. Worth noting about both the study sites is that post-monsoon has been instrumental in creating marked difference in species assemblage of the segregated sub-sites (G-PB as well as S-Bw) with remaining sub-sites, which otherwise showed higher similarity during other seasons (Table 3a and b).

The PCA (Figure 6a) has shown to segregate the sub-sites of Site 1 not as physical habitats but in terms of three seasons, since all monsoonal sub-sites laid within the top-left quadrant, the post-monsoonal ones in the bottom-left and the pre-monsoonal ones spanned the two right quadrants. X-axis (first component) of the biplot (Figure 6a) revealed that salinity, conductivity, TDS, turbidity and temperature of water were highly associated with the increase in population of maximum zooplankton species due to positive loadings [*H. viduus* (Gurney, 1967); *K. cochlearis* (Gosse, 1851); *Diaphanosoma sarsi* Gauthier, 1951; *Moina brachiata* (Jurine, 1820); *Mesocyclops thermocyclopoides* (Claus, 1857); *Ephemeropterus barroisi* Richard, 1894; *P. vulgaris* Carlin, 1943; *Neodiptomus schmackeri* (Poppe and Richard, 1892); *H. mira* (Hudson, 1871); *Filinia novaezealandiae* Shiel and Sanoamuang, 1993]. Whereas a decrease in population of few other species [*Keratella tropica* (Apstein 1907), *Polyarthra* sp., *Lecane bulla* (Gosse, 1851), *Anuraeopsis fissa* Gosse, 1851 and *Philodina citrina* Ehrenberg, 1832] was indicated by negative loading on the same axis, which in turn flourished with increase in BOD. The former 10 species were also seen to flourish at all sub-sites of Site 1 only during pre-monsoon. The biplot in Figure 6b revealed that turbidity and water temperature were

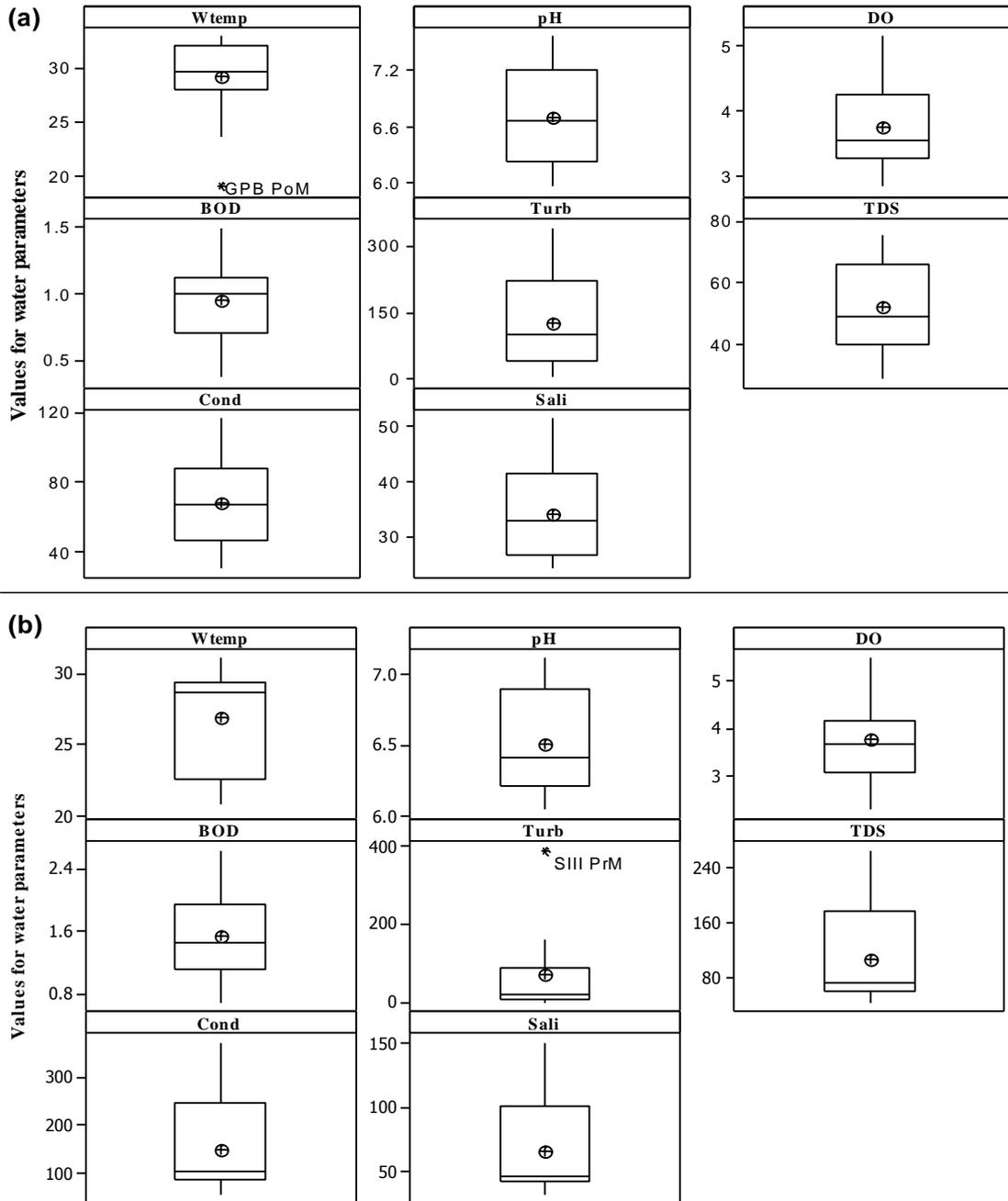


Figure 4. Physicochemical parameters recorded from (a) Site 1, and (b) Site 2. Abbreviations in panels are explained with respective units of measurement in 'Materials and methods'. *=Outlier observation; box=> Interquartile range box = Middle 50% of the data; Middle line= median; Symbol within box=> mean; Whiskers - Extend to the maximum/minimum data point within 1.5 box heights from the top/bottom of the box.

found to influence increase in population of all (*P. vulgaris*, *D. sarsi*, *Diaphanosoma excisum* Sars, 1885, *P. citrina*, *M. thermocycloides*, *A. fissa*, *Brachionus quadridentatus* Hermann 1783, *Conochilus natans* (Seligo, 1900), *L. bulla*, *M. micrura* and *H. viduus*) but two species that were present at Site 2. Simultaneously, DO and BOD coupled together to throw large negative loadings on first component, these parameters showed positive association with increase in population of two species (*K. cochlearis* and unidentified species 2). pH, TDS, salinity and

conductivity were clustered close together in Site 2 in a similar way as their grouping in Site 1, but these four parameters had large positive loadings on second component at Site 2.

The dendrogram analyses (Figure 7) have highlighted slightly different results between Site 1 and Site 2. Attributes of sub-site G-PB during pre-monsoon was quite far from the clustering of sub-sites G-I, G-II, G-III and G-IV for Site 1 (84%-96%), indicating that summer fragmentation in this wetland led to a lot of differences in zooplankton composition

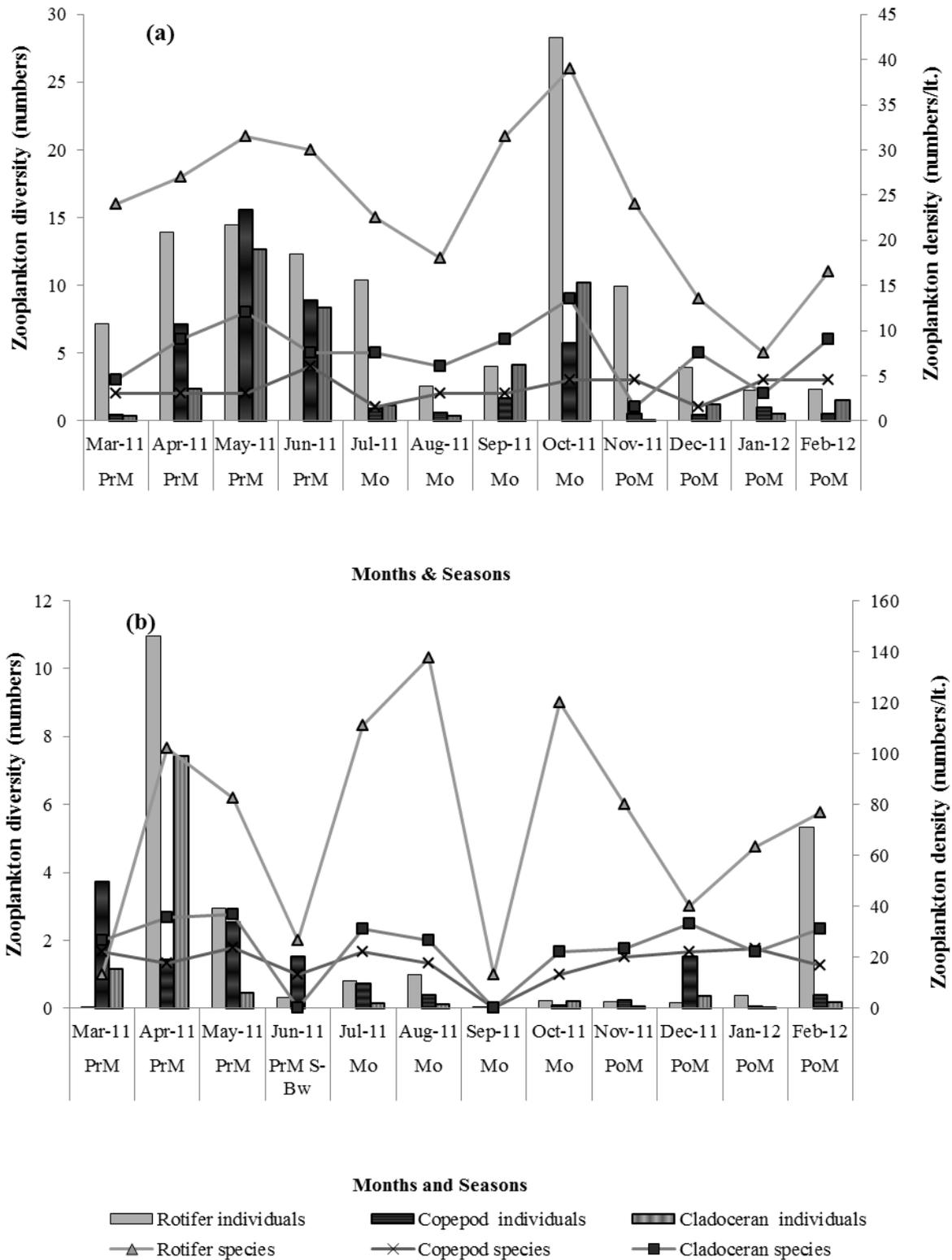


Figure 5. Aggregate monthly fluctuation of zooplankton diversity and density at (a) Site 1 and (b) Site 2.

at local sub-sites. However, monsoon and post-monsoon periods exhibited very similar species composition. Total cluster analysis diagram has also depicted closest similarity (98%) between G-III and G-IV during post-monsoon period. The sub-sites within Site 2 displayed closest relations (93%-98%)

during monsoon period; whereas results showed differences of S-III from the rest of the sub-sites depicting only 84% similarity during pre-monsoon. Both sites S-I and S-II were found to be very close (97%) in respect of species composition even during pre-monsoon. Considering comparison of both sites

Table 3. Community Similarity indices for mean zooplankton density at selected sub-sites of two study sites, across 3 major seasons

Sub-site-season	G-I PoM	G-I PrM	G-I Mo	G-II PoM	G-II PrM	G-II Mo	G-III PoM	G-III PrM	G-III Mo	G-IV PoM	G-IV PrM	G-IV Mo	G-PB PoM	G-PB PrM	G-PB Mo
G-I PoM	×			11			12			9			2		
G-I PrM		×			17			7			20			18	
G-I Mo			×			19			17			15			20
G-II PoM	0.665			×			14			10			<i>1</i>		
G-II PrM		0.296			×			9			21			21	
G-II Mo			0.316			×			16			14			8
G-III PoM	0.493			0.305			×			10			<i>1</i>		
G-III PrM		0.278			0.553			×			11			10	
G-III Mo			0.263			0.290			×			12			12
G-IV PoM	0.168			0.390			0.180			×			<i>1</i>		
G-IV PrM		0.336			0.387			0.298			×			21	
G-IV Mo			0.409			0.352			0.288			×			18
G-PB PoM	0.087			0.022			0.010			0.038			×		
G-PB PrM		0.231			0.388			0.356			0.361			×	
G-PB Mo			0.353			0.582			0.239			0.372			×

Sub-site-season	S-I PoM	S-I PrM	S-I Mo	S-II PoM	S-II PrM	S-II Mo	S-III PoM	S-III PrM	S-III Mo	S-Bw PoM	S-Bw PrM	S-Bw Mo
S-I PoM	×			12			12			7		
S-I PrM		×			7			9			8	
S-I Mo			×			15			10			12
S-II PoM	0.103			×			10			8		
S-II PrM		0.374			×			13			13	
S-II Mo			0.488			×			10			13
S-III PoM	0.309			0.165			×			7		
S-III PrM		0.067			0.233			×			8	
S-III Mo			0.206			0.180			×			9
S-Bw PoM	0.047			0.029			0.070			×		
S-Bw PrM		0.127			0.555			0.012			×	
S-Bw Mo			0.399			0.358			0.144			×

*G= Site 1 (Gurguripal); I, II, III, IV, and PB =>sub-sites of Site 1; S= Site 2 (Sundra); I, II, III and Bw=>sub-sites of Site 2; PoM=post-monsoon; PrM=pre-monsoon; Mo=monsoon. *Left side columns:* fractional values indicate C_N (Bray and Curtis, 1957) between respective sub-sites; *Upper right side:* whole numbers indicate 'j' for seasonal pair of sub-sites; italicised values indicate relatively lowest 'j'; values in bold indicate >50% or <10% C_N between any 2 pair of sub-sites within same season.

together (Figure 7), S-Bw solely set itself apart from all other sub-sites as a segregated habitat (70%-86%) irrespective of seasons and monsoons and post-monsoons brought most of the sub-sites under close clusters (94% similarity) in spite of being locally or regionally located.

Discussion

This study has added 22 new records to the previous list of rotifers from freshwater wetlands of the district (Pradhan and Chakraborty, 2008; Halder *et al.*, 2008). However, this number is much less than that found in floodplains of north-eastern part of India (Sharma, 2005; Sharma, 2010) and freshwater riverine networks of the south-west Bengal (Pradhan and Chakraborty, 2008). The diversity, species composition and percentage of surface coverage of macrophytes have appeared to be important density dependant factors determining the density and

diversity of aquatic invertebrate faunal (Cottenie *et al.*, 2003; Van de Meutter *et al.*, 2008). In concordance with these workers, the occurrence of some rotifers in one of the sites and their absence in the other site may infer that particular species of Rotifera exhibited habitat preference influenced by macrophytes. However, there were some species which did not exhibit any such preference, inferring that the rest were common to the region. It may be true that the existence of a rotifer in any particular place is not determined by the processes of dispersal, colonization, and establishment, but rather that the habitat selects which organisms thrive (Walsh *et al.*, 2007). Contrarily, some species are known to have high habitat selectivity (Kaya *et al.* 2010). Sorensen's similarity indices (Table 1) with respect to zooplanktonic diversity indicate moderate similarity, but those for aquatic plants and abiotic parameters clearly indicate the contrasting nature of both study sites because of moderate dissimilarity between them.

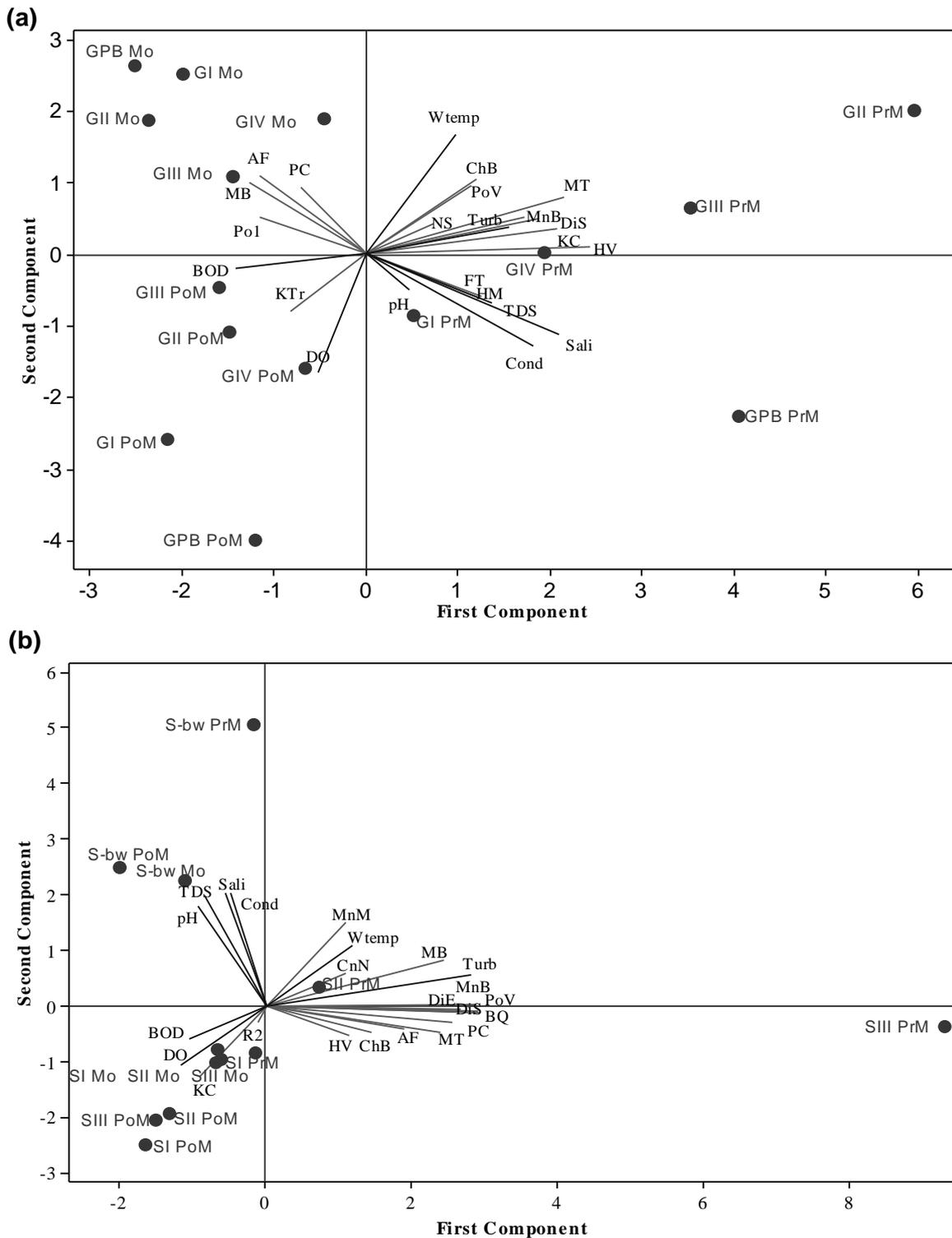


Figure 6. Principal Components Analyses of water quality parameters (blue project lines) and important species composition (green project lines) in the seasonal sub-sites of: (a) Study Site 1 and (b) Site 2. Abbreviations refer to the zooplankton species listed in Table 4. These biplots illustrate only those species that were either/both dominant (relative abundance >2.1%) or frequent.

Joniak *et al.* (2007) and Wallace *et al.* (2005) emphasized that the similarity of rotifer communities is most strongly influenced by particular habitat and season. This was proved in the present research study too, where season has been found to be a major factor in determining the bulk species of a habitat. Further,

macrophytes influenced the colonization of few zooplankton species unique to a particular local habitat.

Because of the discontinuity of water flow between sub-sites in this study, postmonsoon exhibited least similarities among zooplankton

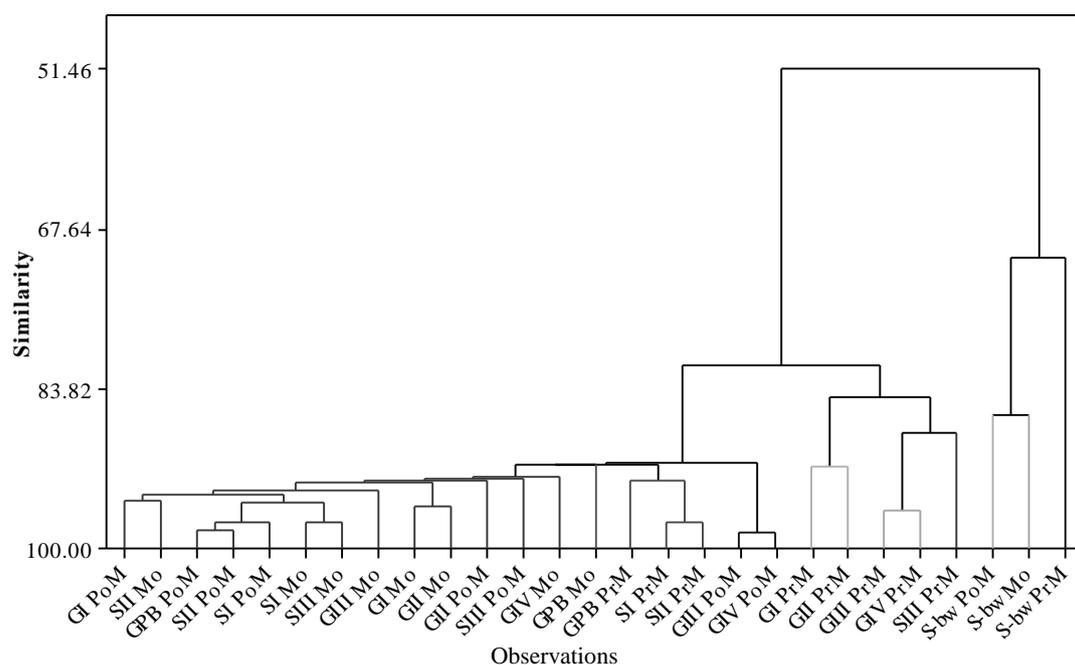


Figure 7. Dendrogram showing similarities among various sub-sites during each season on the basis of physicochemical attributes, macrophytes and important zooplanktonic components of both sites.

Table 4. List of important zooplankton species recorded in this study during 2011-2012

Species	Abbreviation
Phylum: Rotifera	
<i>Anuraeopsis fissa</i> Gosse, 1851	AF
<i>Brachionus quadridentatus</i> Hermann 1783	BQ
<i>Conochilus natans</i> (Seligo, 1900)	CnN
<i>Filinia novaezealandiae</i> Shiel and Sanoamuang, 1993	FT
<i>Hexarthra mira</i> (Hudson, 1871)	HM
<i>Keratella cochlearis</i> (Gosse 1851)	KC
<i>Keratella tropica</i> (Apstein 1907)	KTr
<i>Lecane bulla</i> (Gosse, 1851)	MB
<i>Philodina citrina</i> Ehrenberg, 1832	PC
<i>Polyarthra vulgaris</i> Carlin, 1943	PoV
<i>Polyarthra</i> sp.	Po1
Unidentified species 2	R2
Phylum: Arthropoda	
Subclass: Copepoda	
<i>Mesocyclops thermocyclopoides</i> Harada, 1931	MT
<i>Heliodyptomus viduus</i> (Gurney, 1916)	HV
<i>Neodyptomus schmackeri</i> (Poppe and Richard, 1892)	NS
Order: Cladocera	
<i>Ephemeropterus barroisi</i> (Richard, 1894)	ChB
<i>Diaphanosoma excisum</i> Sars, 1885	DiE
<i>Diaphanosoma sarsi</i> Richard, 1894	DiS
<i>Moina micrura</i> Kurz, 1874	MnM
<i>Moina brachiata</i> (Jurine, 1820)	MnB

communities of fragmented sub-sites for both study sites. Values of 'j' were mostly high for pairwise combinations of the sub-sites belonging to the Site 1 during monsoon and pre-monsoon in contrast to those

during post-monsoon. Walsh *et al.* (2007) stated the fact that there would be relatively little change in rotifer composition among large interconnected lakes or from year to year, is a paradox. The species

composition of G-II showed maximum similarity with G-PB during monsoon ($C_N=0.582$) due to overflow, in contrast to post monsoon, when connectivity was disrupted. This suggests that simple connectivity may render similar species assimilations for nearest sub-sites only and is not sufficient to homogenise the composition of entire water body. Cottenie *et al.* (2003) have suggested that, even in their system of highly interconnected ponds, local environmental constraints can be strong enough to structure local communities. Fontaneto *et al.* (2008) found that Bdelloids showed low species diversity but high habitat selectivity. In addition they claimed that where dispersal appeared to be rare, habitat availability tended to limit the ability of colonists to become established.

The potential of organisms to disperse among habitat patches within metacommunities depends on the distance and type of connections among patches (Shurin *et al.*, 2000). Site 1 showed substantial dispersal while Site 2 exhibited negligible spatial dispersal within wetland metacommunities because of effective fragmentation, which is in accordance with the findings of Cottenie and De Meester (2003) and Declerck *et al.* (2011b). Connectivity between subcomponents of present study, probably by passive water movement in a complex manner, is found to be similar to case of large lakes, which corroborates the findings of Leibold *et al.* (2004). Therefore the present study emphasizes the actual heterogeneity in spite of apparent homogeneity of selected water bodies.

It is observed that local habitats within a wetland may manifest extremely low to high similarity (Table 3), but in spite of the contrasting nature of both wetlands, there is a close similarity in the species richness of each group of organisms (Rotifera, Copepoda or Cladocera) as well as total zooplankton richness (Table 1). Interestingly, a series of common species, occurring at both the sites, although quite low in their density, are responsible for bringing in the similarity between the two studied wetlands. Such a reorganised phenomenon at regional level may hint towards a Complex Adaptive System within the metacommunity (Figure 1). Walsh *et al.* (2007) found surprisingly high species richness in the arid ephemeral pond systems which fits our finding about Site 2 exhibiting substantial zooplankton richness, although being temporary in nature. Wallace (2002) opined that rotiferan species abundance can differ markedly and unfortunately, even short term sampling schedules can miss the details of population peaks. In tune with the fact, rotifers (particularly *P. vulgaris*) have been found to dominate both the sites, but particular copepods and cladocerans equally shared the dominance in Site 2 (Figure 3). Regional species diversity and density patterns across months showed distinct trends with nearly synchronised peaks for rotifer, copepod and cladocera together in both sites (Figure 5).

Studying the distribution of zooplankton species on the basis of physicochemical parameters (Figure 6a and 6b) revealed one strong cluster for each site. Maximum species were found to be associated with water temperature and turbidity in both the sites whereas only a couple of them seemed to vary along DO and BOD. Such finding is partly true for temperature as stated by Wallace *et al.* (2005) but is otherwise different from the authors due to the difference in the ecological nature of the wetlands (desert versus lateritic forest). Figure 7 has suggested that the trajectory of species composition got hugely diverged at sub-sites of Site 2 only during pre-monsoon but important species composition in S-Bw remains more or less unaltered before and after monsoon. Moreover, sub-sites of both sites illustrated substantially high similarity among them during monsoon and post-monsoon, although being located at far away regions. In spite of above-mentioned variations in the individual site, the zooplankton communities of both sites have been found to converge on a similar assemblage of taxa annually at regional scale (Table 1). Cadotte (2006) showed that dispersal affects richness at the local community scale, but not at the metacommunity scale. The results from present study lead us to accept the hypothesis of CWCD stating that locally coexisting species communities within each site are less similar to each other than random aggregate draws from the two regional water bodies.

Wallace *et al.* (2005) stated that communities vary widely among different habitats, which appears to be due to the influence exerted by the local edaphic conditions. This was corroborated in the current study where constituent species tended to fluctuate within a wetland enjoying similar ecological conditions. In conclusion, the present paper has reflected the fact that stronger partitioning between adjacent local habitats led to more heterogeneity between inhabiting plankton populations, making seasonal influence secondary. Contrarily, even slight connectivity was supposed to be sufficient to homogenise the majority community of a wetland (enabling successful intra-site colonisation). This highlighted season as a primary factor which directly or indirectly governed the regional metacommunity.

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