RESEARCH ARTICLE

Depth distribution of zooplankton in relation to limnological gradients under different stratification and interannual regimes in a deep, tropical crater lake

Peter O. Sanful^{1,*}, Samuel Aikins² and Robert E. Hecky³

¹ Department of Fisheries and Water Resources, School of Natural Resources, University of Energy and Natural Resources (UENR), P.O. Box 214, Sunyani, Ghana

² Department of Theoretical and Applied Biology, Kwame Nkrumah University of Science and Technology (KNUST), Kumasi, Ghana

³ Biology Department and Large Lakes Observatory, University of Minnesota-Duluth, 2205 East Fifth Street, Duluth, MN 55812, USA

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Abstract – Zooplankton vertical distribution was studied in Lake Bosumtwi to understand how spatial and temporal variations in the water column affected diurnal and nocturnal patterns. Biweekly samples were collected for 24 consecutive months at the deepest point from 2005 to 2006. Water column properties shaping habitat suitability, namely temperature, light intensity, dissolved oxygen and phytoplankton biomass, varied markedly with depth but less with season. Most zooplankton stayed in the epilimnion continuously and their distribution was unaltered by lake stratification, mixing and restratification. Species dwelt permanently in the epilimnion without any necessity to migrate. Reduced water column variability and resultant weak selective pressures suppressed greater dispersion of species. *Chaoborus ceratopogones* (Theobald) was the main invertebrate predator and performed upward and downward movements on a diel cycle. Competing prey species overlapped extensively in spatial and temporal degree of habitat use. *Chaoborus*, however, segregated in deep water during the day, thereby minimizing prey vulnerability and promoting coexistence among predators and prey. During night-time residence, prey species may be exposed to increased predation risk from *Chaoborus* but gains in reproductive potential in warm, food-rich surface waters may offset losses to mortality. Our results suggest that high degree of habitat constancy and consequently weak selective pressures contributed to the lowered behavioural responses of zooplankton. The persistently skewed distribution of zooplankton is adaptive to predation and competition and promotes species coexistence. This behaviour will optimize growth and reproductive benefits over the cost of descent to suboptimal conditions in deep water.

Keywords: Lake Bosumtwi / *Mesocyclops bosumtwii* / vertical distribution / tropical / water column parameters

1 Introduction

Compared to shallow lakes, deep thermally stratified tropical lakes exhibit sharp vertical gradients in physico-chemical parameters that create depth habitats of variable quality for zooplankton species (MacIntyre, 2012). Variation in temperature, dissolved oxygen, food concentration, light intensity, competition and predation risk with depth define habitat suitability and influence habitat choice of zooplankton populations (Leibold, 1990; Andersen and Nival, 1991; Winder et al., 2003; Stratton and Kessler, 2007; Khalifa et al., 2015). The distribution of zooplankton often is a response to the spatio-temporal dynamics of the physical environment within which they live (Wetzel, 2001; Hansson et al., 2007).

By contrast, the lack of physical partitioning in shallow unstratified lakes simplifies the aquatic habitat (Burks et al., 2002) and result in uniform dispersion of zooplankton (Mavuti, 1992). Stratified waterbodies therefore offer greater scope of discrete depth-habitats for diverse zooplankton to inhabit (Bini et al., 2001). The observed distribution patterns are the outcome of active movement of organisms in response to shifts in habitat quality (Mendonça et al., 2015; Picapedra et al., 2015) or passive vertical transport generated by mixing events (Kramer et al., 1997).

Both abiotic and biotic variables interact to determine zooplankton distribution in lakes. Predation by fish and invertebrates (*Chaoborus*) and competition for resources affect patterns of spatial segregation and succession of zooplankton communities (Zaret and Suffern, 1976; Demott, 1989; Dawidowicz et al., 1990; Wissel et al., 2003). These selective

*Corresponding author: pospanf@yahoo.com

pressures induce behavioural changes in organisms by displacing them from optimal to suboptimal habitats (Gliwicz, 1986). The location of refuges in deep water mediates the impact of biotic forces on zooplankton and helps shape the character of vertical distribution (Primicerio, 2000; Wissel *et al.*, 2003).

Zooplankton vertical migration behaviour is an important ecological trait that enhances overall fitness of organisms (Enright, 1977; Williamson *et al.*, 1996). The main driver of migratory activities is avoidance of capture from visually hunting fish (Zaret and Suffern, 1976). To minimize spatial overlap with competitors and predators, species may exploit different habitats (Primicerio, 2000). Thus, the specific depth-location of a species is the outcome of trade-offs among several competing decisions on habitat choice (Brown, 1998; Lampert *et al.*, 2003; Kessler and Lampert, 2004). Various theories suggest that organisms derive multiple advantages by optimizing their vertical locations in the water column to maximize fitness (Williamson *et al.*, 1996; Pearre, 2003). Habitat stability may therefore promote a stabilizing effect on habitat use by organisms occupying specific habitats (Hanski, 1988).

Seasonal changes such as lake mixing and restratification are examples of physical upsets to habitat suitability. The resultant changes broaden the habitable volume and homogenize the water column occupied by organisms (Kramer *et al.*, 1997). This ensures greater range of dispersion and consequently active segregation of species along the water column is curtailed (Kramer *et al.*, 1997). Water movements generated by wind-induced turbulence overpower the swimming capabilities of organisms and spread organisms across an increased oxygenated volume (Spitael, 2007; Heald, 2015). This downward movement may heighten predation risk by exposing prey species to deep-dwelling predators. These seasonal oscillations can substantially alter the pattern of distribution (Burns and Mitchell, 1980; Primicerio, 2000; Wong *et al.*, 2012) and compel organisms to occupy suboptimal depths at the expense of their overall fitness (Gliwicz, 1986; Lampert, 1993; Wissel and Ramcharan, 2003). The vast majority of deep African tropical lakes are permanently stratified with muted seasonality of their water columns (MacIntyre, 2012). The rare occurrence of full mixing events implies that active habitat selection of zooplankton will be less pervasive. This may possibly be the signature distribution of tropical zooplankton resident in deeper lakes.

Despite numerous studies on tropical African zooplankton, an extremely poor record of research work regarding their behavioural ecology exists. The impact of this research gap is even more apparent in the face of limnological regime shifts due to climate change and anthropogenic factors. Seasonal and multiyear studies are therefore required to improve our understanding of water column dynamics and responses of zooplankton organisms. The aim of this study therefore is to provide insight into how seasonality in water column structure in deep, stratified tropical African lakes affects distribution patterns of zooplankton.

2 Materials and methods

2.1 Study site

Lake Bosumtwi is a deep tropical lake. In recent times, it has shifted from holomictic – completely mixed to meromictic –

partially mixed (Turner *et al.*, 1996a; Puchniak *et al.*, 2009). The closed-basin lake is characterized by a long water residence time and reduced flushing rates (Turner *et al.*, 1996b). It occupies a nearly circular depression created by a meteorite that impacted the crater site 1.07 million years ago (Koeberl *et al.*, 2007). The lake is located at 06°30' N and 01°25' W in the south-central part of Ghana along the West African coast and lies in the path of the annual migration of the Intertropical Convergence Zone (ITCZ) (Koeberl *et al.*, 2007) (Fig. 1). It has a crater diameter 10.5 (±0.5 km), a lake-surface diameter of 8–8.5 km, maximum depth of 78 m and surface area of 52 km² (Koeberl *et al.*, 1997). The lake's limnology is closely approximated to regional climate variability (Puchniak *et al.*, 2009). The closed-basin structure means that it lacks inflow and outflow channels with water levels driven by the precipitation-evaporation balance and making the lake extremely sensitive to climate variability (Turner *et al.*, 1996b). High rainfall seasonality is characterized by maximum precipitation in May/June with a secondary peak in September/October.

Mean conductivity, temperature, dissolved oxygen, salinity and pH within the top 30 m of the water column are 1150 $\mu\text{S cm}^{-2}$, 28.14 °C, 52.35% saturation, 0.32 psu and 8.9, respectively. The water column is stable with persistent stratification all year round and a permanently anoxic deep water underlying a mixed layer of variable depth and oxygen content (Puchniak *et al.*, 2009). Mixing occurs strongly in August and weakly in January, but in certain years, the August circulation may be less prominent (Puchniak *et al.*, 2009). Pronounced mixing events can liberate H₂S from deep water often leading to massive fish kills (Turner *et al.*, 1996a; Puchniak *et al.*, 2009). Entrainment of nutrient-rich hypolimnetic water triggers phytoplankton productivity during this period (Awortwi, 2009). Algal chlorophyll concentration in the mixed layer ranges between 0.002 and 32 $\mu\text{g L}^{-1}$ with an annual mean of 10 $\mu\text{g L}^{-1}$. The phytoplankton community is dominated by Cyanobacteria (Poste *et al.*, 2008; Awortwi, 2009). Previous studies characterized the zooplankton community as consisting of only nine taxa namely an endemic copepod *Mesocyclops bosumtwii* (Mirabdulayev *et al.*, 2007), a dense *Chaoborus* larval assemblage, several rotifer species and a small-sized cladoceran *Moina micrura* (Kurz) (Sanful *et al.*, 2012). The major rotifer species are *Brachionus calyciflorus* (Pallas) and *Hexarthra intermedia* (Wiszniewski). Species that are uncommon in the water column include *Brachionus dimidiatus* (Bryce), *Keratella cochlearis* (Gosse), *Filinia pejeri* (Hutchinson) and *Filinia camascela* (Myers) (Sanful *et al.*, 2012). A seasonal band of green and purple sulphur bacteria peaks in metalimnetic layers (12.5–15 m) at the hypoxic–anoxic interface between March and July.

2.2 Zooplankton sampling

Discrete quantitative samples on day-time vertical distributions were collected biweekly between January 2005 and December 2006 at an index central station 06°30' N and 01°25' W between 11 h:30 min and 00 h:30 min. The limnological season was classified as stratified (most months), mixing (January, July, August) and restratifying (September and October). Samples were collected from eleven discrete depths as follows: surface (0), 1, 2, 5, 8, 10, 12.5, 15, 20, 25 and 30 m of depth using a 6 L van Dorn water bottle to take

Fig. 1. Map of Lake Bosumtwi showing catchment boundary (broken lines) and its geographical location in the study country and continent. Lake map modified from [Shanahan \(2006\)](#).

triplicate samples at each depth. A total of 18 L of water containing zooplankton at each depth was filtered from the Van Dorn samples through a 25 μ m mesh. Based on prior knowledge of the water column structure, the sampling depths were segmented into epilimnetic (surface, 1, 2, 5 m), metalimnetic (8, 10, 12.5, 15 m) and hypolimnetic (20, 25 and 30 m) layers. Filtered zooplankton was preserved with 4% formalin.

2.3 Diel (24-h) vertical migration (DVM) studies

DVM studies were conducted on three dates corresponding to the stratified, mixing and restratifying events. Triplicate

samples were collected with a 6-L Van Dorn sampler at eleven discrete depths compartmentalized into epilimnion (surface, 1, 2, 5 m), metalimnion (8, 10, 12.5, 15 m) and hypolimnion (20, 25 and 30 m) at 6-h intervals beginning from 12 h:00 min of the first day to 06 h:00 min of the next day. Concurrent dissolved oxygen and temperature parameters were profiled with a Hydrolab H₂O 6SBP multiprobe from a depth 50 m due to restricted cable of the Hydrolab. Notwithstanding, all three thermal layers were conveniently sampled with the 50 m mark well into the hypolimnion over the 78 m depth of the lake. Samples were stored in 125 mL glass bottles and preserved with 4% formalin.

2.4 Subsampling and enumeration procedures

Zooplankton was counted from 5 mL subsamples. More than 200 individuals of the most common species were counted (McCauley, 1984). In contrast, ≥ 50 individuals of the less common species were usually counted from several subsamples from a Sedgwick-Rafter counting chamber mounted on a Zeiss inverted microscope at $100\times$ magnification.

2.5 Physicochemical measurements

The underwater light intensity was measured with a flat-plate LI-COR 190R quantum sensor (LI-COR Biosciences, Lincoln NB). Measurements were taken at different depths from the surface to the depth where the light intensity was approximately 1% of surface irradiance, usually down to the metalimnion between 8 and 10 m. A Hydrolab H₂O 6SBP multiprobe (Hydrolab Corporation, Austin, Texas, 1991) was used to capture 50 m-depth profiles of temperature and dissolved oxygen.

2.6 Phytoplankton biomass measurement

Phytoplankton biomass data were obtained from contemporaneous phytoplankton studies (Awortwi, 2009). Samples were usually concentrated into 125 mL subsamples after filtering through a mesh. Samples were usually obtained from a 6-L Van Dorn water bottle used to sample phytoplankton at biweekly intervals at ten discrete depths (surface, 1, 2, 5, 8, 10, 12.5, 15, 20, 30). These depths were similarly categorized into epilimnetic, metalimnetic and hypolimnetic layers. The subsamples were immediately preserved with 1 mL acid Lugol solution and subsequently stored in a dark, cool container for further analysis in the laboratory. Phytoplankton species were enumerated from settled 2 mL samples observed under an inverted Zeiss microscope in a 2 mL Utermohl chamber at $400\times$ magnification and converted to wet weight biomasses through approximation of cell volume to geometrical formulae that best fits the shape of the cell.

2.7 Data analysis

Measured physicochemical parameters were categorized into independent group variables corresponding to distinct water layers. Seasonal variations were classified on the basis of stratified, mixing and restratifying conditions of the lake. The vertical density gradients of the zooplankton species served as the dependent variables. A two-way analysis of variance (ANOVA) and *t*-tests were used to examine whether dissolved oxygen, temperature and phytoplankton biomass varied significantly with depth and season. Data analysis and statistical tests were performed with Sigma Plot Version 10, SYSTAT 10 (Systat Software Inc.). Data were examined at the 5% level of statistical significance. The seasonal correspondence in depth distribution of physicochemical variables and zooplankton species densities were analyzed with both Spearman's Rank (pairwise) and Pearson's (listwise) correlations.

3 Results

3.1 Vertical gradients in limnological variables

Temperature, dissolved oxygen and phytoplankton biomass showed strong gradients between 10 and 15 m depth during the stratified period with a steep thermocline co-occurring with a strong oxycline in 2005 and 2006 (Fig. 2). Light distribution was bimodal with a highly illuminated upper epilimnion and darker metalimnion and hypolimnion (Tab. 1). Mean lake transparency was 1.6 ± 0.41 m over the two years. The shallowest euphotic mean depth of 1.05 ± 0.28 m was recorded during the restratifying period. During the stratified period, the mean epilimnetic, metalimnetic and hypolimnetic depths were 8, 4 and 32 m, respectively over the sampling depth of 50 m (Fig. 2). Lake stratification was characterized by well-defined gradients in light intensity, temperature, dissolved oxygen and phytoplankton biomass (Fig. 2). Statistically, during 2005 and 2006, the seasonal water column variation in temperature, dissolved oxygen, phytoplankton biomass and light intensity were all significant at the 5% probability level (Tab. 2).

3.2 Interannual patterns of depth variability of limnological parameters

Seasonal temperature, dissolved oxygen and phytoplankton biomass depth profiles in 2005 were correlated with that of 2006 by performing a Spearman's pairwise rank correlation analysis to compare the degree of similarity in the water column structure between the two years. All these parameters showed remarkable significant differences at $p < 0.05$ (Tab. 3).

3.3 Density gradients of zooplankton

The summary statistics for the maximum and minimum densities of zooplankton and their respective means, standard deviations and significant differences among mean species densities are shown (Tab. 4). Adults, copepodites and nauplii of *M. bosumtwii* were predominant at all depths inhabited by zooplankton. However, most zooplankton species were highly concentrated in the epilimnion (Tab. 4). Overall, copepods showed the strongest gradients across all seasons decreasing dramatically in numbers from the epilimnion to the hypolimnion (Fig. 3). The hypolimnion was devoid of zooplankton at most times except *Chaoborus*, which showed an inverse distribution in the water column (Fig. 4). Statistically, adults of *M. bosumtwii* did not show any significant variation across depth and season at $p > 0.05$, $n = 15$ (Tab. 5). A similar pattern of distribution was exhibited by conspecifics where depth and seasonality of the water column structure did not exert any strong vertical density gradient on copepodites ($p > 0.05$, $n = 15$) and nauplii ($p > 0.05$, $n = 15$). All three developmental stages of *M. bosumtwii* all showed significant seasonal variations among the stratified, mixing and restratifying periods only in the epilimnion ($p < 0.05$, $n = 15$). Differences in the metalimnion and hypolimnion over the same season were not significant at ($p > 0.05$, $n = 15$). For *B. calyciflorus*, densities varied significantly in the epilimnion at ($p < 0.05$,

Fig. 2. Depth profiles of temperature, dissolved oxygen and phytoplankton biomass during stratified, mixing and restratifying periods.

$n = 20$) but variations in the metalimnion ($p > 0.05$, $n = 20$) and hypolimnion ($p > 0.05$, $n = 20$) were not significant. Both *H. intermedia* and *Chaoborus* did not exhibit any statistical relationship among depth and across seasons ($p > 0.05$, $n = 20$) and ($p > 0.05$, $n = 20$), respectively.

3.4 Interannual patterns of depth variability of zooplankton species density

Correspondence analysis showed that zooplankton species demonstrated significant interannual variability in the patterns

Table 1. Summary statistics of maximum, minimum, mean and standard deviation of temperature, dissolved oxygen (DO) and phytoplankton biomass. Epilimnion (n)=255, metalimnion (n)=153, hypolimnion (n)=153. Probability values calculated for vertical differences in physicochemical parameters among epilimnion, metalimnion and hypolimnion. Sample size (n): temperature (20), DO (20), phytoplankton biomass (21), light intensity (7), Secchi depth (7).

Parameter	Epilimnion				Metalimnion				Hypolimnion				<i>P</i> -value
	Max	Min	Mean	Std	Max	Min	Mean	Std	Max	Min	Mean	Std	
Temperature (°C)	32.61	26.56	29.43	1.36	29.98	26.82	27.84	0.75	27.98	26.81	27.05	0.21	<0.05
DO (mg L ⁻¹)	12.18	0.92	6.30	2.52	10.25	0.10	2.76	2.54	8.93	0.09	1.29	2.09	<0.05
Phytoplankton biomass (mg wt m ⁻³)	6375	208	2162	1264	3856	148	1238	799	2094	34	441	336	<0.05
Light intensity (μmol s ⁻¹ m ⁻²)	1050	6.5	265.77	299.96	0	0	0	0	0	0	0	0	<0.05
Secchi depth (m)	2.6	0.8	1.6	0.41	0	0	0	0	0	0	0	0	<0.05

Table 2. Seasonal mean and standard deviation values of physicochemical variables in each stratum during 2005 and 2006. Data for light intensity was not obtained in 2006 due to technical challenges with light meter. Epilimnion (n)=255, metalimnion (n)=153, hypolimnion (n)=153. Light intensity for stratified season (n)=22, mixing season (n)=19 and Secchi depth (n)=4.

Physicochemical variable	Stratified			Mixing			Restratifying		
	Epi.	Meta.	Hypo.	Epi.	Meta.	Hypo.	Epi.	Meta.	Hypo.
2005									
Temperature (°C)	30.37 ± 1.01	27.59 ± 0.39	27.11 ± 0.17	27.46 ± 0.55	27.29 ± 0.37	27.08 ± 0.26	28.59 ± 1.31	27.04 ± 0.22	26.8 ± 0.01
Phyto. biomass (mg wt m ⁻³)	688 ± 367	443 ± 231	208 ± 201	1644 ± 1108	1219 ± 791	667 ± 546	2953 ± 1569	986 ± 665	470 ± 359
DO (mg L ⁻¹)	6.73 ± 2.11	0.59 ± 0.61	0.44 ± 0.61	3.63 ± 0.63	4.02 ± 1.30	1.50 ± 1.51	5.02 ± 2.51	0.91 ± 1.01	0.37 ± 0.33
Light intensity	195.50 ± 260.99	0	0	344.3 ± 328.46	0	0	0	0	0
Secchi depth	1.75 ± 0.17	0	0	1.35 ± 0.1	0	0	1.05 ± 0.28	0	0
2006									
Temperature (°C)	30.50 ± 0.71	28.30 ± 0.69	27.00 ± 0.19	28.50 ± 0.58	27.97 ± 0.67	27.20 ± 0.29	28.82 ± 0.93	27.55 ± 0.21	27.22 ± 0.10
Phyto. biomass (mg wt m ⁻³)	1970 ± 1085	726 ± 312	385 ± 174	2050 ± 952	1302 ± 846	396 ± 219	2744 ± 1238	1126 ± 515	447 ± 283
DO (mg L ⁻¹)	6.33 ± 1.58	2.92 ± 2.66	2.33 ± 2.88	6.88 ± 1.69	5.15 ± 3.43	2.36 ± 2.69	8.33 ± 2.06	1.76 ± 1.65	0.12 ± 0.02
Secchi depth	1.70 ± 0.2	0	0	1.53 ± 0.3	0	0	1.35 ± 0.19	0	0

Table 3. Spearman rank correlation comparing differences in seasonality of limnological variables in the water column between 2005 and 2006.

Parameter	Stratified	Mixing	Restratifying
Dissolved oxygen	0.53*	0.48*	0.84*
Temperature	0.89*	0.66*	0.94*
Phytoplankton biomass	0.42*	0.42*	0.64*

* Significance of the correlation and absence of (*) shows that relationship is not significant. Number of observations for stratified (n =43), mixing (n =55), restratifying (n =44).

of vertical distribution (Tab. 6). Most species showed significant correlations (p <0.05) between the mixing and restratifying periods with values of correlation coefficients (R^2) ranging from 0.24 for *M. bosumtwii* adults to 0.53 recorded for *B. calyciflorus*. There were no similarities in the

vertical distribution profiles between the stratified periods in 2005 and 2006. *Chaoborus* movements in the water column showed dissimilar patterns from year to year with no correlations in the structure of distribution in the water column (p >0.05).

Table 4. Summary statistics including maximum, minimum, mean and standard deviation of population densities of each species in the individual water stratum. Epilimnion (n)=255, metalimnion (n)=153, hypolimnion (n)=153.

Species/developmental stage	Epilimnion				Metalimnion				Hypolimnion			
	Max	Min	Mean	Std	Max	Min	Mean	Std	Max	Min	Mean	Std
Copepod adults*	93 746	1250	4760	10 546	62 331	1500	1548	6314	18 749	2333	165	1560
Copepodites*	313 154	1500	43 953	54 832	191 659	1917	5535	38 224	158 327	2083	1909	13 769
Nauplii*	481 480	1083	22 441	66 435	104 829	83	6339	13 216	4167	583	156	727
<i>Moina micrura</i>	19 833	1000	430	1902	2250	1250	50	313	0	0	0	0
<i>Brachionus calyciflorus</i>	102 329	1333	4476	14 556	20 833	1000	556	2576	31 249	1167	620	4166
<i>Hexarthra intermedia</i>	26 164	83	2808	4596	6250	2083	108	622	6250	0	36	477
<i>Chaoborus ceratopogones</i> *	6250	83	172	696	252 083	83	2649	20 460	34 000	83	2773	4130

*Significance of mean species densities among epilimnion, metalimnion and hypolimnion at $p < 0.05$. **Fig. 3.** Diurnal depth distribution of adults, copepodites and naupliar stages of the copepod *M. bosumtwii* during stratified, mixing and restratifying periods.

Fig. 4. Diurnal depth distribution of *M. micrura*, *H. intermedia*, *B. calyciflorus* and *Chaoborus* during stratified, mixing and restratifying periods.

Table 5. Variation of mean densities of zooplankton taxa within epilimnion, metalimnion and hypolimnion at $p < 0.05$ significance level. Sample size (n) is given in bracket. NS – not significant.

Parameter	Stratified	Mixing	Restratisfying
Copepod adults	NS	NS	NS
Copepodites	NS	$p < 0.05$ (15)	$p < 0.05$ (12)
Nauplii	NS	$p < 0.05$ (15)	NS
<i>B. calyciflorus</i>	$p < 0.05$ (12)	NS	NS
<i>H. intermedia</i>	NS	NS	NS
<i>Chaoborus</i>	NS	NS	NS

Table 6. Seasonal mean and standard deviation of population densities in each stratum during 2005 and 2006. Epilimnion (n) = 255, metalimnion (n) = 153, hypolimnion (n) = 153.

Species/developmental stage	Stratified			Mixing			Restratifying		
	Epi.	Meta.	Hypo.	Epi.	Meta.	Hypo.	Epi.	Meta.	Hypo.
2005									
Copepod adults	5562 ± 7441	993 ± 2274	0	2406 ± 5578	777 ± 1688	155 ± 602	11 826 ± 14 398	7999 ± 19 080	2343 ± 6628
Copepodites	16 057 ± 12 323	2694 ± 3962	0	60 796 ± 50 831	25 865 ± 32 012	5433 ± 11 066	98 454 ± 100 638	24 519 ± 55 506	17 041 ± 46 430
Nauplii	370 ± 927	4110 ± 8226	13 714 ± 26 363	21 002 ± 13 308	15 283 ± 11 984	1805 ± 3420	42 319 ± 81 233	9221 ± 17 431	506 ± 1277
<i>Moina micrura</i>	535 ± 1183	0	0	40 ± 200	300 ± 791	0	0	0	0
<i>Brachionus calyciflorus</i>	937 ± 1948	0	0	25 695 ± 31 615	4633 ± 7215	5972 ± 12 371	0	0	0
<i>Hexarthra intermedia</i>	2672 ± 4347	0	0	2225 ± 3060	417 ± 862	417 ± 1613	1531 ± 2404	0	0
<i>Chaoborus ceratopogones</i>	0	542 ± 928	618 ± 625	140 ± 485	278 ± 1013	2528 ± 4916	542 ± 928	2562 ± 75	431 ± 1235
2006									
Copepod adults	1583 ± 3047	0	0	3280 ± 7636	106 ± 408	0	879 ± 1011	278 ± 649	0
Copepodites	43 740 ± 39 360	2875 ± 7196	0	39 931 ± 47 959	3094 ± 2988	0	23 294 ± 34 407	1431 ± 2619	0
Nauplii	2883 ± 6472	2159 ± 4250	0	7309 ± 8400	4500 ± 6167	956 ± 3212	10 216 ± 13 730	5805 ± 10 782	0
<i>Moina micrura</i>	463 ± 1116	0	0	0	0	0	0	0	0
<i>Brachionus calyciflorus</i>	0	0	0	833 ± 1901	1500 ± 387	0	3812 ± 5693	0	0
<i>Hexarthra intermedia</i>	3590 ± 5678	0	0	2426 ± 3635	278 ± 732	0	4684 ± 5052	521 ± 1802	0
<i>Chaoborus ceratopogones</i>	96 ± 295	632 ± 1032	1972 ± 2067	17 ± 83	1678 ± 5312	5094 ± 4063	308 ± 677	638 ± 677	2403 ± 1598

3.4.1 Variation of zooplankton species densities with limnological variables

Densities of adults, copepodites and nauplii stages of *M. bosumtwii* were positively correlated with physicochemical variables and phytoplankton biomass profiles in the water column across all seasons and years (Tab. 7). An inverse relationship was observed by the *Chaoborus* distribution patterns with limnological variables and *H. intermedia* did not exhibit statistical relationships during the mixing season.

3.5 Seasonality of DVM Patterns

No zooplankton species and developmental stages of *M. bosumtwii* performed active day and night migration in the water column over the three limnological seasons (Figs. 5–7). Most species inhabited the epilimnion and metalimnion en masse throughout the period. Even though numbers of *Chaoborus* were relatively higher in surface waters at night, density-driven mass movements were not detected. A greater dispersion in the water column was, however, observed during the mixing period. The analyses of DVM patterns showed that temporal changes in the densities of individual species among the various water strata were weakly correlated and yielded poor statistical results (range of $R^2 = 0.14–0.89$, $p > 0.05$).

4 Discussion

Lake Bosumtwi exhibited distinct limnological cycles and spatio-temporal dynamics of the water column. The significant depth of the lake permitted establishment of a thermal structure based on pronounced temperature and density gradients between water masses. These characteristics commonly depicted by stratified lakes feature a resource-rich, growth-enhancing epilimnion and a deeper, resource-poor, growth-limiting hypolimnion separated by an intermediate metalimnion (Wetzel, 2001). Variations in the water column structure due to mixing and restratification cycles also occurred. Combined with stratification, they defined the seasonality of the lake. This seasonality of Lake Bosumtwi like most deep African lakes has prolonged stratification and collapse of thermal stability are only ephemeral (Puchniak *et al.*, 2009; MacIntyre, 2012). The extended stratification period stabilized the water column and maintained consistent habitat conditions for zooplankton. The clear seasonal changes produced by these distinct lake events however yielded little impacts on patterns of zooplankton distribution.

The role of thermocline deepening and lake mixing in shaping distribution patterns of zooplankton is well-documented (Spitael, 2007; Cantin *et al.*, 2011). Limnological seasonality was marked by reduced amplitude of water column dynamics through limited span in mixing and restratification processes. Lake mixing broadened the habitable volume for zooplankton by extending their range of distribution. This mainly occurred due to oxygenation of anoxic depths. The downward mixing of oxygen will also force *Chaoborus* to deeper depths to accomplish the same degree of refuge. Consequently oxygen has the effect of reducing predation by *Chaoborus* and therefore total predation by forcing *Chaoborus* down to deeper depths. The increased delivery of dissolved

Table 7. Spearman rank correlation between species densities of zooplankton and limnological variables during 2005 and 2006.

Species	Stratified			Mixing			Restratifying		
	DO	Temp.	Phyto. biomass	DO	Temp.	Phyto. biomass	DO	Temp.	Phyto. biomass
2005									
Copepod adults	0.57*	0.56*	0.56*	0.17*	0.08	0.04	0.33*	0.38*	0.49*
Copepodites	0.74*	0.74*	0.56*	0.51*	0.19*	0.12*	0.58*	0.59*	0.66*
Nauplii	0.64*	0.64*	0.56*	0.45*	0.11*	0.09*	0.43*	0.58*	0.62*
<i>H. intermedia</i>	0.75*	0.75*	0.34	0.17*	−0.01*	0.05	0.50*	0.51*	0.28*
<i>Chaoborus</i>	−0.61*	−0.59*	−0.40	−0.28	−0.17*	−0.53*	−0.05*	0.13*	0.03
2006									
Copepod adults	0.37*	0.34*	0.33*	0.44*	0.34*	0.40	0.46*	0.46*	0.26*
Copepodites	0.35*	0.49*	0.39*	0.49*	0.59*	0.37*	0.76*	0.75*	0.58*
Nauplii	0.35*	0.34*	0.32*	0.45*	0.29*	0.41*	0.43*	0.54*	0.36*
<i>H. intermedia</i>	−0.42*	−0.65*	−0.55*	−0.39*	−0.52*	−0.55	0.70*	0.63*	0.40
<i>Chaoborus</i>	−0.42*	−0.65*	−0.55*	−0.39*	−0.52*	−0.62	−0.59*	−0.55*	−0.46*

* Significance of the correlation and absence of (*) shows that relationship is not significant. Number of observations for stratified ($n = 44$), mixing ($n = 55$), restratifying ($n = 44$).

oxygen to anoxic depths allowed copepods to also occupy deeper layers but this displacement was short-lived and less instructive. The increased dispersal of copepods could be explained by either active or passive mechanisms. However, because copepods did not previously inhabit deeper waters, their increased densities could be attributed entirely to vertical transport by water currents. The latter is supported by evidence of the role of physical forces in distributing zooplankton passively in the water column (Mavuti, 1992; Kramer *et al.*, 1997; Kizito, 1998).

Knowledge of mechanisms underlying habitat selection is key to understanding zooplankton distribution. Majority of species stayed in the epilimnion and used this single habitat without migration to exploit other deep strata. The preference for the epilimnion may be adaptive permitting organisms to maximize growth and development potential (Threlkeld, 1980; Orcutt and Porter, 1983; Stich and Lampert, 1984). Constancy of the physical environment favoured continuous epilimnetic residence. This suppressed any possible alterations to distribution patterns of species. The position of organisms at any specific depth in a stratified lake is suggested as a trade-off among conflicting decisions on habitat choice (Lampert, 2005). Persistence of zooplankton in the epilimnion may therefore confer an advantage on organisms because in deep water, growth and reproductive performance decline with decreasing temperature and food scarcity (Ringelberg, 2009). Spatial segregation with *Chaoborus* reduced predation risk on prey in the epilimnion. Coupled with poor food and growth conditions in the hypolimnion, descent by organisms was discouraged and severely restricted. Such situations commonly result in diminished zooplankton migration (Gliwicz and Pijanowska, 1988; Leibold, 1990; Lampert, 2005). The lack of migration further highlights the importance of predation in determining prey distribution (Zaret and Suffern, 1976; Pearre, 2003; Mendonça *et al.*, 2015). It is possible that zooplankton may develop specialized abilities to use the epilimnion more

efficiently due to consistency in habitat use. Temporal changes in the size of predator populations and limiting food resources may undermine the adaptation process by increasing predation and competition. This may compel organisms to migrate deeper into suboptimal conditions in the hypolimnion, therefore altering community structure (Zaret and Suffern, 1976; Primicerio, 2000). However, these biotic forces were weakened by extensive spatial overlaps between prey and invertebrate predators.

Only *Chaoborus* carried out “normal” DVM – daytime descent into deeper depths and night-time ascent to surface layers – on a diel cycle. This movement was detected rather on a limited scale. The DVM activity undertaken by *Chaoborus* prevented coexistence with its prey populations mainly confined to the epilimnion. *Chaoborus* ascent at night led to a shared habitat with prey organisms that did not depart from surface waters even though the presence of their predators increased risk of capture. The lack of response from prey demonstrates that the densities of predators are either well below the threshold required to induce migratory activity or prey may compensate for mortalities with increased reproductive potential (Fejes *et al.*, 2003). For prey to be forced to abandon a preferred habitat, predation pressure must exceed a specific threshold to trigger descent (Zaret and Suffern, 1976). Non-migrant animals may suffer high rates of respiration and mortalities in surface waters but could balance these losses with high food supply and increased fecundity (Dawidowicz and Loose, 1992). This behaviour is complemented by stability of the epilimnetic habitat, which has adaptive value for optimizing metabolic and reproductive fitness (Hanski, 1988). The lack of migration further suggests that predatory losses of species due to fish are weak or they would be higher if they migrated down during the day and be exposed to *Chaoborus*.

Competition is an important determinant of zooplankton distribution (Nogrady *et al.*, 1993). There was high overlap in habitat use among competing herbivore species given the

Fig. 5. Diel vertical migration (DVM) patterns of zooplankton taxa during the stratified season.

degree of stability in the habitat. This degree of spatial overlap increases vulnerability of prey to predation and intensifies interspecific competition (Quintana *et al.*, 2015). Competitors often limit overlaps in habitat use to overcome inequalities in competitive abilities (Nogrady *et al.*, 1993; Primicerio, 2000). The influence of competition on prey species may be evident in the distribution pattern of key herbivores in the lake. Major herbivore species, mainly *B. calyciflorus*, *H. intermedia* and

M. micrura, compete for limited quantities of edible algal food, given the abundance of toxic cyanobacteria in the phytoplankton community (Awortwi *et al.*, 2015). These types of organisms are also heavily preyed upon by *Chaoborus* (Moore and Gilbert, 1987; Moore *et al.*, 1994) and the interactions can contribute substantially to temporal and spatial structuring of zooplankton communities (Miller and Kerfoot, 1987; Rothhaupt, 1990). Larger organisms are predation-prone due

Fig. 6. Diel vertical migration (DVM) patterns of zooplankton taxa during the mixing season.

to the increased visibility to fish feeders (Zaret and Suffern, 1976; Stich and Lampert, 1981; Gliwicz, 1986) but small-sized organisms such as rotifers may escape detection and thereby reduce losses (Zaret, 1980; Gliwicz and Pijanowska, 1988). This explains why rotifers selected to stay in the epilimnion for most part of the year despite the strong presence of *Chaoborus*.

Fish predation is largely regarded as a proximate factor in altering patterns of distribution and overall structure of

zooplankton communities (Zaret and Suffern, 1976). Due to the absence of fish data, the influence of fish predation on *Chaoborus* could not be well accounted for. However, the suspicion is that the dominant native haplochromine fishes mainly composed of cichlids may exploit zooplankton inefficiently because of the low visibility, which restricts their feeding on larger organisms like *Chaoborus*. Haplochromines are reported to be facultative zooplanktivore sight feeders

Fig. 7. Diel vertical migration (DVM) patterns of zooplankton taxa during the restratifying season.

(Poste *et al.*, 2008) and in Bosumtwi, detection is limited by high phytoplankton turbidity due to large unconsumed biomass controlled by cyanobacteria (Awortwi *et al.*, 2015). Low fish predation may give prominence to *Chaoborus* in regulating distribution patterns in the lake as has been noted by Lagergren

et al. (2008) who documented the control exerted by invertebrate predators in DVM of other zooplankton. There is further evidence to suggest that at high fish population densities, feeding patterns of pelagic zooplanktivores may alter zooplankton community structure providing evidence for strong selective

pressures to induce migratory behaviour (Hecky, 2006). This tendency may, however, be weakened by the high spatial segregation between *Chaoborus* and the fish community living in the mixed layer. The absence of strong planktivory often accounts for the lack of migratory activity in prey (Dini *et al.*, 1993) although hypoxia/anoxia below the mixed layer may also be a barrier to migration if species are not adapted to such conditions. *Chaoborus* is an example of species adapted to low oxygen, thus allowing them to have a refuge from predation (Gade, 1985; Hazanato, 1992).

5 Conclusion

In conclusion, Lake Bosumtwi possessed a water column that displayed significant variation in depth but limited seasonality. Low variability in vertical distribution patterns of zooplankton was associated with equally low seasonal variation in water column structure. Habitat consistency restricted most populations to the epilimnion and this may be evidence of lack of strong selective pressures to alter habitat choice and habitat use. *Chaoborus* performed discernible DVM. The strategies for coexistence included spatial segregation and temporal overlaps of prey with predators and maintenance of low densities of herbivores.

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