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RESEARCH ARTICLE

Influences of environmental parameters and phytoplankton productivity on benthic invertebrates in a tropical oligotrophic lake, northern Malaysia

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Abstract

Studies that associate environmental parameters with aquatic organisms in man-made lakes remain limited by accessibility and interest particularly in many Asian countries. With missed opportunities to monitor environmental transitions at Lake Kenyir, our knowledge of lake transition is restricted to the non-mixing shallow waters only. Triplicate monthly benthic invertebrate samples were collected concurrently with various environmental parameters at three locations (zones A–C) of Kenyir Lake, Malaysia. Our results affirmed that the northeast part of Lake Kenyir is oligotrophic. Abundance of phytoplankton, total suspended solids, phosphate, nitrite and nitrate drive the abundance of various groups of benthic invertebrates. All of these extrinsic variables (except phosphate) negatively influenced the density of Trichoptera and positively influenced (P<0.05) the densities of Polychaeta, Oligochaeta, Bivalvia, Gastropod, Isopoda and Copepod in all zones. Phosphate negatively influenced the density of Trichoptera and positively influenced (P<0.05) the densities of Oligochaeta, Bivalvia and Copepod. Its influences on the Polychaeta, Gastropod and Isopoda densities were zone-specific. Overall, seasons equally influenced the relationships between extrinsic and response variables in all zones. The results of this study are useful to evaluate the lake's environmental quality, in conservation and in similar projects involving environmental handling, monitoring and recovery.

Keywords Ecology · Extrinsic factors · Intrinsic variables · Water quality · Trichoptera · Plankton · Detrended Correspondence Analysis · PERMANOVA · Man-made lake

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Introduction

Aquatic organisms are highly responsive to the changes in their surrounding environment driven by water chemistry. Therefore, environmental parameters may determine spatio-temporal distribution of sensitive aquatic species such as benthic invertebrates. Benthic invertebrates actively participate in the exchange of nutrients between the sediment and the overlying water. Thus, they play a vital role in the energy flow and nutrient cycling and foundation of aquatic food webs (Rahman et al. 2008a; Lucca et al. 2010). Nonetheless, it is not necessarily true that all environmental parameters influence the abundance of benthic invertebrates (Hernandez et al. 2014; Rahman 2015a).

While observing changes in environmental parameters may be interesting for their effects on aquatic organisms from a research perspective, the protection of biodiversity in water bodies and thus stability of environmental parameters is also of great interest for aquatic ecosystems (Rahman et al. 2008b). Relationships between various environmental parameters and aquatic organisms in natural lakes are well established through significant research efforts. Most studies (e.g. Lisboa et al. 2011; Habib and Yousuf 2014; Alanoca et al. 2016; Zhang et al. 2016; Ji et al. 2020) focus on natural instead of man-made lakes despite the development of many such lakes worldwide. Studying such man-made systems can be hampered if only comparing these to what is known of natural lakes especially because these lakes evolve with time and thus contain temporally unique ecosystems (Wilk-Wozniak et al. 2014). Thus, researchers studying man-made lakes need to be cognisant that any comparison with natural lakes may be an unrealistic approach for understanding their ecology (Jackson et al. 1983; Schultz 1991). For instance, the surroundings of natural lakes are often shaped by geomorphic changes (i.e. over very long time scales) that result in stable habitat features that contribute to relatively predictable and stable food chains and associated ecosystem services (Nelson et al. 2018). Comparatively, the swelling of natural rivers to form artificial lakes unearth underlying resources and minerals while submerging existing vegetation and other biotic components, creating a very different ecological template to natural lake bottoms.

Apart from degradation, natural lakes undergo thermal fluctuations depending on tributary activity and depth. Over very long time scales, only selected organisms evolve to adapt to such changes through natural selection. It would be difficult to simulate this adaptation strategy *in situ* because accessibility is always limited by littoral layers (from decaying and degradation) as well as unexplored sections with uncertain depths. Hence, the only possible means to explore adaptation is by monitoring low trophic organisms like producers (the planktonic organisms) and primary consumers (benthic invertebrates) along with the environment of exposure (water properties) so that ecological support systems in man-made lakes can be clearly understood.

Studies in great lakes like Lake Superior, Lake Huron, Lake Erie, Lake Baikal, Great Salt Lake and Grand Canyon developed different forms of understanding because history, geologic processes and weather records were formed from early curiosities and inquiries. Comparatively, man-made lakes are developed to produce reservoirs for water supply or flood mitigation by damming rivers. The historical timeline of man-made lakes ranges from decades to centuries, whereby these young lakes may still have tributaries that constantly flow to maintain the lake's depth. Information on the formation and types of biota in man-made lakes are limited to pre-lake explorations, and environmental impact assessment reports. Environmental monitoring is indispensable for the analysis of the ecological status, providing subsidies for the elaboration of management and conservation strategies. Lake Kenyir, which is the largest man-made lake in Southeast Asia with an area of 260 km^2 and its knowledge gaps relating to water quality and current biota, inspired this study. Lake Kenyir was formed during 1985 through the damming of the Kenyir and Terengganu Rivers. The majestic forests of Terengganu Nature Reserve surround these rivers and have evolved since the formation of the Sunda Plains.

Climate change is another important issue that may cause long-lasting impacts on global aquatic ecosystems particularly freshwater lakes. Due to global climate change, many aquatic systems have experienced increases in their water temperature of 0.1–1.0 °C per decade in the past 20–30 years (Ormerod and Durance 2012). Such changes in water temperature are expected to have negative consequences on freshwater lake invertebrate communities in various ways, including altered community composition (Daufresne et al. 2004), range distribution (Hickling et al. 2005) and trophic interactions (Quinlan et al. 2005). Changes in water quality due to climate change will also affect invertebrate communities in freshwater lakes. Invertebrate community diversity in freshwater lakes is especially at high risk from climate change. The combination of increasing human exploitation coupled with climate change will likely lead to reduced biodiversity of freshwater lakes with only tolerant species remaining . Therefore, reduction in ecosystem services from aquatic ecosystems may be severely decreased due to climate change. This will likely have significant and often negative social, cultural and economic consequences. Hence, understanding how man-made lakes function will help not only to manage them for their health but also to provide ecosystem services that could be critical for future human needs.

In aquatic systems, abundance of benthic invertebrates is generally correlated with a range of environmental factors including trophic state or degree of eutrophication (Tszydel et al. 2015; Ding et al. 2016; Wang and Tan 2017; Svensson et al. 2018). Benthic invertebrates also indirectly accelerate the mineralization of decaying organic matter into inorganic forms such as phosphates and nitrates (Boyd 1970; Lucca et al. 2010). While the influence of various environmental factors on benthic invertebrates is reported separately in many cases, benthic invertebrates in aquatic ecosystems are influenced by numerous, simultaneously interacting environmental factors. Understanding the influence of environmental factors is of great challenge and, therefore, the relative importance of those environmental factors on benthic invertebrate communities is rarely quantified in Asian tropical man-made lakes. Therefore, the primary aim of this study was to assess the influence of various environmental factors and phytoplankton abundance on various groups of benthic invertebrate dynamics at both temporal and spatial scales with different water depths in Lake Kenyir.

Methods

Study site and experimental design

Lake Kenyir is a reservoir constructed by damming the Kenyir River and its sub-tributaries. Fitting the criteria of a man-made lake (Taub 1984), the vast water reservoir is situated in the northeastern Malaysian peninsular. At this location, the monsoon period is from October to March and non-monsoon period is from April to September. Acessability to Lake Kenyir is limited to road networks whereas the inner sections comprising of islands and islets are only accessible through water vessels like house- and speed boats. This study was carried out at the northeast section of Kenyir Lake for a period of 1 year (January–December 2016). We selected this area to avoid confounding effects due to anthropogenic activity as this area is protected by the authority. We visually observed significant amounts of bottom mud in each sampling site during the study. The sediment structure of all sampling sites appeared similar (sandy clay) based on our broad visual observation at the time of sampling. According to Norfaizal et al. (2015), soil structure of the sampling area ranges from sandy clay to sandy clay loam.

All measured variables were studied at three zones with three different water depths: zone A (mean depth: 6.3±0.6 m), zone B (12.3±2.5 m) and zone C (19.7±1.5 m) (Fig. 1). Each zone was subdivided into 3 sampling sites, which were considered replications. The distance between any two sampling zones was approximately 3 km and the distance between any two sampling sites in each zone was approximately150 m.

Collection of water quality and chlorophyll-a data

A series of water quality parameters (temperature, dissolved oxygen (DO), pH, nitrite (NO_2–N), nitrate (NO_3–N), ammonia (total ammonia nitrogen), phosphate (PO_4–P), total suspended solid (TSS) and chlorophyll-a (Chl-a) were determined monthly between 9:00 and 11:00 h 30 cm above the bottom at each sampling site. Temperature, dissolved oxygen and pH were recorded directly at each sampling site using a portable Hydrolab equipment (HydrolabMinisonde® water quality multiprobes). Water samples were collected by taking 1-L sample from each sampling site with a Van Dorn water sampler. The samples were then used for nitrogenous and phosphorus nutrients, TSS and Chl-a determination. Total ammonia nitrogen and PO_4–P were analysed spectrophotometrically following Stirling (1985). Nitrate (cadmium reduction method) was determined according to APHA (1998). Total suspended solid was determined according to Stirling (1985). Chl-a was determined spectrophotometrically after acetone extraction according to Boyd (1979). Chl-a was determined instead of phytoplankton abundance as the relative concentration of chlorophyll is indicative of phytoplankton biomass (Desortova 1981; Jenkerson and Hickman 2007; Rahman 2021). Temperature, dissolved oxygen and pH of surface water were also recorded frequently 30 cm below the water surface. They were statistically similar between 30 cm below the water surface and 30 cm above the bottom.

Trophic state of the lake was determined using the TRIX index, which indicates the trend towards eutrophication. This multivariate index was calculated using the following equation:

$$\mathrm{TRIX} = \left(\mathrm{Log}_{10}((\mathrm{Chl–a}) \times |\%\mathrm{DOd}| \times \mathrm{DIN} \times \mathrm{SRP}) + \mathrm{K}]\right)/\mathrm{m}\Big)$$

where Chl-a is the concentration of chlorophyll-a (µg L^{-1}); |% DOd| is the absolute deviation from the dissolved oxygen percent saturation; DIN is the dissolved inorganic nitrogen (nitrate + nitrite + total ammonia) (µg L^{-1}); and SRP is the soluble reactive phosphorus (µg P L^{-1}). The constants $K = 1.5$ and $m = 12/10 = 1.2$ are the scale coefficients introduced to fix the lowest index value and define the extension of the related trophic scale, from 0 to 10 TRIX units (Pettine et al. 2007).

Collection of benthic data

Triplicate benthic samples were collected monthly in each sampling zone with a Ponar grab (area: 15.2 cm × 15.2 cm). In each sampling site, one bottom mud sample was collected and washed through a 200-µm mesh size sieve. Benthos remaining on the sieve were preserved in a plastic vial containing a 10% buffered formalin solution. In the laboratory, a Rose Bengal ($C_{20}H_2O_5Cl_4I_4K_2$) solution (100 mg L^{-1}) was added to each sample to stain benthic invertebrates and reduce sorting time. All organisms were sorted with dissecting forceps and identified up to the class level under a stereomicroscope. We did not undertake finer levels of identification because we were interested in the influences of various environmental parameters and phytoplankton productivity on broad-scale community differences of benthic invertebrates. Identification keys used for benthic invertebrates were after Brinkhurst (1971) and Pinder and Reiss (1983).

Data analysis

Data collected from October to March were considered under monsoon season, whereas data collected from April to September were considered under non-monsoon season in all statistical analysis (Rahman 2021). All data were checked for normality and homogeneity of variance before analysis. Data were analysed using a repeated-measures one-way ANOVA (analysis of variance) to compare the mean variation in water quality parameters, Chl-a and benthic invertebrates among sampling zones and among sampling months. Sampling zone was considered a main factor and sampling month was treated as a sub-factor. If a factor was significant, differences between means were analysed by Tukey's tests for unplanned multiple comparisons of means (at $P \leq 0.05$ level of significance). ANOVA was performed using IBM SPSS statistics 20v.

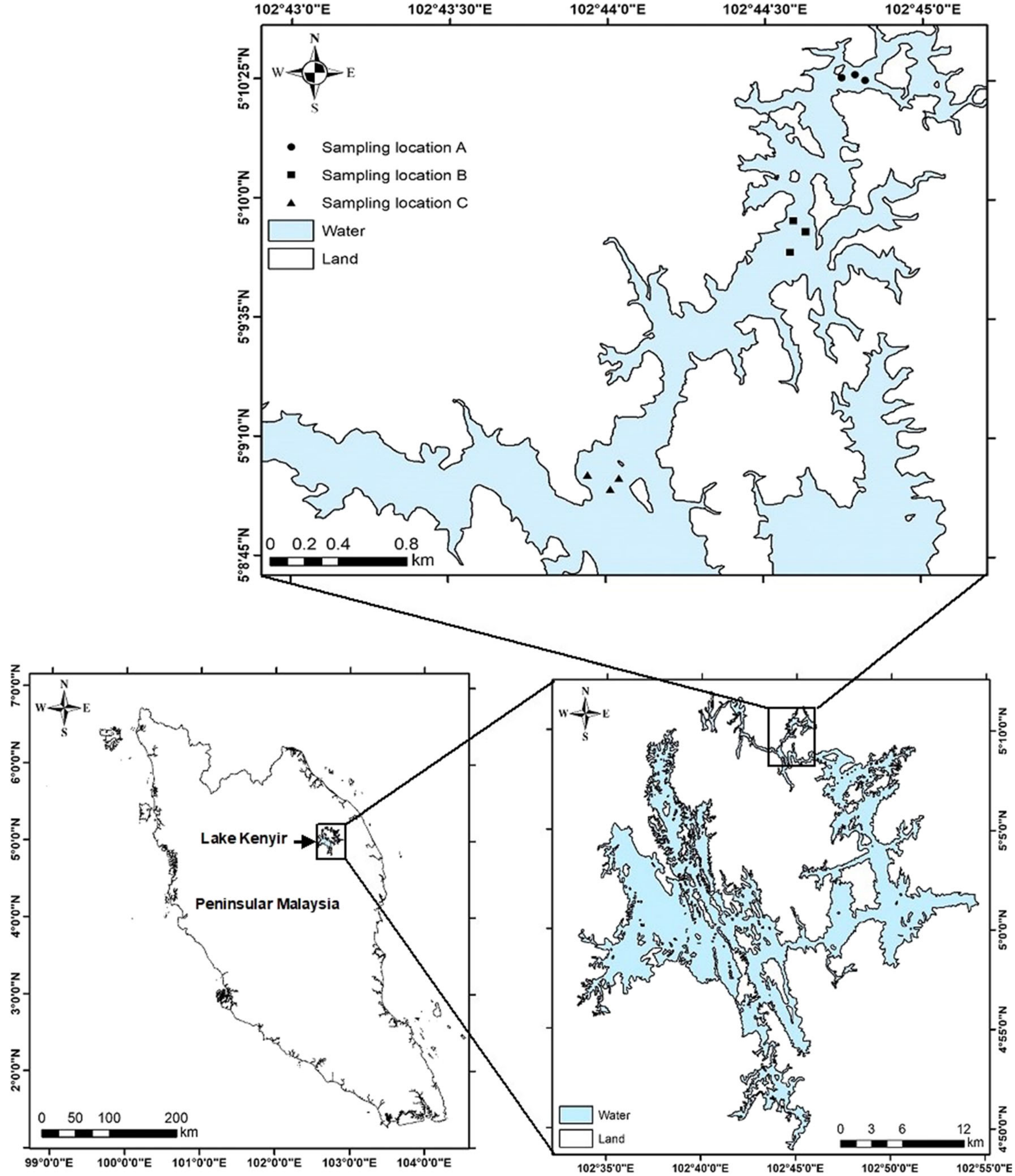

Fig. 1 Topographical representation of sampling zones (zone A, zone B and zone C) in the northeast waters of Lake Kenyir

For multivariate ordinations, two different datasets were used: (1) water quality—DO, water temperature, pH, nitrate, nitrite, ammonia, phosphate, chlorophyll-a and TSS; (2) various groups of benthic invertebrates—Polychaeta, Oligochaeta, Bivalvia, Gastropoda, Isopoda, Copepoda and Trichoptera abundance. We calculated a canonical correlation index among the two datasets to understand the highest direct explanatory power. The highest canonical correlation index indicates the highest direct explanatory power. Based on the highest canonical correlation index, water quality datasets were used as explanatory variables (extrinsic factors), and benthos datasets were used as response variables (intrinsic variables) in multivariate ordinations. First, a DCA (detrended correspondence analysis) was performed to understand prevailing patterns of the response variables in relation with the explanatory variable gradient. Ordination axes smaller than two standard deviations indicated linear or monotonic responses, suggesting that the RDA (redundancy analysis) was the best method for direct gradient analysis (ter Braak and Smilauer 1998; Rahman et al. 2008b). RDA was run with variables centred and standardized by subtracting the mean and dividing by the standard deviation. The significance of the first ordination axis and the significance of the first four canonical axes together were evaluated with Monte Carlo permutation tests using 1000 permutations. RDA was used to directly explain the variation in the response variables from the variation in the explanatory variables.

Following the results of the RDA, permutational multivariate analysis of variance (PERMANOVA) with the DistLM model was used to investigate the significant influence of environmental factors on the density of benthic invertebrates (Baldanzi et al. 2013). The PERMANOVA analyses were done using PRIMER v7 (Anderson 2008), while both DCA and RDA were performed using CANOCO v4 (ter Braak and Smilauer 1998).

Results

Effects of season, zone and their interaction on environmental parameters

The effects of sampling season, sampling zone and their interaction on water quality parameters, the concentration of chlorophyll-a and TRIX index are presented in Table 1. Their effects were not significant (P>0.05) on nitrate, ammonia, TSS, chlorophyll-a concentration, or TRIX index. TRIX index varied from 1.63 to 3.41, with the minimum value in zone C during monsoon and the maximum value in zone B during non-monsoon. All water quality parameters were statistically similar (P>0.05) in all sampling zones except DO with significantly higher (P<0.05) concentration in zone A (the shallowest zone) compared to zones B and C. DO concentration in zones B and C were statistically similar (Table 1). Among all water quality parameters, only water temperature, pH, nitrite and phosphate concentration had seasonal effects. The monsoon season showed a significant increase in pH and phosphate concentration (P<0.05), while water temperature and nitrite concentration were decreased (P<0.05). There were no interaction effects of season and sampling zone (P>0.05) for any of the water quality parameters (Table 1).

Effects of season, zone and their interaction on benthic invertebrates

All observed benthic invertebrates belonged to 10 classes: Polychaeta, Oligochaeta, Bivalvia, Gastropoda, Isopoda, Copepoda, Mysida, Insecta (Trichoptera larvae), Hirudinea and Arachnida. The Trichoptera were the predominant class that contributed the highest percentage (69.2%) of the total benthic fauna followed by the Copepoda (10.6%), Bivalvia (8.2%), Polychaeta (6.1%), Oligochaeta (1.9%), Isopoda (1.7%), Gastropoda (1.3%), Hemiptera (0.2%), Hirudinea (0.1%), Arachnida (0.1%) and Mysida (0.1%). Unidentified benthic invertebrate contributed 0.6% of total benthic fauna. Hemiptera, Hirudinea, Arachnida, Mysida and unidentified benthic fauna were very rarely observed and were not significantly different among sampling time and among sampling zones. Therefore, those classes are not presented.

Table 1 Effects of zone and season on various water quality parameters and TRIX index at the northeast part of Lake Kenyir based on one-way repeated-measures ANOVA. Mean with no superscript in common differ significantly (P<0.05)

Variable	Significance (p value)			Tukey's test				
	Zone (Z)	Season (S)	Z×S	Zone			Season	
				Zone A	Zone B	Zone C	Monsoon	Non-monsoon
Temperature (°C)	ns	**	ns	31.05±0.30	31.14±0.30	31.07±0.29	29.86±0.17	32.31±0.17
DO (mg L^{-1})	*	ns	ns	6.31±0.10^{a}	5.72±0.21^{b}	5.67±0.29^{b}	5.79±0.23	6.01±0.10
pH	ns	**	ns	6.99±0.10	6.89±0.11	6.94±0.10	7.12±0.11	6.75±0.05
Nitrate (mg L^{-1})	ns	ns	ns	0.747 ±0.104	0.792 ±0.102	0.775 ±0.097	0.819 ±0.085	0.724±0.079
Nitrite (mg L^{-1})	ns	**	ns	0.007 ±0.001	0.007 ±0.001	0.007 ±0.001	0.006 ±0.000	0.008±0.001
Ammonia (mg L^{-1})	ns	ns	ns	0.021 ±0.002	0.019 ±0.001	0.018 ±0.001	0.020 ±0.001	0.019±0.001
Phosphate (μg L^{-1})	ns	**	ns	8.71±0.92	8.48±0.95	9.54±1.11	10.41±1.02	7.41±0.45
TSS (g L^{-1})	ns	ns	ns	0.018 ±0.002	0.019 ±0.002	0.014 ±0.002	0.016 ±0.002	0.018±0.002
Chlorophyll-a (μg L^{-1})	ns	ns	ns	2.41±0.14	2.35±0.17	2.43±0.15	2.41±0.12	23.86±1.32
TRIX index	ns	ns	ns	2.71±0.05	2.65±0.06	2.66±0.07	2.69±0.04	2.66±0.05

Data are means ± standard error (SE). TSS = total suspended solid; DO = dissolved oxygen. Mean with no superscript in common differ significantly (P<0.05)

The effects of sampling season, sampling zone and their interaction on all classes of benthic invertebrates are presented in Table 2. Polychaeta, Bivalvia, Copepoda, Trichoptera and total benthic invertebrates were statistically different ($P<0.05$) among the sampling zones, whereas Oligochaeta, Gastropoda and Isopoda were statistically similar ($P>0.05$) in all sampling zones. The mean density of Polychaeta was higher in zone B than in zone C. It was statistically similar when comparing zone A versus zone B and zone A versus zone C. The mean density of Bivalvia, Copepoda, Trichoptera and total benthic invertebrates was higher at zone A compared to zone B and zone C. Their densities in zone B and zone C were statistically similar ($P>0.05$). Seasonal effects on all groups of benthic invertebrates were not significant except Gastropoda and Isopoda, both of which were higher during non-monsoon season compared to monsoon season. Interaction effects of sampling season and sampling zone on all groups of benthic invertebrates were non-significant ($P>0.05$).

Benthic invertebrates explained by environmental parameters and phytoplankton density

The first canonical axis and the first four canonical axes combined were statistically significant at the 5% level for the RDA using explanatory variables (water quality parameters and phytoplankton (Chl-a)) and the response variable (density of various groups of benthic invertebrates). The first two significant axes explained 83.8% of the variance in benthic invertebrate density and 91.6% of the benthic invertebrate—water quality and phytoplankton relationship in zone A, 82.2% and 93.5% of these relationships in zone B and 80.9% and 84.9% of these relationships in zone C (Table 3). The influence of extrinsic factors on response variables was almost the same among sampling zones (Tables 3 and 4, Figs. 2, 3 and 4). The first RDA axis was positively correlated with the density of all groups of benthic invertebrates (except Trichoptera), which scored high on the first RDA axis in all zones (Table 3, Figs. 2, 3 and 4). This axis negatively correlated with Trichoptera. This axis may therefore be interpreted as a 'benthic invertebrates' axis, positively correlated with TSS, nitrate, nitrite, phosphate, chl-a and TRIX index. All of these extrinsic variables (except phosphate) negatively influenced ($P<0.05$) the density of Trichoptera and positively influenced ($P<0.05$) the densities of Polychaeta, Oligochaeta, Bivalvia, Gastropoda, Isopoda and Copepoda densities in all zones (Table 4, Figs. 2, 3 and 4). Phosphate negatively influenced ($P<0.05$) the density of Trichoptera and positively influenced ($P<0.05$) the densities of Oligochaeta, Bivalvia and Copepoda. Its influences on the Polychaeta, Gastropoda and Isopoda densities were zone-specific. It significantly and positively influenced Polychaeta in zone B, and Gastropoda and Isopoda in all zones except zone C. Water temperature, pH, DO and ammonia had no significant influence ($P>0.05$) on any groups of benthic invertebrates. Overall, monsoon and non-monsoon season equally influenced the relationships between explanatory and response variables in all zones (Figs. 2, 3 and 4).

Discussion

Environmental parameters and trophic state

This is the first known study that provides empirical evidence about the trophic state of a man-made tropical freshwater lake, Lake Kenyir. The trophic state of a water body is frequently

Table 2 Effects of sampling zone and season on mean (± standard error) densities (ind. m^{-2}) of benthic invertebrate groups in collected from the northeast part of Lake Kenyir based on one-way repeated-measures ANOVA

Group of benthic fauna	Significance (p value)			Tukey's test				
	Zone (Z)	Season (S)	Z×S	Zone			Season	
				Zone A	Zone B	Zone C	Monsoon	Non-monsoon
Polychaeta	*	ns	ns	$18.0±8.0^{ab}$	$90.2±41.0^{a}$	$2.4±1.7^{b}$	18.4±8.6	55.3±27.1
Oligochaeta	ns	ns	ns	10.8±5.8	18.0±6.1	6.0±3.1	8.0±3.8	15.2±4.6
Bivalvia	*	ns	ns	$79.3±17.9^{a}$	$26.4±8.0^{b}$	$40.9±10.5^{b}$	52.9±11.2	44.9±10.5
Gastropoda	ns	*	ns	13.2±5.1	8.4±6.2	2.4±1.7	2.4±1.8	13.6±5.1
Isopoda	ns	*	ns	15.5±6.7	12.0±3.7	2.4±1.7	4.8±2.7	15.2±4.5
Copepoda	*	ns	ns	$115.3±23.8^{a}$	$34.8±8.6^{b}$	$39.6±11.4^{b}$	56.1±11.5	70.4±16.0
Trichoptera	*	ns	ns	$594.0±113.2^{a}$	$329.4±66.1^{b}$	$321.0±51.8^{b}$	450.5 ±74.7	379.1±61.1
Total benthic invertebrates	*	ns	ns	$846.6±98.7^{a}$	$530.2±77.5^{b}$	$414.7±44.9^{b}$	593.1 ±71.2	601.2±63.2

*$P≤0.5$; ns, not significant (P>0.05). Mean with no superscript in common differ significantly ($P<0.05$)

Table 3 Redundancy analyses (RDA) of water quality and phytoplankton (chlorophyll-a) explaining density of benthic invertebrate groups at three sampling zones Lake Kenyir

Statistics	Axis 1	Axis 2	Axis 3	Axis 4
Zone A				
Eigenvalues	0.777	0.042	0.024	0.010
Density of benthic invertebrate–water quality and phytoplankton correlation	0.802	0.391	0.321	0.173
Cumulative % variance of benthic invertebrate density	77.9	83.8	85.6	86.9
Cumulative % variance of benthic invertebrate density–water quality and phytoplankton relation	89.3	91.6	95.1	97.3
Zone B				
Eigenvalues	0.669	0.159	0.015	0.011
Density of benthic invertebrate–water quality and phytoplankton correlation	0.874	0.512	0.356	0.143
Cumulative % variance of benthic invertebrate density	66.1	82.2	83.8	84.5
Cumulative % variance of benthic invertebrate density–water quality and phytoplankton relation	77.8	93.5	94.4	96.8
Zone C				
Eigenvalues	0.796	0.044	0.021	0.013
Density of benthic invertebrate–water quality and phytoplankton correlation	0.775	0.447	0.212	0.131
Cumulative % variance of benthic invertebrate density	72.6	80.9	85.5	87.4
Cumulative % variance of benthic invertebrate density–water quality and phytoplankton relation	78.3	84.9	92.4	94.2

Total variance=1.000; RDA was statistically significant at $P \leq 0.05$

estimated using the TRIX index (Vollenweider et al. 1998; Boikova et al. 2008; Primpas and Karydis 2011; Rahman and Hamidah 2020). The TRIX index at all studied zones of Lake Kenyir was lower than 4 throughout the year, indicating the northeast part of lake Kenyir was oligotrophic (Pettine et al. 2007; Table 5). This conclusion is further supported by the abundance of benthic invertebrates in the lake bottom sediments, in which Trichoptera dominated 69.2% of the total benthic invertebrate abundance. Trichoptera normally live in oligotrophic water bodies with low nitrogenous and phosphorous nutrients (Lenat and Penrose 1996; Hamid and Rawi 2017). The oligotrophic state finding is also supported by the high oxygen concentration in water near the sediment as observed by Lucca et al. (2010) in a tropical oligotrophic lake (Lake Caco, Brazil). Our result is supported by Hou et al. (2012), who stated that soil of rainforest and rainforest lakes are limited in labile nutrients as most nutrients are captured and stored in the root systems of the characteristically dense tree layer. Therefore, water in rainforest lakes are generally low in productivity (Rouf et al. 2008).

Our results indicate that the water body of Lake Kenyir was warm and well oxygenated. There was no marked difference in the physical and chemical (except DO) characteristics of the water among the sampling zones, indicating relative spatial homogeneity. The observed higher DO concentration at the shallowest zone is also observed in other similar studies (Corbi and Trivinho-Strixino 2002; Jager and Walz 2002). As expected, monsoon season was characterised by comparatively higher rainfall, decreased temperature and increased pH. Monsoon season also increased phosphate concentration in water. This might be due to runoff from the surrounding rainforest which transported phosphate to the lake water during monsoonal rains (Abdallah and Barton 2003). The observed decreased nitrite concentration in water near the bottom sediment during monsoon season is not straightforward but could potentially be related to a number of factors as bacteria produce nitrite as an unstable and intermediate product from nitrate to ammonia and vice versa.

Abundance of benthic inverteabrates

The density of benthic invertebrates varied little (P>0.05) between seasons, indicating relative seasonal homogeneity of benthic invertebrates in comparison with other studies conducted in tropical lakes (Lima et al. 2013). Similar results were also observed by Magalhaes et al. (2015) in a tropical (Taperacu) estuary in Brazil. We observed very little variation in benthic invertebrate densities, which might be related to the fact that seasonal changes in most environmental variables were modest and did not incur strong seasonal trends in density of benthic invertebrates (Efitre et al. 2001). According to Peeters et al. (2004), environmental homogeneity is accompanied by a decrease in the variation of benthic invertebrate density. The observed high density of total benthic invertebrates in the shallowest zone concurs with other studies conducted in tropical lakes (Hernandez et al. 2014). Increased benthic macroinvertebrate density with decreasing water depth is a common phenomenon observed in lakes associated with spatial homogeneity of environmental parameters (Hernandez et al. 2014; Cleto-Filho and Arcifa 2006). In the present study, spatial

Table 4 PERMANOVA (with DistLM) pseudo-Fs and significance (*P* value) for the influence of various extrinsic factors on various benthic invertebrate groups

Extrinsic factors	Polychaeta		Oligochaeta		Bivalvia		Gastropoda		Isopoda		Copepoda		Trichoptera	
	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*
Zone A														
Temperature	0.18	0.701	0.12	0.740	1.17	0.311	0.40	0.542	0.01	0.954	0.66	0.438	0.00	0.984
DO	0.17	0.682	0.12	0.657	1.68	0.207	0.29	0.608	0.56	0.465	1.93	0.168	0.84	0.371
pH	0.23	0.656	0.21	0.676	3.47	0.066	0.50	0.509	0.96	0.297	0.01	0.957	0.07	0.781
Nitrate	23.63	0.001	14.13	0.002	171.28	0.001	20.62	0.001	27.04	0.001	88.41	0.001	143.80	0.001
Nitrite	8.09	0.005	8.44	0.008	43.47	0.001	15.32	0.001	56.94	0.001	24.82	0.001	29.64	0.001
Ammonia	0.27	0.637	0.12	0.731	0.01	0.978	2.46	0.138	1.45	0.237	0.27	0.608	0.01	0.964
Phosphate	2.96	0.097	31.95	0.001	4.50	0.031	6.02	0.013	3.62	0.048	13.93	0.001	6.32	0.020
TSS	20.49	0.001	17.29	0.001	99.89	0.001	24.80	0.001	27.51	0.001	108.57	0.001	169.97	0.001
Chlorophyll-a	23.13	0.001	14.51	0.001	125.71	0.001	19.23	0.001	23.53	0.001	109.77	0.001	175.23	0.001
TRIX	15.55	0.001	10.15	0.002	67.15	0.001	15.16	0.002	16.66	0.001	94.80	0.001	53.52	0.001
Zone B														
Temperature	0.45	0.502	0.78	0.401	1.80	0.190	1.36	0.307	0.63	0.435	2.21	0.145	0.11	0.750
DO	3.79	0.061	3.61	0.059	0.09	0.750	1.91	0.152	0.01	0.948	0.96	0.335	3.50	0.057
pH	0.30	0.571	0.15	0.693	1.83	0.151	1.96	0.135	3.05	0.101	3.64	0.070	2.29	0.143
Nitrate	7.17	0.010	8.76	0.013	65.02	0.001	12.78	0.001	39.32	0.001	58.94	0.001	164.96	0.001
Nitrite	18.45	0.002	23.92	0.001	76.21	0.001	28.43	0.001	50.93	0.001	89.15	0.001	103.37	0.001
Ammonia	1.74	0.199	1.08	0.299	0.06	0.800	2.09	0.153	0.00	0.989	0.01	0.940	1.43	0.248
Phosphate	8.36	0.007	9.18	0.008	6.78	0.010	6.67	0.014	6.89	0.017	6.31	0.026	6.02	0.011
TSS	5.46	0.021	9.19	0.002	47.38	0.001	5.81	0.008	36.51	0.001	34.37	0.001	80.02	0.001
Chlorophyll-a	10.42	0.005	11.70	0.001	68.57	0.001	12.39	0.001	42.78	0.001	73.08	0.001	182.25	0.001
TRIX	8.88	0.005	10.35	0.006	44.89	0.001	10.16	0.002	23.80	0.001	42.65	0.001	167.67	0.001
Zone C														
Temperature	0.06	0.794	0.13	0.716	0.16	0.690	0.00	0.985	0.06	0.783	0.00	0.985	0.44	0.523
DO	1.06	0.231	0.00	0.995	3.86	0.053	0.81	0.346	0.89	0.308	3.76	0.052	0.01	0.901
pH	0.39	0.507	0.03	0.868	1.24	0.283	0.05	0.819	0.23	0.610	1.15	0.296	0.43	0.533
Nitrate	5.02	0.034	6.61	0.017	11.81	0.006	5.70	0.023	4.92	0.039	11.97	0.001	21.83	0.001
Nitrite	15.54	0.008	18.31	0.003	8.27	0.011	10.93	0.010	8.73	0.019	14.42	0.001	30.16	0.001
Ammonia	3.35	0.146	0.70	0.368	0.66	0.408	3.35	0.125	3.35	0.177	1.61	0.222	0.10	0.740
Phosphate	0.59	0.494	3.90	0.045	16.76	0.002	0.50	0.569	0.37	0.621	13.98	0.001	4.52	0.044
TSS	4.87	0.016	11.43	0.001	51.65	0.001	21.64	0.001	8.29	0.004	67.05	0.001	113.04	0.001
Chlorophyll-a	7.30	0.004	11.37	0.001	24.02	0.001	4.04	0.049	5.81	0.026	24.10	0.001	35.55	0.001
TRIX	4.04	0.047	6.02	0.022	10.90	0.007	5.74	0.020	11.08	0.004	10.79	0.005	14.74	0.002

heterogeneity of both benthic invertebrate density and environmental parameters indicated that both spatial and seasonal effects on benthic invertebrates were marginal (Peeters et al. 2004). Thus, the mechanism of benthic invertebrate dynamics was complex and influenced by a combination of factors, which are discussed in the following section in relation to RDA.

Prior to this study, there was no information on the benthic invertebrate population in Lake Kenyir. Therefore, it is not possible to strictly compare the density of benthic invertebrates observed in the present study with those in the literature (Table 6), because of differences in environmental parameters, trophic state and benthic invertebrate collection sieve, all of which greatly influence the density of benthic invertebrate communities. In Lake Kuriftu (an eutrophic lake), Ethiopia, a very high density of benthic invertebrates (20,443 ind m^{-2}) was reported by Ayele and Mengistou (2013), while a very low density of 168±29 ind m^{-2} had been recorded from the Aiba Reservoir (an eutrophic reservoir), Nigeria, by Atobatele and Ugwumba (2010). Generally, the density of benthic invertebrates is much higher in eutrophic lakes compared to oligotrophic lakes (Pamplin and Rocha 2007). However, the

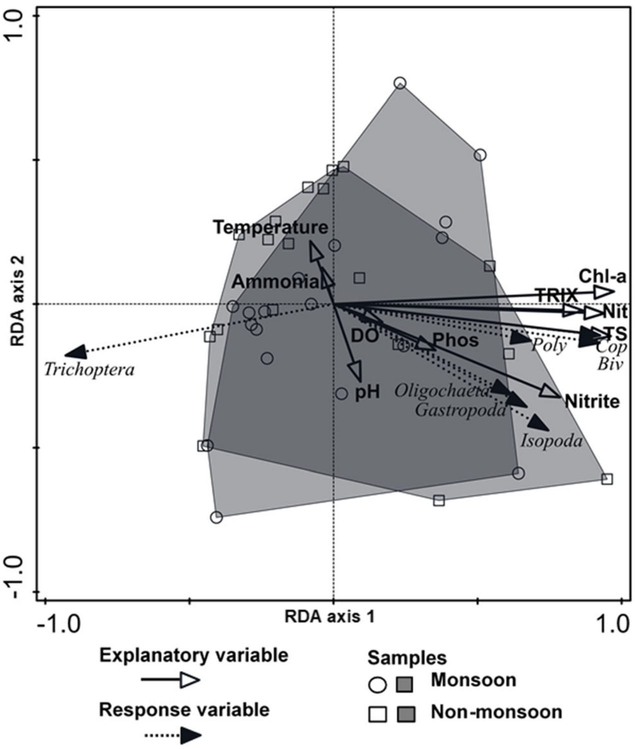

Fig. 2 Redundancy analysis (RDA) biplot (first two axes) of various benthic invertebrate groups explained by lake water quality and phytoplankton (chlorophyll-a) abundance at the sampling zone A. Ammonia, total ammonia (NH_4^+ + NH_3); DO, dissolved oxygen; TS, total suspended solids, Chl-a, chlorophyll-a; Nit, nitrate; Phos, phosphate; *Poly*, Polychaeta; *Cop*, Copepoda; *Biv*, Bivalvia

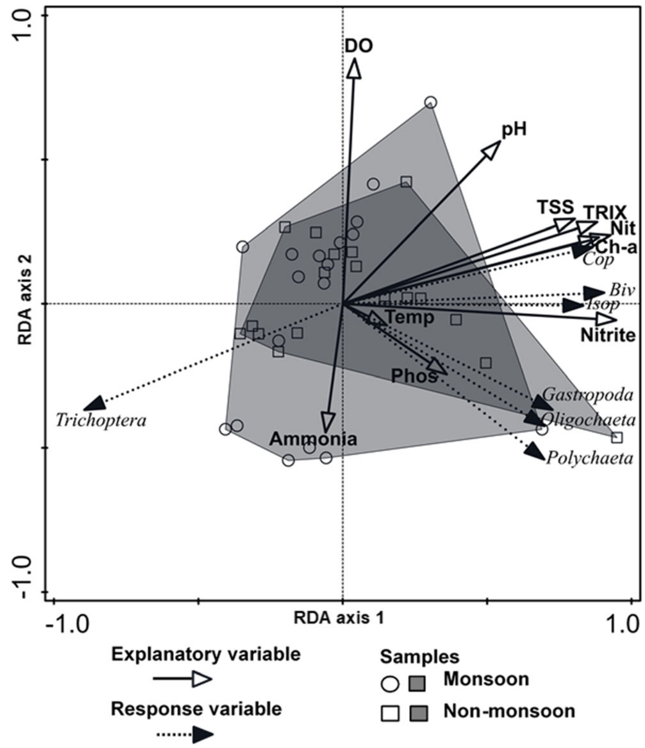

Fig. 3 Redundancy analysis (RDA) biplot (first two axes) of various benthic invertebrate groups explained by lake water quality and phytoplankton (chlorophyll-a) abundance at the sampling zone B. Nit, nitrate; Ammonia, total ammonia (NH_4^+ + NH_3); Phos, phosphate; Temp, water temperature; DO, dissolved oxygen; TSS, total suspended solids, Ch-a, chlorophyll-a; *Cop*, Copepoda; *Biv*, Bivalvia; *Isop*, Isopoda

observed density of benthic invertebrates in Lake Kenyir reflects the results of Lucca et al. (2010), who reported benthic invertebrate density of 584±33 in the sediment of a tropical oligotrophic lake (Lake Caco, Brazil) using 210-μm benthos collection sieve. In Malaysia, a range of benthic invertebrates 107–511 indi. m^{-2} was recorded in a tropical forest stream by Nor Zaiha et al. (2015). Sediment type also plays an important role in structuring benthic invertebrates (Donohue and Irvine 2003). However, observed benthic invertebrates in the present study might not be influenced by the sediment type as the sediment structure was similar in all sampling site based on our broad visual observation at the time of sampling.

We observed that Trichopterans dominated all zones in both seasons in sediments of Lake Kenyir. Previous studies showed that Trichoptera was a dominant group in a Malaysian river (Nor Zaiha et al. 2015). The observed higher density of Trichopterans might be due to leaf litter from the surrounding rainforest as leaf litter can be used as food and shelter for Trichopterans (Eggert and Burton 1994; Campos and Gonzalez 2009; Suhaila et al. 2014). This can be further supported by the results observed by Roque et al. (2003), who observed a higher density of Trichopterans at the forest segment of tropical streams in southwestern Brazil. Tropical lakes provide a wide variety of habitat for aquatic insects, forming 10 to 90% of total benthic organisms in these ecosystems (de Brito-Junior et al. 2005; Jorcin and Nogueira 2008; Lucca et al. 2010). However, a higher density of Trichopterans in Lake Kenyir is an indicator of oligotrophic water characterised by the low phytoplankton abundance and nitrogenous and phosphorous nutrients and high DO in lake water (Barbour et al. 1999; Pamplin et al. 2006; de Moor and Ivanov 2008). The observed non-significant seasonal variation of Trichopteran concurs with Efitre et al. (2001), who observed no seasonal variation of Trichopteran density in lake Nabugabo, Uganda.

Environmental influence on benthic inverteabrates

This study provides a unique contribution towards the primary literature describing various environmental parameters and phytoplankton abundance affecting the various groups of benthic invertebrates in Lake Kenyir. By sampling across a full 12-month cycle in nine sampling sites and collecting benthic invertebrates, phytoplankton and various water quality data, we have delineated the relative importance of key variables such as water temperature, concentration of ammonia, TSS, nitrate, nitrite and phosphate and phytoplankton abundance affecting the density of benthic invertebrates in Lake Kenyir.

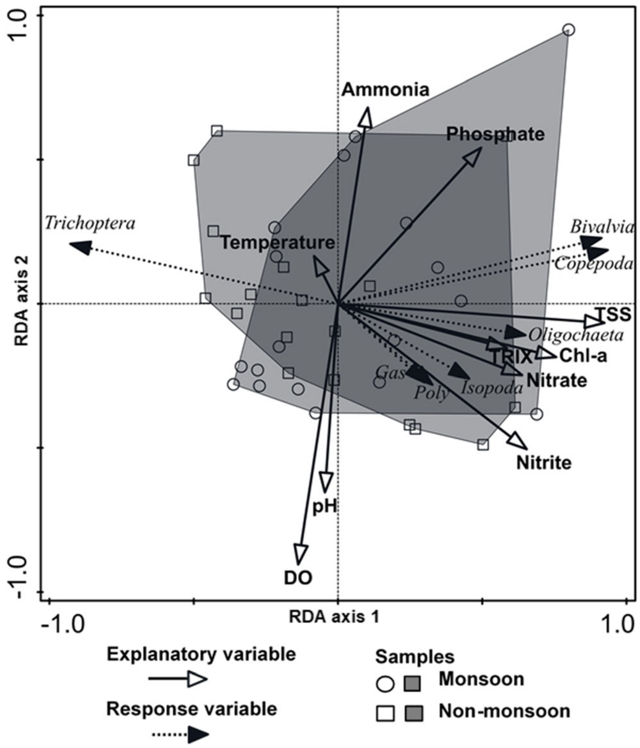

Fig. 4 Redundancy analysis (RDA) biplot (first two axes) of various groups of benthic invertebrate densities explained by lake water quality and phytoplankton (chlorophyll-a) abundance at the sampling zone C. Ammonia, total ammonia ($NH_4^+ + NH_3$); DO, dissolved oxygen; TSS, total suspended solids, Chl-a, chlorophyll-a; *Poly*, Polychaeta; *Gas*, Gastropoda

The water quality and phytoplankton availability dataset clearly explained the overall variation in benthic invertebrates well for each of the three sampling zones (first two canonical axes explained 91.6%, 93.5% and 84.9% variance of the benthic invertebrate density–water quality and phytoplankton relation in zone A, zone B and zone C, respectively) with sufficient data, but clearly with divergent benthic invertebrates' group-specific importance.

Our study indicated that the density of benthic invertebrate communities was limited by various environmental variables and by their adaptation to specific environments. We observed that the density of Trichopterans was negatively influenced by phytoplankton abundance, TRIX index and the concentration of nitrate, nitrite, phosphate and TSS in water, indicating eutrophication negatively influence their density. This concurs with Houghton (2004), who mentioned that Trichopteran species are intolerant of organic matter and, therefore, they can be used as an important water quality indicator (Barbour et al. 1999; Berlin and Thiele 2002; Koperski 2011). Houghton (2004) also observed a decrease in Trichopterans with increasing organic matter in aquatic habitats. According to Pamplin et al. (2006) and Koperski (2011), Trichopterans are very sensitive to oxygen and organic matter content in water, living in sediment with low organic matter content and high dissolved oxygen concentration. Although the organic matter content in the lake sediment was not measured, low nitrogenous and phosphorous nutrients, a high DO concentration and a neutral pH suggest a low organic matter content in the sediment.

Table 5 The TRIX index and their related trophic state (Pettine et al. 2007)

TRIX index	State water quality	Level of eutrophication	Trophic state
0< to ≤4	High-quality	Low	Oligotrophic
4< to ≤5	Good	Medium	Mesotrophic
5< to ≤6	Moderate	High	Eutrophic
6< to ≤10	Poor and degraded	Elevated	Hypertrophic

In the present study, all groups (except Trichopterans) of benthic invertebrates were positively influenced by increasing trophic state as they were positively correlated with phytoplankton abundance, TRIX index and the concentration of nitrate, nitrite, phosphate and TSS in water. Similar positive correlation of benthic invertebrate density with the concentration of nitrate and phosphate and the abundance of phytoplankton are reported in many studies (Rahman 2015b). The observed positive relationship of benthic of invertebrate (except Trichopterans) density with the concentration of nitrate and phosphate might be due to their preference of eutrophic water, living in sediment with abundant organic matter (Suriani et al. 2007; Zerlin and Henry 2014). According to Ndaruga et al. (2004), Oligochaeta are tolerant of organic pollution. Most of the Oligochaeta and Gastropod species prefer eutrophic water, living in sediment with high organic matter loads (Laamrani et al. 1997; Suriani et al. 2007). Published information (e.g. Jyvasjarvi et al. 2013; Hernandez et al. 2014) indicated that TSS caused by dead phytoplankton and other organic particles increased the abundance of benthic invertebrates except Trichopterans. TSS that are largely comprised of organic matter are generally used as food for most of the benthic invertebrate species found here.

Concentration of ammonia in water near the bottom sediments did not influence benthic invertebrate population in Lake Kenyir. Other environmental parameters such as temperature, DO and pH had no influence or a very minimum influence (P>0.05) on benthic invertebrates depending on sampling location although several other studies observed a significant influence of temperature, DO and pH on benthic invertebrate population in lakes (Pamplin and Rocha 2007; Lucca et al. 2010; Abong o et al. 2015). In the present study, water temperature, pH and DO and ammonia concentration did not act as limiting factors for observed benthic invertebrate groups as these parameters were likely at either optimum levels that would enhance optimum growth of the invertebrates or at least not present at deleterious levels. Our study was restricted to the northeastern part of the lake, and a large

Table 6 Reported density (individual m^{-2}) of benthic invertebrates (BI) in various tropical and sub–tropical freshwater lakes worldwide

Density of BI	Location of study	Trophic state	Mesh size of sieve (μm)	References
513±43	Lake Malawi	Oligotrophic	200	Abdallah and Barton (2003)
2475±2714	Americana Reservoir, Brazil	Eutrophic	210	Pamplin et al. (2006)
4256±6300	Americana Reservoir, Brazil	Eutrophic	210	Pamplin et al. (2006)
562–851	Ponte Nova Reservoir, Brazil	Oligotrophic	210	Pamplin and Rocha (2007)
297–1255	Mangueira lake, Brazil	Oligo-mesotrophic	250	Wurdig et al. (2007)
584±33	Lake Caco, Brazil	Oligotrophic	210	Lucca et al. (2010)
744–15,300	Peri lagoon (freshwater), Brazil	-	250	Lisboa et al. (2011)
4388–18,251	Lake Kuriftu, Ethiopia	Eutrophic	200	Ayele and Mengistou (2013)
597±493	Lake Kenyir, Malaysia	Oligotrophic	200	Present study

proportion of this huge water body still needs to be investigated. The composition of bottom sediment was not determined in the laboratory during the study period. Further studies of benthos as well as composition of bottom sediment (particle-size distribution and organic matter content) are required for the entire lake.

Conclusion

This study showed that functional analysis of environmental parameters and abundance of phytoplankton provided an understanding on relationships with benthic invertebrates in a man-made lacustrine ecosystem that has thus far been absent in published literature. Key findings indicate that the northeast part of Lake Kenyir is oligotrophic. Abundance of benthic invertebrates was limited by TSS, nitrogenous and phosphorus nutrients and abundance of phytoplankton. Other factors such as competition for space and resources and predation of invertebrates by fish and birds, not included in the present analyses, may also have an impact on the structure of the benthic community and should be assessed in future research. Nevertheless, the results of this study can be useful to the ecology of benthic invertebrates and to evaluate the lake's environmental quality to guide conservation efforts especially for similar projects involving environmental management and recovery of both new and older lakes. The relationship between the observed variables needs to be regularly monitored to have more in-depth understanding about the ecology of benthic invertebrates in relation to future climate change.

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Data availability The data that support the findings of this study are available from the corresponding author on reasonable request.

Declarations

Ethical approval and consent to participate Permission to work in Lake Kenyir was obtained from the Department of Fisheries, Malaysia (Jabatan Perikanan Malaysia) (reference: Ptk. Tr. 2706 Jld. 1 (19)). All benthos were handled in accordance with Malaysian code for the care and use of animal for scientific purpose (MyCode). Animal ethics clearance for this study was obtained from the Institutional Animal Care and Use Committee (reference: IIUM/518/14/4/IACUC) before commencing this research.

Consent for publication Not applicable

Competing interests The authors declare no competing interests.

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