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ORIGINAL RESEARCH

Constructed treatment wetlands provide habitat for zooplankton communities in agricultural peat lake catchments

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Abstract Zooplankton are an essential component of healthy functioning lake and wetland ecosystems. Despite this, zooplankton communities within constructed treatment wetlands (CTWs) in agricultural landscapes remain unstudied. Taxa richness, total abundances and community composition were evaluated for zooplankton assemblages from three habitat types (lakes, CTWs and drainage ditches) within five intensive agricultural peat lake catchments in New Zealand. Relationships to water quality, physicochemical and biotic habitat variables were examined. Zooplankton were dominated by cladocerans, copepods, ostracods and rotifer taxa, representing a range of communities typical of lake and pond habitats. CTWs supported species otherwise absent from lake and drain habitats, increasing the overall biodiversity of the highly-modified peat lake catchments. Taxa richness of CTWs was higher than that of drains, and a few CTWs had greater diversity than several lakes. The morphological variables area and depth contributed to the greatest differences between habitats, followed by pH, inorganic nitrogen, conductivity and temperature. Correspondingly, zooplankton communities were significantly influenced by habitat area, depth and pH, as well as ammonium, phosphate, water temperature, dissolved oxygen, and macrophyte cover. Opportunities were explored for refining CTW designs to enhance zooplankton biodiversity and potentially improve treatment efficiency through increasing the complexity and diversity of CTW habitat niches.

Keywords Zooplankton · treatment wetlands · intensive agriculture · biodiversity · peatlands · shallow lakes

Introduction

Constructed treatment wetlands (CTWs) are used globally as technologies to improve water quality (Kadlec and Knight 1996) and are effective in reducing levels of suspended solids, nitrogen and phosphorus, as well as organic matter and pathogens (Vymazal 2007; Vymazal and Kröpfelová 2008; Kadlec 2010; Dunne et al. 2012). CTWs are designed and created to emulate and enhance the natural processes and functions of wetland ecosystems involving wetland vegetation, soils, and microbial and aquatic communities (Mitsch and Gosselink 2007; Kadlec and Wallace 2008). The efficacy of CTWs depends upon the functionality, resilience and ecological integrity of the wetland ecosystems ability to acclimate to changes in hydrology, pollutant loads and water chemistry. Ecological integrity integrates physical, chemical and biological integrity; the latter refers to an ecosystem's capacity to support and maintain a balanced, integrated, and adaptive biological system with a full range of elements, processes and biotic interactions (Karr 1996).

Biodiversity is an essential component of biological integrity. As part of this biodiversity, zooplankton communities provide a critical link for the flow of energy and nutrients between primary producers and higher trophic levels (Gray

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et al. 2012; Kattel 2012). Such assemblages are also important in maintaining the ecological integrity of shallow lakes and wetlands (Moss et al. 2003; Van den Broeck et al. 2015), and have been included in a number of biotic indices developed to evaluate the ecological quality and integrity of wetlands (Lougheed and Chow-Fraser 2002; Boix et al. 2005). Zooplankton communities of wastewater treatment ponds, including high rate algal ponds, have been well researched, primarily regarding removal or control of zooplankton that can limit algal production and reduce treatment efficacy (Schlüter et al. 1987; Montemezzani et al. 2015). Methods for manipulating zooplankton community composition and relative abundances within aquaculture ponds have also been extensively researched (Geiger 1983; Piasecki et al. 2004; Milstein et al. 2006). Yet, in contrast to studies of such intensively managed and controlled pond systems, no detailed studies exist of zooplankton within agricultural CTWs. Knowledge of community composition, feeding guilds and habitat preferences of zooplankton within CTWs could contribute to improved treatment system design and help to optimise the assimilation of nutrients and reduction of pathogens.

Wetlands, including swamp, marsh, fen and peat bog ecosystems, as well as numerous peat lakes, were once key landscape features in the central Waikato region of New Zealand (Shearer 1997), supporting a diverse indigenous and endemic flora and fauna (Lowe and Green 1987). However, wetlands and lakes have declined in abundance, size and ecological integrity following extensive peatland drainage, cultivation and conversion to pasture beginning in the late 1800s (Hunt 2007). Wetland extent in the Waikato has been reduced by approximately 92% from an estimated pre-human area of >356,000 ha to c. 28,000 ha. Wetland areas have been largely replaced by highly productive, intensive dairy farming (MfE and StatsNZ 2015). Many of the remaining 31 peat lakes in the Waikato region have poor water quality and frequent cyanobacterial algal blooms, resulting from elevated nutrient and sediment levels associated with this change in land use (Hamilton et al. 2010), causing loss of much of their natural character and native biodiversity (Shearer 1997; Beard 2010).

Restoration actions are currently being implemented in several Waikato peat lake catchments to reduce nutrient and sediment runoff and improve lake water quality (Waikato 2006; Peters et al. 2008). Methods include retiring areas of marginal pasture to create esplanade reserves, fencing and planting of riparian and wetland areas around the lake margins and along the banks of inlet waterways, and creation of free surface-flow CTWs to intercept inflows and improve water quality. Within such highly modified, intensive agricultural landscapes, CTWs may feasibly enhance the biodiversity of the lake catchment through provision of habitat isolated from toxic algal blooms and adverse environmental conditions ubiquitous within the lakes themselves.

In this study, we assessed the biodiversity of CTWs by examining zooplankton communities from different aquatic habitats in five shallow peat lake catchments with intensive dairy production as the predominant land use. Habitat types, comprising lakes and their associated CTWs and drainage ditches (heavily modified and/or channelised artificial streams, referred to as drains herein), were studied as part of a greater body of research examining whether CTWs are effective tools for peat lake restoration. Zooplankton community composition was predicted to differ between habitat types, driven primarily by differences in habitat size (area and depth) and complexity (emergent macrophyte cover), water quality variables, and the presence or absence of fish. Based on these factors, we predicted that the biodiversity of zooplankton in CTWs would be higher than that of drains and lower than those of lake habitats.

Our key objectives were to:

(i) compare zooplankton communities (taxa richness, abundances and community composition) between CTW, lake, and drain habitat types;
(ii) examine environmental mechanisms driving differences in the zooplankton communities; and
(iii) discuss opportunities for refining CTW designs to enhance zooplankton biodiversity.

Methods

Study sites

The research was carried out in the central Waikato region, New Zealand (37.8 S, 175.2 E), where there are a number of shallow peat lakes located within agricultural catchments which are almost entirely used for intensive dairy production. Five shallow peat lakes were selected as study sites where CTWs have been implemented as mitigation tools for the inflows of the lakes: Kainui, Kaituna, Komakorau, Koromatua and Serpentine North. These were the only Waikato lakes with CTWs at the time the research was conducted and the CTWs were similar in age, constructed between 1999 and 2001. Lakes Kainui and Kaituna are within the Kainui restiad peat bog in the Waikato District, north of Hamilton city. Lake Koromatua is on the edge of the Rukuhia restiad peat bog, while Lake Serpentine is on the fringe of the Moanatuatua restiad peat bog, both in the Waipa District south of Hamilton city (Clarkson et al. 2004). The central Waikato has a temperate maritime climate with annual rainfall across the lake catchments (approximately 35 km from north to south) ranging from 1100 mm to 1300 mm (Dravitzki and McGregor 2011).

Three habitat types were sampled within each lake catchment and included five lakes, eight drains, and 27 CTWs (40 sampling locations in total). The location of the study lakes and positioning of habitat types within their catchments are provided in Fig. 1. A summary of the lake morphologies, trophic status, Trophic Level Index (TLI; Burns et al. 2000), water clarity, average concentrations of chlorophyll *a* (Chl *a*), total phosphorus (TP) and total nitrogen (TN), the number of major inflows to each lake, and the number of CTWs and their site codes is given in Table 1.

Field Sampling

Sites were sampled in late summer (2–8 February) 2011, following two weeks of persistent heavy rain (c. 215–235 mm across the study area), causing refilling of the CTWs after a dry spring and early summer (c. 125–135 mm over the preceding 12 weeks) (CliFlo 2017). We acknowledge that our sampling is a snapshot of the late-austral summer zooplankton community and environmental conditions, and that greater zooplankton diversity and variety of conditions would likely be encountered if seasonal or higher frequency sampling was undertaken. Single measurements of physicochemical variables were made at each site, including wetted area, depth, connectivity with the downstream lake (high = 3, medium = 2, low = 1, no connectivity = 0), as well as water temperature, dissolved oxygen concentration (DO), specific conductivity and pH, using a YSI 6000 UPG Multi Parameter Sonde (Yellow Springs Instruments, Ohio, USA). Area of the lakes was calculated from digitised aerial images (2016), and was measured manually in the field for CTWs and drains (over the 10 m reach surveyed). Sites with ‘no connectivity’ to the downstream lake occurred where the original drain outlet had been filled to create a ‘filtration’ outlet for the CTW.

Water samples for measurement of nutrients, Chl *a*, suspended solids and zooplankton were collected concurrently from the middle of CTWs and drains from a depth of approximately 0.3 m using a 1 L measuring jug on a 2 m pole. Samples were collected from lake habitats at a similar depth, from platforms built by duck-hunters which extend out into the lake approximately 5–10 m from the shore.

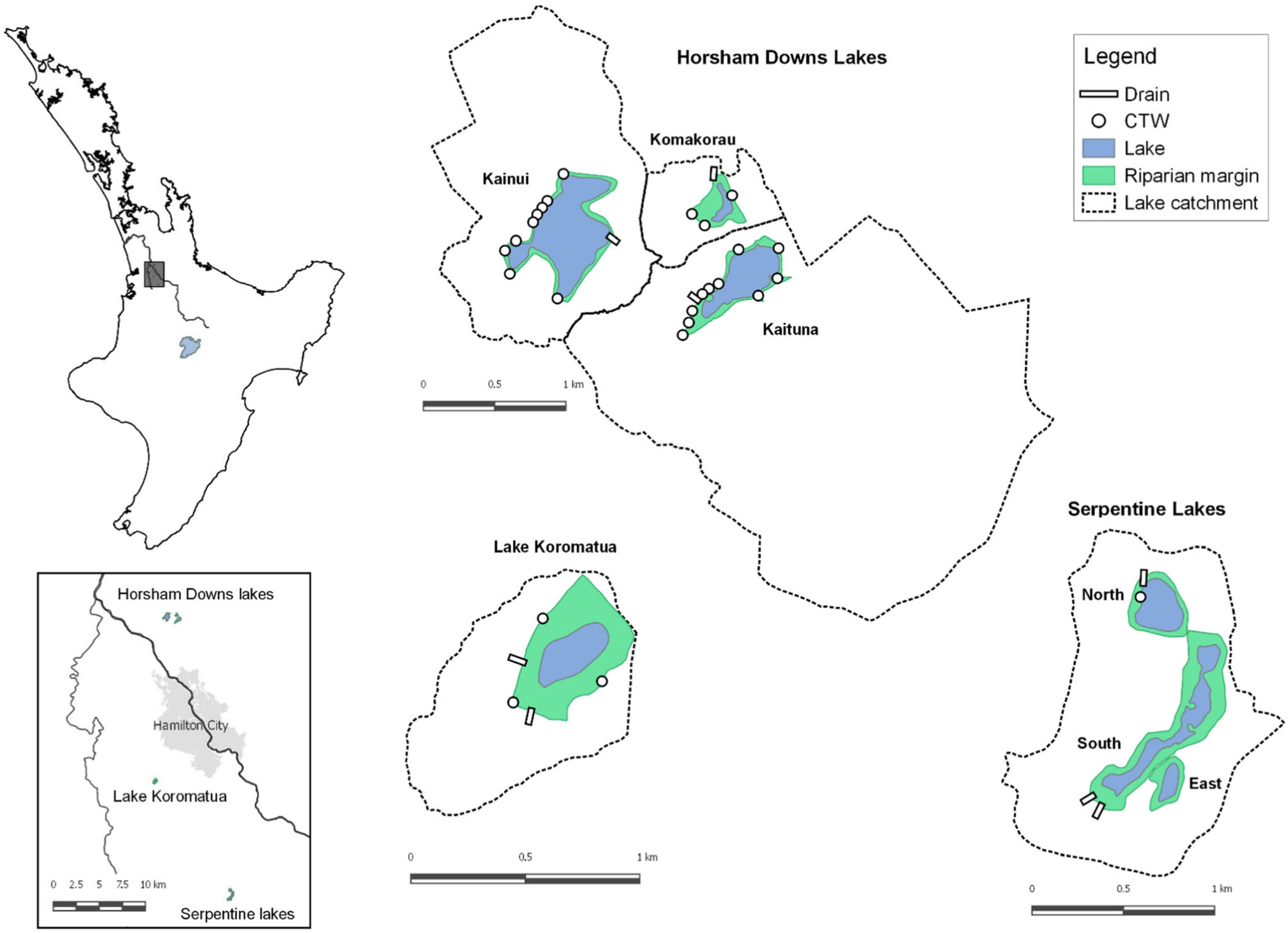


Fig. 1 Location of studied peat lakes in the central Waikato (inset), North Island, New Zealand. Lake areas of open water and riparian margins were digitised from 2016 aerial photographs. Catchment boundaries were delineated from 2008 LiDAR (Light Detection and Ranging) data (source; Waikato Regional Council)

Table 1 Characteristics of the study lakes including morphology, trophic status, Trophic Level Index (TLI), water clarity, and average concentrations of chlorophyll *a* (Chl *a*), total phosphorus (TP) and total nitrogen (TN), number of major in-flows, number of CTWs and CTW codes

Lake	Kainui	Kaituna	Komakorau	Koromatua	Serpentine North
Lake code	KN	KT	KO	KR	SN
Lake area (ha)	25	15	3	7	5
Max. depth (m)	6.7	1.3	1.1	0.8	3.8
Catchment area (ha)	260	589	619	67	163
Trophic state	Hypertrophic	Hypertrophic	Hypertrophic	Hypertrophic	Eutrophic
TLI	6.18	6.00	6.22	6.99	4.48
Secchi depth (m)	0.50	0.32	0.20	0.14	2.02
Chl *a* (mg m^{-3})	45	6	9	32	4
TP (mg m^{-3})	72	208	200	938	48
TN (mg m^{-3})	3041	2509	2488	1492	570
Inflows (*n*)	10	10	3	3	2
CTWs (*n*)	9	10	3	3	1
CTW codes	KN1, KN2, KN3, KN4, KN5, KN6, KN7, KN8, KN9	KT1, KT2, KT3, KT4, KT5, KT6, KT7, KT8, KT9, KT10	KO1, KO2, KO3	KR1, KR2, KR3	SN1

Source (excluding CTWs): Hamilton et al. (2010)

Water samples for particulate and filterable nutrients were collected in 50 ml centrifuge tubes (Greiner Bio1, Germany) and for suspended solids in opaque 1 L bottles. Filterable nutrient samples were syringe-filtered (Whatman GF/C 0.45 μm) in the field and the filter paper retained and wrapped in aluminium foil for Chl *a* analysis. Samples were placed on ice after collection, with nutrient and Chl *a* samples frozen upon return to the laboratory. Water samples for suspended solids analyses were stored in the dark at 4 °C and processed in the laboratory within three days of collection.

Biotic variables measured included percentage cover of emergent macrophytes, visual presence/absence of iron flocculants, and observed presence/absence of fish. A minimum of two G-minnow traps were set per CTW and drain over four nights of trapping. Fish were identified to species level using descriptions from McDowall (2000). The presence/absence of fish for the lakes was determined from the literature, and percentage cover of emergent macrophytes estimated for the entire lake shore using aerial photographs. Iron flocculants were measured by the presence of rust-coloured particles collected on the filter paper retained for Chl *a* analyses.

Zooplankton samples were collected by pouring 3 to 10 L of water through a zooplankton net (40 μm mesh) and were immediately preserved in ethanol (> 50% final concentration) before subsequent identification and enumeration in the laboratory.

Sample analyses

Chlorophyll *a* samples were analysed using a calibrated fluorometer following acetone extraction (Arar and Collins 1997). Filtered nutrient samples were analysed for concentrations of ammonium (NH_4-N), phosphate (PO_4-P), nitrate + nitrite (NO_3–N + NO_2-N) and nitrite (NO_2–N). Concentrations of nitrate were determined by the difference between NO_3-N + NO_2-N and NO_2-N. Analyses were carried out using an Aquakem 200 discrete analyser (Thermo Fisher) with standard colorimetric methods (Federation and American Public Health Association 2005). Limits of detection were 0.001 mg N L^{-1} for NO_2-N, NO_3–N, 0.002 mg N L^{-1} for NH_4-N and 0.001 mg P L^{-1} for PO_4-P. Total P and TN were determined following alkaline persulphate digestion (Federation and American Public Health Association 2005) and analysis for PO_4-P and NO_3-N + NO_2-N, respectively, using a Lachat QuickChem® Flow Injection Analyser (FIA + 8000 Series, Zellweger Analytics, Inc.). Concentrations of total organic nitrogen (ORG-N) were calculated by subtracting the sum of NH_4-N, NO_3–N and NO_2-N from TN.

Suspended solids samples were filtered in the laboratory through pre-combusted (550 °C for 2 h) and pre-weighed glass microfibre filters (Whatman GF/C 0.5 μm). Total suspended solids (TSS) concentrations were determined gravimetrically following drying (105 °C for a minimum of 8 h) and volatile suspended solid (VSS) concentrations were determined following subsequent ashing (550 °C for 4 h). Non-volatile suspended solids (Non-VSS) were calculated from the difference between TSS and VSS.

Zooplankton samples were enumerated in the laboratory using a dissecting microscope at c. 30× magnification until at least 300 individuals, or the whole sample, was counted. Identification was performed using a compound microscope to the lowest level practical, using standard taxonomic guides (Shiel 1995; Chapman et al. 2011).

Statistical analyses

Taxa richness for zooplankton was calculated as the total number of taxa present in each sample. Relative abundances of major zooplankton groups; cladocerans, copepods (including calanoids, cyclopoids and copepod nauplii), ostracods, rotifers and 'others' (including amphipods, dipterans, hemipterans, hydracarina and tardigrades) were calculated for each habitat type and compared using Kruskal-Wallis single factor analysis (Statistica Software version 8.0; Statsoft, Tulsa, OK, USA). The relative abundances of major zooplankton groups were first estimated for each site ($n = 40$) and then averaged across habitat types (lake $n = 5$, CTW $n = 27$, drain $n = 8$) to derive mean relative abundances. This method was chosen as it better incorporated the variability among the sites within each habitat type.

Multivariate analyses were undertaken using Primer 6 (version 6.1.15, Primer-E Ltd., Plymouth Marine Laboratory, Plymouth, U.K) with the PERMANOVA + add-in (version 1.0.5) to determine whether habitat differences existed between lakes, CTWs and drains (based on environmental variables), and to assess patterns of zooplankton community composition. The environmental variables included in analyses were physicochemical (mean depth, area, water temperature, DO, specific conductivity and pH), water quality-related (NH_4-N, NO_3-N, Org-N, PO_4-P, Non-VSS and VSS) and biotic (Chl *a*, percentage cover of emergent macrophytes, iron flocculant and fish presence/absence). All analyses of environmental variables were based on Euclidean distance matrices (Biondini et al. 1991) performed on $\log(x + 1)$ transformed and standardised data (zero mean and unit variance). All analyses of zooplankton data were based on Bray-Curtis similarity matrices (Bray and Curtis 1957) and performed on square-root transformed data as recommended by Anderson et al. (2008).

Prior to undertaking multivariate analyses, a Pearson correlation was performed to identify any highly correlated physicochemical variables. Connectivity was excluded from this analysis as it was not applicable to lake samples, as well as TN and TP due to high correlations with Org-N and PO_4-P, respectively. Individual nutrient species were selected for inclusion as they had stronger relationships with zooplankton community composition than TN and TP alone. Volume was excluded due to high correlations with area and depth measurements.

The variation in environmental variables among habitats was analysed using a single factor (habitat type) permutational multivariate analysis of variance, PERMANOVA (Anderson 2001a; Anderson et al. 2008). A Type III PERMANOVA for unbalanced designs was performed and significance was determined by 9999 unrestricted permutations of the raw data (Anderson 2001b; Anderson and ter Braak 2003). Pair-wise comparisons of group (habitat) means were completed in the case of a significant factor effect to assess between which pairs of habitat types significant differences occurred (McArdle and Anderson 2001). Variables contributing most to the variation among habitats were then identified using similarity percentage analysis (SIMPER), which calculates the average dissimilarity between all pairs of samples and assesses the relative dissimilarity contributed by each variable (Clarke 1993).

The variation in zooplankton community composition between habitat types was similarly evaluated using a single-factor Type III PERMANOVA with pair-wise comparisons of group (habitat) means completed to assess levels of significance. The taxa contributing most to differences in zooplankton community composition between habitat types were determined using the SIMPER procedure.

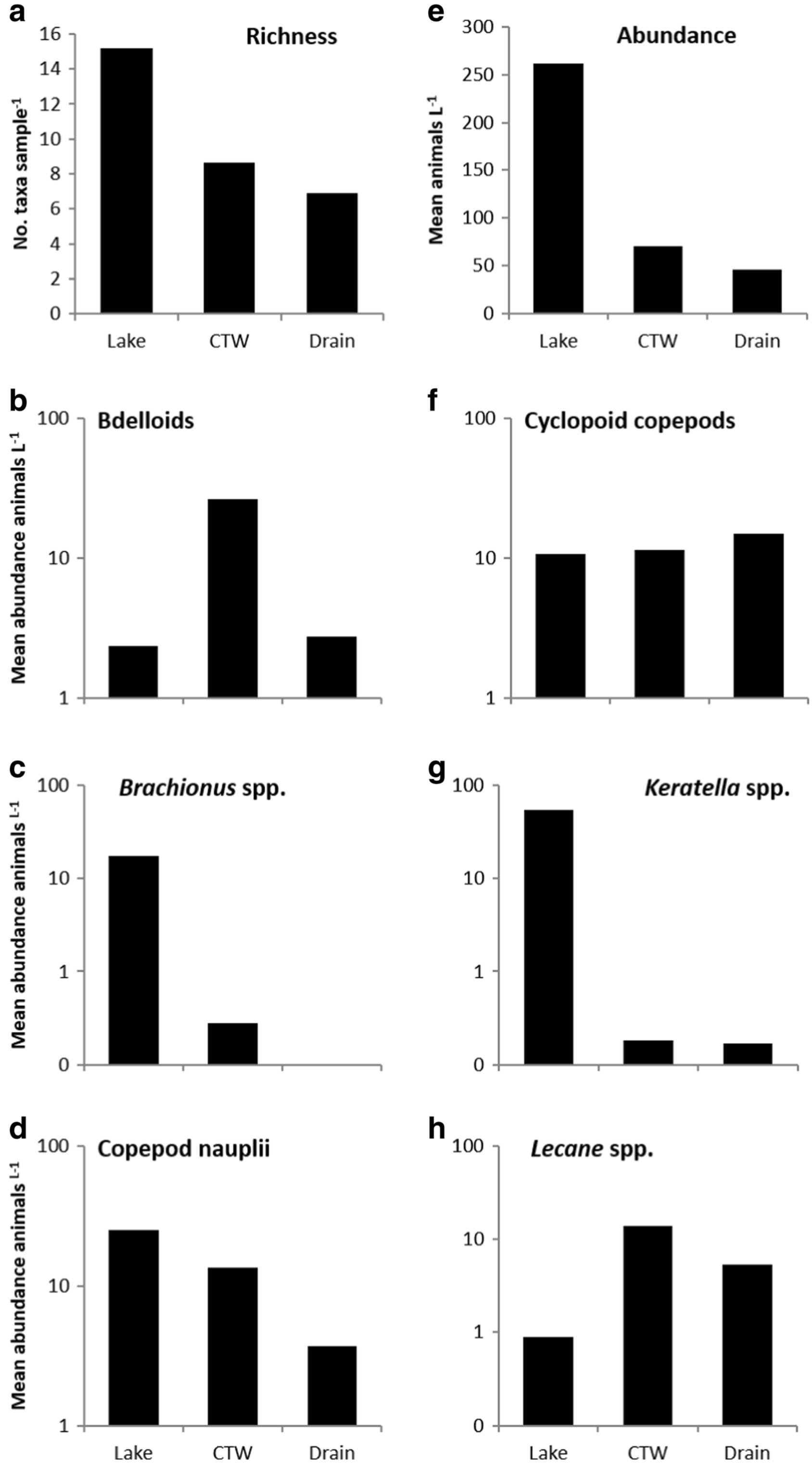
Non-parametric multifactor multiple regression, using the Distance-based Linear Modelling routine in Primer 6 (DistLM), was used to test for the influence of environmental habitat variables (physicochemical, water quality-related and biotic attributes) in structuring the variation in zooplankton community composition (Anderson et al. 2008). The DistLM procedure tests for significant differences in multivariate response variables to explanatory variables based on a selected distance-based measure in the form of a resemblance matrix (Anderson et al. 2008). The step-wise selection procedure based on 9999 permutations was used to select and test habitat variables with an adjusted R^2 selection criterion to eliminate insignificant variables.

Results

Zooplankton community composition

Seventy-three taxa were identified from the three habitat types, including 7 cladoceran, 3 copepod, and 55 rotifer species, ostracods and 8 macroinvertebrate taxa (amphipods, dipterans, hemipterans, hydracarinas and tardigrades). Total number of taxa recorded for each habitat type was greatest from CTWs (52), followed by lakes (40), and drains (20) (S.I. **Table 7**). Lake samples had the highest, although variable, mean taxon richness (15.2, SD = 4.9) followed by CTWs (8.7, SD = 3.8) and drains (6.8, SD = 2.9; Fig. 2a). Similarly, mean zooplankton total abundance was highest in lake samples (262 animals L^{-1}), followed by CTWs and then drain samples (70 and 46 animals L^{-1}, respectively; Fig. 2e). Differences in mean total abundances and richness of zooplankton were not statistically significant amongst habitat types due to high within-group variability. Lakes Komakorau and Koromatua had highest taxa richness (21 and 19, respectively), while the greatest richness from CTW habitats was recorded from KN1 (entering Lake Kainui) and

Fig. 2 Mean values for taxa richness and total abundance of zooplankton (**a**, **e**) and total abundances of zooplankton species most dissimilar between habitat types including; Bdelloids (**b**), *Brachionus* spp. (**c**), Copepod nauplii (**d**), Cyclopoid copepodites (**f**), *Keratella* spp. (**g**) and *Lecane* spp. (**h**) plotted on a $\log_{10}$-scaled axis for each habitat type (lake, CTW and drain)



KR2 (entering Lake Koromatua) (both 16). The CTW KT2, adjacent to Lake Kaituna, had the lowest richness with only cyclopoid copepodites and copepod nauplii recorded from the sample despite the CTW having high lake connectivity and a large area (1080 m^2).

Lake zooplankton assemblages were distinctly different from CTW and drain communities (SIMPER analysis, average Bray-Curtis dissimilarities 83.7 and 86.6, respectively). Differences were driven by the predominance of cladocerans, particularly the rotifers *Brachionus calyciflorus* and *Keratella* *tropica* (Fig. 2c, g), as well as *Polyarthra vulgaris, Synchaeta longipes*, and the cladoceran *Bosmina meridionalis* (Table 2), all of which were at higher abundances in lake habitats but virtually absent from the CTWs and drains. Cumulatively, these taxa, as well as high densities of copepod nauplii, accounted for 45% and 48% of the lake-CTW and lake-drain differences, respectively (Table 2).

There was a relatively subtle difference in the dominant taxa typical of drain and CTW habitats, which is reflected by an average dissimilarity of 67.9 derived from the SIMPER analysis (Table 2) and represented graphically in Fig. 2. Cumulatively, cyclopoid copepodites (10.8), copepod nauplii (9.3) and bdelloid rotifers (9.9) contributed 44.1% to the dissimilarity between CTW and drain zooplankton assemblages (Table 2). High relative abundances of *Lecane* spp. within CTW habitats (Fig. 2h) also contributed to 17% of the community compositional differences in comparison to drain habitats (Table 2).

Comparison of the relative abundances of the major zooplankton groups (cladocerans, copepods, ostracods and rotifers) for each habitat type supported the finer-scale differences between zooplankton assemblages determined by the SIMPER analysis. Cladocerans and calanoid copepods were significantly more abundant in lake habitats compared with CTWs and drains (Table 3). Copepod nauplii and cyclopoid copepodids were common within each habitat (Fig. 2d, f), but differed in their relative abundances (Table 3). Rotifers were also significantly more abundant in lake and CTW habitats

Table 2 SIMPER analysis (square-root transformed data) showing the main taxa contributing to the variation in community composition between lake-CTW and drain-lake habitats, and at least 80% between drain-CTW habitats

Species	Mean abundance	Mean abundance	Mean dissimilarity	Contribution %
	Drain	Wetland		
Cyclopoid copepodites	2.83	2.14	10.76	15.8
Bdelloids	1.21	3.13	9.94	14.6
Copepod nauplii	1.57	2.91	9.33	13.7
Lecane rhytida	0.59	1.27	6.08	9.0
Ostracods	1.55	0.27	4.04	5.9
Cephalodella intuta	0.83	0.42	3.12	4.6
Lecane hamata	0.14	0.68	2.75	4.1
Mosquito larvae	0.55	0.33	2.74	4.0
Lecane lunaris	0.84	0.30	2.67	3.9
Lepadella patella	0.24	0.40	2.02	3.0
Cephalodella tenuiseta	0.07	0.34	1.55	2.3
Mean dissimilarity = 67.9				
	Lake	Wetland		
Keratella tropica	5.31	0.05	8.14	9.7
Bosmina meridionalis	4.60	0.06	7.36	8.8
Polyarthra vulgaris	4.15	0.00	6.22	7.4
Brachionus calyciflorus	2.53	0.02	5.38	6.4
Copepod nauplii	4.47	2.91	5.20	6.2
Synchaeta longipes	2.56	0.00	5.05	6.0
Bdelloids	1.08	3.13	4.38	5.2
Cyclopoid copepodites	2.39	2.14	4.30	5.1
Mean dissimilarity = 83.7				
	Drain	Lake		
Keratella tropica	0.14	5.31	8.66	10.0
Bosmina meridionalis	0.00	4.60	7.98	9.2
Polyarthra vulgaris	0.00	4.15	6.61	7.6
Copepod nauplii	1.57	4.47	6.31	7.3
Brachionus calyciflorus	0.00	2.53	5.92	6.8
Synchaeta longipes	0.00	2.56	5.47	6.3
Cyclopoid copepods	2.83	2.39	4.86	5.6
Mean dissimilarity = 86.6				

Contribution % is the proportion of dissimilarity between habitat pairs contributed by each taxa

Table 3 Relative abundance (%) of zooplankton groups Cladocerans, Copepods (including Calanoids, Cyclopoids and nauplii), Ostracods, Rotifers and Others for lake, CTW and drain habitats

Relative zooplankton abundance (%)

	Lake	Wetland	Drain
Zooplankton			
Cladocerans	25.02^a	1.77^b	0.30^b
Copepods	18.19	44.96	59.24
(Calanoids)	$(1.55)^a$	$(0.03)^b$	$(0)^b$
(Cyclopoids)	(4.37)	(13.96)	(39.51)
(Nauplii)	(12.27)	(30.98)	(19.74)
Ostracods	0.51	0.56	8.71
Rotifers	56.17^a	50.92^a	28.62^b
TOTAL	**99.89**	**98.22**	**96.88**
Others			
Amphipods	0	0	0.37
Diptera	0.06	1.69	2.75
Hemiptera	0	0.09	0
Hydracarina	0.05	0	0
Tardigrades	0	0.01	0
TOTAL	**0.11**	**1.78**	**3.12**

These measurements represent the mean abundance in which the relative abundance of each zooplankton taxon was estimated for each site ($n = 40$) then averaged across habitat type (lake $n = 5$; CTW $n = 27$, drain $n = 8$). Letters in superscript denote significant differences ($P < 0.05$) between habitat types

compared with drains (Table 3), due to the relatively high abundances of bdelloids and *Lecane* spp. within CTW habitats (Fig. 2b, h).

Environmental variables

Lake habitats were significantly larger and more alkaline than CTWs and drains, and both lake shore and CTW habitats had significantly greater depths than drains (Table 4). Mean values of physicochemical, biotic and water quality variables were not significantly different between habitat types due to high variability within habitats.

Based on PERMANOVA, habitat type accounted for a significant proportion of the variation in biotic and abiotic environmental variables across all sites ($F_{pseudo} = 4.78$, $P = 0.0001$). Pairwise comparisons indicated significant differences between each habitat type (Lake, Drain $t = 2.72$; Lake, CTW $t = 2.10$; Drain, CTW $t = 2.07$, $P < 0.01$). The morphological variables area and depth contributed to the greatest dissimilarity between habitat types, followed by pH, inorganic-N and conductivity (SIMPER results, Table 5.) Water temperature was also important, contributing to 6.8% of the dissimilarity between lake and CTW habitats, and 7.7% between lake and drain habitats.

Habitat variables influencing zooplankton communities

Habitat type was determined by PERMANOVA to account for a significant proportion of the variation in zooplankton community composition ($F_{pseudo} = 3.59$, $P = 0.0001$). Pairwise comparisons indicated significant differences between each habitat type based on zooplankton community composition (Lake-Drain $t = 2.19$, $P < 0.01$; Lake-CTW $t = 2.21$, $P < 0.01$; Drain-CTW $t = 1.40$, $P < 0.05$).

The DistLM procedure assigned the greatest proportion of the variation in zooplankton community composition among habitat types to area (22.1%) followed by pH (16.7%) and NH_4-N (10.4%; Table 6). Area was a key driver of the difference between lakes and CTWs, as well as between lakes and drains based on SIMPER analyses (Table 5), while differences in pH were significant between lakes and CTWs. The DistLM marginal tests also determined water temperature and DO were significant drivers of the variation in community composition between lake habitats and CTWs, as well as between lakes and drains (Table 6).

The DistLM analysis indicated conductivity and depth were significant explanatory variables, reflecting differences between CTWs and drains, and supporting previous analyses (Table 5). PO_4-P was a significant explanatory variable in marginal tests due to elevated concentrations in CTWs (mean = 0.24 mg N L^{-1}) compared to lakes and drains (0.06 and 0.01 mg N L^{-1}, respectively). Finally, NH_4-N concentration, iron flocculant and emergent macrophyte cover, each of which were elevated in drains, were also identified as significant by the DistLM marginal tests (Table 6), supporting the SIMPER results (Table 5). Mean NH_4-N concentrations from drains (0.22 mg N L^{-1}) were twice as high as those from CTWs (0.11 mg N L^{-1}) and more than five-fold greater than lake concentrations (0.04 mg N L^{-1}; Table 5).

Discussion

Zooplankton diversity

Our results suggest agricultural CTWs support greater zooplankton diversity than drain habitats and can increase the overall biodiversity of highly modified peat lake catchments. For example, within the catchment of Lake Kainui, 15 taxa were recorded from the lake itself, five additional taxa were recorded from drains, and a further 17 taxa from CTW habitats. Collectively, CTWs had the highest total diversity (54 taxa) followed by lakes (40) and then drains (20) (S.I. Table 7). Mean zooplankton taxa richness for CTWs (c. 9) was intermediate between lake (15) and drain (6) habitats, although no significant differences were apparent due to high variability within habitat types.

Table 4 Mean (± standard deviation) of environmental variables including physicochemical, biotic and water quality for each habitat type

Environmental Variables		Habitat Type								
		Lake (n = 5)			CTW (n = 27)			Drain (n = 8)		
Physicochemical										
Area	(m^2)	108000^a	±	91,627	237^b	±	408	10^b	±	4
Depth	(m)	0.81^a	±	0.11	0.90^a	±	0.36	0.22^b	±	0.10
Connectivity	(H/M/L = 3/2/1)	3.00*	±	0	1.93	±	0.87	1.88	±	0.35
Temperature	(°C)	24.1	±	2.0	21.8	±	1.9	20.9	±	2.2
Conductivity	(mS cm^{-1})	0.18	±	0.04	0.25	±	0.05	0.20	±	0.09
DO	(mg L^{-1})	6.72	±	3.82	3.92	±	4.16	2.59	±	2.07
pH		6.84^a	±	1.24	5.09^b	±	0.72	5.52^b	±	0.52
Biotic										
Macrophytes	(% cover)	7	±	3	34	±	33	65	±	33
Chl *a*	(μg L^{-1})	48.8	±	50.8	27.6	±	27.2	6.6	±	10.1
Fish	(P/A = 1/0)	1	±	0.00	0.48	±	0.51	0.38	±	0.52
Iron floc	(P/A = 1/0)	0.24	±	0.26	0.50	±	0.42	0.90	±	0.47
Water quality										
NH$_4$-N	(mg L^{-1})	0.04	±	0.04	0.11	±	0.15	0.22	±	0.34
NO$_3$-N	(mg L^{-1})	0.11	±	0.10	0.12	±	0.19	0.41	±	0.57
Org-N	(mg L^{-1})	3.92	±	1.81	3.18	±	1.19	2.37	±	1.16
PO$_4$-P	(mg L^{-1})	0.06	±	0.10	0.24	±	0.45	0.01	±	0.01
VSS	(mg L^{-1})	20.5	±	22.2	20.3	±	21.4	15.8	±	14.9
NVSS	(mg L^{-1})	13.5	±	17.7	12.7	±	13.6	8.9	±	9.7

Letters in superscript denote significant differences (Kruskal Wallis test, $P < 0.01$) between habitat types. Connectivity with downstream lake being High, Medium, or Low (3, 2, 1, respectively). * lakes were considered to have high connectivity as there is unimpeded flow for exchange of water and aquatic organisms throughout the habitat

The diversity of zooplankton from the habitats in our study is comparable to that from freshwater ecosystems elsewhere. For example, zooplankton taxa richness for our CTW habitats was similar to floodplain ponds of Truman Lake, a reservoir in Missouri (Medley and Havel 2007), midsummer zooplankton assemblages from wetlands in the mid-west USA (Beaver et al. 1999), and small (area < 1 ha) shallow lakes in south-eastern Wisconsin, USA (Dodson et al. 2005). The lower taxa richness of drain habitats in this study was similar to that of agriculturally impacted wetlands in Wisconsin (mean 3.8) studied by Dodson and Lillie (2001), while richness from lakes Komakorau (21) and Koromatua (19) was similar to eutrophic shallow lake ecosystems in the northern hemisphere (Søndergaard et al. 2005), as well as a number of lakes in the North Island of New Zealand (Duggan et al. 2001).

Notably, two of the CTWs (KN1 and KR2) had greater taxa richness (both 16) than lakes Kainui (15), Kaituna (12) and Serpentine South (9), despite having considerably smaller areas (0.2 and 0.02 ha compared to 25, 15, and 5 ha, respectively). Søndergaard et al. (2005) similarly found a weak relationship between zooplankton taxa richness and habitat size following an investigation of almost 800 Danish shallow lakes (median depth 1.5 m), ranging from 0.01 to 4200 ha, going on to suggest that ponds and small lakes are important biodiversity components in agricultural landscapes. CTWs KN1 and KR2 were relatively complex habitats, with deep (> 1 m) and shallow (< 0.5 m) zones, areas of open water and moderate macrophyte cover; thus, greater zooplankton diversity may be expected owing to a greater range of potential habitats and niches (Lucena-Moya and Duggan 2011).

Zooplankton assemblages & functional attributes

CTW-zooplankton assemblages differed from lake and drain communities owing to relatively few cladocerans and a predominance of rotifers, primarily comprising large numbers of bdelloid rotifers and *Lecane* species. Bdelloid rotifers are primarily benthic and are able to survive extended dry periods via anhydrobiosis (Crowe et al. 1992), making them well adapted to CTW habitats in artificially drained agricultural peat lake catchments where water levels can fluctuate widely. Like most rotifers, bdelloids are suspension feeders and thrive on dead organic matter and bacteria (Ricci 1984). Along with excess sediment and nutrients, pathogenic bacteria have been identified as one of New Zealand's three major water quality problems (MfE and StatsNZ 2017). Runoff from agricultural

Table 5 SIMPER analysis showing the environmental variables contributing up to 70% of the variation among lake, CTW and drain habitats

Variable	Mean value	Mean value	Mean value of dissimilarity	Contribution %
	Drain	CTW		
Depth (m)	0.22	0.90	3.64	10.7
NO_3-N (mg L^{-1})	0.41	0.12	3.12	9.2
Conductivity (mS cm^{-1})	0.197	0.254	2.94	8.7
Chlorophyll *a* (μg L^{-1})	6.57	27.55	2.46	7.3
Org-N (mg L^{-1})	2.37	3.18	2.19	6.5
NH_4-N (mg L^{-1})	0.22	0.11	2.18	6.4
PO_4-P (mg L^{-1})	0.01	0.24	2.14	6.3
Macrophytes (% cover)	65	34	2.10	6.2
Iron floc (P/A = 1/0)	0.9	0.5	2.01	5.9
Mean dissimilarity = 33.90				
	Lake	CTW		
Area (m^2)	108,000	237	5.93	15.6
pH	6.84	5.09	5.39	14.2
Temperature (°C)	24.12	21.83	2.58	6.8
Org-N (mg L^{-1})	3.92	3.18	2.28	6.0
DO (mg L^{-1})	6.72	3.92	2.25	5.9
Conductivity (mS cm^{-1})	0.176	0.254	2.20	5.8
Chlorophyll *a* (μg L^{-1})	48.81	27.55	2.14	5.7
NVSS (mg L^{-1})	13.46	12.69	2.05	5.4
Mean dissimilarity = 37.91				
	Drain	Lake		
Area (m^2)	10	108,000	10.30	20.7
Temperature (°C)	20.89	24.12	3.83	7.7
pH	5.52	6.84	3.63	7.3
Chlorophyll *a* (μg L^{-1})	6.57	48.81	3.62	7.3
Org-N (mg L^{-1})	2.37	3.92	3.54	7.1
Macrophytes (% cover)	65	7	3.19	6.4
NH_4-N (mg L^{-1})	0.22	0.04	2.88	5.8
Iron floc (P/A = 1/0)	0.9	0.2	2.83	5.7
Mean dissimilarity = 50.00				

Mean values for each variable have been back-transformed to original values to clarify dissimilarities. Contribution % is the percentage of dissimilarity between habitat groups contributed by each variable

catchments is known to transport pathogenic bacteria including *Escherichia coli*, *Salmonella*, *Campylobacter* and *Shigella*, as well as the pathogenic protozoans *Cryptosporidium* and *Giardia* (Hooda et al. 2000; Jamieson et al. 2002; Ballantine and Davies-Colley 2014). Bacterivorous zooplankton have been shown to reduce pathogenic bacteria from water (Schallenberg et al. 2005) and are likely to play an important role in the treatment efficiency of CTWs in agricultural landscapes. Therefore, the prevalence of these species in the CTWs of this study is encouraging.

While zooplankton such as bdelloids feed directly on bacteria, metazooplankton including calanoid and cyclopoid copepods as well as large cladocerans such as *Ceriodaphnia dubia* (Galbraith and Burns 2010), consume bacteria indirectly via predation on ciliates (Hansen 2000). Bacterivorous ciliates are important for reducing bacterial densities in effluent from sewage treatment plants (Curds et al. 1968; Madoni 2003) and may also suppress viruses (Pinheiro et al. 2007). The calanoid copepod *Calamoecia lucasi* was abundant in Lake Koromatua and present in CTW KR2 and lakes Kainui, Komakorau, and Serpentine North, while *C. dubia* was present in CTWs KN5 and KT5 as well as Lake Kainui. Furthermore, early copepodid instars (copepod nauplii and cyclopoid copepodites), which feed preferentially on ciliates (Hansen 2000), were prevalent in CTW habitats, comprising approximately 45% of relative abundances. The presence of these zooplankton species in the CTWs of this study is promising as they may contribute

Table 6 Results from DistLM analysis of environmental variables driving variation in zooplankton community composition among lake, CTWs and drain habitats

Marginal Tests		Step-wise Sequential Tests			
Variable	**Pseudo-F**	**Variable**	**Pseudo-F**	**Cum (%)**	**Prop (%)**
Area	3.50**	Area	3.50**	8.4	22.1
pH	3.01**	pH	2.76**	14.8	16.7
Iron Flocculant	2.40**	NH_4-N	1.76*	18.7	10.4
Temperature	2.31**	Conductivity	1.68 n.s	22.5	9.8
Macrophytes	1.93*	Iron Flocculant	1.55 n.s	25.9	8.9
DO	1.89*	Temperature	1.47 n.s	29.0	8.3
NH_4-N	1.92*	Depth	1.46 n.s	32.1	8.1
Conductivity	1.87*	DO	1.36 n.s	35.0	7.5
PO_4-P	1.81*	Macrophytes	1.50 n.s	38.1	8.1
Depth	1.76*				
Fish	1.73*				
NVSS	1.75*				
Chlorophyll *a*	1.40 n.s				
VSS	1.38 n.s				
NO_3-N	1.36 n.s				
Org-N	1.27 n.s				

** P < 0.01; * P < 0.05; n.s = not significant; Cum (%) = Cumulative percentage of variance; Prop (%) = Proportion of explained variance

to reducing pathogenic bacterial communities entering the downstream lakes. Wilcock et al. (2012) likewise suggest that enhancing communities of bacterivorous microorganisms is likely to increase the efficacy of agricultural wetland treatment systems through consumption of harmful bacteria.

Drain-zooplankton assemblages differed from CTWs and were driven by a lack of rotifers and relatively large numbers of ostracods, cyclopoid copepodites and mosquito larvae. Drain habitats generally supported lower zooplankton diversity and abundances, exempting the drain site of Lake Kainui (KND). KND had low macrophyte cover compared to other drain habitats as a result of being cleared in the preceding spring, which may have contributed to greater zooplankton taxa richness (11) and higher abundances (247 animals L^{-1}).

Lake-zooplankton assemblages were distinctly different from CTW and drain communities, due to greater abundances of cladocerans and pelagic rotifer species. Cladoceran zooplankton play a vital role in energy transfer and food web dynamics (Kattel 2012) and were particularly abundant in lake habitats, comprising a quarter of the zooplankton community. The cladoceran *Bosmina meridionalis* was one of the dominant species from our lake samples, second only to the rotifer *Keratella tropica*, each species being commonly abundant in eutrophic New Zealand lakes (Duggan et al. 2002). Interestingly, two species more typical of lakes with low trophic state, *Polyarthra vulgaris* and *Synchaeta longipes*, were abundant in lakes Koromatua and Serpentine North, respectively, despite the lakes being highly eutrophic.

Habitat characteristics

Each habitat type supported significantly different zooplankton communities (refer to results of PERMANOVA and pairwise comparisons), including between drains and CTWs. Habitat morphologies including surface area, water depth and macrophyte cover were most strongly associated with variations in zooplankton composition, whilst significant water quality parameters included pH, conductivity, iron flocculant and concentrations of PO_4-P and inorganic-N. Drain habitats were smaller and shallower than CTWs, with dense macrophyte cover, high concentrations of NH_4-N and NO_3-N, and high frequency of iron flocculant occurrence. CTW habitats were intermediate in size between lakes and drains, relatively deep and with high Chl *a*, Org-N and VSS concentrations, indicative of elevated phytoplankton biomass. Levels of PO_4-P were also highest in CTWs, particularly in those with low pH. Lakes were naturally the largest habitats and moderately deep with warmer water temperatures, high DO and neutral pH. Similar to CTW habitats, lakes had elevated Chl *a*, Org-N and VSS concentrations due to high phytoplankton densities, which in turn supported greater zooplankton abundances.

As evidenced by the results from this study, dense macrophyte cover in small, shallow watercourses suppresses phytoplankton growth and can cause stagnant, reducing conditions, elevating NH_4-N levels. Nonetheless, while excessive macrophyte growth can have negative impacts on stream communities (Collier et al. 1999), macrophytes improve the structural complexity of freshwater habitats and strongly influence community structure and diversity (Warfe and Barmuta 2006; Lucena-Moya and Duggan 2011).

Macrophytes are an important refuge against predation for pelagic cladocerans, as described by Timms and Moss (1984) following observations of different water clarity between connected shallow wetland ecosystems in the Norfolk Broads. The size of macrophyte beds is also important, particularly for populations of horizontally migrating cladocerans such as *Ceriodaphnia* and *Bosmina* species. Lauridsen et al. (1996) suggest numerous small refuges (c. 2 m diameter) are likely to support higher densities of these species rather than single large refuges (> 10 m diameter), which are more typically dominated by macrophyte-associated, non-migrating cladocerans such as *Chydorus* and *Simocephalus* species. Each of the aforementioned cladoceran species occurred in a number of the lake and CTW habitats in our study; thus, it is possible similar dynamics may occur in Waikato peat lake ecosystems. Furthermore, the structural complexity of different macrophytes provides habitat niches favoured by different zooplankton taxa (Lucena-Moya and Duggan 2011). Thus, the variety of emergent, submerged and floating macrophytes within a wetland ecosystem will influence zooplankton biodiversity and biomass.

Finally, many of the CTWs in this study were designed to capture coarse sediment to reduce infilling of the shallow peat lakes downstream. While deposited sediment was not measured in this study, the effects of sedimentation, particularly in cultivated catchments, requires consideration as populations of most zooplankton taxa can persist over long periods through egg banks (Hairston 1996). Gleason et al. (2003) investigated the effects of sediment loads from intensive agricultural activities on the emergence of zooplankton from wetland soil egg banks and found burial by sediment as little as 0.5 cm deep reduced invertebrate emergence by 99%. Duggan et al. (2002) also found limited diversity in lakes with high sediment loads. Designing CTWs with distinct areas of open water and variable depths, by incorporating sedimentation forebays as well as open-water habitats isolated from sediment inputs, will help to minimise any adverse sedimentation effects on zooplankton communities and promote greater diversity.

Conclusions

CTWs can improve the overall biodiversity of highly-modified peat lake catchments, by supporting zooplankton species otherwise absent from lake and drain habitats. Zooplankton taxa richness and abundances were broadly higher from CTWs than drain habitats, and a few CTWs supported greater diversity than several lakes. The results from our research suggest CTWs afford dual benefits for peat lake restoration within intensive agricultural landscapes through provision of habitat for zooplankton communities as well as water quality improvements.

To further enhance zooplankton communities, we propose creating CTWs with variable depths and areas deeper than existing drains, with larger areas of open water and moderate to low levels of diverse macrophyte cover. Opportunities exist to manipulate the influence of macrophyte beds through careful design, construction, plant selection and maintenance to support targeted zooplankton species which can sustain grazing on phytoplankton and improve water quality treatment (Schriver et al. 1995). Just as recent research has extended our knowledge of zooplankton population dynamics within high rate algal ponds in support of improved wastewater treatment (Montemezzani et al. 2016, 2017), expanding our understanding of the lifecycles and habitat requirements of bacterivorous zooplankton and ciliates in wetlands could additionally inform CTW designs to improve operational efficiency whilst concurrently supporting greater zooplankton biodiversity.

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