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Spatial, Environmental, and Biotic Determinants of Zooplankton Community Composition in Subarctic Lakes and Ponds in Wapusk National Park, Canada

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Abstract

Northern regions are expected to experience large environmental change over the next few decades. The response of biota will depend on changes in the local environment, regional processes that influence lake connectivity, and species interactions. In 2008, we surveyed 92 lakes and ponds across Wapusk National Park, located on the southwestern shore of Hudson Bay. At each site we assessed water chemistry and zooplankton community composition. In an effort to understand how the aquatic ecosystems will respond to future environmental change, we determined local characteristics (e.g., water chemistry), regional spatial factors (e.g., dispersal), and biotic interactions (e.g., species associations) influencing community composition. Important environmental variables included lake area, pH, ionic composition, total phosphorus, and chlorophyll *a*; however, spatial variables explained more variation than environmental variables, suggesting that dispersal is an important driver of zooplankton composition in this region. Additionally, species exhibited negative co-occurrence patterns, suggesting biotic interactions are important in structuring the zooplankton communities. As environmental conditions change and the distribution of habitat (i.e., coastal fen, interior peatland, and spruce forest) shifts, evidence that the park's zooplankton community is spatially structured coupled with our suspicion that zooplankton are likely to experience high dispersal levels in Wapusk leads us to suggest zooplankton may indeed be able to track changing environmental conditions within the park, although it remains unclear how species interactions will modify this expectation.

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Introduction

One of the primary goals of community ecology has long been the identification of the factors that control the distribution of species (Hubbell, 2001), a task imbued with particular importance given predictions of future environmental change (Meehl et al., 2007). Species distributions, and the ecosystem functions that species provide, are likely controlled by environmental factors that determine which ecological niches are available, and spatial factors that determine species' access to those niches (Leibold et al., 2004). Furthermore, both classes of factors are expected to play a role in determining how ecosystems respond to environmental change, as the extent to which ecosystem functions will be affected by environmental change likely depends on the ability of a biota to adapt to new environmental conditions (Bell and Gonzalez, 2009), as well as its ability to disperse and thus track those environmental conditions (Leibold and Norberg, 2004; Bell and Gonzalez, 2011).

Wapusk National Park (WNP), located on the southwestern shore of Hudson Bay near Churchill, Manitoba, provides an attractive system to study this interaction between environmental conditions and dispersal capabilities of aquatic organisms. Water is a prominent feature on the landscape, covering ~40% of the 11,475 km^2 total area of WNP. Within the park, there are over 10,000 lakes/ponds embedded in regions differing in lake density and connectivity. Canada's subarctic is expected to experience dramatic changes in temperature in the near future (Christensen et al., 2007) and is generally a region where biota are poorly understood and in need of long-term monitoring (Rouse et al., 1997). The park itself contains a wide range of environmental conditions (Symons et al., 2012), which creates strong potential for niche differentiation among different species, and the park's high concentration of water bodies provides the potential to examine the importance of spatial factors in a habitat likely to have high dispersal potential for aquatic organisms, such as zooplankton.

Zooplankton are a diverse group of aquatic organisms adapted to a wide variety of environmental conditions, and they play an important role in trophic energy flow through their ecosystems (Strecker and Arnott, 2008). It has been long established that zooplankton have strong dispersal capabilities, largely due to the potential for many members of the group to form stress-tolerant resting stages (e.g., Proctor, 1964). Consequently, it is widely hypothesized that zooplankton distributions are closely tied to environmental conditions (Leibold et al., 2004), and, presumably, the species' fundamental or realized niches (Hutchinson, 1957). Indeed, this link between environmental conditions and zooplankton distributions has some strong experimental and field support (e.g., Cottenie et al., 2003; Cottenie and De Meester, 2004; Beisner et al., 2006; Strecker et al., 2008; Gray et al., 2012).

Conversely, it has also been hypothesized that various factors are capable of disrupting the relationship between biota and niche optima. For example, high dispersal conditions may create mass-effects situations where species disperse so rapidly that they are

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present even in suboptimal habitats (Leibold et al., 2004), and in habitats where communities are already well established, strong preexisting biotic interactions may prevent new species from establishing (Shurin, 2000). Indeed, the potential for such priority effects is high in zooplankton, given their rapid generation times and potential to form "banks" of resting stages (De Meester et al., 2002). Furthermore, the neutral perspective hypothesizes that some species distributions may not reflect differing responses to environmental variation, but rather that community composition may be a result of both stochastic competitive dynamics among roughly equivalent member species, and spatial factors that affect species access to habitats (Hubbell, 2001). There is a near consensus now that ecological equivalence is unlikely for broad groups of organisms; however, there is evidence that small groups of species may be ecologically similar, causing stochasticity to be a major factor driving community dynamics (Vellend, 2010).

The metacommunity paradigm now popular in ecology represents a synthesis position which recognizes that environmental conditions likely have some impact on species distributions, but that the influence of the environment is tempered by spatial influences, be they low dispersal that prevents species from accessing habitats to which they are well suited, or high dispersal that maintains species in habitats to which they are poorly adapted. Here we examine a large data set of zooplankton communities over a marked environmental gradient in Canada's subarctic that is well suited to analyze the extent to which zooplankton distribution is a result of environmental conditions, spatial structure, competition, or some mix of all of these factors. We had three goals: (1) to reveal important environmental drivers of zooplankton community composition; (2) to determine the relative importance of local environmental conditions compared to spatial variables (i.e., dispersal); and (3) to evaluate the extent to which species interactions shape local community composition. These analyses will help inform on the extent to which changing environmental factors are likely to affect zooplankton communities, and thereby influence broad-scale ecosystem function, in a region expected to undergo significant change.

Methods

WATER AND ZOOPLANKTON SAMPLING

From 22 July to 3 August 2008 we used a helicopter to sample 92 lakes/ponds in Wapusk National Park. These lakes/ponds were distributed throughout many different types of land cover, which have been grouped into three main habitat types: spruce forest, interior peatland, and coastal fen. Spruce forest is used to describe areas of lichen spruce bog and regenerating burn areas; interior peatland is used to describe areas of lichen melt pond bog and lichen peat plateau bog; and coastal fen describes areas of sedge bulrush-poor fen, sedge-rich fen, and sphagnum larch fen (land cover classification from Brook, 2005). Water bodies were named arbitrarily by the order they were sampled and latitude/longitude, and physical/chemical characteristics are listed in Appendix Tables A1–A3. Most lakes/ponds were small, having depths usually <0.5 m and surface area between 0.05 and 945 ha (median = 4 ha). Near shore at each site, we took in situ measurements of temperature and dissolved oxygen using a YSI 600OMS probe (YSI Incorporated, Yellow Springs, Ohio, USA). Weather was variable during the sampling period, and water temperature was correlated with the daily average air temperature (Pearson correlation, $r = 0.21$, $p = 0.04$). Water samples were collected 10–20 cm below the surface for water chemistry and chlorophyll *a* analyses. Water was filtered through a 75-μm mesh to remove zooplankton. For the analyses of major ions (Cl, SO_4, Ca, Mg, K, Na, SiO_2), nutrients (total phosphorus [TP], filtered and unfiltered, NO_3-NO_2, NH_3, total nitrogen [TN]), alkalinity, dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), specific conductivity, and pH, water samples were sent to Environment Canada's National Laboratory for Environmental Testing at the Canada Centre for Inland Waters (Burlington, Ontario) (EC, 1994). DIC, DOC, and filtered TP samples were filtered through a 0.45-μm cellulose-acetate filter. TP samples were preserved with 1 mL of 30% H_2SO_4 prior to shipping. For chlorophyll *a* analysis, a known volume of water was filtered through a glass fiber filter (Whatman GF/C, pore size 1.2 μm), which was frozen until extraction. Chlorophyll *a* concentration was then determined using a Turner Designs TD700 fluorometer following a 24-h methanol extraction. Qualitative zooplankton samples were collected from each lake by horizontally towing a 75-μm mesh conical net through the water for approximately 10 m. Samples were immediately preserved in 70% ethanol for future identification.

Crustacean zooplankton were enumerated using a Leica MZ16 microscope at 40× magnification and were usually identified to species, except *Alona* spp. and chydorids, which were identified to genus; copepod juveniles and harpacticoids, which were identified to order; and ostracods, which were identified to subclass. A target of 200 individuals for each of crustaceans and rotifers, not including juveniles, was processed in successive subsamples of a defined volume. All crustaceans were identified using the keys of Brooks (1959), Wilson and Yeatman (1959), Smith and Fernando (1978), Dussart (1985), De Melo and Hebert (1994), and Hebert (1995). Rotifers were identified to genus for monogonont rotifers and to class for bdelloid rotifers. All rotifers were identified using Edmondson (1959) and Stemberger (1979). Given that we used 75-μm mesh to sample the zooplankton community, we are only considering the subset of the rotifer community >75 μm in size.

Lake/pond surface area and proximity to other lakes/ponds were assessed using ArcGIS 9.3. Lakes/ponds were derived from cloud-free Landsat 7 imagery from August 2001.

CANONICAL CORRESPONDENCE ANALYSIS

A multivariate ordination technique, canonical correspondence analyses (CCA), was used to determine if zooplankton taxonomic composition was related to environmental variables. First, unidentified monogonont and all insect/arachnid/cnidarian taxa were removed. Second, extremely rare species were removed (<5% occurrence) as they can have a disproportionate effect on ordination results (Quinn and Keough, 2002). Exceptions were made for *Bosmina freyi,* which was lumped with *Bosmina liederi* to create the new taxon *Bosmina* spp., and for *Ilyocryptus acutifrons*, which was lumped with *Ilyocryptus sordidus* to make *Ilyocryptus* spp. Zooplankton relative abundances were Hellinger-transformed to reduce the influence of rare species, and zeros that are common in community data (Legendre and Gallagher, 2001). A CCA was appropriate because gradient lengths were long (>3) (ter Braak and Šmilauer, 1998). Correlations between environmental variables were investigated using variation inflation factors (VIFs). The ion-related data were highly correlated, so a principal component analysis (PCA) was completed using a correlation matrix of altitude, DIC, alkalinity, calcium, log(magnesium), log(specific conductivity), log(sulfate), log(silicate), log(potassium), log(sodium), and log(chloride). The first principal component of this PCA explained 90.3% of the variation in ion-related data between lakes/ponds and was used as an environmental variable for future analyses. After completing the PCA, all VIFs were <10, therefore all variables were retained (Quinn and Keough, 2002). The environmental variables, transformed where desirable to improve normality, included log(TN), log(TP), log(Area), log(Chl), log(DOC), temperature, pH, and the first principal component axis of the ion PCA. Unfortunately, we have limited information on predators in the lakes/ponds. Two of the largest lakes (Mary and Lee Lakes) have fish based on reports of fishing; however, the majority of the survey ponds are likely fishless because they freeze to the bottom in winter, owing to their shallow depth. Environmental variables were forward-selected using Monte Carlo permutation tests at $p < 0.05$ with 999 iterations. After variables were selected, Monte Carlo permutation tests were used to determine the significance of constrained axes. The DCA was completed using CANOCO 4.5 (ter Braak and Šmilauer, 2002), and the CCA was completed using R (R Development Core Team, 2012).

VARIATION PARTITIONING OF ENVIRONMENTAL AND SPATIAL VARIABLES

To assess the relative contribution of local environmental conditions and the spatial arrangement of lakes/ponds in the landscape to determining zooplankton community structure, we used a combination of spatial modeling and multivariate ordinations. Spatial modeling of study lakes/ponds was conducted using Moran's eigenvector maps as outlined by Dray et al. (2006). The spatial arrangement of lakes/ponds on the landscape was modeled using four different connection schemes to create connectivity matrices—Delauney triangulation, Gabriel graphs, relative neighbor graphs, and sphere of influence graphs (Dray et al., 2006). Each of these frameworks determines the proximity of lakes/ponds to each other and expresses these distances in a pairwise connectivity matrix. For each framework, the Hadamard product of each connectivity matrix by a variety of spatial weighting matrices (linear = $1 - d_{ij}/d_{max}$, concave down = $1 - d_{ija}^{y}/d_{maxa}^{y}$, and concave up = $1/d_{ijb}^{y}$, for y = 1:20) was calculated to determine the potential spatial weighting matrices, and the model with the lowest Akaike information criterion (AIC) from this set was selected as the best. We then reran the AIC selection process to identify variables to be retained in the model after we had removed all eigenvectors not correlated with Moran's *I,* as these likely do not show spatial structure (Dray et al., 2006). The generation of the spatial predictors was performed using the R packages spdep (Bivand et al., 2012), spacemakeR (Dray, 2010), and their associated packages (R Development Core Team, 2012).

The environmental variables and zooplankton community composition data used in the ordinations for the variance partitioning analyses were the same as the CCA.

Variance partitioning was performed on the zooplankton community composition at different spatial scales within the park. As we felt that rotifers, cladocerans, and copepods were all likely to experience different spatial and environmental regimes, we performed three separate variance partitions, one for each group. Variance partitioning was performed in R using the varpart function of the package vegan in R (Oksanen et al., 2012; R Development Core Team, 2012). This function uses the species, environment, and spatial matrices for redundancy analyses (RDAs) and partial RDAs to calculate R^2_{adj} values that represent the independent and shared variance explained by environment and space. A CCA-based variation partitioning method would be more optimal for our data due to long gradient lengths; however, there are no methods to calculate the adjusted R^2 values for CCA-based variation partitioning (Oksanen et al., 2012).

ANALYSIS OF SPECIES CO-OCCURRENCE PATTERNS

To determine if biotic interactions are important in structuring local community composition, we completed a co-occurrence analysis that determines if there are negative (i.e., segregations) or positive (i.e., aggregations) species associations using the program EcoSim v. 7.0 (Gotelli and Entsminger, 2009). Species data were organized as a presence-absence matrix, where each row was a different species and each column was a different site. This analysis was completed for the total zooplankton community and the rotifers, cladocerans, and copepods separately. The C-score (Stone and Roberts, 1990) was used as an overall measure of species co-occurrence, as it quantifies the average number of checkerboard units (CU) between each species pair. A checkerboard is a submatrix of the form:

$$\begin{bmatrix} 10 \\ 01 \end{bmatrix} or \begin{bmatrix} 01 \\ 10 \end{bmatrix}$$

Therefore, a checkerboard unit represents an instance of negative co-occurrence between two species. To compare between the four different analyses (total zooplankton, rotifers, cladocerans, copepods), the C-score was standardized to account for differences in matrix dimensions. The standardized effect size (SES) = (observed index – mean of simulated indices)/standard deviation of simulated indices. Negative SES values represent positive species co-occurrences, or aggregations, and positive values represent negative species co-occurrences, or segregations (Stone and Roberts, 1990).

To determine the significance of the observed C-scores, Monte Carlo randomizations of community presence-absence data were used to create "pseudo-communities." We used fixed-fixed constraints on the randomized matrices—i.e., row and column constraints that maintain row sums (number of occurrences of each species in the data set remains the same) and column sums (number of species in each site remains the same). This reduces the chance of Type I error (Gotelli and Entsminger, 2009) and is well suited to data recorded across heterogeneous environments (Rooney, 2008). The randomization occurred using an independent swap algorithm in which the original data matrix is shuffled by swapping random checkerboard submatrices after discarding the first 50,000 swaps. C-scores were calculated after 5000 randomized matrices were generated. The average C-score of the simulated matrices is included in the calculation of SES. All SES that are >1.96 or ≤1.96 are significant at $p < 0.05$ and suggest that negative or positive associations are different from potential random patterns (Gotelli and Entsminger, 2009).

DETECTING PROCESSES UNDERLYING SPECIES CO-OCCURRENCE PATTERNS

Ulrich and Gotelli (2013) showed that when there are multiple patterns in the matrices (i.e., both aggregations and segregations) the results of co-occurrence analyses can be misleading. To correctly determine the co-occurrence patterns, they suggest looking at the species pairs that have the highest CU to determine if they are segregating or aggregating (Ulrich and Gotelli, 2013). We looked at the top 2 percent of species pairs with the greatest absolute value of average CUs to determine their co-occurrence patterns (Appendix Fig. A1). Additionally, negative co-occurrence patterns can result from either species interactions or environmental heterogeneity, where species respond in dissimilar ways to underlying environmental variables. To determine the role of environment in structuring the negative species co-occurrences, we looked at the species pairs with the greatest absolute value of average CUs. The relative abundance of each species was plotted against the environmental gradient that they segregated along in the CCA (Appendix Fig. A1).

Results

Lakes and ponds were situated across costal fen, interior peatland, and spruce forest (Fig. 1). Among the 92 lakes/ponds the geographical and environmental conditions varied considerably (Table 1).

A total of 79 taxa were identified from the lakes and ponds in Wapusk National Park (Appendix Tables A1–A3). The most frequently found taxa were *Conochilus* spp. *Daphnia tenebrosa*, *Heterocope septentrionalis*, and *Leptodiaptomus minutus.* The frequency of occurrence for all taxa ranged from 1% to 77%, with an average of 22%. Richness was highest in rotifers and lower in cladoceran and copepod taxa (Fig. 2). Shannon-Weiner diversity was low, ranging from 0.06 to 1.02 with a mean diversity of 0.5 (Fig. 2). Presence/absence data for each lake/pond can be found in Appendix Table A4.

CCA allowed examination of the relationship between lake/pond environmental measures and variation in zooplankton community composition. The first and second axes represent 9.4% and 5.3% of the variation in zooplankton composition, respectively, and were both significant at $p < 0.05$. The significant environmental variables were lake area and chlorophyll *a*, which were mainly associated with axis 1, and pH, ionic composition, and TP, which were associated with axis 2 (Fig. 3). Lakes/ponds located with the three different habitats were separated along axis 1 (ANOVA, $F = 17.5$, $p < 0.001$), with lakes/ponds in the spruce forest region having low axis 1 scores, lakes/ponds in the coastal fen having high axis 1 scores, and lakes/ponds in the interior peatland being evenly distributed across the axis (Fig. 3). The spruce forest lakes/ponds have the lowest axis 1 scores (Tukey honest significant difference [HSD]: spruce forest – coastal fen, $p < 0.001$; spruce forest – interior peatland, $p = 0.003$) associated with large area, high chlorophyll *a* values, and species composition dominated by *Keratella* spp. *Diaptomus nudus* and *Eucyclops serrulatus* (Figs. 3 and 4). Lakes/ponds in the interior peatland region had intermediate axis 1 scores (Tukey HSD: interior peatland – coastal fen, $p = 0.04$; Fig. 3). Finally, the coastal fen lakes/ponds had the highest axis 1 scores associated with small area and low chlorophyll *a* values, dominated by the rotifers *Trichocerca* spp., *Kellicottia* spp., *Synchaeta* spp., and *Notholca* spp. and by harpacticoid copepods (Fig. 4).

Variation partitioning analysis revealed that spatial variables consistently explained more independent variation than environmental variables (Fig. 5 and Table 2). The environmental variables in this study explain less variation in zooplankton community composition than other studies of zooplankton distribution (Fig. 5). When investigating smaller spatial scales (coastal fen, interior peatland, and spruce forest) the independent effect of environment was rarely significantly different from 0, yet the independent effect of spatial variables was often significant (Table 2).

The co-occurrence analysis showed that there were significant negative co-occurrence patterns, or segregations, between zooplankton taxa. The standardized effect size of the co-occurrence analysis was highest in the rotifer assemblage (19.7) and lower in the cladoceran (6.3) and copepod (4.6) assemblages (Fig. 6). Most of the species pairs that had the greatest absolute value of checkerboard units (i.e., contributed the most to the standardized effect size) showed patterns of segregation and did not appear to be responding differentially to environmental gradients (Appendix Fig. A1).

Discussion

The zooplankton communities of Wapusk National Park show comparable crustacean zooplankton diversity to other Subarctic/Arctic ponds at similar latitudes (Hebert and Hann, 1986). The number of crustacean zooplankton taxa we identified (42) represents an increase from the 25 taxa Hebert and Hann (1986) reported in Churchill. This increase is likely due to the larger spatial scale and increased diversity of habitats sampled. The water chemistry of the lakes/ponds (pH, conductivity, TP,

TABLE 1

Median and range of physical and environmental variables from the 92 lakes/ponds sampled.

	Median	Range
Altitude (m)	43	0–86
Surface area (ha)	4.0	0.05–945
Temperature (°C)	17.0	13.2–24.5
pH	7.8	4.3–8.6
Conductivity (µS cm^{-1})	142.5	20–1020
TP (µg L^{-1})	20	8.2–149
TN (µg L^{-1})	976	573–2900
DOC (mg L^{-1})	14.8	6.1–51
Oxygen (mg L^{-1})	9.3	6.7–10.5
Chlorophyll-*a* (µg L^{-1})	4.6	0.7–37.5

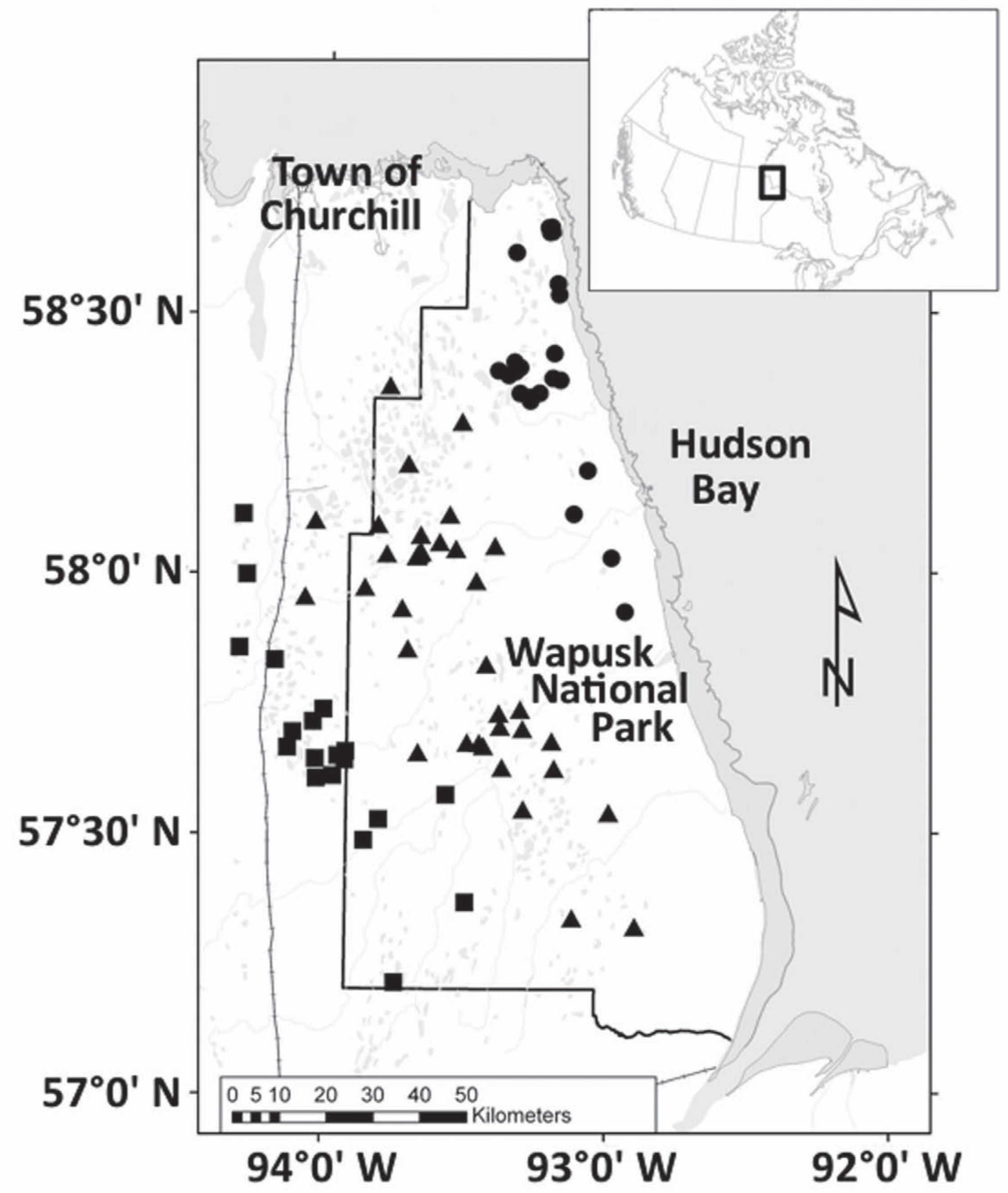

FIGURE 1. Map of the study area, Wapusk National Park. Squares represent lakes/ponds in the spruce forest region, triangles represent lakes/ponds in the interior peatland region and circles represent lakes/ponds in the coastal fen region.

TN, DOC) is within the range found in other shallow ponds in the Arctic, whereas the chlorophyll *a* concentrations were greater than most arctic sites (Rautio et al., 2011). The environmental gradients in the park are large, representing a shift from coastal habitat to inland boreal forest. While the data we collected and gradients we sampled were similar to or greater than those in other systems, where environment was able to explain large amounts of variation in zooplankton community composition (e.g., Rautio, 1998; Cottenie et al., 2001; Steiner, 2004; Strecker et al., 2008; Tavernini et al., 2009), our environmental variables explained relatively little of the variation in community composition.

Our initial goals involved determining the relative importance of environmental and spatial variables in structuring the zooplankton communities of Wapusk National Park. The three models that seemed most likely for our biota included dispersal limitation, species sorting, and mass effects. Of course, while it is possible that different species groups may not fit the same model (even in the same habitat) due to differing dispersal potential, we separated the three taxa in our analyses and found broadly similar results for all three. Species sorting entails a strong correlation between species composition and environmental conditions, and we found a small independent effect of environmental variables,

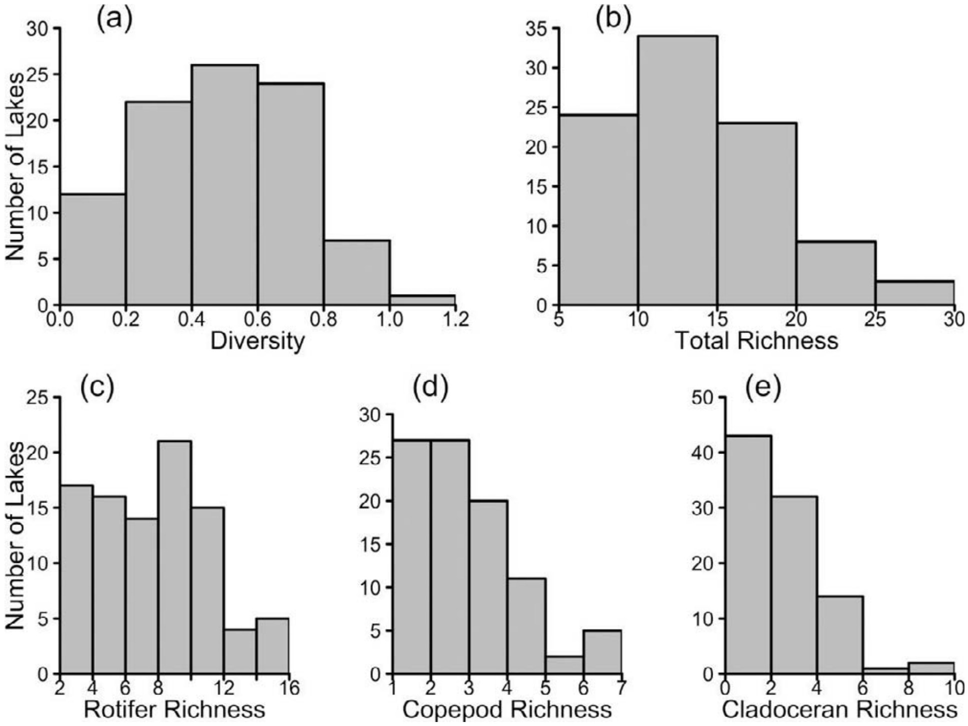

FIGURE 2. The distribution of (a) total community Shannon-Weiner diversity, (b) total richness, (c) rotifer genera richness, (d) copepod species richness, and (e) cladoceran species richness in the 92 lakes/ponds.

especially compared to other studies of zooplankton distribution (Fig. 5). The spatially structured environment component of variation (ES) was relatively large compared to other studies (Fig. 5) and is likely caused by environmental differences between the three spatially separate habitat types (Fig. 3); however, if we consider the most extreme possibility that the entire ES component is an environmental signal, the environmental variables still explain less variation than almost all similar published studies (Fig. 5). There is potential for unmeasured environmental variables that vary with habitat type to increase the importance of the spatial factors (Cottenie et al., 2003), though given the extensive number of environmental factors we sampled, the importance of unmeasured variables is likely low. For example, although there were no data on predators in our analyses, only

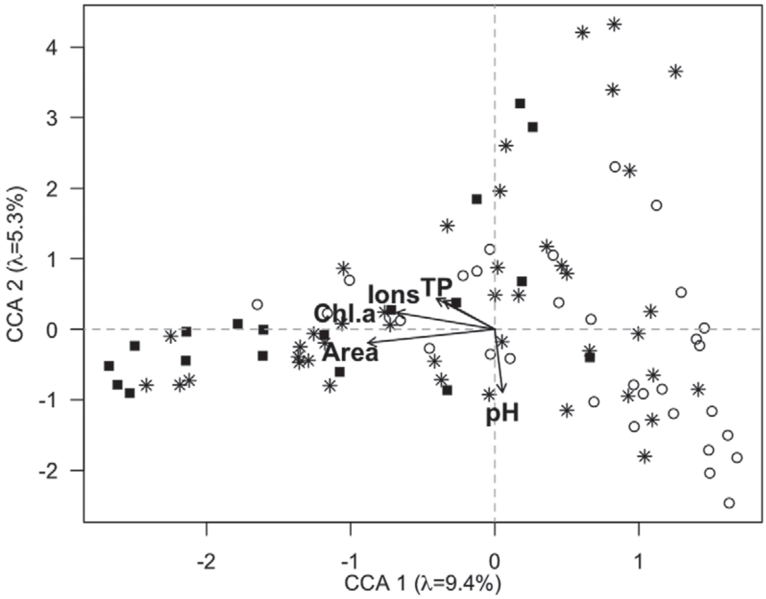

FIGURE 3. CCA biplot of site scores for the 92 ponds. λ represents the percentage of variation explained by each axis. Squares represent lakes/ponds in the spruce forest region, stars represent lakes/ponds in the interior peatland region, and open circles represent lakes/ponds in the coastal fen region.

TABLE 2

The results of variation partitioning analysis; y is the exponent selected for use in the spatial model equation, # Variables represents the number of spatial variables selected for inclusion in the final model, E|S represents the independent variation explained by environmental variables, ES represents the shared variation explained by both environmental and spatial variables, S|E represents the proportion of independent variation explained by spatial variables, and U represents the proportion of unexplained variation.

Region	Taxa	Spatial model	y	# Variables	E|S	ES	S|E	U
Whole Park	Rotifers	Delauney concave down	16	11	0.06*	0.14	0.10*	0.70
	Cladocerans	Gabriel concave down	20	9	0.06*	0.15	0.11*	0.65
	Copepods	Gabriel concave down	3	10	0.06*	0.07	0.25*	0.62
	Crustacean	RNG concave down	2	7	0.03*	0.10	0.16*	0.71
Coastal Fen	Rotifers	SIO concave down	4	4	0.19*	0.01	0.27*	0.52
	Cladocerans	Delauney concave down	2	5	0.07	–0.03	0.21*	0.75
	Copepods	Gabriel concave down	2	5	0.03	0.18	0.27*	0.52
Interior Peatland	Rotifers	Delauney concave down	6	5	0.05	0.15	0.12*	0.68
	Cladocerans	Gabriel concave down	20	4	0.03	0.17	0.06	0.71
	Copepods	SIO concave down	20	6	0.03	0.05	0.21*	0.71
Spruce forest	Rotifers	Delauney concave down	20	2	0.08	0.20	0.03	0.69
	Cladocerans	Delauney concave down	20	1	0.13	0.25	–0.06	0.68
	Copepods	Delauney concave up	1	2	0.04	0.28	–0.12	0.80

Note: significance at $P < 0.05$ is denoted as * for E|S and S|E based on the results of randomization tests. The significance of ES and U cannot be tested.

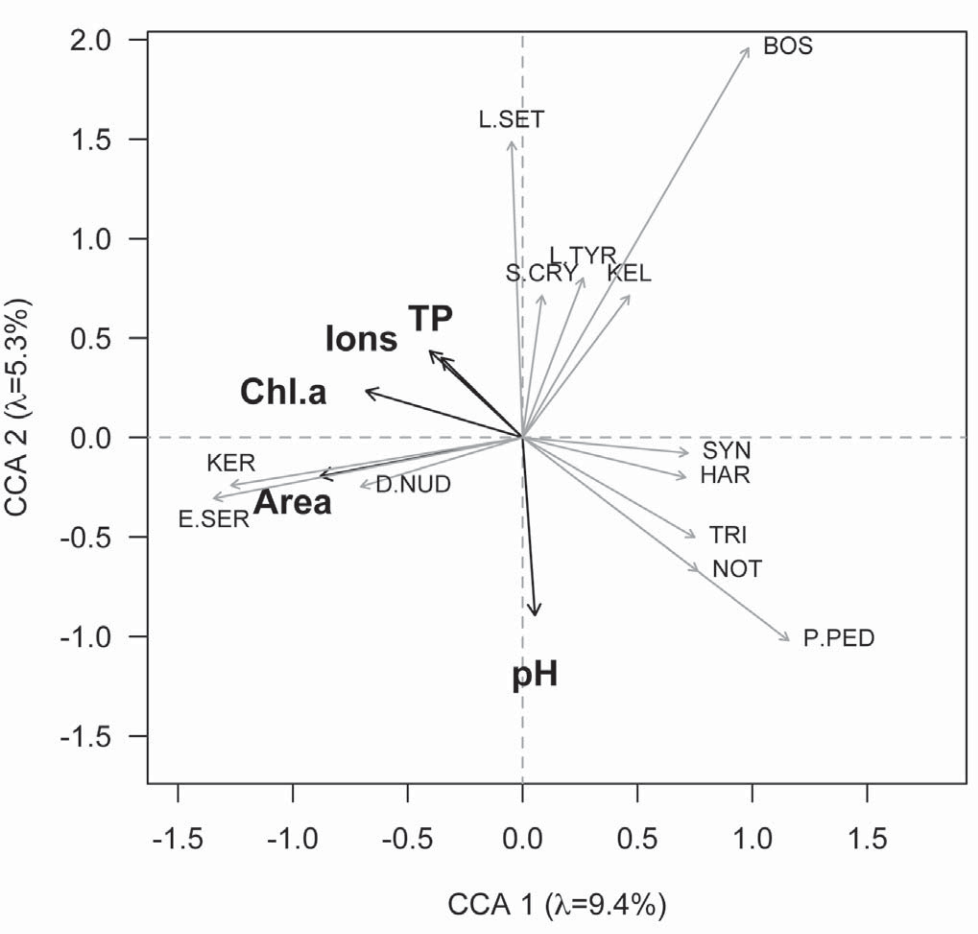

FIGURE 4. CCA biplot of species scores for the 92 lakes/ponds. λ represents the percentage of variation explained by each axis. Only species with scores > 0.7 were plotted for clarity. Abbreviations: L.SET: Latona setifera; L.TYR: Leptodiaptomus tyrelli; S.CRY: Sida crystalline; BOS: Bosmina spp.; KEL: Kellicottia spp.; SYN: Synchaeta spp.; HAR: Harpacticoid copepods; TRI: Trichocerca spp.; NOT: Nothlca spp.; P.PED: Polyphemus pediculus; E.SER: Eucyclops serrulatus; KER: Keratella spp.; D.NUD: Diaptomus nudus.

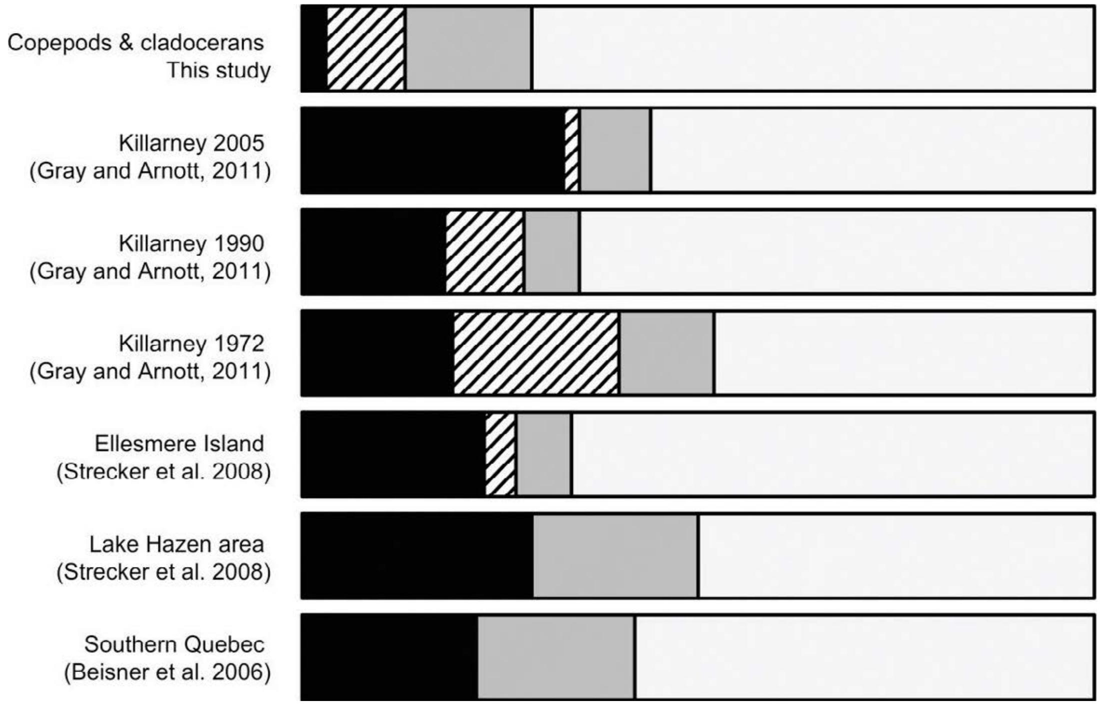

FIGURE 5. Results of variation partitioning analysis from studies of crustacean (i.e., copepod and cladoceran) zooplankton distribution. Black regions represent the independent effect of environment, the hatched regions represent the shared variation between environmental and spatial variables, the shaded regions represent the independent effect of spatial variables, and the white regions represent unexplained variation in community composition.

two of the lakes/ponds have known fish populations, therefore not having this data likely had minor impacts on the results. The independent spatial variables explained a large proportion of variation, suggesting that species sorting was not the sole mechanism occurring at the spatial scale we investigated. When considering the three regions separately, there is some evidence that the taxa are responding to environmental gradients due to high explanatory power of ES, but there is often a significant independent effect of space (Table 2).

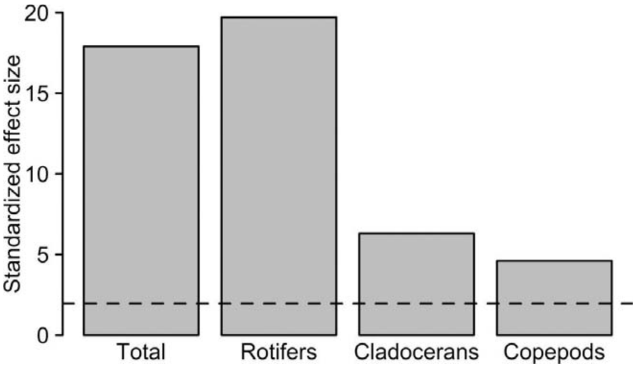

FIGURE 6. Results of co-occurrence analysis for different zooplankton taxa. Significant negative co-occurrence patterns are detected at standardized effect size values above 1.96 (dashed line) at $p < 0.05$.

Three metacommunity models that would involve a strong spatial signal are the “mass effects” metacommunity, where species are over-dispersed into habitats regardless of niche preferences; “neutral” metacommunities, where species are responding to dispersal constraints and stochastic competitive dynamics among equivalent species; and “dispersal limited” metacommunities, where species are unable to access ideal habitats due to dispersal constraints. Unfortunately, despite diametrically different causal mechanisms, these metacommunity models are notoriously difficult to distinguish in terms of pattern, and we have some evidence that argues in favor of each model. In support of the dispersal limitation paradigm, the amount of spatial variation explained decreased with the increasing ability for taxa to disperse (i.e., rotifers, with strong dispersal abilities [Caceres and Soluk, 2002], had spatial variation explaining less variance in composition than in the copepods, which are relatively weak dispersers [Frisch et al., 2012]). Furthermore, the negative co-occurrences among pairs of our species also support the hypothesis that the importance of space is due to dispersal limitation rather than true mass effects, as a mass effects scenario would suggest that species co-occur randomly. Conversely, other evidence suggests that mass effects are more likely than dispersal limitation. Most species had widespread distributions in the park, indicating that species likely have the potential to access all ponds. In addition, we also followed 23 ponds over three years (S. E. Arnott, unpublished data) and found that crustacean zooplankton species turnover averaged 28% per year, which is high compared to temperate lakes (Arnott et al., 1999) and suggests that dispersal (either through space or time via the egg bank) is high in Wapusk. In support of both the mass effects and the neutral model, the strong independent spatial signal could be evidence that environmental gradients are not providing strong selection against arriving species, although we acknowledge that this aspect of the models is difficult to assess in Wapusk because many of the environmental gradients were spatially structured. Perhaps the strongest argument in favor of a high dispersal interpretation of our data is the substantial evidence that zooplankton are capable of dispersing over large distances (De Meester et al., 2002), and the characteristics of our tundra-pond ecosystem (e.g., no trees, flat land, much wind, waterfowl, and ephemeral habitat) suggest that dispersal between lakes/ponds is high. Ultimately, however, we are unable to determine if the spatial signal we detected was due to low or high dispersal in this system; although, as we outline above, there seems to be more evidence for high dispersal. Recently, it has been argued that the models of mass effects, dispersal limitation, species sorting, and neutral dynamics fit on a continuum of dispersal and environmental heterogeneity, and it is difficult to categorize natural systems, as they often share characteristics with more than one paradigm (Logue et al., 2011; Winegardner et al., 2012). Furthermore, it is important to consider the interactions between the amount of dispersal, environmental gradients, and species interactions themselves.

Local interactions between species are also capable of having a strong effect on community composition (Diamond, 1975). Biotic resistance and/or priority effects have been extensively investigated experimentally (e.g., Shurin, 2000; Forrest and Arnott, 2006; Strecker and Arnott, 2010) and have a well-developed theoretical background (Steiner and Leibold, 2004). At the landscape level one way to determine if priority effects or local species interactions are important to community structure is to determine species co-occurrence patterns (Conner and Simberloff, 1979). Negative co-occurrence patterns are expected when species interactions or priority effects are excluding additional species from colonizing a habitat patch. As we found strong negative co-occurrence patterns for all three species groups across the landscape there is reason to expect that priority effects may be important in Wapusk. Conversely, a meta-analysis by Gotelli and McCabe (2002) showed that most biological communities show patterns of negative co-occurrence, however, these patterns may not necessarily be driven by competition, but rather by species responding differently to environmental gradients across the sampling scale. In our study, the species pairs that had the highest negative co-occurrence values (checkerboard units, CUs) were not separated along important environmental gradients, suggesting that different environmental tolerances were not driving the negative co-occurrence patterns and that other ecological processes (e.g., priority effects) were more important in causing the negative co-occurrences, as would be predicted by the neutral model. Indeed, neighboring lakes/ponds with similar chemistry in Wapusk have negatively co-occurring species pairs, indicating that we may even be seeing alternate stable equilibria. Finally, priority effects are expected to be particularly important in smaller habitats (e.g., ponds), as the populations are able to rapidly monopolize the location (Steiner and Leibold, 2004), and when the biota involved reproduce quickly and have the ability to rapidly colonize a space, for example, via a standing egg bank (De Meester et al., 2002). Altogether, these factors suggest that biotic interactions may play an important role in structuring communities, though experimental methods and temporal data will likely be needed to evaluate the importance of priority effects and dispersal in this system.

Overall, the three different habitat types had a large effect on zooplankton community composition, yet there were strong negative species co-occurrences suggesting that species interactions and priority effects may be important in determining species composition in this pond ecosystem. Given that we believe the system to have high levels of dispersal, we expect that zooplankton should be able to track changing environmental conditions. If the cover of coastal fen, interior peatland, and spruce forest habitats is affected by climate change, then this will likely have large implications for the distribution and abundance of aquatic taxa in Wapusk National Park.

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APPENDIX

TABLE A1

Physical data from each lake. All lakes are located in UTM zone 15N. Habitats are coded as CF for coastal fen, IP for interior peatland, and SF for spruce forest.

Lake	Easting	Northing	Habitat	Alt (m)	Perimeter (m)	Area (m^2)
1	489218	6502398	CF	0	3220.68	448,509.14
2	488726	6502263	CF	6	6647.96	1,206,627.8
3	489097	6503372	CF	4	2664.56	162,948.55
4	488462	6503260	CF	9	455.06	10,430.01
5	481559	6497967	CF	11	507.41	15,826.97
6	490643	6488917	CF	3	1508.28	30,464.25
7	496689	6451236	CF	15	3977.64	803,000.39
8	493727	6441921	CF	17	245.99	4041.24
9	504618	6420985	CF	14	1111.45	75,326.77
10	454550	6469608	IP	38	4428.87	678,638.24
11	458428	6452824	IP	51	13,494.42	7,355,228.88
12	438575	6440855	IP	64	1253	109,442.13
13	436298	6424606	IP	69	2801.5	369,129.12
14	423870	6429298	SF	68	3135.07	438,413.61
15	477668	6472606	CF	29	6992.3	2,414,081.66
16	481106	6474501	CF	22	593.59	15,575.21
17	482285	6473296	CF	23	2631.72	318,346.02
18	489283	6470994	CF	18	640.42	18,845.72
19	490864	6470594	CF	13	2936.17	515,929.4
20	486429	6467801	CF	22	690.72	30,700.97
21	479834	6471644	CF	22	590.22	22,533.26
22	481327	6472476	CF	20	971.39	66,329.61
23	469949	6461797	IP	42	443.17	10,741.46
24	451967	6439899	IP	55	627.02	13,563.55
25	453780	6433630	IP	50	668.97	28,599.89
26	461017	6437587	IP	44	4494.8	1,237,986.92
27	467253	6441917	IP	43	1300.63	92,662.47
28	465081	6436022	IP	41	433.95	12,263.25
29	468544	6434580	IP	38	416.55	8374.52
30	476864	6435204	IP	31	1240.24	36,890.46
31	472843	6427697	IP	40	101.37	660.6
32	456995	6421990	IP	55	846.73	47,197.17
33	449094	6426517	IP	57	1771.95	82,968.02
34	455114	6341869	SF	78	1814.41	173,273.53
35	448659	6372359	SF	72	4501.71	1,471,167.02
36	451852	6376829	SF	73	834.39	42,793.17
37	470271	6358883	SF	63	968.16	36,832.31
38	493131	6355549	IP	58	7676.04	1,561,813.1
39	506506	6353689	IP	35	500.31	14,844.78
40	501004	6378089	IP	33	545.08	12,253.51
41	482693	6378858	IP	59	4116.22	1,084,388.62

TABLE A1

Continued.

Lake	Easting	Northing	Habitat	Alt (m)	Perimeter (m)	Area (m^2)
42	460277	6391157	IP	62	4017.11	522,227.27
43	458196	6413330	IP	53	4157.5	398,439.25
44	444888	6391360	SF	72	347.26	7744.64
45	443143	6390456	SF	72	175.87	2188.7
46	444628	6389566	SF	80	601.56	17,630.79
47	442080	6386174	SF	78	4135.21	1,095,172.02
48	438542	6385706	SF	81	10,675.26	3,387,405.74
49	438369	6389876	SF	80	14,407.83	4,018,213.3
50	432428	6392270	SF	86	3935.27	693,671.61
51	433562	6395582	SF	81	1760.25	149,032.51
52	488859	6393433	IP	38	683.5	27,149.88
53	489335	6387584	IP	45	1588.32	177,997.73
54	478186	6387802	IP	49	3960.15	995,816.87
55	470756	6393183	IP	52	3543.77	457,533.27
56	473348	6393093	IP	52	161.07	1286.43
57	474243	6392437	IP	46	506.73	17,467.6
58	477847	6396616	IP	46	1055.3	57,455.51
59	477552	6399426	IP	44	373.09	9564.11
60	482649	6396065	IP	39	937.48	53,445.71
61	482143	6400193	IP	37	5744.59	2,104,963.15
62	474941	6409928	IP	44	6764.67	1,980,167.66
63	501740	6432529	CF	15	174.78	1980.16
64	466223	6381964	SF	57	504.19	13,853.08
65	437937	6397823	SF	79	6949.84	2,299,763.9
66	440175	6400434	SF	79	190.78	2664.79
67	429812	6411004	SF	80	4314.58	984,468.1
68	422247	6413705	SF	80	4117.54	851,507.64
69	423142	6442181	SF	64	980.68	63,525.54
70	461061	6433956	IP	47	1373.8	124,068.02
71	461126	6433953	IP	45	96.68	504.58
72	461097	6433885	IP	48	101.97	612.14
73	460444	6433585	IP	44	302.17	4829.97
74	460501	6433501	IP	43	182.91	2353.1
75	460573	6433514	IP	41	271.05	4917.04
76	460575	6433487	IP	44	145.12	1299.57
77	460113	6433030	IP	43	551.01	12,237.58
78	460211	6433048	IP	42	497.61	11,901.19
79	460287	6432961	IP	46	269.53	5266.75
80	484367	6466246	CF	31	1117.19	70,052.8
81	484437	6466279	CF	24	980.98	49,856.12
82	484444	6466143	CF	25	711.32	29,903.75
83	484371	6466807	CF	24	198	2309.82

TABLE A1

Continued.

Lake	Easting	Northing	Habitat	Alt (m)	Perimeter (m)	Area (m^2)
84	484430	6466768	CF	24	1024.35	21,129.48
85	484514	6466843	CF	23	122.81	1055.72
86	484309	6466742	CF	24	119.93	918.21
87	484304	6466836	CF	22	293.07	3603.9
88	484310	6466953	CF	26	1191.41	48,713.3
89	484150	6466928	CF	24	347.05	8145.8
90	482267	6467768	CF	28	16,906.63	9,450,315.48
91	489595	6476288	CF	13	592.49	16,948.2
92	490368	6491245	CF	3	822.81	24,736.5

TABLE A2

Chemical data from each lake, including: pH, conductivity (Cond, µS cm^{-1}), total nitrogen (TN, mg L^{-1}), total phosphorus (TP, mg L^{-1}), temperature (Temp, C), dissolved oxygen (DO, mg L^{-1}), alkalinity (Alk, mg L^{-1}), chloride (Cl, mg L^{-1}), sulfate (SO_4, mg L^{-1}), dissolved organic carbon (DOC, mg L^{-1}), dissolved inorganic carbon (DIC, mg L^{-1}), calcium (Ca, mg L^{-1}), magnesium (Mg, mg L^{-1}), potassium (K, mg L^{-1}), sodium (Na, mg L^{-1}), and silica (SiO_2, mg L^{-1}).

Lake	pH	Cond	TN	TP	Temp	DO	Alk	Cl	SO_4	DOC	DIC	Ca	Mg	K	Na	SiO_2
1	7.86	888	0.877	0.0223	15.03	10.34	117	190	25.8	6.3	26.4	27.6	16.9	9.55	118	0.28
2	7.74	195	0.816	0.0193	21.6	9.38	68.5	17.9	1.28	6.9	15.6	22.4	4.01	1.11	9.47	0.57
3	8.05	308	0.607	0.0103	19.87	9.07	94.5	38.2	3.51	6.8	21.4	26.2	8.26	2.25	22.6	2.15
4	7.72	237	1.22	0.0207	20.36	9.09	91.4	19.3	0.69	9.1	20.5	29.5	4.91	1.14	10.6	1.75
5	8.19	341	1.54	0.0147	22.56	7.93	133	27.6	4.93	13.6	29.2	39.9	9.51	1.78	16.8	0.61
6	7.97	360	1.16	0.0258	21.34	9.89	95.3	47.8	11.3	8.6	21.3	32.1	6.98	2.43	27.3	1.11
7	7.94	325	1.3	0.0224	23.42	8.47	109	34	3.54	11.2	24.1	35.9	6.59	1.67	20	0.15
8	7.9	286	1.7	0.0229	24.48	7.88	111	20	4.84	20.3	24.6	43	4.71	0.88	9.97	2.22
9	8.27	265	1.02	0.017	23.64	8.03	122	9.83	3.75	13.9	27.3	42.6	5.21	0.86	5.33	0.41
10	7.6	109	0.938	0.0137	21.11	8.14	50.5	3.01	0.76	6.1	11.3	12.5	4.68	0.66	1.96	0.14
11	7.59	137	1.31	0.0302	20.2	8.43	62.8	4.09	1.32	9.5	14.1	16.8	5.32	0.76	2.78	0.12
12	6.96	56.4	2.3	0.0335	21.24	7.58	17.3	3.77	0.11	19.9	3.6	5.48	1.69	0.57	2.45	3.13
13	6.28	28.1	1.35	0.0519	21.29	8.04	5.96	2.71	0.15	16.2	0.7	2.85	0.87	0.58	1.68	1.3
14	6.73	66.1	1.53	0.055	21.47	7.58	13.9	9.22	0.87	13.2	0.9	4.19	1.3	0.75	6.74	0.37
15	7.82	196	0.687	0.0196	16.97	9.8	73.5	15.8	1.69	7.3	16.2	23	4.35	0.93	9.02	0.59
16	7.92	314	1.21	0.0197	16.26	10.35	94.7	38.1	2.8	12.5	21.3	32	7.22	1.33	18.4	1.73
17	7.79	148	0.775	0.0229	17.37	9.48	67.4	4.78	0.97	6.7	15.2	20.9	3.82	0.7	2.77	0.22
18	8.14	290	0.736	0.0185	16.21	9.97	132	14	1.7	8.9	31.6	38.5	8.79	1.02	8.18	1.33
19	8.23	398	0.947	0.0222	15.91	9.74	131	46.8	2.43	10.7	29.8	34.4	6.84	2.09	36.9	0.31
20	8.14	730	1.85	0.0237	15.57	10.06	139	143	5.18	17.2	31.3	58.4	9.75	2.14	69	1.13
21	8.16	384	1.21	0.0177	15.67	9.88	124	46.2	2.66	13.6	28.1	43.4	7.67	1.32	21.1	0.92
22	8.08	255	0.84	0.0123	16.59	9.36	103	18.3	0.92	10	23.4	31.3	6.31	0.76	10	1.41
23	7.91	170	0.69	0.0106	14.4	8.99	77.7	4.81	0.97	12.7	17.5	25.1	4.28	0.62	3.13	0.9
24	6.73	50	1.87	0.057	13.26	9.74	14.4	4.34	0.31	14	2.9	5.08	1.16	0.79	2.81	0.41

TABLE A2

Continued.

Lake	pH	Cond	TN	TP	Temp	DO	Alk	Cl	SO_4	DOC	DIC	Ca	Mg	K	Na	SiO_2
25	7.9	228	0.959	0.0153	13.89	9.57	75.4	24	2.99	17.6	16.5	17.8	9.2	0.91	14.6	1.36
26	8.15	230	0.864	0.017	15.37	10.13	105	8.6	2.5	11.9	24	31.1	7.1	1.03	5.63	0.59
27	8.16	242	1.26	0.012	15.45	10.23	109	9.27	3.83	14.6	24.5	35.8	6.3	0.98	4.86	0.33
28	8.13	251	1.38	0.0165	15.86	10.12	110	11.2	2.03	18.3	25.7	34.6	7.36	0.96	6.08	1.61
29	7.87	157	1.47	0.0082	16.22	9.42	53.8	13.2	0.27	14.8	12.4	20.3	2.94	0.77	5.86	0.46
30	6.75	47.8	1.04	0.0155	16.86	10.05	7.94	7.06	0.07	17.6	1.7	3.58	0.9	0.53	4.28	0.4
31	5.01	56.3	1.9	0.0263	20.52	8.5	2.79	9.76	0.15	39.3	0.7	3.31	1.33	0.35	4.97	0.22
32	7.32	68.9	1.25	0.0271	16.87	9.05	24.8	4.45	0.04	15.1	5.5	7.94	2.23	0.57	2.75	0.41
33	7.18	58.6	1.22	0.0494	16.85	8.62	16.3	4.06	0.36	20.6	3.8	5.91	2.13	0.89	3.07	1.45
34	7.55	80.7	0.677	0.0232	17.13	9.23	36.9	1.12	0.39	14.6	8.3	11.9	2.93	0.55	1.11	0.97
35	7.89	124	0.573	0.0154	16.31	9.58	61.5	1.25	0.59	10.1	14	18.3	4.17	0.81	1.15	0.47
36	5.62	26.6	1.33	0.0754	16.5	8.2	3.02	2.81	0.3	22.8	0.6	2.4	0.56	0.33	2.12	0.32
37	6.97	38.1	1.01	0.0517	16.27	8.98	11.3	2.47	0.09	19.8	2.2	4.92	0.95	0.65	2	1.43
38	7.73	161	1.17	0.0367	16.58	9.14	60	12.2	1.04	10.5	13.6	17.5	4.68	0.79	6.51	0.77
39	7.79	189	0.893	0.0162	16.42	9.84	56.4	21.1	1.79	19	12.6	19.9	4.27	0.78	11.3	1.28
40	7.89	223	1.1	0.0186	18.24	9.34	67.4	25.7	1.77	15	15.6	22.6	5.21	0.91	13.4	1.66
41	7.77	143	1.02	0.0222	17.36	9.74	62.9	5.61	0.38	12.6	14.3	18.1	4.68	0.68	3.52	0.47
42	7.44	59.3	0.68	0.019	17.05	9.23	23.2	2.19	0.19	12.3	5.4	6.68	2.44	0.57	1.62	0.46
43	7.29	74.9	1.61	0.0344	17.95	9.46	23.5	5.31	0.69	21.9	5	8.11	2.79	0.61	3.21	0.7
44	5.49	23.8	0.876	0.149	16.35	7.57	2.72	2.17	0.56	18.3	0.8	2.02	0.43	0.84	1.67	0.63
45	7.49	82.8	0.852	0.0191	16.49	7.88	36.5	1.56	0.15	22.4	7.8	12.2	3.02	0.47	1.52	1.79
46	5.3	20	0.705	0.0262	16.12	7.9	1.57	1.7	0.23	18.9	0.5	2.01	0.49	0.47	1.17	0.36
47	7.51	79.3	0.771	0.035	16.39	10.46	34	2.88	0.49	7.9	7.5	9.51	2.43	0.73	2.56	0.91
48	7.67	94	0.634	0.0147	17.13	9.2	36.5	4.72	0.39	13.3	8	11.6	3.04	0.54	2.69	0.83
49	7.8	121	0.958	0.0257	17.48	10.24	50.2	5.92	0.5	8.4	11.2	13.6	4.06	0.68	3.97	0.57
50	7.67	80.2	0.591	0.0131	17.51	8.39	35.6	1.62	0.68	9.9	7.9	10.9	2.72	0.62	1.23	0.34
51	7.4	75.1	0.678	0.023	18.16	9.17	23.5	6.12	0.39	15.3	5.1	8.63	2.72	0.24	2.47	0.96
52	7.31	71.6	1.44	0.0247	13.21	9.71	21.4	5.45	0.22	20.8	4.6	8.64	1.77	0.39	3.3	1.19
53	8.03	163	0.7	0.0148	15.03	8.9	74.4	4.6	0.39	51	16.6	24	4.61	0.3	2.81	0.83
54	8.07	200	0.909	0.0203	15.46	9.18	81.2	12.4	0.55	47	18.1	24.5	6.19	0.53	6.63	0.63
55	7.94	141	0.875	0.0204	14.25	9.86	64.9	2.51	2.07	17.4	14.5	19.4	5.23	0.35	1.78	0.31
56	4.69	32.9	1.35	0.0286	14.25	9.4	0.17	4.54	0.23	46.9	0.7	1.5	0.71	0.09	2.46	0.08
57	7.71	181	0.745	0.0111	15.46	9.54	44.3	25	1.1	25	9.7	16.5	4.57	0.54	13.3	0.66
58	6.38	28.5	0.877	0.0324	15.68	8.5	4.23	2.9	0.08	17.4	1	2.39	0.59	0.14	1.74	0.42
59	7.98	142	0.915	0.0133	15.83	10.02	60.5	6.16	0.12	15.2	13.2	20.9	3.21	0.23	3.37	1.6
60	8.29	231	0.874	0.0095	18.66	9.75	95.6	11.8	8.07	14.7	19.4	32.4	5.82	0.42	6.05	1.3

TABLE A2

Continued.

Lake	pH	Cond	TN	TP	Temp	DO	Alk	Cl	SO_4	DOC	DIC	Ca	Mg	K	Na	SiO_2
61	8.08	205	1.06	0.0287	17.33	10.26	96.1	5.57	1.56	11	21.6	30.7	5.89	0.32	3.45	0.12
62	8.06	156	0.922	0.0282	16.39	10.3	75.6	2.48	0.18	10.4	17.6	20.5	6.42	0.26	1.52	0.24
63	8.45	1020	1.45	0.02	14.36	9.23	148	224	12.9	21.4	31.9	51.3	18.4	3.45	128	1.29
64	7.22	100	1.5	0.0194	16.81	8.52	14.8	16.1	0.07	21.7	4.1	6.36	2.47	0.47	7.95	0.53
65	7.8	114	0.75	0.0156	17.63	9.52	42.7	6.67	1.8	11.8	9.8	13.6	3.96	0.35	2.92	0.3
66	4.36	35.8	0.971	0.0283	18.44	8.81	–2.11	2.65	0.78	27.9	1	0.98	0.56	0.24	1.61	0.09
67	7.75	118	0.635	0.0208	19.5	9.14	53.3	2.78	2.15	10	11.8	16	3.93	0.32	2.43	0.18
68	7.6	111	0.848	0.0277	20.95	8.57	49.4	4.68	0.1	14	11.1	14.1	4.33	0.39	3.06	0.32
69	6.93	34.1	0.704	0.0206	17.9	8.96	12.6	1.64	0.04	14.1	3.3	3.84	1.5	0.18	1.03	0.4
70	7.72	135	0.985	0.0206	18.89	9.11	60.4	5.11	1.41	20	12.7	14.9	6.83	0.45	2.98	1.23
71	4.31	43.1	1.43	0.03	22.65	7.42	–1.98	4.17	0.76	34.9	1.2	0.7	0.76	0.3	2.47	0.03
72	4.35	43.5	1.51	0.0339	23.08	6.76	–1.68	4.17	1.11	31.6	1.1	0.57	0.82	0.46	2.46	0.05
73	6.52	34	0.98	0.0231	15.41	8.78	6.76	3.93	0.23	20.1	2.3	2.27	1.31	0.28	2.46	1.02
74	5.75	28.3	0.986	0.0276	15.94	9.33	3.21	3.81	0.18	20.4	1.6	1.56	1	0.09	2.28	0.19
75	7.27	67.8	1.05	0.0152	16.95	9.55	21.6	4.87	0.55	25.1	5.1	6.27	3.69	0.18	2.91	0.36
76	6.63	35.9	0.947	0.017	17.08	9.45	7.37	4.02	0.06	21.1	2	2.42	1.58	0.04	2.38	0.48
77	5.38	34.3	0.955	0.0219	15.42	9.37	2.87	5	0.04	27.6	1.2	1.76	1.18	0.14	2.77	0.09
78	6.33	55.2	1.44	0.0194	21.27	8.12	9.27	7.8	0.06	36.4	1.6	3.75	2.46	0.15	4.07	0.78
79	6.57	43	1.13	0.0185	17.96	9.25	8.3	5.05	0.06	27.6	1.9	3.15	2.1	0.05	2.78	0.39
80	8.16	247	0.769	0.0098	15.83	10.03	95.5	19.7	1.12	9.5	20.8	32	5.55	0.64	10.6	1.64
81	8.25	225	0.887	0.0147	17.13	9.8	91.5	15.2	1.15	9.9	20.1	30.1	5.43	0.33	8.5	0.58
82	8.21	245	0.742	0.0109	17.84	10.14	91.1	21.6	1.09	8.8	20.6	30.9	5.43	0.68	11.5	2.38
83	8.55	224	1.33	0.0152	20.15	9.69	98.3	12	1.24	19.6	20.7	35.3	5.21	0.24	6.89	1.19
84	8.22	228	1.36	0.0158	19.26	9.87	86.3	18.4	1.77	17.9	18.6	31.1	4.79	0.43	10.4	1
85	7.92	193	1.86	0.0163	21.75	8.81	69.9	16.5	0.32	24.4	15.8	26.9	4.02	0.13	8.98	1.26
86	8.04	174	2.9	0.0212	24.11	9.07	57.7	16.4	1.35	40.3	11.1	24.8	4.17	0.13	8.29	1.28
87	8.26	141	1.18	0.0202	19.6	9.96	56.8	7.76	0.81	15.2	12.1	19.8	2.8	0.47	4.48	0.87
88	8.36	237	0.667	0.0147	17.02	10.15	99.5	15	0.84	7.8	22.2	32.8	5.71	0.62	8.06	0.19
89	8.3	254	0.681	0.0163	17.43	9.96	109	15.2	0.88	7.7	23.6	36.2	5.89	0.65	8.11	0.28
90	7.97	188	0.964	0.0228	14.79	7.87	70.5	14.7	0.9	6.4	16.1	22.4	4.55	0.47	8.24	0.07
91	8.19	327	1.07	0.0152	14.37	8.39	104	39.8	0.52	11.8	22.9	36.2	6.36	1.09	21.3	0.16
92	8.3	540	0.742	0.0114	14.07	9.42	141	75.2	19.6	7.6	30.9	43.5	12.7	3.4	46.7	3.84

TABLE A3

Chlorophyll-*a* data from each lake.

Lake	Chl-*a* (μg L^{-1})	Lake	Chl-*a* (μg L^{-1})	Lake	Chl-*a* (μg L^{-1})
1	1.3	32	14.8	63	1.8
2	8.1	33	9.1	64	4.5
3	2.1	34	4.7	65	5.2
4	3.9	35	6.8	66	3.5
5	3.2	36	2.6	67	6.0
6	3.4	37	2.9	68	8.7
7	8.3	38	21.2	69	7.9
8	4.2	39	6.3	70	6.2
9	3.5	40	5.5	71	5.7
10	3.3	41	12.0	72	4.6
11	10.6	42	8.6	73	6.6
12	8.7	43	19.6	74	4.8
13	37.5	44	13.6	75	3.9
14	33.5	45	4.0	76	3.1
15	2.3	46	18.3	77	4.6
16	3.2	47	13.0	78	4.1
17	3.6	48	6.2	79	4.1
18	4.8	49	11.0	80	0.7
19	7.7	50	4.3	81	1.4
20	7.1	51	10.0	82	2.2
21	3.3	52	11.4	83	1.6
22	2.9	53	4.4	84	1.5
23	2.8	54	9.0	85	2.3
24	19.5	55	6.9	86	3.6
25	5.5	56	7.9	87	1.7
26	6.9	57	2.0	88	2.0
27	2.9	58	10.8	89	3.3
28	3.7	59	3.2	90	12.4
29	2.0	60	1.3	91	2.6
30	5.6	61	7.6	92	2.1
31	8.4	62	13.4		

TABLE A4

Presence/absence of taxa in each lake.

Lake	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Asplanchna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bdelloid	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	1	0	1	0	1	1
Brachionus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Cephalodella	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Collotheca	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	1	0	0	0	0
Colurella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conochilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conochilus	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
Dicranophorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dipluchlanis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eothinia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Epiphanes/Proales	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euchlanis	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1
Gastropus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Kellicottia	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0
Keratella	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	1
Lecane	0	0	1	1	1	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0
Lepadella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Macrochaetus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monostyla	1	1	0	1	0	1	1	1	0	1	1	1	0	0	1	1	0	1	0	1	1
Mytilina	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0
Notholca	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0
Platyias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ploesma	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1
Polyarthra	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Pleurotrocha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synchaeta	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	1
Testudinella	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Trichocerca	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Trichotria	1	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	1	0	1	1
Unidentified monogonont	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0

TABLE A4

Continued.

Lake	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Asplanchna	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0
Bdelloid	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	0	1	0	1	0	0
Brachionus	0	0	1	0	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0
Cephalodella	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Collotheca	1	1	1	1	1	1	0	0	1	0	1	0	1	1	0	0	1	1	1	1	0
Colurella	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Conochilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conochilus	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1
Dicranophorus	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dipluchlanis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eothinia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Epiphanes/ Proales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euchlanis	0	1	0	1	0	1	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0
Gastropus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Kellicottia	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1
Keratella	1	0	1	0	0	1	1	0	1	0	0	0	1	1	1	1	1	1	1	0	0
Lecane	1	1	1	0	0	0	1	1	0	1	1	0	0	1	1	0	0	1	1	0	0
Lepadella	0	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0
Macrochaetus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Monostyla	1	1	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0
Mytilina	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Notholca	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Platyias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ploesma	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Polyarthra	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	1	0	0
Pleurotrocha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synchaeta	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1	0	0	0	1	0	0
Testudinella	0	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0
Trichocerca	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Trichotria	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0
Unidentified monogonont	0	0	0	1	0	0	1	1	0	1	0	0	0	1	0	1	0	0	0	0	0

TABLE A4

Continued.

Lake	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Asplanchna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bdelloid	0	0	1	1	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0	0
Brachionus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cephalodella	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Collotheca	1	0	0	1	0	1	1	0	1	1	1	1	1	1	0	0	0	1	1	1	0
Colurella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conochilloides	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Conochilus	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	0	0	1	1	0
Dicranophorus	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Dipluchlanis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eothinia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Epiphanes/Proales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euchlanis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1
Gastropus	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
Kellicottia	0	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1	1	0
Keratella	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	0	0	1	1
Lecane	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	1
Lepadella	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Macrochaetus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monostyla	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	1	1	1	1
Mytilina	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Notholca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1
Platyias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ploesma	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1
Polyarthra	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1
Pleurotrocha	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Synchaeta	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	1	0
Testudinella	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Trichocerca	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Trichotria	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1
Unidentified monogonont	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0

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Continued.

Lake	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Asplanchna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bdelloid	1	0	1	0	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1
Brachionus	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1
Cephalodella	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	0	1	1
Collotheca	0	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0
Colurella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conochilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conochilus	0	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0
Dicranophorus	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Dipluchlanis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Eothinia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epiphanes/Proales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euchlanis	1	0	0	1	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	1	1
Gastropus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kellicottia	0	1	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Keratella	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lecane	1	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lepadella	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	0
Macrochaetus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monostyla	1	0	0	1	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1
Mytilina	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	1	1
Notholca	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1
Platyias	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ploesma	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0
Polyarthra	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleurotrocha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synchaeta	1	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	1	1	1	0	1
Testudinella	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	1	1	1
Trichocerca	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichotria	1	0	1	0	0	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1
Unidentified monogonont	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	1	1	1

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Continued.

Lake	85	86	87	88	89	90	91	92
Asplanchna	0	0	0	0	0	0	0	0
Bdelloid	1	1	1	1	1	0	0	1
Brachionus	0	0	0	1	1	0	0	1
Cephalodella	0	1	1	0	1	0	1	1
Collotheca	0	0	0	0	0	0	0	0
Colurella	0	0	0	0	0	0	0	0
Conochilloides	0	0	0	0	0	0	0	0
Conochilus	0	0	1	1	0	1	1	1
Dicranophorus	0	0	0	0	1	0	0	1
Dipluchlanis	0	0	0	0	0	0	0	0
Eothinia	0	0	0	0	0	0	0	0
Epiphanes/Proales	0	0	0	0	0	0	0	0
Euchlanis	1	0	1	1	1	0	1	1
Gastropus	0	0	0	0	0	0	0	1
Kellicottia	0	1	0	0	0	1	1	0
Keratella	0	0	0	0	0	1	0	1
Lecane	1	1	1	1	1	0	1	1
Lepadella	1	1	0	0	1	0	1	0
Macrochaetus	0	0	0	0	0	0	0	0
Monostyla	1	1	1	1	1	0	1	1
Mytilina	1	1	1	1	1	0	1	0
Notholca	1	0	1	1	1	0	1	1
Platyias	0	1	0	0	0	0	0	0
Ploesma	0	0	0	0	0	0	0	0
Polyarthra	0	0	0	0	0	0	0	1
Pleurotrocha	0	0	0	0	0	0	0	0
Synchaeta	0	0	0	1	1	0	1	1
Testudinella	1	1	1	1	1	0	1	1
Trichocerca	0	0	0	0	1	0	0	0
Trichotria	1	1	1	1	1	0	1	1
Unidentified monogonont	1	0	0	0	1	0	0	0

TABLE A4

Continued.

Lake	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Acantholebris curvirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acroperus harpae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Alona sp.	1	1	0	1	1	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1
Alonella nana	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	1	0
Alonella excisa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bosmina liederi	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0
Bosmina freyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chydorus sp.	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	1	1
Daphnia tenebrosa	0	0	0	0	1	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	0
Diaphanosoma brachyurum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eurycercus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holopedium sp.	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0
Macrothrix rosea	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Latona setifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocryptus acutifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ilyocryptus sordidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuroxus denticulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyphemus pediculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scapholebris kingi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sida crystallina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simocephalus serrulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simocephalus vetulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE A4

Continued.

Lake	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Acantholebris curvirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acroperus harpae	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Alona sp.	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Alonella nana	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Alonella excisa	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bosmina liederi	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0
Bosmina freyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chydorus sp.	1	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Daphnia tenebrosa	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	0	1	0
Diaphanosoma brachyurum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Eurycercus sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holopedium sp.	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	1	1
Macrothrix rosea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Latona setifera	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocryptus acutifrons	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocryptus sordidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuroxus denticulatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyphemus pediculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Scapholebris kingi	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sida crystallina	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Simocephalus serrulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simocephalus vetulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE A4

Continued.

Lake	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Acantholebris curvirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acroperus harpae	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Alona sp.	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1	0	1	1	0	0
Alonella nana	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0
Alonella excisa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Bosmina liederi	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Bosmina freyi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chydorus sp.	1	1	1	1	0	0	1	1	1	0	0	0	1	0	0	1	0	1	1	0	1
Daphnia tenebrosa	1	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	1	0	1	1	0
Diaphanosoma brachyurum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eurycercus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Holopedium sp.	1	1	0	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0
Macrothrix rosea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Latona setifera	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Ilyocryptus acutifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocryptus sordidus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuroxus denticulatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyphemus pediculus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Scapholebris kingi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sida crystallina	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Simocephalus serrulatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Simocephalus vetulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE A4

Continued.

Lake	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Acantholebris curvirostris	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acroperus harpae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Alona sp.	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	1	1	1	1
Alonella nana	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	1	1
Alonella excisa	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
Bosmina liederi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bosmina freyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chydorus sp.	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1
Daphnia tenebrosa	1	1	0	1	1	1	1	0	0	1	1	1	0	1	0	1	0	1	1	1	1
Diaphanosoma brachyurum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eurycercus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Holopedium sp.	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0
Macrothrix rosea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Latona setifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ilyocryptus acutifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ilyocryptus sordidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuroxus denticulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Polyphemus pediculus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scapholebris kingi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sida crystallina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simocephalus serrulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Simocephalus vetulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

TABLE A4

Continued.

Lake	85	86	87	88	89	90	91	92
Acantholebris curvirostris	0	0	0	0	0	0	0	0
Acroperus harpae	0	0	0	0	1	0	0	0
Alona sp.	1	0	1	1	1	0	1	1
Alonella nana	0	1	1	0	0	0	1	1
Alonella excisa	0	0	0	0	0	0	0	0
Bosmina liederi	0	0	0	0	0	0	0	0
Bosmina freyi	0	0	0	0	0	0	0	0
Chydorus sp.	1	0	1	1	0	0	1	0
Daphnia tenebrosa	1	0	1	1	0	0	1	0
Diaphanosoma brachyurum	0	0	0	0	0	0	0	0
Eurycercus sp.	0	0	0	0	0	0	0	0
Holopedium sp.	0	0	0	0	0	1	0	0
Macrothrix rosea	0	0	0	0	0	0	0	0
Latona setifera	0	0	0	0	0	0	0	0
Ilyocryptus acutifrons	0	0	0	0	0	0	0	0
Ilyocryptus sordidus	0	0	0	0	0	0	0	0
Pleuroxus denticulatus	1	1	0	0	1	0	0	0
Polyphemus pediculus	0	0	0	0	0	0	0	0
Scapholebris kingi	0	0	0	0	0	0	0	0
Sida crystallina	0	0	0	0	0	0	0	0
Simocephalus serrulatus	0	0	0	0	0	0	0	0
Simocephalus vetulus	0	0	0	0	0	0	0	0

TABLE A4

Continued.

Lake	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Nauplii	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Calanoid copepodid	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1
Cyclopoid copepodid	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1
Harpacticoid copepodid	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	1	1
Epischura lacustris	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0
Diaptomus novidecimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diaptomus nudus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Diaptomus wilsonae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperodiaptomus arcticus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterocope septentrionalis	1	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	0	0
Leptodiaptomus minutus	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1
Leptodiaptomus tyrelli	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0
Skistodiaptomus oregonensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyclops scutifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthocyclops robustus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diacyclops thomasi	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Diacyclops navus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucyclops serrulatus	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
Macrocyclops sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microcyclops rubellus	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Harpacticoid sp.	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1
Ostracoda	1	0	0	0	1	0	0	1	0	1	1	1	0	0	1	1	0	0	1	1	1
Gammarus lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tardigrada	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0

TABLE A4

Continued.

Lake	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Nauplii	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Calanoid copepodid	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cyclopoid copepodid	1	0	1	1	1	1	1	0	1	0	1	1	1	1	0	1	1	0	1	1	1
Harpacticoid copepodid	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epischura lacustris	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	1	1	0	1	1
Diaptomus novidecimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diaptomus nudus	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diaptomus wilsonae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hesperodiaptomus arcticus	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterocope septentrionalis	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	1	0	1	1
Leptodiaptomus minutus	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1
Leptodiaptomus tyrelli	0	0	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0
Skistodiaptomus oregonensis	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	0
Cyclops scutifer	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Acanthocyclops robustus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diacyclops thomasi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
Diacyclops navus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucyclops serrulatus	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Macrocyclops sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microcyclops rubellus	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Harpacticoid sp.	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ostracoda	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0
Gammarus lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tardigrada	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE A4

Continued.

Lake	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Nauplii	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Calanoid copepodid	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Cyclopoid copepodid	0	1	1	1	1	1	1	1	1	0	1	1	0	0	1	1	0	1	1	1	1
Harpacticoid copepodid	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Epischura lacustris	0	0	1	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0
Diaptomus novidecimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diaptomus nudus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Diaptomus wilsonae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperodiaptomus arcticus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0
Heterocope septentrionalis	1	0	0	0	1	1	0	0	0	1	1	1	1	1	0	0	1	0	1	1	0
Leptodiaptomus minutus	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0
Leptodiaptomus tyrelli	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Skistodiaptomus oregonensis	0	0	1	0	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0
Cyclops scutifer	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthocyclops robustus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Diacyclops thomasi	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Diacyclops navus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucyclops serrulatus	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
Macrocyclops sp.	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Microcyclops rubellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Harpacticoid sp.	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Ostracoda	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0
Gammarus lacustris	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tardigrada	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE A4

Continued.

Lake	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Nauplii	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Calanoid copepodid	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cyclopoid copepodid	1	1	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	1	1
Harpacticoid copepodid	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1
Epischura lacustris	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diaptomus novidecimus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diaptomus nudus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diaptomus wilsonae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperodiaptomus arcticus	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0
Heterocope septentrionalis	0	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	1	0	1	1
Leptodiaptomus minutus	0	1	1	1	1	0	0	1	1	0	1	0	1	1	1	1	1	1	1	0	1
Leptodiaptomus tyrelli	0	0	0	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	1	1
Skistodiaptomus oregonensis	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyclops scutifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthocyclops robustus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Diacyclops thomasi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diacyclops navus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucyclops serrulatus	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0
Macrocyclops sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microcyclops rubellus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
Harpacticoid sp.	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Ostracoda	1	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1
Gammarus lacustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tardigrada	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1

TABLE A4

Continued.

Lake	85	86	87	88	89	90	91	92
Nauplii	1	1	1	1	1	1	1	1
Calanoid copepodid	1	1	1	1	0	1	1	1
Cyclopoid copepodid	1	1	1	1	1	1	0	0
Harpacticoid copepodid	0	0	0	0	1	0	1	1
Epischura lacustris	0	0	0	0	0	1	0	0
Diaptomus novidecimus	0	0	0	0	0	0	0	0
Diaptomus nudus	0	0	0	0	0	0	0	0
Diaptomus wilsonae	1	0	0	0	0	0	0	0
Hesperodiaptomus arcticus	0	1	0	0	0	0	0	0
Heterocope septentrionalis	1	1	1	0	0	1	1	0
Leptodiaptomus minutus	0	0	1	0	0	1	0	1
Leptodiaptomus tyrelli	1	1	1	1	0	0	1	0
Skistodiaptomus oregonensis	0	0	0	0	0	0	0	0
Cyclops scutifer	0	0	0	0	0	0	0	0
Acanthocyclops robustus	0	0	0	0	0	0	0	0
Diacyclops thomasi	0	0	0	0	0	0	0	0
Diacyclops navus	0	0	0	0	0	0	0	0
Eucyclops serrulatus	0	0	0	0	0	0	0	0
Macrocyclops sp.	0	0	0	0	0	0	0	0
Microcyclops rubellus	0	0	0	0	1	0	0	1
Harpacticoid sp.	0	0	0	0	0	0	1	0
Ostracoda	1	0	1	1	1	0	1	1
Gammarus lacustris	0	0	0	0	0	0	0	0
Tardigrada	0	0	0	0	0	0	0	0