



The effects of eutrophication and invasive species on zooplankton community dynamics in a shallow temperate lake

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With 8 figures and 1 table

Abstract: Eutrophication (and associated cyanobacterial blooms) and biological invasions are increasingly common problems in aquatic ecosystems, yet their effects on zooplankton community dynamics are not well understood. We examined zooplankton community dynamics from 2005 to 2011 in a tidally-influenced shallow temperate lake (Vancouver Lake, Washington, USA), with particular emphasis on the effects of eutrophication and biological invasions. Cluster analysis, indicator species analysis, and non-metric multidimensional scaling analyses were used to explore interactions between the zooplankton community and multiple environmental stressors. Our results suggest that interannual differences in seasonal zooplankton community succession may be influenced directly by turbidity, cyanobacterial blooms, predatory zooplankton, and invasive crustacean zooplankton, and indirectly by $\text{PO}_4\text{-P}$ availability and temperature. Based on these results, we suggest that two separate management goals – alleviating eutrophication and managing the spread of invasive species – may be in conflict. We recommend future studies on the competition between native and non-native species to better understand the effects of cyanobacterial blooms on the success of non-native species, and the potential long-term consequences of non-native species invasions on zooplankton community dynamics.

Keywords: Invasive zooplankton; cyanobacterial bloom; water quality; environmental stressors; shallow lake; Vancouver Lake

Introduction

Freshwater ecosystems are threatened by multiple stressors, such as eutrophication arising from changing land use practices, and invasions of non-native species arising from increased commercial shipping, recreational boating, and other modes of dispersal. Over the past decade or more, there have been many studies that have investigated the effects of increased nutrient availability on freshwater food web dynamics

and restoration efforts (Jeppesen et al. 1997; Boersma et al. 2008; Glibert et al. 2011). One prominent consequence of eutrophication is the increased intensity and frequency of cyanobacterial blooms (Paerl 2008). Cyanobacterial blooms can in turn affect zooplankton community dynamics by adversely altering the quantity and quality of food available (Christoffersen et al. 1990; Gulati & Demott 1997; Davis et al. 2012; Rollwagen-Bollens et al. 2013) and shifting predation pressure on zooplankton by higher trophic levels (e.g.

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by altering planktivore feeding behavior and intensity) (Jeppesen et al. 1997; Engström-Öst et al. 2006). Thus, eutrophication can have profound and far-reaching effects on zooplankton communities.

Aquatic invasive species can also significantly alter trophic interactions in planktonic food webs (Hooff & Bollens 2004; Strecker & Arnott 2008; Strecker et al. 2011). For example, the invasion of the cladoceran *Bythotrephes longimanus* in Canadian lakes resulted in an overabundance of planktivorous predators which led to a decline in zooplankton prey diversity (Strecker & Arnott 2008; Kelly et al. 2013b). Likewise, the introduction of several species of Asian copepods has caused vast changes in the plankton communities of the San Francisco Estuary (Bollens et al. 2002; Bollens et al. 2011; Bollens et al. 2014; Hooff & Bollens 2004). Yet another example of an aquatic invader is the ctenophore *Mnemiopsis leidyi*, whose introduction to the Black Sea in the 1980s and expansion throughout the Caspian Sea in the 1990s caused declines in the abundance and diversity of native plankton (Roohi et al. 2008; Roohi et al. 2010) and zooplanktivorous fish (Shiganova et al. 2004; Daskalov & Mamedov 2007). Thus, invasive zooplankton can have substantial effects on native zooplankton communities that may ramify throughout aquatic food webs.

Zooplankton are important intermediaries between primary producers and higher trophic level organisms in aquatic ecosystems, by mediating algal growth through grazing and being consumed by zooplanktivorous invertebrates and fishes. Therefore, changes in zooplankton communities over time may serve as important indicators of the effects of eutrophication (Søndergaard et al. 2005; Winder et al. 2009; Jeppesen et al. 2011), as well as the effects of biological invasions (Kelly et al. 2013b; Palmer & Yan 2013).

Variation in zooplankton community composition may also be an important factor to consider in the monitoring and management of freshwater ecosystems (Dijkstra et al. 2011). Freshwater systems are experiencing dramatic changes in land use and development activities, at the same time as climate shifts influence environmental conditions of these systems and their surrounding watersheds. Observational studies and field surveys are essential to investigating and understanding the cumulative effects of multiple stressors on aquatic communities (Dodds et al. 2012; Palmer & Yan 2013), and are a critical complement to, and extension of, experimental programs that are often limited to testing the effects of a single stressor. Moreover, multi-year observational studies contribute to a better understanding of ecosystem dynamics by

identifying relationships and interactions among different measured stressors which can then serve as a springboard for developing future hypothesis-driven experiments (Dodds et al. 2012; Palmer & Yan 2013).

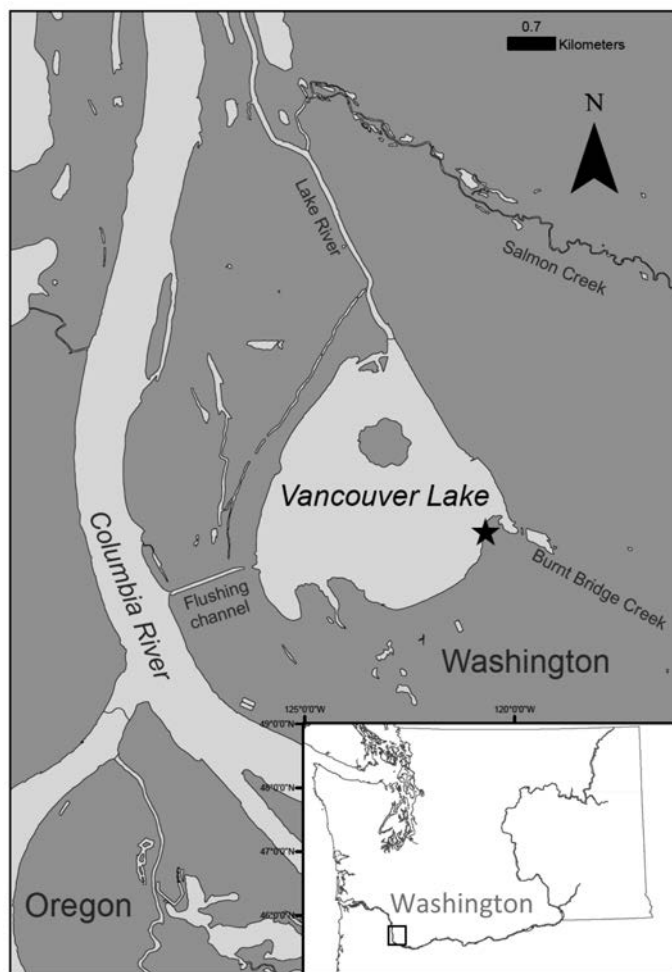
Vancouver Lake, located in the Columbia River floodplain in southwest Washington State, USA, is an ideal model system in which to study the effects of multiple stressors on freshwater communities. Vancouver Lake is a large, shallow, tidally influenced, non-stratifying lake that was historically flushed each spring by the lower Columbia River, but due to diking and reclamation is now hydrologically connected to the river only via a large engineered flushing channel and one small creek. It is a eutrophic lake subject to seasonal toxic cyanobacterial blooms resulting partly from increased phosphorus availability (Lee et al. 2015a) and has been the focus of previous studies to assess the biotic and abiotic influences on phytoplankton dynamics, bloom formation, and cyanotoxin production (Boyer et al. 2011; Rollwagen-Bollens et al. 2013; Lee et al. 2015b). Additionally, the spatial and temporal distributions of several invasive zooplankton taxa in the nearby lower Columbia River have recently been documented (Cordell et al. 2008; Bollens et al. 2012; Smits et al. 2013; Breckenridge et al. 2015; Dexter et al. 2015; Emerson et al. 2015). But to date the interactions among multiple stressors on Vancouver Lake as an interconnected system within the lower Columbia River have not been well studied. Thus, the specific objectives of this 6.5-year observational study (October 2005 through September 2011) in Vancouver Lake were to 1) characterize seasonal zooplankton community succession, and 2) examine how multiple stressors — especially eutrophication and zooplankton invasions — are associated with and likely affecting zooplankton community dynamics.

Methods

Study site

Vancouver Lake is located in southwest Washington State, USA (Fig. 1). It is a shallow (mean depth ~1 m), tidally influenced (but with no salinity intrusions), non-stratifying natural lake within the Columbia River floodplain. Vancouver Lake has two distinct hydrological connections with the Columbia River. First, the flushing channel, located on the southwest side of the lake, contains a one-way floodgate allowing water from the Columbia River to enter into Vancouver Lake when water levels in the river are higher than in the lake. In addition, Lake River connects the north end of Vancouver Lake to the Columbia River ~16 km downstream, and has a bi-directional flow depending on the tidal stage: as the flood tide raises the water level in the Columbia River, Lake River flows into Vancouver Lake, and

Fig. 1. Vancouver Lake, a 630 ha shallow, eutrophic lake located in Clark County, southwest Washington state. Inflows into Vancouver Lake are via the flushing channel, Burnt Bridge Creek, Lake River, and Salmon Creek. Lake River is the only outflow from Vancouver Lake. The filled star represents the sampling station located at the end of a dock at the Vancouver Lake Sailing Club.



as the tide ebbs, Lake River flows out of Vancouver Lake and into the Columbia River. Vancouver Lake also receives freshwater from two small creeks (Burnt Bridge Creek and Salmon Creek) that run through urban, suburban, and semi-rural areas of southwest Washington, representing a drainage area of up to 262 km² of the surrounding watershed. The influence of surrounding land use on water quality variables of Burnt Bridge Creek and Salmon Creek have been previously studied and well described (Deemer et al. 2012).

Previous studies of the aquatic biota of Vancouver Lake have been very limited, but include an in depth analysis of the phytoplankton community composition (including cyanobacteria biomass) from February 2007 through October 2010 (Lee et al. 2015a), as well as studies of microzooplankton grazing (Boyer et al. 2011) and mesozooplankton grazing (Rollwagen-Bollens et al. 2013). The fish community has only been described for the summer of one year (Caromile et al. 2000) and no studies of zooplanktivory have been performed in Vancouver Lake.

Field collections

A study of spatial variability of plankton in Vancouver Lake was undertaken in 2007, with a total of eight littoral and limnetic sites, and a dock station, sampled 10 times each. Kend-

all's tau (τ_b) was then used to examine concordance among sites and demonstrated no significant spatial differences in plankton community composition ($n=10$ per site, $p > 0.05$) (Bollens & Rollwagen-Bollens 2009). Additionally, the depth at the end of the dock sampling site has been shown to be representative of the mean depth of the lake (Sheibley et al. 2014). Based on these results, and ease of access, all subsequent sampling was conducted from the end of the dock located just south of Burnt Bridge Creek (Fig. 1), and all previous samples collected there were deemed representative of the lake as a whole.

We collected samples at least monthly, and when resources allowed, more frequently during suspected bloom periods. More specifically, from October 2005 through February 2007, lake water and plankton samples were collected monthly. From March 2007 to September 2010, lake water and plankton samples were collected monthly (November through February), bi-weekly (March and October), or weekly (April through September). From May 2011 through October 2011, lake water and plankton samples were collected weekly. During each sampling effort a YSI 91 or 6920 was used to measure temperature and dissolved oxygen (DO) from the surface to the bottom, at 0.3 m intervals. Lake water depth and Secchi depth were also measured.

A clean bucket was used to collect surface water samples in triplicate for chlorophyll-*a* (chl-*a*) and kept on ice until trans-

ported back to the laboratory. A 15–25 mL aliquot of lake water from each replicate was then filtered onto GF/F filters and kept frozen at -20°C until fluorometric analysis using a Turner Model 10 AU fluorometer (Strickland & Parsons 1972).

At each sampling time, triplicate zooplankton samples were collected using a 0.5 m diameter, 73 μm mesh net towed vertically from 0.15 m above the lake bottom to the surface. Zooplankton samples were preserved in 5–10% formalin. Well mixed subsamples were taken from whole samples with a Hensen-Stempel pipette, and a minimum of 300 zooplankton individuals were quantified and identified to the lowest taxon possible using a Nikon SMZ 1500 microscope at $10\times$ – $40\times$ magnification. Copepod nauplii were often highly abundant, and were not included in the organism counts because they can overwhelm and dampen overall community composition patterns; however, nauplii of the calanoid copepod *Pseudodiaptomus forbesi* were included in order to examine any significant changes associated with this invasive species. Zooplankton densities were calculated based on volumes filtered (individuals m^{-3}).

From February 2007 through October 2010, additional surface subsamples of 50 mL for analysis of nitrite ($\text{NO}_2\text{-N}$), nitrate ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), orthophosphate ($\text{PO}_4\text{-P}$), and silicate ($\text{SiO}_4\text{-Si}$) were filtered through a 0.45 μm Millipore filter into acid washed plastic bottles and kept on ice until returned to the laboratory. Samples were then frozen and sent to the Marine Chemistry Lab at the University of Washington's School of Oceanography for analysis.

Statistical analyses

Prior to all analyses, zooplankton abundances were $\log +1$ transformed. All nauplii, except for those of *P. forbesi*, and those taxa occurring in $<3\%$ of all samples were excluded. In two cases, taxa were combined to family (e.g. Bosminidae, see explanation in results) and order (e.g. Calanoida) to form a group that included rarer taxa that might have been excluded from the analysis or would otherwise have overestimated the influence of rare taxa.

In order to characterize significantly distinct groupings within the zooplankton community, we used cluster analysis (Clarke 1993), multiple response permutation procedure (MRPP) (Mielke et al. 1981; McCune & Grace 2002), and indicator species analysis (Dufrene & Legendre 1997). Clusters of distinct zooplankton communities were defined by using relative Euclidian distance measure and Ward's method for cluster linkage with 75% of the information retained. This allowed us to examine how similar/dissimilar communities were clustered together and how they changed over time based on the relative abundances and occurrence of zooplankton taxa. MRPP was then used to test the significance of the resulting zooplankton clusters, as well as to determine if there were significant inter-annual differences in the groupings, using ranked Sorenson's distance. Indicator species analysis was then applied to each zooplankton group to determine which zooplankton taxa were most strongly associated with each cluster. Indicator species analysis specifically identifies taxa that best represent each of the resulting zooplankton communities derived from cluster analysis. Taxa that occurred five times or more in one cluster compared to other clusters were considered significantly representative of that particular cluster and deemed "faithful."

We used non-metric multidimensional scaling (NMDS) to detect relationships between zooplankton species abundance

and environmental conditions. NMDS is a robust ordination technique that can be used with non-normally distributed and discontinuous data (McCune et al. 2000). Any sample dates with incomplete data (i.e. missing physical or nutrient data) were excluded. Due to the varying sampling regimes and detection of invasive zooplankton, three NMDS ordinations spanning different time periods were performed to determine the extent of abiotic (physical and nutrient) and biotic (cyanobacteria biomass and non-native zooplankton) influences on changes in zooplankton community composition. All NMDS ordinations were performed using the Sorenson distance measure and the "slow and thorough" autopilot option in PC-ORD (v.5.33), which iteratively searches for the best solution (McCune et al. 2000).

In the first NMDS ordination, we examined how zooplankton community composition varied between October 2005 through September 2010, and May 2011 through October 2011, in response to changes in lake depth, Secchi depth, temperature, season, and chl-*a*. To best capture seasonality in the Pacific Northwest, season was calculated as $\sin(365/360(\text{Julian day}))$, with December 1 set as 0, March 1 as 1, June 1 as 0, and September 1 as -1 . Specifically, we based September 1 as -1 because on average it is the warmest month of the year. Using a metric for seasonality allowed us to assess if other seasonal processes that were not measured (e.g. hours of daylight, changes in flow) might also influence plankton community dynamics. For the second ordination, we examined how zooplankton community composition varied over a shorter period of time for which we had more extensive environmental data: from February 2007 through September 2010, zooplankton composition was assessed in association with lake depth, Secchi depth, DO, nutrient availability, cyanobacteria biomass, and chl-*a*. A detailed description of our process of enumeration of cyanobacteria and other phytoplankton can be found in Lee et al. (2015a). Briefly, cyanobacteria biomass calculations were determined as recommended by APHA (2012); biomass was estimated (Menden-Deuer & Lessard 2000) after calculating biovolume based on geometric shape (Hillebrand et al. 1999).

Finally, in our third ordination, we examined the zooplankton communities and associated environmental data (lake depth, Secchi depth, chl-*a*, temperature, and season) using the combined periods of pre- and post-introduction of invasive zooplankton, i.e., October 2005 – February 2007 and March 2010 – October 2011, respectively. In this third ordination, taxa that were initially combined to a higher classification (i.e. species to family or order) were separated to their lowest taxonomic resolution because they no longer occurred in $<3\%$ of samples. All statistical analyses were performed using PC-ORD version 5.33 software (McCune & Grace 2002).

Results

Environmental variables

Over the 6.5-year study, total lake depth ranged from 0.80 m to 4.9 m and fluctuated seasonally, with increased depth during the spring freshet and decreased depth during the late summer/early autumn (Fig. 2a). Secchi depth ranged from 0.15 m to 2.1 m and followed a similar seasonal pattern as total lake depth (Fig. 2a).

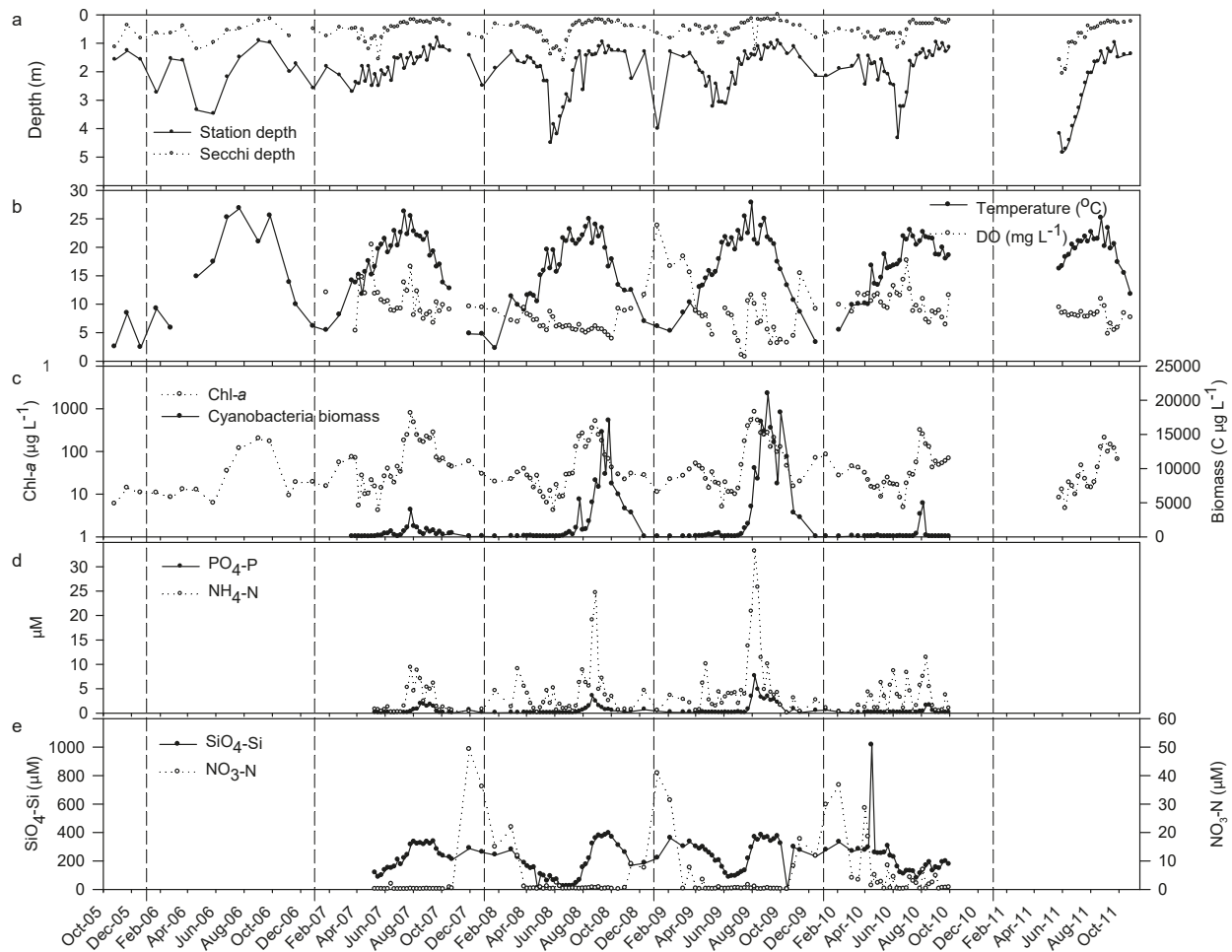


Fig 2. (a) Station depth and Secchi depth, (b) DO and temperature, (c) chl-*a* concentration in Vancouver Lake from October 2005 through September 2010, and May 2011 through October 2011; and cyanobacteria biomass from February 2007 through September 2010. Concentrations of (d) $\text{PO}_4\text{-P}$ and $\text{NH}_4\text{-N}$, and (e) $\text{SiO}_4\text{-Si}$ and $\text{NO}_3\text{-N}$ measured from May 2007 through September 2010.

Temperature ranged from 2.2 °C to 28 °C, and showed a seasonal pattern of warmer temperatures in the summer and cooler temperatures in the winter (Fig. 2b). The warmest summer was observed in 2009 and the coolest summer in 2010 (peaking at 23 °C). DO ranged from very low levels ($<2.0 \text{ mg L}^{-1}$) during the summer months to supersaturated conditions ($>14 \text{ mg L}^{-1}$) during the winter and spring months (Fig. 2b). Chl-*a* ranged from $4.1 \text{ } \mu\text{g L}^{-1}$ to $820 \text{ } \mu\text{g L}^{-1}$ and exhibited intense seasonal peaks during the summer, concurrent with increased temperatures and the onset of cyanobacterial blooms, with the highest values observed in summers of 2007 and 2009 (Fig. 2c). Nutrient data are described in detail in Lee et al. (2015a), but briefly, $\text{PO}_4\text{-P}$ exhibited relatively stronger peaks during the onset of cyanobacterial blooms during the summer months (Fig. 2d). $\text{NH}_4\text{-N}$ fluctuated throughout the year, but similar to $\text{PO}_4\text{-P}$, concentrations were greater

during the summer months (Fig. 2d). $\text{NO}_3\text{-N}$ availability was greatest during the winter months, when chl-*a* was lowest (Fig. 2e). $\text{SiO}_4\text{-Si}$ showed seasonal fluctuations with concentrations greater during the summer and winter, and lower during the spring (Fig. 2e).

Dominant zooplankton groups

A total of 28 zooplankton taxa, excluding nauplii and copepodites, were identified from 171 samples in Vancouver Lake (Table 1). It should be noted that the use of a 73 μm mesh net may have missed some smaller rotifer species. Two seasonal peaks of total zooplankton abundance were observed during most years – one during late spring (May) and one during late summer (August/ September) (Fig. 3a). We observed one peak in total zooplankton abundance in 2006 (spring) and 2011 (summer), which might be attributed to a somewhat reduced sampling frequency in those years

Table 1. Names and occurrences (% of total samples) of zooplankton taxa collected in Vancouver Lake. Taxa occurring in <3 % of samples were not included in statistical analyses.

Taxa	Occurrence (%)
Cladocera	
Bosminidae*	93.57
<i>Daphnia retrocurva</i>	88.89
Other <i>Daphnia</i> sp.	42.69
<i>Chydorus</i> sp.	15.80
<i>Leptodora kindtii</i>	15.79
<i>Ceriodaphnia</i> sp.	9.36
<i>Diaphnosoma</i> sp.	5.26
<i>Eurycerus</i> sp.	4.09
<i>Alona</i> sp.	1.17
Rotifera	
<i>Polyarthra</i> sp.	86.55
<i>Brachionus</i> sp.	74.27
<i>Asplanchna</i> sp.	70.18
<i>Keratella</i> sp.	67.25
<i>Kellicottia</i> sp.	7.02
<i>Filina longiseta</i>	0.58
Copepoda	
Nauplii **	100
Cyclopoida	
Copepodites	99.41
<i>Diacyclops thomasi</i>	97.06
Harpacticoid	3.5
Calanoid	
Copepodites	20.47
<i>Leptodiaptomus</i> sp.	16.96
<i>Pseudodiaptomus forbesi</i>	
Nauplii	16.37
Copepodites	2.34
Adult	1.75
<i>Skistodiaptomus</i> sp.	4.68
Other	
Oligochaeta	2.94
Chironomidae	2.35
Nematoda	1.18
Arachnidae	0.59
Chironomidae	0.59
Polychaeta	0.59

* Bosminidae includes both *B. longirostris* and *B. coregoni*.

** Nauplii includes all copepod nauplii except for *P. forbesi*.

(monthly throughout 2006 and monthly from May through October 2011, vs. weekly during the summer of other years). Cladocera dominated the late spring peak each year, whereas the dominant group observed during late summer peaks varied among cyclopoid copepods, rotifers, and cladocera (Fig. 3b).

Of the copepods, cyclopoids were the most common taxon, dominated nearly exclusively by *Diacy-*

clops thomasi. In addition, calanoid copepods were observed throughout the sampling period (except in 2008); however, they did not contribute substantially to total zooplankton abundance except in 2011. Due to the rare occurrence (<3 %) of adults of the calanoids *Leptodiaptomus* sp., *Skistodiaptomus* sp., and *Pseudodiaptomus forbesi*, these taxa were subsequently combined into “adult calanoid copepods” so as not to exclude them from the analysis. Finally, harpacticoid adults were distinguished, but were rarely present. Among rotifers, six taxa were identified but only five were included in the analysis due to the rarity of one taxon. *Polyarthra* sp., *Asplanchna* sp., and *Brachionus* sp. were present each year; *Keratella* sp. was present each year from 2007 through 2011, but not in 2005 or 2006; and *Kellicottia* sp. was present only in 2010. With respect to cladocerans, *Daphnia retrocurva* was the most abundant of a total of nine cladoceran species identified (Table 1).

Seasonal succession and zooplankton community composition

Results from cluster analysis defined four significant clusters ($A=0.208$, $p<10^{-8}$), suggesting a recurring seasonal succession, as well as significant interannual variability ($A=0.176$, $p<10^{-8}$) (Fig. 3a). Seasonal succession was observed in 2007, 2009 and 2010, with cluster 1 occurring during the winter, clusters 2 and 3 representing the spring, cluster 4 representing the summer, and cluster 2 representing the autumn. Zooplankton assemblages between October 2005 and December 2006 were defined only by clusters 1 and 4, when overall zooplankton abundances were lowest. In contrast, during 2008, clusters 1 and 4 were completely absent, with cluster 2 representing the winter and spring, and cluster 3 representing the summer and early autumn. Additionally, with the absence of cluster 4 in 2008, overall abundances of clusters 2 and 3 were higher than in previous years. In 2011, cluster 1 represented the entire spring and summer, with overall abundances higher than in 2007-2010 (but not 2005 and 2006), and with abundances of other clusters dramatically suppressed (Fig. 3a).

Based on indicator species analysis, cluster 1 was characterized by calanoid copepods, harpacticoid copepods, and all non-daphnid and bosminid cladocerans (Fig. 4a). With the exception of 2008 and 2011, cluster 1 occurred during winter months. From 2005 through 2006, the cladocerans *Ceriodaphnia* sp. and *Chydorus* sp. were especially abundant. The rare occurrence of cluster 1 in 2007 was dominated by harpacticoid copepods. Cluster 1 was the only group represented in 2011

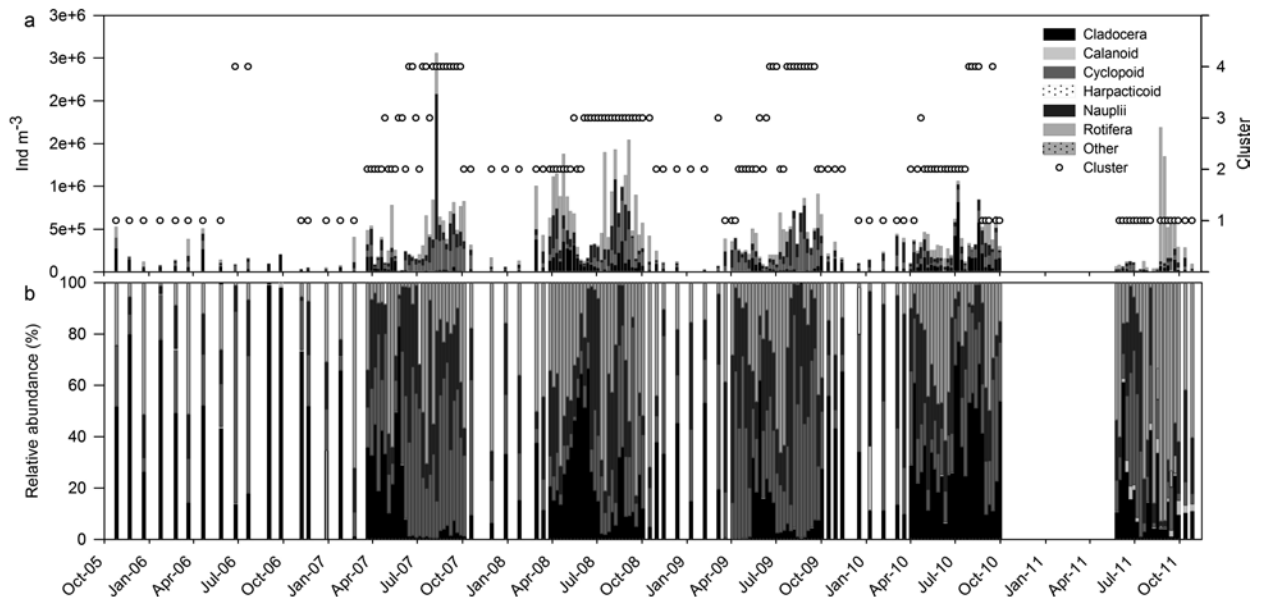


Fig. 3. (a) Distribution of dominant clusters and total zooplankton abundance (individuals m^{-3}), and (b) relative zooplankton abundance (%), October 2005 through October 2011, grouped by order.

and was dominated by calanoid copepods, with overall abundances higher than in the previous four years.

Cluster 2 consisted primarily of the cladoceran family Bosminidae, and the rotifers *Polyarthra* sp., *Asplantha* sp., *Keratella* sp., and *Kellicottia* sp. (Fig. 4b). Abundances of these taxa were low during the winter and variable throughout spring, summer, and autumn. A late spring and late summer bimodal distribution of cluster 2 species abundances was particularly pronounced in 2007, 2008, and 2010. Based on indicator species analysis, *Kellicottia* sp. was the species that best defined this cluster, however it was only detected in 2010.

Cluster 3 was represented by the cladoceran, *D. retrocurva*, and other daphnids (Fig. 4c). Daphnids were largely absent during the winter (as were other zooplankton taxa) and exhibited two peaks in abundance during the late spring and late summer, with the exception of 2011, when daphnids were notably absent during the summer.

Cluster 4 consisted of the cyclopoid copepod *D. thomasi*, cyclopoid copepodites, the rotifer *Brachionus* sp., and the carnivorous cladoceran *Leptodora kindtii* (Fig. 4d). As with clusters 2 and 3, there were striking interannual differences in overall abundance and occurrence of cluster 4 taxa. Cluster 4 defined the summer community each year, with the exception of 2008 and 2011. In 2008, *L. kindtii* was absent during the summer and the zooplankton community was

characterized by cluster 3. In summer 2011, although abundance and occurrence of *D. thomasi* and copepodites were lower compared to previous years, and *Brachionus* sp. exhibited uncommonly high abundances, the zooplankton community was defined by cluster 1.

Abiotic and biotic factors associated with zooplankton community composition

The first NMDS ordination of zooplankton community composition, including the longer time series (2005–2011) but more limited set of environmental variables, resulted in a three dimensional solution of which only axis two was strongly correlated with three of the five environmental variables (stress = 15.28, $r^2 > 0.3$): Secchi depth, season, and chl-*a* (Fig. 5a). Cluster 1 was associated with increased water clarity (deeper Secchi depth) and season. Ordination of sample points representing cluster 1 were more dispersed than other clusters and was largely driven by *Chydorus* sp., and calanoid adults and copepodites ($r^2 > 0.2$), even though other cladoceran taxa are included in this cluster (Fig. 5b). Seasonal summer peaks of chl-*a* showed a strong relationship with Cluster 4. Clusters 2 and 3 occupied an intermediate space of the ordination, suggesting that these clusters exist as transitional conditions across each environmental gradient.

The second ordination, using data from February 2007 through September 2010, was performed to examine whether including additional environmental

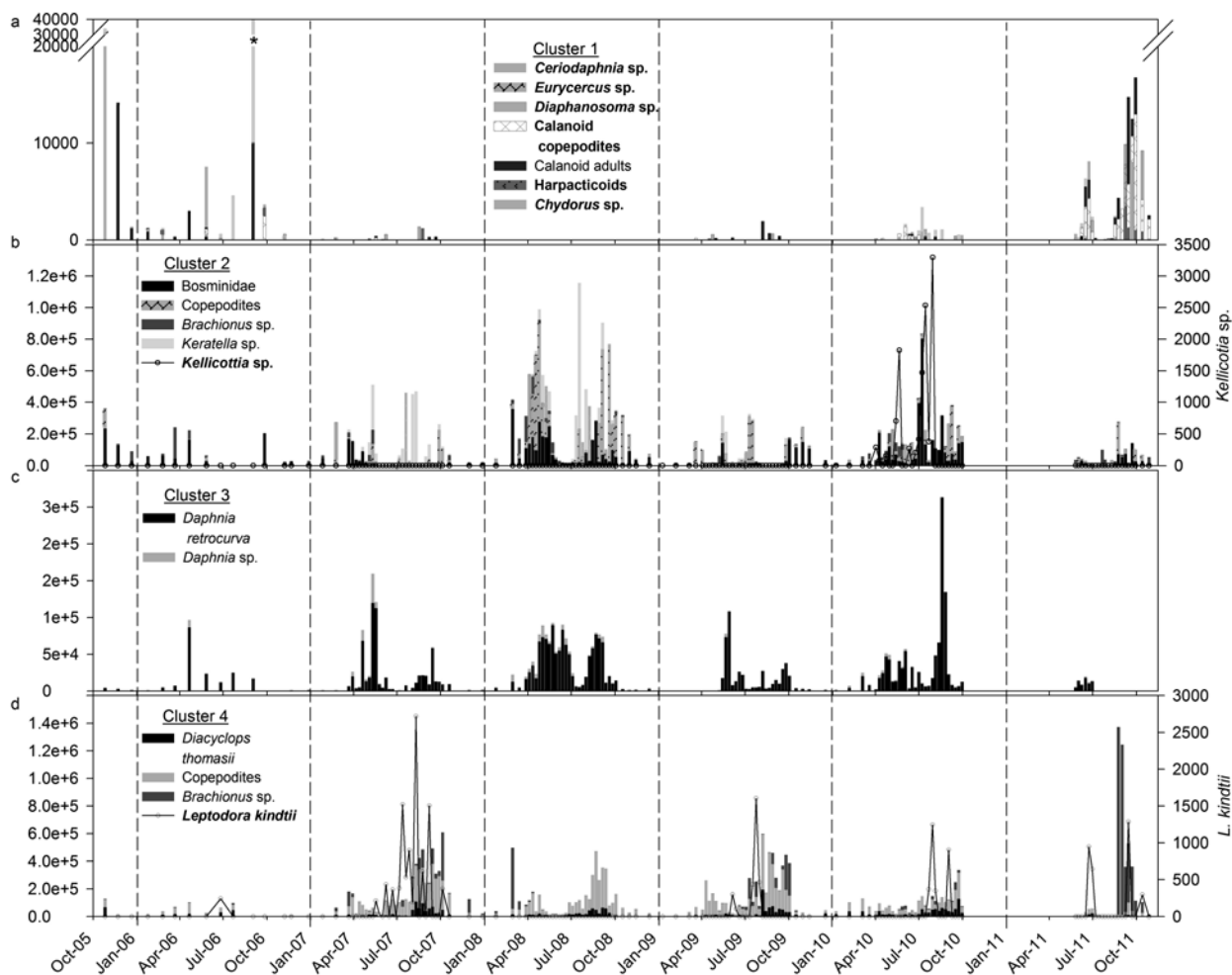


Fig. 4. Panels (a) through (d) show abundance of zooplankton taxa representing each cluster determined by indicator species analysis ($p < 0.05$). Taxa in bold are exclusively faithful to the cluster.

variables, not available in other years (i.e., DO, nutrients, and cyanobacteria biomass), would yield additional insight into the dynamics of the zooplankton community (Fig. 6). A three dimensional solution (stress = 14.95) was reached and included several additional environmental factors associated with zooplankton community composition ($r^2 > 0.2$). Interannual differences were more apparent with this subset of data. Season was associated with clusters 2 and 3 (Fig. 6a) from 2008 and 2010 (Fig. 6b). All annual summer zooplankton communities (clusters 4 and 2) were associated with increased levels of $\text{PO}_4\text{-P}$ and chl-*a*, warmer temperatures, and higher cyanobacteria biomass. High cyanobacteria biomass and chl-*a* defined the annual phytoplankton blooms in Vancouver Lake, specifically from 2007 through 2009, which have been correlated with seasonally eutrophic conditions (as described by increased $\text{PO}_4\text{-P}$); however, in

2010 a significant cyanobacterial bloom was not observed, even though there was an increase in $\text{PO}_4\text{-P}$ (Lee et al. 2015a).

Introduction of non-native zooplankton

Two invasions of non-native zooplankton were detected in Vancouver Lake over the course of our study. The non-native Asian calanoid copepod *Pseudodiaptomus forbesi* was first identified in Vancouver Lake in June 2006 as nauplii, and then in November 2006 as adults (Fig. 7a). With the exception of a single occurrence in April 2009, *P. forbesi* was not observed again until 2010 (Fig. 7a). In 2011 it was abundant in all life history stages (Fig. 7a).

The non-native bosminid cladoceran, *Bosmina coregoni*, was first observed in Vancouver Lake in March 2007. *B. coregoni* first appeared in the Colum-

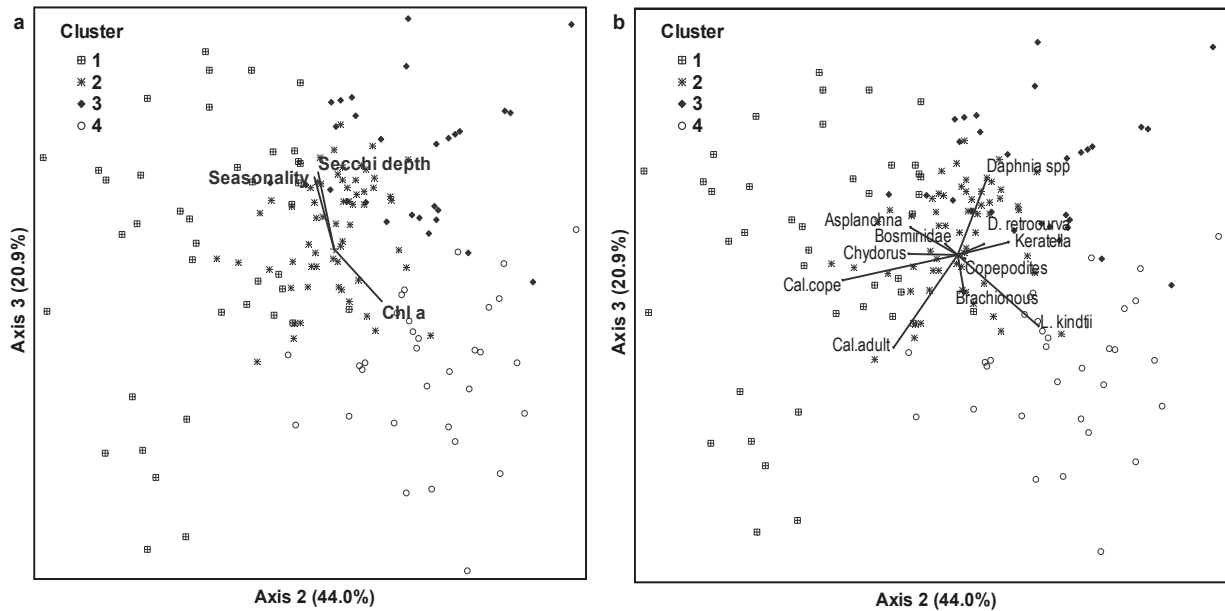


Fig. 5. NMDS ordination of zooplankton samples and environmental conditions from October 2005 through September 2011. Axis 1 (not shown) represented an additional 22.5 % of explained variance among samples. Joint plot cut offs for both environmental vectors (**a**) and species associations (**b**) were set at $r^2 > 0.2$. The magnitude and orientation of the vector represents the strength and direction (positive or negative), respectively, of the association.

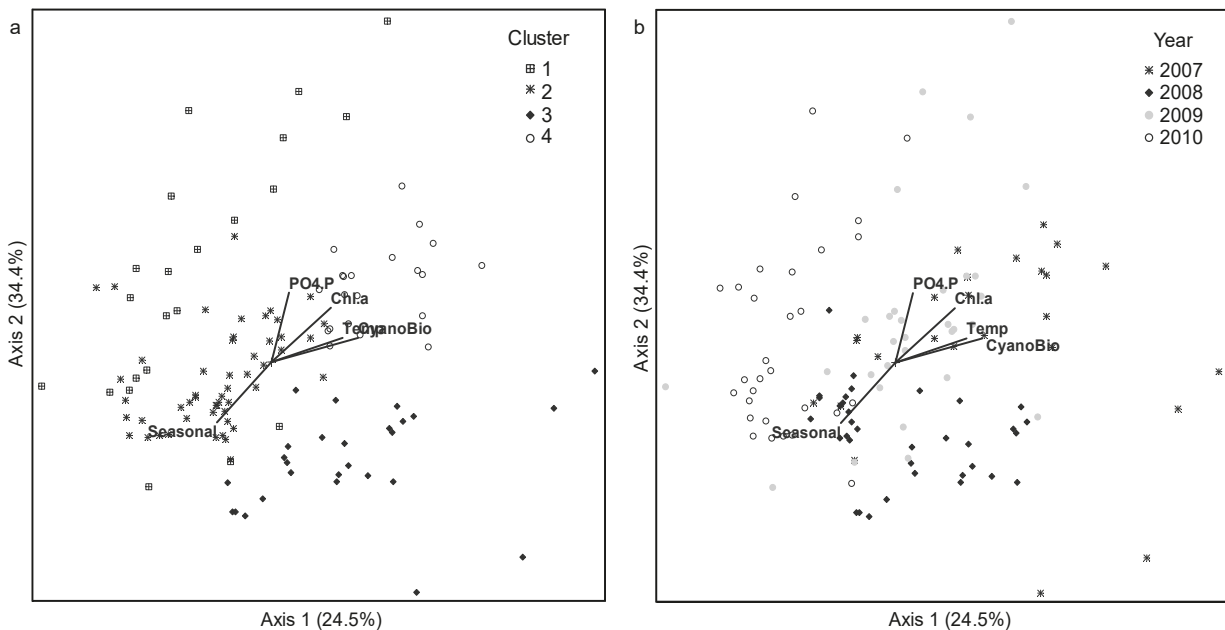


Fig. 6. NMDS ordination of zooplankton samples and environmental variables, including cyanobacteria biomass, in Vancouver Lake. Axis 2 (not shown) represented an additional 34.4 % of explained variance among samples. Joint plot cut offs for environmental vectors were set to $r^2 > 0.2$. Environmental vectors are shown in relation to sampling points defined by zooplankton community clusters (**a**) and year (**b**).

bia River as a single occurrence in September 2006, before a population boom was observed in 2008 (Dexter et al. 2015). All Bosminidae species in Vancouver Lake were initially identified by us as *B. coregoni*, due

to their dominance beginning in March 2007. However, in 2010 we determined that both *B. coregoni* and the native *B. longirostris* were present in Vancouver Lake. Due to the uncertainty in identifications be-

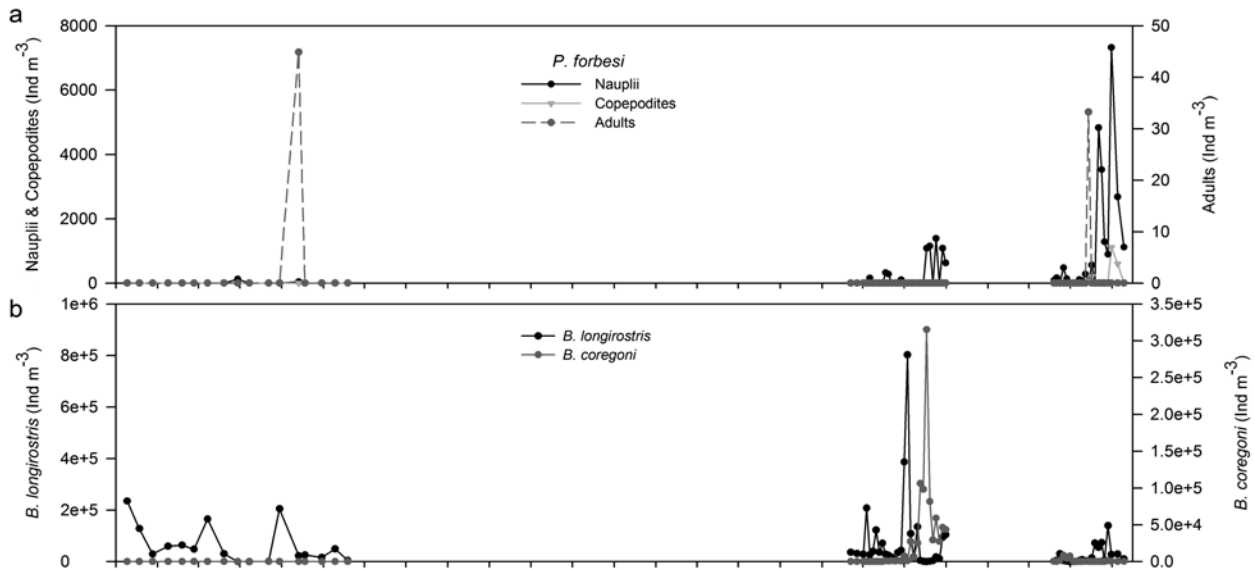


Fig. 7. Occurrence and abundance of non-native zooplankton taxa in Vancouver Lake pre-introduction (October 2005 – February 2007) and post-introduction (March 2010 – October 2011). **(a)** Abundance of *P. forbesi* of different life stages; **(b)** abundances of *B. longirostris* and *B. coregoni*.

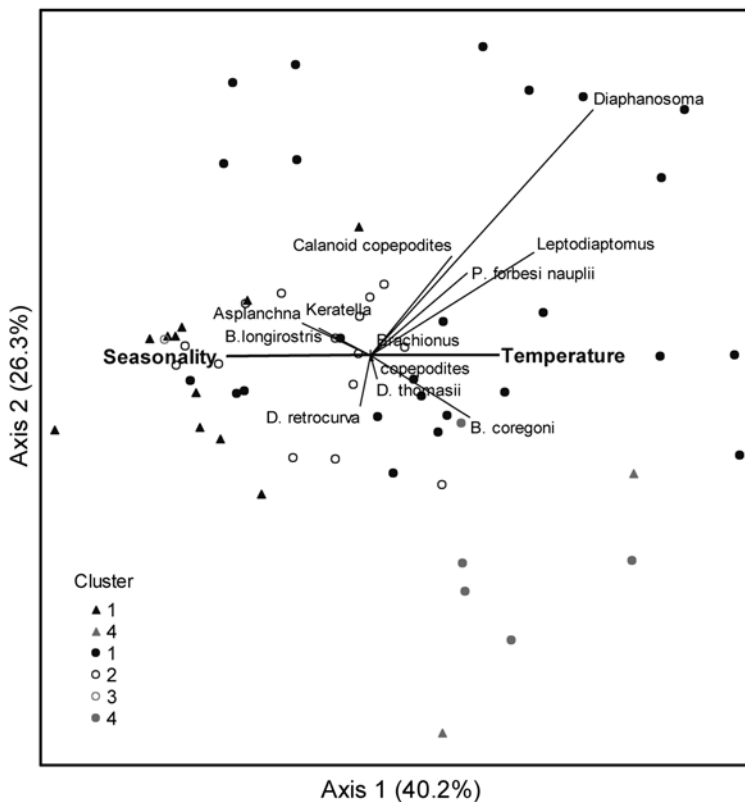


Fig. 8. NMDS ordination of zooplankton samples representing pre-introduction (solid triangles) and post-introduction (circles) of non-native zooplankton. Axis 3 (not shown) represented 19.9% of the explained variance among samples. Joint plot cut offs for environmental and species vectors were $r^2 > 0.2$.

tween 2007 and 2009, *B. coregoni* and *B. longirostris* occurring during this period were combined into a single taxonomic group (family Bosminidae). Bosminids in 2010 and 2011 samples, however, were reliably

identified as either of two separate taxa: *B. coregoni* or *B. longirostris*.

The third and final NMDS ordination was employed for the purposes of examining possible envi-

ronmental associations with zooplankton communities both pre- and post-introduction of non-native zooplankton. The pre-introduction period (October 2005 – February 2006) was defined by the absence of *B. coregoni* and the lack of an established *P. forbesi* population. The post-introduction period (March 2010 – October 2011) was defined by the increased occurrence and abundance of both invasive zooplankters, *P. forbesi* and *B. coregoni* (Fig. 7b).

The NMDS ordination of pre- and post-introduction showed distinctly different groups (stress = 14.29) (Fig. 8). With the exception of two samples, the pre-introduction group consisted of cluster 1 taxa and was strongly associated with season. The post-introduction group predominantly consisted of clusters 1, 2 and 4. After the introduction of both invasive zooplankters, cluster 1 was principally associated with *P. forbesi* and other calanoid copepods. Cluster 2 was largely comprised of rotifers and *B. longirostris*. In contrast, cluster 4 was predominantly represented by *B. coregoni*. Of the post-introduction samples, summer samples of cluster 4 occurred during 2010, and summer samples of cluster 1 occurred during 2011, and both were most strongly associated with temperature. The native *B. longirostris* (cluster 2) was inversely associated with *B. coregoni* (cluster 4).

Discussion

The results of our study suggest that multiple stressors – including cyanobacterial blooms (due to eutrophic conditions) and invasive zooplankton species – influenced seasonal and interannual variability in zooplankton community dynamics in Vancouver Lake.

Effects of eutrophication on zooplankton community dynamics

Environmental variables that strongly influenced zooplankton community dynamics in Vancouver Lake included common characteristics of eutrophic conditions such as increased turbidity, increased $\text{PO}_4\text{-P}$, and cyanobacterial blooms. In particular, $\text{PO}_4\text{-P}$ availability in Vancouver Lake may have had an indirect influence on summertime zooplankton community composition through the stimulation of cyanobacterial blooms. Increased orthophosphate concentrations during summer months in Vancouver Lake were most likely due to a combination of several processes, including wind driven sediment resuspension (Sheibley et al. 2014), anoxia at the sediment-water interface (Lee et al. 2015a), and possibly the release of $\text{PO}_4\text{-P}$

due to grazing (Frost et al. 2004). Recently, Lee et al. (2015a) demonstrated that peaks in $\text{PO}_4\text{-P}$ concentration were significantly associated with the occurrence and duration of large cyanobacterial blooms that occurred in Vancouver Lake during each summer from 2007 to 2009. These authors further found that a very muted bloom dominated more by diatoms than cyanobacteria in 2010 was associated with a lower peak in $\text{PO}_4\text{-P}$ concentration relative to previous summers.

Our results from analysis of zooplankton abundance and taxonomic composition over the same time period (2007–2010) show that the zooplankton communities in 2007 through 2009 were generally similar to each other (defined by rotifer-dominated cluster 2 and *D. thomasi*-dominated cluster 4) and strongly associated with eutrophic conditions of increased cyanobacteria biomass, chl-*a*, temperature, and $\text{PO}_4\text{-P}$. However, the community in 2010 was significantly different (represented by cluster 1 dominated by calanoid copepods) and not strongly associated with either seasonality or eutrophication. Although an annual increase in chl-*a* was observed during the summers of 2010 and 2011, these were noticeably lower than the blooms in 2007–2009. More specifically, we observed a zooplankton community shift from cluster 4 to cluster 1 at the end of the 2010 summer, and the entire 2011 summer community was also defined by cluster 1. This suggests a strong link between zooplankton community structure and seasonally eutrophic conditions, in particular the occurrence (or not) of cyanobacterial blooms.

Effects of cyanobacterial blooms on zooplankton community dynamics have been well studied elsewhere (see review by Ger et al. 2014). Meta-analyses of laboratory studies examining effects of toxic cyanobacteria on zooplankton fitness suggested that although cyanobacteria are not ideal food items, zooplankton responses to cyanobacterial blooms are species-specific and may not be as severely detrimental as previously thought (Wilson et al. 2006; Tillmanns et al. 2008). For example, observational studies of Lake Tai showed that increases in cladoceran populations correlated with an increase in cyanobacteria biomass, but that copepods varied independently from cyanobacteria biomass (Sun et al. 2012). Other studies have shown that smaller cladocerans and copepods are better competitors than larger cladocerans during cyanobacterial blooms (Deng et al. 2008; Wang et al. 2010; Sun et al. 2012), and that larger cladocerans may respond by a decrease in body size while still maintaining a positive growth rate (Sarnelle et al. 2010). Daphnids have been reported to become tolerant to

cyanobacterial toxins when repeatedly exposed to cyanobacteria (Hairston et al. 2001; Sarnelle & Wilson 2005), suggesting that cyanobacteria may act as a selection force on some zooplankton taxa (Hairston et al. 2001). Thus, the composition of the summer zooplankton community in Vancouver Lake may be changing due to an interaction of repeated annual exposure to summer cyanobacterial blooms and the greater prominence of cyanobacteria-tolerant zooplankton taxa.

Predation pressure by carnivorous zooplankton may also affect summer zooplankton community composition (Wojtal et al. 1999; Pichlova & Brandl 2003; Lesutiene et al. 2012). Each year of our study in Vancouver Lake, cladocerans and rotifers tended to dominate the zooplankton community during the spring. Subsequently, in every summer (except 2008) the carnivorous cladoceran, *L. kindtii*, was observed, concomitant with decreased daphnid and rotifer abundances. *L. kindtii* are voracious predators that can cause severe declines in prey populations generally (Wojtal et al. 1999; Chang & Hanazato 2003; Lesutiene et al. 2012), and have been shown to significantly alter zooplankton community structure by preying upon cladocerans and rotifers specifically (Wagner & Benndorf 2007; Wagner et al. 2013). The absence of *L. kindtii* in Vancouver Lake in 2008 may have contributed to the observed increase in abundance of rotifers and daphnids that summer (although our collection methods [e.g. sample volume and net diameter], combined with the evasive capabilities of *L. kindtii*, almost certainly caused us to underestimate the abundance of this predator (e.g. Wojtal et al. 1999)). Direct effects of cyanobacterial blooms on *L. kindtii* are not well known, although a few studies have documented their co-occurrence and the continued predation by *L. kindtii* on available prey (Patoine et al. 2006; Perga et al. 2013). While we observed seasonal and interannual changes in zooplankton community composition in relation to eutrophic conditions in Vancouver Lake, the relative abundance of predatory zooplankton may also have had an effect on zooplankton community composition.

Finally, we observed zooplankton abundances to be positively associated with increased Secchi depth (i.e. water clarity), except during winter months when temperatures were not conducive for zooplankton growth. This relationship could have been due to food availability and/or predation pressure (although the latter was not measured by us). For instance, concomitant with increased Secchi depth, chl-*a* levels were very low, suggesting decreased food availability and/or increased grazing. Conversely, when Secchi depth was low, chl-*a* levels were very high, implying increased

food availability. Another possible interpretation, however, is that low Secchi depths represent periods of high turbidity that may provide zooplankton with refuge from visual predation (Engström-Öst & Mattila 2008; Schulze 2011). Thus, either increased food availability or decreased visual predation may have contributed to the higher zooplankton abundances we observed during summer months. Finally, we acknowledge the potential of fish planktivory to structure zooplankton communities (Brooks & Dodson 1965; Gliwicz et al. 2010; Schulze 2011); however, it was impossible for us to evaluate here, because studies on seasonal fish abundance and zooplanktivory have not been conducted in Vancouver Lake.

Effects of invasive zooplankton

We observed two non-native zooplankton species in Vancouver Lake in the later years of our study: the bosminid cladoceran, *Bosmina coregoni*, and the calanoid copepod, *Pseudodiaptomus forbesi*. In comparing the pre- (2005–2006) and post-invasion (2010–2011) time periods, temperature was the main environmental variable that was associated with both *B. coregoni* and *P. forbesi* nauplii, suggesting that warmer temperatures were conducive for these two species. However, temperature alone does not explain the population abundance patterns of *B. coregoni* observed in 2010 and 2011. Specifically, bosminids were also negatively associated with chl-*a* (Fig. 5b).

Based on native habitat conditions and the spatial and temporal occurrence of *P. forbesi* and *B. coregoni* (in east Asia and Eurasia, respectively), the mechanisms of introduction to Vancouver Lake were most likely different for these two species. *P. forbesi* has been well established throughout the lower Columbia River and upstream in several impoundments since 2005, and has been shown to dominate the zooplankton community of these waters in the late summer/early autumn (Cordell et al. 2008; Bollens et al. 2012; Breckenridge et al. 2015; Dexter et al. 2015; Emerson et al. 2015). Because of its presence throughout the lower Columbia River, introduction of *P. forbesi* to Vancouver Lake was most likely through natural flows from nearby “source” waters, e.g. through the flushing channel or Lake River. Yet, while the introduction of *P. forbesi* in 2010 significantly altered the summer zooplankton community in Vancouver Lake when it first arrived, this Asian copepod did not dominate the zooplankton community of the Lake, as it has in various parts of the Columbia River. It remains to be seen if further re-introductions of *P. forbesi* in Vancouver

Lake will continue to affect zooplankton community composition, including the possibility that this invasive copepod might eventually dominate the summer zooplankton community in the lake.

In contrast, *B. coregoni* has been an established freshwater invader in North America since the 1960s (Deevey & Deevey 1971) via multiple invasions (DeMelo & Hebert 1994), but its introduction to the U.S. Pacific Northwest has been more recent and the effects of its invasion on zooplankton community dynamics and trophic interactions are not well known (Smits et al. 2013; Dexter et al. 2015). *B. coregoni* first appeared in the Columbia River as a single occurrence in September 2006, prior to a population boom in 2008 (Dexter et al. 2015). However, a recurring population of *B. coregoni* in Vancouver Lake was first identified in March 2007, before its detection in the Columbia River estuary, Lake Washington and several other lakes in eastern Washington State (Smits et al. 2013). The patchy occurrence and distribution of *B. coregoni* throughout the state of Washington suggests that its introduction and dispersal may be largely attributed to recreational boating and migratory fowl (Smits et al. 2013).

Overall bosminid cladoceran abundances in Vancouver Lake were high during the spring, and then drastically reduced during the summer. The noticeable increase in bosminid abundances observed in 2010 coincided with a truncated and mild cyanobacterial bloom, with the native *B. longirostris* dominating during the early summer and the invasive *B. coregoni* dominating during the late summer. At present, no studies have examined competitive interactions between *B. longirostris* and *B. coregoni*. Under laboratory conditions, cyanobacterial blooms have been demonstrated to suppress populations of larger cladocerans, while allowing the opportunity for smaller cladocerans, such as *B. longirostris*, and copepods to persist (Lampert 1987; Fulton & Paerl 1988). Yet, *B. coregoni* is larger than *B. longirostris*, and field studies have demonstrated that *B. coregoni* in its native range was positively correlated with cyanobacteria (Deng et al. 2008; Sun et al. 2012), suggesting that *B. coregoni* may be tolerant of cyanobacterial blooms. Similar to daphnids, bosminids have also been shown to adapt to repeated exposure to toxic cyanobacteria (Jiang et al. 2013). Our results indicate that Bosminids (which were dominated by *B. coregoni*) may be adversely affected by cyanobacterial blooms in Vancouver Lake as they are negatively associated with increased levels of chl-*a* (Fig. 5); however, this does not preclude the possibility that *B. coregoni* may eventually become tolerant to cyanobacterial blooms in Vancouver Lake.

Calanoid copepods have been shown to be more sensitive to toxic cyanobacteria compared to other types of crustacean zooplankton (DeMott et al. 1991). In particular, *P. forbesi* in the San Francisco estuary has been shown to be more susceptible to microcystin than other copepods and cladocerans (Ger et al. 2009), yet can nevertheless co-exist with toxic blooms of *Microcystis* sp. because of its selective feeding behavior (Ger et al. 2010). However, no studies have examined the effects of cyanobacterial blooms on different life history stages of *P. forbesi*. In Vancouver Lake, *P. forbesi* consisted mainly of nauplii, with copepodites and adults usually very rare or absent (indeed, adult female *P. forbesi* were never observed by us), although the limited occurrence of *P. forbesi* copepodites and adults in our samples may be due to the truncated sampling regimes in 2010 and 2011, which ceased at the end of September and October, respectively. In the Columbia River, adult *P. forbesi* peak in abundance in late summer and early autumn (Bollens et al. 2012; Dexter et al. 2015; Emerson et al. 2015) and thus we may have missed peak abundances of adult *P. forbesi* in Vancouver Lake in 2010 and 2011. Alternatively, the generally low abundances of *P. forbesi* in Vancouver Lake could have been the result of deleterious effects of cyanobacteria, as has been shown for this and other calanoid copepods (DeMott et al. 1991; Ger et al. 2009). Our results suggest that further investigation of the effects of cyanobacterial blooms on different life stages of *P. forbesi* is warranted.

An established *P. forbesi* population may have detrimental effects on native zooplankton communities. Studies within the Columbia River watershed have shown *P. forbesi* to consume ciliates and diatoms, and may compete for similar prey items as *Diacyclops thomasi*, a seasonally dominant cyclopoid copepod in Vancouver Lake (Rollwagen-Bollens et al. 2013; Bowen et al. 2015). Although we rarely observed *P. forbesi* adults in Vancouver Lake, the increased abundance of calanoid copepods in general in the late spring of 2011 coincided with an overall decrease of other copepods, cladocerans, and rotifers. A similar effect was observed during the late summer of 2011, but a substantial increase of *Brachionus* sp. abundance and the presumed resulting competition for resources might also have contributed to the drastic declines of non-calanoid copepods, cladocerans, and other rotifers compared to previous summers.

Havel et al. (2005) predicted that landscapes consisting of lakes and reservoirs, such as the Columbia River basin, are more susceptible to invasions by non-native species. The Columbia River is a major com-

mercial waterway and can be considered a “hotline” in that it acts as a biodiversity corridor through several different ecosystems throughout the northwest United States and Canada (Décamps 2011). Vancouver Lake is also a recreational destination for sailing, rowing, and fishing, and is directly connected with the Columbia River. Recreational boating has been demonstrated to be an effective vector for spreading invasive plankton (Kelly et al. 2013a). Moreover, the lower Columbia River hosts several other invasive zooplankton species that have not yet been detected in Vancouver Lake (Cordell et al. 2008; Bollens et al. 2012; Breckenridge et al. 2015; Dexter et al. 2015). This suggests that future invasions of Vancouver Lake are likely, lending greater urgency for the need to examine interactions between invasive and native zooplankton, and their implications for higher trophic levels and food web dynamics.

Management implications for Vancouver Lake: a model shallow lake system

Intensive observational studies of shallow, tidally influenced freshwater ecosystems, such as Vancouver Lake, are uncommon. Thus, Vancouver Lake serves as a model system for examining multi-stressor effects in shallow lakes, and the ecosystem consequences and management implications of these stressors.

Eutrophication, as measured by increased turbidity, nutrient and chl-*a* concentrations, and cyanobacteria biomass – common problems facing freshwater systems worldwide – significantly influenced the composition and abundance of the zooplankton community in Vancouver Lake, indicating that management to reduce nutrient addition may also impact zooplankton assemblages with potential effects on planktonic food web dynamics. The presence of invasive zooplankton taxa also resulted in changes to the overall zooplankton community in Vancouver Lake, with potential management implications. Furthermore, there may be a negative interaction in Vancouver Lake between eutrophication (e.g. cyanobacterial blooms) and invasive zooplankton. For instance, in 2010 and 2011 there was a numerical increase in invasive zooplankton species at a time of year (late summer) when cyanobacteria had bloomed in previous years, but did not occur in these two years. While speculative, this suggests that the absence of cyanobacteria blooms in 2010 (Lee et al. 2015a) and 2011 (VLWP 2011) may have facilitated the numerical increase of invasive zooplankton. If cyanobacterial blooms negatively affect invasive zooplankton, management actions aimed at reducing cyanobacterial blooms may contribute to the success and

establishment of introduced species such as *B. coregoni* and *P. forbesi*. Thus, further research is needed to examine interactions between cyanobacterial blooms and invasive zooplankton species.

Finally, long term investigations of understudied systems such as Vancouver Lake are needed to better understand the effects of multiple environmental stressors to help guide future management and restoration efforts, particularly under conditions of climate warming. For example, climate change has been indicated as the cause of changes in zooplankton community dynamics (Gyllström et al. 2005) and increases in temperature have been demonstrated to alter zooplankton community composition by selecting for life history characteristics more resilient to warmer temperatures (Dijkstra et al. 2011). Additionally, asynchronous systems, where the timing of the presence of predator and prey are mismatched, can occur as a result of changes in seasonal meteorological conditions (Straile 2000; Anneville et al. 2010; Wagner et al. 2013). This may be exacerbated if either predator or prey species become replaced by non-native species. Understanding possible interactions among multiple stressors (e.g., eutrophication, invasive species, and climate change) will be important to better managing impaired, interconnected freshwater ecosystems.

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