

Research Article

Seasonal dynamics of zooplankton in Columbia–Snake River reservoirs, with special emphasis on the invasive copepod *Pseudodiaptomus forbesi*

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Abstract

The Asian copepod *Pseudodiaptomus forbesi* has recently become established in the Columbia River. However, little is known about its ecology and effects on invaded ecosystems. We undertook a 2-year (July 2009 to June 2011) field study of the mesozooplankton in four reservoirs in the Columbia and Snake Rivers, with emphasis on the relation of the seasonal variation in distribution and abundance of *P. forbesi* to environmental variables. *Pseudodiaptomus forbesi* was abundant in three reservoirs; the zooplankton community of the fourth reservoir contained no known non-indigenous taxa. The composition and seasonal succession of zooplankton were similar in the three invaded reservoirs: a bloom of rotifers occurred in spring, native cyclopoid and cladoceran species peaked in abundance in summer, and *P. forbesi* was most abundant in late summer and autumn. In the uninvaded reservoir, total zooplankton abundance was very low year-round. Multivariate ordination indicated that temperature and dissolved oxygen were strongly associated with zooplankton community structure, with *P. forbesi* appearing to exhibit a single generation per year. The broad distribution and high abundance of *P. forbesi* in the Columbia–Snake River System could result in ecosystem level effects in areas intensively managed to improve conditions for salmon and other commercially and culturally important fish species.

Key words: Columbia River, invasive copepods, seasonal dynamics, community structure, zooplankton, indicator species

Introduction

Understanding the seasonal dynamics and ecological effects of invasive zooplankton will help managers understand how non-native species are affecting important ecosystem services such as water quality, fisheries and biodiversity. Many studies have addressed the ecological effects of non-native species (Simberloff and Von Holle 1999; Mack et al. 2000; Mooney and Cleland 2001; Sakai et al. 2001), but far fewer have focused on zooplankton (Bollens et al. 2002). Some invasive zooplankton have been shown to affect ecosystem function and structure. For example, the invasive zooplankter *Mnemiopsis leidyi* (Agassiz, 1865), a ctenophore native to the western Atlantic coasts, has had significant trophic effects on food webs in the Black, Caspian, and North Seas (Shiganova et al. 2004; Finenko et al. 2006; Oguz et al. 2008; Roohi et al. 2008; Roohi et al. 2010; Riisgård et al. 2012). Another example is the predatory cladoceran

Bythotrephes longimanus (Leydig, 1860), which has greatly reduced zooplankton species richness and overall plankton abundance in the Great Lakes of North America since its introduction from the Black Sea (Yan et al. 2001; Boudreau and Yan 2003; Strecker and Arnott 2005; Strecker et al. 2006; Strecker and Arnott 2008). Both of these invasions occurred in the 1980s, likely as a result of ballast water exchange.

Several non-native zooplankton species have been introduced to multiple estuaries of the northeast Pacific Ocean, apparently as a result of ballast water discharge (although other vectors may be possible too, e.g., Lodge (1993), Temnykh and Nishida (2012), Suárez-Morales and Arroyo-Bustos (2012), Rothlisberger and Lodge (2013)). For instance, in the San Francisco Estuary (SFE), comprising both the San Francisco Bay and the Sacramento/San Joaquin Delta, no less than nine invasive copepod species have been documented as having successfully established populations (Kimmerer et al. 1994; Bollens et al. 2002; Hooff

and Bollens 2004; Cordell et al. 2007; Bollens et al. 2011; Bollens et al. 2014). More specifically, the invasive copepods *Oithona davisae* (Ferrari and Orsi, 1984), *Limnithona tetraspina* (Zhang and Li, 1976), and *Pseudodiaptomus marinus* (Sato, 1913) make up a significant percentage of the zooplankton community in summer and autumn in the lower SFE (Bollens et al. 2011; Bollens et al. 2014). A fourth introduced carnivorous copepod, *Tortanus dextrilobatus* (Chen and Zhang, 1965), also reaches peak abundances in the SFE during autumn (Hooff and Bollens 2004). These invasive zooplankton species are suspected of first colonizing the SFE, and then making their way into nearby Northeast Pacific estuaries, including the Columbia River Estuary (CRE) (Cordell et al. 2008; Bollens et al. 2012). The genus *Pseudodiaptomus* is a well-known estuarine invader worldwide, particularly *P. marinus* (Fleminger and Kramer 1988; Barry and Levings 2002; Jiménez-Pérez and Castro-Longoria 2006; Medeiros et al. 2006; Brylinski et al. 2012). A congener of *P. marinus*, *Pseudodiaptomus inopinus* (Burckhardt, 1913), has become established in the Chehalis River Estuary in Washington State, where it peaks in abundance in the summer and autumn, and is a large part of the diet of invertebrate predators (Bollens et al. 2002; Cordell et al. 2007). A second congener, *Pseudodiaptomus forbesi* (Poppe and Richard, 1890), was discovered in the SFE in 1987 and in the CRE in 2002, and is thought to have arrived at both locations via ballast water exchange (Orsi and Walter 1991; Cordell et al. 2008). The seasonal dynamics of *P. forbesi* near the mouth and the freshwater reach of the CRE has recently been considered by Bollens et al. (2012) and Dexter et al. (unpubl. data), respectively, but the dynamics of this species farther upstream in the Columbia-Snake River complex remains unknown.

The Columbia River is vital to both the ecology and economy of the Pacific Northwest of the United States. The Columbia River has been highly modified by man, often to the detriment of important ecological and economic resources. Pacific salmon (*Oncorhynchus* spp.) were once abundant in the Columbia River system but now many populations are listed as threatened or endangered under the U.S. Endangered Species Act. Hydroelectric development and the concomitant effects of the impoundment of the Columbia and Snake Rivers are commonly thought to be major factors in the decline of Pacific salmon. Pacific salmon are also a culturally significant species to indigenous tribes. The development of the Columbia

River Basin has also resulted in an increase in global shipping traffic, a possible vector for invasive species.

The distribution and abundance of Columbia-Snake River zooplankton—either native or invasive—have been little studied in the past. Scarola (1968) briefly summarized the zooplankton species present in the McNary Dam reservoir over one year, with weekly sampling in the summer and irregular sampling in other seasons. Harris (1979) described the zooplankton of several lakes and reservoirs in the Lower Snake River drainage; however this study only listed the dominant crustacean species present in summer, winter, and spring. Neitzel et al. (1983) carried out weekly surveys of zooplankton over the course of a year in the Hanford reach of the Columbia River, and described how their relative abundances varied seasonally.

The arrival and subsequent establishment of *P. forbesi* has potential implications for the native zooplankton community of the Columbia-Snake River system, as well as for fishes, notably the endangered and threatened salmonid species that are native and endemic to this river system. Columbia-Snake River zooplankton species have been described in reference to the diets of migrating salmonids, e.g., in the Lower Columbia River Estuary (Craddock et al. 1976; Kirn et al. 1986), the Middle Columbia River (Dauble et al. 1980; Muir and Emmett 1988; Rondorf et al. 1990; Muir and Coley 1996), and the Lower Snake River (Rondorf et al. 1990; Muir and Coley 1996). However, these studies rarely included detailed (species-specific) analyses of zooplankton. Haskell et al. (2006) examined American shad (*Alosa sapidissima* Wilson, 1811) diet and physical and environmental forcing of zooplankton from 1994 to 1996, but only from August to November. While these studies took place in and around the downstream reservoirs of the mainstem Columbia-Snake River reservoirs, there are no previous studies that include multi-year, monthly surveys of zooplankton communities in multiple reservoirs within the system. Specifically in regard to *P. forbesi*, previous studies have been limited to matters of distribution (Bollens et al. 2002; Cordell et al. 2008; Bollens et al. 2012; Breckenridge et al. 2014), diet (Ger et al. 2009; Ger et al. 2010; Bowen et al. unpubl. data) or predation (Adams et al. unpubl. data).

Thus this study had three objectives. The first was to quantify and describe the seasonal and interannual abundance and distribution of zooplankton in four Columbia-Snake River reservoirs, including three reservoirs with and one reservoir without the invasive copepod *P. forbesi*. The second was to

relate variation in these zooplankton assemblages to various physical and biological factors. The third objective was to describe the seasonal succession of life-stages of the invasive *P. forbesi* in these reservoirs.

Methods

Study site

The Columbia River drains a basin of 671,000 km², containing land in the United States and Canada (Ebel et al. 1989). The Snake River is the largest tributary of the Columbia River and comprises 49% of the Columbia's total catchment area (Ebel et al. 1989). Because the Columbia–Snake River system drains a variety of climate zones from alpine to coastal, we sampled reservoirs that exhibited variation in topography and variety in sub-basin terrestrial habitat type. Samples were collected in four reservoirs: the Bonneville, John Day, and Priest Rapids dam reservoirs on the Columbia River and the Ice Harbor dam reservoir on the Snake River (Figure 1, Table 1). The dominant land types surrounding the John Day, Ice Harbor, and Priest Rapids reservoirs are shrub-steppe and agricultural land. The Bonneville reservoir intersects the Cascade mountain range, leading to a set of characteristics unique amongst the reservoirs in this study. The eastern (upstream) half of the Bonneville reservoir is surrounded by interior grassland, mixed conifer forest, and Ponderosa Pine-dominated forest. The western (downstream) half of the Bonneville reservoir lies within mesic lowland conifer-hardwood forest.

Field methods

Zooplankton and environmental samples were collected monthly from the forebay of each reservoir, between July 2009 and June 2011. All sampling sites were between 3 and 8 km upstream from their respective dams at the deepest point in the river (Bonneville = 27 m, John Day = 55 m, Ice Harbor = 36 m, Priest Rapids = 26 m). This point was typically at or near the center of the river, except at Bonneville, where the deepest waters occur close to the north shore. Triplicate zooplankton samples were collected at each site via vertical haul of a 0.5-m diameter, 73- μ m mesh zooplankton net from 0.5 m off the reservoir bottom to the surface. A flow meter in the mouth of each net determined the volume of water filtered. Samples were rinsed from the net and preserved with a 5% solution of buffered formalin.

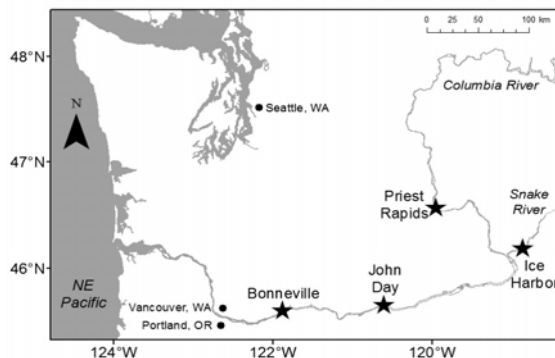


Figure 1. Locations of sampled reservoirs. Stars indicate sampling sites.

For each zooplankton tow, environmental measurements (temperature, dissolved oxygen, turbidity, conductivity, and pH) were collected at the surface using a YSI 6920 V2 sonde multimeter. During year two (2010–2011) only, surface water for chlorophyll measurements was collected with a clean bucket and subsamples placed in opaque 60 ml bottles. Samples were kept cold until they could be filtered and chlorophyll *a* concentrations determined in the lab, within 48 hours of collection. Mean monthly freshwater discharge, as measured at the Beaver Army Terminal (Station 14246900), was obtained from the National Water Information System (NWIS 2012). This station is located 146 km downstream of Bonneville Dam, and was chosen in order to describe seasonal and interannual patterns of freshwater discharge in the Columbia River watershed as a whole.

Laboratory methods

Aliquots from each preserved zooplankton sample were taken from a homogenized whole sample with a Hensen-Stempel pipette. Individuals were then identified to the lowest possible taxon (Edmondson 1959; Balcer et al. 1984; Thorp and Covich 2010; Cordell 2012) using a Nikon SMZ 1500 microscope, and enumerated until 300 non-naupliar specimens were identified. Thorp and Covich (2010) identified an *Acanthocyclops vernalis-robustus* species complex, and we have used this key to identify the copepod discussed in this study as *A. robustus* (Sars, 1863). Chlorophyll *a* concentrations were determined fluorometrically (Holm-Hansen and Riemann 1978). The 60 mL water samples were vacuum-filtered through Whatman 25 mm GF/F glass microfiber filters, then placed in a vial and treated with acetone.

Table 1. Selected characteristics of reservoirs in this study. Surface area, capacity, and max depth are data from the National Inventory of Dams. Retention time was estimated using data from United States Army Corps of Engineers and Columbia Basin Fish Passage Center.

	Bonneville	John Day	Ice Harbor	Priest Rapids
River	Columbia	Columbia	Snake	Columbia
Length	75 km	122 km	51 km	29 km
Surface area	83.4 km ²	222.6 km ²	33.9 km ²	30.7 km ²
Capacity	3.42×10^8 m ³	6.54×10^8 m ³	5.01×10^8 m ³	2.36×10^8 m ³
Max depth	30 m	56 m	34 m	34 m
<i>P. forbesi</i>	present	present	present	absent
Retention time	2.5 days	8.9 days	6.5 days	1.3 days

Table 2. List of mesozooplankton species identified, ranked by total abundance. Taxa not found in <5% of samples and not included in statistical analyses: Mollusca, Arachnida, Isopoda, and Mysidae. Copepod nauplii (n=22,713) and *P. forbesi* nauplii (n=17,623) also not included in statistical analyses.

	Taxon	Total Number	Percentage
Cladocera	<i>Bosmina longirostris</i>	11,304	12.51
	<i>Daphnia retrocurva</i>	4,228	4.68
	<i>Eurycercus lamellatus</i>	1,994	2.21
	<i>Eubosmina coregoni</i>	1,806	2.00
	Other <i>Daphnia</i>	768	0.85
	<i>Chydorus sphaericus</i>	561	0.62
	<i>Moina</i> sp.	316	0.35
	<i>Diaphanosoma birgei</i>	115	0.13
	<i>Ceriodaphnia laeustris</i>	94	0.10
	<i>Camptocercus</i> sp.	30	0.03
	<i>Leptodora kindtii</i>	10	0.01
Copepoda	<i>Pseudodiaptomus forbesi</i>	11,605	12.85
	Diaptomidae juveniles	8,359	9.25
	<i>Leptodiaptomus ashlandi</i>	1,690	1.87
	<i>Skistodiaptomus</i> spp.	541	0.60
	<i>Epischura laeustris</i>	44	0.05
	Cyclopoid juveniles	20,426	22.61
	<i>Diacyclops thomasi</i>	2,962	3.28
	<i>Acanthocyclops robustus</i>	797	0.88
	<i>Eucyclops</i> sp.	93	0.10
	<i>Mesocyclops edax</i>	72	0.08
	Harpacticoida	1,226	1.36
Rotifera	<i>Brachionus</i> sp.	12,838	14.21
	<i>Asplanchna</i> sp.	4,928	5.46
	<i>Kellicottia</i> sp.	522	0.58
	<i>Keratella</i> sp.	85	0.09
	<i>Polyarthra</i> sp.	74	0.08
Other	Oligochaeta	1,200	1.33
	Polychaeta	565	0.63
	Nematoda	453	0.50
	Chironomidae	329	0.36
	Amphipoda	116	0.13
	Bivalvia	80	0.09
	Ostracoda	38	0.04
	Tardigrada	31	0.03
	Insecta	25	0.03
Total		90,325	100.00

After 24 hours of acetone immersion, the solution was poured into a glass vial and chlorophyll *a* concentration was measured using a Turner Designs 10-AU fluorometer.

Statistical analyses

Zooplankton densities (individuals/m³) were calculated based on microscopic counts and volumes filtered. Due to their extremely high abundance, copepod nauplii were not included in statistical analyses, but were included in *P. forbesi* life stage analysis. Species present in <5% of samples were also not included in statistical analyses (Table 2). Kruskal-Wallis (χ^2), a non-parametric analysis of variance, was used to test for differences in environmental variables (Zar 1999).

The relationship between zooplankton community structure and environmental forcing was analyzed using non-metric multidimensional scaling (NMDS), an ordination technique (Clarke 1993; McCune and Grace 2002). NMDS ordination used Sorenson's (Bray-Curtis) distance measure, and the ordination that best described the data while maintaining a low stress value was chosen (Kruskal and Wish 1978). Environmental variables were correlated to ordination axes using Pearson's *r*. This ordination technique was accompanied by cluster analysis, which clearly defined distinct zooplankton communities. Cluster analysis used Sorenson's (Bray-Curtis) distance measure, and flexible-beta linkage method, with $\beta = -0.25$. Cluster Analysis revealed four distinct clusters within the ordination that were defined by similarity between the respective zooplankton samples and which were strongly indicative of seasons. A summer/autumn cluster (July–October) was characterized by a mean temperature of 19.0°C and high zooplankton abundance. A winter cluster (December–June) was characterized by a mean temperature of 8°C and low zooplankton abundance. A spring cluster (March–May) was characterized by temperatures similar to the winter cluster (mean=9°C), but exhibited higher zooplankton abundance than winter. Finally, a transitional cluster (July, November–December) was characterized by a mean temperature of 13.9°C and moderate zooplankton abundance. These clusters formed the basis of subsequent analyses described below, but will not be discussed further. Finally, Indicator Species Analysis defined the specific taxa that were most strongly descriptive of each cluster, based on faithfulness and exclusivity of each species to that group (Dufrêne and Legendre 1997). Species that had Indicator Values five times greater in a group than any of

the other three groups were considered strong indicator species of that group. Multidimensional analyses were performed using the PC-ORD (version 5.10; MjM Software Design, Gleneden Beach, Oregon) statistical software package for Windows. The stress value provided by PC-ORD is a value between 0 and 100 that provides a measure of goodness of fit of the ordination to the underlying similarity matrix. Univariate statistical tests, ANOVAs, and non-parametric equivalents were performed using SigmaStat (version 3.5; SigmaStat Software, Inc., Richmond, California) for Windows.

Results

Seasonal and interannual variation of zooplankton and environmental variables

A total of 130,661 zooplankton specimens from 61 taxa were identified from 288 samples (Table 2). The most abundant species were the invasive calanoid copepod *P. forbesi*, the cladoceran *Bosmina longirostris* (Müller, 1776), the rotifer *Brachionus* sp., and the cyclopoid copepod *Diacyclops thomasi* (Forbes, 1882). Copepods made up 52.9% of the total number of identified specimens, with cladocerans and rotifers making up 23.5% and 20.4%, respectively. Copepod nauplii, identified as either belonging to *P. forbesi* or not, were present in most samples. Total mesozooplankton abundance was significantly greater in 2009–2010 than 2010–2011 ($p=0.009$, $df=1$, Figure 2). Conversely, mean monthly river discharge was significantly greater in 2010–2011 than in 2009–2010 ($\chi^2=13.231$, $p<0.001$, $df=1$), and varied seasonally in the predicted manner (higher in late winter–early summer, and lower in early summer–late winter; Figure 2). Water temperature ranged from 4°C in January and February to almost 25°C in July and August (Figure 2), but was not significantly different between sites ($\chi^2=0.355$, $p=0.949$, $df=3$) or years ($\chi^2=0.379$, $p=0.538$, $df=1$).

Zooplankton community structure showed consistent patterns of seasonal variation and succession (Figures 3, 4). The invasive copepod *P. forbesi* dominated the zooplankton community in three of four reservoirs during autumn, and rotifers dominated in spring when *P. forbesi* was very rare. A pulse of *P. forbesi* occurred in late summer and early autumn in Bonneville and John Day reservoirs, but was delayed and muted in Ice Harbor, and was non-existent in Priest Rapids (Figure 3). Overall zooplankton abundance was very low year-round in the uninvaded Priest Rapids reservoir (Figure 3).

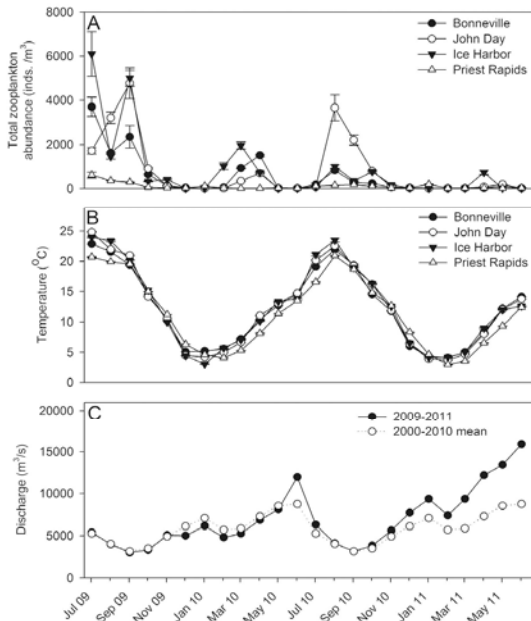


Figure 2. Mean (± 1 SE) total zooplankton abundance (individuals/m³) (A) and mean (± 1 SE) surface temperature (B) of the sample sites in this study. Panel C shows mean monthly discharge of the Columbia River, both during the study (closed circles) and a ten-year average (open circles).

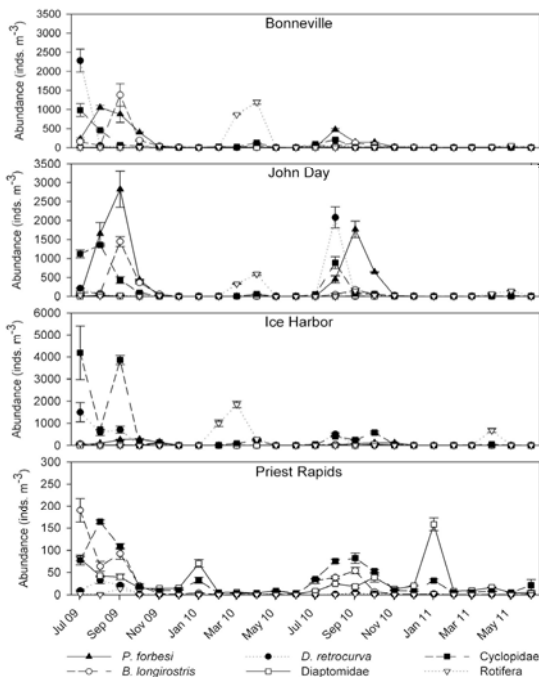


Figure 3. Mean (± 1 SE) abundance (individuals/m³) of main zooplankton taxa in each of the four Columbia–Snake River system reservoirs. Note different scale on Ice Harbor and Priest Rapids panels.

Multi-dimensional zooplankton community analysis

NMDS ordination produced a three-dimensional solution with a stress of 8.33 after 119 iterations that explained 68.1% of the seasonal and interannual variation in the mesozooplankton communities (Figure 5). This is considered to be a “good” level of stress for a NMDS ordination, and thus this ordination has a low risk of misinterpretation (Kruskal and Wish 1978; McCune and Grace 2002). After interpreting the scree plot, the ordination with the highest degree of parsimony between number of axes and amount of variation explained was one with 3 axes. This ordination was significantly different than that of a randomized Monte Carlo solution ($p=0.004$).

The NMDS ordination revealed a clear seasonal progression of zooplankton communities in the invaded reservoirs (Figure 6). Axis 1 appeared to explain little variation in the system (16.1%), except for a group of samples in which the zooplankton community was dominated by rotifers, and was quite different from the rest of the samples in the ordination. As a result, Axis 1 partially described a gradient of species richness and (Shannon) diversity. Axis 2 described the largest amount of variation (46.7%) in the zooplankton community data. Summer and winter communities occurred high and low on this axis, respectively. Additionally, overall zooplankton abundance tended to vary along Axis 2, with increasingly higher total abundance occurring higher on this axis. A trend becomes clear when interpreting these axes of variation between each of the four reservoirs. The three reservoirs that have been invaded by *P. forbesi* (Bonneville, John Day, and Ice Harbor) show a consistent, seasonal pattern of variation in zooplankton abundance and community structure. The zooplankton community in the uninvaded Priest Rapids reservoir displayed minimal variation over the course of the two-year study, and was similar to the communities of the three reservoirs invaded by *P. forbesi* only during the winter (Figures 5, 6).

The environmental variables correlated most strongly with Axis 1 were species richness (Pearson's $r=-0.652$) and species diversity ($r=-0.659$). Axis 2 was strongly correlated with temperature ($r=0.754$) and total zooplankton abundance ($r=0.726$), and negatively correlated with dissolved oxygen ($r=-0.592$) and freshwater discharge ($r=-0.487$). We excluded Axis 3 from interpretation due to low explanatory power (5.3% of variation) and poor correlation with biotic and abiotic variables. When the ordination

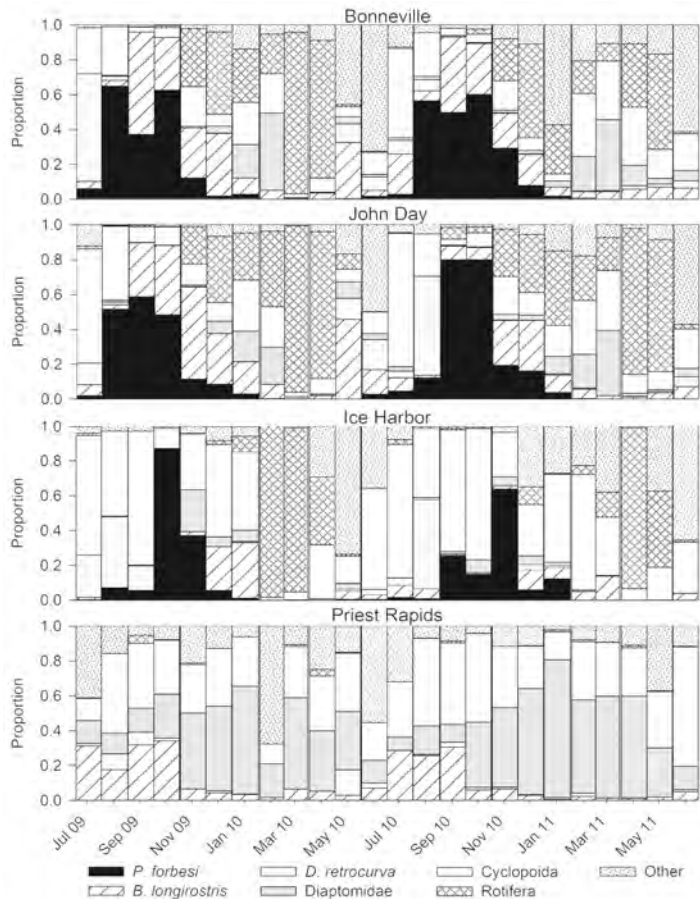


Figure 4. Mean monthly proportional abundance of main zooplankton taxa in each of four Columbia – Snake River reservoirs from July 2009 to June 2011.

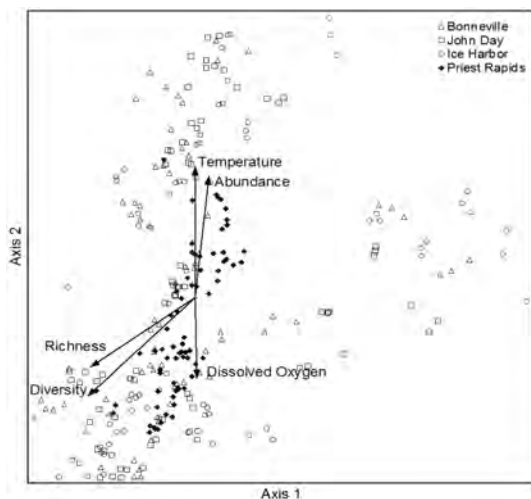


Figure 5. Joint plot of NMDS ordination of zooplankton samples from Middle Columbia and Snake River reservoirs, July 2009 – June 2011 and environmental correlates of ordination axes. Vector cutoff for correlates is $r^2=0.3$. Stress = 8.33. Samples are coded by reservoir.

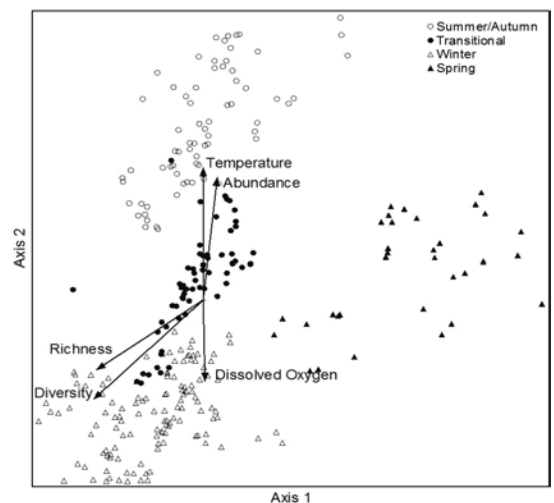


Figure 6. Joint plot of NMDS ordination of zooplankton samples from Middle Columbia and Snake River reservoirs, July 2009 – June 2011, and environmental correlates of ordination axes. Vector cutoff for correlates is $r^2=0.3$. Stress = 8.33. Samples are coded by clusters defined in cluster analysis.

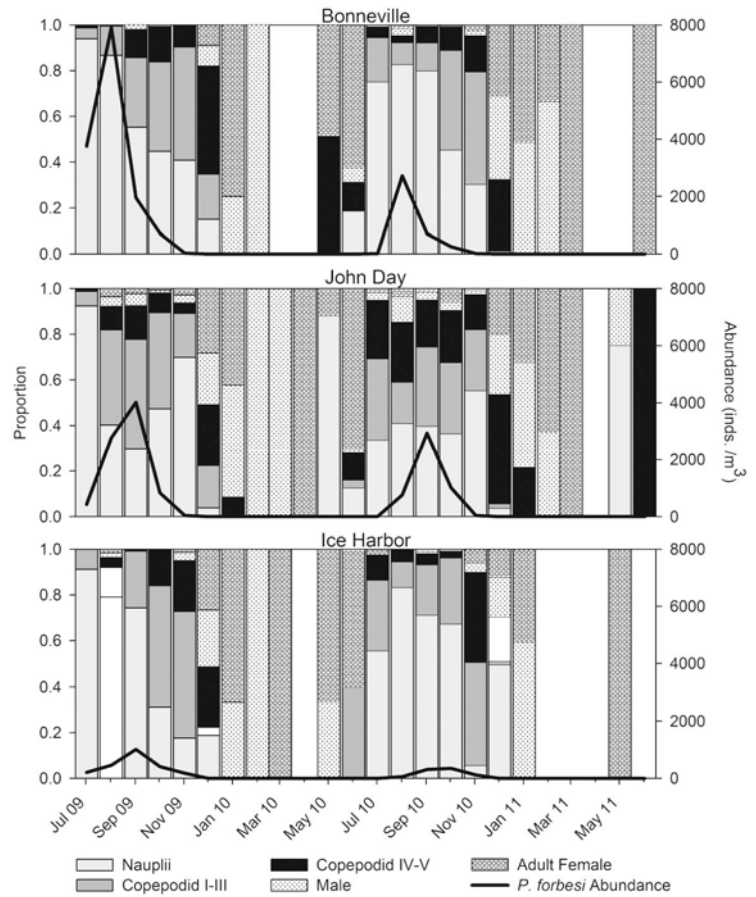


Figure 7. Life stage distribution of *P. forbesi* in three invaded reservoirs of the Columbia–Snake River system.

Table 3. Indicator values for taxa with significant Monte Carlo *p*-values (<0.05) for season-based clusters. Bold values indicate strong indicator values for respective cluster (5x that of any other cluster).

		Summer/Autumn	Transitional	Winter	Spring	<i>p</i> -value
Cladocera	<i>Bosmina longirostris</i>	78	15	0	2	0.0002
	<i>Daphnia</i> spp.	31	8	0	0	0.0164
	<i>Daphnia retrocurva</i>	61	1	0	0	0.0002
	<i>Eubosmina coregoni</i>	16	9	0	0	0.0004
	<i>Eurycerus lamellatus</i>	1	0	1	49	0.0014
Copepoda	<i>Pseudodiaptomus forbesi</i>	99	0	0	0	0.0002
	Diaptomidae I-III	13	43	9	4	0.0008
	Diaptomidae IV-V	13	38	8	6	0.002
	<i>Leptodiaptomus ashlandi</i>	0	25	8	1	0.0478
	<i>Skistodiaptomus</i> spp.	9	35	1	0	0.0002
	Cyclopidae I-III	89	5	0	4	0.0002
	Cyclopidae IV-V	56	10	1	22	0.016
	<i>Diacyclops thomasi</i>	57	9	1	15	0.0022
	<i>Acanthocyclops robustus</i>	68	1	0	0	0.0002
Rotifera	<i>Asplanchna</i> sp.	9	14	1	46	0.0006
	<i>Brachionus</i> sp.	0	0	0	99	0.0002

is viewed along Axes 1 and 2 (Figure 5), seasonal and geographic variation in the zooplankton community can be described by 2 orthogonal gradients, one of water temperature and total zooplankton abundance, and the other of species richness and diversity.

As previously noted, chlorophyll *a* was only collected during the 2nd year of the study. When a NMDS ordination was run on year 2 data separately, chlorophyll *a* concentration did not correlate to zooplankton community variation on any axis, with the strongest Pearson's correlation of $r = -0.170$. Thus, chlorophyll abundance was not considered to have any significant explanatory power, and is not considered further.

Seasonal progression of P. forbesi life stages

The life stages of *P. forbesi* in the three invaded reservoirs showed a clear pattern of seasonal progression (Figure 7). The *P. forbesi* populations were dominated by nauplii in early to mid-summer, C I-III copepodites in late summer, and C IV-V copepodites in early autumn. Adults made up the majority of the population of *P. forbesi* from late autumn (high abundances) through spring (very low abundances) (Figure 7). While we did not assess the ovigerity of adult female *P. forbesi* (eggs can become detached during collection and processing of samples), eggs were qualitatively observed to be most abundant during late summer/early autumn and ceased to be present until late the following spring.

Indicator species analysis

Of the 36 species and life-stage groups that were included in the Indicator Species Analysis, 8 were strong indicators of a cluster (Table 3). The invasive calanoid copepod *P. forbesi*, the native cyclopoid copepods *D. thomasi* and *A. robustus*, and the cladocerans *B. longirostris* and *Daphnia retrocurva* (Forbes, 1882) were strong indicators of the summer/autumn cluster. The winter cluster had no significant indicator species associated with it, but was most accurately described by very low total zooplankton abundance and high species evenness. The cluster representing spring zooplankton communities was best described by the cladoceran *Eurycercus lamellatus* (Mueller, 1776) and the rotifer genera *Asplanchna* and *Brachionus*. Native calanoid copepod species *Leptodiaptomus ashlandi* (Marsh, 1893) and *Skistodiaptomus* spp. best described the fourth, transitional cluster.

Discussion

Zooplankton community and environmental forcing

The three invaded reservoirs in this study demonstrated the expected summer–autumn seasonal peaks in zooplankton abundance (Figures 3, 4), which were dominated by cladocerans, cyclopoid copepods, and *P. forbesi*. The peaks of the cladocerans *B. longirostris* and *D. retrocurva* in the early summer were consistent with other studies in the region, with *Daphnia* typically peaking just before *Bosmina* (Chapman et al. 1985; Haskell et al. 2006). *Diacyclops thomasi* accounted for the majority of the cyclopoid copepods in our study, with a small percentage made up of *A. robustus*. *Acanthocyclops robustus* was common in our samples, but never abundant. Similar to the findings of Bollens et al. (2012) in the Lower CRE, *P. forbesi* and *D. thomasi* in the reservoirs overlapped considerably in both time and space. It is currently unknown what sort of competition may be occurring between these species, in either adult or larval stages. Adult *D. thomasi* is known to consume ciliates and soft-bodied rotifers at very high rates (Brett et al. 1994; Brandl 2005; Rollwagen-Bollens et al. 2012). Adult *P. forbesi* is also known to consume ciliates, but can also effectively graze on diatoms and dinoflagellates (Bouley and Kimmerer 2006; Bollens et al. unpubl. data). Further studies of the actual (rather than the potential) competition between native and invasive copepods in the Columbia River, including various life history stages (e.g., adults vs. nauplii), are warranted.

Total zooplankton abundance in the four reservoirs was very low during the early winter months, and remained so until a small peak of native calanoid copepods occurred in mid- and late winter. The most abundant native calanoid copepod during this period was *L. ashlandi*. The much less common genus *Skistodiaptomus* co-occurred with *L. ashlandi* during the winter. Immediately after the small peak of native calanoids, a bloom of rotifers (*Asplanchna* and *Brachionus*) occurred in the spring (Figures 3, 4). This bloom is likely due to a presumed increase in primary productivity in the spring, as rotifer abundance has been shown to be explained more by food availability than by the abundance of predators (Yoshida et al. 2003). The trophodynamics of these rotifers have been extensively studied in other systems, and while both genera are known to be grazers, *Asplanchna* is also a voracious

facultative predator, with *Brachionus* being one of its prey (Nandini et al. 2003; Brandl 2005; Sarma and Nandini 2007; Van der Stap et al. 2007; Yin and Niu 2008; Wen et al. 2011).

Despite our ordination explaining 68% of the total variation in the zooplankton community of Columbia–Snake River reservoirs (Figure 5), a considerable amount of the overall variation remains unexplained. One recent study of the variation in crustacean zooplankton community structure of the Missouri River found that the distance from the closest upstream dam was the strongest explanatory factor (Dickerson et al. 2010). This metric was not strongly correlated with the variation in community composition in our data. However, we did not analyze samples along a longitudinal gradient within reservoirs. As stated previously, chlorophyll *a* concentration was also not strongly explanatory of zooplankton community variation. Some portion of the unexplained variation in our zooplankton data may be associated with nutrient concentrations (although our lack of correlation between zooplankton and chlorophyll may suggest otherwise) or residence time of reservoirs, variables that we did not routinely measure. Other factors that warrant further study include planktivory by fishes and invertebrates, competition between zooplankton taxa, and primary production (as opposed to merely using chlorophyll *a* as a proxy for standing stock of phytoplankton).

Spatial variation in zooplankton

Some of the spatial variability in zooplankton we observed among reservoirs may be due to how recently *P. forbesi* has invaded the system. While Ice Harbor was similar to Bonneville and John Day in overall community structure, the muted annual peaks of *P. forbesi* in this reservoir may be a result of the species' gradual and only recent upstream range expansion. That is, the Bonneville and John Day reservoirs may represent more "established" populations of *P. forbesi* in the system. In addition to occurring about a month later than in the other two invaded reservoirs, the conditions that define the summer cluster (high temperature and high zooplankton abundance) at Ice Harbor also last about a month longer. Because temperature was not different between sites, we suspect variation in nutrient availability (not measured) may influence primary productivity at Ice Harbor, thereby potentially limiting the annual peak of *P. forbesi*.

Different physical characteristics of the reservoirs and their geographic location within the Columbia

and Snake River systems may also be influencing between-site variation in zooplankton communities. For instance, the channel morphology, water retention times, and seasonal and daily flow patterns vary by reservoir in relation to their position within the Columbia River Basin and Columbia River hydro-electric system (Table 1). Daily and seasonal discharge patterns at individual dams are often the result of dam operations structured to meet regional energy demands (Hamlet et al. 2002; Payne et al. 2004). Seasonal discharge also varies because of efforts to improve survival of migrating juvenile salmon (Plumb et al. 2006). Regulated discharge patterns have been shown to affect plankton dynamics in other riverine systems (Perry and Perry 1991; Jassby 2005). Also, the floodplain and upland areas of the reservoirs we sampled have disparate vegetation communities that are structured by precipitation gradients, land use activities (e.g., agricultural, timber harvest), and urbanization.

Nutrient inputs resulting from agricultural practices, irrigation withdrawals and returns, and urbanization all have the potential to affect plankton dynamics (Kobbia et al. 1991; Henley et al. 2000; Jassby 2005). The Ice Harbor reservoir, formed by the last dam on the Snake River, is the shallowest reservoir in this study, and may have higher nutrient levels from agricultural runoff (U.S. Army Corps of Engineers 2000). In contrast, the Priest Rapids reservoir's comparatively low zooplankton abundance may be a result of the more arid landscape and lower agricultural runoff upstream of its dam (Arntzen et al. 2013). It seems unlikely that differences in the zooplankton abundance we observed would be due to differential planktivory in the reservoirs. The introduced American shad is highly abundant downstream in the Bonneville and John Day reservoirs where zooplankton abundances are high, but very low in abundance or non-existent in Priest Rapids (Hasselman et al. 2012). Shorter water residence times may also partially account for the differences in zooplankton abundance seen in the Priest Rapids reservoir, as well as the muted and delayed peak abundance of *P. forbesi* in the Ice Harbor reservoir. Low nutrient concentrations (and thus low primary productivity) and/or short water residence times may also explain the absence of a spring bloom in rotifer abundance in Priest Rapids that was present in the other three reservoirs. The Priest Rapids Reservoir also shows a markedly different zooplankton community overall, as it is dominated year-round by native calanoid (*L. ashlandi*) and cyclopoid (*D. thomasi*) copepods. Moreover, the Priest Rapids reservoir exhibited higher species

richness and species diversity than the invaded reservoirs in summer and autumn (Figures 5, 6), in large part due to the dominance of rotifers and *P. forbesi* in the invaded reservoirs during those times. The role of nutrients and residence times in influencing reservoir zooplankton communities warrants further attention.

Temporal variation in zooplankton

We observed striking seasonal variation in the zooplankton of the Columbia–Snake River reservoirs. The summer/autumn cluster of zooplankton was characterized by the indicator species *B. longirostris*, *D. retrocurva*, and native copepods *D. thomasi* and *A. robustus*, in addition to *P. forbesi*, which accounted for the vast majority of the crustacean zooplankton in the reservoirs. This suite of co-occurring cladoceran and copepod species has been previously documented in the Columbia–Snake River system (Scarola 1968; Harris 1979; Neitzel et al. 1983; Rondorf et al. 1990; Haskell et al. 2006) and elsewhere in the temperate northern hemisphere (Brooks and Dodson 1965; Yan and Pawson 1997; Mabee 1998; Semenova 2009).

The transitional cluster was strongly associated with the native calanoid copepods *L. ashlandi* and three species from the genus *Skistodiaptomus* (all in very low numbers). These copepods never dominated the zooplankton community of the invaded reservoirs to the extent that *P. forbesi* did, but in the uninvaded Priest Rapids reservoir, they accounted for a high proportion of total zooplankton abundance during most of the year (Figure 4).

No indicator species were associated with the winter cluster, when overall zooplankton abundance was very low. The low mean water temperature (8°C) during this period, and associated low primary productivity in winter, may explain this low abundance of zooplankton. A lack of indicator species in the winter cluster points to increased variation and diversity in the zooplankton communities that define this cluster.

The spring cluster was comprised of samples that were dominated by the rotifers *Asplanchna* and *Brachionus*. Rotifer populations have been shown to be strongly controlled by temperature (Wen et al. 2011), so it is possible that these rotifers are blooming in response to a temperature threshold. However, the average water temperature in our spring cluster (9°C) is not significantly different than that of the winter cluster. Another possible explanation is that *Brachionus* and *Asplanchna* are responding to an increase in primary production brought on by increased nutrient

availability in the spring. Yet another possible consideration is residence time; however peak rotifer abundance occurred at an annual low in residence time as a result of increased precipitation and snowmelt, as well as the associated increase in dam spill (Ebel et al. 1989; Thornton et al. 1990).

Differences in observed zooplankton abundances between years may have been due to different discharges in 2009 and 2010. All three major zooplankton groups (copepods, cladocerans, and rotifers) exhibited much-reduced peaks in 2010–2011 compared to 2009–2010, which corresponded with a significant increase in freshwater discharge in 2010–2011. With increased freshwater discharge, planktonic taxa may be advected through the reservoirs before they can take advantage of the increased primary productivity and refugia that reservoirs may provide.

The seasonal increase in crustacean zooplankton abundance we observed during summer and autumn is a typical pattern in temperate aquatic systems (Ebel et al. 1989; Yan and Pawson 1997; Kehayias et al. 2008; Stich et al. 2009; Bollens et al. 2012). Our ordination shows that water temperature is the environmental variable most strongly associated with increased zooplankton composition and abundance, especially *P. forbesi* (Figure 6). However, water temperature is likely only a proximate factor driving seasonal changes in zooplankton, and is probably affecting biotic processes (e.g., food, growth, reproduction, predation) that are the ultimate factors governing seasonal changes in zooplankton. Conversely, the concentration of dissolved oxygen was the next strongest environmental variable, and was inversely related to temperature, as expected.

The association of peak abundances of *P. forbesi* with seasonal peaks in water temperature (Spearman's $\rho = 0.624$, $p < 0.001$) has also been documented in the Lower Columbia River Estuary (Cordell et al. 2008; Bollens et al. 2012) and in the San Francisco Bay–Sacramento/San Joaquin Delta (Kimmerer et al. 1994; Kimmerer and Orsi 1996). This annual pattern of *P. forbesi* abundance may make this invasive species one of particular interest with respect to global climate change. That is, increasing regional temperatures and earlier onset of summer may affect the abundance and duration of *P. forbesi*'s summer/autumn dominance of the zooplankton community in Columbia–Snake River reservoirs. Because water temperatures greater than 25°C are inhospitable to the majority of temperate crustacean zooplankton species (Moore et al. 1996), global climate change may have the potential to cause

considerable biotic change to the already highly invaded Columbia and Snake Rivers.

Pseudodiaptomus forbesi and other invasive zooplankton

Pseudodiaptomus forbesi has now become well established in several Columbia–Snake River reservoirs, although its abundance varies geographically. In the Ice Harbor reservoir, this represents an invasion of more than 520 km upstream from the mouth of the Columbia River. Recent studies have found that reservoirs can facilitate invasions of zooplankton, possibly due to the physical characteristics of reservoirs that differ from those of natural lakes (Thornton et al. 1990; Havel et al. 2005; Banks and Duggan 2009), such as sedimentation rates, nutrient cycling, and thermal stratification. The *P. forbesi* specimens we collected in the Ice Harbor reservoir were upstream of five hydroelectric dams, and their presence there may have been facilitated by the reservoirs impounded by these dams. On the other hand, the Priest Rapids reservoir was not invaded by *P. forbesi*. This is likely due to the lack of barge traffic above the Hanford Reach of the Columbia River, which is located below the Priest Rapids Dam. This lack of barge traffic may deprive *P. forbesi* of a vector necessary for upstream dispersal. The Hanford Reach is the only remaining free-flowing reach of the Columbia River that is not tidally influenced, and may represent a physical barrier to the invasion of *P. forbesi*.

We have presented the first known description of the annual life stage distribution of *P. forbesi* in the Columbia River (Figure 7). *P. forbesi* in the reservoirs we sampled had a clear progression of life stages that suggests a single annual generation. The timing of ovigerity in *P. forbesi* is similar to that of two other invasive congeners, *P. inopinus* (Cordell et al. 1992; Cordell and Morrison 1996) and *P. marinus* (Grindley and Grice 1969; de Olazabal and Tirelli 2011). However, we are uncertain about the dynamics of the eggs of *P. forbesi*. Dormant eggs of freshwater copepods have been found to degrade more slowly than those of rotifers, meaning that the hardier copepod eggs may increase invasion potential (Briski et al. 2011). It is still unknown how *P. forbesi* might overwinter in the Columbia–Snake system. Thus, while the exact mechanism(s) remain to be elucidated, it is clear that *P. forbesi* has been able to successfully colonize and exploit the Columbia–Snake River system, such that it now dominates the late summer/autumn zooplankton community. These findings are similar to that of Bollens et al. (2012) in

the lower CRE, as well as Bouley and Kimmerer (2006) in the SFE.

As for the potential for longer term changes, our summer and autumn data from 2009–2011 can be compared with that of Haskell et al. (2006) from 1994–1996 to examine potential long-term (15-year) changes in both zooplankton abundance and community composition in the John Day reservoir. Total zooplankton abundances in 1995 and 1996 were similar to those in our study, but total abundance was noticeably higher in 1994 than in 2009–2011. The zooplankton community in the John Day reservoir from 1994 to 1996 was predominantly made up of the same taxa as in 2009–2011 (*Daphnia*, *Bosmina*, and copepods); however, the marked difference between the two study periods is the dominance of *P. forbesi* in 2009–2011. *Pseudodiaptomus forbesi* now makes up a significant portion of the zooplankton community during the late summer and autumn in the John Day reservoir, and has seemingly replaced a peak of cyclopoid copepods that was present during the same season in 1994–1996. Peaks in abundance of *Daphnia* in August and *Bosmina* in the autumn appear to have remained unchanged. A rank-abundance correlation analysis of summer/autumn samples from 1994–1996 and 2009–2011 in the John Day reservoir indicates that the crustacean zooplankton communities are not correlated (Kendall's $\tau_b = 0.083$, $p = 0.114$), suggesting possible long-term changes; although such a direct comparison is confounded by the use of different mesh sizes for sampling (153 μm by Haskell et al. 2006 vs. 73 μm in the present study) and different sampling depths. Substantial changes in zooplankton community structure after the establishment of an exotic zooplankter have been shown elsewhere, e.g., Harp Lake, Ontario, Canada (Yan and Pawson 1997; Yan et al. 2002), Lake Winnipeg, Manitoba, Canada (Suchy et al. 2010), Rybinsk Reservoir, Russia (Lazareva 2010), the Caspian Sea (Shiganova et al. 2004; Roohi et al. 2008; Roohi et al. 2010) and the San Francisco Estuary (Winder and Jassby 2011).

The invasion of *P. forbesi* in the Columbia–Snake Rivers could have important implications for higher trophic level species, some of which are also non-native invasive species. The most visible vertebrate invader in this system is the American shad (*Alosa sapidissima*), which may compete with native juvenile salmonids, especially Chinook salmon (*Oncorhynchus tshawytscha*, Walbaum, 1792), for zooplankton prey. Zooplankton make up the vast majority of the diet of juvenile American shad in the John Day reservoir, with a

significant portion made up of copepods (Haskell et al. 2006). Whether American shad prey on *P. forbesi* relative to native zooplankton is unknown. Hatchery-reared juvenile Chinook salmon were recently determined experimentally to prefer native cladocerans (*D. retrocurva*) over *P. forbesi*, but showed no preference between native *Cyclopidae* spp. and *P. forbesi* (Adams et al., unpubl. data). How these invasive zooplankton-fish interactions ramify through Columbia–Snake River food webs is currently unknown.

Summary

The results of our two-year, multi-reservoir study show four distinct seasonal zooplankton communities in Columbia–Snake River reservoirs. The invasive copepod *P. forbesi* was abundant in three reservoirs; the zooplankton community of the fourth reservoir consisted entirely of native species. The composition and seasonal succession of zooplankton were similar in the three invaded reservoirs: a bloom of rotifers occurred in spring, native cyclopoid and cladoceran species peaked in abundance in summer, and the invasive copepod *P. forbesi* was most abundant in late summer and autumn. In the uninvaded reservoir, total zooplankton abundance was very low year-round. Overall, seasonal patterns of zooplankton community structure were most strongly predicted by water temperature. *Pseudodiaptomus forbesi* appears to have a single annual generation, and to overwinter in these reservoirs as adults. The food web implications of the invasion of *P. forbesi* are largely unknown and thus warrant further research, especially as it pertains to various salmon populations that depend on zooplankton for food during critical points in their growth and development.

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