

Persistent vs. ephemeral invasions: 8.5 years of zooplankton community dynamics in the Columbia River

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Abstract

Nonindigenous aquatic species are becoming increasingly common in coastal and inland waters, largely due to the global transport of zooplankton via commercial shipping and recreational boating. The cost of mitigation and lost income due to invasive zooplankton is estimated in the billions of dollars annually, yet we know little about the temporal dynamics of these invaders. Analysis of an 8.5-year (June 2005–December 2013) zooplankton time series from the Columbia River revealed contrasting patterns of invasion dynamics between species, cyclical periods of community invasion, and key environmental variables that constrain populations of invasive zooplankton. We identified four seasonal zooplankton communities (autumn/invaded, winter/barren, spring/rotifer, and transitional) that are strongly correlated with changes in chlorophyll content and water temperature, with peak abundances of invasive zooplankters occurring during periods of maximum water temperature. Additionally, we observed contrasting patterns of phenology between persistent and ephemeral invasive populations, with successful invaders exhibiting delayed annual peaks in population abundance. Two invasive zooplankters—the copepod *Pseudodiaptomus forbesi* and larval Asian clam *Corbicula fluminea*—dominate the zooplankton community in late summer and early autumn. Likewise, our results support conclusions from a growing body of literature that delayed phenology may be a key functional trait for successful invaders.

Nonindigenous aquatic species are nearly ubiquitous in urbanized coastal estuaries, largely due to the global transport of zooplankton via ballast water (Carlton and Geller 1993; Ruiz et al. 2000; Bollens et al. 2002). Perhaps the most well-documented zooplankton invasions are the introductions of the ctenophore, *Mnemiopsis leidyi*, that led to fisheries collapses in the Black Sea (Shiganova 1998), and the introduction of zebra and quagga mussels that led to large-scale community shifts in the U.S. Great Lakes (Vanderploeg et al. 2002; Cuhel and Aguilar 2013). Economic impacts of invasive species total \$120 billion annually in the U.S. (Pimentel et al. 2005) and over 1000 aquatic introductions have been reported from Western Europe (Gollasch 2006).

On the U.S. West Coast, several estuaries have experienced high-impact invasions by exotic species of zooplankton resulting in large-scale community shifts (Cordell et al. 2008; Winder and Jassby 2011). In the U.S. Pacific Northwest, the list of successful planktonic invaders includes four species of calanoid copepods (*Sinocalanus doerrii*, *Limnoithona tetraspina*, *Pseudodiaptomus inopinus*, and *Pseudodiaptomus forbesi*), a bosminid cladoceran (*Bosmina coregoni*), and larval Asian clams (*Corbicula fluminea*) (Bollens et al. 2012; Smits

et al. 2013; Breckenridge et al. in press). Among these invasive species, copepods of the genus *Pseudodiaptomus* have emerged as the most seasonally abundant members of the zooplankton community in at least 11 rivers in Oregon and Washington (Bollens et al. 2002; Cordell et al. 2008; Bollens et al. 2012). In the Columbia River, *Pseudodiaptomus* is represented by *P. forbesi*, which attains seasonal abundances several orders of magnitude greater than all native species of zooplankton combined (Cordell et al. 2008; Bollens et al. 2012). While several studies have examined spatial distribution and abundance of invasive zooplankton in the Columbia River (Cordell et al. 2008; Bollens et al. 2012; Breckenridge et al. in press) the temporal dynamics of these species are not well understood. More broadly, explicit study of the temporal dynamics of aquatic invasive species beyond a typical 2–3 year study period has been relatively rare in any system (Bollens et al. 2002; Schaber et al. 2011).

Investigation of the temporal dynamics of an invader can yield key insights into ecological impacts and environmental constraints of aquatic invasions. For example, seasonal exclusion of native taxa and reduced community stability was observed in Bahia Blanca estuary, Argentina, after introduction of the copepod, *Eurytemora americana*, and the barnacle, *Balanus glandula* (Hoffmeyer 2004). Likewise, a

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detailed study of the phenology of *M. leidy* in the central Baltic Sea, Schaber et al. (2011) found that unfavorable water conditions during the breeding season precluded the existence of a self-sustaining population, and that seasonal blooms were likely due to annual reintroduction from more hospitable bodies of water.

Investigation of temporal dynamics can also provide insight into the general principles of invasion biology which can only be observed on decadal time scales, for example, invasion lag-phases (Mack et al. 2000) and cycles of boom and bust (Simberloff and Gibbons 2004). For example, Strayer et al. (2011) examined invasive zebra mussel populations in the Hudson River across a multidecadal time scale and found dramatic long-term changes in survivorship, age structure, and filtration rates that were undetected in several short-term studies.

After introduction, many invasive species experience a prolonged period of small population size before undergoing explosive population growth (Simberloff and Gibbons 2004). The duration of this invasion lag phase is highly variable between species and has been variously attributed to the difficulty of detecting exponential increase in small populations and/or genetic changes that occur after introduction (Mack et al. 2000). Because newly introduced species often undergo this period of low abundance, the early detection abilities of a given sampling program can be estimated from the detection rates of rare native taxa (Hoffman et al. 2011). Although it is difficult to completely exclude the possibility that a rare species has escaped observation, program-wide detection rates can provide an estimated maximum population size for any species that may have escaped detection (Hoffman et al. 2011). Although early detection of introduced species is now an objective of many zooplankton sampling programs, there have been few attempts to create a generalized detection model for rare taxa (but see Harvey et al. 2009; Hoffman et al. 2011).

Finally, a growing body of literature indicates that the annual timing of life history events can be an important factor in the success of invasive taxa. However, the study of phenology (broadly defined as the annual timing of biological processes) as a determinant of invasion success has been largely restricted to terrestrial plant communities (Godoy and Levine 2014). Several invasive members of the Columbia River zooplankton community exhibit a highly seasonal distribution (Bollens et al. 2012; Emerson et al. in press), but the degree to which these phenological patterns have influenced the invasion success of these species is unknown.

Here, we examine the phenology of invasive zooplankton in the Columbia River, as well as investigate broader issues of detection, persistence, and stability of invasive populations. We conducted our analyses using a time-series of monthly zooplankton samples collected from a single location over an 8.5-year time period. Specifically, we addressed the following four objectives: (i) identify and characterize

the seasonal zooplankton communities in the freshwater reach of the Columbia River estuary; (ii) quantify relationships between population cycles of invasive zooplankton species and environmental factors; (iii) compare the temporal dynamics of ephemeral introduced populations with those of persistent invasive populations; and (iv) evaluate the threshold of detection for our sampling program to detect rare and newly arrived species.

Methods

Site description

The Columbia River Basin drains an area of 669,300 km² covering portions of seven western U.S. states and the Canadian province of British Columbia (Simenstad et al. 1990). The Columbia River travels a length of 1954 km and discharges on average 224 billion m³ of annual outflow into the Pacific Ocean near Astoria, Oregon (Simenstad et al. 1990). Hydrology of the Columbia River is largely driven by accumulation of snowpack during winter and snowmelt during spring and early summer, although the approximately 214 impoundments of the river are presently managed so as to reduce seasonal variation in flow (Payne et al. 2004). Large commercial fisheries for anadromous fishes such as Steelhead trout, chinook, coho, chum, and sockeye salmon exist on the Columbia River, with several fish stocks falling under the protection of the U.S. Endangered Species Act (Simenstad et al. 1990).

Samples were collected from a pier in the Columbia River in Vancouver, Washington (45.6222°N, 122.6772°W), approximately 170 river km from the mouth of the Columbia River and 66 km downstream from the Bonneville dam, which is the furthest downstream impoundment on the river. The pier is approximately 20 m long and sampling occurred approximately 10 m from the shore, with water depths ranging seasonally from 8 m to 11 m. Hydrological conditions at this location are high flow with no thermal stratification, and mean water depth of 9.5 m. During our period of study, water temperature at river bottom ranged from 2.8°C to 21.8°C, with peak temperatures occurring in August. Chlorophyll *a* (Chl *a*) ranged from 0.1 µg L⁻¹ to 23.3 µg L⁻¹, with peak values occurring in the spring. The site is upstream of any saltwater intrusion but is tidally influenced.

Sample and data collection

We collected zooplankton samples and environmental data monthly between June 2005 and December 2013. On each date, we collected three replicate zooplankton samples via vertical net tows from a depth of one meter above river bottom to the surface using a 73-µm mesh, 0.5 m diameter ring net with attached flowmeter (General Oceanics). Plankton samples were fixed in a 5–10% buffered formalin solution in the field for later taxonomic processing. We measured salinity, temperature, and water clarity on each sampling date with a YSI 85 temperature/salinity probe (YSI

Incorporated) and Secchi disk. Temperature and salinity data were collected at two-meter intervals from surface to bottom. We collected triplicate samples of surface water using a bucket and kept them chilled in 70 mL opaque bottles until filtration and analysis for Chl *a* concentration. We obtained river discharge data from the United States Geological Survey (<http://www.waterdata.usgs.gov>).

Laboratory methods

A minimum of 200 non-naupliar organisms were subsampled from aliquots of each sample using a Stempel pipette, which were identified and enumerated using a Leica MZ6 stereomicroscope (Leica Microsystems). Identification to the genus or species level was made for most rotifers and microcrustaceans using Thorp and Covich (2010). We converted counts of individual taxa to density (individuals m^{-3}) by multiplying each count by the ratio (volume of sample : volume of subsample), and then dividing by the total volume of water sampled. Two replicate samples were processed for each date. We excluded nauplii abundance from all statistical analyses and aggregated rare taxa (those present in less than 5% of samples) into higher taxonomic groups for multivariate community analysis.

We measured Chl *a* concentrations fluorometrically via the acidification method (Strickland and Parsons 1972) using a Model 10-AU fluorometer (Turner Designs).

Statistical analyses

We conducted multivariate community analysis through Non-Metric Multidimensional Scaling (NMDS), cluster analysis, indicator species analysis, and the BIOENV correlation procedure according to Field et al. (1982) and Clarke and Ainsworth (1993). All multivariate analyses were conducted using the vegan package (Oksanen et al. 2013) for R version 2.15.2. Patterns of community similarity among samples were identified through NMDS ordination of untransformed species counts utilizing the Bray–Curtis distance measure (Kruskal 1964). The goodness of fit between data and NMDS results were evaluated by the unit of “stress,” which evaluates the degree of mismatch between the rank order of distances in the data and the rank order of distances on the ordination, with values less than 0.2 considered to be a good fit (Field et al. 1982). Each monthly sample was also assigned to a community group through hierarchical agglomerative clustering of monthly samples. Hierarchical clustering was conducted on a dissimilarity matrix of species abundances utilizing the Bray–Curtis distance measure and the group average linkage algorithm. The final number of community groups was chosen based on the maximum number of clusters that were stable across multiple cluster-building algorithms (complete linkage, single linkage, and group average) (Field et al. 1982).

Correlations between multivariate patterns of species abundance and environmental factors were identified with the BIOENV non-metric correlation procedure (Clarke and

Ainsworth 1993), which identifies the most parsimonious suite of environmental variables that explains variation in community structure between samples. BIOENV models are evaluated by the Spearman harmonic rank correlation, which can assume values ranging from 0 (no correlation between rank orders) to 1 (perfect correlation between rank orders) (Clark and Ainsworth 1993). Environmental factors contained within the best fit BIOENV model were plotted as vectors on the final NMDS ordination with the “envfit” function in the vegan package, which produces a goodness of fit statistic (r^2), the significance of which we assessed using a Monte Carlo randomization test based on 1000 permutations. Finally, we identified species that were characteristic of each community group through indicator species analysis of abundance values (Dufrene and Legendre 1997) and assessed statistical significance of association values through a Monte Carlo permutation test.

We estimated our sampling program’s threshold of detection for rare taxa through three complementary approaches. First, we estimated minimum population size required for reliable detection (defined as detection at least once per year) by regressing average population size against the number of observations for each taxon. Second, species accumulation curves were created to estimate the rate at which new species were detected with increased number of samples (Kindt et al. 2006). Finally, the true size of the species pool was estimated using the “specpool” function within the vegan package, which uses algorithms developed by Smith and van Bell (1984) to extrapolate the number of species in a given pool based on the distribution of species across samples.

Results

Seasonal variation of zooplankton and environmental variables

A total of 59,432 specimens from 63 taxa were identified from 205 zooplankton samples collected between June 2005 and December 2013. Table 1 shows the taxonomic diversity among these samples, excluding copepod nauplii and rare species. Copepods comprised 44.7% of all individuals, with cladocerans and rotifers accounting for 19.5% and 15.5%, respectively. Four species comprised 58.7% of total zooplankton abundance: the invasive calanoid copepod *P. forbesi* (20.2%), the cladoceran *Bosmina longirostris* (15.3%), the rotifer *Brachionus* sp. (12.1%), and larvae of the invasive bivalve *C. fluminea* (11.1%). Invasive taxa comprised 31.8% of total zooplankton abundance (Fig. 2). Previously unknown in the Columbia River Estuary, the invasive cladoceran *B. coregoni* was first detected in September 2006, and comprised 0.5% of total abundance across our time series (Table 2). Three of the invasive calanoid copepods previously recorded elsewhere in the Columbia River, *S. doerrii*, *L. tetraspina*, and *P. inopinus*

Table 1. List of zooplankton taxa present in samples collected from the Columbia River from June 2005 to December 2013. *P. forbesi* nauplii ($n = 10,619$) and other copepod nauplii ($n = 3322$) were excluded, as were taxa observed in less than 5% of samples. Species are ranked by total abundance and bold text denotes invasive species.

	Taxon	Total number	% Total	
Cladocera	<i>B. longirostris</i>	7956	17.50%	
	<i>Daphnia retrocurva</i>	717	1.58%	
	<i>Chydorus</i> sp.	242	0.53%	
	<i>B. coregoni</i>	237	0.52%	
	<i>Eurycerus</i> sp.	231	0.51%	
	<i>Moina</i> sp.	169	0.37%	
	<i>Chydorus sphaericus</i>	154	0.34%	
	<i>Alona quadrangularis</i>	131	0.29%	
	Other Cladocera	117	0.26%	
	<i>Daphnia mendotae</i>	111	0.24%	
	Copepoda	<i>P. forbesi</i>	10,501	23.10%
		Cyclopidae I-III	2820	6.20%
<i>D. thomasi</i>		1410	3.10%	
Harpacticoid		720	1.58%	
<i>Acanthocyclops robustus</i>		450	0.99%	
Diaptomidae I-III		432	0.95%	
Diaptomidae IV-VI		188	0.41%	
<i>Skistodiaptomus</i> sp. adult		85	0.19%	
<i>Leptodiaptomus</i> sp. adult		49	0.11%	
<i>Eucyclops</i> sp. Adult		30	0.07%	
<i>Mesocyclops</i> sp.		29	0.06%	
Other Calanoid		26	0.06%	
Rotifera		<i>Brachionus</i> sp.	6267	13.78%
		<i>Asplanchna</i> sp.	1796	3.95%
Other		<i>C. fluminea</i>	5776	12.70%
	Oligochaeta	1941	4.27%	
	Nematoda	987	2.17%	
	Polychaeta	944	2.08%	
	Chironomidae	524	1.15%	
	Tardigrada	110	0.24%	
	Hydra	85	0.19%	
	Amphipoda	57	0.13%	
	Insecta	46	0.10%	
	Arachnida	37	0.08%	
Ostracoda	31	0.07%		
Total		45,467	100.00%	

Table 2. Observations of *B. coregoni* in the Columbia River from June 2005 to December 2013

Year	Annual abundance (individuals m^{-3})	Peak abundance (individuals m^{-3})	Month of peak abundance
2005	—	—	—
2006	2.50	2.50	September
2007	—	—	—
2008	300	265	July
2009	211	169	May
2010	1010	846	April
2011	26.6	11.2	August
2012	90.3	45.8	October
2013	17.0	6.71	June

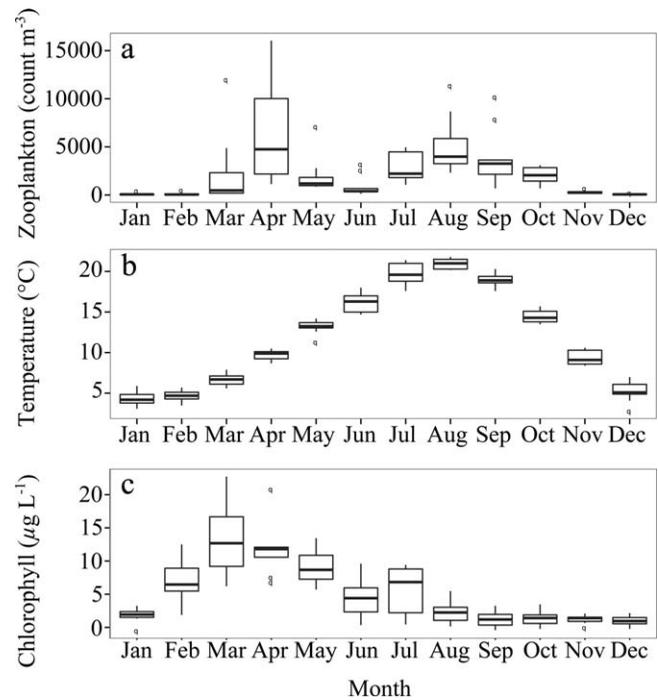


Fig. 1. Monthly values for (a) total zooplankton abundance, (b) water temperature, and (c) Chl *a* concentration. Outliers are points further than 150% of the distance between the median and the interquartile range.

(Cordell et al. 1992; Bollens et al. 2012), were not detected in our time series.

Total zooplankton abundance over the 8.5-year sampling period was bimodally distributed within an annual cycle (Fig. 1a), with an initial peak in early spring comprised primarily of native rotifers (*Brachionus* sp.), and a second peak in late summer-early autumn comprised primarily of the invasive copepod *P. forbesi* and the invasive bivalve *C. flumi-*

nea (Fig. 2a). Total zooplankton abundance ranged from 10 individuals m^{-3} to 16,032 individuals m^{-3} , with the proportion of invasive taxa ranging seasonally from 0% in late spring to a maximum of 97.2% in late summer (Fig. 2b).

Cluster analysis and indicator species analysis

Our hierarchical clustering of community data identified four community groups that were strongly indicative of seasons during the year. To simplify discussion of groups, we assigned each community group a name based on defining characteristics and seasonality. A late summer-early autumn

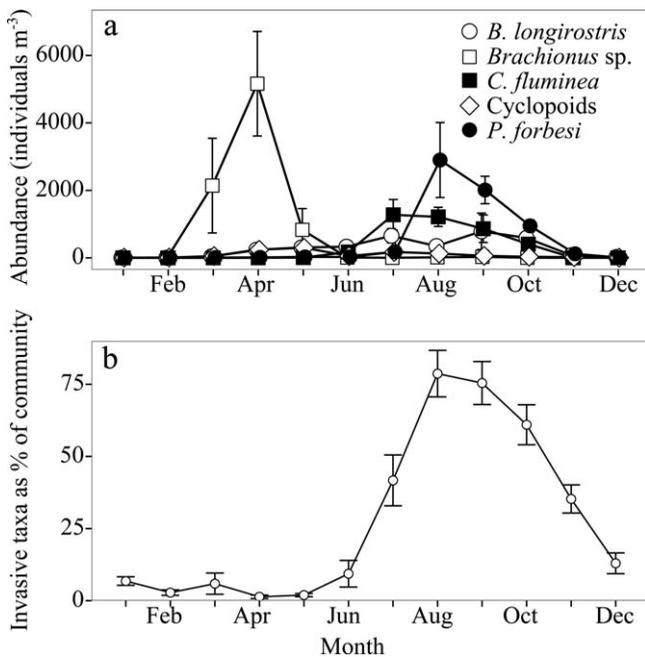


Fig. 2. (a) Mean (\pm SE) monthly abundance of the five most abundant zooplankton taxa and (b) Mean (\pm SE) monthly percentage of total zooplankton abundance comprised of invasive taxa. The five species shown in panel a comprise 90% of all zooplankton abundance observed during the period of study. *P. forbesi* and *C. fluminea* are invasive in the Columbia River.

cluster (“Autumn/Invaded”) was associated with high water temperature (mean = 18.1°C), a strong peak in the abundance of the two invasive species *P. forbesi* and *C. fluminea*, and high total zooplankton abundance (mean = 3446 individuals m⁻³). The Autumn/Invaded community occurred from May to December, but with August–October as the most frequent months of occurrence (Fig. 3).

A winter cluster (“Winter/Barren”) was associated with low water temperature (mean = 4.7°C) and extremely low total zooplankton abundance (mean = 21 individuals m⁻³). The Winter/Barren community was composed of a diverse and even assemblage of rotifers, cladocerans and copepods. The Winter/Barren community occurred from December to February, with equal frequency of occurrence in each of these months.

A spring cluster (“Spring/Rotifer”) was associated with intermediate temperature (mean = 9.9°C), high Chl *a* concentration (12.1 μ g L⁻¹), peak abundance of rotifers, and high total zooplankton abundance (mean = 5826 individuals m⁻³). Occurrence of the Spring/Rotifer community ranged from March to May, with April as the most frequent month of occurrence.

Finally, a transitional cluster (“Transitional”) was associated with intermediate temperature (mean = 8.8°C), moderate zooplankton abundance (mean = 332 individuals m⁻³), and 33% higher species richness than other community groups. This community was largely composed of taxa that

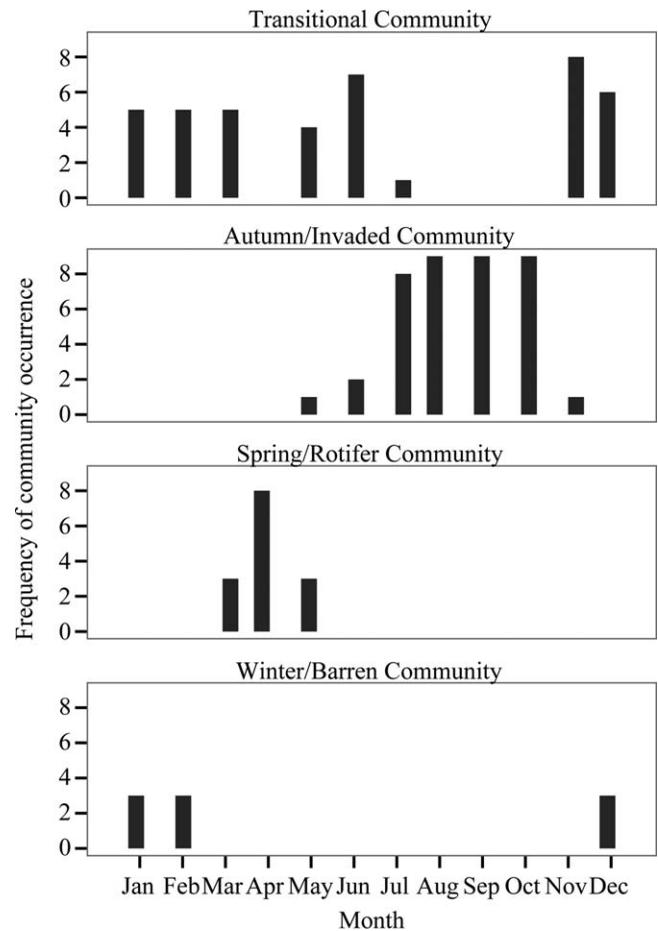


Fig. 3. Timing and frequency of occurrence for each of four community groups in 8.5-year dataset.

do not have strong seasonal peaks in abundance. The Transitional community occurred in all months except April, August, September, and October. Mean temperature, zooplankton abundance and diversity for each community are given in Table 3.

Indicator species analysis identified 15 taxa as significant indicator species for at least one community group (Table 4). Four taxa (*C. fluminea*, *P. forbesi*, *B. longirostris*, and *D. retrocurva*) were significant indicators of the Autumn/Invaded community, nine taxa (*Brachionus* sp., *Diacyclops thomasi*, *Asplanchna* sp., cyclopoid copepodites I–III, Diaptomid copepodites IV–VI, nematodes, tardigrades, chydorid cladocerans, and aquatic mites) were indicators of the Spring/Rotifer community, and two taxa (chironomid larvae and harpacticoid copepods) were indicators for all community groups except the Winter/Barren community.

Multidimensional analysis of zooplankton communities and environmental factors

NMDS was used to produce a two dimensional ordination of community data with a stress value of 0.09 at final

Table 3. Mean \pm standard deviation (SD) for selected attributes of zooplankton community groups.

Community name	Mean zooplankton abundance	Mean species richness	Mean species evenness	Mean temperature
Transitional	332 \pm 304	20.8 \pm 3.6	0.73 \pm 0.10	8.9 \pm 4.5
Autumn/Invaded	3450 \pm 2460	15.2 \pm 4.2	0.47 \pm 0.14	18.2 \pm 3.0
Spring/Rotifer	5830 \pm 4780	15.5 \pm 3.2	0.37 \pm 0.17	10.0 \pm 2.2
Winter/Barren	20.9 \pm 11.1	15.4 \pm 3.4	0.87 \pm 0.06	4.7 \pm 1.3

Table 4. Indicator species analysis results for taxa with significant association with at least one seasonal community. Association values range from 0 to 1. Bold text denotes invasive species.

Taxa	Community Association	Association value	p-value
C. fluminea	Autumn/Invaded	0.614	0.005
P. forbesi	Autumn/Invaded	0.535	0.010
<i>B. longirostris</i>	Autumn/Invaded	0.462	0.005
<i>D. retrocurva</i>	Autumn/Invaded	0.325	0.045
<i>Brachionus</i> sp.	Spring/Rotifer	0.705	0.005
<i>D. thomasi</i>	Spring/Rotifer	0.535	0.005
Cyclopidae (stage I–III)	Spring/Rotifer	0.535	0.005
Nematoda	Spring/Rotifer	0.528	0.005
<i>Asplanchna</i> sp.	Spring/Rotifer	0.457	0.005
Tardigrada	Spring/Rotifer	0.419	0.005
Chydoridae	Spring/Rotifer	0.416	0.015
Diaptomidae (stage IV–VI)	Spring/Rotifer	0.376	0.035
Arachnida	Spring/Rotifer	0.342	0.030
Chironomidae	Autumn/Invaded, Spring/Rotifer, and Transitional	0.393	0.015
Harpacticoid copepods	Autumn/Invaded, Spring/Rotifer, and Transitional	0.372	0.035

configuration (Fig. 4). The Spring/Rotifer and Autumn/Invaded community groups each had high zooplankton abundance but occurred under different chlorophyll and temperature regimes. The succession of community groups across the time series was cyclical, with the Autumn/Invaded, Winter/Barren, and Spring/Rotifer communities always separated by the Transitional community for a period of at least one month. The BIOENV correlation procedure identified two parameters that best explained the observed community data across our time series: temperature and Chl *a* concentration, and yielded a Spearman harmonic rank correlation of 0.57 (Table 5).

Phenological patterns and interannual variation of invasive species

The invasive cladoceran *B. coregoni* was first observed in the Columbia River through the detection of a lone individual in September 2006, with an estimated abundance of 2.5 individuals m^{-3} . In 2008, *B. coregoni* underwent a rapid population boom and reached peak abundance of 247 individuals m^{-3} , then remained at this level for several years, before rapidly declining in 2011. In 2013, *B. coregoni* was observed at the lowest abundance since its initial detection (Table 2,

Fig. 5). The timing of annual peak abundance of *B. coregoni* was highly variable, ranging from April to October, with equal frequency of occurrence for each month.

In contrast to this boom and bust pattern observed in *B. coregoni*, the invasive copepod *P. forbesi* was consistently abundant (mean of 3558 individuals m^{-3}), although peak abundance was several times larger than average in 2010 (10,725 individuals m^{-3}) and several times smaller than average in 2013 (748 individuals m^{-3}). Annual peak abundance of *P. forbesi* only occurred in August or September, with six and three occurrences, respectively (Fig. 5). *P. forbesi* was first observed in the Columbia River in 2002 (Cordell et al. 2008) and has, thus, far persisted at high levels of abundance for at least 12 years.

Peak abundances of the three invasive species of zooplankton occurred under a narrow range of temperature and chlorophyll conditions (Fig. 6). Most annual peaks for *B. coregoni* and all peaks for *P. forbesi* and larval *C. fluminea* occurred during high temperature-low chlorophyll conditions, which are characteristic of the Autumn/Invaded community. Annual peak abundance of *P. forbesi* occurred at an average temperature of 20.6°C (range = 18.6–21.8°C) and average Chl *a* concentration of 2.4 $\mu g L^{-1}$ (range = 0.76–

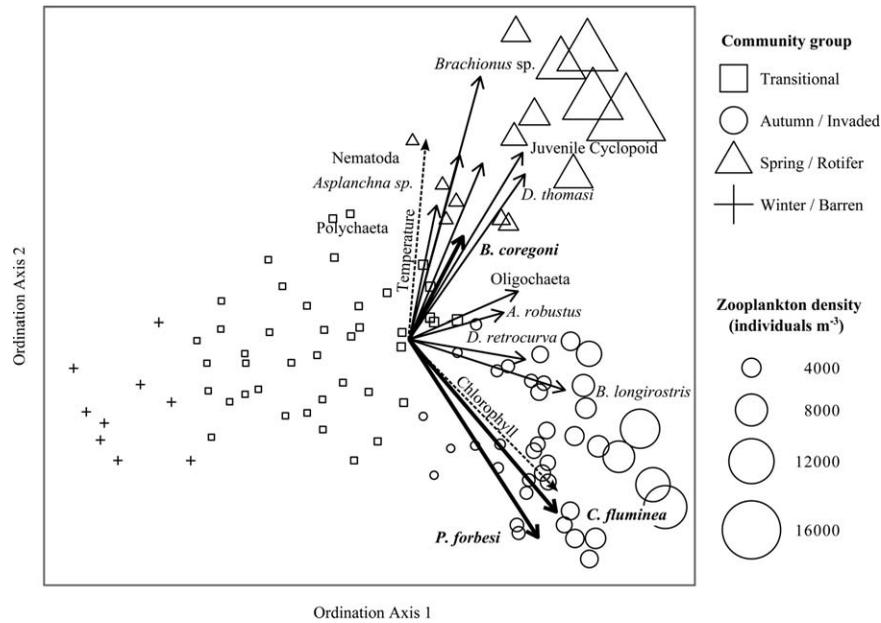


Fig. 4. NMDS ordination (stress = 0.09) of community data with gradients of temperature ($r^2 = 0.77$, $p < 0.001$) and chlorophyll ($r^2 = 0.53$, $p < 0.001$) plotted as vectors (in dashed lines) and indicator species plotted as vectors (in solid lines). Invasive species are emboldened. Symbol size is scaled by total zooplankton abundance in each sample and symbol shape corresponds to community groups derived from hierarchical clustering.

5.46 $\mu\text{g L}^{-1}$). *C. fluminea* peak abundance occurred at an average temperature of 19.7°C (range = 17.6–21.4°C) and average Chl *a* concentration of 4.6 $\mu\text{g L}^{-1}$ (range = 0.96–8.23 $\mu\text{g L}^{-1}$). Annual peak abundance of *B. coregoni* occurred at an average temperature of 15.9°C (range = 10.2–20.3°C) and average Chl *a* concentration of 8.6 $\mu\text{g L}^{-1}$ (range = 2.71–21.42 $\mu\text{g L}^{-1}$).

Although all three invasive species peaked in abundance during periods of high temperature, greater than average temperatures did not correspond to larger annual peaks in abundance (*P. forbesi*, $r^2 = 0.0$, $p = 0.525$; *C. fluminea*, $r^2 = 0.02$, $p = 0.321$; *B. coregoni*, $r^2 = 0.33$, $p = 0.135$). However, there was a strong and highly significant correlation between Chl *a* concentration and peak abundance of both *P. forbesi* ($r^2 = 0.56$, $p = 0.012$) and *B. coregoni* ($r^2 = 0.92$, $p = 0.002$), although the direction of the correlation was negative for *P. forbesi* and positive for *B. coregoni*.

Detection of rare taxa

Our results indicate that most species were detected within the first six months of each year, and that species with abundances greater than one individual m^{-3} were unlikely to escape detection in any single year. Average abundance and frequency of detection had a strong positive correlation ($r^2 = 0.78$, $p < 0.001$), and improvements in detection plateaued above average abundances of 10 individuals m^{-3} (Fig. 7). Species with average population size greater than one individual m^{-3} were detected in at least 20% of samples (i.e., ca. 2.5 occurrences per year).

Species accumulation decreased sharply after collection of six samples, and the rate of increase approached zero after

Table 5. Summary of best fit BIOENV models for permutations including up to four environmental parameters.

Number of parameters in model	Parameters in best fit model	Correlation
1	Temperature	0.5581
2 (best fit model)	Temperature, chlorophyll	0.5702
3	Temperature, chlorophyll, month	0.5330
4	Temperature, chlorophyll, month, day length	0.5083

collection of 12 samples, which is in broad agreement with our observed patterns of species accumulation for individual sampling years (Fig. 8). Likewise, total species richness (including undetected species) was estimated at 35 species, which matches the number of records in our observed species pool. The extrapolated value for species richness did not vary with the choice of species accumulation index. This result indicates that the occurrence of undetected species in our time-series was unlikely given the rate of species accumulation and duration of the observational record.

Discussion

Seasonal succession and unequal invasion

The Columbia River is a heavily invaded body of water, but the seasonal zooplankton communities are unequally

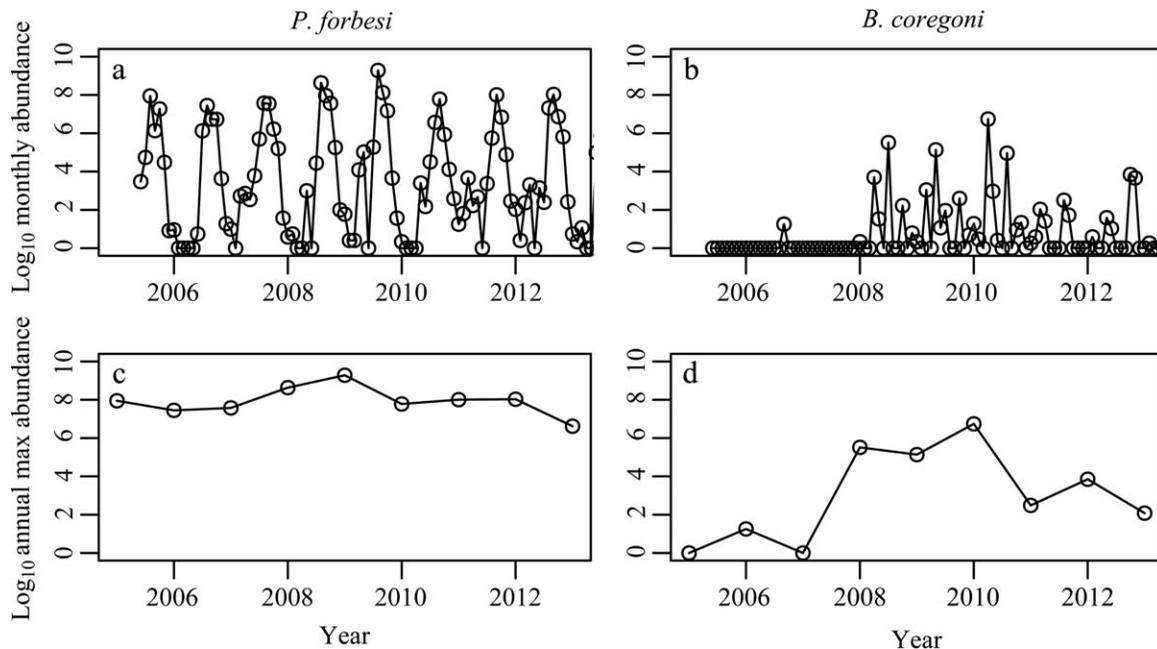


Fig. 5. (a, b) Monthly abundance and (c, d) yearly peak abundance for *P. forbesi* and *B. coregoni* plotted across the period of study. Abundance values are plotted on a log_{10} scale.

invaded, oscillating in a predictable annual pattern between a state of dominance by native taxa in the winter and spring, and a heavily invaded state in summer and autumn. These seasonal communities are largely comprised of native rotifers in the spring and two species of invasive zooplankton in the autumn: a calanoid copepod (*P. forbesi*) and larvae of the Asian clam (*C. fluminea*). A similar oscillation between dominance by native taxa in the winter/spring and invasive taxa in summer/autumn has been observed for San Francisco Estuary zooplankton (Bollens et al. 2014) and fishes (Gewant et al. 2012).

Patterns of zooplankton succession in the Columbia River were strongly associated with changes in temperature and phytoplankton abundance (Chl *a* concentration). Our sampling program did not extend to most zooplankton predators (i.e., macroinvertebrates and fishes), and thus, we are unable to determine the extent to which predation also acts as a driver of succession in this system. The narrow temperature range under which the Autumn/Invaded community occurs indicates that physiological constraints may be an especially strong driver of temporal dynamics for that community group. Regional climate models for the Pacific Northwest indicate that average air temperatures are expected to increase in the region by more than 2°C by the end of the 21st century (Payne et al. 2004), which may lengthen and move forward the period of optimal water conditions for invasive zooplankton. In addition to the direct effects of atmospheric warming, expected changes in precipitation across the Columbia River basin are expected to alter sea-

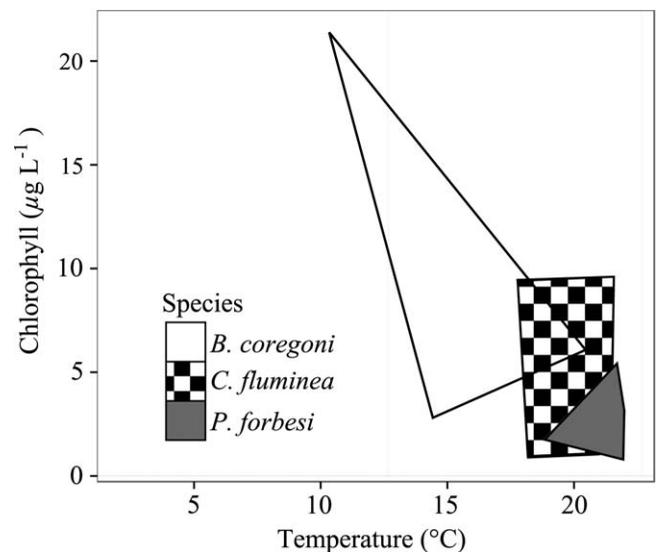


Fig. 6. The occurrence of peak abundance of three invasive taxa in temperature and chlorophyll "space."

sonal streamflow patterns to reduce river flow during warm seasons (Hamlet 2011). Although geographic expansion of many invasive species is expected under future climate conditions (Bellard et al. 2013), our study suggests that ecosystems which contain temperature-limited invasive species may be particularly sensitive to climate-induced expansion of invasions.

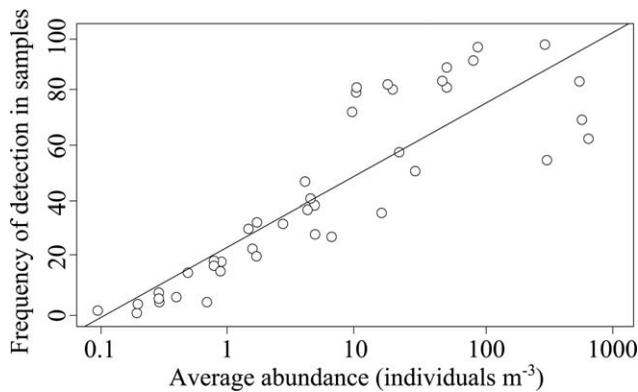


Fig. 7. Average abundance for each taxon across entire time series vs. percentage of samples in which those taxa were detected. Regression line $r^2 = 0.78$, $p < 0.001$.

Water temperature has been similarly identified as a driver of zooplankton community succession in several other northeast Pacific estuaries, for example, the San Francisco Estuary (Gewant and Bollens 2005; Bollens et al. 2011, 2014) and Willapa Bay, Washington (Graham and Bollens 2010), although other factors such as salinity, coastal upwelling, and the extent of marine influence can also be important drivers. In other estuaries, the effects of temperature are mixed. For instance, delays or early onset of seasonal zooplankton community succession of up to a month were linked to interannual variation in water temperature in a Greenland fjord (Arendt et al. 2012). Conversely, a study of seasonal succession in three Japanese estuaries found that zooplankton community succession was independent of water temperature and instead strongly correlated with annual changes in turbidity and salinity (Suzuki et al. 2013). Although changes in salinity and flow regime are strongly associated with zooplankton community succession in the lower Columbia River Estuary (Bollens et al. 2012; Breckenridge et al. in press), we found neither to be drivers of zooplankton succession in the freshwater reach of the estuary.

While the role of predation in driving seasonal succession of zooplankton communities in the Columbia River remains unclear, juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and northern pikeminnow (*Ptychocheilus oregonensis*) have been shown to exhibit strong selectivity for native copepods over the invasive *P. forbesi* (J. Adams et al. unpubl.). Given the sheer abundance of *P. forbesi*, the observation of differential predator selectivity between it and native zooplankton suggests that a reordering of the trophic structure of the late summer and early autumn food web has likely occurred in the Columbia River. This potential for trophic disruption is further supported by A. Bowen et al. (unpubl.), who found that high ingestion rates and opportunistic omnivory of *P. forbesi* may provide a strong competitive advantage against the common native cyclopoid *D. thomasi*. Our

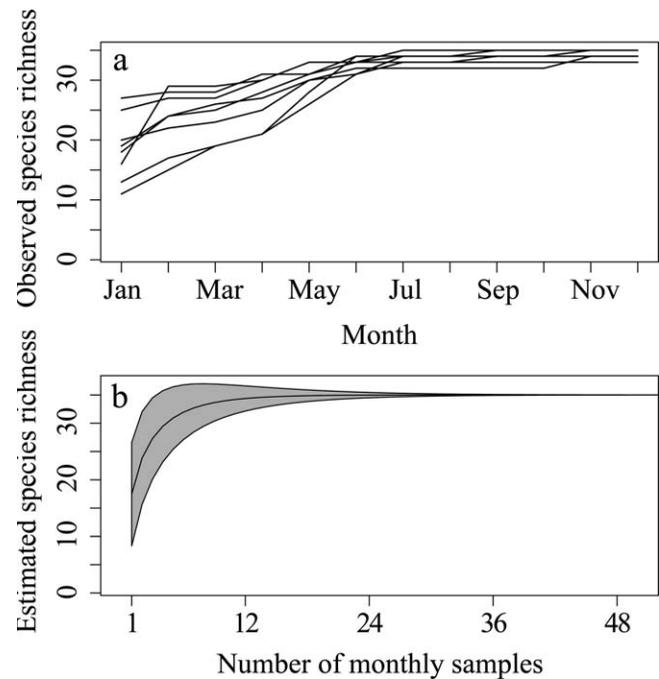


Fig. 8. (a) Observed and (b) estimated rates of species accumulation with increasing number of samples. Observed species richness is plotted cumulatively for each complete year of sampling (2006–2013).

research echoes the findings of Naiman et al. (2012), in that even in relatively well-studied bodies of water such as the Columbia River, the trophic interactions between native and non-native members of the community are almost entirely unknown, although potentially profound.

Detection of rare and newly introduced taxa

Species accumulation theory predicts that the number of species discovered during community sampling will increase logarithmically with increasing sampling effort, eventually approaching an asymptote (Hoffman et al. 2011). Thus, species accumulation curves are useful for identifying an optimal level of sampling effort for detection of rare taxa. Species accumulation curves appear to have performed well with our dataset, with our estimated rate of species accumulation in broad agreement with observed rates across each year of study.

We have shown that across our sampling program most species are detected within the first six months of each year, and that the presence of taxa undetected across the entire duration of our sampling program is unlikely. However, several native (and at least one invasive) species of zooplankton have almost certainly persisted for multiple years at abundances below our threshold for reliable detection. The invasive cladoceran *B. coregoni* was not detected in our sampling program until a lone individual was found on the 16th month of sampling (September 2006), and it remained undetected again for an additional 16 months. Independent

observation of *B. coregoni* in the Columbia River in 2008 by Smits et al. (2013) at an abundance of 0.12 individuals m^{-3} supports the existence of a population of *B. coregoni* smaller than our threshold of detection (one individual m^{-3}) during this period. Poor detection rates of *B. coregoni* during what appears to have been an invasion lag phase suggest that our long-term sampling program at one location is not optimally suited for rapid detection of newly introduced species.

By comparing our estimated threshold of detection against the population size of species known to inhabit the Columbia River, we have been able to estimate whether undetected species are truly absent or merely persisting at levels of abundance below our threshold of detection. Of the three species of invasive copepods (*S. doerri*, *P. inopinus*, and *L. tetraspina*) which have been observed in brackish portions of the Columbia River Estuary (Cordell et al. 1992; Bollens et al. 2012; Breckenridge et al. in press), all were completely absent from upstream samples of our 8.5 year-time series. In contrast, the most infrequently detected species in our study, the predatory cladoceran *Leptodora kindtii*, was observed on six separate dates across our 8.5-year time series. Persistence of the three undetected invasive copepod species during our period of study would require population levels of at least an order of magnitude lower than *L. kindtii*, which is inconsistent with previously reported abundances of these taxa (Cordell et al. 1992, 1996, Bollens et al. 2002, 2012). Previous observations of *P. inopinus* have been restricted to brackish portions of the Columbia River Estuary (Cordell et al. 1992; Bollens et al. 2012), and the complete absence of this species from our study site suggests an inability to colonize freshwater portions of the estuary.

The estimation of the efficacy of our sampling program to detect rare taxa has allowed us to make a clear distinction between lack of observation and lack of occurrence, and to draw conclusions about the temporal dynamics of populations that do occur at our study site. However, caution is required in applying these results to sampling programs of a different design. Detection of zooplankton is highly dependent on collection method, and on the degree of spatial heterogeneity of populations. Additionally, because our estimation of the threshold of detection averages out seasonal peaks and interannual variation, it should not be used to predict detection in any single sample, but rather as a generalized estimate of detection across a multiyear sampling program.

Persistent dominance vs. boom-and-bust invasions

Zooplankton invasions in the Columbia River have resulted in large populations that have persisted for decades (e.g., *P. forbesi* and *C. fluminea*) and in unstable cycles of boom and bust (e.g., *P. inopinus*). For example, the calanoid copepod *P. inopinus* was first observed in the Columbia River in 1990 where it was found to be highly abundant in the lower estuary (Cordell et al. 2008). Surveys undertaken in 2002 (Cordell et al. 2008); presently congeneric invasive

copepod (*P. forbesi*) has become seasonally abundant (Bollens et al. 2012; Breckenridge et al. in press). Similarly, we observed the establishment of the invasive cladoceran *B. coregoni*, as well as its subsequent population boom and decline. It is unclear whether *B. coregoni* will stabilize at a reduced population size, undergo periodic cycles of boom-and-bust, or disappear from the Columbia River completely.

The boom-and-bust invasion dynamics of *P. inopinus* and *B. coregoni* contrast strongly with the persistent dominance of the invasive copepod *P. forbesi* and larval Asian clam, *C. fluminea*. Populations of *P. forbesi* have stably persisted across our 8.5-year time series without any clear trend toward increase or decrease, while *P. inopinus* appears to have been extirpated from the Columbia River (Cordell et al. 2008). The coincident timing of the arrival of *P. forbesi* in the Columbia River and the disappearance of *P. inopinus* from the lower estuary (Cordell et al. 2008) is highly suggestive of competitive exclusion by the later arriving species. Several examples of displacement of a highly successful invasive species by the subsequent arrival of a closely related species have been reported previously. For example, the Asian black rat (*Rattus rattus*) was displaced from much of Western Europe by the Norway rat (*Rattus norvegicus*) and the black South American fire ant (*Solenopsis richteri*) was displaced from the southern United States by subsequent arrival of the red South American fire ant (*Solenopsis invicta*) (Simberloff and Gibbons 2004).

The continued persistence of *P. inopinus* in at least 10 other U.S. Pacific Northwest estuaries where *P. forbesi* has not become established (Cordell et al. 2008) provides further support for competitive exclusion. It remains unclear which traits have allowed *P. forbesi* to persist in the Columbia River while *P. inopinus* has declined or vanished, but there are indications that *P. inopinus* is restricted to a narrower range of salinity. Surveys undertaken in 1990 found *P. inopinus* to be highly abundant in the lower estuary but absent at an upstream site located at river kilometer 85 (Cordell et al. 1992). In contrast, *P. forbesi* has been observed at least 500 km upstream of the estuary and into the lower Snake River (Cordell et al. 2008; Emerson et al. in press).

Competitive exclusion by a closely related species could also contribute to the unstable dynamics of *B. coregoni*, as the closely related *B. longirostris* is one of the most abundant native members of the community. A review of well-documented boom-and-bust invasions by Simberloff and Gibbons (2004) found that for the majority of studies density-dependent mortality (such as exhaustion of resources or increased pathogenic load) was frequently invoked as the causal agent of population decline. However, density-dependent causes of mortality seem unlikely in the case of *B. coregoni* in the Columbia River because peak populations of *B. coregoni* were far smaller than those of the native congener *B. longirostris*.

The ecological impacts of planktonic invasion in the Columbia River are difficult to understand given the context

of multiple contemporaneous invasions. For example, the presence of invasive bivalves in a community can alter trophic interactions, nutrient cycling, water clarity, and benthic substrate (MacIsaac 1996; Sousa et al. 2014). While it is unclear if the presence of *C. fluminea* in the Columbia River has been facultative or inhibitive to the establishment of subsequent invaders, the high abundances and synchronized phenology between *P. forbesi* and larvae of *C. fluminea* suggest that these two taxa are unlikely to be direct competitors. However, the feeding habits of larval *C. fluminea* have not been well characterized, and although there is evidence that feeding does occur during the planktonic larval phase (King et al. 1986), prey selection must presently be inferred from the nonselective feeding habits observed in adults (Boltovskoy et al. 1995).

Finally, our research supports a growing body of literature that suggests the annual timing of life history events can be an important factor in the invasional success of introduced taxa. Godoy and Levine (2014) found that stabilizing niche selection favors the establishment of invasive species with a large phenological offset from native members of the community, which tends to insulate newly arrived species from direct competition from established species. *P. forbesi* and *C. fluminea* both exhibit a large phenological offset from native members of the community, and this may play some part in their invasional success. Likewise the large phenological overlap between *B. coregoni* and several abundant species of rotifers may account for the unstable dynamics of *B. coregoni*. Additionally, some predators in the Columbia River are anadromous (e.g., juveniles of several salmonid species), while many others are resident (e.g., sticklebacks, mysids and juvenile pikeminnow), but all of these predators are known planktivores (juvenile *O. tshawytscha*: Bollens et al. 2010; *Gasterosteus aculeatus* and *Neomysis mercedis*: Bollens et al. 2002; and juvenile *P. oregonensis*: Beamesderfer 1992). Thus, seasonal predation pressure on zooplankton in the Columbia River would be expected to vary under differing phenological patterns, but with a magnitude that is presently unknown.

Although long-term population cycles are not unknown in aquatic invasions (Sousa et al. 2014), we observed cyclical periods of community invasion with contrasting patterns of phenology between persistent and ephemeral invasive populations. Our results support findings from terrestrial plant communities that a delayed phenology relative to native taxa may be a key functional trait for successful invaders. We have also found that peak abundances of dominant invasive zooplankters are restricted to periods of maximum water temperature, with implications that anthropogenic climate change may increase the habitability of the Columbia River for invasive taxa. In looking toward the future, zebra and quagga mussels have recently crossed the U.S. continental divide (Wong et al. 2010) and are now threatening the Columbia River Basin, adding to the importance of continuing these long-term plankton time series as a means of inves-

tigating new introductions, population persistence, and ecological impacts of aquatic invasive species.

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