

LETTER

Native and invasive zooplankton show differing responses to decadal-scale increases in maximum temperatures in a large temperate river

Eric Dexter ^{1,*} Stephen M. Bollens ^{1,2} Gretchen Rollwagen-Bollens ^{1,2}

¹School of the Environment, Washington State University, Vancouver, Washington; ²School of Biological Sciences, Washington State University, Vancouver, Washington

Scientific Significance Statement

It has been widely proposed that increasing global temperatures will promote the geographic spread of invasive species, yet few studies have examined the effects of increasing temperatures on existing populations of invaders. Here, we examine long-term temperature trends across a 70-year series of daily records from the lower Columbia River (Washington and Oregon), and assess the correlation between interannual variability in water temperature and the abundance of several native and invasive zooplankton species using an overlapping 12-year series of monthly zooplankton samples. Our results show a clear pattern of increasing water temperatures, with negative correlations between elevated late summer temperatures and the abundance of all examined native species, thus suggesting that long-term warming may promote conditions more favorable for several presently-established invasive zooplankton species.

Abstract

It has been widely proposed that increasing global temperatures will promote the geographic spread of invasive species, yet few studies have examined the effects of increasing temperatures on existing populations of invaders. Here, we examine temperature trends across a 70-year series of daily records from the lower Columbia River (Washington and Oregon), and assess the correlation between interannual water temperature variability and the abundance of several native and invasive zooplankton species using a 12-year series of monthly zooplankton samples from a nearby station. Our results show a clear pattern of increasing temperatures in the river, with a negative correlation between elevated late summer temperatures and the abundance of all examined native taxa, but none of the examined invasive taxa. Our study supports the hypothesis that anthropogenic climate change may promote conditions more favorable to previously established populations of invasive zooplankton species.

*Correspondence: eric.dexter@unibas.ch

Present address: The University of Basel, Department of Environmental Sciences, Basel, Switzerland

Author Contributions Statement: ED conducted data collection, statistical analysis, and led manuscript preparation. SMB and GRB designed and supervised the study approach and field collection. All three authors contributed to the interpretation of data and preparation of the manuscript.

Data Availability Statement: All data files and R scripts associated with this manuscript may be found at the FigShare digital repository under the address: <https://doi.org/10.6084/m9.figshare.8289053>.

Associate editor: María González

Additional Supporting Information may be found in the online version of this article.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Biological invasions are an increasingly widespread aspect of global environmental change (Vitousek et al. 1996; Cuhel and Aguilar 2013; Simberloff et al. 2013), and it has been proposed that increasing global temperatures will promote both the spread of aquatic invasive species and increase the severity of invasion impacts (e.g., Stachowicz et al. 2002; Hellmann et al. 2008). This hypothesis arises from the facts that successful invaders tend to tolerate a wide range of environmental conditions and typically possess a strong capacity to colonize disturbed habitats (Grabowski et al. 2007; Hellmann et al. 2008). A growing body of observational studies, laboratory experiments, and modeling efforts link climate change and invasion spread (e.g., Stachowicz et al. 2002; Winder et al. 2011), although this pattern is far from universal (Hilbish et al. 2010).

Invasion is a complex multistep process that encompasses introduction, establishment, and persistence—with each stage potentially governed by different factors (Williamson 2006; Theoharides and Dukes 2007). Most efforts to study the relationship between climate change and invasion have centered upon the establishment of new invasions, in particular, the geographic expansion of well-known invaders into warming habitats. Here, we explore the latter stage of the invasion process (persistence) and examine the manner in which increasing global temperatures may affect the population dynamics of well-established invasive species.

Our study focuses on the lower Columbia River (CR) (Oregon and Washington), which exhibits strong seasonal succession of zooplankton communities, with summer and autumn communities typically dominated by several highly abundant invasive species (Dexter et al. 2015). The calanoid copepod *Pseudodiaptomus forbesi*, and planktonic juveniles of the clam *Corbicula fluminea*, are by far the most abundant invaders within the lower river and upper estuary, often comprising more than 90% of all zooplankton in late summer and early autumn (Dexter et al. 2015; Emerson et al. 2015). Both species are known to tolerate much higher temperatures than presently occur in the CR. *C. fluminea* is endemic to freshwaters across Asia, Africa and Australia (Sousa et al. 2008), and *P. forbesi* inhabits waters in the Yangtze River region which may exceed 30 °C (Zhang et al. 2018).

Over the next several decades, an increase in temperature of ~3.0°C is predicted for the U.S. Pacific Northwest (Mote and Salathé 2010). Temperatures are predicted to increase by ~4.5°C by 2095 for the Columbia River Basin, which includes portions of seven U.S. states and two Canadian provinces (Hamlet and Lettenmaier 1999). We propose that increasing temperatures will promote conditions favoring the growth of warm-water invaders such as *P. forbesi* and *C. fluminea* over locally-adapted native species, allowing for both increased abundance and earlier emergence in warmer years. Based upon prior observations (Dexter et al. 2015), we hypothesize that native species will show a positive association with earlier summer warming, but respond negatively to rising maximum temperatures in late summer.

Several unusually warm climate events have unfolded across this region in recent years (e.g., Kintisch 2015), thereby providing an opportunity to examine these hypotheses under the extreme conditions that foreshadow a warmer climate of the future. We therefore conducted a series of regression-based analyses to examine the long-term temperature trends in the lower CR (~70 years), and the relationship between short-term (inter-annual) variation in temperature and population density for several native and invasive zooplankton species. Specifically, we examined: (a) if a decadal-scale warming trend could be detected in the lower CR; (b) if CR zooplankton showed a consistent response to interannual temperature variation; and (c) if invasive zooplankton were more tolerant of extreme temperatures than native members of the community.

Methods

Study site and sample collection

The CR drains an area of 669,300 km² across the U.S. Pacific Northwest region (Simenstad et al. 1990). Rates of river flow are heavily influenced by the timing of spring and summer snowmelt, although more than 200 impoundments on the river have greatly reduced seasonal variation in flow relative to historical patterns (Payne et al. 2004). We collected zooplankton samples from a pier located in Vancouver, Washington (45.62°N, 122.68°W), approximately 170 river km upstream from the mouth of the CR and 64 km downstream from the Bonneville Dam—the furthest downstream impoundment on the river (Fig. S1). This site is characterized by high flow with no thermal stratification, and water depths ranging seasonally from 8 to 11 m (Dexter et al. 2015). We sampled from this location every month within January 2005–December 2016, yielding a total of 144 continuous monthly samples. During each instance, we collected three zooplankton samples via vertical net tows from 1 m above river bottom to the surface using a 73-μm mesh, 0.5-m diameter ring net with attached flowmeter (General Oceanics). Zooplankton samples were fixed in a 10% buffered formalin solution for later taxonomic processing.

In the laboratory, a minimum of 200 non-naupliar organisms were identified from aliquots of each sample using a Leica MZ6 stereomicroscope (Leica Microsystems) at 40× magnification. Specimens were identified to the lowest possible taxonomic rank using Thorp and Covich (2009), with most individuals identified to the genus or species level. We converted specimen counts to density (individuals m⁻³) by multiplying each count by the ratio of sample volume to aliquot volume, and dividing by the total volume of water filtered. Two replicate samples were processed for each sampling date, with the third reserved as backup.

Long-term temperature data

We obtained long-term temperature and river flow data from daily records collected at the Bonneville Dam (~64 km

upstream of study site) spanning January 1950–June 2017 (Columbia Basin Research 2018). Bonneville Dam water temperatures were monitored at a depth of ~14 m in the forebay near the turbine intakes. These hypolimnetic temperatures were representative of riverine temperatures at the downstream zooplankton sampling site due to the reservoirs being run-of-the-river with short residence times. For the purposes of model validation, we also obtained long-term water temperature records from two additional upstream monitoring sites: the Dalles Dam (~100 km upstream of our study site) and the McNary Dam (~300 km upstream) (Columbia Basin Research 2018). Pacific Decadal Oscillation (PDO) indices and Southern Oscillation Index (SOI) values were obtained electronically from the U.S. National Oceanic and Atmospheric Administration (NOAA) for the period spanning January 1950–June 2017 (National Centers for Environmental Information 2018).

Analysis of long-term water temperature trends

Long term trends in water temperature (1951–2017) were assessed via generalized least squares regression of daily temperature records from the Bonneville Dam forebay and several regionally-relevant climatic variables: PDO index, SOI index, and CR flow rates (volume/s). Temperature values were de-seasoned by standardizing each observation against the monthly mean and then converting to z-scores. The full model was structured as $temperature \sim time + PDO + SOI + River\ flow$, with an AR(1) autocorrelation structure applied to the error term (Zuur et al. 2009). Time was expressed as the number of years elapsed since $t = 0$. The best-fit regression model was selected from this full model via backwards p -value selection for both (1) the entire data series and (2) seasonal subsets of the series: winter (December–February), spring (March–May), summer (June–August), and fall (September–November). p -Values were adjusted for multiple comparisons across all five models using the False Discovery Rate method (Benjamini and Hochberg 1995). Models were fit using maximum likelihood estimation for model selection, and the final model was re-fit using restricted maximum likelihood (REML). Regression model assumptions were validated via graphical examination of residuals according to the approach recommended in Zuur et al. (2009). Model results were validated using the same procedure applied to data from the two additional upstream sites. All regressions were performed in R version 3.2.2 using the nlme package (version 3.1.128—Pinheiro et al. 2018).

Analysis of individual taxa response to elevated temperatures

In order to test the hypothesis that interannual variation in summer water temperatures strongly affects zooplankton abundances in the CR, we developed a series of general linear models for the six most abundant zooplankton taxa during summer months: *Daphnia* sp. (native), *Bosmina longirostris* (native), cyclopoid copepodites and adults (native), juvenile

C. fluminea (invasive), *P. forbesi* copepodites and adults (invasive), and *P. forbesi* nauplii (invasive). Note that “*Daphnia* sp.” corresponds to a mixture *D. mendotae* and *D. retrocurva* (which are difficult to differentiate at most life stages) and “cyclopoid copepodites and adults” corresponds to *Diacyclops thomasi* and *Acanthocyclops robustus* (for the same reason). We modeled the nauplii of *P. forbesi* (which are easily distinguished from other nauplii) but not cyclopoid nauplii, which we rarely observed in summer months. Also note that planktonic *C. fluminea* represent only the juvenile life-stage of the clam, not the benthic adults.

All models were formulated as $\log(abundance) \sim month \times temperature$, with temperature modeled as a continuous variable and month set as a factor (i.e., ANCOVA—analysis of covariance). When significant $month \times temperature$ interaction terms were present, the models were interpreted only with respect to the interaction terms, not either term singly. We accomplished this by calculating the conditional coefficients of the interaction terms in the model (i.e., the changes in the coefficient for temperature conditional on the value of month), along with 95% confidence intervals for these coefficients using the interplot package version 0.2.1 for R (for methodological details see Solt et al. 2018). p -Values were adjusted for multiple comparisons across all six models using the False Discovery Rate method (Benjamini and Hochberg 1995).

Results

Long term trends in water temperatures

We detected a statistically significant increase in water temperature at the Bonneville Dam monitoring station across the period spanning 1951–2017 (Fig. 1A), a trend which was also apparent at both upstream dams (Figs. S2 and S3). At all sites, the best-fit regression model contained three parameters: time, PDO, and river flow. River temperatures were negatively associated with increasing flow, positively associated with high PDO index values, and positively correlated with time (expressed as years). When this modeling process was repeated with seasonal subsets of the data, PDO was significant in only spring and winter. In all instances, SOI was dropped during model selection due to strong collinearity with PDO.

This warming trend was most apparent in the summer and fall months (Fig. 1B). Across the entire period of study, median August water temperatures at the Bonneville Dam increased approximately 2°C, with the period of greatest increase occurring between 1970 and 1980 (Fig. 1C). This rapid increase around the 1980s accords with the well-documented reversal in the polarity of the PDO in 1976–1977 (Miller et al. 1994; Mantua and Hare 2002). Moreover, the number of extreme heat events at this site (defined as water temperatures > 22°C) has increased in recent decades. The partial decade spanning 2010–2016 shows at least a two-fold increase in the frequency of these extreme heat events compared to any other decade in the nearly 70-year data

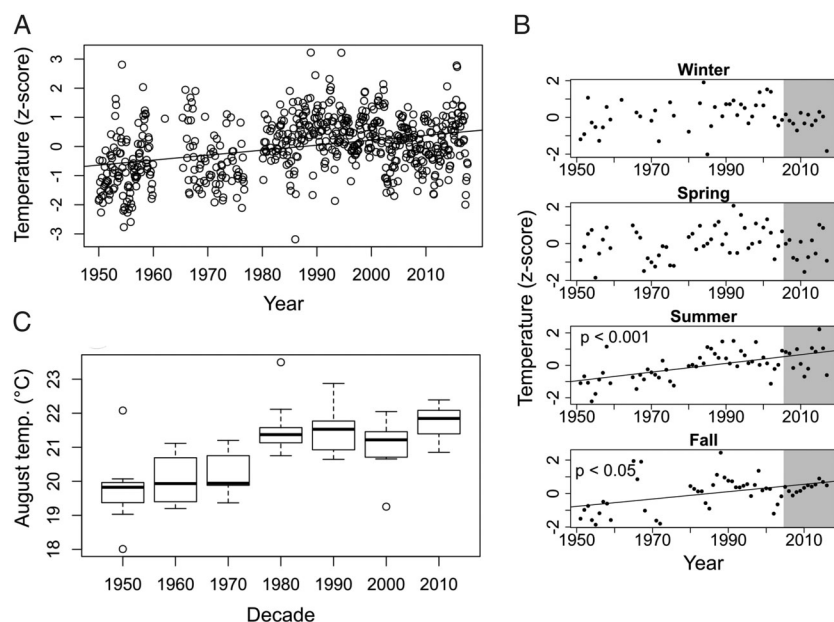


Fig. 1. (A) Daily Columbia River water temperature at the Bonneville Dam forebay averaged by month for the entire time-series. (B) Seasonal subsets of the Bonneville Dam time-series with the 12-year zooplankton series shaded in gray. A significant positive relationship between water temperature and time was observed for the complete series ($p < 0.001$), summer ($p < 0.001$), and fall ($p < 0.05$). (C) Median and interquartile ranges for August water temperature at the Bonneville Dam forebay by decade. Across the period of study, median August water temperatures increased approximately 2°C, with the period of greatest increase occurring between 1970 and 1980.

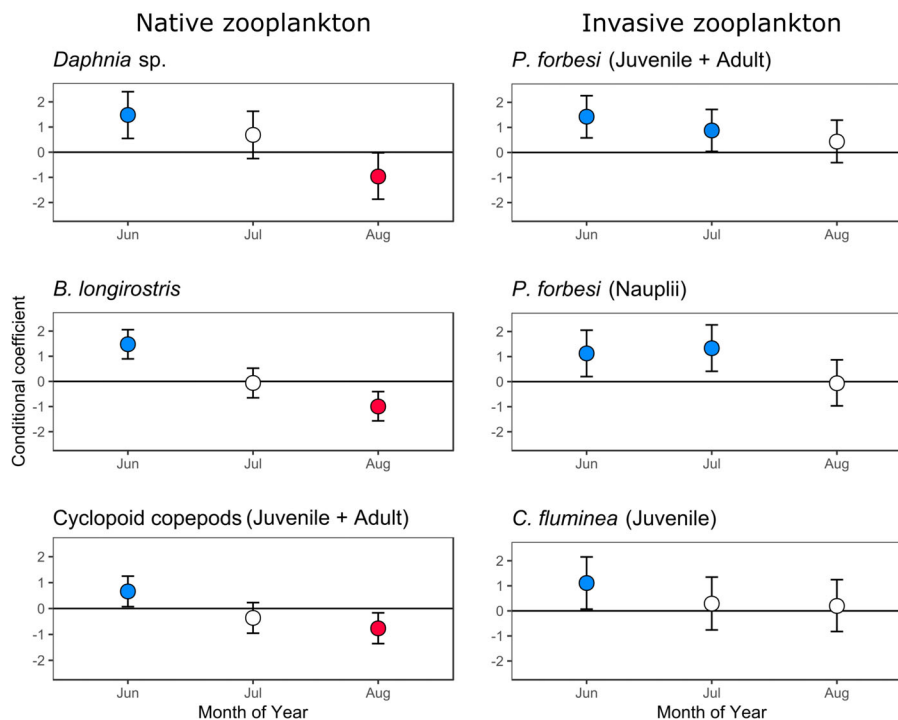


Fig. 2. The conditional coefficient of the interaction term for the linear regression model $abundance \sim temperature \times month$ for the six most abundant zooplankton taxa during the summer months in the Columbia River. Parameter estimates and confidence intervals are shown for each taxon, with positive effects of temperature in blue, negative effects in red, and nonsignificant effects in white.

series. This pattern remains unchanged when the raw number of events are standardized to account for several intermittent gaps in the time series during the 1960s and 1970s. Long-term temperature data from the two upstream dams show similar trends of increasing temperatures in recent decades and recent years (i.e., 2010–2016) (Figs. S2 and S3).

Individual zooplankton taxa responses to elevated summer water temperatures

The six zooplankton taxa most abundant during summer months all showed significant interactions between interannual variation in abundance and temperature (Fig. 2). The magnitude and direction of this interaction varied across species and season, but followed some general patterns. In early summer, elevated water temperatures were associated with

greater abundances of both native and invasive species. In late summer, elevated water temperatures were associated with decreased abundances of native taxa, but not invasive taxa. In some instances, the magnitude of correspondence between interannual variations in water temperature and abundance was striking. In the strongest case, 81% of the interannual variation in the June abundance of the native cladoceran *B. longirostris* could be explained by water temperature alone (Fig. 3). This positive correlation breaks down for *B. longirostris* in mid-summer (July), and then becomes strongly negative when water temperatures reach their annual peak in late summer (August). In contrast, no evidence for negative effects of elevated water temperatures were observed for any of the invasive taxa. As higher water temperatures tend to be correlated with decreased water flow in the summer months, these patterns may reflect some degree of concentration of the zooplankton community. However, the magnitude of interannual variation in summer month flow (~ fivefold difference between minimum and maximum) was far less than the corresponding interannual variation in population densities (~ 10^5 fold difference).

Discussion

We observed a clear pattern of increasing water temperatures over the past 70 years at several sites in the lower CR. This pattern of increase is most apparent in summer months, with median August temperatures at the Bonneville Dam showing an increase of approximately 2°C over the period of 1950–2018. Similarly, extreme heat events appear to be increasing in frequency, with a two-fold increase in the number of average monthly water temperatures exceeding 22°C in the period of 2010–2016 relative to any other decade examined. Our study was not designed to partition this warming trend into components of river management, regional climatic cycles, and global climate change, although our findings accord with regional predictions for anthropogenically induced climate change (Hamlet and Lettenmaier 1999; Mote and Salathé 2010). The sharp increase in summer water temperatures that we observed between 1970 and 1980 (although striking) may be a special case, as this period of rapid warming closely corresponds to a rapid shift in the polarity of the PDO in 1976–1977 (Miller et al. 1994; Mantua and Hare 2002). Irrespective of the ultimate drivers of this warming trend, it is clear that plankton communities in the CR have experienced steadily increasing temperatures across recent decades, and that this increase has been greatest during summer months.

In temperate latitudes, annual changes in temperature across seasons far exceed the magnitude of interannual variation within seasons. Nonetheless, interannual variation in temperature may have a profound effect on the phenology and abundance of plankton populations (Berger et al. 2007). Many species of zooplankton exhibit temperature-dependent

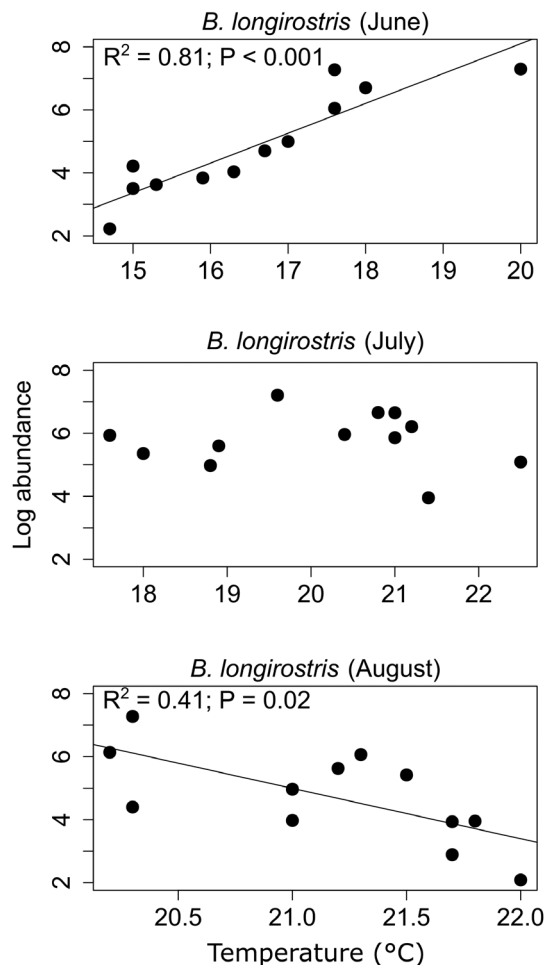


Fig. 3. The $\log(x + 1)$ abundance of *B. longirostris* plotted against water temperature for each summer month (June, July, August) during the 12-year period of study. For each month, an ordinary least squares model of the form $\text{abundance} \sim \text{temperature}$ was fitted with the corresponding p -value (adjusted for multiple comparisons using FDR) and R^2 shown on each plot. Regression lines are shown only for months with a significant correlation between temperature and abundance.

growth rates, and interannual variation in water temperatures may affect the seasonal succession of predators and prey, or drive phenological mismatches in life-history events. Our results show that CR zooplankton populations are highly responsive to interannual variations in temperature, and that the response is taxon-specific. Each zooplankton taxon that we examined showed a positive association between abundance and water temperature in early summer (June), when water temperatures hovered around 16°C. In contrast, interannual variation (i.e., increase) in late summer temperatures yielded negative associations for all examined native taxa, but none of the invasive taxa.

These associations may represent several different mechanisms. On one hand, the patterns that we observed may reflect differing physiological capacities to tolerate elevated water temperatures. Negative correlations between peak water temperatures in late summer and the density of several native species may reflect a physiological threshold beyond which fitness declines relative to warm-water tolerant invaders. Alternatively, shifting patterns of abundance might reflect earlier onset of seasonal community succession, but not necessarily an overall change in population size. Such associations could be driven by direct effects (e.g., warmer temperatures promoting earlier emergence of *P. forbesi* from overwintering eggs) or indirect effects (e.g., increased food abundance in warmer years supporting earlier reproduction in *C. fluminea*), or combinations of both, as these interpretations are not mutually exclusive. For example, multiple species of non-indigenous ascidians in coastal New England exhibit both earlier recruitment in response to warmer winters as well as greatly increased growth rates (relative to native ascidians) in response to warmer summers (Stachowicz et al. 2002). As our taxonomic groupings represent populations (e.g., *P. forbesi*), assemblages (cyclopoid copepods), and reproductive events (*C. fluminea* juveniles), we propose that our results likely reflect multiple mechanisms.

With respect to the continued expansion and long-term persistence of these invaders, our results have clearly differing implications. Zooplankton populations often exhibit highly seasonal dynamics, and possess a temporal as well as geographic range. The geographic range of *P. forbesi* has remained static across the Pacific Northwest for several decades (Dexter et al. 2020), but our results highlight a potential for expansion in temporal range. Warming conditions may push *P. forbesi* into greater contact with an early-season zooplankton community, or extend the persistence of *P. forbesi* into the characteristically depauperate months of early winter. The implications for *C. fluminea* are likely quite different, as populations of benthic adults persist across the entire year. The number of juveniles released may reflect conditions in previous months that control number and quality of eggs produced, fertilization success, and number of larvae brooded in the gills. Thus, while our models show a similar response to elevated temperatures in both invasive taxa, the biological interpretation of this response may be highly species specific.

Although our data reveal a clear set of associations, there are some important limitations to bear in mind. The frequency of our sampling events (once per month) does not provide sufficient resolution to differentiate shifts in phenology from an overall change in total population density across an entire year. These hypotheses might be discriminated in future studies through examination of the succession of the various life-stages of these zooplankton taxa, more frequent sampling, additional measures of seasonal change (e.g., onset of the spring phytoplankton bloom or stratification in nearby lakes), or perhaps through a time-frequency based approach to signal processing (Katz et al. 2011). Furthermore, our ability to understand the wider ecological implications of these findings would be greatly enhanced by the inclusion of additional sampling sites in the CR, especially in the brackish waters of the lower estuary and the lentic waters of upstream reservoirs. Nonetheless, we can conclude that given the clear warming trends we have observed and the affinity (or at least tolerance) that several invaders show for the warmest conditions in the CR, we predict that summer conditions in the CR may increasingly favor the growth of invasive zooplankton over native species in coming decades.

REFERENCES

- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B Methodol.* **57**: 289–300. <http://dx.doi.org/10.1111/j.2517-6161.1995.tb02031.x>.
- Berger, S. A. and others 2007. Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton. *Oecologia* **150**: 643–654. doi: [10.1007/s00442-006-0550-9](https://doi.org/10.1007/s00442-006-0550-9).
- Columbia Basin Research. 2018. Columbia river DART (data access in real time), [accessed 2018 March 1]. Available from <http://www.cbr.washington.edu/dart>.
- Cuhel, R. L., and C. Aguilar. 2013. Ecosystem transformations of the Laurentian great Lake Michigan by nonindigenous biological invaders. *Ann. Rev. Mar. Sci.* **5**: 289–320. doi: [10.1146/annurev-marine-120710-100952](https://doi.org/10.1146/annurev-marine-120710-100952).
- Dexter, E., S. M. Bollens, G. Rollwagen-Bollens, J. Emerson, and J. Zimmerman. 2015. Persistent vs. ephemeral invasions: 8.5 years of zooplankton community dynamics in the Columbia River. *Limnol. Oceanogr.* **60**: 527–539. doi: [10.1002/lno.10034](https://doi.org/10.1002/lno.10034).
- Dexter, E., S. M. Bollens, J. Cordell, and G. Rollwagen-Bollens. 2020. *Zooplankton invasion on a grand scale: Insights from a 20-year time-series across 38 Northeast Pacific estuaries*. *Ecosphere*. <http://dx.doi.org/10.1002/ecs2.3040>.
- Emerson, J. E., S. M. Bollens, and T. D. Counihan. 2015. Seasonal dynamics of zooplankton in Columbia-Snake River reservoirs, with special emphasis on the invasive copepod *Pseudodiaptomus forbesi*. *Aquat. Invasions* **10**: 25–40. doi: [10.3391/ai.2015.10.1.03](https://doi.org/10.3391/ai.2015.10.1.03).

- Grabowski, M., K. Bacela, and A. Konopacka. 2007. How to be an invasive gammarid (Amphipoda: Gammaroidea)—comparison of life history traits. *Hydrobiologia* **590**: 75–84. doi:[10.1007/s10750-007-0759-6](https://doi.org/10.1007/s10750-007-0759-6).
- Hamlet, A. F., and D. P. Lettenmaier. 1999. Effects of climate change on hydrology and water resources in the Columbia River basin. *J. Am. Water Resour. Assoc.* **35**: 1597–1623. doi:[10.1111/j.1752-1688.1999.tb04240.x](https://doi.org/10.1111/j.1752-1688.1999.tb04240.x).
- Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. *Conserv. Biol.* **22**: 534–543. doi:[10.1111/j.1523-1739.2008.00951.x](https://doi.org/10.1111/j.1523-1739.2008.00951.x).
- Hilbish, T. J., P. M. Brannock, K. R. Jones, A. B. Smith, B. N. Bullock, and D. S. Wetthey. 2010. Historical changes in the distributions of invasive and endemic marine invertebrates are contrary to global warming predictions: The effects of decadal climate oscillations. *J. Biogeogr.* **37**: 423–431. doi:[10.1111/j.1365-2699.2009.02218.x](https://doi.org/10.1111/j.1365-2699.2009.02218.x).
- Katz, S. L., S. E. Hampton, L. R. Izmet'eva, and M. V. Moore. 2011. Influence of long-distance climate Teleconnection on seasonality of water temperature in the World's largest Lake—Lake Baikal, Siberia. *PLoS One* **6**: e14688. doi:[10.1371/journal.pone.0014688](https://doi.org/10.1371/journal.pone.0014688).
- Kintisch, E. 2015. 'The Blob' invades Pacific, flummoxing climate experts. *Science* **348**: 17–18. doi:[10.1126/science.348.6230.17](https://doi.org/10.1126/science.348.6230.17).
- Mantua, N. J., and S. R. Hare. 2002. The Pacific decadal oscillation. *J. Oceanogr.* **58**: 35–44. doi:[10.1023/A:1015820616384](https://doi.org/10.1023/A:1015820616384).
- Miller, A. J., D. R. Cayan, T. P. Barnett, N. E. Graham, and J. M. Oberhuber. 1994. The 1976–77 climate shift of the Pacific Ocean. *Oceanography* **7**: 21–26.
- Mote, P. W., and E. P. Salathé. 2010. Future climate in the Pacific Northwest. *Clim. Change* **102**: 29–50. doi:[10.1007/s10584-010-9848-z](https://doi.org/10.1007/s10584-010-9848-z).
- National Centers for Environmental Information. 2018. Teleconnections, [accessed 2018 November 29]. Available from <https://www.ncdc.noaa.gov/teleconnections/>.
- Payne, J. T., A. W. Wood, A. F. Hamlet, R. N. Palmer, and D. P. Lettenmaier. 2004. Mitigating the effects of climate change on the water resources of the Columbia River basin. *Clim. Change* **62**: 233–256. doi:[10.1023/B:CLIM.0000013694.18154.d6](https://doi.org/10.1023/B:CLIM.0000013694.18154.d6).
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2018. nlme: Linear and nonlinear mixed effects models. R package version 3.1-140. Available from <https://CRAN.R-project.org/package=nlme>.
- Simberloff, D. and others 2013. Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* **28**: 58–66. doi:[10.1016/j.tree.2012.07.013](https://doi.org/10.1016/j.tree.2012.07.013).
- Simenstad, C., L. Small, C. McIntire, D. Jay, and C. Sherwood. 1990. Columbia River estuary studies - an introduction to the estuary, a brief-history, and prior studies. *Prog. Oceanogr.* **25**: 1–13. doi:[10.1016/0079-6611\(90\)90002-J](https://doi.org/10.1016/0079-6611(90)90002-J).
- Solt, F., Y. Hu, and B. Kenkel. 2018. interplot: Plot the effects of variables in interaction terms. Version 0.2.1. for R. Available from <https://CRAN.R-project.org/package=interplot>.
- Sousa, R., C. Antunes, and L. Guilhermino. 2008. Ecology of the invasive Asian clam *Corbicula fluminea* (Müller, 1774) in aquatic ecosystems: An overview. *Ann. Limnol. - Int. J. Limnol.* **44**: 85–94. doi:[10.1051/limn:2008017](https://doi.org/10.1051/limn:2008017).
- Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proc. Natl. Acad. Sci.* **99**: 15497–15500. doi:[10.1073/pnas.242437499](https://doi.org/10.1073/pnas.242437499).
- Theoharides, K., and J. Dukes. 2007. Plant invasion across space and time: Factors affecting nonindigenous species success during four stages of invasion. *New Phytol.* **176**: 256–273. doi:[10.1111/j.1469-8137.2007.02207.x](https://doi.org/10.1111/j.1469-8137.2007.02207.x).
- Thorp, J. H., and A. P. Covich. 2009. *Ecology and classification of north American freshwater invertebrates*. Academic Press.
- Vitousek, P., C. D'Antonio, L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *Am. Sci.* **84**: 468–478.
- Williamson, M. 2006. Explaining and predicting the success of invading species at different stages of invasion. *Biol. Invasions* **8**: 1561–1568. doi:[10.1007/s10530-005-5849-7](https://doi.org/10.1007/s10530-005-5849-7).
- Winder, M., A. D. Jassby, and R. Mac Nally. 2011. Synergies between climate anomalies and hydrological modifications facilitate estuarine biotic invasions. *Ecol. Lett.* **14**: 749–757. doi:[10.1111/j.1461-0248.2011.01635.x](https://doi.org/10.1111/j.1461-0248.2011.01635.x).
- Zhang, K., M. Xu, Q. Wu, Z. Lin, F. Jiang, H. Chen, and Z. Zhou. 2018. The response of zooplankton communities to the 2016 extreme hydrological cycle in floodplain lakes connected to the Yangtze River in China. *Environ. Sci. Pollut. Res.* **25**: 23286–23293. doi:[10.1007/s11356-018-2144-6](https://doi.org/10.1007/s11356-018-2144-6).
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer-Verlag.

ACKNOWLEDGMENTS

Funding for this research was provided by a U.S. Environmental Protection Agency STAR graduate fellowship grant (#FP91780901-0) awarded to E. Dexter and S. Bollens. All authors certify that they have no financial or personal conflicts of interest in the subject matter or materials discussed in this manuscript.

Submitted 31 January 2020

Revised 01 May 2020

Accepted 16 May 2020