



# Seasonal and interannual variation in lower Columbia River phytoplankton (2005–2018): environmental variability and a decline in large bloom-forming diatoms

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**ABSTRACT:** Understanding the influence of biotic and abiotic factors on riverine phytoplankton dynamics is challenging, particularly as anthropogenic stressors such as eutrophication, invasive species, and climate change alter these relationships. We examined a 14 yr (January 2005 to December 2018) dataset of phytoplankton and water quality variables, along with zooplankton and nutrient concentrations, from the Columbia River (the largest river in the US Pacific Northwest) to identify seasonal and interannual patterns of phytoplankton assemblage structure and their environmental associations. Non-metric multidimensional scaling, cluster, and indicator species analyses revealed: (1) a diatom/flagellate cluster in spring/summer, associated with chlorophyll *a*, discharge, ciliates, and Sarcodina; (2) a cyanobacteria/chlorophyte cluster in late summer/early fall, associated with higher water temperatures, increased clarity, the invasive copepod *Pseudodiaptomus forbesi*, and veligers of the invasive Asian clam *Corbicula fluminea*; and (3) a mixed-taxa winter cluster of minimal abundance and biomass. Nutrients were not strongly associated with the observed structural patterns. Phytoplankton bloom duration varied interannually, between years with short springtime blooms vs. years when blooms extended across multiple months. Springtime blooms of the diatom *Asterionella formosa* decreased in recent years, giving way to blooms of a mixed diatom assemblage. Further, high temperature, low discharge, and more invasive zooplankton were associated with cyanobacterial blooms, suggesting that increased temperature and reduced river flows predicted due to climate change in the Pacific Northwest may lead to further impacts on the late summer/early fall Columbia River plankton community.

**KEY WORDS:** Diatoms · Cyanobacteria · *Asterionella* · Invasive species · Climate change

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## 1. INTRODUCTION

As an autochthonous carbon supply, phytoplankton provide a major energy source for metazoan food webs (Reynolds & Descy 1996, Thorp et al. 2006), and thus form the base of riverine ecosystem productivity. Phytoplankton abundance and species composition are controlled by a wide range of abiotic and biotic factors, such as water column mixing, temper-

ature, nutrient and light availability, and zooplankton grazing (Sommer et al. 2012, Winder & Sommer 2012). Variability in these regulatory processes can alter the structure of phytoplankton assemblages, resulting in seasonal dynamics and interannual variation in bloom timing and magnitude (Reynolds 1989, Sterner 1989, Reynolds & Descy 1996). Determining which factors govern phytoplankton dynamics in rivers is further complicated by the compounding

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anthropogenic stressors acting upon freshwater systems, including eutrophication, flow modification, species invasions, and climate change (Dudgeon et al. 2006, Vörösmarty et al. 2010, Isaak et al. 2012, Reid et al. 2019). Long-term studies examining relationships between phytoplankton and environmental factors are thus vital to improving our understanding of these community dynamics in large river ecosystems; however, such studies are somewhat rare in the riverine ecology literature. With this as motivation, we conducted a 14 yr study to characterize the phytoplankton assemblage patterns and environmental associations in the lower Columbia River (CR), the largest river in the Pacific Northwest region of the USA.

Abiotic processes that strongly influence phytoplankton dynamics in riverine systems are commonly altered as a result of anthropogenic flow modification. Flow dynamics alter the concentration of suspended solids in the water column, causing variation in turbidity and light penetration; thus, riverine systems often favor diatoms, as these species are efficient harvesters of light at low intensity (Dokulil 1994, Reynolds et al. 1994). In addition, water temperature may directly influence phytoplankton abundance and composition, due to species-specific thermal growth optima (Reynolds 2006), or indirectly, by preventing or enhancing vertical mixing and subsequently modifying nutrient fluxes (Winder & Sommer 2012). The creation of dams and reservoirs, increasingly common along large rivers (Grill et al. 2015), affects many of these abiotic processes by altering discharge rates and timing (Nilsson et al. 2005), water temperatures (Poole & Berman 2001), and nutrient cycling and transport (Humborg et al. 2000, Ittekkot et al. 2000, Ahearn et al. 2005, Bosch 2008, Nilsson & Renöfält 2008). Indeed, temperature-controlled vertical mixing is likely to exert stronger control over phytoplankton dynamics in impounded reservoirs or areas of reduced flow, creating spatially distinct assemblages along the river continuum. In some cases, high phytoplankton growth rates in reservoirs serve to provide inocula for downstream communities (Reynolds & Descy 1996, Talling and Prowse 2010, Bortolini et al. 2017).

Biotic processes, such as grazing by crustacean zooplankton, have often been considered less important than abiotic processes in governing phytoplankton dynamics in large rivers (Reynolds & Descy 1996, Wehr & Descy 1998), and although laboratory and modeling studies have shown the importance of zooplankton grazing in regulation of lentic freshwater phytoplankton abundance and composition (Billen et al. 1994, Rollwagen-Bollens et al. 2013, Bowen et al.

2015), field studies examining this relationship in rivers are limited (Kobayashi et al. 1996).

Zooplankton can feed selectively, and thereby have a direct influence on phytoplankton composition (DeMott 1986, Cowles et al. 1988, Hong et al. 2013). Zooplankton grazing may even cause cascading effects if heterotrophs are preferentially consumed, thereby releasing some (but not all) phytoplankton taxa from predation (Sommer 2008, Saage et al. 2009, Rollwagen-Bollens et al. 2013, 2018). Rotifers, commonly abundant in rivers, are suggested to have a greater ability than other zooplankton to influence riverine phytoplankton assemblages, potentially due to faster generation times than other zooplankton taxa (Reynolds & Descy 1996, Gosselain et al. 1998). Grazing by bivalves may also be particularly relevant to riverine phytoplankton dynamics, as it may significantly decrease phytoplankton biomass (Strayer et al. 1999), may be selective to particular phytoplankton taxa (Baker & Levinton 2003, Bolam et al. 2019), and can indirectly influence nutrient and light dynamics in freshwater ecosystems (Vaughn & Hakenkamp 2001).

Long-term (>10 yr) studies of the Elbe and Rhine Rivers revealed that phytoplankton biomass in both systems is strongly regulated by abiotic factors, particularly discharge (Hardenbicker et al. 2014). By contrast, in the Meuse River, increases in bivalves (*Corbicula* spp.) have coincided with a notable decline in phytoplankton in the past decade, and model results show that effects of invasive filter feeders also have consequences for nutrient cycling and other ecosystem processes (Pigneur et al. 2014). These examples of contrasting control by abiotic and biotic processes on riverine phytoplankton assemblages emphasize the need to consider systems individually and over long time periods to understand factors governing phytoplankton dynamics.

The CR is the largest river in the US Pacific Northwest and is highly altered by anthropogenic stressors. Hydroelectric dams, which alter discharge and disrupt ecosystem connectivity and river habitats (Liermann et al. 2012, Grill et al. 2015), are numerous on the CR, and its watershed has been impacted by substantial agricultural land use change over the past century (Matheussen et al. 2000). The CR has also experienced a number of aquatic species invasions, most notably the Asian copepod *Pseudodiaptomus forbesi* (Bollens et al. 2012, Dexter et al. 2015, Emerson et al. 2015) and the Asian clam *Corbicula fluminea* (Hassett et al. 2017). Invasive species can alter indigenous community structure, biodiversity, and ecosystem function (Havel et al. 2015). For instance,

selective feeding on autotrophic and heterotrophic microplankton has been exhibited by both *P. forbesi* (Bowen et al. 2015) and *C. fluminea* (Bolam et al. 2019), with evidence for avoidance of cyanobacterial taxa by both species. However, the relationships between, and relative importance of, these abiotic and biotic processes on long-term phytoplankton dynamics in the lower CR have not been investigated.

In this study, we examined 14 yr of monthly phytoplankton and environmental data collected from the lower CR to address 2 overarching research questions: (1) How do the patterns of phytoplankton abundance and composition in the lower CR vary seasonally and interannually? (2) Which abiotic and biotic variables are most closely associated with variation in phytoplankton composition? Our findings allow us to better understand phytoplankton seasonal and interannual variability in the lower CR and provide insights into the relationships between phytoplankton assemblages and anthropogenic stressors, such as climate change and species invasions, in large river systems.

## 2. MATERIALS AND METHODS

### 2.1. Study system

The CR is 1954 km long, has a catchment area of 660 480 km<sup>2</sup>, and a mean annual discharge of ~5500 m<sup>3</sup> s<sup>-1</sup>, measured at The Dalles, OR, USA (Simenstad et al. 1990). Dams are common features within the CR Basin, providing hydroelectric power generation, improved navigation, flood control, irrigation, recreation, and water supply. There are 11 major hydroelectric dams on the mainstem CR and hundreds of smaller impoundments along its tributaries (Simenstad et al. 1990).

Our sampling station was located approximately 10 m from shore at a pier in Vancouver, WA, USA (45° 37' 20" N, 122° 40' 38" W), which is located 66 river km downstream from the lowest mainstem hydropower project (Bonneville Dam) and approximately 170 river km upstream of the mouth of the river at the Pacific Ocean (Fig. 1). Hydrologically, the river is well mixed at this site, as river flow is high and the water col-

umn is not known to thermally stratify (Dexter et al. 2015). The 4 major dams on the lower CR are 'run-of-river,' i.e. designed to maintain consistent flow and minimal storage. Phytoplankton abundances were not found to be different above and below the lowest 2 dams (Bonneville and The Dalles dams) in a recent study (Rose et al. 2019b).

### 2.2. Sample collection and data acquisition

We collected samples of plankton and water quality variables from the CR on a monthly basis from January 2005 to December 2018, with only 1 missing month in the time series (March 2016). Surface water samples were collected in triplicate using a clean bucket on each sampling date. For phytoplankton, 200 ml sub-samples were taken from each bucket

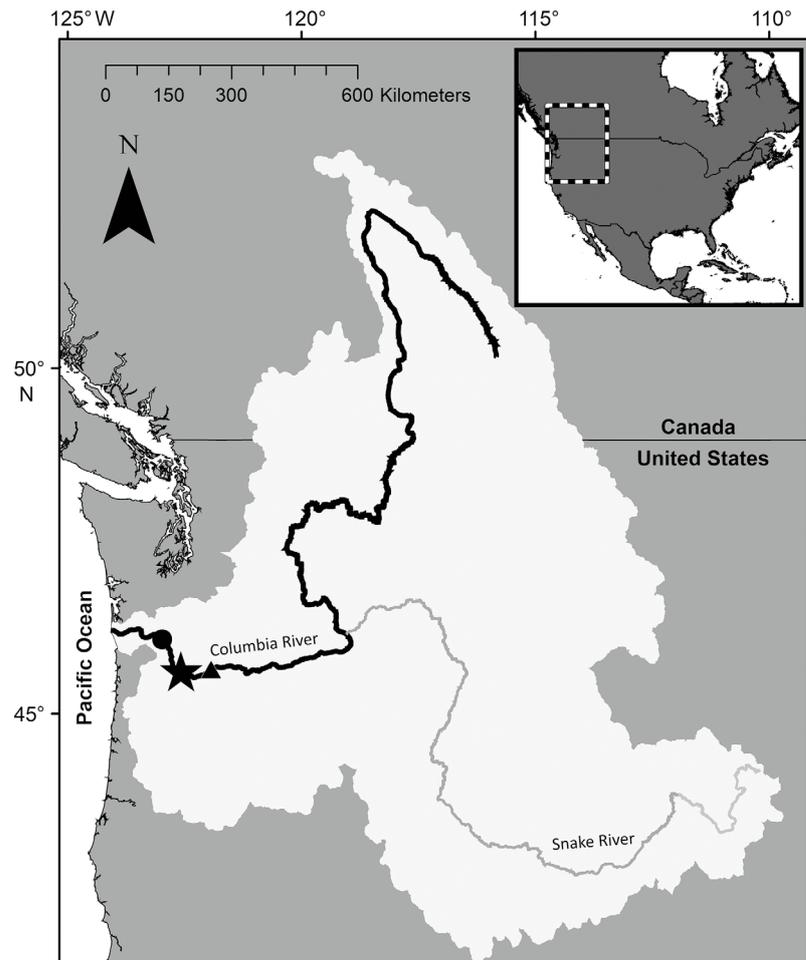


Fig. 1. Columbia River Basin (light gray; shown with the Columbia River and its major tributary, the Snake River) in the Pacific Northwest region of the USA. The sampling location near Vancouver, WA, is marked with a star, and the location of the Bonneville Dam is marked with a black triangle. Black circle shows Port Westward (formerly Beaver Army Terminal)

and immediately preserved in the field by transferring into amber bottles pre-filled with Lugol's iodine solution, to a final dilution of 5%. Additional water sub-samples (70 ml) were taken from each bucket, stored in amber bottles, and kept on ice during transportation back to the lab for determination of chlorophyll (chl) *a* concentration.

Water temperature and salinity profiles were obtained using a YSI 85, an EC 300, or a YSI Pro 2030 water quality probe, recording values every 2 m from the surface to the bottom. We also concurrently recorded river depth and Secchi disk depth. We acquired river flow data from the CR Data Access in Real Time (DART) database ([www.cbr.washington.edu/dart](http://www.cbr.washington.edu/dart)). We calculated mean monthly discharge in  $\text{m}^3 \text{s}^{-1}$  using hourly data recorded at the Bonneville Dam from January 2005 through December 2018.

We also utilized mesozooplankton data collected concurrently at our site from January 2005 to December 2016. Zooplankton were collected via triplicate vertical tows from a depth of 1 m off the river bottom to the surface using a 73  $\mu\text{m}$  mesh, 0.5 m diameter plankton net and preserved in the field using 5–10% buffered formalin. For taxonomic identification, sub-samples were taken from homogenized, preserved samples using a Stempel pipette; a minimum of 200 non-naupliar organisms were counted using a Leica MZ6 stereomicroscope. Microcrustaceans and rotifers were identified to the lowest taxon possible (Thorp & Covich 2010). Counts of individual organisms were converted to density ( $\text{ind. m}^{-3}$ ) for further analysis. For a full description of methods used for zooplankton enumeration, see Dexter et al. (2015). Mesozooplankton data were binned into the following taxonomic categories for further analysis—Cladocera, Copepoda: cyclopoid, Copepoda: calanoid (*P. forbesi*), Rotifera, and bivalve veligers (*C. fluminea*). Nauplii were excluded from these analyses. All observed species of Cladocera and cyclopoid Copepoda were native, with the exception of rare observations of the non-indigenous cladoceran *Bosmina coregoni* (Smits et al. 2013).

Nutrient data were acquired from the United States Geological Survey (USGS) National Water Information System Web Interface (<https://nwis.waterdata.usgs.gov/nwis/qwdata>). Filtered water quality samples were collected from the CR at Port Westward, OR, formerly Beaver Army Terminal (46° 10' 53" N, 123° 10' 55" W), approximately 82 river km downstream from our plankton collection site. We used measurements of nitrite + nitrate ( $\text{NO}_2 + \text{NO}_3\text{-N}$ ), orthophosphate ( $\text{PO}_4\text{-P}$ ), total ammonia ( $\text{NH}_3 + \text{NH}_4\text{-N}$ ), and silica ( $\text{SiO}_2$ ), all in  $\text{mg l}^{-1}$ . Samples were collected on a nearly monthly basis from 2005 to 2018

(less frequently in fall and winter months). An average was calculated when multiple values existed for a given month. One value of  $\text{NH}_3 + \text{NH}_4\text{-N}$  (April 2011) was excluded from our analysis because it was 30× greater than the next highest value.

### 2.3. Laboratory methods

To determine chl *a* concentration, we filtered 70 ml aliquots of river water through Whatman GF/F filters. Filters were put into glass scintillation vials and placed in a freezer for at least 24 h, but fewer than 6 d. Chl *a* was extracted by adding 20 ml of 90% acetone to the vials and placing them back in the freezer for 24 h. Chl *a* concentration was determined fluorometrically, according to the acidification method (Arar & Collins 1997), using a Turner Model 10-AU fluorometer.

Two of the 3 replicate preserved microplankton samples from each date were separately settled using Utermöhl chambers in preparation for enumeration and identification. Aliquots ranged from 9.5 to 200 ml, to ensure adequate cell densities, and were settled for at least 15 h before examination with a Leica DMI 4000B inverted microscope at 400× magnification (and 630× where necessary). We identified and counted at least 300 cells from fields along slide transects (Kirchman 1993). We included all phytoplankton, defined here to include autotrophic/mixotrophic protists and cyanobacterial taxa, and heterotrophic protists (ciliates and Sarcodina) between 5 and 200  $\mu\text{m}$ , and identified these to genus and species, where possible, following Patterson & Hedley (1992) and Wehr et al. (2015). Biomass estimates ( $\mu\text{g C l}^{-1}$ ) were calculated according to Hillebrand et al. (1999) and Menden-Deuer & Lessard (2000). To facilitate consistent comparisons among taxa, our counting unit for all taxa was individual cell, rather than colony. Resulting phytoplankton data were binned into the following 6 major taxonomic groups for visual presentation—diatoms, dinoflagellates, flagellates (including cryptophytes, chrysophytes, synurophytes, and euglena), chlorophytes, cyanobacteria, and rhodophytes.

### 2.4. Data analysis

We used a cluster analysis approach (Clarke 1993) to identify distinct groups among phytoplankton samples throughout the entire 14 yr study period. Phytoplankton abundance data were transformed ( $\log_{10} + 1$ ) prior to analysis. Hierarchical agglomerative clustering was performed using Bray-Curtis

dissimilarity measures and the group average linkage clustering method. We used a multiple-response permutation procedure (Mielke et al. 1981) to test whether the resultant clusters were significantly different from one another. We then found species strongly indicative of each cluster through indicator species analysis (Dufrene & Legendre 1997), using relative abundance and frequency of species within each cluster, and assessed significance of the associations using a Monte Carlo permutation test.

We assessed patterns in phytoplankton composition among samples through ordination with non-metric multidimensional scaling (NMDS), using transformed ( $\log_{10} + 1$ ) abundance data and a Bray-Curtis dissimilarity measure (Kruskal 1964). We selected NMDS as a method of ordination because of its broad application in community ecology and sound performance on non-normal and discontinuous data (McCune & Grace 2002). We conducted the ordination 3 times, using the previous best solution as a new random start each time, to find the best solution with the lowest stress value (Minchin 1987). Taxa present in less than 5% of samples were excluded from analysis to reduce the influence of rarely occurring species on assemblage analysis (McCune & Grace 2002). The goodness-of-fit between the NMDS ordinations and our data was evaluated by calculating a stress coefficient, or a measure of the relationship between the rank order sample positions in ordination space and the rank order dissimilarities in the original data, using a guidance value of  $<0.2$  as a sound representation of community relationships (Clarke 1993). We further tested if stress evident in our NMDS ordinations was lower than that achievable in ecological null models using randomized data via a permutation procedure (Dexter et al. 2018).

To determine which combination of abiotic and biotic environmental variables best explained patterns in phytoplankton composition, we utilized a non-parametric BIOENV correlation procedure (Clarke & Ainsworth 1993). In this analysis, the phytoplankton community ordination was related to all combinations of factors in our environmental dataset (i.e. physical variables, chl *a*, and  $\log_{10}$ -transformed mesozooplankton abundances) to determine the most parsimonious combination of factors that explains variation in phytoplankton assemblages in the lower CR. A best-fit combination of environmental variables was identified by comparing patterns in the phytoplankton ordination with these variables, and evaluated using a Spearman's harmonic rank correlation coefficient ( $r_s$ ). Variables identified in the best-fit model were then included in vector fitting, via re-

gression, on the NMDS ordination to allow visual assessment of strength and direction of relationships with phytoplankton assemblages. Goodness-of-fit to the phytoplankton assemblage patterns of each variable included in vector fitting was measured with a correlation coefficient ( $r^2$ ) and evaluated for significance using 1000 permutations in a Monte Carlo randomization test.

Because the mesozooplankton and nutrient data each only partially overlapped with our phytoplankton time series, the combination of NMDS and BIOENV described above was conducted 3 times: (1) using monthly phytoplankton samples from 2005 to 2018 accompanied by the variables chl *a*, temperature, discharge, depth, salinity, ciliates, and Sarcodina; (2) using monthly phytoplankton data and all aforementioned variables from 2005 to 2016, plus our mesozooplankton time series (Cladocera, cyclopoid Copepoda, Rotifera, *P. forbesi*, and *C. fluminea* veligers); and (3) using monthly phytoplankton and mesozooplankton data from 2005 to 2016 as well as the acquired USGS nutrient data in addition to all previously used environmental variables. This allowed us to compare all environmental variables across different portions of our phytoplankton time series, and avoided the limitations of using statistical methods which are unable to perform properly when there are zeros in the data (as was common in our dataset). Multivariate community analyses were performed using R version 3.6.1 (R Core Team 2019) and the packages 'vegan' (Oksanen et al. 2019) and 'labdsv' (Roberts 2016).

We further analyzed phytoplankton assemblage data to explore 3 possible changes in species composition and bloom magnitude that we observed over our 14 yr time series. In each case, data were  $\log_{10}$ -transformed to meet test assumptions of data distribution and variance prior to linear regression analysis. First, we tested the relationship between river discharge and phytoplankton bloom magnitude during springtime (March–May), when both river flow and phytoplankton biomass are typically at their annual peak. A springtime mean ( $n = 3$ ) was calculated for phytoplankton biomass ( $\mu\text{g C l}^{-1}$ ) and river discharge ( $\text{m}^3 \text{s}^{-1}$ ) for each year (2005–2018). Second, we observed a measurable decrease in the abundance of the diatom *Asterionella formosa* starting in 2013; we therefore compared annual means of *A. formosa* ( $\log_{10}$  transformed) abundance from 2005–2012 to those of 2013–2018 using a Mann-Whitney *U*-test.

Finally, to investigate whether apparent increases in cyanobacteria abundance in the latter years of our

study period were statistically significant, we compared total cyanobacteria  $\log_{10}$ -transformed abundance between years using a Kruskal-Wallis and post-hoc Dunn's comparison test, with p-values adjusted for multiple comparisons using the false discovery rate method (Benjamini & Hochberg 1995). It was not possible for us to use parametric analyses to test the relationships between phytoplankton taxa and all of the other environmental variables in our dataset, for the reasons stated above, i.e. non-normal and discontinuous data, and the presence of multiple zeros. Univariate analyses were completed using R version 3.6.1 (R Core Team 2019).

### 3. RESULTS

#### 3.1. Abiotic environmental variables

Many of the environmental factors we measured in the CR exhibited strong seasonal variability. River discharge ranged from 2381 to 13 440  $\text{m}^3 \text{s}^{-1}$ , and lowest and highest discharge occurred annually in September/October and April/May/June, respectively (Fig. 2a and see Fig. S1a in the Supplement at [www.int-res.com/articles/suppl/a087p029\\_supp.pdf](http://www.int-res.com/articles/suppl/a087p029_supp.pdf)). Surface water temperatures ranged between 2.5 and 22.5°C, with lowest temperatures in December/January and highest temperatures in July/August (Fig. 2b; Fig. S1b). Secchi disk depth varied over time, ranging from 0.5 to 6.0 m, but generally followed a trend inverse to that of river discharge (Fig. 2c; Fig. S1c). Total water depth ranged between 7.8 and 15 m, and was generally shallowest in August/September/October and deepest in April/May/June (Fig. 2d; Fig. S1d). Salinity was ~0.1 PSU throughout the study period (data not shown).

$\text{PO}_4\text{-P}$  concentration averaged 0.030  $\text{mg l}^{-1}$  over the 14 yr study period and was highly variable, particularly between 2008 and 2013 (Fig. S2a), with no strong seasonal pattern (Fig. 2e).  $\text{NO}_2\text{+NO}_3\text{-N}$  concentrations ranged between 0.002 and 0.726  $\text{mg l}^{-1}$  (Fig. S2b), were highest from January to March, and decreased throughout the spring to a low in July and August (Fig. 2f).  $\text{NH}_3\text{+NH}_4\text{-N}$  concentrations averaged 0.110  $\text{mg l}^{-1}$ , with high variability and elevated values between 2008 and 2012 (Fig. S2c), and highest values evident in late spring and late summer (Fig. 2g).  $\text{SiO}_2$  concentration was also highly variable, particularly from 2007 through 2014, and ranged from 0.07 to 17  $\text{mg l}^{-1}$  (Fig. S2d) and was generally highest in March–May and lowest in June–August (Fig. 2h).

#### 3.2. Biotic environmental variables

Abundances of mesozooplankton taxa showed seasonal and interannual variability in peak density between 2005 and 2016 (Fig. S3). Cladoceran density typically increased during spring and summer and reached lowest densities in late fall/winter (Fig. S3a). Cyclopoid copepods were generally less abundant than Cladocera, but were similarly most abundant in spring and summer (Fig. S3b). Unlike Cladocera and copepods, rotifers generally exhibited one strong seasonal peak in the spring (Fig. S3c). Both invasive zooplankton species, the Asian copepod *Pseudodiaptomus forbesi* and veligers of the Asian clam *Corbicula fluminea*, had peak densities in late summer/early fall (Fig. S3d,e). Of the microzooplankton (heterotrophic protist) taxa collected between 2005 and 2018, ciliates were consistently more abundant than Sarcodina, with both exhibiting one or more peaks of abundance throughout spring and summer (Fig. S3f,g). Chl *a* concentration, used in vector analysis as a proxy for phytoplankton biomass, was commonly highest in spring; however, during some years, elevated chl *a* concentration persisted into summer and early fall (Fig. 3a).

#### 3.3. Phytoplankton composition

A total of 72 phytoplankton taxa were identified from our samples (Box 1). Total phytoplankton abundance ( $\text{cells ml}^{-1}$ ) increased from February until ~April/May and then decreased to a minimum in December/January of each year (Fig. 3b). Generally, the annual pattern in total phytoplankton biomass ( $\mu\text{g C l}^{-1}$ ) followed that of total abundance (Fig. 3c). However, the timing and magnitude of the annual phytoplankton bloom varied interannually. Phytoplankton abundance and biomass commonly peaked between March and May; however, in some years, the annual bloom period extended into late summer (e.g. 2008, 2009, and 2013) and even into fall (e.g. 2017, 2018) (Fig. 3). Phytoplankton abundance and biomass were regularly dominated by diatoms, with flagellates comprising a greater proportion in months when diatom biomass was low. Cyanobacteria were numerically abundant during peak phytoplankton bloom periods (typically during spring, except in 2017 and 2018), but usually did not comprise a significant proportion of community biomass (Fig. 3). However, in years when the bloom period extended into late summer and fall (e.g. 2017 and 2018), cyanobacteria comprised a greater proportion of phytoplankton abundance and biomass (Fig. S4).

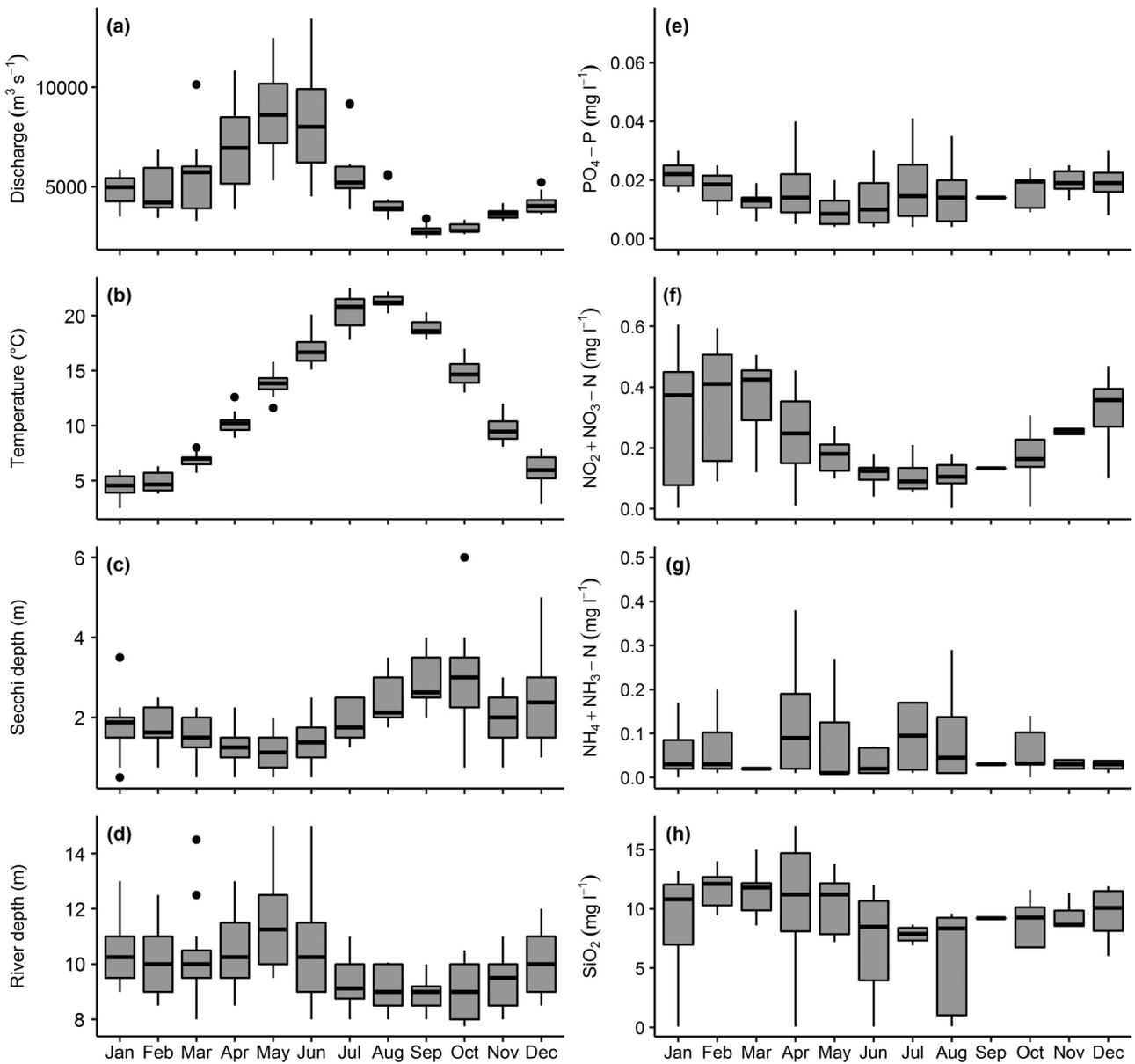


Fig. 2. Median and interquartile range of monthly values for (a) discharge, (b) water temperature, (c) Secchi disk depth, and (d) river depth at the study site based on data collected from the Columbia River 2005 through 2018. Outlying points have values beyond  $1.5\times$  the median and interquartile range. Median and interquartile range of mean monthly nutrient concentrations, including (e) phosphate, (f) nitrite plus nitrate, (g) total ammonia nitrogen, and (h) silica collected between January 2005 and December 2018 at Port Westward (formerly Beaver Army Terminal) in the lower Columbia River (USGS unpubl. data). Outlying points are not shown

### 3.4. Phytoplankton cluster analysis

We identified 3 phytoplankton assemblage clusters using hierarchical agglomerative clustering of abundance data from the entire study period (2005–2018; Fig. 4), which were significantly different from each other according to the multiple-response permutation procedure ( $A = 0.146$ ,  $p < 0.001$ ). Clusters were evaluated using environmental variables that were deter-

mined to be most closely associated with assemblage patterns using the BIOENV correlation procedure.

Cluster 1 primarily included samples from February to June and was associated with moderate water temperatures (mean =  $12.0^{\circ}\text{C}$ ), shallow Secchi disk depths (mean =  $1.6\text{ m}$ ), and increased chl *a* concentration (mean =  $8.98\ \mu\text{g l}^{-1}$ ). According to indicator species analysis, Cluster 1 was characterized by a ‘diatom/flagellate’ assemblage, which included pri-

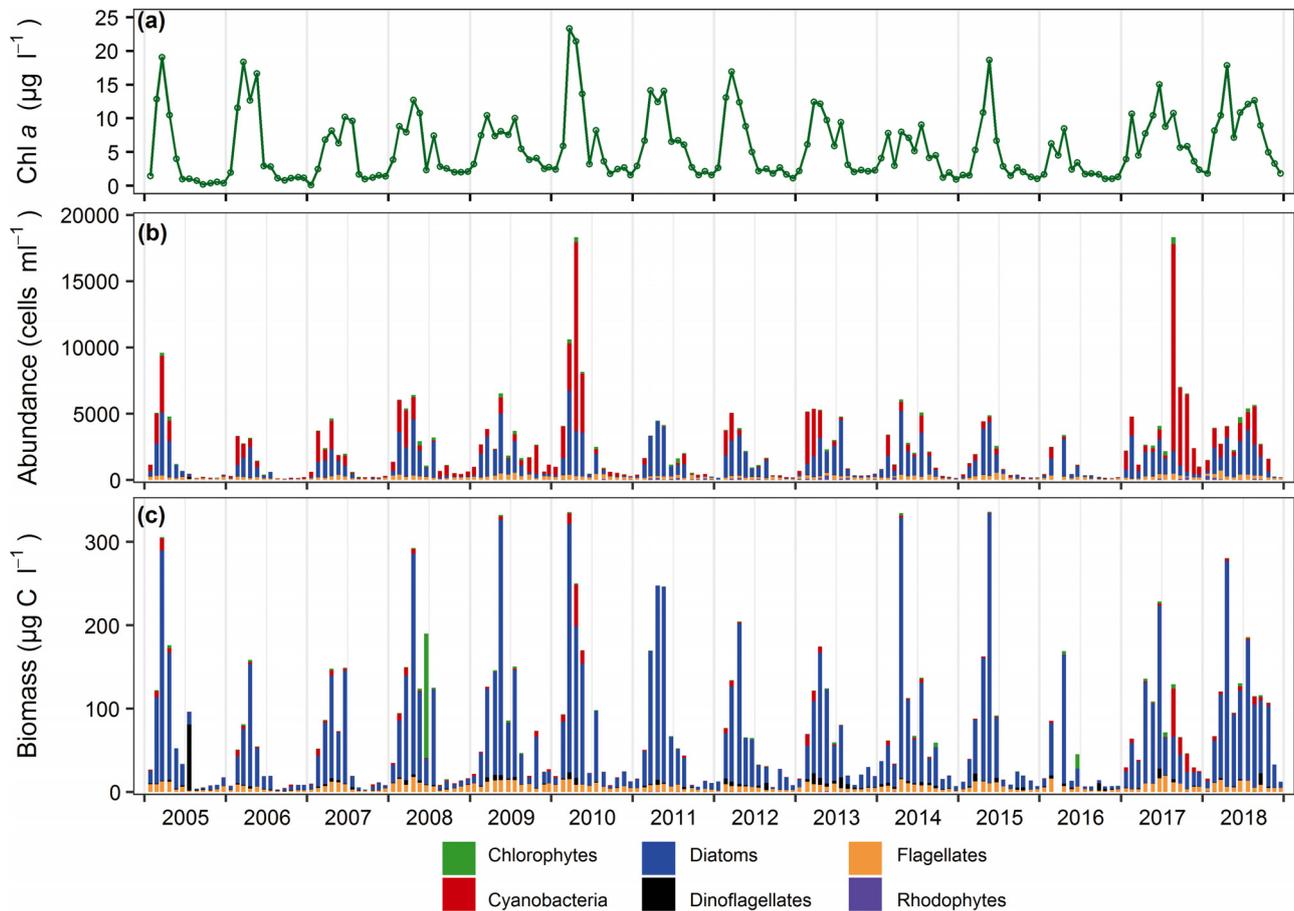


Fig. 3. (a) Chlorophyll a concentration, (b) abundance, and (c) biomass of 6 major taxonomic categories of Columbia River phytoplankton collected near Vancouver, WA (USA), from January 2005 to December 2018

Box 1. Columbia River, USA, phytoplankton taxa present in >5% of samples from January 2005 to December 2018

<b>Bacillariophyceae</b>	<i>Amphora</i> spp., <i>Asterionella formosa</i> , <i>Aulacoseira</i> spp., <i>Aulacoseira</i> sp. (spiral morphology), <i>Cocconeis</i> spp., <i>Cyclotella</i> spp., <i>Cymbella</i> spp., <i>Diatoma</i> spp., <i>Fragilaria capucina</i> , <i>Fragilaria crotonensis</i> , <i>Gomphonema</i> spp., <i>Gyrosigma</i> spp., <i>Hantzschia</i> spp., <i>Melosira</i> spp., <i>Navicula</i> spp., <i>Nitzschia</i> spp., <i>Nitzschia fruticosa</i> , <i>Nitzschia sigmaidea</i> , <i>Rhoicosphenia abbreviata</i> , <i>Skeletonema</i> spp., <i>Stephanodiscus</i> spp., <i>Surirella</i> spp., <i>Synedra</i> spp., <i>Synedra ulna</i> , <i>Tabellaria fenestrata</i> , unknown chain centric, unknown pennate
<b>Chlorophyta</b>	<i>Actinastrum</i> spp., <i>Ankistrodesmus</i> spp., <i>Characium</i> spp., <i>Chlamydomonas</i> spp., <i>Coelastrum</i> spp., <i>Dictyosphaerium</i> spp., <i>Eudorina</i> spp., <i>Golenkinia</i> spp., <i>Kirchneriella</i> spp., <i>Micractinium</i> spp., <i>Monoraphidium</i> spp., <i>Oocystis</i> spp., <i>Pandorina</i> spp., <i>Pediastrum</i> spp., <i>Scenedesmus</i> spp., <i>Acutodemus acuminatus</i> (formerly <i>Scenedesmus acuminatus</i> ), <i>Scenedesmus linearis</i> , <i>Desmodesmus communis</i> (formerly <i>Scenedesmus quadricauda</i> ), <i>Schroederia setigera</i> , <i>Schroederia spiralis</i> , <i>Sphaerocystis</i> spp., <i>Tetraedron</i> spp., <i>Tetrastrum</i> spp., unknown chlorophyte
<b>Chrysophyta</b>	<i>Dinobryon</i> spp., <i>Stelaxomonas</i> spp.
<b>Cryptophyta</b>	<i>Cryptomonas</i> spp., unknown flagellate
<b>Cyanophyta</b>	<i>Dolichospermum</i> spp. (formerly <i>Anabaena</i> ), <i>Aphanizomenon flosaquae</i> , <i>Aphanocapsa</i> spp., <i>Aphanothece</i> spp., <i>Coelosphaerium</i> spp., <i>Merismopedia</i> spp., <i>Microcystis</i> spp., <i>Oscillatoria</i> spp., unknown cyanobacteria
<b>Dinophyta</b>	Athecate prolate dinoflagellate, athecate round dinoflagellate, <i>Peridinium</i> spp., thecate prolate dinoflagellate, thecate round dinoflagellate
<b>Euglenozoa</b>	Euglenoid
<b>Rhodophyta</b>	<i>Batrachospermum gelatinosum</i>
<b>Synurophyceae</b>	<i>Mallomonas</i> spp.

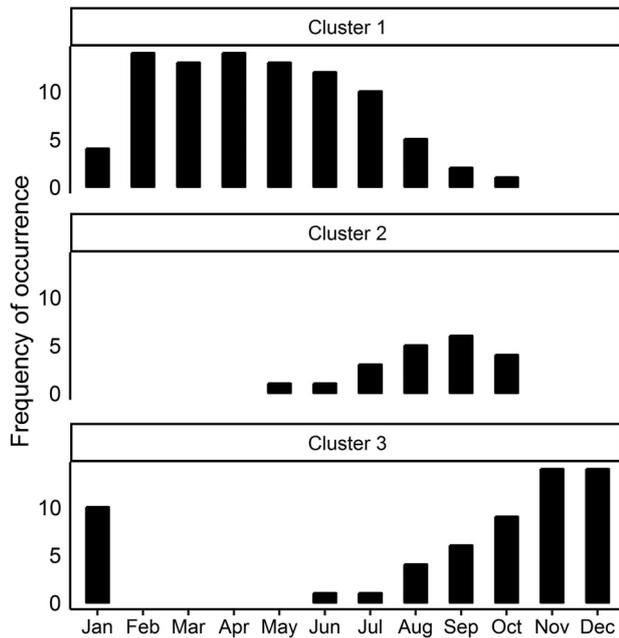


Fig. 4. Monthly frequency of occurrence for each phytoplankton community cluster in the Columbia River from January 2005 to December 2018. Cluster 1 = diatoms/flagellates; Cluster 2 = cyanobacteria/chlorophytes; Cluster 3 = mixed taxa

mainly large diatom species, with some flagellates, a few green algae, and 1 cyanobacteria taxon (Table 1).

Cluster 2 predominantly included samples from August to October and was associated with warmer water temperatures (mean = 18.8°C), deeper Secchi disk depths (mean = 2.7 m), and reduced chl *a* concentration (mean = 2.88  $\mu\text{g l}^{-1}$ ). Indicator species analysis revealed that Cluster 2 was characterized by a 'cyanobacteria/green algae' assemblage, including multiple cyanobacteria and green algae genera, a few diatoms, and a dinoflagellate taxon (Table 1).

Cluster 3 primarily included samples from November to January and was associated with cooler water temperatures (mean = 10.8°C), moderate Secchi disk depths (mean = 2.3 m), and lowest chl *a* concentration (mean = 1.81  $\mu\text{g l}^{-1}$ ). Cluster 3 predominantly included samples from winter when phytoplankton abundance was low and of a mixed assemblage; no individual taxa were found to be significantly indicative of Cluster 3.

Based on these statistical analyses, we defined the phytoplankton clusters as (1) 'diatoms/flagellates,' (2) 'cyanobacteria/chlorophytes,' and (3) 'mixed taxa,' which primarily occurred in spring/early summer, late

Table 1. Community clusters determined through hierarchical agglomerative clustering of phytoplankton abundance data (2005–2018). Indicator species analysis was used to find taxa significantly associated with a given cluster ( $p < 0.05$ ). Taxa with highly significant associations ( $p \leq 0.001$ ) are in **bold**, cyanobacteria genera are underlined. Abiotic and biotic associations are positively associated with the indicated phytoplankton community cluster

Community cluster	Season	Indicator taxa	Abiotic associations	Biotic associations
<b>Cluster 1: diatoms/flagellates</b>	Spring/summer	<b><i>Synedra</i>, <i>Asterionella</i>, <i>Fragilaria crotonensis</i>, <i>Mono- raphidium</i>, <i>Nitzschia</i>, <i>Aulacoseira</i>, <i>Cyclotella</i>, <i>Dinobryon</i>, <i>Mallomonas</i>, <i>Chlamydomonas</i>, <b>unknown flagellate</b>, <i>Micractinium</i>, athecate round dinoflagellate, <u><i>Aphanizomenon flosaquae</i></u>, unknown chlorophyte, <b><i>Tabellaria fenestrata</i>, <i>Stelexomonas</i>, <i>Cryptomonas</i>, <i>Fragilaria capucina</i>, <i>Ankistrodesmus</i></b></b>	Discharge	Chl <i>a</i> , Sarcodina, Ciliates
<b>Cluster 2: cyanobacteria/chlorophytes</b>	Late summer/fall	<b><u><i>Microcystis</i></u>, <i>Navicula</i>, <u><i>Aphanocapsa</i></u>, <i>Scenedesmus</i> sp., <i>Cocconeis</i>, <i>Scenedesmus linearis</i>, <i>Dictyosphaerium</i>, <i>Tetraedron</i>, <u><i>Merismopedia</i></u>, <i>Nitzschia fruticosa</i>, <i>Rhoicosphenia abbreviata</i>, <i>Pandorina</i>, <i>Sphaerocystis</i>, <i>Coelastrum</i>, <i>Eudorina</i>, thecate prolate dinoflagellate, <u><i>Oscillatoria</i></u></b>	Temperature, clarity	<i>Pseudodiatomus forbesi</i> , <i>Corbicula fluminea</i> veligers
<b>Cluster 3: mixed taxa</b>	Winter			

summer/fall, and winter, respectively, although with some interannual variation. The duration of the diatom/flagellate cluster in spring/summer was shortest in 2016, lasting through April, and longest in 2017 and 2018, lasting through October and September, respectively. The cyanobacteria/chlorophyte cluster of late summer/fall usually lasted for a shorter time than diatoms/flagellates (~1–3 mo), occurred early in 2016 (May/June) and did not occur during 2011–2013 or in 2017. The disappearance of the cyanobacteria/chlorophyte cluster from 2011–2013 was coincident with reduced July water temperatures ( $<19^{\circ}\text{C}$ ) between 2010 and 2013, which were the lowest water temperature measurements for July over the 14 yr study period. The mixed taxa cluster occurred once in June 2010, accompanied by reduced phytoplankton abundance relative to other summer months, and again in 2016, lasting from July through December.

### 3.5. Phytoplankton assemblage relationships with abiotic and biotic factors

NMDS analysis of the entire phytoplankton abundance dataset (2005–2018) resulted in a 3-dimensional ordination with a stress value of 0.13 (Fig. 5). The permutation test of Dexter et al. (2018) further validated our ordination by determining that the stress value for our data matrix could not have occurred if strong species interactions were absent ( $z = -61.6$ ,  $p = 0.002$ ). Analysis using the BIOENV correlation procedure on all abiotic and biotic factors collected monthly from 2005 to 2018 ( $n = 167$ ) revealed that the model with the combination of factors which best explained patterns in the phytoplankton assemblage data ( $r_s = 0.5188$ ; Table S1) included temperature ( $r^2 = 0.65$ ), Secchi disk depth ( $r^2 = 0.34$ ), chl *a* ( $r^2 = 0.60$ ), and ciliates ( $r^2 = 0.70$ ; Fig. 5).

An NMDS ordination (3 dimensions, stress = 0.13), permutation test ( $z = -55.0$ ,  $p = 0.002$ ), and BIOENV procedure were also conducted with the mesozooplankton data that were collected concurrently with the first 12 yr of our phytoplankton data (2005–2016;  $n = 143$ ). The model with the combination of factors that best explained patterns in our phytoplankton assemblage data ( $r_s = 0.5357$ ; Table S2) included Secchi disk depth ( $r^2 = 0.35$ ), chl *a* ( $r^2 = 0.60$ ), discharge ( $r^2 = 0.47$ ),

ciliates ( $r^2 = 0.70$ ), Sarcodina ( $r^2 = 0.46$ ), the invasive Asian copepod *P. forbesi* ( $r^2 = 0.66$ ), and veligers of the invasive Asian clam *C. fluminea* ( $r^2 = 0.57$ ; Fig. 6).

The third and final NMDS (3 dimensions, stress = 0.13), permutation test ( $z = -44.60$ ,  $p = 0.002$ ), and BIOENV procedures were conducted using 12 yr of our phytoplankton data (2005–2016,  $n = 101$ ) and associated abiotic and biotic factors (including mesozooplankton) that corresponded with nutrient samples. The BIOENV model with the combination of factors that best explained phytoplankton assemblage patterns ( $r_s = 0.5431$ ; Table S3) included temperature ( $r^2 = 0.65$ ), Secchi disk depth ( $r^2 = 0.38$ ), chl *a* ( $r^2 = 0.61$ ), ciliates ( $r^2 = 0.69$ ), and *P. forbesi* ( $r^2 = 0.60$ ).

### 3.6. Analysis of temporal changes in phytoplankton composition and bloom magnitude

Interannual variation in springtime (March–May) phytoplankton biomass ( $\mu\text{g C l}^{-1}$ ) followed a trend inverse to that of spring river discharge over the study period. Linear regression analysis revealed this inverse trend to be significant ( $n = 14$ ,  $p = 0.04$ , adjusted  $r^2 = 0.24$ ; Fig. 7).

*Asterionella formosa*, *Aulacoseira* spp., *Cyclotella* spp., *Fragilaria crotonensis*, and *Stephanodiscus* spp. were the dominant diatom taxa by biomass in the CR throughout the study period. *A. formosa*, which commonly comprised the greatest proportion of springtime diatom biomass, exhibited marked seasonality, with a rapid increase from February to March/April followed

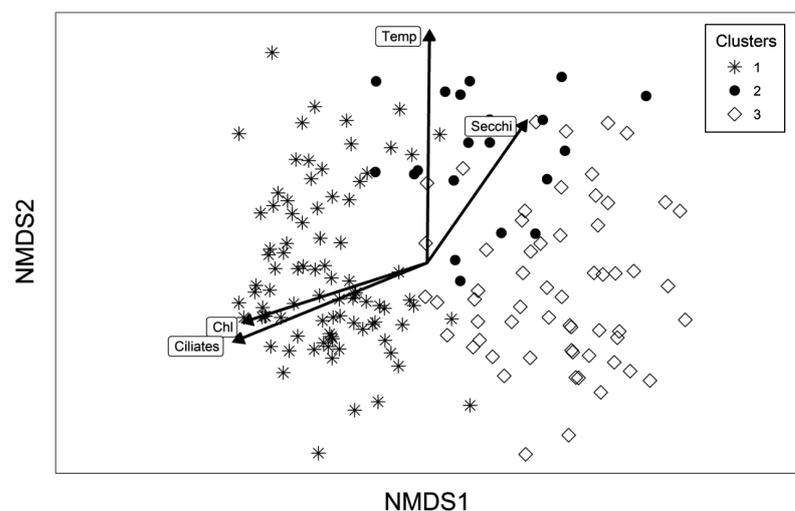


Fig. 5. Non-metric multidimensional scaling (NMDS) ordination (stress = 0.13) plotted with directional vectors for gradients of the abiotic variables of temperature ( $r^2 = 0.65$ ), Secchi disk depth ( $r^2 = 0.34$ ), ciliates ( $r^2 = 0.70$ ), and chlorophyll *a* concentration ( $r^2 = 0.60$ ) measured between 2005 and 2018. Only significant ( $p < 0.001$ ) variables were fitted to this ordination

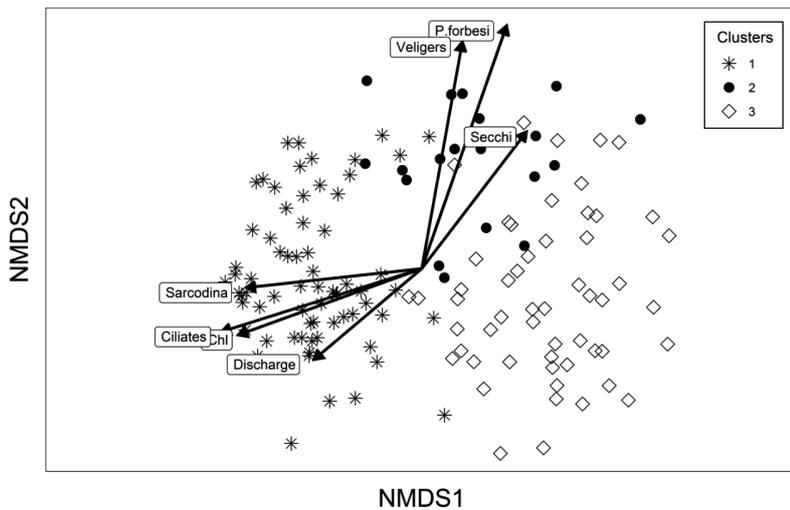


Fig. 6. Non-metric multidimensional scaling (NMDS) ordination (stress = 0.13) plotted with directional vectors for gradients of Secchi disk depth ( $r^2 = 0.35$ ), ciliates ( $r^2 = 0.70$ ), discharge ( $r^2 = 0.47$ ), Sarcodina ( $r^2 = 0.46$ ), the invasive copepod *Pseudodiaptomus forbesi* ( $r^2 = 0.66$ ), veligers of the invasive clam *Corbicula fluminea* ( $r^2 = 0.57$ ), and chlorophyll *a* concentration ( $r^2 = 0.60$ ), measured over the period from 2005 to 2016. All fitted variables were highly significant ( $p < 0.001$ )

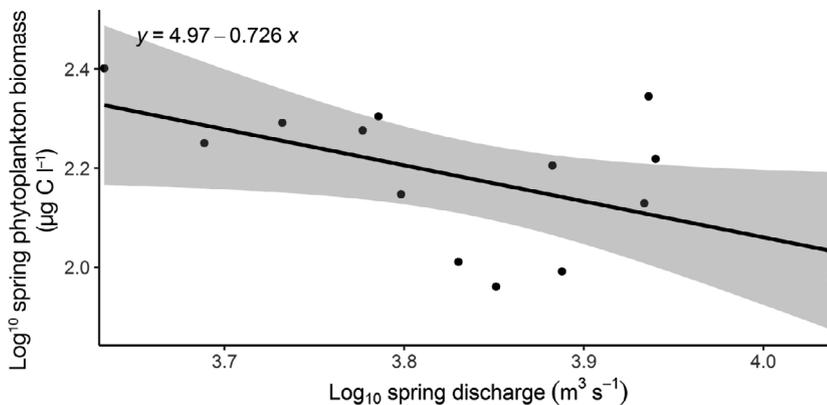


Fig. 7. Relationship between springtime (March–May) mean phytoplankton biomass and discharge in the Columbia River measured over the period from 2005 to 2018 ( $p = 0.04$ , adjusted  $r^2 = 0.24$ , shown with 95% CI in gray)

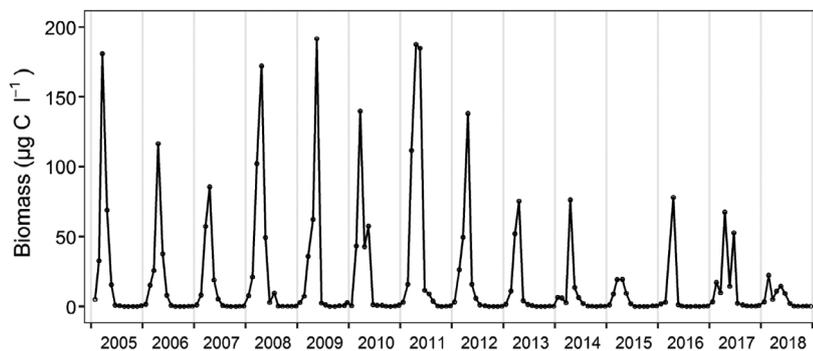


Fig. 8. Biomass of *Asterionella formosa* collected near Vancouver, WA (USA), from 2005 to 2018

by a decrease from March/April to June of each year (Fig. 8). However, the magnitude of the springtime peak of *A. formosa* declined in 2013 and remained at reduced levels through 2018. A Mann-Whitney *U*-test revealed that mean annual abundance of *A. formosa* was significantly lower in the years 2013–2018 compared to 2005–2012 ( $w = 0$ ,  $p < 0.001$ ). *Stephanodiscus* spp., *Cyclotella* spp., and *Aulacoseira* spp. exhibited the most seasonal variability, and frequently had multiple peaks throughout the summer and early fall (Fig. S5). Mean cyanobacteria abundance was greatest in 2017, followed by 2010 and 2018, and abundance significantly differed between years ( $\chi^2 = 41.58$ ,  $df = 13$ ,  $p < 0.001$ ). Although cyanobacteria abundance was noticeably elevated in recent years (2017 and 2018), and each of these years had greater mean cyanobacteria abundance than the previous 6 yr, these differences were not significantly different from other peak years in the study period (Table S4).

#### 4. DISCUSSION

We found that 3 major seasonal phytoplankton assemblages occurred in the lower CR from 2005 to 2018: (1) a spring/early summer diatom/flagellate assemblage associated with chl *a*, elevated discharge, ciliates, and Sarcodina; (2) a late summer/fall cyanobacteria/chlorophyte assemblage associated with greater water temperatures, increased water clarity, the invasive copepod *Pseudodiaptomus forbesi*, and veligers of the invasive Asian clam *Corbicula fluminea*; and (3) a mixed winter assemblage of low annual abundance and biomass. Our results also revealed a decrease in the abundance of *Asterionella formosa* in recent years, resulting in a transition from an early springtime diatom bloom dominated by *A. formosa* to a bloom of mixed taxa.

#### 4.1. Seasonal variation in phytoplankton composition

The phytoplankton assemblages in the CR generally exhibited a regular seasonal pattern each year. A 'diatom/flagellate' assemblage (Cluster 1) in spring/early summer comprised the typical major bloom period, which transitioned to a late summer/early fall 'cyanobacteria/chlorophyte' assemblage (Cluster 2), and finally to a 'mixed taxa' assemblage (Cluster 3) of low abundance that regularly occurred from November to January. These patterns of phytoplankton seasonality are similar to those of other large river systems, which are commonly known to be diatom-dominated, and seasonal decline of this taxon in large rivers is thought to be strongly influenced by concurrent decreases in flow and turbidity that remove competitive advantages for many diatom genera (Reynolds & Descy 1996, Wehr & Descy 1998). A summer transition to assemblages with higher proportions of chlorophytes has been noted in the Danube River (Dokulil & Donabaum 2014), and with higher proportions of cyanobacteria in the Ohio River (Wehr & Thorp 1997) and River Thames (Moorhouse et al. 2018).

Environmental conditions in the CR also varied seasonally from 2005 through 2018. During springtime, water temperature increased, while Secchi disk depth decreased, coincident with increasing phytoplankton biomass. Discharge also increased in spring months due to timing of the spring freshet and seasonal dam spill. This seasonal increase and decrease in discharge lagged just behind that of chl *a* in our 14 yr record. During late summer/early fall, water temperatures were warmest and coincided with reduced river discharge, decreased water depth, increased Secchi disk depth, and periods of high chlorophyte and cyanobacteria abundance. Such variation in environmental factors are common in freshwater systems of mid-latitude regions, where temperatures are strongly seasonal, and discharge corresponds with timing of the springtime freshet and rainy season.

#### 4.2. Interannual variation in phytoplankton assemblages

From 2005 to 2018, springtime (~March–May) diatom/flagellate blooms were common, although at times phytoplankton abundance and biomass remained elevated into late summer (2008, 2009, 2014) and even into fall (2017 and 2018). The cyanobacteria/chlorophyte cluster generally occurred for 1–3 mo

between ~July and September, but only appeared for 1 mo in fall 2010 and then did not occur again until August/September of 2014. Interestingly, while many factors likely contributed to this pattern, July water temperatures were noticeably low ( $\leq 19^{\circ}\text{C}$ ) from 2010 to 2013. Cyanobacteria growth rates are optimized at higher temperatures relative to algal species (Carey et al. 2012). Both higher water temperatures (Bussi et al. 2016, Cha et al. 2017, Wood et al. 2017) and reduced discharge and turbidity (Hoetzel & Croome 1994, Cha et al. 2017) have been shown to increase cyanobacteria abundance in rivers. Thus, reduced July water temperatures in the CR between 2010 and 2013 likely played a role in the absence of the cyanobacteria/chlorophyte cluster during that time. Although total cyanobacteria were apparently elevated in recent years (2017–2018), this was not a significant increase from all previous years.

An inverse relationship between phytoplankton biomass and discharge occurred in the spring (March–May), with greater biomass occurring during years with lower discharge. Variation in spring discharge thus likely contributed to the interannual variation in spring phytoplankton bloom timing and magnitude in the lower CR. The inverse relationship between phytoplankton and discharge has been observed in other CR studies over shorter time frames (Sullivan et al. 2001, Maier & Peterson 2017, Rose et al. 2019b), as well as in other larger rivers in Europe, including the Rhine, Elbe (Hardenbicker et al. 2014), and Danube (Schmidt 1994), and in the Neuse River estuary, North Carolina, USA (Valdes-Weaver et al. 2006). This relationship is characteristic of large rivers as distinct from smaller river systems, in which algae are commonly benthic and a positive relationship exists between chl *a* and discharge (Reynolds & Descy 1996, Wehr & Descy 1998).

Starting in 2013, the diatom/flagellate cluster began to last into late summer/fall, a period when phytoplankton abundance and biomass had previously been low. In contrast, the prominent spring-blooming diatom *A. formosa* began to decline in abundance and biomass in 2013, and remained low throughout the latter part of our study period (2013–2018). *Aulacoseira* spp., *Cyclotella* spp., *Fragilaria crotonensis*, and *Stephanodiscus* spp. exhibited interannual variability, but no taxon clearly increased coincident with the decline in *A. formosa*. These changes in phytoplankton blooms may thus have larger-scale food web implications, such as alterations in quantity and timing of available autochthonous energy to support secondary (e.g. zooplankton) or tertiary producers (e.g. planktivorous fishes), particularly if the

longer bloom period noted in recent years (2017–2018) continues.

We are unsure of the mechanisms that caused a decline in *A. formosa*, as there were no clear changes in biotic and abiotic factors that coincided with the marked decline in this diatom. The Asian clam *C. fluminea* is known to filter-feed on diatoms (Bolam et al. 2019) and may play a role in reductions in *A. formosa*. Feeding studies conducted on the Asian copepod *P. forbesi* from the lower CR showed that this species exhibited a preference for diatoms (Bowen et al. 2015), although it peaks in abundance in late summer (Dexter et al. 2015) when *A. formosa* is no longer abundant. All diatom taxa observed in our study, especially *A. formosa*, are also known to be parasitized by zoosporic chytrid fungi in the lower CR (Maier & Peterson 2014, 2017). While *A. formosa* is often considered large and inedible for many mesozooplankton grazers, chytrids may also be feeding on the diatoms, passing nutrients on to grazers that ingest the more manageable zoospores (i.e. via the 'mycoloop') (Kagami et al. 2007, 2011). Conditions for chytrid parasitism of diatoms in the CR may be most ideal during early spring, when water temperatures are cool and light levels are increasing (Reynolds 2006). Thus, it is possible that chytrid infection of *A. formosa* and grazing may have played dual roles in the recent decline of this taxon. While not quantified in our study, chytrid zoospores were regularly observed on larger diatom taxa in our samples (data not shown).

Abiotic influences may also play a role in the decline of *A. formosa*. Climate changes, such as warmer and wetter winters, may influence algal populations through altered nutrient dynamics and river discharge rates in areas of production (George et al. 2007), which may result in altered inocula for downstream populations (Descy & Gosselain 1994). Although we did not see evidence of decline in other diatom taxa, downstream silicate limitation of diatom production has been noted in other highly regulated river systems (Humborg et al. 2000, Ittekkot et al. 2000) and may play a role in the CR as well.

#### 4.3. Phytoplankton assemblage associations with biotic and abiotic factors

The diatom/flagellate cluster was strongly associated with chl *a* concentration; this is unsurprising, as this cluster aligned with the spring/summer bloom, when abundance and biomass were typically highest. Ciliates and Sarcodina were also strongly posi-

tively associated with this cluster. Notably, our analysis showed that ciliates and Sarcodina were more strongly associated with phytoplankton assemblages than were cladoceran or cyclopoid copepod grazers in the CR. One possibility is that these micrograzers increased in abundance with the diatom/flagellate cluster in response to a growing food supply. Grazing pressure by ciliates has been noted to significantly affect phytoplankton standing crop in rivers, thus influencing algal bloom timing and magnitude in these systems (Quinlan et al. 2009). Rotifers have also exhibited high grazing rates on riverine algae, even creating a shift toward larger, inedible taxa (Gosselain et al. 1998). However, many of the diatom taxa indicative of this cluster are large and less readily consumed by small grazers (Sommer et al. 1986, Kagami et al. 2007).

We did not measure zooplankton grazing rates in our study, and we recognize that increases in zooplankton abundance do not necessarily result in higher grazing impact on phytoplankton, due to both biotic (e.g. species-specific, stage-specific, and allometric feeding relationships) and abiotic (e.g. temperature, turbulence) factors. However, it is possible that grazing pressure from these smaller-bodied heterotrophs could have played a role in reinforcing the dominance of diatoms in Cluster 1 by consuming smaller non-diatom cells, thereby releasing larger diatoms from competition with other algal species, as has been observed in other freshwater systems (Lazzaro 1997, Boyer et al. 2011, Rollwagen-Bollens et al. 2013, 2018). Future studies of CR zooplankton grazing rates are recommended, in that they would allow for the exploration of possible causal relationships between zooplankton grazing and phytoplankton community structure.

Increased water clarity, as measured by Secchi disk depth, was associated with the cyanobacteria/chlorophyte cluster in summer/early fall. It is likely that water clarity increased due to multiple factors. Discharge is reduced during late summer/early fall months, as is precipitation, which likely reduces concentrations of suspended solids in the water column. Moreover, total phytoplankton abundance and biomass were also typically lower when the cyanobacteria/chlorophyte cluster was present in late summer/early fall. Reductions in both suspended sediment and phytoplankton biomass may increase light penetration in the water column and enhance growth conditions for chlorophytes and cyanobacteria, no longer favoring diatom taxa that are better adapted to low light intensities (Reynolds & Descy 1996, Reynolds 2006). A similar decrease in turbidity

and increase in riverine cyanobacteria has been noted in the Lower Darling River, Australia (Mitrovic et al. 2011).

Nutrients were not strongly associated with phytoplankton community patterns in the lower CR according to our analysis, in sharp contrast to findings in an adjacent floodplain lake that is hydrologically connected to the lower CR (Lee et al. 2015, Rose et al. 2017). However, a previous study in the CR also found that increases in phytoplankton did not correspond with decreased nutrient concentrations (Prahl et al. 1997). This finding is not uncommon among large river systems; other studies have shown that nutrients are not as likely to have as strong an influence on phytoplankton productivity and community structure in large rivers as they do in lakes, due in part to the predominant physical influences of turbulent flow, high discharge, and light limitation in rivers (Reynolds & Descy 1996, Wehr & Descy 1998, Salmaso & Zignin 2010, Hardenbicker et al. 2014). However, long-term studies in the Rhine showed that a reduction in nutrients, especially phosphorus, resulted in a reduction in phytoplankton biomass and an increase in species diversity (Friedrich & Pohlmann 2009). Although physical (i.e. temperature, clarity, discharge) and biological (i.e. zooplankton) factors measured in this study were most strongly associated with phytoplankton assemblage patterns, the seasonal signatures in nutrient concentrations, particularly apparent for  $\text{NO}_2+\text{NO}_3\text{-N}$  and  $\text{SiO}_2$ , suggest that measurable uptake by phytoplankton occurred and that there was an underlying role of nutrients in phytoplankton dynamics in the lower CR. It is also possible that by including different forms of nutrients, such as total nitrogen and phosphorus, further analyses may uncover additional relationships with phytoplankton assemblage patterns. Overall, we did not find a strong correlation between dissolved nutrient concentrations and phytoplankton assemblages in the CR, despite the typically important role of nutrients in phytoplankton (Reynolds 2006, Wehr et al. 2015) and cyanobacterial bloom dynamics (Paerl 2014, Bussi et al. 2016, Rose et al. 2019a) in other freshwater systems.

#### 4.4. Phytoplankton assemblage associations with anthropogenic stressors

The 2 invasive species, the Asian copepod *P. forbesi* and veligers of the Asian clam *C. fluminea*, were both strongly associated with the cyanobacteria/chlorophyte cluster during late summer/early fall. Previous re-

search has shown that both taxa peak in abundance during late summer in the CR, coincident with higher temperatures and reduced chl *a* (Dexter et al. 2015, Hassett et al. 2017). *P. forbesi* may increase in abundance when water temperatures are in an optimal range, co-occurring with the cyanobacteria/chlorophyte community. Also, feeding studies have demonstrated the preference of *P. forbesi* for diatoms and ciliates and avoidance of cyanobacteria in the CR (Bowen et al. 2015); thus, high densities of *P. forbesi* are likely to reinforce the dominance of cyanobacteria. Similarly, adult *C. fluminea* have been shown to avoid consuming cyanobacteria (Bolam et al. 2019), and may also play a role in reinforcing the cyanobacteria/chlorophyte cluster in late summer/fall in the CR.

Elevated water temperature was also strongly associated with the cyanobacteria/chlorophyte cluster. Warmer water temperatures may increase abundance of cyanobacterial species within phytoplankton communities because of their high thermal growth optima relative to algal cells (Reynolds 2006, Paerl 2014, Visser et al. 2016) and may also influence toxin production (Walls et al. 2018). Warmer temperatures are generally thought to cause an ecological shift toward smaller species, within both phytoplankton and bacterial assemblages (Daufresne et al. 2009), which may further favor cyanobacteria and small chlorophyte taxa. Warming of river waters associated with climate change has also been noted at broader regional scales in the US Pacific Northwest (Isaak et al. 2012). Recent studies of the CR have identified summertime warming of water temperatures of  $\sim 2^\circ\text{C}$  in the last several decades (Petersen & Kitchell 2001, Dexter et al. 2020), and that the increase in summer water temperature is negatively related to native, but not invasive, zooplankton taxa (Dexter et al. 2020). Our results show that a cyanobacteria-dominated summer/early fall phytoplankton assemblage exists in the CR and is strongly positively associated with temperature. The occurrence of late summer cyanobacteria-dominated assemblages in the CR should be monitored in the future, particularly if elevated water temperatures occur for a longer duration during late summer months, as predicted in future climate change scenarios for the Pacific Northwest. In addition, as our BIOENV models explained  $\sim 50\%$  of the variance in phytoplankton assemblage patterns, further studies may reduce unexplained variance by including measures of water column light intensity, mixing depth, turbulent flow, and a broader array of nutrient measures.

Over the past 150 yr, the CR has experienced a great deal of anthropogenic flow modification (e.g.

navigation and irrigation) which has resulted in a deepened river channel, reduced mean water level (especially during low flow periods), and a higher flow velocity (Helaire et al. 2019). Mean annual discharge has decreased, due to climatic changes and irrigation withdrawal, and as a result, peak spring discharge has both decreased in magnitude and occurs earlier in the season (Naik & Jay 2011). Many of these physical river characteristics were strongly associated with different phytoplankton assemblages in our analyses. If these trends continue in the future, altered springtime discharge is likely to further influence the timing and magnitude of the springtime phytoplankton bloom and reinforce the low flow conditions associated with warmer temperatures, cyanobacteria, and invasive zooplankton taxa in late summer in the lower CR.

## 5. CONCLUSIONS

Results of our 14 yr field study in the lower CR revealed 3 distinct phytoplankton clusters specific to spring/summer, late summer/fall, and winter months and showed that the magnitude and duration of these assemblages vary on an interannual basis. We found that the diatom/flagellate cluster of the spring/summer has sometimes expanded into late summer and even fall months in recent years. There has also been a notable decline in the diatom *Asterionella formosa* from ~2013 to 2018, which may be influenced by biotic factors (i.e. grazing and parasitism) but requires further study to clarify. If this reduction in *A. formosa* represents a persistent change, future studies should seek to establish underlying cause(s) and determine potential food web implications of this change, as this diatom has historically been a common and prominent springtime bloom-forming taxon in the CR. The higher than average abundances of cyanobacteria in 2017 and 2018, while greater than the previous 6 yr, did not result in statistically significant differences compared to previous years of our study. Nevertheless, abundances of cyanobacteria in the CR should be closely monitored in the future given the dual forces of climate change (increasing temperature) and grazing by invasive species which promote conditions that favor cyanobacteria.

Our study revealed that temperature, light regime (water clarity), and discharge were important abiotic factors associated with phytoplankton assemblages in the CR, but that nutrients were not as strongly associated with observed structural patterns. Dis-

charge, which varied inversely with springtime phytoplankton biomass, was at annually low levels with the occurrence of the cyanobacteria/chlorophyte cluster during late summer/fall, concurrent with warm water temperatures. Discharge is predicted to increase during winter, with earlier spring peak flows, and decrease throughout summer and fall under future climate scenarios for the CR Basin (Hamlet & Lettenmaier 1999), while water temperatures are predicted to continue rising in summer months (Isaak et al. 2012, Pachauri et al. 2014). Biotic factors are also important, as we found ciliates, Sarcodina, *Corbicula fluminea* veligers, and the copepod *Pseudodiaptomus forbesi* to be strongly associated with phytoplankton assemblages in the CR, lending support to an important, if also poorly understood, role of grazers in riverine phytoplankton dynamics.

Determining the biotic and abiotic drivers of phytoplankton dynamics in large river systems is critical for resource management, particularly in rivers where water is managed to meet many diverse needs. Our findings show that biotic factors (i.e. zooplankton) and physical abiotic factors (i.e. temperature, clarity, discharge) both have an important role in phytoplankton dynamics in the lower CR, but the relative importance alternates seasonally along with phytoplankton assemblage structure and total biomass. Further studies should focus on riverine communities most affected by climate change and species invasions (e.g. our late summer/early fall cyanobacteria/chlorophyte assemblage), as this could lead to loss of biodiversity and reduced ecosystem function (Dudgeon et al. 2006, Havel et al. 2015, Reid et al. 2019).

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