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The effects of run-of-river dam spill on Columbia River microplankton

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Abstract

Dams, increasingly common in riverine systems worldwide, are particularly prevalent on the Columbia River (CR) in the United States. Hydroelectric projects, including both storage and run-of-river (i.e., minimal storage) structures, on the mainstem CR highly manage water flow, often by releasing water over (rather than through) dams as "spill." To test the effects of run-of-river dam spill on microplankton abundance and composition, we sampled above and below two dams in the lower CR before and during spill conditions in spring 2016 and during and after spill conditions in late summer 2007. We tested the effects of location (i.e., above vs. below dams), spill condition (i.e., before, during, and after spill), and their interaction on microplankton abundance. Generally, diatoms were most abundant during springtime, whereas cyanobacteria were most abundant in late summer. Most taxa were not significantly different in abundance above and below dams, regardless of spill status; although cyanobacteria abundance was marginally higher below dams in summer 2007 (p = .04). Abundances of all taxa were significantly different between pre-spill and spill periods in spring 2016, whereas only diatom and flagellate abundances were significantly different between spill and post-spill periods in summer 2007. We conclude that spill conditions may influence microplankton abundance, but are not likely to affect microplankton communities on either side of run-of-river dams on the CR. This is important information for dam managers concerned about ecosystem impacts of spill.

KEYWORDS

cyanobacteria, diatoms, flagellates, phytoplankton, run-of-river reservoirs, turbulent mixing

1 | INTRODUCTION

Riverine systems have been drastically altered by humans on a global scale. Freshwater resources, aquatic habitats, and biodiversity are threatened as a result of watershed development, industrialization, and impoundments (Nilsson, Reidy, Dynesius, & Revenga, 2005; Vörösmarty et al., 2010). Dams are well known among such stressors for altering river hydrology, sediment transport, and nutrient dynamics (Graf, 1999; von Schiller et al., 2016). Deleterious effects of dams on anadromous fish populations are also well studied (Cooper et al., 2017; Harnish, Sharma, McMichael, Langshaw, & Pearsons, 2014; Lawrence, Kuparinen, & Hutchings, 2016). However, much less is known about the potential effects of dams on microplankton—a group that includes autotrophic and heterotrophic/mixotrophic protists, as well as photoautotrophic cyanobacteria. Alterations to microplankton communities, which form the base of pelagic food webs that support invertebrates and fishes, may also have consequences for aquatic ecosystem dynamics.

Dams alter physical and chemical processes in riverine ecosystems and may, therefore, influence microplankton abundance and community composition through multiple mechanisms. Dams influence thermal regimes by altering water volume and discharge and via height-selective release of water from thermally stratified reservoirs (Olden & Naiman, 2010), which may affect microplankton community structure due to species-specific thermal growth optima (Reynolds, 2006). Dam operations allow careful management of river flow to address the various needs of diverse stakeholders (e.g., irrigation, fish passage, flood control, hydroelectric production, recreation, and navigation). Some hydroelectric dams further alter river flow by periodically releasing water over the spillway and by-passing turbines—conditions referred to as "spill." Spill may be used to facilitate fish passage or to lower reservoir levels prior to seasonal water inflows (e.g., from rain or snowmelt).

Spill has long been known to cause gas supersaturation hazardous to fish (Ebel & Raymond, 1976); however, relatively little is known about potential effects of spill on other aquatic species (Williams, 2008). Changes in water flow, including spill, may alter suspended sediment load and water column turbidity (Kondolf, 1997; Ligon, Dietrich, & Trush, 1995). Increased sediment load may in turn influence microplankton community structure, as turbidity is inversely related to light penetration and thus may affect competition for light among phytoplankton taxa (Holz, Hoagland, Spawn, Popp, & Andersen, 1997; Huisman et al., 2004). Thus, dams have the potential to influence microplankton dynamics through several mechanisms caused by impoundment and spill.

Of particular concern is the potential for flow impoundment imposed by dams to enhance cyanobacteria abundance (Paerl & Paul, 2012). Cyanobacterial blooms are a current problem for freshwater systems globally and have been noted in many impounded riverine (Guo et al., 2018; Oliver, Dahlgren, & Deas, 2014; Remmal, Hudon, Hamilton, Rondeau, & Gagnon, 2017) and adjacent floodplain lake ecosystems (Rollwagen-Bollens, Lee, Rose, & Bollens, 2018; Rose, Rollwagen-Bollens, & Bollens, 2017). Altered thermal regimes in reservoirs that result in warmer waters and stratification may increase the likelihood of cyanobacterial dominance (Cha, Cho, Lee, Kang, & Kim, 2017; Paerl & Paul, 2012). Dams may also modify the river environment by increasing river residence time, thus reducing turbulent flow and mixing (Graf, 1999; Ligon et al., 1995). Some species of cyanobacteria gain motility through regulation of buoyant gas vesicles (Reynolds, Oliver, & Walsby, 1987) and therefore have a considerable competitive advantage in areas of reduced flow, such as reservoirs (Huisman, Matthijs, & Visser, 2005; Paerl et al., 2016). Artificially increasing mixing is a management strategy sometimes used to limit cyanobacteria growth (Visser, Ibelings, Bormans, & Huisman, 2016); therefore, increased flow due to spill has the potential to reduce riverine cyanobacteria populations (Mitrovic, Hardwick, & Dorani, 2011).

The Columbia River (CR) has experienced significant flow modification since the 19th century and is an important generator of hydroelectric power in the U.S. Pacific Northwest. Within the Federal Columbia River Power System, 14 large-scale hydroelectric dams on the mainstem CR, including five storage and nine run-of-river multi-purpose dams, are managed in close coordination by the U.S. Army Corps of Engineers (Bonneville Power Administration, 2004). Unlike storage dams, run-of-river dams have limited water storage and are more reliant upon river flow rate for power generation. The regulation of water flow through, and over, CR run-of-river dams changes the residence times of river water above these dams, often creating conditions in which flow rates are substantially lower and residence times are substantially longer than would occur without impoundment. Therefore, water behind run-of-river dams is variously referred to as pondage, a headpond, or a reservoir. In the Federal Columbia River Power System, the river just upstream of a run-of-river dam is referred to as a reservoir, and we use this term throughout this article.

Annual spill periods on CR dams are coordinated to support anadromous fish passage, and typically are initiated in early April, with spill occurring continuously through August. This results in distinct flow conditions between spill and non-spill periods. Despite the regularity of spill in the CR, studies examining ecosystem effects caused by the transition to and from spill conditions are lacking and typify the overall lack of studies specifically examining ecosystem effects of run-of-river systems compared with larger, storage dams.

Recent research has described CR zooplankton community structure and phenology (Bollens, Breckenridge, Cordell, Rollwagen-Bollens, & Kalata, 2012; Breckenridge, Bollens, Rollwagen-Bollens, & Roegner, 2015), including the abundance and impact of aquatic invasive species such as zooplankton (Dexter, Bollens, Rollwagen-Bollens, Emerson, & Zimmerman, 2015; Emerson, Bollens, & Counihan, 2015) and bivalves (Bolam, Rollwagen-Bollens, & Bollens, 2019; Hassett et al., 2017). Although much is known about plankton communities in the CR, the potential effects of run-of-river dam spill on microplankton have not been examined. We therefore carried out a field study comparing community composition and abundances of six microplankton taxonomic groups (i.e., diatoms, chlorophytes, dinoflagellates, ciliates, flagellates, and cyanobacteria) above and below two run-of-river dams during conditions of spill and non-spill. We hypothesized that conditions of water flowing over, rather than through, dam structures during spill would result in reduced abundance and altered community composition of the microplankton immediately below the dams versus within reservoirs just above the dams. Moreover, we hypothesized that no such differences would occur during non-spill conditions (i.e., when water passes through, but not over, the dams). This is the first study to examine the effects of spill versus non-spill conditions from run-of-river dams on microplankton in the CR and, to our knowledge, in riverine systems generally.

2 | MATERIALS AND METHODS

2.1 | Study sites

The CR has a catchment area of 660,480 km^2 spanning two Canadian provinces and seven U.S. states (Simenstad, Small, David McIntire, Jay, & Sherwood, 1990). We sampled at Bonneville (45°38′39″N, 121°56′

26″W) and The Dalles (45°36′44″N, 121°08′04″W) Dams—the two most downstream run-of-river hydropower dams in the mainstem CR (Figure 1). We collected samples at a total of 12 sites—six at each dam (Figure 2). At each dam, two sites were located downstream, and four were located upstream of the structure within the reservoir (henceforth referred to as “below dam” and “above dam,” respectively). Below dam sites were both located mid-channel. Above the dams, two sites were located mid-channel, and two sites were located in near-shore waters on either side of the reservoir to form a cross-channel transect that passed through the farthest upstream mid-channel site. Sample sites were located approximately 0.5 and 3 km below dams and 1 and 8 km above dams (Table 1).

Ideally, all sampling (i.e. before, during, and after spill conditions) would have been conducted within the same year; however, due to constraints of resource availability, sampling had to be carried out partially in 2007 and again in 2016. Environmental conditions were similar in both years; average monthly discharge ranged from 2,569–7,634 m^3/s in 2007 and 2,661–8,002 m^3/s in 2016 (data accessed from http://www.cbr.washington.edu/dart), and water temperature ranged from 3.9–21.5°C in 2007 and 5.8–22.2°C in 2016 (Rose et al., in prep.). Although both years experienced similar overall conditions of temperature and discharge, river temperatures are generally lower in spring and higher in late summer, whereas discharges are generally higher in spring and lower in late summer.

2.2 | Field collections

Field sampling was conducted before and after the onset of spill conditions in spring 2016 and during and after the end of the spill period in late summer 2007. We describe and discuss these two sampling efforts in a temporal sequence based on season, rather than sampling year, in order to consider conditions when spill begins before considering the conditions when spill ends. There were four sample collections in spring 2016—two before and two during spill conditions. Specifically, sampling was conducted within 3 weeks and 1 week before the onset of spill (March 15–16 and April 6–7, respectively) and within 1 week and 3 weeks after spill began (April 11–12 and May 3–4, respectively). We also sampled near the end of spill conditions (August 28–29) and again 1 week after spill had ended (September 10–11) in 2007. Each set of sample collections occurred over 2 days in order to obtain samples from all 12 sites.

2.3 | Laboratory methods

Samples of river water for microplankton identification and analysis of chlorophyll *a* (chl *a*) concentration in spring 2016 were collected from the surface at all sites, using a clean bucket, whereas additional near-bottom (~0.5 m above river bed) samples were collected using a Van Dorn water sampler at one site below and two mid-channel sites above both dams on all occasions. During the August and September 2007 sample periods, water was collected at the surface and near-bottom at every sampling location, except in September when inclement weather restricted sampling to only one site above Bonneville Dam (Figure 2).

Subsamples (70–100 ml) of water for chl *a* analysis were stored in amber bottles and kept on ice for transportation back to the lab, whereupon an aliquot of 70–140 ml was filtered through a Whatman GF/F filter. Filters were then stored in the freezer for at least 24 hr,

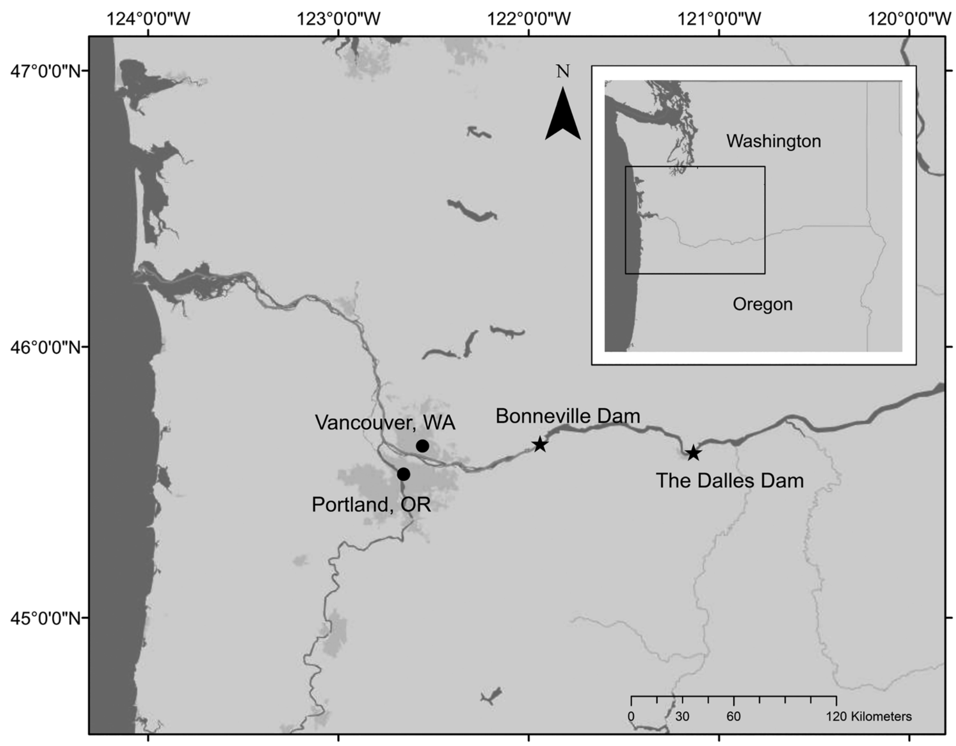

FIGURE 1 Location of Bonneville and The Dalles Dams in the lower Columbia River in the Pacific Northwest, United States

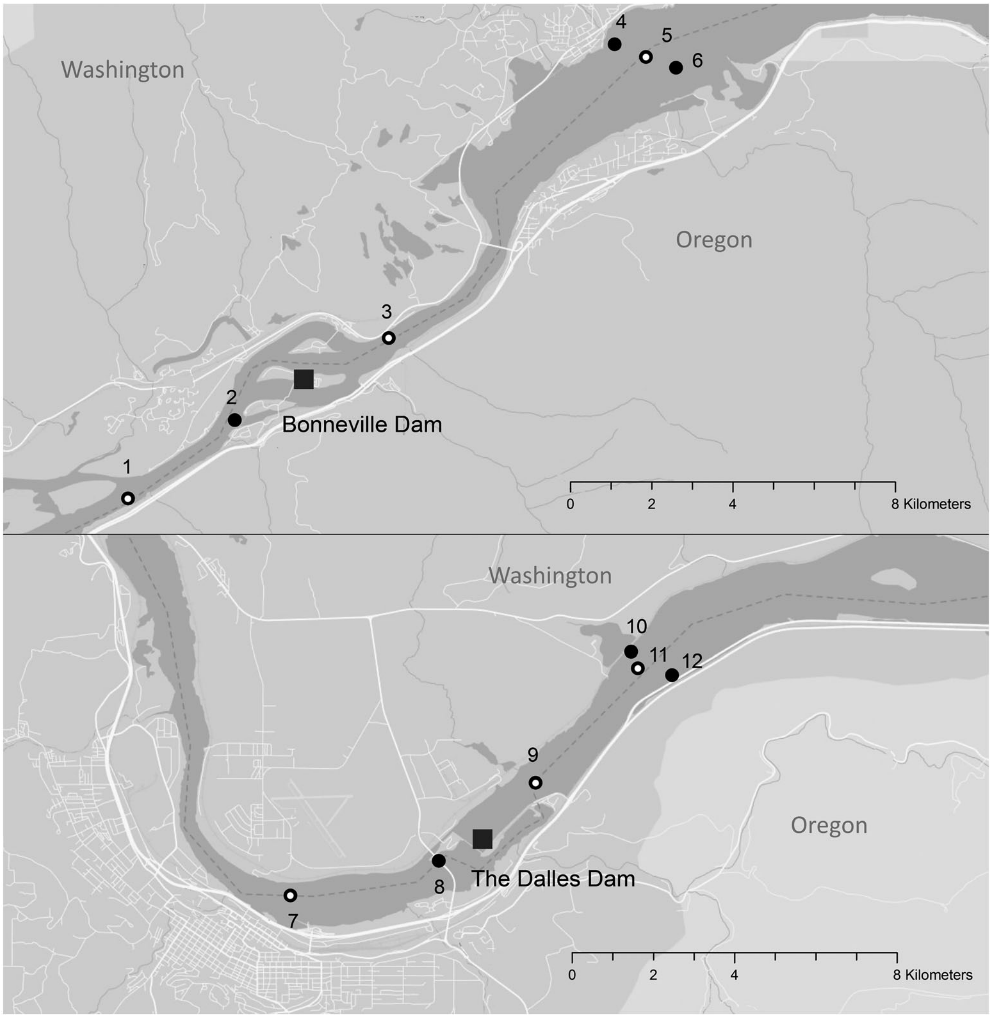

FIGURE 2 Sample site locations above and below Bonneville and The Dalles Dams in the lower Columbia River. Open circles represent sites where both surface and deep-water samples were collected in 2016

TABLE 1 Average river channel depth and distance from dam for each sampling site

Site	Dam	Distance from dam (km)	Average river depth (m)
1	Bonneville	−2.28	12.7
2	Bonneville	−2.14	13.2
3	Bonneville	1.27	24.9
4	Bonneville	7.95	10.5
5	Bonneville	8.13	12.4
6	Bonneville	8.38	6.5
7	The Dalles	−3.28	15.0
8	The Dalles	−0.57	15.2
9	The Dalles	1.53	76.3
10	The Dalles	2.84	8.2
11	The Dalles	4.18	31.8
12	The Dalles	3.04	6.8

Note. Negative values indicate distances below dams.

but no more than 7 days. Chl *a* was extracted from the filters in 20 ml of 90% acetone while in the freezer for 24 hr. Chl *a* concentration was determined using a Turner Model 10 AU fluorometer according to the acidification method (Strickland & Parsons, 1972).

Subsamples (200 ml) of river water collected to assess microplankton abundance and taxonomic composition were immediately preserved in the field in 5% Lugol's iodine solution. In the laboratory, aliquots of 20–40 ml were settled via the Utermöhl (1958) method for 24 hr before identification with a Leica DMI 4000B inverted microscope at 400× magnification (630× where necessary). We counted at least 300 organisms from fields along slide transects (Kirchman, 1993) from each sample. Although the term microplankton commonly refers to organisms between 20 and 200 μm, we also counted phytoplankton and protists as small as 5 μm in order to include all identifiable members of each taxonomic group. Cyanobacteria cells are commonly smaller than 5 μm, but colonies are typically within the microplankton size range; therefore, we enumerated all cells within colonies to maintain consistent units for comparison of abundance among all taxa. Individual cells were identified to genus and species, where possible, using Wehr, Sheath, and Kociolek (2015) and Patterson and Hedley (1992). Biomass estimates were calculated according to Hillebrand, Dürselen, Kirschtel, Pollingher, and Zohary (1999) and Menden-Deuer and Lessard (2000). Organisms were binned into the following six taxonomic categories for statistical analyses: diatoms, dinoflagellates, flagellates, ciliates, chlorophytes, and cyanobacteria.

2.4 | Statistical analyses

Abundance data from both dams were pooled (i.e. considered as replicates) into "above" and "below" categories for each taxonomic group to allow for statistical comparisons. To justify data pooling, preliminary comparisons were made between abundances measured at each sample site and depth (i.e., mid-channel surface, mid-channel deep, near-shore surface, and near-shore deep) in the above dam category and again for the sites and depths in the below dam category, for both dams on each sample date. Kruskal–Wallis tests were used for these preliminary comparisons because of non-normal data distributions and showed no significant differences between microplankton abundances collected from sites within the above dam category, or within the below dam category, for any taxonomic group within any sample period in 2007 or 2016 (years considered separately).

We used two-way analysis of variance (ANOVA) to test the effects of (a) location relative to dam (above vs. below), (b) spill condition (e.g., before, during, or after spill), and (c) possible interaction of location and spill condition, on the abundance of each microplankton group. Tests were conducted separately for 2007 and 2016 data; in 2016, comparisons of microplankton abundance were made between samples collected before and after spill (3 weeks and 1 week pre-spill onset in spring, 1 week and 3 weeks after spring onset of spill) and in 2007 between samples collected during and after spill (1 week before the end of spill conditions and 1 week after spill had ended). Abundance was never zero for a given location or sample date for any two-way ANOVA; tests were calculated using type III sums of squares due to unequal sample sizes above versus below the dams. Within any given test, all data contributing to the test were either transformed (using log, square, or cube root) or untransformed in order to meet test assumptions of normality and/or homoscedasticity. Data were verified as meeting test assumptions using Levene's and Shapiro–Wilk tests. Where relevant, post hoc tests to determine significance of between-group differences were conducted using Tukey's honest significant difference tests.

Where data did not meet assumptions of parametric tests (i.e., ciliate and dinoflagellate abundances in 2007), Kruskal–Wallis tests were applied to compare abundances above and below dams across sample periods. In total, 10 two-way ANOVA (six tests with 2016 data and four tests with 2007 data) and two Kruskal–Wallis tests (with 2007 data) were undertaken to test for differences in abundance of each microplankton group above and below dams during conditions of spill and non-spill. Anticipating that differences between groups would be small and detecting a false positive (Type I error) would be unlikely, we did not adjust experiment-wise error rates in response to multiple tests to maintain a lower Type II error rate. All statistics were conducted using R software (Core Team, 2018).

We recognize that low statistical power due to small sample size (n = 6 below dams and n = 12 above dams) is a limitation of our study. To explore this, a t test and power analysis was performed on diatom abundance above and below dams in March 2016 ($t = -0.50$, $df = 16$, $p = .63$, $\alpha = .05$, $1 - \beta = .076$). No significant difference in abundance was found, and such a small effect size (5.7% difference in abundance) would require much larger power to detect. However, our sample size would allow us to detect a change in abundance of ~25%, an effect size that, although not small, would likely be of ecological importance.

3 | RESULTS

3.1 | Effects of springtime transition from non-spill to spill conditions (2016)

Chl a concentration, a proxy for phytoplankton carbon biomass, ranged from 3.6 to 5.6 μg/L 3 weeks before the onset of spill in mid-March, 5.2 to 7.2 μg/L 1 week before spill in early April, 3.9 to 5.9 μg/L 1 week after the onset of spill in mid-April, and 1.0 to 2.3 μg/L 3 weeks into the spill period in early May (Figure 3). Microplankton abundance was dominated by diatoms, followed by cyanobacteria and flagellates, during each sample period (Figure 4). Regarding biomass, microplankton was dominated by diatoms on all

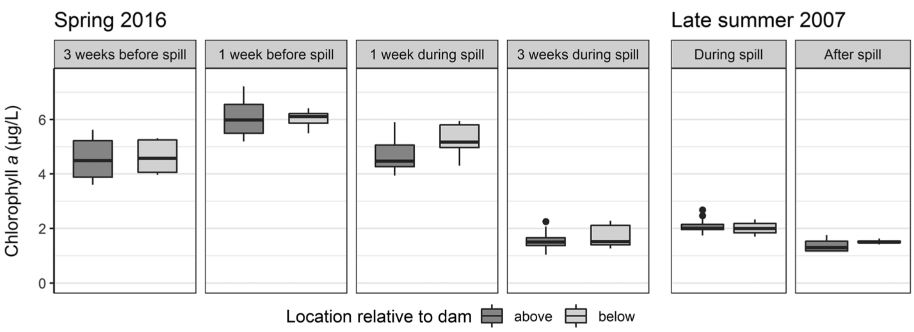

FIGURE 3 Chlorophyll a concentration above and below dams (Bonneville and The Dalles combined) before and during spill conditions in spring 2016 (four sampling periods) and during and after spill conditions in late summer 2007 (two sampling periods)

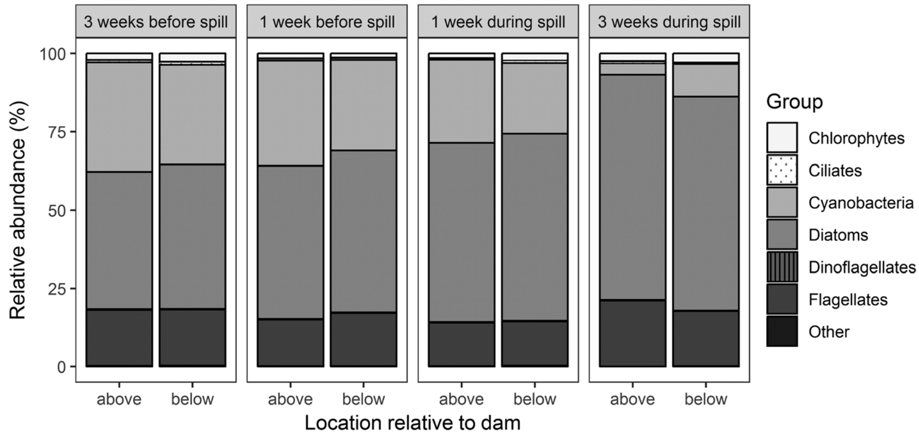

FIGURE 4 Relative abundance of microplankton groups above and below dams (Bonneville and The Dalles combined) before (two dates) and during (two dates) spill conditions in spring 2016

spring sample dates, whereas ciliate and flagellate biomass were subdominant (Figure S1).

There was no significant interaction effect in any two-way ANOVA conducted using spring 2016 data (non-spill to spill conditions). Two-way ANOVA results from spring 2016 further showed no significant effect of sample location relative to dam (i.e., above or below) on abundance of any microplankton taxon (Table 2; Figure 5). However, abundances were significantly different between spill and non-spill conditions for all microplankton groups (Table 2). Post hoc analyses showed that diatom abundance differed between all four sample dates, gradually increasing in abundance from 3 weeks before the onset of spill to 1 week after spill began and then decreasing to their lowest abundance 3 weeks after the onset of spill in May (Figure 5). Cyanobacteria, dinoflagellate, and ciliate abundances were significantly lower 3 weeks after spill initiation in May compared with all other sample periods. Flagellate abundance increased in the first week after spill onset compared to pre-spill, and decreased again after 3 weeks of spill conditions.

TABLE 2 Results of two-way ANOVA testing the effects of location (above vs. below) and spill condition (before vs. during spill) on abundance of microplankton groups in spring 2016

Group	Location	Spill condition	Interaction
Two-way ANOVA			
Diatoms	$F = 0.285$ $p = .60$	$F = 53.7$ $p < 2e{-}16$***	$F = 0.515$ $p = .67$
Cyanobacteria	$F = 0.087$ $p = .77$	$F = 33.7$ $p = 3.4e{-}13$***	$F = 1.72$ $p = .17$
Flagellates	$F = 0.0078$ $p = .93$	$F = 40.03$ $p = 1.1\ e{-}14$***	$F = 1.44$ $p = .24$
Chlorophytes	$F = 0.291$ $p = .59$	$F = 3.73$ $p = .016$*	$F = 0.180$ $p = .91$
Ciliates	$F = 1.38$ $p = .24$	$F = 9.27$ $p = 2.2e{-}05$***	$F = 2.29$ $p = .087$
Dinoflagellates	$F = 1.34$ $p = .25$	$F = 18.7$ $p = 8.2e{-}09$***	$F = 0.422$ $p = .74$

Abbreviation: ANOVA, analysis of variance.

*$p < .05$. **$p < .01$. ***$p < .001$.

3.2 | Effects of late summer transition from spill to non-spill conditions (2007)

Chl *a* concentrations ranged from 1.7 to 2.7 μg/L during spill conditions in late August 2007 and 1.2 to 1.7 μg/L just after spill cessation in early September (Figure 3). In August, during spill, cyanobacteria were dominant in abundance, followed by diatoms and chlorophytes (Figure 6). In September, after spill ended, cyanobacteria remained dominant, but chlorophytes had higher relative abundance than diatoms. Diatoms were dominant with respect to biomass throughout August to September 2007, followed closely by chlorophytes (Figure S2).

There was no significant interaction effect in any two-way ANOVA conducted with the data collected during the late summer spill to non-spill transition in 2007. Two-way ANOVA results revealed a marginally significant effect of location (i.e., above or below dam) on cyanobacteria abundance in 2007, with higher abundance below dams ($F = 4.4$, $p = .04$; Figure 7; Table 3). None of the other microplankton groups differed in abundance by sample location (Table 3). Diatoms ($F = 5.7$, $p = .02$) and flagellates ($F = 7.0$, $p = .01$) showed significant variation in abundance between sampling periods (i.e., during vs. after spill), with both groups more abundant in August, during spill conditions, compared with September, after spill had ended (Figure 7).

4 | DISCUSSION

Our overarching objective for this study was to determine how run-of-river dam spill conditions affect microplankton abundance and composition in the CR. Overall, our results reveal that there is little to no short-term (days) effect on microplankton abundance of passing over or through run-of-river dams under the operational practices at the time of our sampling. It is possible that we were unable to detect subtle changes in abundance or to measure signs of cell stress or damage

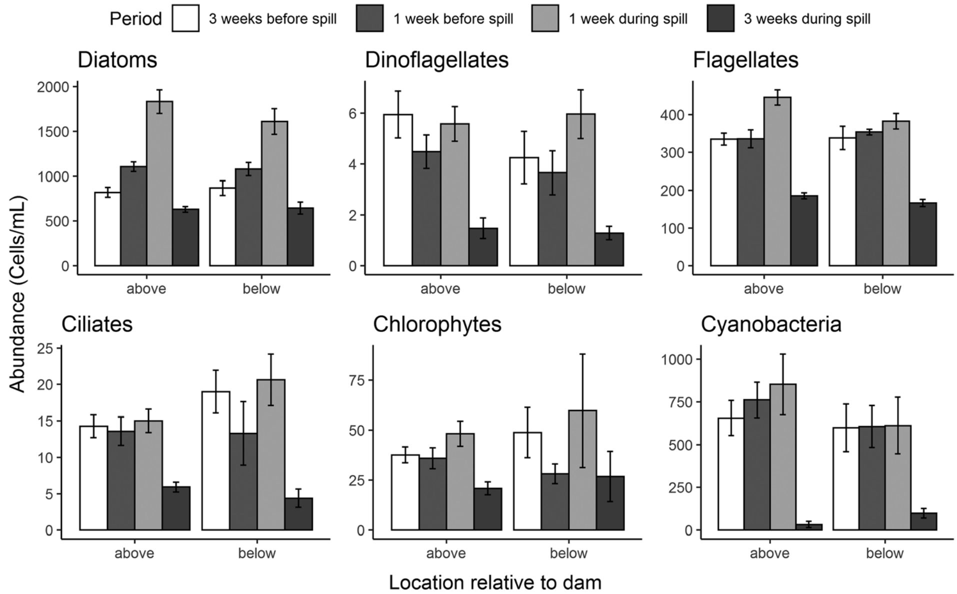

FIGURE 5 Mean (±*SE*) abundance of each microplankton taxon above and below dams (Bonneville and The Dalles combined) during all sample periods (twice before and twice during spill) in spring 2016

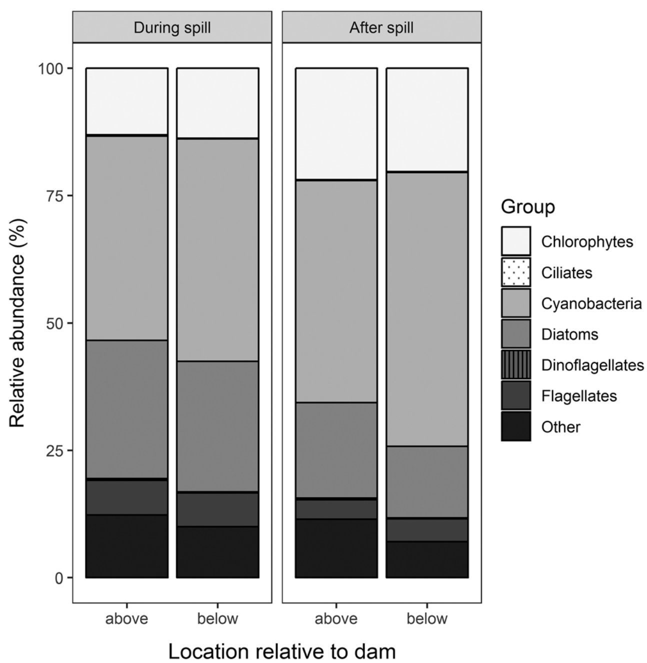

FIGURE 6 Relative abundance of all microplankton groups above and below dams (Bonneville and The Dalles combined) during and after spill conditions in late summer 2007

detectable by other methods, such as evaluation of photosynthetic efficiency and release of dissolved organic material (Garrison & Tang, 2014). However, the lack of statistically significant different abundances above versus below the Bonneville and Dalles dams may be considered encouraging news for dam managers who are concerned about the effects of run-of-river dam operations on microplankton communities.

On the other hand, abundances of all microplankton groups, except chlorophytes, were significantly different between pre-spill and spill conditions in spring 2016, with these taxa being substantially higher in overall abundance 1 week after the onset of spill compared with pre-spill and then much lower in abundance than pre-spill after 3 weeks of spill conditions. Variation in abundance over the course of 6 weeks is not surprising for microorganisms whose populations respond rapidly to environmental changes. However, because of the relatively short time between the pre-spill sampling (April 6–7) and sampling after spill onset (April 11–12), it is possible that the increase in diatom and flagellate populations over this time is at least partly attributable to the onset of spill conditions themselves. Interestingly, during the transition from spill to non-spill conditions in late summer 2007, diatoms and flagellates were also significantly more abundant during spill conditions than after spill, providing further support for the possible beneficial influence of spill on these taxonomic groups.

Turbulent mixing, which may be caused by natural river flows and increased by passage through or over dams, may increase diatom abundance through resuspension of cells and by increasing nutrient fluxes into boundary layers surrounding cells. Diatoms are large, heavy, non-motile cells with high sinking velocities in quiescent waters (Reynolds, 2006) and thus may benefit from turbulence through resuspension into light-rich surface waters (Fraisse, Bormans, & Lagadeuc, 2015; Huisman et al., 2004), particularly where nutrients are not limiting (Arin et al., 2002; Margalef, 1978). Diatoms are well adapted to limited light levels (Litchman & Klausmeier, 2008), making them strong competitors for light in turbulent waters where vertical position in the water column (and thus access to light) frequently varies. Enhanced growth rates resulting from increased nutrient fluxes to cells in well-mixed waters is also likely to benefit diatoms, particularly larger cells (Karp-Boss, Boss, & Jumars, 1996). Large diatom cells, which have low surface area to volume ratios, have exhibited higher growth rates under turbulent conditions due to increased nutrient transport into their potentially nutrient-depleted boundary layers, whereas smaller

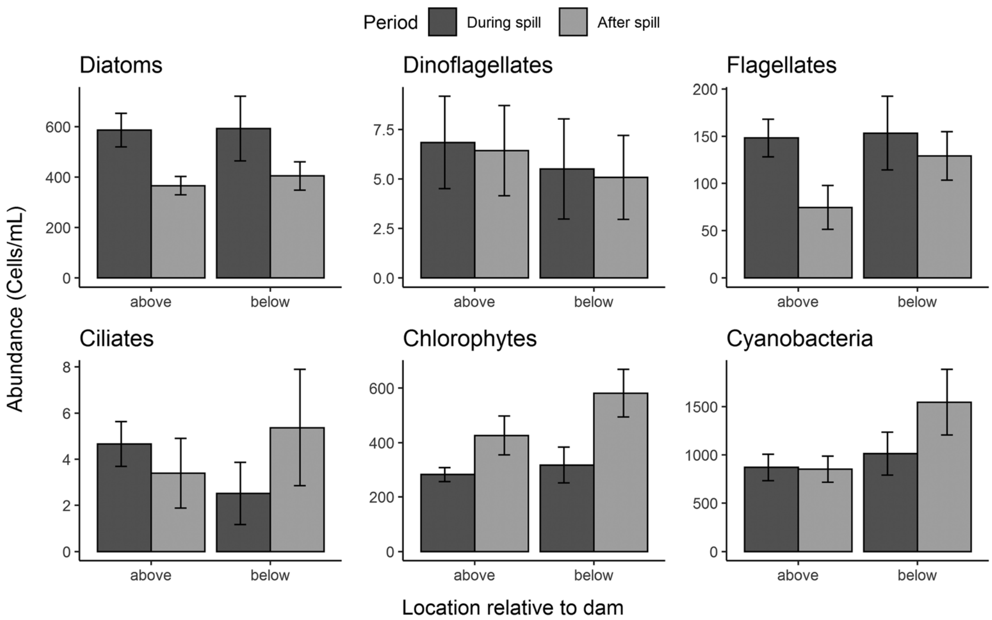

FIGURE 7 Mean (±*SE*) abundance of each microplankton taxon above and below dams (Bonneville and The Dalles combined) during and after spill conditions in late summer 2007

TABLE 3 Results of (a) two-way ANOVA testing the effects of location (above vs. below) and spill condition (during vs. after spill) on microplankton abundance and (b) Kruskal–Wallis analysis of abundance across location and sample periods in late summer 2007

Group	Location	Spill condition	Interaction
Two-way ANOVA			
Diatoms	F = 0.10 p = .75	F = 5.7 p = .02*	F = 0.06 p = .81
Cyanobacteria	F = 4.4 p = .04*	F = 0.0058 p = .94	F = 1.2 p = .27
Flagellates	F = 3.40 p = .07	F = 7.0 p = .01*	F = 1.7 p = .20
Chlorophytes	F = 3.3 p = .08	F = 3.7 p = .06	F = 1.2 p = .28
Kruskal–Wallis			
Ciliates	χ^2 = 1.9; p = .60		
Dinoflagellates	χ^2 = 0.21; p = .97		

Abbreviation: ANOVA, analysis of variance.

*p < .05. **p < .01. ***p < .001.

cells did not show a similar response (Arin et al., 2002; Peters, Arin, Marrasé, Berdalet, & Sala, 2006). Thus, increased turbulence during spill in the CR may create conditions that are sufficiently different from non-spill conditions to enhance diatom abundance.

Growth benefits from increased nutrient uptake facilitated by motion are likely similar for phytoflagellates (e.g., *Cryptomonas*; Sommer, 1988). Turbulent mixing can also increase predator–prey encounter rates (Dolan, Sall, Metcalfe, & Gasser, 2003; Prairie, Sutherland, Nickols, & Kaltenberg, 2012), which may be beneficial for heterotrophic flagellates. Turbulent conditions caused increased growth and grazing on bacteria by the nanoflagellate *Paraphysomonas* sp. (Delaney, 2003) and increased clearance rates for weak swimming or non-motile flagellate species (i.e., choanoflagellates and helioflagellates), but not for more motile flagellate and ciliate species (Shimeta, Jumars, & Lessard, 1995). Therefore, increased exposure to nutrients and improved grazing rates for species with low motility may help to explain why flagellate abundance increased with spill conditions in our study, even though similar increases were not seen in more highly motile groups, such as dinoflagellates and ciliates.

Unlike modest levels of small-scale turbulence, intense turbulence (i.e., potentially caused by spill) may be detrimental to some microorganisms. Short bursts of high-intensity turbulence were noted to cause stress, measured as release of nutrients and dissolved organic material, and cell death in two diatoms (Garrison & Tang, 2014). Breakage of diatom chains may also occur as a result of strong hydrodynamic forces (Young, Karp-Boss, Jumars, & Landis, 2012). However, although the long-chain forming diatom *Fragilaria crotonensis* was common in samples we collected from the CR before and during spill conditions in 2016, no consistent trend in chain length was noted above and below dams (data not shown). Although we did not measure hydrodynamic forces directly, our findings suggest that levels of turbulence caused by run-of-river dams in the CR are likely below that which causes reduced growth and mortality to diatoms.

Studies examining the effects of run-of-river dams generally focus on migrating fish populations (Gibeau, Connors, & Palen, 2016), whereas studies on plankton communities are limited (Zhou et al., 2009; Zhou, Tang, Wu, Fu, & Cai, 2008) and have not considered effects of spill versus non-spill conditions. In contrast to our findings, one study that included sample sites surrounding a storage and run-of-river dam found that phytoplankton abundance was greater in reservoir sites above dams, and the community composition had increased proportions of chlorophytes, chrysophytes, and cyanobacteria when compared with the diatom-dominated mainstem and the same river reaches prior to dam construction (Li et al., 2013). However, a study examining effects of multiple hydropower dams found that although phytoplankton richness was greater in unregulated compared with regulated river reaches, there was no difference in phytoplankton abundance between reservoir and non-reservoir sites (Nogueira, Ferrareze, Moreira, & Gouvêa, 2010). Also similar to our results, a study conducted in the Ohio River found that the effect of low-head dams on phytoplankton was generally subtle, with no consistent pattern above and below dams across taxonomic groups and time periods (Wehr & Thorp, 1997).

We had also hypothesized that the relatively reduced flow in reservoirs above run-of-river dams would lead to higher abundances of cyanobacteria compared with reaches just below the dams; however, this was not supported by our results. It seems likely that, under the current conditions in the CR, constant flow and short residence time (~1–2 days) in these run-of-river reservoirs (and typical of such systems) may be sufficient to prevent cyanobacterial bloom formation. Our results are supported by other studies describing the influence of flow on cyanobacteria abundance, in which deliberate pulses of higher flow (Mitrovic et al., 2011) and artificial mixing or flushing (Paerl et al., 2016; Visser et al., 2016) have been used successfully to mitigate cyanobacterial blooms associated with lakes and reservoirs.

Diatoms are the major phytoplankton taxon in the CR. Diatoms generally dominated the CR phytoplankton community throughout most sampling periods (i.e., late summer 2007 and spring 2016), similar to results presented in previous research conducted in the lower CR (e.g., Bolam et al., 2019; Bowen, Rollwagen-Bollens, Bollens, & Zimmerman, 2015). However, although diatoms dominated the community throughout spring (March to May 2016), cyanobacteria were the most abundant taxon in the late summer (August to September 2007). These results are not surprising; cyanobacteria abundance commonly reaches its peak in late summer, when water temperatures are at an annual high and discharge low, as is the case in the CR. Such a transition from numerical dominance by diatoms in the spring to cyanobacteria in the summer has been noted in other large river systems (Baker & Baker, 1981; Wehr & Thorp, 1997).

Similarly, total microplankton abundance in our samples was much higher in spring than late summer, which corresponds with annual peaks in chl *a* concentration in the CR (Dexter et al., 2015). Sullivan, Prahl, Small, and Covert (2001) also found diatoms to be the major phytoplankton taxon in the CR, noting an annual springtime bloom, and described an inverse relationship between diatom production and river flow. This supports our interpretation that the lower abundances of nearly all microplankton taxa we observed during May 2016 (3 weeks into the spill period) was influenced by several weeks of persistent, increased flow resulting from spill.

5 | CONCLUSION

Our study showed that spilling water through or over run-of-river dams causes minimal to no effect on the abundance of microplankton taxa above versus below dams in the lower CR. These results may be encouraging for hydroelectric system managers concerned with the potential ecosystem impacts of dam operations. On the other hand, our results also suggest that spill conditions influence overall microplankton abundance compared with non-spill conditions, with diatoms and flagellates possibly benefitting from spill conditions. Thus, we recommend that future research be conducted with higher frequency sampling of microplankton before, during, and after periodic spill events in impounded and unimpounded river reaches to disentangle the effects of dam spill from that of seasonal and interannual variation in other environmental (biotic and abiotic) factors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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