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Spatial variation in dinoflagellate recruitment along a reservoir ecosystem continuum

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Physical and chemical gradients across ecosystems, such as stream-to-lake continua within human-made reservoirs, provide valuable opportunities to examine how organisms respond to changing environments. We quantified the rate of dinoflagellate recruitment across a small reservoir to test the hypothesis that organisms are controlled by different factors along a reservoir continuum. We predicted that recruitment would be tightly coupled with reservoir physics in the riverine zone and closely related to water chemistry in the lacustrine zone. For the dominant dinoflagellate genus in the reservoir, *Peridinium*, recruitment from the sediments accounted for a median of 16% of increases in pelagic cell abundance throughout the summer. As predicted, *Peridinium* recruitment rates at the riverine site were correlated with physical variables, while at the lacustrine site, recruitment rates were highly correlated with water chemistry (e.g. nutrient ratios and dissolved oxygen). Recruitment patterns of the second most common genus, *Gymnodinium*, were not correlated with environmental variables, though *Gymnodinium*'s much lower densities suggest that its dynamics were controlled by other factors. Our results reveal that the physical–biological coupling controlling algal recruitment, which can play a large role in pelagic population growth and bloom formation, can vary substantially on a spatial gradient within even a small reservoir.

KEYWORDS: algal life history; *Gymnodinium*; *Peridinium*; phytoplankton; population ecology

INTRODUCTION

Organisms that live along abiotic gradients within an ecosystem, also referred to as an ecosystem continuum, provide a rich opportunity to examine physical–biological coupling (Whittaker, 1967; Hart and Finelli, 1999; Carmack and Wassman, 2006; Harrison *et al.*, 2008). Gradients provide the opportunity to quantify not only how the abundance of a species changes with varying environmental conditions (Brown, 1984; Tilman, 1993; Austin, 2002; McGill *et al.*, 2007), but also how organisms within the same species may respond differently to changing physical and chemical factors (Austin, 2002; Oksanen and Minchin, 2002; Vonlanthen *et al.*, 2009). The effects of gradients on populations have been extensively studied along salinity gradients in estuaries (Bouvier and del Giorgio, 2002; Crump *et al.*, 2004; Harrison *et al.*, 2008) and littoral-to-pelagic gradients within lakes (Schindler *et al.*, 1996; Vonlanthen *et al.*, 2009). However, less is known about how changing environmental conditions along a lotic to lentic gradient in reservoirs affect freshwater populations.

Many reservoirs are constructed by damming rivers, creating an ecosystem continuum of riverine to lacustrine conditions and providing an ideal opportunity to examine how environmental constraints may change within the same ecosystem (Thornton *et al.*, 1990; Wetzel, 1990). In a typical run-of-the-river reservoir, the physical and chemical environment exhibits marked changes from the upstream riverine zone to the downstream lacustrine zone near the dam (Kimmel and Groeger, 1984; Thornton *et al.*, 1990; Wetzel, 1990). In the riverine zone, inflow dynamics dominate the local environment; this reservoir zone experiences shorter local hydraulic residence times, higher sedimentation and more flushing of nutrients relative to downstream (Kimmel and Groeger, 1984). In contrast, the lacustrine zone experiences longer local residence times and is characterized by a deeper, lake-like basin with less temporal variability in physical conditions. As the name implies, the transitional zone is characterized by intermediate local residence times, sedimentation and nutrient flushing. Thus, the reservoir continuum provides an excellent opportunity to investigate how population dynamics vary with environmental conditions.

Here, we investigated how the responses of two phytoplankton taxa to environmental conditions vary along a reservoir ecosystem continuum. While most studies exploring population responses to environmental gradients in reservoirs have been conceptual (Kimmel and Groeger, 1984; Thornton *et al.*, 1990; Wetzel, 1990), recent empirical work indicates that the importance of different environmental drivers controlling phytoplankton population growth changes along this continuum (Cunha and Calijuri, 2011; Rychtecký and Znachor, 2011). In the riverine zone, algal population growth is often limited by light due to high flow and sedimentation rates (Kimmel and Groeger, 1984; Lind, 2002; Cunha and Calijuri, 2011), while in the lacustrine zone, algal population growth may be limited by internal nutrient dynamics (Kimmel and Groeger, 1984; Lind, 2002). In the transitional zone, primary production may be affected by both upstream (physics) and downstream (nutrient cycling) controls (Kimmel and Groeger, 1984; Lind, 2002). We predicted that phytoplankton population dynamics would be tightly coupled with changes in the physical environment in the riverine zone and most closely related to water chemistry in the lacustrine zone. In the transitional zone of the reservoir, recruitment patterns would be driven by both physical and chemical conditions.

We tested this hypothesis using two dinoflagellate taxa, *Peridinium* and *Gymnodinium*. Dinoflagellates are common in many aquatic systems and can be observed in all three reservoir zones because of their cosmopolitan distribution (Pollingher, 1988). Dinoflagellates can play a critical ecological role because they are a high-quality food source to higher trophic levels (Breteler *et al.*, 1999) and are often mixotrophic (Stoecker, 1999). They are the dominant taxa that produce harmful algal blooms in estuaries and oceans (Paerl, 1988; Hallegraeff, 1993; Anderson *et al.*, 2002; Sellner *et al.*, 2003), and occasionally produce blooms in freshwater systems (Nakamoto, 1975; Yamada *et al.*, 1998; Rengefors and Legrand, 2001; Hirabayashi *et al.*, 2007). Because dinoflagellate blooms can cause taste and odor problems in drinking water (Anderson *et al.*, 2002), understanding the factors that control their population dynamics is important for the management of drinking water reservoirs.

Dinoflagellate life cycles are complex (Pfiester and Anderson, 1987), and certain critical steps in their life history may play disproportionately large roles in their population dynamics (Park and Hayashi, 1993; Nehring, 1996; Sanderson and Frost, 1996). For example, pelagic populations are subsidized by recruitment from dormant cysts in the sediments (Park and Hayashi, 1993; Sanderson and Frost, 1996). These cysts can overwinter from preceding years and provide a seed bank of genetic variability for future populations (Pfiester and Anderson, 1987; Rengefors, 1998). Successful recruitment from the sediments to the water column typically plays an important role in increasing pelagic populations (Park and Hayashi, 1993; Nehring, 1996; Sanderson and Frost, 1996).

Past work suggests that dinoflagellate recruitment can be stimulated by light (Binder and Anderson, 1986; Anderson *et al.*, 1987; Pfiester and Anderson, 1987; Rengefors *et al.*, 2004), water column mixing (Hansson *et al.*, 1994; Hansson, 1995) and water temperature (Rengefors and Anderson, 1998; Rengefors *et al.*, 2004), but is inhibited by anoxia (Rengefors and Anderson, 1998). Most of these factors vary longitudinally along a reservoir ecosystem continuum, as well as temporally within a season, creating the opportunity to evaluate their combined effects on dinoflagellate recruitment. Although multiple studies have examined the drivers of dinoflagellate recruitment in marine systems and natural freshwater lakes, much less is known about dinoflagellate recruitment in reservoirs.

To examine changes in *Peridinium* and *Gymnodinium* population dynamics along the reservoir ecosystem continuum, we measured recruitment and pelagic populations for both taxa in a drinking water reservoir throughout one summer season. We quantified the rate of cells leaving the sediments in the riverine, transitional and lacustrine zones of the reservoir, and examined how recruitment rates in the different zones responded to temporal changes in physical and chemical variables throughout the sampling period.

METHODS

Study site

Falling Creek Reservoir (FCR) is a small, eutrophic impoundment located in Vinton, VA, USA (37.30°N, 79.84°W). The reservoir is a drinking water source owned and managed by the Western Virginia Water Authority. The reservoir catchment is primarily forested, and includes one primary inflow stream that contributes ~95% of incoming water to FCR (Fig. 1; Gerling *et al.*, 2016). The inflow discharge rate is measured every 15 min on an INW Aquistar PT2X pressure sensor (INW, Kirkland, WA, USA) at a weir on the stream located ~250 m before it enters the reservoir.

FCR represents a continuum of a lotic to lentic ecosystem, with a shallow, more "riverine" zone (maximum depth in thalweg = 4 m) near the inflow, a "transitional" zone (maximum depth = 7 m), and a deep "lacustrine" zone (maximum depth = 9.3 m) at the reservoir deep hole (Fig. 1).

Dinoflagellate recruitment and pelagic population sampling

In 2014, we sampled dinoflagellate recruitment in FCR throughout the summer stratified period (6 June through 22 September) by collecting cells recruiting from the sediments into algal recruitment traps. Each recruitment trap consisted of a 90 mm-diameter transparent glass funnel attached to a white 250-mL plastic collection bottle, following the design of Carey *et al.* (2008). The traps were weighted and suspended ~20 cm above the sediments, with the opening of the funnel oriented downwards to collect organisms leaving the sediments, following previously used recruitment trap methods (Hansson, 1996a; Carey *et al.*, 2008).

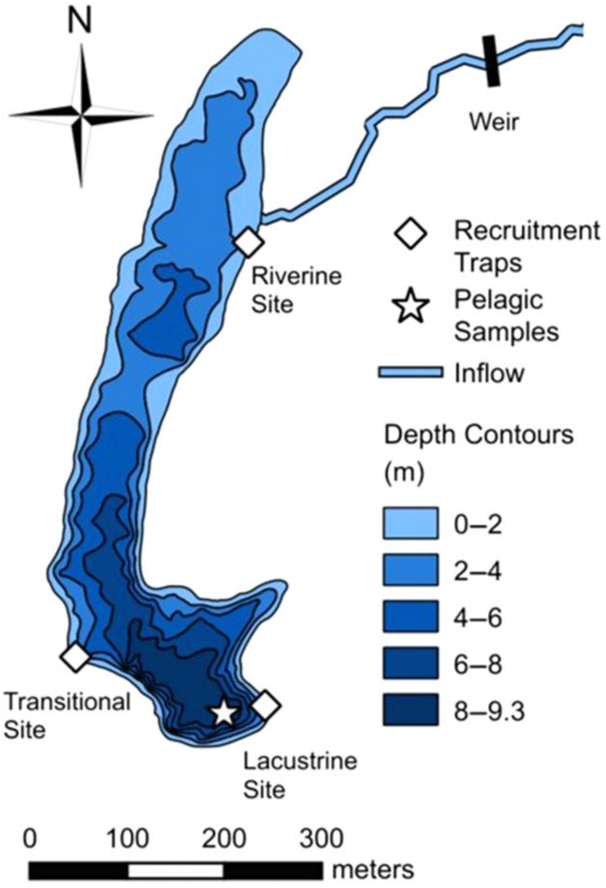

Fig. 1. Bathymetric map of Falling Creek Reservoir, Vinton, VA, USA. Two replicate recruitment traps were deployed at each of the three reservoir zones: riverine, transitional and lacustrine. The location of water chemistry and pelagic dinoflagellate sampling is denoted by a star. The inflow rate was measured at the weir entering the reservoir.

We deployed traps at three sites that corresponded to the reservoir's riverine, transitional and lacustrine reservoir zones (Fig. 1). Each recruitment site contained duplicate traps hanging ~1 m apart. Previous studies have demonstrated that most dinoflagellate recruitment takes place from shallow sediments (Anderson *et al.*, 1987; Hansson *et al.*, 1994), so we suspended the replicate recruitment traps from metal garden hooks (hereafter, recruitment trap masts) over ~1 m deep sediments. To stabilize the masts, we drilled holes in the bottom of 19-L plastic buckets, inserted the bottom prongs of the masts through the bucket bottoms, sank the buckets into the sediments and then filled buckets with large rocks to anchor the masts. Masts were deployed in early May, giving disturbed sediments 4 weeks to stabilize before recruitment traps were hung on the masts on 6 June.

In this study, we defined the recruitment period as the duration of time extending from the day the traps were deployed until the day before they were sampled. We collected the contents of the recruitment traps weekly until late August, and then every 7–14 days through the end of September as recruitment rates decreased in late summer. On each sampling day, a snorkeler removed the trap by plugging the funnel stem to prevent contamination from surface waters and bringing the sample bottle to the surface. The contents of the sample bottle were poured into a dark brown 250-mL plastic bottle and preserved immediately with Lugol's iodine solution. To prevent biofilm accumulation inside the recruitment traps, we replaced the trap bottles on each sampling day with fresh 250-mL bottles filled with tap water. Glass funnels were wiped clean or new funnels were substituted to ensure that they remained transparent throughout the monitoring period. After the cleaned recruitment traps were ready for deployment, we again plugged the funnel opening to prevent the tap water from leaking out while slowly lowering replacement traps back into position underwater. We took care not to disturb the sediments around the traps during deployment or sample collection. The recruitment trap mast in the lacustrine zone fell over on 13 August, and the mast in the riverine zone fell on 15 September; we were not able to reinstall these traps without disturbing the sediments.

We calculated recruitment rates into each trap according to standard methods (Hansson, 1996a, 1996b; Carey *et al.*, 2008). First, we quantified the number of cells of the two dominant dinoflagellate taxa (*Peridinium* and *Gymnodinium*) by subsampling the contents from each recruitment sample. We first homogenized the sample by stirring with a pipettor, then pipetted 0.1 mL subsamples into a Palmer–Maloney counting chamber. Using a Nikon Eclipse TS100 inverted microscope at ×100 magnification, we counted multiple transects in the counting chamber. Overall, 10 subsamples were enumerated per recruitment trap; all microscopy was conducted by K.D.H. These counts were then converted to dinoflagellate recruitment rates in units of cells $m^{-2}\,d^{-1}$ for each taxon.

We examined randomly chosen replicates from sample collection days with the highest recruitment rates to verify dinoflagellate taxonomy; cells in these samples were identified to species when possible by an external expert (A. St. Amand, Phycotech, Inc.) using an Olympus BX51 microscope at ×400 magnification.

To estimate the pelagic densities of each genus, we collected integrated phytoplankton samples approximately biweekly throughout the monitoring period from the deep hole (denoted by a star in Fig. 1). Pelagic samples were collected with a plastic tube sampler (9 cm diameter). We lowered the bottom of the tube to 4 m depth and capped the top of the tube to create a vacuum and ensure that no water was lost as we retrieved the tube bottom. The integrated epilimnetic water was added to a bucket and mixed thoroughly to homogenize the sample. We added 250 mL of this water to a dark brown sample bottle, which was preserved with Lugol's solution as described above. These samples were stored out of direct sunlight until microscopic analysis. Because the epilimnion was well-mixed through the summer (based on thermal profiles), we assume that these samples from one site are representative of pelagic dinoflagellate populations throughout the reservoir. We estimated pelagic dinoflagellate densities by settling 25–50 mL of preserved sample into a 5-mL counting chamber and counting cells on the Nikon Eclipse TS100 inverted microscope at ×100 magnification following the protocol of Utermöhl (1958).

Environmental monitoring

To investigate which environmental variables might drive dinoflagellate recruitment, we collected physical, chemical and weather data in the reservoir catchment and at the deep hole throughout the monitoring period. Thus, this study is focused on how dinoflagellate responses to the same set of measured environmental variables varied along the reservoir ecosystem continuum, and not on how the environmental variables themselves changed among reservoir zones – we did not monitor each variable in each reservoir zone. This approach is consistent with previous recruitment studies that compared recruitment data from multiple benthic sites with one pelagic site within a water body (Hansson, 1993; Rengefors *et al.*, 2004; Carey *et al.*, 2014).

Catchment-scale variables included weekly mean inflow rate, mean residence time and mean solar radiation. We used daily flow averages from the inflow weir to calculate mean inflow rate and mean hydraulic reservoir residence time for each recruitment period, following the methods described by Gerling *et al.* (2016). Additionally, because light availability can be a major factor in driving recruitment patterns (Binder and Anderson, 1986; Anderson *et al.*, 1987), we obtained incoming shortwave radiation (solar irradiance) data on a 15-min time scale from the Roanoke Regional Airport, located ~15 km from FCR. Similar to the procedure for daily flow data, we averaged the shortwave radiation measurement from noon on each day in a recruitment period to estimate the mean noon solar irradiance. Using radiation measured at noon vs. averaged over a longer midday period did not alter the findings from the statistical analyses.

Environmental data collected weekly at the reservoir deep hole included temperature, dissolved oxygen, turbidity, Schmidt stability, thermocline depth, Secchi depth and nutrients. We used a 4 Hz CTD (conductivity, temperature and depth) SBE 19plus profiler (Seabird Electronics, Bellevue, WA, USA) to collect high-resolution

(~0.1 cm resolution) profiles of temperature, dissolved oxygen and turbidity at the approximate midpoint of each ~7 d recruitment period. We then subsampled these CTD profiles to extract the temperature, dissolved oxygen and turbidity as potential predictors of recruitment at 1.0 m depth to match the depth of recruitment traps. In addition, we used the full CTD temperature profiles to calculate reservoir Schmidt stability and thermocline depth using the *rLakeAnalyzer* package (Winslow *et al.*, 2015), which calculates physical limnology metrics in the R statistical environment (R version 3.2.0, R Development Core Team, 2015). On each sampling date, we also estimated water transparency using a Secchi disk and collected water samples to measure total and soluble fractions of nitrogen (N) and phosphorus (P).

For nutrient sampling, we used a 4 L Van Dorn sampler (Wildco Supply Company, Yulee, FL, USA) to collect water from 1.6 m depth, which corresponded to the depth of the drinking water intake valve closest to the recruitment trap depth. After this water was homogenized in a bucket, a subsample was collected for total nutrient analysis and a second subsample for soluble nutrient samples was syringe-filtered in the field with 0.7 μm Whatman GF/F filters, both in acid-washed bottles. All samples were then frozen until laboratory analysis on a Lachat flow-injector analyzer (Lachat ASX 520 Series, Lachat Instruments, Loveland, CO, USA). Total N (TN) and total P (TP) concentrations were analyzed using USGS method I-4650-03, and soluble samples for ammonium (NH_4^+), nitrate–nitrite ($NO_3^- - NO_2^-$) and soluble reactive P (SRP) were analyzed following the Quik-ChemMethod 10-115-10-1-B. We used these nutrient concentrations to calculate the molar ratios of TN:TP and dissolved inorganic N (DIN, the sum of NH_4^+ and $NO_3^- - NO_2^-$) to dissolved inorganic P (DIP, estimated as SRP).

Statistical analyses

To evaluate the temporal coherence (*sensu* Kratz *et al.*, 1987) in recruitment rates within and across the riverine, transitional and lacustrine sites, we calculated Spearman's nonparametric correlation of recruitment rates for all possible pairs of sites for each taxon following Carey *et al.* (2008, 2014).

To test the prediction that dinoflagellate recruitment is more closely related to the physical environment in the riverine zone and to water chemistry in the lacustrine zone, we quantified the association between the monitored environmental variables and the temporal recruitment patterns of each taxon in each reservoir zone. First, we ln-transformed the recruitment rates for each taxon to meet the assumption of normality. Then, because many of our environmental variables were closely correlated ($|r| = 0.60 - 0.84$), we used principal components analysis (PCA) in the R *vegan* package (Oksanen *et al.*, 2015) to summarize the variability in the weekly averages for the catchment variables and the deep-hole environmental variables at the midpoint of each recruitment period. To interpret the resulting principal components (PC), we plotted the rank-ordered loading values for each variable, and used the inflection points in these plots to determine which variables loaded most heavily onto each PC. Finally, we calculated Pearson correlations between mean ln-transformed ($n = 2$ replicates) recruitment rates in each sample site and the scores from PC 1 and 2 to evaluate the associations between recruitment and potential multivariate drivers in each zone of the reservoir.

Contribution of recruiting cells to pelagic populations

To estimate the importance of recruitment to pelagic dinoflagellate populations, we calculated the percent recruitment contribution during sample periods when the pelagic population increased using standard methods (Karlsson-Elfgren *et al.*, 2003; Carey *et al.*, 2008). First, we used *Peridinium* and *Gymnodinium* recruitment rates to estimate the total number of cells entering the epilimnion during each recruitment period: we converted the median recruitment rate across all six traps (in cells $m^{-2}\,d^{-1}$) to total recruiting cells (cells d^{-1}) by multiplying recruitment rates by the area of FCR in the 0–2 m depth stratum. This assumes that the recruitment rates observed in traps at 1 m depth were representative of recruitment throughout FCR's 0–2 m stratum, a reasonable – and conservative – assumption, since reservoirs typically have steep bathymetry between the littoral and pelagic zones. Pelagic samples were typically collected on the same days as environmental samples, not recruitment trap samples, so we used daily estimates of dinoflagellate recruitment to estimate the total recruitment from 0 to 2 m during each pelagic sample. Next, we multiplied the observed pelagic density of *Peridinium* or *Gymnodinium* (in cells L^{-1}) by the total epilimnetic volume to estimate the abundance of total epilimnetic cells, and then calculated the net change in pelagic density from the previous sampling period (the change in total epilimnetic cells). Finally, we calculated the relative contribution of recruitment to the change in the pelagic population using the following equation:

$$\text{recruitment contribution} = \frac{(\text{median total recruitment from } 0-2\text{ m})}{(\Delta \text{ total epilimnetic cells})} \quad (1)$$

where changes in pelagic *Peridinium* or *Gymnodinium* populations not explained by recruitment rates were attributed to reproduction, cell death (e.g. due to grazing and lysis) and/or cell loss (e.g. due to discharge from the reservoir, forming cysts and leaving the pelagic life stage).

To provide some measure of uncertainty around the % recruitment contribution, we repeated the calculation using the minimum and maximum observed recruitment across all traps in each recruitment period ($n = 6$ through August 13, but $n = 4$ or 2 after masts fell down).

RESULTS

Recruitment patterns and contribution to pelagic populations

Recruitment rates of *Peridinium* and *Gymnodinium* varied spatially and temporally through the monitoring period (Fig. 2), with pulses of high recruitment occurring at different times at each site throughout the summer. *Peridinium* recruitment rates were up to ~2–10 × higher than *Gymnodinium* (Fig. 2), and *Peridinium* composed the majority of all recruiting dinoflagellate cells (50–100% of total cells in every trap each week) in FCR. *P. wisconsinense* was determined to be the dominant *Peridinium* species in the reservoir on the days when recruitment was highest; *Gymnodinium* was unable to be identified via microscopic methods.

Throughout the summer, *Peridinium* recruitment rates of replicate traps within a reservoir site were more closely correlated than recruitment rates among sites (Fig. 3), even though the maximum distance between sites was <1 km. The highest correlation was observed for replicate recruitment traps within the riverine site; traps within the transitional and lacustrine sites were also highly correlated. Sites furthest from each other (riverine and lacustrine) were the least correlated (Fig. 3). Importantly, *Peridinium* recruitment rates within sites did not exhibit significant temporal autocorrelation at 1 and 2 week lags (Pearson's r, $P > 0.06$ for all replicates).

In contrast, *Gymnodinium* recruitment patterns were not closely correlated between site replicates within either the riverine or the lacustrine zone (Fig. 3). *Gymnodinium* recruitment in the transitional zone was correlated between replicates (Fig. 3); this site also generally exhibited the highest rates of *Gymnodinium* recruitment through the summer. No other traps among the three different sites exhibited strong correlations. *Gymnodinium* recruitment rates were not autocorrelated between replicates (Pearson's r, $P > 0.12$ for all replicates), but mean *Gymnodinium* recruitment did exhibit temporal coherence at the lacustrine site ($P = 0.019$), preventing us from comparing mean *Gymnodinium* recruitment with PC scores to analyze *Gymnodinium* along the reservoir continuum.

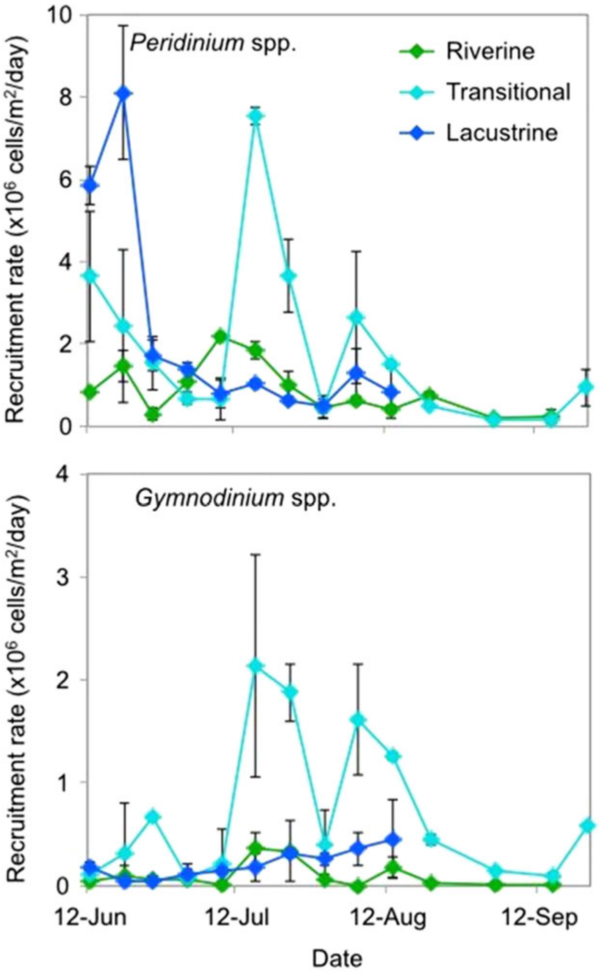

Fig. 2. Mean ± 1 standard error of recruitment rates of *Peridinium* (top) and *Gymnodinium* (bottom) at three reservoir zone sites in Falling Creek Reservoir during summer 2014; note the different *y*-axis scales. The riverine and lacustrine series are truncated because their recruitment trap masts fell down during the sampling period.

Recruitment patterns and pelagic populations appear to have been more closely synchronized at the beginning of the monitoring period for both *Peridinium* and *Gymnodinium* than at the end of the summer (Fig. 4). For both taxa, pulses in recruitment lined up with peaks in pelagic populations in late June and mid-July; in August and September, the correspondence between changes in recruitment rates and pelagic abundances was weaker. These patterns were robust regardless of if the reservoir-wide minimum, median and maximum recruitment rates were being examined. Overall, the median recruitment rate was closer to the minimum rate than to the maximum rate during most recruitment sample periods (Fig. 4), but weeks with the highest maximum recruitment rates were closely coupled with peaks in pelagic populations for both genera (Fig. 4).

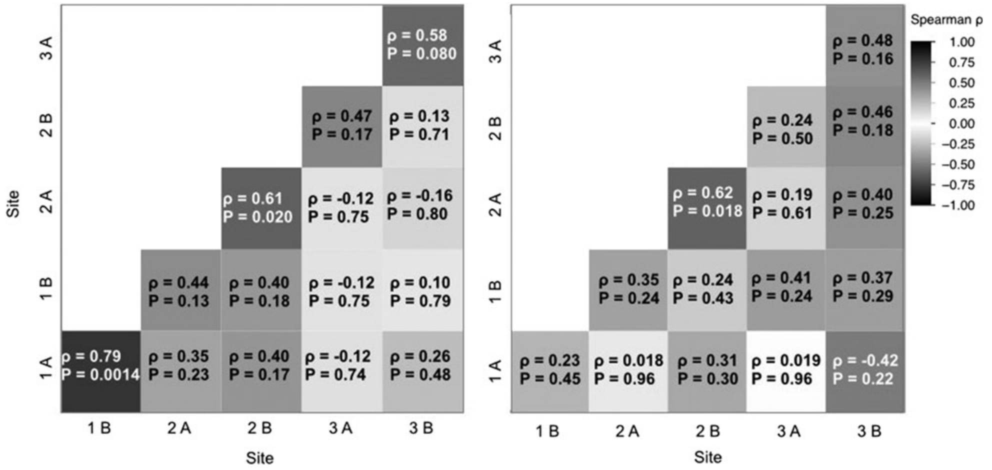

Fig. 3. Spearman's ρ nonparametric correlations of *Peridinium* (left) and *Gymnodinium* (right) recruitment rates among all recruitment trap replicates in Falling Creek Reservoir in summer 2014. Site 1 = riverine zone, site 2 = transitional zone and site 3 = lacustrine zone; letters A and B denote replicate traps within each site. Darker colors indicate more closely correlated replicates, with white denoting Spearman's ρ correlations of $\rho = 0$ and black denoting $\rho = \pm 1.0$. Sites 1 ($n = 13$) and 3 ($n = 10$) have fewer sample periods than site 2 ($n = 14$) because the recruitment trap masts fell over.

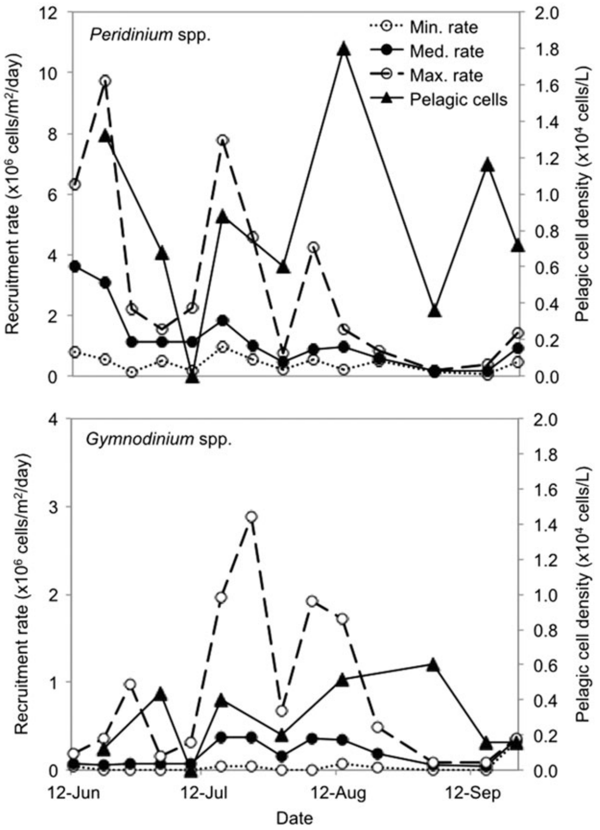

Fig. 4. Minimum, median and maximum observed recruitment rates (gray lines, calculated across all standing traps at that time period) and pelagic cell concentrations (black line) of *Peridinium* (top) and *Gymnodinium* (bottom) in Falling Creek Reservoir during summer 2014. Note that the recruitment rate scales differ between panels.

Recruitment from the sediments contributed to the pelagic population growth of both dinoflagellate taxa. In summer 2014, there were three sample periods when the pelagic *Peridinium* population increased, allowing us to estimate the contribution of recruiting cells to pelagic populations. Median *Peridinium* recruitment rates contributed 6–16% of pelagic population growth in summer 2014 (S1). *Gymnodinium* pelagic populations increased in four sample periods, and *Gymnodinium* recruitment contributed 3–150% of population growth (S1). The 150% contribution estimate was observed in the week of 18 August and was due to recruitment rates that were higher than the pelagic population increase, indicating that some recruiting cells did not remain in the pelagic population (e.g. due to grazing, senescence and discharge from the reservoir).

Environmental conditions in the reservoir

We observed seasonal changes in physics and water chemistry at the reservoir's deepest site throughout the monitoring period (Figs 5 and 6). Water temperature at the depth of the recruitment traps warmed throughout June to August before decreasing in September (Fig. 5H). Throughout the summer, FCR exhibited stratified conditions, with a well-mixed epilimnion extending to ~3 to ~4 m depth (Fig. 5B). Schmidt stability decreased toward the end of the monitoring period as the reservoir approached autumn turnover (Fig. 5A). Due to dry summer conditions, inflow stream flow rate was lowest toward the end of the summer (Fig. 5C), resulting in an increase in hydraulic residence

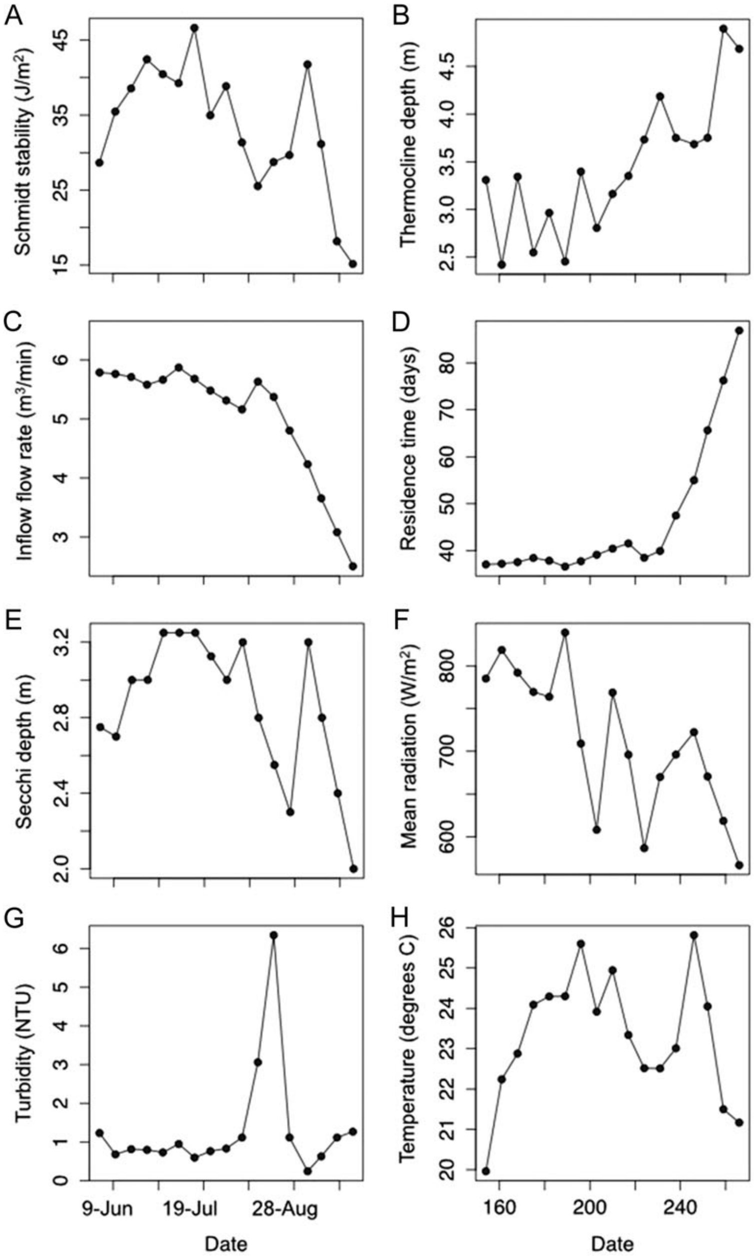

Fig. 5. Reservoir physical variables: Schmidt stability (**A**), thermocline depth (**B**), inflow flow rate (**C**), residence time (**D**), Secchi depth (**E**), mean radiation (**F**), turbidity (**G**) and temperature (**H**) in Falling Creek Reservoir during summer 2014. Variables (A–E) strongly loaded onto PC1.

time (Fig. 5D). In contrast, Secchi depth and mean noon solar radiation did not follow a clear seasonal pattern (Fig. 4E and F); both were highest in mid-summer (early July) and fluctuated toward the end of the monitoring period. Total and soluble N:P ratios, as well as concentrations of total and dissolved N and P fractions, were dynamic through the sampling season, yet suggested N limitation because DIN:DIP ratios were consistently <4 (Fig. 6G). Epilimnetic dissolved oxygen concentrations fluctuated throughout the summer but remained above 0.219 mM (Fig. 6F).

The PCA partitioned the physical and chemical variables into two separate multivariate axes (Fig. 7, S2), which together explained 67.5% of the variance. Physical environmental variables loaded strongly on PC1 (Fig. 7, S2). Inflow rate, solar radiation, Schmidt stability and Secchi depth loaded positively onto this axis, while mean residence time and thermocline depth

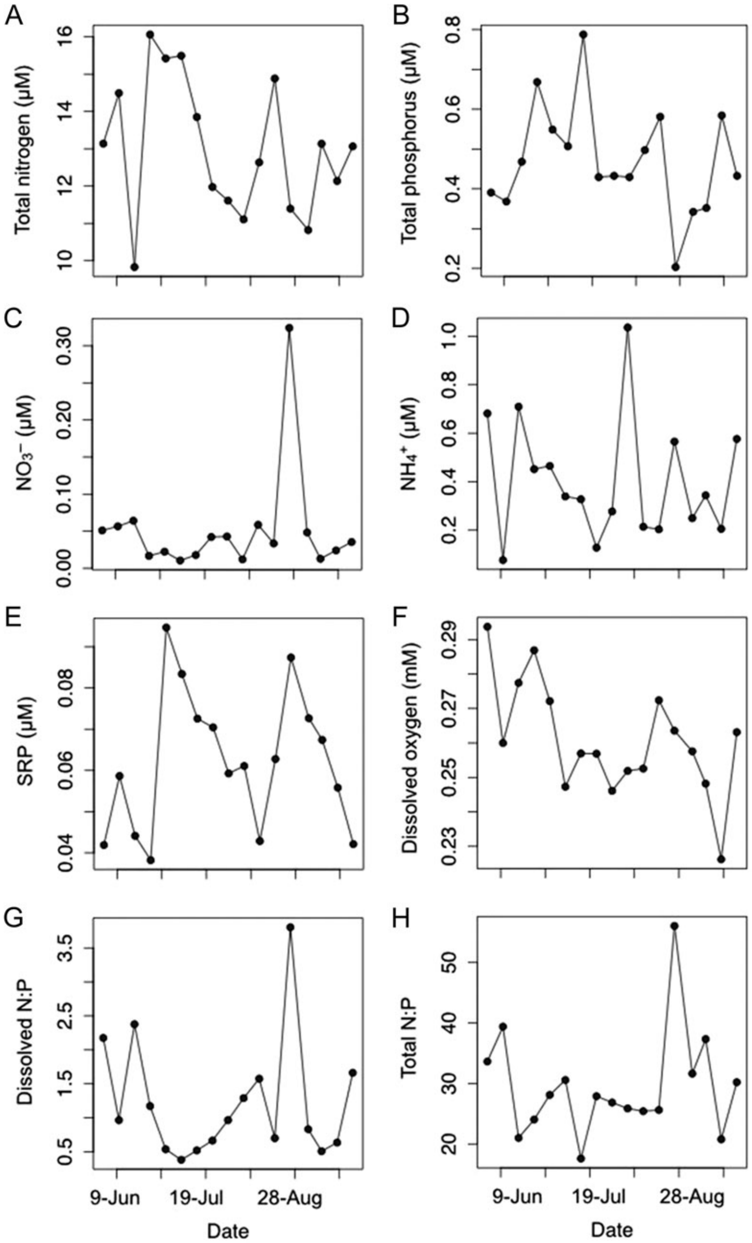

Fig. 6. Water chemistry variables: total nitrogen (**A**), total phosphorus (**B**), nitrate (NO_3^-, **C**), ammonium (NH_4^+, **D**), soluble reactive phosphorus (SRP, **E**), and dissolved oxygen (**F**) concentrations, and dissolved (**G**) and total (**H**) N:P molar ratios in Falling Creek Reservoir, summer 2014. Dissolved and total N:P fractions (G and H) were included in the PCA and strongly loaded onto PC2.

loaded negatively. In comparison, chemical environmental variables loaded strongly on PC2 (Fig. 7, S2). Dissolved oxygen and N:P ratios loaded positively onto this axis, while Secchi depth loaded negatively.

Plotting the PC scores for each sample period with the eigenvectors of environmental variables illustrates the multivariate changes in the FCR environment over the monitoring period (Fig. 7): the position of each sample period relative to environmental loadings highlights the temporal variability in FCR and how the relative importance of environmental variables changed through the summer. For example, the variability among sampling periods was driven more by nutrients and dissolved oxygen earlier in the season, but then became dominated by physical drivers (radiation, inflow rate, Schmidt stability and Secchi depth) during midsummer. Throughout the rest of the summer, with the exception of week 13 (25 August–1 Septmber), physical

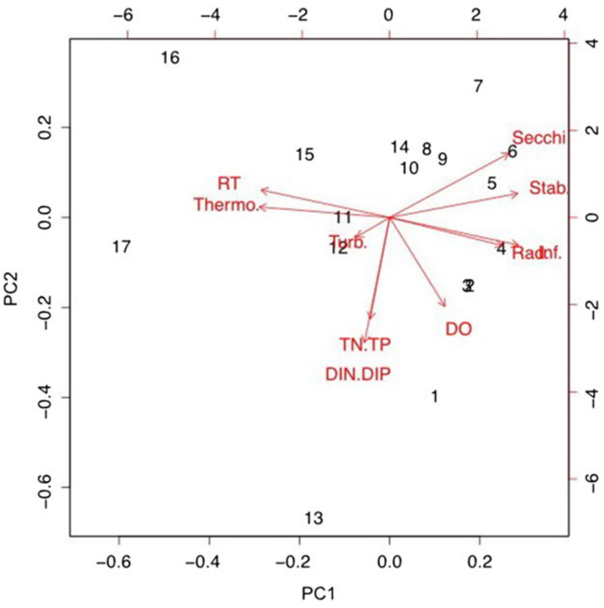

Fig. 7. Biplot of observations (i.e. recruitment sample periods, numbered 1–17 in chronological order, weeks 2 and 3 overlap) and eigenvectors of environmental variables throughout the recruitment monitoring period in FCR. Bottom and left axes are normalized PC scores for the observations; top and right axes are loadings for the environmental variables; length of the arrows represents the weight of their loadings onto PC1 (which explains 47.5% of variance) and PC2 (20% of variance). Environmental variables (clockwise from top) are abbreviated as follows: Secchi = Secchi depth; Stab. = Schmidt stability; Inf = mean inflow flow rate; Rad = mean radiation; DO = dissolved oxygen; TN:TP = total N:P; DIN.DIP = soluble N: P; turb. = turbidity; thermo. = thermocline depth; and RT = mean residence time.

drivers, primarily residence time, thermocline depth and turbidity, dominated reservoir dynamics (Fig. 7).

Relationship between recruitment and environment

Peridinium recruitment patterns in the three reservoir zones indicate differential sensitivity of *Peridinium* recruitment to physical and chemical environmental factors along a riverine-to-lacustrine reservoir continuum (Fig. 8). Consistent with expectations, ln-transformed recruitment rates of *Peridinium* were positively correlated with the physical variables that loaded on PC1 at the riverine site and with the chemical variables that loaded on PC2 at the lacustrine site (Fig. 8), but not vice versa. At the transitional site, *Peridinium* recruitment rates were weakly positively related to both PC1 and PC2 (Fig. 8). We did not repeat these analyses for *Gymnodinium* due to lack of coherence between replicates within a site (Fig. 3) and temporal autocorrelation at the lacustrine site.

DISCUSSION

An improved understanding of the factors controlling phytoplankton population dynamics is needed to better predict blooms in drinking water reservoirs. Our study demonstrates that recruitment from the sediments, a life history stage that is often overlooked in phytoplankton models, was an important factor promoting the pelagic population growth of two cosmopolitan dinoflagellate taxa in FCR. Our calculations indicate that median *Peridinium* recruitment contributed 6–16% of pelagic population increases, and median *Gymnodinium* recruitment contributed 2–106% of its population growth (S1). Previous studies have estimated that algal recruitment rates contribute <10% of pelagic populations (Trimbee and Harris, 1984; Barbiero and Kahn, 1994; Hansson *et al.*, 1994), but recruitment of some cyanobacteria can contribute up to ~45% of pelagic populations as reviewed by Carey *et al.* (2014). Though our estimates of recruitment contribution were highly variable each week, our data suggest that recruitment plays a larger role subsidizing dinoflagellate pelagic populations in FCR than in other freshwater systems; however, it is important to keep in mind that our data only cover one summer season. Dinoflagellates have slow division rates relative to other phytoplankton (Reynolds, 2006), so cells recruiting from the sediments may be provide an especially important subsidy for their pelagic populations.

Moreover, our results suggest that recruitment may be particularly important in reservoirs with short residence times (mean = 47 days in FCR in summer 2014), compared to natural lakes. Our estimates of the contribution of recruitment to pelagic populations were conservative because we assumed that recruitment from sediments deeper than 2 m was negligible; FCR's thermocline fluctuated between 2.5 and 3.5 m during the high recruitment period in early summer (Fig. 5A), and Hansson *et al.* (1994) found that recruitment of the dinoflagellate *Ceratium hirundinella* below the thermocline was negligible during summer stratification. Hence, recruitment likely occurred from the 2–3.5 m strata in FCR, contributing additional recruiting cells to the pelagic population. Furthermore, we estimated the importance of recruitment using the median recruitment rate calculated for each sample period, but if recruitment rates were spatially heterogeneous, then benthic subsidies to pelagic populations may actually be higher than our estimates. These estimates would be improved by including more pelagic sample sites to address horizontal patchiness in pelagic populations; however, we note that many previous studies have also only used one pelagic site to estimate recruitment contribution from multiple littoral recruitment traps

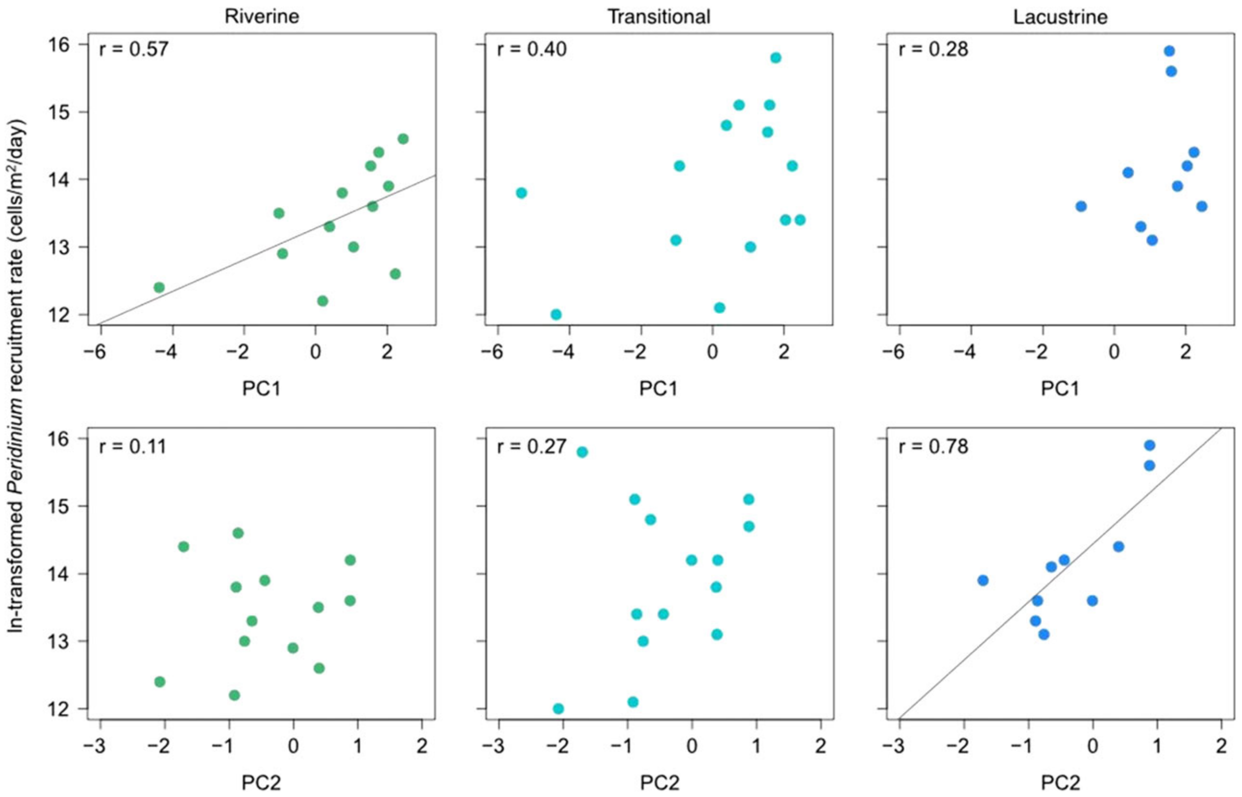

Fig. 8. Ln-transformed mean *Peridinium* recruitment rates for each reservoir zone (lacustrine: left panels; transitional: center panels; and riverine: right panels) and PC scores (PC1: top panels, physical drivers; PC2: bottom panels, chemical drivers). Regression lines are shown for relationships with $r > 0.5$.

(Hansson *et al.*, 1994; Rengefors *et al.*, 2004; Carey *et al.*, 2014).

Throughout the monitoring period, *Peridinium* spp. was the dominant recruiting dinoflagellate taxon and had up to 50 × higher recruitment rates and 7 × higher pelagic abundances than *Gymnodinium* (Figs. 2, 4). *Peridinium*'s dominance is likely due to multiple factors, which may include differences in the abundance of dormant cysts in the seed bank or different growth rates in the pelagic zone. Though both genera have been placed in the same Reynolds phytoplankton functional classification (Reynolds *et al.*, 2002; Niesel *et al.*, 2007), a survey of 24 German reservoirs over five years revealed that *Peridinium* and *Gymnodinium* very rarely co-occurred at high biovolumes (Niesel *et al.*, 2007). Niesel *et al.* (2007) concluded that this was due to slight differences in their realized niche, and competition may also prevent the two genera from co-occurring. In these systems, *Gymnodinium* was more likely to dominate when TP concentrations were <0.32 μM and had a narrower pH tolerance (pH 6–7) than *Peridinium* (Niesel *et al.*, 2007). These results support *Peridinium*'s dominance in FCR, which exhibited TP concentrations between 0.36 and 0.77 μM (Fig. 6) and pH concentrations between 6.2 and 8.2 in summer 2014 (C.C.C., unpublished data).

The strong temporal coherence within our reservoir sites but lack of coherence among sites indicate that *Peridinium* recruitment is likely driven by similar environmental cues within a site but different environmental variables among sites. In contrast, *Gymnodinium* recruitment may be driven by factors other than environmental cues, or be responding to environmental cues at much finer spatial scales than *Peridinium*. Dinoflagellate recruitment can be heavily influenced by internal regulation, i.e. endogenous clocks within resting cysts (Anderson *et al.*, 1987; Rengefors and Anderson, 1998), which we did not measure but may have influenced recruitment patterns of *Gymnodinium* recruitment in FCR. Because *Gymnodinium* was not controlled by site-specific variables, we focused on *Peridinium* to test our hypothesis that recruitment in the riverine zone would respond to physical variables, while recruitment in the lacustrine zone would be driven by changes in chemistry.

Changes in physical and chemical conditions are usually confounded in natural systems because they generally occur concurrently. Here, the unsupervised PCA separated the physical and chemical variables, providing an opportunity to examine how *Peridinium* responded to physical vs. chemical drivers across a reservoir continuum. Our results suggest that this dinoflagellate population may be driven by different factors in different reservoir zones, which has important implications for algal management in reservoirs. More broadly, our study contributes to the growing literature (Lind and Barcena, 2003; Cunha and Calijuri, 2011; Rychtecký and Znachor, 2011) that has observed very different phytoplankton dynamics in the riverine vs. lacustrine zones of a reservoir. Longer-term studies spanning more than one summer are needed to determine the extent that interannual variability mediates recruitment sensitivity to different environmental factors along the reservoir ecosystem continuum.

The two dinoflagellate taxa exhibited substantial variability in recruitment rates among reservoir zones (Fig. 3). In the riverine zone of the reservoir, variability in *Peridinium* recruitment was most closely related to physical conditions (Fig. 8). This is likely because phytoplankton growth in the upstream riverine zone is often driven by physical variables, such as light availability and flow rate (Kimmel and Groeger, 1984; Lind, 2002; Cunha and Calijuri, 2011). The riverine zone is usually shallower and narrower than transitional and lacustrine zones; therefore, inflow flow rate should be relatively more important. Although we assumed a well-mixed epilimnion based on nutrient and thermal profiles, it is possible that nutrients were less limiting at the riverine site because of inflowing nutrient-rich stream water, thus reducing the relative sensitivity of algal recruitment to changing nutrient dynamics in comparison to physical conditions.

In the lacustrine zone, *Peridinium* recruitment rates were less sensitive to physics and instead more closely related to changes in nutrient chemistry (Fig. 8). As expected, *Peridinium* recruitment rates were strongly related to PC2 scores ($r = 0.78$), which were driven by N:P ratios and dissolved oxygen concentrations, in spite of the shorter recruitment time series at this site. Reservoir lacustrine zones experience longer local residence times than upstream regions, and nutrient supply in this zone is usually driven more by internal nutrient cycling than external inflows (Kimmel and Groeger, 1984). Thus, algal growth in downstream lacustrine zones is less closely coupled with reservoir physics and tends to be driven by internal nutrient chemistry (Kimmel and Groeger, 1984; Lind, 2002; Cunha and Calijuri, 2011). Dinoflagellate growth is often limited at low (<16) N:P ratios (reviewed by Elser *et al.*, 1990), and FCR experienced strong N limitation (dissolved N:P < 4) in summer 2014. Consequently, it follows that *Peridinium* recruitment rates in the lacustrine zone were highest during periods heavily influenced by increasing N:P ratios.

Our environmental variables were measured either at the reservoir deep hole (Secchi depth, nutrient chemistry, temperature, turbidity and dissolved oxygen), or at the whole-reservoir scale (incoming solar radiation, inflow flow rate, reservoir residence time, Schmidt stability and thermocline depth). Thus, our results reveal varied responses of dinoflagellates to the same core set of environmental drivers, and not changes in those environmental variables, along the reservoir continuum. Further investigation should include sampling environmental variables and dinoflagellate pelagic abundances in each reservoir zone to improve our understanding of the factors driving dinoflagellate recruitment along the reservoir continuum. For example, our estimates of residence time were calculated for the whole basin, but local residence time in each zone is likely substantially different. Additionally, our data only span one summer, similar to the vast majority of recruitment studies reviewed by Carey *et al.* (2014), but a longer field study would provide greater insight into recruitment dynamics, especially for rare taxa, such as *Gymnodinium*, which may have very different densities between years (Hansen and Carey, 2015).

CONCLUSIONS

Our results demonstrate that recruitment plays an important role in pelagic population dynamics of the two dominant dinoflagellates in FCR. Because dinoflagellates can form problematic blooms that represent a major water quality concern (Nakamoto, 1975; Paerl, 1988; Yamada *et al.*, 1998; Hirabayashi *et al.*, 2007), understanding the factors driving dinoflagellate recruitment, as well as the importance of recruitment to pelagic bloom formation, may improve reservoir management. In reservoirs with short residence times, such as FCR, pelagic phytoplankton population dynamics may depend heavily on recruitment, and response of recruitment patterns to environmental factors may be extremely variable spatially. We note that the maximum distance between reservoir recruitment trap sites in FCR was <1 km, indicating that the controls of dinoflagellate population dynamics can change rapidly over a short distance along the reservoir continuum. Our data provide insight to the spatial variation in phytoplankton recruitment, but we note that longer field studies are needed to confirm and strengthen these conclusions. Consequently, we advocate consideration of both the spatial heterogeneity of environmental conditions and the changing response of algal recruitment along the reservoir continuum to improve management of dinoflagellate blooms in reservoirs.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plankton Research* online.

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