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PRIMARY RESEARCH PAPER

Feeding rates and prey selection of the invasive Asian clam, *Corbicula fluminea*, on microplankton in the Columbia River, USA

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Abstract The Asian clam, *Corbicula fluminea,* was introduced into North America in the 1920s—first observed in the Columbia River—and has expanded its range across the continent and into South America and Europe, yet little is known about its ecology and potential to impact food webs. To evaluate prey selectivity and feeding rates of *C. fluminea*, we conducted laboratory feeding experiments using water from two distinct Columbia River environments (unimpounded river and reservoir) during July and October 2016. The mean clearance rate on microplankton was 270 (± 53.6 SE) ml water clam^{-1} h^{-1} and mean ingestion rate was 2.45 (± 0.83 SE) µg C clam^{-1} h^{-1}, although rates varied with season and location. In the reservoir in July, clams preferred diatoms and showed an avoidance of dinoflagellates and flagellates; during October in the unimpounded river, clams preferred flagellates while showing a significant avoidance of cyanobacteria. Diatoms were dominant at both sites, and were ingested by clams; however, clams ingested cyanobacteria at very low rates. Substantial consumption of microplankton such as diatoms and rejection of cyanobacteria by *C. fluminea* may provide competitive advantages to cyanobacteria, leading to microplankton community composition shifts and other changes to food webs in the Columbia River.

Keywords Bivalve grazing · Selective feeding · Plankton community composition · Suspension feeding · Aquatic invasive species

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Introduction

Aquatic invasive species (AIS) are an increasing concern due to their potential to significantly affect the aquatic systems to which they are introduced and become established. In particular, invaders have been shown to impact biodiversity by altering community composition and abundances in freshwater systems (Rahel, 2002), and declines in freshwater biodiversity, in part due to invasions, are expected to continue in coming decades (Sala et al., 2000). This is especially true in regard to invasive freshwater bivalves. For instance, in South America, the presence of the golden mussel, *Limnoperna fortunei* (Dunker, 1857), led to a decrease in crustacean and rotifer zooplankton

abundances (Rojas Molina & de Paggi, 2008; Rojas Molina et al., 2012), although mussel veligers can sometimes be an additional source of nutrition for larval fishes (Paolucci et al., 2010). Two more notorious invasive bivalves, the zebra [*Dreissena polymorpha* (Pallas, 1771)] and quagga [*Dreissena bugensis* (Andrusov, 1897)] mussels, have been a topic of great concern in the eastern and central United States (US) since their introduction into the Great Lakes region in 1988 (Ludyanskiy et al., 1993). *D. polymorpha* can cause large decreases in phytoplankton abundance and biomass (Caraco et al., 1997; Karatayev et al., 1997) and selectively consume specific phytoplankton taxa (Naddafi et al., 2007). *D. polymorpha* has also been implicated in the promotion of harmful cyanobacteria blooms in two of the US Great Lakes (Huron and Erie) (Vanderploeg et al., 2001), and in a similar vein, *L. fortunei* has been linked to increased *Microcystis* abundance in the Salto Grande Reservoir in Argentina (Cataldo et al., 2012). Similarly, *D. bugensis* caused declines in all phytoplankton taxa except chlorophytes and cyanobacteria in another Great Lake (Michigan) (Fahnenstiel et al., 2010). While *D. polymorpha* and *D. bugensis* have not yet been detected in the US Pacific Northwest (though *D. bugensis* has invaded other parts of the western US [Wong et al., 2010]), a different invasive bivalve—the Asian clam *Corbicula fluminea* (O. F. Müller, 1774)—has been established there since the 1930s (McMahon, 1983). Despite its current widespread distribution in the region (Dexter et al., 2015; Hassett et al., 2017), the impacts of this invasive bivalve are largely unknown.

Corbicula fluminea is a freshwater, veneroid bivalve endemic to Southeast Asia, Africa, and the Pacific Islands (McMahon, 1983). *C. fluminea* shells were first identified in the US Pacific Northwest in 1924 in the Columbia River and, in three separate invasion events, spread throughout the entire continental US (Counts, 1981). Following the US invasion, *C. fluminea* was identified as an invader in both South America and Western Europe (Mouthon, 1981; Ituarte, 1994; Sousa et al., 2005). *C. fluminea* are highly effective suspension feeders and large populations can process substantial volumes of water in short periods of time (Beaver et al., 1991; Pigneur et al., 2014); for instance, in the Potomac River in the northeast US, a population of Asian clams was capable of filtering the entire water column in 3–4 days (Cohen et al., 1984). However, studies of *C. fluminea* have typically evaluated phytoplankton as a single prey group, with possible selection for specific taxa only rarely considered.

Taxonomic prey selection by *C. fluminea* was first examined by Boltovskoy et al. (1995) using gut content analysis, which showed that *C. fluminea* did not preferentially select for specific phytoplankton taxa in a South American river. Subsequently, Atkinson et al. (2011) suggested that *C. fluminea* preferentially selected prey in the Flint River of the southeast US based on size (individual prey between 0.3 and 10 μm), but showed no taxonomic preference. However, Way et al. (1990) found Asian clams to selectively consume particles up to 16 μm in size, and Way et al. (1989) suggested that the clams' gills can effectively sort particles up to 20 μm in size.

While taxon-specific selection has not yet been definitively demonstrated in *C. fluminea*, there is a substantial literature on selective feeding by other invasive freshwater bivalves. For instance, the feeding behavior of *D. polymorpha* is particularly well documented. In Lake Erken, Sweden, *D. polymorpha* preferentially selected for cryptophytes, chrysophytes and dinoflagellates over diatoms, chlorophytes and cyanobacteria (Naddafi et al., 2007). When preferred taxa were not seasonally available in Lake Erken, mussels shifted to consumption of the next highest quality prey available—diatoms (Naddafi et al., 2007). *D. polymorpha* has also been shown to select for cultured *Microcystis aeruginosa* (Kützing, 1846) over other prey options (Baker et al., 1998; Dionisio Pires et al., 2004). Similarly, *D. bugensis* has shown selective preference for unicellular cyanobacteria and diatoms (Tang et al., 2014).

River impoundments can create spatial differences in river phytoplankton communities through alteration of residence times in different portions of the river, potentially altering prey available to bivalve suspension feeders in these systems. Li et al. (2013) noted a decrease in diatom dominance and an increase in dominance by chlorophytes and cyanobacteria due to longer residence times in reservoirs following impoundment of the Mekong River. River impoundment has been shown to cause shifts of dominance in phytoplankton communities when compared to open, free-flowing river systems (Holz et al., 1997) and while run-of-river impoundment provides shorter residence times than large storage reservoirs, it has

been shown to cause similar changes in microplankton assemblages (Li et al., 2013). Given the effects of impoundment on phytoplankton community composition, consumption by *C. fluminea* could vary significantly in portions of rivers that are dammed versus those that are free-flowing.

Numerous invasions by aquatic species have been documented in the Columbia River, including plankton, fish, and crustacean taxa (Bollens et al., 2002; Cordell et al., 2008; Bollens et al., 2012; Smits et al., 2013, Dexter et al., 2015; Emerson et al., 2015; Lee et al., 2016; Hassett et al., 2017; Dexter et al., 2018). Given the additional threat posed by the spread of quagga and zebra mussels (undetected in the Columbia River Basin to date) to the already heavily invaded Columbia River ecosystem, it is important to understand the ecology and possible food web effects of other invasive bivalves in the region, beginning with the already established *Corbicula fluminea*.

To this end, we conducted laboratory feeding experiments to evaluate potential taxon-specific feeding on microplankton (cells 5–200 μm) by adult *C. fluminea* in the lower Columbia River. We had two main objectives (1) to evaluate potential selective feeding of *C. fluminea* for or against specific microplankton taxa; and (2) to evaluate the consumption rates of *C. fluminea* incubated in river water of seasonally variable microplankton composition. Given that temperate phytoplankton communities typically change composition through seasonal succession, we chose to undertake feeding trials in two different times of the year (July and October) in which river flow and the plankton community are substantially different (Dexter et al., 2015). Moreover, we chose two distinct portions of the river (unimpounded river vs. impounded reservoir sites) to allow us to evaluate clam consumption of microplankton in two different habitats.

Methods

Study site

The Columbia River is the second largest river in the United States, draining an area of 660,480 km^2 in the US Pacific Northwest and is responsible for up to 90% of the freshwater discharged into the Pacific Ocean in the area between the San Francisco Bay and the Straits of Juan de Fuca (Simenstad et al., 1990). Additionally, the Columbia River contains important recreational, commercial, and tribal fisheries, including several members of the genus *Oncorhynchus* (e.g., chinook, sockeye salmon), white sturgeon [*Acipenser transmontanus* (Richardson, 1836)], American shad [*Alosa sapidissima* (A. Wilson, 1811)], and Pacific smelt [*Thaleichthys pacificus* (Richardson, 1836)]. This massive freshwater system is very important to the US Pacific Northwest; 70% of the electrical energy supplied to the region comes from thirty dams on the river and 1.4 million hectares of agricultural lands are irrigated by the river (Payne et al., 2004). The Columbia River is generally well mixed vertically and thus well oxygenated throughout the water column (Dexter et al., 2015).

We collected adult clams from two locations in the Columbia River for use in three clam feeding experiments conducted in July and October 2016. The first location was Blurock Landing, a public access beach along a free-flowing section of the Columbia River in Vancouver, WA, USA (45°39′56.76″N, 122°45′33.37″W; Fig. 1). This site (hereafter referred to as "river") is approximately 162 river km upstream of the mouth of the Columbia River at Astoria, OR, USA, and approximately 73 km downstream from the Bonneville Dam, the most downstream of 30 hydroelectric dams along the mainstem of the Columbia River. The river at this location is tidally influenced but contains no salt water. Sediment at this location is sandy and silty, with moderate macrophyte cover in areas not exposed by tidal changes. Clams are frequently exposed during low tide at this site. The site is frequently used for recreational swimming in summer months and experiences heavy commercial and recreational boat traffic in mid-river.

The second location where we collected water for our experiments was the Bonneville Reservoir at Hood River, OR, USA (45°42′54.81″N, 121°30′13.38″W; Fig. 1), approximately 38 km upstream of the Bonneville Dam to represent a reservoir site (hereafter referred to as "reservoir"). This reservoir site is more sandy than the river site, with heavy macrophyte cover. Water level here varies seasonally as a result of changes in water release through the dam, unlike the river site where water level changes as a result of tidal stage and the seasonal hydrograph.

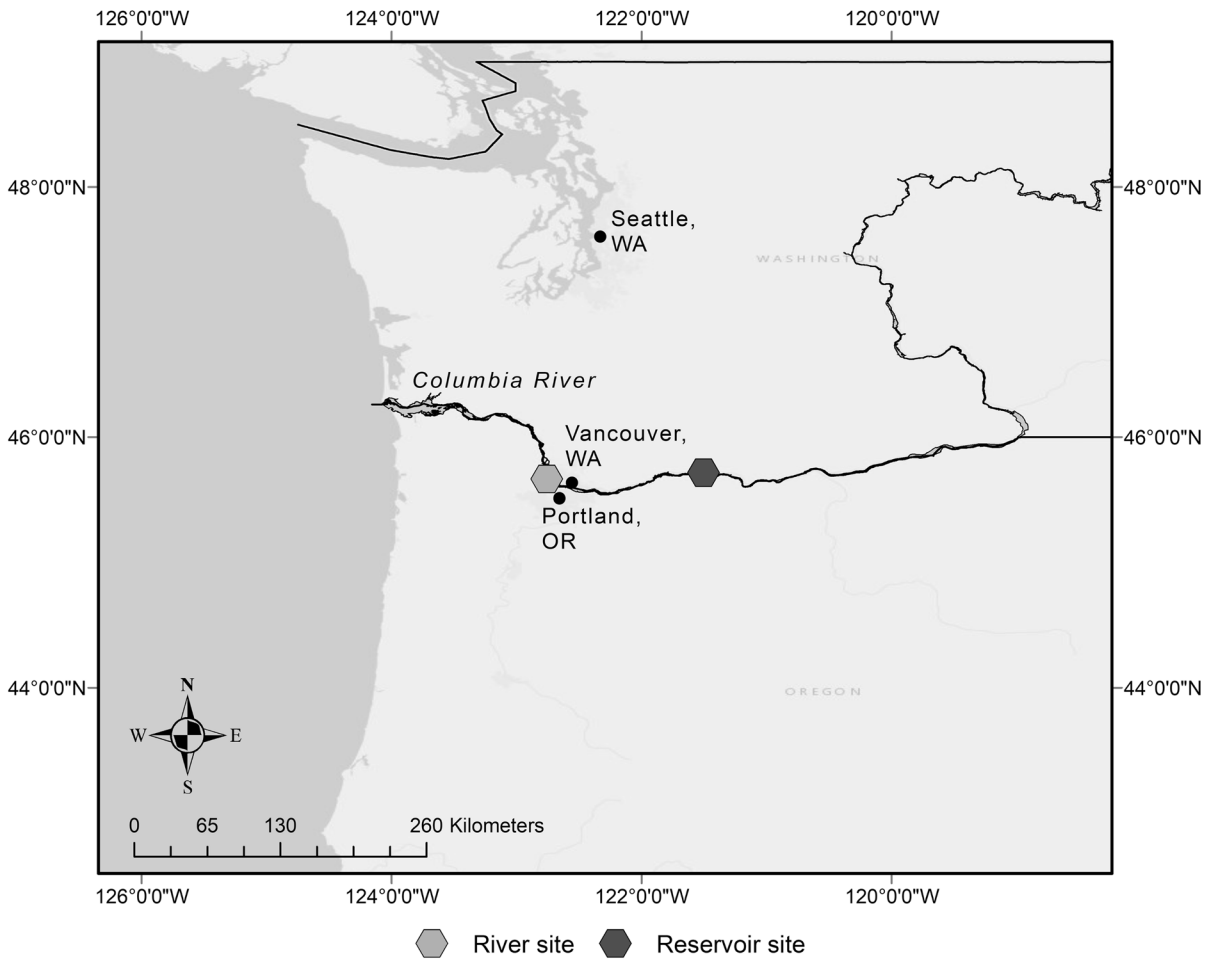

Fig. 1 Map of reservoir and river site locations on the Columbia River, USA

Field collections

Adult clams (> 1 cm valve width) were collected in shallow (~ 1 m) water at the river site. Clams were visually identified on top of or buried in shallow sediment and extracted with a flat-ended shovel. Adult clams were sifted from the sediment using a 4-mm wire mesh basket and transferred into a bucket of ambient river water. Clams were transported back to the laboratory within 6 h, and acclimated in a temperature-controlled room at ambient river temperature in unfiltered river water collected from the corresponding site in each experiment.

Water from both the river and reservoir sites was collected in shallow (~ 1 m) water in transparent 10- or 20-l plastic Nalgene® carboys. Carboys were held just under the surface, pointed upstream, and allowed to completely fill to avoid air pockets and minimize turbulence inside the carboy. Carboys were stored in a temperature-controlled room at ambient river or reservoir temperatures. Carboy lids were unscrewed to allow gas exchange and lights were set to a timer matched to an 8-h night cycle. Clams and water for all experiments were held in these conditions for 24 h prior to each clam feeding experiment. Grazing, and subsequent pseudofeces production, by clams during this pre-experiment acclimation period was accounted for during microplankton enumeration (see "Microplankton enumeration" section below).

Clam feeding experiments

Feeding experiments (Fig. 2) were carried out at ambient water temperature for each site in a

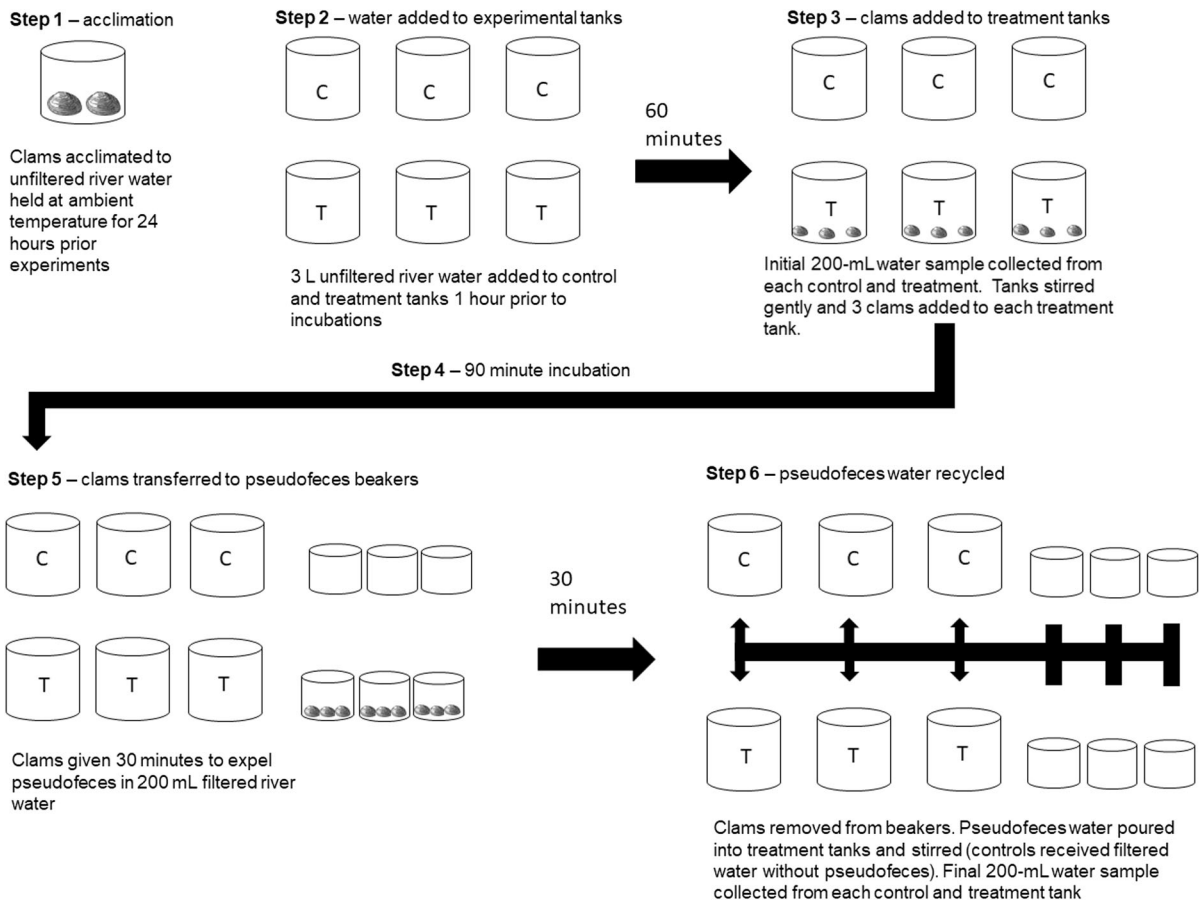

Fig. 2 Schematic diagram of feeding experiments. Steps occured in chronological order. Control and treatment tanks are marked "C" and "T," respectively

temperature-controlled room. During July, water temperature was 20°C at the river site and 21°C at the reservoir site. During October, water temperature was 15°C at the river site. Prior to each experiment, adult clams were separated into bins of six sizes based on valve width (1.20–1.59 cm, 1.60–1.99 cm, 2.0–2.39 cm, 2.40–2.79 cm, 2.80–3.19 cm, 3.20–3.60 cm). This method was intended to determine the most abundant size groups and to remove undue influence of particularly large or small clams. One hour before each experiment, six high-density polyethylene containers were filled with 3 l each of water from either the river or reservoir site; 3 containers served as controls and 3 as treatment containers. Because we did not have sufficient clams to select all of our experimental specimens from any one size class, we had to combine specimens across two size classes (and thus we were unable to test for differences in feeding due to clam size). Specifically, 6 clams of the most abundant size class (1.60–1.99 cm) and 3 clams of the second most abundant size class (2.0–2.39 cm), for a total of nine clams within the 1.60–2.39 cm size range, were selected and placed in a 1-l glass beaker containing unfiltered water collected from the same site as the clams for 1 h prior to the experiment. Subsequently, three of the 9 clams were randomly selected and placed in each of the 3 treatment containers.

At the start of the feeding experiments (t = 0 h), containers were gently stirred and an initial 200-ml water sample was collected from the surface of each control and each treatment container for microplankton community analysis (Fig. 2). Microplankton samples were immediately preserved in 10 ml of 5% Lugol's solution in opaque bottles. Immediately following this, 3 clams were randomly selected from

the holding container and placed into each of the 3 treatment containers. Clams were observed to ensure that they opened their valves and extended their siphons, and were allowed 90 min in the feeding experiment containers. While these incubations were short in duration, we did not stir the experimental tanks during incubation, and thus we cannot preclude the possibility of sinking cells.

Following the 90 min (t = 1.5 h) of feeding in the containers, clams were transferred to glass beakers containing 200 ml of 0.22 µm filtered river (or reservoir) water to allow them to expel pseudofeces (Fig. 2). It is likely that clams also expelled feces during this time; however, only pseudofeces were considered for the purposes of this study due to their potential to contain viable cells (Vanderploeg et al., 2001). After 30 min (t = 2 h), clams were removed and pseudofeces were gently broken up with a magnetic stir bar before being gently poured back into the treatment containers to account for microplankton removed from the water column by clams but not consumed (Fig. 2). Following addition of pseudofeces to treatment containers, a 200-ml final water sample was collected from each control and treatment container and preserved in 5% Lugol's solution for microplankton analysis (Fig. 2).

We also collected water samples for analysis of chlorophyll *a* throughout the feeding experiments. Four 60-ml samples were collected from experimental containers pre- and post-feeding experiment, as well as before and after the addition of pseudofeces. One sample was also collected from pseudofeces beakers prior to magnetic stirring, for a total of five chlorophyll samples per replicate. Chlorophyll samples were filtered through Whatman GF/F filters immediately after the experiments had ended. Filters were wrapped in foil and frozen for at least 24 h prior to extraction in 20 ml of acetone for an additional 24 h. Chlorophyll *a* concentrations from the acetone samples were measured on a Turner Model 10 AU fluorometer following the acidification method (Strickland & Parsons, 1972).

Microplankton enumeration

Microplankton samples were settled via the Utermöhl method prior to microscopic analysis. For control replicates, 35-ml subsamples were settled into settling chambers for 18 h prior to enumeration. For treatment replicates, 50-ml subsamples were settled to account for removal of microplankton by clams. Settled subsamples were examined under a Leica DMI 4000B inverted microscope at 400×. Individual microplankton cells were sized and identified to family, or genus when possible (Wehr & Sheath, 2002). All microplankton (cells 5–200 µm) were counted and identified until a total of 300 individuals per subsample was reached.

We calculated the abundance of microplankton in each control and treatment container, at both the initial and final time points, as the number of cells present per volume of incubation water (3 l). However, since the clams had been acclimated in unfiltered experimental water prior to the incubation period, and likely ejected unconsumed cells into the incubation water as pseudofeces during the incubation (Vanderploeg et al., 2001), we calculated a correction factor that we applied to the initial abundance values measured in each experiment. The correction factor (CF) was calculated as $CF = Chl_F/Chl_I$, where Chl_F represents the amount of chlorophyll *a* in experimental tanks after pseudofeces were added and Chl_I represents the amount of chlorophyll *a* in experimental tanks before pseudofeces were added. Initial phytoplankton abundances were then modified by the following equation $C_{ic} = C_{icu} * CF$, where C_{ic} is the adjusted abundance of cells in the initial controls, C_{icu} is the unadjusted abundance of cells in initial controls, and CF is the correction factor described above.

Consumption rates

To measure consumption of microplankton by *C. fluminea*, we calculated clearance rates (CR; ml water clam^{-1} h^{-1}) and ingestion rates (IR; µg C clam^{-1} · h^{-1}) of six major microplankton taxonomic groups (ciliates, chlorophytes, cyanobacteria, diatoms, dinoflagellates, and flagellates) as well as total microplankton in each replicate and control container following the methods of Marin et al. (1986). Clearance rates were calculated as $CR = \left[\frac{V*g}{N}\right]$, where V is feeding incubation volume, N is the number of clams per container, and g is the grazing mortality coefficient (t^{-1}). The grazing mortality coefficient (g) was defined as $g = r - \left[\frac{\ln\left(\frac{C_{ft}}{C_{ic}}\right)}{t}\right]$, where r is the

microplankton growth rate in control samples (t^{-1}), C_{ft} is the abundance of cells (cells ml^{-1}) in final treatment samples, C_{ic} is the abundance of cells from initial control samples, and t represented feeding experiment time in hours. The microplankton growth rate (r) in control replicates is defined as $r = \left[\frac{\ln\left(\frac{C_{fc}}{C_{ic}}\right)}{t}\right]$, where C_{fc} is the abundance of cells from final controls. Ingestion rates were calculated as $IR = CR \times B_{ic}$, where B_{ic} is the initial biomass of microplankton taxa in the initial controls. Biomass (μg C l^{-1}) in these samples was based on a conversion of biovolume to carbon following the methods of Menden-Deuer & Lessard (2000). Differences in ingestion rates were evaluated using a Kruskal–Wallis one-way ANOVA followed by Mann–Whitney U-tests for post hoc pairwise comparisons; microplankton community abundances in these experiments were found to be non-normally distributed and as such, a non-parametric test was selected.

Clam feeding selectivity

To measure differential preference for specific taxa by *C. fluminea*, we used two different approaches. First, we compared clearance rates of the clams for each major prey taxon within each experiment using one-way ANOVA (Zar, 1996) followed by Tukey's HSD tests for post hoc pairwise comparisons. Significant differences ($P < 0.05$) in the clearance rates may suggest differential preference of microplankton taxa by grazers (Rollwagen-Bollens et al., 2013). Second, we calculated an electivity index (E^*; Vanderploeg & Scavia, 1979; Rollwagen-Bollens et al., 2013) that compares proportions of taxa in the grazer's diet to proportions of taxa available in the environment. While selectivity indices are often sensitive to variation in the relative abundance of prey, Vanderploeg & Scavia's E^* index has been suggested for use in such cases (Confer & Moore, 1987). To estimate E^*, we first calculated the abundance of prey cells of a given prey taxon (i) consumed by clams (R_i) as $R_i = \left[\frac{N_{ic} - N_{fc}}{2}\right] - N_{ft}$, where N_{ic} is the mean abundance of cells in initial control samples, N_{fc} is the abundance of cells in final control samples, and N_{ft} is the abundance of cells in the final treatments. Following this, we calculated the proportion of cells in the clams' diet (r_i) and the proportion available for consumption in the experiments (n_i), where $n_i = \frac{N_{ic}}{\sum_{j=1}^{m} N_{jc}}$, $r_i = \frac{R_{ic}}{\sum_{j=1}^{m} R_{jc}}$, and m is the number of prey taxa available. E^* was then calculated as $E_i^* = \frac{W_i - \frac{1}{m}}{W_i + \frac{1}{m}}$, where $W_i = \frac{\frac{r_i}{n_i}}{\sum_{j=1}^{m} \frac{r_j}{n_j}}$. Electivity ($E^*$) of 0 indicates a neutral preference for a prey taxon. Positive values up to + 1.0 represent increasing preference for a prey taxon, while negative values down to − 1.0 indicate increasing avoidance of a prey taxon. In some cases involving rare taxa (i.e., taxa in very low absolute and relative abundance), R_i was calculated as a negative value, due to instances in which those taxa were not observed in samples from control beakers, but were then observed in very low abundance in final treatment samples. We interpreted such negative R_i values as an absence of those taxa in the clams' diet, and therefore set R_i to 0 for further calculations of E^* for those taxa. E^* values were tested for significant difference from zero through one-sample t-tests.

Results

Microplankton abundance and biomass

Microplankton abundance (Fig. 3a) was higher in July (summer) than October (fall) at the river site. In July, diatoms were the dominant taxon followed by somewhat lower abundances of flagellates, chlorophytes, and cyanobacteria, and substantially lower abundances of dinoflagellates and ciliates. In October, cyanobacteria increased somewhat in abundance and became the dominant taxon, whereas other taxa declined. Microplankton biomass (Fig. 3b) was similarly higher in July than October at the river site and was heavily dominated by diatoms. At the reservoir site during July, abundance was more evenly distributed between diatoms, flagellates, chlorophytes, and cyanobacteria (Fig. 3a), whereas biomass was dominated by diatoms (Fig. 3b).

Microplankton composition

The relative abundances of the major microplankton taxonomic categories at the river site and the reservoir site were relatively similar during July (Fig. 4). More

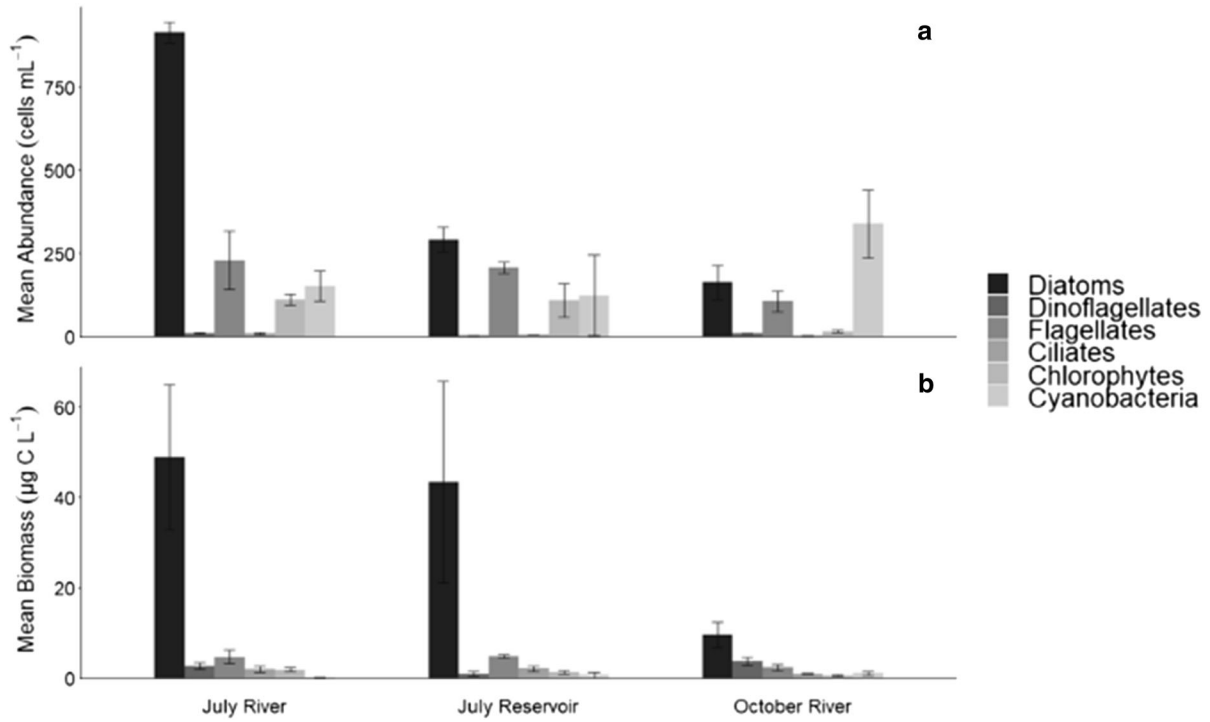

Fig. 3 Abundance (**a**) and biomass (**b**) (mean ± SE) of microplankton taxa at two sites in the Columbia River in July and October 2016

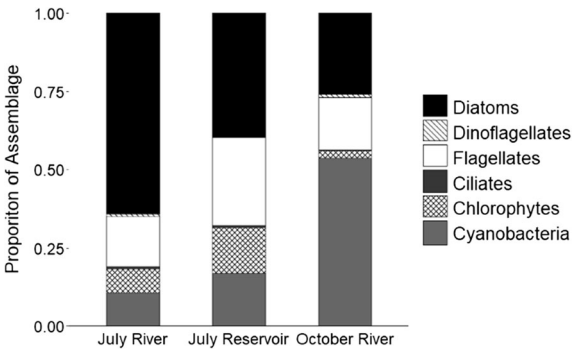

Fig. 4 Relative abundances of microplankton taxa at two sites in the Columbia River during July and October 2016

specifically, at both the river and reservoir sites, *Cyclotella* sp. was the most abundant diatom taxon, while *Aulacoseira* sp. were also common. *Melosira* sp. and *Fragillaria* sp. diatoms were also abundant at the river site, while the reservoir diatom assemblage included high numbers of *Gomphonema* spp. which were not present at the river site. Flagellates and chlorophytes at both sites were dominated by cryptomonads and *Monoraphidium* sp, respectively. Cyanobacteria at both sites were dominated by *Aphanocapsa* sp., *Merismopedia* sp., and *Oscillatoria* sp., with the highest abundance and biomass occurring in October at the river site.

Clearance rates

Clearance rates for microplankton taxa by clams in our experiments averaged 270 (± 53.6 SE) ml water clam^{-1} h^{-1}, but varied with season and location (Fig. 5). Note that negative clearance rates are an indication of prey avoidance by a suspension-feeding grazer, since the grazing rate coefficient (g) used to calculate clearance rate is negative when there are higher abundances of prey taxa present in treatments with grazers than in control treatments at the end of a feeding incubation. Overall, clams cleared microplankton at higher rates at the river site in both seasons than at the reservoir site. However, no significant differences in clearance rates were evident among microplankton taxa in July in either the river or reservoir, while in October in the river the clearance rate of clams on cyanobacteria was significantly lower

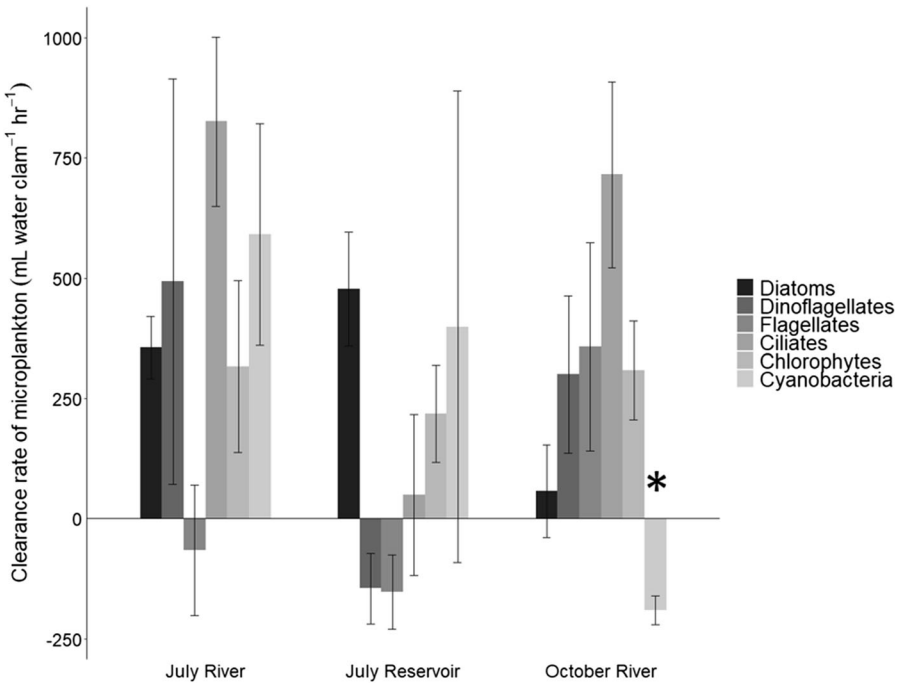

Fig. 5 Clearance rates (ml water clam^{-1} h^{-1}; mean ± SE) of adult *C. fluminea* on microplankton taxa at two sites in the Columbia River in July and October 2016. Statistical analyses were only performed within experiments. Asterisk denotes significant difference in clearance rate within an experiment

($F = 4.24$, $P = 0.019$) than for all other prey taxa (Table 1; Fig. 5).

Electivity indices

Mean electivity indices indicated no preference for or against any taxon by adult *C. fluminea* in the river in July (Fig. 6). Clams showed a preference for diatoms and an avoidance of dinoflagellates and flagellates in the reservoir in July (Fig. 6). Conversely, clams showed a preference for flagellates and an avoidance of diatoms in the river in October (Fig. 6).

Ingestion rates

Mean ingestion rate of microplankton by clams in our experiments was 2.45 (± 0.83) µg C clam^{-1} h^{-1}. Clams ingested diatoms at significantly higher rates than other prey groups in the reservoir ($\chi = 12.7$, $P = 0.03$) in July (Table 2, Fig. 7). Similarly, while there was no significant difference in ingestion between overall prey groups in the river in July ($\chi = 9.26$, $P = 0.1$), pairwise comparisons indicated significantly higher ingestion of diatoms than chlorophytes ($P = 0.017$), cyanobacteria ($P = 0.006$), and flagellates ($P = 0.005$) (Table 2). In October at the river site, ingestion rates were uniformly low and did not vary between microplankton prey taxa ($\chi = 8.27$, $P = 0.14$), except for cyanobacteria, for which ingestion rates were significantly lower than other taxa in all three experiments (Table 2, Fig. 7).

Discussion

Microplankton assemblage

Microplankton composition, abundance, and biomass observed in our study are generally consistent with those of previous studies in the Columbia River, but with some notable differences. The biomass of flagellates, cyanobacteria, and diatoms is consistent with previous work in the lower reaches of the Columbia River (Bowen et al., 2015); however, diatom abundance at our river site in July was substantially higher than recorded in previous studies in the lower Columbia River (Bowen et al., 2015; Breckenridge et al., 2015). Dominance of microplankton assemblages by diatoms is not uncommon in temperate rivers in spring and early summer, as shown in both the Meuse River in Belgium (Gosselain et al., 1994) and the Ebro River in Spain (Sabater et al., 2008), however, typically in mid-summer, chlorophytes have become dominant in these assemblages.

Table 1 Results of one-way ANOVA for clearance rates of microplankton by *C. fluminea*

Clearance rates					
July river					
df	SS	MS	*F*	*P*	
5	1351283	270257	1.71		
	Cyanobacteria	Diatoms	Dinoflagellates	Flagellates	Chlorophytes
Ciliates	0.136	0.700	0.900	0.136	0.630
Cyanobacteria		0.975	0.999	0.383	0.952
Diatoms			0.998	0.781	0.999
Dinoflagellates				0.544	0.993
Flagellates					0.839
July reservoir					
df	SS	MS	*F*	*P*	
5	1016264	203253	2.6	0.087	
	Cyanobacteria	Diatoms	Dinoflagellates	Flagellates	Chlorophytes
Ciliates	0.744	0.464	0.950	0.942	0.972
Cyanobacteria		0.999	0.338	0.326	0.977
Diatoms			0.146	0.139	0.858
Dinoflagellates				1.000	0.618
Flagellates					0.600
October river					
df	SS	MS	*F*	*P*	
5	1394050	278810	4.24	**0.019**	
	Cyanobacteria	Diatoms	Dinoflagellates	Flagellates	Chlorophytes
Ciliates	**0.010**	0.072	0.403	0.552	0.424
Cyanobacteria		0.834	0.249	0.165	0.236
Diatoms			0.849	0.709	0.831
Dinoflagellates				0.999	1.000
Flagellates					0.999

Pairwise comparisons are Tukey's HSD tests. Values in bold indicate statistical significance ($P < 0.05$) within each experiment

In our study, diatoms remain dominant in mid-summer with a relatively low presence of chlorophytes. In October, dominance in the microplankton assemblage in the Columbia River shifted from diatoms to cyanobacteria while in the studies discussed above, diatoms resumed dominance of the microplankton assemblage in fall communities (Gosselain et al., 1994, Sabater et al., 2008).

Diet selectivity of Asian clams in the Columbia River

We assessed the diet selectivity of *C. fluminea* based on differential clearance rates on prey taxa as well as an index of electivity. *C. fluminea* clearance rates for different prey taxa varied considerably in our experiments, but in general, were comparable to ranges reported from previous laboratory experiments, e.g., 41.2–151 ml water clam^{-1} h^{-1} in the Potomac River (Cohen et al., 1984), 66.4–145 ml water clam^{-1} h^{-1} in the Tombigbee, Ouachita, and Tangipahoa Rivers (Way et al., 1990) and 109–1370 ml water clam^{-1} h^{-1} in the Chowan River (Lauritsen, 1986). In addition, one field study conducted in the Lower Rhine River measured filtration rates of 364–745 ml water clam^{-1} h^{-1} in spring and 94–111 ml water clam^{-1} h^{-1} during fall (Vohmann et al., 2010). While it is possible that temperature differences in our experiments affected clam clearance rates (20–21°C in July, 15°C in October), variation in clearance rates by *C. fluminea* has been shown to respond weakly to differences in temperature

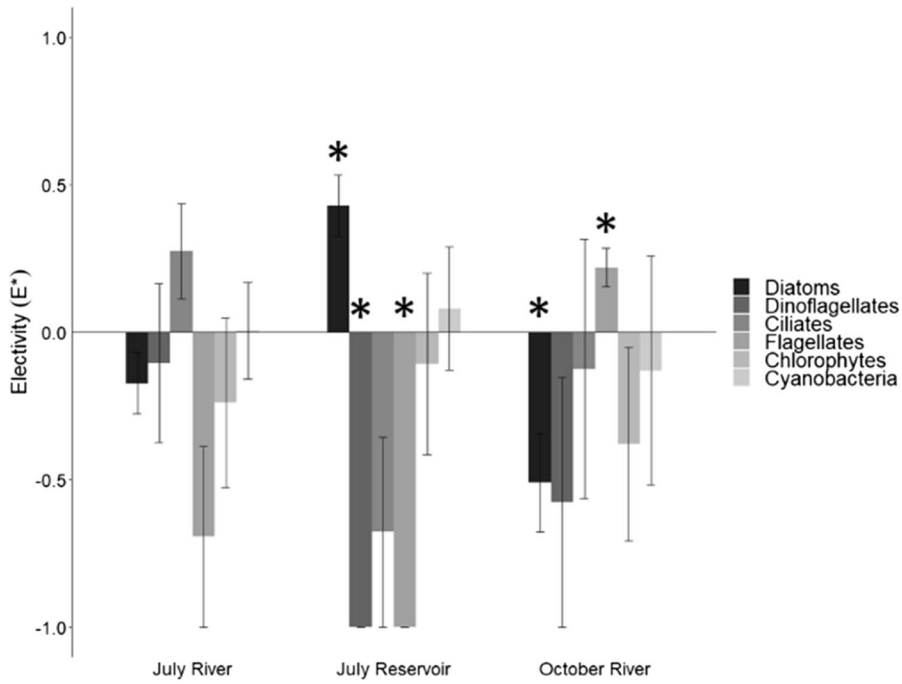

Fig. 6 Electivity indices (E^*; mean ± SE) calculated from clam feeding experiments conducted using water from two sites in the Columbia River during July and October 2016. Positive values represent preference of clams for a particular taxon, and negative values represent avoidance of that taxon. Asterisks denote E* values significantly different from 0

(Viergutz et al., 2012), with these authors suggesting that clearance rates are likely more heavily influenced by other factors.

During the summer (July), we found no significant differences in clearance rates of *C. fluminea* among prey taxa at either the river or reservoir site. This lack of selectivity is consistent with previous studies on selection by *C. fluminea.* For instance, Boltovskoy et al. (1995) recorded no significant differences in the consumption of phytoplankton taxa through a comparison of gut contents and prey items available in the Paraná River delta in Argentina. Similarly, Atkinson et al. (2011) demonstrated a lack of taxonomic selectivity in adult clams, although they did show size selectivity (i.e., a preference for smaller cells). In our study, however, clams showed significantly lower clearance rates on small cyanobacteria in the river in October. Evidence for selective preference by other invasive bivalves (specifically dreissenids) for cyanobacterial taxa is mixed in the literature. Baker et al. (1998) found that *D. polymorpha* in the Hudson River preferentially selected cultured *M. aeruginosa* over other prey and thus promoted increases in diatom concentrations. Selection for *M. aeruginosa* over diatoms and chlorophytes was also observed by Dionisio Pires et al. (2004). The closely related *D. bugensis* has also shown selective preference for large diatoms and unicellular cyanobacteria (Tang et al., 2014). Conversely, several other studies indicated a rejection of cyanobacteria by dreissenids. In a study of *D. polymorpha* feeding on the toxic cyanobacterium *M. aeruginosa*, mussels rejected the cyanobacteria in Lakes Erie and Huron (Vanderploeg et al., 2001). Similarly, *D. bugensis* has been shown to reject chlorophytes and colonial cyanobacteria in the US Great Lakes (Fahnenstiel et al., 2010; Tang et al., 2014).

Our electivity (E^*) analysis, in contrast to the clearance rates, indicated differences in selectivity by clams between study sites in our summer experiments. In the reservoir, clams showed a preference for diatoms and a strong avoidance of dinoflagellates and flagellates. Dinoflagellates in our study were represented mostly by *Peridinium* sp. 20–25 µm in size, near the maximum prey size that *C. fluminea* can process (Way et al., 1990). However, in the river in October, clams showed a preference for flagellates while avoiding diatoms. It is possible that differences in selection by clams in these experiments were due to differences in prey assemblages at the river and reservoir locations, perhaps caused by different hydrodynamics at these impounded (reservoir) versus unimpounded (river) sites. As river impoundment has been demonstrated to alter microplankton

Table 2 Results of Kruskal–Wallis one-way ANOVA for ingestion rates of microplankton by *C. fluminea*

Ingestion rates					
July river					
df		χ^2		*P*	
5		9.26		0.1	
	Cyanobacteria	Diatoms	Dinoflagellates	Flagellates	Chlorophytes
Ciliates	0.159	0.062	0.485	0.141	0.282
Cyanobacteria		**0.006**	0.168	0.469	0.336
Diatoms			0.057	**0.005**	**0.017**
Dinoflagellates				0.150	0.295
Flagellates					0.309
July reservoir					
df		χ^2		*P*	
5		12.7		**0.03**	
	Cyanobacteria	Diatoms	Dinoflagellates	Flagellates	Chlorophytes
Ciliates	0.216	0.039	0.157	0.157	0.201
Cyanobacteria		**0.009**	0.455	0.455	0.062
Diatoms			**0.003**	**0.003**	0.178
Dinoflagellates				0.500	**0.033**
Flagellates					**0.033**
October river					
df		χ^2		*P*	
5		8.27		0.14	
	Cyanobacteria	Diatoms	Dinoflagellates	Flagellates	Chlorophytes
Ciliates	**0.013**	0.258	0.439	0.424	0.323
Cyanobacteria		0.058	**0.009**	**0.008**	**0.039**
Diatoms			0.211	0.200	0.424
Dinoflagellates				0.485	0.270
Flagellates					0.258

Pairwise comparisons are Mann–Whitney *U*-tests. Values in bold indicate statistical significance ($P < 0.05$) within each experiment

assemblages in both storage (Holz et al., 1997) and run-of-river impoundments (Li et al., 2013), it is important to consider differences in selectivity by Asian clams in the unimpounded and impounded portions of the Columbia River (our river and reservoir sites).

Our variable results on selective feeding align with conflicting observations of other invasive freshwater mussels in lentic versus lotic systems. For instance, *D. polymorpha* has been shown to prefer cryptophytes over other taxa in the Great Lakes (Vanderploeg et al., 2001; Fahnensteiel et al., 2010), as well as in a European lake (Naddafi et al., 2007). Naddafi et al. (2007) also found *D. polymorpha* to exhibit a preference for dinoflagellates and a weak avoidance of diatoms. However, Vanderploeg et al. (2001) showed a rejection of cyanobacteria (*M. aeruginosa)* by *D. polymorpha* in Lake Huron (lentic), but Baker et al. (1998) showed a selective preference for this same taxon in the Hudson River (lotic). It is possible that differences in hydrology of lentic and lotic systems (similar to our river and reservoir sites) alter assemblage and grazing dynamics enough to cause changes in bivalve feeding selectivity between systems. Indeed, in the Columbia River, clams showed a preference for diatoms at the reservoir site where flow rate is lower and the smaller diatom *Gomphonema* spp. was present, but showed avoidance of diatoms at the river site when the much larger *Melosira* sp. and *Fragillaria* sp. were common. In the case of flagellates, however, both sites were dominated by the same group (*Cryptomonas* sp.), yet clams avoided this taxon

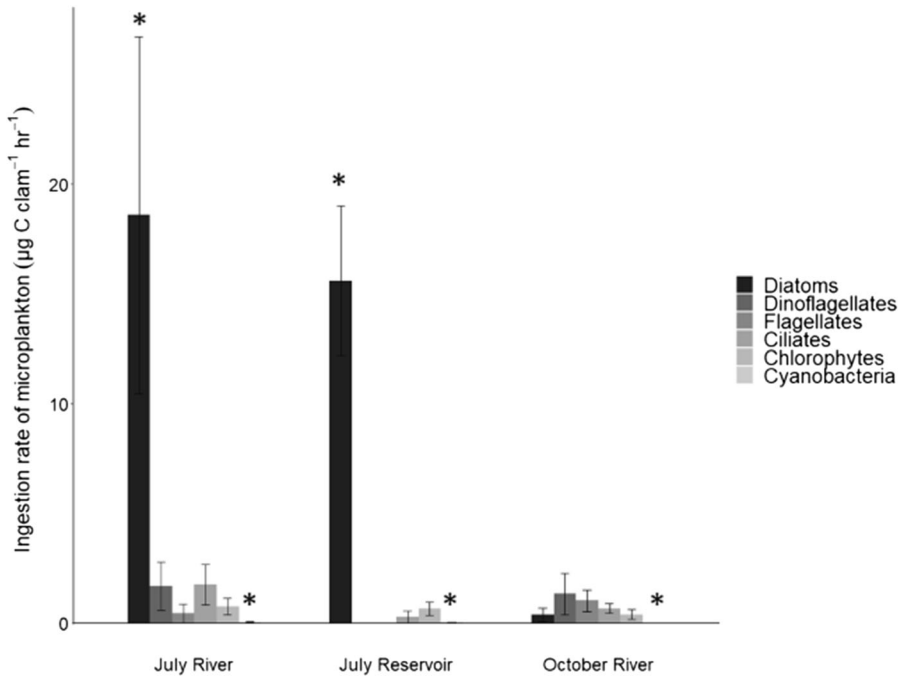

Fig. 7 Ingestion rates (µg C clam^{-1} h^{-1}; mean ± SE) of adult *C. fluminea* on microplankton taxa from feeding experiments conducted at two sites in the Columbia River during July and October 2016. Asterisks denote significant difference in ingestion rates within an experiment

in the reservoir water and strongly preferred them in river water.

Ingestion of microplankton taxa by Asian clams

While there were few differences in the preference of *C. fluminea* for microplankton taxa between our river and reservoir sites, the clams ultimately ingested diatoms at significantly higher rates than other taxa in our summer experiments at both sites. High consumption of diatoms is supported in the literature, as shown in both gut content analysis (Boltovskoy et al., 1995) and laboratory experiments (Hakenkamp et al., 2001). However, in our study, diatom consumption by clams declined substantially between summer and fall. In our study, differences in ingestion rates of diatoms by clams were likely due to the change in abundance between July and October and/or morphological differences between diatoms in these experiments. That is, in July, most diatoms were individual, unchained cells dominated by *Cyclotella* sp., whereas in October, most of these *Cyclotella* sp. cells were aggregated into long chains. As *C. fluminea* cannot effectively sort particles > 20 µm (Way et al., 1989), it is not surprising to see ingestion rates of diatoms decline when cells form long chains. Along with differences in size and morphology, microplankton taxa have a broad range of nutritional value. For example, cryptomonads contain higher amounts of organic nutrients (proteins, carbohydrates) than diatoms per unit cell volume (Moal et al., 1987). Similarly, in a study on lipid composition, cryptomonads were shown to have higher percentages of polyunsaturated fatty acid chains than chlorophytes and cyanobacteria (Ahlgren et al., 1990). While the role of microplankton nutritive value may be important to prey selection by *C. fluminea*, we were unable to assess this in our study.

Cyanobacterial taxa in our study formed large clusters of cells (*Aphanocapsa* sp., *Merismopedia* sp.) or long filaments (*Oscillatoria* spp.), and this morphology, in conjunction with their extremely low biomass, is one possible explanation for our extremely low ingestion rates of clams on cyanobacteria. This is similar to the inability of invasive zebra mussels (*D. polymorpha*) to consume colonial cyanobacteria (Bastviken et al., 1998; Vanderploeg et al., 2001). Alternatively, low consumption of cyanobacterial taxa by *C. fluminea* could be an aversion to potentially toxic strains. This aversion has been repeatedly observed in *D. polymorpha* (Vanderploeg et al., 2001; Dionisio Pires & Van Donk, 2002; Juhel et al., 2006), with mussels showing weaker aversion to non-toxic strains. Conversely, the veneroid clam *Corbicula*

leana (Prime, 1867)—suggested by Komaru et al. (2013) to be genetically indistinguishable from *Corbicula fluminea*—showed no difference in selection for toxic versus non-toxic *Microcystis* (Pham et al., 2015).

All other microplankton prey taxa in our study (dinoflagellates, flagellates, ciliates, and chlorophytes) were consistently consumed by clams at low to moderate rates. Similarly, Boltovskoy et al. (1995) undertook a study of *C. fluminea* gut contents in the Paraná River in Argentina and observed low consumption of non-diatom taxa (with the important caveat that diatoms are likely to persist longer in guts due to frustules). Hakenkamp et al. (2001) also showed no effect of filter-feeding by *C. fluminea* on ciliates and small flagellates, in agreement with our study, but showed a decline in abundance of large flagellates, which were rare in our samples.

Potential of Asian clam feeding to promote cyanobacterial blooms

Asian clams exhibited a significant avoidance of cyanobacteria when colonial taxa were present at our river site in October. As mentioned above, this is likely a result of the inability of *C. fluminea* to manipulate large prey items (e.g., colonial clusters of cells) when sorting particles across their gills, or possibly an aversion to cyanobacterial toxins. Similarly, *L. fortunei* has been shown to select for single-celled *Microcystis* while avoiding colonies in the Salto Grande Reservoir, Argentina, and concurrently promoting *Microcystis* growth (Boltovskoy et al., 2013). An avoidance of cyanobacteria by *D. polymorpha*, and consequent promotion of cyanobacterial blooms, has also been demonstrated in several observational and laboratory studies. In Great Lakes Huron and Erie, *D. polymorpha* initially filtered cyanobacteria from the water, but then ejected them as pseudofeces and resuspended viable cells into the water column, promoting an increase in the abundance of potentially harmful cyanobacteria, which were uncommon prior to the establishment of *D. polymorpha* (Vanderploeg et al., 2001). Similarly, in Oneida Lake, New York an increase in frequency of blooms of *Aphanizomenon* was noted following establishment of *D. polymorpha* (Horgan & Mills, 1997). Another study showed a concurrent increase in *Microcystis* biomass and microcystin toxin levels in freshwater lakes in southern Michigan associated with the presence of *D. polymorpha* (Knoll et al., 2008). In Lake Michigan, *D. bugensis* caused declines in phytoplankton taxa except for chlorophytes and cyanobacteria (Fahnenstiel et al., 2010) and in Lake Huron, *D. bugensis* has been shown to reject colonial cyanobacteria (Tang et al., 2014). While these studies occurred in lentic systems with little flow, a similar avoidance of cyanobacteria by *C. fluminea* in the lower Columbia River, as demonstrated in October in our river experiment, may significantly alter phytoplankton communities and lead to an increase in already frequent cyanobacterial blooms in other parts of this region (Jacoby & Kann, 2007; Lee et al., 2015a, b; Rose et al., 2019).

Previous studies in the Columbia River Basin have shown cyclopoid copepods to indirectly increase cyanobacterial bloom frequency or intensity through consumption of other microplankton (e.g., diatoms) that compete with cyanobacteria (Rollwagen-Bollens et al., 2013; Bowen et al., 2015; Rollwagen-Bollens et al., 2018), a trend documented in other systems as well (Olson et al., 2006; Urrutia-Cordero et al., 2015). Comparable to these copepod feeding impacts, selective avoidance of cyanobacteria by the Asian clam *C. fluminea* could potentially result in enhanced cyanobacterial growth and blooms. Such blooms can have broader, negative food web effects by reducing water quality, outcompeting beneficial phytoplankton taxa, and increasing mortality in higher trophic level predators (e.g., Moustaka-Gouni et al., 2006; Havens, 2008; Paerl & Otten, 2013). In addition to the effects of clam feeding on harmful cyanobacteria, it is possible that ingestion and selection by clams may have similar effects on other taxa (e.g., diatoms) that could ramify through the food web.

Conclusion

Adult *C. fluminea* in our study consumed diatoms, the dominant microplankton taxon in both abundance and biomass, at significantly higher rates than other microplankton taxa during summer. While clams in our study generally were only rarely selective in their feeding, we observed several instances of avoidance of certain microplankton taxa, most notably cyanobacteria. Rejection of filtered but unwanted organisms by bivalves can lead to resuspension of viable cells into

the water column, promoting population increases of these taxa relative to other prey taxa that are both filtered and consumed. The selective rejection of cyanobacteria by *C. fluminea* that we observed, when combined with likely future eutrophication and warming, may pose serious ecological consequences to the Columbia River Basin, and potentially other areas invaded by these clams, by increasing the frequency and intensity of harmful cyanobacteria blooms.

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