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**Research Article**

# Abundance and growth of the invasive Asian clam, *Corbicula fluminea*, in the lower Columbia River, USA

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## Abstract

The Asian clam, *Corbicula fluminea*, is a broadly distributed and abundant invasive species, yet many aspects of its biology are not well understood. Based on previous research by other investigators, we hypothesized that abundance, population growth rate, and individual growth rate of *C. fluminea* would increase with temperature, chlorophyll-*a*, and dissolved oxygen. We sampled *C. fluminea* at two sites in the lower Columbia River (CR), USA. Modal progression analyses indicated a life span of 2–3 years. A generalized linear mixed model (GLMM) predicting the abundance of *C. fluminea* indicated a significant negative association with chlorophyll-*a* concentration, whereas a GLMM predicting the population growth rate of *C. fluminea* indicated a significant positive association with dissolved oxygen. The GLMM predicting the individual growth rate of *C. fluminea* indicated the individual growth rate was not significantly related to any individual environmental variable. Overall, these results emphasize that the biology of *C. fluminea* in the CR is similar in many regards to other populations studied in temperate regions globally, but that important spatial differences can occur between sites separated by 60 km within the same river system.

**Key words:** invasive species, population biology, aquatic ecology, North America

## Introduction

The Asian clam, *Corbicula fluminea* (Müller, 1774), is a widespread and abundant invasive species in many mid-latitude regions of the world, including North America, South America and Europe (Karatayev et al. 2005; Sousa et al. 2008a; Lucy et al. 2012). Its reproductive strategies, growth, and tolerance of variable environmental conditions have allowed this species to become established and thrive in many freshwater environments (Sousa et al. 2008a). *Corbicula fluminea* poses threats to the ecosystems in which it invades. For instance, *C. fluminea* can deplete algal abundance in large water bodies, negatively impacting native species (Ilarri et al. 2014; Ferreira-Rodríguez et al. 2018). In the Meuse River in northwest Europe, the filter feeding of *C. fluminea* caused a 70% decrease in phytoplankton abundance, thereby impacting the entire food web (Pigneur et al. 2014). *Corbicula fluminea* invasions can also clog infrastructure at industrial facilities as a result of the mucus secreted during the juvenile stage (Foster et al. 2013).

The biology of *Corbicula fluminea* has been well studied in several parts of its invasive range. In the Lower Delta of the Paraná River, Argentina, length frequency analysis indicated a single reproductive period for *C. fluminea* between mid-summer and early fall, but with three different age cohorts present, suggesting a life span of 3 years (Cataldo and Boltovskoy 1998). Moreover, several environmental variables have been found to influence the population dynamics of *C. fluminea*. For example, it has been shown that temperature can affect individual growth rate (Cataldo and Boltovskoy 1998) as well as clam shell size and body mass (Denton et al. 2012; Rosa et al. 2012). Additionally, food availability has been implicated as an important factor in growth and reproductive capacity of *C. fluminea* in the lower Rhine River, Germany (Viergutz et al. 2012). Also, there were significant seasonal differences in population growth rate, being highest in summer compared to late fall in the Paraná River, Argentina, likely resulting from differences in temperature and food availability (Cataldo and Boltovskoy 1998). Additionally, dissolved oxygen levels have been positively correlated with individual growth of *C. fluminea* (Belanger 1991; Ilarri et al. 2011), whereas low pH was associated with decreased population growth and abundance (Ilarri et al. 2011). These associations between environmental variables and clam growth suggest the potential for significant spatial and temporal variations in the biology of *C. fluminea*.

Although it is clear that *C. fluminea* is a prolific and impactful invader, the body of research on *C. fluminea* in the Columbia River [CR], North America, in which it was first introduced in 1938 (Counts 1981), is very limited. Benthic surveys in the lower CR demonstrated densities of adult and juvenile *C. fluminea* up to 722 clams m$^{-2}$, with density negatively correlated with silt and clay and positively correlated with the percentage of volatile solids (McCabe et al. 1997). Moreover, the zooplankton community of the lower CR is dominated by newly released *C. fluminea* juveniles in late summer and early autumn (Dexter et al. 2015, 2020a, b). Planktonic *C. fluminea* juveniles were found to be associated with cyanobacteria and higher water temperatures in the CR (Hassett et al. 2017). Recent research on the feeding rate (Rollwagen-Bollens et al. 2021) and feeding selectivity (Bolam et al. 2019) of adult *C. fluminea* in the CR indicated selective ingestion of flagellates and avoidance of cyanobacteria. This previous research illustrates the high abundance and potential impacts of *C. fluminea*, yet very little is known about the basic biology (e.g., individual and population growth rates) of this invader in the CR.

The first objective of this study was to estimate the abundance and population growth rate of *C. fluminea* in the lower CR and how they vary seasonally, interannually and spatially. We hypothesized that the abundance and population growth rates of *C. fluminea* would be highest during the summer months, when *C. fluminea* reproduce and juveniles recruit to the population (Cataldo and Boltovskoy 1998; Dexter et al. 2015; Hassett et al.

2017). The second objective was to estimate the individual growth rate of *C. fluminea* in the CR and examine seasonal, interannual, and spatial variability. We hypothesized that individual growth rates would be greatest during summer months, when water is warmest and phytoplankton and microphytobenthic algae are abundant (Dauble et al. 1985; Denton et al. 2012; Viergutz et al. 2012; Rosa et al. 2012). Our third and final research objective was to explore whether chlorophyll-*a* [chl-*a*], temperature, dissolved oxygen [DO] and pH were associated with abundance, population growth rates, and individual growth rates of *C. fluminea* in the CR. We hypothesized that temperature and chl-*a* concentration would be positively correlated with abundance, population growth rate, and individual growth rate (Dauble et al. 1985; Denton et al. 2012; Viergutz et al. 2012), whereas DO, which can affect the amount of time *C. fluminea* actively feeds (Belanger 1991; Ilarri et al. 2011), and pH would be negatively correlated with the abundance, population growth rate, and individual growth rate of *C. fluminea* (Ringwood and Keppler 2002). This study is designed to provide new knowledge into the biology of *C. fluminea,* in a region where it has not prevously been studied, and that could be vital to managing this global invader.

## Materials and methods

### *Study species*

The juvenile stage of *C. fluminea* is characterized by a semi-buoyant mucoid secretion which allows juveniles to disperse quickly and far away from the parent clam (Foster et al. 2013). *Corbicula fluminea* are also hermaphroditic and capable of androgenesis, a rare asexual male reproductive strategy (Hedtke et al. 2008) which enables single male individuals to initiate reproduction in isolation and has been shown to lead to rapid reproduction and colonization of new substrate (Gomes et al. 2016). This is a dramatic advantage for *C. fluminea* over native clams and mussels in the CR that reproduce with glochidia (parasitic larvae) that require native fish species to act as vectors for dispersal (Thomas et al. 2010).

### *Study area*

The CR Basin drains an area of 669,300 km$^2$ spanning the northwestern United States and southwestern Canada. The CR flows 1,954 kms from its headwaters to the Pacific Ocean and acts as the boundary between the states of Washington and Oregon (Simenstad et al. 1990). The CR is a highly modified system with a substantial number of impoundments, which provides consistent hydropower and flood control for the region (Payne et al. 1995).

Field collections of *C. fluminea* were done at two locations in the CR: one at Blurock Landing, in Vancouver, Washington (45°39′57″N; 122°45′33″W) (hereafter referred to as “Blurock”) and the other at Kalama, Washington

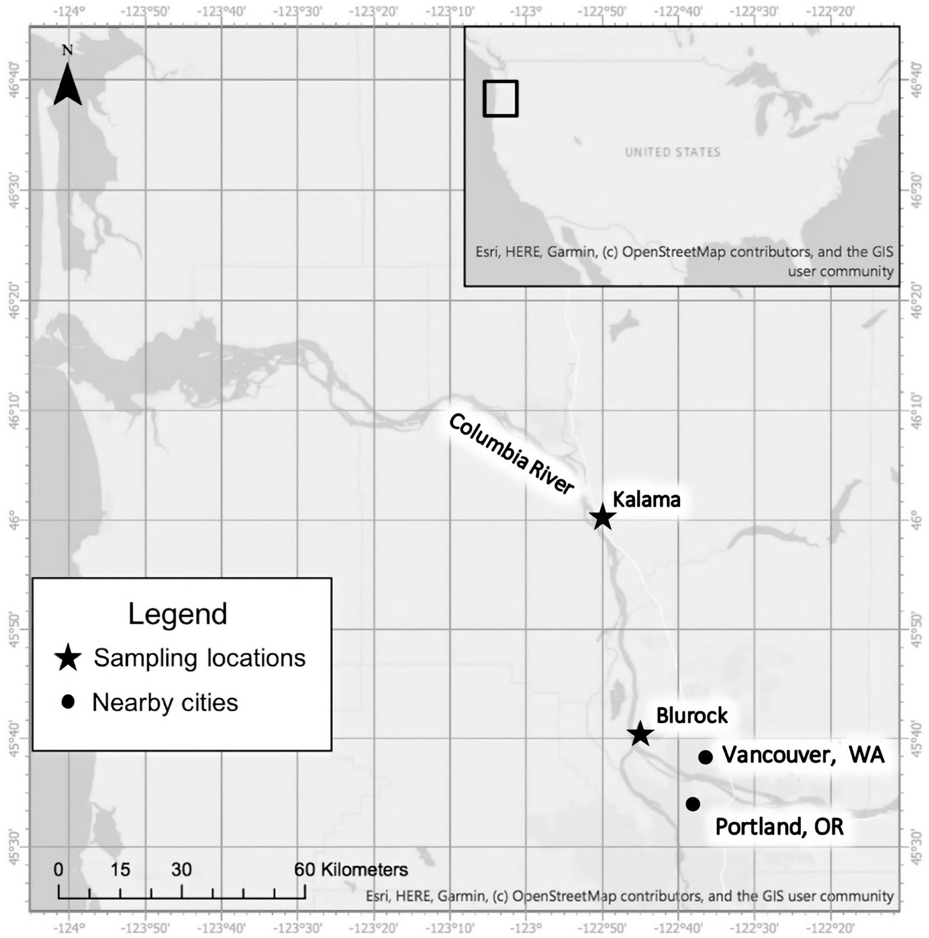

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**Figure 1.** Map of the study area. The two sampling sites (Blurock and Kalama) on the lower Columbia River are marked with stars. Nearby metropolitan areas of Vancouver, Washington (WA) and Portland, Oregon (OR) are marked with circles.

(46°3′7″N; 122°52′26″W) (hereafter referred to as “Kalama”) (Figure 1). Both sites are entirely freshwater, but have a tidal range of approximately 1.5 m, which varies seasonally. These two sampling sites were chosen because preliminary observations indicated that they both had accessible and abundant populations of *C. fluminea* (e.g., Bolam et al. 2019) and because they are separated by 60 km, and might therefore have different environmental conditions that could affect the growth and condition of *C. fluminea*. For instance, Kalama is a relatively undeveloped site just downriver of the confluence with the Kalama River, whereas Blurock is directly downriver from two metropolitan areas (Vancouver, Washington and Portland, Oregon) and receives more human foot traffic than Kalama. Blurock is immediately downriver of the confluence with the Willamette River, a historically polluted river that flows through Portland, Oregon and contains elevated levels of polychlorinated biphenyls (PCBs) (Sethajintanin et al. 2004). Moreover, Blurock is located next to a U.S. Environmental Protection Agency superfund site in Vancouver, WA associated with a previous aluminum smelter that contains soil contaminated with cyanide and fluoride (Johnson and Norton 1988). Kalama is located approximately

30 km downriver of the confluence with Lake River, which connects Vancouver Lake with the CR. Vancouver lake is a shallow eutrophic lake plagued by seasonal cyanobacterial blooms (Rollwagen-Bollens et al. 2013, 2018; Lee et al. 2015), in contrast to the CR further upstream, which only rarely experiences cyanobacteria blooms (Rose et al. 2021).

### *Sample collection and processing*

Field collections were undertaken at Kalama in 2017, 2018, and 2019 and at Blurock in 2018 and 2019, and occurred approximately every two weeks, beginning in early summer and ending in mid-fall each year (sampling during other seasons proved impossible because of high river flows and water depths). There were a few occasions during these periods when sampling was not possible because of flooding or beach closures. All field collections were undertaken around low tide. At each site, the "high tide" mark was located and then a 30.5 m transect was laid out parallel to the shoreline, comprised of 20 sections, each 1.53 m in length. During each bi-weekly sampling period, 1–3 transect sections were randomly selected for sampling. The same transect section was never sampled more than once and different transects were used each year. Once a transect section was selected, sampling occurred directly offshore of the section, in water depth of 30 cm, using a 1 m by 1 m quadrat. The GPS coordinates of the center of the quadrat were recorded. Measurements of temperature, pH and DO were taken at the center of the quadrat using a YSI ProPlus probe (YSI Incorporated). Before disturbing the sediments, 70 ml of river water was collected in a dark container and placed on ice for subsequent chlorophyll analysis back in the laboratory. All visible clams in the surface of the 1m by 1m quadrat were collected by hand, put into a pre-labeled container, and preserved with 70% buffered ethanol. Next, the surface 15 cm of sediments within the quadrat were rinsed through a 2 mm sieve to remove any remaining clams and the contents were transferred to the same pre-labeled container. This collection method was replicated for a second or third randomly generated quadrat, until a minimum of 100 clams were obtained at each site on each date. If at least 100 clams were obtained from the first quadrat, then no additional quadrats were sampled. A total of 7,980 clams were collected in this study, for an average of 163 clams per site per date.

Once in the laboratory at Washington State University Vancouver, water samples were vacuum filtered through GF/F filters and the filter papers were stored in a freezer. Chl-*a* concentrations were then determined using a Model 10-AU fluorometer (Turner Designs) following the acidification method (Strickland and Parsons 1972; Arar and Collins 1997). Within a week following each field collection, the shell length (SL) of each individual clam was measured with electronic calipers (Adoric Electronic Digital Caliper) to the nearest 0.01 mm.

### *Data manipulation and statistical analyses*

Differences in the measured environmental variables (chl-*a* concentration, temperature, DO, and pH) between Kalama and Blurock during 2018 and 2019 (the only years when both sites were sampled) were assessed in R using Welch's t-tests to accommodate unequal variances.

Population growth rate refers to the change in abundance over time. The average abundance of *C. fluminea*, measured here as density (# of individuals m$^{-2}$), for each sampling date and site was calculated using the R statistical software (R Core Team 2013). These data were then used to calculate realized rates of population growth (r) over time (t) using the exponential growth equation: $N_t = N_o e^{rt}$.

Individual growth rate refers to the change in size (SL, in this case) of an individual clam over time. Clam individual growth rates were calculated using modal progression analysis (e.g., Bollens et al. 1992; Sousa et al. 2008a; Colwell et al. 2017). This method involves tracking recognizable cohorts, identified using size frequency distributions, over time. Changes in the mean SLs for each cohort over time are inferred to be individual growth rates. To accomplish this, clams were first binned into 1 mm SL bins and the resulting data input into the Food and Agriculture Organizations of the United Nations Fisheries Stock Assessment tool (FiSAT II) (Gayanilo et al. 2005). Using FiSAT II, length-frequency data were separated into modal groups, or cohorts, and then for each respective modal group, a mean SL was determined (Bollens et al. 1992; Gayanilo et al. 2005). The mean SL of a given mode (or cohort) was then visually connected through time to determine a growth rate (change in SL per unit time) for each modal group (Bollens et al. 1992; Gayanilo et al. 2005).

Univariate linear regressions, with abundance, individual growth rate or population growth rate as the dependent variable, and each of the measured environmental variables (chl-*a* concentration, temperature, DO and pH) as a predictor variable, were performed in R using the package "car" (Fox and Weisberg 2019) and visualized using "ggplot2" (Wickham 2016).

Generalized linear mixed modeling (GLMM), using the R package "car" (Fox and Weisberg 2019), was undertaken to investigate the relationship between abundance, population growth rate, or individual growth rate (dependent variables) and potential predictor variables (chl-*a* concentration, temperature, DO, pH, year, location, and cohort). This is similar to methods used in recent studies of bivalve populations (Basen et al. 2011; Hold et al. 2013; Meseck et al. 2018). The continuous predictor variables (chl-*a* concentration, temperature, DO, pH, and cohort) were standardized to a mean of 0 and standard deviation 1 to calculate standardized effect sizes. This allows for the comparison of the magnitudes of the coefficients (Schielzeth 2010). Mixed effects were included with year and location (Kalama or Blurock) to evaluate the importance of interannual and spatial variation. The link function for each GLMM was chosen by comparing the

AIC values for the global model with each of the possible link functions (log, identity, power). To allow the use of the log link function, which cannot handle negative numbers, the value of one was added to the population growth rate and individual growth rate values before analysis. Before undergoing model selection, the "vif()" function in the R package "car" (Fox and Weisberg 2019) was used to calculate the variance inflation factor (VIF) to assess collinearity. Variables that returned VIF values greater than 5 were considered collinear, in which case one collinear variable was removed from the model until all VIF values were less than 5. The preferred (best) model was selected using the "StepAIC" function in the "MASS" package in R (Venables and Ripley 2002). This is a stepwise function that systematically removes the least significant variables until the model with the best explanatory power is achieved. StepAIC selects for the combination of the fewest explanatory variables with the best explanatory power. Pseudo R-squared values were calculated by subtracting the ratio of the residual deviance to the null deviance from 1, and then used to assess the amount of variation explained by the GLMMs. The best GLMMs describing abundance, population growth rate, and individual growth rate included the log link. For all GLMMs, the VIF values were less than 5 for all variables, and therefore there was no collinearity.

## Results

### *Environmental conditions*

Temperature peaked in late summer of each year at each site but showed greater interannual variation at Kalama (Figure 2A, B), and was higher overall at Blurock than Kalama (Welch's t-test: $t = 2.06$, $df = 106$, $p = 0.042$). Chl-*a* concentration at Kalama showed one or two peaks during summer or early fall in 2017 and 2018, but was lower and less variable in 2019 (Figure 2C). Chl-*a* concentrations at Blurock showed a decreasing trend throughout the sampling period in 2018 and 2019, with only a minor peak in late summer of 2018 (Figure 2D). Chl-*a* concentration over the study period was higher at Kalama than Blurock (Welch's t-test: $t = -5.20$, $df = 114$, $p = 1.73e^{-6}$). DO at Kalama was highest in early summer, oscillated around 9 mg/L, and then increased during fall of all years (Figure 2E). DO at Blurock generally decreased through summer, until September or October, and then increased or plateaued for the remainder of fall (Figure 2F). Overall, DO was higher at Blurock than Kalama (Welch's t-test: $t = 2.95$, $df = 79$, $p = 0.004$). The pH at Kalama had a peak in late summer and then increased steadily, with secondary peaks in late fall (Figure 2G). The pH at Blurock gradually increased throughout the sampling period in 2018, with a peak in mid-October, whereas pH peaked in late July and mid-October in 2019 (Figure 2H). Overall, pH was not significantly different between sites.

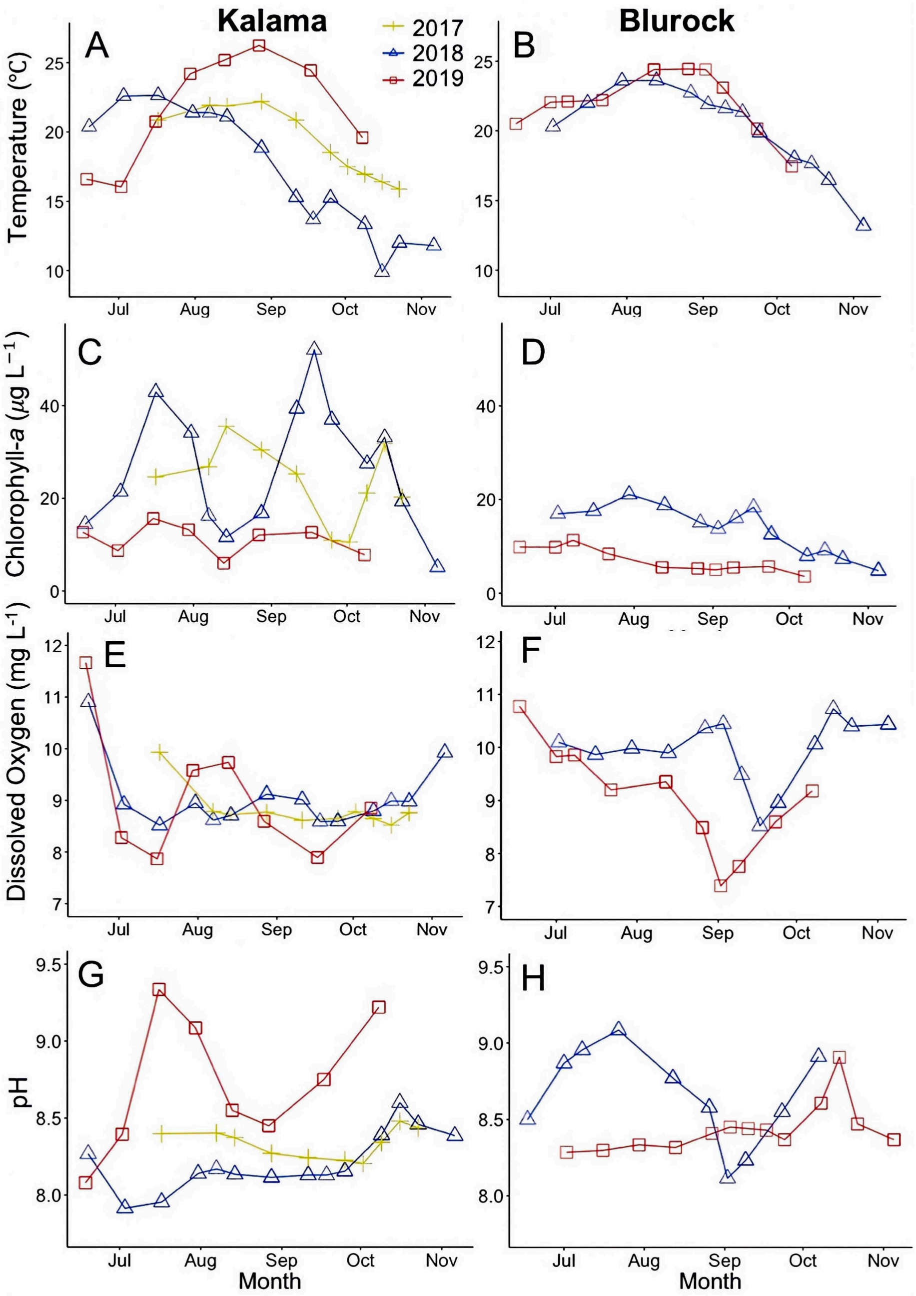

**Figure 2.** Temperature (A, B), chlorophyll-*a* (C, D), dissolved oxygen (E, F), and pH (G, H) at Kalama in 2017 (yellow), 2018 (blue) and 2019 (red), and at Blurock in 2018 (blue) and 2019 (red). This color scheme applies to other captions.

### *Abundance and population growth rates*

The abundance of *C. fluminea* at Kalama ranged from 16.5–500 clams m$^{-2}$, but varied considerably both seasonally and interannually (Figure 3A). Peak abundances in 2017, 2018, and 2019 were 174 clams m$^{-2}$, 500 clams m$^{-2}$, and 299 clams m$^{-2}$, respectively. Seasonally, abundance at Kalama showed either one or two peaks each year. In 2017, the first abundance peak occurred in late summer, with another faint peak occurring in early fall. In 2018 there were two well-defined peaks in abundance, with the first occurring in early summer and the second in early fall. In 2019 there was an early summer peak in abundance, but not a clear secondary peak in fall. Population growth

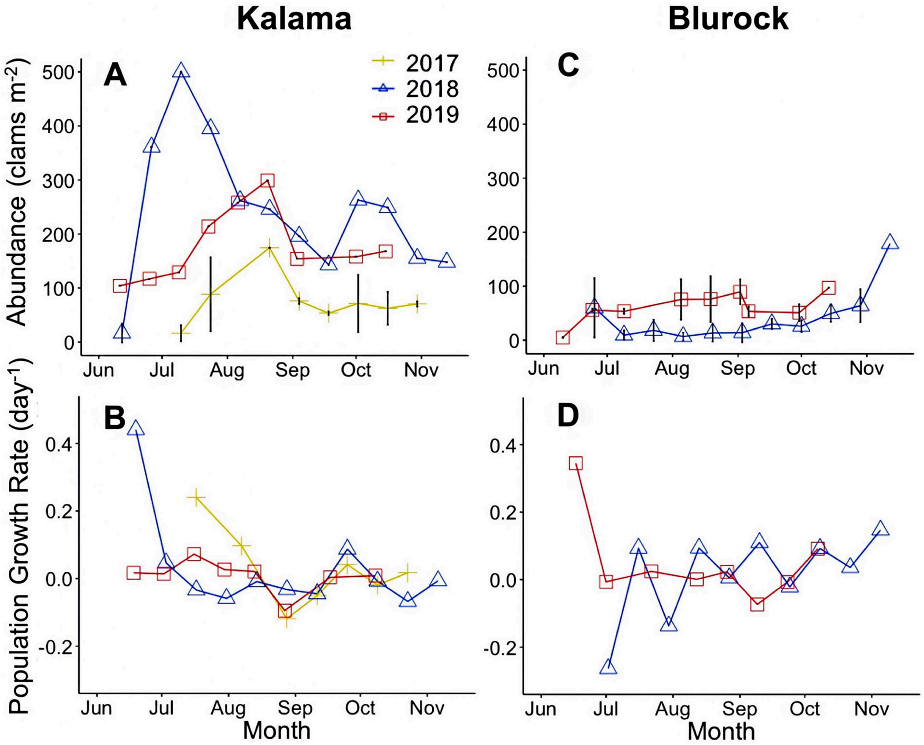

**Figure 3.** Abundance (A, C) and population growth rate (B, D) at Kalama in 2017, 2018, and 2019, and at Blurock in 2018 and 2019. Error bars for abundance estimates are included for dates on which multiple samples were collected.

rates at Kalama were consistently low, ranging from −0.119 to 0.097 day$^{-1}$, except for a notable peak in early summer of 2017 (0.240 day$^{-1}$) and 2018 (0.441 day$^{-1}$) (Figure 3B).

At Blurock, the abundance of *C. fluminea* ranged from 5.00–174 clams m$^{-2}$, and did not vary much seasonally (except for the clear recruitment peak in late fall of 2018), but did vary interannually, with overall abundances being greater in 2019 than in 2018 (Figure 3C). However, peak abundances at Blurock were 174 clams m$^{-2}$ in 2018 and 97 clams m$^{-2}$ in 2019. Abundances at Blurock were lowest in early August 2018 (7.00 clams m$^{-2}$) and early June 2019 (5.00 clams$^{-2}$). Overall, abundance was higher at Kalama than Blurock (Welch's t-test: $t = 13.71$, $df = 98$, $p = 2.20e^{-16}$). Population growth rates at Blurock were variable but generally low (e.g., −0.136 day$^{-1}$ to 0.146 day$^{-1}$) except for the very low value of −0.263 day$^{-1}$ in early summer of 2018 and the very high value 0.345 day$^{-1}$ in early summer of 2019 (Figure 3D). Overall, the population growth rates of *C. fluminea* were not significantly different between sites.

Univariate linear regressions of abundance and individual environmental variables at Kalama indicated that temperature was the only variable significantly related to abundance ($t = 2.49$, $df = 73$, $p = 0.015$) (Supplementary material Figure S1). At Blurock, univariate linear regressions indicated that chl-*a* and temperature were the only variables significantly related to abundance ($t = -10.16$, $df = 43$, $p = 5.25e^{-13}$ and $t = -2.82$, $df = 43$, $p = 0.007$, respectively) (Figure S1).

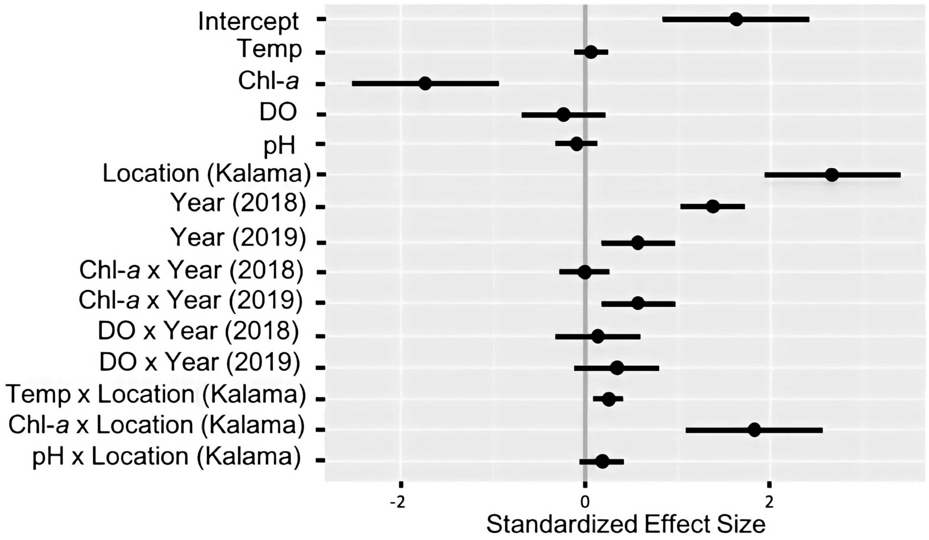

**Figure 4.** Mean and 95% confidence intervals for the coefficients for each environmental variable (and their interactions) resulting from the GLMM describing the abundance of *C. fluminea*. All variables not shown were not retained in the best model. An "x" indicates an interaction effect between variables.

The best GLMM to describe the abundance of *C. fluminea* indicated that abundance was negatively correlated with chl-*a* concentration (t = −4.44, df = 104, p = $2.21e^{-5}$) and varied with location (t = 7.35, df = 104, p = $4.56e^{-11}$) (Figure 4). There was significant interannual variation with abundance being higher in 2018 (t = 8.029, df = 104, p = $1.51e^{-12}$) and 2019 (t = 2.87, df = 104, p = 0.005) when compared with 2017. Although temperature, pH, and DO were not significant predictors of abundance, the best model (pseudo $R^2$ = 0.912) included these variables as parameters (Figure 4). The relationships between the abundance of *C. fluminea* and chl-*a* and DO varied with year and were included as mixed effects in the model. The relationship between abundance of *C. fluminea* and temperature and chl-*a* varied with location and were included as mixed effects (t = 3.11, df = 104, p = 0.002 and t = 4.985, df=104, p = $2.45e^{-6}$, respectively). The relationship between the abundance of *C. fluminea* and pH also varied with location, although not significantly, and was included as a mixed effect. The most important predictors of the abundance of *C. fluminea*, as indicated by standardized effect size, were location, chl-*a*, and the interaction between location and chl-*a* (Figure 4).

Univariate linear regressions of population growth rate and individual environmental variables at Kalama indicated that chl-*a* was the only variable related to population growth rate (t = 2.33, df = 65, p = 0.023) (Figure S2). At Blurock, univariate linear regression indicated that temperature and DO were related to population growth rate (t = −2.97, df = 37, p = 0.005 and t = 2.87, df = 37, p = 0.006, respectively) (Figure S2).

The best GLMM to describe the population growth rate of *C. fluminea* indicated that population growth rate was positively correlated with DO (t = 2.92, df = 88, p = 0.004) and location (t = −2.49, df = 88, p = 0.015)

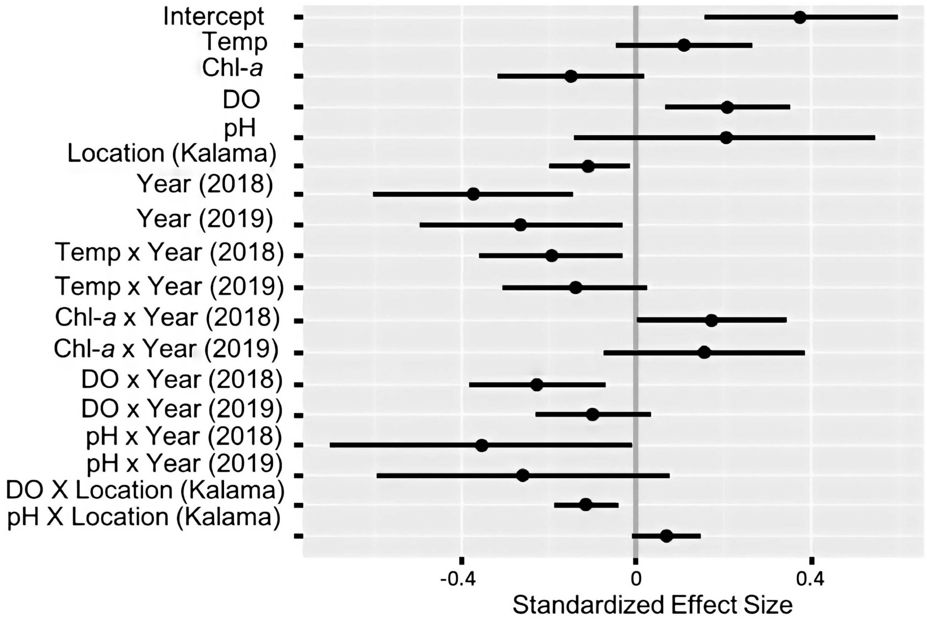

**Figure 5.** Mean and 95% confidence intervals for the coefficients for each environmental variable (and their interactions) resulting from the GLMM describing the population growth rate of *C. fluminea*. All variables not shown were not retained in the best model. An “x” indicates an interaction effect between variables.

(Figure 5). There was significant interannual variation, with population growth rate being lower in 2018 (t = −3.32, df = 88, p = 0.001) and 2019 (t = −2.30, df = 88, p = 0.024) when compared with 2017. Although temperature, chl-*a*, and pH were not significant predictors of population growth rate, the best model (pseudo $R^2 = 0.346$) included these variables as parameters (Figure 5). The relationships between the population growth rate and the measured environmental variables varied with year, with the relationship being different in 2018 for temperature (t = −2.42, df = 88, p = 0.018), chl-*a* (t = 2.02, df = 88, p = 0.046), DO (t = −2.97, df = 88, p = 0.004) and pH (t = −2.05, df = 88, p = 0.043). Similarly, the relationship between abundance of *C. fluminea* and DO varied with location (t = −3.25, df = 88, p = 0.002) and was included as a mixed effect in the model. The relationship between the population growth rate of *C. fluminea* and pH also varied with location, although not significantly, and was included as a mixed effect. The most important predictors of the population growth rate of *C. fluminea*, as indicated by standardized effect size, were year, DO, pH, and the interaction between pH and year, and between DO and year (Figure 5).

### *Cohort analysis and individual growth rates*

Modal progression analysis of length-frequency data from Kalama revealed five statistically distinct cohorts in 2017 and four cohorts each in 2018 and 2019 (Figure 6). However, in 2017 the two youngest cohorts both appeared during the sampling period and therefore it is likely that both cohorts represent young-of-the-year recruits. Clams corresponding to new recruits at Kalama ranged in SL from 3–11 mm. The second cohort in 2018 and 2019

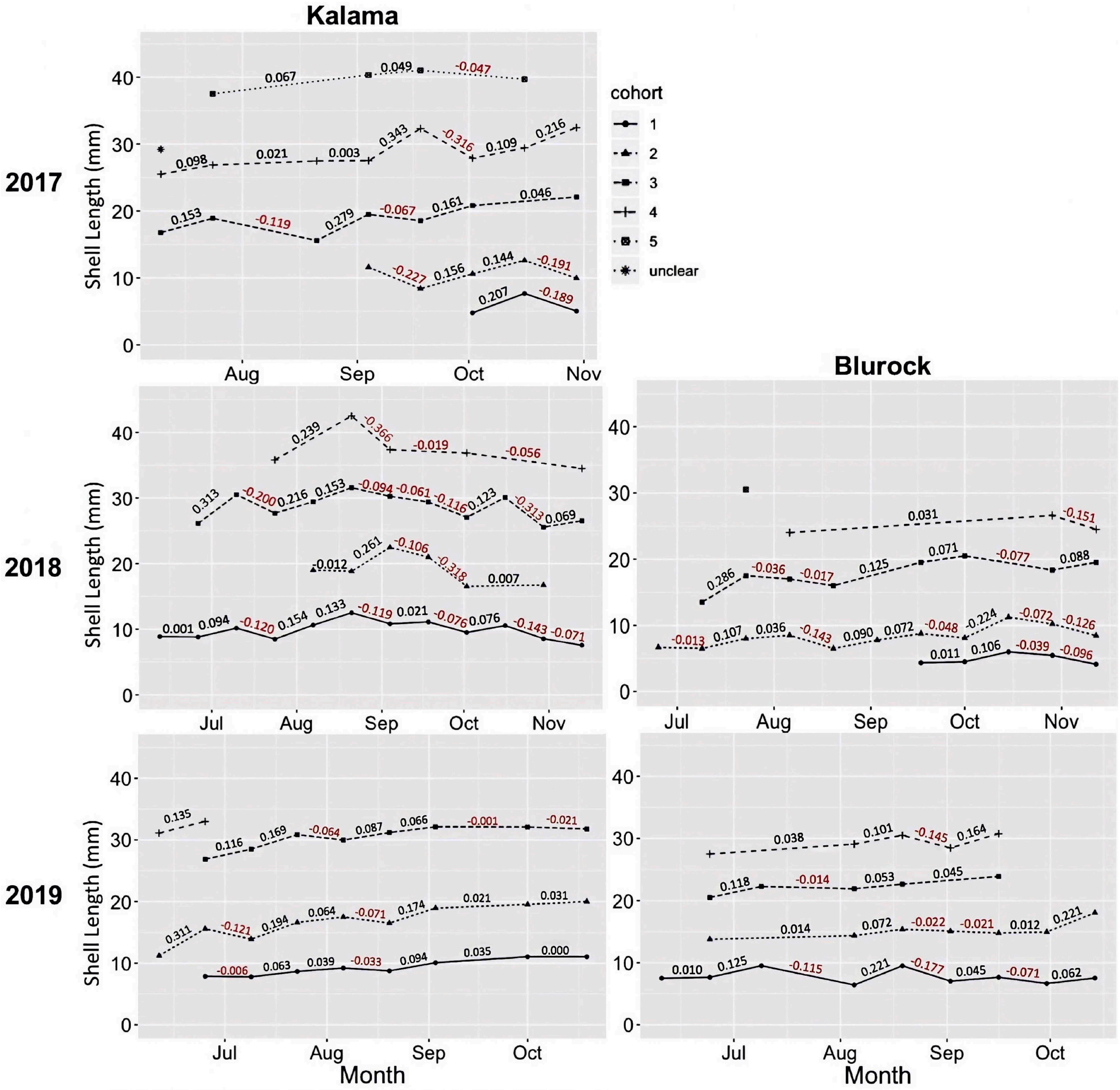

**Figure 6.** Individual growth rates from modal progression analysis with FiSAT software for Kalama in 2017, 2018 and 2019 and Blurock in 2018 and 2019. Each point represents the mean shell length of a cohort and the individual growth rate is calculated as the change in the mean shell length of that cohort between two consecutive sampling periods. A cohort is expressed as a line connecting a series of points over time. Positive slopes indicate positive individual growth rates, in mm day$^{-1}$ (numbers in black), and negative slopes indicate negative individual growth rates (numbers in red). The cohorts are labeled one to five, with one representing the youngest cohort of new recruits and five representing the oldest cohort.

and the third cohort in 2017 corresponded to one-year old clams and ranged in size between 10–20 mm. Two-year old clams in cohort three in 2018 and 2019 and cohort four in 2017 ranged in size from 20–30 mm. The oldest cohort of clams at Kalama, ranging in size from 28–40 mm, was represented by the fourth cohort in 2018 and 2019 and the fifth cohort in 2017, and had an approximate age of four years (these clams were not abundant and were not collected every sampling period).

At Blurock, modal progression analysis of length-frequency data revealed five distinct cohorts in 2018 and four cohorts in 2019 (Figure 6). The two

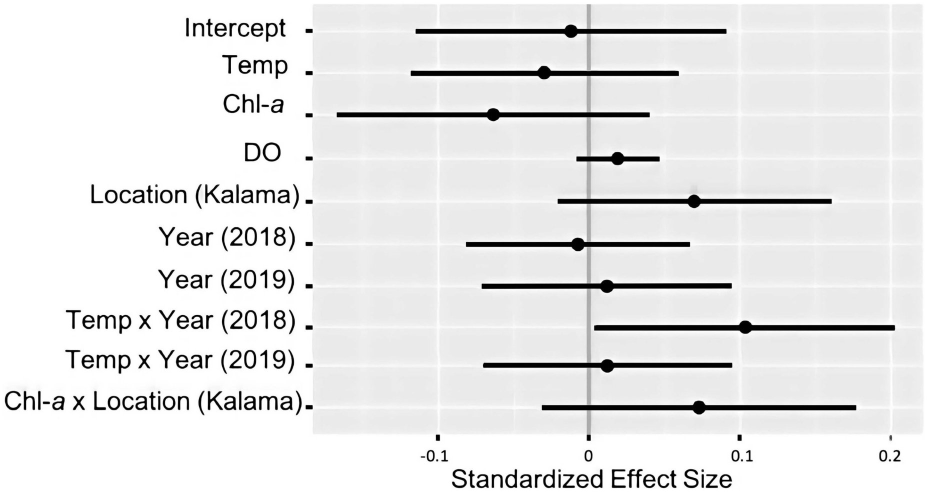

**Figure 7.** Mean and 95% confidence intervals for the coefficients for each environmental variable (and their interactions) resulting from the GLMM describing the individual growth rate of *C. fluminea*. All variables not shown were not retained in the best model. An "x" indicates an interaction effect between variables.

youngest cohorts in 2018 were new recruits of < 10 mm. The third cohort in 2018 and the second cohort in 2019 likely correspond to one-year old clams that ranged in SL from 10–22 mm. The two-year old clams in cohort three in 2019 and cohort four in 2017 ranged in SL from 20–28 mm. The oldest cohort of clams at Blurock, with an approximate age of three years and a SL of 25–32 mm, was represented by the fourth cohort in 2019 and was only observed once in late July 2018.

Individual growth rates of *C. fluminea* were not significantly different between sites. At Kalama, individual growth rate of *C. fluminea* ranged from −0.366 mm day$^{-1}$ to 0.343 mm day$^{-1}$, with an overall mean of 0.040 mm day$^{-1}$. At Blurock, individual growth rate of *C. fluminea* ranged from −0.177 mm day$^{-1}$ to 0.286 mm day$^{-1}$, with an overall mean of 0.030 mm day$^{-1}$. The overall mean individual growth rate of *C. fluminea* in this study was 0.035 mm day$^{-1}$.

Analysis of the univariate relationships between the individual growth rate of *C. fluminea* and individual environmental variables at Kalama indicated that temperature was the only variable related to individual growth rate ($t = 2.027$, $df = 118$, $p = 0.046$) (Figure S3). At Blurock, none of the individual environmental variables were significantly related to individual growth rate (Figure S3).

The best GLMM used to describe the individual growth rate of *C. fluminea* indicated that it did not vary significantly with any environmental variable (Figure 7). Although temperature, chl-*a*, and DO were not significant predictors of individual growth rate, the best model included these variables as parameters (Figure 7). The relationship between the individual growth rate of *C. fluminea* and temperature varied with year, with the interaction effect being significant for 2018 ($t = 2.095$, $df = 110$, $p = 0.038$), and was included as a mixed effect in the model. The standardized effect size of the GLMM coefficients indicated that the interaction between temperature and year is the most important predictor of individual growth rate (Figure 7). However, this best fit model explained very little of the variance in individual growth rate of *C. fluminea* (pseudo $R^2 = 0.138$).

## Discussion

### *Abundance and population growth rates*

The seasonal patterns in the abundance of *C. fluminea* were different at Kalama and Blurock. As we predicted, abundance at Kalama was highest during the summer in all years, when temperature and food (chl-*a*) were highest. This pattern of seasonal abundance is typical of many populations of *C. fluminea* in Asia, Europe, and North America (Morton 1977; Aldridge and McMahon 1978; Hornbach 1992; Mouthon 2001). For example, in the Saone River at Lyon, France, *C. fluminea* exhibited one reproductive period spanning summer and fall, with two distinguishable peaks in abundance, corresponding to peaks in recruitment (Mouthon 2001).

At Blurock, in contrast, the pattern in the seasonal abundance of *C. fluminea*—with peaks in November and early October—is atypical for populations in North America, Europe, and Asia (Morton 1977; Aldridge and McMahon 1978; Hornbach 1992; Mouthon 2001). However, it is important to note that preliminary sampling in 2016 at Blurock (data not shown) suggested a large die-off event preceding our 2017 sampling, which could explain the difference between our observations at Blurock in 2018 and 2019 and those observed by other investigators elsewhere. Overall, chl-*a* concentrations were significantly lower and temperatures were significantly higher at Blurock than at Kalama. Thus, potential food limitation during the summer months, when metabolism is increased in response to warmer temperatures, could account for the lower recruitment and abundance of *C. fluminea* that we observed at Blurock. However, it is also possible that there were one or more unaccounted variables limiting the abundance of *C. fluminea* during the summer months at Blurock. For example, seasonal variation in predation on *C. fluminea,* while not evaluated in our study, could account for the low abundance in summer at Blurock. Sturgeon have been shown to feed on *C. fluminea* in the CR, with increased feeding activity in spring and summer compared to fall (McCabe et al. 1993).

While we present both univariate and GLMM results, our discussion focuses on the GLMM analyses as they provide a more comprehensive and ecologically relevant interpretation of our data. GLMM analysis indicated that DO was a significant predictor of population growth of *C. fluminea*, as we hypothesized and has been observed by others (Belanger 1991; Ilarri et al. 2011). However, abundance and population growth rates were not significantly related to temperature or pH, contrary to our hypotheses and to the findings of others (Cataldo and Boltovskoy 1998; Denton et al. 2012).

It is possible that pH did not have a significant impact on abundance or population growth rate because the pH never fell below 8 at either site. *Corbicula fluminea* has been shown to tolerate pH as low as 6.5 with adequate calcium levels (Sousa et al. 2008b). Although temperature was not a significant predictor of either abundance or population growth rate, temperature was retained as a parameter in both of the best models, and the coefficients were both positive, consistent with the positive relationship we hypothesized and which has been observed elsewhere. For instance, Denton et al. (2012) reported an increase in reproductive activity of *C. fluminea* at warmer temperatures. Moreover, we observed abundance to be significantly *negatively* related to chl-*a* concentration, also contrary to our hypotheses, although this relationship varied significantly with location. This negative relationship with chl-*a* and interaction with location were also among the most important predictors of *C. fluminea* abundance. It is possible that *C. fluminea* at one or both of our two sites were relying on non-phytoplankton sources of food, such as benthic microbes, and therefore not showing the anticipated relationship with chl-*a* concentration. *Corbicula fluminea* can pedal feed (bioturbate sediments and feed on benthic microbes) as well as suspension feed and has been shown to consume benthic flagellates, bacteria, and diatoms, even in the presence of abundant prey in the water column (Hakenkamp et al. 2001). In addition, some of the unexplained variation in our data is likely due to the fact that abundance and growth of *C. fluminea* are the result of environmental conditions not at any given point in time (as we have modeled them here), but rather, as the result of environmental conditions integrated over the preceding weeks or even months (a modeling exercise that was beyond the scope of the current study). It is also possible that a range of life history traits (e.g., dispersal patterns, mortality rates, age and size at maturity, etc.) may be responsible for the different patterns in abundance and population growth rate that we observed.

### *Cohort analysis and individual growth rates*

New young-of-the-year recruits of *C. fluminea* at both Kalama and Blurock were less than 15 mm in SL and one-year old clams ranged in size from 13–25 mm, which is comparable to other studies (Hornbach 1992; Stites et al. 1995; Cataldo and Boltovskoy 1998; Denton et al. 2012). We found two-year old clams ranged from 20–33 mm in SL and three-year old clams ranged from 30–43 mm in SL. However, it can be problematic to equate cohorts with ages in *C. fluminea,* as is commonly done with other bivalves, because multiple cohorts can appear over a single reproductive period (Cataldo and Boltovstoy 1998; Li et al. 2017). Indeed, we observed two distinct cohorts of new recruits occurring at Kalama in 2017, as well as at Blurock in 2018. Nevertheless, our results suggest a life span of approximately

2–3 years for *C. fluminea*, as has previously been observed for populations in North and South America (Hornbach 1992; Cataldo and Boltovskoy 1998).

The average individual growth rate of *C. fluminea* in this study was 0.035 mm day$^{-1}$, which is similar to previous studies (Cataldo and Boltovskoy 1998; Sousa et al. 2008a; Vohmann et al. 2010). For example, Vohmann et al. (2010) reported individual growth rates ranging from 0.007 to 0.115 mm day$^{-1}$, depending on food concentration. Although temperature was included in our best GLMM predicting individual growth rate of *C. fluminea* at Kalama and Blurock, none of the measured environmental variables were significant predictors. Overall, individual growth rate was negatively associated with temperature and chl-*a* (although not significantly so). This is contrary to our hypotheses and the findings of previous studies (Dauble et al. 1985; Foe and Knight 1986; Crespo et al. 2015). However, the interaction effect between temperature and year was significant and the most important predictor of individual growth rate, indicating that interannual variation is important. While temperature, chl-*a*, and DO were included in the best explanatory GLMM, these and other variables explained little of the variation in individual growth rate (pseudo $R^2 = 0.138$). Therefore, we are likely missing one or more factors important to predicting the individual growth rate of *C. fluminea* at our sites. For example, alternate sources of food, such as benthic algae, were not measured by us. Similarly, calcium is a necessary element of bivalve shell formation and has been indicated as an important predictor of *C. fluminea* production (Zhao et al. 2017), but was not measured by us. Also, several studies have found that sediment characteristics are an important indicator of bivalve growth, with individual growth generally highest in sandy sediment and lower in gravel and clay sediments (Grizzle and Lutz 1989; Grizzle and Morin 1989; de la Huz et al. 2002). This is thought to occur because fine sediment can easily be suspended in the water column and limit the filter feeding efficiency of benthic suspension feeders, while coarse sediment can inhibit burrowing activity (de la Huz et al. 2002).

Additionally, food quality is another potentially important predictor of individual growth rate that we did not evaluate. Food quality generally, and lipid content specifically, can affect the somatic growth rate of *C. fluminea* (Basen et al. 2011). More specifically, growth rates of *C. fluminea* were highly correlated with sterol and fatty acid content, as well as elemental nutrient levels (C:P and C:N) of the food source (Basen et al. 2011). Similarly, the presence of toxic cyanobacteria may limit the filter feeding activity and individual growth of *C. fluminea* (Foe and Knight 1986; Basen et al. 2011). Overall, somatic growth rates of *C. fluminea* have been shown to be higher in the presence of abundant eukaryotic algae and reduced in the presence of cyanobacteria (Foe and Knight 1986; Basen et al. 2011). It is likely that measuring and including dissolved calcium, benthic algal abundance, sediment characteristics and food quality in future predictive models would help account for the variation in individual growth rate of *C. fluminea*.

With respect to modal progression analysis, we offer a caution – while a valuable tool for studying the biology of a species, it is not without its limitations. For example, modal progression analysis can result in negative individual growth rates such as those occasionally observed in this study. Negative growth rates can occur as a result of size selective predation, e.g., by predators preferentially selecting larger prey and thus shifting the size distribution of the remaining prey to smaller individuals over time. In the CR, large sturgeon feed on *C. fluminea* and commonly select for larger benthic prey items (McCabe et al. 1993). Similarly, crabs, birds, and other fish have been shown to exhibit size-selective predation on bivalves (Schneider 1981; Macchiusi and Baker 1991; Torres et al. 2012) and are all potential predators of *C. fluminea* in the CR. Another process that could yield negative individual growth rates as determined by modal progression analysis is continuous recruitment of newly settled, small clams throughout the summer and fall, which would decrease the mean SL of the (apparent) cohort. Thus, the individual growth rates derived from our modal progression analysis, especially the negative rates, should be interpreted with caution.

There is another possible explanation for why the GLMMs predicting population growth rate and individual growth rate of *C. fluminea* explained substantially less variance (pseudo $R^2 = 0.346$ and 0.138, respectively) than the GLMM predicting abundance (pseudo $R^2 = 0.912$). This could be due, in part, to population growth rate and individual growth rate being calculated metrics, which therefore contain more error, whereas abundance is a direct observation, and necessarily contains less error.

### *Summary and conclusions*

We observed marked differences in the biology of *C. fluminea* at our two sites in the lower CR (Kalama and Blurock), as well as some differences between seasons and years. At Kalama, abundance followed the pattern previously observed in North and South America and which we hypothesized for the CR: highest abundance in the summer, with a secondary peak in fall. At Blurock, however, abundance was lower during the summer and peaked in the fall. Modal progression analyses indicated a life span of 2–3 years for *C. fluminea* at both sites in the lower CR, with new young-of-the-year recruits (< 15 mm), one-year old (13–25 mm), two-year old (20–33 mm), and three-year old (30–43 mm) clams present. The GLMM model predicting the abundance of *C. fluminea* indicated a significant negative association with chl-*a* concentration, whereas the GLMM predicting the population growth rate of *C. fluminea* indicated a significant positive association with DO. The GLMM predicting the individual growth rate of *C. fluminea* was not significantly related to any individual environmental variable; however, the interaction between temperature and year was significant. Finally, other environmental variables not measured by us, such as dissolved calcium, benthic algae, sediment characteristics and food quality, should be included in future studies of abundance and growth of *C. fluminea*. This study provides new knowledge on the biology of *C. fluminea,* in a region where it is abundant but poorly studied, and which may prove valuable for managing or preventing the spread of *C. fluminea* in similar environments. Overall, this study emphasizes that the biology of *C. fluminea* in the lower CR is similar in many regards to other populations studied in temperate regions of North America, South America and Europe, but that important spatial differences in biology can occur between sites separated by 60 km within the same river system.

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## Authors' contributions

SH: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, writing – original draft, writing – review and editing. SB: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, ethics approval, funding provision, writing – original draft, writing – review and editing.

## Ethics and permits

We, the authors, have complied with the institutional and/or national policies governing the humane and ethical treatment of the experimental subjects (however, all research pertaining to this article concerned invertebrates and did not require any research permit(s)). We are willing to share the original data and materials if so requested.

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**Supplementary material**

The following supplementary material is available for this article:

**Figure S1.** Relationship between the abundance (clams m$^{-2}$) of *Corbicula fluminea* and chlorophyll-*a* concentration, temperature, dissolved oxygen and pH.

**Figure S2.** Relationship between the population growth rate (day$^{-1}$) of *Corbicula fluminea* and chlorophyll-*a* concentration, temperature, dissolved oxygen and pH.

**Figure S3.** Relationship between the individual growth rate (mm day$^{-1}$) of *Corbicula fluminea* and chlorophyll-*a* concentration, temperature, dissolved oxygen and pH.

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http://www.reabic.net/aquaticinvasions/2022/Supplements/AI_2022_Henricksen_Bollens_SupplementaryMaterial.pdf