

Salvador Robb-Chavez ORCID iD: 0000-0003-2735-8240

Broadscale distribution, abundance and habitat associations of the invasive Asian clam
(*Corbicula fluminea*) in the lower Columbia River, USA

Salvador B. Robb-Chavez¹ (Corresponding Author, sbchavez@wsu.edu)

Stephen M. Bollens^{1, 2} (sbollens@wsu.edu)

Gretchen Rollwagen-Bollens¹ (rollboll@wsu.edu)

Timothy D. Counihan³ (tcounihan@usgs.gov)

¹School of the Environment, Washington State University, 14204 NE Salmon Creek Ave,
Vancouver, WA 98686, USA

²School of Biological Sciences, Washington State University, 14204 NE Salmon Creek
Ave, Vancouver, WA 98686, USA

³U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research
Laboratory, 5501A Cook-Underwood Road, Cook, WA 98605, USA

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ABSTRACT

The Asian clam, *Corbicula fluminea*, is an invasive freshwater bivalve that has established populations across the globe and is known to have deleterious effects on natural and human systems. Yet, despite being present in the Columbia River (CR) for nearly a century, little is known about this invader's basic biology and ecology in this large river system. Thus, we undertook a field study to assess its i) broadscale distribution and abundance, and ii) associations with habitat characteristics in the lower CR. During 2019-20, *C. fluminea* were collected from 27 shore-based stations spanning 481 river kilometers of the lower CR, along with several habitat characteristics (bank slope, temperature, dissolved oxygen, pH, salinity, conductivity, chlorophyll-*a* concentration, and sediment composition and % organic matter). *C. fluminea* abundance ranged from 0-430 ind. m⁻². Most sites with abundances >100 ind. m⁻² were located downstream of Bonneville Dam, while most sites with abundances < 100 ind. m⁻² were located upstream. Generalized linear models predicting the abundance of *C. fluminea* indicated significantly positive correlations with water temperature and % sand, and negative correlations with bank slope and sedimentary % organic matter. We also reviewed the global literature on abundance and habitat associations of *C. fluminea* and compared this with our own results. Our investigation represents the greatest spatial extent at which *C. fluminea* has been studied in the CR and our results provide a better understanding of the basic biology and ecology of this global invader, as well as provide natural resource managers with information on habitat conditions favorable for this invasive bivalve within temperate river ecosystems.

Keywords: Aquatic Invasive Species, Generalized Linear Model, Ecological association, Large temperate river, Freshwater bivalve

List of Acronyms/Abbreviations

AIC

Akaike information criterion

Δ AIC

AIC difference

°C

degrees Celsius

C. fluminea

Corbicula fluminea

chl-*a*

chlorophyll-*a*

Cond.

conductivity

cm

centimeter

CR

Columbia River

DO

dissolved oxygen

Dw

dry weight

Flow

water flow

g

gram

GLM

generalized linear model

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<i>I_w</i>	ignited weight
km	kilometer
km ²	square kilometer
m ³	cubic meter
m	meter
m ⁻²	per square meter
mg/L	milligrams per liter
μm	micron
ml	milliliter
mm	millimeter
Nutr.	dissolved nutrients
OM	organic matter
Peb./Stone	gravelly sediment and/or cobbles
PERSAND	% sand

PERSILT

% silt

PM

particulate matter

PSU

practical salinity unit

Redox

redox potential

RKM

river kilometer

sal

salinity

$\mu\text{S}/\text{cm}$

microsiemens per centimeter

SL

shell length

slope

bank slope

Temp.

water temperature

Turb.

turbidity

VIF

variance inflation factor

INTRODUCTION

The Asian clam, *Corbicula fluminea*, is a freshwater bivalve native to Asia, Australia and Africa which has successfully invaded aquatic systems throughout North America,

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Europe, and South America (Karatayev et al. 2007, Crespo et al. 2015, Benson and Williams 2021). Asian clams possess a variety of life history traits which enable successful colonization into invaded habitats, including short time to sexual maturation, rapid growth rate, and high fecundity (Sousa et al. 2008a, Gomes et al. 2016). The ability to self-fertilize through androgenesis (Hedtke et al. 2008, Pigneur et al. 2012) and thus to seed a population with a single individual, coupled with the dispersal capabilities of their semi-buoyant larvae and tolerance of a wide range of environmental conditions (McMahon 1999), further enables the successful invasion of *C. fluminea* outside of its native range.

The harmful effects of *C. fluminea* on both ecosystems and human economies in its invaded range are significant. High filter-feeding rates of *C. fluminea* were shown to be responsible for a 70% decrease in phytoplankton abundance in the Meuse River, northwest Europe (Pigneur et al. 2014). Elsewhere, grazing activity by *C. fluminea* was found to negatively impact food sources for pelagic species (Hwang et al. 2004) and influence changes to epibenthic community assemblages (Ilarri et al. 2014). *C. fluminea* can be classified as an intermediate sediment re-worker in the soft-bottomed waterways where it invades, as its pedal feeding activity pushes larger particles further down into the substrate, which can alter natural patterns of sediment mixing and biogeochemical cycling (Majdi et al. 2014). *C. fluminea* feeding can further alter natural nutrient cycling in invaded systems by increasing the amount of organic matter deposited in the substrate when conditions are favorable for its suspension feeding and reducing organic matter deposition when conditions favor pedal feeding. More specifically, where *Corbicula* and unionids co-occur, a shift in animal-influenced nutrient cycling from control by native

species to control by invasive species can occur (Hakenkamp et al. 1999, Hopper et al. 2022). As for economic impacts, high densities of mucus-secreting pediveliger larvae spawned by *C. fluminea* can clog pipes or other infrastructure such as heat exchangers, resulting in over a billion dollars in remediation costs annually (McMahon 1999, Pimentel et al. 2005, Foster et al. 2022).

Co-occurrence of *C. fluminea* and native unionid mussels may contribute to lower growth rates and degraded physiological condition of native mussels in areas with high *C. fluminea* density as a result of competition for space or food (Ferreira-Rodriguez et al. 2018, Haag et al., 2021). In the Columbia River (CR), *C. fluminea* abundance has greatly eclipsed that of native unionid mussels (McCabe et al. 1997, Helmstetler and Cowles 2008), partially due to the ability of *C. fluminea* to self-fertilize and thus establish a population from a single individual following disturbance (Hedtke et al. 2008), while unionids must rely upon native fish populations (often imperiled) for dispersion of mussel larvae (Haag et al. 1998, Haag 2012). Trophic niche overlap between *C. fluminea* and native unionid mussels (Modesto et al. 2021), including a shared preference for larger algal taxa and avoidance of cyanobacteria (Bartsch et al. 2017), can lead to competition for food (Haag et al. 2021) which favors *C. fluminea* due to its high filtration rate (Bolam et al. 2019).

C. fluminea generally tolerates a wide range of substrata, from large bare stones to fine silt, as well as a broad range of water temperatures (2°-30°C), allowing the clam to establish populations in high to mid-latitudes in both oligo- and eutrophic freshwater systems (McMahon 1999, Castañeda et al. 2018, Benson and Williams 2021). Previous investigations in the CR have shown *C. fluminea* abundance to be positively correlated

with temperature and negatively correlated with chlorophyll-*a* (chl-*a*) concentration (Henricksen and Bollens 2022), while larval abundance is positively correlated with temperature (Hassett et al. 2017). Other studies have shown *C. fluminea* abundance to be positively correlated with well-oxygenated, sandy sediments containing little organic matter in a Brazilian lagoon (Silveira et al. 2016) but positively correlated with coarser sediments and high organic matter content in Iberia (Sousa et al. 2008b, Ferreira et al. 2014). However, the current taxonomic status of the genus *Corbicula* in Europe has recently been questioned (Morhun et al. 2022), suggesting that multiple different species and/or hybrids may be present, thereby complicating the interpretation of the above results. Nevertheless, inconsistent findings in the literature prompt further investigation into which environmental variables are most closely associated with successful invasion and high density of *C. fluminea*.

C. fluminea was first observed in the CR circa 1938, likely reaching the Pacific Northwest of the United States via the accidental introduction of larvae from ballast water or purposeful importation as a food item (Crespo et al. 2015, Foster et al. 2022). *C. fluminea* has since become well established in the CR (Henricksen and Bollens 2022), reaching population densities of up to 722 individuals m⁻² (McCabe et al. 1997). Despite these 80+ years of occurrence in the CR, as well as its known harmful effects in other invaded ecosystems, only a very limited body of scientific literature exists on the ecology of pelagic juveniles (Dexter et al. 2015, Hassett et al. 2017, Dexter et al. 2020a, b) and benthic adult *C. fluminea* in the CR (McCabe et al. 1997, Bollens et al. 2021, Rollwagen-Bollens et al. 2021, Henricksen and Bollens 2022), particularly regarding this species' habitat associations.

This investigation sought to address three knowledge gaps in the population ecology of *C. fluminea* in the lower CR. Given the limited spatial extent of the previous studies in the CR referenced above, our first objective was to determine the broadscale (> 100 km) distribution and abundance of *C. fluminea* throughout the lower CR. Our second objective was to determine which habitat characteristics (i.e., bank slope, water temperature, dissolved oxygen, salinity, conductivity, pH, sediment particle size, sediment organic matter content, and chl-*a* concentration) are significant predictors of *C. fluminea* abundance in the lower CR. More specifically, we hypothesized that habitats dominated by sandy sediment (diameter 500 µm-2mm) containing little fine clay or silty sediments (diameter < 125 µm), lower chl-*a* concentration, and warmer water temperatures (up to 25°C; Rosa et al. 2012) would support the greatest abundances of *C. fluminea*. Our third and final objective was to review the extant literature on the distribution and abundance of *C. fluminea*, especially in relation to environmental variables, in its invaded range of North America, South America, and Europe, as well as its native range in Asia, Africa, and Australia, and to compare these findings to our results from the lower CR.

METHODS

Study Area

The CR flows 1,954 km from its headwaters in British Columbia, Canada, through two US states and into the northeastern Pacific Ocean at Astoria, OR, USA, draining a basin covering 660,480 km² and with a mean annual discharge of 224 billion m³ (Simenstad et al. 1990). The CR is the largest river on the west coast of North America and is highly altered by human activities. The mainstem has been impounded for hydropower, flood

control, irrigation, and navigation, resulting in substantial changes to natural water temperature and discharge patterns (Hinrichsen et al. 2013). Human activities have enhanced nonnative species introductions, further impacting the basin, and the CR is a heavily invaded ecosystem as a result (Bollens et al. 2002, Dexter et al. 2015, 2020a, b, c).

We collected *C. fluminea* of shell length (SL) >2 mm, along with samples of associated environmental variables, in the region of the CR that separates the western portions of Washington state and Oregon state, USA (the “lower” CR) (Figure 1). We conducted two broadscale sampling efforts (once in September-October of 2019 and once again in September-October 2020) to collect clams from 27 shore-based stations (each station consisting of a 15 m transect) located on both banks of the river along a span of 481 river kilometers (RKM) from Cathlamet, WA (most downstream extent) to Richland, WA (most upstream extent). These stations, publicly accessible and on public land, were selected by identifying potential areas for riverbank access on foot via satellite imagery (Google, 2019) and encompassed wadeable, free-flowing reaches of the CR located below the most downstream impoundment (Bonneville Dam), as well as sites further upstream within the impounded Bonneville Reservoir, Lake Celilo (behind The Dalles Dam), Lake Umatilla (behind John Day Dam), and Lake Wallula (behind McNary Dam).

Sample Collection in the Field

Triplicate quadrat samples were collected in the same fashion at each site. First, three survey flags were placed at 5-m intervals for a total length of 15 m along the water’s edge at each of the 27 stations. At each flag location, a 1-m² quadrat was placed on the adjacent river bottom at 30 cm water depth, and its geographic location was recorded.

Bank slope perpendicular to the thalweg of the river was measured using a digital inclinometer, then temperature (°C), dissolved oxygen (mg/l), salinity (PSU), conductivity (µS/cm), and pH of the overlying water were measured with a YSI ProPlus model multiparameter sonde. A 70-ml water sample was collected from surface water in an amber bottle and placed on ice in a cooler for subsequent fluorometric analysis of chl-*a* in the laboratory. Next, a 250 ml sediment sample was collected from within the top 15 cm of the substrate within the sample quadrat after carefully sieving it through a 2mm mesh sieve contained within a steel mixing bowl to remove any *C. fluminea* of > 2 mm SL present within. This sediment sample was then transferred to a plastic sample jar and returned to the laboratory for sediment size fractionation analysis. In 2020 only, a second 250-ml sediment sample was collected for total organic carbon analysis using the same procedure. Finally, the entirety of the top 15 cm of substrate remaining within each sample quadrat was sieved through a #10 Tyler (2 mm mesh) sediment sieve to collect all *C. fluminea* individuals of SL > 2 mm. All *C. fluminea* thus collected were placed in jars and preserved in the field with 70% sodium bicarbonate-buffered ethanol.

Sample Processing in the Laboratory

All samples were transferred to the laboratory at Washington State University, Vancouver, within 8 hours of collection. In the laboratory, the chilled 70 ml water samples were vacuum filtered through GF/F filters, placed within aluminum foil-wrapped scintillation vials and frozen for later processing. Chl-*a* concentrations were then determined with a Model 10-AU fluorometer (Turner Designs) via the acidification method (Strickland and Parsons 1972, Arar and Collins 1997). All *C. fluminea* specimens in each quadrat sampled were enumerated. Sediment samples for grain size analyses were

dried at 60 °C in a drying oven for 72 hours or until all moisture was evaporated, then sediments were size fractioned by sieving through a series of nested sediment sieves (4 mm, 2 mm, 500 µm, 250 µm, 125 µm). Total mass of each sediment sample for OM analysis (from 2020 samples only) was measured after drying overnight in a drying oven at 60 °C to remove any excess moisture, then sieved through a 4-mm sediment sieve. The masses of the sample portions > 4 mm and < 4 mm were recorded. A portion of each OM sample < 4mm was placed in a pre-weighed 30-ml porcelain crucible, the weight of the filled crucible was recorded, and then ignited at 500 °C for two hours. Total crucible weight was recorded once the sample was cool enough to handle, and the OM content as % loss-on-ignition was calculated as $[(Dw - Iw) / Dw] * 100$, with Dw corresponding to dry sample weight and Iw corresponding to ignited sample weight (Schulte et al. 1991, Sutherland 1998, Bisutti et al. 2004).

Data Processing and Statistical Analyses

Univariate negative binomial family generalized linear modeling (GLM) regressions, with *C. fluminea* abundance within each 1 m² quadrat sampled as the response variable and each of the measured environmental parameters as explanatory variables, were performed on two data sets: i) the entirety of our 2019-2020 data set (absent the 2020 OM data) (N=162) and ii) only the 2020 data set (which included OM) (N=81). This type of regression analysis was chosen over simple linear regression because of the numerous observations with zero values in the response variable (abundance), which gave rise to overdispersion. These univariate GLM regression analyses were undertaken in R using the “MASS” package (Venables and Ripley 2002) and visualized with “ggplot2” (Wickham 2016).

After initially exploring the data via univariate regressions (Supplemental Figure 1), subsequent multivariate GLM regressions for each of the two data sets (2019-20 and 2020-only) were undertaken. Clam abundance was the dependent variable, with bank slope, water temperature, DO, salinity, conductivity, pH, chl-*a*, % sand, % silt, and OM (2020-only) as the explanatory variables. First, a Poisson family GLM was selected for modeling clam abundance counts using the “stats” package in R (R Core Team, 2013). This GLM was evaluated for overdispersion by fitting a quasipoisson GLM to determine the value of the dispersion parameter (theta). A negative binomial GLM was then fit to the data using the “glm.nb” function in the R package “MASS” (Venables and Ripley 2002). Next, the quasipoisson and negative binomial GLMs were evaluated for zero inflation using the “check_zeroinflation” function in the “performance” R package (Lüdecke et al. 2021). Due to the highly overdispersed nature of the clam abundance data (theta=80.74) and accurate prediction of zeros (98% predicted vs. observed), the negative binomial GLM was selected for interpretation of the abundance data. Model fit was validated by plotting residuals of simulated data from the negative binomial GLM against observed values using the “simulateResiduals()” function in the R package “DHARMa” (Hartig 2022). As OM samples were only collected in 2020, a separate negative binomial GLM was fit to these data to evaluate the relationship between the suite of environmental variables (including OM) and *C. fluminea* abundance following the same procedures of model evaluation and selection as described above. Collinearity amongst explanatory variables in all GLMs was assessed by calculating variance inflation factors (VIF) amongst variables using the “vif” function in the R package “car” (Fox and Weisberg 2019).

Next, the best models for interpretation were selected using stepwise Akaike information criterion (AIC) analysis by removing least-significant explanatory variables from each global model until the combination of covariates with the lowest possible AIC value was determined (Venables and Ripley 2002). AIC was used to compare fit between regression models to find the most parsimonious set of parameters, which explained the greatest amount of variation in the data. This was done by discarding models using unnecessary parameters (Bozdogan 1987). Nagelkerke R-squared values for the negative binomial GLMs fit to the abundance data were calculated using the “rsq” function in the R package “rsq” (Zhang 2021). Nagelkerke R-squared is a pseudo R-squared value calculated in lieu of a traditional R-squared value (which cannot be calculated for a negative binomial family GLM) and is interpreted as a measure of information content compared to an intercept model rather than explained variance (Cameron and Windmeijer 1996). Finally, the point measurements of continuous predictor variables for each multivariate model were standardized to mean 0 and standard deviation 1 to compare effect size using the “jtools” package (Long 2022), then visualized using the “ggplot2” package in R (Wickham 2016).

Literature Review

A literature review of previous studies on *C. fluminea* distribution, abundance and habitat associations was conducted using the Web of Science database in 2021. Search terms included “*Corbicula fluminea*” and “habitat,” “distribution,” “abundance,” or “density.” Additional searches included “*Corbicula fluminea*” and each of the individual environmental variables included in our regression analyses above (i.e.: “slope,” “temperature,” “DO,” “salinity,” “conductivity,” “pH,” “chlorophyll,” “sand,” “silt,” or

“OM.”), as well as “flow.” Relevant results from articles identified in our searches (i.e., those containing quantitative information regarding *C. fluminea* abundance and at least one of the above environmental variables) were compiled into tables.

RESULTS

Environmental Conditions

Throughout the study area (Figure 1), bank slope ranged from 0.0-26.0° with no discernable longitudinal spatial trend (Figure 2A). Water temperature ranged between 9.8 and 26.0 °C and increased from upstream to downstream (Figure 2B). Dissolved oxygen values ranged from 6.4-13.8 mg/l, trending higher upstream (Figure 2C). Salinity exhibited a consistently narrow range from 0.00-0.18 PSU throughout the study area (Figure 2D), while conductivity ranged from 78-331 $\mu\text{S}/\text{cm}$ (Figure 2E), with both lacking any discernible spatial pattern. The range of pH was 7.17-9.98, decreasing downstream in 2019, but with no obvious pattern in 2020 (Figure 2F). Chl-*a* concentration ranged from 1.36-419 $\mu\text{g}/\text{L}$, without a longitudinal trend (Figure 2G), while % sand ranged from 0.01-97.1%, with higher values observed below RKM 300 (Figure 2H). The % silt content ranged from 0.05-93.3%, with little spatial pattern (Figure 2I). Sediment organic matter content (OM, collected in 2020 only) ranged from 0.10-17.8% and did not exhibit a spatial trend (Figure 2J). The correlation between any two environmental variables is given in Supplemental Figure 2.

Distribution and Abundance of *C. fluminea*

We collected 6,318 clams over the course of our study in 2019 and 2020. The abundance of *C. fluminea* ranged from 0-430 (mean = 39) clams m^{-2} (Figure 3). The sample site with the greatest abundance (430 ind. m^{-2}) was located at Gresham, OR near the confluence of

the Sandy River with the CR (RKM 193). Most of the sample sites with abundances greater than 100 ind. m⁻² were located downstream of Bonneville dam, while most of the sites with abundances < 100 ind. m⁻² were located upstream (Figure 2K, Figure 3). Of the 162 quadrats sampled, 50 were found to have no *C. fluminea* present (0 ind. m⁻²).

Abundance of *C. fluminea* in Relation to Environmental Variables

The most parsimonious negative binomial multivariate GLM (Nagelkerke R-squared = 0.22) using both years' data indicated that *C. fluminea* abundance was positively correlated with water temperature ($z = 3.41$, $p = 6.42e^{-4}$) and % sand ($z = 2.20$, $p = 2.79e^{-2}$), and negatively correlated with bank slope ($z = -6.10$, $p = 1.07e^{-9}$) (Figure 4). Bank slope and water temperature were the most important predictors of *C. fluminea* abundance, as indicated by standardized effect sizes (Figure 4). AIC values of models resulting from stepwise analysis of negative binomial GLMs using 2019-2020 environmental and *C. fluminea* abundance data are shown in Supplemental Table 1. When the 2020 data (which included OM) were considered separately, the most parsimonious negative binomial GLM (Nagelkerke R-squared = 0.57) indicated that *C. fluminea* abundance was positively correlated with water temperature ($z = 3.92$, $p = 8.85e^{-5}$) and percent silt ($z = 2.58$, $p = 9.65e^{-3}$), while being negatively correlated with bank slope ($z = -6.52$, $p = 7.01e^{-11}$) and sedimentary organic matter content ($z = -3.21$, $p = 1.35e^{-3}$) (Figure 5). Chl-*a* and salinity were retained in the best GLM of the 2020 data, despite being non-significant predictors. Bank slope, water temperature, and sedimentary organic matter content were the most important predictors of *C. fluminea* abundance in 2020, as indicated by standardized effect sizes (Figure 5). AIC values of models resulting

from stepwise analysis of negative binomial GLMs using only 2020 environmental and *C. fluminea* abundance data are shown in Supplemental Table 2.

Literature Review

Our literature search returned 73 relevant articles. Results from articles pertaining to *C. fluminea* distribution and abundance were compiled in Table 1, while published studies, which tested the relationship of *C. fluminea*'s abundance with individual environmental variables (positive, negative, or non-significant) were compiled in Table 2.

DISCUSSION

Distribution and Abundance of *C. fluminea*

Our study provides one of the most geographically extensive examinations of *C. fluminea* distribution within a lotic system of North America and adds new insights into the broadscale distribution and spread of this global invader. The distribution of *C. fluminea* in the lower CR varied spatially but showed little temporal (interannual) variability during 2019 and 2020. Most sites with high (>100 ind. m^{-2}) abundance were located downstream of Bonneville Dam (RKM 56 – 235), while most sites where *C. fluminea* was absent or in low abundance (<100 ind. m^{-2}) were located upstream of the dam (RKM 235 – 537) in both years. The observed abundance differential above and below this first impoundment of the CR may arise from favorable habitat conditions located downriver (i.e., temperature, sandy substrate; Figure 2) compared to those located upriver of Bonneville dam. Peak abundance within our study sites (430 ind. m^{-2}) was comparable to a previous shore-based investigation in the CR, which reported peak abundance of 500 ind. m^{-2} (Henricksen and Bollens 2022), but was lower than the maximum value (722 ind. m^{-2}) reported in the only main-channel CR benthic invertebrate survey known to include

C. fluminea (McCabe et al. 1997). Overall, our results on the abundance of *C. fluminea* in the CR generally comport with the findings of previous regional studies.

Our results of *C. fluminea*'s maximum abundance in the CR are consistent with some previous North American studies but are considerably lower than many other studies from this continent (Table 1). For instance, Eng (1977) reported a maximum *C. fluminea* abundance of 131,200 ind. m⁻² in central California. More recent studies from Lake Tahoe, California reported *C. fluminea* abundances exceeding our findings by a factor of two (Denton et al. 2012, Wittman et al. 2012a, Wittman et al. 2012b). Several investigations of *C. fluminea* abundance from the east coast of the US and Canada also found peak abundances exceeding those found in our study. For instance, thermal plumes from power generating facilities in Canada's St. Lawrence River, where *C. fluminea* is otherwise absent due to inhospitably cold temperatures, harbored clam populations up to seven times those found in our study (Simard et al. 2012, Castañeda et al. 2018). Several studies along the United States Atlantic coast found even higher maximum abundances: 11,522 ind. m⁻² (Graney et al. 1980); 1,467 ind. m⁻² (Cohen et al. 1984); and 2,000 ind. m⁻² (Kelley et al. 2022). In the St. Clair River in the North American interior, French and Schloesser (1996) reported peak abundances (2,106 ind. m⁻²), over twice those in the CR. Collectively, these studies indicate that the CR harbors less dense populations of Asian clams than many other bodies of freshwater in North America. However, it is important to note that our study sampled relatively few (3) quadrats across a longer extent of the river, whereas other studies focused on smaller scale variability by sampling more quadrats over a smaller span of a given river.

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As for Europe, more than half of the 33 published studies we found reported peak abundances greater than our findings in the CR (Table 1). These include Ireland (17,872 ind. m⁻²; Caffrey et al. 2011, Minchin 2014, Sheehan et al. 2014, Minchin and Boelens 2018); the United Kingdom (2,500 ind. m⁻²; Aldridge and Müller 1993); Belgium (5,000 ind. m⁻²; Nguyen and De Pauw 2002); the Iberian peninsula (11,500 ind. m⁻²; Modesto et al. (2013); and Bulgaria's Danube River (16,560 ind. m⁻²; Hubenov et al. 2013). Within the River Lima estuary on the Iberian Peninsula, Sousa et al. (2006) reported that abundance was diminished compared to other estuarine systems due to the presence of environmental contaminants. In contrast, our observed abundances within the CR sometimes exceeded abundances reported in the European interior, e.g., in Poland's Oder and Vistula Rivers, where winter temperatures are regarded as unsuitable for *C. fluminea* survival and clams make use of thermal refugia via warmed power plant effluent (Bonk et al. 2018, Urbańska et al. 2018, Cebulska and Krodkiewska 2019). In addition, as *C. fluminea* is a more recent invader of Europe than the Pacific Northwest of the United States (Karatayev et al. 2007), one should keep in mind the common phenomenon of invasive species density being greater in earlier phases of an invasion event (Blackburn et al. 2011).

In South America, only one investigation, in the Parana River delta of Argentina (Boltovskoy et al. 1997), found greater *C. fluminea* abundance than our observations in the CR, whereas eight other South American studies reported abundances below those of the CR, including in the Argentinian lowlands (Reyna et al. 2013, Reshaid et al. 2017), Patagonia (Labaut et al. 2021), and tropical/subtropical areas of Brazil (Franca et al. 2007, Paschoal et al. 2015, Silveira et al. 2016) (Table 1).

Reports of *C. fluminea* abundance within its native range of Asia, Australia and Africa are scarce, but reported abundances in Asia (Cai et al. 2011, Zhang et al. 2019) are lower than those reported in our study of the CR. Reporting of *C. fluminea* distribution in Africa is limited to a single study in its invaded range of Morocco, but which did not report abundances (Clavero et al. 2012). Interestingly, our findings of *C. fluminea* abundance within the CR generally fall below those of other temperate waterbodies throughout Europe and elsewhere in North America, while exceeding those in tropical/subtropical areas similar to those in the clam's native range of Asia. It is possible that the CR represents a system with some physiochemical limiting factors or predation pressures which constrain the abundance of *C. fluminea* (as discussed in the next section).

Abundance of *C. fluminea* in Relation to Environmental Variables

The most parsimonious GLM model of our 2019-2020 data indicated a significantly negative relationship of *C. fluminea* abundance with bank slope, while indicating significant positive relationships with water temperature and % sand. The most parsimonious GLM model for the 2020 data (which included OM) indicated a significant positive relationship with % silt, and significant negative relationships with salinity and percent OM. Because the GLM of our 2019-2020 data set contained twice the number of data points as the GLM of our 2020 data, we have greater confidence in the former results, and thus we will focus our discussion therein. However, because OM was a significant negative predictor in the multivariate regression of the 2020 data (recall that OM data were not collected in 2019), we also consider the role of OM as a significant predictor of *C. fluminea* abundance. Taken as a whole, our results from these two GLMs

are in some instances similar to, but in many cases quite different from, previously published studies.

Our results support findings of a positive relationship between *C. fluminea* abundance and temperature. We compiled results from the published literature on how *C. fluminea* abundance is related to various environmental variables (Table 2). A positive relationship between temperature and *C. fluminea* abundance is well documented, both in terms of broadscale distribution (McMahon 1999, Crespo et al. 2015, Gama et al. 2016), as well as at smaller spatial scales. For instance, several studies report *C. fluminea* making use of habitats proximal to artificial thermal refugia within otherwise inhospitably cold environments (Simard et al. 2012, Bonk et al. 2018, Castañeda et al. 2018, Urbańska et al. 2018, Cebulska and Krodkiwska 2019). However, several other investigations found that temperature was not a significant predictor of *C. fluminea* abundance when considered at smaller spatial scales (e.g., 13-370 km) in North America (Brown et al. 2007, Cooper 2007, Sedlacek and Schoenebeck 2015, Henricksen and Bollens 2022), Europe (Sousa et al. 2008, Franco et al. 2012), and South America (Pereira et al. 2017). Our results showed a warming trend from upstream to downstream in the CR, where the greatest *C. fluminea* abundances were found. This includes the greatest single-site abundance (430 ind. m⁻²) at the confluence of the Sandy River and the CR, near Gresham, OR at RKM 193 – a highly developed reach of the CR, surrounded by impervious surfaces and industrial land uses. Compared with more rural areas upstream, these urbanized landscapes absorb greater quantities of infrared energy which is then transferred via runoff to the CR, potentially causing spikes in water temperature during spring and early summer (Chang and Lawler 2011) coinciding with the phenology of *C.*

fluminea spawning activity in the CR (Dexter et al. 2015, Hassett et al. 2017, Henricksen and Bollens 2022). Warmer temperatures may also positively affect biological rate processes of *C. fluminea*, such as feeding (Rollwagen-Bollens et al. 2021).

Bank slope was the other environmental variable consistently identified as a negatively significant predictor of *C. fluminea* abundance in our models. When considered as a proxy for high flow, steep riverbank slopes likely have implications for the ability of planktonic early juvenile Asian clams to settle. Sample sites where the bank is less sloped, such as those on the inside curve of a riverbend, represent areas of lower energy flow compared to areas located on the outer curve (Naiman and Bilby 1998). However, large, impounded rivers such as the CR may behave differently than those which are smaller and free-flowing (Hatten and Batt 2010). In fact, our observation of a significant negative correlation between slope and temperature (Supplemental Figure 2) suggests that less steeply sloped regions of the river are likely more quiescent, less advective, and thus more prone to local warming. Early juvenile Asian clams utilize mucoid secretions and a ciliated velum to remain suspended in the water column until settlement occurs via a single byssal thread attachment to the substratum, whereby further transport may occur due to turbulent flow (McMahon 1999). Thus, shallow-sloped reaches of the riverbank may allow for greater settlement by *C. fluminea* due to a lack of turbulent flow that could otherwise cause re-suspension and transport. However, the extant literature is mixed on whether flow has positive, negative, or non-significant effects on *C. fluminea* abundance. For instance, Urbanska et al. (2018) found abundance to be positively related to flow in a Polish canal that experienced anoxia, with clam distribution being limited to high-flow areas exhibiting higher oxygen levels. In contrast, Bodis et al. (2011) found *C. fluminea*

abundance to be negatively related to flow, with clams being more abundant in larger, more quiescent watercourses compared to faster-flowing waters. In any event, we found that bank slope was a negative predictor of *C. fluminea* abundance in the lower CR. Regarding the relationship between sediment characteristics (e.g., % sand, % silt, and % OM) and clam abundance, our findings differ somewhat (but not always consistently) from those of previous investigations. Of the 21 previously published studies that reported relationships with sediments (Table 2), 11 reported a significant positive relationship between the sandy substrate and *C. fluminea* abundance. Silveira et al. (2016), however, reported both a positive relationship to percent sand as well as a negative relationship with OM (as we observed). Our finding of a negative relationship between abundance and % OM may be related to sediment samples containing a higher % of OM also exhibiting lower % sand, which was found to be a positive predictor of abundance. Sousa et al. (2008b) also found a positive relationship between clam abundance and sandy substrata, but in contrast to our results, reported a positive relationship to OM. Belanger et al. (1985) also found a positive relationship between OM and clam abundance in their North American study. Still, others (the remainder of known studies that included sandy sediment composition as an explanatory variable) reported sand content as being non-significant in predicting *C. fluminea* abundance (McCabe et al. 1997, Brown et al. 2007, Franco et al. 2012, Ferreira-Rodriguez and Pardo 2014, Sedlacek and Schoenebeck 2015, Pereira et al. 2016, Patrick et al. 2017, Castañeda et al. 2018, McDowell et al. 2018, Modesto et al. 2018). The often-limited spatial extent of these previous studies may play a role in their lack of significant findings, as they were often constrained to shorter reaches of a given river or portions of lentic bodies exhibiting

lesser variation in substrate composition (Brown et al. 2007). Interestingly, our results do not support our hypothesis of a negative relationship between clam abundance and percent silt, since the only significant result from our models (the multivariate GLM of 2020 data) indicated a positive relationship. We interpret this as further evidence of this species' ability to inhabit a wide range of sediment types, from bare rock to fine sediment (McMahon 1999). Moreover, *C. fluminea* shares the ability with many other bivalves to rework the structure of underlying sediment through pedal feeding, thus allowing it to be successful in multiple sediment types (Vaughn and Hakenkamp 2001, Sousa et al. 2009). With regard to chl-*a* concentration, we found no significant relationship with clam abundance, contrary to our hypothesis (based on earlier findings of Henricksen and Bollens 2022). Other investigators (Brown et al. 2007, Sousa et al. 2008b, Franco et al. 2012, Modesto et al. 2013) reported similar non-significant relationships between clam abundance and chl-*a*. Indeed, no other studies known to us reported a positive relationship between adult or juvenile *C. fluminea* abundance and chl-*a* concentration (Table 2), although one study reported a negative correlation (Henricksen and Bollens 2022). Chl-*a*, while often used as a proxy for the presence of food for filter-feeding bivalves, does not fully reflect the availability of preferred food sources for a given species, especially in the context of *C. fluminea*'s pedal feeding capabilities. Bolam et al. (2019) showed that *C. fluminea*'s food preferences change over the course of summer and fall in the CR, with clams preferring diatoms in the summer and flagellates in the fall, and generally avoiding cyanobacteria. Thus, the abundance of chl-*a*, as was used in our current study and many previous studies by others (Table 2), has only limited utility in assessing the role of food availability in regulating *C. fluminea* abundance, and thus

future studies could consider more taxon-specificity in their assessment of food quantity and quality.

Other environmental variables, not measured by us in this study, are also likely to be important in regulating the abundance of *C. fluminea*, in particular calcium (and potentially other ions) and predation. For example, Bollens et al. (2021) found that calcium concentrations necessary for supporting invasive bivalves like *C. fluminea* and *Dreissena* spp. are sufficient throughout the lower CR; however, the influence of organic or other inorganic nutrients have yet to be assessed in the CR. Sousa et al. (2008b) found evidence that nutrient concentrations (i.e., nitrate and ammonia) were negatively correlated with *C. fluminea* abundance in Portugal's Minho River estuary, while indicating water hardness, a proxy for inorganic nutrient (i.e., calcium) concentration, was positively correlated with abundance (Table 2). With regard to predation, Castro et al. (2018) determined *C. fluminea* was less palatable to predators (i.e., European eel, common carp, Louisiana crawfish) in its invaded range than were native bivalves. Despite this, white sturgeon are known to feed upon *C. fluminea* within the lower CR and elsewhere on the US west coast (McCabe et al. 1993, Rochman et al. 2017), while crayfish (which are present in the CR; Sorenson et al. 2012) may be important consumers of *C. fluminea* (Covich et al. 1981, Pereira et al. 2016). Whether such predation is sufficient to limit Asian clam abundance in the CR remains to be determined.

Summary and Conclusions

We observed the Asian clam (*C. fluminea*) to be broadly distributed and more abundant in the lower CR than previously reported in its home range in Asia and in tropical/subtropical areas of its invaded range of South America, but generally less

abundant than in other invaded temperate areas within North America and Europe. We found *C. fluminea* abundance within the lower CR to be positively associated with warmer water temperatures and sandy substrate, while being negatively associated with steeper bank slopes and sedimentary organic material content. Our results are therefore consistent with most (but not all) previous studies from other regions around the globe (Tables 1 and 2). We note that the roles of food availability and predation in influencing the population dynamics of *C. fluminea* are areas in particular need of further research. Our investigation represents the greatest spatial extent at which the distribution and abundance of *C. fluminea* have been studied in the CR. We expect near-shore areas of shallow-sloped riverbanks exhibiting warmer water temperatures, sandy substrate, and little sedimentary organic material to be locations ripe for invasion by *C. fluminea*. By elucidating the relationship of *C. fluminea* abundance to environmental variables, our results provide a better understanding of the basic biology and ecology of this global invader while providing natural resource managers with information on habitats that may be susceptible to future invasions, which are expected to increase under likely climate change scenarios (Crespo et al. 2015, Dexter et al. 2020a)

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DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are stored at Washington State University Vancouver in Vancouver, Washington, United States, and are available from the authors upon reasonable request.

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FIGURE LEGENDS



Figure 1 Map of the lower Columbia River study area. Filled squares represent near-shore stations sampled in 2019-2020.

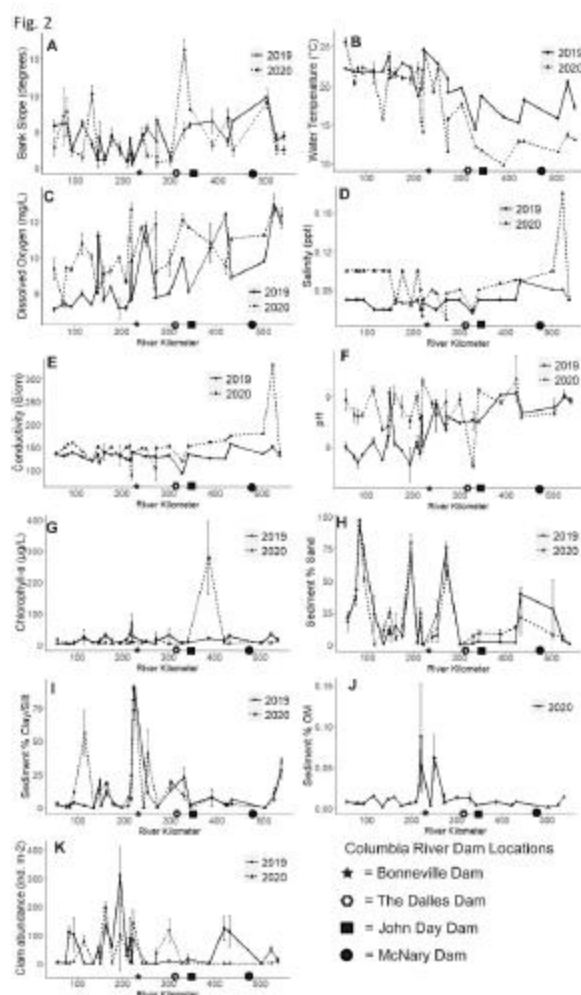


Figure 2 Environmental variables (mean + SE) collected across the study area: (A) bank slope, (B) water temperature, (C) dissolved oxygen, (D) salinity, (E) conductivity, (F) pH, (G) chlorophyll-*a*, (H) percent sand, (I) percent clay/silt, (J) percent OM, and (K) abundance values per sampling station in 2019 (solid lines, circles) and 2020 (dashed lines, triangles). Low river kilometer (RKM) values correspond to downstream areas within the study area, with high RKM values upstream. Locations (RKM) of Bonneville Dam (stars), The Dalles Dam (hexagons), John Day Dam (squares) and McNary Dam (circles) are denoted on the x-axis.

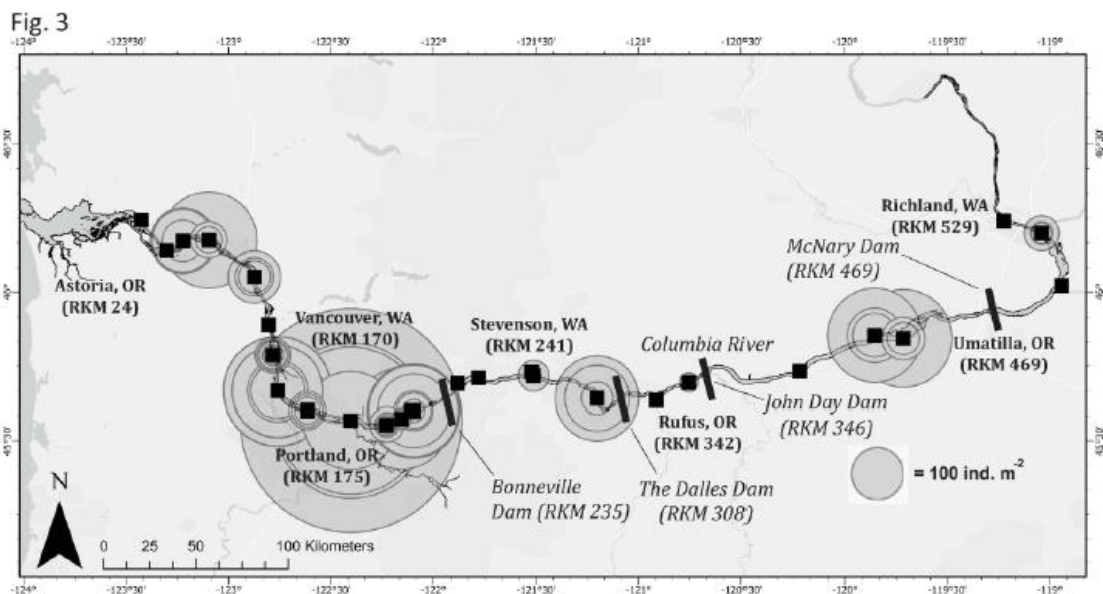


Figure 3 Map of *Corbicula fluminea* abundance throughout the study area in 2019-2020, where filled squares represent sampling stations, black bars represent dam locations and clam abundance (ind. m⁻²) is represented as proportionally sized circles. RKM = river kilometer.

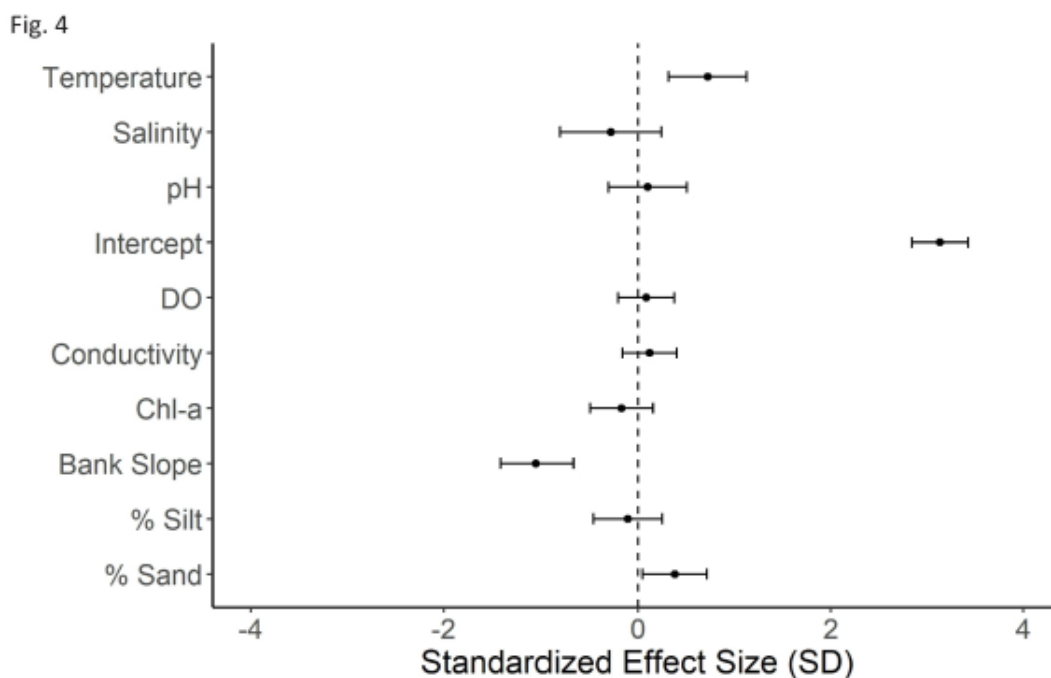


Figure 4 Standardized effect size (mean and 95% confidence intervals) of environmental variables within the generalized linear model on the abundance of *Corbicula fluminea* throughout the study area (2019-2020 data).

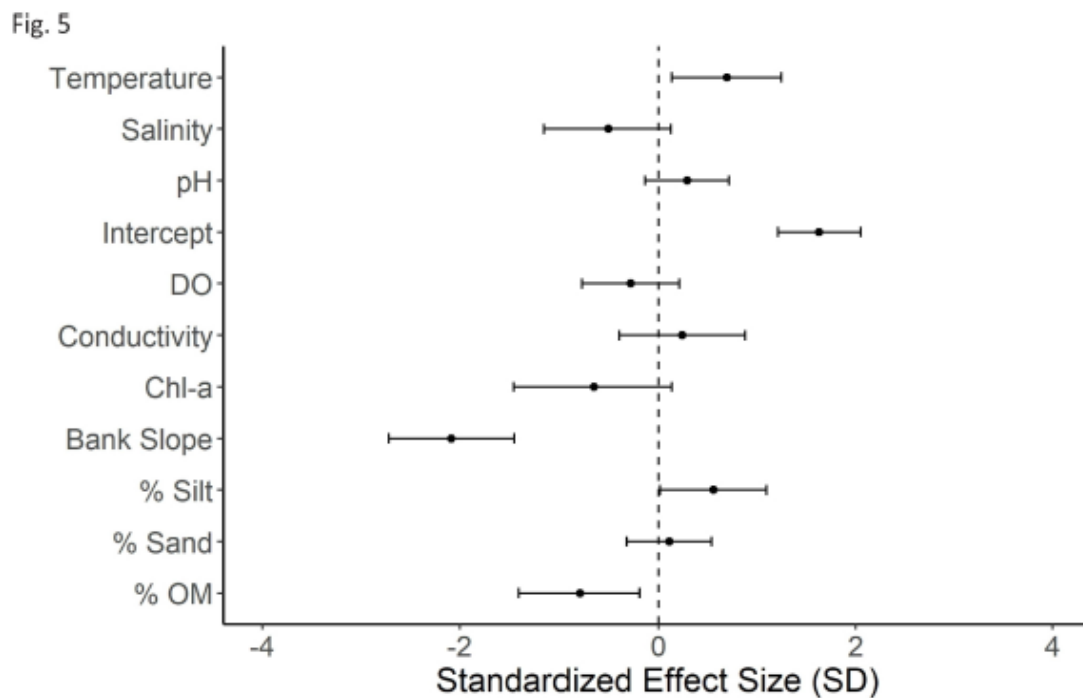


Figure 5 Standardized effect size (mean and 95% confidence intervals) of environmental variables within the generalized linear model on the abundance of *Corbicula fluminea* throughout the study area (2020 data [containing OM] only).

TABLES

Table 1 Summary results from known published studies (by continent) of *C. fluminea* distribution and abundance (ind. m⁻², unless otherwise noted). n/a indicates that abundance was not reported. RKM = river kilometers.

Continent	Authors (Year)	Spatial Extent (km)	Abundance (ind. m ⁻² , unless noted)	Location
Asia	Cai et al. (2011)	2,338 ²	905	China lake
	Perova and Pryanichnikova (2019)	430 RKM	20	Russia reservoir
	Zhang et al. (2019)	13,400 km ²	8.05	Chinese lake basin

Africa	Clavero et al. (2012)	~400 km	n/a	North African river basins (3)
North America	Eng (1977)	125 km	131,200	California canal
	Graney et al. (1980)	2.45 km	11,522	Virginia river
	Hartfield and Cooper (1983)	125,443 km ²	n/a	Mississippi rivers
	Cohen et al. (1984)	~60 RKM	1,467	Maryland river
	Belanger (1991)	20 RKM	968	Louisiana River
	Diaz (1994)	1.35 RKM	1,433	Virginia River
	French and Schloesser (1996)	14.5 km	2,106	Michigan River
	McCabe et al. (1997)	113 RKM	722	Columbia River (United States)
	Karatayev et al. (2003)	71.51 ²	0-49.6	Texas River
	Karatayev et al. (2005)	695,662 ²	n/a	Texas lakes and rivers
	Vaughn and Spooner (2006)	14,400 km ²	2,401	Oklahoma, Arkansas rivers
	Brown et al. (2007)	~120 RKM	201	California watershed
	Cooper (2007)	13 RKM	0-690	North Carolina River
	Denton et al. (2012)	~20km of shoreline	2,832	Nevada Lake
	Simard et al. (2012)	4 RKM	4,695	Quebec River
	Wittmann et al. (2012a)	4 km of shoreline	2,793	California Lake
	Wittmann et al. (2012b)	10 km of shoreline	4,103	California Lake
	Sedlacek and Schoenebeck (2015)	370 RKM	629	Texas River
	Barba-Macias et al. (2017)	~150 RKM	98	Mexico rivers/lakes
	Patrick et al. (2017)	152 ²	0-225	Alabama, Florida basin
	Castañeda et al. (2018)	~7.5 RKM	0-7,501.9	Quebec River
	Smith et al. (2018)	~840 km of shoreline	0-20.9	Laurentian great lake
	McDowell and Byers. (2019)	40 RKM	7-483	Georgia rivers
	Douglass et al. (2020)	~480 RKM	26 · person · hr ⁻¹	Ohio river
	Henricksen and Bollens (2022)	60 km	5-500	Columbia River (United States)
	Kelley et al. (2022)	~350 RKM	0-2,000	Alabama, Tennessee basins
	Ring and Woolnough (2022)	5,230 km ²	0.24 g/cm ³	Michigan basin
	Robb-Chavez et al. (this study)	481 RKM	0-917.03	Columbia River (United States)
Europe	Araujo and Ramos (1993)	24 km	n/a	Portugal river

	Aldridge and Müller (2001)	12 km	2,500	Britain rivers
	Mouthon (2001)	0.048 ²	164-934	France river
	Nguyen and De Pauw (2002)	~100 km	5-5,000	Belgium rivers/canals
	Beran (2006)	83 RKM	<100	Czech Republic river
	Sousa et al. (2006)	2 RKM	0-60	Portugal river
	Schmidlin and Baur (2007)	~40RKM	1-600	Switzerland, Germany, France river
	Sousa et al. (2008)	~15 RKM	80-4,185	Portugal, Spain river
	Elliott and Ermgassen (2008)	~15 RKM	1,000	Britain River
	Perez-Quintero (2008)	1,300 ² (invaded area of Iberian penin.)	n/a	Spain, Portugal basins
	Morais et al. (2009)	52 km	7-360 · person · hr ⁻¹	Spain, Portugal basin
	Marescaux (2010)	210,016 ²	n/a	France rivers
	Bódis et al. (2011)	160 RKM	736	Hungary river
	Caffrey et al. (2011)	~32 RKM	9,636	Ireland river
	Franco et al. (2012)	25 RKM	542-1,142	Portugal estuary
	Schmidlin et al. (2012)	~225 km	n/a	Switzerland lakes
	Sousa et al. (2012)	~170 RKM	2,280	Portugal rivers
	Hubenov et al. (2013)	441 RKM	16,560	Bulgaria rivers
	Kamburska et al. (2013)	212.5 ²	1,249	Italy lake
	Ferreira-Rodriguez and Pardo (2014)	~15 RKM	3,150	Spain river
	Sheehan et al. (2014)	~3 RKM	17,872	Ireland river
	Modesto et al. (2013)	21 RKM	4-11,500	Portugal estuary
	Minchin et al. (2014)	~293 ² , 216 RKM	1,500-4,500	Ireland river
	Crespo et al. (2017)	~15 RKM	0-1,900	Portugal estuary
	Pereira et al. (2017)	~15 RKM	4.1-3,076.9	Portugal ditches/brooks
	Ferreira-Rodriguez et al. (2017)	~300km	n/a	Portugal, Spain rivers
	Bonk et al. (2018)	210	2.0-6,694.5	Poland river
	Minchin and Boelens (2018)	223 ² , 60 RKM	>1,800	Ireland lakes
	Paganelli et al. (2018)	15 RKM	0-1,483	Italy river
	Urbanska et al. (2018)	~1 km	0-78	Poland rivers
	Cebulska and Krodkiewska (2019)	~12 RKM	16-118	Poland river
	Gama et al. (2020)	6 km	0-12.71	Portugal river
South	Boltovskoy et al.	~0.02	430-10300	Argentina

America	(1997)			river/estuary
	Cazzaniga and Perez (1999)	5 RKM	n/a	Argentina river
	Franca et al. (2007)	~200	10-100	Brazil river
	Reyna et al. (2013)	~80 RKM	12	Argentina river
	Paschoal et al. (2015)	0.0625	160-630	Brazil reservoir
	Silveira et al. (2016)	19 ²	0-700	Brazil lagoon
	Reshaid et al. (2017)	~140 RKM	0-53.23	Argentina river
	Hunicken et al. (2019)	12 RKM	84-125	Argentina estuary
	Labaut et al. (2021)	~200 RKM	133-519	Argentina river

Table 2 Summary results from all known published studies (by continent) of *Corbicula fluminea* abundance as related to environmental variables (“Flow” = water flow, “Temp.” = water temperature, “DO” = dissolved oxygen, “Cond.” = conductivity, “Sal.” = salinity, “Chl-*a*” = chlorophyll-*a* concentration, “OM” = sediment organic matter, “Sand” = sandy sediment composition, “Silt” = silty sediment composition, “Peb./Stone” = gravelly sediment and/or cobbles, “Nutr.” = dissolved nutrients [Ca⁺, NH₄⁺, PO₄, P, N], “Redox” = redox potential, “Depth” = water depth, “PM” = suspended particulate matter, “Turb.” = turbidity). A significantly positive or negative relationship to each environmental variable is indicated with + or -, respectively. Non-significant relationships are indicated as “ns,” with blanks indicating that the environmental variable was not measured/assessed. Studies marked with an asterisk (*) indicate that biomass, rather than abundance, was the response variable.

Continent	Authors (Year)	Environmental Correlate																
		Flow	Temp.	DO	Cond.	Sal.	pH	Chl- <i>a</i>	OM	Sand	Silt	Peb./Ston	Nutr.	Redox	Hard.	Depth	PM	Turb.

												e						
Nort h Ame rica	Belang er et al. (1985)								+	+								
	Belang er (1991)			+														
	McCa be et al.(199 7)									ns	-	ns				ns	+	
	Karata yev et al. (2003)									+	-							
	Vaugh n and Spoon er (2006)	-								ns	n s	-						
	Brown et al. (2007)	ns	ns	n s	ns			ns		ns	n s	ns				ns	n s	
	Coope r (2007)		ns		ns				+	+	-					ns		
	Simar d et al. (2012)		+															
	Sedlac ek and Schoe nebeck (2015)	ns	ns	n s	ns	n s	n s			ns	n s	ns				-	-	ns
	Patrick et al. (2017)									ns	n s	ns				-		
	Castan eda et al. (2018)	+	+	n s	ns					ns	n s	ns				-		+
	McDo well et al. (2018)									ns	n s	-						
	Henric ksen and Bollen s (2022)		ns	n s			n s	-										
	Kelley	+								+	-		ns			-		

	et al. (2022)																	
	Robb-Chavez et al. (this study)	-	+	ns	ns	ns	ns	ns	-	+	ns							
Euro pe	Schmidlin and Baur (2007)	-								+	ns	ns						
	Sousa et al. (2008b))*		ns			ns	ns	ns	+	+	ns		- (N, NH ₄ ⁺)	+	+		ns	
	Bodis et al. (2011)	-								+	-				+			ns
	Caffrey et al. (2011)									+								
	Franco et al. (2012)	+	ns	ns		-	ns	ns	ns	ns	ns		ns				ns	
	Ferreira-Rodriguez and Pardo (2014)					-	ns		+	ns	ns	ns						
	Modes to et al. (2013) *	-	+	ns	ns	-	ns	ns	ns	ns	ns		+	(P, PO ₄)			ns	
	Ferreira-Rodriguez et al. (2017)												+	(Ca ⁺)				
	Paganelli et al. (2018)									+		ns						
	Gama et al. (2020)									+	+	-				-		
South America	Silveira et al. (2016)								-	+	ns					ns		
	Pereira	ns	ns	n	ns		n		n	ns	n	ns	ns			ns	n	ns

	et al. (2017)			S			S		S		S						S	
Global Mod eling	McDo well et al. (2014)		+				+				+		- (N H ₄ ⁺)				-	
	Gama et al. (2016)	[Environmental correlates found to be less significant predictors than mean lowest temperature (regional) and elevation]																