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Temperature-dependent functional response of the invasive Asian clam, *Corbicula fluminea,* feeding on natural phytoplankton

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ABSTRACT
The invasive suspension-feeding Asian clam, *Corbicula fluminea*, is abundant and broadly distributed in temperate rivers and lakes, yet its feeding dynamics, including how feeding rate varies as a function of prey density (i.e., functional response) and temperature, are not well known. We therefore undertook feeding experiments using adult *C. fluminea* and varying concentrations of natural phytoplankton prey (measured as chlorophyll *a* concentration). Clearance (filtration) rates adjusted to clam wet weight (WW) did not vary with food concentration at either 15.0 or 20.5 °C and averaged 57.5 and 167.6 mL g^{-1} WW h^{-1}, respectively. Ingestion rate, however, increased linearly with increasing food concentration at both 15.0 and 20.5 °C. Both clearance rate and ingestion rate showed strong temperature dependence, with Q_{10} coefficient values of 6.99 and 5.65, respectively. These high feeding rates support the emerging view that this species is capable of extensive ecological impacts in both its native range and invaded habitats.

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aquatic invasive species; bivalve suspension feeding; feeding rate; Q_{10} coefficient; temperature dependence

Introduction

The rate at which an organism feeds often varies as a function of food density (i.e., functional response; sensu Holling 1959) and is a foundational concept in physiological ecology, population biology, and community ecology. Suspension-feeding bivalves generally increase ingestion rate with increasing food density, although the exact nature of this relationship varies within and between species (see reviews by Winter 1978, Jorgensen 1996, Beninger 2009, Pascoe et al. 2009, Riisgård et al. 2011). Of particular interest is whether a given species exhibits either (1) a threshold concentration below which clearance (filtration) and ingestion do not occur or (2) a saturation concentration above which ingestion rate is maximal and constant. Temperature can also be important in regulating functional response, especially in poikilothermic animals such as bivalves, where a change of 10 °C (as often occurs seasonally in temperate regions) can elicit a ~2–3-fold change in physiological rates (Pisek et al. 1973, Gosling 2003, Saucedo et al. 2004, Braby and Somero 2006, Lurman et al. 2014, Xiao et al. 2014, Hraoui et al. 2020).

The Asian clam *Corbicula fluminea* is endemic to freshwater habitats in Southeast Asia, Africa, and the Pacific Islands (McMahon 1983), but it invaded North America in the early 20th century (Counts 1981) and subsequently spread throughout temperate Europe and South America (Mouthon 1981, Ituarte 1994, Karatayev et al. 2005, Sousa et al. 2005, 2008). This abundant and widespread invader is known to consume phytoplankton (Cohen et al. 1984, Beaver et al. 1991), which in turn can have ramifications for entire aquatic food webs (Ilarri et al. 2014, Pigneur et al. 2014, Ferreira-Rodríguez et al. 2018, Bolam et al. 2019). However, few studies have examined the dynamics of feeding by *C. fluminea* (e.g., how feeding rate may vary with food density) and how functional response in turn may vary with temperature. Indeed, knowing the rate at which this organism feeds, and more specifically how feeding rate varies as a function of food concentration and temperature, has implications for both fundamental science (e.g., the first principles of physiological ecology) as well as applied science (e.g., invasion and conservation biology).

We therefore undertook a series of laboratory incubation experiments with adult *C. fluminea* fed a natural assemblage of phytoplankton prey to measure their clearance rates (mL g^{-1} WW h^{-1}) and chlorophyll *a* (Chl-*a*) ingestion rates (µg g^{-1} WW h^{-1}) as a function of food density. We hypothesised that clearance rate would not change with increasing food concentration, except possibly by decreasing after reaching a saturating

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concentration of food, and that ingestion rate would increase with increasing food concentration (e.g., Holling Type I curve), possibly plateauing and remaining constant after reaching a saturating concentration of food (e.g., a Holling Type II curve). In addition, we investigated the potential for seasonal temperature effects (i.e., Q_{10} effects) by running experiments at 2 different temperatures, during summer and autumn. We hypothesised that both clearance rate and ingestion rate would increase with increasing temperature, consistent with a Q_{10} of 2.0–3.0.

Study site

Our experiments were conducted using live clams and the ambient planktonic prey assemblage collected at 2 beaches along the lower stretch of the Columbia River in the Pacific Northwest region of the United States. The 2 sites were located 100 and 155 river km upstream of the river mouth at Astoria, Oregon, USA. The Columbia River is a highly invaded ecosystem (Bollens et al. 2002, 2012, Emerson et al. 2015, Connelly et al. 2020, Dexter et al. 2020a), with *C. fluminea* a conspicuous component of the plankton as juveniles (Dexter et al. 2015, Hassett et al. 2017, Dexter 2020b) and the benthos as adults (McCabe et al. 1997, Bolam et al. 2019).

Methods

We conducted a series of feeding experiments in July and October 2016 with adult *C. fluminea* clams incubated in Columbia River water across a range of available prey concentrations. We describe our methods for selecting sites, collecting live clams and experimental incubation water, and conducting the feeding experiments, including details specific to the functional response component of the experimental design.

On the day prior to each set of experiments, adult clams (>1 cm valve width) were collected by hand from the sediment at ~10–20 cm water depth at the farthest downstream site (Blurock Landing; 45°39′56.76″N, 122°45′33.37″W) and transferred into a bucket filled with ambient river water. At the same time, unfiltered river water containing the phytoplankton prey assemblage for the incubations was collected from 2 Columbia River sites, Blurock Landing and the Bonneville Reservoir (45°42′54.81″N, 121°30′13.38″W), both sites where clams were known to be abundant, using separate 10 or 20 L Nalgene carboys held just under the surface while pointing upstream until completely filled. The clams and filled carboys were transported back to the laboratory at Washington State University, Vancouver, within 6 h of collection. Clams were added to the carboys and stored in a temperature-controlled room at ambient temperatures under a 16:8 h light:dark cycle for 24 h.

In the laboratory prior to each set of experiments, unfiltered river water containing the natural assemblage of phytoplankton (× = ambient phytoplankton concentration) was diluted to 0.25× and 0.50× using 0.22 μm-filtered river water from the same location as the diluent. In addition, ambient river water was concentrated using 0.22 μm reverse filtration until reaching 2×. The experimental design then consisted of a set of control containers without clams and 4 treatment conditions (0.25×, 0.5×, 1×, and 2×) with added clams ($n = 3$ per container), each with 3 replicates. Clams used in the experimental treatments were first acclimated to their respective treatment water for 30 min (although some investigators prefer a longer acclimation period, we chose to keep this relatively short and tractable), after which they were transferred to incubation containers with fresh treatment water for 90 min and then removed. The wet weight (WW) of each experimental clam was measured following the experiments to calculate weight-specific feeding rates.

During each set of functional response experiments, 60 mL subsamples were removed from each initial control, final control, and final treatment incubation container and filtered over Whatman GF/F filters. The filters were wrapped in foil and frozen for a minimum of 24 h and a maximum of 7 d, and then Chl-*a* was extracted and measured using a Turner Model 10-AU fluorometer according to Strickland and Parsons (1972). Clearance rate (mL g^{-1} WW h^{-1}) and Chl-*a* ingestion rate (μg g^{-1} WW h^{-1}) from each feeding incubation were then calculated according to Marin et al. (1986), with corrections applied for gut-filling during acclimation and pseudofeces release during the incubations (see Bolam et al. 2019 for details). Initial statistical analysis indicated no differences between rates measured using the river water from 2 different locations (collected ~55 river km apart), and thus these data were combined, but all data were otherwise analyzed separately between months (Aug vs. Oct).

In addition, values of Q_{10} were calculated for the 2 sets of functional response experiments using the equation:

$$Q_{10} = (R_2/R_1)^{\frac{10^\circ C}{T_2 - T_1}},$$

where R = feeding rate at temperature T, 1 = October experiments (15.0 °C), and 2 = July experiments (20.5 °C).

To assess the influence of prey concentration on clam feeding rates (i.e., functional response), regressions were performed using the *car* package (Fox and Weisberg 2018) in R programming software (R Core Team 2015). The effect of temperature on the relationship between prey concentration and clam feeding rates (clearance and ingestion rates) was analyzed using analysis of covariance (ANCOVA).

Results and discussion

Clearance rates

Clearance rates of adult *C. fluminea* did not vary with food concentration at either 15.0 or 20.5 °C (neither monthly regression had a slope significantly different from 0; Jul: $F = 3.46$, $p = 0.08$; Oct: $F = 0.79$, $p = 0.38$; Fig. 1a). The average clearance rate was 57.5 mL g^{-1} WW h^{-1} at 15.0 °C (Oct) and 167.6 mL g^{-1} WW h^{-1} at 20.5 °C (Jul). We found no apparent threshold effect (food concentration below which no clearance occurred) or apparent saturation effect (food concentration above which clearance rate declined; Fig. 1a).

Our measured clearance rates of adult *C. fluminea* are near the high end of the range reported by other investigators (Table 1) but with some notable caveats. First, previous studies of *C. fluminea* feeding used a wide range of experimental techniques and reported their results using many different units (Table 1), all of which complicate comparison among studies. The units of our calculated clearance rates (mL g^{-1} WW h^{-1}) are comparable to those reported by Prokopovich (1969) and Cohen et al. (1984), although both of these previous studies were conducted at higher temperatures (20.0—26.5 °C) than our study (15.0 and 20.5 °C), and only Cohen et al. (1984) and Beaver et al. (1991) used natural prey (as we did). Prokopovich (1969) reported clearance rates of 20–150 mL g^{-1} WW h^{-1}, comparable to, if slightly lower than, our measured rates 2–250 mL g^{-1} WW h^{-1}. Cohen et al. (1984) reported rates of 13.8–33.9 mL g^{-1} WW h^{-1}, considerably lower than our measured rates. These findings are especially surprising given that our experimental temperatures were several degrees lower than those of Cohen et al. (1984). By comparison, Silverman et al. (1995) reported a clearance rate of 264 mL g^{-1} live weight h^{-1}, slightly higher than our maximal rate, although these investigators used cultured *E. coli* rather than natural prey (as we did). Generally speaking, clearance rates reported in previous studies (Table 1) are comparable or somewhat lower than our measured clearance rates.

Ingestion rates

The average Chl-*a* ingestion rate of adult *C. fluminea* was 0.159 µg g^{-1} WW h^{-1} at 15.0 °C and 0.412 µg g^{-1} WW h^{-1} at 20.5 °C. Overall, our measured ingestion rates ranged from 0 to 1.0 µg g^{-1} WW h^{-1}. Bolam et al. (2019) is the only previous study reporting ingestion rates with which we can make direct comparisons (Table 1), and even this comparison requires applying a C:Chl-*a* conversion. We are unaware of any direct measurements of C:Chl-*a* in the Columbia River, although Prahl et al. (1998) used a literature value of 50, even though this ratio is known to vary seasonally, spatially, and with nutrient conditions (e.g., Riemann et al. 1989). Nevertheless, applying a C:Chl-*a* ratio of 50, we can convert the ingestion rate of Bolam et al. (2019) to 0–0.4 µg g^{-1} WW h^{-1}, which falls within the lower range that we report here. However, it is notable that our higher ingestion rate measurements were made at twice (2×) natural prey concentrations, whereas those of Bolam et al. (2019) were made at ambient (1×) prey concentrations.

Our ingestion rate results showed a strong dependence on food concentration at both temperatures; that is, ingestion increased linearly with increasing food concentration (both monthly regressions had slopes that were highly significantly different from zero; Oct: 15.0 °C, $F = 21.07$, $p = 0.0002$; Jul: 20.5 °C, $F = 24.99$, $p = 0.0001$; Fig. 1b). We found no apparent threshold effect (food concentration below which ingestion ceased) or apparent saturation effect (food concentration above which ingestion was maximal and constant; Fig. 1b).

In general, the shape of our functional response curve (ingestion as a function of food density; Fig. 1b) for *C. fluminea* resembled a Holling Type I curve (Holling 1959; i.e., no evidence of saturation, although this may have been a result of our inability to create highly concentrated food conditions). Because of limitations of our reverse filtration method to highly concentrate food, we were only able to manipulate food density up to a level of twice ambient conditions, or Chl-*a* ~8 µg L^{-1}. Chl-*a* in the Columbia River is below this level for much of the year, but during the late winter/early spring phytoplankton bloom period, it can often reach concentrations exceeding 10 µg L^{-1} (Dexter et al. 2015). We therefore recommend that future studies use higher concentrations of food than we were able to achieve to better test for possible saturation effects in feeding. This modification might require the use of cultured prey, which would likely achieve higher prey concentrations, but would also present the trade-off of being less natural than the field-collected prey assemblages used in our experiments.

Also, we found little evidence for a threshold effect on the feeding of *C. fluminea*; only 1 of the 2 regression lines (ingestion during Oct; Fig. 1b) suggests a possible cessation of feeding at low food levels. This particular aspect of the feeding dynamics of *C. fluminea* also warrants further investigation.

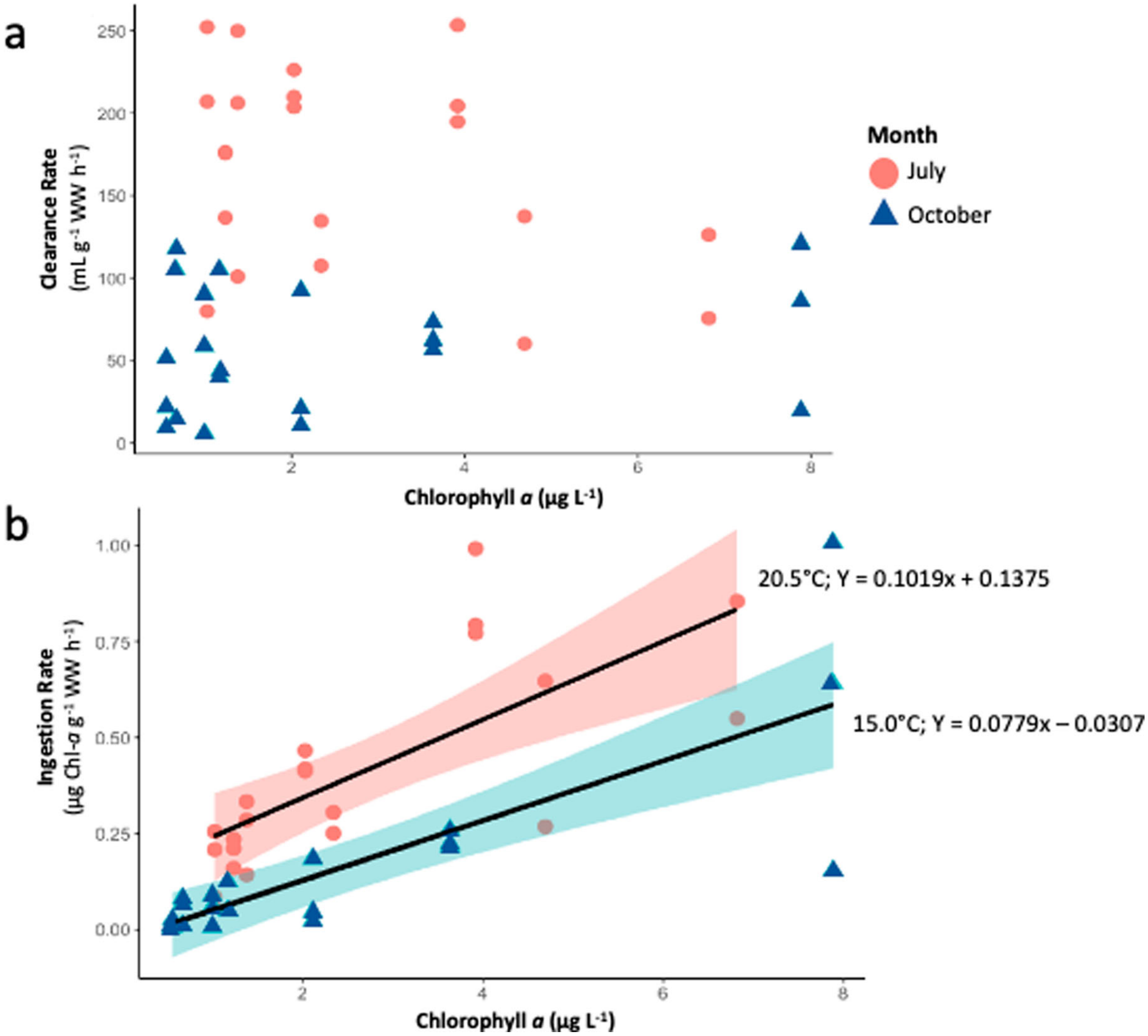

Figure 1. Experimentally determined (a) clearance rates and (b) Chl-*a* ingestion rates of adult *C. fluminea* as a function of food density (Chl-*a* concentration of natural microplankton collected from the Columbia River during July and October 2016). Solid lines are results of linear regressions; shaded areas are 95% confidence intervals. Both regression lines in panel (b) had slopes significantly different from zero ($p < 0.001$).

Note that all our clearance and ingestion rates, irrespective of temperature, were based on assessing abundance of food by measuring bulk Chl-*a* concentration, which masks any possible effects that variable prey taxonomic composition might have on feeding. For instance, *C. fluminea* is known to be selective in its feeding (Way et al. 1989, 1990, Atkinson et al. 2011, Bolam et al. 2019), as are many other bivalves (Levinton et al. 1998, Dionisio Pires et al. 2004, Naddafi et al. 2007, Tang et al. 2014). Moreover, the compositions of the natural (ambient) prey in our 20.5 °C (Jul) experiments and our 15.0 °C (Oct) experiments were necessarily different. Bolam et al. (2019) reported that the microplankton composition in the Columbia River during July predominantly consisted of diatoms, with lower abundances of flagellates, chlorophytes, cyanobacteria, dinoflagellates, and ciliates, whereas in October, cyanobacteria became the dominant taxon while other taxa declined in relative abundance. Thus, we cannot rule out the possibility that the lower clearance and ingestion rates we observed in October compared to July were depressed because of the higher relative abundance of less desirable cyanobacteria prey rather than due to lower temperature alone. More generally, differences in the microplankton prey composition between our 2 experiments, not evident by measuring Chl-*a* alone, may have affected (in unknown ways) the feeding rates and Q_{10} values (discussed later) measured in our experiments. Moreover, seasonal variation in (1) clam size and (2) clam physiological state (not measured by us) may also have contributed to the different results in our 2 feeding experiments. Finally, the acclimation period used in any given experiment may affect the results, as might

Table 1. Summary results from known peer-reviewed experimental studies of *C. fluminea* feeding. n/a = not available; WW = wet weight and DW = dry weight.

					Clam size range	
Authors and year	Clearance rate range	Ingestion rate range	Prey medium	Temperature	Length	Weight
Beaver et al. 1991	705–727 mL clam^{-1} h^{-1}	n/a	Natural ambient prey	24 °C	21–23 mm	n/a
Bolam et al. 2019	0–800 mL clam^{-1} h^{-1}	0–18 µg C clam^{-1} h^{-1}	Natural ambient prey	15 and 20.5 °C	16–24 mm	7.6–12.6 g WW
Buttner and Heidinger 1981	300–800 mL clam^{-1} h^{-1}	n/a	Cultured *Scenedesmus* sp.	21–24 °C	n/a	0.8–7.4 g soft tissue
Cohen et al. 1984	13.8–33.9 mL g^{-1} WW h^{-1}	n/a	Natural ambient prey	26.5 °C	n/a	2.3–7.1 g WW
Foe and Knight 1986	2.8–4.5 mL g^{-1} DW h^{-1}	n/a	Cultured diatom taxa	20 °C	n/a	n/a
Lauritsen 1986	109–1370 mL clam^{-1} h^{-1}	n/a	Cultured algae	8–31 °C	21.2–24.1 mm	n/a
Liu et al. 2009	1.0–5.5 mL mg^{-1} DW h^{-1}	200–2500 cells mg^{-1} DW h^{-1}	Cultured toxic and non-toxic *Microcystis aeruginosa* and *S. obliquus*	25 °C	20–25 mm	n/a
Prokopovich 1969	20–150 mL g^{-1} WW h^{-1}	n/a	Suspended solids	20–24 °C	13–36 mm	0.8–23 g WW
Rollwagen-Bollens et al. (this study)	2–250 mL g^{-1} WW h^{-1}	0–1.0 µg Chl-*a* g^{-1} WW h^{-1}	Natural ambient prey	15 & 20.5 °C	16–24 mm	7.6–12.6 g WW
Silverman et al. 1995	264 mL g^{-1} WW h^{-1}	n/a	Cultured *E. coli* in artificial pondwater	Room temperature	23–25 mm	7.9 g WW
Viergutz et al. 2012	320–1400 mL clam^{-1} h^{-1}	n/a	Cultured *Chlorella vulgaris*	15–21 °C	12–20 mm	n/a
Way et al. 1990	10–610 mL clam^{-1} h^{-1}	n/a	2 µm micro-spheres	15 °C	n/a	50–400 mg ash free DW
Zhao and Liu 2018	80–400 mL g^{-1} soft tissue h^{-1}	n/a	Cultured *Chlorella vulgaris*	20 °C	18–25 mm	n/a

using lentic (standing water) versus lotic (flowing water) experimental conditions.

Temperature dependence

Both clearance rates and ingestion rates of adult *C. fluminea* showed strong temperature dependence. For clearance rates, we used the average rate for each temperature reported earlier to calculate a Q_{10} of 6.99. For ingestion rates, we used the average rate for each temperature reported earlier to calculate a Q_{10} of 5.65.

The Q_{10} values we observed for *C. fluminea* were high. For instance, Q_{10} values in the range of 2.0–3.0 are typical of poikilothermic animals in general (Gosling 2003, Saucedo et al. 2004). The only published Q_{10} values for *C. fluminea* known to us are from Xiao et al. (2014), who reported values ranging from 0.65 to 1.83. However, Peck et al. (2002) reported Q_{10} values of 1.9–5.0 for the bivalve *Laternula elliptica*, and Johnson and Brinkhurst (1971) reported Q_{10} values as high as 9.76 for *Pisidium* clams. Thus, our Q_{10} value of 5.65 for ingestion rate of *C. fluminea*, while high, falls within the range observed for other bivalves, and our Q_{10} value of 6.99 for clearance rate of *C. fluminea* is at the exceptionally high end of this range. We note, however, that our Q_{10} values were based on measuring rates at only 2 temperatures and should therefore be viewed with appropriate caution.

Conclusions

Overall, our results suggest that the Asian clam *C. fluminea* can feed at notably high rates, especially at high food concentrations (consistent with a Type I functional response), and that feeding by *C. fluminea* also shows a high degree of temperature dependence (as indicated by Q_{10} values of 5.65 for ingestion rate and 6.99 for clearance rate). The high feeding rates support the emerging view that this invasive species is capable of extensive ecological impacts in both its native range and its many invaded habitats.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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