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Research Article

Distribution, abundance and condition of an invasive bivalve (*Corbicula fluminea*) along an artificial thermal gradient in the St. Lawrence River

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Abstract

The Asian clam *Corbicula fluminea* has been introduced to lakes and rivers worldwide, but its physiological requirements generally restrict its distribution to water temperatures of ≥ 2 °C. In north temperate areas of North America, *C. fluminea* therefore occurs primarily in artificially heated waterbodies. In November 2009, *C. fluminea* was discovered for the first time in the St. Lawrence River within the thermal discharge plume of the Gentilly-2 nuclear power plant, in which the species had developed an abundant and persistent population. In summer 2011, the distribution, abundance and body condition of *C. fluminea* were sampled in sections of the river immediately upstream and for several kilometres downstream of the power plant. The thermal plume extended as far downstream as 4 km, and *C. fluminea*'s population density declined along this distance. A generalized linear mixed model indicated that *C. fluminea*'s local population density was related negatively to water depth and positively to temperature, turbidity and flow velocity, with temperature having the greatest influence. At stations closer to the discharge source, clams were larger and had a higher mean body condition. However, when temperatures exceeded 30 °C in the discharge canal during mid-summer, body condition was maximal outside the canal at 1.5 km downstream of the discharge source. Thus, although the plume provided a winter thermal refuge for *C. fluminea*, it created a temperature gradient that encompassed both the upper and lower tolerance limits of the species. The *C. fluminea* population was extirpated during the winter months when normal temperatures were re-established following permanent cessation of power plant activity in December 2012.

Key words: Asian clam, freshwater, invasive species, physiological ecology, population dynamics, power plant, water temperature

Introduction

Since the 1800s, the Great Lakes–St. Lawrence River basin has been transformed by successive invasions of nonnative species that have altered water quality, biodiversity, food webs and ecosystem processes (Ricciardi 2006). Over 85 nonnative species of invertebrates, fishes, plants and algae have been reported in the St. Lawrence River (de Lafontaine and Costan 2002; Ricciardi 2006) and in many cases their colonization was facilitated by shipping activity, recreational water use and anthropogenic disturbances (Hudon and Carignan 2008; de Lafontaine and Costan 2002). Aquatic systems are more susceptible to invasions when they are subject to frequent disturbance or have been extensively modified (Moyle and Light 1996; Havel et al. 2005; Sorte et al. 2013). In particular, the modification of temperature regimes through climate change (Sorte et al. 2013; Floury et al. 2013) or the discharge of thermal effluent (Langford 1990) affects the survival, growth, reproduction and the distribution of aquatic organisms (Caissie 2006; Walther 2010; Urian et al. 2011; Floury et al. 2013; McDowell et al. 2017) and mediates the invasion success of introduced species (Fey and Cottingham 2012; Oyugi et al. 2012; Meek et al. 2012). Although the thermal requirements of subtropical/tropical species prevent most of them from becoming established in temperate environments (Coutant 1977; Leach 2003; Bomford et al. 2010), artificially heated waters can provide such species with a refuge from severe winter temperatures and thus enable their northern range expansion (Langford 1990). Conceivably, these refuge populations could expand into natural environments as thermal barriers are lifted under climate change (Floury et al. 2013).

In November 2009, the Asian clam *Corbicula fluminea*—a globally invasive subtropical freshwater bivalve (Crespo et al. 2015)—was discovered in the thermal plume of the Gentilly-2 nuclear power plant (hereafter known as G2NPP) in Bécancour, Québec (Simard et al. 2011; Simard et al. 2012). This is the first record of *C. fluminea* for the St. Lawrence River and the coldest freshwater system in which the species has been found. The thermal discharge of G2NPP prevented the formation of ice in this section of the river by maintaining water temperatures at ~10 °C above ambient throughout the winter (Langlois and Vaillancourt 1990). A frequently cited study suggested that *C. fluminea* cannot survive prolonged exposure to temperatures below 2 °C (Mattice and Dye 1975), fostering the conventional view that the species can exist only in artificially heated waters where it occurs in temperate regions (McMahon 1983; but see McMahon 1999). However, populations exposed to low winter temperatures have been discovered in lakes in New York State (M. Modley, Lake Champlain Basin Program, pers. comm.; E. Cvetanovska and A. Morden, McGill University, unpubl. data) and Ireland (Minchin 2014), and previously in a Michigan river (Janech and Hunter 1995). Thus, it is conceivable that *C. fluminea* could colonize the entire freshwater section of the St. Lawrence River as winter temperatures continue to rise with climate change (Hudon et al. 2010).

Corbicula fluminea is a highly successful invader owing largely to its early maturation and hermaphroditic fertilization—traits that allow populations to recover quickly after being exposed to harsh environmental conditions (McMahon 2002). Dense filter-feeding populations can greatly reduce suspended particles from the water column, thereby promoting prolific macrophyte growth and fundamental habitat changes that can restructure benthic and pelagic communities (Lauritsen 1986; Phelps 1994; Ilari et al. 2012). The tissues of *C. fluminea* sequester heavy metals and other contaminants, which are released into the water column following mass mortality events (boom-bust cycles) or are transferred directly to molluscivores (Robinson and Wellborn 1988; Inza et al. 1997; McMahon 1999; Liao et al. 2008; Patrick et al. 2017). Furthermore, rapid accumulation of clams in water intake systems causes municipal and industrial biofouling problems that incur annual costs of billions of dollars in the United States (Isom 1986).

The thermal plume produced by G2NPP offered an outdoor laboratory to compare the life history and population dynamics of *C. fluminea* along a thermal gradient. We sampled clams at stations inside and outside the thermal plume to test the following predictions: i) *C. fluminea*'s distribution is restricted to the thermal plume, and ii) its age, iii) body condition, iv) biomass and v) reproductive capacity decline with distance from the discharge source. Given that *C. fluminea* requires 15–16 °C for reproduction and suffers high mortality as temperatures approach 2 °C (McMahon 1999), it was not expected to survive or reproduce outside the plume. Temperature was hypothesized to be the major abiotic factor limiting the growth and reproduction of *C. fluminea*, but local abundance was expected to be affected by additional factors including sediment particle size and flow velocity; the species reportedly attains higher densities in coarse sand and gravel substrates (McMahon 1983; Schmidlin and Baur 2007; Bodís et al. 2011) and in shallow, flowing and well-oxygenated areas (McMahon 1983).

Methods

Our study site is a section of the St. Lawrence River surrounding the G2NPP at Bécancour, Quebec (46º23′42.51″N; 72º21′23.53″W). The G2NPP had been in operation and functioning at 50–100% of its maximum capacity from 1983 to December 2012, throughout which it experienced random reactor stoppages for varying periods of days to weeks (Langlois and Vaillancourt 1990). During its operation, a thermal plume extended at least 4.0 km downstream from the power plant. In the discharge canal, water temperatures were typically 13–18 °C higher than ambient, and this difference attenuated downstream and varied throughout the year (Simard et al. 2012). For this study, we divided the plume area into four sections defined by distance and temperature: the first section was in the 600 m discharge canal, whereas the second, third and fourth sections were 600–1450 m, 1450–2600 m, and 2600–4000 m downstream of the discharge source, respectively. Each section included three transects and three sampling stations per transect.

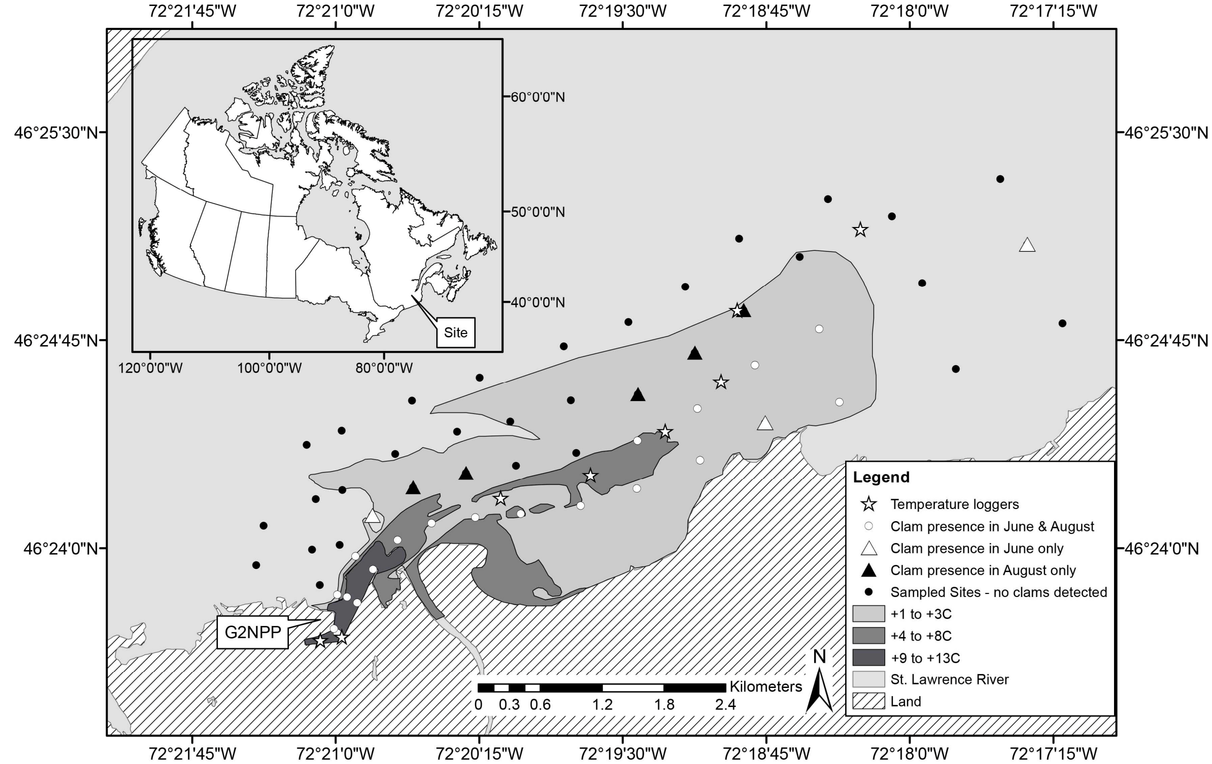

Figure 1. Map of the thermal plume generated by the Gentilly-2 nuclear power plant on the St. Lawrence River (Quebec, Canada) showing the thermal plume, sampled sites, temperature logger locations and *C. fluminea* distribution.

Distribution and abundance of C. fluminea *and environmental variables*

In October 2010, we deployed digital loggers (HOBO TidbiT v2 Temperature Data Loggers), anchored at the river bottom, along the thermal plume to record water temperature hourly until retrieved in May 2011 (N = 207 days); two temperature loggers in the canal were retrieved in August 2011 (N = 296 days). During summer 2011, we sampled 36 stations along the previously defined 4-km section of the plume (Figure 1). These were located within 12 transects (3 stations per transect) perpendicular to the shore. As a consequence of stations selected based on their accessibility throughout the summer, the distance between transects and between stations varied slightly (on the order of meters). In addition, we sampled 20 stations outside the plume (7 upstream, 6 downstream and 7 north of the plume). Because the phenology of *C. fluminea* is mediated largely by temperature (e.g. single or biannual reproductive periods during summer months), sampling was conducted in June and August (McMahon 1999). At each station, we took three petite ponar grabs (152 × 152 mm sample area) lowered from a boat; thus, we obtained 168 samples. We visually recorded the presence or absence of macrophytes in our petite ponar grabs. Sediment size was examined by spreading the sediment from each petite ponar grab evenly in a tray and visually determined the percent coverage of particular substrate types within a pre-marked 0.0625 m^2 quadrat (Jones and Ricciardi 2005). These measurements were multiplied by their respective phi-values ($\varphi = -\log_2$ [mean particle diameter, in mm]) of each substrate type and then summed to give the mean sediment size per station (cf. Mellina and Rasmussen 1994; Jones and Ricciardi 2005). We sieved the collected sediment through a 500 µm mesh and preserved the invertebrates in 75% ethanol. At each sample station, we measured depth (m) using a depth sounder, and temperature (°C), conductivity (µs/m) and dissolved oxygen (mg/L) just above the sediment using a digital YSI (Pro 2030) meter. We measured flow (m/s) using a digital flow meter (Swoffer model 3000), and transparency (cm) using a Secchi tube at the surface of the water. Subsequently, we sorted the preserved samples under a dissecting microscope and removed all macroinvertebrates from the sediment.

All three grabs from the early-summer sampling were processed; however, owing to time constraints, only two grabs per station were sorted for the late-summer sampling. All *C. fluminea* obtained from the sorted grab samples were counted and measured.

Body condition, reproductive status and size structure of clams

All adult *C. fluminea* (> 6 mm) were kept in 75% ethanol for a maximum of two weeks prior to examination of their body condition. We measured the length (parallel to the umbo) of the clams to the nearest 0.01 mm using digital vernier calipers. We dissected each adult clam and noted the presence/absence of brooding larvae in the gills to determine their reproductive status (Britton and Morton 1982). The tissue was removed from the shell with a scalpel, and its preserved wet weight was measured to the nearest 0.0001 g. Tissues and shells were placed in an oven at 70 °C for 24 hours, to obtain their dry mass (Cataldo et al. 2001). Juvenile clams (<6 mm length) were measured under a dissecting microscope using a stage micrometer, but were not weighed and thus were excluded from the condition analysis. Size class frequencies of all clams were graphed and the peaks of histograms were identified as cohorts (Schmidlin and Baur 2007). The size-frequency distributions for populations in each of these sections were measured in both June and August.

Statistical analysis

Environmental factors were compared between stations inside and outside the thermal plume using ANOVA, for June and August separately. We also compared the same factors between the canal and the rest of the plume (ROP), using ANOVA and Tukey's post-hoc test. Relationships between the environmental factors and distance from the discharge source were tested using least-square regression for normally distributed data, and Spearman correlation for non-normally distributed data.

To determine which environmental factors explained variation in local abundances, we fitted a generalized linear mixed model (GLMM) using R (Bates et al. 2011; R Development Core Team 2012). Given that multiple grabs per station were taken at two different time periods, "station" and "sampling period" were treated as random effects in the model (Bolker et al. 2009; Zuur et al. 2009). Fixed effects in the model were temperature (°C), depth (m), dissolved oxygen concentration (mg/L), specific conductivity (µs/m), transparency (cm), flow velocity (m/s), sediment size (phi-scale) and the presence/absence of macrophytes. Conductivity and transparency were not used in the same model because these variables were correlated (Pearson correlation, r = 0.6, $p < 0.001$). To account for overdispersion, we included individual observations (i.e. each grab) as a random effect (Bolker et al. 2009). We used Akaike's Information Criterion (AIC) and the information-theoretic approach to achieve the most parsimonious and biologically relevant inferences about the roles of these environmental factors. The model with the lowest AICc score and highest Akaike weight (ω_i) were assumed to be the best suited to explain trends in the data; models with a difference in AICc (Δ_i) less than 2 are considered equivalent (Burnham and Anderson 2002). To assess the differences in AIC scores and "a priori" hypotheses, we tested ten models using the "drop1" function (R Development Core Team 2012). Variables were removed from the model if they showed no substantive change in AIC values (Bolker et al. 2009).

We compared the condition of *C. fluminea* 1) inside the discharge canal versus the ROP, and 2) in June versus August, by a two-factor analysis of covariance (ANCOVA) with dry weight as the dependent variable, shell length as the covariate, and station and time as factors (Glantz and Slinker 2001; IBM Corp. 2011). We aimed to use restricted size classes of the clams to maximize overlap between all stations, but it was difficult to obtain sufficient numbers of clams of the same size class because of differences in population dynamics between the canal and the ROP. The early-summer samples consisted of 32 clams (7–28 mm) for the canal, and 45 clams (6–12 mm) for the rest of the plume. The late-summer samples consisted of 131 clams (6–12 mm) for the canal and 73 clams (6–13 mm) for the rest of the plume. Assumptions of normality, homogeneity of regression slopes, and homogeneity of variance were tested and supported. Contingency tests on the proportion of gravid clams were conducted to compare differences in reproductive status between sampling periods (June versus August) and location (inside or outside the canal). Lastly, maximum shell length and biomass were regressed against distance from the discharge source.

Results

Population density of C. fluminea *and environmental variables*

Sampling in June 2011 revealed a mean population density of 275.9 ± 146.3 clams m^{-2} across the 4-km plume (Table 1), but abundance was highly skewed

Table 1. Densities of live *C. fluminea* observed downstream of the G2NPP over time.

Date	Density (m^{-2}) Entire plume	 Canal	Source
Nov 2009	303 ± 132	841 ± 125	Simard et al. 2011
Aug 2010	3380 ± 1315	5339 ± 2500	Simard et al. 2012
Oct 2010	n/a	2151.8 ± 63.2	This study
June 2011	275.9 ± 146.3	832.9 ± 113.2	This study
Aug 2011	1618.3 ± 650.5	5290.9 ± 2211	This study
May 2012	382.5 ± 153.3	1026.6 ± 358.6	Hamelin 2013; unpubl. data
Sep 2012	940.7 ± 217.5	2237.2 ±179.8	Hamelin 2013; unpubl. data
June 2013	0	0	This study
Aug 2013	0	0	This study

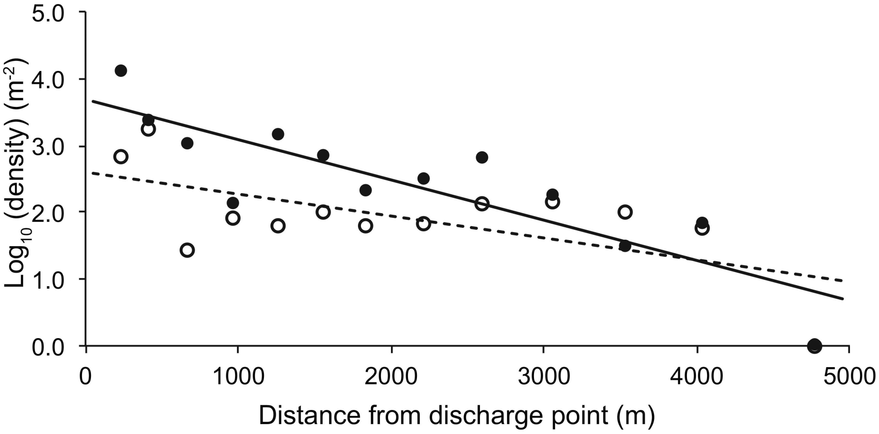

Figure 2. Relationship between the log-transformed *C. fluminea* density (clams m^{-2}) and distance from the discharge source (m) in June (dashed line) and August (solid line). Line fitted by least-squares regression, June: $y = -0.0003x + 2.604$, $r^2 = 0.344$, $p = 0.0206$; August: $y = -0.0006x + 3.693$, $r^2 = 0.744$, $p = 0.0001$.

toward the canal area, which supported a higher density (832.9 ± 113.2 m^{-2}) than the rest of the plume (90.3 ± 10.8 m^{-2}). We found only a single individual (a juvenile clam) outside the pre-defined plume at 5.5 km downstream from the discharge source (Figure 1). Environmental conditions in the river were substantively modified by the thermal plume; depth and dissolved oxygen were lower, whereas temperature and specific conductivity were higher, inside the plume compared to sites beyond (Supplementary material Table S1).

In August, *C. fluminea*'s population density (1618.3 ± 650.5 m^{-2} across all sampling stations) was nearly 6-fold higher than in June, with 13 times as many clams in the canal (5270.9 ± 2211 m^{-2}) than in the ROP (400.8 ± 173.2 m^{-2}). No individuals were collected outside the plume area (Figure 1). Temperature remained higher in the plume and was the only environmental variable that differed from outside the plume.

In both June and August, the population density of *C. fluminea* decreased log-linearly (June: $p = 0.02$, $r^2 = 0.344$, $N = 13$; August: $p = 0.0001$, $r^2 = 0.72$, $N = 13$) with distance downstream from the discharge source and the linear relationship did not statistically differ between sampling periods, June and August (ANCOVA, $F_{3,22} = 2.886$, $p = 0.104$; Figure 2). Only one physical variable, mean point temperature, was correlated with distance downstream from the discharge source (Figure 3a); the same pattern was confirmed using thermograph data from October 11, 2010 to August 2, 2011 (Figure 3b).

Of the ten multivariate models tested to explain *C. fluminea* density based on “a priori” hypotheses, three were supported ($\Delta_i < 2$, Table 2). The top model, explaining 39% of the variation ($\omega_i = 0.390$), included a positive effect of temperature and flow velocity and a negative effect of depth and transparency (“Model 4”; Table 3).

Body condition and population size structure

Body condition of the clams was examined separately for the canal and ROP, because these locations differed in most environmental variables (Table S2). Temperatures in the canal in August were significantly higher than temperatures recorded in the ROP at any time during the year (ANOVA, $p < 0.001$, $F_{3,68} = 12.85$; Tukey's post hoc tests; Table S2).

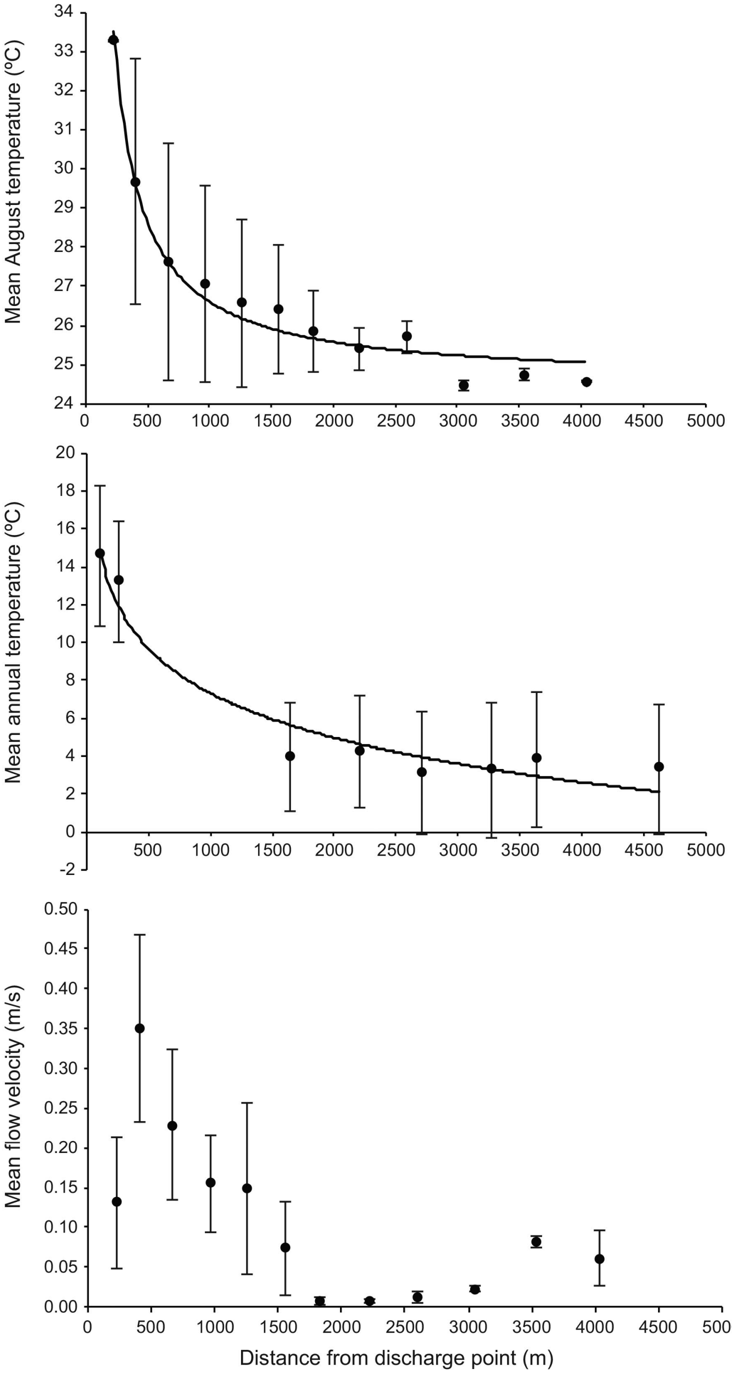

Figure 3. a) Mean temperature sampled in August along the thermal gradient. Line fitted by least-squares regression: $y = 24.55 + 2050.62/x$, $r^2 = 0.975$, $p < 0.001$. b) Mean temperature recorded hourly between October 2011 and May 2012, against distance from the heat source. Line fitted by least-squares regression: $y = -3.39 \ln(x) + 30.78$, $r^2 = 0.953$, $p < 0.001$. c) Mean flow velocity recorded in August along the thermal gradient ($p > 0.05$). June data followed the same trends. Error bars for one standard deviation; where error bars are not visible, the error is smaller than the size of the marker.

The dry mass-shell length relationships for adult clams collected in the canal did not differ between sampling periods (ANCOVA, $F_{1,276} = 0.251$, $p = 0.617$), but did differ from those of the ROP (ANCOVA, $F_{1,276} = 5.827$, $p = 0.016$; Figure 4). There was a significant interaction between station and time (ANCOVA, $F_{1,276} = 6.995$, $p = 0.009$). For a standard shell length of 8.3 mm, the dry tissue weights for clams in the canal and the ROP were identical in June (~ 0.0038 g, ANCOVA, $F_{1,74} = 0.003$, $p = 0.953$). By contrast, in August, clams in the ROP were in better condition than those in the canal (i.e., 0.0044 versus 0.0034 g (~ 22% reduction), respectively, ANCOVA, $F_{1,201} = 28.129$, $p < 0.01$).

Table 2. Summary of the generalized linear mixed models and their corresponding AICc values predicting the abundances and occurrence of *Corbicula fluminea* for the summer sampling with sampling station, grab and time as random factors.

Model[a]	Model ID	K	AICc	Δ_i	ω_i
Depth + flow + temp + trans	4	8	468.83	0.00	0.39
Depth + temp + trans	5	7	469.52	0.69	0.28
Depth + DOconc + flow + temp + trans	3	9	470.78	1.94	0.15
Temp + trans	6	6	471.64	2.80	0.10
Depth + DOconc + flow + temp + trans	2	10	472.35	3.51	0.07
Depth + DOconc + flow + macro + sed + temp + trans	1	11	474.55	5.71	0.02
Depth + DOconc + flow + temp	8	8	496.04	27.20	0.00
DOconc + temp + trans	10	8	496.14	27.30	0.00
Temp	7	5	501.98	33.15	0.00
Depth + flow + sed	9	7	533.92	65.09	2.9 E -15

[a] Depth: water depth (m); DOconc: dissolve oxygen concentration (mg/L); temp: temperature (ºC); trans: water transparency (cm); flow: flow velocity (m/s); sed: sediment type (phi-scale); macro: presence/absence of macrophytes.
K: Parameter count includes intercept and variance.

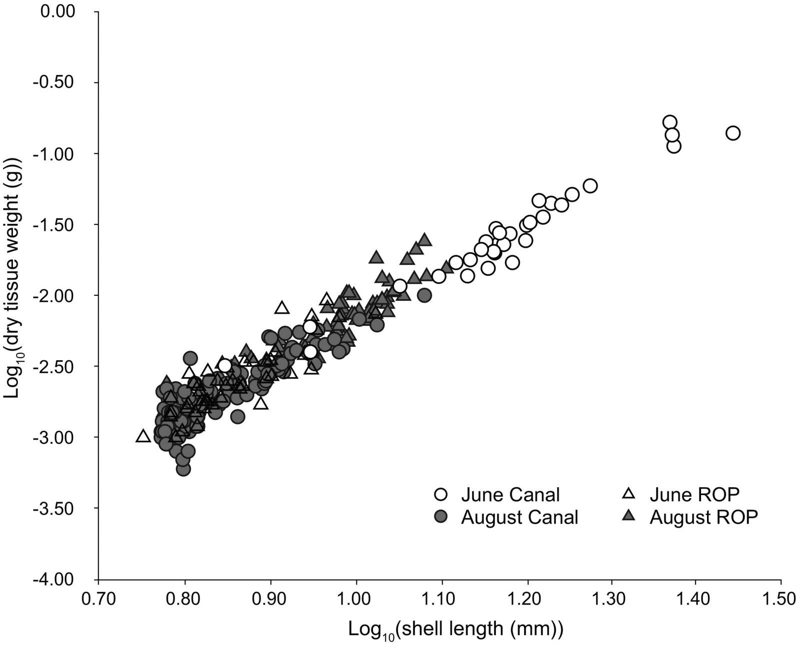

Figure 4. Log$_{10}$transformed dry tissue weight (g) versus log10transformed shell length (mm) for *Corbicula fluminea* adults (> 6mm), in the canal and ROP in June and August, 2011. Lines fitted by least-squares regression: June Canal: $\log_{10}$mass = 3.16 $\log_{10}$length – 5.32 ($r^2 = 0.95$, $p < 0.001$); June ROP: $\log_{10}$mass = 3.30 $\log_{10}$length – 5.45 ($r^2 = 0.74$, $p < 0.001$); August Canal: log10mass = 3.12 $\log_{10}$length – 5.34 ($r^2 = 0.77$, $p < 0.001$); August ROP: $\log_{10}$mass = 2.99 $\log_{10}$length – 5.11 ($r^2 = 0.83$, $p < 0.001$). Condition was greater for August ROP (ANCOVA, p = 0.016).

In June, there was a negative relationship between mean shell length and the distance from the discharge source, with a mean shell length ranging from 20.8 ± 4.6 mm nearest the discharge source to 7.2 ± 0.9 mm at the edge of the plume ($p < 0.001$, $r^2 = 0.80$, N = 12, Figure 5a). By August, however, the relationship between distance and mean shell length of clams was no longer significant ($p > 0.05$, Figure 5b).

Biomass of *C. fluminea* was inversely related to distance from the discharge source in June ($p = 0.002$, $r^2 = 0.635$, N = 12, Figure 5c), but not in August ($p > 0.05$, Figure 5d). The reproduction of *C. fluminea* is also influenced by its position in the thermal plume and by sampling date. There were more brooding clams in the canal than in the downstream

Table 3. Results from the generalized linear mixed model with the lowest AICc score, using variable/fixed effects and random factors (station, grab and time) unique to Model 4, AICc = 468.8.

Variable	Coefficient	Standard Error	p-value
Depth	−0.246	0.131	0.0614
Transparency	−0.050	0.009	6.77e-09
Flow	1.866	1.074	0.0824
Temperature	0.531	0.052	< 2e-16

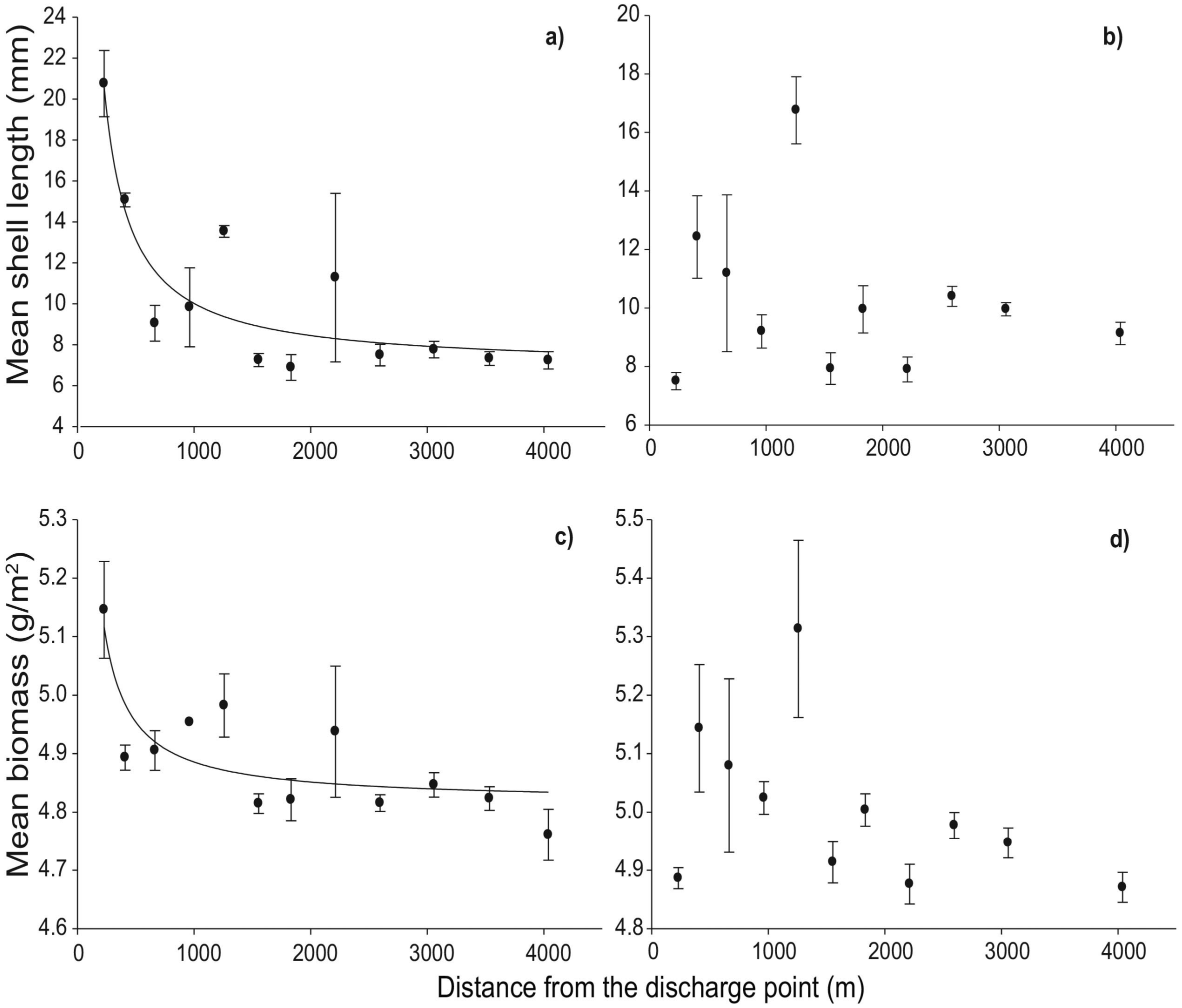

Figure 5. The mean shell length (mm) of adult *C. fluminea* along the thermal gradient in a) June 2011, line fitted by least-squares regression: $y = 3137.6/x + 6.879$, $r^2 = 0.80$, $p < 0.001$. b) August 2011, no relationship between the variables, $p > 0.05$. The biomass (dry tissue weight g/m^2) of *C. fluminea* along the thermal plume in c) June, line fitted by least-squares regression: $y = 68.463/x + 4.817$, $r^2 = 0.635$, $p = 0.002$; d) August, no relationship between the variables, $p > 0.05$. The error bars represent standard error; where the error bars are not visible, the error is smaller than the marker size.

plume area in June, whereas the opposite is true in August, suggesting that clams reproduce earlier in the canal ($\chi^2 = 29.21$, df = 1, $p < 0.001$).

The size-frequency distributions of clams in all four sections of the river suggest at least 3 cohorts throughout the summer (Figure 6). For June, there appears to be a trend of decreasing cohort number from the discharge source: four cohorts in the canal, three cohorts in Sections 2 and 3, and only two cohorts in Section 4. No such trend is discernible for August. In June, the maximum shell lengths for the cohorts were 28 mm, 14.2 mm, 10.6 mm (one outlier at 19.5 mm) and 9.3 mm in the canal and Sections 2, 3 and 4, respectively.

Discussion

The limiting effect of temperature and other abiotic variables

In the St. Lawrence River, the thermal plume generated by the G2NPP provided a refuge habitat for *C. fluminea* characterized by water temperatures consistently warmer than ambient, although other abiotic factors varied during summer. Only one individual was discovered beyond the thermal plume: a juvenile clam collected downstream of the maximum extent of the plume.

Our model selection highlights water temperature as the most significant predictor of the abundance

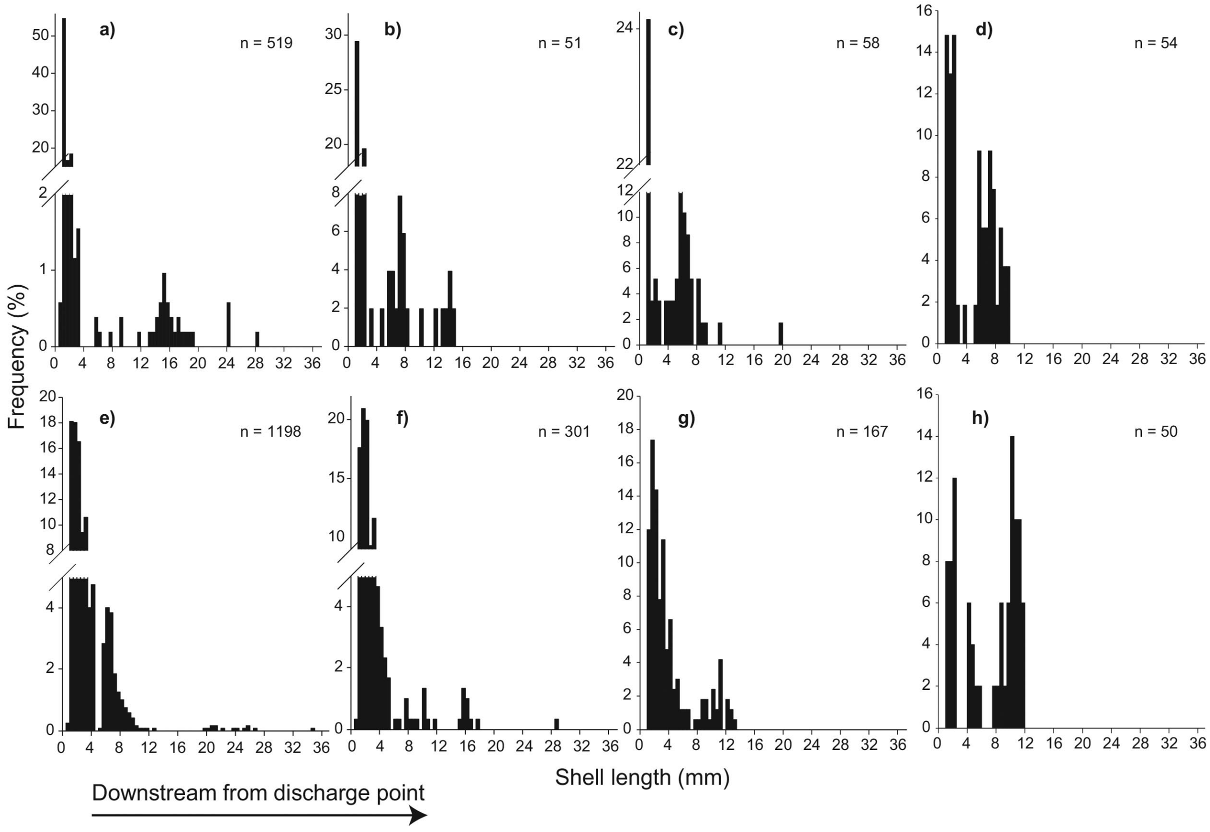

Figure 6. Frequency histogram of *C. fluminea*'s size classes in the canal in June 2011: a) canal, b) Section 2, c) Section 3, d) Section 4; and in August 2011: e) canal, f) Section 2, g) Section 3, h) Section 4. Each peak in the figure represents a potential cohort. Sample sizes indicated in figure.

and distribution of *C. fluminea* in the river. Accordingly, densities of *C. fluminea* are consistently highest inside the discharge canal (Table 1) and decline with distance downstream. Removing temperature from the model yielded the lowest AICc score. The same relationship with temperature is found for biomass and clam size in June, but disappears by August, likely because late-summer temperatures within the canal became suboptimal for feeding, growth and reproduction. Throughout the winter months, the temperature of the canal was consistent and predictable, except when the G2NPP was shut down for brief periods of maintenance. Temperatures never fell to *C. fluminea*'s putative cold tolerance limit of 2 °C, but frequently exceeded its upper tolerance limit of 30 °C. By contrast, temperatures logged at 1.5 km and 4.5 km from the discharge source in the thermal plume were more variable, often falling below 2 °C in winter, but never exceeding 30 °C in the summer (Figure S1).

Although *C. fluminea* tolerates indefinite exposure to temperatures between 2 °C and 34 °C in the laboratory, its filtration rate, oxygen uptake and reproduction are all significantly depressed when temperatures exceed 30 °C (Habel 1970; Mattice and Dye 1975; Cherry et al. 1980; McMahon 1983; McMahon 1999). Temperature loggers in the discharge canal of G2NPP recorded water temperatures above 30 °C for 39 days between June and the first week of August 2011 (Figure S1); based on temperatures recorded manually during sampling events, we suspect that they remained above 30 °C for the entire month of August. Despite the potential physiological stress that such high temperatures might have imposed on *C. fluminea,* its population density was positively correlated with temperature, possibly because of reproduction that likely occurred in June. The recruits in the canal may not have been exposed to the sub-optimal temperatures long enough to cause mass mortality in June; but their body condition, growth and biomass were significantly reduced by August.

The local abundance of *C. fluminea* was reduced in deeper and more transparent waters, and enhanced in areas subject to higher flow velocity. Most studies suggest that *C. fluminea* prefers shallow habitats (Dresler and Cory 1980; Bagatini et al. 2007; Brown et al. 2007), although some have reported either positive, or an absence of, depth effects on its distribution and density (Schmidlin and Baur 2007; Cooper 2007). We speculate that high flows in the plume might contribute to the re-suspension of organic material from the sediment, providing more nutrients to the clams. The filtration activities of an abundant *C. fluminea* population can reduce turbidity (Cohen et al. 1984; Lauritsen 1986; Phelps 1994), so a negative correlation between turbidity and clam density might be expected; however, our study found higher densities in more turbid waters. In this area of the river basin, nutrient inputs from agricultural land contribute to the river's productivity (Hudon and Carignan 2008), and tidal activity (of up to 1.5 m) likely causes re-suspension of sediment (cf. Howarth et al. 1996) including organic material, which could support larger clam populations. Unfortunately, no chlorophyll or nutrient samples were collected to test these hypotheses.

Finally, because *C. fluminea* is reported to reach higher densities in well-oxygenated sediments such as sand and gravel (McMahon 1983; McMahon 1999; Schmidlin and Baur 2007), we expected sediment particle size to predict its local abundance. However, the abundance of clams collected across a broad range of sediment types was unrelated to sediment size. In sum, although several abiotic variables may contribute to the distribution and abundance of this northern population of *C. fluminea,* temperature appears to be the principal limiting factor.

Body condition of clams

The body condition of *C. fluminea* was significantly lower in the canal in August, suggesting exposure to suboptimal conditions. Indeed, between the months of July and August, the canal experienced over 39 days in which temperatures exceeded 30 °C (Figure S1), a critical limit that is believed to provoke interrupted growth, feeding and reproduction in *C. fluminea* (McMahon 1983). By contrast, clam body condition in the ROP increased from June to August (Bush et al. 1974; Mattice and Dye 1975; McMahon 1999). With increasing clam density, the population in the canal may also have been subjected to density dependent stressors (Phelps 1994), but we found no significant difference in the density gradient between the two sampling periods (Figure 2).

Although interpretation of observed changes in body condition can be confounded by the loss of gametic tissue during reproductive events (Williams and McMahon 1989), this is not the case here, as temperatures most conducive to the release of pediveligers (~ 25 °C, Aldridge and McMahon 1978) occurred in the ROP in August. In the canal, however, potentially lethal temperatures (34.5 ± 0.7 °C) were recorded in mid-July (Figure S1), suggesting it is frequently suboptimal habitat during summer months. Warm summer events can cause a reduction in body mass and an increase in mortality of *C. fluminea* (Weitere et al. 2009; McDowell et al. 2017). Thus, the positive effects of a warmer winter may be counteracted to some extent by the negative effects of higher peak summer temperatures in the canal. The pronounced decline in density along the plume (Figure 2) co-occurring with the seemingly minor changes in tissue of adult clams (Figure 3) is explained by a large number of juveniles in the canal, which were excluded from the condition analysis.

Population structure and growth analysis

The size distribution and the presence of gravid clams indicated a well-established reproducing population of *C. fluminea* in 2011. Results obtained from size-frequency histograms supported our prediction of a declining number of cohorts along the length of the plume, but only in June. Similarly, mean shell length was inversely related to distance from the discharge in June, consistent with our prediction, although this correlation too was not observed in August. Shell length at sampling stations closest to the canal declined through summer, whereas it increased in the ROP. This asymmetric pattern could result from 1) a die-off of older individuals in response to detrimentally high temperatures in the canal; 2) high recruitment of juveniles in the canal; 3) density-dependent processes including intraspecific competition; or 4) differential growth of smaller clams, causing them to attain shell lengths similar to those of older, slow-growing individuals, thereby obscuring cohorts. Differential growth would not increase the median shell lengths very rapidly, but it would account for larger maximum shell lengths. The maximum shell lengths for each cohort increased by ~ 3 mm, whereas the median and minimum shell length for the cohorts increased by ~ 1 mm. Given that population densities along the thermal plume were similar in June and August, it is unlikely that density-dependent processes explain the patterns observed.

In June, the measured size classes suggest that the age of the clams (estimated following Schmidlin and Baur 2007) spanned < 1 to 4 years (0.5–28.0 mm) in the canal and < 1 to 2 years immediately downstream (0.5–14.2 mm). We hypothesize that the annual range of water temperatures in the canal (4.1–36.0 °C) permits winter survival, earlier growth, and earlier and potentially more frequent reproductive events, thereby generating a higher number of annual cohorts. Our results also suggest the possibility of some clams overwintering in the ROP, but such individuals may simply result from different growth stages emigrating from the canal. Individuals with a shell length of ≤ 14 mm may drift downstream using a mucous string or byssal thread when exposed to water current (Prezant and Chalermwat 1984; McMahon 1999), potentially skewing size frequency histograms for clams at downstream stations by adding intermediate size classes between peaks. Frequent drifting may have similarly led to misinterpretation of the number of cohorts in the ROP.

Consistent with the expectation that exposure to low winter temperatures reduces the fitness of *C. fluminea* and heightens mortality (Muller and Baur 2011), age (inferred from size) class declined with downstream distance from the discharge source. Based on the observed mean shell size (10.6 mm) in June, we infer that clams located at stations between 2.6 km to 4 km downstream managed to reach sexual maturity (normally attained at 6–10 mm; McMahon 1983) within 1–3 months following winter, despite being exposed to an average winter temperature of 2.1 ± 0.1 °C (49 days ≤ 2 °C). However, between 2.6 km to 4 km downstream, the largest individual (9.3 mm) was probably less than a year old, perhaps reflecting a more limited survival and growth in average winter temperatures of 1.0 ± 0.1 °C (95% of days ≤ 2 °C). It is possible that our age estimates were confounded by environmental conditions severe enough to limit clam growth in the ROP and produce older clams of smaller size; in such a case, individuals of 9.3 mm in June could conceivably have overwintered. Furthermore, the collection of a 19.5 mm individual (seemingly too large to be accounted for by downstream migration) also suggests that some individuals might have been able to overwinter at the far end of the plume.

Evidence of temperature sensitivity after power plant closure

The assumption that *C. fluminea* cannot survive below 2 °C (McMahon 1983; McMahon 1999) is derived from a temperature tolerance experiment that was unable to acclimate the clams to 2 °C (Mattice and Dye 1975). Subsequent studies and field observations suggested that *C. fluminea* can adapt to near-freezing temperatures when acclimated to winter conditions (Habel 1970; Janech and Hunter 1995; Kreiser and Mitton 1995; Muller and Baur 2011). Adding further evidence that the species can tolerate colder temperatures was the discovery in 2010 of an overwintering population of *C. fluminea* in Lake George (New York), a north temperate waterbody that does not receive heated effluent. However, the recent closure of G2NPP provided an opportunity to verify whether *C. fluminea* can survive in the St. Lawrence River under natural winter conditions. During the operation of G2NPP, temperatures in the ROP frequently dropped below 2 °C, but natural minimum temperatures in the river are close to 0 °C and can remain near freezing for many weeks. A survey of the system following the shutdown of G2NPP indicated that a mass die-off occurred over the winter of 2012–13; sampling in June 2013 revealed extraordinary numbers of intact empty shells: 418.6 ± 122.8 m^{-2} – nearly 30 times higher than in the previous year, May 2012 (14.4 ± 7.2 m^{-2}). Sampling in June and August 2013 failed to locate living clams (Table 1), consistent with the view that the G2NPP plume had provided a critical thermal refuge for *C. fluminea* in the St. Lawrence River.

Conclusions

The G2NPP thermal plume offered a unique experimental environment for studying the population dynamics of this thermophilic invasive species. To date, no populations of *C. fluminea* have been discovered in areas of the river beyond the plume, and no living clams have been collected in the original plume section since 2012. Sampling in the summer of 2013 suggests that the population was extirpated soon after cessation of the G2NPP's operation.

Within the thermal plume, *C. fluminea* populations were most abundant at relatively warm, shallow, turbid sites exposed to higher flows. Density and body condition of clams differed across different plume sections and times of year, corresponding with spatiotemporal variation in water temperature. Remarkably, the plume created a temperature gradient that encompassed both the upper and lower thermal tolerance limits of *C. fluminea*. Significant differences in temperature between the canal and ROP were coupled with physiological and phenological differences in *C. fluminea* populations in these river sections. The onset of reproduction, indicated by the presence of gravid females, occurred earlier in the canal than in the ROP. In August, condition indices suggest that extreme temperatures in the canal restricted growth, whereas body condition was maximal in the ROP. Thus, the environment in the canal was optimal during the winter, but sub-optimal or even detrimental in late summer. These results are consistent with the observed general pattern of stronger responses to climate change by aquatic animals, particularly non-native species (Weitere et al. 2009; Sorte et al. 2013; McDowell et al. 2017).

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Supplementary material

The following supplementary material is available for this article:

Table S1. Environmental variables recorded at sampling stations inside and outside the thermal discharge plume of the Gentilly-2 Nuclear Power Plant (St. Lawrence River, Quebec) in 2011.

Table S2. Comparisons (using ANOVA and Tukey's post-hoc test) of environmental variables in the thermal discharge plume of the Gentilly-2 Nuclear Power Plant (St. Lawrence River, Quebec) in the early and late summer 2011.

Figure S1. Average daily temperature in the canal and mean daily water temperature from October 26, 2010 to May 20, 2011.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Castaneda_etal_SupplementaryMaterial.pdf