Fundam. Appl. Limnol., Arch. Hydrobiol. Vol. 176/3, 249–262
Stuttgart, March 2010 **Article**

Influence of conductivity on life history traits of exotic and native amphipods in the St. Lawrence River

Åsa Kestrup[1] and **Anthony Ricciardi**[1,*]

Redpath Museum, McGill University, Montreal, Canada

With 8 figures and 6 tables

Abstract: We compared the survival, growth and fecundity of the Ponto-Caspian amphipod *Echinogammarus ischnus* and the North American amphipod *Gammarus fasciatus* across a range of conductivities in a fluvial lake at the confluence of the St. Lawrence and Ottawa rivers (Quebec, Canada). Previous work has found that water chemistry (conductivity) regulates the direction and intensity of intraguild predation between these two species. Because *E. ischnus* evolved in ion-rich waters, we hypothesized that low conductivity has a negative effect on its life history traits, whereas *G. fasciatus* would be more tolerant. Consistent with this hypothesis, *E. ischnus* is abundant along the south shore of the lake in water of high conductivity (300 µS/cm), but rare along the north shore where conductivity is subject to strong fluctuations (85–230 µS/cm). In laboratory experiments using water with low (108 µS/cm), high (300 µS/cm) and intermediate (50:50 mix) conductivities, both species showed reduced growth at low conductivity, but *E. ischnus* also suffered higher mortality. *E. ischnus* collected from both shores did not differ in size-specific fecundity, size at reproduction, or size of adults. On the north shore, *E. ischnus* was present in low abundance at one site and absent from another site where it had been recorded in previous years. We conclude that low conductivity negatively affects the growth rate and mortality of *E. ischnus,* which is apparently eliminated from the north shore during periods of strong influx of ion-poor water from the Ottawa River, but re-establishes populations temporarily when higher conductivity is restored.

Key words: amphipod, conductivity, calcium, *Echinogammarus*, *Gammarus*, life history, water chemistry.

Introduction

Amphipods have successfully invaded fresh- and brackish water systems in North America and Europe (Jazdzewski 1980, Dermott et al. 1998, bij de Vaate et al. 2002), sometimes causing the decline or exclusion of native species (Dick & Platvoet 2000, Kinzler & Maier 2003). The invasion success and impacts of aquatic invaders vary through space and time, and studies have recently begun to relate this variation to local physico-chemical conditions (Costanzo et al. 2005, Thomsen & D'Antonio 2007, Alcaraz et al. 2008). Among amphipods, variation in the concentration of dissolved ions (conductivity) has been shown to govern whether species replacement or exclusion will occur, by regulating the intensity and direction of intraguild predation between native and exotic species (Dick & Platvoet 1996, Kinzler & Maier 2003, MacNeil et al. 2003, Kestrup & Ricciardi 2009). However, to understand why a particular abiotic factor limits the success of an invader, we must examine the effect of the factor at different stages of its life history (Berezina & Panov 2004, Alcaraz & Garcia-Berthou 2007) and how its response may differ from that of native competitors (Kestrup & Ricciardi 2009). Very little is known about the influence of the abiotic environment

---

Authors' address:

[1] Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec, Canada H3A 2K6.

[*] Corresponding author; e-mail: tony.ricciardi@mcgill.ca
asa.kestrup@mcgill.ca

www.schweizerbart.de
DOI: 10.1127/1863-9135/2010/0176-0249
1863-9135/10/0176-0249 $ 3.50

on the life history traits of aquatic invaders, although dissolved ions (salinity or conductivity) are among the most commonly studied factors (Haynes & Cashner 1995, Work & Gophen 1999, Berezina & Panov 2004, Alcaraz & Garcia-Berthou 2007). Furthermore, to date, no study has simultaneously examined the influence of variation in water chemistry on the life history traits of an aquatic invader and the native species with which it is interacting.

A concentration of dissolved ions beyond the tolerance range of an aquatic organism results in osmotic stress (Sutcliffe 1984). Among crustaceans in particular, calcium is a key element for maintaining an impermeable membrane necessary for osmoregulation, especially at the time of moult (Zehmer et al. 2002), and is essential for growth of the exoskeleton and for regulating intracellular processes (Wright 1979). When exposed to levels of conductivity or calcium at the lower limit of their tolerance range, crustaceans may suffer reduced growth, lower reproduction and increased mortality (Rukke 2002, Zehmer et al. 2002, Jeziorski & Yan 2006, Ashforth & Yan 2008). Identification of such tolerance limits is therefore necessary for predicting (i) which environments are susceptible to invasion by a crustacean and (ii) the conditions in which its performance and fitness (and thus impact) are maximal.

In this study, we examined the life history traits of native and exotic amphipods exposed to different concentrations of dissolved ions, to determine how two competing species differ in their response to local variation in water chemistry. The Ponto-Caspian amphipod *Echinogammarus ischnus* has replaced the North American amphipod *Gammarus fasciatus* throughout much of its invaded range in the North American Great Lakes (Dermott et al. 1998), but more than a decade after the invasion the two species coexist in Lake St. Louis – a fluvial lake near Montreal, Quebec, with strong gradients in the concentration of dissolved ions (Palmer & Ricciardi 2004). Although *E. ischnus* is a euryhaline species with a reported upper salinity tolerance of 23 ‰ and able to survive short-term exposure to highly saline water (30 ‰), its lower ionic tolerance is not known (Jazdzewski 1980, Ellis & MacIsaac 2009). This is of interest as *E. ischnus* has invaded lakes and rivers with salinities of < 0.1 ‰ in Europe and North America (Jazdzewski 1980, Dermott et al. 1998, Palmer & Ricciardi 2004).

Here, we examine the role of low conductivity as a factor limiting the invasion success of *E. ischnus* and contrast this species' performance to that of *G. fasciatus*. Given that *E. ischnus* has evolved in ion-rich waters (Cristescu & Hebert 2005), while *G. fasciatus* is a freshwater species, we hypothesized that exposure to low conductivity would have a negative influence on the life history traits of the invader, but little or no influence on the life history traits of the native amphipod. Specifically, we predict that at low conductivity the invader would suffer from reduced growth and lower survival, and be less fecund (i.e. a lower proportion of adult females would be ovigerous, and ovigerous females would carry fewer eggs). However, if the individuals on both sides of the river have adapted to local water conditions, those in low-conductivity habitats may be more tolerant than individuals from high-conductivity habitats (Bijlsma & Loeschcke 2005).

Methods

These hypotheses were tested in a combination of laboratory experiments and field observations using Lake St Louis as a study and collection site. A natural gradient of conductivity exists in the lake because it receives ion-rich water from the St. Lawrence River along its south shore (conductivity 305 µS/cm, calcium 36.3 mg/L, salinity 0.15 ‰) and ion-poor water from the Ottawa River along its north shore (conductivity 80 µS/cm, calcium 8.3 mg/L, salinity 0.04 ‰) (Centre St-Laurent 2003). *E. ischnus* is abundant along the south shore and scarce along the north shore, where conductivity fluctuates greatly depending on the relative discharge of the two rivers (Å Kestrup, unpubl. data; Palmer & Ricciardi 2004). We used two study sites on the south shore (Chateauguay West, 45°21.80 N, 73°47.20 W and Chateauguay East, 45°22.52 N, 73°46.55 W, Fig. 1) and two sites on the north shore (Valois Bay, 45°26.37 N, 73°46.48 W and Lachine, 45°26.01 N, 73°41.17 W), where both species have previously been recorded. The natural fluctuations of conductivity and calcium concentration in the study system were observed by measuring these two parameters biweekly at all four sites from mid-May to mid-September 2008 (10 occasions). Water chemistry variables (O_2, conductivity, temperature) were measured with an electronic meter (YSI 85 DO/Cond/Salinity Meter), while water for calcium measurements was collected just above the river bottom in clean plastic bottles, and stored at 4 °C in a refrigerator until analysed < 3 days later (LaMotte Model PHT-CM-DR-LT). The relationship between conductance and calcium concentration at the different sites was tested in least squares regressions.

Laboratory experiments

The survival and growth of juveniles of both species in different conductivity and calcium levels were tested in a laboratory experiment. Water with high conductivity and calcium concentration (HC) (conductance: 300 µS/cm, calcium: 37.8 mg/L) was collected from Chateauguay East on the south shore, and water from the Ottawa River (LC) with low conductivity and calcium concentration (conductance: 107.7 µS/cm, calcium: 16.8 mg/L) was collected from a site on the north shore at the western end of the Island of Montreal (Place St Louis, 45°25.03 N, 73°52.68 W). During late July and early August 2008, ovigerous fe-

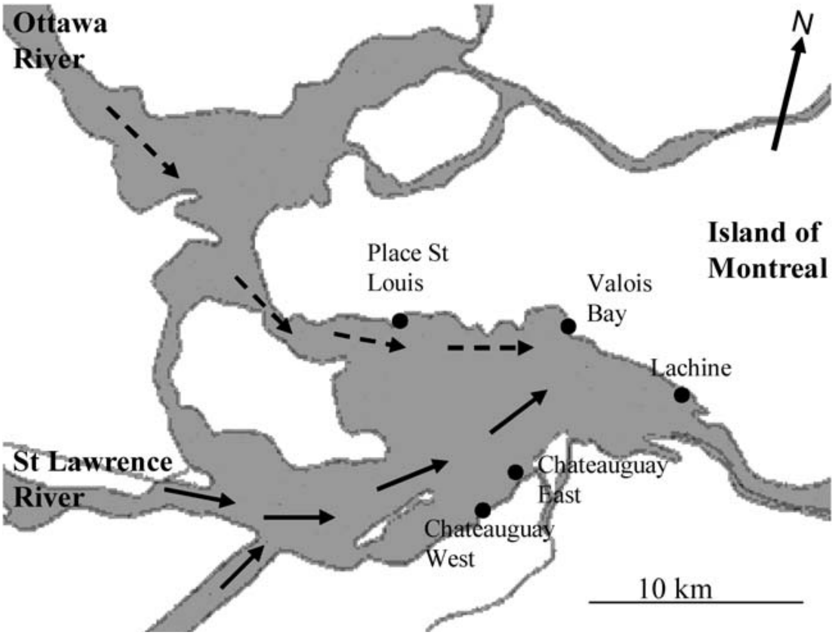

Fig. 1. Sites for collection of amphipods and sampling of water chemistry.

males and precopula pairs of both species were collected from Chateaguay West. In Lachine on the north shore, only native females were collected, as very few ovigerous *E. ischnus* females were encountered. In the laboratory, the precopula pairs were allowed to mate and the ovigerous females were placed in individual trays (400 mL) of filtered water: initially HC water for those from the south shore and LC water for those from the north shore. All trays were kept in a chamber at constant temperature (20 °C) and a light regime of 15:9 hrs light:dark. The amphipods were exposed to the following treatments: 1) *E. ischnus* in HC, IC or LC water; 2) *G. fasciatus* from the south shore in HC, IC or LC water; and 3) *G. fasciatus* from the north shore in LC water. The last treatment served to test if survival of *G. fasciatus* individuals from the south and north shore differ in their tolerance to LC water. To acclimatize the females to low conductivity-conditions, two thirds of the females from the south shore were placed in a 50:50 mix of low- and high- conductivity water (IC). The following day, half of these females were placed in pure LC water. The trays were checked daily over a period of 11 days, and hatched juveniles were transferred to individual trays (118 mL) with filtered water of the same type as in the parental tray. The *E. ischnus* juveniles came from 26 females, while the *G. fasciatus* juveniles came from 17 females from the south shore and 5 females from the south shore. Animals were fed ‘catfish food pellets’ (a mixture of plant and animal matter) *ad libitum*. Five days after hatching, 30 juveniles of visibly good condition were chosen for each treatment. The head length (i.e. from the tip of the rostrum to the rear edge of the head) of each individual was measured using a Wild Heerbrugg stereo microscope with a micrometer eyepiece. Head length was used as a proxy for the total body length (Gonzalez & Burkart 2004); we confirmed this relationship by measuring the head length and the total straight body length (tip of the rostrum to the tip of the telson) of 80 individuals of both species and found a strong positive correlation (linear regression: $R^2 = 0.97$ for *E. ischnus* and $R^2 = 0.94$ for *G. fasciatus*, both $p < 0.001$). To prevent the amphipods from moving while being measured, they were placed on a piece of mesh (mesh size 63 µm or 1 mm, depending on the size of the individual) in a Petri dish. The juveniles were grown for 6 weeks. Mortality was measured weekly and head length was measured every 2 weeks. Following measurement, the amphipod was transferred to a container with clean water and fresh food. After 6 weeks, the animals were preserved in 70 % alcohol, and both head length and total body length were measured immediately after preservation. Differences in growth between treatments (using head length) were analyzed in repeated-measures ANOVAs, one per species, with water type/origin as the fixed factor and head size as the repeated measure, followed by Tukey’s post-hoc test. Differences in the total length at the end of the experiment were tested in one-way ANOVAs. The specific growth rate (% length increase/day) per two-week period was determined and tested in a repeated-measures ANOVA with species, water and origin as fixed factors, and time as repeated measures. Individuals were used as replicates in the analysis. We did not control for juveniles coming from the same female. Differences in survival among treatments during the 5 days after hatching and during the experiment were tested using Chi-square analyses followed by the Marascuilo (1966) procedure, which allows comparison of all possible pairs of proportions.

Field sampling

To examine growth rate and fecundity *in situ*, amphipods were collected from the two sites on the south shore and the two sites on the north shore on July 17–18 and August 7–8, 2008. Amphipods were collected using a variety of methods: Plastic trays (21 cm width, 34 cm length, 12 cm depth) filled to the brim with cobble and nylon mesh (1 × 1 m) attached to bricks were deployed at each site at 0.5–1 m depths and left undisturbed for 3 weeks to be colonized by amphipods. Rocks were also collected from each site on the sampling date in order to collect a minimum of 300 individuals per species per site. As all size classes of both species were collected using these methods, it is unlikely that differences in sampling techniques between sites may have affected the results. In the lab, all amphipods were stored in 70 % alcohol and later identified to species. The total straight length of each individual (from the tip of the rostrum to the base of the telson) of all *E. ischnus* and subsamples of ca. 300 *G. fasciatus* per site was measured using a stereo microscope with an eye-piece micrometer. Individuals of lengths below 2.4 mm were not included in the study because species identification characters were not fully developed (although *E. ischnus* uropods are generally quite distinct, the inner rami on newly hatched *G. fasciatus* are difficult to discern). Females were identified by the presence of brood plates, and males by the presence of genital papillae. *G. fasciatus* individuals larger than 5.3 mm and *E. ischnus* individuals larger than 4.5 mm were classified as adults, based on the size of the smallest ovigerous female found in the samples. Females carrying eggs or hatched juveniles in their brood pouches were recorded as gravid. The number of eggs per female was counted only if all eggs in the brood were intact (i.e. none had hatched). Our data on fecundity compared with data collected in 1996 at sites in Lake Erie and western Lake Ontario (Dermott et al. 1998), where conductivity and calcium concentrations are relatively high (conductivity: 234–290 µS/cm, and calcium 30–38 mg/L; R. Dermott, Great Lakes Laboratory for Fisheries, Burlington, Ontario, pers. comm.).

Storage in alcohol may cause reductions in the weight and size of aquatic invertebrates (Lasenby et al. 1994, Black & Dodson 2003, Wetzel et al. 2005), but this is unlikely to have biased our length measurements because all of the specimens we collected were measured consistently after a time interval of approximately 4 weeks since preservation.

The size-specific fecundity of females was analyzed in ANCOVAs with body length as the covariate, site as a fixed factor and the number of eggs per female as the dependent variable. Egg numbers were square-root transformed to meet the assumption of homogeneity of variances. Each species was analyzed separately. Where slopes were heterogenous, the Wilcox procedure was used to identify ranges of the covariate for which the group means were significantly different (significance level $p < 0.05$). The partial fecundity index, defined as the mean brood size/female size, was also estimated for each species at the different sites and compared in one-way ANOVAs followed by Tukey's post-hoc test (Grabowski et al. 2007). Differences in the partial fecundity index of the two species at the sites where they co-occur were tested in independent samples t-tests with Bonferroni correction. The size of males and females at the different sites were also compared in independent samples t-tests with Bonferroni correction. Deviation of the sex ratio from 1:1 was tested in a binomial test. Differences in the proportion of ovigerous individuals among adult females at the different sites were tested using Chi-square analyses followed by the Marascuilo procedure.

To estimate growth rate in the field, cohorts were followed between sampling dates. Cohorts were identified by Bhattacharya's (1967) method, using the software FiSAT II. Differences in growth rate between sites were tested in a one-way ANOVA (*G. fasciatus*) or an independent samples t-test (*E. ischnus*).

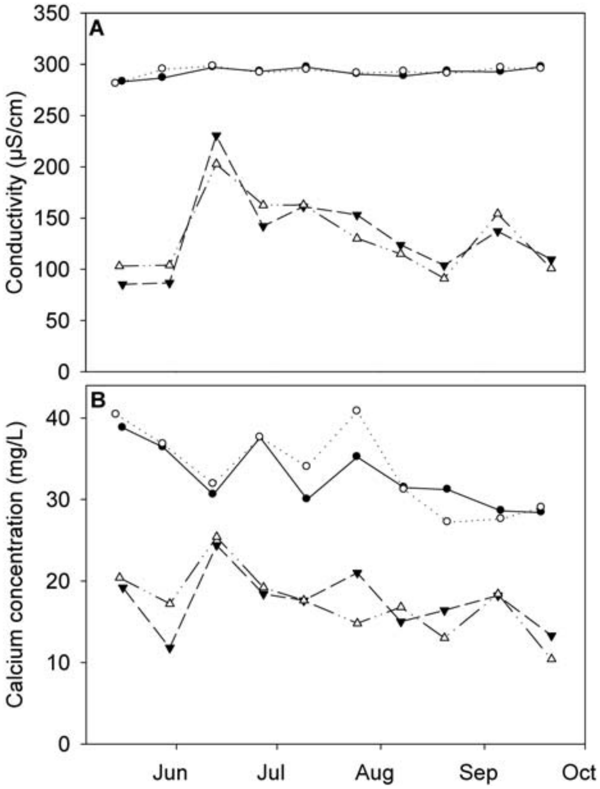

Fig. 2. Variation in conductivity **(A)** and calcium concentration **(B)** in Chateauguay West (filled circles) and East (open circles) on the south shore, and Valois Bay (filled triangles) and Lachine (open triangles) on the north shore of Lake St. Louis.

Results

Conductivity remained high and fluctuated less throughout the season at the south shore sites (283–297.5 µS/cm at Chateauguay West and 281.0–298.0 µS/cm at Chateauguay East) than at the north shore (85–230.5 µS/cm at Valois Bay and 90.9–202.7 µS/cm at Lachine; Fig. 2). The calcium concentration was also higher at the south shore, but its fluctuations were of similar magnitude on both shores (28.4–38.8 mg/L and 27.2–40.8 mg/L at Chateauguay West and East, respectively, and 11.8–24.4 mg/L and 10.4–25.4 mg/L at Valois Bay and Lachine, respectively). Temporal variation in calcium concentration and conductance were positively correlated at the north shore sites (Valois Bay: $p = 0.010$, $R^2 = 0.59$, $F_{1,9} = 11.43$, Lachine: $p = 0.017$, $R^2 = 0.53$, $F_{1,9} = 8.99$), but negatively correlated at Chateauguay West ($p = 0.016$, $R^2 = 0.54$, $F_{1,9} = 9.30$), whereas there was no correlation at Chateauguay East (NS; Fig. 3).

Laboratory experiment

The eggs of both species hatched successfully to produce viable offspring in all three types of water. *G. fasciatus* juveniles hatched 8–10 days and *E. ischnus* juveniles hatched after 9–11 days, following fertilization. Juvenile *E. ischnus* suffered higher mortality in

LC water during the acclimatization period (the first 5 days after hatching), with a survival of only 61 %, compared to 83 % and 89 % in the HC and IC treatments, respectively ($\chi^2 = 11.8$, df = 2, p = 0.002). By contrast, *G. fasciatus* survival was similar across treatments, 81–92 % (NS). Throughout the experiment, the number of dead individuals increased gradually. After two weeks, mortality of *E. ischnus* in LC water was higher (> 50 %) than in the other treatments (HC-10 % and IC-20 %), while mortality of *G. fasciatus* was relatively low (17–30 %) in all treatments. After 6 weeks, survival differed among treatments for *E. ischnus* ($\chi^2 = 20.40$, df = 2, $p < 0.0001$; Fig. 4a), whereas *G. fasciatus* survival did not differ among treatments ($\chi^2 = 2.83$, df=3, NS; Fig. 4b). The survival of *E. ischnus* was significantly lower ($p < 0.05$) at LC (20 %) than at IC (60 %) and HC (77 %), while there was no significant difference in mortality at IC and HC.

Similarly, the growth (change in head length as a function of time) of *E. ischnus* (Fig. 5a) differed between treatments (rmANOVA, $F_{2.44} = 13.08$, $p < 0.001$), being lower at LC than at IC and HC ($p < 0.001$), although there was no difference between IC and HC (Tukey's post-hoc, p = 0.75). The growth of *G. fasciatus* also varied across treatments ($p < 0.001$, $F_{3.65} = 20.77$, Fig. 5b); its growth in both LC-treatments was lower than in HC and IC treatments ($p \leq 0.001$), but there was no significant difference between the two LC treatments or between IC and HC treatments. Using the total length after 6 weeks in a

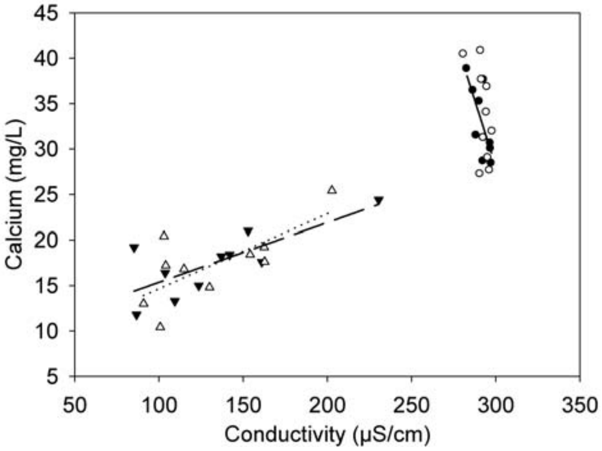

Fig. 3. Relationship between calcium concentration and conductivity at the sample sites on the north shore (Valois Bay – filled triangles and Lachine – open triangles) and the south shore (Chateauguay East – open circles and Chateauguay West – closed circles) of Lake St. Louis. In Valois Bay (dashed line) and Lachine (dotted line) the relationship was positive, while it was negative in Chateauguay West (solid line).

Table 1. Specific growth rate (% length increase/day) of native and exotic amphipods exposed to water with high, intermediate and low conductivity in the laboratory.

		Specific growth rate		
Species	Treatment	0 – 2 wks	2 – 4 wks	4 – 6 wks
E. ischnus	HC	2.1	1.1	0.7
	IC	1.2	1.1	1.4
	LC	0.8	0.8	0.7
G. fasciatus	HC	3.1	2.5	1.9
	IC	2.7	2.0	2.3
	LC	2.0	2.1	2.0
	LC-LC	2.3	1.4	1.7

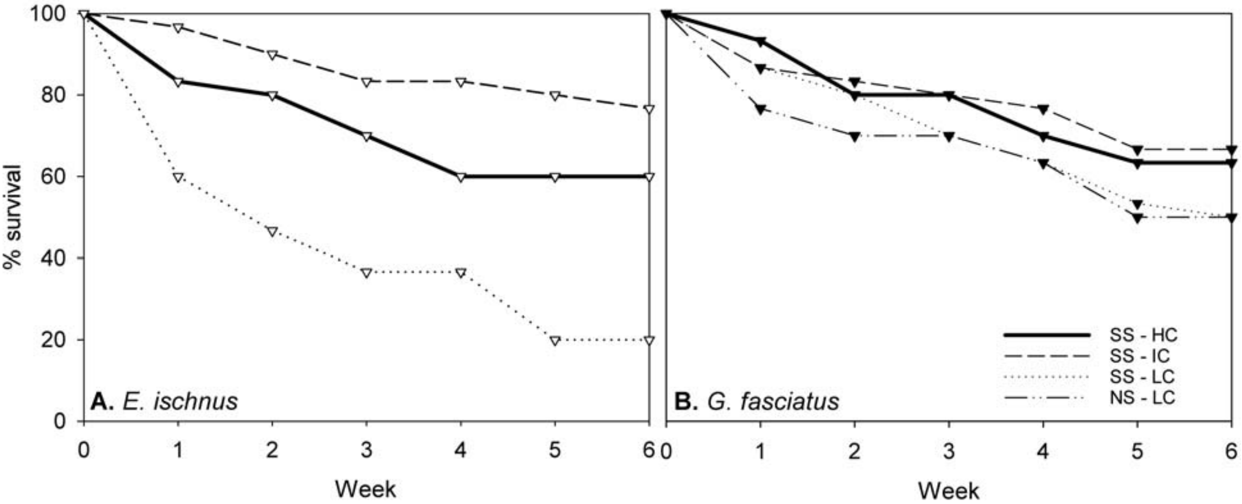

Fig. 4. Survival of *E. ischnus* **(a)** and *G. fasciatus* **(b)** from the north shore (NS) and the south shore (SS) in water of low (LC), intermediate (IC) and high conductivity (HC).

one-way ANOVA gave identical results. The specific growth rate of both species decreased with increasing age ($F_{2,116} = 18$, $p < 0.001$) (as has been observed for other amphipods; Piscart et al. 2003), increased with conductivity ($F_{2,116} = 14.33$, $p < 0.001$), and was higher for *G. fasciatus* than *E. ischnus* in all treatments ($F_{1,116} = 341.31$, $p < 0.001$; Table 1). There was no effect of origin ($F_{1,116} = 0.58$, NS).

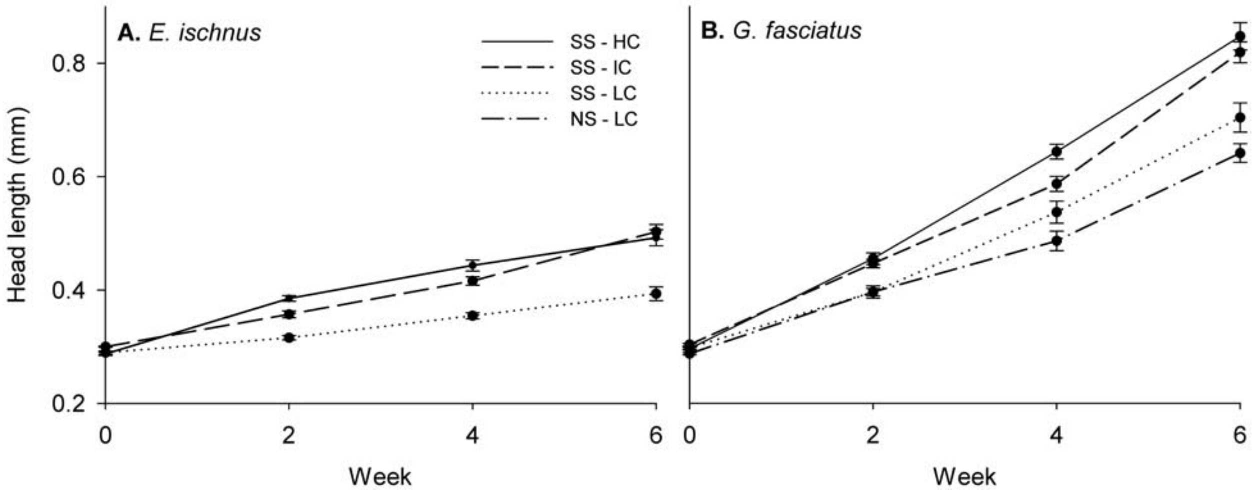

Fig. 5. Growth rate of *E. ischnus* **(a)** and *G. fasciatus* **(b)** from the north shore (NS) and the south shore (SS) in water of low (LC), intermediate (IC) and high conductivity (HC).

Table 2. Analysis of size-specific fecundity of *E. ischnus* and *G. fasciatus*.

Size-specific fecundity					
			E. ischnus		
Linear regression					
Site	*N*	*F (df)*	*P*	R^2	*Equation*
Chateauguay W	46	25.495 (1,45)	<0.001	0.37	y= –1.399 + 0.664 * female length
Chateauguay E	56	37.916 (1.55)	<0.001	0.41	y= –1.203 + 0.637 * female length
Valois Bay	6		>0.05		
Lower Great Lakes	55	91.069 (1,54)	<0.001	0.63	y= –1.952 + 0.748 * female length
ANCOVA					
Independent variables	*df*	*F*	*P*		
Site	2	0.273	0.761		
female length	1	139.825	<0.001		
Total	157				
			G. fasciatus		
Linear regression					
Site	*N*	*F (df)*	*P*	R^2	*Equation*
Chateauguay W	50	65.617 (1,49)	<0.001	0.58	y= –1.816 + 0.720 * female length
Chateauguay E	50	78.080 (1,49)	<0.001	0.62	y= –2.403 + 0.824 * female length
Valois Bay	53	8.665 (1,52)	0.005	0.15	y= –0.30 + 0.393 * female length
Lachine	49	22.375 (1,48)	<0.001	0.32	y= –2.976 + 0.880 * female length
Lower Great Lakes	42	134.178 (1,41)	<0.001	0.77	y= –0.871 + 0.641 * female length
ANCOVA					
Independent variables	*df*	*F*	*P*		
Site	4	2.336	0.056		
female length	1	180.653	<0.001		
Interaction site * fem lgth	4	2.528	0.041		
Total	244				

Field sampling

Fecundity

The size-specific fecundity of *E. ischnus* did not differ among the HC sites and the lower Great Lakes (Fig. 6a, Table 2). Too few gravid females were found in Valois Bay to allow a statistical comparison of both sides of the river; however, the size-specific fecundity of the few females found in Valois Bay was within the same range as the other samples (Fig. 6a). By contrast, the size-specific fecundity of *G. fasciatus* differed among sites (i.e. there was an interaction between site and female length; Table 2). Large *G. fasciatus* females were less fecund in Valois Bay than at the other four sites (Fig. 6b); these differences were significant for individuals of length > 7.3 mm at Lachine, > 6.5 mm at Chateauguay East, > 6.7 mm at Chateauguay West, and > 5.8 mm in the lower Great Lakes. In addition, smaller females in the lower Great Lakes were more fecund than those in Lachine (< 7.0 mm) and Chateauguay West (< 7.3 mm). The highest number of eggs recorded in gravid *G. fasciatus* females at the different sites were 17 (Valois Bay), 30 (Lachine), 24 (Chateauguay West) and 30 (Chateauguay East). For *E. ischnus* females, the highest number of eggs ranged from 12 at Valois Bay to 19 at Chateauguay East.

The partial fecundity index of *E. ischnus* was not significantly different between sites ($F_{3,162} = 0.2$, N. S., Table 3). The partial fecundity of *G. fasciatus* differed between sites ($F_{4,243} = 11.1$, $p < 0.001$), and was higher in the lower Great Lakes than at all sites in Lake St Louis ($p \leq 0.001$), except for Chateauguay East (NS),

Table 3. Partial fecundity index (mean brood size/female size).

Partial fecundity index (mean ± SE)	*G. fasciatus*	*E. ischnus*
Lachine	1.41 ± 0.10	N. A.
Valois	1.10 ± 0.07	1.20 ± 0.23
Chateauguay	1.60 ± 0.09	1.16 ± 0.07
Peninsula	1.33 ± 0.06	1.13 ± 0.08
Lower Great Lakes	1.93 ± 0.13	1.21 ± 0.08

Table 4. Size at the onset of reproduction and of the largest females and males found.

Species	Site	Smallest size at female sexual maturity (mm)	Largest male	Largest female
E. ischnus	Chateauguay W	4.6	9.6	7.8
	Chateauguay E	4.7	10.7	8.1
	Valois Bay	5.8	8.3	7.9
G. fasciatus	Chateauguay W	5.4	11.9	8.9
	Chateauguay E	5.5	17.0	9.2
	Valois Bay	5.4	10.9	10.7
	Lachine	5.5	10.7	8.9

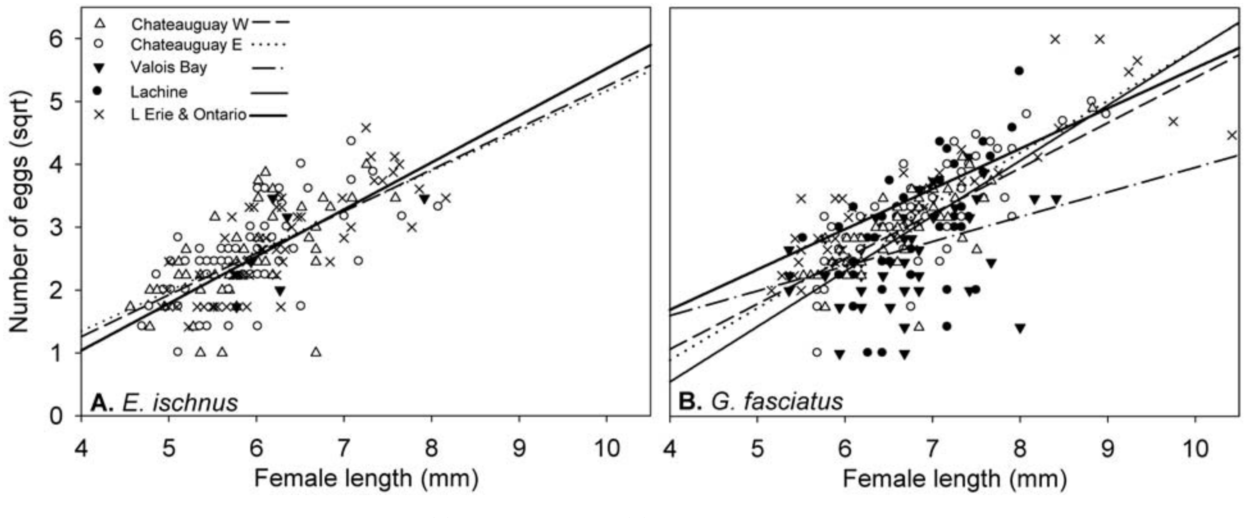

Fig. 6. Size-specific fecundity of *E. ischnus* (**a**) and *G. fasciatus* (**b**) at the different sampling sites.

and was higher in Chateauguay East than in Valois Bay (p = 0.001). The partial fecundity of *G. fasciatus* was higher than that of *E. ischnus* at only two sites: the lower Great Lakes and Chateauguay East ($t_{95} = 5.1$, $p < 0.001$ and $t_{104} = 3.8$, $p < 0.001$, respectively). At the other sites, the partial fecundity of the two species did not differ significantly.

E. ischnus generally began reproducing at a smaller size than *G. fasciatus* (Table 4). In both species, males were generally larger than females (t-tests, $p < 0.01$, unequal variances assumed), with the exception of *E. ischnus* at Valois Bay. The larger size classes were comprised almost entirely of males.

Table 5. Sex ratio in the adult population tested against a ratio of 1:1.

Site	N	Proportion gravid females	 nongravid females	 males	Sex ratio (f/m)	Binomial tests p (sex ratio)
G. fasciatus						
Chateauguay W	544	0.414	0.112	0.474	1.109	ns
Chateauguay E	385	0.317	0.119	0.564	0.774	0.0072
Valois Bay	480	0.300	0.215	0.485	1.060	ns
Lachine	511	0.358	0.174	0.468	1.138	ns
E. ischnus						
Chateauguay W	249	0.289	0.193	0.518	0.930	ns
Chateauguay E	289	0.253	0.197	0.550	0.818	0.0497
Valois Bay	26	0.231	0.231	0.538	0.857	ns

Table 6. Mean cohort length and growth between sampling dates for *E. ischnus* and *G. fasciatus*.

South shore	*G. fasciatus*					*E. ischnus*				
Site	TL (mm)		Size increase			TL (mm)		Size increase		
	July 18	Aug 8	Absolute (mm)	Relative (%)	Daily (%)	July 18	Aug 8	Absolute (mm)	Relative (%)	Daily (%)
Chateauguay W	2.80	3.85	1.05	38	1.53		3.0			
		6.63				3.12	4.84	1.72	55	2.11
	6.38	9.02	2.64	41	1.66	4.91	6.67	1.76	36	1.47
	8.66					6.16				
Chateauguay E	3.70	4.62	0.92	25	1.06		2.90			
	4.86	6.70	1.84	38	1.54	3.40	5.00	1.60	47	1.85
	6.35	8.99	2.64	42	1.67	4.85	7.21	2.36	49	1.91
	8.19	10.62	2.43	30	1.24	6.55				
	11.44									
North shore	*G. fasciatus*					*E. ischnus*				
	TL (mm)		Size increase			TL (mm)		Size increase		
	July 17	Aug 7	Absolute (mm)	Relative (%)	Daily (%)	July 17	Aug 7	Absolute (mm)	Relative (%)	Daily (%)
Valois Bay		2.96								
	3.40									
		6.07								
	6.58	8.18	1.60	24	1.04	3.80	4.80	1.00	26	1.12
	8.35						6.12			
	10.22									
Lachine		3.37								
	3.33	4.98	1.65	50	1.93					
	4.66	6.73	2.07	44	1.77					
	6.27	8.65	2.38	38	1.54					
	7.34									
	8.78									

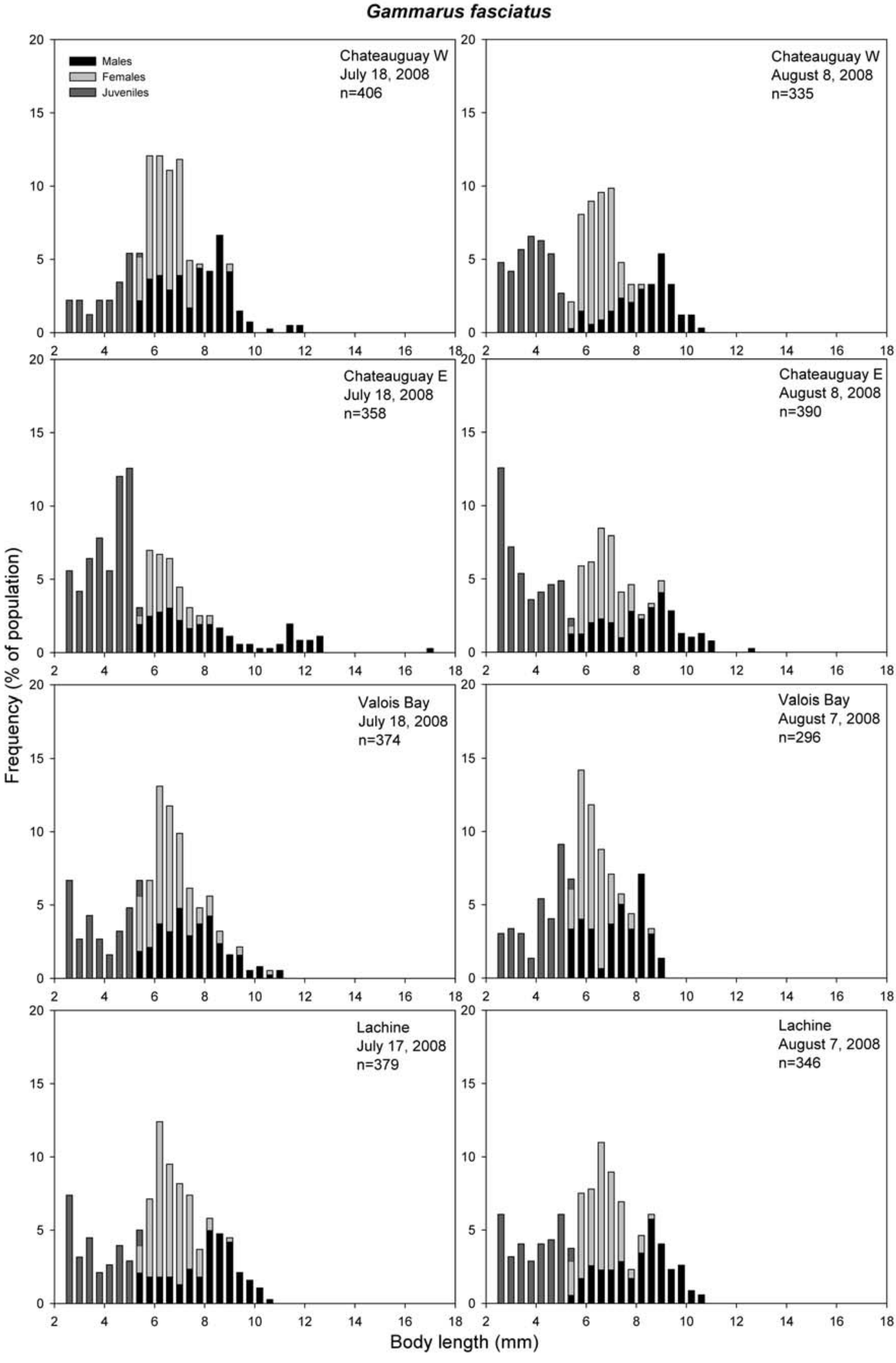

Fig. 7. Size distribution of *G. fasciatus* at the four sampling sites in July and August 2008.

Sex ratio and proportion of ovigerous females

Populations of both species were dominated by males at one site (Chateauguay East), but the sex ratio was not significantly different from unity at the other sites (Table 5). The proportion of ovigerous individuals among adult *G. fasciatus* females varied across sites ($\chi^2 = 27.232$, df =3, $p < 0.0001$), differing between Chateauguay West (79 %) and the two sites on the north shore (Valois Bay 58 %, and Lachine 67 %), and between Chateauguay East (73 %) and Valois Bay. There was no significant difference between sites on the same shore. By contrast, the proportion of ovigerous adult females of *E. ischnus* did not differ among sites ($\chi^2 = 0.678$, df = 2, NS), and was 60 % at Chateauguay West, 56 % at Chateauguay East, and 50 % at Valois Bay.

Growth rate in the field

There was no difference in growth rate between sites (*G. fasciatus*: $F_{2,8} = 2.28$, NS; *E. ischnus*: t = –0.27, NS). The growth rate of *E. ischnus* appeared lower at Valois Bay (1.1 %) than at the two HC sites (1.5–

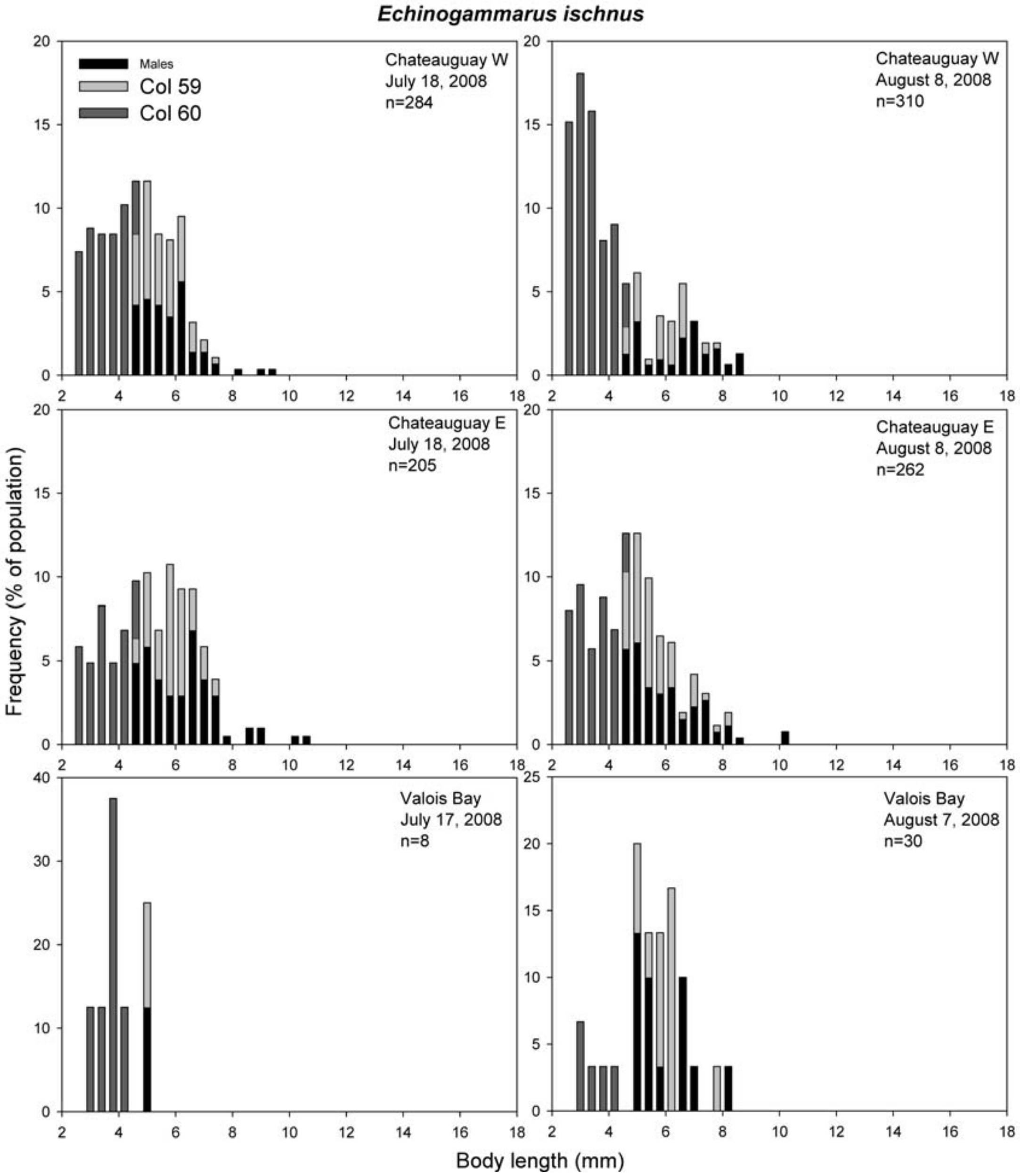

Fig. 8. Size distribution of *E. ischnus* at the three sampling sites in 2008

2.1 %), but the small number of individuals found at the site makes the estimate uncertain. For both species, it was possible to identify and follow multiple cohorts from the first to the second sampling dates (Figs 7 and 8, Table 6). During this time period, conductivities at Valois Bay and Lachine varied from 103–153 µS/cm and 112–130 µS/cm (and [Ca^{2+}] was 15–21 mg/L and 15–17 mg/L), respectively. For *G. fasciatus*, 2 and 4 cohorts were followed in Chateauguay West and East respectively, 3 cohorts in Lachine, and only one cohort in Valois Bay. For *E. ischnus*, two cohorts were followed at each of the HC sites, and one cohort in Valois Bay.

Discussion

Growth experiment in the laboratory

Low conductivity appears to be stressful to native and exotic amphipods, as it resulted in reduced growth rate for both species in our laboratory experiments. However, it has a stronger negative effect on the invader, which suffered higher mortality. The pattern of mortality is similar to what was observed for *Gammarus pseudolimnaeus* along a calcium gradient (Zehmer et al. 2002). In that study, although general osmoregulatory failure did not prevent intermoult *G. pseudolimnaeus* from living in water with low Ca-levels, animals died quickly as they moulted, resulting in a gradual increase in mortality as moulting was not synchronized within the population (Zehmer et al. 2002). The loss of the exoskeleton during moulting exacerbates osmotic stress as the permeability to water increases, and the influx of water is higher for animals in a medium with lower concentrations of dissolved ions (Lockwood & Inman 1973). Surprisingly, *G. fasciatus* individuals from the north shore were not more tolerant to low conductivity than those from the south shore, suggesting no local adaptation of *G. fasciatus* to low conductivity.

In the laboratory experiment, the specific growth rate of *E. ischnus* was lower than that of *G. fasciatus* in all treatments. The specific growth rate of *G. fasciatus* was higher than what has been recorded for other species of freshwater amphipods at similar temperatures and comparable to that recorded for *Dikerogammarus villosus* (1.6–2.6 for males, 1.7–2.3 for females) – another Ponto-Caspian amphipod that has successfully invaded European inland waters (Piscart et al. 2003). In the laboratory, the growth rate of *E. ischnus* was as high as that of *G. fasciatus* only among newly hatched individuals in favourable conditions (i.e. HC). In the field, we found no clear differences in the growth rate of *G. fasciatus* across sites. It was not possible to compare the growth rates of *E. ischnus* at both shores of the lake as it was found in very low abundances at one site on the north shore, and absent from another site where it had been recorded previously (Palmer & Ricciardi 2004). However, our laboratory results indicate that the growth rate of the native amphipod is higher than that of the exotic amphipod, contrary to the popular assumption that invasive species exhibit more rapid growth than closely-related native species (Piscart et al. 2003).

Sex ratio and fecundity in the field

The sex ratios of both species were in accordance with previous records from other regions. Previous studies found the sex ratio to be dominated by males (e.g. *G. fasciatus* in Lake Erie; Clemens 1950) or to fluctuate in dominance between genders (e.g. *E. ischnus* in Lichenskie Lake, Poland; Konopacka & Jesionowska 1995). *E. ischnus* females started reproducing at a smaller size than *G. fasciatus*, regardless of the water chemistry. The size-specific fecundity of *G. fasciatus* was more variable across sites than of *E. ischnus*, and was lower at Valois Bay than in the lower Great Lakes. *E. ischnus* size-specific fecundity did not differ between the sites with high conductivity and the lower Great Lakes. The smallest maximal brood size of both species was recorded at Valois Bay. The variation in fecundity across sites appears not to depend on conductivity, as the sites on the north shore followed different patterns.

Few studies have examined the relationship between water chemistry and brood size. Arnér & Koivisto (1993) observed that the size-specific fecundity of the cladoceran *Daphnia magna* peaked at 4 ‰, whereas Glazier et al. (1992) found no relationship in a study of *Gammarus minus* across a wide range of calcium and conductivity (5–72 mg/L and 36–424 µS/cm). Alcaraz and Garcia-Berthou (2007) measured an increase in reproductive investment of the mosquitofish (*Gambusia holbrooki*) in more stressful environments. In our study, the partial fecundity of *E. ischnus* did not differ between sites and, unexpectedly, was much lower in our study system (1.13–1.21) than in central Europe (2.21; Grabowski et al. 2007). Our results thus contrast the observed European pattern of exotic amphipods having a higher partial fecundity than native amphipods (Grabowski et al. 2007, Pöckl 2007).

The majority of the females of both species were gravid, the exception being *E. ischnus* in Valois Bay, where only 50 % of the females carried eggs. The proportion of *G. fasciatus* females carrying eggs was also lowest in Valois Bay. Thus, Valois Bay may be more stressful for *G. fasciatus* than the other sites for reasons unrelated to conductivity. The lack of relationship between water chemistry and the percentage of ovigerous females of gammarid amphipods is consistent with other studies (Glazier et al. 1992).

Influence of conductivity on life history of amphipods

There is very limited published information on the conductivity and calcium requirements of *G. fasciatus* and *E. ischnus*, even though the tolerance of *G. fasciatus* to other abiotic factors such as temperature and oxygen has been examined (e.g. Sprague 1963, Thibault & Couture 1982). Creaser (1935) recorded the presence of *G. fasciatus* in a West Virginia stream at a calcium concentration of 10.8 mg/L and its absence downstream at a calcium concentration of 4 mg/L. The recorded levels of calcium along the north shore in our survey (minimum $[Ca^{2+}] = 10.4$ mg/L) are therefore within the known tolerance range of *G. fasciatus*. Moreover, this species was found at all sites on both shores in this study as well as in a previous survey (Palmer & Ricciardi 2004). While our lab experiment suggests that a conductivity and calcium concentration of 108 µS/cm and 17 mg/L, respectively, result in high mortality of juvenile *E. ischnus*, the species was present at low abundance at Valois Bay when conductivity was 102.7 µS/cm. This species may tolerate short exposure to low conductivity, but is weakened in this environment. Previously, we found that *E. ischnus* survived well with conspecifics in enclosures *in situ* at conductivities of 169–177 µS/cm and calcium levels of 21–27 mg/L, but was vulnerable to intraguild predation from *G. fasciatus* (Kestrup & Ricciardi 2009).

The populations of *E. ischnus* along the north shore of Lake St. Louis are not persistent (this study; Palmer & Ricciardi 2004); individuals are found there only occasionally and at low abundances. The presence of juveniles and ovigerous females in our study and in archived samples (Palmer & Ricciardi 2004) suggests that either *E. ischnus* establishes reproducing populations infrequently along the north shore, or these are sink populations of individuals dispersed from sites upstream where *E. ischnus* are abundant (e.g. Point-du Moulin on Ile Perrot). Its intolerance to low conductivity is the most probable reason why *E. ischnus* has not established permanent self-sustaining populations along the north shore. Conductivity regularly fluctuates to levels near 100 µS/cm, which results in increased mortality among juveniles, whereas adult individuals generally are more tolerant to unfavourable conditions (Berezina & Panov 2004, Bravo et al. 2007, Roche et al. 2009). *E. ischnus* may be able to survive exposure to low conductivity water during intermoult periods, but suffers higher mortality when moulting (Zehmer et al. 2002). In addition to mortality caused by osmotic stress, crustaceans are also more vulnerable to predation during this period (Bailey et al. 2006). Our study covered only a 5-month period during the summer, and it is possible that it omitted periods in which the lowest values of conductivity and calcium occurred. While there are no long-term data series of these parameters in Lake St Louis, daily measurements throughout 2007 of the conductivity in the Ottawa River at Carillon show fluctuations between 69–152 µS/cm, with the periods with the lowest values occurring in February–March (69 µS/cm) and June-July (65 µS/cm). If these periods coincide with periods of high influx into Lake St Louis, it is possible that the conductivity along the north shore can be even lower than 100 µS/cm (Myriam Rondeau, Environment Canada, unpubl. data).

The physiological tolerance of an invader is a major determinant of the potential range it can invade, as shown for amphipods (Wijnhoven et al. 2003, Berezina & Panov 2004), cladocerans (Work & Gophen 1999) and mosquitofish (Haynes & Cashner 1995, Alcaraz & Garcia-Berthou 2007). However, in order to properly assess the tolerance of a species, it is important to consider multiple life history stages, which may respond in a different way to different levels of the same factor. An example is a study of the Baikalian amphipod *Gmeniloides fasciatus* in the Gulf of Finland, which revealed strong differences in salinity tolerance among adults, juveniles and embryos that limit the amphipod's occurrence in brackish waters (Berezina & Panov 2004). Thus, despite a broader tolerance of many invaders to abiotic factors, some euryhaline species are less tolerant than native freshwater species to low conductivity and salinity (Wijnhoven et al. 2003, Jokela & Ricciardi 2008). Ion-poor environments may therefore constrain the spread and impact of these euryhaline invaders.

Conclusions

Conductivity influences the growth and survival of amphipods, but has no strong influence on their size-specific fecundity and size at reproduction. Although its tolerance to a wide range of salinities has allowed *E. ischnus* to successfully invade new environments in Europe and North America, its survival is diminished in areas of low conductivity, which provides an advantage or refuge for native competitors such as *G. fasciatus* in Lake St. Louis.

Human activities (e.g. organic pollution) have facilitated some invasions (Jazdzewski et al. 2004, MacNeil et al. 2004, Piscart et al. 2005), but declining calcium levels in northern lakes resulting from acidification (Jeziorski et al. 2008) may ultimately exclude invaders with high calcium requirements, such as Ponto-Caspian crustaceans. High biotic potential (i.e. a strategy for rapid colonization, involving early maturation, high number of generations per year and high fecundity) is a trait often shared by invaders (Devin & Beisel 2007, Grabowski et al. 2007). However, as pointed out by other authors (Devin & Beisel 2007, Dick 2008), high biotic potential alone does not guarantee successful establishment or dominance following establishment. Indeed, our results show that the success and dominance of *E. ischnus* in the lower Great Lakes (Dermott et al. 1998) cannot be attributed to greater reproductive ability. Devin & Beisel (2007) claim that invasive species exhibit a particular ecological profile (traits related to tolerance to abiotic conditions) rather than a biological one (e.g. life history traits such as body size, life span and reproduction). However, we believe that a better predictor of the invasion success and relative dominance of amphipods is a broad tolerance to the abiotic environment combined with being a stronger intraguild predator.

Acknowledgements

We thank G. D'Avignon, R. Kipp, E. Litvack, R. Marrotte, K. O'Sullivan, and B. Romaguer for helpful assistance in the lab and in the field. We also thank Dr Ronald Dermott at the Department of Fisheries and Oceans for generously sharing data from Lakes Erie and Ontario, and Myriam Rondeau at Environment Canada for generously sharing data of conductivity-measurements in the Ottawa River. This research was funded by the Canadian Aquatic Invasive Species Network.

References

Alcaraz, C., Bisazza, A. & Garcia-Berthou, E., 2008: Salinity mediates the competitive interactions between invasive mosquitofish and an endangered fish. – Oecologia **155:** 205–213.

Alcaraz, C. & Garcia-Berthou, E., 2007: Life history variation of invasive mosquitofish (*Gambusia holbrooki*) along a salinity gradient. – Biol. Conserv. **139:** 83–92.

Arnér, M. & Koivisto, S., 1993: Effects of salinity on metabolism and life history characteristics of *Daphnia magna*. – Hydrobiologia **259:** 69–77.

Ashforth, D. & Yan, N. D., 2008: The interactive effects of calcium concentration and temperature on the survival and reproduction of *Daphnia pulex* at high and low food concentrations. – Limnol. Oceanogr. **53:** 420–432.

Bailey, R. J. E., Dick, J. T. A, Elwood, R. W. & MacNeil, C., 2006: Predatory interactions between the invasive amphipod *Gammarus tigrinus* and the native opossum shrimp *Mysis relicta*. – J. N. Amer. Benthol. Soc. **25:** 393–405.

Berezina, N. A. & Panov, V. E., 2004: Distribution, population structure and salinity tolerance of the invasive amphipod *Gmelinoides fasciatus* (Stebbing) in the Neva Estuary (Gulf of Finland, Baltic Sea). – Hydrobiologia **514:** 199–206.

Bhattacharya, C. G., 1967: A simple method of resolution of a distribution into Gaussian components. – Biometrics **23:** 115–135.

bij de Vaate, A., Jazdzewski, K., Ketelaars, H. A. M., Gollasch, S. & van der Velde, G., 2002: Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. – Can. J. Fish. Aquat. Sci. **59:** 1159–1174.

Bijlsma, R. & Loeschcke, V., 2005: Environmental stress, adaptation and evolution: an overview. – J. Evol. Biol. **18:** 744–749.

Black, A. R. & Dodson, S. I., 2003: Ethanol: a better preservation technique for *Daphnia*. – Limnol. Oceanogr. Methods **1:** 45– 50.

Bravo, M. A., Cameron, B. & Metaxas, A., 2007: Salinity tolerance in the early larval stages of *Carcinus maenas* (Decapoda, Brachyura), a recent invader of the Bras d'Or Lakes, Nova Scotia, Canada. – Crustaceana **80:** 475–490.

Centre St-Laurent, 2003: St. Lawrence water masses. Environment Canada. http://www.qc.ec.gc.ca/csl/inf/inf010_e.html. Accessed 07-10-2008

Clemens, H. P., 1950: Life cycle and ecology of *Gammarus Fasciatus* Say. – Contrib. Stone Lab., Ohio University **12:** 1–63.

Costanzo, K. S., Kesavaraju, B. & Juliano, S. A., 2005: Condition-specific competition in container mosquitoes: The role of noncompeting life-history stages. – Ecology **86:** 3289–3295.

Creaser, E. P., 1935: Some notes on the ecological requirements or the amphipod *Gammarus fasciatus*. – Ecology **16:** 665–666.

Cristescu, M. E. A. & Hebert, P. D. N., 2005: The "Crustacean Seas" – an evolutionary perspective on the Ponto-Caspian peracarids. – Can. J. Fish. Aquat. Sci. **62:** 505–517.

Dermott, R., Witt, J., Um, E. M. & Gonzalez, M., 1998: Distribution of the Ponto-Caspian amphipod *Echinogammarus ischnus* in the Great Lakes and replacement of native *Gammarus fasciatus*. – J. Great Lakes Res. **24:** 442–452.

Devin, S. & Beisel, J. N., 2007: Biological and ecological characteristics of invasive species: a gammarid study. – Biol. Invasions **9:** 13–24.

Dick, J. T. A., 2008: Role of behaviour in biological invasions and species distributions; lessons from interactions between the invasive *Gammarus pulex* and the native *G. duebeni* (Crustacea : Amphipoda). – Contrib. Zool. **77:** 91–98.

Dick, J. T. A. & Platvoet, D., 1996: Intraguild predation and species exclusions in amphipods: The interaction of behaviour, physiology and environment. – Freshwat. Biol. **36:** 375–383.

Dick, J. T. A. & Platvoet, D., 2000: Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. – Proc. R. Soc. Lond. Ser. B : Biol. Sci. **267:** 977–983.

Ellis, S. & MacIsaac, H. J., 2009: Salinity tolerance of Great Lakes invaders. – Freshwat. Biol. **54:** 77–89.

Glazier, D. S., Horne, M. T. & Lehman, M. E. 1992; Abundance, body-composition and reproductive output of Gammarus minus (Crustacea, Amphipoda) in 10 cold springs differing in pH and ionic content – Freshwat. Biol. **28:** 149–163

Gonzalez, M. J. & Burkart, G. A., 2004: Effects of food type, habitat, and fish predation on the relative abundance of two amphipod species, *Gammarus fasciatus* and *Echinogammarus ischnus*. – J. Great Lakes Res. **30:** 100–113.

Grabowski, M., Bacela, K. & Konopacka, A., 2007: How to be an invasive gammarid (Amphipoda : Gammaroidea)-comparison of life history traits. – Hydrobiologia **590:** 75–84.

Haynes, J. L. & Cashner, R. C., 1995: Life history and population dynamics of the western mosquitofish – a comparison of natural and introduced populations. – J. Fish. Biol. **46:** 1026–1041.

Jazdzewski, K., 1980: Range extensions of some gammaridean species in European inland waters caused by human activity. – Crustaceana Suppl. **6:** 84–107.

Jazdzewski, K., Konopacka, A. & Grabowski, M., 2004: Recent drastic changes in the gammarid fauna (Crustacea, Amphipoda) of the Vistula River deltaic system in Poland caused by alien invaders. – Divers. Distrib. **10:** 81–87.

Jeziorski, A. & Yan, N. D., 2006: Species identity and aqueous calcium concentrations as determinants of calcium concentrations of freshwater crustacean zooplankton. – Can. J. Fish. Aquat. Sci. **63:** 1007–1013.

Jeziorski, A., Yan, N. D., Paterson, A. M., DeSellas, A. M., Turner, M. A., Jeffries, D. S., Keller, B., Weeber, R. C., McNicol, D. K., Palmer, M. E., McIver, K., Arseneau, K., Ginn, B. K., Cumming, B. F. & Smol, J. P., 2008: The widespread threat of calcium decline in fresh waters. – Science **322:** 1374–1377.

Jokela, A. & Ricciardi, A., 2008: Predicting zebra mussel fouling on native mussels from physicochemical variables. – Freshwat. Biol. **53:** 1845–1856.

Kestrup, Å. M. & Ricciardi, A., 2009: Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean. – Biol. Invasions **11:** 2095–2105.

Kinzler, W. & Maier, G., 2003: Asymmetry in mutual predation: possible reason for the replacement of native gammarids by invasives. – Arch. Hydrobiol. **157:** 473–481.

Konopacka, A. & Jesionowska, K., 1995: Life-history of *Echinogammarus ischnus* (Stebbing, 1898) (Amphipoda) from artificially heated Lichenskie lake (Poland). – Crustaceana **68:** 341–349.

Lasenby, D. C., Yan, N. D. & Futter, M. N., 1994: Changes in body dimensions of larval *Chaoborus* in ethanol and formalin. – J. Plankton Res. **16:** 1601–1608.

Lockwood, A. P. & Inman, C. B. E., 1973: Changes in apparent permeability to water at molt in amphipod *Gammarus duebeni* and isopod *Idotea linearis*. – Comp. Biochem. Physiol. **44:** 943–952.

MacNeil, C., Bigsby, E., Dick, J. T. A., Hatcher, M. J. & Dunn, A. M., 2003: Differential physico-chemical tolerances and intraguild predation among native and invasive amphipods (Crustacea); a field study. – Arch. Hydrobiol. **156:** 165–179.

MacNeil, C., Prenter, J., Briffa, M., Fielding, N. J., Dick, J. T. A., Riddell, G. E., Hatcher, M. J. & Dunn, A. M., 2004: The replacement of a native freshwater amphipod by an invader: roles for environmental degradation and intraguild predation. – Can. J. Fish. Aquat. Sci. **61:** 1627–1635.

Marascuilo, L. A., 1966: Large-sample multiple comparisons. – Psych. Bull. **65:** 280–290.

Palmer, M. E. & Ricciardi, A., 2004: Physical factors affecting the relative abundance of native and invasive amphipods in the St. Lawrence River. – Can. J. Zool. **82:** 1886–1893.

Piscart, C., Devin, S., Beisel, J. N. & Moreteau, J. C., 2003: Growth-related life-history traits of an invasive gammarid species: evaluation with a Laird-Gompertz model. – Can. J. Zool. **81:** 2006–2014.

Piscart, C., Moreteau, J. C. & Beisel, J. N., 2005: Biodiversity and structure of macroinvertebrate communities along a small permanent salinity gradient (Meurthe River, France). – Hydrobiologia **551:** 227–236.

Pöckl, M., 2007: Strategies of a successful new invader in European fresh waters: fecundity and reproductive potential of the Ponto-Caspian amphipod *Dikerogammarus villosus* in the Austrian Danube, compared with the indigenous *Gammarus fossarum* and *G. roeseli*. – Freshwat. Biol. **52:** 50–63.

Roche, D. G., Torchin, M. E., Leung, B. & Binning, S. A., 2009: Localized invasion of the North American Harris mud crab, *Rhithropanopeus harrisii*, in the Panama Canal: implications for eradication and spread. – Biol. Invasions **11:** 983–993.

Rukke, N. A., 2002: Effects of low calcium concentrations on two common freshwater crustaceans, *Gammarus lacustris* and *Astacus astacus*. – Funct. Ecol. **16:** 357–366.

Sprague, J. B., 1963: Resistance of 4 freshwater crustaceans to lethal high temperature and low oxygen. – J. Fish. Res. Board Can. **20:** 387–415.

Sutcliffe, D. W., 1984: Quantitative aspects of oxygen uptake by *Gammarus* (Crustacea, Amphipoda) - a critical review. – Freshwat. Biol. **14:** 443–489.

Thibault, Y. & Couture, R., 1982: Upper thermal resistance of *Gammarus fasciatus,* Say (Crustacea, Amphipoda) and its use in situations of thermal shock. – Can. J. Zool. **60:** 1339–1346.

Thomsen, M. A. & D'Antonio, C. M., 2007: Mechanisms of resistance to invasion in a California grassland: the roles of competitor identity, resource availability, and environmental gradients. – Oikos **116:** 17–30.

Wetzel, M. A., Leuchs & H. Koop, J. H. E. 2005: Preservation effects on wet weight, dry weight, and ash-free dry weight biomass estimates of four common estuarine macro-invertebrates: no difference between ethanol and formalin. – Helgol. Mar. Res. **59:** 206–213.

Wijnhoven, S., van Riel, M. C. & van der Velde, G., 2003: Exotic and indigenous freshwater gammarid species: physiological tolerance to water temperature in relation to ionic content of the water. – Aquat. Ecol. **37:** 151–158.

Work, K. A. & Gophen, M., 1999: Factors which affect the abundance of an invasive cladoceran, *Daphnia lumholtzi*, in US reservoirs. – Freshwat. Biol. **42:** 1–10.

Wright, D. A., 1979: Calcium regulation in intermoult *Gammarus pulex*. – J. Exp. Biol. **83:** 131–144.

Zehmer, J. K., Mahon, S. A. & Capelli, G. M., 2002: Calcium as a limiting factor in the distribution of the amphipod *Gammarus pseudolimnaeus*. – Amer. Midl. Nat. **148:** 350–362.

Submitted: 24 June 2009; accepted: 06 April 2010.