

Effects of ontogenetic stage and density on the ecological role of the signal crayfish (*Pacifastacus leniusculus*) in a coastal Pacific stream

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Abstract. Ontogenetic stage and density of consumers can affect the intensity of their roles within a community. These roles can be further complicated in a heterogeneous environment, where a consumer might have disparate effects in different microhabitat types. We conducted an enclosure experiment in a small temperate stream to test the differential ecological roles of adults and juveniles of the signal crayfish (*Pacifastacus leniusculus*) in 2 microhabitat types. In addition, we manipulated numbers of each stage to create a gradient of density (and biomass). Enclosures contained 1, 2, or 3 adults, or 4, 8, or 12 juveniles. Control enclosures lacked crayfish. We added leaf packs the 4 corners of the enclosures to provide a primary resource for crayfish and other invertebrates and to provide a detritus-based microhabitat. After 6 wk, we collected the leaf packs and a cobble-bottom (Surber) sample from the center of the enclosures. We used cobble-bottom samples to analyze the composition of the community in the cobble microhabitat. Leaf-pack breakdown rate was positively related to crayfish biomass for adults and juveniles. Leaf-pack invertebrate community composition and abundance were negatively affected by crayfish presence, but these results were independent of crayfish ontogenetic stage and total biomass. The composition of the cobble-bottom invertebrate community was not significantly affected by the presence of crayfish, regardless of density or ontogenetic stage. This result might have been the consequence of the cannibalistic tendencies of *P. leniusculus* or of possible indirect effects of crayfish (e.g., bioturbation or chemical cues). Our study is among the first to be done on the ecology of *P. leniusculus* in its native environment. The fact that our results do not agree with those found in other studies for this organism might reflect the fact that most of what we know about this organism comes from research done where it has been introduced.

Key words: ecology, environmental heterogeneity, freshwater ecosystem, microhabitat, ontogeny.

Determining the role of a certain species within an ecosystem is complex because this role is a function of more than its mere presence in an area. For example, many species exhibit ontogenetic niche shifts, which correspond to different ecological roles through development (Werner and Gilliam 1984, Olson 1996, Hjelm et al. 2000). Behavioral shifts during development result in ecological differences between ontogenetic stages that are not simply a result of higher biomass of larger individuals. Ontogenetic niche shifts can increase complexity of species interactions and can have important consequences for community dynamics (Ebenman 1988, Taylor et al. 2001). Increased diversity in a species' ecological role can be caused by behavioral differences through ontogeny. In addition, the density of a species in a specific area can have

major effects on the local community. A species might be found in higher densities in certain microhabitat types, a pattern that can lead to context-dependent effects on the community at local scales. Context-dependent effects are especially likely in heterogeneous environments, such as lotic and lentic freshwater environments, where the potential for diverse microhabitat structure exists. Indeed, the heterogeneous nature of stream ecosystems requires a thorough investigation into the spatial component of a species' ecology (McIntosh et al. 2004).

Freshwater crayfish of many genera undergo ontogenetic niche shifts with respect to dietary preference. Juveniles are primarily carnivorous (e.g., Abrahamsen 1966, Parkyn et al. 1997, Whitledge and Rabeni 1997, Guan and Wiles 1998), whereas adults are omnivorous (e.g., Lodge et al. 1994, Whitledge and Rabeni 1997, Creed and Reed 2004, Usio and Townsend 2004). The need for a protein-rich diet for small

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crayfish often has been cited as a primary reason behind the ontogenetic niche shifts (Momot 1995, Whitley and Rabeni 1997). The diminished ability of large crayfish to obtain small, fast-moving invertebrates as prey also has been identified as an important factor (Abrahamsson 1966, Nyström et al. 1999). However, Parkyn et al. (2001) have shown that adults are indeed capable of obtaining aquatic invertebrate prey, and that these food sources make up a substantial part of their diet. Others (e.g., Nyström et al. 1999, Stenroth and Nyström 2003) suggest that the ingestion of detritus of vascular leaves by crayfish provides the energy required for maintenance, whereas energy for growth is provided by protein-rich sources. However, the biofilm that grows on detritus probably is easily digested and highly nutritious (Whitley and Rabeni 1997).

The ecological role of sexually mature crayfish has been studied extensively, but the role of juveniles is not as clearly characterized. In stream systems, adults have substantial roles as predators (Momot 1995, Parkyn et al. 1997, Whitley and Rabeni 1997, Usio 2000, Usio and Townsend 2004) and processors of vascular plant detritus (Hury and Wallace 1987, Parkyn et al. 1997, Whitley and Rabeni 1997, Schofield et al. 2001, Hollows et al. 2002, Creed and Reed 2004), and several researchers have proclaimed their significant role in stream ecosystems. Little is known about the ecology of juvenile crayfish (but see Parkyn et al. 2001). Thus, adult and juvenile members of a single species could have different roles in the stream ecosystem.

The ecology of large crayfish often has been studied using single individuals in enclosures (e.g., Creed and Reed 2004; but see discussion for some notable exceptions) without taking into account the ecological impacts of crayfish density or microhabitat use. However, *Pacifastacus leniusculus* (Dana) often is patchily distributed in streams, with areas of high density (usually areas of low flow and high organic matter buildup) and areas of low density (fast-moving riffles with little debris buildup) (CAB, personal observation). Thus, great disparity in ecological effects might exist between crayfish in these different microhabitat types.

We hypothesized that juvenile and adult crayfish would have different ecological roles in the detritus-based stream communities where they occur naturally and that increased crayfish density (biomass) would alter these effects. We asked how crayfish ontogeny and density (and their interaction) would affect the community. On the basis of the ontogenetic niche shifts described above, we predicted a decrease in abundance and diversity of the invertebrate community in

response to juvenile crayfish and diminished leaf pack dry mass because of consumption by adult crayfish. We predicted that these effects would intensify with increasing crayfish density to a point, after which crayfish would be limited by intraspecific aggression. We expected the effects to be more substantial in leaf-pack microhabitat than in cobble-bottom microhabitat. We used a controlled enclosure experiment to test our hypotheses.

Methods

Study species and study site

We used *P. leniusculus*, the only crayfish native to British Columbia, in our experiments. Its natural range extends from northern California to southern British Columbia (Bondar et al. 2005b); however, most of what is known about the ecology of this species comes from studies where it is an introduced species. The species was widely introduced to many parts of Europe and Asia in the mid- to late 1900s after losses of native European and Asian species from the crayfish plague (Abrahamsson and Goldman 1970, Svardson 1995).

We conducted our experiment in the University of British Columbia's Malcolm Knapp Research Forest, in southwestern British Columbia in the Coastal Western Hemlock biogeoclimatic zone. We worked in Spring Creek, a 2nd-order stream with a riffle-pool, cobble-dominated geomorphology (described in Richardson 1992, Reece and Richardson 2000, Negishi and Richardson 2006) within the research forest. Riparian vegetation surrounding Spring Creek consists primarily of red alder (*Alnus rubra*) with a smaller representation of vine maple (*Acer circinatum*), whereas the dominant forest cover is largely Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*).

Experiment

We conducted a randomized complete block experiment that contrasted effects of crayfish ontogenetic stage and density on leaf pack mass and invertebrate community abundance and composition in leaf packs and in mixed cobbles on the bottom (on the basis of Surber samples). We constructed enclosures (length = 90 cm, width = 90 cm, height = 50 cm) of 1.25-cm diameter polyvinyl chloride pipe and plastic hardware cloth (mesh size = 1 cm²), and dug them into the streambed to a depth of 30 cm so that the water inside the enclosures was between 15 and 20 cm deep. We created microhabitat structure within the enclosures by placing four 5-g ($\pm 1\%$) leaf packs in each (at the

corners), and allowed the packs to condition for 10 d before the start of the experiment. We made leaf packs from senescent leaves of red alder that had been collected from the riparian area of Spring Creek in the previous autumns and air-dried in the laboratory. We weighed the leaves, then rewetted them, bound them with wire-based garden ties, and affixed them to the inside of the enclosures.

We based crayfish treatment densities on the range of natural field densities of crayfish per linear meter of stream at 5 sites on Spring Creek (CAB, unpublished data). Adult treatments had 1, 2, or 3 individuals (average orbital carapace length [OCL] = 32.5 mm)/enclosure with average total biomass of 23.8, 44.4, and 72.0 g/enclosure, respectively. Juvenile treatments had 4, 8, or 12 individuals (average OCL = 18.5 mm [1–2-y-old crayfish according to Guan and Wiles 1998]), with average total biomass of 19.4, 30.0, and 49.1 g/enclosure, respectively. A control treatment consisted of enclosures with no crayfish. We replicated all treatments in 4 complete blocks (1 replicate of each treatment/block), spaced out along Spring Creek. We did the enclosure experiment on a homogeneous reach of the stream (~100 m in length), with a depth of ~30 cm and cobble and gravel substrate.

Once crayfish were inside, we covered the tops of the enclosures with galvanized steel hardware cloth (mesh size = 1 cm²) to allow maximum exposure to light while preventing crayfish from escaping or predators from entering. We ran the experiment for 6 wk, from early June to mid-July 2002, at which time stream temperature was between 8 and 12°C. We brushed the sides and tops of the enclosures 2×/wk to prevent debris buildup.

Sampling

We removed leaf packs and crayfish from the enclosures at the end of the experiment. In 1 of the 3-adult treatments only 1 adult survived, and in 1 of the 2-adult treatments only 1 adult survived. We took Surber samples (250- μ m mesh, 2-min sampling time, 1 sample/enclosure) from the center of each enclosure. We washed leaves thoroughly of any debris and invertebrates, air-dried them for 72 h, and weighed them. We washed all debris and invertebrates removed from the leaves into a large basin that was subsequently drained through a sieve with 63- μ m mesh. We stored the invertebrates from the leaf packs and Surber samples in 70% ethanol for subsequent analysis. We identified invertebrates to genus under a dissecting microscope, and counted them in 2 size categories (large: ≥ 1 mm, small: 0.5–1 mm).

Data analysis

We analyzed effects of biomass (a continuous variable) within ontogenetic stage on leaf-pack dry mass and leaf-pack and cobble-bottom invertebrate communities with a blocked analysis of covariance (ANCOVA), with crayfish ontogenetic stage as the main treatment effect (juvenile vs adult) and biomass as the covariate (excluding the control treatment). We calculated Simpson's index of diversity to assess effects of crayfish on taxonomic diversity. We analyzed the effect of crayfish treatment (including the control) on leaf-pack dry mass and leaf-pack and cobble-bottom invertebrate communities with a 2-way analysis of variance (ANOVA) for block design (4 blocks). In each case (ANCOVA leaf pack, ANCOVA cobble bottom, ANOVA leaf pack, ANOVA cobble bottom), we used a nonsequential Bonferonni correction for the p -values to account for the large number of tests. We carried out preplanned orthogonal contrasts on all analyses (see tables for descriptions). We used the MIXED procedure with the maximum likelihood method in SAS (version 9.1; SAS Institute, Cary, North Carolina) with $\alpha = 0.0045$ (Bonferonni-corrected value).

Results

Crayfish effects on leaf-pack decomposition

Crayfish biomass had a significant negative effect on leaf-pack dry mass (ANCOVA, biomass as covariate, $F_{1,13} = 32.33$, $p < 0.0001$; Fig. 1A); however, this effect was not dependent on ontogenetic stage ($F_{1,13} = 2.59$, $p = 0.132$) and the stage \times biomass interaction was not statistically significant ($F_{1,13} = 0.00$, $p = 0.977$). The slope of the crayfish biomass to leaf-pack dry mass relationship was -0.06 for both adult and juvenile crayfish. This result reiterates that the decrease in leaf-pack dry mass was not strictly proportional to the increase in crayfish biomass; i.e., the 95% confidence intervals around the slope (-0.0226 to -0.097) did not overlap with slope = -1 .

Crayfish treatment significantly affected leaf-pack breakdown rate ($F_{6,17} = 8.79$, $p = 0.0002$). Final leaf-pack dry mass differed significantly between the 3-adult and 1-adult treatments (ANOVA, orthogonal contrast, 3-adult vs 1-adult: $F_{1,17} = 28.97$, $p < 0.0001$; Fig. 1B). The mean final leaf-pack dry mass did not differ between crayfish and control treatments (ANOVA, orthogonal contrast, control vs crayfish: $F_{1,17} = 0.8$, $p > 0.05$). The block effect was significant for the ANCOVA ($F_{3,13} = 13.6$, $p = 0.0003$) and the ANOVA ($F_{3,17} = 14.18$, $p < 0.0001$).

Microhabitat-dependent effects of crayfish

Leaf-pack community.—Overall, total invertebrate abundance was significantly lower in crayfish than in control treatments (ANOVA; Table 1), but Simpson's index of diversity did not differ significantly between crayfish and control treatments (ANOVA; Table 1). Neither total invertebrate abundance nor species diversity was significantly affected by crayfish biomass or ontogenetic stage (ANCOVA; Table 1). The predominant taxa on the leaf packs were the nemourid stonefly *Zapada*, orthoclad chironomids, acarid mites, Tipulidae, Chironomini, and Tanypodinae. Abundances of all other taxa were too low to analyze statistically.

Abundances of *Zapada* spp. (Fig. 2A), total number of shredders (Fig. 2B), Orthocladiinae (Fig. 2C), Acari (Fig. 2D), and Tipulidae (Fig. 2E) on leaf packs were significantly lower in crayfish than in control treatments (ANOVA, orthogonal contrast, control vs crayfish; Table 1). The effects of crayfish on the number of total shredders, acarid mites, Tipulidae, *Zapada*, and Orthocladiinae were independent of crayfish biomass or ontogenetic stage (ANCOVA; Table 1). No significant interactions were detected between ontogenetic stage and biomass. Thus, the presence of crayfish had a strong negative effect on the abundances of these taxa, but the same effect was realized for 72 g of adult as for 20 g of juvenile crayfish.

The abundances of large Chironomini and Tanypodinae on leaf packs were significantly lower in crayfish than in control treatments, but the abundances of small Chironomini and Tanypodinae did not differ significantly between control and crayfish treatments (ANOVA; Table 1, Fig. 3A, B). The effects of the crayfish on the abundance of large Chironomini and Tanypodinae were independent of crayfish biomass and ontogenetic stage (ANCOVA; Table 1).

Cobble-bottom community.—Total invertebrate abundance in the cobble-bottom community was slightly <900 individuals/enclosure. Crayfish treatment, biomass, and ontogenetic stage did not significantly affect total abundance or the abundances of individual taxa in the cobble-bottom community (ANOVA, orthogonal contrasts, control vs crayfish, all p values > 0.05; ANCOVA; Table 2). The predominant taxa in the cobble samples were orthoclad chironomids, nemourid stoneflies (*Zapada* spp.), and baetid and leptophlebiid mayflies. No size-dependent effects of crayfish were detected for any taxon (Fig. 4A–D), including Chironomini and Tanypodinae, 2 taxa that showed size-specific responses to crayfish in leaf packs.

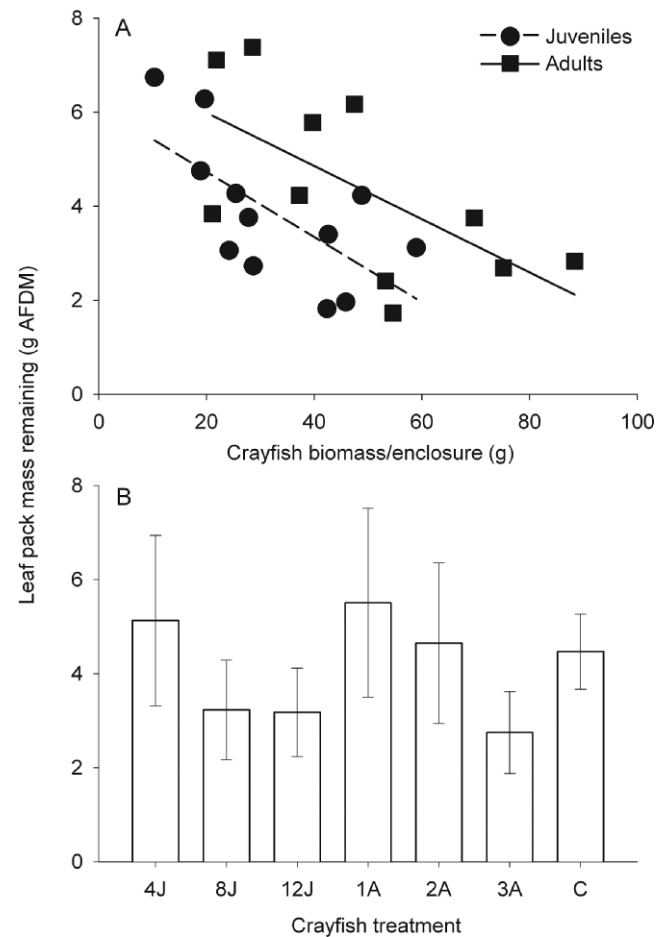


FIG. 1. Mean (± 1 SE) leaf-pack dry mass remaining in enclosures at the end of the experiment (after 6 wk) along gradients of adult and juvenile crayfish biomass (biomass as a covariate) (A), and in each crayfish treatment (B). AFDM = ash-free dry mass, 4J = 4 juvenile, 8J = 8 juvenile, 12J = 12 juvenile, 1A = 1 adult, 2A = 2 adult, 3A = 3 adult, C = control.

Discussion

Crayfish effects on leaf-pack decomposition

We found no statistically significant difference in final leaf-pack dry mass between treatments with or without (control) crayfish. Adult crayfish have been described as having major effects on the rate of leaf decomposition in other donor-controlled stream ecosystems (Creed and Reed 2004, Parkyn et al. 1997, 2001, Whitledge and Rabeni 1997, Schofield et al. 2001, Hollows et al. 2002, Huryn and Wallace 1987). However, Usio and Townsend (2004) found that the rate of leaf decomposition was similar in stream channels with and without crayfish, a result they attributed to the compensatory grazing and shredding capabilities of the invertebrate community. A similar form of functional compensation probably occurred in

TABLE 1. *F*-values for analysis of variance (ANOVA) testing the effects of crayfish treatment (1, 2, or 3 adults, 4, 8, or 12 juveniles, no crayfish control) and block and for analysis of covariance (ANCOVA) testing the effects of ontogenetic stage (excluding no-crayfish control) and block with crayfish biomass as a covariate on the responses of leaf-pack invertebrates. Preplanned orthogonal contrasts for the ANOVA included control vs all crayfish treatments (shown below), and 3 adults vs 1 adult (not shown because none were significant). Statistical significance after sequential Bonferonni correction was judged at $\alpha = 0.0045$. * = $p < 0.0045$, ** = $p < 0.00045$.

Response variable	ANOVA			ANCOVA		
	Treatment (df = 6,17)	Block (df = 3,17)	Contrast (control vs crayfish)	Biomass (df 1,13)	Stage (adult vs juvenile, df = 1,13)	Block (df 3,13)
Total shredders	6.11*	1.87	30.87**	0.42	0.00	2.01
Total <i>Zapada</i>	3.42	5.03	15.54*	0.09	0.04	6.44*
Total Orthocladinae	6.66*	0.91	32.78**	1.55	0.46	0.30
Total Acari	8.31**	2.09	33.77**	6.01	3.90	0.72
Total Tipulidae	5.55*	2.74	28.72**	5.08	0.56	5.50
Chironomini (>1 mm)	2.66	0.96	12.39*	0.95	0.03	2.18
Chironomini (0.5–1 mm)	1.47	1.79	2.60	0.01	0.44	2.36
Tanypodinae (>1 mm)	5.18*	0.55	23.70**	1.55	0.05	1.42
Tanypodinae (0.5–1 mm)	1.61	1.53	5.01	0.04	0.17	2.77
Total invertebrates	6.50*	2.07	32.62**	0.51	0.07	2.17
Simpson's index	2.29	5.87	0.01	0.15	2.55	4.79

our study because the shredding invertebrate guild was much more abundant in control than in crayfish enclosures.

In our study, leaf-pack dry mass was negatively related to biomass of both adult and juvenile crayfish. This result indicates that higher crayfish biomass (regardless of ontogenetic stage) can negatively influence leaf biomass in areas where leaf debris accumulates. We expected a higher (statistically significant) rate of loss of leaves in enclosures with adult than in enclosures with juvenile crayfish because other researchers have found that the magnitude of crayfish effects is positively related to crayfish biomass (Parkyn et al. 1997). Instead, we found that the rates of loss did not differ between adult and juvenile treatments, controlling for total biomass. We speculate that the highly aggressive nature of *P. leniusculus*, as opposed to other crayfish species (including *Paranephrops planifrons*, the subject of the study by Parkyn et al. 1997), might be the cause of the nonproportional decrease in leaf biomass relative to crayfish biomass; i.e., the rate of leaf litter decline decreased with increased crayfish density. *Pacifastacus leniusculus* is frequently described as aggressive and cannibalistic (Tierney et al. 2000, Westman and Savolainen 2001, Pockl and Pekny 2002, Nakata and Goshima 2003), characteristics that we also noted during our study. Stenroth and Nyström (2003) found only minor differences in rates of leaf breakdown between enclosures with 2 different densities of *P. leniusculus*. In a few cases during our study (see results), ~4 to 5 wk into the experiment, one of the adult crayfish in an enclosure was either severely injured or killed by

another, resulting in a large mass gain of one individual and mass loss in another. Corkum and Cronin (2004) found that feeding by *Orconectes propinquus* in experimental treatments with high food availability was limited by mutual interference.

Crayfish effects on the invertebrate community

Research on the direct and indirect effects of crayfish in food webs of several streams suggests that their role as predators on several invertebrate taxa can be substantial (Momot 1995, Parkyn et al. 1997, Whitley and Rabeni 1997, Usio 2000, Stenroth and Nyström 2003, Creed and Reed 2004). For example, the New Zealand crayfishes *P. planifrons* (Parkyn et al. 2001) and *Paranephrops zealandicus* (Hollows et al. 2002) prey directly on gastropods, cased caddisflies, chironomids, oligochaetes, and ephemeropterans. Gut-content analyses of the crayfishes *Orconectes luteus* and *Orconectes punctimanus* showed that chironomids, ephemeropterans, and trichopterans were preferred prey (Whitley and Rabeni 1997). In other studies, crayfish were associated with decreased density of some invertebrate taxa in leaf packs (e.g., Usio 2000, Usio and Townsend 2004), but whether the reductions were a result of direct or indirect interactions is not known because these studies did not provide evidence of direct predation. Our study also does not provide insight as to whether the effects of crayfish are caused by direct predation or indirect effects of crayfish presence. However, Bondar et al. (2005a) used gut content and stable isotope analyses of crayfish from this population and showed that the crayfish were not

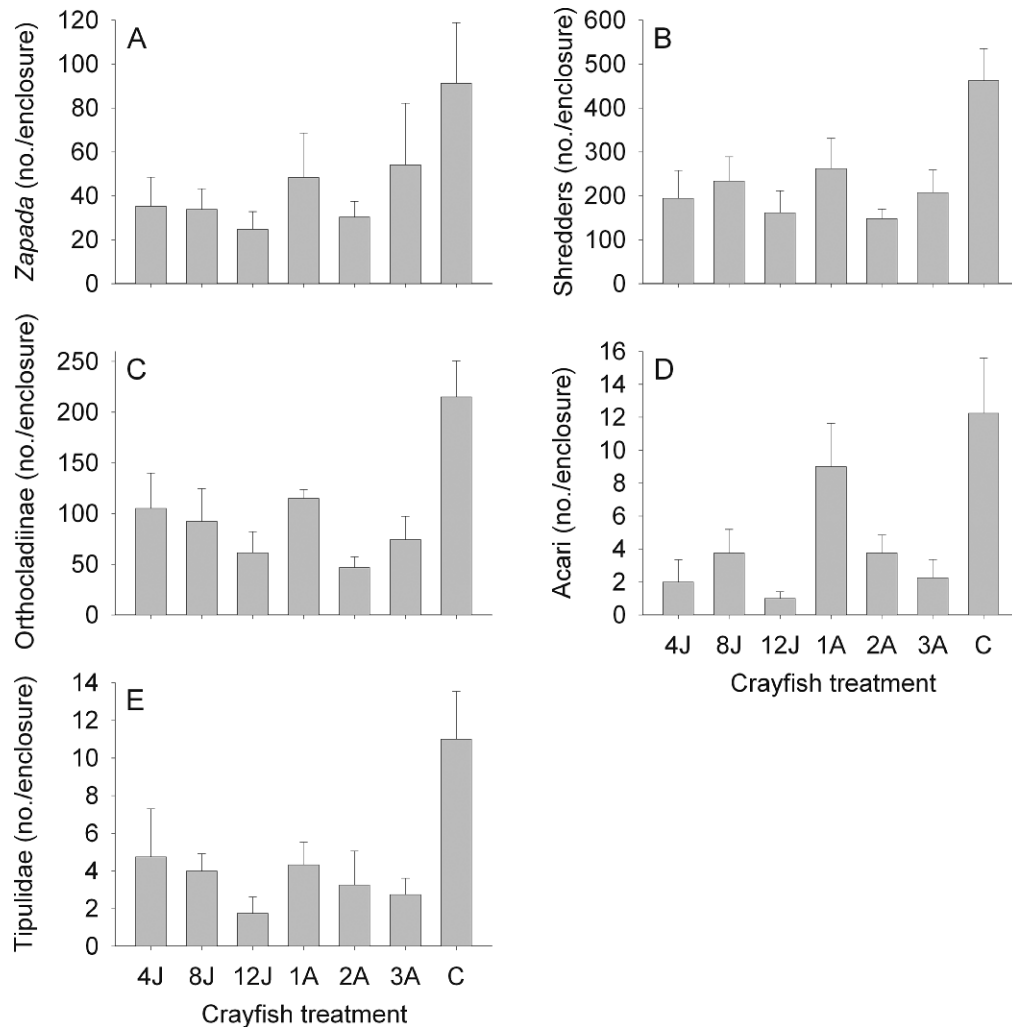


FIG. 2. Mean (+1 SE) abundance of *Zapada* spp. (A), shredders (B), Orthocladiinae (C), Acari (D), and Tipulidae (E) in leaf packs in enclosures in each crayfish treatment. 4J = 4 juvenile, 8J = 8 juvenile, 12J = 12 juvenile, 1A = 1 adult, 2A = 2 adult, 3A = 3 adult, C = control.

directly preying on invertebrates. Instead the bulk of their diet consisted of detrital material and detrital biofilm. Therefore, the crayfish effects on leaf-pack invertebrate communities in our study might be largely the result of indirect mechanisms.

Indirect effects of crayfish are likely to be the result of physical disturbance and sediment removal on the leaf packs or a predatory chemical cue released by the crayfish. Sediment removal by crayfish can have a large effect on stream communities (e.g., Parkyn et al. 1997, Creed and Reed 2004, Usio and Townsend 2004, Zhang et al. 2004). Pringle et al. (1993) showed that bioturbation by large decapod crustaceans (aytid shrimp) profoundly affects the composition of invertebrate communities of tropical streams.

Crayfish can indirectly affect stream invertebrate groups, such as snails (e.g., Alexander and Covich

1991, Covich et al. 1994, Hoverman et al. 2005), amphibians (e.g., Saenz et al. 2003), and fish (e.g., Kusch and Chivers 2004), through chemical cues. Such cues might induce emigration of invertebrates from areas of low or high crayfish density. Several stream invertebrate taxa have the ability to sense chemical cues from predators (e.g., Soluk and Collins 1988, Dahl 1998). Mayfly nymphs exhibit several antipredator behaviors in the presence of chemical cues from *Orconectes rusticus* (Richmond and Lasenby 2006). McIntosh et al. (2002) showed that a critical threshold (above which drift takes place) of such cues from brook trout (*Salvelinus fontinalis*) might exist for the mayfly *Baetis bicaudatus*. We suspect that such a threshold might exist for chemical cues exuded from *P. leniusculus*. If the threshold was exceeded in our low juvenile crayfish density treatments, then it seems

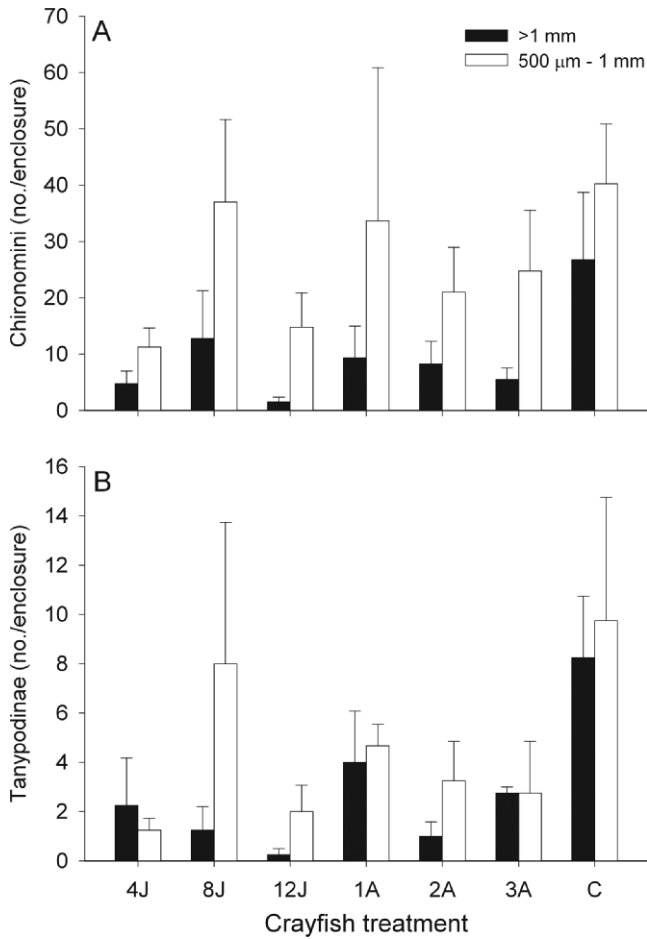


FIG. 3. Mean (+1 SE) abundance of small (0.5–1 mm) and large (>1 mm) Chironomini (A) and Tanypodinae (B) in leaf packs in enclosures in each crayfish treatment. 4J = 4 juvenile, 8J = 8 juvenile, 12J = 12 juvenile, 1A = 1 adult, 2A = 2 adult, 3A = 3 adult, C = control.

reasonable that the effects of crayfish on invertebrates in leaf packs would be the same at all crayfish densities, regardless of ontogenetic stage or total crayfish biomass. Investigation of invertebrate responses to crayfish cues in their immediate environment and whether a critical threshold exists for such responses are areas that merit future study.

Size-specific responses of chironomids to crayfish (i.e., negative effects on large Chironomini and Tanypodinae, no effect on small individuals) have been reported for other chironomid taxa (e.g., Creed and Reed 2004, Usio and Townsend 2004). The responses of different instars to chemical or bioturbation disturbances of crayfish could be vastly different, and might explain this result. Allan (1978) found that early instars or small taxa are less constrained in their habitat choices and drift periodicity than are large individuals, and this flexibility might make them less

prone to drift in response to environmental perturbations.

Crayfish did not affect the total abundance of invertebrates or species diversity in cobble areas of the enclosures. This result is contrary to literature that predicts facilitation of collector invertebrates by the leaf-shredding activities of the crayfish (the shredder-collector facilitation hypothesis; Heard and Richardson 1995). In addition, Creed and Reed (2004) noticed that heptageniid mayflies were more abundant in treatments with than without crayfish, something we did not observe with the leptophlebiid mayflies in our samples.

A predator might affect the community in some habitat types within a system, and not in others (Gibson et al. 2004). Habitat-specific effects might explain why species that were strongly affected in leaf packs were not affected in cobble. We hypothesize from these results that crayfish did not spend much time foraging in the cobble-bottom areas of the enclosures, and instead spent most of their time in the debris-filled areas. This hypothesis fits with the pattern of distribution of crayfish among habitats in Spring Creek. Crayfish are found most often in high densities in areas with substantial organic matter accumulations. Mark-recapture studies confirm long-term residence of crayfish in such areas (CAB and JSR, unpublished data), and our study shows that crayfish had the strongest ecological effects in this microhabitat within the enclosures. Thus, intensity or direction of ecological effects of crayfish appears to vary among invertebrate taxa and microhabitats in which they are studied.

No effect of crayfish ontogenetic stage

The ecologies of some organisms differ vastly among ontogenetic stages (e.g., Polis 1988, Mittelbach and Persson 1998, Persson and Brönmark 2002). We did not detect ontogenetic effects in our study, although we expected to find them. We observed similar effects of crayfish on leaf pack invertebrates in all treatments, regardless of ontogenetic stage. This result indicates that adult and juvenile crayfish had similar ecological roles. It is possible that the juveniles used in our experiment (mean OCL = 18.5 mm, corresponding to a 2-y-old crayfish) already had undergone an ontogenetic shift and were functionally the same as adults. However, Parkyn et al. (2001) demonstrated that *Paranephrops planifrons* underwent an ontogenetic shift in diet at OCL = 20.0 mm, a conclusion based on gut content analysis of crayfish with OCL <20 mm and >20 mm. Guan and Wiles (1998) reported that *Pacifasticus leniusculus* juveniles

TABLE 2. *F*-values for analysis of variance (ANOVA) testing the effects of crayfish treatment (1, 2, or 3 adults, 4, 8, or 12 juveniles, no crayfish control) and block and analysis of covariance (ANCOVA) testing the effects of ontogenetic stage (excluding no-crayfish control) and block with crayfish biomass as a covariate on the responses of the most abundant cobble-bottom invertebrates (see Fig. 4 for data). Statistical significance after sequential Bonferroni correction was judged at $\alpha = 0.0038$. * = $p < 0.0038$.

Response variable	ANOVA		ANCOVA		
	Treatment (df = 6,10)	Block (df = 2,10)	Biomass (df = 1,8)	Stage (adult vs juvenile, df = 1,8)	Block (df = 2,8)
<i>Zapada</i> spp. (0.5–1 mm)	3.33	2.57	5.92	8.94	6.45
<i>Zapada</i> spp. (>1 mm)	3.69	3.44	7.01	2.48	2.62
Orthocladiinae (0.5–1 mm)	0.20	5.08	0.19	0.17	3.85
Orthocladiinae (>1 mm)	2.06	8.51	2.31	0.01	7.94
<i>Baetis</i> (0.5–1 mm)	2.43	1.59	1.54	0.09	1.71
<i>Baetis</i> (>1 mm)	2.40	6.21	9.99	6.08	9.96
<i>Paraleptophlebia</i> (0.5–1 mm)	1.26	2.29	1.67	2.02	3.76
<i>Paraleptophlebia</i> (>1 mm)	0.77	6.70	7.48	2.41	2.99
Chironomini (0.5–1 mm)	0.56	3.58	0.66	1.52	4.53
Chironomini (>1 mm)	3.12	28.81**	1.77	0.68	16.12*
Tanypodinae (0.5–1 mm)	1.00	2.97	2.25	0.45	7.52
Tanypodinae (>1 mm)	0.78	3.89	0.88	0.33	5.11
Total invertebrates	1.15	2.83	2.77	2.69	4.19

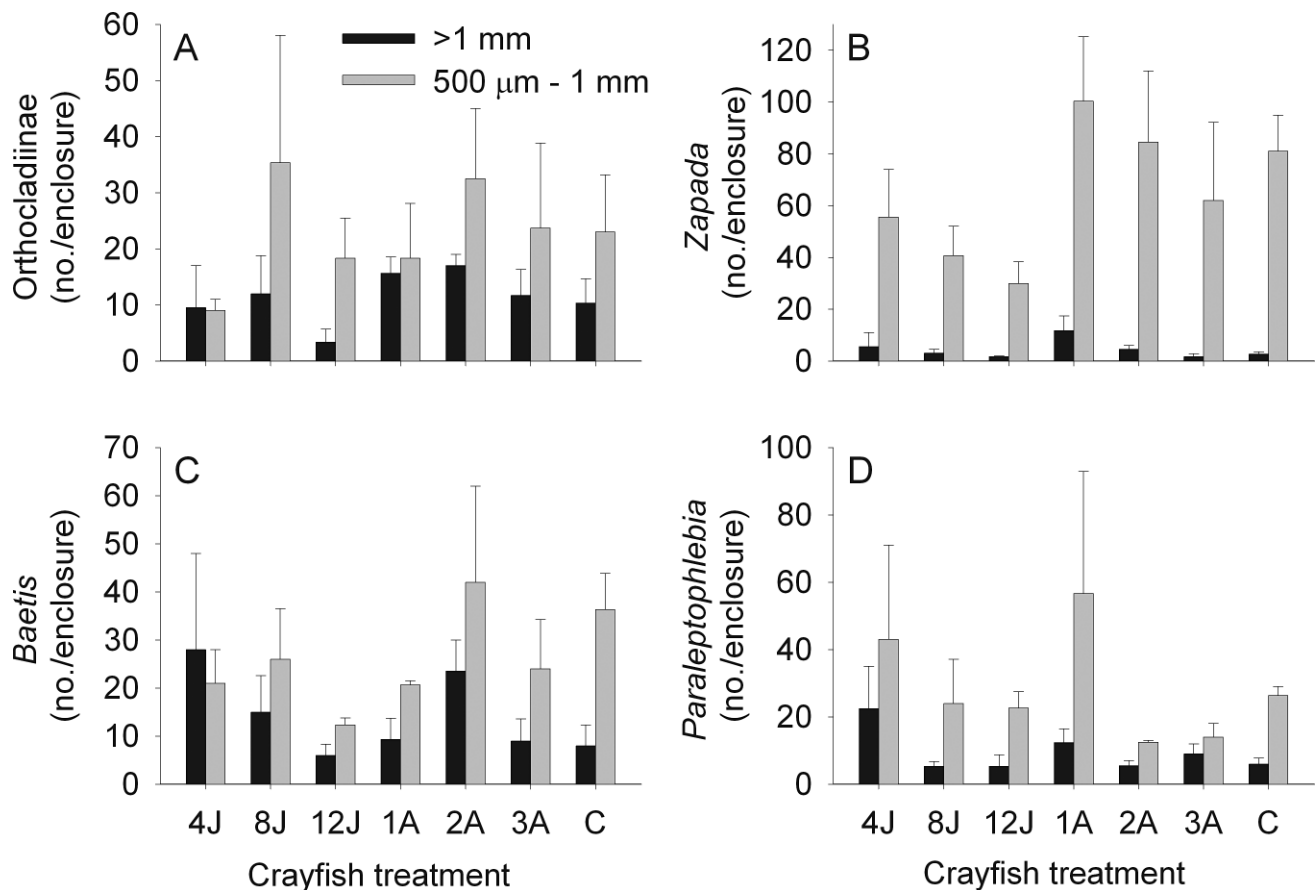


FIG. 4. Mean (+1 SE) abundance of small (0.5–1 mm) and large (>1 mm) Orthocladiinae (A), *Zapada* spp. (B), *Baetis* (C), and *Paraleptophlebia* (D) cobble bottoms of enclosures in each crayfish treatment. 4J = 4 juvenile, 8J = 8 juvenile, 12J = 12 juvenile, 1A = 1 adult, 2A = 2 adult, 3A = 3 adult, C = control.

with OCL >20 mm were far more carnivorous than were adults with a carapace length of 33 to 45 mm (in our study, juvenile OCL = 18.5 mm, adult OCL = 32.2 mm). We maintain that the juvenile crayfish used in our study were small enough to require a high-protein diet to sustain rapid growth. Thus, they should have been more predatory than the adults, which molt only once or twice per year (Shimizu and Goldman 1983). Future work should examine the ecology of young-of-the-year juveniles to determine whether an ontogenetic shift in diet occurs earlier in the life cycle than ~2 y. Comparison of young-of-the-year and adult *P. leniusculus* in their native habitat would address the question of whether an ontogenetic difference in their ecology exists.

Most research on the ecology of *P. leniusculus* in lotic environments (e.g., Guan and Wiles 1998, Stenroth and Nyström 2003, Bubb et al. 2004) has been undertaken where the species is introduced. For example, in a Swedish stream, *P. leniusculus* was a substantial predator on several invertebrate taxa. It affected predatory invertebrates and Ephemeroptera strongly, but did not affect Diptera and Plecoptera (Stenroth and Nyström 2003). Our results were just the opposite, in that *P. leniusculus* affected Diptera and Plecoptera strongly, but did not affect Ephemeroptera. In a British stream, several ontogenetic stages of *P. leniusculus* preyed directly on Chironomidae and Ephemeroptera, and juveniles preyed specifically on Coleoptera (Guan and Wiles 1998). Our present study did not address direct predation, but we have shown elsewhere (Bondar et al. 2005a) that *P. leniusculus* does not prey directly on invertebrates in our study system. Thus, we conclude that *P. leniusculus* had only indirect effects on the invertebrate community in our study. Such disparate results illustrate that the ecology of a species in an environment where it is introduced can differ markedly from its ecology within its native range. *Pacifastacus leniusculus* has negative effects on native crayfish populations in areas where it has been introduced (e.g., *Astacus astacus* in Europe, Westman et al. 2002; *Cambaroides japonicus* in Japan, Nakata and Goshima 2006). Thus, *P. leniusculus* appears to be involved in agonistic interspecies interactions in these areas. Comparative research on the ecology of *P. leniusculus* as an introduced and native species could provide insight into the contrasting roles it plays in different parts of the world.

Acknowledgements

We are grateful for the field assistance of Kathleen Bottriell on this project. We appreciate funding from the Forest Sciences Program (British Columbia),

Natural Sciences and Engineering Research Council (Canada), the University of British Columbia, and a Günter and Cordula Paetzold fellowship (to CAB). In addition, we thank Bill Neill, Scott Hinch, Diane Srivastava, Ross Thompson, and members of the StARR (Stream and Riparian Research) laboratory for their helpful comments on earlier versions of this manuscript. Declaration regarding the use of animals: We, the authors of this manuscript, declare that the experiments comply with the current laws of Canada.

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Received: 17 June 2008

Accepted: 12 January 2009