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Intraguild interactions and large-scale population patterns

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Abstract. Competitive interactions, including interference and intraguild predation, occur in many aquatic food webs and influence large-scale patterns of abundance, especially in lentic habitats. In a study of small coastal streams in eastern Canada, we found patterns suggesting that abundances of a predatory invertebrate, *Sweltsa onkos* (Plecoptera:Chloroperlidae), are influenced by another predator, *Rhyacophila vibox* (Trichoptera:Rhyacophilidae). Larval densities of the 2 species were inversely correlated, and mortality of larval *S. onkos* tended to be higher in streams with many *R. vibox*. Abundance and mortality of a 3rd predatory species, *Isoperla montana* (Plecoptera:Perlodidae), were unrelated to abundances of the other species. Laboratory behavioral observations confirmed that interactions between *R. vibox* and *S. onkos* were asymmetrical; high densities of *R. vibox* led to higher injury and mortality rates and lower growth rates of *S. onkos*, whereas *S. onkos* had no effect on *R. vibox* growth or mortality. Previous work has shown that *R. vibox* reaches high densities only in streams with few or no fish, and we conclude that the relative abundances of *S. onkos* and *R. vibox* in the study streams might be influenced by differences in vulnerability to intraguild and fish predation.

Key words: intraguild interactions, competition, behavior, aquatic invertebrates, Rhyacophilidae, Chloroperlidae, Perlodidae, streams.

The importance of biotic interactions, such as competition or predation, in structuring stream communities has been a point of contention for decades (e.g., Grossman et al. 1982, Creed 2006, Lepori and Malmqvist 2007). Competition is sometimes thought to play a relatively minor role in streams because of high levels of disturbance (Wagner 2005, Schmera et al. 2007). However, many studies have demonstrated density-dependent population dynamics linked to resource limitation (Wallace et al. 1999, Rowe and Richardson 2001, Taylor et al. 2002), competition for nonfood resources (e.g., net-building sites for filtering Trichoptera; Lancaster et al. 1988, Funakoshi 2005), and interference in predatory invertebrates (Hildrew et al. 2004).

The many examples of microhabitat and diet partitioning in invertebrates, often enhanced by temporal segregation of life cycles, strongly suggest a significant past or current role for interspecific competitive interactions in streams. Manipulations of consumers or their resources have demonstrated negative effects of one species on the growth, survivorship, or abundance of another (e.g., Richardson 1991, Feminella and Hawkins 1995, Slavik et al.

2004). Behavioral interference often is observed among predatory invertebrates, and effects include changes in behavior (avoidance, reduced activity, reduced foraging) (Elliott 2003b), physical displacement from preferred locations (Haden et al. 1999), and predation (Woodward and Hildrew 2002).

Relating small-scale species interactions to larger-scale patterns of distribution can be challenging (Wiley et al. 1997, Cooper et al. 1998). In general, scaling up is expected to occur when small-scale processes are not swamped by phenomena important at larger scales, e.g., disturbance, dispersal, or effects on different life stages (Peckarsky et al. 1997). Intraguild predation (often coupled with fish predation) is an interaction that influences large-scale distributional patterns in lentic environments. Species composition tends to vary in a predictable manner from temporary ponds without large predators, through semipermanent habitats with large predatory invertebrates, to permanent habitats with fish (McPeck 1990, Wellborn et al. 1996, Wissinger et al. 1996, 2003, Stoks and McPeck 2003). Species are prevented from extending their distributions to more permanent habitats by predation (intraguild or fish), or are excluded from less permanent habitats by intraguild predators or intolerance of abiotic conditions. Species composition in streams follows a similar

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environmental gradient, from temporary, fishless, often headwater streams, through permanent reaches with fish, with further gradients in fish species composition depending on stream size or order (Creed 2006). Similar mechanisms might drive transitions in stream invertebrate community composition. Stream invertebrates clearly differ in their vulnerability to fish, and good examples of strong fish effects on invertebrate communities can be found (e.g., Gilliam et al. 1989, Meissner and Muotka 2006). Asymmetric intraguild interactions influence distributional patterns, e.g., segregated distributions of 2 predatory caddisflies (Martin 1985) and effects on foodweb structure by an invasive dragonfly (Woodward and Hildrew 2001). However, we know of no example in which a pattern of inverse abundances is produced by a combination of vulnerability to a top predator and intraguild interactions.

Up to 13 (average 9) species of relatively large predatory invertebrates, most of which are rare, coexist in small coastal streams in eastern Canada. One species, *Rhyacophila vibox* (Trichoptera:Rhyacophilidae), emerges in high numbers only from streams without or with very few fish (Sircom and Walde 2009). We asked if 2 of the other common and widespread members of the predator guild, *Sweltsa onkos* (Plecoptera:Chloroperlidae) and *Isoperla montana* (Plecoptera:Perlodidae), showed patterns of abundance and larval mortality that were suggestive of intraguild interactions with *R. vibox*. We then determined if growth, mortality, and behavioral responses measured in laboratory streams provided mechanisms that explained field patterns. Our goal was to determine if differences in vulnerability to intraguild predation could explain variation in the distribution and mortality of predatory invertebrates.

Methods

Study area and organisms

The field study was conducted in small (~5 km long), parallel, and unconnected low-order streams that drain a 220- to 260-m-high basalt ridge and empty into the Bay of Fundy in eastern Canada (lat 45.1°N, long 64.9°W). The landscape is mixed forest, dominated by red spruce, yellow and white birch, and various maple species, and contains small-scale farms (mostly small pastures and hayfields) and wood-cutting operations. Two groups (~65 km apart) of 4 adjacent streams (0.5–2 km apart) were selected for sampling (Appendix). Sampling reaches (2–6 m wide) were 200 to 300 m long, 500 to 800 m upstream from the stream mouths, at elevations between 30 and 50 m above sea level. Substrate was mostly small to large

cobble on bedrock with scattered boulders and stretches of exposed bedrock in some streams. The streams are prone to spates during heavy rain and at snowmelt and have greatly reduced water flow in late summer/early autumn. Five of the 8 streams have resident populations of small brook trout (*Salvelinus fontinalis*), and one stream also has American eels (*Anguilla rostrata*). No other fish species are present. Fish surveys were done in late July and early August 2004 when streams were reduced to small pools connected by limited surface flow. An electroshocker was passed through ~20 pools in each sampling reach. The pools were small enough that it was unlikely that fish were missed. Fish density was calculated from estimates of pool area, on the basis of length and width.

Benthic larval censuses were done in autumn 2004 (6–7 November, 18–19 December) and spring 2005 (2–3 April, 28–29 April). Streams were ice-covered from January through March, and emergence of *Sweltsa onkos* and *I. montana* and pupation of *R. vibox* began in May. *Rhyacophila vibox* and *I. montana* have a predominantly 1-y life cycle, whereas *S. onkos* has a 2-y life cycle. Otherwise, phenologies are similar: emergence occurs from mid-May through July, eggs are laid shortly after emergence, and early instar larvae can be collected in September.

Estimates of larval abundance of the 3 focal species (*R. vibox*, *S. onkos*, and *I. montana*) were obtained by allowing colonization of mesh bags (~1-cm mesh) that each covered ~300 cm² on the stream bottom. Each bag contained 7 pieces of substrate of standardized sizes (maximum dimensions: one 14–16 cm, one 10–12 cm, three 7–10 cm, two 4–6 cm); the smallest and largest stones corresponded to the 25th and 50th percentiles of substrate sizes found in the streams. Artificial samplers have well-known sets of advantages and disadvantages (Rosenberg and Resh 1993). The important advantages for our study were the ability to take equivalent samples from different streams and to obtain repeated samples from the same locations over time, while minimizing substrate disturbance. Local stones of appropriate sizes were used to avoid problems with preferences for or against introduced materials.

We standardized colonization time among streams to minimize biases in comparisons of density and mortality rates across streams. Thirty bags, in groups of 10 (~50 m between groups, ~5 m between bags), were deployed in each stream ~6 wk before the 1st sampling date and remained in the streams throughout the census period. Bags were placed in areas of moderate flow, and pools, depositional areas, and scours were avoided. Two weeks before each sam-

pling date, the bags were checked and any that had washed out were returned to the stream. Larval samples were obtained by retrieving the bags with a 250- μm -mesh net to minimize loss, and then agitating and scrubbing each bag in a bucket of water for 30 s. Bags were returned to the stream. The extracted organisms and debris were placed immediately in dilute ethanol and then preserved in 70% ethanol in the laboratory.

Estimates of abundance (number of larvae collected/bag) and size distributions (mass) were obtained for each species in each stream on each sampling date. Individual larvae were wet-weighed on a microbalance 4 to 6 wk after collection. Time of weighing was standardized to prevent biases in estimates among dates or streams caused by mass loss in ethanol.

Species-specific larval mortality rates were estimated for each stream. Autumn larval mortality was assessed from November and December counts (n) ($\ln[(n_{\text{Dec}} + 0.1)/\ln(n_{\text{Nov}} + 0.1)]$) and winter mortality was assessed similarly from December and early April counts. We focused on the 2nd-y cohort of *S. onkos*, i.e., those individuals that were to emerge in April, and did not include the 1st-y cohort, i.e., individuals <0.1 mg in November and December and <0.2 mg in April, in analyses. A few very small *R. vibox* (<0.2 mg), probably the result of delayed hatching, were present in April and were omitted from analyses.

Laboratory experiments

Laboratory experiments focused on *R. vibox* and *S. onkos* because of the negative association observed for the species abundances and mortality in the field. Larvae were maintained at different densities (a mixed additive/substitutive design) in artificial stream tanks (see below), and growth and mortality were monitored over 2-wk periods. Eight experimental treatments were used: single-species treatments at densities of 1 larva/stream tank (4 replicates/species), 2 larvae/stream tank (3 replicates/species), and 4 larvae/stream tank (2 replicates/species) and mixed-species treatments at densities of 2 larvae and 4 larvae (equal numbers of each species) per stream tank (3 replicates). Laboratory densities were 0.4 to 1.7/100 cm², comparable with field densities in late April (on the basis of mesh bag samples) of 0.3 to 3.7/100 cm². Two trials were conducted (28 March–11 April, 16–30 April).

Experimental animals (predators and prey) were collected from the study streams a few days before each run, transported in leaf material on ice, and weighed in the laboratory. The predators were kept in

individual mesh-sided vials in an aerated tank for 48 h to standardize hunger level and facilitate gut clearing, and then reweighed. Late instars of both species were used. Mean initial masses (\pm SD) were: *R. vibox*, 21 \pm 0.7 mg; *S. onkos*, 6.6 \pm 0.2 mg. At the end of the experiment, predators were isolated for 48 h before weighing. *Simulium* sp. was selected as prey because both species consumed them readily in the laboratory, for ease of collection, and visibility. Prey were maintained in a tray of circulating water until needed. Prey density was maintained at 10/stream tank; missing and dead individuals were replaced each afternoon.

Experiments were conducted in 24 clear plastic circular stream tanks (outer diameter = 20 cm) placed in 4 racks (6 tanks per rack), each rack with its own water supply and lighting. Water (buffered, dechlorinated municipal water) was pumped from a lower reservoir to an upper reservoir, and water from the upper reservoir was gravity-fed to each stream tank through individual tubes at current speeds of \sim 10 cm/s. Each tank had a center screened drain that maintained water depth at 5 cm and allowed the water to enter the lower reservoir. Substrate was a single layer of white aquarium gravel (2–5 mm) and a single refuge stone (4 \times 6 cm) collected from a study stream. The tanks were housed in an environmental chamber at a constant 7 \pm 2°C (similar to April water temperatures in the field), and a 11:13 h light:dark cycle. Daytime light levels were 255 lux, produced by 2 fluorescent tubes positioned 60 cm above the stream tanks in each rack. These conditions do not entirely mimic natural stream conditions, but they establish the potential for one species to interfere with or prey upon the other.

Growth rate was assessed as the difference in gut-cleared mass between the beginning and end of the experiment, divided by initial mass. Prey consumption was estimated as total prey missing. A control run with only prey indicated that prey did not disappear in the absence of predators. Per capita daily consumption was calculated as total consumption/stream tank divided by the number of predators in the tank and the length of the trial. At the end of the 1st trial, we noticed that many of the *S. onkos* were missing appendages. For the 2nd trial, all *S. onkos* were checked for intact appendages (legs, cerci, antennae) at the beginning of the experiment, and each individual received an injury score at the end of the trial (1 point for each lost appendage, or a significant portion thereof, e.g., $\frac{1}{2}$ an antenna).

Predator activity was monitored during five 1-h periods (predawn: 0700 h, postdawn: 0815 h, midday: 1300 h, predusk: 1800 h, postdusk: 1915 h) on 5 d

during each trial. Lights were on from 0800 h to 1900 h each day. Midnight (0100 h) observations were made during the 2nd trial. The location and activity (moving or not) of each predator were noted at 15-min intervals during each observation period. Activity for each observation period was the proportion of observed movement episodes relative to total possible movement episodes; e.g., in a stream tank with 2 *R. vibox*, 8 movement episodes were possible: 2 individuals × 4 observation times.

Prey activity was assessed on 2 nights in each trial. Each tank was photographed with a 3-megapixel digital camera just before the lights went out and again just after they came on the following morning. Prey were counted in each image and their position compared between time periods. Any prey that had changed position by >1 body length were deemed to have moved. Movement in each tank was expressed as the proportion of prey that changed position.

Statistical analyses

Analyses used standard general linear model methods ($\alpha = 0.05$). Field abundances were \sqrt{x} -transformed to improve normality. In analyses of the laboratory data, trial was treated as a fixed factor and was omitted when insignificant to increase statistical power. All abundances were treated as covariates. Predator activity was analyzed using a repeated-measures analysis, with time of day as the within-subjects factor. Activity and growth (both proportions) were arcsine(x)-transformed.

Results

Field patterns

Larval size distributions suggested a 1-y life cycle for *R. vibox* in these streams (Fig. 1A, B), as found in southern Quebec (MacKay 1969). The small *R. vibox* larvae found in spring might have hatched late (a few 1st instars were found in mid-December). *Isoperla montana* also appeared to have a 1-y life cycle, but 2 *S. onkos* cohorts appear to be present (Fig. 1A, B), indicating a 2-y life cycle, as seen in southern Ontario (Harper 1973). In November, modal mass of the 2nd-y cohort of *S. onkos* was slightly greater than that of *R. vibox* or *I. montana* (Fig. 1A), but in the spring, *R. vibox* was considerably larger than *S. onkos* (Fig. 1B). *Rhyacophila vibox* was always much larger than the 1st-y *S. onkos*, and the period during which many 2nd-y *S. onkos* were larger than many *R. vibox* was quite short. As in other streams (MacKay 1969), *R. vibox* grew rapidly in autumn. By early November, 35% of larvae were 4th or 5th instars.

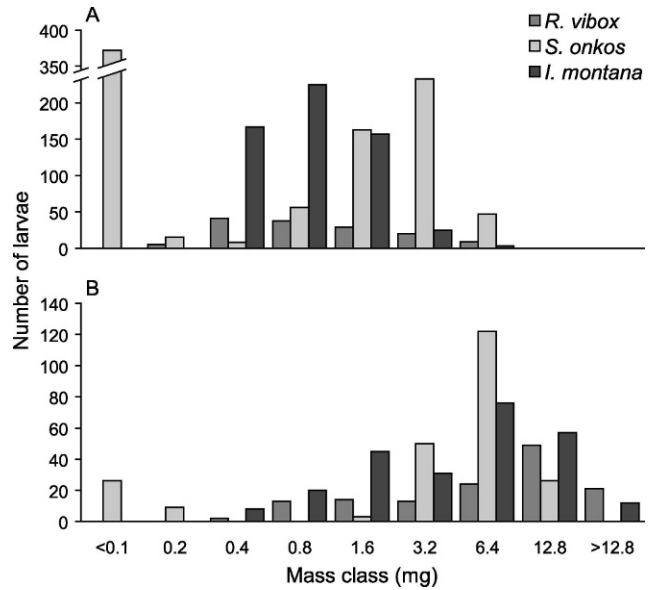


FIG. 1. Size (mass) distribution of larval *Sweltsa onkos*, *Isoperla montana*, and *Rhyacophila vibox* collected in November (A) and late April (B).

Predator abundances varied greatly among the 8 streams, with up to 7-fold differences between streams for *I. montana*, 16-fold differences for *R. vibox*, and >50-fold differences for *S. onkos*. In autumn, significantly fewer *S. onkos* were found in streams with many *R. vibox* than in streams with fewer *R. vibox* ($R^2 = 0.72$, $F_{1,6} = 15.53$, $p = 0.01$; Fig. 2A), and the relationship persisted, but was weaker, in spring ($R^2 = 0.54$, $F_{1,6} = 4.97$, $p = 0.07$; Fig. 2B). Mortality of *S. onkos* tended to be higher in autumn (November–December; $R^2 = 0.045$, $F_{1,6} = 5.96$, $p = 0.06$; Fig. 2A) and winter (December to early April, $R^2 = 0.75$, $F_{1,3} = 8.77$, $p = 0.06$; Fig. 2B) in streams with more *R. vibox* than in streams with fewer *R. vibox*. Abundances of *S. onkos* and *R. vibox* were not related to *I. montana* abundance ($0.25 < p < 0.96$) or mortality ($0.21 < p < 0.79$). Mortality rates of *S. onkos* or *R. vibox* were not related to abundances of *I. montana* ($0.12 < p < 0.73$). *Rhyacophila vibox* was abundant only in streams without fish (Fig. 3).

Interactions in laboratory streams

During the laboratory experiments, *R. vibox* was observed attacking and consuming *S. onkos* once. Almost 40% of *S. onkos* (7 of 18) kept with *R. vibox* over the 2 trials died or disappeared. In contrast, only 8% (3 of 36) of *S. onkos* kept alone or with conspecifics died or disappeared (Fig. 4A). On average, *S. onkos* lost 3 appendages, or portions thereof, in tanks with *R. vibox* and <1 appendage when kept alone or with

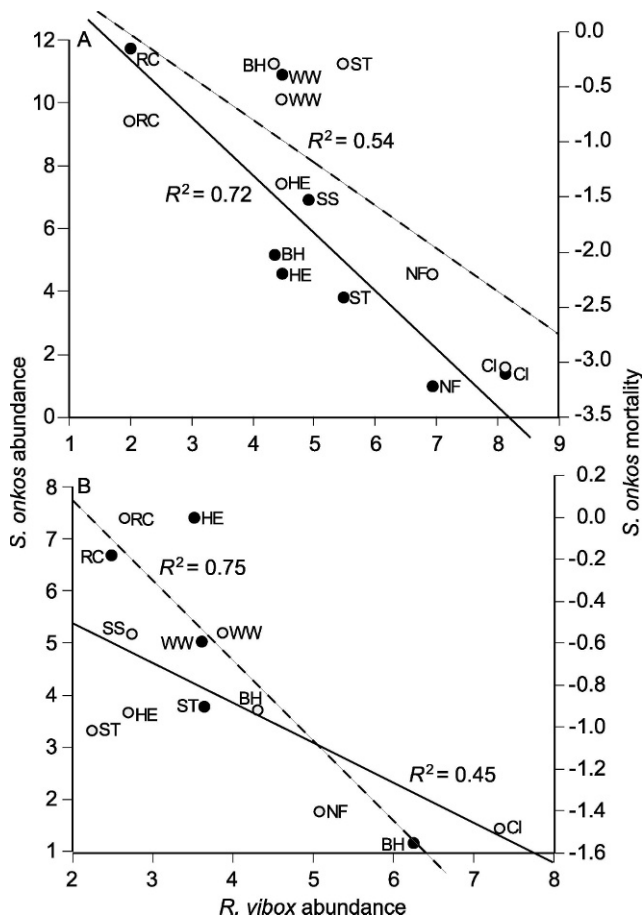


FIG. 2. Relationships between *Sweltsa onkos* abundance (filled markers, solid lines) and mortality (open marker, dashed lines) and *Rhyacophila vibox* abundance ($\sqrt{[\text{number}/\text{sample bag}]}$) in autumn (A) and winter/spring (B). Fit lines and R^2 values are for linear regressions.

conspecifics (Fig. 4B). The percentage of *R. vibox* that died or disappeared was similar when kept with *S. onkos* (11%) as when kept with conspecifics (14%) (Fig. 4A).

The relative sizes of *R. vibox* and *S. onkos* in the laboratory study (3-fold difference in mean wet mass) were similar to their relative sizes in the field in spring (2.3-fold difference). However, individuals used in the single-species treatments were significantly larger at the beginning of the experiment than were individuals used in the multispecies treatments (~40% by mass). These larger individuals had significantly different behavior and growth patterns than smaller individuals, so they were not included in analyses of growth or activity. Larger *S. onkos* were much less active than smaller *S. onkos* ($F_{1,26} = 7.09$, $p = 0.01$), and larger *R. vibox* grew less than smaller *R. vibox* ($F_{1,21} = 25.56$, $p < 0.001$).

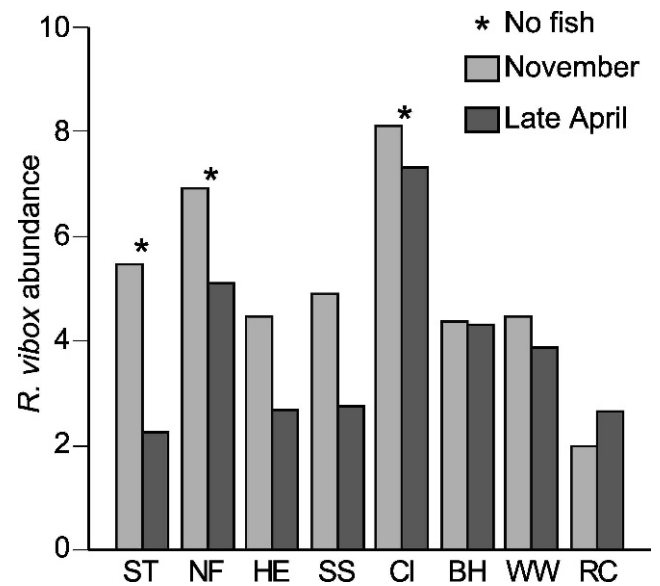


FIG. 3. Mean abundance ($\sqrt{[\text{number}/\text{sample bag}]}$) of *Rhyacophila vibox* in November and late April in each stream. Streams are ordered from west to east. Fishless streams are indicated with an asterisk. ST = Starratt Brook, NF = Number Five Brook, HE = Healeys Brook, SS = Sheep Shearer Brook, CI = Cobby Irving Brook, BH = Black Hole Brook, WW = Woodworth Creek, RC = Ross Creek Brook.

Growth of *S. onkos* was significantly lower in the high-density multispecies treatment than in the other treatments (Fig. 5A). Growth of *S. onkos* responded to the interactive effect of experimental densities of conspecifics (N_{onkos}) and *R. vibox* (N_{vibox}) ($F_{1,10} = 4.80$, $p = 0.05$). *Sweltsa onkos* did not grow in the high-density multispecies treatment, but its mass increased by 14 to 18% in the other treatments (Fig. 5A). Activity of *S. onkos* differed between trials ($F_{1,9} = 15.42$, $p = 0.003$) and responded significantly to N_{vibox} ($F_{1,9} = 27.27$, $p = 0.001$) and the trial \times N_{onkos} interaction ($F_{1,9} = 10.96$, $p = 0.01$). *Sweltsa onkos* was more active in the presence of *R. vibox* (10–11% moving) than when with conspecifics (~5% moving) (Fig. 5B). Growth of *R. vibox* did not differ significantly among treatments (Fig. 6A) but did differ between trials ($F_{1,11} = 10.04$, $p = 0.01$). Activity of *R. vibox* responded significantly to the interactive effects of $N_{onkos} \times N_{vibox}$ ($F_{1,10} = 5.26$, $p = 0.04$) and trial \times N_{onkos} ($F_{1,10} = 8.47$, $p = 0.02$). *Rhyacophila vibox* tended to be less active when *S. onkos* was present than in single-species treatments, but only in the 1st trial (Fig. 6B). Growth rates of *R. vibox* were lower, and activity was more erratic in the 2nd than in the 1st trial, perhaps because some individuals were nearing pupation.

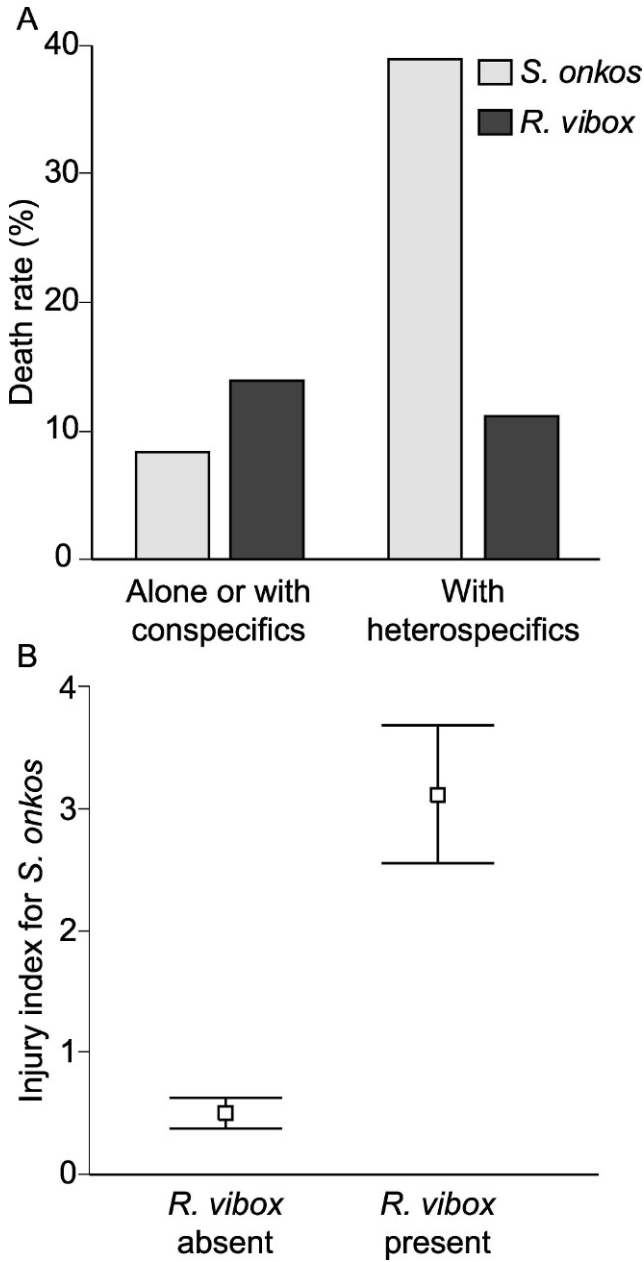


FIG. 4. Effect of the presence of *Rhyacophila vibox* on rates of disappearance/death (A) and mean (± 1 SE) number of missing appendages (B) for *Sweltsa onkos* in laboratory streams.

Per capita prey consumption (estimated from number of missing prey) was not affected by density of *S. onkos* or *R. vibox*. Prey consumption was low, averaging 0.3 prey per predator per day (range 0–0.8). However, this estimate did not include possible partial prey consumption, and both predators were observed partially consuming and then abandoning prey. Some of the dead prey found in the stream tanks had almost certainly been partially eaten, but it was

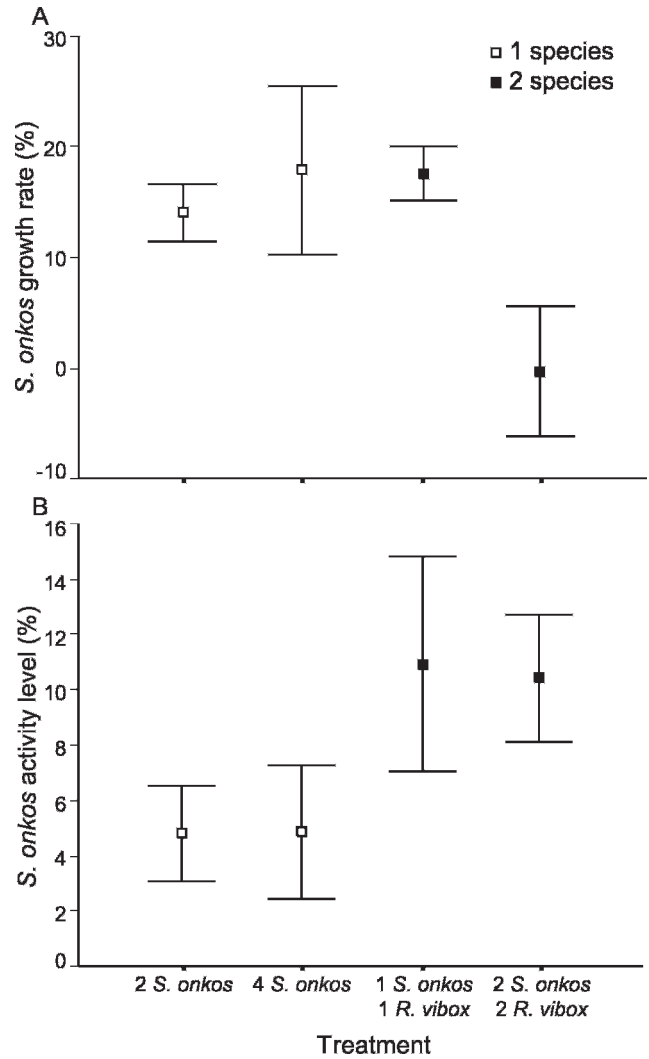


FIG. 5. Mean (± 1 SE) relative growth rate (% increase in mass) (A) and activity level (% moving) (B) of *Sweltsa onkos* in response to experimental densities of conspecifics and *Rhyacophila vibox* in laboratory streams.

not possible to assess partial feeding quantitatively. The number of dead prey per predator (0.3 ± 0.2 , range = 0.1–0.9) was not related to predator density. Movement of prey was unaffected by the density of either predator.

Rhyacophila vibox was significantly more active than *S. onkos* ($F_{1,26} = 11.26, p = 0.002$). Both predators had a diel pattern of activity, with less movement during the day and more during the night (Fig. 7). *Sweltsa onkos* activity dropped rapidly from 16% to 4% within the 1st h after the lights were turned on in the morning. *Rhyacophila vibox* activity remained high after dawn, and significant activity was observed at midday. *Rhyacophila vibox* was most active just before dawn, whereas *S. onkos* was most active at midnight (Fig. 7).

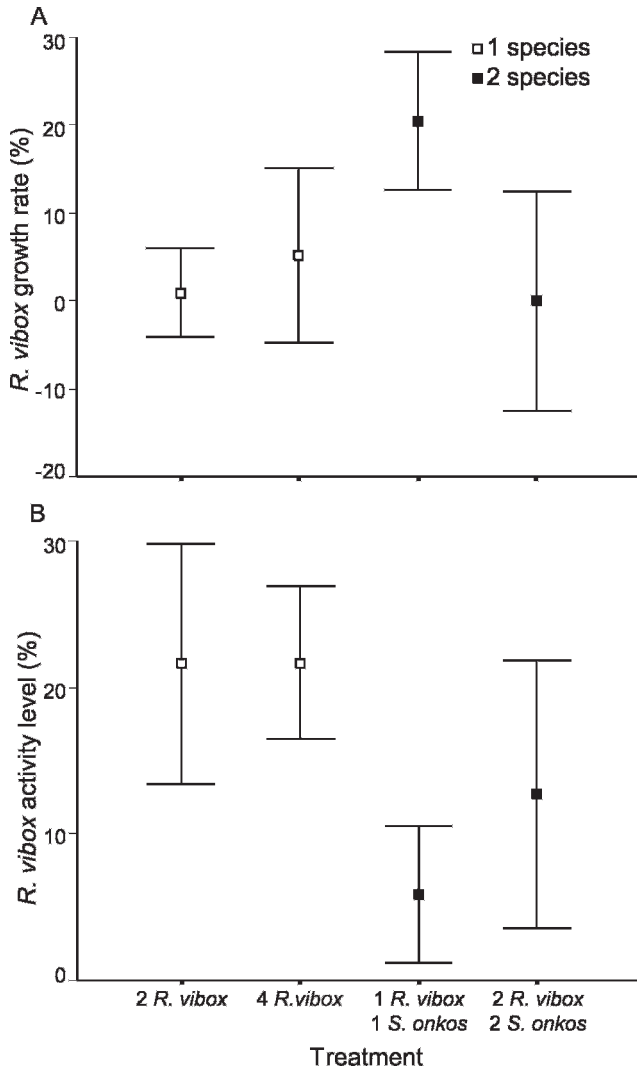


FIG. 6. Mean (± 1 SE) relative growth rate (% increase in mass) (A) and activity level (% moving) (B) of *Ryacophila vibox* in response to experimental densities of conspecifics and *Sweltsa onkos* in laboratory streams.

Discussion

Large-scale patterns of abundance and mortality for 2 species of predatory invertebrates from small coastal streams indicated a potentially important role for intraguild interactions and were concordant with mechanisms identified at much smaller scales. *Sweltsa onkos* were more abundant in streams with few *R. vibox*, and mortality rates for *S. onkos* tended to be lower in streams with few *R. vibox*. In the laboratory, *R. vibox* increased mortality and injury rates, and, at the higher density, reduced growth rates of *S. onkos*. Thus, mortality patterns in the field and behavior in the laboratory suggest that some of the variation in abundance of *S. onkos* among streams might be a consequence of intraguild interactions.

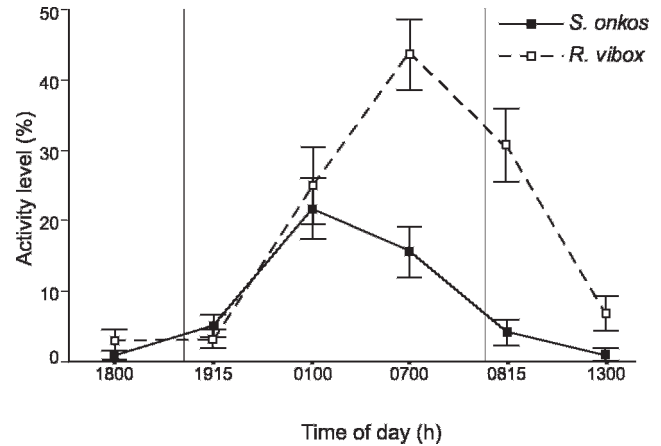


FIG. 7. Mean (± 1 SE) diel activity of *Sweltsa onkos* and *Ryacophila vibox* across treatments and trials. Vertical lines indicate the time at which the lights went out (left) and came on (right).

In lentic environments, the importance of intraguild interactions varies along a gradient from fishless temporary habitats through fishless semi-permanent and permanent habitats to permanent habitats with fish. Intraguild interactions tend to be most significant in the middle of the continuum (Stoks and McPeck 2003). If a similar pattern exists along a permanence/fish gradient in lotic habitats, then intraguild predation should have the largest effects on invertebrate predator guild composition in streams without fish.

The full gradient from temporary to permanent streams was not represented in our study. Even in fishless streams, pools were connected by some flow throughout the season in most years. The absence of sufficiently large or deep pools probably excludes fish from some streams. Thus, the streams in our study range from permanent streams with resident populations of brook trout to permanent/semipermanent streams without fish. Brook trout spend much of their time in pools, but we have routinely observed them in riffles, habitat in which *R. vibox* usually is found. The generally high activity levels and tendency of *R. vibox* to remain active after dawn (Fig. 7) contrast with the strongly diel pattern observed for *S. onkos* and reported for other *Rhyacophila* species (*Rhyacophila nubila* and *Rhyacophila dorsalis*) commonly found in streams with trout (Fjellheim 1980, Elliott 2005). This high level of daytime activity probably increases the vulnerability of *R. vibox* to visual, day-foraging brook trout. In our streams, *R. vibox* adults emerge in large numbers only from streams with very few or no trout (Sircom and Walde 2009), and high densities of larvae occur only in fishless streams. Thus, strong effects of

R. vibox on other species should be restricted to fishless streams.

The interactions between *R. vibox* and *S. onkos* were very asymmetrical, as are most intraguild interactions in stream food webs (Peckarsky 1991, Woodward and Hildrew 2001, 2002, Elliott 2003b, Lancaster et al. 2005). *Rhyacophila vibox* clearly was dominant in these interactions, and injured and sometimes consumed *S. onkos*. Nonlethal interference (changes in foraging rate, microhabitat use) can significantly affect survival and distribution of aquatic taxa (Peckarsky 1991, Muotka and Penttinen 1994, Elliott 2003a, b, Jonsson and Malmqvist 2003). Increased activity and slower growth rates, with presumed consequences on size, could affect survival of *S. onkos* and almost certainly would reduce reproductive output. Links between size and lifetime fecundity have been shown for other *Sweltsa* species (Yoshimura et al. 2003).

The variation in relative abundances of *S. onkos* and *R. vibox* in the study streams could be explained as a consequence of different vulnerabilities to fish vs intraguild predation. This trade-off has been documented several times in lentic habitats. For example, intraguild interactions determined dominance among limnephilid caddisflies only in habitats without salamander predators (Wissinger et al. 1996, 2003), and the distribution of *Enallagma* spp. (Zygoptera) reflected a strong trade-off between vulnerability to fish and dragonfly (intraguild) predation (McPeck 1990, 1998). We suspect that analogous patterns (shifts from vulnerability to intraguild predators to vulnerability to fish as a determinant of species composition) might be common along the transition from fishless streams or reaches to those with fish.

We cannot eliminate the possibility that the negative correlation between *S. onkos* and *R. vibox* is caused by factors other than interspecific interactions. However, among the factors that we have measured (11 variables including prey composition, canopy cover, substrate size, and water chemistry), only stream size explains the variation in abundance of *S. onkos* (Sircom and Walde 2009). *Rhyacophila vibox* and *S. onkos* differ in tolerance of high flow (JS, unpublished data). Related stonefly taxa also prefer lower flow habitats (e.g., Muotka 1993) and forage less effectively at high flow than does *Rhyacophila* (Malmqvist and Sackmann 1996). However, our small study streams (where *S. onkos* is rare) tend to have lower rather than higher current velocities (JS, personal observation). Unmeasured factors could be responsible for the correlation, e.g., flow refuges (sensu Lancaster and Hildrew 1993) could be fewer or less accessible in small streams. However, the link between both mortality and abundance of *S. onkos*

and abundance of *R. vibox* and the supporting behavioral observations point to intraguild interactions as the most likely causal factor examined to date.

Growing evidence indicates that biotic interactions, including intraguild interactions, sometimes influence large-scale patterns of abundance (e.g., Wissinger et al. 1996, 2003, Stoks and McPeck 2003). The stream-scale correlations between mortality and abundance of one predator with the abundance of another, and the correspondence with individual behavior, indicate that large-scale phenomena do not overwhelm the consequences of some key biotic interactions in these streams. Much can be gained by integrating experiments and observations at multiple scales, despite the difficulties associated with such studies (e.g., Peckarsky et al. 1997, Wiley et al. 1997, Cooper et al. 1998, McIntosh et al. 2002). Such an approach will be required to determine if large-scale effects of intraguild interactions in streams are more likely to occur in semipermanent/permanent streams without vertebrate predators.

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APPENDIX. Fish biomass and physical/chemical characteristics of the study streams. Sites are ordered from west to east (see Fig. 3 for stream names). Catchment area, main stem length, and gradient were obtained from digital topographic maps. Mean substrate size is the average maximum dimension of 50 rocks selected at 2-m intervals along a 100-m transect. Canopy cover is the average of measurements taken at 1-m intervals from bank to bank (10 transects/stream). Chemical analysis was performed by the Environmental Chemistry lab at QEII Hospital, Halifax, Nova Scotia, on samples collected at base flow (early July).

Variable	ST	NF	HE	SS	CI	BH	WW	RC
Fish biomass (g/m ²)	0	0	9.3	2.5	0	3.5	2.9	6.7
Catchment area (km ²)	7.8	3.0	4.9	7.4	4.1	8.5	10.6	6.5
Main stem length (km)	5.3	4.0	4.4	5.3	3.1	5.9	6.0	5.0
Gradient (%)	4.2	4.8	4.5	3.7	4.4	3.6	3.0	3.5
Mean substrate size (cm)	27.4	24.7	24.9	27.4	18.3	18.2	19.6	15.3
Canopy cover (%)	55	82	57	90	89	56	58	91
pH	7.6	7.5	7.4	7.6	7.5	7.6	7.7	7.5
Conductivity (μS/cm)	158	133	86	114	80	65	111	64
Alkalinity (mg/L CaCO ₃)	22	18	12	18	23	20	27	19