

Risk-sensitive foraging by juvenile signal crayfish (*Pacifastacus leniusculus*)

C.A. Bondar, K. Zeron, and John S. Richardson

Abstract: Feeding behavior of carnivorous and herbivorous organisms is commonly explained in terms of nutritional requirements. However, feeding behavior of omnivorous organisms is difficult to predict and may not be based on nutritional requirements alone. To assess the plasticity of feeding behaviors exhibited by an omnivore, we conducted a feeding experiment using juvenile signal crayfish (*Pacifastacus leniusculus* (Dana, 1852)), both alone and in the presence of conspecifics and predators. Crayfish were presented with three types of food (chironomids, mayflies, and woody debris) in experimental enclosures, and the food type consumed and time to consumption were recorded. Although the same overall food choice (chironomid larvae) was made in all trials, the time it took for the juvenile crayfish to make a food selection was longer in the presence of adult conspecifics (both male and female) and adult cutthroat trout (*Oncorhynchus clarkii* (Richardson, 1836)). Food selection also took longer, although not significantly, in the presence of conspecific juvenile crayfish, and no changes in behavior were noted in the presence of young-of-the-year (YOY) cutthroat trout. The altered behavior of the juvenile crayfish observed in the presence of adult fish and crayfish can lead to context-dependent effects of this omnivore on its community. Ecologists must be increasingly aware that the feeding of omnivores may not be solely based on nutritional criteria.

Résumé : Le comportement alimentaire des organismes carnivores et herbivores s'explique généralement par leurs besoins nutritifs. Cependant, le comportement alimentaire des organismes omnivores est difficile à prédire et peut ne pas être basé sur les seuls besoins nutritifs. Afin de déterminer la plasticité des comportements alimentaires chez un omnivore, nous avons mené une expérience d'alimentation chez des jeunes de l'écrevisse signal (*Pacifastacus leniusculus* (Dana, 1852)), seuls et en présence d'animaux de même espèce et de prédateurs. Nous avons fourni trois types de nourriture (chironomides, éphémères et débris ligneux) aux écrevisses dans des enclos expérimentaux et nous avons noté le type de nourriture consommée et le temps requis pour cette consommation. Bien que le même choix général de nourriture (chironomides) soit fait dans tous les essais, le temps requis par les jeunes écrevisses pour faire un choix de nourriture est plus long en présence d'écrevisses adultes (tant mâles que femelles) de même espèce et de truites fardées (*Oncorhynchus clarkii* (Richardson, 1836)) adultes. La sélection de la nourriture est aussi plus longue, mais pas de façon significative, en présence de jeunes écrevisses de même espèce; il n'y a pas de changement de comportement alimentaire en présence de jeunes truites fardées de l'année. Le changement de comportement des jeunes écrevisses observé en présence de poissons et d'écrevisses adultes peut entraîner des effets de cet omnivore sur sa communauté qui varient selon le contexte. Les écologistes doivent de plus en plus être conscients que l'alimentation des omnivores peut ne pas être basée seulement sur des critères nutritifs.

[Traduit par la Rédaction]

Introduction

Omnivory in aquatic food webs has been recognized as a widespread occurrence (Menge and Sutherland 1987; Polis and Strong 1996). However, food choices made by omnivorous organisms are difficult to predict because an understanding of when and why different food groups are more

likely to be consumed is required. Most often it is assumed that nutritional constraints uniquely determine the food-mixing behavior of omnivores; however, several other factors may ultimately play a role (Singer and Bernays 2003). Factors such as predation risk, density of a preferred food source, biotic interactions (both intraspecific and interspecific), and microhabitat use all contribute to the dietary

Received 23 June 2006. Accepted 3 October 2006. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 15 December 2006.

C.A. Bondar,¹ K. Zeron,² and J.S. Richardson. Department of Forest Sciences, The University of British Columbia, 3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

¹Corresponding author (e-mail: carinb@interchange.ubc.ca).

²Present address: Department of Natural Resource Management, 2041-2424 Main Mall, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

choices of an omnivore, which may lead to selection of food sources that are suboptimal in terms of nutrition. For example, it has been well established that freshwater predatory invertebrates often incorporate algae and detritus (nutritionally poor food choices) into their diets, though the reasons for this inclusion are poorly understood (Lancaster et al. 2005).

The effects of predation on feeding behavior have traditionally been observed through an organisms' feeding rate on one specific food type (Sih 1982; Gilliam and Fraser 1987); however, few studies have investigated how predation risk affects the feeding behavior of omnivores. Understanding the mechanisms contributing to food choice in omnivorous organisms is important both in terms of the feeding ecology of the omnivores themselves and in terms of the potential effects of omnivorous organisms on their surrounding communities. The dynamics of food selection can ultimately dictate whether omnivory stabilizes population, community, and food web dynamics (Singer and Bernays 2003).

Stream-dwelling crayfish have been shown to be true omnivores (Pimm and Lawton 1978), having both plant- and animal-based components in their diets (Whitledge and Rabeni 1997; Parkyn et al. 2001; Hollows et al. 2002). In addition to the omnivory observed within age classes, crayfish have also been described to exhibit "life-history omnivory" (Woodward and Hildrew 2002), in that there are shifts in the feeding behavior of crayfish through development. Juvenile crayfish have traditionally been described as carnivorous and adults as detritivorous, and this trend has been shown for many crayfish genera (e.g., Abrahamsson 1966; Parkyn et al. 1997; Whitledge and Rabeni 1997). However, the ontogenetic shifts previously described in the literature may not be ubiquitous to all crayfish genera. In particular, research on the North American signal crayfish, *Pacifastacus leniusculus* (Dana, 1852), in its native environment has documented that juveniles feed primarily on conditioned woody debris found in the streambed (Bondar et al. 2005), in contrast with the primary food base of aquatic invertebrates found by other authors (e.g., Stenroth and Nyström 2003).

Although a certain amount of nutrition is clearly available from detrital food sources via the biofilm (Whitledge and Rabeni 1997), growth rates were significantly higher when crayfish were raised on a diet of invertebrates in comparison with detritus (Bondar et al. 2005). Juvenile *P. leniusculus* are therefore making foraging decisions that are not entirely based on the nutritive value of the food source, leading to the question about what determines the behavioral aspects of food choice in this omnivore.

There are several reasons why juvenile *P. leniusculus* may select food that is not optimal in terms of its nutritional value. Members of this species are aggressive and exhibit strong cannibalistic tendencies at several ontogenetic stages, especially by adults (Guan and Wiles 1998). Juvenile and adult *P. leniusculus* are found in similar stream habitats in their native environment, in areas of low flow and high debris buildup (C.A. Bondar, unpublished data). Although crayfish in these areas can be quite dense, the woody debris and other vascular detritus provide an abundance of refugia. In addition to the threat of intraspecific cannibalism, there is

a threat of predation for juvenile crayfish from other sources. Cutthroat trout (*Oncorhynchus clarkii* (Richardson, 1836)) are numerous in small streams containing crayfish and adults prey on juvenile *P. leniusculus* in Spring Creek (C.A. Bondar, personal observation). Little is known about the relationship between juvenile crayfish and juvenile cutthroat trout; however, these organisms are known to coexist in similar areas of the stream.

We used field-based choice experiments to assess the food selections made by *P. leniusculus* juveniles. Specifically, we asked whether juvenile crayfish would select invertebrate prey over woody debris when given a choice in a nonthreatening environment and whether the feeding behavior of these organisms would be influenced by the presence of conspecifics (adult or juvenile crayfish) or predators (cutthroat trout). Owing to the aggressive, cannibalistic nature of this species, we expected there to be a strong negative impact of the presence of adult crayfish (no food choice, attempting to seek refuge instead of feeding). We used both male and female adult crayfish in this study to determine whether there was an influence of adult gender on juvenile behavior. Similarly, as adult cutthroat trout have been shown to actively prey on juvenile *P. leniusculus*, we expected to see a strong negative influence of their presence. The presence of conspecific juvenile crayfish was expected to alter the time to a decision, but not the overall choice, and the presence of young-of-the-year (YOY) cutthroat trout was not expected to alter the behavior of the juvenile crayfish, as there is little size difference between these two organisms.

Methods

The choice experiments took place in Spring Creek (see descriptions in Reece and Richardson 2000; Negishi and Richardson 2003), a second-order stream located in The University of British Columbia's Malcolm Knapp Research Forest. YOY juvenile *P. leniusculus* (orbital carapace length (OCL) average 11.01 mm, range 8.2–12.5 mm) were hand-netted and kept in 25 L plastic containers without food for 48 h prior to being tested. Lids were kept on the containers to minimize disturbance and predation by birds and mammals. The vessels containing the crayfish were kept in the stream to maintain cool temperatures. River rocks (3–5 cm) purchased from a landscape supplier were thoroughly washed and placed in the containers with the crayfish to provide them with hiding places without providing any food.

Small (5 L) plastic vessels were used for the food choice tests. Purified water from the laboratory was brought to the stream site so that the water was free of any chemical signals that might influence the crayfish. The food choices added at random places to each vessel were as follows: five pieces of conditioned woody debris (approximately 1 cm × 1 cm), 10 live chironomid larvae, and five live baetid mayfly (Ephemeroptera) nymphs. The invertebrates were chosen based on their occurrence in diets of crayfish (including *P. leniusculus*) from other research (Guan and Wiles 1998; Hollows et al. 2002). Food sources were added to the enclosures 2 min prior to the addition of the crayfish. Crayfish were placed in the enclosures (one per trial) within the confines of a piece of 5.25 cm PVC tubing held vertically

and were given 3 min to acclimatize prior to being released. Subsequent to the release of the crayfish, the PVC tubing was removed from the vessel. The first item eaten by the crayfish was taken to be a positive trial for that food source. Time to consumption was also recorded. If a trial progressed for 20 min without consumption of a food item, it was not included. Only one trial was performed in each enclosure before rinsing and re-adding the food sources. A total of 19 trials were performed this way; each crayfish was used only once.

For the treatments involving the reaction of the juvenile crayfish to potential predators or conspecifics, a basket (13.0 cm diameter) made of 0.32 cm plastic mesh was hung in the center of the vessel so that the presence of the added fish or crayfish could be experienced by the juvenile crayfish without the surface area of the arena being altered in any way. Mesh was used so that chemical signals could easily permeate the vessel and also so that the entire floor of the treatment area would be visible once the basket was in place. The treatment organism was added to the basket, and the basket was suspended over the treatment area for 2 min prior to the addition of the food sources. Trials then proceeded as outlined above. A total of 14 juvenile feeding trials were performed for each of the following added organisms: adult female crayfish (OCL < 30 mm), adult male crayfish (OCL < 30 mm), conspecific juvenile crayfish (OCL ~ 11 mm), juvenile (mass ~ 0.5 g) and adult (mass ~ 10 g) cutthroat trout. The added organisms were caught by hand-netting in Spring Creek, except for adult cutthroat trout, which were caught in minnow traps. These organisms were held without food in minnow traps (adult crayfish and fish) or plastic vessels (juvenile fish) within the stream for 24 h prior to the experiment. All treatments were conducted during daylight hours, in a shaded area of the streambank.

Data analysis

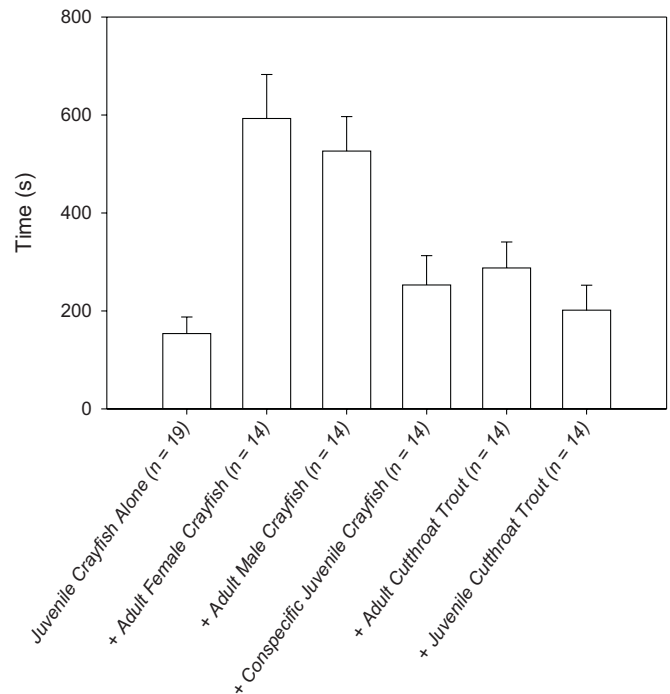
Data were analyzed in a one-way ANOVA using the MIXED procedure in SAS/STAT[®] version 8e (SAS Institute Inc. 2004) for the choice made by the juvenile crayfish for all treatments. The time to a choice for each treatment was assessed in the same manner, and treatments were compared using post hoc contrasts.

Results

For each of the choice treatments apart from the cutthroat trout, there was one trial for which the crayfish did not make a choice within 20 min. Otherwise, all trials for all treatments yielded the same result: the crayfish ate the chironomid larvae. It was noted in a few instances that the crayfish attempted to obtain a mayfly; however, they were never successful in this endeavor. Often, crayfish would climb over the wood fragments to reach a chironomid or would turn them over with their chelipeds if a chironomid had crawled underneath it. The crayfish never selected the wood as a food source in these trials.

The amount of time before a food item was consumed by the crayfish varied between treatments (Fig. 1). It was significantly faster when the crayfish were alone or with conspecific juveniles or cutthroat trout as opposed to when they

Fig. 1. Time to first food choice by young-of-the-year *Pacifastacus leniusculus* alone and in the presence of various other members of the stream community. In all cases, the first food choice was a chironomid. A statistically significant difference in the time to a choice was detected between the treatments containing adult crayfish and all other treatments (ANOVA post hoc contrast, $P = 0.0001$ for both adult female and male crayfish vs all other treatments). Numbers of replicates for each trial was $n = 19$ for juvenile crayfish alone and $n = 14$ for each of the other trials with added individuals. Error bars indicate standard error.



were with adult crayfish (significant contrasts for alone versus with adult female ($P < 0.0001$) or adult male ($P < 0.0001$)). The time to consumption was 285% and 242% longer in the presence of adult female and male crayfish, respectively. There was no statistically significant difference in the time it took for the juvenile crayfish to consume a food item in the presence of either female or male adult crayfish. Although there were no statistically significant differences in the time to consumption for the alone, conspecific juvenile crayfish, or cutthroat trout trials, there was a trend of increased time with any introduced organism. Time to consumption was 31%, 64%, and 87% longer in the presence of YOY cutthroat trout, conspecific juvenile crayfish, and adult cutthroat trout, respectively. Although not statistically significant, there was a trend of increased time to consumption in the presence of adult cutthroat trout ($P = 0.10$).

In the trials where juvenile crayfish were alone, several unsuccessful attempts to obtain mayflies occurred. This happened with 26% of individuals (5 of 19 individuals), as opposed to an average of 6% across all other trials (4 of 70 individuals). In each of the five individuals that attempted to obtain mayflies in the juvenile crayfish alone treatment, there was an average of three tries per individual, while there was only one for those crayfish in the other treatments where these attempts occurred.

The movement patterns of the crayfish differed between trials. In trials with adult crayfish and adult cutthroat trout,

the juvenile crayfish were still and movements were slow as opposed to when they were alone or with conspecific juveniles or YOY fish. Movements became especially limited or would cease altogether when the adult crayfish or fish within the cages were active.

Discussion

Although gut content and stable isotope analyses have demonstrated that YOY juvenile *P. leniusculus* in Spring Creek have a substantial portion of woody debris (and almost no invertebrates) in their diet (Bondar et al. 2005), wood was not the food source consumed under any circumstances during this experiment. Why are invertebrates not a larger part of the natural diet of juvenile *P. leniusculus*? The answer may come in part from the clear inhibition exhibited by the juvenile crayfish in the presence of adult crayfish and, to a lesser extent, the large cutthroat trout. Despite the fact that the larval chironomids were always chosen, the time to consumption was much longer, suggesting a degree of inhibition. In addition, the movement patterns of the juvenile crayfish in the presence of adult crayfish and fish suggested a greater degree of caution.

The threat of cannibalism by larger conspecifics has been shown to alter foraging decisions in other organisms as well. For example, Sih (1992) documented that avoidance of cannibalistic adults for juvenile aquatic insects (*Notonecta hoffmanni* Hungerford, 1925) was achieved by a reduction in movement, similar to the results of our study. If the threat of cannibalism to juvenile crayfish was causing a restriction of movement, the ingestion of woody debris may be a by-product of the increased risk. Since crayfish are omnivorous, and therefore have the capacity to feed on several food types, the presence of adults may shift juveniles to a diet that is composed largely of detritus, a more easily obtained food source. The woody debris may serve a dual function as a refuge from predators and a food source. Although chironomids and other invertebrates may also be present in areas with an abundance of woody debris, juvenile crayfish may refrain from ingesting them if a great deal of movement is required to do so. The occasional ingestion of invertebrates may occur for this reason, although stable isotope data (Bondar et al. 2005) show that generally this does not occur to a large extent.

Although not statistically significant, our results show a pattern of reduced movement and inhibition of feeding behavior of the juvenile crayfish in the presence of the large cutthroat trout, leading us to speculate that adult cutthroat trout have impacts on the ecology of these organisms. The lack of significance found in our study may be a result of the fact that our experiments took place during daylight hours as opposed to at night. Indeed, Nyström (2005) found a greater effect of fish on the activity level of *P. leniusculus* outside of refugia during the night. However, Söderback (1994) researched the behavior of juvenile *P. leniusculus* in the presence of adult European perch (*Perca fluviatilis* L., 1758) and found a strong antipredator response in pool-based experiments conducted during daylight hours. The latter study found the use of refugia in experimental pools was greater in the presence of perch. Although we did not use refugia in this study, we speculate that larger pieces of

woody debris in Spring Creek may serve such a function for juvenile crayfish and serve secondarily as a food source. Further work should incorporate this possibility by providing juvenile crayfish with a choice between edible and nonedible types of refugia. Additionally, the effects of cutthroat trout on juvenile crayfish behavior should be investigated at several times of day and night.

When juvenile crayfish were alone in the choice trials, several unsuccessful attempts to obtain the mayflies occurred. Crayfish were clearly unable to obtain the mayflies, as we did not observe any successful captures. However, they were almost always successful in capturing a chironomid on their first attempt. This shows that there may be some food sources that would be preferable to the crayfish but are too costly to obtain both in terms of energy expenditure and the potential exposure to predators through increased movement (since no attempts to obtain mayflies occurred when any other organism was present in the vessel). Several researchers have speculated that adult crayfish are detritivorous because of their inability to obtain small, fast-moving invertebrates in their large chelipeds (Abrahamsson 1966; Nyström et al. 1999). This study shows that the same may be true of juvenile crayfish for certain fast-moving invertebrates, such as the baetid mayflies used in our experimental vessels. The fact that the crayfish were always able to obtain a chironomid, even when they had to overturn wood pieces to find them, shows that this should be a likely food source for them in the absence of predation risk in a natural setting.

Our research has demonstrated that predation risk can affect the feeding behavior of omnivores, and we speculate that this may be the reason for the inclusion of nutritionally-poor items in the diet in a natural setting. The decreased movement patterns and the increased time to food consumption may be contributing factors to the seemingly poor diet of juvenile *P. leniusculus* in Spring Creek. Feeding behavior of omnivorous organisms presents ecologists with a substantial challenge. However, detailed studies on feeding behavior will provide a broader insight into the circumstances that govern when a switch in food choice takes place. This in turn will lead to a greater knowledge of the complex web of ecological impacts that omnivores have on their communities.

Acknowledgements

The authors gratefully acknowledge the field assistance of Lee-Ann Hamilton and Megan Harrison. This paper was improved with the helpful comments of Per Nyström and one anonymous reviewer. The research was funded by the Natural Sciences and Engineering Research Council of Canada, the Forest Sciences Program (B.C.), The University of British Columbia, and a Gunter and Cordula Paetzold graduate fellowship to CAB.

References

- Abrahamsson, S.A. 1966. Dynamics of an isolated population of the crayfish, *Astacus astacus* Linné. *Oikos*, **17**: 96–107.
- Bondar, C.A., Bottrill, K., Zeron, K., and Richardson, J.S. 2005. Does tropic position of the omnivorous signal crayfish (*Pacifastacus leniusculus*) in a stream food web vary with life history

- stage or density? *Can. J. Fish. Aquat. Sci.* **62**: 2632–2639. doi:10.1139/f05-167.
- Gilliam, J.F., and Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, **68**: 1856–1862. doi:10.2307/1939877.
- Guan, R., and Wiles, P.R. 1998. Feeding ecology of the signal crayfish *Pacifastacus leniusculus* in a British lowland river. *Aquaculture*, **169**: 177–193. doi:10.1016/S0044-8486(98)00377-9.
- Hollows, J.W., Townsend, C.R., and Collier, K.J. 2002. Diet of the crayfish *Paranephrops zealandicus* in bush and pasture streams: insights from stable isotopes and stomach analysis. *N.Z. J. Mar. Freshw.* **36**: 129–142.
- Lancaster, J., Bradley, D.C., Hogan, A., and Waldron, S. 2005. Intraguild omnivory in predatory stream insects. *J. Anim. Ecol.* **74**: 619–629. doi:10.1111/j.1365-2656.2005.00957.x.
- Menge, B.A., and Sutherland, J.P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* **130**: 730–757. doi:10.1086/284741.
- Negishi, J.N., and Richardson, J.S. 2003. Responses of organic matter and macroinvertebrates to placements of boulder clusters in a small stream of southwestern British Columbia, Canada. *Can. J. Fish. Aquat. Sci.* **60**: 247–258. doi:10.1139/f03-013.
- Nyström, P. 2005. Non-lethal predator effects on the performance of a native and an exotic crayfish species. *Freshw. Biol.* **50**: 1938–1949. doi:10.1111/j.1365-2427.2005.01438.x.
- Nyström, P., Brönmark, C., and Graneli, W. 1999. Influence of an exotic and a native crayfish species on a littoral benthic community. *Oikos*, **85**: 545–553.
- Parkyn, S.M., Rabeni, C.F., and Collier, R.J. 1997. Effects of crayfish (*Paranephrops planifrons*: Parastacidae) on in-stream processes and benthic faunas: a density manipulation experiment. *N.Z. J. Mar. Freshw. Res.* **31**: 685–692.
- Parkyn, S.M., Collier, R.J., and Hicks, B.J. 2001. New Zealand stream crayfish: functional omnivores but trophic predators? *Freshw. Biol.* **46**: 641–652. doi:10.1046/j.1365-2427.2001.00702.x.
- Pimm, S.L., and Lawton, J.H. 1978. On feeding on more than one trophic level. *Nature (London)*, **275**: 542–544. doi:10.1038/275542a0.
- Polis, G.A., and Strong, D.R. 1996. Food web complexity and community dynamics. *Am. Nat.* **147**: 813–846. doi:10.1086/285880.
- Reece, P.F., and Richardson, J.S. 2000. Benthic macroinvertebrate assemblages of coastal and continental streams and large rivers of southwestern British Columbia, Canada. *Hydrobiologia*, **439**: 77–89. doi:10.1023/A:1004105820586.
- SAS Institute Inc. 2004. SAS/STAT[®]. Version 8e [computer program]. SAS Institute Inc., Cary, N.C.
- Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology*, **63**: 786–796. doi:10.2307/1936799.
- Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *Am. Nat.* **139**: 1052–1069. doi:10.1086/285372.
- Singer, M.S., and Bernays, E.A. 2003. Understanding omnivory needs a behavioral perspective. *Ecology*, **84**: 2532–2537.
- Söderback, B. 1994. Interactions among juveniles of two freshwater crayfish species and a predatory fish. *Oecologia (Berl.)*, **100**: 229–235.
- Stenroth, P., and Nyström, P. 2003. Exotic crayfish in a brown water stream: effects on juvenile trout, invertebrates and algae. *Freshw. Biol.* **48**: 466–475. doi:10.1046/j.1365-2427.2003.01020.x.
- Whitledge, G.W., and Rabeni, C.F. 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. *Can. J. Fish. Aquat. Sci.* **54**: 2555–2563. doi:10.1139/cjfas-54-11-2555.
- Woodward, G., and Hildrew, A.G. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.* **71**: 1063–1074. doi:10.1046/j.1365-2656.2002.00669.x.