

Intraspecific mass-scaling of field metabolic rates of a freshwater crayfish varies with stream land cover

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Abstract. We investigated the effect of land cover on the metabolic scaling of the freshwater crayfish, *Orconectes rusticus*, by comparing the field metabolic rate (FMR) of populations from streams flowing through different natural and agricultural land cover. When data from all streams were pooled, the metabolic mass-scaling exponent was approximately 0.71. However, both the strength and nature of FMR-mass relationships varied among streams (slopes from 0.61 to 0.91). This variability in scaling exponents was significantly correlated with two types of land cover, the proportion of monoculture (row cropping) agriculture (positive slope, $P < 0.02$, $R^2 = 0.75$) and the proportion of wetlands (negative slope, $P = 0.05$, $R^2 = 0.57$), in the riparian zone of each stream. In a complementary laboratory study, we found the metabolic response of crayfish to differ among animals consuming plant and animal based foods. Crayfish consuming animal-based foods had higher respiration rates than conspecifics consuming plant-based foods. As *O. rusticus* exhibits variable feeding rates and foraging behavior, differences in the availability and quality of food that accompany changes in catchment land cover provides a potential mechanism for the observed site-dependence of FMR-mass scaling. Intraspecific variability of FMR-mass scaling in stream crayfish and its relationship to catchment land use is further evidence that organismal physiological flexibility and acclimation to specific environments complicates efforts to use general mass-scaling laws to explain disparate ecological phenomena.

Key words: invertebrate ecology; land use; metabolism; Ontario; *Orconectes rusticus*; respiration; stream ecosystems.

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INTRODUCTION

Metabolism consists of the chemical reactions that are central to the maintenance and proliferation of life. The rate at which these reactions occur is intimately tied to an organism's body size. This relationship between animal mass and metabolism has long been recognized (e.g., Kleiber 1932) and has generally been described by the allometric relationship, $R = aM^b$, where the metabolic rate (R) of an organism is related to

its mass (M) to the power of a scaling exponent (b) and modified by a scaling coefficient (a). Such observations of mass-metabolism scaling and a set of derived models have been used to explain widely disparate ecological phenomena (Brown et al. 2004). However, there is accumulating evidence of systematic deviations among scaling exponents within and among species (Dodds et al. 2001, Bokma 2004, Glazier 2005, White et al. 2007). Variation in intraspecific scaling thus appears to be quite common and related to a

set of connected biological and environmental factors (Glazier 2005). For example, variability in scaling exponents has been found to reflect organism lifestyle (Killen et al. 2010), the physiological state of the organism (Glazier 2010), and ontogenetic shifts in habitat use (Riisgård 1998, Glazier 2005, Glazier 2006). Here, we assess whether variability in mass-metabolism scaling among conspecific populations can be explained by the ecological setting of its habitat, which has previously received relatively little study.

Stream ecosystems are well-suited for the study of how the metabolic allometry of organisms varies across a gradient of environmental conditions. Stream ecosystems are highly dynamic, heterogeneous environments and are strongly affected by numerous internal (e.g., stream flow) and external processes (e.g., canopy cover). Small streams are especially influenced by adjacent terrestrial environments, which can provide much of the stream's energy base. Removal of riparian vegetation reduces these external inputs and simultaneously increases surface irradiance and internal primary production. These effects of changing riparian vegetation can be amplified by agriculture in the catchment, which acts as a major source of nutrients (Fitzpatrick et al. 2007), affects food web structure (Goetz and Fiske 2008) and alters a range of species traits (e.g., benthic macroinvertebrate foraging strategies) in stream residents (Doledec et al. 1999). The dynamic stream environment and its sensitivity to catchment land cover would thus appear to have the potential to alter the physiology of resident organisms.

Crayfish are benthic invertebrates that can dominate the biomass of communities in some streams (Huryn and Wallace 1987). Crayfish are omnivorous and have been found to consume variable amounts of animal (Momot 1995), plant (Guan and Wiles 1998) and detrital food sources (Huryn and Wallace 1987, Stenroth et al. 2006). In general, they have strong dietary preferences for animal-based foods when multiple food sources are present (Momot 1995, Correia and Anastacio 2008). This omnivorous diet, particularly if animal mass-dependent, could alter crayfish metabolism if diet differences lead to changes in metabolic rate. Diet quantity and quality have

been found repeatedly to strongly affect mass-specific respiration rates in taxonomically diverse animals (e.g., McNab 1986, Bozovic 1995, Anderson and Jetz 2005, Zhou and Wang 2009). Land cover effects on the relative availability of crayfish prey types could thus lead to variable mass-metabolism scaling but the magnitude and nature of these effects have yet to be examined.

In this study, we measured the field metabolic rates of the freshwater crayfish, *Orconectes rusticus*, collected from streams flowing through different land cover in southern Ontario, Canada. We determined whether mass-metabolism scaling varied among streams and whether differences among streams were related to riparian land cover. We also examined a potential dietary explanation for stream-specific mass-metabolism scaling by measuring crayfish metabolic responses to changes in diet (from plant- to animal-based) and by generally examining the effects of catchment land use on important components of stream food webs.

METHODS

Stream characterization

We studied the metabolism of crayfish collected from seven 4th order streams located in southern Ontario, Canada. This region is characterized by high amounts of agriculture, which we differentiate into two categories, monoculture and mixed-agriculture. We defined monoculture to include land primarily and continuously used to grow row crops such as soybeans and corn. This land cover is associated with yearly till and high rates of fertilizer application. In contrast, mixed-agriculture is characterized by rotational crops such as grains and hay and typically requires only irregular tilling and minimal fertilization. Our previous work has shown that monoculture is a highly intensive form of agriculture, which elevates export of nutrients, primarily nitrogen (Wilson and Xenopoulos 2009, Williams et al. 2010) in receiving streams. In contrast, stream nutrient concentrations or microbial activity do not strongly relate to mixed agriculture, which is considered a less intensive form of agriculture. For this study, we quantified land cover in the upstream riparian zone, defined as a 100 m strip on each stream bank extending 100 m upstream from the point of sampling,

using existing land cover data and digital elevation models with ArcMap 9.0 (ESRI 2004) as described in Wilson and Xenopoulos (2008). Riparian land cover was chosen because it is representative of total catchment cover, but more predictive of terrestrial-stream interactions (Gregory et al. 1991). In addition, riparian land cover is highly correlated with the land cover of the entire watershed in this area ($r > 0.75$; Wilson and Xenopoulos 2008, Williams et al. 2010). Streams were chosen to ensure a gradient of agricultural and natural land cover was included in our study (see Table 1 for summary).

Stream crayfish sampling

We quantified field metabolic rates (FMR) of crayfish as representative of their metabolic rates as they are residing in the stream. Crayfish were sampled in 2008 (August and September) and 2009 (August) after crayfish had completed spring mating and bearing of offspring. Crayfish across a wide size range were collected with dip nets from each selected stream location. Immediately following capture, animals were placed into respiration chambers (0.5 or 1.0 L blackened mason jars) that contained local stream water, sealed, and semi-submerged in a shaded area of the stream to maintain ambient temperatures. Oxygen concentration and temperature were measured using an O₂ probe (Hach, Mississauga, Ontario, Canada; model Id40; detection limit ~0.01 mg O₂/L) after a period of acclimation (10–15 min) and then again 20–40 min later. This acclimation duration was chosen to ensure O₂ concentration in the chambers remained above 4 mg O₂/L after the respiration incubation. Furthermore, we employed a two-point measure-

ment approach to ensure minimal oxygen contamination associated with probe activity. Preliminary work demonstrated that, at most, 0.01 mg O₂/L is added to the water by probe reinsertion, which is well below our observed signal (2–6 mg O₂/L decline). During each sampling event, at least 2 additional chambers lacking crayfish were used to eliminate the effect that stream water alone had on the change in oxygen concentrations. Following the final oxygen measurement, each crayfish was placed on ice and the volume of water within the chamber was recorded. After returning to the laboratory, crayfish were frozen and stored. Frozen crayfish were subsequently placed in plastic cups and dried at 60°C for >72 h before being weighed to the nearest milligram on an analytical balance.

Metabolism-food experiments

We assessed the effect of food type on crayfish metabolic rate with a complementary laboratory study. Crayfish were collected from a non-study stream and acclimated to lab conditions for 4 weeks. Each crayfish was confined to its own aquarium, and provided refuge, aerated river water and commercial aquarium fish food. Following this period, animals ($n = 7$) were deprived of food for one week and randomly assigned to either rich or poor quality food treatments. The distinction between rich and poor foods was made based on previous studies (Olsson et al. 2008), which found animal based diets (high quality) result in greater growth than plant based diets (low quality). Animals in poor quality treatments were fed maple leaves, in excess, which had been placed for one month in a non-study stream. Animals in high quality treatments were provided with a commercial brine-shrimp fish-food in excess. After 4 weeks in their respective food conditions, animals were separated from their food sources and placed in experimental chambers 20 min prior to initial oxygen readings. Crayfish respiration and dry mass were measured as described above for animals studied in the field component of the study.

Statistical analyses

FMR was calculated as the per unit change in oxygen concentration, corrected for the oxygen consumption in crayfish-free chambers. This con-

Table 1. Percent land cover in riparian zones of each stream site. Other types of land cover included forage fields, idle or abandoned fields, and developed areas and were not included in this analysis.

Site	Forest	Monoculture	Mixed agriculture	Wetland	Other
Beaverton	8.60	9.50	19.1	46.4	16.4
Cavendish	24.7	17.1	10.3	28.0	19.9
East Cross	20.2	18.5	17.2	31.5	12.6
Fish	5.60	43.5	11.8	0.10	38.9
Indian	48.6	8.20	6.70	10.9	25.6
Teeswater	17.4	20.8	10.5	25.3	36.0
Uxbridge	17.8	13.2	14.4	32.2	22.4

centration change was then multiplied by chamber volume to determine total oxygen consumption rate. Temperature (T) corrections were performed according to the Q_{10} method ($R_{\text{corrected}} = R_{\text{measured}} \times 10^{(T_{\text{corrected}} - T_{\text{measured}})(\log Q_{10})/10}$) outlined by White and Seymour (2003), where $Q_{10} = 1.49$ as per Wiens and Armitage (1961). All field and laboratory respiration rates were corrected to 22.0°C, which was the average temperature found across sites and sampling years. In most cases (10 of the 12 samplings), stream temperature deviated less than 3.0°C from 22.0°C and resulted in relatively minor adjustments to crayfish metabolic rates.

Relationships between mass and FMR were assessed using standard major axis (SMA) estimations on log-log transformed data that included both years on the software SMATR (Falster et al. 2006). This analysis provides a robust method to assess whether there was a common mass-metabolism scaling relationship among all streams (Warton et al. 2006). As we did not find a common slope, we further tested for differences among streams using post-hoc multiple comparisons with the SMATR software. Least-squares regression was then used to assess the relationship between stream-specific scaling exponents to multiple characteristics of riparian land cover using SAS (version 9.0). For the food type-metabolic rate experiment, differences between the two food types were assessed using an independent two-sample *t* test.

RESULTS

Stream effects on mass-metabolism scaling

Similar to much work involving mass-metabolic scaling (e.g., Brown et al. 2004), we first assessed the relationship between mass and FMR without a consideration for ecological context. This across-stream analysis of all available data revealed a strong allometric relationship between FMR and mass (Fig. 1A), with a scaling exponent of 0.71. There was considerable variation in the individual FMRs of crayfish of any given mass (Fig. 1A) and a significant stream-effect on the FMR-mass relationship ($P = 0.032$). To further assess the nature of this stream-specific effect, we examined the relationships between crayfish FMR and mass for each stream separately. These stream-specific FMR-mass relationships general-

ly had a better fit, with six of the seven streams having a higher R^2 (than the across stream relationship) despite smaller ranges in mass (Fig. 1B–H). Correspondingly, several stream-specific scaling exponents were significantly different from each other (Fig. 2). In particular, the scaling exponent of Fish Creek ($b = 0.91$) was significantly greater than four other streams including a low scaling exponent of 0.61 in Teeswater Creek (Fig. 2).

The relationship of scaling exponents and land cover

Stream-specific scaling exponents were significantly correlated with some aspects of riparian land cover, although the nature and fit of these relationships were specific to land cover type (Table 2). Of natural riparian cover, sites with proportionally more wetlands were associated with lower scaling exponents (Table 2), while forested areas were not related to stream-specific scaling ($P > 0.05$). Scaling exponents also related to monoculture but not mixed agriculture (Table 2). We found a significant, positive relationship between stream scaling exponents and the proportion of stream riparian zones in monoculture agriculture. This type of land use explained a significant proportion ($R^2 = 0.75$) of between-stream variability in crayfish scaling exponents.

The metabolic response to food quality

We found the metabolic rates of laboratory-held *O. rusticus* to vary in response to food type. Between the two food types, mass-specific metabolic rates were significantly higher for crayfish fed the animal-based food (mean and standard deviation = 0.74 ± 0.17 mg $O_2 \cdot g$ dry mass $^{-1} \cdot h^{-1}$) compared to the plant based food (mean and standard deviation = 0.48 ± 0.12 mg $O_2 \cdot g$ dry mass $^{-1} \cdot h^{-1}$; independent-samples *t*-test, $t(13) = 3.28$, $P = 0.006$). There was no significant difference in crayfish mass between rich (mean and standard deviation = 2.32 ± 0.59 g dry mass) and poor (mean and standard deviation = 2.17 ± 0.82 g dry mass) food treatments (independent-samples *t*-test, $t(13) = 0.56$, $P = 0.58$).

DISCUSSION

The FMR-mass scaling of *O. rusticus*, when data from all streams were pooled, was found to

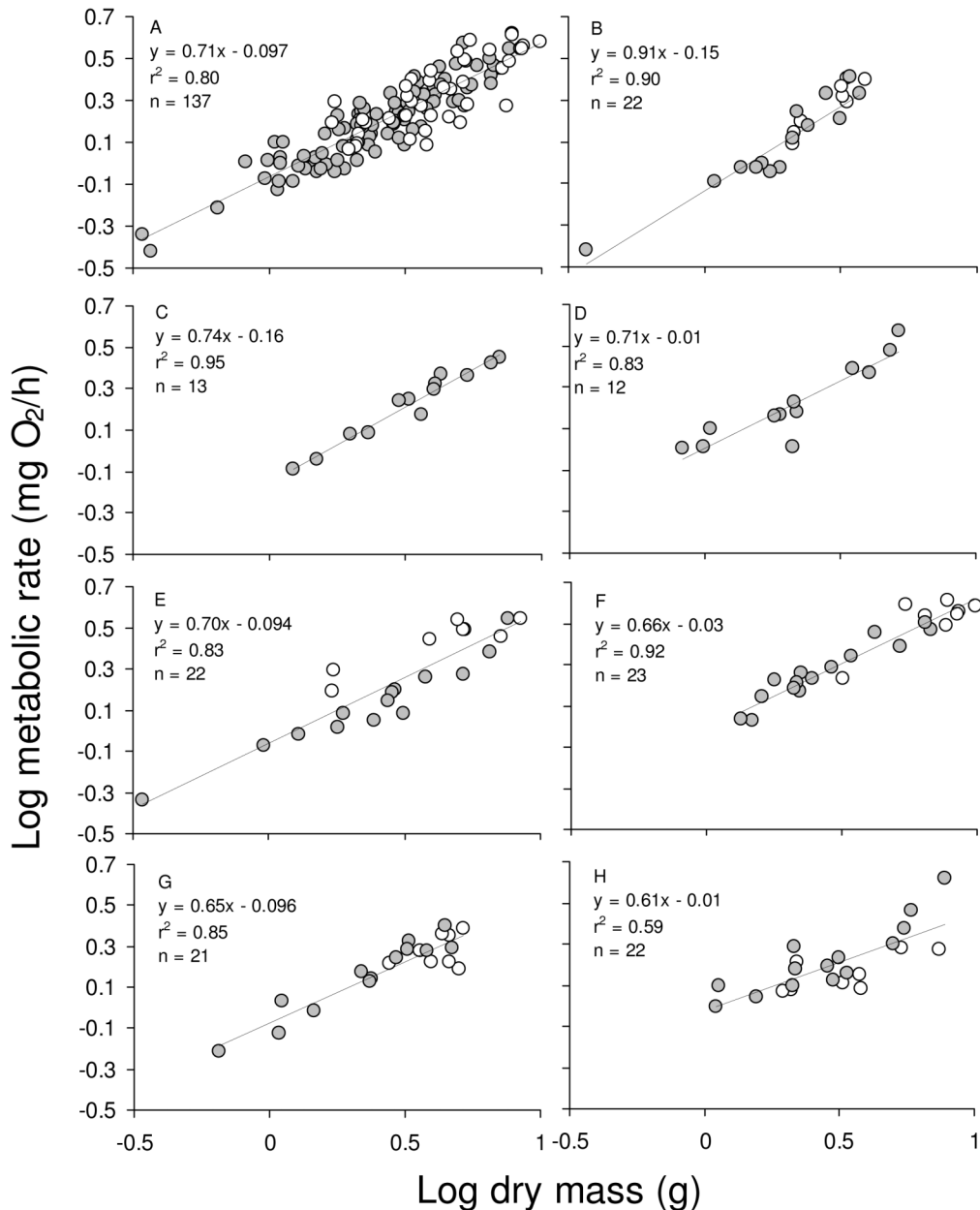


Fig. 1. Log-log plot of the temperature corrected (22°C) field metabolic rate against mass for: (A) all sites together, (B) Fish Creek, (C) East Cross, (D) Cavendale, (E) Indian, (F) Teeswater, (G) Beaverton and (H) Uxbridge. The reported regression statistics are of combined data from 2008 (open circles) and 2009 (closed circles) where both years are available.

be 0.71. However, when each stream was considered separately, we found there was a range in FMR-mass scaling exponents (0.61–0.91) and generally a better fit; 7 of 8 streams had individual R^2 higher than the global relationship.

These stream-specific scaling exponents include two values (0.91, 0.61) that approximately bracket the range of mass-metabolic scaling exponents found among diverse groups of organisms (Glazier 2005). In addition, this range of inter-

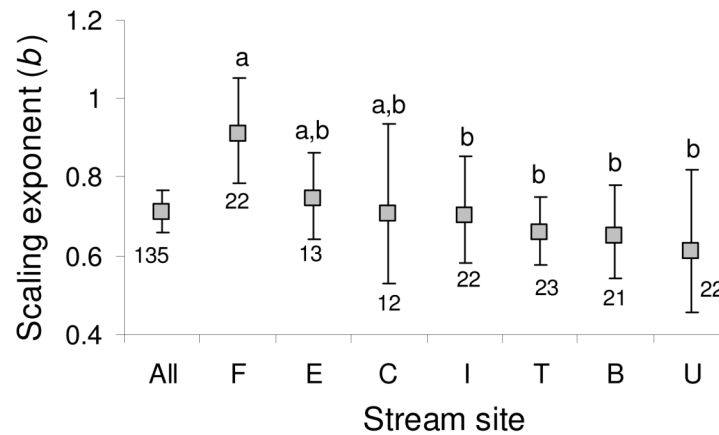


Fig. 2. Scaling exponents of the allometric relationships between field metabolic rate and crayfish mass. Shown are the mean and 95% confidence intervals with sample sizes indicated below. Scaling exponents with different characters indicate significant differences. Category abbreviations refer to all sites combined (All), Fish Creek (F), East Cross (E), Cavandale (C), Indian (I), Teeswater (T), Beaverton (B) and Uxbridge (U).

Table 2. Relationships between crayfish mass-metabolic scaling exponents and land cover in the stream's upstream riparian zone.

Riparian land cover	Slope	Intercept	<i>n</i>	<i>P</i>	<i>R</i> ²
Monoculture	0.0071	0.58	7	0.01	0.75
Mixed agriculture	-0.0100	0.84	7	0.21	0.30
Forest	-0.0008	0.73	7	0.82	0.01
Wetland	-0.0048	0.83	7	0.05	0.57

stream scaling exponents is similar to that seen in compilations of other aquatic invertebrates, both intra- and interspecifically (Glazier 2005, Glazier 2006). Our results thus demonstrate variable FMR-mass scaling that diverges at finer spatial scales from the 'global' scaling value for *O. rusticus* found for all streams grouped together. This result of spatial scale-dependency is quite common in ecology (Levin 1992) and is further evidence that studies of metabolic scaling need to carefully consider the spatial- and environmental-context of the organism of study.

The site-dependence of metabolic scaling found here related to some, but not all, measures of riparian land cover, which likely reflects the physiological responses of crayfish to the numerous effects that land cover can have on the stream environment. For example, monoculture agriculture in this region primarily uses row crops and is generally associated with high till, heavy fertilization, and the application of pesticides.

In contrast, streams flowing from wetlands tend to have less suspended solids and lower nutrient concentrations (Johnston et al. 1990). In general, these changes in stream habitat may alter its overall suitability, the supply of nutritional resources, and the level of stress endured by resident crayfish. Unfortunately, it is difficult to determine which specific stream characteristic is responsible, in part, because of the multiple physical, chemical, and biological differences associated with streams and their land use (Table 3). For instance, greater agricultural monoculture in stream catchments can be accompanied with more suspended solids, greater supplies of dissolved nutrients, different hydrological processes, altered biological communities, changes in light and temperature, and greater areas of soft substrates (Table 3).

The size and direction of these relationships between scaling exponents and particular land cover categories as documented here nevertheless requires explanation. In general, a plausible mechanism for variable allometric scaling of crayfish FMR among streams would need to: 1) elicit a size-related response of metabolic rate that 2) varies among streams. For example, the increased FMR-mass scaling exponents in agricultural streams could result from lower respiration rates in small crayfish, greater respiration rates of larger crayfish, or a combination of both. This size-dependency of the effect adds complex-

Table 3. Stream ecosystem responses to increasing monoculture agriculture in the upstream catchment.

Stream response	With increasing monoculture	Source
Piscivorous/ insectivorous fish†	Unimodal; absent at extremely high monoculture	Wilson and Xenopoulos (2011)
Leaf respiration†	Increases	M. A. Xenopoulos (<i>unpublished data</i>)
Total dissolved nitrogen†	Increases	Wilson and Xenopoulos (2009)
Total dissolved phosphorus†	No change	Wilson and Xenopoulos (2009)
Invertebrate P and N excretion†	Increases	James et al. (2007)
Microbial activity†	Increases	Williams et al. (2010)
Microbially-derived DOC†	Increases	Wilson and Xenopoulos (2009)
Fish and invertebrate community	Variable	Yates and Bailey (2010)
Functional diversity of animal communities	Decreases	Flynn et al. (2009)
Macroinvertebrate diversity	Decreases	Weijters et al. (2009)
Macroinvertebrate biomass	Increases	Delong and Brusven (1998)
Fish diversity	Decreases	Weijters et al. (2009)
Internal:external energy source	Increases	Feminella et al. (1989)

Note: A dagger indicates responses measured in streams from this study's geographic region.

ity to any explanation as it requires differently sized-crayfish to respond differently to the same change in the environment. Consequently, there would seem to be few, relatively simple hypotheses that meet both of these requirements.

Crayfish feeding and diet are plausible explanations for the variable FMR-mass scaling exponents observed here given their strong effects on metabolism and size-dependent nature. Feeding, in and of itself, is well-known to increase metabolic rates due to the energy cost of specific dynamic action (SDA; Jobling, 1983). Differences in the frequency and quantity of consumption could translate into different FMR for the same-sized crayfish residing in different streams. For this mechanism to explain our observations, smaller crayfish in non-agricultural streams would need to feed more compared to their conspecifics in agricultural streams and/or larger crayfish would need to feed less in non-agricultural compared to agricultural streams. However, with no data on the recent feeding history of the crayfish, gut fullness, or of prey abundance, this explanation is currently difficult to evaluate. Future work should thus focus on carefully documenting the effects of food availability and feeding history on FMR of stream crayfish, the effects of land use on the quantity of food available to differently sized stream crayfish, and whether this can fully explain scaling exponents that vary among streams.

Another potential complementary and non-exclusive explanation is the quality of food ingested by crayfish. Despite crayfish being omnivorous, food selectivity exists when multi-

ple resource types are present in lab and stream settings (Momot 1995, Correia and Anastacio 2008, Olsson et al. 2008). For example, crayfish positively select aquatic invertebrates from mixed food sources and increase their growth rates (Ahvenharju and Ruohonen 2005, Olsson et al. 2008). In our laboratory experiment, the metabolic rates of *O. rusticus* were different between invertebrate-only and plant-only diets. The greater metabolic rates associated with invertebrate-based foods likely reflects the greater rates of growth in crayfish consuming this food (Ahvenharju and Ruohonen 2005). For food selectivity to account for variable crayfish metabolism, the relative availability of different food types would need to vary among streams flowing through catchments having different land cover. Agricultural streams are known to have different invertebrate communities and an overall greater abundance of aquatic invertebrates (e.g., Delong and Brusven 1998; Table 3). In our study streams, we have found that invertebrate abundance on rocks (per cm²) positively relates to riparian monoculture ($P < 0.05$, $R^2 = 0.22$; D. Spooner and M. Xenopoulos, *unpublished data*).

For diet composition to explain the stream-dependence of crayfish metabolic scaling, these differences in the availability of different food types would also need to translate into size-dependent changes in diet composition. For example, examination of crayfish stomach contents have found, within the same environment, smaller crayfish generally consume greater proportions of aquatic invertebrates than their larger

conspecifics (Guan and Wiles 1998, Reynolds and O'Keefe 2005; although see Stenroth et al. 2006). Comparisons of crayfish stomach contents between pasture and forested streams have also found ontogenetic shifts in diet to be related to land cover (Parkyn et al. 2001). However, greater invertebrate consumption by small crayfish and a shift to plant-based food in larger crayfish should produce a flatter mass-metabolism relationship in high agriculture streams. This is opposite of our primary result that greater scaling exponents were found in agriculturally influenced streams. Consequently, while altered crayfish diet composition across a body mass gradient could produce different metabolic responses, its ability to explain the variable mass-specific relationships that we observed appears limited in the absence of any information on ontogenetic dietary shifts in crayfish from Ontario streams.

There are other potential explanations that should also be carefully considered and remain difficult to fully rule out. Crayfish responses to predatory fish, the abundance of which can vary among streams, could also directly or indirectly affect their metabolic rates. For example, predator cues can directly increase metabolic rates in freshwater fish (Sunardi et al. 2007) and could similarly affect crayfish respiration. Alternatively, predatory fish might indirectly alter the metabolism of stream crayfish by altering their foraging behavior (and its effects on feeding and subsequently on mass-metabolism scaling as detailed above). As fish are well-known size selective predators and often limited by gape width, this explanation also includes a size-dependence component. However, we have found no evidence that insectivorous and/or piscivorous fish increase in streams from this region having agricultural catchments (Table 3; Wilson and Xenopoulos 2011). Nevertheless, future efforts should determine if and how crayfish diet and predator responses vary among streams having different land cover and their ability to alter metabolism rates of differently sized crayfish.

FMR-mass scaling was found to significantly vary among crayfish originating from streams across a land use gradient. This metabolic flexibility across crayfish populations, which could not be accounted for by mass or temperature, was significantly related to the type of land cover in the upstream riparian zone. As previ-

ously documented for other invertebrates (Glazier 2005), our results demonstrate a significant systematic deviation away from non-variable, mass-dependent metabolic scaling among populations of a single species. The prevalence, physiological causes, and ecological implications of variable mass-scaling of metabolism among populations and its landscape correlates merit further consideration.

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