Metabolic Rate Interacts with Resource Availability to Determine Individual Variation in Microhabitat Use in the Wild

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ABSTRACT: Ecological pressures such as competition can lead individuals within a population to partition resources or habitats, but the underlying intrinsic mechanisms that determine an individual’s resource use are not well understood. Here we show that an individual’s own energy demand and associated competitive ability influence its resource use, but only when food is more limiting. We tested whether intraspecific variation in metabolic rate leads to microhabitat partitioning among juvenile Atlantic salmon (Salmo salar) in natural streams subjected to manipulated nutrient levels and subsequent per capita food availability. We found that individual salmon from families with a higher baseline (standard) metabolic rate (which is associated with greater competitive ability) tended to occupy faster-flowing water, but only in streams with lower per capita food availability. Faster-flowing microhabitats yield more food, but high metabolic rate fish only benefited from faster growth in streams with high food levels, presumably because in low-food environments the cost of a high metabolism offsets the benefits of acquiring a productive microhabitat. The benefits of a given metabolic rate were thus context dependent. These results demonstrate that intraspecific variation in metabolic rate can interact with resource availability to determine the spatial structuring of wild populations.

Keywords: Atlantic salmon, individual specialization, intraspecific competition, niche width, Salmo salar, standard metabolic rate.

Introduction

Individuals within a population can vary considerably in their patterns of resource use, even when accounting for differences in their age, sex, and body size (Bolnick et al. 2003; Araújo et al. 2011). In many species, co-occurring individuals specialize in different resources within the same habitat or use different but adjacent microhabitats (Werner and Sherry 1987; Svanbäck and Eklöv 2002; Kobler et al. 2009; Edwards et al. 2011). Ecological factors such as intraspecific competition (Svanbäck and Bolnick 2007; Sheppard et al. 2018), parasitism (Britton and Andreou 2016; Pegg et al. 2017), and predation (Araújo et al. 2011) can determine the degree to which individuals partition their resource use. Intraspecific niche variation, in turn, can feed back to influence important ecological and evolutionary processes such as population dynamics, community structure, ecosystem flux (Hughes et al. 2008; Bolnick et al. 2011; Violle et al. 2012), adaptive divergence, and speciation (Bolnick et al. 2009).

Variation in resource use is thought to occur because individuals differ in their rank preferences, the criteria by which they rank resources, and/or their ability to obtain their preferred resource, for example, if they are socially dominant versus subordinate (Ekman and Askenmo 1984; Svanbäck and Bolnick 2005; Tinker et al. 2009; Araújo et al. 2011). However, the underlying intrinsic mechanisms that determine an individual’s resource use are not well understood. There is some evidence that organismal traits associated with morphology (Robinson 2000; Svanbäck and Bolnick 2007), digestive ability (Olsson et al. 2007), cognition (Persson 1985; Werner and Sherry 1987), and personality (Kobler et al. 2009; Mittelbach et al. 2014; Toscano et al. 2016) play a role in promoting the existence and persistence of individual specialization. For example, intraspecific variation in aggression levels can lead to habitat partitioning among conspecifics (Kobler et al. 2011). Energy is needed to acquire resources, but whether an individual’s own energy requirements and physiological potential for metabolic activities determine its resource use is not clear.
The baseline energetic cost of living (defined as standard metabolic rate [SMR] in ectotherms and basal metabolic rate in endotherms; Hulbert and Else 2000) can differ up to threefold among individuals in a population (Burton et al. 2011). These intraspecific differences in metabolism are repeatable within individuals (Auer et al. 2016, 2018b) and consistent within families (Pough and Andrews 1984; Docker et al. 1986; Steyermark and Spotila 2000; Pakkasmaa et al. 2006; Robertsen et al. 2014) across a wide variety of taxa. While some of the variation in metabolism can be attributed to early environmental and maternal effects (Burton et al. 2011), there is increasing evidence that metabolic rates are heritable and thus that there is a genetic basis to observed differences in metabolism at both the individual and family levels (Nespolo et al. 2005; Nilsson et al. 2009; Wone et al. 2009; Pettersen et al. 2018). Metabolic rate is also known to covary with a range of physiological and behavioral traits that influence resource acquisition and may determine individual-level choices in resource use. For example, individuals with a faster baseline metabolic rate tend to have a higher meal-processing capacity (Millidine et al. 2009), activity levels (Careau et al. 2008), daily energy expenditure (Auer et al. 2017), boldness, competitive dominance, and territorial aggression (Biro and Stamps 2010).

Laboratory studies show that faster metabolic rates mean a higher cost of living that can be beneficial for growth and survival when food availability is high but disadvantageous when food is scarce (Bochdansky et al. 2005; Armstrong et al. 2011; Burton et al. 2011; Killen et al. 2011; Auer et al. 2015a). Individual differences in metabolism and associated traits may therefore lead to partitioning of microhabitats that differ in their productivity. Specifically, individuals with a higher metabolic rate may need to compete more for access to productive habitats to meet their higher energy demands. In contrast, individuals with lower metabolic rates may use less productive sites because of reduced costs associated with competition and/or because they are displaced from more favorable microhabitats by dominant individuals with higher metabolic rates.

Increased intraspecific competition can lead to higher levels of individual specialization within a population (Araújo et al. 2011; but see Jones and Post 2016), so the degree to which metabolic rate determines habitat use may also depend on per capita resource availability. Specifically, individuals may fare equally well across different habitat types regardless of their metabolic rate when resource levels are high, since competition for those resources will be relaxed. In contrast, low resource levels may lead to heightened competition, which would force less competitive individuals into suboptimal microhabitats and/or drive individuals to partition their habitat use in a way that meets their metabolic demands. There is some evidence that differences in metabolic rate can lead to habitat partitioning among species: introduced rainbow trout (Oncorhynchus mykiss) with higher metabolic rates displace native west-slope cutthroat trout (Oncorhynchus clarkii) with lower metabolic rates from more productive downstream sites (Rasmussen et al. 2011). However, the role of energy metabolism in determining habitat use at the intraspecific level and across gradients of resource availability has not yet been investigated.

We examined the link between intraspecific variation in metabolic rate and microhabitat use among juvenile Atlantic salmon (Salmo salar) in natural streams subjected to manipulated levels of nutrients and subsequent per capita food availability. Juvenile salmonids inhabit small tributary streams where they feed predominantly on drifting macroinvertebrates carried in the water current. As a consequence, differences in foraging profitability between microhabitats can be stark: fast-flowing areas (termed “rifles”) with higher densities of drifting prey are directly adjacent to pools where water flow is minimal and prey availability is much lower (Logan and Brooker 1983; Brown and Brussock 1991; Nislow et al. 1998, 1999; Brooks et al. 2017). After hatching and leaving their nests in late spring, the majority of surviving juveniles defend access to foraging sites within the same territory throughout their first summer (Steingrimsson and Grant 2003, 2008). They spend much of their time holding position against or near the substratum surface, darting out to capture drifting prey or defend against intruders (Grant and Kramer 1990; Nislow et al. 1998, 2010; Steingrimsson and Grant 2008). Access to favorable foraging locations is critical for growth and survival, and territorial defense of feeding sites can lead to dominance hierarchies within a given microhabitat (Nislow et al. 2010).

As part of a larger study examining the ecological effects and evolutionary consequences of nutrient levels for freshwater ecosystems (Auer et al. 2018a; McLennan et al. 2019), we planted embryos from full-sibling Atlantic salmon families in equal distribution and density across 10 replicate tributary streams of the River Conan in northern Scotland (see app. A for description of study sites; apps. A–F are available online). Nutrient levels are naturally low in upland streams, but they have been depressed further in this particular catchment because of a lack of marine-derived nutrient input from spawning salmon parents in combination with nutrient export via emigration of juveniles stocked as embryos (Nislow et al. 2004). Five of the streams received a nutrient boost to simulate the deposition of postspawning parents (high-nutrient streams hereafter), while the five remaining streams did not receive nutrients and served as reference sites (low-nutrient streams hereafter; Auer et al. 2018a). Nutrient restoration led to a nearly twofold increase in macroinvertebrate prey abundance.
and biomass but not fish density (fig. 1; Auer et al. 2018a), thereby generating higher per capita food availability and subsequent fish growth in streams with high compared with low nutrient levels (fig. 1). Juvenile salmonids are food limited in the wild, but aggression during territorial defense typically declines with increasing food availability (Slaney and Northcote 1974; Toobaie and Grant 2013; Bailey et al. 2019). In addition, intraspecific resource competition occurs not just via interference but also exploitative mechanisms, notably, via shadow competition whereby fish defending upstream territories, simply by virtue of their position, have priority access to drifting prey and deplete the resources available to those farther downstream (Hughes 1992; Elliott 2002; Einum et al. 2011). As such, increased per capita food availability provides strong evidence that nutrient restoration relaxed levels of intraspecific resource competition.

Here we combine measurements of SMR from laboratory-reared juveniles of each family (Auer et al. 2018a) with fine-scale observations of their siblings’ microhabitat use and subsequent growth rates in these same 10 streams to examine whether variation in SMR at the family level influences the distribution and performance of conspecifics among microhabitats. Nutrient restoration had no differential effects on embryo-to-juvenile survival among families differing in their SMR in either low- or high-nutrient streams (Auer et al. 2018a), thereby allowing us to examine and compare juvenile microhabitat use and growth among the same diversity of metabolic phenotypes across stream types. By comparing sites with manipulated food levels, we provide experimental evidence that intraspecific variation in metabolic rate can interact with resource availability to determine the spatial structuring of wild populations.

Material and Methods

Rearing and Planting out of Embryos

We used in vitro fertilization over a 3-day period in December 2015 to create 30 full-sibling families from the eggs and sperm of wild returning adult salmon caught in a fish trap on the River Blackwater (fig. A1; figs. A1, A2, D1 are available online). Only female grilse (those fish spending only one winter at sea as confirmed by scalimetry; Shearer 1992) were used in the crosses to control for maternal life history. Egg size has a positive effect on growth and subsequent body size (Einum et al. 2004) but varies little within clutches (Einum and Fleming 2004), so a sample of eggs from each clutch was preserved in a 5% buffered formalin solution (Fleming and Ng 1987) for later determination of mean egg mass per family and its inclusion in

Figure 1: Mean (±SE) abundance (A) and biomass (B) of macroinvertebrate prey as well as density (C) and fork length (D) of juvenile salmon in streams with low (blue; n = 5) versus high (green; n = 5) nutrient levels. Estimates for invertebrates are given as the mean catch per unit effort for 1-min samples taken at three locations at each of 50, 25, and 0 m above the downstream limit of each experimental reach. Fish density was estimated using depletion curves from triple-pass electrofishing capture rates in each stream. Data and results are from Auer et al. (2018a).
growth analyses (see below). A small sample of adipose fin was taken from each of the adults for genotyping, so that all offspring could subsequently be assigned to one of the 30 families. Embryos were transported to a nearby hatchery, where they were reared overwinter in family-specific trays under identical water and temperature (mean ± 1 SE: 4.4° ± 0.03°C) conditions in a single flow-through stream system.

In late February 2016, we planted out a subset of these embryos into artificial nests (McLennan et al. 2016) constructed within a 300 m² reach in each of 10 study streams (75–100 m in length, depending on stream wet width; table A1; tables A1, B1, E1, F1 are available online). Each stream reach received 100 embryos from each of the 30 families (n = 3,000 total in each stream), equating to a density of 10 embryos per square meter that is within the range of observed spawning densities (Fleming 1996). HOBO data loggers (Onset Computer, Bourne, MA) were also placed in each stream at the time of embryo deposition and recorded temperature every 4 h (fig. A2). At the same time, we selected a second subset of siblings from each of the 30 families and transferred them to the University of Glasgow, where we measured their metabolic rates during the juvenile stage (see below). Juveniles were housed in family-specific compartments in a flow-through stream system where they experienced the same water and temperature conditions. Using data from these same streams collected in previous years, temperature in the laboratory was gradually increased to approximate thermal conditions experienced by their siblings in the wild (fig. A2).

**Manipulation of Intraspecific Resource Competition**

To manipulate levels of food availability, we increased nutrient levels in five of the study streams (selected randomly) by adding analogue carcasses in the form of dried hatchery salmon pellets (Skretting, Invergordon, UK) to the experimental reaches at the time of embryo planting (Auer et al. 2018a). Five 3-kg carcass analogues were deposited at equidistant points along each experimental reach to simulate the death and decomposition (Pearsons et al. 2007) of ~25 adult salmon carcasses (Williams et al. 2009; Guyette et al. 2013, 2014). The five remaining study streams served as low-nutrient reference sites.

We determined the effect of nutrient treatment on per capita food availability by quantifying the density of juvenile salmon in relation to the abundance and biomass of their macroinvertebrate prey. We sampled macroinvertebrates between late May and early June 2016 in each of the 10 streams, corresponding to the time that juveniles are establishing territories, having emerged from the nest in early May. Nutrient restoration led to a marked increase in both the abundance and biomass of macroinvertebrates within the prey size range (<1 mm in width) for juvenile salmon (fig. 1A, 1B and Auer et al. 2018a; app. B).

We then estimated juvenile densities and growth rates by triple-pass electrofishing in July 2016. Electrofishing was conducted in two different sections within each experimental reach, each section 10–20 m in length. Lengths of the two sections differed among streams, since longer sections were needed to estimate fish densities from depletion curves of triple-pass electrofishing capture rates in more sparsely populated streams (app. A). The remaining areas of each experimental reach were also electrofished (generally one pass). We measured all captured fish (n = 1,242) for fork length (±0.01 mm) under a mild anesthetic (clove oil 20 ppm) and clipped a small portion of their anal fin before their release for later genotyping and family assignment (app. C). The nutrient manipulation resulted in a marked increase in juvenile growth (fig. 1C) but no change in juvenile density in the high- compared with the low-nutrient streams (fig. 1D; Auer et al. 2018a). Together with measures of macroinvertebrate food supply, these estimates of fish density and growth demonstrate strong treatment differences in per capita food availability (fig. 1; Auer et al. 2018a).

**Juvenile Microhabitat Availability and Use**

At the time of fish sampling, the two sections within each stream (detailed above) were further subdivided into subsections 2 m long for assessment of microhabitat use and availability (see below), and the location (subsection) of each fish (n = 902) was noted upon capture. We characterized the microhabitat by quantifying water velocity in each subsection. Water velocity can be used to predict the profitability of a given stream position since it has a major effect on the rate of food delivery to juvenile salmon feeding territories and thereby their bioenergetics and subsequent growth and survival (Hughes and Dill 1990; Hughes 1992; Nislow et al. 1999, 2000). Water velocity was categorized into five flow classes, following SFCC (2007): class 1 = still (water still or eddy and silent), 2 = pool (water flow slow, eddying, and silent), 3 = glide (water flow moderate to fast but silent and unbroken), 4 = run (water flow fast, unbroken standing waves at surface, silent), and 5 = riffle (water flow fast, broken standing waves at surface, audible). We estimated the proportion of each flow class to the nearest 5% by visual assessment and used those proportions to calculate a flow index for each subsection as 

\[ F_i = \sum_{j=1}^{c} F_j p_{ij}, \]

where \( F_i \) is the flow index for each subsection, \( F_j \) is the flow class, and \( p_{ij} \) is the proportion of the flow class in the \( i \)th subsection. The flow index thus ranged from 1 to 5, with higher values indicating faster-flowing water. Subsections
were 2 m in length, since this area encompasses the range of territory sizes observed in the study species (Keelley and Grant 1995; Hedger et al. 2005; Steingrimsson and Grant 2008).

**Juvenile Metabolic Rates**

We linked individual microhabitat use to family-level metabolic rate by measuring SMRs of siblings from each family that were selected haphazardly during the embryo stage and reared in the laboratory. SMRs were measured over a 10-day period during the last two weeks of June 2016, approximately 2 months after first feeding \((n = 10\) juveniles per family). SMR was measured at 12°C (to approximate the temperature experienced by their siblings in the field at that time; fig. A2) and over a 20-h period as the rate of oxygen consumption using continuous flow-through respirometry, following methods described in (Auer et al. 2015b). After their metabolic rate measurements, we weighed the fish (±1 mg) and measured them for fork length (±0.01 mm) under a mild anesthetic (benzocaine 40 mg L\(^{-1}\)). At the time of measurement, juveniles in the laboratory were on average slightly smaller but within the size range of their siblings captured roughly 3–4 weeks later in the field (mean fork length ±1 SE: lab: 39.24 ± 0.17 mm, range 29.90–46.80, \(n = 300\); field: 48.81 ± 0.22 mm, range 29.62–70.20, \(n = 902\)). Family-level SMR was consistent within families (log-likelihood ratio test: \(\chi^2 = 5.3, P < .05\)) after controlling for differences in body mass (app. D; Auer et al. 2018a).

**Statistical Analyses**

We first compared the mean and variance of microhabitat availability between low- and high-nutrient streams using linear mixed models with stream as a random effect. Differences in the variance among stream types were assessed using log-likelihood tests that compared the fit of the model with and without separate error variances for each nutrient treatment. The same approach was used to compare the mean and variance of individual microhabitat use versus availability in each stream. Comparisons between use and availability were conducted separately for each stream, since microhabitat use of juveniles is constrained by microhabitat availability in the stream that they are living (i.e., they do not move among streams).

Second, we examined whether individual microhabitat use varied as a function of mean family-level SMR within and across streams with low versus high nutrient levels using a linear mixed model that included stream and family as random effects. Since microhabitat use is a function of availability within each stream, flow index was standardized for each stream before analysis. Body size may also affect or be affected by microhabitat use (Armstrong et al. 2003; Hedger et al. 2005), so fork length and its interaction with treatment were initially included in the model but subsequently removed since they were not statistically significant (fork length: \(F_{1,88} = 0.16, P = .689\); treatment × fork length: \(F_{1,88} = 0.62, P = .431\)). We then tested whether individual body size (as an index of growth, since all juveniles were the same age) differed among mean family-level metabolic phenotypes and stream types, first across the microhabitat gradient (i.e., at the population level) and then after taking microhabitat use into account (by including microhabitat score as a covariate). Stream and family were included as random effects. Body size can be a positive function of Julian date of sampling (fish have reached a bigger size later in the season) and initial egg size (Einum et al. 2004) and a negative function of local juvenile density (Nislow et al. 2010), so these three factors were included as covariates in the analyses of growth. The mean egg mass of each family was used as the measure of its egg size. The density of juveniles (per square meter) in each subsection was quantified by dividing the number of juveniles captured in each subsection by the subsection wet area. SMR was standardized to a common body size of 1 g before its inclusion in analyses. All analyses were conducted using SAS 9.4 (SAS Institute, Cary, NC). Effects were considered significant when \(P < .05\).

Our mixed model approach using mean family-level SMR assumes that the mean is known without error, which is not strictly the case. We therefore conducted these same analyses of metabolic rate using a Bayesian approach that takes error in the estimate of SMR into account. The results were qualitatively the same (app. E), so we present results from the generalized mixed models here in the main text.

**Results**

Microhabitats within each stream’s experimental reach ranged from pools with slow-moving water to faster-flowing riffle areas (fig. 2). The flow index for water velocity differed among individual streams in both its mean \((F_{9,26} = 24.92, P < .001)\) and variance \((\chi^2 = 27.97, P < .001)\) but did not differ between treatments (mean: \(F_{1,8} = 0.61, P = .458\); variance: \(\chi^2 = 0.0, P = 1.00\)). Juvenile salmon used the different microhabitats according to their availability within each stream (table 1; fig. 3). However, fish families were nonrandomly distributed across those microhabitats (fig. 4). Specifically, a family’s mean SMR was a significant predictor of microhabitat use in low- but not high-nutrient streams (table 2; treatment: \(F_{1,8} = 0.71, P = .425\); SMR: \(F_{1,8} = 4.69, P = .031\); treatment × SMR: \(F_{1,8} = 10.89, P = .001\)). Within low-nutrient streams,
individuals from families with a higher SMR on average used faster-flowing microhabitats than individuals from families with lower SMRs (fig. 4A; $P < .001$), but there was no link between metabolic rate and microhabitat use in high-nutrient streams (fig. 4B; $P = .425$).

SMR was a significant predictor of fork length in high- but not low-nutrient streams (table 2; fig. 5; treatment: $F_{1,8} = 8.18$, $P = .021$; SMR: $F_{1,887} = 3.57$, $P = .059$; treatment × SMR: $F_{1,887} = 4.67, P = .031$) after controlling for the positive effects of Julian date of sampling.

Figure 2: Microhabitat availability for Atlantic salmon (Salmo salar) juveniles in 10 headwater streams with either low (blue) or high (green) nutrient levels in the northern highlands of Scotland. Plotted are the percentages of each of five different microhabitat types within each stream’s experimental reach that were categorized based on water velocity as being still = water still or eddying and silent; pool = water flow slow, eddying, and silent; glide = water flow moderate to fast but silent and unbroken; run = water flow fast, unbroken standing waves at surface, silent; and riffle = water flow fast, broken standing waves at surface, audible. Streams are 1: A Chomair, 2: An Eilean Ghuirm, 3: Coire nan Laogh, 4: Coire Bhuic, 5: Mhartuin, 6: Chaiseachain, 7: Coire a Gormachain, 8: Gleann Chorain, 9: Gleann Meinich, and 10: Scardroy.

| Stream name          | Mean Variance | Summary of results for tests of microhabitat use versus availability |
|----------------------|---------------|---------------------------------------------------------------------|
|                      | $F$ | df | $P$ | $\chi^2$ | $P$ |                      |
| Low nutrient:        |     |    |     |          |     |                      |
| A Chomair            | .25 | 1, 122 | .621 | 0 | 1.000 |
| An Eilean Ghuirm     | .83 | 1, 52 | .365 | 2 | .327 |
| Coire nan Laogh      | .23 | 1, 175 | .631 | 0 | 1.000 |
| Coire a Bhuic        | .17 | 1, 85 | .685 | 1.1 | .147 |
| Mhartuin             | .01 | 1, 67 | .995 | 1.0 | .159 |
| High nutrient:       |     |    |     |          |     |                      |
| Chaiseachain         | .56 | 1, 82 | .454 | 0 | 1.000 |
| Coire a Gormachain   | .27 | 1, 80 | .604 | 2 | .327 |
| Gleann Chorain       | .01 | 1, 132 | .964 | 0 | 1.000 |
| Gleann Meinich       | .34 | 1, 82 | .561 | .1 | .376 |
| Scardroy             | .18 | 1, 141 | .670 | .1 | .376 |

Note: Microhabitat availability and use by juvenile Atlantic salmon (Salmo salar) were measured in 10 headwater streams with low versus high nutrient levels in the northern highlands of Scotland. $\chi^2$ tests comparing use versus availability were based on one degree of freedom; $P$ values were halved, since tests examined whether the variance was greater than zero. Microhabitat use did not differ from availability within any of the 10 streams.
Differences in metabolic rate can lead to habitat partitioning at the species level (Rasmussen et al. 2011). Here we show that variation in metabolic rate can also lead to microhabitat partitioning within a species. However, links between metabolic rate and microhabitat use depended on nutrient levels and subsequent per capita food availability. The effect on microhabitat use was clear: individuals from families with different metabolic rates used similar microhabitats in high-nutrient streams where food availability was higher, whereas the same phenotypic differences led to divergent microhabitat use in streams with low nutrient levels. In particular, individuals from families with a higher SMR tended to occupy faster-flowing areas (i.e., runs and riffles), compared with individuals with a lower metabolic rate, but only in low-nutrient streams.

Intraspecific resource competition often leads to increased individual specialization but can vary in its effect

Figure 3: Microhabitat use (upper bars, colored) versus microhabitat availability (lower bars, gray) for juvenile Atlantic salmon (Salmo salar) in 10 headwater streams with either low (n = 5; blue) or high (n = 5; green) nutrient levels. Microhabitats were classified based on an index of their water velocity that ranged from 1 (still water) to 5 (fast-flowing riffles). See “Material and Methods” for calculation of water velocity index and table 1 for statistical details on comparisons of microhabitat use versus availability.
on total niche width at the population level (Bolnick et al. 2003; Araújo et al. 2011). Here we found that changes in per capita food availability did not lead to a change in the range of microhabitats used, since microhabitat use at the population level did not differ from availability within each stream, nor did it differ between nutrient treatments. Rather, changes in per capita food availability led to a shift in how different metabolic phenotypes partitioned their microhabitat use, that is, who used which microhabitat.

Differential effects of metabolic rate across stream types suggest that resource availability magnifies the energetic constraints that govern microhabitat selection. Specifically, individuals can meet their baseline energy needs regardless of microhabitat quality in high-nutrient streams where food is more readily available, but they are forced to partition their microhabitat use in a manner that meets their metabolic demands in low-nutrient streams where intraspecific resource competition is likely to be stronger. Partitioning

| Microhabitat use | Growth |
|------------------|--------|
| Intercept        | .01 ± .05 | .20 | .845 | 52.22 ± 1.86 | 28.06 | <.001 |
| Treatment        | -.06 ± .07 | -.84 | .425 | -7.64 ± 2.67 | -2.86 | .021 |
| SMR              | -3.66 ± 4.59 | -.80 | .425 | 47.90 ± 16.12 | 2.97 | .003 |
| SMR × treatment  | 21.32 ± 6.46 | 3.30 | .001 | -50.22 ± 23.24 | -2.16 | .031 |
| Local density    | … | … | … | -1.10 ± .29 | -3.74 | <.001 |
| Julian date      | … | … | … | .75 ± .26 | 2.84 | .005 |
| Initial egg mass | … | … | … | .12 ± .01 | 12.47 | <.001 |

Note: Parameter estimates for treatment are for high- relative to low-nutrient streams. The model for growth also accounts for variation in local fish density, Julian date of sampling, and initial mean egg mass of each family. All predictors are centered on their mean value (standard metabolic rate: 0.171 mg O₂ h⁻¹; local density: 0.92 juveniles m⁻²; Julian date: 199; initial egg mass: 98.1 mg).
of microhabitats can occur because of individual variation in competitive ability and/or trade-offs in resource use (Bolnick et al. 2003; Araújo et al. 2011). Individuals with a higher SMR, by definition, have a higher baseline energy demand, so they are expected to place a heavier premium on gaining access to more productive microhabitats, particularly when food is limited. It is unclear, though, whether individuals with a lower metabolic rate occupied less productive microhabitats in low-nutrient streams because they prefer them or because they were displaced from more productive microhabitats by individuals with a higher metabolic rate. In common with a number of other species, individual salmon with a higher SMR are more dominant and routinely win territorial contests against individuals with a lower SMR under simplified laboratory conditions (Metcalfe et al. 1995; Cutts et al. 2001; Biro and Stamps 2010). However, mesocosm experiments also show that their competitive advantage weakens with increasing habitat complexity and decreased predictability of food sources (Reid et al. 2011, 2012), indicating that they may not be able to fully monopolize the most favorable microhabitats under similar conditions in the wild. Their lack of growth advantage, despite occupying more productive habitats, also suggests that there are trade-offs in microhabitat use.

Body size, as an index of growth, was a positive function of metabolic rate, but only in high-nutrient streams. In low-nutrient streams, individuals from families with higher metabolic rates did not have a growth advantage. Laboratory studies suggest that a higher SMR is beneficial when food levels are high but is disadvantageous when food levels decline (Reid et al. 2011; Auer et al. 2015a; Zeng et al. 2017a, 2017b). This context-dependent advantage of a higher SMR has been attributed, in part, to a higher food-processing capacity (rates of intake, processing, and digestion) among individuals with higher metabolic rates (Millidine et al. 2009; Zeng et al. 2017a) that is advantageous when food levels are high, but whose benefit is outweighed by the costs of a higher baseline maintenance cost when food levels decline (Zeng et al. 2017a). For example, Atlantic salmon individuals with a higher SMR can process meals up to twice as fast as conspecifics with a lower metabolic rate (Millidine et al. 2009). In addition, studies across a wide diversity of animal taxa find that individuals with a higher SMR tend to have higher activity levels compared with conspecifics with a lower SMR (reviewed in Biro and Stamps 2010; Careau et al. 2008). These physiological and behavioral differences may explain the growth advantage of a high metabolic rate in the high-nutrient streams. However, individuals from families with higher metabolic rates did not have a growth advantage in low-nutrient streams, despite occupying more productive microhabitats. Together, these results suggest that links between metabolic rate and growth can be mediated not only by food availability but also by the costs of foraging and territory defense associated with occupying different microhabitat types. Runs and riffles typically have a higher density of drifting macroinvertebrate prey and have a faster water velocity than pools (Hughes and Dill 1990; Hughes 1992; Nislow et al. 1998, 1999), so the payoff in terms of energy intake is potentially larger than it is for pool microhabitats. However, foraging in and defending priority access to faster-flowing microhabitats is also more challenging because energetic expenditure on swimming can increase (Fausch 1984; Enders et al. 2003) and prey capture (i.e., energy intake) can decrease (Hughes and Dill 1990; Nislow et al. 1999) with increasing water velocity. In addition, aggressive defense of foraging locations can take away from time and energy otherwise devoted to foraging (Elliott 1990; Cutts et al. 2001). Trade-offs between energy conservation versus priority of access to food are therefore likely to play an increasingly larger role in determining rank microhabitat preferences as per capita food availability decreases and the strength of intraspecific competition increases. As a result, less competitive individuals, that is,  

![Figure 5: Growth performance as a function of family-level standard metabolic rate in full-sibling families (n = 29) of juvenile Atlantic salmon (Salmo salar) in 10 headwater streams with either low (blue; n = 5) or high (green; n = 5) nutrient levels. Metabolic rates were standardized to a common body mass of 1 g. Plotted are values corrected for the fixed effects of local juvenile density, Julian date of sampling, and initial egg mass as well as the random effects of stream and family. P values are from tests of whether slopes (coefficients) differ from zero. Data are a slightly smaller subset of the larger sample analyzed in Auer et al. (2018a), since microhabitats were quantified in subsections of the larger experimental area in each stream.](image-url)
those with lower metabolic rates and typically subordinate status, will benefit from adopting a low-cost–low-return strategy (Metcalfe 1986) of selecting slower-flowing but less productive microhabitats.

Our results provide evidence that metabolic rate and per capita food availability have interactive effects on microhabitat use. However, our study design did not allow us to distinguish between microhabitat use versus choice since we focused only on the microhabitat use of survivors and did not measure how survival varied as a function of microhabitat use. While there was no relationship between SMR and survival in either stream type (Auer et al. 2018a), we cannot discount that observed patterns of survival, particularly in low-nutrient streams, could be because of the differential survival of metabolic phenotypes within different microhabitats, rather than differences in their microhabitat choice. To tease apart these two alternative mechanisms, selection gradient analyses are needed to examine how survival varies as a function of metabolic phenotype within and across different microhabitats.

Many organisms live in complex environments that provide opportunities for niche partitioning in both space and time. How individuals assort themselves and use resources within that environment can, in turn, affect their own fitness (Morris and Davidson 2000; Nilsen et al. 2004). Here we show that members of a wild population can be distributed among microhabitats according to their family-level metabolic phenotype, which could have consequences for the ecological dynamics of populations (Hughes et al. 2008; Bolnick et al. 2011; Violle et al. 2012) and the evolutionary trajectories of species (Bolnick et al. 2009). Understanding which organismal traits play a role in determining habitat use, and how their influence is determined by ecological conditions, is therefore important for predicting larger-scale patterns and processes. Given that metabolic rate reflects the energetic costs of maintaining the tissues and functions needed to sustain life (Auer et al. 2017) and that energy is considered the central currency in foraging and habitat use decisions (Werner et al. 1983; Piccolo et al. 2014), variation in metabolic rate among individuals likely plays an important role in determining the spatial distributions and patterns of resource use across a wide range of species.

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Statement of Authorship
S.K.A., S.M., J.D.A., K.H.N., and N.B.M. conceived the project; S.K.A., G.J.A., S.M., J.D.A., K.H.N., D.M., R.D.B., and N.B.M. planned the experiments. S.K.A., G.J.A., S.M., D.M., and H.K.D. undertook the artificial fertilization of salmon eggs. S.K.A., G.J.A., and S.M. planted eggs and analogue carcasses out into streams. S.M. reared salmon eggs in the hatchery and sampled invertebrates. S.K.A., G.J.A., and D.M. measured egg mass and juvenile metabolic rates. S.K.A., G.J.A., S.M., H.K.D., T.A.J.M., D.M., R.D.B., and N.B.M. recaptured and measured fish. H.K.D. and T.A.J.M. measured stream habitat parameters. Data were analyzed by S.K.A., R.D.B., and D.J.T. The manuscript was written by S.K.A., with input and final approval from all authors.

Data and Code Availability
Data supporting the results are archived in the Dryad Digital Repository (https://doi.org/10.5061/dryad.sxksn030f; Auer et al. 2020).

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