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

Sonya K. Auer,[1,2,*] Ronald D. Bassar,[2] Daniel Turek,[2] Graeme J. Anderson,[1] Simon McKelvey,[3,†] John D. Armstrong,[4] Keith H. Nislow,[5] Helen K. Downie,[4] Thomas A. J. Morgan,[4] Darryl McLennan,[1] and Neil B. Metcalfe[1]

1. Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, United Kingdom; 2. Williams College, Williamstown, Massachusetts 01267; 3. Cromarty Firth Fishery Trust, Inverness, United Kingdom; 4. Marine Scotland–Science, Freshwater Fisheries Laboratory, Pitlochry, United Kingdom; 5. USDA Forest Service Northern Research Station, Amherst, Massachusetts 01003

Submitted October 30, 2019; Accepted February 28, 2020; Electronically published July 6, 2020

Online enhancements: appendixes. *Dryad data:* https://doi.org/10.5061/dryad.sxksn030f.

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 intra- and interspecific 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.

* Corresponding author; email: sonya.auer@gmail.com.

† Deceased (December 2, 2018).

ORCIDs: Auer, https://orcid.org/0000-0002-2604-1535; McLennan, https://orcid.org/0000-0002-8566-9437; Metcalfe, https://orcid.org/0000-0002-1970-9349.

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DOI: 10.1086/709479

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, 2018*b*) 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. 2015*a*). 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 westslope 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 "riffles") 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 (Steingrímsson and Grant 2003, 2008). There 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; Steingrímsson 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. 2018*a*; 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 Conon 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. 2018*a*). Nutrient restoration led to a nearly twofold increase in macroinvertebrate prey abundance

and biomass but not fish density (fig. 1; Auer et al. 2018*a*), 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. 2018*a*) 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. 2018*a*), 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

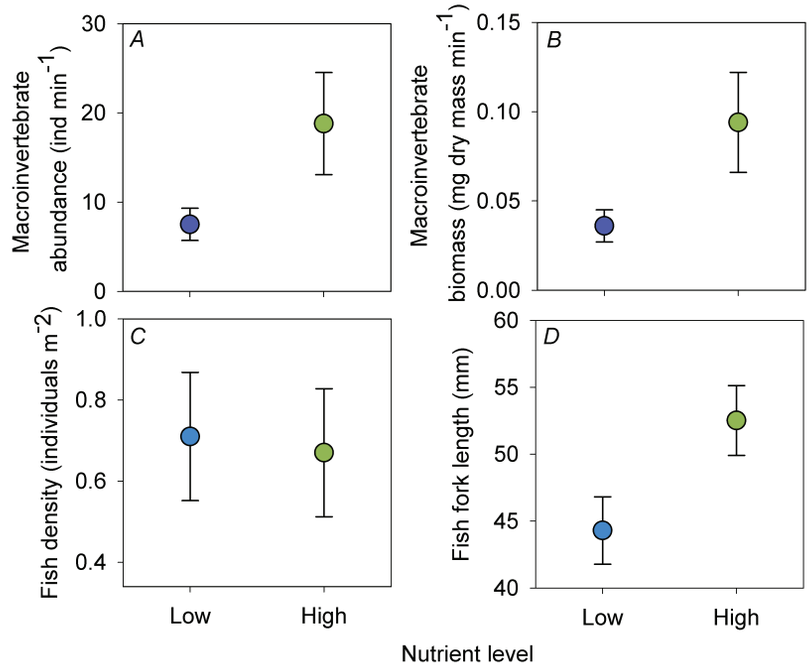

Figure 1: Mean (±SE) abundance (*A*) and biomass (*B*) of macroinvertebrate prey as well as density (*C*) and fork length (*D*) of juvenile salmon in streams with low (blue; $n = 5$) versus high (green; $n = 5$) nutrient levels. Estimates for invertebrates are given as the mean catch per unit effort 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. (2018*a*).

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 m^2 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. 2018*a*). 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. 1*A*, 1*B* and Auer et al. 2018*a*; 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. 1*C*) but no change in juvenile density in the high- compared with the low-nutrient streams (fig. 1*D*; Auer et al. 2018*a*). 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. 2018*a*).

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 eddying 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 $F_i = \sum_{c=1}^{x} F_c p_{i,c}$, where F_i is the flow index for each subsection i, F_c is the flow class, and $p_{i,c}$ is the proportion of the flow class in the ith 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 (Keeley and Grant 1995; Hedger et al. 2005; Steingrímsson 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. 2015*b*). 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. 2018*a*).

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: $F_{1,888} = 0.16$, $P = .689$; treatment × fork length: $F_{1,888} = 0.62$, $P = .431$).

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: $F_{1,890} = 4.69$, $P = .031$; treatment × SMR: $F_{1,890} = 10.89$, $P = .001$). Within low-nutrient streams,

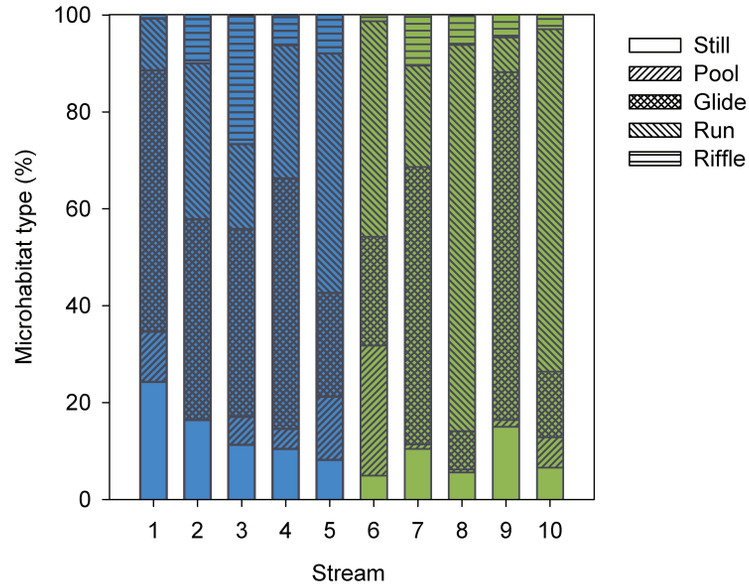

Figure 2: Microhabitat availability for Atlantic salmon (*Salmo salar*) juveniles in 10 headwater streams with either low (blue) or high (green) nutrient levels in the northern highlands of Scotland. Plotted are the percentages of each of five different microhabitat types within each stream's experimental 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.

individuals from families with a higher SMR on average used faster-flowing microhabitats than individuals from families with lower SMRs (fig. 4*A*; $P < .001$), but there was no link between metabolic rate and microhabitat use in high-nutrient streams (fig. 4*B*; $P = .425$).

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

Table 1: Summary of results for tests of microhabitat use versus availability

	Mean			Variance	
Stream name	*F*	df	*P*	χ^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. χ^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.

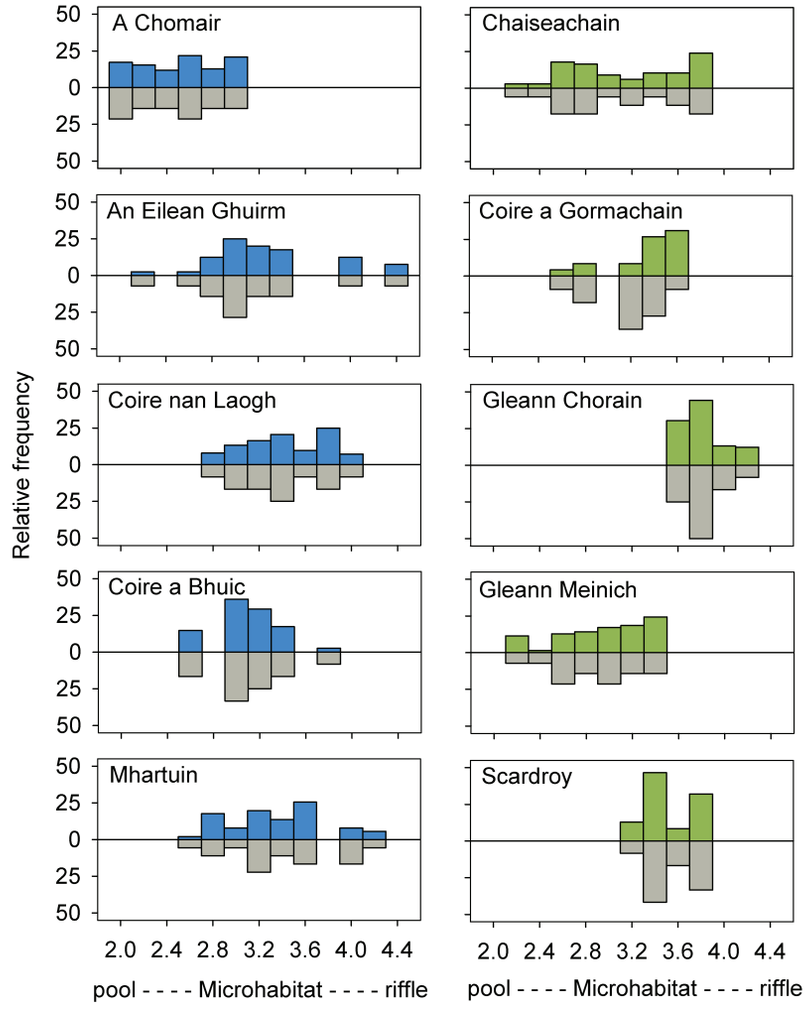

Figure 3: Microhabitat use (upper bars, colored) versus microhabitat availability (lower bars, gray) for juvenile Atlantic salmon (*Salmo salar*) in 10 headwater streams with either low ($n = 5$; blue) or high ($n = 5$; green) nutrient levels. Microhabitats were classified based on an index of their 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.

($F_{1,887} = 8.04$, $P = .005$) and initial egg mass ($F_{1,887} = 155.54$, $P < .001$) and the negative effects of local juvenile density ($F_{1,887} = 14.01$, $P < .001$). There was no link between metabolic rate and growth in low-nutrient streams (fig. 5; $P = .893$), but within high-nutrient streams, individuals from families with a higher SMR tended to be larger compared with those with lower SMRs (fig. 5; $P = .003$). Results were qualitatively the same when taking variation in microhabitat use into account (app. F).

Discussion

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

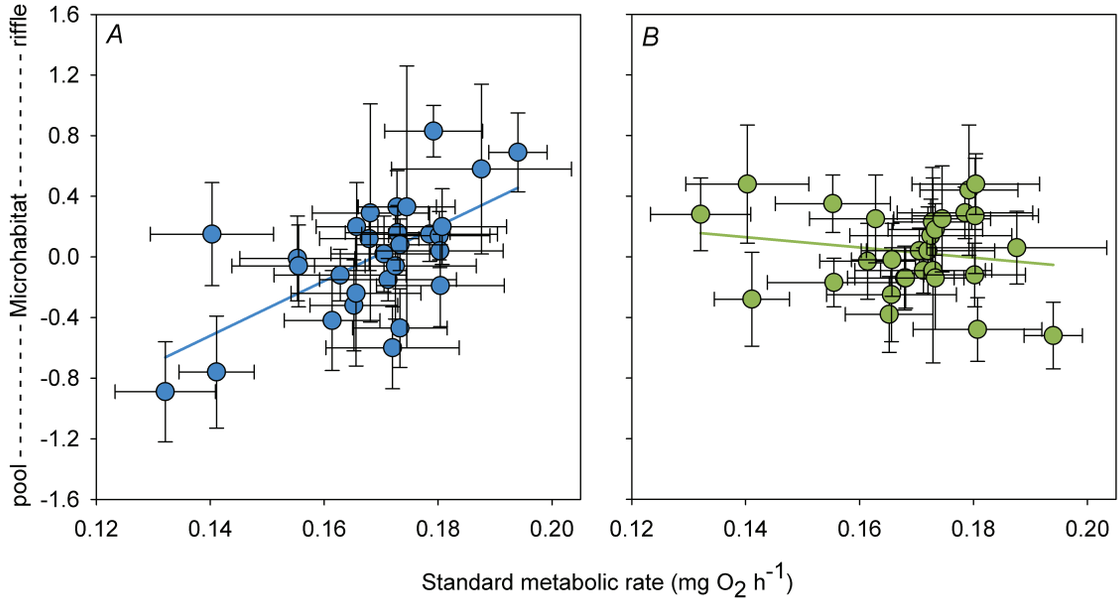

Figure 4: Microhabitat use as a function of family-level standard metabolic rate in full-sibling families ($n = 29$) of juvenile Atlantic salmon (*Salmo salar*) in 10 headwater streams with either low (*A*; blue; $n = 5$) or high (*B*; green; $n = 5$) nutrient levels. Microhabitats were classified based on an index of their water velocity that ranged from 1 (still water) to 5 (fast-flowing riffles) and standardized on a per-stream basis before analysis. Standard metabolic rate is standardized to a common body size of 1 g. Plotted are values corrected for the random effects of family and stream. *P* values are from tests of whether slopes (coefficients) differ from zero; see text for more statistical details.

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

Table 2: Summary of results for tests examining the effect of mean family-level standard metabolic rate (SMR) on microhabitat use and growth of juvenile Atlantic salmon (*Salmo salar*) in uplands streams with low versus high nutrient levels in the northern highlands of Scotland

	Microhabitat use			Growth		
	$\beta \pm 1$ SE	t	P	$\beta \pm 1$ SE	t	P
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 O_2 h^{-1}; local density: 0.92 juveniles m^{-1}; Julian date: 199; initial egg mass: 98.1 mg).

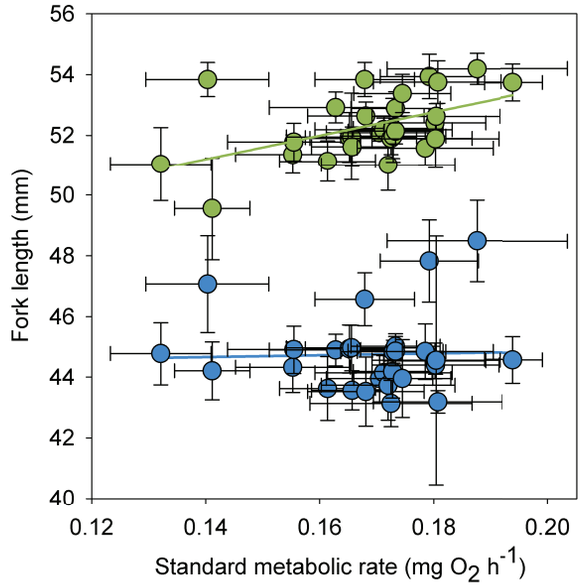

Figure 5: Growth performance as a function of family-level standard metabolic rate in full-sibling families ($n = 29$) of juvenile Atlantic salmon (*Salmo salar*) in 10 headwater streams with either low (blue; $n = 5$) or high (green; $n = 5$) nutrient levels. Metabolic rates were standardized to a common 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. (2018*a*), since microhabitats were quantified in subsections of the larger experimental area in each stream.

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. 2015*a*; Zeng et al. 2017*a*, 2017*b*). 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. 2017*a*) 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. 2017*a*). 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,

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. 2018*a*), 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.

Acknowledgments

We acknowledge our deceased coauthor, Simon McKelvey, who devoted his life's work to the protection and management of Atlantic salmon. We also thank D. Stewart from Marine Scotland Freshwater Fisheries Laboratory for determining the age of salmon parents from scalimetry; E. Rush, R. Golobek, and M. Golobek of the Cromarty Firth Fishery Trust for helping with the artificial fertilization of eggs and planting out of eggs and nutrients; G. Law, R. Phillips, and A. Kirk for helping to maintain fish in the laboratory; and L. McKelvey, K. Salin, D. Orrell, A. Gauthey, R. Auer, and M. Brydon for assistance during electrofishing. Two referees provided helpful comments on the manuscript. All procedures were carried out under the jurisdiction of the UK Home Office project license (PPL 70/8794) governed by the UK Animals Scientific Procedures Act 1986. The authors declare no competing interests. This research was supported by European Research Council Advanced Grants (322784 and 834653) to N.B.M.

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).

Literature Cited

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters 14:948–958.

Armstrong, J. D., P. Kemp, G. Kennedy, M. Ladle, and N. Milner. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research 62:143–170.

Armstrong, J. D., K. J. Millidine, and N. B. Metcalfe. 2011. Ecological consequences of variation in standard metabolism and dominance among salmon parr. Ecology of Freshwater Fish 20:371–376.

Auer, S. K., Bassar, R. D., Turek, D., Anderson, G. J., McKelvey, S., Armstrong, J. D., Nislow, K. H., et al. 2020. Data from: Metabolic rate interacts with resource availability to determine individual variation in microhabitat use in the wild. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.sxksn030f.

Auer, S. K., G. J. Anderson, S. McKelvey, R. D. Bassar, D. McLennan, J. D. Armstrong, K. H. Nislow, et al. 2018*a*. Nutrients from salmon parents alter selection pressures on their offspring. Ecology Letters 21:287–295.

Auer, S. K., R. D. Bassar, K. Salin, and N. B. Metcalfe. 2016. Repeatability of metabolic rate is lower for animals living under field versus laboratory conditions. Journal of Experimental Biology 219:631–634.

Auer, S. K., S. S. Killen, and E. L. Rezende. 2017. Resting vs active: a meta-analysis of the intra-and inter-specific associations between minimum, sustained, and maximum metabolic rates in vertebrates. Functional Ecology 31:1728–1738.

Auer, S. K., K. Salin, G. J. Anderson, and N. B. Metcalfe. 2018*b*. Individuals exhibit consistent differences in their metabolic rates across changing thermal conditions. Comparative Biochemistry and Physiology A 217:1–6.

Auer, S. K., K. Salin, A. M. Rudolf, G. J. Anderson, and N. B. Metcalfe. 2015*a*. Flexibility in metabolic rate confers a growth advantage under changing food availability. Journal of Animal Ecology 84:1405–1411.

———. 2015*b*. The optimal combination of standard metabolic rate and aerobic scope for somatic growth depends on food availability. Functional Ecology 29:479–486.

Bailey, C., L. Andersson, M. Arbeider, K. Bradford, and J. Moore. 2019. Salmon egg subsidies and interference competition among stream fishes. Environmental Biology of Fishes 102:915–926.

Biro, P. A., and J. A. Stamps. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends in Ecology and Evolution 25:653–659.

Bochdansky, A., P. Grønkjær, T. Herra, and W. Leggett. 2005. Experimental evidence for selection against fish larvae with high metabolic rates in a food limited environment. Marine Biology 147:1413–1417.

Bolnick, D., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. Rudolf, et al. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26:183–192.

Bolnick, D. I., L. K. Snowberg, C. Patenia, W. E. Stutz, T. Ingram, and O. L. Lau. 2009. Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. Evolution 63:2004–2016.

Bolnick, D. I., R. Svanbäck, James A. Fordyce, Louie H. Yang, Jeremy M. Davis, C. D. Hulsey, and Matthew L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161:1–28.

Britton, J. R., and D. Andreou. 2016. Parasitism as a driver of trophic niche specialisation. Trends in Parasitology 32:437–445.

Brooks, A. J., B. Wolfenden, B. J. Downes, and J. Lancaster. 2017. Do pools impede drift dispersal by stream insects? Freshwater Biology 62:1578–1586.

Brown, A. V., and P. P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. Hydrobiologia 220:99–108.

Burton, T., S. Killen, J. Armstrong, and N. Metcalfe. 2011. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proceedings of the Royal Society B 278:3465–3473.

Careau, V., D. Thomas, M. Humphries, and D. Réale. 2008. Energy metabolism and animal personality. Oikos 117:641–653.

Cutts, C., C. Adams, and A. Campbell. 2001. Stability of physiological and behavioural determinants of performance in Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences 58:961–968.

Docker, M., T. Medland, and F. Beamish. 1986. Energy requirements and survival in embryo mottled sculpin (*Cottus bairdi*). Canadian Journal of Zoology 64:1104–1109.

Edwards, M. A., A. E. Derocher, K. A. Hobson, M. Branigan, and J. A. Nagy. 2011. Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic. Oecologia 165:877–889.

Einum, S., and I. A. Fleming. 2004. Environmental unpredictability and offspring size: conservative versus diversified bet-hedging. Evolutionary Ecology Research 6:443–455.

Einum, S., M. T. Kinnison, A. P. Hendry, and S. Stearns. 2004. Evolution of egg size and number, Pages 126–153 *in* A. P. Hendry and S. C. Stearns, eds. Evolution illuminated: salmon and their relatives. Oxford University Press, New York.

Einum, S., G. Robertsen, K. H. Nislow, S. McKelvey, and J. D. Armstrong. 2011. The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. Oecologia 165:959–969.

Ekman, J. B., and C. E. Askenmo. 1984. Social rank and habitat use in willow tit groups. Animal Behaviour 32:508–514.

Elliott, J. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. III. The role of territorial behaviour. Journal of Animal Ecology 59:803–818.

———. 2002. Shadow competition in wild juvenile sea-trout. Journal of Fish Biology 61:1268–1281.

Enders, E. C., D. Boisclair, and A. G. Roy. 2003. The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 60:1149–1160.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379–416.

Fleming, I. A., and S. Ng. 1987. Evaluation of techniques for fixing, preserving, and measuring salmon eggs. Canadian Journal of Fisheries and Aquatic Sciences 44:1957–1962.

Grant, J. W. A., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47:1724–1737.

Guyette, M. Q., C. S. Loftin, and J. Zydlewski. 2013. Carcass analog addition enhances juvenile Atlantic salmon (*Salmo salar*) growth and condition. Canadian Journal of Fisheries and Aquatic Sciences 70:860–870.

Guyette, M. Q., C. S. Loftin, J. Zydlewski, and R. Cunjak. 2014. Carcass analogues provide marine subsidies for macroinvertebrates and juvenile Atlantic salmon in temperate oligotrophic streams. Freshwater Biology 59:392–406.

Hedger, R., J. Dodson, N. Bergeron, and F. Caron. 2005. Habitat selection by juvenile Atlantic salmon: the interaction between physical habitat and abundance. Journal of Fish Biology 67:1054–1071.

Hughes, A. R., B. D. Inouye, M. T. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. Ecology Letters 11:609–623.

Hughes, N. F. 1992. Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior

Alaska. Canadian Journal of Fisheries and Aquatic Sciences 49:1999–2008.

Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039–2048.

Hulbert, A., and P. L. Else. 2000. Mechanisms underlying the cost of living in animals. Annual Review of Physiology 62:207–235.

Jones, A. W., and D. M. Post. 2016. Does intraspecific competition promote variation? a test via synthesis. Ecology and Evolution 6:1646–1655.

Keeley, E. R., and J. W. Grant. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 52:186–196.

Killen, S. S., S. Marras, and D. J. McKenzie. 2011. Fuel, fasting, fear: routine metabolic rate and food deprivation exert synergistic effects on risk-taking in individual juvenile European sea bass. Journal of Animal Ecology 80:1024–1033.

Kobler, A., T. Klefoth, T. Mehner, and R. Arlinghaus. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? Oecologia 161:837–847.

Kobler, A., G. E. Maes, Y. Humblet, F. A. Volckaert, and M. Eens. 2011. Temperament traits and microhabitat use in bullhead, Cottus perifretum: fish associated with complex habitats are less aggressive. Behaviour 148:603–625.

Logan, P., and M. Brooker. 1983. The macroinvertebrate faunas of riffles and pools. Water Research 17:263–270.

McLennan, D., J. Armstrong, D. Stewart, S. Mckelvey, W. Boner, P. Monaghan, and N. Metcalfe. 2016. Interactions between parental traits, environmental harshness and growth rate in determining telomere length in wild juvenile salmon. Molecular Ecology 25:5425–5438.

McLennan, D., S. K. Auer, G. J. Anderson, T. C. Reid, R. D. Bassar, D. C. Stewart, E. Cauwelier, et al. 2019. Simulating nutrient release from parental carcasses increases the growth, biomass and genetic diversity of juvenile Atlantic salmon. Journal of Applied Ecology 56:1937–1947.

Metcalfe, N. 1986. Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. Journal of Fish Biology 28:525–531.

Metcalfe, N. B., A. C. Taylor, and J. E. Thorpe. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Animal Behaviour 49:431–436.

Millidine, K. J., J. D. Armstrong, and N. B. Metcalfe. 2009. Juvenile salmon with high standard metabolic rates have higher energy costs but can process meals faster. Proceedings of the Royal Society B 276:2103–2108.

Mittelbach, G. G., N. G. Ballew, and M. K. Kjelvik. 2014. Fish behavioral types and their ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 71:927–944.

Morris, D. W., and D. L. Davidson. 2000. Optimally foraging mice match patch use with habitat differences in fitness. Ecology 81:2061–2066.

Nespolo, R. F., D. M. Bustamante, L. D. Bacigalupe, and F. Bozinovic. 2005. Quantitative genetics of bioenergetics and growth-related traits in the wild mammal, *Phyllotis darwini*. Evolution 59:1829–1837.

Nilsen, E. B., J. D. Linnell, and R. Andersen. 2004. Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*. Journal of Animal Ecology 73:44–50.

Nilsson, J. Å., M. Åkesson, and J. Nilsson. 2009. Heritability of resting metabolic rate in a wild population of blue tits. Journal of Evolutionary Biology 22:1867–1874.

Nislow, K. H, C. Folt, and D. Parrish. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. Ecological Applications 9:1085–1099.

———. 2000. Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. Transactions of the American Fisheries Society 129:1067–1081.

Nislow, K. H., J. D. Armstrong, and J. W. Grant. 2010. The role of competition in the ecology of juvenile Atlantic salmon. Pages 171–197 *in* Ø. Aas, A. Klemetsen, S. Einum, and J. Skurda, eds. Atlantic salmon ecology. Blackwell, West Sussex, UK.

Nislow, K. H., J. D. Armstrong, and S. McKelvey. 2004. Phosphorus flux due to Atlantic salmon (*Salmo salar*) in an oligotrophic upland stream: effects of management and demography. Canadian Journal of Fisheries and Aquatic Sciences 61:2401–2410.

Nislow, K. H., C. Folt, and M. Seandel. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 55:116–127.

Olsson, J., M. Quevedo, C. Colson, and R. Svanbäck. 2007. Gut length plasticity in perch: into the bowels of resource polymorphisms. Biological Journal of the Linnean Society 90:517–523.

Pakkasmaa, S., O.-P. Penttinen, and J. Piironen. 2006. Metabolic rate of Arctic char eggs depends on their parentage. Journal of Comparative Physiology B 176:387.

Pearsons, T. N., D. D. Roley, and C. L. Johnson. 2007. Development of a carcass analog for nutrient restoration in streams. Fisheries 32:114–124.

Pegg, J., D. Andreou, C. Williams, and J. Britton. 2017. Consistent patterns of trophic niche specialization in host populations infected with a non-native copepod parasite. Parasitology 144:945–953.

Persson, L. 1985. Optimal foraging: the difficulty of exploiting different feeding strategies simultaneously. Oecologia 67:338–341.

Pettersen, A. K., D. J. Marshall, and C. R. White. 2018. Understanding variation in metabolic rate. Journal of Experimental Biology 221.

Piccolo, J. J., B. M. Frank, and J. W. Hayes. 2014. Food and space revisited: the role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. Environmental Biology of Fishes 97:475–488.

Pough, F. H., and R. M. Andrews. 1984. Individual and sibling-group variation in metabolism of lizards: the aerobic capacity model for the origin of endothermy. Comparative Biochemistry and Physiology A 79:415–419.

Rasmussen, J. B., M. D. Robinson, A. Hontela, and D. D. Heath. 2011. Metabolic traits of westslope cutthroat trout, introduced rainbow trout and their hybrids in an ecotonal hybrid zone along an elevation gradient. Biological Journal of the Linnean Society 105:56–72.

Reid, D., J. D. Armstrong, and N. B. Metcalfe. 2011. Estimated standard metabolic rate interacts with territory quality and density to determine the growth rates of juvenile Atlantic salmon. Functional Ecology 25:1360–1367.

———. 2012. The performance advantage of a high resting metabolic rate in juvenile salmon is habitat dependent. Journal of Animal Ecology 81:868–875.

Robertsen, G., J. D. Armstrong, K. H. Nislow, I. Herfindal, S. McKelvey, and S. Einum. 2014. Spatial variation in the relationship between performance and metabolic rate in wild juvenile Atlantic salmon. Journal of Animal Ecology 83:791–799.

Robinson, B. W. 2000. Trade offs in habitat-specific foraging efficiency and the nascent adaptive divergence of sticklebacks in lakes. Behaviour 137:865–888.

SFCC. 2007. Scottish Fisheries Co-ordination Centre Habitat Surveys Training Course Manual.

Shearer, W. M. 1992. Atlantic salmon scale reading guidelines, International Council for the Exploration of the Sea, Copenhagen.

Sheppard, C., R. Inger, R. Macdonald, S. Barker, A. Jackson, F. Thompson, E. Vitikainen, et al. 2018. Intragroup competition predicts individual foraging specialisation in a group-living mammal. Ecology Letters 21: 665–673.

Slaney, P., and T. Northcote. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. Journal of the Fisheries Board of Canada 31:1201–1209.

Steingrímsson, S. Ó., and J. W. Grant. 2003. Patterns and correlates of movement and site fidelity in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 60:193–202.

———. 2008. Multiple central-place territories in wild young-of-the-year Atlantic salmon *Salmo salar*. Journal of Animal Ecology 77:448–457.

Steyermark, A. C., and J. R. Spotila. 2000. Effects of maternal identity and incubation temperature on snapping turtle (*Chelydra serpentina*) metabolism. Physiological and Biochemical Zoology 73:298–306.

Svanbäck, R., and D. I. Bolnick. 2005. Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. Evolutionary Ecology Research 7:993–1012.

———. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B 274:839–844.

Svanbäck, R., and P. Eklöv. 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. Oecologia 131:61–70.

Tinker, M. T., M. Mangel, and J. A. Estes. 2009. Learning to be different: acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specializations. Evolutionary Ecology Research 11:841–869.

Toobaie, A., and J. W. Grant. 2013. Effect of food abundance on aggressiveness and territory size of juvenile rainbow trout, *Oncorhynchus mykiss*. Animal Behaviour 85:241–246.

Toscano, B. J., N. J. Gownaris, S. M. Heerhartz, and C. J. Monaco. 2016. Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. Oecologia 182:55–69.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, et al. 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology and Evolution 27:244–252.

Werner, E. E., G. G. Mittelbach, D. J. Hall, and J. F. Gilliam. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64:1525–1539.

Werner, T. K., and T. W. Sherry. 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin's finch" of Cocos Island, Costa Rica. Proceedings of the National Academy of Sciences of the USA 84:5506–5510.

Williams, K., S. Griffiths, K. Nislow, S. McKelvey, and J. Armstrong. 2009. Response of juvenile Atlantic salmon, *Salmo salar*, to the introduction of salmon carcasses in upland streams. Fisheries Management and Ecology 16:290–297.

Wone, B., M. W. Sears, M. K. Labocha, E. R. Donovan, and J. P. Hayes. 2009. Genetic variances and covariances of aerobic metabolic rates in laboratory mice. Proceedings of the Royal Society B 276:3695–3704.

Zeng, L.-Q., L. Wang, G.-N. Wang, Y. Zeng, and S.-J. Fu. 2017*a*. The relationship between growth performance and metabolic rate flexibility varies with food availability in juvenile qingbo (*Spinibarbus sinensis*). Comparative Biochemistry and Physiology A 212:56–63.

Zeng, L.-Q., A.-J. Zhang, S. S. Killen, Z.-D. Cao, Y.-X. Wang, and S.-J. Fu. 2017*b*. Standard metabolic rate predicts growth trajectory of juvenile Chinese crucian carp (Carassius auratus) under changing food availability. Biology Open 6:1305–1309.

References Cited Only in the Online Enhancements

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships from freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343.

Bird, D., and Y. Prairie. 1985. Practical guidelines for the use of zooplankton length-weight regression equations. Journal of Plankton Research 7:955–960.

de Valpine, P., D. Turek, C. J. Paciorek, C. Anderson-Bergman, D. T. Lang, and R. Bodik. 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. Journal of Computational and Graphical Statistics 26:403–413.

Maitland, P. 1965. The feeding relationships of salmon, trout, minnows, stone loach and three-spined stickle-backs in the River Endrick, Scotland. Journal of Animal Ecology 34:109–133.

Mills, D. H. 1964, The ecology of the young stages of the Atlantic salmon in the River Bran, Ross-shire. HM Stationery, Edinburgh.

Taylor, B. W., A. R. McIntosh, and B. L. Peckarsky. 2001. Sampling stream invertebrates using electroshocking techniques: implications for basic and applied research. Canadian Journal of Fisheries and Aquatic Sciences 58:437–445.

Vandeputte, M., S. Mauger, and M. Dupont-Nivet. 2006. An evaluation of allowing for mismatches as a way to manage genotyping errors in parentage assignment by exclusion. Molecular Ecology Notes 6:265–267.

Wankowski, J. 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon, *Salmo salar*. Journal of Fish Biology 14:89–100.

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