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The physiological costs of prey switching reinforce foraging specialization

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Summary

1. Sympatric speciation is thought to be strongly linked to resource specialization with alternative resource use acting as a fundamental agent driving divergence. However, sympatric speciation through niche expansion is dependent on foraging specialization being consistent over space and time.

2. Standard metabolic rate is the minimal maintenance metabolic rate of an ectotherm in a post-absorptive and inactive state and can constitute a significant portion of an animal's energy budget; thus, standard metabolic rate and growth rate are two measures frequently used as an indication of the physiological performance of individuals. Physiological adaptations to a specific diet may increase the efficiency with which it is utilized, but may have an increased cost associated with switching diets, which may result in a reduced standard metabolic rate and growth rate.

3. In this study, we use the diet specialization often seen in polymorphic Arctic charr (*Salvelinus alpinus*) populations to study the effects of different prey on standard metabolic rate and growth rate as well as the effects that early prey specialization may have on the ability to process other prey types efficiently.

4. We found a significant effect of prey type on standard metabolic rate and growth rate. Furthermore, we found evidence of diet specialization with all fish maintaining a standard metabolic rate and growth rate lower than expected when fed on a diet different to which they were raised, possibly due to a maladaptation in digestion of alternative prey items.

5. Our results show that early diet specialization may be reinforced by the elevated costs of prey switching, thus promoting the process of resource specialization during the incipient stages of sympatric divergence.

Key-words: Arctic charr, ecological speciation, evolution, foraging specialization, growth rate, optimal foraging, physiology, standard metabolic rate, sympatric speciation

Introduction

A major theme emerging from our understanding of how ecologically driven speciation occurs in sympatry is that it is frequently linked with resource specialization (Dieckmann & Doebeli 1999; Nosil 2012). There is considerable evidence that intraspecific foraging specialisms are an important step driving the early stages of divergence in sympatry (Knudsen *et al.* 2006; Grant & Grant 2011). Resource use specialization has very significant consequential effects on the ecology for the individual exhibiting a resource specialism (Skúlason & Smith 1995). These effects include habitat use (Heithaus & Dill 2006), fitness (Cucherousset *et al.* 2011), growth (Metcalfe 1986) and reproduction (Dewsbury 1982; Suryan, Irons & Benson 2000). Individuals exhibiting different specialisms may also differ in some or all of these characteristics as a consequence. Such effects are the foundation of the concepts of ecological speciation (Skúlason & Smith 1995; Skúlason, Snorrason & Jónsson 1999). Examples of ecological speciation in sympatry have been shown in plants (Ostevik *et al.* 2012), insects (Grant 1949; Coyne & Orr 1997), birds (Smith & Skúlason 1996) and fish (Adams *et al.* 1998; Hatfield & Schluter 1999; Rogers & Bernatchez 2007; Elmer *et al.* 2014).

Where examples of sympatric divergence exist they are thought to be the result of either strong intraspecific

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competition and/or the availability of new and often novel prey types. Sympatric divergence is more likely to occur when alternative resources are discrete and the behavioural skills and anatomical tools needed to efficiently exploit them are contrasting (Snorrason *et al.* 1994; Skúlason, Snorrason & Jónsson 1999; Amundsen, Bøhn & Våga 2004; Kahilainen & Østbye 2006). Thus, divergent selection can operate differentially on a diverse array of morphological, behavioural and physiological traits to increase foraging efficiency on alternative prey types (Svanbäck & Eklöv 2003). Traits required for high foraging efficiency can be genetically inherited, or ontogenetic, arising through phenotypic plasticity (Via 1993); or a combination of both (Adams & Huntingford 2002). However, for evolved traits to manifest through plasticity alone, any foraging specialism must lead to increased fitness and be maintained over a significant portion of an animal's life. For example, learned behaviours that increase foraging efficiency may help to maintain long-term foraging specialization and as a consequence expose individuals specializing on different prey to different selection regimes. Mechanisms such as search image formation (Stanton 1984) and specific prey foraging techniques (Hughes & Seed 1981; Guillemain, Duncan & Fritz 2001) can increase the cost of prey switching for individuals specializing on a single prey type, and thus promote long-term specialization.

Optimal foraging theory predicts that a decrease in foraging efficiency associated with switching prey increases with the level of behavioural difficulty in acquiring that prey (Hughes 1979; Hughes & Seed 1981). It has also been shown that subtle differences in morphology between individuals can help maintain specialization by increasing foraging efficiency on different prey types (Garduño-Paz & Adams 2010). For example, differences in gill raker spacing and mouth shape in both the three-spined stickleback (*Gasterosteus* spp.) and European white fish (*Coregonas laveratus*) (Kahilainen & Østbye 2006) have been shown to have dramatic effects on their foraging efficiency on benthic or planktonic resources (Schluter 1993).

Physiological adaptations to foraging specialization are less well understood and not as well documented, likely due to their cryptic nature (van Leeuwen, Rosenfeld & Richards 2011). Standard metabolic rate (SMR) and growth rate are two frequently used measures of the physiological performance of individuals (van Leeuwen, Rosenfeld & Richards 2011). Differences in food quantity (van Leeuwen, Rosenfeld & Richards 2011; Auer *et al.* 2015a) and food type (McNab 1986; McBride & Kelly 1990; Yang & Joern 1994; Starck 1999a, b; van Leeuwen *et al.* 2015; Rosenfeld *et al.* 2015) have been shown to influence SMR, which can in turn affect the growth rate of the individual (van Leeuwen, Rosenfeld & Richards 2011; Auer *et al.* 2015b). Therefore, physiological adaptation to increase conversion efficiency of novel prey types may manifest as differences in SMR and growth rate in response to varying food types.

Standard metabolic rate, which is equivalent to basal metabolic rate in endotherms, is the minimal maintenance metabolic rate of an ectotherm in a post-absorptive and inactive state and can constitute a significant portion of an animal's energy budget (Finstad *et al.* 2007). Standard metabolic rate which has been found to be consistent across an individual's life span, is thought to be inherited and there can be up to a threefold difference among individuals (see review in Metcalfe, van Leeuwen & Killen 2016). Comparative studies have shown that SMR is of ecological and evolutionary importance (Glazier 2005; Steyermark *et al.* 2005; Careau *et al.* 2008; Artacho & Nespolo 2009; Burton *et al.* 2011). Differences in physiology have been shown to be a result of ecologically driven selection pressures that can drive and maintain the coexistence of incipient species of lake fish (Dijkstra *et al.* 2011; Evans *et al.* 2012). Differences in SMR can be underpinned by environmental factors, such as resource acquisition (Alvarez & Nicieza 2005; Steyermark *et al.* 2005), which can affect physiology and life-history trajectories making SMR a useful metric for understanding the role of physiology in the occurrence of resource specialization.

Variation in SMR and growth rate among contrasting genotypes is partly rooted in larger digestive tracts and maximum food rations that contribute to a higher SMR (Rosenfeld *et al.* 2015; Allen, Rosenfeld & Richards 2016). Digestive tracts have already been shown to be phenotypically plastic and respond to changes in food availability and prey nutrition (McNab 1986; McBride & Kelly 1990; Yang & Joern 1994; Starck 1999a, b; Armstrong & Bond 2013) with increased food rations leading to increased surface area and microtopography of the intestine (Rosenfeld *et al.* 2015). Studies investigating food quality have shown that animals eating a low-quality diet may evolve lower metabolic rates in order to balance their energetic requirements (McNab 1986). Because lipids have low metabolic activity, differences in SMR may reflect differences in lipid stores, with individuals that have greater lipid stores also having a lower mass-specific SMR (Rosenfeld *et al.* 2015). Furthermore, McNab (1986) found that individuals fed low-quality diets (e.g. low protein and lipid content) also had reduced internal organ mass, potentially resulting in a lower SMR. In contrast, McBride & Kelly (1990), Yang & Joern (1994) and Starck (1999a, b) found a positive correlation between the amount of indigestible material in a diet and organ size with individuals that had larger organs having a higher metabolic rate.

The Arctic charr (*Salvelinus alpinus*) has been frequently recorded exhibiting sympatric resource polymorphisms most frequently occurring as foraging specialisms (Snorrason *et al.* 1994). The two most commonly reported sympatric ecotypes are a pelagic form which specializes on zooplankton prey and a benthic form that specializes on macro invertebrate prey (Malmquist *et al.* 1992; Snorrason *et al.* 1994; Adams *et al.* 1998; Hooker *et al.* 2016).

In this study, we use Arctic charr to investigate the potential effects of early prey specialization on SMR and growth rate using three different prey items, one from the pelagic environment and two from the benthic environment. Furthermore, we test if there were any effects on SMR and growth rate associated with diet switching. The main objectives of this study were (i) to compare the effect of different diets typical of specialization in the wild on SMR and growth rate, and (ii) to establish the role of physiology and its effect on the development of resource specialization using SMR and growth rate as a proxy in Arctic charr from a lineage that had not differentiated into planktonic and benthivorous specialists in the period since the last glaciation from anadromous ancestors.

Materials and methods

FISH CARE AND PREPARATION

Arctic charr were acquired in February 2014 as eggs from a cultured anadromous brood stock. This brood stock was chosen because the anadromous stock provided an undifferentiated lineage with which to test the diversification potential of diet specialization and to avoid potential confounding effects (genetic and non-genetic) as a result of using eggs from parents which were themselves benthic or pelagic specialists. Eggs were transported to the Scottish Centre for Ecology and the Natural Environment (SCENE, Loch Lomond, Glasgow). Upon arrival, the eggs from six full-sib families were placed in separate meshed rearing baskets suspended in a holding tank at a constant temperature room. Constant temperature rooms were illuminated using fluorescent tubes on a 10 L : 14D cycle, controlled with a timer. Water was supplied directly from Loch Lomond and was maintained at 4·0 ± 0·5 °C. Developmental rate and time of sampling was measured in degree-days (dd; the cumulative water temperature for a known period of time in days), this commenced when all fish had hatched. Fish reached the 'first feed' stage at approximately 102dd when the yolk sac was almost exhausted and fish started to actively seek food. At this point, chopped liver was introduced *ad libitum* as an exogenous food source. At 328dd, 16 offspring from each of the six different families of Arctic charr were evenly mixed ($N = 96$) and then distributed across six aquaria ($N = 16$ fish per aquarium). All aquaria measured 48 × 30 × 22 cm, thus providing two replicates of each diet treatment. All aquaria were supplied with water from Loch Lomond on a flow through system at ambient temperature which ranged from 5 to 16 °C.

DIETARY TREATMENTS

From 328dd fish were fed one of three diet types; *Daphnia pulex*; bloodworm (*Chironomus* sp. larvae); or *Gammarus pulex*, all three prey are commonly found in the stomachs of sympatric polymorphic lake-dwelling Arctic charr in the wild (Adams & Huntingford 2002; Knudsen *et al*. 2006). *Daphnia pulex* represented a pelagic prey item, whereas bloodworm and *G. pulex* represented benthic prey items. The mass and nutritional composition for each prey type is given in Table 1. During the rearing period, which ran from 12 March 2014 to 17 October 2014 (approximately 2303dd), fish were fed to satiation three times daily at 4-h intervals. These groups are henceforth referred to as *Daphnia* fish, bloodworm fish or *Gammarus* fish (Fig. 1).

Table 1. Size and nutritional content of the different prey items. All nutritional information is provided by BCUK Aquatics, Lincolnshire, England

Food	Mass (mg)	Protein (%)	Fat (%)	Fibre (%)	Moisture (%)
Daphnia	0·76 (SD 0·025)	5·0	0·7	1·0	90·0
Bloodworm	12·1 (SD 1·41)	5·0	0·5	0·9	89·0
Gammarus	15·92 (SD 2·79)	8·0	1·0	1·2	89·8

During the rearing period leading up to oxygen uptake and growth rate measures, aquaria were supplied daily with 45 g (wet weight) of food from one of the three diet types discussed above. Food items were thawed prior to feeding. To ensure that any observed changes in SMR and growth rate were the result of diet type and not simply quantity, fish were fed to satiation to help reduce differences in food acquisition as a result of dominance hierarchies. Food ration sizes large enough to ensure satiation were calculated prior to the experiment by placing known amounts of food into an aquarium and observing the point at which the addition of food resulted in no additional feeding response.

MEASUREMENT OF GROWTH RATE AND SMR

Twenty-two fish from each diet treatment were randomly selected from aquaria. At this stage each individual was marked with a visible implant elastomer (Northwest Marine Technology, Inc., Shaw Island, WA, USA), and equally distributed across two replicate aquaria (11 fish per tank) measuring 48 × 30 × 22 cm keeping diet type discrete. The remaining fish were used as part of an additional study. Two assessments of growth rate and SMR were then obtained for each of the marked fish. The first assessment of growth rate and SMR (Stage 1) were obtained for fish on their starting (initial) diet (Fig. 1). At the start of Stage 1, fish were weighed to ±0·01 g. At the end of this stage (20–22 days) fish were starved for 24 h, reweighed to ±0·01 g and subject to metabolic measurement. Starving fish for 24 h allowed sufficient time for fish to evacuate their guts prior to oxygen uptake measurements. Individual fish were placed into one of 22 darkened glass respirometer chambers (30 mm diameter, 80 mm length, 56·6 mL volume) to minimize fish activity during measurements (Cutts, Metcalfe & Taylor 2002) and allowed to settle for 18–20 h to acclimatize and come to rest before oxygen consumption measures commenced. All oxygen uptake measurements were taken between 06.00 and 12.00 h. Immediately after oxygen uptake measurement, the 22 fish from each starting diet were divided randomly into two groups of 11 fish. Each group of fish was then fed one of the two alternative diets, for example, fish raised on bloodworm were fed either *Daphnia* or *Gammarus*; fish raised on *Daphnia* were fed either bloodworm or *Gammarus*; and fish raised on *Gammarus* were fed either bloodworm or *Daphnia* (Stage 2). These new diets continued for a further 20–22 days, after which fish were again starved for 24 h, reweighed so that growth rate and SMR could once again be determined (Fig. 1).

Oxygen uptake was measured using flow-through respirometery (Steffensen 1989), whereby the rate of oxygen consumption by the fish is measured as a reduction in oxygen concentration between the water flowing into, and out of, the respirometer (holding the fish). By definition, SMR should be measured on fish which are not growing, that is, fish that are on a maintenance

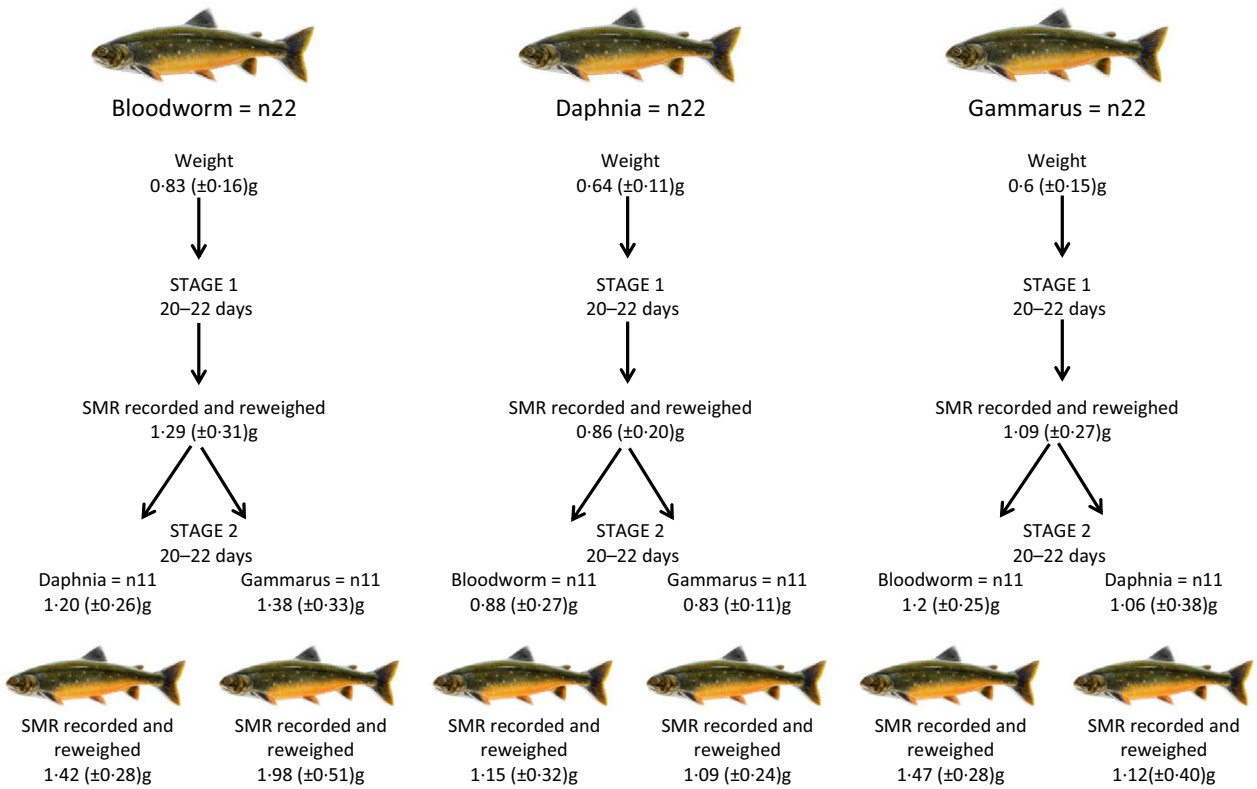

Fig. 1. Schematic showing experimental design, including sample size for each stage and mean weights and standard deviation for each sample group. [Colour figure can be viewed at wileyonlinelibrary.com]

ration, and therefore the term 'apparent SMR' is more appropriate. For consistency, throughout this manuscript the use of the term SMR is taken to mean 'apparent SMR'.

Water was supplied from a central header tank to the respirometry chambers using 4 mm diameter tubing attached to a manifold. An air stone in the header tank of the respirometer apparatus kept inflow water fully saturated with oxygen. Water oxygen concentration exiting the chamber was measured using an oxygen meter (FireStingO_2 oxygen meter; Pyro Science GmbH, Aachen, Germany) fitted with four oxygen probes; each probe was calibrated daily. The average flow rate of the water was 0·07 L h^{-1} (approximately 1 mL min^{-1}); this was adjusted (±) to ensure that there was at least a 10% drop in oxygen concentration between the inlet and outlet of each respirometer, although concentrations never dropped below 80% oxygen saturation. Flow was controlled using micro-valves positioned at the inlet of the respirometer chambers. The flow rate for each chamber was calculated by weighing the amount of water (to 0·01 g) that exited the chamber in a 60-s period and was measured at the same time as oxygen concentration measurements were taken. The respirometry apparatus was located inside a constant temperature room, held at 13·3 °C (±0·1 °C). The rate of oxygen consumption was determined using the following equation (Ege & Krogh 1914):

$$MO_2(\text{whole}) = V_w \Delta C_w O_2$$

where V_w is the flow rate (L h^{-1}) of water through the respirometer and $\Delta C_w O_2$ is the difference in the oxygen concentration between the inflow and outflow water (mL L^{-1}). The concentration of oxygen was calculated by correcting ppO_2 (partial pressure of oxygen) for barometric pressure and multiplying by αO_2 (μmol L^{-1} $torr^{-1}$), the solubility coefficient at the observed temperature. SMR was determined using two oxygen uptake measurements taken 3 h apart with the average of these two measurements used for statistical analysis. If the two measurements differed by greater than 10%, a third measure was taken.

STATISTICAL ANALYSES

Instantaneous growth rates of fish (% bodyweight gain per day) were calculated as 100{[log (final mass)−log (initial mass)]/time elapsed (days)} (Ricker 1975).

Given the increase in fish mass over the course of the experiment, and the effect of mass on metabolism and growth, we used size-corrected residual values for SMR (rSMR) and growth (rGrowth) in subsequent analysis. Size-corrected values were calculated as residuals from the regression of absolute oxygen consumption (SMR) or growth on mass (g) (all log transformed) for all fish. However, the use of residuals in this way have recently been criticised because they remove the possibility of identifying potential effects where variable co-correlation occurs (Freckleton 2002; McCoy *et al.* 2006). Both SMR and growth are notoriously variable in salmonid fish (Cutts, Metcalfe & Taylor 1998). One strength of the study design presented here is that we were able to track changes in metabolic rate and growth with diet change in individual fish, thereby reducing within group variation caused by individual differences. However, to ensure a robust analysis of SMR and growth between diet treatments and to ensure our analysis was not biased by the use of size-corrected residuals, we first tested our data using a generalized linear mixed effect model

(GLMM) with fish mass as a covariate and individual as random effect. A *post-hoc* test was used to extract all relevant comparisons. In addition, the same comparisons were further tested using the additional power of the paired *t*-test to reduce the effect of between individual variation. We tested for the effect of diet type (Stage 1) (bloodworm, *Daphnia* and *Gammarus*) on SMR and growth using an ANOVA. To test for the effect of diet switching on SMR and growth, we again used residuals (as described above) to compare the SMR and growth of individual fish before (Stage 1) and after (Stage 2) the diet switch using a paired *t*-test. Finally, residual values of SMR and growth of fish on their raised diets (Stage 1) were again used to compare against the two other groups that had been switched to that respective diet. For example, the SMR and growth of bloodworm fish being fed bloodworm (Stage 1) were compared with the SMR and growth of *Daphnia* fish and *Gammarus* fish being fed bloodworm (Stage 2) using a linear model. Models included raised diet (explanatory variable) and SMR or growth (response variables).

Standard metabolic rate data were log transformed to linearize the data and meet assumptions of normality and homogeneity of variance. Mass measurements were log transformed following an application of a constant of one to allow transformation of negative values, which occurred as a result of some individuals having a mass of less than 1 g. All analyses were conducted using R version 3.1.0 statistical software (R Development Core Team 2015).

Results

STAGE 1: THE EFFECT OF INITIAL DIET

During Stage 1 there was a significant effect of prey type on SMR ($F_{2,63} = 86{\cdot}73$, $P < 0{\cdot}0001$) (Fig. 2a) and growth rate ($F_{2,63} = 10{\cdot}68$, $P < 0{\cdot}0001$) (Fig. 2b). Fish feeding on *Gammarus* had the highest SMR and growth, whereas fish feeding on *Daphnia* had the lowest SMR and growth (Table 2). A GLMM on raw data showed an identical effect (Table S1, Supporting Information).

Table 2. Between diet (Stage 1) pairwise *post-hoc* differences in rSMR (overall $P < 0{\cdot}0001$) and rGrowth (overall $P < 0{\cdot}0001$). Residual SMR was compared as μmol h^{-1} g^{-1} bodyweight (log), rGrowth was compared as percent bodyweight gain per day (log)

Diet comparison	*t*-test rSMR	*t*-test rGrowth
Bloodworm vs. *Daphnia*	Significantly higher $t_{63} = 5{\cdot}95$, $P < 0{\cdot}001$	Significantly higher $t_{63} = 2{\cdot}67$, $P = 0{\cdot}03$
Bloodworm vs. *Gammarus*	Significantly lower $t_{63} = -7{\cdot}20$, $P < 0{\cdot}001$	Lower $t_{63} = -1{\cdot}93$, $P = 0{\cdot}14$
Daphnia vs. *Gammarus*	Significantly lower $t_{63} = -13{\cdot}16$, $P < 0{\cdot}001$	Significantly lower $t_{63} = -4{\cdot}60$, $P < 0{\cdot}001$

STAGE 2: THE EFFECT OF DIET SWITCHING

When diet type was switched there was a significant effect on individual SMR (Fig. 3a) and growth (Fig. 3b). Fish feeding on Bloodworm showed a significant decrease in SMR and growth when switched to *Daphnia* or *Gammarus*, however, during Stage 1, fish feeding on *Gammarus* had a significantly higher SMR and growth. Contrastingly, fish feeding on *Daphnia* showed a significant increase in SMR but a significant decrease in growth when switched to bloodworm or *Gammarus*. Finally, a decrease in SMR and growth was observed when fish feeding on *Gammarus* were switched to *Daphnia* or bloodworm (Table 3). The same pattern was found using a GLMM analysis, however, as this test was not as sensitive as the paired *t*-test because of a high level of inter-individual variation in SMR, some results were not significant (Table S2).

Interestingly, the SMR of fish switched to an alternative diet (Stage 2) was always significantly lower compared to the SMR of the fish that were raised on that diet (Stage 1) (Fig. 4a). For example, fish fed on a *Daphnia* or *Gammarus*

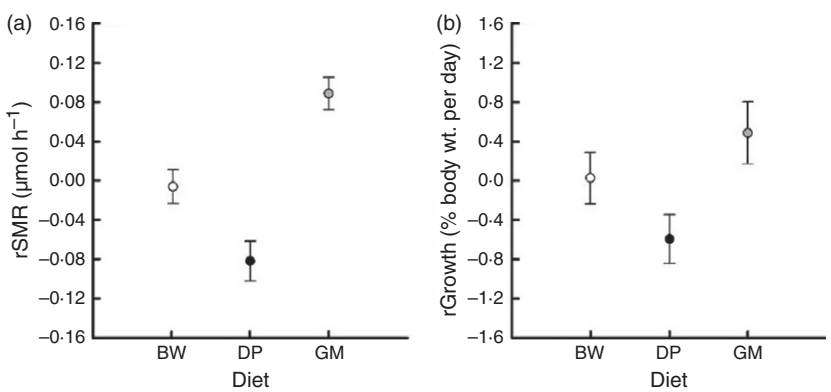

Fig. 2. Body mass-corrected rSMR (a) and rGrowth rates (b) for fish on each diet during Stage 1 (initial diet). Fish raised on bloodworm are depicted with white symbols, *Daphnia* with black and *Gammarus* with grey. Diets at the time the SMR and growth measurements were taken are represented by initials on the *X* axis (BW, bloodworm; DP, *Daphnia*; GM, *Gammarus*). For clarity of presentation, measures of SMR and growth are expressed as residuals, after correction for body mass (rSMR; rGrowth); residuals were calculated from the regression equation of absolute oxygen consumption (μmol h^{-1}) or growth (% body weight per day) on body mass (g) for the full sample size of fish, plotted on double logarithmic axes. Error bars represent 95% confidence intervals. See text for statistical analysis.

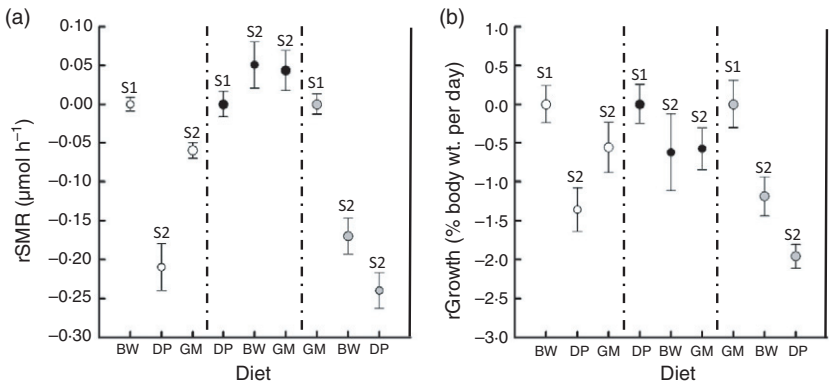

Fig. 3. Body mass corrected rSMR (a) and rGrowth (b) measured when fish were fed their initial diet (S1) and being fed alternative diets (S2). Each set of coloured symbols depicts the same fish on their raised diet (S1) and the diet they were switched to (S2). Fish raised on bloodworm are depicted with white symbols, *Daphnia* with black and *Gammarus* with grey. Diets at the time the SMR and growth measurements were taken are represented by initials on the *X* axis (BW = bloodworm, DP = *Daphnia*, GM = *Gammarus*). For clarity of presentation, measures of SMR and growth are expressed as residuals, after correction for body mass (rSMR; rGrowth); residuals were calculated from the regression equation of absolute oxygen consumption (μmol h^{-1}) or growth (% body weight per day) on body mass (g) for the full sample size of fish, plotted on double logarithmic axes. Error bars represent 95% confidence intervals. See text for statistical analysis.

Table 3. Results from paired *t*-tests comparing individual's rSMR and rGrowth during Stage 1 and following a switch in diet, Stage 2. Residual SMR was compared as μmol h^{-1} g^{-1} bodyweight (log), rGrowth was compared as percent bodyweight gain per day (log)

Diet change	rSMR Increase/decrease	rGrowth Increase/decrease
Bloodworm raised fish switched to *Daphnia*	Significant decrease $t_{10} = -13{\cdot}51$, $P < 0{\cdot}001$	Significant decrease $t_{10} = -7{\cdot}02$, $P = 0{\cdot}001$
Bloodworm raised fish switched to *Gammarus*	Significant decrease $t_{10} = -7{\cdot}65$, $P = <-0{\cdot}001$	Significant decrease $t_{10} = -3{\cdot}82$, $P = 0{\cdot}02$
Daphnia raised fish switched to Bloodworm	Significant increase $t_{10} = 2{\cdot}98$, $P = 0{\cdot}028$	Significant decrease $t_{10} = 3{\cdot}35$, $P = 0{\cdot}02$
Daphnia raised fish switched to *Gammarus*	Significant increase $t_{10} = 3{\cdot}11$, $P = 0{\cdot}02$	Significant decrease $t_{10} = 2{\cdot}26$, $P = 0{\cdot}03$
Gammarus raised fish switched to Bloodworm	Significant decrease $t_{10} = -11{\cdot}81$, $P < 0{\cdot}001$	Significant decrease $t_{10} = -8{\cdot}92$, $P < 0{\cdot}001$
Gammarus raised fish switched to *Daphnia*	Significant decrease $t_{10} = -17{\cdot}67$, $P < 0{\cdot}001$	Significant decrease $t_{10} = -13{\cdot}412$, $P < 0{\cdot}001$

diet and switched to a bloodworm diet (Stage 2) had a significantly lower SMR and growth than fish feeding on bloodworm (Stage 1). Similarly, fish fed on a bloodworm or *Gammarus* diet and switched to *Daphnia* (Stage 2) had a significantly lower SMR and growth than *Daphnia* fish fed *Daphnia* (Stage 1). Finally, fish fed bloodworm or *Daphnia* had a significantly lower SMR when switched to *Gammarus* (Stage 2) than *Gammarus* fish fed on *Gammarus* (Stage 1). A similar trend was also observed for growth but was not statistically significant (Fig. 4b; Table 4). Again the GLMM showed the same pattern in the results but some *post-hoc* results were not significant (Table S3).

Discussion

The type of diet juvenile Arctic charr were initially exposed to following first feeding had a significant effect on SMR and growth rate after the effect of body mass was accounted for. Fish fed on *Daphnia* had the lowest SMR and growth rate with fish feeding on *Gammarus* having the highest. Furthermore, when fish were switched to a diet different to the one on which they were raised their fitness (measured as SMR and growth) was significantly reduced. All fish had a lower SMR and lower growth when fed a diet different to the diet they were raised on when compared to fish raised on that diet. Our results show that early diet specialization may be reinforced by the elevated physiological costs of prey switching.

One possible explanation for the differences in SMR may be due to variation in the length or surface area of the intestine which has been shown to be highly plastic in juvenile salmonids (Armstrong & Bond 2013). It is therefore plausible that differences in protein content, palatability and prey size between those prey used in this study may have led to differences in intestinal development.

Fish fed *Gammarus* exhibited the highest SMR and growth. Because all fish were fed *ad libitum*, our results are likely a developmental response as a result of prey

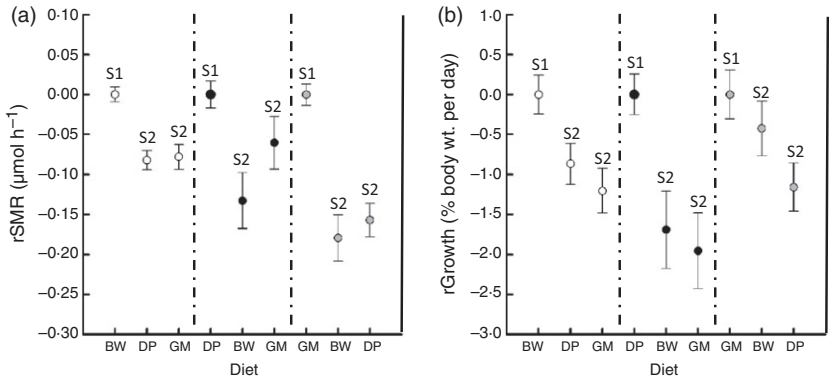

Fig. 4. Body mass corrected SMR g^{-1} body mass (a) and residual growth g^{-1} body mass (b) measured when fish were on their initial diet (S1) and fish from an alternative initial diet being fed the same diet (S2). Each set of coloured symbols depicts the diet at the time the SMR and growth measurements were taken. Bloodworm diet is depicted with white symbols, *Daphnia* with black and *Gammarus* with grey. Initial diets (that fish were raised on) are represented by initials on the *X* axis (BW = bloodworm, DP = *Daphnia*, GM = *Gammarus*). For clarity of presentation measures of SMR and growth are expressed as residuals, after correction for body mass (rSMR; rGrowth); residuals were calculated from the regression equation of absolute oxygen consumption (μmol h^{-1}) or growth (% body weight per day) on body mass (g) for the full sample size of fish, plotted on double logarithmic axes. Error bars represent 95% confidence intervals. See text for statistical analysis.

Table 4. Pairwise *post-hoc* differences in rSMR and rGrowth of fish from different initial diets being fed the same diet. Residual SMR was compared as μmol h^{-1} g^{-1} bodyweight (log), rGrowth was compared as percent bodyweight gain per day (log)

Diet comparison	SMR	Growth
Bloodworm raised fish vs. *Daphnia* raised fish fed on bloodworm	Significantly higher $t_{41} = 9{\cdot}74$, $P < 0{\cdot}001$	Significantly higher $t_{41} = 4{\cdot}50$, $P < 0{\cdot}001$
Bloodworm raised fish vs. *Gammarus* raised fish fed on bloodworm	Significantly higher $t_{41} = 9{\cdot}24$, $P < 0{\cdot}001$	Significantly higher $t_{41} = 6{\cdot}23$, $P < 0{\cdot}001$
Daphnia raised fish vs. bloodworm raised fish fed on *Daphnia*	Significantly higher $t_{41} = 7{\cdot}27$, $P < 0{\cdot}001$	Significantly higher $t_{41} = 6{\cdot}39$, $P < 0{\cdot}001$
Daphnia raised fish vs. *Gammarus* raised fish fed on *Daphnia*	Significantly higher $t_{41} = 3{\cdot}32$, $P = 0{\cdot}005$	Significantly higher $t_{41 \ =} \ 7{\cdot}38$, $P < 0{\cdot}001$
Gammarus raised fish vs. bloodworm raised fish fed on *Gammarus*	Significantly higher $t_{41} = 12{\cdot}85$, $P < 0{\cdot}001$	Higher $t_{41} = 1{\cdot}78$, $P = 0{\cdot}191$
Gammarus raised fish vs. *Daphnia* raised fish fed on *Gammarus*	Significantly higher $t_{41} = 11{\cdot}24$, $P < 0{\cdot}001$	Significantly higher $t_{41} = 4{\cdot}83$, $P < 0{\cdot}001$

type and not as a result of differential food intake across diet types or those associated with behaviours within the aquaria. The higher protein and fat content of *Gammarus* relative to other prey types may provide one mechanism for growth and SMR differentials. However, a similar trend was also observed in fish fed bloodworm, with these individuals having a higher SMR and growth than those fish fed *Daphnia* despite having similar protein content. This suggests that protein content alone is likely not responsible for diet-related differences in SMR and growth observed in this study.

Daphnia and *Gammarus* have a hard exoskeleton which is likely costly to digest (Swaffar & O'Brien 1996; van Leeuwen *et al.* 2015) compared to soft-bodied bloodworm. This could explain the higher initial SMR and growth observed in fish feeding on bloodworm compared to those feeding on *Daphnia*. As the energy demand to breakdown the exoskeleton of the *Daphnia* increases without the added benefit of greater protein and fat content, the consumer is likely to respond in a similar way as individuals subjected to low food rations, leading to a decrease in SMR (van Leeuwen, Rosenfeld & Richards 2011) and growth. However, this does not explain why fish fed *Gammarus* had a higher SMR than fish fed bloodworm. This could be partly explained by the ratio of exoskeleton to internal tissue which will be higher in *Daphnia*. Because they are smaller, the number needed to be consumed to equal that of a single *Gammarus* would be greater and therefore so would the amount of exoskeleton ingested.

Prey size may also be of relevance to the patterns observed for SMR and growth with larger prey (*Gammarus*) resulting in an elevated SMR and growth, as has been shown in other animals (Andrade, Cruz-Neto & Abe 1997; Secor & Faulkner 2002; Secor & Boehm 2006; Millidine, Armstrong & Metcalfe 2009). For example, Secor & Boehm (2006) found that larger meals increased the Specific Dynamic Action of mole salamanders (*Ambystomatidae*) and is maintained in individuals with a higher metabolic

rate (Andrade, Cruz-Neto & Abe 1997; Fu, Xie & Cao 2005; Millidine, Armstrong & Metcalfe 2009).

Interestingly, a switch in diet from one that maintained a low SMR and growth to a diet that maintained a higher initial SMR and growth did not always result in an increase in either. Instead SMR and growth was decreased in fish feeding on bloodworm when they were switched to *Gammarus* despite a *Gammarus* diet maintaining the highest SMR and growth during the initial feeding stages of the experiment (Stage 1). *Daphnia* raised fish showed a slight increase in SMR when switched to bloodworm or *Gammarus* but in both cases growth and SMR remained lower than fish on a continuous bloodworm or *Gammarus* diet. In addition, growth decreased when *Daphnia* fish were switched to an alternative higher quality diet. These results suggest a maladaptation in the assimilation efficiency of the alternative prey type. Surprisingly, this apparent maladaptation seemed to persist regardless of whether the diet switch represented an increase or decrease in prey quality. This suggests that deviating from a familiar prey type to an alternative prey type results in a metabolic discontinuity and ultimately a growth cost even over the relatively short feeding trials in our study. Although the mechanism through which these growth and metabolic rate costs arise remains to be tested, fish in the wild are often exposed to periods of high and low seasonal abundance of a single prey type (Parnell *et al.* 2013).

Physiological or anatomical specialization to increase efficiency in converting a specific prey type to energy may involve differences in the digestive tract that arises during development and thus may not be reversible. That being said, the digestive anatomy of other taxa has been shown to be flexible (Piersma & Lindström 1997; Starck 1999a, b; McWilliams & Karasov 2001) with some species adapting their anatomy on a seasonal basis (McWilliams & Karasov 2001). This may therefore be to some extent reversible. If the digestive tract were to 'retool' itself in an attempt to adapt to different prey following a diet, an increase in SMR would be expected, however, this was not seen in our study. From this study it appears that any physiological adaptation is not immediately reversible as there was no evidence of this after 3 weeks (the duration of stage 2).

The decrease in growth after a change in diet that was observed in our study may have multiple causes. The decrease in growth may be caused by an increase in metabolic costs resulting in a drop in conversion efficiency of energy. However, SMR decreased making this an unlikely cause, thus a loss in conversion efficiency due to some form of maladaptation of the digestive tract to an alternative prey type is much more likely resulting in a reduction in growth. Reduced efficiency may be caused by the gut not being able to fully up-regulate to its maximum capacity due to a miss-match with the composition of the new diet. An alternative is that reduced anabolic metabolism caused by a decrease in growth resulting from less assimilated energy available. As a result of this down-regulation in growth, a decrease in SMR occurs caused by a reduction in available energy.

Factors that may affect energy assimilation may be underpinned by differences in the gross anatomy as a result of being fed different diets during critical developmental periods. Digestive organs have been shown to adjust their size depending on the type of prey being consumed. This can affect SMR because digestive organs have a high mass-specific SMR. Variation in SMR may also arise from differences in digestive chemicals and their quantities/ratios needed to break down prey as these will likely differ according to the prey type. If the digestive chemicals produced differ in their type and quantity so might the gland cells associated with their production. These can alter the molecular physiology caused by different diets thus contributing to variation in SMR (Burton *et al.* 2011).

Optimal foraging theory predicts significant advantages to individuals specializing in feeding on a small range of prey items but this is highly dependent on an ecological context. The optimal foraging model estimates a search time threshold which is defined by when it becomes beneficial to start foraging on an alternative prey item (Pyke, Pulliam & Charnov 1977; Pyke 1984). If there are unaccounted digestive or metabolic costs of specializing on a single prey type that reduce growth efficiency following a prey switch, then this maladaptation to novel prey has the potential to stabilize foraging specializations by increasing the search time threshold above which prey switching is beneficial during periods of low primary prey abundance thus significantly contributing to ecological speciation through novel niche expansion.

Logically, the physiological and growth costs of prey switching shown here should also decrease the fitness of intermediate phenotypes that display reduced foraging specialization. In addition to the individual fitness benefits, such resource specialisms may also have long-term evolutionary consequences by providing an additional mechanism that re-enforces the benefits of diet specialization that drives evolutionary divergence.

Current conceptual models of ecologically driven evolution have resource specialisms and in particular foraging specialisms as the first step of early divergence (Skúlason, Snorrason & Jónsson 1999; Parsons *et al.* 2014). Quantitative modelling has reinforced differential resource specialisms within species as the most important ecological variable enabling divergence in symaptry (Dieckmann & Doebeli 1999) and empirical studies have demonstrated how early stable foraging specialization may arise (Malmquist *et al.* 1992; Robinson 2000; Garduño-Paz & Adams 2010; Siwertsson *et al.* 2013). Despite this, the study presented here is one of the first to show that in addition to the morphological and behavioural optimal foraging advantages to individuals that specialize, there can also be significant physiological advantages in maintaining foraging specialization once they have become established. These physiological advantages can provide further stability in the adoption of foraging specialisms. Our study

elevates the physiological costs of diet specialization to the same level of significance in evolutionary divergence as phenotypic and behavioural foraging specilizations, supporting the importance of cryptic differentiation in digestive metabolism as an important dimension on the integrated phenotype.

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Data accessibility

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.v65m0 (Hooker, van Leeuwen & Adams 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Between diet (Stage 1) pairwise *post-hoc* differences from the GLMM in SMR (overall $P < 0{\cdot}0001$) and Growth (overall $P < 0{\cdot}0001$). Standard metabolic rate was compared as μmol h^{-1} g bodyweight (log). Growth was compared as per cent bodyweight gain per day (log).

Table S2. Results from GLMM comparing individual's SMR and growth during Stage 1 and following a switch in diet, Stage 2. SMR was compared as μmol h^{-1} g^{-1} bodyweight (log). Growth was compared as per cent bodyweight gain per day (log).

Table S3. Results from GLMM comparing individual's SMR and growth of fish from different initial diets being fed the same diet. SMR was compared as μmol $h^{-1}g^{-1}$ bodyweight (log), growth was compared as per cent bodyweight gain per day (log).