

If and when: intrinsic differences and environmental stressors influence migration in brown trout (*Salmo trutta*)

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Abstract Partial migration is a common phenomenon, yet the causes of individual differences in migratory propensity are not well understood. We examined factors that potentially influence timing of migration and migratory propensity in a wild population of juvenile brown trout (*Salmo trutta*) by combining experimental manipulations with passive integrated transponder telemetry. Individuals were subjected to one of six manipulations: three designed to mimic natural stressors (temperature increase, food deprivation, and chase by a simulated predator), an injection of exogenous cortisol designed to mimic an extreme physiological challenge, a sham injection, and a control group. By measuring length and mass of 923 individuals prior to manipulation and by monitoring tagged individuals as they left the stream months later, we assessed whether pre-existing differences influenced migratory tendency and timing of migration, and whether our manipulations affected growth, condition, and timing of migration. We found that pre-existing differences predicted migration, with smaller individuals and individuals in poor condition having a

higher propensity to migrate. Exogenous cortisol manipulation had the largest negative effect on growth and condition, and resulted in an earlier migration date. Additionally, low-growth individuals within the temperature and food deprivation treatments migrated earlier. By demonstrating that both pre-existing differences in organism state and additional stressors can affect whether and when individuals migrate, we highlight the importance of understanding individual differences in partial migration. These effects may carry over to influence migration success and affect the evolutionary dynamics of sub-populations experiencing different levels of stress, which is particularly relevant in a changing world.

Keywords Partial migration · Brown trout · Cortisol · Passive integrated transponder · Life-history strategy

Introduction

Partial migration, where some individuals in a population migrate and others remain resident, occurs in many taxa (Jonsson and Jonsson 1993; Chapman et al. 2011a), including insects (Roff and Fairbairn 2007), birds (Lundberg 1988), mammals (Avgar et al. 2013), and fish (Chapman et al. 2012a, b). Migratory phenotypes can arise as an evolutionary stable strategy when residents and migrants have equivalent fitness, or as a conditional strategy when migration is determined by individual asymmetries (Gross 1987; Chapman et al. 2011a). Obligate migration occurs when individuals adopt a fixed strategy, which may be genetically determined or due to canalization of a plastic trait (Terrill and Able 1988). In contrast, facultative migration is induced above a certain threshold linked to a developmental switch-point or an individual's current energetic state

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(Brodersen et al. 2008; Chapman et al. 2011b). In fish, most evidence suggests that environmental influences on individual growth and condition are primarily responsible for the induction of the migratory phenotype as well as timing of migration (e.g., Forseth et al. 1999; Acolas et al. 2012). However, observational studies of naturally occurring variation in growth and condition are confounded by correlated individual differences in the ability to both acquire and utilize food resources (Metcalf 1998). Few studies have manipulated environmental stimuli to see which proximate mechanisms affect growth and condition, and thus, migration strategy, and none have manipulated multiple variables simultaneously. It is important to understand the effects of proximate mechanisms at the individual level to be able to understand the effects of partial migration at the population level (Brodersen et al. 2008).

Vertebrates are subjected to many natural and anthropogenic stimuli (stressors) that activate the hypothalamic–pituitary–adrenal/interrenal axis and cause a stress response, which is accompanied by elevated plasma glucocorticoids (GCs; i.e., corticosterone or cortisol: Iwama 1998; Wingfield and Romero 2001; Barton 2002; Romero 2004; Baker et al. 2013). As a result of increased GCs, energy reserves are mobilized, elevating the metabolic rate and restricting the availability of energetic resources for growth and reproduction (Pankhurst and Van Der Kraak 1997; Redding et al. 1986; Fullerton et al. 2000). For example, in fish, exhaustive exercise (Gamperl et al. 1994; Eros and Milligan 1996; Donaldson et al. 2010; Madaro et al. 2016), food deprivation (Sumpter et al. 1991; Lendvai et al. 2014), and thermal challenges (Strange et al. 1977; Folke-dal et al. 2012) have all been shown to result in increased concentrations of the circulating GC cortisol. In the short-term, this response is intended to promote survival, but if sustained may reduce fitness (Wingfield and Romero 2001; Schreck 2010). There is a paucity of studies that assess how activation of the stress response may carry over (see Harrison et al. 2011; O'Connor et al. 2014) and affect subsequent life-history decisions (Crespi et al. 2013; Crossin et al. 2016).

Brown trout (*Salmo trutta*) are a freshwater salmonid species native to various regions of Europe. Although there is extensive life-history variation within and among populations of brown trout, in most areas juveniles hatch in freshwater tributaries in the spring and spend 1–3 years in their natal stream before either migrating to lakes or the sea, or staying and assuming residency (Cucherousset et al. 2005; Boel et al. 2014). The decision to migrate, in congeneric salmon, (*Salmo salar*) is made in late summer (Metcalf 1990; Metcalf and Thorpe 1992). The specific decision window for brown trout is not known, but is likely sometime in the fall (Midwood et al. 2014), and is strongly affected by individual condition (Cucherousset et al. 2005;

Olsson et al. 2006; Wysujack et al. 2009) though maternal effects or genetic factors may also play a role when individual differences interact with environmental factors (Paez et al. 2011; Van Leeuwen et al. 2016).

Several hypotheses regarding the causes of partial migration have been developed (reviewed in Chapman et al. 2011a), but most have been tested in the avian literature, and lack testing in other taxa to determine the generality of these ideas. To better understand the ecological factors that may promote the evolution of partial migration, we examined the carryover effects of three treatments designed to mimic natural environmental perturbations on growth and whether they affected migration in juvenile brown trout. To test the fasting endurance hypothesis (Ketterson and Nolan 1976; Boyle 2008; Jahn et al. 2010), we simulated scarce food conditions by reducing foraging opportunities. To test the predation vulnerability hypothesis (Skov et al. 2010), we chased the fish to simulate a sustained encounter with a predator. To test the thermal tolerance hypothesis (Ketterson and Nolan 1976), we increased the holding temperature of fish. In each case, we predicted that stressed individuals (food limited, chased, or thermally challenged) should have lower mass and condition, and migrate sooner and more often compared to controls. To compare with these natural stressors, we used an exogenous manipulation of cortisol and a sham treatment, a common approach to study the effects of stressors on wild fish (Sopinka et al. 2015; Crossin et al. 2016). We predicted that the experimental addition of high levels of cortisol would have greater effects compared to the other stressed treatments, and that these effects would be greater, than in sham or controls. We also utilized natural variation in growth and condition to assess whether our manipulations mimicked natural determinants of migration.

Methods

Study location

The Villestrup Stream is located in north-central Jutland, Denmark, running mainly through agricultural land before entering the Baltic Sea in the Mariager Fjord, and is fed by groundwater with a low annual discharge ($1.1 \text{ m}^3 \text{ s}^{-1}$; del Villar-Guerra et al. 2014). This stream contains a population of brown trout that includes both resident and migratory individuals, and juvenile brown trout generally migrate the spring following the year they hatch (i.e., <1 year of age) with migrants outnumbering residents by 4–30% (Midwood et al. 2015; Winter et al. 2016). The system has been the subject of extensive research over the past decade using uniquely coded passive integrated transponder (PIT) tags (see Gibbons and Andrews 2004) implanted in fish and a

stream-spanning fixed antenna array to study the behavior and survival of individual brown trout. A single PIT station (model TIRIS S-2000, Texas Instruments) consisting of two looped swim-through antennas spaced 10 m apart is present 400 m upstream from the mouth where it enters the fjord, allowing for detections of individuals leaving the stream (Zydlewski et al. 2006). Detection efficiency of the antennas [number of individuals detected at one antenna that were also caught in the trap (see below)] was 86.7%, almost identical to another study in the same river (86.5%; Winter et al. 2016).

Tagging and treatments

From October 21 to October 29, 2014, brown trout parr <21 cm (see Table 1 for sizes) were collected using backpack electrofishing (Scubla ELT 60 II GI; 300 volts). Fish were anesthetized in a 0.3 g l⁻¹ benzocaine solution, measured for total length (± 1 mm) and wet mass (± 0.1 g), and tagged using a 23 mm PIT tag (Texas Instruments, RI-TRP-RRHP, 134 Hz, 0.6 g mass in air, Plano, Texas, USA). On each day, a different section of the stream was electrofished, encompassing approximately 1.8 km total distance. The closest capture point to the PIT antenna was 7 km upstream. Each day, captured fish were haphazardly assigned to one of the six treatments: control, cortisol, sham, food deprivation, chase, and thermal challenge, and we attempted to ensure similar size distributions in each treatment. After treatments were applied, fish were allowed

to recover and were released on the same day of capture (except food deprivation; see below) and at the site of capture. See Table 1 for treatment sample sizes.

For the temperature treatment, we used two identical 80 l containers placed on top of each other, each with 25 l of fresh stream water and connected by two tubes for water exchange. The upper container contained the fish (in batches of 15) and an air stone, while the lower container had a heating element and a pump to circulate the water. The heating element was turned on for ten minutes before fish were introduced into the upper container. Water temperature was measured every 10 min. The temperature was held at 4.2 ± 0.05 °C above ambient temperature for 30 min by turning the heating element on or off, which likely elevates cortisol (Quigley and Hinch 2006). After 30 min, 15 liters of stream water were added to the heating container and the gravity return tube was removed so that the extra water from the top container flowed to the ground. Additional fresh river water was added to the heating chamber to replace the lost water, decreasing the water temperature. Fish were removed from the container when the temperature reached 0.5–1.0 °C above ambient temperature or after 20–30 min following the start of the cooling phase.

The chase treatment consisted of transferring a pair of fish into a donut-shaped container (approximately 1 m in diameter, with a 20 cm hole in the middle). Fish were then chased by hand for 3 min, which resulted in most fish no longer responding to external physical stimuli and likely elevates cortisol (O'Connor et al. 2009).

The food deprivation treatment used four 100 l containers with numerous holes (approximately 7.5 mm in diameter) to allow water to flow through. The container was placed in the stream with stones and rocks at the bottom. Fish (60 per container) were left in the container in the stream for 2 weeks. This procedure did not completely deprive fish of food as small invertebrates could enter the container through the holes, but it reduced foraging opportunities on larger invertebrates. Mass was again measured after fish had been in the containers for 2 weeks, and we found that the treatment did result in a loss of mass (paired *t* test, $t_{237} = -8.68$, $p < 0.0001$, average loss = 0.88 g) similar to a food deprivation study conducted in spring (Midwood et al. 2016). Another study where fish were recaptured after two weeks during the same time period showed that fish gained mass during this period (Birnie-Gauvin et al. in review), indicating this loss of mass was not just due to smoltification or general temporal trends.

Cortisol fish received an intracoelomic injection of a suspension of vegetable shortening (100% vegetable shortening, Crisco, OH, USA) and hydrocortisone 21-hemisuccinate (Sigma-Aldrich, St. Louis, MO, USA, Product #H2882-1G), using a dosage of 0.01 ml shortening

Table 1 Mean \pm SE initial and recapture length, mass, and condition factor for *Salmo trutta* in six treatments

Treatment	N	Length (cm)	Mass (g)	Condition factor
Initial capture				
Control	224	14.44 \pm 0.14	31.02 \pm 1.04	0.965 \pm 0.004
Thermal challenge	225	14.06 \pm 0.12	28.23 \pm 0.84	0.965 \pm 0.004
Chase	225	14.25 \pm 0.13	29.38 \pm 0.89	0.962 \pm 0.004
Food deprivation	243	14.10 \pm 0.11	28.35 \pm 0.76	0.968 \pm 0.004
Cortisol	231	14.03 \pm 0.14	28.14 \pm 0.91	0.955 \pm 0.004
Sham	224	14.31 \pm 0.13	29.72 \pm 0.89	0.958 \pm 0.004
Trap recapture				
Control	54	15.75 \pm 0.23	34.05 \pm 1.66	0.844 \pm 0.006
Thermal challenge	52	15.11 \pm 0.19	30.30 \pm 1.18	0.860 \pm 0.007
Chase	54	15.95 \pm 0.22	35.01 \pm 1.38	0.849 \pm 0.008
Food deprivation	54	15.55 \pm 0.19	32.20 \pm 1.13	0.842 \pm 0.006
Cortisol	5	16.31 \pm 0.85	36.16 \pm 4.65	0.823 \pm 0.031
Sham	46	15.45 \pm 0.26	32.49 \pm 1.52	0.860 \pm 0.009

There were no treatment effects for either initial or recaptured fish

per 1.0 g of fish. This resulted in a cortisol dosage of 100 mg kg⁻¹ of fish, which elevates baseline plasma cortisol in brown trout to supraphysiological levels (above 200 ng ml⁻¹) for at least 9 days (Birnie-Gauvin et al., in review). Thus, our cortisol treatment was designed to represent an extreme physiological challenge. Sham fish were injected with only vegetable shortening at the same dosage and controls were only PIT-tagged.

To evaluate size and growth, migrating fish were recaptured from March 18 to June 4, 2015 using a passive trap located approximately 20 m downstream of the PIT station. This technique does not allow us to evaluate survival, as the trap only captured fish that migrated downstream. Fish were measured and weighed as described above. We calculated specific growth rate (SGR) using the equation $(\log Y_2 - \log Y_1) / (t_2 - t_1) \times 100$, where Y_1 is the mass at the time of tagging (t_1) and Y_2 is the mass at the time of recapture (t_2). We calculated condition factor using the formula $K = (\text{mass}/\text{length}^3) \times 100$ (Ricker 1975).

Migration

We used detections from the PIT station to determine date of migration, as the PIT station operated continuously, and therefore, provided information on migration timing even when the trap was not operating. We defined fish as migrants if they were detected at the PIT station or caught in the trap.

Statistical analysis

We used ANOVAs to evaluate whether treatments initially differed in mass, length, or condition factor, and whether treatments affected daily growth rate. Mass and length were log transformed to achieve normality. As migration date could not be transformed to achieve normality, we used Spearman rank correlations to test whether date of migration was related to initial mass, initial condition, or specific growth rate. We used a Kruskal–Wallis H test to test whether the treatment affected migration date and used the Steel–Dwass method (the non-parametric equivalent to a Tukey HSD) to determine differences among treatments. We used logistic regression to determine whether initial mass or initial body condition affected migratory tendency. As there were different numbers of fish in each treatment, to determine treatment effects on migratory tendency, we used a Chi-square test to compare the number of fish that migrated past the PIT station relative to the total number of fish in each treatment. To visualize treatment effects on migratory timing, we plotted the Julian date that fish migrated past the PIT station by treatment using a Kaplan–Meier product-limit survival curve. All analyses were conducted using JMP v12.1.0 (SAS Institute).

Results

The initial length, mass, and condition factor did not differ among any treatments (ANOVA, all $p > 0.14$). Fewer cortisol fish were recaptured at the trap than any other treatment (χ^2 test, $p < 0.0001$; Table 1), resulting in imprecise estimates for growth in this treatment that should be interpreted with caution. In migratory individuals, food-deprived fish had lower growth rates than chased and thermally challenged fish though none differed from controls, while sham fish grew less than controls ($F_{5,259} = 9.16$, $p < 0.0001$; Fig. 1). Average growth rate for cortisol fish did not differ from any other treatment, though mean values were low and similar to sham (Fig. 1).

Trout were detected moving downstream from October 26 until June 15 (Fig. 2) and most fish (55%) passed the PIT station between March 26 and May 6, consistent with other studies showing some autumn migration with a peak in spring (Winter et al. 2016; Aarestrup et al. 2017). Fewer cortisol-treated fish (8%) successfully migrated than any other treatment (range 31–44%) (χ^2 test, $p < 0.0001$; Table 2). However, the cortisol fish that did migrate passed the PIT station sooner than any other treatment except food deprivation and thermal challenge, and was the only group that differed from controls ($\chi^2 = 18.62$, $p = 0.0023$; Table 2; Fig. 2). Note that most cortisol-treated fish migrated before the trap was operational (trap opened on Julian date = 144), resulting in more data on migration timing than for SGR in this treatment group. Individuals with an unknown fate (which either became residents or died) were initially different from migratory individuals: fish that were smaller upon initial capture were more likely

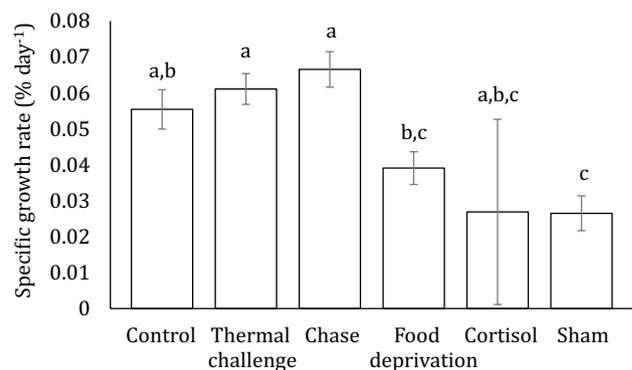


Fig. 1 Specific growth rate (% day⁻¹) of *Salmo trutta* in response to six treatments: control (no manipulation, $n = 52$); thermal challenge (held at 4.2 ± 0.05 °C above ambient for 30 min, $n = 54$); chase (hand chased for 3 min, $n = 54$); food deprivation (no access to large invertebrates for 2 weeks, $n = 54$); cortisol (injected with 100 mg kg⁻¹ solution of cortisol, $n = 5$); and sham (injected with vegetable shortening, $n = 46$). Values are mean \pm SE. Different letters indicate significant differences

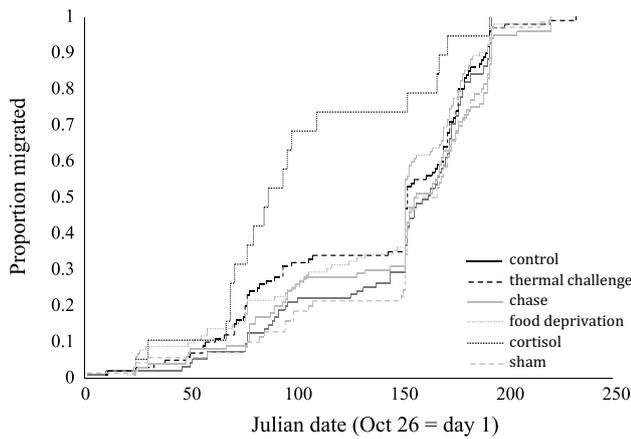


Fig. 2 Kaplan–Meier product-limit survival fit of Julian date (where Oct 26 = day 1) that brown trout (*Salmo trutta*) migrated in response to six treatments (see text for treatment details). Cortisol-treated fish migrated sooner than controls

to migrate than larger fish (logistic regression, $\chi^2 = 6.37$, $p = 0.012$; migrated = 27.3 g, unknown = 30.1 g); and fish initially in poor condition were also more likely to migrate than fish in better condition (logistic regression, $\chi^2 = 7.84$, $p = 0.005$; migrated = 0.956, unknown = 0.966).

Within treatments, migration timing was positively related to specific growth rate (SGR) for thermal stress and food deprivation (thermal stress: $r_s = 0.37$, $n = 52$, $p = 0.0062$; food deprivation: $r_s = 0.42$, $n = 54$, $p = 0.0018$; Fig. 3; all other $p > 0.50$).

Discussion

To better understand the ecological factors that may promote the evolution of partial migration in fish, we examined the consequences of natural variation and three treatments designed to mimic natural environmental perturbations on growth and migration. We found that both natural variation and environmental perturbations affected migration, along with our most severe physiological challenge,

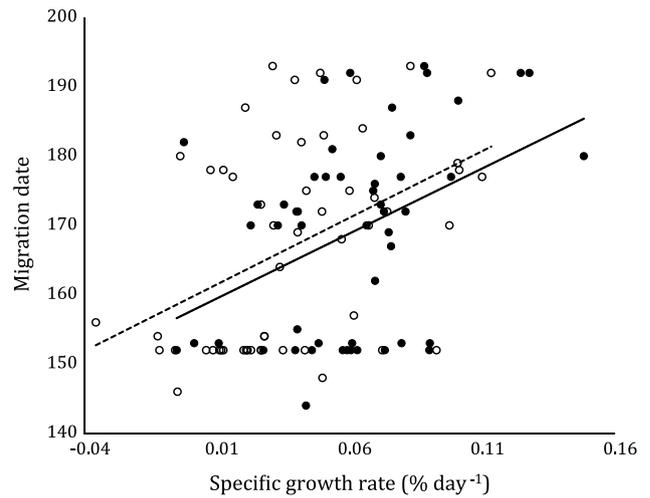


Fig. 3 Migration date (where Oct 26 = day 1) was positively related to specific growth rate (SGR) within thermal stress (*solid points, solid line*, $n = 52$) and food deprivation (*open points, dashed line*, $n = 54$) treatments

supraphysiological levels of cortisol. This increases the generality of two hypotheses (susceptibility to food deprivation and temperature stress) proposed to explain individual variation in migration rate. Our results support the hypothesis that migration in this system is at least a partly phenotypically plastic trait and is likely affected by a threshold state.

Pre-existing natural variation

Smaller, fast-growing individuals are expected to migrate due to higher metabolic rates, and therefore, should be more constrained by low food availability (Chapman et al. 2012b). However, empirical evidence for this pattern has been mixed. Compared to residents, migratory individuals have been found to be smaller (Morinville and Rasmussen 2003; Theriault and Dodson 2003; Skov et al. 2008, 2010) or larger (Bohlin et al. 1994; Olsson et al. 2006; Acolas et al. 2012), have lower body condition (Wysujack et al. 2009; Boel et al. 2014), and have higher (Olsson et al.

Table 2 Timing of migration (mean and median) for *Salmo trutta* detected at the PIT station after treatments were applied (where Oct 26 = day 1)

Treatment	Number passing PIT station	Mean date (\pm SE)	Median date (min, max)
Control	95 (42.4%)	147.0 \pm 4.7 ^a	163 (1, 193)
Thermal challenge	100 (44.4%)	136.8 \pm 5.3 ^{a,b}	153 (10, 233)
Chase	100 (44.4%)	145.8 \pm 5.1 ^a	156.5 (23, 221)
Food deprivation	102 (42.0%)	135.6 \pm 5.2 ^{a,b}	152 (20, 221)
Cortisol	19 (8.2%)	100.5 \pm 11.0 ^b	87 (24, 192)
Sham	70 (31.2%)	150.6 \pm 5.7 ^a	161.5 (1, 221)
All trout	486 (35.4%)	141.0 \pm 2.3	154 (1, 233)

Letters indicate significant differences for average passage date

2006; Kerr and Secor 2009; Acolas et al. 2012) or lower (Morinville and Rasmussen 2003) growth rates. In contrast, the patterns within migratory individuals are more consistent: early migrants are larger (Jonsson 1985; Metcalfe et al. 1990; Bohlin et al. 1996; Theriault and Dodson 2003; Paez et al. 2011), in better condition (Brodersen et al. 2014), and have higher growth rates (Metcalfe et al. 1990; Forseth et al. 1999; Theriault and Dodson 2003) compared to late migrants. We found that individuals that were smaller and in poor condition during the fall migrated, whereas low growth rate individuals under stress (temperature and food deprivation) migrated earlier. Some of these contrasting results across studies might be due to different processes acting on variation within migrating individuals compared to determining whether an individual becomes a migrant. For example, in systems where the smaller individuals migrate, are early migrants still larger than later migrants, or is that pattern only found when larger individuals are migratory? Future studies would benefit from separating hypotheses related to variation in timing of migration within a season (within-year variation), from ones related to whether migratory individuals undertake migration in one year versus the next year (between-year variation), and from those related to migration strategy (migratory versus resident).

As we did not attempt to recapture fish in the stream, we cannot know for sure whether fish that did not pass the PIT station died or assumed residency in the stream (Midwood et al. 2015). Thus, our results relating initial mass and condition to migratory phenotype may be confounded by differential mortality of residents versus migrants. However, in-stream survival is generally higher for larger than smaller individuals (Acolas et al. 2012) and many studies that did recapture individuals found similar patterns, where migratory individuals are smaller (Morinville and Rasmussen 2003; Theriault and Dodson 2003) and have lower body condition (Wysujack et al. 2009; Boel et al. 2014) than residents, supporting the interpretation that individuals that were larger and in better condition chose the residency strategy. Thus, despite not knowing what fraction of the rest of the population died overwinter or lived and assumed residency in the stream, we have evidence that migratory fish already differed from the rest of the population in the fall, which likely reflects current life-history decisions as the decision to migrate is thought to occur prior to this time (Metcalfe et al. 1990; Metcalfe and Thorpe 1992; Midwood et al. 2014).

Experimental manipulations

Food availability is commonly cited as the most important determinant of individual energetic state and thus migration (Nordeng 1983; Gross 1987; Tipping and Byrne 1996;

Brodersen et al. 2008; Wysujack et al. 2009) because it moves the environmental threshold and thus affects whether facultative migrants cross their internal threshold and express migratory behavior (Pulido 2011; Brodersen et al. 2014). For example, food deprivation caused earlier migration in red-spotted newts (*Notophthalmus viridescens*; Grayson and Wilbur 2009), and both hatchery brown trout and Atlantic salmon (*S. salar*) fed reduced rations migrated faster than those on normal rations (Lans et al. 2011). The fasting endurance hypothesis predicts that food deprivation should affect individuals differently: those with small body size and/or high growth rate should migrate sooner (Chapman et al. 2011a). Though we found no overall effect on absolute migration date in food deprived individuals compared to controls, another study depriving juvenile trout of food for the same duration in the spring did find that food deprivation resulted in both a later migration date and fewer migratory individuals (Midwood et al. 2016). Instead, we found that phenotypes were differentially affected within the treatment so that individuals with a lower daily growth rate migrated sooner, which is not consistent with the fasting endurance hypothesis. It may be that dominance hierarchies or aggression also contributed to the stress of this treatment due to the relatively high densities in the food deprivation containers, resulting in a more complex interaction. In our system, migratory individuals were already the smaller individuals in the population, and it appears that low growth rate individuals within the smaller size class crossed the decision threshold for migration earlier than fast-growers (Olsson et al. 2006; Pulido 2011).

The effects of temperature on migration are generally linked to body size and sensitivity to weather events (Chapman et al. 2011a). Similar to food deprivation, we found that temperature did not affect absolute migration date or overall growth rate but that among individuals exposed to the short-term thermal challenge, those with a lower daily growth rate migrated sooner. In other salmonids, individuals raised at high temperatures were physiologically prepared to become migrants earlier than those at lower temperatures (Handeland et al. 2004), indicating that long-term thermal challenges can change migration date. Models also suggest changes in life-history trajectories can occur with very small sustained increases in average temperature (Benjamin et al. 2013), though we did not evaluate that here. The changes observed in these studies were likely driven by the effects of long-term temperature elevation on metabolism and/or growth rate. Our thermal exposure was very short-term (4.2 °C above ambient for 30 min), which is likely why it did not have an overall effect on migration timing, yet it did have differential effects on timing among individuals. The effect on timing is probably due to individual variation in sensitivity to short-term stressful events, as our thermal challenge was unlikely to have long-term

effects on an individual's metabolism. In response to stream warming, trout start migrating (Otero et al. 2014), suggesting that even small temperature changes can have far-reaching implications on the ability of trout to successfully migrate (Jonsson and Jonsson 2009).

Predation vulnerability may be highly dependent on individual phenotype related to conspicuousness, morphology, or behavior (Chapman et al. 2011a). We did not measure those characteristics, which may explain why exposure to a simulated predation event did not affect migration and was not related to our physiological measure of growth. It is also possible that one bout of simulated attack did not represent a high enough predation risk to affect individuals. The risk of predation may also involve a trade-off with growth potential leading to more complex interactions (Skov et al. 2010). Future studies would benefit from more integrated studies of whole-animal trait interactions (Armbruster et al. 2014).

We found that physiological condition in the fall (mass and body condition) determined whether an individual migrated, but only the most extreme treatment (supraphysiological levels of cortisol), which resulted in the lowest specific growth rate, also caused an absolute earlier migration date, similar to previous studies of the effect of cortisol (Midwood et al. 2015). Though it is tempting to conclude that cortisol also inhibited the migratory phenotype, as fewer cortisol-treated fish migrated than controls, the effect of cortisol on migratory status may instead be due to high mortality of cortisol-treated fish (Pickering 1989; Midwood et al. 2014, 2015) regardless of strategy, or to specific mortality of migratory individuals that were moving downstream earlier (compared to control treatment) and thus were more exposed to predation than other fish that migrated later en masse (Aarestrup et al. 2002). Because we did not recapture individuals and cannot determine survival of cortisol-treated residents, we cannot conclude that the low number of cortisol-treated fish that migrated reflects a strategy switch. Thus, despite theoretical support (see Zera and Harshman 2001), a definitive demonstration that elevated cortisol mediates not only variation in migratory timing, but also dichotomous life-history choices, is still lacking.

The timing of stressful events has to coincide with the appropriate window where individuals are still plastic enough to make the decision to migrate. In fish, this decision is likely governed by an individual's assessment of their current state and future energetic trajectory, which can happen as long as 7–10 months before they could migrate to the sea (reviewed in Metcalfe 1998). These assessments may happen even earlier, as even a 1-week difference in the timing of fry emergence affected subsequent migratory strategy in Atlantic salmon (Metcalfe and Thorpe 1992).

We found that cortisol-treated fish had the lowest values for specific growth rate and migrated earlier than control fish. Combined with the growth rate-based effects for thermally challenged and food-deprived fish on migration date, this suggests that in migratory trout, an individual may continue to assess its state over a longer period of time and respond appropriately. However, the same cortisol treatment applied to juvenile brown trout in the spring resulted in similar decreases in mass, but no change in timing of migration (Midwood et al. 2014), suggesting the window affecting timing of migration does end before spring in this species. This strongly supports the hypothesis of condition-dependent migratory timing in trout, where the environment affects individuals and their timing of migration differently.

Conclusions

The factors that influence the decision to migrate are complex, and include morphology, physiology, and behavior (Chapman et al. 2011b). Our objective was to assess the effect of various natural and manipulated stressors on growth, condition, and migration. We found that pre-existing natural variation in physiological status (mass and condition) predicted migratory status in the fall, suggesting that individuals had already made the decision to migrate at that time. However, we also found that layering an additional fall stressor (cortisol, food deprivation, and thermal challenge) affected the timing of migration within the migratory phenotype, in contrast to a similar study where a spring stressor did not affect migratory timing (Midwood et al. 2014). This has important implications for three reasons: one, there may be two thresholds that affect migration—one related to the decision to migrate, which is made early, and one related to the timing of migration, which is flexible for much longer; two, the timing of stressful environmental perturbations is important for affecting migratory timing; and three, stressful events that make individuals change their timing of migration can change the life-history dynamics of a population. If these early migratory individuals are more susceptible to predation, experience sub-optimal sea temperatures or lower food availability, are less able to forage at sea or are more susceptible to other stressors (Heugens et al. 2001; Holmstrup et al. 2010; Thorstad et al. 2012), the population may experience a reduction in abundance with cascading carryover effects on ecosystem function (Theriault et al. 2008; O'Connor et al. 2014). These complex interactions provide us with the unique opportunity to evaluate the interaction of physiology, behavior, and life-history with ecological and evolutionary processes, particularly as individuals face a changing world (Wingfield 2008).

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Author contribution statement JDM, ADMW, KA, and SJC conceived and designed the experiments. JDM, MHL and ADMW performed the experiments. KSP and KB-G analyzed the data. KSP and KB-G wrote the manuscript; other authors provided editorial advice.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All applicable institutional and/or national guidelines for the care and use of animals were followed. Methods were approved by Carleton University (Protocol Number 315774) and the Danish Technical University (protocol number: 2013-15-2934-00808).

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