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Food and temperature stressors have opposing effects in determining flexible migration decisions in brown trout (*Salmo trutta*)

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Abstract

With rapid global change, organisms in natural systems are exposed to a multitude of stressors that likely co-occur, with uncertain impacts. We explored individual and cumulative effects of co-occurring environmental stressors on the striking, yet poorly understood, phenomenon of facultative migration. We reared offspring of a brown trout population that naturally demonstrates facultative anadromy (sea-migration), under different environmental stressor treatments and measured life-history responses in terms of migratory tactics and freshwater maturation rates. Juvenile fish were exposed to reduced food availability, temperatures elevated to 1.8 °C above natural conditions, or both treatments in combination over 18 months of experimental tank rearing. When considered in isolation, reduced food had negative effects on the size, mass and condition of fish across the experiment. We detected variable effects of warm temperatures (negative effects on size and mass, but positive effect on lipids). When combined with food restriction, temperature effects on these traits were less pronounced, implying antagonistic stressor effects on morphological traits. Stressors combined additively, but had opposing effects on life-history tactics: migration increased and maturation rates decreased under low food conditions, whereas the opposite occurred in the warm temperature treatment. Not all fish had expressed maturation or migration tactics by the end of the study, and the frequency of these "unassigned" fish was higher in food deprivation treatments, but lower in warm treatments. Fish showing migration tactics were smaller and in poorer condition than fish showing maturation tactics, but were similar in size to unassigned fish. We further detected effects of food restriction on hypo-osmoregulatory function of migrants that may influence the fitness benefits of the migratory tactic at sea. We also highlight that responses to multiple stressors may vary depending on the response considered. Collectively, our results indicate contrasting effects of environmental stressors on life-history trajectories in a facultatively migratory species.

Introduction

Against the backdrop of rapid global change, organisms are increasingly exposed to a variety of pressures stemming from anthropogenic activities (Sanderson *et al.* 2002). Temperature increases, habitat degradation, pollution, exploitation, and land use changes are examples of pressures, or "stressors", that contribute to recent patterns of population and biodiversity decline, and altered ecosystem functioning (Walther *et al.* 2002; Parmesan 2006). While much research has addressed the effects of individual stressors, in practice, stressors rarely occur in isolation, and it is imperative we also understand the combined effects of multiple stressors (Breitburg *et al.* 1998) in order to better forecast and manage species' responses to global change (Côté *et al.* 2016). This is not necessarily straightforward however, with co-occurring stressors – defined here as biotic or abiotic changes beyond the range typically experienced under natural conditions (Breitburg *et al.* 1999; Crain *et al.* 2008) – potentially acting additively, synergistically, or antagonistically (Folt *et al.* 1999; Crain *et al.* 2008).

Although a growing body of research is now expanding beyond single-stressor approaches, uncertainty still surrounds the net effects of co-occurring stressors, and empirical studies have provided mixed results. Meta-analyses suggest that synergistic effects dominate in the marine sphere (Crain *et al.* 2008; Harvey *et al.* 2013; Przeslawski *et al.* 2015), but antagonistic effects (Byrne and Przeslawski 2013) and additive effects (O'Gorman *et al.* 2012) have also been reported. In freshwater systems, which are particularly sensitive to multi-faceted change (Ormerod *et al.* 2010), antagonistic effects of multiple stressors are most prevalent (Jackson *et al.* 2016).

The effects of stressors may be highly context-specific. For example, increased temperature is a stressor likely to be experienced almost universally across natural systems, yet the impacts of warming at the individual level can range from positive to negative depending on whether optimum performance temperatures are exceeded (Huey and Stevenson 1979; Sinclair *et al.* 2016). Moreover, stressor effects can differ depending on the trait/response, or the level of organisation considered *e.g.* warming can increase individual metabolic and feeding rates, but may reduce survival, cause population/species extinctions (Petchey *et al.* 1999; Fussmann *et al.* 2014) or alter community stability due to long-term changes in species' interaction strengths (Rall *et al.* 2010). Predicting stressor effects at multiple levels is likely to be additionally challenging when more than one stressor is involved (Galic *et al.* 2018).

An understudied aspect of multiple stressors is how effects at the individual level shape life-history trajectories, which in turn may mediate how stressors scale up to influence higher-level (e.g. population, community, ecosystem) processes. One fundamental decision that many animals face, which is associated with a broad range of life-history and eco-evolutionary consequences, is whether to migrate or not. Facultative migration – the phenomenon whereby individuals retain the capacity to adopt either a migratory or a non-migratory life-style – is common across many animal taxa (Lack 1943; Swingland and Greenwood 1984; Lundberg 1987; Kaitala *et al.* 1993; Chapman *et al.* 2011), with well documented examples in birds (Berthold and Querner 1982; Lundberg 1988; Pulido *et al.* 1996; Newton 2008), ungulates (Ball *et al.* 2001; Cagnacci *et al.* 2011; Hebblewhite and Merrill 2011), zooplankton (Hansson and Hylander 2009), and fishes (Northcote and Ward 1985; Jonsson 1985; Chapman *et al.* 2012; Dodson *et al.* 2013). Environmental stresses such as limited food or inclement temperatures often appear to play a role in driving individuals to migrate (Chapman *et al.* 2012). Alternative migratory phenotypes have often been considered within the framework of the "environmentally-cued threshold model" (Tomkins and Hazel 2007; Piche *et al.* 2008; Pulido 2011; Buoro *et al.* 2012), in which tactic frequencies are controlled by the relationship between an environmentally-sensitive status trait (*e.g.* physiological condition or energy status) and an inherited threshold, assumed to be genetically variable. If the status trait exceeds the threshold, or "switch point", residency occurs; if not, migratory tactics are adopted. Environmental factors are likely to be important drivers of migratory tactics at both proximate and ultimate levels, yet few studies have addressed how facultatively migratory species respond to pressures arising from environmental change (Doswald *et al.* 2009), either in isolation, or when stressors act in combination.

Salmonine fishes (trouts, salmons, and charrs) represent an excellent group to study multiple stressor effects (McGinnity *et al.* 2009; de Eyto *et al.* 2016). In facilitating obligate freshwater spawning, salmonines display a suite of migratory phenotypes, encompassing residents that remain in natal streams their entire lives, individuals that migrate to larger rivers or lakes (potomodromy), and others still that undertake a marine migration before returning to fresh water to spawn (anadromy) (Klemetsen *et al.* 2003; Dodson *et al.* 2013; Ferguson *et al.* 2019; Nevoux *et al.* 2019). The migration *versus* residency decision represents a trade-off, where the benefits of migration (avoiding abiotic or biotic stresses in the natal stream, exploiting better food resources in the new environment, which translate into higher growth and thus higher fecundity or mating success) must be balanced against the costs (energetic demands of

migration, physiological stress of changing environments/habitats, a potentially increased risk of predation) (Kendall *et al.* 2014). Environmental conditions in natal fresh waters can interact with intrinsic physiological traits to determine alternative migratory tactics, *e.g.* if food resources cannot support growth or metabolism in early life, the resulting energetic deficit may promote migration. Food resources have been shown to directly (Davidsen *et al.* 2014; Jones *et al.* 2015; Archer *et al.* 2019) and indirectly influence migration (Olsson *et al.* 2006; Wysujack *et al.* 2009; O'Neal and Stanford 2011). Similarly, because temperature profoundly influences biological processes (Gillooly *et al.* 2001; Dell *et al.* 2011), temperature effects on physiological status traits/energetic balance likely make it an important environmental determinant of migratory decisions. Higher temperatures have been associated with increased anadromy *in lieu* of maturation in steelhead trout *Oncorhynchus mykiss* (Sloat and Reeves 2014), but under experimental conditions of constant food supply. Warming is likely to be accompanied by reductions in freshwater macroinvertebrate abundance (Durance and Ormerod 2007), with potentially synergistic effects if elevated metabolic demands induced by warming are compounded by low food availability.

Environmental stressors may also act to affect the performance of individuals once a migratory decision has been made. Although migration potentially confers many benefits on individuals, the ensuing costs mean that environmental conditions experienced prior to out-migration might further affect the future success of migrants, both during migration and in the subsequent environment (river, lake, or sea) (McCormick *et al.* 2009a). Sea-migration in particular requires substantial physiological remodelling for transitioning to salt water, and the changes in physiological regulation of ions, colouration, and body shape (collectively termed "smolting", (Tanguy *et al.* 1994)) necessitate an expensive investment by individuals that is likely to begin long before the migration is initiated, and hence may be affected by environmental stressors. Empirical evidence suggests that once the migratory decision is made, migrants divert resources towards accelerated growth (Metcalfe 1998). Smolt survival at sea is positively related to size (Ward and Slaney 1988) and, as such, favourable freshwater conditions may produce larger and more successful migrants, with associated fitness benefits altering the migration-residency trade off.

Here we present the results of an experimental laboratory study of physiology, migration and maturation of brown trout, using the F1 progeny of wild-caught parents from a population that exhibits facultative migration in nature. We aimed to explore if, and how, life-history decisions are shaped by individual and interactive effects of two putative extrinsic environmental

stressors. Specifically, we aimed to: (i) determine the effects of food restriction and elevated temperature on a range of physiological traits (size, mass, condition, lipids); (ii) assess the life-history consequences, in terms of migratory tactics and maturation decisions, of these stressors (both in isolation and combined); and (iii) explore how environmental stressors affect future migratory performance. We expected that food reduction and elevated temperature would each increase the prevalence of migratory tactics, with potentially synergistic effects when the stressors were combined. We also expected stressors to negatively affect future migratory capacity of anadromous individuals by reducing potential for fast growth (and thus reducing smolt viability), or by inhibiting osmoregulation in salt water.

Materials and Methods

Study population and fish rearing

Brown trout brood stock from a wild population were caught by seine-netting in November 2015 in Tawnyard Lough, an upland lake of 56 ha in the Erriff catchment (National Salmonid Index Catchment) in the west of Ireland (53° 37´ 0.00" N: 09° 40´ 17.10" W). Tawnyard Lough is fed primarily by the Glendavoch river, and a number of smaller tributaries (Figure S1). Brown trout primarily spawn within the Glendavoch River and move downstream as fry or parr to Tawnyard Lough, a distance of a few hundred metres to kilometres, depending on where spawning occurred. Tawnyard Lough produces a large run of out-migrating anadromous juveniles (smolts), with annual estimates of 500 to 3000 smolts enumerated at the outflow of the Lough over the last 30 years (Gargan *et al.* 2016). An unknown proportion of the population remain within the lake, and undergo several years of freshwater growth before returning to the natal stream to spawn. While the migration phenotypes of the brood stock could not be determined unambiguously in this study (because external signs of prior migration are not completely unambiguous in this system), we assumed that the frequencies of migratory/resident phenotypes among our brood stock were broadly representative of naturally occurring frequencies, given that brood stock were obtained haphazardly. Moreover, our goals in this study were not to test explicitly for inherited variation in migration tactics, but rather to explore proximate (environmental) drivers. The *caveat* must be kept in mind, however, that any environmental effects we document are contingent on the genotypic composition of our sample.

Each ripe female (n = 7) was stripped of eggs, which were then split into two batches, and each batch was fertilised by the milt of a single male (n = 10) (*i.e.* each female was mated to two

males, creating fourteen full-sib families). Due to constraints in obtaining brood stock and variation in the timing of when females were ripe to be stripped, eggs were fertilised on three occasions in November and December 2015 (see Table S1 fertilisation/ brood stock crossing details). Fertilised eggs from each crossing were incubated separately in standard Heath trays in the nearby Burrishoole hatchery. Prior to exogenous feeding, fry from the late November/early December fertilisations (hereafter "Nov-Dec fertilisation group") were transferred to a rearing facility at University College Cork (Aquaculture and Fisheries Development Centre). Here, families were mixed, and fry were held in a 100 L growth tank on a recirculating aquaculture system (RAS), maintained by a conditioning unit at a seasonally varying temperature regime approximating that of the catchment from which the brood stock were obtained (i.e. the annual cycle in mean weekly temperatures in the nearby Burrishoole catchment for the preceding three years, see Figure S2. Due to initial logistical constraints in achieving low temperatures, temperatures in winter 2015 were higher than the mean ambient temperatures (Figure S2). Fry were fed *ad libitum* with commercially available trout pellets (Skretting Ltd., Norway) to facilitate their transition to exogenous feeding (by June 2016), and were then fed *ad libitum* until the experimental phase began. Fish experienced a constant photoperiod (12:12 hours of light: dark) during this initial rearing phase. Due to logistical constraints, an additional group of fry from the first fertilisation event (termed "Nov fertilisation group") was maintained at a natural temperature regime in a flow-through tank at the Burrishoole hatchery facility, where they transitioned to exogenous feeding via *ad libitum* feeding with the same trout pellets. Fry from the Nov group were transported to the UCC rearing facility in May 2016, and reared in a 100 L tank, in the same RAS and under the same conditions as the Nov-Dec fertilisation group. Due to size differences (Nov group fish were larger than Nov-Dec group fish by the beginning of the experiment) the two fertilisation groups were reared in separate tanks for the duration of the study to prevent emergence of feeding hierarchies.

Experimental treatments

The study and all associated procedures were carried out with ethical approval from Health Products Regulatory Authority (HPRA) Ireland, under HPRA project license AE19130/P034, and individual licenses AE19130/1087, AE19130/I200, AE19130/I201 and AE19130/I202). The experimental phase ran for an 18-month period from December 2016 to June 2018 with all fish humanely euthanized at the end of the experiment.

Juvenile brown trout were randomly allocated across eight 520L tanks at the end of November 2016 (initial n = 140 per tank for Nov-Dec group, and n = 35 per tank (filled to 203L) for Nov group), each assigned one of two temperature treatments and one of two food treatments. Water flowed continually through tanks to prevent the build-up of waste, returned to a central sump via mechanical filtration, and was treated with protein skimming, biofiltration and UV skimming. Weekly monitoring of water quality indicated that levels of pH, nitrate, nitrite, and ammonia were well within acceptable ranges for fish health. Mortality during the experimental phase was minimal (4%). To avoid compromising water quality with excessive biomass, fish were culled haphazardly (n = 229 in total across all treatments) over the two years of tank rearing, with equal densities in terms of fish numbers (fish per L) maintained across treatment groups and equal biomass densities (g per L) maintained between fertilisation groups. Fish culled in this manner were not included in the analyses.

To explore the individual and interactive effects of food restriction and temperature in determining migratory tactics, food and temperature treatments were applied in isolation and in combination for both fertilisation groups for the duration of the experimental phase. The two food treatments were: (i) high food treatment*:* fish fed recommended daily rations for optimal growth calculated as a percentage of their body mass and adjusted for seasonally-changing temperatures (Skretting Ltd., Norway); and (ii) low food treatment: fish fed 25% of optimal daily rations. A value of 25% of optimal daily rations was chosen for the low food treatment because similar restrictions have previously been shown to reduce the frequency of residency in adfluvial brown trout (Wysujack *et al.* 2009). The two temperature regimes were achieved by passing water through one of two conditioning units that maintained two temperature treatments as follows : (i) cool temperature treatment: temperatures matching the natural, seasonally-varying, temperature regime for the Erriff catchment; and (ii) warm temperature treatment: temperatures elevated by 1.8 °C ± 0.55 (SD) above the cool temperature treatment. The cool treatment ranged from 5.9 - 16.4 °C (mean temperature = 10.9 °C ± 3.2 SD) and the warm treatment ranged from 7.5 - 18.2 °C (mean temperature = 12.7 °C ± 3.2 SD). An increase of 1.8 °C for the warm temperature treatment was chosen because this is in line with increases of 1 - 3 °C projected to occur under climate change scenarios (IPCC 2014). While both treatments remained within sub-lethal ranges for brown trout (Forseth *et al.* 2009; Jonsson and Jonsson 2009), the warm temperature treatment was considered "stressful" because the maximum temperatures in the warm treatment approached upper thermal growth limits for brown trout (18.7 °C). Optimal temperatures for growth have been estimated to be between

13.1 – 13.9 °C (Elliott and Hurley 2000; Hari *et al.* 2006; Elliott and Elliott 2010; Kovach *et al.* 2016). Temperatures in the warm treatment remained above this for twice as long as those in the cool treatment, which remained closer to optimal growth conditions. Food rations were reduced over four weeks and temperature was increased by 0.5 ºC per week to minimise stress. Food was dispensed to each tank *via* automatic feeders (Arvo-Tec Oy, Huutokoski, Finland) during daylight hours. Feeders delivered regular pulses of food, with the frequency of pulses adjusted according to food treatment (i.e. fewer pulses for low food treatments). Within each treatment, absolute rations were adjusted on a monthly basis to account for changes in body mass and temperature.

Data collection and life-history determination

Within each food and temperature treatment combination, 25 – 30 fish from each fertilisation group were lightly anaesthised with MS-222 and marked with unique colour combinations of visible implant elastomer (VIE) tags (Northwest Marine Technology Ltd., Washington, USA), allowing for re-identification of individuals. Fork length and mass were measured at key periods throughout the study [Late-November in 2016 (prior to initiation of treatments), February, April, June, July, September, December in 2017, and April in 2018].

All fish were checked weekly for morphological indicators of smolting from March to June in each of 2017 and 2018, the period corresponding to the natural migratory period in the wild for this population (Gargan *et al.* 2016). Wild smolts typically migrate out of the Erriff system aged between 1+ and 4+, with the large majority doing so aged 2+ or 3+ (approximately equal numbers of each) (Gargan *et al.* 2016). Smolting is a precursor to downstream migration in several salmonines, and comprises a number of morphological, behavioural and physiological changes. We used the following morphological indicators to assess smolting [following Tanguy *et al.* 1994)]: silvering/loss of parr marks; pronounced lateral line (*i.e.* clearly visible and raised to the touch); transparent fins; and fusiform shape (pointed snout, slimmer body, and elongated caudal peduncle) (Riddell and Leggett 1981; Hard *et al.* 1999; Villar-Guerra *et al.* 2019). Fish that clearly matched three of these criteria were classed as smolts. In spring 2017, no fish matched the morphological criteria for smolts. In spring 2018, fish that matched the morphological criteria for smolts were transferred to salt water at 30 ppt for 24 hours to assess hypo-osmoregulatory function. Seawater "challenges" are used as an indicator of anadromy capacity, where the ability to regulate ion concentrations (*e.g.* to maintain plasma chloride concentration) in sea water is a measure of saltwater tolerance, or physiological

"readiness" of smolts for seawater entry (Clarke 1982; McCormick *et al.* 1998; Schultz and McCormick 2012; McCormick 2012). Fish were monitored during this period to ensure that any fish showing signs of failing the challenge (loss of equilibrium) could be removed and euthanised (though no fish showed signs of failure in our study). After the 24 hour seawater challenge, fish were euthanised with an overdose of MS-222. The mass and fork length of each individual was recorded, and a blood sample was obtained from the caudal vasculature using a 21 gauge needle and a 2.6ml heparinised syringe. Blood samples were centrifuged at 8000 rpm for 3 minutes, and the plasma aliquot was siphoned off, stored at -80 °C and later measured for plasma chloride concentration as an indicator of osmoregulatory performance. Four to six gill filaments were placed in 100µl of ice-cold SEI buffer (150 mmol l^{-1} sucrose, 10 mmol l^{-1} EDTA, 50 mmol l^{-1} imidazole, pH 7.3) and frozen at -80 °C for later measurement of gill Na^+/K^+-ATPase (NKA) activity.

All fish (classed morphologically as smolts or non-smolts) were dissected in spring 2018 to visually determine sex and maturation status based on gonad development. Mature males had enlarged white testes or running milt. Maturing males had visible or moderately enlarged testes but no running milt. Mature females had visible eggs in the body cavity. Immature fish (unconfirmed sex at the time of sampling) were later genotyped to determine genotypic sex using a microsatellite sex marker. The natural spawning period for the wild population-of-origin is in late autumn/early winter, and the migratory period is in the spring (Gargan *et al.* 2016). Since freshwater maturation generally precludes migration in brown trout (Jonsson 1985; Dellefors and Faremo 1988; Dębowski and Dobosz 2016) any fish showing signs of maturing without having migrated to sea are considered to be on a non-anadromous trajectory, while smolts which undertake marine migrations are immature. We thus classed fish as smolts (migratory tactic) if they matched the morphological criteria for smolts and were immature. Fish were classed as mature (residency tactic) if they showed signs of maturation at the time of sampling. Fish that were immature and did not match the morphological criteria for smolts had an unknown life history at the time of sampling and were classed as "unassigned". Whole body lipid content (%) was measured for all smolts and a random sample of mature (n = 107) and unassigned (n =19) fish using a CEM Smart trac5 system of integrated heating and nuclear resonance (CEM Corporation, Matthews, NC, USA) on individual homogenised fish samples (Toussaint *et al.* 2002; Keeton *et al.* 2003; Nielsen *et al.* 2005). Plasma chloride concentration was measured by coulometric titration using a Jenway PCLM3 chloride meter (FishVet Group, Oranmore, Ireland) for all smolts and a random sample of non-smolts (n = 107 mature fish and

n = 18 unassigned fish). Gill NKA activity was measured following McCormick *et al.* (2009) for a random sample of smolts and non-smolts (n = 25 smolts, n = 135 mature fish and n = 22 unassigned fish).

Statistical analysis

To test if food and temperature acted as stressors at the level of individual traits underpinning migration (Aim 1), we explored factors affecting fork length, mass and condition of fish across the study period within a mixed effects modelling framework (*nlme* package (Pinheiro *et al.* 2019)). We calculated condition factor as:

$$Condition\ factor\ = \frac{mass\ (g)}{fork\ length\ (cm)^{b}} \times 100$$

Where *b* is the slope estimated from the linear relationship between log (mass) and log(fork length) (Bolger and Connolly 1989). The mixed effects models included time (continuous variable representing weeks since start of experiment), a quadratic term for time (to account for non-linearity of traits through time), food treatment, temperature treatment, fertilisation group, and sex as fixed effects, and individual identity as a random effect to account for multiple measurements on some individuals. We included an interaction between food treatment and temperature treatment (to test for synergistic or antagonistic effects of food and temperature), and a three-way interaction (food treatment × temperature treatment × time) to test whether trajectories diverged through time according to treatment combination. To compare single stressor effects with combined stressor effects, we carried out pairwise comparisons across all levels of the food × temperature interaction using Tukey post-hoc tests (*emmeans* package (Lenth 2019)).

To test whether trait trajectories were similar in mature fish and smolts, we created additional mixed effects models with time, a quadratic term for time, migratory tactics (categorical variable, two levels: smolt/mature), sex, and fertilisation group as fixed effects, an interaction between time and migratory tactics, and a random effect of individual identity. We excluded unassigned fish in this comparison of "status" traits, as we could not determine their life-history trajectory *i.e*. some of the unassigned fish may have been on a migratory trajectory, but were deferring actual migration until a later age. For all of the above models, temporal autocorrelation of the response variable was accounted for by modelling an autoregressive error structure as a first order lag function of time. Separate models were constructed for z-

standardised measures of length, mass and condition, and normal errors were assumed in each case.

We similarly used mixed effects models (normal errors) to explore factors influencing variation in final measurements of traits (z-standardised length, condition, and whole body lipids) at the end of the study. We included food treatment, temperature treatment, fertilisation group, sex, and an interaction between food treatment and temperature treatment as fixed effects, and date of terminal sample (categorical variable with 8 sampling dates) as a random effect. Additional mixed effects models tested for differences in final measurements of status traits according to migratory tactics (migratory tactic, sex and fertilisation group included as fixed effects, and terminal sample date as a random effect).

To test if food and temperature treatments affected life-history tactics (Aim 2), we built three generalized linear models (GLMs) with a logit-link function and binary life-history response variables. One GLM predicted smolt status (binary response: 1 = smolt, 0 = non-smolt), a second GLM predicted maturation (binary response: 1 = mature, 0 = immature), and a third GLM tested for differences in expression of any life-history tactics by the end of the study (*i.e.* by age 2+, second year of life) (binary response: 1 = unassigned, 0 = smolt or mature). All GLMs included the categorical variables: food treatment, temperature treatment, sex, fertilisation group, and an interaction between food and temperature treatments.

To explore variation in osmoregulatory performance, we first tested for differences in gill NKA activity (log transformed) and plasma chloride concentration between smolts and non-smolts using mixed effects models (normal errors). Each model included life-history tactic, fertilisation group, and sex as fixed effects, and terminal sampling date as a random effect. We retained the "unassigned" life-history class in these analyses to determine if unassigned fish showed signs of hypo-osmoregulatory capacity in salt water relative to mature fish, suggesting that these unassigned fish were in fact on a smolting trajectory but were yet to express morphological indicators of smolting. Post-hoc pairwise comparisons between life-history tactics were carried out using the *emmeans* package (Lenth 2019).

We explored the mechanisms underpinning osmoregulatory capacity by fitting a GLM (normal errors) to gill NKA activity as a function of size-corrected plasma chloride concentration in smolts and non-smolts. Because hypo-osmoregulatory capacity generally increases with size in brown trout (Finstad and Ugedal 1998), we corrected for size in this analysis by using the residuals of the linear relationship between plasma chloride and fork length. Finally, we

assessed how food and temperature treatments influenced osmoregulatory capacity of smolts (Aim 3) using mixed effects models. Separate models (normal errors) were constructed for z-standardised gill NKA activity and plasma chloride concentration, with food treatment, temperature treatment, sex, fertilisation group, fork length (a covariate to correct for body size effects), and a food × temperature interaction included as fixed effects, and terminal sample date as a random effect.

Marginal R^2 values for mixed effect models were calculated using the *MuMIn* package in R (Barton 2019). We used likelihood ratio tests (LRT) to assess statistical significance of predictor variables for all models at a 5% alpha level, and non-significant interaction terms were excluded to interpret main effects. Analysis was carried out in R version 3.5.3 (R Core Team 2019), and all models were checked against assumptions of the given model (independence, non-normality of residuals, heteroscedasticity and multicollinearity).

Results

At the termination of the experiment, 349 fish were assigned a life-history tactic (30 smolts and 319 mature fish) and 76 fish were classed as "unassigned" (Table 1). The frequency of smolting varied by food and temperature treatments. Overall, the proportion of smolts (averaged across Nov and Nov-Dec fertilisation groups) was highest in the low food–cool temperature treatment (18.9 %), with the lowest proportion in the high food–warm temperature treatment (0.9 %), and intermediate proportions in low food–warm temperature (4.6 %) and high food–cool temperature treatments (3.8 %). The highest proportion of mature fish was in the high food–warm temperature treatment (92.5 %), followed by similar proportions in high food–cool temperature (75.2 %) and low food–warm temperature treatments (75.0 %). Maturation was lowest in the low food-cool temperature treatment (57.6 %).

Morphological trait trajectories

Physiological trait trajectories diverged through time in response to food treatment, temperature treatment, and fertilisation group (Figure 1A, Table 2). The models for length (marginal $R^2 = 0.68$) and condition factor (marginal $R^2 = 0.33$) retained significant interactions between food treatment and temperature treatment, food treatment and time, and temperature treatment and time (Table 2). The model for mass (marginal $R^2 = 0.61$) retained a significant time × food × temperature interaction (Table 2). Fertilisation group had a significant effect on length ($\chi^2 = 57.17$, df = 1, $p < 0.001$), mass ($\chi^2 = 24.49$, df = 1, $p < 0.001$), and condition factor ($\chi^2 = 8.73$, df = 1, $p = 0.003$), with fish in the Nov fertilisation group tending to be larger and

heavier than those in the Nov-Dec group, and in marginally lower condition. There was no significant effect of sex on length (χ^2 = 0.73, df = 1, p = 0.394), mass (χ^2 = 2.01, df = 1, p = 0.156) or condition factor (χ^2 = 0.29, df = 1, p = 0.591) across the study. When food and temperature stressors were experienced in isolation (*i.e.* a single treatment applied) fish receiving the low food treatment were smaller (post hoc comparison of low food–cool temperature *versus* high food-cool temperature treatment: t-value = 12.06, $p < 0.001$), lighter (t-value = 13.26, $p < 0.001$) and in poorer condition (t-value = 10.74, $p < 0.001$). Fish in the warm temperature treatment were also smaller (warm temperature-high food *versus* cool temperature-high food treatment: t-value = 3.23, p = 0.007), lighter (t-value = 3.66, p = 0.002), but in similar condition (t-value = 1.41, p = 0.495) (Figure 2A,B,C). The positive interaction term between food treatment and temperature treatment indicated that effects of combined stressor treatments on length, mass, and *K* were less than we might expect based off their effects in isolation.

Fish also varied in length (marginal R^2 = 0.55), mass (marginal R^2 = 0.36) and condition factor (marginal R^2 = 0.16) trajectories according to migratory tactics, with smolts tending to be smaller than mature fish across the duration of the study period (χ^2 = 15.55, df = 1, $p < 0.001$). The significant interaction between migratory tactics and time for mass and condition factor (Figure 1B, Table 3) indicated smolts gained less mass, with lower condition trajectories (Figure 2D,E,F).

Morphological traits at the end of the study

At the end of the experiment, fish varied in length, condition and whole body lipids depending on food treatment, temperature treatment, life-history tactics and fertilisation group (Figure 3A, B). The models describing final length (marginal R^2 = 0.48) and condition (marginal R^2 = 0.38) each retained a significant interaction between food treatment and temperature treatment but the model describing whole body lipids (marginal R^2 = 0.41) did not (Table 4). We detected significant negative main effects of food treatment (χ^2 = 63.44, df = 1, $p < 0.001$) but positive effects of temperature treatment (χ^2 = 3.91, df = 1, p = 0.048) on lipid levels (Figure 3A). The significant positive interaction term (Figure 3A) indicated an antagonistic effect of food and temperature treatments on length and condition (Figure 3C, D, and E). Fertilisation group significantly affected length (χ^2 = 4.56, df = 1, p = 0.033) and condition (χ^2 = 5.15, df = 1, p = 0.023). Fish in the Nov fertilisation group tended to be larger but in poorer condition, with similar lipid levels (χ^2 = 0.02, df = 1, p = 0.880) to those in the Nov-Dec group. There was no

significant effect of sex on length (χ^2 = 0.14 df = 1, p = 0.712), condition (χ^2 = 2.60, df = 1, p = 0.107) or lipids (χ^2 = 1.91, df = 1, p = 0.167).

Life-history tactics significantly affected length (χ^2 = 4.80, df = 1, p = 0.036), condition (χ^2 = 19.62, df = 1, p < 0.001) and lipids (χ^2 = 13.87, df = 1, p = 0.002). Overall, smolts were smaller than mature fish, with lower condition values, and higher lipid levels (Figure 3B, C, D, E). Smolts and unassigned fish were similarly sized (χ^2 = 0.35, df = 1, p = 0.554), with similar lipid levels (χ^2 = 1.49, df = 1, p = 0.222), though smolts had lower condition values (χ^2 = 07.48, df = 1, p = 0.006) (Figure S3).

Migratory tactics

The model describing the probability of smolting had significant effects of food treatment (χ^2 = 16.50, df = 1, p < 0.001), temperature treatment (χ^2 = 14.08, df = 1, p < 0.001), fertilisation group (χ^2 = 7.09, df = 1, p = 0.008) and sex (χ^2 = 4.34, df = 1, p = 0.037). The interaction between food treatment and temperature treatment was not significant (LRT for model with and without interaction term: χ^2 = 0.02, df = 1, p = 0.882). Food restriction increased the probability of smolting whereas the warm temperature treatment decreased the probability of smolting (Figure 4A, B). Males were less likely to smolt than females, and fish in the Nov fertilisation group were less likely to smolt than those in the Nov-Dec group (Figure 4A, B).

The model describing the probability of maturing also had significant effects of food treatment (χ^2 = 19.13, df = 1, p < 0.001), temperature treatment (χ^2 = 17.49, df = 1, p < 0.001), sex (χ^2 = 15.90, df = 1, p < 0.001), but the effect of fertilisation group was not significant (χ^2 = 1.04, df = 1, p = 0.308). The interaction between food treatment and temperature treatment was not significant (LRT for model with and without interaction term: χ^2 = 0.99, df = 1, p = 0.319). In contrast to effects on smolting, the high food treatment increased the probability of maturing, as did the warm temperature treatment (Figure 4C, D). Males were less likely to mature than females in all treatments (Figure 4C, D).

The model describing the probability of being unassigned a life-history tactic included significant effects of food treatment (χ^2 = 5.62, df = 1, p = 0.018), temperature treatment (χ^2 = 4.91, df = 1, p = 0.027), sex (χ^2 = 34.05, df = 1, p < 0.001) and fertilisation group (χ^2 = 7.69 df = 1, p = 0.006). The interaction between food treatment and temperature treatment was not significant (LRT for model with and without interaction term: χ^2 = 3.31, df = 1, p = 0.069). Fish were significantly more likely to be unassigned a life history in either the low food or cool temperature treatments, as were males, and fish from the Nov fertilisation group (Table 5).

Osmoregulatory performance

Gill NKA activity varied according to life history (χ^2 = 56.74, df = 2, p < 0.001), but was not affected by sex (χ^2 = 1.28., df = 1, p = 0.258) or fertilisation group (χ^2 = 0.72, df = 1, p = 0.397). Post hoc testing showed smolts had significantly higher NKA activity than mature fish (t = -7.41, df = 172, p < 0.001) and unassigned fish (t = 5.15, df = 172, p < 0.001; Figure 5A). Similarly, plasma chloride concentration was significantly affected by life history (χ^2 = 52.14, df = 2, p < 0.001), with no significant effect of sex (χ^2 = 2.75, df = 1, p = 0.097) or fertilisation group (χ^2 = 2.03, df = 1, p = 0.154). Smolts had significantly lower plasma chloride concentration after saltwater exposure than mature fish (t = 5.56, df = 144, p < 0.001) and unassigned fish (t = -6.77, df = 144, p < 0.001; see Figure 5B). Size-corrected plasma chloride concentration decreased significantly with gill NKA activity in smolts (χ^2 = 14.18, df = 1, p < 0.001, Figure 5C), however there was no significant relationship between size-corrected plasma chloride concentration and gill NKA activity in non-smolts (χ^2 = 1.79, df = 1, p = 0.180, Figure 5D).

After accounting for the significant effect of body size (χ^2 = 5.97, df = 1, p = 0.015), the model describing plasma chloride concentration in smolts (marginal R^2 = 0.49) did not retain a significant food × temperature treatment interaction (LRT: χ^2 = 0.26, df = 1, p = 0.610). We detected a significant main effect of food treatment on plasma chloride concentration (χ^2 = 5.29, df = 1, p = 0.021), where the high food treatment was associated with lower chloride values (Figure 6A, B). There was no significant effect of temperature treatment (χ^2 = 2.26, df = 1, p = 0.133), sex (χ^2 = 1.60, df = 1, p = 0.205) or fertilisation group (χ^2 = 2.77, df = 1, p = 0.096) on chloride concentrations. Mixed model analysis indicated non-significant effects of fork length (χ^2 = 0.06, df = 1, p = 0.814), food treatment (χ^2 = 0.03, df = 1, p = 0.862), temperature treatment (χ^2 = 0.85, df = 1, p = 0.358), sex (χ^2 = 2.47, df = 1, p = 0.116) and fertilisation group (χ^2 = 3.53, df = 1, p = 0.060) on gill NKA activity in smolts (marginal R^2 = 0.20, Figure 6A). Overall, this indicates positive direct effects food treatment (independent of size) on saltwater tolerance of smolts, which were not reflected in gill NKA activity. See Tables S6 and S7 for parameter estimates from the mixed effect models.

Table 1: Percentage of brown trout (n = 425), F1 offspring of wild trout, classed as smolts (i.e. migratory tactic) or non-smolts (mature or unassigned) after two years of experimental tank-rearing. Offspring were derived from brood stock gametes fertilised in November and December 2015 (coded here as early November = "Nov" and late November/early December = "Nov-Dec"). Values correspond to percentages for each category (broken down by sex) of the total number of fish per tank (where each tank corresponds to a given food treatment by temperature regime combination, i.e. a single row in the table). Sample size (n) given in brackets after the %.

Food	**Temperature**	**Fertilisation**	**% Smolts (n)**		**% Mature (n)**		**% Unassigned (n)**	
		Group	*Female*	*Male*	*Female*	*Male*	*Female*	*Male*
Low	Cool	Nov	6.1 (2)	3.0 (1)	48.5 (16)	6.1 (2)	6.1 (2)	30.3 (10)
Low	Cool	Nov-Dec	15.1 (11)	8.2 (6)	19.2 (14)	39.7 (29)	8.2 (6)	9.6 (7)
Low	Warm	Nov	0 (0)	0 (0)	51.5 (17)	36.4 (12)	3.0 (1)	9.9 (3)
Low	Warm	Nov-Dec	2.7 (2)	4.0 (3)	41.3 (31)	28.0 (21)	2.7 (2)	21.3 (16)
High	Cool	Nov	2.9 (1)	0 (0)	32.4 (11)	32.4 (11)	5.9 (2)	26.5 (9)
High	Cool	Nov-Dec	2.8 (2)	1.4 (1)	43.7 (31)	36.6 (26)	2.8 (2)	12.7 (9)
High	Warm	Nov	0 (0)	0 (0)	61.8 (21)	23.5 (8)	2.9 (1)	11.8 (4)
High	Warm	Nov-Dec	1.4 (1)	0 (0)	48.6 (35)	47.2 (34)	0 (0)	2.8 (2)

Table 2: Results of the mixed effect model analysis for length, mass and condition trajectories of brown trout exposed to food and temperature stressors. The results of the model selection procedure on interaction terms are given, and the selected model for each response is highlighted in bold. The models included a random effect of individual identity and a first-order autoregressive correlation structure with respect to time (weeks of experimental treatment) was also modelled.

Model	**df**	**AIC**	**logLik**	***L*-ratio**	***p*-value**
Length ~ time*food*temperature + time^2 + fertilisation + sex	14	1222.8	-597.4		
Length ~ time*food + time*temperature + time^2 + food*temperature + fertilisation + sex	13	1222.5	-598.3	1.8	0.186
Length ~ time*food + time^2 + food*temperature + fertilisation + sex	12	1229.7	-602.8	9.1	0.003
Length ~ time*temperature + time^2 +food*temperature + time^2 + fertilisation + sex	12	1422.2	-699.1	201.6	< 0.001
Length ~ time*food + time*temperature + time^2 + fertilisation + sex	12	1236.1	-606.1	15.6	< 0.001
Mass ~ time*food*temperature + time^2 + fertilisation + sex	14	1667.1	-819.6		
Mass ~ time*food + time*temperature + time^2 + food*temperature + fertilisation + sex	13	1672.6	-823.3	7.5	0.006
Condition ~ time*food*temperature + time^2 + fertilisation + sex	14	3023.4	-1497.7		
Condition **~ time*food + time*temperature + time^2 + food*temperature + fertilisation + sex**	13	3022.4	-1498.2	0.9	0.337
Condition ~ time*food + time^2 + food*temperature + fertilisation + sex	12	3029.8	-1502.9	9.4	0.002
Condition ~ time*temperature + time^2 +food*temperature + time^2 + fertilisation + sex	12	3059.6	-1517.8	39.3	< 0.001
Condition ~ time*food + time*temperature + time^2 + fertilisation + sex	12	3027.3	-1501.7	7.0	0.008

Table 3: Results of the mixed effect model analysis for length, mass and condition trajectories of brown trout in the experiment with life-history classed as either smolts (i.e. migratory) or freshwater mature across the study period. The results of the model selection procedure on interaction terms are given, and the selected model for each response is highlighted in bold. The models included a random effect of individual identity and a first-order autoregressive correlation structure with respect to time (weeks of experimental treatment) was also modelled.

Model	**df**	**AIC**	**logLik**	***L*-ratio**	***p*-value**
Length ~ time*life-history + time^2 + sex + fertilisation	10	1300.6	-640.3		
Length ~ time + life- history + sex + fertilisation	9	1298.9	-640.4	0.2	0.637
Mass ~ time*life-history + time^2 + sex + fertilisation	10	1836.0	-908.0		
Mass ~ time + life- history + time^2 + sex + fertilisation	9	1843.6	-912.8	9.7	0.002
Condition ~ time*life-history + time^2 + sex + fertilisation	10	2674.4	-1327.2		
Condition ~ time + life- history + time^2 sex + fertilisation	9	2678.8	-1330.4	6.4	0.011

Table 4: Results of the mixed effect model analysis for length, condition, and whole body lipids of brown trout exposed to food and temperature stressors at the end of the experimental study period. The results of the model selection procedure on interaction terms are given, and the selected model for each response is highlighted in bold. The models included a random effect of terminal sample date.

Model	**df**	**AIC**	**logLik**	***L*-ratio**	***p*-value**
Length ~ food*temperature + fertilisation + sex	8	901.5	-422.8		
Length ~ food + temperature + fertilisation + sex	7	916.5	-451.3	16.98	< 0.001
Condition ~ food*temperature + fertilisation + sex	8	1034.0	-509.0		
Condition ~ food + temperature + fertilisation + sex	7	1036.9	-511.5	4.94	0.026
Lipids ~ food*temperature + fertilisation + sex	8	375.5	-179.8		
Lipids ~ food + temperature + fertilisation + sex	7	375.7	-180.8	2.18	0.140

Table 5: Parameter estimates with associated standard errors (SE) for three binomial generalised linear models (GLM) predicting smolt (migratory) probability (dummy coded: smolt = 1, non-smolt = 0), freshwater maturation (dummy coded: mature/maturing = 1, immature = 0), and "unassigned" life-history tactics (dummy coded: unassigned = 1, smolt/mature = 0) in brown trout (n = 425). The reference level of each factor is in brackets, i.e. effects in all models were contrasted against female fish from the Nov-Dec fertilisation in the High food and Cool temperature treatment. Statistical significance was assessed at $p < 0.05$.

Effect	**Estimate**	**SE**	**t-value**	***p*-value**
GLM of probability of smolting:				
Intercept (High-Cool, Female, Nov-Dec fertilisation)	-2.559	0.494	-5.176	< 0.001
Food: Low	1.811	0.513	3.533	< 0.001
Temperature: Warm	-1.621	0.481	-3.372	0.001
Fertilisation group: Nov	-1.341	0.569	-2.358	0.018
Sex: Male	-0.849	0.417	-2.037	0.042
GLM of probability of maturation:				
Intercept (High-Cool, Female, Nov-Dec fertilisation)	1.879	0.284	6.625	< 0.001
Food: Low	-1.054	0.248	-4.242	< 0.001
Temperature: Warm	1.004	0.247	4.073	< 0.001
Fertilisation group: Nov	-0.261	0.255	-1.023	0.306
Sex: Male	-0.963	0.248	-3.888	< 0.001
GLM of probability of being unassigned a life history:				
Intercept (High-Cool, Female, Nov-Dec fertilisation)	-2.923	0.366	-7.986	< 0.001
Food: Low	0.644	0.276	2.337	0.019
Temperature: Warm	-0.601	0.274	-2.192	0.028
Fertilisation group: Nov	0.784	0.281	2.789	0.005
Sex: Male	1.655	0.311	5.320	< 0.001

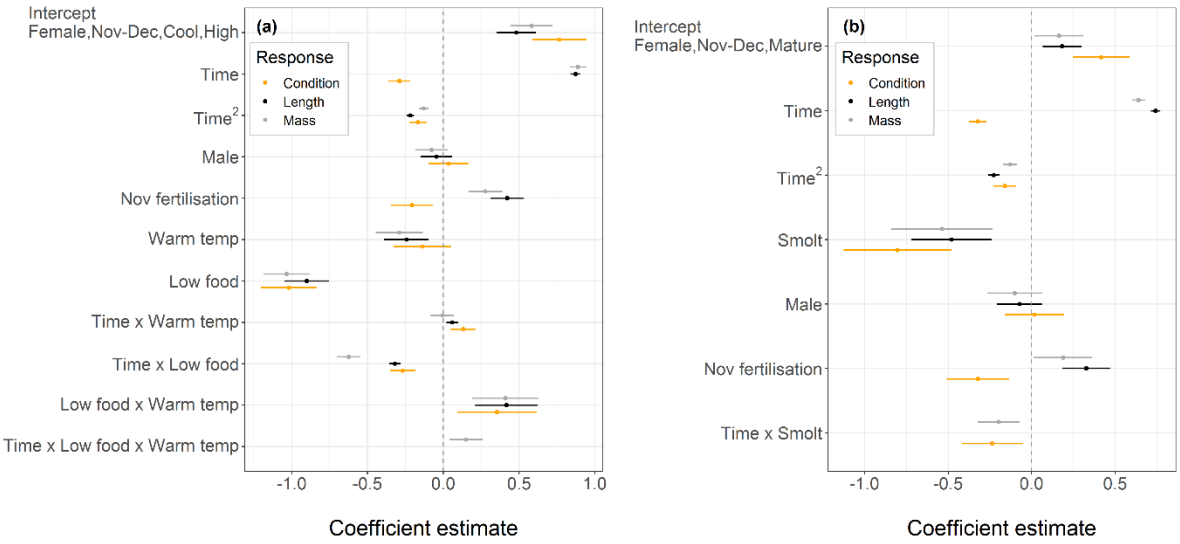


Figure 1: Coefficient estimates (± associated standard errors) of mixed effects models describing z-standardised length, mass and condition trajectories of brown trout offspring (derived from wild-caught parents from a facultatively anadromous population) that were (A) exposed to food and temperature stressors and (B) classified as adopting either smolt (migratory tactic) or freshwater maturing (non-migratory/resident) tactics after 18 months of tank rearing.

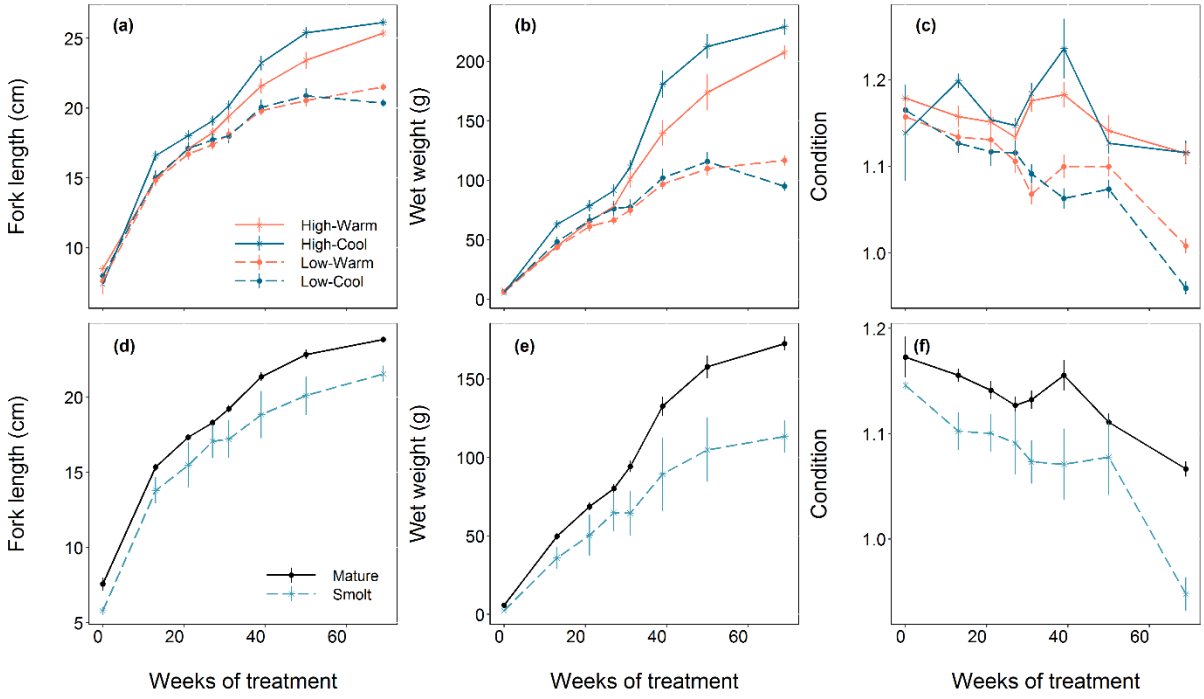


Figure 2: Trajectories of fork length, mass, and condition of brown trout offspring (derived from wild-caught parents from a facultatively anadromous population) under different food treatments and temperature treatments (A, B, C), and classed according to life-history tactics (D, E, and F). Food and temperature treatments are denoted in the format "Food-Temperature" (High or Low food, and Warm or Cool temperature) and life histories were classed as either smolt (migratory tactics) or mature (non-migratory). Week 0 = end of November 2015, when fish were 10 to 11 months old (Nov-Dec and Nov group, respectively).

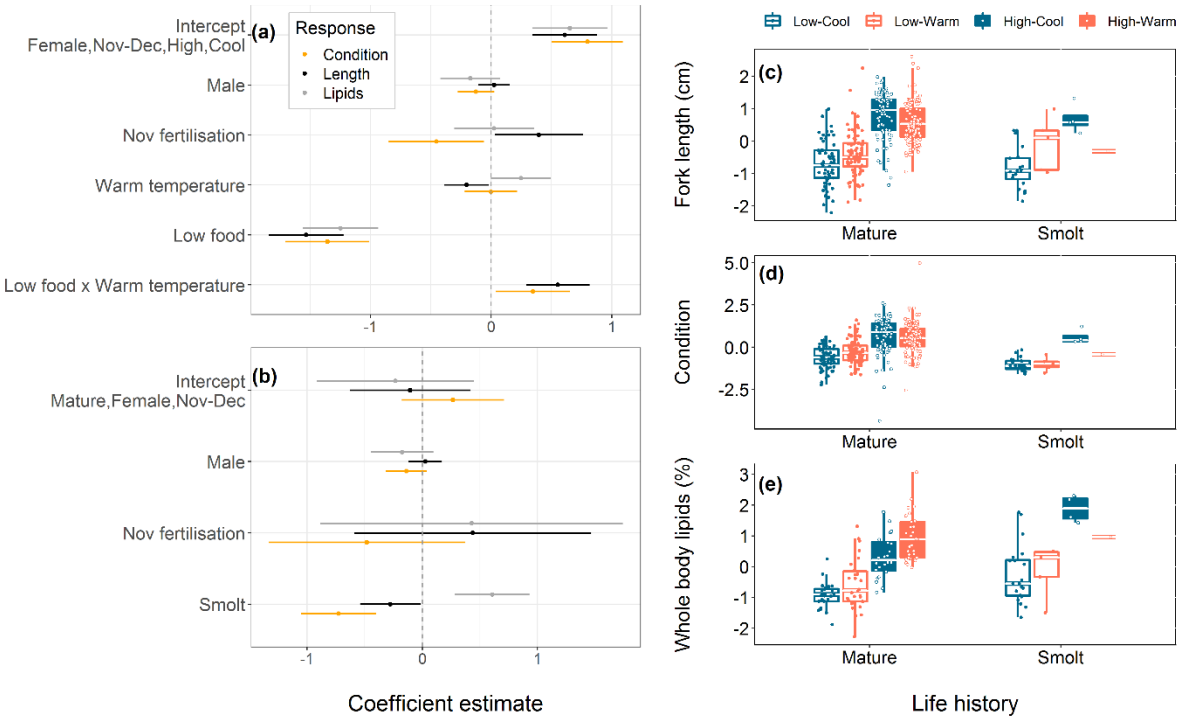
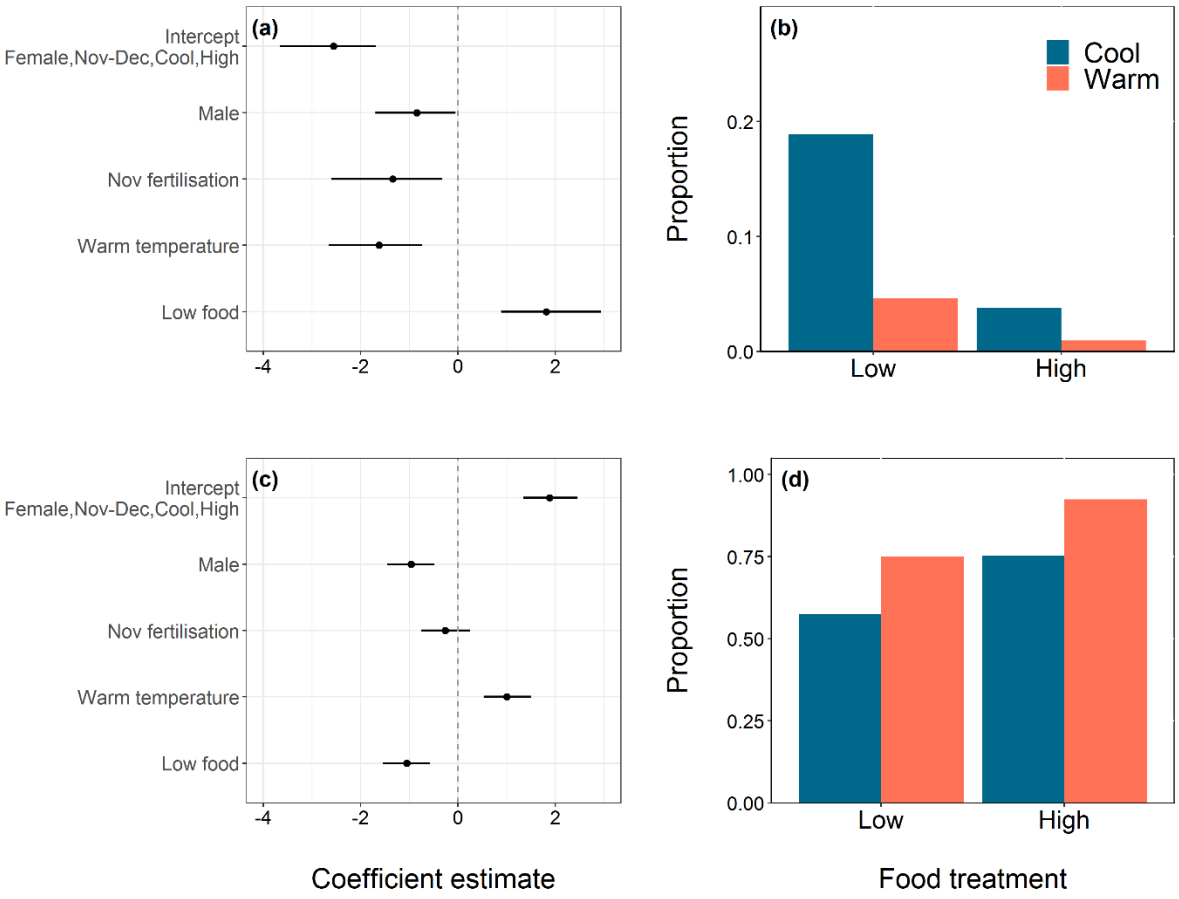


Figure 3: Coefficient estimates (± standard errors) from mixed effect models describing effects of (A) food treatment and temperature treatment and (B) migratory tactics on z-standardised final measures of length, condition, and whole body lipids of brown trout offspring classed as either smolts (migratory) or freshwater mature (non-migratory/resident) at the end of the experimental study (Spring 2018). Median values of (C) length, (D) condition, and (E) whole body lipids are represented by the white horizontal lines in each box in (C), (D), and (E). Food and temperature treatments are denoted in the format "Food-Temperature" (High or Low food, and Warm or Cool temperature). Note that only one smolt was recorded in the High-Warm treatment, and thus there is no corresponding white line for the median in the High-Warm treatment.



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Figure 4: Co-efficient estimates (± 95% confidence intervals) of GLMs describing probability of adopting (A, B) migratory and (C, D) maturation tactics in brown trout (n = 425, F1 offspring of wild trout from naturally facultatively anadromous population). Fish were classed as smolts or maturing after 18 months of tank rearing under varying food restriction and temperature

580 treatments.

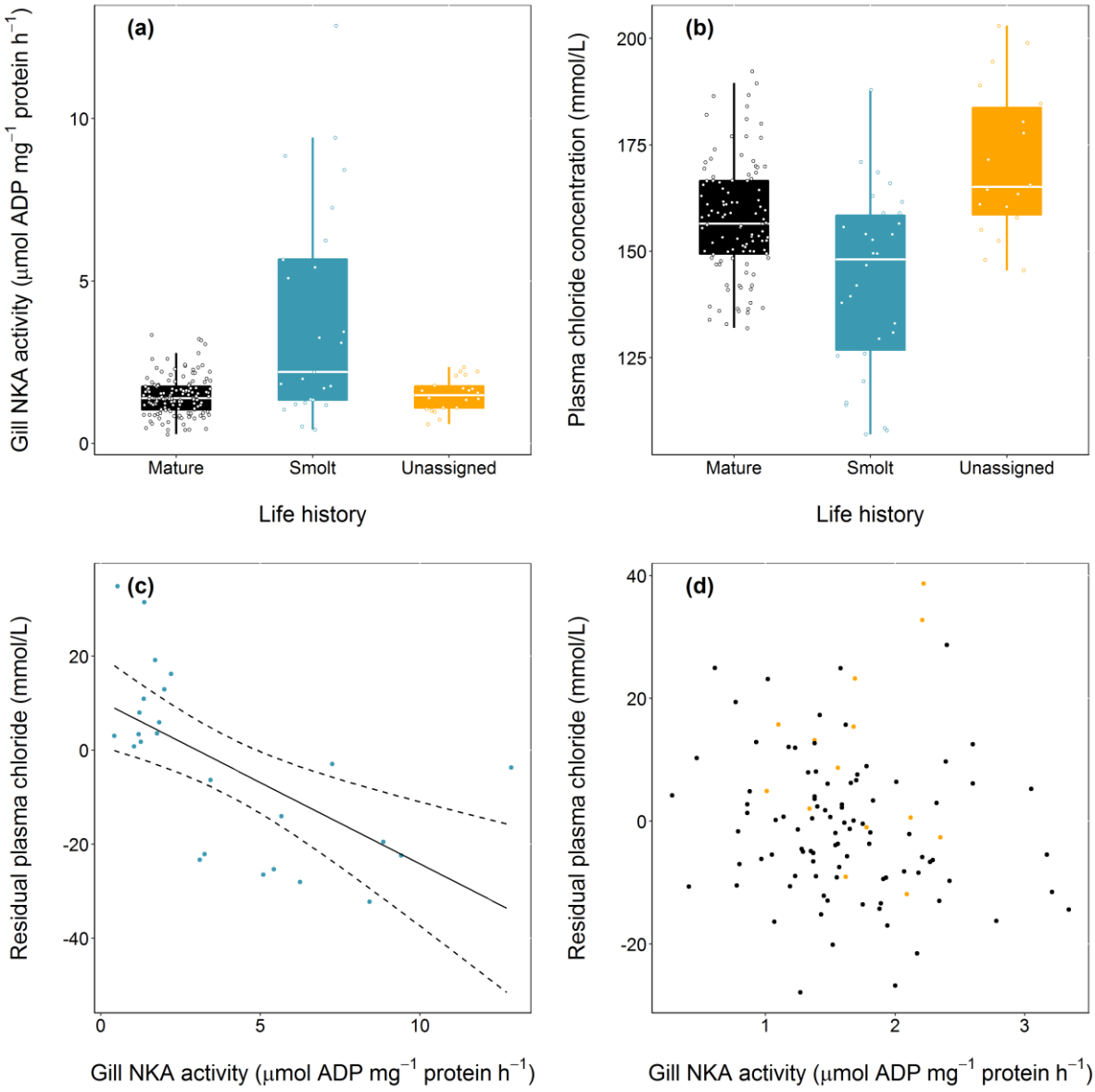


Figure 5: Variation in (A) gill NKA activity, and (B) plasma chloride concentration of brown trout – classed as smolts (migratory tactics) and mature (non-migratory), or unassigned a life-history tactic – after 24 hours in salt water (30 ppt salinity). Size-corrected plasma chloride concentration was negatively related to Gill NKA activity in (C) smolts (dashed line = 95% confidence interval) but there was no relationship in (D) non-smolts (mature and unassigned fish).

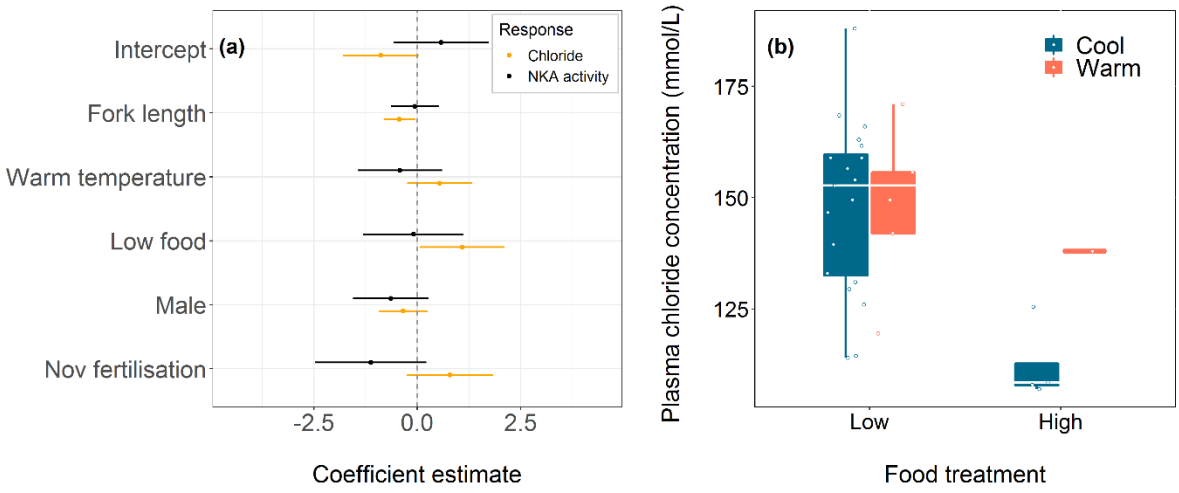


Figure 6: Coefficient estimates (± 95% confidence intervals) from the mixed effects models describing z-standardised (A) gill NKA activity and plasma chloride concentration of brown trout smolts after a 24 hours in salt water (30 ppt salinity). Variation in plasma chloride concentration of smolts according to food treatment is shown in (B), where the white lines in each box represent the median. Note that only one smolt was recorded in the High-Warm treatment, and thus there is no corresponding white line for the median in the High-Warm treatment.

Discussion

Accelerating global change is exposing ecosystems to a multitude of co-occurring stressors, the implications of which are uncertain, particularly for migratory populations. Here we showed that food restriction increased the occurrence of a migratory phenotype (smolts), but conversely elevated temperature reduced smolting rates in favour of increased freshwater maturation (a phenotype consistent with a residency tactic). The observed effects on life-history were underpinned by complex, interactive effects of these putative stressors on underlying status traits associated with migratory decisions.

Effects of multiple stressors on underlying morphological traits

While stressors applied in isolation generally appeared to have negative effects on morphological traits, the effects of warming were less pronounced than food restriction, and varied depending on the response considered. Though fish at higher temperatures were smaller than their counterparts in the cool treatment, they maintained similar condition trajectories, and indeed had higher lipid stores at the end of the study, suggesting temperature may alter patterns

of energy allocation in different ways to food restriction. Smaller sizes and higher lipid stores might arise if investment into gonadal development is prioritised over somatic growth earlier when environmental conditions appear favourable for early growth (*i.e.* the warm temperature treatments) (Jonsson *et al.* 2013), supported by the high prevalence of mature fish in warm treatments. Interestingly, the cumulative effects of food restriction and temperature were less than expected, based on their effects in isolation, suggesting complex antagonistic interactions between the stressors, whereby increased temperatures reduced body size and mass at high, but not low, food levels. The dampened response to temperature when combined with food restriction could perhaps be explained by metabolic rate depression under low food conditions, which has previously been documented in food-limited brown trout (Auer *et al.* 2015, 2016). This, together with overall reduced consumption rates, may simply have swamped any effects of temperature on growth in the low food treatments. Indeed, bioenergetics modelling of stream-dwelling rainbow trout growth has indicated growth may be more affected by factors influencing food intake rates (such as reduced overall food availability) than by direct effects of temperature, particularly during warmer summer months (Railsback and Rose 1999).

Effects of multiple stressors on migration

The antagonistic effects of food restriction and higher temperatures on physiological traits were not apparent at the level of migratory tactics. Indeed, opposing (additive) effects of these putative stressors on migratory phenotypes seemed initially to be counterintuitive. While an increase in the migratory tactic in response to food limitation is in line with previous work (Olsson *et al.* 2006; Wysujack *et al.* 2009; O'Neal and Stanford 2011; Jones *et al.* 2015; Archer *et al.* 2019), surprisingly, a temperature increase of 1.8 °C above the natural temperature regime of the source catchment reduced smolting rates. An energy limitation scenario (where an environmental stressor may act to prevent individuals from reaching genetically determined maturation thresholds) was supported in our results at the level of the status traits. Future migrants (*i.e.* smolts) were consistently smaller than fish that matured in fresh water (*i.e.* residents) and differences in mass and condition trajectories indicated migrants were energetically deficient (relative to mature fish). Energetic limitation appeared to be associated with low food availability, but less so with warmer temperatures.

Warmer temperatures have been proposed to generally increase the frequency of migrants through energetic limitation, if associated elevated metabolic demands are not offset by increased energetic intake (Sloat and Reeves 2014; Kendall *et al.* 2014). However, warming

can have a range of context-dependent impacts on patterns of energy acquisition and allocation in salmonines, which in turn may lead to a diversity of effects on life histories. For example, warmer temperatures are associated with higher levels of growth up until some thermal optimum (Jensen 1990; Forseth and Jonsson 1994; Elliott *et al.* 1995; Ojanguren *et al.* 2001; Jonsson *et al.* 2013), but bioenergetics modelling shows that optimal temperatures for growth are negatively related to daily ration amount and body size (Beauchamp 2009). Thus, higher temperatures could either increase or decrease average somatic growth, depending on food supply, the current distribution of fish sizes, and proximity to thermal growth optima. High somatic growth, along with high body condition and lipids, has been linked to increased freshwater maturation in facultatively migratory salmonines (Jonsson and Jonsson 1993; Dodson *et al.* 2013; Hecht *et al.* 2015), but other studies have found that faster growing juveniles may be more likely to migrate at earlier ages and smaller sizes because they are more energetically constrained by limited food availability (owing to much higher metabolic costs) than slower growers (Forseth *et al.* 1999). Moreover, migration tendency is linked to the relative productivity of marine and freshwater habitats, with anadromy more prevalent in areas where the marine environment offers better opportunities for feeding and growth (*e.g.* in higher latitudes) (Gross *et al.* 1988). Although the temperature stressor we simulated in our study is in line with projected climate warming scenarios of 1–3 °C (IPCC 2014), our warm temperature treatment remained largely within the optimal temperature range for growth in brown trout of 13–17 °C (Elliott *et al.* 1995; Elliott and Hurley 2000; Ojanguren *et al.* 2001) (maximum temperature in the warm treatments was 18.2 °C). It is therefore likely that warmer temperatures did not tip most individuals into an energetic deficit, thus fish were more likely to mature, rather than to smolt, in the warm treatments.

Bioenergetic modelling of migratory variation in steelhead trout has suggested that reductions in food resources can be mediated or exacerbated by water temperatures to alter expression of life histories (Benjamin *et al.* 2013). Few studies have empirically tested the cumulative effects of food supply and temperature on migratory tactics, but from our study, it appears these two environmental stressors may act additively, rather than synergistically, at least for populations that are well within their thermal limits. Moreover, the positive effect of temperature on maturation, coupled with negative temperature effects on the frequencies of smolts and unassigned fish, indicates here that warming acts to hasten the expression of life histories, driving earlier maturation instead of migration. Similar changes in life-history dynamics have been predicted in partially migratory masu salmon (*O. masou*), where favourable early growth

conditions associated with warming promoted maturation over migration and caused an overall decline in life-history diversity (Morita *et al.* 2014).

Antagonistic effects of temperature and food on physiological traits (presumed to underpin migratory decisions) were not translated at the level of migratory tactics (where the putative stressors combined additively). Our results provide additional evidence that multiple stressors can alter ecological responses in unexpected ways, sometimes termed "ecological surprises" (Paine *et al.* 1998). This suggests that effects of stressors can vary depending on the level of organisation, or indeed the response, that is measured (Galic *et al.* 2018). It also underscores how environmental factors may affect migratory decisions directly, and not solely through environmentally induced changes in putative cueing traits. For example, temperature can affect gene expression with long-lasting consequences for future behaviour and life history (Jonsson and Jonsson 2019). There is some evidence to support that warming, in particular, can directly alter life-history tactics *e.g.* temperature hastened maturation at smaller sizes in nine-spined sticklebacks (*Pungitius pungitius*) independently of temperature-mediated growth (Kuparinen *et al.* 2011). Changes in somatic growth or energy allocation due to antagonistic effects of stressors therefore adds an additional layer of complexity to our ability to infer future migratory tactics from patterns of juvenile growth.

Early life conditions affect migration propensity

The effects of fertilisation group on migratory propensity was an unexpected outcome of our study. While the relatively small numbers of brood stock used makes it difficult to draw conclusions regarding differences between fertilisation groups, which most likely stem from inherited genetic effects or epigenetic/parental effects, differences might nonetheless reflect non-inherited variation arising from early-life environment that has knock-on effects for future phenotype (Burton and Metcalfe 2014). Moreover, differences in the timing of readiness for reproduction/fertilisation also indicates differences among brood stock (e.g. spawning site in the wild) that may have translated into genetic or parental effects, rather than an effect of fertilisation date *per se*. Although both fertilisation groups experienced the same food restriction and temperature treatments, phenotypic differences that were established before the application of treatments continued throughout the experimental phase of the study (*e.g.* fish from the Nov fertilisation group, whilst larger, tended to be in poorer condition), supporting genetic/ parental effects as factors which may be equally as important as downstream environmental conditions. Interestingly, individuals in the earlier fertilisation group were more

likely to be classed as "unassigned" by the end of the study. Delayed phenotypic expression of migratory tactics can be reconciled with the existence of multiple decision windows, where an initial window determines the overall migration *versus* residency decision but then subsequent windows determine the actual age at which migrants become smolts, and residents mature (Ferguson *et al.* 2019). Age at smolting, and age at maturation, may involve similar threshold mechanisms as the overarching migration decision but perhaps with different status traits playing the role of 'trigger'; *e.g.* size or growth rates may determine age at smolting in Atlantic salmon but lipid levels may determine age at first maturation (Rowe *et al.* 1991; Jonsson and Jonsson 1993, 2005). Complex environmental stressor effects on these various cues could then increase or decrease overall life-history diversity through temporal variation in migration or maturation patterns. In the Erriff system from which our brood stock was obtained, seaward-migration of wild fish is typically undertaken by smolts at two or three years after hatching (Gargan *et al.* 2016), with potentially up to half of smolts migrating at age 3+. Similarly, although the age distribution of mature residents is unknown for the Erriff system, maturation at ages of 3+ and older is likely. As such, the patterns we observed might have reflected stressor effects on age at migration or age at maturity, in addition to effects on tactic choice *per se*. At least in relation to food restriction, we have no reason to expect that the increased smolting rates we observed in our low food treatments at age 2+ would have been counter-balanced by increased maturation rates at age 3+ of the remaining unassigned fish; if anything, these were likely to have been simply delaying actual smolting until an older age, and therefore larger size (given that larger smolts are more likely to survive the critical transition to the marine environment). In other words, smolting rate differences measured across ages 2+ and 3+ combined, if the experiment had been continued for an additional year, were likely to have been even more pronounced between food treatments. It is less obvious whether the same can be said for temperature effects, but we have no *a priori* reason to expect that age 3+ smolting rates would respond in the opposite direction to sustained higher temperatures than age 2+ smolting rates.

Stressor effects on future migratory capacity

A final aim of our study was to assess if exposure to multiple stressors influenced the capacity of migratory individuals to successfully transition to sea water (an indicator of future migratory success). Smolts generally showed heightened hypo-osmoregulatory performance relative to non-smolts (for a given fish size as indexed by reduced plasma chloride levels following seawater exposure), which was associated with increased Na^+,K^+-ATPase activity, a key

enzyme involved in ion regulation. This is in agreement with many previous studies in salmonines that have described high NKA activity in smolts, which is related directly to ability to maintain homeostasis in seawater (McCormick *et al.* 1998, 2009b, 2013; Nilsen *et al.* 2007). We had expected the addition of stressors might further influence the hypo-osmoregulatory performance of smolts through negative effects on size, irrespective of enzyme activity, and indeed, we did detect a size dependency in plasma chloride levels, which was not reflected in gill NKA activity. Size-dependent increases in salinity tolerance that are independent of the size-dependent smolt decision have also been previously established for salmonines (McCormick *et al.* 1998). Thus, though the overall frequency of smolting was lower in optimal growth conditions (*i.e.* high food regimes in our study), the small number of smolts that were produced under these good growing conditions were larger and in better condition than their counterparts exposed to less favourable conditions. Intriguingly, we detected an additional negative effect of food restriction on hypo-osmoregulatory performance that was independent of size. Food limitation could potentially contribute to competitive interactions between individuals, emergence of dominance hierarchies, and generally heightened physiological stress, with implications for seawater tolerance and survival of brown trout (Pickering 1989; Sigholt and Finstad 1990; Liebert and Schreck 2006; Midwood *et al.* 2014). Collectively, these results suggest that food deprivation may act as a stressor to migrants, which may have negative impacts for survival at sea (Ward and Slaney 1988), and possibly reduce the overall fitness of the migratory life history.

Implications and considerations

Considerable uncertainty still surrounds how environment and genetics integrate, via mediating physiological traits, to influence complex life-history patterns of facultatively migratory species (Crozier *et al.* 2008). Here, we focused on two stressors that are likely to occur in synchrony based on projections of global change, with important implications for an experimentally reared population of trout that can be extrapolated to wild populations, though some caveats should be noted. Whilst macroinvertebrate abundance and size are indeed projected to shrink with rising temperatures across the range of brown trout distribution (Durance and Ormerod 2007), in natural systems trout have been shown to track shifts in prey community assemblies (Woodward *et al.* 2010) or even become more selective in diet as temperatures increase (O'Gorman *et al.* 2016). Furthermore, given that our study population originated from a relatively cool catchment, it is possible that temperature increases in similar systems will primarily serve to increase fish growth/energetic status and promote residency,

although this very much depends on how other key factors such as food supply, flow rates, biotic factors also respond to climate change. Any reductions in anadromy would likely alter the transfer of nutrients between freshwater and marine systems, with consequences for wider ecosystem processes (Doughty *et al.* 2016). If warming results in overall decreases in life-history diversity within populations (*e.g.* Benjamin *et al.* 2013; Morita *et al.* 2014) that are coherent over broad spatial scales, this could lead to a reduction in the "portfolio effect" in salmonines, whereby maintaining a range of phenotypic diversity buffers aggregations of populations and even entire species from changing environmental conditions (Schindler *et al.* 2015).

Expanding our approach to additional populations, including those that are closer to their thermal limits, *e.g.* in southern Europe, may alter the patterns we observed here (Almodóvar *et al.* 2012). There is some evidence for genotype by temperature interactions in key phenotypic traits in salmonines (Doctor *et al.* 2014) but the role of intrinsic factors relative to environmental context requires further exploration (Ferguson *et al.* 2017). Common garden or reciprocal transplant style experiments in the wild would help to elucidate the mechanisms underpinning responses to multiple stressors in migratory species, whilst also incorporating the complexities of natural systems, such as changes in prey community structure, or abiotic correlates of warming (*e.g.* reduced oxygen/flow) (Clews *et al.* 2010). Nevertheless, our study has important implications for the development of management strategies to conserve facultatively migratory salmonines, a culturally iconic group in global decline due to aquaculture expansion, habitat degradation, and climate change (Costello 2009; Limburg and Waldman 2009).

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