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ARTICLE

Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (*Oncorhynchus mykiss*) life histories

Matthew R. Sloat and Gordon H. Reeves

Abstract: We reared juvenile *Oncorhychus mykiss* with low and high standard metabolic rates (SMR) under alternative thermal regimes to determine how these proximate factors influence life histories in a partially migratory salmonid fish. High SMR significantly decreased rates of freshwater maturation and increased rates of smoltification in females, but not males, after 1 year of rearing. Warmer water temperatures significantly decreased rates of freshwater maturation and increased rates of smoltification in both sexes. Variation in individual growth influenced the probability of adopting anadromy or freshwater residency as life histories, but produced paradoxical results. Individuals with the highest growth performance within their respective temperature treatments had a higher probability of freshwater maturation, but warmer temperatures decreased freshwater maturation despite significantly increasing somatic growth. Whole-body lipid content was significantly lower for fish reared in the warm temperature treatment, which may explain the decreased probability of freshwater maturation for individuals exposed to warmer temperatures. Our results indicate that changes in somatic growth induced by altered thermal regimes can influence the relationship between body size and the probability of maturation. Accordingly, somatic growth may not be a robust predictor of shifts in the prevalence of anadromy and residency in partially migratory salmonids when compared across thermal regimes.

Résumé : Nous avons élevé des truites arc-en-ciel (*Oncorhynchus mykiss*) juvéniles caractérisées par des taux métaboliques standards (TMS) faibles et élevés dans différents régimes thermiques afin de déterminer l'influence de ces facteurs sur les cycles biologiques d'un salmonidé partiellement migrateur. Des TMS élevés se sont traduits par une réduction significative des taux de maturation en eau douce et une augmentation des taux de smoltification des femelles, mais non des mâles, après un an d'élevage. Des températures d'eau plus chaudes entraînaient une réduction significative des taux de maturation en eau douce et une augmentation des taux de smoltification des deux sexes. Les variations de la croissance individuelle ont eu une influence sur la probabilité d'adoption de l'anadromie ou de la résidence en eau douce comme types de cycle biologique, produisant toutefois des résultats paradoxaux. Une probabilité accrue de maturation en eau douce était associée aux individus présentant les plus fortes performances de croissance pour un traitement thermique donné, mais les températures plus chaudes, tout en accélérant de manière significative la croissance somatique, entraînaient une réduction de la maturation en eau douce. Le contenu lipidique corporel était significativement plus faible chez les poissons élevés à plus haute température, ce qui pourrait expliquer la plus faible probabilité de maturation en eau douce pour les individus exposés à des températures plus élevées. Nos résultats indiquent que les modifications de la croissance somatique provoquées par des changements au régime thermique peuvent influencer la relation entre la taille du corps et la probabilité de maturation. Par conséquent, la croissance somatique pourrait ne pas être une variable explicative robuste des variations selon le régime thermique de la prévalence de l'anadromie et de la résidence chez les salmonidés partiellement migrateurs. [Traduit par la Rédaction]

Introduction

In many taxa, individuals express a wide array of migratory behaviors (Dingle 1996). For some individuals, ontogenetic niche shifts involve migrations of thousands of kilometres, while other individuals remain sedentary by comparison, completing their entire lives within a narrow home range. Such a diversity of migratory behavior is termed partial migration (Chapman et al. 2011) and is exhibited by several species of salmonid fish (Jonsson and Jonsson 1993; Dodson et al. 2013). Partially migratory salmonid populations often consist of anadromous fish that undergo marine migrations before reaching maturity, as well as freshwater residents that complete their entire life cycle in freshwater ecosystems. Partially migratory populations of *Oncorhynchus mykiss* may comprise both an anadromous form (commonly known as steelhead) and freshwater residents (rainbow trout) (Seamons et al. 2004; McPhee et al. 2007; Christie et al. 2011). Both forms spawn in streams in late winter through spring, and the young live as parr in fresh water for 1 or more years before they either smolt and migrate to sea or mature and complete their life cycle entirely within fresh water. Anadromous and resident forms commonly interbreed and produce offspring capable of adopting either life history (e.g., Christie et al. 2011).

The expression of anadromy or freshwater residency is shaped by a variety of proximate mechanisms. Factors affecting energy acquisition and allocation during juvenile rearing may be especially important influences on the adoption of anadromy or residency as life history tactics (e.g., Forseth et al. 1999; Morinville and

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Rasmussen 2003; McMillan et al. 2012). These factors may be intrinsic (determined in part by individual variation in physiological attributes; Piché et al. 2008) or extrinsic (shaped by the environment encountered early in life; Morita et al. 2000; Wyusjak et al. 2009). A key intrinsic trait influencing both energy acquisition and allocation is standard metabolic rate (SMR), a measure of the rate at which an animal partitions energy to maintain basic physiological function. In salmonids, SMR may vary several-fold among individuals even after accounting for variation in body mass (Enders and Scruton 2005; Tyler and Bolduc 2008). SMR is positively associated with dominance rank within salmonid social hierarchies (e.g., Metcalfe et al. 1995; Yamamoto et al. 1998; McCarthy 2001), and individuals with higher SMR tend to obtain feeding territories with the highest rates of food delivery (Reid et al. 2011). However, improved access to food resources facilitated by possessing a higher SMR comes at a cost in terms of the efficiency with which high SMR individuals can assimilate energy obtained from those resources (Millidine et al. 2009; Van Leeuwen et al. 2011). For a given rate of food intake, individuals with higher SMR may have substantially less surplus energy to allocate to growth and maturation (Reid et al. 2011). Because energy budgets directly affect growth and developmental trajectories, individual variation in SMR is likely to have an important proximate influence on salmonid life histories.

Temperature may also influence growth and development in partially migratory salmonids through its direct effects on fish metabolism and energy allocation (Clarke and Johnston 1999; Tocher 2003). Predicting the consequences of altered thermal regimes for salmonid life histories can be particularly challenging, however, because of the complex physiological responses of ectotherms to changes in temperature (Berrigan and Charnov 1994; Bernardo and Reagan-Wallin 2002). Temperature influences not only the balance of energy lost and gained through metabolism, consumption, and assimilation (Myrick and Cech 2000), but also the pathways by which individuals allocate assimilated energy to competing functions such as maintenance, growth, storage, and maturation (Berg et al. 2011). For example, juvenile salmonids exposed to lower stream temperatures tend to allocate more energy towards storage at a cost to somatic growth (Berg et al. 2011; McMillan et al. 2012). Temperature-driven changes in energy storage during juvenile rearing may have important consequences for salmonid life histories because energy reserves in the form of mobilizible lipids are needed to initiate the maturation process (Simpson 1992; Tocher 2003; Trombley and Schmitz 2013). However, the effect of temperature on the adoption of anadromous or resident life histories in partially migratory salmonids has received little attention to date. Because of anticipated warming of stream ecosystems from global climate change (e.g., van Vliet et al. 2011; Isaak et al. 2012), an improved understanding of the proximate influence of temperature on the adoption of anadromous and resident life histories is needed to forecast potential effects of altered thermal regimes on partially migratory salmonid populations.

In this study, we determined the effects of individual variation in energy metabolism and rearing temperature on the expression of anadromous or freshwater resident life histories in partially migratory steelhead and rainbow trout (*O. mykiss*). To examine the effects of energy metabolism on life histories in a large number of individuals, we separated a cohort of juvenile fish into subordinate and dominant behavioral groups based on competitive outcomes in stream mesocosms. We demonstrate that under the conditions of our study, behaviorally dominant fish had higher mean SMR than behaviorally subordinate fish. We then reared behaviorally dominant and subordinate groups (high SMR and low SMR groups, respectively) under two alternative thermal regimes until fish exhibited phenotypic traits associated with anadromous and freshwater resident life histories. We hypothesized that (*i*) high SMR groups would have lower rates of freshwater residency and higher rates of smoltification than low SMR groups (Morinville and Rasmussen 2003) and (*ii*) fish exposed to colder rearing temperatures would increase energy allocation towards storage and exhibit increased rates of freshwater maturation (McMillan et al. 2012). By tracking individual body size throughout the experiment, we determined how temperature, SMR, and individual growth trajectories influenced life history expression in this phenotypically plastic species.

Materials and methods

Collection and rearing of experimental animals

We used a full-sibling group of juvenile *O. mykiss* spawned from anadromous parents from the Clackamas River, Oregon, USA, for this experiment. Fish were obtained as fertilized eggs from Oregon Department of Fish and Wildlife's Clackamas River Hatchery. Immediately after fertilization, eyed eggs were transferred to Oregon State University's Salmon Disease Laboratory, Corvallis, where they were incubated at 10 °C until completion of yolk-sac absorption and the onset of exogenous feeding, at which point they were selected for inclusion in the experimental trials.

Determination of fish dominance status

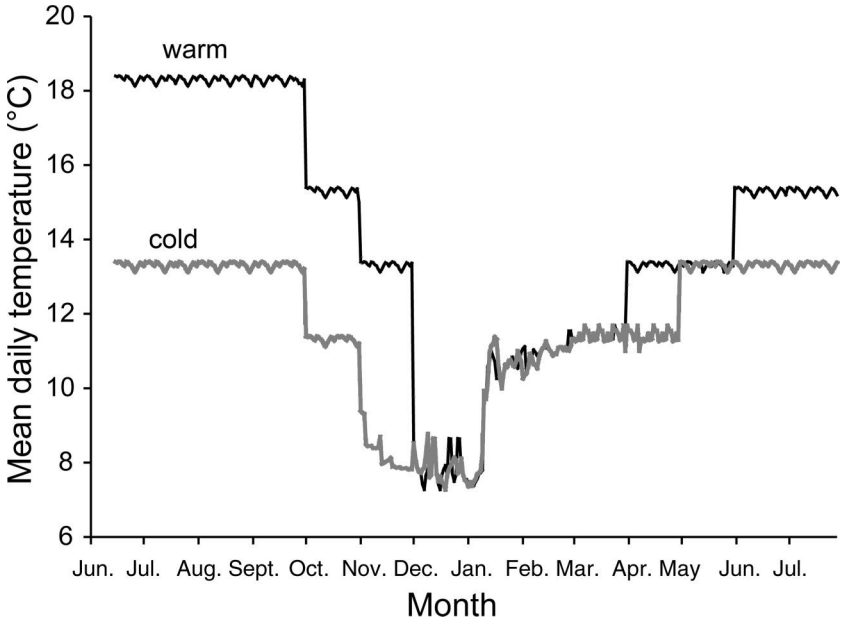
In preparation for the rearing experiment, we separated fish into competitively subordinate and competitively dominant groups based on competitive outcomes in stream mesocosms. To determine the relative competitive ability of fish, we stocked 12 streams at densities of 100 fish·m^{-2} and allowed fish to either establish and defend feeding territories or disperse into a one-way fish trap at the downstream end of each stream (Keeley 2001). The goal of this procedure was to allow competition for feeding territories to segregate a large number of individuals into two groups that differed in competitive ability and correlated physiological attributes such as SMR. Because of a strong positive correlation between metabolic rate and competitive ability in salmonines (e.g., Metcalfe et al. 1995; Yamamoto et al. 1998; McCarthy 2001), we expected fish that successfully established and defended feeding territories within the stream mesocosms to have, on average, higher standard metabolic rates than dispersing fish (Reid et al. 2011; Sloat 2013).

Stream mesocosms consisted of 2.4 m × 0.5 m rectangular channels with gravel substrate and a one-way fish trap at the outflow. Water depth was a uniform 15 cm and flow rate was approximately 2 m^3·h^{-1}. Three 14 cm × 5 cm × 8 cm bricks were evenly spaced down the center of each stream to provide physical structure for fish orientation. We provided food to each stream via automated belt feeders that dispensed 1.44 g of Biodiet starter feed (Bioproducts, Warrenton, Oregon, USA; 18% lipids, 53% proteins, digestible energy density 18.8 kJ·g^{-1}) to the head of the channel over a 12 h period beginning at 0700 each day. Directional flow within the streams distributed food throughout the channel. We removed dispersing fish from the trap each day and held them in a single 100 L tank. We continued this procedure until approximately 35 fish remained in each channel, a period lasting 4 or 5 days, at which point we captured the remaining fish and held them in a separate 100 L tank. Previous experiments using this methodology demonstrated that competition for feeding territories mediated through agonistic behavior is the mechanism segregating territorial and dispersing fish (Sloat 2013).

Dyad competition trials between territorial and dispersing fish

To test the assumption that dispersing juveniles were competitively excluded from the stream mesocosms, we determined the competitive outcomes of contests between a subsample of territorial fish and dispersing fish in dyad trials. Territorial and dispersing fish, as determined from the stream mesocosms, were size-matched and paired in 25 dyads. Fish from each dyad were then individually marked using colored visible implant elastomer (VIE)

Fig. 1. Water temperatures in warm and cold experimental thermal regimes from June 2010 to July 2011.



injected within dorsal fin tissue before being placed in a simulated stream environment consisting of 0.45 m long × 0.15 m wide × 0.15 m deep channels. The channels had directional flow and a natural substrate of gravel. Food was provided by introducing individual frozen brine shrimp through a feeding tube located at the head of each channel. We used brine shrimp as food because of the ease of controlled delivery of individual food items to the channels; preliminary trials with individual territorial and dispersing fish demonstrated that they immediately recognized brine shrimp as food. Fish were allowed 24 h to acclimate to the channels and then were observed during controlled feeding to determine differences in the direction of agonistic interaction and rate of food acquisition among individuals. Within each dyad, we considered fish with the highest combined score of agonistic interactions initiated and food acquired to be dominant.

Respirometry

We measured SMR in a randomly selected subset of territorial and dispersing fish to determine potential differences in energy metabolism between these groups. We used intermittent-flow respirometry in four separate glass respirometry chambers, which allowed measurement of SMR on four individuals per day. Two chambers each were submerged in two 100 L tanks supplied with a constant inflow of oxygenated water at 13 °C. Respirometry chambers were housed within opaque black plastic so that fish were visually isolated from each other and any light sources during the respirometry trials. Water was supplied to each chamber via two submersible centrifugal pumps. A flush pump supplied oxygenated water from the 100 L water bath. A second pump recirculated water through the chamber in a closed loop. Oxygen concentration was measured using a fiber optic oxygen sensor and oxygen meter (Oxy-4 mini oxygen instrument, Loligo Systems, Tjele, Denmark) sealed within a flow-through cell in line with the recirculating pump. To measure oxygen consumption, the flush pump was intermittently turned off, during which time the depletion of oxygen in the respirometry chamber was measured. Measurement of oxygen consumption was made at approximately 7 min intervals during a 16 h period from 1600 on the day each trial began to 0800 on the following day. The flush pump was turned back on in between each SMR measurement to restore the oxygen content of the chamber back to premeasurement levels. Control of the recirculating and flush pumps and calculation of oxygen consumption rates were automated using AutoResp software (Loligo Systems). Blank trials were performed over 16 h and showed that no microbial oxygen use was present.

Prior to being placed in respirometry chambers, all fish were held without food for 30 h to ensure gut clearance and that fish were in a postdigestive state during SMR measurement. We measured fish mass to the nearest 0.01 g using an electronic balance and fish volume to the nearest millilitre using water displacement in a graduated cylinder immediately before placing fish in the respirometry chambers. Measuring these parameters facilitated the automated calculation of oxygen consumption rates. Oxygen consumption rates were plotted graphically, and SMR was estimated as the median of the lowest six measurements recorded over the 16 h measurement period, which typically occurred >9 h after the fish were introduced to the chambers. Because of logistical constraints, we could not conduct respirometry trials until 9 months after the behavioral assessments were performed. Previous research has shown that relative rates of energy metabolism in laboratory-reared salmonids are stable over periods of 6–9 months (e.g., McCarthy 2000; Cutts et al. 2001), suggesting that our SMR measurements are still likely to reflect relative differences between fish groups at the time that dominance status was assessed.

Experimental rearing

We used a two-by-two factorial design to test the effects of rearing temperature and SMR on growth and development in juvenile *O. mykiss*. We reared 24 groups of 30 fish each in a series of 100 L tanks. These consisted of 12 groups of high SMR (territorial) fish and 12 groups of low SMR (dispersing) fish, as determined using the stream mesocosms. Six groups of fish of each type were subjected to one of two thermal regimes that differed by 2.5 °C mean annual water temperature. The warm regime consisted of seasonally adjusted temperatures between 6 and 18 °C and the cold regime ranged between 6 and 13 °C (Fig. 1). These temperature regimes mimicked the natural range of temperature variation among stream habitats available to the source population, which diverge during spring, summer, and fall, and are less variable during winter (M. Sloat, unpublished data). Water temperature was adjusted using in-line heater and chiller units. Water temperatures were monitored at 1 h intervals using water temperature data loggers (HOBO Pro v2, Onset Corp., Pocasset, Massachusetts, USA). Fish were reared under a seasonally adjusted photoperiod

typical for the source population (~45 °N). Fish were hand-fed with pellet feed (Bioproducts, Warrenton, Oregon, USA; 20% lipids, 40% proteins, digestible energy density 18.2 kJ·g^{-1}) twice daily at a ration size of 3% mean body mass per day, adjusted monthly for fish growth. We tracked the size of individual fish using VIE marks in unique combinations of color and mark location. At monthly intervals from June 2010 to July 2011, we anaesthetized all fish and measured fork length (FL) to the nearest millimetre and mass to the nearest 0.01 g.

Mortality over the approximately 13-month-long growth trials ranged from one to six individuals per tank, with no difference in mortality among treatment groups (ANOVA, effect of temperature: $F_{[1,22]} = 3.81$, $P = 0.19$; effect of SMR: $F_{[2,22]} = 0.48$, $P = 0.62$). We maintained constant fish densities within each tank by replacing mortalities with fish of a similar SMR category reared at similar density under the appropriate thermal regime. Data from replacement fish were not analyzed. A logistical failure resulted in excessive fish mortality (>50%) in one tank within the cold temperature × high SMR treatment. Data from this tank were not analyzed.

Determination of life histories

We determined the life history trajectory of individual fish using a combination of visual examination and dissection. During May and June 2011, the period when smolts from the source population normally migrate to sea, we visually assessed each fish to determine whether their phenotypic characteristics were consistent with smoltification. During this period, smolts become silver in color, lose parr marks and fin coloration, and their morphology becomes more fusiform (Jonsson 1985; Tanguy et al. 1994; Nielsen et al. 2003). In July 2011, we euthanized all fish and dissected their gonads to determine sex and maturation stage. Fish were categorized as mature, maturing, or not maturing depending on the stage of gonad development. Maturation status in males was determined by visual examination of testes. Maturing fish had moderately enlarged white testes visible without microscopy, but without running milt (Jones and Orton 1940; McMillan et al. 2012). Fully mature males had enlarged white testes and running milt. Nonmaturing males had gonads visible only with the aid of microscopy and aceto-carmine stain (Guerrero and Shelton 1974). Maturation status in females was determined by histology. Ovaries were removed and fixed in formalin, then dehydrated through a graded series of ethanol baths, and embedded in paraffin wax, thin-sectioned to 5 μm, and stained with hematoxylin-eosin to aid in visualization of oocytes. Developmental stage (oogenesis) was determined by light microscopy (Nagahama 1983). No females were fully mature at the end of the growth trials, but females were classified as maturing in preparation for reproduction in the subsequent spring if oocytes had advanced to lipid droplet stage at the time of sampling (Nagahama 1983; Campbell et al. 2006). Males and females that did not exhibit the phenotypic characteristics of smolts and did not possess maturing gonads were considered to have undetermined life histories. At the conclusion of the study, whole-body lipid content was determined in a random selection of 30 males and 30 females per life history type per temperature treatment. Whole-body lipid content (to the nearest 0.01%) was determined using the acid hydrolysis method (Reynolds and Kunz 2001).

Data analysis

Data for males and females were treated separately in all analyses. To test for treatment effects on the proportion of fish maturing during the experiment, we performed analysis of variance (ANOVA) on arcsine square-root-transformed data. To determine treatment effects on growth trajectories, we performed repeated-measures ANOVA (ANOVAR) on monthly mean mass for tank replicates. We also analyzed patterns of individual fish growth to determine if treatment effects on life history expression primarily operated through effects on somatic growth. Individual mass trajectories were described by a Gompertz growth equation (Winsor 1932), a model of asymptotic growth that is commonly used to describe the growth form of fish (Quinn and Deriso 1999):

$$m_t = m_\infty e^{-e^{-k(t-I)}}$$

where m is mass, t is age, m_∞ is the asymptotic size, k is growth rate, and I is the age at the growth curve inflection point (Fig. 2). The model was fitted to the monthly individual mass measurements using nonlinear least-squares regression.

We also investigated potential seasonal growth effects on life history expression by calculating absolute growth in mass (g·day^{-1}) for each fish during the summer–fall (July–November), winter (November–March), and spring (March–June) periods. We then performed logistic regression using these growth parameters and treatment levels to estimate the probability that an individual fish would either smolt or mature. The full statistical model for this analysis was

$$\text{logit}[p(m)] = \beta_0 + \beta_1(T) + \beta_2(M) + \beta_3(m_\infty) + \beta_4(k) + \beta_5(I) + \beta_6(g_s) + \beta_7(g_w) + \beta_8(g_{spr}) + \beta_9(m_f) + \alpha + \varepsilon$$

where T is temperature regime; M is SMR category; m_∞, k, and I are Gompertz growth curve parameters, as previously described; g_s, g_w, and g_{spr} are summer, winter, and spring absolute growth rates, respectively; m_f is mass at the end of the growth trials; α represents a random tank effect; and ε is a random error term. These mixed effect models were fitted using the lmer procedure in the lme4 library (Bates et al. 2013) in R 2.12.1 (R Development Core Team 2010). We used Akaike's information criterion (AIC) to select the most parsimonious model, given the data, from the set of candidate models (Burnham and Anderson 2002). The model with the smallest AIC value was regarded as the most plausible, and models within two AIC units of the model with the lowest AIC value were considered to be equally supported by the data.

Results

Competitive behavior and energy metabolism

Dyad trials

When placed in dyads with dispersing fish, territorial fish consumed 78% of the introduced food items ($\chi^2 = 24.11$, df = 1, $P < 0.001$), initiated 79% of agonistic encounters ($\chi^2 = 6.37$, df = 1, $P = 0.012$), and were considered dominant in 20 of 25 trials (80%). Consequently, territorial fish that we inferred to be competitively dominant within stream mesocosms were 16 times more likely than dispersing fish to be dominant when the two types of fish were paired in dyads ($\chi^2 = 15.68$, df = 1, $P < 0.001$).

Standard metabolic rate

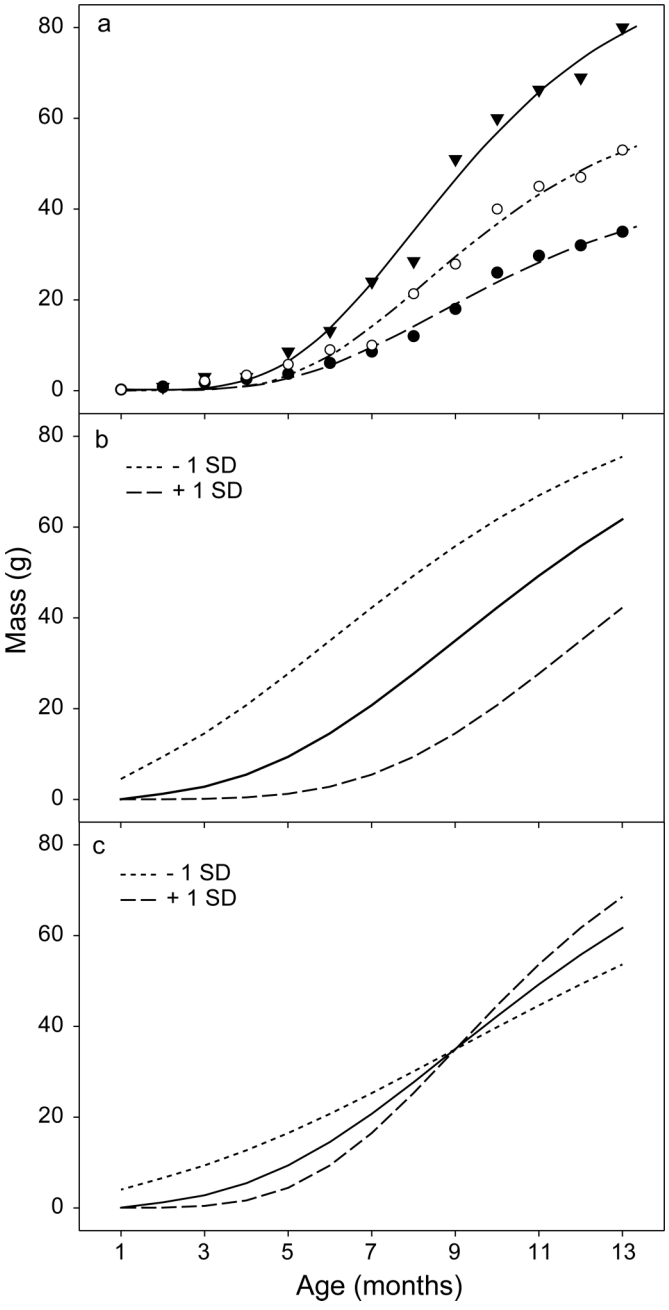
Territorial fish had significantly higher SMR than dispersing fish (Fig. 3). Territorial fish shared a common slope with dispersing fish in regressions of log(mg O_2· h^{-1}) on log(mass) ($F_{[1,38]} = 0.02$, $P = 0.88$), but had a significantly higher intercept ($F_{[1,38]} = 9.83$, $P = 0.008$). Consequently, for a given body mass, territorial fish had, on average, a 1.0 mg O_2·h^{-1} higher SMR relative to dispersing fish (Fig. 3), demonstrating a significant difference in energy metabolism between nominally "high SMR" and "low SMR" fish groups included in the rearing trials.

Rearing trials

Treatment effects on maturation

There was no difference in the proportion of males and females within any of the treatment groups ($\chi^2 = 2.54$, df = 3, $P = 0.47$). On average, among the four combinations of SMR type and rearing temperature, 22% to 42% of females initiated maturation during

Fig. 2. (*a*) Three examples of the Gompertz growth equation fit to individual mass-at-age data for three *O. mykiss*. Age is expressed as months after hatching. (*b*) An illustration of variation in the inflection point (*I*). For a fixed asymptotic size (m_∞) and growth rate (*k*), growth curves are plotted for the mean *I* (solid line) and one standard deviation above (dashed line line) and one standard deviation below (dotted line) the mean. (*c*) An illustration of variation in *k*. For a fixed m_∞ and *I*, growth curves are plotted for the mean *k* (solid line) and values one standard deviation above (dashed line) and one standard deviation below (dotted line) the mean.



the experiment (Fig. 4). No females were capable of reproduction by the end of the experiment, but maturing females had reached the lipid droplet stage of oocyte development (Nagahama 1983; Campbell et al. 2006) in preparation for reproduction the following spring. Temperature had a significant negative effect on the proportion of females maturing (ANOVA on arcsine square-root-transformed data, $F_{[1,19]} = 22.81$, $P < 0.001$). The mean proportion of

Fig. 3. The relationship between standard metabolic rate and mass for juvenile *O. mykiss* that established territories (solid circle, solid line) within stream mesocosms and those that dispersed (open circle, dashed line) into a one-way emigration trap.

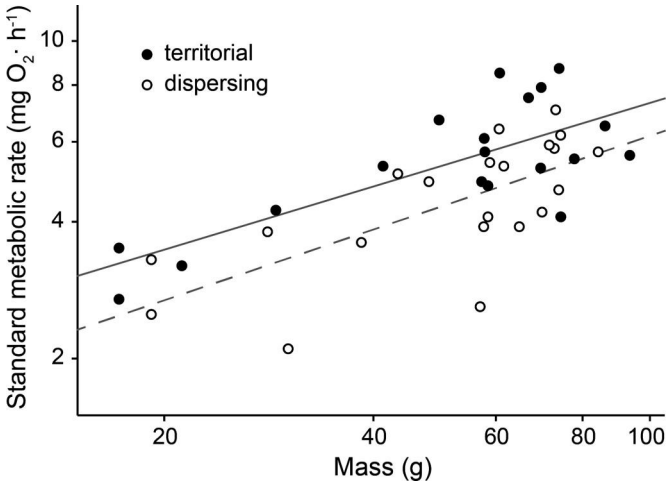
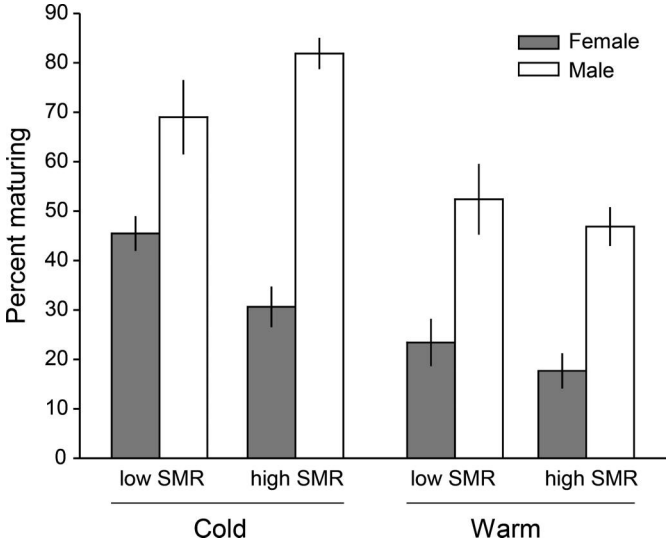


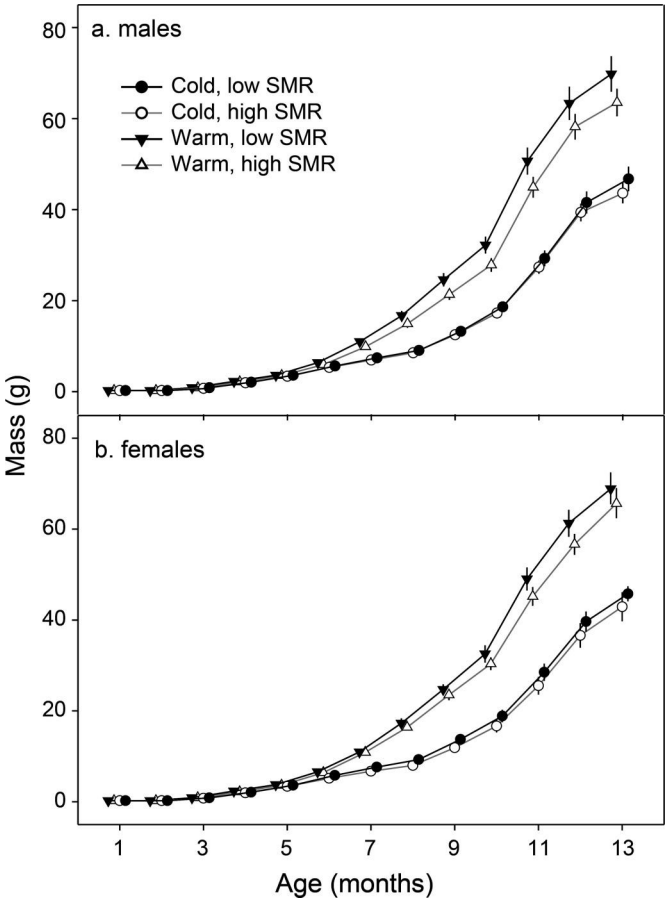
Fig. 4. Mean rates of maturation (%) for male and female *O. mykiss* by SMR type and temperature treatment. Error bars represent ±1 SE.



females maturing under the cold thermal regime was 18% greater (95% confidence interval (CI) = 9%–28%) than in the warm regime. SMR type had a weak but significant effect on female rates of maturation (ANOVA, $F_{[1,19]} = 5.11$, $P = 0.036$). High SMR females had a 9% (95% CI = 1%–17%) lower mean rate of maturation, after allowing for the effects of temperature on life history expression. We could not determine the life history phenotype of 6% of females, with neither temperature nor SMR type having an effect on the proportion of undifferentiated females (ANOVA, effect of temperature: $F_{[1,19]} = 0.001$, $P = 0.97$; effect of SMR: $F_{[1,19]} = 2.81$, $P = 0.11$).

Overall, the mean rate of male maturation during the experiment was 30% higher (95% CI = 21%–40%) than in females. Among the four combinations of SMR type and rearing temperature, 47% to 82% of males initiated maturation (Fig. 4). Temperature had similar effects on life history expression in males as in females; males exposed to the cold thermal regime had a 26% (95% CI = 16%–35%) higher rate of maturation (ANOVA on arcsine square-root-transformed data, $F_{[1,19]} = 19.40$, $P < 0.001$) than those exposed to a warm thermal regime. SMR type did not influence life history expression in males (ANOVA, $F_{[1,19]} = 0.39$, $P = 0.54$). Although

Fig. 5. Mean mass-at-age for (*a*) male and (*b*) female *O. mykiss* over the 12-month period from June 2010 to July 2011. Data are organized by SMR type and temperature treatment. Error bars represent ±1 SE.



overall male maturity rates were lower in warmer temperatures, the proportion of maturing males that were fully mature at the end of the experiment was 56% (95% CI = 41%–69%) higher in the warm temperature treatment (ANOVA, $F_{[1,19]} = 61.96$, $P < 0.001$). We could not determine the life history phenotype of 6% of males, with neither temperature nor SMR type having an effect on the proportion of undifferentiated males (ANOVA, effect of temperature: $F_{[1,19]} = 0.30$, $P = 0.59$; effect of SMR: $F_{[1,19]} = 1.13$, $P = 0.30$).

Effect of growth form on O. mykiss *life histories*

For both males and females, increased rearing temperature significantly increased the change in fish mass over time (ANOVAR, effect of temperature in females: $F_{[1,231]} = 89.76$, $P < 0.001$; effect of temperature in males: $F_{[1,231]} = 53.81$, $P < 0.001$). Growth trajectories among temperature treatments began to diverge in November (Fig. 5), giving rise to a significant temperature × date interaction (ANOVAR, temperature × date interaction in females: $F_{[1,12]} = 1249.54$, $P < 0.001$; temperature × date interaction in males: $F_{[1,231]} = 42.61$, $P < 0.001$). In both males and females, high SMR fish had a consistently lower mean mass-at-age than low SMR groups (Fig. 5). However, the magnitude of the size difference between SMR types never reached statistical significance for either males or females in either temperature treatment (ANOVAR, effect of SMR in females: $F_{[1,12]} = 0.02$, $P = 0.88$; effect of SMR in males: $F_{[1,231]} = 0.06$, $P = 0.80$).

In general, the Gompertz growth model fit individual growth trajectories very well, with R^2 values between 0.94 and 0.99. For some fish (4%), estimates of the asymptotic size parameter were highly uncertain (i.e., $P > 0.10$), and these individuals were removed from subsequent analyses of growth form and life history expression. For the remainder of fish, the Gompertz model provided individual estimates of the growth rate parameters m_∞, k, and I (Table 1). The best-approximating logistic regression model of life history expression in female *O. mykiss* included significant effects of parameters m_∞ and I, as well as effects of temperature treatment and SMR type (Table 2). Female maturation was positively associated with m_∞ and negatively associated with I (Table 2), indicating that, on average, females with higher estimated asymptotic size and an earlier occurrence of inflection in the estimated growth curve had a higher probability of maturation (Fig. 6). Interpretation of the effect of variation in I on individual growth trajectories is aided by Fig. 2. For a given asymptotic size and growth rate, fish with lower values of I have relatively greater mass earlier in life. Consequently, the negative effect of I on the probability of female maturation suggests that females that were relatively larger at younger ages had a higher probability of maturation. In addition to these growth parameters, rearing temperature and SMR type also influenced the probability of female maturation, with individuals reared under warm temperatures or

Table 1. Summary of the growth parameters asymptotic size (m_∞), growth rate (k), and growth inflection (I) from a Gompertz growth model fit to individual trajectories in mass-at-age in male and female *O. mykiss* expressing maturing or smolting phenotypes when reared under cold and warm thermal regimes.

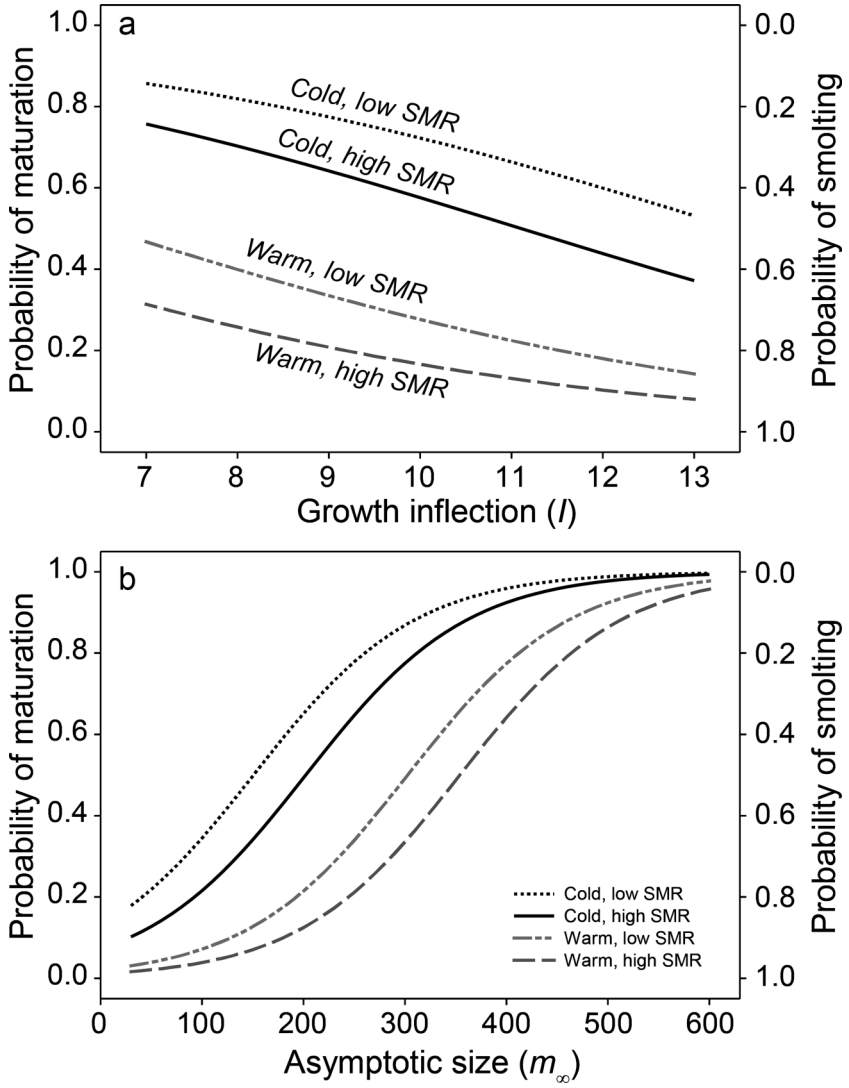
	m_∞	k	I
Temperature and life history category	Mean ± SE	Mean ± SE	Mean ± SE
Female			
Cold			
Smolt	142.27±10.51	0.166±0.007	11.29±0.38
Mature	225.72±19.92	0.179±0.007	10.05±0.35
Warm			
Smolt	151.12±6.74	0.213±0.006	9.39±0.26
Mature	234.56±25.46	0.216±0.011	9.15±0.32
Male			
Cold			
Smolt	143.82±26.77	0.061±0.014	9.20±0.23
Mature	182.46±14.43	0.077±0.009	9.46±0.39
Warm			
Smolt	155.12±8.09	0.064±0.007	10.87±0.59
Mature	182.12±12.00	0.085±0.009	11.45±0.33

Table 2. Best-approximating mixed-effects logistic regression models of the probability of maturation in female and male *O. mykiss*.

Variable	Coefficient ± SE	z value	P
Female			
Intercept	1.530±0.935	1.636	0.102
T	−1.920±0.374	−5.132	<0.001
M	−0.651±0.307	−2.122	0.034
m_∞	0.013±0.002	5.152	<0.001
I	−0.277±0.088	−3.170	0.002
Male			
Intercept	−0.148±0.627	−0.236	0.814
T	−1.793±0.333	−5.378	<0.001
m_∞	0.005±0.002	2.872	0.004
k	4.909±2.184	2.248	0.025

Note: Variables retained in the best-approximating models include temperature (T), SMR category (M), and the Gompertz growth parameters asymptotic mass (m_∞), age at the inflection point (I), and growth rate (k) estimated for individual fish. Model selection was based on minimum AIC values. Tank replicate was included as a random effect in all models.

Fig. 6. Predicted probability of life history expression in high SMR and low SMR female *O. mykiss* reared under cold and warm thermal regimes as a function of variation in (*a*) growth inflection (*I*) and (*b*) asymptotic size (m_∞). Probability curves for *I* and m_∞ were estimated by using mean values for other growth parameters included in the best-approximating multiple logistic regression model of female life history expression (Table 2). In this analysis, probability of maturation (left *y* axis) is the reciprocal of the probability of smolting (right *y* axis).



belonging to high SMR groups having a lower probability of maturation (Table 2). Since the logistic regression analysis only included those females exhibiting attributes of freshwater-maturing or smolting phenotypes, the estimated probability of maturation represents the reciprocal of the probability of smolting (Fig. 6). Consequently, the reaction norms illustrated in Fig. 6 represent probabilistic thresholds for the adoption of either freshwater resident (rainbow trout) or anadromous (steelhead) life histories in female *O. mykiss* under the conditions of our study.

For male *O. mykiss*, the best-approximating logistic regression model of life history expression included significant effects of the Gompertz growth model parameters m_∞ and *k*, as well as effects of temperature (Table 2). Male maturation was positively associated with m_∞ and *k* (Table 2), indicating that, on average, males with higher estimated asymptotic size and higher growth rate had a higher probability of maturation (Fig. 7). Temperature had a negative effect on the probability of male maturation (Table 2; Fig. 7). As with the analysis of females, the logistic regression analysis only considered those males expressing either freshwater-maturing or smolting phenotypes, so that the reaction norms illustrated in Fig. 7 represent probabilistic thresholds for the adoption of either freshwater resident or anadromous life histories in male *O. mykiss* under the conditions of our study.

Whole-body lipids

Mean whole-body lipid content for females at the end of the experiment was 9.2% (±0.28% SE). When pooled across tank replicates, there were small but significant differences in whole-body lipid content between life history types and temperature regimes (ANOVA, effect of temperature: $F_{[1,116]} = 22.91$, $P < 0.001$; effect of life history: $F_{[1,116]} = 29.78$, $P < 0.001$). Females reared under the cold regime had a mean whole-body lipid content of 9.8%, which was 1.1% (95% CI = 0.8%–1.5%) greater than in females reared under the warm regime (Fig. 8). Maturing females had a mean whole-body lipid content of 9.9%, which was 1.3% (95% CI = 1.0%–1.6%) greater than in smolting females (Fig. 8).

For males, mean whole-body lipid content was 9.1% (±0.28% SE). Males reared at cold temperatures had a mean whole-body lipid content that was 1.4% (95% CI = 0.9%–1.9%) higher than males reared under warm temperature (ANOVA, $F_{[1,116]} = 11.69$, $P < 0.001$). We did not detect differences in whole-body lipid content between life history types in males (ANOVA, $F_{[1,116]} = 0.82$, $P = 0.37$).

Fig. 7. Predicted probability of life-history expression in male *O. mykiss* reared under cold and warm thermal regimes as a function of variation in (*a*) growth rate (*k*) and (*b*) asymptotic size (m_∞). Probability curves for *k* and m_∞ were estimated by using mean values for other growth parameters included in the best-approximating multiple logistic regression model of male life history expression (Table 2). In this analysis, probability of maturation (left *y* axis) is the reciprocal of the probability of smolting (right *y* axis).

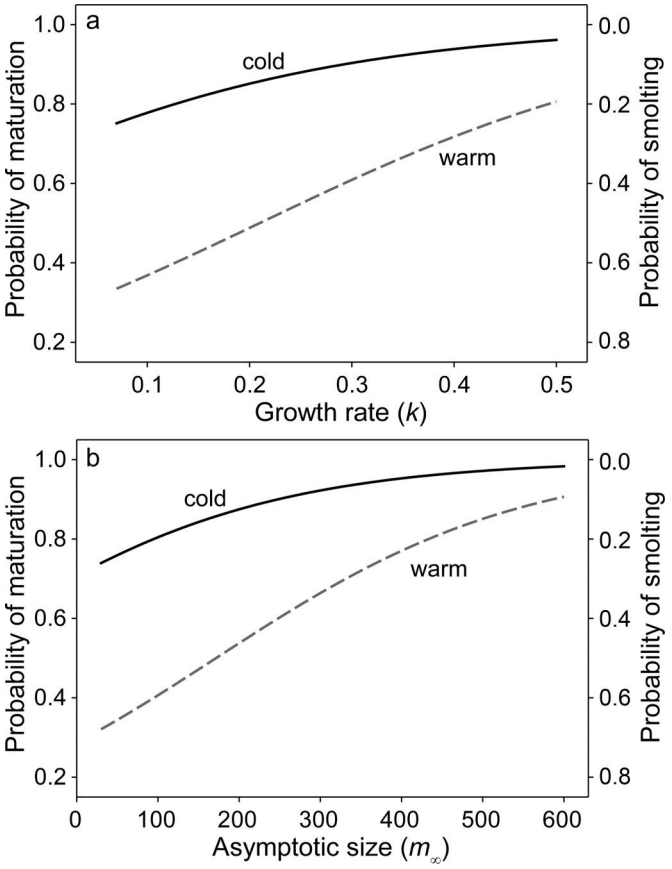
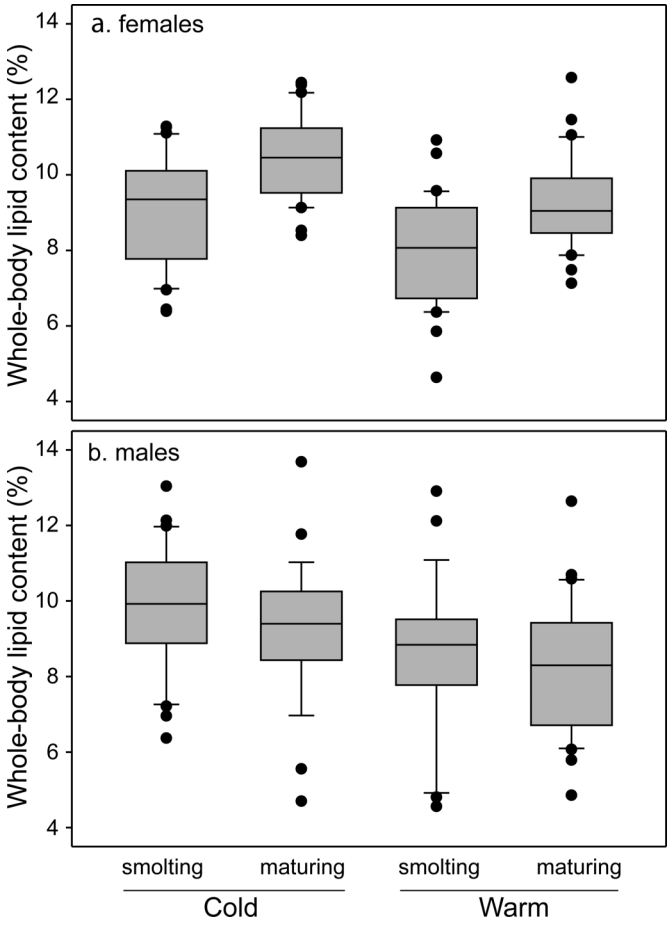


Fig. 8. Whole-body lipid content for smolting and maturing (*a*) female and (*b*) male *O. mykiss* reared under a cold and warm thermal regime. Whiskers represent lines to data that are no more than 1.5 times the interquartile range. Top lines of boxes denote the 75th percentile, bottom lines the 25th percentile, and middle lines the means. Filled circles denote outliers.



However, the analysis of whole-body lipid content among life history types in males is likely confounded by the timing of our sampling relative to developmental stage. Male samples included fully mature fish that were exuding milt. Fully mature males had a mean whole body lipid content of 8.0%, which was 1.3% (95% CI = 0.2%–2.4%) lower than that of males in the process of maturation for reproduction in the subsequent spring. The lower whole-body lipid levels in fully mature males was likely due to changes in proximate composition during conversion of lipid from storage to gonad development, as well as loss of material during sampling.

Discussion

Understanding the suite of proximate factors influencing anadromy and freshwater residency is one of the most fundamental aspects of managing partially migratory salmonids and a basic step towards predicting their response to environmental change. Our experiment with partially migratory *O. mykiss* yielded several salient results. First, we found that individual variation in energy metabolism influenced *O. mykiss* life histories. Females in high SMR groups had lower rates of freshwater maturation (residency) and higher rates of anadromy than those in low SMR groups. High SMR groups also had consistently lower mean growth rates than low SMR groups, regardless of sex, although differences among groups did not reach statistical significance. Taken together, however, these results suggest that high SMR groups had proportionally less surplus energy available after meeting their higher metabolic costs of maintenance of basic physiological function, which resulted in small differences in fish size, but significant differences in the prevalence of anadromy and freshwater residency in females. We did not observe a significant effect of SMR on male life histories. The lack of an effect of SMR in males may be due to the lower energetic costs of maturation in males relative to females (Fleming and Reynolds 2004). Male gonads constitute as little as 3% of total somatic energy, whereas females may contain 30% of their total energy in gonads (Jonsson and Jonsson 2003; Jonsson et al. 2012). Because males need less energy for gonadal development, they may be less likely to be energetically constrained from maturation by intrinsic differences in metabolism.

Investigations of partially migratory brown trout (*Salmo trutta*) (Forseth et al. 1999) and brook trout (*Salvelinus fontinalis*) (Morinville and Rasmussen 2003) have also demonstrated that migratory individuals have higher metabolic expenditures than residents. These findings support the hypothesis that individuals with high metabolic expenditures are energetically constrained from freshwater maturation and are more likely to undergo feeding migrations before reaching maturity. However, previous investigations have not been able to partition the total metabolic costs of migratory individuals into energy used for activity, specific dynamic action, or SMR. Consequently, they could not differentiate between met-

abolic expenditures attributable to either the direct effects of intrinsic physiological variation (e.g., variation in SMR) or the indirect energetic consequences of habitat selection (e.g., Fausch 1984) and agonistic behaviors spent in defense of feeding territories (e.g., Cutts et al. 1998). Our results suggest that the adoption of anadromy or freshwater residency as life histories is, at least in part, a direct consequence of individual variation in SMR.

The segregation of fish into high and low SMR groups in our study was facilitated by behavioral processes that influenced competition for feeding territories during early ontogeny. SMR is known to be positively associated with boldness, aggression, and other traits that influence competitive dominance (reviewed in Careau et al. 2008; Biro and Stamps 2010; Burton et al. 2011). As with several previous studies (e.g., Metcalfe et al. 1995; Cutts et al. 2001; McCarthy 2001), we found that fish that successfully established territories in stream environments had, on average, higher SMR than individuals that were forced to disperse. In Atlantic salmon (*Salmo salar*), social dominance has been linked to SMR and the age at which individuals initiate marine migrations as smolts (Metcalfe et al. 1995). Our results extend the linkages between individual variation in behavior, physiology, and salmonid life histories to include not only the timing of life history transitions among anadromous individuals, but also the adoption of either anadromy or residency as alternative life history tactics.

A second major finding of our experiment was the strong effect of temperature on *O. mykiss* life histories. Warmer rearing temperatures significantly increased rates of anadromy and decreased freshwater maturation in both males and females. Previous research has linked increases in somatic growth to higher probabilities of freshwater maturation in partially migratory salmonids (reviewed in Jonsson and Jonsson 1993; Dodson et al. 2013). However, our study produced paradoxical results with regard to the effect of temperature on growth and maturation. Within each temperature treatment, individuals with higher somatic growth performance had the highest probability of freshwater maturation, but an increase in rearing temperature among treatments reduced rates of freshwater maturation in females and males by 18% to 26%, respectively, despite improving somatic growth rates by approximately 30% to 40%, respectively. These results indicate that changes in somatic growth mediated by temperature may alter the relationship between body size and the probability of maturation. Accordingly, changes in somatic growth induced by changing thermal regimes may not be a robust predictor of shifts in the prevalence of anadromy and residency in partially migratory salmonids.

Studies of other teleosts have also demonstrated an effect of temperature on maturation independent of the direct effects of temperature on somatic growth (Dhillon and Fox 2004; Kuparinen et al. 2011). Kuparinen et al. (2011) demonstrated that increased rearing temperature induced a reduction in age and size at maturation in male ninespine sticklebacks (*Pungitius pungitius*) that could not be explained solely by somatic growth differences across temperature treatments. In Japanese medaka (*Oryzias latipes*), age and size at maturity increased with increasing rearing temperature even when somatic growth rates were manipulated to remain constant across thermal regimes (Dhillon and Fox 2004). Baum et al. (2005) found that exposure to increased water temperatures elevated the length threshold for male parr maturity in Atlantic salmon. These findings provide additional evidence that temperature can alter the correlation between somatic growth and the probability of maturation and emphasize that the proximate factors influencing maturation decisions in ectotherms are not limited to body size alone (Bernardo and Reagan-Wallin 2002).

Somatic growth represents one of several competing pathways by which energy is allocated within ectotherms (e.g., Morinville and Rasmussen 2003; Berg et al. 2011), and body size only partially reflects an individual's history of energy acquisition and assimilation. For example, individuals of a similar size may have significantly different energy densities depending on their relative allocation of energy to growth versus storage (Craig et al. 1978). Rearing temperature appears to exert a strong influence on energy allocation, with exposure to colder temperatures resulting in increased energy storage along latitudinal and altitudinal gradients (Berg et al. 2011) and within catchments among streams with relatively cold versus warm thermal regimes (McMillan et al 2012). Within our study, whole-body lipid content was significantly higher for both males and females under the cold temperature treatment, which may explain the increased probability of freshwater maturation for individuals exposed to a cooler thermal regime. Patterns of female maturation within each temperature treatment were consistent with this hypothesis, as maturing females had significantly higher mean whole-body lipid content than female smolts. Our data on male whole-body lipid content were inconclusive, but this was probably due to a mistiming of sampling with developmental stage in males. The high proportion of fully mature males in the sample of fish measured for whole-body lipids probably confounded our analysis because of changes in proximate composition during conversion of lipid stores to mature gonads and through loss of material during sampling. Overall, our results are similar to those of McMillan et al. (2012), who found that a reduction in whole-body lipid levels increased the estimated size threshold for freshwater maturation in *O. mykiss*. These results suggest that patterns of lipid storage may help account for changes among thermal environments in the association between body size and the probability of maturation. Thus, the "independent" effects of temperature on age and size at maturation observed elsewhere (Dhillon and Fox 2004; Kuparinen et al. 2011) could possibly be explained by examining the effects of temperature on additional components of energy budgets such as energy storage (e.g., McMillan et al. 2012).

The results of our study have several implications for the conservation of partially migratory salmonids, particularly in light of potential alterations to stream thermal regimes from global climate change and other anthropogenic influences. Our results provide experimental support for the observations of McMillan et al. (2012) that warmer temperature regimes that maximize growth at the expense of energy storage will reduce the probability of freshwater maturation. However, we caution against the interpretation that warmer thermal regimes will result in a higher abundance of anadromous individuals, as the numerical abundance of salmonids commonly decreases with increasing temperature (e.g., Li et al. 1994; Ebersole et al. 2001; Zoellick 2004). Consequently, an increase in the proportion of anadromous individuals within populations may be offset by decreases in total population size. Nevertheless, our results point to a strong role for temperature in the processes shaping anadromy and freshwater residency. They also highlight some of the challenges of predicting the effect of environmental change on phenotypically plastic species with complex life histories. Recent efforts to model the influence of climate warming on life history expression in salmonids have focused on the bioenergetic effects of increased temperature on body size (e.g., Benjamin et al. 2013). Generally, model predictions suggest that increases in somatic growth due to favorable increases in stream temperature will result in an increase in freshwater-maturing phenotypes (Benjamin et al. 2013). However, our results suggest that an emphasis on somatic growth and body size may omit important components of energy allocation strategies that influence salmonid life histories. Because temperature may alter energy allocation in important ways that are not captured by measuring somatic growth alone, a mechanistic understanding of the physiological responses to altered thermal regimes is needed to forecast effects of climate change.

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