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ORIGINAL PAPER

# Latitude and altitude differentially shape life history trajectories between the sexes in non-anadromous brown trout

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**Abstract** We used two different approaches involving two organizational levels and spatial scales to explore altitudinal and latitudinal variation in life histories of non-anadromous brown trout *Salmo trutta*. First, we studied the factors influencing the maturation of individuals from populations in northern Spain. Second, we explored the effects of altitude (range 40–1,340 m) and latitude (range 40.6–61.7°N) on longevity, maximum length, length and age at maturity, and fecundity, comparing Spanish and Norwegian populations. Individual maturation was determined by length, age, and sex, and at a given size and age individuals were more likely to mature at higher altitudes. Brown trout lived longer but attained smaller sizes at higher latitudes. Both males and females matured at an older age with increasing latitude, but latitude affected their life-history strategies differentially. Males matured at smaller sizes with increasing latitude and altitude, which may indicate that their maturation threshold depends on the growth potentiality of the river since they compete with other males from the same population. The opposite effects were detected in females. Since female fecundity increases strongly with size there may be a size below which maturation has strong fitness costs. Brown trout are extraordinarily plastic, allowing persistence in a wide variety of environments. In the context of climate change, latitudinally based studies are important to predict potential effects of climate change, especially at the southern edge of species distribution.

**Keywords** Maturity · Reproduction · Life-history strategies · Europe · Salmonids

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## Introduction

Life history theory proposes that natural selection shapes the timing and duration of various key events in an organism's life in order to maximize fitness (Roff 1992; Stearns 1992). The various life history events are linked to growth, reproduction and survivorship through trade-offs. Different selection regimes may lead to variation in traits such as age and size at maturity (Kozłowski and Uchmański 1987). This is especially so for species with indeterminate growth due to the trade-off between early reproduction and future growth. How resources are allocated to growth and current reproduction impact on the residual reproductive value, which depends strongly on the length of the reproductive life span (Kozłowski and Uchmański 1987; Charnov et al. 2007). Thus, the benefits of being large and the costs of becoming large have to be balanced (see Blanckenhorn 2000). Further, males and females invest differently in reproduction (Hendry et al. 2004) and while variation in female body size is mainly driven by fecundity selection, male size is usually a sexually selected trait (Arak 1988). Hence, different costs and benefits may favour the selection of different life-history strategies between sexes.

Key events in an organism's life depend not only on trade-offs or on the physiology of an individual, but also on environmental variation. Temperature is the major environmental variable that influences performance of ectotherms since locomotion, immune function, sensory input, foraging ability, courtship, feeding and growth are thermally sensitive (see Angilletta et al. 2002 for a review). Temperature, together with photoperiod and food availability, is also among the most important factors that vary with latitude, and correspondingly latitudinal gradients in life-history traits have been described in many species from different taxa (e.g. Hjernquist et al. 2012).

Salmonid fishes have been intensively studied and a large variation in life history traits has been described both among and within species (see for example Fleming 1998; Thorpe 1990). Salmonids such as salmons and trouts have mating systems where females compete for suitable breeding sites whereas males compete intensively for spawning opportunity (e.g. Fleming and Reynolds 2004; Esteve 2005; Jonsson and Jonsson 2011). Although all salmonid species spawn in fresh water, many of them, especially of the genus *Salmo* and *Oncorhynchus*, are anadromous and have a marine phase (Nelson 2006). Juvenile fish (also known as parr) feed in freshwater for a variable time period before going through a smolt transformation, a physiological and morphological process to preadapt to life in the sea (Folmar and Dickhoff 1980). Migrating individuals spend a variable amount of time at sea before returning to the river where they were born to reproduce (Keefer and Caudill 2014). This is a generalised life cycle, as many species display a high variability in life histories encompassing populations that range from being fully freshwater resident to anadromous (Klemetsen et al. 2003; Quinn 2005; Jonsson and Jonsson 2011), as well as including populations where mature parr and anadromous males coexist (Jonsson and Jonsson 1993, Hutchings and Myers 1994, Aubin-Horth et al. 2006).

Brown trout *Salmo trutta* L. is a model species for the study of variation in life-history traits due to its wide geographic distribution and great life history variation (Klemetsen et al. 2003; Cucherousset et al. 2005; Jonsson and Jonsson 2011). Latitudinal variation in life history traits has especially been studied in anadromous *S. trutta* from northern areas of its European distribution (Jonsson and L'Abée-Lund 1993). Smolt age, sea-age at maturity, and longevity are known to be influenced by clinal variation in environmental factors (L'Abée-Lund et al. 1989; Jonsson and L'Abée-Lund 1993). However, when river conditions are favourable for growth and/or migration is prevented, populations are often non-anadromous, i.e., they spend their whole life in freshwater. Many populations are also completely confined to rivers and streams and the environmental conditions in running water have a strong influence on life history since freshwater habitat characteristics fluctuate in the short term (Jonsson and Jonsson 1993; Nicola and Almodóvar 2002). Recently, Parra et al. (2009) described the spatial variation in growth of stream resident *S. trutta* in southern European populations and found that growth varied along an altitudinal gradient. Further, at a larger latitudinal scale they found that length-at-age decreased with increasing latitude. Hence, environmental changes along altitudinal or latitudinal gradients influence growth and may lead to clinal variations in other life-history traits. Furthermore, male and female traits may differ due to differential selection pressures (see Serbezov et al. 2010). Female fecundity is strongly dependent on body size (Elliott 1995), and larger females normally dig deeper nests and defend them more successfully (Crisp and Carling 1989). In contrast, male size is mainly affected by sexual selection. Therefore, optimal age and size at maturity may differ between sexes. When an individual matures is most likely linked to proximate cues such as physiological status during a critical period when maturation is initiated (Thorpe 2007). Thus, when reserves and growth rate are above some genetically determined thresholds, maturation is triggered (Thorpe 1990; Baum et al. 2004).

Here, we investigate variation in life history of stream-resident *S. trutta* at two different spatial scales. We are interested in unravelling the effects of altitude and latitude on age and length at maturity, longevity, and maximum length, and also if these effects differ between males and females. Firstly, we focus on variation in life-history traits at a regional scale to investigate which factors influence the maturation threshold of individuals from populations in Northern Spain. The reported differences in growth along the altitudinal cline in the area (Parra et al. 2009) suggest that there is variation in other traits, similar to previous observations made in Atlantic salmon *Salmo salar* L. (Baum et al. 2004). Hence, potential differences in growth opportunity set by altitudinal gradients may lead to different life-history strategies so that age at maturity is expected to increase with altitude and/or size at maturity is expected to decrease with altitude. Employing a second approach, we still focus on the effects of an altitudinal gradient but within a large-scale study, comparing life-history traits from populations inhabiting the southern periphery of the distribution (latitude 40°–43°) with populations from Norway (latitude 61°). Considering the latitudinal difference in water temperature, we expect age at maturity and longevity to increase with latitude. Predictions with regards to length at maturity are not as clear since previous observations were taken from anadromous populations where individuals experience different events along a life span.

## Materials and methods

### Study areas

The analysis of regional variation in age and size at maturation was carried out with *S. trutta* individuals from four rivers in the Bay of Biscay drainage (Araxes, Leitzarán, Urumea, and Bidasoa) and seven rivers in the Mediterranean Ebro River drainage (Erro, Urrobi, Irati, Salazar, Eska, Ultzama, and Arga) (Fig. 1; Table 1). Between four and 17 sampling sites were selected in each river, depending on its size and number of tributaries. Sampling sites corresponded to first to fifth-order rivers and were located at an altitude ranging from 40 to 895 m. Median summer discharge ranged from 0.05 to 3.70 $m^3 s^{-1}$ and mean daily summer temperature ranged between 11.6 and 17.4 °C (for further details see Ayllón et al. 2010).

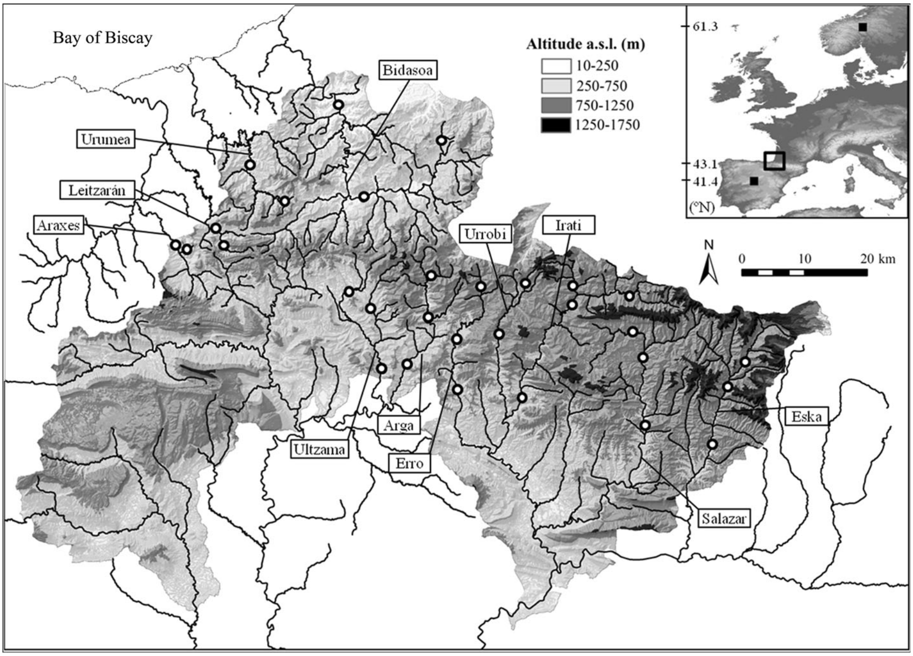

**Fig. 1** Map of the study area in northern Spain, showing the location of sampling sites in Bay of Biscay and Ebro drainages. The location of the rivers in Europe is also shown (*open square*), as well as that from the rivers in central Spain and Norway (*solid squares*)

For the global analysis of latitudinal and altitudinal variation in life-history patterns we used averaged population data from the abovementioned rivers and also data from populations at the southern and northern areas of *S. trutta* distribution. Seven rivers belonging to two Atlantic drainages from the centre of the Iberian Peninsula, Tagus River drainage (Jarama, Dulce, Gallo, Cabrillas, and Hoz Seca) and Douro River drainage (Cega and Eresma) were used; the system and sampling is described in Nicola and Almodóvar (2002). In addition, we used data from seven localities in five Norwegian rivers (Bellbekken, Gjesa, Ulvåa, Søre Osa, and Nordre Bjøråa; see Olsen and Vøllestad 2003 for further details) (Table 1). All the individuals included in the analyses were non-anadromous. The Ebro, Tagus and Douro Rivers drainages populations are landlocked, while the other samples were determined as non-anadromous after inspection of the size/scale growth pattern.

## Sampling

For the analysis of regional variation in age and size at maturity, electrofishing with a 2,200 W DC generator took place every year from 1993 to 2004 at the end of the growing season in the Ebro and Bay of Biscay drainages. Fish were anaesthetized with MS-222 (tricaine methanesulphonate), fork length (L, to the nearest mm) and weight (to the nearest g) were measured, and scales were taken for age determination following the Dahl-Lea methodology (Dahl 1910; Lea 1910). At the beginning of the 1996 spawning season (mid-September), individuals were captured and immediately frozen in dry ice at −80 °C until

**Table 1** Summary of mean (standard deviation) population characteristics of the brown trout populations used to study latitudinal and altitudinal clines in life history traits

| Area | Ebro drainage | Bay of Biscay drainages | Central Spain | Norway |
|---|---|---|---|---|
| No. rivers | 8 | 4 | 6 | 5 |
| No. individuals | 610 | 409 | 142 | 8,943 |
| Altitude | 693.6 (135.20) | 269.4 (148.95) | 1,207.3 (168.48) | 349.1 (67.40) |
| Latitude | 42.9 (0.07) | 43.1 (0.07) | 41.4 (0.43) | 61.3 (0.26) |
| b | 2.7 (0.63) | 2.0 (0.61) | 2.3 (0.57) | 1.88 (0.08) |
| $L_{0+}$ | 73.2 (9.48) | 69.1 (10.87) | 75.2 (15.32) | 48.6 (5.59) |
| $L_{minM}$ | 155.5 (31.25) | 158.3 (30.53) | 133.5 (7.78) | 123.4 (23.68) |
| $L_{minF}$ | 165.2 (28.75) | 150.2 (18.36) | 150.7 (13.15) | 146.1 (25.11) |
| $A_{matM}$ | 1.32 (0.478) | 1.55 (0.522) | 1.50 (0.548) | 2.00 (0.577) |
| $A_{matF}$ | 1.58 (0.507) | 1.64 (0.505) | 1.83 (0.408) | 3.14 (1.069) |
| $A_{max}$ | 2.91 (0.490) | 3.23 (0.794) | 3.33 (0.408) | 4.29 (0.951) |
| $L_{max}$ | 254.8 (36.39) | 239.6 (49.72) | 244.1 (55.47) | 178.7 (13.99) |

Individual data from Ebro and Bay of Biscay drainages were used in the analysis of factors affecting maturation and population data from the four areas were used in the analysis of altitudinal and latitudinal variation in life-history traits

b is the exponent of the length-fecundity relationship, $L_{0+}$ (mm) is mean length the first year of life, M and F stand for "males" and "females", respectively, in the different traits analysed: $L_{minM}$ and $L_{minF}$ (mm) are minimum length at maturity of males and females, $A_{matM}$ and $A_{matF}$ are age at maturity (50 % of a cohort) of males and females. $A_{max}$ is age when 10–15 % of a cohort is still alive, and $L_{max}$ (mm) is the mean length of the age-class correspondent to $A_{max}$. The five Norwegian rivers included seven locations where sample sizes varied from 426 to 2,039 individuals

subsequent analysis in the laboratory. There they were dissected and eviscerated and sex was determined. Gonad maturity stages were determined using the method of Nikolsky (1963). The total number of ripe eggs in the ovaries in maturity stage IV–V (i.e., when they have achieved their maximum weight and it is assumed that the individual will spawn that season) gave the individual fecundity of females.

Then, for these rivers from the Ebro and Bay of Biscay drainages, as well as for those used in the global analyses (Central Spain and Norway) we calculated several reproductive traits:

- $A_{matF}$ and $A_{matM}$: age at maturity was the age when 50 % of a cohort was mature, calculated for females (F) and males (M) separately.
- $L_{minF}$ and $L_{minM}$: minimum observed length (mm) of a mature male or female in the population, considering females and males separately.
- Fecundity: we estimated the fecundity-length relationship ($F = aL^b$, where F is fecundity, a and b are constants and L is length) for female *S. trutta*. We then used the exponent b (the slope of the log–log regression) for between-population comparison.

We also wanted to analyse the longevity of trout in the studied populations by means of the size and age they reach at the end of their lives. Because observed maximum length and observed maximum age come from individual data, they may be biased and difficult to compare among populations (see Rochet 1998), so we estimated:

- $A_{max}$: maximum age was the age when 10–15 % of a cohort is still alive.
- $L_{max}$: maximum length was the mean length of the age-class corresponding to $A_{max}$.

### Data analyses

First, to study the maturation pattern of *S. trutta* in northern Spain (the Bay of Biscay and Ebro drainages, see Table 1) we analysed individual data by means of mixed effects multiple logistic regression performed with the lme4 package in R (Bates et al. 2012). Fork length, age, sex, and standardized altitude (i.e., transformed to have mean 0 and standard deviation 1) were used as the fixed effects, while maturation stage ($1 = \text{mature}$, $0 = \text{immature}$) was used as the dependent variable, river as the random effect, the link function was specified as logit and the error structure modeled as binomial. Altitude was included as a proxy for growth opportunity with potential implications on other life-history traits including maturation (see Baum et al. 2004). Akaike's Information Criterion adjusted for small samples (AICc, Burnham and Anderson 2002) was used to select the best model. When competing models were equally supported (i.e., $\Delta\text{AIC} < 2$, Burnham and Anderson 2002) we obtained the average model by means of the MuMIn package in R (Bartoń 2013). Further, to assess the predictive power of each of the predictor variables (including interactions) we calculated their "relative importance" as the sum of the Akaike model weights over all the candidate models ($\Delta\text{AIC} < 2$) which included the explanatory variable.

Second, to analyse the large-scale spatial variation of the different traits, we employed data from the abovementioned drainages, and also included population data from central Spain and Norway. The models were fitted using the lme4 package in R (Bates et al. 2012). Similarly to the previous analysis, when competing models were equally supported ($\Delta\text{AIC} < 2$) we calculated the average model and the relative importance of the variables included. We separately regressed $A_{\text{matF}}$, $A_{\text{matM}}$, $L_{\text{minF}}$, $L_{\text{minM}}$, $A_{\text{max}}$, $L_{\text{max}}$, and b, as dependent variables, using latitude, altitude and their interaction as predictors. Altitude and latitude were standardized by subtracting the mean from each raw score and then dividing the difference by the standard deviation. Further, to test for variation in relative size at maturity we used $L_{\text{max}}$ as an independent covariate in separate models using $L_{\text{minF}}$ and $L_{\text{minM}}$ as dependent variables. This latter analysis aimed to depict the size at which the event of maturity takes place with respect to the maximum size, i.e., the "relative length at maturity". Given that $L_{\text{min}}$ and $L_{\text{max}}$ are likely to vary widely, the relative length at maturity will indicate whether the individuals matured at a smaller or larger size compared to the potential $L_{\text{max}}$ of a certain population.

## Results

A total of 1,019 individuals were analyzed in the populations from the Ebro and Bay of Biscay drainages, which were composed of relatively large fish (Table 1). Maximum age was around 3 years, indicating a short life span. Both males and females matured between the first and the second year of life. Further, the data from central Spain were similar to those found in northern Spain. Finally, trout from the populations in Norway were generally smaller, matured older (especially females) and lived longer.

Regarding the study of the maturation pattern of *S. trutta* individuals from northern Spain, four models had comparable statistical support ($\Delta\text{AIC} < 2$) for the mixed effects logistic regression analysis, so we calculated an average model (Table 2). As expected, maturation probability increased with increasing length, age, and altitude, all factors with a relative importance of one. The magnitude of these effects differed between the sexes, so that for a given length, age and altitude there was an increase in the probability of maturity

**Table 2** Results of multiple logistic regression analyses for maturation status (0 immature, 1 mature)

| Variable | Model 1 Estimate | Model 2 Estimate | Model 3 Estimate | Model 4 Estimate | Average model Estimate | Relative Importance |
|---|---|---|---|---|---|---|
| Intercept | −11.978 | −12.051 | −12.066 | −12.080 | **−12.027** | **–** |
| L | 0.046 | 0.046 | 0.047 | 0.047 | **0.046** | **1.00** |
| age | 5.843 | 5.913 | 5.839 | 5.770 | **5.846** | **1.00** |
| alt | 0.185 | 0.606 | 0.450 | 0.180 | **0.325** | **1.00** |
| sex (M) | 2.250 | 2.270 | 2.187 | 2.545 | **2.293** | **1.00** |
| age × L | −0.015 | −0.016 | −0.015 | −0.015 | **−0.015** | **1.00** |
| age × sex (M) | −1.633 | −1.646 | −1.602 | −1.590 | **−1.624** | **1.00** |
| alt × sex (M) | 0.376 | 0.387 | – | 0.374 | **0.379** | **0.83** |
| L × sex (M) | – | – | – | −0.002 | **−0.002** | **0.17** |
| alt × L | – | −0.003 | – | – | **−0.003** | **0.22** |
| ΔAICc | 0 | 1.33 | 1.84 | 1.93 | **–** | |
| $w_i$ | 0.44 | 0.22 | 0.17 | 0.17 | **–** | |

Fork length, age, sex, standardized altitude, and their two way interactions were used as fixed effects. Only the best 4 models within ΔAICc < 2 are shown. Akaike weights ($w_i$) are also indicated

Sex (M) refers to males, L is fork length of an individual, age is age of an individual, alt is altitude of the river, and x indicates interaction between two variables

Average model estimate and relative importance of the variables are indicated in bold

for males. Several interactions modified these main effects. The probability of maturity rose less steeply with length for older individuals. Besides, a negative interaction between sex and age attenuated the increase in probability of maturity for older males. With a lower relative importance, the probability of males being mature was increased in high altitude rivers whereas their increase in probability of maturity with length was lessened. Finally, the increase in the probability of maturity with altitude was lower for larger individuals.

In the large-scale analysis, the impact of latitude and altitude differed for the various life-history traits, and there were also differences between male and female strategies (Table 3; Fig. 2). Consistent with our predictions, average models showed that $A_{max}$ increased with increasing latitude and altitude as well as with their interaction, whereas $L_{max}$ decreased towards the north. Age at maturity also varied as expected, with both $A_{matM}$ and $A_{matF}$ being higher with an increase in latitude, altitude and their interaction. Length at maturity, however, varied differently with latitude and altitude in males and females. In the case of males, $L_{minM}$ decreased with both latitude and altitude (relative importance 1.00 and 0.76 respectively), but when it was considered with respect to $L_{max}$ (relative length at maturity) the relative importance of either of these geographical clines diminished (to 0.50 and 0.61) since $L_{minM}$ increased with increasing $L_{max}$, which had the highest relative importance (0.89). Conversely, when considering females, $L_{minF}$ increased with latitude, altitude and their interaction, although those changes were of lower relative importance than in the case of males (0.49, 0.39 and 0.24 respectively). When considering the relative length at maturity, $L_{minF}$ increased with $L_{max}$, which had the highest relative importance (1.00), and also increased with increasing latitude, altitude and their interaction, with lower relative importance (0.45, 0.21 and 0.21 respectively). Finally, the exponent (b) of the length-fecundity relationship increased with altitude but decreased with latitude and with the interaction between altitude and latitude (relative importance 1.00, 1.00 and 0.66 respectively) which implies a higher fecundity per body mass unit in

**Table 3** Results of regression analyses testing the variation of mean life-history traits with altitude (alt), latitude (lat) and their interaction (lat × alt)

| Dependent variable | | Intercept | lat | alt | lat × alt | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|---|
| b | Model 1 | 2.592 | 0.184 | 0.792 | 1.499 | 0 | 0.66 |
| | Model 2 | 2.448 | −0.369 | 0.382 | | 1.33 | 0.34 |
| | **Average model** | **2.543** | **−0.004** | **0.653** | **1.499** | – | – |
| | **Importance** | **–** | **1.00** | **1.00** | **0.66** | – | – |
| $A_{max}$ | Model 1 | 3.275 | 0.883 | | | 0 | 0.40 |
| | Model 2 | 3.275 | 1.013 | 0.330 | | 0.11 | 0.38 |
| | Model 3 | 3.444 | 1.667 | 0.814 | 1.773 | 1.26 | 0.22 |
| | **Average model** | **3.311** | **1.102** | **0.505** | **1.773** | – | – |
| | **Importance** | **–** | **1.00** | **0.60** | **0.22** | – | – |
| $L_{max}$ | Model 1 | 2.366 | −0.103 | | | – | – |
| $L_{minM}$ | Model 1 | 2.162 | −0.085 | −0.052 | | 0 | 0.55 |
| | Model 2 | 2.162 | −0.065 | | | 1.71 | 0.24 |
| | Model 3 | 2.175 | −0.034 | −0.014 | 0.140 | 1.93 | 0.21 |
| | **Average model** | **2.165** | **−0.070** | **−0.042** | **0.140** | – | – |
| | **Importance** | **–** | **1.00** | **0.76** | **0.21** | – | – |
| $A_{matM}$ | Model 1 | 1.512 | 0.437 | | | 0 | 0.44 |
| | Model 2 | 1.512 | 0.527 | 0.230 | | 0.52 | 0.34 |
| | Model 3 | 1.657 | 1.087 | 0.644 | 1.517 | 1.31 | 0.23 |
| | **Average model** | **1.545** | **0.615** | **0.396** | **1.517** | – | – |
| | **Importance** | **–** | **1.00** | **0.56** | **0.23** | – | – |
| $L_{minF}$ | Model 1 | 2.188 | | | | 0 | 0.36 |
| | Model 2 | 2.188 | −0.025 | | | 0.76 | 0.25 |
| | Model 3 | 2.220 | 0.097 | 0.095 | 0.326 | 0.83 | 0.24 |
| | Model 4 | 2.188 | | 0.015 | | 1.80 | 0.15 |
| | **Average model** | **2.196** | **0.035** | **0.064** | **0.326** | – | – |
| | **Importance** | **–** | **0.49** | **0.39** | **0.24** | – | – |
| $A_{matF}$ | Model 1 | 1.884 | 1.291 | 0.454 | | 0 | 0.65 |
| | Model 2 | 2.028 | 1.846 | 0.865 | 1.505 | 1.25 | 0.35 |
| | **Average model** | **1.934** | **1.484** | **0.597** | **1.505** | – | – |
| | **Importance** | **–** | **1.00** | **1.00** | **0.35** | – | – |

| Dependent variable | | Intercept | lat | alt | lat × alt | $L_{max}$ | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|---|---|
| $L_{minM}$ | Model 1 | 2.162 | −0.049 | −0.049 | | 0.059 | 0 | 0.27 |
| | Model 2 | 2.162 | | | | 0.079 | 0.05 | 0.26 |
| | Model 3 | 2.162 | | −0.035 | | 0.085 | 0.23 | 0.24 |
| | Model 4 | 2.162 | −0.028 | | | 0.062 | 1.52 | 0.13 |
| | Model 5 | 2.162 | −0.085 | −0.052 | | | 1.83 | 0.11 |
| | **Average model** | **2.162** | **−0.058** | **−0.044** | | **0.072** | – | – |
| | **Importance** | **–** | **0.50** | **0.61** | | **0.89** | – | – |

**Table 3** continued

| Dependent variable | | Intercept | lat | alt | lat × alt | $L_{max}$ | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|---|---|
| $L_{minF}$ | Model 1 | 2.188 | | | | 0.064 | 0 | 0.55 |
| | Model 2 | 2.188 | 0.019 | | | 0.075 | 1.69 | 0.24 |
| | Model 3 | 2.216 | 0.127 | 0.087 | 0.287 | 0.071 | 1.96 | 0.21 |
| | **Average model** | **2.194** | **0.069** | **0.087** | **0.287** | **0.068** | – | – |
| | **Importance** | **–** | **0.45** | **0.21** | **0.21** | **1.00** | – | – |

Only the models within ΔAICc < 2 are shown as well as their Akaike weight ($w_i$) value with respect to the best model. b is the exponent of the length-fecundity relationship, $L_{minM}$ and $L_{minF}$ are minimum length at maturity of males and females, respectively, $A_{matM}$ and $A_{matF}$ are age at maturity (50 % of a cohort) of males and females, $A_{max}$ is age when 10–15 % of a cohort is still alive, and $L_{max}$ is the mean length of the age-class correspondent to $A_{max}$

Average model estimate and relative importance of the variables are indicated in bold

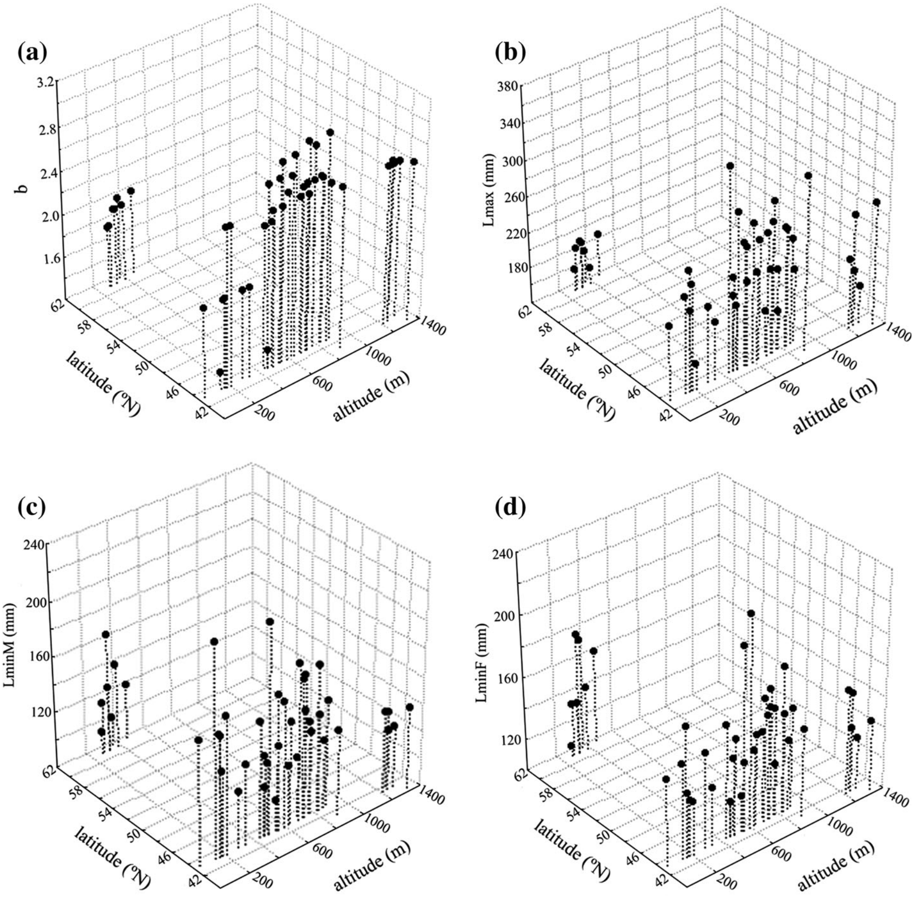

**Fig. 2** *Scatterplots* of **a** b, the exponent of the length-fecundity relationship; **b** $L_{max}$ (mm), mean length of the age-class correspondent to the maximum age ($A_{max}$, see text); **c**, **d** $L_{minM}$ and $L_{minF}$ (mm), minimum length at maturity of males and females respectively; versus altitude and latitude

individuals from higher altitude populations whereas those from populations at higher latitude would make a lower reproductive effort per body mass unit.

## Discussion

The studied life-history traits of stream-resident *S. trutta* largely varied across the altitudinal gradient and between populations from the southern and northern areas of the species distribution. At a smaller scale, maturity of an individual from populations in northern Spain was determined by its length, age, and sex, but also by altitude. Further, at a wider European scale longevity and age at maturity increased with altitude and latitude, consistent with our predictions. There were also geographical effects on male and female size at maturity, although the outcome was different between the sexes: males matured at a smaller size and also at a smaller relative size, whereas females matured at both a larger size and larger relative size.

Policansky (1983) predicted that fish under stable conditions with abundant food will "mature as soon as they are developmentally able to do so". Variation in abiotic (Parra et al. 2009) as well as biotic (Parra et al. 2011) factors leads to large spatiotemporal variability in the growth of *S. trutta* in northern Spain. Conditions in this area are generally favourable for the growth of this species, as water temperature is normally high but below the upper limit for growth during the growing season, a period that can last for more than 3 months at these latitudes. Besides, maturation in the subsequent breeding season is triggered earlier based on growth history (Jonsson and Jonsson 2011). Together, this can explain why the populations studied are short-lived and early maturing, similar to what has been described for other populations at the southern edge of the distribution of the species (e.g. Nicola and Almodóvar 2002). Moreover, a negative interaction between age and length supports the idea that maturity is not determined by a specific age or size but that it results from a combination of both traits, as suggested by Jonsson et al. (1984) for cutthroat trout *Oncorhynchus clarkii* (Richardson) and Dolly Varden *Salvelinus malma* (Walbaum). Age has also been described as affecting the size-maturity relationship in *S. salar* (Baum et al. 2004) and whitespotted char *Salvelinus leucomaenis* (Pallas) (Morita and Morita 2002). Stearns and Koella (1986) proposed that "most organisms mature neither at a fixed size nor a fixed age, but along an age-size trajectory". Given that reproduction implies growth and survival costs (Roff et al. 2006), maturation at a specific age would make slow-growing individuals mature at a size with lower fecundity, whereas maturation at a fixed length may delay maturation and thus increase pre-reproductive mortality for slow-growing individuals (Morita and Morita 2002).

Consistent with our predictions, individuals at a given size and age were more likely to be mature at high altitude sites in northern Spain. Further, *S. trutta* lived longer but attained smaller size at higher latitude. Metabolism is governed by temperature (see e.g. Atkinson 1994; Wootton 1998), so decreased rates of physiological processes occur as temperature decreases northwards and/or upwards. This thermal variation leads to altitudinal and latitudinal differences in growth and in other traits that co-evolve with growth, as has been described for many fish species (Mills 1988; Colby and Nepszy 1981; Mann et al. 1984; Heibo et al. 2005; Blanck and Lamouroux 2007). By delaying maturity, trout from northern and high elevation sites are able to dedicate all the surplus energy to growing for a longer period with the subsequent relative increase in fecundity, as well as increasing their total fitness by means of a longer life span. The main benefit of delaying maturation is an increase in body size, whereas the main cost is a decrease in the probability of surviving to first reproduction (Blanckenhorn 2000). Interestingly, the outcome of this trade-off between age at maturity and longevity is influenced by the environment in species belonging to a wide diversity of taxa (e. g. McAdam et al. 2007 in squirrels; Barret et al. 2010 in salamanders; Hjernquist et al. 2012 in frogs; Le Henanff et al. 2013 in lizards).

The slope of the length-fecundity relationship decreased with latitude indicating a reduced reproductive effort. Williams (1966) predicted a lower reproductive effort per reproductive time for longer-lived individuals. Charnov et al. (2007) refined this concept to the "Lifetime Reproductive Effort" which considers the reproductive effort by unit time multiplied by the average adult life span and is suggested to be constant among different species. In this study, those northern populations where growth is limited might have a less steep length-fecundity relationship so that more energy can be assigned to growth for as long as possible. This could imply decreased lifetime fecundity with respect to southern populations, but in combination with an older age at maturity and extended reproductive life span, it may actually increase the potential maximum length and the number of reproductive events, thus balancing lifetime total fecundity.

Also male trout tended to mature at smaller size with increasing altitude and/or latitude, in consonance with the idea that size at maturity reflects the growth opportunities of the river (Baum et al. 2005; Jonsson and Jonsson 2011). Male fitness is probably not as strongly determined by body size as for females (but see Serbezov et al. 2010), and it decreases when the number of competitors increases (Baum et al. 2005), so the expected benefits of delaying reproduction to increase body size are therefore much smaller in males. Competitors are expected to be smaller in sites with lower growth opportunities and/or higher altitude, therefore influencing male maturation thresholds. Morita et al. (2009) found that male *S. leucomaenis* inhabiting small rivers matured at smaller size and used refuges to increase their success with a sneaker strategy (to sneak fertilizations in the nests of large fighter males, see Gross 1991). Similarly, Baum et al. (2004) described size as a key for the early maturity of *S. salar* within a population, but not between populations, indicating the importance of the status relative to other males of the population. For this same reason, no geographical trends were detected in the relative size at maturity of males, indicating that maturation occurs at a similar point within the growing trajectory along a lifespan in places with different growing opportunities.

Contrastingly, female trout matured at older ages with increasing altitude and latitude and there were no geographical effects in their minimum size at maturity, but their relative length at maturity increased with increasing latitude. Although we acknowledge we are working with estimates that are dependent on sample size, so these results have to be considered cautiously, our findings may indicate that the thermal variation along altitudinal and latitudinal axes not only slows down physiology but also delays emergence (Elliott et al. 2000) and shortens the growing season (Dmitriew 2011). This leads to population differences in mean body size which are not only dependent on the age of individuals but also on the effective number of days available for growth per year (English et al. 2012; Hjernquist et al. 2012). Hence, northern *S. trutta* have a shorter growing season to accumulate reserve tissue to survive a longer winter. Since growth and reproduction compete directly for resources, northern and high-altitude conditions limit the opportunity for early maturation, especially in female trout, which would have to invest in growth for a longer period and so mature later. In the end, since growth rate, maximum size and longevity are partially determined by environmental conditions, life history traits like age at maturity are adjusted accordingly to maintain evolutionary fitness (Jennings and Beverton 1991).

To conclude, two contrasting life-history patterns were found in stream-dwelling *S. trutta* populations from very distant areas within the species distribution. The direction and strength of change in life-history traits with latitude was shaped by altitude and was also sex-specific. Sexual differences in energy allocation induce further differences in important life-history traits between males and females, which in organisms with indeterminate growth may imply different growth trajectories (see e.g. Hjernquist et al. 2012 in 11 species of frogs; Laver et al. 2012 in Komodo dragon *Varanus komodoensis* Ouwens; Zhang and Lu 2013 in 33 urodele species). Our findings are an example of a broad variability in life-history traits in *S. trutta*. The wide distribution of the species allows the colonization of habitats differing spatially and temporally. Thus, life-history strategies of conspecific populations vary accordingly as a consequence of phenotypic variability (see Jonsson and Jonsson 2011 and references therein), either caused by phenotypic plasticity or by local adaptation. Present day climate change intensifies the environmental constraints that already affect many thermally sensitive species, especially in the southern edge of their distribution (e.g. Root et al. 2003; Almodóvar et al. 2012). Latitudinally based studies are therefore important for the prediction of potential effects of global warming because of the latitudinal variation of key environmental parameters, which may be representative of climate-driven changes in life history traits over time (Power et al. 2005).

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