

# Unravelling the effects of water temperature and density dependence on the spatial variation of brown trout (*Salmo trutta*) body size

Irene Parra, Ana Almodóvar, Daniel Ayllón, Graciela G. Nicola, and Benigno Elvira

**Abstract:** This study looks at the relative influence of water temperature and density dependence on the spatial variation in body size of 126 brown trout (*Salmo trutta*) cohorts from 12 Iberian rivers over a 12-year period. Mean cohort mass and length of age groups 0+ to 2+ varied significantly among sampling sites because of the concurrent effect of water temperature and density dependence. Density in suitable habitat had a limiting role that influenced potential maximum growth of cohorts, and water temperature differentiated these cohorts in two groups of sites with high and low potential maximum growth. Water temperature had a positive cumulative effect on body size of all age classes. However, body size of age-0 trout was nonlinearly influenced by short-term exposure to extreme water temperature. Thus, extremely high temperatures became a limiting factor and had deleterious effects on growth. There were intracohort and intercohort effects of density dependence throughout the life span, which were mainly due to the density in the available suitable habitat of trout of the same age or older. The present study supports the hypothesis that both density-dependent and density-independent processes are crucial for the understanding of population dynamics and that their relative importance varies across scales of space and time.

**Résumé :** L'étude s'intéresse à l'influence relative de la température de l'eau et de la dépendance de la densité sur les variations spatiales de la taille du corps pour 126 cohortes de truite brune (*Salmo trutta*) de 12 rivières ibériennes, sur une période de 12 ans. La masse des cohortes et la longueur moyenne des groupes d'âge de 0+ an et 2+ ans variaient de manière significative selon le site de prélèvement, en raison des effets concomitants de la température de l'eau et de la dépendance de la densité. La densité dans les habitats convenables, jouait un rôle limitant qui influait sur la croissance maximum potentielle des cohortes, alors que la température de l'eau différençiait ces cohortes selon deux groupes de localités, qui présentaient des croissances maximums potentielles élevée et faible, respectivement. La température de l'eau avait un effet cumulatif positif sur la taille du corps pour toutes les classes d'âges. Toutefois, l'exposition de courte durée à des températures d'eau extrêmes avait un effet non linéaire sur la taille du corps des truites de 0 an. Les températures extrêmement élevées devenaient ainsi un facteur limitant et avaient des effets néfastes sur la croissance. Des effets intracohorte et intercohort de la dépendance de la densité étaient présents tout au long de la durée de vie, ces effets étant principalement dus à la densité dans l'habitat convenable disponible de truites du même âge ou plus vieilles. L'étude appuie l'hypothèse voulant que des processus dépendants et indépendants de la densité soient nécessaires pour expliquer la dynamique des populations et que l'importance relative de ces deux types de processus varie en fonction de l'échelle spatiale et temporelle.

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## Introduction

Fish growth is inherently linked to population dynamics, and therefore, its study and the elucidation of the numerous factors underlying body size variation is a central topic in fish ecology research (Lorenzen 2008). Body size of salmonids is limited by diverse factors that operate across space and time and induce variations in size within and among populations (Davidson et al. 2010; Bal et al. 2011; Jonsson and Jonsson 2011). However, these factors do not operate at all times or places, so their effects cannot be easily isolated

(Dunham et al. 2002). In fact, they may be interrelated, and one factor may reduce the influence of others. Consequently, a clear understanding of the effects of the factors that have the greatest influence on fish body size requires analysis of data over a wide spatial and temporal scale.

Brown trout (*Salmo trutta*) is widely distributed geographically and exhibits large interpopulation variations in body size (Nislow 2001; Vøllestad et al. 2002; Nicola and Almodóvar 2004), making it an excellent target for research on spatial variability in body size. Water temperature is considered the key environmental factor determining the variation

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**I. Parra, A. Almodóvar, D. Ayllón, and B. Elvira.** Department of Zoology, Faculty of Biology, Complutense University of Madrid, E-28040 Madrid, Spain.

**G.G. Nicola.** Department of Environmental Sciences, University of Castilla-La Mancha, E-45071 Toledo, Spain.

**Corresponding author:** Ana Almodóvar (e-mail: [aalmodovar@bio.ucm.es](mailto:aalmodovar@bio.ucm.es)).

in mean body size across populations, since it directly affects the individual's metabolism and feeding rate (Elliott 1994; Jonsson and Jonsson 2011). However, interpopulation variations in body size have also been shown to be density-dependent (Jenkins et al. 1999; Lobón-Cerviá 2007). Increased population density decreases the quantity and (or) quality of available per capita resources (e.g., Elliott 2002; Ward et al. 2006) and increases competition for territories that differ in feeding opportunities and thereby in growth potential for the fish (Ward et al. 2007). Clearly, the effects of density dependence on growth may derive from competition among members of either the same cohort or different cohorts. So as described by Hughes and Grand (2000), distribution at equilibrium of a size-structured population of growth-maximizing fish would depend not only on both the food an individual can get in a specific patch and the number of other fish that forage in this same patch (as predicted by the Ideal Free Distribution Theory; Fretwell and Lucas 1970), but also on water temperature and on the existing asymmetry in competitive abilities among individuals of different sizes.

To date, however, studies on body size variation of brown trout have only detected the effect of either water temperature or density dependence but not the concurrent effect of the two (e.g., Egglishaw and Shackley 1977; Elliott 1994; Lobón-Cerviá 2005). It may be difficult to detect both effects if one is predominant over the other, the spatial and (or) temporal scale of the study is not sufficiently large (see Jenkins et al. 1999; Lobón-Cerviá 2005), or the measures employed to evaluate density do not accurately characterize the level of fish crowdedness owing to differences in quality among habitat patches (see Parra et al. 2011). Both "raw" (density or biomass) or allometrically scaled measures of abundance, such as "effective density" (Post et al. 1999) or "percent habitat saturation" (Grant and Kramer 1990), may at times not be accurate indicators of potential for intraspecific competition, as they do not consider the availability of suitable habitat for fish. Habitat characteristics can stimulate the operation of density dependence, since not all positions provide the same payoff. Thus, the quality and quantity of feeding territories will eventually limit growth (Newman 1993). To accurately describe the level of crowdedness experienced by individuals, abundance should be measured with regard to the habitat that is suitable for fish (density in suitable habitat (DSH), i.e., the habitat in which fish can experience positive growth), since it is the space individuals actually compete for.

Habitat selection patterns and territory size requirements change throughout brown trout ontogeny (Ayllón et al. 2010a, 2010b). Thus, it is necessary to differentiate growth patterns by life stages. Constraints for body size at one stage may have consequences for later growth and associated life history traits. For instance, embryonic incubation temperature affects food conversion efficiency later in life (Rungruangsak-Torrissen et al. 1998), growth trajectories are determined by the first growing period (Vincenzi et al. 2008, Parra et al. 2009), and fecundity and egg size are positively related to female body size (Elliott 1984), with potential effects on survival and fitness of subsequent generations. Therefore, for predicting potential life history strategies and population trajectories, it is essential to understand which stages are affected by density-dependent growth and whether the operation of density dependence is qualified by environ-

mental factors, as well as to estimate the relative importance of each potential contributory factor along ontogeny (Davidson et al. 2010).

The aim of this work is to study the relative influence of water temperature and density dependence on the body size of brown trout. Twelve years of data (1993–2004) were analysed from 12 rivers in four different basins. The hypothesis presented is that both water temperature and DSH have a concurrent effect on body size. Whether the relative influence of these two factors varies throughout the ontogeny of the fish was also tested.

## Materials and methods

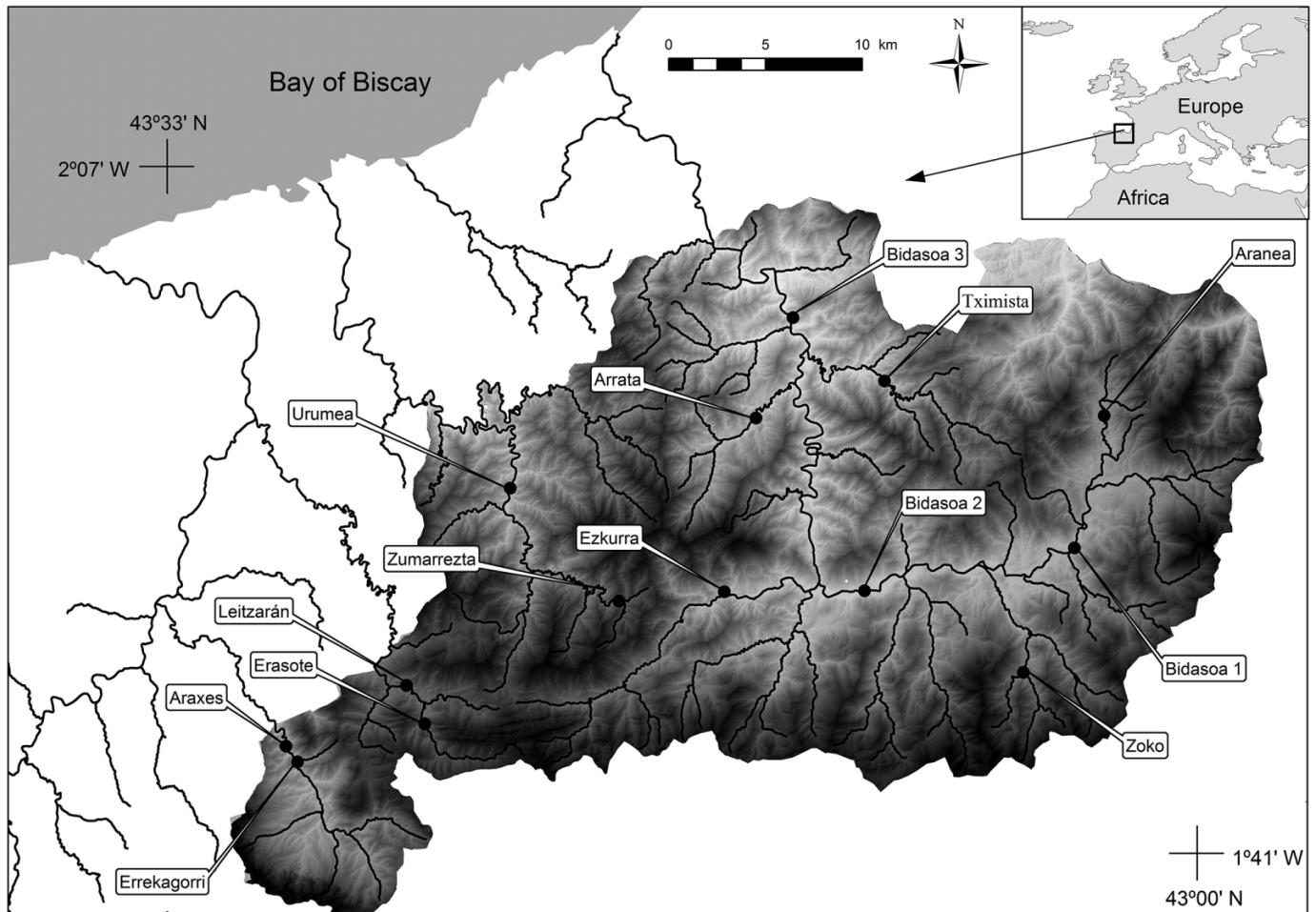
### Study area

Twelve rivers from the Bay of Biscay drainage were sampled annually during 1993–2004 (Fig. 1). One sampling site was selected for each river, except for River Bidasoa, which is the longest, where three sampling sites were located (Bidasoa 1 to 3). Sampling sites corresponded to first- to fifth-order streams and were located from 43°03'N to 43°16'N and from 1°29'W to 2°W, at an altitude ranging from 40 to 490 m. Brown trout is the prevailing fish species throughout the area, and its populations only comprise freshwater resident individuals. Less common species are European eel (*Anguilla anguilla*), Pyrenean gudgeon (*Gobio lozanoi*), Ebro nase (*Parachondrostoma miegi*), Pyrenean minnow (*Phoxinus phoxinus*), Pyrenean stone loach (*Barbatula barbatula*), and Atlantic salmon (*Salmo salar*), while Ebro barbel (*Luciobarbus graellsii*), rainbow trout (*Oncorhynchus mykiss*), and Adour sculpin (*Cottus aturi*) are rare. Consequently, interspecific competition levels are considered low. Ionic content is similar among the rivers, and water quality is in accordance with the limits set by Directive 2006/44/EC of the European Parliament (Council Directive 2006). Sampling sites were chosen to include the broad variability of environmental conditions and habitat saturation levels of the area. The "percent habitat saturation" measures the percentage of the streambed occupied by the territories of all trout in the stream. It was used for an a priori assessment of the level of stream habitat saturation, calculated by means of an allometric territory size relationship specifically developed for brown trout (Ayllón et al. 2010a). Percent habitat saturation values ranged between 6.9% and 75.5% within the study area.

### Fish assessment

Electrofishing with a 2200 W DC generator took place every year at the end of the main growing period (September, when individuals experience an overall reduction in growth) from 1993 to 2004. Individuals were anaesthetized with MS-222 (tricaine methanesulfonate, Sigma-Aldrich, St. Louis, Missouri, USA), measured (fork length,  $L$ , to the nearest mm), weighed ( $M$ , to the nearest g), and scales were taken for age determination. Then, the individuals were returned alive into the river.

The maximum likelihood method (Zippin 1956) and the corresponding solution proposed by Seber (1982) for three removals assuming constant-capture effort was applied to estimate fish densities (trout·ha<sup>-1</sup>) with variance for each age-class and each sampling site.

**Fig. 1.** Digital elevation model of the study area, showing the location of the sampling sites.

### Water temperature

Water temperature was measured with data loggers (Minolog Vemco, Ltd.; <http://www.vemco.com>) permanently placed in each site between July 2004 and October 2005. Maximum and minimum readings of each 24 h period were averaged to calculate mean daily temperature. We then fitted site-specific simple linear regression models with daily recorded water temperature as the dependent variable and daily air temperature data provided by the closest meteorological station as the independent variable ( $R^2$  of developed models ranged from 0.79 to 0.95). Finally, we calculated back historical time series of water temperature at each site based on historical air temperature time series. From the obtained data series, we calculated degree-days ( $^{\circ}D$ ,  $^{\circ}C$ ) for the period from March to September to include the cumulative thermal conditions experienced by trout during the main growing period and maximum mean temperature during 7 consecutive days from March to September ( $T_{\max 7d}$ ,  $^{\circ}C$ ) to study potential effects of physiological stress on growth. Seven days is the usual standard to estimate thermal tolerance of fish to short-term exposure (e.g., Elliott and Elliott 2010). Values were typical of temperate rivers. Rivers Urumea, Araxes, Leitzarán, and their tributaries (Rivers Zumarrezta, Errekagorri, and Erasote, respectively) had lower water temperatures, with mean values during the main growing period (March–September) ranging between 11.7 and 12.4  $^{\circ}C$ , while  $T_{\max 7d}$  was 15.1–15.7  $^{\circ}C$

and  $^{\circ}D$  was 2498–2658. Recorded values were higher for the remaining rivers, River Bidasoa and its tributaries Aranea, Zoko, Ezkurra, Arrata, and Tximista, which had mean temperatures during the main growing period oscillating between 14.1 and 15.8  $^{\circ}C$ ,  $T_{\max 7d}$  ranging between 18.4 and 22.5  $^{\circ}C$ , and  $^{\circ}D$  between 3074 and 3388.

### Physical habitat simulations and DSH

We used DSH (i.e., the number of individuals per square metre of suitable habitat) to measure fish crowdedness. We used the weighted usable area (WUA; an index of the quality and quantity of available habitat) as a proxy for suitable habitat. WUA dynamics were modelled using the physical habitat simulation system (PHABSIM; Milhous et al. 1989). In outline, PHABSIM simulations quantify the available suitable habitat for an aquatic species and its life stages in terms of the combination of stream hydraulics and channel structure at a particular discharge. PHABSIM modelling is based on the assumption that aquatic species will react to changes in their hydraulic environment. These changes are simulated as a function of discharge through different hydraulic models, and their suitability for the target species and life stages is then evaluated through a biological model of habitat selection (the habitat suitability criteria, HSC). Consequently, changes in hydraulic conditions cause changes in the amount and quality of available habitat. The standard output of PHAB-

SIM simulations is the curve that relates the WUA ( $\text{m}^2\text{-ha}^{-1}$ ) with stream flow.

Topographic, hydraulic, and channel structure data required to perform PHABSIM simulations were collected at each study site during August of 2004 following the data collection procedures described by Bovee (1997). Physical habitat variables (depth, velocity, substrate, and cover) were measured every 1 m along transects placed perpendicular to the flow. The percentage (%) of substrate and cover were visually estimated within a 1  $\text{m}^2$  quadrat. Substrate was classified according to modified categories from classification by Platts et al. (1983) as silt (particle size less than 0.8 mm), sand (0.8–4.7 mm), gravel (4.8–76.0 mm), cobble (76.1–304.0 mm), boulder (more than 304.0 mm), and bedrock. We defined cover as any element other than substrate that can provide protection to fish against predators or adverse environmental conditions. The type of cover was classified as vegetation (aquatic or overhanging), woody debris, undercut bank, combined cover (combination of vegetation and woody debris), pools, and under cascade. Transects were selected to best describe the longitudinal distribution of all types of mesohabitats (cascade, rapid, riffle, run, and pool) present within the site and were weighted by the proportion of site length they represented. An average of  $6.4 \pm 2.2$  transects were sampled per site. Sample length at study sites was 10 to 15 channel widths long, that is, two morphological cycles according to the general precepts of alluvial river morphology on the spacing of successive riffles (Leopold et al. 1964). Average length of study sites was  $99.3 \pm 22.6$  m, and average assessed area of study sites was  $886.1 \pm 261.1$   $\text{m}^2$ .

To model brown trout habitat selection, site-specific depth, velocity, and channel index (a variable combining substrate and cover features) preference curves for young-of-the-year (0+), juvenile (1+), and adult (2+) life stages were built, following methods described in Ayllón et al. (2010b). In the present study, the channel index was established as a combination of substrate and cover features. Whenever an element providing cover was present, it was considered the main structural element of the quadrat, whereas dominant substrate represented channel index when no cover elements were available in the quadrat. Field samplings conducted to collect habitat use and habitat availability data were designed to minimize the uncertainty in WUA curves derived from HSC development (see Ayllón et al. 2012). HSC varied as a function of both local site-specific hydraulic and morphological features and catchment-scale physical attributes. Aranea, Erasote, and Zumarrezta study sites corresponded to the river reach typology (RT) 1 described in Ayllón et al. (2010b), while Errekagorri and Zoko corresponded to RT 2, Arrata, Leitazarán, and Tximista to RT 3, Araxes to RT 4, Bidasoa 1 to RT 5, Ezkurra to RT 6, Urumea to RT 7, and Bidasoa 2 and 3 to RT 8. HSC developed for every kind of reach typology are fully described in Ayllón et al. (2010b).

Historical time series of mean summer discharge (July–September) for the 12-year study period (1993–2004) were provided at each study site by the closest gauging stations. Then, mean summer WUA time series for each age-class were obtained by coupling WUA curves as a function of discharge with discharge time series. Habitat competition analyses sensu Waddle (2001) were performed to model spatial segregation of cohorts due to intercohort competition and,

hence, to avoid an overestimation of suitable habitat for each age-class. Since there is a certain degree of overlap in habitat preferences among age-classes, there are PHABSIM cells where one age-class is better suited (i.e., has a higher composite suitability index) than another age-class and other cells where the converse is true. The competition analysis quantifies the total shared WUA where one age-class dominates over the other one and vice versa. We considered that in areas where younger age-classes have less favourable habitat conditions they cannot out-compete older ones with more suitable habitat, being finally displaced, so that this WUA is not added to total available suitable habitat. Analyses of habitat competition between age-classes were made using the effective habitat analysis program (HABEF) within PHABSIM system. Further methodological aspects of competition analyses can be checked in Waddle (2001). As a final step, DSH (trout- $\text{m}^{-2}$  WUA, i.e., number of individuals per square metre of WUA) were calculated from density data and physical habitat simulation results for every age-class, year, and site (results are summarized in Table 1).

## Data analyses

### *Analyses of cohort-specific mass vs. DSH and water temperature*

We explored the existence of spatial differences in the cumulative effect of both water temperature and DSH on mean body size of brown trout through a life span by means of regression analyses. Mean cohort-specific mass ( $M$ ; mean mass of an individual averaged during the first 3 years of life, i.e., age classes 0+ to 2+, within each cohort) was used as the dependent variable. Fixed effects included in the model selection process were cohort density in suitable habitat ( $\text{DSH}_C$ ) and a variable measuring water temperature, either cumulative degree-days during the main growing period (March–September) along the first 3 years of life ( $^{\circ}\text{D}_C$ ) or maximum mean temperature during 7 consecutive days from March to September averaged for the first 3 years ( $T_{\text{max}7\text{d}C}$ ). A squared term of  $T_{\text{max}7\text{d}C}$  was included to test for nonlinear effects of extreme water temperatures. Cohort-year was included as a random effect to look for a temporally stable spatial relationship between the variables.

We first tried to find the optimal random structure by comparing the beyond optimal linear mixed effects (LME) model, containing cohort-year as a random effect, with the beyond optimal generalized least squares (GLS) model by means of Akaike information criterion (AIC) values based on restricted maximum likelihood (REML) estimation. Once the optimal random structure was found, we looked for the optimal fixed structure. We used an information-theoretic approach (Burnham and Anderson 2002) to select the best model, since they allow objective selection of the model most consistent with the data while balancing the trade-off between precision and bias. We constructed a set of candidate models resulting from different combinations of the fixed effects, including all meaningful interactions, and compared the AIC values based on maximum likelihood estimation.

To further describe the relationship between DSH and body size, we performed quantile regressions with cohort-specific mass ( $M$ ) as dependent and  $\text{DSH}_C$  as independent variables. While least squares regression predicts an expected

**Table 1.** Density in suitable habitat (DSH; mean  $\pm$  standard deviation; trout-m<sup>-2</sup> WUA) for three trout age-classes and the average experienced by a cohort during the first 3 years of life, throughout the 12-year study period at 14 sampling sites from the Bay of Biscay.

| Sampling site | DSH <sub>0</sub> | DSH <sub>1</sub> | DSH <sub>2</sub> | DSH <sub>C</sub> |
|---------------|------------------|------------------|------------------|------------------|
| Araxes        | 2.14 $\pm$ 1.705 | 0.57 $\pm$ 0.490 | 0.38 $\pm$ 0.331 | 1.09 $\pm$ 0.800 |
| Errekagorri   | 3.66 $\pm$ 2.171 | 0.95 $\pm$ 0.579 | 0.64 $\pm$ 0.336 | 1.75 $\pm$ 0.970 |
| Erasote       | 4.94 $\pm$ 3.357 | 1.12 $\pm$ 0.479 | 0.65 $\pm$ 0.132 | 2.19 $\pm$ 1.352 |
| Leitzarán     | 1.20 $\pm$ 0.845 | 0.56 $\pm$ 0.775 | 0.13 $\pm$ 0.044 | 0.72 $\pm$ 0.528 |
| Urumea        | 2.71 $\pm$ 2.340 | 0.72 $\pm$ 0.751 | 0.41 $\pm$ 0.223 | 1.43 $\pm$ 1.028 |
| Zumarrezta    | 3.11 $\pm$ 2.600 | 1.06 $\pm$ 0.733 | 0.72 $\pm$ 0.336 | 1.87 $\pm$ 1.042 |
| Bidasoa 1     | 1.58 $\pm$ 1.598 | 0.60 $\pm$ 0.359 | 0.22 $\pm$ 0.066 | 0.90 $\pm$ 0.614 |
| Bidasoa 2     | 0.63 $\pm$ 1.055 | 0.42 $\pm$ 0.199 | 0.18 $\pm$ 0.092 | 0.46 $\pm$ 0.407 |
| Bidasoa 3     | 0.08 $\pm$ 0.074 | 0.28 $\pm$ 0.161 | 0.11 $\pm$ 0.076 | 0.15 $\pm$ 0.047 |
| Aranea        | 3.13 $\pm$ 3.133 | 0.94 $\pm$ 0.428 | 0.43 $\pm$ 0.181 | 1.73 $\pm$ 1.196 |
| Zoko          | 3.79 $\pm$ 4.043 | 1.12 $\pm$ 0.532 | 0.65 $\pm$ 0.274 | 2.00 $\pm$ 1.578 |
| Ezkurra       | 2.78 $\pm$ 1.995 | 0.83 $\pm$ 0.534 | 0.47 $\pm$ 0.300 | 1.63 $\pm$ 0.815 |
| Arrata        | 2.12 $\pm$ 1.219 | 0.66 $\pm$ 0.281 | 0.33 $\pm$ 0.173 | 1.03 $\pm$ 0.472 |
| Tximista      | 2.33 $\pm$ 1.459 | 0.53 $\pm$ 0.164 | 0.11 $\pm$ 0.067 | 1.14 $\pm$ 0.512 |

value of the dependent variable as a function of one or more independent variables, quantile regression analyses all portions of a distribution and allows estimations of a limit, a potential maximum value of the dependent variable (McClain and Rex 2001; Dunham et al. 2002; Cade and Noon 2003). In this context, a limiting factor sets the upper limit for the response variable so the output cannot be better than indicated by the limiting factor, but it could be worse if other factors are also affecting the response (Milhous and Bartholow 2006). We performed bootstrapped (1000 repetitions) quantile regression estimates of the 5th, 25th, 50th, 75th, and 95th quantiles (Q5, Q25, Q50, Q75, and Q95, respectively) using STATA (StataCorp; <http://www.stata.com>). We then tested whether water temperature was related to the residuals from quantile regressions.

#### Analyses of length-at-age vs. DSH and water temperature

We also tested whether spatial variability in length-at-age ( $L_x$ ) was driven by differences in water temperature conditions (of both long-term cumulative,  $^{\circ}D$ , and short-term acute exposures,  $T_{\max 7d}$ ) and variations in both the life-stage-specific density in suitable habitat (DSH <sub>$x$</sub> ) of the current cohort (intracohort effects) and DSH <sub>$x$</sub>  of accompanying cohorts (intercohort effects). As for the cohort analysis, we first studied the random structure of the models with year as random effect to account for sampling-year differences and to look for a yearly stable spatial relationship between the variables. After finding the optimal random structure of the model, we constructed a set of candidate models to define the optimal fixed structure. We considered that  $L_x$  of trout may be affected either by DSH of the three age-classes considered in this work, only by the DSH of its own age-class, or also by the DSH of the immediately younger or older age-classes, as it is more plausible that they compete for territory and food. We also allowed for the possibility of nonlinear effects of extreme water temperature ( $T_{\max 7d}$ ). All meaningful interactions of fixed effects were also included.

We used log-transformed density,  $L_x$ , and cohort-specific mass to perform all the analyses, since previous studies (e.g., Jenkins et al. 1999; Imre et al. 2005) have shown negative power functions as descriptors of relationships between abundance and body size. We checked that correlation between

variables measuring DSH was always weak ( $|r| < 0.5$ ), and we never included both water temperature variables within the same model to avoid collinearity. The models were fitted using the nlme package in R (Pinheiro et al. 2011). We chose the model with the lowest AIC value, and whenever competing models were equally supported (i.e.,  $\Delta AIC < 2$ , Burnham and Anderson 2002) we picked the one with the lower number of parameters as long as all parameters were significant. We recalculated the coefficients of the chosen model with REML estimation. The relative independent contribution of the variables in the final model was evaluated by means of hierarchical partitioning (Chevan and Sutherland 1991), using the hier.part package in R (Walsh and McNally 2009).

## Results

#### Analyses of cohort-specific mass vs. DSH and water temperature

AIC values indicated that the LME model was not better than the GLS model, so cohort-year was not included as random factor. The best GLS model explaining variance in cohort-specific mass ( $M$ ) included DSH<sub>C</sub> and water temperature ( $^{\circ}D_C$ , Table 2). It explained 57% of the total variance in  $M$  and showed that  $M$  significantly increased with  $^{\circ}D_C$  and decreased with DSH<sub>C</sub>, the contribution of DSH<sub>C</sub> to the model being considerably higher (Table 3).

All quantile regressions were significant (Table 4). Increasing DSH caused a decrease in cohort-specific mass, since the slopes of the analysed quantiles were negative throughout the range of quantiles (Fig. 2; Table 4). Slopes were not significantly different through the range of quantiles ( $P > 0.05$ ). Data points were not randomly distributed regarding the estimated quantiles, but their distribution matched the two growth patterns described by Parra et al. (2009) for the rivers of the area. The rivers described as the high-growth group were consistently near the upper quantiles, whereas the rivers from the low-growth group were closer to the lower quantiles (Fig. 2). Water temperature was significantly correlated to residuals from all quantile regressions; Pearson's  $r$  increased with quantile from Q5 ( $r = 0.19$ ,  $P < 0.05$ ) to Q95 ( $r = 0.31$ ,  $P < 0.001$ ).

**Table 2.** Models fit to cohort-specific mass ( $M$ ) and length-at-age  $x$  ( $L_x$ ).

| Model  | $\Delta AIC$ | $w_i$ |
|--|--------------|-------|
| <b>Cohorts</b>   |              |       |
| $DSH_C + {}^\circ D_C$   | 0.00         | 0.44  |
| $DSH_C + T_{\max 7dC} + T_{\max 7dC}^2$  | 1.32         | 0.23  |
| $DSH_C + T_{\max 7dC} + T_{\max 7dC}^2 + DSH_C \times T_{\max 7dC}$  | 2.28         | 0.14  |
| $DSH_C + {}^\circ D_C + DSH_C \times {}^\circ D_C$   | 2.70         | 0.11  |
| $DSH_C$  | 3.27         | 0.09  |
| $T_{\max 7dC} + T_{\max 7dC}^2$  | 77.10        | 0.00  |
| ${}^\circ D_C$   | 86.89        | 0.00  |
| <b><math>L_0 +</math></b>  |              |       |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2$  | 0.00         | 0.21  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times T_{\max 7d}$   | 1.52         | 0.10  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_0 \times {}^\circ D$   | 1.72         | 0.09  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times DSH_2$   | 2.12         | 0.07  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D$   | 2.65         | 0.06  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times DSH_2 + DSH_0 \times T_{\max 7d}$                      | 2.78         | 0.05  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_0 \times DSH_2 + DSH_0 \times {}^\circ D$  | 2.88         | 0.05  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_0 \times DSH_2$  | 2.98         | 0.05  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times DSH_1$   | 2.98         | 0.05  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times DSH_1 + DSH_0 \times T_{\max 7d}$                      | 2.99         | 0.05  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_0 \times DSH_1 + DSH_0 \times {}^\circ D$  | 3.11         | 0.04  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times DSH_1 + DSH_0 \times DSH_2$                            | 3.13         | 0.04  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_0 \times DSH_1$  | 3.41         | 0.04  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times DSH_1 + DSH_0 \times DSH_2 + DSH_0 \times T_{\max 7d}$ | 3.75         | 0.03  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_0 \times DSH_1 + DSH_0 \times DSH_2 + DSH_0 \times {}^\circ D$                   | 3.81         | 0.03  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_0 \times DSH_1 + DSH_0 \times DSH_2$   | 3.97         | 0.03  |
| $DSH_0 + DSH_1 + T_{\max 7d} + T_{\max 7d}^2$  | 12.25        | 0.00  |
| $DSH_0 + DSH_1 + {}^\circ D + DSH_0 \times {}^\circ D$   | 12.55        | 0.00  |
| $DSH_0 + DSH_1 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times T_{\max 7d}$   | 12.76        | 0.00  |
| $DSH_0 + DSH_1 + {}^\circ D$   | 13.63        | 0.00  |
| $DSH_0 + DSH_1 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times DSH_1$   | 14.21        | 0.00  |
| $DSH_0 + DSH_1 + {}^\circ D + DSH_0 \times DSH_1 + DSH_0 \times {}^\circ D$  | 14.46        | 0.00  |
| $DSH_0 + DSH_1 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times DSH_1 + DSH_0 \times T_{\max 7d}$                              | 14.75        | 0.00  |
| $DSH_0 + DSH_1 + {}^\circ D + DSH_0 \times DSH_1$  | 15.61        | 0.00  |
| $DSH_0 + {}^\circ D + DSH_0 \times {}^\circ D$   | 32.38        | 0.00  |
| $DSH_0 + T_{\max 7d} + T_{\max 7d}^2 + DSH_0 \times T_{\max 7d}$   | 33.21        | 0.00  |
| $DSH_0 + T_{\max 7d} + T_{\max 7d}^2$  | 35.31        | 0.00  |
| $DSH_0 + {}^\circ D$   | 36.08        | 0.00  |
| <b><math>L_1 +</math></b>  |              |       |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_1 \times DSH_2$  | 0.00         | 0.31  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_1 \times DSH_0 + DSH_1 \times DSH_2$   | 1.75         | 0.13  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_1 \times DSH_2 + DSH_1 \times {}^\circ D$  | 2.12         | 0.11  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_1 \times DSH_2$   | 2.21         | 0.10  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_1 \times DSH_0 + DSH_1 \times DSH_2 + DSH_1 \times {}^\circ D$                   | 3.69         | 0.05  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_1 \times DSH_0 + DSH_1 \times DSH_2$                            | 4.02         | 0.04  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_1 \times DSH_2 + DSH_1 \times T_{\max 7d}$                      | 4.20         | 0.04  |
| $DSH_1 + DSH_2 + {}^\circ D + DSH_1 \times DSH_2$  | 4.22         | 0.04  |
| $DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_1 \times DSH_2$   | 4.28         | 0.04  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D$   | 4.39         | 0.03  |
| $DSH_0 + DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_1 \times DSH_0 + DSH_1 \times DSH_2 + DSH_1 \times T_{\max 7d}$ | 6.00         | 0.02  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_1 \times DSH_0$  | 6.12         | 0.01  |
| $DSH_1 + DSH_2 + {}^\circ D + DSH_1 \times DSH_2 + DSH_1 \times {}^\circ D$  | 6.12         | 0.01  |
| $DSH_1 + DSH_2 + T_{\max 7d} + T_{\max 7d}^2 + DSH_1 \times DSH_2 + DSH_1 \times T_{\max 7d}$                              | 6.23         | 0.01  |
| $DSH_0 + DSH_1 + DSH_2 + {}^\circ D + DSH_1 \times {}^\circ D$   | 6.27         | 0.01  |

**Table 2** (concluded).

| Model   | $\Delta AIC$ | $w_i$ |
|---|--------------|-------|
| <b>DSH<sub>1</sub> + DSH<sub>2</sub> + °D</b>   | 6.56         | 0.01  |
| DSH <sub>0</sub> + <b>DSH<sub>1</sub></b> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$  | 7.05         | 0.01  |
| <b>DSH<sub>1</sub> + DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$  | 7.72         | 0.01  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + °D + DSH <sub>1</sub> × DSH <sub>0</sub> + DSH <sub>1</sub> × °D   | 8.05         | 0.01  |
| DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + °D + DSH <sub>1</sub> × °D  | 8.52         | 0.00  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>1</sub> × $T_{max7d}$   | 8.58         | 0.00  |
| DSH <sub>0</sub> + <b>DSH<sub>1</sub></b> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>1</sub> × DSH <sub>0</sub>  | 8.72         | 0.00  |
| DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>1</sub> × $T_{max7d}$  | 9.17         | 0.00  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>1</sub> × DSH <sub>0</sub> + DSH <sub>1</sub> × $T_{max7d}$                                 | 10.39        | 0.00  |
| <b>DSH<sub>0</sub> + DSH<sub>1</sub> + °D</b>   | 17.29        | 0.00  |
| DSH <sub>0</sub> + <b>DSH<sub>1</sub></b> + °D + DSH <sub>1</sub> × DSH <sub>0</sub>  | 19.20        | 0.00  |
| <b>DSH<sub>0</sub></b> + DSH <sub>1</sub> + °D + DSH <sub>1</sub> × °D  | 19.29        | 0.00  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + °D + DSH <sub>1</sub> × DSH <sub>0</sub> + DSH <sub>1</sub> × °D  | 21.20        | 0.00  |
| <b>DSH<sub>0</sub> + DSH<sub>1</sub></b> + $T_{max7d}$ + $T_{max7d}^2$  | 21.46        | 0.00  |
| DSH <sub>0</sub> + <b>DSH<sub>1</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>1</sub> × DSH <sub>0</sub>   | 23.37        | 0.00  |
| <b>DSH<sub>0</sub></b> + DSH <sub>1</sub> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>1</sub> × $T_{max7d}$  | 23.46        | 0.00  |
| <b>DSH<sub>1</sub> + °D</b>   | 24.60        | 0.00  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>1</sub> × DSH <sub>0</sub> + DSH <sub>1</sub> × $T_{max7d}$  | 25.35        | 0.00  |
| <b>DSH<sub>1</sub></b> + $T_{max7d}$ + $T_{max7d}^2$  | 26.39        | 0.00  |
| DSH <sub>1</sub> + °D + DSH <sub>1</sub> × °D   | 26.46        | 0.00  |
| DSH <sub>1</sub> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>1</sub> × $T_{max7d}$   | 28.38        | 0.00  |
| <b>L<sub>2</sub> +</b>  |              |       |
| <b>DSH<sub>0</sub> + DSH<sub>1</sub> + DSH<sub>2</sub> + °D</b>   | 0.00         | 0.20  |
| <b>DSH<sub>0</sub> + DSH<sub>1</sub> + DSH<sub>2</sub></b> + °D + DSH <sub>2</sub> × DSH <sub>1</sub>   | 0.61         | 0.14  |
| <b>DSH<sub>0</sub></b> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + °D + DSH <sub>2</sub> × °D   | 1.54         | 0.09  |
| <b>DSH<sub>0</sub></b> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + °D + DSH <sub>2</sub> × DSH <sub>0</sub>   | 1.62         | 0.09  |
| <b>DSH<sub>0</sub></b> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + °D + DSH <sub>2</sub> × DSH <sub>1</sub> + DSH <sub>2</sub> × °D   | 2.10         | 0.07  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + °D + DSH <sub>2</sub> × DSH <sub>0</sub> + DSH <sub>2</sub> × DSH <sub>1</sub>   | 2.20         | 0.07  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + DSH <sub>2</sub> + °D + DSH <sub>2</sub> × DSH <sub>0</sub> + DSH <sub>2</sub> × °D   | 2.39         | 0.06  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + DSH <sub>2</sub> + °D + DSH <sub>2</sub> × DSH <sub>0</sub> + DSH <sub>2</sub> × DSH <sub>1</sub> + DSH <sub>2</sub> × °D                                   | 3.25         | 0.04  |
| <b>DSH<sub>0</sub> + DSH<sub>1</sub> + DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × DSH <sub>1</sub>  | 3.36         | 0.04  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$  | 3.86         | 0.03  |
| <b>DSH<sub>1</sub> + DSH<sub>2</sub> + °D</b>   | 4.17         | 0.02  |
| <b>DSH<sub>0</sub></b> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × DSH <sub>0</sub>  | 4.58         | 0.02  |
| <b>DSH<sub>0</sub></b> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × $T_{max7d}$   | 4.68         | 0.02  |
| <b>DSH<sub>1</sub> + DSH<sub>2</sub></b> + °D + DSH <sub>2</sub> × °D   | 5.11         | 0.02  |
| <b>DSH<sub>0</sub></b> + DSH <sub>1</sub> + DSH <sub>2</sub> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × DSH <sub>1</sub> + DSH <sub>2</sub> × $T_{max7d}$                                 | 5.13         | 0.02  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × DSH <sub>0</sub> + DSH <sub>2</sub> × DSH <sub>1</sub>                            | 5.30         | 0.01  |
| <b>DSH<sub>1</sub> + DSH<sub>2</sub></b> + °D + DSH <sub>2</sub> × DSH <sub>1</sub>   | 5.30         | 0.01  |
| <b>DSH<sub>1</sub> + DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$  | 5.78         | 0.01  |
| <b>DSH<sub>1</sub> + DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × DSH <sub>1</sub>  | 6.23         | 0.01  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + DSH <sub>2</sub> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × DSH <sub>0</sub> + DSH <sub>2</sub> × $T_{max7d}$                                       | 6.33         | 0.01  |
| DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + °D + DSH <sub>2</sub> × DSH <sub>1</sub> + DSH <sub>2</sub> × °D  | 6.69         | 0.01  |
| DSH <sub>1</sub> + <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × $T_{max7d}$  | 6.79         | 0.01  |
| DSH <sub>0</sub> + DSH <sub>1</sub> + DSH <sub>2</sub> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × DSH <sub>0</sub> + DSH <sub>2</sub> × DSH <sub>1</sub> + DSH <sub>2</sub> × $T_{max7d}$ | 7.13         | 0.01  |
| <b>DSH<sub>2</sub> + °D</b>   | 7.42         | 0.00  |
| DSH <sub>2</sub> + °D + DSH <sub>2</sub> × °D   | 7.81         | 0.00  |
| DSH <sub>1</sub> + DSH <sub>2</sub> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × DSH <sub>1</sub> + DSH <sub>2</sub> × $T_{max7d}$  | 7.95         | 0.00  |
| <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$  | 7.99         | 0.00  |
| <b>DSH<sub>2</sub></b> + $T_{max7d}$ + $T_{max7d}^2$ + DSH <sub>2</sub> × $T_{max7d}$   | 8.64         | 0.00  |

**Note:** The models are ordered by  $\Delta AIC$  value, which shows the difference between a model and the chosen model. Akaike weights ( $w_i$ ) are also shown. Significant effects of predictors ( $P < 0.05$ ) are indicated in bold. DSH<sub>x</sub> is density in suitable habitat of an age-class, °D is degree-days from March to September, and  $T_{max7d}$  is maximum mean temperature during 7 consecutive days. Year was included as a random effect in all models.

**Table 3.** Parameter estimates of density in suitable habitat (DSH, trout·m<sup>-2</sup> WUA) and water temperature (°D, degree-days from March to September;  $T_{\max 7d}$ , maximum mean temperature during 7 consecutive days; °C) from regression models best explaining variations in average cohort-specific mass ( $M$ ) and length-at-age ( $L_x$ ) of brown trout from a 12-year study period (10 cohorts) in 14 sampling sites from the Bay of Biscay.

| Dependent variable | Model summary                    | Fixed factor                        | Coefficient | Relative contribution (%) | $P$    |
|--------------------|----------------------------------|-------------------------------------|-------------|---------------------------|--------|
| $M$                | GLS<br>$R^2 = 0.58$ ; $df = 123$ | (Intercept)                         | 1.05834     | —                         | <0.001 |
|                    |                                  | °D <sub>C</sub>                     | 0.00012     | 12.2                      | <0.05  |
|                    |                                  | DSH <sub>C</sub>                    | -0.46471    | 87.8                      | <0.001 |
| $L_{0+}$           | LME<br>$R^2 = 0.56$ ; $df = 131$ | (Random intercept)                  | 0.17710     | —                         | >0.05  |
|                    |                                  | $T_{\max 7d}$                       | -0.00157    | 31.3                      | <0.01  |
|                    |                                  | $T_{\max 7d}^2$                     | 0.06372     | —                         | <0.05  |
|                    |                                  | DSH <sub>0</sub>                    | -0.02394    | 17.4                      | <0.01  |
|                    |                                  | DSH <sub>1</sub>                    | -0.03689    | 22.2                      | <0.01  |
| $L_{1+}$           | GLS<br>$R^2 = 0.52$ ; $df = 143$ | (Intercept)                         | 0.98366     | —                         | <0.001 |
|                    |                                  | °D                                  | 0.00004     | 14.8                      | <0.01  |
|                    |                                  | DSH <sub>0</sub>                    | -0.01865    | 16.0                      | <0.05  |
|                    |                                  | DSH <sub>1</sub>                    | -0.10248    | 33.9                      | <0.001 |
|                    |                                  | DSH <sub>2</sub>                    | -0.07836    | 35.3                      | <0.001 |
| $L_{2+}$           | GLS<br>$R^2 = 0.61$ ; $df = 141$ | DSH <sub>1</sub> × DSH <sub>2</sub> | -0.07443    | —                         | <0.05  |
|                    |                                  | (Intercept)                         | 1.08392     | —                         | <0.001 |
|                    |                                  | °D                                  | 0.00005     | 20.1                      | <0.001 |
|                    |                                  | DSH <sub>0</sub>                    | -0.01506    | 14.9                      | <0.05  |
|                    |                                  | DSH <sub>1</sub>                    | -0.01913    | 12.2                      | <0.05  |
|                    |                                  | DSH <sub>2</sub>                    | -0.08730    | 52.8                      | <0.001 |

**Note:** The relative independent contribution of each predictor (given as a percentage of explained variance) is shown. GLS, generalized least squares; LME, linear mixed effects.

**Table 4.** Quantile regressions of average cohort-specific mass ( $M$ ) vs. density in suitable habitat (DSH<sub>C</sub>) of brown trout from a 12-year study period (10 cohorts) in 14 sampling sites from the Bay of Biscay.

| Quantile | Model                                     | pseudo- $R^2$ | $P$    |
|----------|---|---------------|--------|
| Q5       | $M = 13.02 \times \text{DSH}_C^{(-0.56)}$ | 0.22          | <0.001 |
| Q25      | $M = 20.03 \times \text{DSH}_C^{(-0.56)}$ | 0.32          | <0.001 |
| Q50      | $M = 25.74 \times \text{DSH}_C^{(-0.51)}$ | 0.35          | <0.001 |
| Q75      | $M = 35.63 \times \text{DSH}_C^{(-0.46)}$ | 0.38          | <0.001 |
| Q95      | $M = 57.41 \times \text{DSH}_C^{(-0.38)}$ | 0.29          | <0.001 |

#### Analyses of length-at-age vs. DSH and water temperature

AIC values indicated that the LME model with random intercept was better than the GLS model. The optimal fixed structure included both intracohort DSH (DSH<sub>0</sub>) and intercohort DSH (DSH<sub>1</sub> and DSH<sub>2</sub>) and  $T_{\max 7d}$  in a nonlinear fashion (Table 2). No interaction terms were included. It explained 56% of the variance, and the highest relative influence was that of intercohort DSH (Table 3).

Regarding length on the second and third year of life ( $L_{1+}$  and  $L_{2+}$ ), the best-supported models did not include year as a random effect. In both cases, fixed effects were DSH of the three age-classes and °D (Table 2). Besides, the scaling rate of  $L_{1+}$  with DSH<sub>1</sub> was significantly and negatively affected by DSH<sub>2</sub>, whereas no interaction terms were included in the model for  $L_{2+}$ . The chosen models explained 52% and 61% of the variance in  $L_{1+}$  and  $L_{2+}$ , respectively (Table 3).  $L_{1+}$  was mainly and equally affected by both DSH<sub>1</sub> and DSH<sub>2</sub>, whereas spatial variation of  $L_{2+}$  was mainly explained by variations in DSH<sub>2</sub>. The effect of water temperature was lower on  $L_{2+}$  than on  $L_{1+}$ .

To sum up, increased water temperature and decreased both intracohort and intercohort DSH resulted in increased  $L_x$ , irrespective of age-class. However, we also detected a significant nonlinear effect of short-term extreme water temperature exposure on length at the first year of life, so that  $L_{0+}$  was reduced at  $T_{\max 7d}$  values above 20.3 °C. While the effect of water temperature weakened along ontogeny, the influence of intracohort density increased markedly with age.

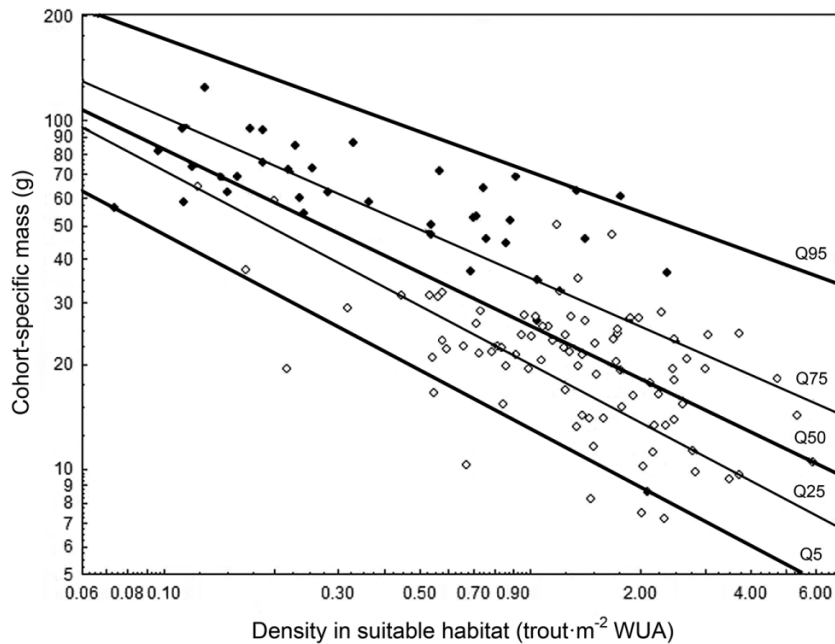
#### Discussion

Both density-dependent and density-independent processes drive brown trout body size variations across study populations. This was revealed by the fact that both water temperature and intracohort and intercohort DSH were significantly correlated with  $L_x$  across the populations studied and by a cumulative effect of both variables on the mass of a cohort. Alone, temperature is known to drive interpopulation variations in growth (Jensen et al. 2000; Nicola and Almodóvar 2004; Forseth et al. 2009), as does fish density (Vøllestad et al. 2002; Grant and Imre 2005; Parra et al. 2011). The combined effects of the two factors, however, had remained elusive.

Spatial variation in cohort-specific mass across the studied populations was explained by a negative effect of DSH and a positive effect of water temperature. The relative influence of both factors differed, however, the effect of DSH being stronger. Likewise, an analysis of  $L_x$  showed that water temperature exerted a higher influence on body size during the first year of life (0+) but also that this effect diminished throughout ontogeny. The effect of density dependence on growth, on the other hand, rose with increasing fish age, as previ-



**Fig. 2.** Quantile regressions (Q5, Q25, Q50, Q75, and Q95) of average cohort-specific mass vs. density in suitable habitat rate of brown trout from a 12-year study period (10 cohorts) in 14 sampling sites from the Bay of Biscay. Solid symbols and open symbols refer to high-growth and low-growth patterns, respectively, described in Parra et al. (2009).



ously shown by Arnekleiv et al. (2006) for Atlantic salmon. Thus, when the first 3 years of life were considered together, density dependence overrode the effects of water temperature in explaining differences in cohort-specific mass.

Quantile regressions showed that maximum cohort-specific mass declined with increasing levels of fish crowdedness experienced throughout the life span. Nevertheless, the dispersion of data from the maximum potential body size set by DSH suggested that unexplained variability in cohort-specific mass may be due to factors other than density dependence. The parallel slopes of the quantiles indicated that these factors do not interact with DSH but rather their effects are additive (Cade et al. 1999). Furthermore, water temperature was positively correlated with the residuals from the analysis, establishing two types of rivers, in accordance with Parra et al. (2009). Cohorts from large main courses, characterized by higher water temperature and (or) lower altitude and thus higher prey productivity, were associated with the highest quantiles (75th and 95th), whereas cohorts from smaller main courses and tributaries, located at higher altitude and with lower water temperature and food supply, were generally associated with the lowest quantiles (from the 5th to the 50th). Shima and Osenberg (2003) suggested that the covariation of both density-independent factors and density-dependent processes may obscure the detection of density dependence. In our study, the dispersion of data in the point cloud within the range of densities where cohorts from both the high- and low-growth river types overlapped may have masked the effect of density dependence on body size. This was not the case because the broad spatio-temporal scale used in the present study provided a wide enough range in DSH to detect the growth effect. However, in other instances it is necessary to account for spatial variability in environmental factors to detect density-dependent effects, which might otherwise remain cryptic.

In the analyses of  $L_x$ , a year effect was only detected when measuring the size of age-0 trout. Year effects may include yearly differences in variables such as extreme flow events or food availability, and this variation does not seem to be strong enough to affect the body size of older trout. Water temperature had a higher impact on the length of age-0 trout when compared with older trout. Incubation temperature could have influenced the date of emergence from the stream bed and may have caused interpopulation differences in emergence time (Elliott and Hurley 1998; Ojanguren and Braña 2003; Nicola et al. 2009), which would lead to variations in the length of trout after the first growing period (Ojanguren and Braña 2003; Nicola and Almodóvar 2004). Water temperature may also influence the physiology of fish, causing differences in enzymes related to food conversion efficiency (Rungruangsak-Torrissen et al. 1998) as discussed by Jonsson et al. (2005) for Atlantic salmon. Thus, this higher thermal effect on growth in the first year, whether it be direct or indirect, together with an expected higher prey productivity in warmer rivers, would establish spatial differences in growth between the rivers from the first year of life. In addition, ontogenetic changes in optimal temperature for growth, together with the improved ability of older individuals to move toward preferred temperature areas (Morita et al. 2010), may progressively diminish the effect of water temperature on growth performance throughout the life span.

Furthermore, the length of age-0 trout was influenced by a nonlinear effect of maximum water temperature. Thus, trout grew larger with increasing temperature up to values where extreme temperatures became limiting and had deleterious effects on growth. This harmful effect of extreme maximums on the body size of alevins but not on older individuals may be related to the allometric relationship between volume and the fish's surface area, which makes youngest life stages more susceptible to both extreme maximum and minimum

temperatures (Brett 1952) as well as to temperature fluctuations (Elliott 1994). Additionally, increased swimming performance allows juveniles and adults to move toward cooler areas during extreme temperature events. These results are of special importance under the current scenario of climate change, since freshwater conditions are projected to worsen (higher temperatures and longer droughts; Intergovernmental Panel on Climate Change 2007), this being especially critical at the southern edge of the distribution range of brown trout (Jonsson and Jonsson 2009; Almodóvar et al. 2012), where these populations are located. As shown by our findings, warmer water would affect the growth of recruits, with subsequent effects on reproduction and fitness, and may eventually affect future recruitment and survival of the populations.

Brown trout were smaller in rivers with higher DSH (higher potential for intraspecific competition) irrespective of considered age-class. The relationships were power negative (i.e., the effect is stronger for lower values of DSH). Brown trout size-at-age was affected by both intracohort and intercohort DSH, although the major effects were exerted by intracohort density and density of older cohorts. The negative effect of increased intracohort density on the spatial variation of body size of salmonids has been previously reported (e.g., Imre et al. 2005; Lobón-Cerviá 2007). It was also expected that body size of a certain cohort increases as density of older cohorts decreases (e.g., Jenkins et al. 1999; Nordwall et al. 2001; Lobón-Cerviá 2005), since individuals of younger age-classes are able to use more profitable stream positions. In this way, a higher density of older cohorts not only had a direct negative effect on body size of trout on the second year of life, but also magnified the deleterious effect of intracohort density. The reverse effect, a negative influence of younger age-classes on the growth of older trout, may seem less direct, but it could be explained by interference competition mechanisms. Since habitat preferences of different age-classes typically overlap in a higher or lesser degree (see Ayllón et al. 2009, 2010b), there are stream habitats that are concurrently suitable for the different age-classes. When these habitats are more suitable for younger trout, the occupation of these marginal habitats by older individuals is only energetically profitable when the density of younger competitors is low. Despite the fact that younger individuals cannot out-compete older ones, increasing density of younger trout results in increased metabolic costs associated with guarding and defending territories and thus reduces the growth of older trout. Similar results were found by Kvingedal and Einum (2011) in Atlantic salmon. In addition, higher densities of younger age-classes would depress growth of older ones through exploitative competition for food, since even if younger individuals cannot out-compete older ones they can consume prey that otherwise would have been available to older age-classes.

This study shows that water temperature and DSH are concurrently acting on the body size of stream-dwelling brown trout, with the relative influence of both factors on body size changing throughout ontogeny. Water temperature would mainly affect growth the first year of life, with potential harmful effects in the case of short-term exposure to extreme water temperatures. The operation of intracohort and intercohort density dependence throughout the life span would also determine the wide spatial differences in body size observed

across rivers. The findings add new insights into the key role of both density-dependent and density-independent processes on population dynamics and their differential influence across scales of space and time.

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