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Ontogenetic variation in density-dependent growth of brown trout through habitat competition

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SUMMARY

1. Density-dependent growth has been widely reported in freshwater fishes, but the ontogenetic evolution of competition and its subsequent effects on growth through a life span remains unclear.
2. Patterns of competition can be described by integrating population abundance data with habitat-modelling results. Weighted usable area (WUA; m^2 WUA ha^{-1}) curves are obtained for each flow value and are then coupled with demographic data to obtain the occupancy rates (trout m^{-2} WUA, the density of a given age class related to its suitable habitat) of the WUA for every age class, year and site.
3. We examined a long-term data series searching for temporal variation in the influence of habitat occupancy rate on the growth of brown trout *Salmo trutta*. We tested whether (i) mean cohort mass (mean mass of the cohort during the first 3 years of life) is affected by the occupancy rate experienced across a life span; and (ii) the occupancy rate experienced at different ages influenced mean body size.
4. We observed a consistent negative power relationship between average cohort mass and mean occupancy rate through a life span, indicating that stronger cohorts were related to a reduced growth, with likely consequences for individual fitness.
5. The effects of occupancy rate on size-at-age were mainly detected in the size attained at the second year of life, but they were because of the competition at different times. Thus, the level of competition varied through ontogeny, in some of the rivers affecting growth since the first year of life, whereas in most of the rivers the main effects on body size resulted from the competition during the second year of life.
6. Occupancy rate appears more appropriate than density for assessing the occurrence of habitat competition in freshwater fishes, since it encompasses the differences in quantity and quality of suitable habitat for each age class.
7. Our study highlights the importance of density-dependent growth as a key process in the dynamics of brown trout populations, its temporal variation depending on the temporal changes of density and the variation of competition associated with the habitat capacity for each life stage.

Keywords: density dependence, life history, physical habitat simulation, population dynamics, Salmonids

Introduction

Density-dependent growth has been described in both marine (Lorenzen & Enberg, 2002) and freshwater fishes (e.g. Byström & García-Berthou, 1999; Jenkins

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et al., 1999; Imre, Grant & Cunjak, 2005; Lobón-Cerviá, 2005, 2007; Schram *et al.*, 2006). High population densities cause competition for resources, which become depleted as a consequence of the increased abundance of individuals (Heath, 1992). This competition is often asymmetric between and within size classes in structured populations, and thus, it changes as a function of the environment and/or ontogenetic stage (Werner, 1994). The operation of density on fish growth usually results in interannual variations in fecundity, recruitment and in size-at-maturity, which ultimately affect fitness (Lobón-Cerviá *et al.*, 1997; Cowan, Rose & DeVries, 2000; Jonsson *et al.*, 2001; Nicola & Almodóvar, 2002). Salmonids are a useful system for the study of density-dependent growth as they usually live in seasonally variable environments where they often defend territories (Vøllestad & Olsen, 2008). Some authors have concluded that growth is density-independent (Egglishaw & Shackley, 1977; Mortensen, 1977) or that the effects of density on growth are restricted to low-density populations, whereas density-dependent losses would occur at high densities (Imre *et al.*, 2005). Elliott (1990a, 1994, 2009) found that increasing density did not affect mean mass of the population, but decreased the variation in the individual mass around the mean value. Newman (1993) further predicted that high densities could lead to an increase in the number of slower growers with a consequent increase in the variance of growth.

Many studies have been made to explore density dependence in salmonids, especially in brown trout, *Salmo trutta* L., sometimes expressing abundance either as the total number or total biomass (Jensen, Forseth & Johnsen, 2000; Vøllestad, Olsen & Forseth, 2002; Grant & Imre, 2005), which underestimates differences in the intensity of density-dependent interactions related to body size (Post, Parkinson & Johnston, 1999). Besides, previous studies have not yet elucidated the possible effects of the temporal variation in competition level on the growth of brown trout. Grant & Imre (2005) concluded that density-dependent growth occurs in the first year of life but only at low densities, whereas mortality and emigration increase with increasing density. Young-of-the-year is a stage with a high competition for resources (Milner *et al.*, 2003) but the conditions experienced during this first period also have consequences on growth that can persist through a lifetime (Nicola & Almodóvar, 2004; Parra *et al.*, 2009). Therefore, long-term studies including older fish are needed to elucidate the temporal variation in the effects of density on fish growth. Moreover, fish growth could also show cohort effects, i.e. growth may be affected by the maternal and the environmental conditions during the first year of life. Therefore, cohort strength could have effects over individual growth within each cohort (Lobón-Cerviá, 2005), these effects being evident on fitness through generations (Davey *et al.*, 2006; Vincenzi *et al.*, 2008).

Fish growth is related to the quality of the foraging territories (Newman, 1993; Ward *et al.*, 2007), and habitat characteristics can stimulate the operation of density dependence. Several authors have developed some measures to characterise the intensity of density-dependent interactions by accounting for the allometry in food consumption, like 'effective density' (Post *et al.*, 1999), or in space requirements, such as percent habitat saturation (PHS, Grant & Kramer, 1990). PHS measures the per cent of the streambed occupied by the territories of all salmonids in the stream and has been used by some authors to assess the level of competition (e.g. Grant & Imre, 2005; Lobón-Cerviá, 2005). However, PHS may sometimes be misleading when defining thresholds to the operation of density dependence, since it ignores the proportion of streambed suitable for the population, which is the space individuals actually compete for. Competition levels may differ greatly between populations presenting similar PHS values when the availability of suitable habitat also differs widely. Therefore, the use of habitat occupancy rates (i.e. the density of a given age class related to its suitable habitat) would be a more appropriate measure of competition for the study of density-dependent responses. Physical habitat is much determined by the interaction of the structural features of the stream channel and the hydrological regime (Maddock, 1999). Suitable habitat for an aquatic species and life stage can be estimated as a function of streamflow through physical habitat simulation models. By coupling hydraulic data with biological data, these models simulate the temporal evolution in habitat quality and quantity in relation to flow conditions. Ultimately, the patterns of competition can be depicted by integrating population abundance data with habitat-modelling results.

This study analyses the occurrence of density-dependent growth in nine contrasting populations of stream-living brown trout from the southern species distribution, where a previous study has revealed wide spatial differences in brown trout growth patterns (Parra *et al*., 2009). We used two complementary approaches to analyse the influence of intraspecific competition on the growth of brown trout. First, we hypothesised that growth can be affected by intracohort occupancy rate through a life span. Thus, stronger cohorts are expected to have smaller cohort-specific masses. To test this prediction, we compared the cohort-specific occupancy rate and mass of nine populations during 12 years. Second, we aimed to elucidate the period when the effect of competition on growth is greatest, by analysing the relationships between size-at-age by cohort and year and the occupancy rate on the current and previous years.

Methods

Study area

Data were collected in the north of Spain, during 1993–2004. Nine rivers from the Bay of Biscay drainage were sampled at nine sampling sites corresponding to first- to fifth-order streams and located from 43°03′ to 43°13′N and from 1°29′ to 2°′W. These sites included a wide range of environmental conditions and habitat saturation levels within the area. Saturation of habitat capacity was measured through the PHS (Grant & Kramer, 1990; Table 1) calculated by means of an allometric territory size relationship specifically developed for brown trout (Ayllón *et al*., 2010a). Brown trout is the most common fish species in the rivers, and its populations comprise only resident individuals. Environmental characteristics of the study sites are detailed in Parra *et al.* (2009).

Fish assessment

Electrofishing with a 2200-W DC generator took place every year at the end of the growing period from 1993 to 2004. Individuals were anaesthetised with MS-222 (tricaine methanesulfonate; Sigma-Aldrich, St. Louis, MO, U.S.A.), 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.

Fish densities (trout ha^{-1}) with variance were estimated separately for each sampling site by applying the maximum likelihood method (Zippin, 1956) and the corresponding solution proposed by Seber (1982) for three removals assuming constant-capture effort. Population estimates were carried out separately for each year class.

Physical habitat simulations and occupancy rate

Habitat modelling was performed using the physical habitat simulation (PHABSIM) system (Milhous, Updike & Schneider, 1989). PHABSIM simulations determine the potentially available habitat for an aquatic

Table 1 Habitat suitability metrics for three trout age classes throughout the 12-year study period at nine study rivers: the area occupied by trout territories (percent habitat saturation, PHS); the proportion of suitable habitat available in the reach (weighted usable area, WUA/total reach area; % WUA); and the average of suitable habitat saturation by age class (WUA S), quantified as the annual ratio between PHS and %WUA. Note that values shown for each metric for each river are the means of the 12 calculated annual values and therefore the 12-year mean values for WUA S do not necessarily correspond exactly to the ratios between the 12-year means for PHS and %WUA

	0+			1+			>1+		
River	PHS	% WUA	WUA S	PHS	% WUA	WUA S	PHS	% WUA	WUA S
Araxes	6.2	8.1	0.81	9.1	11.8	0.77	9.9	20.5	1.01
Errekagorri	12.3	13.5	0.98	13.7	17.9	0.79	8.3	12.4	1.10
Erasote	14.0	12.5	1.30	22.0	20.1	1.11	39.5	47.0	1.24
Urumea	4.2	4.9	0.99	9.2	9.6	1.24	7.4	12.0	0.96
Zumarrezta	6.2	8.5	0.78	19.0	6.3	0.84	12.2	15.8	1.16
Bidasoa	4.1	6.4	0.81	17.8	19.8	0.90	5.2	11.9	0.63
Aranea	9.5	10.7	1.06	28.6	29.2	0.98	18.8	29.0	0.86
Zoko	7.1	8.1	0.89	9.8	26.6	0.73	10.1	11.5	1.01
Arrata	5.6	4.9	1.19	9.8	11.6	0.85	2.4	3.7	0.78
Mean	7.7	8.6	0.98	16.5	17.0	0.91	12.6	18.2	0.97
Maximum	14.0	13.5	1.30	28.6	29.2	1.24	39.5	47.0	1.24
Minimum	4.1	4.9	0.78	9.1	6.3	0.73	2.4	3.7	0.63

species and its life stages as a function of discharge by coupling a hydraulic model with a biological model of habitat selection (the habitat suitability criteria, HSC). PHABSIM modelling is based on the assumption that aquatic species will react to changes in the hydraulic environment. These changing conditions on stream hydraulics are simulated as a function of discharge, and their suitability for an aquatic species and its life stages is evaluated through the HSC. Consequently, changes in hydraulic conditions cause changes in the amount and quality of available habitat. The standard output of PHABSIM simulations is the curve that relates the weighted usable area (WUA; m^2 WUA ha^{-1}, an index of the quality and quantity of available habitat) with streamflow.

Topographic, hydraulic and channel structure data needed to carry out PHABSIM simulations were collected at each study site during the summer of 2004 following the data collection procedures described by Bovee (1997). Physical habitat variables (depth, velocity, substrate and cover) were measured every one metre along transects placed perpendicular to the flow. These transects were selected to best describe the longitudinal distribution of all types of mesohabitats present within the site and were weighted by the proportion of site length they represented. For this purpose, at least two transects were located at each mesohabitat type. Sample length at study sites was 5–7 times the average channel width, in accordance with the general precepts of alluvial river morphology on the spacing of successive riffles (Leopold, Wolman & Miller, 1964). Average length of study sites was 99.9 ± 8.0 m, and average assessed area of study sites was 805.4 ± 168.1 m^2.

Results from PHABSIM are extremely sensitive to the accuracy of HSC used in the model, so site-specific depth, velocity and channel index (a variable combining substrate and cover features) preference curves for YOY (0+), juvenile (1+) and adult (>1+) life stages were built. To do this, electrofishing was carried out at each study site to define habitat use. Captured trout were measured (fork length, to the nearest mm) and assigned to one of the aforementioned age classes. Numbered tags were dropped wherever a trout was captured, and depth, current velocity, substrate and cover were measured afterwards in a 1-m^2 quadrat. Data collected for hydraulic and habitat simulations were used to estimate habitat availability. Univariate preference curves were developed for each age class according to standard methods (Ayllón *et al*., 2009).

Historical time series of mean summer discharge 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 was obtained by coupling WUA curves as a function of discharge with discharge time series. Habitat competition analyses were performed to model spatial segregation of cohorts because of competition and hence to avoid an overestimation of potential available habitat for each age class. In the areas where direct competition occurs, there are cells where one age class is better suited 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 shared areas where younger age classes have less favourable habitat conditions, they cannot out-compete older ones with more suitable habitat, being finally displaced, so this shared WUA was not added to total available habitat. Analyses of habitat competition between age classes were made using the HABEF program within PHABSIM system. Methodological aspects of competition analyses are described in Waddle (2001).

Finally, occupancy rates of the WUA (trout m^{-2} WUA, i.e. number of individuals per square metre of WUA) were calculated from demographic data and physical habitat simulation results for every age class, year and site.

Data analysis

Two different approaches were used to explore density-dependent growth. Firstly, the cumulative effect of cohort strength on the growth of brown trout through a life span was analysed by regressing the cohort-specific occupancy rate, i.e. the mean occupancy rate (Or_i) during the first 3 years of life of cohort i (age classes 0+ to 2+, well represented in all the studied rivers) and cohort-specific mass (M_i, g), i.e. mean mass of the cohort i during the first 3 years of life.

Secondly, to identify the period when the effect of competition on growth is greatest, length-at-age (L_x, cm) was compared to the life stage-specific occupancy rate ($Or_{x,\ i}$). Length-at-age x on year i was also compared with life stage-specific occupancy rate experienced by these individuals on year $i-1$, when they were age $x-1$ ($Or_{x-1,\ i-1}$), as well as with the mean occupancy rate of the time interval from year $i-1$ to year i [$(Or_{x-1,\ i-1} + Or_{x,\ i})/2$].

Previous studies (Crisp, 1993; Jenkins *et al.*, 1999) have shown negative power functions as descriptors of relationships between abundance and growth and therefore we used log-transformed variables to perform all the analyses by means of linear regression models. Whenever L_x was significantly related to the occupancy rate in different life stages, multiple regression analyses were used to detect the highest effect on L_x.

Results

Cohort-specific growth

Cohort-specific mass was related to cohort-specific occupancy rate in all the studied rivers (Fig. 1). These relationships were negative power and highly significant, explaining between 59 and 82% of the mass variance. Thus, cohorts that showed higher occupancy rates during the first 3 years of life were smaller on average. Therefore, as expected, growth was affected by the density of conspecifics through a life span in overall populations.

Effects of occupancy rate on size-at-age

Length at the first year of life (L_{0+}) was related to the occupancy rate at this life stage ($Or_{0+,\ i}$) in one river (Fig. 2; growth pattern 1), probably because in the rest of the rivers the effect of $Or_{0+,\ i}$ was exerted throughout the first year of life and its effects were detected in L_{1+}. Consequently, the most consistent relationships were detected when analysing length of trout on their second year of life (L_{1+}). L_{1+} was negatively related to the mean occupancy rate on the period from 0+ to 1+ (Or_{0-1+}) in eight of nine studied rivers. When partitioning the effects of intracohort competition during the 0+ to 1+ period, we observed that L_{1+} was significantly related to the occupancy rate experienced the previous year as 0+ ($Or_{0+,\ i-1}$) in eight of nine rivers, whereas in seven rivers L_{1+} was related to the occupancy rate of 1+ trout observed the current year ($Or_{1+,\ i}$) (Fig. 2). Thereafter, multiple regression analyses showed that the highest amount of L_{1+} variance was explained by $Or_{0+,\ i-1}$ in the four rivers where habitat saturation (WUA S, Table 1), and thus competition levels at YOY stage, were higher than at the cohort's second year of life (Table 1, growth pattern 2). In the remaining five rivers, where habitat saturation levels were higher at the juvenile stage, $Or_{1+,\ i}$ was the variable that explained the highest proportion of the variance (growth pattern 3). In one of these five rivers, L_{1+} was only related to $Or_{1+,\ i}$. Therefore, the time when the operation of density dependence on L_{1+} is stronger was conditioned by the intensity of competition on year $i-1$ relative to year i, that is, the stage with higher competition would have the strongest effects on L_{1+}.

In addition, length at the third year of life (L_{2+}) was influenced by the mean occupancy rate on the period 1+ to 2+ (Or_{1-2+}) in half of the rivers. In two of them, L_{2+} was related to the occupancy rate of this age class ($Or_{2+,\ i}$) while the occupancy rate experienced the previous year as 1+ ($Or_{1+,\ i-1}$) was also related to L_{2+} in three rivers (Fig. 2). In the river where the occupancy rate of both years had significant effects on L_{2+}, multiple regression analyses showed that the highest amount of variance was explained by $Or_{1+,\ i-1}$.

Overall, intraspecific competition would have exerted effects on growth at different moments in the populations. It begins when density approaches carrying capacity, reaches a peak in the life stage when saturation comes closest to carrying capacity and then lessens after a long period of growth restriction.

Discussion

In nine rivers and over a 12-year period, there was a consistent negative power relationship between the mean occupancy rate of cohorts and their cohort-specific masses, indicating a strong influence of the conditions experienced through a life span on the growth of a cohort. As expected, stronger cohorts were associated with a reduced growth throughout their lives. Thus, the natural alternation of favourable and unfavourable years would give rise to weak and strong cohorts and would make the population fluctuate around its carrying capacity. This mechanism could also be crucial for the recovery of populations after disturbance events and provide new evidence for the relevance of density-dependent growth in population dynamics and hence in population regulation and persistence. To date, most cohort studies on vertebrates have evaluated the influence of conditions in the first year of life, which

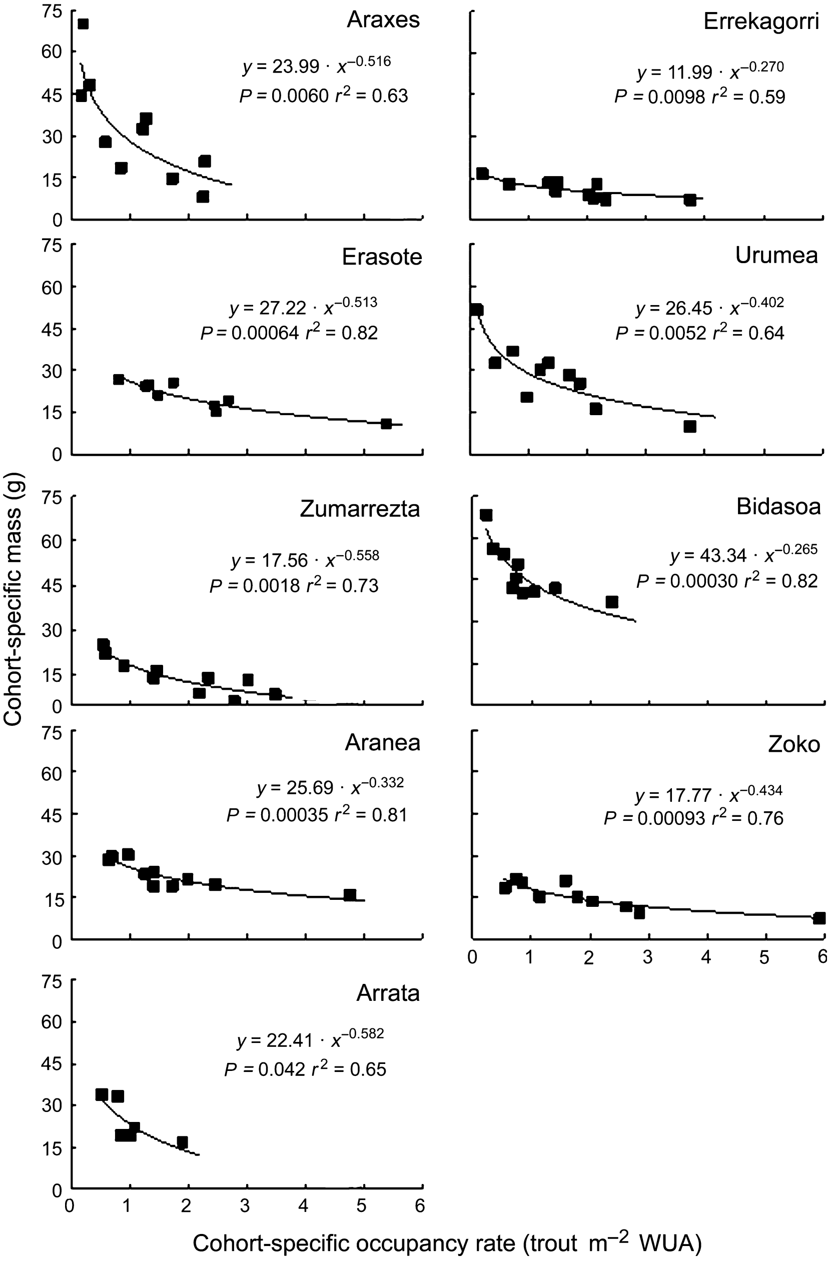

Fig. 1 Cohort-specific mass versus cohort-specific occupancy rate for ten cohorts (1993–2002) of brown trout from nine rivers.

comprises a high proportion of total growth, on the adult fitness (e.g. Lindström, 1999; Gaillard *et al.*, 2003; Descamps *et al.*, 2008). Moreover, it is a well-known fact that circumstances during early life in fishes have long-lasting influences on growth and thus affect age at maturity (Jonsson *et al.*, 2001; Olsen & Vøllestad, 2005), fecundity (Nicola & Almodóvar, 2002) and egg size (Ojanguren, Reyes-Gavilán & Braña, 1996), therefore shaping individual fitness (Metcalfe & Monaghan, 2001) and finally the strength of subsequent cohorts. However, vertebrate growth is significant during more than 1 year, especially until maturity is reached, so taking a longer period into account appears to be necessary when studying long-term cohort effects.

Previous studies of salmonids have often focused on density-dependent growth of individuals during their first year of life (e.g. Crisp, 1993; Keeley, 2001; Grant & Imre, 2005; Imre *et al.*, 2005) but the effects of density may also be detected in older age classes (Jenkins *et al.*, 1999; Cowan *et al.*, 2000; Bohlin *et al.*, 2002; Lobón-Cerviá, 2005; Davey *et al.*, 2006). A deeper knowledge of

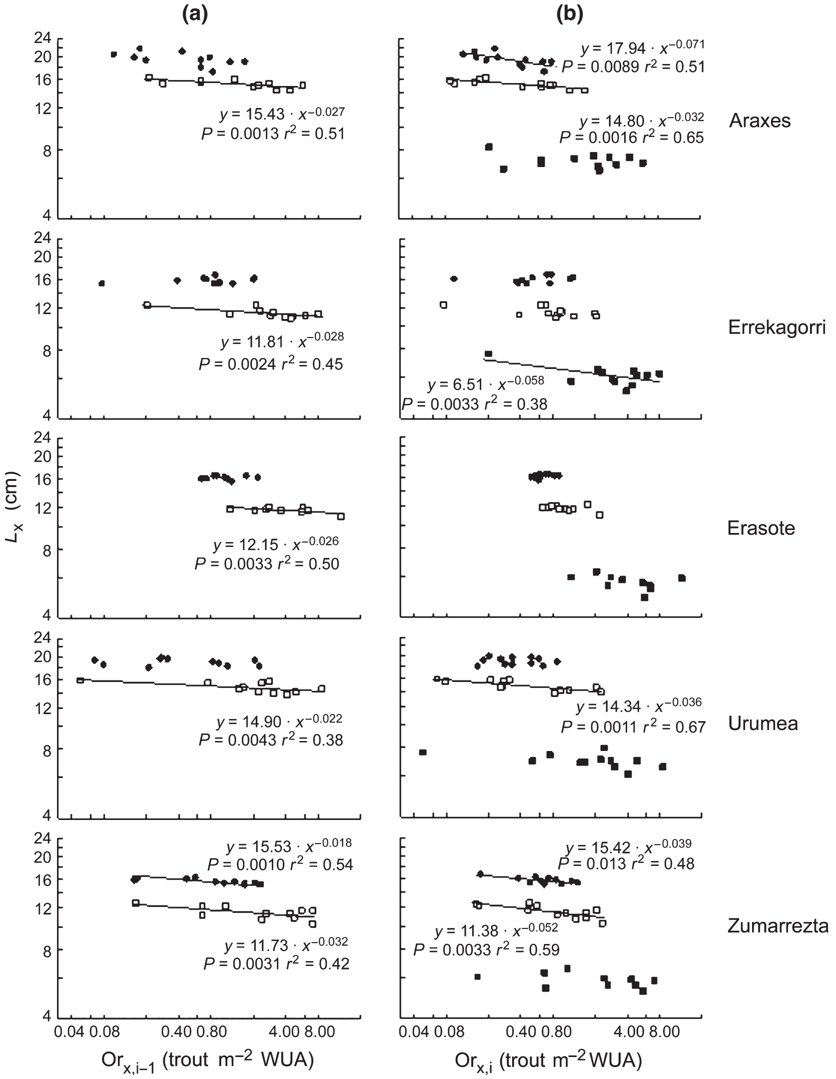

Fig. 2 Average fork length relative to (a) occupancy rate of 1+ and 2+ trout in year *i*-1, when they were age-0+ (open squares) and age-1+ (filled circles) trout, respectively and to (b) occupancy rate of 0+ (filled squares), 1+ (open squares) and 2+ (filled circles) trout in year *i*. Lines indicate significant regressions.

the stage when competition exerts the strongest effect on growth during the life span of a cohort could be of major importance for understanding competitive interactions and their consequences in population dynamics. With that purpose, we carried out a year-to-year study and, as a result, we observed that in all the studied rivers the main effects of competition on growth were detected in the size attained at the second year of life. However, these effects resulted from different levels of competition at diverse times through the life span. Thus, in some rivers, competition was high enough to induce a reduction in growth since the first year of life, whereas in the rest of the rivers competition exerted the highest influence on growth during the second year of life. In some populations, the size of trout in the third year of life was still affected by the levels of competition at previous stages. These results, considered as a whole, show different temporal patterns of density-dependent growth through a life span.

The proportion of available habitat varies between rivers and between age classes since habitat requirements change over ontogeny (e.g. Armstrong *et al.*, 2003; Ayllón *et al.*, 2010b), leading to different patterns of evolution of competition through life, as a result of the temporal variation of the density-habitat capacity relationship. Thus, the initial recruitment and the evolution of occupancy rate while trout increase their body size would make competition start sooner or later and hence also its effects on growth. If occupancy rate was high enough to limit growth very soon after emergence, the effects

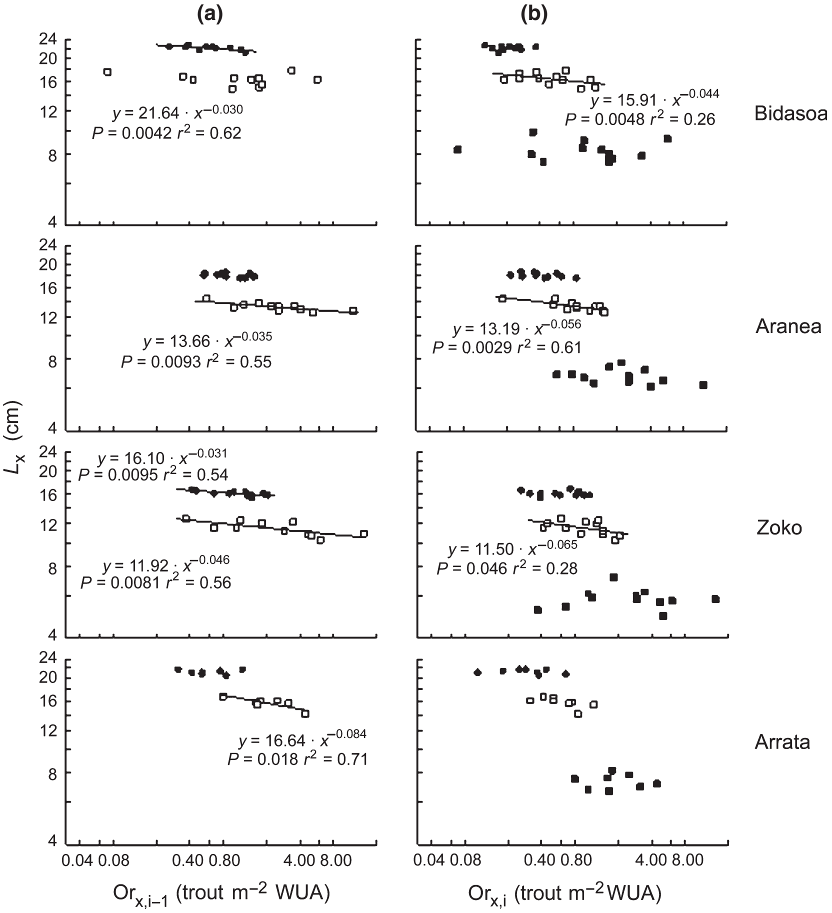

Fig. 2 *Continued.*

on growth could be detected in the length of trout at a younger age. This first scenario concurs with the situation observed in the first of the growth patterns described in this work (growth pattern 1). Despite the fact that an early effect of competition on growth is a common situation previously described in the salmonid literature (e.g. Crisp, 1993; Keeley, 2001; Grant & Imre, 2005; Imre *et al.*, 2005), we only detected this pattern in one river. Nevertheless, it has been suggested that YOY would be primary regulated through density-dependent mortality (Elliott, 1994) since smaller individuals would be more susceptible to starve by increased food deprivation via competition than older ones (Bohlin *et al.*, 2002; Einum, Sundt-Hansen & Nislow, 2006). Later in ontogeny, individuals have a higher capacity to survive a density-dependent reduction in energy intake so the major effects of increased competition would be observed on growth (Einum *et al.*, 2006). Therefore, if the increase in competition happened close to the summer samplings, the effects on growth would probably not be detected in the length of trout in their first year of life, but could be strong enough to have effects on the size attained the following year (growth pattern 2). A time lag between resource limitation and the response to it has been previously considered as a possible explanation in cases of lack of density dependence in survival (Byström & García-Berthou, 1999), although to our knowledge there are no previous demonstrations of a delayed effect of limited resources on growth. In contrast, if the increase in competition happened later in time, the main effects on growth would also be detected in the size attained on the second year of life, but they would be mostly because of the competition experienced that same year (growth pattern 3).

We acknowledge that because of the observational nature of our data, further experimental work is needed to reveal the underlying mechanisms of competition. However, our findings provide evidence that the use of habitat occupancy instead of fish abundance data is a better approach to detect the direct effects of intraspecific competition on growth. Thus, density and biomass, which have been traditionally employed to assess fish abundance, may not give an accurate estimation of real competition levels as they do not consider the availability of suitable habitat for fish. Grant & Kramer (1990) used the percentage of the stream area occupied by salmonid territories as a measure of habitat saturation for a given density (PHS), but Grant *et al.* (1998) recommended a calibration of PHS values that is equivalent to the carrying capacity for each population. Grant & Kramer (1990) already suggested the possibility of an increase in the predictive power of PHS considering only suitable habitat. In fact, the probability of observing a density-dependent response would have been extremely low in the present work from PHS values (Table 1). Besides, there are some cases when the principle of PHS may not be applicable, such as populations in which individuals behave as multiple central-place foragers instead of defending single-place territories (e.g. Steingrímsson & Grant, 2008), or in populations in which juveniles and adults cease to be territorial (e.g. Elliott, 1990b). Hence, occupancy rate is a more accurate measure of intraspecific competition than density or biomass, since it encompasses differences in quantity and quality of available habitat for each age class. In addition, as reckoned in the present study, occupancy rate considers the effects of intercohort interactions for available habitat through competition analyses, thus avoiding an overestimation of potential available habitat for each age class. Of course, it should be kept in mind that available habitat for study years is calculated from simulated hydraulic conditions and not from data collected year-to-year. Therefore, despite there being different indicators of hydraulic models performance so that the quality of hydraulic simulations can be checked, some deviance from real hydraulic conditions is expected. The density approach has been used worldwide in studies of the effects of population abundance on growth and performance of animal species. However, the observed relationship between density and growth may not be because of a direct causal relationship, but may result from growth being affected mainly by intraspecific competition for habitat or food resources (e.g. Mysterud *et al.*, 2002; Girish & Saidapur, 2003; Eitam, Blaustein & Mangel, 2005; Toïgo *et al.*, 2006).

We conclude that the approach of using occupancy rates instead of density or biomass is a step towards a more complete understanding of density-dependent growth and its effects on population dynamics. The present work also undermines the idea that density-dependent responses are tightly related to high- or low-density populations, as formerly argued (Jenkins *et al.*, 1999; Lobón-Cerviá, 2005), since for a given density, occupancy rate could vary widely between rivers with high differences in suitable habitat. While there is an ongoing debate about the relevance of density-dependent growth on the dynamics of brown trout populations and the accuracy of the measures employed to detect it, our study provides direct evidence of the critical role of density dependence as a key factor determining size-at-age in brown trout. Further, the operation of density dependence across a life span adopted different patterns, shaped by the river-specific variation of suitable habitat through ontogeny. As the use of occupancy rate has been shown to improve the accuracy of density measures, further work in other fish species and vertebrate taxa represents a future challenge for empirical and theoretical work.

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