Ecology and Evolution

Can migrants escape from density dependence?

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Abstract

Migration is thought to maximize growth by enabling individuals to escape from density dependence, but this has rarely been tested at the individual level in natural populations. We employed linear mixed modeling of the spacing between consecutive scale growth rings to reconstruct individual growth profiles of a paradigmatic fish migrant, the sea trout (*Salmo trutta*) and related these to estimates of year class strength over a 13-year period. Variation in scale growth was 1.3 times greater among individuals than within individuals in freshwater and 10 times greater at sea. Scale growth was inversely related to year class strength, both in freshwater (before migration) and at sea (after migration). Competition for patchily distributed resources is the most plausible explanation of the negative density-dependent growth observed in freshwater and, to a lesser extent, in the marine environment. Our study provides some of the strongest evidence for a role of density dependence in determining partial migrations because although migrants can maximize growth by moving into the sea, they do not appear to become free from density dependence constraints completely. This has implications for conservation and suggests that sea trout and other anadromous fish displaying partial migrations may not be best managed on a river by river basis, but rather from a broader, coastal perspective.

Introduction

Understanding temporal fluctuations in the abundance and growth of organisms has long been a key challenge in population ecology (Krebs 2009) and density dependence is perhaps one of the most ubiquitous endogenous regulators (Brook and Bradshaw 2006). Consideration of density dependence regulation is also important for managing exploited populations because the effects of fishing mortality can vary markedly depending on the degree of compensatory versus additive mortality, which is ultimately a function of density dependence (Minto et al. 2008). Yet, the effects of density dependence may not become noticeable unless one repeatedly samples at the individual level (Vøllestad and Olsen 2008) because most organisms become more mobile as they grow, and

ontogenetic changes in per capita resource requirements can cause the relationship between density and resource abundance to change over time (Begon et al. 1996). This is particularly the case for migratory species, where individuals may be able to "escape" competition by moving between habitats (Poethke et al. 2007; Mobæk et al. 2009), thereby making it difficult to detect density dependence regulation.

Salmonids are well suited for studying density dependence because juveniles pass through a critical time for survival soon after emergence from spawning redds (Elliott 1994; Garcia de Leaniz et al. 2000) when competition for food and space is intense (Van Zwol et al. 2012), and many populations include both resident and migratory individuals (partial migration, Wysujack et al. 2009; Acolas et al. 2012). Most density dependence studies have

made use of time series based on stock–recruitment relationships to infer density-dependent regulation at the early juvenile stage. For example, researchers have compared egg densities against juvenile survival (Nicola et al. 2008), or against body size (Einum et al. 2006). However, this approach assumes that density is a valid metric of the intensity of competition experienced by individuals, which may not be the case if resources are patchily distributed and sampling area is unrelated to the spatial scale of the species (Berryman 2004). An effect of density on growth may also be difficult to detect in such studies if resident fish have a larger than average size or emigration is size dependent (Elliott 1994; Jenkins et al. 1999). Density needs to be measured in relation to the mobility of the organism under study (Jenkins et al. 1999) and the spatial distribution of resources (Berryman 2004; Finstad et al. 2009), but these may not always be known. A second limitation of observational studies is that fitness metrics, such as survival or growth, are often collected for a small subset of individuals, typically over a short time period. For example, density estimates of juvenile salmonids are typically inferred (and scaled up) from a necessarily limited number of small stream sectors, which can restrict statistical inferences. Similar limitations also exist for growth studies because the number of individuals that can be recaptured is typically small, which seriously limits the number of repeated measures that can be obtained. In addition, small alevins are usually difficult or even impossible to mark individually (Kaspersson and Höjesjö 2009), which is unfortunate since this the stage where the impact of density on fitness is most likely to be manifested (Elliott 1994).

The analysis of the spacing between consecutive growth rings (circuli) found in bone structures such as scales or otoliths can be used to reconstruct the growth trajectories of individuals with much more detail than is usually possible through mark and recapture (Campana and Thorrold 2001). In addition, because the analysis of growth circuli represents repeated measures on the same individuals, linear mixed effects models can be used to increase the power and accuracy of statistical inferences (van de Pol 2012). Here, we used a 13-year time series with estimates of year class strength for two populations of migratory brown trout (*Salmo trutta*) to test the hypothesis that early freshwater growth, but not marine growth, is suppressed at high population densities. We employed upstream trap records of sea trout (i.e., the marine ecotype of brown trout) returning as adults to rivers to spawn in order to estimate annual indices of year class strength during the freshwater and early marine stage, standardized to a common body size. We tested for density dependence by examining variation in juvenile growth reconstructed from analysis of adult scales in relation to year class strength indices, derived from data on parental abundance.

Brown trout displays extensive morphological and ecological plasticity and often includes both resident and anadromous (sea trout) morphotypes that can coexist and interbreed within a single population (Caballero et al. 2012). More than 95% of individuals at the southern limit of the distribution migrate to sea after 2 or 3 years in freshwater (Marco-Rius et al. 2012). Sexual maturity can be reached after a few months in the estuary, or delayed following 1–3 years of feeding at sea (Caballero et al. 2006). The incidence of iteroparity can vary markedly among populations, but it is typically 10–40% at the southern range of the species (Caballero et al. 2012).

Freshwater systems are typically more resource limited than marine environments (Ross 1986), and density-dependent growth is thought to be caused by exploitative competition for food, rather than by interference competition for space in freshwater (Grant and Imre 2005), although both mechanisms may operate and result in identical density–growth relationships (Ward et al. 2007). In the sea, in contrast, the effect of density on salmonid growth is thought to be mediated exclusively through completion for food (Peterman 1984) as it is assumed that it would be difficult for fish to monopolize space or defend marine resources (Snover et al. 2005). Our expectation, therefore, was that variation in freshwater growth would track changes in year class strength, whereas variation in marine growth would be largely independent of density if juveniles migrate to "escape" competition.

Materials and Methods

Study populations

We examined temporal variation in density-dependent growth in two contrasting populations of migratory brown trout (sea trout) from Galicia (NW Spain), one from a large watershed (R. Ulla – 2804 km^2) and one from a much smaller catchment (R. Lerez – 449 km^2). Sea trout were caught in upstream traps on their returning marine migration each year during 1999–2010, the body size was measured (fork length, mm) and a sample of scales collected before the fish were returned upstream by fishery officers. The two rivers differ markedly in accessible stream length for sea trout (R. Lerez – 25 km, R. Ulla – 102 km) and estuary size (R. Lerez – 99 km^2, R. Ulla – 238 km^2), and also likely in the strength of density-dependent effects (Caballero et al. 2006; Marco-Rius et al. 2012). Thus, sea trout from the much smaller River Lerez migrate to sea at a smaller mean smolt size (174 ± 9.1 mm) than those from the larger R. Ulla (220 ± 12.4 mm), mean smolt ages being similar (R. Ulla,

2.04 ± 0.13 years; R. Lerez, 2.12 ± 0.12 years; Marco-Rius et al. 2012).

Scale analysis and growth profiles

We randomly chose scales from 60 adult sea trout per river and year from the historical scale collection, and selected 2–5 scales with clear (nonregenerated) nuclei for each fish to prevent bias due to loss of the first few growth rings. We made acetate impressions of the scales with the aid of a pressure roller, scanned these with a Minolta MS 6000 (Konica Minolta, Tokyo, Japan) microfilm scanner at 23–50× magnification, and saved them as high-resolution TIFF images as in Kuparinen et al. (2009).

ImageJ v. 1.4.1 (Abràmoff et al. 2004) was employed to digitize the position of each growth ring, to identify the annual growth rings (annuli), and to measure the intercirculi spacing along the 360º scale axis with reference to a calibrated scale bar in order to derive measures of scale growth (Marco-Rius et al. 2013). The freshwater and marine ages were determined based on the number of annuli and the point of entry of smolts into the sea (beginning of marine phase) was noted based on the change from a concave to a convex curvature of the first marine circulus (Marco-Rius et al. 2012). We considered scale growth patterns between the scale focus and the first freshwater winter as a measure of early juvenile growth in freshwater, and between the point of entry into the sea and the first marine winter as a measure of early marine growth (postsmolt growth, PSG; Friedland et al. 2006). Using only the first part of the freshwater and marine phases (common to all individuals) avoids problems due to age effects and assumes that intercohort density-dependent effects are similar for yearling and underyearling individuals in terms of growth potential (Kvingedal and Einum 2011). The first three scale circuli were not taken into account in the analysis due to the possibility of scale regeneration during early growth. In total, we analyzed scales of 453 sea trout from the R. Lerez and 490 sea trout from the R. Ulla.

Reliability of scale analysis

A paired *t*-test was used to assess nonrandom deviations in scale radii between the original scales and their acetate impressions (*n* = 30) in order to quantify potential bias in scale measurements arising from pressure from the hand roller. To ascertain the precision of the scale analysis, we estimated the repeatability of the point of entry into the sea and of the end of the first freshwater growing season by measuring the scales of 30 individuals twice in a double-blind fashion and calculating the intraclass correlation coefficient (α-Cronbach) as per Kuparinen et al. (2009). The Pearson correlation coefficient was used to

evaluate the strength of the association between scale length and fish length, and thus to assess whether scale size could be used as a proxy for fish body size. Precision in scale measurements (resolution 0.01 mm; CV = 17.1%) was better than that of body size measurements (resolution 1 cm; CV = 19.2%), and the former was therefore preferred to examine growth variation among migratory trout, as we had also found in previous studies (Marco-Rius et al. 2012, 2013). We used scale growth as the trait of interest, rather than back-calculated body size from scale measurements because the latter introduces additional errors caused by low precision of body size measurements taken in the field, and uncertainty about the precise nature of the function linking scale growth to body growth (Marco-Rius et al. 2013).

Data analysis

We modeled variation in year class strength by considering the annual number of returning sea trout caught in two upstream traps at the end of the fishing season (R. Lerez, mean trap catch = 347 sea trout/year, range: 203–610; R. Ulla mean trap catch = 350 sea trout/year, range: 212–596), standardized to a common body size (Lerez, 347.3 mm; Ulla, 350.3 mm) in order to factor in variation in size-dependent fecundity. We assumed that annual variation in trap catches reflected variation in spawning escapement (and thus on egg deposition) and derived indices of year class strength for each cohort and smolt year (i.e., year of seaward migration) taking into account the age structure of these populations (Marco-Rius et al. 2012) to factor in the relative contribution of overlapping age classes. For example, the index of year class strength for the 2000 cohort (i.e., juveniles hatching during 2000) was estimated from the number of adult spawners caught ascending each river during the 1999–2000 spawning season. Likewise, an index of smolt strength for the same year (2000) was calculated by summing the strengths of the 1999, 1998, and 1997 cohorts weighted by the known proportions of 1-, 2-, and 3-year-old smolts, respectively.

We employed linear mixed modeling to assess individual variation on the spacing between consecutive growth circuli (intercirculi spacing) using the protocol described in Zuur et al. (2009) for nested data using the Bayesian Information Criterion (BIC; see Data S1 for details). Beginning with the saturated model, we identified on the basis of deletion tests a simplified model (the minimal adequate model) that had only significant terms but statistically the same level of fit than the saturated model (Crawley 2007). The effects of river and year class strength on freshwater intercirculi spacing were examined with the following fixed effects saturated model:

$$I \sim C \times S_{\mathrm{H}} \times R$$

where I is the freshwater intercirculi spacing (until the first freshwater winter), C is the circuli pair being considered (i.e., the pair of consecutive growth rings deposited along the scale radius that represent two consecutive time periods), S_{H} is the standardized year class strength at hatching adjusted for variation in adult body size and juvenile age structure, and R is the river identity. All the possible interactions were included in the model. Likewise, to model variation in marine scale growth, we considered the following saturated structure:

$$I \sim C \times R \times S_{\mathrm{M}} \times FW$$

where I is the marine intercirculi spacing (until the first marine winter), C is the circuli pair being considered, S_{M} is the standardized year class strength at smolting (taking into account the smolt age of the population) adjusted for variation in adult body size, R is the river identity, and FW is the scale radius at the end of the first winter in freshwater. As previously described, all interactions were included in the model. We used the squared root of the dependent variable in every model to help normalize error terms.

Random effects were tested in both saturated models, and these were assumed to be independent among individuals and to follow a normal distribution with mean zero and variances σ^2_{a} and σ^2_{b}, respectively; the observation error $\varepsilon_{i,j}$, was also assumed to be independent and normally distributed. We calculated variance components to determine the relative strengths of within and among individual differences in intercirculi spacing, and allowed for autocorrelation in intercirculi spacing by considering an autoregressive (AR) model of order one in the autocorrelation structure. This provided a better fit to the data than a model without correlated serial errors. We run models incorporating the effect of year class strength at various time lags (-4 to $+4$) to account for the fact that competition experienced by migrants at sea may also be affected by earlier and later year classes. All analyses were performed on R 2.15.0 language (R Development Core Team 2012) using the nlme 3.1-103 package (Pinheiro et al. 2012).

Results

Scale reliability

There was no significant distortion of scale radius due to the impression process ($t_{29} = 0.547$, $P = 0.465$), indicating that acetate impressions gave an accurate, unbiased representation of scale size. Repeatabilities of scale size

were high, both for smolt scale length (α-Cronbach = 0.879) and for scale size attained at the end of the first freshwater growing season (α-Cronbach = 0.898). Scale radius and fork length were positively correlated ($r = +0.747$, $P = 0.001$), and the relationship was not different among rivers ($F_{1,941} = 0.326$, $P = 0.568$) allowing us to use scale measurements to reconstruct changes in body size regardless of river identity.

Determinants of individual variation in freshwater growth

Inspection of freshwater growth profiles, obtained by plotting circuli number against cumulative scale length (Fig. 1), reveals considerable variation in growth slopes among individuals, as well as between rivers and years. Annual scale growth differed significantly among years, both in freshwater (R. Ulla $F_{9,489} = 2.82$, $P = 0.005$, Fig. 2A; R. Lerez $F_{11,452} = 7.15$, $P < 0.001$, Fig. 2B) and in the sea (R. Ulla $F_{11,489} = 3.43$, $P < 0.001$, Fig. 2C; R. Lerez $F_{11,452} = 1.89$, $P = 0.04$, Fig. 2D).

The minimal adequate model of intercirculi spacing in freshwater according to the model selection procedure described in Data S1 included all three main effects, that is, circuli number, year class strength, and river identity. None of the interactions was significant, and these were removed from the model following Zuur et al. (2009). The inclusion of an autocorrelation structure, as well as of random intercepts and slopes, was found necessary to adequately describe the freshwater growth of sea trout. Inspection of parameter estimates (Table 1) and fitted values (Fig. 3) indicates that there is considerable variation in the growth slope of individuals within the same cohort, and that early scale growth decreases rapidly from the first summer until the first freshwater winter. Freshwater growth differs significantly between the two neighboring rivers, with sea trout from the R. Ulla growing faster (i.e., displaying wider intercirculi spacing) than those from the R. Lerez.

Determinants of individual variation in marine growth

As with freshwater growth, the minimal adequate model of intercirculi spacing during the first marine growing season included the effects of circuli number, year class strength, and river identity. The terms capturing variation in freshwater size, as well as all the interactions, were not significant and were removed. As with freshwater growth, the inclusion of random effects and a correlation structure was necessary to adequately describe marine growth of sea trout (Table 2). Inspection of fitted values during
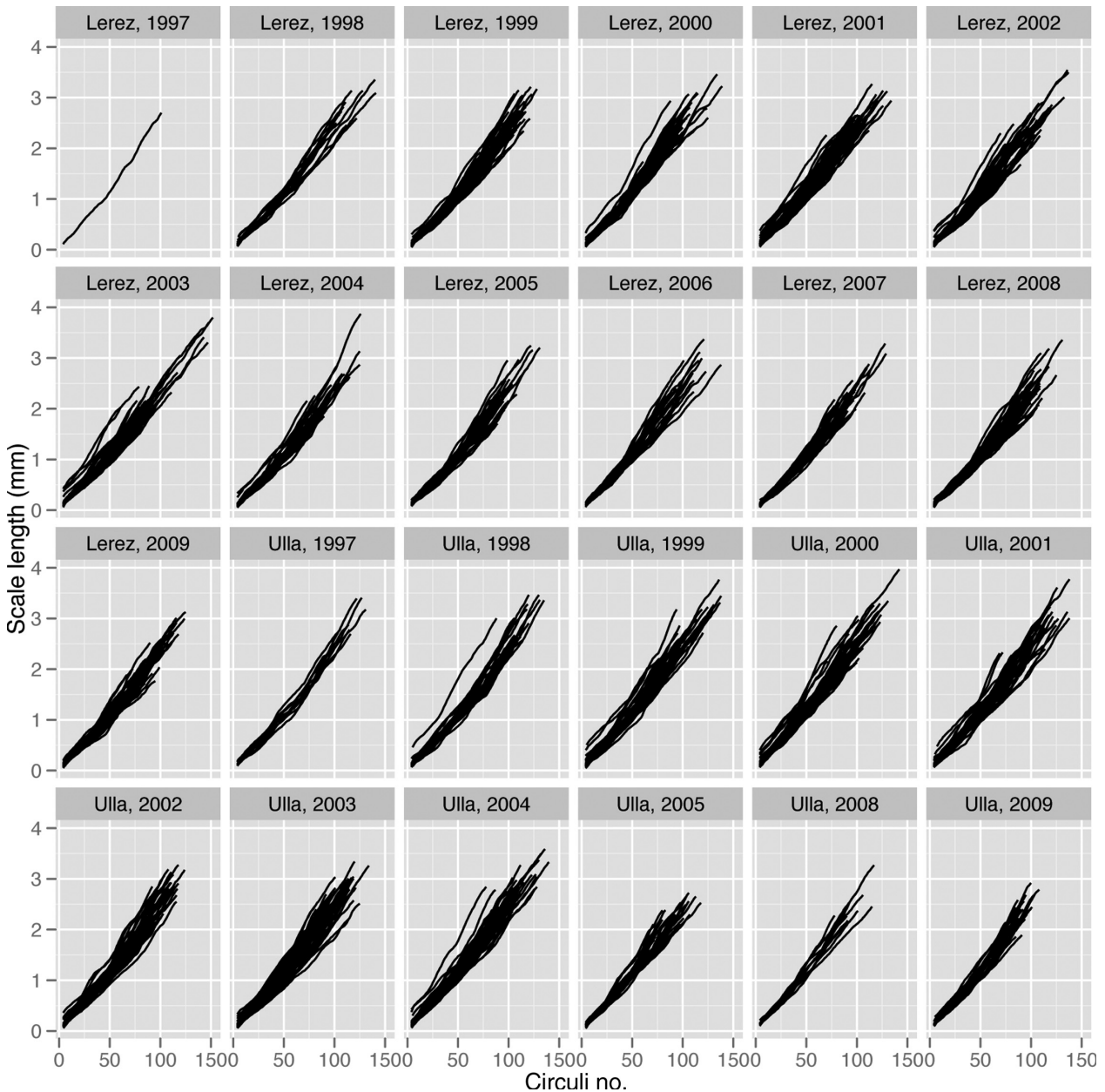
Figure 1. Freshwater scale growth profiles (cumulative scale growth, mm) of sea trout from the R. Lerez (*n* = 453) and the R. Ulla (*n* = 490) stratified by year of seaward migration (smolt year).

the first summer at sea displayed in all cases a positive slope, reflecting a period of rapid, accelerated growth (Fig. 4). Parameter estimates indicated that sea trout from the R. Ulla grew faster in the sea (as they did in freshwater) than those from the R. Lerez.

Partition of variance components

Analysis of variance components indicated that variation among individuals in freshwater intercirculi spacing (R.

Lerez 25%, R. Ulla 29%) was similar to within individual variation (R. Lerez 23%, R. Ulla 19%). In contrast, variation in marine growth was much higher among individuals (R. Lerez 27%, R. Ulla 32%) than within individuals (R. Lerez 2%, R. Ulla 3%).

Density-dependent growth

The negative, statistically significant sign of the parameter estimates for year class strength on intercirculi spacing
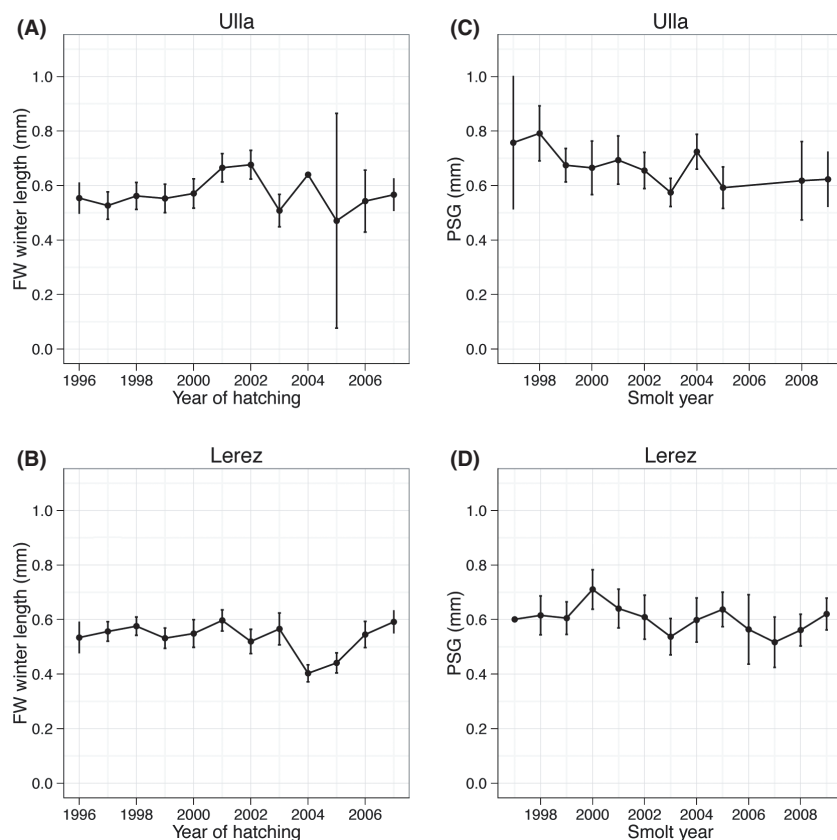
Figure 2. Temporal changes in scale growth (mm, mean ± 95 CI) of sea trout during the first year in freshwater (A and B) and during the first marine growing season (postsmolt growth, C and D) in the rivers Ulla and Lerez.

Table 1. Parameter estimates of mixed effects modeling of intercirculi spacing (square root) during the first year in freshwater.

Effects	Estimate	SE	t-value	P-value
Fixed				
Intercept	0.167	0.813×10^{-3}	207.70	<0.001
Circuli no.	−0.002	3.703×10^{-5}	−47.78	<0.001
River	0.305×10^{-2}	8.567×10^{-4}	3.56	<0.001
Year class strength	-6.310×10^{-6}	2.711×10^{-6}	−2.32	0.020
Random (SD)				
Intercept	0.011			
Slope (circuli)	0.001			
Residual	0.018			
Correlation structure				
Corr	0.267			

Random effects are indicated by the standard deviation of slope and intercept. Minimal adequate linear mixed effects model (LMM): Intercirculi spacing)$^{0.5}$ = River + Year class strength + Circuli no.

indicates that parental abundance (and thus likely offspring abundance) had a negative effect on the subsequent growth of juveniles. The density-dependent effect on growth was c. 2.5 times stronger in freshwater (Table 1, parameter estimate -6.31×10^{-6}, $P = 0.020$) than at sea (Table 2, parameter estimate -2.55×10^{-6},

$P = 0.048$), although confidence intervals overlapped and as such parameters are based on different types of data, they may not be directly comparable. The absence of significant interaction terms suggests that the negative effect of density on growth was same for both rivers. Models of marine scale growth lagged at 1–4 years were not significant, with model fit becoming increasingly poorer with increasing time lags (BIC lag1 = −96,965.25, BIC lag2 = −82,305.8, BIC lag3 = −71,133.14, BIC lag4 = −63,639.08) suggesting that there was little, if any, evidence for interference competition at sea among individuals of different smolt years.

Discussion

Our study suggests that growth of juvenile sea trout, a species exhibiting partial migrations (Wysujack et al. 2009; Acolas et al. 2012) is suppressed at high population densities, not only in freshwater but, to a lesser extent, also in the marine environment. Under the assumption that scale size and intercirculi spacing are both positively related to somatic growth – assumptions that are generally upheld by empirical evidence in salmonids (Marco-Rius et al. 2012) and other fishes (Cheung et al. 2007), we found that temporal fluctuations in year class strength had a marked

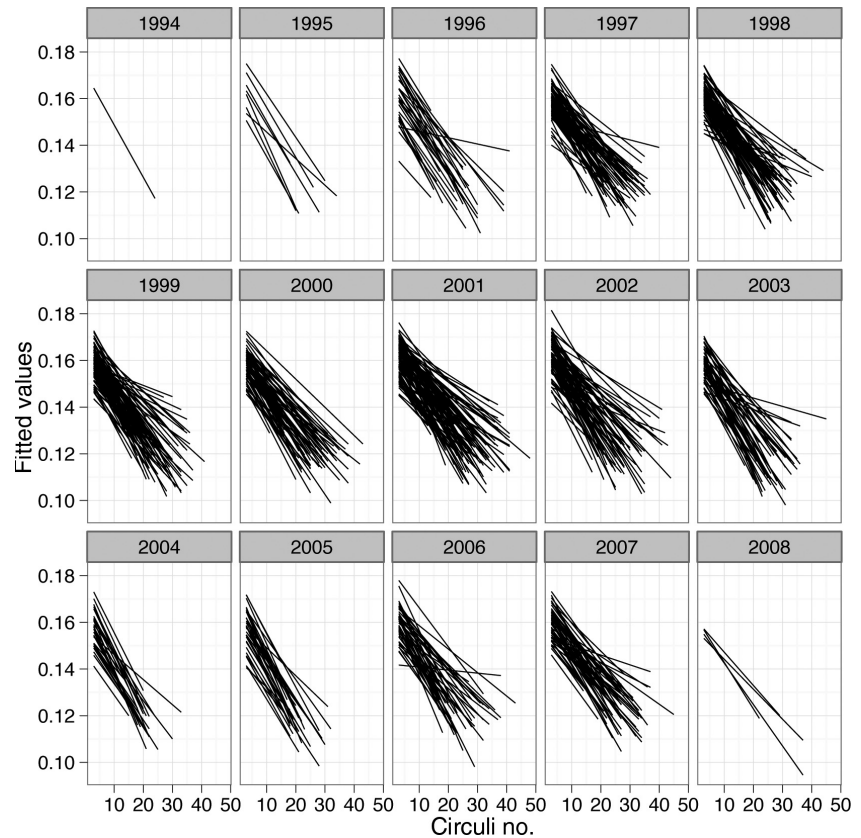**Figure 3.** Fitted values of mixed effects model describing intercirculi spacing during the first year in freshwater according to year of hatching.

Table 2. Parameter estimates of mixed effects modeling of intercirculi spacing (square root) during the first marine growing season (post-smolt growth).

Effects	Estimate	SE	*t*-value	*P*-value
Fixed				
Intercept	0.020	0.727×10^{-3}	27.57	<0.001
Circuli no.	1.504×10^{-4}	1.011×10^{-5}	14.88	<0.001
River	1.797×10^{-2}	0.036×10^{-3}	4.98	<0.001
Smolt year strength	-2.550×10^{-6}	1.278×10^{-6}	−1.98	0.048
Random (SD)				
Intercept	2.718×10^{-3}			
Slope (circuli)	3.949×10^{-5}			
Residual	8.565×10^{-3}			
Correlation structure				
Corr	0.564			

Random effects are indicated by the standard deviation of slope and intercept. Minimal adequate linear mixed effects model (LMM): Intercirculi spacing)$^{0.5}$ = River + Smolt year strength + Circuli no.

effect on juvenile growth at two different life-history stages, and at two different spatial scales.

Annual fluctuations in salmonid abundance are usually large (Nicola et al. 2008) and can be expected to have large effects on intra- and intercohort competition (Einum et al. 2011), which should be manifested in changes in individual growth (Parra et al. 2011); strong density-dependent effects on growth have been demonstrated at population level in many salmonids (e.g., Rich et al. 2009; Crozier et al. 2010). Yet, such effects have been much more difficult to detect at the individual level, as growth data derived from mark and recapture are often restricted to a few time events and tend to provide only a snapshot of growth performance (Vincenzi et al. 2012). In contrast, growth circuli continue to be deposited over the entire lives of many fishes, and once formed, remain unchanged (Cheung et al. 2007). These characteristics afford the fine resolution necessary to quantify individual variation in fish growth, and as our study shows, to test for density-dependent effects at the individual level.

Selection can act strongly on salmonid body size (Garcia de Leaniz et al. 2007) and we found large differences in scale growth increments of sea trout from two neighboring rivers, highlighting the marked effect that spatial heterogeneity and local conditions can have on salmonid growth (Foldvik et al. 2010). In general, density–dependent effects were stronger in freshwater than at sea, and also stronger in the river Lerez (with less accessible area and poorer juvenile growth) than in the much larger River Ulla. These results are consistent
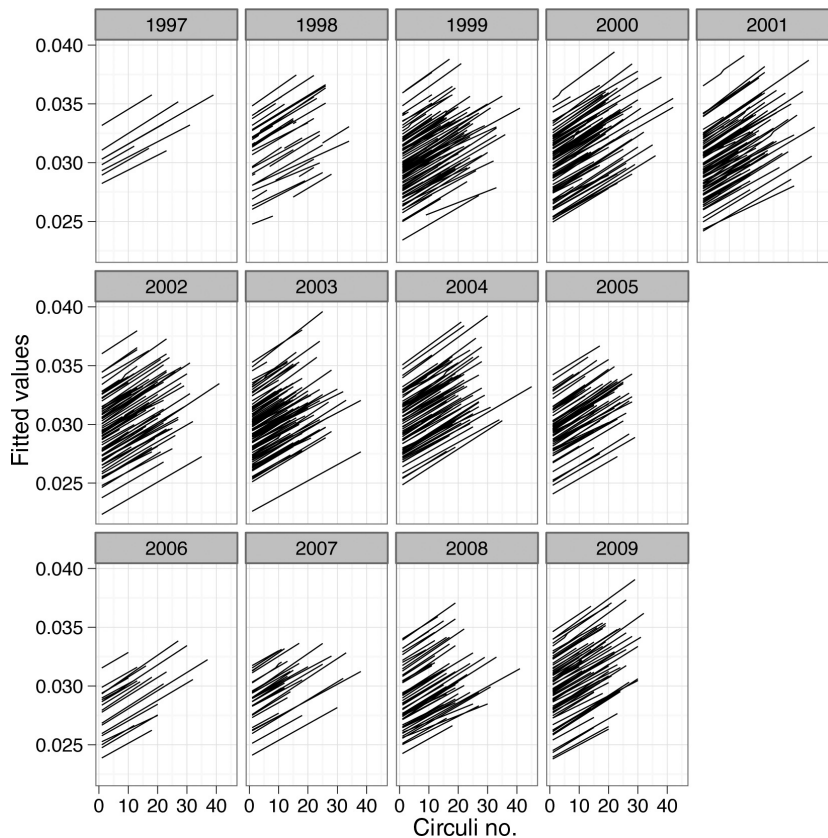
Figure 4. Fitted values of mixed effects model describing intercirculi spacing during the first marine growing season (postsmolt growth, PSG) according to year of smolting. For comparisons, circulus number one represents transition into the marine environment for all fish.

with resource competition being the chief reason for negative density-dependent effects on salmonid fitness (Finstad et al. 2009). Migratory salmonids typically move in small shoals when they enter the sea in order to minimize predation (Dutil and Coutou 1988) and are able to exploit a wider range of prey resources than in freshwater (Hansen and Quinn 1998), so marked density-dependent effects are perhaps less likely to occur at sea.

Density-dependent growth at sea has not been reported before for anadromous brown trout, but this may reflect the difficulty of detecting such a process in a coastal species with a relatively short marine phase, as well as the limited power of simple scale growth analysis (Marco-Rius et al. 2012). Negative density-dependent marine growth appears to be relatively common among other migratory salmonids (e.g., Atlantic salmon – Hansen and Quinn 1998; coho salmon – Emlen et al. 1990; sockeye salmon – Martinson et al. 2008), although it is most readily apparent during the late marine phase (Ruggerone et al. 2006). Unlike in freshwater, where density-dependent growth is well explained by territorial behavior and interference competition, similar underlying mechanisms at sea remain obscure (Snover et al. 2005). Seasonal migrations can result in high concentrations of sea trout close to shore as the species rarely moves more than

100 km offshore in this area (Caballero et al. 2006). Productivity in these coastal waters is regulated by short, localized upwelling episodes that reappear with a frequency of 14 ± 4 days (Álvarez-Salgado et al. 2000) resulting in patchily distributed and temporally abundant prey that provide the conditions necessary for marine density dependence effects to develop. On the other hand, we found no evidence for lagged effects on marine growth, suggesting that density dependence at sea results chiefly from the effect of single smolt cohorts (i.e., smolts entering the sea on the same year) rather than from the effects of multiple year classes.

Although our study did not consider the potential effect of other marine fish (including sea trout from other nearby populations, as well as other marine fishes), the two study populations occupy adjacent estuaries and are the largest in the area (Caballero et al. 2006; Marco-Rius et al. 2012). It could also be argued that if marine growth of sea trout depended on the presence of other, unaccounted fish competitors, failure to include these would have likely introduced random noise, making it more difficult (not less) to detect density-dependent marine growth.

Our analysis of variance components indicates that variation in intercirculi spacing was larger between individuals than within individuals, both in freshwater and at sea.

This supports the contention that intercirculi spacing is a good indicator of individual growth performance (Marco-Rius et al. 2012, 2013) and can be used to examine how individuals respond to density dependence regulation. Migration has been viewed as a strategy to "escape" from harsh conditions (Hebblewhite and Merrill 2009) which can protect offspring against density dependence (Economou 1991). Salmonid alevins are thought to benefit from dispersal early in life through improved growth at the expense of increased risk of predation (Einum et al. 2011), and our study indicates that seaward migration may confer similar benefits as sea trout smolts appear to benefit from reduced density dependence during the first marine growing season. This is consistent with the existence of marine compensatory growth, whereby individuals that grow poorly in freshwater are able to catch up later during their marine life (Marco-Rius et al. 2012), presumably because competition is weaker during the postmigratory than the premigratory phase (Snover et al. 2005).

However, our results also indicate that sea trout do not escape completely from density dependence constraints by migrating into the sea, and that their marine growth is still impacted by the presence of conspecifics, presumably due to competition for food (Peterman 1984). Recent models predict that density dependence could help maintain partial migrations if, as our study of sea trout indicates, resident and migratory individuals are subjected to density-dependent forces of varying strength before and after migration (Taylor and Norris 2007). The findings of our study have implications for conservation and management because despite strong homing behavior on this species, the existence of negative density-dependent growth at sea suggests that sea trout should not be managed on a river by river basis and that populations may be better conserved taking a wider, coastal perspective.

Acknowledgments

Author Contribution

F. M. R. and C. G. L. conceived and designed the study, analyzed the data, and wrote the manuscript. P. C. coordinated the collection and long-term storage of samples. P. M. and P. C. supervised the study, provided editorial advice, and helped to finance the work.

Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. R code and details of linear mixed effects model selection, following Zuur et al. (2009).