Modelling carrying capacity dynamics for the conservation and management of territorial salmonids

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ABSTRACT

Inherent in the carrying capacity notion is the basic idea of a maximum population a particular level of resources can support over a period of time. Knowledge of carrying capacity is essential for wildlife conservation since it is intrinsic in determining how much habitat must be conserved to maintain healthy populations. Further, this concept has been the cornerstone of the management of exploited animal and plant populations. Yet the question about what determines carrying capacity for territorial species and how it can be quantified has been long neglected by ecological research. We propose a novel method to model carrying capacity dynamics for territorial salmonids, which can be further applied to any territorial species as long as they are principally limited by habitat conditions. In our model, maximum abundance is limited by environmentally induced fluctuating habitat conditions and regulated through territorial behaviour. Carrying capacity is estimated as the amount of habitat available divided by the expected individual territory area for a given life stage. We tested whether the model was capable of explaining the annual fluctuations in densities of brown trout *Salmo trutta* from 12 Mediterranean populations for a 12-year study period. We observed not only that density of the different life stages tracked carrying capacity dynamics, but also that the eventual cohort performance was affected by both inter-cohort competition and intensity of intracohort competition experienced in the previous year. Likewise, recruitment depended on the levels of carrying capacity saturation experienced by adult stock the year before. In any case, resilience decreased with carrying capacity. Such results suggest that restoration measures attempting to increase population abundance through stocking, increased breeding dispersion or cohort survival may reduce the performance of both the enhanced and competing cohorts. Further, high exploitation rates may lead populations occurring at low carrying capacities to extinction.

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1. Introduction

Carrying capacity has been defined in many different ways (e.g. see reviews by del Monte-Luna et al., 2004; Pulliam and Haddad, 1994), so that its concept has remained controversial and elusive, to the point that there is a great uncertainty about how it should be used and measured and, indeed, what information can be inferred from it for wildlife conservation and management (Goss-Custard et al., 2002). Nevertheless, inherent in the carrying capacity notion is the basic idea of a maximum population that can be supported over a period of time for a particular level of resources. But carrying capacity is not a static number. Because both available resources and the requirements of a species change over time, carrying capacity is always changing, across seasons, years and through ontogeny. Population numbers of animals are therefore never constant from year to year, but rather fluctuate around an inter-annual mean carrying capacity that reflects the average environmental conditions over the long term (Jonsson and Jonsson, 2011). However, the carrying capacity of an environment is not only determined by the abundance and distribution of limited resources but also by how individuals compete for their use. This notion is especially relevant in organisms that compete via both exploitation and interference because behavioural responses induced by aggressive interactions typically result in a much reduced exploitation of the limited resource than could be accounted for by resource depletion alone (Begon et al., 2006). In territorial species, the behavioural adjustment of the size and shape of territories has profound consequences for their population regulation, demography, and spatial ecology (Adams, 2001). Yet, surprisingly, the question about what determines the carrying capacity for territorial species has been long neglected by ecological research (López-Sepulcre and Kokko, 2005).

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The concept of carrying capacity has played an important role in the study and management of animal and plant populations, being the cornerstone of the management of exploited renewable resources (Hilborn et al., 1995). Harvest models need specific information on carrying capacity, maximum population growth rate and abundance to estimate the maximum sustainable yield (Sibly et al., 2003). When the management goal lies in the conservancy side, estimation of carrying capacity provides a basis for evaluating the conservation status of populations and for assessing the changes in population dynamics resulting from anthropogenic impacts (Ayllón et al., 2012). Regarding fish population management, carrying capacity is needed to determine the target spawning escapement (Elliott and Elliott, 2006), the size of fish passage facilities (Clay, 1995), the optimal allocation of instream flow (Cardwell et al., 1996) or the probability of population persistence (Hilderbrand, 2003), as well as to calibrate population dynamics models (e.g., Dumas and Prouzet, 2003; Sabaton et al., 1997).

Carrying capacity is therefore an essential parameter in population management and modelling, though it is rarely estimated since it is extremely difficult to quantify (Morris and Mukherjee, 2007). The traditional approach to determining carrying capacity for anadromous salmonids has been through stock-recruitment analysis (Potter et al., 2003). However, this approach has proven to be imprecise in most cases since it requires long-time data series including a wide range of run sizes, which are usually not available in the majority of salmonid populations (Cramer and Ackerman, 2009). Carrying capacity for both stream-dwelling and anadromous salmonids has also been estimated from historical maximum habitat occupancies (e.g., Capra et al., 2003; Dumas and Prouzet, 2003). This approach is also burdened with the necessity of long data series and estimates of carrying capacity may be biased by extraordinary explosions in population numbers that may not reflect a long-term sustainable level. In addition, historical values of maximum habitat occupancy in a stream reach are difficult to extrapolate to other streams or even to other reaches within the same stream. Process-based bioenergetic models have also been used to predict carrying capacity for drift-feeding salmonids (e.g., Hayes et al., 2007). Though promising, these complex models require detailed data of composition, abundance and spatial patterns of invertebrate drift as well as the development of drift-foraging models describing the feeding habits and energetics of target species, so their generalization to other species or river systems must be considered with caution.

In this work we propose a novel method to estimate the carrying capacity for territorial salmonids. In the proposed model, maximum abundance is limited by environmentally induced fluctuating habitat conditions and regulated through territorial behaviour. The quantity of suitable habitat available for fish of a given age is estimated as a function of discharge using physical habitat simulations, and the maximum number of fish that can be sustained is estimated as the area of suitable habitat divided by the expected individual territory area for the given aged cohort. We tested whether the model is capable of explaining the annual fluctuations in young-of-the-year, juvenile and adult densities in brown trout *Salmo trutta* L. populations from twelve Mediterranean rivers.

2. Materials and methods

2.1. Rationale of the model

We define carrying capacity as the maximum density of fish a river can naturally support during the period of minimum available habitat. That is, habitat quantity (the area that generates positive growth and survival for an organism across a riverscape, i.e. the usable habitat) and quality (realised growth and survival rates in different habitat types) would determine the maximum number of individuals in a stream. Since stream habitats change spatially and temporally, life histories and demographic traits of conspecific populations also vary in space and time, so that the habitat acts as a template for the ecology of salmonid species (Jonsson and Jonsson, 2011). Consequently, spatio-temporal variations in population density of salmonids are typically related to changes in habitat conditions (Klemetsen et al., 2003; Milner et al., 2003). Though physical habitat structure and prey abundance jointly determine both habitat quantity and quality (Rosenfeld and Taylor, 2009), for the purposes of modelling, we considered physical habitat the main environmental factor limiting population size. Given the territorial nature of salmonids and their energetic requirements, there is clearly a limit to the number of fish that any habitat can support (Grant and Kramer, 1990; Milner et al., 2003). Hence territory size will set the maximum number of individuals that a stream can sustain, providing the link between available habitat and carrying capacity.

The rationale of the approach is simple: at low population densities, individuals will establish large territories at habitats of the highest quality; but with increasing density, individuals will be progressively forced to defend territories of increasingly smaller size and to occupy sub-optimal habitats (Bult et al., 1999; Newman, 1993). However, there is a threshold of habitat quality in which it is not profitable in terms of energy gain to defend a territory, so that individuals will either display an alternative behaviour (non-territoriality or floating), emigrate or die (Elliott, 1994; Newman, 1993). Consequently, as the habitat becomes increasingly saturated with territories, the probability of observing density-dependent losses increases (Grant and Kramer, 1990). Yet the prior operation of density-dependence on growth would moderate the magnitude of population decline due to density-dependent mortality and emigration, so that the population would be maintained at the highest possible abundance (Keeley, 2001; Lobón-Cerviá, 2007). Although density-dependent effects on growth are generally stronger at low densities, density-dependent growth patterns actually depend on the distribution of habitat quality within the stream (Ward et al., 2007). The point when all suitable habitats are saturated with territories representing the minimum spatial requirements of individuals corresponds to the stream carrying capacity.

2.2. The model

The dynamics of stream physical habitat can be modelled by means of physical habitat simulation models. These models simulate the temporal evolution of habitat quality and quantity in relation to flow conditions. Physical habitat is characterized by means of the key habitat features limiting distribution and abundance of salmonids, which are typically considered to be depth, current velocity, substrate and cover (see review by Armstrong et al., 2003). Hydraulic conditions (depth and velocity) are simulated through hydraulic models. The suitability of channel structure (substrate and cover) and simulated hydraulic conditions for an aquatic species and its life stages is then assessed by means of habitat suitability models (the habitat suitability criteria, HSC). The HSC are commonly depicted as habitat selection curves, which represent habitat preference under the prevailing biotic and abiotic conditions in any particular stream, so that they can be seen as operational applications of the realized ecological niche (Rosenfeld, 2003). The standard output of physical habitat simulations is the curve that relates the weighted usable area (WUA; m² WUA ha⁻¹, an index combining quality and quantity of available habitat) with stream flow.

It is usually assumed that the niche separation of different fish sizes and salmonid species is enough to keep intercohort and interspecific competition at low levels (Milner et al., 2003).
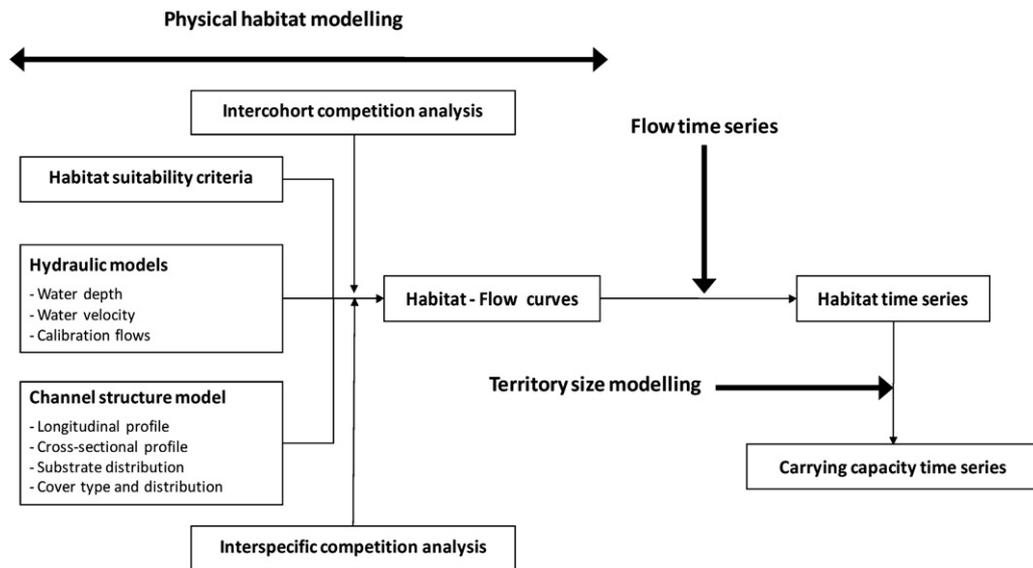
Fig. 1. Schematic representation of the approach proposed for estimating stream carrying capacity for territorial salmonids.

However, different studies have shown that habitat selection patterns (Bohlin, 1977), survival and movement (Nordwall et al., 2001), individual growth rate (Kaspersson and Höjesjö, 2009), body size and energetics (Einum and Kvingedal, 2011; Kvingedal and Einum, 2011; Nordwall et al., 2001) of a cohort may be significantly affected by the density of not only older but also younger cohorts. Likewise, interspecific competition can decrease population density and lead to reduced growth and survival in salmonid populations (Jonsson and Jonsson, 2011). Consequently, habitat competition analyses must be performed to model active spatial segregation due to intercohort and interspecfic competition when estimating available suitable habitat for the different life stages.

In the proposed model, territory size is the proximate factor that limits maximum potential abundance (Fig. 1). Although some factors, such as competitor density and food abundance (e.g. Keeley, 2000) or visual isolation (Imre et al., 2002), can affect territory size in salmonids, body size is considered its strongest determinant (e.g. Elliott, 1990; Keeley and Grant, 1995; Keeley and McPhail, 1998). Consequently, the space required and defended by individuals of any size can be estimated by means of an allometric territory size relationship. Since in our proposed approach available suitable habitat is measured through WUA, which is an index that combines quantity and quality and not a measure of actual area, the territory size model must account for variations in territory quality. The model would estimate the same territory size irrespective of habitat quality otherwise, while actually territory size should increase with decreasing habitat quality. In this case, estimates of carrying capacity would be highly sensitive to the distribution of habitat quality contributing to WUA within the stream, so that applying the same territory size model to streams differing in habitat quality distribution might be a source of considerable bias. In Mediterranean systems, summertime likely limits a stream's carrying capacity for salmonids because it represents the convergence of increasing fish length and territory size requirements during the growing season, and decreasing stream flow and thus available suitable habitat. Therefore, carrying capacity is estimated for every age class through the ratio $K_i = WUA_i/T_i$ where K_i is the carrying capacity of age-class i (trout ha^{-1}), WUA_i is the mean summer WUA of age-class i (m^2 ha^{-1}) and T_i quantifies the mean territory size of trout of age-class i (m^2 trout^{-1}), being calculated as the area of the territory that would be defended by an average-sized individual of age-class i. Density-dependent growth functional relationships should be included when estimating territory size.

2.3. Case study: the Aragón River basin

2.3.1. Study area

We applied the proposed method in 19 sites located in 12 rivers from the Aragón River basin, a Mediterranean drainage (Fig. 2). Sites corresponded to second to fourth-order streams and were located between latitudes 42°30′ and 43°03′N and longitudes 0°43′ and 1°32′W, at an altitude ranging from 540 to 870 m. We selected sampling sites to represent all the existing variability of environmental conditions within the area, which are fully described in Ayllón et al. (2010a). Studied brown trout populations occur in allopatry and comprise exclusively stream-dwelling individuals. The rivers are not currently stocked. Median summer discharge ranged from 0.03 to 0.74 m^3 s^{-1} and mean daily summer water temperature ranged between 12.3 and 16.6 °C.

2.3.2. Carrying capacity modelling

Habitat modelling was carried out by means of the Physical Habitat Simulation system (PHABSIM; Milhous et al., 1989). In PHABSIM, the longitudinal distribution of different habitat types within the stream is described through transects placed perpendicular to the flow. Along each transect, measurements of physical habitat variables are made at regular intervals to describe their lateral distributions and gradations. As a result, the study site is depicted as a mosaic of cells, each one characterized by its area, structural features (substrate and cover) and hydraulic conditions (water depth and velocity), which are a function of flow (Waddle, 2001).

We conducted habitat surveys to collect the topographic, hydraulic and structural data required to perform PHABSIM simulations at each site during August 2004. The data collection procedures are fully described elsewhere (Ayllón et al., 2010b, in press). We assessed an average ($\pm$SD) length of 100.8 ± 23.4 m and an average ($\pm$SD) area of 816.2 ± 381.7 m^2 per study site. We used the reach-type specific HSC described in Ayllón et al. (2010a) to characterize YOY (0+), juvenile (1+) and adult (>1+) brown trout habitat selection. Hydraulic data were calibrated in PHABSIM following procedures set out in Waddle (2001). We used the HABEF program within PHABSIM system to model spatial segregation of cohorts and to avoid therefore an overestimation of available suitable habitat for each age class. Since there is a certain degree of overlap in habitat preferences among age classes (see Ayllón et al., 2009, 2010a), there is a potential for intercohort competition in
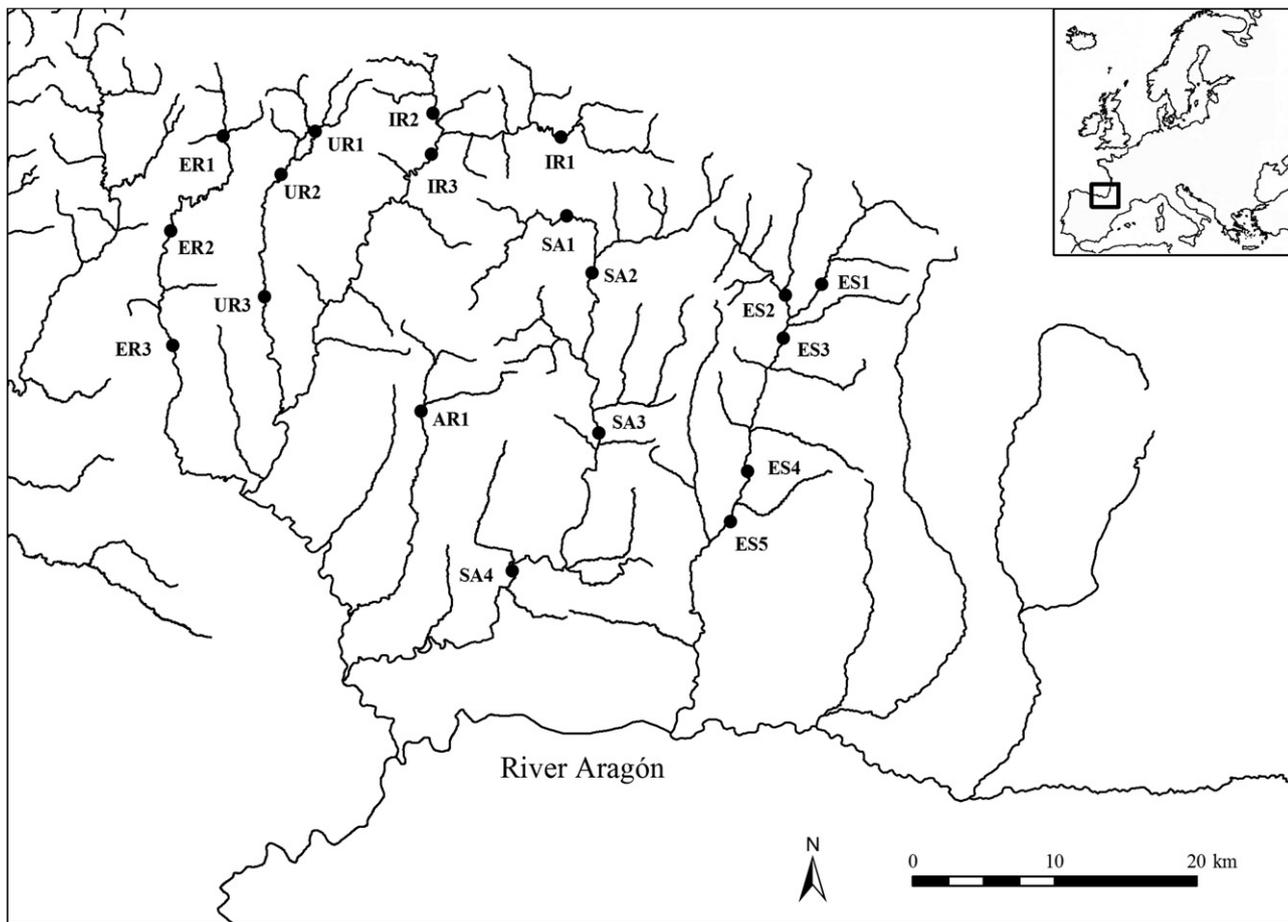
Fig. 2. Map of the study area showing the sampling sites located in the Eska (ES), Salazar (SA), Areta (AR), Irati (IR), Urrobi (UR) and Erro (ER) river sub-basins.

some areas of the stream. This results in 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. We quantified the total shared WUA where one age class dominated over the other 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 was not added to total available habitat. Further methodological aspects of HABEF analyses can be checked in Waddle (2001).

Historical flow time series for the 12-year study period (1993–2004) were provided at each study site by the closest gauging stations. Hydrological analyses performed by means of IHA V7 software (The Nature Conservancy, Olympia, WA) showed that no extreme flood episodes occurred during the study period. Consequently, it was assumed that no significant changes in the channel structure and morphology have occurred during the 1993–2004 period. Then, summer (July–September) habitat time series for each age class were obtained by coupling WUA curves as a function of flow with flow time series. Mean summer WUA was calculated as the daily average for each age-class and year. Finally, habitat time series were translated into carrying capacity time series by means of an allometric territory size relationship specifically developed for brown trout (Ayllón et al., 2010b): $\mathrm{Log}_{10} T = (2.64 - 0.96 \times \text{age category}) \times \mathrm{Log}_{10} L - (2.72 - 0.90 \times \text{age category})$, where T (m^2 of WUA) is territory size, L (cm) is length and age category is 0 for fish $\leq$9 cm (YOY) or 1 for fish >9 cm (older trout). Note that because of the approach used to develop this relationship (see Ayllón et al., 2010b), territory size is directly calculated in WUA units, so derived estimates of carrying capacity would be fairly robust to variation in

the distribution of habitat quality within a stream. Length–density relationships were used to estimate average length-at-age in populations where growth was density-dependent (unpublished data). Average length-at-age was used in the rest of study populations.

2.3.3. Fish assessment

Brown trout populations were sampled by electrofishing every summer (August–September) from 1993 to 2004. Trout were anaesthetized with tricaine methane-sulphonate (MS-222) and individuals were measured (fork length, to the nearest mm) and weighed (to the nearest g). Scales were taken for age determination and fish were returned alive into the river. All procedures complied with the Spanish and European Union legislation on animal care and experimentation. Fish density (trout ha^{-1}) with variance was 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.

2.3.4. Data analysis

We explored the existence of spatial differences in carrying capacity among sites through one-way analysis of variance (ANOVA) and subsequent Tukey's test. Significant deviance of observed densities from estimated carrying capacities was tested for each age-class and site by means of t-tests.

We tested whether annual fluctuations in the number of individuals of a certain life stage (YOY, juvenile and adult) were driven by variations in carrying capacity, the levels of crowdedness (i.e., carrying capacity saturation) experienced by these individuals the

previous year and the levels of crowdedness experienced by individuals of accompanying life stages. The level of carrying capacity saturation was measured as the relationship between observed density and estimated carrying capacity (D/K ratio) and was used as a proxy for intensity of competition among individuals. We fitted linear mixed effects models with the nlme package in R (Pinheiro et al., 2011) and performed subsequent model selection with sequential removal of non-significant fixed effects and subsequent model comparisons using log-likelihood ratios according to the procedure recommended by Zuur et al. (2009). Density of life stage x at year i ($D_{x,i}$), as dependent variable, was regressed against the life stage-specific carrying capacity ($K_{x,i}$), the level of carrying capacity saturation experienced by these individuals on year $i-1$ when they were age $x-1$ ($D_{x-1,\,i-1}/K_{x-1,\,i-1}$) and the level of carrying capacity saturation experienced by each accompanying life stage y at year i ($D_{y,\,i}/K_{y,\,i}$) as fixed effects. In the case of YOY trout, $D_{0+,i}$ was regressed against the level of carrying capacity saturation experienced by adult trout the previous year ($D_{>1+,\,i-1}/K_{>1+,\,i-1}$). Squared terms of ($D_{x-1,\,i-1}/K_{x-1,\,i-1}$) and ($D_{>1+,\,i-1}/K_{>1+,\,i-1}$) were included to test for potential non-linear effects of past carrying capacity saturation levels. All interaction terms were also included in the models. Finally, study site was included as a random factor (random intercept) to induce a correlation structure between observations within the same site.

Assumptions of normality of distributions and homogeneity of variances were verified through Shapiro–Wilk and Levene's tests, respectively. The significance level for all statistical tests was set at $\alpha = 0.05$.

3. Results

There were significant spatial differences in estimated carrying capacity (K) among study sites (ANOVA, $F_{18,205} = 154.1$, $P < 0.0001$). Post hoc Tukey's test differentiated four homogeneous groups of sites depending on this parameter (Table 1): the first group (high K) comprised only one site (average $K = 14,800$ trout ha^{-1}); the second group (medium K) was formed by seven sites (average $K = 5168$ trout ha^{-1}, range 4831–6136 trout ha^{-1}); the third group (low K) included five sites (average $K = 3648$ trout ha^{-1}, range 3218–4008 trout ha^{-1}); finally, six sites formed the fourth group (very low K) (average $K = 2037$ trout ha^{-1}, range 1316–2641 trout ha^{-1}).

Four out of the 19 sites had a total population density (D) significantly below estimated carrying capacity (t-test, $P < 0.01$). In these sites, all age-classes presented a D significantly lower than K (t-test, $P < 0.05$). A total of five, four and seven sites had a YOY, juvenile and adult D, respectively, significantly lower than K (Table 1).

Density of YOY depended on estimated YOY K and the D/K ratio of adult trout the previous year in a non-linear fashion, and was significantly and negatively affected by the D/K ratio of juvenile trout (Table 2). The model best explaining annual fluctuations of juvenile D included juvenile K and a non-linear relationship with the D/K ratio of juvenile trout at the year before, when they were YOY. Reciprocally, juvenile D was significantly and negatively affected by the D/K ratio of YOY trout at the same year (Table 2). Adult D increased significantly and linearly with estimated K and non-linearly with the D/K ratio of adult trout at the year before, when they were juveniles (Table 2). No interaction terms were included in any of the best explaining models. Finally, we re-ran regression analyses using D instead of D/K ratio as a proxy for intensity of inter and intracohort competition. In all regression analyses, D/K ratio performed better than D in terms of explaining a larger amount of variation and identifying a larger number of significant variables.

The previous analyses indicate that YOY and juvenile trout interacted in an antagonistic manner. Carrying capacity saturation of either life stage decreased with increasing levels of crowdedness experienced by individuals of the other life stage (Fig. 3a). By contrast, the performance of adult trout was not affected by the levels of K saturation of accompanying life stages (Fig. 3b). Simultaneously, increasing saturation of K by a cohort of either YOY or juvenile trout increased the probability that this cohort approached or even exceeded estimated K the following year until a certain threshold of K saturation is reached (Fig. 3a and b). The same effect was observed in YOY density as a function of the saturation levels experienced by adult trout the previous year (Fig. 3a). The relative magnitude and rate of change of the deviation of estimated D from K were higher at lower values of K irrespective of considered life stage.

4. Discussion

Determining the maximum number of individuals a certain system can support and how this productivity can be affected by human actions is a primary goal for population conservation and management. All management strategies should be rooted on a clear understanding of the primary drivers of population size trends and variability (Dochtermann and Peacock, 2010). In the present study, we set out a method to estimate the carrying capacity of the environment for territorial salmonids. We showed that estimated stream carrying capacity together with intra and intercohort density-dependent processes were capable of explaining between 63 and 79% of the annual variation in YOY, juvenile and adult brown trout densities.

Estimated carrying capacity alone accounted for between 39 and 56% of annual fluctuations in density. However, YOY and juvenile densities are mutually affected by the level of crowdedness experienced by the competing cohort, suggesting a negative density-dependent regulation of each life stage over the other. Density of younger cohorts does not exert any negative effect on adults, though. The biological interpretation of the effects of density in suitable habitats of juveniles on YOY performance is simple: at low densities, juveniles would occupy only high quality habitats so that suboptimal habitats can be taken up by surplus of YOY; with increasing juvenile density, the habitat that remains available decreases and so does YOY density; eventually, at juvenile densities over carrying capacity, individuals without territories would even occupy a fraction of the YOY habitat, setting their numbers below carrying capacity.

The negative effect of YOY habitat oversaturation on juvenile trout is less intuitive. Either interference competition for space or exploitative competition for food seem equally plausible underlying behavioural mechanisms. As predicted by habitat suitability models, there are stream habitats that are concurrently suitable for both age-classes. When the suitability of these habitats is higher for juveniles, they will out-compete YOY trout. On the contrary, when these habitats are more suitable for YOY trout, the occupation of these marginal habitats by juveniles is only energetically profitable at low density of YOY competitors. Increasing numbers of YOY increases the metabolic costs associated to vigilance and defence of territories, reducing their growth potential till rendered unsuitable (Hixon, 1980; Titus, 1990). Additionally/alternatively, higher densities of YOY would reduce performance of juveniles through exploitative competition for food, since younger individuals can consume prey that otherwise would have been available to older ones even if they cannot win competition for territories. So the overall net effect of increasing YOY density would be a decrease in habitat quality for juveniles. Kvingedal and Einum (2011) observed that reduced habitat quality due to competition with YOY resulted in reduced individual growth rate in juvenile Atlantic salmon *Salmo salar* L. Likewise, Parra et al. (2012) showed that mean body size of juvenile brown trout decreased with increasing YOY density
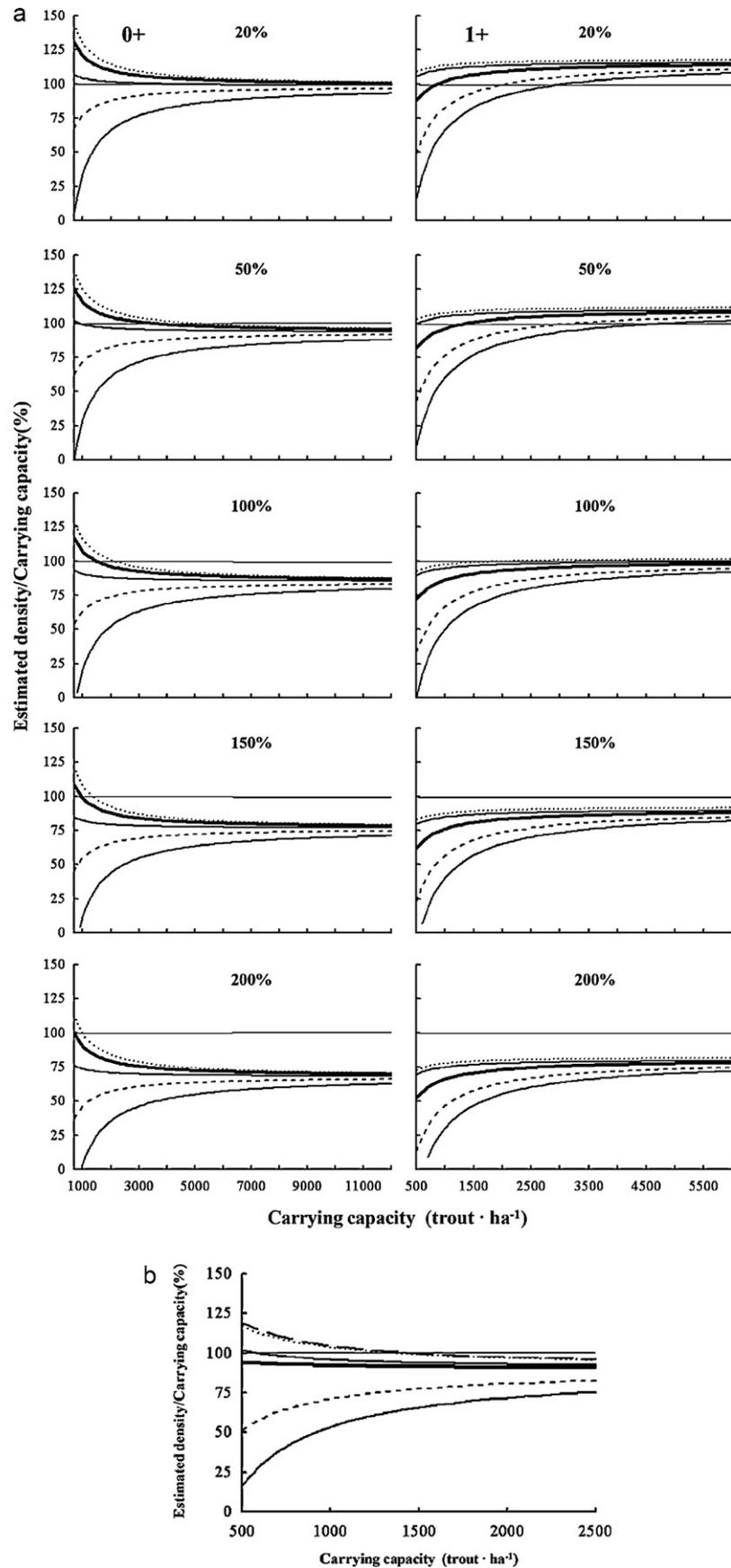
Fig. 3. (a) Carrying capacity saturation, expressed as the relationship between model estimates of density and carrying capacity (D/K ratio), along a gradient of carrying capacity for YOY (0+) and juvenile (1+) trout as a function of the levels of carrying capacity saturation experienced by the competing life stage (from 20 to 200%, depicted from top to bottom). YOY D/K ratio varies with the levels of carrying capacity saturation experienced by adult (>1+) trout the previous year, while juvenile D/K ratio varies with the levels of carrying capacity saturation experienced by YOY trout the previous year (20% thin solid line, 50% dashed line,

Table 1

Mean (±standard deviation) estimated carrying capacity (total and by age-classes) and category of study sites. Significant deviance of density from carrying capacity with its probability (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) is also shown.

Site	K category	Total K (trout ha^{-1})	K 0+ (trout ha^{-1})	K 1+ (trout ha^{-1})	K >1+ (trout ha^{-1})
ES1	Low	3604 ± 925	1526 ± 672	1391 ± 237	687 ± 104
ES2	Medium	5560 ± 1140	2225 ± 810	1647 ± 404	1687 ± 374
ES3	Medium	4992 ± 964	2448 ± 681	1725 ± 183	819 ± 153
ES4	Very low	2641 ± 823	$1753 \pm 591*$	508 ± 127	380 ± 13
ES5	Very low	$1669 \pm 302**$	$1045 \pm 218*$	$247 \pm 60*$	$377 \pm 42***$
SA1	Low	3218 ± 516	1671 ± 360	999 ± 162	549 ± 44
SA2	Low	3831 ± 437	1529 ± 315	1694 ± 344	607 ± 70
SA3	Very low	$2287 \pm 361***$	$935 \pm 273***$	$706 \pm 97***$	$647 \pm 126***$
SA4	Very low	$2475 \pm 519***$	$1256 \pm 348***$	$465 \pm 168***$	$754 \pm 166***$
AR1	Very low	$1316 \pm 339***$	$772 \pm 167***$	$282 \pm 130*$	$262 \pm 80*$
IR1	Medium	4850 ± 798	2811 ± 474	1514 ± 319	524 ± 63
IR2	Medium	4850 ± 433	2140 ± 581	1624 ± 226	$1085 \pm 108**$
IR3	Low	4008 ± 724	2494 ± 417	1177 ± 348	337 ± 25
UR1	High	$14,800 \pm 1919$	8702 ± 1477	4436 ± 846	1661 ± 253
UR2	Medium	4955 ± 500	1780 ± 384	2453 ± 278	$722 \pm 60**$
UR3	Low	3577 ± 495	1381 ± 364	1374 ± 163	822 ± 105
ER1	Medium	6136 ± 1291	2567 ± 1071	2189 ± 264	1380 ± 107
ER2	Medium	4831 ± 570	2327 ± 549	1671 ± 298	833 ± 102
ER3	Very low	1835 ± 208	1088 ± 463	572 ± 146	$175 \pm 22*$

Table 2

Summary of the best linear mixed effects models explaining annual variations in density of YOY (0+), juvenile (1+) and adult (>1+) brown trout *Salmo trutta* from a 12-year study period in 19 sampling sites from the Aragón River basin.

Dependent variable	Model summary	Fixed factors	Coefficients	P
$D_{0+,i}$	$R^2 = 0.63$; $F = 74.7$; d.f. = 219; $P < 0.001$	(Intercept)	-702.9	<0.01
		$K_{0+,i}$	0.917	<0.001
		$(D_{1+,i}/K_{1+,i})$	-3.847	0.04
		$(D_{>1+,i}/K_{>1+,i})$	-8.590	0.10
		$(D_{>1+,i-1}/K_{>1+,i-1})$	21.484	<0.001
		$(D_{>1+,i-1}/K_{>1+,i-1})^2$	-0.087	<0.001
$D_{1+,i}$	$R^2 = 0.79$; $F = 160.2$; d.f. = 219; $P < 0.001$	(Intercept)	-536.6	<0.001
		$K_{1+,i}$	1.010	<0.001
		$(D_{0+,i}/K_{0+,i})$	-1.640	0.04
		$(D_{>1+,i}/K_{>1+,i})$	-0.015	0.14
		$(D_{0+,i-1}/K_{0+,i-1})$	7.780	<0.01
		$(D_{0+,i-1}/K_{0+,i-1})^2$	-0.020	0.05
$D_{>1+,i}$	$R^2 = 0.72$; $F = 153.2$; d.f. = 220; $P < 0.001$	(Intercept)	-503.5	<0.001
		$K_{>1+,i}$	0.903	<0.001
		$(D_{0+,i}/K_{0+,i})$	-0.637	0.35
		$(D_{1+,i}/K_{1+,i})$	-0.748	0.28
		$(D_{1+,i-1}/K_{1+,i-1})$	7.245	<0.001
		$(D_{1+,i-1}/K_{1+,i-1})^2$	-0.020	<0.001

Note: All interaction terms were non-significant.

in suitable habitat. Our results indicate that increased rates of mortality and/or emigration of juvenile individuals towards more profitable habitats are also expected outcomes of such intercohort interactions.

These results entail several implications for managed populations. In populations enhanced through stocking, when the number of stocked fish largely exceeds the stream carrying capacity, not only the future production of the stocked cohort will be decreased through intracohort density-dependent mortality and growth (Einum et al., 2006; Lobón-Cerviá, 2007; Parra et al., 2011, 2012) but also the production of coexisting cohorts will be affected by intercohort competition. Einum et al. (2008) showed that under some circumstances (e.g., when the habitat of younger life stages is limiting or survival is density-dependent) habitat restoration projects focused on increasing breeding dispersion may be ineffective or even detrimental to future adult abundance.

The efficacy of such measures was also highly dependent on intercohort competitive mechanisms (see Einum et al., 2008). Our results point to this same direction given that increased breeding dispersion resulting in oversaturation of YOY habitat is predicted to decrease the density of coexisting juveniles below its carrying capacity, especially in populations with low carrying capacities.

The obtained models also show that within-cohort interactions regulate trout density the year after. That is, the density of a cohort relative to its carrying capacity a given year increases with increasing level of carrying capacity saturation experienced by the cohort the previous year. But as expected, this relationship is non-linear, since at very high saturation levels, intracohort competition is so strong that density-dependent losses occur, depressing realized density below carrying capacity next year. Consequently, enhancing measures leading to improved cohort survival so that the habitat is extremely oversaturated would result

100% thick solid, 150% dotted line, and 200% thin solid line). The line that indicates when estimated density matches carrying capacity is also shown. (b) Carrying capacity saturation, expressed as the relationship between model estimates of density and carrying capacity (D/K ratio), along a gradient of carrying capacity for adult (>1+) trout as a function of the levels of carrying capacity saturation experienced by adult trout the previous year when they were juveniles (20% thin solid line, 50% short-dashed line, 100% thick solid, 150% dotted line, 200% long-dashed line, and 250% thin solid line). The line that indicates when estimated density matches carrying capacity is also shown.

in over-compensatory mortality that would prevent the cohort from reaching its carrying capacity in subsequent years. Interestingly, the maximum cohort performance is accomplished at past saturation levels well over 100%. This suggests that a large number of surplus individuals may remain at the stream reach, even at high intracohort competition levels, by just adopting a non-aggressive energy-minimizing strategy (Puckett and Dill, 1985; Titus, 1990). In fact, the benefits of dispersing may also depend on the abundance of competing cohorts (Einum et al., 2011) and even older age-classes will ultimately have some limit to how well they are capable of homogenizing competitive intensities across stream habitats (Einum et al., 2006).

The relative effect of previous competition on a cohort performance is stabilizing at high carrying capacities. On the contrary, at very low carrying capacities the effect is so strong that the cohort numbers can rapidly decline towards zero. It is expected that as the environment becomes harsher, the effects of density-dependence on population numbers will decrease (Elliott and Elliott, 2006; Nicola et al., 2008, 2009). Most of our study populations presenting a very low carrying capacity are significantly below their maximum potential, being then limited by factors other than habitat capacity, especially by water temperature (see Almodóvar et al., 2012; Ayllón et al., 2012). Weak density-dependent effects are also common in recruitment-limited populations, where recruitment may be insufficient to saturate available habitat for older cohorts (Halpern et al., 2005). Nevertheless, there are also healthy populations that naturally occur at low carrying capacities. In this case, the effects of disturbance events on a specific life stage at a certain time may persist through generations, especially if recruitment is strongly affected, given that recruits numbers are a primary driver of adult abundance (Elliott, 1996) and the total production of a cohort (Lobón-Cerviá, 2009a). In this kind of population, if extreme environmental pressures over recruitment are maintained for a long period of years, they may substantially depress the population growth rate, and thus the population density at equilibrium, and probably lead the population to extinction (Daufresne and Renault, 2006). Therefore, in those populations which show little resilience, a small reproductive stock would not be sufficient to repopulate the streams when environmental conditions re-optimize, contrarily to what has been reported in Atlantic brown trout (Lobón-Cerviá, 2009b) and other salmonid populations (Vincenzi et al., 2008). Consequently, human activities that persistently reduce adult stock below its maximum potential (e.g. angling) may threaten population persistence on the long-term if the pressure is too strong.

Hence in our study populations, the existence of endogenous regulation (whose strength depends on environmental harshness) causes the abundance of different life stages to track the fluctuations of the carrying capacity set by environmental conditions. However, we also observe that the final performance of a cohort is inherently linked to numbers of competing cohorts. All these regulatory mechanisms can be incorporated in the modelling process to increase the predictive power of models of carrying capacity dynamics estimated through the proposed approach. Finally, it is worth noting that this approach can be applied to any territorial animal species as long as they are principally limited by habitat conditions and habitat selection patterns can be modelled as habitat suitability functions.

Acknowledgments

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