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# MODELLING BROWN TROUT SPATIAL REQUIREMENTS THROUGH PHYSICAL HABITAT SIMULATIONS

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### ABSTRACT

Territorial behaviour is often considered the main mechanism regulating salmonid populations and territory size regarded as the proximate factor that limits abundance, being mainly determined by body size. Despite the spatial requirements of young-of-theyear (YOY) brown trout, *Salmo trutta*, have been previously established, there is still a gap in the knowledge about the spatial needs of older individuals. Therefore, we aimed to develop an allometric territory size relationship for YOY, juvenile and adult trout. Territory size was inferred from 12-year demographic data and physical habitat simulations performed at 10 pristine sites where populations showed high and stable densities. When compared to previous models in salmonids, results revealed not only interspecific but also intraspecific significant differences in the size of territories used by individuals of comparable size. Interestingly, the explanatory power of the derived allometric territory size relationships was similar to previous models based on individual observational data. It suggested that despite the fact that results obtained from population data cannot explicitly describe territorial behaviour of individuals, they may represent accurately their spatial requirements. Finally, results suggested that territory volume, and not territory area, scaled with body size at a rate consistent with brown trout metabolic rate, the scaling rate being highly constant at any level of simulated proportion of nonterritorial fish in the population. Consequently, if individuals must increase territories to fulfil energetic demands, the allometry of territory volume seems a better predictor of spatial requirements than territory area. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: habitat selection; habitat simulation models; PHABSIM; salmonids; Salmo trutta; territorial behaviour; territory size; territory volume

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## INTRODUCTION

Salmonids frequently compete with conspecifics for feeding territories in streams, this competition resulting in density dependent responses that increase in intensity as population density approaches carrying capacity (Grant and Kramer, 1990). Therefore, territorial behaviour is often considered the main mechanism regulating salmonid populations (Keeley, 2001), being territory size regarded as the proximate factor that limits abundance (Grant *et al.*, 1998). Population dynamics in territorial species is, in turn, strongly influenced by how territory size is adjusted to ecological conditions (Adams, 2001).

Despite many factors, such as intruder pressure (e.g. Imre *et al.*, 2004), food abundance (e.g. Keeley, 2000) or visual isolation (Imre *et al.*, 2002), can affect territory size in salmonids, previous studies evidence that body size is the strongest predictor (e.g. Grant *et al.*, 1989; Elliott, 1990; Keeley and Grant, 1995; Keeley and McPhail, 1998). Consequently, the area required and defended by individuals of any size can be scaled by an allometric territory size relationship (e.g. Grant and Kramer, 1990).

Former studies of territoriality in salmonids have been conducted under experimental (e.g. Keeley, 2000; Imre *et al.*, 2004) and natural (e.g. Elliott, 1990; Keeley and McPhail, 1998) conditions. In any case, they provide territory size data based on direct observations of territorial individuals. However, since not all individuals are territorial (Puckett and Dill, 1985; Brännäs *et al.*, 2003), the study of territories may provide information regarding the habitat, space and food requirements of dominant individuals in the populations (Grant *et al.*, 1998).

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On the contrary, territory size data derived from studies conducted at a population level would encompass diverse behavioural strategies (territorial, floating or nonterritorial) and aggressiveness levels of both dominant and subordinate individuals. Therefore, this approach would reveal average spatial requirements of fish, which could not be applied to individual-based models but may be relevant to population dynamics modelling.

Estimates of territory size from population density data would introduce, however, a significant bias since not all the wetted stream area is suitable for fish. Physical habitat simulations determine the potentially available habitat, which can be quantified in terms of area (weighted usable area, WUA) or volume (weighted usable volume, WUV), for an aquatic species as a function of discharge. In consequence, indirect estimates of spatial requirements from abundance data must be referred to the WUA (or WUV), since it is a measure that combines habitat quality and quantity available for the different life stages. In populations at carrying capacity, the available WUA or WUV for each life stage would be saturated with territories of an estimated size representing the average minimum spatial requirements of individuals within the life stage.

Brown trout *Salmo trutta* is considered a highly territorial species, chiefly in the alevin stage when the acquisition of feeding territories turns crucial for survival (Titus, 1990) and density dependent mortality strongly operates on recruitment (Nicola *et al.*, 2008, 2009). However, self-thinning processes have been described in brown trout populations for juveniles and adults as space requirements increased and habitat availability declined (Rincón and Lobón-Cerviá, 2002; Lobón-Cerviá and Mortensen, 2006). Therefore, competition for space in juvenile and adult stages is likely to occur when suitable habitat become limiting. Nevertheless, despite the influence of territory size in setting the maximum density of cohorts along their whole life span, up to now only Elliot's (1990) work provides an allometry of territory size for young-of-the-year (YOY) brown trout. This lack of information about the spatial needs of older trout renders necessary to extend the study of territories to juvenile and adult stocks.

It has been suggested that salmonids increase territory size to meet increasing metabolic demands (Keeley and McPhail, 1998; Steingrímsson and Grant, 1999). However, trout would not necessarily increase territory size in relation to body mass consistently with metabolic rate. In neighbouring rivers, a shift in brown trout both habitat selection and foraging patterns occurs after the first winter, trout moving to deeper and slower habitats as they grow (Ayllón *et al.*, in press). As a result, YOY trout may use in a greater extent two-dimensional territories in shallow fast-flowing riffles but as trout grow and move to pool habitats the productivity of the territory would depend on the cross-sectional profile of water flowing over the area. It would be then a three-dimensional territory, the territory volume, which must be scaled as trout grow in size at a rate high enough to meet increasing energy requirements.

The aim of this study was to develop an allometric territory size relationship for YOY, juvenile and adult brown trout, testing the hypothesis that territory volume, and not territory area, must necessarily scale to body size at a rate consistent with metabolic rate. That is to say, we hypothesized that the allometry of territory volume would be a better predictor of brown trout spatial requirements than territory area. We also analysed whether the territory volume hypothesis can be applied to other salmonid species.

## **METHODS**

#### Study area and brown trout populations

This study was carried out in 10 sites located in four rivers from the Ebro River basin, a Mediterranean drainage (rivers Arrañosin, Sorogain, Arga and Orokieta) and five rivers from the Bay of Biscay drainage (rivers Errekagorri, Erasote, Zumarrezta, Aranea and Zoko). One sampling site was selected in each river, except for river Arga, where two sampling sites were located (hereafter Arga 1 and 2). Sampling sites correspond to first to third-order streams and are situated at an altitude ranging from 210 to 895 m. Selected sites represented the highest population densities over the study area (average population density  $\pm$  SD = 9013  $\pm$  2847 trout ha<sup>-1</sup>, n = 120), showing a low interannual variability (mean coefficient of variation  $\pm$  SD = 0.355  $\pm$  0.102, n = 10) during the 12-year study period (1993–2004). Age classes from 0+ to 3+ were represented all years in all study sites and density data for 4+ age class were available in all sites occasionally.

The territory size hypothesis predicts that as a cohort approaches habitat saturation individuals will cease growing, emigrate or die, and that the probability of observing such density dependent responses increases with increasing density or habitat saturation (Grant and Kramer, 1990). Therefore, Percent Habitat Saturation (PHS,

Grant and Kramer, 1990) was calculated for all years and sites. However, instead of comparing observed densities to maximum predicted densities by the allometric territory size relationship developed by Grant and Kramer (1990), densities were compared to maximum habitat capacity defined by maximum observed occupancy rates (e.g. Capra *et al.*, 2003; Gouraud *et al.*, 2008). Average PHS was 56.3% (range 44.8–67.4%) which corresponds to a probability of observing a density dependent response of 0.78 (range 0.70–0.83) according to the logistic model of Grant and Kramer (1990). In fact, spatio-temporal variations in mortality rates of 0+ and 1+ age classes at study sites were density dependent, as well as temporal fluctuations in mortality rates were correlated to density in both age classes in almost all study sites (Almodóvar *et al.*, unpublished data).

Daily average water temperature during growing season ranged from  $12.8^{\circ}$ C to  $15.8^{\circ}$ C at selected sites, these values being included within the optimum range for growth described for brown trout in Mediterranean streams (Nicola and Almodóvar, 2004; Parra *et al.*, 2009). Moreover, maximum water temperature never exceeded the upper critical values for survival in natural conditions (Wehrly *et al.*, 2007). Hence, water temperature was not regarded as a limiting factor at study sites. In addition, no other environmental constraints were detected.

The effect of human impacts over the studied rivers was assessed to determine their ecological status. For this purpose, 21 impact variables identified by Degerman *et al.* (2007) as descriptors of key human pressures that act on fish communities and population structure at different spatial scales were selected (Table I). The 89.25 and 7.0% of measured values across sites corresponded to high and good status impact classes respectively, according to the European Union Water Framework Directive (WFD; 2000/60/EEC). Only a minor proportion of measured impacts (3.75%) were defined as moderate. Results yielded by impact analyses revealed no severe anthropic pressure over the physical, chemical and biological conditions of selected sites. Therefore, studied populations were considered not far from carrying capacity and intraspecific competition for feeding territories assumed to take place.

Electrofishing with a 2200 W DC generator took place every year at the end of the growing period from 1993 to 2004. Prior to sampling, each site was blocked upstream and downstream with nets. Fish densities 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. Brown trout were anaesthetized with MS-222 (tricaine methanesulfonate), measured (fork length, to the nearest mm) and weighed (to the nearest g), and scales were taken for age determination. Individuals were grouped in three age classes, 0+, 1+ and >1+ and average size-at-age was estimated. The fish were placed in holding boxes to recover and then returned back to the stream. There was no mortality of fish or other wildlife caused by the electrofishing, handling and anaesthesia of the fish. The regional environmental agency of Navarre permitted the population studies in the field. All procedures complied with the Spanish and European Union legislation on animal care and experimentation.

## Physical habitat simulations and territory size

Habitat modelling was performed using the Physical Habitat Simulation System PHABSIM (Milhous et al., 1989). Hydraulic and channel structure data required for hydraulic and habitat simulations were collected at each study site during the summer of 2004 following the data collection procedures described by Bovee (1997). Physical habitat variables were measured every 1 m along transects placed perpendicular to the flow. 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 to 7 times the average channel width, in accordance with the general precepts of alluvial river morphology on the spacing of successive riffles (Leopold et al., 1964). Average length of study sites was  $97.2 \pm 21.9$  m, and average assessed area of study sites was  $763.1 \pm 414.5$  m<sup>2</sup>. Average data of measured physical habitat variables are summarized in Table II. Since results from PHABSIM are extremely sensitive to the accuracy of habitat suitability criteria used in the model, 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. 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 (Vismara et al., 2001; Ayllón et al., in press). Historical time series of mean summer discharge for the 12-year study period (1993–2004) were provided at Table I. Selected human impact variables and the scale they apply. Average variable values  $\pm$  SD of sampling sites and the corresponding classes of ecological status (1 = high, 2 = good, 3 = moderate, 4 = poor, 5 = bad). Status classes are described in Degerman *et al.* (2007)

Human impact variableValueClassHuman impact variableVaNatural flow quantity10.99 $\pm$ 21.41-3Connectivity (impassable dams)0.(% deviation)(% deviation)10.99 $\pm$ 21.41-3Connectivity (impassable dams)0.(% deviation)Upstream dam affects siteNo1Land use (% agriculture)0.88 :(% doviation)Norphological conditionNegligible1Urbanization (%)0.91 :Morphological conditionNegligible1Urbanization (%)0.91 :Phosphate (mg1 <sup>-1</sup> )9.26 $\pm$ 2.211Riparian zone (%)90.06Oxygen (mg1 <sup>-1</sup> )0.10 $\pm$ 0.081-2Phosphate function90.06Ammonium (mg1 <sup>-1</sup> )0.11 $\pm$ 0.151-290.06	Segment		River		
Natural flow quantity10.99 $\pm$ 21.41-3Connectivity (impassable dams)0.(% deviation)Upstream dam affects siteNo1Land use (% agriculture)0.88:Upstream dam affects siteNo1Lund use (% agriculture)0.88:Morphological conditionNegligible1Urbanization (%)0.91:Phopped7.81 $\pm$ 0.441Riparian zone (%)90.06Phosphate (mg1 <sup>-1</sup> )0.10 $\pm$ 0.081-21-2Ammonium (mg1 <sup>-1</sup> )0.11 $\pm$ 0.151-2	uman impact variable Value	Class	Human impact variable	Value	Class
Upstream dam affects siteNo1Land use (% agriculture)0.88-temperatureMorphological conditionNegligible1Urbanization (%)0.91-Morphological conditionNegligible1Urbanization (%)0.91-pH7.81 \pm 0.441Riparian zone (%)90.06Oxygen (mg l <sup>-1</sup> )9.26 \pm 2.211Ploodplain lateral movements>5Phosphate (mg l <sup>-1</sup> )0.11 \pm 0.151-21-2	sctivity (impassable dams) 0.00	1	Connectivity (impassable dams)	$0.70\pm0.95$	1–3
$ \begin{array}{llllllllllllllllllllllllllllllllllll$	use (% agriculture) $0.88 \pm 1.99$	1	Land use (% agriculture)	$0.16\pm0.45$	1
$ \begin{array}{cccccc} pH & 7.81 \pm 0.44 & 1 & Riparian zone (\%) & 90.06\\ Oxygen (mg1^{-1}) & 9.26 \pm 2.21 & 1 & Floodplain lateral movements & >9 \\ Phosphate (mg1^{-1}) & 0.10 \pm 0.08 & 1-2 & \\ Ammonium (mg1^{-1}) & 0.11 \pm 0.15 & 1-2 & \\ \end{array} $	ization (%) $0.91 \pm 1.66$	1-2	Urbanization (%)	$0.48\pm0.52$	1
Introduction of fishNo1Impact of fish stockingNo stocking1Exploitation rate (%) $12.6 \pm 14.9$ $1-2$ Impact from other faunaNo1Impact from floraNo1Weed cuttingNever1	an zone (%) 90.06±7.6 plain lateral movements >90%				

## BROWN TROUT SPATIAL REQUIREMENTS

River	Altitude (m)	Summer discharge (m <sup>3</sup> s <sup>-1</sup> )	Width (m)	Depth (cm)	Velocity $(m s^{-1})$	Dominant substrate (%)	Total cover (%)
Arrañosin	895	$0.14\pm0.08$	$6.1 \pm 1.3$	$19.8\pm8.2$	$0.27\pm0.43$	Stone (35.4)	16.7
Sorogain	780	$0.09 \pm 0.08$	$4.5 \pm 1.9$	$15.5\pm6.8$	$0.14\pm0.20$	Bedrock (66.7)	52.2
Arga 1	690	$0.21\pm0.04$	$6.5\pm0.5$	$18.2\pm8.0$	$0.30\pm0.23$	Stone (78.3)	34.8
Arga 2	555	$0.69 \pm 0.13$	$11.7\pm1.7$	$34.9\pm20.6$	$0.25\pm0.53$	Stone (55.2)	36.2
Orokieta	610	$0.15\pm0.09$	$4.3\pm0.5$	$22.5\pm7.8$	$0.39\pm0.41$	Stone (79.0)	57.9
Errekagorri	210	$0.05\pm0.03$	$3.1\pm0.6$	$12.3\pm5.1$	$0.26\pm0.33$	Bedrock (64.3)	57.1
Erasote	490	$0.44 \pm 0.16$	$5.2 \pm 1.0$	$21.0 \pm 14.6$	$0.29\pm0.47$	Bedrock (70.3)	50.0
Zumarrezta	470	$0.09\pm0.06$	$4.0\pm0.9$	$22.7 \pm 14.2$	$0.18\pm0.31$	Boulder (50.0)	80.0
Aranea	300	$0.42 \pm 0.19$	$5.5\pm0.8$	$25.8\pm22.2$	$0.51\pm0.53$	Stone (44.0)	64.0
Zoko	340	$0.17\pm0.08$	$5.0\pm1.5$	$17.0\pm12.9$	$0.31\pm0.32$	Stone (55.0)	35.0

Table II. Physical characteristics (mean  $\pm$  SD) of study sites, sampled during July and August of 2004

each study site by the closest gauging stations. Mean summer WUA and WUV time series for each age class were then obtained by coupling WUA and WUV curves as a function of discharge with discharge time series.

Habitat competition analyses were performed to model spatial segregation of cohorts due to competition and, hence, to avoid an overestimation of potential available habitat for each age class. Analyses of habitat competition between age classes were made using the HABEF programme within PHABSIM system. 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 (or WUV) where one age class dominates over the other one and *vice versa*. We considered that in areas where younger age classes has less favourable habitat conditions they cannot out-compete older ones with more suitable habitat (Railsback *et al.*, 2005), being finally displaced, so that this WUA (or WUV) was not added to total available habitat. Finally, occupancy rates of the weighted usable area (density/WUA) and volume (density/WUV) were calculated from demographic data and physical habitat simulation results for every age class, year and site.

Average territory area and volume were then estimated as the inverse of the WUA or WUV occupancy rate. Firstly, linear regressions were performed with average territory area as dependent variable and average age class fork length and mass as independent variables to derive the allometric relationships. Allometric equations were based on  $\log_{10}$  transformed data to meet statistical assumptions. Secondly, we estimated the territory volume-body size relationship at both population and individual level. On one hand, we followed the same procedure as formerly described for the allometry of territory area to derive the allometric relationship of territory volume at a population level. On the other hand, we used the habitat use data collected during the habitat study to obtain the allometry of an area set by the allometric territory area relationship previously developed. Hence, the territory volume required by each captured fish was calculated as the territory area multiplied by the water depth of the position they occupied. Finally, we regressed territory volume against body mass for all sampled fish based also on  $\log_{10}$  transformed data.

To test whether the territory volume hypothesis works out in salmonids as a general rule, we re-analysed the data provided by Keeley and Grant (1995), and Keeley and McPhail (1998) to estimate the relationship between body mass and territory volume in Atlantic salmon *Salmo salar* and steelhead trout *Oncorhynchus mykiss*.

## Effects of floating and nonterritorial behaviour

We assessed the effects of varying levels (from 0 to 60% of total population density) of individuals displaying a nonterritorial behaviour (nonterritorial *sensu stricto* and floaters) upon regression coefficients of allometric models to render possible comparisons with results from previous studies based on the observation of territorial individuals. Analyses were carried out under a hypothesized scenario where the total proportion of nonterritorial fish in the population (P%) was encompassed by the  $P_i\%$  smallest individuals of each *i* age class. These fish were not taken into account when both age class density and average age class body size (length or mass) were calculated. This

scenario was selected over an alternative one where the proportion of nonterritorial fish (P%) in the population included the  $P_i/2\%$  of both the smallest and largest individuals of each *i* age class, since experimental studies have shown that territorial brown trout individuals were significantly larger than fish adopting a floating or nonterritorial behaviour (Brännäs *et al.*, 2003). The selected scenario is also consistent with experimental observations of Keeley (2001) in steelhead trout. Keeley detected polymodal size-frequency distributions when the smallest and in worst condition fish were given the chance to emigrate at increasing levels of competition or decreasing levels of food abundance. The secondary peaks were suggested to represent individuals using alternate foraging tactics.

#### Statistical analyses

To address possible intra- and interspecific differences in the spatial requirements of individuals, we used oneway analyses of variance (ANOVA) to compare territory estimates observed in our study with the expected values from previous models in salmonids. We contrasted regression slopes between derived models and previous models in the literature by means of *t*-tests. The significance level  $\alpha$  was set at 0.05.

### RESULTS

Brown trout territory area  $(T, m^2)$  estimated from demographic data and physical habitat simulation results (Table III) increased with increasing body length (L, cm) according to the model  $\text{Log}_{10} T = 1.79 \cdot \text{Log}_{10} L - 1.99$   $(F_{1,361} = 931.5, p < 0.0001, r^2 = 0.72)$ . However, a change in the regression function occurred between YOY trout and older individuals (Figure 1a). Both the intercepts (ANCOVA,  $F_{1,359} = 3.92$ , p = 0.048) and the slopes (ANCOVA,  $F_{1,359} = 4.24$ , p = 0.040) of the two regression models differed significantly. Hence, the resulting model was  $\text{Log}_{10} T = (2.64 - 0.96 \cdot \text{age category}) \cdot \text{Log}_{10} L - (2.72 + 0.90 \cdot \text{age category}) (F_{3,359} = 314.0, p < 0.0001, r^2 = 0.72)$ , where age category is 0 for fish  $\leq 9 \text{ cm}$  (YOY) or 1 for fish > 9 cm (older trout). Territory area increased in relation to body mass (M, g) in a similar way (Figure 1b). Analyses revealed significant differences in the intercepts (ANCOVA,  $F_{1,359} = 3.87$ , p = 0.048) and the slopes (ANCOVA,  $F_{1,359} = 4.69$ , p = 0.031) of the regression models. As a result,  $\text{Log}_{10}T = (0.84 - 0.30 \cdot \text{age category}) \cdot \text{Log}_{10}M - (0.98 + 0.26 \cdot \text{age category}) (F_{3,359} = 322.0, p < 0.0001, r^2 = 0.73)$ .

Results were compared to former studies monitoring territory area in salmonids (Figure 2 and Table IV). In the present study, YOY trout required territories significantly larger than the brown trout population studied by Elliott (1990) (ANOVA: p < 0.0001) and other species of salmonids (p < 0.0001) of the same size other than Atlantic salmon and steelhead trout smaller than 5 cm (Figure 2). In contrast, trout larger than 9 cm used territories significantly smaller than overall salmonids (p < 0.0001) and Atlantic salmon (p < 0.0001), but not steelhead trout (p = 0.069), of comparable size. The slope of the territory area versus body length regression for YOY brown trout in the present study was similar to those previously described for salmonids (t-test: t = 0.08, n = 135, p = 0.94),

River	Length 0+	WUA Occ 0+	WUV Occ 0+	Length 1+	WUA Occ 1+	WUV Occ 1+	Length >1+	WUA Occ >1+	WUV Occ >1+
Arrañosin	$6.4 \pm 0.8$	$3.3 \pm 1.3$	20.3 + 7.9	$12.5 \pm 1.7$	$1.6 \pm 0.5$	$7.9 \pm 3.4$	$18.5 \pm 2.4$	$0.7 \pm 0.3$	$3.1 \pm 1.8$
Sorogain	$6.0 \pm 1.1$	$5.6 \pm 4.0$	$33.5 \pm 14.8$	$11.5 \pm 1.2$	$1.2 \pm 0.6$	$7.7 \pm 4.8$	$16.1 \pm 1.8$	$0.8 \pm 0.4$	$4.4 \pm 2.4$
Arga 1	$6.9 \pm 0.9$	$3.4 \pm 1.9$	$19.6 \pm 10.9$	$13.6 \pm 1.3$	$1.0 \pm 0.3$	$5.9 \pm 1.9$	$19.8 \pm 2.7$	$0.7 \pm 0.3$	$4.2 \pm 1.7$
Arga 2	$7.6 \pm 1.1$	$2.5 \pm 1.2$	$9.6 \pm 4.8$	$15.6 \pm 1.9$	$0.7 \pm 0.3$	$1.6 \pm 0.6$	$22.5\pm2.5$	$0.3 \pm 0.2$	$0.5 \pm 0.3$
Orokieta	$7.0 \pm 0.9$	$3.7 \pm 2.4$	$17.0 \pm 14.4$	$13.7\pm1.5$	$0.9 \pm 0.2$	$5.7 \pm 2.6$	$19.3 \pm 2.4$	$0.5 \pm 0.1$	$2.2 \pm 0.9$
Errekagorri	$6.0 \pm 1.0$	$3.7\pm2.2$	$30.3 \pm 17.5$	$11.3\pm1.4$	$0.9\pm0.6$	$5.3\pm2.9$	$16.9\pm2.1$	$0.6 \pm 0.3$	$2.5 \pm 1.2$
Erasote	$5.8\pm0.9$	$4.9\pm3.4$	$31.1 \pm 23.4$	$11.7\pm1.1$	$1.1 \pm 0.5$	$4.6\pm2.0$	$17.2\pm2.3$	$0.6 \pm 0.1$	$1.5\pm0.7$
Zumarrezta	$5.8\pm0.7$	$3.1\pm2.6$	$16.4\pm10.0$	$11.2\pm1.5$	$1.1 \pm 0.7$	$5.3\pm2.8$	$16.8\pm2.5$	$0.7 \pm 0.3$	$2.4 \pm 1.0$
Aranea	$6.7 \pm 1.1$	$3.1 \pm 3.1$	$18.4 \pm 17.0$	$13.3 \pm 1.4$	$0.9 \pm 0.4$	$2.1 \pm 0.9$	$18.8\pm2.7$	$0.4 \pm 0.2$	$0.7 \pm 0.5$
Zoko	$5.7\pm1.9$	$3.8\pm4.0$	$20.6\pm20.7$	$11.4\pm1.7$	$1.1\pm0.5$	$3.8\pm1.9$	$16.6\pm2.1$	$0.6\pm0.3$	$2.2\pm1.0$

Table III. Average ( $\pm$  SD) fork length (cm), weighted usable area WUA (trout m<sup>-2</sup> of WUA) and weighted usable volume WUV (trout m<sup>-3</sup> of WUV) occupancy rates (Occ) for each age class of brown trout

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Figure 1. Relationship between territory area (m<sup>2</sup>) and (a) fork length (cm) and (b) mass (g) for brown trout

steelhead trout (t = 0.35, n = 162, p = 0.73), brook trout (t = 0.31, n = 135, p = 0.76), and brown trout larger than 4 cm (t = 1.41, n = 294, p = 0.16) but not brown trout smaller than 4 cm (t = 4.46, n = 613, p < 0.0001) and Atlantic salmon (t = 2.00, n = 160, p = 0.045), which showed steeper slopes. On the contrary, older trout scaled territories to body length at a significantly lower rate than salmonids (t = 2.18, n = 274, p = 0.031), Atlantic salmon (t = 4.49, n = 299, p < 0.0001) and steelhead trout (t = 2.48, n = 301, p = 0.014). Similar results were obtained when the regression slopes of the territory area versus body mass relationships were compared.

Territory volume (V, m<sup>3</sup>) calculated from population data significantly increased with increasing body mass (Figure 3a). Contrarily to the allometry of territory area, the allometric territory volume relationships did not differ statistically between YOY and older trout, since there were no significant differences in either regression slopes (ANCOVA:  $F_{1,359} = 0.42$ , p = 0.52) or intercepts ( $F_{1,359} = 0.28$ , p = 0.60). Therefore, data were pooled and the regression model describing this relationship was  $\text{Log}_{10} V = 0.76 \cdot \text{Log}_{10} M - 1.63$  ( $F_{1,361} = 842.0$ , p < 0.0001,  $r^2 = 0.70$ , 95%CI for b = 0.71-0.81). When analysing territory volume based on individual data (Figure 3b), the model  $\text{Log}_{10} V = 0.75 \cdot \text{Log}_{10} M - 1.65$  ( $F_{1,365} = 2840.8$ , p < 0.0001,  $r^2 = 0.89$ , 95%CI for b = 0.72-0.78) was obtained. Both models presented almost identical regression slopes (ANCOVA:  $F_{1,726} = 0.04$ , p = 0.84) and intercepts ( $F_{1,726} = 0.11$ , p = 0.74).

The analyses of data from Keeley and Grant (1995) and Keeley and McPhail (1998) showed that the relationship between body mass and territory volume were highly significant in both Atlantic salmon ( $Log_{10}V = 0.96$ 



Figure 2. Comparison of the territory area and fork length relationship, solid line: brown trout, *S. trutta* (thick line: present study; thin line: Elliott, 1990) and brook trout, *S. fontinalis* (dotted line; Grant *et al.*, 1989), a multi-specific study (small dash-dash line; Grant and Kramer, 1990), Atlantic salmon, *S. salar* (dashed line; Keeley and Grant, 1995) and steelhead trout, *O. mykiss* (small-dashed line; Keeley and McPhail, 1998)

Table IV. Slopes (95%CI) of territory area versus fork length and mass linear regression models in salmonid species. Mass coefficients were extracted from Keeley and Grant (1995). All models are based on log<sub>10</sub> transformed data

Species	Length	Mass	Reference
Salmo trutta < 9 cm	2.64 (1.92-3.36)	0.84 (0.58-1.10)	Present study
Salmo trutta > 9 cm	1.68 (1.50–1.86)	0.54 (0.46–0.62)	Present study
Salmo trutta $< 4 \text{ cm}$	3.45 (3.40-3.51)	0.99	Elliott (1990)
Salmo trutta > 4 cm	2.24 (2.17–2.31)	0.82	Elliott (1990)
Salmo salar	3.91 (3.28-4.55)	1.12 (0.91–1.33)	Keeley and Grant (1995)
Oncorhynchus mykiss	2.47 (1.87–3.04)	0.82 (0.63-1.01)	Keeley and McPhail (1998)
Salvelinus fontinalis	2.48 (1.74–3.22)	0.82	Grant et al. (1989)
Multi-specific	2.61 (2.15–3.07)	0.86	Grant and Kramer (1990)

 $Log_{10}M - 1.44$ , p < 0.001,  $r^2 = 0.89$ , 95%CI for b = 0.87 - 1.10) and steelhead trout ( $Log_{10}V = 0.83$  $Log_{10}M - 1.52$ , p < 0.001,  $r^2 = 0.75$ , 95%CI for b = 0.69 - 0.97). Interspecific differences were observed as brown trout, Atlantic salmon and steelhead trout models varied significantly in their intercepts (ANCOVA:  $F_{2,457} = 16.75$ , p < 0.0001) and slopes ( $F_{2,457} = 14.11$ , p < 0.0001). Atlantic salmon had higher territory volumes ( $F_{1,410} = 40.54$ , p < 0.0001) that scaled with body mass at a higher rate ( $F_{1,410} = 34.77$ , p < 0.0001) than brown trout. Meanwhile, steelhead trout required greater territories than brown trout ( $F_{1,412} = 12.54$ , p < 0.0001) although the scaling rates were similar ( $F_{1,412} = 3.51$ , p = 0.061).

The regression slopes of the relationship of both body mass and territory area (ANCOVA:  $F_{6,2513} = 0.016$ , p = 0.99), and body mass and territory volume ( $F_{6,2527} = 1.013$ , p = 0.41) did not differ between different levels of trout displaying a nonterritorial behaviour (Figure 4). In contrast, intercepts varied significantly when body mass was regressed either to territory area ( $F_{6,2513} = 4.00$ , p < 0.001) or territory volume ( $F_{6,2527} = 8.83$ , p < 0.0001). However, these differences were not found when the proportion of nonterritorial individuals was below the 50% of total population density in territory area ( $F_{4,1795} = 1.26$ , p = 0.28) and below 40% in territory volume ( $F_{3,1444} = 1.03$ , p = 0.38).



Figure 3. Relationship between territory volume (m<sup>3</sup>) and body mass (g) for brown trout based on (a) population data, and (b) individual data

#### DISCUSSION

Our findings showed that differences in body size of brown trout accounted for the 72% of the variation observed in territory area, supporting former results based on individual observational data in salmonid species (Grant *et al.*, 1989; Elliott, 1990; Grant and Kramer, 1990; Keeley and Grant, 1995; Keeley and McPhail, 1998). We also observed ontogenetic changes in the allometry of territory area, with YOY trout scaling territories to body size at a significantly higher rate than older trout. Elliott (1990) reported a similar behaviour within the YOY age-class in brown trout, observing a change in the slope of the allometric territory area relationship for trout greater than 4 cm in length. Ontogenetic changes in the territory area occupied by individuals have been described as well for other species of salmonids. YOY Atlantic salmon (Keeley and Grant, 1995) and steelhead trout (Keeley and McPhail, 1998) required relatively larger territories for their body size in comparison to older individuals.

Results revealed interspecific variations in the size of territories required by individuals of a comparable size. YOY trout used larger territories than other species of salmonids while in older trout this behaviour was quite the opposite. Such variations may result from differences in habitat selection patterns or metabolic requirements between species. In addition, salmonids can behave as single or multiple central-place foragers, and the proportion of individuals switching from one to another pattern of space use varies across species and populations



Figure 4. Regression slope (top) and regression intercept (down) of the allometric relationships of territory area for YOY (thin line) and older brown trout (thick line), and territory volume (dashed line) at different proportions (P) of nonterritorial brown trout. Standard errors of the mean are also shown

(Steingrímsson and Grant, 2008). Furthermore, we also detected intraspecific differences, since trout in our study area had significantly larger territories than equally-sized individuals of the population described by Elliott (1990). Salmonids defend territories that vary in size in response to diverse environmental conditions. Hydraulic conditions specially affect territory area and foraging behaviour, since it is directly linked to the availability, distribution and composition of drifting prey (Reid and Thoms, 2008). Territory area typically decreases as habitat quality and complexity (Imre *et al.*, 2002; Dolinsek *et al.*, 2007; Venter *et al.*, 2008), or food abundance (Keeley, 2000) increase. Moreover, biotic factors such as competition with introduced species can modify aggression and foraging behaviour in fish populations (Seiler and Keeley, 2007). Differences in such factors may explain in a great extent the differences observed in territory area. Moreover, territoriality is a flexible rather than a rigid behaviour strategy (Grant, 1997), varying between individuals and populations. Variations in abiotic characteristics such as instream physical habitat features (Johnsson *et al.*, 2000, 2004; Höjesjö *et al.*, 2004) or food availability (Brännäs *et al.*, 2003) between rivers, as well as behavioural differences, resident-migratory behaviour (Lahti *et al.*, 2001) or aggressiveness level (Lahti *et al.*, 2002), between populations may cause changes in brown trout territorial behaviour and spatial ecology.

In the present study, YOY fish scaled territories to body length and mass at a rate similar to other populations of brown trout and different species of salmonids, while older trout did it at a significantly lower rate than those formerly described in salmonid species. Salmonids are thought to increase territory area to meet increasing metabolic demands (Keeley and McPhail, 1998; Keeley, 2000) as the scaling of body mass and territory area in most previous studies (Table IV) is consistent with that predicted by salmonid metabolic rate (average of 0.87, range 0.73–1.05; see Steingrímsson and Grant, 1999). In our study, YOY brown trout scaled territories to body mass with a slope (0.84) included in that range and not significantly different to specific slopes reported for brown trout, ranging from 0.75 (Elliott, 1976) to 0.88 (Beamish, 1964). In contrast, the scaling of territory area to body mass in older trout did not match the hypothetical values that would result from the allometry of metabolic rate. Nevertheless, the allometry of territory volume and body mass (0.76) was almost the same as the scaling coefficient of energy required for metabolism observed in brown trout by Elliott (1976). When we analysed the hypothesis prediction by applying the allometry of territory area to sampled individuals (individual data), we obtained similar

results. Then, if individuals must increase territories to fulfil energetic demands, the allometry of territory volume seems a better predictor of juvenile and adult spatial requirements than territory area in the studied brown trout populations.

We suggest this could be the consequence of geometric differences in space use between age classes. In the studied rivers, trout displayed a similar habitat selection pattern to that described in Ayllón et al. (in press) in neighbouring rivers. YOY trout inhabited shallow riffles selecting two-dimensional territories around velocity shelters close to fast-flowing areas, since they are the most energetically profitable positions (Fausch, 1984). Growing YOY trout would have to increase the size of the two-dimensional territories at a rate consistent with increasing metabolic demands. In contrast, given that swimming capacity (Videler, 1993) and reactive distance to prey (Guensch et al., 2001) increase with body size, larger fish maximize their net energy gain in deeper areas of higher visibility. Therefore, older trout would move to deeper habitats to minimize energy costs selecting resting positions of low water velocity, while maximizing energy intake feeding in the fast-flowing section of the water column. Hence, they would adjust resting-feeding positions in a three-dimensional territory, the territory volume, which must scale to body mass at a rate consistent with increasing energy requirements, according also to the notion that prey detection locations are distributed throughout the reaction volume, not concentrated on its surface (Hughes et al., 2003). This could explain why in some instances the territory area hypothesis may fail in defining maximum density in pool habitats but not in riffles (see Grant and Kramer, 1990). Moreover, we found that the regression slopes of the relationships between body mass and territory volume that we estimated for Atlantic salmon and steelhead trout from Keeley and Grant (1995) and Keeley and McPhail (1998) data were not significantly different to the mean scaling of metabolic rate to body mass in salmonids, being included in its range of variation.

Our results showed that the scaling rates of territory size to mass were consistent and did not change at any level of simulated proportion of nonterritorial fish in the population. Moreover, the area actually defended by territorial fish would not significantly change until the threshold of 40% is reached, when the applicability of developed models may fail. Likewise, conclusions yielded from comparisons to previous works are valid within this range (0-40% of nonterritorial fish in the population). Unfortunately, although Elliott (1990) observed a negligible proportion of YOY brown trout not holding a territory after the critical period, there are no data about the levels of nonterritorial fish in summer time or in older trout in natural systems. The importance of territoriality as a mechanism of population regulation may depend on the proportion of individuals defending territories (Imre et al., 2002). Density dependent responses may also occur in populations regulated through floating when territorial individuals defend fixed territories, as described in several fish, mammal or bird species (López-Sepulcre and Kokko, 2005 and references therein). However, in salmonid species it has been shown that increasing number of competitors lead to decreasing territory size (Keeley and McPhail, 1998; Keeley, 2000; Imre et al., 2004), which also seems to be a general pattern in many other taxa (Adams, 2001; López-Sepulcre and Kokko, 2005). Therefore, proportions of nonterritorial individuals greater than 40%, which result in territories three times larger than predicted by Elliot's (1990) model, would be an unrealistic scenario in the studied rivers since it would not be energetically profitable for territorial trout to defend large territories at high competitor densities in productive and stable environments.

Our results obtained by means of physical habitat simulations and demographic data showed that territory size was strongly correlated to brown trout body size. Interestingly, the explanatory power of the derived allometric territory area and volume relationships was in some instances similar to previous models in salmonids based on the traditional individual observational approach. Then, it seems that despite the fact that results obtained from population data cannot describe territorial behaviour of individuals, they may represent accurately their spatial requirements. In addition, results appear to validate the initial hypothesis that territory volume would be a better predictor of brown trout spatial needs than territory area. Besides, the territory volume was, at least, as good predictor as territory area in the other considered salmonid species, Atlantic salmon and steelhead trout. Finally, the variability observed in territories predicted by different allometric relationships highlights not only interspecific but also intraspecific differences on the grounds of particular local adaptations. As a result, these relationships should be developed and applied specifically to different species or populations, since territory predictions from the model may have profound implications in population management.

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