Spatial distribution of limited resources and local density regulation in juvenile Atlantic salmon

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Summary

1. Spatial heterogeneity of resources may influence competition among individuals and thus have a fundamental role in shaping population dynamics and carrying capacity. In the present study, we identify shelter opportunities as a limiting resource for juvenile Atlantic salmon (*Salmo salar* L.). Experimental and field studies are combined in order to demonstrate how the spatial distribution of shelters may influence population dynamics on both within and among population scales.
2. In closed experimental streams, fish performance scaled negatively with decreasing shelter availability and increasing densities. In contrast, the fish in open stream channels dispersed according to shelter availability and performance of fish remaining in the streams did not depend on initial density or shelters.
3. The field study confirmed that spatial variation in densities of 1-year-old juveniles was governed both by initial recruit density and shelter availability. Strength of density-dependent population regulation, measured as carrying capacity, increased with decreasing number of shelters.
4. Nine rivers were surveyed for spatial variation in shelter availability and increased shelter heterogeneity tended to decrease maximum observed population size (measured using catch statistics of adult salmon as a proxy).
5. Our studies highlight the importance of small-scale within-population spatial structure in population dynamics and demonstrate that not only the absolute amount of limiting resources but also their spatial arrangement can be an important factor influencing population carrying capacity.

Key-words: carrying capacity, density dependence, population regulation, river substrate, spatial heterogeneity.

Introduction

Competition for limited resources and the resulting density-dependent processes are central in governing population dynamics and evolution in natural populations. Density dependence and population regulation is commonly detected in population abundance time series (Bjørnstad & Grenfell 2001). However, in the presence of variable limiting resources, demographic rates may not depend on population density per se, but on the density relative to the level of the limiting resources (e.g. Berryman 1999, 2004). Identification of limiting resources and quantification of their variation is therefore vital to understand and predict population dynamics. The role of temporally varying limiting resources in shaping population dynamics has been documented in many populations (Sæther 1997; Krüger & Lindström 2001; Solberg et al. 2001; Berryman & Lima 2006; Chamaillé-Jammes et al. 2008). However, limiting resources may also vary spatially. Among

populations, differences in the total amount of a limiting resource are often a likely explanation for variation in abundance (e.g. Fleishman et al. 2002; Cermenõ et al. 2008). On a finer scale, there may be spatial variation within populations. This might be a result of individuals tracking spatial variation in habitat quality, such that an ideal free distribution is approximated (e.g. Fretwell & Lucas 1970; Pulliam & Danielson 1991) and there is a growing recognition that within-population spatial heterogeneity of resources will mediate the strength of intraspecific competition, and hence, influence population carrying capacity (e.g. Flather & Bevers 2002; Shima & Osenberg 2003; Forrester & Steele 2004; Wang et al. 2006).

Spatial aggregation of resources influences the strength of density dependence in widely diverging systems from African elephants to reef fishes (e.g. Holbrook & Schmitt 2002; Johnson 2007; Chamaillé-Jammes et al. 2008). For example, competition for enemy-free space within reef structures may result in density-dependent mortality of some fish species (reviewed by Hixon & Jones 2005). Subpopulations can then

be subject to locally operating density-dependent processes where the structural complexity of the habitat governs the strength of density-dependent mortality (Beukers & Jones 1997; Holbrook & Schmitt 2002; Forrester & Steele 2004; Johnson 2007). Such observations raises questions on the importance of spatial structuring. Despite considerable theoretical focus on the spatial aggregations of continuously distributed resources and how this may shape density-dependent processes and ultimately population carrying capacity (e.g. Wiegand *et al.* 1999; Engen, Lande & Sather 2002; Flather & Bevers 2002; North & Ovaskainen 2007), empirical studies are largely lacking.

Stream-living salmonid fishes are among those organisms for which the nature of density dependence is best understood (e.g. Grant & Kramer 1990; Jonsson, Jonsson & Hansen 1998; Milner *et al.* 2003), and where the potential importance of within-population spatial structure for population dynamics is increasingly acknowledged (Einum & Nislow 2005; Einum, Sundt-Hansen & Nislow 2006; Einum *et al.* 2008a,b). They lay eggs in discrete nests on spatially separated patches of suitable substrate (gravel), resulting in a spatially heterogeneous distribution of recruits. This in combination with limited juvenile mobility following emergence from nests causes intense local competition during the first few weeks of their lives (Einum & Nislow 2005; Einum *et al.* 2008a). As juveniles grow, their habitat requirements change (Armstrong *et al.* 2003). In particular, whereas small juveniles depend on areas with low water velocities for successful feeding (Nislow, Sepulveda & Folt 2004), there is an increasing dependence on large streambed interstices used for shelter with increasing body size (Heggenes *et al.* 1993; Valdimarsson & Metcalfe 1998; Finstad *et al.* 2007). Shelter availability is thus a candidate-limiting factor in juvenile salmonids, and one that may become more limiting with increasing juvenile body size.

Shelter availability covaries with streambed variation in stone sizes and substrate embeddedness, both considerably variable on a river (population) scale due to variation in local geomorphology or fine sediment input. Reduced complexity of streambed substrate from external stressors such as land-use changes or river channel engineering has also recently received considerable attention as a potential contributor to the worldwide decline of anadromous salmonid populations (e.g. Suttle *et al.* 2004). Yet, the mechanistic effects of shelter and how it may interact with density in shaping population dynamics remains poorly understood. If shelter represents a limiting factor for juvenile salmonids, spatial variation in shelter availability is predicted to influence local carrying capacities within populations. Here we use a recently developed method for quantifying shelter availability to test for interactions between density and shelter on juvenile Atlantic salmon performance (growth and dispersal) in both replicated semi-natural stream channels and in a natural population. These experimental and observational approaches are then complemented by a comparative one, where we quantify the abundance and spatial distribution of shelters in nine Norwegian salmon rivers and test for effects on adult salmon production.

Material and methods

Experiments were conducted at the Norwegian Institute for Nature Research (NINA) Station, Ims (south-western Norway, 58°54′ N, 5°57′ E) using one-summer-old (0+) first-generation hatchery-reared Atlantic salmon with parents originating from the nearby River Imsa. Hatchery-reared Atlantic salmon use shelters in a similar way to wild salmon, but they tend to share shelters more often (Griffiths & Armstrong 2002). Thus, the use of hatchery fish makes the present experiments conservative with regard to detecting effects of shelter availability on performance. Water to the hatchery and the channels is drawn from a nearby lake. Water temperatures ranged from 0·8 to 7·6 °C (mean 4·5 °C) during the experiments, which is well below the temperature where juvenile Atlantic salmon start to show a winter behavioural pattern and shelter during daytime (c. 10 °C; Fraser, Metcalfe & Thorpe 1993; Heggenes *et al.* 1993). Only natural food items entering through the inlet water, or present in the substrate, were available for the fish.

EXPERIMENT 1: SHELTER × DENSITY AND GROWTH PERFORMANCE

To test for an interaction between shelter and density on growth rate, 10 stream channels were stocked with a high density (12 fish per channel) and 10 with low density (4 fish). The fish were individually tagged (PIT), measured (±1 mm) and weighed (±0·01 g) before being released. The channels (485 × 25 cm) had natural river gravel substrate (mean diameter: 4·3 cm ± 1·8 SD), with water depths ≈ 30 cm and water flow 34·4 (±3·9 SD) L min⁻¹. Monofilament lines were stretched across each stream channel to reduce the risk of predation from birds. Two different shelter treatments were obtained by distributing eight larger rocks (mean diameter 19·4 cm ± 4·2 SD) evenly along each channel. For five channels of each density treatment, all rocks were embedded approximately 2 cm in the gravel substrate to reduce the number of interstitial spaces in the substrate. In the remaining channels, the rocks were placed on top of the substrate, creating shelters. Since the submergence of embedded rocks into the substrate was minor and the water velocities were generally low (< 0·5 cm s⁻¹), the environmental conditions were likely similar between treatments, except for the intended differences in shelter availability.

Two replicates of this experiment were performed over time. Experimental period 1 lasted from 14 December 2006 to 7 February 2007 and period 2 from 26 February to 23 April 2007. Initial wet mass ranged from 11·50 to 27·83 g (mean 20·89 ± 4·16 SD) and from 6·11 to 19·47 (mean 10·50 ± 2·35 SD) in period 1 and 2, respectively. Total length ranged from 100 to 130 mm (mean 120 ± 8 SD) and from 81 to 118 (mean 96 ± 7 SD) in period 1 and 2, respectively. There was no difference in size (total length) of the fish among channels within each experimental period (all $F_{19,159} < 1·15$, all $P > 0·302$). Out of 320 fish released, 57 fish were not recovered at the end of the experiment. There was no effect of shelter or density treatment on the proportion of fish recovered (density, $F_{1,39} = 0·35$, $P = 0·557$; shelter, $F_{1,39} = 2·33$, $P = 0·135$).

Growth performance was measured as $(\log_e M_{end} - \log_e M_{start})/t$, where M_{start} and M_{end} is the wet mass at the start and end of the experiment, respectively, and t is the duration in days. The effects of shelter and density were analysed by a two-way ANOVA, with mean growth from each channel as the dependent variable.

EXPERIMENT 2: SHELTER × DENSITY AND DISPERSAL

Eight stream channels (2·1 × 10·3 m) were used to test for an interaction between density and shelter on dispersal rate. Each channel received

a water flow of 166 L min^{-1}. Water depth varied from 15 to 40 cm (mean 27·5 cm), with the upstream part being shallower than the downstream one. A one-way trap allowing dispersal from the stream channels was placed at the outlet of each channel. Substrate consisted of natural river gravel with variations in stone size composition among stream channels, thus creating a shelter gradient. Shelter was measured as described in Finstad *et al.* (2007), using a 13-mm flexible PVC tube, and quantified as the number of interstitial spaces > 3 cm within a 0·25 m^2 square. For each stream channel, we measured 20 randomly distributed squares, and calculated the mean shelter density.

Two release trials were conducted in this experiment. In the first, we released a high density (42 fish per channel) of juvenile Atlantic salmon into each stream channel. The relationship between shelter availability and fish remaining in the channel at the end of the experimental period (15 December 2006–7 February 2007) was then estimated. In the second trial (28 February–23 April 2007), the number of released fish was set to match the lowest carrying capacity from the first trial (14 fish per channel). Thus, if shelters act as a limiting resource, we predicted the number of fish remaining in the channel in the second trial to be independent of shelter availability.

The fish were individually tagged (PIT), measured (±1 mm) and weighed (±0·01 g) before being released in the stream channels. Wet mass ranged from 21·53 to 50·35 g (mean 34·08 g ± 6·66 SD) in trial 1 and from 28·71 to 55·05 g (mean 38·66 g ± 5·66) in trial 2. Total length ranged from 122 to 159 mm (mean 141 mm ± 6 SD) in trial 1 and from 135 to 162 mm (mean 148 mm ± 7 SD) in trial 2. There were no differences in length of the fish among stream channels within the two periods (trial 1; $F_{7,335} = 1·15$, $P = 0·328$: trial 2; $F_{7,111} = 1·68$, $P = 0·122$).

Dispersal from the stream channels was prevented by a screen placed in front of the outlet during the first 14 days of each trial to allow fish settlement. At the end of the experiment, fish remaining in the stream channel were collected and weighed (±0·01 g). We tested for an interaction between shelter availability and initial density on the number of fish remaining in the channel in an ANCOVA, using density as a categorical variable and log$_e$ shelter availability as a covariate. We also tested for effects on growth performance of the fish recaptured at the end of the experiment.

FIELD STUDY: SHELTER × DENSITY AND APPARENT SURVIVAL

The field study was conducted in the River Nausta, located on the western coast of Norway (Table 1). Shelter availability throughout the whole river was mapped during 26 August 2006 by conducting visual surveys, dividing the river into 81 homogenous sections (size range 1054 to 48 023 m^2, mean 7785 m^2) according to substrate compositions using the dominating and sub-dominating (by area) substrate classes (sand < 2 cm, gravel 2–12 cm, cobble 12–30 cm, boulders > 30 cm and bedrock). Shelter was measured according to Finstad *et al.* (2007), using a 13-mm rubber tube, in three randomly distributed 0·25 m^2 squares within each section.

Without reference to and independent of the shelter availability measurements, 24 fish sampling sites (range 67 to 180 m^2, mean 94 m^2) were distributed along the river. The sites represent the span in the river's physical habitat (mesohabitats; Borsányi *et al.* 2004). On each site, we estimated the densities of initial recruits (YOY) and densities of fish from the same cohort the following year (1+) for three consecutive cohorts by electrofishing in September–October each year from 2003 to 2006. For the 2003, 2004 and the 2005 cohort, 17, 24 and 23 sites were surveyed, respectively. The sites were fished with either 3-, 2- or 1-pass electrofishing (c.f. Bohlin *et al.* 1989; Mitro & Zale 2000). Fish catch probability (*P*) was estimated (Bohlin *et al.* 1989) separately for YOY and older salmon for sites with 3-, or 2-pass electrofishing and a sufficient number of fish caught (3-pass: $n > 20$; 2-pass: $n > 30$). Based on these data, a mean catch probability (P_{mean}) was calculated for YOY ($P_{mean} = 0·47 ± 0·09$SD; $n = 37$) and older salmon ($P_{mean} = 0·62 ± 0·12$SD; $n = 25$). There was no significant difference in estimated catch probability among years either for YOY or 1+ Atlantic salmon ($F_{3,33} = 0·66$, $P = 0·580$ and $F_{3,21} = 0·20$, $P = 0·889$, respectively). Abundance of YOY and 1 + (N_{yoy} and N_{1+}) was then estimated at each site i for each cohort j as:

$$N_{i,j} = T_{i,j} \left[1 - (1 - P_{mean}) \, k_{i,j} \right]^{-1} \qquad \text{eqn 1}$$

where *T* and *k* is the total catch and the number of electrofishing passes, respectively. Finally, salmon abundances were converted to densities and expressed as number of individuals per 100 m^2.

For each site and cohort, we calculated the retention rate from the YOY stage to the 1+ stage as log$_e$(D_{1+}/D_{YOY}) where D_{1+} and D_{YOY} is number of individuals per 100 m^2 for 1+ and YOY, respectively. This is equivalent to the measure λ of population growth among cohorts [log$_e$(D_{t+1}/D_t)], and is hereafter referred to as local population growth, $λ_i$. To test if competition for shelters affected $λ_i$, we fitted variants of the generalized theta-logistic equation (see Table 2 for models). Linear or nonlinear models with either carrying capacity depending on shelter availability, constant carrying capacity or no density dependence were compared (Berryman & Lima 2006;

Table 1. Study rivers included in the between population comparison of shelter availability and distribution

River	Location	Km	Area	*N*	Sh (± SD)	I_a	Catch
Nerøydalselvi	60°52′ N, 6°50′ E	11·2	364 438	54	7·3 (6·1)	2·0	1 617
Flomselvi	60°51′ N, 7°06′ E	4	123 345	40	10·0 (6·0)	2·8	1 219
Lærdalselvi	61°06′ N, 7°29′ E	24·7	1 070 105	95	7·1 (5·0)	1·5	11 602
Nausta	61°30′ N, 5°43′ E	10	630 591	49	4·1 (4·1)	1·2	7 320
Gaula	61°22′ N, 5°41′ E	13	1 009 052	37	4·8 (5·1)	2·3	6 045
Jølstra	61°27′ N, 5°51′ E	7·7	469 329	34	5·7 (4·4)	4·1	4 105
Eidselva	61°54′ N, 6°00′ E	10	407 954	56	6·3 (5·0)	3·7	831
Vigda	63°18′ N,10°11′ E	9·3	78 278	358	4·5 (3·5)	5·9	645
Børsa	63°19′ N,10°04′ E	5·4	44 993	151	4·6 (3·1)	2·6	628

Latitude and longitude for river mouth (location) is given along with length (km, kilometres) and area in square metres (area) of the stretch used by Atlantic salmon, number of transects measured for shelter availability (*N*), mean shelter availability (Sh), index of aggregation (I_a) as well as maximum Atlantic salmon catch in kilograms (catch).

Table 2. Alternative models for change in number of fish from a given cohort per sampling site ($\lambda = D_{1+}/D_{YOY}$)

Model	k	AIC_c	ΔAIC_c	w	R^2
(1) $\log_e(\lambda) = r_m[1 - (D_{YOY})^\theta]$	3	201·08	36·83	< 0·000	0·06
(2) $\log_e(\lambda) = r_m[1 - (D_{YOY}/K)]$	3	210·64	46·39	< 0·000	0·19
(3) $\log_e(\lambda) = r_m[1 - (D_{YOY}/K)^\theta]$	4	203·27	39·02	< 0·000	0·19
(4) $\log_e(\lambda) = r_m[1 - (D_{YOY}/\alpha SH)]$	3	191·39	27·13	< 0·000	0·30
(5) $\log_e(\lambda) = r_m[1 - (D_{YOY}/\alpha SH)^\theta]$	4	164·25	0	0·999	0·55

D_{YOY} is initial cohort density (number of YOY per 100 m^2), SH is shelter availability, r_m, θ, K and α are estimated parameters. Number of parameters (k), AIC$_c$ values (AIC$_c$), relative change in AIC$_c$ measured against best model fit (ΔAIC$_c$), Akaike weights (w) and R^2 are shown.

Chamaillé-Jammes *et al.* 2008). We used Akaike information criteria corrected for small sample size (Burnham & Anderson 2002) to select the most parsimonious model (AIC$_c$) and the model with the lowest AIC$_c$ value is considered superior. The full model taking into account the carrying capacity of a given site depending on shelter availability is:

$$\log_e(\lambda_i) = r_m[1 - (D_{YOY,i,j}/\alpha * SH_i)^\theta] + \epsilon \qquad \text{eqn 2}$$

where r_m is the maximal intrinsic population growth rate, $D_{yoy,i,j}$ is the recruit abundance (YOY Atlantic salmon at site i for cohort j), SH_i is local shelter availability with a scaling coefficient α, θ is the shape parameter ($\theta = 1$ is a linear model) and $\in$ is a stochastic error term. Under the assumption that carrying capacity of a given site is not influenced by shelter availability, $\alpha * SH_i$ is fixed, representing a constant carrying capacity (K). Models were fit by nonlinear regression using the nls library in the program R (Bates & Watts 1988; Bates & Chambers 1992).

We tested if measurement errors could produce spurious density dependence in our data (c.f. Freckleton *et al.* 2006) by generating data sets with random measurement error but without density dependence by re-sampling from a simulated data set. Using the observed initial distribution of YOY abundances and assigning randomly drawn (i.e. density independent) λ_i's from its observed normal distribution (mean $1·0 \pm 1·2$ SD), we generated new 1+ abundances. Sampling was then simulated using sampling efficiencies (p_{mean} values) as observed from the original data set ($0·47 \pm 0·09$ SD and $0·62 \pm 0·12$ SD for YOY and 1+, respectively). The probability that the observed relationship between YOY abundance and λ_i was generated by sampling error was then assessed as the proportion of the simulated data sets having an equal or more negative relationship than the original field data.

FIELD SURVEY: AMONG-RIVER VARIATION IN SHELTER DISTRIBUTION AND POTENTIAL EFFECTS ON CARRYING CAPACITIES

To examine the extent of variation in abundance and spatial distribution of shelter availability among populations, we conducted detailed shelter surveys in nine Norwegian rivers during August 2006 (Table 1). Furthermore, we evaluated the potential importance of such variation for population carrying capacity, using maximal values in catch statistics time series from sport fisheries (www.laksereg.no) as a proxy. Although having inherent limitations as a tool for stream productivity (e.g. variation in fishing effort, unreported catch, sea mortality), the statistics likely reflect large-scale variations in river production (Crozier & Kennedy 2001; Thorley *et al.* 2005; L'Abée-Lund, Haugen & Vøllestad 2006). Thus, in the absence of more detailed smolt (juveniles migrating to sea) production

estimates, catch statistics presently represent the best available data for such analyses.

The whole river accessible for Atlantic salmon was surveyed for shelter availability by distributing three 0·25 m^2 squares randomly along cross-sections of the river, with cross-section intervals varying from 100 to 350 m among rivers (depending on the total river length, Table 1). The total number of shelters measured at each cross-section was used as a measure of shelter availability at that site. To compare the spatial distribution of shelters among rivers, we used the index of aggregation (I_a) calculated using SADIE (Perry & Dixon 2002; Perry *et al.* 2002). The index of aggregation is the distance to regularity (i.e. equal shelter counts across all transects) for the observed data divided by the mean distance to regularity for permuted data sets (i.e. transect shelter counts randomly ordered) based on the original observations. Thus, I_a is not sensitive to variation in spatial scale for observations or difference in length among rivers. Low I_a values indicate an even (random) distribution of shelters, whereas high values indicate more patchy shelter distribution.

Maximum reported catch (in kilograms) of adult Atlantic salmon per riverbed area unit was used as a proxy for population carrying capacity. Routines for collecting catch statistics improved during 1970s and only catches from 1970 and onwards were used. We used maximum rather than average catch because several of the smaller rivers have very low reported catch in many years, due to poor reporting or poor fishing conditions. We excluded the 1979 catches from the River Nausta from the analyses since large releases of smolts likely caused return rates far above the natural capacity. Reported biomass was used rather than numbers of fish since numbers and proportions of the different sea-year classes varies both within (over time) and among rivers (e.g. L'Abée-Lund, Vøllestad & Beldring 2004). Larger mean sizes may compensate for increased mortality caused by increased time spent at sea, whereas number of fish do not. Furthermore, maximum adult salmon catch in kilograms correlated considerably better with river size (and hence presumably smolt production) than the numbers of fish caught (catch in kilograms vs. riverbed area; Pearson $r = 0·89$, $P = 0·001$; catch number; Pearson $r = 0·56$, $P = 0·184$). Riverbed areas accessible for anadromous salmonids from 1:50 000 maps (Norway digital) were used to estimate catch per river area, with the exception of the two smallest rivers, Børsa and Vigda, where maps did not include area measures for the whole of the river. In these, we used width measurements for every 25 m collected during the shelter survey to calculate riverbed area. Both our own width measurements and digital maps are based on vegetation free area and are thus corresponding measures. All statistics were $\log_e$ transformed to normalize the data before further analyses. In addition to correlating catch per m^2 with the index of shelter I_a, we used AIC$_c$ to select among linear models with maximum adult salmon catch as dependent variable and riverbed area and I_a as explanatory variables.
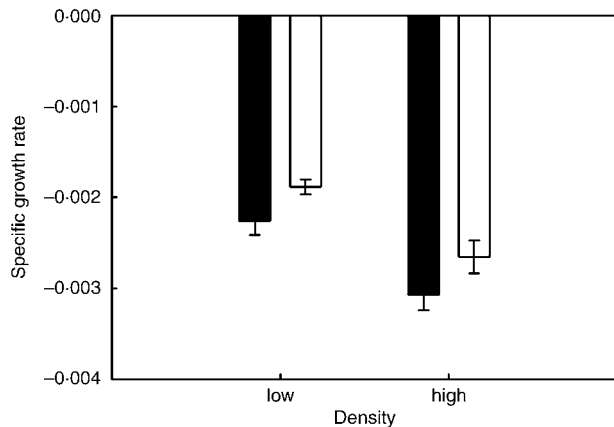
Fig. 1. Effect of density and shelter on mean specific growth rate of juvenile Atlantic salmon in stream channels for both experimental trials combined. High and low density is 12 and four fish per stream channel, respectively. Black bars are low shelter treatment (all large stones embedded) and white bars are high shelter treatment (none of the large stones embedded).

Results

EXPERIMENT 1: SHELTER × DENSITY AND PERFORMANCE

All fish lost mass during the experiment (mean $-2 \cdot 09$ g $\pm 1 \cdot 14$ SD) and mean specific growth rates (mean $-0 \cdot 0026 \pm 0 \cdot 0009$ SD) ranged from $-0 \cdot 001$ to $-0 \cdot 0039$ among stream channels. Average mass specific growth rates were lower in trial two than in trial one ($-0 \cdot 0028 \pm 0 \cdot 0004$ SD and $-0 \cdot 0021 \pm 0 \cdot 0006$ SD, respectively). Both shelter and density treatment affected the average specific growth rates in each stream channel. Mass loss increased with increasing density and decreasing shelter (Fig. 1), and the relationships between mass loss, density and shelter were similar in both experimental periods (density, both $F_{1,36} > 21 \cdot 79$, $P < 0 \cdot 001$; shelter, both $F_{1,36} < 5 \cdot 17$, $P > 0 \cdot 037$; density × shelter, both $F_{1,36} < 1 \cdot 12$, $P > 0 \cdot 30$). There was no significant interaction effect between shelter and density.

EXPERIMENT 2: SHELTER × DENSITY AND DISPERSAL

There was a significant increase in the number of fish remaining in the stream channels at the end of the experiment with increasing shelter availability for the high-density treatment (Fig. 2a). In the low-density treatment, there was no relationship between fish remaining and shelter availability, and there was a significant interaction effect between density and shelters on the number of fish remaining in the channels (density, $F_{1,12} = 83 \cdot 31$, $P > 0 \cdot 001$; shelter, $F_{1,12} = 78 \cdot 06$, $P = 0 \cdot 027$; density × shelter, $F_{1,12} = 5 \cdot 60$, $P = 0 \cdot 035$). This supports the prediction that the carrying capacity of the streams depended on shelter availability, and that surplus fish left the arena. All fish that remained in the streams at the end of the experiment lost mass (mean $-3 \cdot 30 \pm 1 \cdot 31$ SD) and mean specific growth rate ($-0 \cdot 0018 \pm 0 \cdot 0006$ SD) ranged from $-0 \cdot 0024$ to $-0 \cdot 0004$ among stream channels (Fig. 2b). There was no relationship between
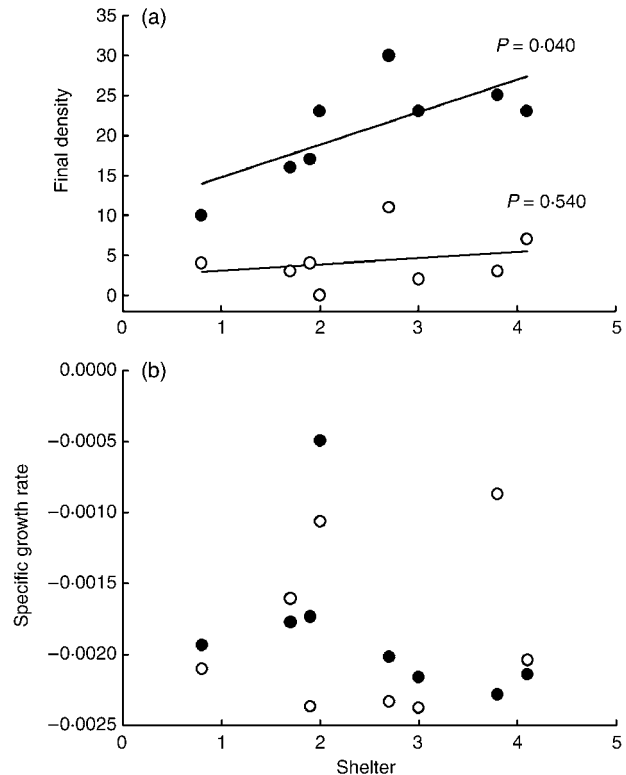

Fig. 2. Measured number of shelters against final density (a) and mean specific growth rate in each stream channel (b) for fish remaining in the stream channels. Closed circles represent high density treatment (42 fish released) and open circles represent low density treatment (14 fish released). Solid line is least square regression lines for the relationship between shelters and fish remaining in the stream at the end of the experiment (high density treatment; $10 \cdot 70 \pm (4 \cdot 23$ SE$) + 4 \cdot 06$ shelter $\pm (1 \cdot 56$ SE$)$, $R^2 = 0 \cdot 45$, $P = 0 \cdot 40$). No significant relationship was found between shelters and number of fish remaining at the low density treatment.

mean performance of the fish remaining in each channel (specific growth rate) and initial density or shelter availability (density, $F_{1,15} = 0 \cdot 16$, $P = 0 \cdot 695$; shelter, $F_{1,15} = 2 \cdot 18$, $P = 0 \cdot 165$; shelter × density, $F_{1,15} = 0 \cdot 62$, $P = 0 \cdot 444$).

FIELD STUDY: SHELTER × DENSITY AND APPARENT SURVIVAL

There was large spatial variation in recruitment. Local density of YOY Atlantic salmon varied from 0 to 385 individuals per 100 m^2 (mean 92 ± 82 SD) among sampling sites. Similarly, density of 1-year-old juveniles varied from 0 to 186 individuals per 100 m^2 (mean 32 ± 33 SD). There was no detectable difference in YOY densities between cohorts or effect of shelter availability on YOY density (cohort, $F_{2,63} = 0 \cdot 048$, $P = 0 \cdot 959$; shelter, $F_{2,63} = 0 \cdot 37$, $P = 0 \cdot 541$; shelter × cohort, $F_{2,63} = 0 \cdot 22$, $P = 0 \cdot 799$). Mean density of 1-year-old juveniles varied among cohorts and increased with shelter availability. However, there was no detectable differences among cohorts in the relationship between shelter availability and densities of 1 year olds (cohort, $F_{2,63} = 8 \cdot 13$, $P < 0 \cdot 001$; shelter, $F_{2,63} = 29 \cdot 48$, $P < 0 \cdot 001$; shelter × cohort, $F_{2,63} = 0 \cdot 44$, $P = 0 \cdot 644$).
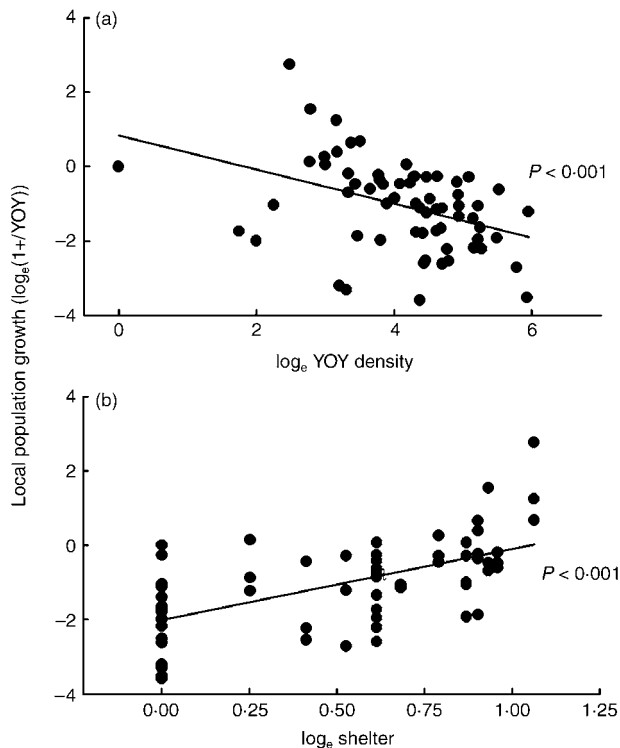
Fig. 3. Ratio between YOY Atlantic salmon densities and 1+ density the following year (local population growth) in the River Nausta plotted against (a) YOY density and (b) shelter density. All variables are $\log_e$ transformed. Figure show all cohorts pooled with *P* values from least square regression fit (solid line). All relationships were significant also when cohorts were analysed separately (all $P < 0.030$).

Fig. 4. Predicted density of 1+ as a function of YOY density (D_{YOY}) from model 5 in Table 2 plotted separately for shelter densities (SH) 0, 2, 4 and 6 shelters per 0.25 m².

There was large spatial variation in the local population growth through ontogeny. The density ratio between YOY and 1 year olds [$\log_e(\lambda)$] varied from -3.9 to 2.7 (mean -1.5 ± 1.2 SD). Although most sampling sites had a net decrease in the number of individuals of a given cohort over time [$\log_e(\lambda) < 0$], some sites had a net increase [$\log_e(\lambda) > 0$]. This positive density ratio was mainly found in sites with low initial density of YOY fish and high shelter availability (Fig. 3). Accordingly, local population growth through ontogeny decreased with increasing density of initial recruits (Fig. 3a) and increased with increasing shelter availability (Fig. 3b). The negative relationship between initial recruit density and density ratio [$\log_e(\lambda)$] was unlikely to be a result of sampling error. The estimated sampling error did only produce a simulated slope coefficient that was more negative than the observed in less than 0.1% of the simulations. The modelled sampling efficiency had to be decreased below realistic values ($P_{mean} < 0.15 \pm 0.1$ SD) in order to make it likely that the simulated slope was equal or higher than the observed (i.e. sampling error producing a larger scaling between $\log_e(\lambda)$ and YOY density than observed in more than 5% of the simulations).

The spatial variation in local population growth was related to variation in carrying capacity caused by variation in shelter availability. Confronting different models of local population growth demonstrated that the local density ratio [$\log_e(\lambda)$] was
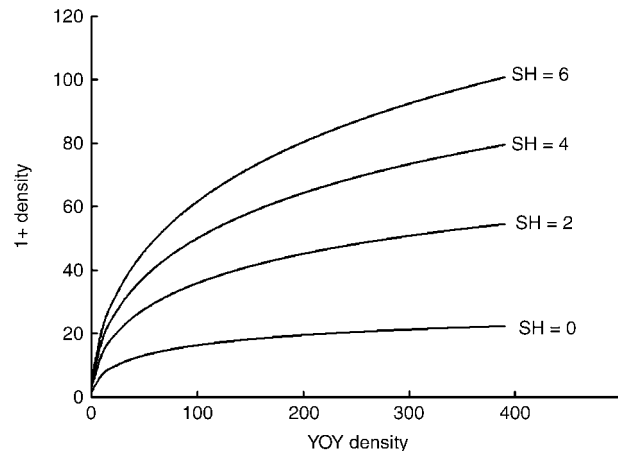
best described by a theta logistic model including a nonlinear effect of carrying capacity scaled according to shelter availability, rather than alternative models not including shelter availability or density dependence (Table 2). Modelled local density ratios [$\log_e(\lambda)$] were positive for sampling sites with low initial density of YOY salmon, indicating a net immigration to low density patches. In such patches, the density ratios were only weakly dependent on shelter availability. In contrast, the most negative density ratios were found in patches with high initial densities, and the ratios increased rapidly with increasing shelter availability. The effects of shelter availability on estimated carrying capacity are illustrated by plotting modelled effect of YOY density on 1+ density (Fig. 4). Maximum-modelled 1+ density increased with increasing shelter availability.

FIELD SURVEY: AMONG-POPULATION VARIATION IN SHELTER DISTRIBUTION AND CORRELATIONS TO CATCH STATISTICS

There was large variation in both mean shelter availability and shelter distribution among the surveyed rivers (Fig. 5). Mean shelter availability ranged from 4.12 to 10.0 measured shelters per transect (Table 1). The index of shelter aggregation (I_a), measured as normalized distance to regularity, varied from 1.15 to 5.88 among rivers. Estimated I_a differed significantly from a random distribution ($P < 0.026$) for all but the two lowest values (1.15 and 1.47, $P < 0.282$). The highest index of aggregation was found in the Rivers Jølstra and Vigda, which had high shelter availability in upper or lower parts of the river stretch accessible to Atlantic salmon. In contrast, the River Nausta had low shelter aggregation. Here, shelters were patchy distributed but high and low shelter patches were more evenly distributed along the stretch. There was no relationship between the mean shelter density in each river and I_a (Pearson $r = 0.39$, $P = 0.444$).

A negative trend (Pearson $r = -0.64$, $P = 0.060$) was found between maximum catch of adult Atlantic salmon per square
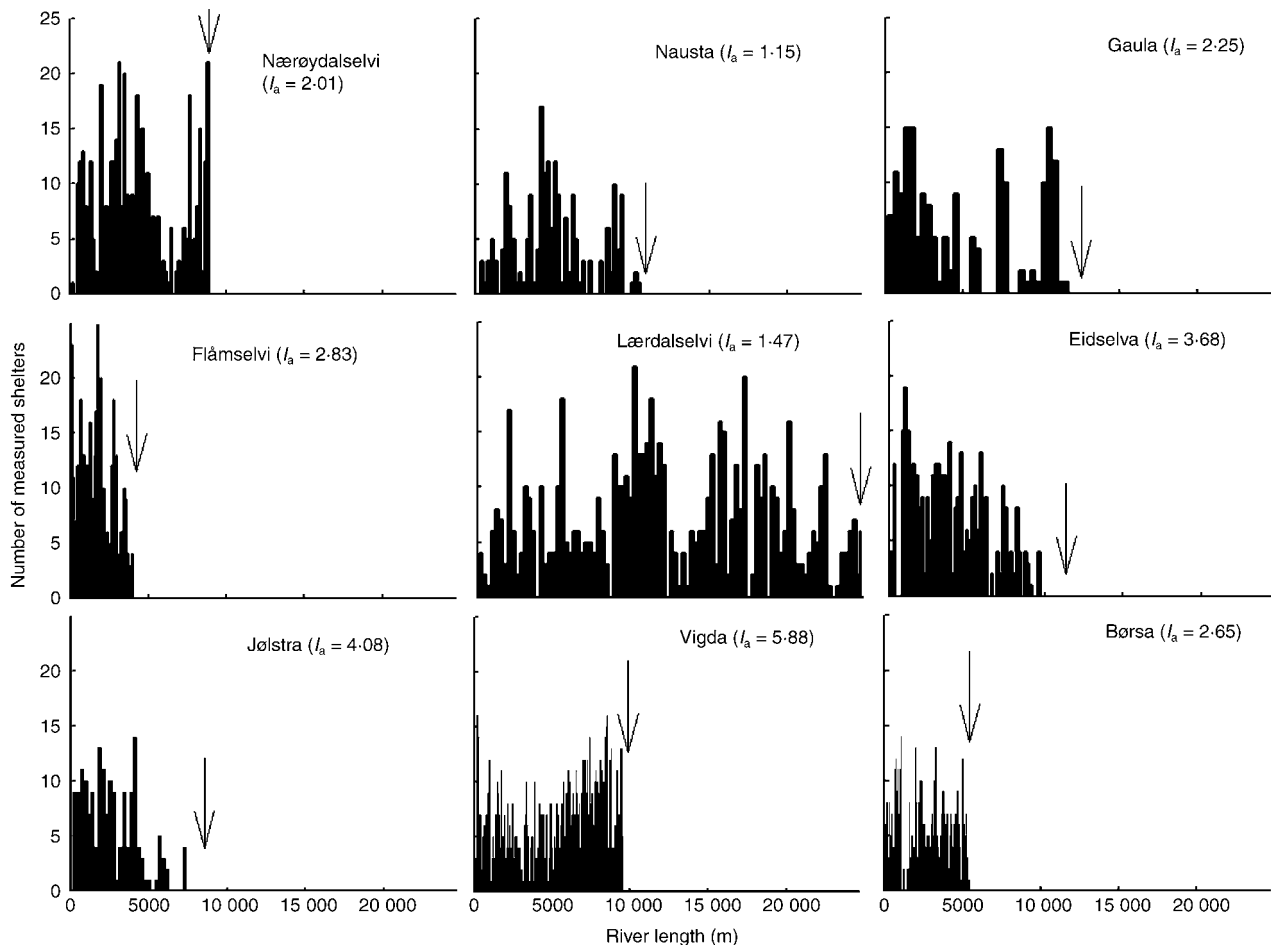
Fig. 5. Distribution of shelters along the stretch used by Atlantic salmon in the nine surveyed rivers (see Table 1 for location). Bars represent number of shelters measured in each transect and arrow indicate the end of the river. The estimated distance to regularity (I_a) is also given. Note that the scale of the bars varies according to distance between transects.

metre and the measure of shelter spatial aggregation (I_a), whereas no relationship was found to mean shelter availability (Pearson $r = 0.001$, $P = 0.998$). The relatively low numbers of rivers explored constrain further analyses. Nevertheless, including both riverbed area and shelter distribution (I_a) as covariates in a linear model with adult salmon catch as dependent variable gave illustrating results. Although the differences in AIC_c values were too small to draw definite conclusions, the full model including both river area and shelter distribution (I_a) gave the most parsimonious model (AIC_c: full model 23·8, riverbed area only 24·8, I_a only 33·2).

Discussion

In the present study, we identify a limiting resource for juvenile Atlantic salmon and demonstrate how the spatial distribution of this resource may influence carrying capacity on both within population and among population spatial scales. In experiments, winter growth was related to shelter availability and fish density in a closed system, but not in an open system where the fish dispersed according to a carrying capacity set by shelter availability, causing resident fish to obtain similar

growth across shelter treatments. These results were corroborated by data from a natural population showing local population growth during the first year of life to decrease with increasing local recruitment and decreasing local shelter availability. Finally, the within-river spatial arrangement of shelters were found to vary considerably in a multi-river comparison, and salmon populations in rivers with evenly distributed shelters tended to be more productive than populations in rivers where shelters were heterogeneously distributed. The present study therefore highlights the importance of spatial resource heterogeneity in population dynamics and indicates that not only the absolute amount of limiting resources but also their spatial arrangements are important factors regulating population carrying capacity.

In the first experiment, we showed how the winter growth performance of juvenile Atlantic salmon can be positively influenced by shelter availability and negatively by fish density. All fish in the experiment had net mass loss comparable to wild juvenile Atlantic salmon during winter (e.g. Næsje *et al.* 2006). A likely explanation for the negative energetic effects of reduced shelter availability is increased metabolism (Millidine, Armstrong & Metcalfe 2006; Finstad *et al.* 2007),

likely due to increased anti-predator behaviour and alertness (Hawkins, Armstrong & Magurran 2004), or alternatively, more aggressive interactions resulting from shelter competition (Harwood *et al*. 2002). In the second experiment, fish could leave the streams by a one-way trap. Here, low number of shelters resulted in high dispersal at high initial densities, whereas dispersal was not related to shelters at lower initial densities, matching apparent carrying capacity of streams. Furthermore, whereas there were significant effects of both density and shelters on energetic performance for fish kept in the closed system, this was not the case in the open system. These observations thus support that shelters is a limiting resource and that the fish distribute according to a given carrying capacity set by shelter availability.

Our detailed observational data from a wild population demonstrated how local shelter availability can explain spatial variation in local carrying capacity. We could not determine the relative importance of dispersal and mortality on local population growth. The magnitude of the difference in energetic performance across shelter availabilities observed in our experimental treatments is likely to result in survival differences for juvenile salmonids in a natural setting, which depend on energy reserves to survive the winter (Finstad *et al*. 2004; Biro *et al*. 2004). Sheltering is also an anti-predator behaviour (Heggenes *et al*. 1993; Grand & Dill 1997; Valdimarsson & Metcalfe 1998) and the amount of shelters may therefore influence local mortality rates through effects on predation rates. However, it is also apparent that dispersal played a prominent role in shaping the spatial variation in local population growth. This is evident in patches with low initial recruitment and high shelter availabilities, where the number of 1+ fish was higher than the preceding number of recruits. Thus, local population growth may have been determined jointly by local mortality and dispersal rates.

Our comparison of spatial shelter distribution demonstrates a considerable among-river variation. Interestingly, the population in which we demonstrated effects of shelter on local carrying capacity (the River Nausta) was the one with the least heterogeneous distributed shelters among the nine rivers surveyed (Fig. 5), suggesting that similar effects can be just as strong, if not stronger, in other rivers. The heterogeneity in shelter availability is governed by riverbed substrate composition, ultimately resulting from variation in landscape topography, land use and the watershed's geological history and source-sink dynamics of sediments creates a natural variation in shelter availability throughout the river (Rice & Church 1998). In addition, degradation of stream habitats from external stressors such as land-use changes and deforestation in the catchment area or internal disturbances such as engineering of river channels will affect substrate composition and its spatial distribution. These types of anthropogenic disturbances have received considerable attention as contributors to the observed worldwide decline of salmonid populations (e.g. Parrish *et al*. 1998; Suttle *et al*. 2004).

The present study illustrates how increased spatial variation in a resource that is shown to be limiting on a local scale may decrease the overall population's carrying capacity more or less independent of the absolute level of the resource, likely due to aggregation effects (review by Englund & Cooper 2003). Limits to dispersal have been demonstrated for salmonids even in small streams (Bohlin *et al*. 2002) and the spatial scale of a typical salmon river (e.g. means for Norwegian rivers 21·1 km, median 11·5, $n = 156$; L'Abée-Lund *et al*. 2004) makes it likely that ideal free distributions of fish may be hampered. Furthermore, dispersal may induce increased mortality through predation or energetic costs. Thus, a highly heterogeneous distribution of this limiting resource may cause increased on-site mortality and/or increased mortality associated with dispersal costs as the resource becomes more and more limiting with increasing body size. Furthermore, at sites with very high shelter availability, it is likely that other factors than shelter (e.g. territory sites) may be the limiting factor. This may explain the observed trend towards salmon populations in rivers with evenly distributed shelters to be more productive than populations in rivers with more patchy shelter distribution irrespective of the populations mean shelter availability.

The present and recent work on salmonids represent important steps towards a more complete empirically based understanding of small-scale spatial habitat structure and its effects on population dynamics. The predicted ecological patterns should apply to the wide range of organisms showing high fecundity, discrete breeding locations and low offspring mobility. Such organisms are predicted to experience intense local competition and density dependence during the initial juvenile stages (Einum & Nislow 2005). The spatial distribution of breeding areas within a population can influence the resulting juvenile distribution and their performance over surprisingly small spatial scales (two orders of magnitude smaller than the spatial extent of the population for Atlantic salmon, Einum *et al*. 2008a). As a consequence, the spatial pattern of egg deposition is predicted to strongly influence patterns of density-dependent mortality and equilibrium adult abundance (Einum *et al*. 2008b). For organisms with high juvenile growth potentials, the limitations on dispersal ability can be predicted to decrease rapidly with age, and individuals may to an increasing degree respond to high local competition by increasing their emigration rates (Einum *et al*. 2006). However, even for these older stages there will ultimately be some limit to how well they are able to homogenize competitive intensities (Einum *et al*. 2006), perhaps particularly related to the inability to sample all potential areas and obtain the required information. Indeed, the among-river comparison in the present study indicates that the spatial heterogeneity of a resource that is increasingly limiting for older and more mobile stages can influence population productivity. Based on these recent advances, it appears clear that the local-scale within-population spatial distribution of individuals, being initially dictated by maternal breeding decisions and shaped by dispersal abilities and the distribution of limiting resources (which may themselves change throughout the life cycle), adds another layer of complexity to the dynamics of many wild populations, and represents a substantial challenge for future empirical and theoretical studies.

Acknowledgement

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