

Predicting population responses to restoration of breeding habitat in Atlantic salmon

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Summary

1. Habitat degradation is seriously threatening stream biodiversity and productivity world-wide. For salmonid fish, restoration projects in disturbed systems commonly aim at increasing the availability of suitable breeding habitats, but expectations of effects on population abundance based on explicit models are lacking.

2. We used a spatial population model to predict how breeder dispersion may influence population dynamics of salmonids. Simulations involved changing the relative abundance of habitat suitable for two juvenile size classes (small fry and larger parr), the type of density-dependent regulation (effects on survival only vs. effects on survival and growth) and intercohort competitive mechanisms.

3. Increased breeding dispersion could alter patterns of density-dependent mortality and increase equilibrium adult abundance and maximum sustainable yield (MSY). However, there was a strong interaction between stage-specific habitat abundance and breeding dispersion. The most pronounced effects of breeding dispersion were observed under intermediate levels of fry habitat abundance.

4. When fry habitat was abundant, density-dependent mortality was most intense during the parr stage, and increased breeding dispersion did not increase adult abundance or MSY. In fact, when populations were regulated in the parr stage, increased breeding dispersion could cause decreased adult abundance because of the effects of intercohort competition. This negative effect only occurred, however, when competition among juveniles was symmetric (no age or size advantage).

5. *Synthesis and applications.* The population effects of restoring breeding habitat can differ among environments, and we have demonstrated how these differences can be understood in the light of stage-specific density dependence. Increasing spatial dispersion of breeders may often be an efficient measure for conserving threatened populations and increasing yields in fished populations. However, if direct evidence or habitat considerations suggest that fish populations experience density-dependent mortality during the parr stage, attempts to increase abundance through increased breeding distribution or artificial stocking should be avoided, as these are likely to be ineffective or even detrimental. The difference between fishing rates providing maximum sustainable yield and extinction is particularly small for such populations, suggesting that fish managers should adopt a conservative and flexible regulation regime.

Key-words: carrying capacity, exploitation, habitat restoration, individual based modelling, intercohort competition, local density dependence, population regulation, spatial modelling

Introduction

Habitat protection and restoration are integral elements in the conservation and management of streams and rivers (Giller 2005). The aim of such measures is often to increase the abun-

dance of a target species that is particularly vulnerable or of high commercial or recreational value. Habitat restoration projects in north temperate zone streams and rivers are often aimed at increasing the abundance of anadromous salmonids (Bash & Ryan 2002; Hendry *et al.* 2003). There has been considerable concern over the declines in abundance of these species in recent decades (Nehlsen 1997; ICES 2000). It is believed that much of this decline can be ascribed to human alterations of the physical stream habitat, with an added

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complication that many of the species are heavily fished (e.g. annual fishing rates of Atlantic salmon *Salmo salar* L. exceed 50% in many populations; ICES 2000). At least for some species, the presence of density dependence in freshwater (Elliott 1994; Jonsson, Jonsson & Hansen 1998; Einum 2005) and its absence for adults at sea (Jonsson, Jonsson & Hansen 1998) suggests that restoration of stream habitat should have the potential to increase viability and yield of salmonid populations.

When managing salmonid populations there is the complication that different life stages utilize different habitat types even within freshwater (Armstrong *et al.* 2003), therefore habitat restoration needs to consider ontogenetic changes in habitat use and determine which habitat types are likely to be limiting abundance. Competition for habitat in juvenile salmonids is likely to be high during the initial period following emergence from nests, because of discrete breeding locations and limited early juvenile dispersal abilities (Crisp 1995; Fleming 1996; Webb *et al.* 2001; Einum *et al.* 2008). Accordingly, high local density during this initial juvenile stage is found to cause high mortality (Einum & Nislow 2005). The spatial distribution of breeding habitats may therefore play an important role in limiting early juvenile abundance.

Degradation of breeding habitat as a result of anthropogenic disturbance is well documented (Opperman *et al.* 2005) and a number of river restoration projects aim to improve the abundance of suitable breeding habitat (Bash & Ryan 2002). When successful, such measures increase the spatial dispersion of breeding. However, in many situations it is unclear whether increased breeding dispersion and accompanying increased early survival actually translates into higher adult populations. For species with indeterminate growth, individual resource requirements increase through ontogeny, leading to potential intense competition (i.e. density dependence) during later juvenile stages (Yoda *et al.* 1963; Begon, Firbank & Wall 1986). Furthermore, following initial settlement, juvenile salmon rapidly increase their dispersal abilities (Einum, Sundt-Hansen & Nislow 2006). This may lead to a decoupling of adult population abundance from survival during early life stages (Armstrong & Nislow 2006). Thus the spatial component is integral to population ecology and has to be incorporated in models to make them sufficiently realistic.

We developed a model based on a conceptual framework for salmonid population regulation (Nislow, Einum & Folt 2004) to examine the importance of incorporating the spatial component. The model was parameterized with data from Atlantic salmon and used to predict how adult abundance and maximum sustainable yield (MSY) may be influenced by the spatial dispersion of breeding habitats. A modelling approach to these issues is particularly valuable because it also enables us to predict how alternative juvenile competitive mechanisms and stage-specific habitat abundances influence effects of breeding habitat dispersion. Furthermore, it may serve as an example of how spatial modelling may contribute to the understanding of population dynamics and management of other organisms with similar ontogenetic changes in habitat use (Werner & Gilliam 1984), density heterogeneity (Folt & Schulze 1993) and dispersal abilities (Roff 1991).

Methods

The model employs a super-individual approach, which enables modelling of large populations by grouping individuals that are identical in any respect relevant to the model (Scheffer *et al.* 1995). Two group criteria were used: spatial location (i.e. section of a stream) and cohort. For eggs, each super-individual contained the eggs of a maternal super-individual. Number of real individuals, body size (or egg size) and size class (see below) were linked to each super-individual and then followed with daily increments (Fig. 1).

SPATIAL HABITAT STRUCTURING AND SIZE CLASS DIVISIONS

The model stream was divided into sections delineated by patches of breeding habitat, and these patches were uniformly distributed along the stream such that, for a given number of breeding patches, all sections were of equal length. For the single breeding patch scenario this was situated on the upstream end of the stream. Each section was longitudinally homogeneous in juvenile habitat availability. Juvenile salmonids of different sizes occupy different habitat types (reviewed by Heggenes 1990) and in the model this was accommodated by specifying, for each section, habitat availability as the proportion of area suitable for each of two size classes. An empirically validated bioenergetics model suggests that suitable habitats differ among small and large juveniles during their first summer of growth (Nislow, Folt & Parrish 1999, 2000), with the earliest stage following emergence from nests (1–2 months, equivalent to body sizes up to 1 g) requiring particularly slow water currents. Larger juveniles utilize faster flowing, deeper water and require coarser substrate for sheltering (reviewed by Armstrong *et al.* 2003). Thus, in the model, juveniles were divided into two size classes, with the smallest class (body mass up to 1 g) representing juveniles during their first 1–2 months of life (fry) and the larger class (parr) consisting of juveniles larger than 1 g.

EMERGENCE AND INITIAL SETTLEMENT

Timing of emergence of juveniles from model nests occurred according to established relationships between temperatures and development rate (Crisp 1981, 1988). At emergence, individuals dispersed downstream (Elliott 1986) and occupied the first available downstream territory. Although some upstream migration may occur, this is expected to be limited during emergence, with respect to both frequency and distance (García de Leániz, Fraser & Huntingford 2000; Einum & Nislow 2005). Limitations to successful dispersal following emergence are common across salmonid species (Elliott 1986; Richards & Cernera 1989; Trotter 1989; Fjellheim, Raddum & Barlaup 1995), suggesting a survival cost of post-emergent dispersal. Such costs can be because of an increased risk of predation (increased predator encounter rate from drift-feeding fish) and reduced opportunities for feeding. In the model, dispersal survival costs during initial settlement increased linearly with distance from 0 (no additional mortality) to 1 (100% mortality) if the juveniles dispersed further than a maximum dispersal distance. Fish dispersing out of the lowermost section were lost from the population. Field studies of dispersal rates from nests of known location all suggest that there is negligible successful dispersal beyond 1 km downstream of nests during the first summer (Crisp 1995; Webb *et al.* 2001; Einum & Nislow 2005). Thus we used a maximum dispersal distance at emergence of 1 km.

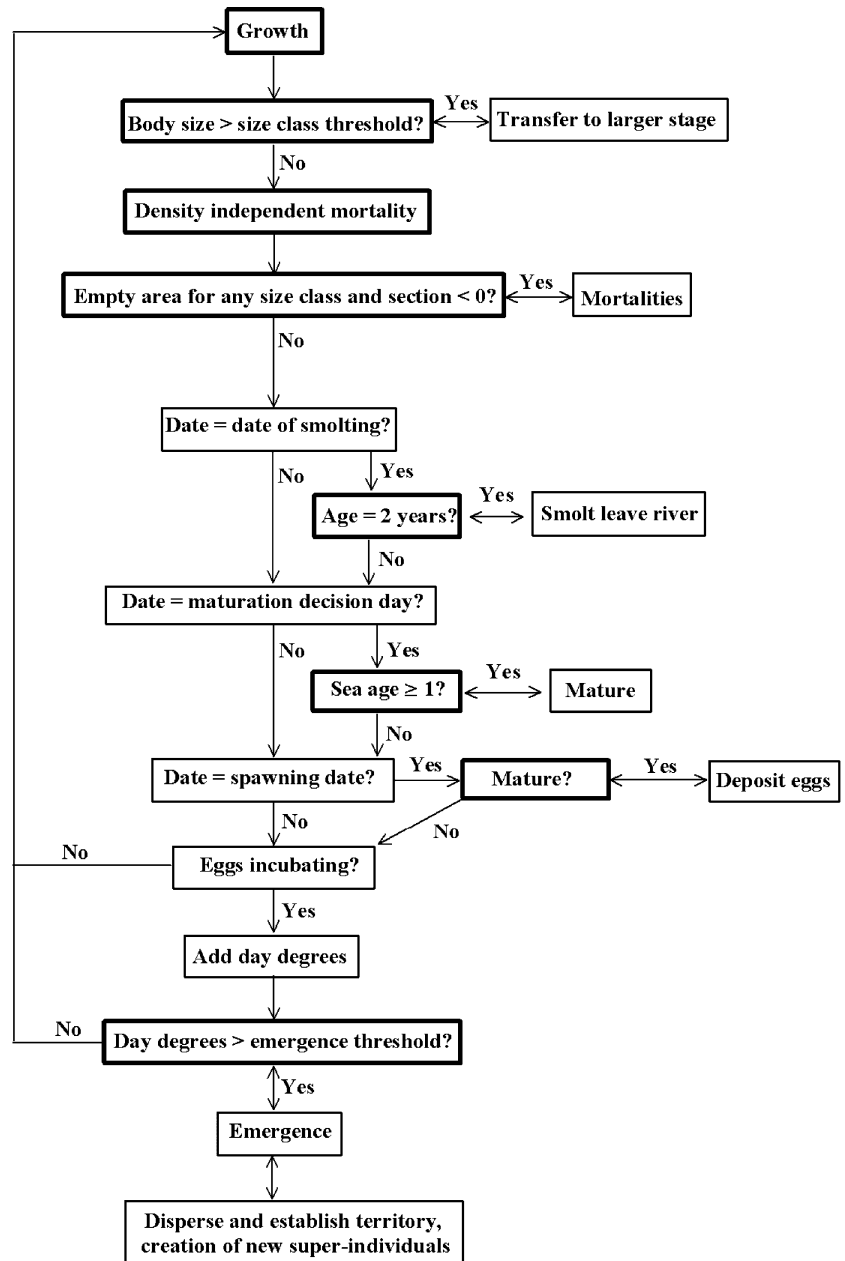


Fig. 1. Flow chart of the population model. Boxes with bold frames represent loops over super-individuals, except for 'Empty area for any size class and section < 0?', which represents loops over size classes and sections. Double-headed arrows indicate a return to the loop after the action has been imposed.

SURVIVAL FOLLOWING INITIAL SETTLEMENT

Juveniles were modelled to occupy a defended patch of habitat (i.e. territory) at any given time, with the patch area increasing with body size according to empirical relationships (Keeley & Grant 1995; see Appendix S1 in the supplementary material).

Simulated streams were divided into sections of equal length and habitat characteristics, with breeders distributed in equal numbers among sections. In such cases, the total juvenile area requirements change in parallel among sections. Thus, if the total area requirement for a given juvenile size class exceeds that available within each section, no successful movement and subsequent establishment of excess fish can occur among sections. Thinning (i.e. loss of individuals belonging to the given section and size class) was then imposed. Two different scenarios for such density-dependent losses were simulated, one where competition was symmetric within the given size class (henceforth referred to as non-selective thinning)

and one where competition was asymmetric and the youngest fish present within the size class were removed sequentially (selective thinning). Thus these two scenarios span the range of possible strengths of positive size selection during density-dependent mortality. In addition to density-dependent mortality, the model imposed density-independent mortality in the simulations based on data from the River Imsa (Jonsson, Jonsson & Hansen 1998; see Appendix S1 in the supplementary material).

GROWTH AND MIGRATION TO SEA

Growth rates depended on water temperatures and growth parameters according to existing growth models, and were modelled as being either density-independent or density-dependent (Elliott & Hurley 1997; Forseth *et al.* 2001; see Appendix S1 in the supplementary material). Juveniles migrated to sea as 2-year-old smolt on 1 May (Jonsson, Jonsson & Hansen 1990).

MATURATION AND BREEDING

At sea, the body mass of individuals on a given day was modelled as a function of body mass the previous day and growth parameters according to existing growth models (Ostrovsky 1995; Forseth *et al.* 2001; see Appendix S1 in the supplementary material). The daily mortality rate at sea was set to a constant value of $Z_{\text{daily}} = 0.00713$, corresponding to a smolt-to-grilse mortality (500 days) of 92.6% (Hutchings & Jones 1998), similar to that observed in River Imsa (table 1 in Jonsson, Jonsson & Hansen 2003). From each super-individual at sea, 83% of the individuals matured after one sea winter and 17% after two sea winters, according to the observed proportions of sea ages in the River Imsa (Jonsson, Hansen & Jonsson 1991). If maturing, the fish stopped growing and entered the river on 15 September (Jonsson, Jonsson & Hansen 1990). Female fecundity increased with body mass (g) following Jonsson, Jonsson & Fleming (1996) (fecundity = $5.104 \text{ body mass}^{0.86}$). Egg mass was set equal to the mean observed in the River Imsa (0.117 g; Jonsson, Jonsson & Fleming 1996). The resulting juvenile body mass (g) at emergence was related to egg mass (g) as: body mass = 1.45 egg mass (Einum & Fleming 2000a). Females spawned on 1 December (peak spawning time in the River Imsa; Heggberget 1988) in the same location as they were born. Atlantic salmon males commonly mature precociously as parr. Although this may have some costs in terms of growth and survival rates (Myers 1984), we assumed no such effects in the present model and the adult sex ratio was assumed to be 1 : 1.

SIMULATIONS

To predict how equilibrium adult abundance (adult returns to river) and patterns of density dependence can be influenced by habitat availability and breeding dispersion, we simulated population dynamics of hypothetical rivers of proportions typical for those inhabited by salmon (total length 50 km, width 10 m), with various habitat availabilities. Mean monthly water temperatures in the river were obtained using data from the River Imsa from 2003 (NINA Research Station, Ims). We let proportions of suitable habitats for fry vary between 1% and 99%, whereas the remaining area for each scenario was set to be suitable for parr. Thus the total area of habitat available was constant for a given river length and only relative proportions of the two types varied. For each habitat scenario we predicted effects of level of breeding dispersion (simulated by varying the number of breeding locations from 1 to 10 uniformly distributed along the length of the stream, see above) on equilibrium adult abundance and loss rates for different juvenile size classes. For a given simulation, the model was run until it approached stability (coefficient of variation of adult abundance over 10 consecutive years < 1%).

To examine the relative contribution of mortality during different size classes to the total juvenile mortality, loss rates (k) were calculated at equilibrium for each size class and scenario as:

$$k = \log(N_{t-1}/N_t) \quad \text{eqn 1}$$

where N_{t-1} represents the number of individuals from a cohort entering a size class, and N_t is the number of individuals from the same cohort surviving to enter the next size class.

To test for differences in the intensity of density dependence for the different size classes under various environmental scenarios, we examined how loss rates changed with number of individuals recruiting into a size class. The loss rates of a cohort can be expressed as a function of the logarithm of recruits (N_{t-1}) as:

$$k = \alpha_0 + \alpha_1 \log N_{t-1} \quad \text{eqn 2}$$

where α_1 is an estimate of the strength of direct density dependence, being equal to 0 if no density dependence occurs and increasing in value as the intensity of density dependence increases (Bjørnstad, Falck & Stenseth 1995). To estimate α_1 we let the model run to stability before disturbing the system by reducing or increasing N_{t-1} by 5% for one cohort, calculating loss rates, and then estimating α_1 .

To examine how fishing rates can influence the equilibrium population size under different environmental scenarios, we performed simulations in which a temporally stable adult fishing rate was imposed upon adults returning to the river. Fishing was non-selective with regard to sex and breeding location, and rates varied from 1% to 99% among simulations. To reduce the number of possible combinations, simulations were conducted for fry habitat abundance values of 5%, 50% and 90%, and for each of these populations with 1–10 breeding locations were simulated. For a given combination of fry habitat abundance and breeding dispersion, fishing was imposed annually until the new adult abundance equilibrium was reached. These results were similar under non-selective and selective thinning, and we therefore present only those obtained under non-selective thinning.

Results

STAGE-SPECIFIC DENSITY DEPENDENCE

The intensity of density dependence differed strongly between size classes in a given environment and across habitat availability scenarios for a given size class (Fig. 2). Few breeding locations and little fry habitat resulted in intense competition amongst the fry and thus strong density dependence. The same conditions resulted in few fry surviving to become parr, much parr habitat, and thus little competition and weak density dependence on the parr. Thus the parameter space for density dependence for fry was the mirror image of that for parr (e.g. Fig. 2a vs. Fig. 2e, etc.). For a given proportion of habitat suitable for fry, increased breeding dispersion generally resulted in lower density dependence for fry and higher density dependence for parr. This happened because increased breeding dispersion increased the total amount of suitable habitat available for fry within their maximum dispersal distance, which increased the fry carrying capacity.

Patterns of density dependence were qualitatively similar under density-independent and density-dependent growth (e.g. Fig. 2a vs. Fig. 2b) and under size-selective and non-selective thinning (e.g. Fig. 2a vs. Fig. 2c). Quantitatively, the largest differences in patterns of density-dependent mortality were evident between scenarios with density-dependent vs. density-independent growth. Under density-dependent growth, the potential for density-dependent mortality increased for fry (e.g. Fig. 2a vs. Fig. 2b) and decreased for parr (e.g. Fig. 2e vs. Fig. 2f). This was because of a reduction in parr body size (and hence territory size) prior to smoltification under density-dependent growth. Thus, more parr survived to smoltification, producing more adults and higher egg deposition relative to the habitat available for fry, which then led to increased fry density-dependent mortality.

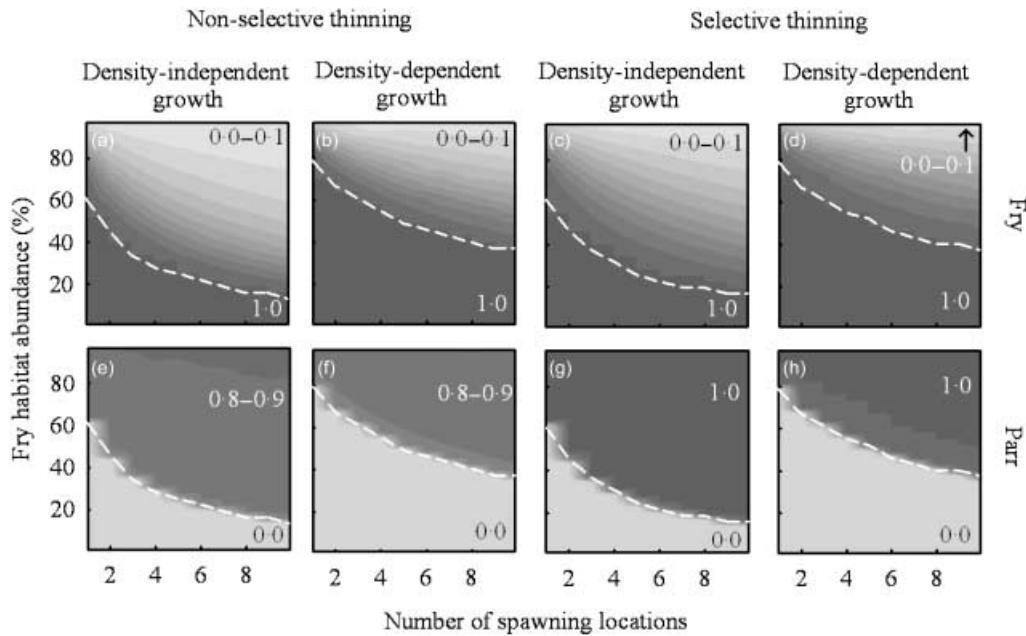


Fig. 2. Intensity of density dependence (α_1) for fry (upper panels) and parr (lower panels) Atlantic salmon as a function of number of spawning locations and fry habitat abundance under different thinning and density-dependent growth rate scenarios. Darker shading indicates stronger density dependence (higher values of α_1 , indicated by numbers). Dotted lines indicate the fry habitat value maximizing adult abundance for each value of number of spawning locations.

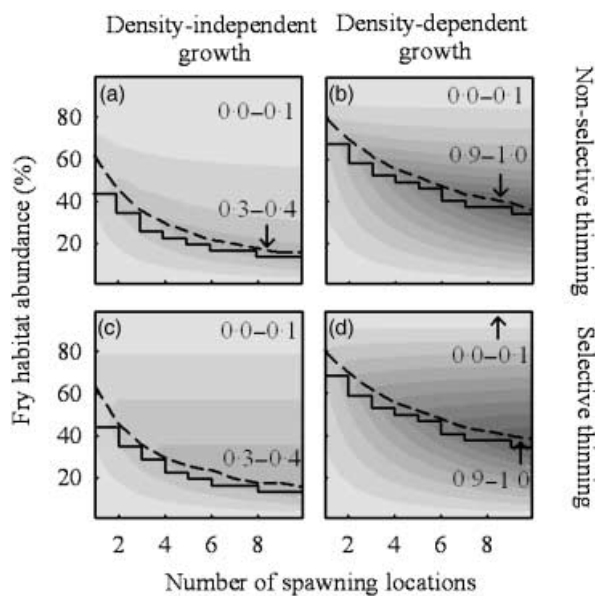


Fig. 3. Relative adult abundance (observed/maximum among all simulations) as a function of number of spawning locations and fry habitat abundance values. Darker shading indicates higher abundance (indicated by numbers). Dotted lines indicate the fry habitat value maximizing adult abundance for each value of number of spawning locations, and solid lines are contour lines for $\alpha_1 = 0.0$ from Fig. 2 indicating threshold values for density-dependent mortality in parr (0 below line, positive above).

ADULT ABUNDANCE

Adult abundance generally increased with increasing breeding dispersion (Fig. 3). However, the magnitude of this effect depended strongly on fry habitat abundance. The strongest

increase in adult abundance in response to increases in breeding dispersion was observed at fry habitat abundance values between *c.* 20% and 40% (Fig. 3). The combination of breeding dispersion and fry habitat maximizing adult abundance consistently coincided with the values for onset of parr density-dependent mortality (Fig. 2). Thus the optimal fry habitat abundance values were those that simultaneously minimized fry and parr density-dependent mortality. These patterns were qualitatively similar under density-dependent and density-independent growth (e.g. Fig. 3a vs. Fig. 3b). However, maximum adult abundance increased under density-dependent growth (Fig. 3). Again, this was caused by the reduction in body size (and hence territory size) in parr prior to smoltification under density-dependent growth, which allowed a larger proportion of the habitat to be suitable for fry without resulting in density-dependent mortality of parr.

Adult abundance changed less with increased breeding dispersion at low and high levels of fry habitat. If fry habitat abundance was very low (*< c.* 10%) and breeding dispersion was low, few fry survived the initial emergence period when dispersal was restricted. However, because fry habitat was scarce these few survivors were sufficient to fill all vacant habitat after the initial fry settlement, when limitations to dispersal were relaxed. Hence weak or no positive effects of increasing breeding dispersion were observed (Fig. 3). At the other extreme, if fry habitat was very abundant (*> c.* 60%), the population was regulated during the parr stage (Fig. 2), and increasing the recruitment into the parr stage by increasing breeding dispersion did not increase adult abundance (Fig. 3). In fact, when values of fry habitat abundance and breeding dispersion were sufficient to cause regulation during the parr stage, adult abundance actually decreased with increasing

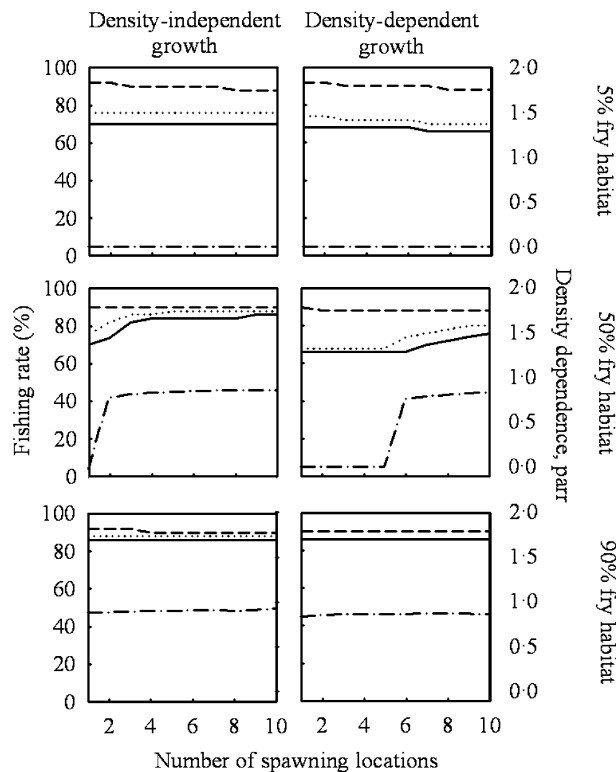


Fig. 4. Modelled adult Atlantic salmon fishing rates giving the maximum sustainable yield (solid lines), reducing equilibrium adult abundance by 20% (dotted lines) or causing population extinction (dashed lines) under different environmental and behavioural scenarios. Dashed-dotted lines indicate intensity of density dependence (α_1) for parr in the absence of fishing.

breeding dispersion (Fig. 3a,b), under scenarios where thinning was non-selective (no size or age advantage for intercohort interactions). In contrast, if thinning was selective (larger individuals win competitive interactions) this effect did not occur (Fig. 3c,d). In these scenarios, adult abundance reached an asymptote as breeding dispersion increased.

POPULATION RESISTANCE TO FISHING

Fishing rates causing extinction were invariably high (c. 90%), indicating an overall high resistance to fishing mortality (Fig. 4). Fishing rates giving a MSY were usually below those causing a 20% reduction in equilibrium adult abundance (Fig. 4). Populations with density-dependent mortality occurring on the parr stage (e.g. the 90% fry habitat scenarios in Fig. 4) showed a somewhat higher resistance to fishing (measured as mortality required to reduce equilibrium abundance by 20%) than those being regulated exclusively during the fry stage (e.g. the 5% fry habitat scenarios in Fig. 4). Furthermore, MSY varied greatly in magnitude among the different environmental and behavioural scenarios (Fig. 5). The greatest effect of breeding dispersion on MSY was observed for intermediate values of fry habitat abundance (Fig. 5), which was consistent with the relationships between breeding dispersion and adult abundance in non-fished populations (Fig. 3).

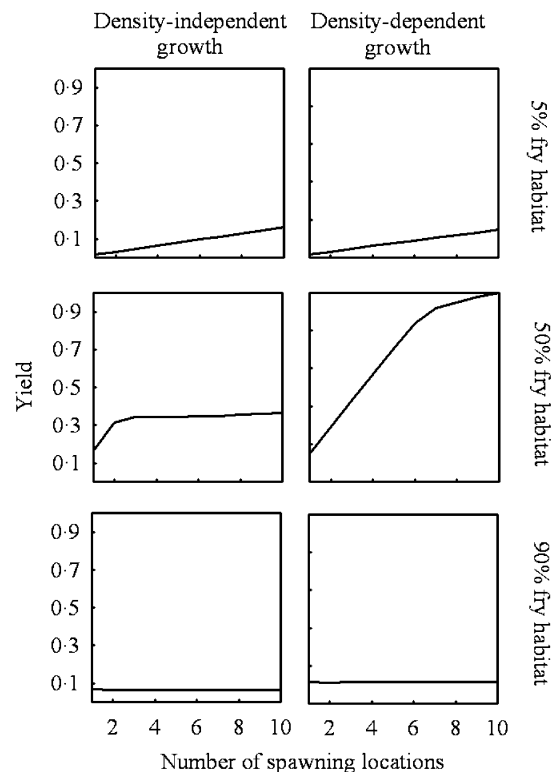


Fig. 5. Modelled maximum sustainable yield (observed/maximum among all simulations) of adult Atlantic salmon under different environmental and behavioural scenarios.

Discussion

The success of restoration strategies is thought to depend on details of the ecology and behaviour of individuals (Jansson *et al.* 2005). For anadromous salmonids, increasing the availability of breeding habitat through increased access (fish passages) and channel bed improvements (gravel augmentation or gravel cleaning) is an important component of many restoration efforts (Kondolf, Vick & Ramirez 1996; Hendry *et al.* 2003). However, theoretical models predicting population effects of such efforts across environments have been lacking. This problem is exacerbated by the typical absence of monitoring of ultimate effects (Bash & Ryan 2002). In the present study we approached these problems by developing a spatially explicit model that predicts the population consequences of breeding habitat dispersion. Under many scenarios increased breeding dispersion caused reduced local competition for habitat during the earliest juvenile stage (i.e. reduced density-dependent mortality for fry), increased adult abundance and increased MSY. However, strong interaction effects between stage-specific habitat abundance and breeding dispersion emerged, and the most pronounced effects of breeding dispersion were observed under intermediate habitat abundance values for the smallest life stage. Thus population effects of increased breeding dispersion can differ among systems, related to which juvenile life stage is likely to be limited by competition for habitat.

How can this information be used to help guide management activities? This is an important question as our model results indicate that, under some scenarios, increasing breeding dispersion can be ineffective or detrimental. We offer three suggestions. First, in situations where important attributes of fry or parr habitat are obviously restricted, restoration efforts should be focused on increasing habitat availability before increasing breeding dispersion. For example, in channelized rivers with little or no bank complexity or lateral habitat, the abundance of slow-flowing microhabitats allowing successful fry foraging (Nislow, Folt & Parrish 1999, 2000) is likely to be low. Increasing the availability of fry habitat should then take precedence over increasing breeding dispersion. Secondly, in situations where stage-specific habitat availabilities are unclear, it may be possible, using stocking experiments or monitoring data, to test for density-dependent parr survival. If parr survival is density-dependent, increasing breeding dispersion is likely to be ineffective (Fig. 3). Finally, for fishery managers, the risk of serious declines in population size when setting a long-term fixed proportion quota aiming at MSY (e.g. by simply limiting the duration of the fishing season) is considerable. Furthermore, such risks will be substantially larger in populations that are regulated during the parr stage. Although such populations tolerate higher fishing rates at MSY, the difference between fishing rates giving MSY and extinction is much less (Fig. 4). Thus, if direct evidence or habitat considerations suggest that populations experience density-dependent mortality during the parr stage, it is particularly important to adopt a conservative and flexible regulation regime.

Our results also indicate the importance of understanding the details of population mechanisms when modelling the effects of management actions. Most significantly, in scenarios where stage-specific habitat abundances caused density-dependent mortality during the parr stage (i.e. low parr habitat abundance), effects of breeding dispersion depended on intercohort competitive mechanisms. Under symmetric competition, the number of parr from a given cohort was reduced by recruitment of younger cohorts, and adult abundance actually decreased with increasing breeding dispersion. Such effects may be expected whenever the number of individuals in a given subadult life stage and from a given cohort is reduced as a result of competition with recruits from a younger cohort entering the same life stage. In the presence of such effects, management measures aimed at increasing population abundance by releasing captive reared individuals over multiple consecutive cohorts (a common management practice for many fish species; Fjellheim & Johnsen 2001; Leber *et al.* 2004) or habitat manipulations that increase recruitment into the limited stage (e.g. by improving breeding opportunities) can actually cause a reduction in population abundance. It should be emphasized that this effect differs from the intracohort interactions causing over-compensatory mortality and dome-shaped stock-recruitment curves. Populations experiencing such 'intercohort dilution' may be described well by asymptotic stock-recruitment curves. In contrast, under asymmetric competition (i.e. older and larger juveniles win) adult abundance did not change with increas-

ing breeding dispersion. Effects of intracohort variation in salmonid body size on the outcome of competitive interactions has been well studied in the laboratory. However, whereas some studies suggest that body size advantages can be strong (Johnsson, Nöbbelein & Bohlin 1999) others find only weak or no evidence for such effects (Huntingford *et al.* 1990; Metcalfe, Taylor & Thorpe 1995; Metcalfe, Valdimarsson & Morgan 2003). Furthermore, intercohort competition includes both effects of age and body size, and less is known about how these in combination influence competitive abilities. Finally, competitive abilities measured in the laboratory may not always manifest under field conditions (Martin-Smith & Armstrong 2002). Further resolution of these basic science issues is key to determining the probability of over-compensatory responses to increases in parr recruitment.

The present findings emphasize the importance of understanding which stages are under density-dependent regulation in order to develop a proper focus for management efforts (Benton & Grant 1999; Armstrong *et al.* 2003) and demonstrate how consideration of behavioural ontogenetic changes and habitat availability can help to achieve such an understanding. Failing to do so may prevent further progress in this important area of ecology, and the history of salmonid research may serve as an illustration of this. In some long-term population studies and short-term experiments, high mortality and intense density dependence occurred very early in the life history (Elliott 1994; Einum & Fleming 2000a,b; Nislow, Einum & Folt 2004; Einum & Nislow 2005; Einum 2005), with little evidence for significant density dependence in later juvenile life stages (Elliott 1994). In contrast, negative relations between density and body mass or age may represent evidence for density dependence occurring throughout juvenile life (Elliott 1993; Bohlin *et al.* 1994; Grant *et al.* 1998; Steingrímsson & Grant 1999; but see Dunham & Vinyard 1997; Armstrong 1997). Thus previous empirical studies have failed to reach a consensus regarding the issue of when during the juvenile stage regulation occurs. The present model shows that such lack of consensus may be a result of real differences in how populations are regulated, because of differences in habitat abundance for different stages and/or differences in the spatial dispersion of breeders. Although some fry habitat abundance estimates (e.g. 14% of total wetted area; Nislow, Folt & Parrish 2000) suggest the greatest potential for density-dependent mortality during the fry stage based on the results presented here, more empirical information on habitat availability for different size classes and the spatial distribution of breeders across populations is required to obtain more specific predictions regarding the ontogenetic dynamics of density dependence in salmon.

Any model of biological systems necessarily involves the use of simplifying assumptions. Here, we modelled situations with temporally (among-years) and spatially (within-river) constant environmental conditions. Although this is certainly never the case for real populations, as indicated by fluctuating population abundances (Nickelson & Lawson 1998; Einum *et al.* 2003; Isaak *et al.* 2003), it allowed us to address important questions regarding population abundance and density dependence under an equilibrium situation.

The choice of input parameter values may also influence model results. One advantage of the present model is that input parameters other than those of direct interest (i.e. habitat types and breeding distribution) were obtained primarily from a single well-studied population. Because this particular combination of parameter values has been proved to allow the existence of a viable population of salmon, and as it is not known whether averages of parameter values from multiple populations would be evolutionary or ecologically stable, this approach seemed superior to using parameters from several populations.

The underlying behavioural mechanisms may differ from those assumed, again influencing the model results. For example, the observation that habitat use changes with increasing body size is accommodated in the present model by dividing juveniles into two size classes and by letting these utilize different habitat types. Although this assumption is based on empirical observations and bioenergetic modelling, deviations from this pattern may occur. Yet complete absence of stage structure in habitat use seems unlikely in most cases, and the present approach represents a compromise between realism and generality. Life-history diversity was limited to variation in age at maturity and a corresponding variation in size at maturity, fecundity and egg size. Although a range of life-history strategies and tactics are present within salmonid populations (Hendry & Stearns 2004), these were the ones we considered to be the most important in relation to the issues addressed in the present study.

Whereas our model was developed using the biological particulars of Atlantic salmon, the general approach and insights should be valid for the wide range of organisms with size-structured populations exhibiting ontogenetic niche shifts (Werner & Gilliam 1984) and where variation in mobility causes the spatial scale of density dependence to differ among stages (Ray & Hastings 1996). For such organisms, ensuring sufficient spatial dispersion of breeding habitat may in many cases be an efficient measure to conserve threatened populations and increase yield in fished populations. However, in the presence of intercohort dilution, management measures such as stocking or habitat manipulation, attempting to increase abundance of size-structured populations, may not only be inefficient but even detrimental if the targeted stage is not limiting abundance. This illustrates the importance of applying knowledge about basic ecological mechanisms to achieve successful restoration of disturbed systems (Jansson *et al.* 2005).

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Model details and parameter values.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2008.01464.x>

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