

Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon

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Two separate field experiments were performed in the U.S.A. and Norway with stocked Atlantic salmon *Salmo salar*. In the Norwegian experiment, the offspring of early-spawning fish which had larger eggs and emerged a few days before offspring of later spawning fish had consistently higher survival rates. In the U.S.A. experiment, stream sections with higher proportions of favourable foraging locations during the critical period (the transition from dependence on maternally-derived yolk reserves to independent feeding) had lower loss rates of fish stocked as unfed fry. These results provide support for the critical period concept (CPC) in Atlantic salmon, underscores the utility of a manipulative approach to achieve further advances in knowledge of Atlantic salmon ecology and provide additional guidance to management and restoration. A mechanistic, conceptual model for density dependence is presented to identify important knowledge gaps that remain to further evaluate the importance of the CPC for Atlantic salmon population regulation.

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Key words: Atlantic salmon; critical period; density-dependence; habitat suitability.

INTRODUCTION

High mortality during the transition from dependence on maternally-provided yolk reserves to exogenous feeding has been shown to be a strong determinant of cohort strength in a number of fish species (Sinclair, 1989). If cohort strength is essentially set by events during this relatively short period of time, understanding the mechanisms involved in population regulation during this critical period may be a means to effective management. These considerations may be particularly relevant to stream salmonids. In the Critical Period Concept (CPC), the ultimate mechanism underlying a critical period for survival derives from specific habitat requirements for oviposition and incubation (Armstrong *et al.*, 2003) combined with potentially limited dispersal from incubation sites (Gustafson-Marjanen & Dowse, 1983; Beall *et al.*, 1994; De Leaniz *et al.*, 2000; Webb *et al.*, 2001). Relatively few juveniles (referred to as fry during the first 2–3 months after emergence) find suitable microhabitats (appropriate feeding

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territories and refuges from predation and high flows) resulting in high, strongly density-dependent mortality rates (Elliott, 1985) during the first weeks after emergence. The importance of the CPC depends on to what degree it can explain overall population regulation, or in other words whether density-dependent mortality during the critical period reduces competition and the potential for density dependence for later life-history stages.

A complex web of proximate mechanisms underlies density dependence in stream salmonids, an understanding of which is necessary to predict when the CPC is likely to apply to salmonid populations (*i.e.* in which cases early density-dependent mortality is the main regulating factor). The mechanisms can be outlined and summarized in a conceptual model of how density dependence may occur in juvenile stream-living salmonids (Fig. 1). The model can be used to identify the factors to consider when comparing the probability for density dependent processes to occur for different age- or size-classes. Generally, at any given point in time, a population can be thought of as consisting of two types of individuals: occupants and dispersers. Occupants are individuals that defend a required resource against other individuals, typically a feeding location for territorial salmonids, whereas dispersers are individuals that do not presently occupy such locations. Density dependence in the population is a result of the influence of effective density, which can be thought of as the density that each individual experiences at a given time (*e.g.* number of encounters with other individuals per time interval) (Lloyd, 1967; Folt & Schulze, 1993), and is jointly determined by cohort size, individual territory size, area of habitat

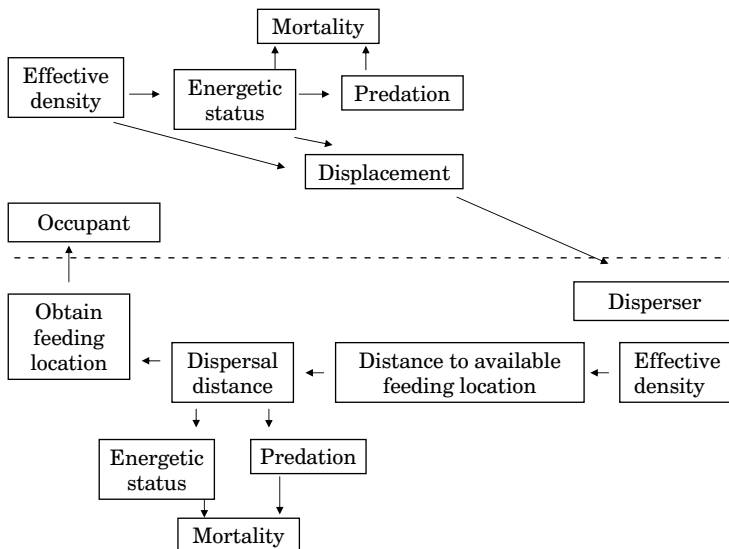


FIG. 1. A conceptual model of density-dependent processes in stream-living juvenile salmonids. Area above and below ----- represents effects of effective density on occupants (individuals that defend a required resource against other individuals) and dispersers, respectively. ←, the sequential actions of different factors (□) affecting the probability of survival of the two types of individuals, and the probability for transition from occupant to disperser status and *vice versa*.

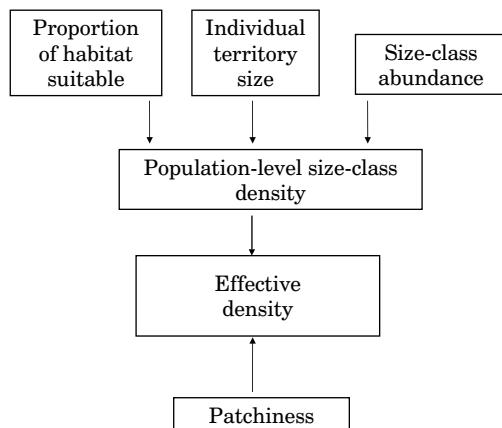


FIG. 2. Factors influencing effective density for stream-living juvenile salmonids. The diagram describes how cohort size, individual territory size, area of habitat suitable for occupancy and population patchiness co-determine the effective density (the density experienced by individual fish).

suitable for occupancy and population patchiness (Fig. 2). For occupants, effective density may influence their energetic status (*e.g.* time and energy spent on competitive interactions), which then may influence risks of mortality (predation, parasitism and starvation). Effective density may also influence the probability for dispersal, both due to the effect on the probability of displacement by a superior competitor, or through effects on energetic status. For dispersers, effective density will influence the distance to an available feeding location, and through that the dispersal distance required to becoming an occupant. The distance required to disperse can be thought of as representing a cost to the individuals in terms of energy and predation, which ultimately translates to a risk of mortality.

In spite of this complexity, simple predictions arise from the CPC that can be tested with stocking experiments. For example, if critical period mortality results from intense competition for territories, individuals that are competitively superior are predicted to have higher survival than competitive subordinates during the critical period. Competitive superiority in salmonids is generally associated with larger body size and early emergence (Metcalf, 1998; Einum & Fleming, 2000*a, b*; Letcher *et al.*, in press). It remains unclear, however, whether competitive advantage results in a critical period survival advantage under all environmental conditions (Good *et al.*, 2001). To test this prediction, effects of body size and timing of emergence on survival could be investigated by manipulating stocking conditions. Similarly, if there is intense competition for suitable territories, an increase in the availability of suitable habitats is predicted to result in increased survival during the critical period. Availability of appropriate microhabitats has been shown to be associated with overall survival in Atlantic salmon *Salmo salar* juveniles (Folt *et al.*, 1998; Nislow *et al.*, 1999, 2000), but there have been no studies explicitly comparing survival during the critical period with habitat availability in the same period. This prediction could be tested by stocking similar numbers of juvenile Atlantic salmon in reaches covering a range of levels of available microhabitat and measuring fish survival in each site during the critical period.

Understanding the implications of CPC for population performance and salmonid production can lead to more effective management of declining salmonid populations. As an example, due to widespread population extirpation and decline of anadromous Atlantic salmon (Parrish *et al.*, 1998) fish culture and stocking are currently being used to enhance or restore populations throughout the historic range of this species. Many programmes rely on culture and stocking strategies (using cultured eggs and unfed fry) that may significantly impact both the intrinsic condition of fish (size, developmental status and genetic composition) and the environments they experience (temperature, current speed, predators and competitors) during the critical period. The understanding of this vital period could be enhanced by the use of experiments with controls on factors such as parentage, density, timing and location of stocking. Control of these key variables is much more feasible with stocking experiments than with wild populations. Stocking experiments, with a long history in salmonid ecology, have been used effectively to address basic issues such as the role of predation (Henderson & Letcher, 2003), interspecific (Kennedy & Strange, 1986) and intraspecific (Whalen & Labar, 1994) competition and developmental status (Letcher & Terrick, 2001) in determining juvenile performance.

Two separate stocking experiments were carried out (Table I) to test predictions of the CPC as it relates to juvenile anadromous Atlantic salmon: (1) greater competitive advantage during the critical period increases fry growth and survival and (2) Increased survival during the critical period is associated with greater availability of suitable habitats. The mechanistic, conceptual model for density dependence was then used to identify important knowledge gaps that remain to incorporate the CPC into a broader ecological perspective. The overall goals of the study were to understand the implications of these predictions for Atlantic salmon stocking and restoration programmes.

TABLE I. Summary characteristics for the two studies used to evaluate predictions of the Critical Period Concept (CPC) for stream dwelling juvenile Atlantic salmon

| River | Location | Question | Stocking technique | Sampling interval (months) | Performance attributes measured |
|---------------------------------|-------------------|----------|--------------------|----------------------------|---------------------------------|
| River Bjørnbettelva | Central Norway | 1 | Eyed eggs | 2 | Survival L_T Dispersal |
| Connecticut River (tributaries) | North-east U.S.A. | 2 | Unfed fry | 1.5–2 | Loss rate L_T Mass |

Question 1, Does greater competitive advantage during the critical period increase fry growth and survival?

Question 2, Is increased survival during the critical period associated with greater availability of suitable habitats?

Stocking technique, developmental stage at which Atlantic salmon fry were stocked; Sampling interval, the time between stocking and sampling.

MATERIALS AND METHODS

RIVER BJØRNBETTELVA: PREDICTION 1

The field experiment was conducted in the River Bjørnbettelva (63°27' N; 9°54' E), a tributary to the River Ingdalselva, central Norway. Previously there were no Atlantic salmon in the River Ingdalselva due to a natural migration barrier close to the sea, but the river has for the last decade been stocked with adult Atlantic salmon to establish a naturally reproducing population. No spawning has occurred in the River Bjørnbettelva, and spawning in the River Ingdalselva occurs several km upstream of the River Bjørnbettelva (B.O. Johnsen, pers. comm.). The section of the River Bjørnbettelva used in this study extends from the outlet and upstream 1848 m to an impassable waterfall. Mean length and width of habitat units in the study section were 9.7 m (range: 1.2–71.4 m) and 3.5 m (range: 1.1–11.3 m), respectively. Riffles were the dominant habitat type throughout the river, but these were regularly interspersed with stretches of glides and pools (unpubl. data).

In the autumn of 2001, 10 full-sib family groups from the River Måna, central Norway, were produced at the Norwegian Gene Bank Hatchery, Haukvik, central Norway. To establish competitive differences between groups of fry, half of these were from fish that matured early in the season, and the other half from later maturing fish. This resulted in fish that differed in fertilization time (23 November and 12 December). Using incubation temperature data and the model for development of salmonid eggs (Crisp, 1981, 1988) the median date of emergence for these two groups was estimated to be 3 and 6 June [early (EE) and late emerging (LE) groups]. The groups also differed in egg size, with mean \pm s.d. egg mass at the eyed stage of EE = 140 ± 21 mg and LE = 102 ± 12 mg (*t*-test, d.f. = 8, $P = 0.008$). Each family group was reared separately until the eyed-egg stage, at which point the early and late fertilized groups were given different thermal otolith banding patterns (Volk *et al.*, 1999). Single marks were created by short-term (5°C, 48 h) increases in incubation temperature, with the distance between each mark being determined by the period incubated at ambient temperature between two marking episodes. Then, 10 different release groups were produced using these eggs, where each group had an equal contribution from each family group, but where the total number of eggs (range 100–1100) differed among groups. These different release groups were then given distinct otolith banding patterns to enable identification of group origin.

Some of the eggs from the EE groups had hatched by the end of the marking procedure, and thus could not be used in the releases. The number of eggs from each fertilization group in each release group was therefore prior to the counted 'outplanting'. The different groups were placed in 13.5 × 5.5 × 6.5 cm plastic, coarse-mesh incubation boxes (Vibert[®], Federation of Fly Fishermen, Bozeman, MT, U.S.A.), which were buried in artificial nests, with each nest being located *c.* 150 m apart in the River Bjørnbettelva on 2 May. Egg survival at each station was estimated on 17 June, when the Vibert boxes were excavated and their contents checked. Egg mortalities were subtracted from egg release numbers to give number of hatched eggs because the focus of the study was on differences between EE and LE fish occurring during and following emergence. Low egg mortality (range: 0.0–4.3%) indicated that oxygen supply in nests was high, and thus egg mortality could be assumed to be non-selective relative to fertilization time and egg size (Einum *et al.*, 2002). This enabled the number of EE and LE eggs hatching from each nest to be estimated.

During 29 July to 1 August the whole stream was electrofished to recapture as many as possible of the surviving juveniles. This was done by dividing the river into 143 different sections from the outlet up to 100 m above the uppermost nest, with most sections comprising a single habitat unit. Each section was electrofished three times unless two or fewer juveniles were caught during the second round, and population estimates were made using a modified Zippin maximum-likelihood method (Bohlin *et al.*, 1989). The area above these sections up to the waterfall was divided into 10 m sections and electrofished in a similar manner. At least 30 min was allowed between each round of electrofishing for any given section. All juvenile Atlantic salmon caught were

anaesthetized in clove oil, killed and frozen for later otolith analyses. Otolith analyses were performed on every second Atlantic salmon recaptured (*i.e.* according to their numbers given during sampling) using standard techniques. Analyses of reference material of fish from the different groups retained in the hatchery confirmed that the marking procedure produced the predicted banding patterns. Survival rates of EE and LE groups from each nest were calculated by multiplying the numbers identified by two (half of the fish were analysed) and then dividing by the number of hatched eggs of that type from that nest. In addition to survival and individual total length (L_T), median absolute dispersal distance (location at capture relative to nest location), was calculated for EE and LE fish in each nest. To test whether EE and LE groups differed with respect to survival, size and dispersal distances, paired *t*-tests were used.

CONNECTICUT RIVER: PREDICTION 2

The goal of this study was to test whether survival of Atlantic salmon fry is determined by the availability of suitable microhabitats during a potential critical period. The study was conducted in six sites located in small rearing tributary streams in the northern Connecticut River basin (between 42°86' and 43°55' N; 27°55' and 27°70' W), in central and southern Vermont, U.S.A. (Nislow *et al.*, 1999), that in previous studies were found to differ with respect to habitat characteristics. Study sites were *c.* 100 m long, located in small (<30 km² drainage area) upland streams dominated by coarse gravel and cobble substrata, with stream widths under typical late spring conditions of 5–8 m. Between 1 and 15 May 1997, unfed Atlantic salmon fry were stocked at a density of 50 fry per stocking unit (stocking unit = 100 m² of stream habitat; standard densities for rearing tributaries in the basin) into study sections (remaining habitat in the streams was stocked at similar densities). Age-0 year Atlantic salmon size and abundance were estimated using three-pass electrofishing censuses conducted 45–55 days after stocking. Immigration and emigration from the plots were restricted during electrofishing passes using blocking nets, and there was a 30 min wait between passes. All salmonids [brook trout *Salvelinus fontinalis* (Mitchill) and Atlantic salmon] were anaesthetized using clove oil, identified, weighed (wet mass to the nearest 0.01 g) and then returned to the stream.

The availability of foraging locations favourable for growth has been shown to be a primary determinant of habitat quality for age-0 year Atlantic salmon (Folt *et al.*, 1998; Nislow *et al.*, 2000). Earlier studies in these systems found that age-0 year Atlantic salmon in their first month after stocking choose territories with current speeds <0.18 m s⁻¹ which are most likely to result in high foraging rates, and that these locations are frequently in limited supply during this period (Nislow *et al.*, 2000). To determine differences in habitat quality among sites, microhabitat measurements were collected following the protocol established by Nislow *et al.* (1999). In three sampling sessions separated by *c.* 1 week intervals between stocking and electrofishing, measurements were made at 1 m intervals along bank-to-bank transects established at 25 m intervals in each study plot. The percentage of sample points <0.18 m s⁻¹ current speed was used as an index of habitat suitability. Linear regression was used to test the relationship between habitat suitability, fry survival and fry growth (change in mean mass or L_T from stocking to sampling) across the six study sections. The daily proportion lost (K) (Elliott, 1985) was used as a proxy for survival because fry were unmarked: $K = (N_{\text{stocking}} - N_{\text{sampling}}) t^{-1}$, where N_{stocking} and N_{sampling} are number of fish at stocking and sampling and t is the time (days) between these events.

RESULTS

RIVER BJØRN BETTELVA: PREDICTION 1

A total of 1105 juvenile Atlantic salmon were recaptured. Catchability was high (estimated to 0.83 using the Zippin procedure, Bohlin *et al.*, 1989),

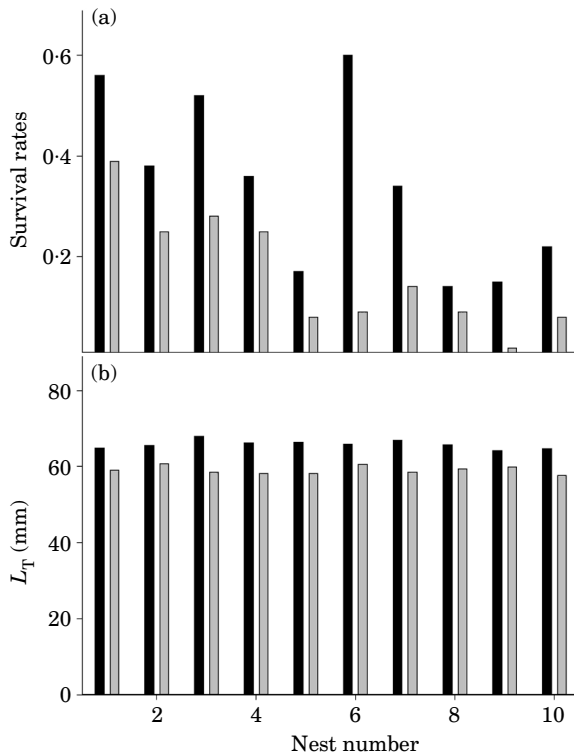


FIG. 3. Differences in (a) survival (*t*-test, d.f. = 9, $P = 0.002$) and (b) total length (*t*-test, d.f. = 9, $P < 0.001$) between early-fertilized (■, competitive dominant) and late-fertilized (▣, competitive subordinate) Atlantic salmon fry in the River Bjørnbettelva in 2002.

probably due to the small size of the river and low summer flow; total proportion of surviving juveniles that was recaptured was estimated to be 0.97. The distribution of fish originating from the different nests reflected to a large degree the distribution of nests, although some dispersal had occurred, with the median absolute dispersal distance being 92 m (range: 0–1500 m).

Across the range of density and habitat conditions in the River Bjørnbettelva, fry belonging to the EE group had significantly higher survival (mean \pm s.e. = 0.34 ± 0.05) than LE fry (0.17 ± 0.04) [Fig. 3(a)] (*t*-test, d.f. = 9, $P = 0.002$). The EE fry also maintained their size advantage over LE fry, and were >10% larger (mean \pm s.e. = 65.8 ± 0.4 mm L_T) (*t*-test, d.f. = 9, $P < 0.001$) than LE fish (59.1 ± 0.3 mm L_T) [Fig. 3(b)] at capture. No significant differences between the dispersal of EE *v.* LE fish were observed (*t*-test, d.f. = 9, $P = 0.594$).

CONNECTICUT RIVER: PREDICTION 2

Both habitat availability and fry loss rates varied substantially among the study sites. Estimates of the proportional availability of suitable habitats (as predicted from the foraging-based habitat suitability model) ranged from *c.* 13 to 40% of total stream habitat area. Streams with higher gradients and larger drainage areas maintained higher spring flows and consequently lower availabilities of low

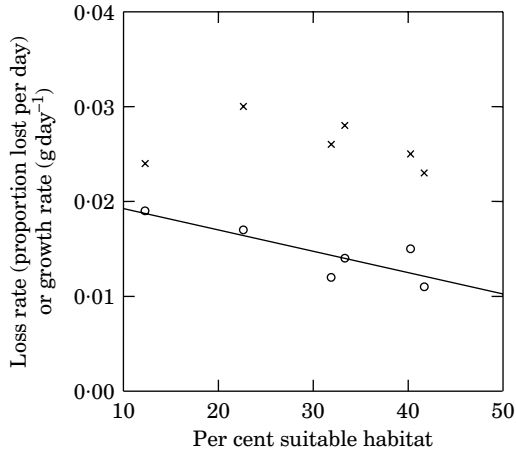


FIG. 4. Effect of per cent suitable habitat on Atlantic salmon growth in mass (x) ($P > 0.05$) and loss rates (proportion lost) (o) in six study sites in the Connecticut River in 1997. The curve for loss rate and per cent suitable habitat was fitted by $y = -0.00023x + 0.22$ ($r^2 = 0.70$, $n = 6$, $P < 0.05$).

current speed microhabitats required by Atlantic salmon fry in their first month after stocking. Similarly, the proportion lost of fry varied considerably across study sites (0.55 to 0.98 fry unit⁻¹ day⁻¹) translating into a loss of <60 to $>95\%$ of fry over the interval between stocking and sampling. Loss rates of Atlantic salmon fry during the potential critical period after stocking were significantly lower in study sections with lower availabilities of model-predicted suitable habitats ($n = 6$, $r^2 = 0.70$, $P < 0.05$) (Fig. 4). Variation in habitat suitability explained 70% of the total variation in loss rates, with a 10% decrease in habitat suitability corresponding to *c.* 15% increase in fry loss rates. In contrast, there was no relationship between mean fry L_T or mass with variation in habitat suitability across the six sites.

DISCUSSION

Stocking experiments with juvenile Atlantic salmon proved to be an effective way to test predictions of the CPC for stream salmonids. Results of two separate stocking experiments supported one of the major tenets of the CPC, that competition for suitable territories influences high juvenile mortality in the first weeks after emergence or stocking.

In the River Bjørnbettelva study, dominance status significantly affected survival and growth during the potential critical period. A major advantage of this study was that individuals were identifiable with respect to nest origin and emergence group, and essentially no fish dispersed out of the nearly 2 km study site (a waterfall prevented upstream migration, and no recaptures were made in the main river or in the lower 100 m of the stream). It was therefore possible to conclude that mortality, and not dispersal, was responsible for fry losses during the critical period. Consistent with the extensive body of literature on the importance of competitive relationships in stream salmonids (Metcalf, 1998; O'Connor *et al.*, 2000), EE fish, with their prior residence and a greater egg size

advantages, had significantly greater survival than LE fish. Previous studies employing manipulations of fertilization time and egg size in Atlantic salmon identified strong causal effects of these two traits on juvenile survival in the wild (Einum & Fleming, 2000*a, b*). Knowledge of such causal relationships is necessary to predict evolutionary dynamics of traits (Mitchell-Olds & Shaw, 1987). The ecological effect of natural variation in such traits, however, is not necessarily identical to those detected from manipulations, because potential correlations between the focal trait and other maternal or genetic traits may counteract single trait effects. The present study demonstrated that the effect of natural variation in fertilization time and egg size in Atlantic salmon is similar in direction to those where such traits were manipulated, with early and large emergers having a survival advantage over later, smaller emergers.

Effects of differences in competitive ability have important implications for culture and stocking supplementation, specifically when unfed fry are stocked into streams with some wild reproduction. If supplementation fish are stocked, or emerge from stocked eggs earlier than wild fish, there may be negative impacts on wild fish (Letcher *et al.*, in press). Another important concern is that many stocking programmes, in order to increase survival and recruitment, place unfed fry, after acclimatization, in a stream every few metres to achieve a stocking density of 50 m⁻². This procedure potentially bypasses strong selection on fry performance during this early critical period, which may decrease the rate of local adaptation in restored or supplemented populations (Hendry *et al.*, 2003).

A second line of evidence supporting competition for suitable sites as a mechanism underlying the CPC for stream salmonids comes from the Connecticut River study. Differences in the probability of obtaining suitable territories caused by differences in habitat availability among study sites was associated with differences in fry loss rates. These results complement the Bjørnbettelva study, which showed that differences in the probabilities of obtaining suitable sites were determined by differences in competitive ability. Connecticut River study sites predicted to have a higher availability of suitable foraging habitats had lower loss rates of fry during the potential critical period for survival. These results reinforce those of Nislow *et al.* (1999, 2000, 2004) that habitat suitability during the critical period has a strong influence on overall capacity of streams to support juvenile production. It was not possible to determine the extent to which loss rates were due to mortality *v.* dispersal in this experiment. Results from the Bjørnbettelva study, however, suggest that successful dispersal beyond the 100 m scale during this period may be uncommon for juvenile Atlantic salmon. This indicates that loss rates primarily reflect mortality during this period, a conclusion which has been supported by other studies (Elliott, 1994). Further, even if loss rates are to some extent due to dispersal, they still reflect the ability of particular stream sections to support fry throughout the critical period (Nislow *et al.*, 1999). In contrast to loss rates, there was no relationship between availability of suitable habitat and size of fry at the end of the critical period. This lack of a relationship also supports the CPC, in that while fewer fry find suitable habitats when availability is low, the growth rates of those that do are not predicted to differ (Elliott, 1985; Nislow *et al.*, 1999).

The role of habitat during a potential critical period for survival has important implications for stocking and restoration. The Connecticut River study indicates that relatively small differences in the availability of suitable microhabitats, well within the range of both natural variation, and variation associated with habitat manipulation (Nislow *et al.*, 1999), can have substantial impacts on juvenile survival. Identifying rearing streams with high availabilities of suitable habitat, and restoring habitat in low production streams may therefore help to improve Atlantic salmon production. The proviso is that this effect will be contingent on correlated variation in other determinants of Atlantic salmon growth and survival. An additional option for enhancement programmes, where critical period survival may be limiting would be to bypass this period by stocking juveniles at later life-history stages (*i.e.* fed fry or parr). Previous research on survival and growth of fed and unfed Atlantic salmon fry, however, have failed to demonstrate consistent differences in their survival (Letcher & Terrick, 2001). Moreover, the use of older juveniles in stocking programmes has a number of potential negatives (Einum & Fleming, 2001), including bypassing important natural selection events as well as increased hatchery resources and rearing costs.

While the present studies largely support the CPC, important knowledge gaps remain to incorporate this concept into a broader ecological perspective. In particular, the 'success' of the CPC should not be used in isolation to infer at what juvenile stage Atlantic salmon populations are regulated. In theory, density-dependent processes may occur during later juvenile stages as well, and this may buffer any effects of temporal variation in critical period survival. With reference to the conceptual model of density-dependent mechanisms (Fig. 1), the relevant question becomes 'does the intensity of these mechanisms decrease or increase as fish grow?'. This, in essence, is what determines whether later bottlenecks or self-thinning counteracts density dependence during the critical period. Two factors may be particularly relevant in this context. First, as the fish grow they increase their resource requirements due to allometric relations (food or territory size). Thus, everything else being equal, resource requirements of a cohort increase as the individuals increase in body size. This is the argument for why self-thinning should occur in juvenile salmonids (Bohlin *et al.*, 1994; Dunham & Vinyard, 1997; Grant *et al.*, 1998; Steingrímsson & Grant, 1999). Armstrong (1997), however, suggested that self-thinning might not occur if density-dependent mortality is high post-emergence, which is consistent with his analysis of several long-term datasets. A caveat regarding this argument, however, is that as the fish grow they start using different resources, and thus the amount of resources available may change. In terms of feeding habitats, evidence suggest that the amount of suitable habitat increase as fish size increase, thus potentially reducing the effect of increased resource demand per individual (Nislow *et al.*, 2000). It is also possible, however, that certain resources can be in short supply for larger fish (*e.g.* shelters, Armstrong & Griffiths, 2001 and pools, Rincon & Lobon-Cervia, 2002), thus resulting in long dispersal distances and increased potential costs. Thus, predicting any direct effect of body size on effective density requires detailed knowledge about all such mechanisms and considerations of body size-resource requirement allometries in isolation may be overly simplistic.

The second important factor to consider is that mobility may change as fish size increases, and this may influence effective density. For stream salmonids, effective density may be extremely high during the critical period, when hundreds or thousands of individuals emerge from redds at discrete locations suitable for spawning. Combined with the large demand on habitat resulting from these high densities, previous studies have shown that a relatively small percentage of total stream habitat may provide suitable territories (Nislow *et al.*, 1999, 2000). This combination of factors suggests a high risk of displacement for occupants and long distances to available feeding locations for 'dispersers'. Dispersal during the critical period may also be particularly costly, due to high risk of predation (Henderson & Letcher, 2003). If this cost of dispersal is lower for larger fishes, they may be more able to reduce effective density through dispersal and homogenization of densities within the population. In other words, larger fishes may be able to use areas within the stream that cannot be reached during the critical period due to their distance from spawning habitats, and this may reduce the mean effective density experienced for larger fishes. Yet, in the paucity of data on costs of dispersal of different sized fishes, the magnitude of this effect remains unknown, and will likely also depend on the spatial arrangements of different habitat types (including spawning habitat) within the stream.

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References

- Armstrong, J. D. (1997). Self-thinning in juvenile sea trout and other salmonid fishes revisited. *Journal of Animal Ecology* **51**, 519–526.
- Armstrong, J. D. & Griffiths, S. W. (2001). Density-dependent refuge use among over-wintering wild Atlantic salmon juveniles. *Journal of Fish Biology* **58**, 1524–1530. doi: 10.1006/jfbi.2001.1554
- Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M. & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* **62**, 143–170.
- Beall, E., Dumas, J., Claireaux, D., Barriere, L. & Marty, C. (1994). Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. *ICES Journal of Marine Science* **51**, 1–9.
- Bohlin, T., Hamrin, S., Heggberget, T. G., Rasmussen, G. & Saltveit, S. J. (1989). Electrofishing – theory and practice with special emphasis on salmonids. *Hydrobiologia* **173**, 9–43.
- Bohlin, T., Dellefors, C., Faremo, U. & Johlander, A. (1994). The energetic equivalence hypothesis and the relation between population-density and body-size in stream-living salmonids. *American Naturalist* **143**, 478–493.
- Crisp, D. T. (1981). A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. *Freshwater Biology* **11**, 361–368.
- Crisp, D. T. (1988). Prediction, from temperature, of eyeing, hatching and 'swim-up' times for salmonid embryos. *Freshwater Biology* **19**, 41–48.

- De Leaniz, C. G., Fraser, N. & Huntingford, F. A. (2000). Variability in performance in wild Atlantic salmon from a single redd. *Fisheries Management and Ecology* **7**, 489–502.
- Dunham, J. B. & Vinyard, G. L. (1997). Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1025–1030.
- Einum, S. & Fleming, I. A. (2000a). Highly fecund mothers sacrifice offspring survival to maximise fitness. *Nature* **405**, 565–567.
- Einum, S. & Fleming, I. A. (2000b). Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* **54**, 628–639.
- Einum, S. & Fleming, I. A. (2001). Implications of stocking: ecological interactions between wild and released salmonids. *Nordic Journal of Freshwater Research* **75**, 56–70.
- Einum, S., Hendry, A. P. & Fleming, I. A. (2002). Egg-size evolution in aquatic environments: does oxygen availability constrain size? *Proceedings of the Royal Society of London B* **269**, 2325–2330.
- Elliott, J. M. (1985). Population regulation for different life-stages of migratory trout *Salmo trutta* in a lake district stream, 1966–83. *Journal of Animal Ecology* **54**, 617–638.
- Elliott, J. M. (1994). *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.
- Folt, C. L. & Schulze, P. (1993). Spatial patchiness, individual performance and predator impacts. *Oikos* **68**, 560–566.
- Folt, C. L., Nislow, K. H. & Power, M. E. (1998). Scale considerations in Atlantic salmon research. *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 1–14.
- Good, S. P., Dodson, J. J., Meekan, M. G. & Ryan, D. A. J. (2001). Annual variation in size-selective mortality of Atlantic salmon fry. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1187–1195.
- Grant, J. W. A., Steingrímsson, S. O., Keeley, E. R. & Cunjak, R. A. (1998). Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 181–190.
- Gustafson-Marjanen, K. I. & Dowse, H. B. (1983). Seasonal and diel patterns of emergence from the redd of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 813–817.
- Henderson, J. N. & Letcher, B. H. (2003). Predation on stocked Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 32–42.
- Hendry, A. P., Letcher, B. H. & Gries, G. (2003). Estimating natural selection on stream-dwelling Atlantic salmon: implications for the restoration of extirpated populations. *Conservation Biology* **17**, 795–805.
- Kennedy, G. J. A. & Strange, C. (1986). The effects of intra- and inter-specific competition on the survival and growth of stocked juvenile Atlantic salmon and resident trout. *Journal of Fish Biology* **28**, 479–489.
- Letcher, B. H. & Terrick, T. D. (2001). Effects of developmental stage at stocking on growth and survival of Atlantic salmon fry. *North American Journal of Fisheries Management* **21**, 102–110.
- Letcher, B. H., Dubrueil, T., O'Donell, M. J., Obedzinski, M., Griswold, K. & Nislow, K. H. (in press). Effects of variation in timing and manner of fry introduction on Atlantic salmon growth, survival and life history expression. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Lloyd, M. (1967). Mean crowding. *Journal of Animal Ecology* **36**, 1–11.
- Metcalfe, N. B. (1998). The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 93–103.
- Mitchell-Olds, T. & Shaw, R. G. (1987). Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* **41**, 1149–1161.
- Nislow, K. H., Folt, C. L. & Parrish, D. L. (1999). Favorable foraging locations for age-0 Atlantic salmon: application to the restoration of populations and habitats. *Ecological Applications* **9**, 1085–1099.

- Nislow, K. H., Folt, C. L. & Parrish, D. (2000). Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. *Transactions of the American Fisheries Society* **129**, 1067–1081.
- Nislow, K. H., Sepulveda, A. J. & Folt, C. L. (2004). Mechanistic linkage of hydrologic regime to summer growth of age-0 Atlantic salmon. *Transactions of the American Fisheries Society* **133**, 79–88.
- O'Connor, K. I., Metcalfe, N. B. & Taylor, A. C. (2000). The effects of prior residence on behavior and growth rates in juvenile Atlantic salmon (*Salmo salar*). *Behavioral Ecology* **11**, 13–18.
- Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D. & Reeves, G. H. (1998). Why aren't there more Atlantic salmon? *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 281–287.
- Rincon, P. A. & Lobon-Cervia, J. (2002). Nonlinear self-thinning in a stream-resident population of brown trout (*Salmo trutta*). *Ecology* **83**, 1808–1816.
- Sinclair, A. R. E. (1989). Population regulation in animals. In *Ecological Concepts. British Ecological Society Symposium* (Cherrett, J. M., ed.), pp. 197–241. Oxford: Blackwell Scientific Publications.
- Steingrímsson, S. Ó. & Grant, J. W. A. (1999). Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. *Journal of Animal Ecology* **68**, 17–26.
- Volk, E. C., Schroder, S. L. & Grimm, J. J. (1999). Otolith thermal marking. *Fisheries Research* **43**, 205–219.
- Webb, J. H., Fryer, R. J., Taggart, J. B., Thompson, C. E. & Youngson, A. F. (2001). Dispersion of Atlantic salmon (*Salmo salar*) fry from competing families as revealed by DNA profiling. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 2386–2395.
- Whalen, K. G. & LaBar, W. (1994). Survival and growth of Atlantic salmon fry stocked at varying densities in the White River, Vermont. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2164–2169.