

A temporally stable spatial pattern in the spawner density of a freshwater fish: evidence for an ideal despotic distribution

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Abstract: We explore the causal basis for a temporally stable spatial pattern in the density of spawning individuals of a freshwater fish. Based on a comparatively long-term set of data spanning one decade, reproductively active brook trout (*Salvelinus fontinalis*) inhabiting a near-pristine river on Cape Race, southeastern Newfoundland, occupy areas of either high or low density. Compared with their low-density counterparts, high-density aggregations are typically more than 30 times denser despite occupying only 4% of the available habitat. High-density areas are characterized by slower flow and suspected groundwater or bog-water seepage, attributes likely to increase the probability of offspring survival in Freshwater River. Disparity in density between high- and low-density aggregations declined as total population size increased, a pattern consistent with the predictions of the ideal free distribution. The larger body sizes of trout in the high-density aggregations may prevent others from occupying the most preferred spawning habitat. This spatial pattern in spawner density is consistent with that predicted by an ideal despotic distribution, although we cannot discount the influence that Allee effects might have on the distributional patterns of spawning individuals at low population sizes.

Résumé : Nous explorons chez un poisson d'eau douce les bases causales d'un patron spatial temporairement stable dans la densité des individus au moment de la fraye. D'après un ensemble de données à relativement long terme prélevées au cours d'une décennie, les ombles de fontaine (*Salvelinus fontinalis*) en reproduction active dans une rivière quasiment à l'état sauvage à Cape Race, sud-est de Terre-Neuve, se retrouvent dans des zones ou de forte ou de faible densité. Par comparaison avec les rassemblements de faible densité, les rassemblements plus denses ont typiquement une densité plus de 30 fois plus élevée, alors qu'ils occupent seulement 4 % de l'habitat disponible. Les zones de forte densité se caractérisent par un débit plus faible et des infiltrations présumées d'eau souterraine ou d'eau de tourbière, des caractéristiques susceptibles d'améliorer la survie des rejetons dans la rivière Freshwater. La disparité entre les densités des rassemblements de forte et de faible densité diminue à mesure que la population augmente, un patron compatible avec les prédictions de la distribution libre idéale. Les tailles corporelles plus grandes des ombles dans les rassemblements de forte densité peuvent empêcher les autres poissons d'occuper les habitats les plus recherchés pour la fraye. Ce patron spatial de densité des reproducteurs est compatible avec les prédictions de la distribution idéale despotique, bien que nous soyons obligés de prendre aussi en considération l'influence que pourraient exercer les effets d'Allee sur les patrons de répartition des individus qui frayent aux faibles densités de population.

[Traduit par la Rédaction]

Introduction

One of the fundamental objectives of ecology is to seek explanations for patterns of spatial heterogeneity in animal density. Although considerable work has focused on causal mechanisms underlying spatial variability in fish abundance, most patterns in density have been interpreted as being reflective of a spatial concordance with the suitability of feeding resources (e.g., Tyler and Gilliam 1995). Many of these distributions have been interpreted within the theoretical constructs of the ideal free distribution (e.g., Girard et al. 2004; MacLean et al. 2005), such that animals are assumed to distribute themselves among habitats of different quality

in accordance with the latter's suitability (Fretwell and Lucas 1970; Fretwell 1972). For example, at low densities, individuals are predicted to occupy only the highest quality habitat. However, as density increases, the suitability of this habitat is assumed to decline. At the density at which the suitability of the highest-quality habitat equals the suitability of the habitat with the next-highest quality, individuals are predicted to begin occupying both habitats as overall population density increases further.

Despite its considerable potential for explaining spatial distributions of animals in the wild, little attention has been directed to exploring the degree to which spatial variability in the distribution of reproductive individuals might be ex-

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plained within the theoretical constructs of the ideal free distribution. Here, based on a comparatively long-term set of data (6 years spanning one decade), we explore the causal basis for a temporally stable spatial pattern in the density of spawning individuals of a freshwater fish. Brook trout (*Salvelinus fontinalis*) are endemic to eastern North America and spawn during autumn in egg nests, or redds. The eggs incubate in the bottom substrate during winter, whereafter the young emerge from the substrate in spring. The quality or suitability of spawning habitat appears to be related, in part, to the magnitude of groundwater seepage (e.g., Curry and Noakes 1995; Blanchfield and Ridgway 1997; Essington et al. 1998), possibly because of the latter's influence on the temperature, siltation probability, and oxygen concentration experienced by the developing embryos (Benson 1953; Blanchfield and Ridgway 2005; Warren et al. 2005). In addition to these physical attributes, we wish to use the predictions that emerge from an ideal free distribution based approach to explore the degree to which spatial variability in breeding habitat suitability might be affected by the quality and quantity of mates or by competitors for mates.

To minimize the influence of anthropogenic disturbance on spatial distribution patterns, we undertook our research on a near-pristine, riverine population of brook trout (*Salvelinus fontinalis*) at the northeastern edge of its geographical range that has been studied since the late 1980s (e.g., Hutchings 1993; Hutchings and Gerber 2002; Wilson et al. 2004). Our general goal was to seek explanations for spatial variability in the distribution of spawning brook trout. Our specific objectives were (i) to determine whether spatial differences in spawner densities are stable over time, (ii) to quantify physical differences in available spawning habitat, and (iii) to examine whether patterns in spatial variability in the density of reproductive individuals can be explained by an ideal free distribution, or a variant thereof.

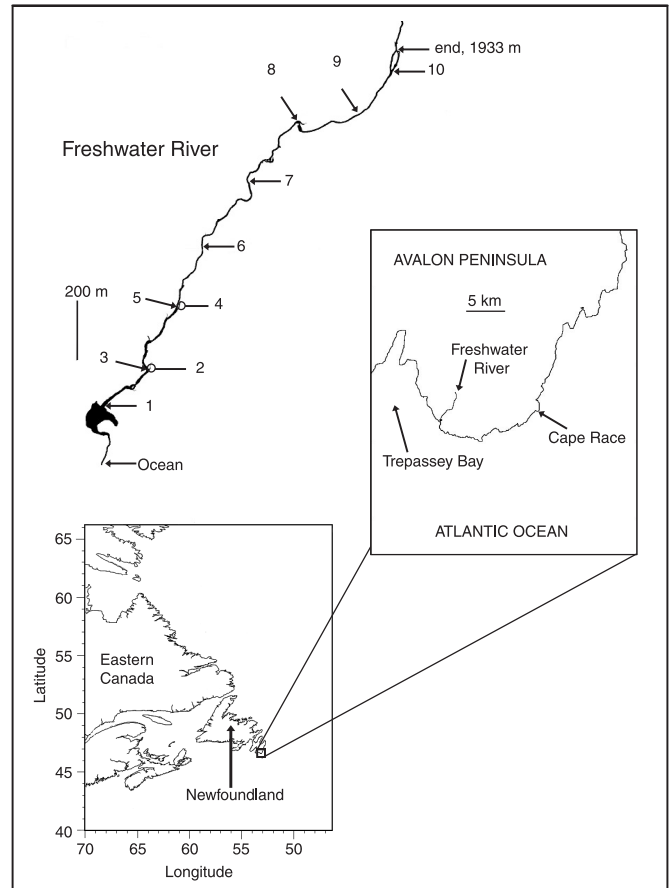
Materials and methods

Study site

Brook trout is the only fish species in Freshwater River, southeastern Newfoundland (Fig. 1). The river flows for 4.5 km across a subarctic barren and is almost entirely comprised of riffles. It is unaffected by anthropogenic disturbance, there is virtually no soil in the catchment, and there is very little fine sediment in the river. Immigration from other populations is physically impossible (a 50 m cliff separates the river from the sea). Natural predators of trout are absent and there is no fishing mortality (Hutchings 2006). On average, individuals mature at young ages (2–3 years) and small sizes (80–100 mm) (Hutchings 1993). Females have low fecundity but produce large eggs (fewer than 100 eggs of 4–5 mm in diameter) and have relatively high reproductive investment (gonadosomatic indices of 15%–20%). Overwinter survival of postreproductive individuals is low (10%–15%) (Hutchings 1994).

Based on three years (1987–1989) of observational data on the distribution of redds (J.A. Hutchings, unpublished data), brook trout spawn throughout Freshwater River. The redds comprise two forms. The first is identified by areas of disturbed gravel created by females during the construction of their egg nests. The second is identified by the presence

Fig. 1. Freshwater River and its geographic location in relation to eastern Canada. The downstream boundaries of each of the 10 sampling sections are shown. The study area extended between the downstream end of section 1 and ended 1933 m upriver at the upstream end of section 10.



of eggs distributed, rather than buried, at the base of pebble–cobble substrate. As reported below, substrate particle size does not vary within Freshwater River at spatial scales up to hundreds of square metres.

Sampling protocol

Brook trout were sampled during autumn in 1993, 1995–1998, and 2002 and during spring in 1994 and 1996–2000. Individuals were acquired using an electrofisher (model 12A; Smith-Root Inc., Vancouver, Washington) with single sweeps of each section being conducted annually at a constant voltage and amperage by the same individual (J.A.H.). Based on resampling of trout from cordoned sections (J.A. Hutchings, unpublished data), electrofisher capture efficiencies do not differ between riffles and flats in Freshwater River. Fish were anaesthetized with CO₂ in accordance with Canadian Council on Animal Care protocols, measured, and allowed to recover fully before release to their general area of capture. Body size was estimated as fork length measured directly on each individual and as weight estimated indirectly from sex-specific length (L) to weight (W) regressions for this population (males, $\log(W) = -4.45 + 2.77\log(L)$; females, $\log(W) = -4.84 + 2.97\log(L)$) (Hutchings 1990). All fish reported as males or females

were sexually mature, based on external characteristics (Hutchings 2006); we were unable to determine the sex of immature individuals based on external examination.

The study area was ~1.9 km in length and extended upstream from where the river enters a pond near the ocean (Fig. 1). The collection technique enabled any potential aggregations of brook trout to be identified on a very small spatial scale. Fish were documented in groups from more than 30 segments of the river, each of which was separated by short (less than 1 m) stretches of fast-flowing water. We pooled these segments into 10 sections for temporal comparisons given that the exact delineation of some of the smaller subsections was not always consistent among years. Based on the electrofisher catch data, trout were evenly distributed within each of the 10 sections such that areas of densely aggregated trout were not detected in the sections that were characterized overall by low densities of spawning individuals. Seven of the 10 sections (mean length = 265 m) were in the main channel and corresponded to the most prominent features of river morphology (Table 1). Sections 2 and 4 were relatively small (15 and 13 m long, respectively) outpockets directed upstream from the river channel into the surrounding bog (Fig. 1). Section 10 comprised the eastern channel (81 m long) bounding a small island in the middle of the river.

Habitat characteristics

Stream characteristics were quantified on 5 and 6 October 2004 during the spawning period. A stratified random sampling approach was employed such that each of the 10 sections identified in Fig. 1 contained a minimum of 11 sample sites. In the larger sections, there was one sample site for every 10 m of stream length. The position of each of these sites was randomly selected as a distance upstream (1 m bins) from the downstream boundary of each section. At each sample site, data were obtained from a random selection of the midpoint of the left, center, or right third of the stream width.

At each sample site, we measured stream width and depth to the nearest centimetre and water temperature to the nearest 0.1 °C. Water current ($\text{cm}\cdot\text{s}^{-1}$) was estimated by recording the time taken for an orange to float to the sampling site from a location 2 m upstream. Substrate was scored to an index of coarseness, using a modified Wentworth scale (Bain et al. 1985). The categories were as follows: 0, vegetation; 1, sand, silt, or clay; 2, gravel (2–16 mm); 3, pebble (17–64 mm); 4, cobble (65–256 mm); 5, boulder (>256 mm); and 6, bedrock. A grid containing four 15 cm × 15 cm squares was placed at each sample site and the dominant substrate category in each square was recorded.

Statistical analyses

Density was estimated as the number of fish captured per unit area of stream channel within each section, using the mean width and length data reported in Table 1 (lengths of sections 2 and 4 are given above). Density differences among river sections were analyzed using analysis of variance (ANOVA) and Tukey post-hoc analyses to determine whether sections could be grouped into categories. These analyses indicated that three sections could be grouped as high-density spawning aggregations and seven sections as

Table 1. Physical characteristics of the 10 study sections in Freshwater River, Newfoundland.

Section	Distance upstream of river mouth (m)	N	Mean width (m)	Mean depth (cm)	Mean temperature (°C)	Mean current ($\text{cm}\cdot\text{s}^{-1}$)	Mean relative particle size	Mean relative particle variability
1	0–230	23	3.1±1.0	23±6.8	13.8±0.0	37±12.4	2.4±2.2	0.47±0.81
2	230	11	2.0±0.7	25±3.4	10.2±0.6	2±0.0	4.1±0.4	0.47±0.43
3	230–489	23	2.9±0.9	24±9.6	13.8±0.0	32±9.4	2.8±1.8	0.37±0.69
4	489	11	1.9±0.3	25±5.5	10.1±0.8	13±9.0	1.9±1.5	0.99±0.96
5	489–742	25	2.6±0.4	23±9.8	13.8±0.0	35±8.9	3.8±1.5	0.44±0.63
6	742–1102	36	2.7±0.8	25±8.6	13.8±0.1	33±12.5	3.4±1.5	0.56±0.86
7	1102–1398	29	2.5±0.5	24±8.6	13.8±0.0	33±13.0	1.5±1.9	0.36±0.81
8	1398–1698	27	1.9±0.5	25±6.6	13.3±0.1	38±11.3	3.5±1.3	0.67±0.93
9	1698–1852	15	2.6±0.8	24±8.4	13.3±0.1	31±8.5	3.5±1.6	0.43±0.74
10	1852–1933	12	2.9±1.3	18±9.4	12.5±0.5	20±10.0	3.5±2.0	0.35±0.45

Note: Sections 2 and 4 comprise side branches off the main riverbed; section 10 comprises the eastern channel around a small island; all other sections are located within the main river channel. Sections 2, 4, and 10 were occupied by high-density spawning aggregations of brook trout (*Salvelinus fontinalis*). Relative particle size (mean coarseness) is the section average of the mean particle score within a sample site (four 15 cm × 15 cm quadrants); relative particle variability is the section average of the standard deviation in particle scores within a sample site. N is the number of locations randomly sampled in each section; section means are shown with ±1 standard deviation.

low-density spawning aggregations. The relative amount of variation in density explained by sex, aggregation category, and sections within category was determined using nested ANOVA (replicates were years). A nested ANOVA was used to determine the influence of sex, aggregation category, sections within a category, and years within section on individual fish length. Correlation analysis was used to describe changes in density of fish in high- and low-density aggregations as a function of population size. Habitat characteristics of high- and low-density areas were compared using a nested multivariate analysis of variance (MANOVA). The dependent variables were river width, depth, current velocity, temperature, substrate coarseness (mean of the four squares, no longer a rank, following Bain et al. (1985)), and substrate variability (standard deviation of the four squares, no longer a rank). The independent variables were the aggregation category and sections nested within each aggregation category. We undertook residual analyses to evaluate the assumptions implicit to parametric statistics; α was set at 0.05.

Results

Spawning aggregations

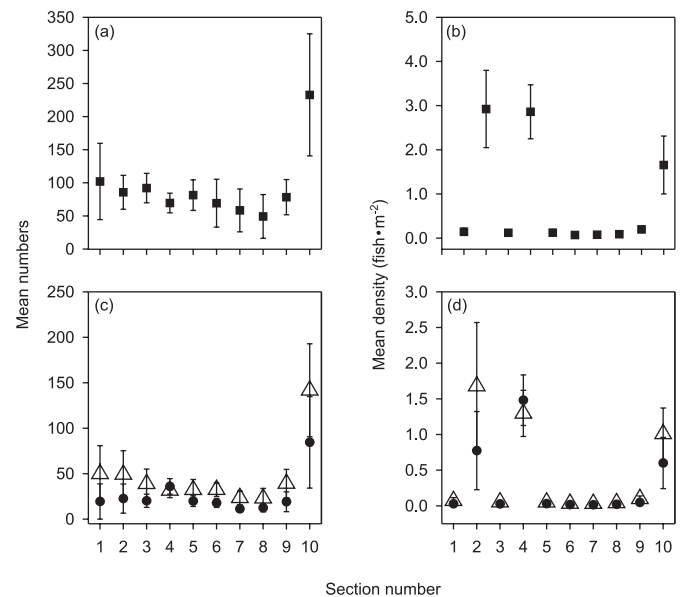
Autumn fish density differed among sections for all fish ($F_{[9,50]} = 53.46$, $p < 0.001$), mature males ($F_{[9,45]} = 23.33$, $p < 0.001$), and mature females ($F_{[9,46]} = 20.84$, $p < 0.001$) (Fig. 2). Post hoc analyses indicated that sections 1, 3, and 5–9 were consistently similar to one another but different from sections 2, 4, and 10. The former sections (1, 3, 5–9) were categorized as low-density aggregations (LAGG) and the latter as high-density aggregations (HAGG). The three HAGG areas comprised 3.9% of the total study area. Most (82%) of the variability in spawner density among years could be explained by the HAGG and LAGG categories. An additional 2% of the variability was explained among sections within the HAGG and LAGG areas, whereas sex accounted for only 1% of the variability; 14% of the variation was unexplained. On average, densities of mature brook trout were 33 times higher in the HAGG areas.

Characteristics of high- and low-density spawning aggregations

Spawners in the high- and low-density aggregations differed significantly in body size in autumn (Fig. 3), with males and females in the LAGG areas being 11% shorter (32% lighter) and 10% shorter (31% lighter), respectively, than those in the HAGG areas. Comparing the sexes, females were 15% percent longer and 53% heavier than males. All four levels of the nested ANOVA explained significant amounts of variation in body size ($p < 0.010$). Sex accounted for most of the explained variability in fish length (26%), followed by the HAGG and LAGG areas (9%), sections within the HAGG and LAGG areas (2%), and years within sections (1%).

Spawning females outnumbered spawning males, with the average sex ratio (female to male) being 2.0 in the LAGG areas and 1.6 in HAGG areas. There were, thus, relatively more males per female in the high-density spawning aggregations. An ANOVA with sections nested within the HAGG and LAGG categories and using years as replicates indicated that this difference was not quite significant

Fig. 2. Estimates of mean abundance of brook trout (*Salvelinus fontinalis*) in autumn, expressed in (a and c) numbers and (b and d) densities over 6 years in different sections of Freshwater River. Study sections, ranging from 1 (the lowermost section) to 10 (the uppermost section), are shown on the x axis. (a and b) Data for sexed and unsexed individuals are included; (c and d) reproductive males (●) and reproductive females (△) are distinguished. Data represent the mean \pm 1 standard deviation (among-year variation). Error bars are present for all means but are too small to be observed in some cases.



($F_{[1,8]} = 1.97$, $p = 0.072$). A female-biased sex ratio was evident throughout the river with the exception of one of the spawning aggregations (section 4; Fig. 2).

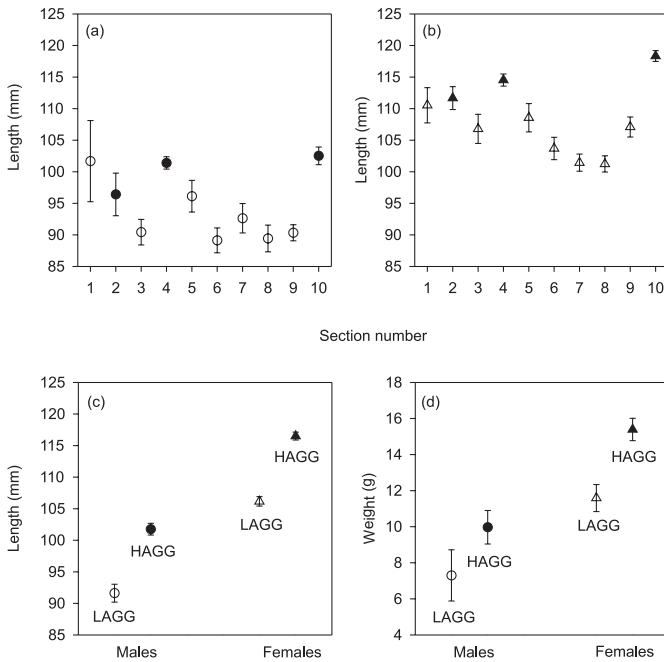
Seasonal variability in aggregation densities

Although the spatial disparity in density between the HAGG and LAGG areas in autumn was also evident in spring, the difference in density was much less pronounced (Fig. 4). Based on an ANOVA with only the HAGG–LAGG categories and sections nested within categories as the two factors (sex was excluded given that these data were not available for trout sampled in spring), 91% of the variation in density during autumn was explained by the HAGG–LAGG areas as compared with 70% during spring. On average, fish densities (all ages combined) were 29 times higher in HAGG areas than in LAGG areas during autumn, but only three times higher during spring.

Effect of population size on spatial disparity in spawner density

During the 6 years of autumn sampling, the total number of brook trout collected (including all mature and immature individuals), using the same amount of electrofishing effort, ranged between 811 and 1084 (Fig. 5). The spatial disparity in spawner density between the HAGG and LAGG areas declined significantly as the total number of fish increased ($N = 6$ years, Spearman ranked $r = -0.943$, $p < 0.020$; Fig. 5). Density increased significantly with total catch in the LAGG areas (Spearman ranked $r = 1.000$, $p < 0.010$), but tended to

Fig. 3. Mean body size of mature brook trout (*Salvelinus fontinalis*) inhabiting high-density aggregations (HAGG; solid symbols) and low-density aggregations (LAGG; open symbols) in Freshwater River. Data are separated by sex in the upper panels (a, males; b, females) and by aggregation type in the lower panels (c, fork length; d, predicted weight). Data represent mean \pm 1 standard error (a and b, among years; c and d, among sections).



decrease in the HAGG areas (Spearman ranked $r = -0.657$, $p < 0.200$).

Physical attributes of the areas occupied by high- and low-density spawning aggregations

There were significant differences in the physical attributes of the areas occupied by the high- and low-density aggregations of spawning individuals (Table 1), based on the results of a nested MANOVA (Pillai's = 0.99178; $F_{[6,3]} = 60.350$, $p = 0.003$). Post hoc nested ANOVAs indicated that high-density areas were characterized by significantly slower water current (11.8 vs. 34.1 $\text{cm}\cdot\text{s}^{-1}$; $F_{[1,8]} = 51.92$, $p < 0.001$) and lower water temperature (11.0 vs. 13.7 $^{\circ}\text{C}$; $F_{[1,8]} = 53.15$, $p < 0.001$) when compared with low-density areas. By contrast, there were no significant differences in river width ($F_{[1,8]} = 1.41$, $p = 0.263$), depth ($F_{[1,8]} = 0.95$, $p = 0.341$), substrate coarseness ($F_{[1,8]} = 0.09$, $p = 0.769$), or fine-scale substrate variability ($F_{[1,8]} = 0.82$, $p = 0.375$) between the HAGG and LAGG areas.

Discussion

Spatial patterns in the density of breeding individuals were temporally stable within a near-pristine, riverine population of brook trout over the period of at least one decade. Spawners could be distinguished as occupying areas of either high or low density, the former comprising only 4% of the river. The disparity in density between high- and low-density aggregations, the former being 13–59 times higher than the latter on an annual basis, declined as total popula-

Fig. 4. Estimates of mean abundance of brook trout (*Salvelinus fontinalis*) in spring expressed as (a) numbers and (b) densities and pooled by sex over 6 years in different river sections. Study sections, ranging from 1 (the lowermost section) to 10 (the uppermost section), are shown on the x axis. Data represent the mean \pm 1 standard deviation (among-year variation).

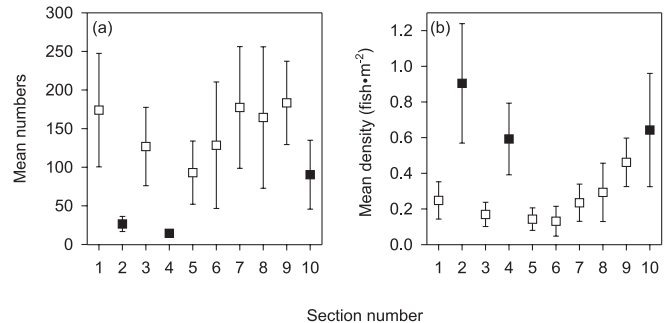
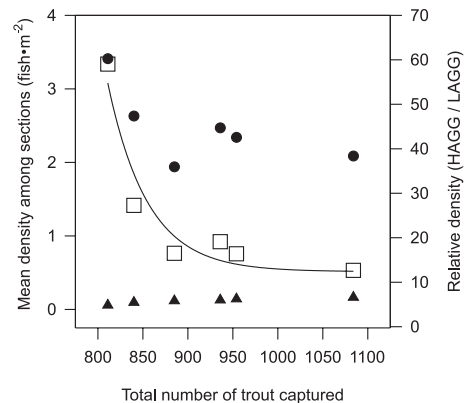


Fig. 5. Fish density as a function of population size over 6 years. Left axis: high-density aggregations (HAGG, ●); low-density aggregations (LAGG, ▲); right axis: ratio of HAGG to LAGG (□), with fitted curve.



tion size increased. Mature individuals within high-density aggregations were significantly larger than those in low-density aggregations. Although high-density areas were characterized by slower flow and lower temperatures, the latter is unlikely to be caused by the former given that numerous short segments of river contained areas of slow current but only the three short segments with high-density aggregations of brook trout were characterized by lower temperatures.

Natural selection may favour individuals that spawn in the areas where the highest densities of trout were recorded. We hypothesize that the comparatively short length of the river coupled with the mortality consequences of being displaced over a 50 m waterfall into the ocean favours females that spawn in areas of comparatively slow-moving water, thus reducing the probability of physical displacement of the young following their emergence from the egg nests. The lower temperatures in these areas may suggest the presence of the seepage of groundwater or bog water, the former having been hypothesized to enhance the survival of brook trout embryos (Curry and Noakes 1995; Essington et al. 1998). Thus, we interpret the differential currents and water temperatures in the areas occupied by the high-density spawning

aggregations to be indicative of a higher-quality spawning habitat. This interpretation is supported by our observation that the disparity in trout abundance between high- and low-density areas was an order of magnitude greater in autumn, during the spawning period, than in spring.

A key prediction of the ideal free distribution is that the disparity in density between habitats of variable quality should decline as total population size increases (Fretwell and Lucas 1970; Fretwell 1972). In accordance with this expectation, we find that the disparity in density between high and low spawner aggregations declined as total population size increased. We interpret this finding to be reflective of a greater reduction in the quality of the areas occupied by the high-density aggregations. As density increases, competition for spawning sites by females and for mates by males would also be expected to increase. With increasing population size, females might be favoured to forgo preferred spawning sites, and males to forgo the increased density of potential mates, by increasingly spawning in low-density aggregation areas. There is qualitative evidence to support our prediction that the quality of spawning habitat in the HAGG areas declines with increasing density. These three sections are the only areas in which redd superimposition, or nest re-use, has been observed in Freshwater River (J.A. Hutchings, unpublished data).

However, if the spawning habitat available to high-density aggregations is superior to that available to low-density aggregations, we would not have anticipated an absolute (albeit not statistically significant, possibly because of limited statistical power) decline in the density of the high-density aggregations with increased population size. Such a decline, if biologically meaningful, might be indicative of an Allee effect, reflected by increases in individual fitness (and population growth rate) with increases in population density (Courchamp et al. 1999; Stephens and Sutherland 1999). In the absence of Allee effects, as population size increases, individuals are predicted to settle in different habitats at a rate that maintains equal suitability. However, when present, once a secondary habitat is occupied, it may become advantageous for individuals to vacate the first habitat and to occupy another or for newly arriving individuals to settle alternative secondary habitats at a higher rate (Fretwell 1972; Greene and Stamps 2001). Thus, in the presence of an Allee effect, a small increase in population size has the potential to alter spatial distributional patterns dramatically (Fretwell 1972). Within the context of our study, as population size increases from a low level, fitness might also be expected to increase because of increased availability of potential mates to males and because of the fitness advantages to females concomitant with increased genetic and phenotypic variability of potential mates.

Two assumptions of the ideal free distribution are that individuals are free to occupy the habitat most suitable to them and that all individuals within a habitat gain equal fitness benefits by being there (Fretwell and Lucas 1970; Fretwell 1972). However, when dominant individuals occupy the highest-quality habitats to the exclusion of subordinates, the distribution is no longer considered “free” and is often referred to as being despotic (Fretwell 1972).

If spawning brook trout are distributed in accordance with an ideal free distribution, we would have predicted the aver-

age size of individuals to have been the same in the high- and low-density aggregations. However, under an ideal despotic distribution, individuals may compete for preferred spawning sites such that areas of higher density are predicted to contain individuals that have a competitive advantage. Mature brook trout in the high-density aggregations in Freshwater River were significantly larger than their low-density counterparts. If larger size is associated with dominance (Hutchings 1991; Hakoyama and Iguchi 2001), then individuals may not be “free” to occupy habitats of variable suitability. Given our observation that high-density spawners are significantly larger than low-density spawners, we interpret our results as being consistent with the hypothesis that the spawning distribution of brook trout can be explained as an ideal despotic distribution.

Although ideal free and ideal despotic distributions have been invoked to explain spatial patterns in animal densities (Haugen et al. 2006), most studies have focused on the degree to which spatial patterns in density can be explained by spatial variability in foraging activity and (or) food resources (e.g., Tyler and Gilliam 1995; Girard et al. 2004; MacLean et al. 2005), rather than by spatial variability in the quality of mates and breeding habitat. Hakoyama and Iguchi (2001), for example, argued that the spatial distribution of amago trout (*Oncorhynchus masou ishikawae*) was despotic because of the ability of larger individuals to exclude smaller fish from high-quality food patches under laboratory conditions. Based on a field manipulation experiment, Calsbeek and Sinervo (2002) concluded that the dominant morph of side-blotched lizards (*Uta stansburiana*) was better able to modify its distribution to maximize territory quality, a finding consistent with the expectations of a despotic distribution.

In summary, we conclude that spatial patterns in spawner density of a riverine salmonid are consistent with those predicted by an ideal despotic distribution. Habitat quality varies with both the physical and biological attributes of potential spawning areas. Higher-quality habitats in this river appear to be characterized by slow water flow and groundwater or bog-water seepage. At small population sizes, we predict that females would prefer these areas to increase the survival probabilities of their offspring and that males would prefer these areas because of increased availability of potential mates. Allee effects might also affect the distributional patterns of spawning brook trout at low densities, although our data are limited in this regard. As population size increases, it appears as though lower-quality spawning areas have an increased probability of being occupied, indicative presumably of a decline in the suitability of the preferred spawning areas. There is also reason to believe that higher-quality individuals prevent others from occupying the most preferred spawning areas. The temporal stability of spawner densities over a 10-year period suggests that observed distributional patterns do not represent spurious responses to short-term, environmental variation.

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