

A field test of simple dispersal models as predictors of movement in a cohort of lake-dwelling brook charr

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Summary

1. Dispersal can be a major determinant of the distribution and abundance of animals, as well as a key mechanism linking behaviour to population dynamics, but progress in understanding dispersal has been hampered by the lack of a general framework for modelling dispersal.
2. This study tested the capacity of simple models to summarize and predict the lake-wide dispersal of an emerging cohort of young-of-the-year brook charr *Salvelinus fontinalis*, over 12 surveys conducted during a 2-month period.
3. The models are based on two types of dispersal kernel, the normal distribution from a simple diffusion process, and a Laplace distribution depicting exponential decay of the frequency of dispersers away from the point of origin. In all, four models were assessed: one-group diffusion (D1S) and exponential (E1S) models assuming homogeneous dispersal behaviour within the cohort, and two-group diffusion (D2S) and exponential (E2S) models accounting for intrapopulation differences in dispersal between sedentary and mobile individuals.
4. A rigorous cross-validation, based on calibrating the models to the distributions from the first two surveys only and then validating them on the remaining 10 distributions, was used to compare model predictions with observed values for five properties of the dispersal distributions: counts in individual shoreline sections; mean lateral displacement, variance and kurtosis of displacements; and the percentage of long-distance dispersers.
5. Substantial intrapopulation heterogeneity in dispersal behaviour was apparent: 83% of all individuals were estimated to be sedentary and the remainder mobile. Remarkably, the two-group exponential model E2S – calibrated to data from only two surveys conducted 3.5 and 8.5 days after the beginning of emergence – predicted reasonably well all properties of the spatial distribution of the cohort until the end of the study, 7 weeks later.
6. Standardized measures of mobility derived from simple models may lead to better understanding of population dynamics and improved management. Specifically, the ability to accurately predict long-distance dispersal may be critical to assessing population persistence and cohort strength whenever key habitats, such as refugia or productive areas supporting a large proportion of the cohort, are sparsely distributed or distant from the point of origin.

Key-words: diffusion and exponential mixtures, intrapopulation heterogeneity, Gaussian and Laplace distributions, leptokurtic dispersal kernel, *Salvelinus fontinalis*.

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Introduction

Dispersal can be a major determinant of the distribution and abundance of animals, as well as a key mechanism linking behaviour to local and regional population dynamics (Clobert *et al.* 2001). Dispersal plays a fundamental role in regulating local densities, allowing for population spread and redistribution, and ensuring population persistence in highly variable environments (Stacey & Taper 1992). Despite this broad ecological importance, progress in predicting and quantifying dispersal has been hampered by the lack of a general framework for modelling dispersal (Turchin 1998). However, parameter values from fitted models can be used as standardized measures of dispersal for comparing mobility across populations or species and examining the ecological determinants and evolutionary implications of mobility (Rodríguez 2002; Skalski & Gilliam 2003).

Many studies of movement have focused on modelling the dispersal kernel describing the probability distribution of displacement distances from a known point of origin (e.g. Porter & Dooley 1993; Kot, Lewis & van den Driessche 1996). Two continuous probability distributions, the normal and negative exponential, are commonly used as approximations to the decline in frequency of observations as dispersal distance increases away from a source of dispersers (Turchin 1998; Okubo & Levin 2001). Use of the normal distribution as a dispersal model derives from the time-dependent solution of the random walk equation describing diffusive spread.

In contrast to the normal, or diffusion, model, the negative exponential model considers the spatial distribution that arises after a fixed time interval. Various biological mechanisms may generate negative exponential distributions, e.g. when local competition drives dispersal, opposing a natural tendency for philopatry, and animals settle as soon as they find an uncontested patch of suitable habitat (Porter & Dooley 1993). The close connections between diffusion and exponential models sometimes go unrecognized. Exponential dispersal kernels can be derived by modifying diffusion models in various ways, for example, by adding a term for advection toward the origin, or specifying an appropriate compound distribution (Okubo & Levin 2001). Diffusion and exponential models therefore have mechanistic underpinnings and a stronger conceptual grounding than do more phenomenological models (Turchin 1998).

Two key features of dispersal kernels, the kurtosis and the shape of the tails of the distribution, have received particular attention. Dispersal distributions are often strongly leptokurtic because displacements over very short or very long distances are more frequent, and those over intermediate distances more rare, than expected under a normal distribution (Kot *et al.* 1996). Both the diffusion model (mesokurtic; kurtosis = 0) and the negative exponential model (leptokurtic; kurtosis = 3) may be poor fits if the observed kurtosis

greatly exceeds 3. Leptokurtic dispersal is often modelled by incorporating intrapopulation heterogeneity in movement rates in two-group models that combine separate dispersal distributions, one for a sedentary component of the population, the other for a mobile component (Skalski & Gilliam 2000; Rodríguez 2002).

A variety of ecological processes depend critically on the shape of the tails of the dispersal kernel, which determines the frequency of long-distance dispersal events. For example, such events have important implications for propagation velocity of invading species, persistence in fluctuating and heterogeneous environments, preservation of metapopulation dynamics in fragmented landscapes, maintenance of genetic diversity, and population responses to climate change (Stacey & Taper 1992; Kot *et al.* 1996; Latore, Gould & Mortimer 1999; Cain, Milligan & Strand 2000; Clobert *et al.* 2001; Clark *et al.* 2003). Consequently, the ability of dispersal models to accurately characterize the frequency of long-distance dispersers is of theoretical interest (Paradis, Baillie & Sutherland 2002). One-group models that assume homogeneous dispersal behaviour have thin kernel tails and often underestimate the probability of long-distance movements (Kot *et al.* 1996; Skalski & Gilliam 2000; Rodríguez 2002), potentially leading to misinterpretation of the role of dispersal at landscape and larger scales. In contrast, two-group models have heavier tails that decline more slowly with distance and can therefore hold a greater proportion of the dispersing population.

For many animal species, natural dispersal is difficult to monitor and model. Common limitations in field studies include the difficulty of delimiting the population and potential range of dispersal, the need for handling the organisms in mark–recapture studies, and the small sample sizes and number of dispersal distributions examined. However, the natal dispersal of lake-dwelling brook charr *Salvelinus fontinalis* (Mitchill) has simplifying characteristics that facilitate the application and testing of dispersal models. Spawning often occurs at only one littoral location with groundwater upwelling, providing a single source of natal dispersers for the entire lake (Ridgway & Blanchfield 1998). The cohort emerges gradually from the spawning site and spreads slowly around the lake margins over a period spanning approximately 2 months (Snucins, Curry & Gunn 1992; Curry, Noakes & Morgan 1995). High rates of predation in open waters result in restriction of young of year (YOY) dispersal to a shallow corridor of inundated shoreline around the lake margins, where large numbers of fish can be readily observed by snorkelling during the emergence and dispersal of a cohort (Biro & Ridgway 1995; Biro, Ridgway & Noakes 1997). Therefore, frequency distributions of dispersal distance can be obtained repeatedly without marking the fish, and movement can be conveniently modelled along a single spatial dimension. To our knowledge, this unique pattern of dispersal of a whole cohort over its entire range has not been studied before in any vertebrate

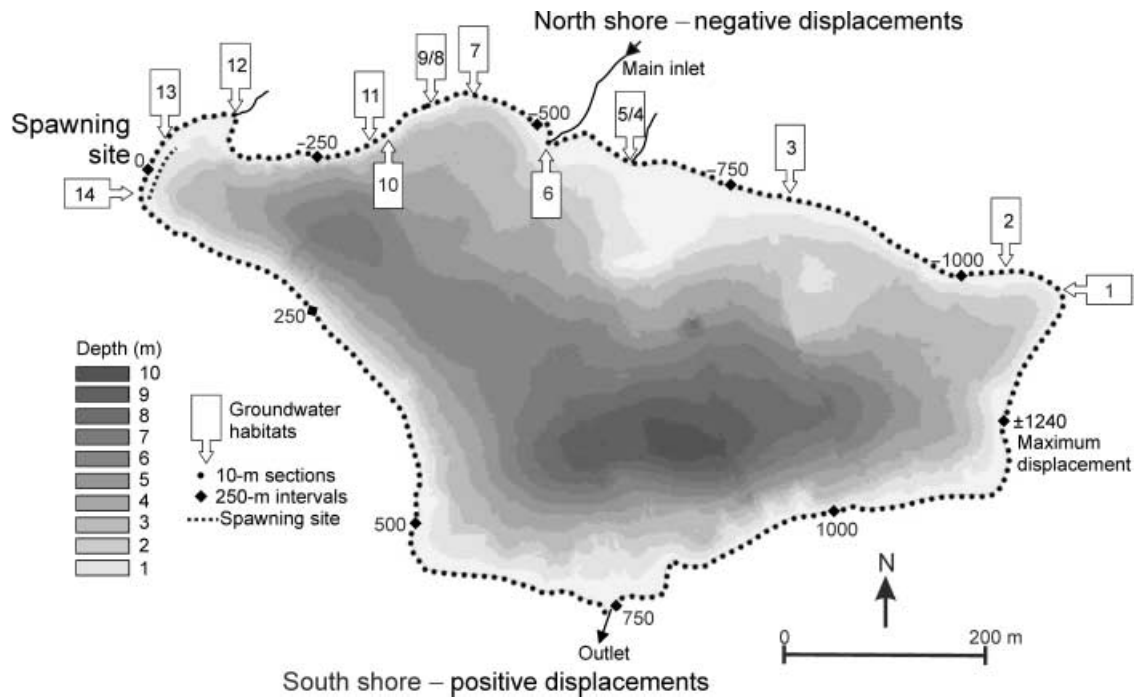


Fig. 1. Bathymetric map of Mykiss Lake, showing the single spawning site from which brook charr dispersed, groundwater sources, inlet and outlet streams. Shoreline sections (10 m) covering the lake perimeter (2480 m) and displacement distances at 250-m intervals are shown.

population. Previous studies have documented fine-scaled intrapopulation variation in movement behaviour of dispersing YOY salmonids in still-water environments (McLaughlin, Grant & Kramer 1992; Biro & Ridgway 1995; Biro *et al.* 1997), providing further motivation for comparing one- and two-group dispersal models in this system. Additionally, knowledge about the tails of the dispersal distribution is helpful in assessing whether YOY salmonids can avoid detrimental warm temperatures by reaching cool groundwater refugia distant from the spawning site.

The present study examines the usefulness of simple dispersal models for summarizing and predicting the lake-wide dispersal of an emerging cohort of YOY brook charr, over 12 surveys conducted during a 2-month period. The models are based on two types of dispersal kernel, the normal distribution arising from a simple diffusion process, and a Laplace distribution depicting exponential decay of the frequency of dispersers away from the point of origin. In all, four models were assessed: one-group diffusion and exponential models assuming homogeneous dispersal behaviour, and two-group diffusion and exponential models accounting for intrapopulation heterogeneity. The models assume that dispersal proceeds from an instantaneous point source, along a single spatial dimension, independently of habitat heterogeneity, and at rates determined by constant diffusion or displacement coefficients. Behavioural interactions among individuals and density dependence are not considered. The two-group models allow for intrapopulation heterogeneity in dispersal rates, but assume that the proportions of

sedentary and mobile individuals are fixed. A cross-validation approach based on calibrating the models to the distributions from the first two surveys only and then validating them on the remaining 10 distributions was used to evaluate model predictions of the spatial distribution of fish counts and four aggregate measures of dispersal. The robustness of predictions to violation of model assumptions was also assessed.

Methods

STUDY SITE AND DATA COLLECTION

The dispersal of a cohort of YOY brook charr along the lake shoreline was studied in Mykiss Lake (2480 m perimeter, 23.5 ha), Algonquin Provincial Park, Ontario, Canada (45°40' N 78°13' W) in the spring of 2003. Mykiss Lake has an unexploited, self-sustaining population of brook charr with high densities of YOY. A single littoral spawning site spans approximately 60 m of shoreline on the west end of Mykiss Lake (Fig. 1). Two types of groundwater habitat along the north shore of the lake act as thermal refugia during the summer: three seasonally flowing inlet streams, fed primarily by shallow groundwater, and 14 zones of groundwater discharge (Borwick, Buttle & Ridgway 2006; see Fig. 1). None of the inlet streams hold resident populations of brook charr, but during the spring one stream drains a smaller lake holding a small population. A permanent block net was set across this stream at the outlet of the smaller lake to prevent downstream migration into Mykiss Lake. Temperatures in groundwater

Table 1. Date, time since beginning of emergence, shoreline temperature in nongroundwater habitat (daily mean), total counts of fish over all sections sampled, fraction of dispersal range sampled (F), and estimated cohort size (total counts $\times F^{-1}$) for 12 lake-wide surveys of YOY brook charr

Survey	Date	Time (days)	Temperature ($^{\circ}\text{C}$)	Total counts	Fraction sampled	Cohort size
1	26, 27 April	3.5	6.7	64	1	64
2	30 April; 2, 3 May	8.5	8.6	218	1	218
3	6, 7 May	13.5	10.9	365	1/3	1095
4	10, 11 May	17.5	14.0	1064	1/2	2128
5	14, 15 May	21.5	12.3	1045	1/2	2090
6	19, 20 May	26.5	15.9	737	1/3	2211
7	23, 24 May	30.5	14.8	703	1/3	2109
8	27, 28 May	34.5	15.3	673	1/3	2019
9	2, 3 June	40.5	15.5	359	1/3	1077
10	8, 9 June	46.5	18.0	372	1/3	1116
11	14, 15 June	52.5	18.3	332	1/3	996
12	20, 21 June	58.5	21.2	250	1/3	750

habitats and at a single shoreline location without groundwater discharge (260 m from the centre of the spawning site, north shore), were recorded at 8-min intervals (StowAway TidbiT loggers, Onset Computer, Bourne, MA, USA).

The lake shoreline was delimited into 248 sections, each 10 m in length, which collectively covered the entire lake perimeter (Fig. 1). Field observations began on 26 April, which closely coincided with the start of the emergence period (as determined by field observations of embryonic YOY with residual yolk sac), and continued until 21 June. Over this period, the spatial distribution of YOY was determined 12 times, in surveys conducted 3–5 days apart, by visually counting YOY brook charr while snorkelling the lake perimeter (Table 1). Counts were made between 08.00 and 18.30 h by a single observer (MFC) that moved across 10-m sections, staying within 1 m from the edge of the inundated shoreline vegetation and woody debris, and called counts through the snorkel to a second observer floating offshore in a canoe. YOY in Mykiss Lake are consistently found close to the surface and to structural cover such as fallen trees projecting offshore over deeper water, and do not appear to be disturbed by the presence of an observer (Biro & Ridgway 1995). Fallen trees were carefully surveyed by swimming out from shore on one side and returning to shore on the other. YOY in shallow, inaccessible areas were counted from above the surface while the observer knelt on the substrate. Sampling time per section was 5.45 ± 2.16 min (mean \pm SD for 24 sections without offshore trees). All YOY counted within a given section were assigned a common dispersal distance, measured from the midpoint of the section to the midpoint of the spawning site.

Counts were made in all sections along the full range of the spatial distribution of YOY in the first two surveys. Once the distribution of YOY covered the entire shoreline, it was not feasible to inspect carefully all 248 sections within a short period of time. Therefore, for surveys 3–12, counts were made only for a subsample of sections from strata of equal length distributed uni-

formly over the entire lake perimeter. In surveys 4 and 5, two sections were randomly sampled from individual strata comprising four sections each, and in the remaining surveys one section was randomly sampled from strata comprising three sections each, so that either one-half or one-third of the lake perimeter was sampled in each of these surveys (Table 1). Sampling began at a randomly selected section and continued around the lake perimeter in a randomly determined direction. Although YOY did migrate up the three inlet streams, only YOY observed within the boundaries of the lake shoreline were considered in this study. A permanent net set across the Mykiss Lake outlet was checked regularly and used to monitor emigration. When the 10-m section encompassing the outlet was sampled in one of the 12 surveys, captured YOY were assigned the dispersal distance corresponding to that section (735 m) and released to the stream.

To assess the accuracy of the counting technique, 52 10-m sections distributed around the lake were sampled twice, first at normal search speed and again, 5 min later, using as much time as necessary to ensure detection of all YOY present. Sections sampled twice had representative levels of cover and first sample counts covering the full range of counts recorded in this study. Because accuracy of counts declined with increasing YOY abundance, a fitted power function was used to correct all counts from the 12 surveys: corrected count = 0.85 (original count) $^{1.20}$; $r^2 = 0.97$; $n = 52$; $P < 0.0001$.

To confirm that YOY dispersal was primarily along the lake shoreline rather than in deeper water, fine-meshed gillnets (12.5 mm stretched mesh, 0.1 mm filament diameter; Lundgrens Fiskredskap, Stockholm, Sweden) were set at the west end of Mykiss Lake, where YOY densities were highest. Six gillnets (10 m \times 1.5 m) were set along the bottom of the lake and perpendicular to the shoreline (depth range: 0.5–4 m), from 16.00 h on 22 May to 10.00 h on 23 May. This procedure sampled the area beyond the edge of the inundated shoreline vegetation, where YOY brook charr were observed most frequently in a study using nets of the same specifications

(Venne & Magnan 1995). A similar survey was conducted on 19 and 20 July to determine whether disappearance of YOY from most of the lake shoreline by the last survey in late June could be due to movement to deeper, cooler waters. Thirteen nets were set on the bottom throughout the lake in offshore regions (depth range: 3–6 m). No YOY brook charr were captured in netting surveys in May or July, although cyprinids of similar size as YOY (May only) and numerous 1- and 2-year-old brook charr were caught (May and July). These observations, together with those of Biro & Ridgway (1995) and Biro *et al.* (1997) strongly suggest that the YOY cohort was restricted to the shallow shoreline of Mykiss Lake throughout the 12 surveys.

DISPERSAL MODELS

The models evaluated here were based on two types of dispersal kernel, $f(x,t)$, specifying the probability density function of dispersers along a single dimension of space, x (distance from the point of origin), at different times, t . The first type of kernel is the normal distribution arising from a simple diffusion process:

$$f(x,t) = \frac{1}{2\sqrt{\pi Dt}} \exp\left(\frac{-x^2}{4Dt}\right)$$

where D is a diffusion coefficient ($\text{m}^2 \text{day}^{-1}$) quantifying the rate of spread from the point of origin. The second type of kernel, depicting exponential decay of the frequency of dispersers to either side of the point of origin, is a Laplace distribution modified to allow for temporal variation in δ , the mean lateral displacement of dispersers (m):

$$f(x,t) = \frac{1}{2\delta_t} \exp\left(-\frac{|x|}{\delta_t}\right)$$

specifically, $\delta_t = \delta_0 t^r$, where δ_t is the mean lateral displacement up to time t (d), δ_0 is the mean lateral displacement 1 day after the onset of dispersal, and the exponent r determines how the lateral displacement changes through time. For both types of kernel, the distributions are symmetric about the origin.

The kernels described above are one-group models assuming that the population comprises a single component that is homogeneous with regard to movement behaviour, i.e. that all individuals share a common displacement parameter. To account for potential heterogeneity arising from the presence of population components differing in movement behaviour, dispersal kernels were also combined as discrete mixtures of two distributions, one for sedentary individuals and the other for mobile individuals, to form two-group models (Skalski & Gilliam 2000; Rodríguez 2002) of the general form:

$$f(x,t) = p g_s(x,t) + (1-p) g_m(x,t)$$

where $f(x,t)$ is the dispersal kernel for the entire population, p is the proportion of sedentary individuals in

the population (assumed constant through time), $g_s(x,t)$ is the dispersal kernel for sedentary individuals, and $g_m(x,t)$ is the dispersal kernel for mobile individuals. In all, four dispersal models were assessed: the one-group diffusion (D1S) and exponential (E1S) kernels, and the two-group diffusion (D2S) and exponential (E2S) kernels. For the D2S model, the diffusion kernels g_s and g_m had different diffusion coefficients, whereas for the E2S model the exponential kernels g_s and g_m had different mean lateral displacements but a common exponent r . Although both diffusion and exponential models can account for asymmetrical dispersal about the origin (e.g. by incorporating a term for directional drift in advection–diffusion models; Skalski & Gilliam 2000), only symmetric models were considered here because there was little evidence for directed dispersal of YOY brook charr in Mykiss Lake (see Results, below).

Because the lake perimeter forms a closed loop, discrepancies between the spatial distribution predicted assuming an infinite domain of dispersal and that observed in the lake can result from ‘looping’ movement of fish beyond ± 1240 m from the spawning site, the maximum displacement observed (Fig. 1). Looping movements appeared to be negligible only for the first two surveys (see Results, below). Therefore, prior to calculation of all predicted values, the dispersal kernels were adjusted to account for truncation of the spatial range of observation at 1240 m, i.e. for the fact that displacements > 1240 m would not have been recorded correctly. Compound probability densities over the truncated range, $h(x,t)$, were obtained for all models as the sum of densities for displacements that do not traverse the boundary 1240 m from the spawning site, $f(x)$, those that traverse exactly once, $f(x \pm L)$, and those that traverse exactly twice, $f(x \pm 2L)$:

$$h(x,t) = \sum_{i=-N}^N f(x + iL,t); \quad -\frac{L}{2} \leq x \leq \frac{L}{2},$$

where L is the lake perimeter and index i takes integer values (Fig. 2). For all models, the area under the density function $h(x,t)$ was always > 0.999 when $n = 2$. The compound densities $h(x,t)$ model the spatial distribution of the whole cohort along the truncated range of observation and are used for model comparisons, but truncation is an arbitrary observational constraint the importance of which varies from lake to lake as a function of perimeter length. Therefore, substantive ecological interpretation of dispersal behaviour should be based on the dispersal kernels $f(x,t)$, which better reflect how the fish would actually move along an unbounded domain of dispersal, independently of truncation.

MODEL FITTING AND CROSS-VALIDATION

A two-step approach based on cross-validation was used to assess model predictions. The lake-wide dispersal distributions from the 12 surveys were split into two subsets, a calibration subset consisting of the distributions

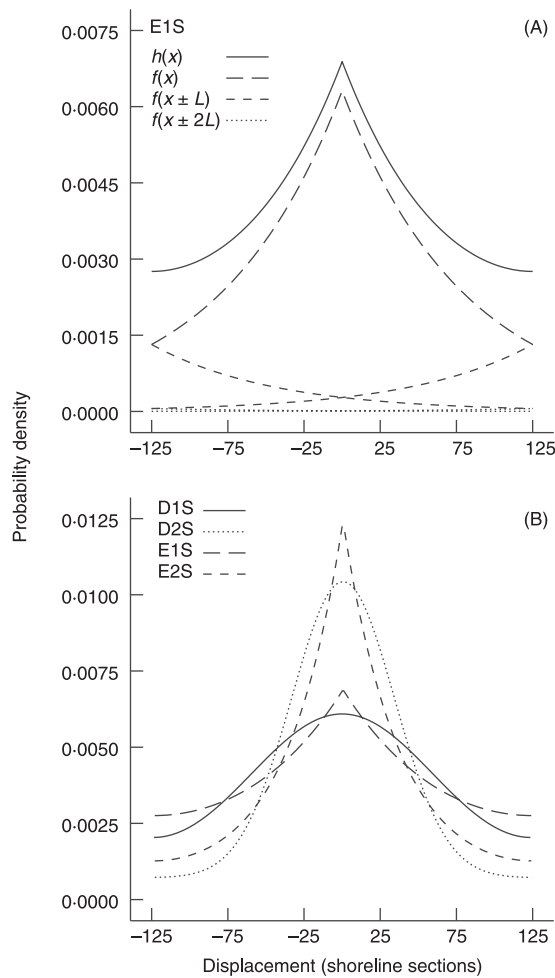


Fig. 2. (A) Compound dispersal kernel, $h(x)$, arising from 'looping' movement beyond the boundary at ± 1240 m ($L/2$) from the spawning site. The curves depict predicted densities for the one-group exponential model, E1S, on survey 12. (B) Predicted compound kernels for the one- and two-group diffusion and exponential models on survey 12. Displacements in the north (negative values) and south (positive values) directions are given in shoreline sections (10 m).

from the first two surveys only, and a validation subset consisting of the remaining 10 distributions. In the calibration step, parameter estimates for the four models were obtained by minimizing the sum of negative log-likelihoods over all of the observed displacement distances simultaneously for the first two surveys. Then, keeping these parameter values fixed, the models were used to predict the dispersal distributions for the 10 remaining surveys, i.e. predictions for surveys 3–12 were projections based on model fits to data from only the first two surveys. A similar approach was used in a previous study of fish dispersal, in which models calibrated to data from the first two of four surveys were validated against data from the last two surveys (Skalski & Gilliam 2000).

In the validation step, model predictions were compared with observed values for five properties of the dispersal distributions: (1) counts of YOY brook

charr in individual shoreline sections; (2) mean lateral displacement (the mean, or first moment, of distances from the point of origin, in absolute value, i.e. ignoring dispersal direction); (3) variance of displacements (the second moment of distances from the point of origin, which measured spatial spread of the cohort from the spawning site); (4) kurtosis of displacements (g_2 , the fourth moment of distances from the point of origin, standardized for variance, a measure of the shape of the 'shoulders' of the distribution); and (5) the percentage of YOY brook charr in the 'tail' region of the dispersal distributions, defined arbitrarily as the 12 shoreline sections most distant from the spawning site in either direction around the lake (24 sections in all, covering 10% of the lake perimeter; -1120 to -1240 m and 1120 to 1240 m; Fig. 1).

For the first property of the dispersal distributions, counts in individual shoreline sections, model performance was assessed by comparing the relationship between observed and predicted counts for each of the 12 surveys with that expected if model predictions were unbiased (corresponding to a 1 : 1 relation). Predicted counts for a section x metres away from the spawning site at time t , $C_{\text{pred}}(x, t)$, were obtained from the relation:

$$C_{\text{pred}}(x, t) = \frac{H(x, t)}{\sum_j H(x, t)} \sum_j C_{\text{obs}}(x, t),$$

where $H(x, t)$ is the proportion obtained from the compound density function $h(x, t)$, and $C_{\text{obs}}(x, t)$ the observed count, at position x and time t . The summation index j runs through all sections examined by the snorkeller at time t . This formula apportions the total counts spatially so that the proportion of counts at a given position matches that derived from the compound density function. For the four remaining properties of the dispersal distributions, models were evaluated by comparing the temporal trajectories of observed and predicted values and assessing the mean error of prediction over surveys 3–12. Because the variance of the observed values and the deviation between observed and predicted values tended to increase with the magnitude of the observed values, two measures of error incorporating different weighting functions for the deviations were used; weighted squared error: $w(x_{\text{obs}} - x_{\text{pred}})^2$, where w is inversely proportional to the variance of x_{obs} , and relative error: $|x_{\text{obs}} - x_{\text{pred}}|/x_{\text{obs}}$.

Variations and confidence intervals for observed values were obtained by assuming an underlying binomial distribution for proportions, and by bootstrapping for statistical moments (percentile method; 10 000 draws). Confidence intervals for model parameters and predicted trajectories were obtained by bootstrapping based on individual draws that randomly sampled 64 observations from survey 1 and 218 from survey 2 (cf. Table 1), to mimic the actual sampling scheme. For all models, the predicted statistical moments and proportion of YOY under the tails of the compound density function $h(x, t)$ were obtained by numerical integration. Calculations

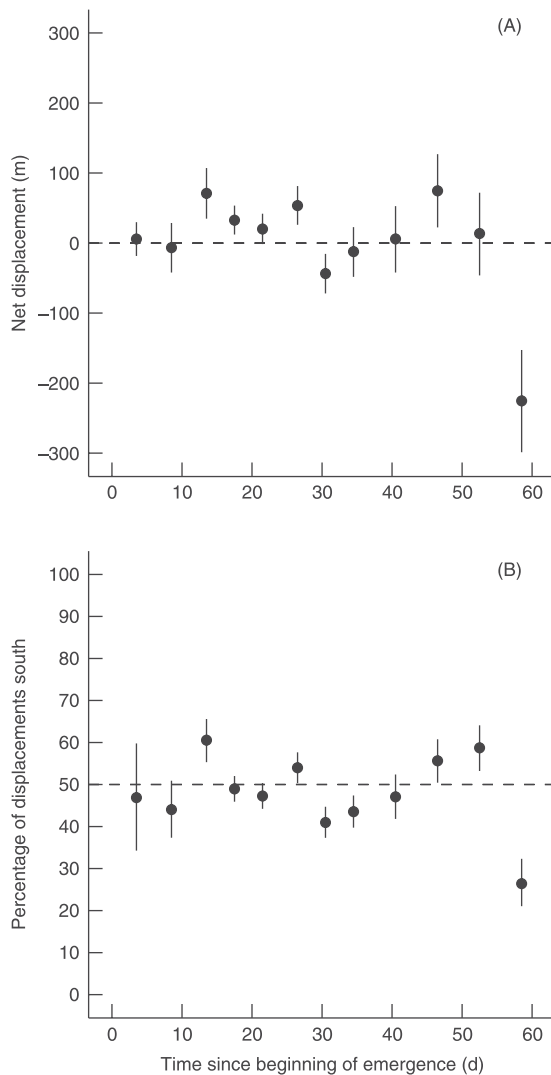


Fig. 3. Movements of YOY brook charr about the spawning site over the 12 lake-wide surveys. (A) Net displacement, calculated as the mean of displacements from the spawning site in the north (negative values) and south (positive values) directions. (B) Percent of individuals that moved to the south of the spawning site. The dashed horizontal line represents the centre of the spawning site. Vertical lines depict 95% confidence intervals.

were done in the R environment (version 2.1.0; R Development Core Team 2005).

Dispersal of a hypothetical cohort was simulated to compare the predictions of the four models for movement along an unbounded spatial domain. The bootstrap fits of the dispersal kernels, $f(x,t)$, were used to obtain predicted values for the mean lateral displacement and the percentage of long-distance displacements expected after 58.5 days. Long-distance displacements were defined arbitrarily as those > 1240 m away from the spawning site, to provide an estimate of the percentage of the cohort that moved beyond that boundary. However other boundaries for long-distance displacement could have been used as well, because the ecologically interesting question is how predictions of the four models

Table 2. Parameter estimates and bootstrap confidence intervals for models fitted to the dispersal distributions of YOY brook charr for the first two surveys. Units are $100 \text{ m}^2 \text{ day}^{-1}$ for the diffusion coefficients, D , and m for the mean lateral displacement of dispersers, δ_0 . The proportion of sedentary fish is given by p . Parameters for the two-group models are indexed by s for the sedentary component and m for the mobile component

Model	Parameter	Estimate	(95% confidence interval)
Diffusion			
D1S	D	36.79	(25.42, 49.70)
D2S	D_s	9.73	(5.86, 12.85)
	D_m	160.47	(85.50, 242.32)
	p	0.820	(0.687, 0.897)
Exponential			
E1S	δ_0	30.12	(18.59, 47.17)
	r	0.804	(0.543, 1.074)
E2S	δ_{0s}	35.34	(19.23, 59.52)
	δ_{0m}	106.38	(44.44, 227.27)
	r	0.572	(0.284, 0.881)
	p	0.832	(0.649, 0.930)

differ when fish displacements can be observed precisely, i.e. in the absence of looping.

Results

There was no consistent directional bias of the dispersing YOY cohort over the duration of the study (Fig. 3). Movements were distributed symmetrically about the centre of the spawning site until the last sampling date, when the mean displacement was biased to the north shore, where all stream inlets and sources of groundwater discharge were located (Fig. 1). Shoreline temperatures in groundwater habitat were $\leq 18^\circ\text{C}$, the approximate thermal limit for YOY brook charr (Power 1980), over the study period and remained below or near 18°C in nongroundwater habitat until the last sampling date, when they attained 21°C (Table 1). Changes in the estimated cohort size (Table 1), as well as estimates from a model of egg development as a function of incubation temperature (M. F. Coombs, unpublished data), suggest that most of the cohort emerged within a 2-week period. Cohort size remained approximately constant over surveys 4–8 and declined markedly over the last four surveys in June (Table 1).

Models fitted to the YOY distributions from the first two surveys (Table 2) adequately described the subsequent redistribution of YOY over the full 2-month dispersal period (Fig. 4). Both two-group models indicated that sedentary individuals were preponderant in the cohort (Table 2). All models tracked the main temporal trend in the data, a decline in density near the spawning site accompanied by symmetric lateral displacement away from the spawning site. Sections with exceptionally high density relative to model predictions ('outliers') were evenly distributed to either side of the spawning site and did not seem to be systematically associated

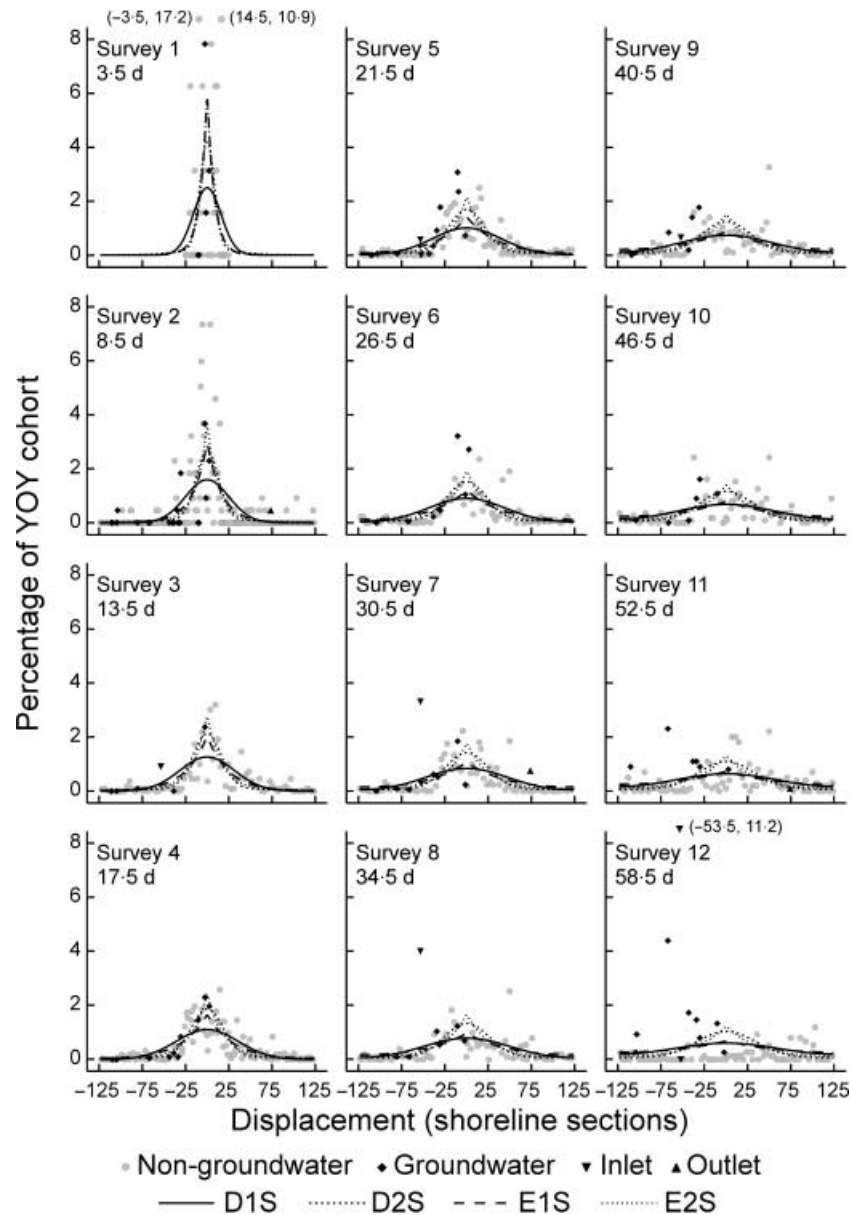


Fig. 4. Spatial distribution of YOY brook charr in different habitats (symbols), and model predictions (lines) for the 12 lake-wide surveys. Predictions for surveys 3–12 are projections from the compound density function $h(x, t)$, based on fits of the kernel $f(x, t)$ to data from only the first two surveys. Extreme values are given at top of the plot for surveys 1 and 12. Distances from the spawning site in the north (negative values) and south (positive values) directions are given in shoreline sections (10 m). Time since the beginning of emergence is specified for each survey and runs from top to bottom, then left to right.

with specific habitat types, with the exception of the last sampling date, when all outliers in the north shore were associated with groundwater habitats (Fig. 4).

Plots of observed vs. predicted counts for individual shoreline sections revealed structural shortcomings in the one-group models (Fig. 5). The deviations of the lowest smoothers from the 1 : 1 line indicate that both models tended to underestimate high counts ($x_{\text{obs}} > \sim 15$) and overestimate intermediate counts ($x_{\text{obs}} \sim 5$), consistent with the graphical depiction of the one-group spatial distributions for many of sampling dates (Fig. 4). Furthermore, the ranges of predicted counts were markedly restricted relative to those of observed counts: 5–6% of observed counts exceeded the maximum count

predicted by D1S and 3·0% of observed counts exceeded that predicted by E1S. Predicted counts for the two-group models were better aligned with the 1 : 1 line, but both models tended to overestimate counts at intermediate and high values, as shown by the deviation of the lowest smoothers from the 1 : 1 line. This bias was generally smaller for E2S than for D2S. Coverage of the range of observed counts by predictions of the two-group models was better than for the one-group models: 1·7% of observed counts exceeded the maximum count predicted by D2S and 0·8% of observed counts exceeded that predicted by E2S.

Because the range of observation was truncated at ± 1240 m, predicted statistical moments did not remain

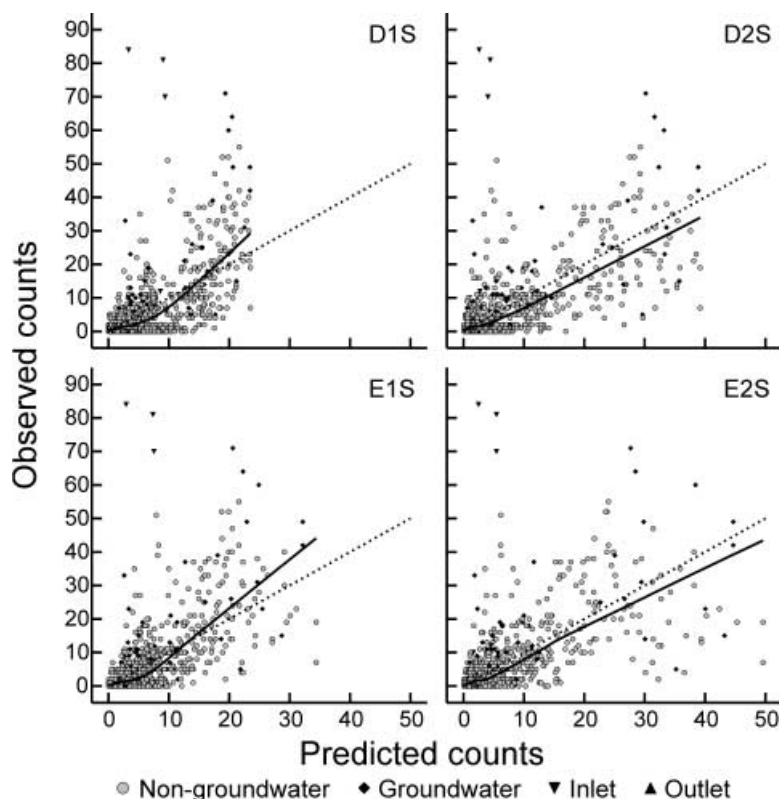


Fig. 5. Observed vs. predicted counts in individual shoreline sections, combined across all 12 surveys, for the one- and two-group diffusion and exponential models. Lowest regressions (solid line) and 1 : 1 lines (dotted) are shown. Habitat types are coded by symbols.

constant or vary linearly as would be expected sometimes in the absence of truncation (e.g. linear increase of variance in time and constant kurtosis for D1S; Fig. 6). The temporal trajectories of the mean lateral displacement and variance were more accurately predicted by D1S and E2S than by D2S and E1S, which generally underestimated (D2S) or overestimated (E1S) both measures over the 10 validation surveys (Fig. 6A,B; Table 3). Coverage of confidence intervals for predicted trajectories was poor for D2S (Fig. 6A,B).

The kurtosis of displacement distances was near zero on the initial survey (indicating mesokurtosis), increased rapidly on the second survey, and then declined progressively toward mesokurtosis (Fig. 6C). Over the 10 validation surveys, E2S tracked the variation in kurtosis more closely than the three other models, which underestimated (D1S, E1S) or overestimated (D2S) the kurtosis (Fig. 6C; Table 3).

The percentage of YOY in the tail region of the dispersal distributions increased over the study period but was highly variable (Fig. 6D). However, the agreement of predicted and observed trajectories (Fig. 6D) and the weighted squared error (Table 3) indicate that E2S matched the observed temporal trend more closely than the other models, although relative error for E2S (0.516) was slightly higher than that for D2S (0.502). It is noteworthy that after 58.5 days the one-group models had a higher percentage of YOY in the tail region than the two-group models (cf. Fig. 2B), which have higher kurtosis and thus heavier tails. This apparent discrepancy arises because this percentage depends not only on kurtosis but also on the variance, which was higher for the one-group models (Fig. 6B).

The two measures of error yielded the same rank orderings of model performance with one exception, per cent under the tails of the distribution for D2S and E2S; for these two models, the change in rank order was determined by small differences in the measures of error (Table 3). Overall, among the four models considered only E2S had adequate predictive performance and coverage of confidence intervals relative to the other models for all properties of the spatial distribution: counts, mean lateral displacement, variance, kurtosis, and percentage under the tails (Figs 5 and 6; Table 3).

In the simulations of dispersal along an unbounded spatial domain, the expected values of mean lateral displacement were broadly comparable for D1S, D2S and E2S but were markedly higher for E1S (Fig. 7A). Results for E2S, the model with the best performance, suggest that < 10% of the cohort (mean = 9.8%; median = 8.2%) had moved > 1240 m at the end of the

Table 3. Model prediction errors over surveys 3–12. The mean weighted squared error (WSE) and mean relative error are given for four properties of the spatial distribution of the cohort. The **best** (in bold) and second-best (underlined) performances are indicated for each property

Property of spatial distribution	Measure of error	Model			
		D1S	D2S	E1S	E2S
Mean lateral displacement	WSE	2805.7	5987.1	5194.3	<u>3403.0</u>
Variance $\times 10^4$		<u>157720</u>	219357	668631	79721
Kurtosis		0.945	1.747	0.573	<u>0.668</u>
Percent under tails		0.907	<u>0.683</u>	3.265	0.528
Mean lateral displacement	Relative error	0.135	0.211	0.195	<u>0.147</u>
Variance $\times 10^4$		<u>0.201</u>	0.266	0.418	0.156
Kurtosis		1.052*	1.142*	0.741*	<u>0.752*</u>
Percent under tails		0.659	0.502	1.312	<u>0.516</u>

*Absolute error, $|x_{\text{obs}} - x_{\text{pre}}|$, is given instead of relative error because kurtosis is not on a ratio scale.

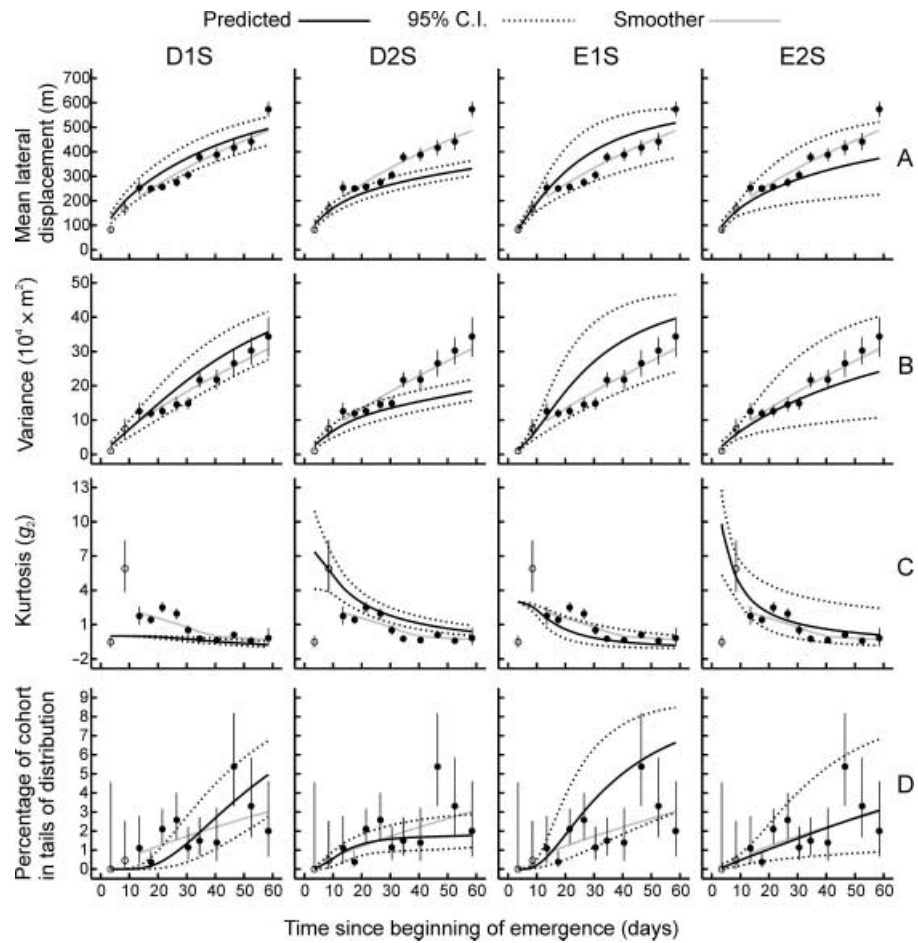


Fig. 6. Observed dispersal properties (circles) and model predictions (lines). (A) Mean lateral displacement from the spawning site, (B) variance and (C) kurtosis of displacement distances, and (D) percentage of YOY brook charr in the 24 shoreline sections most distant from the spawning site. Predictions for surveys 3–12 (filled circles) are projections from only the first two surveys (empty circles). Smoother curves for surveys 3–12 are provided for reference (power functions for A, B and D; lowess for C because kurtosis is not on a ratio scale). In C, $g_2 = 0$ indicates mesokurtosis. Also shown are 95% confidence intervals for the observed data (vertical lines) and predicted trajectories (dotted lines).

study (58.5 days). The exponential models had greater uncertainty about the expected values and more skewed distributions than the diffusion models. A similar pattern, greater expected values for E1S and greater uncertainty and skew for the exponential models, also held for the percentage of long-distance displacements (Fig. 7B).

Discussion

This study provides evidence that simple quantitative models can yield useful predictions of fish dispersal in a natural field setting. Both two-group models pointed to substantial intrapopulation variation in movement behaviour and indicated that sedentary individuals predominated in the cohort. Remarkably, model E2S – calibrated to data from only two surveys conducted 3.5 and 8.5 days after the beginning of emergence of the cohort of YOY brook charr – predicted reasonably well all the examined properties of the spatial distribution of the cohort until the end of the study, 7 weeks later (Figs 5 and 6). These results suggest that dispersal

Table 4. Dispersal properties for a hypothetical cohort moving along an unbounded domain of dispersal. Expected values of statistical moments and percentage of the cohort moving beyond a given distance, K , are given for the two-group exponential model E2S. Mean lateral displacements are indexed by s for the sedentary component and m for the mobile component. See text for full description of parameters

Property	Equation
Mean lateral displacement	$p\delta_{is} + (1 - p)\delta_{im}$
Variance	$p2\delta_{is}^2 + (1 - p)2\delta_{im}^2$
Kurtosis	$24 \frac{p\delta_{os}^4 + (1 - p)\delta_{om}^4}{(p2\delta_{os}^2 + (1 - p)2\delta_{om}^2)^2} - 3$
Percentage of cohort moving beyond distance K	$100 \left(pe^{-\frac{K}{\delta_{is}}} + (1 - p)e^{-\frac{K}{\delta_{im}}} \right)$

behaviour of YOY brook charr in Mykiss Lake is temporally stable, a finding supported by previous work on Mykiss Lake documenting heterogeneity in fine-scale movements of dispersing YOY brook charr (Biro &

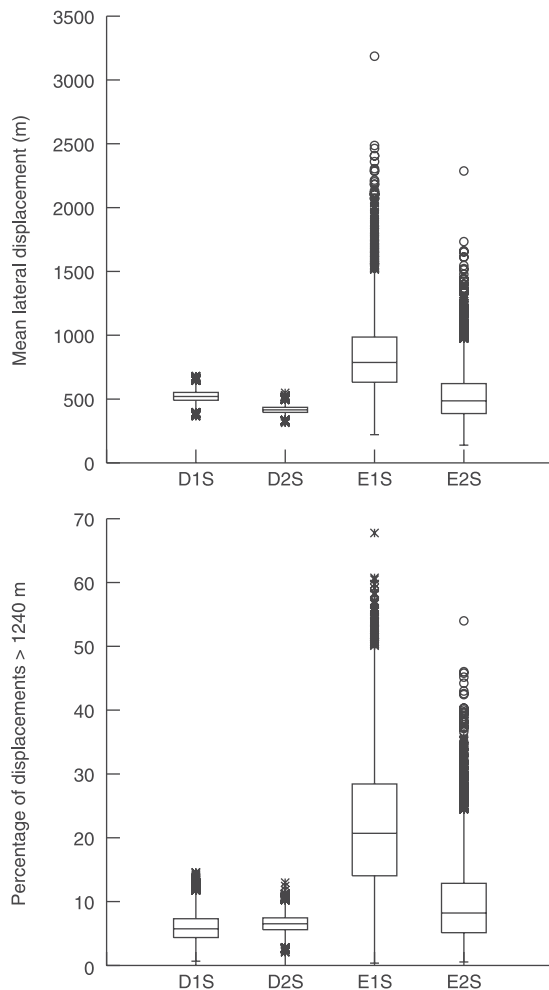


Fig. 7. Predicted dispersal of YOY brook charr moving over an unbounded spatial domain. The boxplots depict the expected distribution of (A) mean lateral displacement, and (B) percentage of long-distance dispersers in the cohort (displacements > 1240 m away from the spawning site), 58.5 days after the beginning of emergence. Predicted values are projections from the dispersal kernel $f(x,t)$, based on 10 000 bootstrap fits to data from only the first two surveys.

Ridgway 1995; Biro *et al.* 1997) and consistent behaviour of marked individuals over time (P. A. Biro, unpublished data). In a review of studies on movement in stream salmonids, sedentary individuals predominated in most of the 27 populations examined; however, the proportion of individuals in the sedentary and mobile components varied considerably among populations (Rodríguez 2002). Beyond this statistical evidence, there is considerable biological evidence of intrapopulation heterogeneity in movement behaviour of salmonids (e.g. McLaughlin *et al.* 1992; Bradford & Taylor 1997; Brännäs & Eriksson 1999; Steingrímsson & Grant 2003), as well as catfish (Sakarís, Jesien & Pinkney 2005), catostomids (Jeffres *et al.* 2006), cyprinids (Skalski & Gilliam 2000), rivulines (Fraser *et al.* 2001) and sculpins (Petty & Grossman 2004), and many of these studies suggest that individual differences are persistent.

Simple models are appealing because they can describe dispersal properties with few parameters and do not

require tailoring to system-specific detail. Model simplicity, however, may require reliance on stringent assumptions and preclude insight into detailed mechanism. Some model assumptions were clearly violated in this study: emergence of the cohort was concentrated over a period of 2 weeks, the spawning site was not strictly a point source, and shoreline habitats had markedly contrasting thermal regimes (Fig. 1). Failure to meet model assumptions may explain some of the discrepancies between observations and model predictions, such as the aggregation of individuals in coldwater habitats on the last survey (Fig. 4). Similarly, the spatial extent of the spawning site, which spanned a 60-m stretch, may have contributed to the relatively 'flat-topped' spatial distribution of YOY and near-zero kurtosis on the first survey (Figs 4 and 6). As well, increase in cohort size following the first two surveys may have led to density-dependent increase in dispersal rate and underestimation of the lateral mean displacement and variance by the two-group models in the post-calibration surveys (Fig. 6). The cross-validation procedure indicated that predictions of E2S were robust to violation of these assumptions. More generally, these results illustrate that cross-validation can be useful in identifying influential processes omitted from the models through examination of discrepancies between observations and model predictions.

A practical advantage of the exponential models relative to the diffusion models is that analytic solutions can be found for various useful descriptors of the spatial distribution (Rodríguez 2002; Table 4), whereas for the diffusion models these descriptors must be obtained by numerical integration. For example, in the presence of sedentary and mobile components, the mean lateral displacement for E2S is a simple weighted average of the values for each component (Table 4). For individuals moving along an unbounded domain, the expected mean lateral displacement (m) after t days, based on parameter values in Table 2, is given by the simple power function: $42.3 t^{0.572}$.

The simulations of dispersal along an unbounded spatial domain (Fig. 7) show the value of model comparisons based on multiple properties of the spatial distribution. Reliance on single measures of dispersal, such as mean lateral displacement, can be misleading because the variance of the distribution is critical to processes such as propagation velocity of undesirable species and diseases, population persistence, meta-population dynamics, maintenance of genetic diversity, and population responses to climate change, the outcomes of which may be determined by relatively few organisms in the tails of the distribution.

Theoretical results suggest that, when there is no directional asymmetry in dispersal and the dispersal domain consists of uniformly suitable habitat, long-distance dispersal will not contribute to population persistence (Lockwood, Hastings & Botsford 2002). However, when habitat required for survival is sparsely distributed, long-distance dispersal can have a major

impact on population persistence (Latore *et al.* 1999). Long-distance dispersal may be critical for determining cohort strength of YOY brook charr whenever key habitats, such as groundwater refugia or rearing grounds, are distant from the spawning site. The decline in abundance of YOY observed in June suggests that cohort strength may be linked ultimately to the proportion of the cohort that reaches thermal refugia before seasonal warming restricts subsequent dispersal and renders large sectors of the lake shoreline uninhabitable. The proportion of long-distance dispersers in a population can therefore have implications for population persistence of lake-dwelling brook charr. Consequently, the ability of models such as E2S to predict long-distance dispersal makes them potentially useful tools for management.

Establishing mechanistic connections between individual-level behaviour and population spread is a promising area for further research. It would be interesting to know whether models generating leptokurtosis, such as the random walk with advection toward the origin, can use field estimates of directional bias in individual movements to replicate the observed kurtosis and tail shape of the dispersal distribution at the population level. As well, standardized measures of mobility derived from simple models based on dispersal kernels may prove useful in identifying the ecological determinants of dispersal and assessing their relative importance in different environmental contexts. For example, the roles of food availability and YOY density could be assessed through comparisons of standardized measures of mobility across lakes differing in productivity or cohort size.

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