

## MODELING DIFFUSIVE SPREAD IN A HETEROGENEOUS POPULATION: A MOVEMENT STUDY WITH STREAM FISH

GARRICK T. SKALSKI<sup>1</sup> AND JAMES F. GILLIAM

*Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695-7617 USA*

**Abstract.** Using a mark–recapture technique in a small temperate stream, we described the movement of four fish species over a five-month period and developed a mathematical model that described the observed movement patterns. The movement distributions were generally leptokurtic, and two of the four species demonstrated some degree of upstream bias. There was little difference in movement among species or through time. There were no temporal correlations in probability of movement, movement direction, or distance moved. The spatial spread of the most abundant species, bluehead chubs, over a four-month period was characterized by upstream bias, diffusion-like spread, and persistent leptokurtosis. Bluehead chubs demonstrated complex relationships between probability of movement and size and growth, while creek chubs showed only an effect of size on probability of movement. Further, growth of individual bluehead chubs was correlated through time. These empirical results suggest the hypothesis that heterogeneity in phenotypic attributes, such as size and growth, is related to heterogeneity in movement behavior.

A diffusion–advection model of bluehead chub movement, structured with two subgroups that dispersed at different rates (“fast fish” and “slow fish”), was parameterized and validated with the field data. This model with heterogeneity in movement rates generated the leptokurtic pattern observed in the field data, in contrast to the classic diffusion model without population heterogeneity, which produces a normal distribution.

The results from this work suggest that heterogeneity in fitness-influencing attributes such as size and growth could explain heterogeneity in individual-level movement behavior and might underlie the leptokurtic patterns that have been observed at the population level in numerous field studies.

*Key words:* diffusion–advection model; dispersal behavior; fish; kurtosis; mark–recapture; movement behavior; *Nocomis leptocephalus*; population heterogeneity; *Semotilus atromaculatus*; stream.

### INTRODUCTION

Organism movement and dispersal arise as key determinants of population structure and function in a variety of ecological settings. In many circumstances understanding dispersal is important because movement is a key mechanism underlying the dynamics of populations (Holmes et al. 1994), particularly those with explicit spatial structure (Kareiva 1990). Previous results, garnered mostly from mathematical models, have shown that rates of dispersal can influence metapopulation dynamics (Hanski and Gilpin 1991), predator–prey interactions (Taylor 1990, 1991, Holyoak and Lawler 1996), the coexistence of competitors (Goldwasser et al. 1994, Warren 1996), and community structure (Tilman 1994, Warren 1996). A quantitative understanding of movement rates can be important in ecological applications; the management of species invasions (Hengeveld 1992, Kot et al. 1996), biocontrol practices (Walde 1994, Brodmann et al. 1997, Ives and Settle 1997), pest outbreaks (Turchin and Thoeny 1993), and fragmented populations (Fahrig and Merriam 1994) all hinge on predicting and understanding rates of movement. Consequently, re-

search that can describe and explain patterns of organism movement can be useful in a variety of settings, encompassing many basic and applied interests.

The goals of this analysis are to empirically and theoretically describe the spatial spread of stream fish and to provide an explanation for a departure from normality (leptokurtosis) that these and other movement data show. These results can then be interpreted in light of their implications for the dispersal dynamics of populations in general.

In this paper the focus is on tracking the movement of individuals (the “Lagrangian” view) as a path to understanding, mechanistically, the spatial spread of the population as a whole (the “Eulerian” view). The practical difficulties of following large numbers of organisms through space and time are a substantial hindrance in field studies, and thus empirical information is rare for many taxa in many systems (Okubo 1980, Turchin 1998). Ecologists have used simple diffusion (Skellam 1951, Kareiva 1982, 1983, Turchin and Thoeny 1993), correlated random walk (Kareiva and Shigesada 1983, Kareiva and Odell 1987, McCulloch and Cain 1989), and Markov chain (Kareiva 1982) models to describe dispersal data for various insects. Perhaps the strongest gains in dispersal ecology have been theoretical. Okubo (1980) and Turchin (1998)

Manuscript received 14 September 1998; revised 31 March 1999; accepted 20 April 1999.

<sup>1</sup> E-mail: gtskalsk@unity.ncsu.edu



PLATE 1. Durant Creek, Wake County, North Carolina, USA. Photograph by Garrick T. Skalski.

have provided useful accounts of the contribution of mathematics to dispersal theory, but the empirical validity of previous mathematical work has yet to be thoroughly evaluated. In summary, no synthesis of dispersal patterns has emerged from the field data and no consensus has been reached on the appropriateness of the various models of dispersal.

We analyzed data from a five-month mark–recapture study of an entire stream fish community. Stream fish communities are convenient and unique systems for quantitative movement studies for several reasons. First, a number of species are usually available for capture and study in any one stream at densities sufficient for making statistical inferences, allowing for simultaneous examination of the movement of potential predators, prey, and competitors. Second, stream fish can be individually marked, a technique that provides more information than mass marking methods. Third, because of their natural abundance, movement by stream fish can be observed while the organisms are at their natural densities in their natural habitats, eliminating the need to transplant and augment marked populations. Finally, because small streams can be conceptualized as one-dimensional habitats, the mathematical and statistical analysis is relatively simple, mitigating the need for laboratory or mesocosm settings.

We analyzed the dispersal of stream fish both empirically and theoretically in an attempt to describe and explain the patterns of movement. The classic simple diffusion model, which predicts that movement distances are normally distributed and that the variance of distances moved increases linearly with time, represents our null model of organism movement (Skellam 1951). Thus, in an effort to describe the pattern within a conceptual framework, we tested the hypothesis that the patterns of fish movement are consistent with those predicted in the Skellam model by describing the general statistical form of the movement data and testing the hypothesis that the distribution of distances moved

is normally distributed. We also tested the hypothesis that the variance of distances moved of dispersing fish increases linearly with time.

In an effort to understand the mechanisms underlying movement patterns, we related several measured variables to the observed patterns of movement. Specifically, we tested whether movement patterns vary among species, through time, with fish size, or with the growth of individuals. We also tested for temporal correlations in the probability of movement, and the direction and distance of displacement of dispersing individuals.

Because some of the empirical results suggested a hypothetical mechanism that could describe the observed movement patterns, we also constructed and parameterized a mathematical model of movement that incorporated this mechanism and tested the hypothesis that this model (i.e., the mechanism of movement) could describe the spatial spread of fish over a four-month time period. We also compared the performance of our model (i.e., hypothesis) to that of two alternative models (i.e., hypotheses) using three different evaluation criteria. Finally, we reconcile the empirical and theoretical results via a discussion of patterns and processes in stream fish movement and suggest opportunities for future research.

#### EMPIRICAL STUDY: METHODS

##### *Study site*

The study took place in a 1-km length of Durant Creek as it flows through the Durant Nature Park, Raleigh, North Carolina, USA (see Plate 1). Durant Creek joins the Neuse River 4 km below the study area. The creek varied in depth from ~2 cm in the shallowest riffles to 1.5 m in the deepest pools and varied in width from 1 to 4 m. The substrate varied in size from sand to boulders to bedrock. The channel morphology was characterized by alternating riffle, run, and pool segments that averaged 10–15 m in length. Although much

of the catchment consisted of secondary succession hardwood forest within the park's boundaries, most of the headwaters drained suburban residential areas; the creek showed some sedimentation and flash floods throughout the study period. Visually, aquatic insect densities appeared low; however caddisflies (Hydropsychidae), dobsonflies (*Corydalus cornutus*), crane-flies (*Tipula* spp.), water striders (Gerridae), midges (Chironomidae), and damselflies (Zygoptera) were observed in larval and sometimes adult forms throughout the study. Crayfish (Cambaridae) were, by far, the most frequently observed invertebrate taxa.

We captured 14 species of fish over the course of the study: bluehead chub (Cyprinidae: *Nocomis leptocephalus*), creek chub (Cyprinidae: *Semotilus atromaculatus*), rosyside dace (Cyprinidae: *Clinostomus funduloides*), redbreast sunfish (Centrarchidae: *Lepomis auritus*), yellow bullhead (Ictaluridae: *Ameiurus natalis*), American eel (Anguillidae: *Anguilla rostrata*), swallowtail shiner (Cyprinidae: *Notropis procne*), white shiner (Cyprinidae: *Notropis albeolus*), margined madtom (Ictaluridae: *Noturus insignis*), green sunfish (Centrarchidae: *Lepomis cyanellus*), bluegill sunfish (Centrarchidae: *Lepomis macrochirus*), mosquitofish (Poeciliidae: *Gambusia affinis*), warmouth sunfish (Centrarchidae: *Lepomis gulosus*), and a darter (Percidae: *Percina* spp.) (Menhinick 1991). The first five species listed are thought to be residents based, at least, on observations of reproductive-sized adults and abundant young-of-the-year occurring at some point during the study. Of these, bluehead chubs and creek chubs were the two most abundant species in the creek. The others may be immigrants that were born in downstream areas and reservoirs that feed nearby creeks in the catchment.

#### Sampling methods

From 15 March 1996 through 15 August 1996 we carried out a mark-recapture study in Durant Creek with sampling occurring at 1-mo intervals (interval length chosen arbitrarily) for a total of six sampling occasions. Using a backpack electrofisher (Model 12A POW, Smith Root, Incorporated, Vancouver, Washington, USA) and 0.6-cm mesh block seines, we shocked sampling sites (37 sites) one at a time, always moving upstream from site to site. We carried out two passes at each site. We held captured fish in the stream in mesh laundry baskets set a few centimeters into the water and weighted with rocks until processing. All fish greater than ~40 mm total length were then anesthetized in a buffered solution of MS-222 (tricaine methanesulfonate), individually marked with elastomer tags (for details see *Marking method*), measured for total length, allowed to recover in the baskets, and then released into cover (underwater brush, rocks, undercut banks) in the middle of the site from which they were captured.

We marked and released fish in a 400-m section of creek, which consisted of 37 sampling sites, or patches.

Our sites were defined by the stream's channel morphology: alternating pools, runs, and riffles. Fish captured and marked with our methods inhabited two types of discrete habitat patches along the stream's continuum: pools and runs. Thus our sampling sites were defined as the pools and runs along the stream's continuum. The sites were similar in length and averaged 10–15 m long. Areas upstream and downstream of the 400-m section were searched for marked fish with equal electrofishing effort (two passes with block nets). The area 180 m downstream of the marking area was searched on all recapture occasions (April–August). The area 50 m upstream of the marking area was searched during the April recapture and the area 180 m upstream of the marking area was searched during the final August recapture. Sampling within any given month was completed within 3–5 d.

#### Marking method

We marked fish using an elastomer tagging method (Northwest Marine Technologies, Shaw Island, Washington, USA). A fluorescent liquid is mixed with a catalyst, which initiates a chemical reaction whereupon the material hardens into a flexible solid after ~3 h. This mixture was injected under the skin of fish using a 29-gauge "tuberculin" syringe, producing a small sliver of visible, flexible material. By combining four elastomer colors with 10 anatomical positions, up to 760 fish could be uniquely marked ( $720 = ({}^9P_4)^2$  with two injections, plus  $40 = ({}^9P_4)^1$  with a single injection).

We marked individuals >40 mm total length from all captured species, producing a total of 610 marked fish over the course of the study. Of these we recaptured a total of 478 fish, representing 237 different individuals. Four species produced enough data to justify a statistical analysis: bluehead chub (216 recaptures), creek chub (123 recaptures), redbreast sunfish (54 recaptures), and rosyside dace (28 recaptures).

#### Statistical bias and weighting

We quantified patterns of movement using histograms that charted the frequency distribution of distances moved, where distance moved was in units of sites, or patches, corresponding to our sampling sites. These distributions will be called "movement distributions." We arbitrarily assigned downstream movement negative values of net displacement and upstream movement positive values.

Because it is physically impossible to search indefinitely upstream and downstream of the marking area for marked fish, the resulting sample of distances moved by fish may be biased: the tails of the movement distribution are subject to undersampling. For some statistical procedures this is irrelevant, but for others it is important. The amount of undersampling can be diminished by searching farther upstream and downstream for marked fish. Not all of the information in the tails of the distribution is lost, however. Out to a

point on the tail of the distribution the amounts by which points are undersampled are known. By weighting observations at these points according to the degree of undersampling an estimate of the real distribution can be calculated out to a point (Porter and Dooley 1993). To assess undersampling we weighted the data accordingly and compared weighted and unweighted movement distributions statistically. Preliminary analyses showed unweighted and weighted distributions to be both visually and statistically indistinguishable (via a Kolmogorov-Smirnov test; Sokal and Rohlf 1981). Therefore we used unweighted distributions for all analyses.

In an effort to simultaneously maximize power and minimize bias in our diverse array of analyses we constructed two data sets from the field data: I and II. Data Set I consists of all of our observations on movement and was used to test hypotheses regarding species, size, and growth effects on movement, as well as to estimate the variance and kurtosis of movement distributions. Data Set II is a subset of Data Set I which corrects for our uneven sampling effort upstream vs. downstream of the 400-m mark and release section; Data Set II is the set of observations recovered when we searched for marked fish at least 10 sites upstream and downstream of every release site, and when our upstream effort equaled our downstream effort. Data Set II was used to test for upstream bias, normality, temporal effects and correlations, to estimate the mean and skewness of movement distributions, and to parameterize and evaluate mathematical models.

In every case below, we pooled data over all sampling sites to generate movement distributions. Further, every movement distribution, unless specified otherwise, represents movement over a 1-mo time interval.

#### *The movement distribution*

We conducted tests of the general statistical properties of the movement distributions. We tested the hypothesis of symmetry in the movement distributions, in terms of both numbers of moves and median distance moved. We used a  $\chi^2$  test (Sokal and Rohlf 1981) to compare the number of fish that moved downstream to those that moved upstream. We used a Mann-Whitney  $U$  test (Sokal and Rohlf 1981) to compare the median distance of displacement by fish that moved downstream to the median distance traveled by those that had moved upstream. We also tested the hypothesis that movement distributions were normal using D'Agostino's test for normality (Sokal and Rohlf 1981). The kurtosis (Zar 1996) of the movement distributions was also estimated for each species. We analyzed data that were pooled over all months for each of the four species. Symmetry and normality were tested using Data Set II, while kurtosis estimates used Data Set I.

#### *Species and time effects*

We compared movement distributions of the four species with Kolmogorov-Smirnov tests, to test for dif-

ferences in movement among species. Bluehead chub movement was compared to that of creek chubs for each of the five months. Because of small samples sizes for the other two species (redbreast sunfish and rosyside dace), we pooled data for these species over all months and evaluated species effects using all pairwise combinations of the four species, with bluehead chubs and creek chubs pooled across months for this comparison. All tests of species effects used Data Set I.

Finally, we analyzed time effects for pairwise combinations of the five months for bluehead chubs and creek chubs using Data Set II. We did not analyze temporal effects for rosyside dace and redbreast sunfish due to small sample sizes.

#### *Size and growth effects*

We tested the hypothesis that movement behavior was related to the size and growth of fish. For bluehead chubs and creek chubs we tested the hypotheses that probability of movement varied with size and growth using probit regression (Sokal and Rohlf 1981; 0 = stay, 1 = move), pooling data over all months. The statistical significance of the independent variables was evaluated using the  $\chi^2$  likelihood ratio statistic computed using a backward elimination algorithm. This statistic addresses whether the presence of a given independent variable in the probit model results in a significant improvement in the model's description of the data. The relatively small number of recaptures of redbreast sunfish and rosyside dace prevented our use of probit regression to analyze these data. For these species we asked if "movers" and "stayers" differed in size and growth. "Movers" were defined to be fish which showed nonzero net displacement over a recapture interval, and "stayers" were defined to be fish which showed zero net displacement over a recapture interval (did not move from the previous collection site). We compared mean size (total length in millimeters at the start of the recapture interval) and growth (net change in total length during the recapture interval) of movers to that of stayers, using a two-tailed  $t$  test (Sokal and Rohlf 1981).

Considering only movers, using Spearman rank correlation (Sokal and Rohlf 1981), we tested for relationships between distance moved and both size and growth of the four species. For each of the four species we pooled data over all recapture intervals to achieve reasonable sample sizes.

To further explore the relationship between growth and movement we tested for temporal relationships in growth rate for bluehead chubs and creek chubs captured in three consecutive months (i.e., data from two consecutive recapture intervals). We tested the hypothesis that the growth of individual fish during the second recapture interval was related to their growth during the first interval using linear regression (Sokal and Rohlf 1981). Next, we asked whether probability of movement in the two intervals varied with growth

TABLE 1. Estimates of kurtosis (with standard error and sample size [ $n$ ] reported in parentheses) for bluehead chubs, creek chubs, redbreast sunfish, and rosieside dace.

Species	Recapture interval	Kurtosis (1 SE, $n$ )	$P$
Bluehead chub	All intervals	7.34 (0.39, 157)	<0.002
	March–April	3.45 (0.78, 35)	
	April–May	0.61 (0.74, 39)	
	May–June	3.64 (0.85, 29)	
	June–July	6.38 (0.83, 30)	
	July–August	3.00 (0.92, 24)	
Creek chub	All intervals	6.65 (0.52, 84)	<0.002
	March–April	0.27 (1.06, 17)	
	April–May	1.65 (1.06, 17)	
	May–June	0.53 (1.09, 16)	
	June–July	4.84 (1.04, 18)	
	July–August	3.37 (1.09, 16)	
Redbreast sunfish	All intervals	3.56 (0.85, 29)	<0.01
Rosieside dace	All intervals	1.82 (1.04, 18)	>0.1

Note: The bound on the  $P$  value resulting from the test of the hypothesis that the kurtosis is zero is reported for each species.

rate in the two intervals using probit regression, pooling movement measurements over the two intervals; thus there are two movement observations for each pair of growth observations. All size and growth analyses used Data Set I.

#### Temporal correlations in movement

For bluehead chub and creek chub data pooled together to avoid small sample sizes, we tested for temporal correlations in the probability, direction, and distance of movement for fish that were recaptured in any three consecutive months. We tested the hypothesis that the probability that a fish moved or stayed over a given recapture interval depended upon whether it had moved or stayed during the previous interval using a  $\chi^2$  test. Also via a  $\chi^2$  test, we tested the hypothesis that the direction a fish moved during a given recapture interval depended upon its direction of movement during the previous interval. That is, we tested the hypothesis that whether a fish moved upstream, downstream, or remained stationary during a recapture interval depended upon whether the fish moved upstream, downstream, or remained stationary during the previous recapture interval. Finally, we tested the hypothesis that the distance a fish moved during a given recapture interval depended upon the distance it had moved during the previous interval using Spearman rank correlation. We did not analyze temporal correlations for redbreast sunfish and rosieside dace because of small sample sizes. All analyses for temporal correlations used Data Set II.

#### Spatial spread through time

Finally, we analyzed the spatial spread of bluehead chubs and creek chubs through time. This analysis describes the population-level movement of fish as they spread from a hypothetical single release point. Pooling data over all months, we estimated the mean, variance, skewness, and the kurtosis of the movement distribution over a four-month period of movement for each

species (Sokal and Rohlf 1981, Zar 1996). The estimates of variance and kurtosis were computed with Data Set I, while those of the mean and skewness were estimated with Data Set II.

To test the hypothesis that the variance of distances moved increased linearly with time, we regressed the estimated variance of distances moved on time using the polynomial equation  $y = c_0 + c_1t + c_2t^2$ , where  $y$  is the variance and  $t$  is time; the hypothesis predicts  $c_0 = 0$ ,  $c_1 > 0$ , and  $c_2 = 0$ .

## EMPIRICAL STUDY: RESULTS

### The movement distribution

The movement distributions of each of the four species deviated from normality (for each case: D'Agostino's test:  $D \ll 0.0001$ ,  $P < 0.01$ ). Leptokurtosis was a general feature of the movement distributions; that is, the distributions had higher peaks and longer tails than a corresponding normal distribution, and thus accounted for some of the departure from normality (Table 1, Fig. 1). Bluehead chub, creek chub, and redbreast sunfish movement distributions were significantly leptokurtic. The point estimates of kurtosis were positive in every recapture interval for bluehead chubs and creek chubs, and in no case was platykurtosis (kurtosis  $< 0$ ) indicated.

Two of the four species showed some degree of upstream bias. Bluehead chubs showed a clear upstream bias ( $\chi^2 = 7.19$ ,  $df = 1$ ,  $P = 0.0073$ ), and rosieside dace were also more likely to move upstream ( $\chi^2 = 4.57$ ,  $df = 1$ ,  $P = 0.0325$ ). Creek chubs and redbreast sunfish, however, showed no bias in direction of movement (creek chubs:  $\chi^2 = 0.26$ ,  $df = 1$ ,  $P = 0.6055$ ; redbreast sunfish:  $\chi^2 = 0.33$ ,  $df = 1$ ,  $P = 0.5637$ ). The median distance moved upstream was not statistically different from the median distance moved downstream for any of the four species (for each case: Mann-Whitney  $U$  test:  $P > 0.05$ ).

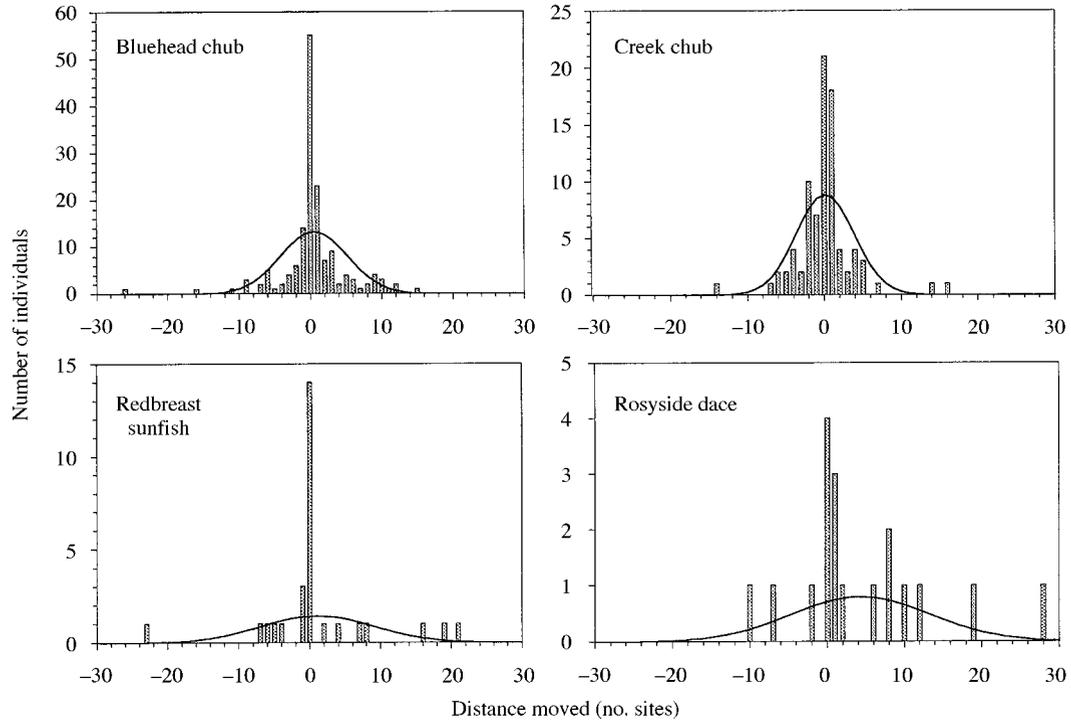


FIG. 1. Movement distributions over 1 mo for bluehead chubs, creek chubs, redbreast sunfish, and rosyside dace. The corresponding normal probability density functions parameterized with the mean and variance from the data are shown for each distribution. Data are pooled over all recapture intervals.

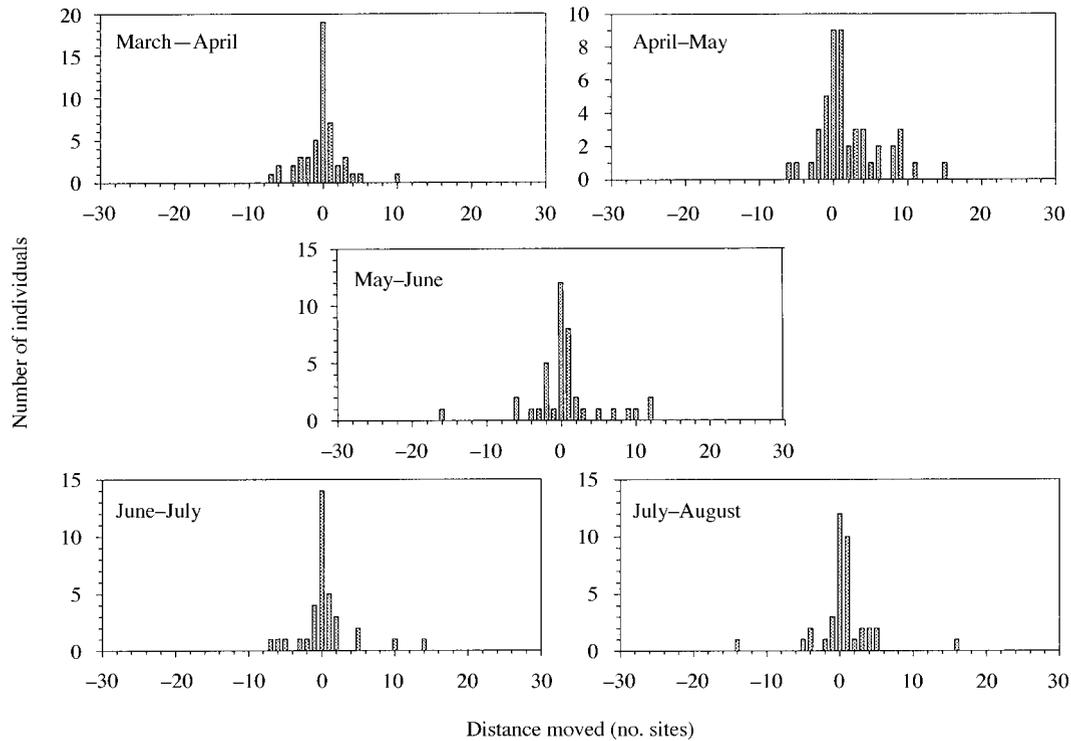


FIG. 2. Movement distributions for bluehead chubs and creek chubs pooled over the two species within each of the five recapture intervals.

### Species and time effects

Neither species nor time had strong effects on the patterns of fish movement. There was little difference among the movement distributions of the four species (Fig. 1). Bluehead chub and creek chub movement distributions were not statistically different in any of the five recapture intervals using the Bonferroni criterion for multiple comparisons (for each of five contrasts: Kolmogorov-Smirnov test:  $P > 0.01$ ). By this same criterion no species effects were detected when the data were pooled over all recapture intervals (for each of five contrasts: Kolmogorov-Smirnov test:  $P > 0.01$ ).

Time of the recapture interval had little overall effect on the movement distributions of bluehead chubs and creek chubs (Fig. 2). The movement distributions from the five recapture intervals were not statistically different (for each of 10 contrasts per species: Kolmogorov-Smirnov test:  $P > 0.0025$ ) for both bluehead chubs and creek chubs using the Bonferroni criterion.

### Size and growth effects

Both the size and growth of fish tended to vary with degree of movement within recapture intervals, but the effects were variable among the species. For bluehead chubs (Fig. 3) probability of movement varied with both size ( $\chi^2 = 7.22$ ,  $df = 1$ ,  $P = 0.0072$ ) and growth ( $\chi^2 = 5.16$ ,  $df = 1$ ,  $P = 0.0232$ ), showing a nonlinear response caused by the interaction of size and growth effects ( $\chi^2 = 6.42$ ,  $df = 1$ ,  $P = 0.0113$ ). Probability of movement increased with size in slow-growing individuals, but decreased with size in fast-growing individuals. For bluehead chubs, the data did not differ significantly from the best-fit probit model ( $\chi^2 = 147.81$ ,  $df = 145$ ,  $P = 0.4196$ ), and growth did not vary with size (linear regression:  $F_{1,153} = 0.62$ ,  $P = 0.4308$ ). In contrast, probability of movement in creek chubs (Fig. 3) was positively related to size ( $\chi^2 = 11.22$ ,  $df = 1$ ,  $P = 0.0008$ ), but did not vary significantly in response to growth ( $\chi^2 = 2.73$ ,  $df = 1$ ,  $P = 0.0983$ ). For creek chubs, the data did not differ significantly from the best-fit probit model ( $\chi^2 = 51.39$ ,  $df = 47$ ,  $P = 0.3058$ ), and growth did not vary with size (linear regression:  $F_{1,79} = 1.81$ ,  $P = 0.1820$ ). The effect of size and the effect of growth on probability of movement both differed between the two chub species (species  $\times$  size:  $\chi^2 = 4.29$ ,  $df = 1$ ,  $P = 0.0383$ ; species  $\times$  growth:  $\chi^2 = 8.15$ ,  $df = 1$ ,  $P = 0.0043$ ).

For the redbreast sunfish and rosyside dace, movers were similar to stayers in terms of both size (redbreast sunfish:  $t = 1.86$ ,  $df = 27$ ,  $P = 0.0734$ ; rosyside dace:  $t = -0.25$ ,  $df = 16$ ,  $P = 0.8069$ ) and growth (redbreast sunfish:  $t = -0.56$ ,  $df = 26$ ,  $P = 0.5812$ ; rosyside dace:  $t = -0.32$ ,  $df = 16$ ,  $P = 0.7530$ ).

Of those fish that did move, size showed no consistent relationship with distance moved (Fig. 4). Size had no effect on the distances moved by bluehead chubs ( $R_s = -0.1349$ ,  $N = 157$ ,  $P = 0.0921$ ) or creek chubs

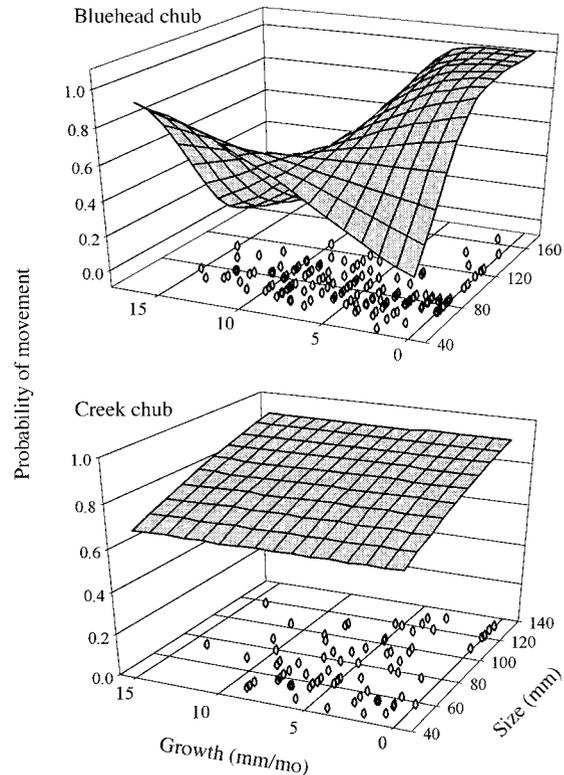


FIG. 3. The probit model predictions for the response of probability of movement to size and growth for bluehead chubs and creek chubs. Models include only those independent variables that were judged statistically significant by the likelihood ratio test. Points in the size/growth plane show the values of size and growth for which we have empirical observations.

( $R_s = -0.0158$ ,  $N = 63$ ,  $P = 0.9022$ ). The same was true for rosyside dace ( $R_s = 0.1019$ ,  $N = 14$ ,  $P = 0.7289$ ). Redbreast sunfish, however, demonstrated a negative relationship between distance moved and size ( $R_s = -0.6844$ ,  $N = 14$ ,  $P = 0.0069$ ); given that they did move, smaller fish moved farther than larger fish.

Growth also had little effect on distance moved for those fish that did move. For all four species growth showed no relationship with distance moved (Fig. 5; bluehead chub:  $R_s = 0.0624$ ,  $N = 153$ ,  $P = 0.4437$ ; creek chub:  $R_s = 0.1391$ ,  $N = 62$ ,  $P = 0.2810$ ; rosyside dace:  $R_s = 0.0480$ ,  $N = 14$ ,  $P = 0.8706$ ; redbreast sunfish:  $R_s = 0.1780$ ,  $N = 14$ ,  $P = 0.5426$ ).

The analysis of the growth rates of chubs which had been caught on three consecutive occasions showed that growth rates were positively correlated through time in bluehead chubs (linear regression:  $F_{1,66} = 23.08$ ,  $P < 0.0001$ ) and showed a nonsignificant positive trend in creek chubs (linear regression:  $F_{1,28} = 1.13$ ,  $P = 0.2962$ ). We then tested the hypothesis that probability of movement varied with growth rate in the two recapture intervals. Both intervals of growth had significant effects on the movement of bluehead chubs (first

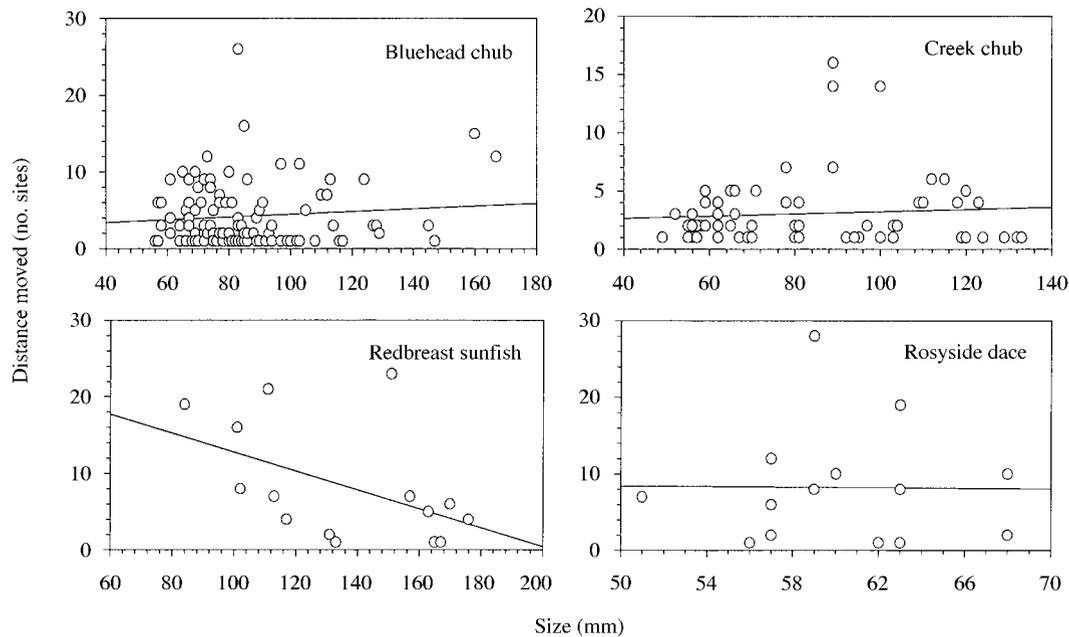


FIG. 4. The relationship between absolute value of distance moved and size (total length, mm) for each of the four species, given that distance moved was  $>0$ . Data are pooled over all five recapture intervals for all species.

interval:  $\chi^2 = 4.37$ ,  $df = 1$ ,  $P = 0.0366$ ; second interval:  $\chi^2 = 10.07$ ,  $df = 1$ ,  $P = 0.0015$ ), but the relationship was complex: the probability of movement also depended on the interaction among growth rates in the two intervals (Fig. 6;  $\chi^2 = 15.45$ ,  $df = 1$ ,  $P = 0.0001$ ). For bluehead chubs, the data did not differ significantly from the best-fit probit model ( $\chi^2 = 76.81$ ,  $df = 65$ ,  $P = 0.1499$ ). Neither interval of growth affected creek chub movement (first interval:  $\chi^2 = 0.48$ ,  $df = 1$ ,  $P = 0.4873$ ; second interval:  $\chi^2 = 0.004$ ,  $df = 1$ ,  $P = 0.9453$ ).

#### Temporal correlations in movement

Bluehead chubs and creek chubs showed no statistically significant temporal correlations in movement. Whether a chub moved during a recapture interval did not depend on whether it had moved the previous recapture interval ( $\chi^2 = 1.97$ ,  $df = 1$ ,  $P = 0.5787$ ). However, there was a nonsignificant trend in the data toward a positive correlation: the proportions of fish that did not move during a recapture interval were 25% and 39%, respectively, for fish which did and did not move during the previous recapture interval (if no correlation, the expected proportions are identical). The direction that a chub moved during a recapture interval did not vary with its previous direction of movement ( $\chi^2 = 3.88$ ,  $df = 4$ ,  $P = 0.8678$ ). Distances moved during consecutive time intervals showed no relationship (Spearman rank correlation:  $R_s = 0.0590$ ,  $N = 84$ ,  $P = 0.5939$ ).

#### Spatial spread through time

The spatial spread of the chub species was characterized by a constant rate of spread: the variances of the movement distributions increased linearly with time (Fig. 7). The estimated intercept, linear, and quadratic terms followed the pattern predicted by classic theoretical work on simple diffusion, i.e., zero intercept, positive slope, and zero quadratic term (Skellam 1951). (For bluehead chub, intercept,  $t = 0.28$ ,  $P = 0.7949$ ; linear,  $t = 10.16$ ,  $P = 0.002$ ; quadratic,  $t = 0.50$ ,  $P = 0.6700$ . For creek chub, intercept,  $t = 0.33$ ,  $P = 0.627$ ; linear,  $t = 7.30$ ,  $P = 0.0053$ ; quadratic,  $t = -1.17$ ,  $P = 0.3630$ .) However, the movement distributions of the two chubs differed in important ways. Bluehead chubs showed upstream bias and leptokurtosis over all four months, as evidenced by positive estimates of the mean, skewness, and kurtosis (Table 2). In contrast, creek chubs showed little evidence of persistent upstream bias, and their leptokurtosis, while evident in the first three months, showed a decreasing trend with time, vanishing by the fourth month (Table 2).

#### THEORETICAL STUDY: METHODS

##### A model of fish movement

Having gained some insight into potential mechanisms that underlie movement patterns in stream fish, we now construct a mathematical model that builds upon our empirical information. We focus only on the bluehead chub because their data are most extensive among the taxa we examined.

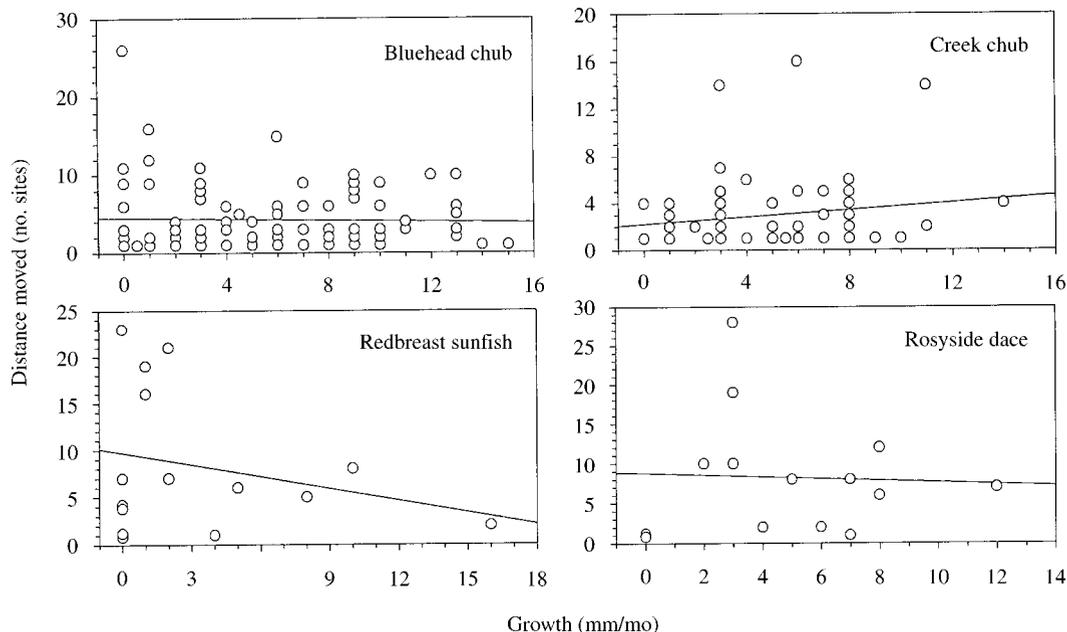


FIG. 5. The relationship between absolute value of distance moved and growth (total length, mm/mo) for each of the four species, given that distance moved was >0. Data are pooled over all five recapture intervals for all species.

The field data for bluehead chubs suggest four prominent features of fish movement. First, there is a relationship involving “population heterogeneity,” or the variability among individuals. Population heterogeneity in movement is related to population heterogeneity in other traits. In particular, size and growth rate are related to movement behavior in a complex manner. Second, the movement distributions are noticeably leptokurtic, with high peaks and long tails. Third, the var-

iance increased linearly with time, a property consistent with diffusive spread. Finally, the movement of bluehead chubs was characterized by an upstream bias that persisted through four months.

Thus we desired to construct a diffusion model that could generate upstream bias and leptokurtosis. Assuming no recruitment over the time interval of interest, the classic model of simple diffusion in a homogeneous population (Skellam 1951) can be extended to predict upstream bias by adding an advection component (Zabel and Anderson 1997, Turchin 1998). This model predicts the density of organisms,  $P(x, t)$ ,

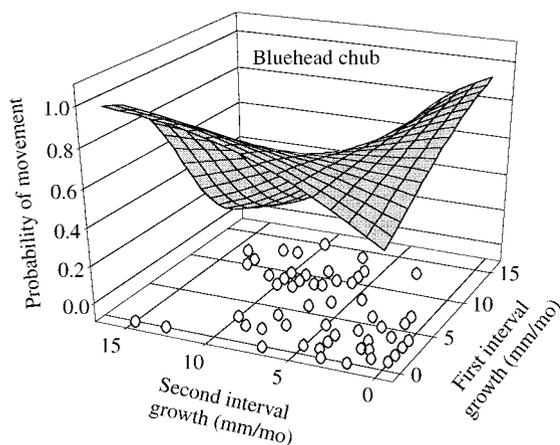


FIG. 6. The probit model predictions for the response of probability of movement to growth in two consecutive recapture intervals in bluehead chubs. The model includes only those independent variables that were judged statistically significant by the likelihood ratio test. Points in the growth plane show the values of growth in the two intervals for which we have empirical observations.

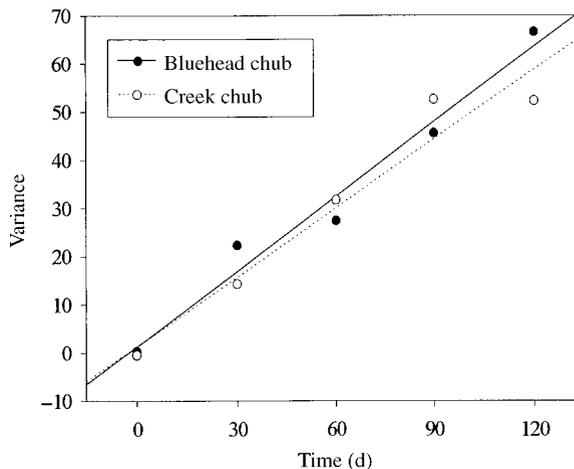


FIG. 7. The relationship between time and variance in distance moved for bluehead chubs and creek chubs. Data are pooled over all recapture intervals.

TABLE 2. Estimates of the mean, variance, skewness, and kurtosis of the movement distributions (frequency distribution of number of sites moved) for dispersing bluehead chubs and creek chubs over a 4-mo period.

Time (d)	Mean (1 SE, <i>n</i> )	Variance (1 SE, <i>n</i> )	Skewness (1 SE, <i>n</i> )	Kurtosis (1 SE, <i>n</i> )
<b>Bluehead chub</b>				
0	0 (0, 190)	0 (0, 190)	n/a	n/a
30	1.13 (0.35, 134)*	22.29 (5.42, 157)	0.44 (0.43, 134)*	7.34 (0.39, 157)*
60	1.57 (0.50, 86)*	27.40 (7.86, 101)	0.95 (0.31, 86)*	6.37 (0.48, 101)*
90	3.19 (0.80, 59)*	45.64 (14.03, 69)	0.87 (0.25, 59)*	4.58 (0.57, 69)*
120	2.44 (0.77, 32)*	66.62 (30.69, 44)	1.08 (0.22, 32)*	7.51 (0.70, 44)*
<b>Creek Chub</b>				
0	0 (0, 161)	0 (0, 161)	n/a	n/a
30	-0.03 (0.44, 76)	14.30 (4.57, 84)	0.82 (0.43, 76)*	6.65 (0.52, 84)*
60	1.00 (0.70, 57)	31.67 (8.74, 60)	1.10 (0.31, 57)*	2.61 (0.61, 60)*
90	2.62 (1.25, 34)*	52.64 (18.19, 35)	0.75 (0.25, 34)	2.24 (0.78, 35)*
120	2.38 (1.58, 21)	52.35 (17.62, 21)	0.73 (0.22, 21)	0.40 (0.97, 21)

Note: Standard errors and sample sizes (*n*) are shown in parentheses.  
 \*Estimates that are significantly different from zero ( $P < 0.05$ ).

through space *x*, and time *t*, via solution of the partial differential equation

$$\frac{\partial P}{\partial t} = D \left( \frac{\partial^2 P}{\partial x^2} \right) - \beta \frac{\partial P}{\partial x} \tag{1}$$

with diffusion rate *D*, and advection rate  $\beta$ ; in the Skellam (1951) model,  $\beta = 0$ . Yet this model is unable to predict leptokurtic spread because its solution for the initial and boundary conditions that correspond to our field data (a hypothetical instantaneous, single point release of  $P_0$  fish) is the normal distribution,

$$P(x, t) = \left( \frac{P_0}{2\sqrt{\pi Dt}} \right) \exp \left( \frac{-(x - \beta t)^2}{4Dt} \right) \tag{2}$$

with mean  $\beta t$ , and variance  $2Dt$  (Turchin 1998). However, as observed by Okubo (1980) a movement distribution that is the sum of two normal distributions with unequal variances is leptokurtic. Thus, population heterogeneity in movement can generate leptokurtosis, a hypothesis that is consistent with our empirical information since population heterogeneity in size and growth was related to population heterogeneity in movement.

We now extend the classic “population homogeneity” model described in Eqs. 1 and 2 by considering a model of a heterogeneous population consisting of two subgroups, “fast fish” and “slow fish,” each moving by simple diffusion with upstream advection along a line of patches (“fast” and “slow” do not imply “move” and “stay,” respectively; fast fish can either move or stay, as can slow fish). If  $F(x, t)$  is the density of rapidly diffusing fish, or fast fish, in patch *x* at time *t*, and  $S(x, t)$  is the density of slowly diffusing fish, or slow fish, in patch *x* at time *t*, then the equations describing the spatial spread are

$$\frac{\partial F}{\partial t} = D_F \left( \frac{\partial^2 F}{\partial x^2} \right) - \beta_F \frac{\partial F}{\partial x} \tag{3}$$

for fast fish, and

$$\frac{\partial S}{\partial t} = D_S \left( \frac{\partial^2 S}{\partial x^2} \right) - \beta_S \frac{\partial S}{\partial x} \tag{4}$$

for slow fish, where  $D_F$  is the diffusion coefficient for fast fish,  $D_S$  is the diffusion coefficient for slow fish, and  $\beta_F$  and  $\beta_S$  are the rates of upstream advection for fast and slow fish, respectively. Because Eqs. 3 and 4 are uncoupled, the solution to this population heterogeneity model for  $P(x, t)$ , the spatial-temporal density of fish given an instantaneous point release of  $P_0$  fish, is the weighted sum of the solutions to Eqs. 3 and 4, so

$$P(x, t) = Z \left( \frac{P_0}{2\sqrt{\pi D_F t}} \right) \exp \left( \frac{-(x - \beta_F t)^2}{4D_F t} \right) + (1 - Z) \left( \frac{P_0}{2\sqrt{\pi D_S t}} \right) \exp \left( \frac{-(x - \beta_S t)^2}{4D_S t} \right) \tag{5}$$

where *Z* is the proportion of the population that is composed of fast fish. If  $Z = 1$  or  $Z = 0$ , Eq. 5 reduces to Eq. 2, the solution to the homogeneity model, i.e., the classic diffusion-advection model of a homogeneous population.

The variance in position given by Eq. 5 is

$$\text{Var}(X) = 2(ZD_F + (1 - Z)D_S)t + (Z)(1 - Z)(\beta_F - \beta_S)^2 t^2 \tag{6}$$

a quadratic function in time, *t*. This model admits the possibility of a nonlinear increase in variance with time, although the nonlinear component can be negligible over some time periods if the increase in variance due to the difference in advection rates is small relative to the diffusive spread within subgroups. When the advection terms are equal, Eq. 6 reduces to a linear equation in time, where the variance is the weighted average of the two subgroups.

Our empirical evidence that variability in the size and growth of bluehead chubs is related to their movement behavior motivates the concept of population het-

erogeneity in the model, but we do not know the basis for this heterogeneity. We do not attempt to mechanistically link size or growth to movement behavior in this model. Heterogeneous movement behavior could arise from a variety of types of population heterogeneity, including variation in size, growth, predation hazard, mating success, morphology, sex, or genotype per se (Gilliam and Fraser, *in press*). Eqs. 3 and 4 best describe scenarios where the movement behavior of individuals is fixed over a time scale that consists of many of the movement decisions in an individual's lifetime; e.g., when variation in movement behavior is caused by variation among individuals in sex, morphology, or genotype per se. However, under many scenarios Eqs. 3 and 4 will be good approximations over some time scales, such as those likely to include empirical studies; e.g., when variation in movement behavior is caused by variation among individuals in size, growth, predation hazard, or mating success. Our intent is that our analysis (1) presents sufficient evidence to justify population heterogeneity as a hypothesis for explaining leptokurtosis and (2) motivates research that attempts to identify mechanisms of heterogeneous movement in natural populations.

#### Evaluating the models

Using field data (Data Set II) on the spatial spread of bluehead chubs after one month and two months of movement we estimated the parameters of the model via a maximum likelihood fit of Eq. 5 to our field data (Hilborn and Mangel 1997). Parameters were estimated from the simultaneous, maximum likelihood fit of the model to the one- and two-month movement distributions. We then used the model with these parameters to predict the spatial spread of fish after three and four months of movement. We validated the model by comparing its predicted distributions to those from field data collected over the same time interval (three and four months). For each month we compared the overall form of the model's predicted distributions to that shown in the data using a two-tailed, one-sample Kolmogorov-Smirnov test. Parameterization of the population heterogeneity model with one- and two-month data and validation of the model's projected distributions after three and four months is a good test of the model's structure.

A stronger method for evaluating the population heterogeneity model is to examine its ability to describe the field data relative to alternative models. Therefore we parameterized two competing models: (1) the population homogeneity model consisting of one subgroup of diffusing fish, the classic simple diffusion-advection model with one diffusion coefficient and one upstream advection rate (two parameters total), and (2) a population heterogeneity model that consisted of three subgroups of diffusing fish, each having their own rates of diffusion (three parameters) and advection (three parameters), and relative proportions (two parameters)

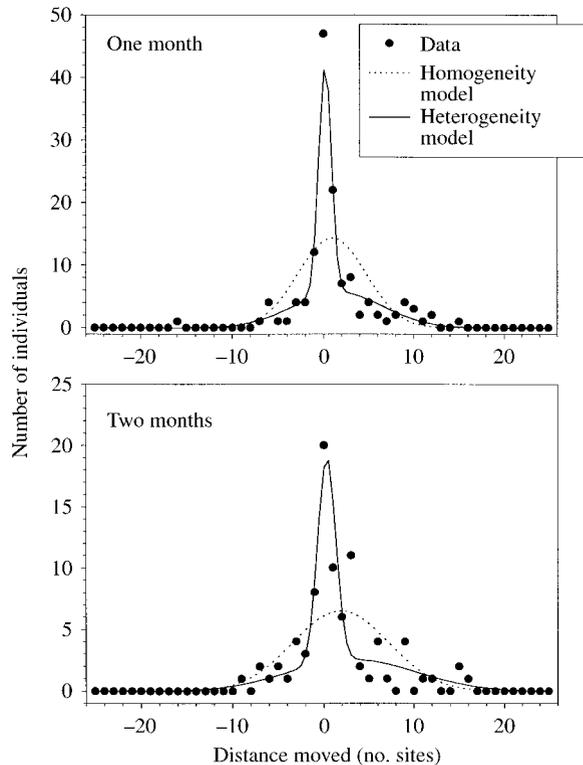


FIG. 8. The parameterizing fit of the population homogeneity and heterogeneity models to the field data after 1 and 2 mo of movement from a point release.

for a total of eight parameters. Our two alternative models were parameterized by the maximum likelihood fit to the data described above.

To evaluate our competing models we computed the net and absolute values of the deviations (deviation = model value - data value) between model and data values. We then compared these measures of fit among the competing models. Because the models have differing numbers of parameters we also conducted likelihood ratio tests using  $\chi^2$  statistics (Hilborn and Mangel 1997). These tests evaluate competing models by considering both fit to the data and number of parameters.

#### THEORETICAL STUDY: RESULTS

The population heterogeneity model described the spatial spread of fish over the 4-mo time period, and captured features of the spatial spread not described by the homogeneity model. For the heterogeneity model, the movement distributions of model fish fit well to those of real fish during the parameterization using the first 2 mo of data (Fig. 8). Estimates of diffusion coefficients for the heterogeneity model were consistent with the estimates of the advection rates: fish that diffused at a faster rate also showed greater upstream advection (Table 3). Parameters estimated from this fit were then used to predict movement distributions over

TABLE 3. Maximum likelihood parameter estimates (and 95% confidence intervals) for the population heterogeneity model with two subgroups.

Parameter	Symbol (units)	Estimate (95% CI)
Diffusion coefficient for fast fish	$D_F$ (sites <sup>2</sup> /d)	0.4119 (0.3189, 0.5461)
Diffusion coefficient for slow fish	$D_S$ (sites <sup>2</sup> /d)	0.0080 (0.0048, 0.0142)
Upstream advection for fast fish	$\beta_F$ (sites/d)	0.0541 (0.0284, 0.0801)
Upstream advection for slow fish	$\beta_S$ (sites/d)	0.0051 (-0.0001, 0.0104)
Proportion of fast fish	$Z$ (no. of fast fish/total no. of fish)	0.5222 (0.4388, 0.6077)

3- and 4-mo intervals, and the predictions of the heterogeneity model after 3 and 4 mo of movement also agreed with the empirical movement distributions (Fig. 9). In each case the heterogeneity model distribution is statistically indistinguishable from the empirical distribution (one-sample, two-tailed Kolmogorov-Smirnov test; 3 mo:  $D = 0.1349$ ,  $N = 59$ ,  $P > 0.20$ ; 4 mo:  $D = 0.1478$ ,  $N = 32$ ,  $P > 0.20$ ). The population heterogeneity model matched the leptokurtosis, variance, and overall distribution of the movement data.

In contrast, the simple diffusion model of a homogeneous population (the homogeneity model) substantially underestimated the center of the movement distributions for all months, while consistently overestimating the frequency of moves of intermediate length

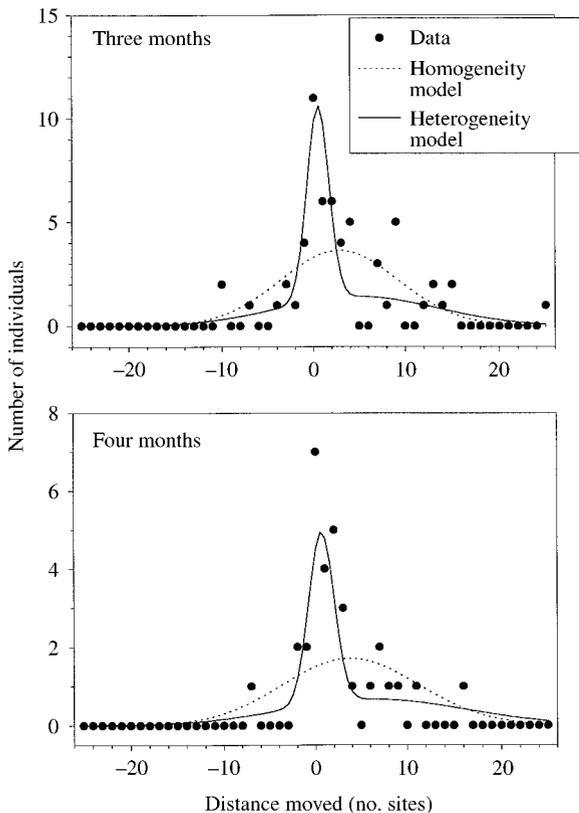


FIG. 9. The validation and fit of the population homogeneity and heterogeneity population models to the data after 3 and 4 mo of movement from a point release.

(Figs. 8 and 9); the homogeneity model was statistically distinguishable from the field data (Kolmogorov-Smirnov test; 3 mo:  $D = 0.1857$ ,  $N = 59$ ,  $P < 0.05$ ; 4 mo:  $D = 0.3153$ ,  $N = 32$ ,  $P < 0.05$ ). Analysis of the total net deviation (model - data) of the simple diffusion model at each distance moved, summed over all months and both directions of movement, quantitatively corroborated this visual trend (Fig. 10A). Both models with increased heterogeneity (two and three subgroups) showed little, if any, systematic bias relative to the field data.

Analysis of the total magnitude of deviation (absolute value of model - data), summed over all months

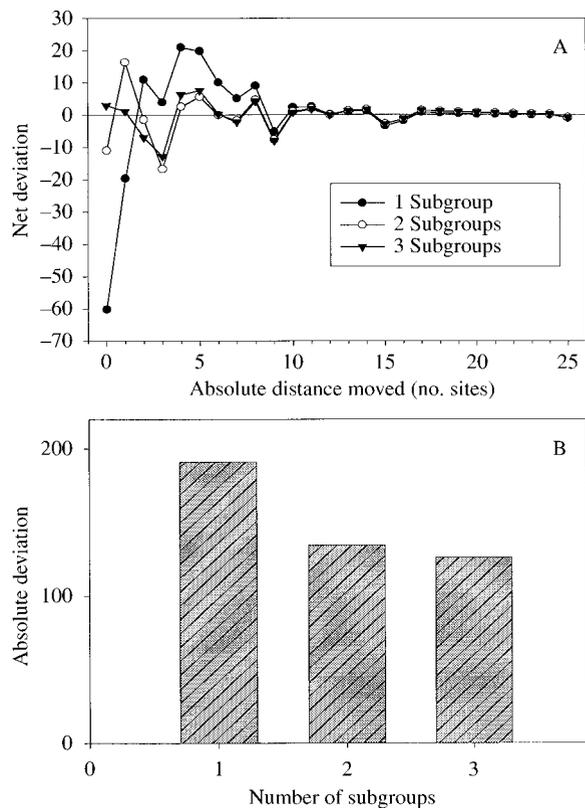


FIG. 10. The fit of the models consisting of one (homogeneity model), two (heterogeneity model), and three diffusing subgroups analyzed as (A) the total net deviations summed over all months and both directions, and (B) the total absolute deviations summed over all months and distances moved.

and distances moved, showed that a model population consisting of two diffusing subgroups is a dramatic improvement over the simple diffusion of a single subgroup, but a model population consisting of three diffusing subgroups results in little improvement in fit over the model consisting of only two subgroups (Fig. 10B). However, the likelihood ratio tests showed that both of the heterogeneity models produced significant improvements in fit relative to the homogeneity model (one subgroup vs. two subgroups:  $\chi^2 = 121.36$ ,  $df = 3$ ,  $P < 0.0001$ ; one subgroup vs. three subgroups:  $\chi^2 = 137.32$ ,  $df = 6$ ,  $P < 0.0001$ ), and the addition of a third subgroup of diffusing fish, although improving the fit only slightly quantitatively, nonetheless resulted in a statistically significant improvement in the model's performance (two subgroups vs. three subgroups:  $\chi^2 = 15.96$ ,  $df = 3$ ,  $P = 0.0012$ ).

## DISCUSSION

### *Characterizing stream fish movement*

Leptokurtosis was a feature of the movement distributions for three of the four species we studied over a one-month time interval. Over longer time scales leptokurtosis persisted over a four-month period for bluehead chubs and over a three-month period for creek chubs. Leptokurtosis appears in many other studies of movement by stream fish (e.g., Harcup et al. 1984, Heggenes et al. 1991, Gowan and Fausch 1996, Gilliam and Fraser, *in press*), and other taxa (Kareiva 1982, Brown and Zeng 1989, Olesen and Warncke 1989, Kot et al. 1996), dating to Dobzhansky and Wright's (1943) classic studies of fruit flies. Given its apparent pervasiveness, understanding the genesis of leptokurtosis should be an important contribution to ecology in general. For example, qualitative behavior of biological invasions depends upon the shape of the tails of the movement distribution (Kot et al. 1996, Turchin 1998); a species following our population heterogeneity model, which is the weighted sum of normal distributions, would have exponentially bounded tails and should not exhibit the unbounded invasion speeds that some other leptokurtic distributions can generate (Kot et al. 1996). Additionally, a population following the population heterogeneity model shows persistent leptokurtosis, a pattern consistent with the bluehead chub data with which the model was parameterized; however, the creek chub data indicated convergence to normality by the fourth month, and we suggest a modification of the heterogeneity model (i.e., allowing for exchange of individuals between "fast" and "slow" subgroups) that could account for that phenomenon (see below, *Extending the model*).

We observed upstream bias in the movement behavior in two of the four taxa that we studied. Upstream bias has been documented in studies of stream fish movement (e.g., Gatz and Adams 1994, Gowan and Fausch 1996), but does not appear to be a general pat-

tern (e.g., Stott 1967, Harcup et al. 1984, Clapp et al. 1990, Heggenes et al. 1991, Gilliam and Fraser, *in press*). Patterns of directionality may depend on fish density (Schlosser 1995) and time of year (Gowan and Fausch 1996). Mechanisms underlying directionality, or lack thereof, warrant further investigation.

Over our sampling period (March–August) the time of year and species had little effect on the movement behavior of these stream fish. Other studies have shown seasonal (Clapp et al. 1990, Gatz and Adams 1994, Gilliam and Fraser, *in press*) and species (Stott 1967, Hill and Grossman 1987, Gatz and Adams 1994, Schlosser 1995) effects to occur in some cases, but not in others. Since the majority of the individuals in the populations we studied were nonreproductive we suspect that the similarities in the movement distributions among species and recapture intervals reflect similarities in the perception and quality of resource patches (i.e., availability of food, safety from predators) among species and through time.

### *Population heterogeneity as an explanation for leptokurtosis*

The central goal of this study was to explore the relationship between phenotypic variability and movement behavior at the individual level and extend this relationship as a mechanism for population-level patterns of movement. We used empirical data to test for relationships between phenotype and the movement of individuals and utilized mathematical models to examine the relationship between individual variability in movement and population-level dispersal.

Empirically we found that size and growth were related to movement behavior using data on the two chub species. Moreover, bluehead chubs had a measurable level of population heterogeneity demonstrated by temporal correlations in growth: components of the population were persistently fast growers and others were persistently slow growers. Furthermore, probability of movement varied with growth over the course of two consecutive recapture intervals. Thus, we have observed that population heterogeneity in fitness-influencing attributes such as size and growth was related to heterogeneity in movement behavior. Others have shown similar relationships for a variety of taxa (e.g., Hart and Resh 1980, Kohler 1984, Kareiva and Odell 1987, Turchin 1998, Gilliam and Fraser, *in press*).

The modeling analysis indicated that population heterogeneity in movement behavior per se, regardless of its basis, can generate the population-level patterns observed in the field data, particularly the leptokurtosis.

Interestingly, although growth rates of bluehead chubs were temporally correlated and growth rates were in turn correlated with probability of movement, probability of movement was not temporally correlated through time at our temporal scale of measurement (1 mo). However, there was a nonsignificant trend that suggested correlation for bluehead chub and creek chub

data pooled together: of those fish that did move during a recapture interval, only 25% did not move during the following recapture interval, while of those fish that did not move during a recapture interval, 39% also did not move during the following recapture interval (if no correlation, the expected proportions are identical). For bluehead chub data considered alone, the proportions not moving during a recapture interval were 33% and 50%, respectively, for fish that had moved and had not moved during the previous recapture interval, but the trend is not statistically significant ( $\chi^2 = 1.67$ ,  $df = 1$ ,  $P = 0.6447$ ). In comparison, the population heterogeneity model with two subgroups, parameterized with the bluehead chub data alone, predicts that the proportions not moving ( $\int_{-0.5}^{0.5} P(x, 30) dx$ : the proportion centered at patch  $x = 0$  at the end of a 30-d interval) are 24% and 50%, respectively, for fish which had moved and not moved previously. This correlation arises because "fast" fish are more likely to move from the starting patch than are "slow" fish; moves are independent between recaptures within the fast and slow subgroups, but since fast fish remain fast and slow fish remain slow, the correlation exists for the total population. Studies of the short-term movement behavior of fish have shown that populations may demonstrate heterogeneity in individual movement behavior that is consistent with our modeling analysis (Kennedy 1981, Grant and Noakes 1987, McLaughlin et al. 1992, Bradford and Taylor 1997).

Our empirical results relating size and growth to movement motivate the hypothesis of population heterogeneity to describe leptokurtic movement patterns, but we do not know the basis for that heterogeneity. The correlation between growth and movement over one-month time scales suggests that it is persistent at that time scale and could act as a basis for population heterogeneity in movement behavior. Further studies are needed to define the roles of size and growth in determining movement behavior. Defining the exact quantitative costs and benefits of movement in terms of fitness could be difficult, but would prove useful in understanding heterogeneity in movement distributions, and therefore the kurtosis observed at the population level. A key, albeit difficult, step will be to explicitly link individual-level movement behavior *within an interacting population* to population-level patterns of dispersal (Turchin 1991, 1998, Tyler and Rose 1997).

Genetic explanations for leptokurtosis are also possible. Models have shown that population heterogeneity in movement is possible under certain scenarios (Hamilton and May 1977, McPeck and Holt 1992). Empirically, Sokolowski et al. (1997) have identified a single locus in fruit flies that influences movement behavior. They have identified fruit flies which move at variable rates—a result that agrees well with the seminal work of Dobzhansky and Wright (1943). Future work should uncover the relative influences of en-

vironmental and genetic effects on movement behavior in terms of fitness.

#### *Extending the model*

Since leptokurtosis is a common pattern in movement data, a model of movement with population heterogeneity, such as that described here, may prove useful whenever spatial structure is implicated. A benefit of this model is that it takes advantage of the diffusion framework for modeling population-level movement, which has a strong mathematical base (Okubo 1980, Turchin 1998). The linear increase in variance observed in our data is consistent with predictions from simple diffusion models (Skellam 1951; see Eq. 2), suggesting that although the Skellam model fails to describe the leptokurtosis, the diffusion approach is appropriate for quantifying stream fish movement (Zabel and Anderson 1997). The population heterogeneity model has the potential to accommodate linear or nonlinear increases in variance, depending on the values of the advection parameters (see Eq. 6). In the case of applying the model to the bluehead chub movement data the nonlinear effect exists because the advection term for fast fish is larger than that for slow fish, but the magnitude of the difference is negligible relative to the magnitudes of the diffusion coefficients; therefore the nonlinear effect is negligible over the four-month time scale for which we have data.

While the population heterogeneity model with two subgroups was a significant improvement upon the classic single subgroup (homogeneity) model, the heterogeneity model with three subgroups was, in turn, a statistically significant improvement upon the two subgroup version. However, we also note that the improvement in fit was quantitatively slight relative to the gain between the homogeneity model and the two subgroup heterogeneity model (Fig. 10B). Nonetheless, the prospect that increasing the number of subgroups can increase the model fit, perhaps significantly so, raises the specter of "parameter explosion" as three or more subgroups are modeled. An alternative would be to generalize the population heterogeneity idea by considering dispersing populations as having continuous probability distributions of diffusion coefficients. Thus, one or two parameters describing that distribution would replace the two or three diffusion coefficients for our present heterogeneity models. Advection might be then modeled as a correlate of diffusion if, e.g., faster diffusers also show greater advection, as in our present case.

Another extension of the model presented here would be to allow for exchange of individuals between the fast fish and the slow fish subgroups and to explore the relationship between exchange rate and kurtosis. Exchange among subgroups could account for the patterns of kurtosis observed in the creek chub: significant leptokurtosis after one month of movement followed by a decline in kurtosis and culminating in mesokurtosis

(i.e., kurtosis = 0) after four months of movement. Our empirical data suggest a shift in the composition of the creek chub population from heterogeneity to homogeneity that could be described by the heterogeneity model with exchange. For creek chubs captured in three consecutive months, movers composed 64% of the population during the first recapture interval and increased in relative abundance to compose 92% of the population during the second recapture interval; this suggests that the population became increasingly homogenized over the course of our study. In contrast, for bluehead chubs captured in three consecutive months, movers composed 60% of the population during both the first and second recapture interval; this suggests that the bluehead chub population maintained its heterogeneity over the course of our study. Numerical results suggest that exchange rates can influence population heterogeneity over time and therefore determine patterns of leptokurtosis (G.T. Skalski, *unpublished data*). Linking exchange rates to individual-level behavior would complete the relationship between foraging behavior at the individual level and leptokurtosis at the population level, thereby allowing population patterns to be interpreted in terms of the evolutionary fitness of individuals.

Future work in basic and applied ecology should incorporate population heterogeneity into models of movement and compare the results to situations lacking population heterogeneity. Theoretical results suggest that population heterogeneity in movement rates may explain certain species invasions (Shigesada et al. 1995) and increase the rate of spread of dispersing populations (Goldwasser et al. 1994, Kot et al. 1996). This approach should be applied to other situations where movement is thought to be important, including metapopulation dynamics, species interactions (McCaughey et al. 1996), and the conservation of fragmented populations. Such a comparison could be particularly interesting if heterogeneous movement is related to other forms of population heterogeneity, such as size, growth, genetic composition, or fitness.

#### ACKNOWLEDGMENTS

We thank John Connors of Durant Nature Park and his staff for allowing access to the study site. Harold Brady, Ken Collins, Brad Taylor, Peter Guillozet, Eric Harrold, Elizabeth Workman, Tyler Stanton, Eleanor Dunn, Vann Stancil, and Dawn O'Hara helped with the mark-recapture study. Steve Ellner, Jim Rice, Martha Groom, and Jacquelin Dietz provided useful suggestions. Financial support was provided by the U.S. National Science Foundation and the Agricultural Research Service of North Carolina State University.

#### LITERATURE CITED

- Bradford, M. J., and G. C. Taylor. 1997. Individual variation in dispersal behavior of newly emerged chinook salmon (*Oncorhynchus tshawytscha*) from the Upper Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Science* **54**:1585–1592.
- Brodmann, P. A., C. V. Wilcox, and S. Harrison. 1997. Mobile parasitoids may restrict the spatial spread of an insect outbreak. *Journal of Animal Ecology* **66**:65–72.
- Brown, J. H., and Z. Zeng. 1989. Comparative population ecology of eleven species of rodents in the Chihuahuan desert. *Ecology* **70**:1507–1525.
- Clapp, D. F., R. D. Clark, Jr., and J. S. Diana. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. *Transactions of the American Fisheries Society* **119**:1022–1034.
- Dobzhansky, T., and S. Wright. 1943. Genetics of natural populations, X. Dispersion rates in *Drosophila pseudoobscura*. *Genetics* **28**:304–340.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50–59.
- Gatz, A. J., and S. M. Adams. 1994. Patterns of movement of centrarchids in two warmwater streams in eastern Tennessee. *Ecology of Freshwater Fish* **3**:35–48.
- Gilliam, J. F., and D. F. Fraser. *In press*. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology*.
- Goldwasser, L., J. Cook, and E. D. Silverman. 1994. The effects of variability on metapopulation dynamics and rates of invasion. *Ecology* **75**:40–47.
- Gowan, C., and K. D. Fausch. 1996. Mobile brook trout in two high elevation streams: re-evaluating the concept of restricted movement. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:1370–1381.
- Grant, J. W. A., and D. L. G. Noakes. 1987. Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. *Journal of Animal Ecology* **56**:1001–1013.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature* **269**:578–581.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**:3–16.
- Harcup, M. F., R. Williams, and D. M. Ellis. 1984. Movements of the brown trout, *Salmo trutta* L., in the River Gwyddon, South Wales. *Journal of Fish Biology* **24**:415–426.
- Hart, D. D., and V. H. Resh. 1980. Movement patterns and foraging ecology of a stream caddisfly larva. *Canadian Journal of Zoology* **58**:1174–1185.
- Heggenes, J., T. G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences* **48**:757–762.
- Hengeveld, R. 1992. Potential and limitations of predicting invasion rates. *Florida Entomologist* **75**:60–72.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, New Jersey, USA.
- Hill, J., and G. D. Grossman. 1987. Home range estimates for three North American stream fishes. *Copeia* **1987** (2): 376–380.
- Holmes, E. E., M. A. Lewis, J. E. Banks, and R. R. Veit. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* **75**:17–29.
- Holyoak, M., and S. P. Lawler. 1996. Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. *Ecology* **77**:1867–1879.
- Ives, A. R., and W. H. Settle. 1997. Metapopulation dynamics and pest control in agricultural systems. *American Naturalist* **149**:220–246.
- Kareiva, P. M. 1982. Experimental and mathematical analyses of herbivore movements: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* **52**:261–282.
- Kareiva, P. M. 1983. Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture experiments. *Oecologia* **57**:322–327.
- Kareiva, P. M. 1990. Population dynamics in spatially com-

- plex environments: theory and data. *Philosophical Transactions of the Royal Society of London (B)* **330**:175–190.
- Kareiva, P. M., and G. Odell. 1987. Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *American Naturalist* **130**:233–270.
- Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* **56**:234–238.
- Kennedy, G. J. A. 1981. Individual variation in homing tendency in the European minnow, *Phoxinus phoxinus* (L.). *Animal Behavior* **29**:621–625.
- Kohler, S. L. 1984. Search mechanisms of a stream grazer in patchy environments: the role of food abundance. *Oecologia* **62**:209–218.
- Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* **77**:2027–2042.
- McCauley, E., W. G. Wilson, and A. M. de Roos. 1996. Dynamics of age-structured predator-prey populations in space: asymmetrical effects of mobility in juvenile and adult predators. *Oikos* **76**:485–497.
- McCulloch, C. E., and M. L. Cain. 1989. Analyzing discrete movement data as a correlated random walk. *Ecology* **70**:383–388.
- McLaughlin, R. L., J. W. A. Grant, and D. L. Kramer. 1992. Individual variation and alternative patterns of foraging movements in recently emerged brook charr (*Salvelinus fontinalis*). *Behaviour* **120**:286–301.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* **140**:1010–1027.
- Menhinick, E. F. 1991. The freshwater fishes of North Carolina. North Carolina Wildlife Resources Commission, Raleigh, North Carolina, USA.
- Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, New York, New York, USA.
- Olesen, J. M., and E. Warncke. 1989. Temporal changes in pollen flow and neighborhood structure in a population of *Saxifraga hirculus* L. *Oecologia* **79**:205–211.
- Porter, J. H., and J. L. Dooley. 1993. Animal dispersal patterns: a reassessment of simple mathematical models. *Ecology* **74**:2436–2443.
- Schlosser, I. J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology* **76**:908–925.
- Shigesada, N., K. Kawasaki, and Y. Takeda. 1995. Modeling stratified diffusion in biological invasions. *American Naturalist* **146**:229–251.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196–218.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Freeman, San Francisco, California, USA.
- Sokolowski, M. B., H. S. Pereira, and K. Hughes. 1997. Evolution of foraging behavior in *Drosophila* by density-dependent selection. *Proceedings of the National Academy of Science* **94**:7373–7377.
- Stott, B. 1967. The movements and population densities of roach (*Rutilus rutilus* (L.)) and gudgeon (*Gobio gobio* (L.)) in the River Mole. *Journal of Animal Ecology* **36**:407–423.
- Taylor, A. D. 1990. Studying metapopulation effects in predator-prey systems. *Biological Journal of the Linnean Society* **42**:305–323.
- Taylor, A. D. 1991. Metapopulations, dispersal, and predator-prey dynamics: an overview. *Ecology* **71**:429–433.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.
- Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**:1253–1266.
- Turchin, P. 1998. Quantitative analysis of movement and spatial population dynamics. John Wiley, New York, New York, USA.
- Turchin, P., and W. T. Thoeny. 1993. Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. *Ecological Applications* **3**:187–198.
- Tyler, J. A., and K. A. Rose. 1997. Effects of individual habitat selection in a heterogeneous environment on fish cohort survivorship: a modelling analysis. *Journal of Animal Ecology* **66**:122–136.
- Walde, S. 1994. Immigration and the dynamics of a predator-prey interaction in biological control. *Journal of Animal Ecology* **63**:337–346.
- Warren, P. H. 1996. The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. *Oecologia* **105**:132–140.
- Zabel, R. W., and J. J. Anderson. 1997. A model of the travel time of migrating juvenile salmon, with an application to Snake River spring chinook salmon. *North American Journal of Fisheries Management* **17**:93–100.
- Zar, J. H. 1996. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.