Sex-biased dispersal in a salmonid fish

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We tested the hypothesis that dispersal is sex biased in an unexploited population of brook trout, *Salvelinus fontinalis*, on Cape Race, Newfoundland, Canada. Based on the assumptions that trout are promiscuous and that reproductive success is limited primarily by either number of mates (males) or fecundity (females), we predicted that males would disperse greater distances than females. We also tested the hypothesis that trout populations comprise stationary and mobile individuals, predicting that males have greater mobility than females. Based on a mark–recapture study of 943 individually tagged fishes, 191 of which were recaptured over 5 years, we find strong support for our hypothesis of male-biased dispersal in brook trout. Averaged among all 11 resampling periods, males dispersed 2.5 times as far as females; during the spawning period only, male dispersal exceeded that by females almost fourfold. Both sexes were heterogeneous with respect to movement, with a lower incidence of mobility among females (29.6%) than males (41.1%); mobile males dispersed six times further than mobile females. We conclude that this sex bias reduces mate competition among male kin and decreases the probability that males will reproduce with related females.

Keywords: sex-biased dispersal; brook trout; stationary and mobile individuals; Newfoundland; *Salvelinus fontinalis*

1. INTRODUCTION

Dispersal is one of the most fundamental life-history responses to spatially and temporally variable environments. Movement potentially influences individual fitness, population dynamics, genetic variation within populations, gene flow among populations and the probability of colonizing new habitats (Roff 2002). For a number of species of birds and mammals, one sex disperses greater distances than the other. When the fitness consequences of acquiring and defending breeding resources differ between males and females, Greenwood (1980, 1983) predicted that the sex that gains more from prior ownership of a territory (males in birds, females in mammals) would be favoured by selection to disperse less. In addition to resource competition, sex biases in dispersal also appear to covary with mating system. Females disperse further than males in socially monogamous birds (Greenwood 1980; Greenwood & Harvey 1982), whereas dispersal tends to be male biased among polygamous and promiscuous mammals (Dobson 1982).

Patterns of sex-biased dispersal have been variously ascribed to inbreeding avoidance, competition for mates and competition for breeding resources (Pusey 1987; Johnson & Gaines 1990). Based on game-theoretic models of kin selection, Perrin & Mazalov (1999, 2000) concluded that competition among kin, on its own or in conjunction with inbreeding avoidance, can produce the patterns of movement that are widely documented for mammals and birds. The primary reason for this is that competition among kin reduces inclusive fitness and should thus be avoided.

The question of whether avoidance of kin competition can lead to sex differences in dispersal appears to depend

on the likelihood that males and females compete for the same resources. This can be viewed as the difference in relative magnitude of two types of competition among kin. The term ‘local mate competition’ (LMC) was coined by Hamilton (1967) to describe competition for mates by relatives of the same sex. In polygamous mating systems, within which male reproductive success is likely to be limited primarily by the number of females with whom they mate, LMC is probably higher for males. By contrast, ‘local resource competition’ (LRC; Clarke 1978) among relatives for limited breeding resources is likely to be greater among females when males contribute little, if any, parental investment. Perrin & Mazalov (2000) argue that the strength of the sex bias in dispersal patterns depends on a balance between local competition among kin for mates (LMC) and for resources (LRC). When local competition affects males and females equally (monogamous systems), or when female reproductive success is limited primarily by externally derived breeding resources in polygynous or promiscuous systems, dispersal is not expected to be sex biased. Alternatively, male-biased dispersal will be favoured within populations for which:

- (i) males and females are not monogamous;
- (ii) male reproductive success is limited primarily by the number of mating opportunities, leading to high LMC in the absence of dispersal; and
- (iii) female reproductive success is limited primarily by her own rate of processing resources, rather than by the resources themselves, resulting in low or negligible LRC in the absence of dispersal (Perrin & Mazalov 2000).

There is reason to believe that these conditions for male-biased dispersal exist in the fish family Salmonidae (trout, salmon and char etc.). With few exceptions (e.g. grayling and *Thymallus* spp.), salmonids reproduce in

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autumn during a two to five week spawning period. Once a female has selected a site for egg deposition, she is courted by more than one male who aggressively competes with other males for the opportunity to fertilize her eggs (Fleming 1998; Marschall *et al.* 1998). Genetic studies of individual reproductive success support the assumption that salmonids are promiscuous (Garant *et al.* 2001; Jones & Hutchings 2002), and the absence of any form of parental care by males, including nest site preparation and construction, is consistent with the hypothesis that a male's reproductive success is limited primarily by the number of females with whom he can mate. Among fishes for which parental care is either minimal or lacking, it is commonly held that a female's reproductive success is limited primarily by the number of eggs that she is able to produce (Stearns 1992; Wootton 1998; Roff 2002).

To date, studies of sex-biased dispersal have been limited almost entirely to birds and mammals. With the possible exception of one marine species (the great white shark *Carcharodon carcharias* (Pardini *et al.* 2001)), there is little evidence that dispersal by females differs significantly from that by males within or among natural populations of fishes. This paucity of empirical work provided impetus for our examination of sex-biased dispersal in a riverine salmonid fish endemic to eastern North America, the brook trout (*Salvelinus fontinalis*). The mating system and reproductive behaviour of this species appears to be well described by the three conditions on which Perrin & Mazalov (2000) predicted dispersal to be male biased. Thus, our study provided an opportunity to test their prediction. Second, the analytical framework recently developed by Rodriguez (2002) to model the movements of stream-dwelling fishes allowed us to test the hypotheses that brook trout populations comprise stationary and mobile individuals, reflecting individual variation in mobility, and that males have greater mobility than females. Following Howard (1960), we consider dispersal to be 'the permanent movement an individual makes from its birthsite to the place where it reproduces or would have reproduced had it survived and found a mate'.

2. MATERIAL AND METHODS

(a) Study population

The population of brook trout inhabiting Freshwater River on Cape Race, southeastern Newfoundland, Canada, for which extensive life-history data are available (Hutchings 1991, 1993, 1994, 1996), is ideally suited for ecological study. Brook trout is the only fish in the river and the population is not subjected to avian forms of predation, negating the potential influence of interspecific competition and predation on life history and movement; in addition, the population is unexploited and is otherwise unaffected by anthropogenic disturbance (Hutchings 1993, 1994, 1996). The 50 m cliff at which the river enters the sea effectively prevents migration to other rivers, rendering the population closed and genetically distinct (Ferguson *et al.* 1991). Freshwater River is 2.2 km in length; average width and depth measure 3.41 ± 1.98 (s.d.) m and 16.8 ± 7.3 cm, respectively. From a life-history perspective, Freshwater River trout mature at small sizes (80–100 mm), at young ages (2–3 years) and experience low post-reproductive, overwinter survival (10–15%). Females are distinguished by the production of fewer than 100 large eggs (typically 4–5 mm diameter) and high

proportional allocation of body tissue to gonads (15–20% of body weight).

(b) Mark-recapture experiment

Passive integrated transponder (PIT) tags (Biomark) were used to document the movements of 943 trout in Freshwater River. PIT tags are small (12.0 mm × 2.1 mm) glass cylinders comprised of a coil and an integrated circuit, programmed to transmit one of some billions of codes. An induction coil is used to energize each tag, causing them to transmit their corresponding 10-digit alphanumeric code to the digital display of the reader in which the coil is housed. The tags were inserted into the body cavity of anaesthetized individuals through a 3 mm long incision immediately anterior to the base of the anal fins. The adipose fin was marked by a fin clip to identify tagged individuals upon recapture.

Trout were initially captured by an electrofisher (Smith-Root Model 12A) from one of 38 sections of river averaging 27.5 ± 3.3 (s.e.) m in length. These river sections, separated by very short (less than 1 m) stretches of fast-flowing water, were chosen to correspond broadly to prominent features of stream morphology. Tags were inserted into 354 individuals between 11 June and 17 June 1995, and into 589 individuals between 11 June and 13 June 1996. All fishes were returned to their stream section of capture once they had fully recovered from the tagging procedure. Post-tagging mortality was nil prior to the return of fishes to the river. To sample tagged individuals, the entire length of the 2.2 km long unobstructed section of river upstream of the mouth was electrofished twice annually in spring (between 26 May and 13 June) and in autumn (between 26 September and 3 October) from 1995 until 2000, when the number of recaptures had declined to nil. During the resampling phase of the study, the river was divided into 59 sections, averaging 33.9 ± 2.7 (s.e.) m in length. The average section-length did not differ between the tagging and recovery periods ($F_{1,95} = 2.21$, $p = 0.14$). The timing of the autumn sampling periods coincided with spawning, which allowed us to sex any tagged individuals, using external characteristics (e.g. extrusion of milt, visible evidence of eggs beneath the body wall and sexual differences in the shape of the urogenital opening).

(c) Statistical analyses

Differences in mean dispersal distance between the sexes were initially examined by one-way analyses of variance; statistical significance was based upon 1000 randomizations of the data (Manly 1991). We then modelled the frequency distributions of lifetime distances travelled by individuals from the locations at which they were originally marked. Here, we fit our movement data to the continuous, negative exponential functions developed by Rodriguez (2002) to describe the frequency distribution of the number (N) of individuals recaptured between the lower (X_L) and upper sections (X_U) of various distance classes away from the location of original capture, i.e. $N(X_L, X_U)$.

To obtain the expected number of individuals recaptured in a given distance class

$$N(X_L, X_U) = N_0 s \pi C(X_L, X_U), \quad (2.1)$$

where N_0 is the number of individuals originally marked, s is the probability of survival during the study period, π is the probability of recapture, and $C(X_L, X_U)$ represents one of two cumulative distribution functions to describe the proportion of marked individuals recaptured between the lower (X_L) and upper (X_U) boundaries of each distance class. The form of the

cumulative distribution function depends on whether the population is best described as a homogeneous group of individuals, all of whom have similar probabilities of dispersal, or whether the population is heterogeneous, being comprised of a relatively stationary group and a relatively mobile group. For relatively homogeneous populations,

$$C(X_L, X_U) = e^{-\lambda X_L} - e^{-\lambda X_U}, \quad (2.2)$$

where λ is the inverse of mean dispersal distance. For more heterogeneous populations,

$$C(X_L, X_U) = p(e^{-\lambda_s X_L} - e^{-\lambda_s X_U}) + (1 - p)(e^{-\lambda_m X_L} - e^{-\lambda_m X_U}), \quad (2.3)$$

where λ_s and λ_m represent the inverse of mean dispersal distances for stationary and mobile individuals, respectively, and p is the proportion of stationary individuals in the population. Equations (2.2) and (2.3) are referred to as the one- and two-group models.

Treating each sex separately, the one- and two-group models were fitted to the observed number of recaptures in 29×50 m distance classes, ranging from 0 (those fishes recaptured in the stream sections in which they were originally marked) to 1400 m (those fishes recaptured 1376–1425 m from the sections in which they were originally marked). Two parameters were estimated for the one-group model ($N_0 s \pi$ and λ) and four for the two-group model ($N_0 s \pi$, p , λ_s , λ_m). Parameter estimates were those that minimized the residual sum of squares for each model, as determined by the nonlinear regression model function in S-PLUS (Venables & Ripley 1998). (Although 943 fishes were initially marked, the number of tagged males and females could not be ascertained because of the low confidence with which individuals can be sexed externally in June. This is why N_0 had to be estimated in combination with the parameters s and π .)

To determine the nonlinear function that provided the better fit to the dispersal data for male and female trout, the Akaike Information Criterion (AIC), corrected for small sample size (Hurvich & Tsai 1989), was calculated for the one- and two-group models. The model that provided the better fit to the observed data was the model with the lower AIC.

3. RESULTS

(a) Direct estimates of dispersal

The recapture of marked individuals allowed for direct estimation of dispersal by brook trout in Freshwater River. Of the 943 trout marked with PIT tags, 273 (29.0%) were recaptured at least once. Among the recaptured individuals were 94 males, 97 females and 82 fishes of undetermined sex. The average number of recaptures per recaptured individual was independent of sex, distance from tagging location and year of tagging ($F_{4,193} = 0.83$, $p = 0.459$) and averaged 1.50 ± 0.06 for all 191 sexed individuals. The maximum number of individual recaptures was six, recorded for a male tagged in 1996, at a length of 95 mm, and recaptured twice annually from 1997 to 1999.

There were no significant differences in body size at tagging between recaptured males and females within or between years. The average lengths of recaptured females tagged in 1995 (89.9 ± 2.7 (s.e.) mm, $n = 21$) and in 1996 (94.0 ± 1.1 mm, $n = 76$) did not differ from the lengths of

Figure 1. Dispersal distances of female ($n = 97$) and male ($n = 94$) brook trout in Freshwater River, Cape Race, Newfoundland. The positive values represent dispersal upstream of an individual's tagging location; the negative values represent dispersal downstream of an individual's tagging location.

recaptured males tagged in 1995 (95.1 ± 0.9 mm, $n = 24$; $F_{1,43} = 1.74$, $p = 0.194$) or in 1996 (94.7 mm ± 1.4 , $n = 70$; $F_{3,187} = 0.92$, $p = 0.431$), respectively. Pooling data for fishes tagged in 1995 and 1996, the average length of recaptured males and females was 94.1 ± 1.3 mm and 93.1 ± 1.1 mm, respectively.

Dispersal, operationally defined here as the distance between an individual's last known location and its tagging location, was independent of body size. Among females, there was no association between length at tagging and lifetime displacement from each individual's tagging location ($r = -0.05$, $p = 0.63$). Although the negative correlation between length and dispersal distance among males was statistically significant ($r = -0.21$, $p = 0.042$), the variation in dispersal distance explained by length was very low (4.4%). Indeed, the exclusion of a single outlier (a 77 mm male that had dispersed 1360 m) rendered the correlation insignificant ($r = -0.15$, $p = 0.14$).

Male brook trout dispersed almost 2.5 times the distance traversed by females. On average, males displaced themselves 195.4 ± 36.5 m ($n = 94$) from their tagging location compared with 81.5 ± 23.4 m ($n = 97$) by females ($F_{1,189} = 7.01$, $p = 0.009$). Among the few (5.2%) females that dispersed more than 250 m, these movements were undertaken in an upstream direction from the site of initial tagging (figure 1). By comparison, of the 23.4% of males that dispersed more than 250 m, roughly equal numbers moved upstream and downstream of their tagging location.

(b) Effects of spawning on individual movement

The differences in displacement from tagging location between the sexes differed between the spring and autumn recapture periods (table 1). Average dispersal by males recaptured in autumn immediately prior to spawning was significantly different from that by males recaptured during the non-spawning period and by females irrespective of recapture period ($F_{3,279} = 5.37$, $p = 0.001$). Although

Table 1. Distance between final recapture and tagging locations (± 1 s.e.) by male and female brook trout during non-spawning (spring) and spawning (autumn) recapture periods in Freshwater River, Newfoundland.

recapture period	sex	distance from tagging location (m)		
		mean	median	<i>n</i>
non-spawning	male	91.5 $\pm$ 29.8	0	79
	female	73.9 $\pm$ 23.9	2.0	85
spawning	male	229.5 $\pm$ 47.9	77.5	54
	female	63.8 $\pm$ 21.6	12.0	65

Figure 2. Frequency distribution of dispersal distances by male (open triangles) and female (closed triangles) brook trout in Freshwater River, Cape Race, Newfoundland. The lines represent the fit of the dispersal data to the two-group model (equation (2.3)) described in § 2.

average dispersal distance during the non-spawning period did not differ between sexes ($F_{1,162} = 0.22$, $p = 0.64$), the distance travelled from the tagging location by males recaptured during the spawning period was almost four times greater than that of females ($F_{1,117} = 11.14$, $p = 0.001$). Among females, there were no differences in distance travelled from tagging location between the spawning and non-spawning seasons ($F_{1,148} = 0.09$, $p = 0.763$).

(c) *Quantitative models of dispersal*

For both males and females, the two-group model provided a better fit to the frequency distributions of dispersal distances than the one-group model (figure 2). Among females, the AIC for the two-group model (residual standard error = 0.0056, $p < 0.001$) was 14.64 less than the AIC for the one-group model. Similarly, among males, the AIC for the two-group model (residual standard error = 0.0106, $p < 0.001$) was 11.26 lower than that for the one-group model. Differences in AIC of more than 7 indicate a clearly superior fit of the data to the model with the lower AIC (Burnham & Anderson 1998). The better fit provided by the two-group model indicates that both sexes contain a mixture of stationary and mobile individuals, as indicated by visual inspection of figures 1 and 2. Based on the estimates of p for each of the two-group

models (table 2), 41.1% of the male population comprises mobile individuals compared with 29.6% for females. The parameter combination $N_0 s \pi$ for the two-group models was the same for both sexes (94.0 ± 4.0 s.e.).

Parameter estimates for λ_s and λ_m in the two-group model provide additional support for the observation that male trout disperse greater distances than females. Calculated as $\log(2)/\lambda_s$ (Rodriguez 2002), the median dispersal distance of stationary individuals was similar between sexes, being 7.5 and 10.8 m for males and females, respectively (table 2). However, comparing the mobile fractions of the male and female populations, the median dispersal distance ($\log(2)/\lambda_m$) of males (346.6 m) was six times greater than that of females (57.8 m).

To examine whether stationary and mobile individuals differed phenotypically from one another, we compared the average lengths of mobile and stationary males and females, using the estimates of p derived from the two-group models (table 2). Ranking individuals by dispersal distance (from lowest to highest), we considered mobile individuals to be represented by the upper $(1 - p)$ fraction of individuals within each sex, that is, the uppermost 41.1% and 29.6% of males and females, respectively. Stationary individuals would thus represent the lowest percentage of p of the male and female populations, respectively. Comparing the average length at tagging, stationary males (96.6 ± 1.7 (s.e.) mm) and stationary females (95.0 ± 1.3 mm) were significantly longer, respectively, than mobile males (90.5 mm; $F_{1,92} = 5.72$, $p = 0.018$) and mobile females (89.0 ± 1.7 mm; $F_{1,95} = 7.25$, $p = 0.008$).

4. DISCUSSION

We draw two primary conclusions from our study of movement by marked individuals in an unexploited population of brook trout. First, we reject the null hypothesis that dispersal does not differ between the sexes; there is considerable evidence of male-biased dispersal in brook trout. Second, neither males nor females can be considered homogeneous groups of individuals with respect to movement. Rather, males and females are each represented by stationary and mobile components, a reflection of individual differences in lifetime movement within the river. All else being equal, males dispersed almost 2.5 times as far as females throughout their lives. Comparing the mobile components of each sex, males dispersed six times further than females, the sex for which the incidence of stationarity was also higher.

Table 2. Parameter estimates for the two-group model and estimates of median dispersal ($\log(2)/\lambda$) by male and female brook trout in Freshwater River, Newfoundland.

sex	population component	parameter estimate (s.e.)	median dispersal distance (m)
male	mobile	$\lambda_m = 0.002$ (0.001)	346.6
	stationary	$\lambda_s = 0.092$ (0.009)	7.5
	proportion stationarity	$p = 0.589$ (0.039)	—
female	mobile	$\lambda_m = 0.012$ (0.002)	57.8
	stationary	$\lambda_s = 0.064$ (0.005)	10.8
	proportion stationarity	$p = 0.704$ (0.047)	—

We have interpreted the distance between an individual's final recapture location and its tagging location as being indicative of an individual's dispersal from its location of birth. Given that the youngest individuals among those that were tagged were 1 or 2 years of age (based on two length-at-age keys (Hutchings 1993; A. J. Wilson, unpublished data)), our absolute estimates of dispersal probably represent underestimates of the true dispersal distances, an underestimation that will not qualitatively affect our results. Crucial to the interpretation of our results, however, is our implicit assumption that males and females either do not differ in dispersal prior to attaining 70 mm in length or that female dispersal during the first 1 or 2 years of life is greater than males. Although we are unaware of any empirical basis for believing that females disperse further than males prior to maturity, it is an assumption that merits future testing.

To our knowledge, only one other study has documented statistically significant differences in within-population dispersal between the sexes in fishes. Comparing the mitochondrial DNA of great white sharks off South Africa, Australia and New Zealand, Pardini *et al.* (2001) concluded that males are more likely to undertake trans-oceanic migrations than females. Although empirical examinations of sex-biased dispersal in fishes are few, there is reason to believe that male-biased dispersal may not be uncommon, at least among those species for which males provide no parental care and for which female reproductive success is not limited by access to breeding resources. Within a population of rock-dwelling cichlids from the *Pseudotropheus* (*Maylandia*) complex, Knight *et al.* (1999) based their conclusion of male-biased dispersal on sexually divergent, albeit statistically nonsignificant, associations between relatedness and movement. Based on their finding that female guppies (*Poecilia reticulata*) preferentially associate with other females in spatially discrete schools, Griffiths & Magurran (1998) proposed that males may be more mobile than females within populations, allowing them to move opportunistically among schools in search of mates. Among populations, Hard & Heard (1999) reported a male bias in the straying of hatchery-reared chinook salmon (*Oncorhynchus tshawytscha*) to non-natal rivers, although it is not clear whether this difference could be attributed to higher at-sea mortality among females, a sex difference in survival that has been documented for other Pacific salmon (Holtby & Healey 1990). Evidence that dispersal may not differ between sexes is available for pink salmon (*O. gorbuscha* (Thedinga *et al.* 2000)), killifish (*Rivulus hartii* (Gilliam & Fraser 2001)) and galjoen (*Coracinus capensis* (Attwood & Bennett 1994)).

We conclude that male-biased dispersal in brook trout provides support for the prediction of Perrin & Mazalov (2000) that male-biased dispersal is favoured in promiscuous mating systems within which male reproductive success is limited primarily by mating opportunities, and female reproductive success is limited primarily by the ability to process, rather than to compete for, resources. Salmonids are promiscuous spawners (Fleming 1998; Marschall *et al.* 1998; Garant *et al.* 2001; Jones & Hutchings 2002), and the lack of parental care indicates that male reproductive success is limited primarily by the number of mates. The observation that distances from tagging location were greater among males recaptured during spawning than by males recaptured during non-spawning periods (table 1) is consistent with the hypothesis that dispersal by males is associated with mating.

Our suggestion that reproductive success in female brook trout is limited primarily by the ability to process resources, rather than by the resources themselves, is not unreasonable. It is generally assumed that fecundity in indeterminately growing organisms, which increases allometrically in most fishes (Wootton 1998), is limited primarily by a female's ability to process food resources and to transfer the energy gained to somatic growth and gonadal tissue (Stearns 1992; Roff 2002). Although we do not discount the possibility that female reproductive success can be affected by the availability of suitable spawning substrate, we are unaware of any studies that have documented density-dependent competition by salmonid females for nest sites in the wild. Indeed, for the brook trout inhabiting Freshwater River, considerable within-river variation in spawning density indicates that nest sites may not be limiting. Among 54 sections of Freshwater River sampled annually between 1993 and 1999, the number of spawning females per square metre ranged between 0.01 and 2.90 (J. A. Hutchings, unpublished data). Even within the primary breeding sites in the river, spawning densities vary three- and fourfold, indicating that spawning substrate may not typically constitute a limiting resource.

Brook trout appear to be heterogeneous with respect to mobility. For both males and females in Freshwater River, some individuals could be identified as stationary and others as mobile, with the percentage of mobile individuals being greater among males. Differences in mobility have been previously documented for brook trout. In early life, for example, short-term variation in behaviour is associated with individual differences in foraging strategy. Some individuals are relatively sedentary (sit-and-wait tactic), whereas others tend to be active (active search tactic) (Biro & Ridgway 1995; McLaughlin *et al.* 1999),

although body size, body shape and level of aggression appear to be correlated with mobility (McLaughlin *et al.* 1994, 1999). Although mobile brook trout were statistically smaller than stationary individuals in Freshwater River, it is not clear that the average 6 mm difference between the two types is biologically meaningful. Based on the fit of movement data to the one- and two-group models described in equations (2.2) and (2.3), Rodriguez (2002) previously concluded that brook trout populations comprise stationary and mobile components. Indeed, based on his analysis of 17 studies encompassing six species of salmonids, Rodriguez (2002) proposed that within-population differences in mobility can often be considerable.

Until further research on sex-biased dispersal has been conducted on salmonids, or on fishes in general, we have no means of assessing the generality of our findings. However, if male-biased dispersal is not uncommon, it could have important consequences for patterns of gene flow among populations and for the persistence of salmonid populations, many of which have either been extirpated or face increased risks of extinction (e.g. Nehlsen *et al.* 1991; COSEWIC 2002; NRC 2002). For example, if males are more likely to colonize rivers following the extirpation of local populations, natural re-colonization could be a relatively slow process because of comparatively low dispersal by females. Another consequence of male-biased dispersal may be that females within a population are more related to one another than males, an observation that has been made in river otters (*Lontra canadensis*) the males of which disperse greater distances than females (Blundell *et al.* 2002). Similarly, if migration rates are male biased, estimates of effective migration rate derived from mark-recapture studies may significantly overestimate the degree of genetic similarity between putative populations given the higher variance in individual reproductive success that is typical of males.

In summary, we provide direct quantitative evidence of male-biased dispersal in fishes. For the study population of Newfoundland brook trout, we propose that greater dispersal by males reduces mate competition among kin and decreases the probability that males will spawn with related females. Given the potential consequences of sex-biased dispersal to life history, fitness, genetic variation and conservation biology, we suggest that there is considerable merit in undertaking mark-recapture and genetic studies of sex-biased dispersal in fishes.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.