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Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes

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Abstract

Natal homing is a hallmark of the life history of salmonid fishes, but the spatial scale of homing within local, naturally reproducing salmon populations is still poorly understood. Accurate homing (paired with restricted movement) should lead to the existence of fine-scale genetic structuring due to the spatial clustering of related individuals on spawning grounds. Thus, we explored the spatial resolution of natal homing using genetic associations among individual Chinook salmon (*Oncorhynchus tshawytscha*) in an interconnected stream network. We also investigated the relationship between genetic patterns and two factors hypothesized to influence natal homing and localized movements at finer scales in this species, localized patterns in the distribution of spawning gravels and sex. Spatial autocorrelation analyses showed that spawning locations in both sub-basins of our study site were spatially clumped, but the upper sub-basin generally had a larger spatial extent and continuity of redd locations than the lower sub-basin, where the distribution of redds and associated habitat conditions were more patchy. Male genotypes were not autocorrelated at any spatial scale in either sub-basin. Female genotypes showed significant spatial autocorrelation and genetic patterns for females varied in the direction predicted between the two sub-basins, with much stronger autocorrelation in the sub-basin with less continuity in spawning gravels. The patterns observed here support predictions about differential constraints and breeding tactics between the two sexes and the potential for fine-scale habitat structure to influence the precision of natal homing and localized movements of individual Chinook salmon on their breeding grounds.

Keywords: Chinook salmon, dispersal, fine-scale genetic structure, movement, natal homing, spatial autocorrelation

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Introduction

The life histories of many animals involve round-trip migrations between habitats used for breeding, feeding, refuge, and other essential functions (Dingle 1996). Natal homing, in which an individual returns to its site of origin (Greenwood & Harvey 1982), is a key feature of this type of migration and is a hallmark of the life history of many salmonid fishes (e.g. of the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*). Despite the fact that homing is well-recognized and the physiological and behavioural mechanisms enabling natal homing in the freshwater phase have been extensively studied (e.g. Quinn & Dittman 1990; Dittman & Quinn 1996; Nevitt & Dittman 2004; Ueda 2005), the spatial scale of homing within local, naturally reproducing salmon populations is still poorly understood (Hendry *et al*. 2004; Quinn 2005).

Natal homing can be viewed as a hierarchical phenomenon in salmonids, with various selective pressures acting at

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different points in the return journey. At broad spatial scales (i.e. among rivers or 'natal regions' supporting distinct populations) the most important factor leading to the evolution of homing appears to be selection for returning individuals to appropriate habitats for breeding. Homing should increase the likelihood of successful reproduction if individuals returning to their natal habitat to breed are better suited to specific environmental conditions (Cury 1994; Hendry *et al*. 2004; Kolm *et al*. 2005). Indeed, the majority of individuals for most salmonids home successfully to their natal region; those that do not are identified as 'strays' (Hendry *et al*. 2004; Quinn 2005).

At smaller spatial scales homing patterns are less well known (Hendry *et al*. 2004; Quinn 2005). Work on homing in sockeye salmon (*Oncorhynchus nerka*) indicates that many individuals can home with high spatial resolution to specific incubation sites (i.e. specific stream reaches, ponds, or beaches in a natal lake, Varnavskaya *et al*. 1994; Quinn *et al*. 1999; Stewart *et al*. 2003; Quinn *et al*., in press). Individuals that distribute away from these natal sites within a population assumedly do so because they simply home less accurately or because they move purposefully to seek mates or suitable spawning locations (Esteve 2005). We describe this within-population movement as 'localized movement' to avoid confusion with the term 'straying', which is generally used to describe failure to home at a larger spatial scale, i.e. among populations (Cury 1994; Rieman & Dunham 2000; McDowall 2001; Hendry *et al*. 2004; Quinn 2005).

The spatial distribution and relatedness of individual salmon within a population therefore will be determined by a balance between precise natal homing and localized movements regardless of cause (see Blair & Quinn 1991; Dittman & Quinn 1996; Stewart *et al*. 2003; Rich *et al*. 2006). In this scenario, individual fish are likely to alter their homing and movement behaviour in response to various biological and habitat factors and for several reasons male and female salmon might adopt different strategies or be under different constraints. For instance, even where other pressures for precise homing are strong, some movement from specific natal spawning sites may be beneficial to avoid inbreeding between siblings or competition for mates (Pusey & Wolf 1996; Bentzen *et al*. 2001; Taggart *et al*. 2001; Garant *et al*. 2005). Given the breeding behaviour of Pacific salmon (genus *Oncorhynchus*, on which we focus), theory predicts that males should move more than females. Female Pacific salmon construct and defend nests or redds, which are excavated in stream gravels (Groot & Margolis 1991; Quinn & Foote 1994; Quinn 1999), whereas males play no significant role in this regard (Esteve 2005). In such mating systems the need to choose appropriate nesting sites is more important for females than for males (Greenwood 1980; Perrin & Mazalov 2000). It is intuitive that strong homing could facilitate strategic nest-site choices by females who gained experience with natal habitats as juveniles (see, e.g. Quinn *et al*. 1999; but see also Hendry *et al*. 2004). Furthermore, because females are paired physically with their nests their mating events are more likely to occur either nearby or within the same redd (Bentzen *et al*. 2001), whereas males, which face higher reproductive competition (Fleming 1998; Quinn 1999), may mate with females in various locations and over longer time periods (Healey & Prince 1995; Quinn *et al*. 1996; Esteve 2005). Thus, although both monogamous and polygamous matings have been documented for each sex in Pacific salmon (Wilson & Ferguson 2002; Mehranvar *et al*. 2004; Seamons *et al*. 2004; Kuligowski *et al*. 2005), the spatial and temporal nature of these matings may differ. This combination of factors may be expected to increase the precision of natal homing in females over males as well as constrain a female's ability to move once an initial nesting site has been chosen (Foote 1990; Hendry *et al*. 1995).

The spatial structure of spawning habitats may also be expected to influence the resolution of natal homing at fine scales and engender sex biases in localized movement. For instance, regions of a watershed with more fragmented spawning habitat may be characterized by greater environmental heterogeneity, providing an increased 'signal' in the localized olfactory cues fish use to determine natal sites and enabling more precise natal homing (see review in Hendry *et al*. 1995; Dittman & Quinn 1996; Stewart *et al*. 2003; Rich *et al*. 2006). Furthermore, where spawning gravels are continuous, females may be able to make more widespread exploratory forays before choosing an ultimate nesting site and therefore be more likely to breed further from their natal reach. If spawning habitat is fragmented or patchy, females moving shorter distances from their natal area would more likely encounter unsuitable conditions and return to their natal area to breed. Natal homing may thus be more accurate and localized movements more constrained for females in regions with fragmented distributions of spawning habitats.

In the case of males, individuals should seek as many mating opportunities as possible, although the relationship between this behaviour and habitat structure is more difficult to predict and may vary between initial exploratory movements during first arrival to a stream and subsequent movement after dominance hierarchies are established (Rich *et al*. 2006). On one hand, males in continuous habitat may not need to move very far to find mating opportunities, while in fragmented habitats longer-distance movements may be more likely as females are patchily distributed (see Rich *et al*. 2006 for similar but slightly contrasting predictions). In contrast, continuous habitat may facilitate scouting movements and lead to multiple matings across a larger spatial extent, while patchy or fragmented habitat may constrain movement by males. The costs of movement in these cases are somewhat unclear. Intuitively, movement

at these spatial scales should not be energetically costly for migratory salmon that travel many thousands of kilometres in their lifetimes (Healey 1991). At the same time, the increased aggression encountered by males moving into habitats with established dominance hierarchies may engender very real costs for male salmon (Rich *et al*. 2006). Male movement strategies may also be influenced by female densities, which will affect the likelihood of being successful in encountering mates with a 'sit and wait' strategy (Quinn 2005; Anderson 2006).

If the spatial structure of spawning habitats and sex-specific breeding strategies are important in shaping fine-scale homing and movement behaviour in salmon, their signatures should be evident in patterns of genetic relatedness among individual fish within river networks. Accurate homing and limited subsequent movement should lead to the existence of fine-scale genetic structuring due to the spatial clustering of related individuals on spawning grounds. Previous work within our study site, a network of streams considered to be a 'natal region' for Chinook salmon (*Oncorhynchus tshawytscha*) in central Idaho, USA, suggested genetic structure among local populations was influenced (albeit weakly) by basin and tributary geometry (Neville *et al*. 2006). In this study, we investigated structure at finer scales, asking whether localized patterns in the distribution of spawning gravels and sex were related to the magnitude and spatial extent of positive autocorrelation among individual genotypes in this system. Spatial autocorrelation statistics describe the degree to which self-similarity in a variable trait changes with distance, and have been used extensively in ecology and evolution to address a wide array of questions (Sokal & Oden 1978; Diniz-Filho & Malaspina 1995; Koenig 1999). In contrast to many studies in plants (e.g. Ruckelshaus 1996; Hardy *et al*. 2000; Kalisz *et al*. 2001; Marquardt & Epperson 2004; Snall *et al*. 2004; Vekemans & Hardy 2004), the use of spatial autocorrelation for evaluating genetic structure in animals has been limited because their higher dispersal potential is generally assumed to prohibit fine-scale genetic structure (Peakall *et al*. 2003; Double *et al*. 2005). However, the homing behaviour of salmon may be expected to create fine-scale genetic structure despite migrations covering thousands of kilometres in some cases. Here, we predicted that the spatial extent of genetic clustering would correspond with the spatial extent of clustering among Chinook salmon redds (the presence of which we assumed was an indicator of suitable habitat), providing evidence for the influence of the localized geometry of spawning gravels on natal homing. More specifically, we predicted genetic autocorrelation should be more pronounced in the portion of the study site with greater discontinuity in suitable spawning gravels. Secondly, we predicted genetic structuring would be most evident in females, which may be expected to home more accurately and are more closely constrained to local environments and less able to move during breeding.

Methods

Species and study system

Data were collected in 2002 from the Middle Fork Salmon River (MFSR), a relatively pristine tributary of the larger Snake and Columbia River systems, which drains 7330 km^2 of mountainous habitat in central Idaho (Fig. 1). Populations from the MFSR comprise a distinct 'major grouping' in the Interior Columbia River and are thus considered reproductively and demographically independent of other such groups (McClure *et al*. 2003). Chinook salmon begin entering the MFSR in early summer and stage for various periods of time (from weeks to months) before spawning in August and early September. Females construct redds by excavating stream substrates to form depressions within which eggs are deposited and buried (Healey 1991; Esteve 2005). As eggs are deposited, they are fertilized by one or more males and embryos incubate in the gravel to emerge as fry the following spring. Juveniles generally spend 1 year in their natal area before migrating seaward (Bjornn 1971), where they undergo rapid growth for 1–3 years. Most adult Chinook salmon returning to the MFSR are 4–5 years old (Kiefer *et al*. 2002).

During the Pleistocene, the upper sub-basin of the MFSR (including Sulphur creek and above; Fig. 1) was glaciated (McPhail & Lindsey 1986; Utter *et al*. 1989; Meyer & Leidecker 1999). Due to this historical geomorphic influence, the upper and lower sub-basins of the system differ in the composition of stream habitat. Deposits of glacial sediments in the upper sub-basin have created wide, open valleys (Bond & Wood 1978) with extensive reaches of pool-riffle sequences used by spawning salmon. In contrast, streams in the lower sub-basin flow through narrow, V-shaped valleys supporting short, noncontinuous reaches of spawning habitat (Isaak & Thurow 2006).

Data collection and analyses

Sampling. In August and September of 2002, tissue was obtained from adults that died on the spawning grounds throughout most of the occupied spawning areas in the MFSR (middle sections of the river were inaccessible, Fig. 1) and stored in 95% ethanol. The location of each carcass was recorded using a Global Positioning System (GPS; accuracy approximately < 12 m, although it should be noted that some carcasses may have drifted downstream). Total genomic DNA was extracted using DNeasy extraction kits (QIAGEN Inc.). Polymerase chain reactions (PCRs) and fragment analyses using an Applied Biosystems PRISM 3730 automated sequencer were performed by the Nevada Genomics Center (Reno, NV). Of an initial working set of 10 loci, we chose a subset of eight that could be genotyped reliably. The eight microsatellite loci, references, GenBank Accession nos, and PCR and thermal conditions are given in Table 1.

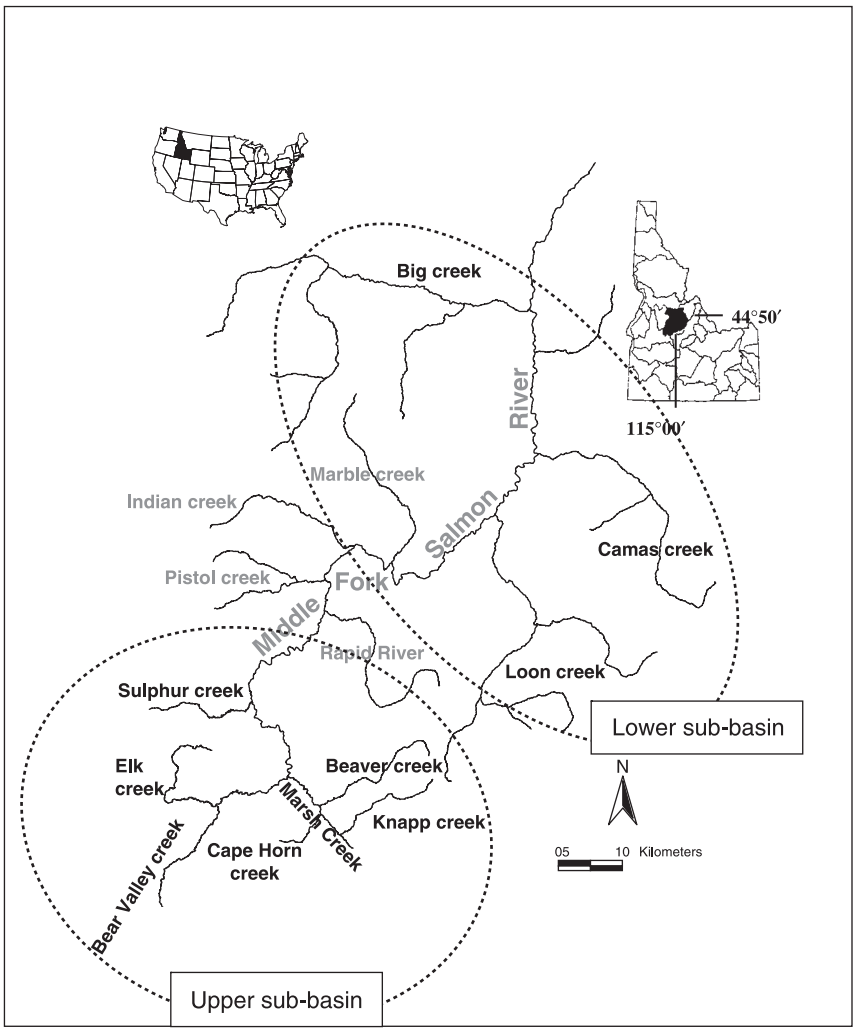

Fig. 1 Stream network in the Middle Fork Salmon River, Idaho used by Chinook salmon for spawning. Genetic samples were obtained from carcasses found within those major spawning aggregations shown with names of tributaries in black bold (tributaries with grey names were unsampled). Areas referred to as the upper- and lower-sub-basins in the text are circled.

Table 1 Microsatellite markers used to genotype Chinook salmon sampled in the Middle Fork Salmon River, with references and GenBank Accession no. Also given are the thermal protocols, and the amount of dNTPs and forward and reverse primer used in each 10-μL PCR

Marker	Reference	GenBank no.	Thermal protocol	dNTPS	Primer F/R
Otsg68	(Williamson *et al*. 2002)	AF393187	95° for 2 mins; 94°, 62°, and 72° each at 40 s, cycled 44 times; 72° for 5 min	0.5 μL	0.1 μL
Otsg249	(Williamson *et al*. 2002)	AF393192	‘	‘	‘
Ots3	(Banks *et al*. 1999)	AF107031	95° for 2 mins; 94°, 53°, and 72° each at 40 s, cycled 44 times; 54° for 40 min	0.54 μL	0.2 μL
Ots2M	(Greig & Banks 1999)	*	95° for 2 mins; 94°, 60°, and 72° each at 40 s, cycled 44 times; 60° for 40 min	‘	‘
Ogo4	(Olsen *et al*. 1998)	AF009796	‘	0.8 μL	‘
Ots10M	(Greig & Banks 1999)	*	‘	‘	‘
OtsD9	(Naish & Park 2002)	AY042709	‘	‘	‘
Ssa408	(Cairney *et al*. 2000)	AJ402725	‘	‘	‘

*, modifications of original primers (ots10 and ots2): ots2m F-GCC TTT TAA ACA CCT CAC ACT TAG
ots2m R-TTA TCT GCC CTC CGT CAA G
ots10M F-GGG CAT GTG TGT GTA GAA AGA
ots10M R-GGT CCC ATT GTC ATT ACT GCT AC

PCRs were performed in 10-μL reactions, each with 1 μL Titanium buffer, 0.2 μL Titanium *Taq*, approximately 20 ng of DNA, the dNTP and primer amounts given in Table 1, and the remainder made-up with water. Individuals were genotyped manually by Neville using GENEMAPPER version 3.0 (Applied Biosystems). The quality of DNA in many of our tissue samples was poor due to degradation of carcasses in the field. For quality control, therefore, we amplified each individual three times at each locus. Individuals were genotyped at a locus only if amplified successfully, consistently, and unambiguously at minimum twice for heterozygotes and three times for homozygotes.

Distribution of genotypes. We used the program GENALEX (version 5.1, Peakall and Smouse 2001; see also Peakall & Smouse 2005) to estimate the spatial extent and magnitude of positive correlation among individual multilocus genotypes across the landscape. GENALEX calculates the multilocus autocorrelation coefficient r among individual genotypes falling within various spatial distance classes. The r correlation coefficient is similar to Moran's I coefficient, and ranges from –1 to +1 (Peakall *et al*. 2003). The program requires matrices of squared genetic distances between all individuals, which were calculated as outlined in Peakall *et al*. (1995) and Smouse & Peakall (1999) and entered along with matrices of stream distances between all individuals. GENALEX determines error about r by bootstrapping, using random draws with replacement of the relevant pairwise comparisons for a given distance class. The estimated autocorrelation coefficient r is evaluated against the hypothesis of no autocorrelation ($r = 0$). The 95% confidence interval about the null hypothesis of no autocorrelation was determined by random permutation (see Peakall *et al*. 2003). Because GENALEX cannot handle missing data, we limited our dataset to individuals genotyped for at least six of the eight loci. In a few cases (see Results), we filled in remaining missing genotypes with the most common genotype (Peakall & Smouse 2001; Foley *et al*. 2004; Peakall & Smouse 2005). All analyses were performed with 1000 bootstraps and permutations.

The correlation coefficient r and associated error intervals were visualized as correlograms, which display r in relation to distance, i.e. across increments, or bins, for a given distance class (see Fig. 3 for examples). For instance, for a correlogram based on a distance class of 10 km, r is displayed for comparisons between individuals falling within the bins of 0–10 km, 10–20 km, 20–30 km, etc. We used distance classes of 1, 2, 5, 10, 20, and 40 km, which spanned both the smallest and largest spatial resolution possible for our dataset in each sub-basin. Within a given correlogram, we evaluated the magnitude and spatial extent of nonrandom genetic associations among individuals. The latter was based on the point at which r crosses the x-axis (= 0 autocorrelation). We also used a more conservative graphical interpretation that incorporates uncertainty in the r estimate and error about the null hypothesis of zero autocorrelation ($r = 0$, see above); in this framework, we accepted significant autocorrelation to exist only at distances where the point estimate of r is greater than the 95% confidence interval about zero and where the bootstrapped error bars about r are greater than zero (see Peakall *et al*. 2003).

Observed patterns of autocorrelation are the composite result of the true spatial patterns of genetic structure and the distance classes evaluated, which dictate which individuals and the number of individuals that are incorporated in to each estimate of r (Peakall *et al*. 2003; Vekemans & Hardy 2004). The spatial scale (distance class) for which data are summarized and analysed can therefore influence the outcome of spatial autocorrelation analyses. Thus, while the spatial extent of significant autocorrelation (i.e. the distance to which autocorrelation is positive, as interpreted either graphically or by the x-intercept as noted above) can be interpreted legitimately for a given spatial distance class or correlogram, it may change when evaluating different distance classes (Peakall *et al*. 2003). Therefore, we also evaluated composite graphs containing the results from the first distance bin assessed in each single correlogram, meaning that individuals were pooled into successively larger classes (0–1, 0–2, 0–5 km, etc., see also Primmer *et al*. 2006). This approach enables examination of how data pooling affects autocorrelation, and thus allows better evaluation of the true extent of detectable positive autocorrelation (see Double *et al*. 2005).

Based on habitat differences between the upper and lower sub-basins, we evaluated genetic autocorrelation patterns within each sub-basin separately. To evaluate differences in genetic autocorrelation between male and female salmon, we also estimated r separately for each sex.

Distribution of redds. Redd surveys were undertaken in 2002 as part of a complementary study, and further details of field and validation methods can be found in Isaak & Thurow (2006). Briefly, Chinook salmon redds were censused throughout the MFSR using low-level helicopter flights at the end of the spawning season. All redd locations were georeferenced using GPS. In sections where heavy tree canopy prevented aerial recording, GPS coordinates of redd locations were taken by trained observers who walked the stream.

Under the assumption that the occurrence of redds indicated the presence of suitable habitat, we quantified habitat patchiness based on the spatial extent of autocorrelation in the presence or absence of redds for comparison with genetic data. An Arc/Info macro was used to segment the stream network into 500-m intervals and assign redds to the appropriate stream segment (Isaak *et al*., unpublished). Autocorrelation analyses were performed

Fig. 2 Chinook salmon redd distributions from 2002 surveys in the Middle Fork Salmon River, Idaho. Each symbol represents one redd. Area in grey demarcates redds that were surveyed aerially, but were not included in autocorrelation analyses because of a lack of genetic samples from this region for comparison.

similarly to those using genotypes, i.e. with the approach of Peakall & Smouse 2001) but based on patterns in the presence or absence of redds between all paired stream segments in a given distance class. For these analyses, entries in the 'habitat distance matrix' consisted of a 0 distance if either both or neither stream segments in a pair contained redds (0–0 or 1–1 occupancy patterns) and a distance of 1 for pairs where one segment contained at least one redd and the other had no redds (0–1 or 1–0, see Peakall *et al*. 2003), thus characterizing at a given spatial scale the continuity among stream segments in the presence or absence of redds. This habitat matrix was compared to a geographical distance matrix giving the pairwise stream distances between the centres of all stream segments. Spatial autocorrelation in redd presence-absence was evaluated separately for each sub-basin and included only redds in these sub-basins (i.e. redds surveyed in the middle of the system where we had no genetic samples were excluded from analyses, see Figs 1 and 2).

Results

To provide a foundation for comparison with genetic data, we present results from analyses of spatial patterns among redds first.

Distribution of redds

Seventeen hundred thirty redds were built throughout 710 km of stream in the MFSR in 2002, for an overall average density of 2.44 redds/km (Fig. 2). In regards to the upper and lower sub-basins where we had genetic samples, 905 redds were built in the upper sub-basin throughout 175 km of stream for an average density of 5.18 redds/km,

and in the lower sub-basin there were 704 redds built throughout 313 km of stream for an average density of 2.25 redds/km.

Visual assessment of redd distributions suggested significant clumping of redds throughout the MFSR (Fig. 2), which was confirmed empirically by results from the analysis of autocorrelation in redd presence-absence among stream segments: positive autocorrelation was found for almost all distance classes evaluated, indicating that the distribution of redds was significantly nonrandom in both sub-basins. For each sub-basin, Table 2 summarizes the distance to which autocorrelation was positive based on both a graphical interpretation of significance (see Methods) and on the *x*-intercept. Figure 3 displays a subset of the same data graphically, using example correlograms for a 1- and 5-km distance, which show the autocorrelation statistic *r* as a function of distance.

In the upper sub-basin, autocorrelation in redd presence-absence was positive and significant for the first distance bin of every distance class evaluated and the spatial extent of autocorrelation was generally greater than that in the lower sub-basin, suggesting that redds were spatially clumped or more continuous for larger distances in the upper sub-basin (Table 2). For instance, for a 1-km distance class, autocorrelation remained positive out to 8 km or 14.8 km, respectively, based on either a graphical or *x*-intercept interpretation of significance (Fig. 3 panel a top; Table 2). In the lower sub-basin for a 1-km distance class, positive autocorrelation extended to 5 km (graphical interpretation) and 6.6 km (*x*-intercept; Fig. 3 panel b top). Similarly, when using a larger distance class of 5 km, positive autocorrelation in the upper sub-basin extended to 10 km when interpreted graphically, and to 32.8 km based on the *x*-intercept (Fig. 3 panel a bottom, Table 2). In the lower sub-basin for a 5-km distance class, autocorrelation was positive to 5 km (graphical interpretation) and 9.3 km (*x*-intercept; Fig. 3 panel b bottom, Table 2). With the exception of the 40-km distance class, where no

Table 2 Results of spatial autocorrelation analyses of Chinook salmon redd presence-absence among stream segments in the Middle Fork Salmon River. The table presents the spatial extent of positive autocorrelation, i.e. the distance to which autocorrelation was significantly positive as defined both by graphical interpretation using error (see Methods for description) or the *x*-intercept. For each, the upper sub-basin ('Upper') and lower sub-basin ('Lower') were analysed and interpreted separately. NS, not significant, meaning that the null hypothesis of 0 autocorrelation was not rejected for the first distance bin in that distance class, and therefore no spatial extent of autocorrelation could be defined

Distance class (km)	Distance of graphical significance (km)		*x*-intercept (km)	
	Upper	Lower	Upper	Lower
1	8	5	14.8	6.6
2	8	6	15.5	7.1
5	10	5	32.8	9.3
10	10	10	35.8	19.5
20	20	20	41.6	29.7
40	40	NS	55.7	0

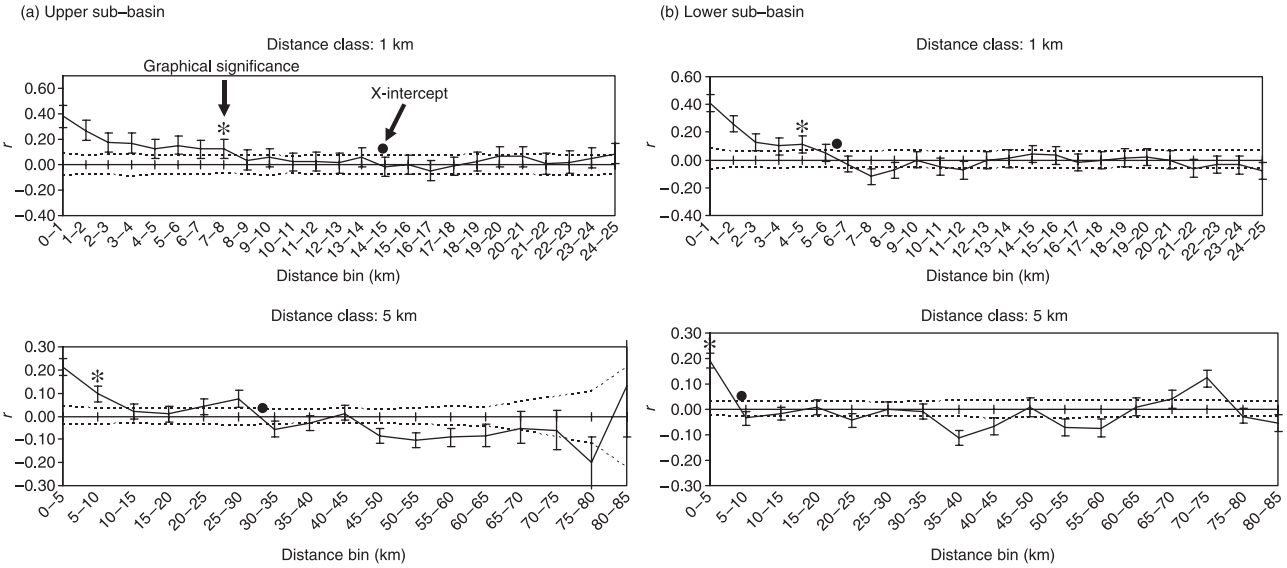

Fig. 3 Selected correlograms showing the autocorrelation coefficient *r* in relation to distance based on distance classes of 1 and 5 km for Chinook salmon **redd presence-absence** among stream segments in the Middle Fork Salmon River. Correlograms for the upper sub-basin are at left (a), those for the lower sub-basin are at right (b). Dashes bracket the 95% confidence intervals about the 0 autocorrelation value, representing the null hypothesis of no spatial structure; 95% confidence limits about *r* indicated by error bars. Distances to which autocorrelation was positive and significant based on graphical interpretation and the *x*-intercept are indicated by * and ●, respectively.

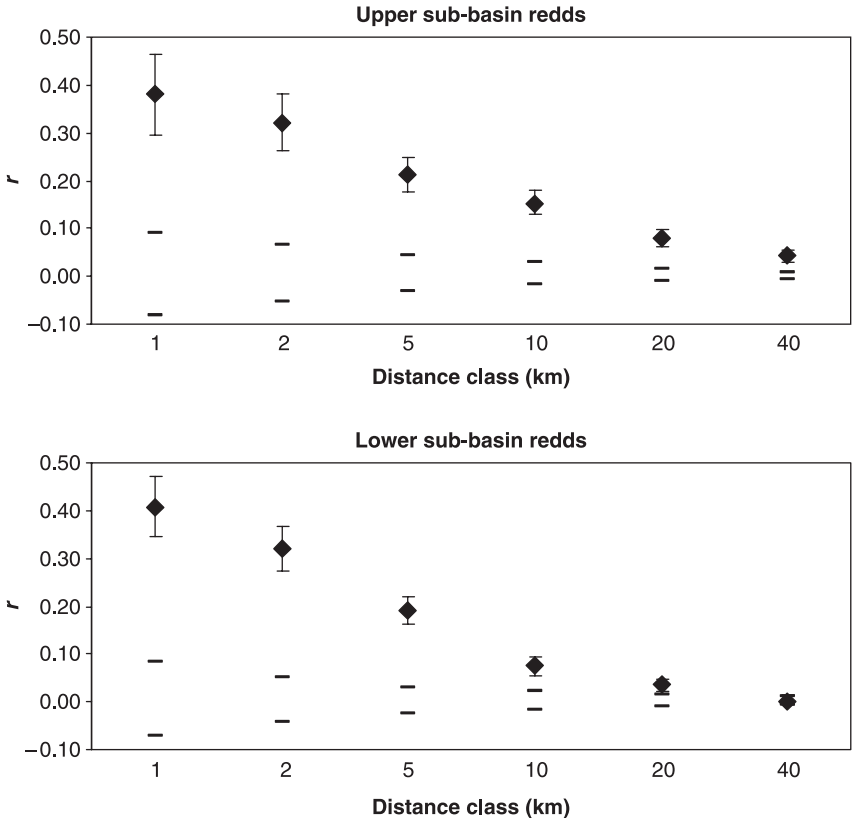

Fig. 4 Composite graph showing the autocorrelation statistic from the first distance bin in each single correlogram for Chinook salmon **redd presence-absence** in the upper (top) and lower (bottom) sub-basins. Thus, *r* was estimated as stream segments were pooled into successively larger distance classes, i.e. 0–1 km, 0–2 km, 0–5 km, etc. Dashes bracket the 95% confidence intervals about the 0 autocorrelation value, representing the null hypothesis of no spatial structure; 95% confidence limits about *r* indicated by error bars. This graph demonstrates how autocorrelation is affected by the distance class assumed, and shows the scale at which positive autocorrelation could be detected in each basin.

autocorrelation was observed in the lower sub-basin, the *x*-intercept was always substantially larger in the upper than in the lower sub-basin. The spatial extent of autocorrelation based on graphical interpretation was also larger in the upper sub-basin for the first three distance classes but was equal at larger distance classes (Table 2). Furthermore, oscillations between positive and negative autocorrelation (e.g. Fig. 3a, b lower graphs) suggest that spawning sites occurred in clusters with intervening spaces of unused habitat in both sub-basins, but such patchiness was slightly more apparent in the lower sub-basin (see also Peakall *et al*. 2003).

In the composite graphs where stream segments were pooled into successively larger distance classes (i.e. using the first distance bin from each correlogram), the extent of detectable autocorrelation was similar for each sub-basin; both sub-basins showed significant autocorrelation at every spatial scale (i.e. distance class) evaluated with the exception of the 0–40 class in the lower sub-basin (Fig. 4).

In summary, at all spatial scales except for the largest distance class in the lower sub-basin, redds were not randomly distributed but rather showed significant spatial clustering. However, for a given distance class (i.e. correlogram) the spatial extent of spawning gravels was generally larger and more continuous in the upper sub-basin than in the lower sub-basin.

Distribution of genotypes

The final number of individuals included in our dataset was 370. The number of single-locus missing genotypes that had to be substituted with common genotypes comprised less than 1.2% of the total. Of those individuals missing genotypes, five individuals were missing two genotypes, the rest were missing one.

Substantial differences were found in genetic autocorrelation patterns both between sub-basins and between the sexes. Thus, we felt it would be inappropriate to pool across either of these factors and we present only the results for sex by sub-basin analyses. For each sub-basin and each sex, Table 3 summarizes the distance to which autocorrelation was positive based on both a graphical interpretation of significance (see Methods) and on the *x*-intercept. Males were not genetically autocorrelated in either basin at any spatial scale, as *r* was effectively 0 for the first bin of each distance class evaluated and the null hypothesis of no autocorrelation could not be rejected. Thus, no distance or *x*-intercept could be defined for males at any scale. These results can be seen graphically in Fig. 5, which again is a composite graph showing *r* for the first distance bin from each single correlogram; here, the *r* statistic for males was always zero regardless of what distance class was used.

Table 3 Results of spatial autocorrelation analyses of male and female Chinook salmon **genotypes** in the Middle Fork Salmon River. For each distance class, the table presents the spatial extent of positive autocorrelation among individual genotypes, i.e. the distance to which autocorrelation was significantly positive as defined by graphical interpretation using error (see Methods for description) or the *x*-intercept. For each, males and females from the upper sub-basin ('Upper') and lower sub-basin ('Lower') were analysed and interpreted separately. NS, not significant, meaning that the null hypothesis of 0 autocorrelation was not rejected for the first distance bin in that distance class, and therefore no spatial extent of autocorrelation could be defined

	Distance of graphical significance				*x*-intercept (km)			
Distance class	Male Upper ($N = 84$)	Female Upper ($N = 156$)	Male Lower ($N = 32$)	Female Lower ($N = 98$)	Male Upper ($N = 84$)	Female Upper ($N = 156$)	Male Lower ($N = 32$)	Female Lower ($N = 98$)
1	NS	1	NS	2	0	2.2	0	9.8
2	NS	NS	NS	2	0	0	0	13.4
5	NS	NS	NS	5	0	0	0	13.6
10	NS	NS	NS	10	0	0	0	17.2
20	NS	NS	NS	20	0	0	0	37.1
40	NS	NS	NS	40	0	0	0	91.3

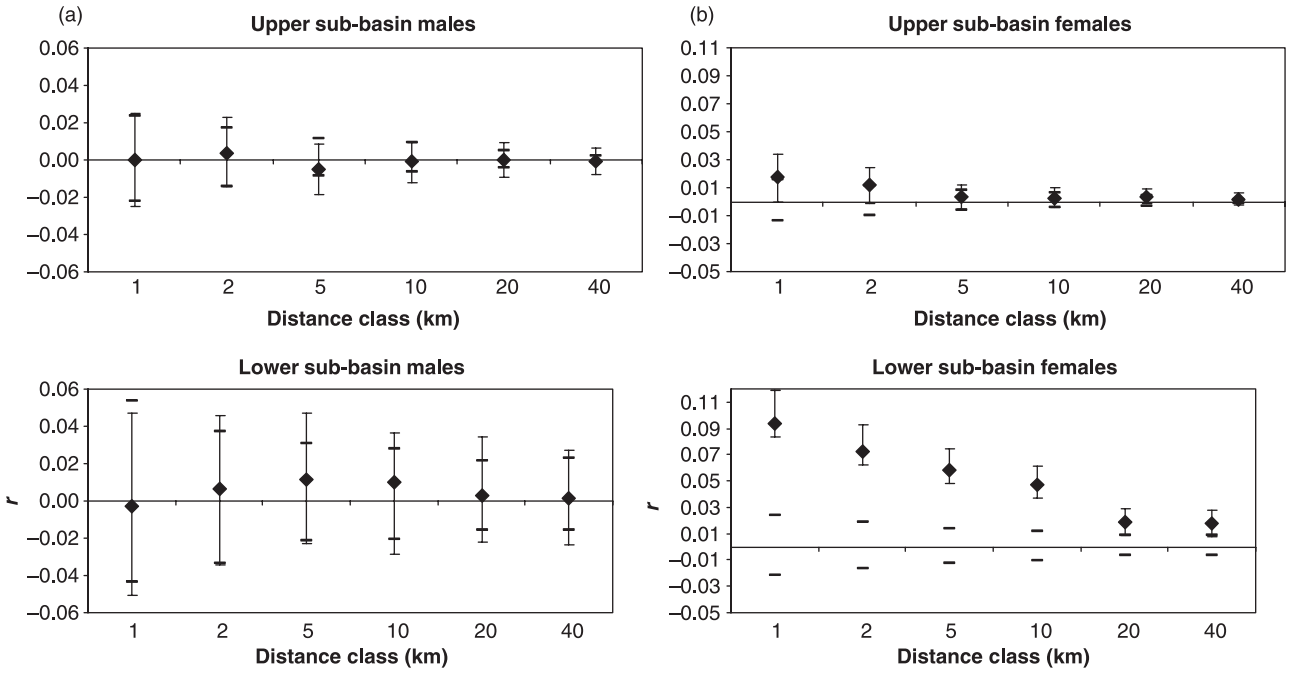

Fig. 5 Composite graph showing the autocorrelation statistic from the first distance bin in each single correlogram for male (left) and female (right) Chinook salmon **genotypes** in the Middle Fork Salmon River in the upper (top) and lower (bottom) sub-basins. Thus, *r* was estimated as genotypes were pooled into successively larger distance classes, i.e. 0–1 km, 0–2 km, 0–5 km, etc. Dashes bracket the 95% confidence intervals about the 0 autocorrelation value, representing the null hypothesis of no spatial structure; 95% confidence limits about *r* indicated by error bars. This graph demonstrates how autocorrelation is affected by the distance class assumed, and shows the scale at which positive autocorrelation could be detected for each sex in each basin.

In the upper sub-basin, female genotypes were non-randomly distributed for the smallest distance class (1 km), with a spatial extent of 1 km for graphical interpretation of significance, and an *x*-intercept of 2.2 km (Table 3, Fig. 5). Female autocorrelation was effectively zero for larger distance classes in the upper sub-basin and so no spatial extent or *x*-intercept could be defined at these scales. In the lower sub-basin, however, female genotypes showed strong and significant autocorrelation at all distance classes assessed. The spatial extent of positive autocorrelation among female genotypes in the lower sub-basin ranged from 9.8 to 91.3 km based on the *x*-intercept, or from 2 to 40 km when interpreted graphically (Table 3).

In comparing autocorrelation between males and females as individuals of each sex were pooled into successively larger distance classes in the composite graph, Fig. 5 (top) demonstrates that genetic associations were weak overall in the upper sub-basin and the strength of genetic autocorrelation did not differ between the sexes there, while females in the lower sub-basin were positively autocorrelated for all distance classes and had significantly stronger autocorrelation than males for 1 and 2 km distance classes but not for others (Fig. 5 bottom).

Discussion

Previous work in this system based on more traditional analyses, where individuals from each tributary were pooled a priori into 'populations', revealed weak but significant genetic structure among tributaries despite evidence of on-going gene flow. Relatively stronger differentiation was observed between the two sub-basins, but no difference was found in the degree of differentiation among tributaries within each sub-basin (Neville *et al*. 2006). Here, autocorrelation analyses of individual genotypes have revealed that genetic structuring also occurs at much finer scales and varies between sub-basins. The patterns observed here support predictions about potential ecological and evolutionary factors hypothesized to influence the precision of natal homing and localized movements of individual Chinook salmon within populations on their breeding grounds.

Spatial autocorrelation analyses of redds showed that spawning locations in both sub-basins were spatially clumped, but the upper sub-basin generally had a larger spatial extent to the continuity of redd locations than the lower sub-basin, where the distribution of redds and associated habitat conditions were more patchy. We were unable to make clear predictions as to the influence of this pattern of habitat structure on genetic structure among males, which ultimately showed no genetic clustering in either sub-basin at any scale. Homing may be inaccurate or reproductive competition may be strong enough for males that they are equally likely to move in either of the habitat contexts presented in our system, leading to a lack of genetic autocorrelation among individuals. Interestingly, a recent mark-resighting study of male sockeye salmon showed that males moved little from their selected stream area after an initial period of exploratory movement when they first reached the spawning grounds (Rich *et al*. 2006), supporting observations of strong male site-fidelity in other studies of sockeye salmon (Hendry *et al*. 1995; Stewart *et al*. 2004). Rich *et al*. (2006) postulated that this site fidelity could lead to fine-scale genetic structure. However, as these authors noted, both restricted movement and strong natal homing are prerequisites to such structure in salmon. Our data suggest that either a lack of fine-scale homing in the first place or movement at some stage subsequent to homing led to genetic mixing and no structuring in males in our system. These genetic data thus add a critical missing piece to efforts to understand the interaction among natal homing, localized movement, and genetic structure.

Spatial genetic patterns for females varied in the direction predicted between the two sub-basins, with much stronger autocorrelation among female genotypes in the sub-basin with less continuity in spawning gravels. This is consistent with the notion that female Chinook salmon in the more continuous habitat of the upper sub-basin either home less precisely or may be able to move about more freely to prospect for suitable nesting sites, leading to greater genetic mixing and less apparent structure. In contrast, in the lower sub-basin where suitable spawning habitat is patchier, both the requirements of spatially accurate homing and restricted movement must have been met to create the fine-scale genetic structuring observed in females. Consequently, a prominent sex-bias in genetic patterns was observed in the lower sub-basin, with a weaker but still significant sex-bias in the upper sub-basin at the finest spatial scale (1-km distance class). Sex-biased dispersal has been demonstrated in many mammals and birds (Greenwood 1980; Dobson 1982; Leturque & Rousset 2004) but we still know little about this phenomenon in salmonid fishes, particularly at finer spatial scales. In the salmonids, differences in ecological constraints as well as evolutionary selective pressures may be expected to produce male-biased movement and dispersal, although investigations of sex-biased dispersal have been somewhat equivocal. Male-biased straying has been observed at larger spatial scales (i.e. among rivers) in Chinook salmon in some cases (Hard & Heard 1999) but not in others (Unwin & Quinn 1993). In two studies of brook charr (*Salvelinus fontinalis*, Hutchings & Gerber 2002) and brown trout (*Salmo trutta*, Bekkevold *et al*. 2004) males were found to stray more than females among streams, but in a different brook charr system sex-biased dispersal was scale-dependent in that males strayed more among neighbouring streams but females strayed more at longer distances (i.e. across a lake, Fraser *et al*. 2004). As in our study, male-biased dispersal in these systems has been suggested to be the result of avoidance of kin competition and inbreeding, and the higher reproductive competition in males (Hutchings & Gerber 2002; Fraser *et al*. 2004). It is important to note, however, that most previous studies (including the above) have investigated straying among populations, and straying at these larger spatial scales possibly involves different selective pressures than the fine-scale within-population movement emphasized here. In general, very little is known about the transition between the act of homing to natal populations at broader spatial scales and movement related to the selection of the spawning sites or mates within these populations leading to the genetic patterns we observed.

Many factors may have affected both our results and their relevance to understanding homing and localized movement

in salmon. For instance, our samples did not include small nonmigratory males (see Garcia-Vazquez *et al*. 2001; Blanchfield *et al*. 2003) and were possibly biased against fully representing smaller males (jacks) that return to spawn after only 1 year at sea (see, e.g. Zhou 2002). At larger spatial scales, these fish have been shown in some cases to have different straying patterns from larger males, but the results from previous studies have been highly variable. For instance, Hard & Heard (1999) found that younger fish strayed more than older individuals, while several studies reported less straying in jacks than older individuals (Quinn & Fresh 1984; Quinn *et al*. 1991; Labelle 1992) and Candy & Beacham (2000) found no relationship between straying and age. It would be difficult therefore to predict in what capacity males employing these reproductive strategies might influence the spatial distribution of genetic variability, but we emphasize that our results apply only to larger and older males.

Additionally, it is possible that the difference we observed between the two sub-basins in the strength of sex bias is related to differences in statistical power to detect such a bias across the watershed. While in the upper sub-basin a sex bias in genetic autocorrelation existed only at the finest spatial scale (1-km distance class), a sex bias may have existed at larger spatial scales but it may have been too weak for detection with the loci and sampling scheme used here. Anything but an extreme sex bias (e.g. 90% vs. 10% dispersal for the two sexes) can be difficult to detect with genetic data, as statistical power decreases rapidly as the bias in dispersal decreases (Goudet *et al*. 2002). Even if the sex bias was only slightly lower in the upper basin, our power to detect it may have been much less. The fact that a sex bias was detected in the lower sub-basin indicates that the bias in that region was strong (see Goudet *et al*. 2002).

The power to detect autocorrelation in our study may also be influenced by varying sample sizes between the sub-basins and sexes. In most cases, this bias should be conservative, as larger sample sizes were used in the region where autocorrelation was weakest or lacking. The one place where our ability to detect autocorrelation may have been poor was in males in the lower sub-basin, but the centre of the confidence intervals surrounding r in this case was always close to zero and thus increased sample size is unlikely to have changed this result.

Differences in sample sizes were, however, largely due to natural differences in the density of spawners between the two sub-basins, which may be a confounding factor in this study. Population density is known to affect the spatial distribution of individuals and social interactions in both sexes in salmonids. Low population densities may induce males to move further in search of mating opportunities (Quinn 2005), as they are unlikely to encounter females using a 'sit and wait strategy' when females are scarce. Recent work on coho salmon (*Oncorhynchus kisutch*) spawning at low densities demonstrated greater movement in males than females, and male movement was inversely correlated with female densities (Anderson 2006). However, another recent study showed little effect of density on movement in sockeye salmon (Rich *et al*. 2006). In other scenarios, higher population densities may increase aggression among males and lead to reduced movement, and females competing for space at high densities may be more limited in redd-site choices and forced to move to suboptimal habitats as population densities increase (Quinn 1999; Esteve 2005). Although relatively low compared to historical levels, abundances of Chinook salmon in the MFSR during our sampling period were the highest in decades, and as fish have expanded back into the system they have generally been at higher densities in the upper sub-basin (Isaak *et al*. 2006). Depending on the relative importance of the above behaviours, different densities in the two sub-basins may have shaped the genetic patterns we observed. Ultimately, however, variations in density mirror differences in available spawning habitat between the two sub-basins (Isaak *et al*. 2006) and thus spawning habitat would still be considered the fundamental factor influencing relative differences in homing and movement behaviour between these two regions.

Finally, it is important to emphasize that the spatial distribution of genotypes in current time, as described here, does not necessarily reveal genetic patterns that emerge from successful breeding and consequently shape population-level genetic divergence. Rather, the spatial distribution of genotypes shows where individuals were when we sampled them and how related they were to each other, whether or not they bred in that location (or at all). For instance, a scenario that is not unlikely is that males and females have similar abilities and tendencies to home to their natal stream, but distribute differently once on their natal spawning grounds in response to various ecological and reproductive pressures. Some of the males we sampled may in fact have even bred at their natal incubation site and then moved to the location where they were collected in search of additional mates, contributing to the largely random patterns in male genotypes observed here. Other individuals of both sexes included in our sample may not have bred at all (see Healey & Prince 1998) or have been transported to their collection location by currents following breeding at a given site (e.g. Zhou 2002). These scenarios may still foster the among-tributary differentiation found previously in our system (Neville *et al*. 2006) but also allow for the individual-based genetic patterns observed here that reflect differences in localized movement between the sexes. Furthermore, because spatial patterns based on individual genotypes reflect movement in 'real time', as opposed to the long-term averaged rates of gene flow characterized by traditional genetic analyses (e.g. F_{ST}), patterns observed here may be dynamic in response to

the many biological and habitat factors that are temporally variable in such systems. Further study of how such fine-scale genetic structure among individuals changes across time in response to these factors would be a fruitful area of research.

Concluding remarks

Understanding the spatial scale of genetic structuring is an important focus of many conservation efforts (Primmer *et al*. 2006), and it has been argued that the spatial extent of genetic clustering quantified by autocorrelation analyses should be used to characterize units of conservation concern (Diniz-Filho & Telles 2002). In this light, individuals at distances where autocorrelation among genotypes is positive are considered related and 'redundant', and thus the spatial extent of genetic autocorrelation can be used to understand the geographical distances that relate to diversity. The differences in spatial genetic autocorrelation between the two sexes revealed here make it difficult to define generalized population-level patterns (see Diniz-Filho & Telles 2002). However, our results provide insight into the potential fine-scale homing abilities of females (leading to genetic structuring at scales as small as 1 km), and suggest that males may be important agents of movement and possibly gene flow in this system. Overall, the sex bias in genetic structure likely reflects differential constraints and selective pressures facing each sex. Finally, the spatial structure of spawning areas across the landscape likely had important influences on the scale of genetic structuring observed in both sexes. Thus, both intrinsic characteristics of individuals (sex) and extrinsic factors (landscape structure) were associated with the scale of natal homing and localized movements and the potential for dispersal. The importance of these critical influences underscores the need to integrate the biology of the organism in question (see also Double *et al*. 2005) when attempting to understand the relevance of the spatial distribution of individuals revealed by spatial autocorrelation of genotypes.

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