ORIGINAL PAPER

Fluctuating sex ratios, but no sex-biased dispersal, in a promiscuous fish

Sofía Consuegra · Carlos García de Leániz

Abstract Dispersal in birds and mammals tends to be female-biased in monogamous species and male-biased in polygamous species. However results for other taxa, most notably fish, are equivocal. We employed molecular markers and physical tags to test the hypothesis that Atlantic salmon, a promiscuous species with intense male-male competition for access to females, displays male-biased dispersal. We found significant variation in sex ratios and in asymmetric gene flow between neighbouring salmon populations, but little or no evidence for sex-biased dispersal. We show that conditions favouring male dispersal will often be offset by those favouring female dispersal, and that spatial and temporal variation in sex ratios within a metapopulation may favour the dispersal of different sexes in source and sink habitats. Thus, our results reconcile previous discrepancies on salmonid dispersal and highlight the need to consider metapopulation dynamics and sex ratios in the study of natal dispersal of highly fecund species.

Keywords Sex ratios · Sex-biased dispersal · Asymmetric gene flow ·
mtDNA · Microsatellites · Atlantic salmon · Metapopulation

Introduction

Natal dispersal, the movement of juveniles from their place of birth to the place of first reproduction (Greenwood 1980), constitutes one of the most pervasive and influential animal life-history traits (Clobert et al. 2001). Dispersal modulates the

Present Address:
S. Consuegra (✉)
Department of Biological Sciences, University of Wales Swansea, Swansea SA2 8PP, UK
e-mail: s.consuegra@swansea.ac.uk

S. Consuegra
Gatty Marine Institute, University of St. Andrews, St. Andrews, Fife KY16 8LB, Scotland, UK

C. G. de Leániz
Department of Biological Sciences, University of Wales Swansea, Swansea SA2 8PP, UK

persistence and demography of species (Hanski 1999), buffers populations against stochastic events (Cadet et al. 2003) and environmental fluctuations (Friedenberg 2003), and reduces the likelihood of local extinctions (Poethke et al. 2002). By dispersing, individuals can attain higher fitness if they reduce competition from kin, minimise the likelihood of inbreeding, or encounter better habitats or less crowded patches (Perrin and Mazalov 1999, 2000). In small or bottlenecked populations, immigration can slow down genetic drift and prevent the loss of genetic variation (Aars and Ims 2000). However, because dispersal also has costs, it imposes an upper limit to gene flow, and hence to population differentiation and to adaptive divergence (Hendry 2004; but see Garant et al. 2005).

The advantages of dispersal are thought to result from a balance between inbreeding avoidance and local competition avoidance (Perrin and Mazalov 1999, 2000). If such balance differs between the sexes, perhaps because one sex invests more in parental care or in territorial defence than the other, then sex-biased dispersal would ensue depending on the mating system. In monogamous species like birds (Greenwood 1980) or some mammals (Favre et al. 1997) females tend to be the dispersing sex, while in promiscuous mammals males tend to disperse more (Dobson 1982), as their parental investment is lower. Dispersal in polygamous species results from an equilibrium between ''local mate competition'' and ''local resource competition'' and how they affect both sexes (Perrin and Mazalov 2000). When males compete for females in absence of local resource competition (only local mate competition operates) or when only males compete (e.g. the number of females is limited), males tend to be the dispersing sex. In contrast, when competition for limited resources affects both males and females, the dispersing sex tends to be independent of the mating system (Perrin and Mazalov 2000). However, because natal dispersal is essentially context-dependent (Clobert et al. 2001), there are several exceptions and counter-examples to this general pattern, which can be too simplistic for some taxa (e.g. LeGalliard et al. 2003).

Salmonids have been proposed as strong candidates for male-biased dispersal based on their polygamous mating system (Hutchings and Gerber 2002; Bekkevold et al. 2004). However, metapopulation dynamics, and spatial variation in sex ratios or in resources, can also affect natal dispersal (Cohen and Levin 1991; Holt and McPeek 1996), and the question remains controversial (Hendry et al. 2004). For example, chum salmon displays male-biased dispersal in some populations (Hard and Heard 1999) but not in others (Unwin and Quinn 1993), while in brook trout males are the predominantly dispersing sex in some cases (Hutchings and Gerber 2002) and females in others (Fraser et al. 2004).

Estimates of dispersal rates have been obtained directly by mark and recapture (Thedinga et al. 2000), radiotracking (Blundell et al. 2002) or the use of stable isotopes (Caudill 2003). However direct methods are not easily applicable to all species, and they only estimate the ability of individuals to disperse, not their ability to reproduce effectively in a new habitat (Prugnolle and de Meeus 2002). In contrast, indirect genetic estimates of dispersal provide additional information on the migrants that effectively reproduce (i.e. contribute to gene flow). Genetic methods that compare markers with different modes of inheritance (e.g. sex-specific versus nuclear markers) have been widely used to reveal historical patterns of gene flow (e.g. Escorza-Treviño and Dizon 2000), although comparisons between markers can be complicated because of their different modes of inheritance and rates of evolution.

Different markers can provide discordant dispersal estimates, and should ideally be used in combination (Wilson et al. 2004).

We have recently demonstrated that asymmetric levels of gene flow and high dispersal rates can help to maintain genetic variation in Atlantic salmon living in marginal habitats (Consuegra et al. 2005a). Here we use molecular markers and physical tags to test for sex-biased dispersal in the same Atlantic salmon metapopulation, and examine the consequences of spatial and temporal variation in sex ratios on gene flow between neighbouring rivers. To our knowledge, this is the first study that combines sex-ratio data with physical tagging and genetic methods to test for sex-biased dispersal in a highly fecund species.

Material and methods

Origin and type of samples

Adipose fin clips and scale samples were collected from wild anadromous Atlantic salmon entering the rivers Asón ($n = 121$), Pas ($n = 200$), Nansa ($n = 249$), and Deva ($n = 130$) during 1996–2000, as described in Consuegra et al. (2002, 2005a, b). These are short (<40 km), neighbouring rivers, located near the southernmost limit of the species' endemic distribution and all within a 90 km radius of each other. Individuals were sampled throughout the year, assigned to their appropriate cohort (1993–1998; see Consuegra et al. 2005a) and a subsample of fish sexed by gonadal dissection in the case of angled fish (March–July), or by stripping and inspection of secondary sexual characters in the case of spawners sampled during or near the breeding season (September–December).

Statistical analysis of sex ratios

The sex ratio (SR = no. of males/no. males + no. females) of anadromous breeders was calculated from annual samples of returning adults caught from September onwards (after the end of the fishing season, hence were representative of spawning escapement) during 1985–2002; we excluded from analysis annual samples of less than 10 spawners. The sex ratio of 209 smolts (seaward migrating juveniles) was calculated by dissection of the gonads from samples collected during the 1986–1988 spring migrations in the rivers Ason (n: 49) and Nansa (n: 29), and during the 1994 spring migration in the nearby river Eo (n: 131). As this a destructive procedure, data on smolt sex ratios were necessarily limited in these endangered populations.

The incidence of mature male parr (males that mature in freshwater at an early age before going to sea) was estimated by manual expression of the milt in electrofishing surveys carried out in the fall, stratified by age classes. Differences from 50:50 expectations in smolt and adult sex ratios were assessed by constructing 95% binomial confidence intervals (Wilson and Hardy 2002) and by calculating exact binomial probabilities. We also employed the binomial test to test for evidence of sex-biased marine mortality, comparing the sex ratio of returning adults with the sex ratio of emigrating smolts. Log-linear analysis and log-likelihood ratios were employed to test for temporal and spatial heterogeneity in sex ratios within and across populations (Wilson and Hardy 2002).

Microsatellite and mitochondrial DNA analysis

Total DNA was extracted from adipose fin clips and amplified for five tetranucleotide microsatellites (SSsp1605, SSsp2201, SSsp2210, SSsp2213 and SSsp2216; Paterson et al. 2004) as in a previous study (Consuegra et al. 2005a). One microlitre of the extracted DNA was used to amplify a 1400-bp fragment in the ND1 region, followed by digestion with four restriction enzymes (*Hae*III, *Hin*fI, *Rsa*I and *Dra*I) as in Consuegra et al. (2002). In total 687 fish were typed for mtDNA (including 209 females and 165 males) and 664 fish were typed for microsatellite variation (including 100 females and 76 males).

Estimates of gene flow for biparental and maternally inherited markers

We compared the extent of population structuring and gene flow for biparental (microsatellites) and maternally inherited (mtDNA) markers by analysis of molecular variance (AMOVA) based on F_{ST} and Φ_{ST} statistics using ARLEQUIN v.2.0 (Schneider et al. 2000). The significance of the covariance components was tested using 1,000 permutations of the data. The number of migrants exchanged per generation between populations was estimated using the program MIGRATE v2.3 (Beerli and Felsenstein 2001), based on mtDNA (*n*: 687) and microsatellite data (*n*: 664). MIGRATE estimates directional (including asymmetrical) gene flow using a maximum-likelihood approach based on the coalescent theory and was considered the most appropriate approach because symmetry in gene flow could not be assumed in our populations (Consuegra et al. 2005a). For each river, we pooled data from all year classes to increase the power of the tests, as populations had shown temporal stability in haplotype and allele frequencies over the period of study (Consuegra et al. 2002, 2005b). We estimated gene flow among the four populations, but as no tagging data was available for the river Deva, we considered three of them (Ason, Pas and Nansa) to make genetic estimates of dispersal rates comparable to those obtained from physical tagging (see below). Initial estimates of θ and gene flow were based on F_{ST} estimated from the data. The program was run five times and the results were averaged between runs.

Estimates of sex-biased dispersal based on microsatellite loci

We ran six simulations with MIGRATE (3 for each sex) to compare migration rates among the sexes based on microsatellite variation. The estimated number of migrants was averaged for each sex in each population, and statistical significance was assessed by constructing approximate confidence intervals (Beerli and Felsenstein 2001). We also carried out five specific tests with the FSTAT software (v2.9.3) to test for differences in natal dispersal between the sexes, as detailed in Goudet et al. (2002). First, we compared the inbreeding coefficient (F_{IS}) of males and females under the assumption that the more dispersing sex should have a higher F_{IS} than the more philopatric sex. Likewise, we tested for statistical differences between the sexes in the fixation index (F_{ST}) assuming that the more philopatric sex should display more genetic differentiation between populations than the more dispersing sex. We then calculated the degree of relatedness of males and females, under the assumption that individuals of the more dispersing sex should be less related to another than those of the more philopatric sex. We

calculated mean assignment indices (mAIc) for males and females, corrected for different levels of gene diversity between populations (AIc, Favre et al. 1997). Positive values of AIc indicate that a genotype is more likely to belong to a resident individual, while negative values indicate potential dispersers. Since immigrants will tend to have lower AIc values than resident fish, the more dispersing sex should tend to have lower mAIc values than the more philopatric sex. Finally, we tested for differences between the sexes in the variance of the assignment indices (vAIc), under the assumption that the dispersing sex should show greater variance. According to Goudet et al. (2002), in cases where dispersal rates are high (>4%)—as it was the case for these populations Consuegra et al. (2005a)—the most powerful tests for detecting sex-biased dispersal are those that compare F_{ST} and mAIc values between the sexes. We performed one tailed-tests by 10,000 permutations of the data to test the null hypothesis that males should be the most dispersing sex, first using data from only one cohort (1997 year class), as recommended by Goudet et al. (2002), and then pooling data from all six cohorts (1993–1998), corresponding to the years 1996–2000.

Estimates of sex-biased dispersal based on mark and recapture studies

Sex-biased dispersal was also estimated by examining the location of recapture of 166 hatchery-reared native adults of known sex that had been coded-wire tagged (CWT) and stocked as juveniles in their home rivers (Asón, Pas and Nansa). All angled fish plus a sample of spawners were screened (without replacement) for tags in each river every year, and the fish classified as ''homers'' (philopatric) or ''strayers'' (dispersers) depending on whether they had returned to spawn in their home river or in other rivers.

Results

Sex ratios of migrant juveniles and adult spawners

Data on the sex ratio of smolts from the three different populations was combined as there was no significant heterogeneity in frequencies between samples (log-likelihood ratio = 1.603, df = 2, p = 0.449). The sex ratio (SR = proportion of males) of 209 smolts was 0.359 (95% binomial CI = 0.308–0.409) indicating a highly significant excess of females (64%) amongst seaward migrants (binomial test, p = 0.000). On the other hand, log-linear analysis revealed a significant 3-way interaction between year, river, and sex of anadromous spawners (likelihood ratio = 21.260, df = 8, p = 0.007). Thus, the sex ratio of anadromous breeders fluctuated significantly from year to year in all populations (log-linear analysis; Ason, likelihood ratio = 36.110, df = 13, p = 0.001; Pas, likelihood ratio = 23.10, df = 5, p = 0.000; Nansa, likelihood ratio = 42.570, df = 13, p = 0.000; Deva, likelihood ratio = 8.320, df = 3, p = 0.040), being significantly different from the smolt sex ratio in 45% of the cases and from an even sex ratio in about 40% of the years (Fig. 1a). The sex ratio of anadromous spawners differed significantly between populations (likelihood ratio = 18.579, df = 3, p = 0.000), being generally male-biased in the rivers Nansa and Deva, and female-biased in the rivers Ason and Pas (Fig. 1b).
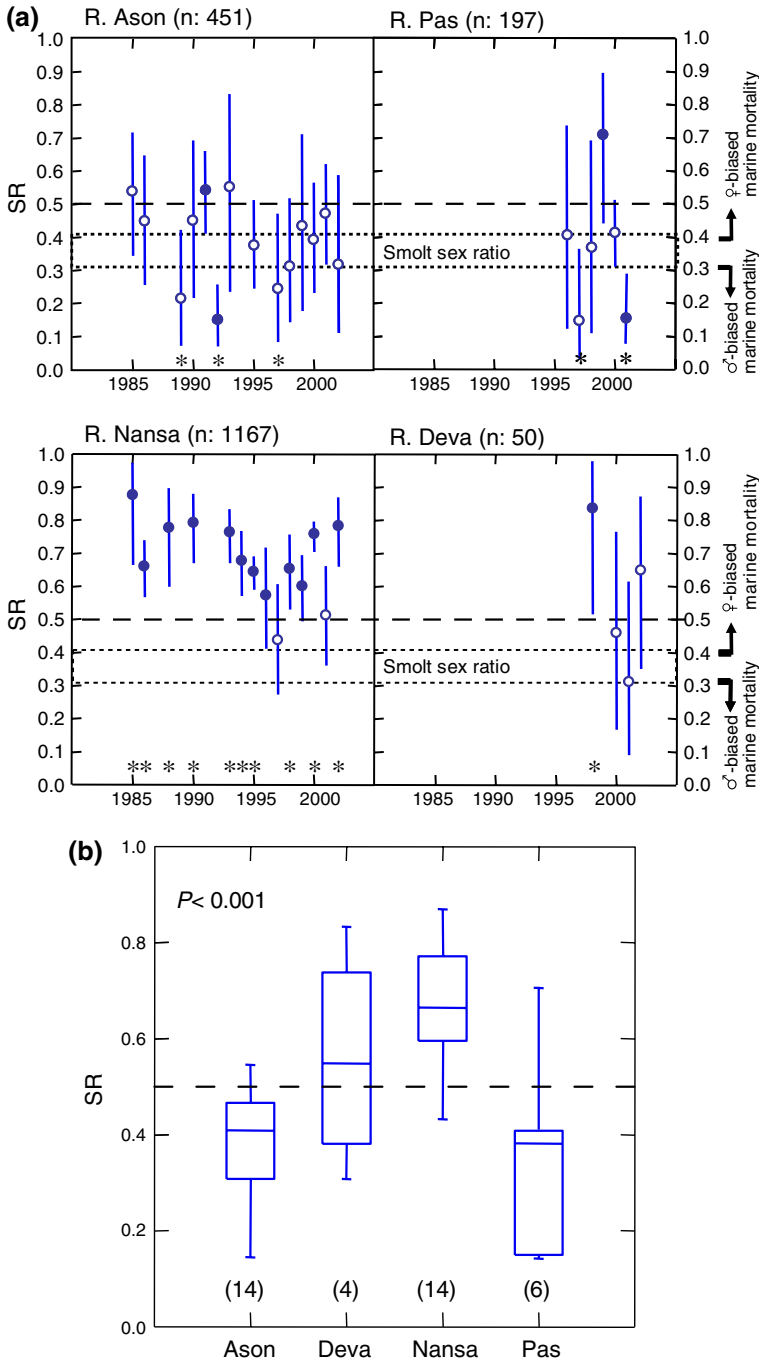
Results from electro-fishing surveys during the breeding season revealed a high incidence of early sexual maturation amongst male parr in freshwater. Thus, 58.8% of male parr (20/34) had reached sexual maturity as 0 + during their first autumn,

◀**Fig. 1** (**a**) Temporal fluctuations in the sex ratio (*SR*, proportion of males ± 95% CI) of anadromous spawners in four neighbouring Atlantic salmon populations; dashed line indicates 50:50 sex ratio and dotted range indicates sex ratio of emigrating smolts ± 95% CI. Asterisks indicate spawning years with significant departures from equal sex ratios while closed symbols denote years with significant departures from the smolt sex ratio, indicative of female-biased (above the line) or male-biased (below the line) adult marine mortality. (**b**) overall variation in the sex ratio of anadromous spawners in each population; number of annual samples shown in parentheses

and 77.4% of males (65/84) matured in subsequent years (1 + /2). Thus, the majority of males in these southern populations have the opportunity to reproduce before going to sea, thereby strongly biasing the sex ratio of spawners.

Population structuring and rates of dispersal among rivers

Genetic differentiation between populations was low, although significant for both microsatellite ($F_{ST} = 0.011$, $p = 0.000$, $n = 176$) and mtDNA ($\Phi_{ST} = 0.017$, $p = 0.046$, $n = 374$) markers. The results of running MIGRATE with mitochondrial DNA and microsatellite data indicated high rates of migration between populations and confirmed the asymmetric pattern of gene flow revealed in a previous study (Consuegra et al. 2005a). However, gene flow estimates based on mitochondrial DNA were unrealistically high (data not shown) probably due to the limited sequence variation between mtDNA haplotypes in Iberian salmon populations (Consuegra et al. 2002). Nevertheless, all five runs of the program gave similar estimates and indicated the same general pattern of asymmetrical exchange between rivers. Both mitochondrial and nuclear markers indicated that the river Asón exchanged least migrants, while the river Nansa displayed the greatest rate of exchange (Table 1). Absolute rates of exchange between rivers based on microsatellite estimates were in the range 186–234 migrants per generation (62 to 78 fish per year based on a typical 3-year generation time). The direction of migration varied, however, depending of the marker being analysed. Results from microsatellites indicated that the river Pas acted as net source while the river Asón, and to a lesser extent the river Nansa, acted as sinks (Table 1), which is just the opposite pattern inferred from mitochondrial DNA.

Table 1 Maximum likelihood estimates (MLE) and approximate 90% confidence limits (0.05 and 0.95 percentiles) of the number of migrants per generation (*M*), based on genetic variation at five microsatellite loci

	Migrants per generation (M)				Source population		
	0.05	MLE	0.95		Ason	Nansa	Pas
Ason → Nansa	21.7	23.1	24.6	Emigration	71.0	127.9	130.3
Nansa → Ason	40.0	42.5	45.1	Immigration	115.6	106.5	76.1
				Exchange	186.6	234.4	206.4
Ason → Pas	18.5	19.8	21.1				
Pas → Ason	37.5	40.0	42.5				
Nansa → Pas	32.3	33.9	35.6				
Pas → Nansa	50.7	52.9	55.1				

Results shown are the averages of five runs using the program MIGRATE

Genetic assessment of sex-specific dispersal

For mitochondrial DNA, no significant population differentiation was detected when samples were analysed by sex, although the degree of sex-specific structuring was somewhat larger for females (Female $\Phi_{ST} = 0.028$, $p = 0.054$, $n = 209$) than for males (Male $\Phi_{ST} = 0.012$, $p = 0.229$, $n = 165$). In contrast, both females and males showed significant population structuring with respect to microsatellite loci, with slightly more male than female differentiation between populations (Female $F_{ST} = 0.012$, $p = 0.010$, $n = 100$; Male $F_{ST} = 0.016$, $p = 0.029$, $n = 76$). Maximum likelihood estimates of migration rates based on microsatellite data were not statistically different between males and females in the rivers Ason (males = 36.4 ± 4.2, females = 32.2 ± 3.3) and Pas (males = 47.2 ± 4.6, females = 40.2 ± 3.4). However, migration appeared to be significantly male-biased ($p < 0.01$) in the River Nansa (males = 50.2 ± 5.0, females = 35.4 ± 3.1).

Except for males showing a slightly higher inbreeding coefficient, F_{IS} (indicative of male dispersal), the trend in the four other tests of sex-biased dispersal was more indicative of female-biased dispersal (lower F_{ST}, lower relatedness, lower assignment, and higher variance in females; table 2). However, none of the tests were statistically significant in any of the samples (one cohort, and all cohorts combined).

Mark and recapture study

Analysis of the location of recapture of 166 adult salmon that had been micro-tagged as juveniles also failed to show any significant evidence for sex-biased dispersal (Table 3). The distribution of sexes amongst adults that returned to their river of

Table 2 Results of five tests of sex-biased dispersal in Atlantic salmon using microsatellite nuclear markers, showing one-tailed probabilities that males disperse more than females

	Sex	N	Test of sex-biased dispersal				
			F_{IS}	F_{ST}	Relatedness	$mAIc$	$vAIc$
1997 cohort	Females	55	0.196	0.013	0.021	-0.236	5.082
	Males	53	0.204	0.038	0.063	+0.245	3.853
	P		0.456	0.973	0.971	0.872	0.719
1996–2000 runs	Females	100	0.116	0.010	0.017	-0.189	8.685
	Males	76	0.173	0.012	0.020	+0.249	6.954
	P		0.256	0.657	0.644	0.856	0.781

Results shown are for one single cohort (1997 cohort), and for several spawning years (1996–2000 runs)

Table 3 Sex ratio (SR, proportion of males ± 95% binomial CI) of anadromous adults returning from the sea to spawn in their river of origin (homers) or in other rivers (strayers) based on the recapture of native fish tagged as juveniles with unique coded wire tags (CWT)

Population	Philopatric (homers)				Dispersers (strayers)			
	N	Males	Females	SR	N	Males	Females	SR
Ason	19	9	10	0.47 ± 0.23	3	0	3	–
Pas	49	18	31	0.37 ± 0.14	25	15	10	0.60 ± 0.20
Nansa	70	45	25	0.64 ± 0.12	0	0	0	–
Total	138	72	66	0.52 ± 0.05	28	15	13	0.53 ± 0.19

origin ('homers') was almost identical to the distribution of sexes amongst fish that returned to spawn in a different river ('strayers'; likelihood ratio = 0.010, df = 1, p = 0.975), even when the river Nansa (with no strayers) was excluded from analysis (likelihood ratio = 1.261, df = 1, p = 0.261). When considered individually, no significant differences were found in the distribution of sexes amongst homers and strayers in any of the rivers where straying was detected (Ason, Fisher exact test p = 0.257; Pas Fisher exact test p = 0.128).

Discussion

In Atlantic salmon, as in all salmonids, polygamous promiscuity and male-biased operational sex ratios are probably the norm (Fleming 1996, 1998), with females commonly mating with more than one male (e.g. Jones and Hutchings 2001), and males attempting to fertilize as many females (e.g. Taggart et al. 2001). Under these conditions, natal dispersal may be expected to be biased in favour of males, at least when controlling for migratory tendency (Hendry et al. 2004). Yet, and contrary to theoretical predictions for promiscuous mating systems (Perrin and Mazalov 2000), we found little or no evidence for male-biased dispersal in our study. Only in the River Nansa, the population with the most male-skewed sex ratio, was there any evidence for male-biased dispersal, albeit only in one of the tests performed. Several reasons could account for this.

   First, it is possible that none of the genetic tests we employed was sufficiently powerful to detect differences in dispersal among the sexes (Goudet et al. 2002; Prugnolle and de Meeus 2002), though we used one-tailed tests, two different markers with different modes of inheritance, and a single cohort to attain maximum possible power (Goudet et al. 2002). Although eight or more loci are typically required to test for sex-biased dispersal (Goudet et al. 2002), and evidence from FSTAT tests alone should be treated with caution before rejecting male-biased dispersal (Prugnolle and de Meeus 2002), physical tagging and population structuring tests also failed to detect any difference in natal dispersal between the sexes. Population structuring in our study was 1.54 times stronger for maternally inherited mtDNA than for biparentally inherited microsatellites, which is not markedly different from the expected ratio of 2.56, based on the fourfold lower effective size of mtDNA (Birky et al. 1989) corrected by the observed excess of females among smolts (64%). This indicates that gene flow must have been similar between the sexes, despite a strong female bias among migrants. Further, when analysed by sex, mtDNA structuring was the same for males and females in all populations. Although females showed slightly more structuring than males between populations, the difference was not high enough to infer male-biased dispersal and probably reflects inter-population differences in sex ratios (e.g. Escorza-Treviño and Dizon 2000). Indeed, migration rate estimates were only significantly male-biased in the population with the most male-skewed sex ratio. If anything, females—not males—appeared to be the more dispersing sex.

   Secondly, our dispersal estimates may have been affected by the movement of fish to or from unsampled, 'ghost' populations (Slatkin 2005). Although this is unlikely at the spatial scale considered, sex-biased dispersal could have been present at larger geographical scales (i.e. between metapopulations). However, we found little or no evidence of physically tagged adults straying to or from other systems. It appears,

instead, that natal dispersal was largely sex-independent in the four studied Atlantic salmon populations, despite a strong male-biased operational sex ratio and a large difference in reproductive investment between the sexes. This contrasts with results showing male-biased dispersal in chinook salmon (Hard and Heard 1999) and brook trout (Hutchings and Gerber 2002; Fraser et al. 2004), but is in agreement with results for most other salmonids, including the close relative, the brown trout (Table 4). Analysis of 24 dispersal studies in fishes suggests that natal dispersal may be sex-independent in most cases (50%), being largely unrelated to mating system, life history strategy or reproductive guild across species (Table 4). Moreover, studies showing male–biased dispersal (29%) appear to be as frequent as those showing female-biased dispersal (21%).

Why are then such seemingly large discrepancies in sex-biased dispersal between closely related salmonid species, and even between populations within the same species? Indeed, why do fish, unlike birds or mammals, often fail to conform to models of sex-biased dispersal based on their mating system? We argue that natal dispersal in salmonid metapopulations, and possibly in other fish species, will often be sex-independent because:

(i)   conditions favouring the dispersal of males can be just as frequent or strong as those favouring the dispersal of females
(ii)   fluctuating sex ratios may favour male dispersal in some years but not in others; and
(iii)   metapopulation dynamics may favour the dispersal of different sexes in source and sink habitats

Differences in sex-specific life history strategies, a common phenomenon in salmonids (e.g. Fleming 1996) and other fishes (e.g. Huse 1998), can favour either male or female dispersal, or tend to cancel each other. For example, the fact that gene flow was the same for both sexes despite a strong preponderance of females amongst smolts suggests that female Atlantic salmon incurred higher migratory mortalities than males, as reported for other salmonids (Holtby and Healey 1990; Spidle et al. 1998; Tamate and Maekawa 2004). Indeed, the proportion of females among anadromous breeders was typically lower than it would have been expected from the sex ratio of emigrating smolts, again suggesting that females incurred a higher marine mortality in most years. Conversely, there must have been strong factors favouring female-mediated gene flow to offset the strongly male-biased operational sex ratio. In Atlantic salmon, anadromous females tend to mature at an older age (and thus stay longer at sea and attain a larger size) than anadromous males (Fleming 1998), and this may explain their additional marine mortality. Anadromous females in our study were on average 25% older than anadromous males (data not shown), and although we did not incorporate sex-specific differences in age at maturity in our analysis, this would have resulted in an additional female mortality at sea. Thus, while an excess of females among smolts will result in greater scope for female dispersal, the higher marine survival of males may compensate for it. Similarly, while males may attain a higher degree of iteroparity by maturing in freshwater before migrating to sea (mature male parr; see below), females may compensate by surviving better than anadromous males after spawning, and consequently by being able to breed more than once (Fleming 1996). Therefore,

Table 4 Evidence for sex-biased natal dispersal in fishes

Species	Life history[d]	Mating system[e]	Breeding frequency[f]	Fertilization	Reproductive guild	Sex-biased dispersal[g]	Method[h]	Reference
Sharks								
Carcharodon carcharias	M	?	I	Internal	Live bearer	M	G	Pardini et al. (2001)
Isurus oxyrinchus	M	?	I	Internal	Live bearer	M	G	Schrey and Heist (2003)
Barbus haasi	S	P	I	External	Non-guarder egg scatterer	0	T	Aparicio and De Sostoa (1999)
Rivulines								
Rivulus hartii	S	P	I	External	Non-guarder egg scatterer	0	T	Gilliam and Fraser (2001)
Cardinalfishes								
Apogon niger	S	M?	I	External	Bearer external brooder	F	T	Okuda (1999)
Sunfishes								
Micropterus salmoides	S	P	I	External	Guarder nester	0	T	Schleusner and Maughan (1999)
Flounders								
Pleuronectes platessa	M	P	I	External	Non-guarder egg scatterer	0	G	Hoarau et al. (2004)
Billfishes								
Makaira nigricans	M	P	I	External	Non-guarder egg scatterer	0	G	Buonaccorsi et al. (2001)
Poeciliids								
Poecilia reticulata	S	P	I	Internal	Live bearer	M	T	Croft et al. (2003)
Poecilia reticulata	S	P	I	Internal	Live bearer	0	G	Russell et al. (2004)
Cichlids								
Pseudotropheus zebra	S	P	I	Internal	Bearer external brooder	M	G	Knight et al. (1999)
Pseudotropheus callainos	S	P	I	Internal	Bearer external brooder	M	G	Knight et al. (1999)
Eretmodus cyanostictus	S	M	I	External	Bearer external brooder	F	G	Taylor et al. (2003)
Neolamprologus multifasciatus	S	M	I	External	Non-guarder brood hider	F	T	Schradin and Lamprecht (2000)
Neolamprologus pulcher	S	M	I	External	Non-guarder brood hider	0	G,T	Stiver et al. (2004)
Salmonids								
Salvelinus fontinalis	S	P	I	External	Non-guarder brood hider	M	T	Hutchings and Gerber (2002)

Table 4 Continued

Species	Life history[d]	Mating system[e]	Breeding frequency[f]	Fertilization	Reproductive guild	Sex-biased dispersal[g]	Method[h]	Reference
Salvelinus fontinalis	S	P	I	External	Non-guarder brood hider	M/F[b]	G	Fraser et al. (2004)
Salvelinus malma	S	P	I	External	Non-guarder brood hider	F	T	Koizumi et al. (2006)
Oncorhynchus tshawytscha	M	P	S	External	Non-guarder brood hider	0	T	Unwin and Quinn (1993)
Oncorhynchus tshawytscha	M	P	S	External	Non-guarder brood hider	M	T[a]	Hard and Heard (1999)
Oncorhynchus nerka	M	P	S	External	Non-guarder brood hider	0	T	Thedinga et al. (2000)
Salmo trutta	M	P	I	External	Non-guarder brood hider	0	G	Hansen et al. (2001)
Salmo trutta	M	P	I	External	Non-guarder brood hider	0/M[c]	G	Bekkevold et al. (2004)
Salmo salar	M	P	I	External	Non-guarder brood hider	0	G,T	This study

[a] Transplant

[b] Marginal effect (P = 0.05) and only in some rivers, depending on scale

[c] Not significant

[d] Migratory type. S = Sedentary, M = Migratory

[e] Mating system. M = monogamous/parent bonding, P = Polygamy/Polyandry

[f] Breeding frequency. I = Iteroparous, S = Semelparous

[g] Sex-biased dispersal. 0 = sex independent, M = male-biased, F = female-biased

[h] Methods. G = genetic methods, T = physical tags

variation between the sexes in survival or in life-history traits, most notably in age at maturity, will affect the scope for sex-biased dispersal in salmonids, as shown for other species (e.g. Palo et al. 2004).

Although little is known about inter-sexual competition in salmonids, sex-specific differences in migratory behaviour have been found at all stages of development (emerging alevins: Nagata and Irvine 1997; emigrating smolts: Tamate and Maekawa 2004; returning adults: Morbey 2000), suggesting that more than one life stage may be sensitive to cues about sex-specific competition. For some populations, early sexual maturation in freshwater has perhaps the greatest potential effect on natal dispersal in anadromous Atlantic salmon, favouring either male or female-mediated gene flow. Mature parr are almost invariably males (Fleming 1998), which causes a strong male-bias in the operational sex ratio, and should lead to increased male-male competition and, hence, to male-biased dispersal. Thus, the high incidence of mature male parr observed in Iberian salmon populations should have resulted in a strong male-biased dispersal in our study. However, early sexual maturation also increases male mortality in freshwater relative to females (e.g. Myers 1984), which may explain the preponderance of females among emigrating smolts (Fig. 1), and which should result in greater scope for female-mediated gene flow. Given that early parr maturation is possibly heritable (Glebe and Saunders 1986, Garant et al. 2002; but see Fleming and Reynolds 2004), and that parr cannot survive in sea water (and thus cannot contribute to gene flow among watersheds), the spawning of mature male parr will tend to favour the spread of non-dispersing (resident) genes in the population (e.g. Lundqvist et al. 1994), constraining male-mediated gene flow and further exacerbating the effect of female-biased dispersal. Thus, whether male parr maturation favours male or female dispersal (or has no effect) probably varies spatially and temporally, depending on the sex ratio of anadromous spawners, the relative incidence of mature male parr in the spawning population, and the additional mortality associated with early reproduction. The fact that the sex ratio of anadromous populations typically shows little or no relation to the proportion of males maturing in freshwater (Fleming 1998) suggests that males and females incur similar life-time mortalities, thereby negating some of the advantages of sex-biased dispersal.

Because the advantages of natal dispersal depend chiefly on what the individual does in relation to other individuals in the group (Dobson and Jones 1985, Clobert et al. 2001), optimal dispersal strategies may be expected to differ between the sexes, and also to vary with varying sex ratios. Our study indicates that the sex ratio of anadromous breeders can fluctuate greatly between years, and also among rivers, in a salmonid metapopulation. Two populations had a male-biased sex ratio (Deva, Nansa), while two populations tended to be female-biased (Ason, Pas). The direction of gene flow varied depending on the molecular marker being used, perhaps due to local differences in sex-biased dispersal between neighbouring populations (e.g. Fraser et al. 2004) with different sex ratios. Physical tagging and maternally-inherited mtDNA indicated that gene flow was predominantly from the smallest (river Ason) to the largest (Rivers Nansa and Pas) populations according to a ''source/ sink'' system independent of habitat quality (Kawecki and Holt 2002), while bi-paternally inherited microsatellites indicated the opposite trend. This suggests that males and females may have dispersed differently in source and sink habitats, as indicated by the greater rate of migration of males in the River Nansa (a potential sink). The mark and recapture study, although non-significant, also indicated that

more males dispersed from the Pas while more females dispersed from the Ason. This suggests that spatial variation in sex ratios may favour the dispersal of a different sex in source and sink habitats, depending on the relative degree of resource competition and local mate competition. Moreover, temporal fluctuations in sex ratios may have helped to homogenize sex-biased gene flow, since conditions that favour the dispersal of males in some years may favour the dispersal of females in other years (Massot and Clobert 2000). A similar interaction between sex ratio and dispersal was observed by Marzluff and Balda (1989) in a flock living bird (pinyon jay), where females tended to leave flocks dominated by females to join flocks dominated by males. Temporal and spatial variation in sex ratios, therefore, may act together to prevent persistent sex-bias dispersal in Atlantic salmon metapopulations.

The estimated exchange of migrants in our study was high and seemed to conform to a metapopulation structure with asymmetric gene flow helping to maintain genetic variation in small, depressed salmon populations (Consuegra et al. 2005a). Although the mere existence of a metapopulation does not necessarily imply the absence of sex-biased dispersal (Caudill 2003), metapopulation dispersal may be sex-independent if the exchange of migrants is primarily driven not by the mating system, but by the risk of local extinction (Cohen and Levin 1991; Holt and McPeek 1996). Therefore, whether natal dispersal is sex-biased or not may also depend on the size and conservation status of the populations (Poethke et al. 2002). Indeed, natural recolonization of extirpated populations is largely independent of gender (e.g. Blundell et al. 2002). This has important implications for the persistence and restoration of fish populations, particularly at low densities, since fisheries exploitation can inadvertently target one sex (e.g. Consuegra et al. 2005b) and disrupt natal dispersal.

Most models of adaptive sex ratios predict that sex ratios should favour the sex that experiences the lowest competition (when both sexes disperse the same), and the dispersal of the sex that experiences the strongest local competition, when the sex ratio is constant (Ranta et al. 2000; Perrin and Mazalov 2000). In consequence, one would expect that the joint evolution of spawner sex ratio and dispersal should result in the sex ratio being biased towards one sex and dispersal being biased towards the opposite sex. However, the Atlantic salmon populations studied here do not fit this pattern, as the only population with evidence for male biased dispersal (R. Nansa) also shows a male-skewed sex ratio, while the other three populations do not show biased dispersal, despite having male or female skewed sex ratios. This is because dispersal can have multiple causes (Dobson and Jones 1985), and the results of the joint evolution of sex ratio and dispersal cannot always be predicted from the independent evolution of each trait. For example, Leturque and Rousset (2004) showed that when there is resource competition between males and females in polygynous species both, sex ratios and dispersal, can be biased towards the same sex (males). Additionally, if dispersal is costly and only one sex disperses at an optimal rate, the sex ratio should be biased toward the sex with optimal dispersal, rather than towards the sex that disperses the most (Leturque and Rousset 2004). Thus, the evolution of sex-biased dispersal and the evolution of sex-ratios may act in opposite ways, and as our study clearly indicates, cannot be studied independently of each other.

In summary, our study indicates that despite a polygamous mating system with strong male-male competition, the Atlantic salmon populations we have studied do not show sex-biased dispersal. We suggest that for salmonid metapopulations, differences in sex-specific life history strategies, and spatial and temporal variation in sex ratios, will commonly favour the dispersal of both sexes.

References

Aars J, Ims RA (2000) Population dynamic and genetic consequences of spatial density-dependent dispersal in patchy populations. Am Nat 155:252–265

Aparicio E, de Sostoa A (1999) Pattern of movements of adult Barbus haasi in a small Mediterranean stream. J Fish Biol 55:1086–1095

Beerli P, Felsenstein J (2001) Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. Proc Natl Acad Sci USA 98:4563–4568

Bekkevold D, Hansen MM, Mensberg KD (2004) Genetic detection of sex-specific dispersal in historical and contemporary populations of anadromous brown trout Salmo trutta. Mol Ecol 13:1707–1712

Birky CW, Fuerst P, Maruyama T (1989) Organelle diversity under migration, mutation and drift: equilibrium expectations, approach to equilibrium, effects of heteroplasmic cells, and comparisons to nuclear genes. Genetics 121:613–627

Blundell GM, Ben-David M, Groves P, Bowyers RT, Geffen E (2002) Characteristics of sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations. Mol col 11:289–303

Buonaccorsi VP, McDowell JR, Graves JE (2001) Reconciling patterns of inter-ocean molecular variance from four classes of molecular markers in blue marlin (Makaira nigricans). Mol Ecol 10:1179–1196

Croft DP, Albanese B, Arrowsmith BJ, Botham M, Webster M, Krause J (2003) Sex-biased movement in the guppy (Poecilia reticulata). Oecologia 137:62–68

Cadet C, Ferrière R, Metz JAJ, van Baalen M (2003) The evolution of dispersal under demographic stochasticity. Am Nat 162:427–441

Caudill CC (2003) Measuring dispersal in a metapopulation using stable isotope enrichment: high rates of ex-biased dispersal between patches in a mayfly metapopulation. Oikos 101:624–630

Clobert J, Nichols JD, Danchin E, Dhondt A (2001) Dispersal. Oxford University Press, Oxford, UK

Cohen D, Levin SA (1991) Dispersal in patchy environments: the effects of temporal and spatial structure. Theor Popul Biol 39:63–69

Consuegra S, García de Leániz C, Serdio A, González Morales M, Straus LG, Knox D, Verspoor E (2002) Mitochondrial DNA variation in Pleistocene and modern Atlantic salmon from the Iberian glacial refugium. Mol Ecol 11:2037–2048

Consuegra S, Verspoor E, Knox D, García de Leániz C (2005a) Asymmetric gene flow and the evolutionary maintenance of genetic diversity in small, peripheral Atlantic salmon populations. Cons Genetics 6:823–842

Consuegra S, García de Leániz C, Serdio A, Verspoor E (2005b) Selective exploitation of early running fish may induce genetic and phenotypic changes in Atlantic salmon. J Fish Biol 67(Suppl. A):130–146

Dobson FS (1982) Competition for mates and predominant juvenile dispersal in mammals. Anim Behav 30:1183–1192

Dobson FS, Jones WT (1985) Multiple causes of dispersal. Am Nat 126:855–858

Escorza-Treviño S, Dizon AE (2000) Phylogeography, intraspecific structure and sex-biased dispersal of Dall's porpoise, Phocoenoides dalli, revealed by mitochondrial and microsatellite DNA analyses. Mol Ecol 9:1049–1060

Favre L, Balloux F, Goudet J, Perrin N (1997) Female-biased dispersal in the monogamous mammal Crocidura russula: evidence from field data and microsatellite patterns. Proc R Soc Lond B264:127–132

Fleming IA (1996) Reproductive strategies of Atlantic salmon: ecology and evolution. Rev Fish Biol Fish 6:379

Fleming IA (1998) Pattern and variability in the breeding system of Atlantic salmon (Salmo salar), with comparisons to other salmonids. Can J Fish Aquat Sci 55:59–76

Fleming IA, Reynolds JD (2004) Salmonid breeding systems. In: Hendry AP, Stearns SC (eds) Evolution illuminated. Salmon and their relatives. New York: Oxford University Press, pp 264–294

Fraser DJ, Lippé C, Bernatchez L. (2004) Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (Salvelinus fontinalis) Mol Ecol 13:67–80

Friedenberg NA (2003) Experimental evolution of dispersal in spatiotemporally variable microcosms. Ecol Lett 6:953–959

Garant D, Fontaine P-M, Good SP, Dodson JJ, Bernatchez L (2002) The influence of male parental identity on growth and survival of offspring in Atlantic salmon (Salmo salar). Evol Ecol Res 4:537–549

Garant D, Kruuk LEB, Wilkin TA, McCleery RH, Sheldon BC (2005) Evolution driven by differential dispersal within a wild bird population. Nature 433:60–64

Gilliam JF, Fraser DF (2001) Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. Ecology 82:258–273

Glebe BD, Saunders RL (1986) Genetic factors in sexual maturity of cultured Atlantic salmon (Salmo salar) parr and adults reared in sea cages. Can Sp Pub Fish Aquat Sci 89:24–29

Goudet J, Perrin N, Waser P. (2002) Tests for sex-biased dispersal using bi-parentally inherited genetic markers. Mol Ecol 11:1103–1114

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Hansen MM, Kenchington E, Nielsen EE (2001) Assigning individual fish to populations using microsatellite DNA markers. Fish Fisher 2:93–112

Hanski I (1999) Metapopulation ecology. Oxford University Press, New York

Hard JJ, Heard WR (1999) Analysis of straying variation in Alaskan hatchery chinook salmon (Oncorhynchus tshawytscha) following transplantation. Can J Fish Aquat Sci 56:578–589

Hendry AP (2004) Selection against migrants contributes to the rapid evolution of ecologically dependent reproductive isolation. Evol Ecol Res 6:1219–1236

Hendry AP, Castric V, Kinnison MT, Quinn TP (2004) The evolution of philopatry and dispersal. In: Hendry AP, Stearns SC (eds) Evolution illuminated. Salmon and their relatives. Oxford University Press, New York, pp. 52–91

Hoarau G, Piquet AM T, van der Veer HW, Rijnsdorp AD, Stam WT, Olsen JL (2004) Population structure of plaice (Pleuronectes platessa L.) in northern Europe: a comparison of resolving power between microsatellites and mitochondrial DNA data. J Sea Res 51:183–190

Holt RD, McPeek MA (1996) Chaotic population dynamics favors the evolution of dispersal. Am Nat 148:709–718

Holtby LB, Healey MC (1990) Sex-specific life history tactics and risk-taking in coho salmon. Ecology 71:678–690

Huse G. (1998) Sex-specific life history strategies in capelin (Mallotus villosus). Can J Fish Aquat Sci 55:631–638

Hutchings JA, Gerber L. (2002) Sex-biased dispersal in a salmonid fish. Proc R Soc Lond B269:2487–2493

Jones MW, Hutchings JA (2001) The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic salmon. Heredity 86:675–684

Kawecki TJ, Holt RD (2002) Evolutionary consequences of asymmetric dispersal rates. Am Nat 160:333–347

Knight ME, Van Oppen MJ H, Smith HL, Rico C, Hewitt GM, Turner GF (1999) Evidence for male-biased dispersal in Lake Malawi cichlids from microsatellites. Mol Ecol 8:1521–1527

Koizumi I, Yamamoto S, Maekawa K. (2006) Female-biased migration of stream-dwelling Dolly Varden in the Shiisorapuchi River, Hokkaido, Japan. J Fish Biol 68:1513–1529

Le Galliard J-F, Ferrière R, Clobert J. (2003) Mother-offspring interactions affect natal dispersal in a lizard. Proc R Soc Lond B270:1163–1169

Leturque H, Rousset F. (2004) Intersexual competition as an explanation for sex-ratio and dispersal biases in polygynous species. Evolution 58:2398–2408

Lundqvist H, McKinnell S, Fängstam H, Berglund I. (1994) The effect of time, size and sex on recapture rates and yield after river releases of Salmo salar smolts. Aquaculture 121:245–257

Massot M, Clobert J. (2000) Processes at the origin of similarities in dispersal behaviour among siblings. J Evol Biol 13:707–719

Mazluff JM, Balda RP. (1989) Causes and consequences of female biased dispersal in a flock-living bird, the pinyon jay. Ecology 70:316–328

Morbey Y. (2000) Protandry in Pacific salmon. Can J Fish Aquat Sci 57:1252–1257

Myers RA (1984) Demographic consequences of precocious maturation of Atlantic salmon (Salmo salar) Can J Fish Aquat Sci 41:1349–1353

Nagata M, Irvine JR (1997) Differential dispersal patterns of male and female masu salmon fry. J Fish Biol 51:601–606

Okuda N. (1999) Female mating strategy and male brood cannibalism in a sand-dwelling cardinalfish. Anim Behav 58:273–279

Palo JU, Lesbarrères D, Schmeller DS, Primmer CR, Merilä J. (2004) Microsatellite marker data suggest sex-biased dispersal in the common frog Rana temporaria. Mol Ecol 13:2865–2869

Pardini AT, Jones CS, Noble LR, Kreiser B, Malcolm H, Bruce BD, Stevens JD, Cliff G, Scholl MC, Francis M, Duffy C A J, Martin AP (2001) Sex-biased dispersal of great white sharks. Nature 412:139–140

Paterson S, Piertney SB, Knox D, Gilbey J, Verspoor E. (2004) Characterization and PCR multiplexing of novel highly variable tetranucleotide Atlantic salmon (*Salmo salar* L.) microsatellites. Mol Ecol Notes 4:160–162

Perrin N, Mazalov V. (1999) Dispersal and inbreeding avoidance. Am Nat 154:282–292

Perrin N, Mazalov V. (2000) Local competition, inbreeding, and the evolution of sex-biased dispersal. Am Nat 155:116–127

Poethke HJ, Hovestadt T. (2002) Evolution of density-and patch-size-dependent dispersal rates. Proc R Soc Lond B269:637–645

Prugnolle F, de Meeus T. (2002) Inferring sex-biased dispersal from population genetic tools: a review. Heredity 88:161–165

Ranta E, Lummaa V, Kaitala V, Merilä J. (2000) Spatial dynamics of adaptive sex ratios. Ecol Let 3:30–34

Russell ST, Kelley JL, Graves JA, Magurran AE (2004) Kin structure and shoal composition dynamics in the guppy, Poecilia reticulata. Oikos 106:520–526

Schleusner CJ, Maughan OE (1999) Mobility of largemouth bass in a desert lake in Arizona. Fish Res 44:175–178

Schneider S, Roessli D, Excoffier L (2000) ARLEQUIN ver 2.000: a sofware for populations genetics data analysis. Geneve: Genetics and Biometry Laboratory, University of Geneve

Schradin C, Lamprecht J. (2000) Female-biased immigration and male peace-keeping in groups of the shell-dwelling cichlid fish Neolamprologus multifasciatus. Behav Ecol Sociobiol 48:236–242

Schrey AW, Heist EJ (2003) Microsatellite analysis of population structure in the shortfin mako (Isurus oxyrinchus). Can J Fish Aquat Sci 60:670–675

Slatkin M. (2005) Seeing ghosts: the effect of unsampled populations on migration rates estimated for sampled populations. Mol Ecol 14:67–73

Spidle AP, Quinn TP, Bentzen P. (1998) Sex-biased marine survival and growth in a population of coho salmon. J Fish Biol 52:907–915

Stiver KA, Dierkes P, Taborsky M, Balshine S. (2004) Dispersal patterns and status change in a cooperatively breeding cichlid Neolamprologus pulcher: evidence from microsatellite analyses and behavioural observations. J Fish Biol 65:981–105

Taggart JB, McLaren IS, Hay DW, Webb JH, Youngson AF (2001) Spawning success in Atlantic salmon (Salmo salar L.): a long-term DNA profiling-based study conducted in a natural stream. Mol Ecol 10:1047–1060

Tamate T, Maekawa K (2004) Female-biased mortality rate and sexual size dimorphism of migratory masu salmon, Oncorhynchus masou. Ecol Freshw Fish 13:96–103

Taylor MI, Morley JI, Rico C, Balshine S. (2003) Evidence for genetic monogamy and female-biased dispersal in the biparental mouthbrooding cichlid Eretmodus cyanostictus from Lake Tanganyika. Mol Ecol 12:3173–3177

Thedinga JF, Wertheimer AC, Heintz RA, Maselko JM, Rice SD (2000) Effects of stock, coded-wire tagging, and transplant on straying of pink salmon (Oncorhynchus gorbuscha) in southeastern Alaska. Can J Fish Aquat Sci 57:2076–2085

Unwin MJ, Quinn TP (1993) Homing and straying patterns of chinook salmon (Oncorhynchus tshawytscha) from a New Zealand hatchery: spatial distribution of strays and effects of release date. Can J Fish Aquat Sci 50:1168–1175

Wilson AJ, Hutchings JA, Ferguson MM (2004) Dispersal in a stream dwelling salmonid: inferences from tagging and microsatellite studies. Cons Genetics 5:25–37

Wilson K, Hardy ICW (2002) Statistical analysis of sex ratios: an introduction. In: Hardy ICW (eds) Sex ratios: concepts and research methods. Cambridge University Press, Cambridge, UK, pp 48–92