Dispersion patterns of kin in young-of-the-year Atlantic salmon (*Salmo salar* L.) in Catamaran Brook, New Brunswick

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Abstract

Dispersion patterns of kin in young-of-the-year Atlantic salmon (*Salmo salar* L.) in Catamaran Brook, New Brunswick

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Movement allows organisms to respond to heterogeneity in physical and biological conditions both at the individual and population level. Studying the movement of young stream fishes has proven to be problematic because of the difficulty of tagging small fishes using traditional techniques. In this study, recently developed microsatellite markers were used as a method of tagging individual young-of-the-year (YOY) Atlantic salmon (*Salmo salar* L.). First, the association between the local-scale distribution patterns of 81 territorial YOY salmon and their degree of relatedness in a natural stream was tested. No significant association between relatedness and distance at the local scale was found. Focal fish were not more related to their nearest-neighbour (mean $r_{x,y} = -0.004$) than to randomly selected fish (mean $r_{x,y} = 0.005$), nor were they more related to their four nearest-neighbours (mean $r_{x,y} = -0.01$) than to non-neighbours (mean $r_{x,y} = -0.007$). Second, 97 anadromous adults moving into the stream to spawn, four redd locations, as well as 313 of their offspring were sampled in a 1.6 km reach of Catamaran Brook. The initial dispersal of offspring from the four redd locations and resulting long-range dispersion patterns of families were mapped. The average dispersal distance of 69 YOY salmon from the sampled redd locations ranged from 50 – 955m downstream, and 9 – 154m upstream. Five maternal and nine paternal

half-sibling families were recaptured over an average dispersion distance (linear distance between the most upstream and most downstream sites of capture) of 1340m and 1018m, respectively. Four full-sibling families were identified with an average dispersion distance of 945m. The redd location (for sampled redds) and the most upstream location of a family (linear distance of the most upstream location of capture to the mouth of the brook) were combined and analysed as one variable. Dispersion distance was significantly, and positively correlated with redd or upstream location, with most families dispersing to the mouth of the brook. Third, alternative mating strategies take place in Atlantic salmon males, whereby both anadromous adults and precocious parr compete for fertilization opportunities with anadromous females. The present study suggests that precocious male parr may have fertilized up to 53% of the 313 sampled YOY salmon. This intensive field sampling allowed for the detection of the initial dispersal from redds and the large-scale dispersion of YOY salmon, which would not have been possible using alternative tagging methods. The results of the present study contributes to the understanding of dispersal and dispersion patterns of YOY salmon in freshwater habitats, and are applicable to the conservation and management of salmonid populations.

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Chapter 1

Chapter 2

General Introduction

Movement allows organisms to respond to heterogeneity in physical and biological conditions in order to increase their growth, survival and reproductive success (Kahler et al. 2001) both at the individual and population level. The degree to which salmonids move in a stream has been controversial. Increasing evidence suggests that stream fishes undergo a wide range of movements both within and between individuals (Gowan et al. 1994), challenging the view that stream fishes are sedentary (Gerking 1959). Many factors, such as resource competition at high densities, affect whether or not an animal moves. However, individuals are expected to move if movement will increase their fitness (Baker 1978; Hanski 1999).

Female Atlantic salmon (*Salmo salar* L.) spawn in a small area of a stream (reviewed by Fleming 1998) with several anadromous and/or precocious male parr (Jones 1959). The dispersal of young-of-the-year (YOY) salmonids from the resulting redds (i.e. gravel nests) is a critical period during early life history of salmonids in terms of survival (Elliott 1994). Most YOY salmonids are reported to move less than 1 km downstream after emerging from a redd (Egglishaw & Shackley 1973; Kennedy 1982; Harding 1986 cited in Hay 1989; Marty & Beall 1989; Beall et al. 1994; Webb et al. 2001). However, most of these studies are based on artificial redds and our knowledge of salmon dispersal from natural redds is limited. Of these previously mentioned studies, only the YOY salmon dispersal study reported in Hay (1989) is based upon a natural redd. The dispersal of kin from redds result in local-scale dispersion patterns. After the initial dispersal from redds, most YOY salmon are sendentary (Steingrímsson & Grant 2003).

In experimental studies involving high habitat quality conditions (i.e. high food abundance and/or low predation risk) (Brown & Brown 1993a), individuals are known to respond differentially toward relatives (i.e. kin-biased behaviour; Hepper 1991). These results suggest that establishing a territory next to kin increases both direct and indirect fitness, by reducing the aggression of dominant fish, increasing the foraging rate and growth rate of subordinate kin (Brown & Brown 1996) and thereby, increasing over-winter survival.

Unfortunately, little is known about kin-biased behaviour in wild populations of salmonids. Few studies have addressed this issue (e.g. Hansen et al. 1997; Fontaine & Dodson 1999; Mjølnerød et al. 1999; Carlsson & Carlsson 2002; Carlsson et al. 2004) and the results are equivocal. Sampling is almost always done by electrofishing and, therefore, the precise location of YOY kin in the stream is usually unknown (but see Fontaine & Dodson 1999).

Traditional tagging techniques, such as passive integrated transponder (PIT) (Armstrong et al. 1996) and visible implant elastomer tags (Dewey & Zigler 1996), are limited to larger sized fish, unlike genetic markers which are effective for all sizes of fish. Using genetic markers as a "tagging" method, the objectives of my study were (1) to test for the presence of kin-biased dispersion patterns in wild YOY Atlantic salmon by using a relatively non-invasive capture technique (i.e. snorkelling with dip nets) to map the distribution of kin at a local scale, and (2) to estimate both upstream and downstream dispersal of young-of-the-year Atlantic salmon from natural redds, and the dispersion patterns of siblings.

Chapter 1. Local-scale dispersion of young-of-the-year Atlantic salmon (*Salmo salar* L.) suggests no evidence of kin-biased settlement in a natural stream

Introduction

The concept of kin selection was first proposed in *The Origin of Species* when Darwin suggested that natural selection can operate at the family level, as well as on single organisms (Wilson 1975). Kin selection occurs when relatives behave to increase the genetic fitness of the whole group, at the expense of the direct fitness of some of the members in the group (Wilson 1975). Kin selection is amplified when individuals respond differentially toward relatives, known as kin-biased behaviour (Hepper 1991). Kin-biased behaviour is mediated by a mechanism of kin recognition (i.e. the ability to identify relatives), which has been the subject of many studies in eusocial insects, amphibians, birds and mammals (Hepper 1991). The advantages of kin recognition are numerous and include behaviour such as mate selection (inbreeding avoidance), avoidance of cannibalism, and helping one's relatives (increasing inclusive fitness) (reviewed in Ward & Hart 2003).

Hamilton (1964) suggested that helping kin, or not competing against kin, can be beneficial if the benefits received by related individuals (i.e. indirect fitness) outweigh the costs to the individual's direct fitness. Inclusive fitness is defined as the sum of an individual's own fitness (i.e. direct fitness) plus the sum of all increases in fitness of its relatives caused by the individual (i.e. indirect fitness) (Wilson 1975). If k is defined as the ratio of the gain in fitness of relatives divided by the loss of personal fitness and r as the relatedness of that individual to another, then "altruistic" behaviour towards kin is

favoured if : $k > 1/r$. For example, an individual choosing to help a full-sibling (i.e. $r = 0.5$) instead of reproducing would increase their inclusive fitness if their full-sibling's fitness increased by more than two times (Wilson 1975).

A wide range of kin-biased behaviour has been observed including avoiding kin in winter refuges in Atlantic salmon (Griffiths et al. 2003), migration with kin by smolts in Atlantic salmon (Olsén et al. 2004) and schooling of kin in foraging brook charr (*Salvelinus fontinalis*) (Fraser et al. 2005). In a number of controlled experimental studies, Brown and Brown (1993a) were the first to explore the link between kin-biased behaviour, and growth rate, a component of inclusive fitness, with territorial behaviour in juvenile salmonids. In high quality habitat (i.e. high food abundance and/or low predation risk), juvenile rainbow trout (*Oncorhynchus mykiss*) siblings are less aggressive towards each other, and gain more weight, compared to non-kin groups (Brown & Brown 1993a). Establishing a territory next to kin would increase both direct and indirect fitness, by reducing the aggression of dominant fish, increasing the foraging rate and growth rate of subordinate kin (Brown & Brown 1996) and thereby, increasing over-winter survival.

Unfortunately, little is known about kin-biased behaviour in wild juvenile salmonids. Only a few field studies have addressed this issue (e.g. Hansen et al. 1997; Fontaine & Dodson 1999; Mjølnerød et al. 1999; Carlsson & Carlsson 2002; Carlsson et al. 2004) and the results are equivocal. Mjølnerød et al. (1999) reported a weak but significant negative association between relatedness and geographical distance (within 300m) in juvenile Atlantic salmon. Related YOY brown trout (*Salmo trutta* L.) were found closer together than expected by chance in one of two streams (Carlsson et al. 2004). In another study however, YOY and 1+ brown trout in a stream avoided kin

(Carlsson & Carlsson 2002). In all three studies, sampling was done by electrofishing, which is a relatively crude way of determining local dispersion patterns. Hence, the question of whether YOY kin were holding adjacent territories in the stream could not be answered. At a smaller spatial scale, Fontaine and Dodson (1999) individually captured YOY Atlantic salmon using a diver-operated electrofishing device, and concluded that kin are not found in adjacent territories up to 10 days after emergence from redds (i.e. gravel nests).

The purpose of my study was to test whether YOY Atlantic salmon settle closer to kin than to non-kin. This is the first study using genetic markers and a non-invasive capture technique (i.e. snorkelling with dip nets) to test kin-biased dispersion patterns in wild YOY Atlantic salmon. This sampling technique ensured reliable location information for each fish prior to capture.

Materials and Methods

In the field

This study is based upon a wild Atlantic salmon population in Catamaran Brook (46-52.7'N, 66-06.0'W), New Brunswick, a third order tributary of the Little Southwest Miramichi River. Each autumn, adult salmon migrate into the brook to spawn. A counting fence and fish trap, 216m upstream from the mouth of the brook, is maintained by the staff of the Catamaran Brook Research Station during the spawning season to monitor the entry and exit of spawning individuals.

In October and November of 2003, 97 anadromous adults, were caught at the counting fence and fish trap as they migrated into and out of Catamaran Brook. A total of 31 females and 66 males were tagged, measured (i.e. fork length in cm), fin-clipped, and subsequently released past the fish trap in the direction they were moving. To identify individual fish, a Floy Tag was attached to the dorsal fin of each adult and a piece of caudal fin (~0.5 cm^2) was clipped and preserved in 95% ethanol for genetic studies. If an adult was already tagged, the tag number was recorded and a fin-clip was collected. Because of high water levels, the fence was removed from October 27 to November 3, 2003, allowing untagged adults to move into the brook. Therefore, not all anadromous adults were sampled. When the fence was reassembled and functional, some untagged and previously tagged adults were caught, sampled and released before migrating out of the brook toward the sea.

From August 28 to September 1st, 2004, the putative offspring of the 2003 spawning season were sampled by snorkelling in an 8x38-m study site located at the mouth of the brook, approximately two months after emergence from redds. The site was chosen because of the high density (0.3 – 1 per m^2) of YOY salmon. Sampling was done in the afternoons (between 13h00 and 18h00) when approximately 60% of YOY salmon are active (Breau 2003). Each fish was caught by a diver using dip nets, swimming upstream, to minimize the chance of scaring and chasing the fish out of established territories. A brightly-painted orange marker was placed at the site of capture. Only one fish was caught at a time and brought to shore for processing and then gently released by the diver back into the stream near its location of capture. On shore, the mass (± 0.01 g) and fork length (± 0.1 cm) of each fish were measured and an adipose fin-clip (~0.1-0.2

cm^2) was taken and preserved in 95% ethanol for genetic studies. After five consecutive days, 91 YOY salmon were captured and their location (i.e. (x,y) coordinates to the nearest cm) were recorded (Fig. 1.1; protocol in Steingrímsson & Grant 2003).

In the laboratory

Genomic DNA extractions and DNA amplification

Genomic DNA was extracted for both the adults (n = 97) and YOY samples (n = 81) from ~25 mg of tissue and complete adipose fin, respectively, using the QIAGEN DNeasy Tissue Kit (QIAGEN Inc., Mississauga, Ontario, catalogue # 69506). Of the 91 YOY samples collected, only 81 could be used in the genetic analysis. Fish numbers 16, 18, 22, 24, 26, 42, 46, 47, 48 and 64 were not genotyped (Fig. 1.1).

All samples were successfully amplified using the polymerase chain reaction (PCR) at eight polymorphic tetranucleotide microsatellite loci: SSsp1605, SSsp2215, SSsp2210, SSsp2213, SSspG7, SSsp2216 (Paterson et al. 2004), Ssa197 and Ssa202 (O'Reilly et al. 1996). Tetranucleotide microsatellites are polymorphic (reviewed in Jarne & Lagoda 1996) and easier to resolve than di- or trinucleotides, since they show minimal PCR artefacts such as stuttering, which may complicate one's ability to correctly score allele sizes (O'Reilly et al. 1996). The PCR reaction consisted of a 'master mix' (V_f= 24 μl) of PCR reaction buffer [20 mM Tris-Cl pH 9.5, 25 mM KCl, 0.05% Tween-20, 100 μg/ml Bovine Serum Albumin and 1.5 mM $MgCl_2$], 0.2 mM dNTPs, 0.2 pmol/μl forward and reverse primers, 0.05 units/μl TAQ polymerase. The forward primer was labelled with a fluorescent molecule (for details, see *Genotyping* section below). One to four microlitres (μl) of genomic DNA (DNA was not quantified) were added to each sample.

A negative control, where no DNA was added to the reaction, was included in each experiment. The following PCR thermal cycling conditions were used: initial denaturation at 96°C for 3 min, 35 cycles of 96°C for 30 sec (denaturation), 58°C for 30 sec (annealing), and 72°C for 30 sec (elongation), and a final extension at 72°C for 5 min. For loci Ssa197 and Ssa202, the same conditions were used, except the annealing temperature was set to 55°C. To check that PCR amplification was successful, several samples were randomly chosen, run on a 1% agarose gel, and stained in a 0.5 μg/ml ethidium bromide solution to view on the Syngene Digital Imaging Station (Syngene, Frederick, Maryland).

Genotyping

To determine the size of the DNA fragments (i.e. microsatellite alleles) generated by PCR, the forward primer of each primer pair was labelled (OPERON Technologies, California) at the 5'-end with one of three fluoresceins (fluorescent dyes), 6-FAM (blue), TET (green) or HEX (yellow), to permit detection of the amplified DNA fragments on the ABI 310 Genetic Analyzer (ABI 310) (Applied Biosystems, Foster City, California). Using these dyes, three multiplexed groups were formed: (1) SSsp1605(6-FAM)-SSsp2215(TET)-SSsp2210(HEX), (2) SSsp2213(6-FAM)-SSspG7(TET)-SSsp2216(HEX), and (3) Ssa197(6-FAM)-Ssa202(TET). Each group was run separately on the ABI 310 in 15 μl of formamide, along with 0.l-0.15 μl of the size standard, GeneScan™-500 [TAMRA]™ (red), also labelled with a fluorescent dye. Standardization between runs was done by comparing and overlapping the size standard for up to 48 consecutive runs using the GENOTYPER v. 3.7 NT software.

Data analyses

Scoring alleles

Allele sizes were determined from the raw data generated by the ABI 310 using the software GENOTYPER. For each locus, size range of each allele was determined and alleles were manually scored for each individual. A third DNA fragment (128 bp) was present in every individual genotyped at locus SSsp2216, and was omitted from further analyses.

Hardy-Weinberg equilibrium, linkage disequilibrium, detection of null alleles and allele size mis-identification due to stuttering

To verify that the population was in Hardy-Weinberg (HW) equilibrium, the following tests were performed. The web-based software, GENEPOP v.3.4 (http://wbiomed.curtin.edu.au/genepop/genepop_op1.html) (Raymond & Rousset 1995), was used to test for the HW equilibrium, linkage disequilibrium of the eight loci used, and calculate allelic frequencies and observed heterozygosity values for each locus. When an allele fails to amplify by PCR (i.e. a null allele), usually due to mutations in the flanking regions of a microsatellite locus, heterozygotes may be mis-identified as homozygotes. The MICRO-CHECKER v. 2.2.3 software (Oosterhout et al. 2004) was used to test for the presence of null alleles and mis-identification of allele size due to stuttering in the data set. Stuttering occurs when the polymerase in a PCR reaction slips off of the DNA it is amplifying by one, two or three microsatellite repeats, thereby creating secondary allele fragments. These fragments are a common artefact during genotyping experiments,

and may create a problem in determining an allele size. All tests were corrected for multiple comparisons using the Bonferroni correction ($\alpha = 0.05/8 = 0.00625$), except for the linkage disequilibrium test, which was corrected for 28 pair-wise comparisons ($\alpha = 0.05/28 = 0.00178$) (Sokal & Rohlf 1995).

Kinship determination

Scored alleles for the adults and YOY were analysed using the Parental Allocation of Singles in an Open System (PASOS) v.1.0.0.1 software (Duchesne et al. 2005) and PEDIGREE v.3.0 software (http://herbinger.biology.dal.ca/pedigree/) (Smith et al. 2001). Parental assignment to offspring was performed using the software PASOS in order to create groups of siblings with at least one parent in common. Since not every individual in the site is expected to be assigned to an adult, the software PEDIGREE was also used to partition individuals into groups of siblings in the absence of parental information, thereby including all of the 81 offspring sampled at the site in the analysis.

The degree of genetic relatedness of offspring dyads (i.e. pairs of offspring) was estimated using pair-wise relatedness values ($r_{x,y}$) calculated using the KINSHIP v.1.3.1 software (Queller & Goodnight 1989) for 81 offspring (i.e. 3240 dyads). Relatedness ($r_{x,y}$) can be estimated using the equation $R = \sum_x \sum_k \sum_l (P_y - P^*) / \sum_x \sum_k \sum_l (P_x - P^*)$; where $R = r_{x,y}$; x = individuals in the data set; k = loci analysed; l = allelic position; P_x = the frequency within individual x of the allele found at x's locus k and allelic position l; P_y = the frequency of that same allele in the pair-wise comparison between individual x and its "partner" y – the individual to which you want to measure x's relatedness; and P^* = the frequency of the same allele in the population at large, with all putative relatives of

x excluded (Queller & Goodnight 1989). Half-siblings and full-siblings are defined as having one or two parents in common, respectively. Theoretically, unrelated, half-sibling and full-sibling individuals have a mean pair-wise relatedness value ($r_{x,y}$) of 0, 0.25, and 0.50, respectively. Using the potential parental genotypes, 30 000 pairs of unrelated, half-sibling and full-sibling offspring were simulated to identify the likelihood of the misclassification of full-sibling dyads as half-siblings or unrelated, and half-sibling dyads as unrelated. Due to the overlap of the distribution of expected values from each of the genetic relationships (i.e. unrelated, half-sibling or full-sibling), threshold-relatedness values are necessary to recognize siblings (at least half-siblings) and full-siblings in the data set ($\alpha = 0.05$) (procedure described in Blouin et al. 1996).

Relatedness as a function of linear distance

Two comparisons were used to test for a relationship between relatedness and distance. In the nearest-neighbour analysis, each YOY in the site was tested to see if its nearest-neighbour (i.e. the YOY with the shortest linear distance) was more closely related (based on $r_{x,y}$ values from the software KINSHIP) than a random YOY in the site. In an analysis of the four nearest-neighbours, each YOY in the site was tested to see if its four nearest-neighbours (i.e. four YOY with the shortest linear distances), were more related (based on $r_{x,y}$ values from the software KINSHIP) than the average relatedness of all other YOY in the site.

On a larger spatial scale, a Mantel test using the R-Package v. 4.0d6 software (Casgrain & Legendre 2001) was performed to test for a correlation between the pair-wise relatedness matrix (output file obtained from KINSHIP) and the pair-wise distance

matrix, assembled manually from the equation $c^2=a^2+b^2$ with the (x,y) coordinates of each fish location incorporated [$a = (x_j - x_i)$; $b = (y_j - y_i)$; where (x_i, y_i) coordinates describe the location for fish (i) and (x_j, y_j) coordinates describe the location for fish (j), in a given pair-wise comparison] to find the shortest distance (c) between each pair of YOY.

Results

Allelic diversity, Hardy-Weinberg equilibrium, linkage disequilibrium, and null allele detection

All loci were polymorphic. The number of alleles ranged from 9 - 27 in the adults (mean = 15.6) and 7 - 18 alleles in the offspring (mean = 11.6). Six of the eight loci in the 97 adults and seven of the eight loci in the 81 offspring were in Hardy-Weinberg (HW) equilibrium (Table 1.1). Heterozygote deficiency was detected for SSsp2213 and SSspG7 in adults and no heterozygote deficiency was detected for the offspring. Linkage disequilibrium for the eight loci used in this study was detected in both adults and in offspring (i.e. 5 of 28 and 7 of 28 pair-wise comparisons, respectively). The presence of a null allele at locus SSsp2213 was detected in the adults only. No evidence of mis-identification of allele size due to stuttering was found at any locus, as determined by the software MICRO-CHECKER.

Relatedness of young-of-the-year salmon

The relatedness values of offspring dyads (i.e. pairs of fish) were determined (Fig. 1.2). Based on the simulation data of offspring from potential parental genotypes (i.e. adult genotypes), I selected two threshold-relatedness values. The threshold value of $r_{xy} \geq 0.489$ yielded full-sibling dyads with 95% of half-sibling dyads and 99.96% of unrelated individuals rejected. Consequently, the full-sibling group included 54% of all full-sibling dyads (Fig. 1.3). The threshold value $r_{xy} \geq 0.240$ yielded a group of sibling dyads with 95% of unrelated individuals rejected and included 94% of all full-sibling dyads and 53% of all half-sibling dyads (Fig. 1.3). Unrelated individuals will exhibit a normal distribution around a mean $r_{xy} = 0$, which explains the negative values of relatedness.

Determination of sibling groups

Out of 97 adults, four anadromous females (with a probability of correctness of 93.5%, as calculated by the software PASOS; Appendix 1A) and 10 anadromous males (with a probability of correctness of 88.1%, as calculated by the software PASOS; Appendix 1B) were assigned successfully to 30 offspring and 18 offspring, respectively, for a total of 41 of the 81 YOY in the site (Table 1.2). Of the 41 offspring, seven had two parents assigned to them, two of which were full-siblings (fish 2 & 12) and genetically identical at eight loci (i.e. one fish was sampled twice). Therefore, no full-siblings could be identified using parental information. Two females accounted for 28 of the 30 assigned offspring. The software PASOS created five maternal and paternal half-sibling groups (i.e. parents with more than one assigned offspring) (Table 1.2).

Because 40 of 81 offspring were unassigned to adults (using the software PASOS), the software PEDIGREE was used to include all 81 offspring to construct half- and full-sibling groups without the use of parental information. A total 45 of 81 offspring and 30 of 81 offspring were partitioned significantly (1000 iterations; group cohesion score $\alpha = 0.05$) into eight half-sibling families (Appendix 1C) and into nine full-sibling families (Appendix 1D), respectively, including a total of 46 of 81 offspring at the Mouth site, since full-sibling families were nested within half-sibling families (Table 1.3).

Four pairs of fish were found to be genetically identical at all eight loci ($r_{x,y} = 1.0$; as calculated using the software KINSHIP): fish numbers 1 & 7, 2 & 12, 3 & 19, and 11 & 20. These pairs of fish were likely the same fish captured on two different days (Appendix 1E).

Determination of relatedness of neighbours

Focal fish were not significantly more related to their nearest-neighbours (mean $r_{x,y}$ = -0.004) than to a randomly selected (mean $r_{x,y} = 0.005$) fish (paired t = -0.308, df = 80, $p = 0.759$). Similarly, focal fish were not significantly more related to their four nearest-neighbours (mean $r_{x,y}$ = -0.01) than to non-neighbours (mean $r_{x,y}$ = -0.007) (paired t = -0.213, df = 80, $p =$ 0.832). No correlation was found between the pair-wise relatedness and pair-wise distance matrices of the 81 YOY in the site (Mantel test; t = -0.190, n = 81, $p = 0.425$) (Fig. 1.4).

Discussion

Only two of the eight loci for the adults, and one of the eight loci for the offspring showed a significant deviation from the Hardy-Weinberg (HW) equilibrium. Furthermore, no heterozygote deficiencies were detected for the offspring. The observation that locus SSsp2213 was not in HW equilibrium in both adults and offspring may be the result of a null allele detected at this locus. Omitting SSsp2213 from the analyses would not affect the results since only one of the offspring (fish 53) assigned to the adult male 819 would be omitted from the analysis (refer to Tables 1.2 and 1.3) and two offspring would be added (fish 56 assigned to male 820 and fish 53 assigned to male 801; when SSsp2213 was included, male 820 did not have any assigned offspring). Omitting locus SSsp2213 would also reduce the estimated correctness probabilities of assigning female and male adults to offspring from 93.5% to 87.9% and 88.1% to 82.7%, respectively. Linkage disequilibrium was not expected since all of the loci chosen for this study have been mapped and shown not to be linked (Gilbey et al. 2004).

There was no significant association between relatedness ($r_{x,y}$) and distance (m) at two different spatial scales, even with the bias of four pairs of genetically identical fish included as eight individual fish. These results disagree with the findings of laboratory studies that have demonstrated the presence of kin-biased behaviour in territorial salmonids at the local scale (e.g. Brown & Brown 1996). Habitat quality and population density may have contributed to the lack of evidence of kin-biased behaviour of YOY salmon in the field.

Perhaps habitat quality in the study site was too low (i.e. food was limited and/or predation risk was high) for kin-biased behaviour to be beneficial (Brown & Brown 1993a). Food abundance and predation risk, which were not measured in this study, are known to alter the degree to which salmon exhibit kin-biased behaviour under laboratory settings. When habitat quality is high (i.e. high food abundance and/or low predation risk) subordinate fish gain more weight, a component of fitness for juvenile salmonids (Hutchings & Jones 1998), by associating with dominant kin than with non-kin (Brown & Brown 1996). Habitat quality has also been shown to influence kin-biased behaviour in common frog (*Rana temporaria*) tadpoles (Pakkasmaa & Laurila 2004). In low quality habitats (i.e. food was limited), no kin-biased associated benefits (i.e. increased growth) were detected compared to when habitat quality was high (i.e. food was in excess).

Population density may also explain why kin-biased behaviour is observed in the laboratory but not in a natural habitat. Densities of YOY at the Mouth site may have been too low (0.27 fish per m^2) for the fish to have exhibited kin-biased behaviour. Other field studies reporting equivocal results had similar densities: 0.36 – 2.6 fish per m^2 in YOY salmonids (Fontaine & Dodson 1999; Carlsson et al. 2004). In contrast, in laboratory studies density varied between 1 – 9 fish per m^2 (Brown & Brown 1993a; 1993b; Brown et al. 1996). Future studies in the laboratory using low densities and in nature using high densities of YOY salmonids might help resolve the issue.

Figure 1.1. Mapped locations ((x,y) coordinates) of 91 young-of-the-year Atlantic salmon caught at the Mouth site at Catamaran Brook in the summer of 2004. Zero is the left bank of the 8x38-m site. Note: the x-axis is exaggerated.

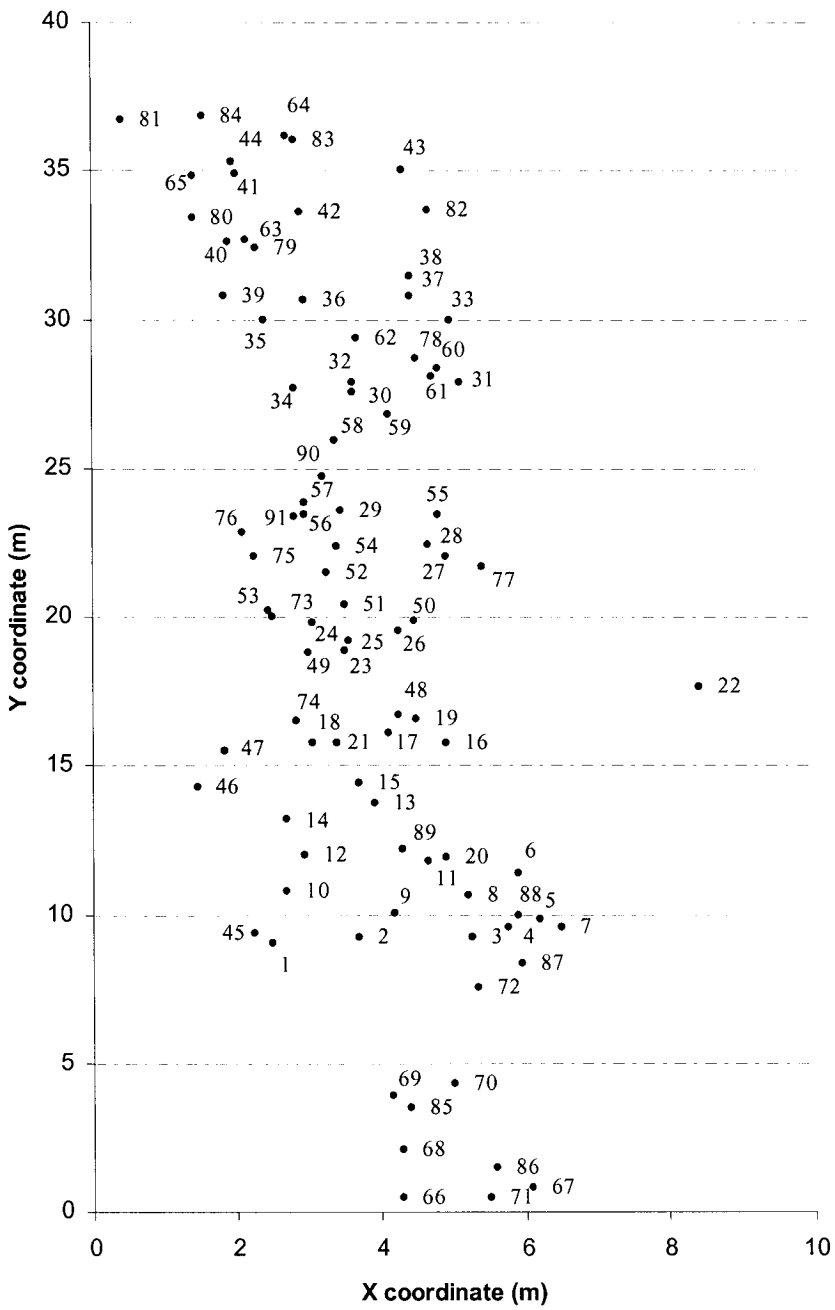

Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81
84
64
44
83
43
65
41
80
42
82
63
40
79
38
37
39
36
33
35
62
78
60
32
31
34
30
61
58
59
90
57
55
76
91
56
29
28
75
54
52
27
77
53
73
51
50
24
25
26
49
23
22
48
74
18
19
47
21
17
16
46
15
13
14
89
12
20
6
11
10
9
8
88
5
7
45
2
3
4
1
87
72
69
70
85
68
86
67
66
71

Figure 1.2. Relatedness values ($r_{x,y}$) for offspring dyads calculated using the software KINSHIP for the Mouth site at Catamaran Brook (n = 81 fish; n = 3240 dyads).

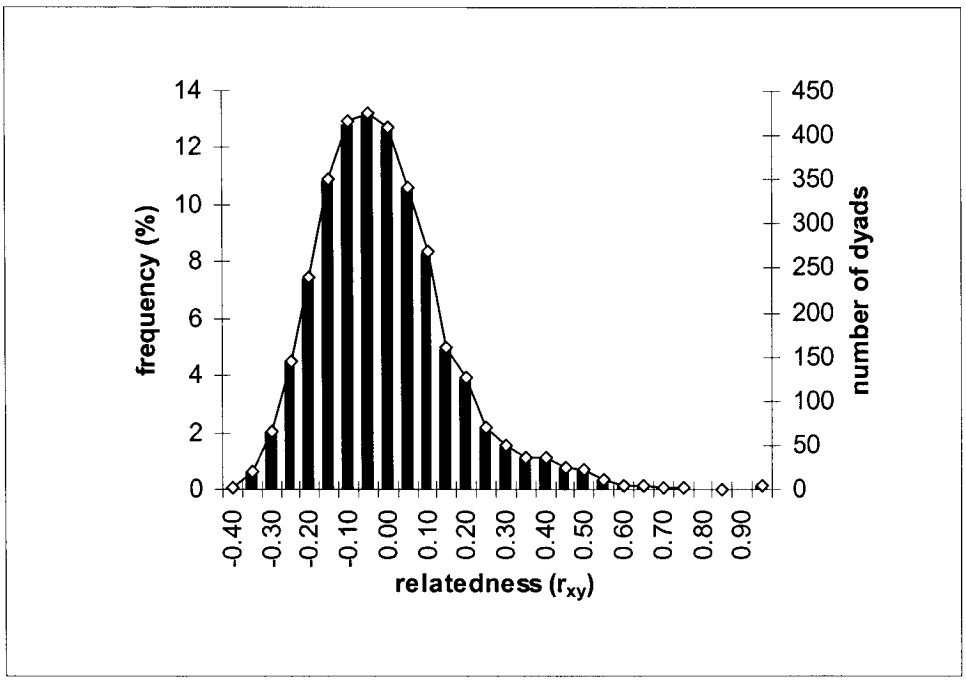

frequency (%)
number of dyads
relatedness (r_{xy})
0
2
4
6
8
10
12
14
0
50
100
150
200
250
300
350
400
450
-0.40
-0.30
-0.20
-0.10
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90

Figure 1.3. Frequency distribution of 30,000 simulated offspring dyads from spawning adult genotypes. The threshold value $r_{xy} \geq 0.489$ yields full-sibling dyads and the threshold value $r_{xy} \geq 0.240$ yields sibling dyads.

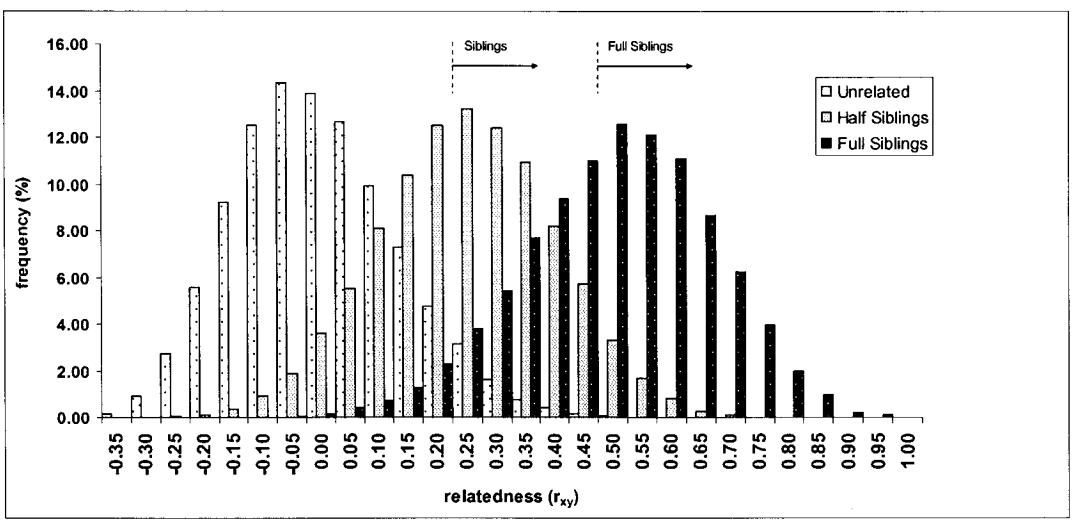

16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
frequency (%)
Siblings
Full Siblings
Unrelated
Half Siblings
Full Siblings
-0.35
-0.30
-0.25
-0.20
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
0.50
0.55
0.60
0.65
0.70
0.75
0.80
0.85
0.90
0.95
1.00
relatedness (r_{xy})

Figure 1.4. Pair-wise relatedness as a function of pair-wise distance in young-of-the-year Atlantic salmon (n = 81 fish; n = 3240 dyads). Siblings (having at least one parent in common) [95th percentile threshold value $r_{x,y}$ = 0.240; full line] and full-siblings [95th percentile threshold value $r_{x,y}$ = 0.489; broken line] are identified. Mantel test; t = -0.190, n = 81, p = 0.425.

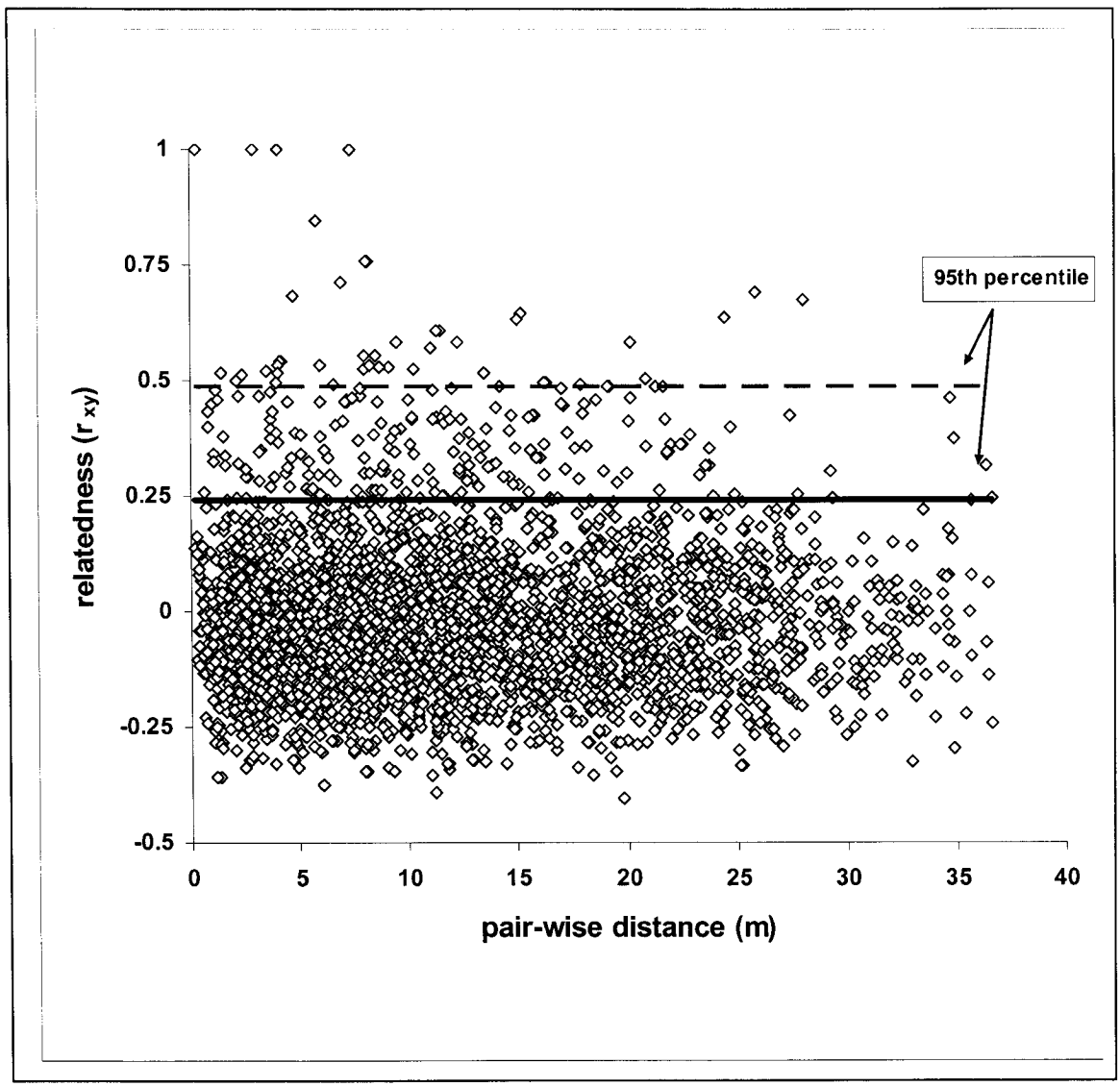

1
0.75
0.5
0.25
0
-0.25
-0.5
relatedness (r_{xy})
95th percentile
0
5
10
15
20
25
30
35
40
pair-wise distance (m)

Table 1.1. Allelic diversity, expected and observed homozygosity and Hardy-Weinberg (HW) equilibrium test results for (a) 97 adults captured in the fall of 2003 and (b) 81 offspring sampled in the Mouth site of the Lower Reach in the summer of 2004.

Locus	No. Alleles	No. Expected Homozygotes	No. Observed Homozygotes	Heterozygote Deficiency p-value	HW equilibrium p-value
(a) Adults					
SSsp1605	11	17.52	19	0.282	0.059
SSsp2215	15	15.05	9	0.918	0.544
SSsp2210	9	40.94	40	0.663	0.767
SSsp2213	15	10.07	23	< 0.001*	< 0.001*
SSspG7	16	9.46	15	< 0.001*	0.005*
SSsp2216	27	7.49	9	0.073	0.428
Ssa197	16	10.71	14	0.283	0.114
SSa202	16	8.63	9	0.585	0.177
(b) Offspring					
SSsp1605	12	12.22	11	0.840	0.218
SSsp2215	14	13.11	10	0.888	0.010
SSsp2210	7	27.79	29	0.592	0.837
SSsp2213	12	11.33	16	0.133	0.001*
SSspG7	14	8.37	6	0.872	0.296
SSsp2216	18	7.65	13	0.045	0.021
Ssa197	16	9.04	5	0.977	0.237

Table 1.1 continued...

Ssa202	16	8.57	5	0.954	0.093

**significant, $\alpha = 0.0062$ after Bonferroni correction*

Table 1.2. Assignment of female (n = 4 of 31) and male (n = 10 of 66) anadromous adults to offspring (n = 41 of 81) at the Mouth site, Catamaran Brook using the software PASOS.

Adult	No. of offspring	Offspring name
female 827	15	2, 5, 6, 12, 14, 50, 56, 58, 59, 62, 67, 68, 75, 76, 84.
female 837	13	4, 11, 20, 21, 23, 30, 34, 39, 44, 55, 61, 73, 82.
female 834	1	17.
female 779	1	57.
male 897	3	2, 12, 82.
male 809	4	3, 19, 37, 55.
male 824	4	13, 17, 62, 65.
male 803	1	15.
male 819	1	53.
male 780	1	67.
male 3083	1	69.
male 842	1	72.
male 843	1	86.
male 801	1	91.

Table 1.3. Half-sibling (n = 45 of 81) and full-sibling (n = 30 of 81) families (for a total of 46 offspring) in the Mouth site at Catamaran Brook using the software PEDIGREE.

Family name	No. of offspring	Offspring name
(a) Half-siblings		
Family 1	9	1, 7, 15, 27, 29, 31, 38, 51, 85.
Family 2	9	11, 20, 21, 23, 39, 44, 55, 61, 73.
Family 3	8	5, 14, 50, 56, 59, 68, 75, 76.
Family 4	5	3, 8, 19, 37, 69.
Family 5	5	10, 43, 53, 54, 89.
Family 6	4	2, 12, 52, 67.
Family 7	3	4, 30, 34.
Family 8	2	6, 84.
(b) Full-siblings		
Family 1	6	11, 20, 21, 23, 55, 73.
Family 2	4	27, 31, 38, 85.
Family 3	4	3, 8, 19, 37.
Family 4	3	2, 12, 52.
Family 5	3	1, 7, 51.
Family 6	3	10, 33, 89.
Family 7	3	4, 30, 34.
Family 8	2	6, 84.
Family 9	2	14, 50.

Chapter 2. Dispersion patterns of young-of-the-year Atlantic salmon (*Salmo salar* L.) in Catamaran Brook, New Brunswick, as revealed by microsatellite analysis

Introduction

Movement allows organisms to respond to heterogeneity in physical and biological conditions in order to increase their growth, survival and reproductive success (Kahler et al. 2001). At an individual level, dispersal can be a response to a spatially and temporally variable environment (Hutchings & Gerber 2002). At a population level, the movement of individuals serves to rescue small populations from local extinction within a metapopulation (Brown & Kodric-Brown 1977).

An individual is expected to move if movement will increase its fitness (Baker 1978; Hanski 1999). On a local scale, factors that may affect whether or not an animal moves include: reduction of sibling competition, inbreeding avoidance, resource competition at high densities (density-dependent dispersal), conspecific attraction at low densities, and escaping imminent extinction (Hanski 1999).

The degree to which salmonids move in a stream has been a controversial topic. Gerking (1959) suggested that stream fishes have restricted movements within home ranges. The view that stream fishes are sedentary persisted in the literature until challenged by Gowan et al. (1994). Increasing evidence suggests that stream fishes undergo a wide range of movements, such as passive and active dispersal of fry, diel movements and long-range migrations (Gowan et al. 1994).

The question of whether YOY Atlantic salmon in Catamaran Brook are sedentary or mobile was studied by Steingrímsson and Grant (2003). They tagged fish using

fluorescent elastomer tags injected under the skin (Dewey & Zigler 1996) in early July at a fork length of 30.1 – 55.3 mm. YOY salmon are sendentary; most move less than 10m in 60 days (Steingrímsson & Grant 2003). Unfortunately, fish emerging from gravel nests are too small to tag (i.e. 26 mm, Randall 1982), so the initial dispersal from redds could not be studied. Adult females deposit up to 14 000 eggs (Scott & Crossman 1979). Consequently thousands of siblings emerge from a nest and potentially compete for resources, presumably favouring the dispersal away from the redd, and downstream (Hume & Parkinson 1987; Steingrímsson & Grant 2003). Moreover, Imre (2003) clearly demonstrated that density-dependent growth occurs in YOY salmon at Catamaran Brook; growth rate decreases as density increases.

Most YOY salmonids are known to move less than 1 km downstream after emerging from a redd (Egglishaw & Shackley 1973; Kennedy 1982; Harding 1986 cited in Hay 1989; Marty & Beall 1989; Beall et al. 1994; Webb et al. 2001), searching for suitable habitat, which is likely to be in shallow, slow areas of the stream (Keeley & Grant 1995). Initial densities as high as 10 YOY salmon per m^2 over short distances near the redd after emergence have been estimated (Beall et al. 1994). Therefore, dispersal of YOY fish may be an important means of maximizing the use of available habitat (Crisp 1993). Similarly, YOY salmon were shown to disperse up to 950m from locations where they were stocked; many dispersed less than 500m and most dispersed less than 20m (Crisp 1995). Few studies report upstream dispersal (range 90 - 166m) from a redd location (e.g. Egglishaw & Shackley 1973; Harding 1986 cited in Hay 1989; Webb et al. 2001). Our knowledge of the dispersal of YOY fish from natural redds is limited. Of

these previously mentioned studies, only the dispersal of YOY salmon reported in Hay (1989) originated from a natural redd.

Genetic markers are an ideal way to study the movement of fishes because unlike traditional tags (e.g. PIT or elastomer tags), genetic markers can be used for all sizes of fish. Furthermore, very little tissue is needed (0.1-0.2 cm^2) for genetic analyses, which allows for live (non-destructive) sampling of small or endangered populations.

The purpose of this study was to estimate both the upstream and downstream dispersal of YOY Atlantic salmon from natural redds, and the dispersion patterns of siblings. Spawning adults were sampled as they migrated through a counting fence at Catamaran Brook, New Brunswick. The offspring of these adults were sampled at 14 electrofishing sites (Cunjak et al. 1993) in the Lower Reach of Catamaran Brook, New Brunswick. In addition, the dispersal of offspring from four known redds was described.

Materials and Methods

Refer to Materials and Methods of Chapter 1 for details of methods used in Chapter 2. Any additional methods used in this chapter are described below.

In the field

Each autumn, adult salmon migrate into the brook to spawn. A counting fence and fish trap, 216m upstream from the mouth of the brook, is maintained by the staff of the Catamaran Brook Research Station during the spawning season to monitor the entry and

exit of spawning individuals (Fig. 2.1; Table 2.1). In October and November of 2003, 97 anadromous adults (31 females and 66 males) were caught at the counting fence and fish trap as they migrated into and out of Catamaran Brook. Spawning individuals also include precocious male parr, which were not sampled in this study. For sampling methods, refer to Chapter 1.

During a spawning event, a single anadromous female digs one or more gravel nests, collectively called a redd (reviewed in Fleming 1998) with a surface area ranging from 2 – 6 m^2 (de Gaudemar et al. 2000) and spawns with several anadromous and/or parr males (Jones 1959). During the spawning season in October and November of 2003, the locations of four redds were mapped (Table 2.1) in collaboration with Laura Weir, a PhD candidate at Dalhousie University. Geographical coordinates were recorded (Fig. 2.1) using a Global Positioning System (GPS) and markers were placed at the banks of the brook to facilitate sampling of these selected redds in April of 2004 for genetic analysis.

Catamaran Brook is composed of four study reaches covering over 3 km of the brook: the Lower Reach, Gorge Reach, Middle Reach and Upper Reach (Cunjak et al. 1993). In July 2004, a total of 13 sites were electrofished in the Lower Reach (~1.65 km), and in August and September 2004, one site was snorkelled at the mouth of the brook (site from Chapter 1). During electrofishing, two barrier nets were used to prevent the upstream and downstream movement of fish out of the site. Each site was sampled three to six times by an electrofishing crew (500 volts, Backpack Electrofisher Smith-Root Inc. Model 12-B, Vancouver, Washington State, U.S.A.). A two-man lip-seine (i.e. fishing net) was used to capture the temporarily stunned fish. Every fourth YOY salmon captured

was sampled for genetic analysis. For sites L1, L2, L4 and L5, fewer crew members were available, so only one pass by the electrofishing crew was completed, and no barrier nets were used; all captured fish were sampled. Refer to Chapter 1 for sampling methods of the Mouth site. All YOY salmon caught by electrofishing and by snorkelling were weighed (± 0.1 g), measured (i.e. fork length ± 0.1 cm) and a sample of adipose tissue (~0.1-0.2 cm^2) was collected and preserved in 95% ethanol for genetic analysis. Linear distances, along the mid-line of the brook, of each site or redd location from the mouth of the brook and the site area were measured (Table 2.1). In addition, GPS coordinates were recorded (Fig. 2.1).

In the laboratory

Genomic DNA extractions, DNA amplification and Genotyping

For the 313 YOY sampled, genomic DNA was extracted from the complete adipose fin. Refer to Chapter 1 for genomic DNA extraction, PCR amplification and genotyping protocols used.

The maternal genotypes of the four redds (16, 18, 19 and 57) were determined by Laura Weir in the Marine Gene Probe Laboratory at Dalhousie University by genotyping the DNA extracted from fertilized eggs from each redd at five loci: SSsp2215, SSsp2210, SSsp2213, SSsp2216 (Paterson et al. 2004) and Ssa197 (O'Reilly et al. 1996). Calibration of the two data sets (i.e. four redd mothers' genotypes generated by Laura Weir and 31 trap-caught mothers' genotypes generated by myself) was necessary because the two labs use different genotyping equipment. In order to compare and integrate the data generated

from each lab, ten individuals from redd 18 were genotyped and alleles were determined independently in each laboratory from the same DNA stock. Furthermore, the calibration was verified by matching the most frequent alleles at each locus between both data sets. A sixth locus, SSspG7 was used to compare the redd females to the fish trap females. The most frequent alleles of SSspG7 were compared between these two data sets in order to match the genotypes.

Data analyses

Presence of young-of-the-year siblings per site

The KINSHIP v.1.3.1 software (Queller & Goodnight 1989) was used to assign relatedness values ($r_{x,y}$) to YOY salmon (n = 313) sampled in all Lower Reach sites. Refer to Chapter 1 for details.

Dispersal and dispersion of siblings

The Parental Allocation of Singles in an Open System (PASOS) v.1.0.0.1 software (Duchesne et al. 2005) was used to assign parents to offspring to create maternal half-sibling, paternal half-sibling, and full-sibling groups. The maternal genotypes obtained from the four sampled redds were included together with the maternal parental data set used for assigning mothers to offspring. A positive control was used by combining the ten offspring from redd 18 (used in the calibration procedure described in the *Genotyping* section above) with the 313 offspring sampled, whereby the software PASOS was

expected to assign the female parent at redd 18 to these ten offspring. Dispersion data were obtained by plotting the number of siblings captured per site in the Lower Reach.

Estimation of the total number of anadromous adults

The Petersen method was used to estimate the total number of spawning adults (caught and uncaught) at Catamaran Brook in the fall of 2003: $N = [(M+1)(C+1)/(R+1)] -1$; where N = total number of spawning anadromous adults, M = number of individuals tagged going upstream into the brook, C = number of individuals caught moving downstream out of the brook and R = number of recaptured individuals found in C (Seber 1973).

Statistical analyses

The dispersion distance for a family was defined as the linear distance between the most upstream and most downstream sites (midpoint distances from the mouth of the brook) containing members of that family. This measure will underestimate the actual dispersion distance of a family because of the limited number of recapture locations and sampled fish (Fig. 2.1; Table 2.1). The median location for a family was the distance from the mouth of the brook at which the median fish of each family was captured. The redd location is the linear distance of the location of the redd sampled from the mouth of the brook. When the redd location was unknown, the upstream location of a family was used. The upstream location is the linear distance between the most upstream site where a family was captured and the mouth of the brook. Dispersal distances could only be calculated for the four families in which the location of the redd was known. However,

the dispersion distances of all families were analysed regardless of whether or not the redd location was known. SPSS v.12.0.1 for Windows software was used for all statistical tests.

Results

Population structure

Using the Petersen method, an anadromous population of 172 adults (95% confidence interval (CI) = 126.6 – 271.8) was estimated, of which an estimated 125 were anadromous males (CI = 81.3 – 236.9) and 46 were anadromous females (CI = 30.7 – 101.9). The fence efficiency was estimated to be 56.4% (CI = 35.7% - 76.4% efficient) in the fall of 2003, since 97 of the estimated 172 adults were caught at the fish trap.

Allelic diversity, Hardy-Weinberg equilibrium, linkage disequilibrium, and null allele detection

The number of alleles per locus ranged from 9 - 27 in the adults (mean = 15.6) (Table 1.1) and 9 - 23 in the offspring (mean = 14) (Table 2.2), providing sufficient genetic polymorphism (Fig. 2.2) for parental assignment and kinship determination (Bernatchez & Duchesne 2000). For example, at the most polymorphic locus, SSsp2216, the two most frequent alleles occurred in 17.8% and 10.7% of individuals in the population, whereas at the least polymorphic locus, SSsp2210, the two most frequent alleles occurred in 52.2% and 28.6% of individuals.

For the 313 offspring sampled, only one of the eight loci (Table 2.2) did not differ from the Hardy-Weinberg (HW) equilibrium. Linkage disequilibrium for the eight loci used in this study was detected in 10 of 28 pair-wise comparisons. Heterozygote deficiency (Table 2.2) and the presence of a null allele at locus SSsp2213 were detected. No evidence of mis-identification of allele size due to stuttering was found at any locus, as determined by the software MICRO-CHECKER.

Relatedness of young-of-the-year salmon

While most YOY caught in the Lower Reach were unrelated (mean $r_{xy} = 0.004 \pm 0.165$ at all sites), the right-skewed distributions indicated the presence of some related individuals at most sites (Fig. 2.3; Table 2.3).

The mating system

All four female parents at redds were assigned to offspring. The female parent at redd 16 was assigned to 11 offspring, only one of which was assigned to a male parent. The female parent at redd 18 was assigned to six offspring; two had a different male parent assigned. The female parent at redd 19 was found to be genetically identical at six loci (SSsp2215, SSsp2210, SSsp2213, SSspG7, SSsp2216 and Ssa197) to the female adult 837, one of the 31 female adults caught at the fish trap. Since, the probability of two individuals having the same genotype at six loci is extremely low, female 837 was assumed to be the female parent at redd 19. Female 837 was assigned to 49 offspring, 17 of which were assigned to four different male parents. The female parent at redd 57 was assigned to three offspring, none of which were assigned a male parent (Table 2.4).

Of the 31 female adults, 7 were assigned to offspring. The number of assigned mates per female ranged from 0 to 6 (median = 1) (Table 2.4). Of the 66 male adults, 20 were assigned to offspring. The number of assigned mates per male ranged from 0 to 2 (median = 1). While all female parents are anadromous adults, male parents are either anadromous adults or precocial parr. Hence, a higher proportion of offspring was expected to be assigned to the captured anadromous females compared to males. Of the 313 offspring, 132 were assigned to anadromous females, but only 62 were assigned to anadromous males ($\chi^2_1 = 25.26, p < 0.001$). If this gender difference in assignment of offspring is an unbiased estimate of the success of anadromous parents, I estimate that anadromous males fertilized only 47% of all offspring (i.e. 62/132); and, therefore, precocial parr may have fertilized 53% of offspring.

Dispersal from redds

The female parents at the four redds were assigned to offspring in the 14 sites sampled, with an estimated correctness probability of 78%, as calculated by the software PASOS. The positive control confirmed the reliability of assignments: the female parent at redd 18 was assigned to her 10 offspring (i.e. eggs collected from redd 18). Because female Atlantic salmon tend to spawn in a small section of a stream (reviewed in Fleming 1998), the dispersion of her offspring can be used to estimate dispersal distance from the redd.

The female parent at redd 16 was assigned to 11 offspring: seven were captured downstream of the redd (50-542m) and four were captured upstream of the redd (26-132m). The female parent at redd 18 was assigned to six offspring: four were captured downstream (63-556m) and two were captured 13m upstream. The female parent at redd

19 (identified as female 837) was assigned to 49 offspring: 32 were captured downstream (75-955m) and 17 were captured upstream (37-154m). The female parent at redd 57 was assigned to three offspring: two were found downstream (201-818m) and one 9m upstream (Fig. 2.4).

If an offspring is an independent datum, then fish tend to disperse more frequently downstream (n = 45) than upstream (n = 24) ($\chi^2_1 = 6.39, p = 0.011$) and farther downstream (median = 542m) than upstream (median = 154m) (Mann-Whitney test, z = -4.94, n = 69, $p < 0.001$). These trends were similar at all four redds, despite the differing sampling effort upstream and downstream of each redd.

Dispersion of maternal, paternal and full-siblings

A total of five maternal half-sibling families (from females caught at the fish trap; median size = 6, mean = 17.7) were resolved with an average dispersion distance of 1340m. Dispersion distance is defined as the linear range in which half-sibling and full-sibling families (i.e. two or more assigned offspring) were caught in the brook. Female parents 827, 837, 779, 787, 834, 817 and 796 were assigned to offspring with an estimated correctness probability of 93.5%, as calculated by the software PASOS (Table 2.4; Appendix 2A).

A total of nine paternal half-sibling groups (median size = 3, mean = 5.7) were resolved with an average dispersion distance of 1018m and an estimated correctness probability of 88.1%, as calculated by the software PASOS, for assigning fathers to offspring (Table 2.4; Appendix 2A). The dispersion distance was expected to be smaller for offspring of anadromous females than for offspring of anadromous males, because

anadromous males may spawn repeatedly throughout the brook, as in brook trout (Hutchings & Gerber 2002), whereas females tend to spawn in a small area of the stream (reviewed in Fleming 1998). However, dispersion distance for maternal offspring did not differ significantly from paternal offspring ($t = 1.12$, $df = 12$, $p = 0.286$). Moreover, a total of four full-sibling groups were identified with an average dispersion distance of 945m (Appendix 2A). The four full-sibling groups are composed of only two mothers. These two mothers had the two largest half-sibling groups detected by parental assignment (Appendix 2A). Since no differences were detected between maternal and paternal offspring, all dispersion distances from offspring of anadromous parents and dispersal distances from offspring of females at redds were analysed together (Table 2.5).

For sibling groups determined using parental assignment (i.e. PASOS software) and including siblings dispersing from the four redds, dispersion distance was positively correlated with redd or upstream location (Pearson's correlation, $r = 0.812$, $n = 17$, $p < 0.001$), but was not significantly correlated with number of offspring per family or median distance. These continuous variables and gender of adults were included in an analysis of covariance. Dispersion distance was significantly related only to redd or upstream location (Fig. 2.5). Contrary to my expectation, there was no significant difference between dispersion distance of offspring of female and male adults. Furthermore, most data lie on or just below the 1:1 line. This pattern indicated that dispersion distance of families does not seem limited by the movements of offspring but by the upstream location of the family, likely a surrogate for redd location. The two points above the line, for redds 16 and 19, were the result of offspring dispersing

upstream. The few points that were well below the line were represented by small families (n = 2 – 6).

Discussion

Seven of the eight loci in the offspring sampled at the 14 sites in the Lower Reach (n = 313) showed a significant deviation from the Hardy-Weinberg (HW) equilibrium. Several possibilities could account for this. First, in the fall of 2003, an estimated 172 adults migrated into Catamaran Brook to spawn in three of the four reaches: Lower Reach, Gorge Reach and Middle Reach. However, only the Lower Reach offspring were sampled in this study. Therefore, not all genotypic frequencies expected in the offspring can be expected in my sample, since only 1/3 of the stream length was sampled. Second, for a population to be in HW equilibrium, it should have a randomly-mating population with no migration and no selection. The complex mating system in Atlantic salmon may violate some of these assumptions. For example, the sex-ratio ratio in this population is male-biased (i.e. 66 anadromous males plus mature parr vs 31 anadromous females).

Dispersion distance increased the farther into Catamaran Brook adults moved to construct redds. In contrast with the abundant literature of dispersal of YOY salmonids of less than 1 km from artificial redds (Egglishaw & Shackley 1973; Kennedy 1982; Marty & Beall 1989; Beall et al. 1994; Webb et al. 2001), maternal and paternal offspring, on average, dispersed greater than 1 km (1340m and 1018m, respectively). Similarly, the only other study to have examined dispersal of YOY salmon from a natural redd reported a maximal dispersal of 743m downstream and 166m upstream (Harding 1986 cited in

Hay 1987). In this study, upstream dispersal was detected for offspring from all four redds (range 9m – 154m). Our results demonstrated that regardless of where the redd or upstream location of a family was, most families dispersed to the mouth of the brook. Sampling design should account for long-range dispersion of siblings and is of high importance when assuming that the fish at one site may not be related to fish at another. Hansen et al. (1997) suggested that sampling of YOY individuals should be done over long river stretches greater than 100m. My results suggest that the sampling should be spaced over much larger distances (> 1 km) in order to avoid a biased sampling of YOY siblings.

The lack of a difference between dispersion distances for male and female half-sibling groups is consistent with the findings of Taggart et al. (2001). In Atlantic salmon, more than 50% of both sexes contributed to more than one redd, often greater than 1 km apart (Taggart et al. 2001). Furthermore, females were shown to spawn in one or two redds per female in a semi-natural stream, but spawned in two to seven redds per female in a natural stream (de Gaudemar et al. 2000). This behaviour may increase the probability of survival of some of the progeny from stochastic events, such as floods, in a natural stream (Fleming 1996). In contrast, male brook trout move more than females during the spawning season (Hutchings & Gerber 2002).

According to the current literature, mature male parr may fertilize 23% – 40% of eggs when one or more anadromous males are present (Hutchings & Myers 1988; Thomaz et al. 1997; Jones & Hutchings 2001; 2002). We calculated that mature male parr may have fertilized up to 53% of the sampled offspring in Catamaran Brook in 2004. This high success rate for male parr deserves further investigation.

In summary, the use of genetic markers revealed that (1) the average dispersal distance of YOY salmon from the four sampled redd locations ranged from 50 – 955m downstream, and 9 – 154m upstream, (2) the average dispersion distance of maternal (1340m) and paternal (1018m) families were greater than 1 km and not significantly different from each other, (3) the dispersion distance of YOY salmon is limited by the redd or upstream location of a family: the more upstream a redd is located, the larger the dispersion distance, and (4) up to 53% of the offspring sampled in this study may have been fathered by precocious parr.

Figure 2.1. Map of the Lower Reach of Catamaran Brook, New Brunswick. GPS coordinates of the sampling and redd sites are represented by white and black dots, respectively. The following labels were used. Ri: riffle; B: bedrock; Ru: run; L: Lower Reach site with undescribed habitat; R: redd; F: flat; P: pool. A description of the sites is provided in Table 2.1.

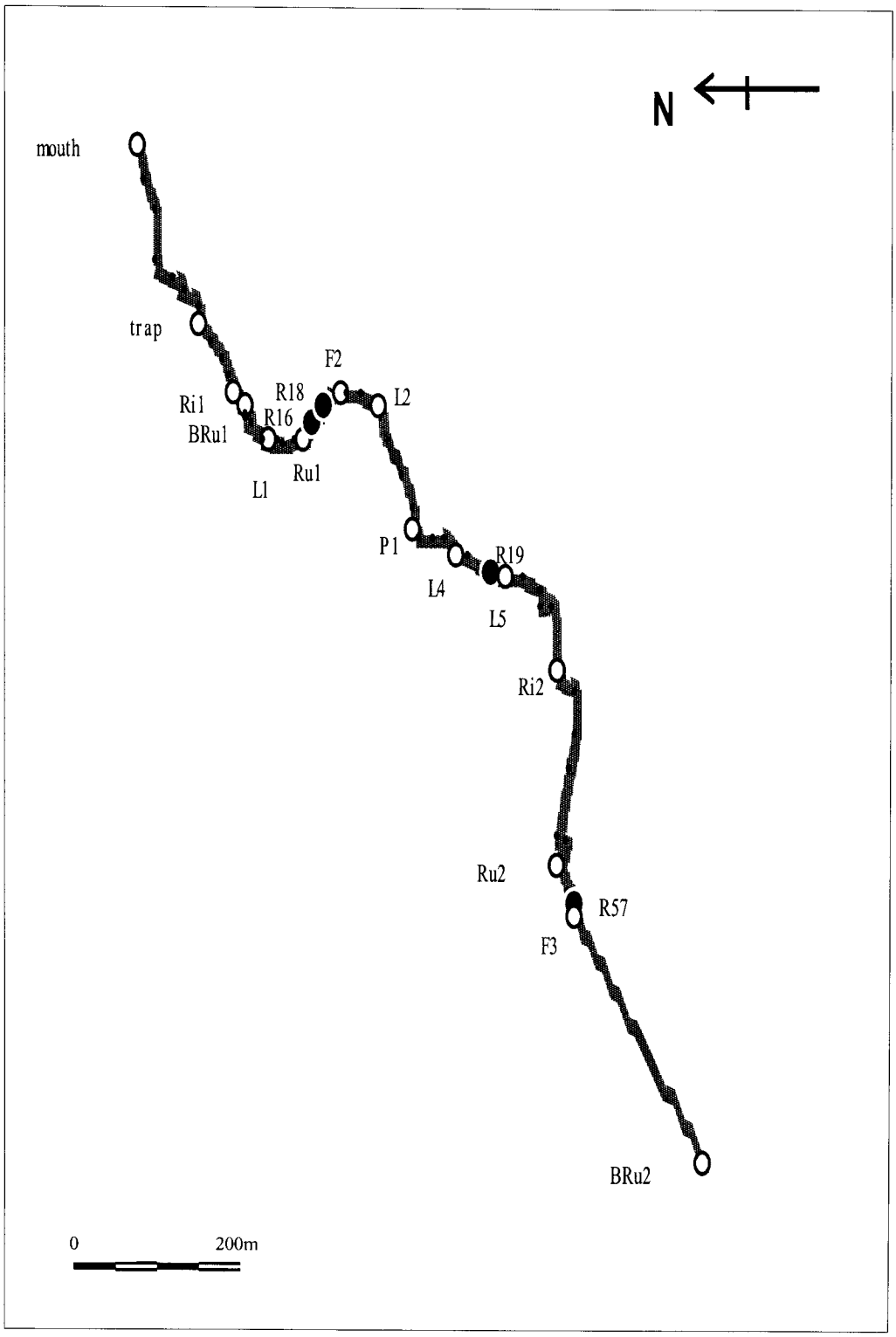
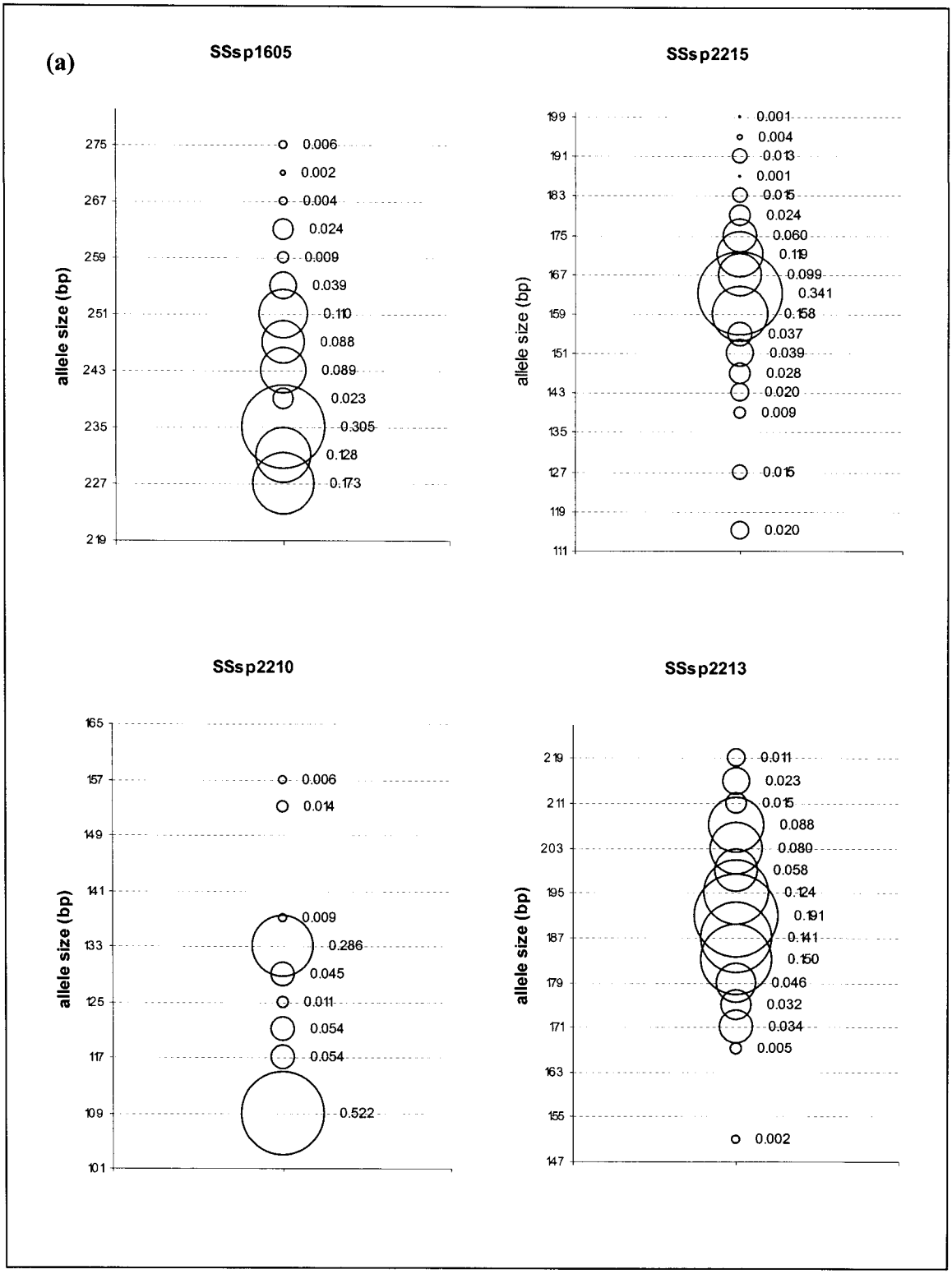

N
mouth
trap
Ri1
BRu1
R18
R16
F2
L2
Ru1
L1
P1
R19
L4
L5
Ri2
Ru2
R57
F3
BRu2
0
200m

Figure 2.2. Population allele frequencies for (a) SSsp1605, SSsp2215, SSsp2210 and SSsp2213, and (b) SSspG7, SSsp2216, Ssa197 and Ssa202. Alleles are represented by circles. Circle size is proportional to allele frequencies of the sampled population (i.e. 97 adults and 313 offspring). Frequencies are shown numerically next to each circle.


(a)
SSsp1605
allele size (bp)
275
267
259
251
243
235
227
219
0.006
0.002
0.004
0.024
0.009
0.039
0.110
0.088
0.089
0.023
0.305
0.128
0.173
SSsp2215
allele size (bp)
199
191
183
175
167
159
151
143
135
127
119
111
0.001
0.004
0.013
0.001
0.015
0.024
0.060
0.119
0.099
0.341
0.158
0.037
0.039
0.028
0.020
0.009
0.015
0.020
SSsp2210
allele size (bp)
165
157
149
141
133
125
117
109
101
0.006
0.014
0.009
0.286
0.045
0.011
0.054
0.054
0.522
SSsp2213
allele size (bp)
219
211
203
195
187
179
171
163
155
147
0.011
0.023
0.015
0.088
0.080
0.058
0.124
0.191
0.141
0.150
0.046
0.032
0.034
0.005
0.002

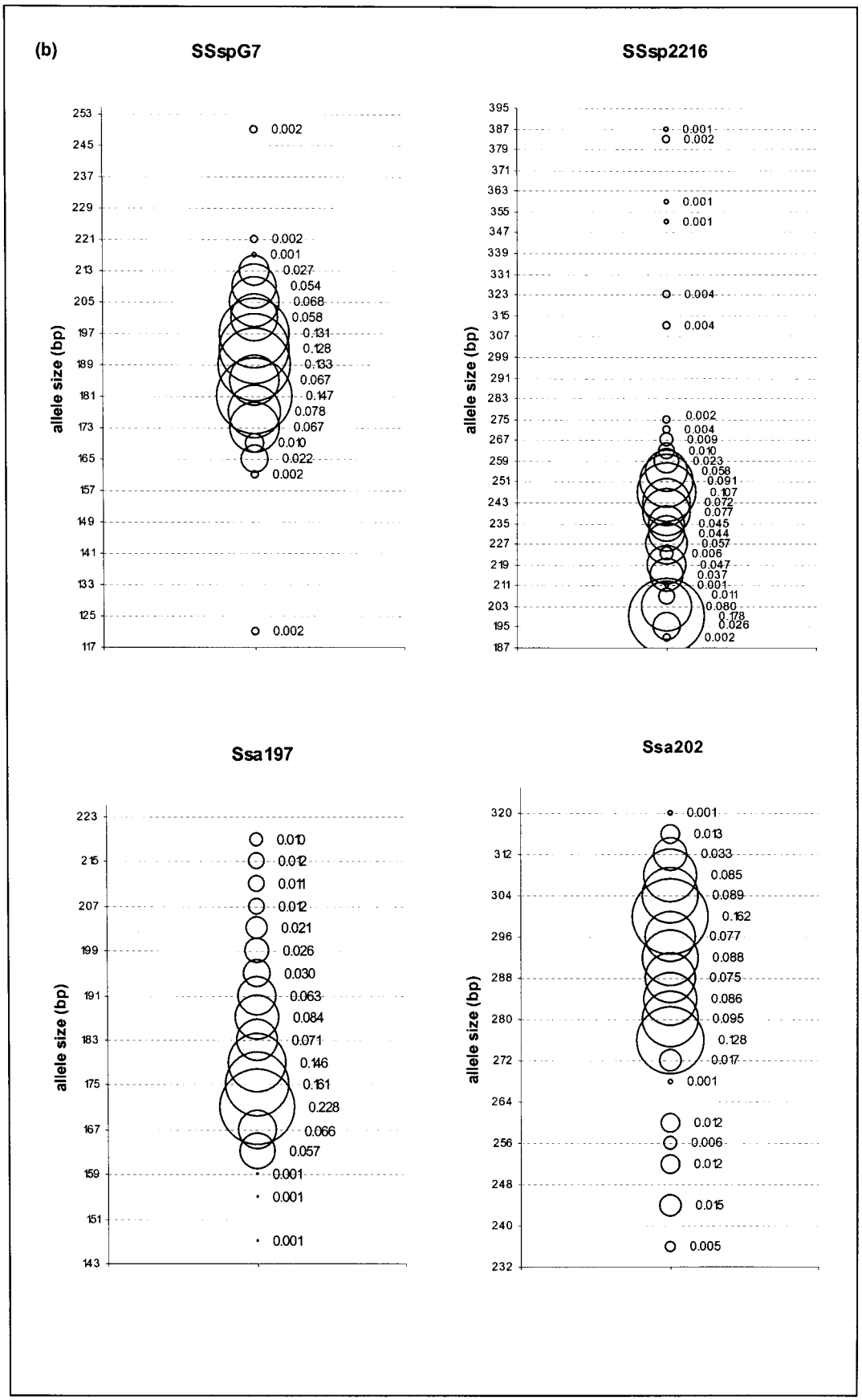

(b)
SSspG7
SSsp2216
Ssa197
Ssa202
allele size (bp)

Figure 2.3. Observed relatedness values of young-of-the-year Atlantic salmon dyads per site. Dyads of individuals are classified as either unrelated ($r_{xy} < 0.240$), siblings having at least one parent in common ($r_{xy} \geq 0.240$), or full-siblings ($r_{xy} \geq 0.489$). The midpoint distance of each site from the mouth of the brook is indicated in parentheses.

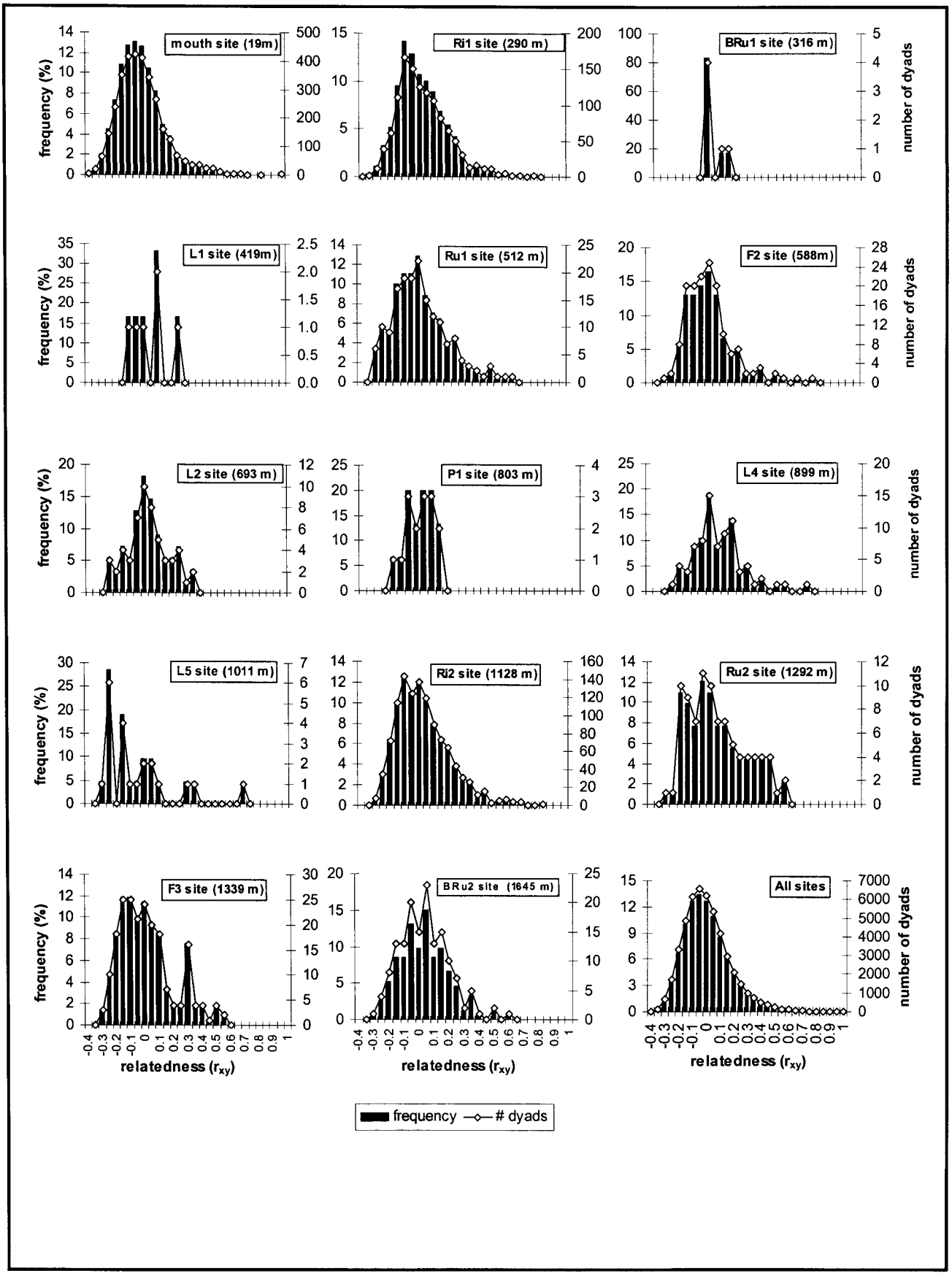

mouth site (19m)
Ri1 site (290 m)
BRu1 site (316 m)
L1 site (419m)
Ru1 site (512 m)
F2 site (588m)
L2 site (693 m)
P1 site (803 m)
L4 site (899 m)
L5 site (1011 m)
Ri2 site (1128 m)
Ru2 site (1292 m)
F3 site (1339 m)
BRu2 site (1645 m)
All sites
frequency (%)
number of dyads
relatedness (r_{xy})
frequency
dyads

Figure 2.4. Dispersal of maternal half-siblings from redds. Black arrows indicate the location of the redd in the brook.

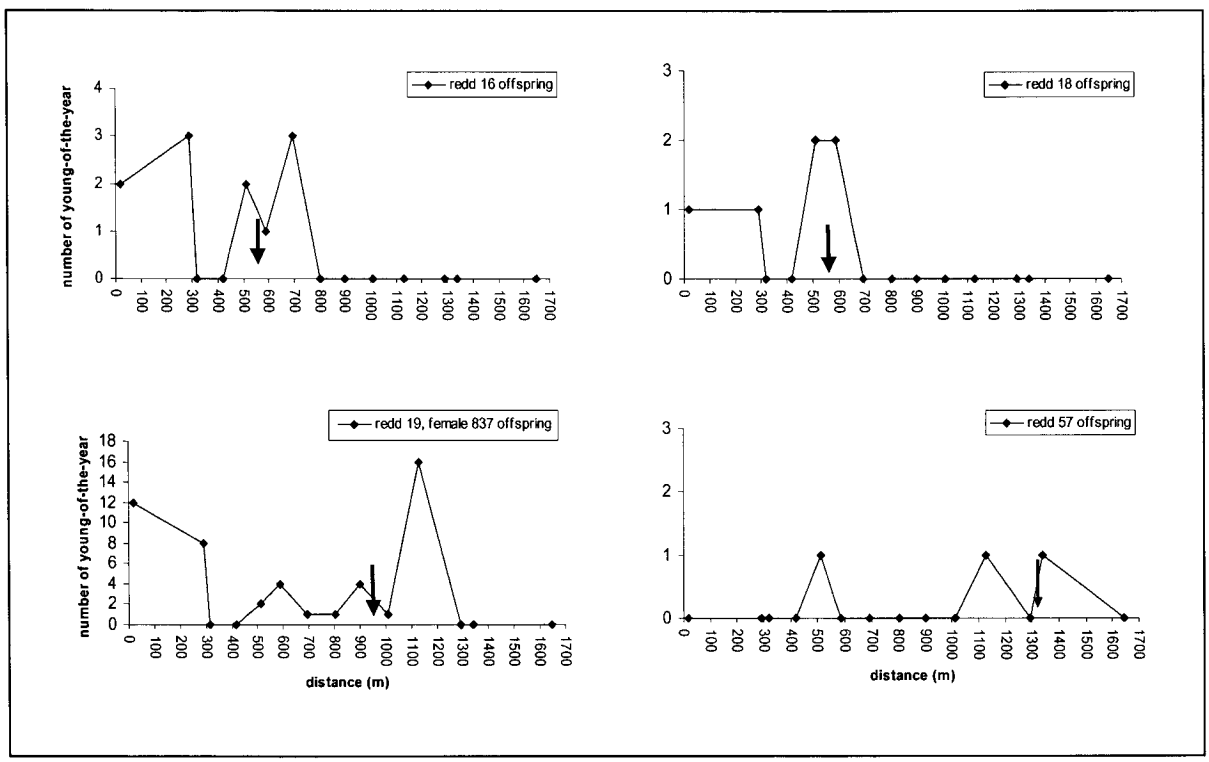

redd 16 offspring
number of young-of-the-year
redd 18 offspring
redd 19, female 837 offspring
number of young-of-the-year
distance (m)
redd 57 offspring
distance (m)

Figure 2.5. Dispersion distance and redd location of offspring of female (n = 8) and male (n = 9) anadromous parents.

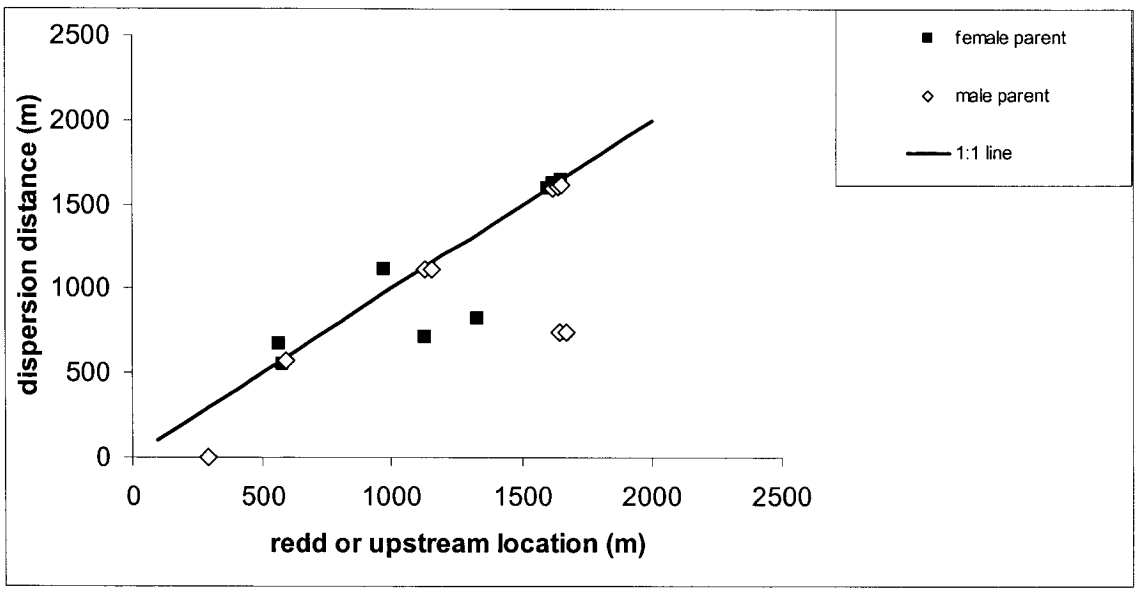

2500
2000
1500
1000
500
0
dispersion distance (m)
0
500
1000
1500
2000
2500
redd or upstream location (m)
female parent
male parent
1:1 line

Table 2.1. Distance to sites (midpoint) and redds from the mouth of Catamaran Brook and the number of young-of-the-year salmon sampled in the summer of 2004.

Site or redd	Distance (m)	Number of young-of-the-year sampled	Date sampled	Site area (m^2) or redd length (m)
Mouth	19	81	28 Aug – 1 Sept	304
Riffle 1	290.5	49	07 July	227
Bedrock Run 1	316.5	4	08 July	90
L1	418.9	4	31 July	74
Run 1	511.7	19	08 July	67
Redd 16	561.5	-	25-26 April	1.9
Redd 18	574.9	-	25-26 April	2.0
Flat 2	587.6	18	09 July	192*
L2	693.4	11	31 July	84
Pool 1	802.6	6	27 July	103
L4	899.4	13	31 July	116
Redd 19	974.4	-	25-26 April	2.9
L5	1011.4	7	31 July	65
Riffle 2	1128.5	48	10 July	138
Run 2	1291.6	14	11 July	85
Redd 57	1329.8	-	25-26 April	2.5
Flat 3	1338.8	21	11 July	177
Bedrock Run 2	1645.3	18	12 July	85

* *based on measurements in 2003*

Table 2.2. Allelic diversity, expected and observed homozygosity and Hardy-Weinberg (HW) equilibrium test results for 313 offspring captured in all Lower Reach sites in the summer of 2004.

Locus	No. alleles	No. expected homozygotes	No. observed homozygotes	Heterozygote deficiency p-value	HW equilibrium p-value
SSsp1605	13	52.35	50	0.894	< 0.001*
SSsp2215	17	61.94	59	0.889	< 0.001*
SSsp2210	9	108.39	115	0.371	0.790
SSsp2213	14	40.02	69	< 0.001*	< 0.001*
SSspG7	16	32.29	25	0.967	< 0.001*
SSsp2216	23	27.91	38	0.095	< 0.001*
Ssa197	17	43.94	33	0.993	0.003*
Ssa202	18	31.43	19	0.999	< 0.001*

**significant, $\alpha = 0.0062$ after Bonferroni correction*

Table 2.3. Number of sibling and full-sibling dyads per site, based on pair-wise relatedness values determined using the software KINSHIP; unrelated dyads have a $r_{xy} < 0.240$, sibling dyads having at least one parent in common have a $r_{xy} \geq 0.240$, and full-sibling dyads have a $r_{xy} \geq 0.489$.

Site	# Sibling dyads	# Full-sibling dyads	# Unrelated dyads	Total dyads
Mouth	244 (7.5%)	43 (1.3%)	2953 (91.1%)	3240
Riffle 1	131 (11.1%)	19 (1.6%)	1026 (87.2%)	1176
Bedrock Run 1	0	0	6 (100%)	6
L1	1 (16.7%)	0	5 (83.3%)	6
Run 1	22 (12.9%)	5 (2.9%)	144 (84.2%)	171
Flat 2	11 (7.2%)	3 (2.0%)	139 (90.8%)	153
L2	6 (10.9%)	0	49 (89.1%)	55
Pool 1	0	0	15 (100%)	15
L4	9 (11.5%)	1 (1.3%)	68 (87.2%)	78
L5	3 (14.3%)	1 (4.8%)	17 (81.0%)	21
Riffle 2	129 (11.4%)	23 (2.0%)	976 (86.5%)	1128
Run 2	19 (20.9%)	2 (2.2%)	70 (76.9%)	91
Flat 3	34 (16.2%)	5 (2.4%)	171 (81.4%)	210
Bedrock Run 2	17 (11.1%)	2 (1.3%)	134 (87.6%)	153

Table 2.4. The proportion of offspring unassigned to female and male anadromous mates.

Parent	No. anadromous mates	No. offspring	Offspring unassigned to anadromous mates (%)
female of redd 16	1	11	90.9
female of redd 18	2	6	66.7
female 837 of redd 19	4	49	65.3
female of redd 57	0	3	100.0
female 827	6	54	74.1
female 779	0	11	100.0
female 787	1	6	83.3
female 834	1	2	50.0
female 817	1	1	100.0
female 796	1	1	100.0
male 897	2	15	0.0
male 824	2	10	20.0
male 809	2	6	50.0
male 823	1	6	83.3
male 3083	1	3	66.7
male 819	0	3	100.0
male 801	1	3	66.7
male 828	0	3	100.0
male 836	1	2	0.0
male 842	0	1	100.0
male 843	0	1	100.0

Table 2.4 continued...

male 816	0	1	100.0
male 849	1	1	0.0
male 846	0	1	100.0
male 780	1	1	0.0
male 730	0	1	100.0
male 803	0	1	100.0
male 783	1	1	0.0
male 838	0	1	100.0
male 820	1	1	0.0

Table 2.5. Redd location and dispersion distance (linear distance of a family in the brook), and median family location (median linear location of a family in the brook) of offspring of female and male anadromous parents.

Parent	No. offspring	Dispersion distance (m)	Median family location[1] (m)	Redd or Upstream location[1] (m)
female of redd 16	11	674.4	511.7	561.5
female of redd 18	6	555.9	511.7	574.9
female of redd 19 = 837	49	1109.5	587.6	974.4
female of redd 57	3	827.1	1128.5	1329.8
female 827	54	1626.3	1011.4	1645.3
female 779	11	1626.3	693.4	1645.3
female 787	6	709.6	1014	1128.5
female 834	2	1626.3	832.2	1645.3
male 897	15	1109.5	1128.5	1128.5
male 824	10	1626.3	709.5	1645.3
male 823	6	745.9	1128.5	1645.3
male 809	6	568.6	19	587.6
male 801	3	1626.3	899.4	1645.3
male 819	3	1109.5	316.5	1128.5
male 3083	3	1626.3	1645.3	1645.3
male 828	3	0	290.5	290.5
male 836	2	745.9	1272.4	1645.3

[1] Reported as meters from the mouth of Catamaran Brook.

General Conclusions

The purpose of my thesis was to use genetic techniques to gain new insights into the dispersal and dispersion patterns of YOY salmon in a natural stream. Traditional tagging methods (e.g. PIT or elastomer tags) used in the past are limited to larger stream fishes and could not be used to tag YOY dispersing from redds. However, genetic markers can address this limitation. Moreover, genetic markers can be effectively used to describe the long-distance dispersal of a family from a point of origin in the brook (i.e. a redd) without having to resample the brook over time, since no recaptures of the same individuals are necessary.

In Chapter 1, I tested whether kin settled closer to one another than to non-kin. Using genetic information I showed that siblings are present and dispersed in the site. Focal fish were not more related to their nearest-neighbour (mean $r_{x,y} = -0.004$) than to randomly selected fish (mean $r_{x,y} = 0.005$), nor were they more related to their four nearest-neighbours (mean $r_{x,y} = -0.01$) than to non-neighbours (mean $r_{x,y} = -0.007$).

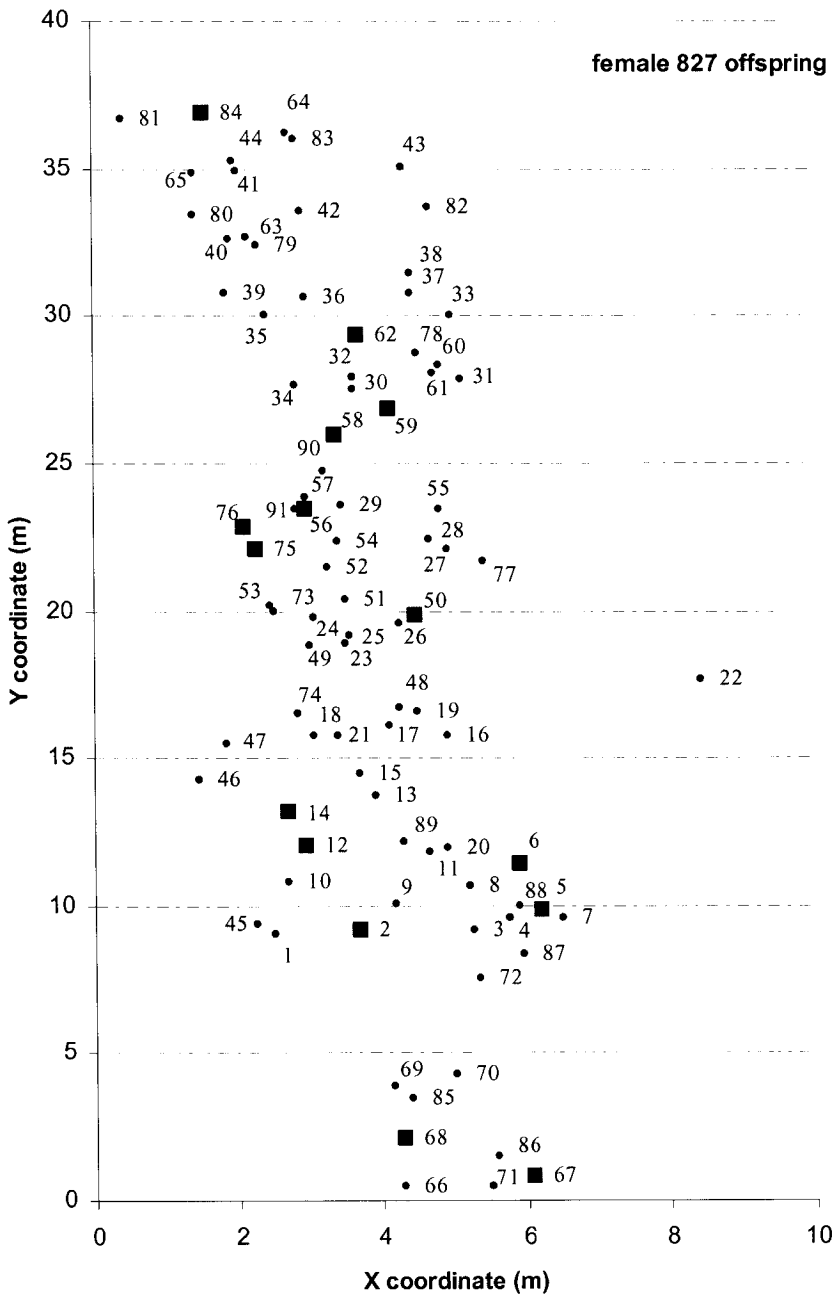
In Chapter 2, I quantified the dispersal of YOY from redds and the dispersion of siblings in Catamaran Brook. Ninety-seven anadromous adults, four natural redds and 313 YOY offspring were sampled. This extensive sampling and the use of genetic markers revealed that the extent of the initial dispersal of offspring from redd locations and the resulting long-range dispersion (i.e. > 1 km) were much farther than reported in previous studies (i.e. < 1 km). My results suggest that dispersion distance of families is not limited by the movement of offspring but by the upstream location of the family, likely a surrogate for redd location.

The novelty of this study was the use of genetic markers to infer maternal genotypes from four redds, and together with the genotypes of the 97 sampled adults, to assign parentage to the 313 offspring sampled in a natural stream. Not only did YOY salmon disperse upstream from every redd sampled, but families also dispersed much farther downstream than what was previously reported in the literature. The results of this study contribute to furthering our knowledge of YOY freshwater salmonid behaviour with possible applications to designing programs for conservation and management of salmonid populations worldwide.

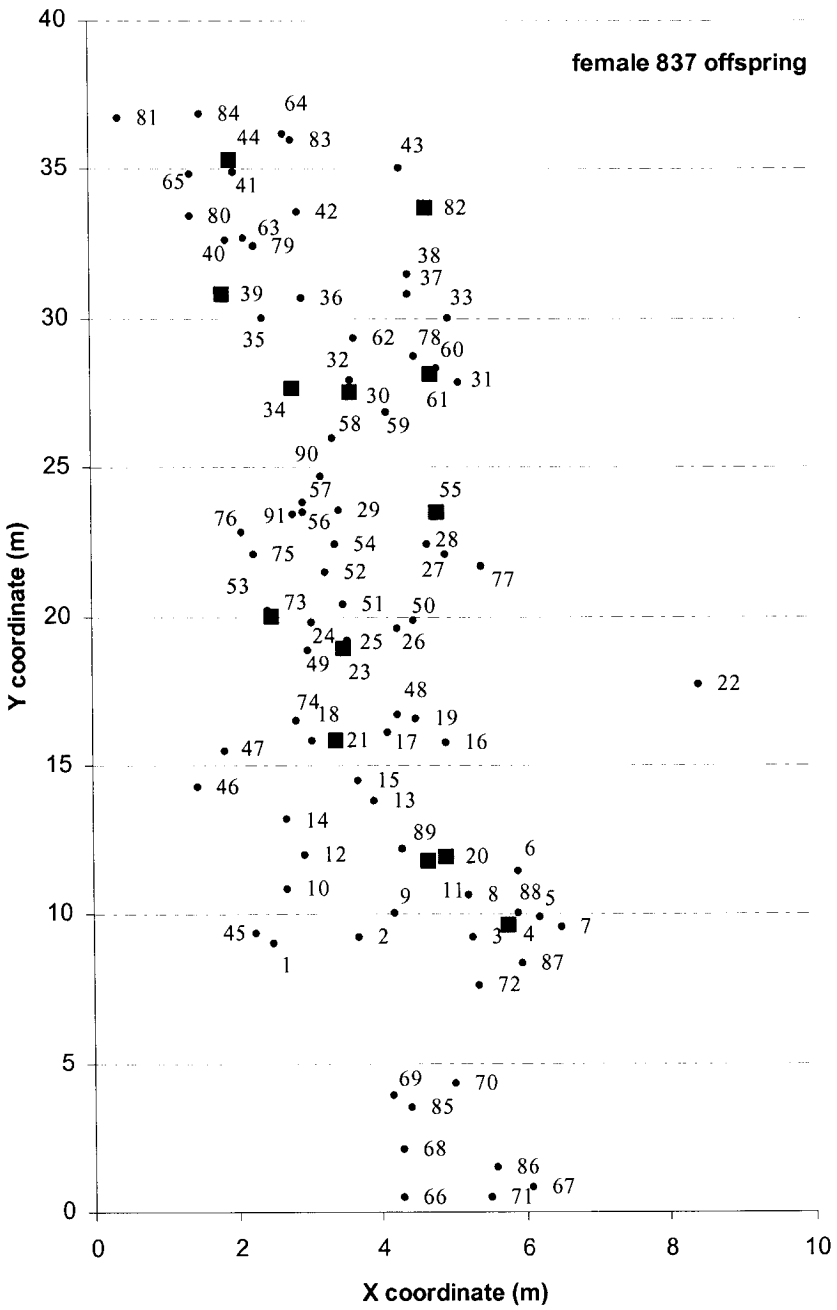
Appendices Chapter 1

Appendix 1A. Location of offspring (solid squares) of adult females (a) 827 and (b) 837 at the Mouth site, Catamaran Brook. Refer to Table 1.2 for details.

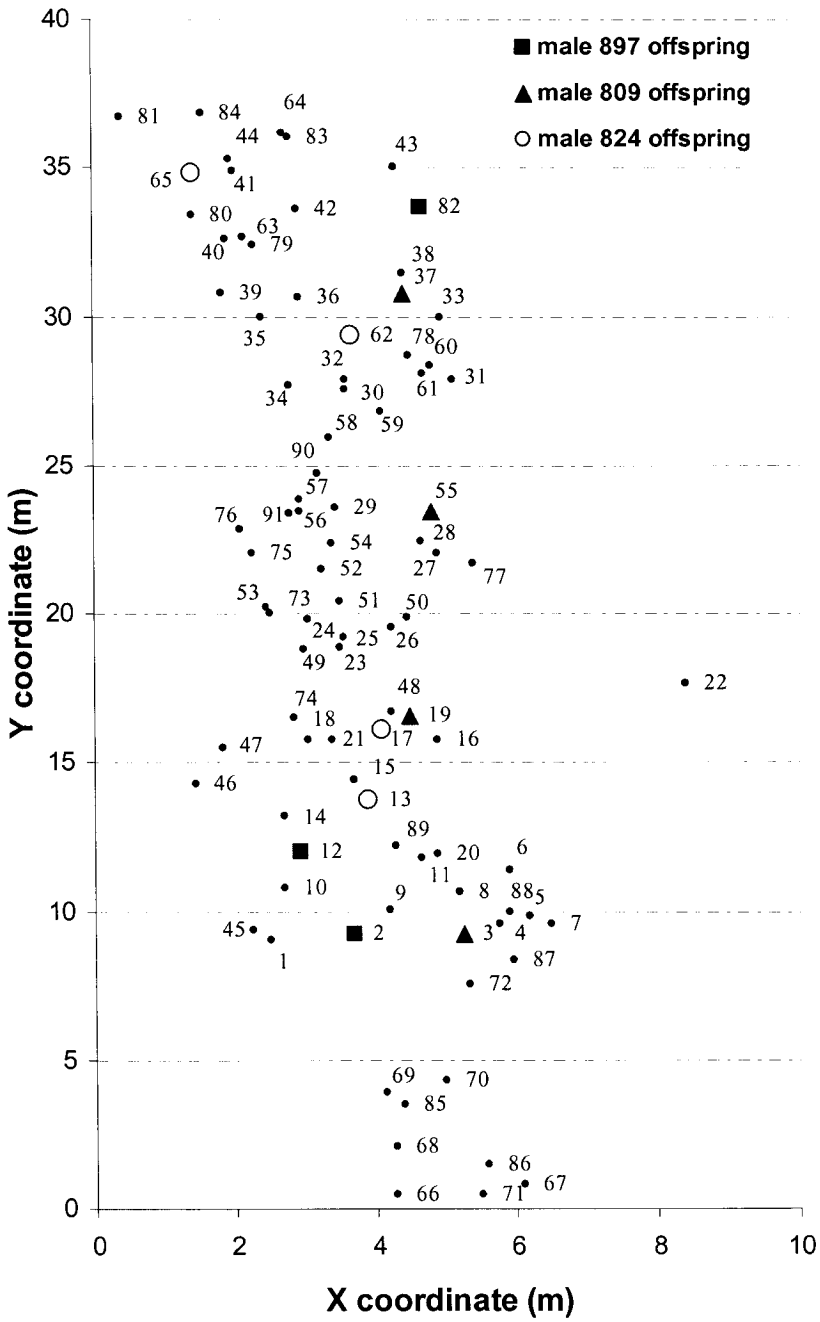
(a)


female 827 offspring
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81 84 64 44 83 43 65 41 80 42 82 63 40 79 38 37 39 36 33 35 62 78 60 32 30 61 31 34 58 59 90 57 55 76 91 29 56 28 75 54 27 77 52 53 73 51 50 24 25 26 49 23 22 48 74 18 19 47 21 17 16 46 15 13 14 89 12 20 6 11 10 9 8 88 5 7 45 2 3 4 1 87 72 69 70 85 68 86 71 67 66

(b)

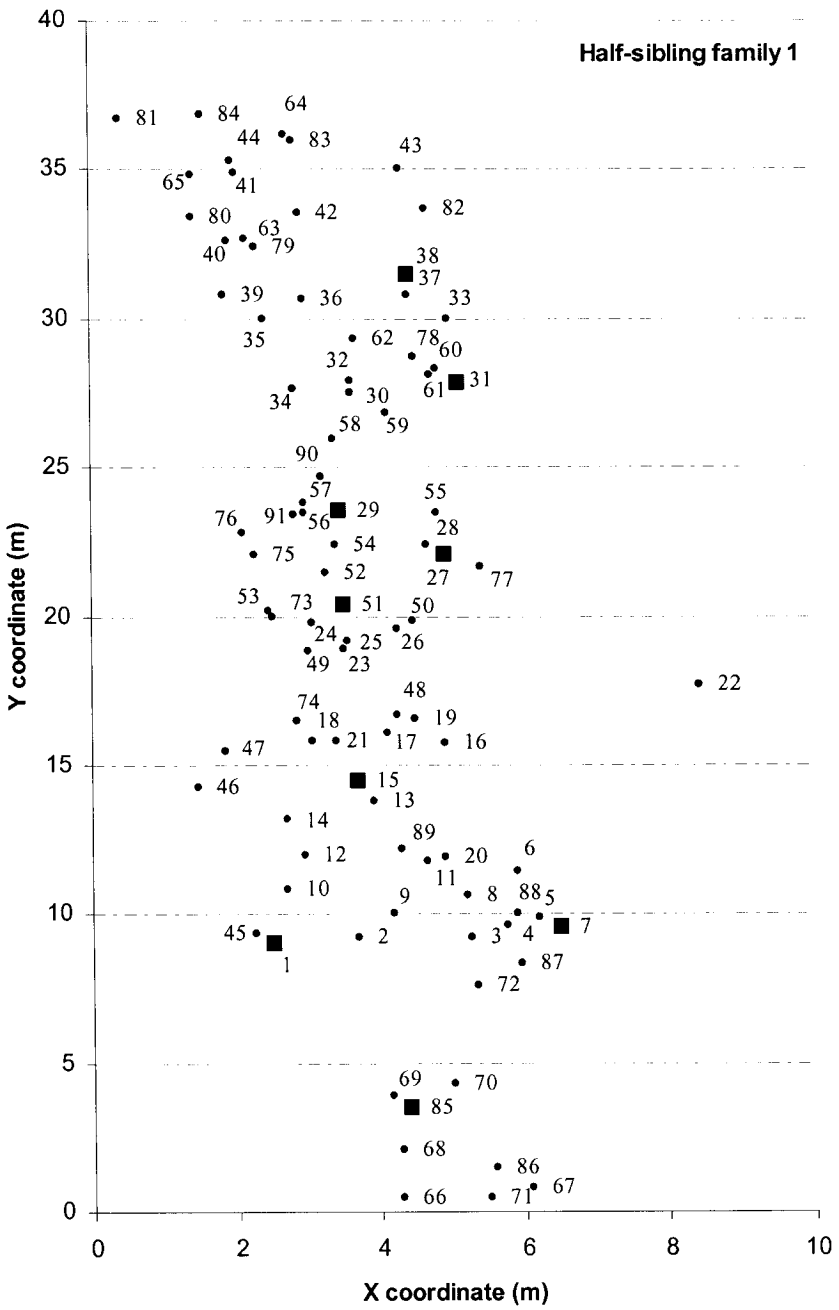

female 837 offspring
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81 84 64 44 83 43 65 41 80 42 82 63 40 79 38 37 39 36 33 35 62 78 60 32 31 30 61 34 58 59 90 57 55 76 91 56 29 54 28 75 52 27 77 53 73 51 50 24 25 26 49 23 22 48 74 18 19 47 21 17 16 46 15 13 14 89 12 20 6 10 9 11 8 88 5 45 2 3 4 7 1 87 72 69 70 85 68 86 67 66 71

Appendix 1B. Location of offspring of adult males 897, 809 and 824 at the Mouth site, Catamaran Brook. Refer to Table 1.2 for details.

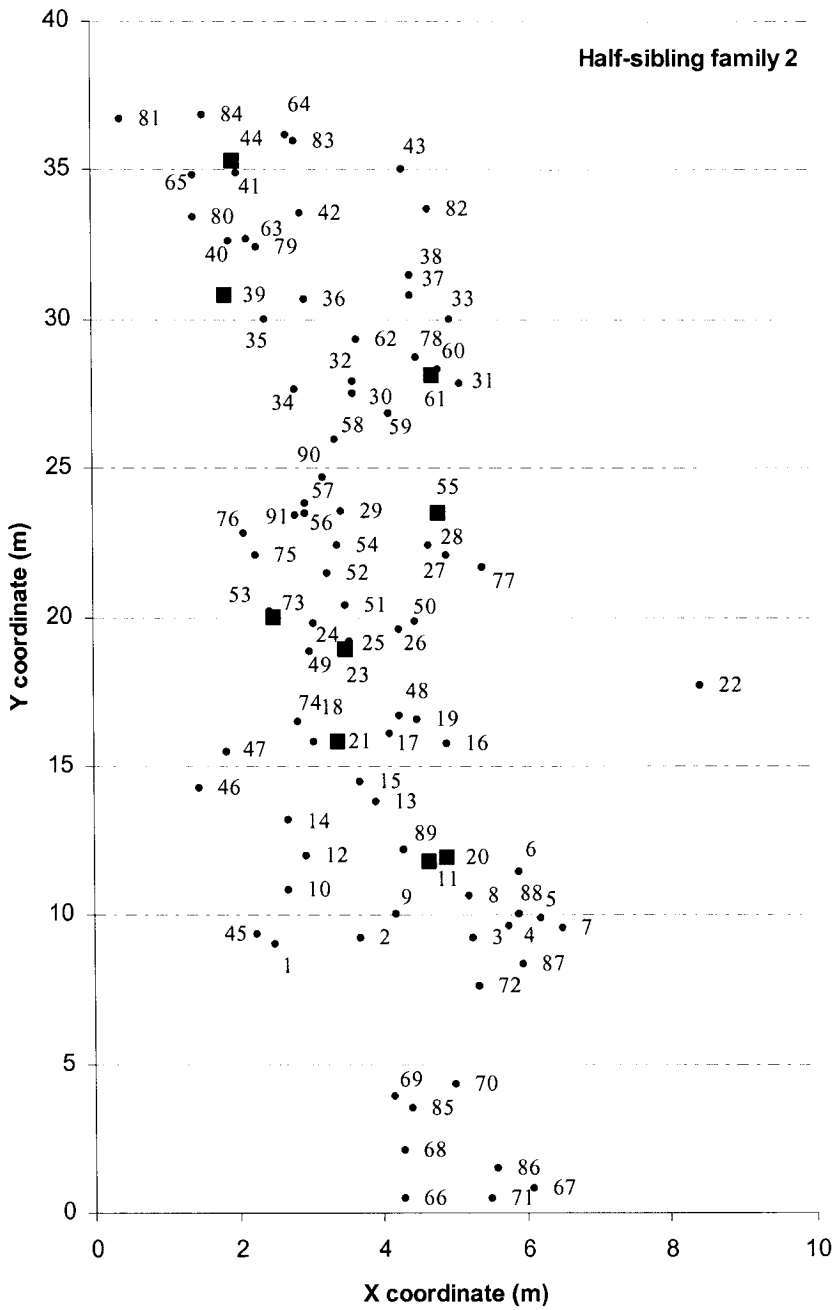

male 897 offspring
male 809 offspring
male 824 offspring
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10

Appendix 1C. Location of half-sibling offspring (solid squares unless indicated otherwise) (a) family 1, (b) family 2, (c) family 3, (d) families 4 and 5, (e) families 6, 7 and 8 at the Mouth site, Catamaran Brook. Refer to Table 1.3 for details.

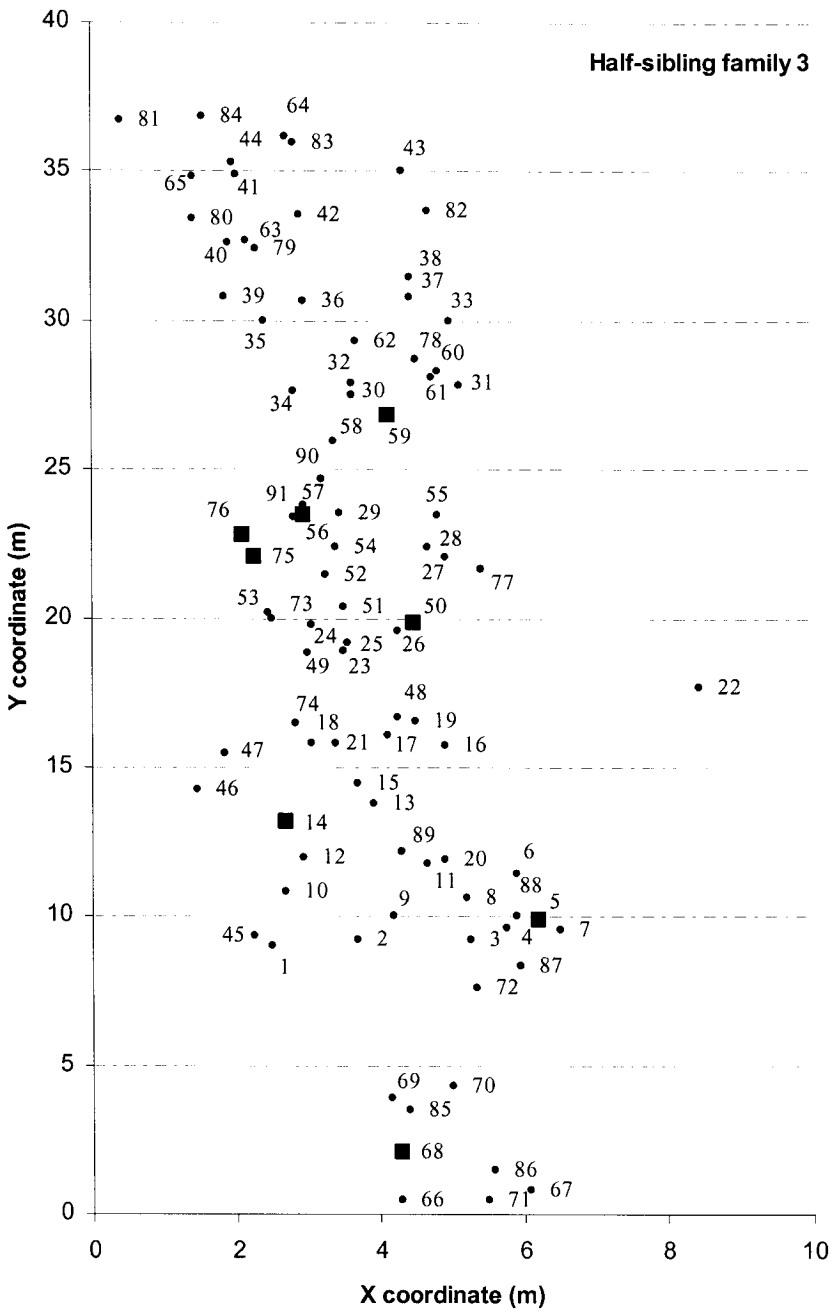
(a)


Half-sibling family 1
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81 84 64 44 83 43 65 41 80 42 82 63 40 79 38 37 39 36 33 35 62 78 60 32 31 61 34 30 58 59 90 57 55 76 91 56 29 28 75 54 27 77 52 53 73 51 50 24 25 26 49 23 22 48 74 18 19 47 21 17 16 15 46 13 14 89 12 20 6 11 10 9 8 88 5 45 2 3 4 7 1 87 72 69 70 85 68 86 67 66 71

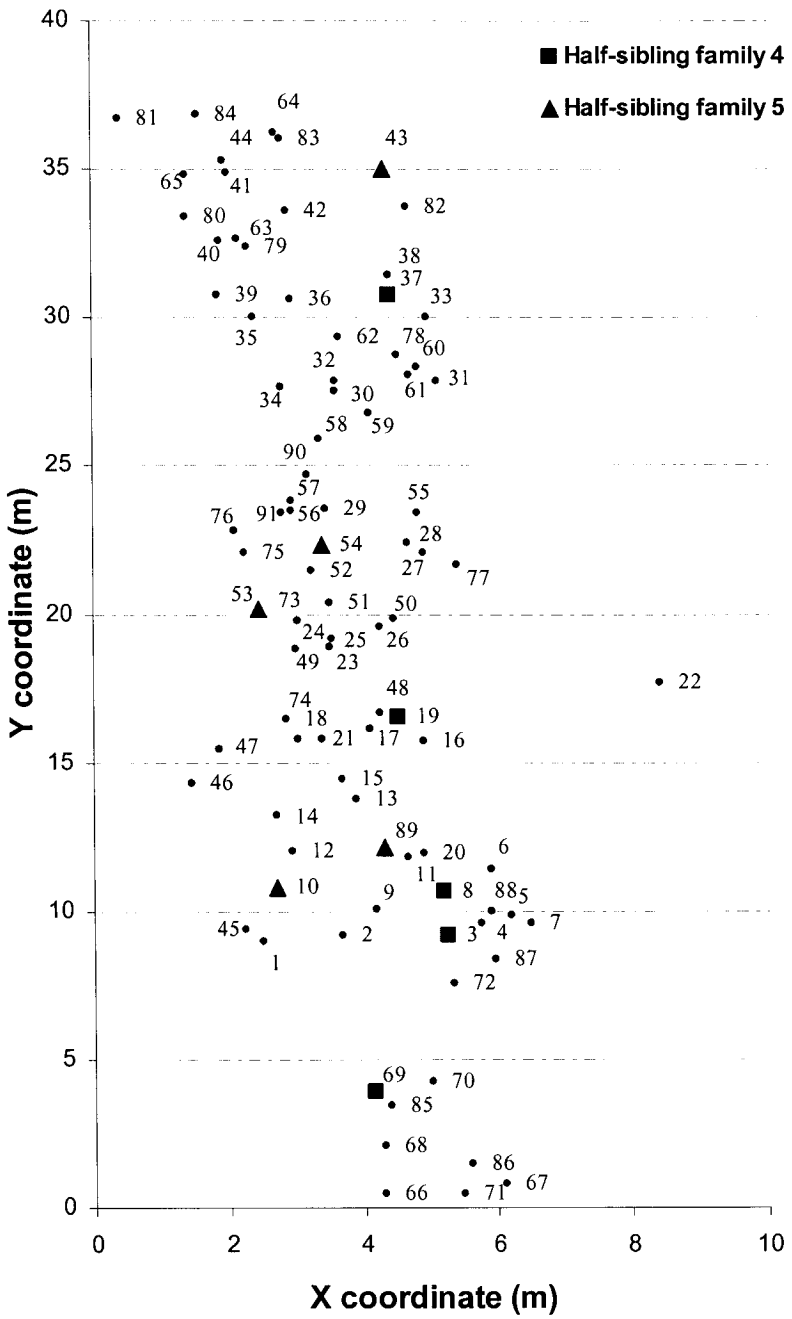
(b)


Half-sibling family 2
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81 84 64 44 83 43 65 41 80 42 82 63 40 79 38 37 39 36 33 35 62 78 60 32 31 34 30 61 58 59 90 57 55 76 91 56 29 28 75 54 27 77 52 53 73 51 50 24 25 26 49 23 22 48 74 18 19 47 21 17 16 15 46 13 14 89 12 20 6 11 10 9 8 88 5 45 2 3 4 7 1 87 72 69 70 85 68 86 66 71 67

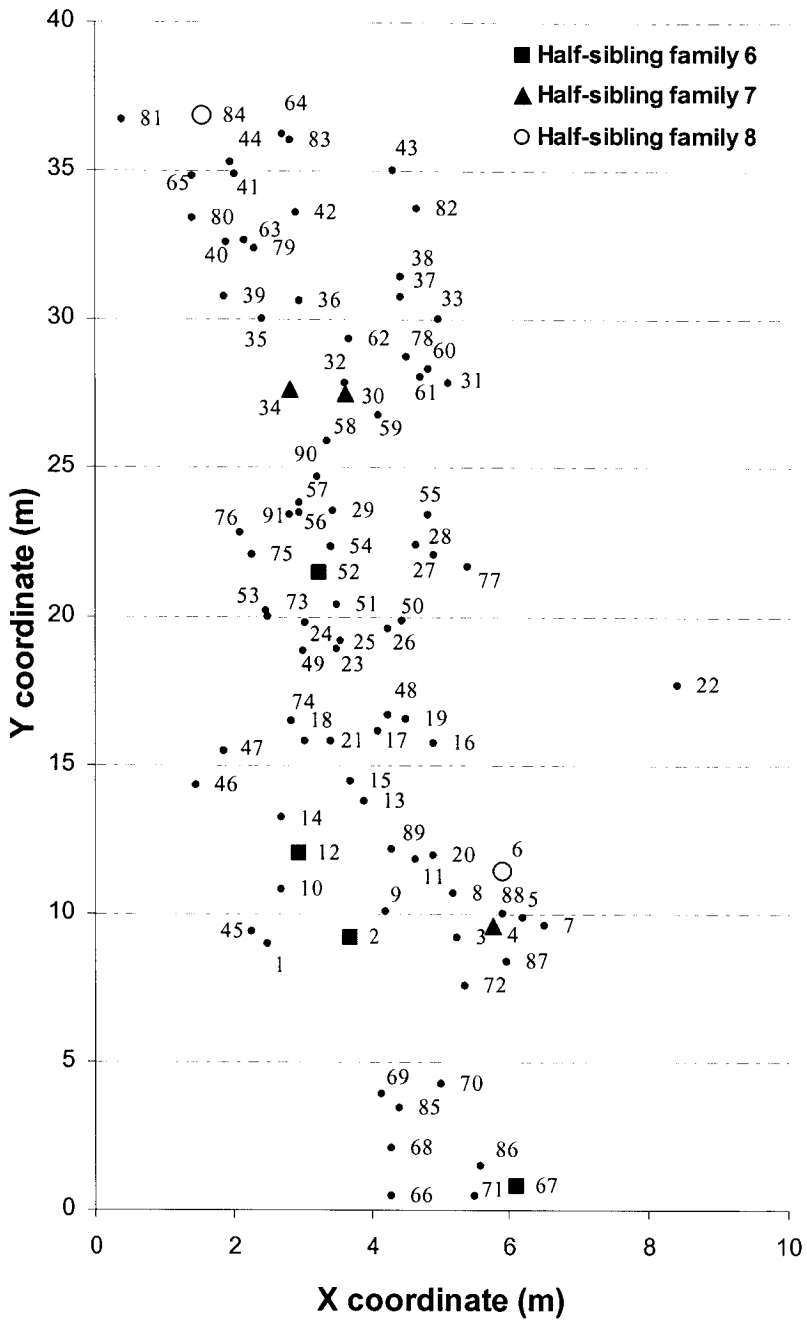
(c)


Half-sibling family 3
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81 84 64 44 83 43 65 41 80 42 82 63 40 79 38 37 39 36 33 35 62 78 60 32 30 61 31 34 58 59 90 91 57 55 76 29 56 54 28 75 52 27 77 53 73 51 50 24 25 26 49 23 22 48 74 18 19 47 21 17 16 46 15 13 14 89 12 20 6 11 88 10 9 8 5 45 2 3 4 7 1 87 72 69 70 85 68 86 66 71 67

(d)

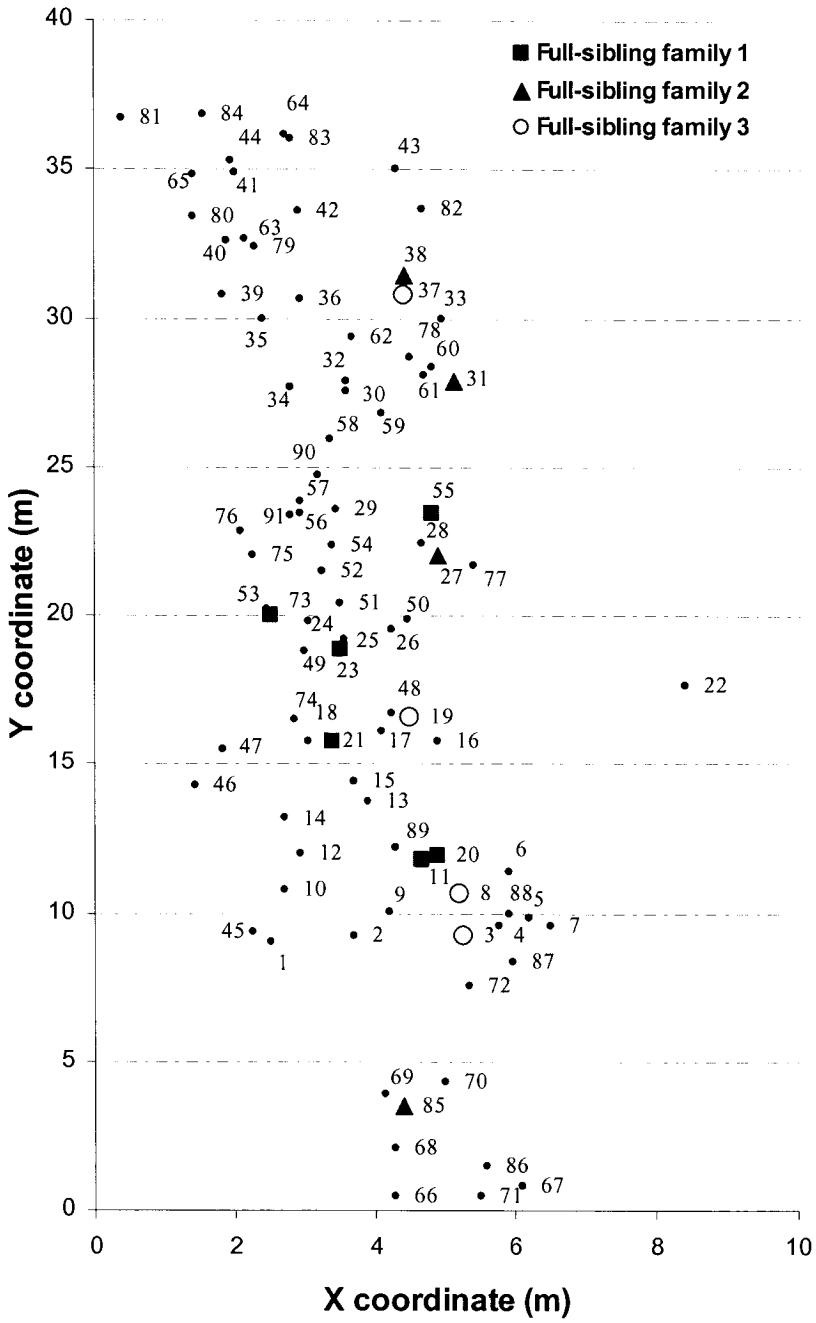

Half-sibling family 4
Half-sibling family 5
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81 84 64 44 83 43 65 41 80 42 82 63 40 79 38 37 39 36 33 35 62 78 60 32 31 34 30 61 58 59 90 57 55 76 91 56 29 28 75 54 52 27 77 53 73 51 50 24 25 26 49 23 22 48 74 18 19 21 17 16 47 15 46 13 14 89 12 20 6 11 10 9 8 88 5 7 45 2 3 4 87 1 72 69 70 85 68 86 67 66 71

(e)

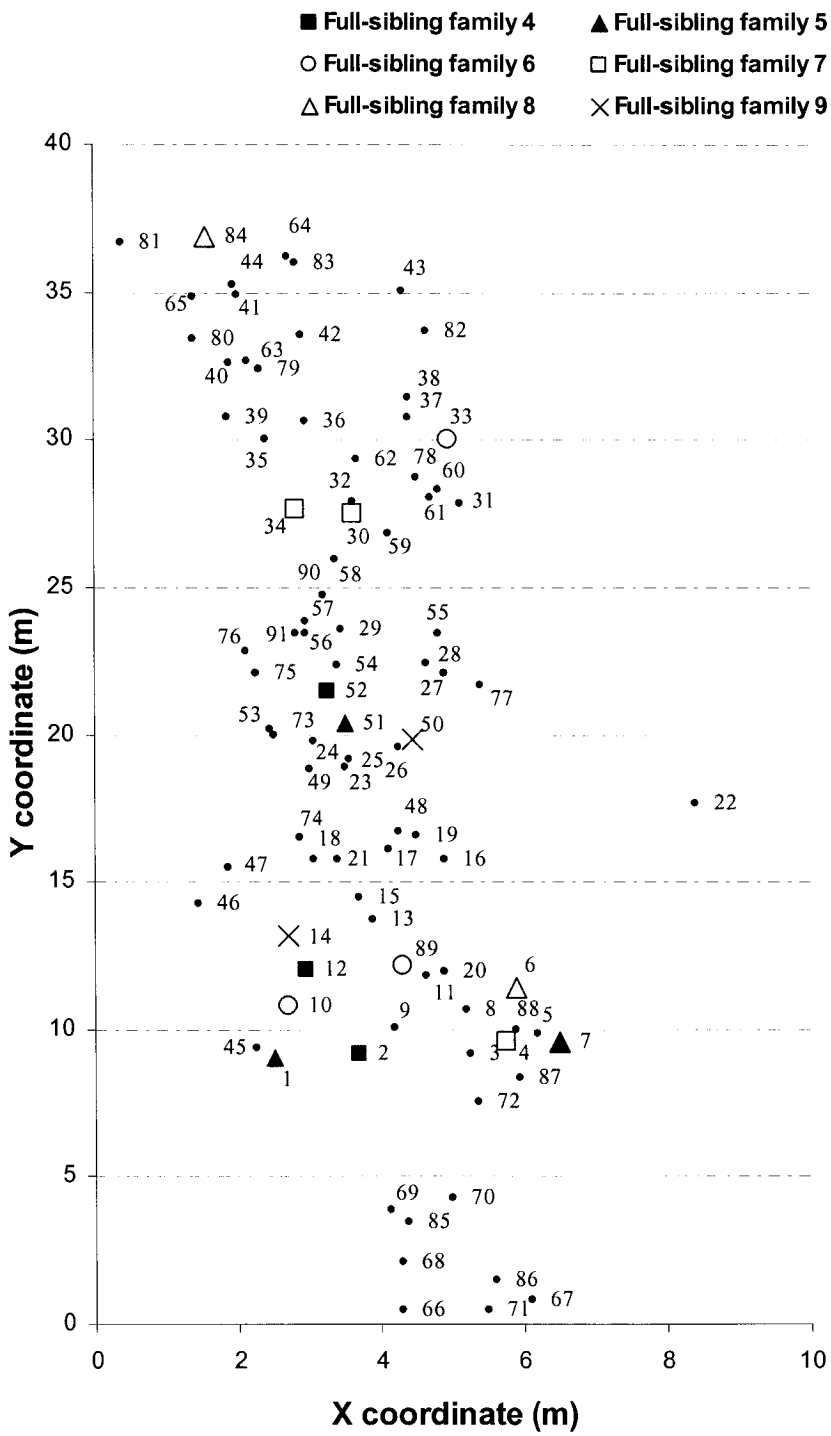

Half-sibling family 6
Half-sibling family 7
Half-sibling family 8
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81 84 64 44 83 43 65 41 80 42 82 63 40 79 38 37 39 36 33 35 62 78 60 32 31 34 30 61 58 59 90 57 55 76 91 56 29 28 75 54 27 77 52 53 73 51 50 24 25 26 49 23 22 48 74 18 19 47 21 17 16 46 15 13 14 89 12 20 6 11 10 9 8 88 5 7 45 2 3 4 87 1 72 69 70 85 68 86 66 71 67

Appendix 1D. Location of full-sibling offspring (a) families 1, 2 and 3, (b) families 4-9 at the Mouth site, Catamaran Brook. Refer to Table 1.3 for details.

(a)


Full-sibling family 1
Full-sibling family 2
Full-sibling family 3
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10
81 84 64 44 83 43 65 41 80 42 82 63 40 79 38 39 36 37 33 35 62 78 60 32 61 31 34 30 58 59 90 57 55 76 91 56 29 28 75 54 27 77 52 53 73 51 50 24 25 26 49 23 22 48 74 18 19 47 21 17 16 46 15 13 14 89 12 20 6 11 10 9 8 88 5 45 2 3 4 7 1 87 72 69 70 85 68 86 67 66 71

(b)


Full-sibling family 4
Full-sibling family 5
Full-sibling family 6
Full-sibling family 7
Full-sibling family 8
Full-sibling family 9
Y coordinate (m)
X coordinate (m)
0
5
10
15
20
25
30
35
40
0
2
4
6
8
10

Appendix 1E. Sample calculations of the probability of sharing identical genotypes across eight loci for offspring sampled at the Mouth site of Catamaran Brook.

Sample Calculations

Four pairs of offspring have identical alleles at all eight loci.

Example. *When one parent is known:*

A range of probabilities can be calculated to take into account the genotype of the second, unknown parent. Based on the occurrence of homozygosity at these eight loci for each sampled adult in our data set (n = 97) we can calculate that most individuals (~47%) are homozygous at 1 of the 8 loci. Only one individual (~1%) was homozygous at 5 of the 8 loci. The former scenario was used to estimate the most probable case of homozygosity in the unknown parent, and the latter was used as an indication of what the worst case scenario might be.

⇒ For fish 3 & 19, their genotype:

230/246, 151/**167**, 109/**121**, **191**/191, 197/**209**, 203/**251**, 171/**175**, 279/**287**

Male parent 809 is known, thus one allele matches the offspring (bolded):

230/234, 163/**167**, **121**/129, 187/**191**, 201/**209**, 199/**251**, 175/**175**, **287**/291

From the offspring, we can infer one of the two alleles of the female parent:

246/x, 151/x, 109/x, 191/x, 197/x, 203/x, 171/x, 279/x.

The number of possible genotypes per locus is calculated as follows for:

(1) the most probable case of homozygosity (1 of 8 loci are homozygous):

4x4x4x4x4x4x2x2 = 16384, thus 1/16384 chance that 3 & 19 are two different fish with identical genotypes

(2) the worst case scenario (5 of 8 loci are homozygous):

4x4x4x2x2x2x2x1 = 1024, thus 1/1024 chance that 3 & 19 are two different fish with identical genotypes.

⇒ Therefore, the chance that 3 & 19 are different fish with identical genotypes ranges from 1/16384 to 1/1024.

⇒ Similarly, with one known parent, the chance that fish 11 & 20 are different fish with identical genotypes ranges from 1/8192 to 1/512.

⇒ With two known parents, the chance of fish 2 & 12 = 1/8192.

⇒ With two unknown parents, the chance of fish 1 & 7 = 1/324.

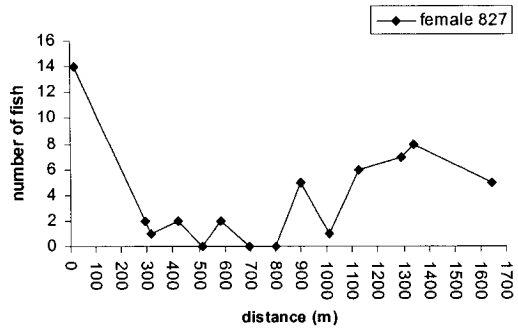
Conclusion:

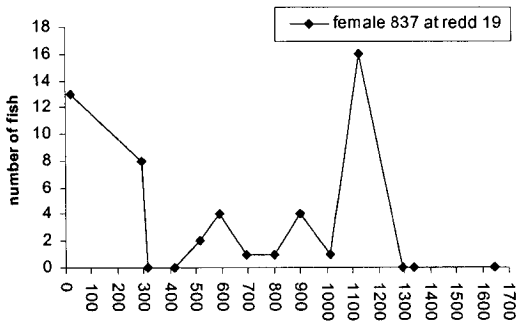
These four pairs are most probably four fish, and not eight.

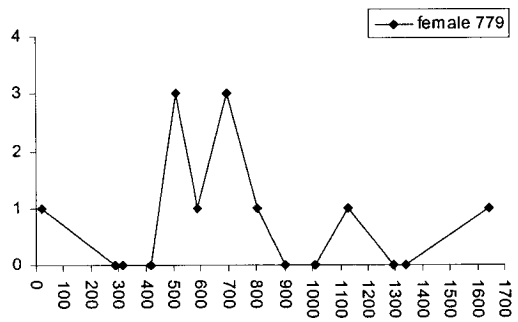
Appendices Chapter 2

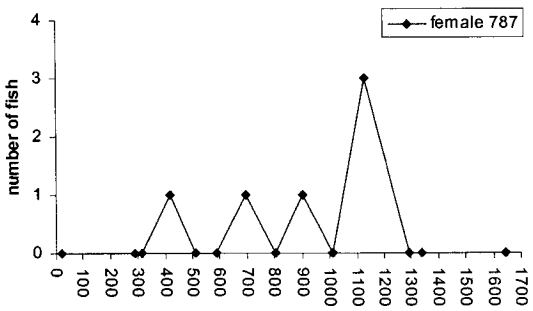
Appendix 2A. Dispersion patterns of (a) maternal half-siblings, (b) paternal half-siblings and (c) full-siblings captured downstream of a putative redd location. Refer to Table 2.5 for details.

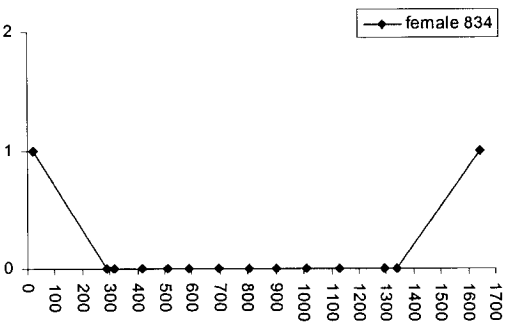
(a)

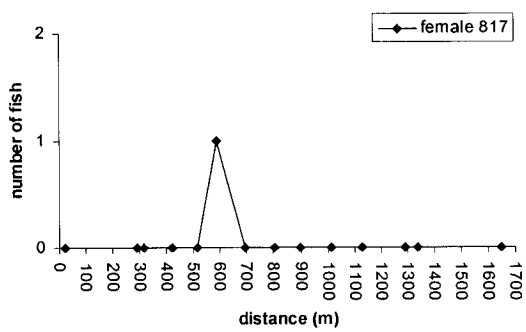

female 827
number of fish
distance (m)

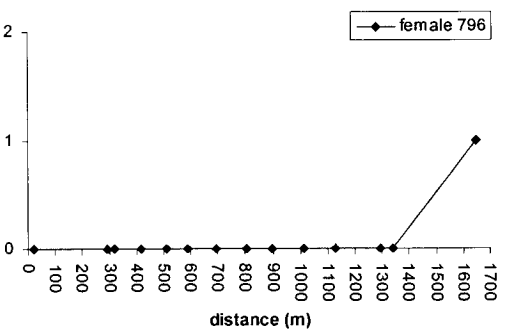

female 837 at redd 19
number of fish


female 779

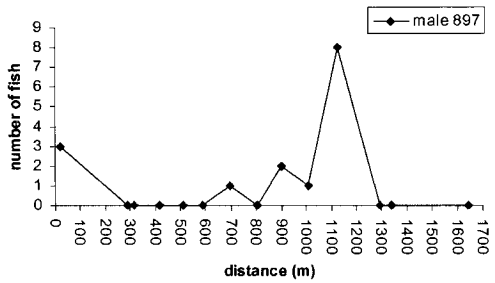

female 787
number of fish

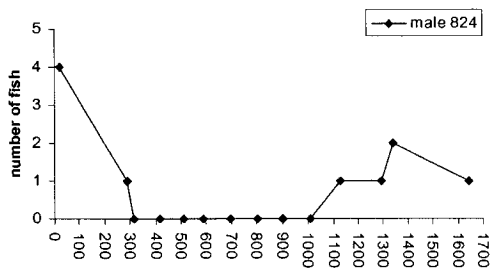

female 834

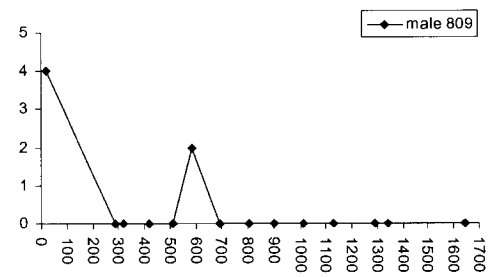

female 817
number of fish
distance (m)

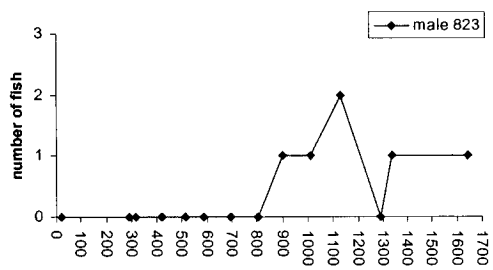

female 796
distance (m)

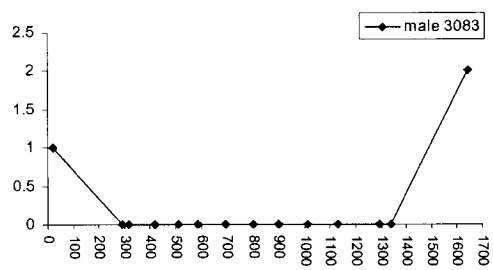
(b)

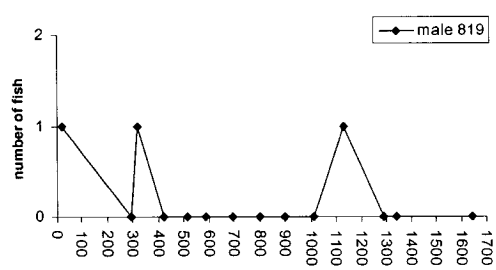

male 897
number of fish
distance (m)

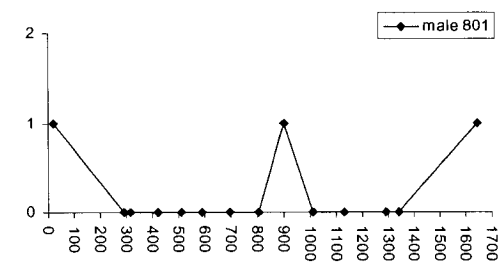

male 824
number of fish

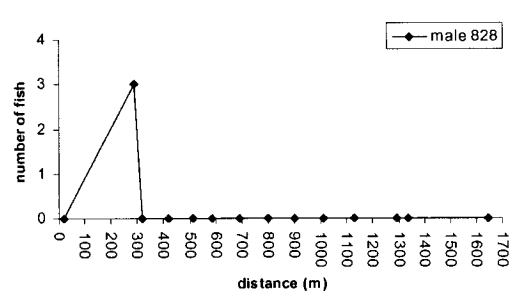

male 809

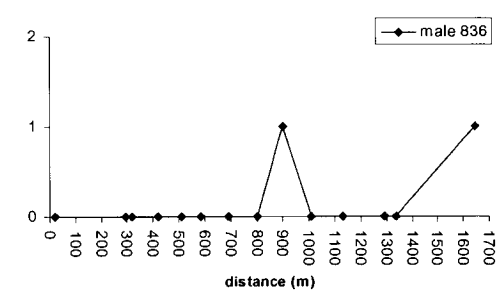

male 823
number of fish

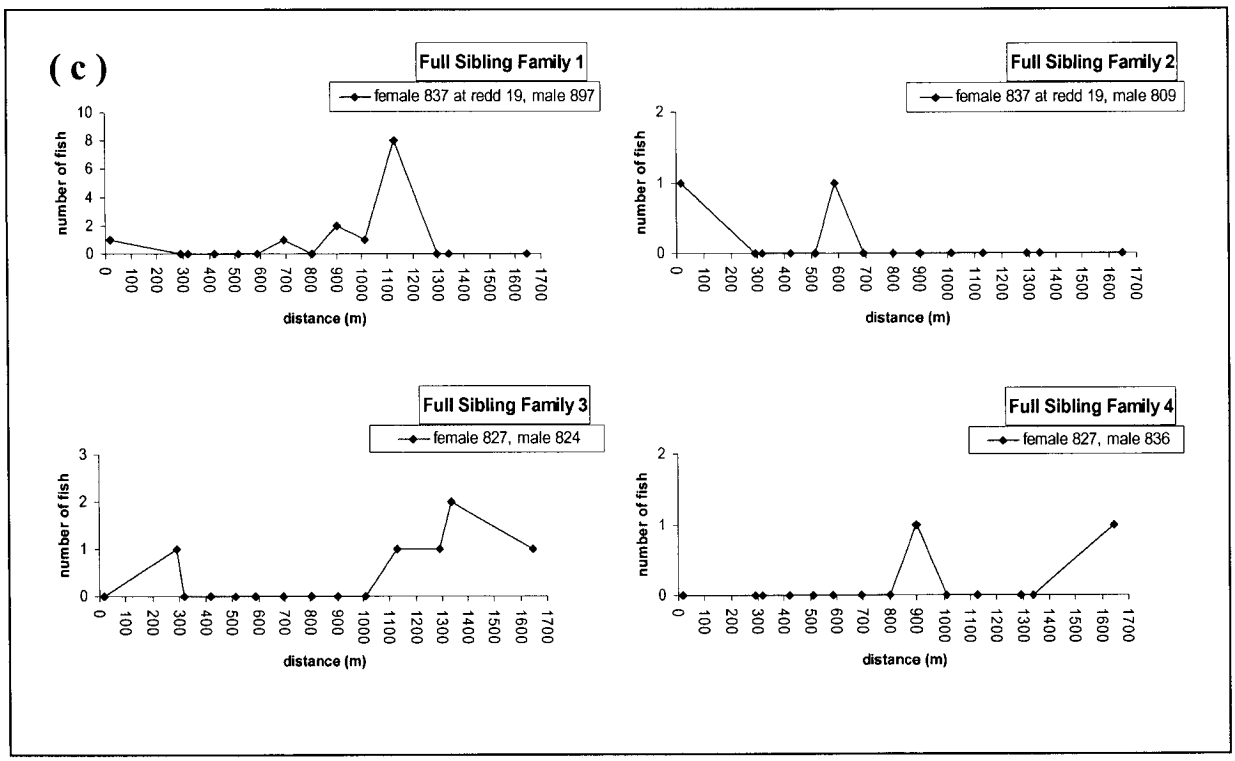

male 3083


male 819
number of fish


male 801


male 828
number of fish
distance (m)


male 836
distance (m)


(c)
Full Sibling Family 1
female 837 at redd 19, male 897
number of fish
distance (m)
Full Sibling Family 2
female 837 at redd 19, male 809
number of fish
distance (m)
Full Sibling Family 3
female 827, male 824
number of fish
distance (m)
Full Sibling Family 4
female 827, male 836
number of fish
distance (m)

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