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The Genetics and Ecology of Atlantic salmon (*Salmo salar*) decline in chalk streams

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1. ABSTRACT

This study analysed the population genetics and ecology of *Salmo salar* in two chalk rivers, the River Frome and River Piddle, Dorset, U.K. The number of adults returning to spawn in these rivers has declined over the past ten years, reflecting the global trend in reduced river *S. salar* population sizes. It is possible that a reduction in population size leads to a reduction in genetic diversity and thus to a reduction in fitness. This study aimed to determine the distribution and density of juvenile *S. salar* (parr) in the river, estimate the level of current genetic variability, determine the extent, pattern and stability of genetic differentiation, investigate the relationship between genetic variability and ecology and estimate long term changes in genetic variation.

Juvenile *S. salar* density was surveyed by electric fishing in summer and autumn for three consecutive years, 1998, 1999 and 2000, at twenty sites on the River Frome and two sites on the River Piddle. Between 14-16 sites were sampled at any one time and 5 sites were sampled in November 1998. Fin clips were removed for genetic analysis and the juveniles returned to the stream.

The density of juveniles varied between sites and between years; the lowest density was 0.027 and the highest density was 49.49 individuals per 100 m^2. Density was not dependent on distance of site from source or on flow rate category. High densities were found at sites where gravel cleaning had been carried out indicating success of this technique in promoting survival at the egg stage. Evidence of Brown trout (*Salmo trutta*) predation/competition influence on salmon parr density was found, which has profound management implications in a river with a declining salmon population and where trout are stocked.

High site fidelity of parr, measured by the number of marked juveniles at the same sites in Autumn, was detected. Detection of low numbers of 1+ parr indicate that most juveniles smolt after one year due to rapid growth in a productive chalk stream. Habitat quality was assessed using the HABSCORE model. Large variation in parr density relative to habitat quality score was detected. Significant variation in parr length between sites was detected. A significant correlation between parr growth rate and density was detected in 1998. Positive correlations were found between juvenile mean length and river flow rate category, which may have consequences for differential survival rates within the catchment.

Microsatellite markers were used to estimate genetic variability and population structure. Microsatellites are highly variable and have previously been used to test for genetic differentiation among salmonid populations within rivers. A large number of salmonid microsatellite primers are published. Fifteen primers were purchased and six primers were optimised. PCR products were run out on polyacrylamide gels and visualised by silver staining.

All microsatellite loci were polymorphic; between 5 and 13 alleles were detected per locus. Numbers of alleles detected were lower than numbers detected in other rivers, however the number of alleles is highly dependent on sample size. Allelic richness standardised per individual (ARi) was calculated to permit comparison across sites and with other studies. In the rivers Frome and Piddle, ARi was lowest at locus Ssa 289 and highest at locus Ssa 197. At four loci, ARi detected in this study was lower than in nine Canadian and three European rivers.

Observed heterozygosity over all loci was between 0.494 (July 1998) and 0.648 (October 2000). Observed heterozygosity varied between loci; loci Ssa 289 and Ssosl 417 were lower than the other four loci. Expected heterozygosity (Ht) corrected for sample size, over all loci, was between 0.698 (November 1998) and 0.737 (July 1998). Over all loci, no site had a particularly low Ht. Ht varied between loci and was lowest at locus Ssa 289. Allele sizes were equivalent to other studies except locus Ssosl 417 which was larger in the rivers Frome and Piddle samples than in other studies of *S. salar*.

Allele frequency data were used to estimate population structure. A total of 33 1+ parr were sampled over the three years. No significant differentiation was detected between 0+ and 1+ parr of the same cohort year, however, none of the 1+ parr could be assigned to a sample site, therefore 1+ parr were excluded from further analyses. Very low but significant differentiation was detected between years. Low but significant differentiation was detected between Summer and Autumn samples in each of the three years, therefore population structure of Summer and Autumn samples was analysed separately.

Population structure was estimated using Wright's F statistics to measure correlation of alleles over all sites (F_{IT}), between sites (F_{ST}) and within sites (F_{IS}). Over 6 loci, significant total F_{IT} was detected at each time (F_{IT} 0.179-0.329). Significant F_{ST} was detected at each time except November 1998 (F_{ST} 0.031-0.066). Significant F_{IS} was detected at each time (0.153-0.31). Locus Ssa 197 had the highest percentage contribution to overall loci F statistics at four sample times and Ssa 289 had the lowest percentage contribution at all sample times. The estimation of over all sites F_{IS} was much higher at locus Ssosl 417 than at all other loci, therefore locus Ssosl 417 was removed and all further estimations used five loci only. Over 5 loci, significant F_{IT} was detected at each sample time, however the values were lower than the 6 locus estimates (F_{IT} 0.075 to 0.226). Significant F_{ST} was detected at each sample time, except November 1998 (F_{ST} 0.03 to 0.052). Significant F_{IS} was detected at each sample time and both the values and the levels of significance were reduced (F_{IS} 0.044 to 0.202).

Significant F_{IS} was detected at between two and ten sites per sample time. Significant F_{IS} was detected at Moreton Ford at 5 sample times, at Norris farm at 4 sample times and at Lewell Mill at 3 sample times. Estimation of high, significant F_{IS} at a site could be due to a small number of adults spawning at that site. Numbers of adults per site could not be monitored in this system, however number of redds per site was counted in January 2000. In July 2000, high significant F_{IS} was detected at Lewell Mill and Moreton Ford which corresponds to the low numbers of redds at these sites. Seven redds were observed at Waterbarn Stream, July 2000; F_{IS} at this site was low and not significant.

Significant differentiation between sites was detected for a large number of pairwise comparisons. Pairwise F_{ST} values were between 0.0005 and 0.1126. Significant differentiation between sites may be due to non-random return of adults to spawn or due to sampling small numbers of families. Non-random return of adults to spawn may be due to migration to the natal spawning site or migration to sites with specific environmental characteristics. Significant positive correlation of pairwise F_{ST} and geographical distance between sites was detected only in July 2000.

River flow rate category was estimated at all sites. River temperature was estimated at eight sites in Summer and Autumn 2000. River temperature was converted to optimal degree days. Between May and July optimal degree days were between 73% and 84 % of the maximum

possible. A significant positive correlation between May to July optimal degree days and distance of site from source was detected. No correlation between optimal degree days and flow rate category were detected. No relationship between temperature and fish length were detected.

No correlation between genetic differentiation between sites (pairwise F_{ST}) and differences in environmental characteristics (temperature converted to optimal degree days and flow rate category) was detected at any sample time.

The possibility of sampling small numbers of families per site could be ruled out if isolation by distance was detected or if temporal stability of site allele frequency was detected. Isolation by distance was detected in one sample time only and temporal stability of site allele frequency was not detected for either 1998-1999 or 1999-2000 therefore the possibility that small numbers of families were sampled per site can not be ruled out.

DNA was extracted from 1421 scales, removed by anglers from adult *S. salar* in the River Frome between 1963 to 1997. Scales were aged by counting the number of rings, however age information was not available for all scale samples. Scales were analysed by cohort year. Allele frequency data were used to estimate correlation of alleles within a cohort year, and no significant values were estimated. Significant correlation between adult population size and number of alleles was detected at locus Ssosl 85, however the number of alleles detected in a population is dependent on sample size therefore measures of genetic variability, corrected for population size, should be used to compare between years. No correlation between adult population size and allelic richness or between expected heterozygosity was detected.

2. INTRODUCTION

2.1 Background

The rivers Piddle and Frome are an ideal system for a detailed study of *Salmo salar* spatial and temporal genetic variation and population structure. The adult population size in the Frome from 1970 to present is known and an archive scale collection, dating from 1960, has allowed changes in number of adults returning to spawn and changes in population age structure to be monitored. The rivers Piddle and Frome are chalk streams that have never been stocked with salmon.

A global decline has occurred in *S. salar* populations. This is reflected both in total catch data (Mills et al. 1999) and rod catch data (Welton et al. 1999). In some rivers reduced population size is due to large barriers to migration which prevent adults from reaching spawning sites.

S. salar in the Frome were historically exploited by a stone weir at Wareham, in place from the 14th Century. The population was nearly completely destroyed by 1850, and use of the weir was prohibited in 1861 (Solomon 2000). The number of salmon returning to spawn has since recovered. Barriers to migration such as mills at East Stoke and Bindon were first documented in the 1910s (Solomon 2000). The first possible barrier to upstream migration of adults is the mill channels at East Stoke (ES). Obstructions have been removed and it has been observed that the resistivity counter does not cause a barrier to movement. Old hatch channels at Bindon Millstream (BM) do not present a barrier to migration providing the flow rate is sufficiently high. Former mill structures at East Burton (EB) were found to have no effect on migration providing that the sluices were kept free of weed. A weir at Waterbarn Stream (WS) operated by the Environment Agency did not pose a barrier to migration provided flow rate was sufficiently high. It was stated that by 1986, no major obstacles exist to upstream movement of adults (Solomon 2000).

The total number of adults returning to spawn has been monitored since 1970 by a fish counter at East Stoke (Grid reference SY870867). Data from the fish counter, combined with information from an archive scale collection, revealed that the population has declined and the age structure has altered. Prior to 1991, the average numbers of adult *S. salar* ascending the Frome was around 2500 per annum, with a maximum of 4000 in 1988. Since 1991, mean numbers of adults have reduced to an average of less than 1000 per annum (Figure 1.1) (Welton et al. 1999).

A multi sea winter (MSW) fish is an individual that stayed at sea at the feeding grounds for more than one year. A disproportionate decline in the multi-sea winter fractions of the population and a decline in the spring run, in which MSW fish predominate, occurred in the Frome and has also been reported in other rivers (Rogan et al. 1993). In the River Frome, a number of adult females survived spawning and spawned again; 28 % of 3 SW and 7 % of 2 SW fish had spawned previously (Welton et al. 1999). Most parr (juvenile salmon in freshwater) smolted (change from parr to smolt, with physiological changes for survival in salt water and colouring change from camouflage markings to silver) at age 1+; data from scales showed that only 12 % smolted at 2+, in contrast with Northern Rivers, where greater proportion of parr remain in the river for more than one year.

Decline of *S. salar* populations is of concern both economically and for species conservation. A detailed description of the extent and structure of genetic diversity is required to inform species management programmes.

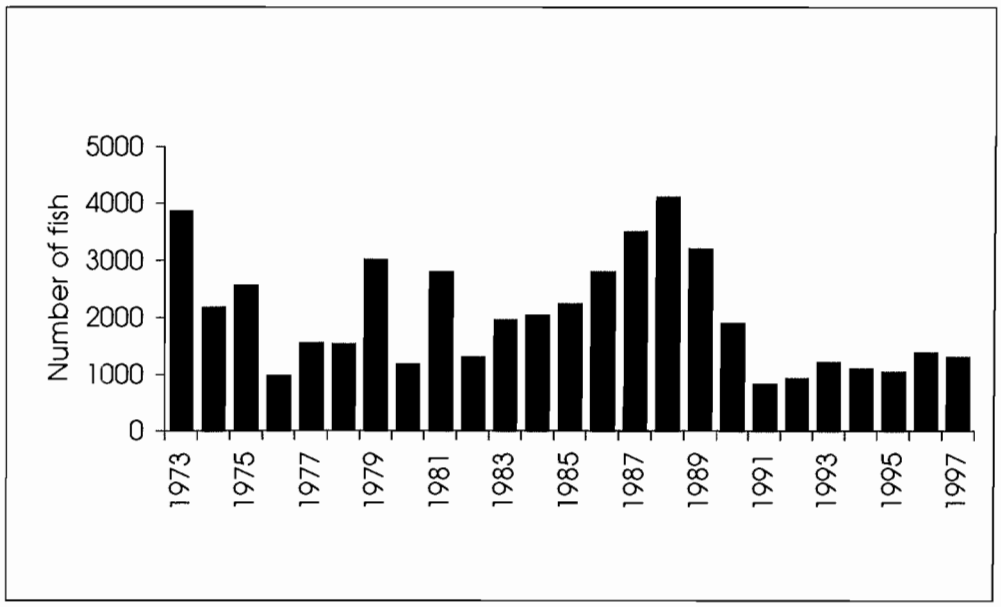


Figure 1.1 Number of adult *S. salar* detected by fish counter on River Frome between 1773 and 1997

2.2 Multi sea winter fish

It has been demonstrated that fish of different sea ages may spawn in different parts of a river system (Summers 1996). On the River Spey spring MSW salmon migrate to and subsequently spawn in the upper reaches while summer MSW fish remain in the lower reaches. Similarly, early running grilse spawn in the upper reaches whilst later running fish remain in the lower reaches (Laughton 1991). Several Spey salmon showed migratory behaviour patterns which indicated homing behaviour associated with increased tributary discharges. Webb and Hawkins (1989) working on the River Dee observed similar patterns.

There has been a dramatic decline in MSW fish in chalk streams and in the overall number of migrating adults. The Test has been particularly affected and the decision was made to supplement stocks with fish of hatchery origin. Scottish stock was chosen for its large MSW component and stocking has been carried out since the late 80s. However, there has been no evidence of an increase in the MSW component of the stock in the Test (Russell et al. 1996). The 1992 juvenile fish of the Test showed distinct differences in allele frequency from wild fish and from previous batches of River Test origin hatchery reared fish (Thompson and Russell 1994). These differences may have been due to using an insufficient number of fish as broodstock resulting in a biased sample (quite possible) or that rearing juveniles under hatchery conditions cause different selection pressures than those found in the wild (unlikely as previous hatchery reared juveniles had the characteristics of wild fish) or from mistaken identity of broodstock, eggs or juveniles during hatchery procedures (possible). It was decided to try to maintain the genetic integrity of the Test stock and monitor the genetic allele frequency of further introductions as well as the stock in general to see if the effects of past stocking with non-Test fish have resulted in any significant change to the genetic make-up of the stock.

Results for 1994 suggest that the allele frequency of adult Test fish has been modified by introductions and are now a "cross" between Test fish and Scottish fish (Russell and James 1994). Even following the decision to try and maintain the genetic integrity of Test stock, hatchery fish introduced in 1995 came from Test/Scottish broodstock of mixed origin and not native Test stock.

A genetic appraisal of salmon stocks on the rivers Avon, Piddle and Frome by MAFF notes that the sAAT-4* allele frequency of chalk stream salmon has been found to be different from other rivers due either to genetic drift or adaptation to the chalk stream habitat (Russell and Child 1996, Russell and James 1995). The apparent genetic modification of the Test and Itchen stock by recent introductions of parr derived from other sources has raised concerns about the potential implications for other south coast chalk streams.

2.3 Genetic variation

A possible outcome of decline in population size is a reduction of genetic variability and fitness. The susceptibility of a species to loss of genetic diversity when population size is reduced is dependent on the distribution of genetic variation within and among populations (Jordan et al. 1992).

Spatial genetic variation and the spatial genetic structure of salmon populations on a continental and between-river scale has been well studied (McConnell et al. 1995, Sanchez et al. 1996, Stahl 1998, Tessier et al. 1997 and Verspoor 1997). However, genetic variation and population structure within-rivers has been less well studied and there is only one previously published study of the temporal component of spatial genetic differentiation of *S. salar* (Garant et al. 2000).

The extent and structure of *S. salar* genetic variation may be influenced by life history and behavioural traits and environmental factors. Little is known about the behaviour of adults in the river with regard to selection of spawning sites. Subdivision of a population within river system can occur if adults return to the natal sites to spawn. Youngson et al. (1994) and Heggberget et al. (1988) have shown that homing occurs to a smaller area than the whole catchment and may be tributary based. Behavioural traits such as assortative mating due to size or time of return and (possible) mating with kin can also lead to genetic structuring. Factors such as migration barriers and physical and environmental differences (pH, pollution, speed of flow, gravel, vegetation, predators) between sites may also lead to genetic differentiation.

Life history traits such as precocious maturation of male parr and repeat spawning by some females can lead to reduction of genetic differentiation between sites within a river. Precocious parr are not constrained by normal mating barriers and spawning may not be site specific. Limited information is available regarding repeat spawners but it is possible that these fish spawn at different sites or even different rivers. It is possible to correlate life history and behavioural traits with patterns of genetic variation, however, further information regarding the heritability of these traits is needed before firm conclusions can be made.

2.4 Long term genetic variation

The long term data for the River Frome provides a unique opportunity to relate changes in genetic variability with changes in number of adults returning to spawn and changes in age structure over a long time period. Scales have been collected by anglers since 1963, however, the number of individuals sampled in any one year varied dramatically, from one in 1983 to 169 in 1974 (Figure 2.4.1.). To allow accurate comparison of genetic variability between years, individuals were analysed by cohort year (Figure 2.4.2).

No other studies exist with such an extensive scale collection, although other studies have used old scale samples and compared genetic variability to current samples. For example, Nielsen et al. (1997) assessed changes in genetic variability of *S. salar* using scales from the 1930s and samples taken in 1989. Reduction in genetic diversity was detected; this may be a result of a genetic bottleneck, however, this may be due to problems comparing adult and juvenile samples.

Allele frequency data can be used to detect reduction in genetic variation (Cornuet and Luikart 1996 and Luikart and Cornet 1998). In this river the number of returning adults did not fall below 1000 for any year, thus the population size remained relatively large. It is possible that effective population sizes were lower than recorded census adult population size for certain years. Changes in effective population size over time can be estimated (Miller and Kapuscinski 1997 and Neigel 1996). Allele frequency data can be used to determine if differences occur based on life history variables (number of years spent in river as parr and number of years at sea before return to spawn) and thus can be used to test if multi-sea winter fish form a separate component of the population. Aspects of *S. salar* life history, for example overlapping generations (Waples and Teel 1990), multiple spawners and the presence of precocious parr, may contribute to low genetic differentiation between years.

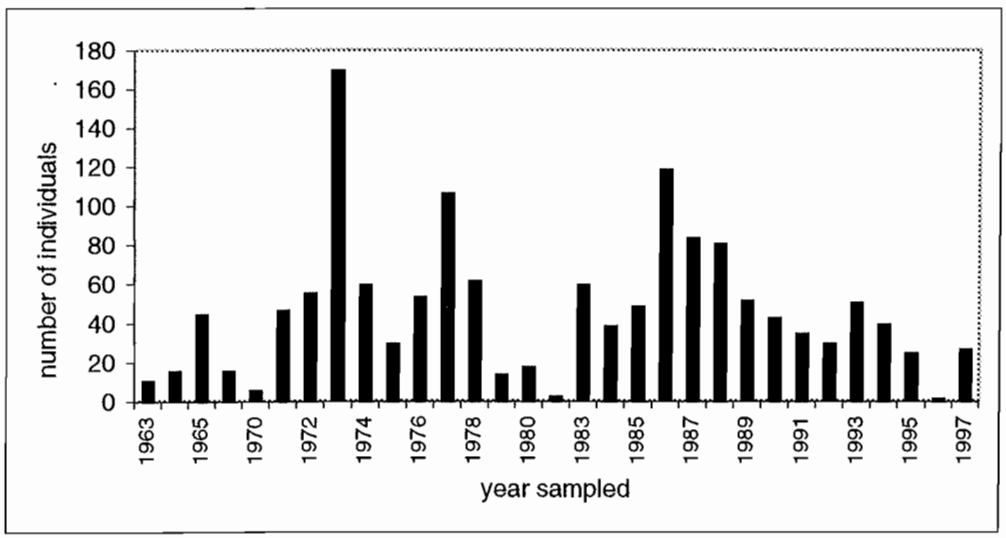


Figure 2.4.1 Number of scale samples per year of return to river

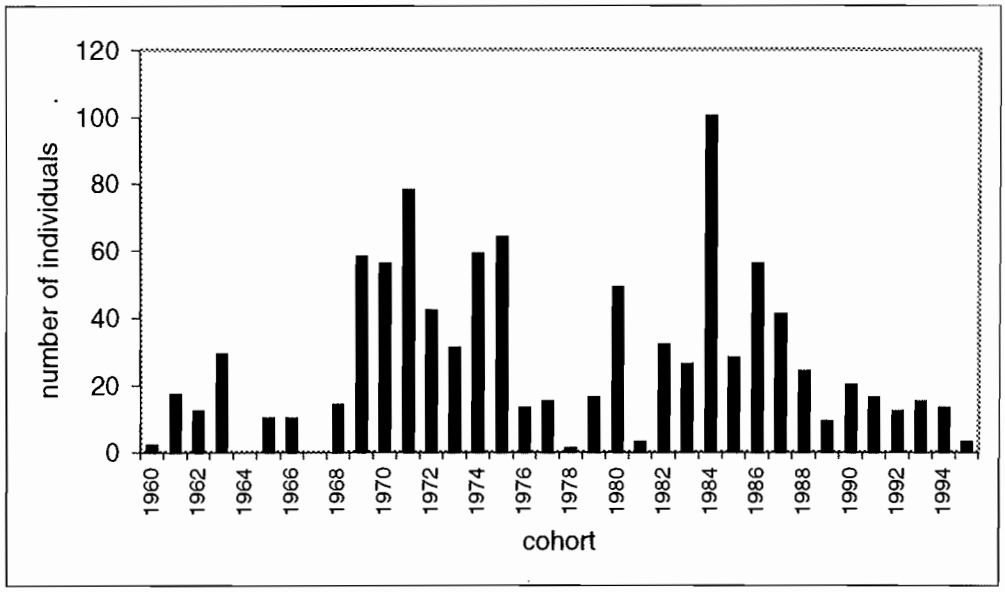


Figure 2.4.2 Number of scale samples per cohort

2.5.1 Sampling concerns

Significant genetic differentiation between sites within a river may be caused by the non-random return of adults to spawn or may be due to sampling small numbers of families per site. Ideally differentiation between spawning populations would be estimated using samples taken from spawning adults or from eggs. However, in many rivers such as the Frome, sampling of spawning adults is not permitted and therefore samples are taken from juveniles at the parr stage. There are a number of factors which must be considered when estimating information about spawning adults by sampling progeny.

The life cycle and behaviour of *S. salar* within chalk streams influences the time of year that sampling can be performed. The age structure of juveniles must also be considered. In the rivers Frome and Piddle, spawning occurs in December/ January and therefore no sampling was permitted before July to ensure that juveniles were sufficiently large to withstand electrofishing and handling. Sampling was non-destructive; juveniles were returned to the river after removal of a fin clip.

There is limited information on the movement of parr within the river throughout the year. It was assumed that young parr remained at the site of hatching. A second sample was taken in Autumn of the same year to assess parr site fidelity. One sample was taken in November 1998 to determine if any juveniles remained in small tributaries late in the year. Previous work has suggested that parr move from small tributaries to the main river in Autumn (Riley, pers. comm.).

Parr can remain in the river for up to 5 years before smolting. In chalk streams most juvenile *S. salar* smolt after one year, however, parr older than 0+ do occur in the rivers Frome and Piddle. Parr of different cohorts may be present at the same site, and previous studies (Beacham and Dempson 1998) have deliberately sampled parr of different age groups. Results from studies where allele frequencies of parr of different cohorts have been pooled, should be viewed with caution; allele frequencies may not be stable over time, parr older than

0+ may have migrated from the site where they hatched and parr older than 0+ may be precociously mature. Parr of different cohorts should not be pooled unless detected allele frequencies are temporally stable and it can be proved that older parr have not migrated from the site where they hatched. Precocious parr occur in the Frome, although it is impossible to quantify the exact proportions without destructive sampling.

Study sites were selected on the basis of good habitat for juvenile salmon with the likelihood that sufficient individuals would be sampled for genetic analysis. Distribution maps of redd (gravel structure containing eggs) counts for 1980/1981 and 1982/1983 (Wessex water authority) (Solomon 2000) indicate that suitable spawning sites occur over the entire river. Redds were observed from the tidal limit of the River Frome at Wareham to 5 km upstream of Dorchester. On the river Piddle, redds were observed from the tidal limit to Tolpuddle and upstream to Bere Regis (Bere Stream).

It is possible that sample sites selected do not correspond to a 'population'. Populations are defined as groups of individuals with constrained among-populations interbreeding, but with random mating within each population (Verspoor 1997). It may be possible that two populations have been pooled or when sample sites are adjacent it is possible that samples are in fact from one population.

2.5.2 Sampling small numbers of families per site

Detection of significant genetic differentiation between sites may indicate that adults returned non-randomly to spawn. However, significant differentiation may be detected when sampling small numbers of families per site (Hansen et al. 1997) or due to sampling large numbers of offspring from a small number of spawning adults with no reproductive isolation (Allendorf and Phelps 1981). An estimation of the population size and effective population size at each site would indicate if the 'Allendorf' effect occurs. However numbers of adults per site were not available in this system.

It is possible to use allele frequency data to test if small numbers of families are sampled per site. Detection of 'isolation by distance' (IBD); correlation of genetic differentiation between sites and geographical site distance apart, would allow the possibility of sampling small numbers of families to be ruled out. There is no expectation of significant positive correlation between pairwise F_{ST} and geographic distance between sites if small numbers of families were sampled. In resident populations genetic differentiation between sites may increase over time due to drift. Isolation by distance can occur as a gene flow is reduced with increasing site distance apart. However, these expectations are not necessarily met in migratory species such as *S. salar*.

It is not expected that allele frequency differences caused by a small number of adults per site or from sampling small numbers of families per site to be stable over time. In this study, we devised a test of temporal allele correlation. If the observed spatial structure is stable over consecutive years then significant genetic differentiation can be attributed to non-random return of adults and not to sampling effects.

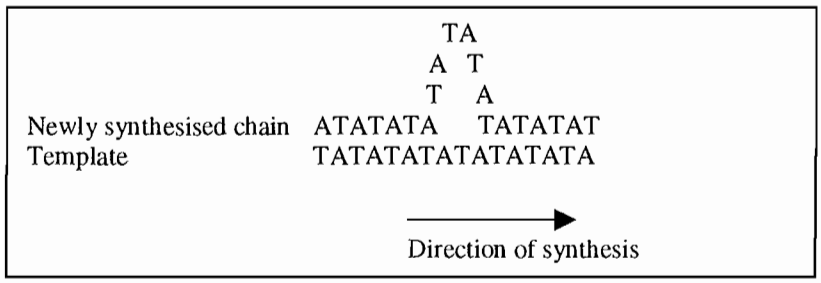
2.6 Genetic markers

Genetic markers known as microsatellites have become the marker of choice for estimation of genetic variability and population structure. Microsatellites are regions of DNA where a short sequence is sequentially repeated and can be defined by repeat length and number of repeats. Repeat units are generally between one and five base pairs (Jarne and Lagoda 1996). Microsatellites are classified into dinucleotides (eg ATATAT), trinucleotides (eg GTCGTCGTC) and tetranucleotides (eg CTCACTCACTCA). Many microsatellites are pure repeats, however, compound ((eg $(CA)_n(CTCA)_n$)) and interrupted repeats (eg $(TC)_{10}N_n(TC)_3$) have also been isolated. Microsatellites are variable, co-dominant and have relatively large numbers of alleles per locus. Microsatellite size may be under selection however it is generally assumed that microsatellites are not under selection pressure ('neutral'). Microsatellite loci are generally polymorphic in natural populations, however compound and interrupted loci tend to be less polymorphic, possibly due to reduced slippage during replication. Null alleles are caused by mutations in primer annealing sequence and can be detected by testing against expected frequencies under Hardy Weinberg equilibrium, provided that heterozygote deficiencies have no other origin (Jarne and Lagoda 1996).

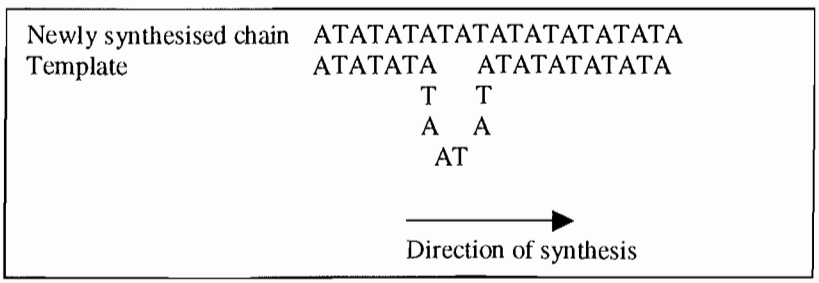
No prior sequence knowledge is required to develop or utilise microsatellites therefore they are useful in species of conservation interest where limited knowledge of the genetics. Microsatellites developed in one species can be used to investigate genetic variability in related species, however, mutation in the primer binding site may cause failure of some cross-species amplification (Chambers and MacAvoy 2000). Higher polymorphism and larger alleles are generally found in the species in which the primers were characterised. Cross species amplification may be problematic if a chromosomal replication has occurred, for example, (McConnell et al. 1995b) reported that a microsatellite, cloned from *S. salar*, appeared to be tetraploid in *S. trutta* having three to four alleles per individual.

Mutation may occur by slipped strand mis-pairing or recombination during replication, resulting in the loss or gain of one or more repeat units (Chambers and MacAvoy 2000).

Repeats are added when the newly synthesised DNA chain loops out;



Repeat units are removed if the template loops out;



Several mutation models have been proposed and have been tested with observed and simulated data to explain observed and simulated allele frequencies. The Stepwise Mutation Model (SMM) assumes that mutation will add or remove a single unit to or from the existing allele with equal probability. The Infinite allele model (IAM) assumes each mutation creates a new allele. The K-allele model assumes that K allelic states are possible, mutation at a given allele occurs with the probability u/k-1 to a particular allele. Debate continues over which model best describes observed data, and a number of different statistical methods have been developed to incorporate these.

Point mutations can occur in microsatellites producing imperfect repeats which are less variable than perfect repeats, possibly due to reduced slippage mutation rate. It is possible that the longest stretch of uninterrupted repeat units has the strongest effect on slippage mutation rate (Anon 2000). As mutations add and remove units from a microsatellite a series of allele sizes develops. The number of alleles in a population are controlled by mutation, migration and drift. Microsatellites appear to have an upper size limit and rarely exceed a few tens of times the repeat unit; it is possible that loss of repeats is more common with large alleles or involves larger deletions with less efficient repair.

The mutation rate of a microsatellite locus can be estimated from direct counting of mutations from pedigrees or indirect estimation from linkage data and by comparing observed and theoretical values. Rates of mutation differ between species but values between 10^{-5} to 10^{-2} mutations per meiosis have been observed (Anon 2000).

Microsatellites have complex structures and complex histories, therefore it is possible that alleles of identical size have resulted from different lineages. Size homoplasy at microsatellite loci was analysed by Viard et al. (1998) in five interrupted and/or compound repeats in *Apis mellifera* (honey bee), *Bombus terrestris* (bumble bee) and *Bulinas truncatus* (freshwater snail). Fifteen different sized fragments were composed of 31 different sequences, with between one to seven different sequences per same-sized product. Size homoplasy was detected mainly between populations. If similarly large numbers of alleles are hidden in analyses of salmonid populations then there could be serious implications for estimations of genetic variation and population structure.

Populations are screened for genetic variation using primers, short (e.g. 20 bp) sections of DNA which designed to be complementary to a region upstream and a region downstream of the microsatellite. The selected microsatellite region is amplified using the polymerase chain reaction (PCR). Different sized alleles can be readily separated on polyacrylamide gels and visualised using silver staining.

2.7 Statistical tests

2.7.1 Degree of non-random mating

Differences in observed allele frequency can be used to characterise population structure. The deviation of allele frequencies from expected, given random mating, can be estimated using F statistics (Wright 1951). Wright defined the correlation between the presence or absence of an allele in uniting gametes (correlation coefficient) and defined a set of correlations for subdivided populations. For a population divided into a series of subpopulations, three quantities were defined: F_{IS} – the correlation between uniting gametes within a subpopulation compared with the correlation between gametes selected randomly from within that

subpopulation; F_{IT} – the correlation between uniting gametes in the whole population compared with the correlation between gametes selected randomly from the whole population; and F_{ST} – the correlation between gametes selected randomly within subpopulations compared with the correlation between gametes selected randomly from the whole population. These correlations are related by the formula $(1-F_{IT}) = (1-F_{IS}) \times (1-F_{ST})$. F_{IT} measures the extent of non-random mating with the whole population, F_{IS} measures the extent of non-random mating within subpopulations and F_{ST} the extent to which alleles occur in the same subpopulation.

2.7.2 Coancestry

θ is a parameter called coancestry, the correlation between alleles in different individuals within a subpopulation. θ is akin to an intra-class correlation coefficient. Cockerham (1969, 1973) discussed the properties of this parameter and its relationship to Wright's F_{ST}. The important difference is that F_{ST} (and the other F-statistics) consider alleles in gametes, whereas θ is concerned with alleles within individuals. In other words, for individuals A and B, F-statistics are concerned with the correlation between alleles in a randomly selected gamete produced by A and a randomly selected gamete produced by B. In the coancestry approach, the correlations are between a randomly selected allele from A and a randomly selected allele from B. If meiosis is regular, the correlations are identical. Differences between F_{ST} and θ can arise under particular systems of mating in groups of individuals (Cockerham, 1973), but estimates of θ can be considered estimates of F_{ST} (Weir & Cockerham, 1984).

2.7.3 Estimating F_{ST}

The most commonly used method of estimating F_{ST} is that of Weir & Cockerham (1984). They actually derive an estimator, $\hat{\theta}$, of θ, but they consider that their formula also serves as an estimator of F_{ST} (it should be noted that $\hat{\theta}$, not θ itself, is the estimator of F_{ST}). Weir & Cockerham use this particular notation, because they consider θ to be a parameter unambiguously, whereas F_{ST} has been defined both as a parameter and its estimator.

Weir and Cockerham (1984) used an analysis of variance approach to derive an expression for $\hat{\theta}$. Consider a single locus with two alleles A and a with overall frequencies p and (1-p) respectively. Arbitrarily assign values of X=1 for A and X=0 for a. If X_{ijk} denotes the value (0 or 1) for the ith allele in the jth individual in the kth population, then the total variance of X can be partitioned as follows:

$$X_{ijk} = p + a_k + b_{jk} + w_{ijk}$$

where a_k represents the difference (from overall p) in the frequency of A in population k (with variance of the set of a_k equal to σ_a^2), the b_{jk} denote differences between individuals within populations (variance σ_b^2), and the w_{ijk} represent differences between alleles within individuals (variance σ_w^2). The total variance of $X = p(1-p) = \sigma_T^2 = \sigma_a^2 + \sigma_b^2 + \sigma_w^2$. Let $\hat{\sigma}_a^2$, $\hat{\sigma}_b^2$ and $\hat{\sigma}_w^2$ (with $\hat{\sigma}_T^2 = \hat{\sigma}_a^2 + \hat{\sigma}_b^2 + \hat{\sigma}_w^2$) denote the analysis of variance sample estimates of the variance components.

The expected value of $\hat{\sigma}_a^2$ equals p(1-p)θ; so θ (and hence F_{ST}) can be estimated by

$$\hat{\theta} = \hat{\sigma}_a^2 / \hat{\sigma}_T^2$$

which is an estimator of the proportion of the total variance that is due to differences in the mean allele frequency among populations.

Weir & Cockerham take the above equation and modify it so that the estimates of the variance components are corrected for the (potentially) small number of subpopulations sampled and the (potentially) small and unequal number of individuals sampled within each subpopulation.

There are different ways of treating loci with more than two alleles and for combining data from several loci. Weir & Cockerham's (1984) suggested approach, which is widely used, is to calculate the overall $\hat{\theta}$ as

$$\hat{\theta} = \sum_r \sum_s \hat{\sigma}_{a(rs)}^2 / \sum_r \sum_s \hat{\sigma}_{T(rs)}^2$$

which is effectively an average of the individual $\hat{\theta}$ values ($\hat{\theta}_{(rs)} = \hat{\sigma}_{a(rs)}^2 / \hat{\sigma}_{T(rs)}^2$) for each allele s of each locus r, weighted by respective total variances ($\hat{\sigma}_{T(rs)}^2$). The simple, uncorrected form of the equation for $\hat{\theta}$ is used for clarity. A different approach to multiple alleles and loci has been proposed by Long (1986), but most standard population genetics computer programs (e.g. Goudet, 1995; Raymond & Rousset, 1995) use Weir & Cockerham's formula for $\hat{\theta}$ to calculate F_{ST} estimates from data from multiple loci and alleles.

2.7.4 Testing significance

Several methods have been proposed for testing the significance of $\hat{\theta}$. Weir & Cockerham (1984) suggested bootstrapping over loci when data are from multiple loci, and jackknifing over populations for single or small numbers of loci. The bootstrap approach has been criticised by Raymond & Rousset (1995a) and Van Dongen (1995) largely because most data sets have insufficient independent (i.e. unlinked) loci. Van Dongen (1995) suggested that more than 20 independent loci are necessary in order that the bootstrap distribution is more-or-less continuous and does not exhibit 'peculiar' properties because of the limited number of possible values the re-sampled estimate can take.

An alternative to bootstrapping is a one-sided randomisation test. Here alleles are randomly allocated among subpopulations, preserving the original sample sizes, and $\hat{\theta}$ is calculated from the randomised data. Multiple iterations (say 10000) of this procedure generates the distribution under the null hypothesis that $\theta = 0$. If the observed $\hat{\theta}$ is greater than 95% of the $\hat{\theta}$ values generated from randomised data, the null hypothesis (θ = 0) is rejected. If the estimate of F_{IS} is significant, alleles within individuals are not independent and the correct units of permutation are genotypes (Goudet, 1995). The testing of $\hat{\theta}$ is discussed in detail by Raymond & Rousset (1995b) and Goudet *et al.* (1996).

2.7.5 Testing significance of multiple comparisons

Rice (1989) stated that 'when a group of two or more tests are scanned and P values of the component tests are used to determine where significance occur, if no adjustment is made then the probability of a type I error increases monotonically with increasing number of tests'. In 100 tests, when the null hypothesis is true, then 5 significant tests will be obtained at the 5% level. When a large number of tests are performed the Bonferroni correction should be applied. The nominal level (e.g. 5 %) is divided by the number of tests to give the adjusted nominal level which is indicative only as some tests may not be possible. This method of correction is very conservative.

2.7.6 Temporal stability of the observed pattern of spatial differentiation

A test was devised (by R.T. Clark, CEH Dorset), to assess temporal stability of allele frequency by determining if the average F_{ST} between years at the same site was lower than the average F_{ST} between years at different sites. F_{ST} within sites between years ($F_{ST}W$) and F_{ST} between sites between years ($F_{ST}B$) was calculated and pairwise F_{ST} values were ranked. Q_1, the mean rank of pairwise $F_{ST}W$, and Q_2, the mean rank of pairwise $F_{ST}B$, were calculated. The test statistic Q is given by

$$Q = \frac{Q_1 - Q_2}{(n \times n/2)}$$

The significance of the test result was obtained by a Mantel type randomisation test. If return of adults is non-random then a higher temporal correlation of alleles at the same site is expected, Q_1 will be less than Q_2 therefore Q is negative.

2.7.7 Allelic richness

The observed number of alleles in a sample is highly dependent on sample size, therefore a measure of allelic 'richness' can be calculated (El Mousadik and Petit 1996). The expected number of alleles in a sub-sample of 2n genes is estimated, given that 2N genes have been sampled $(N \geq n)$.

Allelic richness, Rs,

$$Rs = \sum_{i-l}^{n} \left[1 - \frac{\binom{2N-Ni}{2n}}{\binom{2N}{2n}} \right]$$

where Ni is the number of alleles of type i among the 2N genes. Each term under the sum corresponds to the probability of sampling allele i at least once in a sample of size 2n. If allele i is so common that we are certain to sample it -when 2n > (2N-Ni)- the ratio is undefined but the probability of sampling the allele is set to 1. The programme FSTAT v2.9.3. (Goudet 2001) uses the above formula for Rs; over all samples, the same sub-sample size n is kept, but N is altered to the overall samples number of individuals genotyped at the locus. Allelic richness, standardised per individual, can be used to compare genetic variability between sites and also between studies.

2.7.8 Assignment of 1 + parr

1 + parr were assigned to the reference population using a likelihood frequency-based method devised by Paetkau et al. (1995). An individual is assigned to the population in which that individual's genotype is most likely to occur. Multilocus assignment is the product of the assignment likelihoods for each locus. When an allele in the individual is absent from the population sample, the estimate of the corresponding allele frequency is zero, thus eliminating the population. However, the allele may be rare and therefore not represented in the sample. This problem can be overcome by replacing null frequencies by a small constant frequency (0.01). The set of reference populations may not include the true population of origin of an individual, thus a confidence measure is obtained. Multilocus genotypes are simulated by randomly taking alleles according to population frequencies.

2.8 Objectives

Survey the rivers Frome and Piddle to identify the distribution and density of juvenile *S. salar* and estimate stability over three consecutive years.

Estimate the level of genetic variability of *S. salar* within the Rivers Frome and Piddle and determine the extent, pattern and temporal stability of genetic differentiation, over three consecutive years.

Analyse factors such as differences in environmental variables, which may cause genetic differentiation within a river.

Estimate changes in genetic variation in the Frome *S. salar* population since 1963, using DNA extracted from scales sampled from adults returning to spawn, and relate genetic changes to changes in population size and age structure.

3. METHODS

3.1 Sites

The Rivers Frome and Piddle discharge into Poole Harbour, Dorset, UK. Twenty sites were sampled on the River Frome and two sites were sampled on the River Piddle (Table 3.1.1) For site locations see site map, section 3.8.

Table 3.1.1 Juvenile *S. salar* sample sites on the Rivers Frome and Piddle, Dorset

	Site code
River Piddle	
Trigon Farm	TF
Bere Stream	BS
River Frome	
West Holme	WH
E. Stoke Millstream	ESMS
East Stoke	ES
Wool Stream	WO
Bindon Millstream	BM
Waterbarn Stream	WS
East Burton	EB
Tadnoll Winfrith	TW
Dereck's Tadnoll	DT
Tadnoll Knap Mill	TK
Moreton Carrier	MC
Moreton Ford	MF
Norris Mill Farm	NF
Lewell Mill	LM
South Winterbourne	SW
Dorchester Sewerage	DS
Greys Bridge Carrier	GB
Railway	RW
Whitfield Hatches	HA
Muckleford Bridge	MB

3.2 Sampling

Over 2300 salmon parr were sampled at 7 occasions over three years. 16 sites were sampled in July 1998, 16 sites were sampled in September 1998, 5 sites were sampled in November 1998, 16 sites were sampled in July 1999, 16 sites were sampled in September 1999, 15 sites were sampled in July 2000 and 14 sites were sampled in October 2000 (Table 3.2.1). Due to the small numbers of juveniles present at sites Dorchester Sewage Works (DS) and Dereck's Tadnoll (DT) in 1998, these sites were not sampled in following years.

Table. 3.2.1 *S. salar* juveniles sampled from sites on the Rivers Frome and Piddle at seven sample times

Sample time	Sites sampled
July 1998	GB NF LM EB ES ESMS WS HA MB TW SW WO MC MF DT DS
September 1998	GB NF LM EB ES ESMS WS HA MB TW SW WO MC MF DT DS
November 1998	GB ESMS WS BM WO
July 1999	BS WH GB NF LM EB ES ESMS WS HA BM TW SW WO MF RW
September 1999	BS WH GB NF LM EB ES ESMS WS HA MB BM TW SW WO MF
July 2000	BS WH GB NF LM EB ES ESMS WS HA BM TW SW WO MF
October 2000	BS GB NF LM EB ES ESMS WS HA MB BM SW WO MF

Quantitative samples of juvenile salmon were taken from each of the pre-determined sites, using multiple shock, catch depletion, electric fishing methods. Each site was electric fished at 100 Hz pulsed dc, with stream width determining the use of either single or twin anodes. Population estimates (exact minimum likelihood) were calculated from the multiple shock catch data at each site using the program "Remove 2" (Clarke 1992). Where very low numbers of fish were caught and population estimates could not be calculated, densities based on the total number of fish caught were used as the best minimum density estimate.

All salmon parr were retained in bins and fork length measured to the nearest mm. 0+ salmon were sedated in 2 Phenoxyethanol and a small portion of one of the pelvic fins removed from each individual. This was preserved in absolute ethanol for subsequent DNA analysis. Alternate fins were clipped at adjacent sites to provide an indication of subsequent parr mobility and/or migration. Scales were removed from any salmon parr thought to be older than 0+ to determine the age. After processing, all fish were returned to the same section of river alive. On the September/October surveys of each year, pelvic fins were examined for previous clips and recorded accordingly to assess recapture efficiency.

To make a crude assessment of the potential predators present at each site, pike (>20cm), eels (>30cm) and trout (>15cm) were counted during the first shock. This did not provide an estimate of population size or density but did however provide a standard comparison between sites to assess the relationships between the number of potential predators and the population size of salmon parr.

3.3 Habitat quality and availability

An independent, predictive model, based on a series of real, physical habitat and geographical measurements, called HABSCORE, was used to assess the quality of available habitat at each site and whether sites were at full carrying capacity for 0+ salmon. HABSCORE is a system for measuring and evaluating stream habitat features and can be used to evaluate the suitability of the stream for salmonid fish. It is based on species and age-specific empirical statistical models, which relate predicted fish populations to observed habitat variables.

When the electric fishing survey was completed at each site, 'HABSCORE V' HAB*forms* were completed for the same section of river. HABSCORE was recorded on a standard questionnaire

form. Data from the completed forms were then put into the HABSCORE software package and the model run to obtain the predictions. Two output values are generated; the Habitat Quality Score (HQS) and the Habitat Utilisation Index (HUI). The HQS gives predicted estimates of fish abundance at each site, expressed as the expected density of fish per $100m^2$ of streambed, under "pristine" conditions. The HUI is a measure of the extent to which the habitat is used by salmonids (estimated by difference between the observed density and the HQS). These two values give the theoretical natural carrying capacity of the stream.

For this study version V of the model was used as this is designed to be suitable for all river and stream types and not just (as with earlier versions of the model) upland streams. Data collected for HABSCORE have also been used to determine any intra-site variation in habitat, between surveys and to establish any relationships between habitat/geographical factors and population density or growth rate.

3.4 Parr growth rate

The growth rate of the fish at each site was assessed by comparing the Instantaneous Growth Rate (G) of the fish (the growth over a unit of time) between sampling times.

$$G = \log_e w_2 - \log_e w_1 / \Delta t \qquad \textit{Eqn 3.4.1}$$

Where w_1 and w_2= mean weight of fish at time t_1 and t_2 respectively.

Variable river conditions between years meant that whilst the summer sampling was always carried out in July the autumn sampling time varied. In 1999, for example, river conditions resulted in some sites being sampled in September and some in October. For this reason the value for the time interval (Δt) was taken as the number of days between sampling.

Three values of G were calculated for each year.
A/ Growth between 1st May and the July sampling date (assuming a weight of fish of 0.15 g on 1st May (Elliott & Hurley 1997)).
B/ Growth between the July sampling and the autumn sampling.
C/ Growth between 1st May and the autumn sampling.

In all cases weights were calculated from observed lengths using the equation

$$W(g) = aL(cm)^b \qquad \textit{Eqn 3.4.2.}$$

Values of a = 0.01313 and b = 2.9058 were taken from published length / weight coefficients for juvenile salmonids in October (Crisp et al 1997).

3.5 Genetic analysis

3.5.1 DNA extraction

DNA was extracted following a modification of the Beacham and Dempson (1998) method. One fin clip was digested in 300 µl of Chelex Buffer A (5 % Chelex, 100 mM NaCl, 50 mM Tris, 1% Triton, 10mM EDTA) with 3 mg proteinase K and 0.1 mg RNAse, overnight at 37 °C with rotation. The supernatant was removed from digested samples, 300 µl of Chelex Buffer B

was added and extracts were stored at –20 °C. This is a very rapid extraction technique and minimises the risk of cross transfer of samples.

3.5.2 Microsatellite primer selection and optimisation

Over 40 salmonid microsatellite primers sequences are published which have potential use for characterising *Salmo salar* genetic variability. Primers cloned from *Salmo salar* will be most likely to amplify scorable products, however, previous studies have shown that primers can amplify across species, therefore primers cloned from *Salmo trutta*, *Oncorhynchus* sp. (Pacific salmon) and *Salvelinus* sp. (Charr) may be useful. Primers were selected on the basis of published information regarding product size polymorphism and heterozygosity. Primers amplifying a small product were preferred; smaller product size is especially important if DNA is degraded. Tetranucleotide repeats were preferred due to reduced likelihood of stutter bands. The extent of previous publication for use to characterise population structure was also considered.

Fifteen primers, cloned from *S. salar* were selected; Ssa 202, Ssa 171, Ssa 197 (O'Reilly et al. 1996), Ssa 289 (McConnell et al. 1995a), Ssosl 85, Ssosl 417 (Slettan et al. 1997), Ssa 4, Ssa 14 (McConnell et al. 1995b), Ssa 85 (O'Reilly et al. 1996), Ssosl 438, Ssosl 439, Ssosl 444, (Slettan et al. 1997), F43, 20.19 and D30 (Sanchez et al. 1996) and tested using DNA extracted from River Frome *S. salar* fin clips. For details of published microsatellite repeat structure, size and heterozygosity for these primers see Appendix Section 7.3.5., Table 7.3.5.1. Two primers, cloned from *S. trutta,* μ60 (Estoup et al. 1993) and μ73 (Estoup et al. 1993), and two primers cloned from *Oncorhynchus,* Ogo1a (Olsen et al. 1998) and F_{GTI} (Sakamoto et al. 1994), were tested using DNA extracted from fin clips, despite no previous publications for use in *S. salar*. For details of published microsatellite structure, size and heterozygosity for these primers see Appendix Section 7.3.5., Table 7.3.5.2.

Previous studies have used primers from species other than *S. salar*, for example, μ3, μ79.1 and μ79.2 cloned from *S. trutta* (not published, source quoted in Tessier et al. 1997), Omy 27 and Omy 28 (C. Herbinger, not published) cloned from *Oncorhynchus* and Sfo-23, cloned from *Salvelinus* (Angers et al. 1995). These primers were not used due to difficulties in obtaining the primers sequences and also due to the problem that primers from more distantly related species are less likely to amplify the correct product, may have a large degree of stutter or may be monomorphic. For details of published microsatellite structure, size and heterozygosity for primers μ3, μ79.1, μ79.2, Omy 27, Omy 28 and Sfo-23, see Appendix Section 7.3.5., Table 7.3.5.3.

Further primer sequences, cloned from *S. salar* are available, however, eight 'Ssosl' primers cloned from *S. salar* by (Slettan et al. (1997) were not selected as these have not previously been used for population studies, some have large products and had overlapping products. Three primers cloned by Martinez et al. (1999) were also not selected as the products had a high degree of stutter. For details of published microsatellite structure, size and heterozygosity for these primers see Appendix Section 7.3.5., Table 7.3.5.4.

PCR conditions were determined experimentally, as published conditions were generally too stringent. DNA concentration was not quantified and an arbitrary amount of 0.2 μl was used as a template in a reaction mix of standard buffer, amount of Taq and standard $MgCl_2$, primer and dNTP concentration. TMAC and formamide were added to some reactions to increase specificity.

3.5.3 PCR conditions

PCR amplifications were performed in 10 µl reaction volumes using 0.2 µl DNA extract, 10 mM Tris, 50 mM KCl, 15 mM $MgCl_2$, 1 % Triton 100, 1.0 mM dNTP, 2 pmol forward and 2 pmol reverse primer and 0.01 µl Taq DNA polymerase. Amplification was performed on a Hybaid 96 well OmnE, using the cycle profile: 2 min at 95 °C x1; 1 min at 94 °C, 30s at AT[a], 40 s at 72 °C x5; 1 min at 90 °C, 1 min at AT[b], 50s at 72 °C x28. TMAC and formamide were added to some reactions to increase specificity. Generally a lower annealing temperature (AT) than the published AT was used.

3.5.4 Product visualisation and scoring

PCR products were visualised to single base resolution on 6 % denaturing polyacrylamide gels and stained with silver staining kit (Promega). Alleles were scored on the basis of relative size and reference samples were used to standardise scoring across gels. A 100 bp ladder and a 25 bp ladder (Promega) were used to size products.

3.6. Genetic analysis of scale samples

Scales were removed by anglers from adult *S. salar* migrating upstream in the river Frome. Scales were stored dry in envelopes at room temperature. The age of the fish was determined by counting the number of scale rings, however, age information was not determined for all of the scale samples. DNA was extracted from a 1421 scales, using the modified Chelex method (Section 3.5.1) and genetic variability was assessed using microsatellite markers (Sections 3.5.2. to 3.5.4).

3.7 Statistical analysis of genetic variability and population structure

Allele frequency data were used to estimate genetic variation and population structure. Number of individuals per sample site and over all sites were calculated per sample time and allele frequencies per sample site and over all sites were estimated. Genetic diversity was calculated per locus, per site and over all sites at each sample time. Number of alleles, observed heterozygosity and expected heterozygosity under Hardy-Weinberg equilibrium were calculated using the programme FSTAT v2.9.1. (Goudet 2000) and allelic richness standardised per individual was calculated using FSTAT v2.9.3. (Goudet 2001).

Observed heterozygosity (Ho) was calculated using $Ho = 1- \Sigma_k \Sigma_i P_{kii}/ np$, where P_{kii} is the frequency of genotype AiAi in the sample k and np is number of samples.

Expected heterozygosity weighted by sample size, was calculated using

$$H_{sk} = \frac{n_k}{n_k - 1}\left(1 - \sum p_{ik}^2 - H_{ok}/2n_k\right)$$

where n_k is the size of sample k, P_{ik} is the frequency of allele A_i in sample k and H_{ok} is the observed proportion of heterozygotes in sample k.

Weir and Cockerham's (1984) estimators of F, θ and f were used to characterise population structure. F, θ and f are considered to be estimators of Wright's (1951) F statistics; F_{IT}, F_{ST} and F_{IS} respectively.

Comparisons between sample times for Ho, Ht, F_{IS} and F_{ST} was calculated using a between-groups test, FSTAT v2.9.3 (Goudet 2001). For each group the average (over samples and loci) of the chosen statistic was calculated then OS_x was calculated using equation 3.7.1.

Equation 3.7.1.

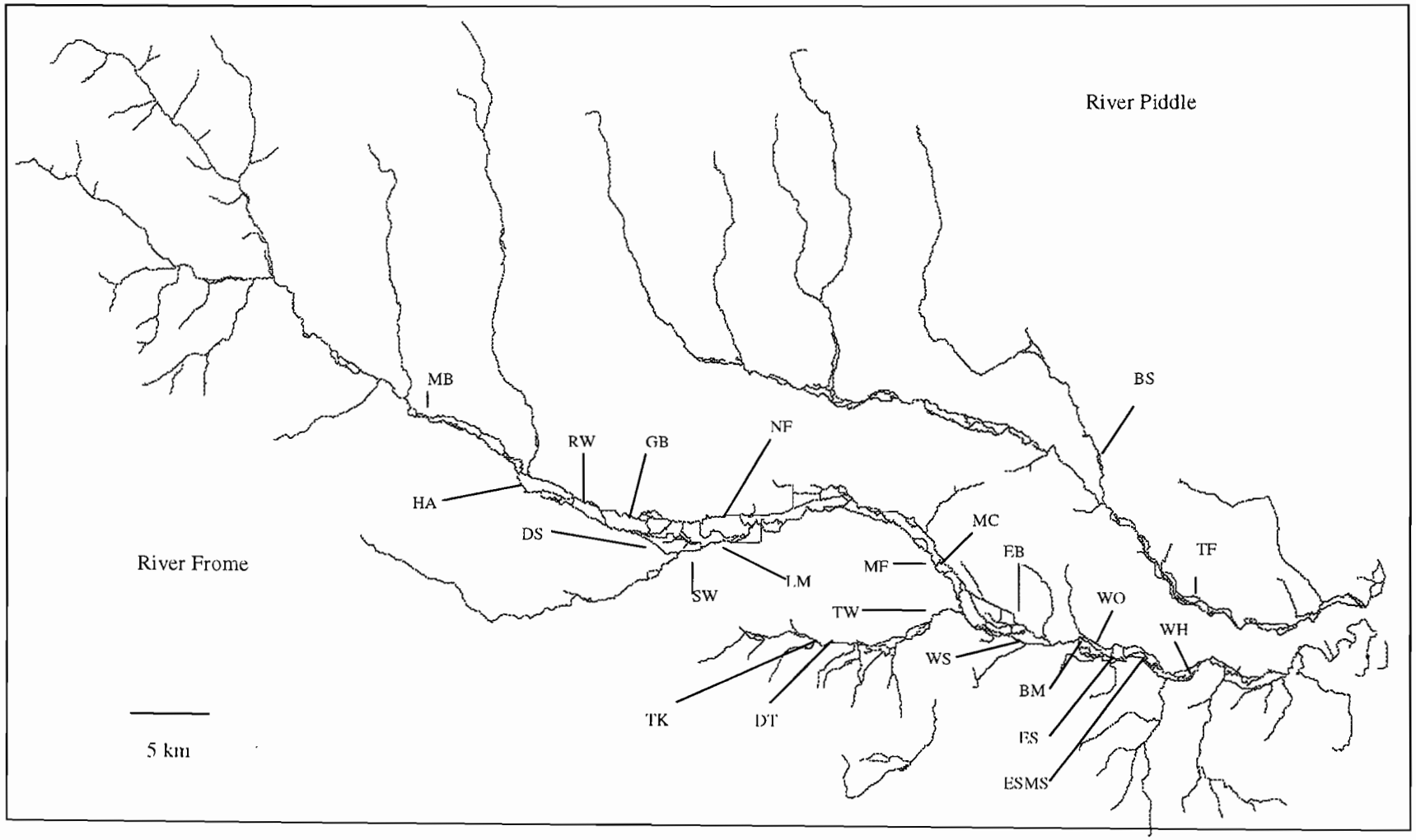
$$OS_x = \sum_{i=1}^{nbsubgrps-1} \sum_{j=i+1}^{nbsubgrps} (x_i - x_j)^2$$

Permutation was used to assess the significance of the statistic OSx. Whole samples were allocated at random to the different groups (keeping the number of samples in each group constant), and Sx calculated from the randomised data set. The P-value of the test is the proportion of randomised data sets giving a larger Sx than the observed OSx.

The significance of correlation between pairwise F_{ST} and geographic distance was tested using Mantel randomisation. The temporal stability of observed spatial differentiation was tested by estimation of temporal allele frequency stability, using a method devised by R. T. Clark (Raybould et al., in press). Parr of 1+ age group were assigned to the reference population using GeneClass v1.0.2 (Cornuet et al. 1999) (programme http://www.ensam.inra.fr/YRLB/geneclass.html).

3.8 Location of 22 sampling sites on the rivers Piddle and Frome, Dorset

Sites were plotted onto the river network using a map based on digital spatial data licensed from the Centre for Ecology and Hydrology Moore (1994)



River Piddle
TF Trigon Farm
BS Bere Stream

River Frome
WH West Holme
ESMS East Stoke Millstream
ES East Stoke
WO Wool Stream
BM Bindon Millstream
WS Waterbarn Stream
EB East Burton

TW Tadnoll Winfrith
DT Dereck's Tadnoll
TK Tadnoll Knap Mill

MC Moreton Carrier
MF Moreton Ford
NF Norris Mill Farm
LM Lewell Mill
SW South Winterbourne
DS Dorchester Sewerage
GB Greys Bridge Carrier
RW Railway
HA Whitfield Hatches
MB Muckleford Bridge

4. RESULTS

4.1 Sampling

Juvenile *S. salar* were sampled by electric fishing from the rivers Frome and Piddle at seven sample times; July 1998, September 1998, November 1998, July 1999, September 1999, July 2000 and October 2000. A total of 22 sites were sampled however, a maximum of 16 sites was electrofished at any one time.

Over all sample times, 33 1+ parr were sampled from 9 sites on the River Frome and one site on the River Piddle, the Bere Stream (Figure 4.1.1.). No parr older than 1+ were sampled. It is possible that some 1+ parr were precociously mature. Maturity of precocious parr can only be determined after dissection; in this study it was deemed important that all parr were returned to the river alive, therefore the percentage of precocious parr was not assessed.

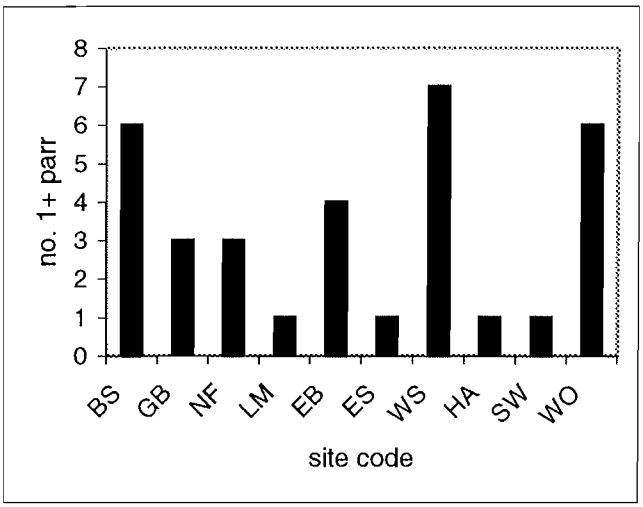


Figure 4.1.1 Number of 1+ parr sampled in the rivers Frome and Piddle, combined total per site for 1998, 1999 and 2000

4.1.1 Electric fishing efficiency

Electric fishing efficiency is affected by many factors including width and depth of the stream, discharge, turbidity and macrophyte biomass as well as operator differences. In this study, the fishing team remained constant thus reducing error. Electric fishing efficiency was calculated for each site on each occasion (Table 4.1.1.). Electric fishing efficiency was generally very high, falling below 60% on only four occasions.

4.1.2 Parr mortality

It was assumed that most density-dependent mortality had taken place before the July sampling times, when fish were marked, however, there would have been some further natural mortality. Although there is no direct assessment of mortality of parr due to fin clipping, all fish were held in recovery bins after marking, and all were released in good condition. Thus mortality due to this process was considered minimal. The possibility of mortality of marked parr between Summer and Autumn samples must be taken into account when estimating the percentage of individuals recaptured at a site in Autumn.

4.1.3 Mark-recapture estimates

Removal of a fin clip from each fish for genetic analysis gave the opportunity to investigate site fidelity of salmon parr. Percentage recapture gives an estimate of site fidelity, however, efficiency of electric fishing and the possibility of parr mortality must be taken into account. Recapture rates varied between 0% and 90%, and varied both between sites and between years (Table 4.1.1.). Recapture rates were adjusted by the electric fishing efficiency for each site to give the best estimate of the recapture rate. More than 10% recovery of marked fish was found for 70% of the sites and in one quarter of sites >25% recapture was recorded. The results show high fidelity to site for salmon parr over the period July to September in each year although results are low enough in most places to be certain that genetic samples come from several spawning sites and are not just the progeny of a single set of parents.

Table 4.1.1 Percentage recapture of salmon parr, originally fin clipped in June, at 13 sites on the River Frome, Dorset. The values given in column 1 for each year were recalculated using the efficiency of electric fishing to give the best estimate of recapture rate (middle column).

	Sep-98			Sep-99			Oct-00		
SITE	% Recapture	Recalculated from EF efficiency	EF efficiency	% Recapture	Recalculated from EF efficiency	EF efficiency	% Recapture	Recalculated from EF efficiency	EF efficiency
Whitfield Hatches	57	81	70	0	0	65	24	28	86
G B Carrier	44	65	68	23	28	83	24	29	83
South Winterbourne	43	45	95	30	51	59	15	18	85
North Stream (NMF)	4	5	80	9	13	67	10	14	71
Lewell Mill	23	37	62	14	17	81	10	14	72
Moreton Ford	4	6	68	14	15	91	6	7	83
Tadnoll Heath	22	27	82		0	94	43	59	73
East Burton	10	23	44	30	71	42	4	6	68
Waterbarn Stream	13	17	76	28	62	45	3	4	83
Bindon Mill Stream	13			3	4	70	8	9	90
Wool stream		0	86				9	11	84
E Stoke	13	15	87	40	63	64	0	0	67
ESMS	35	39	89	90	106	85	12	16	75

4.1.4 Parr density

Density of 0+ parr was estimated from the standard catch depletion method. The variation in density between sites in any year was high. Per site density varied between 0.19 and 14.7 individuals per 100 m^2 in July 1998, between 1.02 and 15.08 individuals per 100 m^2 in September 1998, between 0.252 and 6.97 individuals per 100 m^2 in November 1998, between 0.027 and 22.13 in July 1999, between 0.088 and 12.75 individuals per 100 m^2 in September 1998, between 6.3 and 49.49 individuals per 100 m^2 in July 2000 and between 1.7 and 10.13 individuals per 100 m^2 in October 2000 (Table 4.1.2.).

Table 4.1.2 Density of 0+ salmon parr in the River Frome at 19 sites in the study period 1998-2000 (*= not sampled)

Site	JULY 1998	SEPT 1998	NOV 1998	JULY 1999	SEPT 1999	JULY 2000	OCT 2000
Muckleford Bridge	0.19	3.72	*	0.11	2.54	*	3.72
Whitfield Hatches	0.82	2.12	*	2.82	1.95	6.3	3.74
Dorchester S/W	0	1.02	*	*	*	*	*
Greys Bridge	1.54	7.45	3.01	4.92	4.29	8.55	7.59
South Winterbourne	3.43	4.27	*	7.12	6.82	29.97	5.79
Norris Mill	1.72	4.18	*	18.32	12.75	6.47	1.7
Lewell Mill	7.65	9.65	*	6.56	7.52	11.81	7.79
Morton Ford	14.7	13.69	*	7.11	2.54	10.82	7.2
Morton Carrier	0.92	1.31	*	*	*	*	*
Owermoigne Tadnoll	0	1.61	*	*	*	*	*
Knapp Tadnoll	0	0	*	*	*	*	*
Winfrith Tadnoll	2.71	3.86	*	3.31	8.7	0	3.65
East Burton	11.7	15.08	*	2.42	9.82	49.69	6.62
Waterbarn Stream	7.65	6.59	2.52	7.43	4.78	12.26	10.13
Wool Stream	0	4.24	5.12	2.76	3.27	24.01	8.19
Bindon Mill Stream	8.8	1.32	6.87	22.13	6.29	33.35	10.05
East Stoke	5.04	3.12	*	1.74	9.85	6.67	9.39
E. Stoke Mill Stream	1.76	5.52	2.75	6.09	6.01	10.11	7.66
West Holme	0	0	*	0.027	0.088	0	0

Density was independent of distance from source (Fig 4.1.2.). Density was independent of flow category of the river ($R^2 < 0.22$ for each of July and September samples in all years (Table 4.1.3.)). There were significant differences between years at many of the sites (non-overlapping confidence intervals) although there was no consistent pattern (Fig 4.1.2.). This variation depends not only on the habitat quality but also the density of spawning fish the previous year. Some sites where salmon parr were not found had suitable habitat for spawning and juveniles but the low number of spawning adults (<1000 compared to up to 4000 in the 1980s) indicates that overall the river is below its carrying capacity.

Table 4.1.3 R^2 values and significance of relationship between salmon parr density and flow rate category

Date	R^2	Degrees of freedom	Significance
JULY 1998	0.1546	14	NS
SEPT 1998	0.2217	16	NS
JULY 1999	0.1777	13	NS
SEPT 1999	4E-05	14	NS
JULY 2000	0.1753	11	NS
SEPT 2000	0.1287	13	NS

(NS not significant)

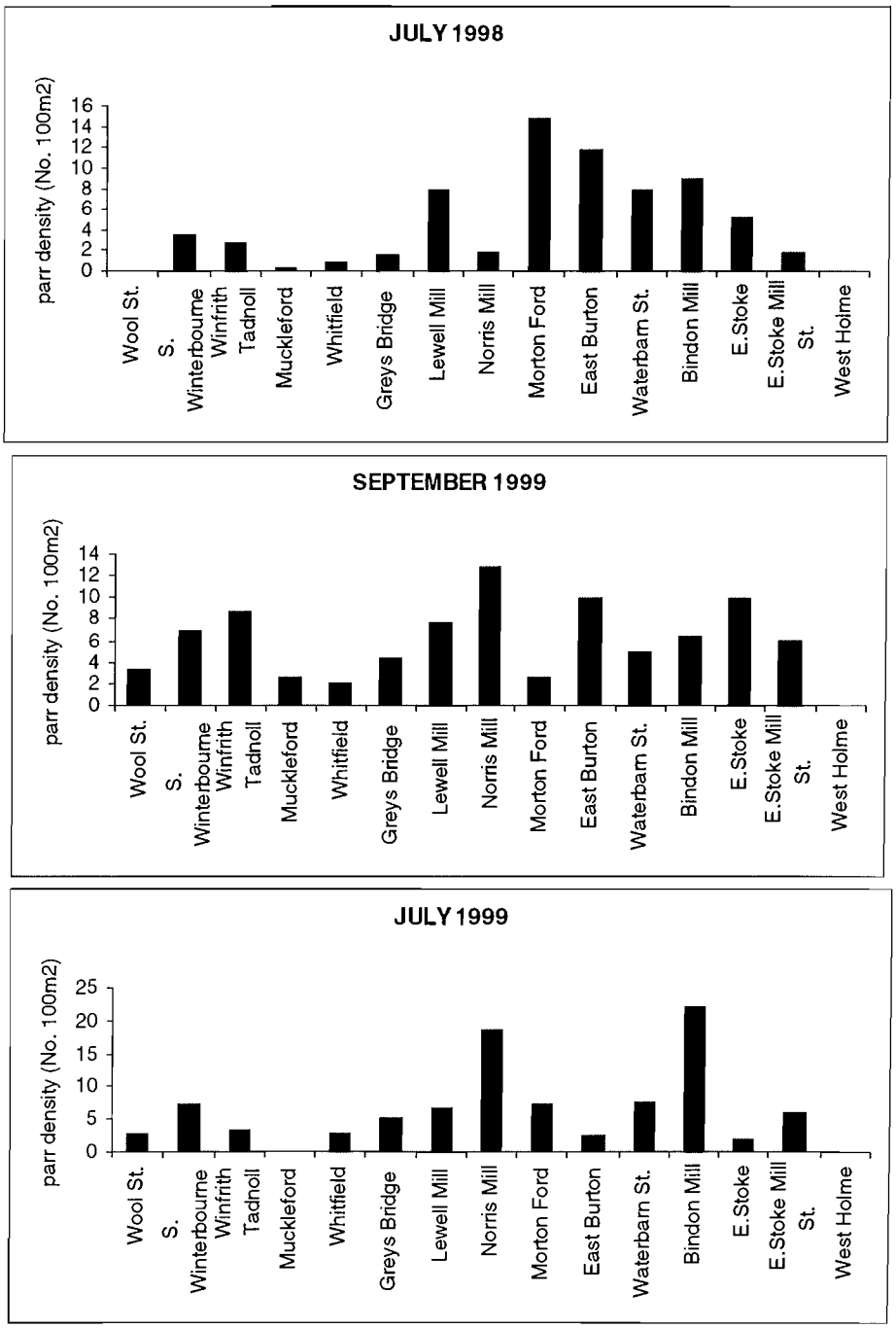


Figure 4.1.2 Density of salmon parr in the River Frome at 6 sample times
(Sites arranged by distance from source)

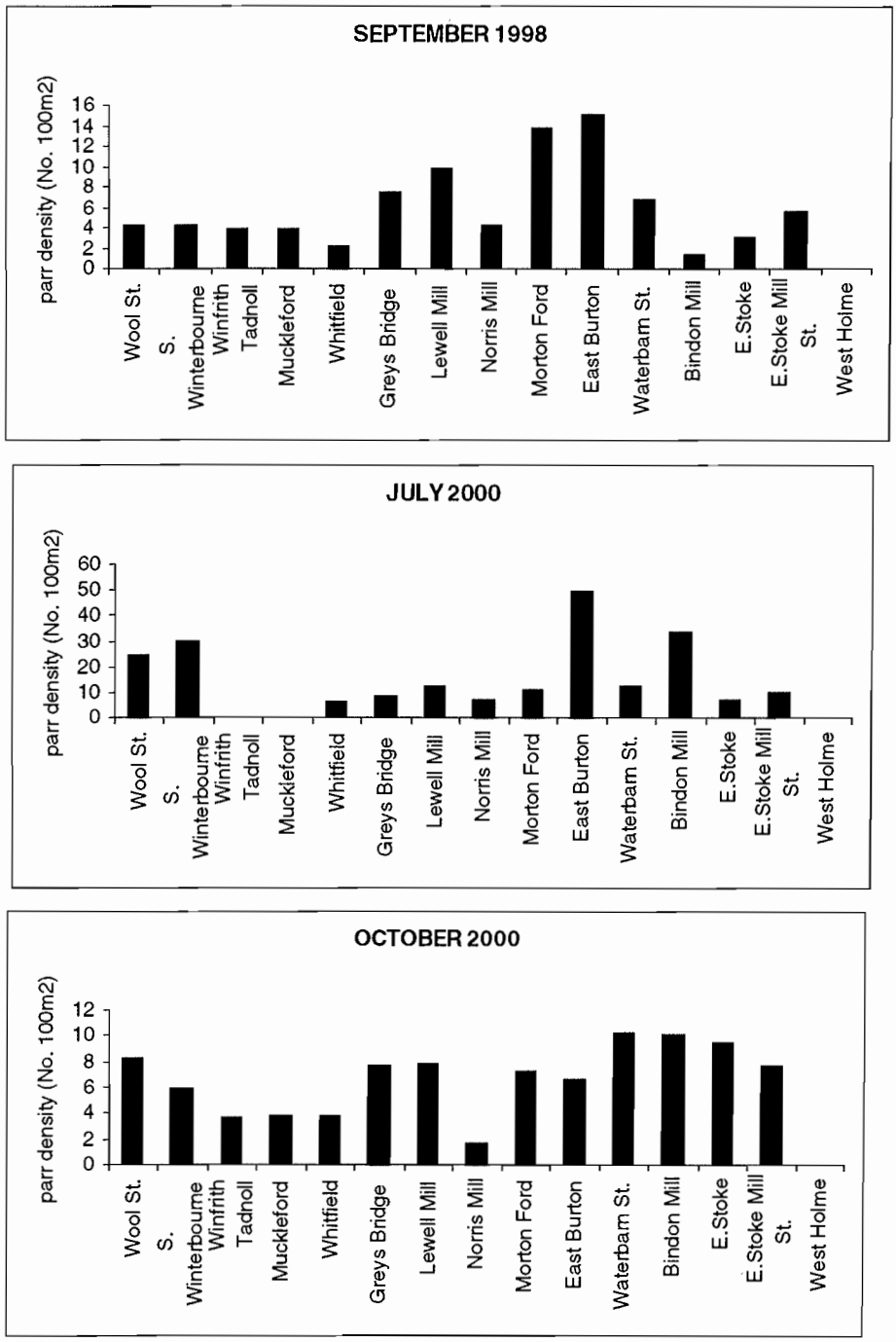


Figure 4.1.2 (Continued)

It was possible to determine density from mark recapture rates and to compare these with the more usual catch depletion method based on repeat electric fishing of a reach of river. In this study, fin clipping for genetic analysis provided such a mark and a density estimate was produced from the recapture data (Table 4.1.4.). The density estimates from mark recapture were higher than those for catch depletion. Catch depletion is the most robust method where electric fishing efficiency is high (as in this study) and this suggests that the number of recaptures was less than it should have been. Both methods depend on immigration and emigration from the study site being equal. However, immigrating individuals would have been unmarked whereas marked fish may have emigrated. This would account for the lower

than expected recapture rate and again is evidence that, although site fidelity is high (see above) there must have been some movement of parr into and out of the study reaches and therefore the sampling for genetic analysis was not necessarily limited to the progeny of a low number of pairs.

Table 4.1.4 Comparison of density estimates for salmon parr at each site using catch depletion (D_{CP}) and mark recapture (D_{MR}) methods

	Sep-98		Sep-99		Sep-00	
Site	D_{CD}	D_{MR}	D_{CD}	D_{MR}	D_{CD}	D_{MR}
Muckleford Bridge	3.72	3.45	0.11	2.2	3.72	*
Whitfield Hatches	2.12	3.43	2.82	*	3.74	16.08
Greys Bridge	7.45	15.8	4.92	18.63	7.59	32.08
S.Winterbourne	4.27	10.03	7.12	18.84	5.79	38.66
Norris Mill	4.18	105.0	18.32	108.14	1.7	57.8
Lewell Mill	9.65	36.51	6.56	54.36	7.79	70.76
Morton Ford	13.69	345.0	7.11	12.6	7.2	112.36
Winfrith Tadnoll	3.86	18.86	3.31	*	3.65	8.4
East Burton	15.08	99.02	2.42	22.4	10.13	226.8
Waterbarn Stream	6.59	45.99	7.43	14.57	6.62	194.37
Wool Stream	4.24	*	2.76	*	8.19	101.64
Bindon Mill Stream	1.32	*	22.13	231.46	10.05	108.53
East Stoke	3.12	23.0	1.74	16.51	9.39	*
E. Stoke Mill Stream	5.52	16.26	6.09	6.6	7.66	59.85
West Holme	0	*	8.8	*	0	*

4.1.5 Effect of predators on density

At the same time that parr were being sampled, information was collected on the number of large eels (>40 cm), large trout (>25 cm) and pike (all sizes) within each section as a possible indication of local predation pressures on stocks of juvenile salmon. In all three years in July, there was a significant inverse relationship between density of salmon parr and the number of predatory trout (Fig 4.1.3.). This may not be a causal relationship as salmon parr and adult trout are known to occupy different habitats. However, all sites were chosen to be good habitats for salmon parr and it is known that adult trout do eat juvenile salmon.

No relationships were found between salmon parr density and the number of predatory eels ($R^2 = 0.0003 - 0.36$, $p>>0.05$). From gut analysis studies, eels are known to eat salmon parr (Mann et al 1989 and pers obs.). Mann (1989) however found that salmon parr are not a large proportion of their diet and given that eels do not occupy the same habitat niche as salmon parr, interactions may be expected to be low; although it is not known whether eels migrate to salmon parr habitats at night to feed.

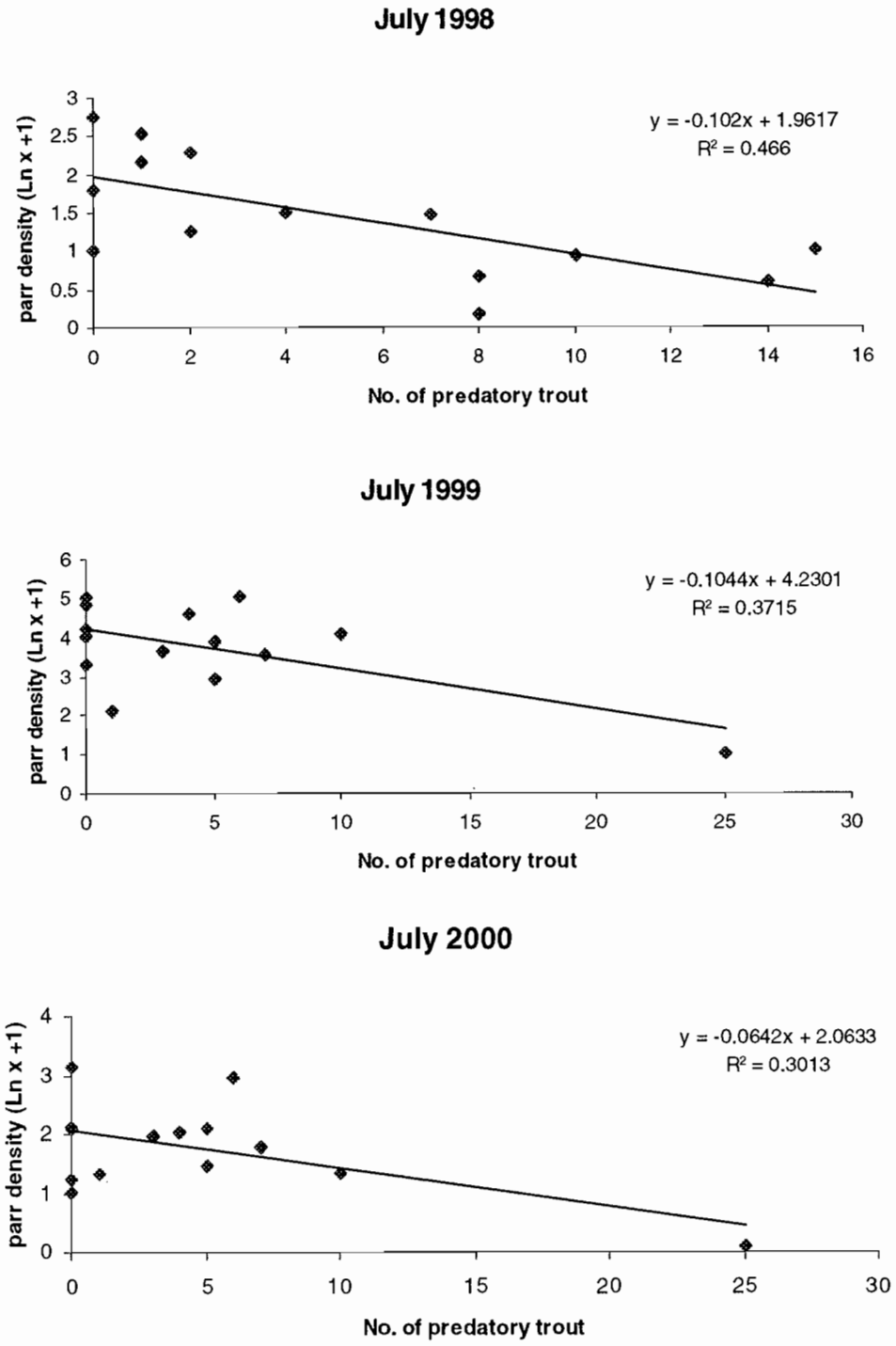


Figure 4.1.3 Relationship between the density of salmon parr and the number of predatory trout in the River Frome

4.1.6 Habitat characteristics

The distributions and population densities of juvenile salmon have been related to measured habitat characteristics determined on the basis of the established HABSCORE V methodology. HABSCORE is a model that, by calculating a Habitat Quality Score (HQS), attempts to predict potential densities of juvenile salmonids. Physical and biotic habitat characteristics are used in the model and it is believed to be an effective predictor of parr densities in all waters.

HQSs were determined for all sites sampled. Predictions depend heavily on link numbers, these are derived from the stream order and the number of tributaries of a given size upstream of a given site. In most cases, predicted scores (equivalent to the carrying capacity of the river at those sites) were far in excess of densities found by electric fishing surveys. Whilst this may have been expected, given the low numbers of salmon in the river compared with historical records, it was felt that the HABSCORE methodology was not appropriate to chalk streams. The scores were recalculated using only tributaries which were known to be appropriate habitats for salmon juveniles, as is the case in all other rivers where this method has been applied, but is not true for chalk streams. This reduced the HQS to a more realistic level.

Densities of salmon parr were related to the HQS as percentages (Table 4.1.5.). Thus values of <100 show densities below the carrying capacity and vice versa. Neither the HQS nor any of the individual habitat categories used in HABSCORE were correlated with parr density. Habitat characteristics used were percentages of submerged vegetation, turbulent shallow water, deep and shallow glides, deep and shallow runs. In all cases, scatter plots of density against percentage of each habitat characteristic showed no discernable pattern. It is clear from results (Table 4.5.) that densities over ten times the carrying capacity were found in places. It should be noted, however, that HABSCORE surveys should be conducted over a range of habitats in one reach. In this case, because large numbers of parr were needed for genetic analysis, sites and habitats were selected where there was a high probability of finding parr and thus the HQS value was based on an unrepresentative section. Given this, however, there was a large variation in density relative to HQS (Table 4.1.5.). For example, low values were found at Muckleford Bridge and Whitfield Hatches. These two sites are upstream of a gauging weir at Dorchester which is known to be a barrier to migration of adults (Solomon 2000). Four sites, Morton Ford, Waterbarn Stream, East Burton and Bindon Millstream showed consistently high results. The gravel at these sites had been pressure washed to remove fine sediment. The survival rate of eggs can be increased between one and two orders of magnitude in this way and is the probable cause of the results. Results also show the importance of side streams as nursery areas for salmon. These include carriers and millstreams, originally man made but now essential in the survival of this threatened species.

Table 4.1.5 Habitat Quality Score (HQS) values and density percentage of the HQS

	Jul-98		Sept-98		Nov-98		Jul-99		Sept-99		Jul-00		Sept-00	
	HQS	D as % of HQS	HQS	D as % of HQS	HQS	D as % of HQS	HQS	D as % of HQS	HQS	D as % of HQS	HQS	D as % of HQS	HQS	D as % of HQS
Muckleford bridge	34.03	1	6.59	56			4.67	19	13.41	2			54.1	28
Whitfield Hatches	41.54	2	27.09	8			7.86	13	15.08	36	111.1	24	36.68	40
Greys Bridge	3.16	49	11.5	65	35.79	8	4.38	39	10.96	112	2.88	1140	10.92	240
S. Winterbourne	4.71	73	0.91	469			4.85	336	2.03	147	14.55	776	2.64	793
Norris Mill	41.47	4	53.63	8			38.17	7	177.1	48	122.2	22	96.7	7
Lewell Mill	12.9	26	15.14	64			20.74	32	23.66	32	35.62	141	204.4	17
Morton Ford	0.7	2100	3.69	371			3.7	470	0.54	192	4.79	894	3.1	857
Winfrith Tadnoll	10.97	25	8.07	48			4.55	49	17.7	73	45.84	0	12.87	99
Waterbarn Stream	4.24	180	5.31	124	22.61	11	2.08	810	12.47	324	9.55	2004	2.6	988
E. Burton	16.66	70	5.25	287			2.29	79	0.59	116	21.09	255	44.77	104
Wool Stream	2.94	0	.68	624	0.44	1164	1.16	217	1.51	238	7.4	1072	6.75	431
Bindon Millstream	2.68	328	1.44	92	2.22	309	2.46	379	1.66	900	13.94	929	13.39	266
E. Stoke	9.81	51	3.62	86			1.23	82	12.02	141	6.94	570	1.89	3238
E. Stke Millstream	10.56	17	6.55	84	7.06	39	10.17	143	4.19	60	87.02	50	8.25	361

4.1.7 Parr length

Significant variation in parr length between sites was detected at each sample time ($p<0.001$). There was no relationship between mean parr length and distance from source ($R^2 = 0.02$-0.25, $p> 0.05$) except for one occasion (July 2000, $R^2 = 0.33$, $p<0.05$). A contributory factor in this is the braided sections of the river and the mill streams, where distance from source is not linked to flow but is dependent on the size and number of channel(s). Length is dependent on growth rate which in turn is influenced by temperature and food availability. Generally, rivers are more productive in the higher flow categories and for individual fish, feeding almost exclusively on drifting invertebrates, the rate of passage of food past their feeding station will increase with increasing flow category and although swimming costs will be greater, the net energy gain should be higher.

4.1.8 Parr growth rate

Comparisons were made between site density and growth rate. In 1998 July salmon parr density was significantly correlated with May to July, July to September and May to September Instantaneous growth rates. Whilst however July salmon parr density was significantly correlated with September density, no correlation between September density and any of the growth rates could be found. In 1999 no correlation between July or September density and growth rates were found; although July density and July to autumn and May to autumn growth rates were only just non-significant. The 1999 July and September densities were not correlated. In 2000 significant correlations were found between July parr densities and July to October and May to October growth rates but as with other years no correlation could be found with autumn densities and growth rates. The July and October parr densities were not significantly correlated.

4.2 Genetic Analysis

4.2.1 DNA extraction

DNA was extracted from 2099 fin clips and stored at –20 °C. DNA remained suitable for amplification by microsatellite primers even after storage for three years. Numbers of samples used for genetic analysis varied between sites and between years (Table 4.2.1 and Figures 4.2.1-4.2.7.)

Table 4.2.1 Numbers of samples used for genetic analysis for 7 sample times

Sample time	No. 0+ parr	No. 1+ parr
July 1998	448	None
September 1998	306	11
November 1998	36	None
July 1999	335	14
September 1999	289	1
July 2000	377	7
October 2000	308	none

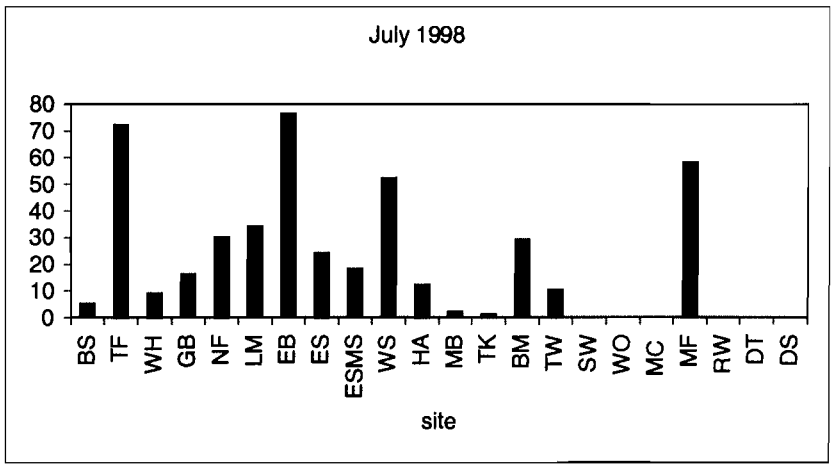


Figure 4.2.1 Number of juvenile *S. salar* analysed per site, Rivers Frome and Piddle, July 1998

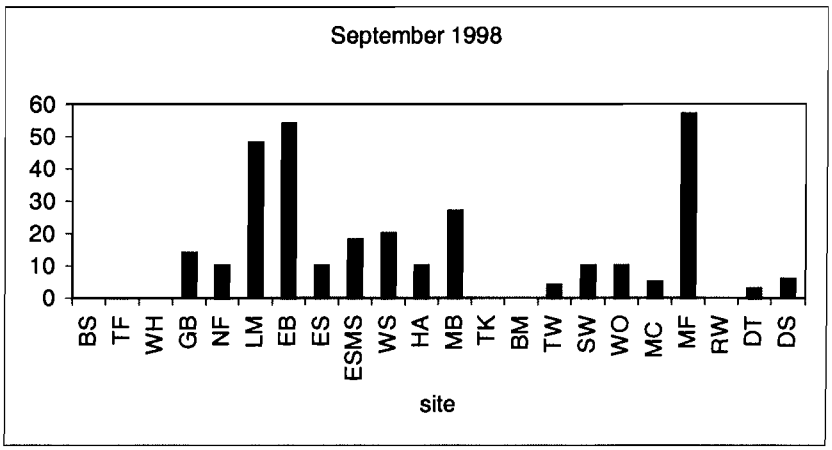


Figure 4.2.2 Number of juvenile *S. salar* analysed per site, Rivers Frome and Piddle, September 1998

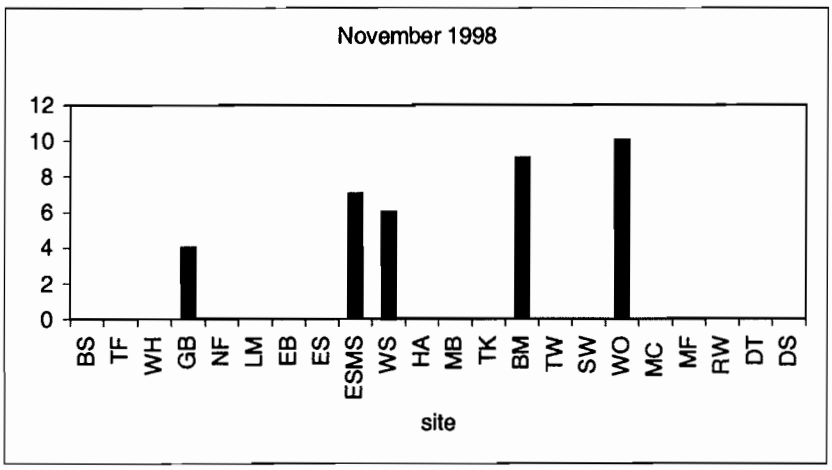


Figure 4.2.3 Number of juvenile *S. salar* analysed per site, Rivers Frome and Piddle, November 1998

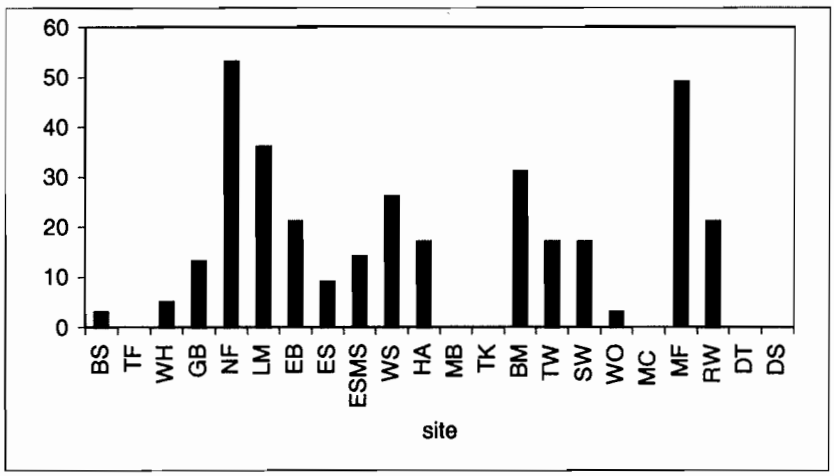


Figure 4.2.4 Number of juvenile *S. salar* analysed per site, Rivers Frome and Piddle, July 1999

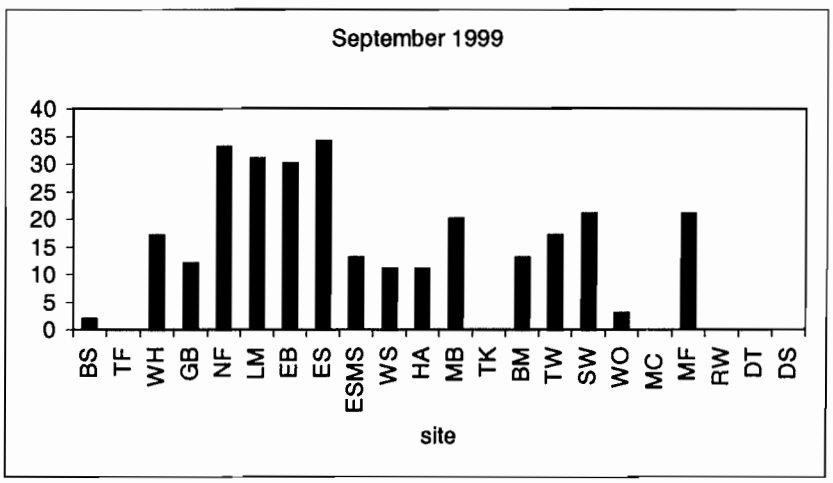


Figure 4.2.5 Number of juvenile *S. salar* analysed per site, Rivers Frome and Piddle, September 1999

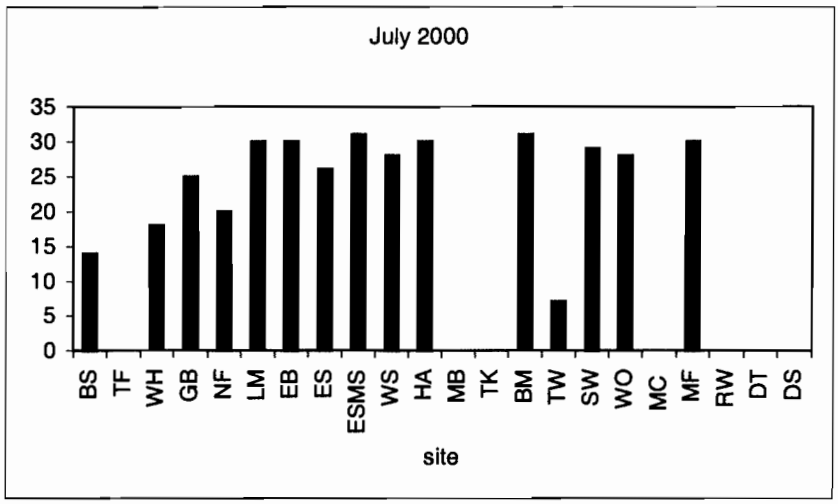


Figure 4.2.6 Number of juvenile *S. salar* analysed per site, Rivers Frome and Piddle, July 2000

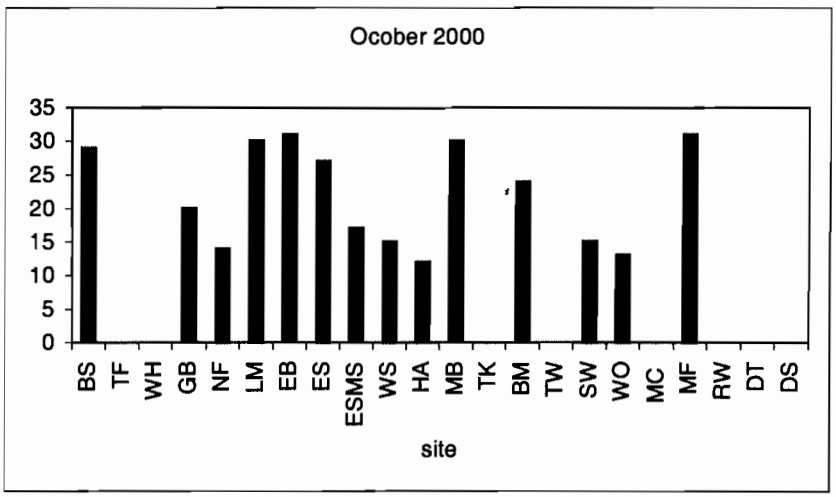


Figure 4.2.7 Number of juvenile *S. salar* analysed per site, Rivers Frome and Piddle, October 2000

4.2.2 Microsatellite optimisation

Of the 15 primers cloned from *S. salar* which were selected on the basis of product size, polymorphism and heterozygosity, PCR conditions were fully optimised for 6 primers; Ssa 202, Ssa 171, Ssa 197, Ssa 289, Ssosl 85 and Ssosl 417 (Table 4.2.2). These primers amplified products which were clearly resolved by size using polyacrylamide sequencing gels. One sample was loaded per lane. Products were visualised using silver staining. Individual fish were scored as either a homozygote (both alleles same size therefore only one band visible) or a heterozygote (two bands visible).

The amount of stutter visible at different loci was dependent on the structure of the microsatellite. Primers Ssa 202 (Figure 4.2.8), Ssa 171 (Figure 4.2.9) and Ssa 197 (Figure 4.2.10), amplify compound microsatellites and had less stutter bands than primers Ssosl 85 (Figure 4.2.11), Ssa 289 (Figure 4.2.12) and Ssosl 417 (Figure 4.2.13) which amplify dinucleotide microsatellites. Locus Ssosl 417 had a band smaller than the other band sizes which appeared in most samples; this band appeared in lanes possessing two larger

bands (Figure 4.2.13, lane 6) therefore this band was excluded from allele scores at this locus (Figure 4.2.14).

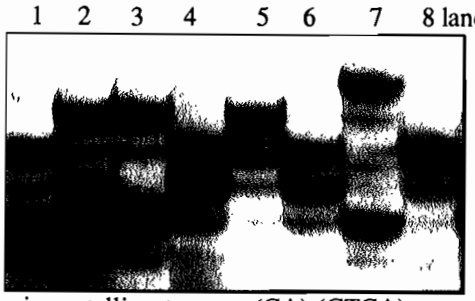
No PCR products were detected with primer Ssa 4 (McConnell et al. 1995) using River Frome *S. salar* DNA. Primer Ssa 14 (McConnell et al. 1995) amplified a monomorphic product when tested with Frome *S. salar* DNA. Primers Ssa 85 (O'Reilly et al. 1996) Ssosl 438, Ssosl 439, Ssosl 444 (Slettan et al. 1997), F43, 20.19, and D30 (Sanchez et al. 1996) required further optimisation.

Two primers cloned from *S. trutta,* μ60 and μ73 (Estoup et al. 1993), were not used to screen the population because a low number of alleles were detected and the amplification products had a large amount of stutter making scoring inaccurate. Of the two primers cloned from *Oncorhynchus* that were tested, primer Ogo1a was rejected due to amplification of monomorphic products, however primer F_{GTI} may be useful after further optimisation.

Table 4.2.2 PCR additives and Annealing Temperatures for 6 microsatellite primers

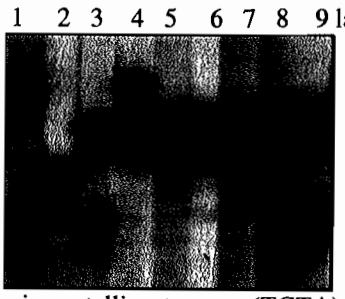
Locus	TMAC	formamide	AT^a/AT^b °C	published AT °C	ramp
Ssa 202	60mM	2.5%	46/50	58	0.5
Ssa 171	60mM	2.5%	46/50	58	0.5
Ssa 197	30mM	1.25%	50/54	58	/
Ssosl 85	/	/	52/56	55	/
Ssa 289	60mM	2.5%	44/48	46	/
Ssosl 417	/	1.25%	58/56	53	/

A ramp of 0.5 was added to the second 72 °C step for primers Ssa 202 and Ssa 171 to increase product yield



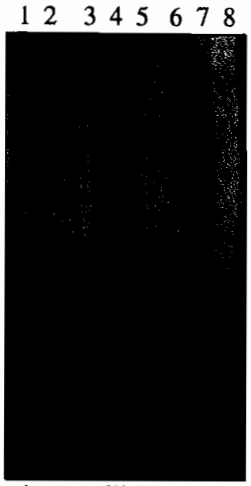
microsatellite structure $(CA)_3(CTCA)_7$

Figure 4.2.8 PCR-amplified microsatellite locus Ssa 202



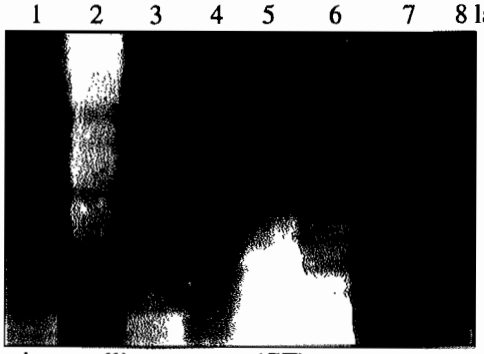
microsatellite structure $(TGTA)_{14}(TG)_7$

Figure 4.2.9 PCR-amplified microsatellite locus Ssa 171



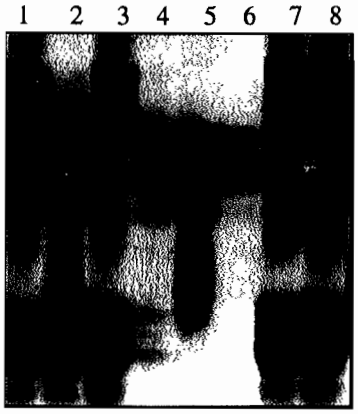
microsatellite structure $(GT)_5C(TG)_4TC(TG)_3A(GTGA)_{15}$

Figure 4.2.10 PCR-amplified microsatellite locus Ssa 197



microsatellite structure $(GT)_{22}$

Figure 4.2.11 PCR-amplified microsatellite locus Ssosl 85



microsatellite structure $(GT)_{12}$

Figure 4.2.12 PCR-amplified microsatellite locus Ssa 289

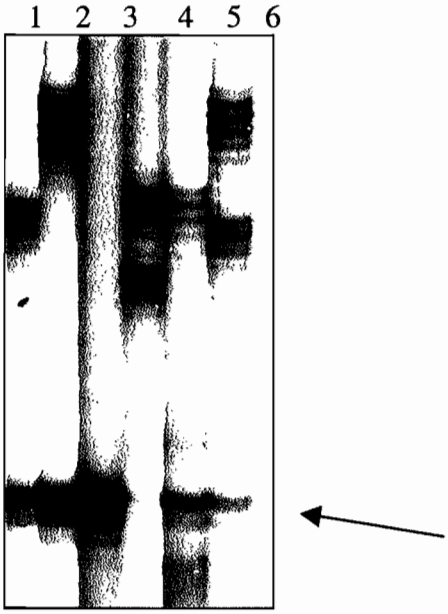
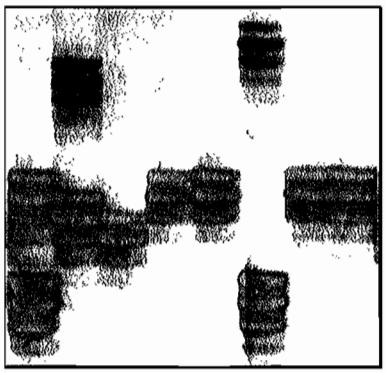


Figure 4.2.13 PCR-amplified microsatellite locus Ssosl 417 including small band



microsatellite structure $(TG)_{25}$

Figure 4.2.14 Locus Ssosl 417, bands used in analysis

4.2.3 Allele size

Alleles were sized using a 100 bp ladder and a 25 bp ladder. This does not allow sizing accuracy of 1 bp, however, size information was used only to compare the relative size ranges of alleles between *S. salar* in the river Frome and published allele size ranges for *S. salar* in other rivers. Allele sizes in bp were not used for analysis of population structure. Alelle sizes for loci Ssa 202, Ssa 171, Ssa 197, Ssosl 85 and Ssa 289 were generally in the same range as previously published allele sizes, however, allele sizes at locus Ssosl 417 were much larger than previously published allele sizes (Table 4.2.3).

Table 4.2.3 Allele size ranges for 6 *Salmo salar* microsatellite loci

locus	Rivers Frome and Piddle *approximate* allele size range bp	published allele size range bp
Ssa 202	250-300	270-320
Ssa 171	250-350	233-267
Ssa 197	200-350	150-200
Ssosl 85	175-200	177-204
Ssa 289	100-150	110-119
Ssosl 417	250-300	159-211

Between-study comparisons of allele sizes should be viewed with caution. At certain loci, some studies detected even sized products and some studies reported odd-sized repeats. For example at locus Ssa 202 $((CA)_3(CTCA)_7)$ Garant et al. (2000) reported odd sized products at intervals of 4 bp and Beacham and Dempson (1998) reported odd sized products at intervals of 4 bp, except for sizes 298 and 303. In contrast, Fontaine et al. (1997), reported even sized products. At locus Ssa 289 $((GT)_{12})$ McConnell et al. (1995) reported odd sized products of 2 bp, however, Beacham and Dempson (1998) reported even sized products of 2 bp difference. Beacham and Dempson (1998) suggested that allele 110 is equivalent to allele 113 in (McConnell et al. 1995). At locus Ssosl 85 $((GT)_{12})$ Garant et al. (2000) and Fontaine et al. (1997) reported even sized products of 2 bp difference, however, (Nielsen et al. 1999) reported odd sized products of 2 bp. At Locus Ssa 197 $((GT)_5C(TG)_4TC(TG)_3A)$ Garant et al. (2000) and Fontaine et al. (1997) reported even sized products of 4 bp difference. Beacham and Dempson (1998) reported even sized products of 4 bp difference, except for alleles 217 and 227.

Compound repeats may mutate at any of the structural units therefore products of a range of sizes may be obtained. It is possible that the PCR reaction added bases to the product. When product sizes are obtained that are not whole numbers, it is possible that differences in rounding up cause some studies to report odd numbers and some to report even numbers. It is possible that e.g. size 240 (Fontaine et al. 1997) is the same allele as size 241 (Beacham and Dempson 1998). Differences in rounding up or down will be more important with dinucleotide repeats.

4.3 Genetic variability

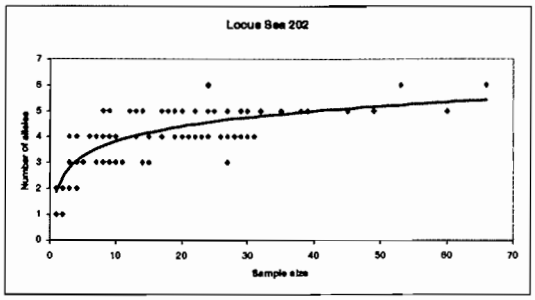
The genetic variability of juvenile *S. salar* sampled from the Rivers Frome and Piddle over three consecutive years was assessed using number of alleles per locus, allelic richness and percentage heterozygosity.

4.3.1 Number of alleles

The six loci used to screen the population for genetic variability were all polymorphic and the number of alleles detected (over all sites) per locus was between 5 and 13. The most highly polymorphic loci were Ssa 197 and Ssosl 85, having 13 alleles each. Twelve alleles were detected at locus Ssa 171, 10 alleles were detected at Ssosl 417 and seven alleles were detected at locus Ssa 202. The least polymorphic locus was Ssa 289 with 5 alleles.

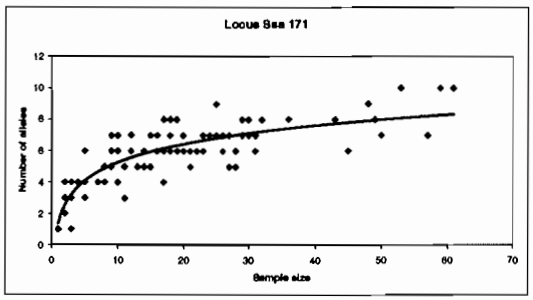
The numbers of alleles detected in the Rivers Piddle and Frome was lower than number of alleles detected in studies of *S. salar* in other rivers. At locus Ssa 197, 20 alleles were detected by Fontaine et al. (1997) (n = 181), 14 alleles were detected by Beacham and Dempson (1998) (n= 145) and 19 alleles were detected by Garant et al. (2000) (n = 343). At locus Ssosl 85, 11 alleles were detected by Fontaine et al. (1997) (n = 176), 16 alleles were detected by Nielsen et al. (1999) (n = 150) and 15 alleles were detected by Garant et al. (2000) (n = 343). At locus Ssa 171, 28 alleles were detected by Fontaine et al. (1997) (n = 173), and 33 alleles were detected by Garant et al. (2000) (n = 343). At locus Ssosl 417, 21 alleles were detected by Nielsen et al. (1999) (n = 150). At locus Ssa 202, 20 alleles were detected by Fontaine et al. (1997) (n = 171), 16 alleles were detected by Beacham and Dempson (1998) (n =113) and 16 alleles were detected by Garant et al. (2000) (n = 343). At locus Ssa 289, 6 alleles were detected by McConnell et al. (1995) (n = 55).

The number of alleles detected per locus is dependent on sample size, due to the presence of many low frequency alleles in natural populations (Nei 1987). It is possible that the differences between the numbers of alleles detected in this study compared to other rivers is due to differences in sample size. Although overall N was larger than 299 at each sample time (except November 1998), some of the sample sizes per site were very small (Appendix 7.4.3, Tables 7.4.3.1 to 7.4.3.7). The observed number of alleles was correlated with sample size at each locus (Figures 4.3.1 to 4.3.6).



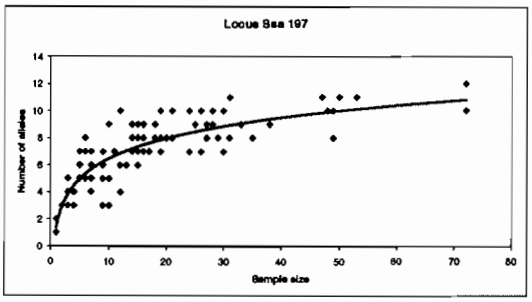
r_p 0.645, significant at p= 0.001

Figure 4.3.1 Observed number of alleles, locus Ssa 202



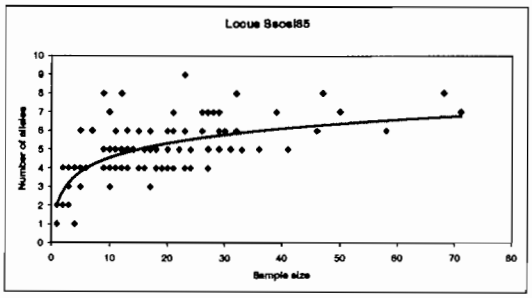
r_p 0.713, significant at p= 0.001

Figure 4.3.2 Observed number of alleles, locus Ssa 171



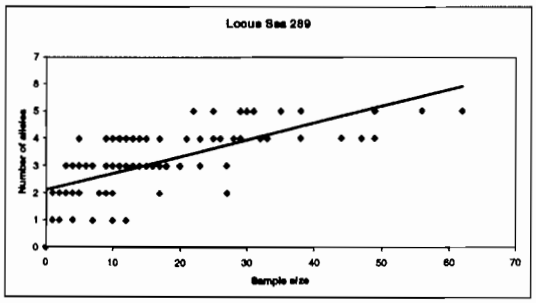
r_p 0.731, significant at p= 0.001

Figure 4.3.3 Observed number of alleles, locus Ssa 197



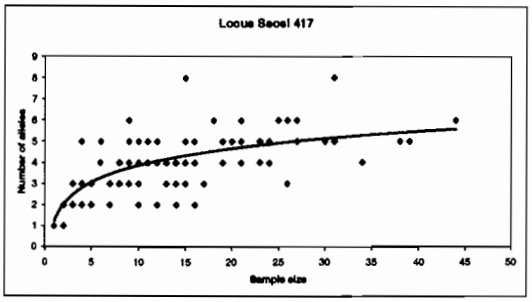
r_p 0.566, significant at p= 0.001

Figure 4.3.4 Observed number of alleles, locus Ssosl 85



r_p 0.666, significant at p= 0.001

Figure 4.3.5 Observed number of alleles, locus Ssa 289



r_p 0.592, significant at p= 0.001

Figure 4.3.6 Observed number of alleles, locus Ssosl 417

4.3.2 Allelic richness

Using numbers of alleles to compare genetic diversity between sites or between studies is not accurate if sample sizes vary. A measure of diversity, independent of sample size, was calculated using the allelic richness of (El Mousadik and Petit 1996) standardised per individual; 'ARi'. ARi was calculated over all sites at six sample times for each locus (Figure 4.3.7.). In this study ARi estimates were between 1.45, at locus Ssa 289 and 1.8, at locus Ssa 197. At locus Ssa171 ARi was 1.76, at locus Ssosl 85 ARi was 1.71, at loci Ssa202 and Ssosl 417 ARi was 1.68.

Published allele frequency data were used to estimate ARi for *S. salar* in Canadian and European rivers. At loci Ssa 197, Ssa 171, Ssosl 85 and Ssa 202 estimates of ARi in this study were lower than ARi estimates for every other river. At locus Ssosl 417, the over all estimate of ARi in this study was equivalent to estimates for other rivers, and at locus Ssa 289 estimates of ARi in this study were within the range of estimates obtained from other studies. It is possible that higher ARi estimates in other rivers are due to the larger adult population sizes, however, adult population size was given for 5 Canadian rivers in Fontaine et al. (1997) only. Over all loci ARi for the 5 Canadian rivers were between 1.81 to 1.89 and adult population sizes were between 1520 and 2271 individuals.

At locus Ssa 197, using allele frequencies from three tributaries of a Canadian river (Beacham and Dempson 1998) average ARi of 1.856 was estimated for the 1986 sample and average ARi of 1.866 was estimated for the 1992 sample. Using allele frequencies for seven Canadian rivers (Fontaine et al. 1997) ARi estimates between 1.825 and 1.912 were obtained and for seven sites on a Canadian river (Garant et al. 2000), ARi of 1.904 was estimated for the 1996 sample and ARi of 1.928 was estimated for 1997 sample. At locus Ssa 171, using

allele frequencies for seven Canadian rivers (Fontaine et al. 1997) ARi was between 1.84 and 1.913. At locus Ssosl 85, using allele frequencies for seven Canadian rivers (Fontaine et al. 1997) ARi was between 1.743 and 1.887. Using allele frequencies from (Nielsen et al. 1999) study, ARi was 1.736 for a Danish river in 1930s and 1989, ARi was 1.76 for a Scottish river (1989) and 1.869 for a Swedish river (1989). Using allele frequencies for seven sites on a Canadian river, ARi was 1.869 in 1996 and 1.879 in 1997 (Garant et al. 2000).

At locus Ssa 202, using allele frequencies from three tributaries of a Canadian river (Beacham and Dempson 1998), average ARi was estimated at 1.875 in 1986 and 1.849 in 1992; using allele frequencies for seven Canadian rivers (Fontaine et al. 1997), ARi was between 1.838 and 1.91 and for seven sites on a Canadian river, ARi was 1.857 in 1996 and 1.889 in 1997 (Garant et al. 2000). At locus Ssosl 417, using allele frequencies from (Nielsen et al. 1999) study, ARi for a Danish river was 1.644 in the 1930s and 1.552 in 1989, ARi was 1.86 for a Scottish river (1989) and 1.867 for a Swedish river (1989). At locus Ssa 289, using allele frequencies for three North American and two European rivers (McConnell et al. 1995), ARi's of 1.305, 1.262, 1.547, 1.756 and 1.544 were estimated. Using allele frequencies for three tributaries of a Newfoundland river (Beacham and Dempson 1998), average ARi in 1986 was 1.638 and average ARi in 1992 was 1.075.

Allelic richness standardised per individual over all loci over all sample times was estimated for the 22 sample sites in this study. Site 2 (TF) had the highest ARi of 1.713 and site 13 (TK) had the lowest ARi of 1.333 (Figure 4.3.8). ARi was calculated per site per locus for July 1998 (Figure 4.3.9.), September 1998 (Figure 4.3.10), July 1999 (Figure 4.3.11), September 1999 (Figure 4.3.12.), July 2000 (Figure 4.3.13) and October (Figure 4.3.14).

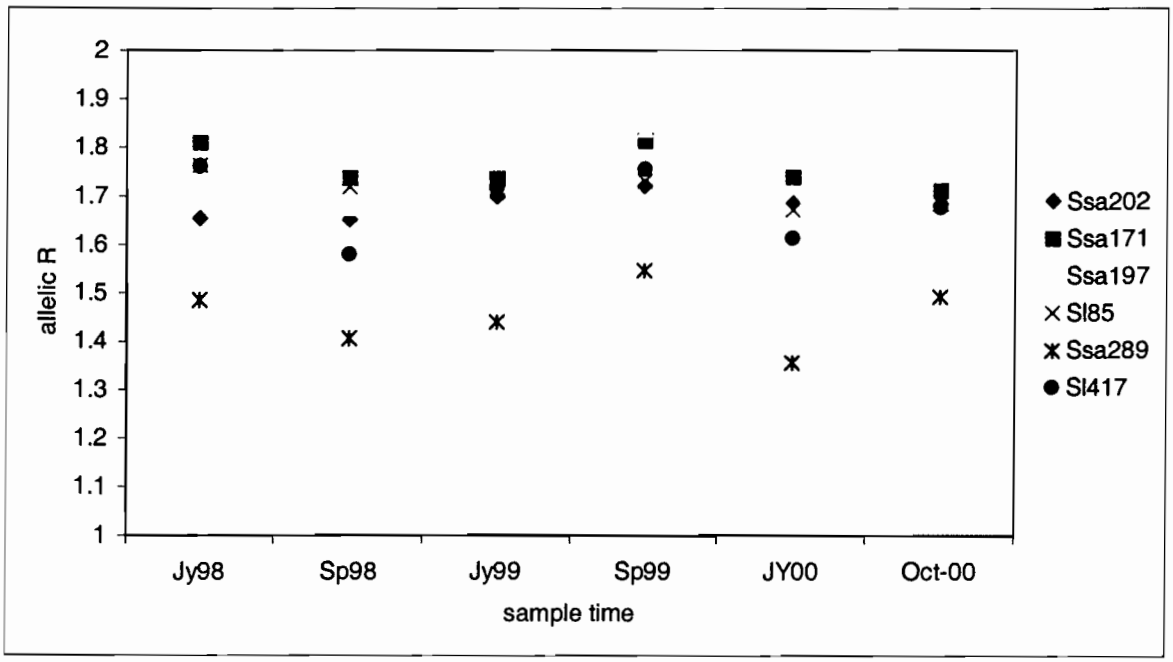


Figure 4.3.7 Allelic richness standardised per individual for six microsatellite loci at six sample times

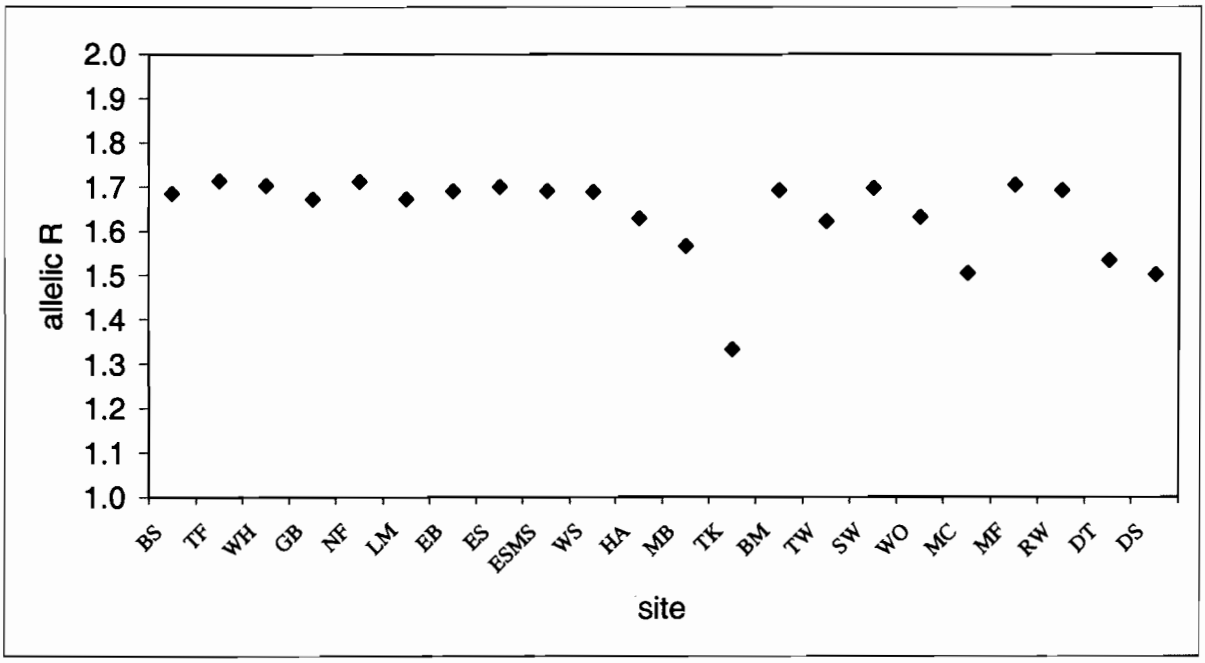
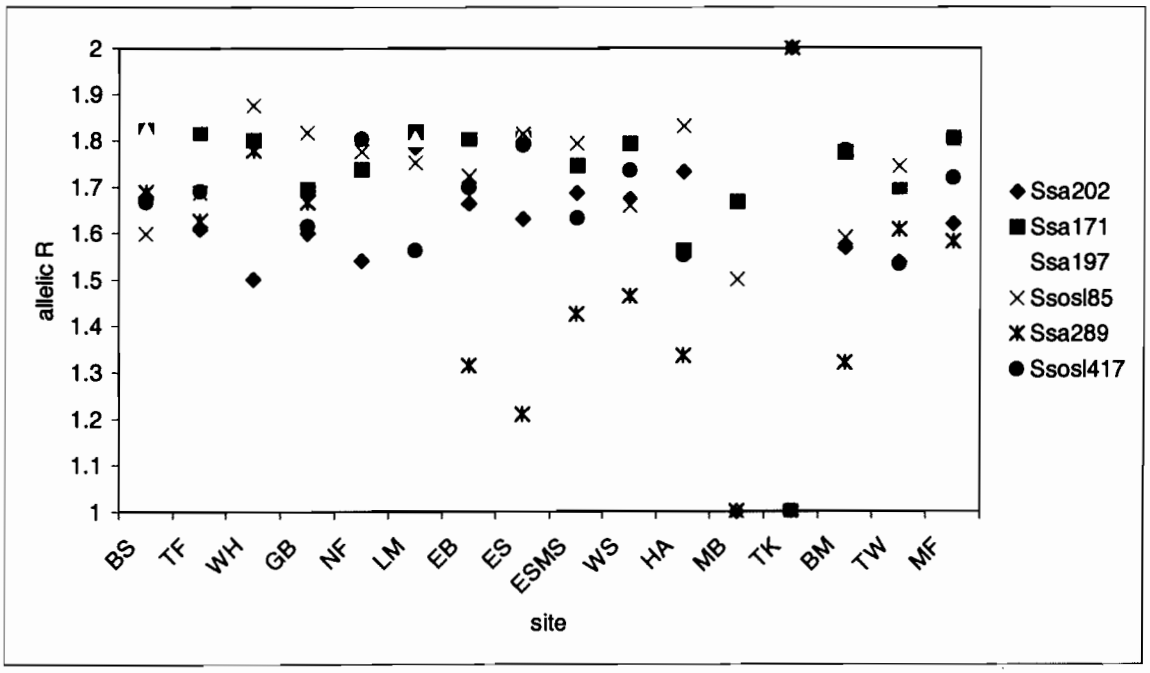


Figure 4.3.8 Allelic Richness standardised per individual, over all loci, over six sample times per site



(TK N= 1)

Figure 4.3.9 Allelic Richness standardised per individual per site for 6 loci, July 1998

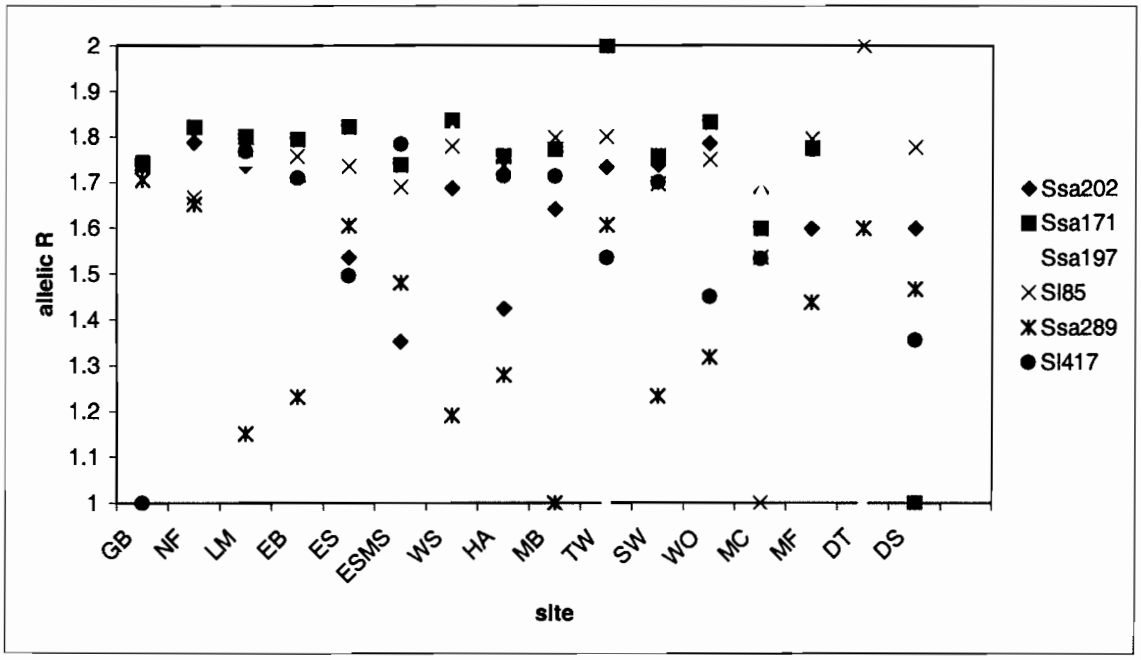


Figure 4.3.10 Allelic Richness standardised per individual per site for 6 loci, September 1998

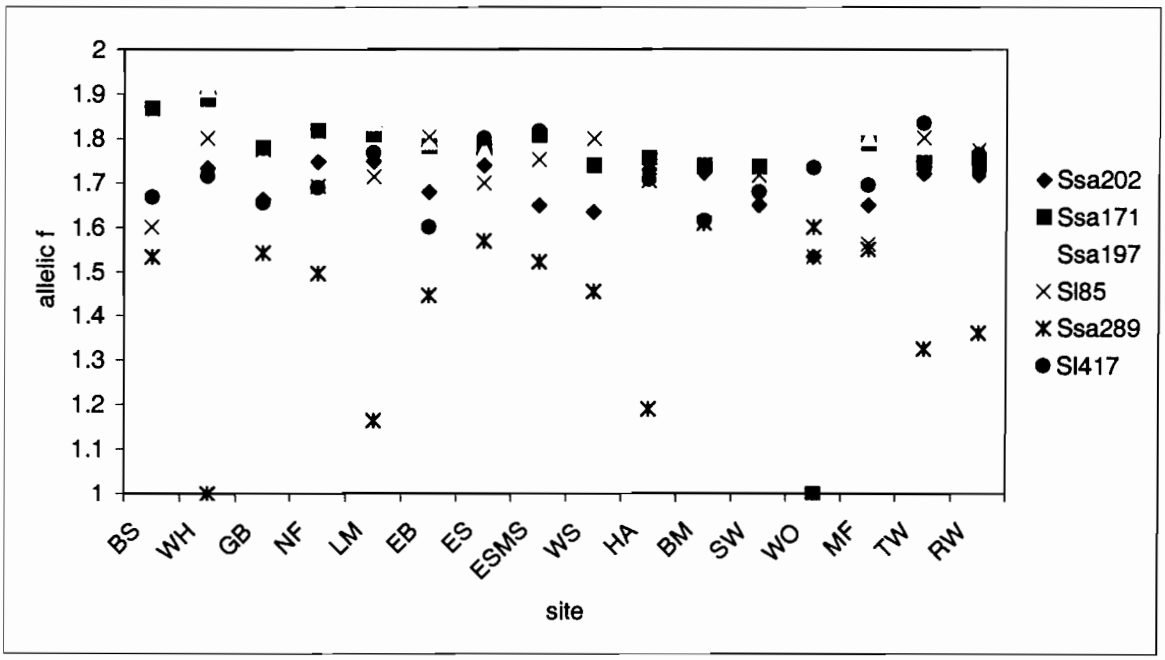


Figure 4.3.11 Allelic Richness standardised per individual per site for 6 loci, July 1999

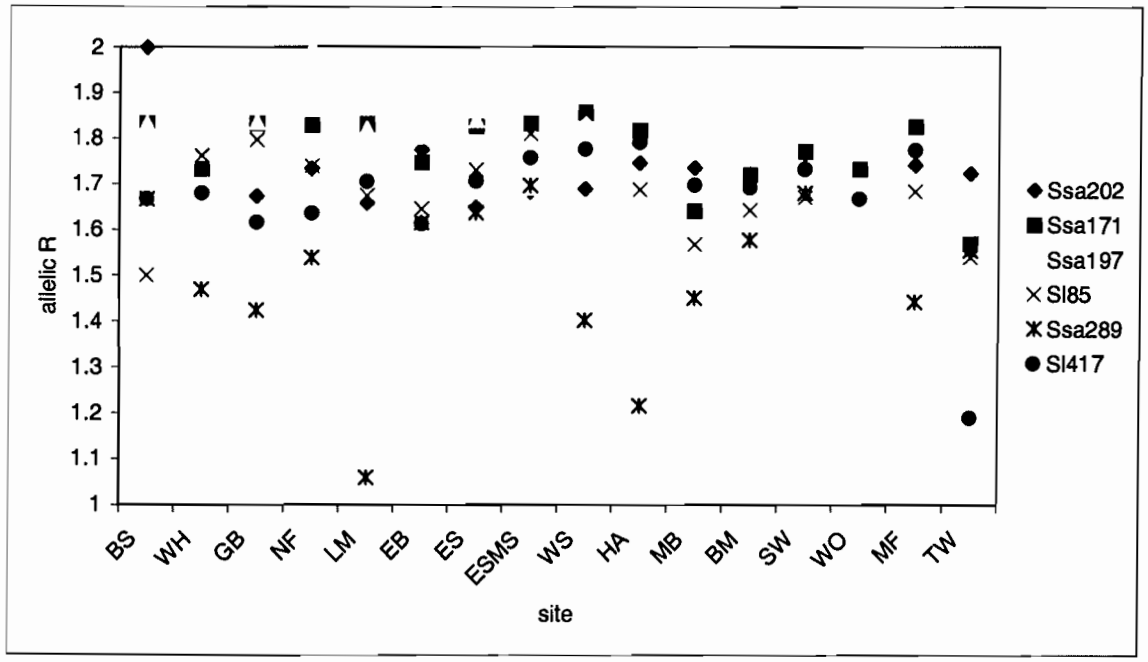


Figure 4.3.12 Allelic Richness standardised per individual per site for 6 loci, September 1999

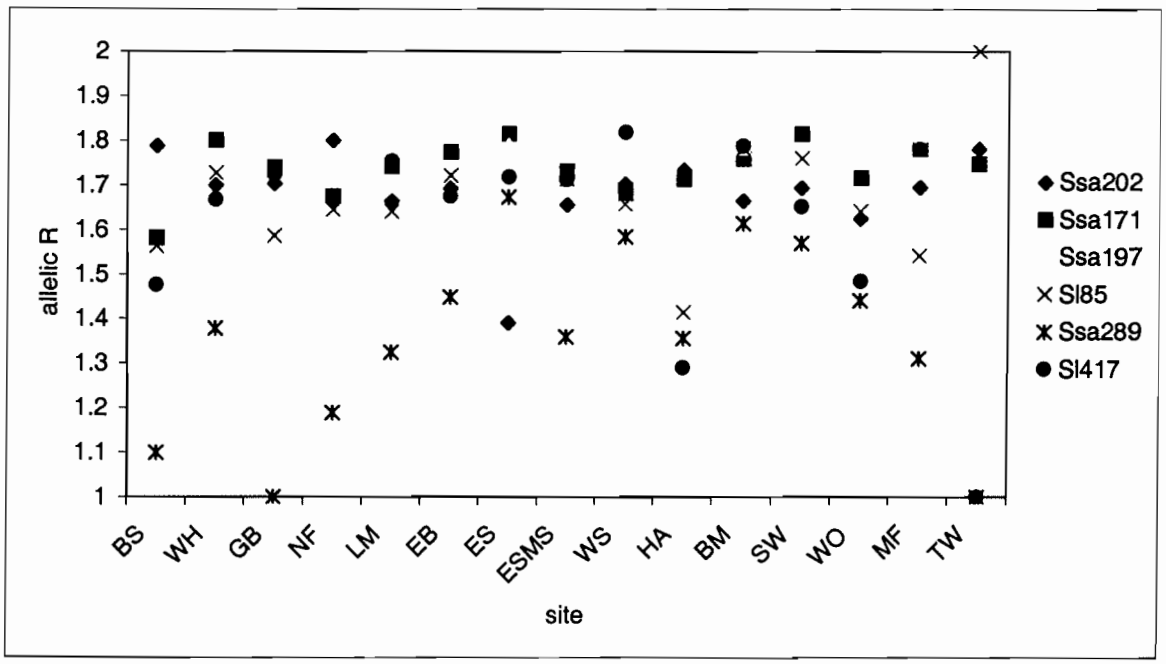


Figure 4.3.13 Allelic Richness standardised per individual per site for 6 loci, July 2000

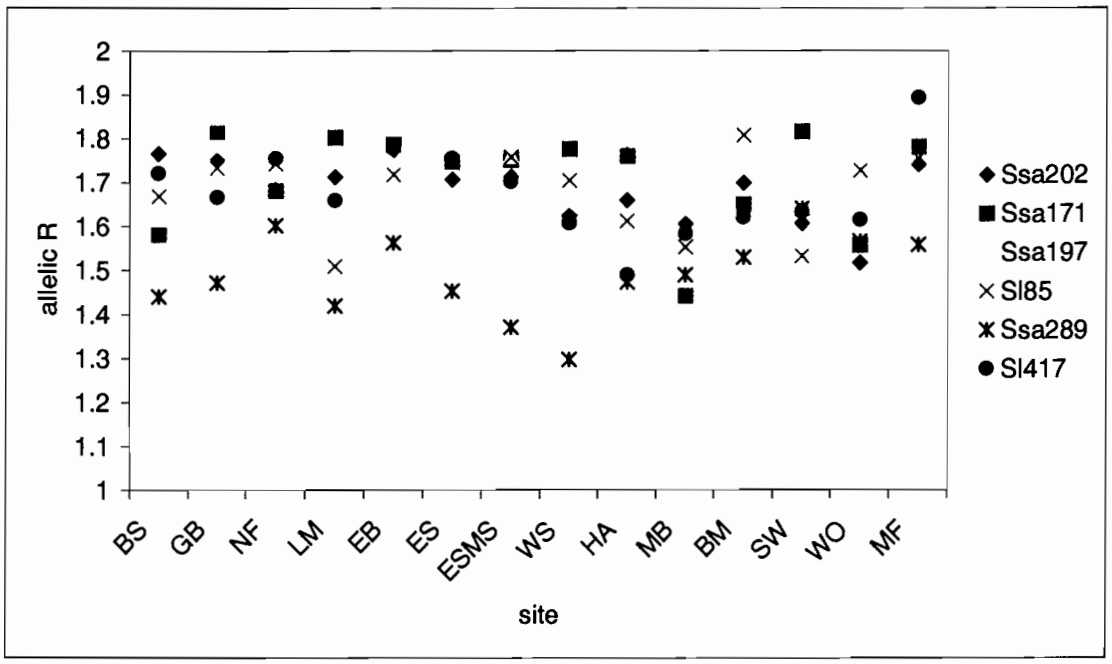


Figure 4.3.14 Allelic Richness standardised per individual per site for 6 loci, October 2000

4.3 3 Observed heterozygosity frequency (Ho)

Observed heterozygosity over all sites over all loci was calculated for six sample times and varied between 0.494 in July 1998 and 0.648 in October 2000 (Figure 4.3.15). No significant difference between summer and autumn over-all sites Ho was detected at any of the sample years, using the between-groups test (Equation 3.7.1, Methods). Significant difference between over all sites Ho in July 1998 and July 1999 ($p = 0.0012$) and between July 1999 and July 2000 ($p = 0.0466$) was detected using the between-groups test (Equation 3.7.1, Methods).

Observed heterozygosity over all sites at seven sample times was lowest at loci Ssa 289 and Ssosl 417 (Figure 4.3.16). Low heterozygosity at these loci has been observed for *S. salar* in other rivers, for example, McConnell et al. (1995) observed heterozygosity of 0.3-0.75 at locus Ssa 289 and Nielsen et al. (1999) observed heterozygosity of 0.31-0.96 at locus Ssosl 417. At locus Ssa 202, Ho was between 0.564, July 1998 and 0.775, July 1999, which is lower than that observed by Fontaine et al. (1997) (Ho 0.86) and Beacham and Dempson (1998) (Ho 0.842-0.862). At locus Ssa 171 Ho was between 0.675, October 2000, and 0.857, September 1999, which is lower than that observed by Fontaine et al. (1997) (Ho 0.94). Locus Ssa 197 Ho was between 0.634, July 1998 and 0.846, October 2000, which is similar to that observed by Fontaine et al. (1997) (Ho 0.86) and Beacham and Dempson (1998) (Ho 0.843-0.858). At locus Ssosl 85 Ho was between 0.601, July 2000, and 0.7, November 1998, which is lower than that observed by Fontaine et al. (1997) (Ho 0.8186) and in the range of that observed by Nielsen et al. (1999) (Ho 0.31-0.82).

Observed heterozygosity per site varied between 0 and 1 (these extreme values are associated with very small sample sizes at certain sites, Appendix section 7.4.3, Tables 7.4.3.1 to 7.4.3.7).

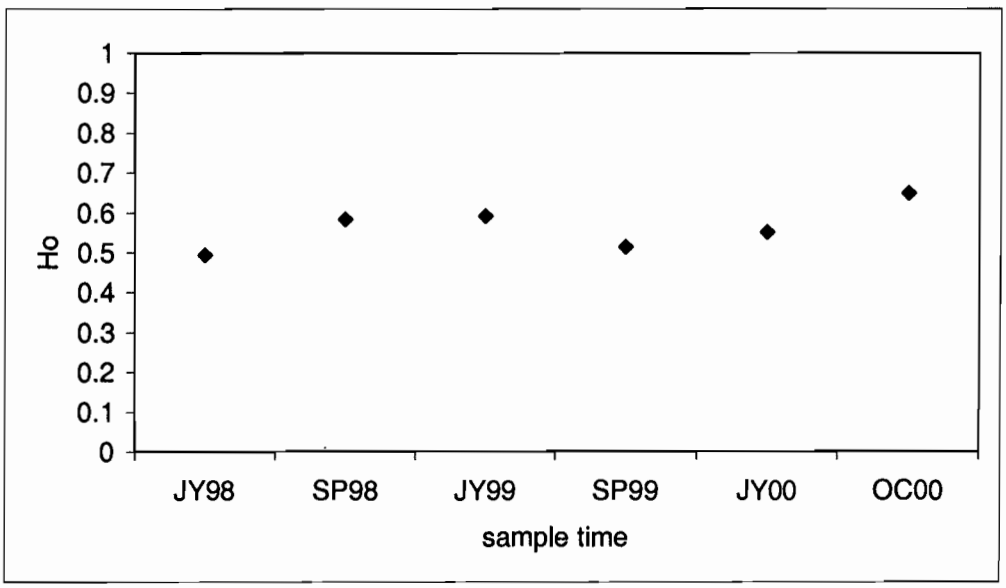


Figure 4.3.15 Observed heterozygosity over all sites over all loci for six sample times

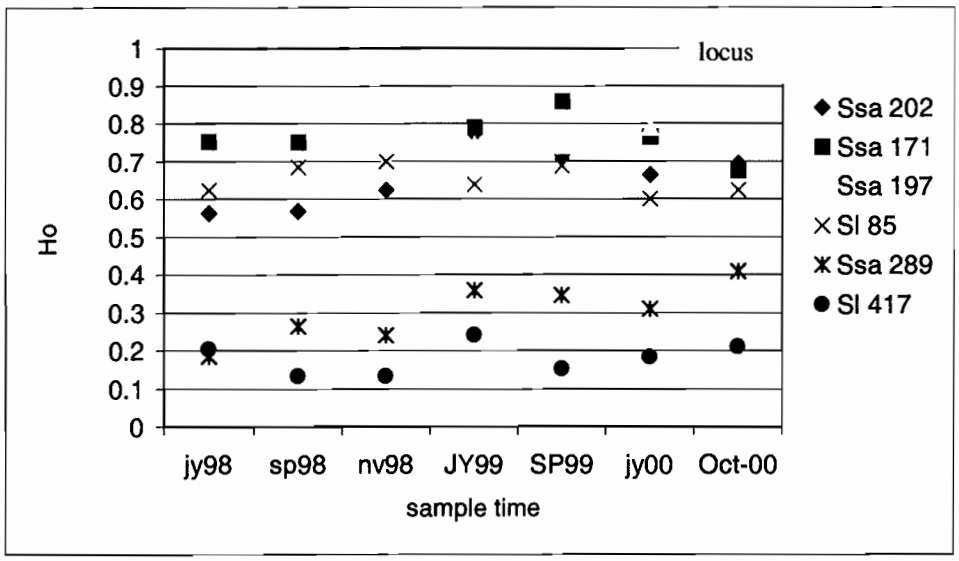


Figure 4.3.16 Observed heterozygosity of *S. salar* overall sites at 7 sample times for 6 microsatellite loci

4.3.4 Expected heterozygosity frequency (Ht)

Expected heterozygosity corrected for differences in sample size (Ht), over all sites over 6 loci estimates were between 0.698 and 0.737 (Figure 4.3.17.). No significant difference between Summer and Autumn over all sites Ht was detected in any of the three years studied.

Expected heterozygosity over all sites was lowest at locus Ssa 289 (Ht 0.39 to 0.542) at all sample times. At locus Ssa 202, Ht was between 0.684 and 0.724; at locus Ssa 171 Ht was between 0.74 and 0.805, at locus Ssa 197 Ht was between 0.794 and 0.857, at locus Ssosl 85 Ht was between 0.706 and 0.773 and locus Ssosl 417 Ht varied from 0.758 to 0.808 (Figure 4.3.18). Expected heterozygosity overall loci over all sample times was lowest at site MC (overall Ht 0.588) and highest at site GB (overall Ht 0.741) (Figure 4.3.19).

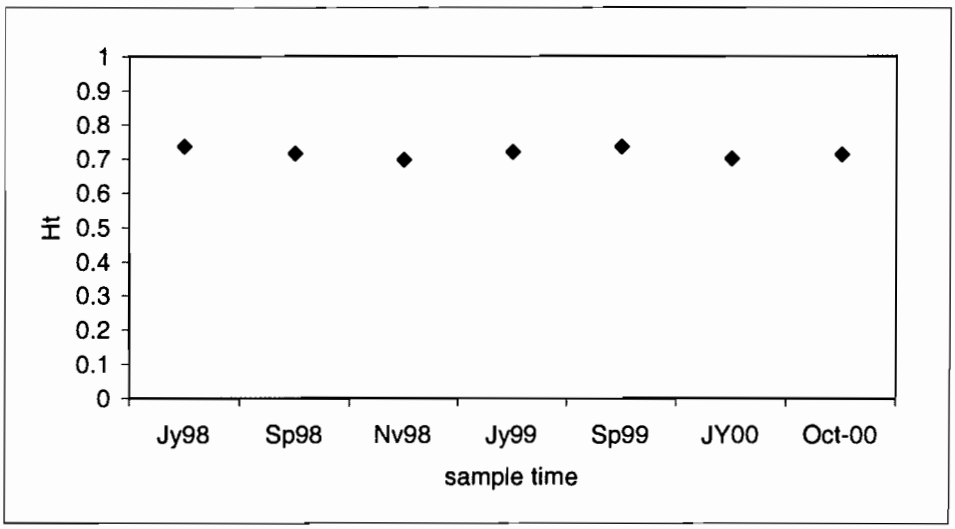


Figure 4.3.17 Expected heterozygosity (Ht) of *S. salar* in the rivers Piddle and Frome over 6 loci, overall sites per sample time

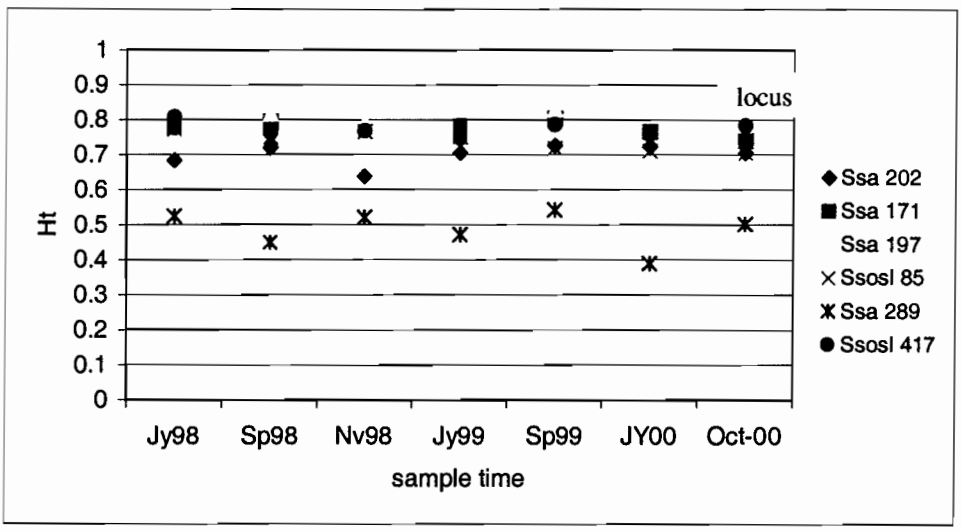


Figure 4.3.18 Expected heterozygosity (Ht) of *S. salar* in the Rivers Piddle and Frome per locus at seven sample times

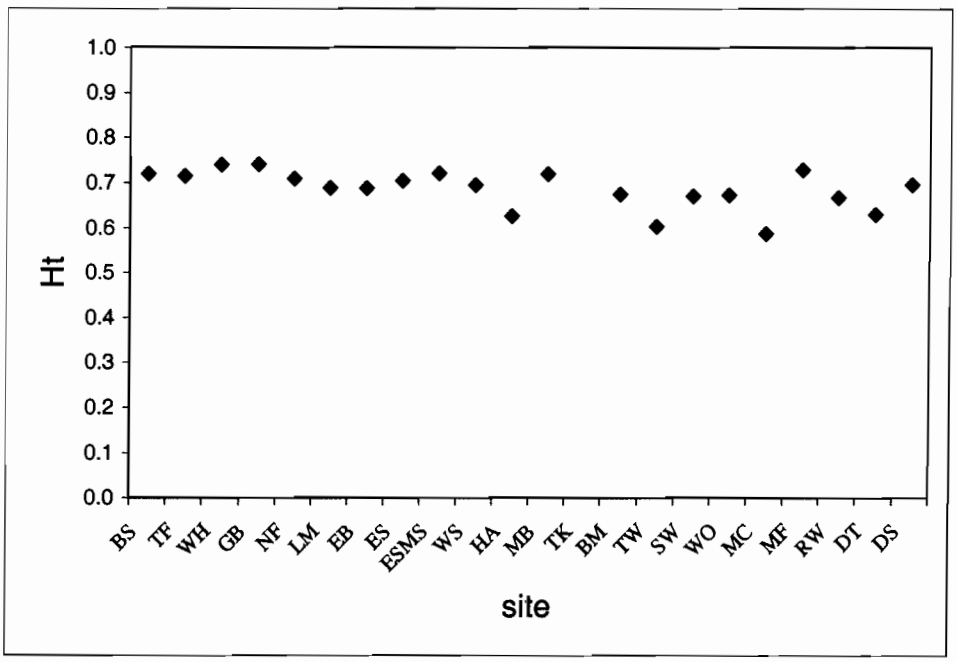


Figure 4.3.19 Expected heterozygosity (Ht) over 6 microsatellite loci over 7 sample times for 22 sample sites

4.4 Allele frequency

Allele frequencies were calculated for each of six loci for each site at each sample time (Appendix Section 7.4.4, Figures 7.4.4.1 to 7.4.4.7) and over all sites per sample time (Figures 4.4.1 to 4.4.41). At locus Ssa 202 allele 4 was at the highest frequency at all sample times (Figures 4.4.1 to 4.4.7). At locus Ssa 171 allele 4 was at the highest frequency at all sample times (Figures 4.4.8 to 4.4.13). At locus Ssa 197 allele 12 was at the highest frequency at all sample times (Figures 4.4.14 to 4.4.20). At locus Ssosl 85 allele 8 was at the highest frequency at all sample times (Figures 4.4.21 to 4.4.27). At locus Ssa 289 allele 4 was at the highest frequency at all sample times (Figures 4.4.28 to 4.4.34). At locus Ssosl 417 allele 4 was at the highest frequency at all sample times except July 1999 when allele 6 occurred at the highest frequency (Figures 4.4.35 to 4.4.41).

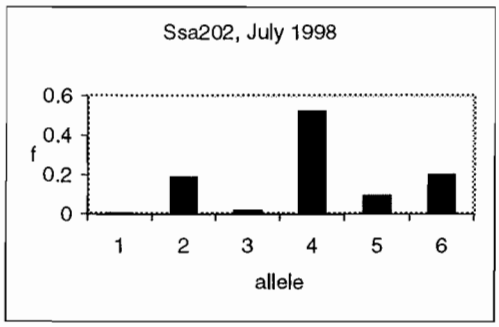


Figure 4.4.1 Allele frequency at locus Ssa 202, over all sites July 1998

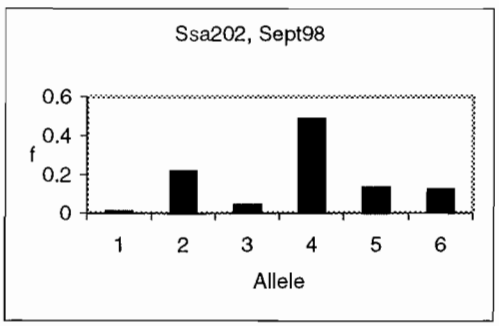


Figure 4.4.2 Allele frequency at locus Ssa 202, over all sites September 1998

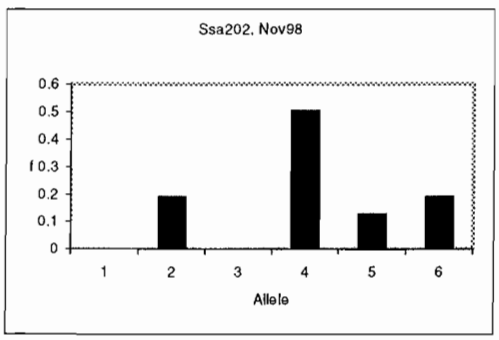


Figure 4.4.3 Allele frequency at locus Ssa202, over all sites, November 1998

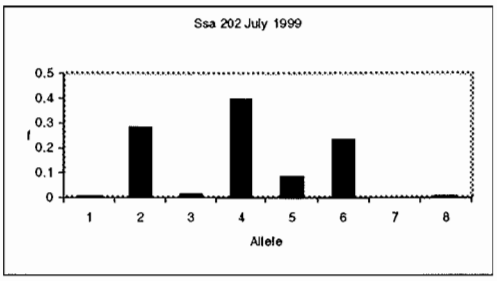


Figure 4.4.4 Allele frequency at locus Ssa 202, over all sites July 1999

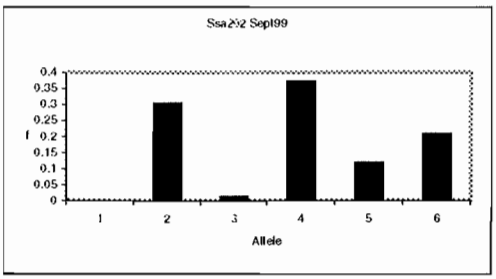


Figure 4.4.5 Allele frequency at locus Ssa 202, over all sites September 1999

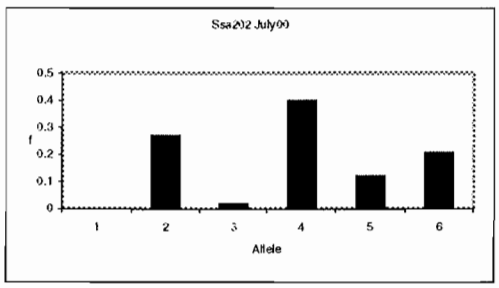


Figure 4.4.6 Allele frequency at locus Ssa 202, over all sites July 2000

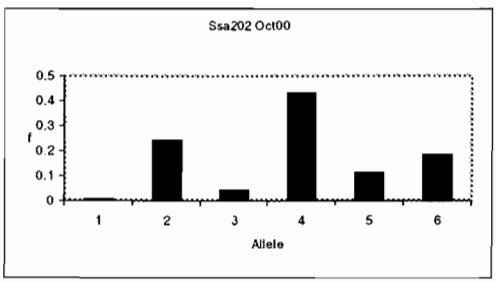


Figure 4.4.7 Allele frequency at locus Ssa 202, over all sites October 2000

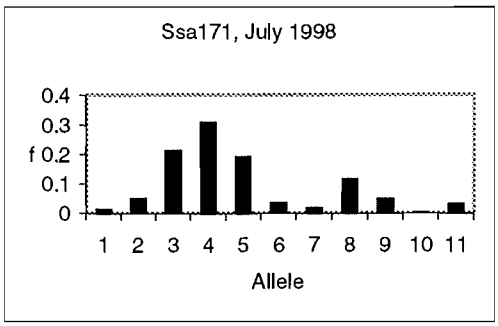


Figure 4.4.8 Allele frequency at locus Ssa 171, over all sites July 1998

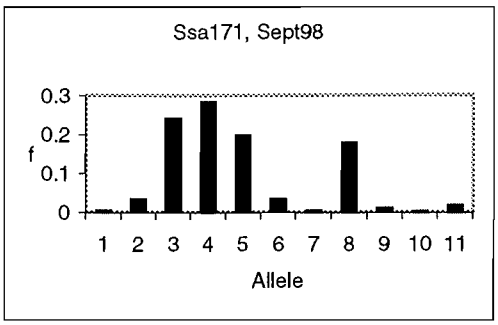


Figure 4.4.9 Allele frequency at locus Ssa 171, over all sites September 1998

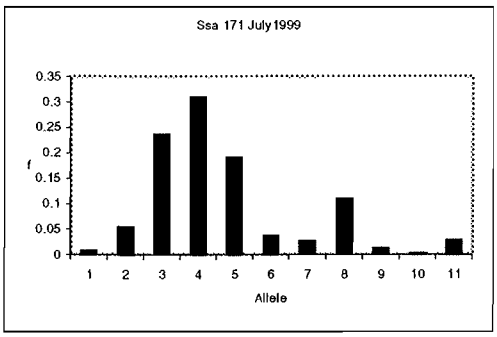


Figure 4.4.10 Allele frequency at locus Ssa 171, over all sites July 1999

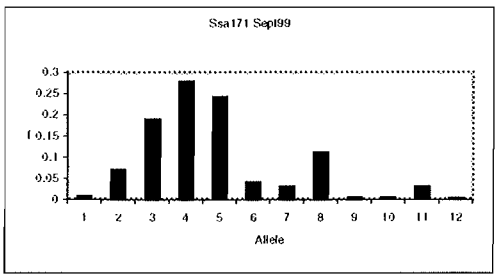


Figure 4.4.11 Allele frequency at locus Ssa 171, over all sites September 1999

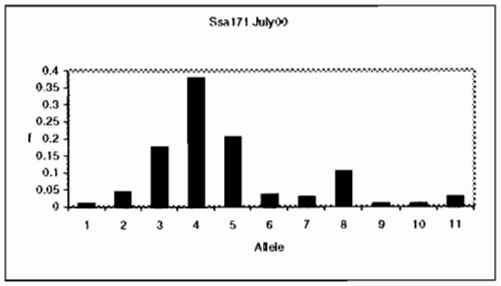


Figure 4.4.12 Allele frequency at locus Ssa 171, over all sites July 2000

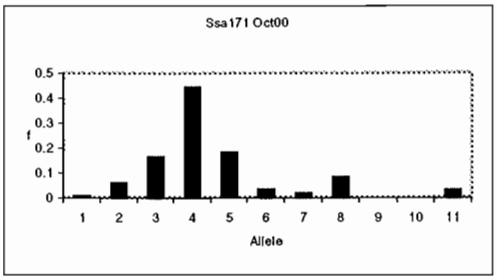


Figure 4.4.13 Allele frequency at locus Ssa 171, over all sites October 2000

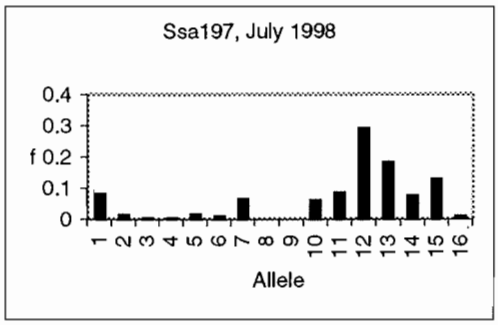


Figure 4.4.14 Allele frequency at locus Ssa 197, over all sites July 1998

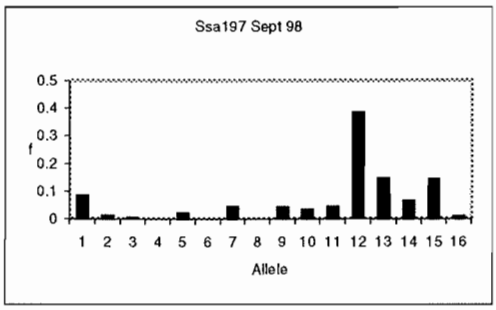


Figure 4.4.15 Allele frequency at locus Ssa 197, over all sites September 1998

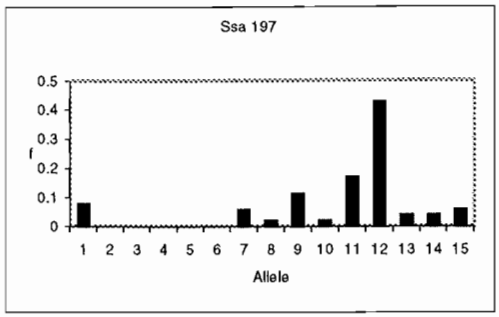


Figure 4.4.16 Allele frequency at locus Ssa 197, over all sites, November 1998

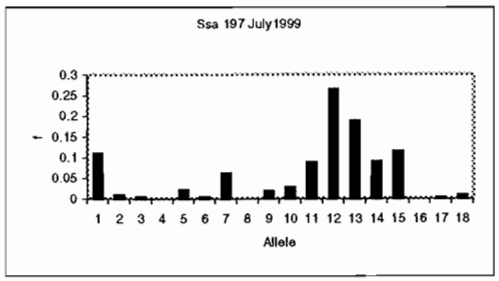


Figure 4.4.17 Allele frequency at locus Ssa 197, over all sites July 1999

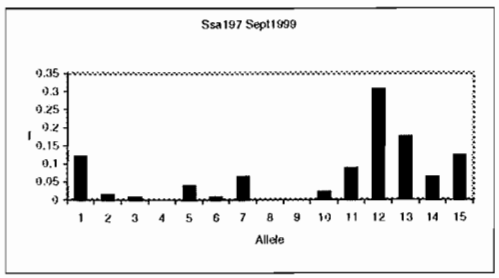


Figure 4.4.18 Allele frequency at locus Ssa 197, over all sites September 1999

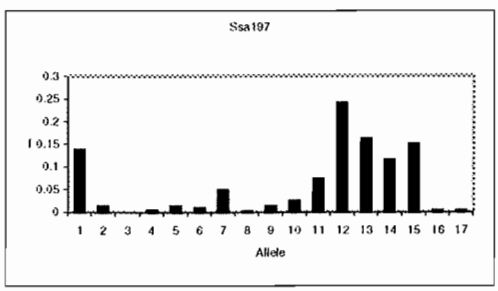


Figure 4.4.19 Allele frequency at locus Ssa 197, over all sites July 2000

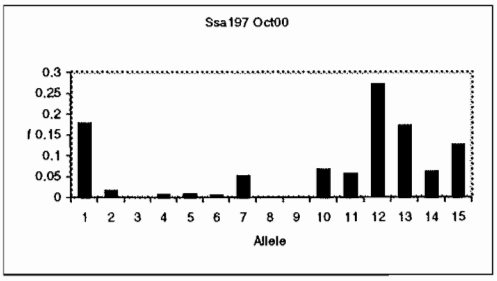


Figure 4.4.20 Allele frequency at locus Ssa 197, over all sites October 2000

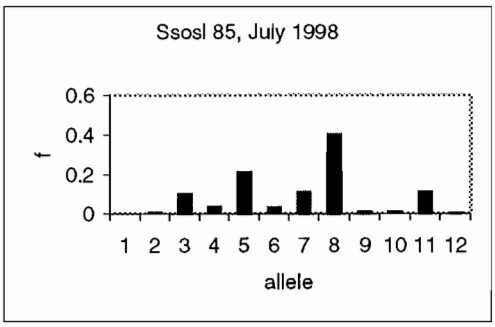


Figure 4.4.21 Allele frequency at locus Ssosl 85, over all sites July 1998

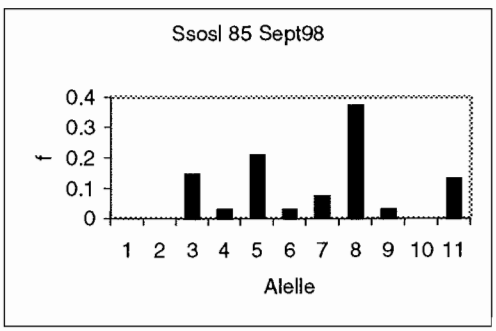


Figure 4.2.22 Allele frequency at locus Ssosl 85, over all sites September 1998

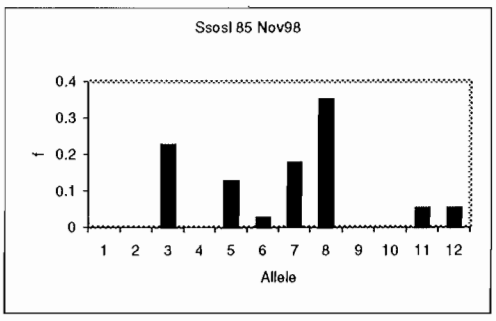


Figure 4.2.23 Allele frequency at locus Ssosl 85 over all sites, November 1998

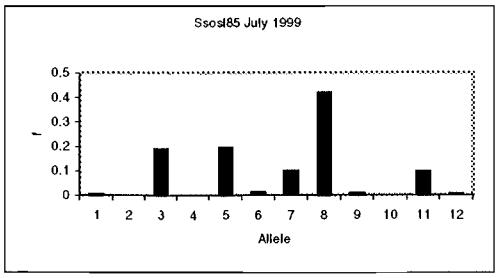


Figure 4.2.24 Allele frequency at locus Ssosl 85, over all sites July 1999

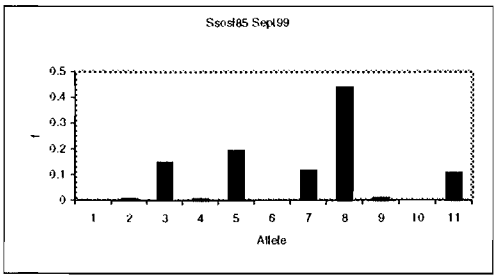


Figure 4.4.25 Allele frequency at locus Ssosl 85, over all sites September 1999

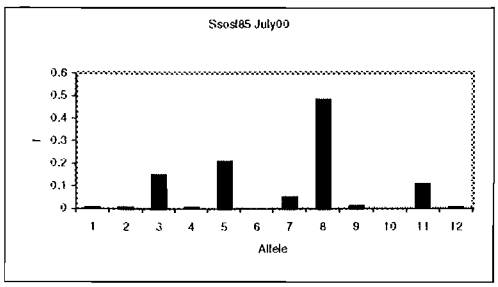


Figure 4.4.26 Allele frequency at locus Ssosl 85, over all sites July 2000

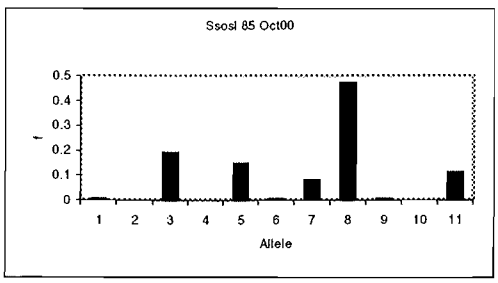


Figure 4.4.27 Allele frequency at locus Ssosl 85, over all sites October 2000

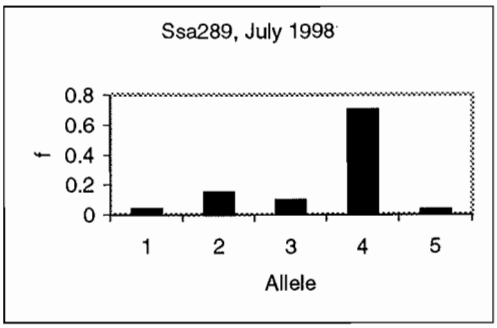


Figure 4.4.28 Allele frequency at locus Ssa 289, over all sites July 1998

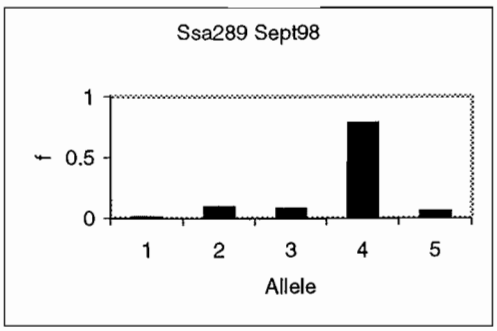


Figure 4.4.29 Allele frequency at locus Ssa 289, over all sites September 1998

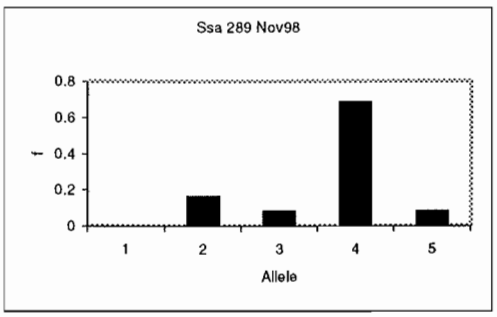


Figure 4.4.30 Allele frequency at locus Ssa 289, over all sites, November 1998

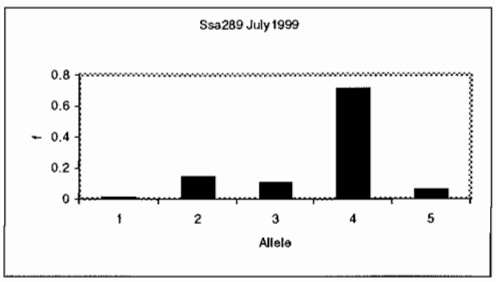


Figure 4.4.31 Allele frequency at locus Ssa 289, over all sites July 1999

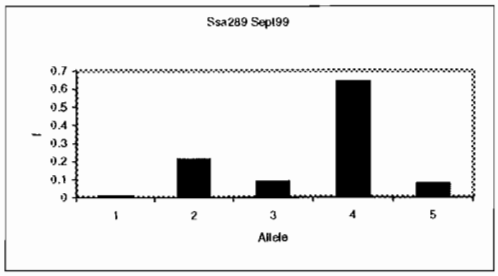


Figure 4.4.32 Allele frequency at locus Ssa 289, over all sites September 1999

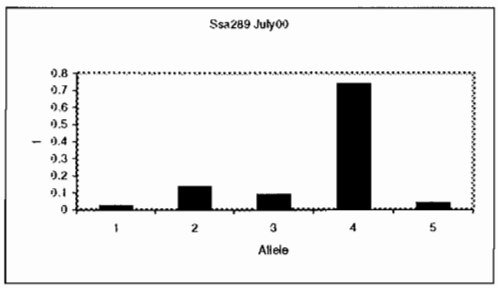


Figure 4.4.33 Allele frequency at locus Ssa 289, over all sites July 2000

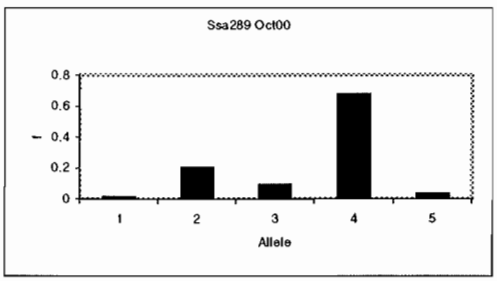


Figure 4.4.34 Allele frequency at locus Ssa 289, over all sites October 2000

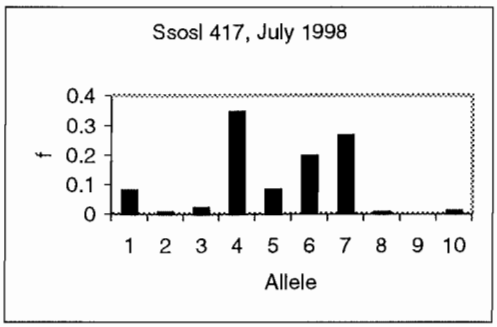


Figure 4.4.35 Allele frequency at locus Ssosl 417, over all sites July 1998

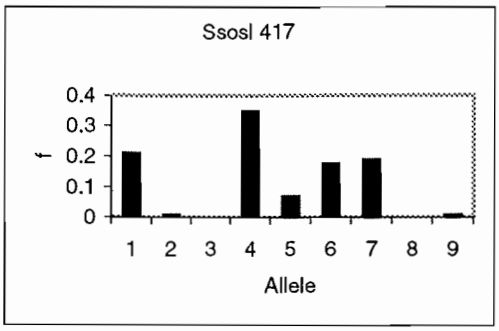


Figure 4.4.36 Allele frequency at locus Ssosl 417, over all sites September 1998

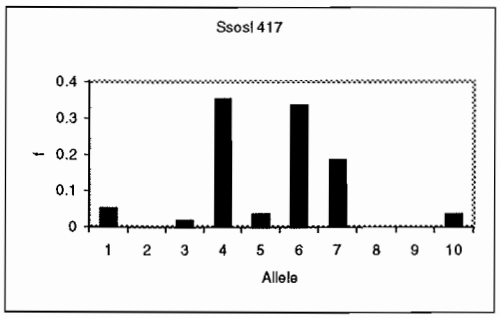


Figure 4.4.37 Allele frequency at locus Ssosl 417, over all sites, November 1998

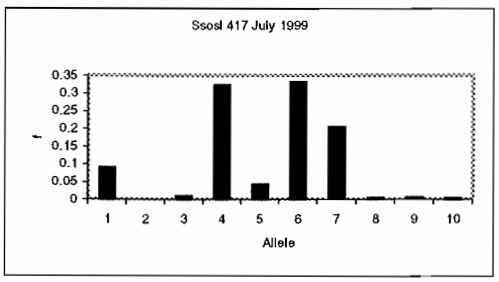


Figure 4.4.38 Allele frequency at locus Ssosl 417, over all sites July 1999

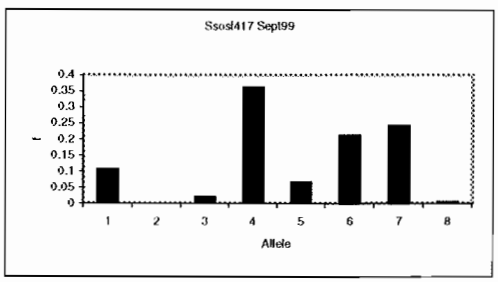


Figure 4.4.39 Allele frequency at locus Ssosl 417, over all sites September 1999

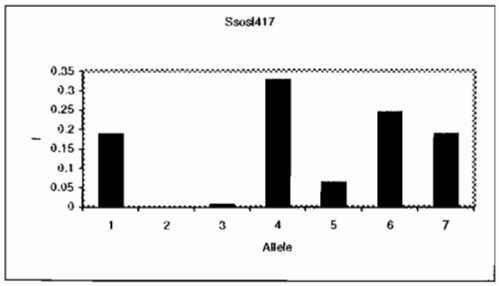


Figure 4.4.40 Allele frequency at locus Ssosl 417, over all sites July 2000

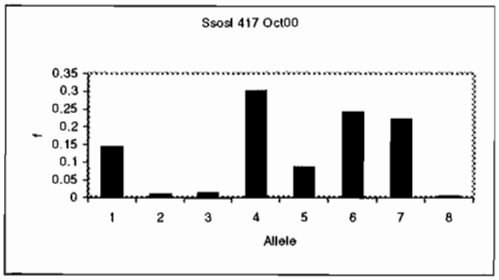


Figure 4.4.41 Allele frequency at locus Ssosl 417, over all sites October 2000

4.5 Population structure

4.5.1 Genetic differentiation of life history types

F_{ST} between 0+ parr and 1+ parr of the same cohort year was estimated to determine if differentiation occurred on the basis of life history type. It is possible that the 0+ samples contained juveniles that will not smolt at 0+. Fourteen 1+ parr were sampled in 1998, however, no 0+ parr of the cohort year were sampled, therefore F_{ST} was not calculated for the cohort year 1997. In the cohort year 1998, 14 1+ parr sampled in July 1999 and one 1+ parr sampled in September 1999 were tested against 0+ parr caught in July 1998. In the cohort year 1999, F_{ST} was estimated between 7 1+ parr sampled in July 1999 and 0+ parr sampled in July 1999. No significant differentiation between 0+ and 1+ parr of the cohort year 1998 was detected (F_{ST} 0.0045^{NS}) and no significant differentiation was detected between 0 + and 1+ parr of the cohort year 1999 (F_{ST} 0.0045^{NS}).

An assignment test was used to determine if 1+ parr had migrated from their natal spawning site. To control for the possibility of change in allele frequency between years the reference populations were of the same cohort. The July sample was selected for assignment populations due to the possibility that parr had migrated by the Autumn. None of the 1+ parr were assigned to one particular reference site at any sample time (Tables 4.5.1.1 to 4.5.1.4) and no pattern of migration from nearby sites and no evidence of downstream migration was detected. Parr older than 0+ were excluded from the analysis of population structure on the basis that none of the 1+ parr could be assigned to a sample site.

Table 4.5.1.1 11 1+ parr sampled in September 1998 assigned to reference 0+ parr sampled July 1998

1+ parr sample site	Assignment site
GB	TF, GB, NF, LM, EB, ES, ESMS, WS, HA, BM, TW, MF
GB	TF, GB, NF, LM, EB, ES, ESMS, WS, HA, BM, TW, MF
GB	TF, GB, NF, LM, EB, ES, ESMS, WS, HA, BM, TW, MF
NF	TF, NF, EB, ES, ESMS, WS, BM, MF
LM	TF, GB, NF, LM, EB, ES, ESMS, WS, HA, BM, TW, MF
EB	TF, NF, LM, EB, ES, ESMS, WS, MF
WS	TF, GB, NF, LM, EB, ES , WS, HA, BM, TW, MF
WS	TF, NF, LM, EB, ES, ESMS, WS, BM , MF
WS	NF, EB, ESMS, BM, MF
HA	NF, ES
WO	TF, NF, LM, EB, ES, ESMS, WS

1+ parr sampled in September 1998 could not be assigned to the cohort of 1997, therefore were assigned to the reference population July 1998, however, these results should be interpreted with caution as it is possible that allele frequencies per site were not stable between consecutive years.

Table 4.5.1.2 Assignment of 14 1+ parr sampled in July 1999 to reference 0+ parr sampled in July 1998

1+ parr sample site	Assignment site
BS	TF, GB, NF, LM, EB, ES, WS, HA, BM, MF
BS	TF, GB, NF, EB, ES, WS, BM, MF
BS	TF, GB, NF, EB, WS, BM, MF
BS	TF, GB, NF, LM, EB, ES, ESMS, WS, HA, BM, MF
NF	TF, GB, NF, LM, EB, ES, ESMS, WS, HA, BM, MF
NF	TF, GB, NF, LM, EB, ES, WS, BM, MF
EB	TF, GB, NF, LM, EB, ES, ESMS, WS, BM, MF
EB	NF, EB, ES, WS, BM
EB	TF, NF, EB, ESMS, WS, BM, MF
WS	TF, GB, NF, LM, EB, ES, ESMS, WS, HA, BM, MF
WS	TF, LM, EB, ES, ESMS, WS, HA, MF
WO	TF, GB, NF, LM, EB, ES, ESMS, WS, HA, MF
WO	TF, NF, LM, EB, ES, ESMS, WS, HA, BM, MF
WO	TF, GB, NF, LM, EB, ES, ESMS, WS, BM, MF

Table 4.5.1.3 Assignment of one 1+ parr sampled in September 1999 to reference 0+ parr sampled in July 1998

1+ parr sample site	Assignment site
ES	NF, LM, HA, TW

Table 4.5.1.4 Assignment of 7 1+ parr sampled in July 2000 to reference 0+ parr sampled in July 1999

1+ parr sample site	Assignment site
BS	BS, WH, GB, NF, LM, EB, ES, ESMS, WS, HA, BM, SW, MF, TH, RW
BS	NF, LM, ESMS, BM, MF, TW
WS	NF, TW
WS	NF, EB, WS, BM, SW, MF, RW
WS	NF, LM, BM, SW, RW
WO	WH, NF, LM, EB, ES, ESMS, WS, HA, BM, MF, TH, RW
WO	NF, LM, EB, ES, WS, BM, MF, RW

Probability of assignment; 10000 simulations at a rejection level of 0.01.Genetic differentiation between years

4.5.2 Genetic differentiation between years

Genetic differentiation was estimated between juvenile *S. salar* sampled in three consecutive years. Summer and Autumn 0+ samples were pooled in each year, as these fish were all of the same cohort. Genetic differentiation between consecutive years was low but significant in both 1998-1999 and 1999-2000 and genetic differentiation across two years, 1998-2000 was higher than across one year (Table 4.5.2).

Table 4.5.2 F_{ST} between three consecutive years

Differentiation between	F_{ST}	p
All sites Summer and Autumn 1998 v All sites Summer and Autumn 1999	0.0053	0.0001
All sites Summer and Autumn 1999 v All sites Summer and Autumn 2000	0.0032	0.0001
All sites Summer and Autumn 1998 v All sites Summer and Autumn 2000	0.0073	0.0001

4.5.3 Genetic differentiation between Summer and Autumn sample times

Juveniles were sampled in Summer (July 1998, July 1999 and July 2000) with the assumption that limited migration from the spawning location will have occurred. It is possible that parr have migrated within the river by the Autumn (September 1998, September 1999 and October 2000). It was not possible to monitor the juveniles directly, however it may be possible to infer behaviour from genetic variability and population structure. If there are no differences between summer and Autumn samples in the same year then these are considered to be replicate samples. Very low but significant differentiation between Summer and Autumn samples was detected in all three years, thus Summer and Autumn samples were not pooled for analysis of population structure (Table 4.5.3).

Table 4.5.3 F_{ST} between Summer and Autumn samples for three years

Differentiation between	F_{ST}	p
July 1998-Septmeber 1998	0.0201	0.0001
July 1999-September 1999	0.0015	0.0106
July 2000-October 2000	0.0029	0.0001

4.5.4 Genetic differentiation between the Rivers Frome and Piddle

The extent of genetic differentiation between the Rivers Frome and Piddle was estimated using F_{ST}. The river Piddle was not sampled in September 1998 and only a very small number of samples were obtained for the River Piddle in July and September 1999. If adult *S. salar* have a strong homing mechanism to the natal river, then it is possible that differentiation may occur even when two rivers are very close. Significant differentiation between the Rivers Piddle and Frome was detected in July 1999, July 2000 and October 2000. No samples were obtained from the river Piddle in September 1998 and samples sizes were very low in July and September 1999 (Table 4.5.4.).

Table 4.5.4 F_{ST} between Piddle and Frome

Sample time	F_{ST} between Piddle and Frome	p	Piddle N
July 1998	0.0339	0.0001	75
July 1999	-0.0601	NS	3
Sept 1999	-0.0227	NS	2
July 2000	0.0741	0.0001	14
Oct 2000	0.0276	0.0001	29

4.6 Over all sites F statistics

4.6.1 Six-locus F statistics

Population structure was estimated using Wright's F statistics. Significant F_{IT} was detected at each sample time; F_{IT} values were between 0.179 and 0.329. Significant F_{ST} was detected at each sample time except November 1998; F_{ST} values were between 0.031 and 0.066. Significant F_{IS} was detected at each sample time; F_{IS} values were between 0.153 and 0.310 (Table 4.6.1). No significant difference was detected between Summer and Autumn 6 loci F_{ST} or for between Summer and Autumn 6 locus F_{IS} for each sample year. No significant difference between 6 locus F_{ST} was detected between July 1998 and July 1999, however, a significant difference ($p < 0.05$) was detected between 6 locus F_{ST} in July 1999 and July 2000. A significant difference between 6 locus overall F_{IS} ($p < 0.01$) was detected between July 1998 and July 1999, however no significant difference was detected between over all F_{IS} in July 1999 and July 2000. Differences between samples times were tested using the between-groups test (Equation 3.7.1, Methods).

Table 4.6.1 F statistics for seven sample times, overall sites for 6 microsatellite loci

Sample time	6 loci F_{IT}	6 loci F_{ST}	6 loci F_{IS}
July 1998	0.316^{****}	0.036^{****}	0.291^{****}
September 1998	0.272^{****}	0.054^{****}	0.230^{****}
November 1998	0.329^{****}	0.028^{NS}	0.310^{****}
July 1999	0.179^{****}	0.031^{****}	0.153^{****}
September 1999	0.207^{***}	0.048^{****}	0.167^{****}
July 2000	0.224^{****}	0.066^{****}	0.169^{****}
October 2000	0.196_{****}	0.048^{****}	0.155^{****}

p 0.05^{*}, p 0.01^{**}, p 0.001^{***} p 0.0001^{****}

p values based on 10000 randomisations; F_{IT} randomisation of alleles over all samples, F_{ST} randomisation of genotypes among samples, F_{IS} randomisation of alleles within samples, proportion equal to or larger than observed.

4.6.2 Percentage contribution of each locus to F statistics

The contribution of each locus to F statistics for each sample time was estimated following the method of Goudet et al. (1994). The highest percentage contribution was due to locus Ssa 197 at four of the sample times and from locus Ssosl 85 at the other two sample times. The highest contribution was between 20.043 % and 24.208 %. Locus Ssa 289 made the lowest contribution at each sample time, between 8.597 % and 12.995 %. Locus Ssosl 417 had the second lowest percentage contribution in each sample time except September 1999; values were between 10.95 and 16.92 (Figures 4.6.2.1 to 4.6.2.6.). The differences between the highest and lowest percentage contribution were 14.9 %, 17.58 %, 10.09 %, 7.05%, 15.71 %, 9.93 % in sample times 1-6 respectively. Thus the loci selected in this study had similar percentage contributions to estimation of population structure.

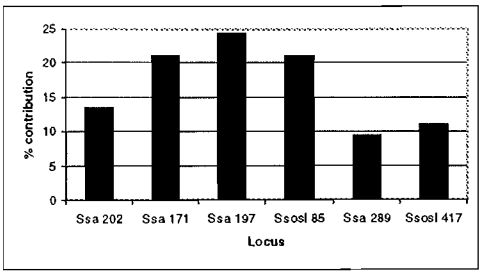


Figure 4.6.2.1 Percentage contribution of each locus to total F statistics, July 1998

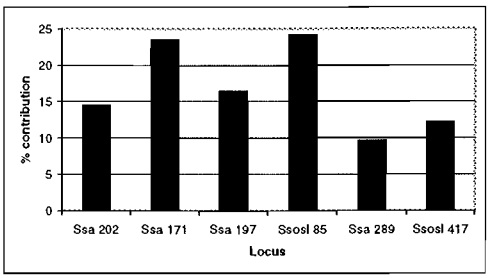


Figure 4.6.2.2 Percentage contribution of each locus to total F statistics, September 1998

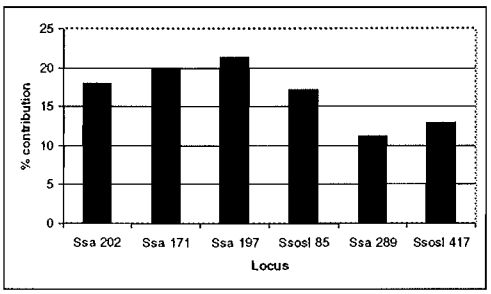


Figure 4.6.2.3 Percentage contribution of each locus to total F statistics, July 1999

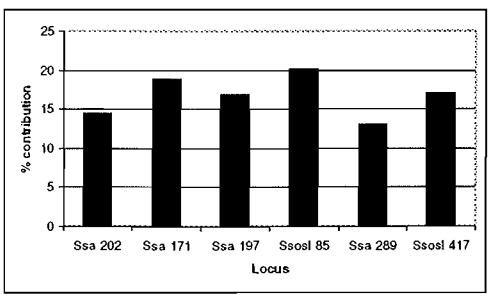


Figure 4.6.2.4 Percentage contribution of each locus to total F statistics, September 1999

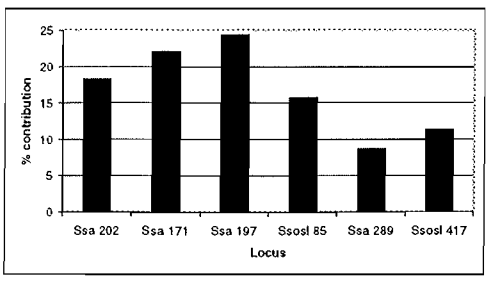


Figure 4.6.2.5 Percentage contribution of each locus to total F statistics, July 2000

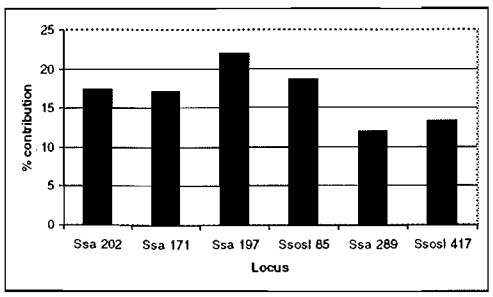


Figure 4.6.2.6 Percentage contribution of each locus to total F statistics, October 2000

4.6.3 Contribution of each locus to over all sites F_{IS} estimation

Very high values of overall sites F_{IS} for each sample time were estimated in this study (Table 4.6.1). The contribution of each locus to estimation of F_{IS} was analysed at seven sample times. F_{IS} values obtained using locus Ssosl 417 were much higher than the average of the other loci and were outside the standard error of the overall locus (including Ssosl 417) value at each sample time (Figure 4.6.3.1 to 4.6.3.6).

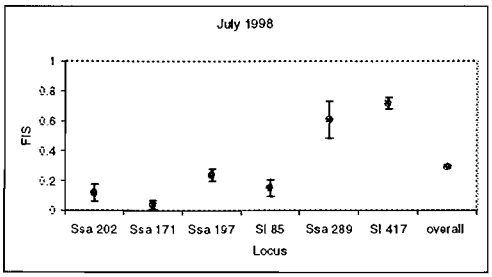


Figure 4.6.3.1 F_{IS} values per locus and over all loci, July 1998

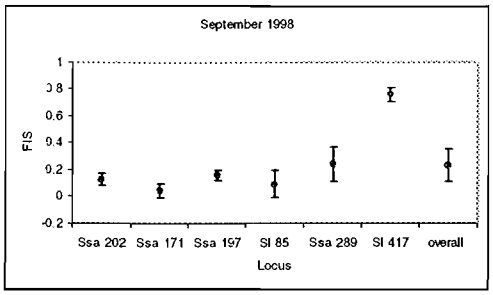


Figure 4.6.3.2 F_{IS} values per locus and over all loci, September 1998

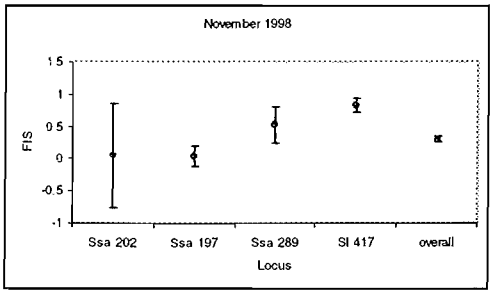


Figure 4.6.3.3 F_{IS} values per locus and over all loci, July 1999

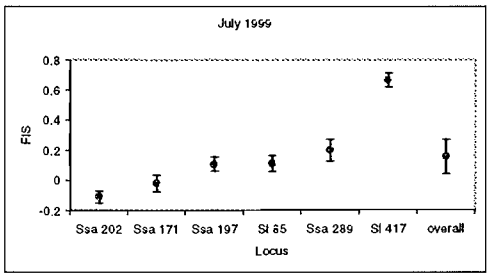


Figure 4.6.3.4 F_{IS} values per locus and over all loci, September 1999

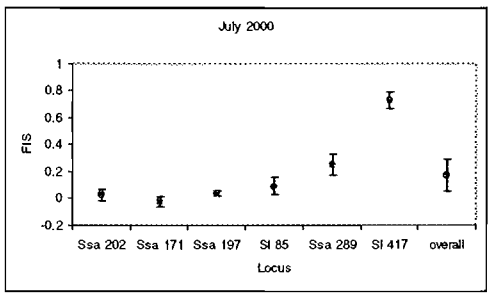


Figure 4.6.3.5 F_{IS} values per locus and over all loci, July 2000

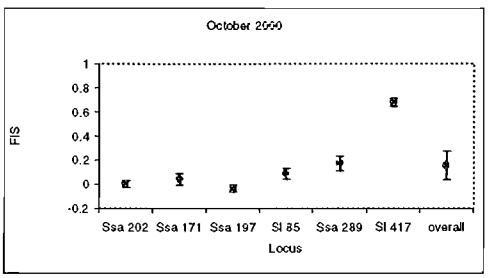


Figure 4.6.3.6 F_{IS} values per locus and over all loci, October 2000

4.6.4 Five-locus F statistics

High F_{IS} values were estimated with six loci including locus Ssosl 417, therefore data from Ssosl 417 were removed and F statistics calculated using 5 loci only. With 5 loci, significant F_{IT} was detected at each sample time (F_{IT} 0.075 to 0.226), significant F_{ST} was detected at each sample time except November 1998 (F_{ST} = 0.03 to 0.052) and significant F_{IS} was detected at each sample time (F_{IS} 0.044 to 0.202) (Table 4.6.4). Estimation of F statistics with 5 loci only resulted in lower estimates of F_{IT} at each sample time (Figure 4.6.4.1), lower estimates of F_{ST} at each sample time except July 1999 (Figure 4.6.4.2) and lower estimates of F_{IS} (Figure 4.6.4.3).

No significant difference was detected between over all sites F_{IT} values for Summer and Autumn in any year. No significant difference was detected between over all sites F_{ST} for Summer and Autumn for any year. No significant difference in F_{ST} values was detected between July 1998 and July 1999 or between July 1999 and July 2000. No significant difference between F_{IS} estimates in July 1999 and July 2000 were detected, however significant differentiation ($p < 0.01$) between F_{IS} in July 1998 and July 1999 was detected. Differentiation between groups was tested using Equation 3.7.1 (Methods).

Table 4.6.4 F statistics for seven sample times over 5 loci (no Ssosl 417)

Sample time	5 loci F_{IT}	5 loci F_{ST}	5 loci F_{IS}
July 1998	0.226^{****}	0.030^{****}	0.202^{****}
September 1998	0.157^{****}	0.046^{****}	0.116^{****}
November 1998	0.200^{**}	0.046^{NS}	0.161^{*}
July 1999	0.076^{****}	0.031^{****}	0.046^{***}
September 1999	0.084^{****}	0.039^{****}	0.046^{**}
July 2000	0.105^{****}	0.052^{****}	0.056^{***}
October 2000	0.075^{****}	0.032^{****}	0.044^{**}

p values based on 10000 randomisations; F_{IT} randomisation of alleles over all samples, F_{ST} randomisation of genotypes among samples, F_{IS} randomisation of alleles within samples, proportion equal to or larger than observed. p 0.05^{*}, p 0.01^{**}, p 0.001^{***} p 0.0001^{****}

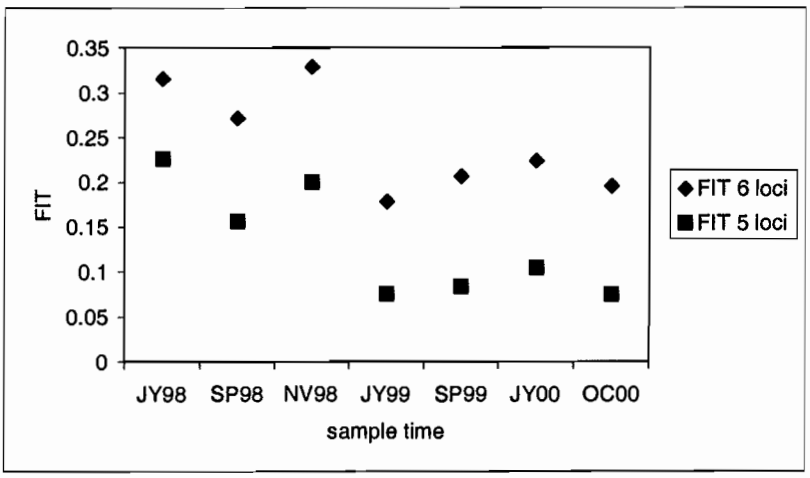


Figure 4.6.4.1 F_{IT} per sample time calculated with 6 loci and with 5 loci

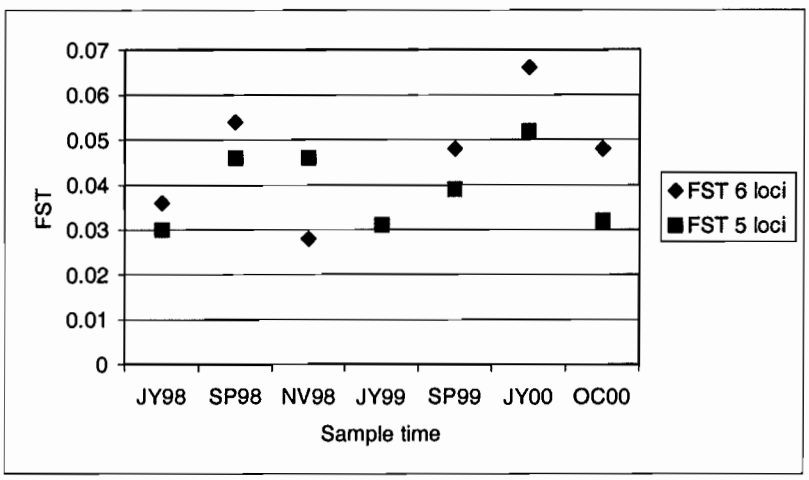


Figure 4.6.4.2 F_{ST} per sample time calculated with 6 loci and with 5 loci

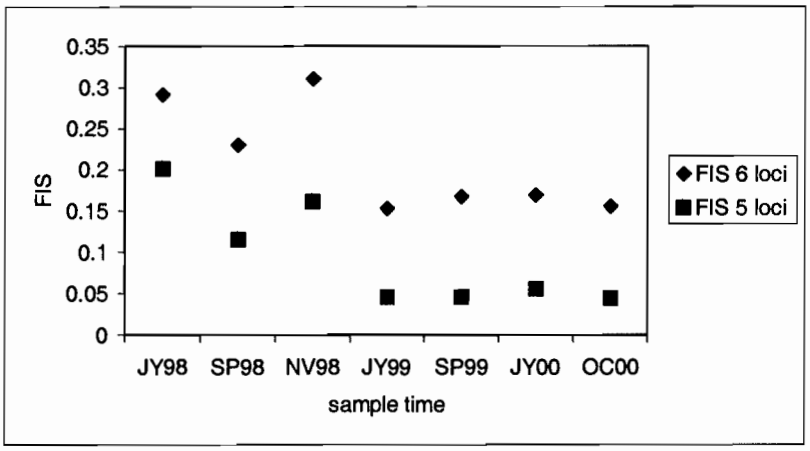


Figure 4.6.4.3 F_{IS} per sample time calculated with 6 loci and with 5 loci

Significant F_{ST} could be due to non-random return of adults to spawn or due to sampling of small numbers of families per site. The possibility of sampling small numbers of families per site can be ruled out if pairwise F_{ST} values were correlated with environmental distances between sites and or differences in environmental variables between sites and if temporal stability of site allele frequency occurred.

Estimates of F_{ST} in July 1998, November 1998 and July 1999 are within the range of previously published estimates of for *S. salar* populations in rivers of similar size; the values for September 1998, September 1999, July 2000 and October 2000 are larger than previously published values. Previous estimates appear to be similar magnitude, independent of the molecular marker and independent of the size of distances between sites. Previous estimates of within river differentiation varied between F_{ST} = 0.0109 (Beacham and Dempson 1998) and F_{ST} = 0.034 (Garant et al. 2000). Percentage differentiation between sites varied between 0.7 $\%^{NS}$ (Jordan et al. 1992) and 3.6 $\%^{SE\ 1.3}$ (Stahl 1998) (1.6 % (O'Connell et al. 1995), 1.6 $\%^{SE\ 0.38}$ (Galvin et al. 1994), 3.4 $\%^{***}$ (Galvin et al. 1996), 3.4 % (McElligott and Cross 1991)).

Estimates of F_{IS} obtained in this study were high, however, it is not possible to compare these to F_{IS} values for other *S. salar* populations. No F_{IS} values for other *S. salar* populations have previously been published, however a population of anadromous Arctic Char (*Salvelinus alpinus*) (Bernatchez et al. 1998) had F_{IS} values of 0.078 to 0.118.

4.7 Five-locus F_{IS} per site

F_{IS} per site varied with locus and sample time (Appendix 7.4.7.1 to 7.4.7.7). Significant F_{IS} was detected at 10 sites in July 1998 (Figure 4.7.1), three sites in September 1998 (Figure 4.7.2), two sites in July 1999 (Figure 4.7.3), four sites in September 1999 (Figure 4.7.4) and July 2000 (Figure 4.7.5) and three sites in October 2000 (Figure 4.7.6). Significant F_{IS} was detected at Moreton Ford (MF) at five sample times, significant F_{IS} was detected at Norris Farm (NF) at four sample times and significant F_{IS} was detected at Lewell Mill (LM) at three sample times (Table 4.7.1).

Table 4.7.1 Sites with significant F_{IS} for 6 sample times

Sample time	Significant F_{IS} at sites
July 1998	TF^{*a}, WH**, NF*, LM^{*a}, EB^{*a}, ES^{*a}, ESMS^{*a}, WS^{*a}, HA^{*a}, MF**
September 1998	NF^{*a}, MB**, MF^{*a}
July 1999	BM***, MF*
September 1999	NF***, EB*, BM*, MF*
July 2000	WH*, LM**, ES^{*a}, MF^{*a}
October 2000	NF**, LM**, MB**

Sig at p 0.05 *, p 0.01 **, p 0.001 ***.
Bonferroni corrected significance; indicative adjusted nominal level (5%) *a.

A large F_{IS} value with low allele number indicates a small number of families. If fish are randomly mating within a site then F_{IS} will be zero, however, if significant F_{IS} is detected within a site, it is possible that more than one population existed at that site; effectively populations have been pooled. The number of adults spawing at a site cannot be directly monitored in this river, however, the number of redds in an area will give an indication of the number of females spawning at a site.

In January 2000 an assessment of the number of redds (salmon spawning areas) was made at 10 sites. Only redds bigger than 50cm in length were noted. This was to reduce the possibility of counting small *S. trutta* (resident Brown trout and sea trout) redds. Crisp (2000) noted that salmon redds are about 3.5 times the length of the female that excavates it. With the minimum length of Frome salmon approximating 45 cm that equals a minimum redd length of around 1.5 m. Thus some small trout or sea trout redds may have been counted in error. Personal observation in the relatively slow flowing chalk streams however indicate that smaller redds may be constructed by salmon and thus only counting redds >1.5 m would miss some redds. No differentiation between salmon and large sea trout redds could be made.

The largest number of redds were detected at Waterbarn Stream (WS), however at all other sites either one or no redds were detected. Waterbarn stream had a low and non-significant F_{IS} as would be expected if a large number of adults spawned at this site, as indicated by the high redd count. High, significant F_{IS} was detected at Lewell Mill (LM) and Moreton Ford (MF) and redd counts at these sites were low, indicating that a small number of adults spawned at these sites.

Table 4.7.2 Number of redds per site in 2000

Site Name	Number of redds	F_{IS} JY00
Muckleford Bridge	No redds seen	0.01^{NS}
Whitfield Hatches	1 redd	0.115^{NS}
Norris Mill	No redds seen	0.006^{NS}
Lewell Mill	1 redd	0.128^{**}
Tadnoll Brook	1 redd	0.007^{NS}
Moreton Ford	No redds seen	0.243^{*a}
East Burton	1 redd	0.038^{NS}
Waterbarn	7 redds	0.051^{NS}
Bindon Millstream	No redds seen	0.01^{NS}
Wool Stream	No redds seen	0.061^{NS}

P value based on 12600 randomisations, p 0.05 *, p 0.01 **, p 0.001***. Indicative adjusted nominal level (5%) was 0.00048, p 5 % adjusted *a.

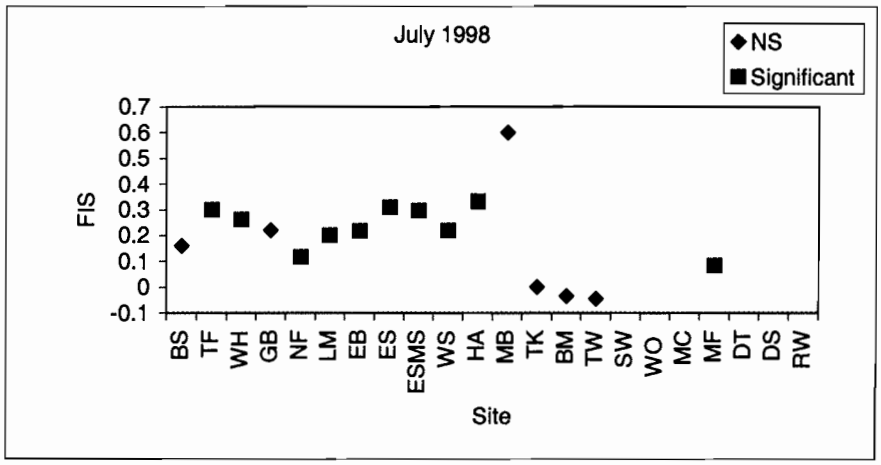


Figure 4.7.1 F_{IS} values per site, July 1998

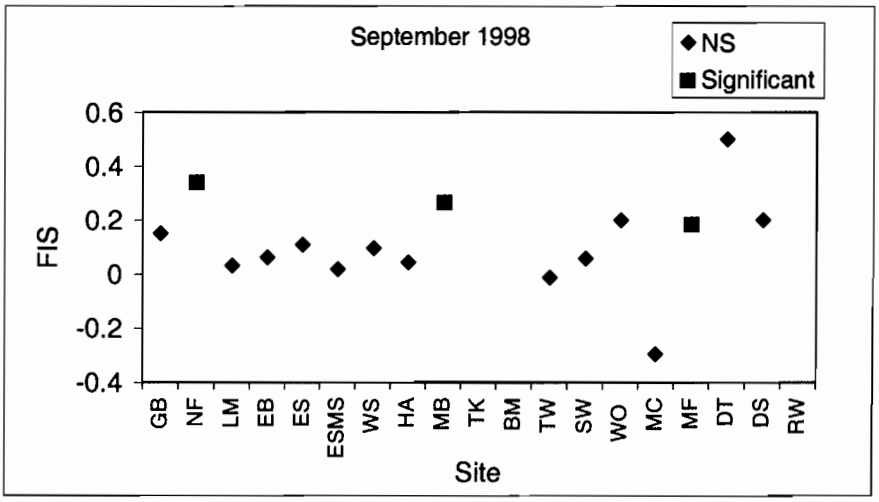


Figure 4.7.2 F_{IS} values per site, September 1998

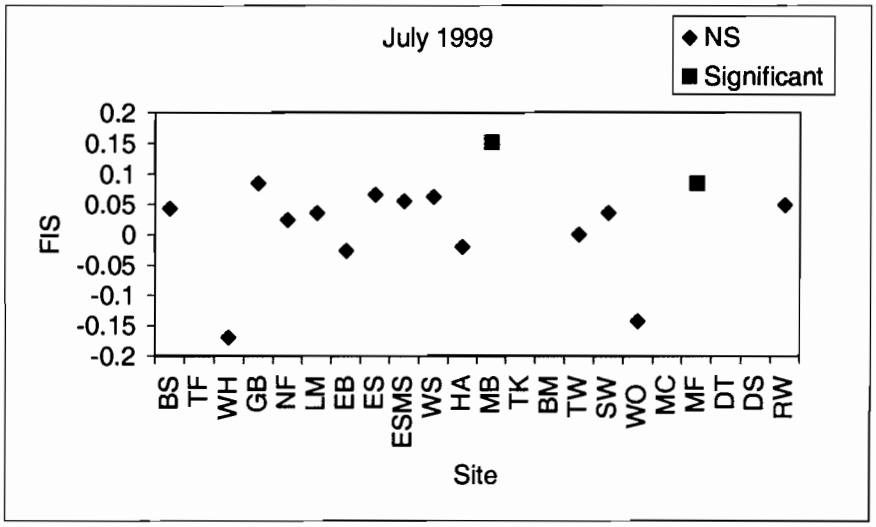


Figure 4.7.3 F_{IS} values per site, July 1999

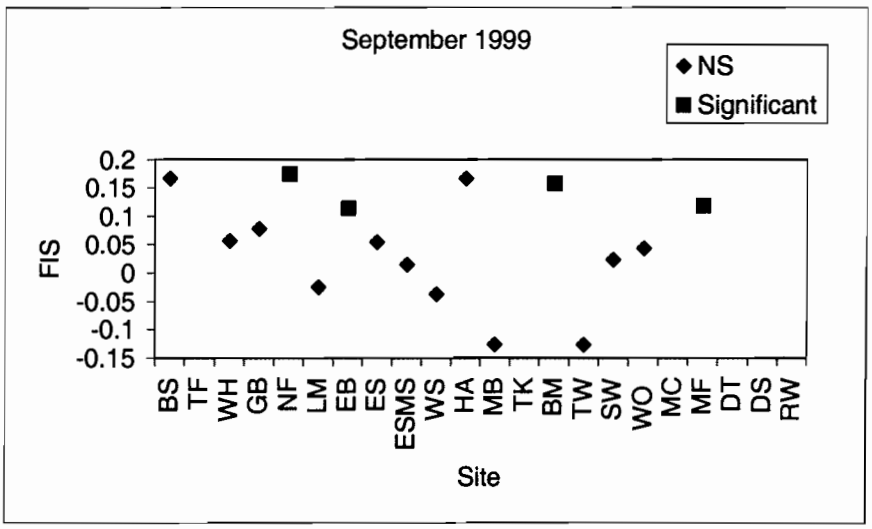


Figure 4.7.4 F_{IS} values per site, September 1999

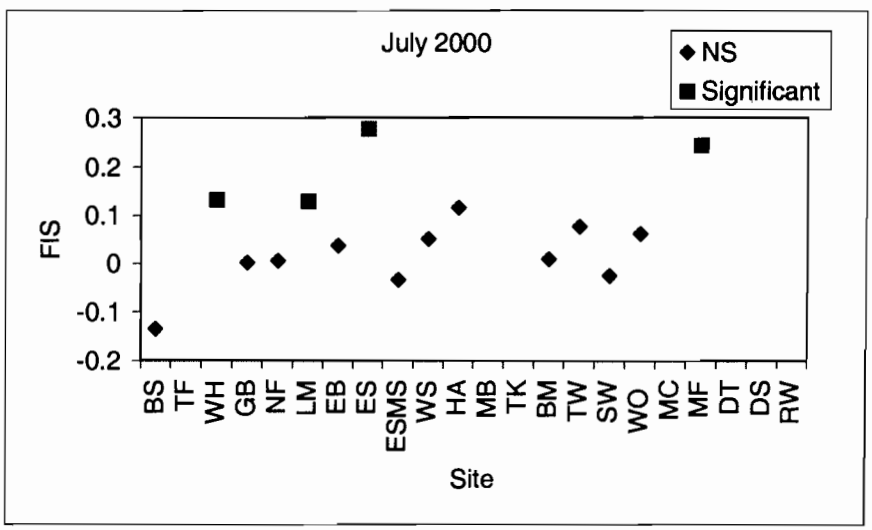


Figure 4.7.5 F_{IS} values per site, July 2000

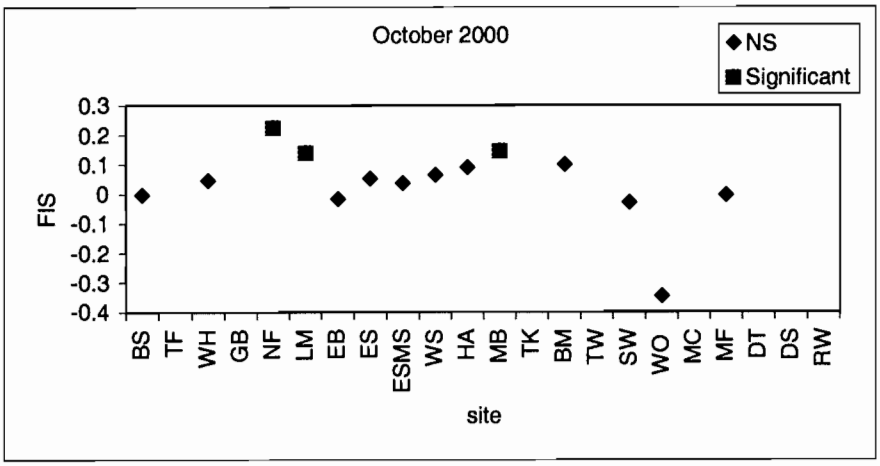


Figure 4.7.6 F_{IS} values per site, October 2000

4.8 Genetic differentiation between sites

4.8.1 Pairwise F_{ST}

F_{ST} was calculated between each pair of sites for each sample time to determine which sites were genetically differentiated and to determine the magnitude of between-site differentiation (Appendix Section 7.4.8, Figures 7.4.8.1 to 7.4.8.7). Significant pairwise F_{ST} estimates were obtained for a large number of sites at each sample time (Figures 4.8.1.1 to 4.8.1.6). Significance of pairwise F_{ST} was obtained by randomisations. Multiple tests were performed, therefore significance was Bonferroni corrected. This correction is very conservative and non-corrected significance values were also noted.

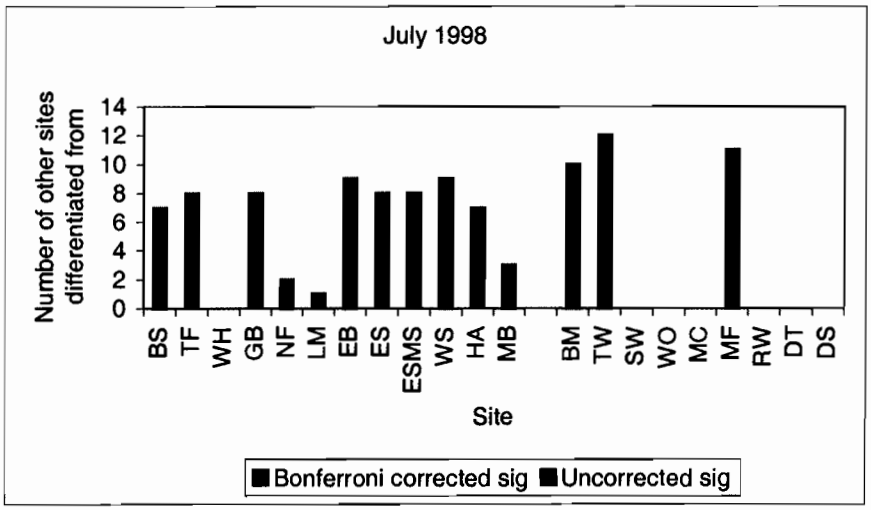


Figure 4.8.1.1 Number of sites that each site was significantly differentiated from in July 1998, total 15 sites

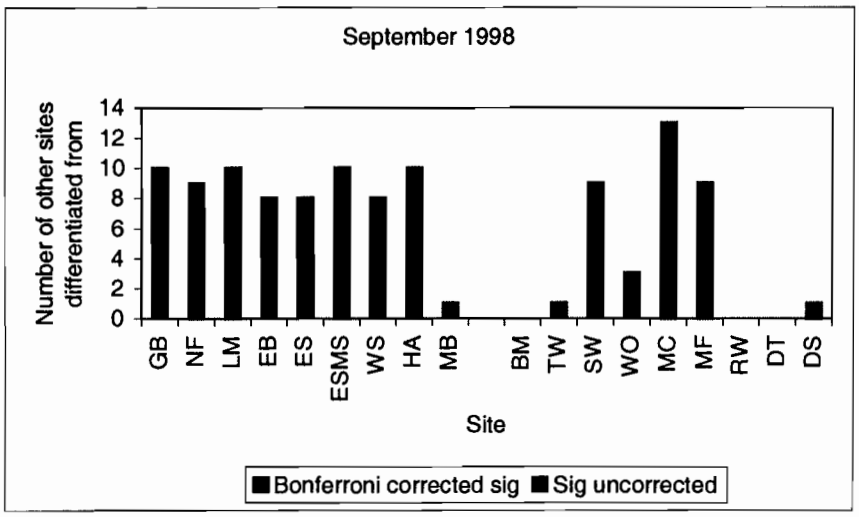


Figure 4.8.1.2 Number of sites that each site was significantly differentiated from in September 1998, total 16 sites

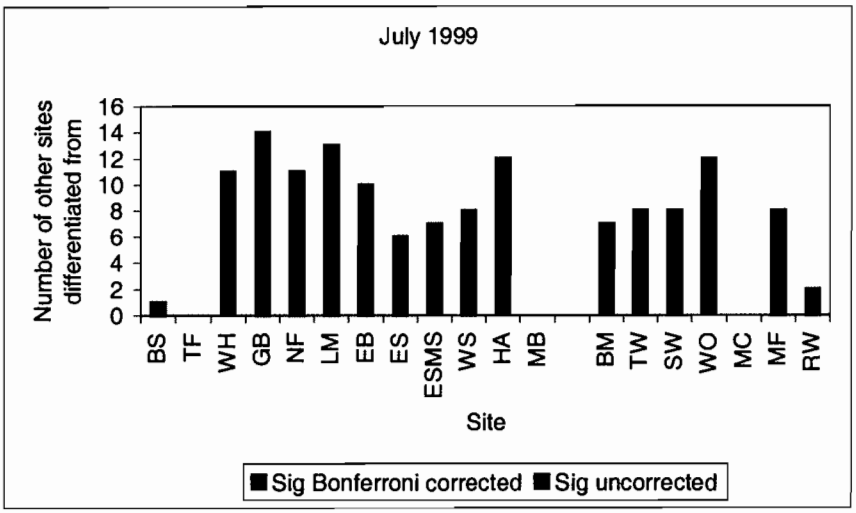


Figure 4.8.1.3 Number of sites that each site was significantly differentiated from in July 1999, total 15 sites

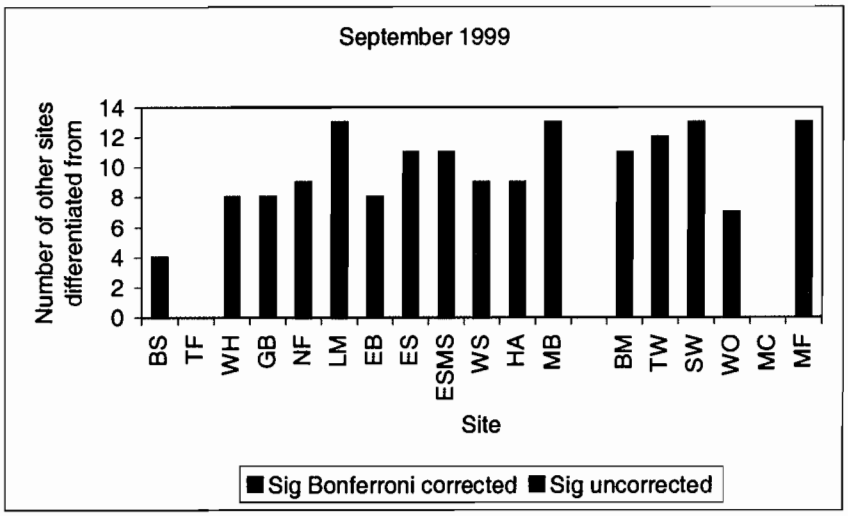


Figure 4.8.1.4 Number of sites that each site was significantly differentiated from in September 1999, total 16 sites

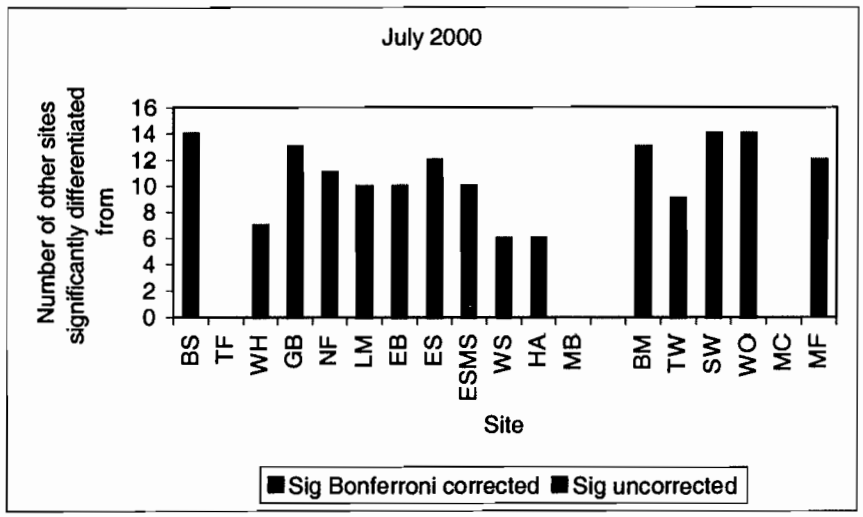


Figure 4.8.1.5 Number of sites that each site was significantly differentiated from, July 2000. Total 15 sites

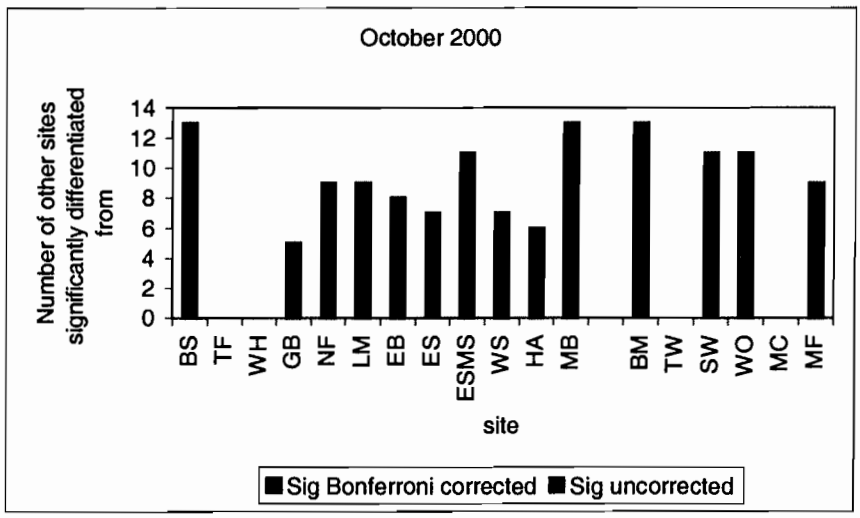


Figure 4.8.1.6 Number of sites that each site was significantly differentiated from, October 2000, total 14 sites

4.8.2 Magnitude of pairwise F_{ST}

The lowest significant pairwise F_{ST} value in July 1998 was 0.0005, between sites EB-WS and the highest significant pairwise F_{ST} value was 0.1126, between sites MB-TW. In September 1998, the lowest significant pairwise F_{ST} value was 0.0167, between sites EB-MF and the largest was 0.2459, between sites HA-MC. In July 1999, the lowest significant pairwise F_{ST} value was 0.0086, between ES-WS and the highest F_{ST} was 0.2224, between WO-SW. In September 1999, the lowest significant pairwise F_{ST} value was 0.0025, between NF-WS and the highest was 0.1157, between SW-LM. In July 2000, the lowest significant pairwise F_{ST} value was 0.0044, between NF-WH and the highest was 0.1720, between NF-ESMS. In October 2000, the lowest significant pairwise F_{ST} value was 0.0098, between NF-ES and the highest was 0.1072, between WO-ESMS (Figure 4.8.2).

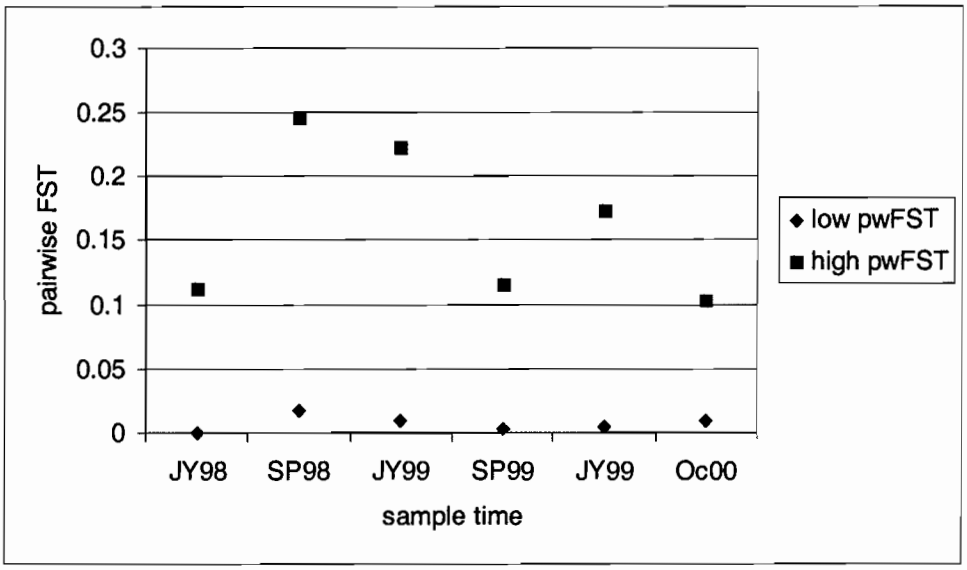


Figure 4.8.2 Lowest and highest pairwise F_{ST} at 6 sample times

4.9 Relationship between genetic population structure and geographical distance between sites

The relationship between population structure and distance between sites can be investigated by sequential pooling of adjacent sites and recalculation of F_{IS} for each pooling group stage and by correlation of pairwise F_{ST} with geographical distance between sites.

4.9.1 Pooling adjacent sites

To determine if substructure occurs in the Rivers Frome and Piddle at a certain level sites were successively pooled and F_{IS} re-calculated for each grouping following the method of Goudet et al. (1994). If substructure occurs at a certain level then a large jump in F_{IS} between the two pooling groups would be observed. In the Rivers Frome and Piddle, successive grouping of sites did not result in a distinct increase in F_{IS} with any pooling stage (Figures 4.9.1 to 4.9.6).

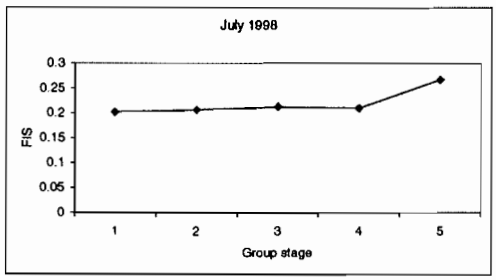


Figure 4.9.1 Change in F_{IS} with sample site pooling, July 1998

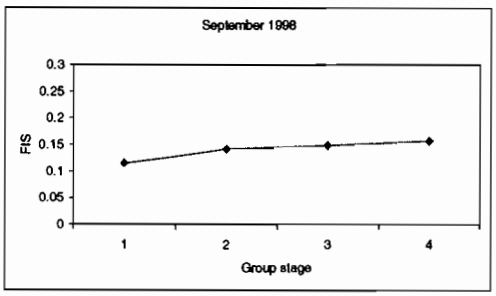


Figure 4.9.2 Change in F_{IS} with sample site pooling, September 1998

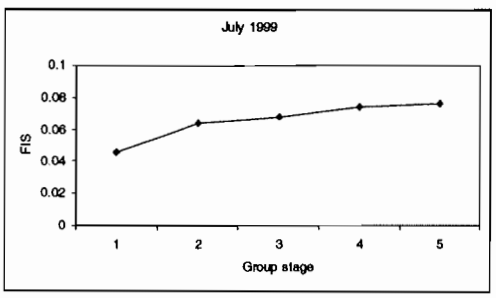


Figure 4.9.3 Change in F_{IS} with sample site pooling, July 1999

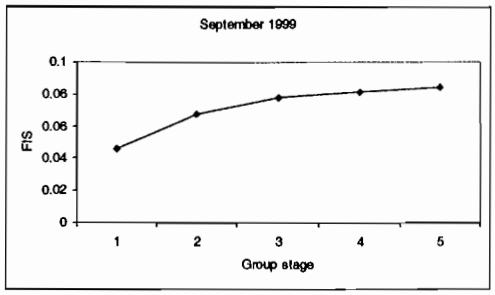


Figure 4.9.4 Change in F_{IS} with sample site pooling, September 1999

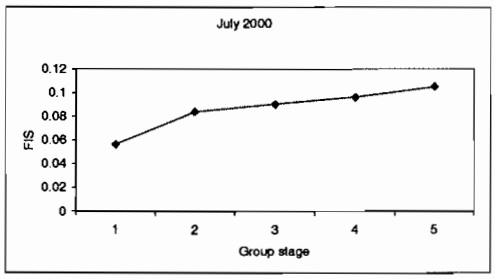


Figure 4.9.5 Change in F_{IS} with sample site pooling, July 2000

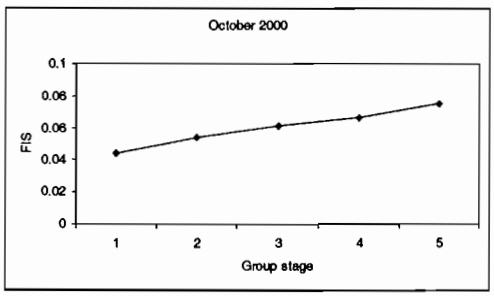


Figure 4.9.6 Change in F_{IS} with sample site pooling, October 2000

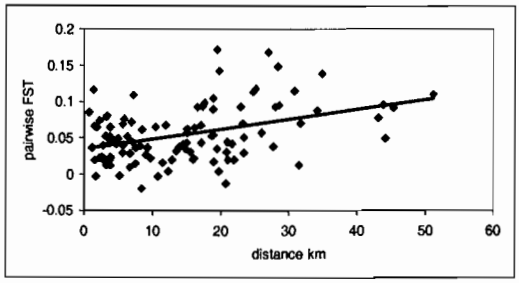
Pooling group stage

Stage 1	No pooling
Stage 2	Piddle (sites 1+2), Frome[a] (sites 3, 8, 9, 14, 17), Frome[b] (sites 7, 10, 13, 15, 18, 19, 21), Frome[c] (sites 4, 5, 6, 16, 20, 22) and Frome[d] (11, 22).
Stage 3	Piddle (sites 1+2), Frome[a+b] (sites 3, 7, 8, 9, 10, 13, 14, 15, 17, 18, 19, 21) and Frome[c+d] (sites 4, 5, 6, 11, 12, 16, 20, 22).
Stage 4	Piddle (sites 1-2) and Frome (sites 3-22).
Stage 5	All sites pooled.

(see site map Section 3, Methods, Figure 3.1. for site names and location);

4.9.2 Geographical distance between sites and pairwise F_{ST}

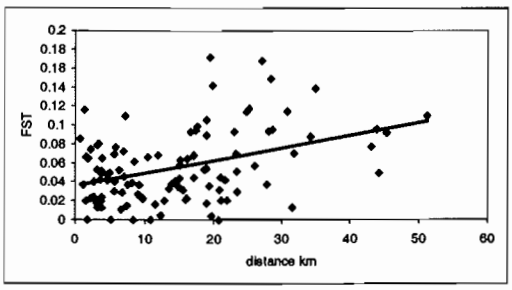
Significant genetic differentiation between sites (pairwise F_{ST}) was detected despite very small geographical distances between sites. The largest distance apart of any pair was 56 km and the smallest distance was 0.74 km. A significant positive correlation between pairwise F_{ST} and geographic distance was observed in July 2000 (Figure 4.9.2.1). No correlation was detected between pairwise F_{ST} and geographic distance at any other sample time (Appendix Section 7.4.9, Figures 7.4.9.1 to 7.4.9.5).



r_p 0.398
p 0.0195

Figure 4.9.2.1 Pairwise F_{ST} and geographic distance between sites, July 2000

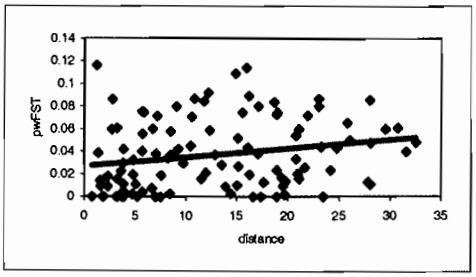
If there are no differences in allele frequency between sites then F_{ST} will be zero. It is possible to obtain negative F_{ST} values if among-individuals variance is greater than the among subpopulations variance. In this study negative pairwise F_{ST} values were obtained at each sample time and is possible that the Rp between pairwise F_{ST} and geographic distance is affected by the inclusion of negative F_{ST} values, therefore negative F_{ST} values were set to zero. In July 2000, changing negative F_{ST} values to zero increased the Rp from 0.398 to 0.402 (Figure 4.9.2.2), however significant correlation was not detected at any other sample time (Appendix Section 7.4.9, Figures 7.4.9.6 to 7.4.9.11).



R_p 0.402
P 0.018

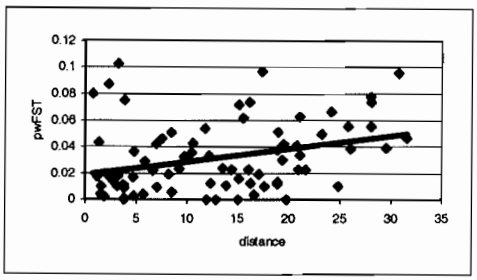
Figure 4.9.2.2 Pairwise F_{ST} and geographic distance between sites, July 2000, negative F_{ST} values set to zero

The relationship between genetic differentiation between sites and geographic distances between sites was investigated using the river Frome samples only. Significant correlation was detected between River Frome pairwise F_{ST} values and distance between sites in September 1999 (Figure 4.9.2.3) and October 2000 (Figure 4.9.2.4). No correlation was detected at any other sample time (Appendix Section 7.4.9, Figures 7.4.9.12 to 7.4.9.14).



Rp 0.213
p 0.033

Figure 4.9.2.3 Pairwise F_{ST} and geographic distance between sites, River Frome only, September 1999, negative F_{ST} values set to zero



Rp 0.314
p 0.0122

Figure 4.9.2.4 Pairwise F_{ST} and geographic distance between sites, River Frome only, October 2000, negative F_{ST} values set to zero

4.10 Environmental characteristics

4.10.1 Flow rate category

Flow rate category was determined at each site. A significant positive correlation between parr length and flow category was detected (Figure 4.10.1.2). Significant relationships were shown for July and September samples in all three years (R^2 = 0.65, $p<0.05$ – 0.92, $p<$ 0.001). As absolute lengths of parr varied between years, comparisons between combined surveys were made on ranked data, largest parr being ranked one (Figure 4.10.1.1). Again significant differences were found between sites indicating that good growth was site specific and not random. Ranked parr lengths for all samples were also significantly correlated with river flow category ($p<0.05$).

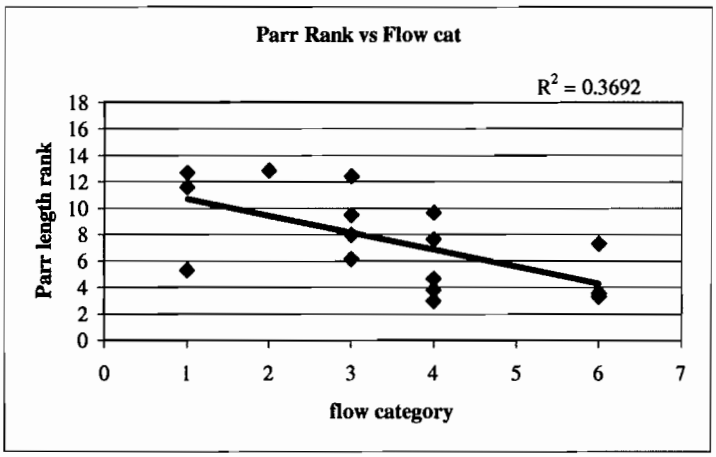


Figure 4.10.1.1 Ranked parr length versus stream order. Note largest parr ranked 1

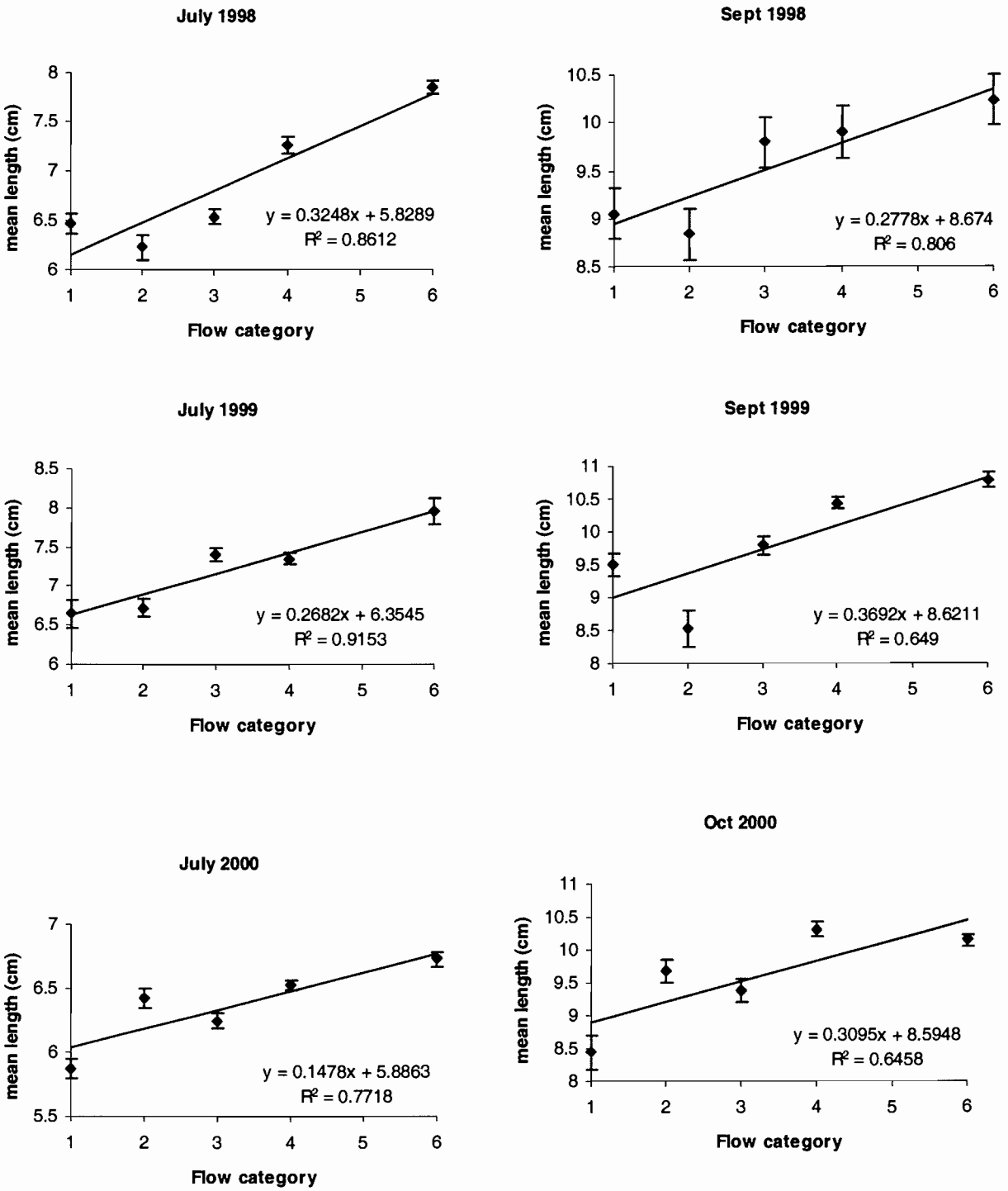


Figure 4.10.1.2 Relationship between mean length of salmon parr (±SE) and flow category in the River Frome

4.10.2 Temperature

Temperature loggers were placed in the river at eight locations. These sites encompassed the majority of the major river biotopes covered by the fish sampling (Table 4.10.2.1.).

Table 4.10.2.1 Locations of temperature loggers and flow category of each site

Logger No	River / Stream	Location	Flow Cat.	Exact location
1	Tadnoll Brook	Winfrith Heath	1	802875
2	Wool Stream	Bindon Abbey	1	854869
3	Bindon Millstream	Bindon Abbey	2	854869
4	R. Frome	Norris Mill	3	738908
5	R. Frome	Lewell Mill	4	739901
6	R. Frome	Muckleford Br.	4	642937
7	East Stoke Millhead	East Stoke	6	870868
8	R. Frome	East Burton	6	824875

Temperature loggers were calibrated against each other prior to placing in the river, a maximum mean variation of 0.27° Celsius was found between them. The variance between loggers was not significant (Moods median test $p<0.01$). The loggers were installed on 19/1/2000 and were set to log temperature every hour. Loggers were downloaded at intervals throughout the year. Final data for analysis was collected on 4/1/2001.

Many studies have shown that fish growth is highly correlated with temperature (Elliott 1975 *et al*, Crisp 2000). There is a threshold temperature below which they do not grow (in salmon 6° Celsius) and temperature requirements for fish are often expressed in degree-days above this threshold. However, growth and temperature is not a linear function. Above the threshold temperature growth rates increase up to an optimal temperature and then decline until an upper limit for growth (or survival) is reached (Table 4.10.2.2).

Table 4.10.2.2 Temperature limits for salmon parr growth (from Elliott & Hurley 1997)

	Salmo salar
Upper temperature limit (TU)	22.5° Celsius
Optimum growth temperature (TM)	15.9° Celsius
Lower temperature limit (TL)	6.0° Celsius

River temperatures were therefore converted to optimised degree days (ODD) in order to more accurately reflect this pattern of temperature influence on growth. Figure 4.10.2.1. shows the values for both degree-days and optimised degree-day for temperature values between 1 and 24° Celsius and clearly shows the differing results obtained from the two methods, with ODD more accurately reflecting the influence of temperature upon the fish growth.

Eqn 1 $ODD = (T-T_{LIM})/(TM-T_{LIM})]$

Where: T = water temperature, T_{LIM} = TL if T⊘ TM or T_{LIM} = TU if T ≥TM.

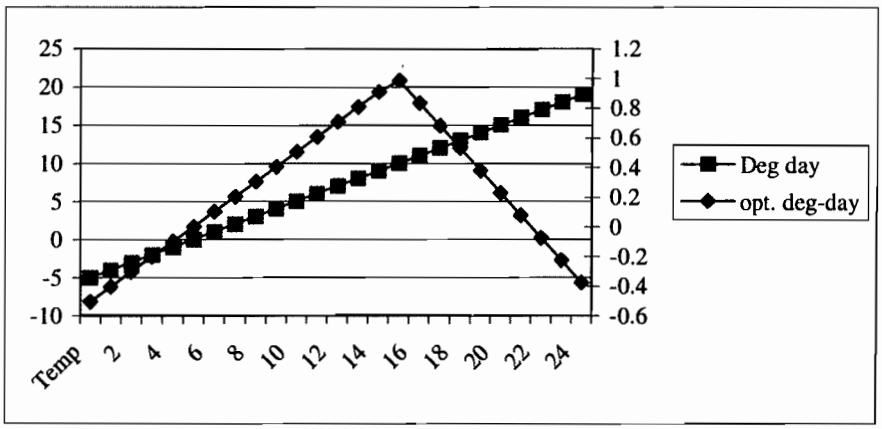


Figure 4.10.2.1 Temperature values of 1-25° Celsius converted to Degree Days >6 and Optimised Degree Days (ODD)

Temperature data were also analysed with reference to the percentage of the maximum optimal temperature for growth over the time periods noted for the Instantaneous Growth rate calculations i.e the observed value compared with the value if the temperature had been 15.9° Celsius.

Between 1st May (nominal gravel emergence date for salmon) and 12th July (average date of summer sampling) values of ODD averaged between 73% and 84% of the maximum possible. In the period between 12th July and 20th October (approximate date of autumn sampling) variation between sites was less, ranging from 79% to 83% of the maximum possible. May to July values were significantly ($p<0.01$) correlated with distance from source of the site, with higher ODD values being found in the furthest downstream sites (Figure 4.10.2.2). July to October values however were not correlated with distance from source. This difference could be due to the higher difference between air and water temperature in the river between May and July compared with between July and October (CEH data).

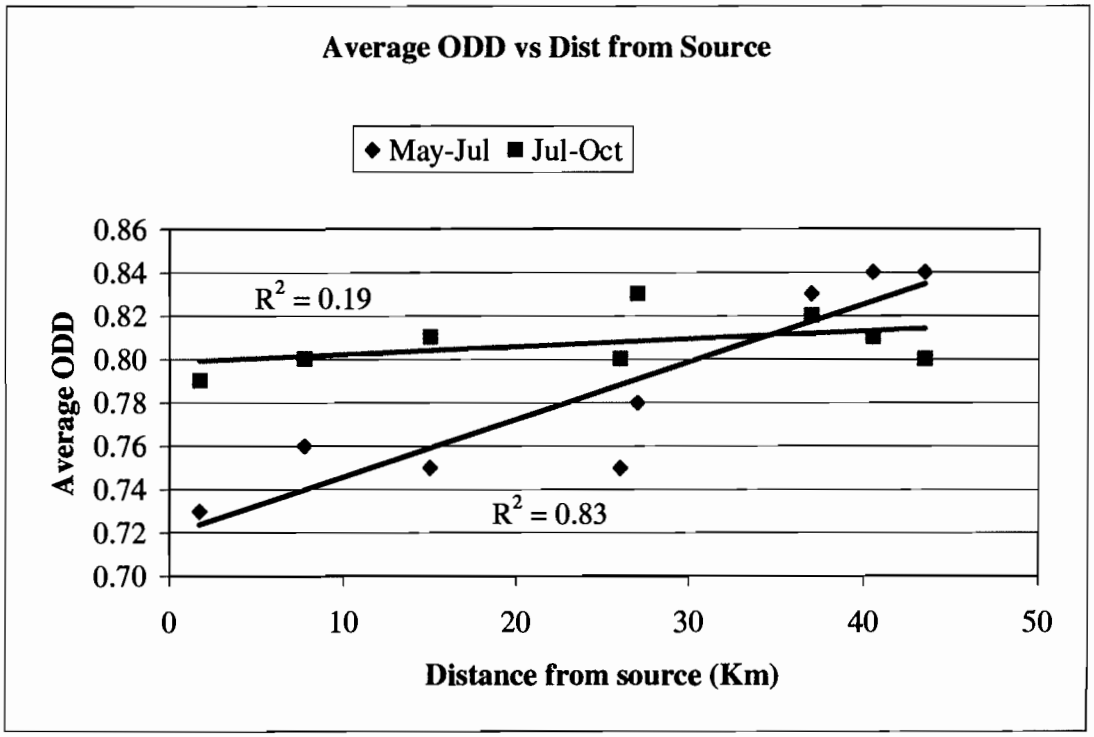


Figure 4.10.2.2 Relationship between Average optimised degree days and distance from source for the periods May to July and July to October

No relationship was found between flow category and May to July or July to October ODD. The ODD values were compared with mean fish length and Instantaneous Growth Rate (G) at each of the sites where the temperature was monitored. No relationship between temperature and mean fish length in July and October or growth rate could be found (Figure 4.10.2.3). In July however the lowest growth rate observed was also associated with the lowest ODD observed between May and July. Likewise in October the two lowest growth rates were associated with the lowest ODD between July and October.

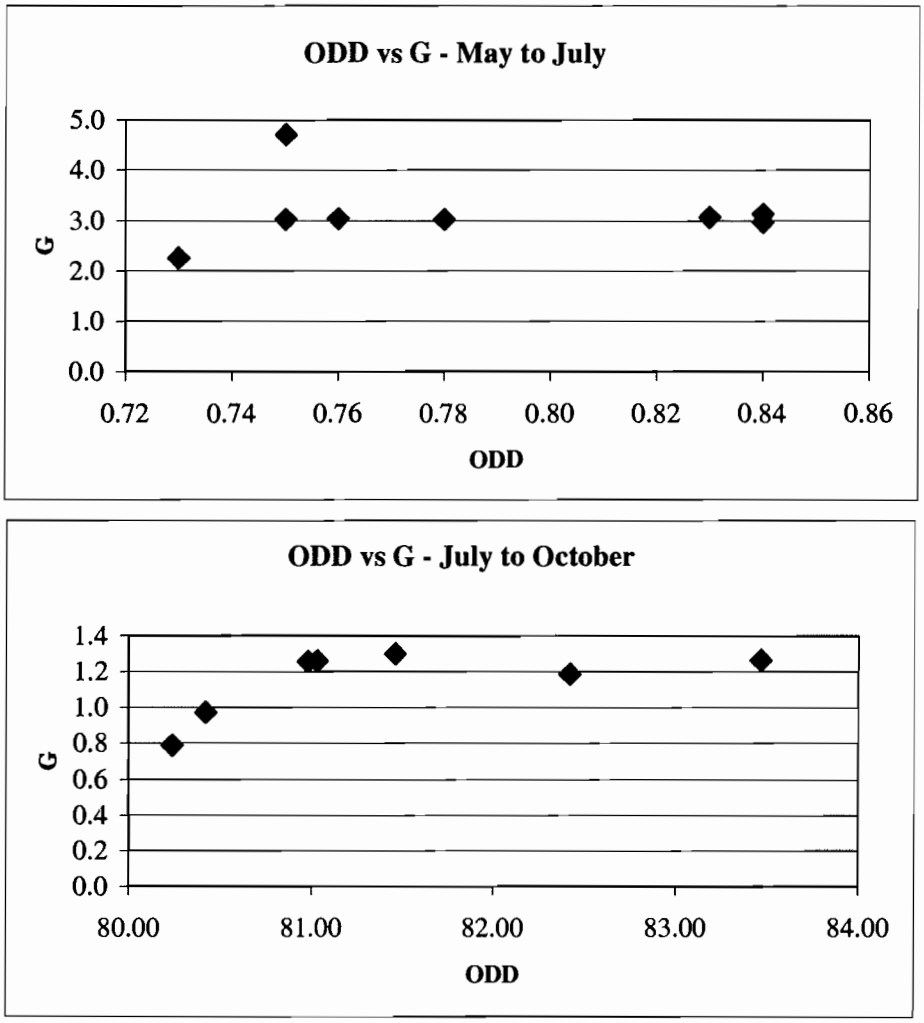


Figure 4.10.2.3 Relationship between salmon parr growth and ODD for the periods May to July (M-J) and July to October (J-O)

4.11 Genetic differentiation and environmental differences between sites

Genetic differentiation was detected between sites, measured as pairwise F_{ST}. Genetic differentiation may be correlated with environmental differences between sites. Environmental differences may be correlated with distance therefore if significant correlation is detected between pairwise F_{ST} and environment, partial regression can be used to control for the effect of one variable while testing the effect of another.

River temperature was measured at seven sites (WH, NF, LM, EB, ES, BM, WO) in July and October 2000 only and river temperature was converted to optimal degree days. Difference in optimal degree days (ODD) was largest between sites BM and WH in July 2000 (Appendix Section 7.4.11, Figure 7.4.11.1) and was largest between sites ES and LM in October 2000 (Appendix Section 7.4.11, Figure 7.4.11.2). No correlation was detected between differences in optimal degree days between sites and pairwise F_{ST} between sites for July 2000 (Rp -0.202, P 0.379) or for October 2000 (Rp 0.197, p 0.392).

Differences in flow rate category were calculated at 13 sites in July 1999, 14 sites in September 1998, 14 sites in July 1999, 15 sites in September 1999, 14 sites in July 2000 and 13 sites in October 2000 (Appendix Section 7.4.11, Figures 7.4.11.3 to 7.4.11.8). No correlation was detected between differences in flow rate category between sites and pairwise F_{ST} at any sample time; July 1998 Rp –0.056, p 0.624, September 1998 Rp 0.144 p 0.174, July 1999 Rp -0.044, p 0.68, September 1999 Rp 0.124, p 0.208, July 2000 Rp 0.042, p 0.693, October 2000 Rp –0.048, p 0.677.

4.12 Temporal stability of site allele frequency

Detection of temporal stability of site allele frequency would indicate that adult *S. salar* returned to the natal site to spawn and would allow the possibility of sampling small numbers of families to be ruled out.

Eleven sites; West Holme, Grey's Bridge, Norris Farm, Lewell Mill, East Burton, East Stoke, East Stoke Millstream, Waterbarn Stream, Whitfield Hatches and Bindon Millstream, were sampled in all three years. Juveniles sampled in the Autumn of each sample year were not used in the analysis because it is possible that these fish may have migrated between sites. F statistics were estimated for just the 11 sites sampled in the Summer of each year. Over 5 loci, significant F_{IT} was detected in each of the three years, significant F_{ST} was detected in each of the three years and significant F_{IS} was detected in each of the three year (Table 4.12.1.).

Table 4.12.1 Summary F statistics over 5 loci over all sites

sample time	N	F_{IT}	F_{ST}	F_{IS}
July 1998	305	0.219^{****}	0.02^{****}	0.203^{****}
July 1999	231	0.067^{****}	0.024^{****}	0.044^{**}
July 2000	283	0.092^{****}	0.045^{****}	0.049^{**}

P values based on 10000 randomisations; F_{IT} randomisation of alleles over all samples, F_{ST} randomisation of genotypes among samples, F_{IS} randomisation of alleles within samples, proportion equal to or larger than observed. p 0.01^{**} $p0.001^{***}$ $p0.0001^{****}$.

Pairwise F_{ST} was calculated across years (Tables 4.12.3 and 4.12.4). A test was applied to estimate the temporal stability of allele frequency. A significant negative value indicates temporal stability of allele frequency within sites. No significant temporal stability of site allele frequencies was detected (Table 4.12.2), thus it is not possible to state that adult *S. salar* returned to natal spawning sites within the Rivers Frome and Piddle in these three years.

Table 4.12.2 Temporal stability of site allele frequency; Q-Test

Year	11 sites sampled in each Summer	Negative F_{ST} values to zero	River Frome only
1998-2000	-0.102^{NS}	/	/
1998-1999	-0.063^{NS}	-0.049^{NS}	-0.022^{NS}
1999-2000	0.031^{NS}	0.018^{NS}	-0.047^{NS}

The power of the test was examined using data from a published study of 7 sites within a river, sampled over two consecutive years (Garant et al. 2000) (Table 4.12.5). Pairwise F_{ST} values were between 0.0077 and 0.0837. A significant negative test value was obtained; Q = -0.259 (p = 0.02) indicating temporal stability of allele frequency in this river.

Table 4.12.3 Pairwise F_{ST} values between 11 sites on the Rivers Frome and Piddle, sampled in July 1998-July 1999

site	JY98 BS	JY98 WH	JY98 GB	JY98 NF	JY98 LM	JY98 EB	JY98 ES	JY98 ESMS	JY98 WS	JY98 HA	JY98 BM
JY99 BS	**-0.0672**	-0.0292	-0.0492 *a	-0.0228	-0.0389	-0.0608	-0.041	-0.0523	-0.0767	-0.0365	-0.0325
JY99 WH	0.0589	**0.0655**	0.0539 *a	0.0198	-0.0216	-0.0133	-0.0289	-0.0199	-0.0093	-0.0196	0.0385 *
JY99 GB	0.0198	-0.0193	**0.0027 *a**	0.006 *a	0.0205 **	0.0157 *a	0.0132	0.0164 **	0.0083	0.0464 *a	0.04 *a
JY99 NF	0.042 **	0.0419	0.017 *a	**0.0372**	0.0244	0.0177 *a	0.016	0.0227 *a	0.0153 *a	0.0418 *a	0.0356 *a
JY99 LM	0.0726 **	0.0913	0.0989 *a	0.056 *a	**0.0409 *a**	0.0304 *a	0.0348	0.0291 *a	0.0379 *a	0.0526 *a	0.0379 *a
JY99 EB	0.0592 *	0.0111	0.0459 *a	0.0332 *	0.0568 *a	**0.0143 *a**	0.018	-0.0031 ***	0.0253 *a	0.0279 ***	0.0295 ***
JY99 ES	0.016 **	0.0173	0.0138 *	0.0377	0.0184 *	0.0009 **	**0.0024**	0.0041 *	-0.0131 **	0.013 **	0.0296 *a
JY99 ESMS	0.027 **	0.0338 *	0.0411 *a	0.0424 *a	0.0364 ***	0.0179 *a	0.0181	**0.0056 ***	0.0125 *a	0.0434 *a	0.0467 *a
JY99 WS	0.0493 ***	0.0075	0.0278 *a	0.0099	0.047 *a	0.0003 *a	0.0034	0.0036 *a	**0.0093 *a**	0.0183 *a	0.0307 *a
JY99 HA	0.0944 *a	0.0989 *	0.0823 *a	0.0519 *a	0.0571 ***	0.0294 *a	0.0316	0.0556 *a	0.0376 *a	**0.0557 *a**	0.0756 *a
JY99 BM	0.0331 **	0.0046	0.0068 *a	0.0352 *	0.0217 *	0.019 *a	0.0234	0.024 *a	0.0118 *a	0.0296 *a	**0.0344 *a**

Table 4.12.4 Paiwise F_{ST} values between 11 sites on the Rivers Frome and Piddle, sampled in July 1999-July 2000

site	JY99 BS	JY99 WH	JY99 GB	JY99 NF	JY99 LM	JY99 EB	JY99 ES	JY99 ESMS	JY99 WS	JY99 HA	JY99 BM
JY00 BS	**0.0757**	0.0913	0.1218 **	0.0942 *a	0.0573 *a	0.0788 *a	0.093	0.1147 **	0.0887 *a	0.0774 ***	0.093 *a
JY00 WH	-0.0828	**-0.0189**	0.0081	0.0021	0.0078	-0.0047	-0.0055	0.0159	-0.0055	0.0052	-0.0055
JY00 GB	0.0017	0.0046	**0.0786 *a**	0.0346 ***	0.0452 *a	0.0438	0.0559	0.0799	0.0646 **	0.0564	0.0637
JY00 NF	-0.0217	-0.0127	0.0346 *	**0.0153**	0.0511 *a	0.0416 **	0.0216	0.056	0.0328	0.0229	0.0198
JY00 LM	-0.0511	0.0109	0.0354 **	0.029 *a	**0.0197 **	0.0044	0.0163	0.0411	0.0076	0.0262	0.0234
JY00 EB	-0.0606	0.0061	0.0107 *	0.0112 ***	0.0279 **	**0.0082**	0.0007	0.0136	0.0048	0.0388 *a	0.0072
JY00 ES	0.0005	0.074 *	0.0147 *	0.0745 *a	0.1063 *a	0.0684	**0.0722**	0.0759	0.0456	0.1025 **	0.0585
JY00 ESMS	-0.0303	-0.0207	0.0284 *a	0.0181 *a	0.0398 *a	0.0205	0.0259	**0.0324 ***	0.011	0.0375 *a	0.0146
JY00 WS	-0.0646	0.0536 *	0.0287 ***	0.0399 ***	0.082 *	0.0462	0.0034	0.0256	**0.0228**	0.0742	0.0129
JY00 HA	-0.0413	0.0571	0.0383 ***	0.0226	0.0639	0.0684	0.0496	0.0897	0.0723	**0.0758**	0.0603
JY00 BM	-0.0392	-0.0037	0.0291 **	0.0164 ***	0.0516 **	0.0235	-0.0073	0.0076	0.0161	0.0472	**-0.0013**

P values obtained after 23100 permutations. Indicative adjusted nominal level (5%) for multiple comparisons is 0.000216. P0.05* (non adjusted), p0.01** (non adjusted), p0.001*** (non adjusted). p 5 % level *a (Bonferoni adjusted).

Table 4.12.5 Pairwise F_{ST} values between 7 sites over two consecutive years, River Sainte-Marguerite, Canada (Garant et al. 2000)

site	PR27 1997	PR81 1997	PR58 1997	NO05 1997	NE06 1997	NE28 1997	XA01 1997
PR27 1996	**0.0129**	0.0175	0.0305	0.0432	0.0192	0.0201	0.0305
PR81 1996	0.0194	**0.026**	0.0369	0.0483	0.0255	0.0323	0.0222
PR58 1996	0.0232	0.0184	**0.038**	0.0411	0.0257	0.038	0.0296
NO05 1996	0.0363	0.0477	0.0837	**0.0396**	0.0582	0.0464	0.0728
NE06 1996	0.0187	0.0174	0.0392	0.0423	**0.0169**	0.0296	0.0270
NE28 1996	0.0077	0.0128	0.0417	0.0269	0.014	**0.0192**	0.0193
XA01 1996	0.0296	0.0409	0.0445	0.0549	0.029	0.0291	**0.0352**

4.13 Long term genetic variation

4.13.1 Number of samples per cohort year

Age information was not available for all the scale samples analysed and only the individuals that could be assigned to the correct cohort year were included in further statistical analysis. At locus Ssa 202, samples from cohort year 1968-1971 and 1992-1995 were analysed, sample sizes were between 1 and 55 (Figure 4.13.1). At locus Ssa 171, samples from 1984 to 1995 were analysed and sample size per cohort year was between 1 and 30 (Figure 4.13.2). At locus Ssosl 85, samples from cohort years 1961-1963, 1965, 1966-1975 and 1982-1995 were analysed and sample sizes were between 1 and 55 (Figure 4.13.3).

Table 4.13.1 Number of scale samples processed

Locus	Total number samples analysed per locus	Number of samples with age information
Ssa 202	339	230
Ssa 171	142	104
Ssosl 85	654	480

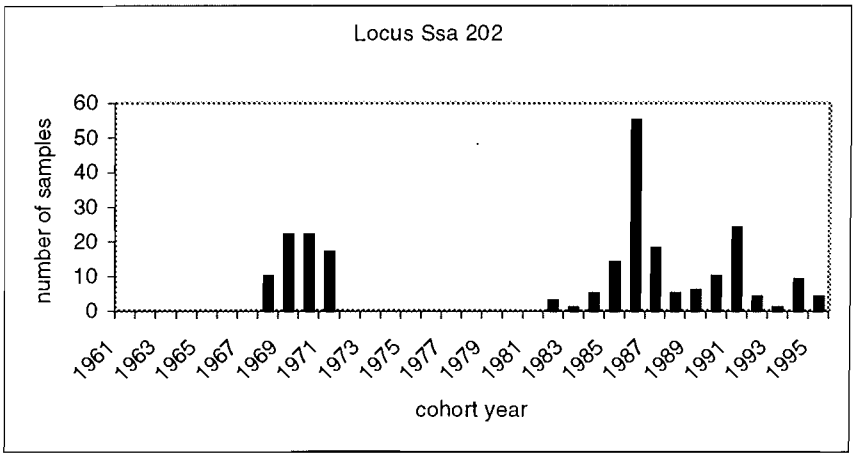


Figure 4.13.1 Number of *S. salar* scale samples per cohort year, locus Ssa 202

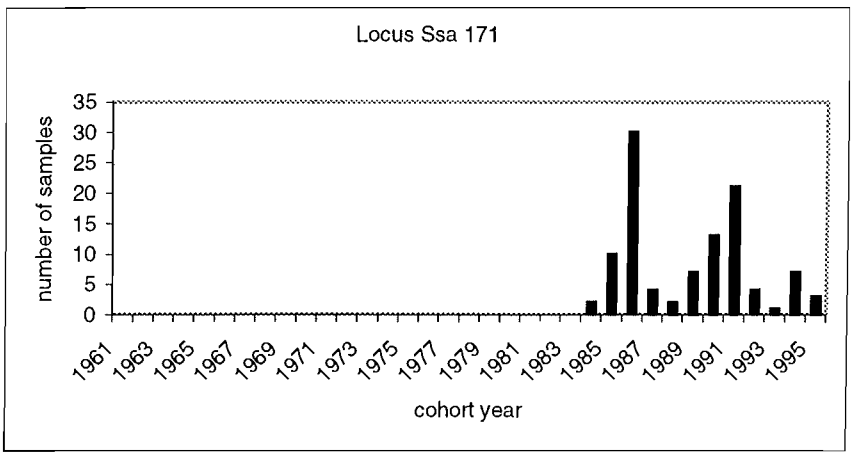


Figure 4.13.2 Number of *S. salar* scale samples per cohort year, locus Ssa 171

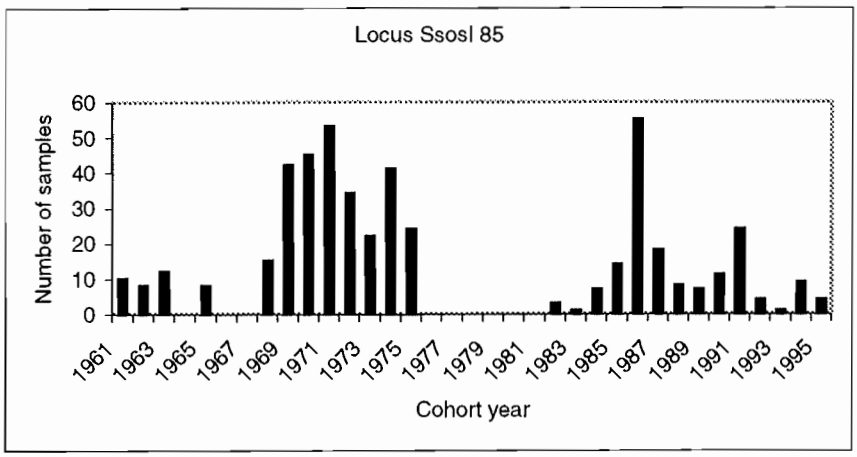


Figure 4.13.3 Number of *S. salar* scale samples per cohort year, locus Ssosl 85

4.13.2 Allele frequency

Allele frequencies per locus per year were calculated. At locus Ssa 202; allele number 1 was detected in each year except 1993. Allele number 2 was detected in 1970, 1971, 1984-1988 and 1991 only, and has the lowest frequency. Allele number 3 was detected in each cohort year and was the most frequent in 11/16 years sampled. Allele number 4 was detected in each year except 1982, 1983, 1985, 1988, 1992 and 1993. Alleles 6 and 7 were not detected in any year of the scale samples analysed, although alleles of this size were detected in the juvenile samples. Allele number 8 was detected in 1982 only (Appendix Section 7.4.13, Figure 7.4.13.1).

At locus Ssa 171, allele number 1 was detected in each year analysed except 1984, 1988, 1989 1993 and 1995. Allele number 2 was detected in each year except 1988 and 1993. Allele number 3 was detected in each year except 1984. Allele number 4 was detected in each year except 1987 and 1993. Allele number 5 was detected in 1989 and 1991 only. Allele number 6 was detected in 1985, 1986, 1989, 1991, 1993, 1994 and 1995. Allele number 7 was detected in four years only; 1985, 1986, 1989 and 1990. Allele number 8 was detected in 1984, 1990 and 1991 only (Appendix Section 7.4.13, Figure 7.4.13.2).

At locus Ssosl 85, allele number 1 was detected in 1986 only. Allele number 2 was detected in 1988 only. Allele number three was detected in each year analysed except 1965, 1983 and 1993. Allele number 4 was detected in 1990 only. Allele number 5 was detected in each year except 1982, 1993 and 1995. Allele number 6 was detected in years 1969, 1971 and 1974 only. Allele number 7 was detected in each year except 1965, 1982–1985 and 1993. Allele number 8 was detected in each year and occurred at the highest frequency in 18 out of the 24 cohort years analysed. Allele 9 was detected in 1969 -1971, 1974 and 1985, only. Allele number 10 was detected in 1961, 1965 and 1970 only. Allele number 11 was detected in each year except 1961, 1983 and 1992-1995 (Appendix Section 7.4.13, Figure 7.4.13.3).

4.13.3 Correlation of alleles within cohort year

Correlation of alleles within each cohort year was estimated per locus and over all. To estimate the correlation, each year was treated as a site and F statistics were calculated. The F_{IS} value output is therefore the measure of allele correlation within a cohort year. Over all loci, allele correlation values per year varied between years and large values were obtained in 1961 and 1982. None of the values were significantly different from zero (Table 4.13.3 and Figure 4.13.3) therefore no substructure was detected within a year and the scale samples taken from adults can be assumed to be a random sample of the total adult population.

Table 4.13.3 Correlation of alleles per year for loci Ssa 202, Ssa 171 and Ssosl 85, and over all three loci

locus	Ssa202	N	Ssa171	N	Ssosl85	N	overall loci F_{IS}
year							
1961					0.5	10	0.5
1962					-0.063	8	-0.063
1963					0.205	12	0.205
1965					-0.228	8	-0.228
1968	0.031	10			-0.067	15	-0.009
1969	0.198	22			0.198	42	0.198
1970	0.134	22			0.064	45	0.099
1971	0.033	17			-0.025	53	0.004
1972					0.146	34	0.146
1973					-0.182	22	-0.182
1974					0.245	41	0.245
1975					0.072	24	0.072
1982	-0.333	3			1	3	0.429
1984	-0.25	5	-0.333	2	0.442	7	-0.109
1985	0.175	14	-0.087	10	-0.233	14	-0.051
1986	-0.01	55	0.322	30	0.024	55	0.118
1987	0.073	18	-0.6	4	0.052	18	-0.135
1988	-0.067	5	-1	2	0.317	8	-0.182
1989	0.2	6	0.032	7	0.2	7	0.146
1990	-0.068	10	0.146	13	-0.087	11	0.001
1991	0.017	24	0.09	21	-0.011	24	0.033
1992	0.294	4	0	4	0	4	0.094
1994	-0.077	9	-0.235	7	-0.293	9	-0.202
1995	0.1	4	0.2	3	-0.286	4	0.037

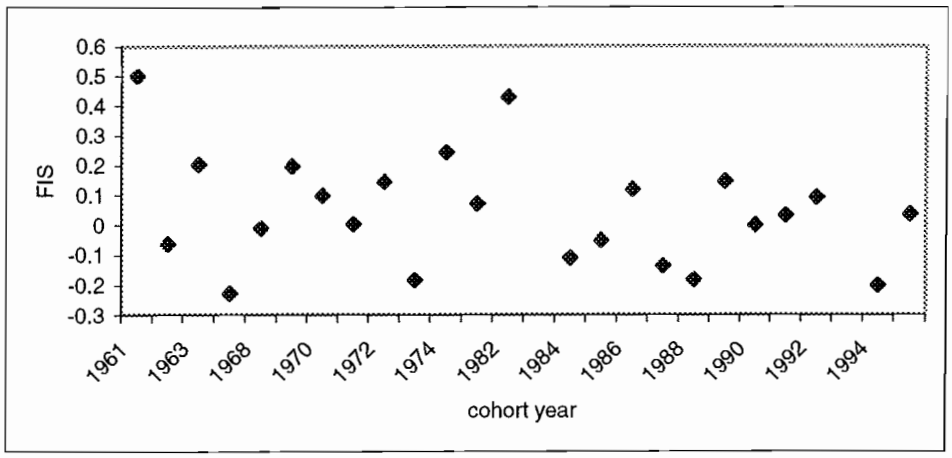


Figure 4.13.3 Correlation of alleles for adult *S. salar* per cohort year over 3 loci

4.13.4 Relationship between population size and genetic variability

Levels of genetic variability may be correlated with population size. Population size was highest in 1988 at 4093 individuals and was lowest in 1991 at 804 individuals (Figure 4.13.4). Population size declined drastically between 1990 and 1991, and since 1991 numbers of adults returning to spawn have been low (between 804 and 1355 individuals).

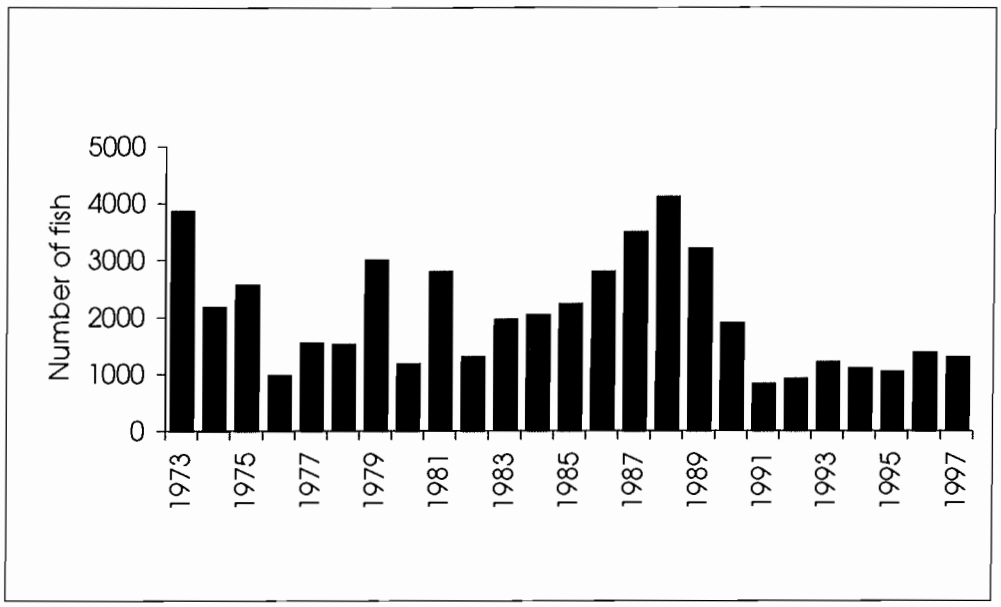


Figure 4.13.4 Numbers of adult *S. salar* detected by fish counter in River Frome, 1973 to 1997

4.13.5 Number of alleles

At locus Ssa 202 the number of alleles detected was lowest in 1983 and 1993 (Figure 4.13.5.1) (N.B. these years had a sample size of 1 individual). A positive correlation between adult population size (numbers of *S. salar* detected by fish counter) in year *a* and numbers of alleles at locus Ssa 202, detected in the progeny of those adults (cohort year *a* +*1*) however this was not significant (Figure 4.13.5.4).

At locus Ssa 171 the number of alleles detected was lowest in 1983 and 1993 (Figure 4.13.5.2) (N.B. these years had a sample size of 1 individual). A positive correlation between adult population size (numbers of *S. salar* detected by fish counter) in year *a* and numbers of alleles at locus Ssa 171, detected in the progeny of those adults (cohort year *a +1*) (Figure 4.13.5.5) was observed, however this was not significant.

At locus Ssosl 85, number of alleles was lowest in 1993 (Figure 4.13.5.3) (N.B. this year had a sample size of 1 individual). A significant positive correlation (Rp 0.699, P 0.003) between adult population size (numbers of *S. salar* detected by fish counter) in year *a* and numbers of alleles detected in the progeny of those adults (cohort year *a +1*) was observed (Figure 4.13.5.6).

The number of alleles detected in a population is highly dependent on sample size. In this study, sample size per cohort varied between one and 55 therefore measures of genetic variation, which are corrected for sample size, should be used to estimate differences between years.

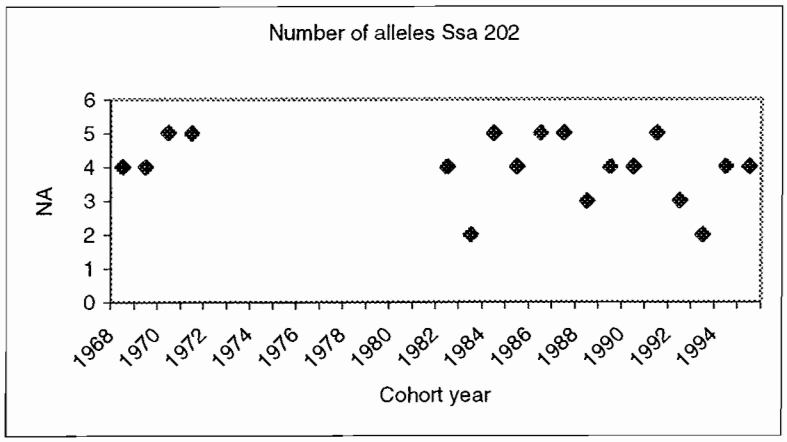


Figure 4.13.5.1 Numbers of alleles detected per cohort year at locus Ssa202, *S. salar* scale samples

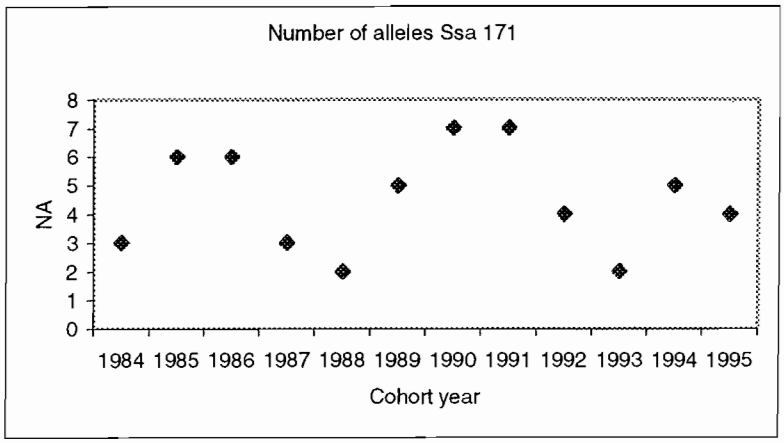


Figure 4.13.5.2 Numbers of alleles detected per cohort year at locus Ssa 171, *S. salar* scale samples

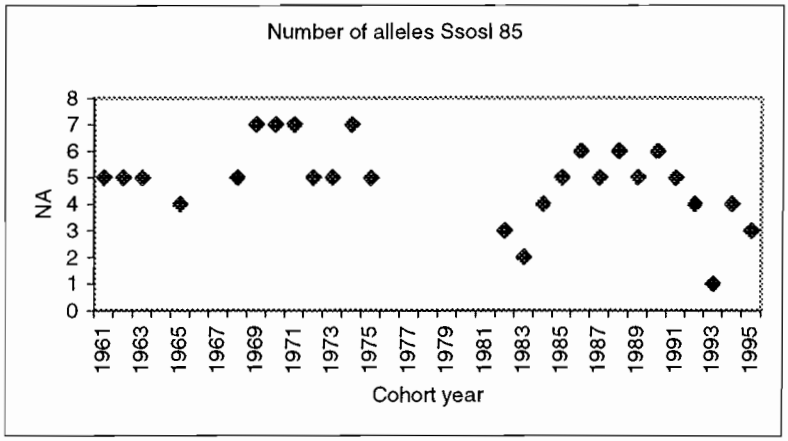
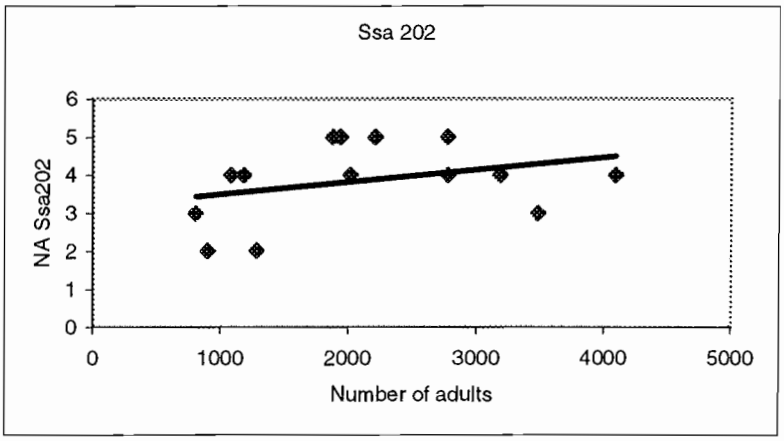
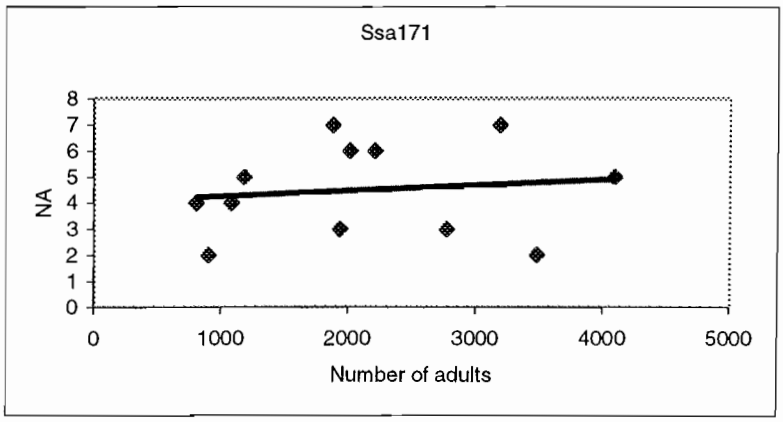


Figure 4.13.5.3 Numbers of alleles detected per cohort year at locus Ssosl 85, *S. salar* scale samples



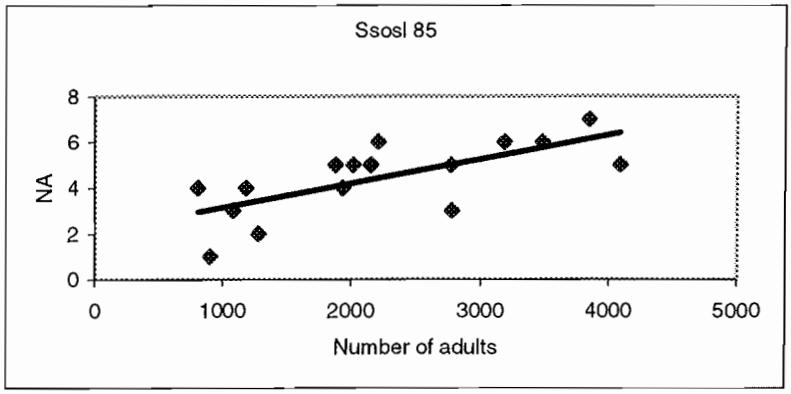
Rp = 0.319, P 0.267

Figure 4.13.5.4 Adult population size in year *a* related to number of alleles detected in progeny (year *a+1*), locus Ssa 202



Rp 0.127, P 0.695

Figure 4.13.5.5 Adult population size in year *a* related to number of alleles detected in progeny (year *a*+1), locus Ssa 171



Rp 0.699, P 0.003

Figure 4.13.5.6 Adult population size in year *a* related to number of alleles detected in progeny (year *a*+1), locus Ssosl 85

4.13.6 Allelic richness (ARi)

ARi can be used to measure change in diversity over time and is useful when archive and current sample sizes are different. Allelic richness over all loci, standardised per individual was lowest in year 1965, and was highest in year 1983 (Figure 4.13.6.1) however correlation of reduced allelic richness with low population size was not detected (Figure 4.13.6.2).

Allele frequency data from current (1989) *S. salar* samples and *S. salar* scale samples (collected 1931-1939) in the Skjern River (Denmark) (Nielsen et al. 1999) were used to calculate allelic richness change over time. The *S. salar* population had declined in this river during the last 50 years. At locus Ssosl 417, ARi was 1.64 for the 1930s scale sample and ARi was 1.55 in 1989.

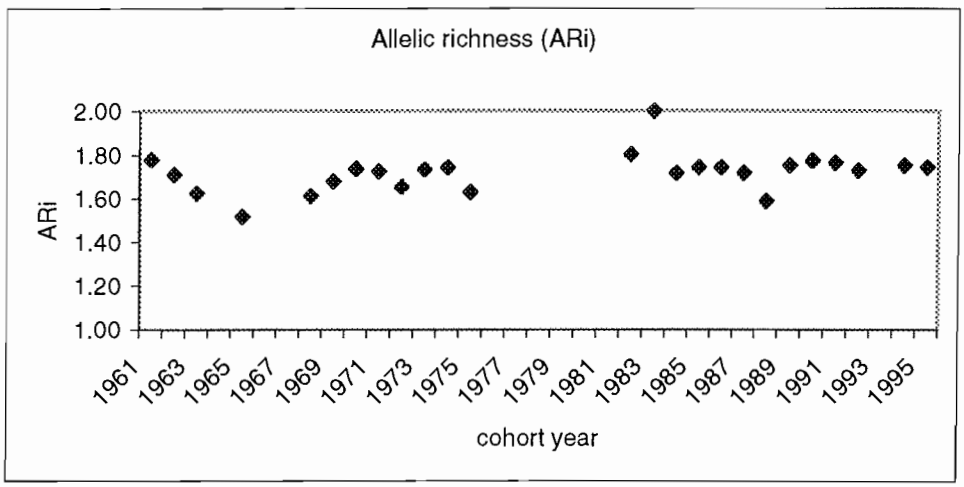
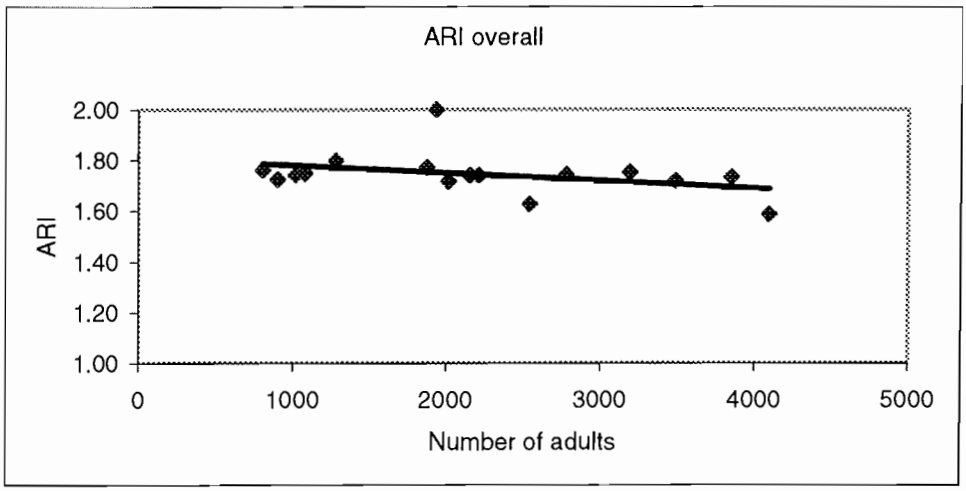


Figure 4.13.6.1 Allelic richness (ARi) over all loci per cohort year of *S. salar* in the River Frome



Rp –0.38, P 0.147

Figure 4.13.6.2 Adult population size in year *a* related to Allelic richness calculated for progeny (year *a*+1), over three loci

4.13.7 Expected heterozygote frequency

Expected heterozygote frequency was lowest in 1965, Ht 0.509 and was highest in 1982, Ht 0.875 (Figure 4.13.7.1). A correlation of low Ht with low adult population size was not detected (Figure 4.13.7.2).

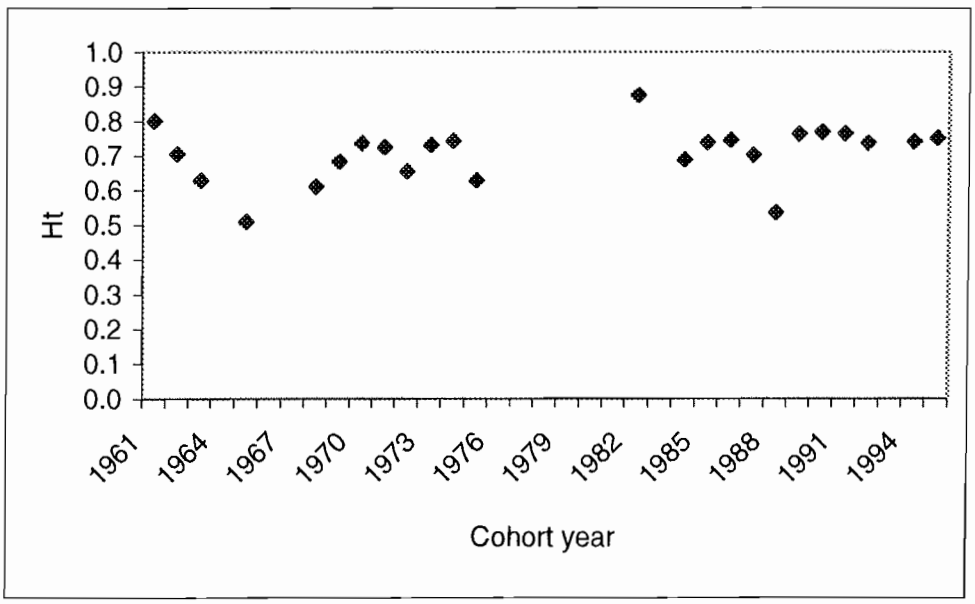
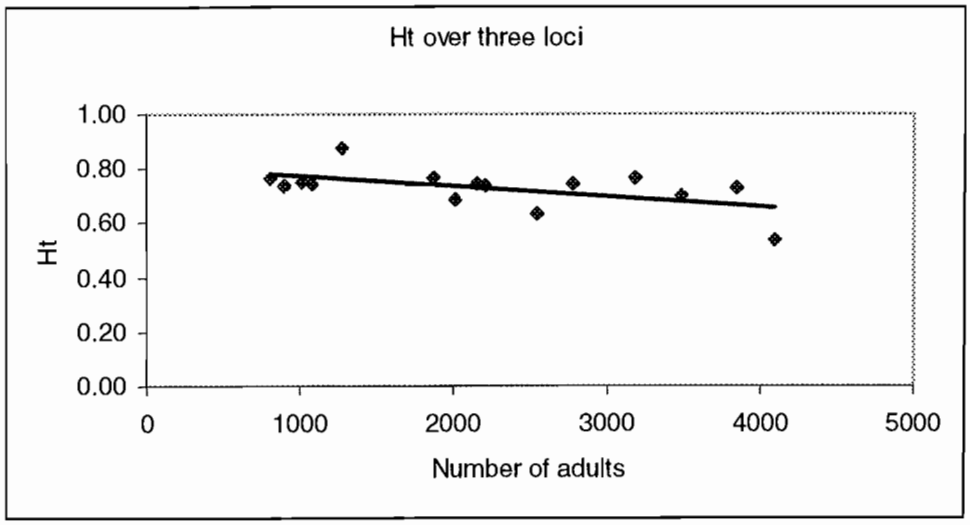


Figure 4.13.7.1 Expected heterozygosity frequency (Ht) of adult *S. salar* per cohort year over 3 loci



Rp –0.563 P = 0.029

Figure 4.13.7.2 Adult population size in year *a* related to expected heterozygote frequency (Ht) calculated for progeny (year *a*+1), over three loci

5. DISCUSSION

5.1 Sampling

In this study sites were sampled on a much smaller scale than previous studies of within-river genetic differentiation, this was due to the very small size of the catchment. Sites were sampled over three consecutive years which allowed stability of environmental characteristics and genetic variability at sites to be analysed over time.

Sample sites were chosen to represent all parts of the catchment. As far as possible, sites where a large number of parr could be collected relatively quickly for genetic analysis were selected, although some sites were chosen in parts of the catchment for which no previous information was available, which often resulted in very small numbers of juveniles being sampled.

The primary aim of the project was to collect large numbers of parr and this required a sampling strategy that was not consistent with that which would have been employed solely for an ecological study. The problems involved with sampling small numbers of families per site and of being certain that juveniles were the spawned in the reach in which they were caught, could have been overcome by sampling directly from eggs or from fish on the spawning grounds. These were our preferred options but the Environment Agency refused permission to sample eggs or breeding adults. This left parr sampling as the only option. During the course of the study, commercial nets were not in operation on the Frome. However, when commercial netting is in operation salmon could be purchased from the operator, movements could be monitored by radiotracking and a DNA sample could be taken to relate spawning behaviour and genetic variability. Direct monitoring would enable the number of adults spawning in a certain area, sex ratio and the input from precocious male parr to be determined.

It is important to have temporal replicates; if we had only sampled in one year we could have made conclusions regarding spatial structure which may not have applied in all years. Juveniles of different age classes should not be used as temporal replicates for spatial analyses; it is possible to test allele frequency stability over time, however it is difficult to be certain of the site of origin of parr older than 0+.

5.2 Site characteristics

At sample sites, potentially suitable habitat was chosen. Sites varied from shallow gravel reaches with no plants to deeper reaches with abundant plants and sand/silt substratum common. No habitat variable was correlated with density of salmon parr. The macrophyte *Ranunculus* spp. is characteristic of chalk streams and was expected to have an influence on the distribution and density of salmon parr. Parr are known to favour a gravel substratum, and good flow for interception of drifting invertebrates. The presence of *Ranunculus* causes changes in both substrate composition and flow and can cause large areas to be sub-optimal for salmon parr. However, a comparison of two adjacent sites on the main river, one with <5% macrophyte cover (Morton Ford) and one with 50-95% cover (East Burton) over the three years showed that both sites had similar high densities of salmon parr in July in all three years (maximum 0.125 individual m^{-2} at East Burton and 0.142 individual m^{-2} at Morton Ford).

Temperature was measured and converted to optimal degree days (ODD). ODD were 73 % to 84 % of the maximum possible. May to July ODD values were significantly correlated with distance from source. No relationship between flow category and optimal degree days was detected. No relationship between optimal degree days and mean parr length or growth rate was detected. These results imply that the limit for optimal growth in the river Frome may be below those published by Elliott & Hurley (1997) for the river Lune.

Parr density varied between sites and between years although there was no consistent pattern. Parr density was not correlated with distance from source or flow rate category. Overall the river is well below its maximum carrying capacity as shown by Habitat Quality Score values. Parr density was higher at sites where gravel had been cleaned and at these sites the theoretical maximum carrying capacity was often exceeded. The density of *S. salar* parr was inversely correlated with numbers of piscivorous brown trout (*S. trutta*). This confirms the predictions given in the Atlantic salmon population model produced for the Frome which suggested that predation by trout could cause deleterious effects on the salmon population and in an extreme scenario could cause the demise of the species (Hilton et al. 2001). This suggests that a management decision should be taken on whether a particular reach or area of river should be operated as a salmon or trout fishery as the conservation of the salmon species could be severely compromised by the addition of large numbers of predatory trout.

5.3 Life history types

Few 1+ parr were detected and no parr older than 1+ were sampled. Little evidence exists to show that site differences are related to use by different age cohorts of salmon. This is contrary to studies in Scotland (River Dee, Aberdeenshire) which showed that different age cohorts used different parts of the catchment and that there were discrete genetic sub-populations (Youngson et al. 1983). However, the River Dee is very long in comparison with the Frome and has several distinct tributaries. The Frome is only 50 km long and spawning is limited to the lower 30 km. It has few tributaries and they are small in comparison to the Scottish rivers. Salmon which do spawn in the tributaries on the Frome generally run up just prior to spawning, however the main spawning grounds are within the main river. Further complications arise due to the braided nature of the river in the middle part of the catchment.

This lack of specific spawning sites for different age cohorts was not unexpected given the differences in physical characteristics compared with studies where sub-populations exist. Although this is a negative result, it still has management implications for the river. It suggests that gravel cleaning which is used to increase the survival of eggs (the most serious mortality bottleneck to the population) cannot be concentrated in any one area to improve the survival of a particular age cohort, in this case multi-sea-winter fish which have shown the largest decrease in numbers.

Differences in parr length between sites was detected. Since a large parr is most likely to give rise to a 1+ smolt and a greater proportion of MSW salmon are derived from 1+ smolts, it follows that parr from different parts of the catchment may have different potentials for production of MSW fish. It is also known that large smolts have a better survival rate, hence are more likely to return as adults to breed. Thus parr inhabiting the lower reaches may be producing a higher return rate than those from further upstream. It is possible that different life history strategies form genetically distinct components of the population. No differentiation was detected between 0+ and 1+ parr of the same cohort year however it was

not possible to determine where the 1+ parr were likely to have hatched, therefore 1+ parr were excluded from analyses of spatial genetic differentiation.

Variation in smolt size (and previously parr length) was greater for grilse x MSW progeny than for either grilse x grilse or MSW x MSW Ritter *et al.* (1986). Thus the differences detected in parr length between sites may be a consequence of the sea age of the breeding adults at each site.

However, Bielak and Power (1986) state that data from 20 rivers showed that there was no relationship between river age and sex or river age and sea age. This study has shown that growth of parr in chalk streams is generally fast and a high proportion smolt at 1+ and are consequently large for their age. The fact that mean parr length was correlated with flow category shows that parr grow faster in main river habitats low down the catchment. Ritter *et al.* (1986) also showed that larger hatchery smolts produced more grilse than smaller smolts again favouring grilse production in the Frome.

Although, in this system, no surveys have shown that MSW salmon favour particular areas to spawn, the lack of reported large salmon in tributaries and in the shallow upper catchment indicates that it is most likely to be within the main river and probably centred on the lower/ middle reaches and therefore gravel cleaning in these areas provides the best method of improving adult returns of this threatened age cohort.

5.4 Genetic analysis

The DNA extraction method used (Chelex-100) has been reported to be unsuitable for long term storage of DNA (Walsh et al. 1991). The original method of Beacham and Dempson (1998) included an autoclave step, this may improve quantity of DNA recovery but DNA is likely to be fragmented. DNA was extracted from some samples using an autoclave step and some problems were encountered when attempting to amplify from this DNA after three years.

Ideally, genetic variation would be analysed using a large number of loci to reduce standard error. Despite the large number of published Salmonid primers, only ten have been used for studies of *S. salar* population structure. It is possible that some published primers are badly designed or that River Frome *S. salar* have sufficiently diverged from source samples to prevent primer binding. Published studies of population structure of *S. salar* do not tend to give any information regarding testing and rejection of additional primers. Some researchers have tested the utility of salmonid primers for amplification of microsatellites in related species. Primers for use with *S. salar* were tested by Olsen et al. (1996) including primers cloned from *S. salar*. Some microsatellites from other species were found to amplify products in *S. salar*, however no amplification was detected using *S. salar* primers Ssa 202 and Ssa 289; Ssa 171 was found to have multiple bands and smearing. This is in direct contrast to this study and to other published studies. *S. salar* are of tetraploid origin and disomic inheritance may not be complete at some loci (Allendorf and Thorgaard 1984). Tetrasomic loci are buffered against genetic drift. Incomplete diploidisation may explain the presence of additional bands, for example at locus Ssosl 417 a smaller band was visible in some lanes.

5.5 Genetic variability

Genetic variability detected in current *S. salar* in the chalk rivers Frome and Piddle, Dorset, UK, was lower than genetic variability detected in *S. salar* populations in Canadian and

European rivers. The rivers used for comparison are all much larger than the rivers Frome and Piddle therefore higher genetic variability in the larger rivers many be due to larger adult population size. However it is possible that these rivers have also undergone a reduction in adult size. Genetic variability of *S. salar* from cohort years between 1961 and 1995 was assessed and no correlation of reduced genetic variability and low adult population size was detected. Thus low genetic variability is not related to the reduction in adult population size in the River Frome since 1989, but may be related to the extreme reduction in adult *S. salar* in the River Frome in 1850.

No loss of alleles was associated with the decline of MSW fish suggesting that spawning occurs between mixed aged fish. Studies have shown that both inherited and developmental factors may influence sea age. Progeny of 1SW (grilse) fish produced proportionately more 1SW offspring than did 2SW and older fish (Ritter *et al.* 1986). Thus, as is the case in the Frome, once the MSW component has reduced significantly, the chances are greater for a grilse x grilse mating resulting in an increase in the proportion of grilse subsequently produced and a grilse dominated population.

Before further statistical analysis of this data, the samples will be screened with 5-6 microsatellite loci and DNA extracted from most recent adult samples (years 1999, 2000 and 2001). This will allow comparison of adult allele frequencies with juvenile allele frequencies in the same year.

Although the measured population size has rarely reduced below 1000 adults, it is possible that the effective population size has been lower in some years. The effective population size for each year could be calculated using modified spatial data models. Other studies have shown large disparity between effective and census population size (Miller and Kapuscinski 1997). The extensive data set for age structure will allow are more accurate estimation of effective population size because known age-at-spawning can be used.

Gene flow between cohorts can be modelled (Waples). This will allow the reproductive success of different life history types to be estimated. The change in age structure over time can be analysed and the possibility that MSW are genetically differentiated can be tested.

5.6 Population structure

Small but significant genetic differentiation between years was detected. Differentiation between years could be due to different sections of the population returning to spawn in each year, however the very low levels of differentiation detected could be due to genetic drift. Life history traits such as overlapping generations and the presence of precocious parr are likely to reduce genetic differentiation between years, by increasing the effective population size.

A high level of site fidelity was detected between Summer and Autumn samples, however genetic differentiation was detected between Summer and Autumn samples in three consecutive years. Autumn samples were not 'missed' in the first sample but have migrated in from elsewhere.

Genetic differentiation was detected, using current samples, between the Rivers Frome and Piddle. Thus differentiation between two rivers can occur even when river mouths are less than 10 km apart and despite the fact that the River Frome was likely to have been

recolonised after the population crash in 1850s from fish which were spawned in the river Piddle.

Significant F_{ST} over all sites was detected at each sample time. Detection of significant F_{ST} could be due to non-random return of adults to spawn or due to sampling a small number of families per site. It is possible to obtain significant differentiation by sampling a large number of offspring from a small number of spawning adults, even though the adults have no reproductive isolation

Non-random return of adults to spawn may be due to migration of adults to the natal spawning sites or spawning at sites with specific environmental characteristics. The possibility of sampling a small number of families per site could be ruled out if pairwise genetic differentiation between sites was correlated with genetic differentiation between sites; if site allele frequencies were temporally stable or if genetic differentiation between sites was correlated with environmental differences between sites.

A low number of adults spawning at a site can be indicated by a high F_{IS} value with low number of alleles. Redds were counted at ten sites in January 2000, this gives an indication of the number of adults spawning at that site. Sites with high F_{IS} had low redd counts and a low non significant F_{IS} was estimated for a site with a large number of redds.

A correlation between genetic differentiation between sites and geographic distance between sites was detected in July 2000 only. Isolation by distance can occur in static populations due to reduced gene flow between distant populations and genetic drift over time. The occurrence of isolation by distance is not necessarily expected with migratory populations that re-constituted each year. Adult salmon returning to spawn are able to move anywhere within the river and if adults do not home to natal spawning sites then no isolation by distance will be detected.

No correlation between environmental differences between sites and genetic differentiation between sites was detected. Few previous studies have explicitly tested for spatio-temporal genetic differences using the same sites over consecutive years. This study used a new method of investigating the percentage of genetic variation attributable to differences in allele frequency in consecutive years. No temporal stability of population structure was detected between years. Temporal stability of site allele frequency was detected in a Canadian river (Garant et al. 2000), thus it can be concluded that there was a tendency for adult *S. salar* to return to the natal spawning sites in this river, in the two years investigated.

In this system, the possibility that adults were returning to the natal sites to spawn or that significant differentiation was due to sampling a large number of offspring from a small number of spawning adults, with no reproductive isolation, could not be distinguished.

5.7 Management recommendations

The River Frome is an SSSI and the salmon population is the only truly wild population in the chalk streams of southern England. An interest in the salmon population of the river Frome has been shown by English Nature. In all other rivers in this area, stocking of fish reared commercially has seriously affected the genetic composition of the wild stock by interbreeding. A consequence of this has been a reduction in fitness. The Frome population historically comprised three age groups of returning adults and it is the multi-sea-winter fish

(especially the 3SW group) that have declined the most. Results from other CEH research on salmon has shown that the smolt production can vary 4-fold from a constant adult stock suggesting that riverine environmental factors are influencing smolt production and that habitat improvement is potentially a tool for fisheries management.

This study has show that there are no genetically distinct sub-populations of salmon nor any areas used exclusively by one age group of adults. This has important management implications in that efforts on habitat improvements to increase juvenile production should be spread throughout the catchment to increase the probability of enhancing MSW stocks. If all life history types are likely to come from any section of the river, then juvenile survival can be promoted at particular sites without prejudicing any section of the population and management efforts can be concentrated on sites where the return is likely to be high. As parr length is positively related to flow category (discharge) and large smolts survive better than small smolts, improvements in these middle/lower areas are likely to increase numbers of smolts.

5.8 Output

Published paper:

Welton, J ., W . C Beaumont, and M Ladle. 1999. Timing of migration and changes in age structure of Atlantic salmon, *Salmo salar* L., in the River Frome, a Dorset chalk stream, over a 24 year period. Fisheries Management and Ecology 6:437-458.

In Press:

Raybould, A F, R T Clarke, J M Bond, R E Welters, and C J Gliddon. in Press. Inferring patterns of dispersal from allele frequency data.

Future publications:

1. Use of microsatellite markers to investigate population structure of *S. salar*; problems of cross species amplification, amplification of monomorphic products and more than two alleles being visible per lane, in relation to chromosome polyploidy.

2. Spatial variation of allele frequency of *S. salar* in the Rivers Frome and Piddle.

3. Temporal aspects of spatial genetic variation. Long term changes in adult population size, age structure and genetic variability of *S. salar* in the river Frome, Dorset.

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7. APPENDIX

7.3.5 Methods, Microsatellite Primer Optimisation

Table 7.3.5.1 Fifteen microsatellite primers cloned from *S. salar* and tested for use in this study

Locus	Repeat type	AT °C	N_A	Size bp	Ho	Published use for population structure analysis
Ssa 202 (O'Reilly et al. 1996)	$(CA)_3(CTCA)_7$	58	18	270-320	0.4-0.8	Beacham and Dempson 1998, Fontaine et al. 1997, Nielsen et al. 1999, Garant et al. 2000.
Ssa 171 (O'Reilly et al. 1996)	$(TGTA)_{14}(TG)_7$	58	29	233-267	0.6-0.9	Fontaine et al. 1997, Tessier et al. 1997, Tessier and Bernatchez 1999, Garant et al. 2000.
Ssa 197 (O'Reilly et al. 1996)	$(GT)_5C(TG)_4TC(TG)_3A$ $(GTGA)_{15}$	58	21	150-200	0.4-0.8	Beacham and Dempson 1998, Fontaine et al. 1997, Tessier et al. 1997 and Tessier and Bernatchez 1999, Garant et al. 2000.
Ssosl 85 (Slettan et al. 1995)	$(GT)_{22}$	55	14	177-204	0.5-0.8	Fontaine and Dodson 1999, Tessier et al. 1997 and Tessier and Bernatchez 1999, Garant et al. 2000.
Ssa 289 (McConnell et al. 1995a)	$(GT)_{12}$	46	6	110-119	0.3-0.9	Beacham and Dempson 1998.
Ssosl 417 (Slettan et al. 1997)	$(TG)_{25}$	53	21	159-211	0.7-0.8	Nielsen et al. 1999.
Ssa 4 (McConnell et al. 1995b)	$(GT)_{39}$	65	30	112-190	0.6-0.89	McConnell et al. 1995b and McConnell et al. 1995a.
Ssa 14 (McConnell et al. 1995b)	$(TC)_{10}N_{15}$ $(TC)_3N_2(AC)_{12}$ $(TC)_3N_5(CA)_4$	57	3	138-145	0.3-0.5	Beacham and Dempson 1998, McConnell et al. 1995b and McConnell et al. 1995a
Ssa 85 (O'Reilly et al. 1996)	$(GT)_{14}$	58	12	110-138	0.3-0.8	O'Reilly et al. 1996 and Nielsen et al. 1999.
Ssosl 438 (Slettan et al. 1997)	$(AC)_{26}AT(AT)_6$	50	7	116-146	0.76	Nielsen et al. 1999.
Ssosl 439 (Slettan et al. 1997)	$(AC)_{30}$	56	7	194	0.73	No published use.
Ssosl 444 (Slettan et al. 1997)	$(AC)_{41}$	58	5	135	0.48	No published use.
F43 (Sanchez et al. 1996)	$(AC/TG)_n$	60	9	96-102	0.5	No published use.
20.19 (Sanchez et al. 1996)	$(AC/TG)_n$	62	4	0.7		No published use.
D30 (Sanchez et al. 1996)	$(AG/TC)_n$	53	5	0.5		No published use

AT annealing temperature, N_A number of alleles, Ho observed heterozygosity.

Table 7.3.5.2 Four microsatellite primers, cloned from species other than *S. salar*, and tested in this study

Primer	Cloned from	N_A	Ho	Allele size bp
µ60 (Estoup et al. 1993)	*S. trutta*	6	0.49	97-111
µ73 (Estoup et al. 1993)	*S. trutta*	?	0.63	140-158
Ogo1a (Olsen et al. 1998)	*Oncorhynchus*	21	183-323	?
F_{GTI} (Sakamoto et al. 1994)	*Oncorhynchus*	7	?	?

AT annealing temperature, N_A number of alleles, Ho observed heterozygosity.

Table 7.3.5.3 Six microsatellite primers cloned from species other than *S. salar*, with previous publication for use with *S. salar*

Primer	Cloned from	N_A	Ho	Allele size bp	Used by	Comments
µ3 (Tessier et al. 1997)	*S. trutta*	11	0.6-0.7	204-216	Tessier et al. 1997, Fontaine et al. 1997.	
µ79.1 (Tessier et al. 1997)	*S. trutta*	6	0.2-0.6	145-161	Tessier et al. 1997.	
µ79.2 (Tessier et al. 1997)	*S. trutta*	2	0.3-0.6	120-122	Tessier et al. 1997.	number of alleles low
Omy 27 (C. Herbinger, not published)	*Oncorhnchus*	17	0.76	?	McConnell et al. 1995b.	
Omy 28 (C. Herbinger, not published)	*Oncorhnchus*	25	0.79	?	McConnell et al. 1995b.	
Sfo-23 (Angers et al. 1995)	*Salvelinus*	12	0.6	114-144	Tessier et al. 1997.	

AT annealing temperature, N_A number of alleles, Ho observed heterozygosity.

Table 7.3.5.4 Eleven published microsatellite primers cloned from *S. salar*

These primers were not purchased

Primer cloned by	Repeat type	AT	N_A	Ho	Allele size bp	Used by	Comments
Ssosl 20 (Slettan et al. 1997)	$(CA)_{24}$	58	6	0.74	120	/	possibly useful dinucleotide prone to stutter
Ssosl 25 (Slettan et al. 1997)	$(TG)_{32}$	58	5	0.670	159	/	possibly useful.
Ssosl 32 (Slettan et al. 1997)	/	55	7	0.82	111	/	long repeat, not sequenced.
Ssosl 34 (Slettan et al. 1997)	$(GT)_{18}$	54	7	0.66	163	/	possibly useful
Ssosl 311 (Slettan et al. 1997)	$(TG)_{38}$	55	23	0.7-0.9	126-170	Nielsen et al. 1999	possibly useful
Ssosl 436 (Slettan et al. 1997)	$(TG)_{41}$	54	10	0.76	127-187	/	possibly useful photo shows stutter
Ssosl 446 A+B (Slettan et al. 1997)	$(AC)_{25}$	56	11	/	132	/	NOT USE alleles overlap, two primer sites very close together.
Ssosl 456 (Slettan et al. 1997)	$(AC)_{12}AG\ (AC)_{10}$	58	1	0	177	/	NOT USE monomorphic
SS 4 (Martinez et al. 1999)	GT	60	14	0.8	184-254	/	heterozygous, large number of alleles, however, not previously used for population studies. Published photo has large amount of stutter.
SS 6 (Martinez et al. 1999)	GT	65	5	0.67	226-268	/	heterozygous, large number of alleles, however, large alleles size, not previously used for population studies and published photo has large amount of stutter.
SS 11 (Martinez et al. 1999)	GT	67	15	0.67	338-390	/	heterozygous, large number of alleles, however, large alleles size, not previously used for population studies and published photo has large amount of stutter.

AT annealing temperature, N_A number of alleles, Ho observed heterozygosity.

7.4.3 Results, Genetic variability

Table 7.4.3.1 Genetic variability at 6 microsatellite loci of *S. salar* in the rivers Piddle and Frome sampled from 16 sites, July 1998
Sample size (N), number of alleles (N_A), expected heterozygosity (Ht), observed heterozygosity (Ho)

locus	BS	TF	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	TK	BM	TW	MF	overall sites
N total	5	72	9	16	30	34	76	24	18	52	12	2	1	29	10	58	448
Ssa 202																	
N	4	60	2	3	24	12	66	20	15	38	5	1	1	9	7	45	312
N_A	3	5	2	3	4	5	6	4	4	5	3	1	2	3	3	5	6
Ht	0.708	0.609	0.5	0.583	0.541	0.795	0.665	0.637	0.686	0.674	0.75	NA	NA	0.576	0.524	0.619	0.684
Ho	0.5	0.533	0.5	0.667	0.5	0.583	0.5	0.4	0.7333	0.6316	0.6	0	0	0.444	0.7143	0.6889	0.5641
Ssa 171																	
N	5	59	3	15	30	32	61	18	16	48	11	2	1	28	10	57	396
N_A	4	10	4	5	7	8	10	7	7	9	5	2	1	6	4	7	11
Ht	0.8	0.818	0.833	0.693	0.739	0.817	0.804	0.802	0.75	0.794	0.568	1	NA	0.774	0.7	0.805	0.779
Ho	1.0	0.7288	0.667	0.7333	0.6	0.875	0.7377	0.8333	0.625	0.7917	0.4545	0	0	0.8214	0.7	0.8421	0.7525
Ssa 197																	
N	5	72	9	15	30	33	72	24	17	49	12	2	1	28	10	50	429
N_A	5	10	7	8	10	9	11	7	7	8	6	3	1	10	5	11	14
Ht	0.85	0.85	0.889	0.795	0.847	0.808	0.837	0.824	0.844	0.831	0.803	1	NA	0.786	0.728	0.859	0.854
Ho	0.6	0.7083	0.6667	0.8667	0.633	0.4848	0.6667	0.5	0.4118	0.551	0.25	0.5	0	0.8929	0.7	0.68	0.634
Ssosl 85																	
N	5	68	9	13	29	32	71	23	17	47	10	2	1	27	9	58	421
N_A	3	8	8	6	7	8	7	9	6	8	7	2	1	7	5	6	11
Ht	0.575	0.689	0.875	0.821	0.776	0.756	0.724	0.824	0.8	0.661	0.839	0.5	NA	0.59	0.743	0.804	0.773
Ho	0.8	0.4706	0.8889	0.7692	0.8276	0.5938	0.5352	0.4348	0.6471	0.5957	0.7	0.5	0	0.6296	0.7778	0.8103	0.6247
Ssa 289																	
N	5	62	5	2	0	0	56	18	17	47	10	2	1	25	9	38	297
N_A	3	5	4	2	NA	NA	5	3	3	4	2	1	2	4	4	5	5
Ht	0.75	0.631	0.85	1	NA	NA	0.316	0.212	0.438	0.469	0.344	0	NA	0.32	0.611	0.585	0.525
Ho	0.2	0.0806	0.2	0	/	/	0.1786	0.1111	0.0588	0.1064	0.2	0	1.0	0.36	0.556	0.3421	0.1852
Ssosl 417																	
N	2	31	0	7	20	13	39	18	15	44	10	2	1	12	3	15	232
N_A	2	8	NA	3	5	3	5	6	4	6	4	2	1	5	2	5	9
Ht	1	0.697	NA	0.667	0.814	0.577	0.706	0.81	0.648	0.74	0.578	1	NA	0.807	0.667	0.738	0.808
Ho	0	0.2258	/	0	0.4	0.2308	0.1538	0.111	0.2	0.2727	0.1	0	0	0.1667	0	0.2	0.2026
over all loci Ht	0.780	0.716	0.789	0.759	0.743	0.751	0.675	0.685	0.694	0.695	0.567	0.875	NA	0.53	0.662	0.735	0.737

Table 7.4.3.2 Genetic variability at 6 microsatellite loci of *S. salar* in the Rivers Piddle and Frome sampled from 16 sites, September 1998
Sample size (N), number of alleles (N_A), expected heterozygosity (Ht) and observed heterozygosity (Ho) per locus per population

locus	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	TW	SW	WO	MC	MF	DT	DS	overall
N total	14	10	48	54	10	18	20	10	27	4	10	10	5	57	3	6	306
Ssa 202																	
N	7	6	32	30	4	15	11	8	8	3	9	4	4	39	0	3	183
N_A	4	4	5	5	2	3	3	3	4	3	4	4	3	5	NA	2	6
Ht	0.786	0.817	0.739	0.704	0.5	0.35	0.7	0.42	0.652	0.667	0.757	0.833	0.667	0.601	NA	0.667	0.719
Ho	0.4286	0.5	0.6563	0.7	0.75	0.4	0.4545	0.5	0.5	1.0	0.4444	0.5	0.75	0.5385	/	0.3333	0.5683
Ssa 171																	
N	12	10	43	50	4	18	19	9	16	2	8	2	5	45	0	1	244
N_A	6	6	8	7	4	6	6	6	6	4	4	3	3	6	NA	1	11
Ht	0.731	0.817	0.8	0.795	0.792	0.737	0.839	0.771	0.785	1	0.741	0.75	0.6	0.777	NA	NA	0.795
Ho	0.9167	0.9	0.7674	0.84	1	0.7778	0.6842	0.5556	0.375	1.0	1.0	1.0	0.6	0.6889	/	0	0.75
Ssa 197																	
N	7	9	38	48	6	15	14	7	0	1	10	6	4	47	1	3	216
N_A	5	3	9	10	8	7	7	6	NA	1	3	7	3	11	1	4	13
Ht	0.774	0.667	0.754	0.707	0.95	0.79	0.808	0.869	NA	NA	0.706	0.917	0.625	0.818	NA	0.833	0.817
Ho	0.8571	0	0.6842	0.5625	0.6667	0.8	0.7857	0.5714	/	0	0.6	0.8333	1.0	0.7021	0	0.6667	0.6781
Ssosl 85																	
N	13	10	39	50	10	18	15	10	26	3	6	4	4	47	1	5	261
N_A	5	3	7	7	4	5	6	5	7	4	4	4	1	8	2	4	8
Ht	0.74	0.661	0.773	0.759	0.744	0.694	0.776	0.722	0.8	0.833	0.7	0.833	0	0.8	NA	0.75	0.749
Ho	0.8462	0.8	0.8718	0.68	0.6	0.5556	0.8667	1.0	0.7692	0.6667	0.6667	0.25	0	/	1	1.0	0.6858
Ssa 289																	
N	14	10	44	32	10	15	15	10	10	4	8	6	4	38	3	5	228
N_A	4	3	4	4	4	3	3	3	1	3	2	3	2	4	2	2	5
Ht	0.728	0.678	0.152	0.232	0.628	0.481	0.19	0.278	0	0.625	0.232	0.317	0.5	0.437	0.667	0.5	0.45
Ho	0.1429	0.2	0.1364	0.2188	0.2	0.4667	0.2	0.3	0	0.5	0.25	0.3333	0.75	0.4474	0.333	0.2	0.2632
Ssosl 417																	
N	2	0	31	30	7	10	0	4	4	4	8	9	5	27	0	5	146
N_A	1	NA	5	5	2	5	NA	3	3	2	4	3	2	6	NA	2	7
Ht	0	NA	0.781	0.719	0.5	0.822	NA	0.833	0.833	0.583	0.732	0.472	0.55	0.782	NA	0.4	0.763
Ho	0	/	0.0968	0.1667	0.4286	0.1	/	0	0	0.25	0.25	0.1111	0.4	0.2593	/	0	0.1333
over all loci Ht	0.752	0.792	0.665	0.653	0.686	0.6546	0.663	0.649	0.768	0.742	0.645	0.687	0.588	0.703	0.667	0.63	0.716

Table 7.4.3.3 Genetic variability at 5 microsatellite loci of *S. salar* in the River Piddle, November 1998
Sample size (N), number of alleles (N_A), expected heterozygosity (Ht) and observed heterozygosity (Ho) per locus per population

site code	GB	ESMS	WS	BM	WO	overall
N total	4	7	6	9	10	36
Ssa 202						
N	4	1	1	2	/	8
N_A	4	2	2	1	/	4
Ht	0.833	NA	NA	0	NA	0.639
Ho	0.75	1	1.0	0	/	0.625
Ssa 197						
N	3	6	4	9	5	27
N_A	3	5	4	5	7	10
Ht	0.667	0.817	0.792	0.563	0.9	0.794
Ho	1.0	1.0	0.5	0.3333	1.0	0.7037
Ssosl 85						
N	3	3	2	5	7	20
N_A	3	4	2	6	6	7
Ht	0.667	0.917	0.5	0.85	0.857	0.767
Ho	1.0	0.6667	0.5	0.8	0.5714	0.7
Ssa 289						
N	3	5	2	7	8	25
N_A	3	4	1	3	2	4
Ht	0.833	0.9	0	0.548	0.232	0.52
Ho	0.3333	0	0	0.4286	0.25	0.24
Ssosl 417						
N	2	6	5	8	9	30
N_A	2	4	3	3	6	7
Ht	1	0.8	0.8	0.714	0.785	0.768
Ho	0.0	0	0	0.125	0.3333	0.1333
over all loci Ht	0.8	0.859	0.697	0.669	0.694	0.698

Table 7.4.3.4 Genetic variability at 6 microsatellite loci of *S. salar* in the rivers Piddle and Frome sampled from 16 sites, July 1999
Sample size (N), number of alleles (N_A), expected heterozygosity (Ht) and observed heterozygosity (Ho) per locus per population

sitecode	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	BM	TW	SW	WO	MF	RW	overall
total N	3	5	13	53	36	21	9	14	26	20	31	17	17	3	49	21	338
Ssa 202																	
N	3	5	13	53	35	21	9	14	26	20	31	17	17	3	49	17	333
N_A	4	3	4	6	5	4	4	3	4	5	4	5	4	2	5	5	7
Ht	0.833	0.725	0.651	0.747	0.747	0.679	0.736	0.648	0.632	0.725	0.724	0.643	0.5	0.647	0.717	0.717	0.706
Ho	1.0	0.8	0.9231	0.8491	0.8286	0.7143	0.7778	0.6429	0.6923	0.9	0.5806	0.8235	0.8235	0.6667	0.7755	0.7059	0.7748
Ssa 171																	
N	3	5	12	53	36	21	9	14	26	20	31	16	17	3	49	17	332
N_A	4	6	7	10	8	6	5	6	6	7	7	6	6	1	8	6	11
Ht	0.833	0.833	0.833	0.833	0.833	0.833	0.778	0.805	0.74	0.753	0.739	0.733	0	0.791	0.744	0.735	0.783
Ho	1.0	1.0	0.6667	0.8679	0.9167	0.9048	0.7778	0.8571	0.6923	0.9	0.7419	0.75	0.8235	0	0.5918	0.8824	0.7892
Ssa 197																	
N	3	5	13	53	35	21	9	14	26	19	31	16	16	3	49	16	329
N_A	5	6	6	11	8	10	5	8	10	10	11	9	9	3	10	7	15
Ht	0.917	0.9	0.856	0.86	0.839	0.794	0.778	0.841	0.853	0.845	0.811	0.86	0.667	0.8	0.863	0.804	0.857
Ho	1.0	1.0	0.6154	0.6981	0.55143	0.7143	0.6667	0.8571	0.8846	0.7368	0.7419	0.75	0.875	1.0	0.8163	0.75	0.7447
Ssosl 85																	
N	3	3	10	46	36	21	9	13	26	20	29	16	16	3	41	18	310
N_A	3	3	5	6	5	7	4	6	6	6	5	5	5	2	5	5	9
Ht	0.583	0.75	0.761	0.691	0.713	0.802	0.722	0.769	0.805	0.708	0.736	0.717	0.667	0.564	0.802	0.775	0.752
Ho	0.667	1.0	1.0	0.7391	0.722	0.8095	0.3333	0.3077	0.5	0.6	0.6552	0.75	0.6875	0	0.4634	0.7222	0.6387
Ssa 289																	
N	3	4	9	49	35	20	9	14	26	20	31	16	17	3	49	17	322
N_A	2	1	3	5	5	3	3	3	4	3	5	3	4	2	4	4	5
Ht	0.667	0	0.569	0.497	0.164	0.445	0.556	0.514	0.453	0.191	0.613	0.676	0.5	0.551	0.323	0.368	0.471
Ho	0	0	0.111	0.3673	0.1714	0.45	0.7778	0.7143	0.5	0.15	0.3548	0.375	0.2941	1	0.4286	0.1765	0.3602
Ssosl 417																	
N	2	4	9	38	21	15	3	10	23	12	27	6	15	3	34	15	237
N_A	2	3	4	5	6	3	3	5	4	4	5	5	4	3	4	8	9
Ht	1	0.833	0.694	0.695	0.777	0.619	0.833	0.85	0.754	0.731	0.622	0.69	0.75	0.699	0.9	0.781	0.748
Ho	0	0	0	0.2368	0.381	0.0667	0.6667	0.2	0.08	0.1667	0.2593	0.1667	0.3333	0.6667	0.3529	0.2667	0.2405
over all loci Ht	0.806	0.808	0.727	0.721	0.679	0.695	0.734	0.738	0.706	0.659	0.708	0.720	0.617	0.675	0.725	0.697	0.719

Table 7.4.3.5 Genetic variability at 6 microsatellite loci of *S. salar* in the rivers Piddle and Frome sampled from 16 sites, September 1999
Sample size (N), number of alleles (N_A), expected heterozygosity (Ht) and observed heterozygosity (Ho) per locus per population.

sitecode	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	TW	SW	WO	MF	overall
total N	2	17	12	33	31	30	34	13	11	11	30	13	17	21	3	21	299
Ssa 202																	
N	1	9	9	24	20	8	21	10	10	7	13	10	15	21	3	17	198
N_A	2	4	5	5	4	5	4	4	3	4	4	4	4	4	3	4	5
Ht	NA	0.674	0.667	0.736	0.658	0.777	0.654	0.678	0.678	0.75	0.731	0.733	0.764	0.833	0.746	0.714	0.727
Ho	1	0.7778	0.7778	0.6667	0.65	0.75	0.4762	0.8	0.9	0.7143	0.8462	0.5	1.0	0.8571	0.3333	0.5882	0.7172
Ssa 171																	
N	2	9	10	24	25	21	23	12	9	8	11	13	17	20	3	17	224
N_A	3	5	7	7	7	5	7	6	7	5	5	5	4	6	3	6	12
Ht	0.75	0.729	0.839	0.83	0.828	0.746	0.822	0.826	0.847	0.804	0.627	0.718	0.764	0.667	0.827	0.566	0.805
Ho	1.0	0.7778	0.7	0.7917	0.96	0.7143	0.9565	1.0	1.0	1.0	0.9091	0.7962	0.6471	1.0	01.0	0.7647	0.8571
Ssa 197																	
N	2	14	11	1	19	27	19	7	10	7	15	12	14	18	3	21	200
N_A	3	7	7	2	7	9	8	7	9	4	6	10	9	8	4	8	12
Ht	0.75	0.786	0.836	NA	0.825	0.806	0.846	0.702	0.856	0.69	0.814	0.909	0.861	0.833	0.774	0.879	0.83
Ho	1.0	0.7143	0.8182	1	0.7368	0.7407	0.5789	0.5714	0.5	0.4286	0.6	0.8333	1.0	0.9444	1.0	0.7619	0.7400
Ssosl 85																	
N	2	14	12	33	28	27	32	11	11	11	20	13	17	21	3	21	276
N_A	2	5	5	5	7	5	6	5	6	4	4	4	3	6	3	4	8
Ht	0.5	0.761	0.803	0.741	0.675	0.648	0.73	0.805	0.85	0.709	0.564	0.644	0.67	0.667	0.687	0.537	0.719
Ho	0.5	0.7857	0.6667	0.697	0.7143	0.5556	0.8125	0.9091	0.9091	0.2727	0.7	0.6154	0.6471	0.7143	1.0	0.5714	0.6884
Ssa 289																	
N	2	17	12	25	17	14	33	13	11	9	17	13	16	20	3	21	243
N_A	2	4	4	5	2	4	4	4	4	3	2	3	3	3	3	4	5
Ht	1	0.478	0.428	0.546	0.059	0.624	0.638	0.712	0.4	0.215	0.449	0.59	0.695	0.833	0.444	0.563	0.542
Ho	0	0.1765	0.3333	0.2	0.0588	0.4286	0.6667	0.3846	0.4545	0.2222	0.5294	0.3077	0.375	0.15	0.333	0.381	0.3457
Ssosl 417																	
N	2	10	10	24	23	27	21	10	8	9	11	8	10	19	2	16	210
N_A	2	3	3	4	4	5	4	5	4	5	4	3	2	5	2	5	7
Ht	1	0.711	0.644	0.647	0.718	0.621	0.718	0.8	0.821	0.833	0.727	0.714	0.744	1	0.8	0.2	0.786
Ho	0	0.1	0.1	0.1667	0.1739	0.1852	0.2381	0	0.125	0.1111	0.0909	0.375	0	0.3158	0	0	0.1524
over all loci Ht	0.8	0.690	0.703	0.7	0.627	0.704	0.735	0.754	0.742	0.667	0.652	0.718	0.75	0.806	0.713	0.577	0.735

Table 7.4.3.6 Genetic variability at 6 microsatellite loci of *S. salar* in the rivers Piddle and Frome sampled from 15 sites, July 2000
Sample size (N), number of alleles (N_A), expected heterozygosity (Ht) and observed heterozygosity (Ho) per locus per population

locus	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	BM	TW	SW	WO	MF	overall
Total N	14	18	25	20	30	30	26	31	28	30	31	7	29	28	30	377
Ssa 202																
N	13	17	23	19	29	25	18	30	23	19	29	7	27	27	29	332
N_A	5	5	4	5	4	5	5	4	4	4	4	4	4	3	4	5
Ht	0.779	0.7	0.701	0.798	0.667	0.694	0.395	0.655	0.704	0.731	0.664	0.691	0.625	0.695	0.786	0.724
Ho	1.0	0.6471	0.8261	0.8421	0.6897	0.6	0.2222	0.6	0.6522	0.7895	0.6522	0.7143	0.8148	0.5926	0.6897	0.6627
Ssa 171																
N	14	17	25	20	30	27	24	31	22	19	29	7	29	28	30	352
N_A	5	8	9	7	8	7	7	6	6	8	8	4	7	6	8	11
Ht	0.585	0.803	0.738	0.674	0.743	0.774	0.813	0.731	0.68	0.713	0.759	0.813	0.712	0.785	0.75	0.767
Ho	0.5	0.7059	0.84	0.7	0.633	0.8515	0.8333	0.7742	0.7273	0.6842	0.7931	0.7143	0.931	0.9286	0.6333	0.7642
Ssa 197																
N	14	18	25	20	29	30	26	30	28	29	31	7	29	28	29	373
N_A	7	9	9	8	8	10	7	10	10	8	8	7	8	9	8	16
Ht	0.824	0.845	0.808	0.837	0.866	0.852	0.79	0.849	0.787	0.857	0.784	0.775	0.765	0.815	0.869	0.858
Ho	0.8571	0.889	0.8	0.75	0.7931	0.8	0.6923	0.9	0.75	0.7586	0.7419	0.7143	0.8276	0.7857	0.7931	0.7882
Ssosl 85																
N	13	12	22	19	16	29	18	29	23	23	26	2	29	24	16	313
N_A	4	4	5	4	4	5	4	6	6	4	7	4	6	4	4	10
Ht	0.554	0.735	0.591	0.645	0.64	0.72	0.685	0.712	0.654	0.412	0.783	0.761	0.645	0.558	1	0.712
Ho	0.7692	0.5833	0.3636	0.6316	0.0625	0.7586	0.3333	0.7586	0.7826	0.5217	0.6923	1.0	0.6897	0.4583	0.0625	0.6006
Ssa 289																
N	10	5	12	10	23	29	23	29	12	5	22	7	25	26	23	262
N_A	2	3	1	2	4	4	4	4	3	2	5	1	5	4	4	5
Ht	0.1	0.4	0	0.189	0.324	0.45	0.68	0.357	0.595	0.4	0.611	0.571	0.444	0.312	0	0.39
Ho	0.1	0.2	0	0.2	0.2174	0.3448	0.3478	0.3793	0.333	0	0.6818	0	0.44	0.2308	0.2174	0.3092
Ssosl 417																
N	14	14	19	19	16	16	13	16	9	12	11	2	24	16	16	224
N_A	2	4	5	4	5	4	4	4	5	2	5	1	5	2	5	6
Ht	0.473	0.687	0.741	0.681	0.763	0.69	0.737	0.727	0.854	0.303	0.818	0.667	0.5	0.798	0	0.758
Ho	0.5714	0.1429	0.1053	0.1579	0.25	0.25	0.2308	0.25	0.2222	0	0.1818	0	0	0	0.25	0.183
over all loci Ht	0.553	0.695	0.716	0.637	0.667	0.697	0.683	0.672	0.712	0.569	0.737	0.743	0.615	0.661	0.852	0.702

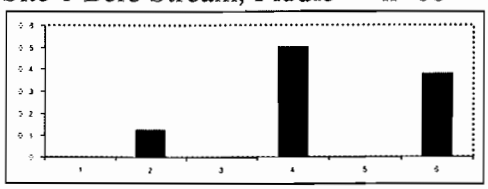
Table 7.4.3.7 Genetic variability at 6 microsatellite loci of *S. salar* in the rivers Piddle and Frome sampled from 14 sites, October 2000
Sample size (N), number of alleles (N_A), expected heterozygosity (Ht) and observed heterozygosity (Ho) per locus per population

sitecode	BS	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	SW	WO	MF	overall
Total N	29	20	14	30	31	27	17	15	12	30	24	15	13	31	308
Ssa 202															
N	29	19	14	30	24	22	13	13	9	28	22	15	13	27	278
N_A	5	5	5	5	6	5	5	4	4	4	4	3	4	5	6
Ht	0.767	0.754	0.681	0.719	0.774	0.708	0.712	0.628	0.674	0.606	0.696	0.6	0.516	0.741	0.706
Ho	0.7586	0.6316	0.7143	0.6667	0.7917	0.6818	0.7692	0.5385	0.4444	0.6071	0.8182	0.8	0.5685	0.7407	0.6942
Ssa 171															
N	27	18	12	23	28	26	17	15	12	28	23	15	11	25	280
N_A	5	8	6	6	6	7	6	5	6	5	6	7	3	9	9
Ht	0.585	0.814	0.689	0.806	0.786	0.748	0.756	0.779	0.758	0.443	0.651	0.812	0.541	0.781	0.74
Ho	0.3704	0.8889	0.5	0.6087	0.8214	0.7308	0.6471	0.7333	0.8333	0.3929	0.6087	0.9333	0.9091	0.8	0.6750
Ssa 197															
N	27	19	14	29	31	27	16	15	9	30	24	15	12	31	299
N_A	8	8	8	8	8	9	8	9	6	7	10	6	4	8	12
Ht	0.808	0.849	0.863	0.868	0.824	0.818	0.756	0.848	0.875	0.813	0.763	0.781	0.648	0.852	0.84
Ho	0.9259	0.8421	0.7857	0.9655	0.871	0.8148	0.875	0.8	0.8889	0.8	0.6667	0.6667	0.9167	0.9355	0.8462
Ssosl 85															
N	27	20	14	29	31	27	17	14	12	30	24	15	12	31	303
N_A	4	5	5	5	5	5	5	5	8	6	5	4	4	5	8
Ht	0.666	0.736	0.75	0.507	0.72	0.748	0.765	0.709	0.617	0.556	0.81	0.529	0.723	0.755	0.706
Ho	0.8148	0.65	0.5714	0.3793	0.6774	0.6667	0.5882	0.6429	0.5	0.3667	0.7083	0.6667	0.8333	0.7419	0.6238
Ssa 289															
N	27	9	9	27	30	25	17	15	7	28	23	15	11	29	272
N_A	2	2	3	3	5	4	2	3	3	4	3	4	3	5	5
Ht	0.44	0.472	0.625	0.412	0.563	0.454	0.371	0.295	0.476	0.493	0.536	0.65	0.555	0.56	0.502
Ho	0.4074	0.444	0.2222	0.2963	0.5667	0.4	0.3529	0.3333	0.4286	0.3214	0.3043	0.4	0.8182	0.4828	0.4081
Ssosl 417															
N	26	14	12	21	25	23	13	9	10	26	17	12	7	4	219
N_A	6	3	5	5	6	5	4	4	3	3	3	5	3	5	8
Ht	0.729	0.692	0.769	0.687	0.79	0.767	0.724	0.625	0.511	0.592	0.634	0.652	0.667	1	0.785
Ho	0.3077	0	0.4167	0.2381	0.2	0.1739	0.1538	0.3333	0.1	0.1923	0.2353	0.25	0	0.25	0.2100
over all loci Ht	0.666	0.720	0.730	0.666	0.743	0.707	0.679	0.647	0.647	0.584	0.682	0.671	0.608	0.782	0.713

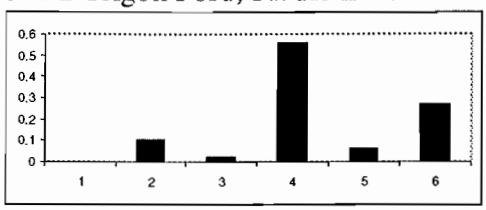
7.4.4 Results Allele frequency

1. Locus Ssa 202

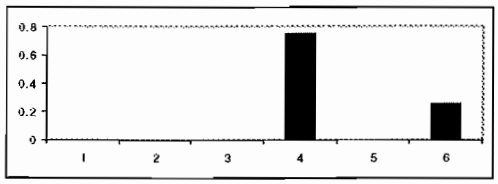
Site 1 Bere Stream, Piddle n=60



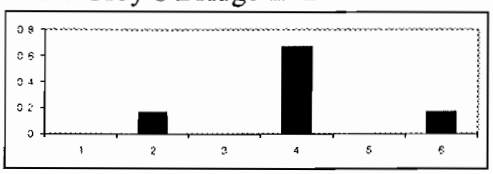
Site 2 Trigon Ford, Piddle n= 4



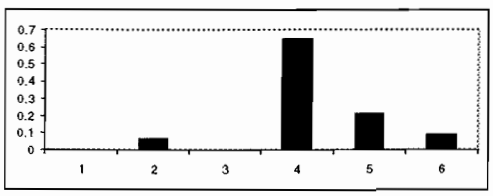
Site 3 West Holme n=3



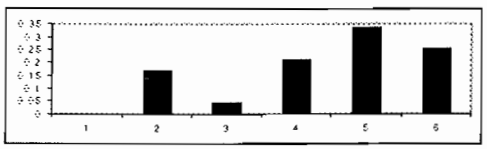
Site 4 Grey's Bridge n=2



Site 5 Norris Farm n= 24



Site 6 Lewell Mill n= 12



Site 7 East Burton n= 66

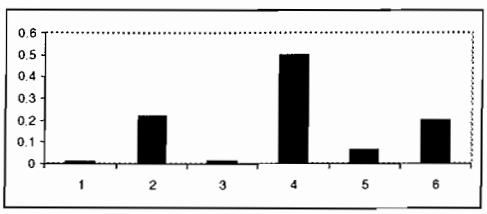
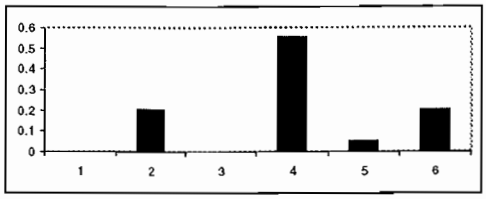
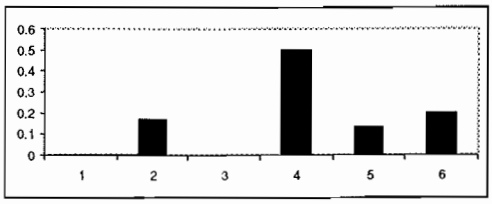


Figure 7.4.4.1 Allele frequencies at 6 microsatellite loci, from *S. salar* sampled at 16 sites on the Rivers Piddle and Frome, July 1998

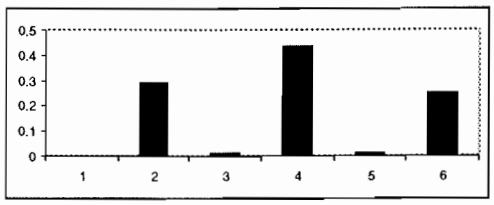
Site 8 East Stoke n= 20



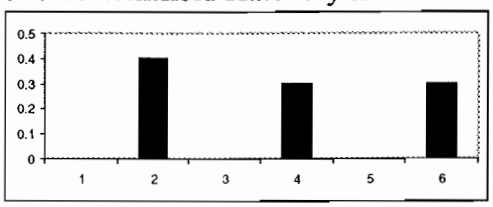
Site 9 ESMS n= 15



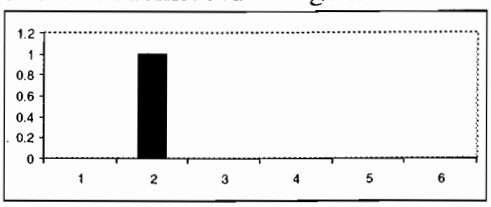
Site 10 Waterbarn Stream n= 38



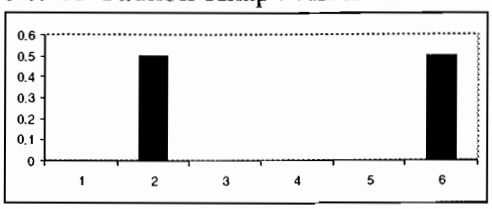
Site 11 Whitfield Hatchery n= 5



Site 12 Muckleford Bridge n= 1



Site 13 Tadnoll Knap Mill n= 1



Site 14 Bindon Millstream n= 9

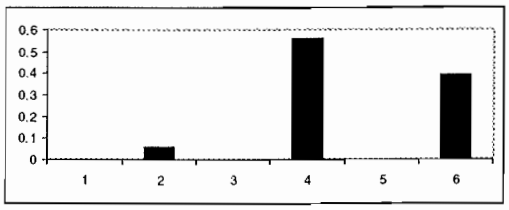
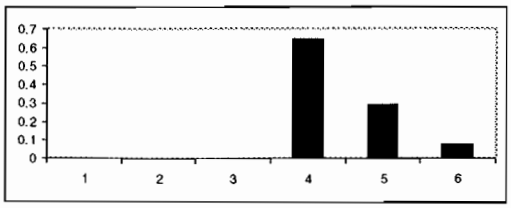
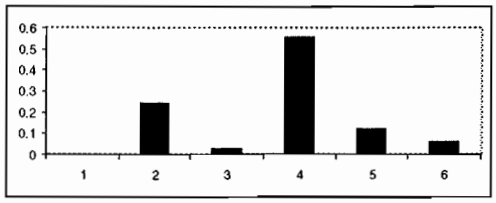


Figure 7.4.4.1 (Continued)

Site 15 Tadnoll Winfrith n= 7

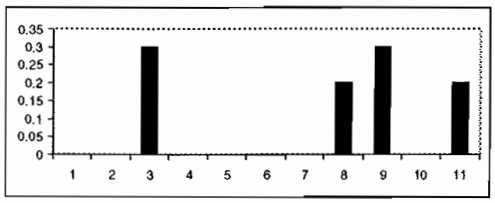


Site 19 Moreton Ford n= 45

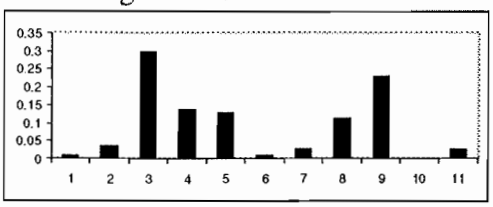


2. Locus Ssa 171

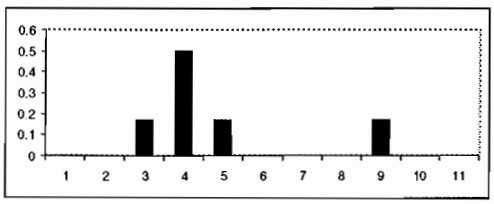
Site 1 Bere Stream, Piddle n= 5



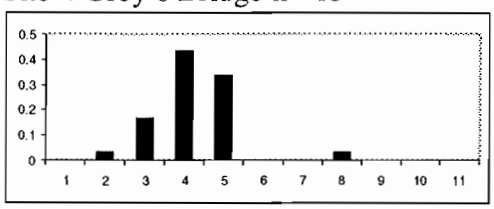
Site 2 Trigon Ford n=59



Site 3 West Holme n=3



Site 4 Grey's Bridge n= 15



Site 5 Norris Farm n= 30

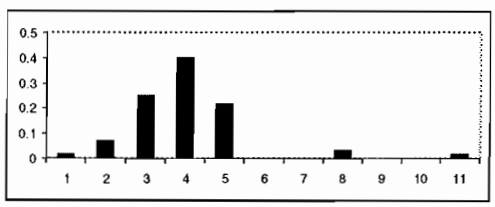
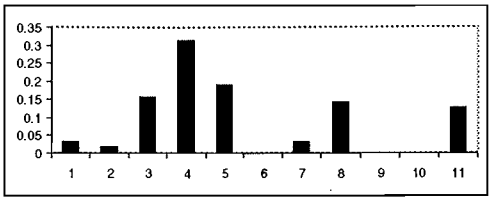
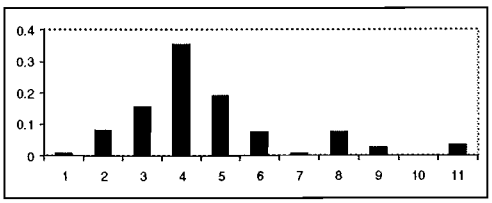


Figure 7.4.4.1 (Continued)

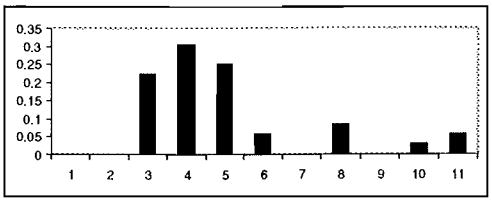
Site 6 Lewell Mill n= 32



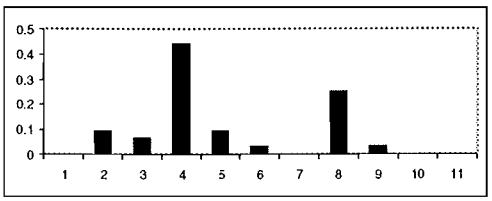
Site 7 East Burton n= 61



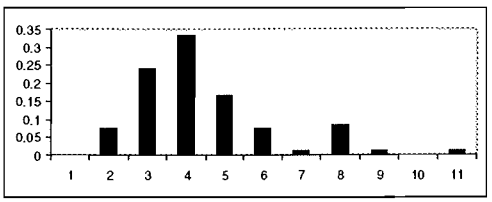
Site 8 East Stoke n= 18



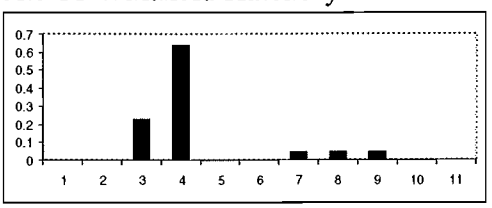
Site 9 ESMS n= 16



Site 10 Waterbarn Stream n= 48



Site 11 Whitfield Hatchery n= 11



Site 12 Muckleford Bridge n= 2

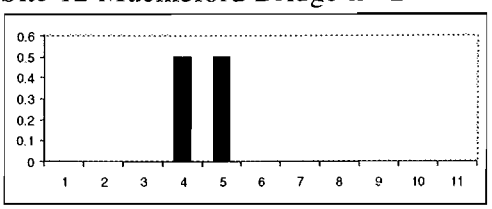
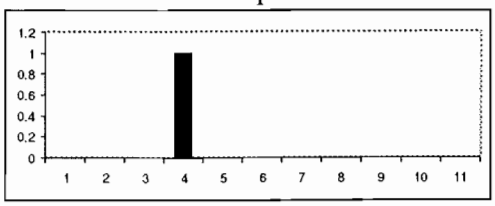
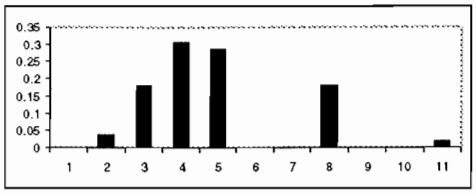


Figure 7.4.4.1 (Continued)

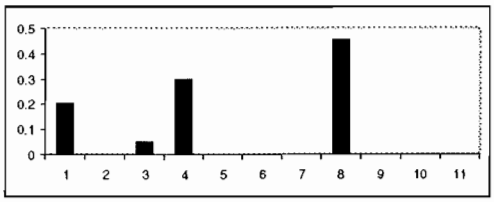
Site 13 Tadnoll Knap Mill n= 1



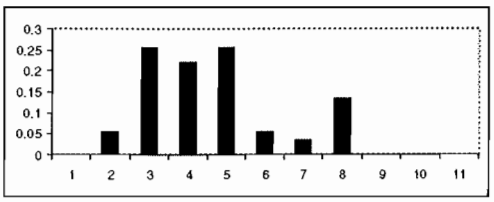
Site 14 Bindon Millstream n= 28



Site 15 Tadnoll Winfrith n= 10

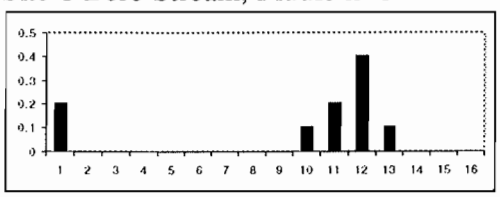


Site 19 Moreton Ford n= 57

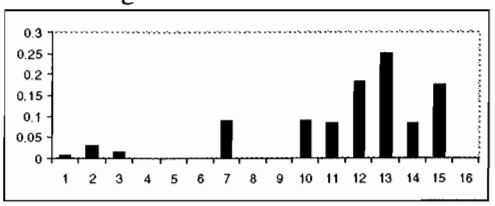


3. Locus Ssa 197

Site 1 Bere Stream, Piddle n=5



Site 2 Trigon Ford n=72



Site 3 West Holme n=9

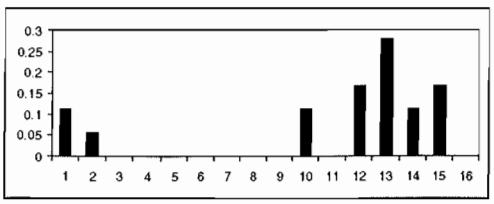
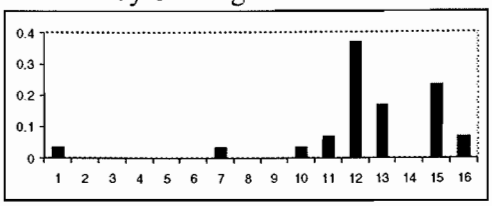
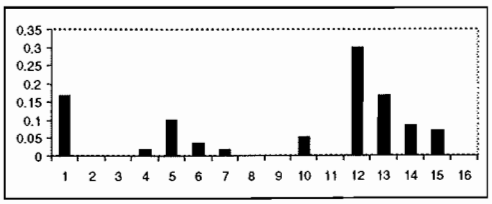


Figure 7.4.4.1 (Continued)

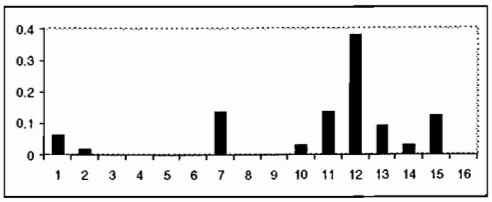
Site 4 Grey's Bridge n=15



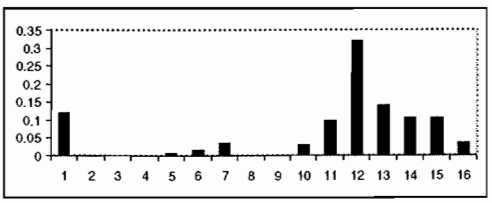
Site 5 Norris Farm n=30



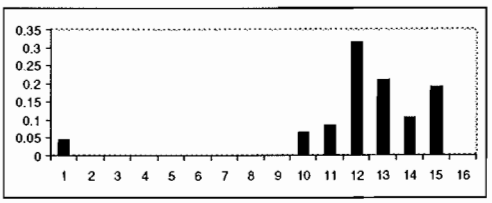
Site 6 Lewell Mill n=33



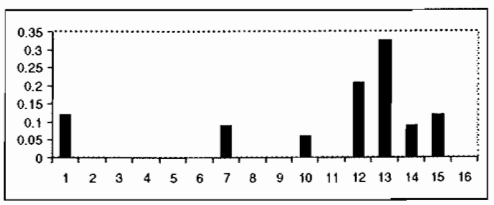
Site 7 East Burton n=72



Site 8 East Stoke n=24



Site 9 ESMS n=17



Site 10 Waterbarn Stream n=49

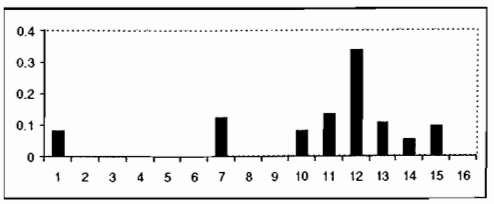
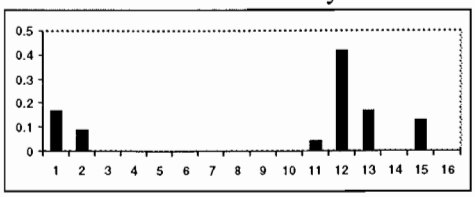
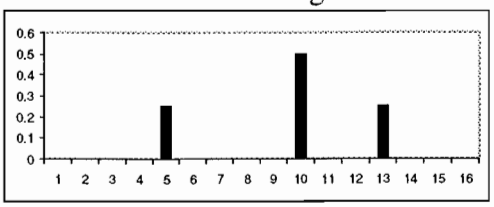


Figure 7.4.4.1 (Continued)

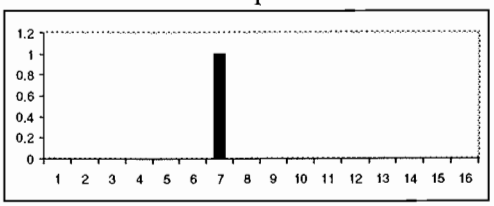
Site 11 Whitfield Hatchery n=12



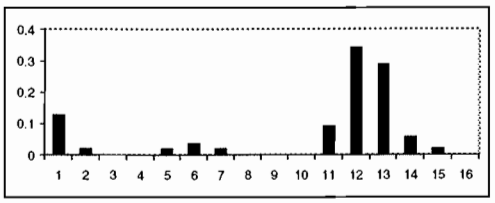
Site 12 Muckleford Bridge n=2



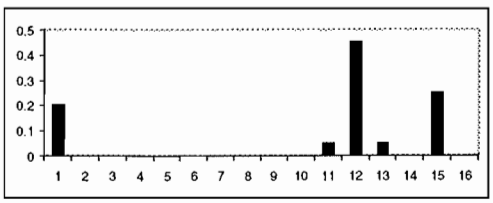
Site 13 Tadnoll Knap Mill n=1



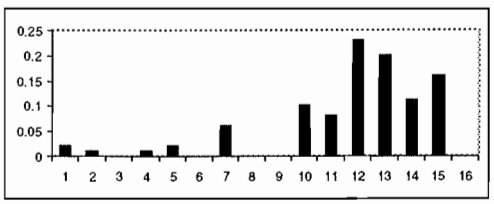
Site 14 Bindon Millstream n=28



Site 15 Tadnoll Winfrith n=10



Site 19 Moreton Ford n=50



4. Locus Ssosl 85

Site 1 Bere Stream, Piddle n=5

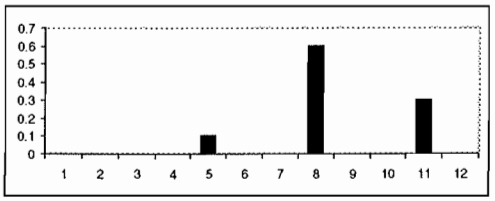
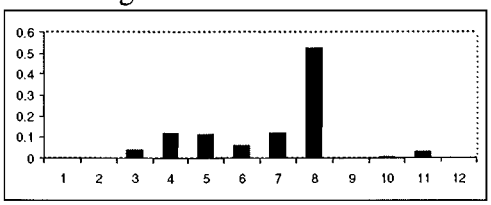
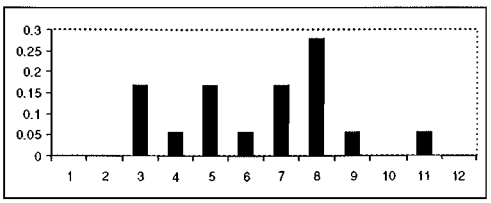


Figure 7.4.4.1 (Continued)

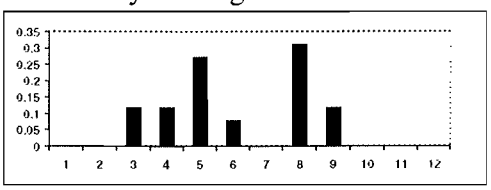
Site 2 Trigon Ford n=68



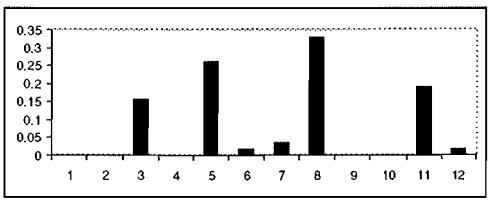
Site 3 West Holme n=9



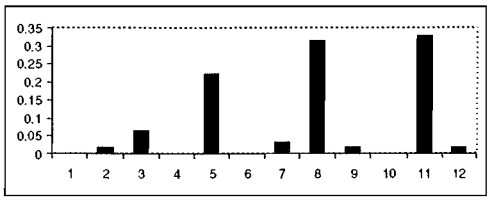
Site 4 Grey's Bridge n=13



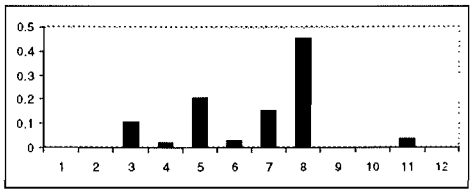
Site 5 Norris Farm n=29



Site 6 Lewell Mill n=32



Site 7 East Burton n=71



Site 8 East Stoke n=23

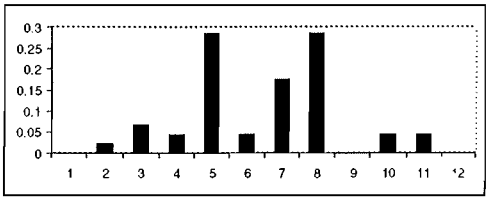
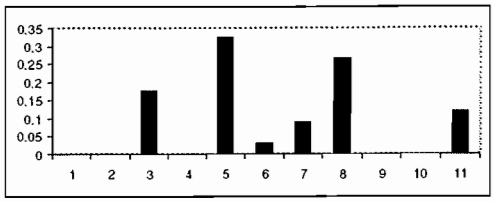
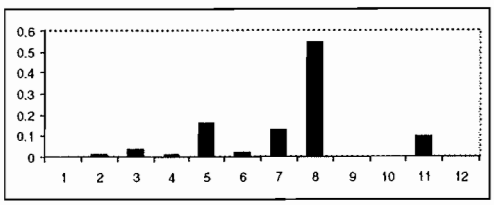


Figure 7.4.4.1 (Continued)

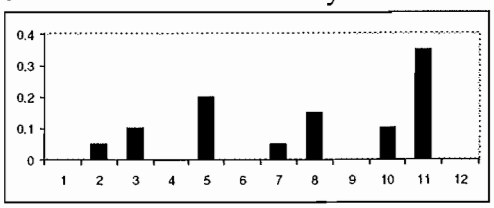
Site 9 ESMS n=17



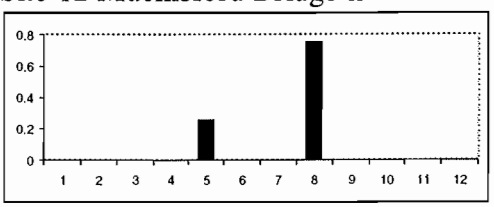
Site 10 Waterbarn Stream n=47



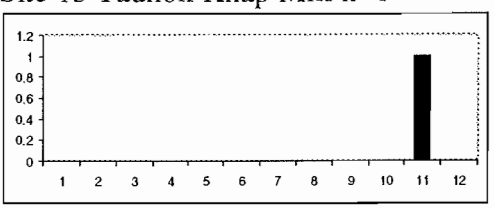
Site 11 Whitfield Hatchery n=10



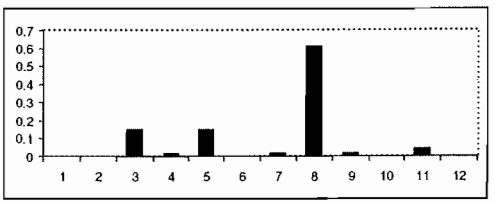
Site 12 Muckleford Bridge n=2



Site 13 Tadnoll Knap Mill n=1



Site 14 Bindon Millstream n=27



Site 15 Tadnoll Winfrith n=9

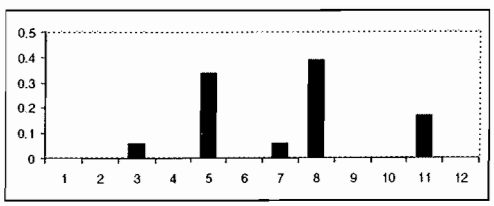
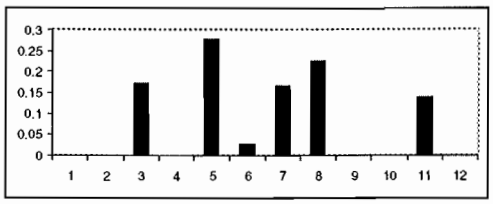


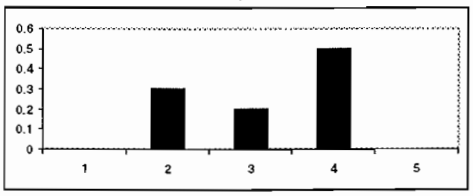
Figure 7.4.4.1 (Continued)

Site 19 Moreton Ford n=58

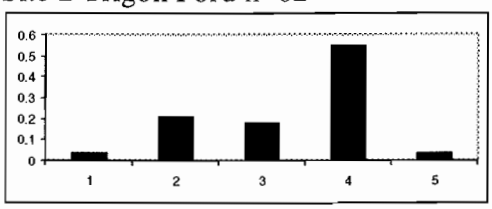


5. Locus Ssa 289

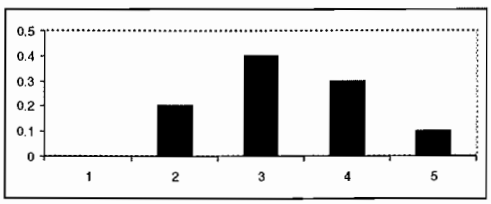
Site 1 Bere Stream, Piddle n=5



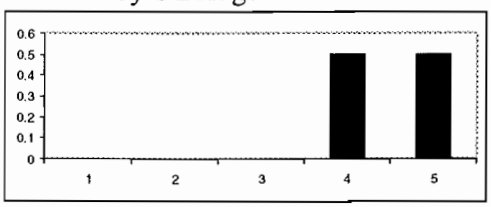
Site 2 Trigon Ford n=62



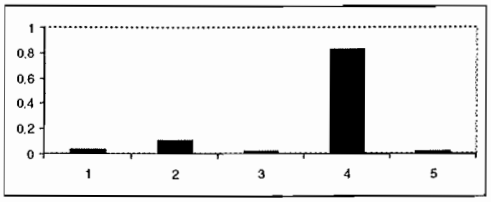
Site 3 West Holme n=5



Site 4 Grey's Bridge n=2



Site 7 East Burton n=56



Site 8 East Stoke n=18

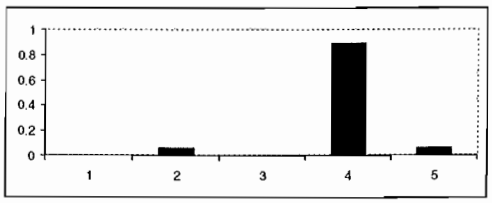
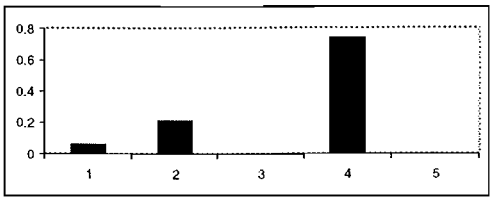
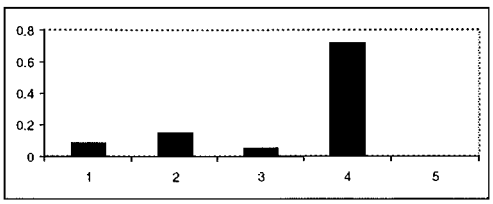


Figure 7.4.4.1 (Continued)

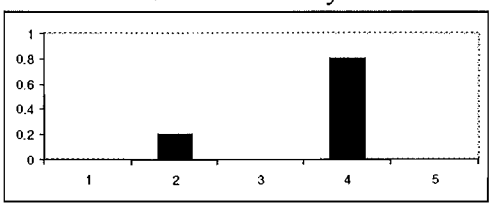
Site 9 ESMS n=17



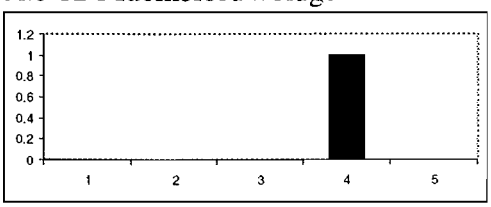
Site 10 Waterbarn Stream n=47



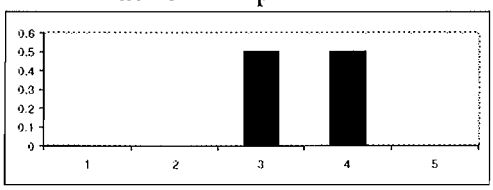
Site 11 Whitfield Hatchery n=10



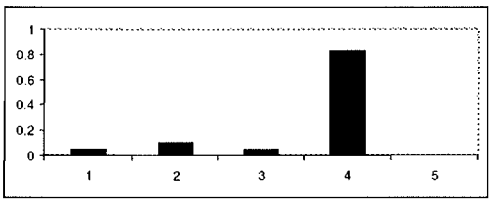
Site 12 Muckleford Bridge n=2



Site 13 Tadnoll Knap Mill n=1



Site 14 Bindon Millstream n=25



Site 15 Tadnoll Winfrith n=9

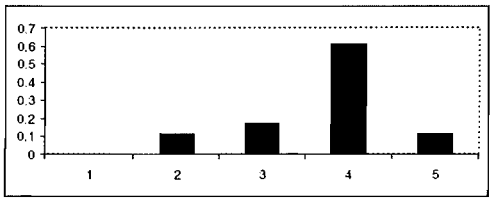
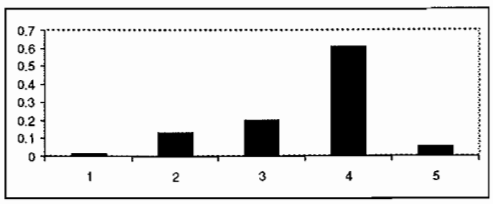


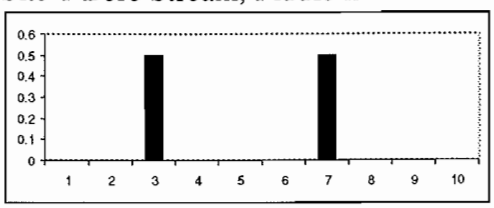
Figure 7.4.4.1 (Continued)

Site 19 Moreton Ford n=38

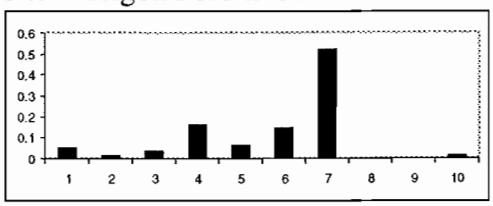


6. Locus Ssosl 417

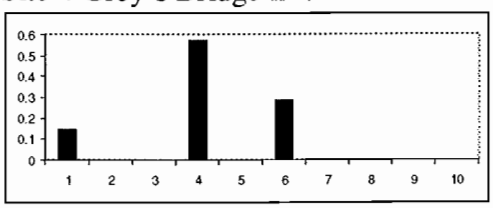
Site 1 Bere Stream, Piddle n= 2



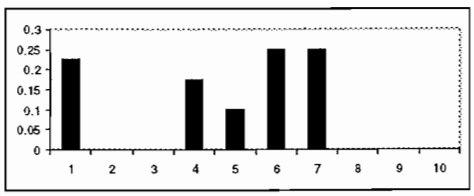
Site 2 Trigon Ford n=31



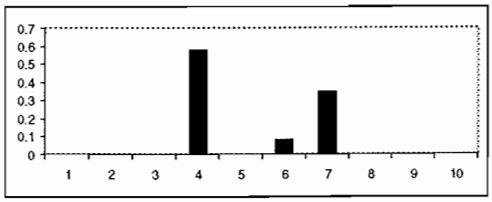
Site 4 Grey's Bridge n=7



Site 5 Norris Farm n=20



Site 6 Lewell Mill n=13



Site 7 East Burton n=39

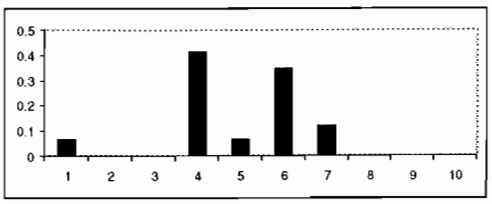
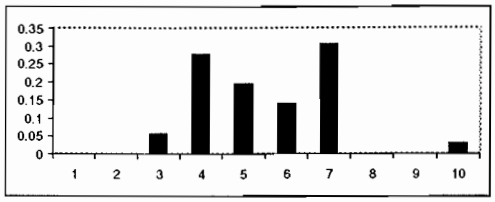
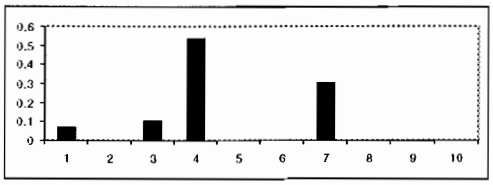


Figure 7.4.4.1 (Continued)

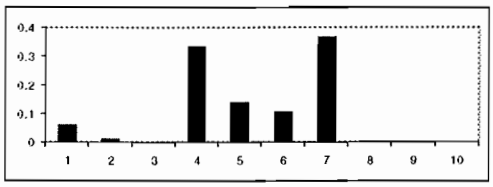
Site 8 East Stoke n=18



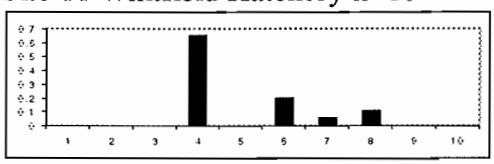
Site 9 ESMS n=15



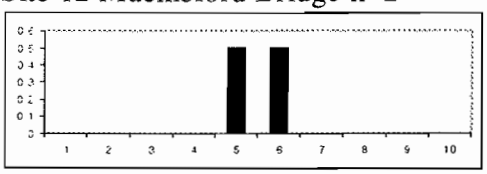
Site 10 Waterbarn Stream n=44



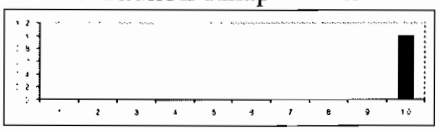
Site 11 Whitfield Hatchery n=10



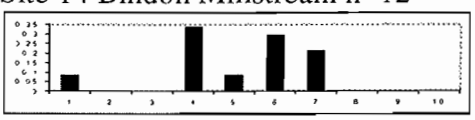
Site 12 Muckleford Bridge n=2



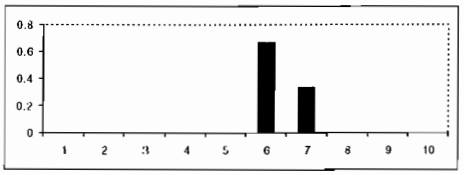
Site 13 Tadnoll Knap Mill n=1



Site 14 Bindon Millstream n=12



Site 15 Tadnoll Winfrith n= 3



Site 19 Moreton Ford n=15

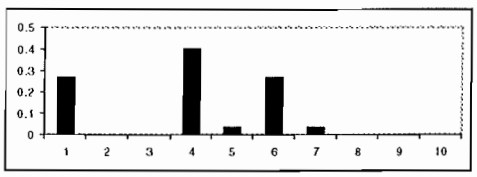
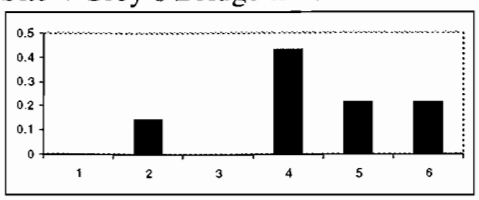


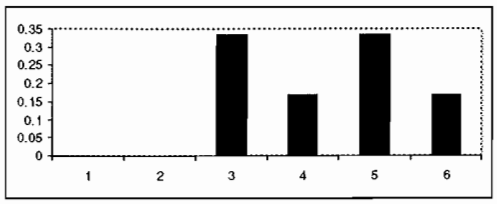
Figure 7.4.4.1 (Continued)

1. Locus Ssa 202

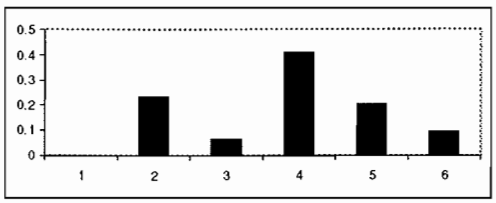
Site 4 Grey's Bridge n= 7



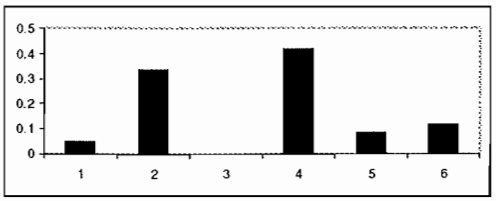
Site 5 Norris Farm n= 6



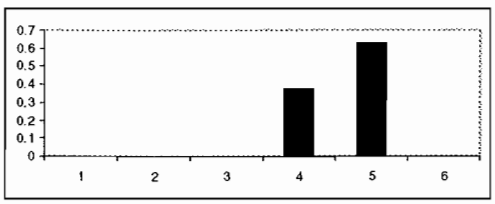
Site 6 Lewell Mill n= 32



Site 7 East Burton n= 30



Site 8 East Stoke n= 4



Site 9 ESMS n= 15

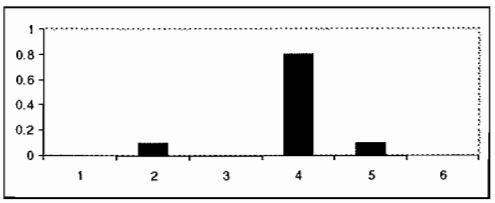
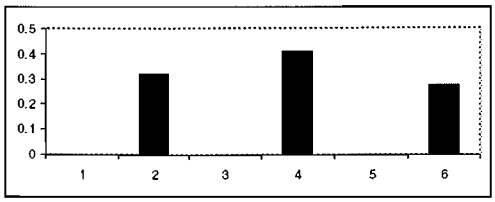
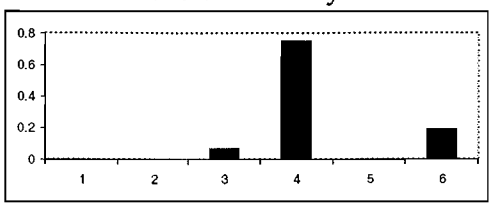


Figure 7.4.4.2 Allele frequencies at 6 microsatellite loci, from *S. salar* sampled at 16 sites on the Rivers Piddle and Frome, September 1998

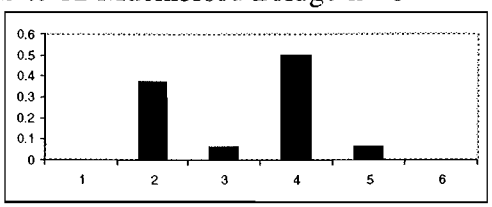
Site 10 Waterbarn Stream n= 11



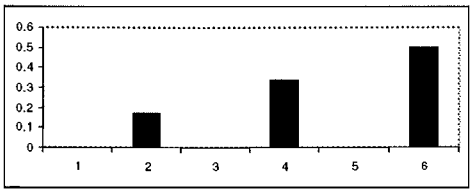
Site 11 Whitfield Hatchery n= 11



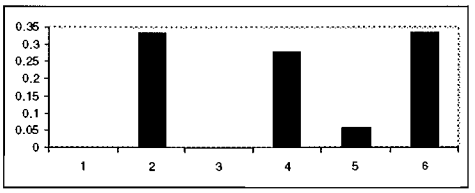
Site 12 Muckleford Bridge n= 8



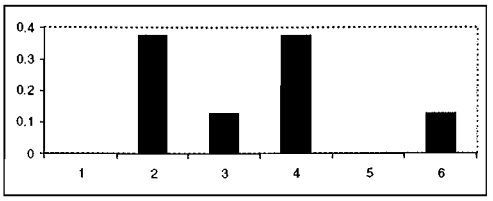
Site 15 Tadnoll Winfrith n= 3



Site 16 South Winterbourne n= 9



Site 17 Wool Stream n= 4



Site 18 Moreton Carrier n= 4

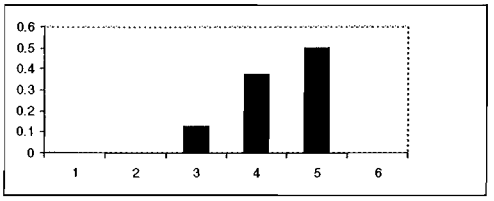
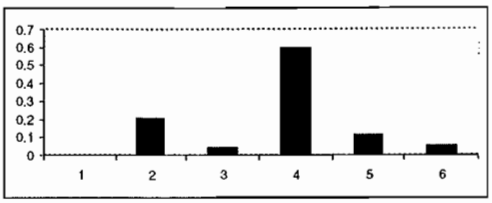
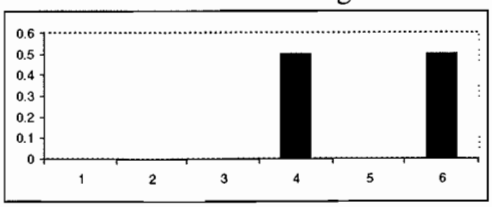


Figure 7.4.4.2 (Continued)

Site 19 Moreton Ford n= 39

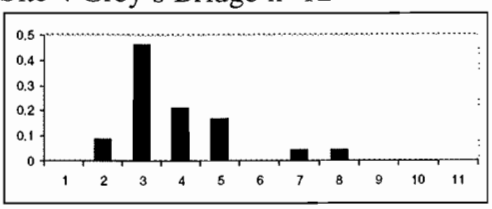


Site 22 Dorchester Sewerage n= 3

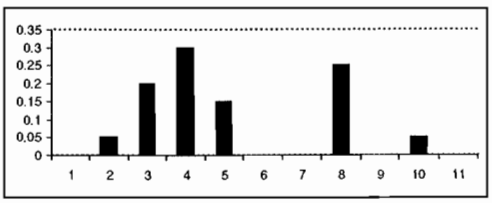


2. Locus Ssa 171

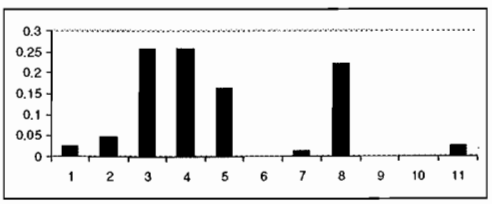
Site 4 Grey's Bridge n=12



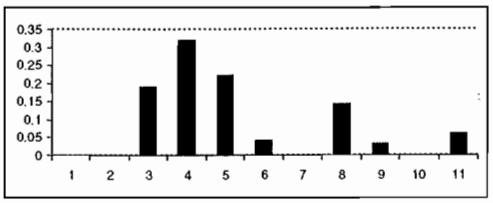
Site 5 Norris Farm n= 10



Site 6 Lewell Mill n= 43



Site 7 East Burton n= 50



Site 8 East Stoke n= 4

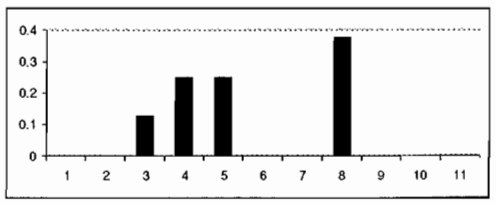
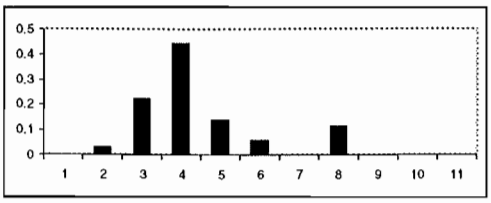
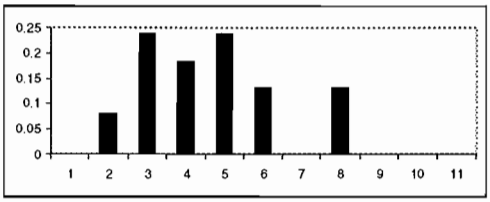


Figure 7.4.4.2 (Continued)

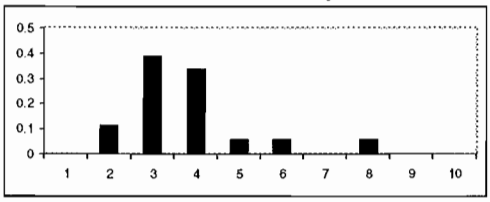
Site 9 ESMS n= 18



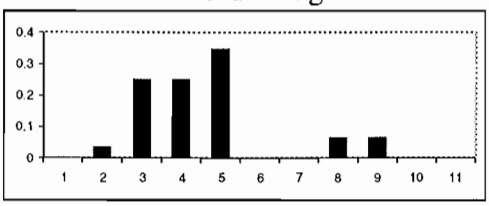
Site 10 Waterbarn Stream n= 19



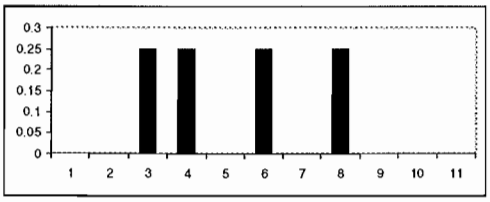
Site 11 Whitfield Hatchery n= 9



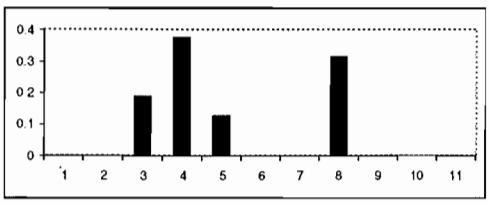
Site 12 Muckleford Bridge n= 16



Site 15 Tadnoll Winfrith n= 2



Site 16 South Winterbourne n= 8



Site 17 Wool Stream n= 2

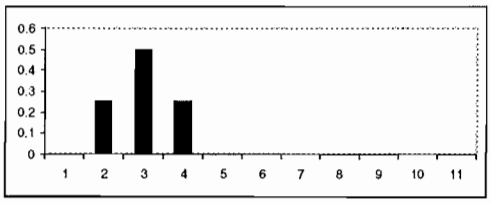
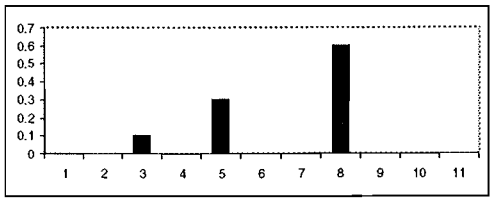
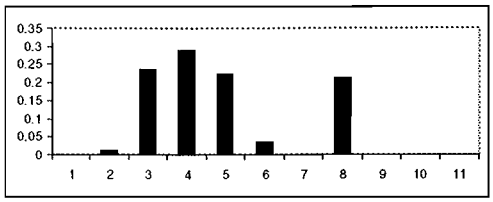


Figure 7.4.4.2 (Continued)

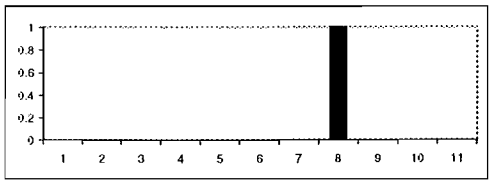
Site 18 Moreton Carrier n= 5



Site 19 Moreton Ford n= 45

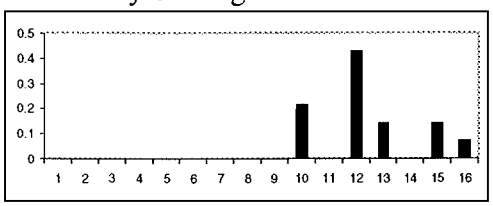


Site 22 Dorchester Sewerage n= 1

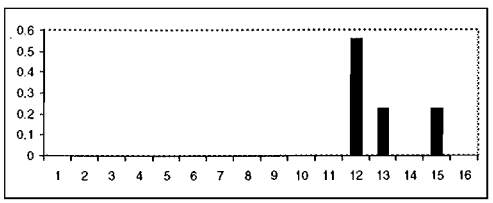


3. Locus Ssa 197

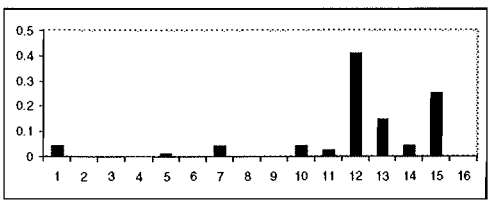
Site 4 Grey's Bridge n= 7



Site 5 Norris Farm n= 9



Site 6 Lewell Mill n= 38



Site 7 East Burton n= 48

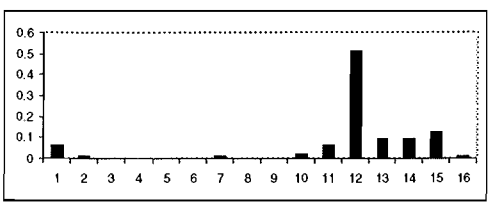
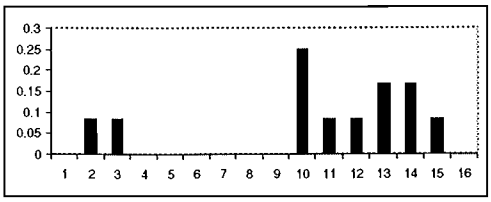
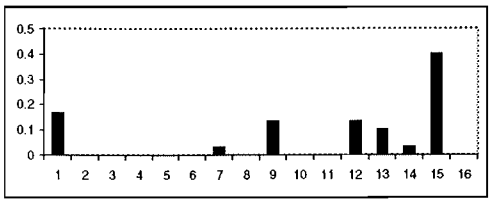


Figure 7.4.4.2 (Continued)

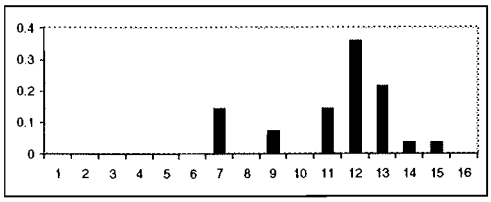
Site 8 East Stoke n= 6



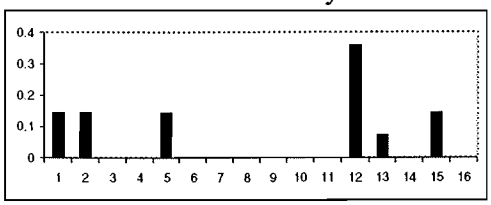
Site 9 ESMS n= 15



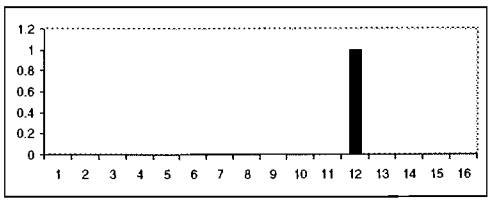
Site 10 Waterbarn Stream n= 14



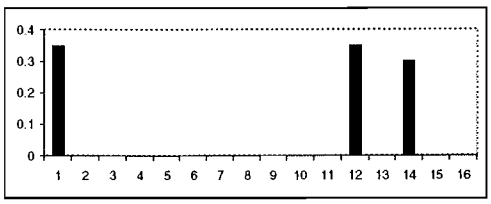
Site 11 Whitfield Hatchery n= 7



Site 15 Tadnoll Winfrith n= 1



Site 16 South Winterbourne n= 10



Site 17 Wool Stream n= 6

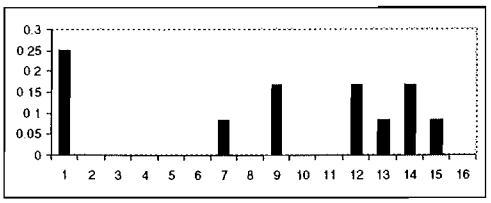
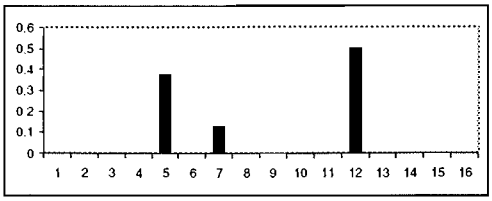
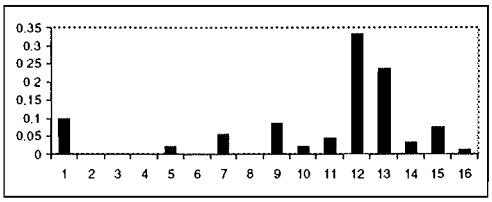


Figure 7.4.4.2 (Continued)

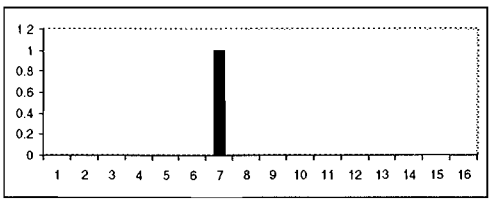
Site 18 Moreton Carrier n= 4



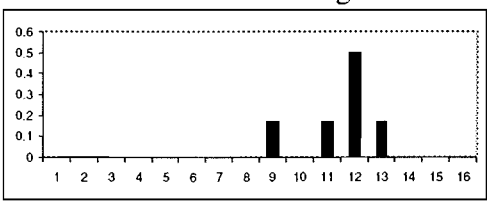
Site 19 Moreton Ford n= 47



Site 21 Dereck's Tadnoll n= 1

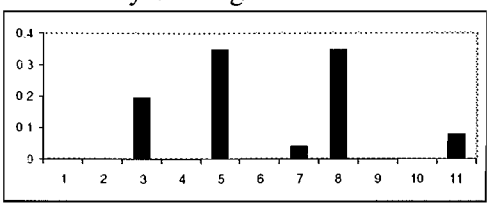


Site 22 Dorchester Sewerage n= 3

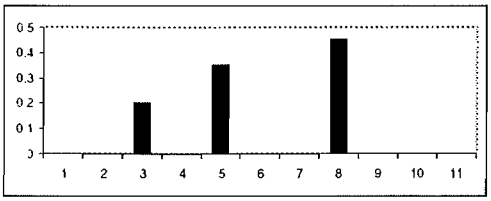


4. Locus Ssosl 85

Site 4 Grey's Bridge n= 13



Site 5 Norris Farm n= 10



Site 6 Lewell Mill n= 39

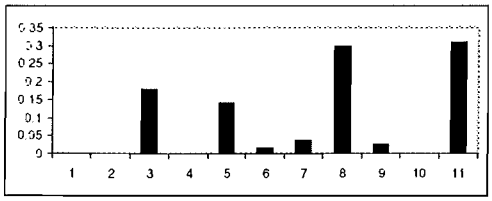
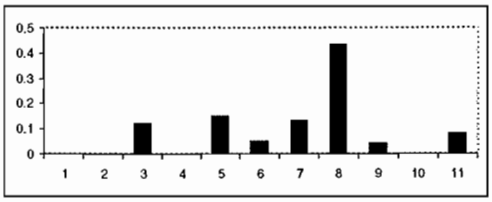
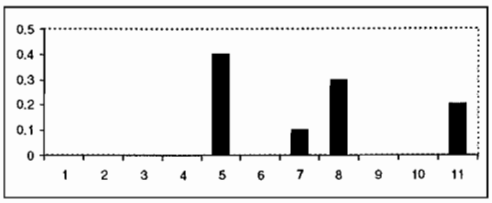


Figure 7.4.4.2 (Continued)

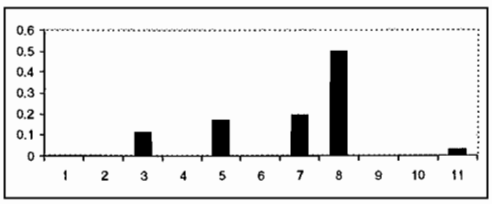
Site 7 East Burton n= 50



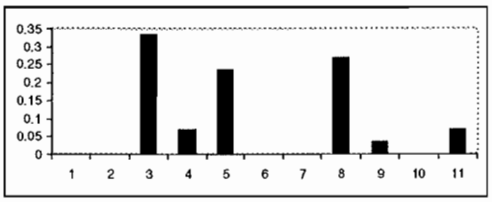
Site 8 East Stoke n=10



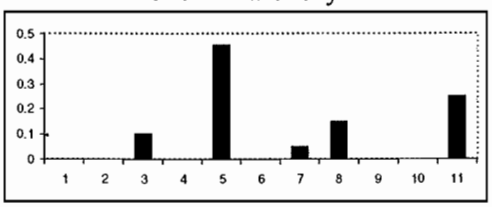
Site 9 ESMS n= 18



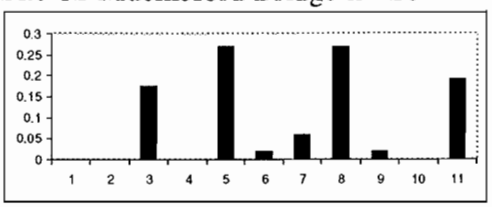
Site 10 Waterbarn Stream n= 15



Site 11 Whitfield Hatchery n=10



Site 12 Muckleford Bridge n= 26



Site 15 Tadnoll Winfrith n= 3

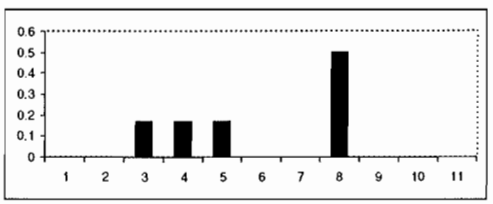
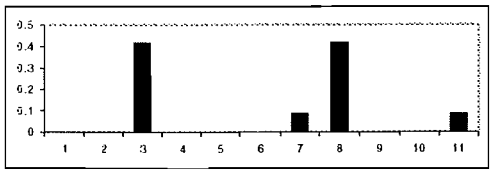
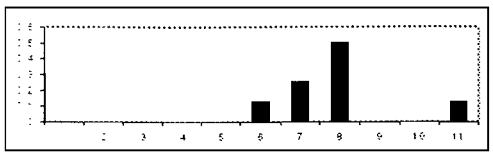


Figure 7.4.4.2 (Continued)

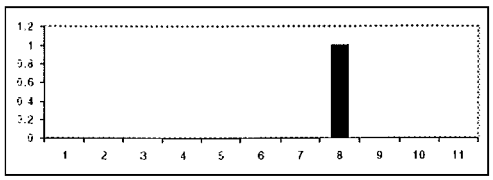
Site 16 South Winterbourne n= 6



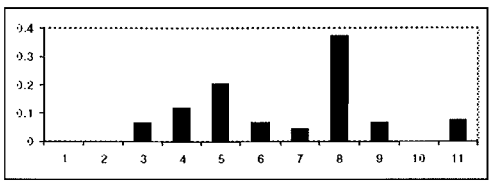
Site 17 Wool Stream n= 4



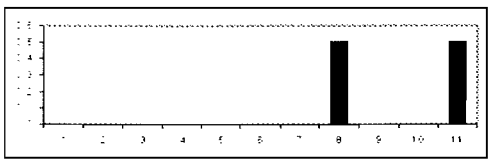
Site 18 Moreton Carrier n= 4



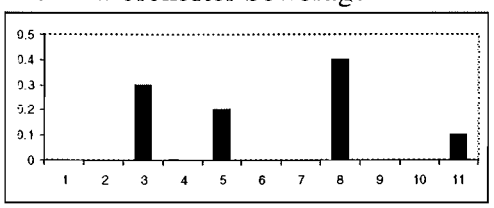
Site 19 Moreton Ford n= 47



Site 21 Dereck's Tadnoll n=1



Site 22 Dorchester Sewerage n= 5



5. Locus Ssa289

Site 4 Grey's Bridge n= 14

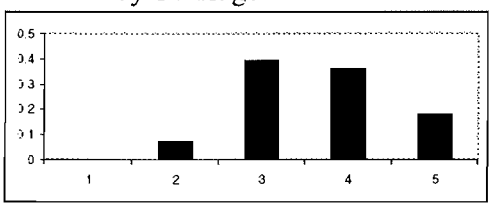
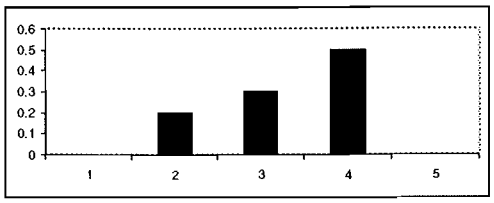
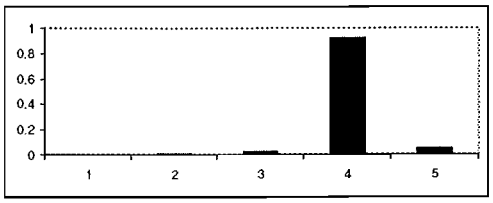


Figure 7.4.4.2 (Continued)

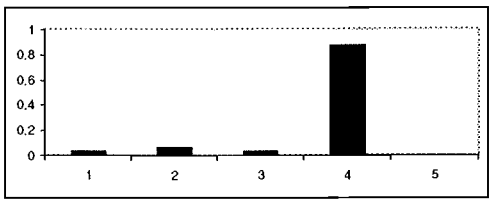
Site 5 Norris Farm n= 10



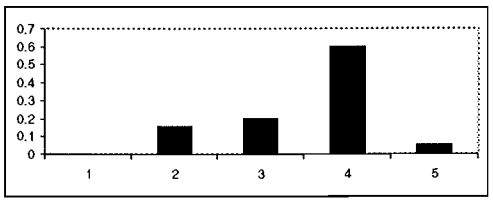
Site 6 Lewell Mill n= 44



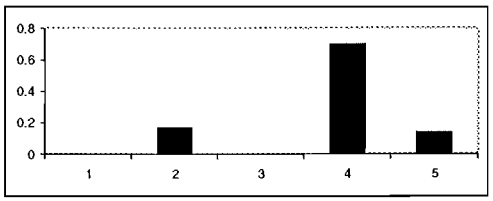
Site 7 East Burton n= 32



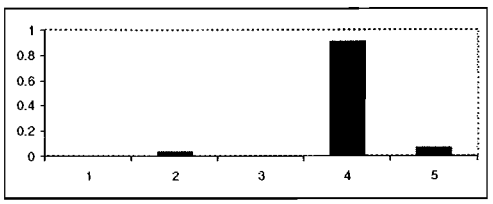
Site 8 East Stoke n=10



Site 9 ESMS n= 15



Site 10 Waterbarn Stream n= 15



Site 11 Whitfield Hatchery n= 10

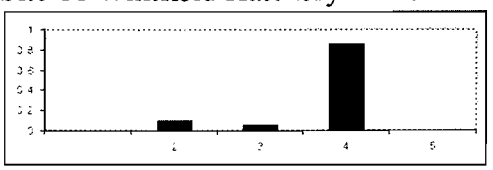
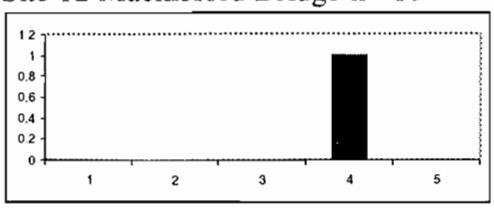
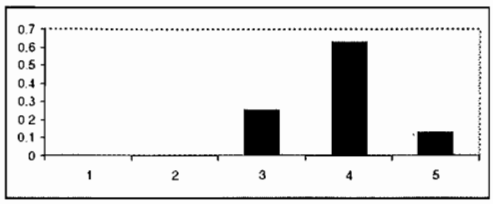


Figure 7.4.4.2 (Continued)

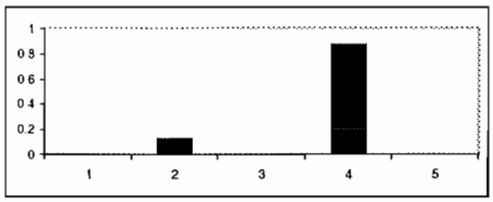
Site 12 Muckleford Bridge n= 10



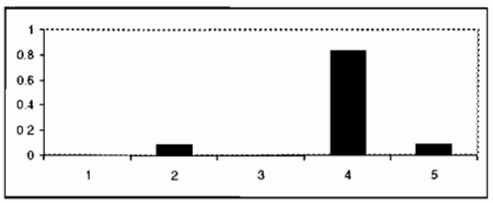
Site 15 Tadnoll Winfrith n= 4



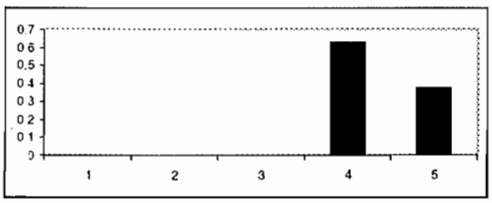
Site 16 South Winterbourne n=8



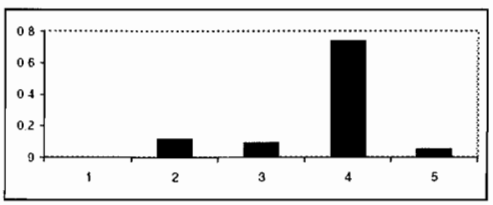
Site 17 Wool Stream n= 6



Site 18 Moreton Carrier n= 4



Site 19 Moreton Ford n= 38



Site 21 Dereck's Tadnoll n=3

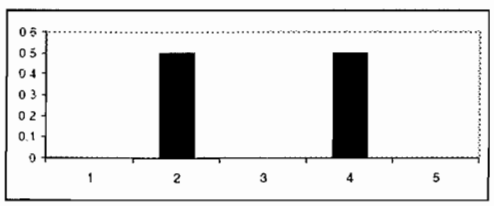
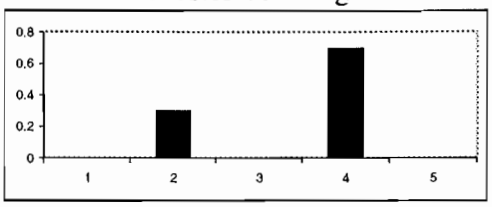


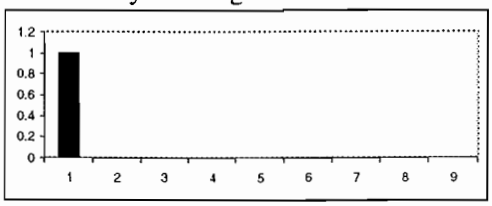
Figure 7.4.4.2 (Continued)

Site 22 Dorchester Sewerage n= 3

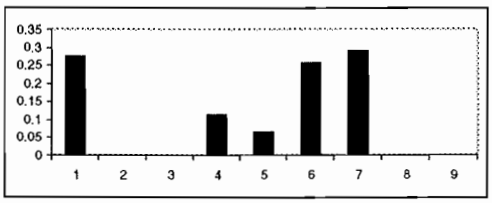


6. Locus Ssosl 417

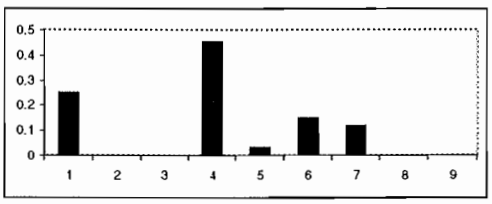
Site 4 Grey's Bridge n=2



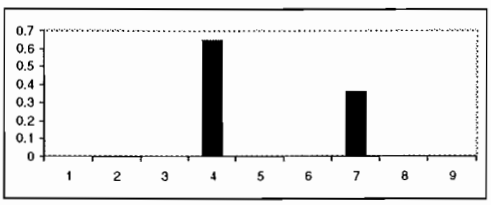
Site 6 Lewell Mill n= 31



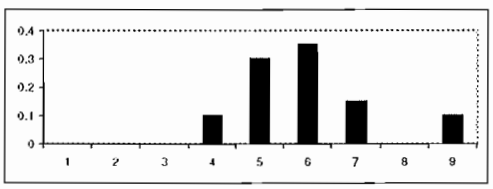
Site 7 East Burton n= 30



Site 8 East Stoke n=7



Site 9 ESMS n= 10



Site 11 Whitfield Hatchery n=4

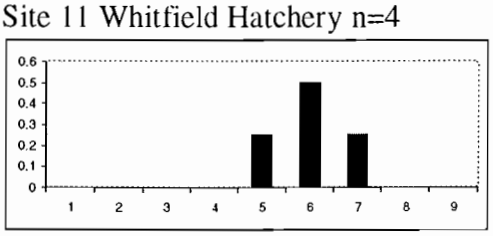
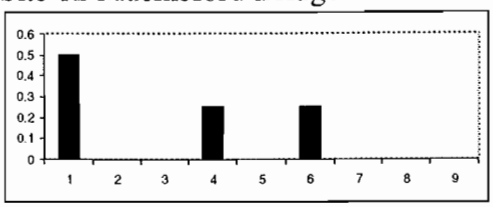
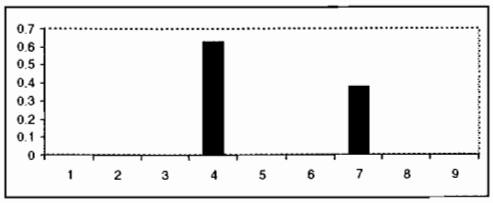


Figure 7.4.4.2 (Continued)

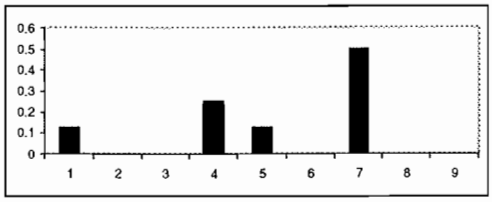
Site 12 Muckleford Bridge n= 4



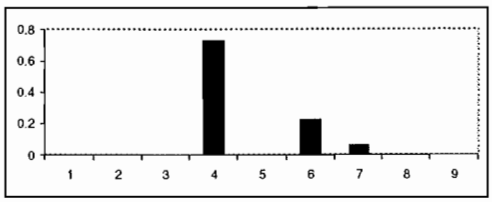
Site 15 Tadnoll Winfrith n= 4



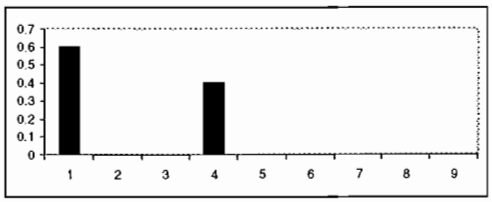
Site 16 South Winterbourne n=8



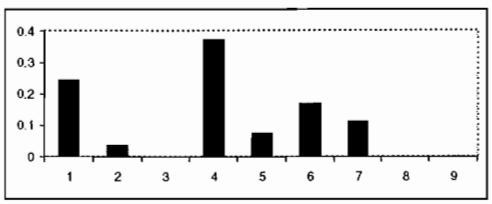
Site 17 Wool Stream n= 9



Site 18 Moreton Carrier n= 5



Site 19 Moreton Ford n= 27



Site 22 Dorchester Sewerage n= 5

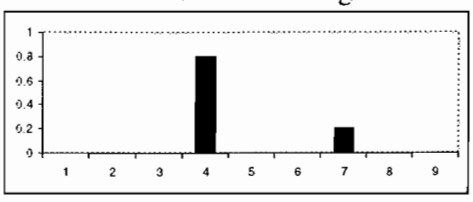
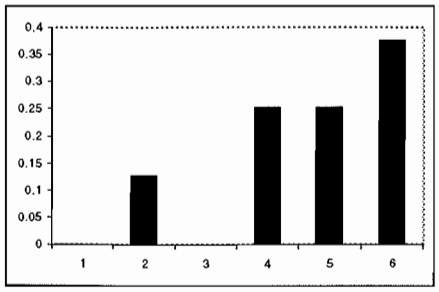


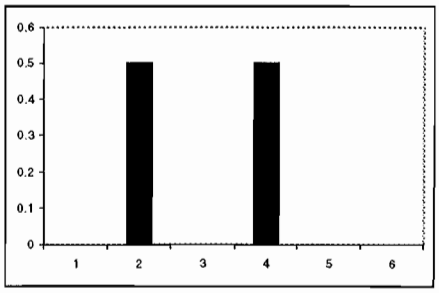
Figure 7.4.4.2 (Continued)

1. Locus Ssa 202

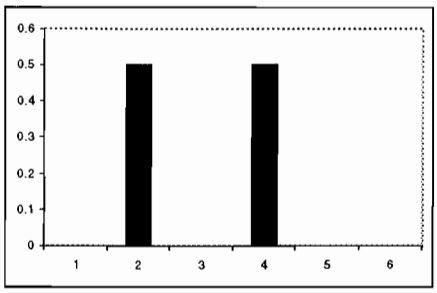
Site 4 GB n=4



Site 9 ESMS n=1



Site 10 WS n=1



Site 14 BM n=2

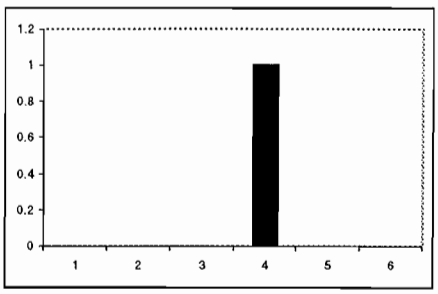
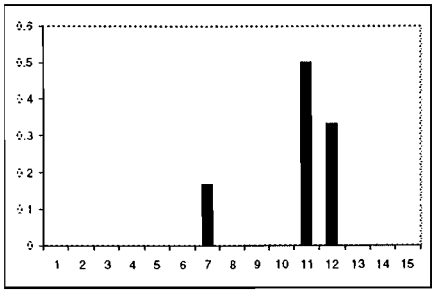


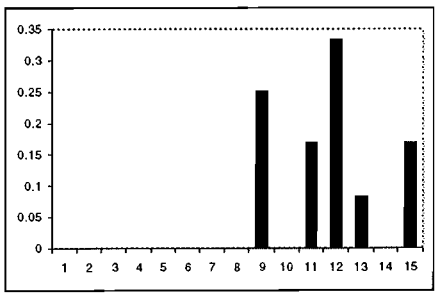
Figure 7.4.4.3 Allele frequencies at 5 microsatellite loci, for *S. Salar* sampled at 5 sites on the River Frome, November 1998

2. Locus Ssa 197

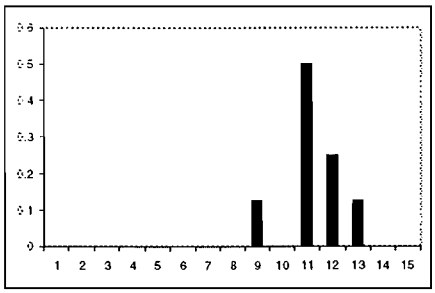
Site 4 GB n=3



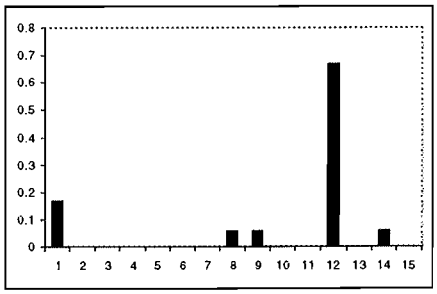
Site 9 ESMS n=6



Site 10 WS n=4



Site 14 BM n=9



Site 17 WO n= 5

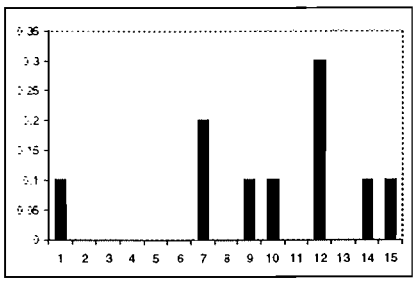
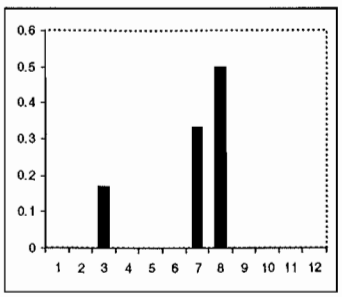


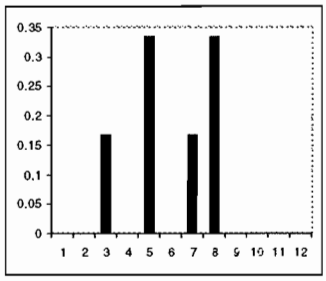
Figure 7.4.4.3 (Continued)

3. Locus Ssosl85

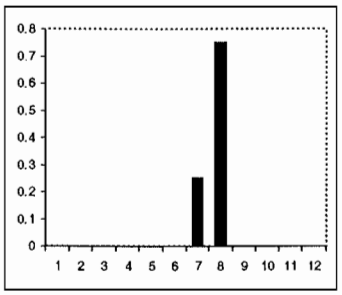
Site 4 GB n=3



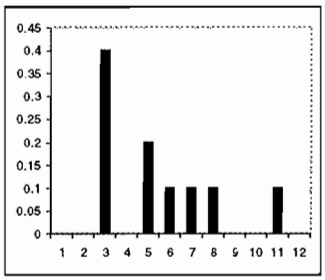
Site 9 ESMS n=3



Site 10 WS n=2



Site 14 BM n=5



Site 17 WO n= 7

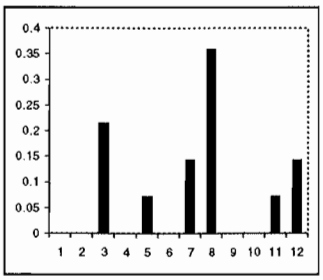
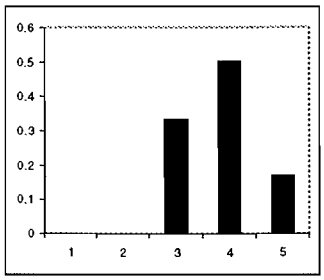


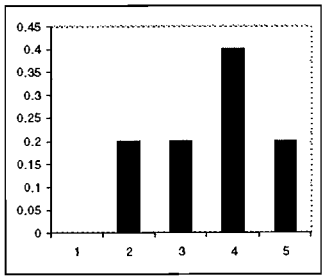
Figure 7.4.4.3 (Continued)

4. Locus Ssa 289

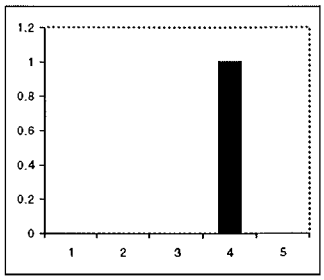
Site 4 GB n=3



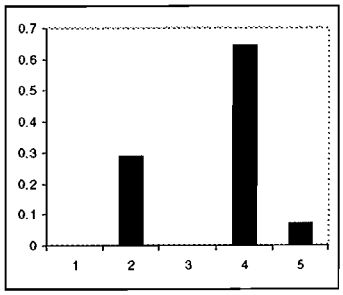
Site 9 ESMS n=5



Site 10 WS n=2



Site 14 BM n=7



Site 17 WO n= 8

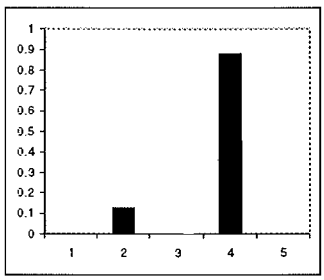
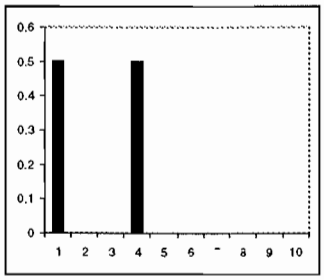


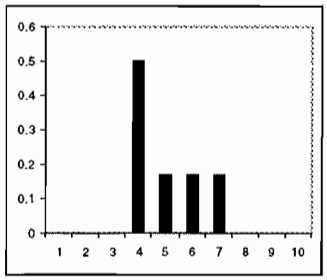
Figure 7.4.4.3 (Continued)

5. Locus Ssosl417

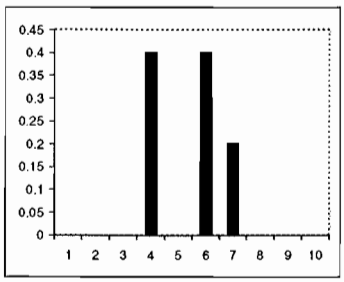
Site 4 GB n=2



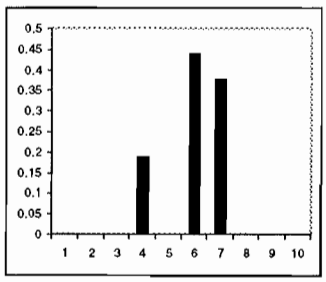
Site 9 ESMS n=6



Site 10 WS n=5



Site 14 BM n=8



Site 17 WO n= 9

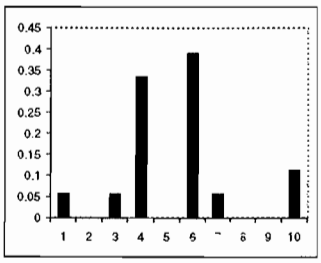
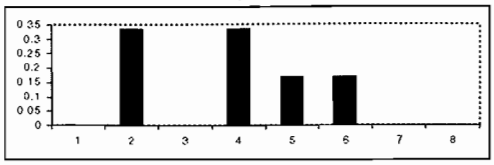


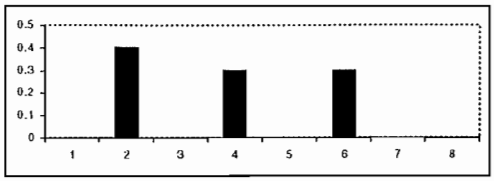
Figure 7.4.4.3 (Continued)

1. Locus Ssa 202

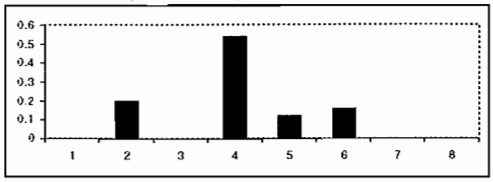
Site 1 Bere Stream, Piddle n=3



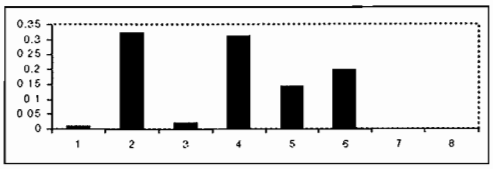
Site 3 West Holme n=5



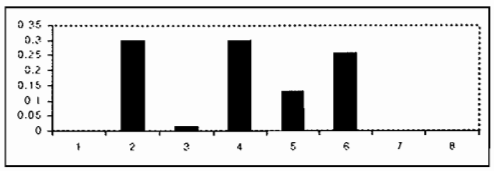
Site 4 Grey's Bridge n=13



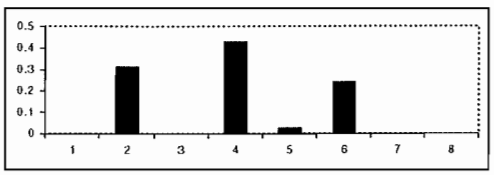
Site 5 Norris Farm n=53



Site 6 Lewell Mill n=35



Site 7 East Burton n=21



Site 8 East Stoke n=9

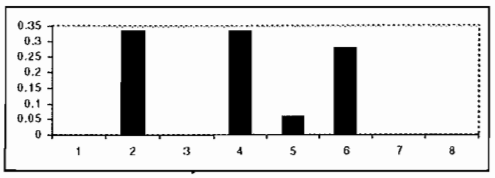
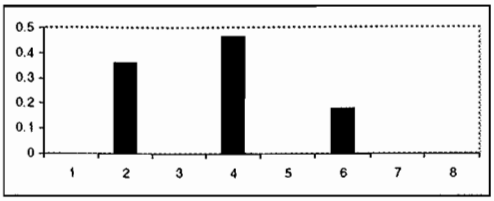
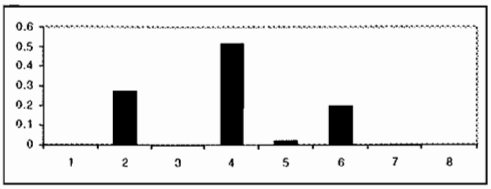


Figure 7.4.4.4 Allele frequencies at 6 microsatellite loci, from *S. salar* sampled at 16 sites on the Rivers Piddle and Frome, July 1999

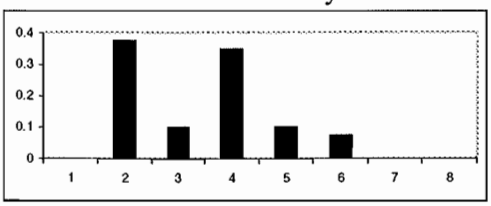
Site 9 ESMS n=14



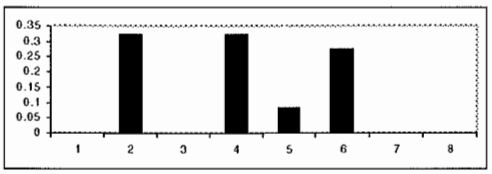
Site 10 Waterbarn Stream n=26



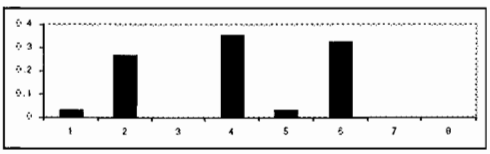
Site 11 Whitfield Hatchery n=20



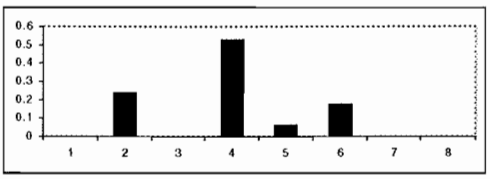
Site 14 Bindon Millstream n=31



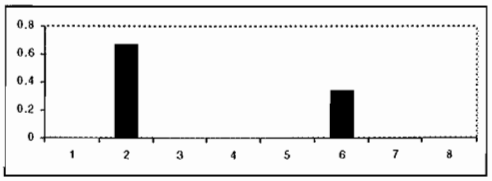
Site 15 Tadnoll Winfrith n=17



Site 16 South Winterbourne n=17



Site 17 Wool Stream n=3



Site 19 Moreton Ford n=49

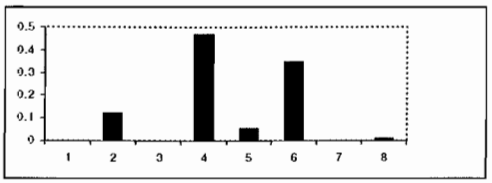
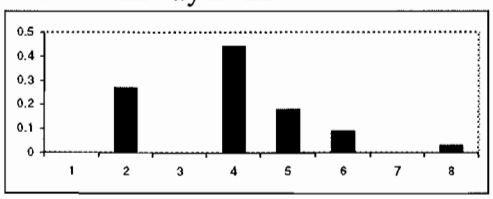


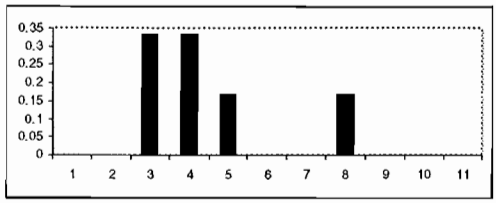
Figure 7.4.4.4 (Continued)

Site 20 Railway n=22

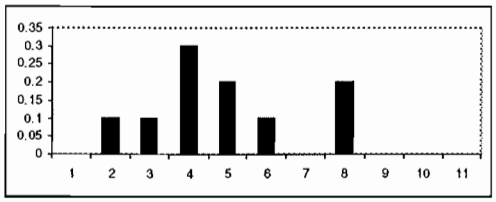


2. Locus Ssa 171

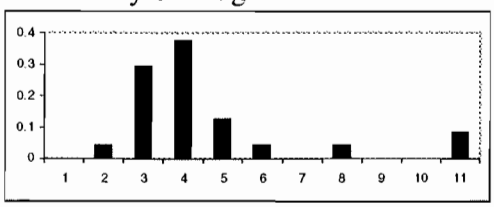
Site 1 Bere Stream, Piddle n= 3



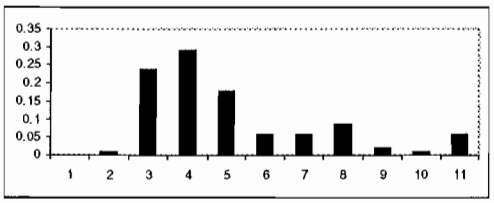
Site 3 West Holme n=5



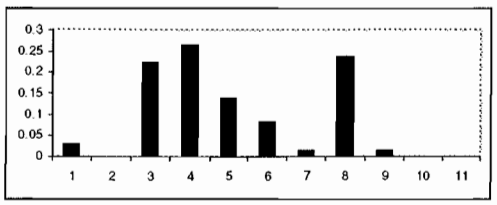
Site 4 Grey's Bridge n=12



Site 5 Norris Farm n=53



Site 6 Lewell Mill n=36



Site 7 East Burton n=21

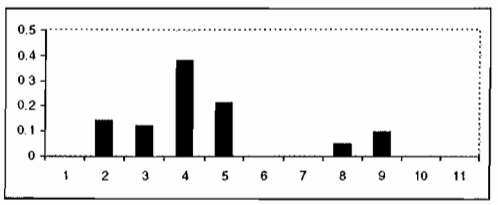
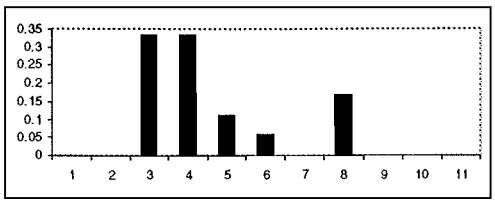
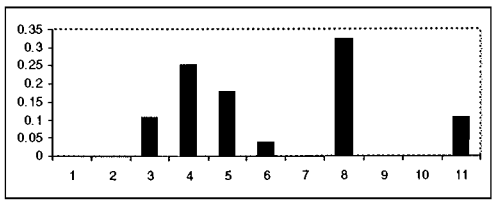


Figure 7.4.4.4 (Continued)

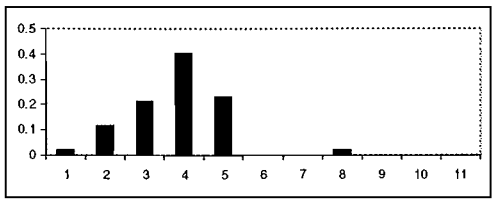
Site 8 East Stoke n=9



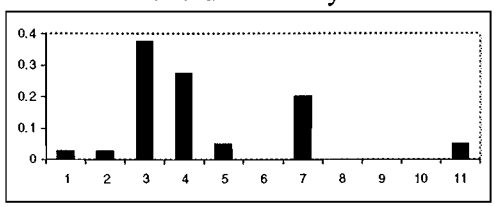
Site 9 ESMS n=14



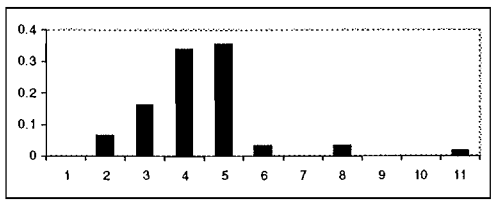
Site 10 Waterbarn Stream n=26



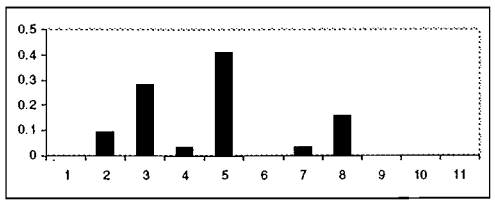
Site 11 Whitfield Hatchery n=20



Site 14 Bindon Millstream n=31



Site 15 Tadnoll Winfrith n=16



Site 16 South Winterbourne n=17

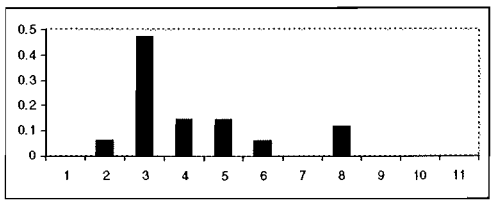
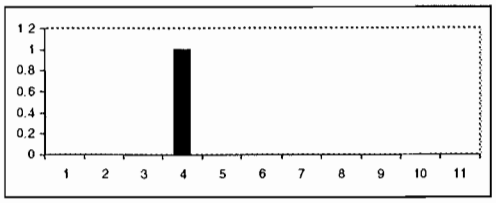
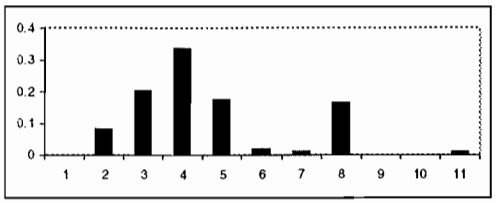


Figure 7.4.4.4 (Continued)

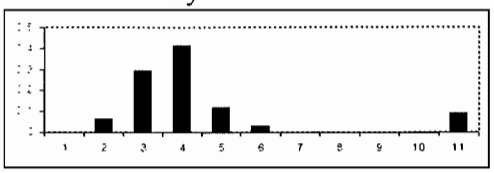
Site 17 Wool Stream n=3



Site 19 Moreton Ford n=49

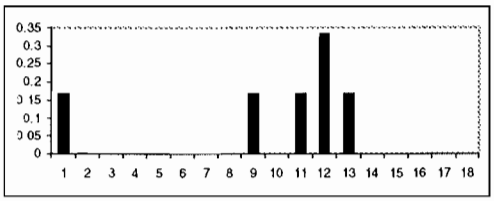


Site 20 Railway n=17

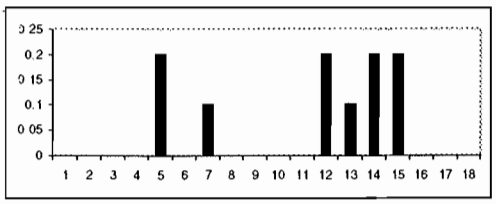


3. Locus Ssa 197

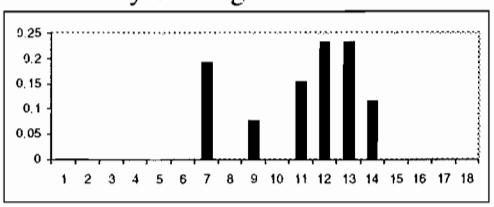
Site 1 Bere Stream, Piddle n= 3



Site 3 West Holme n= 5



Site 4 Grey's Bridge n= 13



Site 5 Norris Farm n= 53

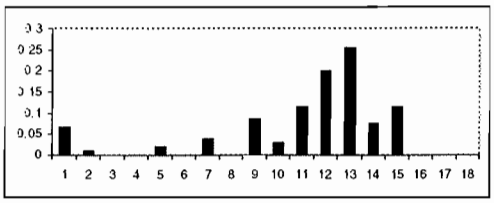
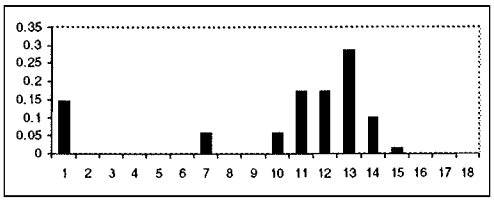
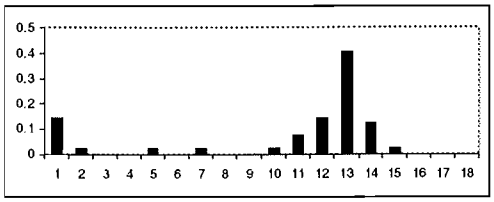


Figure 7.4.4.4 (Continued)

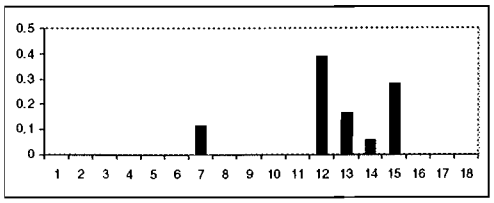
Site 6 Lewell Mill n= 35



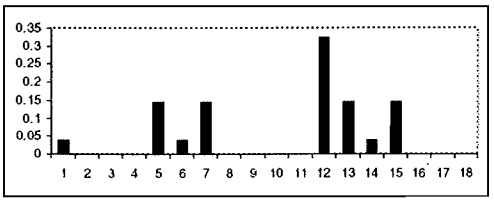
Site 7 East Burton n= 21



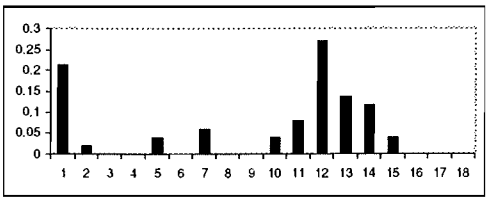
Site 8 East Stoke n= 9



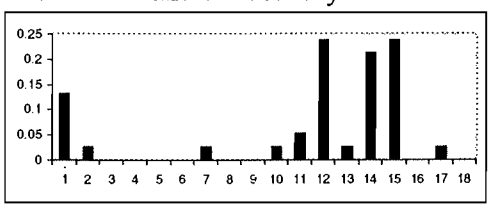
Site 9 ESMS n= 14



Site 10 Waterbarn Stream n= 26



Site 11 Whitfield Hatchery n= 19



Site 14 Bindon Millstream n= 31

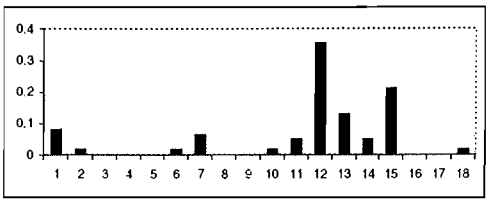
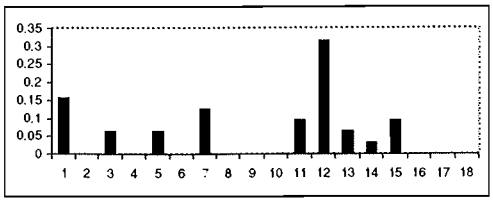
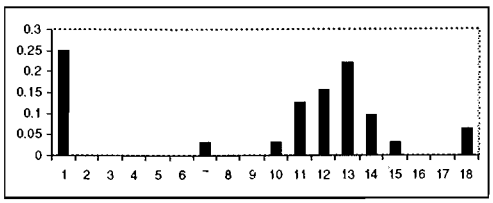


Figure 7.4.4.4 (Continued)

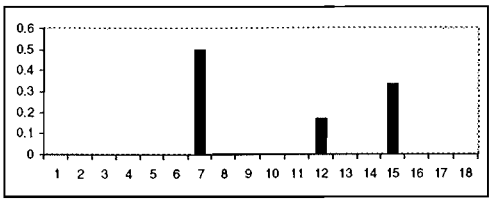
Site 15 Tadnoll Winfrith n= 16



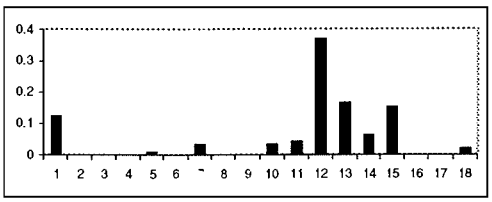
Site 16 South Winterbourne n= 16



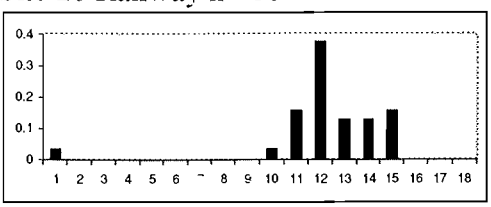
Site 17 Wool Stream n= 3



Site 19 Moreton Ford n= 49

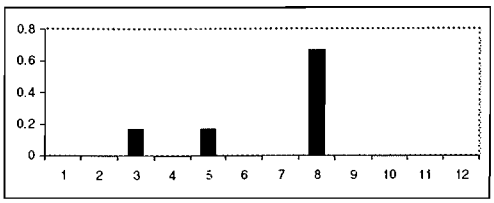


Site 20 Railway n= 16



4. Locus Ssosl 85

Site 1 Bere Stream, Piddle n= 3



Site 3 West Holme n= 3

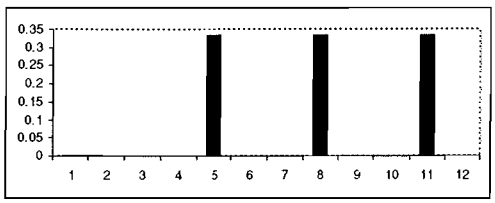
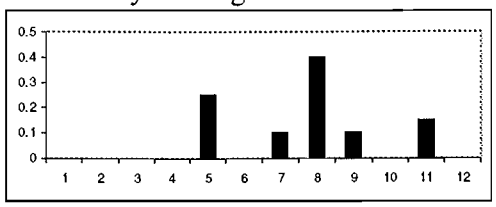
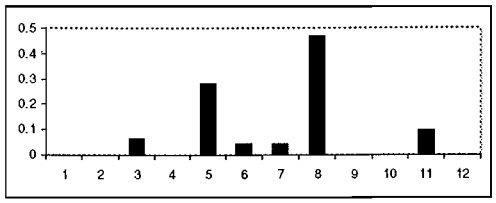


Figure 7.4.4.4 (Continued)

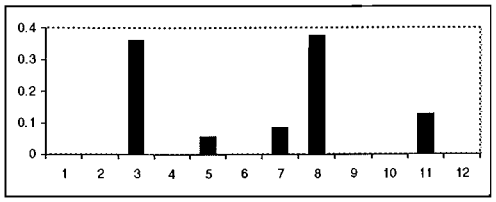
Site 4 Grey's Bridge n= 10



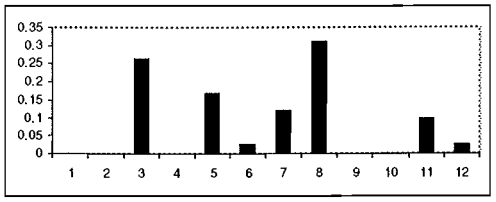
Site 5 Norris Farm n= 46



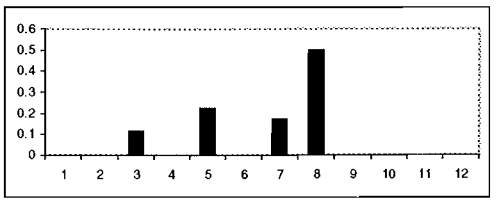
Site 6 Lewell Mill n= 36



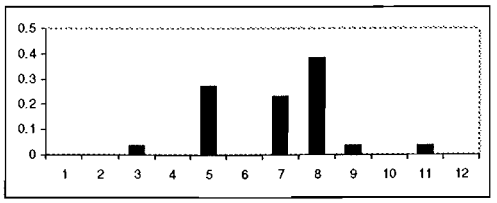
Site 7 East Burton n= 21



Site 8 East Stoke n= 9



Site 9 ESMS n= 13



Site 10 Waterbarn Stream n= 26

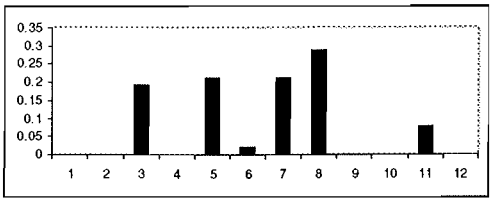
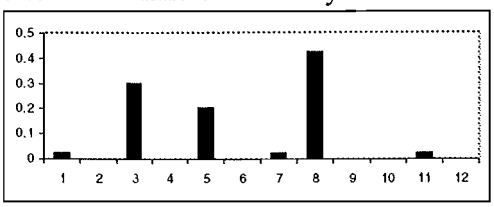
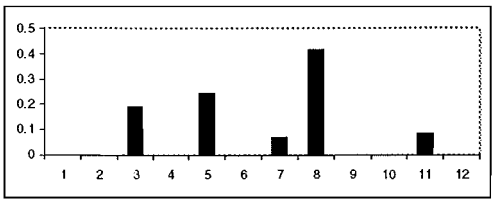


Figure 7.4.4.4 (Continued)

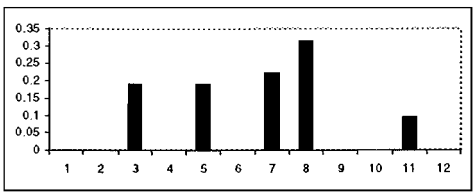
Site 11 Whitfield Hatchery n= 20



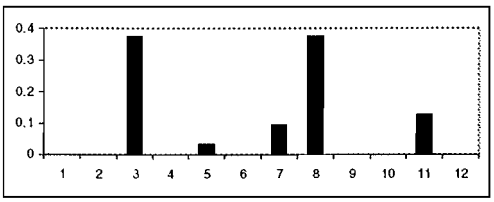
Site 14 Bindon Millstream n= 29



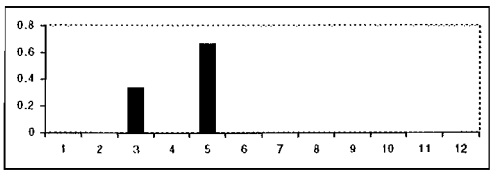
Site 15 Tadnoll Winfrith n=16



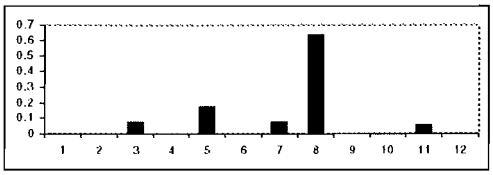
Site 16 South Winterbourne n= 16



Site 17 Wool Stream n= 3



Site 19 Moreton Ford n= 41



Site 20 Railway n=18

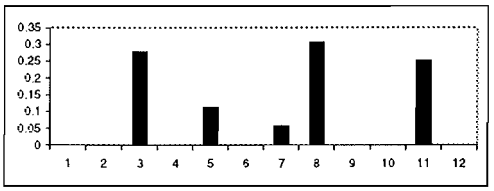
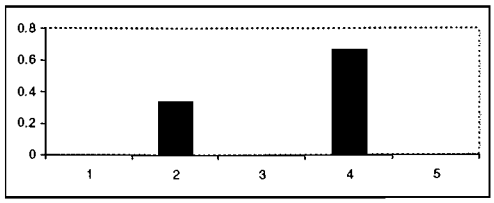


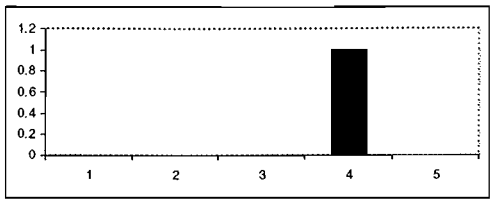
Figure 7.4.4.4 (Continued)

5. Locus Ssa 289

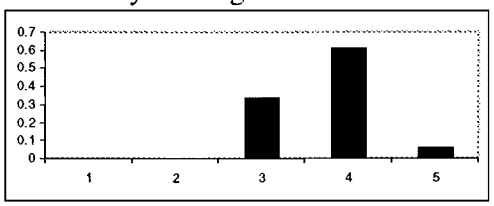
Site 1 Bere Stream, Piddle n= 3



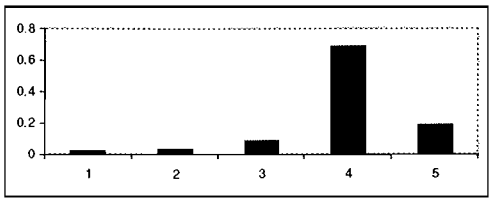
Site 3 West Holme n= 4



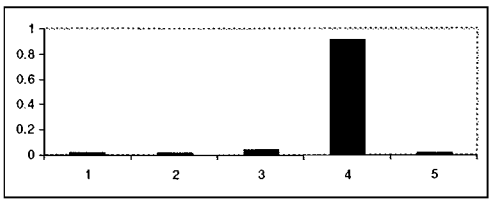
Site 4 Grey's Bridge n= 9



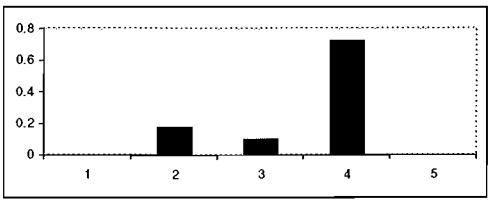
Site 5 Norris Farm n= 49



Site 6 Lewell Mill n= 35



Site 7 East Burton n= 20



Site 8 East Stoke n= 9

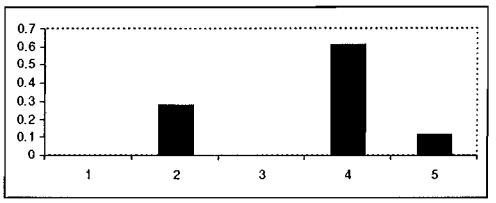
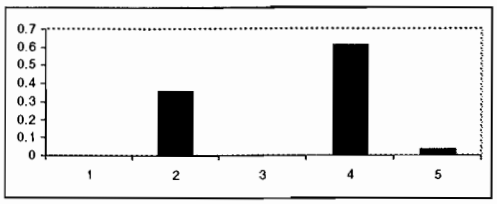
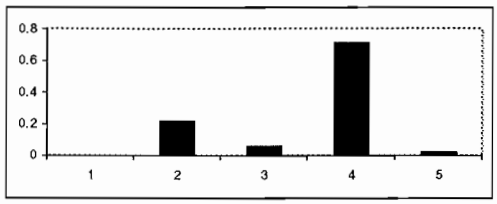


Figure 7.4.4.4 (Continued)

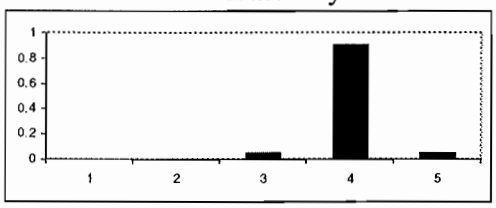
Site 9 ESMS n=14



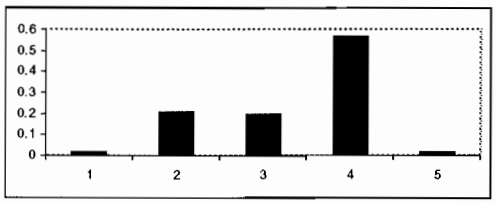
Site 10 Waterbarn Stream n= 26



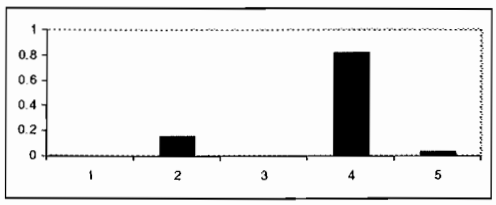
Site 11 Whitfield Hatchery n= 20



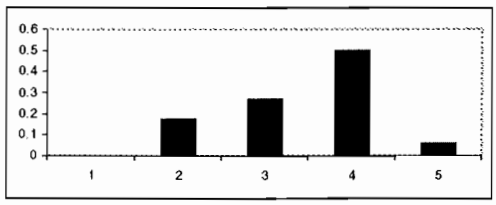
Site 14 Bindon Millstream n= 31



Site 15 Tadnoll Winfrith n= 16



Site 16 South Winterbourne n= 17



Site 17 Wool Stream n= 3

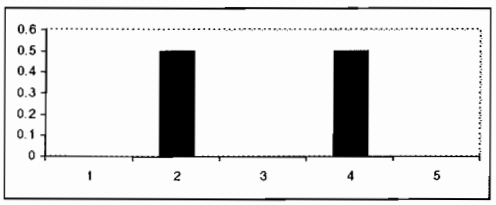
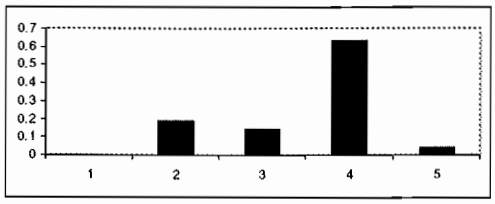
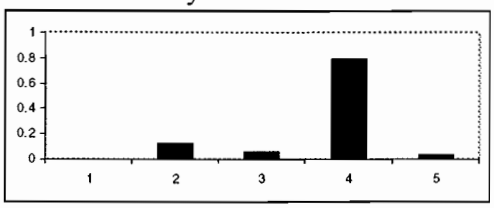


Figure 7.4.4.4 (Continued)

Site 19 Moreton Ford n= 49

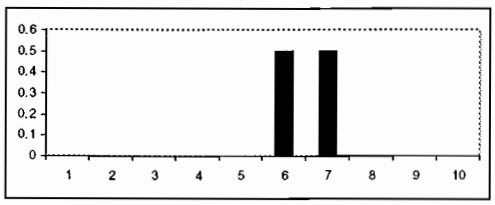


Site 20 Railway n= 17

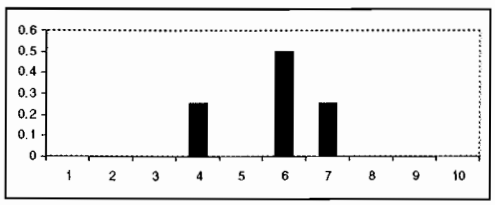


6. Locus Ssosl 417

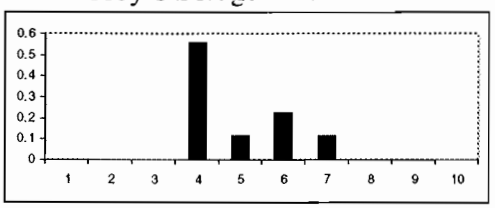
Site 1 Bere Stream, Piddle n= 2



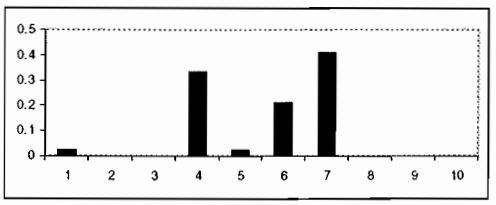
Site 3 West Holme n= 4



Site 4 Grey's Bridge n= 9



Site 5 Norris Farm n= 38



Site 6 Lewell Mill n= 21

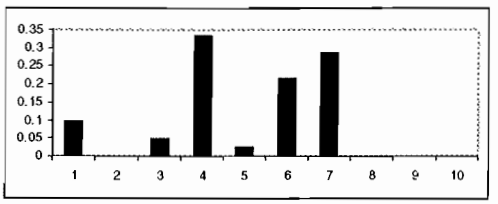
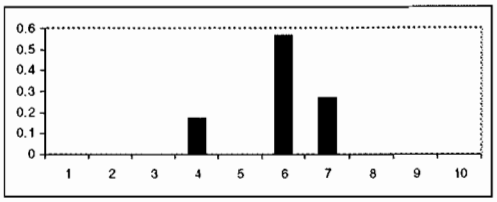
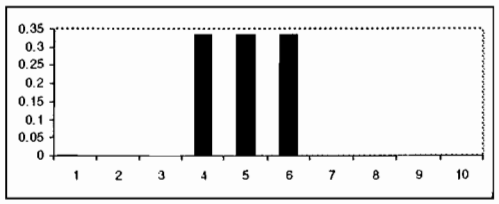


Figure 7.4.4.4 (Continued)

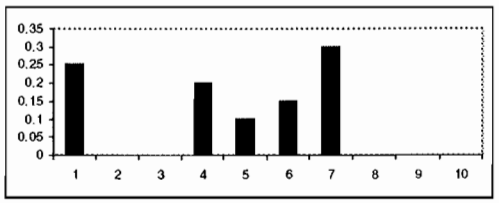
Site 7 East Burton n= 15



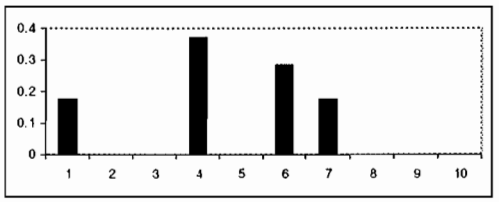
Site 8 East Stoke n= 3



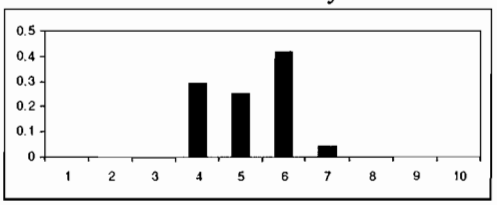
Site 9 ESMS n= 10



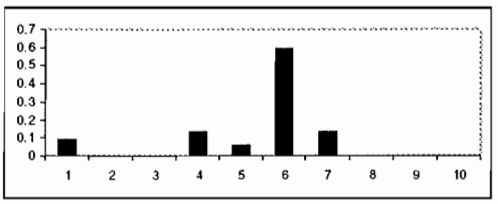
Site 10 Waterbarn Stream n= 23



Site 11 Whitfield Hatchery n= 12



Site 14 Bindon Millstream n= 27



Site 15 Tadnoll Winfrith n= 6

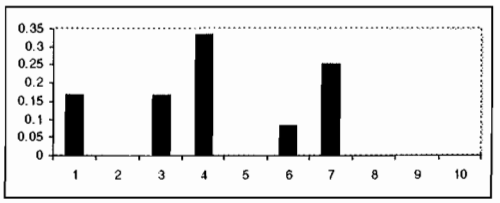
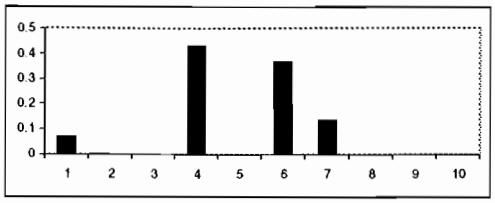
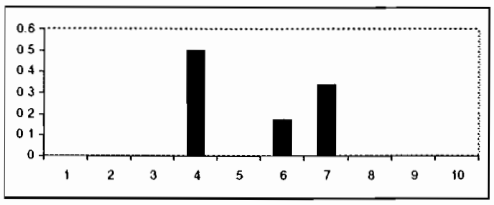


Figure 7.4.4.4 (Continued)

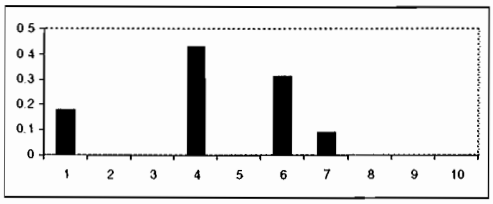
Site 16 South Winterbourne n=15



Site 17 Wool Stream n= 3



Site 19 Moreton Ford n= 34



Site 20 Railway n=15

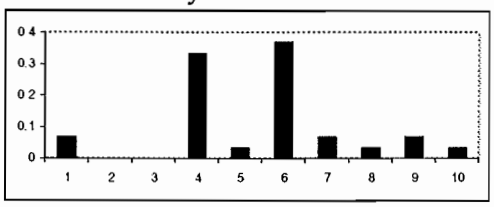
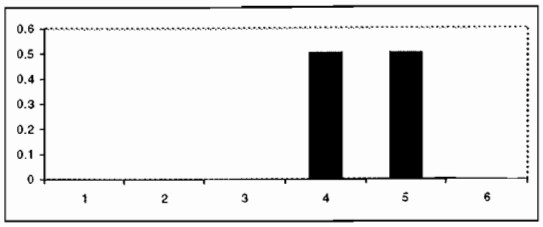


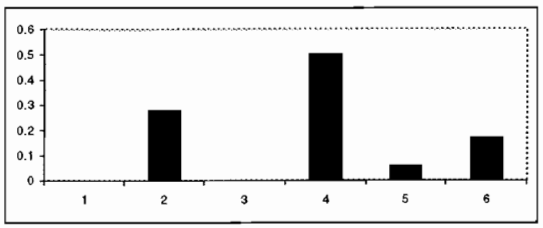
Figure 7.4.4.4 (Continued)

1. Locus Ssa 202

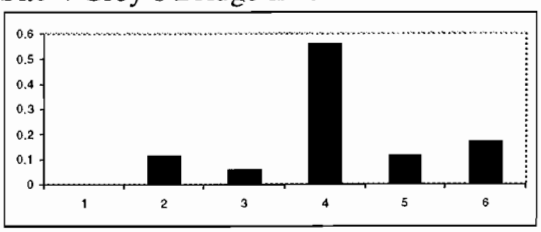
Site 1 Bere Stream, Piddle n= 1



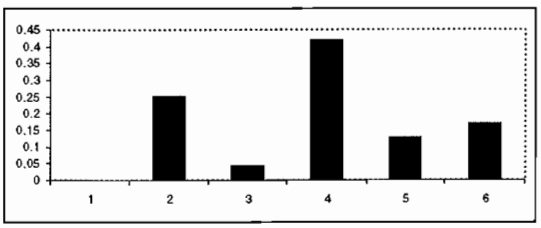
Site 3 West Holme n= 9



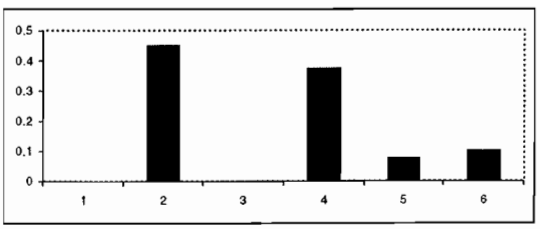
Site 4 Grey's Bridge n= 9



Site 5 Norris Farm n= 24



Site 6 Lewell Mill n= 20



Site 7 East Burton n= 8

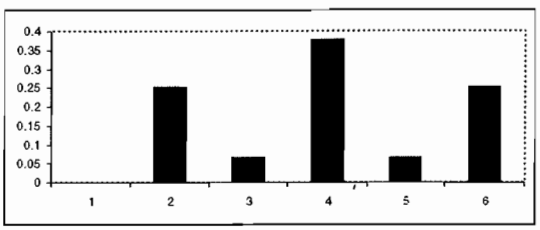
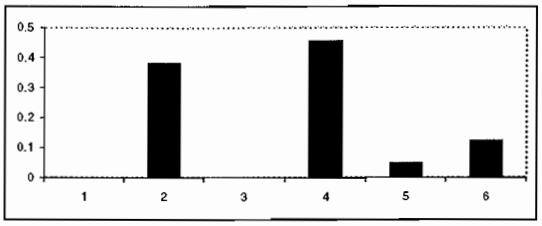
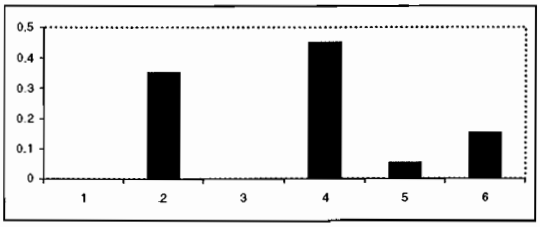


Figure 7.4.4.5 Allele frequencies at 6 microsatellite loci, from *S. salar* sampled at 16 sites on the Rivers Piddle and Frome, September 1999

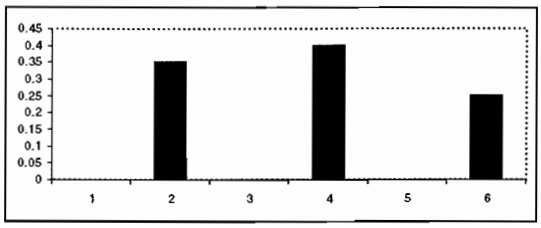
Site 8 East Stoke n= 21



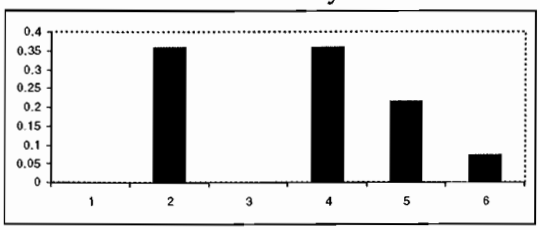
Site 9 ESMS n= 10



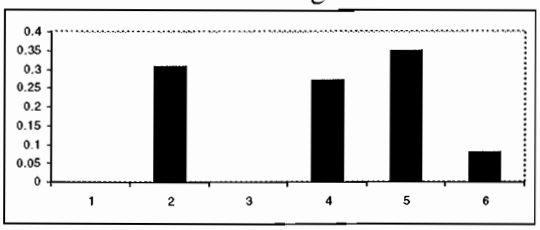
Site 10 Waterbarn Stream n= 10



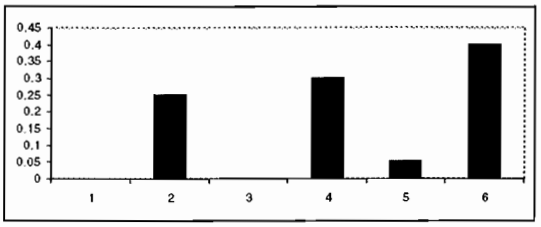
Site 11 Whitfield Hatchery n= 7



Site 12 Muckleford Bridge n=13



Site 14 Bindon Millstream n= 10



Site 15 Tadnoll Heath n= 15

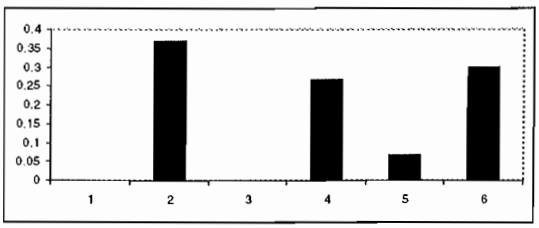
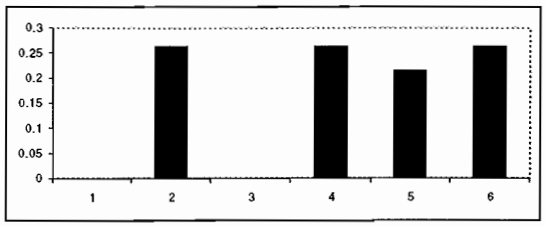
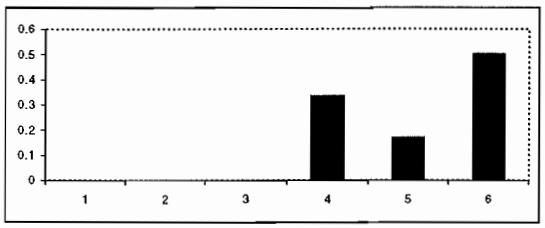


Figure 7.4.4.5 (Continued)

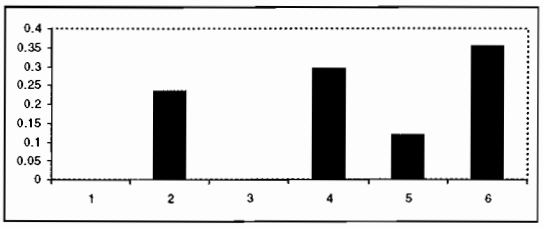
Site 16 South Winterbourne n= 21



Site 17 Wool Stream n= 3

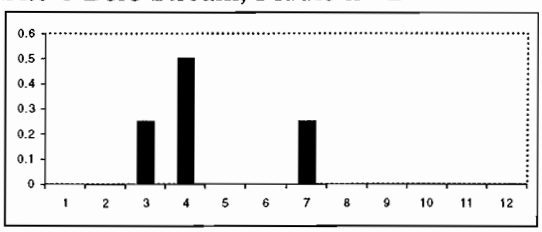


Site 19 Moreton Ford n= 17

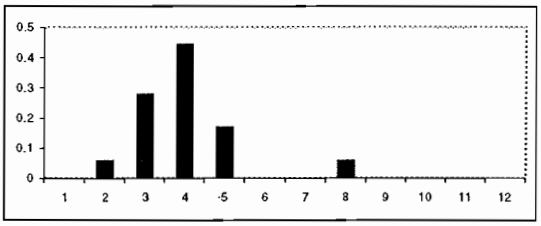


2. Locus Ssa 171

Site 1 Bere Stream, Piddle n= 2



Site 3 West Holme n= 9



Site 4 Grey's Bridge n= 10

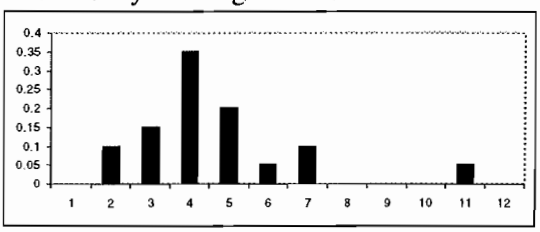
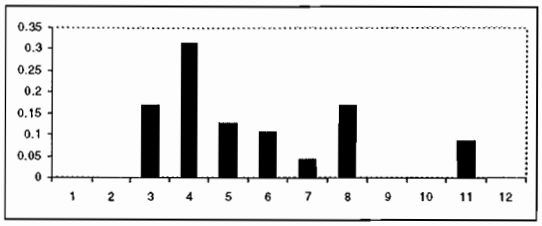
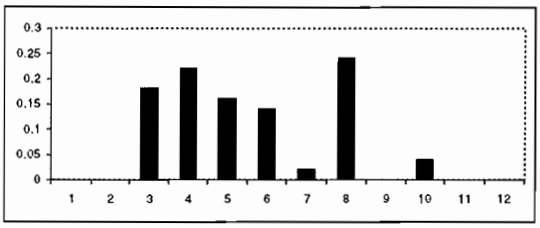


Figure 7.4.4.5 (Continued)

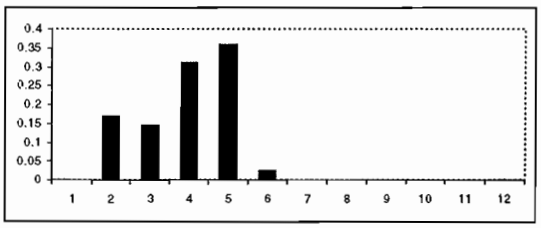
Site 5 Norris Farm n= 24



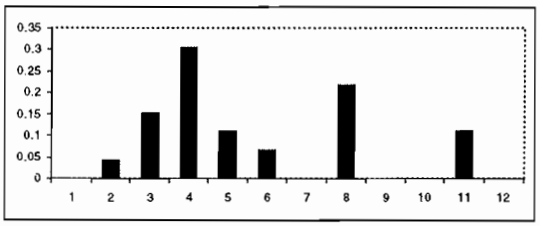
Site 6 Lewell Mill n= 25



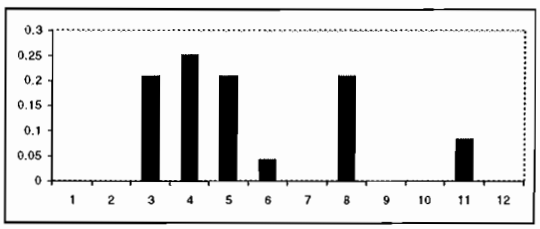
Site 7 East Burton n= 21



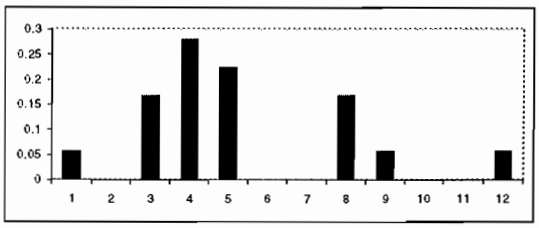
Site 8 East Stoke n= 23



Site 9 ESMS n= 12



Site 10 Waterbarn Stream n= 9



Site 11 Whitfield Hatchery n= 8

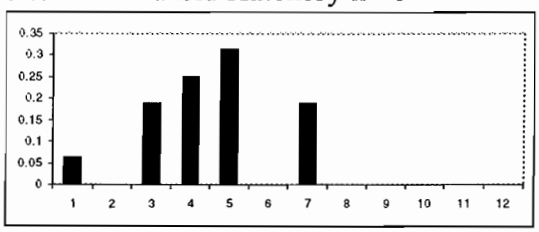
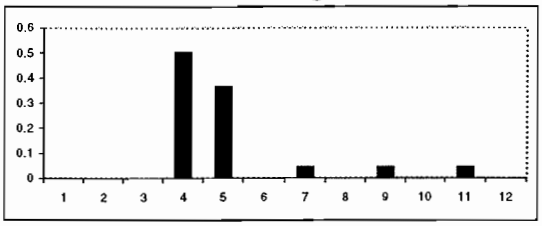
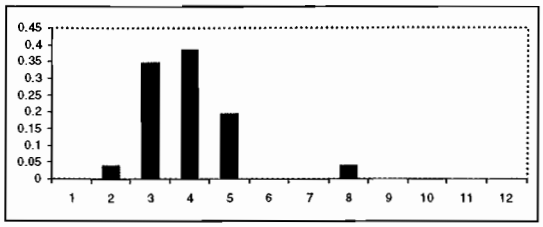


Figure 7.4.4.5 (Continued)

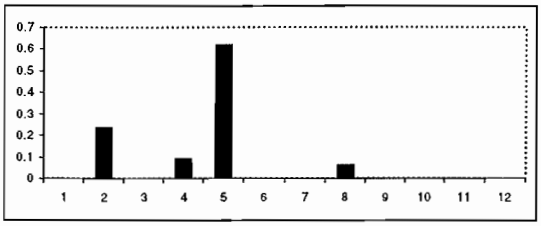
Site 12 Muckleford Bridge n=11



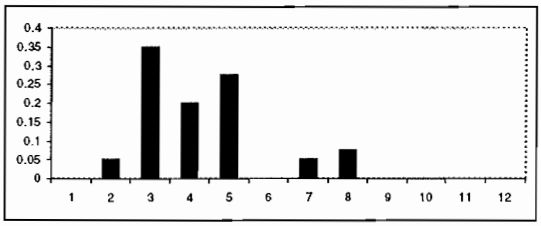
Site 14 Bindon Millstream n= 13



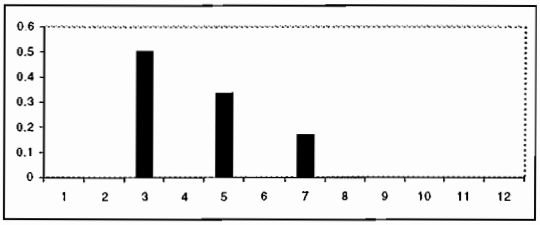
Site 15 Tadnoll Heath n=17



Site 16 South Winterbourne n=20



Site 17 Wool Stream n=3



Site 19 Moreton Ford n=17

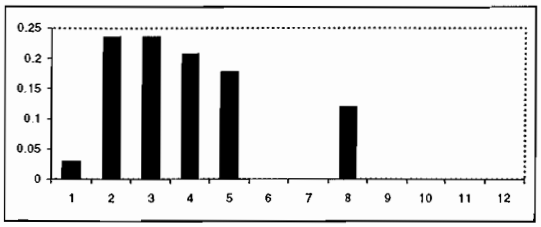
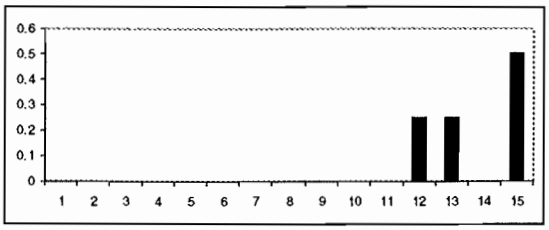


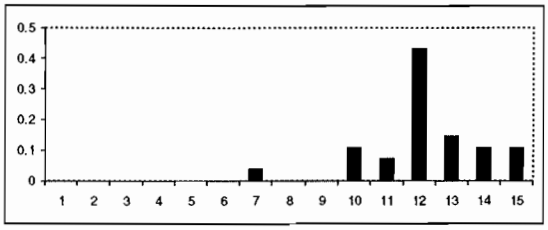
Figure 7.4.4.5 (Continued)

3. Locus Ssa 197

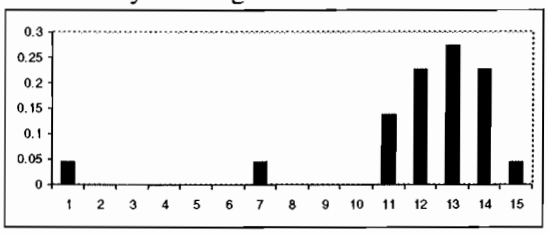
Site 1 Bere Stream, Piddle n= 2



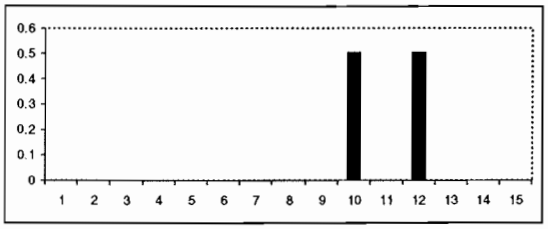
Site 3 West Holme n= 14



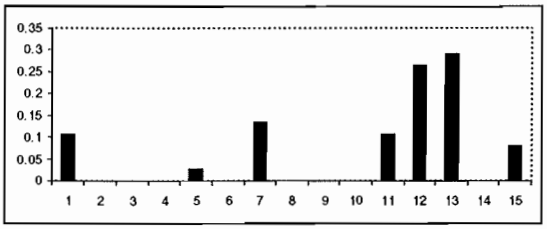
Site 4 Grey's Bridge n= 11



Site 5 Norris Farm n= 1



Site 6 Lewell Mill n= 19



Site 7 East Burton n= 27

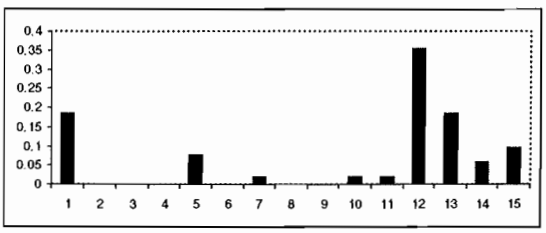
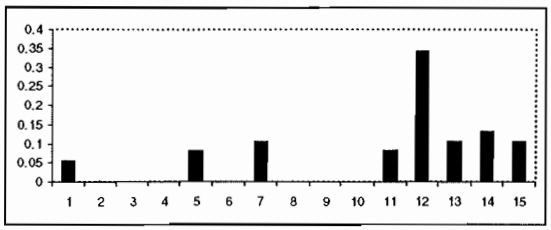
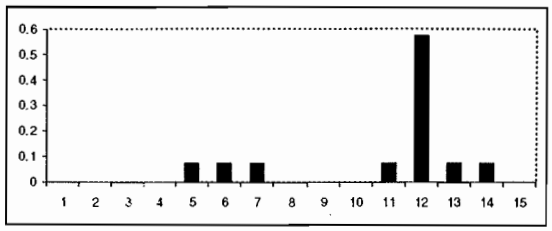


Figure 7.4.4.5 (Continued)

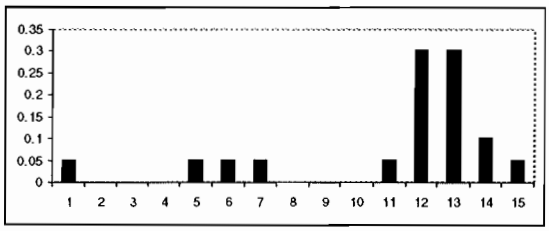
Site 8 East Stoke n= 19



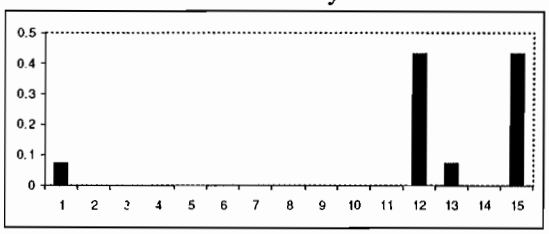
Site 9 ESMS n= 7



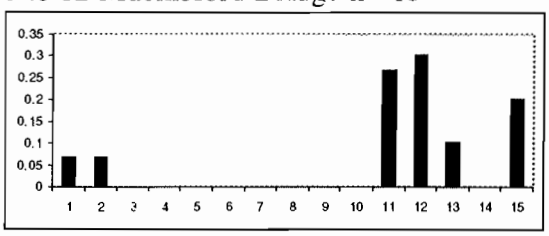
Site 10 Waterbarn Stream n= 10



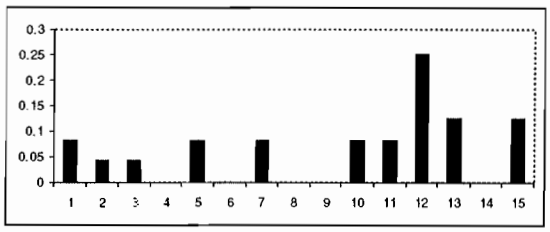
Site 11 Whitfield Hatchery n= 7



Site 12 Muckleford Bridge n= 15



Site 14 Bindon Millstream n= 12



Site 15 Tadnoll Heath n= 14

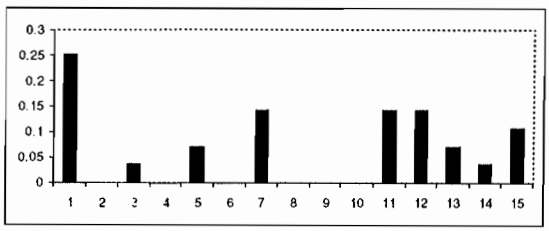
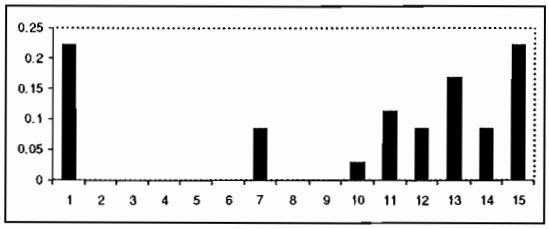
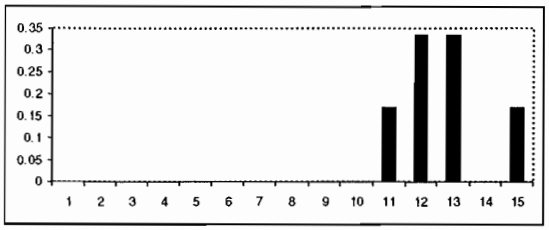


Figure 7.4.4.5 (Continued)

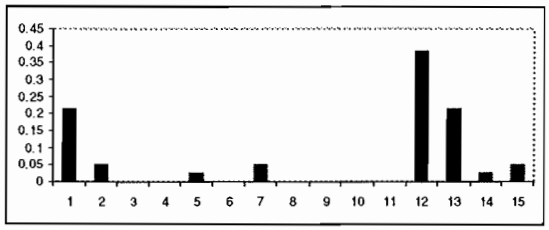
Site 16 South Winterbourne n= 18



Site 17 Wool Stream n= 3

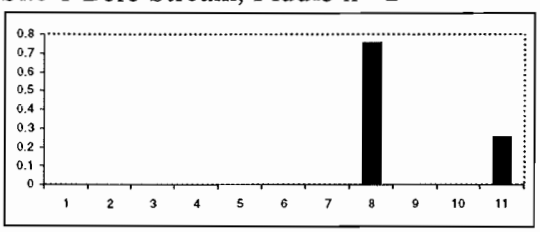


Site 19 Moreton Ford n= 21

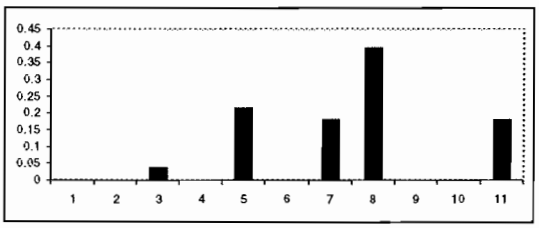


4. Locus Ssosl 85

Site 1 Bere Stream, Piddle n= 2



Site 3 West Holme n= 14



Site 4 Grey's Bridge n= 12

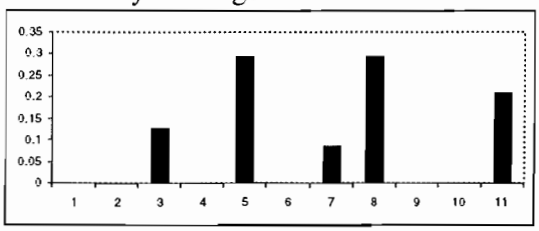
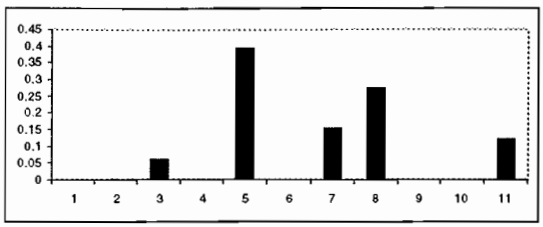
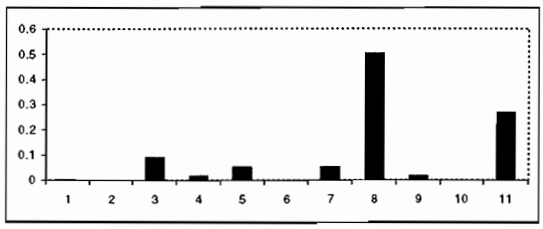


Figure 7.4.4.5 (Continued)

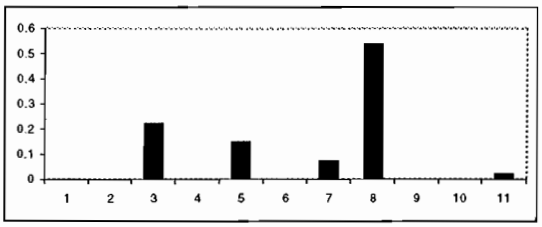
Site 5 Norris Farm n= 33



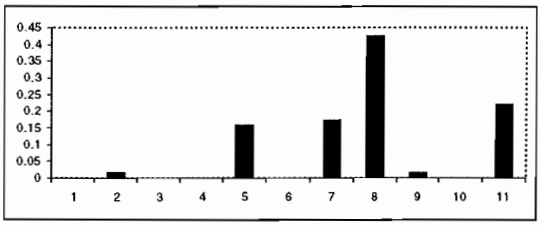
Site 6 Lewell Mill n= 28



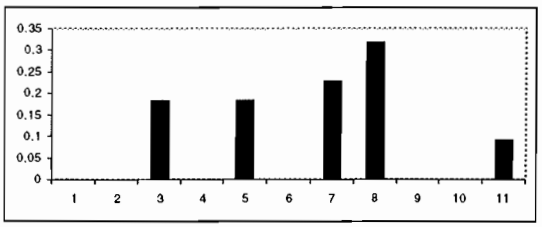
Site 7 East Burton n= 27



Site 8 East Stoke n= 32



Site 9 ESMS n= 11



Site 10 Waterbarn Stream n= 11

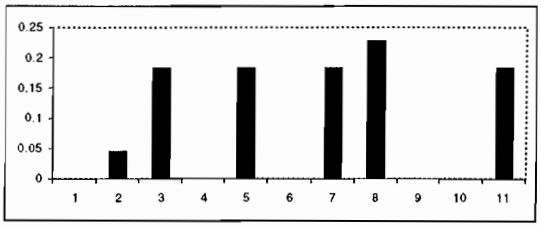
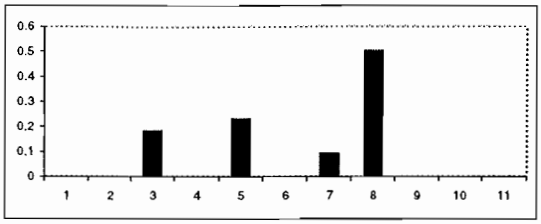
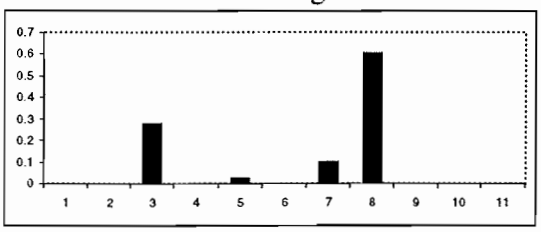


Figure 7.4.4.5 (Continued)

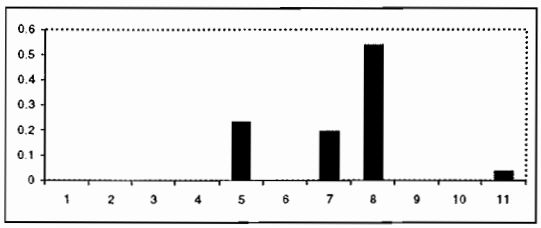
Site 11 Whitfield Hatchery n= 11



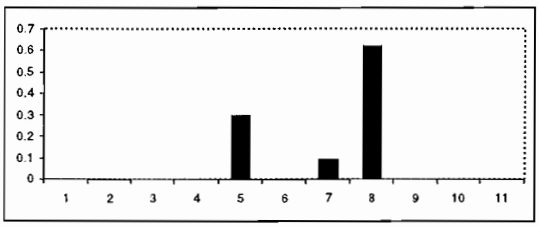
Site 12 Muckleford Bridge n= 20



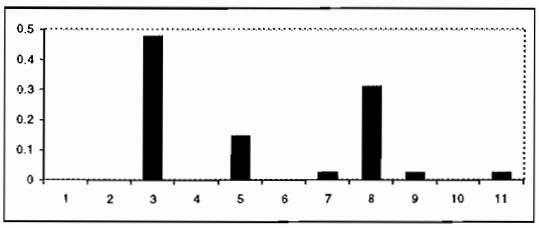
Site 14 Bindon Millstream n= 13



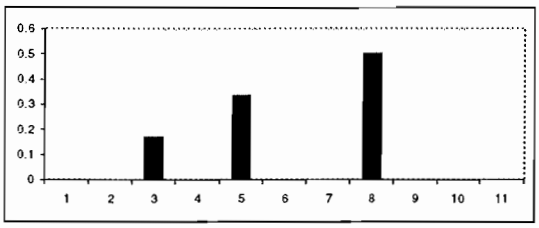
Site 15 Tadnoll Heath n= 17



Site 16 South Winterbourne n= 21



Site 17 Wool Stream n= 3



Site 19 Moreton Ford n= 2

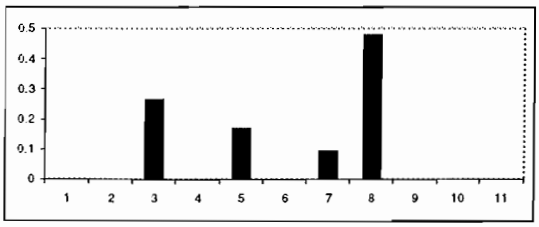
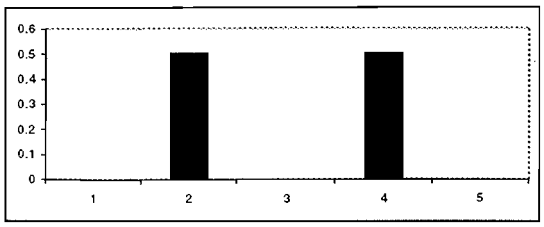


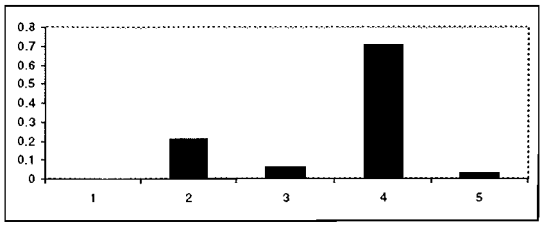
Figure 7.4.4.5 (Continued)

5. Locus Ssa 289

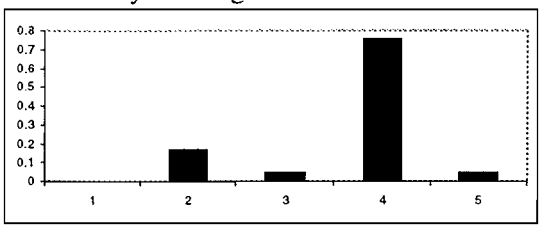
Site 1 Bere Stream, Piddle n= 2



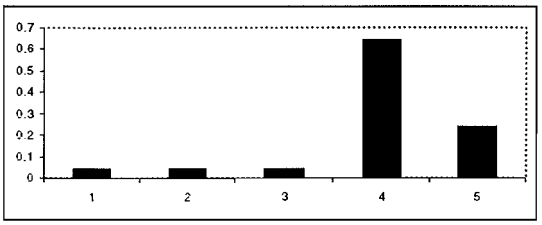
Site 3 West Holme n= 17



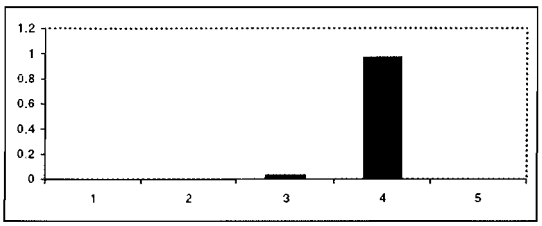
Site 4 Grey's Bridge n= 12



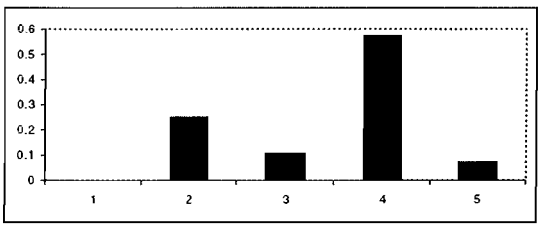
Site 5 Norris Farm n= 25



Site 6 Lewell Mill n= 17



Site 7 East Burton n= 14



Site 8 East Stoke n= 33

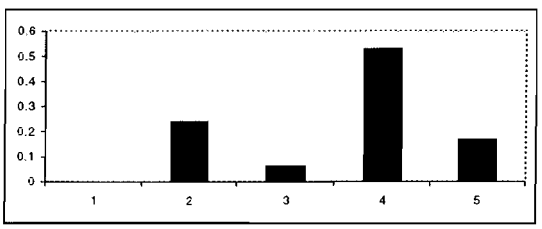
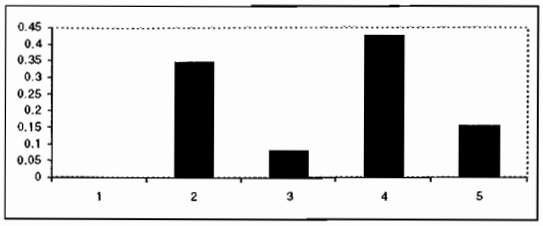
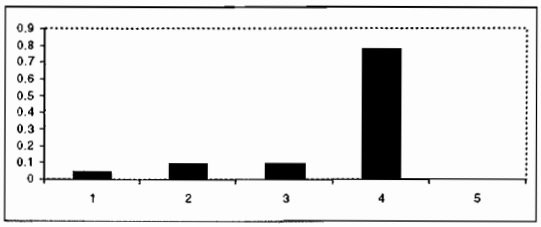


Figure 7.4.4.5 (Continued)

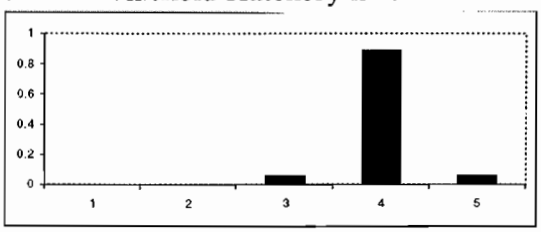
Site 9 ESMS n= 13



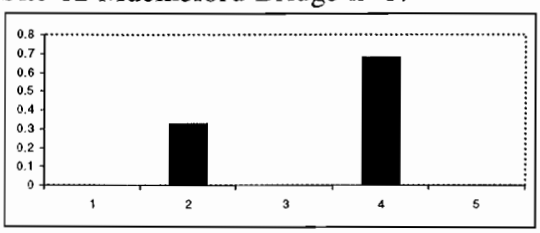
Site 10 Waterbarn Stream n= 11



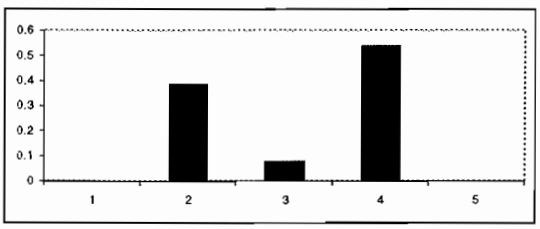
Site 11 Whitfield Hatchery n= 9



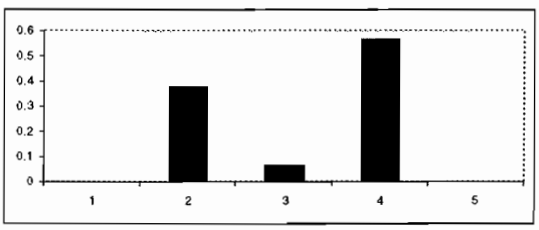
Site 12 Muckleford Bridge n=17



Site 14 Bindon Millstream n= 13



Site 15 Tadnoll Heath n=1



Site 16 South Winterbourne n=20

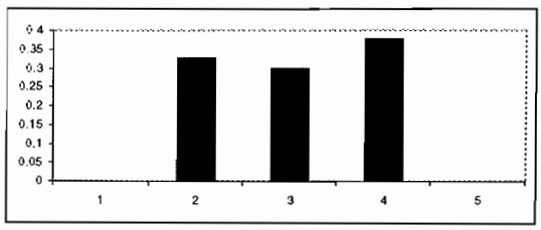
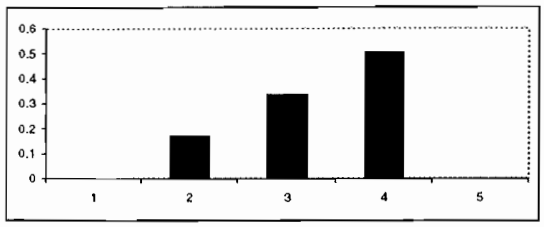
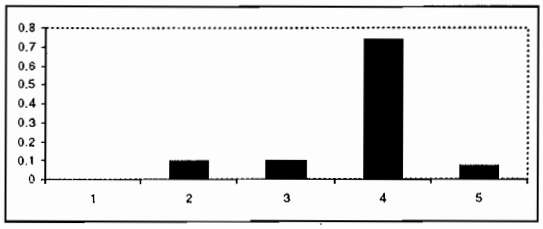


Figure 7.4.4.5 (Continued)

Site 17 Wool Stream n=3

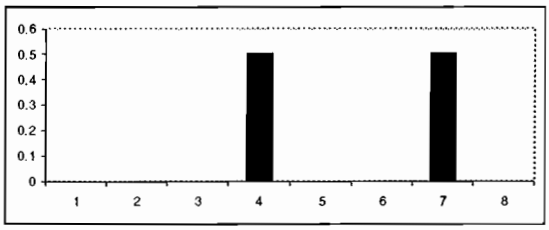


Site 19 Moreton Ford n=21

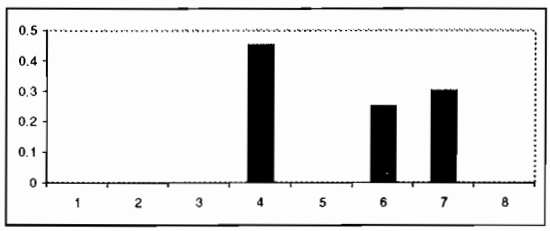


6. Locus Ssosl 417

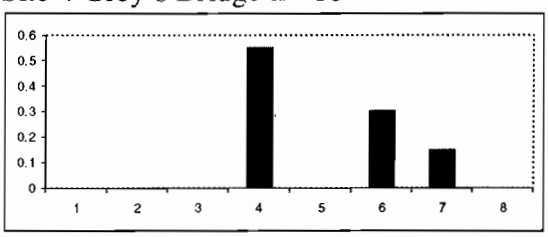
Site 1 Bere Stream, Piddle n= 2



Site 3 West Holme n= 10



Site 4 Grey's Bridge n= 10



Site 5 Norris Farm n= 24

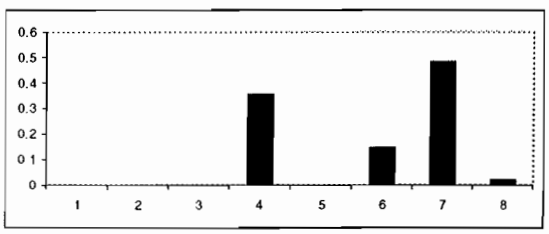
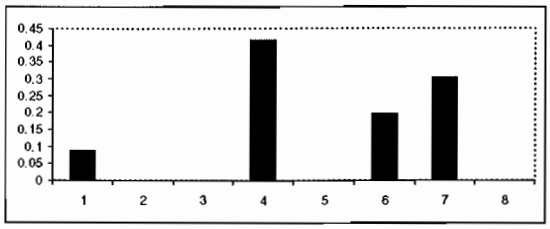
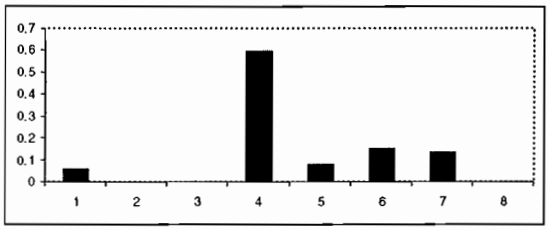


Figure 7.4.4.5 (Continued)

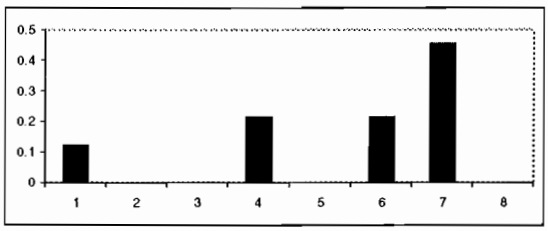
Site 6 Lewell Mill n= 23



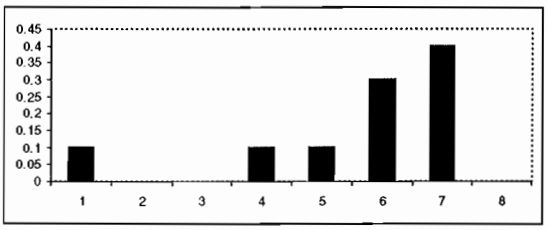
Site 7 East Burton n= 27



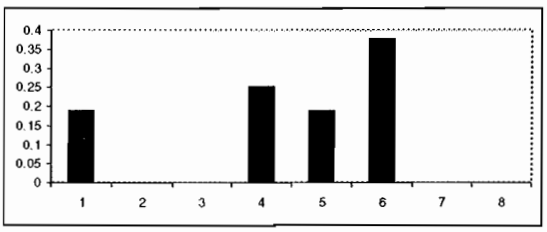
Site 8 East Stoke n= 21



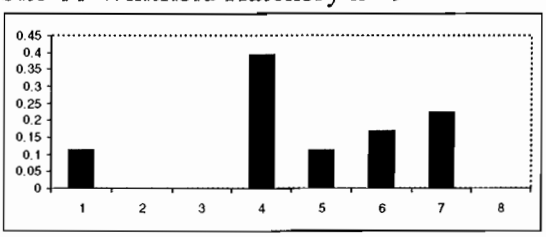
Site 9 ESMS n= 10



Site 10 Waterbarn Stream n= 8



Site 11 Whitfield Hatchery n= 9



Site 12 Muckleford Bridge n=11

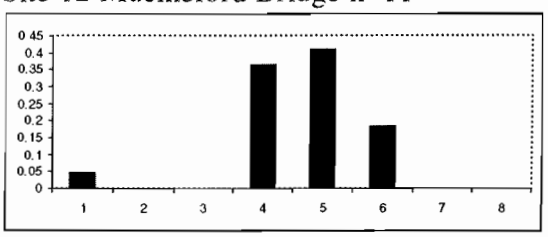
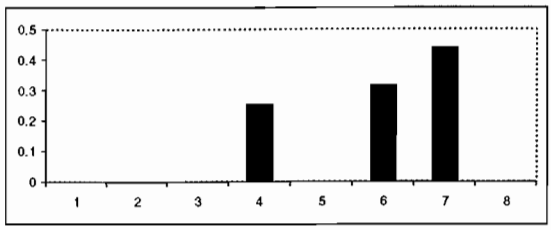
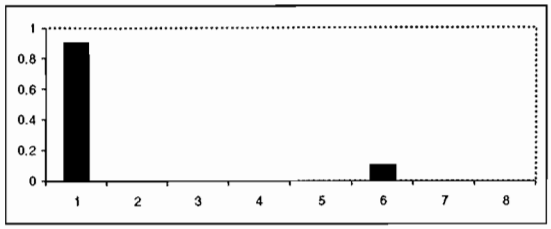


Figure 7.4.4.5 (Continued)

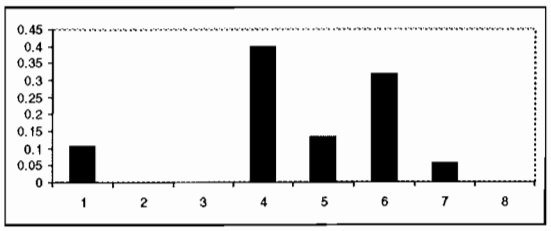
Site 14 Bindon Millstream n= 8



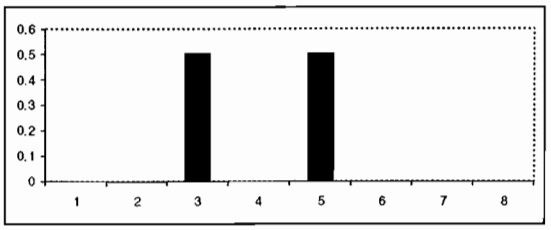
Site 15 Tadnoll Heath n=10



Site 16 South Winterbourne n=19



Site 17 Wool Stream n=2



Site 19 Moreton Ford n=16

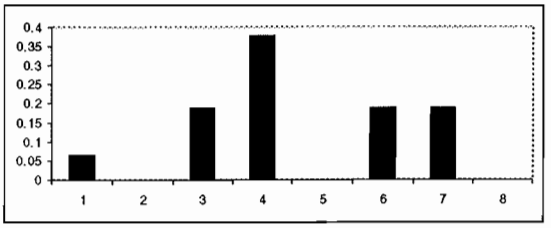
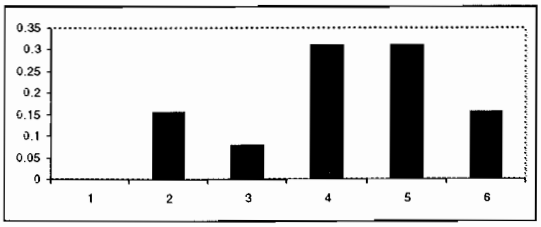


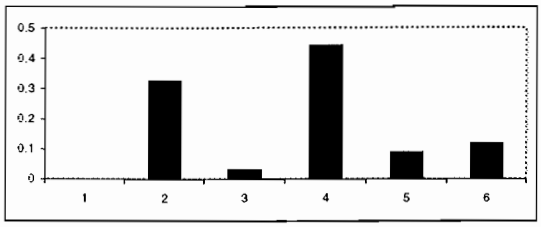
Figure 7.4.4.5 (Continued)

1. Locus Ssa 202

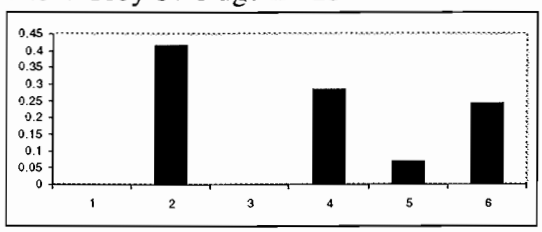
Site 1 Bere Stream n= 13



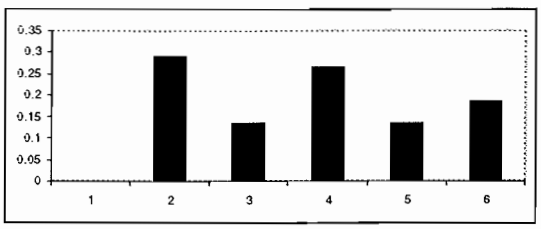
Site 3 West Holme n= 17



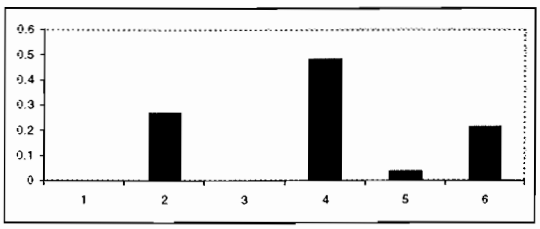
Site 4 Grey's Bridge n= 23



Site 5 Norris Farm n= 19



Site 6 Lewell Mill n= 26



Site 7 East Burton n= 25

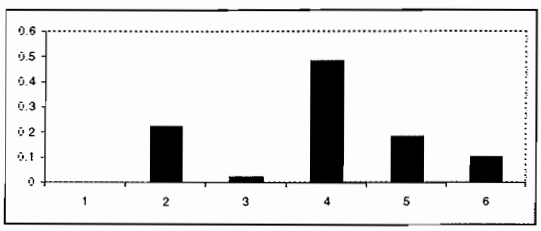
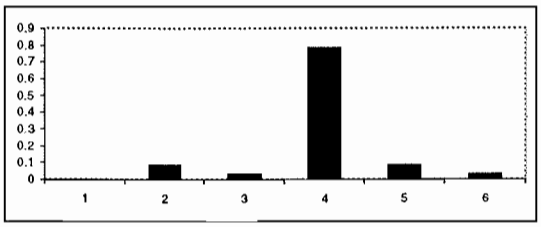
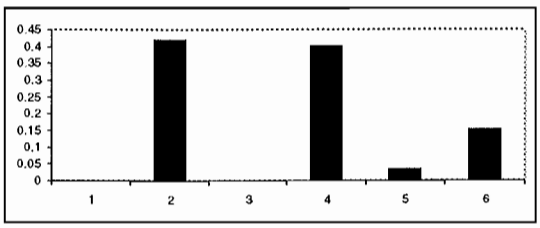


Figure 7.4.4.6 Allele frequencies at 6 microsatellite loci, from *S. salar* sampled at 16 sites on the Rivers Piddle and Frome, July 2000

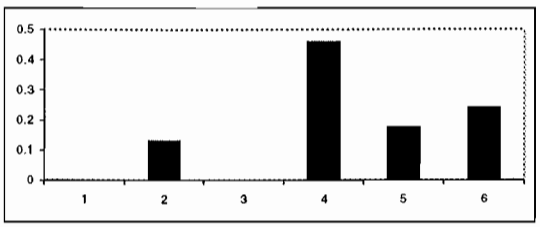
Site 8 East Stoke n= 18



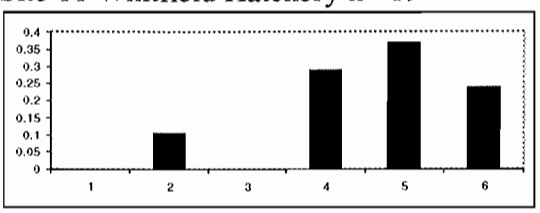
Site 9 ESMS n= 30



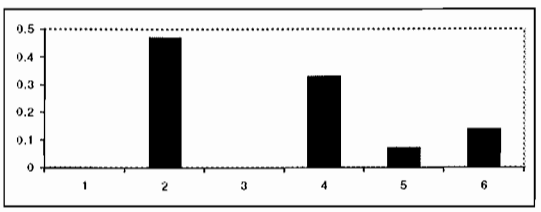
Site 10 Waterbarn Stream n= 23



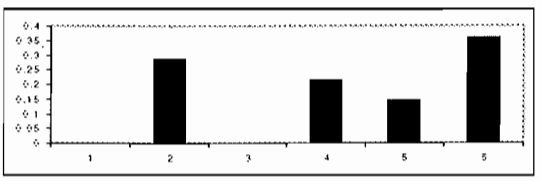
Site 11 Whitfield Hatchery n= 19



Site 14 Bindon Millstream n=29



Site 15 Tadnoll Winfrith n= 7



Site 16 South Winterbourne n=27

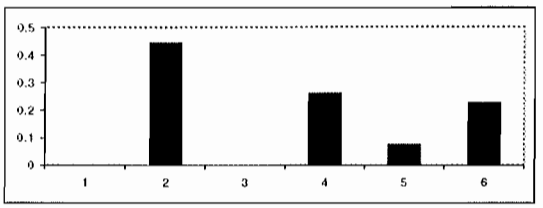
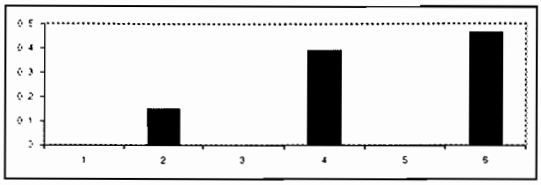
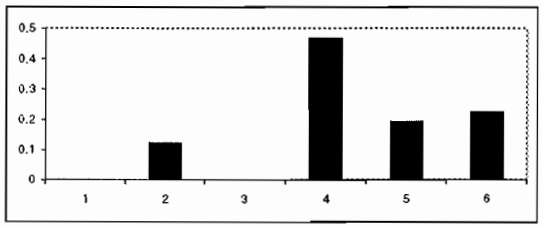


Figure 7.4.4.6 (Continued)

Site 17 Wool Stream n= 27

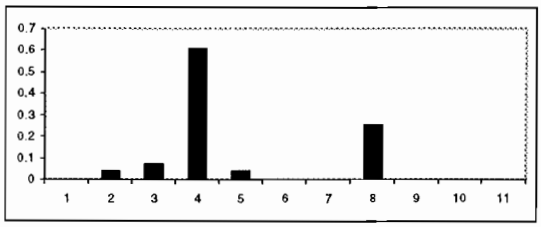


Site 19 Moreton Ford n= 29

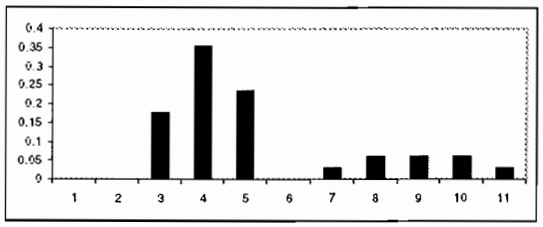


2. Locus Ssa 171

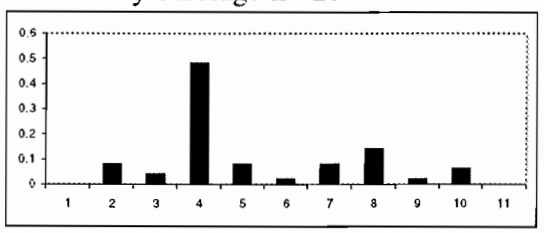
Site 1 Bere Stream n= 14



Site 3 West Holme n= 17



Site 4 Grey's Bridge n= 25



Site 5 Norris Farm n= 20

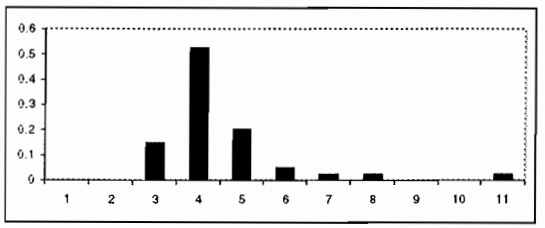
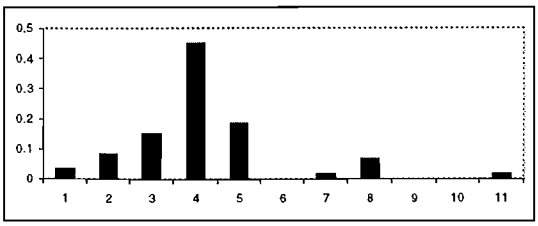
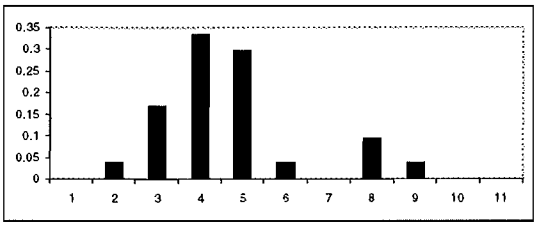


Figure 7.4.4.6 (Continued)

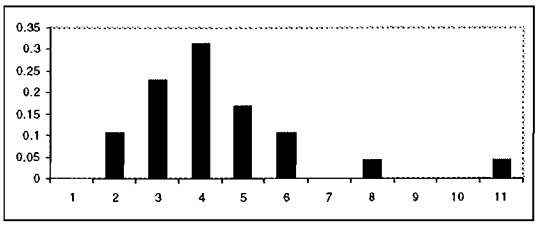
Site 6 Lewell Mill n= 30



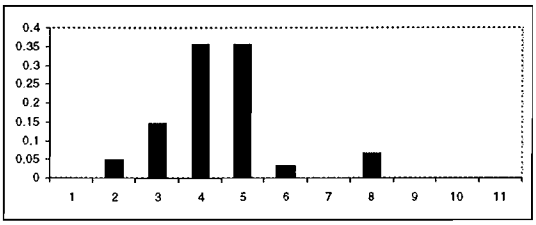
Site 7 East Burton n= 27



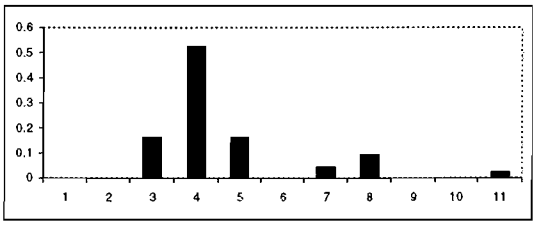
Site 8 East Stoke n=24



Site 9 ESMS n= 31



Site 10 Waterbarn Stream n= 22



Site 11 Whitfield Hatchery n= 19

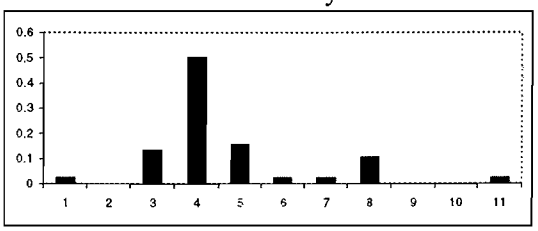
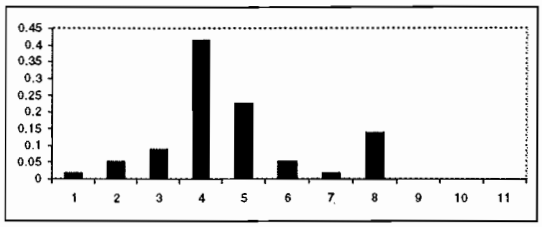
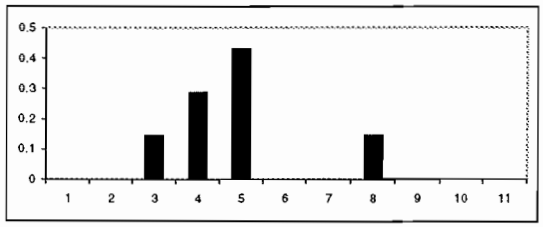


Figure 7.4.4.6 (Continued)

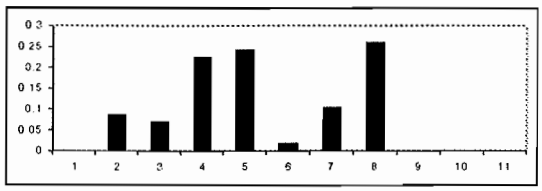
Site 14 Bindon Millstream n= 29



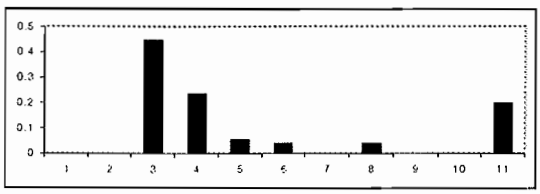
Site 15 Tadnoll Heath n= 7



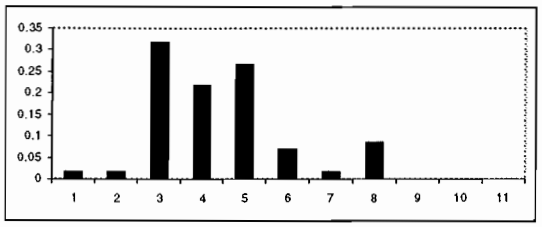
Site 16 South Winterbourne n= 29



Site 17 Wool Stream n= 28



Site 19 Moreton Ford n= 30



3. Locus Ssa 197

Site 1 Bere Stream n= 14

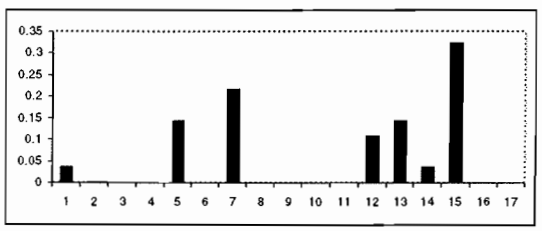
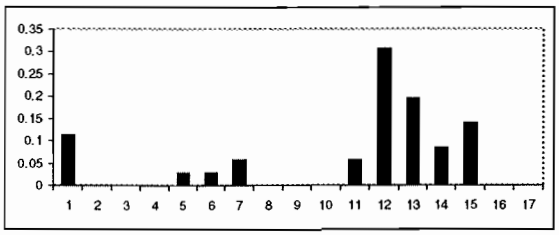
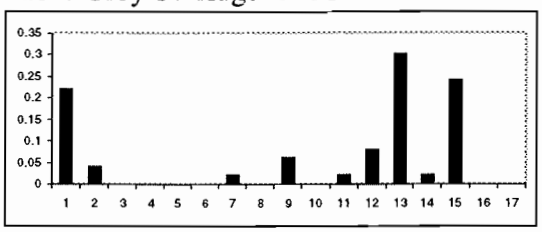


Figure 7.4.4.6 (Continued)

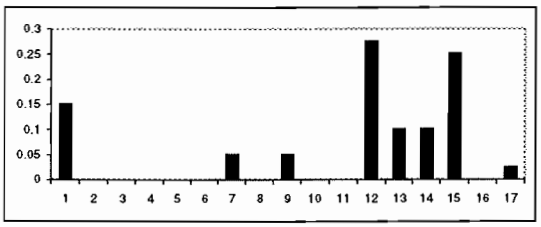
Site 3 West Holme n= 18



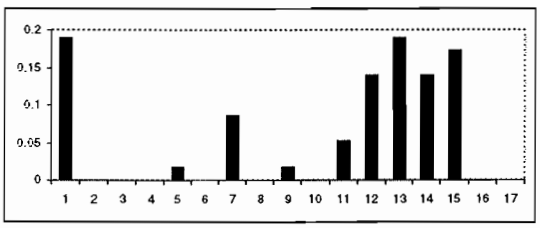
Site 4 Grey's Bridge n= 25



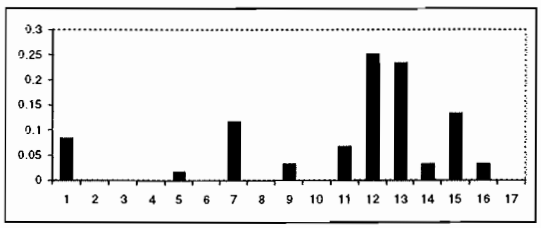
Site 5 Norris Farm n= 20



Site 6 Lewell Mill n= 29



Site 7 East Burton n= 30



Site 8 East Stoke n= 26

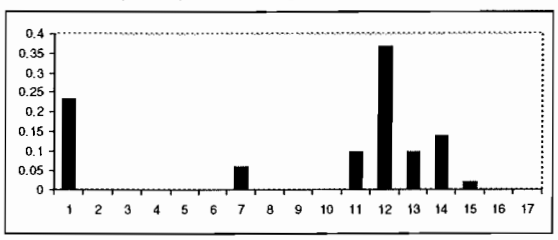
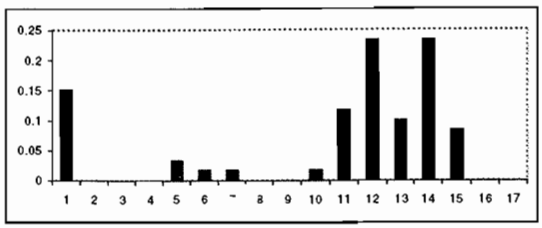
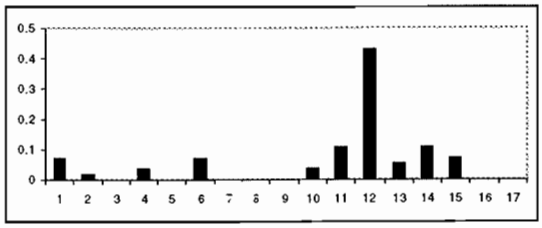


Figure 7.4.4.6 (Continued)

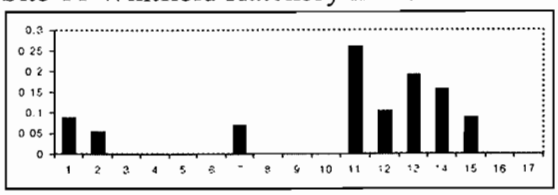
Site 9 ESMS n= 30



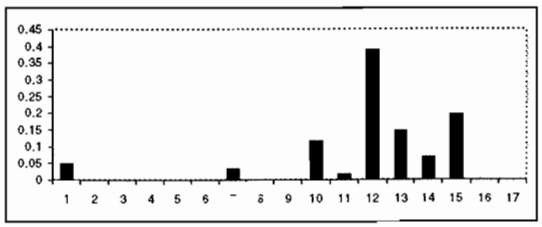
Site 10 Waterbarn Stream n= 28



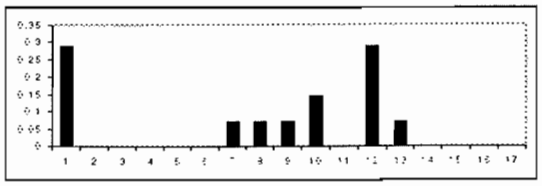
Site 11 Whitfield Hatchery n= 29



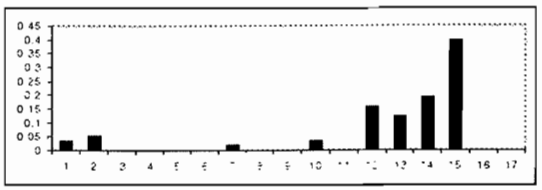
Site 14 Bindon Millstream n= 31



Site 15 Tadnoll Winfrith n= 7



Site 16 South Winterbourne n= 29



Site 17 Wool Stream n= 28

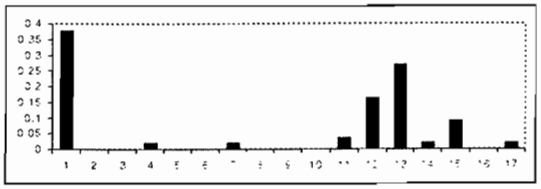
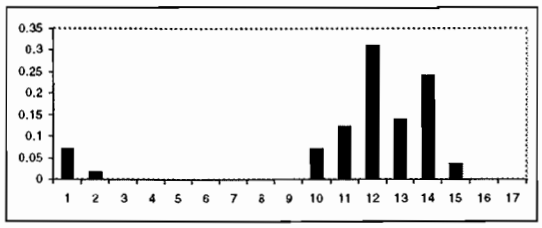


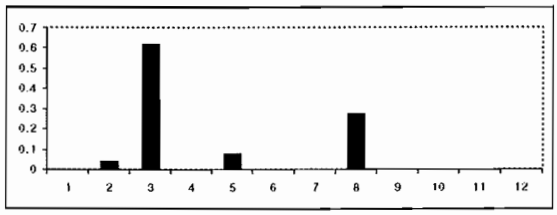
Figure 7.4.4.6 (Continued)

Site 19 Moreton Ford n= 29

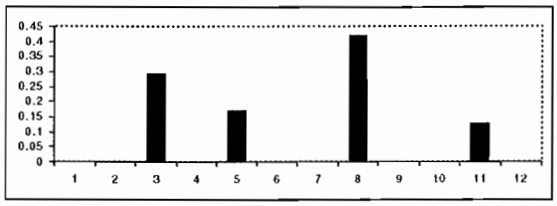


4. Locus Ssosl 85

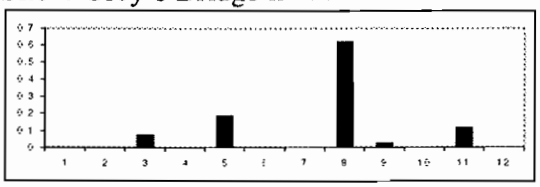
Site 1 Bere Stream n= 13



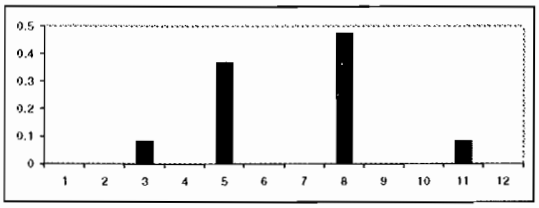
Site 3 West Holme n= 12



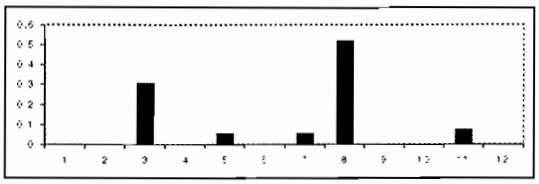
Site 4 Grey's Bridge n= 22



Site 5 Norris Farm n= 19



Site 6 Lewell Mill n= 28



Site 7 East Burton n= 29

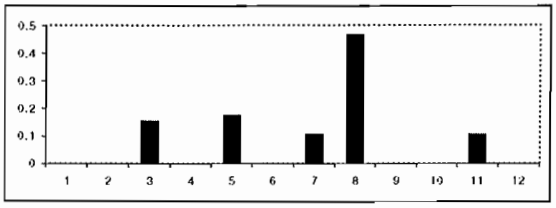
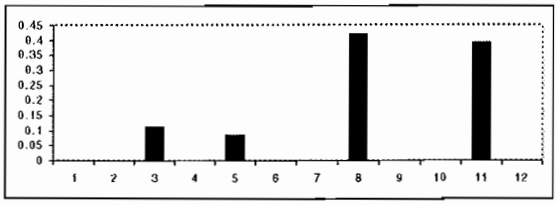
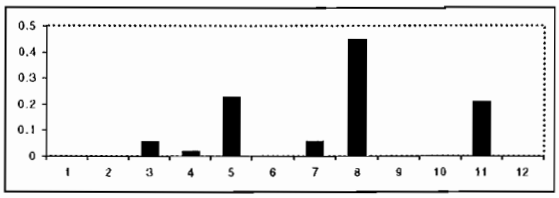


Figure 7.4.4.6 (Continued)

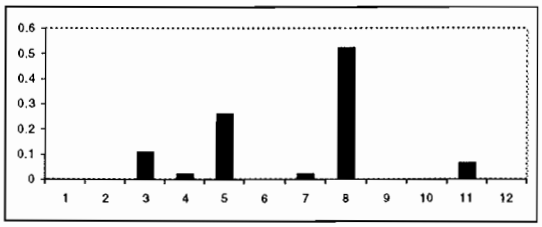
Site 8 East Stoke n=18



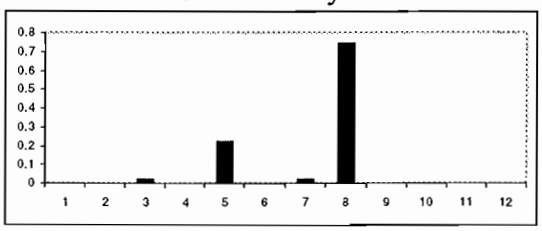
Site 9 ESMS n= 29



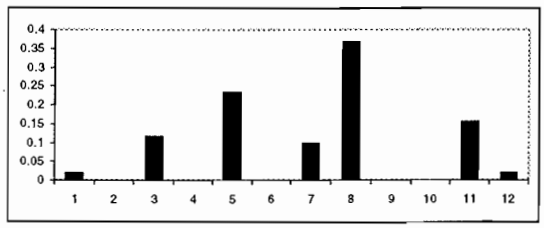
Site 10 Waterbarn Stream n= 23



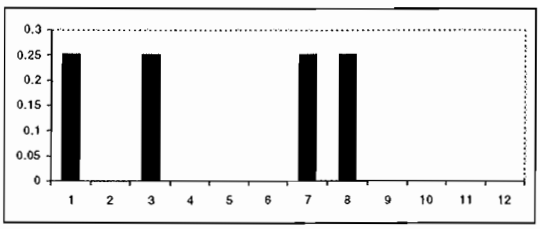
Site 11 Whitfield Hatchery n= 23



Site 14 Bindon Millstream n= 26



Site 15 Tadnoll Winfrith n= 2



Site 16 South Winterbourne n= 29

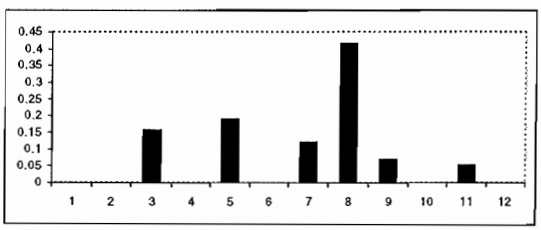
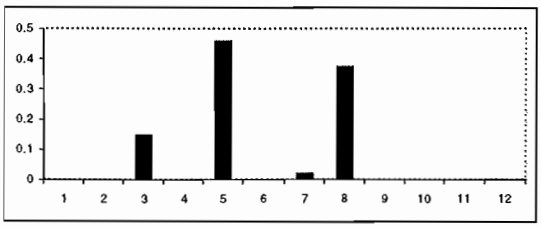
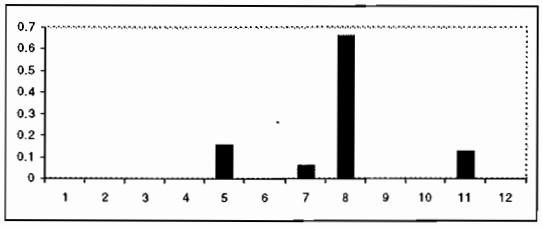


Figure 7.4.4.6 (Continued)

Site 17 Wool Stream n= 24

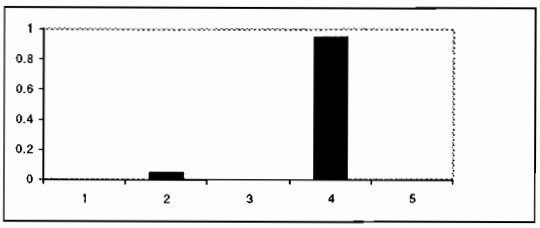


Site 19 Moreton Ford n= 16

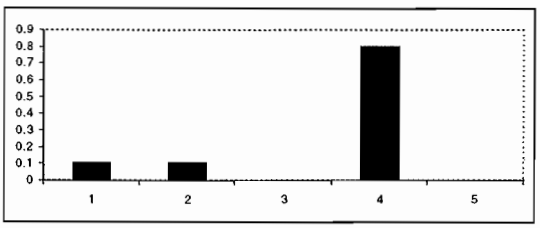


5. Locus Ssa 289

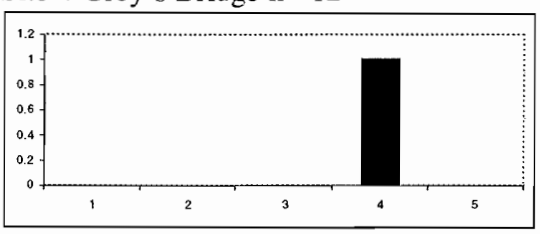
Site 1 Bere Stream n=10



Site 3 West Holme n= 5



Site 4 Grey's Bridge n= 12



Site 5 Norris Farm n= 10

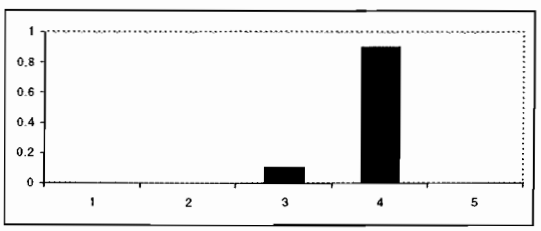
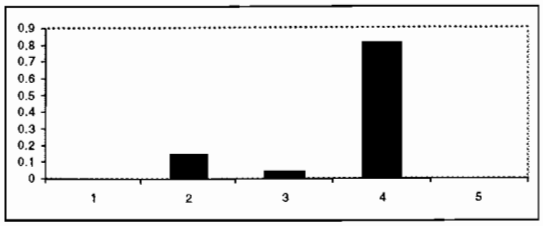
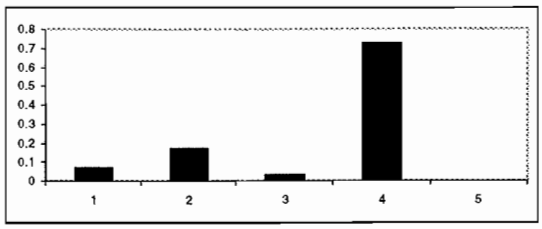


Figure 7.4.4.6 (Continued)

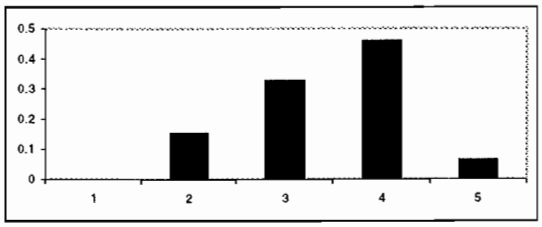
Site 6 Lewell Mill n= 24



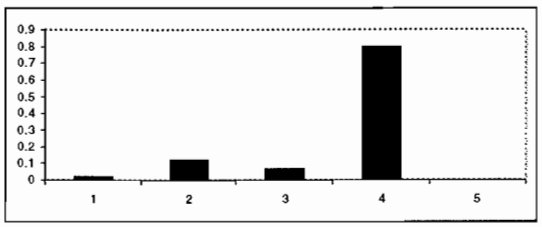
Site 7 East Burton n= 29



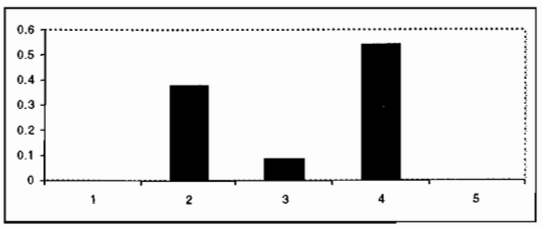
Site 8 East Stoke n= 23



Site 9 ESMS n= 29



Site 10 Waterbarn Stream n= 12



Site 11 Whitfield Hatchery n= 5

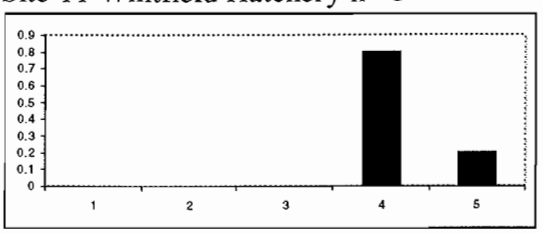
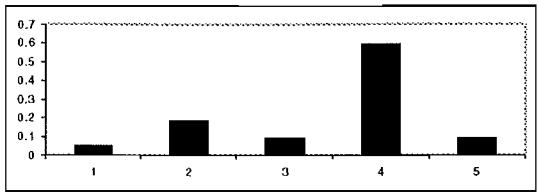
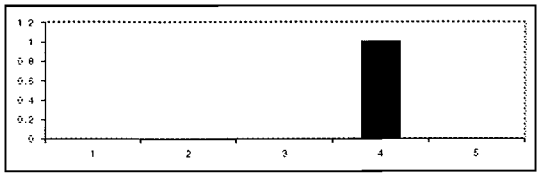


Figure 7.4.4.6 (Continued)

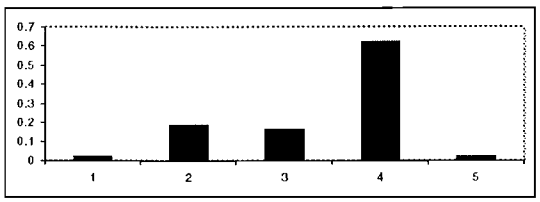
Site 14 Bindon Millstream n= 22



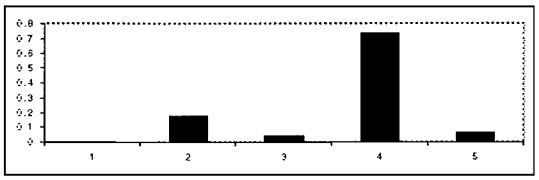
Site 15 Tadnoll Winfrith n= 7



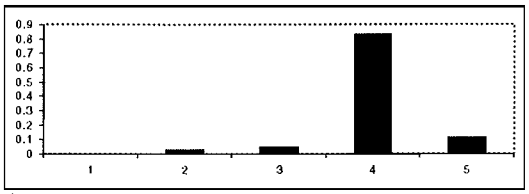
Site 16 South Winterbourne n= 25



Site 17 Wool Stream n= 26

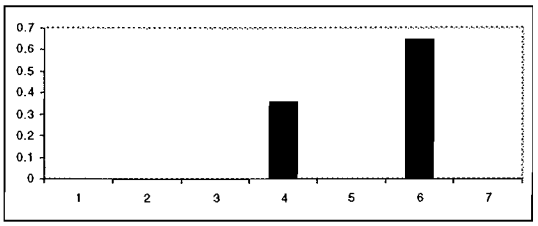


Site 19 Moreton Ford n= 23



6. Locus Ssosl 417

Site 1 Bere Stream n= 14



Site 3 West Holme n= 14

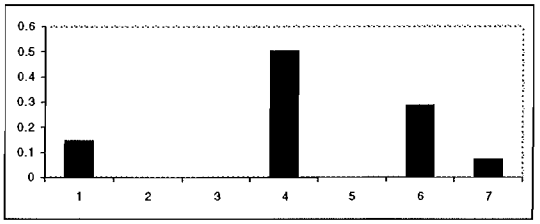
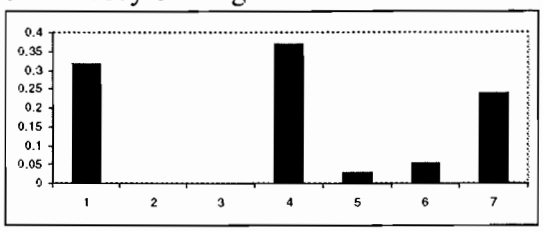
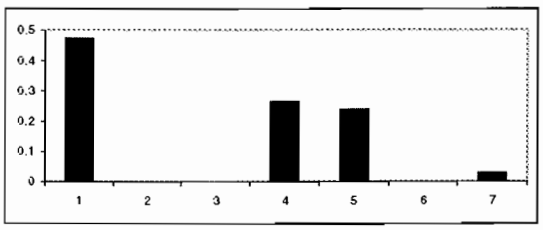


Figure 7.4.4.6 (Continued)

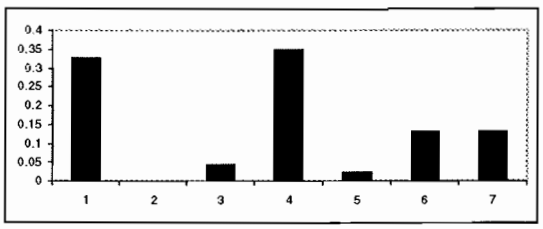
Site 4 Grey's Bridge n= 19



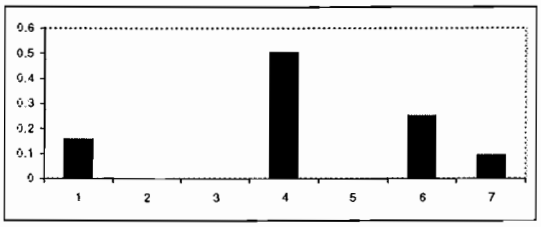
Site 5 Norris Farm n= 19



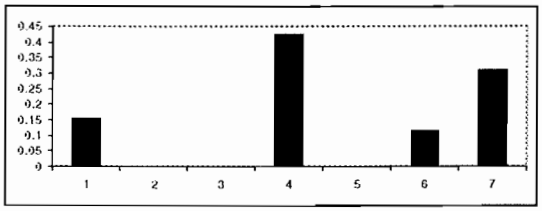
Site 6 Lewell Mill n= 23



Site 7 East Burton n= 16



Site 8 East Stoke n=13



Site 9 ESMS n= 16

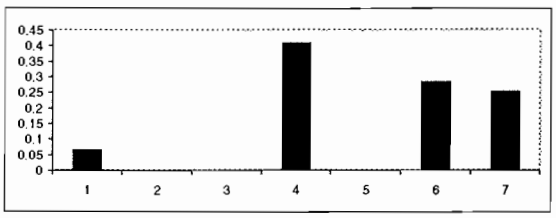
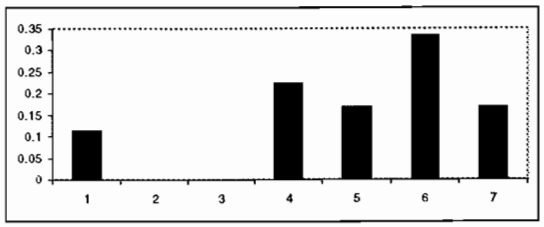
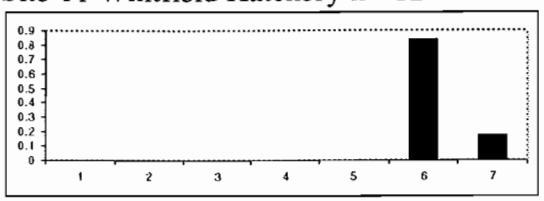


Figure 7.4.4.6 (Continued)

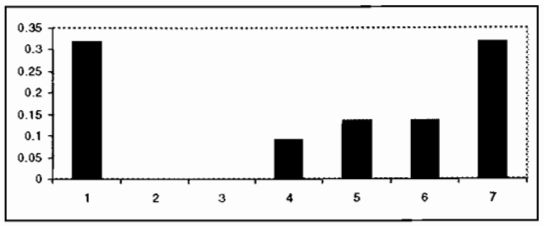
Site 10 Waterbarn Stream n= 9



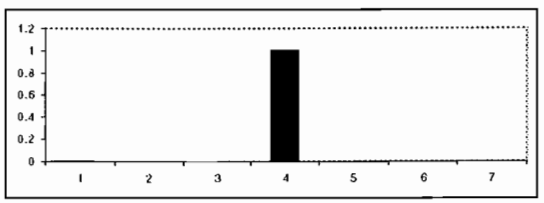
Site 11 Whitfield Hatchery n= 12



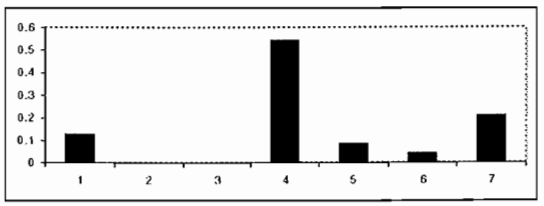
Site 14 Bindon Millstream n= 11



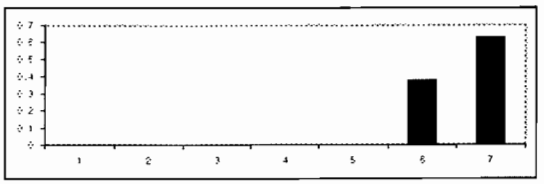
Site 15 Tadnoll Winfrith n= 2



Site 16 South Winterbourne n= 24



Site 17 Wool Stream n= 16



Site 19 Moreton Ford n= 16

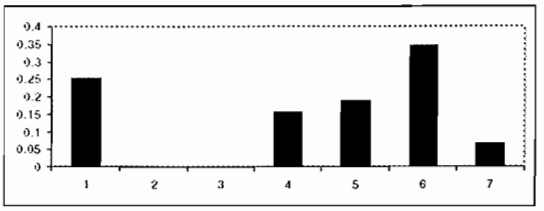
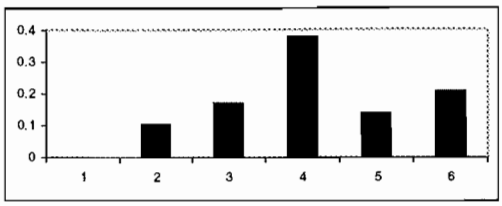


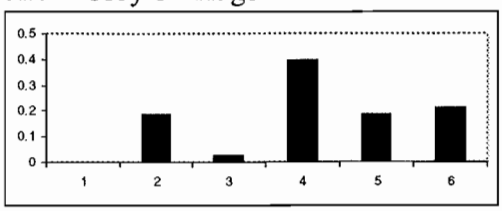
Figure 7.4.4.6 (Continued)

1. Locus Ssa 202

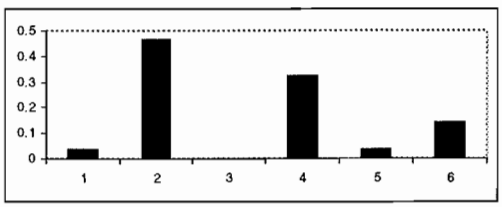
Site 1 Bere Stream n= 29



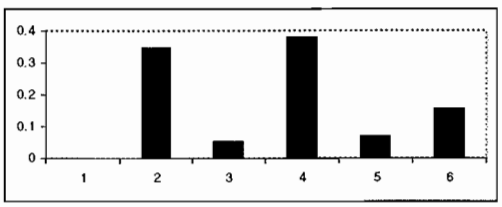
Site 4 Grey's Bridge n= 19



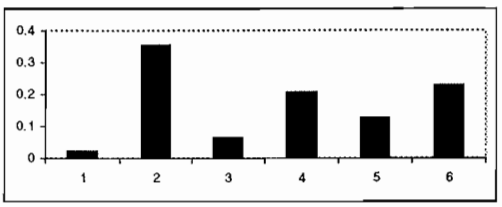
Site 5 Norris Farm n= 14



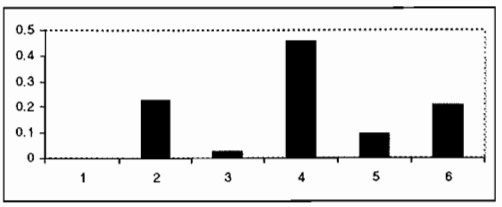
Site 6 Lewell Mill n= 29



Site 7 East Burton n= 24



Site 8 East Stoke n=22



Site 9 ESMS n= 13

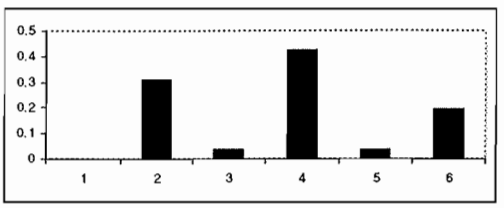
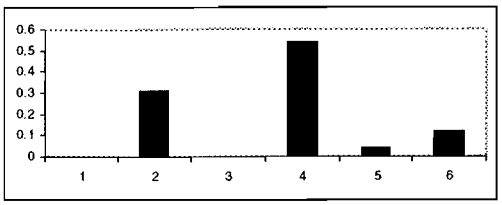
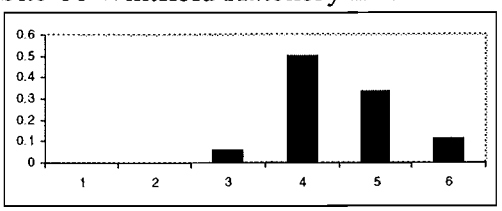


Figure 7.4.4.7 Allele frequencies at 6 microsatellite loci, from *S. salar* sampled at 14 sites on the Rivers Piddle and Frome, October 2000

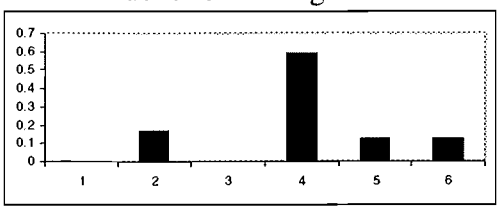
Site 10 Waterbarn Stream n= 13



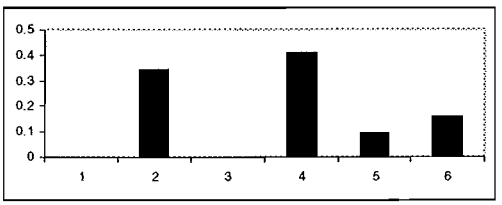
Site 11 Whitfield Hatchery n= 9



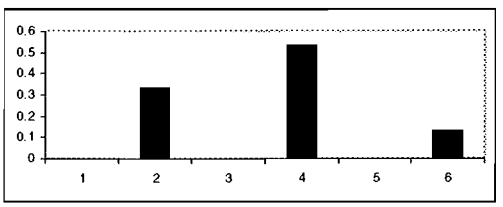
Site 12 Muckelford Bridge n= 28



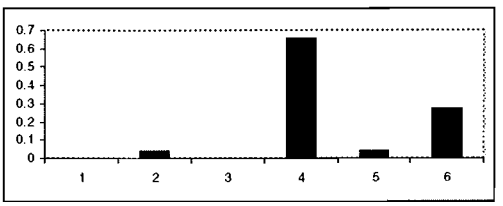
Site 14 Bindon Millstream n= 22



Site 16 South Winterbourne n= 15



Site 17 Wool Stream n=13



Site 19 Moreton Ford n=20

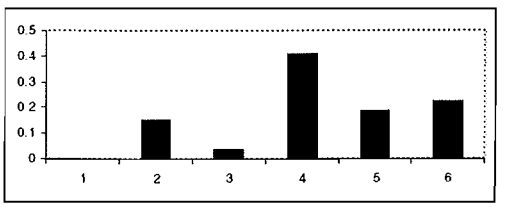
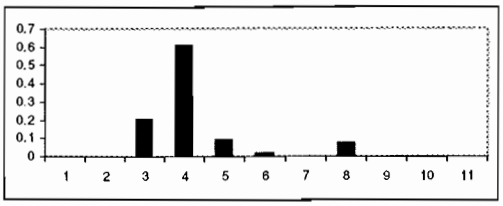


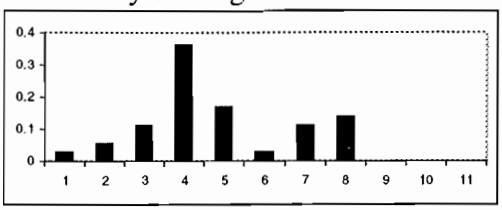
Figure 7.4.4.7 (Continued)

2. Locus Ssa 171

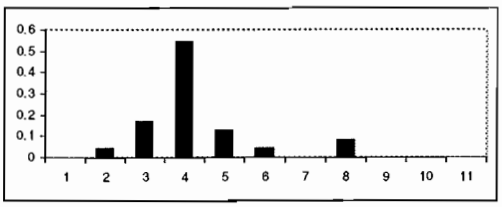
Site 1 Bere Stream n= 27



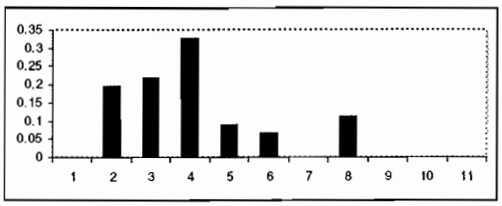
Site 4 Grey's Bridge n= 18



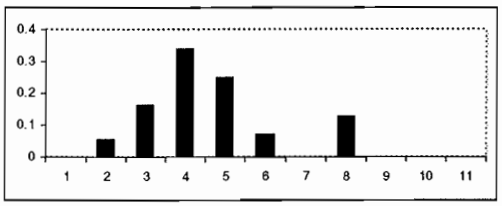
Site 5 Norris Farm n= 12



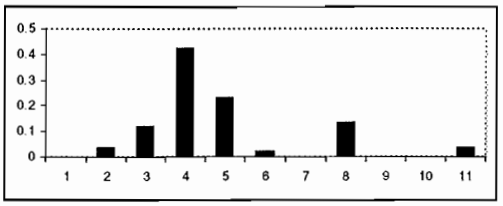
Site 6 Lewell Mill n= 23



Site 7 East Burton n= 28



Site 8 East Stoke n=26



Site 9 ESMS n= 17

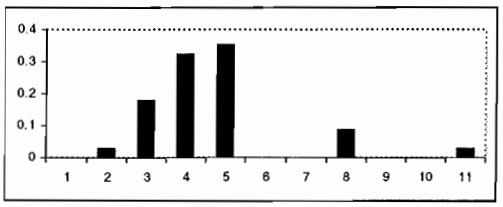
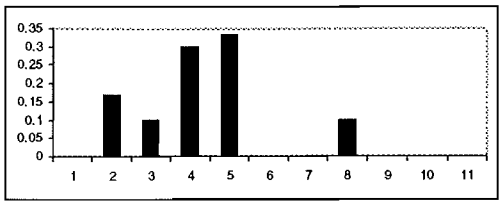
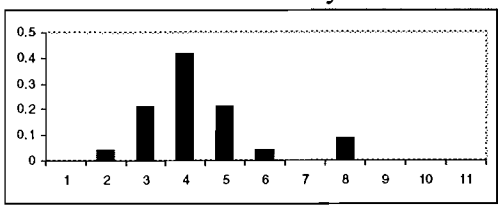


Figure 7.4.4.7 (Continued)

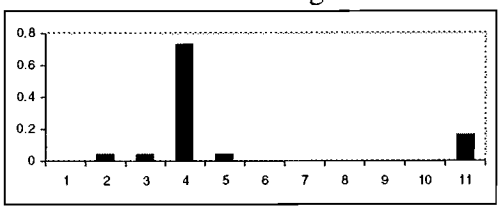
Site 10 Waterbarn Stream n= 15



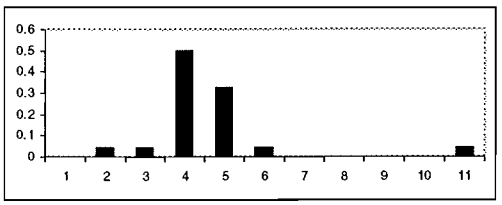
Site 11 Whitfield Hatchery n= 12



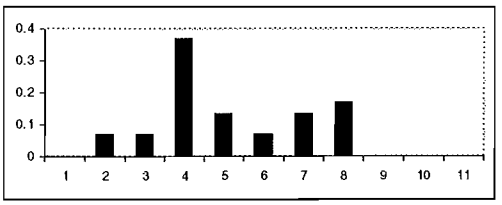
Site 12 Muckelford Bridge n= 28



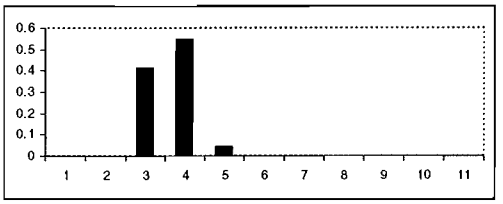
Site 14 Bindon Millstream n= 23



Site 16 South Winterbourne n= 15



Site 17 Wool Stream n=11



Site 19 Moreton Ford n=25

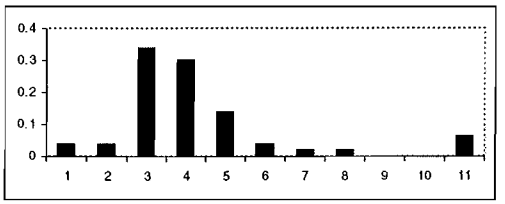
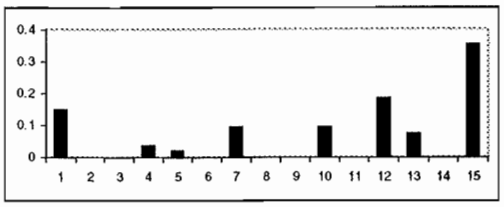


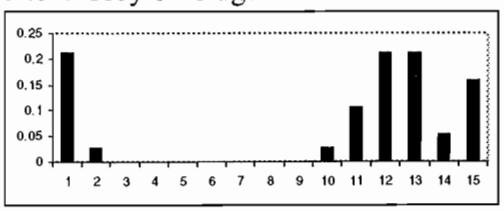
Figure 7.4.4.7 (Continued)

3. Locus Ssa 197

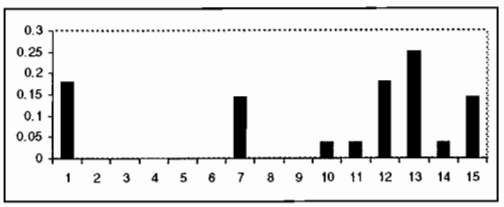
Site 1 Bere Stream n= 27



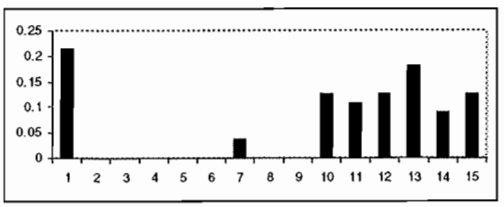
Site 4 Grey's Bridge n= 19



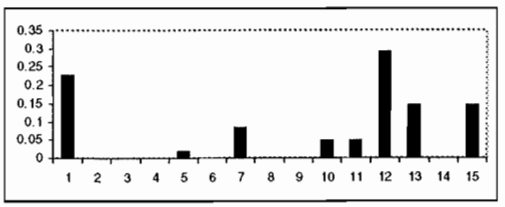
Site 5 Norris Farm n= 14



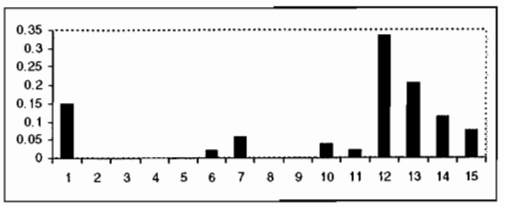
Site 6 Lewell Mill n= 28



Site 7 East Burton n= 31



Site 8 East Stoke n=27



Site 9 ESMS n= 16

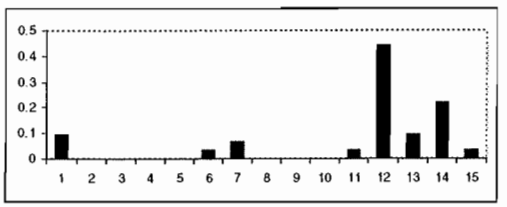
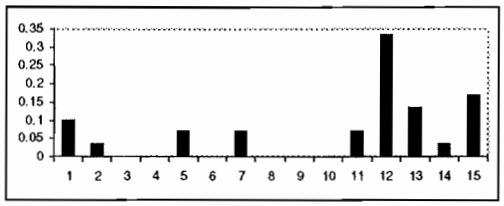
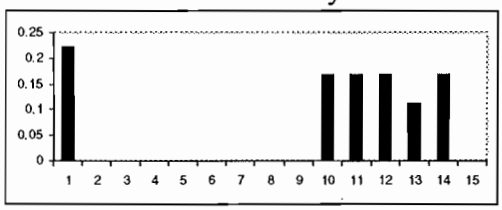


Figure 7.4.4.7 (Continued)

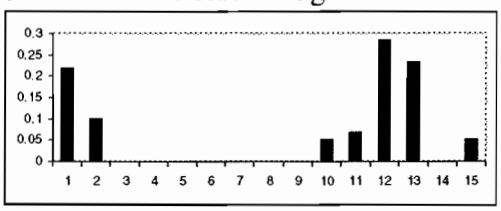
Site 10 Waterbarn Stream n= 15



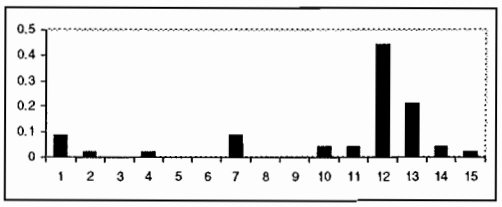
Site 11 Whitfield Hatchery n= 9



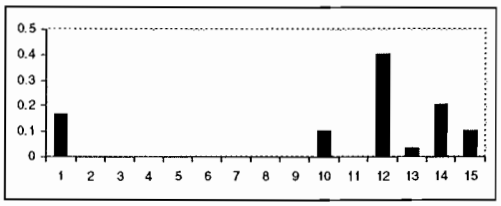
Site 12 Muckelford Bridge n= 30



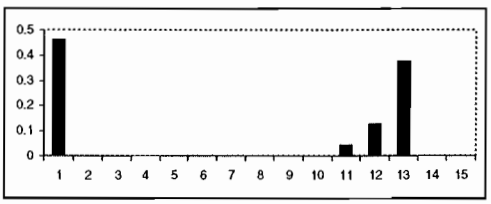
Site 14 Bindon Millstream n= 24



Site 16 South Winterbourne n= 15



Site 17 Wool Stream n= 12



Site 19 Moreton Ford n= 31

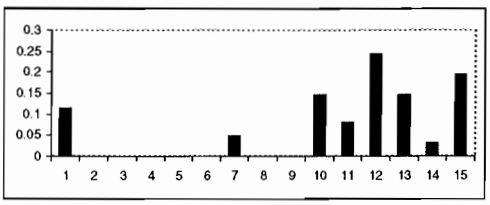
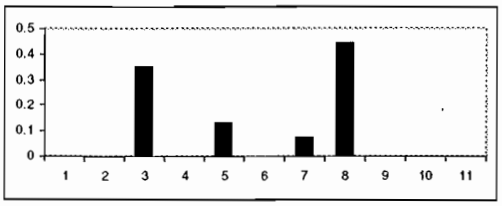


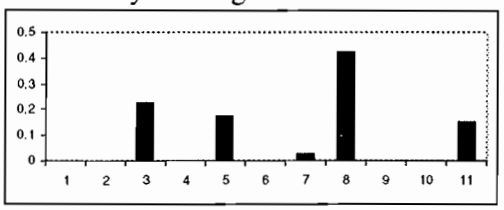
Figure 7.4.4.7 (Continued)

4. Locus Ssosl 85

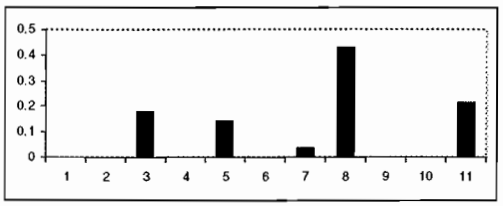
Site 1 Bere Stream n= 27



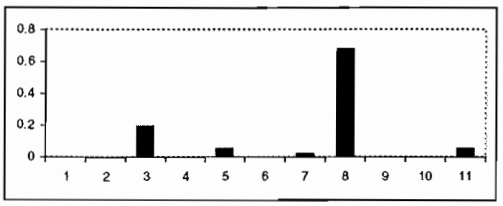
Site 4 Grey's Bridge n= 20



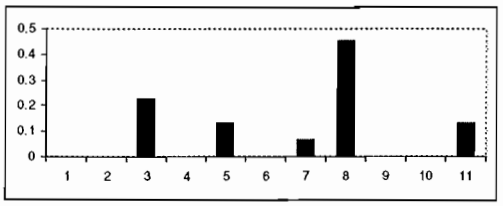
Site 5 Norris Farm n= 14



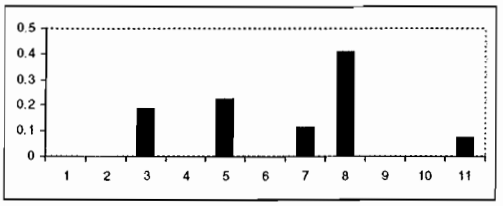
Site 6 Lewell Mill n= 28



Site 7 East Burton n= 31



Site 8 East Stoke n= 27



Site 9 ESMS n= 17

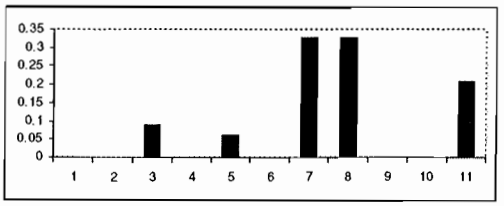
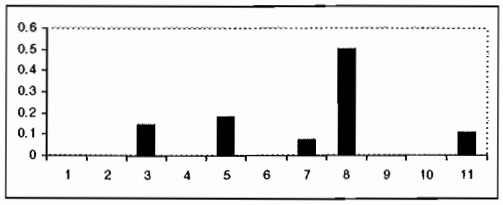
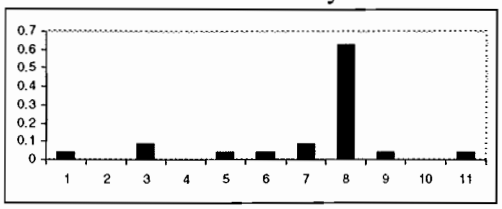


Figure 7.4.4.7 (Continued)

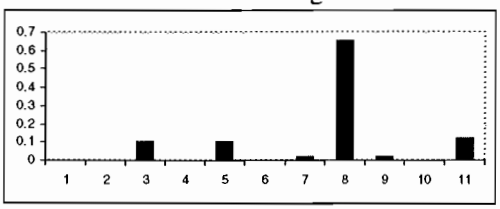
Site 10 Waterbarn Stream n= 14



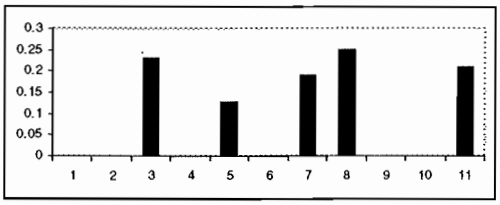
Site 11 Whitfield Hatchery n= 12



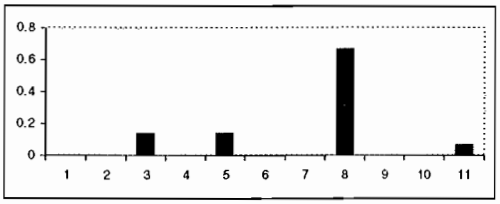
Site 12 Muckelford Bridge n= 30



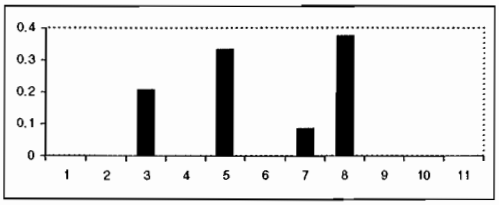
Site 14 Bindon Millstream n= 24



Site 16 South Winterbourne n= 15



Site 17 Wool Stream n= 12



Site 19 Moreton Ford n= 31

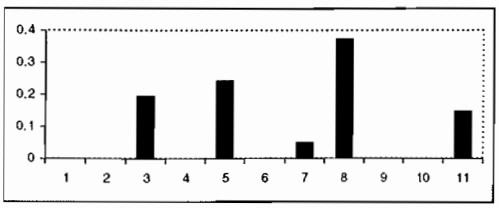
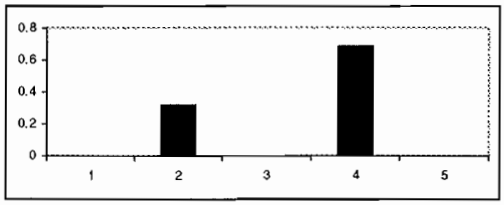


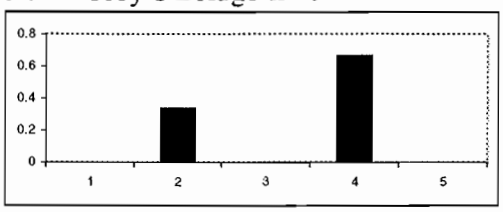
Figure 7.4.4.7 (Continued)

5. Locus Ssa 289

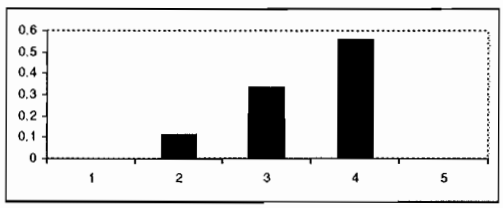
Site 1 Bere Stream n= 27



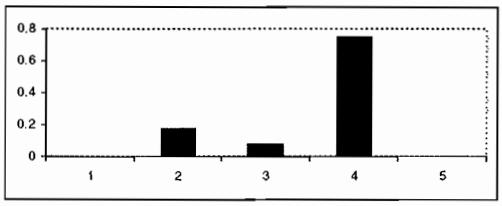
Site 4 Grey's Bridge n= 9



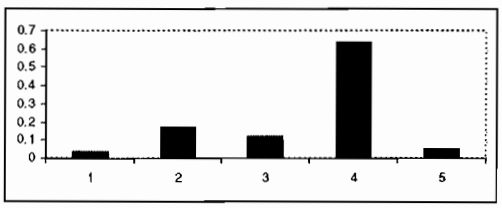
Site 5 Norris Farm n= 9



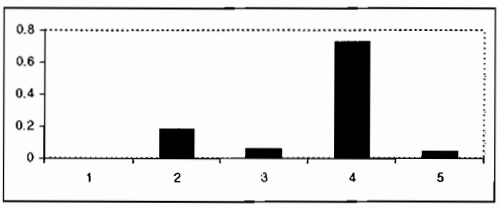
Site 6 Lewell Mill n= 26



Site 7 East Burton n= 30



Site 8 East Stoke n= 25



Site 9 ESMS n= 17

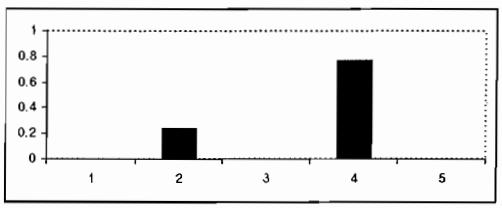
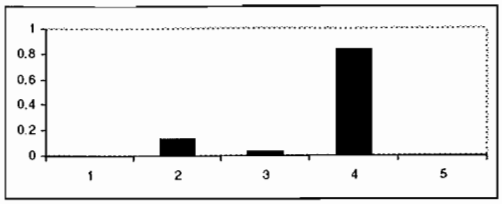
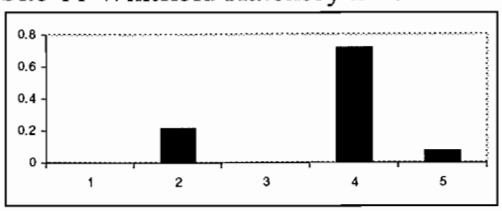


Figure 7.4.4.7 (Continued)

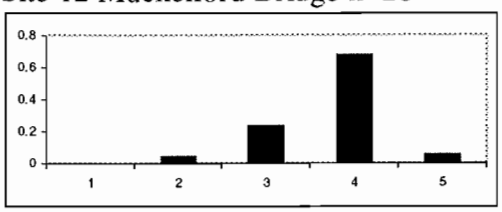
Site 10 Waterbarn Stream n= 15



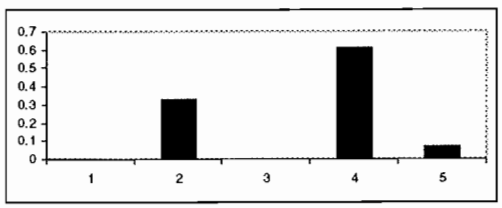
Site 11 Whitfield Hatchery n= 7



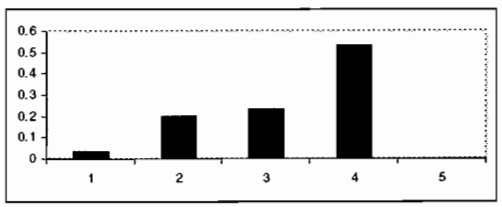
Site 12 Muckelford Bridge n=28



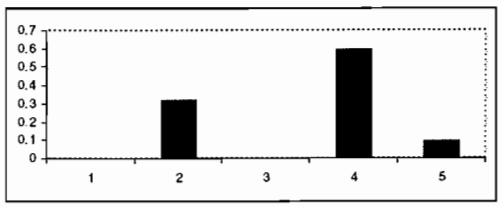
Site 14 Bindon Millstream n= 23



Site 16 South Winterbourne n= 15



Site 17 Wool Stream n=11



Site 19 Moreton Ford n= 29

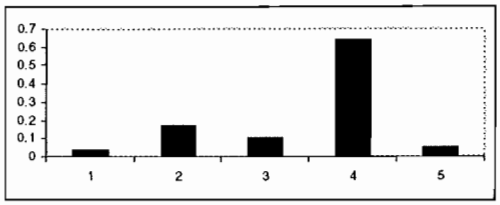
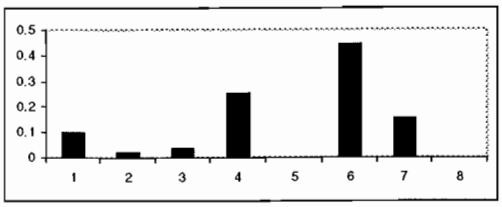


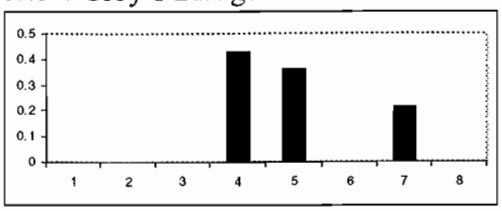
Figure 7.4.4.7 (Continued)

6. Locus Ssosl 417

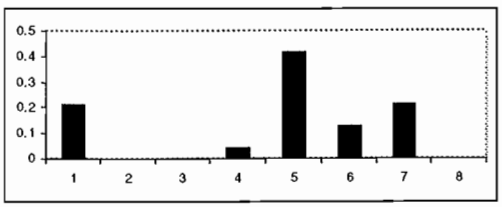
Site 1 Bere Stream n= 26



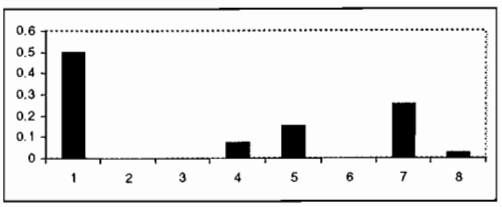
Site 4 Grey's Bridge n= 14



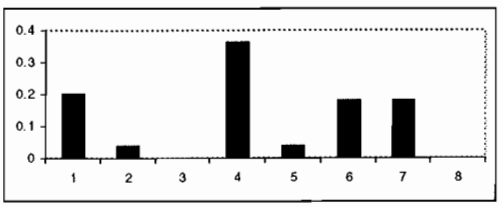
Site 5 Norris Farm n= 12



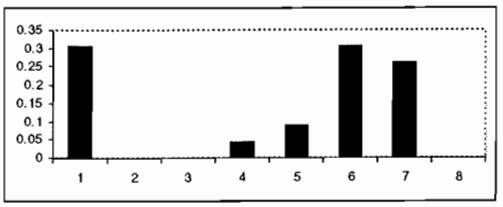
Site 6 Lewell Mill n= 20



Site 7 East Burton n= 25



Site 8 East Stoke n=23



Site 9 ESMS n= 13

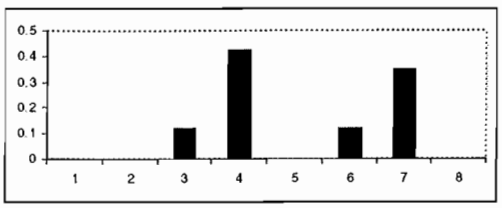
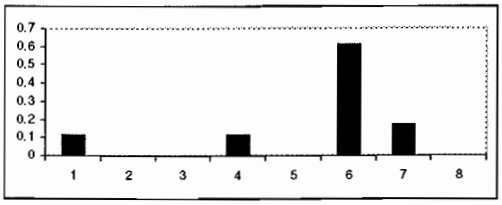
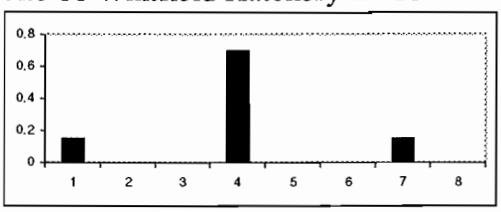


Figure 7.4.4.7 (Continued)

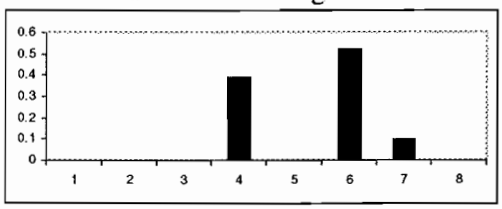
Site 10 Waterbarn Stream n= 9



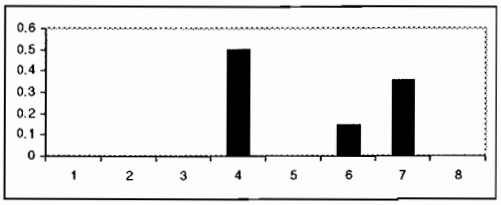
Site 11 Whitfield Hatchery n= 10



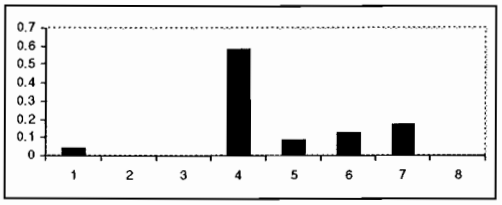
Site 12 Muckelford Bridge n= 26



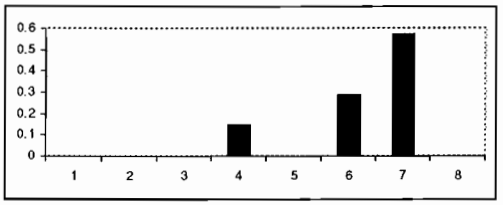
Site 14 Bindon Millstream n= 17



Site 16 South Winterbourne n= 12



Site 17 Wool Stream n= 7



Site 19 Moreton Ford n= 4

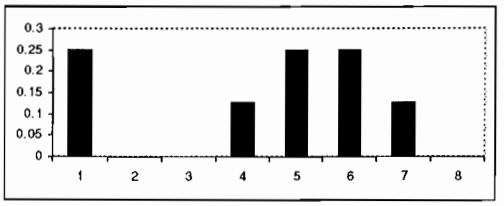


Figure 7.4.4.7 (Continued)

7.4.7. Results, F_{IS} per site

Table 7.4.7.1 F_{IS} per site per locus, over all loci and over 5 loci with Ssosl 417 removed, July 1998

locus	BS	TF	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	TK	BM	TW	MF
N total	5	72	9	16	30	34	76	24	18	52	12	2	1	29	10	58
Ssa 202																
N	4	60	2	3	24	12	66	20	15	38	5	1	1	9	7	45
F_{IS}	0.294	0.125	0	-0.143	0.075	0.267	0.248*	0.372*	-0.069	0.063	0.2	NA	NA	0.229	-0.364	-0.113
Ssa 171																
N	5	59	3	15	30	32	61	18	16	48	11	2	1	28	10	57
F_{IS}	-0.25	0.109	0.2	-0.058	0.188	-0.071	0.082	-0.039	0.167	0.003	0.2	1	NA	-0.062	0	-0.046
Ssa 197																
N	5	72	9	15	30	33	72	24	17	49	12	2	1	28	10	50
F_{IS}	0.294	0.167**	0.25	-0.09	0.252**	0.4*a	0.204*a	0.393*a	0.512*a	0.337*a	0.689*a	0.5	NA	-0.135	0.038	0.208***
Ssosl 85																
N	5	68	9	13	29	32	71	23	17	47	10	2	1	27	9	58
F_{IS}	-0.391	0.317*a	-0.016	0.063	-0.066	0.214*	0.261*a	0.472*a	0.191	0.098	0.166	0	NA	-0.066	-0.047	-0.008
Ssa 289																
N	5	62	5	2	/	/	56	18	17	47	10	1	1	25	9	38
F_{IS}	0.733*	0.872*a	0.765**	1	NA	NA	0.435*a	0.477	0.866*a	0.773*a	0.419	NA	NA	-0.125	0.091*	0.416*a
Ssosl 417																
N	2	31	/	7	20	13	39	18	15	44	10	2	1	12	3	15
F_{IS}	1	0.676*a	NA	1**	0.509*a	0.6**	0.782*a	0.863*a	0.691*a	0.632*a	0.827*	1	NA	0.793*a	1	0.729*a
F_{IS} over all loci	0.338*	0.36*a	0.26**	0.334*	0.203*a	0.262*a	0.316*a	0.418*a	0.357*a	0.293*a	0.406*a	0.714*	NA	0.14*	0.132*	0.192*a
F_{IS} over 5 loci, Ssosl417 removed	0.158	0.299***a**	0.26**	0.22	0.118*	0.201***a**	0.218***a**	0.309***a**	0.296***a**	0.219***a**	0.333***a**	0.6	NA	-0.033	-0.043	0.084**

P value based on 12500 randomisations p 0.05 *, p 0.01 **, p 0.001***. Indicative adjusted nominal level (5%) was 0.0004, 5 % adjusted *a.

Table 7.4.7.2 F_{IS} per locus, over all loci and over 5 loci with Ssosl 417 removed, September 1998

locus	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	TW	SW	WO	MC	MF	DT	DS
N total	14	10	48	54	10	18	20	10	27	4	10	10	5	57	3	6
Ssa 202																
N	7	6	32	30	4	15	11	8	8	3	9	4	4	39	/	3
F_{IS}	0.455	0.388	0.112	0.006	-0.5	-0.143	0.351	-0.191	0.233	-0.5	0.413	0.4	-0.125	0.104		0.5
Ssa 171																
N	12	10	43	50	4	18	19	9	16	2	8	2	5	45	/	1
F_{IS}	-0.254	-0.102	0.041	-0.057	-0.263	-0.055	0.185	0.279	0.523*a	0	-0.349	-0.333	0	0.113	NA	NA
Ssa 197																
N	7	9	38	48	6	15	14	7	/	1	10	6	4	47	1	3
F_{IS}	-0.108	1*a	0.092	0.204**	0.298	-0.012	0.027	0.342	NA	NA	0.15	0.091	-0.6	0.141*	NA	0.2
Ssosl 85																
N	13	10	39	50	10	18	15	10	26	3	6	4	4	/	1	5
F_{IS}	-0.143	-0.21	-0.128	0.104	0.194	0.2	-0.117	-0.385	0.038	0.2	0.048	0.7*	NA	0.468*a	NA	-0.333
Ssa 289																
N	14	10	44	32	10	15	15	10	10	4	8	6	4	38	3	5
F_{IS}	0.804*a	0.705**	0.103	0.059	0.681**	0.03	-0.05	-0.08	NA	0.2	-0.077	-0.053	-0.5	-0.023	0.5	0.6
Ssosl 417																
N	2	/	31	30	7	10	/	4	4	4	8	9	5	27	/	5
F_{IS}	NA	NA	0.876*a	0.768*a	0.143	0.878*a	NA	1*	1*	0.571	0.659**	0.765*	0.273	0.668*a	NA	1
F_{IS} over all loci	0.151*	0.34*a	0.196*a	0.191*a	0.114	0.2**	0.097	0.248*	0.465*a	0.079	0.17*	0.265*	-0.19	0.274*a	0.5	0.302
F_{IS} over 5 loci, Ssosl 417 removed	0.151	0.34***a**	0.032	0.061	0.11	0.017	0.097	0.043	0.265**	-0.013	0.056	0.201	-0.296	0.184***a**	0.5	0.2

P value based on 14400 randomisations. Indicative adjusted nominal level (5%) was 0.00042. p 0.05 *, p 0.01 **, p 0.001***, p 5 % adjusted *a.

Table 7.4.7.3 F_{IS} per locus per population, over all loci and over 5 loci with Ssosl 417 removed, November 1998

locus	GB	ESMS	WS	BM	WO
N total	4	7	6	9	10
Ssa 202					
N	4	1	1	2	/
F_{IS}	0.1	NA	NA	NA	NA
Ssa 197					
N	3	6	4	9	5
F_{IS}	-0.5	-0.224	0.368	0.407	-0.111
Ssosl 85					
N	3	3	2	5	7
F_{IS}	-0.5	0.273	0	0.059	0.333
Ssa 289					
N	3	5	2	7	8
F_{IS}	0.6	1.0**	NA	0.217	-0.077
Ssosl 417					
N	2	6	5	8	9
F_{IS}	1	1*a	1**	0.825	0.575**
F_{IS} over all	0.229	0.515*a	0.522*a	0.369*a	0.223*
F_{IS} over 5 loci Ssosl 417 removed	-0.028	0.367**	0.226	0.203	0.084

P value based on 10000 randomisations 0.05 *, p 0.01 **. Indicative adjusted nominal level (5%) was 0.0025, % adjusted *a.

Table 7.4.7.4 F_{IS} per locus per population, over all loci and over 5 loci with Ssosl 417 removed, July 1999

locus	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	BM	TW	SW	WO	MF	RW
total N	3	5	13	53	36	21	9	14	26	20	31	17	17	3	49	21
Ssa 202																
N	3	5	13	53	35	21	9	14	26	20	31	17	17	3	49	17
F_{IS}	-0.2	-0.103	-0.419	-0.137	-0.11	-0.053	-0.057	0.008	-0.096	-0.241	0.198	-0.149	-0.28	-0.333	-0.199*	0.015
Ssa 171																
N	3	5	12	53	36	21	9	14	26	20	31	16	17	3	49	17
F_{IS}	-0.2	-0.143	0.15	-0.063	-0.135	-0.162	0	-0.065	0.064	-0.196	-0.004	-0.008	-0.123	NA	0.252***	-0.2
Ssa 197																
N	3	5	13	53	35	21	9	14	26	19	31	16	16	3	49	16
F_{IS}	-0.091	-0.111	0.281*	0.188**	0.387*a	0.1	0.143	-0.02	-0.037	0.128	0.085	0.13	-0.017	-0.5	-0.02	0.067
Ssosl 85																
N	3	3	10	46	36	21	9	13	26	20	29	16	16	3	41	18
F_{IS}	-0.143	-0.333	-0.314	-0.07	-0.013	-0.009	0.538	0.6*a	0.379***	0.152	0.11	0.065	0.041	1	0.178	0.068
Ssa 289																
N	3	4	9	49	35	20	9	14	26	20	31	16	17	3	49	17
F_{IS}	1	NA	0.805**	0.261**	-0.046	-0.012	-0.4	-0.39	-0.104	0.214	0.422**	-0.161	0.565***	-1	0.222*	0.52*
Ssosl 417																
N	2	4	9	38	21	15	3	10	23	12	27	6	15	3	34	15
F_{IS}	1	1*	1*a	0.659*a	0.51*a	0.892*a	0.2	0.765*a	0.885*a	0.772*a	0.583*a	0.815**	0.517***	0.111	0.495*a	0.659*a
overall F_{IS}	0.241	0.069	0.232**	0.127**	0.127***	0.111*	0.091**	0.192*a	0.208*a	0.126*	0.215*a	0.169**	0.112*	-0.081	0.154*a	0.162**
F_{IS} over 5 loci Ssosl 417 removed	0.043	-0.169	0.084	0.025	0.036	-0.027	0.066	0.055	0.061	-0.02	0.152***	0	0.035	-0.143	0.083*	0.048

P value based on 13200 randomisations. Indicative adjusted nominal level (5%) was 0.00045. p 0.05 *, p 0.01 **, p 0.001***, p 5 % adjusted *a.

Table 7.4.7.5 F_{IS} per locus per population, over all loci and over 5 loci with Ssosl 417 removed, September 1999

sitecode	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	TW	SW	WO	MF
total N	2	17	12	33	31	30	34	13	11	11	30	13	17	21	3	21
Ssa 202																
N	1	9	9	24	20	8	21	10	10	7	13	10	15	21	3	17
F_{IS}	NA	-0.155	-0.167	0.094	0.012	0.034	0.271	-0.18	-0.328	0.048	-0.158	0.318	-0.4	-0.121	0.6	0.212
Ssa 171																
N	2	9	10	24	25	21	23	12	9	8	11	13	17	20	3	17
F_{IS}	-0.333	-0.067	0.166	0.046	-0.159	0.043	-0.163	-0.211	-0.18	-0.244	-0.449	-0.071	-0.143	-0.308	-0.5	0.076
Ssa 197																
N	2	14	11	1	19	27	19	7	10	7	15	12	14	18	3	21
F_{IS}	-0.333	0.091	0.022	NA	0.106	0.08	0.316**	0.186	0.416**	0.379	0.263*	0.083	-0.138	-0.097	-0.2	0.015
Ssosl 85																
N	2	14	12	33	28	27	32	11	11	11	20	13	17	21	3	21
F_{IS}	0	-0.032	0.17	0.059	-0.058	0.143	-0.113	-0.13	-0.07	0.615**	-0.24	0.045	-0.205	-0.066	-0.5	0.168
Ssa 289																
N	2	17	12	25	17	14	33	13	11	9	17	13	16	20	3	21
F_{IS}	1	0.631**	0.221	0.634*a	0	0.313	-0.045	0.459	-0.136	-0.032	-0.18	0.478	0.333	0.784*a	0.6	0.142*a
Ssosl417																
N	2	10	10	24	23	27	21	10	8	9	11	8	10	19	2	16
F_{IS}	1	0.859*a	0.845***	0.742*a	0.758*a	0.702*a	0.668*a	1*a	0.848*a	0.867*a	0.875*a	0.475	1	0.576*a	1	1*a
overall F_{IS}	0.375	0.195**	0.195**	0.279*a	0.125**	0.201***	0.154***	0.189**	0.127*	0.313***	0.061	0.211**	-0.061	0.115*	0.241	0.283*a
F_{IS} overall, Ssosl 417 removed	0.167	0.057	0.078	0.174***	-0.025	0.114*	0.054	0.015	-0.037	0.167	-0.125	0.158*	-0.126	0.024	0.043	0.118*

P value based on 12600 randomisations p 0.05 *, p 0.01 **, p 0.001***. Indicative adjusted nominal level (5%) was 0.00048, 5 % adjusted *a.

Table 7.4.7.6 F_{IS} per locus per population, over all loci and over 5 loci with Ssosl 417 removed, July 2000

locus	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	BM	TW	SW	WO	MF
Total N	14	18	25	20	30	30	26	31	28	30	31	7	29	28	30
Ssa 202															
N	13	17	23	19	29	25	18	30	23	19	29	7	27	27	29
F_{IS}	-0.284*	0.076	-0.179	-0.055	0.308*	0.136	0.438	0.083	0.073	-0.08	0.013	0.091	-0.179	0.051	0.007
Ssa 171															
N	14	17	25	20	30	27	24	31	22	19	29	7	29	28	30
F_{IS}	0.146	0.121	-0.139	-0.039	0.147	-0.101	-0.024	-0.06	-0.07	0.041	-0.045	0.048	-0.145	-0.305	0.193
Ssa 197															
N	14	18	25	20	29	30	26	30	28	29	31	7	29	28	29
F_{IS}	-0.04	-0.052	0.009	0.104	0.124	0.061	0.124	-0.06	0.047	0.114	0.054	0.178	-0.068	-0.028	0.027
Ssosl 85															
N	13	12	22	19	16	29	18	29	23	23	26	2	29	24	16
F_{IS}	-0.387	0.206	0.385**	0.02	-0.061	-0.054	0.513**	-0.066	-0.196	-0.266	0.116	0	0.094	0.289	0.888*a
Ssa 289															
N	10	5	12	10	23	29	23	29	12	5	22	7	25	26	23
F_{IS}	0	0.5	NA	-0.059	0.101	0.233	0.488***	-0.062	0.439	1	-0.115	NA	0.229	0.48**	0.304
Ssosl417															
N	14	14	19	19	16	16	13	16	9	12	11	2	24	16	16
F_{IS}	-0.209	0.792*a	0.858*a	0.768*a	0.601*a	0.637*a	0.687***	0.656*a	0.74*a	1*a	0.778*a	NA	1*a	1*a	0.687*a
F_{IS} overall loci	-0.146*	0.24*a	0.18*a	0.142**	0.218*a	0.137**	0.351*a	0.091*	0.189***	0.194**	0.152***	0.077	0.134**	0.188**	0.332*a
F_{IS} over 5 loci Ssosl 417 removed	-0.135	0.132*	0.002	0.006	0.128**	0.038	0.278*a	-0.033	0.051	0.115	0.01	0.077	-0.025	0.061	0.243*a

P value based on 12600 randomisations. Indicative adjusted nominal level (5%) was 0.00048. p 0.05 *, p 0.01 **, p 0.001***, p 5 % adjusted *a.

Table 7.4.7.7 F_{IS} per locus per population, over all loci and over 5 loci with Ssosl 417 removed, October 2000

locus	BS	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	SW	WO	MF
Total N	29	20	14	30	31	27	17	15	12	30	24	15	13	31
Ssa 202														
N	29	19	14	30	24	22	13	13	9	28	22	15	13	27
F_{IS}	0.011	0.163	-0.048	0.089	-0.022	0.037	-0.081	0.143	0.34	-0.001	-0.176	-0.333	-0.043	0
Ssa 171														
N	27	18	12	23	28	26	17	15	12	28	23	15	11	25
F_{IS}	0.367**	-0.092	0.275	0.245*	-0.045	0.023	0.144	0.058	-0.1	0.113	0.065	-0.15	-0.681	-0.025
Ssa 197														
N	27	19	14	29	31	27	16	15	9	30	24	15	12	31
F_{IS}	-0.145	0.009	0.089	-0.11	-0.057	0.003	-0.157	0.056	-0.016	0.016	0.126	0.146	-0.415	-0.098
Ssosl 85														
N	27	20	14	29	31	27	17	14	12	30	24	15	12	31
F_{IS}	-0.224	0.116	0.238	0.295	0.059	0.109	0.231	0.093	0.19	0.34**	0.125	-0.261	-0.152	0.018
Ssa 289														
N	27	9	9	27	30	25	17	15	7	28	23	15	11	29
F_{IS}	0.074	0.059	0.644*	0.347*	-0.006	0.119	0.05	-0.129	0.1	0.349	0.432*	0.385	-0.475	0.138
Ssosl 417														
N	26	14	12	21	25	23	13	9	10	26	17	12	7	4
F_{IS}	0.578*a	1*a	0.458**	0.636*a	0.747*a	0.773*a	0.788*a	0.467*	0.804**	0.675*a	0.629*a	0.616**	1**	0.75**
F_{IS} over all loci	0.103*	0.199***	0.267*a	0.224*a	0.119**	0.182*a	0.171**	0.129*	0.183*	0.235*a	0.183***	0.076	-0.1	0.157**
F_{IS} over 5 loci Ssosl 417 removed	-0.003	0.046	0.226**	0.138**	-0.017	0.052	0.038	0.065	0.09	0.145**	0.101	-0.028	-0.346	-0.003

P value based on 12000 randomisations p 0.05 *, p 0.01 **, p 0.001***. Indicative adjusted nominal level (5%) was 0.0005, p 5 % adjusted *a.

7.4.8 Results Pairwise F_{ST} per sample time

Table 7.4.8.1 Pairwise F_{ST} values for *S. salar* at 15 sites, Rivers Piddle and Frome, 5 loci, July 1998

site	BS	TF	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	TW
TF	-0.0178													
WH	-0.0081	-0.018												
GB	**0.0356*a**	0.0222	-0.0578											
NF	0.056	0.0524	-0.0343	-0.001										
LM	0.0245	0.0732	0.0334	0.0388	0.042									
EB	**0.0379****	**0.038***	0.0257	**0.0228****	0.0162	0.0376								
ES	**0.052****	**0.0376*****	0.0206	**0.0079****	0.0084	0.0333	-0.0055							
ESMS	0.0453	**0.0409*****	-0.0019	**0.0171*a**	0.0101	0.0305	**0.0079*a**	**0.0018*****						
WS	0.0092	**0.0281*a**	0.031	**0.0238*a**	0.0374	0.035	**0.0005*a**	**0.0118*a**	**0.0229*a**					
HA	0.0546	**0.0883*a**	0.0439	0.0547*a	**0.0514****	0.0207	**0.0322*a**	0.0265	0.0119	**0.0299*a**				
MB	**0.0879*a**	0.0168	-0.0183	**0.0208*a**	0.0083	0.0509	-0.0108	-0.0193	-0.0172	-0.0137	0.076			
BM	**0.036****	**0.0339*a**	0.0461	**0.0523*a**	0.0368	0.0607	**0.0092*a**	**0.0186****	**0.0274****	**0.0149****	**0.0758****	0.0164		
TW	**0.0444****	**0.0584*a**	0.0394	**0.0395*a**	**0.0356****	0.0457	**0.0456*a**	**0.0461*****	**0.02***	**0.0568*a**	**0.0835*a**	**0.1126*a**	**0.0729*a**	
MF	**0.0466*****	**0.0336*a**	-0.0004	**0.0116*a**	0.016	**0.0447***	**0.0253*a**	**0.0105*a**	**0.0144*a**	**0.0306*a**	**0.0559*a**	0.0349	**0.0548*a**	**0.0403*a**

P-values obtained after 30000 permutations p0.05* (non adjusted), p0.01** (non adjusted) p0.001***(non adjusted).
Indicative adjusted nominal level (5%) for multiple comparisons was 0.000167, p 5 % level *a (Bonferroni adjusted).

Table 7.4.8.2. Pairwise F_{ST} values for *S. salar* at 16 sites, Rivers Piddle and Frome, 5 loci, September 1998

site	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	TW	SW	WO	MC	MF	DT
NF	-0.0015														
LM	**0.0689*a**	**0.0642*a**													
EB	**0.0692*a**	**0.0671*a**	**0.0151*** **												
ES	**0.0341*** **	0.0205	**0.0589***	**0.0874***											
ESMS	**0.0902*a**	**0.1145*a**	**0.0705*a**	**0.0653*a**	**0.0953*a**										
WS	**0.0578*a**	**0.0727*a**	**0.0216***	0.0162	**0.0907****	**0.0909****									
HA	**0.0541*a**	**0.0896*a**	**0.0408*a**	**0.0578*a**	**0.0871****	**0.053*a**	**0.0457*** **								
MB	0.0916	0.109	0.005	0.0041	0.087	0.0713	-0.0008	0.0477							
TW	-0.0368	-0.0254	0.0217	-0.0019	0.0585	0.0506	-0.0446	0.0537	0.0427						
SW	**0.0985*a**	**0.0849*a**	**0.0458*** **	0.0251	**0.1091*** **	**0.1046*** **	**0.0269****	**0.1024*** **	0.041	-0.0377					
WO	**0.0397*** **	**0.0632*** **	0.014	0.0026	0.0815	0.0262	0.0033	0.0281	-0.0238	-0.0612	-0.0001				
MC	**0.1437*a**	**0.094*** **	**0.1452****	**0.1385*a**	**0.1105***	**0.1845*** **	**0.178*** **	**0.2459*a**	0.2232	**0.1405*a**	**0.1889*a**	**0.1659*a**			
MF	**0.0411*a**	**0.0514*a**	**0.0242*a**	**0.0167*a**	0.0401	**0.0292*a**	0.0184	**0.0263*** **	**0.0185***	-0.0244	**0.0502*a**	-0.0049	**0.1109*a**		
DT	0.0841	-0.0497	0.5192	0.3506	-0.0421	0.054	0.3917	0.2228	0.6403	0.0697	0.225	0.1667	0.1798	0.1274	
DS	-0.002	-0.0088	0.0409	0.0169	0.081	0.0831	-0.0294	0.0151	0.0867	-0.0753	0.0058	-0.0026	**0.1698*a**	0.0006	-0.1565

P-values obtained after 27600 permutations p 0.05* (non adjusted), p 0.01** (non adjusted), p 0.001*** (non adjusted).
Indicative adjusted nominal level (5%) for multiple comparisons was 0.000181, p 5 % *a (Bonferroni adjusted).

Table 7.4.8.3 Pairwise F_{ST} values for *S. salar* at 5 sites, no Ssosl 417, River Frome, November 1998

site	GB	ESMS	WS	BM
ESMS	-0.0778			
WS	-0.0585	-0.0227		
BM	0.1552	-0.0086	**0.1648*a**	
WO	0.044	0.0022	0.005	0.0208

P-values obtained after 15000 permutations p0.05* (non adjusted), p0.01** (non adjusted).
Indicative adjusted nominal level (5%) for multiple comparisons is 0.005, p5 % *a (Bonferroni adjusted).

Table 7.4.8.4 Pairwise F_{ST} values for *S. salar* at 15 sites, 5 loci, Rivers Piddle and Frome, July 1999

site	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	BM	SW	WO	MF	TW
WH	-0.006														
GB	-0.0374	**0.0171***													
NF	-0.0505	-0.005	**0.0071****												
LM	-0.0259	**0.0114****	**0.0514*a**	**0.0303*a**											
EB	-0.0267	**0.0128***	**0.0227*a**	**0.0213*a**	**0.0181*a**										
ES	-0.0842	**0.0004***	**0.0166*a**	**0.0022*a**	**0.0406*a**	**0.0248****									
ESMS	-0.0472	0.0001	**0.0328*a**	**0.0304*a**	**0.0624*a**	0.033a	-0.0188								
WS	-0.0429	**0.0071****	**0.0157*a**	**0.0267*a**	**0.0363*a**	-0.0008	**0.0086****	**0.0157*****							
HA	-0.0127	**0.0193*a**	**0.0534*a**	**0.0297*a**	**0.0362*a**	**0.052*a**	0.0286	**0.0713*a**	**0.0378*a**						
BM	-0.0589	**0.003***	**0.0187*a**	**0.0179*a**	**0.0506*a**	**0.0177****	-0.0109	**0.0157*****	0.0107	**0.0467*a**					
SW	-0.0337	**0.072*****	**0.0224*a**	**0.0441*a**	**0.0398*a**	0.0284	0.0324	**0.0568***	0.0256	**0.0544*a**	0.0361				
WO	**0.1591*a**	**0.1711****	**0.1773*a**	**0.1569*a**	**0.2104*a**	**0.1553****	0.1192	**0.1342***	**0.1421****	**0.1982*a**	0.1094	**0.2224*a**			
MF	-0.0585	**0.0273****	**0.0217*a**	**0.0268*a**	**0.0558*a**	**0.0358*a**	-0.0055	0.0241	0.0255	**0.0616*a**	0.0146	0.0438	**0.1983***		
TW	-0.0248	0.003	**0.051*a**	**0.0341*a**	**0.0327*a**	**0.0347*a**	0.0144	0.0205	0.0156	**0.0494*a**	0.0183	**0.0399****	**0.2089*****	**0.0388****	
RW	-0.0399	**0.0043***	**0.0149*a**	0.0221	0.0239	0.0206	0.0126	0.0442	0.0079	0.014	0.019	0.0323	0.1694	0.0384	0.0384

P-values obtained after 23100 permutations p 0.05* (non adjusted), p 0.01**, p 0.001*** (non adjusted).
Indicative adjusted nominal level (5%) for multiple comparisons was 0.000216 p 5 % *a (Bonferroni adjusted).

Table 7.4.8.5 Pairwise F_{ST} values for *S. salar* at 16 sites, Rivers Piddle and Frome, 5 loci, September 1999

Site	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	SW	WO	MF
WH	-0.0395														
GB	-0.0148	-0.0171													
NF	**0.0397***	0.0017	-0.0048												
LM	**0.0689***	**0.0332*a**	0.0419	0.0597											
EB	-0.0259	**0.0027***	0.0102	0.0371	**0.0586*a**										
ES	-0.0252	-0.007	**0.0136****	**0.0126***	**0.0379*a**	**0.0195*a**									
ESMS	0.0099	-0.0044	**0.0257***	0.0094	**0.0742*a**	**0.0077*a**	-0.0128								
WS	0.0243	-0.0133	-0.0145	**0.0025*****	**0.0091*a**	**0.0094*a**	0.0049	**0.0043*****							
HA	-0.0091	**0.0126*a**	**0.0297***	0.0191	**0.0379*a**	0.0169	**0.0427*a**	**0.0497*a**	0.0199						
MB	0.0066	**0.0479*a**	**0.058***	**0.0919*a**	**0.0843*a**	**0.0233*a**	**0.0594*a**	**0.0606*a**	**0.065*a**	0.0325					
BM	-0.0771	-0.0074	**0.0235****	**0.0434*****	**0.0743*a**	-0.0055	**0.0145*a**	**0.0111*a**	**0.0181*a**	**0.0436*a**	**0.0473*a**				
SW	0.0267	**0.0714*a**	**0.0609*a**	**0.086*a**	**0.1157*a**	**0.0283*a**	**0.0723*a**	**0.0539*a**	**0.0515*a**	**0.0746*a**	**0.0706*a**	**0.0397*a**			
WO	-0.0272	**0.0111****	-0.005	**0.0269***	**0.0889*a**	-0.0274	**0.0387*a**	**0.0156*a**	0.009	0.0107	**0.0853*a**	-0.039	-0.0199		
MF	**0.0309***	**0.0159****	**0.0212*a**	**0.0341*a**	**0.0423*a**	-0.0091	**0.0372*a**	**0.0295*a**	**0.0023*a**	**0.0197*a**	**0.0595*a**	**0.0158*a**	**0.0451*a**	-0.0227	
TW	**0.0953***	**0.0865*a**	**0.0834*a**	**0.1085*a**	**0.1134*a**	**0.0224*a**	**0.0716*a**	**0.0796*a**	**0.0795*a**	**0.0863*a**	**0.0756*a**	**0.0403***	**0.0798*a**	**0.0555****	**0.0604*****

P-values obtained after 21000 permutations p 0.05* (non adjusted), p 0.01** (non adjusted), p 0.001*** (non adjusted).
Indicative adjusted nominal level (5%) for multiple comparisons was 0.000238, p 5 % *a (Bonferroni adjusted).

Table 7.4.8.6 Pairwise F_{ST} values for *S. salar* at 15 sites, Rivers Piddle and Frome, 5 loci, July 2000

site	BS	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	BM	SW	WO	MF
WH	**0.0516****													
GB	**0.0958*a**	**0.03*****												
NF	**0.0775*a**	**0.0044***	**0.0203*a**											
LM	**0.0494*****	-0.0124	**0.0243*a**	**0.0246*****										
EB	**0.0705*a**	-0.0186	**0.044*a**	**0.0206*a**	**0.005*****									
ES	**0.1686*a**	**0.0428*****	**0.1427*a**	**0.0992*a**	**0.0685*a**	**0.0486****								
ESMS	**0.1176*a**	-0.0025	**0.0424*a**	**0.172*a**	**0.018*a**	**0.0112*a**	**0.0652*a**							
WS	**0.1149*a**	0.0151	**0.0934*a**	0.0416	0.0383	0.0202	0.0493	0.0406						
HA	**0.1101*a**	0.0382	0.0521	0.0373	0.0458	0.036	0.1143	0.0576	0.0451					
BM	**0.0954*a**	-0.0012	**0.0544*a**	**0.0229*a**	**0.0317*a**	**0.0133****	**0.0668*a**	**0.0129***	**0.0231***	**0.0704*a**				
SW	**0.092*a**	**0.0208*a**	**0.0533*a**	**0.0405*a**	**0.0374*a**	**0.0332*a**	**0.1056*a**	**0.0315*a**	**0.0582*a**	**0.077*a**	**0.0133*a**			
WO	**0.1493*a**	**0.0497*a**	**0.0899*a**	**0.0635*a**	**0.0649*a**	**0.0654*a**	**0.1166*a**	**0.0789*a**	**0.0746*a**	**0.0939*a**	**0.0857*a**	**0.0947*a**		
MF	**0.1388*a**	**0.0166*a**	**0.0686*a**	**0.0394*a**	**0.0371*a**	**0.0182****	**0.0623***	0.0228	0.0422	**0.0208****	**0.0527*a**	**0.0664*a**	**0.0727*a**	
TW	**0.0881*****	-0.0024	**0.0536***	0.0355	0.0215	0.0199	**0.1099*a**	**0.0274***	**0.0809****	**0.0934*a**	**0.0302***	**0.0445****	**0.0695****	0.0291

P-values obtained after 21000 permutations p0.05* (non adjusted), p0.01** (non adjusted), p0.001*** (non adjusted).
Indicative adjusted nominal level (5%) for multiple comparisons is 0.000238, p 5 % *a (Bonferroni adjusted).

Table 7.4.8.7 Pairwise F_{ST} values for *S. salar* at 14 sites, Rivers Piddle and Frome, 5 loci, October 2000

	BS	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	SW	WO
GB	**0.0134*** **												
NF	**0.0442*a**	0.011											
LM	**0.0423*a**	0.0087	0.0153										
EB	**0.0328*a**	-0.0011	-0.002	**0.0124****									
ES	**0.027*a**	-0.0084	**0.0098***	**0.019*****	0.0027								
ESMS	**0.0696*a**	**0.0225****	**0.0419*a**	**0.0511*a**	**0.0221****	0.0021							
WS	**0.0481*a**	0.0036	0.0227	0.0104	0.0098	-0.0092	**0.004****						
HA	**0.0351*****	-0.001	**0.0464****	0.0094	0.03	0.0099	0.0385	0.0226					
MB	**0.0695*a**	**0.051*a**	**0.0331*a**	**0.0539*a**	**0.0663*a**	**0.0388*a**	**0.0956*a**	**0.0554*a**	**0.0363*a**				
BM	**0.053*a**	**0.0119****	**0.0228*a**	**0.0619*a**	**0.0191*a**	**0.0038***	**0.0009***	**0.0179****	**0.0494*a**	**0.0736*a**			
SW	**0.0619*a**	0.0176	**0.0138*a**	**0.0173*a**	**0.0237*a**	**0.0132****	**0.0407*a**	**0.0156*****	**0.0289****	**0.0428*a**	**0.0465*a**		
WO	**0.0622*a**	**0.0375****	**0.0717*a**	**0.0736*a**	**0.0752*a**	**0.0431****	**0.1027*a**	**0.0871*a**	0.0554	**0.0777*a**	**0.0799****	**0.0969*a**	
MF	**0.0248*a**	-0.0017	**0.0191***	**0.0235****	**0.0099***	0.0057	**0.0325*a**	**0.017****	**0.0124****	**0.0628*a**	**0.0335****	0.0356	0.0422

P-values obtained after 19000 permutations p 0.05* (non adjusted), p 0.01** (non adjusted), p 0.001*** (non adjusted).
Indicative adjusted nominal level (5%) for multiple comparisons is 0.000263, p 5 % *a (Bonferroni adjusted).

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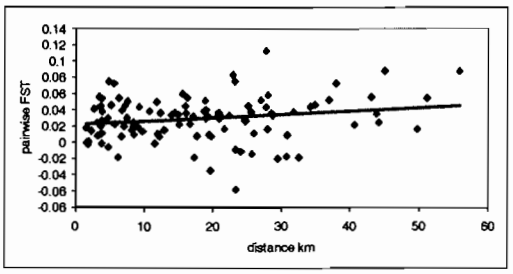
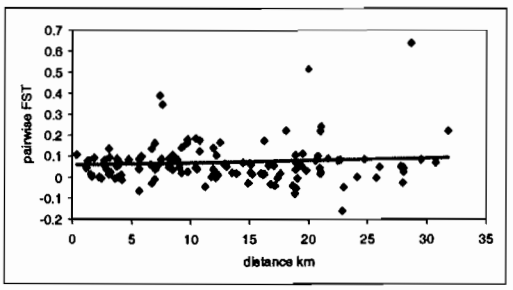
7.4.9 Results, Pairwise F_{ST} and Geographical distance



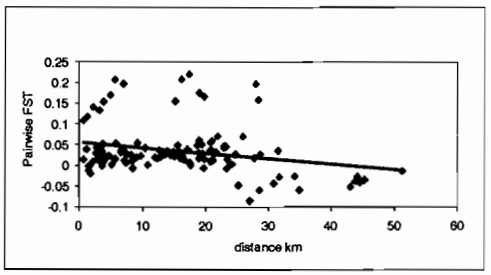
r_p 0.188
p 0.122

Figure 7.4.9.1 Pairwise F_{ST} and geographic distance between sites, July 1998



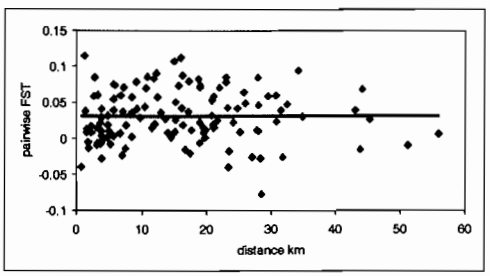
r_p 0.083
p 0.219

Figure 7.4.9.2 Pairwise F_{ST} and geographic distance between sites, September 1998



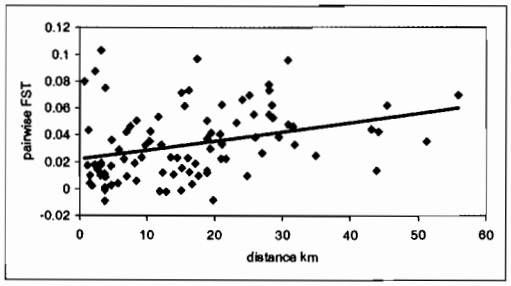
r_p –0.258
p 0.954

Figure 7.4.9.3 Pairwise F_{ST} and geographic distance between sites, July 1999



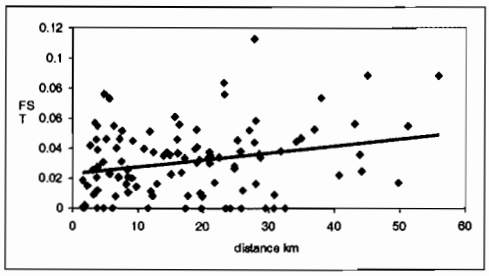
r_p –0.001
p 0.428

Figure 7.4.9.4 Pairwise F_{ST} and geographic distance between sites, September 1999



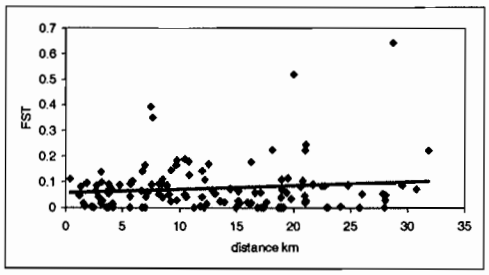
r_p 0.318
p 0.084

Figure 7.4.9.5 Pairwise F_{ST} and geographic distance between sites, October 2000



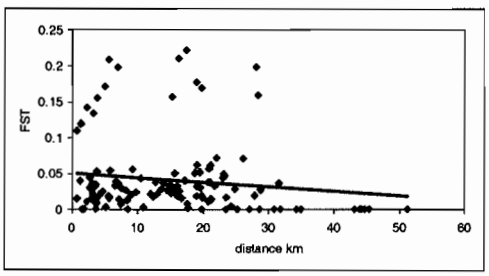
R_p 0.25
P 0.057

Figure 7.4.9.6 Pairwise F_{ST} and geographic distance between sites, July 1998, negative F_{ST} values set to zero



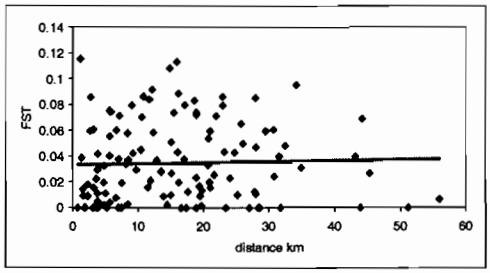
R_p 0.119
P 0.1527

Figure 7.4.9.7 Pairwise F_{ST} and geographic distance between sites, September 1998, negative F_{ST} values set to zero



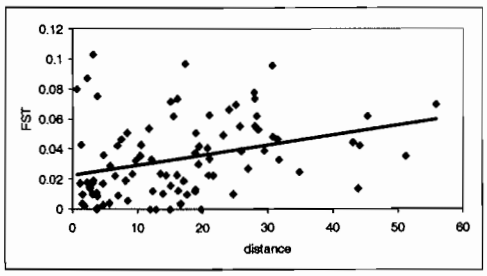
R_p –0.137
P 0.8669

Figure 7.4.9.8 Pairwise F_{ST} and geographic distance between sites, July 1999, negative F_{ST} values set to zero



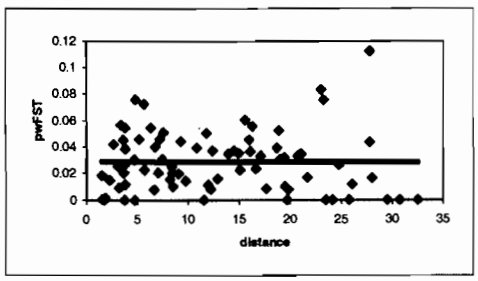
R_p 0.03
P 0.35

Figure 7.4.9.10 Pairwise F_{ST} and geographic distance between sites, September 1999, negative F_{ST} values set to zero



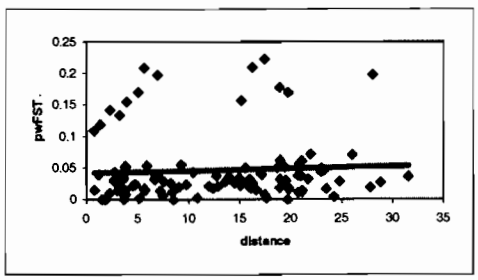
R_p 0.318
P 0.087

Figure 7.4.9.11 Pairwise F_{ST} and geographic distance between sites, October 2000, negative F_{ST} values set to zero



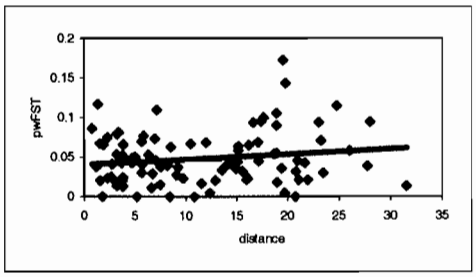
Rp –0.008
p0.5

Figure 7.4.9.12 Pairwise F_{ST} and geographic distance between sites, River Frome only, July 1998, negative F_{ST} values set to zero



Rp 0.54 p
0.237

Figure 7.4.9.13 Pairwise F_{ST} and geographic distance between sites, River Frome only, July 1999, negative F_{ST} values set to zero



Rp 0.157
p0.101

Figure 7.4.9.14 Pairwise F_{ST} and geographic distance between sites, River Frome only, July 2000, negative F_{ST} values set to zero

7.4.11 Results, Genetic differentiation and environmental differences between sites

site	WH	NF	LM	EB	ES	BM
NF	3					
LM	3	0				
EB	8	5	5			
ES	9	6	6	1		
BM	7	4	4	1	2	
WO	6	3	3	2	3	1

Figure 7.4.11.1 Differences in ODD between seven sites in July 2000

site	WH	NF	LM	EB	ES	BM
NF	2					
LM	4	6				
EB	3	5	1			
ES	5	3	9	8		
BM	2	4	2	1	7	
WO	0	2	4	3	5	2

Figure 7.4.11.2 Differences in ODD between seven sites in October 2000

	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	TW
GB	3											
NF	3	0										
LM	2	1	1									
EB	0	3	3	2								
ES	0	3	3	2	0							
ESMS	2	1	1	0	2	2						
WS	3	0	0	1	3	3	1					
HA	2	1	1	0	2	2	0	1				
MB	2	1	1	0	2	2	0	1	0			
BM	4	1	1	1	4	4	2	1	2	2		
TW	5	2	2	2	5	5	3	2	3	3	1	
MF	2	1	1	1	2	2	0	1	0	0	2	3

Figure 7.4.11.3 Differences in flow rate category between 13 sites, July 1998

site	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	TW	SW	WO
NF	0												
LM	1	1											
EB	3	3	2										
ES	3	3	2	0									
ESMS	1	1	0	2	2								
WS	0	0	1	3	3	1							
HA	1	1	0	2	2	0	1						
MB	1	1	0	2	2	0	1	0					
BM	1	1	1	4	4	2	1	2	2				
TW	2	2	2	5	5	3	2	3	3	1			
SW	2	2	2	5	5	3	2	3	3	1	0		
WO	2	2	2	5	5	3	2	3	3	1	0	0	
MF	1	1	1	2	2	0	1	0	0	2	3	3	3

Figure 7.4.11.4 Differences in flow rate category between 14 sites, September 1998

Site	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	BM	TW	SW	WO
GB	3												
NF	3	0											
LM	2	1	1										
EB	0	3	3	2									
ES	0	3	3	2	0								
ESMS	2	1	1	0	2	2							
WS	3	0	0	1	3	3	1						
HA	2	1	1	0	2	2	0	1					
BM	4	1	1	1	4	4	2	1	2				
TW	5	2	2	2	5	5	3	2	3	1			
SW	5	2	2	2	5	5	3	2	3	1	0		
WO	5	2	2	2	5	5	3	2	3	1	0	0	
MF	2	1	1	1	2	2	0	1	0	2	3	3	3

Figure 7.4.11.5 Differences in flow rate category between 14 sites, July 1999

site	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	TW	SW	WO
GB	3													
NF	3	0												
LM	2	1	1											
EB	0	3	3	2										
ES	0	3	3	2	0									
ESMS	2	1	1	0	2	2								
WS	3	0	0	1	3	3	1							
HA	2	1	1	0	2	2	0	1						
MB	2	1	1	0	2	2	0	1	0					
BM	4	1	1	1	4	4	2	1	2	2				
TW	5	2	2	2	5	5	3	2	3	3	1			
SW	5	2	2	2	5	5	3	2	3	3	1	0		
WO	5	2	2	2	5	5	3	2	3	3	1	0	0	
MF	2	1	1	1	2	2	0	1	0	0	2	3	3	3

Figure 7.4.11.6 Differences in flow rate category between 15 sites, September 1999

site	WH	GB	NF	LM	EB	ES	ESMS	WS	HA	BM	SW	WO	MF
GB	3												
NF	3	0											
LM	2	1	1										
EB	0	3	3	2									
ES	0	3	3	2	0								
ESMS	2	1	1	0	2	2							
WS	3	0	0	1	3	3	1						
HA	2	1	1	0	2	2	0	1					
BM	4	1	1	2	4	4	2	1	2				
SW	5	2	2	3	5	5	3	2	3	1			
WO	5	2	2	3	5	5	3	2	3	1	0		
MF	2	1	1	0	2	2	0	1	0	2	3	3	
TW	5	2	2	3	5	5	3	2	3	0	0	0	3

Figure 7.4.11.7 Differences in flow rate category between 14 sites, July 2000

site	GB	NF	LM	EB	ES	ESMS	WS	HA	MB	BM	SW	WO
NF	0											
LM	1	1										
EB	3	3	2									
ES	3	3	2	0								
ESMS	2	2	0	2	2							
WS	0	0	1	3	3	1						
HA	1	1	0	2	2	0	1					
MB	1	1	0	2	2	0	1	0				
BM	1	1	2	4	4	2	1	2	2			
SW	2	2	3	3	3	3	2	3	3	1		
WO	2	2	3	3	3	3	2	3	3	1	0	
MF	1	1	0	1	1	0	1	2	0	2	3	3

Figure 7.4.11.8 Differences in flow rate category between 13 sites, October 2000

7.4.13 Results Long term genetic variability

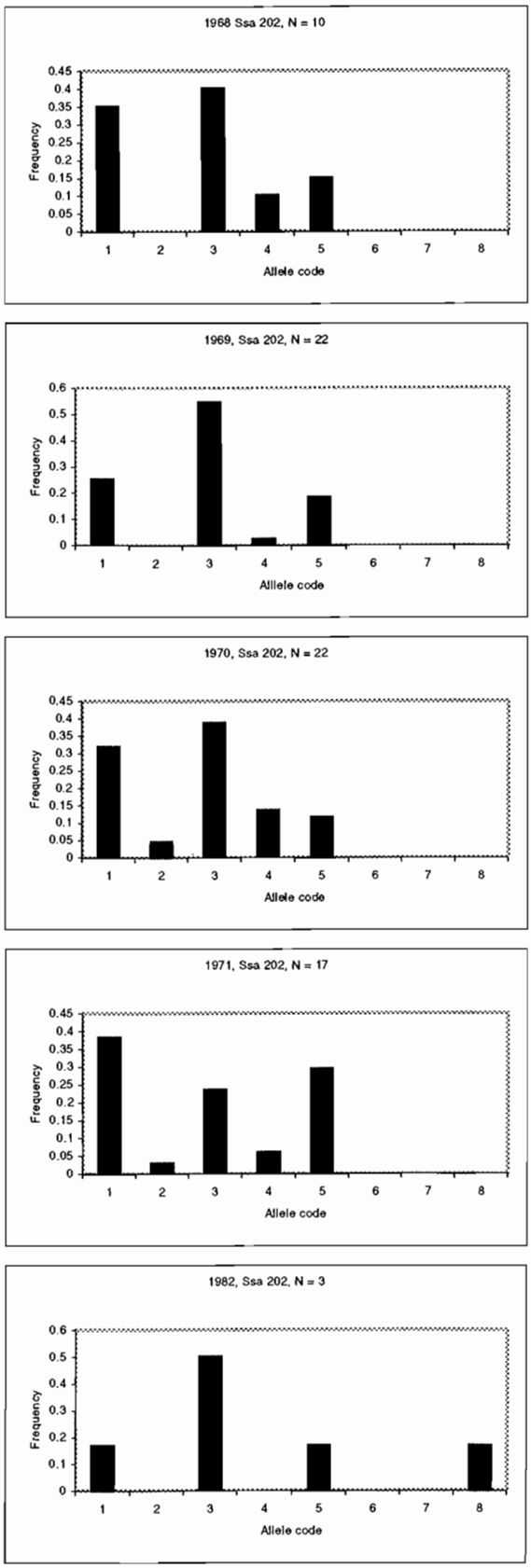


Figure 7.4.13.1 Allele frequency at locus Ssa 202, cohort years 1968-1971 and 1982 to 1995

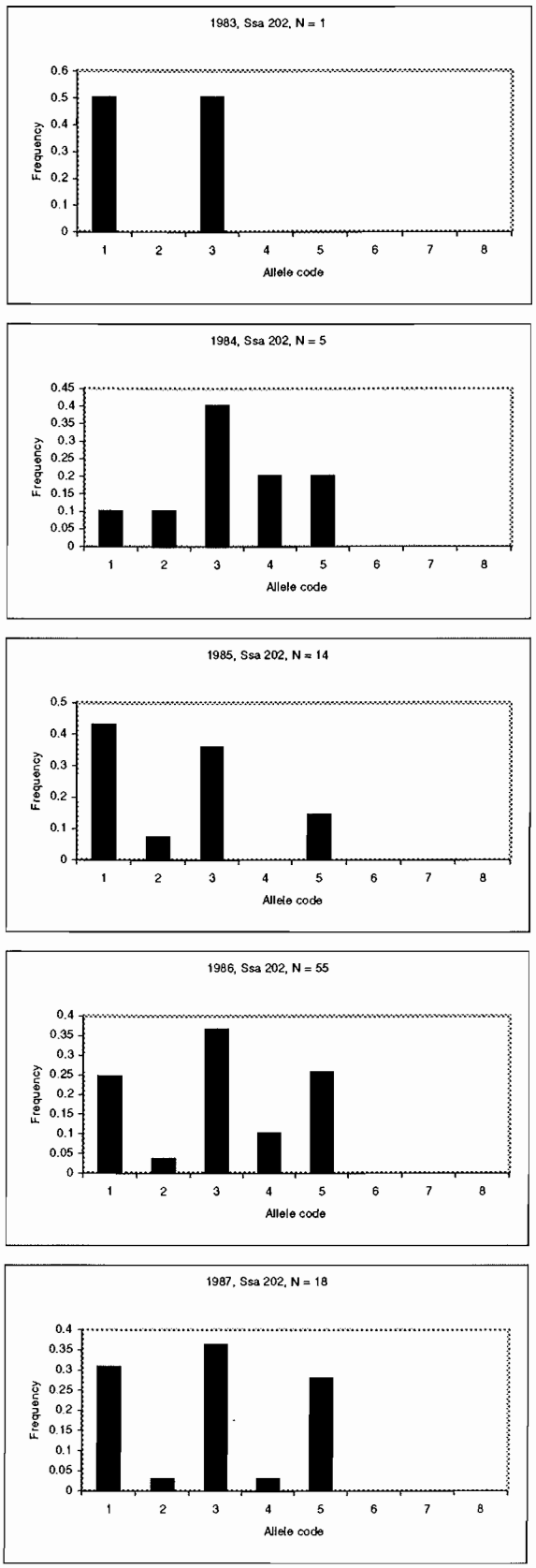
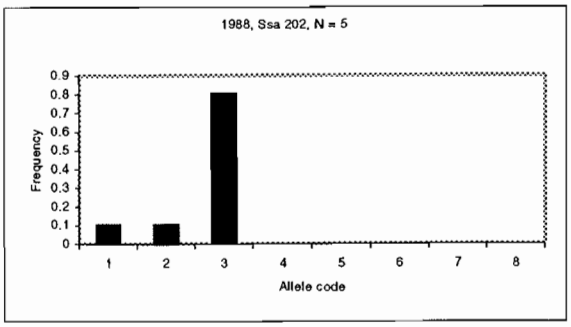
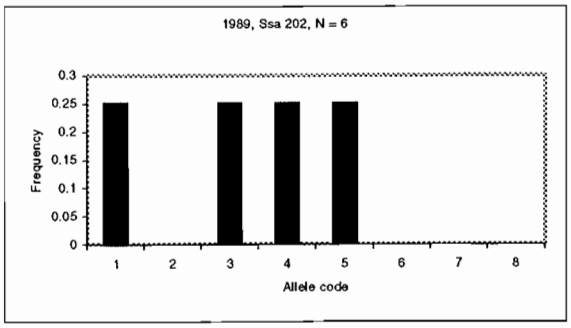
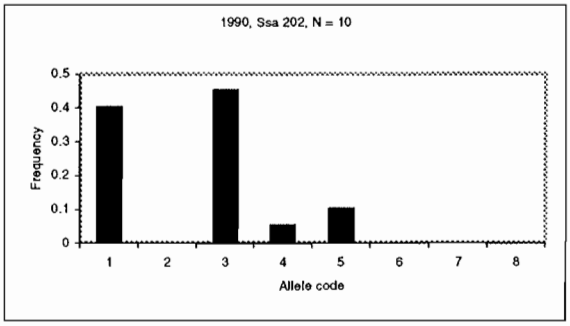
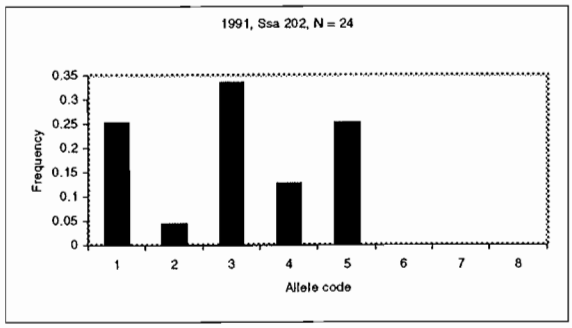


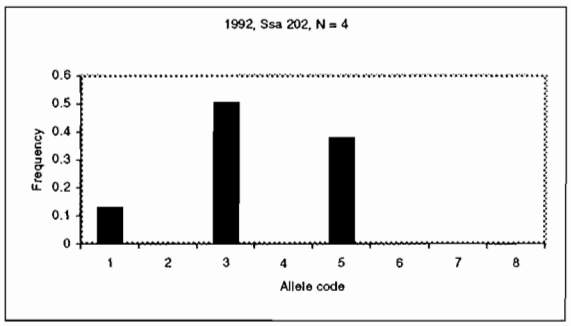
Figure 7.4.13.1 (Continued)

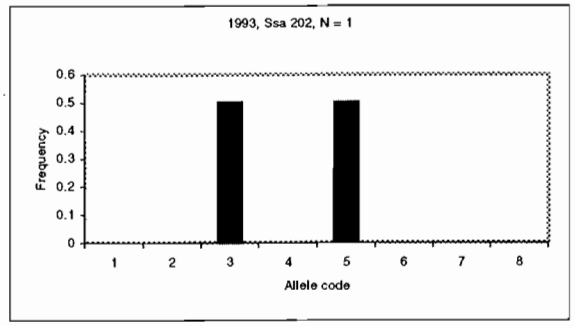


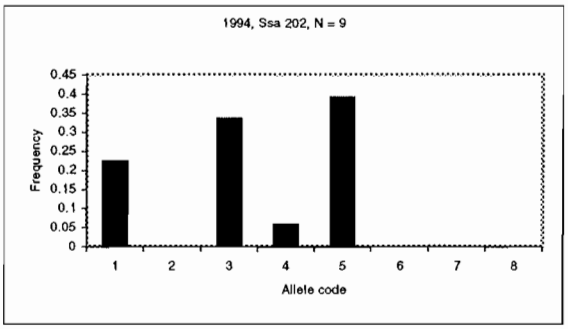


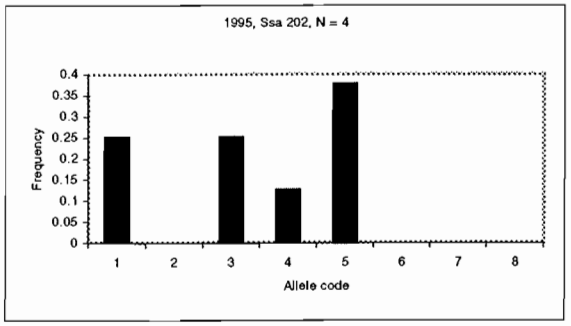












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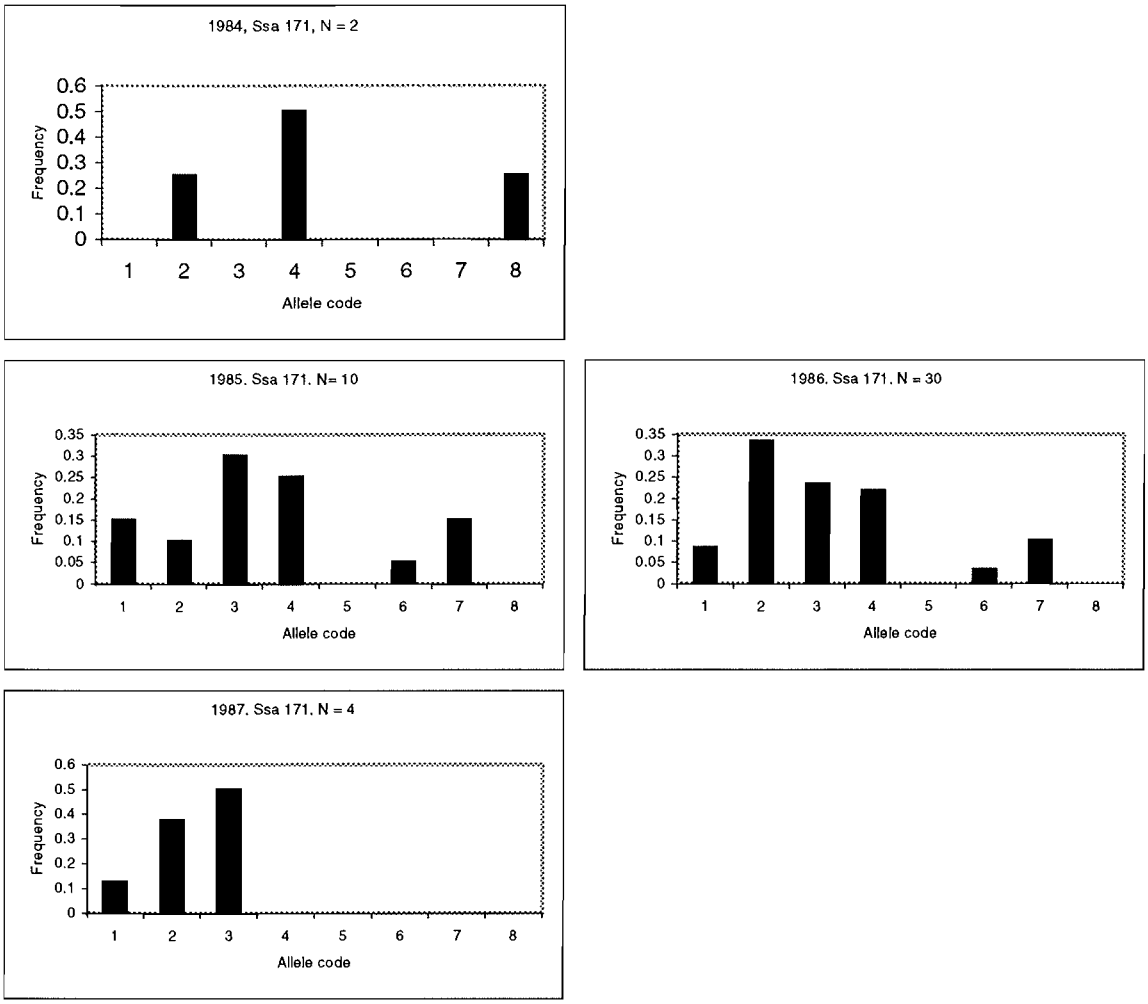
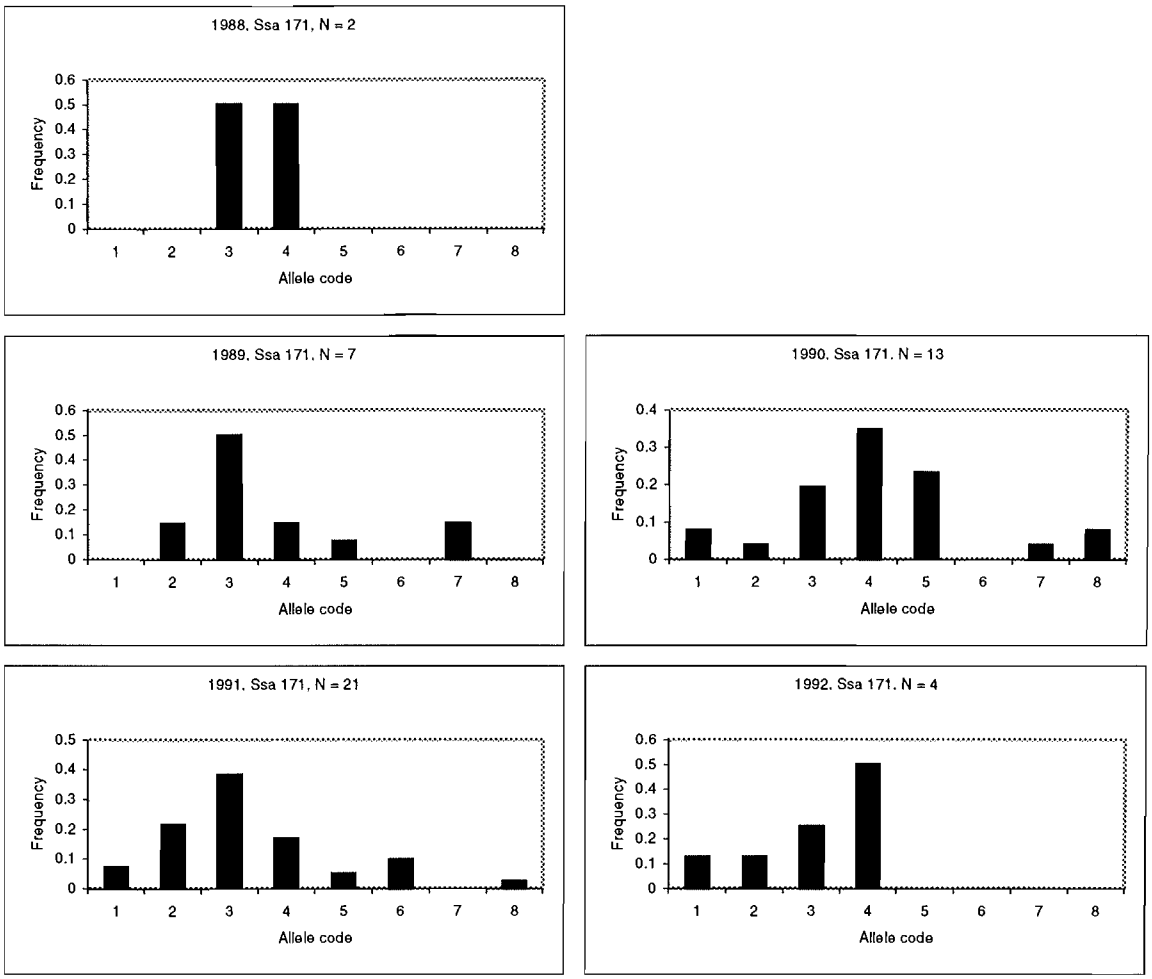


Figure 7.4.13.2 Allele frequency at locus Ssa 171, cohort years 1984 - 1995



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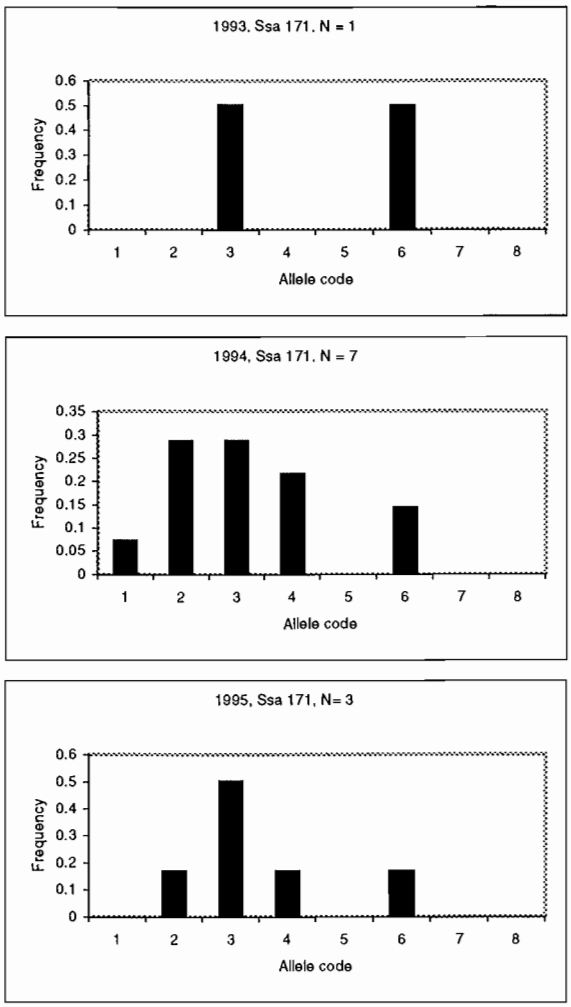

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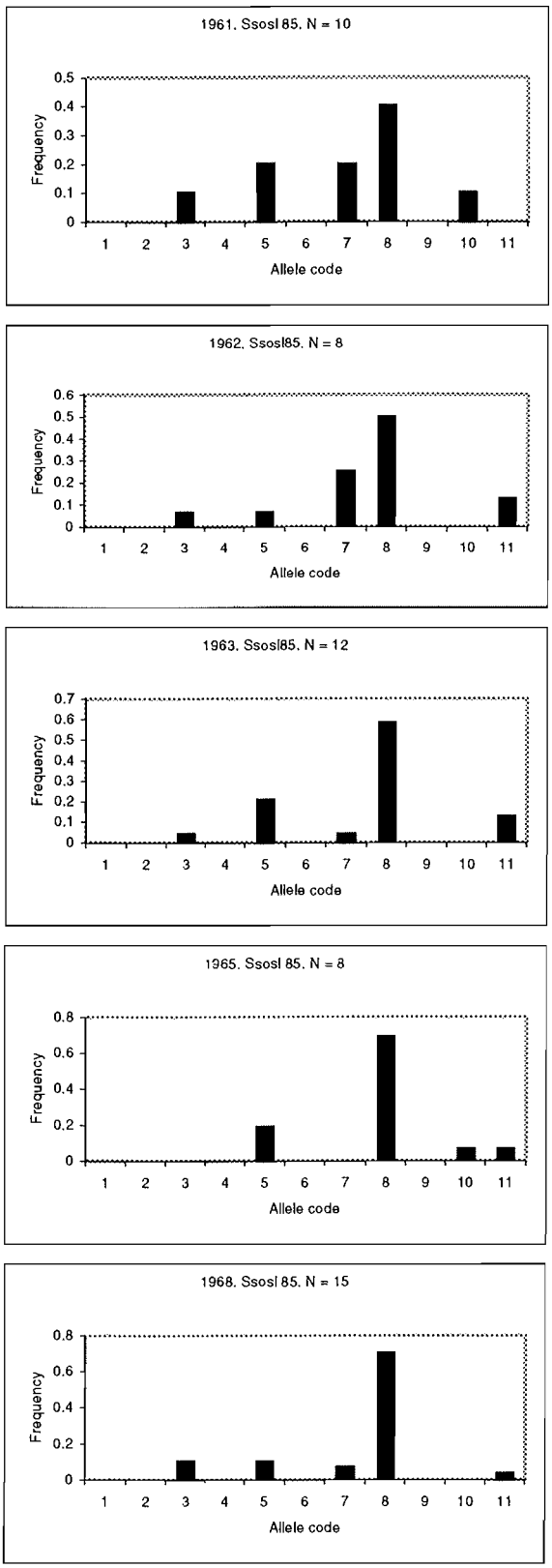
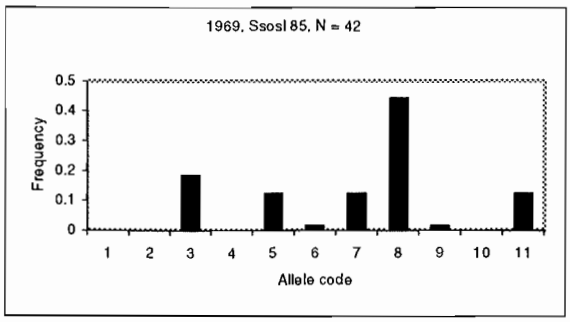
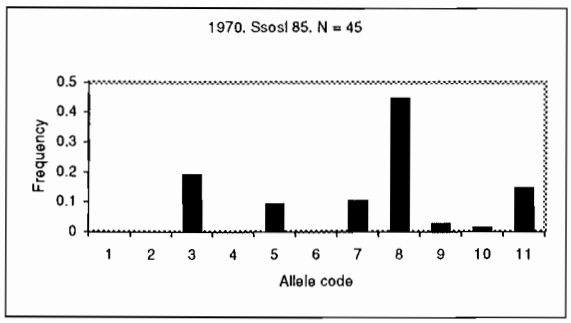
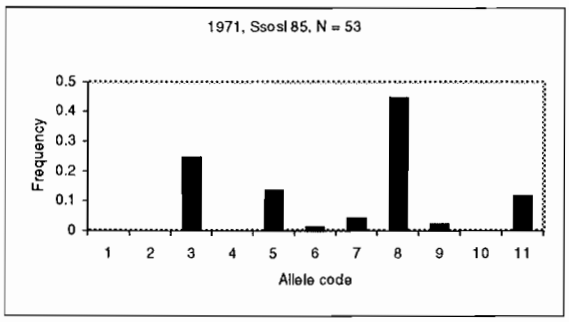
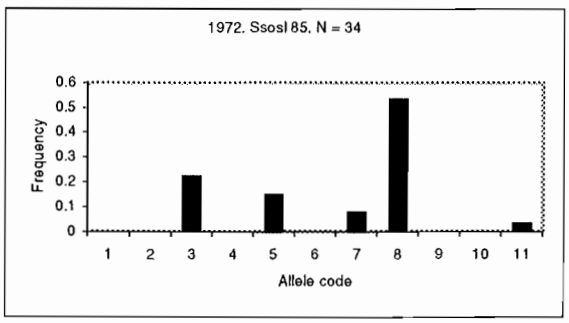


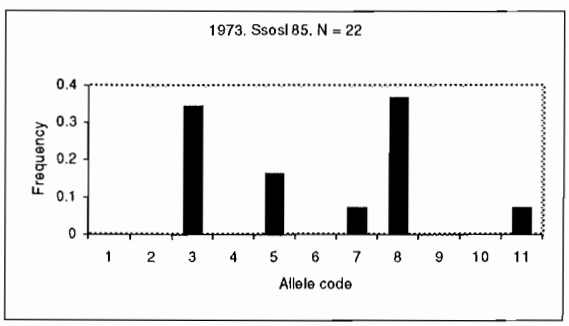
Figure 7.4.13.3 Allele frequency at locus Ssosl 85, cohort years 1961-1963, 1985, 1968-1975 and 1982-1995











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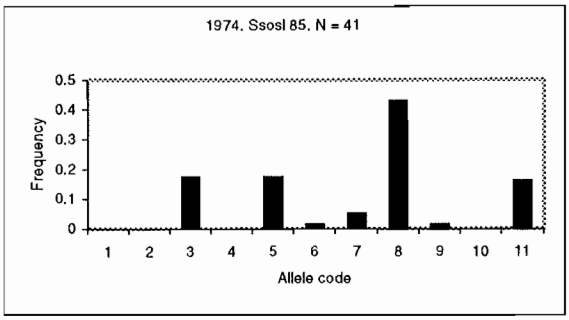

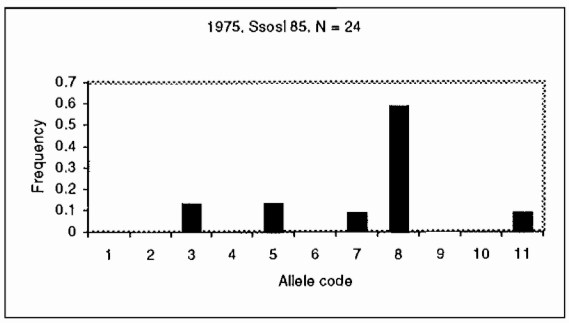

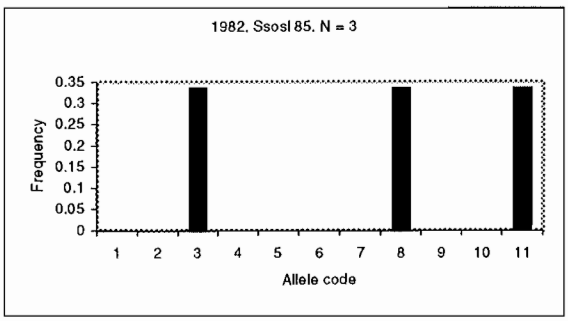

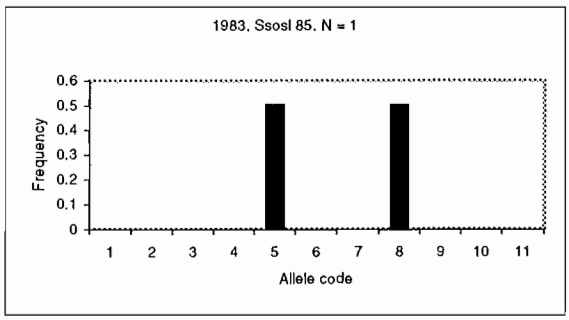

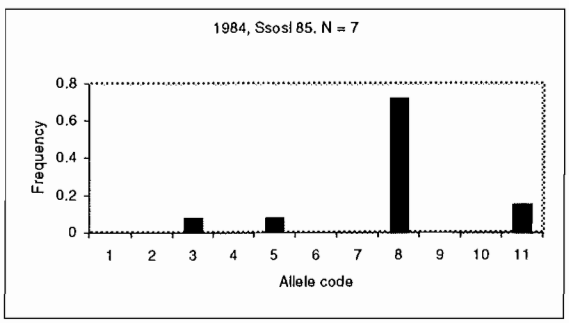

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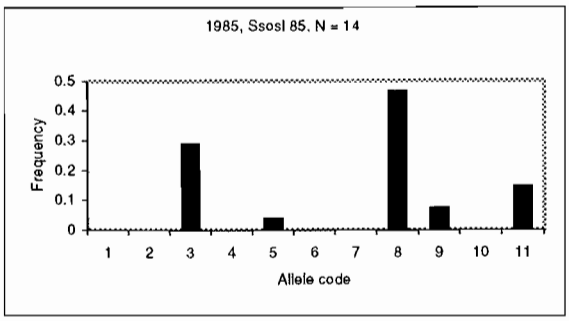

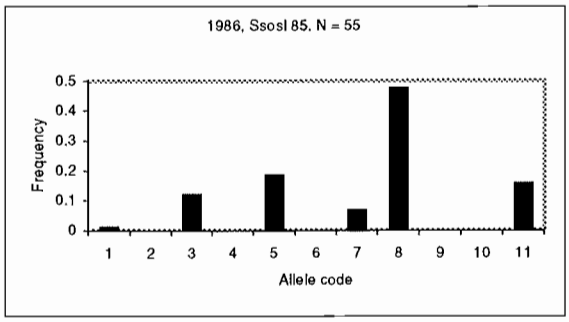

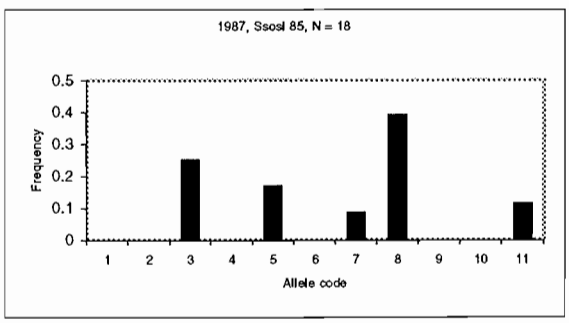

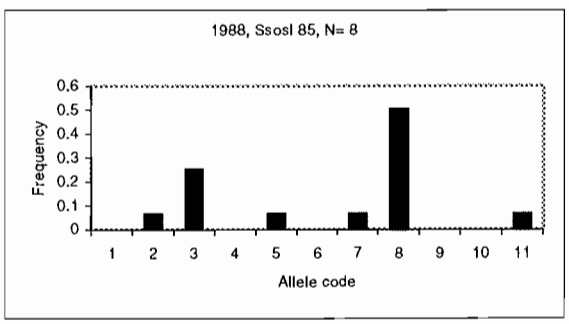

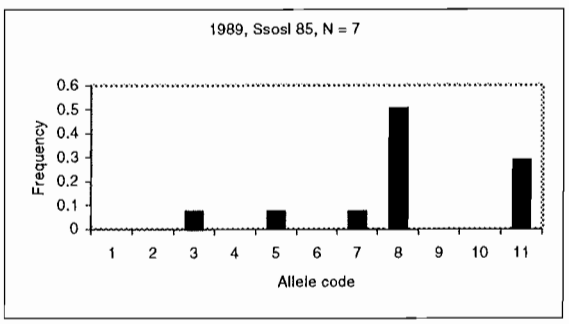

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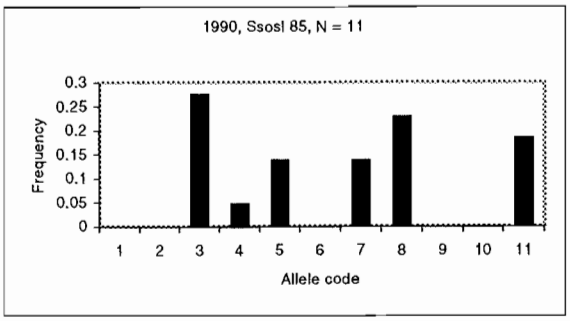

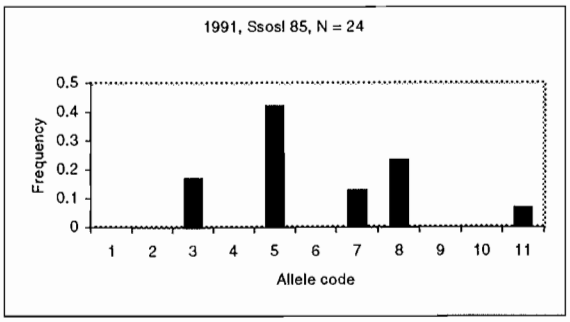

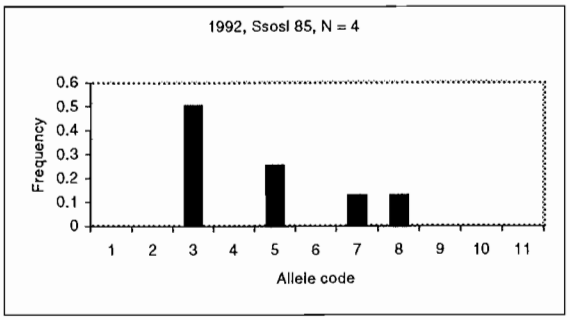

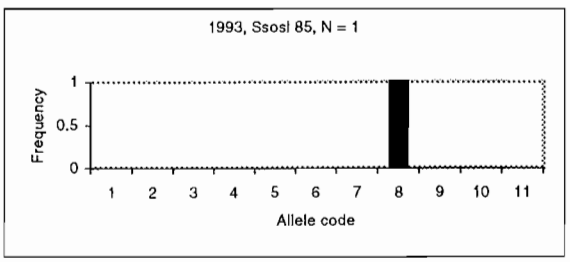

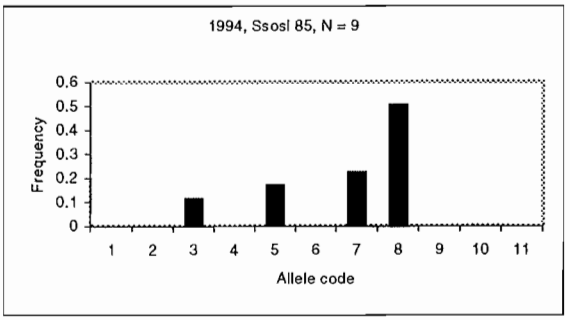

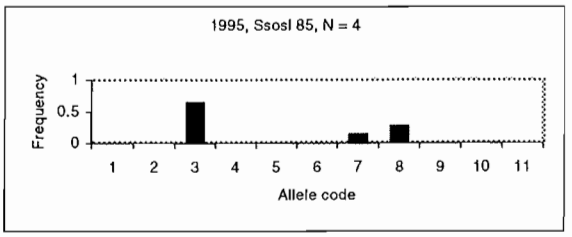

Figure 7.4.13.3 (Continued)

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