Fernandes, Wendy P.A.; Copp, Gordon H.; Riley, William D.. 2016. **Autumn microhabitat breadth differs between family groups of Atlantic salmon parr (Salmo salar) in a small chalk stream.** *Ecology of Freshwater Fish*, 25 (1). 38-47. 10.1111/eff.12189

Autumn microhabitat breadth differs between family groups of Atlantic salmon parr (*Salmo salar*) in a small chalk stream

Wendy P. A. Fernandes[1,2,3], Gordon H. Copp[2,4,5] William D. Riley[2]

[1]Cardiff University, School of Biosciences, Main Building, Museum Avenue, Cardiff, Wales CF10 3LT, UK.

[2]Salmon & Freshwater Team, Centre for Environment Fisheries & Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 0HT, U.K.

[3]Centre for Ecology & Hydrology, Wallingford, Oxford DT2 8ZD, U.K.

[4]Centre for Conservation Ecology & Environmental Science, Bournemouth University, Poole, Dorset, U.K.

[5]Environmental & Life Sciences Graduate Program, Trent University, Peterborough, ON Canada

Correspondence: W. P. A. Fernandes, Cardiff University, School of Biosciences, Main Building, Museum Avenue, Cardiff, Wales CF10 3LT, UK. Email: w.fernandes@live.co.uk

Abstract - The effect of family traits on the microhabitat use by six genetically-distinct groups (three in each year of study) of juvenile Atlantic salmon tagged with passive integrated transponder (PIT) tags was studied via PIT-tag detectors installed on the river bed in a small chalk stream of southern England during Autumn in 2006 and 2007. Canonical correspondence analysis of the molecular and microhabitat data revealed considerable overlap in the microhabitat use of the family groups and notable differences in microhabitat breadth, which was partly influenced by sample size. The data suggest that microhabitat breadth and preferences of wild salmon are influenced by family of origin.

Key words: genotype, adaptive traits, microhabitat use, kinship, family traits.

Introduction

Atlantic salmon *Salmo salar* (L.) have distinct habitat requirements in the wild (Klemetsen et al. 2003). Juvenile Atlantic salmon become highly territorial during the parr stage and growth rates and size distributions are strongly influenced by habitat availability (Armstrong 2010). Modelling studies have demonstrated that parr establish a territory that provides the best balance between energy gain and energy crucial for metabolism, growth and reproduction (Fausch 1984) with a preference shown towards large cobbled areas (Beland et al. 2004). In-stream macrophytes, ligneous debris and marginal bank-side vegetation are also important refuges from predators especially for juveniles (Armstrong et al. 2003; Riley et al. 2006). However, only a small proportion (2–20%) of stream bed microhabitats has suitable characteristics for salmonid territories (Allen 1969), and the loss of suitable habitat is considered a major reason for the decline in stocks of wild Atlantic salmon (Hendry et al. 2003).

Adaptive traits (genotype) play an important role in habitat use, and interactions between genotype and environment lead to localised adaptations (Kaweki & Ebert 2004). Exploitation of optimal microhabitats, i.e. those to which the individual is best suited, will help optimize fitness gains (Kawecki & Ebert 2004), suggesting that microhabitat choices are genetically pre-disposed. It is therefore possible, though as yet unproven, that fish from different parentage will specialise through different microhabitat usage (McLaughlin 1999), and thus family groups are expected to exhibit similar microhabitat preferences.

The aim of the present study was to test the hypothesis that different family groups will differ in the breadth and character of their microhabitat use, each family group exhibiting a distinct microhabitat profile (*i.e.* preferences/avoidances with respect to environmental variables). Microhabitat investigations were carried out on the River Cerne, (River Frome catchment, Dorset), one of the most intensely studied chalk rivers in southern England (*e.g*. Beaumont et al. 1986; Edwards et al. 2009; Hilton et al. 2001; Ibbotson et al. 2004; Welton et al. 1999, 2002), with the specific objectives to: 1) assess the habitat use of tagged salmon parr according to family group; 2) compare the breadth of microhabitat use by family group; and 3) test for differences in microhabitat use profiles amongst family groups.

Materials and Methods

Experimental Set Up

Juvenile salmon were reared from known parents (eggs of one female fertilised with the milt of one male) caught in the River Frome just prior to spawning, anaesthetised (2-phenoxyethanol) and stripped as per Edwards (1978), to create six distinct full-sibling family groups in each of two years (hence, 12 family groups). Adipose tissue samples from the parents were stored in 100% ethanol at 4°C for genetic analysis. Each batch of fertilised eggs (family groups) was placed into stream-side incubators (as per Government of Canada, 1980), one incubator per family group, situated at Watergates Hatchery (Dorchester, Dorset, U.K.) at the source of the Tadnoll Brook, a tributary of the River Frome.

While the salmon emerged from the gravel as fry, baseline weight and fork length (FL) measurements were recorded. Of the 12 distinct family groups created over two years (six family groups in 2006 and six family groups in 2007), three family groups of juvenile Atlantic salmon of similar length (24.8–27.2 mm FL), weight (0.126–0.177 g) and emergence time were chosen to be used in each year, thus providing fish of comparable size and life histories. Within 24 hours of emergence from each incubator, juveniles were stocked in a 1.5 km stretch of the River Cerne during 3 to 9 April 2006 and from 21 March to 9 April 2007. This stream section has not been subjected to management measures, thus providing fish with an undisturbed stream stretch with natural bank-side and in-stream vegetation. Other fishes and lampreys present in the experimental stretch of river included trout *Salmo trutta* (L.), European grayling *Thymallus thymallus* (L.), northern pike *Esox lucius* (L.), European minnow *Phoxinus phoxinus* (L.), European bullhead *Cottus gobio* (L.), stone loach *Barbatula barbatula* (L.), European eel *Anguilla Anguilla* (L.), brook lamprey *Lampetra planeri* (B.) and river lamprey *Lampetra fluviatilis* (L.). Although the River Cerne is suitable for juvenile salmon, barriers to migration prevent adult salmon ascending the river so there was no resident salmon parr population at the time of the experiments

In April 2006, six sites on the river were designated as full-sibling sites and fry from each full-sibling group were released into two sites. An additional six sites were designated as mixed-sibling sites. The full- and mixed-sibling sites were alternated along the river to prevent stream altitude from influencing the results (Fig. 1A). Stream sites were 30 m in length, on average 4 m wide and were separated from one other by 100 m, a distance based on models of existing data (Crisp, 1995)

which show that dispersal distance of most newly hatched salmon is < 20 m downstream. In 2007, to further ensure the genetic integrity of stocked areas, all full-sibling sites were situated upstream from mixed-siblings sites (Fig. 1B) and the distance between stocked sites was increased to 250 m. To utilise the river to its full capacity in the second year of the experiment, the length of full-sibling and mixed-sibling sites was increased to 50 m and 150 m respectively. Initial stocking density in 2006 and 2007 was approximately 2.7 and 4.1 fish m^{-2} respectively. (see Fernandes et al. In press for further details)

After stocking, the fish were given time to establish territories and grow before the sites were sampled by electric fishing, at which time all juvenile salmon caught (parr stage) were tagged with passive integrated transponder (PIT) tags as per Riley et al. (2003) to enable repeated individual identification and the recording of small and large scale movements. Tagging took place during 8–22 August 2006 and 26 July 2007 – 08 August 2007. At the time of tagging in 2006, mean fish FL was 9.45 cm ± (SE) 0.65 cm and mean wet weight 10.48 g ± 0.23 g. In 2007, mean FL was 8.61cm ± 0.06cm and mean wet weight 8.07 g ± 0.17g. The tagged fish (n = 243) differed significantly in FL (Students' t-test: $t_{205} = 9.77$, $P < 0.001$) and wet weight ($t_{205} = 8.63$, $P < 0.001$) between years, however habitat use analysis did not overlap between years. A tissue sample (adipose fin clip) was also taken at the time of tagging (and stored in 100% ethanol) for subsequent genetic analyses to enable family group assignment of juveniles to their parents. Fish were released back to their location of capture following recovery from anaesthesia.

To determine the microhabitat use of each family group, two portable PIT multi-point decoder (MPD) units (Riley et al. 2003) were installed at one single-family and one mixed-family stocked area simultaneously. This was called a 'replicate'. Each MPD unit consisted of 16 flat, plate-shaped antenna discs and PIT tags were detectable when ≤9 cm above each antenna (Riley et al. 2003). Each antenna takes a reading at ≈ 3.2 s intervals and each reading may be considered as a 'point sample' (i.e. the fixed occurrence of an individual fish in time and space). As such, the antenna location constitutes a sampling point (c.f. Riley et al. 2003), *i.e*. a 'point sample' as defined in point abundance sampling for fish microhabitat studies (for a review, see Copp 2010).

In each replicate configuration, the first antenna of each line was placed as close to the river bank as possible (in this case, the left bank) so that bank cover (if present) could also be included as a variable in the data analysis (Fig. 1C). Each antenna was covered with the substrata from the immediate surroundings. The antennae were not visible above the water. Gap size between each antenna within a line (60 cm in 2006 and 30 cm in 2007) was determined from the width of the river sections where the MPD units were installed. In both years, the gap between each line of antennae was 5 m so that as much as possible of each river section was covered within the constraints of the antenna cable lengths (< 10 m). The MPD antenna configuration covered a total area of 6600 m^2 in 2006 and 4500 m^2 in 2007.

The MPD units were moved and installed in the designated sites to generate data for each replicate. In 2006, one entire single-family site and one entire mixed-family site formed the basis of one replicate. In 2007, owing to larger stocked sites, five areas within the single-family sites, and five areas within the mixed-family sites formed the basis of five replicates. Therefore, the MPDs generated data for six replicates carried out over the two-year period. Data collected on the day of installation, and on removal of MPD antennae, were discarded in order to avoid bias due to fish movements in response to disturbance. MPD-generated data was included for four entire days in each of six replicates: i) 5–8 September 2006; ii) 17–20 August 2007; iii) 25–28 August 2007; iv) 4–7 September 2007; v) 12–15 September 2007; vi) 17–20 September 2007.

[FIGURE 1A-C]

Detections of individual PIT tagged fish, including re-occurrences, over the 32 MPD disc antennae (*i.e.* at the same microhabitat) at the two sites over four-day periods were collated into a fish data matrix (192 samples [i.e. antenna records] as rows × 57 tagged fish as columns), which included those antenna (samples) at which no fish detections were recorded. Owing to the large number of detections (of a new fish, or of a fish moving between antennae), the MPD output data were $\log_{10}$ transformed to produce a more even distribution for ease of interpretation.

Microhabitat Data Analysis

At each MPD disc during installation, available microhabitat within a 10 cm radius from the edge of the disc was measured either quantitatively (depth in cm, water velocity in m s^{-1}) or as a proportion (%) of the area: weed cover, bank cover, and three substratum types (as per Copp et al. 1994), i.e. gravel (0.2–5.0 cm), sand (< 0.06–0.2 cm), and silt (< 0.06 cm) (Table 1). Substrata > 5.0 cm were seldom found where antenna were placed and therefore were not included in our analysis. Owing to the limited discharge variability of chalk streams, available microhabitat was assumed to remain constant during each four-day sampling period (e.g. Copp et al. 2005). Comparisons between single-family and mixed-family sites were undertaken using one-way analysis of variance (ANOVA) for water depth and velocity and the Mann-Whitney *U*-test for the other variables.

[TABLE 1]

In preparation for multivariate analysis, the microhabitat data were collated into a data matrix (192 point samples × 7 microhabitat variables) and then converted to semi-quantitative categories, based on the frequency distributions of the variables (as per Copp et al. 1994). Patterns in the microhabitat use of family groups were examined using canonical correspondence analysis (CCA; ter Braak (1986). In CCA, the microhabitat variables were combined into the artificial gradients that best distinguish and separate 'microhabitat breadth', which is only one component of 'niche' (see Copp 2008). The best synthetic gradients, i.e. those that maximise separation of the tagged fish, were selected from the graphical representation of the corresponding eigen values (Persat & Chessel 1989; Mercier et al. 1992) as described in Copp (1990). From the CCA outputs, 'triplots' were generated (*sensu* ter Braak 1986), combining the ordinations for vectors of the microhabitat variables, of the samples coded according to the trial in which they appeared (a = single-family, b = mixed-family. Microhabitat breadth of family groups from the 57 PIT-tagged salmon parr was assessed using ellipses that represent the 90% confidence intervals (Green 1971), whereby the ellipses were plotted on an equal ordination scale (*i.e.* eight units) and the surface areas (in cm^2) of the ellipses were calculated using

MacDraft P.E. v5.5.8 to determine a proxy of mean microhabitat breadth and deviations thereof for each family group.

The distance between the points for each tagged fish (coded by ‘a’ and ‘b’, as above) approximates to their similarity/dissimilarity in terms of appearance in the sampling record, as determined by chi-square distances. The total number of occurrences of tagged fish at each sample (i.e. MPD antenna) was calculated for each family. These figures were converted to $\log_{10}+1$ to reduce skewness, and the matrix cross-tabulated with that of the variables to calculate electivity indices, which were defined as the difference between the frequency of occurrence at sample sites with a specific microhabitat variable and the frequency of that family across all samples (Copp 1992): negative values approaching –0.5 indicate avoidance, whereas positive values approaching +0.5 indicate preference.

Differences in the resulting microhabitat profiles (i.e. 28 electivity indices per family) were tested using the Wilcoxon pair-comparison test. Deviations from expected occurrence of families and microhabitat categories were tested using the Fisher Exact test. The multivariate analyses were undertaken using programmes of the ADE software library (Thioulouse et al. 1997; Chessel & Thioulouse 1998) and the microhabitat profile graphs generated using GraphMu (Thioulouse 1990).

Molecular Analyses

To assign juveniles to their parents, and therefore determine to which family groups they belonged, genomic DNA was extracted (Qiagen tissue DNA extraction kit; catalogue no. 69506) from parental and juvenile fin tissue using the manufacturer's protocol for extracting DNA from animal tissue. DNA yield was quantified on a 1% agarose gel and visualised on a UV transilluminator. Nine microsatellite loci were used in the assignment of parentage, chosen on the basis of their reliability in the use of parentage assignment based on their use in previous salmon genetic studies (Sanchez et al. 1996; McConnell et al. 1995; O’Reilly et al. 1998) and their distinct allelic size range (see Fernandes et al. In press for further details of molecular methods).

The program CERVUS v3 (Marshall 2007) was used to assign each MPD detected parr (n = 57) to their original parental pairs. CERVUS uses an inclusionary approach, which compares the candidate parents’ genotypes with the offspring’s and assesses the relative likelihood (logarithm of

odds) at each offspring's genotype having been inherited from all possible parents. The parent with the highest LOD score is usually assigned as the true parent if its likelihood is significantly higher than the next most likely parent. The mean proportion of sampled candidate mothers and fathers was 100% (six mothers and six fathers: three parent pairs in 2006 and three different parent pairs in 2007). The error rate in likelihood calculations was assumed at 1%.

Results

The number of detections ($\log_{10}$ transformed) did not differ significantly (Kruskal-Wallis test, P = 0.787) between the days (n = 4) of the MPD installation in each replicate site (n = 12), suggesting there was no bias due to possible changes in behaviour following MPD installation. Analysis of microhabitat variables recorded at each MPD disc showed that substratum variables and bank cover did not differ significantly (Mann-Whitney U test, P = 0.25) between single-family and mixed-family sites, however there was a significant difference (ANOVA) in depth ($F_{1, 4088.521}$ = 29.441, P = 0.001) and velocity ($F_{1, 0.294}$ = 5.748, P = 0.003), with mixed-family sites being shallower and faster flowing. Fish from all family groups were detected by the PIT MPD units. Family 4 was the most abundant family group (n = 28), followed by Family 3 (n = 9), and Family 6 (n = 9), Family 2 (n = 5), Family 1 (n = 4), and Family 5 (n = 2). Fish from different family groups were detected in a range of microhabitats (Table 2).

[TABLE 2]

With regard to microhabitat breadth, graphical representation of the CCA eigen values (Fig. 2A–Ca) revealed a break in slope after the third eigen value, indicating that these first three factors (i.e. dimensions) account for the majority of variation in the dataset (Persat & Chessel 1989; Copp 1990; ter Braak & Verdonschot 1995): CA1 for the proportions of gravel, weed cover and bank cover, and to a less extent sand (Fig. 2A-Cb); CA2 for water depth; CA3 for the proportion of sand in the substratum (Fig. 2A-Cc). The CCA triplot revealed considerable overlap in the microhabitat breadth of all family groups (Fig. 2A-Cb and 2A-Cc for CA1 × CA2 and CA1 × CA3, respectively), where mean microhabitat breadth was 46.29 cm^2. The family with the largest microhabitat breadth, and

therefore the greatest positive deviation from the mean, was Family 3 (mean / deviation from mean = 90.1096 cm^2 / 43.8196 cm^2). This was followed by Family 6 (70.0379 / 23.7479 cm^2) and Family 1 (60.4042 / 14.1172 cm^2). The family with the smallest microhabitat breadth, and thus the greatest negative deviation from the mean, was Family 5 (0.0025 / -46.2875 cm^2), followed by Family 2 (15.4613 / -30.8287 cm^2) and Family 4 (41.7232 / -4.5668 cm^2) (Fig. 2A-C).

The microhabitat profiles (Fig. 2A-Cd) were similar for all family combinations except for Family 4, which differed significantly (Wilcoxon's test, $P \leq 0.05$) from families 1, 3 and 6 (Family 5 was excluded from the analysis due to low sample number; $n = 2$). This difference appears to result from the significant ($P < 0.05$) preference in Family 4 for intermediate water depths and velocities as well as the significant ($P < 0.05$) avoidance of any bank cover – the only such significant deviation from expected for this variable. Family 1 microhabitat use did not deviate significantly (Fisher exact test) from the expected frequencies of occurrence except with regard to depth ($P < 0.05$), revealing a preference for deeper waters. Microhabitat use by families 2, 5 and 6 did not deviate from expected, though Family 2 demonstrated a non-significant preference for moderate proportions of weed cover. Family 3 demonstrated significant deviations from expected frequencies with regard to water depth and velocity, and were frequently found in deeper waters of moderately-elevated water velocities (0.21–0.4 m s^{-1}; see Table 2).

[FIGURE 2A-C]

Discussion

Fish from different parentage have been suggested to exploit different microhabitats (McLaughlin 1999), and this was apparent in the significant preferences and avoidances for microhabitat variables (Fig. 2A-Cd) in three family groups of the present study despite considerable overlap in the microhabitat breadth of those families (Fig. 2A-Cb-c). Considerable variation among fish (i.e. wide microhabitat breadth) was evident in most families of the present study.

Preference and avoidance of different habitat types are behaviours that are particularly favoured in the wild, where genetically diverse populations reside. Although the significance of preference and

avoidance from the present study are partly influenced by sample size, and will certainly be influenced by availability of habitat, there is a strong suggestion of a genetic basis for the preference and avoidance of habitat types among the fish in the present study, with different family groups specialising in different microhabitats.

Juvenile Atlantic salmon prefer coarse substrates (> 64 mm) because it provides shelter from high velocities, however in chalk streams where substrate size is generally smaller, macrophytes provide most of the visual barriers between territories and velocity shelters (Hendry & Cragg-Hine, 2000). Juvenile salmon in chalk streams preferred areas with weed cover, which provides shelter from predation risk, particularly at night (Riley et al. 2006, 2009). The highest electivity value observed for weed cover was by Family 2 for proportions of 30–50%, which was the most infrequently encountered category in samples (Table 2). At high densities and limited space, salmonids may use less suitable areas (Riddell et al. 1981), so it is possible that Family 2 in the present study was strongly associated with weeded areas as a result of a trade-off between feeding opportunities and exposure to predation (Milinski & Heller 1978).

In streams, substratum composition is often associated with water velocity (reviewed by Hendry & Cragg-Hine 2003), but this relationship was not apparent in the present study. Water velocity had a minor influence on the ordinations (Fig. 2A-Cb-c), This lack of correlation between water velocity and substratum composition is likely to be due to the relative invariability of the discharge regimes in chalk streams, such as the River Cerne, which results in a relatively uniform bottom substratum (Table 2). Salmon parr typically prefer shallow waters (< 20 cm), with high velocities of 50 to 65 cm s^{-1} (Hendry & Cragg-Hine 2003). However, in this study only families 1, 3 and 4 were significantly associated with intermediate to high depths, and only families 3 and 4 showed a significant preference for intermediate velocity (*i.e.* 0.21–0.6 m s^{-1}) and none with regard to substratum type (Fig. 2B:b-c).

Although not significant, virtually all families in the present study avoided silt and were indifferent to sand. Different levels of marked preference and avoidance were observed for the range of gravel coverage. In the laboratory, overhead cover has been shown to decrease stress response rates and increase growth rate (Pickering et al. 1987), however in the wild, bank cover and closed tree canopy have been shown to reduce in-stream macrophyte growth, thereby diminishing macroinvertebrate

production and diversity (Riley et al. 2009). Despite this, only Family 4 showed a significant avoidance to bank cover whereas this variable was neither preferred nor avoided by fish originating from any other family group in the study (Fig. 2B), and this may suggest a genetic basis for microhabitat specialism.

The number of times individual fish were detected by the MPD was not accounted for. This is because the current study was to gather data about habitat preference, not territory sharing/overlap or dominance. However, it is possible that heterogeneous environments enable fish from fast growing, aggressive family groups to occupy the highest quality habitats. It is also possible that the complexity of the environment may reduce the fitness (i.e. growth rate) of aggressive dominant individuals in relation to subordinates (Höjesjö et al. 2004). Therefore, behavioural variation could be maintained in natural populations, thus allowing subordinate and dominant fish to coexist. Owing to the complexity of salmonid habitat, if any one habitat component is degraded or inadequate, then the productivity of salmonids may decline (Hendry et al. 2003). So, if the environment changes faster than the population is able to adapt, it might quickly become extinct, despite the level of genetic variation present in the stream (Watters et al. 2003). Therefore, in a genetically diverse population (as simulated in this study), individuals could be affected to different degrees and face different probabilities of survival. This is of particular importance for chalk streams where Atlantic salmon are suffering population decline, and where the habitat structure is often modified during periods of river management.

It is notable that only a few variables can be easily measured in the wild, therefore many habitat variables may have been unaccounted for in the present study and what is interpreted as habitat choice may not necessarily focus on the most relevant variable (Bardonnet & Baglinière 2000). Also, previous methods to classify habitat variables, as well as to assess habitat use and preference, differ from study to study (e.g Heggenes, 1990; Heggenes et al. 1993; Bardonnet & Baglinière, 2000), therefore the extrapolation of results from one river system to another may not be simple or appropriate.

Despite some low sample sizes, the present study has shed light on the microhabitat breadth and preference/avoidance among distinct family groups of salmon in a chalk stream. Microhabitat choice is influenced by the family of origin and these findings have important implications for the

management of chalk streams, in particular those with declining numbers of Atlantic salmon, providing fisheries managers with essential information about mixed-family groups and how to reduce intra-specific competition whilst undertaking salmon stocking and re-introduction initiatives.

Acknowledgements

We thank A.T. Ibbotson, M.W. Bruford and S.W. Griffiths for comments during the development of the experiments, R. Moss and D. Stubbing at Watergates Fish Farm, and for assistance in the field L. Scott, W.R.C. Beaumont, A.C. Pinder and M.J. Ives. This study was funded by the University of Cardiff, the Centre for Ecology and Hydrology, the Centre for Environment, Fisheries and Aquaculture Science, Wessex Water and the Environment Agency.

References

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. & Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research 62: 143–170.

Armstrong, J.D. 2010. Variation in habitat quality for drift-feeding Atlantic salmon and brown trout in relation to local water velocity and river discharge, In: Kemp, P.S. ed., Salmonid Fisheries: freshwater habitat management, Oxford: Wiley-Blackwell. pp. 1–22.

Allen, K.R. 1969. Limitations on production in salmonid populations in streams. In: Northcote, T.G. ed., Symposium on salmon and trout in streams. Vancouver: University of British Columbia, pp. 3–18.

Beaumont, W.R.C., Mills, C.A. & Williams, G.I. 1986. Use of a microcomputer as an aid to identifying objects passing through a resistivity fish counter. Aquaculture and Fisheries Management 17: 213–226.

Bardonnet, A. & Baglinière, J.L. 2000. Freshwater habitat of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57: 497–506.

Beland, K.F., Trial, J.G. & Kocik, J.K. 2004. Use of Riffle and Run Habitats with Aquatic Vegetation by Juvenile Atlantic Salmon. North American Journal of Fisheries Management 24:

525–533.

Chessel, D. & Thioulouse, J. 1998. ADE Version 4.0: HyperCard Stacks and Microsoft Quick Basic Programme library for the analysis of environmental data. Universite Lyon I, Villeurbanne.

Copp, G.H. 1990. Recognition of cohorts and growth of larval and juvenile roach *Rutilus rutilus* (L.), using size class ordination of developmental steps. Journal of Fish Biology 36: 803–819.

Copp, G.H. 1992. An empirical model for predicting microhabitat of 0+ juvenile fishes in a lowland river catchment. Oecologia 91: 338–345.

Copp, G.H. 2008. Putting multi-dimensionality back into niche breadth: diel vs. day-only niche separation in stream fishes. Fundamental & Applied Limnology 170: 273–280.

Copp, G.H. 2010. Patterns of diel activity and species richness in young and small fishes of European streams: a review of 20 years of point abundance sampling by electrofishing. Fish & Fisheries 11: 439–460.

Copp, G.H., Guti, G., Rovný, B. & Černý, J. 1994. Hierarchical analysis of habitat use by 0+ juvenile fish in the Hungarian/Slovak flood plain of the River Danube. Environmental Biology of Fishes 40: 329–348.

Copp, G.H., Spathari, S. & Turmel, M. 2005. Consistency of diel behaviour and interactions of stream fishes and invertebrates during summer. River Research & Applications 21: 75–90.

Edwards, D.J. 1978. Salmon and Trout Farming in Norway. Farnham, England: Fishing News Book Limited.

Edwards, F.K., Lauridsen, R.B., Fernandes, W.P.A., Beaumont, W.R.C., Ibbotson, A.T., Scott, L., Davies, C.E. & Jones, J.I. 2009. Re-introduction of Atlantic salmon, *Salmo salar* (L.), to the Tadnoll Brook, Dorset. Proceedings of the Dorset Natural History and Archaeological Society 130: 9–16.

Fausch, D.K. 1984. Profitable stream position for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 64: 441–451.

Fernandes, W.P.A., Griffiths, S.W., Ibbotson, A.T., Bruford, M. & Riley, W.D. In press. Density mediates the role of relatedness in juvenile Atlantic salmon in the wild. Journal of Zoology.

365 Government of Canada 1980. Stream enhancement guide. Vancouver: Government of Canada,
366 Department of Fisheries and Oceans, 82 pp.
367 Green, R.H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs
368 of central Canada. Ecology 52: 543–556.
369 Heggenes, J. 1990. Habitat utilization and preferences in juvenile Atlantic salmon *Salmo salar* in
370 streams. Regulated Rivers Research and Management 5: 341-354.
371 Heggenes, J., Grog, O.M.W., Lindas, O.R., Dokk, J.G., Armstrong, J.D. 1993. Homeostatic
372 behavioural responses in changing environment: brown trout (*Salmo trutta*) become nocturnal at
373 night. Journal of Animal Ecology 62: 295-308.
374 Hendry, K. & Cragg-Hine, D. 2003. Ecology of the Atlantic Salmon. Conserving Natura 2000 Rivers
375 Ecology Series No. 7. English Nature, Peterborough.
376 Hendry, K. & Cragg-Hine, D., O'Grady, M., Sambrook, H. & Stephen, A. 2003. Management of
377 habitat for rehabilitation and enhancement of salmonid stocks. Fisheries Research 62: 171–192.
378 Hilton, J., Welton, J.S., Clarke, R.T. & Ladle, M. 2001. An assessment of the potential for the
379 application of two simple models to Atlantic salmon, *Salmo salar*, stock management in chalk
380 rivers. Fisheries Management and Ecology 8: 189–205.
381 Höjesjö, J., Johnsson, J.I. & Bohlin, T. 2004. Habitat Complexity reduces the growth of aggressive
382 and dominant brown trout (*Salmo trutta*) relative to subordinates. Behavioural Ecology and
383 Sociobiology 56: 286–289.
384 Ibbotson, A.T., Beaumont, W.R.C., Collinson, D., Wilkinson, A. & Pinder, A.C. 2004. A cross-river
385 antenna array for the detection of miniature passive integrated transponder tags in deep, fast
386 flowing rivers. Journal of Fish Biology 65: 1441–1443
387 Kawecki, T.J. & Ebert, D. 2004. Conceptual issues in local adaptation. Ecology Letters 7: 1225–1241.
388 Klemesten, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B.N., O'Connell, M.F. & Mortensen, E.
389 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo* trutta L. and Arctic charr *Salvelinus*
390 *alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12: 1–59.
391 Marshall, T. 2007. CERVUS Version 3.0.3. Field Genetics Ltd.

McConnell, S.K., O'Reilly, P., Hamilton, L., Wright, J.N. & Bentzen, P. 1995. Polymorphic microsatellite loci from Atlantic salmon (*Salmo salar*) – Genetic differentiation of North-American and European populations. Canadian Journal of Fisheries and Aquatic Sciences 52: 1863–1872.

McLaughlin, R.L., Ferguson, M.M. & Noakes, D.L.G. 1999. Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching. Behavioural Ecology and Sociobiology 45: 386–395.

Mercier, P., Chessel, D. & Doledec, S. 1992. Complete correspondence analysis of an ecological profile table: a central ordination method. Acta Oecologica 13: 25–44.

Milinski, M. & Heller, R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus*), Nature 275: 642–644.

O'Reilly, P.T., Herbinger, C. & Wright, J.M. 1998. Analysis of parentage determination in Atlantic salmon (*Salmo salar*) using microsatellites. Animal Genetics 29: 363–370.

Persat, H. & Chessel, D. 1989. Typologie de distributions en classes de taille: intérêt dans l'étude des populations de poissons et d'invertébrés. Acta Œcologica, Œcologia Generalis 10: 175–195.

Pickering, A.D., Griffiths, R. & Pottinger, T.G. 1987. A comparison of the effects of overhead cover on the growth, survival and hematology of juvenile Atlantic salmon, *Salmo salar* (L.), brown trout, *Salmo trutta* (L)., and rainbow trout, *Salmo gairdneri* Richardson. Aquaculture 66: 109–124.

Pinder A.C., Riley W.D., Ibbotson A.T. & Beaumont W.R.C. 2007. Evidence for an autumn downstream migration and the subsequent estuarine residence of 0+ juvenile Atlantic salmon, *Salmo salar* L., in England. Journal of Fish Biology 71: 260–264.

Riddell, B.E., Leggett, W.C. & Saunders, R.L. 1981. Evidence of adaptive polygenic variation between two populations of Atlantic salmon (*Salmo salar*) native to tributaries of the S.W. Miramichi River. N.B. Canadian Journal of Fisheries and Aquatic Sciences 38: 321–333.

Riley, W.D., Eagle, M.O., Ives, M.J., Rycroft, P. & Wilkinson, A. 2003. A portable passive integrated transponder multi-point decoder system for monitoring habitat use and behaviour of freshwater fish in small streams. Fisheries Management & Ecology 10: 265–268.

418 Riley W.D., Ives M. J., Pawson M.G. & Maxwell D.L. 2006. Seasonal variation in habitat use by
419 salmon (*Salmo salar* L.), trout (*Salmo trutta* L.) and grayling (*Thymallus thymallus* L.) in a chalk
420 stream. Fisheries Management and Ecology 13: 221–236.
421 Riley W.D., Pawson M.G. Quayle V. & Ives M.J. 2009. The effects of stream canopy management
422 on macroinvertebrate communities and juvenile salmonid production in a chalk stream. Fisheries
423 Management and Ecology 16: 100–111.
424 Sánchez, J.A., Clabby, C., Ramos, D., Blanco, G., Flavin, F., Vazquez, E. & Powell, R. 1996. Protein
425 and microsatellite single locus variability in *Salmo salar* L (Atlantic salmon). Heredity 77: 423–
426 432.
427 ter Braak, C.J.F. 1986. Canonical Correspondence Analysis: a new eigenvector technique for
428 multivariate direct gradient analysis. Ecology 67: 1167–1179.
429 ter Braak, C.J.F. & Verdonschot, P.F.M. 1995. Canonical Correspondence analysis and related
430 multivariate methods in aquatic ecology. Aquatic Sciences 57: 255–287.
431 Thioulouse, J. 1990. MacMul and GraphMu: two Macintosh programmes for the display and
432 analysis of multivariate data. Computers & Geosciences 8: 1235–1240.
433 Thioulouse, J., Chessel, D., Doledec, S. & Olivier, J.-M. 1997. ADE-4: a multivariate analysis and
434 graphical display software. Statistics & Computing 7: 75–83.
435 Watters, J.V., Lema, S.C. & Nevitt, G.A. 2003. Phenotype management: a new approach to habitat
436 restoration. Biological Conservation 112: 435–445.
437 Welton, J.S., Beaumont, W.R.C. & Clarke, R.T. 2002. The efficacy of air, sound and acoustic bubble
438 screens in deflecting Atlantic salmon, *Salmo salar* (L.), smolts in the River Frome, UK. Fisheries
439 Management and Ecology 9: 11–18.
440 Welton, J.S., Beaumont, W.R.C. & Ladle, M. 1999. Timing of migration and changes in age structure
441 of Atlantic salmon, *Salmo salar* (L.), in the River Frome, a Dorset chalk stream, over a 24-year
442 period. Fisheries Management and Ecology 6: 437–458.
443
444
445
446

447 *Table 1.* Microhabitat variables as converted to semi-quantitative categories (Cat.) from quantitative
448 measurements (depth in cm, water velocity in m s^{-1}) or from proportional (%) measurements (of
449 substratum and cover), based on the frequency distributions of the variables.
450
451 *Table 2.* The microhabitat variables and their semi-quantitative categories for each family of Atlantic
452 salmon (*Salmo salar*) parr in the River Cerne, Southern England, for 5–8 September 2006 and 17
453 August–20 September 2007. Given are the frequencies of occurrence (*f*) of each family in all samples
454 (192 antennae), the total number of occurrences of each microhabitat category ('*n*'; see also Table 1)
455 in samples (i.e. antennae), and the number of samples in which each family group co-occurred with
456 each category.
457
458 *Fig. 1.* **A)** Configuration in 2006 of sites stocked with six single-family (dark shaded) sites and six
459 mixed-family (light shaded) groups of juvenile Atlantic salmon *Salmo salar* into on the River Cerne,
460 (Dorset, England). See methods for stocking densities and channel character. **B)** Configuration in
461 2007 of three single-family (dark shaded) sites and one large mixed-family (light shaded) site (the
462 size of three single-family sites) of Atlantic salmon. See methods for stocking densities and channel
463 character. **C)** Schematic configuration of 16 antennae of a multi-point decoder system MPD (not to
464 scale) installed on a chalk stream. Photo courtesy of CEH.
465
466 *Fig. 2 A–C.* Canonical correspondence analysis triplot ordinations (CA1 × CA2) for Atlantic salmon
467 parr families (1–6) and microhabitat profiles (see Table 1) in the River Cerne (Southern England)
468 between 5–8 September 2006 and 17 August – 20 September 2007, with superimposed ordinations
469 for individual fish coded by site in which they appeared (a = single-family, b = mixed-family), the
470 microhabitat vectors (length indicative of that variable's relative influence on the ordinations) and
471 ellipses representing the 90% confidence intervals (Green, 1971) for that family: **A)** eigen values for
472 the seven canonical dimensions; **B)** triplot of CA1 × CA2; **C)** triplot of CA1 × CA3. **D)** microhabitat
473 electivity profiles (values approaching +0.5 = preference; values approaching -0.5 = avoidance) for
474 that family (all PIT-tagged fish combined). See Table 1 for microhabitat variables and category

numbers). Significant deviations from expected (Fisher-Exact test) are indicated as * ($P \leq 0.05$), ** ($P \leq 0.01$), *** ($P \leq 0.001$).

Table 1. (Fernandes, Copp, Riley)

	Cat. 1	**Cat. 2**	**Cat. 3**	**Cat. 4**	**Cat. 5**	**Cat. 6**
Water depth (cm)	1–24	25–47	48–70			
Water velocity ($m\ s^{-1}$)	< 0.2	0.21–0.4	0.41–0.6	> 0.61		
Weed cover (%)	Absent	1–20	30–50	70–100		
Gravel (%)	Absent	1–19	20–30	40–50	60–75	76–100
Sand (%)	Absent	1–20	21–50	60–100		
Silt (%)	Absent	1–50	60–100			
Bank cover (%)	Absent	1–40	50–80	90–100		

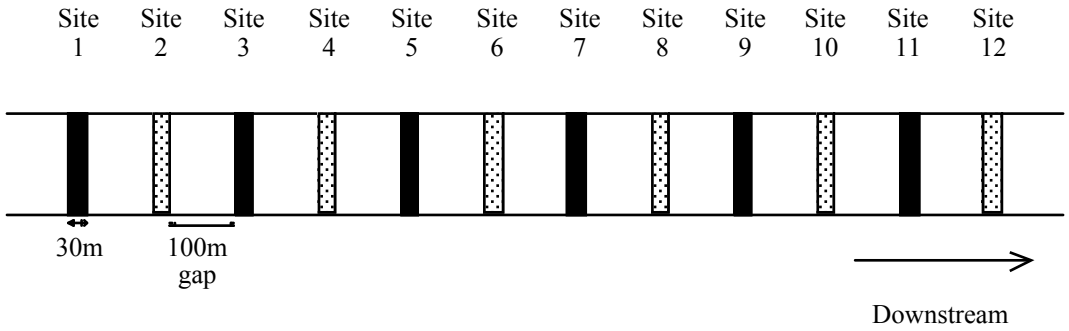
Table 2. (Fernandes, Copp, Riley)

Variable and categories	*f* =	Family 1	2	3	4	5	6
		0.068	0.057	0.099	0.260	0.010	0.052
Water depth (cm)	***n***						
1) 1–24	75	3	2	2	9	1	3
2) 25–47	105	6	9	10	39	1	7
3) 48–70	12	4	0	7	2	0	0
Water velocity (m s^{-1})							
1) < 0.2	70	2	3	2	15	1	4
2) 0.21–0.4	48	5	3	11	10	0	0
3) 0.41–0.6	47	4	5	4	21	0	4
4) > 0.61	27	2	0	2	4	1	2
Weed (%)							
1) absent	157	10	9	14	43	1	7
2) 1–20	15	1	0	2	3	0	2
3) 30–50	7	1	2	2	0	0	0
4) 70–100	13	1	0	1	4	1	1
Gravel (%)							
1) absent	20	1	0	1	4	1	0
2) 1–19	8	0	0	0	0	0	0
3) 20–30	13	2	1	0	4	0	3
4) 40–50	18	1	1	4	3	0	1
5) 60–75	21	3	0	2	2	0	0
6) 76–100	112	6	9	12	37	1	6
Sand (%)							
1) absent	61	1	4	4	16	2	4

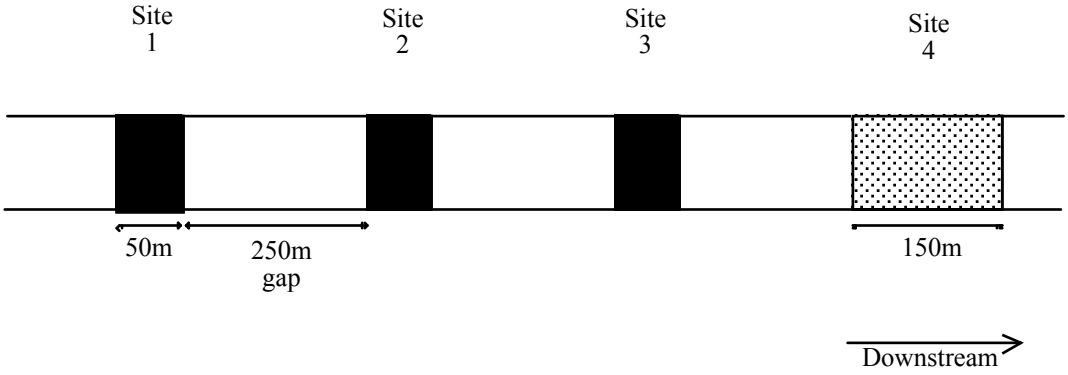
2) 1–20	83	7	7	11	27	0	3
3) 21–50	29	3	0	2	3	0	1
4) 60–100	19	2	0	2	4	0	2
Silt (%)							
1) absent	169	13	11	19	47	2	10
2) 1–50	12	0	0	0	2	0	0
3) 60–100	11	0	0	0	1	0	0
Bank cover (%)							
1) absent	133	13	8	14	43	1	8
2) 1–40	31	0	2	2	4	1	2
3) 50–80	14	0	1	2	3	0	0
4) 90–100	14	0	0	1	0	0	0

Figure 1 a, b and c (Fernandes, Copp and Riley)

A



B



C

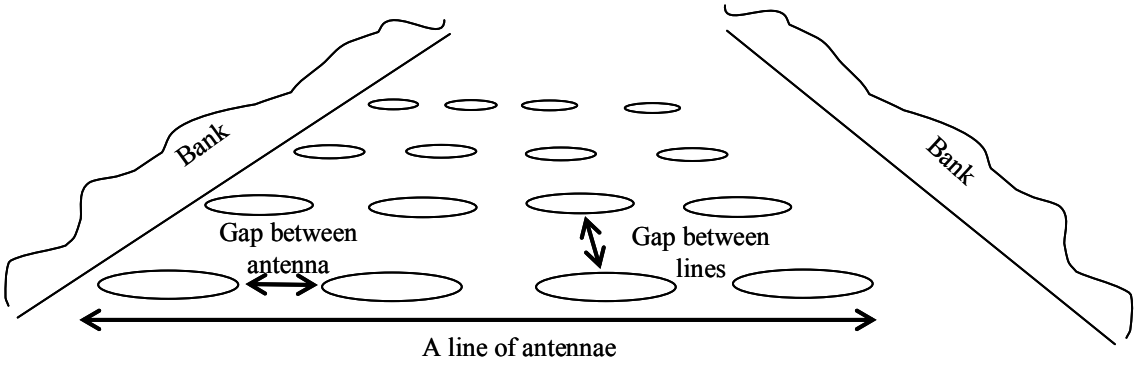
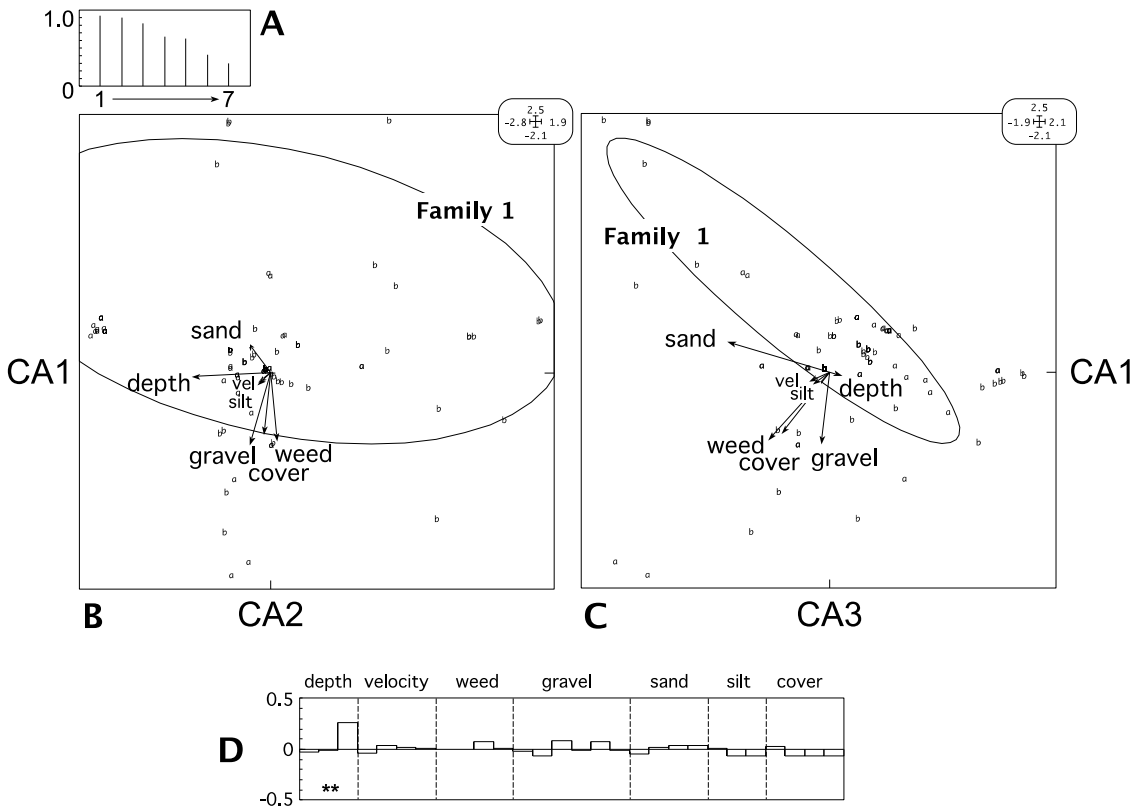
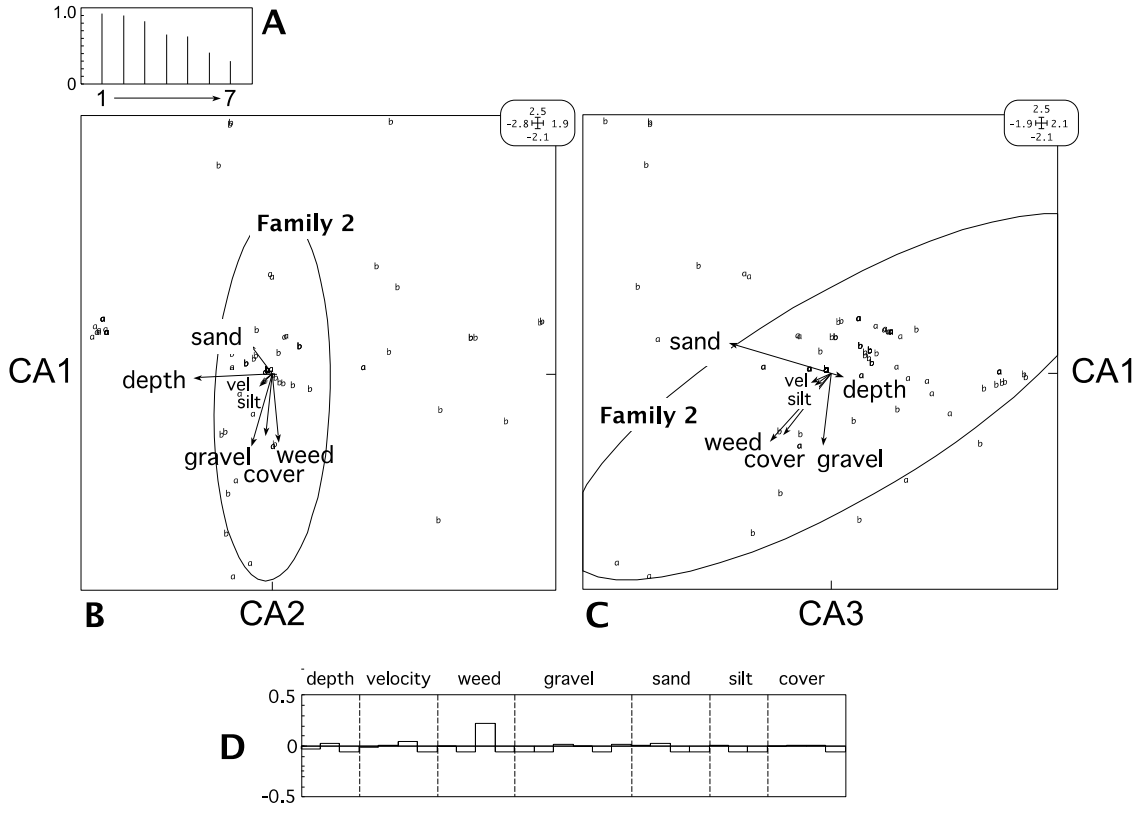


Fig. 2A-C

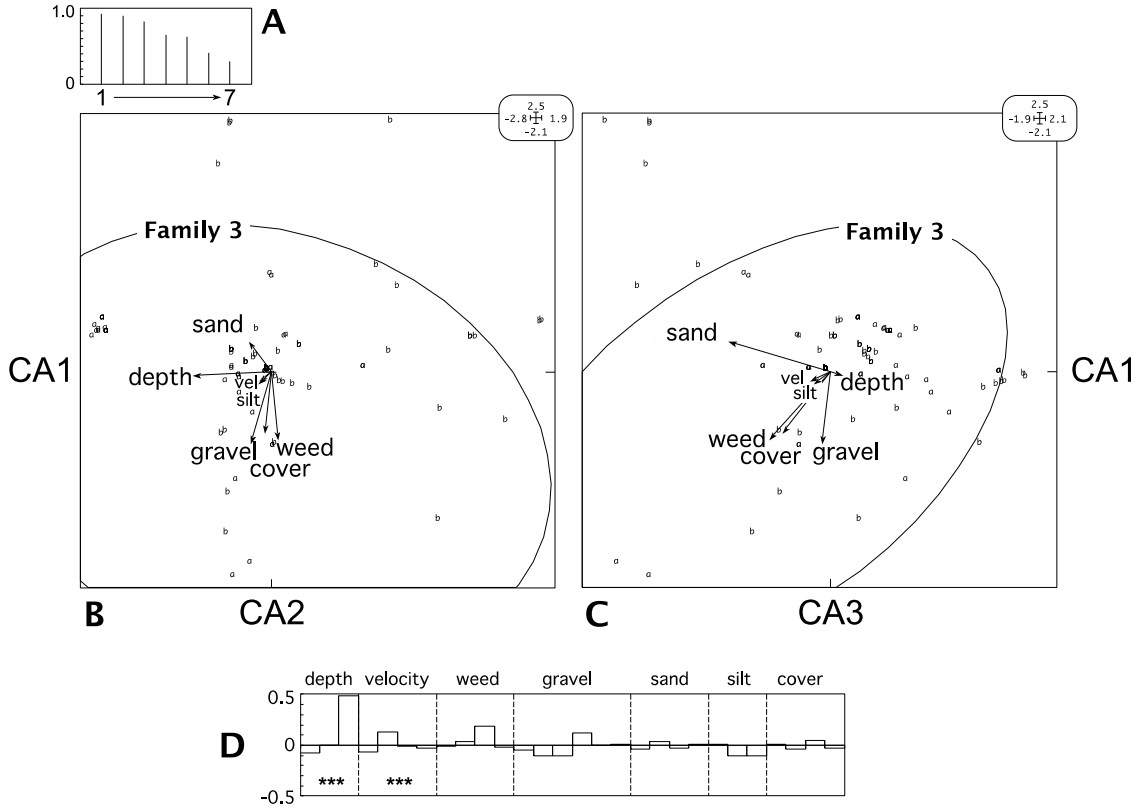
Family Group 1



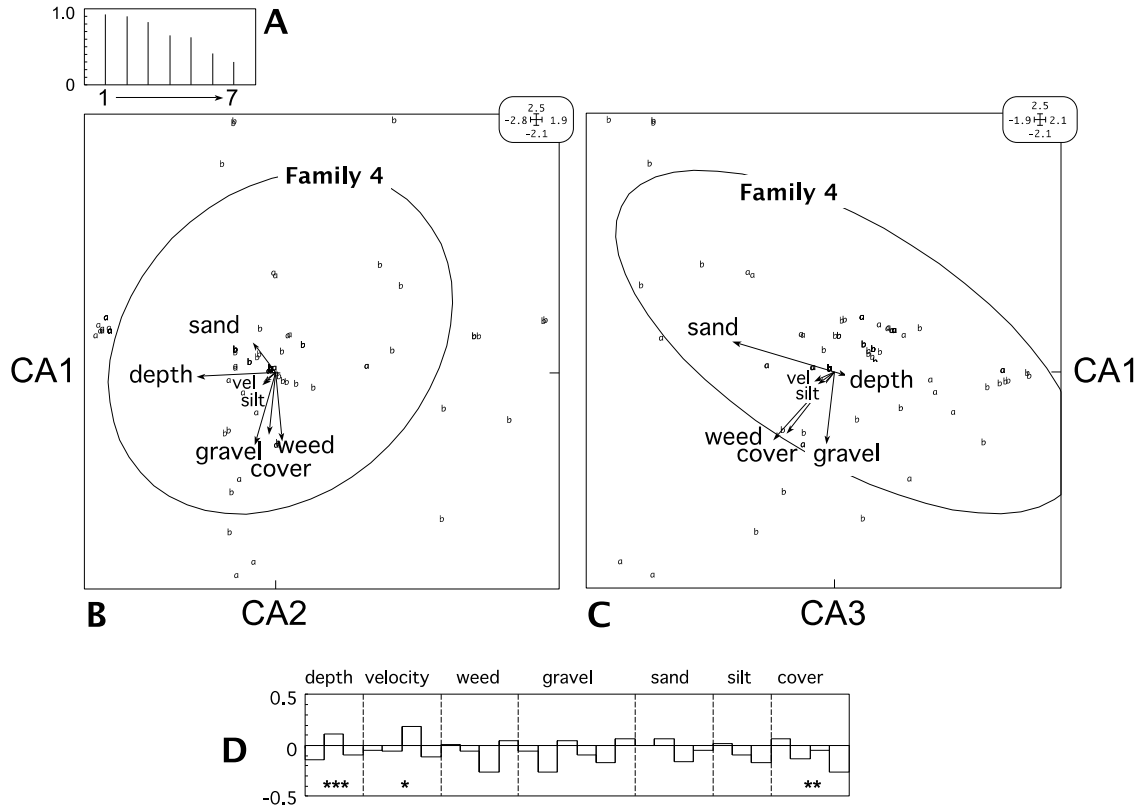
Family Group 2



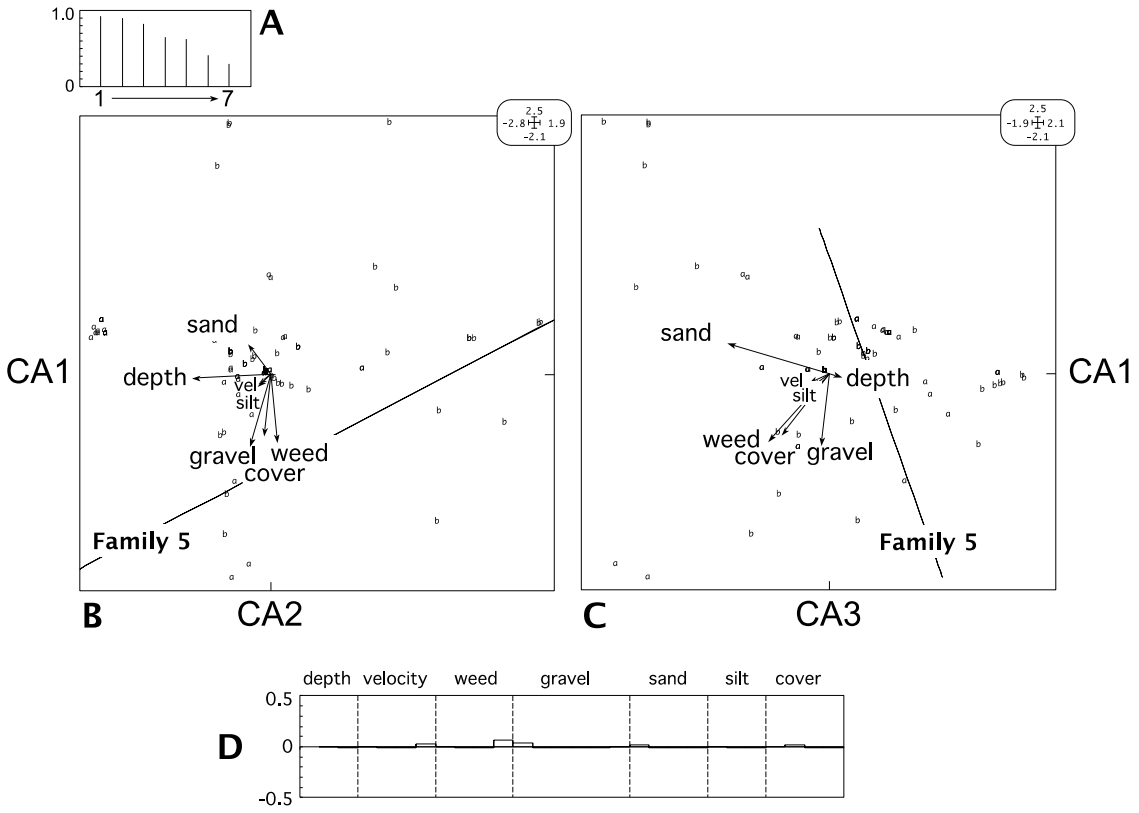
Family Group 3



Family Group 4



Family Group 5



Family Group 6