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Habitat use by the fish assemblages of two chalk streams.

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Patterns of habitat use by fish assemblages in two chalk streams in southern England were examined to identify species preferences with respect to major habitat gradients. Both study sites although differing in some physical habitat characteristics, mainly channel width, water temperature and instream cover, could be similarly arranged along a continuum extending from erosional to depositional habitats. Twelve fish species were collected from stream surveys conducted during July 1993. The habitat was partitioned into six fish species associations that could be assigned to three habitat guilds: depositional (*Barbatula barbatula*, *Gasterosteus aculeatus* and *Anguilla anguilla*), riffle (*Leuciscus leuciscus*, *Thymallus thymallus* and *Salmo salar*) and generalist (*Salmo trutta*, *Phoxinus phoxinus*, *Gobio gobio*, *Cottus gobio*, *Lampetra planeri* and *Pleuronectes flesus*). At low to moderate densities the different species associations were collected in the same habitat patch, but at higher densities there was a clear tendency to mutual avoidance. In particular, large trout appeared as strong interactors that tended to exclude other species from their territories. We hypothesize that the fish assemblage of the Mill Stream and Bere Stream have partitioned the habitat in such a way as to minimize potential competition.

INTRODUCTION

The importance of fish habitat partitioning as a mechanism to facilitate coexistence has been a long debated subject in stream fish community ecology. This controversy has addressed several points: habitat spatio-temporal stability and predictability, competition and predation and phylogenetic constraints (Zaret & Rand, 1971; Schlosser, 1987; Grossman & Freeman, 1987; Angermeier, 1987; Power *et al.*, 1989). Habitat stability and limiting resources promotes strong biotic interactions and as a consequence species display mechanisms to avoid interactions such as food and habitat partitioning (Zaret & Rand, 1971). When the habitat is largely unstable and unpredictable due to the ocurrence of natural disturbances such as floods and droughts, mechanisms to facilitate coexistence are not necessary and species display high microhabitat overlap (Grossman *et al.*, 1982; Grossman & Freeman, 1987). Finally, phylogenetic constraints can be either a consequence of past competitive histories of species, or the only partitioning mechanism in variable environments (Grossman & Freeman, 1987). However, an alternative view suggests that in widespread species, habitat selection is a highly plastic feature that relies upon local spatio-temporal habitat characteristics, rather than a phylogenetically fixed behaviour that affects the structure of the fish assemblage (Angermeier, 1987).

The small chalk streams in southern England are inhabited by a rich fish fauna. The life-histories of the component species have been intensively studied (see Mann, 1989, and references therein). However, as in most North temperate European river systems, neither the patterns of habitat selection of the fish assemblages nor the factors causing it have been examined. These streams possess several features of great interest from a theoretical point of view. The most important of these are the stable patterns of temperature and discharge, and the high productivity. Fluctuations in discharge and temperature are postulated to be the most important sources of environmental variability in streams (Schlosser, 1987; Rahel & Hubert, 1991) and habitat stability has been considered one of the main determinants of species richness in river systems (Horwitz, 1978; Schlosser, 1987). Thus, in these streams the presence of a large number of species in a relatively stable environment suggests *a priori* that deterministic biological factors such as habitat preference and competition should play an important role in structuring stream fish assemblages (Paller, 1994).

The objective of the present study is to determine how habitat features influence fish assemblage structure in two stable and productive streams with similar landscape features.

Specifically our objectives were to (1) describe the assemblage of species associated with major habitat trends, (2) to establish the fish microhabitat preferences and (3) to speculate about the strength and importance of biotic interactions in a system with a high relative stability.

MATERIAL AND METHODS

STUDY AREA

Chalk streams often produce a very stable and predictable environment. Due to the high proportion of discharge from subterranean sources, chalk stream flows and temperatures are strongly buffered against change (Ibbotson *et al.*, 1994). This stability combined with abundance of nutrients, results in extensive instream macrophyte growth. In addition the streams are often shallow and have good light penetration, further enhancing plant growth (Fox, 1978). Primary production in streams is high (500 g dry weight m^{-2}, Westlake *et al*., 1972). Unvegetated chalk streams normally have a bed of flint gravel. Where dense macrophyte growth occurs, fine sediments build up between the stems resulting in the formation of a silt or sand substratum layer. The macrophyte cover is highest during late spring and summer. In late autumn and winter most weeds are washed out and the river bottom is mostly devoid of macrophytes.

This study was carried out on two local hard-water chalk streams, Mill Stream, and Bere Stream. Mill Stream is a divergent channel from the river Frome (Dorset). Bere Stream is a tributary of the river Piddle. Both streams are similar in character and have a patchy distribution of macrophytes. The main macrophyte species found in the study area were: *Ranunculus penicillatus* var *calcareous* (R. W. Butcher), *Rorippa nasturtium aquaticum* (L.) Hayek, *Apium nodiflorum* (L.) Lag. and *Berula erecta* (Huds.) Coville and are partially shaded by riparian trees such as *Salix* sp and *Alnus* sp.

FIELD SAMPLING

The two streams were sampled between the 11th and the 22nd of July 1994. Sampling was carried out between 9 am and 6 pm on warm sunny days. Twenty five transects, evenly spaced at 10 m intervals, were established in each stream. Along each transect one site was sampled as follows (Fig. 1): the first site (in the first transect) was adjacent to one bank, the second (in the second transect) in the centre of the channel and the third (correspondingly in the third channel) adjacent to the opposite bank and so on. At each sampling site fish were captured in an area of approximately 1 m^2 using a pre-positioned electrofishing square (Bain *et al.*, 1985, 1988; Weddle & Lester, 1993). The sampler was a 0.75*0.75 m frame (the effective area of the sampler for the average size of fish captured was approximately 1 m^2) electrified through a 10-m extension cord, which was connected to a Honda EG 1900X generator (230-240 VAC,) positioned on the bank (Fig. 1). Frames were placed over the substratum and left undisturbed for 12-15 min. before sampling (Bain *et al.*, 1985). Sampling was initiated at the most downstream site.

Standard electrofishing equipment tends to drive fish from their original position, resulting in fright bias. Bain *et al*. (1985) observed that the sampling technique employed here minimized fright bias, given that an undisturbed time period of at least 10 minutes is allowed after setting the electrode frames. Also this technique was very effective in immobilizing fish within the electrode frame. This points out that with this sampling technique and sampling design is possible to collect habitat use data on stream fish assemblages very precisely with few investigator bias or effect (Bain & Finn, 1991). Notwithstanding, potentially large fish such as trout could be disturbed while setting the frames in the study area. But, previous estimates of fish density in chalk streams are of a similar order of magnitude (see for instance Mann, 1971).

Electrofishing frame samples were collected using a standardized protocol (Prenda, 1993). The generator was turned on for 1 min. as two collectors approached the frame from downstream and collected the stunned fish with a hand net of 0.25 mm mesh size. The collectors moved back downstream for several minutes and the process was repeated twice giving a total of 3 min. of fish sampling, ensuring in this way that all the fish in the area were sampled. When the generator was turned off, the sampling and adjacent downstream area was throughly examined with the use of an underwater viewer to collect all stunned fish lying on the substratum. All the samples were taken by the same two persons.

All the fish collected were identified and total length measured, to the nearest mm, in the field. A sample of each species was taken to the laboratory where they were weighed (total weight). Fish biomass was calculated using length:weight relationships. In some cases where there were insufficient data for these regressions the length:weight relationships provided by Mann (1971) and Mann & Blackburn (1991) for the same species and study area were applied.

After fish sampling, 10 habitat variables were measured or estimated at each sampling site. Water depth, channel width and active channel width, current velocity at bottom and at 60-70% depth (current meter), percentage of the river bed shaded by stream-side vegetation (visually estimated), instream cover (percentage of the channel bed covered, usually by macrophytes; visually estimated). Substratum coarseness was quantified with a 60 cm square grid divided into 9 20*20 cm sections, applying a modified Wentworth scale (Heggennes *et al.* 1991). Detritus was considered as dead organic material, forming a distinctive layer over the substratum. Its abundance was estimated visually according to the following categories: 0, absent; 1: a small quantity; 2: covers most of the sampling site; 3: very abundant, forming thick layers. Substratum heterogeneity, depth heterogeneity and flow variability were calculated as the standard deviation across sites of substratum coarseness, depth and water current, respectively. Finally, the distance to the nearest shelter was computed as the distance from the sampling site to the nearest structure within the water column capable of covering most of the fish body.

Habitat volume (m^3) in each stream was estimated by multiplying the length of the stream sampled (250 m) by the area of an average section (average width multiplied by average depth). Similarly, discharge (m^3 s^{-1}) was estimated by multiplying the area of an average section by the average water current in each one of the streams studied.

STATISTICAL ANALYSIS

Principal components techniques (hereafter PCA) were used to evaluate fish habitat preferences. A PCA was performed on a habitat variables*sites matrix. The frequency distribution of the first component scores (sampling sites) provided the relative abundance of specific habitat configurations. To test the preferences of each fish species for any particular habitat type, the previously described frequency distribution was compared to the frequency distribution of the sites where each species was present (see Grossman & Freeman, 1987;

Gallardo *et al.*, 1994). A Chi-squared analysis was conducted to determine whether significant differences existed between both frequency distributions. If fish species randomly occupied sampling sites, then distributions for habitat availability and expected frequency should not be significantly different. If a significant result was obtained a partitioned Chi-squared analysis was conducted to determine which classes contributed to statistical significance, i. e. in which habitat type the species was over- or under-represented. To test the effect of habitat variability on fish abundance, biomass and size, the PC1 scores were regressed on fish density and on total length averaged for each site.

To partition the fish assemblage into groups of species with similar distribution a new PCA was applied to a fish density/site matrix.

All variables were tested for normality (normal probability plot or Chi-squared analysis). Those that significantly departed from a reasonable normal distribution were log- (continuous variables) or arcsine-transformed (percentages).

RESULTS

FISH ASSEMBLAGE COMPOSITION AND HABITAT QUALITY

The two study sites differed in habitat volume and flow (Table I), both being greater in Bere Stream. In addition, discriminant analysis of physical habitat variables revealed two groups containing all 25 (100%) of Mill Stream sites and 24 (96%) of Bere Stream sites (Discriminant function, Wilk's lambda=2018, Chi-squared=68.0, $P \leq 0.0001$, 11 df). The variables which most contributed to this classification were channel width, water temperature, instream cover and velocity variability (Table I).

The PCA of habitat variables ordered the sampling sites along an erosional-depositional gradient in both study areas (Fig. 2a). However, in Mill Stream depositional areas were over-represented with respect to Bere Stream (partitioned Chi-squared analysis, $P=0.0032$). The erosional areas coincided with riffles, characterized mainly by high substratum coarseness and faster water current. The depositional areas or lentic sites were characterized by increased detritus and higher cover values (Table II).

A total of 12 species were caught in the two streams sampled: eel (*Anguilla anguilla* L), minnow (*Phoxinus phoxinus* L), bullhead (*Cottus gobio* L), threespined stickleback

(*Gasterosteus aculeatus* L), gudgeon (*Gobio gobio* L), brook lamprey (*Lampetra planeri* Bloch), dace (*Leuciscus leuciscus* L), stone loach (*Barbatula barbatula* L), flounder (*Pleuronectes flesus* L), salmon (*Salmo salar* L), trout (*Salmo trutta* L) and grayling (*Thymallus thymallus* L). Species composition differed between streams (Table III). Mill Stream was dominated numerically by minnows and stone loach whereas in Bere Stream bullhead and salmonids (mainly trout) were most abundant. Total fish density was higher in Mill Stream than in Bere Stream, but some individual species densities were higher in Bere Stream (Table III). Mean fish length was usually larger in Bere Stream (Table III), but total biomass was very similar between sites.

FISH MICROHABITAT PREFERENCES

It was possible to observe habitat preferences in some species within the fish assemblage, but the rest of the species displayed little microhabitat selectivity and were widely distributed accross the available habitat (Fig. 2b). The species with preferences were salmonids that avoided the most depositional areas (partitioned Chi-squared analysis, $P<0.001$, 4 d.f.), and in the case of salmon had preferences for riffles; gudgeon that were over-represented in depositional areas ($P<0.001$); dace that were over-represented in riffle-type reaches; and stickleback that avoided erosional areas and selected depositional ones ($P<0.001$) (Fig. 2b).

Analysing the data from each sampling site separately, in the same way as before, the results are similar, but with a few exceptions. The distribution of gudgeon in Mill Stream and trout in Bere Stream did not depart significantly from random ($P>0.37$, in both cases); salmon in Mill Stream strongly selected riffles and avoided depositional areas ($P=0.005$) while trout had a preference for the intermediate category and still avoided depositional areas; salmon in Bere Stream avoided the intermediate habitat category; finally lampreys were over-represented in Bere Stream intermediate sites but more like riffles ($P=0.001$).

In six of the fish species, density and/or biomass was significantly correlated with the habitat gradient defined by PC1 (Fig. 3). The three-spined stickleback, the stone loach and the lamprey strongly selected sites with higher detritus and cover values. Minnow biomass and trout density both were lowest in riffles in Bere Stream. Finally, eel biomass was highest in Bere Stream riffles (Fig. 3).

To test for the effect of habitat preferences of larvae and immature stone loach and bullhead, the distribution of nursery areas was analysed by PCA in relation to the habitat gradient obtained. Nursery areas were arbitrarily defined as those where the percentage of immature individuals [<45 mm TL, Mann (1971); Welton *et al.* (1983)] was higher than 8% (mean=17.4%, n=5, for stone loach; mean=10.2%, n=7, for bullhead). In the first case, stone loach rearing habitats were over-represented in the most depositional areas and bullhead nursery habitats (actually only found in Bere Stream) were selected between the intermediate and riffle-type habitats (partitioned Chi-squared analysis, $P \leq 0.0001$, in both cases) (Fig. 2b).

Half of the species studied were randomly distributed with the distance to the nearest shelter (Chi-squared test, $P > 0.07$). However, stickleback, gudgeon, dace and grayling preferred open positions; they were over-represented in intermediate distances to refuges and tended to avoid the sites inside sheltered patches ($P < 0.002$).

SPECIES SPATIAL RELATIONSHIPS

The PCA of the fish density/site matrix revealed six groups of species (Table IV). Some of these groups shared habitat patches with similar features. Thus, stone loach, stickleback and eel were mostly found in depositional areas ($P=0.05$); whereas dace, grayling and salmon preferred riffles ($P=0.031$). When the same analysis was applied to a fish biomass/site matrix or to Mill Stream and Bere Stream data separately, similar results were obtained and the fish assemblage was partitioned into 7, 6 and 5 groups of species, respectively. In general, most species were captured accompanied by others, usually between three and six species were collected in the same site (Fig. 4). The only exception being trout that were captured alone in a higher proportion of sites than the rest of species (Fig. 4). To investigate the relationship between each pair of species associations, their densities are represented in a two-dimensional plot (Fig. 5). In most cases, each pair tended to coexist at low to moderate densities, while at higher densities they were separated.

To further analyse the exclusion of other species by trout, their maximum length per sampling point was regressed against the density and biomass of other species (Fig. 6). Trout only shared their territories with minnow, bullhead and salmon.

Eels are potential predators, especially for bullhead (Mann & Blackburn, 1991). The effect of this species on the rest of the fish assemblage was tested and the only significant relationship observed was a positive one between eel size and bullhead density (F=10, 21 d.f., P=0.005, R^2=33.3%).

Thus, combining the habitat preferences with species associations, three habitat guilds could be identified in the study area: riffle, depositional and generalist (Table IV).

DISCUSSION

Usually, increases in species richness and the presence of older age classes have been primarily associated with greater temporal stability and deeper water (Schlosser, 1987). Habitat volume and depth have long been recognised as important factors affecting the maximum size attained by individual fish living in streams (Mahon & Portt, 1985; Harvey & Stewart, 1991). Bere Stream having a greater volume than Mill Stream (and probably being more stable due to its chalk stream properties), contained larger individuals but was less species rich. Also, the proximity of the River Frome may have affected the fish assemblage composition and fish size in the Mill Stream.

At a fine scale, both Mill Stream and Bere Stream study sites could be similarly arranged along a continuum between erosional and depositional habitats. This gradient was obvious in both streams despite the differences in physical character between the sites.

It was possible to identify a habitat partitioning within the fish assemblage of the study area, although some species did not display consistent and/or significant habitat preferences. Some species selected depositional areas, others preferred riffles and the rest (50%) apparently did not select a specific habitat configuration.

Apart from the two-dimensional (longitudinal and transverse) fish distribution observed in Mill Stream and Bere Stream, in general, the fish species found in the study area can be classified according to their preferred position within the water column. Loach, bullhead, lamprey, flounder and eel are bottom-living species and they feed mostly on benthic organisms. Gudgeon, although displaying benthic habits do not have such a strong dependence on the substratum as the latter species (Zweimüller, 1995). Riffle midwater inhabitants included salmonids, grayling and dace. Minnow and stickleback also use midwater, but preferred lentic sites. Thus, the unique restrictions to fish distribution are those derived from riffle availability for riffle midwater column inhabitants. The rest of the species can potentially occupy most of the available habitat, including riffles.

These results are in agreement with previous observations in the study area, but are in contrast with results obtained in other areas. Welton *et al*. (1983), in the Mill Stream, found that loach had a clear preference for macrophyte areas with a substratum of silt, whereas bullhead preference was less consistent and they selected gravel depending only on its size. In contrast, Zweimüller (1995) observed in a small Austrian stream, that stone loach selected shallow and current-exposed locations without clear affinities for a particular substratum. Welton *et al*. (1991) observed that in aquaria loach consumed significantly more prey on gravel substrata than on silt. Thus, according to this, the observed loach substratum preference can be considered as induced or dependent on other factors apart from prey availability. Also the explanation for the observed patterns of distribution can be contradictory. Welton *et al*. (1991) suggested that the observed habitat partitioning between loach and bullhead was a mechanism to avoid competition. In contrast Zweimüller (1995) hypothesized that microhabitat choice by loach and gudgeon was strongly dependent upon abiotic factors such as flow regime.

All these species have a wide distribution in Europe and can be found in an array of different habitats and environmental conditions (Smyly, 1955; 1957; Mills *et al.*, 1983; Mills & Eloranta, 1985; Gaudin & Cailliere, 1990; Doadrio *et al.*, 1991; Lobon-Cerviá *et al.*, 1991, Rundle & Hildrew, 1992; Degerman & Sers, 1993). This indicates that from an evolutionary point of view, these species have developed few habitat adaptations and display an opportunistic behaviour in habitat selection as in other life-history aspects, such as fecundity or lifespan (Maitland, 1965; Mann *et al.*, 1985, Angermeier, 1987). However, this does not exclude the possibility that in specific sites each species selects those microhabitat patches where the cost-benefit relationship is minimized, from an energetic point of view (Werner *et al.*, 1984).

Angermeier (1987) found inconsistent patterns of habitat selection by widespread fish species between sites and dates in some North American streams. This author speculated that the observed patterns of habitat use probably resulted from the trade-off between finding food and avoiding predators, and that this should be fitted to the specificities of particular stream reaches in particular seasons. The lack of precise habitat affinities is intensified if the habitat variations are relatively predictable, as happens in most chalk streams. Here, the annual weed cycle is highly predictable. The main result of this pattern of annual variation is an opportunistic mode of habitat response, with relatively close tracking of variations in patch structure or frequency (Wiens, 1976).

In both the Mill Stream and Bere Stream, fish tended to be distributed randomly among habitats. Thus, the opportunistic mode of habitat distribution and the high fish density and biomass, probably forced the species to distribute themselves so as to minimize potential competitive interactions (Fretwell & Lucas, 1969).

Competitive exclusion and top-down predator-prey interactions have potentially strong effects on fish habitat use in streams (Power *et al.*, 1989). Usually, large predators or competitors determine complementary distribution of prey or subordinate species. In this case, large trout could be strong interactors within the fish assemblage of the study area (Mann *et al.*, 1989). The interacting capacity of a fish is dependent on its size and this in turn is dependent on habitat volume, so higher habitat availability in Bere Stream (larger pools) may have favoured larger trout and stronger interactions than in the Mill Stream. In the latter stream no exclusion of any species could be detected.

Apart from large trout, there was no other apparent strong territorial effect between other species and usually several coexisted in the same microhabitat patch, including bullhead and stone loach long recognized as potential competitors (Smyly, 1957; Hyslop, 1982; Mann, 1989; Welton *et al.*, 1983, 1991). Various species associations based in similar distribution emerged. Excepting the riffle and depositional guilds, the rest of the associations of fish showed no apparent habitat affinities and were randomly distributed with respect to the main habitat gradient. In the case of bullhead and loach, neither in this study nor in previous ones (Welton *et al.*, 1983) have any strong competitive interactions between the species been observed. However, a pollution incident that occurred in the river Frome in 1965, indicated the potential ability of bullhead to outcompete stone loach (Mann, 1989). The bullhead was numerically dominant with respect to stone loach, but the pollution incident selectively affected the bullhead. This event caused a dramatic increase of stone loach abundance. This persisted until the numbers of bullhead recovered, when the population reverted to levels similar to those before the pollution. Thus, it is possible to speculate that the lack of stone loach in Bere Stream was related to the high bullhead density found there. The low availability of large stones to nest could be one of the main factors keeping the bullhead at a low density in Mill Stream, and thus facilitating the thriving loach population in this site.

The species packaging observed in the study area (12 species in six groups distributed into three habitat guilds) seems to be the result of a division of the space available in such a way that potential interspecific interactions were minimized. Removing the effect of the few habitat affinities resulting from adaptive behaviour (riffle inhabitants) and evident exclusion by superior competitors, the rest of the species tended to be distributed following the previously stated rule (minimizing potential negative interactions). This must be general where habitat conditions are within the species tolerance limits. Similarly, Zaret & Rand (1971) found, in a tropical stream, 10 species represented in five distinct groups based on habitat and time separations. They suggested that this was a mechanism to reduce overlap during the time when the resources were in a shortest supply.

These results agree with the suggestion by Maitland (1965), that when a fish assemblage similar to that presented here, occurs in any one part of a river, the different species tend to separate spatially to reduce competition. This spatial separation would be most marked during periods of low flow, such as those occurring during this study.

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TABLE I. Habitat volume, flow and mean values (± 1 ES) of selected habitat variables measured or estimated in Mill Stream and Bere Stream during summer.

	MILL STREAM	BERE STREAM	r (1)
total volume (m^3)	375.76	645.30	
available volume (excluding cover) (m^3)	130.30	370.40	
flow ($m^3 s^{-1}$)	0.31	0.60	
substratum coarseness	5.03 ± 0.17	5.00 ± 0.15	-0.01
substratum heterogeneity	1.26 ± 0.30	1.16 ± 0.15	-0.04
depth (cm)	40.30 ± 1.10	33.60 ± 0.80	-0.22
depth heterogeneity	2.43 ± 0.30	1.98 ± 0.25	-0.16
current velocity ($m s^{-1}$)	0.20 ± 0.01	0.23 ± 0.01	0.11
flow variability	0.08 ± 0.01	0.11 ± 0.01	**0.32***
shade (%)	22.60 ± 8.00	36.90 ± 8.40	0.21
instream cover (%)	27.50 ± 6.30	57.40 ± 7.50	**0.44*****
channel width (m)	5.17 ± 0.30	7.68 ± 0.30	**0.85*****
detritus (%)	1.40 ± 0.20	1.30 ± 0.20	-0.04
water temperature (C)	19.70 ± 0.22	16.90 ± 0.35	**-0.78*****

(1) Pearson correlation coefficent with discriminant function

* P<0.05, ** P<0.01, *** P<0.001

TABLE II. Pearson correlations between the habitat variables included in the PCA and the first principal component. PC1 accounted for 32.5% of total variance. N=50.
* P<0.05, ** P<0.01, *** P<0.001

	r PC1
substratum coarsenes	**0.92*****
water current	**0.86*****
flow heterogeneity	**0.66*****
shade	**0.36****
detritus	**-0.81*****
instream cover	**-0.49*****
depth heterogeneity	**-0.35***
channel width	0.20
depth	-0.20
substratum heterogeneity	0.13

TABLE III. Mean fish density (ind. m^{-2}) and fish size (total length, mm) (± 1 SE) comparison for all fish species caught in the two streams sampled.

	DENSITY			SIZE		
	Mill Stream	Bere Stream	t	Mill Stream	Bere Stream	t
eel	0.88 ± 0.23	0.40 ± 0.12	1.70*	200.0 ± 25.7	358.0 ± 48.9	3.00**
minnow	11.92 ± 2.97	2.40 ± 0.60	3.27**	42.0 ± 0.5	54.8 ± 2.2	-7.41***
bullhead	0.80 ± 0.20	2.20 ± 0.54	-2.42*	36.4 ± 2.2	48.2 ± 2.3	3.21**
stickleback	0.32 ± 0.21	0.20 ± 0.13	0.30	24.5 ± 4.6	31.8 ± 5.9	-1.35
gudgeon	1.76 ± 1.03			103.1 ± 3.6		
brook lamprey	0.44 ± 0.18	0.32 ± 0.17	0.67	125.8 ± 4.4	75.6 ± 9.7	-5.40***
dace	0.32 ± 0.18			154.4 ± 14.3		
stone loach	4.56 ± 1.25			47.3 ± 1.7		
flounder	0.04 ± 0.04			270.0 ± 0		
salmon	0.60 ± 0.25	0.32 ± 0.13	0.64	72.9 ± 1.9	76.8 ± 1.2	-3.34**
trout	0.12 ± 0.07	1.04 ± 0.33	-3.07**	77.3 ± 3.28	124.7 ± 15.0	-2.05[1]
grayling	0.20 ± 0.10			92.4 ± 5.0		
TOTAL DENSITY	21.96 ± 3.68	6.90 ± 1.1	-3.88***			
TOTAL BIOMASS[2]	101.3 ± 26.5	123.8 ± 40.9	-0.24			

* $P<0.05$, ** $P<0.01$, *** $P<0.001$

[1] marginal significance ($0.05<P<0.1$)

[2] g m^{-2}

TABLE IV. Species associations after Pearson correlation with both PC1 and PC2 of principal components analysis of a fish density matrix, and comments on main habitat preferences for each species. 0, + or - in the first position indicates no correlation, significant (P≤0.05) positive and significant negative correlation, respectively with PC1; while in the second position the correlation is referred to the PC2. PC1 accounted for 20.7% of variance and PC2 for 16.1%.

species associations and guilds	habitat preferences
(+,+) *depositional guild*	
stone loach	more abundant in shallow depositional areas, increasingly larger at deeper sites
stickleback	avoided riffles, selected depositional areas at intermediate distances from shelter, more abundant in shallow depositional areas
eel	increased biomass in Bere Stream riffles
(+,-) *riffle guild*	
dace	selected riffles at intermediate distance from shelter, higher abundance and biomass in riffles
grayling	selected intermediate distance from shelter
salmon	avoided depositional areas, selected riffles (Mill) and avoided intermediate habitat categories (Bere)
(-,-) *generalists*	
trout	avoided depositional areas, more abundant in Bere riffles, selected intermediate habitat categories and avoided depositional areas in Mill
(+,0)	
minnow	Higher biomass in Bere depositional areas, random distribution in general
gudgeon	selected depositional areas, random distribution in Mill but at intermediate distance from shelter
(0,+)	
bullhead	random distribution, more abundant in shallow sites
lamprey	selected Bere riffles, higher biomass and density in Mill depositional areas
(0,-)	
flounder	

Figure captions

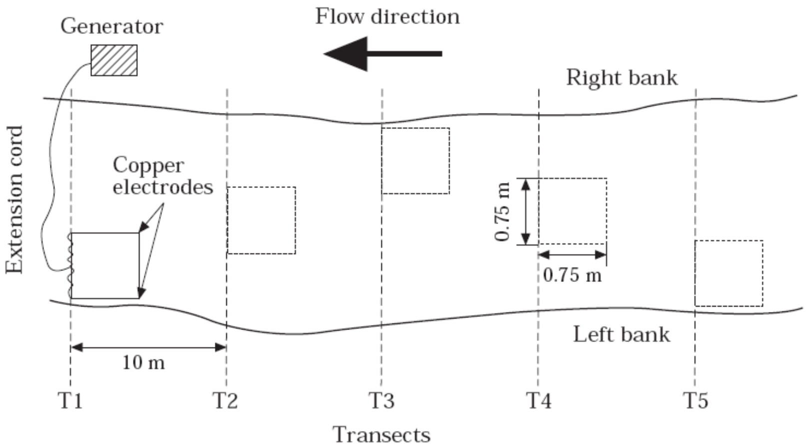

FIG. 1. Field sampling scheme.

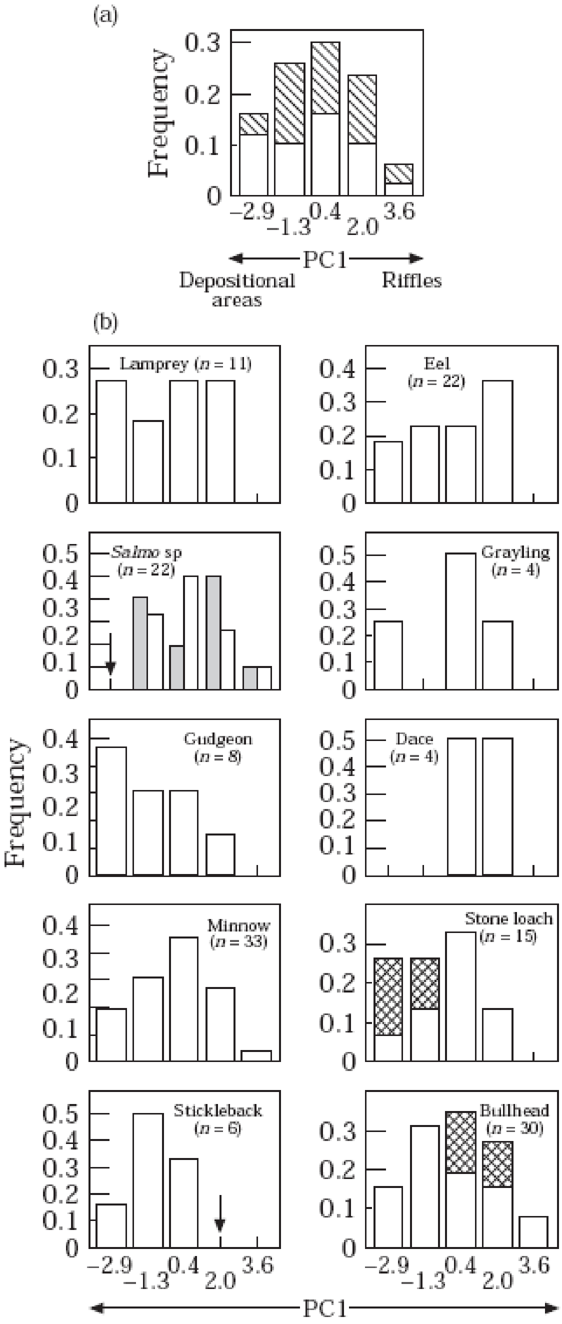

FIG. 2**.** Habitat availability and (b)fish microhabitat preferences in the Mill Stream and Bere Stream. (a) Frequency distribution of first component (PC1) scores of the PCA of stream habitat variables□. Mill Stream (n=25); ▧, Bere Stream (n=25). (b) Frequency distribution of fish species use data. Component categories in which the species was over-represented or under-represented are respectively represented by shaded bars and arrows (partitioned χ^2-analysis, P<0.05). In the case of *Salmo* spp, Atlantic salmon (n=15) and trout (n=13) are represented by ▒ and □, respectively. ▩, Nursery habitat distribution for stone loach and bullhead.

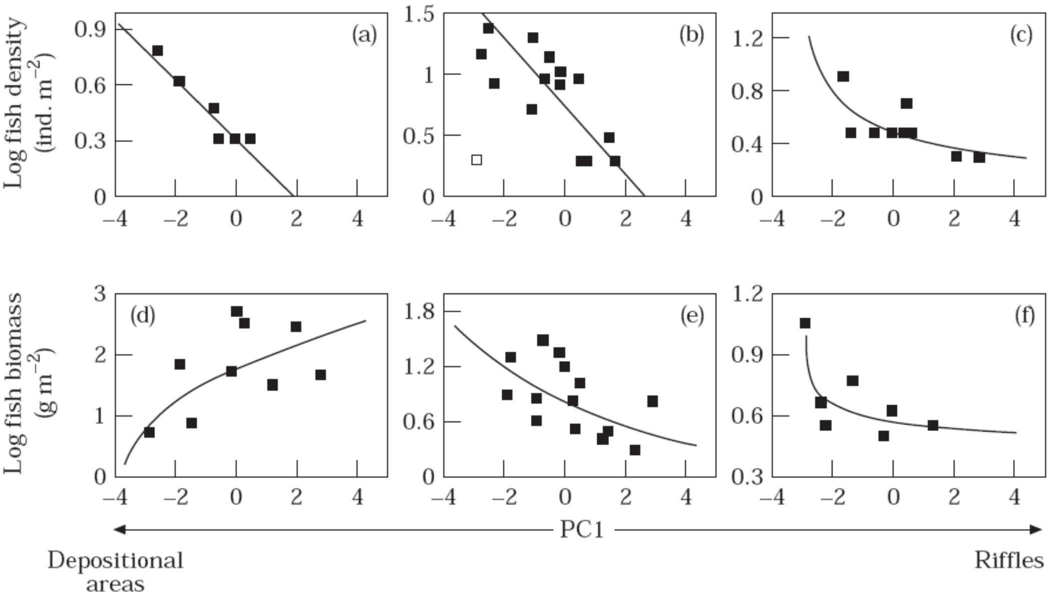

FIG. 3. The effect of depositional-erosional gradient on selected species density and biomass (only the significant relationships are included). Stickleback (Mill and Bere), F=35·5, r^2=89·9%, P=0·004, (b) Stone loach (Mill), F=16·0, r^2=57·1%, P=0·002; (c) trout (Bere), F=15·0, r^2=62·5%, P=0·04; (d) eel (Bere), F=6·2, r^2=47·1%, P=0·041; (e) minnow (Bere), F=5·8, r^2=32·6%, P=0·033; (f) lamprey (Mill), F=10·2, r^2=67·1%, P=0·024.

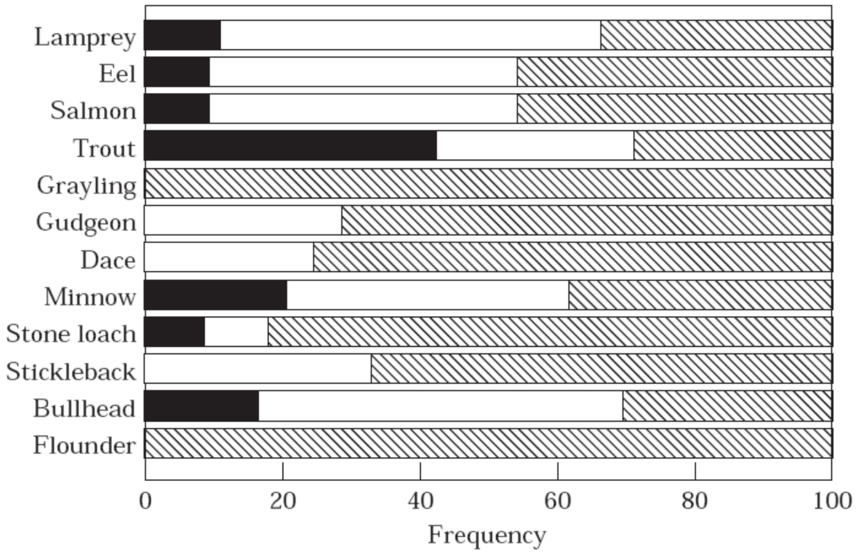

FIG. 4. Frequency distribution of the number of times each species was captured in groups of 1-2 (■), 3-4 (□) or 5-6 (▧) species in both the Mill Stream and Bere Stream.

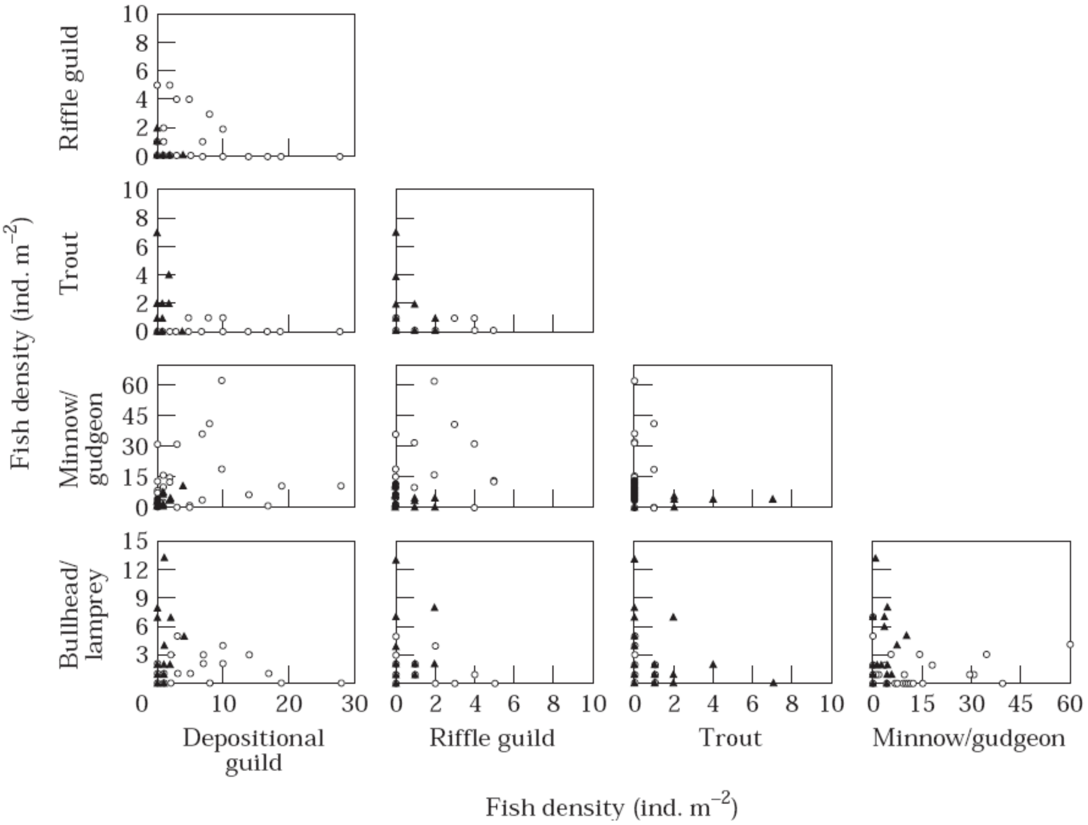

FIG. 5. Biplot of the density of each pair of species associations established in the study area. See Table IV for interpretation of associations. ○, Mill Stream; ▲, Bere Stream.

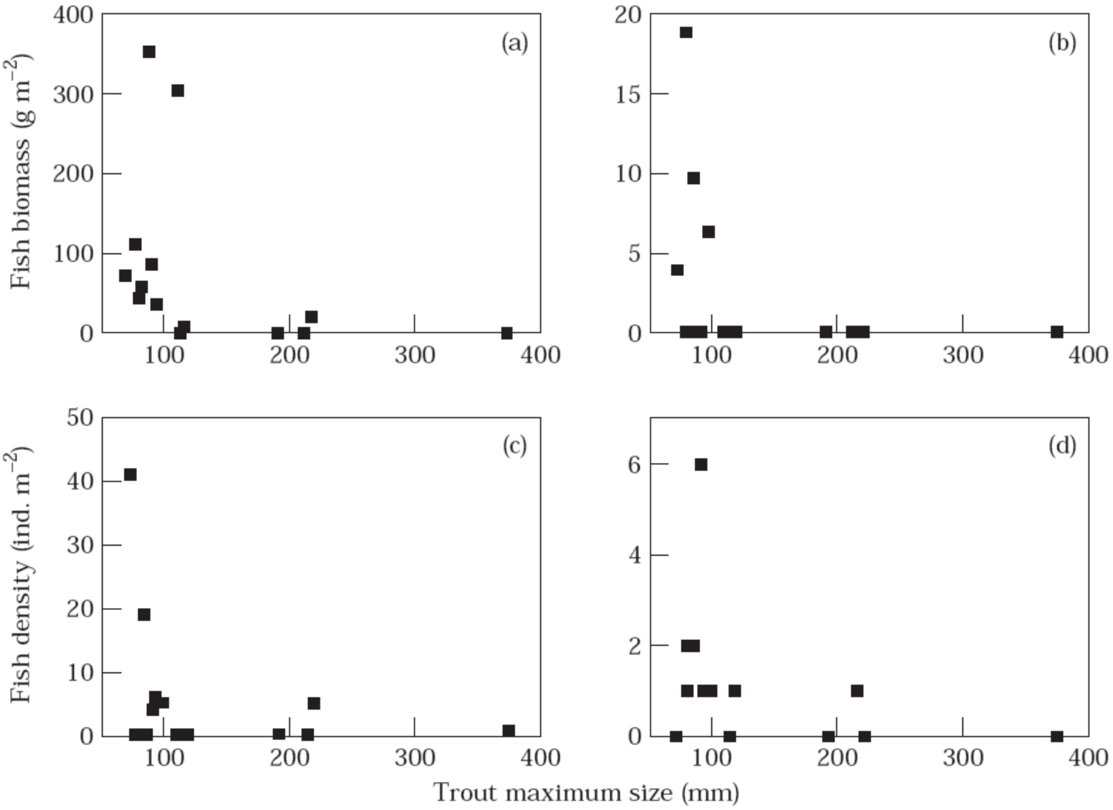

FIG. 6. Relationship between trout maximum size (a), the whole fish assemblage (r^2=66·5%, P=0·0012), (b) salmon biomass (g m^{-2}) (r^2=35·4%, P=0·025) and (c) minnow (r^2=34·6%, P=0·027) and (d) bullhead density (r^2=48·4%, P=0·008) (ind. m^{-2}) in the Mill Stream and Bere Stream.