DIEL AND SEASONAL PATTERNS OF HABITAT USE BY FISH IN A NATURAL SALMONID BROOK : AN APPROACH TO THE FUNCTIONAL ROLE OF THE RIFFLE-POOL SEQUENCE.

J.M. ROUSSEL, A. BARDONNET

INRA, Laboratoire d'Ecologie Aquatique, 65 rue de Saint-Brieuc, 35042 Rennes Cedex, France.

Reçu le 23 mai 1997
Accepté le 17 juillet 1997

Received 23 May, 1997
Accepted 17 July, 1997

ABSTRACT

The spatio-temporal use of the riffle-pool sequence in a natural salmonid brook was studied by day and night for one year on brown trout (*Salmo trutta* L.), bullhead (*Cottus gobio* L.), European minnow (*Phoxinus phoxinus* L.) and stone loach (*Barbatula barbatula* L.). Young-of-the-year brown trouts were more numerous in riffles in spring, whereas older trouts chose pools. A diel pattern of habitat use between riffle and pool was observed for one-year-old individuals, who moved towards riffle during daylight in summer and early fall. Seasonal variations in trout densities were related to movements at a large spatial scale before and after the spawning period. Bullhead preferred riffles to pools, especially young-of-the-year individuals, even if this preference decreased during ontogenesis. On the contrary, minnow chose pools throughout the year and seemed to leave the riffle-pool sequence for spawning, whereas no preference was observed for loach except for riffle during the spawning period. Results and an approach to the functional role of the riffle-pool sequence in lowland salmonid brooks are discussed.

Key-words : brown trout, bullhead, European minnow, stone loach, salmonid brook, riffle-pool sequence, spatial heterogeneity, diel preferences, seasonal preferences, functional habitat.

VARIATIONS JOURNALIÈRES ET SAISONNIÈRES D'UTILISATION DE L'HABITAT PAR LES POISSONS EN RUISSEAU À SALMONIDÉS : UNE APPROCHE DU RÔLE FONCTIONNEL DE LA SÉQUENCE RADIER-PROFOND.

RÉSUMÉ

La succession radier-profond constitue le principal élément d'hétérogénéité géomorphologique en petits cours d'eau à truites peu pentus. Ces deux faciès présentent des caractéristiques d'écoulement radicalement différentes qui supposent des conditions d'habitat elles aussi très différentes. Dans ce travail, l'utilisation spatio-temporelle de la séquence radier-profond a été étudiée de jour et de nuit tout au long de l'année pour les espèces les plus souvent rencontrées dans ce type de ruisseau, à savoir : la truite (*Salmo trutta* L.), le chabot (*Cottus gobio* L.), la loche (*Barbatula barbatula* L.) et le vairon (*Phoxinus phoxinus* L.). Les juvéniles de truite de l'année occupaient préférentiellement les radiers (au moins au printemps) alors que les truitelles d'au moins 1 an ont montré un net choix pour le profond. Les compartiments radier et profond ont été utilisés différemment au cours du nycthémère par les truitelles d'un an, dont une partie se déplaçait vers les radiers le jour en période estivale. Les fluctuations saisonnières de densités ont été expliquées par des différences de recrutement

Article available at http://www.kmae-journal.org or http://dx.doi.org/10.1051/kmae:1997005

annuel et des mouvements de population avant et après la reproduction. Le chabot préférait le radier au profond, cette préférence était très marquée pour les plus jeunes individus puis s'atténuait au cours de l'ontogenèse. Au contraire, le vairon a nettement préféré le profond et aucun changement n'a pu être mis en évidence ; cependant, les faibles densités en juin étaient probablement liées à des déplacements hors secteurs pendant la reproduction. La loche quant à elle était répartie à part égale entre les deux types de faciès, sauf en juin où sa préférence pour le faciès radier était probablement liée à la recherche d'un habitat de reproduction. L'analyse éco-éthologique des résultats obtenus dans ce type de milieu permet d'approcher le rôle fonctionnel de la séquence radier-profond à trois des échelles biologiques de la structure des ichtyocénoses : peuplement, population et individu.

Mots-clés : truite fario, chabot, vairon, loche, ruisseau, séquence radier-profond, hétérogénéité spatiale, préférences journalières, préférences saisonnières, habitat fonctionnel.

INTRODUCTION

Natural salmonid streams provide a large set of physical habitat conditions for the development of aquatic fauna, and fish usually inhabit most available habitats. The stream fish community is generally composed of benthic and nectonic species exhibiting different habitat preferences and segregated according to water depth, velocity and substratum size gradients (GRIFFITH, 1972 ; JONES, 1975 ; BAGLINIÈRE and ARRIBE-MOUTOUNET, 1985 ; GLOVA and SAGAR, 1993 ; GIBSON *et al.*, 1993). Spatial heterogeneity and physical framework are therefore important factors in describing stream fish habitat. In their review, NIEMI *et al.* (1990) concluded that the loss of habitat diversity due to physical alterations of the stream channel was the most common impact associated with long recovery times for fish populations. From FRISSELL *et al.* (1986), physical habitat in streams can be defined as hierarchically nested subdivisions, from the largest scale of the entire river basin and drainage network, to the smallest microhabitat scale which refers to point conditions in the channel. At a median and local scale, an important source of physical habitat heterogeneity depends on geomorphological processes in the stream channel. The channel type, width and slope, combined with flow obstructions in the stream bed (blocks or coarse woody debris), generate particular hydraulic conditions that favour scour and depositional processes. These general mechanisms contribute to the formation of channel geomorphic units, also called habitat types, defined as areas of relatively homogeneous depth, velocity and substratum characteristics. Applications in fishery management have led to the proposal of several classifications of habitat types (BISSON *et al.*, 1982 ; FRISSELL *et al.*, 1986 ; MALAVOI, 1989 ; BRYANT *et al.*, 1992 ; HAWKINS *et al.*, 1993 ; JOWETT, 1993 ; RABENI and JACOBSON, 1993). In spite of variability between observers when naming habitat units (ROPER and SCARNECCHIA, 1995), two basic units correspond to the commonly used terms « riffle » and « pool », a general level of resolution that segregates shallow fast-flowing and deep slow-flowing habitats. In most alluvial valleys, the riffle-pool sequence is a natural habitat feature of the river channel that occurs regularly (see BISSON and MONTGOMERY, 1996 for synthesis). Therefore, the riffle-pool sequence as an entire habitat unit could be of great interest for fishery biologists.

In a one-year study, we evaluated diel and seasonal variations in riffle and pool utilization by fish in a typically alluvial salmonid brook in Brittany, France. Two questions were examined in detail : 1- How is the fish community (species and life stages) divided between riffle and pool habitats ? 2- Are there temporal changes (diel or seasonal) in their habitat type preference (riffle or pool) ? The role of the riffle-pool sequence as a functional habitat feature for fish in salmonid streams and management implications are then discussed.

STUDY SITE

The study was conducted in 1995-96 in the Kerlégan brook, a tributary of the Scorff river, Brittany, France (Figure 1). Its total length is 7.2 km and it drains an area of 20.4 km^2. The mean gradient is 13 m.km^{-1} and the bottom substratum is mainly gravel-sand, which corresponds to the « pool-riffle reach » according to BISSON and MONTGOMERY's stream classification (1996). Brittany has a temperate oceanic climate, and mean daily water temperatures recorded in the brook varied from 17°C (Aug-95) to 5.5°C (Dec-95). Minimum (Jun-95) and maximum (Sep-95) monthly precipitations were 10 mm and 180 mm, respectively. As in most salmonid rivers in Brittany, the development of macrophytes (especially *Ranunculus spp*) also contributes to seasonal modifications on channel hydraulics (HAURY and BAGLINIÈRE, 1996). Carex (*Carex paniculata*) forms the most frequent bankside emergent vegetation and is essentially distributed along pool margins of the brook.

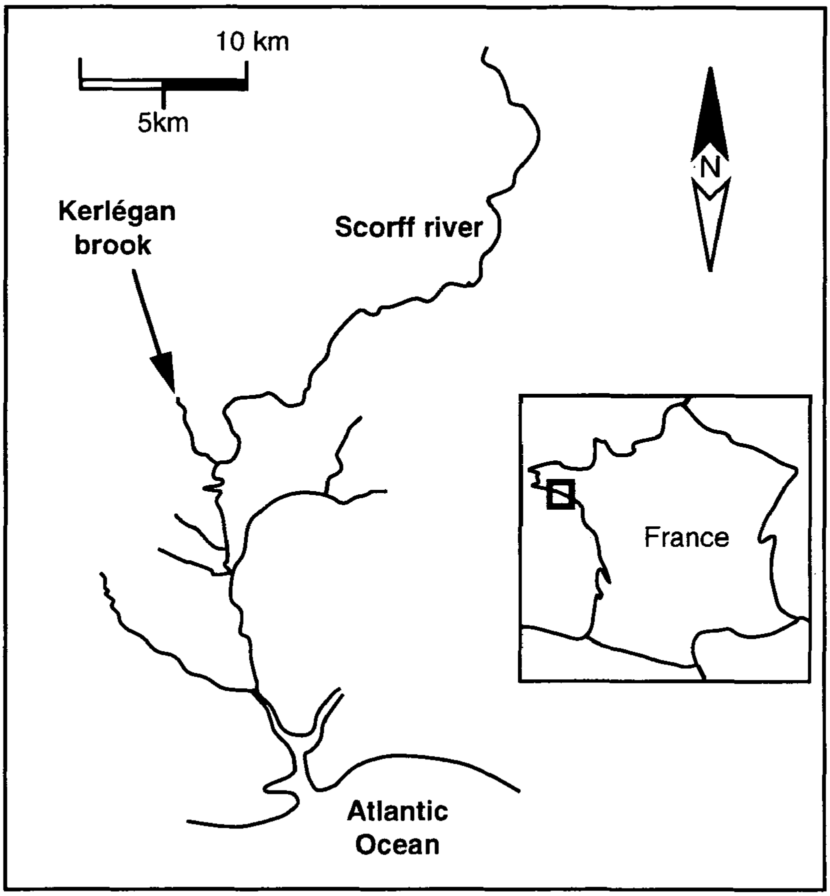

Figure 1
Map of the study site.

Figure 1
Carte du site d'étude.

MATERIALS AND METHODS

Four surveys were conducted in June 1995, October 1995, January 1996 and April 1996. In the kilometre before the confluence with the Scorff river, three similar riffle-pool sequences spaced 50 to 150 metres apart (see Table I for habitat description) were electrofished with an AC generator (200 W, continuous output) using the removal method (DE LURY, 1951). In order to compare day and night densities in the same sequence, in each season, two sequences were electrofished by day (at least 3 h after dawn) and one by night (at least 3 h after dusk). Two weeks later, an inversed sampling (one unit by day, two units by night) was performed. At night, the sampling area was lit with a 500 W halogen spot light. There was no electrofishing during full moon nights. A special dipnet design (mesh 3 mm) pre-positioned across the channel and above the water surface made it possible to partition each sequence in closed riffle and pool habitats synchronously without wading just before electrofishing. When riffles and pools were closed, an operator carrying a 30 cm ring anode waded from the downstream to the upstream end of each sequence. Two other people netted fish with 20 cm ring net handles (mesh 3 mm) and special 60 cm semi-circular section net handles (mesh 3 mm) held flat against the bottom in the riffle. All fish caught were anesthetized (phenoxyethanol), measured (nearest mm) and then released inside the habitat type where they were caught. Each trout was individually marked with a miniature Passive Integrated Transponder (PIT), and scales were sampled to determine age in the laboratory.

Age structure in non-salmonid populations was evaluated by graphic analyses of modes in body length frequencies (BHATTACHARYA, 1967). Mean population densities in pool and riffle were estimated for day and night samples by the CARLE and STRUB method (1978) using Microfish 3.0 software (VAN DEVENTER and PLATTS, 1989). Hypotheses about differences in day and night use of riffle and pool were tested with non parametric Wilcoxon-Mann-Whitney tests (WMW test).

Table I

Mean riffle and pool characteristics and seasonal habitat variations in the three riffle-pool sequences studied.

Tableau I

Caractéristiques mésologiques moyennes et variations saisonnières sur les trois séquences radier-profond de l'étude.

		RIFFLE	POOL
Total length (m)		24	26
Mean width (m)	*Jun. 95*	2.9	2.8
	Oct. 95	2.4	2.7
	Jan. 96	3.1	2.9
	Apr. 96	3.1	2.9
Mean surface area (m^2)		69	73
Mean depth (cm)	*Jun. 95*	8.6	27.2
	Oct. 95	7.1	24.2
	Jan. 96	22.5	41.7
	Apr. 96	15	33
Mean velocity ($cm.s^{-1}$)	*Jun. 95*	23	8
	Oct. 95	14	5
	Jan. 96	51	27
	Apr. 96	20	8
Bottom substrate (Wentworth scale)	*Jun. 95*	gravel	silt - sand
	Oct. 95	and	silt - sand
	Jan. 96	small	sand-gravel
	Apr. 96	cobbles	sand-gravel
Macrophyte cover (%)	*Jun. 95*	83	25
	Oct. 95	42	8
	Jan. 96	33	25
	Apr. 96	75	25
Stream flow ($l.s^{-1}$)	*Jun. 95*	58	
	Oct. 95	28	
	Jan. 96	335	
	Apr. 96	85	

RESULTS

A total of 11 species were caught on each sampling date. Roach (*Rutilus rutilus* L.), dace (*Leuciscus leuciscus* L.), gudgeon (*Gobio gobio* L.), Atlantic salmon (*Salmo salar* L.) and eel (*Anguilla anguilla* L.) were minority species. Numerous juveniles of sea (*Petromizon marinus* L.) and brook (*Lampetra planeri* Bloch) lamprey had buried themselves into the silty habitats of pools, and so inadapted electrofishing precluded correct estimations of their population densities. Bullhead (*Cottus gobio* L.), European minnow (*Phoxinus phoxinus* L.), stone loach (*Barbatula barbatula* L.) and brown trout (*Salmo trutta* L.) represented over 90 % of all individuals caught during the four surveys. These were then more precisely investigated. For each survey, no significant difference was found between the total number of fish caught during the first and the second electrofishings which took place two weeks later ($p>0.10$, WMW test). This indicates that there was no influence of successive electrofishings on species population densities.

Bullhead

Bullhead was the most numerous species in the brook, and represented 57 % of all individuals caught during the entire experiment. No diel difference was observed in its distribution within the riffle-pool sequences (Figure 2). Densities in the pool were constant and significantly lower (1 ind/m^2) than in riffle ($p<0.05$, WMW test). On the contrary, densities in riffle varied from 6 ind/m^2 (Oct-95) to 1.5 ind/m^2 (Jan-96) over the year. These differences were related to demographic changes within the population. Three life stages were clearly identified by body length frequency analysis (Figure 4) : young-of-the-year (0^+), one-year-old (1^+) and older fish ($^{>}1$). 0^+ appeared in electrofishing samples in Jun-95, but densities were probably underestimated because of their small body size (20 mm on average). After a first summer, their mean body size was 38 mm (Oct-95) making them easier to catch. This explains why the highest densities of bullhead were estimated in riffles in Oct-95 (6 ind/m^2), 58 % of which were 0^+. More than 90 % of all 0^+ electrofished came from riffles. During winter, densities strongly decreased for all life stages (1.5 ind/m^2 in Jan-96). The 0^+ still represented 55 % of the total population, but their choice for riffle habitat was less marked (78 %). In spring (Apr-96), 32 % of the new one-year-old cohort was caught in pools, which corresponded to the proportion of the total population that was electrofished in pools. Growth almost stopped during winter, as shown by the mean body size in Apr-96 (39 mm). For older bullheads, mean body sizes showed little increase from summer to winter (from 47.5 to 49.8 mm and from 64.5 to 65.6 mm for 1^+ and $^{>}1$, respectively), suggesting a higher growth rate in spring for this species.

Minnow

No diel difference was found in the distribution of minnow within the riffle-pool sequences (Figure 2). Unlike bullhead, minnow densities were always lower in riffles (from 0 ind/m^2 in Jun-95 to 0.4 in Apr-96) than in pools, and this was significant in Oct-95, Jan-96 and Apr-96 ($p<0.05$, WMW test). However, densities in pools varied from less than 0.1 ind/m^2 (Jun-95) to 2 ind/m^2 (Oct-95) over the seasons. Like for bullhead, these differences were related to demographic changes within the population. Only the young-of-the-year cohort (0^+) was clearly identified from analysis on body length frequencies. 0^+ appeared in the Oct-95 sampling and represented only 32 % of the minnow population (Figure 4). Their mean body size was 30 mm and it was not clear whether the electrofishing had been efficient or not. No 0^+ was caught in Jan-96, and their growth almost stopped in winter as shown by their mean body size in Apr-96 (33 mm) when 29 % of minnow caught were 0^+. No 0^+ and only a few older individuals were electrofished in Jun-95 (Figure 2).

Stone loach

Stone loach densities were globally lower than those of bullhead and minnow (Figure 2). No significant habitat choice was recorded, except in Jun-95 when densities were highest in riffle (0.5 ind/m^2) and lowest in pool (0.1 ind/m^2). No diel difference was found in the distribution

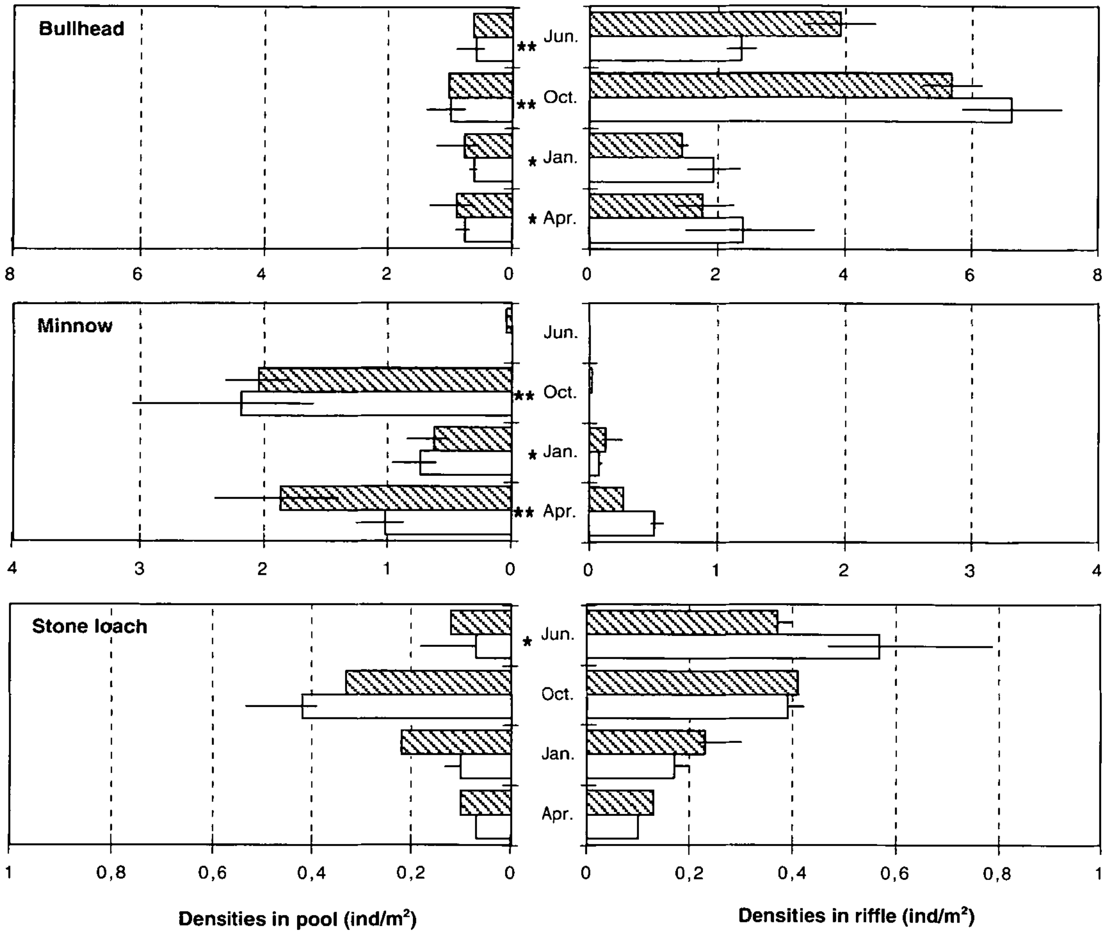

Figure 2

Diel and seasonal densities estimated in riffle and pool for bullhead, minnow and stone loach. Blank and hatched bars represent daylight and night samplings, respectively. Horizontal lines represent a 95 % confidence level for estimated populations ($p<0.05$, Student t distribution). Statistical differences in densities between riffle and pool, by day and night, are estimated by non parametric Wilcoxon-Mann-Whitney tests (* : $p<0.05$; ** : $p<0.01$).

Figure 2

Estimations journalières et saisonnières des densités en radier et en profond pour les chabots, vairons et loches. Les barres blanches et hachurées représentent les échantillonnages de jour et de nuit, respectivement. Les traits horizontaux représentent les intervalles de confiance à 95 % ($p<0,05$, distribution t de Student) des densités estimées. Les différences statistiques de densités calculées entre radier et profond, de jour et de nuit, sont évaluées par des tests non paramétriques de Wilcoxon-Mann-Whitney (* : $p<0,05$; ** : $p<0,01$).

of stone loach within the riffle-pool sequences. Unfortunately, the small amount of individuals caught per season meant that a correct analysis of cohorts in body length frequencies was not possible.

Brown trout

Three age classes were identified for brown trout by scalimetric analysis : young-of-the-year (0^+), one-year-old (1^+) and older fish (>1). Three-year-old trouts represented 21 % of >1 caught for all sampling dates. During the year, mean size-class for 0^+ ranged from 28 mm after

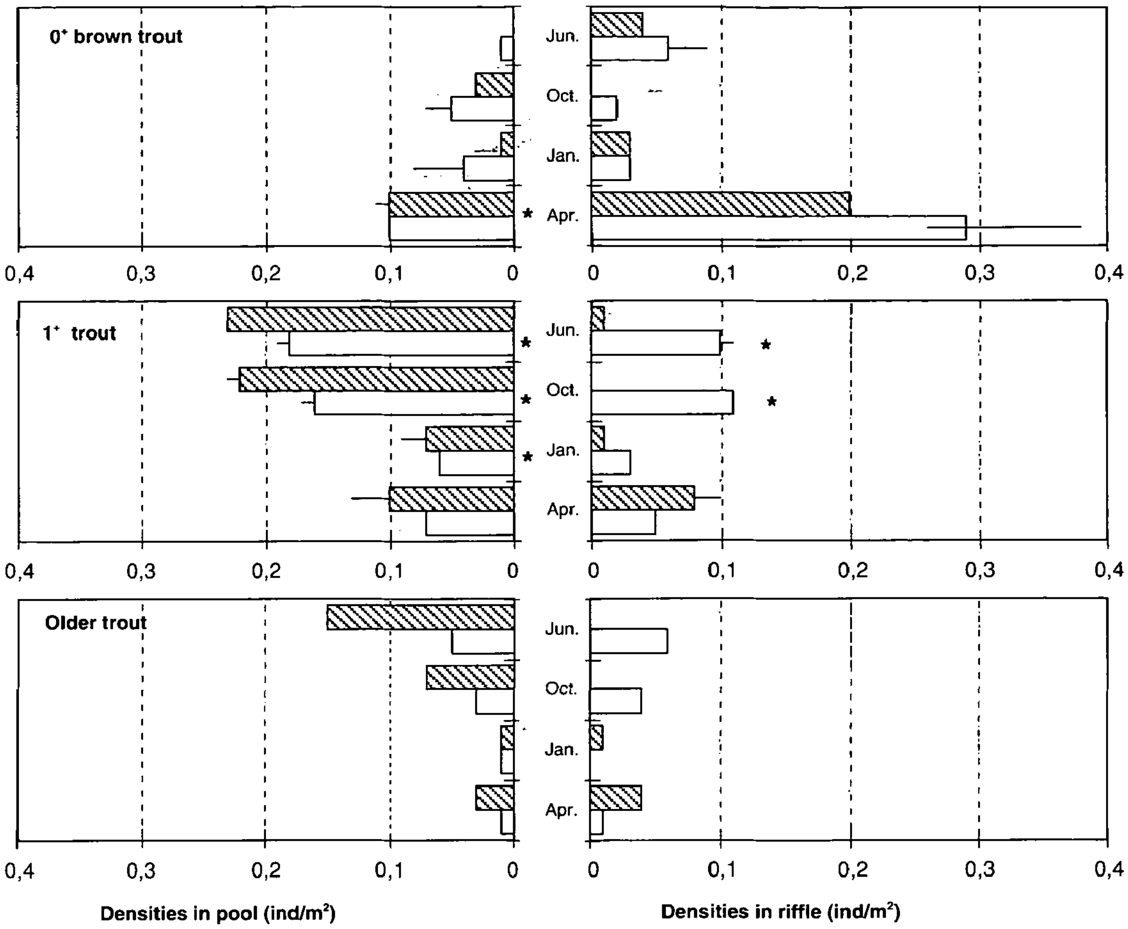

Figure 3

Diel and seasonal age-classes densities for brown trouts estimated in riffle and pool (see Figure 2 for explanations).

Figure 3

Estimations journalières et saisonnières des densités de truites en radier et en profond par classes d'âge (voir Figure 2 pour plus de détails).

emergence to 85 mm in their first winter, from 103 mm to 138 mm for 1^+, and from 164 mm to 185 mm for $^>1$ (Figure 4). Analysis of the seasonal evolution in fork length for individually marked and recaptured 1^+ and $^>1$ trouts showed that individual mean growth was high in summer and stopped in fall and early winter except for one trout (Figure 5). Thereafter, mean body size increased from winter to spring.

The trout population mainly comprised 1^+ fish from Jun-95 to Jan-96 (Figure 3). In 1995, recruitment was very low because of an exceptionally high flood (one per hundred years) during the winter 1994-95. However, the 1996 recruitment was much better and consequently, densities of 0^+ were high in Apr-96 samples. For this period, soon after emergence, 0^+ were significantly more numerous in riffle ($p<0.05$, WMW test). The 1^+ cohort significantly preferred pools from Jun-95 to Jan-96 ($p<0.05$, WMW test), whereas no preference between the two habitat types was observed in Apr-96. Older trouts ($^>1$) showed the same tendencies as 1^+, even if results were not statistically significant. Significant diel differences in 1^+ trout distributions in

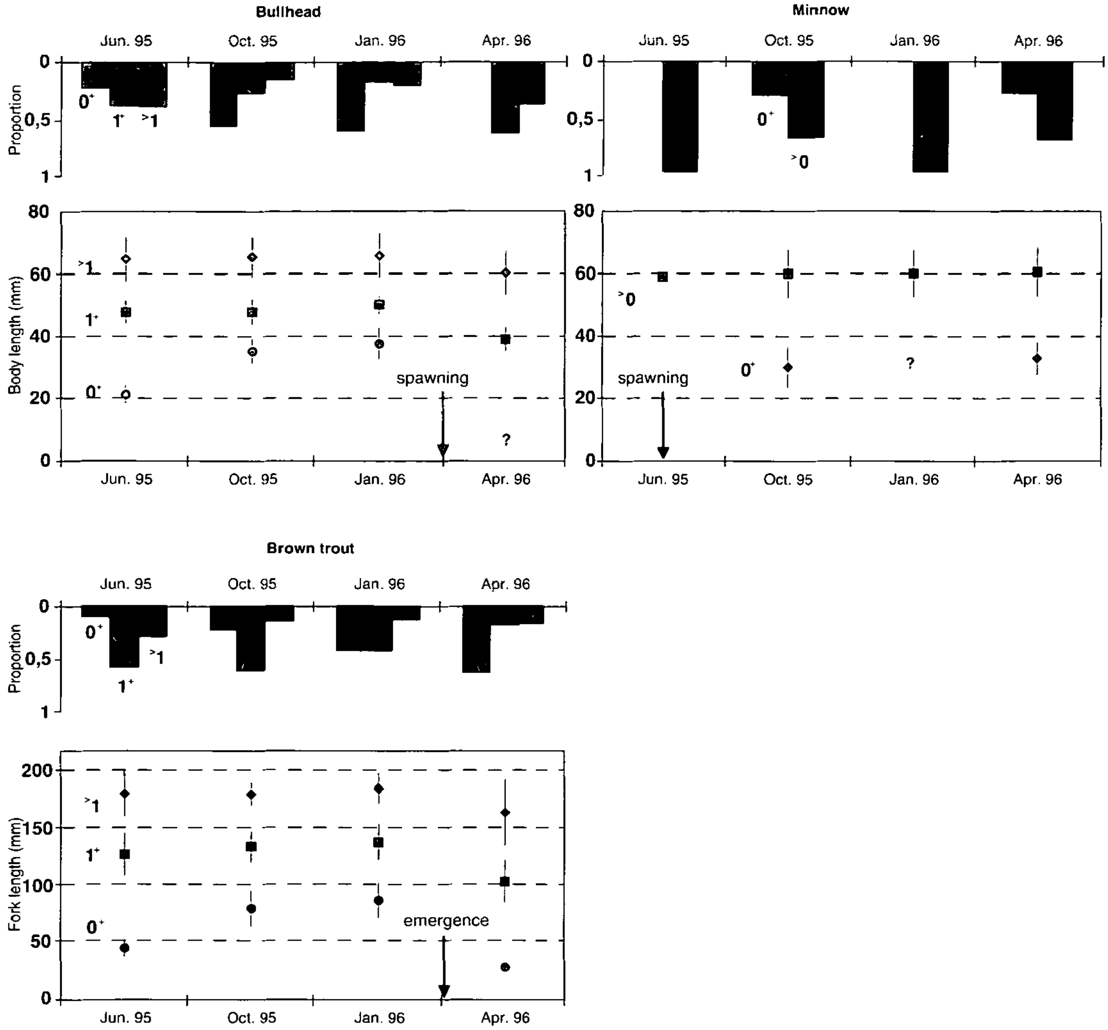

Figure 4

Seasonal variations in age structure for bullhead, minnow and brown trout populations (dark bars), and in mean body sizes for each age class. Vertical lines represent standard deviation (SD).

Figure 4

Variations saisonnières de la composition des populations de chabots, de vairons et de truites selon les classes d'âge (barres noires), et des longueurs moyennes pour chaque classe d'âge. Les traits verticaux représentent les écarts types autour de la moyenne.

riffle were recorded in Jun-95 and Oct-95. For this period, almost all trouts were in pools at night while they used both riffles and pools during daylight. This was significant for 1+, but >1 trouts showed the same temporal pattern.

Analysis of individually marked trouts indicated that 49 % (Jun-95) and 61 % (Oct-95) of fish caught during the first electrofishing were recaptured two weeks later in the same riffle-pool sequence (Figure 6). This riffle-pool fidelity dropped in winter (22 % in Jan-96) and then increased again in spring (30 % in Apr-96). This general pattern was also confirmed in riffle-pool fidelity between seasons.

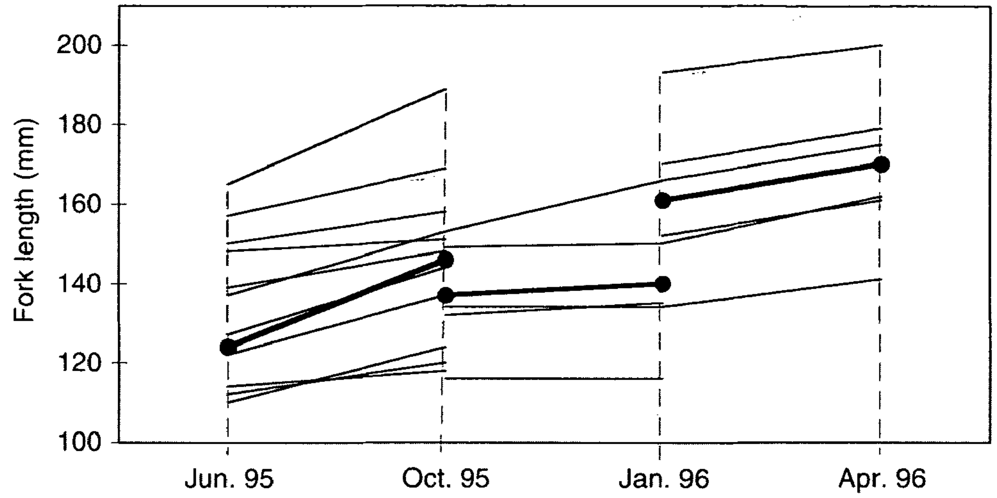

Figure 5

Seasonal variations in fork length for individually marked and recaptured trouts. Light lines represent individual growth, heavy lines mean value.

Figure 5

Variations saisonnières de la longueur fourche des truites marquées et recapturées lors des différentes pêches. Les traits fins représentent la croissance de chaque individu, les traits épais la croissance moyenne.

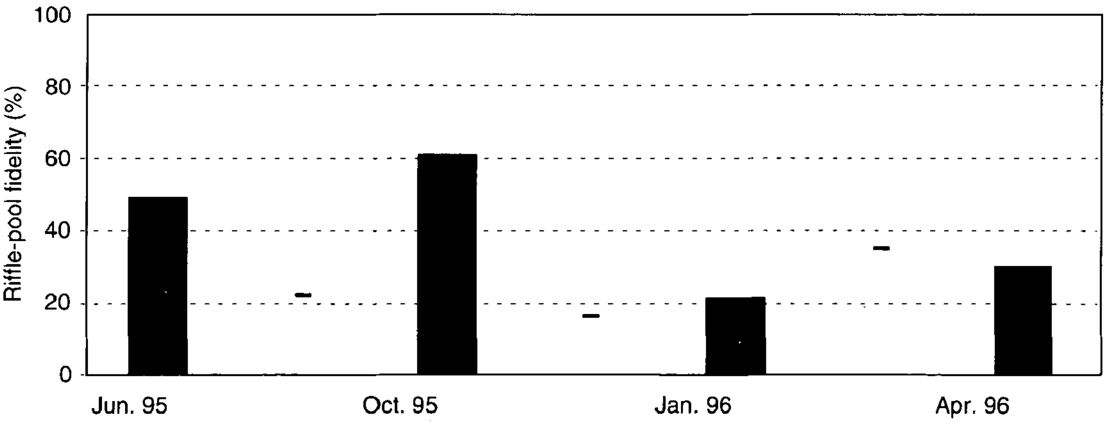

Figure 6

Percentage of individually marked and recaptured trouts in the same riffle-pool sequence two weeks apart for each season (dark bars), and between seasons (horizontal lines).

Figure 6

Pourcentage de truites marquées et recapturées dans la même séquence radier- profond à deux semaines d'intervalle (barres noires), et d'une saison à l'autre (traits horizontaux).

DISCUSSION

Bullhead, minnow, brown trout and stone loach are widely distributed along the longitudinal axis in streams in Brittany (OBERDORFF and PORCHER, 1992). In the Scorff river basin, sympatric populations of these species can occur in the main river (BAGLINIÈRE and ARRIBE-MOUTOUNET, 1985) and in tributaries, where they are the predominant species with eel (BAGLINIÈRE, 1979). Some field and experimental studies have been concentrated on the potential overlap of diets and/or habitat requirements (MAITLAND, 1965 ; MANN and ORR, 1969 ; LIEN, 1981 ; NEVEU, 1981 ; BALTZ *et al.*, 1982 ; WELTON *et al.*, 1983 ; GLOVA, 1987 ; BROWN, 1991), but little is known about the temporal aspect of habitat use. On a seasonal scale, habitat shifts are closely related to the life history of species, like ontogenetic changes in habitat requirements (ELLIOTT, 1986 ; BAGLINIÈRE *et al.*, 1989 ; BALTZ *et al.*, 1991 ; SEMPESKI and GAUDIN, 1995 ; KOCIK and TAYLOR, 1996), spawning (BAGLINIÈRE *et al.*, 1987 ; MEYERS *et al.*, 1992) and overwintering migration (CUNJAK and POWER, 1986 ; SWALES *et al.*, 1986 ; BROWN and MACKAY, 1995), whereas diel habitat shifts usually correspond to circadian rhythms of resting and feeding activities (CAMPBELL and NEUNER, 1985 ; KWAK *et al.*, 1992 ; HEGGENES *et al.*, 1993 ; ROUSSEL and BARDONNET, 1996).

Seasonal changes in densities

For bullhead, the decrease in winter did not affect the structure of the population and the respective percentages of each age class. The density of 1^+ and older individuals in April 1996 is similar to those observed in June 1995. This would indicate that a high winter mortality (more than 50 %) affects the bullhead population. In April 1996, the 0^+ cohort is still missing in electrofishing samples, but their catchability is probably null because of a total body length of less than 10 mm after hatching (SMYLY, 1957). In trout, the decrease recorded in January for the 1994 cohort (1^+) can be explained by the general pattern of upstream spawning migration (which includes 1^+ mature individuals), as described by BAGLINIÈRE *et al.* (1987). Thereafter, there is a small increase in April 1996 for the 1995 cohort density (the new 1^+ cohort). This re-equilibrium in 1^+ densities in the low part of the brook could be the result of a downstream movement from the upper part of the brook initiated in the previous autumn by 0^+, as studied by BAGLINIÈRE *et al.* (1989) in another tributary of the Scorff river. For minnow, a winter decrease was also observed, with 0^+ individuals absent from electrofishing samples. According to diving observations in Kerlégan pools (ROUSSEL and BARDONNET, unpublished data), 0^+ minnow may exhibit a strong winter concealment in carex fine roots along pool margins. This makes catching them by electrofishing very difficult, because of their quiescent behaviour and the low water temperature. Thereafter, the increase in densities in April 1996 is related to the re-appearance of 0^+ in samples. During the breeding period, very few individuals were caught in June 1995. Minnow is a lithophil species that breeds on gravel bars (BALON, 1975). Such spawning areas are characterized by shallow, swift waters (PONCIN, 1996). Because of the high density of spawning shoals, their space partition on spawning areas is very patchy and possibly none of them was present in the sampled areas. For loach, the decrease in density in January and April cannot be explained by population dynamics since densities were too low to identify age classes.

Habitat type choice

Minnow

According to the literature, habitat preferences in European minnow depend on stream size. On a 15 m width station in the Scorff river, BAGLINIÈRE and ARRIBE-MOUTOUNET (1985) observed that densities of minnow in October were the highest in shallow and lotic habitats (about 20 cm depth and from 20 to 40 cm/s). Under similar conditions in the river Nivelle (France), NEVEU (1981) hypothesized that they avoided the deepest habitats (more than 50 cm depth) because of the presence of predators. The increased use of shallow habitat by minnow under predation risk has been recently pointed out under experimental conditions (EKLÖV *et al.*, 1994). However, results on small streams (less than 6 m width) showed that minnow usually inhabit the deepest (more than 30 cm) lentic areas (MAITLAND, 1965 ; JONES, 1975 ;

BAGLINIÈRE, 1979). This corresponds to a preference for pools, as observed in Kerlégan brook for all life stages. The minnow's affinity for cover and shelter structures, especially for coarse woody debris (NEVEU, 1981), macrophytes (LIEN, 1981; MASTRORILLO *et al.*, 1996) or stony bottom substrate (JACOBSEN, 1979 ; BAGLINIÈRE and ARRIBE-MOUTOUNET, 1985), has often been reported by authors. Along the pool margin in the Kerlégan brook, over hanging carex provides a large amount of overhead cover and shelter (underbank, fine roots).

Stone loach

As many loaches were found in pools as in riffles, except in June. This wide distribution in different habitat types was also noted by MAITLAND (1965) and ZWEIMÜLLER (1995) in lowland brooks, even if MAITLAND noticed a slight preference for pools. However, JONES (1975) observed a marked preference for riffle or run (depending on the stream studied), with in all cases the lowest densities in pools. Contradictions in the literature about loach habitat use are common and difficult to clarify. The stone loach is a very discreet species and little is known about its habitat requirements. Despite its strong association with the bottom as a benthic species, SMYLY (1955) did not find any preference for sandy, gravelly and muddy bottoms. The use of shelter during daylight has been described by BURDEYRON (1981), and stone loach did not seem to need any specific structures to exhibit this behaviour since they are able to bury themselves in the sandy bottom. BURDEYRON (1981) observed a seasonal displacement towards areas with aquatic macrophytes in spring and departure at the beginning of fall, and suggested that fish moved in spring to reproduce on macrophytes. This could explain why in June they were more numerous in riffle than in pool, since *Ranunculus spp* mainly developed on riffles (Table I).

Bullhead

Bullheads, like freshwater *Cottidae* in general, are morphologically adapted to hold a position on the bottom in high velocities without energy constraints (FACEY and GROSSMAN, 1992). Depending on the study, they inhabit either fast-flowing (BAGLINIÈRE, 1979 ; BAGLINIÈRE and ARRIBE-MOUTOUNET, 1985 ; COPP, 1992) or slow-flowing habitats (GAUDIN, 1981 ; GAUDIN and CAILLÈRE, 1990). In October, almost all (90 %) young-of-the-year individuals were electrofished in riffles. Riffles in Kerlégan brook may be attractive to bullhead for two different reasons : the use of unembedded cobbles as shelter is well known in freshwater *Cottidae* (BROWN, 1991 ; GREENBERG and STILES, 1993 ; HARO and BRUSVEN, 1994) and stone shelters are in limited number in pools (Table I). The other reason may be trophic : indeed, PETTY and GROSSMAN (1996) reported that patchy distribution in mottled sculpins (*Cottus bairdi* Girard) in large streams was constantly related to prey abundance. A similar patchy distribution could correspond to riffle habitat in the Kerlégan brook, since riffles are known to be higher benthos-producing areas (LOGAN and BROOKER, 1983 ; BROWN and BRUSSOCK, 1991). The use of riffle was more pronounced in 0^+ fish, even if it decreased through the seasons to reach 70 % in April, which corresponded to the total population proportion in riffle. GREENBERG (1991) reported that small benthic fish avoided deep habitats because of a higher predation risk. As they grow, bullheads become less and less vulnerable to fish predation, and at the same time are able to eat larger prey (ANDREASSON, 1971). A shift in feeding habits could lead them to explore deeper habitats. It is then possible that the slight seasonal decrease in preference from riffle nursery areas towards pool habitats may result from a progressive drop in predation risk associated with a change in feeding motivations as the fish grow. Trophic capacities or the number of stone shelters could have fixed the upper density in the pool to about one individual per square metre.

Brown trout

The new 0^+ cohort of brown trout also preferred riffle to pool. As hypothesized for bullhead, young 0^+ might avoid deep areas because of the piscivorous fish predation risk (BARDONNET and HELAND, 1994). On the contrary, 1^+ and older individuals were more numerous in pool habitats for most of the time. This spatial inter-cohort segregation along the water depth gradient has already been described for brown trout in other studies (BOHLIN, 1977 ; EGGLISHAW and SHACKLEY, 1982 ; BAGLINIÈRE and ARRIBE-MOUTOUNET, 1985). A shift from 0⁺ riffle habitats towards deeper areas is established through the seasons, and can be initiated from the beginning of summer (KOCIK and TAYLOR, 1996) or in winter (ELLIOTT, 1986). It could be related to ontogenetic changes in habitat requirements. According to HARVEY and STEWART (1991), as they grow, juvenile brown trouts may become more exposed to diving or wading predators in shallow riffle, and so need to seek shelter in deeper pool habitats. However, habitat change can also correspond to reaching a critical size which may limit competition or even predation from older trouts.

The only observation of a diel use of the riffle-pool sequence came from 1⁺ and older trouts. During the growing season (June-October) when the highest riffle-pool fidelities were recorded for individually marked trouts, they exhibited an increased use of riffle during daylight. A similar movement from pool to riffle during daylight has already been shown under experimental conditions on 1⁺ trouts and related to feeding (ROUSSEL and BARDONNET, 1995). BRIDCUT and GILLER (1993) observed that trouts marked in riffles showed more movements from these habitats than trouts marked in pools, indicating that riffles are occasional rather than regular habitats. Habitat choice within the riffle-pool sequence could then be regarded as a trade-off between potential energy intake and predation risk (FAUSCH, 1984 ; METCALFE *et al.*, 1987), since faster water in riffles is supposed to provide better drift feeding conditions than pools, but is also considered as a more risky area.

The functional role of the riffle-pool sequence

At the riffle-pool scale, two types of temporal changes were identified. Stone loach, 0⁺ trout and bullhead represented examples of seasonal changes, probably linked with a movement to join the spawning site for loach and with ontogenesis for trouts and sculpins. The other temporal change was diel and concerned the increased use of riffle by 1⁺ and older trouts during daylight. These results confirm that fish habitat management in salmonid streams should not be assessed without considering the temporal dimension of fish habitat requirements.

The riffle-pool sequence is an important habitat feature in salmonid streams providing spatial heterogeneity to support freshwater fish development at different biological levels. At the fish community level, it may enhance biodiversity, allowing species with different habitat requirements to cohabit. At the population level, it authorizes age classes exhibiting different habitat preferences to develop in adjoining habitat types. Lastly, at the individual level, it allows the expression of daily behaviour with pools providing nocturnal resting areas for trout feeding in riffle. For these reasons, more attention should be paid to protecting the riffle-pool sequences and spatial heterogeneity on channel hydraulics, since habitat diversity loss appears to be the major cause of long-term alterations in fish populations (NIEMI *et al.*, 1990). According to the literature, the natural dynamics of instream coarse woody debris plays an important role in hydraulic processes associated with riffle-pool formation and stabilization of the channel in different types of streams, including lowland rivers (GREGORY and DAVIS, 1992 ; GREGORY *et al.*, 1992 ; LANGFORD, 1996). Thus, the removal of instream woody debris, which is a usual practice in French stream management, would need to be reconsidered owing to the harmful consequences this custom has on the natural hydraulic processes that are closely related to the riffle-pool sequence formation.

ACKNOWLEDGEMENTS

We would like to thank N. JEANNOT, F. LEFEVRE, F. MARCHAND and many students for their help during the field experiments. We are also grateful to J.Y. MOËLO and to the Scorff Angling Association for electrofishing and experiments facilities. This work was partially financed by the French Conseil Supérieur de la Pêche.

REFERENCES

ANDREASSON S., 1971. Feeding habits of a sculpin (*Cottus gobio* L., Pisces) population. Inst. Freshw. Res., Drottningholm, report n° 51, 30 p.

BAGLINIÈRE J.L., 1979. Les principales populations de poissons sur une rivière à salmonidés de Bretagne-Sud, le Scorff. *Cybium 3,* 53-74.

BAGLINIÈRE J.L., ARRIBE-MOUTOUNET D., 1985. Micro-répartition des populations de truite commune (*Salmo trutta*), de juvéniles de saumon atlantique (*Salmo salar*) et des autres espèces présentes dans la partie haute du Scorff (Bretagne). *Hydrobiologia, 120,* 229-239.

BAGLINIÈRE J.L., MAISSE G., LEBAIL P.Y., PREVOST E., 1987. Dynamique de la population de truite commune (*Salmo trutta* L.) d'un ruisseau breton (France). II - Les géniteurs migrants. *Acta Oecol., Oecol. Appl., 8,* 201-215.

BAGLINIÈRE J.L., MAISSE G., LEBAIL P.Y., NIHOUARN A., 1989. Population dynamics of brown trout, *Salmo trutta* L., in a tributary in Brittany (France) : spawning and juveniles. *J. Fish Biol., 34,* 97-110.

BALON E.K., 1975. Reproductive guilds of fishes : a proposal and definition. *Can. J. Fish. Aquat. Sci., 32,* 821-864.

BALTZ D.M., MOYLE P.B., KNIGHT N.J., 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckel dace, *Rhinichthys osculus. Can. J. Fish. Aquat. Sci., 39,* 1502-1511.

BALTZ D.M., VONDRACEK B., BROWN L.R., MOYLE P.B., 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. *Trans. Am. Fish. Soc., 120,* 166-176.

BARDONNET A., HELAND M., 1994. The influence of potential predators on the habitat preferenda of emerging brown trout. *J. Fish Biol., 45 (suppl. A),* 131-142.

BHATTACHARYA C.C., 1967. A simple method of resolution of a distribution into gaussian components. *Biometrics, 25,* 115-135.

BISSON P.A., NIELSEN J.L., PALMASON R.A., GROVE L.E., 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. *In* ARMANTROUT N.B., Acquisition and utilization of aquatic habitat inventory information, 62-73, American Fisheries Society, Western Division, Bethesda.

BISSON P.A., MONTGOMERY D.R., 1996. Valley segments, stream reaches and channel units. *In* HAUER F.R., LAMBERTI G.A., Methods in stream ecology, 23-52, Academic Press, London.

BOHLIN T., 1977. Habitat selection and intercohort competition of juvenile sea-trout *Salmo trutta. Oikos, 29,* 112-117.

BRIDCUT E.E., GILLER P.S., 1993. Movement and site fidelity in young brown trout *Salmo trutta* populations in a southern Irish stream. *J. Fish Biol., 43,* 889-899.

BROWN L.R., 1991. Differences in habitat choice and behaviour among three species of sculpin (*Cottus*) in artificial stream channels. *Copeia, 3,* 810-819.

BROWN A.V., BRUSSOCK P.P., 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia, 220,* 99-108.

BROWN R.S., MACKAY W.C., 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram river, Alberta. *Trans. Am. Fish. Soc., 124,* 873-885.

BRYANT M.D., WRIGHT B.E., DAVIES B.J., 1992. Application of a hierarchical habitat unit classification system : stream habitat and salmonid distribution in Ward creek, Southeast Alaska. Pacific Northwest Research Station, Research Note PNW-RN-508.

BURDEYRON H., 1981. Activités rythmiques comportementales d'un poisson benthique, la loche, *Noemacheilus barbatulus* L. (*Cobitidae*), dans son milieu naturel et en laboratoire. Ph. D. thesis, University of Lyon (France), 284 p.

CAMPBELL R.F., NEUNER R.G., 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout (*Salmo gairdneri*) observed in western Washington cascade mountain streams. *In* OLSON and WHITE, Proceedings of Symposium on small hydropower and fisheries, 38-49, American Fisheries Society, Denver.

CARLE F.L., STRUB M.R., 1978. A new method for estimating population size from removal data. *Biometrics, 34*, 621-630.

COPP G.H., 1992. An empirical model for predicting microhabitat of 0^+ juvenile fishes in a lowland river catchment. *Oecologia, 91*, 338-345.

CUNJAK R.A., POWER G., 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Can. J. Fish. Aquat. Sci., 43*, 1970-1981.

DE LURY D.B., 1951. On the planning of experiments for the estimation of fish populations. *J. Fish. Res. Board. Can., 8*, 281-307.

EGGLISHAW H.J., SHACKLEY P.E., 1982. Influence of water depth on dispersion of juvenile salmonids, *Salmo salar* L. and *Salmo trutta* L., in a Scottish stream. *J. Fish Biol., 21*, 141-155.

EKLÖV A.G., GREENBERG L.A., KRISTIANSEN H., 1994. The effect of depth on the interaction between perch (*Perca fluviatilis*) and minnow (*Phoxinus phoxinus*). *Ecol. Freshw. Fish, 3*, 1-8.

ELLIOTT J.M., 1986. Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a Lake District stream. *J. Anim. Ecol., 55*, 907-922.

FACEY D.E., GROSSMAN G.D., 1992. The relationship between water velocity, energetic costs and microhabitat use in four North American stream fishes. *Hydrobiologia, 239*, 1-6.

FAUSCH K.D., 1984. Profitable stream positions for salmonids : relating specific growth rate to net energy gain. *Can. J. Zool., 62*, 441-451.

FRISSELL C.A., LISS W.J., WARREN C.E., HARLEY M.D., 1986. A hierarchical framework for stream habitat classification : viewing streams in a watershed context. *Env. Manage., 10*, 199-214.

GAUDIN P., 1981. Eco-éthologie d'un poisson benthique, le chabot, *Cottus gobio* L. (*Cottidae*) : distribution, alimentation et rapports avec la truite, *Salmo trutta* L. Ph. D. thesis, University of Lyon (France), 178 p.

GAUDIN P., CAILLÈRE L., 1990. Microdistribution of *Cottus gobio* L. and fry of *Salmo trutta* L. in a first order stream. *Pol. Arch. Hydrobiol., 37*, 81-93.

GIBSON R.J., STRANSBURY D.E., WHALEN R.R., HILLIER K.G., 1993. Relative habitat use, and inter-specific and intra-specific competition of brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) in some Newfoundland rivers. *Can. Spe. Publ. Fish. Aquat. Sci., 118*, 53-69.

GLOVA G.J., 1987. Comparison of allopatric cutthroat trout stocks with those sympatric with salmon and sculpins in small streams. *Environ. Biol. Fishes, 20*, 275-284.

GLOVA G.J., SAGAR P.M., 1993. A further assessment of trophic and spatial inter-relations of galaxiids and salmonids in New Zealand. *Ecol. Freshw. Fish, 2*, 132-140.

GREENBERG L.A., 1991. Habitat use and feeding behaviour of thirteen species of benthic stream fishes. *Environ. Biol. Fish., 31*, 389-401.

GREENBERG L.A., STILES R.A., 1993. A descriptive and experimental study of microhabitat use by young-of-the-year benthic stream fishes. *Ecol. Freshw. Fish, 2*, 40-49.

GREGORY K.J., DAVIS R.J., 1992. Coarse woody debris in stream channels in relation to river channel management in woodland areas. *Regul. Riv., 9*, 35-43.

GREGORY K.J., DAVIS R.J., TOOTH S., 1992. Spatial distribution of coarse woody debris dams in the Lymington Basin, Hampshire, UK. *Geomorphology, 6*, 207-224.

GRIFFITH J.S., 1972. Comparative behaviour and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Northern Idaho. *J. Fish. Res. Board. Can., 29*, 265-273.

HARO R.J., BRUSVEN M.A., 1994. Effects of cobble embeddedness on the microdistribution of the sculpin *Cottus beldingi* and its stonefly prey. *Great Basin Naturalist, 54*, 64-70.

HARVEY B.C., STEWART A.J., 1991. Fish size and habitat depth relationships in headwater streams. *Oecologia, 87*, 336-342.

HAURY J., BAGLINIÈRE J.L., 1996. Les macrophytes, facteur structurant de l'habitat piscicole en rivière à salmonidés. Etude de microrépartition sur un secteur végétalisé du Scorff (Bretagne-Sud). *Cybium, 20 (suppl. 3),* 111-127.

HAWKINS C.P., KERSHNER J.L., BISSON P.A., BRYANT M.D., DECKER L.M., GREGORY S.V., McCULLOUGH D.A., OVERTON C.K., REEVES G.H., STEEDMAN R.J., YOUNG M.K., 1993. A hierarchical approach to classifying stream habitat features. *Fisheries, 18*, 3-12.

HEGGENES J., KROG O.M., LINDAS O.R., DOKK J.G., BREMNES T., 1993. Homeostatic behavioural responses in a changing environment : brown trout (*Salmo trutta*) become nocturnal during winter. *J. Anim. Ecol., 62*, 295-308.

JACOBSEN O.J., 1979. Substrate preference in the minnow (*Phoxinus phoxinus* L.). *Pol. Arch. Hydrobiol., 26*, 371-378.

JONES A.N., 1975. A preliminary study of fish segregation in salmon spawning streams. *J. Fish. Biol., 7*, 95-104.

JOWETT I.G., 1993. A method for objectively identifying pool, run and riffle habitats from physical measurements. *N. Z. J. Mar. Freshw. Res., 27*, 241-248.

KOCIK J.F., TAYLOR W.W., 1996. Effect of juvenile steelhead on juvenile brown trout habitat use in a low-gradient Great Lakes tributary. *Trans. Am. Fish.* Soc., *125*, 244-252.

KWAK T.J., WILEY M.J., OSBORNE L.L., LARIMORE R.W., 1992. Application of diel feeding chronology to habitat suitability analysis of warm water stream fishes. *Can. J. Fish. Aquat. Sci., 49*, 1417-1430.

LANGFORD T., 1996. Ecological aspects of new forest streams, draining one of Britain's unique areas. *Freshwater Forum, 6*, 2-38.

LIEN L., 1981. Biology of the minnow *Phoxinus phoxinus* and its interactions with brown trout *Salmo trutta* in Ovre Heimdalsvatn, Norway. *Holarctic Ecol., 4*, 191-200.

LOGAN P., BROOKER M.P., 1983. The macroinvertebrate faunas of riffles and pools. *Water Res., 17*, 263-270.

MAITLAND P.S., 1965. The feeding relationships of salmon, trout, minnows, stone loach and three-spined stickelbacks in the river Endrick, Scotland. *J. Anim. Ecol., 34*, 109-133.

MALAVOI J.R., 1989. Typologie des faciès d'écoulement ou unités morphodynamiques des cours d'eau à haute énergie. *Bull. Fr. Pêche Piscic., 315*, 189-210.

MANN R.H.K., ORR D.R.O., 1969. A preliminary study of the feeding relationships of fish in a hard-water and a soft-water stream in southern England. *J. Fish Biol., 1*, 31-44.

MASTRORILLO S., DAUBA F., BELAUD A., 1996. Utilisation des microhabitats par le vairon, le goujon et la loche franche dans trois rivières du sud-ouest de la France. *Ann. Limnol., 32,* 185-195.

METCALFE N.B., HUNTINGFORD F.A., THORPE J.E., 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav., 35,* 901-911.

MEYERS L.S., THUEMLER T.F., KORNELY G.W., 1992. Seasonal movements of brown trout in north-east Wisconsin. *North Am. J. Fish. Manage., 12,* 433-441.

NEVEU A., 1981. Densité et microrépartition des différentes espèces de poissons dans la Basse-Nivelle, petit fleuve côtier des Pyrénées-Atlantiques. *Bull. Fr. Piscic., 280,* 86-102.

NIEMI G.J., DEVORE P., DETENBECK N., TAYLOR D., LIMA A., PASTOR J., YOUNT J.D., NAIMAN R., 1990. Overview of case studies on recovery of aquatic systems from disturbance. *Env. Manage., 14,* 571-587.

OBERDORFF T., PORCHER J.P., 1992. Fish assemblage structure in Brittany streams (France). *Aquat. Living Resour., 5,* 215-223.

PETTY J.T., GROSSMAN G.D., 1996. Patch selection by mottled sculpin (Pisces : *Cottidae*) in a southern Appalachian stream. *Freshw. Biol., 35,* 261-276.

PONCIN P., 1996. Reproduction chez nos poissons. Fédération sportive des pêcheurs francophones de Belgique ASBL, 80 p.

RABENI C.F., JACOBSON R.B., 1993. The importance of fluvial hydraulics to fish habitat restoration in low-gradient alluvial streams. *Freshw. Biol., 29,* 211-220.

ROPER B.B., SCARNECCHIA D.L., 1995. Observer variability in classifying habitat types in stream surveys. *North Am. J. Fish. Manage., 15,* 49-53.

ROUSSEL J.M., BARDONNET A., 1995. Activité nycthémérale et utilisation de la séquence radier-profond par les truitelles d'un an (*Salmo trutta* L.). *Bull. Fr. Pêche Piscic., 337/338/339,* 221-230.

ROUSSEL J.M., BARDONNET A., 1996. Changements d'habitat de la truite (*Salmo trutta*) et du chabot (*Cottus gobio*) au cours du nycthémère : approches multivariées à différentes échelles spatiales. *Cybium, 20 (suppl. 3),* 43-53.

SEMPESKI P., GAUDIN P., 1995. Size-related changes in diel distribution of young grayling (*Thymallus thymallus*). *Can. J. Fish. Aquat. Sci., 52,* 1842-1848.

SMYLY W.J.P., 1955. On the biology of the stone loach *Nemacheilus barbatula* (L.). *J. Anim. Ecol., 24,* 167-186.

SMYLY W.J.P., 1957. The life-history of the Bullhead or miller's thumb (*Cottus gobio* L.). *Proc. Zool. Soc. Lond., 128,* 431-453.

SWALES S., LAUZIER B., LEVINGS C.D., 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. *Can. J. Zool., 64,* 1506-1514.

VAN DEVENTER J.S., PLATTS S., 1989. Microcomputer software system for generating population statistics from electrofishing data - user's guide for Microfish 3.0. Gen. Tech. Rep. INT-254, Ogden, UT : U.S. Department of agriculture, Forest Service, Inter-mountain Research Station, 29 p.

WELTON J.S., MILLS C.A., RENDEL E.L., 1983. Food and habitat partitioning in two small benthic fishes, *Nemacheilus barbatulus* L. and *Cottus gobio* L. *Arch. Hydrobiol., 97,* 434-454.

ZWEIMÜLLER I., 1995. Microhabitat use by two small benthic stream fish in a second order stream. *Hydrobiologia, 303,* 125-137.