

## Fish assemblage structure in Brittany streams (France)

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### Abstract

Fish assemblage structure of 29 Brittany streams is examined. Catchment area, stream gradient, and distance from sources are significantly correlated with species richness. Addition of species with increasing stream size occurs for all streams with no evident longitudinal replacement, suggesting little discontinuity in the stream geomorphology or temperature. Total density of fishes decreases significantly with an increase in stream size but no relation was found between total biomass and catchment area. Headwaters are characterized by short-lived, solitary, and nocturnal feeding species, whereas downstream sites are characterized by long-lived, schooling, diurnal feeding species. Presence of solitary and nocturnal feeding species upstream could be related to predation and/or competition factors. Temporal variation of individual species density varies from an upstream-downstream gradient with the highest variation upstream. Species responsible for this variation were mostly small benthic ones relatively difficult to sample, therefore, the greater temporal variation in upstream areas could be attributed to a deficiency of the sampling methodology.

**Keywords:** Stream fish, behaviour, diversity, Brittany.

*Structure des peuplements piscicoles dans les rivières bretonnes.*

### Résumé

La structure des peuplements piscicoles de 29 rivières bretonnes est examinée. La richesse en espèces est corrélée avec la surface du bassin versant, la pente du cours d'eau et la distance à la source. De l'amont vers l'aval, les peuplements piscicoles évoluent simplement par addition d'espèces, ce qui laisse suggérer une relative homogénéité du milieu. La densité totale de la faune piscicole décroît significativement de l'amont vers l'aval mais aucune corrélation n'apparaît entre la biomasse totale et ce gradient longitudinal. Les peuplements en amont sont caractérisés par des espèces solitaires, très souvent nocturnes et à durée de vie relativement courte alors que plus en aval apparaissent des espèces à comportement grégaire, à mode de vie diurne et à durée de vie plus longue. Cette différence pourrait être attribuée à des facteurs tels que prédation et/ou compétition. La variation temporelle de densité par espèce varie selon un gradient longitudinal et reste plus importante dans la partie amont des cours d'eau. Les petites espèces benthiques sont responsables de cette variation importante en amont. Elles sont difficiles à échantillonner et l'estimation de leur abondance reste aléatoire. Ainsi, la variation temporelle des peuplements plus importante en amont pourrait provenir en partie d'une moins bonne efficacité de pêche concernant ces espèces.

**Mots-clés :** Rivières, poissons, structure des peuplements, écologie, Bretagne.



**Table 1.** – Guilds for common freshwater cyclostomes and fishes captured during this study, including invertivore (I), filter feeders (FF), piscivore (P), omnivore (O), solitary species (S), schooling species (Sc), diurnal feeders (D), and nocturnal feeders (N).

Species	Trophic guild	Solitary or schooling species	Life-span (in years)	Diurnal or nocturnal feeders	Temperature of reproduction (°C)
Petromyzontidae					
<i>Lampetra planeri</i>	FF		3-7		-
Anguillidae					
<i>Anguilla anguilla</i>	I/P	S	*	N	-
Salmonidae					
<i>Salmo salar</i>	I/P	S	*	D;N	5
<i>Salmo trutta fario</i>	I/P	S	8-10	D;N	7
Esocidae					
<i>Esox lucius</i> **	P	S	15-20	D	7
Cyprinidae					
<i>Phoxinus phoxinus</i>	I/O	Sc	5-6	D	10
<i>Gobio gobio</i>	I	Sc	6-7	D	14
<i>Leuciscus leuciscus</i>	I	Sc	15-16	D	10
<i>Leuciscus cephalus</i> **	O/P	Sc	17-21	D	15
<i>Abramis brama</i>	I	Sc	18-20	D	18
<i>Rutilus rutilus</i>	O	Sc	12-14	D	15
<i>Alburnus alburnus</i> **	I	Sc	5-7	D	15
Cobitidae					
<i>Barbatula barbatula</i>	I	S	6-8	N	10
Percidae					
<i>Perca fluviatilis</i> **	I/P	S	10	D	14
<i>Stizostedion lucioperca</i> **	P	S	15	D	12
Cottidae					
<i>Cottus gobio</i>	I	S	4-5	N	12

\* Anadromous or catadromous species; \*\* Rare species.

## Species assignment

Species were classified from literature reports of life history characteristics, principal adult food and feeding behaviour, as summarized by Spillmann (1961), Grandmottet (1983), Philippart and Vranken (1983), Allardi and Keith (1991). Since in Europe fish exhibit substantial geographic variation in life history traits, we used only averaged values available in each category. The assignment of species of fish to feeding groups was difficult because of seasonal changes in fish diets, opportunism and lack of knowledge for a number of species. Only adult fishes were considered. We assigned each species to one of the following trophic groups on the basis of its principal adult food and habitat: Piscivores (P); Invertivores (I); Omnivores (O); Filter feeders (FF) (table 1). Piscivores are fish that eat primarily other fish and crayfish and a smaller amount of aquatic and terrestrial insects. Invertivores include generalized invertivores, surface and water column invertivores and benthic invertivores. We preferred the more general term of invertivores because these fish typically eat crustaceans, oligochaetes, and molluscs, as well as aquatic or terrestrial insects (Oberdorff and Hughes, 1992). Omnivores are fish which consume a wide range of plants, detritus, and material, with at least 25% plants and 25% animals (Karr *et al.*, 1986).

## Statistical analyses

All the relationships during this study were examined using correlations, simple linear regressions, multiple regressions, and analyses of variance.

Catchment area, distance from sources, stream gradient, distance from the ocean, and species richness were were  $\ln$  transformed in order to minimize effects of non-linearity.

To determine the variability in stream fish assemblages we used the coefficient of variation (CV) of population density. CV estimates were calculated by dividing the standard deviation of population estimates by mean abundance (Grossman *et al.*, 1990). To classify CV values, we used the arbitrary classification scheme proposed by Freeman *et al.*, (1988):

**Table 2.** – Correlation matrix of the variables used in regression analysis. SR: species richness; CA: catchment area; SG: stream gradient; DO: distance from ocean; DS: distance from source;  $\ln$ : neperian logarithm.

	$\ln$ DS	$\ln$ CA	$\ln$ SG	$\ln$ DO
$\ln$ CA	0.966			
$\ln$ SG	0.75	0.704		
$\ln$ DO	0.14	0.087	0.006	
$\ln$ SR	0.813	0.828	0.615	0.223

$CV \leq 25\%$  = highly stable,  $25\% < CV \leq 50\%$  = moderately stable,  $50\% < CV \leq 75\%$  = moderately fluctuating,  $CV > 75\%$  = highly fluctuating. Advantages of using CV are described in Grossman *et al.* (1990). All species represented by less than 1 in density (1 individual per 100 m<sup>2</sup>) were eliminated from the analyses (rare species).

## RESULTS

Sixteen species and 12 251 individuals representing 8 families (table 1) were captured at the 50 stations. The most common species was the brown trout *Salmo trutta fario* (35% of the total abundance, and 46% of the total biomass) followed by the eel *Anguilla anguilla* (15.5% of the total abundance and 42% of the total biomass). Among the small species, the sculpin *Cottus gobio* was the most abundant (12% of the total abundance). Species composition and relative abundance of fish were similar to those of a previous study (Baglinière, 1979).

### Species richness versus gradient, distance from source, catchment area, and distance from ocean

We examined relationships between species richness and site characteristics (distance from source, stream gradient, distance from the ocean, and drainage area). Results are summarized in table 2. As expected, species richness increases with lower gradients ( $r^2 = 0.378$ ;  $p < 0.001$ ), increase of distance from source ( $r^2 = 0.66$ ;  $p < 0.001$ ) and increase of catchment area ( $r^2 = 0.686$ ;  $p < 0.001$ ). Catchment area was the best predictor of species richness (fig. 2). There was no significant relation between number of species and distance from the ocean ( $r^2 = 0.05$ ;  $p > 0.05$ ).

### Longitudinal zonation of the fish assemblages

Fish assemblage changes along the longitudinal gradient were due to species addition (table 3). No evidence of species replacement occurred during the study. Headwater sites were characterized by a low species richness dominated by *Salmo trutta fario*.

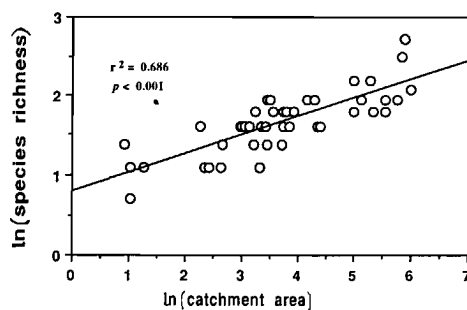


Figure 2. — Plot of species richness versus catchment area in 50 least disturbed sites of 29 Brittany streams.

Table 3. — Distribution of the 16 dominant species along a longitudinal gradient (+ presence; - absence).

Fish species	Catchment area (km <sup>2</sup> )			
	Upstream		Downstream	
	0-100	100-200	200-300	300-400
<i>S. trutta</i>	+	+	+	+
<i>C. gobio</i>	+	+	+	+
<i>B. barbatula</i>	+	+	+	+
<i>L. planeri</i>	+	+	+	+
<i>S. salar</i>	+	+	+	+
<i>A. anguilla</i>	+	+	+	+
<i>P. phoxinus</i>	+	+	+	+
<i>G. gobio</i>	-	-	+	+
<i>P. fluviatilis</i>	-	-	+	+
<i>R. rutilus</i>	-	-	+	+
<i>A. brama</i>	-	-	+	+
<i>L. leuciscus</i>	-	-	-	+
<i>E. lucius</i>	-	-	-	+
<i>A. alburnus</i>	-	-	-	+
<i>L. cephalus</i>	-	-	-	+
<i>S. lucioperca</i>	-	-	-	+

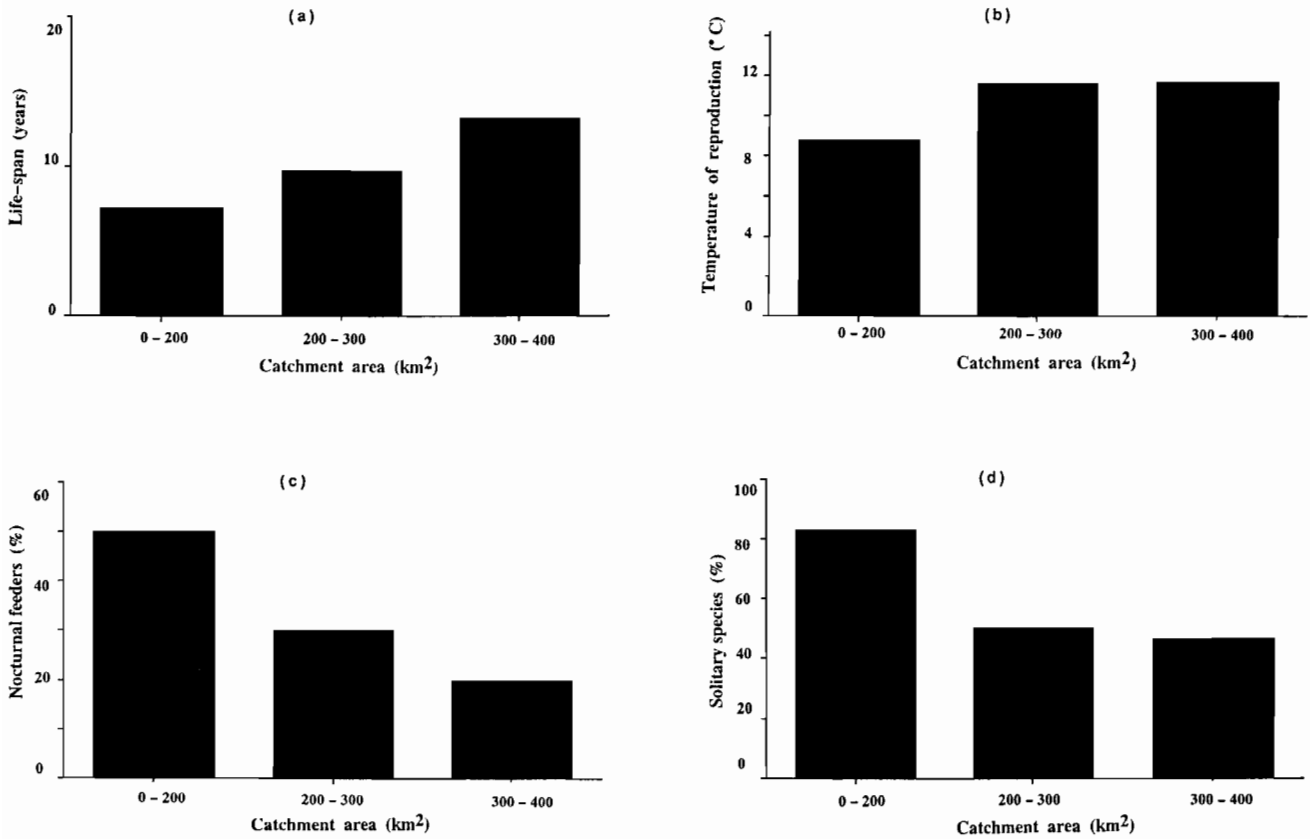
Table 4. — (a) Multiple regression analyses of trout biomass and (b) of trout density versus Ln (catchment area) and Ln (distance from ocean).

Variables	Coefficients	p
(a) Trout biomass vs.		
Ln (catchment area)	-192.7	0.0017
Ln (distance from ocean)	0.493	0.001
Intercept		-
44.57	$r^2 = 0.383$	$p < 0.001$
(b) Trout density vs.		
Ln (catchment area)	-9.23	0.001
Ln (distance from ocean)	7.16	0.009
Intercept		-
27.51	$r^2 = 0.586$	$p < 0.001$

*Anguilla anguilla*, *Barbatula barbatula*, *Phoxinus phoxinus*, and *Cottus gobio* (catchment area 0-200 km<sup>2</sup>), whereas downstream sites supported more complex assemblage with addition of species like *Gobio gobio*, *Rutilus rutilus*, *Leuciscus leuciscus*, *Leuciscus cephalus*, *Abramis brama*, *Perca fluviatilis*, and *Esox lucius* (catchment area 200-400 km<sup>2</sup>).

### Longitudinal variations of total density and biomass of fish assemblages

Total density of fishes (individuals.100 m<sup>-2</sup>) was significantly negatively correlated with catchment area ( $r^2 = 0.295$ ;  $p < 0.001$ ) but no significant relationship was found between total biomass (g.100 m<sup>-2</sup>) and catchment area ( $r^2 = 0.016$ ;  $p = 0.376$ ).



**Figure 3.** — (a) Average life-span of fish species as a function of catchment area; (b) Average temperature of reproduction of fish species as a function of catchment area; (c) Proportion of nocturnal feeders as a function of catchment area; (d) Proportion of solitary species as a function of catchment area.

#### Longitudinal distribution of two most abundant species *Anguilla anguilla* and *Salmo trutta fario*

Both density ( $r^2=0.358$ ;  $p<0.001$ ) and biomass ( $r^2=0.144$ ;  $p<0.05$ ) of eels were significantly negatively correlated with distance from the ocean; nevertheless, the relationship between eel biomass and distance from the ocean was not very high. Individual average weight of eels increased with an increase in distance from the ocean ( $r^2=0.249$ ;  $p<0.01$ ).

Density and biomass of trout were significantly correlated with distance from the ocean and catchment area. Both decreased with an increase in catchment area but increased with an increase of distance from ocean (table 4). The average individual weight of trout was significantly positively correlated with catchment area ( $r^2=0.452$ ;  $p<0.001$ ).

#### Interspecific variation in life and behaviour characteristics of fishes along environmental gradients

We analysed life history characteristics of fish assemblages (*i.e.* average life-span, average reproduction temperature, solitary or schooling species, nocturnal or diurnal feeders) as a function of a longitudinal gradient (catchment area). All these variables were

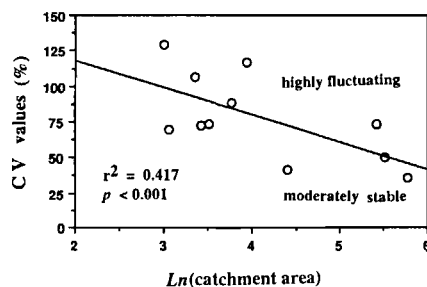
dependent on stream size (fig. 3). Headwater species had a short average life-span and a low average temperature of reproduction; 50% of these species were nocturnal feeders and 85% were solitary. In contrast downstream species had a relatively longer life-span, a higher average temperature of reproduction, were more diurnal feeders (80%) and schooling species (>50%).

#### Temporal variation in fish assemblage structure

We determined the temporal variation in fish assemblages from 11 stations in 8 coastal streams. 4 sites were sampled twice over a 1 year period, 3 sites were sampled twice over a 2 year period, 1 site was sampled twice over a 5 year period, 1 site was sampled twice over a 7 year period, 1 site was sampled twice over a 9 year period, and 1 site was sampled twice over an 11 year period (table 5). Whatever the study time-span, variations of individual species density were higher in headwaters than in downstream areas (fig. 4). According to the CV classification, individual species density varied significantly between moderately stable to highly fluctuating depending on site position along the upstream downstream gradient

**Table 5.** — Coefficient of variation (CV) of individual species density at 11 stations in 8 rivers (see figure 1 for station position on rivers).

Site	River	Catchment area (km <sup>2</sup> )	Time-span (year)	CV% (density)
1	Jet	43.2	1	88
2	Jet	81.7	1	42
3	Trieux	248.8	1	50
4	Trieux	322.3	1	36
5	Saint-Émilion	19.9	2	129
6	Saint-Émilion	30.4	2	72
7	Loup	28.5	2	106
8	Aulne	21.4	5	69
9	Odet	227.2	9	73
10	Théoulas	33.5	11	91
11	Mignonne	51	7	117



**Figure 4.** — Longitudinal changes in CV values (%) of individual species density.

(fig. 4). Species responsible for high values of headwaters individual species density CV were *C. gobio*, *B. barbatula*, and differed from species increasing the CV values downstream *P. phoxinus*, *A. anguilla*, *S. salar*. *C. gobio* and *B. barbatula* were not included in CV analyses downstream because of their low density (<1 individual.100 m<sup>-2</sup>) (table 6).

## DISCUSSION

### Species richness and stream physical variables

Species richness is correlated to varying degrees with different physical variables (stream gradient, distance from sources, catchment area). Catchment area shows the highest correlation among the three variables examined (fig. 2). This synthetic variable reflects other physical ones which could influence fish assemblages (discharge, width, depth, current velocity, temperature, substrate, gradient, elevation) and could be of great use in the comparison of streams in ichthyological studies.

### Longitudinal zonation of fish assemblages

Longitudinal changes in fish composition follow the additive model. There is no evident replacement of species suggesting a weak or non discontinuity in stream geomorphology or temperature (Rahel and Hubert, 1991) and this could be due to the shortness of streams sampled during this study. Numerous studies of temperature stream fish assemblages have shown the same pattern (Kuehne, 1962; Sheldon, 1968; Lotrich, 1973; Horwitz, 1978; Platts, 1979; Beecher *et al.*, 1988). Association of the decline in both density and biomass of headwaters species along the longitudinal gradient with a progressive apparition of warmer water species downstream suggests a possible replacement of species for larger spatial scales. This has been previously confirmed for large European rivers (Balon *et al.*, 1986; Boët *et al.*, 1991; Penczak *et al.*, 1991).

It is interesting to note that this pattern of species addition also follows a trophic gradient consistent with the River Continuum Concept (Vannote *et al.*, 1980). Surface insect feeders are found in headwaters (*S. trutta*), followed by small benthic invertebrate feeders (*C. gobio*, *P. phoxinus*, *B. barbatula*, *G. gobio*),

**Table 6.** — Coefficient of variation of each species density in the 11 stations studied (see table 5 for name of rivers).

Site	Fish species									
	A	B	C	D	E	F	G	H	I	J
1	27	24	135			115	138			
2	12	61	—	—	88	8	—	—	—	—
3	3	—	20	—	158	15	68	38	—	—
4	7	—	50	—	—	38	56	23	—	54
5	21	188	200	—	—	146	92	—	—	—
6	2	213	0	—	—	—	—	—	—	—
7	0	160	160	—	—	—	—	—	—	—
8	16	100	98	—	—	95	36	—	—	—
9	70	—	—	—	15	135	—	—	—	—
10	9	11	9	200	—	76	131	—	200	—
11	51	187	182	—	136	6	138	—	—	—

A: *S. trutta*; B: *C. gobio*; C: *B. barbatula*; D: *L. planeri*; E: *S. salar*; F: *A. anguilla*; G: *P. phoxinus*; H: *G. gobio*; I: *R. rutilus*; J: *L. leuciscus*.

omnivores (*R. rutilus*, *L. cephalus*) and piscivores (*E. lucius*). Trophic diversity of fish assemblages may be related in part to food availability (Li *et al.*, 1987).

#### Population structure of eels and trout

Distribution patterns of eel populations follow a longitudinal gradient with a total density and biomass highest near the ocean and declining with increasing distance from the ocean. Eels colonize streams with younger individuals nearer the ocean, and larger and fewer individuals in upstream sections. This zonation of eel populations in rivers has been reported previously for British streams (Aprahamian, 1988; Naismith and Knights, 1988). They attributed the downstream-upstream shift in age structure to the time required for the eels to reach the upstream sections and to the increase in proportion of females.

Density and biomass of trout populations were positively influenced by distance from the ocean and both decreased with an increase in catchment area. The relationship between trout density, trout biomass and distance from the ocean suggested a weak salinity or temperature tolerance of this species (table 4). The decline of trout density and biomass, and the increase of individual weight with an increase in catchment area showed that trout populations followed a longitudinal zonation contrary to that of eel populations. Individuals were younger and more abundant in upstream areas whereas bigger fishes were fewer but dominant downstream. These results could suggest possible competition and/or predation trends between these two species. Nevertheless recent work of Mann and Blackburn (1991) seems to deny the predation hypothesis. The competition hypothesis is not evident because these species exploit different microhabitats (Neveu, 1981), and eat different food (Mann and Blackburn, 1991).

#### Variation in fish behaviour along longitudinal gradient

Average life-span, average reproduction temperature, percent of solitary species (versus schooling species), and percent of nocturnal feeders (versus diurnal feeders) are all dependent on stream size. Headwaters are characterized by short-lived, solitary, and nocturnal feeder species, with a low temperature of reproduction (<12°C), whereas downstream sites were characterized by long-lived, schooling, diurnal feeder species, with a higher temperature of reproduction.

The increase of species longevity and body size with stream size is a well known phenomenon described previously by Schlosser (1990) and could induce the shift between predominance of nocturnal feeders upstream and diurnal feeders downstream. Small species are more subject to predation (mammals, birds, snakes and fishes) than large species, and could use nocturnal feeding behaviour patterns in response to this threat.

#### Temporal variation in fish assemblages

We found substantial temporal variation of individual species density, this variation differing along an upstream-downstream gradient (fig. 4).

Temporal variation of individual species density downstream was low. Nevertheless, given the life-span of species downstream which encompass the sampling period used during this study (<10 years), this stability could be caused by low recruitment and high survivorship of long-lived species. For this reason, only comparative evaluation of CV values are discussed in this paper without extrapolation to assemblage stability which needed sampling that comprised one mean generation time of the species being examined (Grossman *et al.*, 1990).

There was high temporal variation in individual species density upstream, but this variation was essentially due to small benthic species relatively difficult to sample by electrofishing. These fish tend to sink instead of swimming up after the electrical shock and this greatly reduces sampling efficiency. We suspect that variability of fish density for headwater assemblages is due, partly, to an artefact in the sampling methodology (small benthic species are not sampled in proportion to their relative abundance, therefore, sampling efficiency for these species could show wide variations over time). Nevertheless, another explanation for this temporal variability could be the effect of higher environmental disturbances, such as harsh winter conditions or fluctuations in stream flow, occurring upstream (Horwitz, 1978; Grossman *et al.*, 1990; Schlosser, 1990). This longitudinal pattern of variability in fish density could limit the efficiency of a fish-based index, such as the index of biotic integrity (IBI) (Karr, 1981), to assess anthropogenic disturbances in upstream areas. To alleviate this inconvenience, future studies should focus on whether or not adequate sampling of small benthic species could decrease CV values of individual species density in upstream sections.

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