ENVIRONMENTAL AUDITING

The Fish Fauna of the Doubs River Prior to Completion of the Rhine–Rhône Connection

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ABSTRACT / The part of the Doubs River between Montbéliard and Dôle (France), i.e., downstream from the confluence with the Allan River, will be affected by the Rhine–Rhône connection project. In order to improve the understanding of the Doubs ichthyofauna, aquatic environments of the Doubs were sampled by electrofishing. Fish diversity and the presence of some rheophilic species demonstrated the good ecological quality of some stretches of the Doubs. This quality was due to alternating areas with very diversified aquatic environments (riffles, islands and side-arms, backwaters) and a considerable range of flow velocities. The differences in the structure of the fish communities of the different types of aquatic environments were more qualitative (fish species) than quantitative (number of species and number of fish). However, the mean number of fish was statistically lower in the canals (Freycinet canal and channelized part of the Allan River) than in the main course and in the backwaters. The natural parts of the Doubs (unnavigable reaches) showed the most diversified environmental structure and had the most rheophilic fish communities. Thus, the rheophilic species were well represented, but they proved also the most vulnerable to river regulation. However, the most abundant fishes throughout the Doubs River were generalists with no special requirements for food sources or spawning substrate.

The Rhine–Rhône connection project concerns the part of the Doubs River between Montbéliard and Dôle, i.e., downstream from the confluence with the Allan River. This project is managed by the Compagnie Nationale du Rhône (C.N.R.), a river regulation and management agency. This large ship canal project would be a new waterway through the valleys of the Doubs, Allan, Bourbeuse, Largue, and Ill rivers. The connection between the Rhine and the Saône will be made via 23 reaches (55 m wide, 4.5 m deep) separated by 24 locks (Figure 1C). A Rhine–Rhône connection (for barges less than 400 t) has existed since 1833. The present Freycinet Canal (12 m wide, 2 m deep), named after its builder, connects the Rhine to the Saône. It partly uses the main channel of the Doubs River between l'Isle-sur-le-Doubs and Dôle. Weirs, locks, and occasionally a diversion canal, were built on this reach.

The Doubs receives much domestic effluent, in particular downstream from the towns of Montbéliard, Baume-les-Dames, and Besançon. The river was often ranked in class II of the multiuse quality scale of the Agence de l'Eau Rhône-Méditerranée-Corse (marked pollution) (GREBE 1992). The critical parameters were organic load, ammonium, and phosphorus contents and sometimes metallic pollution (zinc, chromium, cadmium, copper, mainly downstream from Montbéliard). Some tributaries (e.g., the Allan and Savoureuse rivers) are also highly polluted by ammonium and phosphorus.

According to the limnological concept of the biocenotic structure of running waters [i.e., classification system taking into account changes in environmental factors and the occurrence of invertebrate and fish species (Huet 1949, Illies and Botosaneanu 1963, Verneaux 1976)], the ecological status of the Doubs River at the beginning of the 1990s was that of a typical potamon (i.e., a lowland river with an average summer water temperature ≥20°C, coarse to fine sedimentary substrata, eurythermic and rheotolerant species and cyprinids dominant). According to its aquatic fauna, the main course of the river downstream from the confluence with the Allan changed from an epipotamon to a metapotamon (biocenotic classification B7–B9). It showed a good faunistic diversity, but fish species typical of the epipotamon and rhithronic and/or sensitive invertebrate species were only present at low abundances in riffle sectors and downstream from weirs, where the current velocity was high enough to avoid silting. The composition and structure of the aquatic

KEY WORDS: Fish communities; Regulation; Restoration; Floodplain; Large ship canal; Doubs River

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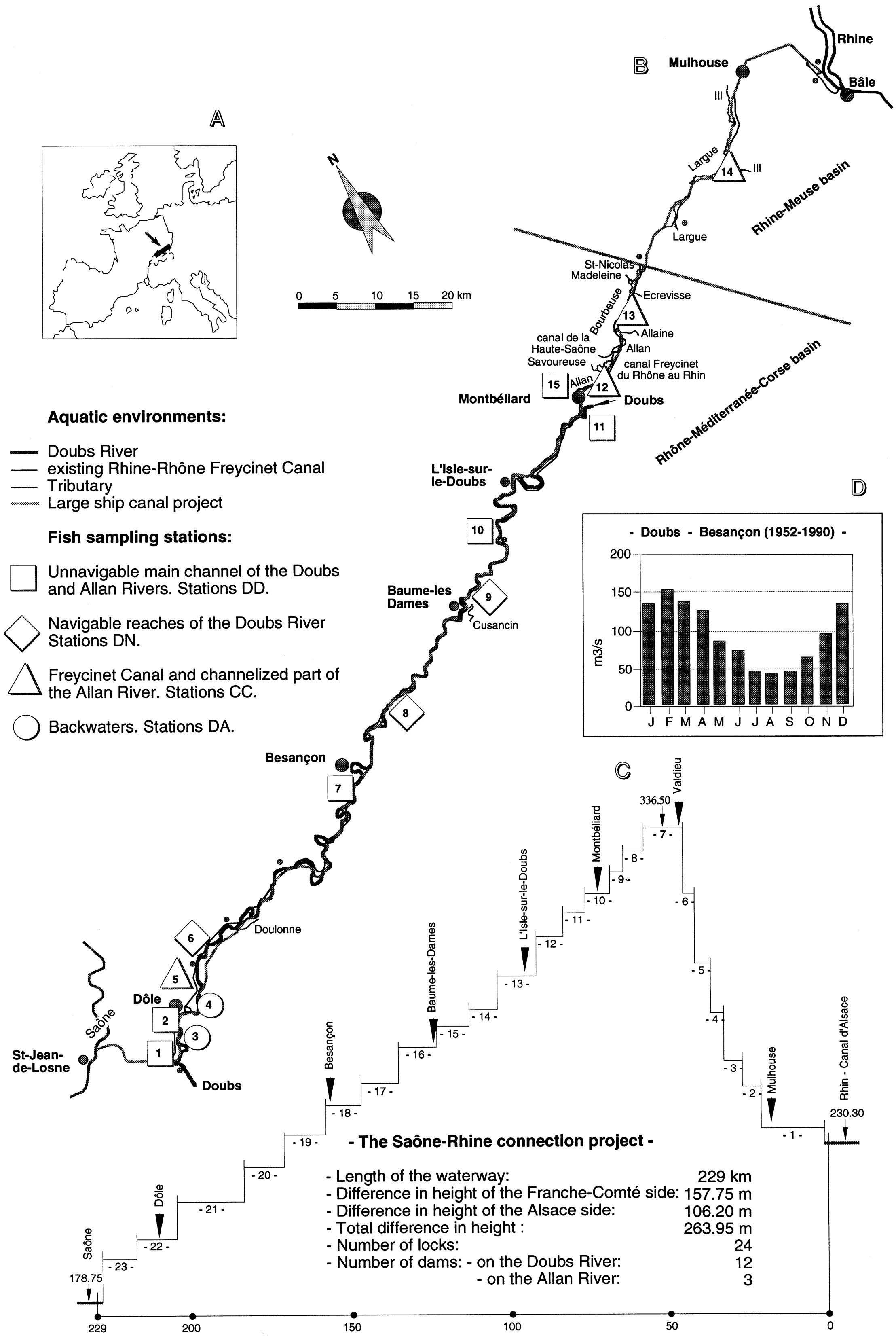


Figure 1. The Rhine–Rhône large ship canal project and location of the 15 sampling stations.

fauna were mainly influenced by organic pollution and environmental alterations such as the erection of weirs at the beginning of the last century (Verneaux 1973, CEMAGREF 1982).

To appreciate the influence of the new waterway on the ecosystems of the Doubs River, studies were needed to update and complement the previous data. Changes in environmental conditions are reflected in corresponding alterations of aquatic community structure and ecosystem functioning. Functional indicators are groups of species descriptive of certain environmental conditions (Bournaud and Amoros 1984, Amoros and others 1987). Plefkin and others (1989) stated that macroinvertebrate and fish communities are the most frequently used indicators. Macroinvertebrates can be used to classify stream biological systems and assess water quality (classification, biological indices) because they integrate the local conditions (chemical quality, habitat structure) and consequently the short-term (species level) as well as long-term (community level) changes. Fruget and others (1996) studied the macroinvertebrate communities of the Doubs River as a part of the Rhine–Rhône connection project. Fish are good indicators of the functioning of freshwater ecosystems, of habitat structure, and of ecological integrity of river systems because of their diverse reproduction, trophic levels and their complex habitat requirements (Schlosser 1985, Schiemer and Spindler 1989, Copp and others 1991).

Data on the fish fauna of the Doubs River are presently available from three sources: Verneaux (1973), the updating of CEMAGREF (1982), and fish inventories of the Jura and Doubs departments (DDAF du Jura 1987, DDAF du Doubs 1990). In order to update and complement these data, several aquatic environments of the Doubs and Allan rivers were sampled by electrofishing in September 1992 and September 1993, respectively.

The objectives of the present study were: (1) to update the existing data base of the ichthyofauna of the Doubs and Allan rivers and of the Rhine–Rhône Freycinet Canal, and (2) to improve the understanding on the functional importance of the backwater areas and overall environmental diversity (ARALEPBP 1993).

Materials and Methods

Study Area

The total length of the future waterway is 229 km including 169 km of the Doubs River. Of these, 71 km of the river would be bypassed by an artificial diversion canal. Most (70%) of the riffles (both natural and artificial ones located downstream from the weirs) will be flooded, several meanders will be cut off, and several islands (and consequently several kilometers of shoreline, i.e., ecotone areas) will be destroyed, one third (near 243 ha) of wetlands (ponds, dead arms, reed beds, etc.) will be filled in, and many (more than 50%) fish spawning areas will be affected.

Because of the geological structure of the catchment area (Jurassic limestone), this part of the river is typified by long seasonal periods of low discharge. The average discharge of the Doubs at Besançon for the 1952–1990 period was 93.5 m^3/s (Figure 1D). Low flow occurs from July to September (discharge <50 m^3/s with an extreme discharge of less than 8 m^3/s) (GREBE 1992). After regulation, nearly 25% of the discharge of the Doubs would be used to operate the locks during low flow.

Field Survey

According to the objectives described previously, the aquatic environments of the Doubs were divided into four categories: the unnavigable main channel of the Doubs and Allan rivers (stations DD), backwaters (stations DA), navigable reaches of the river (station DN), the Freycinet Canal and channelized part of the Allan River (stations CC). Fifteen sampling stations were chosen in these areas (Figure 1B). These stations were distributed from the Alsatian part of the Freycinet Canal to the Doubs River downstream from Dôle. Stations DD11 and DD15 could be considered a priori as reference stations on the Doubs and Allan, respectively, because they were located upstream from the town of Montbéliard in natural stretches of the rivers.

Electrofishing was used to collect point abundance samples (Nelva and others 1979, Persat and Copp 1990, Persat and Olivier 1991). The point sample size was determined by the attractive range of an anode immersed at a fixed depth (nearly 2 m). The anode was dropped suddenly from place to place into the water to surprise the fish. The fishing was performed from a boat. This approach refers to the most elementary unit of ecological perception, the microhabitat. It provides a fractional and systematic sampling of the field area through numerous, small point samples, within an ecosystem or a fluvial reach. This method makes it possible to quickly collect a large number of small point samples in a standardized way. It estimates fish abundance and biomass with a sample unit that is comparable at all levels of ecological perception: the watershed, hydrosystem, biotope, and microhabitat. We collected 300 point samples in September 1992 and September 1993 within a few days under uniform hydrological conditions (low discharges of about 10–12 m^3/s at the Lougres gauging station). Nine environ-

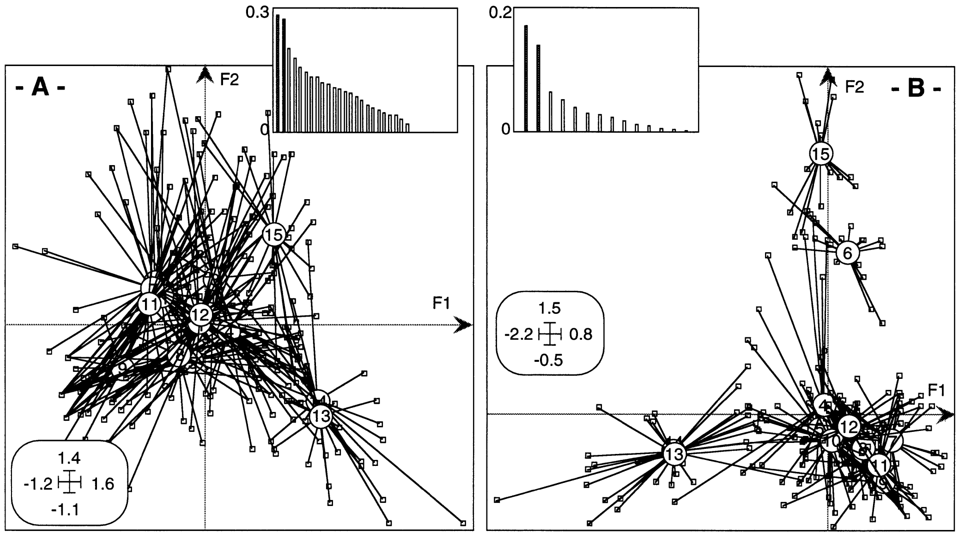


Figure 2. Multiple correspondence analysis (MCA) of the environmental data. **A:** Standard analysis. **B:** Between-station analysis. The circles with the station numbers show to the center of classes and the lines show to the dispersion of samples.

mental variables (bank slope, width, depth, current velocity, substrate, riparian vegetation, aquatic vegetation, perilithon, refuges), divided into 33 categories, were recorded at each point. They provided a brief description of the local (mainly riparian) habitat (Persat and others 1985, Persat and Olivier 1991).

Data Analyses

Environmental data were analyzed using a multiple correspondence analysis (MCA) (Pialot and others 1984, Tenenhaus and Young, 1985). This method is particularly appropriate for the synthetic description of a matrix of qualitative variables.

The community variables, i.e., diversity and density, relative abundance of each species, were calculated for each station and for each type of aquatic environment. The statistical significance of the mean numbers of fish per point sample in the different habitat types was tested using a *t* test. The organization of the communities and its significance were analyzed using a decentered correspondence analysis (DCA), which is well adapted for analyzing the structure of the ichthyofauna collected with the point abundance sampling method (Dolédec and others 1995). This analytical method makes it possible to take into account the sampling effort (i.e., the number of point samples per fishing campaign) of fish communities assessed by electrofishing in large rivers. The analysis was conducted using presence and absence data (each value represented the number of points in which a species was sampled within each fishing station, i.e., 20 sampling points). More details concerning data analyses can be found in Dolédec and Chessel (1991).

Results

Habitat Structure

The standard MCA (Figure 2A) shows that a strong ordination of stations did not exist, except for stations DN9, CC13, CC14, and DD15. The distribution of the sampling points on the F1 $\times$ F2 factorial plane (which only accounted for 21% of the total inertia of the matrix) emphasizes the high degree of heterogeneity within each station. In order to clarify the differences between stations, the data were analyzed with a between-station MCA (Dolédec and Chessel 1989). This analysis only accounted for 22% of the matrix inertia, while the within-station analysis accounted for the remaining 78% and described the large variations in habitat features within the stations. The first two axes of the between-stations analysis accounted for 53% of the inertia (mean value of the occurrence of each category in each station) (Figure 2B). The centers of gravity of the classes (stations) on the F1 $\times$ F2 factorial plane (Figure 2B) form four groups of sites, for which environmental profiles can be drawn (Figure 3): (1) the unnavigable reach of the Allan River (station DD15), one of the two reference stations, with a wide cross-section, a diversified current velocity and a predominantly coarse substrate; (2) a navigable reach upstream from Rochefort Weir (DN6) with a great width and no current; (3) the two upstream stations on the Freycinet Canal (CC13 and CC14), located on either side of the watershed, with a narrow width, a depth of more than 1.50 m, zero current velocity, the presence of artificial banks with vertical slopes, an

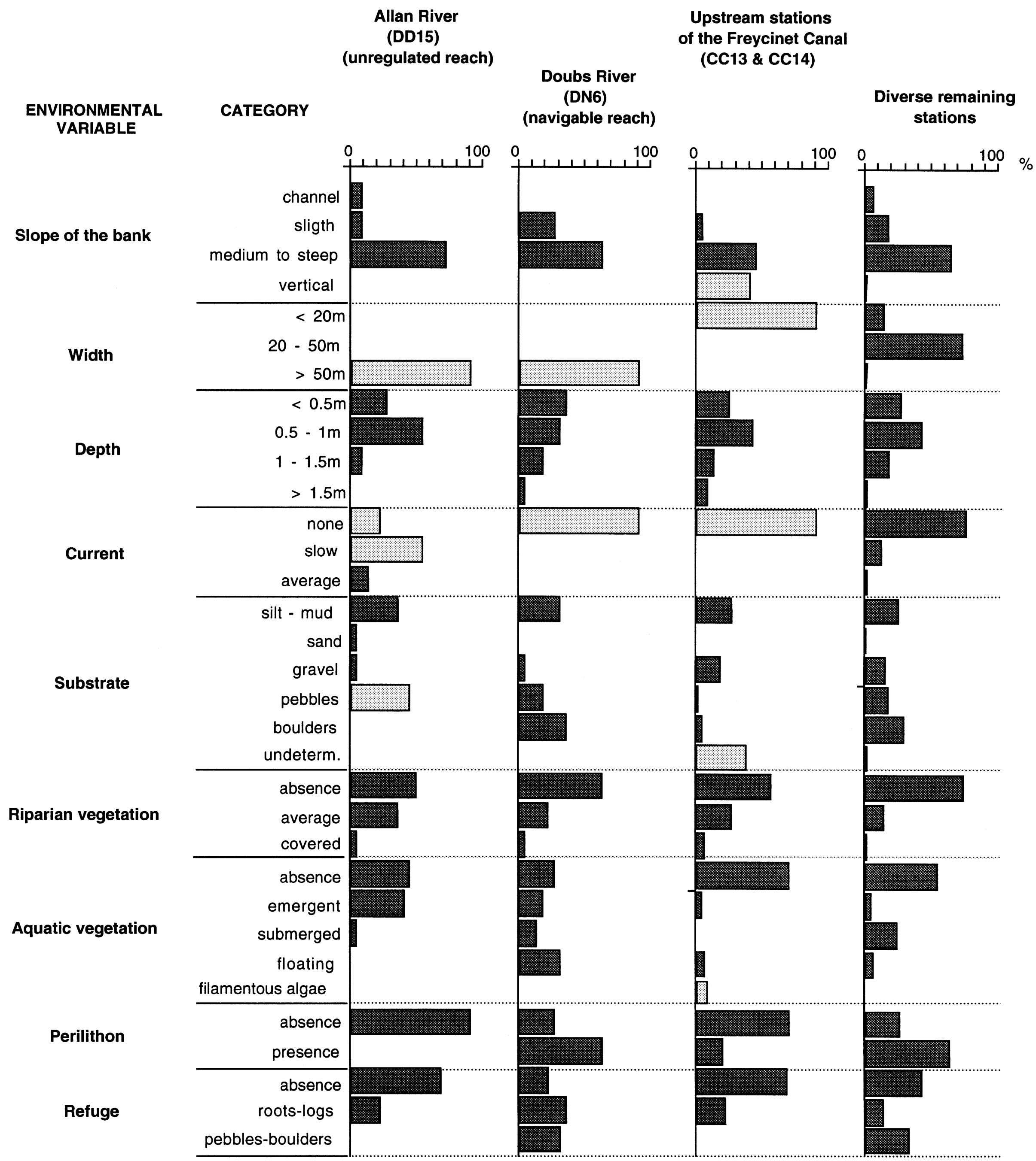


Figure 3. Habitat structure. Environmental profiles of the four groups of sites described by the between-stations MCA.

"undetermined" substrate, and the presence of filamentous algae; and (4) the last group includes the remaining stations without any clear discrimination between them, while a great heterogeneity exists within each station.

The two stations of the main stream (DD15 and DN6) are quite similar on the first axis owing to their width greater than 50 m and to the presence of emergent aquatic vegetation (Phragmites), but they differ on the second axis in their current velocity (diversified in DD15, always zero in DN6) and perilithon (absent in DD15, present in DN6).

The aquatic environments along the Doubs River could not be clearly separated in terms of habitat using our approach. This approach (few sampling campaigns, low flow) was incapable of including the temporal dimension; information about the habitat structure (distribution of current velocities, depth and river

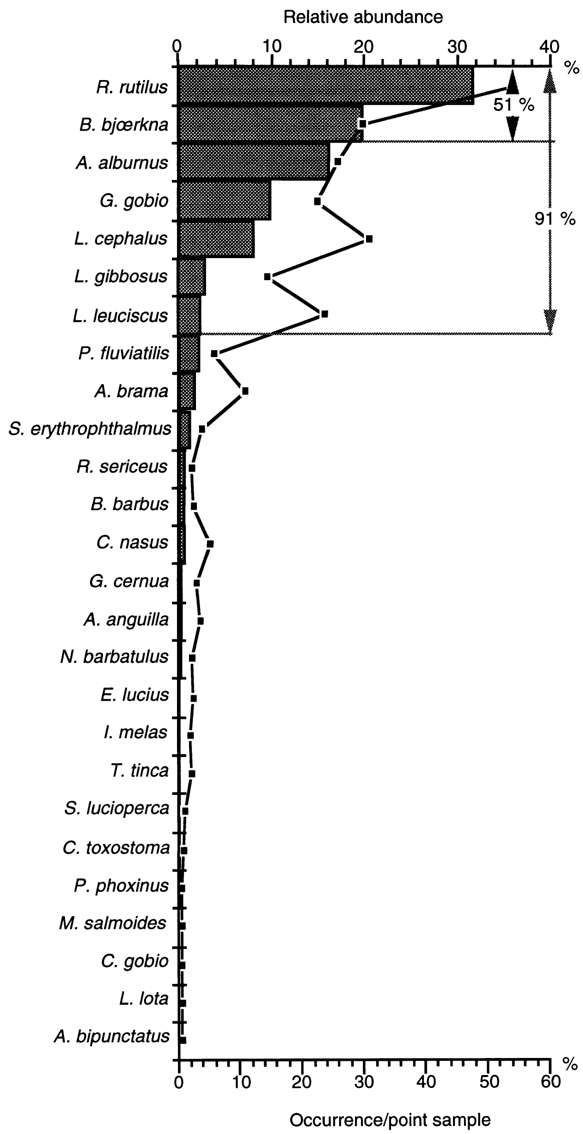


Figure 4. Relative fish abundance (bars) and occurrence (black squares) in point samples.

width) of backwaters during floods or during the spawning periods, for example, is lacking.

Species Composition

Twenty-six fish species were recorded (Figure 4 and Table 1). Six species (brown and rainbow trout, grayling, carp, blageon and wels) were not sampled but were found in the fish inventories (DDAF du Jura 1987, DDAF du Doubs 1990).

The species recorded were either ubiquitous, such as roach (*R. rutilus*) or chub (*L. cephalus*), or had strict ecological requirements, such as the rheophilic (barbel, *B. barbus;* nase, *C. nasus;* southwest European nase, *C. toxostoma;* and stream bleak, *A. bipunctatus*) or the limnophilic species (tench, *T. tinca;* common bream, *A. brama;* and rudd, *S. erythrophthalmus*). Overall, seven species were dominant: roach, white bream, bleak, gudgeon, chub, pumpkinseed, and dace. They accounted for 91% of the total abundance. They also were the most constant species in point samples (Figure 4).

However, some differences in abundance and occurrence existed between environments: for example, in the stations located in the unnavigable main channel, four species were dominant and constant (white bream, roach, bleak, and chub). These ubiquitous species made up 88.5% of the individuals and were present at all the DD stations. Besides these species, rheophilic species such as nase, barbel, and dace were also present but in lower numbers. This diversity reflected the good fishery quality of this type of environment and its high biological interest.

A single sampling campaign was insufficient to show significant differences in diversity and mean number of fish between the types of aquatic environments. It is difficult to estimate how many samples (or what samples size) are actually necessary to catch all species present in large open systems such as large rivers (McDonald and others 1996). It was not possible to test the representativeness of the samples, but it is well known that ‘‘communities dispersed over large areas are more difficult to sample adequately’’ (Baltanas 1992). For these reasons, we can assume that the number of point samples collected in each habitat type was not high enough to allow a statistical comparison of species diversity between these habitat types. However, the mean number of fish per point sample was statistically lower in the canals than in the main course and in the backwaters (Table 2), but no difference existed between the three types of environments in the Doubs river itself.

The highest numbers of species were recorded in the backwater called ‘‘corne des Epiciers’’ (station DA4, 16 species) and in two unnavigable stations of the main channel: Choisey (station DD1, which was the last downstream station and was located in a riffle sector) and Allan (station DD15, one of the two upstream reference stations) (both 15 species). This last station and the other upstream reference station, DD14 located on the Doubs, were the only ones where southwest European nase, *C. toxostoma,* occurred in both stations and stream bleak, *A. bipunctatus,* in DD14, i.e., rheophilic species.

Species Ordination

The sites–species matrix was analyzed using a decentered correspondence analysis. In this analysis, station DA4 was separated into two substations, 4a and 4b, corresponding, respectively, to the main channel of the river at the entrance of the backwater where the first

Table 1. Fish fauna of Doubs River between Montbéliard and Dôle[a]

Code	Common name	Scientific name	Unnavigable main channel (DD)	Backwaters (DA)	Navigable main channel (DN)	Canals (CC)
Php	Minnow	*Phoxinus phoxinus*	*			
Cog	Sculpin	*Cottus gobio*	*			
Nob	Stone loach	*Noemacheilus barbatulus*	*		*	
Chn	Nase	*Chondrostoma nasus*	**	*	*	
Cht	South-west European nase	*Chondrostoma toxostoma*	*			
Lel	Dace	*Leuciscus leuciscus*	**	*	*	
Lec	Chub	*Leuciscus cephalus*	***	**	***	***
Alb	Stream bleak	*Alburnoides bipunctatus*	*			
Gog	Gudgeon	*Gobio gobio*	***	***	***	**
Bab	Barbel	*Barbus barbus*	**	*	*	*
Esl	Pike	*Esox lucius*	*		*	*
Pef	Perch	*Perca fluviatilis*	**	**	**	***
Rhs	Bitterling	*Rhodeus sericeus amarus*	*	**	*	
Leg	Pumpkinseed	*Lepomis gibbosus*	**	**	**	**
Sce	Rudd	*Scardinius erythrophthalmus*	*	**		*
Lol	Burbot	*Lota lota*		*		
Tit	Tench	*Tinca tinca*	*	*	*	*
Abb	Bream	*Abramis brama*	**	**	*	**
Icm	Black bullhead	*Ictalurus melas*		*		*
Rur	Roach	*Rutilus rutilus*	***	***	***	***
Blb	White bream	*Blicca bjoerkna*	***	***	***	**
Ala	Bleak	*Alburnus alburnus*	***	***	***	*
Mis	Black-bass	*Micropterus salmoides*				*
Stl	Pike-perch	*Stizostedion lucioperca*	*			*
Acc	Ruffe	*Acerina cernua*	*	*	*	*
Ang	Eel	*Anguilla anguilla*	*		*	*
Number of species			23	17	17	16

[a]List of species found by electrofishing within each type of aquatic environment in 1992–1993.

***: abundant, **: common, *: rare.

point samples were collected and to the backwater itself. The first three axes of the analysis explain the main structure of the data set (Figure 5A). They only accounted for 52% of the total inertia of the table, highlighting the slight differences between sites in terms of the species composition of the samples. The first axis of the analysis separates the Freycinet Canal and the unnavigable reaches of the river (negative coordinates on this axis) from the backwaters and the navigable reaches (positive values on this axis) (Figure 5B). The Freycinet Canal and the unnavigable reaches are well discriminated by the second axis (the centers of gravity of each habitat type are indicated by circles), while the third axis separates the Freycinet Canal and the navigable stretches (negative scores on the third axis) from the unnavigable main channel and the backwaters (positives scores) (Figure 5C).

Figure 6 shows the simultaneous ordination of species and habitat types along the first three axes of the analysis. The values plotted represent the average occurrence of fish per habitat type. The main results are: Only eurytopic fishes and adults were found in the canals (roach, chub, perch, pumpkinseed) (separation along the second axis). These eurytopic species were also present in the navigable reaches, but together with juveniles (roach, chub, bleak, white bream) (opposition along the first axis). The fish fauna of the unnavigable main channel with its connected backwaters was typical of the ichthyofauna of a river with diversified aquatic environments (separated from the two former habitat types along the third axis). Both rheophilic species (such as minnow, nase, dace, barbel and gudgeon) and ubiquitous or eurytopic species (such as white bream, bleak and roach) were present. The first group was typical of the main channel and was mainly present as adults, whereas the second group was more typical of backwaters and was represented by adults and juveniles. In addition, typical limnophilic species (rudd, bitterling, tench and adult pumpkinseed) were found almost exclusively in the side-arms.

Ecological Significance of the Present Ichthyofauna of the Doubs River

The study of the reproductive guilds (Figure 7A) showed that more than a third of the species (and

Table 2. Characteristic values of taxonomic richness and number of fish in different aquatic environments and *t* tests between mean numbers of fish per point sample in these environments

	Unnavigable main channel (DD)	Back-waters (DA)	Navigable main channel (DN)	Canals (CC)
Stations (N)	6	3	2	4
Point samples (N)	120	60	40	80
Taxonomic richness				
Total species	23	17	17	16
Species/station (mean)	13	11	14	10
Number of individuals				
Total	2094	749	713	403
Mean/point sample	17.43	12.48	17.80	5.02
Standard deviation	25.08	15.19	22.92	7.30
	vs DD	vs DA	vs DN	vs CC
T tests between mean numbers of fish/point sample				
DD	—	1.64	0.085	5.104[a]
DA	—	—	1.29	3.511[a]
DN	—	—	—	3.438[a]
CC	—	—	—	—

[a]Value significant at $P < 0.05$.

nearly three fourths of the individuals) were phytolithophilous (of which 57.8% of the individuals were roach) and phytophilous (of which 92.6% of the individuals were white bream), indicating a great ubiquity. Nevertheless, several typical rheophilic species belonging to the lithophilous reproductive guild (chub, barbel, nase, southwest European nase, stream bleak, and minnow) and psammophilous species (gudgeon) were sampled. This means that the lotic character of the Doubs is still present. However, these species only represented about 10% of the individuals because of the disappearance of some of their spawning sites and/or of the pollution of some reaches of the river (downstream from Besançon for example).

In the part of Doubs concerned by our study, the present fish communities were on the whole typical of the mesopotamon [according to Illies and Botosaneanu (1963); biocenotic classification B8 according to Verneaux (1973, 1976)], that is to say a lowland river with some species more characteristic of side-arms and backwaters (e.g., rudd and tench) (Figure 7B). However, an epipotamic tendency (biocenotical classification B7) appeared in some places, due to the significant presence of gudgeon, barbel, dace, nase, and chub.

According to Verneaux's disturbance index (sensitivity of species to environmental disturbance such as organic pollution or river regulation) the fish communities were composed of moderately (such as rudd or nase) to slightly sensitive species (such as roach or white bream) (Figure 7C). More sensitive species were recorded locally (stream bleak, minnow, stone loach, and sculpin).

The analysis of the diet spectrum of the ten dominant species (relative abundance >1%), according to data available in the literature (Michel and Oberdorff 1995), showed that most of them were able to feed on several food sources. This allowed the dominant species to grow and survive in different environmental conditions, even in the highly artificial biotopes created by river regulation.

The analysis of habitat type preference (according to Persat and others 1994) of the previously mentioned dominant species showed that most of them were eurytopic. They could be found in nearly all habitats (main channel, side-arm, former channel, reservoir). However, it is notable that species highly linked to the lotic main channel (e.g., barbel), or species that need areas with low current velocity, such as backwaters, during some periods of their life cycle (e.g. nase) were not present in the group of dominant species. In contrast, the presence of rudd and tench, more typical of side-arms with a high macrophyte cover, indicated the significant presence of this type of environment. The link with this environment existed because of trophic demands (e.g., zooplankton by white bream), the use of backwaters as winter and flood refuges, or the requirements during the larval and juvenile stages.

Discussion

Ichthyofauna in the Present System

The differences in the structure of the fish communities of aquatic environments of the Doubs River between Montbéliard and Dôle were more qualitative (fish species) than quantitative (number of species and number of fish). However, the mean number of fish was statistically lower in the canals (Freycinet Canal and channelized part of the Allan River) than in the main course and in the backwaters. The natural parts of the Doubs (unnavigable reaches) showed the most diversified environmental structure and the most rheophilic fish communities despite the relatively poor physicochemical quality (e.g., in the reach between Montbéliard and Besançon).

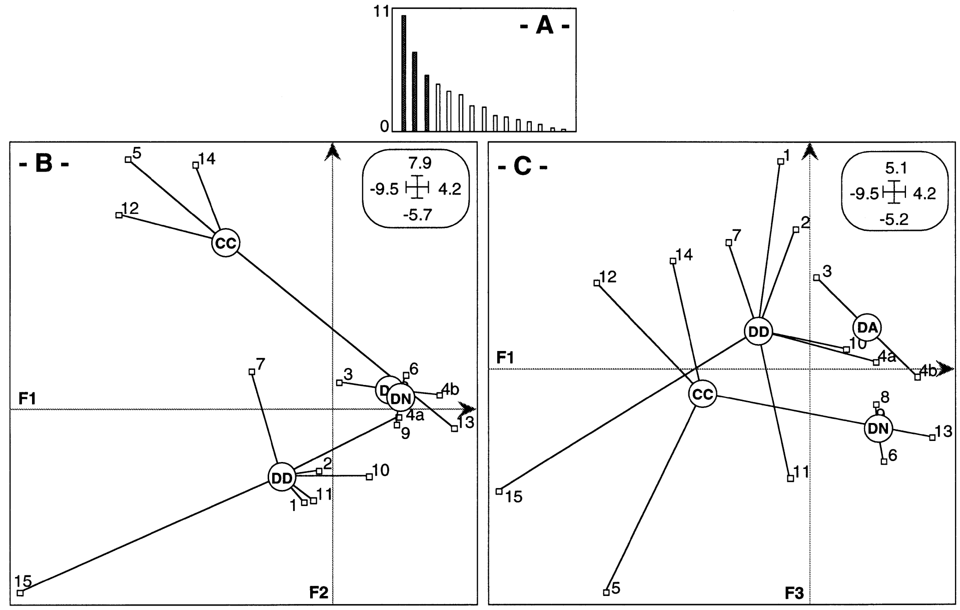


Figure 5. Decentered correspondence analysis (DCA) of the fish fauna. **A:** Eigenvalues. **B** and **C:** Factorial plots F1 × F2 and F1 × F3 of the stations. The centers of gravity of each habitat type are shown in circles.

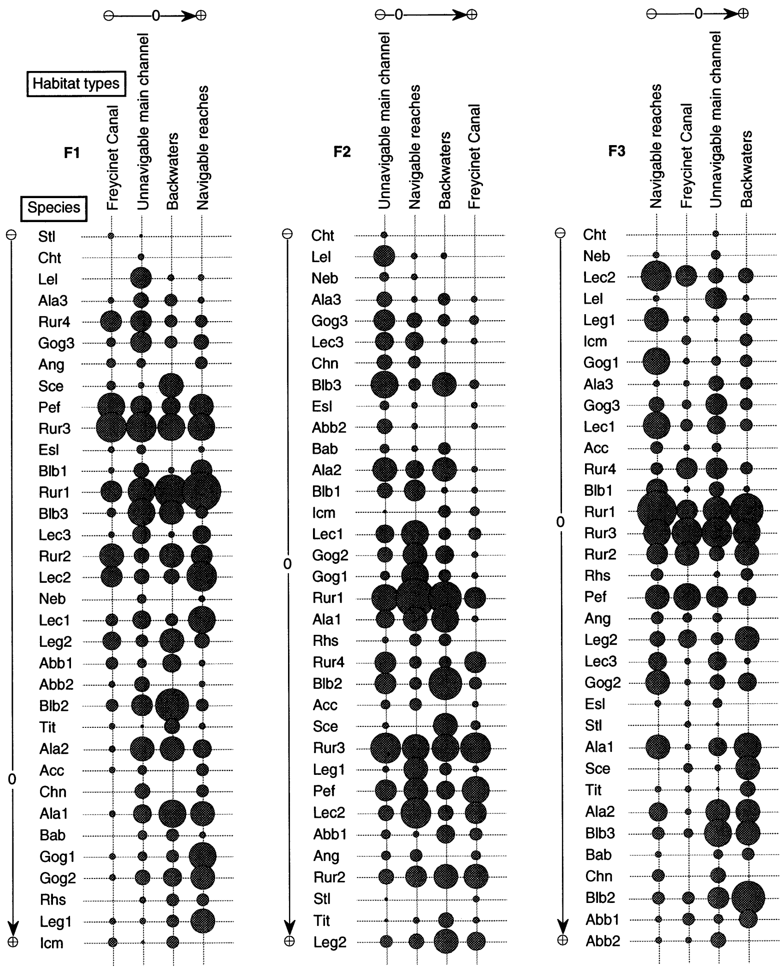
The overall high diversity reflected the potentialities (i.e., the ecological quality) of the river. It was due to the alternation of areas with diversified environments (riffles, several arms, backwaters, etc.) and various ranges of flow velocity. It enabled many species to complete their whole life cycle in good conditions and allowed several ecological guilds to coexist (rheophilic, eurytopic, and limnophilic). The rheophilic species (dace, stream bleak, southwest European nase, minnow, etc.) were well represented, but these were also the most sensitive to river regulation. However, the most abundant fishes throughout the Doubs were generalists (e.g., roach, bleak, and white bream) that had no special requirements for their food sources or for their spawning substrate.

The fish diversity and the presence of some rheophilic species reflected the good ecological quality of some stretches (Allan and Doubs rivers upstream from their confluence, i.e., upstream from Montbéliard; unnavigable sector with connected backwaters downstream from Dôle).

Temporal Changes in Fish Communities over 20 Years

Verneaux was the first to sample the fish communities of the Doubs river at the end of the 1960s and at the beginning of the 1970s. He characterized the part of the river we studied as a typical potamon (a lowland river, biocenotic order B8–B9 according to his classification) (Verneaux 1973, 1981), but the high species diversity masked the low abundance of some species typical of this type of environment that is naturally closer to an epipotamon. The fish communities were mainly influenced by organic pollution and some environmental alterations, such as the erection of weirs at the beginning of the last century. The dominant species were ubiquitous and eurytopic and tolerant towards dissolved oxygen and organic matter content. Rheophilic species occurred only in riffle sectors and downstream from weirs, where the current velocity was high enough to avoid silting. The large organic inputs between Novillars (outflow of a paper factory) and Avanne (outflow of a mill and of the Besançon purification plant) led to a reduction in species richness and species abundances in this stretch of the river. Afterwards, a gradual restoration of water quality was noted, involving higher species abundances and richness, in particular abundance and richness of species typical of the bream zone such as roach, bleak, and white bream. The updating by the CEMAGREF (1982) confirmed these conclusions.

Our study shows that the state of the river has not deteriorated. Ubiquitous and eurytopic species are still dominant, but the faunistic diversity of the main river still exists (cf. total richnesses in Tables 1 and 2) and some rheophilic species are still present. The same was noted for the macroinvertebrate communities (Fruget and others 1996).



SPECIES	total length classes in cm	Code
Alburnus alburnus 1	[0,6[	Ala1
Alburnus alburnus 2	[6,12[	Ala2
Alburnus alburnus 3	[12,17[	Ala3
Anguilla anguilla		Ang
Barbus barbus		Bab
Rhodeus sericeus		Rhs
Blicca bjoekna 1	[0,6[	Blb1
Blicca bjoekna 2	[6,10[	Blb2
Blicca bjoekna 3	[10,32[	Blb3
Abramis brama 1	[0,10[	Abb1
Abramis brama 2	[10,44[	Abb2
Esox lucius		Esl
Leuciscus cephalus 1	[0,8[	Lec1
Leuciscus cephalus 2	[8,15[	Lec2
Leuciscus cephalus 3	[15,46[	Lec3
Rutilus rutilus 1	[0,7[	Rur1
Rutilus rutilus 2	[7,9[	Rur2
Rutilus rutilus 3	[9,17[	Rur3
Rutilus rutilus 4	[17,32[	Rur4
Gobio gobio 1	[0,6[	Gog1
Gobio gobio 2	[6,9[	Gog2
Gobio gobio 3	[9,19[	Gog3
Acerrina cernua		Acc
Chondrostoma nasus		Chn
Noemacheilus barbatulus		Nob
Ictalurus melas		Icm
Perca fluviatilis		Pef
Lepomis gibbosus 1	[0,4[	Leg1
Lepomis gibbosus 2	[4,19[	Leg2
Scardinius erythrophthalmus		Sce
Stizostedion lucioperca		Stl
Tinca tinca		Tit
Chondrostoma toxostoma		Cht
Phoxinus phoxinus		Php
Leuciscus leuciscus		Lel

Figure 6. Simultaneous ordination of species and habitat types along the first three axes of the DCA. The plotted values are the average occurrences of fish species per habitat type. Some species are divided into size classes. The areas of the circles are proportional to the abundance.

Predictions Concerning Implementation of the New Scheme

Human activities such as channelization, construction of levees, navigation, irrigation, etc., highly affect wetlands and rivers (Minshall and others 1985, Schlosser 1991, Johnson and others 1995). These activities generally decrease habitat heterogeneity in the main channel and reduce the interaction of the river with the floodplain and riparian zones (Sedell and Froggatt 1984, Gore and Shields 1995). These disturbances tend to reduce the abundance and diversity of fishes, especially juveniles (Schlosser 1991, Schiemer and others 1991, Schiemer and Zalewski 1992, Weaver and Garman 1994). Changes in the embanked reaches and in the bypassed sections, and the accompanying changes in the lower trophic levels, strongly influence the structure and the dynamics of fish communities. Schiemer and Spindler (1989) showed that a highly structured shoreline is important in providing different classes of current velocity and various food sources. In contrast, artificial embankments are accompanied by a reduced fish fauna with low population densities and eurytopic species. A gradual shift from autochthonous communities to native or introduced competitor or predatory fishes and an impoverishment of the fish fauna with a predominance of habitat generalists and low densities of riverine species are noted. These trends have been demonstrated worldwide in many regulated rivers, e.g., by Krenkel and others (1979) in the Tennessee; Hesse and others (1989) in the Missouri; Carlson and Muth (1989) and Stanford and Ward (1986) in the Colorado; Schiemer and Spindler (1989) and Schiemer and Waidbacher (1992) in the Austrian Danube; and Lelek (1989) and Lelek and Köhler (1989) in the Rhine.

Bain and others (1988) demonstrated, in a northeastern US river, that shoreline habitats harbored over 90% of all fish and most of the species in the river. This result emphasized a shoreline–midstream orientation. How-

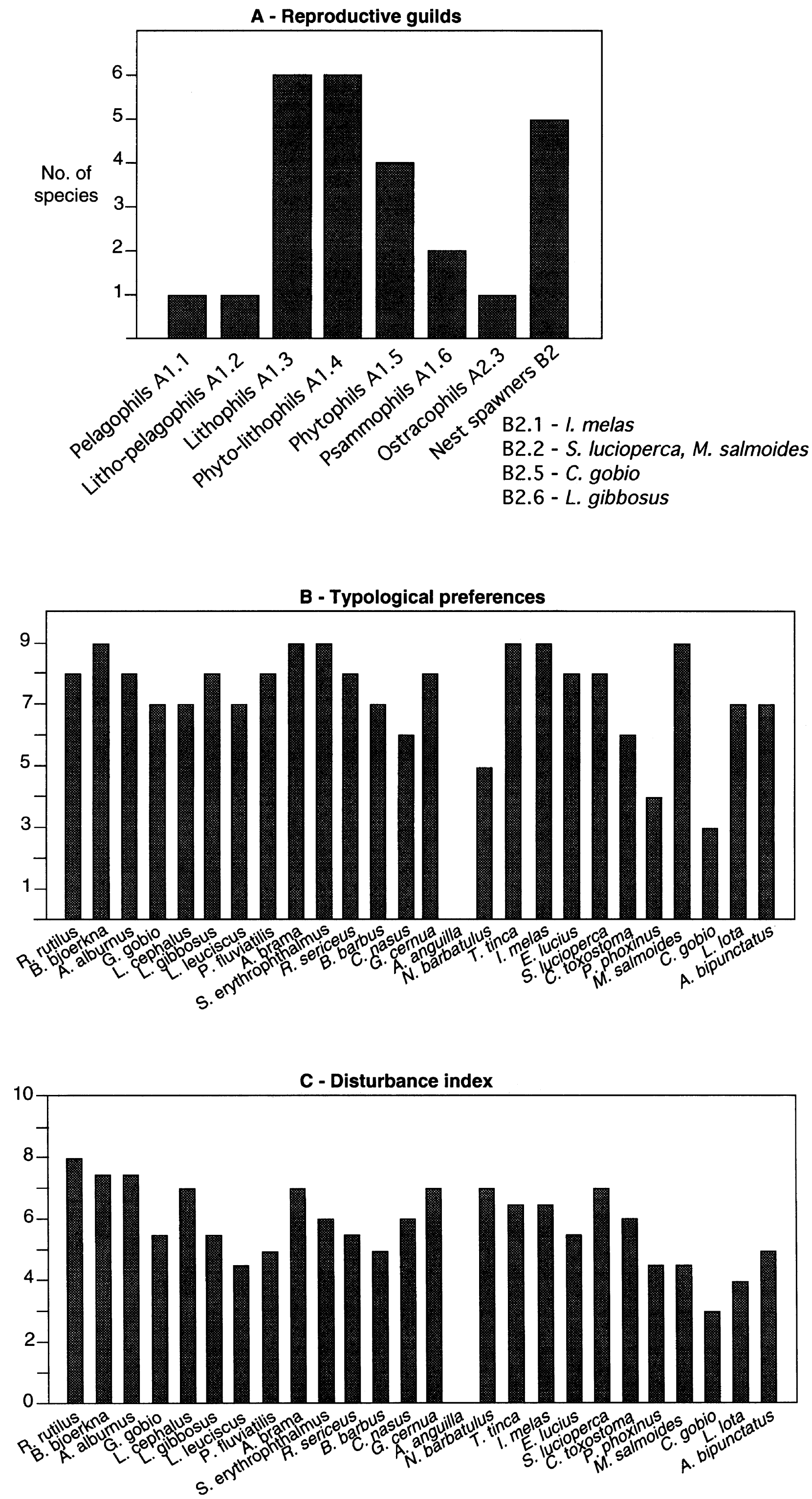


Figure 7. Reproductive guilds according to Balon (1975) (**A**); typological preferences (**B**) and disturbance index (**C**) according to Verneaux (1973). Fish species are classified in **B** and **C** according to their abundance.

ever, the abundant and diverse shoreline fish assemblage was reduced in river reaches with high flow fluctuations (e.g., downstream of dams). Frequent high flow variability imposed functional habitat homogeneity. Without the functional availability of shallow, slow-flowing shoreline habitats, the stream environment became one general type of usable habitat that was dominated by the few habitat generalists and those species specializing on the channel habitat.

Riparian habitats provide essential food supplies and recruitment areas (they are used for spawning and early stages of development) (Persat 1991, Schiemer and others 1991). They represent a fundamental land–inland water ecotone in the dynamics of the river ecosystem. However, these habitats are the first to be disturbed when regulation works begin (Petts and others 1989). For example, Persat (1991) and Persat and others (1995) demonstrated that a reduction in the diversity of the riparian habitats accompanied the construction of further impoundments on the French Upper Rhône and led to a noticeable shift in the fish community structure. The impounded sections became very uniform, with a low number of habitat types corresponding to the embankments, whereas some diversity subsisted in the bypassed sections, which had two main kinds of riparian habitats: one similar to the artificial system, i.e., embankments of the last century, and a specific one, i.e., very large flat and sunny gravel beaches. However, this diversity was much lower than that of the former river banks. Concurrently, some species decreased (salmonids, dace), whereas others increased (roach in the impounded reaches, nase in the bypassed sections). Another consequence of damming on the riparian habitats was the fluctuation in water level (tiding). Tiding mostly affected shallow waters and consequently affected the beaches of rivers, but one of the most important effects of embankments was the heavy reduction of beach areas. Thus, in altering the capacity of the shallows (already reduced by embankments), tiding had the same effect, i.e., the depletion of fry and juveniles, in particular of rheophilic species (Bain and others 1988, Persat and others 1995).

Another example of the influence of regulation was given by the comparison of changes that occurred in fish communities of the three largest European regulated rivers, the Rhine, the Rhône, and the Danube (Persat and others 1995). Facing similar river engineering, the fish communities of these rivers showed similar responses: a reduction in fish biomass, disappearance of major migratory species, disappearance of rheophilic and vulnerable species, and the increase or persistence of a small set of resistant species. All man-made alterations in regulated rivers led to a gradual reduction of the transverse dimension of the hydrosystem by disruption of the connection with lateral waterbodies (side-arms, backwaters, marshes), followed by their drying out or siltation, to a reduction of the submersible areas resulting from straightening and steepening the banks, and to the deepening of the riverbed.

According to the events observed in the Rhine, Rhône, and Danube, the few species resisting human impact are: roach, bream, white bream, chub, bleak, perch, eel, and pike-perch. One common feature of these species is that none live exclusively in standing or running waters but all are able to live in both.

Roach is the great winner of river regulation in Europe (Persat and others 1995). This species has a wide range of feeding techniques, a great fecundity, and is able to spawn on different kinds of substrates such as aquatic plants, submerged branches, and even rip-rap, which are always more or less available in impounded rivers (Schiemer and Wieser 1992).

Aron and Smith (1971) and Arai and Mudy (1983) emphasized the danger of biological exchanges, and consequently of biological introductions, resulting from this type of canal that connects two hydrographic basins, e.g., the transport of species able to supplant autochthonous species, the passage of parasitic diseases, etc. Balon and others (1986) and Bryson (1992) showed that these hazards existed for the new Rhine–Main–Danube connection. These hazards also exist for the future Rhine–Rhône large ship canal. For example, the presence and the development of the wels, *Silurus glanis*, in France and of the parasitic disease called anguillicolosis in the coastal rivers of Languedoc-Roussillon were due to their migration and their extension by the waterways (Allardi 1984, Keith and others 1992, CEMAGREF 1991). Nevertheless the fact that a narrow-gauge connection between the Rhine and Rhône has existed since 1833 would suggest that most possible species transfers between these basins may have already taken place [e.g., recently invading amphipods *Crangonyx pseudogracilis* and *Corophium curvispinum* (Fruget and others 1996)].

Conservation Perspectives and Solutions

Conservation management must take account of the present ecological situation of the Doubs River, i.e., that of a lotic ecosystem with active connections with its backwaters. The primary goal from a conservation perspective must be the maintenance and the improvement of areas that will be highly sensitive to disturbance (such as regulation works). Three main types of conservation solutions may be implemented:

1. Maintenance of at least the average summer dry weather discharge in all the future bypassed sections, i.e., natural sectors. This discharge should be in accordance with the water management policy (French fishery and water laws). The restoration, or at least conservation, of the hydrological regime is the basis of the rehabilitation of regulated river–floodplain systems (Bayley 1995). Travnichek and others (1995) and Bain and Travnichek (1996) indicated that the increase in the minimum water releases in a regulated reach of the Tallapoosa River (Alabama, USA) below a dam improved habitat conditions, restored a diverse fish assemblage more reflective of a riverine system, and pro-

moted the conservation of the riverine fish fauna. Regular flood pulses are vital for the productivity of hydrosystems (Welcomme 1979, Junk and others 1989, Bayley 1989, Sparks 1995). It was proved that fish yield is considerably greater in rivers with connected backwaters and flood pulses than in nearby impoundments where changes in the lateral dimension and flood pulses are absent (Welcomme 1979, 1985, Bain and Boltz 1989, Bayley 1991, Sparks 1995).

2. Maintenance of the diversity of the aquatic environments, in particular through the maintenance of river–floodplain connections. These connections avoid silting up and drying up of side-arms by the regular passage of floods. Backwaters of the Doubs River must be kept permanently connected with the main stream, thus continuing to act as winter and flood refuges and as spawning and hatching areas. A decrease in biological connections will occur if a decrease in morphological connections occurs (Stenseth 1980, Amoros 1991, Fruget 1992). In contrast, lateral integrity of the alluvial system enhances its fish productivity, as shown in different stretches of the Austrian and Slovak Danube by Holcik and others (1981) and Schiemer and Waidbacher (1992), in several dead arms of the Garonne River by Belaud and others (1990), and of the Seine River by Tales and others (1996), or in the regulated Lower Rhône River by Nicolas and Pont (1995). Restoration of physical and biological interactions between the main channel, backwaters, and the floodplain is central to the rehabilitation of regulated rivers (Gore and Shields 1995). The great significance of the floodplain for the reproduction, nursery, and recruitment of fish populations has been well documented (Penaz and others 1991b, 1995, Schiemer and others 1991, Bengen and others 1992). In the Upper Rhône, Penaz and others (1995) showed that the backwater habitats lost their importance as a habitat for fish in a very short time due to the reduced connections with the main channel and due to autogenic processes that accelerated habitat senescence (drying up and invasion by terrestrial plants). Heterogeneity (and consequently diversity) at different ecological levels is fundamental for all types of ecosystems (terrestrial or aquatic) (Haila and Kouki 1994, Winemiller 1995).

3. Maintenance of bank structure and diversity. These aquatic and terrestrial ecotones are important for the biological equilibrium of rivers. Community structure is controlled by the physical conditions of the habitat (Schlosser 1982, Bain and others 1988). Natural banks show great diversity of microhabitats, and they act as biological reserves and nurseries for the species of the main channel (Persat 1991, Schiemer and others 1991). The size of this riverine biological stock is related to the length of natural banks. Microhabitat diversity favors the presence of several ecological guilds. Rivers with diversified habitats, both in the channel and the side-arms or backwaters, are likely to be more productive (Scott and Nielsen 1989, Schiemer and Zalewski 1992, Penaz and others 1991a, 1995). The study of Schiemer and Waidbacher (1992) on the distribution of fish fry in various habitat types in the Austrian Danube downstream from Vienna provided clear evidence that many of the rheophilic species were bound to the inshore zone of the main channel during their early life phase. The lowest population density of the 0+ age class and the lowest species diversity were found along artificial linear embankments (rip-rap). Riverine shoreline structure is thus a decisive characteristic for the existence or disappearance of numerous rheophilic species in the Doubs River. Consequently, linear embankments should be as limited as possible. Shallow sloping and shores covered by vegetation should be developed to create protection zones during floods.

However, if aquatic and/or terrestrial areas are lost, similar environments that function similarly must be created or restored as a compensation (Cairns 1986, Petts 1990). These management recommendations require some deviation from an engineering point of view. Our study can be regarded only as an instantaneous picture. From an ecological perspective, (1) a quality assessment based on adult fish requires long-term studies because the ecological limits of fish become wider with age, and (2) long-term monitoring must be conducted to study man-made disturbances and restoration measures undertaken in the river floodplains (Sparks and others 1990). These are necessary to improve our knowledge of the aquatic environments. The goal of ecosystem management should be to maintain or restore the biological integrity of the ecosystem (Lubinski and others 1995). The concept of biological integrity should be the basis for biological assessment of rivers. It was defined as "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitats of the region" (Angermeier and Karr 1994). This knowledge is essential to our ability to preserve, maintain, and rehabilitate rivers (Petts and others 1989).

Biodiversity must now be considered, both at the species and ecosystem levels, as being of economic value (Lévêque 1994). In management, conservation of biodiversity needs to take into account the environmental economy; biological diversity is also valuable as a resource (Haila and Kouki 1994). The integration of biodiversity preservation into management practices should be a major challenge. The specific ecological features of the systems exploited should be recognized and incorporated into these practices. This calls for close cooperation between fundamental research and applied management. Lessons learned from different regulated rivers around the world suggest that remediation after an impact is enormously more costly than proper mitigative design before the changing of large rivers (Petts and others 1989, Brittain and others 1996).

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