

THE IMPORTANCE OF INSHORE AREAS FOR ADULT FISH DISTRIBUTION ALONG A FREE-FLOWING SECTION OF THE DANUBE, AUSTRIA

V. HIRZINGER,^a H. KECKEIS,^{a*} H. L. NEMESCHKAL^b and F. SCHIEMER^a

^a University of Vienna, Institute of Ecology and Conservation Biology, Althanstrasse 14, A-1090 Vienna, Austria

^b University of Vienna, Institute of Zoology, Althanstrasse 14, A-1090 Vienna, Austria

ABSTRACT

This study analyses bank morphological parameters of inshore areas as significant qualifying criteria for the habitat of riverine fish in large rivers. The mesoscaled (1.04 ± 0.35 km) spatial distribution of adult fish was studied along a 50 km stretch of a free-flowing section of the Austrian Danube. Fish abundance at the inshore zone of the main channel was assessed every month from March 1992 to May 1993, applying stratified random sampling by electrofishing.

In order to calculate river morphological variables, a specific DOS application was programmed taking riverbank profiles, slope of the Danube and mean daily water level into account. The sampling sites by environmental variables were analysed by principal component analysis (PCA). PCA scores, together with the relative densities of each fish species in terms of their proportions per catch, were treated by a simple logistic regression. The different species exhibit specific patterns of statistical probability in terms of distribution and densities at distinct structural inshore types with regard to area, slope, habitat heterogeneity and connectivity parameters.

Large gradually sloping inshore areas are characterized by rheophilic *Chondrostoma nasus*, *Leuciscus idus* and *Abramis balerius*, whereas eurytopic species do not show a consistent pattern. Heterogeneous stretches contain high proportions of *Leuciscus cephalus*, *Abramis brama* and *Abramis ballerus*. Connectivity discriminates strictly riverine species like *Chondrostoma nasus* from rheophilic species which require non-channel habitat during their life history. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: riverine fish; shore line structure; littoral zone; large rivers; Danube; logistic regression; PCA

INTRODUCTION

Numerous ecological studies have focused on the structural habitat requirements of river fish communities (Grossman *et al.*, 1982; Gehrke *et al.*, 1995; Prenda *et al.*, 1997; Martin-Smith, 1998). The functions of main channels and particularly their inshore zones are of major interest. The highway analogy, as a fundamental part of the flood pulse concept (Junk *et al.*, 1989), contradicts the function of the river channel itself as a habitat for riverine fish. It questions the role of main channels as a significant long-term habitat component of the fish assemblage of large floodplain rivers (Galat and Zweimüller, 2001). An alternative hypothesis is that river channels are main habitats for adult fish regardless of seasonal aspects. This approach differs from studies that focus on habitat use during certain life history stages or which exclude certain time periods, for example the spawning season (Angermeier, 1987). Both migrating species and species inhabiting large rivers year-round depend on adequate channel habitats.

Due to water level fluctuations, the main channels of large European rivers are variable environments with temporal differences in habitat availability and inshore heterogeneity (Reckendorfer *et al.*, 1999). Inshore morphology strongly correlates with hydrology, temperature, food availability or shelter and is likely to determine fish community structure (Schiemer and Spindler, 1989; Vanotte *et al.*, 1980). Therefore a key objective in fish ecology is to combine biotic patterns such as fish distribution or association and physical habitat. Stream habitat variation can be determined along a depositional and erosional gradient or as sequences of morphological and hydrological

*Correspondence to: H. Keckeis, University of Vienna, Institute of Ecology and Conservation Biology, Althanstrasse 14, A-1090 Vienna, Austria. E-mail: Hubert.Keckeis@univie.ac.at

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conditions (e.g. pool, riffle and run) (Prenda *et al.*, 1997; Martin-Smith, 1998). A summation of particular physical parameters (e.g. depth, current, substratum or cover) is often used to describe habitat state and is applicable in large rivers as well (Angermeier, 1987).

River alteration through embankment and reinforcement processes in the 20th century led to structurally impoverished main channels. Anthropogenic utilization such as hydroelectric power gain and inland navigation forced laterally migrating rivers into straightened channels and degraded their topology (Ward *et al.*, 1999). The value of the remaining physical habitat structures for a fish fauna and the means by which these structures can be measured in large river sections is of great ecological interest. This has led to the demand for habitat models based exclusively on easily measured parameters (Knapp and Preisler, 1999).

The present study examines habitat classification by focusing on connectivity and depth-dependent variables, which often are considered to be most relevant with regard to habitat complexity and species diversity (Angermeier, 1987). We define bank morphological variables describing slope, size, heterogeneity and connectivity of habitat strata in order to test their significance for the fish community structure. We address the following questions: Do different species show predictable requirements concerning inshore morphological variables? Are main channel habitat conditions reflected in the adult fish community of a local site? Can habitat preferences of ecological guilds (Schiemer and Waidbacher, 1992) be distinguished based on inshore habitat size, slope, heterogeneity and connectivity?

The braided sections of large rivers are valuable but endangered habitats (Persat *et al.*, 1995). Here, we point out the general importance of the Danube's main channel in the last remaining free-flowing section for common fish species, and its role for the integrity of large lowland rivers (Schiemer and Waidbacher, 1992; Schiemer, 2000). The aim is to support the protection and restoration of suitable riverine habitats. Most of the species involved in this study, especially those that require large river habitats, are of conservational concern (Schiemer and Waidbacher, 1992; Galat and Zweimüller, 2001). These main channel habitats need to be investigated because they are seriously affected by anthropogenic changes. Information on suitable habitats for fish is crucial for developing future river management concepts, restructuring efforts and protection measures. Knowledge about the preferred inshore morphology of adult fish should be integrated into these concepts.

STUDY SITE

The study site is a 50 km free-flowing stretch of the Austrian Danube between river kilometre 1945 (north of Vienna) and river kilometre 1895 (near Regelsbrunn) (Figure 1).

Contrary to urgent recommendations that were made in the 1960s, the upper braided free-flowing part was dammed (Lelek, 1976). At present, only two short stretches of the entire Austrian Danube feature near-natural relicts of floodplains (Dister, 1994), of which we sampled one.

Near Vienna, the Danube is a ninth-order river with gravel as the main substrate. It is a large European river: braided channels and gravel bars should dominate the natural state of hydrological and ecological succession at the studied river sections (Persat *et al.*, 1995). The average discharge of the Danube here is $2000 \text{ m}^3 \text{ s}^{-1}$ at a mean slope of 0.043%. The dominant discharge regime is influenced by regular snowmelt in the Alps and by stochastically heavy rainfalls in the catchment area in summer. The predictability of flood events is highest between March and April due to the snowmelt. Over the course of the year the discharge decreases, reaching its minimum in winter. Water temperature in the main channel varies from 0°C in winter to approximately 22°C in summer and shows relatively small daily fluctuations of about 0.5°C.

METHODS

River morphology and hydrology

Channel profile data were used to describe the morphological characteristics of the river banks. These profile data are collected yearly in 100 m intervals.

Hydrological conditions were defined by daily mean water level at the water gauge Orth, 10 km downstream of Vienna. Characteristic water levels and the slope of the Danube were used to calculate the exact water level at the

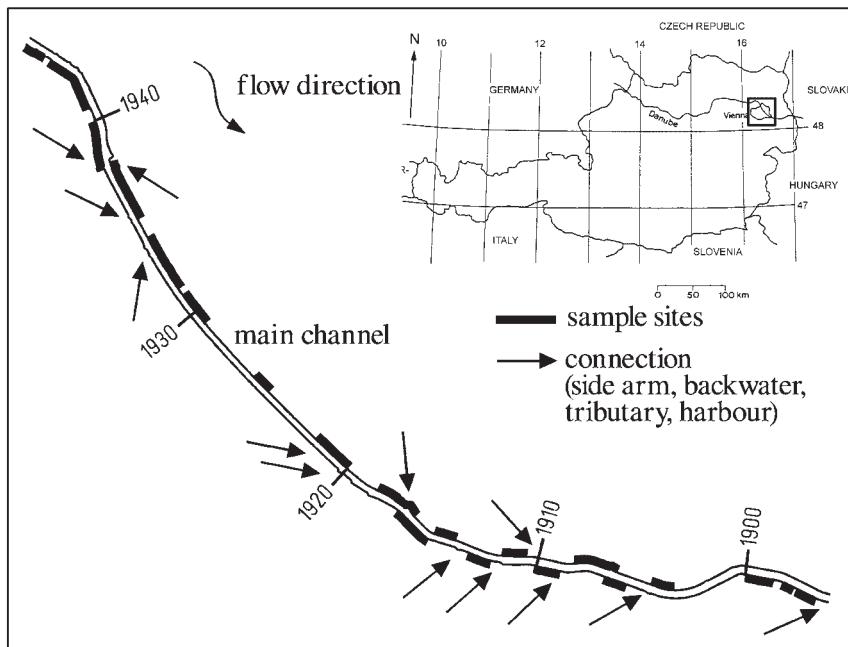


Figure 1. The 50 km stretch of the Danube near Vienna: numbers mark the stream kilometres. The arrows indicate side arms, minor channels, tributaries, backwaters and harbours. The black bars show the sampling sites at both sides of the main channel. Upper right corner: map of Austria, rectangle indicating the location of the study site

point of sampling. Habitat parameters were generated from this morphological and hydrological information using object-orientated vector graphics programmed in C computer language. The following ten variables (1–10) were calculated in order to describe the structural habitat characteristics at a mesoscaled (sampling stretch length = 1.04 ± 0.35 km) spatial level of each site at the time of sampling: three total distances, (1) from the shoreline to 1 m water depth, (2) from 1 to 2 m and (3) from 2 to 3 m water depth (Figure 2a); three surface areas occupied by (4) 0–1 m, (5) 1–2 m and (6) 2–3 m deep water, which together define the habitat size in each particular water depth; (7) the length of the shoreline; and three isobathic lines in (8) 1, (9) 2 and (10) 3 m water depth, which specify the heterogeneity, were also calculated (Figure 2b).

At a reach scale the distances of investigation sites from their closest lateral connection (side-arms, minor channels, tributaries or harbours) were also calculated as a metric variable quantifying the connectivity which defines the accessibility to the most adjacent backwater (Figure 1).

Sampling

Fish distribution was investigated using electrofishing. The 8.5 kW generator produced a direct current of 400–500 V and about 8 A. The anode, consisting of six cables, was fixed at the bow of a 7 m boat, and the copper cathode was placed on the stern (Keckeis *et al.*, 1996). From March 1992 until late May 1993, a series of 147 samples were taken in monthly intervals. The average length of the investigated stretches was 1.04 ± 0.35 km and the length was kept constant for each site (Figure 1). Fish were identified to species level and their relative densities in terms of catch per unit effort (CPUE) were included in the further analysis.

Statistical treatment of the data

River morphological data and catch data were weighted to a distance of 1 km. From the original ten variables representing metric river profile data, three ordination axes were extracted applying principal component analysis (PCA); these axes explain 85.7% of the total variance. Axis interpretations were based on the loadings

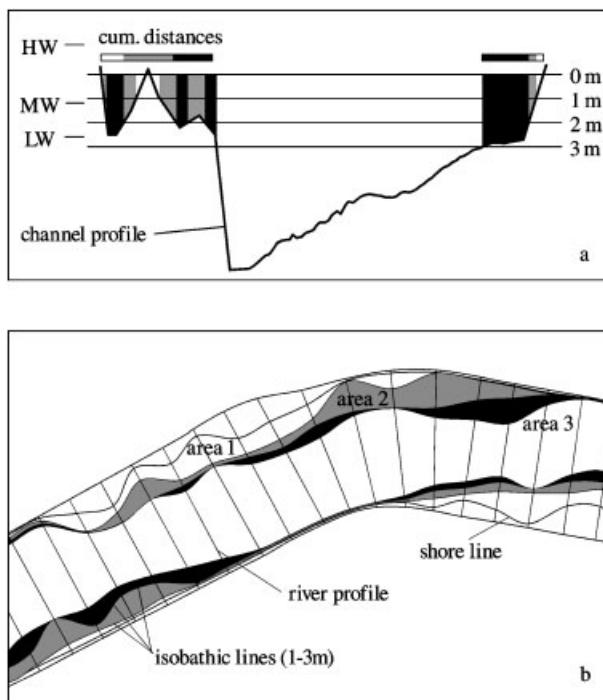


Figure 2. Scheme presenting how the ten morphological variables at the investigated stretches were calculated. (a) Example of a channel profile: cum. distances = cumulative distances from 0–1 (white), 1–2 (grey), 2–3 m (black) water depth; HW = high water level; MW = mean water level; LW = low water level. (b) Bird's-eye view of a 2 km stretch at a selected water level: shoreline, isobathic lines and the areas of the three depth classes (white, grey, black) are given. River profiles in distances of 100 m are indicated by straight lines

of the non-rotated correlation-matrix of components. Connectivity data were transformed to natural logarithm [$y = \ln(1 + x)$] in order to remedy the asymmetric distribution of the original variable.

Fish data were incorporated as relative densities of each fish species in each catch in terms of their proportions per sample (CPUE).

The three PCA factor scores, the connectivity data and the fish data were treated by a logistic regression (for theoretical principles see, for example, Lloyd (1999) or Flury (1997)) using a logit link function (Equation 1). These calculations were made using a module of categorical regression analysis written in VisualBasic for DOS (Nemeschkal, 1999). Significance levels (p) were corrected with respect to Bonferroni inequality (for details see Table IV). In order to reveal two-dimensional plots for each variable of interest from this hyperdimensional analysis, a reduced logistic model (Equation 2) was used; it excluded three of the habitat variables, setting their parameters to zero (Flury, 1997).

$$\pi = g(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4)} \quad (1)$$

This model is used for the ten most abundant species (more than 96.6% of individuals caught; see Figure 3), where π is the probability of occurrence, and $g(x)$ is the expected proportion of a species as a function of the explanatory variables. The parameters of the model are: β_0 is the constant, β_1 , β_2 , β_3 and β_4 are the regression coefficients. The x_1 , x_2 , x_3 and x_4 are the explanatory variables, x_1 is the PCA axis 1, x_2 is the PCA axis 2, x_3 is the PCA axis 3 and x_4 is the transformed connectivity variable.

$$\pi = g(x) = \frac{\exp(\beta_0 + \beta_x)}{1 + \exp(\beta_0 + \beta_x)} \quad (2)$$

The x is the variable of interest.

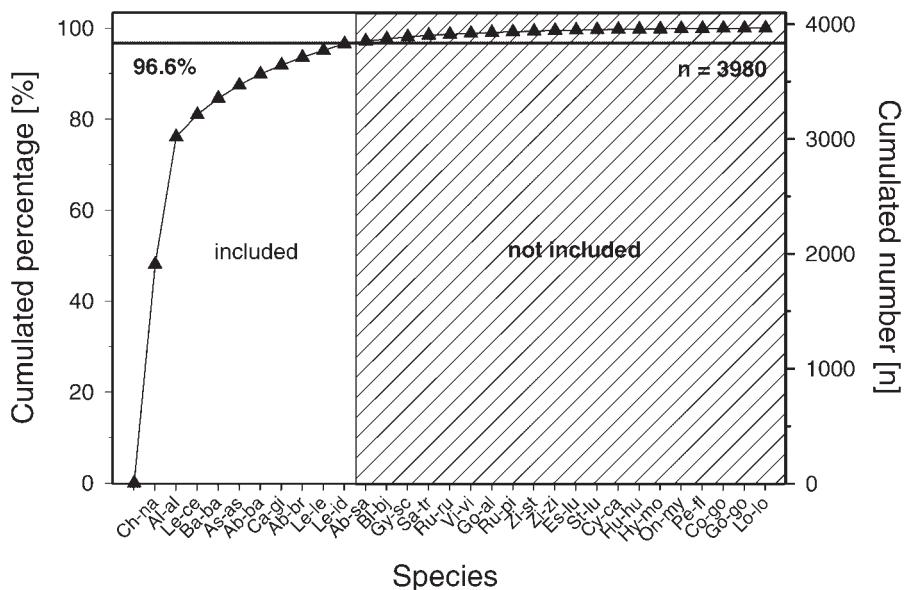


Figure 3. Cumulated relative abundance and cumulated number of the total catch ($n = 3980$). Species: Ch-na, *Chondrostoma nasus*; Al-al, *Alosa alburnus*; Le-ce, *Leuciscus cephalus*; Ba-ba, *Barbus barbus*; As-as, *Aspius aspius*; Ab-ba, *Abramis ballerus*; Ca-gi, *Carassius gibelio*; Ab-br, *Abramis brama*; Le-le, *Leuciscus leuciscus*; Le-id, *Leuciscus idus*; Ab-sa, *Abramis sapo*; Bl-bj, *Blicca bjoerkna*; Gy-sc, *Gymnocephalus schraetzeri*; Sa-tr, *Salmo trutta*; Ru-tr, *Rutilus rutilus*; Vi-vi, *Vimba vimba*; Go-al, *Gobio albipinnatus*; Ru-pi, *Rutilus pigus virgo*; Zi-st, *Zingel streber*; Es-lu, *Esox lucius*; St-lu, *Stizostedion lucioperca*; Cy-ca, *Cyprinus carpio*; Hu-hu, *Hucho hucho*; Hy-mo, *Hypophthalmichthys molitrix*; On-my, *Oncorhynchus mykiss*; Pe-fl, *Perca fluviatilis*; Co-go, *Cottus gobio*; Go-go, *Gobio gobio*; Lo-lo, *Lota lota*.

In order to distinguish different habitats and to reveal distinct groups of sampling sites, a cluster analysis (Ward method, squared Euclidean distance) was used. Significant differences of the three clusters were tested by analysis of variance (ANOVA) for each explanatory variable (see Table V).

RESULTS

The 147 catches yielded a total of 30 species and 3980 individuals. The PCA revealed three axes explaining 85.7% of the total variance in the ten habitat variables measured (Table I). The first axis correlated positively with area down to 1 m water depth, distance from shoreline to 1 m, as well as area and distances between 1 and 2 m water depth. Negative correlation was observed with both distances and area in 2 to 3 m water depth. The second axis was positively correlated with the length of the four isobatic lines; axis three correlated positively with area and distance in 1 to 2 m and 2 to 3 m water depth (Table I). PCA axis 1 will be labelled as 'shallow area', PCA axis 2 as 'deep area' and PCA axis 3 as 'heterogeneity'.

Results of the logistic regressions for the ten most abundant species, which represented over 96.6% of the individuals caught, are shown in Table II and Figure 3. The summarized size data are given in Table III. The remaining 20 species were excluded from the analysis because quantitative analysis of rare species in fish communities is often difficult (Mérigoux *et al.*, 1999). After Bonferroni correction, eight of the ten species considered revealed significant results for at least one variable used in the logistic regression ('shallow area' = PCA axis 1, 'deep area' = PCA axis 2, 'heterogeneity' = PCA axis 3 and the connectivity) (Table IV). *Abramis ballerus*, *Leuciscus cephalus*, *Abramis brama* and *Leuciscus idus* were positively correlated with large, heterogeneous and deep areas. *Leuciscus leuciscus*, *Carassius gibelio* and *Alburnus alburnus* had lower capture probabilities in terms of relative abundance per site with increasing size of area down to 2 or 3 m water depth. *Chondrostoma nasus* showed a negative relationship with heterogeneity and a positive relationship to large areas from 1 to 3 m depth. Four species showed a significant correlation with connectivity. *Leuciscus cephalus* and *Chondrostoma nasus* correlated positively with large distances to the next connection, whereas *Leuciscus idus* and *Alburnus*

Table I. PCA correlation matrix for the ten measured morphological variables and the percentage of explanation for each of the three components based on all samples. Variables 1, 2 and 3 = water depth from 0 to 1, 1 to 2 and 2 to 3 m water depth; dist. = distances at each depth; area = area at each depth; iso 0, 1, 2 and 3 = isobathic lines at 0, 1, 2 and 3 m water depth. Component 1, 2 and 3 = PCA axes 1, 2 and 3

Variable	Component		
	1	2	3
dist 1	0.919	-0.111	0.003
dist 2	0.742	-0.165	0.579
dist 3	-0.588	0.118	0.744
area 1	0.923	-0.084	0.008
area 2	0.721	-0.147	0.607
area 3	-0.565	0.174	0.705
iso 0	0.163	0.877	-0.101
iso 1	0.413	0.792	-0.094
iso 2	0.155	0.900	0.101
iso 3	-0.039	0.905	0.051
Variance			
%	36.5	31.4	17.9
cum. %	36.5	67.9	85.7

alburnus showed a negative correlation. *Barbus barbus* and *Aspius aspius* revealed no significant results (Table IV, species are sorted by correlation pattern).

Between the two most abundant species (*Chondrostoma nasus* and *Alburnus alburnus*, 76%) a contrasting pattern concerning the size of area from 1 to 3 m depth (PCA scores for axis three) was found. Whereas predicted values for *Chondrostoma nasus* increased with increasing size of area in 1 to 3 m water depth, values for *Alburnus alburnus* decreased (Figure 4a). The extrapolated model demonstrated the interrelation between the two species and their demands with regard to certain morphological habitat characteristics (Figure 4b).

The predicted CPUE for connectivity as the macroscaled habitat characteristics were qualified as follows: curves for *Chondrostoma nasus* and *Alburnus alburnus* diverge as the distance to the next connection increases. Sites located far away from any lateral connection showed higher probabilities to catch *Chondrostoma nasus* in contrast to *Alburnus alburnus* (Figure 5a,b).

A hierarchical cluster analysis distinguished three different groups of sampling sites according to the four habitat variables: area 0–2 m, area 1–3 m, heterogeneity and connectivity (Table V). Significance was tested by analysis of variance (ANOVA) ($p \leq 0.001$). Tamhane's post hoc test revealed highly significant differences ($p \leq 0.01$) between the three cluster groups for all parameters except for connectivity in cluster groups 1 and 2.

Cluster group 1 (habitat 1) was characterized by low connectivity, low heterogeneity and large areas at 1 to 3 m water depth. Group 2 (habitat 2) summarized sites with moderate distance to the next connection, moderate values for the heterogeneity and small areas up to 3 m depth. Cluster group 3 (habitat 3) was described by high connectivity, high heterogeneity and large shallow areas.

Habitat 1 showed high capture probabilities for *Chondrostoma nasus* versus *Alburnus alburnus*. Habitat 2 was dominated by catches with high values for *Alburnus alburnus*, and habitat 3 had an intermediate position in which neither *Chondrostoma nasus* nor *Alburnus alburnus* reached extremely high proportions (Figure 6).

DISCUSSION

Several ecological concepts focus on the controlling factors of species associations in large rivers systems. The river continuum concept (RCC; Vanotte *et al.*, 1980) emphasizes carbon dynamics along a longitudinal axis as a major parameter. The flood pulse concept (FPC; Junk *et al.*, 1989) focuses on hydrological dynamics and

Table II. Estimations of the model parameters, standard errors (SE), Wald's statistics (WSt) and p of the logistic model (see Equation 1). β_0 = constant, β_1 = regression coefficient of variable area (0–2 m), β_2 = regression coefficient of variable area (1–3 m), β_3 = regression coefficient of variable heterogeneity, and β_4 = regression coefficient of variable connectivity. Number of samples = 147. Deviance is twice the difference between the log-likelihood of the saturated model and the log-likelihood of the fitted model (for details see Lloyd, 1999, p. 90)

Family	Species	Deviance	Model parameter	Estimation	SE	WSt	p
Cyprinidae	<i>Chondrostoma nasus</i> (L.)	1670.29	β_0	-0.45779	0.06262	-7.31082	<0.00007
			β_1	-0.04080	0.03118	-1.30857	0.19360
			β_2	0.34552	0.03364	10.27029	<0.00007
			β_3	-0.23993	0.04016	-5.97394	<0.00007
			β_4	0.22286	0.05937	3.75393	0.00018
Cyprinidae	<i>Alburnus alburnus</i> (L.)	1796.09	β_0	-0.45541	0.06959	-6.54458	<0.00007
			β_1	-0.65607	0.07104	-9.23484	<0.00007
			β_2	-0.56546	0.03478	-16.25927	<0.00007
			β_3	-0.12991	0.04451	-2.91834	0.00350
			β_4	-0.18445	0.03599	-5.12500	<0.00007
Cyprinidae	<i>Leuciscus cephalus</i> (L.)	1183.95	β_0	-6.18420	0.22893	-27.01299	<0.00007
			β_1	2.67936	0.13286	20.16619	<0.00007
			β_2	0.37990	0.08139	4.66745	<0.00007
			β_3	0.97368	0.09055	10.75261	<0.00007
			β_4	2.17260	0.13445	16.15978	<0.00007
Cyprinidae	<i>Barbus barbus</i> (L.)	264.18	β_0	-3.11453	0.15855	-19.64390	<0.00007
			β_1	-0.09641	0.08303	-1.16119	0.24605
			β_2	0.19073	0.09378	2.03389	0.04236
			β_3	-0.07789	0.10233	-0.76119	0.44725
			β_4	-0.27834	0.16165	-1.72187	0.08543
Cyprinidae	<i>Aspius aspius</i> (L.)	292.40	β_0	-3.58465	0.18599	-19.27383	<0.00007
			β_1	-0.24532	0.08621	-2.84570	0.01314
			β_2	-0.21814	0.09627	-2.26589	0.02382
			β_3	0.37842	0.14159	2.67257	0.00759
			β_4	-0.14692	0.18382	-0.79928	0.42953
Cyprinidae	<i>Abramis ballerus</i> (L.)	256.31	β_0	-5.56802	0.42690	-13.04301	<0.00007
			β_1	1.85460	0.26802	6.91961	<0.00007
			β_2	1.37006	0.21465	6.38286	<0.00007
			β_3	1.80644	0.22160	8.15191	<0.00007
			β_4	-0.50523	0.27376	-1.84550	0.06577
Cyprinidae	<i>Carassius auratus gibelio</i> (BLOCH)	340.19	β_0	-4.09370	0.20325	-20.14110	<0.00007
			β_1	-0.33055	0.08271	-3.99656	0.00007
			β_2	-0.56373	0.08794	-6.41041	<0.00007
			β_3	0.17342	0.14044	1.23486	0.21870
			β_4	0.15481	0.18136	0.85359	0.39533
Cyprinidae	<i>Abramis brama</i> (L.)	230.84	β_0	-4.59035	0.26788	-17.13596	<0.00007
			β_1	0.83617	0.14678	5.69692	<0.00007
			β_2	0.00309	0.11458	0.02696	0.98404
			β_3	0.49189	0.14191	3.46620	0.00054
			β_4	0.51662	0.21360	2.41867	0.01595
Cyprinidae	<i>Leuciscus leuciscus</i> (L.)	160.73	β_0	-4.83007	0.27977	-17.26654	<0.00007
			β_1	-0.48085	0.14107	-3.40851	0.00067
			β_2	-0.07298	0.14826	-0.49226	0.62413
			β_3	-0.00086	0.18704	-0.00462	1.00000
			β_4	0.23675	0.24287	0.97481	0.33205
Cyprinidae	<i>Leuciscus idus</i> (L.)	172.87	β_0	-2.47362	0.32835	-7.53349	<0.00007
			β_1	0.64613	0.17491	3.69403	0.00022
			β_2	0.77446	0.17877	4.33204	<0.00007
			β_3	-0.32759	0.20199	-1.62180	0.10523
			β_4	-3.40992	0.53333	-6.39361	<0.00007

Table III. List of the ten analysed species in this study, their total length (mean, standard deviation, minimum and maximum) sorted by overall number of individuals (n)

Fish species	Length (cm)				
	n	Mean	SD	Min.	Max.
<i>Chondrostoma nasus</i> (L.)	2001	39.0	6.9	10.0	51.5
<i>Alburnus alburnus</i> (L.)	1187	15.0	1.5	8.5	21.5
<i>Leuciscus cephalus</i> (L.)	222	34.4	5.5	11.0	52.0
<i>Barbus barbus</i> (L.)	175	40.1	10.2	16.5	61.5
<i>Aspius aspius</i> (L.)	118	47.1	10.3	21.5	78.0
<i>Aramis ballerus</i> (L.)	97	30.2	3.4	26.0	43.0
<i>Carassius auratus gibelio</i> (BLOCH)	81	26.0	4.2	19.0	39.0
<i>Aramis brama</i> (L.)	77	39.1	7.1	14.0	52.0
<i>Leuciscus leuciscus</i> (L.)	64	21.9	2.9	11.0	27.0
<i>Leuciscus idus</i> (L.)	60	38.2	7.4	19.0	79.0

transversal interactions of limnological systems. The FPC compares the river with a highway that mainly serves for migration purposes. Recent studies suggest a need to revise the perception that main channels of large temperate rivers are mainly used as corridors for the movement of fish (Galat and Zweimüller, 2001; Dettmers *et al.*, 2001).

Here, we attempt to determine association patterns based on simple inshore morphological characteristics under the assumption that the main channel of large rivers is a long-lasting habitat to adult fish. The classification of ecological guilds for fish in the sense of Schiemer and Waibacher (1992) refers to species life history requirements in floodplain systems. We apply this approach to the predictions of our model and to determine which species of different guilds use the main channel as a habitat.

We classified our sampling sites on the basis of simple morphological parameters. (a) Size of area in shallow water down to 2 m depth: the larger this area, the shallower the slope should be and vice versa (see PCA axis 1, Table I). (b) Large areas in slightly deeper water (1–3 m) indicating barren gravel bars (see PCA axis 3, Table I). (c) Habitat heterogeneity expressed by the length of isobatic lines (see PCA axis 2, Table I), analogous to the shoreline length, which describes shoreline diversification used in larval ecology (Schiemer *et al.*, 1991; Wintersberger, 1996). (d) Distance to the next lateral connection with backwaters: this defines accessibility to refuge areas, feeding places or spawning habitats.

Table IV. Bonferroni corrected ($p \leq 1 - (1 - x)^n$; $x = 0.05$; $n = 27$; $p = 0.0018$) correlation matrix of four habitat variables and the ten most abundant species. + or – indicates the positive or negative significant correlation of the species with the environmental variables. n.s. = not significant. ‘area (0–2 m)’ = regression scores of the first PCA axis; ‘area (1–3 m)’ = regression scores for the second PCA axis; ‘heterogeneity’ = regression scores for the third PCA axis; ‘connectivity’ = distance to adjacent connection

Species	‘area (0–2 m)’	‘area (1–3 m)’	‘heterogeneity’	‘connectivity’
Significant				
<i>Aramis ballerus</i> (L.)	+	+	+	n.s.
<i>Leuciscus cephalus</i> (L.)	+	+	+	+
<i>Aramis brama</i> (L.)	+	n.s.	+	n.s.
<i>Leuciscus idus</i> (L.)	+	+	n.s.	–
<i>Leuciscus leuciscus</i> (L.)	–	n.s.	n.s.	n.s.
<i>Carassius auratus gibelio</i> (BLOCH)	–	–	n.s.	n.s.
<i>Alburnus alburnus</i> (L.)	–	–	n.s.	–
<i>Chondrostoma nasus</i> (L.)	n.s.	+	–	+
Not significant				
<i>Barbus barbus</i> (L.)	n.s.	n.s.	n.s.	n.s.
<i>Aspius aspius</i> (L.)	n.s.	n.s.	n.s.	n.s.

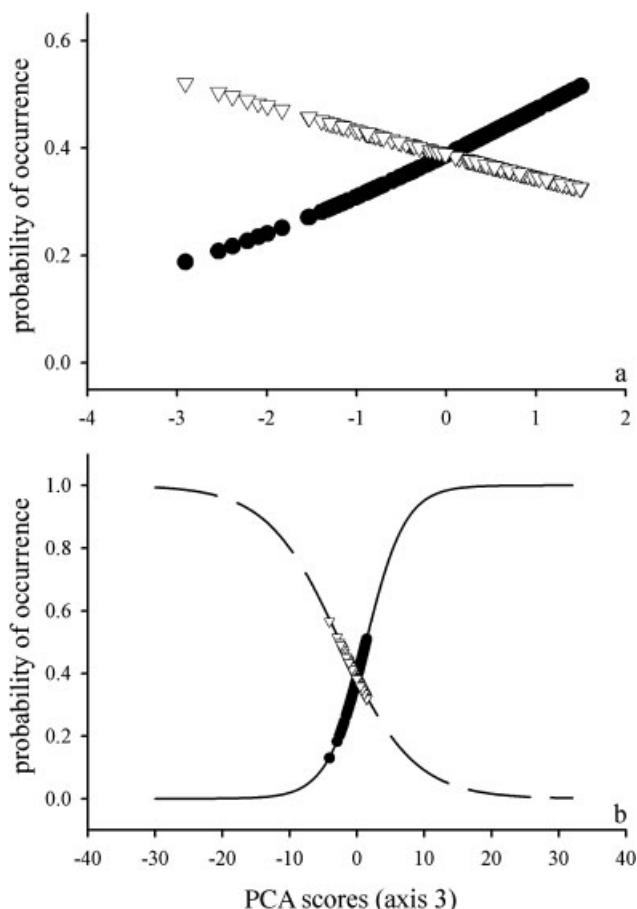


Figure 4. Simplified model (see Equation 2) for the two most abundant species and one explanatory variable, i.e. third PCA axis ('deep area' of 1 to 3 m water depth). (a) Dots indicate the predicted probabilities for *Chondrostoma nasus*; triangles represent the values for *Alburnus alburnus*. (b) Extrapolated curves for (a) show the sigmoidal shape of the logistic regressions

The logistic model predicts relative proportions of different species related to various habitat configurations. Inshore zones dominated by large areas covered with shallow water showed a predominance of rheophilic species, while the abundance of eurytopic species is low. This indicates the importance of large, gradually sloping, near-bank areas for fish species classified as rheophilic, including *Chondrostoma nasus*, *Leuciscus idus* and *Abramis ballerus* (Schiemer and Waidbacher, 1992). *Leuciscus leuciscus* is an endangered species and its abundance in the study area is rather low. Although it is classified as rheophilic, it shows a negative correlation with size of shallow areas. Eurytopic species do not show a consistent pattern concerning the size of area, regardless of shallow or deep water.

With increasing size of area covered by 1 to 3 m deep water, the probability of catching higher proportions of *C. nasus* increases as opposed to *A. alburnus*. This indicates the preference of *C. nasus* for large, deeper and slowly descending areas. Conversely, small areas of 0 to 3 m depth are more likely to yield catches dominated by *A. alburnus* (Figure 6).

With regard to high habitat heterogeneity, i.e. long isobathic lines, the model predicts increasing proportions of *Abramis ballerus*, *Leuciscus cephalus* and *Abramis brama*. These sites represent groynes or island situations with lower water currents and higher temperature (Keckeis *et al.*, 1997). We assume that the feeding conditions and energetic processes in such habitats are positively influenced for these species. Molls (1999) found similar patterns for adult *Abramis bjoerkna* and *Rutilus rutilus* in the main channel of the Rhine. In the same study, *Abramis brama* was abundant in the main channel, proving that this is an accepted habitat. Decreasing abundance with increasing

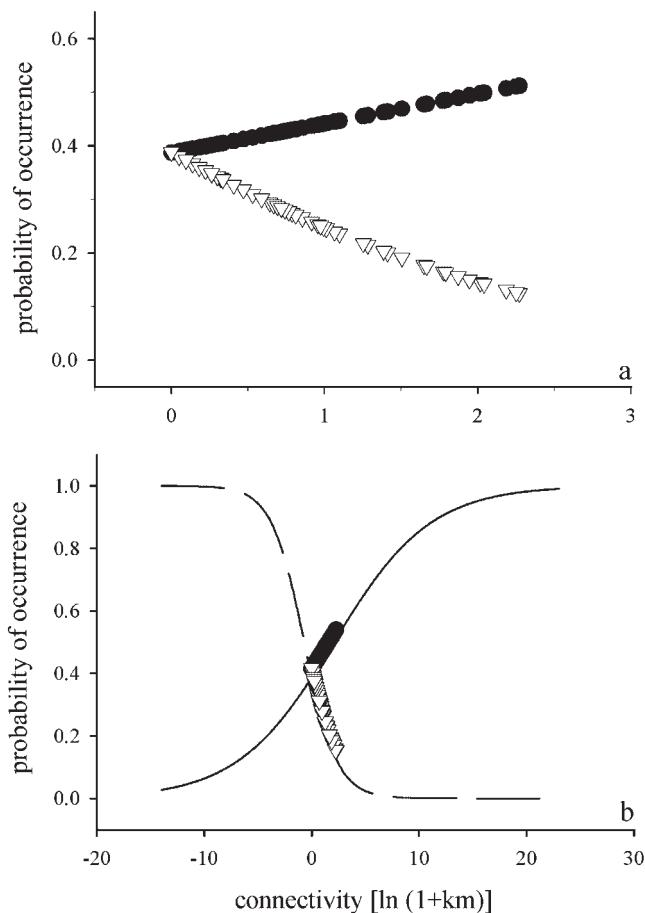


Figure 5. Simplified model (see Equation 2) for the two most abundant species and the macro scaled variable, connectivity. (a) Dots indicate the predicted probabilities for *Chondrostoma nasus*, triangles for *Alburnus alburnus*. (b) Extrapolated curves for (a)

Table V. Means, standard deviations (SD), number of samples for the three cluster groups revealed by hierarchical cluster analysis (Ward method, squared Euclidean distances) and each morphological variable. ANOVA ($p \leq 0.001$) and Tamhane post hoc test ($p \leq 0.01$) showed high significance for all groups and variables except for connectivity in groups 1 and 2

	<i>n</i>	PCA scores			
		area (0–2)	area (1–3)	heterogeneity	connectivity
Cluster group 1	69				
Mean		-0.12	0.45	-0.60	1.10
SD		0.87	0.93	1.02	0.60
Cluster group 2	22				
Mean		-1.45	-1.20	0.18	1.32
SD		0.42	0.85	0.64	0.78
Cluster group 3	56				
Mean		0.72	-0.09	0.66	0.43
SD		0.51	0.69	0.56	0.26

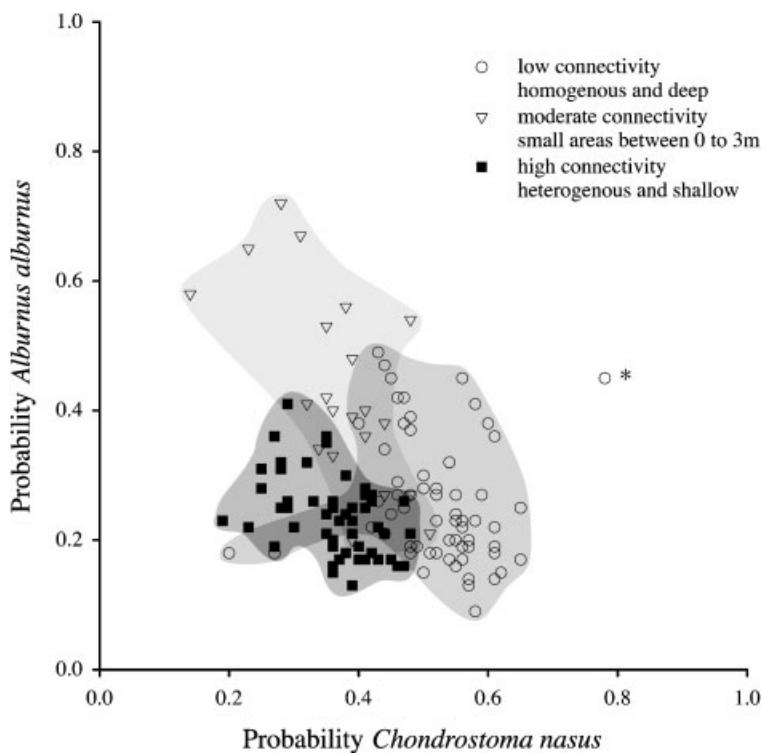


Figure 6. Predicted probability in terms of proportions per catch for *Chondrostoma nasus* versus *Alburnus alburnus* and the three different habitat groups revealed by cluster analysis. Each point represents a sample. Asterisk (*) represents an outlier, not included due to extreme habitat conditions

heterogeneity is predicted for *Chondrostoma nasus*. Analogous trends are implied for *Alburnus alburnus*. Homogeneous habitats with short isobathic lines are represented in the study area as uniformly shaped gravel banks on one hand and as artificial riprap made of angular stones on the other, which evidently differ in their substrate composition. Results for young stages of fish show preferences of rheophilic species for naturally structured habitats, whereas the eurytopic *A. alburnus* was also found in high densities along artificial shorelines (Schiemer and Spindler, 1989). A similar pattern is suggested for adult fish, assuming that low heterogeneity in terms of short isobathic lines describes habitat configurations such as natural gravel bars where riverine species like *C. nasus* should dominate, but also describes man-made channel structures where eurytopic species like *A. alburnus* prevail. Further investigation on this particular variable is certainly required in order to properly distinguish between these two different habitats.

The connectivity is defined as the distance from the investigation site to the connected backwater, harbour or tributary. *Chondrostoma nasus* and *Leuciscus cephalus* showed higher predicted values than *Leuciscus idus* and *Alburnus alburnus*. This discriminates strictly riverine rheophilic species like *Chondrostoma nasus* from rheophilic species like *Leuciscus idus* that also inhabit medium-sized rivers during non-reproducing periods. Schiemer and Spindler (1989) classified *C. nasus* and *L. idus* as abundant and common species in this part of the Danube main channel, but also found *C. nasus* to be periodically abundant in the connected backwaters. *L. cephalus* is very abundant in the river itself, common in connected backwaters, but only rare in disconnected backwaters; it was therefore classified as rheophilic in the cited study which is supported by the present results for connectivity.

We found that distribution patterns of adult fish in the Danube are significantly dependent on area of habitat and habitat heterogeneity and that different species show individual requirements which can be clearly distinguished. Thus, *C. nasus* prefers large, gradually sloping habitats whereas *A. alburnus* does not; *A. ballerus* needs heterogeneous habitats while *C. nasus* does not. Certain species correlate significantly with connectivity, differentiating

strictly riverine species like *C. nasus*, which prefers the main channel throughout its life cycle, from species depending on side arms as a refugium, feeding place or reproductive site (e.g. *L. idus*).

To ensure good habitat quality for a diverse riverine fish fauna in the Danube as an example of a large European river, well-structured inshore zones are required. Meeting the requirements of different species also means providing living space in terms of expanded, gradually sloping inshore areas with varying heterogeneous sections and access to the floodplain and second-order rivers. The conservation and management of large rivers calls for concepts that come as close as possible to the former natural state.

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