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Habitat preference of the sublittoral fish assemblage in a free-flowing section of the Danube River, Austria.

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Abstract

The main channel of the free-flowing section of the Danube River downstream of Vienna (Austria, Europe) is impacted by impoundments upstream and has been altered by flood protection measures, by bank stabilization and maintenance of a navigation channel. In order to provide information for planning of restoration measures, and due to the high indicator value of the fish assemblage, we investigated habitat suitability and patterns of habitat preference of the sublittoral fish assemblage within a selected, representative river reach. The hydraulic information from a 3D numerical model with a high spatial resolution was combined with precise positions of caught individuals. The recording of the position of caught individuals was possible by the application of a newly developed technique which complements standard boat-electro fishing procedures. Combining hydraulic conditions from the hydrodynamic model with the abundance of fish enables the projection of information based on sampling points to area, and to simulate the potential impact of different restoration measures on habitat availability and habitat quality, and may therefore serve as a basis for conservation issues.

Keywords

Large River, river restoration, habitat modeling, species conservation

Introduction

Fish are important elements in the bio-assessment of river ecosystems worldwide (Roset et al. 2007), and are effective in describing the effects of human impacts in relation to natural or near-natural conditions. Several review papers underline the importance of physical habitat structure in determining both the abundance and species composition of stream fishes (Ahmadi-Nedushan et al. 2006, Bovee et al. 1998, Lamouroux et al. 1999, Parasiewicz & Dunbar 2001, Vadas & Orth 2001). An understanding of how hydraulic forces relate to fish habitat will assist in planning restoration projects (Newbury & Gaboury 1987, Rabeni & Jacobson 1993). Management schemes based on a process-oriented view, aiming at nature conservation and predicting expected species distributions, should therefore integrate these findings (Tockner et al. 1998, Schiemer et al. 1999, Schiemer 2000, Porter et al. 2000, Schmutz et al. 2000, Wolter & Bischof 2001).

A large part of the main stem of the free-flowing stretch of the River Danube east of Vienna adjoins the Alluvial Zone National Park, and at the same time it represents an important section for navigation. In order to improve the ecological situation of this site, a pilot reach with a length of 3 kilometers was selected to study the effect of a set of measures (modification of groynes, removal of rip-rap, displacement of shoreline stabilization, river bed stabilization measures) on the fish assemblage. A major reason for the slow recovery of fish faunas of regulated large European rivers is the loss of productive habitats in the main channels (Aarts et al. 2004). Changes in streamflow modify physical habitat (Bain & Finn 1988), therefore we analyzed the effect of discharge on community composition and fish abundance as well as on habitat availability, habitat use and habitat preferences. The results should facilitate the simulation of habitat suitability within the entire river reach and of specific shore types. It should also help localize key habitats and shortfalls, as well as provide a basis for improving habitat conditions for fish in the main stem of the free-flowing Danube east of Vienna.

Material and Methods

Study site

Sampling was carried out in a 3-km-long test reach in the Danube, from river kilometer 1884.50 to 1887.50, which is equivalent to approximately ten times the average width. The samples were taken for the project "Pilot Project Bad Deutsch Altenburg" in the period between beginning of March to late August 2007 in the pilot reach. An overview of the investigation area is shown in Fig. 1.

Table 1: Species number and fish assemblage composition expressed as number of individuals (Ind), abundance (CPUE = catch per unit effort expressed in individuals per minute fishing time) and cumulative percentages ($Perc_{cum}$) of the abundances of single species of the total catch and at different discharge regimes (Q1200, Q1500 and Q1750). Also indicated are the ecological guilds according to SCHIEMER & WAIDBACHER (2002). SD = standard deviation.

			Total catch				Q 1200				Q 1500				Q 1750			
Family	Species	ecolog. Guild	Ind	CPUE	SD	$Perc_{cum}$	Ind	CPUE	SD	$Perc_{cum}$	Ind	CPUE	SD	$Perc_{cum}$	Ind	CPUE	SD	$Perc_{cum}$
Cyprinidae	***Alburnus alburnus***	eurytop	1459	1,3444	**±** 2,839	70,12	580	**1,807**	**± 2,858**	69,31	631	**1,472**	**± 3,008**	76,97	248	**0,793**	**± 2,593**	61,43
Cyprinidae	*Barbus barbus*	rheophil A	139	0,1635	± 0,337	78,65	49	0,158	± 0,404	75,37	40	0,149	± 0,280	84,74	50	0,183	± 0,326	75,65
Cyprinidae	***Leuciscus idus***	rheophil B	58	0,0849	**±** 0,324	83,08	37	**0,192**	**± 0,524**	82,74	15	**0,048**	**± 0,182**	87,27	6	**0,023**	**± 0,094**	77,45
Cyprinidae	*Aspius aspius*	rheophil B	68	0,0827	± 0,178	87,39	22	0,083	± 0,160	85,91	24	0,072	± 0,146	91,02	22	0,094	± 0,221	84,72
Cyprinidae	*Abramis brama*	eurytop	67	0,0722	± 0,176	91,15	25	0,105	± 0,219	89,92	21	0,049	± 0,134	93,59	21	0,066	± 0,168	89,79
Cyprinidae	*Leuciscus cephalus*	eurytop	36	0,0450	± 0,133	93,50	11	0,041	± 0,119	91,48	6	0,025	± 0,077	94,90	19	0,069	± 0,179	95,15
Cyprinidae	*Chondrostoma nasus*	rheophil A	35	0,0332	± 0,121	95,23	17	0,055	± 0,185	93,59	13	0,031	± 0,088	96,50	5	0,016	± 0,057	96,38
Cyprinidae	*Vimba vimba*	rheophil A	9	0,0143	± 0,101	95,98	7	0,033	± 0,155	94,86	2	0,011	± 0,086	97,08				
Salmonidae	*Hucho hucho*	rithrale	9	0,0117	± 0,070	96,59	6	0,022	± 0,081	95,69	1	0,003	± 0,026	97,25	2	0,011	± 0,086	97,24
Cyprinidae	*Abramis bjoerkna*	rheophil B	7	0,0082	± 0,059	97,02	3	0,005	± 0,029	95,89	4	0,019	± 0,097	98,25				
Percidae	*Perca fluviatilis*	eurytop	4	0,0076	± 0,077	97,41	3	0,022	± 0,136	96,72	1	0,002	± 0,018	98,37				
Cyprinidae	*Rutilus rutilus*	eurytop	10	0,0071	± 0,044	97,78	5	0,016	± 0,071	97,35	2	0,003	± 0,026	98,55	3	0,002	± 0,018	97,42
Percidae	*Gymnocephalus schraetser*	rheophil A	2	0,0071	± 0,078	98,15	2	0,023	± 0,138	98,22								
Salmonidae	*Salmo trutta*	rithrale	4	0,0053	± 0,037	98,43	1	0,002	± 0,014	98,29					3	0,014	± 0,062	98,50
Gobiidae	*Neogobius melanostomus*	translocated	6	0,0050	± 0,031	98,69	3	0,007	± 0,038	98,55	3	0,008	± 0,039	98,97				
Gadidae	*Lota lota*	rithrale	2	0,0034	± 0,038	98,87					2	0,010	± 0,065	99,48				
Cyprinidae	*Rutilus pigus*	rheophil A	2	0,0033	± 0,031	99,04	1	0,006	± 0,045	98,79					1	0,004	± 0,032	98,82
Cyprinidae	*Abramis sapa*	rheophil B	6	0,0033	± 0,033	99,21	6	0,010	± 0,058	99,19								
Percidae	*Sander lucioperca*	eurytop	3	0,0024	± 0,014	99,34	2	0,003	± 0,017	99,31	1	0,001	± 0,006	99,52	1	0,003	± 0,015	99,08
Cyprinidae	*Cyprinus carpio*	eurytop	7	0,0021	± 0,019	99,45	2	0,006	± 0,033	99,54					4	0,001	± 0,006	99,14
Cyprinidae	*Carassius gibelio*	eurytop	2	0,0019	± 0,022	99,55					1	0,001	± 0,006	99,57	1	0,005	± 0,037	99,51
Esocidae	*Esox lucius*	eurytop	3	0,0018	± 0,015	99,64	1	0,002	± 0,015	99,61	1	0,001	± 0,007	99,61	1	0,003	± 0,020	99,71
Salmonidae	*Oncorhynchus mykiss*	alien	1	0,0014	± 0,019	99,71					1	0,004	± 0,032	99,83				
Cyprinidae	*Scardinius erythrophthalmus*	stanophil	1	0,0013	± 0,017	99,78									1	0,004	± 0,029	100,00
Gobiidae	*Neogobius kessleri*	translocated	1	0,0011	± 0,015	99,84					1	0,003	± 0,026	100,00				
Cyprinidae	*Leuciscus leuciscus*	rheophil A	2	0,0011	± 0,015	99,90	2	0,004	± 0,027	99,75								
Cyprinidae	*Abramis ballerus*	rheophil B	2	0,0011	± 0,015	99,95	2	0,004	± 0,027	99,89								
Gasterosteidae	*Gasterosteus aculeatus*	translocated	1	0,0006	± 0,008	99,98	1	0,002	± 0,014	99,96								
Siluridae	*Silurus glanis*	eurytop	1	0,0003	± 0,005	100,00	1	0,001	± 0,008	100,00								
	Individuals		1947				789				770				388			
	total species number			29,0				24,0				19,0				16,0		
	species number $sample^{-1}$			2,0	± 2,0			3,0	± 2,0			2,0	± 1,0			2,0	± 1,0	
	Shannon-Wiener Index			0,50	± 0,47			0,58	± 0,52			0,48	± 0,49			0,43	± 0,41	
	$CPUE_{cum}$ $sample^{-1}$			1,9	± 3,1			2,6	± 3,5			1,9	± 3,0			1,3	± 2,7	

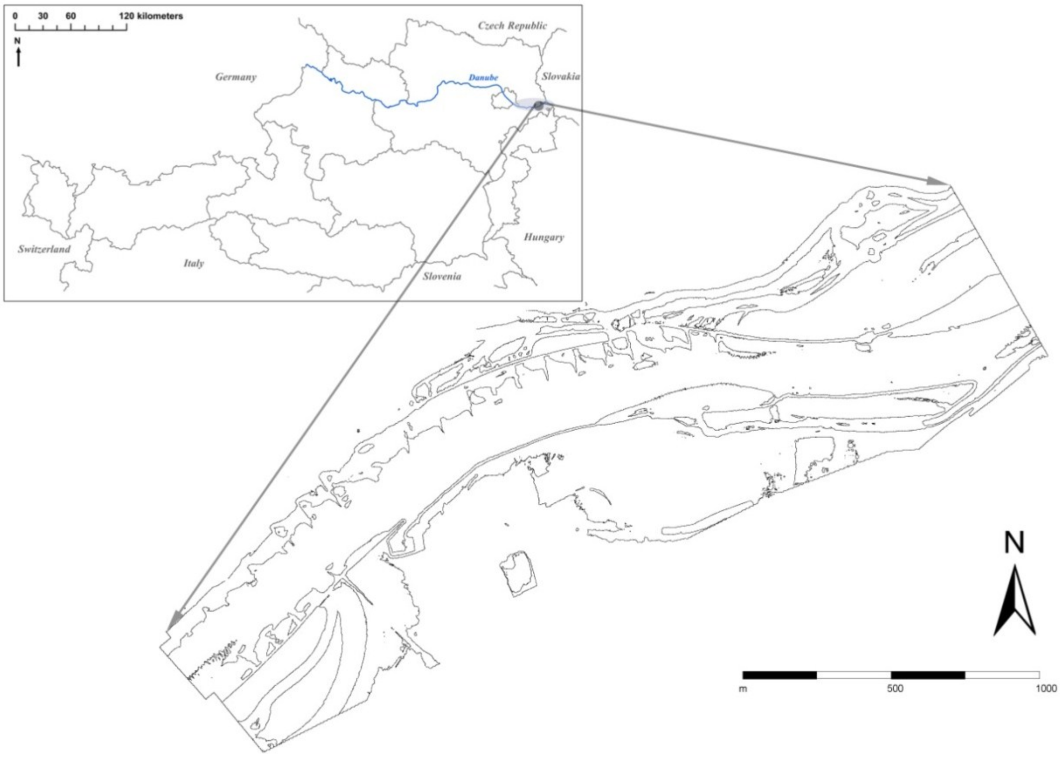

Figure 1:. Location and length of the study site in the free-flowing part of the Danube River east of Vienna, Austria.

Electrofishing

An electrofishing boat equipped with a 300 - 500 V Generator (DC) was used for taking the samples. In order to establish an electric field in the water column, the current was conducted into 6 anodes of 1.25 m length situated in front of the boat and a cathode placed along the side on the back part (Fig. 2). As a standard fishing method a modified continuous line fishing procedure was developed, and from each sample, the combined information on position, water depth and fish-individual number was stored in short time intervals (seconds). Samples were taken during the day along both shores of the river. Sampling proceeded with the flow direction downstream at the speed of the flow velocity or, if velocities were low, slightly faster (FLOTMERSCH & BLOCKSOM 2005). Every second during operation, the geographical position was determined with a dGPS (Leica® GS20, accuracy ± 30 cm) and water depth was measured with a single beam echosounder (Simrad® EQ33). These data were synchronized and stored using the hydrographic software profil2000®. Additionally, every single geographical position where fish were netted was specifically marked and stored separately by the hydrographic software (Fig. 2). This enabled more detailed analyses of occurrence as compared to available standard procedures and provided the required quality of data to analyze habitat use and habitat preference. Overall, 175 samples were taken between March and August 2007; the average length of the lines was 494 ± 306 m and an average catch lasted 6.6 ± 4.5 min. The number of samples was 55 at a river discharge of 1200 m^3s^{-1} (Q1200), and 60 at Q1500 and Q1750, respectively. All collected individuals were immediately placed in containers (1.0 x 0.6 x 0.6 m) which were filled with water from the river. After each catch, they were identified to species, counted and their size (total length; ±1mm) protocolled before they were released back into the river. All individuals from all species caught during one continuous line were considered to represent one sample, because a species/size identification/measurement within one netting operation was not possible due to the short duration. The netting operation lasts only a few seconds, which makes it impossible to protocol all required information of all single individuals during one fishing event. A further point is the simultaneous occurrence of many individuals due to schooling behavior at certain areas. Therefore, this data set cannot be used to analyze species-specific habitat selection.

Statistical analyses

Catch data were standardized to catch per unit effort (cpue, individuals per minute fishing time) to express fish abundance (HAYES et al. 1996). In order to meet the requirements of statistical comparisons, these data were log transformed according to MCCUNE & GRACE (2002) to test for differences between species or species composition of the assemblages between discharge regimes. Calculation of Shannon-Wiener Diversity (H´, MAGURRAN 1988) and tests for differences in species composition were conducted with analysis of similarities (ANOSIM, SIMPER) and nonparametric multidimensional scaling (MDS) using the software Primer 6.1.13®. The Kruskal-Wallis Test (SPSS 16.0®) was applied to compare biodiversity, abundance of single species, and fish sizes observed at different discharges.

Hydrodynamic model

As the parameters required for habitat modeling, i.e. flow velocities or water depths, can only be measured in discrete locations, a three-dimensional hydrodynamic model was employed to allow for an upscaling from the point to the reach scale. For this purpose, the river simulation model RSim-3D (TRITTHART & GUTKNECHT 2007a) was applied. It solves the three-dimensional Reynolds-averaged Navier-Stokes equations using the Finite Volume Method (FVM) on a mesh consisting of arbitrarily shaped polyhedra. This approach has the potential to deliver more accurate results than standard methods when applied to recirculating flows, because it can significantly reduce numerical diffusion (Tritthart and Gutknecht, 2005). Since vortices and recirculation zones are frequently encountered in fields of non-submerged groynes like those present in the Danube River reach, using the polyhedral mesh methodology is particularly advantageous in this case.

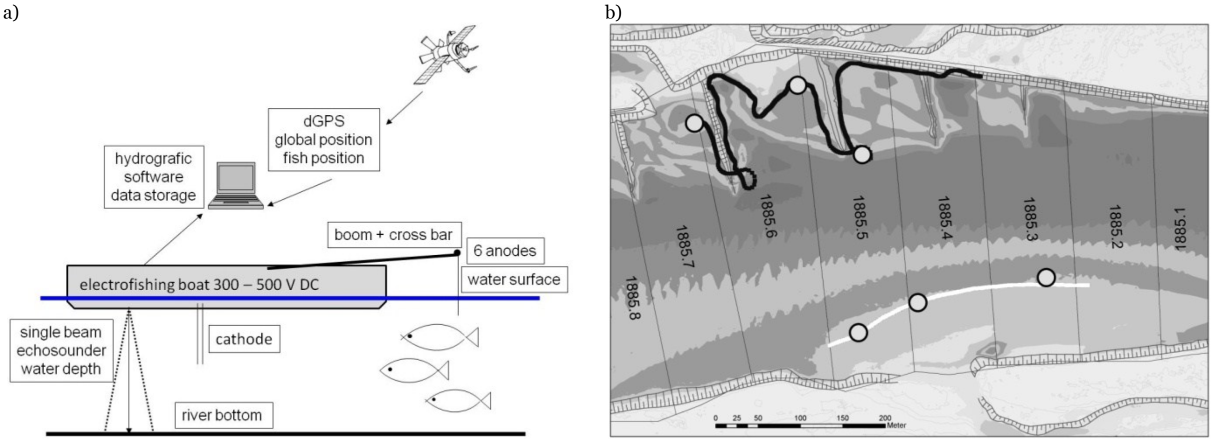

Figure 2:
a) Setup of the electrofishing boat. The position of the boat was recorded synchronously with water depth every second. The positions where fish were encountered were marked separately. These data were transferred to the hydrodynamic model in order to analyze habitat use and habitat preference with regard to water depth and flow velocity. V = Volt, DC = direct current.
b) Map of fishing tracks (green line) in the main channel of the Danube between river kilometer 1885.3 and 1885.6 along a groyne field and at a gravel bar. The red points mark sites where fish were captured.

Numerically, within the RSim-3D model a generalized second-order upwind scheme (BARTH & JESPERSE, 1989) is employed to discretize convective terms in the governing equations, whereas the diffusive terms are discretized using central differences. The SIMPLE method (PATANKAR & SPALDING 1972), reformulated for arbitrarily shaped control volumes, provides coupling of pressure and velocity fields. Turbulence is modeled by means of the standard k-epsilon two-equation turbulence closure (LAUNDER & SPALDING 1974). The position of the free surface is determined by iteratively translating pressure surpluses and deficits in the surface cells into differences of the water surface elevation until the calculated relative pressure is zero everywhere at the surface (TRITTHART & GUTKNECHT 2007a).

The 3D hydrodynamic model set up for the pilot reach at the Danube River covers 3 km as well as an additional stretch of 500 m upstream and 500 m downstream to reduce influences of boundary conditions on the domain of interest. A constant discharge boundary condition was employed at the inlet; known water depth was set at the outlet. After an initial calibration of the model for a discharge of 1930 m^3s^{-1} (mean flow), steady-state simulations were run for a total of ten characteristic discharges from 915 m^3s^{-1} (regulated low flow) to 5060 m^3s^{-1} (highest navigable flow). As the RSim-3D model is based on a bed roughness parameterization employing absolute roughness heights (TRITTHART & GUTKNECHT 2007b), errors for runoffs different from the calibration discharge are considered to be small.

The model was calibrated and validated using separate data sets of velocity and turbulence measurements obtained from ADCP and ADV instrumentation, bed grain size distributions from over 100 samples, gauge hydrographs and officially published water surface elevations for three characteristic discharges (regulated low flow, mean flow and highest navigable flow). Further details of the model validation results for the pilot reach at the Danube River east of Vienna are given in TRITTHART et al. (2009).

Predictive habitat modeling

With regard to the effectiveness of the fishing method, which is based on operating experience, and although 10 percent of the total catch consisted of individuals caught between 3 and 4 m water depth; only data with a water depth shallower than 3 m were considered in the analyses. As normalized probability density functions ranging from 0 to 1, the frequency-of-use graphs (RALEIGH et al. 1986) were applied to determine habitat suitability for the selected Danube reach (equation 1).

$$FUG_i = f_i / f_{[\max]} \qquad \text{(eq. 1)}$$

where: f_i is class frequency and $f_{[\max]}$ is maximum class frequency.

Suitability indices and curves in general indicate the suitability of habitats based on a single parameter. They are computed from empirical frequency distributions, which are standardized based on the most strongly occupied class (BOVEE & COCHNAUER 1977, BOZECK & RAHEL 1992). The class with the largest frequency (highest suitability) receives a SI value of 1. All further classes are weighted after it. The unused classes have the suitability index (SI) 0.

In streams and smaller rivers the documented frequency of individuals is based on visual observation (e.g. snorkeling, HILLMAN et al. 1987). At the Danube, however, due to high suspended load concentration and size of the river, the frequency of individuals was recorded based on mesounit electrofishing. Additionally to the derived suitability indices, habitat preference curves (Ivlev 1961) were derived based on the relation habitat suitability to habitat availability (equation 2).

$Preference = U / A$ (eq. 2)

where: U is class frequency of habitat used and A class frequency of habitat available.

At the Danube, both curves (suitability / preference) were applied for predictive habitat evaluation according to the method of multiplying suitability indices (Bovee, 1986) (equation 3). The application of multiplying suitability indices commonly uses water depth and flow velocity (partially cover) as input parameters (eq. 3).

$$SI_{total} = SI_d \cdot SI_v$$ (eq. 3) concluded

$$SI_{total} = \prod_{i=1}^{I} SI_i$$ (eq. 3)

where: SI_d = Suitability Index depth, SI_v = Suitability Index velocity, SI_{total} = Suitability Index total, SI_i= Suitability index variable;

To gain quantitative (spatially distributed) modeling results, the method of Weighted Usable Area (WUA) (Bovee 1986) was selected as a function of number of grid cells, habitat suitability / preference and area of single grid cell (equation 4).

$$WUA = \sum_{i=1}^{n} HSI_i \cdot A_i$$ (eq. 4)

where: n = total number of grid cells, HSI_i = habitat suitability index, A_i = area of single grid cells (m^2).

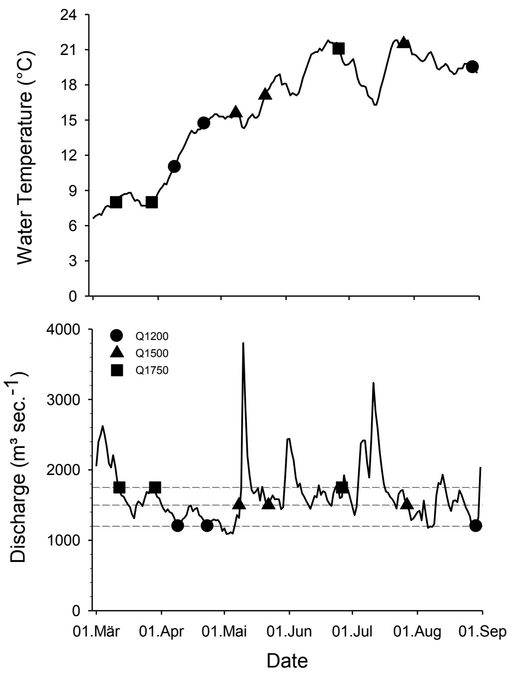

Figure 3: Seasonal course of water temperature (daily average) of the Danube River (water gauge Hainburg, upper graph) and average daily discharge during the investigation period. Symbols reflect sampling dates at different discharge rates. The dashed lines in the lower graph indicate the three applied model-discharge rates.

Results

Species assemblages at different discharges

The discharge of the Danube River during the sampling period ranged from 1090 to 3801 m^3s^{-1}; the average was 1650 m^3s^{-1} (Fig. 3). Water temperature showed an increasing seasonal trend: it rose from 6.6°C in early March to 21.8°C in early August, and then declined slowly to 19.5°C until late August. The modeled discharges of 1200, 1500 and 1750 m^3s^{-1} fitted well with the field situation during sampling (Fig. 3, lower graph).

The total catch from the overall 175 samples was 1947 individuals from 29 fish species. An average catch included 2 individuals of two different species. A large variation between single samples is indicated in the high standard deviation of single species and assemblage composition (Table 1). Total species number decreased from 24 at Q1200 to 19 at Q1500 to 16 at Q1750. A similar trend and significant differences were observed in overall abundance (sum of abundances of every sample) between the three discharges (Kruskal-Wallis Test, $p<0.05$); the lowest value was found at 1750 m^3s^{-1}. No significant relationship between water temperature and species number, or between water temperature and fish abundance, was found. Generally, 4 to 6 species accounted for more than 90 percent of the assemblage in terms of abundance at each discharge situation. Irrespective of the discharge of the river, four fluvial specialists (*Barbus barbus*, *Leuciscus idus*, *Aspius aspius* and *Chondrostoma nasus*) and three generalists (*Alburnus alburnus*, *Squalius cephalus* and *Abramis brama* dominated the total catch. The comparison of the assemblage by means of species accumulation curves (Fig. 4) and by the similarity between samples revealed significant differences between the three discharge regimes. Species accumulation curves at all discharges increased rather steeply; no satiation effect is visible. The steepest increase was observed for Q1200, followed sequentially by Q1500 and Q1750. The pairwise test revealed significant differences between the assemblages at Q1200 vs. Q1750 (R = 0.051, significance level = 0.3%) and between Q1500 and Q1750 (R = 0.03, significance level = 1.8%). No significant differences were found between the assemblage at Q 1200 and Q 1500 (R = 0.002, significance level = 37.6%). A pairwise comparison of abundances of single species between the different discharges revealed that only two species, namely bleak and ide, showed significantly different abundance between the different discharge regimes. The size range (total length) of all captured individuals ranged from 4.5 to 120.0 cm. The most abundant size class was 10-15 cm, which referred mainly to the sizes of the most dominant species, *A. alburnus* (Fig. 5). The size of the characteristic riverine species with high abundances ranged from 40 to approx. 65 cm. Fish sizes at different discharge regimes were not significantly different (p>0.05).

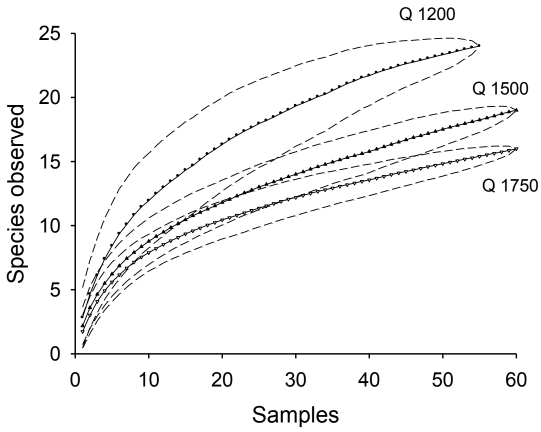

Figure 4: Species accumulation curves of samples taken at different discharge regimes in the pilot reach of the Danube River east of Vienna from March to August 2007.

Habitat use and habitat preference

Habitat availability, habitat use and habitat preferences of the assemblages for water depth and flow velocities at three discharge regimes are given in Fig. 6. At all three analyzed discharge regimes, measured water depth showed a uniform distribution pattern with a maximum frequency at 1.0 to 1.5 m. Water depth classes used by fish showed a similar pattern, but higher frequencies compared to the ones available were observed for the range between 0 up to 1.5 m. The resulting preferences were therefore highest for the depth classes below 1.5 m water depth. A preference-index of 1 was observed for water depths between 0.5 to 1.0 m at Q1200 and Q1500, and for the class 1.0-1.5 m at Q1750. This indicates a change of habitat use with increasing discharge. Preference values for deeper water (> 1.5 m) were distinctly lower at all discharge regimes.

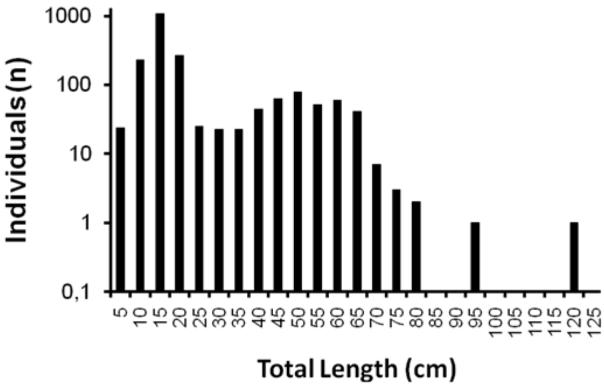

Figure 5: Length (total length, cm) distribution of the total catch. The scale of the x-axis represents size classes (interval 5 cm), note logarithmic scaling of y-axis (number of individuals in each size class).

Flow velocity values (averaged over the water column) revealed a positively skewed distribution pattern at all discharge regimes. In contrast to water depth, an over-proportional use of sites with a velocity between 0.6 and 1.8 ms^{-1} was observed. The highest preference were found for the velocity class between 0.9-1.2 ms^{-1} for all three analysed discharge regimes.

As a result, the combination of the variables water depth and flow velocity revealed a general preference of the assemblages for habitats shallower than 1.5 m, and for an average flow velocity above 0.9 ms^{-1}. With increasing discharge regime, the trend was toward preferring deeper habitats characterized by lower flow velocities.

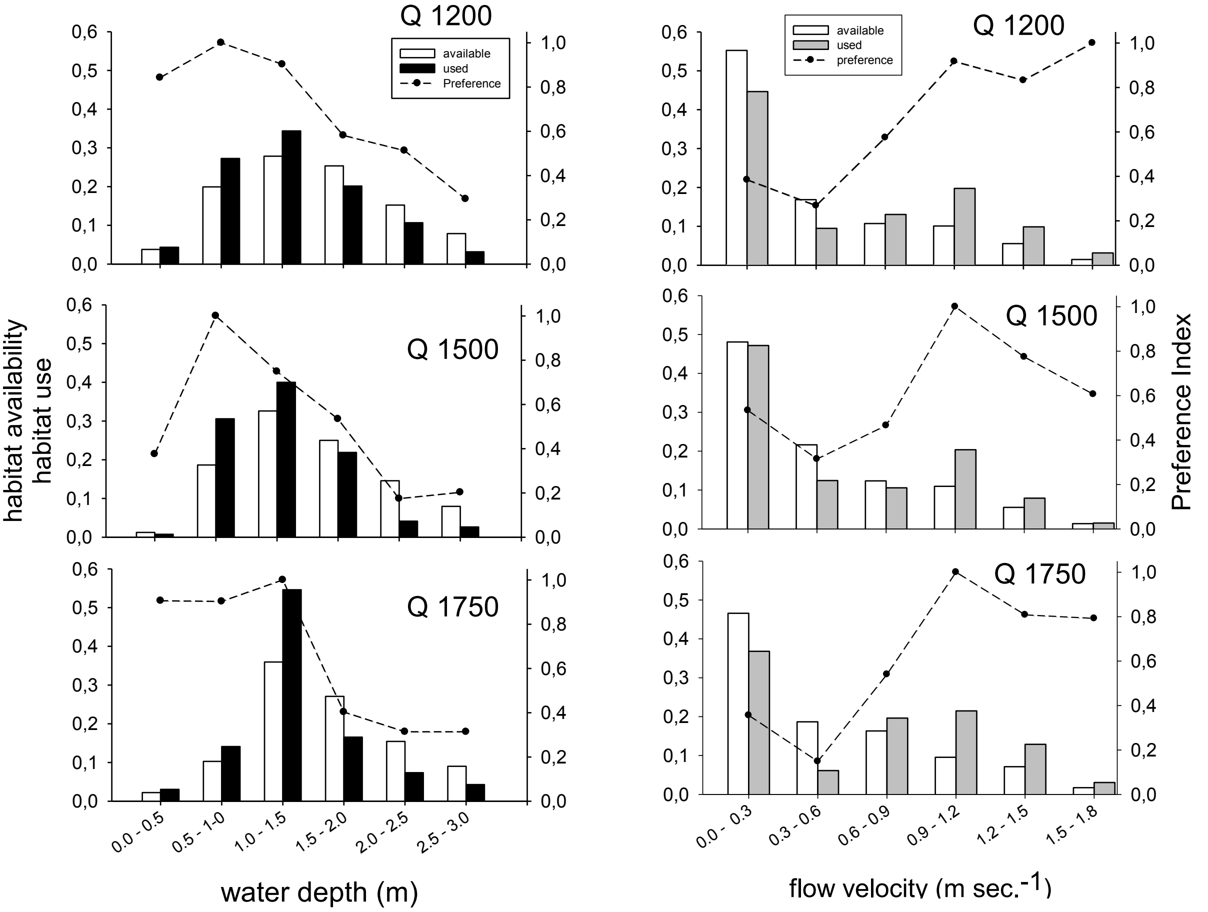

Figure 6: Frequency distributions (left y-scale) of available (white bars) and used water depths (black bars) and flow velocities (grey bars) at different discharge regimes (Q1200, Q1500 and Q1750). Resulting habitat preferences are indicated by symbols and are connected by dotted lines. Habitat preference values refer to the scale of the right y-axis.

Habitat modeling and weighted usable areas

Generally, the riparian zones of each bank showed an almost continuous smaller or wider band of habitats with moderate (≥ 0.4) to highest values (1.0) of habitat suitability of combined depth and flow velocity indices. Large and enclosed areas of high habitat preference values were observed for gravel bars within the test reach (Fig. 7). The areas of highest suitability values within groyne fields were distinctly smaller, unsteady and located upstream of single groynes or related to smaller gravel deposits within the groyne fields. This areal pattern led to overall only small portions of high habitat suitability (areas with a suitability index >0.5) of < 10% at Q1200 and < 5% at Q1500 and Q1750 (Table 2).

Discussion

The sampling design of this study is quantitative and can thus support the future planning of restoration measures in order to improve the ecological condition of the river. It is not, however, appropriate for the analyses of biodiversity, i.e. total number of occurring species (CAO et al. 2001, FLOTEMERSCH & BLOCKSOM 2005, MEADOR 2005, HUGHES & HERLIHY 2007). In a large river like the Danube, a single method may not be appropriate to determine species richness, irrespective of sampling distance, efficiency of the gear and number of samples (CASSELMANN et al. 1990, HAYES et al. 1996, LAPOINTE & CORKUM 2006).

Our sampling sites covered a section of 3 km, which is approx. ten times the average width of the main channel, and our average sample distance of 494 m matches very well with the findings of WOLTER et al. (2004) and FLOTEMERSCH & BLOCKSOM (2005). The latter authors concluded that daytime catches below 4 m water depth and 1000 m along a single bank (or 500 m on a paired bank) is sufficient to characterize sites for bioassessment studies based on quantitative samples. Within the 3 km reach of the regulated main channel, which represents only one type of water body of the whole floodplain (Eupotamon sensu AMOROS & ROUX (1988)), we observed 48 percent of all species recorded in the whole section of the Austrian Danube (total length approx. 270 km) which represented 84 percent of all characteristic species for this type of macrohabitat. The size range and frequency of measured total lengths clearly shows that the sublittoral assemblage is composed mainly of adult individuals. WOLTER & BISCHOFF (2001) found a similar pattern in their study in the main channel of the Oder River. They attributed the presence of bigger fish in the main channel to a habitat preference of older fish for deeper water, and to improved swimming performance with increasing body size. The change of total species number with increasing discharge most notably affected rare species. Nonetheless, other factors such as species-specific reactions to these environmental changes – like movements into other habitats (TAYLOR et al. 1996, WOLTER &

BISCHOFF 2001) – cannot be excluded as underlying factors. The decrease of abundance with increasing water level could be due to a dilution factor or by to movements of individuals from single species into other habitats within the main channel or into connected water bodies of the floodplain, leading to a wider spread of the fish (FLADUNG et al. 2003).

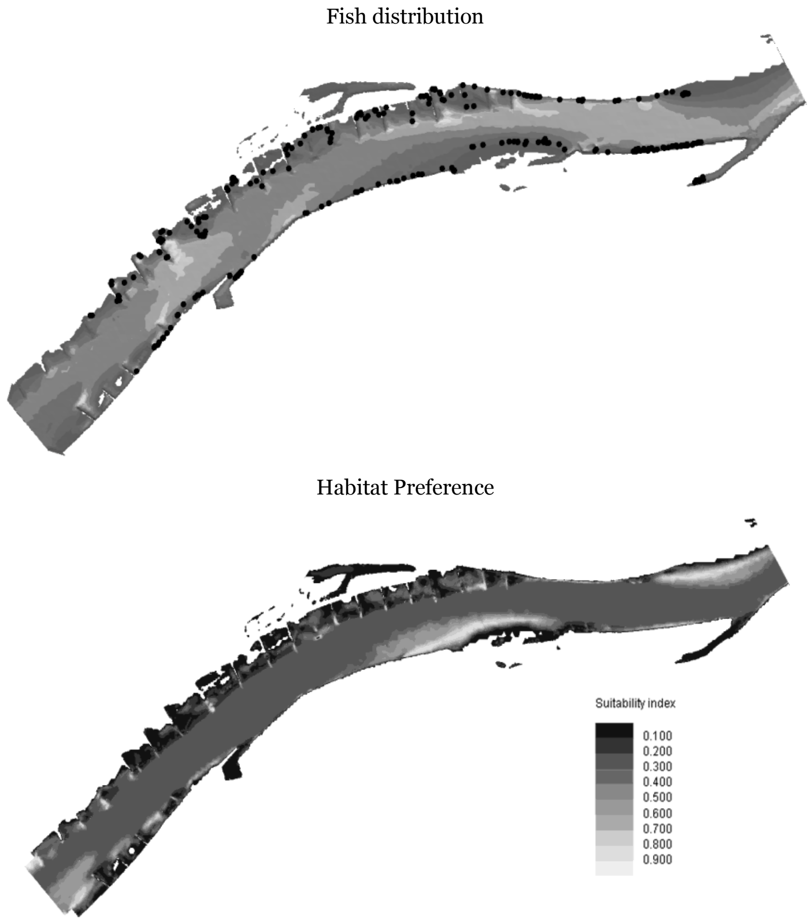

Figure 7: Distribution of areas where fish were caught in the investigated reach at Q1200 (yellow symbols, upper graph) and areas of the reach assigned different categories of habitat preferences (lower graphs) as predicted by the model.

LAMOUROUX et al. (1999) showed that community characteristics in large rivers are strongly influenced by hydraulic niche partitioning: within a geographic region, their statistical hydraulic model explained the large variance of relative species abundance and community structure indices of single reaches. Our study applied a classical instream flow incremental methodology based on a hydrodynamic model with a high spatial resolution and a precise position of caught individuals to estimate the area and position of preferred habitats of the sublittoral fish assemblage in a free-flowing river section. LAPOINTE & CORKUM (2006) recommend studies of habitat use by fish assemblages over studies focusing on single-species. Based on our results, we were able to create habitat suitability curves for water depth and flow velocities for the whole assemblage at three different discharge levels. At all discharges, fish occurred along both sides of the river, indicating a wide use of different habitats. When considering the two variables water depth and flow velocity, however, the habitat model indicated a strong preference for shallow, relatively fast-flowing areas. Projecting the habitat suitability on a 2-dimensional map of the main channel, it turned out that these preferred habitats apply mainly to gravel bars. Such bars represent the few remaining natural structures in the regulated main stem of the Danube. The groynes also revealed areas with highly preferred habitats, especially upstream of the groyne heads, but they are distinctly smaller compared to the gravel bars. Along the inshore areas with rip-rap, the model predicts a thin, continuous line of highly suitable habitats. Artificial structures within a largely modified and regulated river may be the sole sites that provide the required habitat complexity for fish (MADEJCZYK et al. 1998, FLADUNG et al. 2003, BARKO et al. 2004), however, it is unclear whether these structures provide habitat conditions which are required for the long-term development of the populations and for species conservation of the characteristic, native associations. Fish assemblages in regulated rivers often become dominated by generalistic species. Such species can tolerate the changes in habitat availability and structure and can successfully reproduce under these conditions, whereas fluvial specialists disappear or show a declining trend in abundance (SCHIEMER & WAIDBACHER 1992).

Our study revealed the possibility to analyze the patterns of habitat use and habitat preference of a fish assemblage in a large river at different discharges and provides basic information on how flow velocity and water depth – as prominent and easily accessible hydraulic and river morphological variables – relate to fish habitat. The model prediction may help in planning restoration measures, because distinct mesohabitats (gravel bars, groyne fields, rip raps) revealed clear differences in habitat preferences.

Table 2: Areas of different suitability regarding water depth and flow velocities of the pilot reach "Bad Deutsch Altenburg" derived from the hydrodynamic model at different discharge regimes of the Danube River. WUA = weighted usable area; HHS = hydraulic habitat suitability index. WUA (m²) resembles the sum of all areas of single grid cells multiplied by the suitability index of that cell. The HHS (in percent) is related to the total wetted area of a river reach (WUA * wetted area of reach^{-1} * 100).

		water depth		flow velocity		water depth + flow velocity	
	Suitability	Area (m²)	Percent (%)	Area (m²)	Percent (%)	Area (m²)	Percent (%)
Q 1200	0.0-0.1	31795,6	2,5	136147,3	10,6	199012,2	15,5
	0.1-0.2	16874,1	1,3	72168,7	5,6	119441,7	9,3
	0.2-0.3	678768,6	52,7	73000,3	5,7	698088,4	54,2
	0.3-0.4	98697,8	7,7	98469,5	7,7	89933,1	7,0
	0.4-0.5	75017,3	5,8	26284,7	2,0	59961,0	4,7
	0.5-0.6	101899,2	7,9	23888,7	1,9	57860,1	4,5
	0.6-0.7	52581,6	4,1	25096,3	2,0	23240,6	1,8
	0.7-0.8	50980,2	4,0	32164,7	2,5	21960,8	1,7
	0.8-0.9	61233,0	4,8	315202,2	24,5	16489,7	1,3
	0.9-1.0	119182,7	9,3	484607,4	37,7	1042,5	0,1
	Sum	1287029,9	100,0	1287029,9	100,0	1287029,9	100,0
	WUA/HHS	561685,2	43,6	876658,1	68,1	348056,6	27,0
Q 1500	0.0-0.1	47121,7	3,4	107924,2	7,9	259009,1	18,9
	0.1-0.2	158217,3	11,6	68520,7	5,0	886920,6	64,8
	0.2-0.3	812346,3	59,4	52343,7	3,8	79328,5	5,8
	0.3-0.4	54790,2	4,0	98646,4	7,2	57878,9	4,2
	0.4-0.5	49738,4	3,6	104999,9	7,7	29893,1	2,2
	0.5-0.6	51292,3	3,8	28299,3	2,1	21500,7	1,6
	0.6-0.7	55792,6	4,1	624765,9	45,7	16253,7	1,2
	0.7-0.8	58372,7	4,3	153011,5	11,2	11119,1	0,8
	0.8-0.9	49752,8	3,6	90763,9	6,6	5662,8	0,4
	0.9-1.0	30622,1	2,2	38770,9	2,8	479,9	0,0
	Sum	1368046,3	100,0	1368046,3	100,0	1368046,3	100,0
	WUA/HHS	417565,5	30,5	737091,2	53,9	218620,6	16,0
Q 1750	0.0-0.1	21933,9	1,6	158874,2	11,3	261005,2	18,5
	0.1-0.2	13157,1	0,9	88791,4	6,3	122698,8	8,7
	0.2-0.3	11667,1	0,8	123209,2	8,7	896968,2	63,5
	0.3-0.4	1010839,2	71,6	48274,5	3,4	40244,7	2,9
	0.4-0.5	43097,9	3,1	22005,0	1,6	21071,2	1,5
	0.5-0.6	38146,9	2,7	20069,6	1,4	17204,6	1,2
	0.6-0.7	37734,1	2,7	19843,5	1,4	14724,1	1,0
	0.7-0.8	40069,8	2,8	743612,2	52,7	18083,8	1,3
	0.8-0.9	57936,9	4,1	132801,2	9,4	16614,2	1,2
	0.9-1.0	137083,0	9,7	54185,0	3,8	3051,2	0,2
	Sum	1411665,9	100,0	1411665,9	100,0	1411665,9	100,0
	WUA/HHS	594320,0	42,1	850778,1	60,3	325277,5	23,0

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