

SPATIAL AND SEASONAL CHARACTERISTICS OF 0+ FISH NURSERY HABITATS OF NASE, *CHONDROSTOMA NASUS* IN THE RIVER DANUBE, AUSTRIA

Hubert KECKEIS, Gerold WINKLER, Laurence FLORE,
Walter RECKENDORFER and Fritz SCHIEMER

Received April 4, 1997
Accepted November 19, 1997

University of Vienna, Institute of Zoology, Department of Limnology, Vienna

Abstract

The influence of the hydrological regime (water level fluctuations, current conditions), temperature and structural components (substratum, flooded vegetation, woody debris) on the distribution of 0+ nase, *Chondrostoma nasus*, in three nursery habitats (two gravel banks and a sheltered bay: Gb 1, Gb 2 and Bay, respectively) were analysed applying a systematic sampling design. Sampling was carried out from May to August in weekly (May - July) to monthly (July - August) intervals in 1994. Detailed contour maps of each habitat were made by professional surveying. This data set formed the basis for further analysis with a Geographical Information System (GIS). At each site, water current, depth, temperature and fish density were measured at three points perpendicular to the bank in 5 m intervals along 100 m of shoreline. With 1508 points collected in total, substratum, type and density of flooded vegetation, algae, woody debris, canopy were estimated at each sampling point.

Main channel discharge influenced velocity, depth and temperature conditions in each habitat. Fish density, species number and species diversity were distinctly higher at the sheltered Bay compared to the two gravel banks. Within each habitat, nase selected sites with low water current, which was the overwhelming controlling factor for the distribution and occurrence of this species throughout the investigation period: 70% of the total catch was in the velocity range between 1 to 10 cm s⁻¹.

Key words: hydrology, habitat selection, temperature, large river, rheophilic cyprinids, early ontogeny, larvae, juveniles

Introduction

At present, approximately 90% of the shore of the free-flowing stretch of the Danube east of Vienna consists of artificially built rip-rap with a uniform steep slope, only 10% of instream gravel banks originate from natural sediment deposits. According to Persat et al. (1995), this part of the Danube belongs to the large braided section, a type which is most damaged in many European rivers.

Studies on the distribution and abundance of 0+ fish in this part of the Danube revealed that larvae and juveniles of many species occur at distinct sites situated along the main channel (Schiemer & Spindler 1989). A significant positive relationship between the length of the flowage line (Meinck & Möhle 1983) and species number was observed (Schiemer et al. 1991; Wintersberger 1996a), demonstrating the importance of highly diverse inshore structures (gravel banks, bays) as nursery zones for rheophilic fish. The length of the flowage line is an integrative measure incorporating shore structure, current conditions, water depth, substrate and temperature conditions. These

factors, or combinations thereof (their range, course and intensity) determine the quality of riverine 0+ habitats (Zalewski & Naiman 1985; Peňáz et al. 1991; Shields & Hoover 1991; Copp 1992; Wintersberger 1996b).

The long - term patterns of temperature and hydrological conditions may lead to adaptations in the time of spawning or in the embryonic development (Blair et al. 1991; Kamler et al., in press; Jonsson et al. 1991). Therefore analyses of temperature and hydrology at different time scales (long year average, seasonal and diurnal changes) was carried out and compared with the spawning season of *C. nasus*. The locality of spawning areas of riverine cyprinids depend on the hydrological conditions, and it is hypothesised that they should be in the vicinity of the protective nursery zones, because eggs and larvae that are exposed to high mechanical stress probably suffer high mortality (Keckeis et al. 1996). Hydrology determines the availability, size and location of suitable 0+ habitats due to the extension of flooded areas on a large spatial scale (Schiemer et al., in press; Schiemer et al. 1991). Changes in water level and the structural properties of the river margins are likely to predominate the environmental conditions at smaller scale units (i.e. inshore nursery habitat). Therefore the seasonal course and intensity of the water level, and the resulting temperatures, water velocities and water depths at the 0+ nursery habitats may be decisive for fish recruitment in rivers.

Temperature is an important factor in development, metabolism and growth (review in Kamler 1992). Water velocity is relevant for holding position and feeding (Fausch 1984; Flore & Keckeis, in press; Heggenes & Traaen 1988; Scott 1987; Hill & Grossman 1993), as well as for drift rate (i.e. food availability), which is positively related to velocity. Water depth is generally positively correlated with water velocity and plays an important role with regard to predation pressure and habitat selection; shallow sites provide better shelter from predatory fish species (Gilliam & Fraser 1987; Schlosser 1987; Harvey et al. 1988; Bugert & Bjornn 1991; Bugert et al. 1991).

Our main aim was to analyse the relation between habitat structure, hydrology (water level, water current), water depth, temperature conditions and the population of 0+ nase, *Chondrostoma nasus* (L.) at three 0+ nursery areas of Danube. The sites were compared with regard to overall 0+ fish density and species diversity as well as food availability. Furthermore the question of whether 0+ nase are distributed regularly within each habitat, or if they select areas with certain environmental conditions was adressed.

Material and Methods

The study area was located on the right bank of the River Danube between river km 1908.5 and 1910 (Fig. 1). Three different sections of 100 m length were chosen, two situated at river km 1910, representing one sheltered bay with the opening upstream (Bay) and the adjacent gravel bank shore facing the main channel (Gb 1). The third stretch was located at river km 1909 (Gb 2).

Detailed contour maps of each sampling site (ca. 0.5 x 0.5 m) were made by professional surveying (grid of approx. 0.5 x 0.5 m) to ensure exact location of

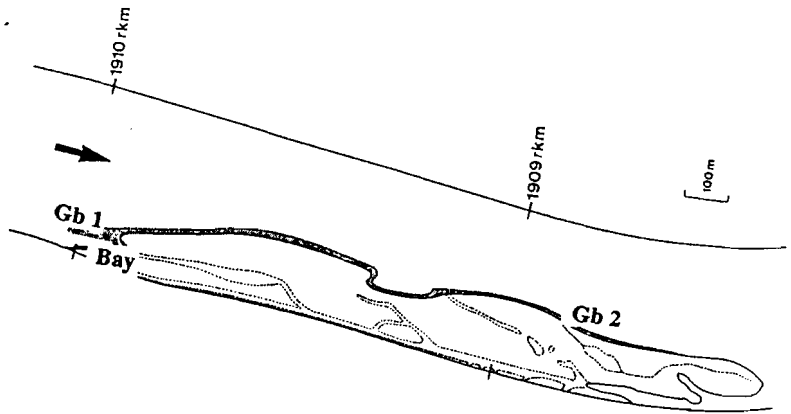
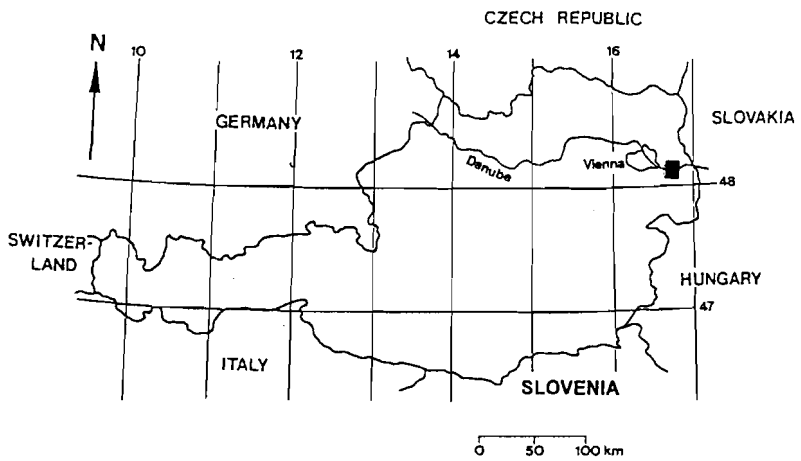


Fig. 1. Location of the study site and sketch of the investigated gravel bank with the three sampling sites.

each sampling point during different hydrological conditions. This data set formed the basis for further analysis with a Geographical Information System (GIS), i.e. detailed maps and overlays of the abiotic conditions (temperature, current, depth) as well as fish distribution patterns and densities at each sampling date (Fig. 2).

Sampling started when the first larvae appeared at the investigation area (visual observations) in May and was carried out in weekly (May - July) to monthly (July - August) intervals in 1994. A systematic sampling design was chosen for the investigations: water current, depth, temperature and fish density were measured at three points (from the shore up to a depth of approx. 0.5 m) in 5 m intervals along a stretch of 100 m shoreline at each site. Altogether 1508 points were analysed. In addition, structural components (substrate, type and density of flooded vegetation, woody debris, canopy) were estimated (Fig. 3). Temperature was measured at each date with a WTW® Oxi 91 probe and

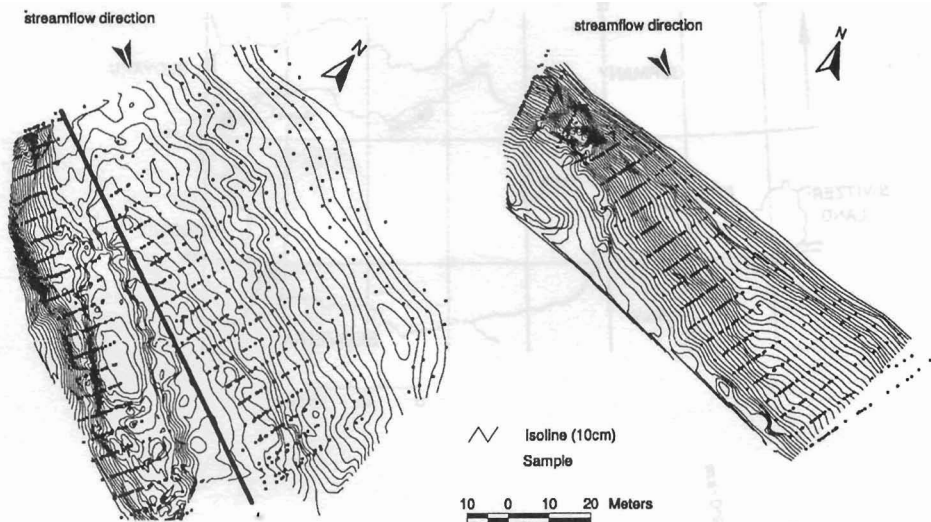


Fig. 2. Bathymetric maps of the three habitats. The black symbols represent all sampling points for depth, velocity, temperature, vegetation and 0+ fish. For details see material and methods and Fig. 3.

additionally at hourly intervals using a data logger (testo® 170) to obtain information about the 24 h cycles. Water level and temperature recordings at hourly intervals from the main channel were provided by the River Authority. Water currents and depths at the habitats were measured at each point with a current meter (Ott C2®; $\pm 0.02 \text{ m s}^{-1}$).

In order to evaluate food availability at each sampling date and each site, three plankton samples of 20 l were taken inshore (approx. 0.2 m from the shore line). Nine drift samples were taken with a drift net (opening 30 x 30 cm, mesh size 100 μm) exposed near the water surface for 3 min. from inshore up to a depth of 0.5 m. Also nine Surber samples (area 0.1024 m^2 , 100 μm mesh size) were taken in a similar manner (Fig. 3). All samples were sieved through a 37 μm (plankton) or 100 μm (drift, benthos) mesh and preserved with 4% formalin. Counting and species determination was carried out in the laboratory using standard techniques (Reckendorfer et al. 1996).

In order to adjust optimally the electronic fishing gear and thus maximise catch efficiency, different anode types and generators (direct current, alternate current) were tested in the National Institute of Fisheries in Scharfling, Upper Austria. Fishing was carried out using a 8.5 kW generator producing a direct current of 400-500 V and ca. 8A. The sampling procedure can be described as a modified „point abundance sampling“ technique (Persat & Copp 1990). An anode of 30 cm diameter was attached to a 4-m pole to minimise disturbance of the fish and was connected to the generator via a 300-m cable to enhance movement. The sphere of action was 0.7 m^2 . A few seconds after exposing the anode to the sampling point, a net was put into the water to collect the fish. 0+ fish were preserved in 4% formalin. Counting, length-measurements and species

determination were carried out in the laboratory. Species were determined using a modified key from Spindler (1988), Koblickaja (1981) and Zweimüller (unpublished).

Principal component analysis (varimax rotation) of the abiotic variables (water current, depth, substrate, temperature, structure flooded terrestrial vegetation, algae) was carried out to reveal which groups of environmental variables are suitable to describe habitat variability (i.e. explained variance of each axis). To evaluate seasonal effects on habitat configuration (e.g. succession and growth of algae, and macrophytes, seasonal changes of flooded areas with terrestrial vegetation) the date was included in the analysis. The significance of the factor loadings were tested by a permutation test (Nemeschkal 1991; Kockeis et al. 1996). The factor scores were coded according to absence/presence of fish and compared using ANOVA to analyse habitat selection.

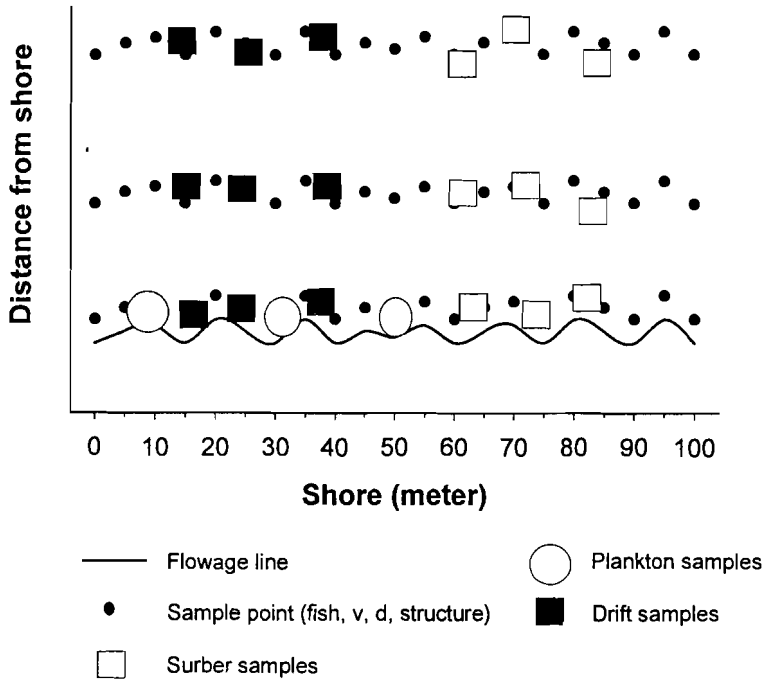


Fig. 3. Applied sampling design for each sampling date and habitat: at 63 points were velocity (v) and depth (d) measured and structural components (flooded terrestrial vegetation and algae) were estimated. Additionally the 0+ fish were collected at each of these points. Three plankton samples were taken inshore, and nine drift and benthos samples were collected along transects at an angle of 90° to the shore up to a depth of 0.5 m.

Results

The long-term pattern (19 years, Fig. 4a) of temperature in the main channel of the Danube at different time scales is characterized by low temperatures from January to late February, followed by a continuous increase to the maximum in August and a decline in December. In 1994 the temperature was rather typical for

the long-term situation, despite more pronounced increases/decreases of the monthly mean values and their variabilities (Fig. 4b). Temperatures increased from 6°C in early March to 22°C in late July/early August, with high daily fluctuations (Fig. 4c). The lines in Figure 4a-4c indicate the preferable spawning temperature of *Chondrostoma nasus*, which lies between 8 and 12°C (P e ě á z et al. 1984), and when projected to the time axes the spawning season for this species would last from late March to late May. This picture is clear when long-term data or yearly data are considered, but the daily fluctuations in Fig. 4c show that temperature already reaches 8°C on March 10, and then fluctuates for several weeks below and above the spawning temperature.

Water level on a long-term scale shows highest values from June to July and lowest values in October/November. From December to late May intermediate levels were observed (Fig. 4d). In 1994, highest values occurred in April; then, the water level decreased continuously up to October, thereafter increasing again slightly (Fig. 4e). Water level shows high fluctuations, both on the long-term and short term-scale. The stochasticity of this variable was most pronounced considering a daily basis: changes of water level of up to 3 m and more occurred within a few days (Fig. 4f).

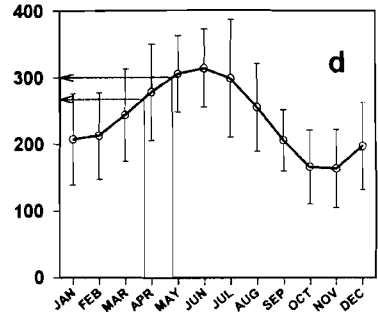
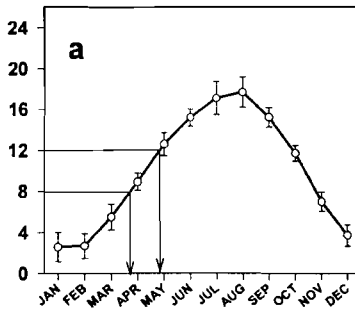
The projection of the spawning season shows that *Chondrostoma* spawns at water levels around mean water plus 0.5 m when most of the gravel banks are flooded (see Fig. 4 d,e), but high fluctuations may occur during this time periods (see Fig. 4f).

At times, the temperature differences in the Bay was distinctly higher than in the Danube and the two gravel banks (Fig. 5a). When plotted against the hydrological conditions, temperature in the sheltered Bay (Fig. 5b) was decoupled from the situation in the main channel, the difference being more than 8°C. However, the Bay habitat dried out at low discharge, i.e. at mean water level minus 0.6 m (indicated in the vertical line in Fig. 5.b). This means that different temperature zones along the shoreline of the Danube are present. Their environmental conditions and existence are significantly influenced by the hydrological regime of the river. The difference is less pronounced at the gravel banks. Inshore temperatures differed maximally 2°C from the main channel at low water level conditions (Fig. 5b).

A similar influence was observed for the variables water current and water depth (Fig. 6). Both, the intensity and pattern were clearly different between the three sites. Water current in the Bay increased slightly with increasing water level; this relationship was much more pronounced at gravel bank 1, where the highest currents were measured. At the gravel bank 2 current speed decreased with increasing water level (in the range from mean water -0.5 m to mean water +1m). Water depth increased linearly with increasing water level at the Bay (steeper slope) and at gravel bank 2. At gravel bank 1, depths remained constant between mean water level -1m and mean water; then, the values increased exponentially. Grain sizes between the three sites were also significantly different: the sediment in the Bay was mainly mud and sand, while at the two gravel banks it consisted of sand, gravel and stones, in average the largest grain size was observed at gravel bank 1.

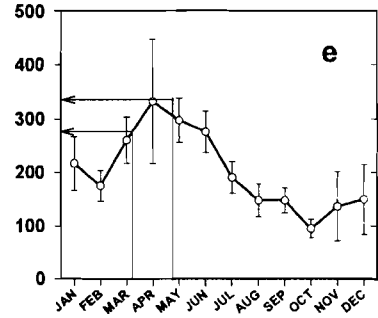
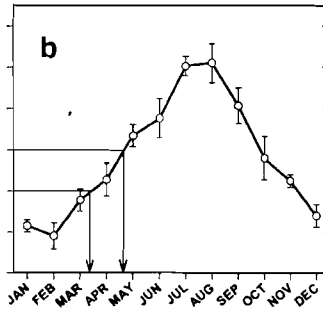
In summary the Bay site can be characterized as having generally low current conditions, distinctly higher temperature below mean water level, and linearly

1975 - 1994



1994

Temperature (°C)



Water level (cm)

Investigation Period

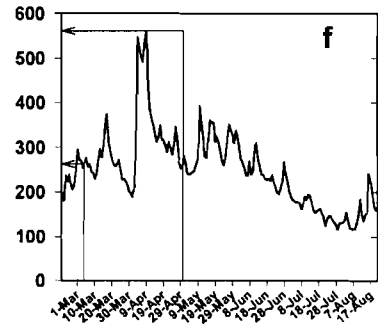
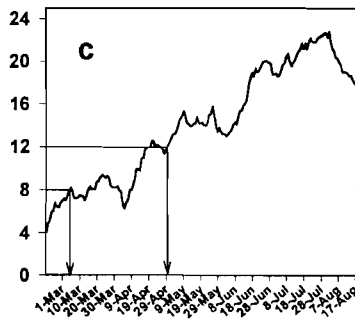


Fig. 4. Temperature (left) and hydrological changes (right) of the Danube at different time scales. The preferential spawning temperature range of *C. nasus* is indicated and projected to the time and water level scale.

increasing water depths with increasing water level conditions (Table 1). At low discharge this site dries out due to the lateral movement of the water body. Gravel bank 1 had strongest currents and stable water depth values over a broad range

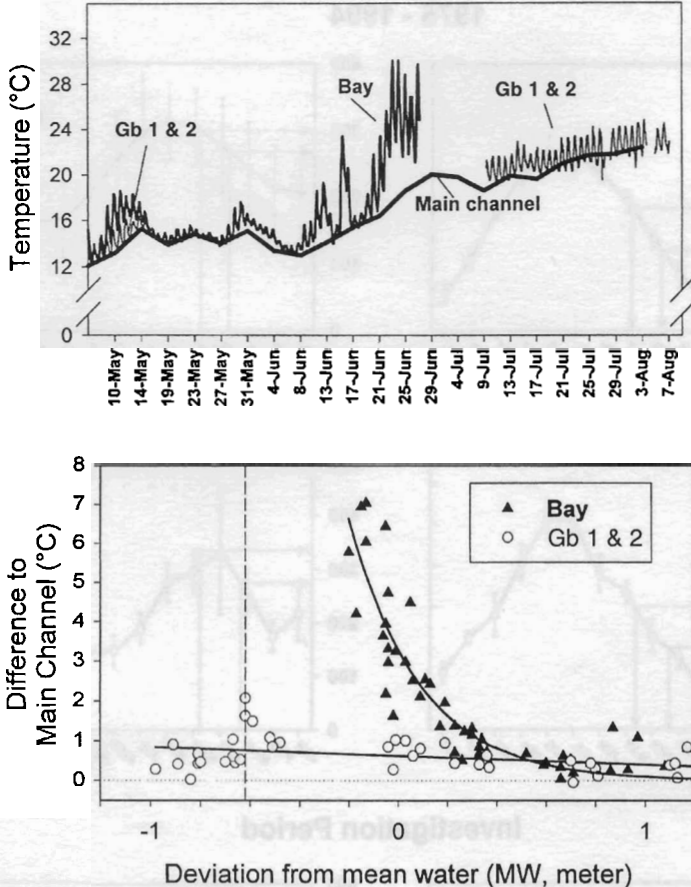


Fig. 5. Seasonal course of temperatures of the main channel and at the three habitats (above) and, below, comparison of the temperature differences at the study sites versus the main channel under different hydrological conditions. MW = long year average (mean water level) from the Danube in Austria (defined by the River Authority). 1 = mean water level plus 1m; -1 = mean water level minus 1m. The vertical line indicates the water level at which the Bay habitat falls dry.

Table 1. Overall characteristics of the main measured abiotic factors (mean values \pm standard deviation) and number of observations (n) at the three sites between May and August 1994.

	Bay	Gb 1	Gb 2
Water velocity (cm sec ⁻¹)	0.03 \pm 0.07	0.32 \pm 0.24	0.17 \pm 0.18
water depth (cm)	44.5 \pm 24.8	32.8 \pm 23.1	41.8 \pm 26.4
water temperature (°C)	17.0 \pm 4.2	16.2 \pm 3.1	15.7 \pm 2.6
grain size (mm)	0.09	26.8	15.7
n	482	459	505

of water levels. At gravel bank 2 water currents decreased with increasing discharge, whereas water depth increased slightly. Both gravel banks had similar but slightly higher temperatures than the main channel (see Fig. 5).

Benthos and drift were dominated by chironomids and Oligochaeta, which accounted for 75% in all samples (for a details see R e c k e n d o r f e r et al. 1996). All food categories (benthic, drift and planktonic prey) were distinctly higher at the Bay habitat than at the other two sites (Table 2).

Table 2. Mean values (\pm standard error) of benthos, drift and plankton at the three sampling sites. Benthos = Individuals per m²; Drift and plankton are given as individuals per m³.

	Bay	Gb 1	Gb 2
Benthos			
Chironomidae	35 925 \pm 13 019 6	13 691 \pm 2 890 9	4 394 \pm 2 025 9
Oligochaeta	71 549 \pm 14 172 6	15 562 \pm 3 191 9	7 157 \pm 1 327 9
TOTAL	333 245 \pm 60 033 6	52 438 \pm 7 445 9	30 656 \pm 6 239 9
Drift			
Chironomidae	-	85 \pm 35 9	31 \pm 5 9
Oligochaeta	-	83 \pm 14 9	96 \pm 14 9
TOTAL	-	295 \pm 59 9	213 \pm 21 9
Plankton			
<i>Brachionus</i>	48 110 \pm 22 499 9	6 518 \pm 2 013 9	7 022 \pm 2 654 9
<i>Keratella</i>	111 182 \pm 36 333 9	28 539 \pm 8 301 9	26 603 \pm 8 519 9
Synchaeta	762 580 \pm 388 474 9	110 736 \pm 33 450 9	99 257 \pm 30 319 9
Rotifera	1 011 303 \pm 467 272 10	173 144 \pm 36 370 9	159 465 \pm 34 197 9

Total individual numbers of 0+ fish were 3.6 - 6 fold higher in the Bay than in Gb 2 and Gb 1, respectively (Table 3). The number of total species (including endangered species) as well as species diversity were higher at the Bay habitat. The total catch was clearly dominated by nase (53.9%), dace, *Leuciscus leuciscus* (15.6%) and barbel, *Barbus barbus* (14.7%). All other species were below 5% of the total catch. The nase was dominant at all three sites, reaching values up to almost 77% at Gb 2; at the other two sites the percentage values are very similar (49.3% at the Bay and 46.6% at Gb 1).

From the PCA, two factors were extracted, explaining 60.3% of the total variance (Table 4, Fig. 7). The variables temperature and date were highly positively correlated with the first axis (Permutation test, $p < 0.001$). Water current, substrate and depth correlated highly positively with the second axis, and structures (flooded terr. vegetation, algae) highly negatively ($p < 0.001$). The first

axis can therefore be interpreted by seasonal variability, and the second axis as abiotic variability. The scores were fish where present in all three habitats where significantly different from those without fish (ANOVA, $p < 0.001$). Monthly differences of microhabitat selection in each habitat are shown in Fig. 8 and in Table 5. In most cases and in all three habitats, the scores with fish present and absent differed significantly. One exception was June, when no significant differences on the first axis (temperature) were observed. Generally, young nase in each habitat were present at points with higher temperature, lower current, shallower depth, finer substrate and more structure compared with the other sampling points. The GIS analysis showed that more than 70% of nase occurred in areas with currents below 10 cm s^{-1} , irrespective of habitat type, hydrological conditions and season (Fig. 9). No significant difference between the number of nase in this areas was observed between the three sites (ANOVA, $p < 0.001$).

Discussion

During the last two decades, increasing recognition has been given to the role of river hydrology and morphology for the ecological integrity and functioning of large river systems (Junk et al. 1989; Schiemer et al., in press; Townsend & Hildrew 1994; Vannote et al. 1980; Ward & Stanford 1995). Detailed knowledge on the functioning and dynamics of rivers and their floodplains at different spatial and time scales is needed to develop management and restoration concepts. Furthermore, practical criteria and measurements are required to enable the ecological evaluation and the comparison of different river systems as well as the transformation of these criteria for river engineers.

The severe channelization of large European rivers reduced fish biomass and lead to the disappearance of migratory and rheophilic species (Persat et al. 1995; Schiemer & Waibacher 1992; Jurařda & Peňáz 1994). Their trophic status, changing habitat requirements throughout their life cycles, and the above-mentioned population changes make riverine fish communities good indicators for the ecological integrity of large river systems (Schiemer et al. 1991; Copp et al. 1991). The indicative value is especially high at critical stages in the life history, i.e. a) the reproductive period due to changes and loss of suitable spawning habitats (Kecckeis et al. 1996) and b) the narrow and specific requirements of the young stages which are critical for recruitment (Schiemer et al. 1991; Schlosser 1985). „Calibrating“ this indicative value demands detailed knowledge of the autecological requirements of the species during critical periods of their life history (Schiemer et al. 1991).

Spawning of *C. nasus* occurs in many European rivers (eastern and western) during April, at temperatures between 8 and 12°C (Peňáz et al. 1984). This temperature range occurs on a long-term pattern in the Danube between late March and late April (see Fig. 4). During this period water levels are slightly above the mean value (long-term pattern), although high short-term fluctuations of both factors may occur, as is demonstrated in Fig. 4c and 4f. Hydrology is a main factor initiating spawning migrations of salmon (Cragg-Hine 1985) and plays an important role for timing of hatching in river-spawning coregonids (Naesje et al. 1995). These two factors also play an important role for the nase with regard to

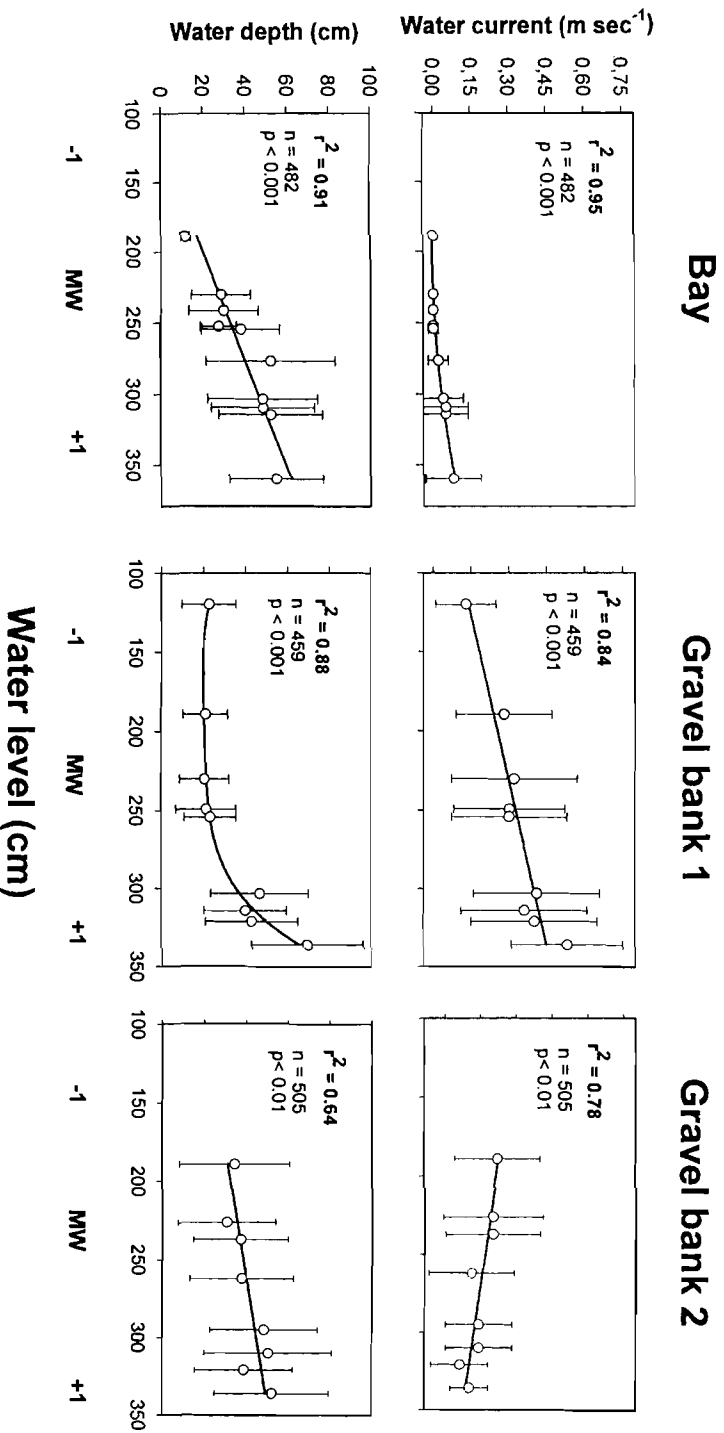


Fig. 6. Relationship between current conditions (above) and water depth (below) at the three habitats and the water level of the Danube. MW = long year average (mean water level) from the Danube in Austria (defined by the River Authority). 1 = mean water level plus 1m; -1 = mean water level minus 1m.

Table 3. Species number, diversity and abundance of the total catch of 0+ fish at the three sites. H' = Shannon diversity index; n = number of individuals; % = percentage of total number.

	Bay		Gb 1		Gb 2		Total	
Species number	14		8		10		14	
endangered species	8		5		5		8	
diversity index H'	1.42		0.92		0.83		1.46	
sample points	482		459		505		1446	
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
<i>Abramis ballerus</i>	2	0.03	-	-	-	-	2	0.02
<i>Abramis brama</i>	149	2.37	2	0.15	10	0.59	161	1.73
<i>Alburnus alburnus</i>	301	4.78	20	1.51	87	5.14	408	4.38
<i>Aspius aspius</i>	2	0.03	-	-	-	-	2	0.02
<i>Barbus barbus</i>	546	8.67	646	48.68	179	10.59	1371	14.72
<i>Blicca bjoerkna</i>	1	0.02	-	-	3	0.18	4	0.04
<i>Chondrostoma nasus</i>	3104	49.29	618	46.57	1300	76.88	5022	53.91
<i>Cottus gobio</i>	7	0.11	2	0.15	1	0.06	10	0.11
<i>Gobio gobio</i>	3	0.05	-	-	-	-	3	0.03
<i>Leuciscus cephalus</i>	216	3.43	-	-	1	0.06	217	2.33
<i>Leuciscus idus</i>	12	0.19	4	0.30	4	0.24	20	0.21
<i>Leuciscus leuciscus</i>	1346	21.38	21	1.58	86	5.09	1453	15.60
<i>Rutilus rutilus</i>	438	6.96	6	0.45	16	0.95	460	4.94
<i>Vimba vimba</i>	3	0.05	-	-	-	-	3	0.03
undet.	167	2.65	8	0.60	4	0.24	179	1.92
TOTAL	6297	100	1327	100	1691	100	9315	100

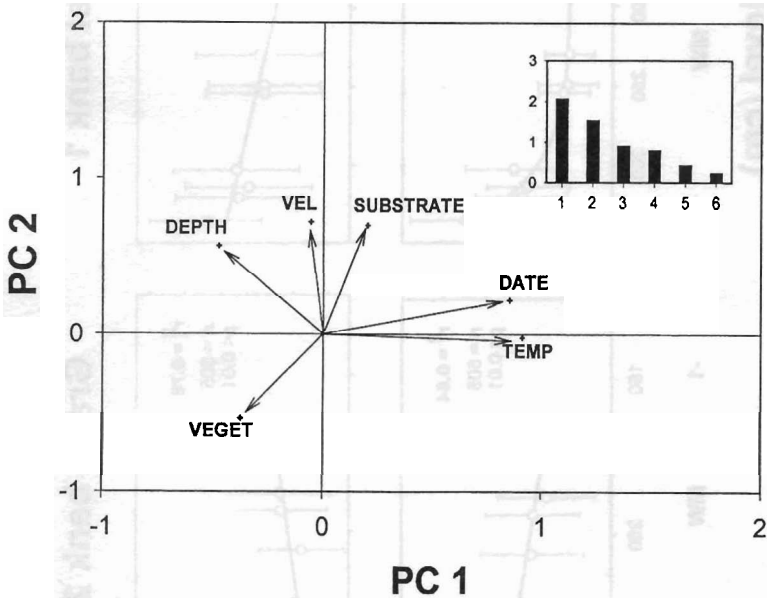


Fig. 7. Rotated factor loadings at the two extracted factor-axes (DEPTH = water depth, VEL = water velocity, TEMP = temperature, VEGET = flooded terrestrial vegetation, algae). The inserted diagram shows the Eigenvalues of the axes. The correlation of the variables with the axes are listed in Table 4.

Table 4. Description of units/codes of the variables of the principal component analysis (above) and the results of the rotated factor matrix with the percentages of explained variance for each axis (below). Highly significant (Permutation test, $p < 0.001$) loadings are printed bold. Number of observations: $n = 1508$.

Variables	Units, Codes	
Water current	cm sec ⁻¹	
Depth	cm	
Temperature	°C	
Substrate		
Mud	1	
Sand	2	
Sand/Gravel	3	
Gravel	4	
Riprap	5	
flooded terrestrial vegetation, algae	0 absent	
(gras, other terr. plants, willos, bushes)	1 present	
	Factor 1	Factor 2
Water current	-0.06	0.72
Depth	-0.48	0.56
Substrate	0.20	0.69
Temperature	0.91	-0.02
Vegetation	-0.38	-0.53
Season	0.85	0.22
Percent of Variance	34.5%	25.8%

timing of the spawning migration and the size of the migrating population into a Danube tributary (K e c k e i s et al., in prep.). In the main channel of the Danube, the highly fluctuating temperatures and water levels may prolonge the spawning period, as indicated in the occurrence of freshly hatched embryos over a long period (May to early June; see W i n k l e r et al., this volume).

The larval and early juvenile stages experience increasing temperatures from 12°C in May up to 20°C in July in the main channel. Within the observed nursery zones, the seasonal course of the temperature was distinctly different from that of the main channel and clearly dependent on the hydrological conditions (see Fig. 5 and 6). Especially at the Bay habitat, where highest densities and species diversity as well as highest food availability was observed (see Table 1 and 2),

Table 5. Habitat selection of nase: comparison of the factor scores of the two extracted axes of each site (Fig. 7) with absence/presence of fish (ANOVA).

	Bay		Gb 1		Gb 2	
	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2
May	<0.001	<0.001	<0.005	<0.001	<0.05	n.s.
June	n.s.	<0.005	n.s.	<0.001	n.s.	<0.01
July	-	-	<0.05	<0.05	-	-
August	-	-	<0.001	<0.001	-	-

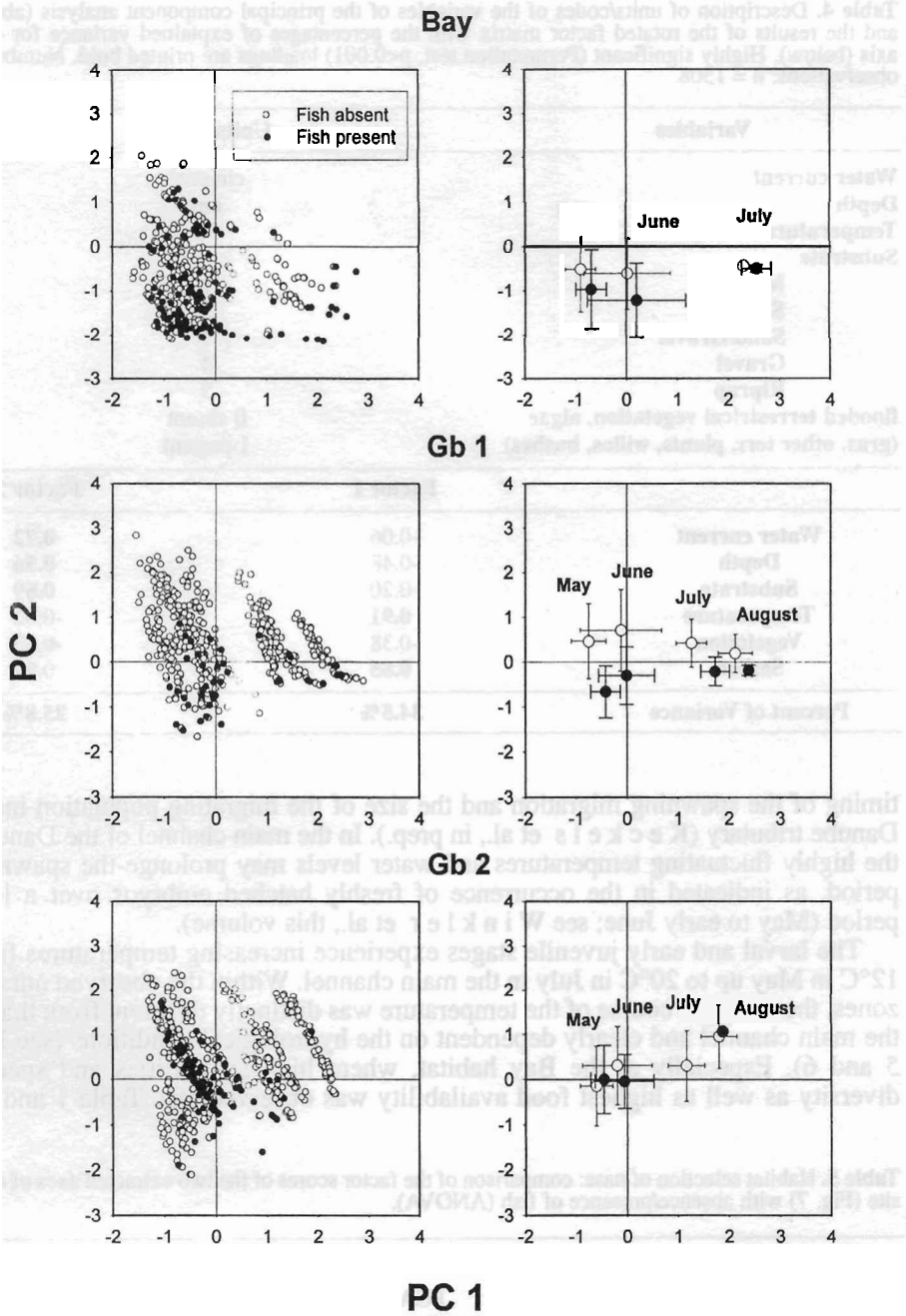


Fig. 8. Factor score plots (varimax rotated) of the three habitats (left) and comparison of pooled scores (mean values \pm standard deviation) of each month (right) to demonstrate the significant seasonal changes at each sampling site. The scores are coded with absence/presence of fish to indicate habitat selection.

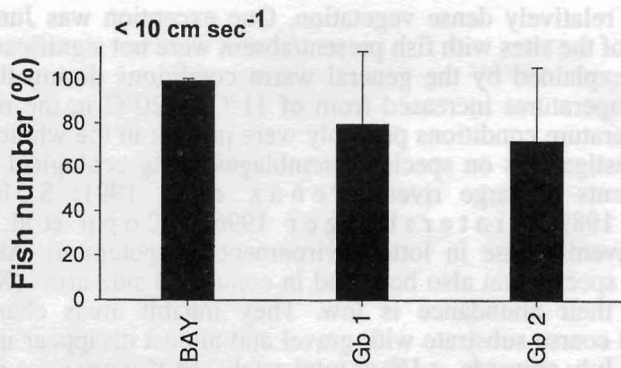


Fig. 9. Occurrence of *C. nasus* within the area of $< 10 \text{ cm s}^{-1}$ water current at the three sampling sites. For comparison, fish number is expressed as a percentage (total catch from each site at each date equals 100%).

the temperature regime becomes decoupled from the conditions in the main channel even at relatively high water level.

However, this type of habitat falls dry at low water level, which on a long-term pattern occurs in autumn (see Fig. 4d); this may also be the case in summer due to the stochastic course of the water level, as was observed during our investigations. This phenomenon plays a role in habitat selection of 0+ fish. Not only do the individuals actively select certain environmental conditions, the shifts of the whole water body determines the amount, position and area of available habitats. River bed structure and the accompanying ecological gradients (S c h i e m e r et al., in press) are highly relevant for the quality of the nursery grounds.

River channelization has altered the areas and connectivity of such habitat types, which limited the accessibility for 0+ fish and prohibited them from reaching the right place at the right time (i.e. disrupted habitat relationships, S c h e i d e g g e r & B a i n 1995); their changing requirements during ontogeny are not fully provided for (B a i n & F i n n 1988; S c h l o s s e r & A n g e r m a i e r 1995; T u r n e r et al. 1994; P e r s a t et al. 1995; W i n t e r s b e r g e r 1996).

The important link between structural properties, hydrological conditions and the 0+ fish fauna is clearly demonstrated in the water current-water level relationships in Fig. 6. The decreasing current speeds with increasing water level at Gb 2 represent the refugial capacity of this zone, which prevent the 0+ fish populations from washing out effects and loss of whole year classes. During flooding events, the density of *C. nasus* decreased in the Bay habitat and increased at Gb 2, located one kilometer downstream (see Fig. 2; S c h i e m e r et al., in press; W i n k l e r et al., this volume). The lower number, unfavourable position and poor succession of diversely structured nursery habitats probably represent a key factor for the decrease of rheophilic fish species in the Danube. The effect on the future development of the population is still unknown and is the topic of ongoing investigations.

In addition, 0+ fish within a particular habitat were not accidentally distributed, as exemplified for nase in Fig. 9. This species selected microhabitats which had slower currents and shallower depths, warmer temperatures, finer

substrate and relatively dense vegetation. One exception was June when the temperatures of the sites with fish present/absent were not significantly different. This can be explained by the general warm conditions during this month, in which the temperatures increased from of 11°C to 20°C in the main channel; suitable temperature conditions probably were present in the whole habitat.

Many investigations on species assemblages along ecological and environmental gradients in large rivers (Peñáz et al. 1991; Schiemer & Spindler 1989; Wintersberger 1996ab; Copp et al. 1991) report larvae and juvenile nase in lotic environments (eupotamon). Although early stages of this species can also be found in connected side arms (Kurmaier et al. 1996) their abundance is low. They inhabit areas characterized by comparabable coarse substrate with gravel and almost disappear in the summer catches (from July onwards, < 1% of total catch; see Kurmaier et al. 1996). In contrast to these findings, 0+ nase dominate the fish association of practically all inshore habitats in the main channel (see Table 3). Within this lotic environment, larvae and juveniles are bound to inshore areas with very slow currents (Fig. 10). Water current is therefore key factor (indicated in the highest correlation with the abiotic factor axes in Table 4) determining habitat suitability for 0+ nase. The high densities of young stages, the favourable abiotic conditions, as well as the high food availability in the Bay habitat lead to the conclusion that such zones are desicive for recruitment of *Chondrostoma nasus* in large rivers.

Acknowledgements

This work was financed by the project P 9600 BIO from the Austrian Research Council (FWF). We gratefully acknowledge the permission to catch fish by the fisheries authority and especially than H. Belanyecz, O. Eggen dorfer and F. Rausch from the local city of Fischamend for their support. The river authority (Österreichische Wasserstraßendirektion) provided the water level and temperature data. We thank our colleagues for their help in the field investigations, and H. Nemeschkal and H. Wintersberger for their discussions. We thank G. H. Copp and P. Jurajda for their comments on an earlier version of this manuscript.

LITERATURE

- BAIN, M.B., FINN, J.T. & BOOK, H.E., 1988: Streamflow regulation and fish community structure. *Ecology*, 69(2): 382-392.
- BLAIR, G.R. & QUINN, T.P., 1991: Homing and spawning site selection by sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Canadian Journal of Zoology*, 69: 176-181.
- BUGERT, R.M., BJORN, T.C. & MEEHAN, W.R., 1991: Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. *Transactions of the American Fisheries Society*, 120: 474-485.
- COPP, G.H., OLIVIER, J.M., PEÑÁZ, M. & ROUX, A.L., 1991: Juvenile fishes as functional descriptors of fluvial ecosystem dynamics: Applications on the River Rhone, France. *Regulated Rivers: Research & Management*, Vol. 6: 135-145.
- COPP, G.H., 1992: Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. In: Wieser, W., Schiemer, F., Goldschmidt, A. & Kotschal, K. (eds.), Environmental biology of European cyprinids. *Environmental Biology of Fishes*, 33: 181-193.
- CRAGG-HINE, D., 1985: The assessment of the flow requirements for upstream migration of salmonids in some rivers of North-West England. In: Alabaster, J.S. (ed.), Habitat modification and freshwater fisheries. *Butterworths*: 209-215.
- FAUSCH, K.D., 1984: Profitable stream posi-

- ons for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology*, 62: 441-451.
- FLORE, L. & KECKEIS, H., in press: The effect of water current on foraging behaviour of the rheophilic cyprinid, *Chondrostoma nasus*, during ontogeny: trade-off energetic benefit-swimming costs. *Regulated Rivers: Research & Management*.
- GILLIAM, J.F. & FRASER, D.F., 1987: Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, 68(6): 1856-1862.
- HARVEY, B.C., CASHNER, R.C. & MATTHWES, W.J., 1988: Differential effects of largemouth and smallmouth bass on habitat use by stoneroller minnows in stream pools. *Journal of Fish Biology*, 33,3: 481-487.
- HEGGENES, J. & TRAAEN, T., 1988: Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *Journal of Fish Biology*, 32: 717-727.
- HEGGENES, J., BRABRAND, A. & SALTVEIT, J.S., 1990: Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. *Transactions of the American Fisheries Society*, 119: 101-111.
- HILL, J. & GROSSMAN, D., 1993: An energetic model of microhabitat use for rainbow trout and rosyzide dace. *Ecology*, 74(3): 685-698.
- JONSSON, N., HANSEN, L.P. & JONSSON, B., 1991: Variation in age, size and repeat spawning of adult atlantic salmon in relation to river discharge. *Journal of Animal Ecology*, 60: 937-947.
- JUNK, W.J., BAYLEY, P.B. & SPARKS, R.E., 1989: The flood pulse concept in riverfloodplain systems. In: Dodge, D.P. (ed.), Proceedings of the International Large River Symposium. *Can. Spec. Publ. Fish. Aquat. Sci.*, 106: 110-127.
- JURAJDA, P. & PEÑÁZ, M., 1994: Fish community of the lower regulated stretch of the River Morava, Czech Republic. *Folia Zool.*, 43(1): 57-64.
- KAMLER, E., 1992: Early life history of fish: An energetics approach. *Chapmann & Hall, London*, 267 pp.
- KAMLER, E., KECKEIS, H. & BAUER-NEMESCHKAL, E., (in press): Temperature-induced changes of survival, development and yolk partitioning in *Chondrostoma nasus*. *Environmental Biology of Fishes*.
- KECKEIS, H., FRANKIEWICZ, P. & SCHIEMER, F., 1996: The importance of inshore areas for spawning nase *Chondrostoma nasus* (Cyprinidae) in a free-flowing section of a large river (Danube, Austria). *Arch. Hydrobiol., Suppl. 113, Large Rivers*, 10, 1-4: 51-64.
- KOBLICKAJA, A.P., 1981: Key for Identifying Young Freshwater Fishes. *Food Industry Publishing House, Moscow (in Russian)*.
- KURMAYER, R., KECKEIS, H., SCHRUTKA, S. & ZWEIMUELLER, I., 1996: Macro- and microhabitats used by 0+ fish in a side arm of the River Danube. *Arch. Hydrobiol. Suppl. 113, Large Rivers*, 10: 425-432.
- NÆSJE, T., JONSSON, B. & SKURDAL, J., 1995: Spring Flood - A primary cue for hatching of river spawning coregonidae. *Canadian Journal of Fisheries and Aquatic Sciences*, 52(10): 2190-2196.
- NEMESCHKAL, H., 1991: Size in land snails (Arianta, Helicidae) as a so-called simple system of characters - A system analyses by means of classification and morphological integration. *Zool. Jb. Syst.*, 118: 149-192.
- PEÑÁZ, M., LUSK, S., SZABÓ, S., LUKSHA, R., SMIRNOVA, E.N., STOROZHENKO, S.S. & TCHEPURNOVA, L.V., 1984: Spawning. In: The undermouth. *Vilnius Mokslas Publishers*, pp: 34-51 (in Russian).
- PEÑÁZ, M., OLIVIER, J.-M., CAREL, G., PONT, D. & ROUX, A.-L., 1991: A synchronic study of juvenile fish assemblages in the French section of the Rhône river. *Acta Sc. Nat. Brno*, 25(5): 1-36.
- PERSAT, H. & COPP, G.H., 1990: Electric fishing and point abundance sampling for the ichthyology of large rivers. In: Cowx, I.J. (ed.), Developments in Electric Fishing. *Fishing News Books, Cambridge*: 197-209.
- PERSAT, H., OLIVIER, J.M. & BRAVARD, J.P., 1995: Stream and riparian management of large braided mid-european rivers, and consequences for fish. In: Armantrout, N.B. (ed.), Condition of the World's Aquatic Habitats. *Proceedings of the World Fisheries Congress, Theme 1. Oxford & IBH Publishing Co, New-Dehli*: 139-169.
- RECKENDORFER, W., KECKEIS, H., WINKLER, G. & SCHIEMER, F., 1996: Water level fluctuation as a major determinant of chironomic community structure in the inshore zone of a large temperate river. *Arch. Hydrobiol., Suppl. 115, Large Rivers*, 11/1: 3-9.
- SCHEIDEGGER, K.J. & BAIN, M.B., 1995: Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia*, 1: 125-135.
- SCHIEMER, F. & SPINDLER, T., 1989: Endangered fish species of the Danube River in Austria. *Regulated Rivers: Research and Management*, 4: 397-407.
- SCHIEMER, F., SPINDLER, T., WINTERSBERGER, H., SCHNEIDER, A. & CHOVANEC, A., 1991: Fish fry associations: important indicators for the ecological status of large rivers. *Verh. Internat. Verein. Limnol.*, 24: 2497-2500.
- SCHIEMER, F. & WAIDBACHER, W., 1992: Strategies for conservation of a Danubian

- fish fauna. In: Boon, P.J., Calow, P. & Petts, G.E. (eds.), *River Conservation and Management*. John Wiley & Sons. Ltd.: 363-382.
- SCHIEMER, F., KECKEIS, H., WINKLER, G., FLORE, L. & RECKENDORFER, W., (in press): Large rivers: ecotonal structure and hydrological properties and their relevance for the fish fauna. *Unesco MAB*.
- SCHLOSSER, I.J., 1985: Flow regime, juvenile abundance and the assemblage structure of stream fishes. *Ecology*, 66(5): 1484-1490.
- SCHLOSSER, I.J., 1987: The role of predation in age- and size-related habitat use by stream fishes. *Ecology*, 68(3): 651-659.
- SCHLOSSER, I.J. & ANGERMAIER, P.L., 1995: Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. *American Fisheries Society Symposium*, 1995; 17: 392-401.
- SCOTT, A., 1987: Prey selection by juvenile cyprinids from running water. *Freshwater Biology*, 17: 129-142.
- SHIELDS, JR, D.F. & HOOVER, J.J., 1991: Effects of channel restabilization on habitat diversity, Twentymile Creek, Mississippi. *Regulated Rivers: Research & Management*, Vol. 6, p. 163-181.
- SPINDLER, T., 1988: Bestimmung der mittel-europäischen Cyprinidenlarven. *Österreichs Fischerei*, 41: 75-79.
- TOWNSEND, C.R. & HILDREW, A.G., 1994: Species traits in relation to a habitat template for river systems. *Freshwater Biology*, 31/3: 265-275.
- TURNER, T.F., TREXLER J.C., MILLER, G.L. & TOYER, K.E., 1994: Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. *Copeia*, 1: 174-183.
- VANNOTE, R.L., MINSHALL, G.W., CUMMINS, K.W., SEDELL, J.R. & CUSHING, C.E., 1980: The river continuum concept. *Can. J. Fish. Aquat. Sci.*, 37: 130-137.
- WARD, J.V. & STANFORD, J.A., 1995: Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research & Management*, 11: 105-119.
- WINTERSBERGER, H., 1996a: Species assemblages and habitat selection of larval and juvenile fishes in the River Danube. In: Sutcliffe, D.W. (ed.), *The ecology of large rivers*. *Archiv Hydrobiol., Suppl. 113, Large Rivers*, 10: 497-505.
- WINTERSBERGER, H., 1996b: Spatial resource utilization and species assemblages of larval and juvenile fishes. *Arch. Hydrobiol., Suppl. 115: 29-44*.
- ZALÉWSKI, M. & NAIMAN, R.J., 1985: The regulation of riverine fish communities by a continuum of abiotic-biotic factors. In: Alabaster, J.S. (ed.), *Habitat modification and freshwater fisheries*. *Published by arrangement with the FAO by Butterworths: 3-9*.

Authors' address:

Hubert KECKEIS,
Gerold WINKLER,
Laurence FLORE,
Walter RECKENDORFER,
Fritz SCHIEMER,

University of Vienna, Institute of Zoology, Department of Limnology, Althanstrasse 14, A - 1090 Vienna, Austria; e-mail: Hubert.Keckeis@univie.ac.at