Towards a Mechanistic Understanding of Urbanization's Impacts on Fish

Christian Wolter

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Introduction

Human population is increasing at a rate of 1.8% per year and urbanization is a global trend. In 2005, there were 3.2 billion urban residents worldwide, representing 49% of the global population (UN 2006). The urban population is projected to increase to 4 billion in 2018 and to more than 5 billion in 2030 (UN 2006). However, in the developed regions 75% of the population lived in urban settlements in 2005. This proportion is expected to increase in Europe from 72% in 2005 to 78% in 2030 and in North America from 81% at present to 87% in 2030 (UN 2006). Urban areas cover only 2.4% on the terrestrial surface of Earth, but their average population density is 52 times that of rural areas (MA 2005). Except coastal areas and island states, the highest average urban population density was found along inland waters with 817 people per km^2 (MA 2005). Indeed, most people believe that urban environmental conditions are deteriorating, and the condition of urban waters is high on their list of worries. Features of urbanization have been reviewed by Paul & Meyer (2001): impervious surface covers, alteration of drainage density and flow dynamics, decreasing groundwater renewing and sediment supply, and increases in surface runoff, water temperature, pollutants, and nutrients. The cumulative effect of various human activities in urban areas profoundly influence urban waters and their biota, either directly by channel modification and habitat degradation or indirectly by land use change and runoff (Booth et al. 2004). The percentage of impervious surface cover has been commonly suggested as the best single predictor of the response of stream biota to urbanization (e.g. Karr & Chu 2000, Allan 2004, Booth et al. 2004, Miltner et al. 2004). However, the threshold values for demonstrated significant biological degradations at the catchment level of 10–15% total impervious area are much below the commonly observed $> 50\%$ impervious cover in metropolitan areas at the regional level (Booth et al. 2004). Karr & Chu (2000) considered biological communities as irreparably damaged if the impervious cover within a watershed ranged between 25–60%. Urbanization is highly positively correlated with both the endangerment of native and the invasion of non-native fish within watersheds and thus, considered as major cause of biotic homogenization (Marchetti et al. 2006). Urbanization tends to favour the persistence of relatively few intolerant, generalist native species, the introduction and establishment of widespread non-natives, and the extinction and extirpation of specialized, intolerant native species (Marchetti et al. 2006).

C. Wolter
Leibniz-Institute of Freshwater Ecology, Berlin, Germany
e-mail: wolter@igb-berlin.de

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But how do urbanized areas and impervious covers impact fish and promote non-native species? What are the basic mechanisms? Non-linear relations between impervious cover and biological communities have been observed, in particular if instream habitats or hydrodynamics were also considered. For example, in Ohio watersheds at sites with relatively undeveloped riparian buffers, the biological integrity was maintained despite high levels of urban land use (Miltner et al. 2004). Accordingly, habitat destruction caused by urban development seemed the primary force driving common species to decline due to resource limitations and enabling different or new species to increase when benefiting from the changed habitats. To analyse this question, between 1992 and 2002 the fish assemblages of 27 Federal waterways have been extensively studied: more than 470 sites were surveyed, 2,100 samples collected, and 336,500 fish recorded representing 35 species. This data set revealed substantial findings on environmental factors structuring local fish assemblages (Wolter & Vilcinskas 1997a, 1998a, Wolter 2000, 2003), environmental pressures (Wolter 2001a, Arlinghaus et al. 2002), urban gradients (Wolter 1997b, 2000, Wolter 1999a), the impact of urbanization on fish abundance (Wolter & Vilcinskas 1996, Wolter 2001b) and population dynamics (Wolter 1998, 1999b, Wolter & Vilcinskas 1998b), and the ecological performance of species (Wolter & Vilcinskas 1997b, Arlinghaus & Wolter 2003).

This paper refers briefly to three main results of the mentioned studies to illustrate the specifics of fish communities in urban waters for the example of the water system of Berlin, Germany, where 3.5 million people reside. Detailed information on methods used, sampling design, environmental variables, species lists etc. are presented in the original papers.

Restricted Structural Diversity Limits Fish Diversity

Fish of urban rivers are generally exposed to higher thresholds of multiple disturbances and in particular to the cumulative effects of altered hydrology and geomorphology. Waters in urban areas are especially embanked, regulated, and their channels fixed, due to an extraordinary high amount of land use in the surroundings, resulting in substantial simplifications of the riverine habitats with monotonous bank structures and few tributary refuges. In the urban waterways studied on average 88% (± 21% standard deviation) of the total bank lines were covered by artificial embankments like rip-rap or sheet pile wall, in contrast to 72% (± 30%) in the rural waterways. In addition, the average number as well as the structural diversity of tributaries was lower in the urban waterways.

The observed fish assemblage patterns differed significantly between the 13 urban and 14 rural waterways surveyed (Fig. 1, Table 2; data from Wolter & Vilcinskas 2000). In urban waters the number of species recorded was generally lower and six native and three non-native fish species were not detected. Typical floodplain species (bitterling, crucian carp, weatherfish, ten-spined stickleback) as well as typical riverine species (chub, zope, stone loach) with more specified habitat requirements disappeared from the urban fish species pool. Dropping abundances and disappearance of intolerant species start immediately with the urbanization of watersheds and result in declining fish diversity (e.g. Boët et al. 1999, Wolter et al. 2000, Paul & Meyer 2001, Wolter et al. 2003). The urban fish communities were dominated by two species, roach and perch accounting for 70% of all fish on average, whilst most of the species were rare, contributing less than 1% each. The observed species inventories ranged from 6–21 in urban and 11–28 in rural waterways. Both the mean number of species and the species diversity (estimated as Shannon's diversity index H') were significantly higher (*Students t* statistics, $p < 0.05$) in rural waters, despite a high amount of habitat destruction in rural waterways. However, urbanization did not impact intolerant species with sensitive habitat requirements only, like chub or pike, but also the abundance of roach, one of the most common eurytopic species in Europe. Roach itself is considered as indicator for environmental degradation by eutrophication (e.g. Oberdorff & Hughes 1992, Oberdorff et al. 1993, Carrel &

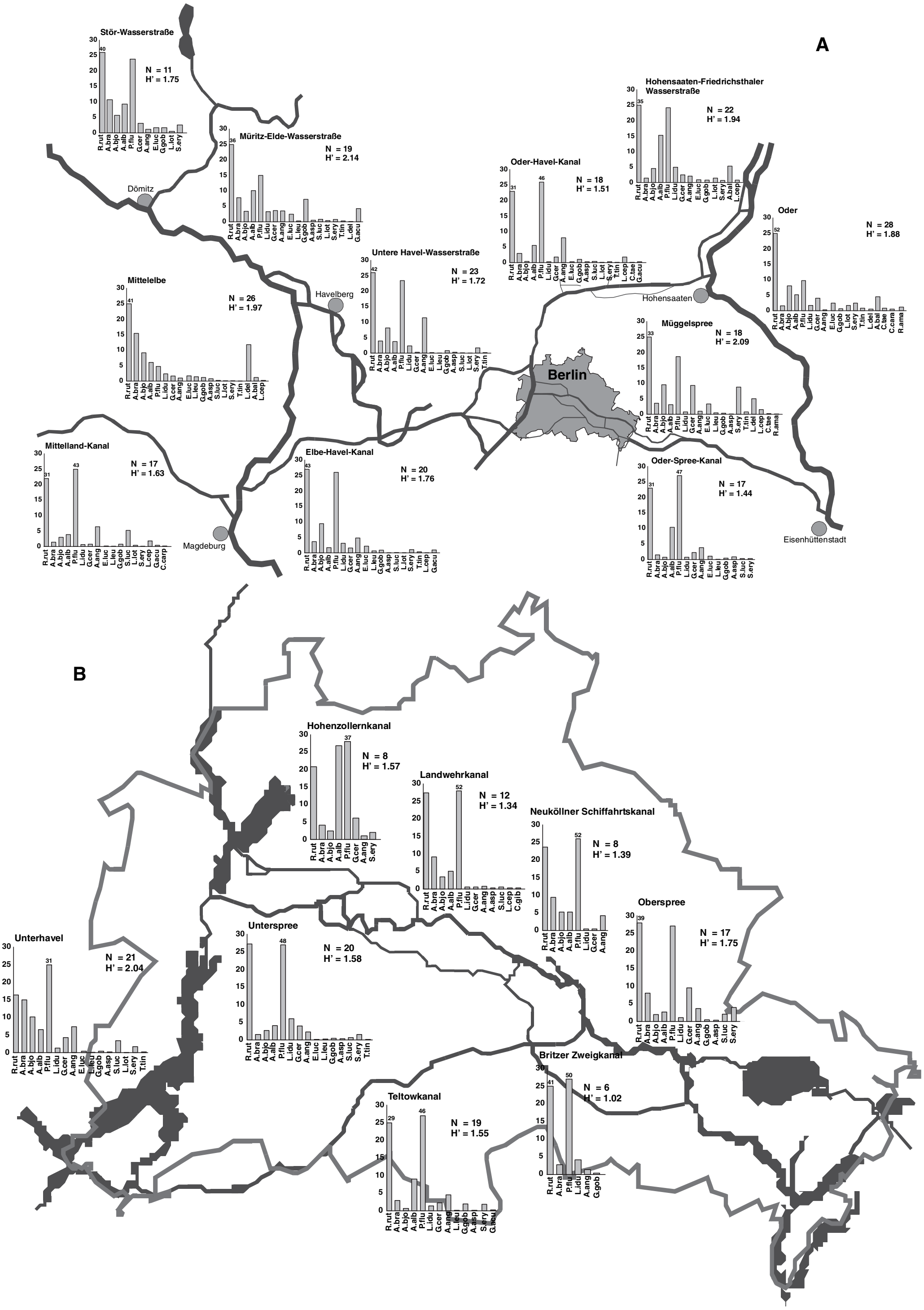

Fig. 1 Relative abundance (%) of the most common fish, species number (N), and Shannon's species diversity (H') in rural (A) and urban (B) waterways surveyed in Berlin and in the NE lowlands in Germany (species abbreviations in Table 2)

Table 1 Main hydro-morphological characteristics of the urban (U) and rural (R) waterways studied (min. = minimum, subm. = submerged, tribs. = tributaries)

Waterway	Length (km)	Min. width (m)	Mean Depth (m)	Mean flow velocity (ms^{-1})	Subm. Macrophytes	Artificial embankment (%)	No. of Tribs. per km	Environment
Britzer Zweigkanal (BZK)	3.4	27.5	2.7	< 0.05	none	100.0	0.00	U
Charlottenburger Verbindungskanal (CVK)	1.7	14.5	2.7	0	none	100.0	0.00	U
Dahme Wasserstraÿe (DaW)	25.0	21.0	1.5	< 0.05	none	74.2	0.36	U
Gosener Kanal (GoK)	2.8	35.0	3.0	< 0.1	none	100.0	0.00	U
Hohenzollernkanal (HZK)	8.2	53.7	3.3	< 0.05	none	100.0	0.36	U
Landwehrkanal (LWK)	10.7	23.0	1.8	0	none	100.0	0.19	U
Neuköllner Schifffahrtskanal (NSK)	4.1	25.0	2.0	0	none	100.0	0.00	U
Oberhavel (OHa)	28.5	54.0	3.5	< 0.1	none	68.1	0.77	U
Oberspree (OSp)	15.0	30.0	2.0	< 0.05	none	96.3	0.38	U
Teltowkanal (TeK)	37.8	27.5	2.7	< 0.05	none	87.6	0.14	U
Unterhavel (UHa)	16.4	46.0	1.5	< 0.1	rare	24.4	0.30	U
Unterspree (USp)	17.8	30.0	2.0	0.1	none	95.2	0.82	U
Westhafenkanal (WHK)	3.1	46.6	3.8	0	none	100.0	0.32	U
Elbe-Havel-Kanal (EHK)	56.8	40.0	3.0	< 0.1	none	93.6	0.32	R
Havelkanal (HvK)	34.9	34.0	3.0	< 0.05	none	99.2	0.20	R
Havel-Oder-Wasserstraÿe (HOW)	135.0	23.0	2.6	< 0.05	rare	89.7	0.28	R
Hohensaaten-Friedrichstaler-Wasserstraÿe (HFW)	42.5	20.0	2.4	< 0.05	none	87.6	0.14	R
Mittelelbe (Elbe)	486.0	200.0	2.9	1.0	rare	10.2	1.07	R
Mittellandkanal (MLK)	321.3	37.0	3.5	< 0.1	none	99.2	0.10	R
Müggelspree (MSp)	35.4	25.0	2.0	0.5	frequent	8.6	7.63	R
Müritz-Elde-Wasserstraÿe (MEW)	120.8	20.0	1.5	0.1	frequent	80.3	0.51	R
Oder (Od)	161.0	200.0	2.2	1.0	none	44.7	0.26	R
Oder-Havel-Kanal (OHK)	49.3	34.0	3.0	< 0.05	frequent	98.8	0.14	R
Oder-Spree-Kanal (OSK)	85.1	28.0	2.0	0.05	none	98.4	0.34	R
Stör-Wasserstraÿe (StW)	19.7	17.0	2.0	0	frequent	87.0	0.18	R
Untere Havel-Wasserstraÿe (UHW)	148.5	46.0	1.8	< 0.1	frequent	50.5	0.69	R
Westoder (WOd)	66.5	43.5	1.8	0.5	none	67.1	0.24	R

Table 2 Means (± SD) of relative abundance (%) and main fish assemblage characters in urban and rural inland waterways (N = number of waterways, ^{a} single records, significance level: $^*p < 0.05$, $^{**}p < 0.01$)

Scientific name	Common name	Urban (N = 13)	Rural (N = 14)
Anguilla anguilla	eel	4.3 ± 3.0	3.8 ± 3.2
Abramis ballerus	zope		3.7 ± 1.8
Abramis bjoerkna	silver bream	4.1 ± 3.5	6.0 ± 3.6
Abramis brama *	common bream	10.3 ± 8.4	4.5 ± 4.2
Alburnus alburnus	bleak	6.9 ± 6.5	8.0 ± 5.2
Aspius aspius	asp	0.3 ± 0.1	0.4 ± 0.4
Carassius carassius	crucian carp		0.2 ± 0.2
Carassius gibelio	prussian carp	0.2 ± 0.1	0.04 ± 0.03
Ctenopharyngodon idella	grass carp		0.005^a
Cyprinus carpio	common carp	0.03 ± 0.01	0.1 ± 0.1
Gobio gobio	gudgeon	0.5 ± 0.5	1.5 ± 1.7
Hypophthalmichthys nobilis	bighead		0.01^a
Leucaspius delineatus	sunbleak	0.1 ± 0.05	2.9 ± 4.4
Leuciscus cephalus *	chub	0.2^a	1.0 ± 0.9
Leuciscus idus	ide	1.6 ± 1.7	2.0 ± 1.5
Leuciscus leuciscus	dace	0.1 ± 0.1	0.3 ± 0.4
Rhodeus amarus	bitterling		0.5 ± 0.5
Rutilus rutilus **	roach	29.5 ± 8.4	39.2 ± 7.0
Scardinius erythrophthalmus	rudd	1.6 ± 1.1	1.7 ± 2.2
Tinca tinca	tench	0.2 ± 0.2	0.3 ± 0.3
Barbatula barbatula	stone loach		0.04^a
Cobitis taenia	spined loach	0.02 ± 0.01	0.2 ± 0.3
Misgurnus fossilis	weatherfish		0.1 ± 0.04
Silurus glanis	wels	0.03 ± 0.01	0.02 ± 0.01
Esox lucius **	pike	0.3 ± 0.2	1.4 ± 1.1
Oncorhynchus mykiss	rainbow trout		0.04^a
Lota lota	burbot	0.04 ± 0.04	0.7 ± 0.7
Gasterosteus aculeatus	3-sp. stickleback	0.2 ± 0.1	1.0 ± 1.4
Pungitius pungitius	10-sp. stickleback		0.06^a
Gymnocephalus cernuus	ruffe	4.2 ± 3.8	2.7 ± 2.2
Perca fluviatilis *	perch	37.7 ± 14.1	24.2 ± 13.2
Sander lucioperca	zander	1.1 ± 1.0	0.8 ± 1.5
Mean number of species *		13.7 ± 4.6	18.8 ± 4.8
Species diversity H′*		1.56 ± 0.24	1.77 ± 0.25
Evenness		0.61 ± 0.07	0.61 ± 0.08
Community Dominance Index		70.0 ± 11.3	64.5 ± 8.6
Total number of individuals		34,828	97,563
Total number of species		23	32

Rivier 1996), but was much (*Students t* statistics, $p < 0.01$) less abundant in the urban than rural waters (Table 2).

These comparisons might be biased by the naturally higher fish species inventories of the large regulated rivers. Thus, we compared the canal fish assemblages separately. In both, urban and rural areas these canals have been artificially constructed according to the same standardized guidelines regarding the navigation-induced physical forces, embankment stability, vessel's drought, canal width, depth, and profile. However, the different land use patterns resulted in slightly lower percentages of artificial embankments, especially of sheet pile walls, and in a higher amount of instream habitats relevant to fish like macrophyte cover, as well as in higher numbers of tributaries in the rural canals (Table 1). These structural differences seemed relevant to fish, because the urban canals showed much (*Students t*, $p < 0.01$) lower mean species number and species diversity than rural canals (Table 3). These findings corresponded very well with those presented in Table 2, and underlined the impact of the heavily reduced structural diversity resulting from urbanization on fishes.

Table 3 Means (± SD) of main fish assemblage characters of artificial navigation canals in urban and rural environments (N = number of canals, significance level: *p < 0.05, **p < 0.01)

Metric	Urban canals (N = 8)	Rural canals (N = 9)
Mean number of species **	11.1 ± 3.8	17.1 ± 3.6
Species diversity H′*	1.43 ± 0.21	1.72 ± 0.27
Evenness	0.61 ± 0.08	0.61 ± 0.08
Community Dominance Index	74.4 ± 10.4	66.8 ± 9.1
Total number of individuals	9,559	29,982
Total number of species	21	28

The particular influence of available tributaries on the fish communities was studied in more detail by comparing 56 sampling sites at the mouth of tributaries within 88 linear stretches (Wolter 2001b). Mean fish species number (10.8 ± 2.09, standard deviation), species diversity ($H' = 1.78 \pm 0.32$), and catch per unit effort CPUE (fish/100 m = 73.3 ± 29.2) were significantly higher (*Students*

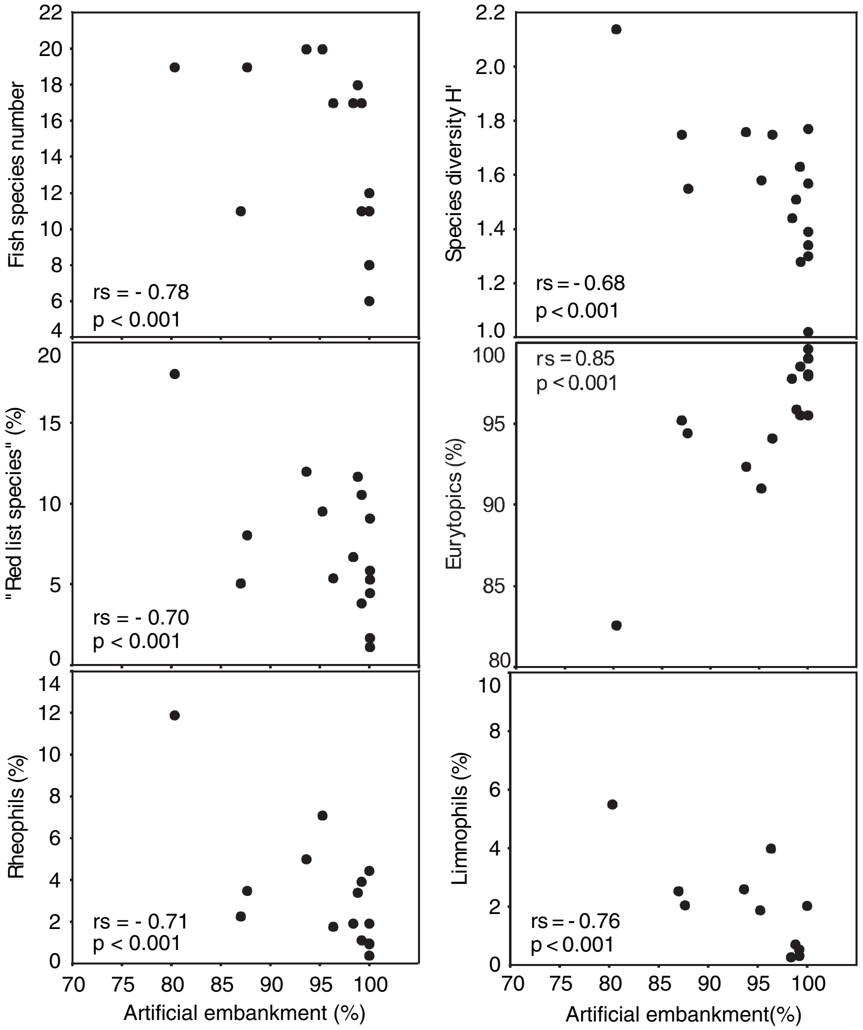

Fig. 2 Spearman rank correlations (coefficient rs) between the percentage of artificial embankment (riprap or sheet pile wall) and various fish community measures (number of waterways N = 19). Redrawn from Wolter (2001b)

t, $p < 0.01$) at tributary sites than at linear canal reaches (fish species number $= 5.7 \pm 2.12$, $H' = 1.19 \pm 0.27$, and CPUE $= 27.3 \pm 8.1$). These findings correspond very well with the observed inverse correlation between distance from tributaries and abundance of eurytopic fish in the free flowing section of the Danube River (Hirzinger et al. 2004), and the importance of off-channel habitats as refuges for fish (Copp 1997). Similarly, ecotone diversity, i.e. diverse instream habitat structures along the banks, has been identified as essential for high fish diversity (Copp 1997, Wolter 2001b, Arlinghaus et al. 2002, Hirzinger et al. 2004). In the Seine River basin a general decrease of specialized fish species has been observed resulting from homogenization of littoral habitats (Boët et al. 1999). Even in lakes the residential development and alterations of littoral habitats caused decreased growth rates and productivity of fish stocks (Schindler et al. 2000) and altered the spatial distribution and aggregation of fish (Scheuerell & Schindler 2004).

Finally, the percentage of artificial embankment requires special consideration as one of the main features of waterways. Except for the large regulated rivers, the proportion of artificial embankments was rather high and typically increased 70–80%, with low differences between rural and urban waterways. However, 80% artificial embankments seemed to be a threshold value, and the gradual increase up to complete embankment significantly impacted fish assemblages. Even the final 10% of the total bank line, if remaining natural or if covered by artificial embankments were reflected in highly significant fish-faunistic differences (Fig. 2, from Wolter 2001b). In waterways with "only" 90% of the shore lines embanked, the observed fish species numbers, species diversity and proportions of rheophilic, limnophilic, as well as threatened fish were significantly higher compared to the completely embanked waterways. The dominance of the most tolerant, eurytopic species significantly increased with shoreline degradation, especially the dominance of perch.

Shore Line Degradation Causes Community Dominance of Perch

Perch (*Perca fluviatilis*) was one of the most widespread fish species in the waters surveyed (Wolter & Vilcinskas 1997a, Wolter et al. 2003). In contrast to the majority of species, perch abundance increased substantially in urban waters (Table 2). Within both rural and urban waters there was a shift of perch abundance along a gradient of artificial embankment, involving a change from the numerical dominance of roach to the dominance of perch in the fish assemblages (Wolter & Vilcinskas 1997b, 1998b). In waterways with predominately natural shorelines, perch were significantly (*Students t*, $p < 0.05$) less abundant (mean 15.43% ± 8.22% standard deviation) than were roach (38.87% ± 4.14%) and other fish species (45.69% ± 8.62%). Contrary to this, the mean perch abundance (42.24% ± 8.83%) exceeded that of roach (32.75% ± 7.82%, $p > 0.05$) and other species (25.01% ± 7.64%, $p < 0.05$) in waterways with predominately artificial shorelines (Fig. 3).

Similar observations were made with respect to total fish biomass: in the more natural waterways, roach was dominating (22.36% ± 5.39%), while the relative biomass of perch was 6.79% ± 3.04%. In contrast, in the more artificial waterways perch became the dominant fish (26.54% ± 2.81%), whilst the mean roach biomass dropped to 19% ± 9.09%. Which factors favoured perch? All waterways investigated were polytrophic to hypertrophic, i.e. the nutrient conditions were favourable to cyprinids, especially roach (Persson et al. 1991, Oberdorff & Hughes 1992, Carrel & Rivier 1996). The competitive superiority of cyprinids involves roach outcompeting juvenile perch (Persson & Greenberg 1990). Limited food resources would favour roach too (Persson & Greenberg 1990, Bergmann & Greenberg 1994), and the only structure competitively favouring perch, submerged vegetation, is lacking in urban waterways: (Persson & Greenberg 1990). Thus, in contrast to the perch dominance observed, a numerical dominance of roach had to be expected.

Roach and perch are the most environmentally tolerant, common and widespread fish species in the waterways studied. Both species require neither specific spawning habitats nor substrata

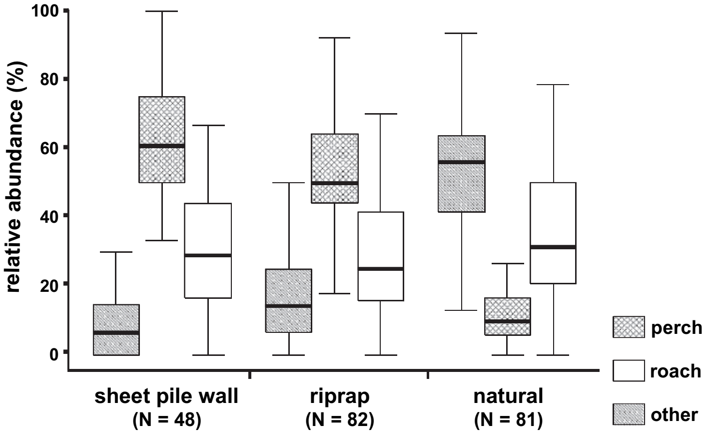

Fig. 3 Occurrence of perch, roach and other species in relation to the type of embankment. The boxes represent 50% of all observations and the whiskers 90%. The thick line marks the median and N the number of sites. Figure redrawn from Wolter & Vilcinskas (1997b)

or hydraulic conditions, and their spawning has been commonly observed. The main difference between both species, or more general between percids and other species, is an ontogenetic habitat shift: larval perch shift their habitat to the pelagic zone immediately after hatching and shift back to the littoral zone at a size range of 11–30 mm depending on the predation pressure in the pelagic (Byström et al. 2003). In contrast, larvae of other species remain in the littoral and essentially depend on shallow, slow flowing nursing habitats. Accordingly, habitat degradations in the littoral zones impacts the recruitment of all fish species with shoreline-bounded larvae. Species with pelagic larvae remain substantially less impacted and thus, the latter become numerical dominant. This pattern might favour perch over other species such as roach under anthropogenic degradations in waterways and urban waters, which has led to the suggestion of perch as an indicator species for structural degradation in regulated rivers and canals (Wolter & Vilcinskas 1997b). This hypothesis has been confirmed empirically by a study of juvenile fish recruitment in a canal, where the availability of littoral habitats was restricted due to commercial navigation (Arlinghaus et al. 2002). The recruitment of juvenile fish in the littoral zone was restricted to bays, oxbows and tributaries due to the high navigation-induced currents in the main channel preventing small juveniles from maintaining shallow low flowing nursing habitats along the banks (Wolter & Arlinghaus 2003, Wolter et al. 2004).

Urbanized Waters Hinder Migrations and Limit Gene Flow

The third example comprises species exchange and gene flow within urban water systems and canals. In selected waterways numerous sites have been surveyed to investigate fish migrations within canals, the suitability of canals as migration routes for fish as well as the barrier effect of navigable locks (Wolter & Vilcinskas 1998b); and population genetic studies were performed to characterize habitat fragmentation and genetic isolation by migration barriers and urbanized river segments (Wolter 1998, 1999b).

Presence-absence and relative abundance data of fish species suggested a barrier effect of extended, nearly still, monotonous watercourses (Wolter & Vilcinskas 1998b). They were less attractive for fish movements and consequently inhibited directional fish migrations. Correspondingly, observed fish invasions proceeded much faster in natural river systems compared to canals. For example, the tubenose goby (*Proterorhinus marmoratus*), a fish species native to the Danube River and recently invading the Rhine River, needed eight years to pass the 171 km long Main-Danube canal (Schadt 2000), but only three years to reach the 895 km distant Rhine Delta in the Netherlands (Tien et al. 2003). However, the barrier effect of such monotonous canals with negligible low flow velocity seemed to be species-specific. While rheophilic specimens terminated their migrations on average at maximum distances of 6–8 km (range 0.5–15 km), no obstructing effects could be observed for eurytopic species, like bleak, common bream, silver bream, roach, and perch. However, possible barrier effects might be hidden by the widespread distribution of eurytopic fish.

Therefore, population genetic analyses have been performed to detect limited gene flow as an indication of restricted fish migrations. Four widespread, eurytopic cyprinids were selected for a population genetic study: common bream, silver bream, roach, and rudd. At the same nine sites, a minimum of 30 specimens each was collected of all four species (details in Wolter 1998, 1999b). Two sites were situated in the urban part of Berlin (Fig. 4), and two reference sites enclose a 155 km long free flowing stretch of the Oder River without any barriers. Thirteen enzyme systems coded by 25 loci were analysed and revealed a high genetic variability of the species examined (details in Wolter 1998, 1999b). The following mean values (± standard error) of intraspecific genetic variability were calculated: common bream (9 subpopulations) percentage of polymorphic $P_{95} = 21.8 \pm 2.1\%$, average observed heterozygosity $H_{obs} = 0.098 \pm 0.010$, average expected heterozygosity $H_{exp} = 0.083 \pm 0.008$; silver bream (9) $P_{95} = 17.8 \pm 1.2\%$, $H_{obs} = 0.082 \pm 0.006$, $H_{exp} = 0.074 \pm 0.006$; roach (9) $P_{95} = 22.2 \pm 2.6\%$, $H_{obs} = 0.091 \pm 0.010$, $H_{exp} = 0.086 \pm 0.008$; and rudd (7) $P_{95} = 17.1 \pm 2.1\%$, $H_{obs} = 0.086 \pm 0.009$, $H_{exp} = 0.079 \pm 0.010$.

The unbiased genetic distances according to Nei (1978) between sites ranged from 0.000–0.037 in common bream, 0.001–0.054 in silver bream, 0.000–0.040 in roach and 0.000–0.044 in rudd. Within rivers between 8.1% (common bream) and 17.4% (rudd) of the genetic variability was attributable to differences between subpopulations, while more than 80% of the observed total genetic variability was due to individual variability within subpopulations. Summarising the results of non-hierarchical F-statistics, the theoretical gene flow between neighbouring samples was restricted in a species-specific manner. The samples from the reference river behaved as one panmictic unit inhabiting a 155 km long Oder river stretch. In contrast, the population genetic structure of the subpopulations from the two urban sites indicated a considerable habitat fragmentation.

In general, two populations are considered as isolated or panmictic respectively, if the theoretical gene flow between them is less than one or more than four effective migrants, i.e. immigrating

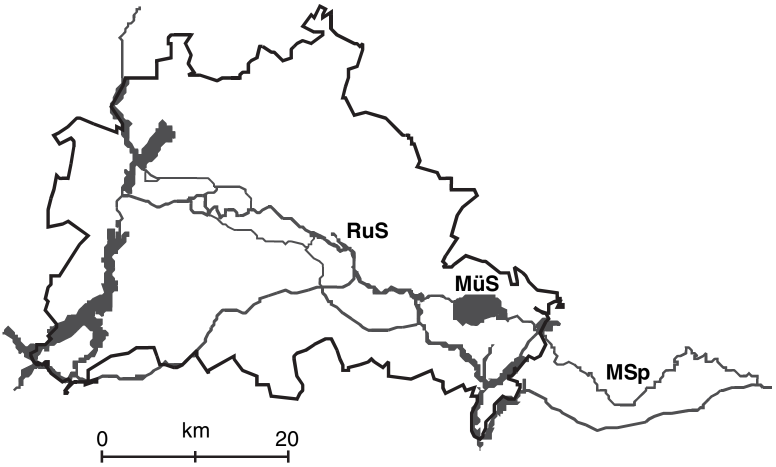

Fig. 4 Location of the sampling sites in two urban flushed lakes, Rummelsburger (RuS) and Müggelsee (MüS) and in the Spree River before entering Berlin

Table 4 Estimated number of effective migrants per generation between neighbouring sites (in parentheses: geographical distance in km / number of weirs between). For sites see Fig. 4

Species	MSp / MüS	MüS / RuS
	(13 / 0)	(13 / 0)
Common bream	5.2	6.3
Silver bream	1.8	10.6
Roach	6.9	3.7
Rudd	0.8	3.0

active spawners per generation (Slatkin & Barton 1989). In the cyprinid species studied, the criteria for a panmictic population will be fulfilled at one to two effective migrants per year only, due to the generation intervals of 2–3 years in roach, 3–4 years in silver bream and rudd, and 4–5 years in common bream. The calculated theoretical gene flow indicated significantly reduced migrations between the urban, channelized river stretch and the more natural Spree River before entering Berlin (MSp, compare Fig. 4) in silver bream and rudd (Table 4).

The value observed in rudd was the absolutely lowest theoretical gene flow of all: 0.8 effective migrants per generation roughly correspond to one spawner every five years entering the urban stretch from upstream rural parts. In addition, roach and rudd subpopulations showed a substantially reduced gene flow in the urban stretch between the sites MüS and RuS (Table 4, for sites see Fig. 4). The observed gene flow pattern did not correspond with geographical distances between sites. The 13 km long channelized river stretch between MüS and RuS restricted the theoretical gene flow similarly to the 155 km long reference stretch in the Oder (3.6 effective migrants per generation between the most upstream and downstream ends in common bream, 3.3 in roach, 10.6 in silver bream). This confirms the conclusions from presence-absence data by Wolter & Vilcinskas (1998b) suggesting a barrier effect of canals and channelized urbanized water stretches. Similar observations were reported by Guinand et al. (1996) from a study of chub in the Rhône basin. They found a strong correlation between genetic and geographic distance in chub from the natural parts of the Rhône River, but no correlation between both distances in chub from the regulated lower Rhône. Mean heterozygosity should increase downstream with absolutely increasing populations of spawners. In contrast, at the most downstream situated site in the urban area of Berlin (RuS) the lowest genetic variability was detected in all four species: in common bream $P_{95} = 16\%$, $H_{obs} = 0.087$; in silver bream $P_{95} = 12\%$, $H_{obs} = 0.049$; in roach $P_{95} = 16\%$, $H_{obs} = 0.057$; and in rudd $P_{95} = 12\%$, $H_{obs} = 0.067$. This loss of genetic diversity was interpreted as an effect of urbanization resulting from both, limited recruitment success and related genetic bottlenecks in urban waters, and restricted individuals exchange. The population genetic studies underlined the barrier effects for fish migrations caused by urbanized water bodies.

Conclusions

In developed urban areas with improved waste water treatments, the water quality is rarely the limiting factor for fish abundance and distribution, but the structural degradation of essential habitats is centrally important (Wolter et al. 2003). Essential habitat structures for fish become bottlenecks and limit fish spawning, recruitment or productivity and therefore, habitat degradation has to be considered as one principal factor of how urbanization impacts fish. The effects on fish assemblages becomes further intensified by altered migration abilities restricting individuals exchange as well as the accessibility of compensatory habitats in the watershed.

It has been argued, that at places where urban development is virtually complete and biological condition at its worst, rehabilitation efforts are unlikely to much improve biological condition

(Booth et al. 2004). However, the findings mentioned above give opposite evidence. If at a very high level of artificial embankment a further reduction of the remaining 10% structured habitats causes a significant decline of fish, then we may also infer that the rehabilitation of 10–20% of the bank line might significantly improve fish abundance and diversity. At least modest improvements seem fully achievable. Improvements in heavily degraded areas can also reduce downstream effects and rehabilitate downstream reaches.

Research needs to both assess the quantity of structural diversity and habitat patterns required to sustain a productive and diverse fish community, and identify the most efficient, technical solutions and measures to improve habitat quality of urban waters for fish by meeting their multiple human uses and social services.

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