ENVIRONMETRICS
Environmetrics (2008)

(www.interscience.wiley.com) DOI: 10.1002/env.948

Spatial metrics and methods for riverscapes: quantifying variability in riverine fish habitat patterns

Céline Le Pichon[1*,†], Guillaume Gorges[1], Jacques Baudry[2],
François Goreaud[3] and Philippe Boët[4]

[1] *Cemagref—HBAN, Parc de Tourvoie, BP44, 92163 Antony, France*
[2] *INRA SAD—Armorique, 65 route de St-Brieuc, CS84215, 35042 Rennes, France*
[3] *Cemagref—LISC, 24 Avenue des landais, 63172 Aubière, France*
[4] *Cemagref—EPBX, 50 avenue de Verdun, Gazinet, 33612 Cestas, France*

SUMMARY

Defining the optimal configuration of all habitats required during a life cycle, called vital habitat, is a necessary step for effective management of riverine fishes and restoration of river habitats. Landscape ecology provides many metrics and methods to study the composition and configuration of habitats, but they need to be adapted for fishes in river environments or riverscapes. For example, hydrographic distance seems more appropriate than Euclidean distance for measuring distances between vital habitats in riverscapes. We adapted some metrics to assess habitats patterns of a threatened cyprinid species (*Barbus barbus*) for natural and artificial riverscapes of the Seine river, France. Composition metrics provided essential quantification of the relative abundance of the vital habitats, whereas configuration metrics were relevant to quantify their spatial arrangement and spatial relationships. Nearest-neighbor hydrographic distance was useful to evaluate the influence of flow variability in the natural riverscape, but was not relevant to discriminate the artificial riverscape from the natural one. Conversely, a proximity index revealed high fragmentation in the artificial riverscape. Spatial habitat relationships between feeding and resting habitats, evaluated with a moving window analysis, provided a map of daily activity patches and emphasized the gaps in the biological continuity of the riverscape. The spatial metrics and methods we adapted to the particularities of the Seine river allowed us to detect natural and artificial variability in fish habitat patterns. They should help in evaluating impacts of habitat alteration and isolation and prioritize preservation and restoration policies in human-impacted rivers. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: GIS mapping; spatial metrics; proximity index; habitat restoration; Barbus barbus

1. INTRODUCTION

Most of the largest river systems in the northern hemisphere are affected by longitudinal and lateral fragmentation and by water regulation (Dynesius and Nilsson, 1994). This is particularly true for

---

*Correspondence to: C. Le Pichon, Cemagref—HBAN, Parc de Tourvoie, BP44, 92163 Antony, France.
†E-mail: celine.le-pichon@cemagref.fr

Received 22 June 2007
Accepted 15 July 2008

European rivers (Petts, 1989) and one of the most severely impaired is the Seine river, which is intimately linked with the megalopolis of Paris (Boët *et al*., 1999). In such a human-impacted riverine ecosystem, fragmentation and the homogenization of aquatic habitats are major threats to stream fish assemblages, which often exhibit declining species richness and low population and recruitment densities (Schiemer and Spindler, 1989; Jurajda, 1995; Belliard *et al*., 1999). These alterations induce a loss of structural complexity and have drastic effects on availability, size, and spatial distribution of vital habitats required for different life stages and activities (Fischer and Kummer, 2000; Lonzarich *et al*., 2000).

Because stream fishes use different patches of vital habitats during daily movements and seasonal migrations, spatial habitat relationships, such as complementation (spatial proximity of non-substitutable resources, also called complementarity), are important to maintain viable populations (Dunning *et al*., 1992). Dams and weirs not only have blocked longitudinal migratory pathways of many well-known diadromous species (sturgeons and salmons) but also have impacted non-diadromous species with long-distance spawning migrations such as rheophilic cyprinids (preference for fast moving water) (Baras, 1994; Ovidio and Philippart, 2002). Fragmentation increases the risk of extinction because it reduces (i) patch colonization, as fish recolonization rates are influenced by the distance from source populations (Detenbeck *et al*., 1992; Lonzarich *et al*., 1998) and (ii) local fish population size (Morita and Yamamoto, 2002). In addition, water regulation disrupts the natural range, timing, and duration of low and high flow events, and the geomorphic processes that create the ever-changing mosaic of aquatic habitats (Junk *et al*., 1989; Richards *et al*., 2002).

For stream fishes, guidelines based on landscape ecology have been proposed for more effective management and conservation (Fausch *et al*., 2002; Rabeni and Sowa, 2002), although there are few practical applications. The use of geographic information systems (GIS)-based approaches is now relatively common for mapping essential fish habitats (Booth, 2001) and has increased the capacity for spatial analysis of freshwater ecosystems (Fisher and Rahel, 2004). However there is still a lack of quantitative measures to compare the spatial structure and connectivity of habitats in different lotic systems (Cooper *et al*., 1997). Connectivity allows for individuals of a species to move from one habitat patch to another habitat patch. Connectivity is a highly studied concept in terrestrial landscape ecology because it plays a crucial role in population persistence (Fahrig and Merriam, 1994). Because it is difficult to evaluate animal movements with empirical movement data, they are often inferred from landscape pattern, which is a surrogate for biological connectivity. Distance-based and area-based metrics, matrix permeability, and species behavior are the main approaches to model connectivity of an entire landscape or habitat patches (Tischendorf and Fahrig, 2000; Moilanen and Hanski, 2001). In aquatic landscapes or riverscapes (Ward, 1998), classical spatial analysis using Euclidean distance is not appropriate and alternative distance measures are needed (Rathbun, 1998; Jensen *et al*., 2006).

In this context, metrics and spatial analysis methods have been adapted to the particularities of rivers: linear and irregularly shaped and dominated by unidirectional water flow. The main objective of our approach was to quantify spatial patterns of fish habitat patches and fish movement at nested scales (patch of vital habitat, daily activity area, sub-population area) (Le Pichon *et al*., 2006a).

This paper examines (i) the use of spatial metrics and methods to quantify the composition and configuration of riverscapes for riverine fish and (ii) the capacity of these metrics to detect the effects of flow variability and human alterations on fish habitat patterns. The metrics were calculated for the vital habitats of a cyprinid species (*Barbus barbus*), affected by habitat alteration and flow regulation in two reaches of the river Seine.

2. MATERIAL AND METHODS

2.1. Study area

The 5th order (Strahler, 1957) alluvial floodplain La Bassée of the Seine river is 100 km upriver from Paris (Figure 1 A). Our study was conducted on two reaches of this 50 m-wide river, each limited upstream and downstream by navigation weirs. The 12 km-long artificial reach (AR) resulted from re-sectioning of the meandering channel in the lower part of the floodplain, followed by rectification in the 1970's. Artificial water bodies connected with the main channel were formed by cut-off meanders and abandoned gravel pits (Figure 1 D). The 22 km-long natural reach (NR) is situated 30 km upstream from the AR. It has few engineering modifications because it was bypassed with a shipping canal. Many natural backwaters occur along the river course, but their connection to the main channel depends on discharge (Figure 1 B, C).

2.2. GIS-based vital habitats mapping

Two GIS maps of the NR were made for discharges near the median (70 m^3/s) and the dry 5-year average flows (38 m^3/s) and covering the spawning period (April–June, gauging station of Pont-sur-

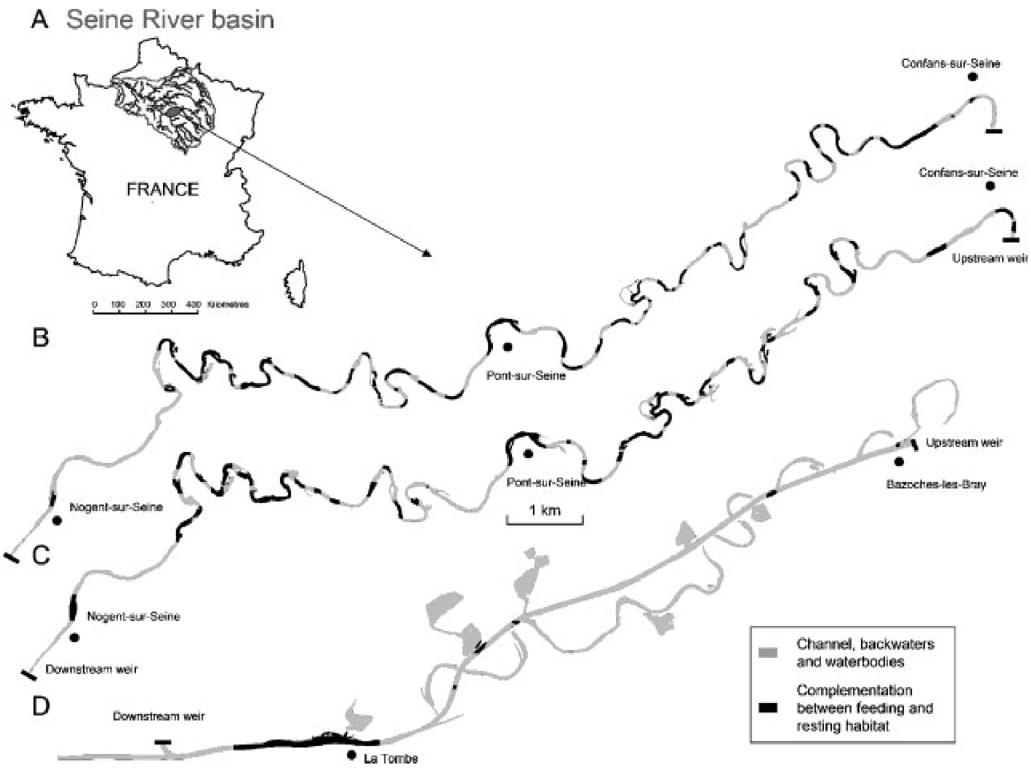

Figure 1. (A) Geographical location of the Seine river basin, France and the ıLa Bassééı alluvial floodplain. (B) natural reach at 38 m3/s; (C) natural reach at 70 m3/s; (D) artificial reach at 80 m3/s. (B–D) Illustration of the moving window analysis using a 120 m squared window to identify complementation between feeding and resting habitats for the different riverscapes

Seine, 1979–2004) (Figure 1). Channel, lateral backwaters boundaries, and environmental variables were located to within 1 m accuracy, with Trimble Pathfinder ProXRS GPS receiver, during a 6 day period in June 2001 for the discharge $70\,\mathrm{m}^3/\mathrm{s}$. Channel boundaries, lateral backwaters, depth < 1 m, and current velocities were modified for the discharge $38\,\mathrm{m}^3/\mathrm{s}$ using field surveys (1996, 2004) and digital orthophotographs (2000) available at this discharge. Few variations in the river morphology were observed between 1996 and 2004 allowing their complementary use for creating the vital habitats maps. One map of the AR was made for the median discharge $80\,\mathrm{m}^3/\mathrm{s}$ (gauging station of Bazoches-les-Bray, 1999–2005) because embankments and constant water level for navigation slightly affect the flooded areas and current velocities. For this reach, channel, artificial water bodies' boundaries, and environmental variables were mapped during a 4-day period in June 2001 and a 3-day period in September 2001. We used the GIS program ArcInfo® to intersect data layers according to species habitat preferences in order to create three vital habitat maps (Table 1) (Le Pichon *et al*., 2006a).

2.3. Computing 2-D oriented hydrographic distance

Calculation of non-Euclidean distance in river networks and estuaries is mainly computed using a network of line segments (Little *et al*., 1997; Torgersen and Close, 2004; Ganio *et al*., 2005; Isaak *et al*., 2007). This approach is difficult to apply to large rivers with connected waterbodies and for riverine fishes moving longitudinally and laterally. An alternative approach, used by Jensen *et al*. (2006) for estuaries, calculates distance in irregularly shaped and heterogeneous environments with the presence of barriers. It uses a cost-weighted distance function, originally proposed by Knaapen *et al*. (1992), known as least-cost modeling (Adriaensen *et al*., 2003). This raster function is based on an eight-neighbor-cell algorithm which allows for movements along the diagonals with a multiplication by the square root of two. The total distance is the minimal sum of the cell size multiplied by the cost assigned to the cell. To calculate hydrographic distance, aquatic habitats were given a cost of one while terrestrial environment (barriers for riverine fishes) is given an infinite cost. We used this approach and added the capability to compute upstream and/or downstream hydrographic distance based on the orientation of the river (Le Pichon *et al*., 2006a). For our approach, we developed a specific program ANAQUALAND 2.0 (Le Pichon *et al*., 2006b) that uses a sparse approximation technique (Saad and Sosonkina, 1999) on large raster data maps in which only a small portion represents the river (1–2% of

Table 1. Selected features of each GIS layer used to build the maps of vital habitat for barbel and nase

GIS layers in vector data structure (polygons)	Resting	Feeding	Spawning
Current velocity[a]: selected classes	V_1, V_2, V_3	V_3,V_4,V_5	V_3,V_4,V_5
Channel, cut-off meander, gravel-pit depth < 1 m: selected bottom substrate		sand, gravel, sand/gravel	gravel, sand/gravel
Banks of channel, cut-off meander, gravel-pit depth <1 m, slope$<45°$: selected bottom substrate	block	sand, gravel, sand/gravel, block	gravel, sand/gravel
Banks of channel, cut-off meander, gravel-pit depth <1 m, slope $> 45°$: selected bottom substrate	block		gravel, sand/grave*l*
Woody debris and Log jam	all		
Riparian cover: roots as shelters	2 m wide		
Natural water bodies connected to main channel	all		

[a] Current velocity in five classes.

V_1: no current velocity; V_2: V<0.2 m/s; V_3: 0.2 m/s <V<0.5 m/s; V_4: 0.5 m/s <V<1 m/s; V_5: V > 1 m/s.

total cells). We chose a 1 m cell size to preserve the sharpness and connectedness, especially narrow resting habitats such as shelters (woody debris or rooted bank), of the initial vector data structure.

2.4. *Composition and configuration metrics*

For river features and patches of vital habitat, we calculated the total and median areas, and the number of patches. Each patch of vital habitat was located in the reach by its hydrographic distance from the upstream edge of the patch to the upstream weir using ANAQUALAND 2.0. The fragmentation of each vital habitat was evaluated with the median nearest-neighbor hydrographic distance and a modified proximity index (Le Pichon *et al*., 2006a). The nearest-neighbor hydrographic distance for a patch of vital habitat was calculated as the edge-to-edge distance along the 2-D river course between a patch and its nearest upstream neighbor. We calculated the proximity index Px (Equation 1), modified from Gustafson and Parker (1994), in which the Euclidean distance is replaced by the hydrographic distance and the search radius is replaced by the search distance:

$$P_{X(Hj/H)} = \sum_{s=1}^{n} \frac{\text{Area}(H_{js})}{(D_{js})^2} \tag{1}$$

where n is the number of vital habitat patches s whose edges were within a search distance of the patch H_j, Area(H_{js}) is the area of patch H_{js}, and D_{js} is the hydrographic distance between patch H_{js} and H_j. The search distance varied from 1 to 2 400 m to take into account movements at the scale of home range size (200–2400 m) (Baras, 1997). A search distance of 100 m meant that all the patches located within 100 m upstream of the upstream edge of the focal patch and 100 m downstream of the downstream edge of the focal patch are taken into account in the index. This dimensionless index increases as patches of the corresponding vital habitat become less isolated and the vital habitat becomes less fragmented in distribution (Gustafson and Parker, 1994).

2.5. *Habitat spatial relationships*

Adult barbel shows diel activity patterns; using mainly resting habitat during the day and feeding habitats at dusk and dawn (Baras, 1997). The distances between these two complementary habitats vary around 60–300 m according to the season and the habitat structure (Baras, 1992). We used two methods to evaluate spatial habitat relationships and tested them with the complementation between feeding and resting habitats. The proximity of resting habitat from each patch of feeding habitat was evaluated with a modified proximity index $Px\ (F_j/R)$ (Equation 2), where n is the number of resting patches s, the edges of which are within a search distance of the patch F_j, Area(R_{js}) is the area of patch R_{js}, and D_{js} the distance between patch R_{js} and F_j. Using the minimum range of distance moved by barbel in a residence area (Baras, 1997), we selected the search distance of 60 m to calculate the proximity of the resting habitat from each patch of feeding habitat. This index allowed the detection of an isolated feeding habitat patch from a complex of resting habitat patches.

$$P_{X(Fj/R)} = \sum_{s=1}^{n} \frac{\text{Area}(R_{js})}{(D_{js})^2} \tag{2}$$

In addition to the proximity index, we developed global maps of complementation patches. We applied a moving-window method derived from image processing that characterizes the landscape

DOI: 10.1002/env

structure in a squared window around each pixel (Schermann and Baudry, 2002). In practice, a spatial index is computed in a square window and its value is allocated to the central pixel. The window is moved systematically through all pixels of the river and a new map of the spatial index is produced. The proportion of feeding (and resting) habitats in a square window of 120 m (60 m from the central pixel) were computed using the CHLOÉ 3.1 software developed by Baudry *et al*. (2005). Complementation areas were defined by the presence of at least 280 m^2 of feeding habitat and 140 m^2 of resting habitat in the 120 m square window; these thresholds were based on expert advice in the absence of data on the ratio between these two vital habitats. We converted these thresholds into percentages according to the window size, and a complementation map was created by overlaying the $\geq$2% proportion feeding habitat map on the $\geq$1% proportion resting habitat map (Le Pichon *et al*., 2006a).

2.6. *Statistical analysis*

We assumed that comparisons between the three riverscapes were valid because their extent and cell size were similar (Hargis *et al*., 1998). Composition and isolation metrics between reaches were compared with the Wilcoxon rank sum (Mann–Whitney) Test for two independent samples using a pairwise procedure (R-Package). We calculated pairwise comparisons between habitats and reaches with corrections for multiple tests using the adjustment methods of Benjamini and Yekutieli, based on the false discovery rate. The null hypothesis that the two distributions were the same was rejected at p-value < 0.05. Comparisons between the proximity indexes of three riverscapes were possible for similar search distances (Hargis *et al*., 1998).

3. RESULTS

3.1. *Riverscape structure*

The quantification of riverscape features: floodplain, channel, natural backwaters, and artificial water bodies provided an estimation of the relative importance of lotic versus lentic habitats. The floodplain length and channel width of the two reaches were quite similar, however the channel length of the AR was half the length of the NR (12 km and 22 km, respectively) emphasizing the rectification of the former (Figure 1). Total area of the channel in the NR represented from 88.5 to 95.7%, depending on discharge, of the river's flooded area, but only 44.7% of the flooded area in the AR (Table 2). The percent of backwater area increased with increasing discharge from 4.3 to 11.5% of flooded area in the NR; mainly due to a doubling of the number of connected backwaters (Table 2). The ratio between backwater area at the two discharges showed that backwaters which became connected at 70 m^3/s (i.e., permanence of 0%) were observed over the entire reach, whereas those which areas are the same at the two discharges (i.e., permanence of 100%) were in the downstream part of the reach (Figure 2). In the AR, water bodies represented the main part of the flooded area and were dominated by large gravel pits and cut-off meanders, as indicated by a very high median area compared to the median area of natural backwaters (Table 2). These results illustrate the shifting nature of the NR with its varying number of connected backwaters, depending on discharge, and the lentic nature of the AR with its large artificial water bodies.

3.2. *Vital habitats*

Because feeding and spawning habitats of the barbel and the nase were located in the main channel, we calculated their total area as a percentage of the channel area (Table 2). The total area of feeding habitat

Table 2. Comparison of composition and fragmentation metrics calculated for river features and vital habitats for barbel and nase. In the same column, the vital habitats sharing at least one common superscript are not significantly different at $p < 0.05$ (Wilcoxon rank sum test)

Riverscape	Features and vital habitat	Total area (m^2)	Total area (% channel area)^1 (% flooded area)^2	Median area (m^2)	Number of patches	Median nearest neighbor distance (m)
Natural reach 38 m^3/s	Channel	1 295 360	95.7^2	—	—	—
	Backwaters	58 290	4.3^2	795	29	—
	Resting habitat	140 616	10.3^2	170^b	187	31^d
	Feeding habitat	226 620	17.5^1	$1\ 023^a$	85	74^c
	Spawning habitat	149 159	11.5^1	994^a	50	98^c
Natural reach 70 m^3/s	Channel	1 296 260	88.5^2	—	—	—
	Backwaters	168 347	11.5^2	890	66	—
	Resting habitat	204 022	14.0^2	176^b	193	37^d
	Feeding habitat	138 846	10.7^1	$1\ 114^a$	58	151^b
	Spawning habitat	85 416	6.6^1	$1\ 490^a$	24	371^a
Artificial reach 80 m^3/s	Channel	875 080	44.7^2	—	—	—
	Water bodies and backwaters	1 080 120	55.3^2	44 163	20	—
	Resting habitat	116 618	5.9^2	4^c	209	76^{abc}
	Feeding habitat	22 640	2.6^1	240^b	25	133^{abc}
	Spawning habitat	20 727	2.4^1	209^b	25	143^{abc}

ranged from 2.6% in the AR to 10.7 and 17.5% in the NR with the higher percentage at 38 m^3/s (Table 2). The lower total area in the AR was a consequence of both a reduction of area patches (p-value < 0.01, Table 2) and a low patch number (25). In the NR, the lower percentage of patch area at 70 m^3/s was attributed to a lower number of patches (58 vs. 85), although patch area was not

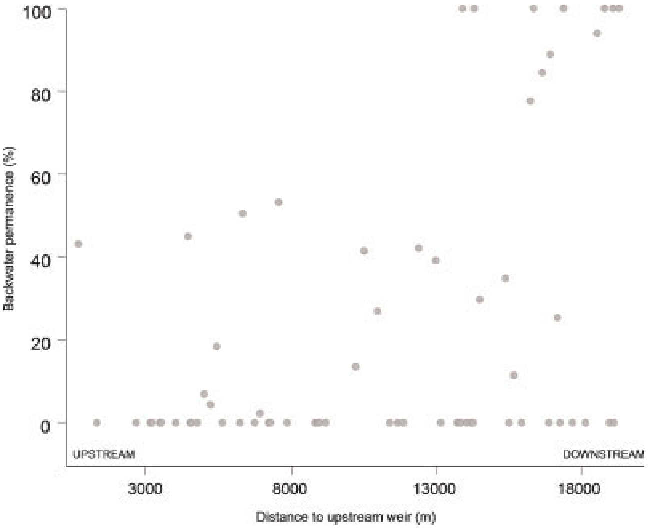

Figure 2. Permanence of backwaters from the upstream to the downstream part of the natural reach. Permanence is the ratio between the backwater area at 38 m^3/s and the backwater area at 70 m^3/s

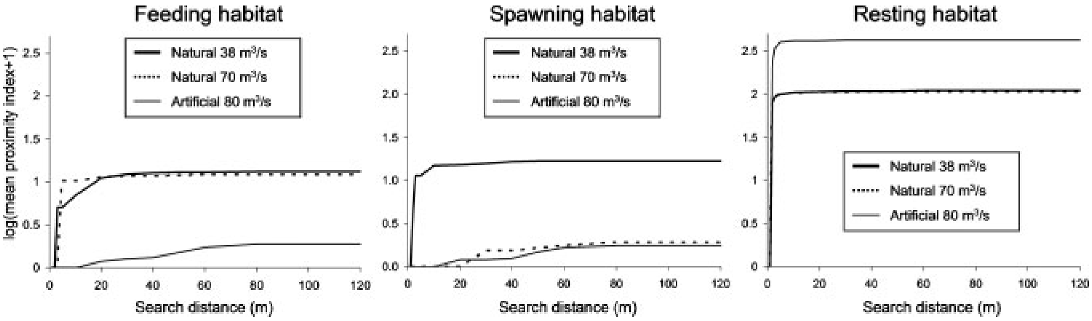

Figure 3. Evolution of the mean proximity index with increasing search distance for the vital habitats in the three riverscapes

significantly different (Table 2). Fragmentation of feeding habitat, evaluated with the nearest-upstream neighbor distance, was different between the two discharges ($p < 0.05$, Table 2) for the NR. This index was not relevant to discriminate the fragmentation in the AR compared to the NR. In contrast, the relationship of mean proximity indexes with increasing search distance showed that feeding habitat in the AR reached a low sill, indicating a fragmentation higher than in the NR at both discharges (Figure 3). In addition, the distribution of proximity indexes (search distance: 60 m) was significantly different between the NR at 38 m^3/s and the AR for feeding habitats, underlying a greater fragmentation in the AR ($p < 0.05$, Figure 4).

The total area of spawning habitat ranged from 2.4% in the AR to 6.6 and 11.5% in the NR with the higher percentage at 38 m^3/s (Table 2). For this habitat type, we observed composition metrics similar to the feeding habitat except for a lower number of patches at 70 m^3/s in the NR (24), which was equal to the number in the AR. In the same way, the mean proximity index curve at 70 m^3/s revealed a fragmentation pattern similar to that observed for the AR (Figure 3). The distributions of proximity indexes (search distance: 60 m) were significantly different between the NR at 38 m^3/s and the AR, but not different between the NR at 70 m^3/s and the AR.

The total area of resting habitat ranged from 5.9% in the AR to 10.3 and 14% in the NR with the higher percentage at 70 m^3/s (Table 2). The composition of this habitat was different from the other vital habitats in the AR; it had the greatest number of patches (ca. 200) and the lowest patch area ($p < 0.05$, Table 2). The highest sills of the mean proximity index curves were reached for this habitat indicating a low degree of fragmentation (Figure 3). The distributions of proximity indexes (search distance: 60 m) were significantly different in the AR, with higher values than in the NR at both discharges (Figure 4).

3.3. Complementation between feeding and resting habitats

The proximity of resting habitat patches to feeding habitat patches along the river course underlined the longitudinal variability at the habitat patch scale (Figure 5). The gaps in the longitudinal sequencing of the proximity index were explained by an absence of feeding habitat patch, especially in the AR, while others were related to feeding habitat patches isolated from a complex of resting habitat patches (Figure 5). In the NR at 70 m^3/s, it was noticeable that many large feeding habitat patches were located in the downstream part of the reach while high proximity indexes were mostly located in the upstream part of the reach (small distances to upstream weir). However, the distributions of these proximity

DOI: 10.1002/env

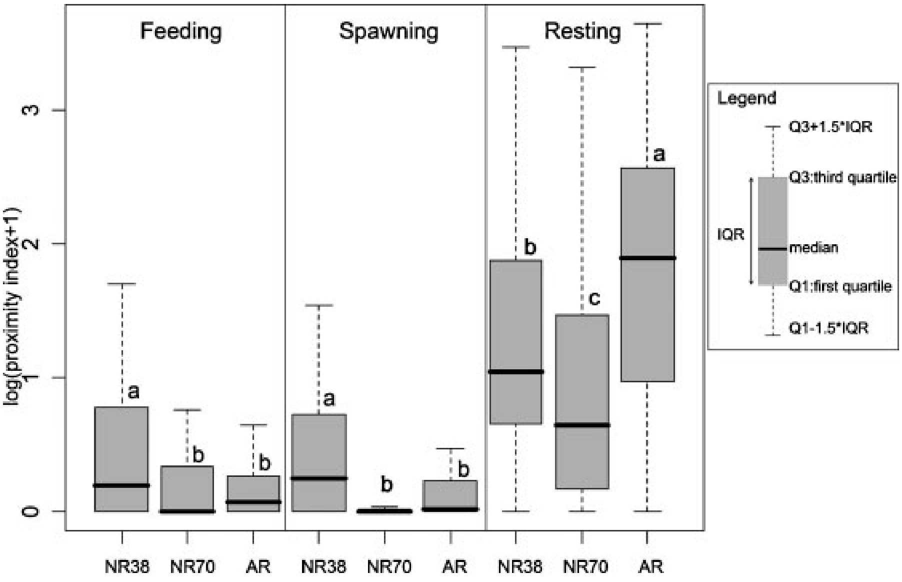

Figure 4. Box plot of the proximity indexes (search distance: 60 m) calculated for the vital habitats in the three riverscapes. For one vital habitat, the riverscapes sharing at least one common superscript are not significantly different at $p < 0.05$ (Wilcoxon rank sum test). NR38: natural reach at 38 m^3/s, NR70: natural reach at 70 m^3/s, AR: artificial reach

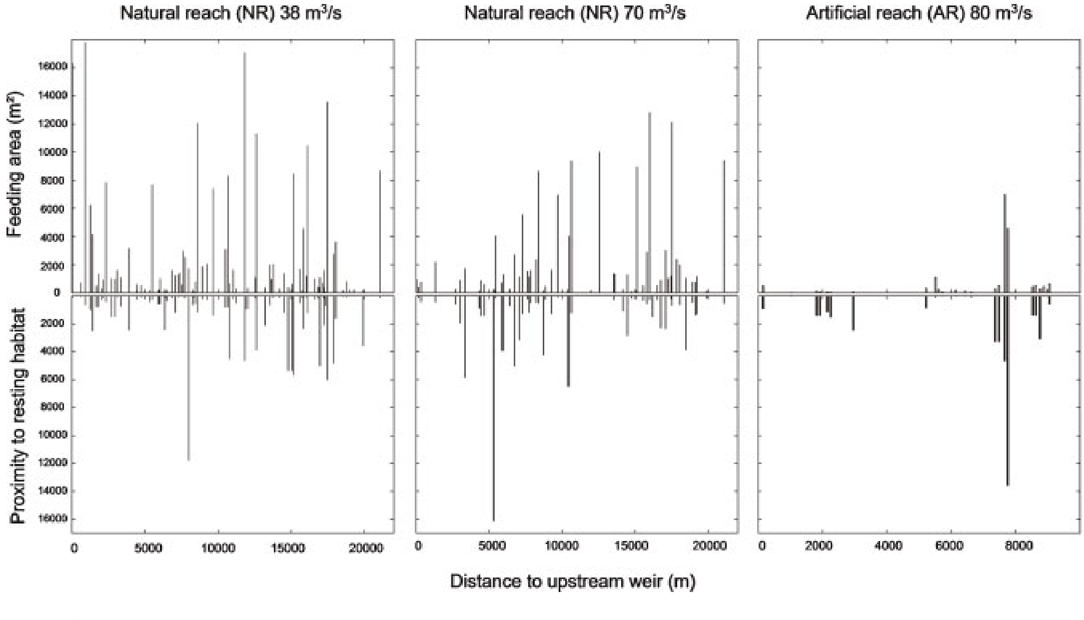

Figure 5. Patch areas of feeding habitat along the river course from upstream to downstream part of each riverscape, and the proximity index of resting habitat from each patch of feeding habitat (search distance: 60 m)

DOI: 10.1002/env

indexes were not significantly different (Wilcoxon rank sum test, $p > 0.05$) between the three riverscapes.

The moving window analysis allowed the identification of complementation areas in which complementation could occur between both feeding and resting habitats (Figure 1). We identified differences between the three riverscapes for median patch area calculated on the complementation maps (Table 3). The estimates of total complementation area increased from 9.0% of the flooded area in the AR to 46.6% in the NR at 38 m^3/s. These differences were both related to a low number of complementation patches in the AR (11) compared to the NR (40–48), and a lower median patch area ($p < 0.01$, Table 3). In the AR, large gaps were observed in the re-sectioning part of the reach (Figure 1 D). The flow fluctuations in the NR influenced the number, sequencing and extent of the complementation patches (Figure 1 B, C).

4. DISCUSSION

4.1. Ability to detect fish habitat pattern

The composition and configuration metrics at the habitat and habitat patch scales revealed different aspects of the spatial organization of these habitats. The total area (in %) provides an estimate of the relative abundance of each vital habitat and the least abundant. Additional information would be required to identify the critical vital habitat, especially the minimum amount of vital habitat and the ratio between vital habitats that are needed to sustain an individual, a shoal, or a population. Using a spatially explicit simulation model, Fahrig (1998) shows that 20% is a threshold below which the configuration of breeding habitat plays an important role in explaining population size and persistence. In our study, the total area of each vital habitat in each riverscape was always under 20% of flooded area, indicating a potential role of vital habitat configuration on fish population. The number of patches associated with the median area of patches provided an evaluation of the fragmentation for the different riverscapes. A careful interpretation was necessary due to the linear shape of the riverscape and because a habitat patch cannot be larger than the width of the channel or the water bodies. A high number of relatively small patches, as is the case for resting habitat, is not an indication of a fragmented habitat because this habitat type consists of essentially small (log jam) and thin (channel bank) features. Nearest-neighbor distance allowed for a comparison between different discharges in the NR, but could not distinguish the highly fragmented AR compared with the NR. This is in accordance with

Table 3. Composition metrics calculated for complementation maps. A window size of 120 m is used for moving window analysis.

Complementation patch characteristic	Natural reach 38 m^3/s	Natural reach 70 m^3/s	Artificial reach 80 m^3/s
Total patch area (m^2)	630 494	530 177	175 315
Total patch area (% flooded area)	46.6	36.2	9.0
Median patch area	9 121^a	11 178^a	2 151^b
Number of patches	48	40	11

^{a,b}On the same row the riverscapes sharing at least one common superscript are not significantly different at $p < 0.05$ (Wilcoxon rank sum test) observations on simulated landscapes for which the nearest-neighbor distance is useful in differentiating inter-patch distances when fragmentation is low (Hargis *et al*., 1998). The nearest-neighbor distance is a simple distance metric that does not account for the amount of habitat patches within the neighborhood and considers only one neighboring patch. The mean proximity index detected the degree of fragmentation of each vital habitat, especially in the AR, because it is a distance-weighted area-based metric. Furthermore, it is a more relevant predictor of immigration rate because it considers areas that are potential sources of dispersers (Bender *et al*., 2003). The proximity index of resting habitats from feeding habitats provided a value for each existing feeding habitat patch, while the complementation map provided a representation at a different scale corresponding to daily activity areas. In addition, this map integrated both the quantities of habitats and the distance between them while the proximity index did not take into account the quantity of focal patches. Visualization of the extent of areas and gaps was informative about their configuration at the reach scale. This could be useful because the existence of aggregated resources may compensate for the negative effects of habitat loss by reducing dispersal mortality (Flather and Bevers, 2002).

4.2. *Ability to detect human alterations*

In highly degraded reaches in which re-sectioning of the meandering channel, embankment and flow regulation occurred simultaneously, most experts would expect there to be an absence of potential habitats for barbel. However, the use of metrics to quantify this and assess the composition and configuration of the remaining habitats was relevant for several reasons. First, composition metrics allowed us to determine how much less area there was of the remaining habitats in the AR compared to a natural channel of the same geomorphological type. In the La Bassée floodplain, the disequilibrium between lotic (feeding and spawning habitats) and lentic habitats in the AR was noticeable through the over-representation of man-made water bodies, which comprised 55% of the flooded area in the AR compared with only 5–11% for natural backwaters in the NR. The high fragmentation of lotic habitats was revealed both by the proximity index and the complementation area map. Knowledge of the composition and configuration of feeding and spawning habitats, which could be limiting vital habitats, is an essential step for identifying critical habitat (Rosenfeld and Hatfield, 2006).

4.3. *Ability to detect flow variability*

Each vital habitat varied markedly between low flow (38 m^3/s) and median flow (70 m^3/s). Lotic habitats (feeding and spawning habitats) increased with decreasing flow as opposed to lentic habitats (resting habitat and nursery habitat located in backwaters), which decreased with decreasing flow. At median flow, many shallow areas (<1 m) disappeared because of the steepness of the banks and increased the fragmentation of spawning habitat. This was observed by Tiffan *et al*. (2002) for rearing habitat of subyearling fall Chinook salmon on a large river (700 m width), which increased as flow decreased. Conversely, in first and second-order streams (1–5 m width) the decrease of flow reduces total lotic habitat (Herger *et al*., 1996; Hilderbrand *et al*., 1999) or modifies the juxtaposition of high quality foraging location for stream salmonids (Gowan and Fausch, 2002). The low number and smaller area of nursery/resting habitat with low flow resulted from less hydraulic connectivity of these lateral backwaters to the river channel (Amoros and Bornette, 2002). The response of a particular vital habitat with discharge is not easy to predict because each habitat is a combination of different variables.

Modeling approaches to map depth and current velocities exist but are mainly restricted to small scales (10^2 m) (Freeman *et al*., 2001), although laser telemetry (bathymetric LIDAR) has allowed for larger-scale studies (10^4 m) (Tiffan *et al*., 2002).

We caution against comparing fish sampling data from different flows or seasons because habitat availability varies in quantity and spatial location. Typically, the barbel seek spawning habitat in April–June, young-of-the-year grow in nursery habitat until September while adults feed in complementation areas from spring to autumn. Thus, dry years (38 m^3/s from spring to autumn) could enhance spawning but limit the access to backwaters used by juveniles the first year. This emphasizes the crucial role of quantifying vital habitat composition and connectivity at different flows, in relation to the seasonal movements of species, to understand fish distribution.

4.4. Management implications

Even though it is often impossible to restore even a portion of the natural fluvial dynamics in highly managed rivers, physical rehabilitation designs are still needed. To be effective in increasing fish abundance, population size and persistence, the appropriate spatial locations of restored vital habitat patches are required, especially in degraded reaches (Pretty *et al*., 2003; Rosenfeld and Hatfield, 2006). The metrics and methods proposed here could be helpful to quantify the ecological integrity of rivers and optimal habitat configuration in NRs, if viable fish populations occur there. They also permit comparisons between different riverscape configurations or restoration scenarios, which are essential to accurately assess the success of rehabilitation designs (Ward *et al*., 2002). The two proximity indexes provide an estimate of the relative value of a habitat patch with respect to vital habitat as well as complementary vital habitat. The identification of high value habitat patches contributes to setting preservation priorities, while identifying low value habitats helps set the spatial context of restoration priorities.

When vital habitats are sparse, complementation requires longer distance movements that could increase mortality risk due to predation or lead to higher energy expenses. Managers could benefit from the knowledge of proposed complementation maps to design policies that improve complementation of vital habitats and could increase local population size (Schrank and Rahel, 2004). The consequences of adding a habitat patch at a specific location could be quantified by calculating the proximity index to see if the habitat patch reduces fragmentation or building a complementation map to see the effect of the local restoration on the entire reach.

5. CONCLUSION AND PERSPECTIVES

We have shown that classical landscape ecology metrics and spatial analysis methods, adapted to the particularities of a river, allowed (i) the detection of different structures in underwater riverscapes in space and time and (ii) the quantification of habitat alteration in an AR compared to a NR of the same floodplain river. Stream ecologists and managers can benefit from the quantitative evaluation of impacts of habitat alteration and isolation in human-impacted rivers. We provided suggestions for identifying limiting vital habitats and appropriate spatial configurations of restored elements.

The ecological relevance of these methods to describe fish distributions should be tested and may require new sampling strategies. Some preliminary results, using a focal patch study (Brennan *et al*., 2002), have shown that the proximity index was correlated with barbel presence (Le Pichon *et al*., unpublished data). Isaak *et al*. (2007) have shown that the strongest predictor of nest occurrence in spawning patches of Chinook salmon was a connectivity index, which is a distance-weighted area-based metrics like the proximity index.

Applying these metrics to other aquatic species requires the knowledge of their vital habitat use and the required range of movements between them. Muti-species studies should investigate possible interactions between vital habitats of different species, because it would provide an assessment of whether or not the habitat restoration for a species at a specific location might affect the essential habitat patch for another species. A general application of these methods to rivers and streams also requires high resolution underwater data over large spatial scales and for different water levels. Riverscape mapping can be difficult depending on the depth range and the transparency of water. A combination of field mapping and remote sensing data must be adapted according to the constraints of the river and the labor and equipment costs. Despite these remaining practical challenges, a GIS-based riverscape approach and spatial metrics and methods provide a flexible framework for the study of the influence of habitat patterns on the spatial distribution of stream fishes.

ACKNOWLEDGEMENTS

We are grateful to William Fisher, Isabelle Durance, Steve Ormerod, Pierre Joly, and Jérôme Belliard for their insightful comments. Many thanks to Thierry Faure and Hughes Boussard for the implementation of ANAQUALAND 1.0 and 2.0. This work is supported by the Environmental Service of Ile-de-France (Diren) to restore the biological connectivity of the Seine river for fishes and the CNRS scientific program ''Piren-Seine.''

REFERENCES

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E. 2003. The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning* **64**: 233–247.

Amoros C, Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* **47**: 761–776.

Baras E. 1992. A study of time and space utilisation strategies in the common barbel *Barbus barbus* (L.). *Cahiers d'Ethologie* **12**: 125–442.

Baras E. 1994. Constraints imposed by high densities on behavioural spawning strategies in the barbel, *Barbus barbus. Folia Zoologica* **43**: 255–266.

Baras E. 1997. Environment determinants of residence area selection by *Barbus barbus* in the River Ourthe. *Aquatic Living Resources* **10**: 195–206.

Baudry J, Boussard H, Schermann N. 2005. Chloe 3.0: freeware of multi-scales analyses on ASCII raster files. Rennes, INRA, SAD-Armorique.

Belliard J, Berrebi-dit-Thomas R, Monnier D. 1999. Fish communities and river alteration in the Seine Basin and nearby coastal stream. *Hydrobiologia* **400**: 155–166.

Bender DJ, Tischendorf L, Fahrig L. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecology* **18**: 17–39.

Boët P, Belliard J, Berrebi-dit-Thomas R, Tales E. 1999. Multiple human impacts by the city of Paris on fish communities in the Seine river basin, France. *Hydrobiologia* **410**: 59–68.

Booth AJ. 2001. Are fisheries geographical information systems merely glorified mapping tools. In *Proceeding of the First International Symposium on Geographic Information Systems (GIS) in Fishery Science*, Nishida T, Kailola PJ, Hollingworth CE (eds). Fishery GIS Research Group: Saitama, Japan; 366–378.

Brennan JM, Bender DJ, Contreras TA, Fahrig L. 2002. Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. In *Integrating Landscape Ecology into Natural Resource Management*, Liu J, Taylor WW (eds). Cambridge University Press: Cambridge; 68–91.

Cooper SD, Barmuta L, Sarnelle O, Kratz K, Diehl S. 1997. Quantifying spatial heterogeneity in streams. *Journal of the North American Benthological Society* **16**: 174–188.

Detenbeck NE, DeVore PW, Niemi GJ, Lima A. 1992. Recovery of temperate-stream fish communities from disturbance: a review of case studies and synthesis of theory. *Environmental Management* **16**: 33–53.

DOI: 10.1002/env

Dunning JB, Danielson BJ, Pulliam HR. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* **65**: 169–175.

Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**: 753–762.

Fahrig L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* **105**: 273–292.

Fahrig L, Merriam G. 1994. Conservation of fragmented populations. *Conservation Biology* **8**: 50–59.

Fausch KD, Torgersen CE, Baxter CV, Li HW. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience* **52**: 483–498.

Fischer S, Kummer H. 2000. Effects of residual flow and habitat fragmentation on distribution and movement of bullhead (*Cottus gobio* L.) in an alpine stream. *Hydrobiologia* **422**: 305–317.

Fisher WL, Rahel FJ. 2004. Geographic information systems applications in stream and river fisheries. In *Geographic Information Systems in Fisheries*, Fisher WL, Rahel FJ (eds). American Fisheries Society: Bethesda, MD; 49–84.

Flather CH, Bevers M. 2002. Patchy reaction-diffusion and population abundance:the relative importance of habitat amount and arrangement. *American Naturalist* **159**: 40–56.

Freeman MC, Bowen ZH, Bovee KD, Irwin ER. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. *Ecological Applications* **11**: 179–190.

Ganio LM, Torgersen CE, Gresswell RE. 2005. A geostatistical approach for describing spatial pattern in stream networks. *Frontiers in Ecology and the Environment* **3**: 138–144.

Gowan C, Fausch KD. 2002. Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes* **64**: 139–153.

Gustafson EJ, Parker GR. 1994. Using an index of habitat patch proximity for landscape design. *Landscape and Urban Planning* **29**: 117–130.

Hargis CD, Bissonette JA, David JL. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology* **13**: 167–186.

Herger LG, Hubert WA, Young MK. 1996. Comparison of habitat composition and cutthroat trout abundance at two flows in small mountain streams. *North American Journal of Fisheries Management* **16**: 294–301.

Hilderbrand RH, Lemly AD, Dolloff CA. 1999. Habitat sequencing and the importance of discharge in inferences. *North American Journal of Fisheries Management* **19**: 198–202.

Isaak DJ, Thurow RF, Rieman BE, Dunham JB. 2007. Chinook salmon use of spawning patches: relative roles of habitat quality, size and connectivity. *Ecological Applications* **17**: 352–364.

Jensen OP, Christman MC, Miller TJ. 2006. Landscape-based geostatistics: a case study of the distribution of blue crab in Chesapeake bay. *Environmetrics* **17**: 605–621.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. In *International Large River Symposium*, Dodge DP (ed.). Canadian Special Publications of Fisheries and aquatic Science: Fisheries and Oceans Canada, Ottawa; 110–127.

Jurajda P. 1995. Effect of channelization and regulation on fish recruitment in a flood plain river. *Regulated River: Research and Management* **10**: 207–215.

Knaapen JP, Scheffer M, Harms B. 1992. Estimating habitat isolation in landscape planning. *Landscape and Urban Planning* **23**: 1–16.

Le Pichon C, Gorges G, Boët P, Baudry J, Goreaud F, Faure T. 2006a. A spatially explicit resource-based approach for managing stream fishes in riverscapes. *Environmental Management* **37**: 322–335.

Le Pichon C, Gorges G, Faure T, Boussard H. 2006b. Anaqualand 2.0: Modelling connectivity in riverscapes. Cemagref: Antony; http://mann.clermont.cemagref.fr/projets/Anaqualand

Little LS, Edwards D, Porter DE. 1997. Kriging in estuaries: as the crow flies, or as the fish swims? *Journal of Experimental Marine Biology and Ecology* **213**: 1–11.

Lonzarich DG, Lonzarich MR, Warren ML. 2000. Effects of riffle length on the short-term movement of fishes among stream pools. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 1508–1514.

Lonzarich DG, Warren ML, Lonzarich MRE. 1998. Effects of habitat isolation on the recovery of fish assemblages in experimentally defaunated stream pools in Arkansas. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 2141–2149.

Moilanen A, Hanski I. 2001. On the use of connectivity measures in spatial ecology. *Oikos* **95**: 147–151.

Morita K, Yamamoto S. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology* **16**: 1318–1323.

Ovidio M, Philippart JC. 2002. The impact of small physical obstacles on upstream movements of six species of fish-synthesis of a 5-year telemetry study in the river Meuse basin. *Hydrobiologia* **483**: 55–69.

Petts GE. 1989. Historical analysis of fluvial hydrosystems. In *Historical change of large alluvial rivers: Western Europe*, Petts GE, Möller H, Roux A-L (eds). John Wiley & Sons: Chichester; 1–18.

Pretty JL, Harrison SSC, Shepherd DJ, Smith C, Hildrew AG, Hey RD. 2003. River rehabilitation and fish populations: assessing the benefit of instream structures. *Journal of Applied Ecology* **40**: 251–265.

Rabeni CF, Sowa SP. 2002. A landscape approach to managing the biota of streams and rivers. In *Integrating landscape ecology into natural resource management*, Liu J, Taylor WW (eds). Cambridge University Press: Cambridge; 114–142.

Rathbun SL. 1998. Spatial modelling in irregularly shaped regions: kriging estuaries. *Environmetrics* **9**: 109–129.

Richards K, Brasington J, Hughes F. 2002. Geomorphic dynamics of floodplains: ecological implications and a potential modelling strategy. *Freshwater Biology* **47**: 559–579.

Rosenfeld JS, Hatfield T. 2006. Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* **63**: 683–698.

Saad Y, Sosonkina M. 1999. Distributed schur complement techniques for general sparse linear systems. *Journal of Science Computing* **21**: 1337–1356.

Schermann N, Baudry J. 2002. Analyse descriptive multi-échelle de la structure d'un paysage: application à la mosaïque d'occupation du sol d'un territoire agricole dans le bocage breton. *Géomatique* **12**: 169–186.

Schiemer F, Spindler T. 1989. Endangered fish species of the Danube river in Austria. *Regulated Rivers: Research & Management* **4**: 397–407.

Schrank AJ, Rahel FJ. 2004. Movement patterns in inland cutthroat trout (*Oncorhynchus clarki utah*): management and conservation implications. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 1528–1537.

Strahler AN. 1957. Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union* **38**: 913–920.

Tiffan KF, Garland RD, Rondorf DW. 2002. Quantifying flow-dependent changes in subyearling fall chinook salmon rearing habitat using two-dimensional spatially explicit modeling. *North American Journal of Fisheries Management* **22**: 713–726.

Tischendorf L, Fahrig L. 2000. On the usage and measurement of landscape connectivity. *Oikos* **90**: 9–19.

Torgersen CE, Close DA. 2004. Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (Lampetra tridentata) at two spatial scales. *Freshwater Biology* **49**: 614–630.

Ward JV. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* **83**: 269–278.

Ward JV, Malard F, Tockner K. 2002. Landscape ecology: a framework for integrating pattern and process in river corridors. *Landscape Ecology* **17**: 35–45.