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A Spatially Explicit Resource-Based Approach for Managing Stream Fishes in Riverscapes

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ABSTRACT / The article describes a riverscape approach based on landscape ecology concepts, which aims at studying the multiscale relationships between the spatial pattern of stream fish habitat patches and processes depending on fish movements. A review of the literature shows that few operational methods are available to study this relationship due to multiple methodological and practical challenges inherent to underwater environments. We illustrated the approach with literature data on a cyprinid species (*Barbus barbus*) and an actual riverscape of the Seine River, France. We represented the underwater environment of fishes for different discharges using two-dimensional geographic information system-based maps of the resource habitat patches, defined according to activities (feeding, resting, and spawning). To quantify spatial patterns at nested levels (resource habitat patch, daily activities area, subpopulation area), we calculated their composition, configuration, complementation, and connectivity with multiple spatial analysis methods: patch metrics, moving-window analysis, and least cost modeling. The proximity index allowed us to evaluate habitat patches of relatively great value, depending on their spatial context, which contributes to the setting of preservation policies. The methods presented to delimit potential daily activities areas and subpopulation areas showed the potential gaps in the biological connectivity of the reach. These methods provided some space for action in restoration schemes.

In human-impacted river corridors, the fragmentation and the homogenization of habitat conditions adversely affect the aquatic fauna. The structural modifications of river corridors are mainly induced by water management and other human activities (Ward 1998), which reduce the spatial and temporal heterogeneity of habitats. In addition, the river system is longitudinally and laterally divided into distinct, almost independent units (Pedroli and others 2002). These human activities impact the river corridor at several spatial scales: pollution at the local scale, channelization at the reach scale, and flow control at the catchment scale. Multiscale habitat alterations have various consequences on the habitats used by organisms, their population biology, and their movement capacities. The distribution of stream fishes is sensitive to these multiscale alterations of river corridors (Schiemer and others 1995; Boët and others 1999). Among these alterations, fragmentation and flow regulation reduce habitat size and quality within and next to the main channel (Rabeni and Jacobson 1993). Splitting habitats and creating barriers are known to isolate fish populations (Morita and Yamamoto 2002), increasing the risk of extinction by reducing the local population size or by disrupting pathways for migration (Baras and others 1994).

Because stream fishes have complex life cycles and movement behaviors, the spatial pattern of their various habitats affect the viability of populations. The life cycles of stream fishes might require distinct habitats for each development stage (larvae, young of the year, adult) and for each activity (feeding, spawning, resting) (Schiemer and others 1995; Baras 1997; Huber and Kirchhofer 1998). Recent works on stream fish movements have challenged the restricted movement paradigm (Gerking 1959) and have shown that some species considered as resident, like the common barbel (*Barbus barbus*) and the nase (*Chondrostoma nasus*), can

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move from 100 m up to several kilometers, depending on exploratory trips or seasonal activities (Gowan and Fausch 1996; Smithson and Johnston 1999; Lucas and Baras 2001). Therefore, large-scale spatial habitat patches relationships, such as complementation (spatial proximity of nonsubstitutable resources), sink/source relations, and neighborhood effects (Dunning and others 1992), can be critical factors for fish population dynamics (Schlosser 1995). Indeed, considering only the availability of one habitat is sometimes not sufficient to explain the spatial distribution of fishes (Freeman 1993): The spatial context of this habitat can be critical. Kocik and Ferreri (1998) improved the understanding of juvenile Atlantic salmon production when mapping the interspersion of spawning and rearing habitats.

Concepts of landscape ecology can be used to analyze the role of spatial patterns in river ecology. The patch-dynamics concept, considering how specific patch characteristics determine biotic and abiotic processes over various scales, was formalised in lotic systems by Pringle and others (1988) and Townsend (1989). The hierarchical patch-dynamics (HPD) concept (Wu and Loucks 1995), viewing ecological systems as nested and hierarchical mosaics of habitat patches, was used for fishes by Schlosser (1991, 1995). A better consideration of longitudinal discontinuities provides a conception of streams as a discontinuous mosaic of patches (Bretschko 1995; Ward and Stanford 1995). This conception also underlines the uniqueness of every reach of a river corridor (Poole 2002). Moreover, fish habitats are dynamic in the relation to longitudinal and lateral hydrodynamic interactions between the elements of the river corridor, which is consistent with the hydrological connectivity concept (Petts and Amoros 1996; Amoros and Bornette 2002). All of these concepts show the importance of embracing the entire, heterogeneous, dynamic, and continuous nature of the river corridor with its abrupt transitions, as pointed out recently by Fausch and others (2002).

River management for biological conservation of stream fishes involves the protection and rehabilitation of habitats and the restoration of the river continuum (Schiemer and Waidbacher 1992; Cowx and Welcomme 1998). Small-scale physical rehabilitation designs (100–1000 m) improving the heterogeneity of depth and current velocities can be ineffective to increase fish diversity because of an inappropriate location in degraded reaches (Pretty and others 2003). An inappropriate location means the isolation from other suitable habitats (complementation) or from a source of available colonizers (sink/source relationships). This assumption is supported by research showing that fish recolonization rates are influenced by the distance from source populations or by differences in the size or distribution of habitats (Detenbeck and others 1992; Lonzarich and others 1998). For example, artificial riffles built to ensure lithophilous spawning must be close to backwater habitats used as nurseries (Schiemer and Waidbacher 1992). The knowledge of movement rates and behaviors in the heterogeneous aquatic environment used by fishes to reach different habitats during the life cycle also contributes to a successful rehabilitation.

The main references to landscape ecology principles in stream studies are as follows: (1) the adoption of a "landscape scale" in streams (Lowe 2002) or (2) the use of terrestrial landscape parameters to explain the distribution of aquatic organisms (Kelly and others 1998; Watzin and McIntosh 1999). Only recently have articles outlined the usefulness of this discipline in the river corridor itself (Ward and others 2002; Wiens 2002) and the need to develop distinct fluvial landscape ecology (Poole 2002). The riverine landscape is increasingly viewed as a "riverscape," a term coined by Ward (1998). However, behind this term are numerous acceptations, depending on which ones, among the six central tenets of landscape ecology proposed by Wiens (2002), are explored. In particular, it could be an aquatic ecosystem within its catchment amenable to study over a wide range of scales (Allan 2004; Harris and Heathwaite 2005).

For stream fishes, guidelines based on landscape ecology have been proposed for more effective management and conservation research (Fausch and others 2002; Rabeni and Sowa 2002). However, practical applications of these concepts dealing with the influence of the spatial pattern of habitat on fish population dynamics remain isolated. Most of the classical approaches are typically site based, with selected sample units of 50–500 m assumed to be representative of the entire river and widely spaced along the river or catchment area. An incomplete view can result from such approaches, missing important phenomena at a larger scale, like the existence of a tributary or a barrier, which can play a role in fish population dynamics. Recently, Baxter (2002) proposed an approach based on landscape ecology that combined continuous and site-based surveys to analyze fish–habitat relationships at landscape scale but without an assessment of their spatial pattern.

This article aims at providing a riverscape approach combined with a set of relevant spatial analysis methods to assess the multiscale relationships between the spatial pattern of fish habitats and processes, depending on fish movements. It has been developed for resident fishes with a freshwater life cycle, but it might be useful for part of the life cycle of diadromous fishes. To illustrate the spatial analysis, we have chosen a rheophilic cyprinid species (*Barbus barbus*) and an actual riverscape: a reach of the Seine River, France. We have used literature data to define habitat preferences and movement capacities for *Barbus barbus*, whereas aquatic habitats of the 20-km reach have been measured in the field. To put some of the methods into practice, we have developed specific tools.

From Underwater Riverscape to Resource Habitat Maps for Stream Fishes

The riverscape approach conceptualizes the river not as sampling points or lines but as a spatially continuous mosaic (Fausch and others 2002). Underwater environments are dynamic and hidden behind a relatively opaque layer that is not directly available to a terrestrial observer (Torgersen 2002). These intrinsic difficulties limit the development of this approach to represent fish habitats and to create maps. In the following subsections, we discuss some methodological and practical challenges of the riverscape approach and we propose choices that might differ from classical approaches of stream ecology.

Representing an Underwater Environment: The Fish Activity Point of View

Usual methods predefine habitat classes using channel geomorphic units as quasidiscrete areas of relatively homogeneous depth and flow (Hawkins and others 1993). In that case, the underwater environment is represented by a single map of fixed channel units (a combination of two variables). These channel units (called pools, glides, rapids, riffles, etc.) are sometimes subjective and depend on the morphological and hydrological properties of the reach as well as the scale of observation, leading to the difficulty of building a general system of classification (Hawkins and others 1993). Nevertheless, each channel unit can be reclassified according to its suitability for a fish species (Toepfer and others 2000; Srivastava and others 2001). This method provides maps of suitability or maps of percentages of suitable area for each previously delimited channel unit, but loses the spatial location of suitable habitat patches.

We predefine habitat classes using an organism-based point of view (Pringle and others 1988), the resource-based concept of habitat (Dennis and others 2003), and a hierarchical partition of the habitat (Kotliar and Wiens 1990; Baguette and Mennechez 2004). The underwater environment is then represented by multiple maps of resource-based habitat patches that are defined in relation to a particular activity for a focal species (resting habitat, spawning habitat, etc.). To allow a spatial delimitation of these habitat patches, we have proposed a classification based on the knowledge of the suitable range of each selected variable for a species: its habitat preferences. Among the relevant variables influencing the different activities of *Barbus barbus*, we selected the ones that can be mapped using available technologies. Variable classes for depth, current velocity, bottom substrate, log jam, and riparian cover are defined according to habitat preferences (Table 1) (Baras 1992; Cowx and Welcomme 1998). This habitat classification allows a more reliable comparison between different reaches because it resolves the problem of subjective classification by geomorphically defined channel units (Meaden 2004). However, this knowledge-based classification might be arbitrary, depending on the validity of biological data in relation to the sampling strategy (Hirzel and Guisan 2002). It especially allows the delimitation of boundaries for each gradient variable and their independent mapping as a mosaic of patches. Each variable is of equal importance and is used and combined with others according to its usefulness for mapping a particular resource habitat.

Increasing the Scope of the Study

Study scales are often influenced by previous educational and traditional methodologies, which could be inappropriate for testing large-scale processes such as migration and dispersal. The usual terms "microhabitat scale," "mesoscale," "macroscale," and "large scale" are not always precisely quantified in meters and remain fuzzy, leading to different acceptations among stream ecologists and even among fish ecologists. Fausch and others (2002) noted the existing gap between the microhabitat (10^{-1}–10^{0} m) and reach-scale (10^{1}–10^{3} m) of most river fish research and the segment scale (10^{3}–10^{5} m) of natural processes and human disturbances. Choosing the right scales requires the definition of the extent and the resolution adapted to the detection of spatial patterns of habitats and to the study of key processes. In scaling theory, the ability to detect patterns at multiple scales is called the scope, or the ratio of extent to grain size (Schneider 2001).

The term "extent" refers to the size of the study area or temporal monitoring and "resolution" means the grain of the data (smallest object or feature dis-

Table 1. Habitat preferences for barbel: body length > 150 mm

Available GIS layers	Resting habitat map	Feeding habitat map	Spawning habitat map
Surface current velocity (m/s)	0–0.5	0.2–1.0	0.2–0.6
Depth (m)	0.3–1.5	0.2–0.5	0.1–0.3
Woody debris: log jam	2 m in diameter		
Selected bottom substrate	Cobble, block	Sand, gravel, pebble	Gravel
Riparian cover: roots as shelters	2 m wide		
Natural water bodies connected to main channel	All		

Source: Adapted from Baras (1992) and Cowx and Welcomme (1998).

cernible in the observations or measurements, minimum mapping unit, pixel size, time interval, etc.). Fish activities, processes, and movement capacities influence the definition of the extent. For mobile species, daily activities occur at the reach level, whereas dispersal occurs at the catchment level (10^5–10^6 m). Spawning migrations might occur at the reach level instead of the segment level for species with restricted movement capacities. For example, considering complementation between daily activities areas and spawning habitat, the extent should be at least 20 km for the nase (*Chondrostoma nasus*) (Lucas and Batley 1996). The scale of human impacts and management is also a determining factor in the definition of the extent (Bayley and Li 1992).

Characterizing the complexity of a habitat requires the use of a relevant resolution (Johnson and Gage 1997). The importance of high-resolution data to study mobile stream fishes has been recently mentioned by Fausch and others (2002) and Rabeni and Sowa (2002). In terrestrial environments, it is assumed that a coarser resolution is suitable for analyzing highly mobile species (Suarez-Seoane and Baudry 2002). However, representing the habitat of mobile fishes might require a higher resolution and a larger extent, in accordance with Torgensen's recommendation (2002) to increase the scope in order to reveal new patterns and relationships between fishes and their environment.

We mapped a 22-km reach with a 50-m-wide channel and lateral water bodies, as a compromise between the presence of upstream and downstream navigation weirs and common barbel spawning migration distances ranging from 2 to 6 km (Lucas and Batley 1996). We used a high resolution of 1 m in a two-dimensional (2-D) representation to reveal the spatiotemporal heterogeneity of longitudinal and lateral fish habitats. It allows the representation of (1) both the main channel and banks, (3) small or thin habitats such as a log jam or bank of boulders, (3) the lateral water bodies for which the aquatic connection with the main channel can be 1 or 2 m wide, depending on the water level, and (4) unique features such as barriers, dams, and other obstacles.

Using a GIS-Based Approach to Map Resource Habitat Patches

With the availability of different high-spatial-resolution remote sensing techniques (Johnson and Gage 1997; Leuven and others 2002; Mertes 2002; Whited and others 2002), geographic information systems (GISs) are increasingly used in freshwater systems (Fisher and Rahel 2004) to spatially delineate fish habitats. Main approaches imply different data layers, representing the environmental variables (depth, current velocity, substrate, temperature, salinity, etc.), that are overlaid to delimit potential areas of fish habitats (Dauble and others 1999) or to predict fish distribution maps (Rubec and others 1998).

We used digital orthophotographs to delineate water boundaries of the channel, corresponding to one discharge. For the same discharge, connected water bodies and variables (depth, current velocities, substrate, log jam, and riparian cover) are located during a field mapping session with an accuracy of 1 m using Differential Global Positioning System (DGPS) equipment, as proposed by Schilling and Wolter (2000). These techniques are chosen as a compromise between high labor costs and relatively low data and equipment costs adapted to turbid water. The different data sources (vector data structure for GPS, raster data structure for aerial imagery) are exported into GIS (ArcInfo®) to create a set of data layers for each variable (Figure 1A). To represent discrete habitat features, a vector GIS data structure is preferred to precisely portray variables (points for logs, polygons for substrate type, islands, etc.). These data layers are combined according to species habitat preferences in order to create resource habitat maps (Figure 1A).

Evaluating the Spatial Pattern of Resource Habitat Patches and Their Spatial Relationships at Various Scales

A Hierarchical Habitat-Based Model

Fish populations in natural or fragmented rivers can be structured like a subdivided population (Lucas and

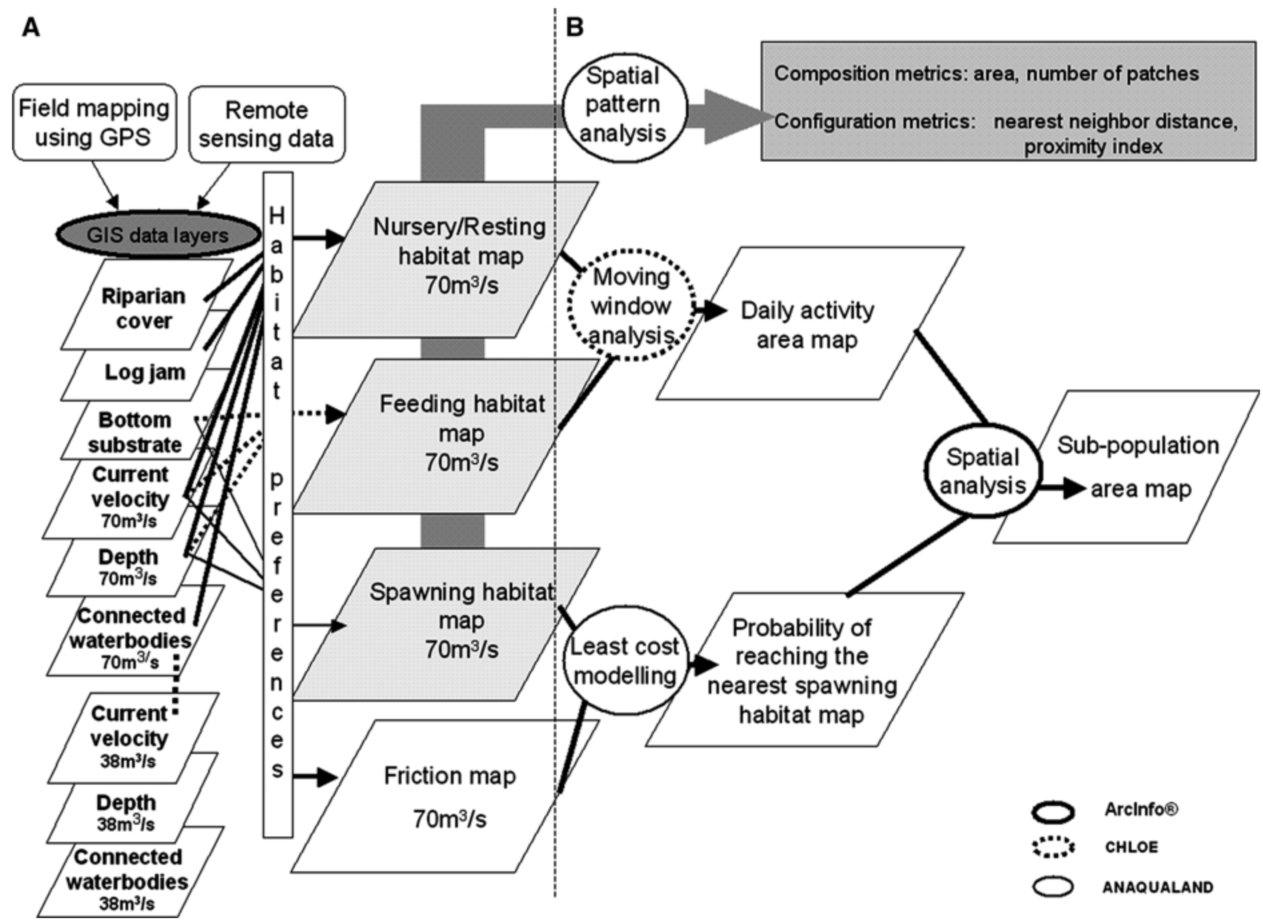

Figure 1. Flowchart of the proposed approach with process steps, spatial analysis methods, and nested products. (**A**) GIS-based maps of resource habitat patches for *Barbus barbus* and a friction map considering the heterogeneity of the whole underwater environment are created using a set of relevant variables and habitat preferences. As some data layers are valuable for one discharge, resource habitat maps and a friction map are created for this discharge. (**B**) Spatial analysis of previous maps to quantify the composition and configuration of habitat patches and their spatial relationships at nested scales.

Batley 1996; Johnston 2000). This subdivided population can be spatially defined by distinct subpopulation areas, containing or not individuals of the species and linked by dispersal migration. Subpopulation areas are defined by the presence and accessibility of all the complementary resources required for a life cycle. For terrestrial species, the spatial structure of potential subpopulation areas is used to model the viability of the population (Pain and others 2000; Jochem and others 2002). A framework to map the spatial structure of a potential subpopulation was proposed by Leuven and Poudevigne (2002).

We adapted this framework for stream fishes and considered each subpopulation area as a hierarchical system, in which the neighborhood relationships between elements of one level define the elements of the upper level (Kotliar and Wiens 1990). Figure 2 illustrates this nested structure using a three-level habitat-based model. At the first level, each resource habitat patch is represented; at the second level, the complementation between resting and feeding habitats defines daily activities areas; at the third level, the complementation between daily activities areas and spawning habitat defines subpopulation areas. The estimation of the complementation between areas at one level takes into account different behaviors and movement capacities. The daily activities area depends on the daily movement capacities, home range size, and foraging behavior, whereas subpopulation areas are related to spawning migration capacities. This model could be modified by adding one level if necessary (e.g., a nursery habitat) or simplified for species requiring few distinct habitats for their life cycle. For single-resource habitat species, the knowledge of the

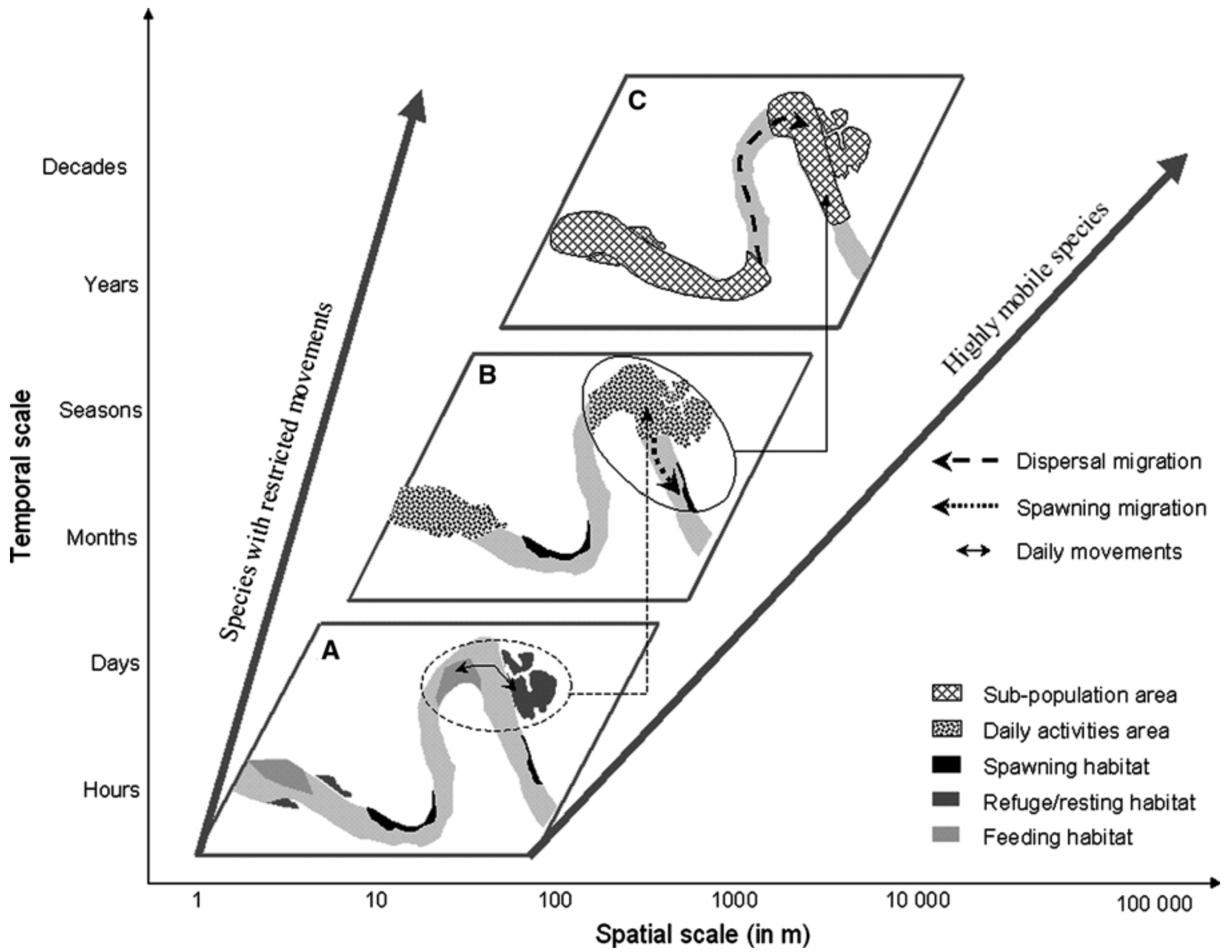

Figure 2. Hierarchical spatiotemporal structure of fish population, inspired by Frissell and others (1986), Schlosser (1995), Pain and others (2000), and Leuven and Poudevigne (2002): (**A**) Resource habitat patch scale; (**B**) daily activities areas scale in which the feeding habitat and the refuge/resting habitat exist and have a complementation relationship; (**C**) subpopulation areas scale in which previous daily activities areas have a complementation relationship with the spawning habitat via spawning migrations. For species with restricted movements, the life cycle might require a spatial scale of 100 m, whereas highly mobile species might necessitate 100 km. The hierarchical structure might also start at the B or C level, depending on whether the species requires a single habitat or various habitats.

minimal area size and maximal movement capacities will delimit the subpopulation area level. At each level of this habitat-based model, spatial analysis methods are proposed to delimit the upper level.

Calculating Areas and Distances in a 2-D River Segment

The spatial analysis of 2-D habitat patches maps, requiring both areas and oriented distances, is implemented using a raster data structure. A 1-m pixel size is chosen to preserve the sharpness of the initial vector data structures, especially with thin resting habitats such as shelters. In order to compute oriented calculations of distance between habitats along the river course (upstream and downstream), we have developed a specific computer GIS program, Anaqualand, which integrates the geometry of the river into the distance between two points or patches and handles large amounts of data composed of few informative pixels (1–2%) through sparse formalism (Saad and Sosonkina 1999).

Quantifying Habitat Patterns at Nested Scales

At the resource habitat patch scale (level A, Figure 2), we used area, number, density, and nearest-neighbor distance to identify the composition and fragmentation of habitats (O'Neill and others 1988; MacGarigal and Marks 1995). We also selected the proximity index (Gustafson and Parker 1994), quantifying the spatial context of a habitat patch in relation

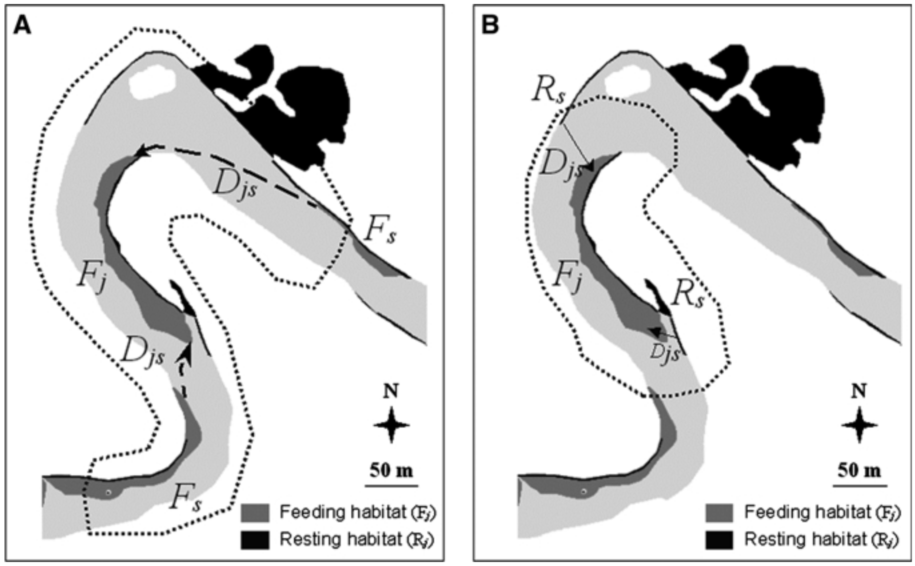

Figure 3. Two proximity indexes calculated for a focal patch F_j; the dashed line delimits the search radius from the edges of the focal patch and D_{js} is the edge-to-edge distance along the 2-D river course. (**A**) The proximity index for a class of habitats (feeding habitats); search radius = 200 m. (**B**) The proximity index for two classes of habitats to evaluate their complementation; this is an example of the proximity of the resting habitat (R_s) to the feeding habitat F_j; search radius = 60 m.

to its neighbors, for its ecological significance, simplicity, and possible adaptability to fish resource habitats, because only area and distance are required. We used the formula modified by MacGarigal and Marks (1995),

$$Px = \sum_{i=1}^{n} \frac{\text{Area}_i}{D_{ix}^2} \quad (1)$$

where n is the number of patches, the edges of which are within a search radius of the patch x, Area_i is the area of patch i, and D_{ix} is the distance between patch i and patch x. The main adaptation is the calculation of each D_{ix} as edge-to-edge distance along the river course using Anaqualand (Figure 3A).

We defined the daily activities area scale using the complementation between feeding and resting habitats. This neighborhood relationship is evaluated with the proximity index of the resting habitat in relation to each feeding habitat (Figure 3B). The daily activities area can be a single resource habitat patch in the case of species that do not use distinct areas to perform these two activities. Global maps of potential daily activities areas were also proposed in addition to previous metrics. We applied a moving-window analysis from image processing, characterizing the landscape structure inside a search radius around each pixel (Schermann and Baudry 2002). In practice, a spatial index is computed in a squared window and its value is assigned to the central pixel. The window is moved systematically along the raster map and a new map of the spatial index is produced. Different spatial indexes, such as relative abundance, richness, diversity, or heterogeneity, are computed using the Chloe software developed by Baudry and others (2005). The proportion of feeding (or resting) habitats is calculated using a relevant window size in relation to the spatial relationship and the species (Figure 4A). Maps of each habitat proportion (Figure 4B) are then overlaid to create a complementation map that represents potential daily activities areas (Figure 4C).

We defined the subpopulation area scale using the complementation between daily activities areas and the connectivity to spawning habitats. The connectivity could be measured by neighborhood indices, such as C_{si} (Hanski 1994), the lacunarity index (Plotnick and others 1993), or the aggregation index (He and others 2000), and modeling approaches. In some modeling approaches, the landscape is considered as a binary system composed of habitat and nonhabitat (Metzger and Décamps 1997; Rushton and others 1997). As the spawning migration might entail long-distance movements and is a vulnerable part of the life cycle (Smith 1991), we considered the biological connectivity of the riverscape as a response of fishes to the heterogeneity of all the habitats traveled through during migration. Modeling approaches of the biological connectivity were implemented using the concept of minimal cumulative resistance (MCR) (Knaapen and others

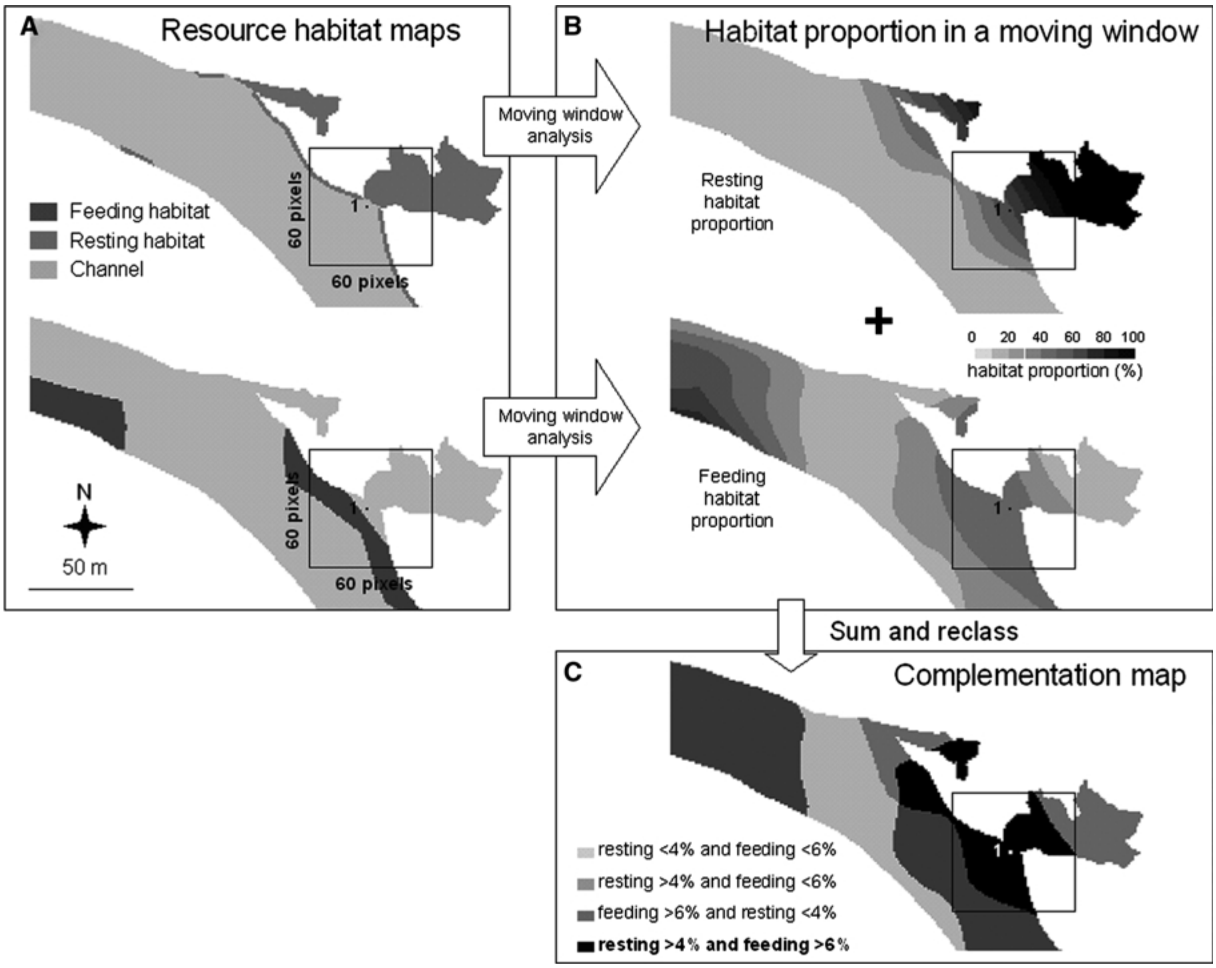

Figure 4. Identification of daily activities areas through complementation maps using the moving-window analysis. Identification of the complementation of stream fish habitats using the moving-window analysis. (**A**) The raster maps of resource habitat patches are computed to create new raster maps of the proportion of each habitat in a 60 × 60-pixel window size. (**B**) Habitat proportions are available from 1% to 100%. These two raster maps are overlaid and then reclassed to identify complementation of the two habitats within a radius of 30 pixels. (**C**) The complementation is defined by thresholds of 4% for resting and 6% for feeding.

1992) or, more recently, the "least cost" model (Adriaensen and others 2003), which assigns to each habitat a value (resistance or permeability) based on energy expenses, mortality risks, and movement costs (Pain and others 2000; Ray and others 2002; Vuilleumier and Prelaz-Droux 2002; Joly and others 2003). We defined a resistance matrix for the barbel based on swimming capacities and predation risks in order to build a friction map (Figure 1A). We applied the MCR for all spawning habitats and built a map of the probability (pixel A_j) of reaching the nearest spawning habitat (pixel B_j) using Anaqualand (Figure 1B). This probability is a decreasing function of MCR and α, in which α is the potential mean distance covered by a fish during the spawning migration. A similar species-specific parameter α_s, called the dispersal coefficient, is used to evaluate connectivity (Vos and others 2001). For the probability computation, we used a decreasing exponential:

$$\mathrm{Proba}\,(A_i) = \mathrm{e}^{-\frac{\min_{Bj}\left[\mathrm{MCR}\,(A_j, B_j)\right]}{\alpha}} \tag{2}$$

The map of the probability of reaching the nearest spawning habitat visually illustrates gaps in the biological connectivity (Figure 5B). By overlaying the daily activities area map (Figure 5A) and the probability map and choosing a threshold probability, we delineated potential areas that might support a subpopulation (Figure 5C). At each scale, one can remove an area that is too small to be either a minimal resource

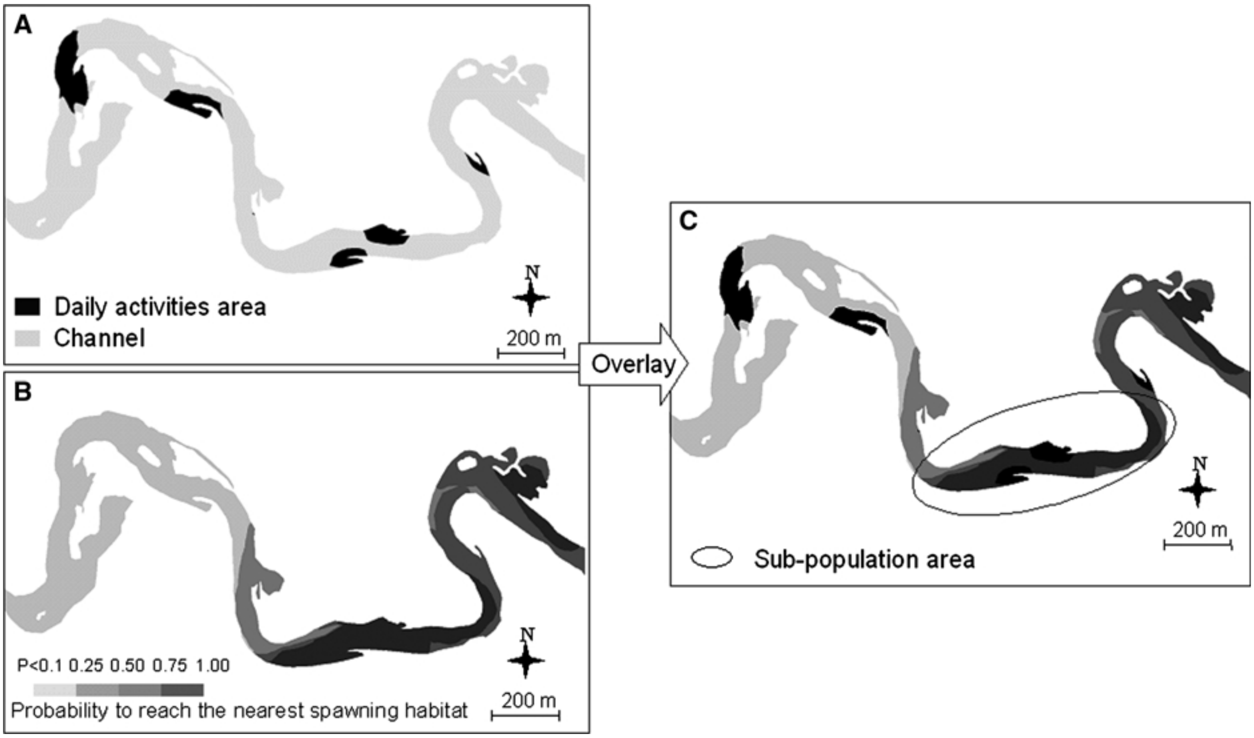

Figure 5. Delimitation of potential subpopulation areas. (**A**) Daily activities areas map using moving-window analysis with Chloe. (**B**) Probability of reaching the nearest spawning habitat map using Equation 2 with Anaqualand. Low probability areas ($P < 0.25$) could be interpreted as gaps in biological connectivity (for spawning). (**C**) The ellipse delimits a potential subpopulation area defined by areas with a high probability of reaching the nearest spawning habitat ($P > 0.75$) and containing daily activities areas.

habitat area, a minimal daily activities area, or a minimal subpopulation area.

Conclusion and Perspectives

The spatial analysis of the riverscape approach attempted to contribute to the fluvial landscape ecology by viewing lotic ecosystems as hierarchical and continuous mosaics of habitat patches. In the case of stream fishes, it meant the following: (1) changing the traditional representation of aquatic habitats and considering the resource habitats that support the entire life cycle, (2) adopting a 2-D large-scale view if necessary, and (3) shifting from site-based to spatially continuous approaches. This approach implied the resolution of different methodological and practical challenges. The main two challenges were mapping resource habitat patches using a GIS-based method and calculating distances in 2-D along the river course. Simple methods were chosen because of the absence of automatic quantification of fish spatial patterns in 2-D. Their ecological relevance was put forward to assess each level of the hierarchical spatial structure of the population. The knowledge of this potential spatial structure should be useful to analyze population viability, to design sampling techniques in order to estimate the abundance of rare or threatened species (Toepfer and others 2000), or to detect isolated populations using genetic methods (Spruell and others 1999). The methods were also proposed for prioritizing the preservation of habitats, designing restoration policies, and testing scenarios following the addition or removal of habitat patches.

Prioritizing Preservation and Restoration Policies

Proposals emerged from this riverscape approach to help define management schemes. Each resource habitat covering the life cycle of the species was represented by one or several maps according to the habitat requirements of the species. Rearing/nursery habitat, feeding habitat, resting/refuge habitat, and spawning habitat patches might be distinct for some species or blend into a single resource habitat patch for others. Methods at the resource habitat level identified potential critical resource habitats, which should allow the prioritization of management policies such as restoration at a relevant location. Mapping resource habitat patches for different species is also useful to assess whether a rehabilitation scheme at a certain location for a given species might destroy critical habitats for other species. The relative value of a habitat patch in relation to its spatial context could be estimated with the proximity index (within the same habitat or between different habitats). The identification of habitat patches of great value contributes to setting preservation priorities, and identifying low-value habitats helps set restoration priorities of their spatial context. The map of the probability of reaching the nearest spawning habitat, or other habitats, illustrates potential gaps in the biological connectivity of a reach, allowing a localization of restoration schemes. All of these spatial analysis methods could be used to simulate different scenarios of restoration. The consequences of the addition of a habitat patch at a specific location could be quantified and visualized using the proposed indexes and maps.

Remaining Challenges

Methodological difficulties still exist when applying this riverscape approach to stream fishes. They are mainly due to the shifting nature of the fish habitat mosaic. Two temporal scales can be distinguished: water-level fluctuations within a period of 1 year, leading to a pulsing connectivity of water bodies, and at the decade-to-century scale, the channel pattern dynamics (Amoros and Bornette 2002; Richards and others 2002). In this context, mapping changing variables is particularly challenging and should be done for a range of relevant flows, depending on processes and species. On the one hand, the availability of bathymetry associated with a hydraulic model at the segment scale makes the creation of depths and current velocities maps for each relevant flow easier (Tiffan and others 2002). On the other hand, only few flows can be mapped using remote sensing and field mapping, and they must be carefully chosen. Relevant flows, according to hydrological conditions of the reach, could be median, dry, or wet 5-yearly flows. By mapping contrasted flows, the range of temporal variation of fish habitats is evaluated (Hilderbrand and others 1999). In some cases, only a particular range of flows is relevant in relation to a specific activity. For example, high flows and inundation maps are required for species using temporary habitats situated in the floodplain for a stage of their life cycle. Pike (*Esox lucius*) migrate from the channel in February to spawn on inundated meadows (Casselman and Lewis 1996). For this species, mapping accessible spawning habitat requires inundation maps, land-cover types, and migrating routes from the channel. In regulated or channeled rivers, water-level fluctuations are often very limited and the riverscape might be "frozen in time" (Ward and others 2002). In such cases, the habitat maps are valid year-round. For intermittent rivers, the validity of habitat maps is restricted to flowing months. The range of temporal variability patterns is critical for understanding the consequences of ecological processes and defining management schemes such as flow regulation. Gustafson (1998) underlined the lack of indices quantifying spatial patterns that include a measure of temporal variation. An integrated parameter of this temporal variation, such as a permanence index, inspired by the aquatic habitat turnover (Ward and others 2002), can be mapped using the set of maps for each flow.

In floodplain rivers with deep and turbid water, the availability of high-resolution data over large spatial scales and for different water levels is also crucial. In that case, panchromatic aerial photography is useful for spotting water boundaries, riparian vegetation, and large woody debris (Muller 1997), but it is ineffective for evaluating water depths. More costly techniques such as laser telemetry (bathymetric LIDAR) and radar interferometry systems could be used for the bathymetry at a resolution of 1 m (Mertes 2002). Multispectral image data, collected with a Compact Airborne Spectrometric Imager (CASI), were used to assess classes of current velocities and bottom substrate (Puestow 2001). However, currently, reliable evaluations of bottom substrate in cloudy waters seem limited to GPS field surveys.

Toward the Validation of the Methods

To validate the ecological relevance of these indexes and maps, spatially continuous surveys of resource habitat patches are needed in order to acquire fish data. Local species abundance can be tested for correlation with the relative value of the habitat patch or its spatial context. Potential subpopulation areas could also be evaluated by sampling juvenile fishes (young-of-the-year) because their distribution is linked to the selection of spawning habitats by adults (Poizat and Pont 1996). Their presence is an appropriate indicator of spawning habitats connected to daily activities areas. Linking specific ecological processes (complementation between two habitats, accessibility of spawning habitat, etc.) to particular spatial analysis methods might provide a tool for predicting said processes using the quantification of spatial patterns.

Despite the remaining methodological and practical challenges, the GIS-based riverscape approach is a flexible framework for the study of the influence of habitat patterns on the spatial distribution of fishes and the enhancement of the detection of areas that might support viable populations. The spatial analysis methods developed for fish habitat patterns might help in evaluating impacts of habitat alteration and isolation and prioritizing preservation and restoration policies.

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