RIVER RESEARCH AND APPLICATIONS

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THE RIVER MACHINE: A TEMPLATE FOR FISH MOVEMENT AND HABITAT, FLUVIAL GEOMORPHOLOGY, FLUID DYNAMICS AND BIOGEOCHEMICAL CYCLING

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ABSTRACT

The dynamics of many large floodplain rivers are dominated by the flood pulse. The high kinetic energy of the erosive flows associated with the flood pulse forms and reforms the river channel. In general, the flood pulse supports the immense abundance and diversity of river life by transporting nutrients and organic matter into backwaters in spring, supporting primary and secondary production during the summer and redistributing these products to channels as water levels recede. Both North American and South American fluvial-dependent large river fishes exhibit complex, system-level longitudinal and/or lateral movements across life stages that allow them to exploit flood pulse-driven spatial heterogeneity and seasonal connectivity to feed, reproduce and avoid harsh conditions. We argue that two hydraulic variables, the magnitudes of velocity and the spatial velocity gradient, are necessary and sufficient to both understand fish 'hydro-navigation' as well as explain patterns in biogeochemistry and fluvial geomorphology and thereby create a new conceptual framework for large floodplain rivers integrating fluid dynamics, channel morphology, biogeochemical cycling and important elements of fish ecology. We illustrate the framework using summary data from the São Francisco River, Brazil that contains sub-basins possessing different levels of impact and also from the lower Paraná River (Argentina) where natural processes can still be studied. We believe the framework is an important element of large river restoration because it directly links the unique physical and chemical processes of large floodplain rivers to life requirements important to fishes and other biota. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS: hydro-geomorphology; river theory; fish migration; biogeochemical cycling; large river ecology; large river fish requirements; large river fish habitat

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INTRODUCTION

Levin (1992) argued that 'the problem of pattern and scale is the central problem in ecology'. Aquatic ecologists manifest Levin's argument by their three decadal searches for spatial and temporal patterns in rivers. This search has generated a series of increasingly complex conceptual models spanning the Nutrient Spiraling Concept (Webster and Patten, 1979), River Continuum Concept (Vannote *et al*., 1980), Serial Discontinuity Concept (Ward and Stanford, 1983), the Flood Pulse Concept (Junk *et al*., 1989), the Patch Dynamics Concept (Pringle *et al*., 1988; Townsend, 1989), the Natural Disturbance Concept (Resh *et al*., 1988), Habitat Templet Concept (Southwood, 1997; Poff and Ward, 1990; Townsend and Hildrew, 1994), the Riverscape Concept (Fausch *et al*., 2002), the Natural Flow Paradigm (Richter *et al*., 1996; Poff *et al*., 1997), and its corollary, the Normative River Concept (Stanford *et al*., 1996), and complementary concepts well contextualized in Thorp *et al*. (2006).

Two related themes emerge from the above body of literature, one theme by its presence and the other by its absence. The theme of natural hydro-geomorphology (NHG) is consistently present in the most recent of the above heuristic constructs, particularly those associated with large rivers. Hydrologic variability and geomorphologic response mould the habitat template upon which natural biodiversity of rivers has evolved and partially determine the erosion, transport and deposition of materials (Wohl *et al*., 2005; Thorp *et al*., 2006; Bertoldi *et al*., 2009). NHG is a critical part of large river restoration and biodiversity conservation and must be

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addressed in water resources management decisions (Poff *et al.*, 1997; Richter *et al.*, 1998). The need for NHG as a target state for river management and restoration is simple to state, intuitive and compelling, but the NHG is seldom observed in *a priori* water resources management decision making because it has not been made sufficiently mechanistic.

The second theme, absent from the literature base describing how large rivers function, is the lack of any consensus, generalized method for quantifying habitat needs of specific large river biota. Without this connection, it is not possible to build models that can be used to reliably forecast the effects of water management actions on biodiversity conservation, nor is it possible to forge any but the most general of hypotheses for scientific testing. Many consider river habitat as patches in a mosaic within a waterscape (e.g. Thorp *et al.*, 2006), but they do not describe precise methods that can be used to quantify habitat as perceived by individual species of aquatic biota. Unfortunately, a concept of habitat as a patch of uniform conditions is not sufficiently comprehensive to accommodate large river systems where a variety of ecological processes take place across multiple scales in a highly dynamic and interconnected ecosystem. This critical scientific gap prevents the NHG and the wealth of scientific studies that underpin it from supporting water resources decision making via incremental, deterministic forecasting or as the basis of scientific hypothesis testing.

The goal of this paper was to answer the questions 'What are aquatic habitats and how can they be envisioned in large floodplain rivers?' by describing a set of principles to guide the development of habitat quantification for large river biota (*sensu* Parasiewicz *et al.*, 2008). The principles should be broad enough that they can be used to develop and execute system-level goals, objectives and scientific hypotheses but quantitative enough that they can be used to select, prioritize and schedule individual projects or other management actions that require quantitative, deterministic forecasts and lead to scientific understanding of individual life stages. We developed the principles by considering the history of the concept of aquatic habitat and then used numerical models to explore and understand realistic fish movements in complex natural flow fields. We explained how these behaviours integrate critical elements of fluvial geomorphology, fluid dynamics, material transport and fish behaviour and thus reconnect back to NHG. We focussed our theory on the iconic fluvial-dependent large fishes whose response to flow or geomorphology change cannot presently be adequately forecast to evaluate different management actions or develop scientific understanding. We then illustrated how the concept can be used to explain observed patterns of fish community composition and abundance in the São Francisco River basin of Brazil.

CONCEPTUAL MODEL RELATING AQUATIC BIOTA TO FLOW AND HYDRO-GEOMORPHOLOGY

Rivers (Poff, 1997; Nestler *et al.*, 2007) and river reaches (Thoms and Parsons, 2002) have been ordinated and assessed along many dimensions, but one useful way of considering rivers, particularly to understand our current habitat concept, is to ordinate them along an arbitrary complexity gradient. The simple end of the complexity gradient is anchored by base flow-dominated streams in simple channels supporting fish communities of low diversity comprised primarily of species that are minimally migratory. The other end of the complexity gradient is anchored by large, flood-pulse rivers in complex geologic settings exhibiting high biodiversity and multi-scale flow patterns in time and space. Many of our ideas about physical habitat quantification can be traced to the use of simple hydraulic variables such as measures of average depth or average velocity in cells of a cross section for the smaller, base-flow systems. However, extrapolation of these habitat concepts met with considerable resistance from biologists working in large, warm water rivers. There is no widely accepted concept of aquatic habitat in hydrologically complex, large (particularly warm water) rivers as bemoaned by Gore and Nestler (1988) and still true today.

Concept of habitat in large, floodplain rivers

The flood pulse drives annual cycles of river processes over a large and diverse spatial domain (Junk *et al.*, 1989; Bunn and Arthington, 2002; Welcomme and Halls, 2004).

The relationship between the flood pulse and subsequent ecological responses in this river has been described by Junk *et al.* (1989) and Junk and Wantzen (2004) for the Amazon basin where the importance of biochemical cycles, particularly for organic carbon, size, dynamics and transport is documented by Richey *et al.* (1991) and McClain (2002). In South American floodplain rivers, either benthic algae (Hamilton *et al.*, 1992; Roesch *et al.*, 2009) or aquatic macrophytes (Hoeinghaus *et al.*, 2007; Jepsen and Winemiller, 2007) are the major organic carbon sources that support river food webs. Both algae and aquatic macrophytes enter aquatic food webs primarily as fine and coarse particulate organic matter which is hydraulically transported in the water column until directly settling onto substrates (Winemiller, 2004). Hydraulic transport processes are important because about 90% of transported organic matter is either sorbed to fine minerals or remains dissolved (Moreira-Turcq *et al.*, 2005). A similar relationship between flood pulse and ecological responses is observed for the lower Paraná River, one of the world's largest rivers and one of the few temperate fluvial systems that still exhibits a natural flood pulse in its lower reaches (Nestler *et al.*, 2007; Baigún *et al.*, 2008).

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Over an annual cycle, the progression of rising water levels, high water and fall of the flood pulse creates a sequence of complex, large-scale hydraulic patterns. The hydraulic forces associated with these patterns transport nutrients, erode, transport and deposit material and create the physical environment for material transformation through chemical and biological processes. As the flood pulse recedes, floodplain dissolved organic carbon and particulate organic carbon and floating aquatic and semiaquatic macrophytes are exported and provide organic matter and nutrients for main channel communities (Junk *et al*., 1989). Dissolved organic carbon represents by far the most important carbon source (Depetris and Paolini, 1991), and floodplain lagoons produce and export reactive and labile organic carbon (Moreira-Turcq *et al*., 2003). The role of the flood for the flow of nutrients and energy through the lower food web compartments and ecosystem productivity has been described for many large river systems, including rivers in Asia (Graaf, 2003; Lamberts and Koponen, 2008) and Africa (Høberg *et al*., 2002).

Within this domain, fluvial-dependent fish have evolved complex, system-scale life history strategies often requiring them to move laterally between the main channel and backwaters or migrate long distances to access critical functional units (FUs) important to different life history stages (Thoms and Parsons, 2002). However, in South America, where temperature variations are less pronounced, the seasonality of water levels assumes a preponderant role affecting the aquatic communities (Agostinho and Zalewski, 1995; de Vazzoler, 1996; Lowe-McConnell, 1999). This connectivity between the fluvial-dependent fishes and FUs is best illustrated with South American detritivorous fishes.

Generally, fish communities of major river systems in South America contain a high proportion of detritivorous fishes (Winemiller, 2004), especially in the families Prochilodontidae, Loricariidae and Curimatidae. They include important fish stocks that in some regions comprise over 50 per cent of the fish community biomass (Bowen, 1983). Fish community biomass in the Paraná and São Francisco rivers is dominated by detritivorous *Prochilodus* species (Franco de Camargo and Petrere, 2001; Winemiller, 2004) whose juveniles remain in lagoons and floodplain channels for 2 years before recruiting to the main channel. These species are critical to overall river health and the abundance of other members of the fish community for three reasons. First, this genus comprises more than half of the fish biomass in permanent habitats of the floodplain, reaching biomasses up to 1000 kg/ha in Paraná (Bonetto *et al*., 1970). Second, its larvae are a critical component of the food consumed by larvae of large piscivorous species that rear in the floodplain (Oldani, 1990). Third, as adults they ingest fine organic matter and flock detritus (Marchese and Ezcurra de Drago, 1992; Fugi *et al*., 1996) and further process the organic matter ultimately produced or transported by processes linked to flood pulse dynamics.

Detritivorous species are not only affected by biogeochemical cycles, but because they are so abundant, they can influence biogeochemical processes associated with NHG of floodplain rivers, even at large scale. Detritivorous species such as *Semaprochilodus* likely influence organic matter content in sediments because they can modify the quantity and nutritional quality of sediments in a floodplain river (Winemiller *et al*., 2006). These species are a critical part of South American large river ecology because they assimilate primary production from highly productive floodplains and transport this carbon to other river areas and even to nutrient-poor ecosystems where they subsidize fish production (Winemiller and Jeppsen, 1998). For this reason, detritivores play a crucial role in carbon and nutrient cycling. They have the capacity to substantially affect the overall fluvial bioenergetics budget (Taylor *et al*., 2006) and can, therefore, be considered as ecosystem engineers (Flecker, 1996). It is impossible to reduce the habitat of *Prochilodus* into simple (average) physical hydraulic variables that are separate from the large-scale processes of large rivers in South America.

How fish respond to flow pattern in rivers

A fuller concept of habitat may be connected to NHG by embracing the entirety of Odum's (1971) definition of habitat '. . .is not only the physical space occupied by an organism, but also its position in environmental gradients. . .' We implement the expanded concept using juvenile salmon outmigration (emigration) as an example. Juvenile salmon may move because of antagonistic social interactions, harsh conditions, food limitations or emigration to adult habitat. During their emigration phase, they may migrate from small natal streams to adult oceanic habitat and, therefore, pass through complex flow fields of a progression of stream sizes from relatively small to relatively large. The hydrodynamic cues they use to make swim path selections in systems that vary widely in size and complexity make them an excellent model to gain insight into how fish generally move through complex flow fields in a variety of fluid and geomorphic settings. Understanding how fish respond to flow fields may also provide insight into how their life history may be integrated into biogeochemical cycles and fluvial geomorphology because both these process are, at least partially, mediated by fluid dynamics.

The swim path selection of juvenile salmon is best understood in the context of the fluvial geomorphology of free-flowing rivers (Nestler *et al*., 2008). In free-flowing rivers, a flow field distorts because of flow resistance (Leopold *et al*., 1964). Without flow resistance, there is no force to distort a unit volume of water once it is set into motion by the force of gravity (Ojha and Singh, 2002). To relate fish swim path selection to flow field distortion, Goodwin *et al.* (2006) proposed a flow field distortion metric 'total hydraulic strain' that embodies the following: (i) linear deformation (whose tensor metric components are normal strain rates); (ii) rotation (whose tensor metric components are angular velocities); and (iii) angular deformation (whose tensor metric components are one-half the true shearing strain rates). Although rotation is not due to normal or shearing strain rates, the same spatial velocity gradients induce both angular deformation (shearing strain) and rotation. The hydraulic variables used to calculate total hydraulic strain are spatial derivatives of velocity and hence embody the second part of Odum's definition.

Two categories of flow resistance, friction resistance and form resistance, occur for subcritical flows (Leopold *et al.*, 1964). A simple, straight, uniform channel produces a flow pattern in which average velocities are lowest nearest a source of friction (such as the channel bottom and edges) with a zero water velocity occurring at the water-channel boundary. Pattern in the total hydraulic strain field is the inverse of pattern in the velocity field, with lowest total hydraulic strain occurring farthest from sources of friction resistance and highest near the sources. Form friction, or drag, is created by large woody debris or rock outcrops projecting into the flow. As in the case of friction resistance, total hydraulic strain associated with form resistance increases towards the signal source. In contrast to bed friction, water velocity increases towards the signal source for form resistance because of local reduction in conveyance area and increased travel distance of water flowing around an obstruction. For example, a fish approaching a stump from the upstream direction will sense increasing total hydraulic strain and an increasing water velocity until boundary effects very close to the obstruction are encountered.

By integrating information between the total hydraulic strain and velocity fields, fish have sufficient information to identify specific channel structures and solid boundaries thereby creating a hydrodynamic 'image' of their immediate surroundings. That is, they have sufficient information to infer the attributes of the solid boundary from pattern in the flow field. They are thus able to move efficiently through a flow field or select habitats with specific hydraulic and geomorphic attributes. In our explanation, we emphasized downstream migration, but the ability of a fish to respond to hydrodynamic cues that signal channel features also allows its migration upstream or to locate and evaluate potential habitat or feeding stations, all in a complex flow field and bed geometry. Although we used juvenile salmon as a model system to describe fish movement, it seems plausible that many other species would use a similar movement cue because all fishes share a common mechanosensory system capable of detecting relative velocity magnitude and hydraulic shear. The lack of appreciation by fish passage designers of the interplay between velocity and hydraulic gradients may be responsible for the lack of success observed for many fishways in South American rivers (Baigún *et al.*, 2007).

The relationship between movement and habitat can be illustrated with the Eulerian–Lagrangian–agent method (ELAM) of analysis (Goodwin *et al.*, 2006). The ELAM is a 'hypothesis tester' to explore different fish movement strategies including the strategy described above. It creates fish in virtual reality that swim within a virtual fluid environment created by a computational fluid dynamics (CFD) model. Using a Reynolds-averaged Navier–Stokes steady-state representation, we create a simple fluid environment with a rectangular cross section (flume walls produce friction resistance) and a centred rectangular prism (produces form resistance) (Figure 1). To recreate fish movement, the ELAM requires a behavioural rule that processes the hydrodynamic information in the immediate vicinity of each virtual fish and then elicits a specific swim selection behaviour. We applied the ELAM to a simple virtual flume using two separate rules. In the first rule (emigration), virtual fish are programmed to swim away from a high value of total hydraulic strain in the downstream direction of highest velocity (Figure 1A) (the complete rule is described in Goodwin *et al.*, 2006). This rule causes virtual fish to move quickly and efficiently through the virtual flume. The second rule is the same as the first rule except that virtual fish swim toward increasing total hydraulic strain while moving downstream (Figure 1B). The second rule causes virtual fish to hug the flume wall, considerably delaying their passage through the flume, and to exhibit a behaviour akin to solid surface foraging behaviour. From this and similar examples, we conclude that two relatively simple hydrodynamic variables, total hydraulic strain and velocity magnitude, when combined into a behaviour rule appear adequate to elicit a variety of seemingly complex migration or habitat selection behaviours. We have successfully used the ELAM to accurately forecast the downstream movement of juvenile salmon at many dams under many operations (Goodwin *et al.*, 2006) as well as the upstream and downstream movements of other species.

While we use juvenile salmon as an example of how a fish may use hydrodynamic cues, it is important to note that the life history of fishes can exhibit impressive diversity. For example, neotropical migratory fish of South America, such as *Prochilodus*, exhibit very different life cycles than North American salmonids (Oldani and Baigún, 2002), although both share the need to move over an extensive spatial domain and correctly time their arrival to locations that meet specific life history requirements. In general, freshwater fish migration in South America can be described as follows. During the rainy season, adults migrate upstream to spawning areas. Spent adults and larvae then move downstream

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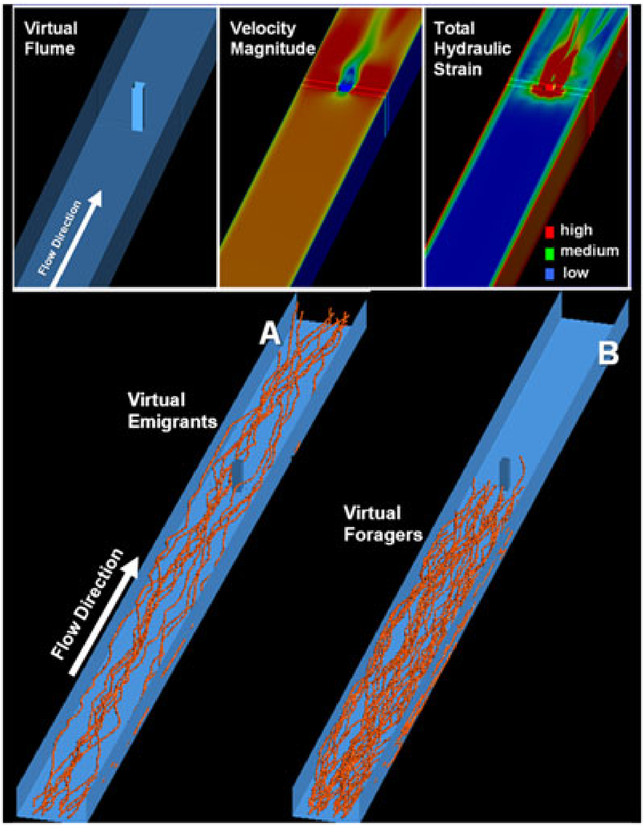

Figure 1. Top. Depiction of virtual flume with rectangular prism and associated contours of velocity magnitude and total hydraulic strain. Bottom. Position of virtual fish after 30 s programmed for migration (left) versus habitat selection (right). Note the affinity of foraging virtual fish for the flume boundary and their reduced net progress towards traversing the flume compared to migrating fish. Computational fluid dynamics modelling performed by staff at IIHR Hydroscience and Engineering, University of Iowa, Iowa City, USA

until they return to the adult habitat from which the population originated (Petrere, 1985). During this downstream movement, the larvae are passively transported into the floodplains (nurseries) along the river channel, where they find favourable conditions for shelter and feeding (Oldani, 1990; Agostinho and Zalewski, 1995; Lowe-McConnell, 1999). Migratory movement differences among different *Prochilodus* populations in South American rivers are common (Winemiller and Jeppsen, 1998) as the life history of each population appears to be in synchrony with the NHG rhythms of the system within which it occurs. This synchrony has been particularly well documented for *Prochilodus* species common to different rivers on the eastern slope of the Andes Mountains (Lucas *et al*., 2001). It would be difficult to capture these interrelationships between NHG and fish ecology using conventional ideas about fish habitat or using a habitat mosaic concept.

Place-specific versus place-searching behaviour

Based on our explorations with virtual fish, we believe that activities of fish in rivers can be broadly separated into two categories from an ecological and life history standpoint: place-specific behaviours or place-searching behaviours. At any one time, a fish can be engaged in one of these activities, but not both, although it may switch rapidly between these activities. Moreover, it may be useful to ordinate different life stages of fish along a gradient that is anchored at one end by life stages that predominantly engage in place-specific activities and anchored at the other end by those that predominantly engage in searching activities. Other strategies may employ various blends of the two activities depending up life stage, environmental gradients and size of the physical domain.

In a place-specific activity, fish maintain their approximate position in an area. For example, a feeding station for a sight-feeding fish such as resident juvenile salmon has the following attributes (Fausch, 1984; Smith *et al*., 2008). The fish bodily locates itself in relatively slow water to minimize the bioenergetic cost of swimming but near a shear zone so that it can dart across the shear zone to capture drifting prey carried near its position by the current. The water velocity across the shear zone must be fast enough to transport prey items at a significant rate but not so fast that the fish must expend substantial energy to return to its original location after feeding. Based on this simple example, two conclusions can be reached about juvenile salmon when they exhibit place-specific activities: specific hydraulic criteria based on water depth and water velocity and variables associated with water velocity such as shear or turbulence can be used to describe feeding station locations (Smith and Brannon, 2007) and these criteria may often be described in terms of absolute values and not relative values. Absolute criteria, keyed to the water velocity on the slow side of the shear zone of the feeding station, are needed because fish must expend energy to maintain position in the face of displacing currents. Therefore, relative difference in velocity across the shear zone does not adequately reflect the bioenergetic realities for a fish trying to maintain position on the slower side of the shear zone. Other aquatic biota that do not move extensively, for example, freshwater mussels, are similarly dependent on the absolute values of relevant hydraulic variables (Morales *et al*., 2006). We believe that the reliance of fish and relatively immobile aquatic taxa on absolute values of hydraulic variables when they engage in place-specific activities causes these activities to be describable using conventional habitat assessment methods that feature relatively simple averaged hydraulic variables. Habitat assessment methods such as the instream flow incremental methodology achieved their early success working on resident fishes in relatively persistent (base flow dominated) systems (Gore and Nestler, 1988).

In searching activities, fish must identify a movement pathway through a complex channel bedform and the hydraulic field it constrains. The motivations for fish to move substantially within a river ecosystem can be varied. Adult fish may move as follows: (i) during spawning migrations; (ii) as they search for feeding zones within the system; (iii) between seasonal or diurnal habitats (e.g. move to overwintering from summer habitats and back again, night and day use habitat); (iv) to search for food as they move; or (v) to search for thermal refuges. Unlike place-based habitat selection strategies used by resident fishes, the hydraulic navigation strategies used by any life stage of a migrating fish to select a path through a complex hydraulic field are generally unknown except for the strategy employed by out-migrating juvenile salmon (Goodwin *et al*., 2006). However, Goodwin *et al.* (2006) speculate that other migrating species may use similar cues because of the similarity of the fish mechanosensory system across species.

Fish that engage in place-searching activities must rely on relative values of hydraulic variables because the domain within which they move may experience substantial changes in bedform and discharge over time and space. Therefore, given this ‘floating baseline condition’ associated with dynamic rivers, it is likely impossible for absolute values of hydrodynamic movement cues to exist that can function over the range of encountered hydraulic conditions as fish migrate along the space–time continuum. For example, if the channel cross section area reduces by 50% and the discharge remains constant, then the average cross section velocity must correspondingly increase by 50% to maintain mass continuity. Consequently, a fixed velocity criterion that identifies the pathway of a migrating fish is unreasonable unless swimming capabilities are exceeded. However, the overall flow pattern may remain essentially the same with some relatively small movement in space of velocity maxima or minima. Use of relative hydraulic variables allows fish to hydro-navigate as discharge changes or as the coarse shape of the channel changes because the basic flow field pattern described as relative values will be more persistent than absolute point values within the field. Moreover, the elegant relationship between geomorphology and hydrodynamic pattern that creates the relative hydraulic signatures used by fish as cues to guide their movement is persistent over geological time as long as bedform and flow field are in dynamic equilibrium.

CONJUNCTION OF LARGE RIVER HYDRO-GEOMORPHOLOGY AND FISH MOVEMENT STRATEGIES

In general terms, the geomorphology of flood-pulse rivers (and other rivers) is determined by hydraulic shear stress acting on the channel boundary. The ELAM described above uses hydraulic strain as the hydraulic variable that cues fish movement. However, both hydraulic shear and strain are related. The hydraulic shear stress in water is proportional to deformation (described via strain rates or velocity gradient) through a constant known as viscosity (Munson *et al*., 2006). Mathematically this is expressed in one dimension as

$$\tau = \mu \frac{du}{dx}$$

where

τ is the shear stress

μ is the viscosity and

$\frac{du}{dx}$ is the velocity gradient or deformation rate.

Therefore, the hydraulic strain field matches the hydraulic shear field. Emigrants, by responding to flow field deformation and velocity magnitude, are also responding to the same hydraulic variables that partially govern the shape of the channel, the erosion, transport and deposition of material and create the physical environment for transformation of nutrients and organic matter. Through their ability to detect flow field distortion and velocity magnitude, large river fishes

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are inextricably coupled to large river hydro-mechanical processes that govern material transport and transformation. Therefore, a concept of habitat for these fishes must include the coupling of large-scale hydrodynamic patterns, fluvial geomorphology and material transport and transformation, all driven by a relatively consistent hydrologic rhythm. For example, adult *Prochilodus* in the Paraná River described earlier can likely detect and concentrate in those habitats with high organic matter in bottom sediments or in the water column (Quirós and Baigún, 1985). Therefore, management and conservation of *Prochilodus* populations, or any fluvial-dependent fish species, must include these processes and their coupling.

The alternative concept leads to a new set of principles that underpin habitat dynamics in large flood pulse rivers consistent with NHG.

Principle 1 - *Importance of fluvial geomorphology*: Principles of fluvial geomorphology lead to basic, understandable and measurable channel-forming processes that produce spatial and temporal patterns at many scales (Nestler and Sutton, 2000) in stream beds (Leopold *et al*., 1964). These processes produce the channel bedforms and substrates that are the physical habitat template perceived by aquatic biota.

Principle 2 - *Importance of hydrodynamic continuity*: A dense and relatively incompressible fluid, like water, exhibits continuity (i.e. there are no breaks or abrupt changes) when forced by gravity and momentum to flow over channel substrates, bedforms and planforms. Therefore, the solid boundary of rivers may best be considered as a continuum of conditions that gradually blend together instead of as relatively sharply delineated areas that comprise a mosaic of conditions.

Principle 3 - *Hydraulic pattern reflects fluvial geomorphology*: Principles 1 and 2 emphasize the relationship between fluid dynamics pattern to physical channel structure that is unique for solid features that vary in shape or size (Smith *et al*., 2005; Buffin-Bélanger *et al*., 2006). That is, the attributes of the physical boundary can be inferred from the behaviour of the fluid pattern if appropriate hydrodynamic variables are measured at correct time and space scales.

Principle 4 - *Importance of hydro-geomorphology*: Hydrogeomorphic processes strongly affect spatial and temporal distributions of biogeochemical cycling of nutrients and carbon, which in turn affect river productivity and food web interactions.

Principle 5 - *Sensing capabilities of the fish mechanosensory system*: The mechanosensory system (used to sense acoustics and water movement) possessed by life stages of all vertebrates that are completely aquatic: (i) is tightly coupled to the fluid medium; (ii) can determine absolute water velocity if a spatial point of reference is available; (iii) can measure spatial and temporal gradients (derivatives) of the flow field; and (iv) can simultaneously collect information over a range of scales (Montgomery *et al.*, 1995).

Therefore, from a fish's perspective, a river is not best represented as a habitat checkerboard or mosaic but as a waterscape of fluid features that gradually blend into one another in much the same way that a landscape, at large scales, is primarily comprised of elevation gradients and not elevation breaks (i.e. cliffs). These fluid features can be described in gradients (i.e. spatial derivatives) over certain space scales coupled to the solid features of the channel. Understanding the fluid environment from a fish's perspective is important for river restoration and to manage the impacts of dams and smaller scale structures that alter river flow fields. Importantly, conventional habitat metrics, such as average depth and velocity, mask gradients and are therefore likely insufficient for linking fish movement among habitats to environmental processes related to geomorphology or to biogeochemical processing. By responding to magnitudes of velocity and velocity gradient, fish are able to make directed (nonrandom) movements in flow fields, within geomorphological complexity and within biogeochemical fields as long as these fields retain their natural interrelationships.

Taken in total, these findings suggest that it is more useful to think of a large river as a machine rather than as an amalgam of habitat patches. The physical structure of the machine is a sloping plane that alters the magnitude and direction of an applied force. The kinetic energy that runs the machine ultimately derives from gravity which drives complex hydrologic rhythms that are, in turn, coupled to local and to global climate patterns. The force generated by the sloping landform and hydrologic rhythm is hydraulic shear which reconfigures the channel and transports material either through the system or to areas where it can settle and be transformed, perhaps over multiple cycles. Importantly, we are not de-emphasizing the importance of autochthonous or allochthonous organic matter in structuring river communities but rather emphasizing the importance of hydrodynamic pattern to the highly advective river ecosystem.

In a large river system, the amount of organic and inorganic materials that is transported and transformed is immense. A fish, by evolving complex life histories and sophisticated movement behaviours, can take advantage of

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the work performed by the river machine as it transports, stores and transforms materials. This enables fish to limit energy expenditure in foraging for widely distributed food when riverine processes naturally accumulate food and organic matter in parts of the river at certain times. Therefore, the primary challenge for fluvial-dependent fishes is not to find specific microhabitats but to synchronize their life history to cues that describe and predict the rhythms of the system so that they can take advantage of the work done by the river. They do this by using basic hydrodynamic cues that allow them to find 'hot spots' and 'hot moments' of biochemical transformation (*sensu* Vidon *et al*., 2010) at a system level. For example, the organic matter available to fishes in the lower Mekong River produces a yield of approximately 2.6 million tons per year (Hortle, 2007). Similarly, the Illinois River provided much of the protein needs for the city of Chicago and was considered to be one of the most productive fisheries ever recorded (Fremling *et al*., 1989). Transport of material is usually considered only in the downstream direction, but upstream migration by fish, particularly salmon and detritivores because they are so abundant, can return biomass and energy to upper-river reaches. In this context, migratory fish are a unique component of the system capable of transporting substantial carbon and nutrients against the natural gradient and therefore, delaying the loss of this material and improving the biological production of the system. Fish also transport larval mussels against the natural gradient that then establish persistent multi-species communities that intercept carbon, cycle it into forms more available to other plants and animals while sequestering carbonates as shell material. The Paraná basin contains more than 50 migratory fish species (Carolsfeld *et al*., 2003). Fragmentation caused by regulation of many South American large rivers has reduced or even eliminated upstream energy flow transported by migratory fish.

The river machine is capable of substantial mass conversion driven by fundamental forces acting across a continuum of time and space scales. Regulation must alter the way the machine works because a substantial part of the kinetic energy of the river is harnessed for power production or other uses that change the magnitude of force and timing of this regime. Sustainable development requires that substantial components of the structure of the river machine and the work that it does be understood and preserved. For example, Amsler and Drago (2009) demonstrated that the Parana River downstream of the large chain of dams located in the Upper basin (Brazil) has lost 60% of its suspended sediments which may, ultimately, reduce the biomass of fish in the river because of the association of organic carbon with river sediments. Biodiversity conservation, particularly for the fluvial-dependent fishes, requires that we understand how their complex life histories and extensive place-searching movement patterns allow them to take advantage of the work performed by the river machine. Without these understandings, the tremendous diversity and abundance of life in large floodplain rivers can neither be conserved nor restored.

Case Studies and Examples

These principles are illustrated by the response of the ichthyofauna in three different reaches of the São Francisco River in Brazil (Figure 2, Table I). Each of the reaches differs substantially in the degree of flow regulation (Figure 3) and associated effects. The lower Velhas River, a major tributary of the middle São Francisco River, is not regulated and still exhibits a pronounced flood pulse. The middle reach of the São Francisco River is heavily regulated by Três Marias Dam (which creates the second largest reservoir of Minas Gerais State). However, tributaries with a confluence downstream of Tres Marias Dam are largely unregulated so that a recovery of the flood pulse occurs with distance downstream of the dam. Finally, the lowest section of the São Francisco River is regulated by eight upstream dams so that the hydrologic signal of the flood pulse has been largely eliminated.

The response of the fish fauna mirrors these different levels of flow regulation. Using the Velhas River fish fauna as a reference, the fish fauna of the middle reach of the São Francisco River with the exception of the reach immediately downstream of the dam is relatively lightly impacted even though the system contains a relatively large upstream dam. Importantly, large numbers of fluvial-dependent fishes occur in this reach although their abundance is reduced. Fluvial-dependent fishes still appear able to migrate to appropriate locations at approximately the right times to take advantage of the work performed by the river machine. Finally, the lower São Francisco is the most regulated reach of the basin because of the operation of eight upstream dams and no substantial unregulated tributaries entering this reach.

As a consequence of river regulation, the kinetic energy regime of the river is substantially impacted, and the material that ordinarily would be transported to the different FUs in an unregulated river instead settles within the reservoirs. Within the reservoir, this material is either lost from the system through sedimentation or contributes towards poor water quality in the seasonally reducing chemical regime of reservoirs instead of settling in the oxidative environment of the floodplain where it could be incorporated into the immense abundance and diversity of life in this river. Energetic pathways also change within fish communities. For example, in Itaipu reservoir in the Parana basin, Hoeinghaus *et al.* (2009) demonstrated that early postimpoundment stages increased ecological efficiency of fisheries production as algivorous–detritivorous species take advantage of detritus accumulation resulting from flooded vegetation and soils.

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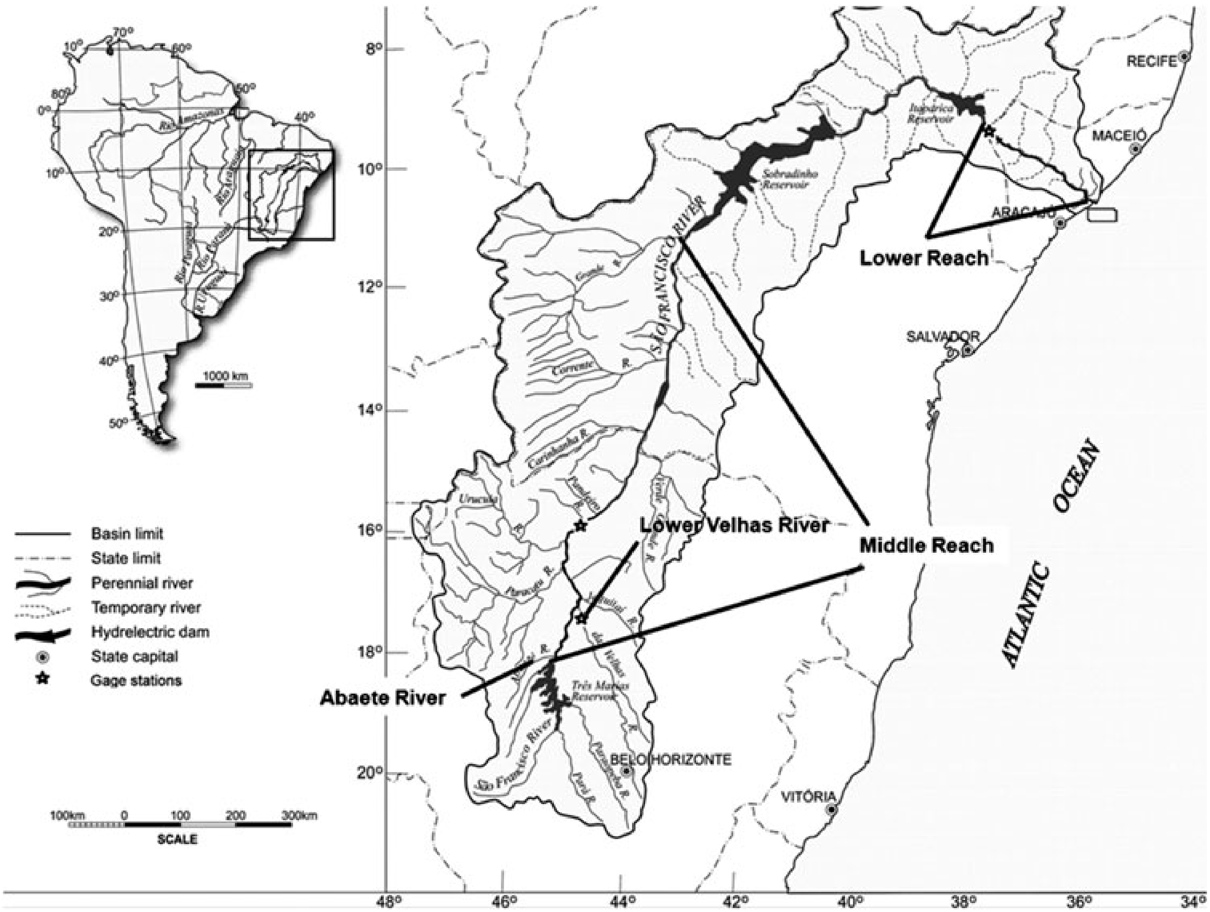

Figure 2. Site map for the São Francisco River of Brazil showing locations of gauges and the Abaete River, the Velhas River and the middle and lower reaches of the São Francisco River

Once Itaipu reservoir stabilized and lentic species increased, ecological efficiency decreased as higher trophic levels become dominant. Not surprisingly, regulated river production is typically much less than in floodplain river systems after trophic upsurge has ended (Jackson and Marmulla, 2000). For example, in the Paraná River basin, the fish yield obtained for reservoirs typically ranges from only 4 to 14 kg/ha (Agostinho *et al*., 2007), and there is an inverse relationship between impoundment area and fish production (Baigun *et al*., 2010). This relationship is caused not only by unfavourable geomorphologic, hydrologic and biogeochemical changes but also because of changes in fish community structure.

Finer scale patterning of fish distribution in response to seasonal changes in water temperature, quantity and quality can also be found in the São Francisco River. Godinho and Kynard (2006) reported that adult female *Prochilodus argenteus* below Tres Marias Dam of the São Francisco River displayed multiple visits to the mouth of the Abaete

Table I. Hydrological and fishery characteristics of three floodplain systems in São Francisco basin, Brazil (based on Sato and Godinho, 2003; Pompeu and Godinho, 2006; Santos, 2009; Santo *et al*., 2009; Santos *et al*., in press)

	São Francisco River floodplain regions		
	Lower Velhas River	Middle São Francisco River	Lower São Francisco River
Elevation	490–510 m	430–500 m	10–90 m
Number of big reservoirs upstream	Zero	One	Eight
Flow regulation	Insignificant	Moderate	Severe
Floodplain fish biodiversity	61 species	48 species	48 species
Large migratory fish extinction?	No	No	Yes
Status of fisheries	No information	Decreased catches	Decreased catches

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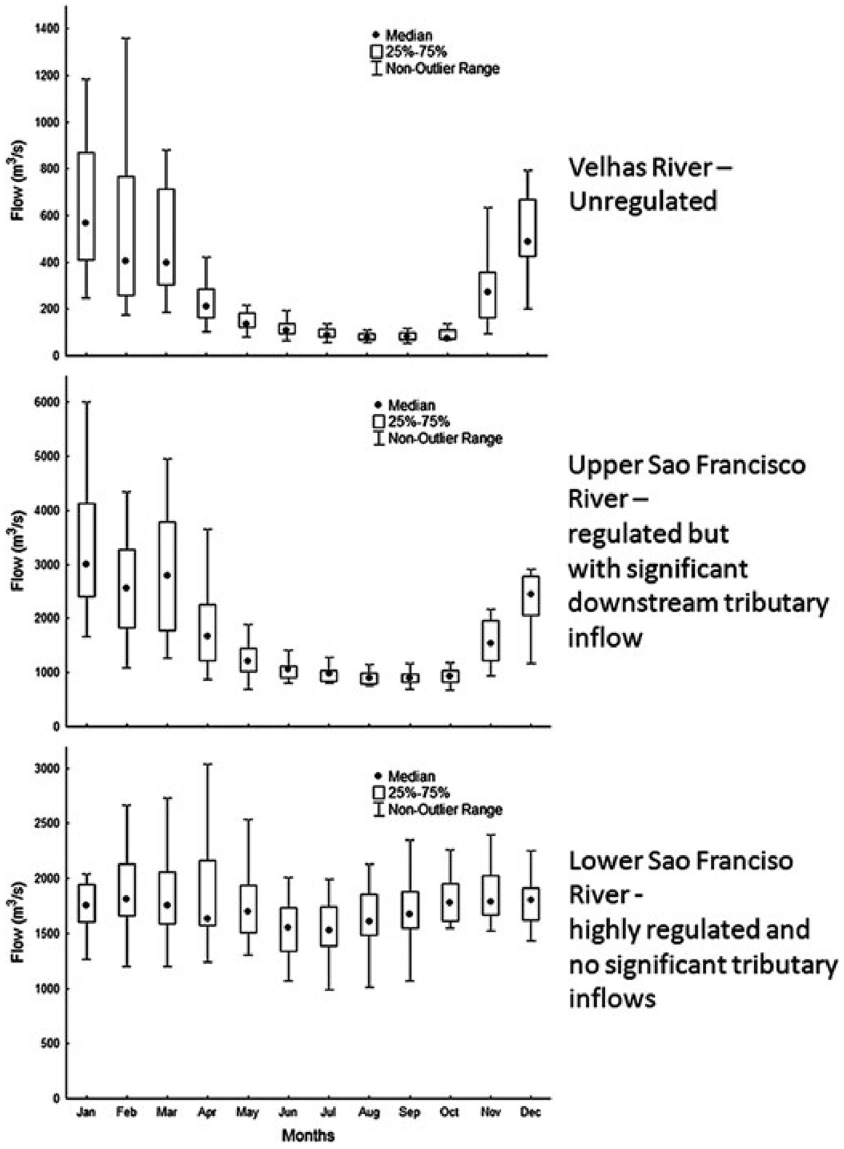

Figure 3. Comparative average anual hydrographs for three reaches within the São Francisco basin. Note the progressive deterioration of the flood pulse from the top plot to the bottom plot. Although the stage at which the river crests its levee is not precisely known, general observations are as follows. The floodplain receives water every year in the Velhas river (Pompeu *et al*., 2005). A large group of floodplain lagoons are flood by a $5000\,\mathrm{m}^3 \times \mathrm{s}^{-1}$ flow (Pompeu and Godinho, 2006) in the middle reach of the São Francisco River. Fishermen report long periods without floodplain submergence in the lower São Francisco River (Santos, 2009)

River (the spawning area for this species) during the spawning season instead of the expected single or reduced number of visits. In contrast, in the middle Paraná River, flow pulses coupled with high temperature trigger a single upstream reproduction migration of this speceis (Oldani, 1990). Godinho and Kynard suggested that unusally frequent spawning could be caused by the mismatch in abiotic variables between where they historically spawned (at the mouth of the unregulated Abaete River) and where these fish must now stage (in the highly regulated São Francisco River main stem below Tres Marias Dam). Water discharged from the Tres Marias Reservoir must have different characteristics from that of the Abaete River because regulation will change water quality and hydrologic pattern. They also demonstrated that temperature and discharge at the Abaete River showed no relation with female *P. argenteus* (sabalo) movements. Therefore, the synchrony was disrupted between the life history of this fish and its cueing variables, such as water temperature or discharge, that signal the state of system-level dynamics of the river and predict its likely seasonal trajectory. The *P. argenteus* population present in the reach between Tres Marias Dam and the downstream confluence with the Abaete River is now genetically distinct from other populations (Hatanaka *et al*., 2006). In addition, adult fish of this subpopulation are smaller than adults of this species occurring further downstream of the confluence with the Abaete River suggesting unfavourable conditions downstream of Tres Marias Dam (Sato *et al*., 1995).

Benthic invertebrate communities are also known to be sensitive to the health of rivers because they are a major pathway of the carbon cycle of temperate rivers. In a major study of paired restored and unrestored European river systems, Jähnig *et al*. (2010) concluded that the lack of difference between the benthic communities of each pair was caused by factors that act at larger (catchment) scales because restoration that changed microscale and mesoscale features appeared ineffective.

Several lessons can be gleaned from the São Francisco River. First, the results show that large fluvial-dependent fishes of the middle reach can be preserved, even in the face of flow regulation, if the river maintains some level of its basic kinetic energy regime, material transport and transformation dynamics and spatial heterogeneity. That is, the fluvial-dependent fishes can still take advantage of the work performed by the river and use their complex life histories and sophisticated movement behaviour to access critical life needs created by the unimpaired functioning of the river.

Second, this progression also illustrates the danger of misapplying habitat metrics to recover or to conserve the biota of large-scale systems. The lower reach of the São Francisco undoubtedly provides micro-hydraulic conditions that support resident fishes because a number of nonmigratory species occur in spite of flow regulation. The danger of characterizing the behaviour of fluvial-dependent fishes using the same microhabitat variables as used for resident fishes, that is, place-selection metrics, becomes clear. Application of these metrics would indicate that microhabitat (e.g. simple average depth, velocity and cover metrics) exists for these species although they have been extirpated. Similar conclusions would be reached for the benthic community of Europe per Jähnig *et al*. (2010). The misapplication of the metrics would lead restoration actions to focus on improved water quality or the provision of fish passage measures and the tight synchrony of these fishes to the flood pulse and associated dynamics would be lost. That is, the river no longer functions as it did prior to regulation, and the fluvial-dependent fishes cannot synchronize their life history and behaviour to the new conditions.

Third, the example and the revised characterization of habitat for large rivers illustrate the danger of reductionist thinking in ecosystem restoration. In a reductionist approach, one would consider separately each of the driving variables that together characterize large rivers. That is, restoration may be considered as separate efforts to restore water quality, reconnect the main channel to the floodplain, or provide for fish passage. However, the realization that these driving variables are interrelated though fluid dynamics patterns in the undisturbed system in which the large river fishes evolved is lost. Therefore, wise stewardship and improved scientific discovery can only result when the time-dependent interrelationships among the driving variables are considered along with their individual mean values and ranges.

CONCLUSIONS

Although a robust and useful theoretical benchmark has been developed to explain how large floodplain river systems work, considerably less effort has been devoted to understand how specific biota, particularly fish, respond to the dynamic, multi-scale habitat variables that define large rivers. Unlike low order rivers where relatively simple geomorphologic and hydraulic variables are useful to define habitat requirements, large floodplain river systems pose formidable challenges due their spatial and temporal complexities. We argue that place-centred habitat assessment is not appropriate to describe holistic characteristics of large river systems. Fish species have developed strategies (e.g. physiological and morphological adaptations, trophic position, migratory movements, growth, recruitment and reproductive patterns) to take advantage of the complexity that is inherent in the river machine concept.

We point out how a general hydro-geomorphic guiding principle based on known or plausible effects of the flood pulse was used to propose general seasonal and spatial patterns in the transport, transformation, production and redistribution of materials within a river corridor. These effects integrate functional and structural linkages among different fluvial components such as floodplains and main and secondary channels. Case studies such as the São Francisco River and the relatively unimpacted middle and lower Paraná system are useful to learn how large river biota, particularly the fish community, are inextricably connected to these structural and functional linkages.

We also conclude that conventional concepts of habitat must be supplemented with a broader perspective that recognizes that fish are capable of at least two behaviours: place-specific behaviours and place-searching behaviours. Conventional approaches to quantify micro-habitat will work well only for fishes that spend most of their time using place-specific behaviours but will not be useful for fishes that spend a substantial part of their time using place-searching behaviours. Without considering place-searching behaviour as a component of habitat and how place searching behaviour allows fish to exploit large river processes, it will not be possible to derive methods necessary to describe the habitat requirements of specific species of large river biota. For this latter group, methods similar to those employed in the ELAM using spatial derivates of the velocity field must be used to understand how these fishes relate to the physical environment of river systems, and therefore how they are integrated into dynamic NHG processes.

The NHG guiding principle was expanded to mechanistically connect environmental fluid dynamics, fluvial geomorphology and biogeochemical cycling via velocity magnitude and hydraulic shear and thereby relate more directly to patterns in the abundance and diversity of large river biota. By studying these patterns in less disturbed large river systems such as the Paraná and São Francisco rivers, valuable information can be gathered and applied to impaired systems, where natural processes are distorted or masked by habitat alterations (Nestler *et al*., 2007). Unlike the general hydro-geomorphology guiding principle, the mechanisms of transport, erosion and deposition of material that derive from it are sufficiently resolved to be evaluated empirically using status and trends monitoring data or process description data. Ideally, these studies would be supported by the same CFD models used to describe movement of emigrants (Goodwin *et al*., 2006) or mussels (Morales *et al*., 2006). That is, CFD modelling can be used to identify and describe the fine-scale erosion and deposition potential of specific parts of the river and its floodplain. Therefore, the mechanisms proposed in this paper can be considered as initial testable hypotheses about how hydro-geomorphology regulates different aspects of biodiversity in large rivers. These hypotheses and others derived in the future can be evaluated and adjusted through the monitoring and assessment phase of adaptive management.

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REFERENCES

Agostinho AA, Gomes LC, Pelicice FM. 2007. Ecologia e Manejo de Recursos Pesqueiros em Reservatorios do Brasil. Ed. Universidade Estadual de Maringa, Maringa, Brazil.

Agostinho AA, Zalewski M. 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Paraná River, Brazil. *Hydrobiologia* **303**: 141–148.

Amsler ML, Drago EC. 2009. A review of the suspended sediment budget at the confluence of the Paraná and Paraguay rivers. *Hydrological Processes* **23**: 3230–3235.

Baigun C, Oldani N, van Damme P. 2010. Represas hidroeléctricas en América Latina y su impacto sobre la ictiofauna. In *Peces de la Amazonía Boliviana:potencialidades y amenazas*, van Damme PA, Carvajal F, Molina J (eds). Ed INIA: Cochabamba; 395–415.

Baigún CRM, Nestler JM, Oldani NO, Goodwin RA, Weber LJ. 2007. Can North American fish passage tools work for South American migratory fishes? *Neotropical Ichthyology* **5**: 109–119.

Baigún CRM, Puig A, Minotti PG, Kandus P, Quintana R, Vicari R, Bo R, Oldani N, Nestler J. 2008. Resource use in the Paraná River Delta (Argentina): moving away from an ecohydrological approach? *Ecohydrology and Hydrobiology* **8**: 245–262.

Bertoldi W, Gurnell A, Surian N, Tockner K, Zanoni L, Ziliani L, Zolezzi G. 2009. Understanding reference processes: linkages between river flows, sediment dynamics and vegetated landforms along the Tagliamento River, Italy. *River Research and Applications* **25**: 501–516.

Bonetto AA, Cordiviola de Yuan E, Pignalberi C, Oliveros O. 1970. Nuevos datos sobre poblaciones de peces en ambientes permanentes del Paraná Medio. *Physis* **30**: 141–154.

Bowen SH. 1983. Detritivory in neotropical fish communities. *Environmental Biology of Fishes* **9**: 137–144.

Buffin-Bélanger T, Rice S, Reid I, Lancaster J. 2006. Spatial heterogeneity of near-bed hydraulics above a patch of river gravel. *Water Resources Research* **42** (4). Art. No. W04413.

Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* **30**(4): 492–507.

Carolsfeld J, Harvey B, Ross C, Baer A (eds). 2003. *Migratory fishes of South América: biology, fisheries and conservation status*. Ottawa International Development Center, The World Bank: Ottawa.

de Vazzoler AEA de M. 1996. *Biologia da Reprodução de Peixes Teleósteos: Teoria e Prática*. EDUEM: Maringá; 169.

Depetris PJ, Paolini JE. 1991. Biogeochemical aspects of South American rivers: the Paraná and the Orinoco. In *Biochemistry of Major World Rivers*, Degens ET, Kempe S, Richey JE (eds). John Wiley and Sons: Chichester; 105–125.

Fausch KD. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* **62**: 441–451.

Fausch KD, Torgersen CE, Baxter CV, Li HW. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience* **52**(6): 483–498.

Flecker AS. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology* **77**: 1845–1854.

Franco de Camargo SA, Petrere M. 2001. Social and financial aspects of artisanal fisheries of middle São Francisco River, MG, Brazil. *Fisheries Management and Ecology* **8**: 163–171.

Fremling CR, Rasmussen JL, Sparks RE, Cobb SP, Bryan CF, Claflin TO. 1989. Mississippi River fisheries: a case history. In *Proceedings of the International Large River Symposium*, Dodge DP (ed). Canadian Journal of Fisheries and Aquatic Sciences, Special Publication 106; 309–351.

Fugi RN, Han S, Agostinho S. 1996. Feeding strategies of five species of bottom-feeding fish of the high Paraná River (PR-MS). *Environmental Biology of Fishes* **46**: 297–307.

Goodwin RA, Nestler JM, Anderson JJ, Weber LJ, Loucks DP. 2006. Forecasting 3-D fish movement behavior using a Eulerian–Lagrangian–agent method (ELAM). *Ecological Modelling* **192**: 197–223.

Godinho AL, Kynard B. 2006. Migration and spawning of radio-tagged Zulega *Prochilodus argenteus* in a dammed Brazilian river. *Transactions of the American Fisheries Society* **135**: 811–824.

DOI: 10.1002/rra

Gore JA, Nestler JM. 1988. Instream flow studies in perspective. *Regulated Rivers: Research and Management* **2**: 93–101.

Graaf, G. 2003. The flood pulse and growth of floodplain fish in Bangladesh. *Fisheries Management and Ecology* **10**: 241–247.

Hamilton SK, Lewis WM, Sippel SJ. 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. *Oecologia* **89**: 324–330.

Hatanaka T, Henrique-Silva F, Galetti PM Jr. 2006. Population substructuring in a migratory freshwater fish *Prochilodus argenteus* (Characiformes, Prochilodontidae) from the São Francisco River. *Genetica* **126**: 153–159.

Høberg P, Lindholm M, Ramberg L, Hessen DO. 2002. Aquatic food web dynamics on a floodplain in the Okavango delta, Botswana. *Hydrobiologia* **470**: 23–30.

Hoeinghaus DJ, Winemiller KO, Agostinho AA. 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. *Ecosystems* **10**: 1019–1033.

Hoeinghaus DJ, Agostinho AA, Gomea LC, Pelicice FM, Okada EK, Latini JD, Kashiwaqui EA, Winemiller KO. 2009. Effects of river impoundment on ecosystem services of large tropical rivers: embodied energy and market value of artisanal fisheries. *Conservation Biology* **23**: 1222–1231.

Hortle K. 2007. Consumption and yield of fish and other aquatic animals from the lower Mekong basin. MRC Technical Paper No. 16. Mekong River Commission, Vientiane, Lao PDR; 87 pp.

Jackson D, Marmulla G. 2000. The influence of dams on river fisheries. In World Commission of Dams, Prepared for Thematic Review II.I: Dams, Ecosystem Functions and Environmental Restoration. Final Report.

Jähnig CJ, Brabec K, Buffagni A, Erba S, Lorenz AW, Ofenböck T, Verdonschot PFM, Hering D. 2010. A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern European rivers. *Journal of Applied Ecology* **47**(3): 671–680. DOI: 10.1111/j.1365-2664.2010.01807.x

Jepsen DB, Winemiller KO. 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. *Ecology of Freshwater Fish* **16**: 267–281.

Junk WJ, Wantzen KM. 2004. The flood pulse concept: new aspects, approaches and applications—an update. In *Proceedings of the Second International Symposium on the Management of the Large Rivers for Fisheries, Volume II*, Welcomme RL, Petr T (eds). FAO Regional Office for Asia and the Pacific: Bangkok, RAP Publication 2004/17; 117–140.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. In *Proceedings of the International Large River Symposium*. Dodge DP (ed). Canadian Special Publication in Fisheries and Aquatic Sciences 106; 110–127.

Lamberts D, Koponen J. 2008. Flood pulse alterations and productivity of the Tonle Sap ecosystem: a model for impact assessment. *Ambio* **37**(3): 178–184. Leopold LB, Wolman MG, Miller JP. 1964. *Fluvial Processes in Geomorphology*. W.H. Freeman and Co.: San Francisco, CA.

Levin SA. 1992. The problem of pattern and scale in ecology. *Ecology* **73**: 1943–1967.

Lowe-McConnell RH. 1999. *Estudos ecológicos de comunidades de peixes tropicais*. Edusp: São Paulo; 535.

Lucas MC, Baras E, Thom TJ, Duncan A, Slavik O. 2001. *Migration of Freshwater Fishes*. Blackwell, Sciences: Oxford.

Marchese M, Ezcurra de Drago I. 1992. Benthos of the lotic environments in the middle Paraná River system: transverse zonation. *Hydrobiologia* **237**: 1–13.

McClain ME (ed). 2002. The Ecohydrology of South American Rivers and Wetlands. IAHS Special Publication 6; 215.

Montgomery JC, Coombs S, Halstead M. 1995. Biology of the mechanosensory lateral line in fishes. *Reviews in Fish Biology and Fisheries* **5**: 399–416.

Morales Y, Weber LJ, Mynett AE, Newton TJ. 2006. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. *Journal of the North American Benthological Society* **25**(3): 664–676.

Moreira-Turcq P, Seyler P, Guyot JL, Etcheber H. 2003. Characteristics of organic matter in the mixing zone of the Rio Negro and Rio Solimões of the Amazon River. *Hydrological Processes* **17**: 1393–1404.

Moreira-Turcq P, Barroux G, Bernardes M, Bonet MP, Maurice-Bourgoin L, Perez M, Seyler P. 2005. In *Dynamics and Biochemistry of River Corridors and Wetlands*, Heathwaite L, Webb B, Rosenberry D, Weaver D, Hayash M (eds). IAHS Publication 294; 19–28.

Munson BR, Young DF, Okiishi TH. 2006. *Fundamentals of Fluid Mechanics*, 5th edition. John Wiley and Sons: Hoboken, New Jersey.

Nestler JM, Sutton VK. 2000. Describing scales of features in river channels using fractal geometry concepts. *Regulated Rivers: Research and Management* **16**: 1–22.

Nestler JM, Baigun CR, Oldani NO, Weber LJ. 2007. Contrasting the middle Paraná and Mississippi rivers to develop a template for restoring large floodplain river ecosystems. *Journal of River Basin Management* **5**(4): 305–319.

Nestler JM, Goodwin RA, Smith DL, Anderson JJ. 2008. Optimum fish passage designs are based on the hydrogeomorphology of natural rivers. *River Research and Applications* **24**: 148–168.

Odum EP. 1971. *Fundamentals of Ecology*. W. B. Saunders Company: Philadelphia.

Ojha CSP, Singh RP. 2002. Flow distribution parameters in relation to flow resistance in an upflow anaerobic sludge blanket reactor system. *Journal of Environmental Engineering* **128**(2): 196–200.

Oldani N. 1990. Variaciones de la abundancia de peces del valle del río Paraná. *Revue D'Hydrobiologíe trop* **23**(1)90: 67–76.

Oldani N, Baigún C. 2002. Performance of a fishway system in a major South American dam on the Paraná River (Argentina–Paraguay). *River Research and Applications* **18**: 171–183.

Parasiewicz P, Nestler JM, Poff NL, Goodwin RA. 2008. Virtual reference river: a model for scientific discovery and reconciliation. 2008. In *Ecological Management: New Research*, Alonso MS, Rubio IM (eds). Nova Science Publishers, Inc.; 189–206. ISBN: 978-1-60456-786-1.

Petrere M Jr. 1985. Migraciones de peces de agua dulce en America Latina: algunos comentarios. *COPESCAL Documento Ocasional, Roma* **1**: 1–17.

Poff NL. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**: 391–409.

Poff NL, Ward JV. 1990. The physical habitat template of lotic systems: recovery in the context of historical pattern of spatio-temporal heterogeneity. *Environmental Management* **14**: 629–646.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime: a paradigm for river conservation and restoration. *Bioscience* **47**: 769–784.

Pompeu PS, Callisto M, Alves CBM. 2005. The effects of urbanization on biodiversity and water quality in the Rio das Velhas basin, Brazil. *American Fisheries Society Symposium* **47**: 11–22.

Pompeu PS, Godinho HP. 2006. Effects of extended absence of flooding on the fish assemblages of three floodplain lagoons in the middle São Francisco River, Brazil. *Neotropical Ichthyology* **4**: 427–433.

Pringle CM, Naiman RJ, Bretschko G, Karr JR, Oswood MW, Webster JR, Welcomme RL, Winterbourn MJ. 1988. Patch dynamics in lotic systems—the stream as a mosaic. *Journal of the North American Benthological Society* **7**(4): 503–524.

Quirós R, Baigún C. 1985. Fish abundance related to organic matter in the Plata River basin, South America. *Transactions of the American Fisheries Society* **114**: 377–387.

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar R. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* **7**: 433–455.

Richey JE, Victoria RL, Salati E, Forsberg BR. 1991. The biogeochemistry of a major river system: the Amazon case study. In *Biochemistry of Major World Rivers*, Degens ET, Kempe S, Richey JE (eds). John Wiley and Sons: Chichester; 57–74.

Richter BD, Baumgartner JV, Powell J, Braun DP. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* **10**(4): 1163–1174.

Richter BD, Baumgartner JV, Braun DP, Powell J. 1998. A spatial assessment of hydrologic alteration within a river. *Regulated Rivers: Research and Management* **14**: 329–340.

Roesch KA, Winemiller LO, Layman CA, Zeiug SC. 2009. Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: evidence from stable isotopes. *Acta Oecologica* **35**: 513–522.

Santo ML, Pompeu PS, Alves CBM, Santos HA, Okuma DKL. 2009. Evaluation of ictiofauna diversity loss due to flow regulation in the lower course of the São Francisco River (Brazil). In *Proceedings of the 7th International Symposium on Ecohydraulics*. Universidad de Concepcion: Concepcion; 10.

Santos ML. 2009. Avaliação das alterações na comunidade de peixes de lagoas marginais do baixo curso do rio São Francisco em função de barramentos. Master Thesis, Federal University of Lavras, Lavras, Brazil.

Santos HA, Okuma DKL, Pompeu PS. in press. Changes in the flood regime of São Francisco River (Brazil) from 1940 to 2006. *Regional Environmental Change*.

Sato Y, Godinho HP. 2003. Migratory fishes of the São Francisco. In *Migratory Fishes of South America: Biology, Fisheries and Conservation Status*, Carolsfeld J, Harvey B, Ross C, Baer A (eds). IDRC/World Bank: Victoria, Canada; 195–232.

Sato Y, Miranda MOT, Bazzoli N, Rizzo E. 1995. Impacto do reservatório de Tres Marias sobre a piracema a jusante da barragem. XI Encontro Brasileiro de Ictiologia; 2.

Smith DL, Brannon EL. 2007. Influence of cover on mean cover hydraulic characteristics in small pool riffle morphology streams. *River Research and Applications* **23**: 125–139.

Smith DL, Brannon EL, Odeh M. 2005. Response of juvenile rainbow trout to turbulence produced by prismatoidal shapes. *Transactions of the American Fisheries Society* **134**(3): 741–753.

Smith DL, Allen MA, Brannon EL. 2008. Characterization of velocity gradients inhabited by juvenile Chinook salmon by habitat type and season. In *Advances in Fisheries Bioengineering. American Fisheries Society, Symposium 61*, Amaral SV, Mathur D, Taft EP III (eds). American Fisheries Society Bethesda: Bethesda, Maryland; 53–70.

Southwood TRE. 1997. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**: 337–365.

Stanford JA, Ward JV, Liss WJ, Frissell CA, Williams RN, Lichatowich JA, Coutant CC. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management* **12**: 391–413.

Taylor B, Flecker AS, Hall RO. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* **5788**: 833–836.

Thoms MC, Parsons M. 2002. Eco-geomorphology: an interdisciplinary approach to river science in *The Structure, Function and Management Implications of Fluvial Sedimentary Systems* (Proceedings of an international symposium held at Alice Springs, Australia, September 2002). IAHS Publ no. 276.

Thorp JH, Thoms M, Delong MD. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* **22**: 123–147.

Townsend CR. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* **8**: 36–50.

Townsend CR, Hildrew AG. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology* **31**: 265–276.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.

Vidon P, Allan C, Burns D, Duval T, Gurwick N, Inamdar S, Lowrance RR, Okay J, Scott D, Sebestyen S. 2010. Hot spots and hot moments in riparian zones: potential for improved water quality management. *Journal of American Water Works Association* **46**(2): 278–298.

Ward JV, Stanford JA. 1983. The serial discontinuity concept of lotic ecosystems. In *Dynamics of Lotic Ecosystems*, Fontaine TD III, Barell SM (eds). Ann Arbor Science Publishers: Ann Arbor, Michigan; 29–42.

Webster JR, Patten BC. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. *Ecological Monographs* **19**: 51–72.

Welcomme R, Halls A. 2004. Dependence of tropical river fisheries on flow. In *Proceedings of the Second International Symposium on the Management of Large Rivers For Fisheries* **2**, Welcomme RL, Petr T (eds). Sustaining Livelihoods and Biodiversity in the New Millennium, 11–14 February 2003. Phnom Penh: 267–283.

Winemiller KO. 2004. Floodplain river food webs: generalizations and implications for fisheries management. In *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries, Volume II. Sustaining Livelihoods and Biodiversity in the New Millennium*, Welcomme R, Petr T (eds). FAO Regional Office for Asia and the Pacific: Bangkok. RAP Publication 2004/17.

Winemiller KO, Jeppsen DB. 1998. Effects of seasonality and fish movements on tropical river flood webs. *Journal of Fish Biology* **53**: 267–296.

Winemiller KO, Montoya JV, Roelcke DL, Layman CA, Cotner JB. 2006. Seasonally varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river. *Journal of North American Benthological Society* **25**: 250–262.

Wohl E, Angermeier PL, Bledsoe B, Kondolf GM, MacDonnell L, Merritt DM, Palmer MA, Poff NL, Tarboton D. 2005. River restoration. *Water Resources Research* **41**: W10301.

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