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Use of Ecohydraulic-Based Mesohabitat Classification and Fish Species Traits for Stream Restoration Design

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Abstract: Stream restoration practice typically relies on a geomorphological design approach in which the integration of ecological criteria is limited and generally qualitative, although the most commonly stated project objective is to restore biological integrity by enhancing habitat and water quality. Restoration has achieved mixed results in terms of ecological successes and it is evident that improved methodologies for assessment and design are needed. A design approach is suggested for mesohabitat restoration based on a review and integration of fundamental processes associated with: (1) lotic ecological concepts; (2) applied geomorphic processes for mesohabitat self-maintenance; (3) multidimensional hydraulics and habitat suitability modeling; (4) species functional traits correlated with fish mesohabitat use; and (5) multi-stage ecohydraulics-based mesohabitat classification. Classification of mesohabitat units demonstrated in this article were based on fish preferences specifically linked to functional trait strategies (i.e., feeding resting, evasion, spawning, and flow refugia), recognizing that habitat preferences shift by season and flow stage. A multi-stage classification scheme developed under this premise provides the basic "building blocks" for ecological design criteria for stream restoration. The scheme was developed for Midwest US prairie streams, but the conceptual framework for mesohabitat classification and functional traits analysis can be applied to other ecoregions.

Keywords: stream restoration; species functional traits; fish mesohabitat classification; Midwest stream habitat; stream ecology; habitat suitability; ecohydraulics; patch dynamics

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1. Introduction

Since the 1990s, stream restoration practice in the Unites States (US) has grown significantly, largely motivated by goals to: improve instream habitat, riparian corridors and water quality, comply with regulations for compensatory mitigation, stabilize channels and banks for land and infrastructure protection, remove fish passage barriers, and enhance aesthetics in urban corridors [1–5]. It must be noted that "restoration" is now broadly used by practitioners in the US to include rehabilitation, revitalization, naturalization, and other river engineering activities. The natural channel design (NCD) approach is the mostly widely used methodology, which requires a reference stream reach as an analog and applied dimensionless geomorphic ratios for planform and channel forms [6–10]. Other restoration design approaches rely on hydrologic/hydraulic analysis coupled with geomorphic principles [11–13]. Practitioners use these approaches to reconfigure channels and commonly install hard structures in order to adjust sediment transport capacity and create stable morphologies [14–16]. Ecological concepts may be incorporated into design but procedures are less methodical predominantly relying on available bioassessment data and professional judgement to place various habitat features. Though the physical sciences are employed to a greater extent than the ecological sciences, the most commonly stated objective for projects is to restore the biological integrity by enhancing habitat and water quality [4,5]. However, recovery of biological integrity from restorations has been mixed depending on how initial project goals were defined, and the organism group (i.e., fish, macroinvertebrates, mussels, periphyton) used to assess outcomes [1,17–24]. Considering the current practices and reported project biological responses, improvements are needed on how to incorporate ecological criteria into the restoration design process, and better understand the potential capacity for ecological recovery within stressed ecosystems.

When ecology is considered in stream restoration design, fluvial geomorphology, engineering hydraulics, and aquatic ecology are generally applied sequentially in this listed order (Figure 1a). This linear design thinking tends to rely on the "build it and they will come" premise for ecological considerations [25,26]. The NCD approach assumes that the selected geomorphic reference provides the physical habitat template needed to enhance the restored reach's biological integrity, but this may not always be the case. For example in low-gradient alluvial streams, construction of weirs to scour a pool (e.g., J-hook and V-cross vanes) may benefit pool habitat species, but riffle habitat specialists may be compromised if the weir reduces riffle length immediately upstream by creating a long backwater glide [19]. Even with favorable restored habitat, the potential species pool for recolonization is dependent on the watershed-scale multiple stressors and reach-scale barriers limiting dispersal [21,27–31]. Recolonization potential at the watershed-scale can be evaluated if adequate bioassessment data are available, and such data are also useful for project scoping [10,24]. Bioassessments guide what basic ecological concepts are incorporated into the geomorphic design, but generally lack the detailed pre-design ecological data needed to specifically target habitat needs. Data needed includes field surveys of sequentially-mapped mesohabitat units and biota; in addition to the use of habitat suitability criteria (HSC) for target species-habitat relationships applied in hydraulic habitat models [32].

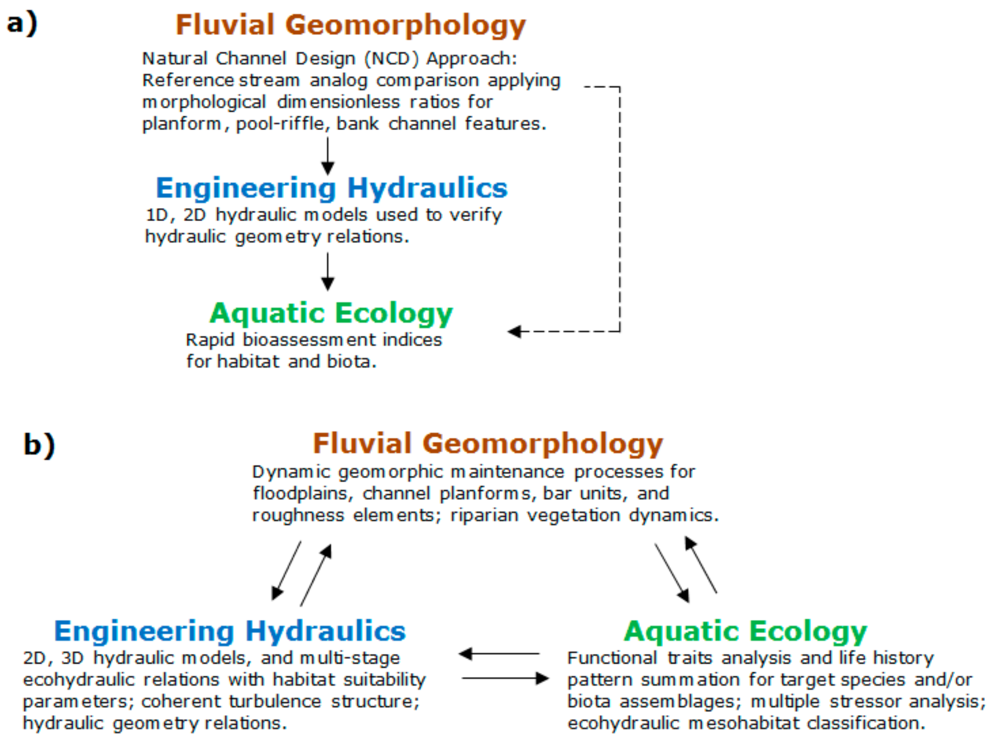

Figure 1. Multidisciplinary design processes for stream restoration: (**a**) as commonly practiced; and (**b**) per an ecohydraulics mesohabitat approach.

1.1. Ecological Concepts: Broad Applications for Stream Restoration

Lake et al. (2007) [33] summarized ecological concepts that are, or can be used to broadly guide stream restoration designs, noting spatial scale and associated processes are critical to project success. Biota distribution and abundance are governed by physical habitat structure spatially organized within a hierarchical structure and each subsequent scale consisting of geomorphic and ecological processes [34–37]. Frissell et al. (1986) [38] describes the classic view of this hierarchical structure within a watershed from segment, reach, channel (pool-riffle) unit to the microhabitat channel bed scale. Physical habitat structure at the reach and channel unit scales can provide refugia from hydrological disturbances (floods and droughts) enhancing ecosystem resilience [27]. The episodic nature of habitat characteristics with respect to flow and other environmental conditions is described by the Patch Dynamics Concept, where the spatio-temporal dynamics of favorable habitat space for biota varies in frequency and duration [39–42]. Patch dynamics recognizes the dominance of abiotic controls on biotic communities associated with habitat heterogeneity, and these controls under natural disturbance regimes promote biodiversity [43]. In general, restoration designs that apply these concepts aim to increase habitat heterogeneity, typically channel reconfiguration and use of instream structures, i.e., weirs, logs, root wads, and lunkers [44,45].

Connectivity within a watershed's riverine corridor can be viewed multidimensionally per longitudinal, lateral, and vertical dimensions, which influence food webs and trophic structure [37,46–49]. The River Continuum Concept [50] as the framework for longitudinal connectivity describes the shifts in tropic dynamics and organism assemblages correlated with allochthonous organic sources in the headwaters to more autochthonous sources in less shaded, larger downstream reaches. To note, this river continuum is inverted in prairie watersheds of the Midwest US [51]. The Flood Pulse Concept [52] describes ecological processes associated with lateral connectivity between the channel and floodplain among different hydrological regimes. Recently more attention has been given to vertical connectivity with stream restoration, characterizing the potential influence of the hyporheic zone on water quality and nutrient reduction [53–56]. Understanding organic matter processing, nutrient cycling, and water quality are all important ecological considerations for stream restoration design [57]. General ecological application of these multidimensional concepts consist of channel modifications with an aim to reduce habitat fragmentation, reconnect the channel with the floodplain for high flows, provide riffle habitat, and revegetate the riparian corridor.

1.2. Habitat and Biological Assessments

Habitat composition and quality are assessed through field surveys that rely on mesohabitat classification schemes, visually identifying habitat units, e.g., pools, riffles, glides, rapids, etc. [58–65]. Environmental agencies accompany mesohabitat surveys with biological surveys for fish and/or macroinvertebrates typically, and both surveys are used to compare with reference stream conditions to generally assess a stream reach's biological integrity [65,66]. Studies assessing the ecological health of streams have extensively relied on linkages between physical habitat quality and biota composition [22,66–70]. Kaufmann et al. (1999) [64] described a field protocol of longitudinally mapping mesohabitat units in sequence, and collecting basic dimensions of each unit and information on riparian vegetation and microhabitat features, i.e., large woody debris (LWD), overhanging bank vegetation, and large rocks. In alluvial systems with less than 2% grade, pool-riffle sequences along the channel bed are a dominant geomorphic and habitat feature if undisturbed [71–76]. Ecologically, pools and riffles are essential because so many lotic species have evolved their body morphology and behaviors to specifically occupy one unit or the other [77–79]. Because projects commonly involve channel reconfigurations at the reach-scale, pool-riffle sequences become a key morphological structure for restoration design [2–5,19]. Success of restoration projects with habitat enhancement objectives requires mesohabitat units to be designed such that geomorphic and hydraulic principles are applied for long-term dynamic stability by self-regulating maintenance processes [32,80,81]. In addition, ecological success of projects may require more detailed information on species-habitat relationships for target species or biota assemblages during the pre-design process.

Recently in the US, there has been a growing need to better assess ecological successes from stream restoration projects, largely driven by the compensatory mitigation regulations under Section 404 of the Clean Water Act [82,83]. Administered by the US Army Corps of Engineers through project permitting, required compensation for loss of stream functions from anthropogenic impacts are offset by restoration in a nearby stream. Under the 2008 Federal Mitigation Rule, mitigation credits used in stream restoration banks require assessing loss of stream functions and quantifying gains from restoration. The difference between restoration gains and pre-restoration losses has been termed "functional lift", where Harmon et al. (2012) [83] frames the analysis protocols as a stream functions pyramid and functional metrics are composited into a score, or lift. The pyramid framework is founded on geology and climate, and consists of five categorical levels with hydrology at its base, and sequentially followed by hydraulics, geomorphology, physicochemical or water quality, and lastly biology. It also relies on NCD methodology for geomorphic metrics, and bioassessments consisting of indices of biotic integrity (IBI) and habitat quality metrics [66]. Expanding on this list of stream functional metrics, many of which are surrogate measures for biological integrity, others have proposed attributes for restoration success as bioindicators focused on assessing ecological processes [4,84–87]. Many of these ecological-process measures are valuable (i.e., primary production, organic matter budgets), but would rarely be used by practitioners due to the expense of data collection and analysis. Hence, the relevance on commonly available bioassessments and habitat quality index scores which are useful for project scoping, and provide general guidance for restoration. As noted in the Introduction above, bioassessment indices need to be disaggregated in order to provide useful pre-design data specifying detailed habitat needs for target species or biota assemblages.

1.3. Hydraulic Habitat Modeling

Hydraulic habitat modeling serves two functions that can be applied to stream restoration design; they are: (1) hydraulic models provide valuable information on geomorphic maintenance processes associated with mesohabitat physical structure; and (2) habitat models utilizing HSC provide the means to apply ecohydraulic principles [88–91]. Mesohabitat preferences by aquatic biota are defined by HSC in which preferences are associated with channel morphology, flow, habitat cover, and physiochemical conditions [92–95]. Among various aquatic organism groups, HSC are most commonly developed for adult fish. Other fish HSC have included multiple life stages, e.g., juveniles, larval, and egg (spawning). Preference relationships primarily include water depth, downstream-orientated velocity, and dominant substrate types where species-specific preferences are scaled from no preference to fully favorable preferred conditions (0 to 1, respectively). Location preferences for fish species are obtained through biological field surveys utilizing pre-positioned areal electrofishing devices (PAEDs) [96]. Developed originally for instream flow incremental methodology in regulated rivers, the Physical Habitat Simulation (PHABSIM) model provides the methodology to link HSC with different flow regimes and channel conditions [93]. With mapped bed substrate types and modeled water depth and velocities for designed channel areas, species preferences per area are summed over the stream reach to generate a single metric termed "weighed usable area" (WUA). PHABSIM is a one-dimensional (1D) model, and limited in application for explicit WUA computations in lateral and floodplain habitats [97,98].

Multidimensional hydraulic models utilizing computational fluid dynamics applications on desktop computers have become more readily available since the 2000s. Tonina and Jorde (2013) [99] reviewed the application of 1D, 2D, and 3D hydraulic models for ecohydraulic studies; in addition to non-numerical models. Hydraulic 2D models based on the depth-averaged St. Venant equation are useful for restoration providing design information in both the longitudinal and lateral dimensions [100–102]. The River2D model also includes a habitat subroutine computing WUAs based on species preference relationships at each user-defined flow cell [103,104]. Non-numerical approaches rely on field surveys coupled with fish occupancy data per classified mesohabitat unit and obtained from PAEDs, e.g., MesoHABSIM [105,106]. They apply statistics to develop multivariate relationships among HSC, habitat hydraulics, and physical features to predict fish occupancy, which can used in channel habitat design [107]. The use of hydraulic habitat models expands the design toolbox for stream restoration, integrating principles from three fundamental disciplines: fluvial geomorphology, engineering hydraulics, and aquatic ecology (Figure 1b). This approach may consider life histories and trait-habitat relationships for target species, or more broadly a composition of biota assemblages but after the geomorphic design parameters have been determined [32,108,109]. Restoring stream habitat based on geomorphic classification of stream reaches can be limiting [29], but coupled with a hydraulic habitat model, species trait-based HSC can be incorporated into restoration design. In general, ecohydraulic models have been used in restoration projects, but their use is minor when considered with the number of projects constructed each year using the NCD method [19,91,102,110–112].

1.4. Developing Ecological Criteria for Stream Restoration Design

It has been suggested that ecological criteria for reach-scale restoration designs could be improved through the use of an ecohydraulic-based mesohabitat survey and species functional traits analysis, including a watershed assessment of the available species pool for recolonization [32]. A trait-based analysis can be completed by specifically linking physical habitat structures with basic biological needs of stream organisms, and fully utilizing existing autecology information on organisms from the potential recolonization pool [20,113–118]. Why an organism occupies a particular stream location at a given time is therefore influenced predominantly by specific channel morphologies and hydraulic conditions [77,80,88,119–124]. Within specific channel morphologies and hydraulic conditions, each species has a unique relationship to the different characteristics of physical stream habitat in order to find the basic biological resources for survival, e.g., food, reproduction, and shelter. Using fish as the "model" organism group, biological resources as trait strategies include: feeding, resting, evasion (escape from predation), spawning, and flow refugia (Table 1). Channel flow patterns have a dominant influence on the organization of biological communities where organisms have evolved to lotic environments that are heterogeneous and temporally variable [43]. The more heterogeneous and complex the physical habitat structure, the greater potential for different species-habitat relationships to occur, which ultimately create more diverse biological communities [21,125–127]. By identifying these relationships based on species functional traits, the ecological significance of process-based hydraulic and geomorphic measures can be systemically developed as ecological design criteria.

This article reviews key principles for stream mesohabitat restoration with an emphasis on integrating fluvial geomorphology, engineering hydraulics, and aquatic ecology; and organized by a fish 'biological needs' framework as presented in Table 1. A multi-stage mesohabitat classification scheme provides the essential link needed to integrate ecohydraulic principles with basic biological needs and geomorphic processes associated with habitat maintenance (Figure 1b). This review focuses on these key principles for Midwest US prairie streams with the objective to demonstrate as a case "region" the fundamental process linkages needed to develop ecological design criteria for mesohabitat enhancement. The linkages are summarized by the following topics:

- Applied geomorphic processes for mesohabitat self-maintenance;
- Mesohabitat-scale ecological concepts;
- Species functional traits relationships with mesohabitats; and
- Ecohydraulic-based, multiple flow-stage mesohabitat classification.

To note, these linkages must be developed conceptually for different physiographic regions with a comprehensive understanding of life histories and traits of the regional species pool. Midwest headwater streams are low-gradient alluvial systems, commonly lack LWD and extensive woody riparian vegetation, and have diverse fish species assemblages. Although this review uses fish as the organism group, macroinvertebrates and other groups can be applied with goals to improve upon ecological criteria for stream restoration design.

Table 1. Basic biological needs or trait strategies for fish guilds organized by flow condition and season: an example for low-gradient alluvial streams in the Midwest US.

Stream Flow Condition	**Season**	
	Summer/Fall	**Winter**
Low and Moderate Base Flows	Feeding Resting Escape from Predation Spawning	Temperature Refuge
High Flows—Floods	Flow Refuge	Flow Refuge

2. Applied Geomorphic Processes for Mesohabitat Maintenance

Two geomorphic scales are relevant to the maintenance processes of mesohabitat units; they are the channel unit (pool-riffle) scale situated hierarchically within the planform (reach) scale [38,128]. Channel units are in the length scale of approximately 1–100 channel widths and reaches are 100–1000 channel widths [35]. In general for the Midwest US, planform types are classified as straight or meandering, and rarely braided [36]. Valley structure and floodplain-channel dynamics exert geomorphic controls on the channel by fixing the longitudinal gradient, and regulating the rate of sediment delivery to the channel. Channel morphology within planforms, including cross-sectional capacity [71,128,129], meander characteristics [130], and local longitudinal profile [131] are dynamically maintained by flood flow events occurring on average every 1–2 years. These flood flows are termed dominant discharge, but practitioners commonly refer to these flows as the bankfull discharge [10,132].

Floodplains are formed by geomorphic processes balancing sediment transport and deposition during flood events and governed by the force-resistance properties of the channel and adjacent riparian areas [129,133–135]. Force is represented as stream power, and resistance consists of a multitude of factors including vegetation, sediment load coarseness, human interventions, etc. Nanson and Croke (1992) [135] classified floodplains based on stream power (energy) and sediment deposition as high- and medium-energy non-cohesive and low-energy cohesive surfaces. Relevant to this review for high-flow habitat refugia are two floodplain process types within the medium-energy non-cohesive classification where stream power ranges from 10 to 60 $W \cdot m^{-1}$. The three floodplain types in meandering channels and associated geomorphic processes at the channel-floodplain interface include:

- Lateral Migrating Floodplains: Lateral point-bar accretion consisting of progressive sediment deposition on the convex bank of a meander bend from helical and divergent flow through the bend [136], which creates elevated and vegetated remnant point bar surfaces;
- Counterpoint Floodplains: Counterpoint accretion occurs within a hydraulic recirculation zone (or large stream eddy) formed against the upstream limb of the convex bank in sharply curving and active migrating bends allowing for fine sediment deposition, which over time form an elevated and vegetated concave bank bench [134]; and
- Abandoned Channel Floodplains: Abandoned-channel accretion occurs in actively migrating channels creating cutoffs followed by overbank vertical accretion, which depending on sediment deposition and location to the active channel the floodplains features include elevated and vegetated remnant channels, and a backwater slough near the mouth of the original channel [137].

Planform characteristics have some control over the regularity of pool spacing [71,128]. For example, in meandering streams with single-loop geometry, pool spacing is highly correlated with meander wavelength, where pools occur at each bend. Within planform reaches, pool-riffle sequences are a product of a mobile gravel-sand bed, in which longitudinally orientated cyclic patterns of erosion and deposition result in pools as local topographic lows and riffles as topographic highs [131]. Pool spacing occurs on average every 5–7 channel unit widths, but the reported range is 1.5 to 23 [72]. Pool-riffle morphology with its unique fluvial properties and spatial pattern represents a stable, but dynamically-varied equilibrium state for channel bed morphology [73–76]. Geomorphic attributes associated with bankfull discharge and pool spacing as noted above are common knowledge and widely applied in the NCD approach for stream restoration [10,44,45].

Less applied directly in restoration design is the velocity-reversal hypothesis, and is the fundamental concept for pool and riffle morphological self-maintenance. This hypothesis defines that during low-flow stages velocities in pools are slow and riffles are relatively fast, and near bankfull high-flows velocities transition where pools are fast and riffles are slow [76,138–143]. A reversal in bed shear stress also occurs from low- to high-flow stages resulting in bed scour in pools and bedload deposition in riffles during high flows. Thus, pools can be distinguished from riffles by their sediment properties, where pools contain more fines and riffles contain a mixed bedload with course gravels and sand. It should be noted that velocity and near-bed shear stress reversals was originally conceived from a 1D hydraulic perspective and based on unit averages.

Geomorphic form and fluvial processes that maintain this pool-riffle morphology are more accurately viewed by 3D channel hydraulics including downstream, lateral, and vertical velocity vectors [144–148]. Channels without major resistance structures will exhibit helical flow patterns which are fundamental to initiation and maintenance of bar structures [149–151]. Arranged together as a bar unit, pool, riffle, and point bar elements are positioned distinctly in a channel meander bend [136]. Pools are located along the outer bank just downstream of the bend apex, riffles are located between bend apices, and point bars are located along the inner bank across from the bend apex. As flow enters the bend it shoals over the point bar forcing flow at the water surface to be directed outward towards the outer bank. In channels without large resistance structures, flow acceleration and deceleration occurs through a pool where flow resistance forms a small, secondary circulation cell with lateral velocities directed toward the inner bank at the water surface. A helical pattern of flow develops through a meander exhibited by transverse or secondary velocity vectors coupled with dominant downstream vectors. It should be noted that multiple helical flows cells can occur in straight channels and the number is dependent on channel width and boundary roughness [152].

Recent studies utilizing 2D and 3D hydraulic models have demonstrated the dominant role of nonuniform flow, secondary circulation patterns, and coherent turbulent structures influencing pool-riffle maintenance processes [152–159]. Expanding to a multidimensional view of hydraulics and sediment routing through pool-riffle, morphological maintenance is explained by flow acceleration at the pool head's cross-sectional constriction during high flows, where flow convergence with maximum velocities and sediment are directed over the point bar rather than the pool thalweg. Whether flow convergence is directed over the point bar is likely dependent on planform, local morphology at the pool entrance, and flow stage, which govern formation of a separation zone and hydraulic recirculation zone over a submerged point bar. It appears flow convergence at the pool head is the dominant driver for development of a secondary circulation cell in the mid-pool area where water depth is deepest, and secondary circulation mobilizes fine sediment [152,154]. Flow deceleration is initiated following the pool front per expanding cross-sectional area and bed slope drop, where MacVicar and Roy (2011) [156] notes from field measurements deceleration correlated spatially with high levels of turbulence intensity. At the tail end of the pool or pool rear, flow deceleration and secondary circulation divergence leads to course sediment deposition into the riffle. Recent interpretation of 3D flow dynamics through the pool suggests that unique ecohydraulic relationships exist among the pool-front, -mid, and -rear areas, in addition to the submerged bar and riffle areas. With the use of a 2D or 3D hydraulic model, maintenance processes associated with velocity- and shear-reversal and flow acceleration-deceleration concepts can be tested during restoration design [19,91,102,159].

While pool spacing is regular in less complex stream reach morphologies where 3D helical flow patterns develop, spacing can be influenced by instream channel structures [128,143]. In streams with large roughness elements, velocity vectors and turbulence intensities scale to these elements, and appear to prevent development of reach-scale 3D helical patterns [91,160]. Scour of alluvial beds occurs very locally from various roughness elements, i.e., LWD, bedrock outcrops, and boulders, which impose a strong local control on pool spacing [139,161]. Pool types have been defined by the formative structure per roughness element or channel feature [162]. The size of the scour zone is dependent of the relative size of the roughness element in relation to channel width, and channel gradient [163,164]. And the spatial position of the scour pool is influenced by local sediment deposition patterns, both longitudinally and laterally [73–76]. Overall, this variability in longitudinal pool spacing is subject to heterogeneity of flow resistance characteristics including the stochastic inputs of large roughness structures to the stream channel and composition of sediment loads. Placement of in-channel structures must be considered during restoration design and appropriately integrated with planform-scale hydraulics, and the number of structures must be related to the available stream power to achieve the channel design outcomes.

3. Applied Ecological Concepts at the Mesohabitat Scale

Many abiotic and biotic environmental factors collectively regulate fish distribution and abundance in streams [122,125,165]. These factors include:

- habitat selection and relative availability of structural requirements in terms of complexity, duration, frequency, and juxtaposition;
- abiotic disturbances such as extremes in flows and temperature; and physiological tolerances to local water quality conditions;
- food availability and food-space-cover relationships;
- resource specialization of fish species; species traits related to body morphology and mode of foraging;
- predator-prey interactions and trophic controls, intra-and inter-specific competitive interactions related to individual size and behavior, and population densities; and
- immigration-extinction and recolonization dynamics.

Fish distribution and abundance are highly variable both temporally and spatially as a function of the multivariate nature of these environmental factors [28,166–169]. The Patch Dynamics Concept offers a valuable perspective of spatiotemporal nature of mesohabitat structure and organism occupancy [40,170,171].

A patch is a spatial unit occupied by an organism and determined by its resource needs [39–42]. It remains subject to scale-dependent functional relationships between biotic interactions and abiotic environmental factors. A patch emphasizes the heterogeneous nature of physical habitat structure, and the temporal changes as environmental conditions vary. Its variable use by individual organisms is a function of spatiotemporal favorability, or less harshness in terms of lotic disturbance regimes [78]. The heterogeneous nature of stream habitat shapes a patch with irregular boundaries, contracting and expanding with the change in flow stage. Because a patch is defined by an organism's resource needs, its space is defined by an ecological process or functional attribute, and has seasonal limits based on individual species' life history and traits. Poff (1997) [114] suggests that species traits data linked with physical habitat attributes can be used to "filter" organism distribution hierarchically among regions and within watersheds. Figure 2 illustrates the importance of the regional species pools and how watershed-scale habitat fragmentation from multiple stressors can influence patch occupancy, in addition to its relevance to stream restoration.

Temporal variability of fish community structure is observed at multiple time scales from hours to years, but within the conceptual framework for mesohabitat use in this article the relevant time scales are the seasonal and flood periods (Table 1). Seasonal fluctuations in fish community structure generally follow a repeatable annual pattern regulated by each species' life history pattern [172–177]. Seasonal fluctuations have been observed in Midwest headwater streams, where fish species richness was greatest in late summer and fall compared to the spring when it was lowest [178,179]. During the winter, mesohabitat use by fish was observed to be preliminarily in deep pools [32]. Expression of species traits and trophic structure strategy are generally related to annual hydrologic variability among different US regions [180]. Poff and Allan (1995) [119] observed hydrologically "stable" streams with fish assemblages characterized as trophic specialists associated with moderate to fast velocities in permanent flows, and hydrologically "variable" streams with fish assemblages characterized as trophic generalists associated with slow velocities in headwater reaches. In part, spatial relations to fish distribution in a watershed and expression of species functional traits cannot be separated from temporal patterns of organization.

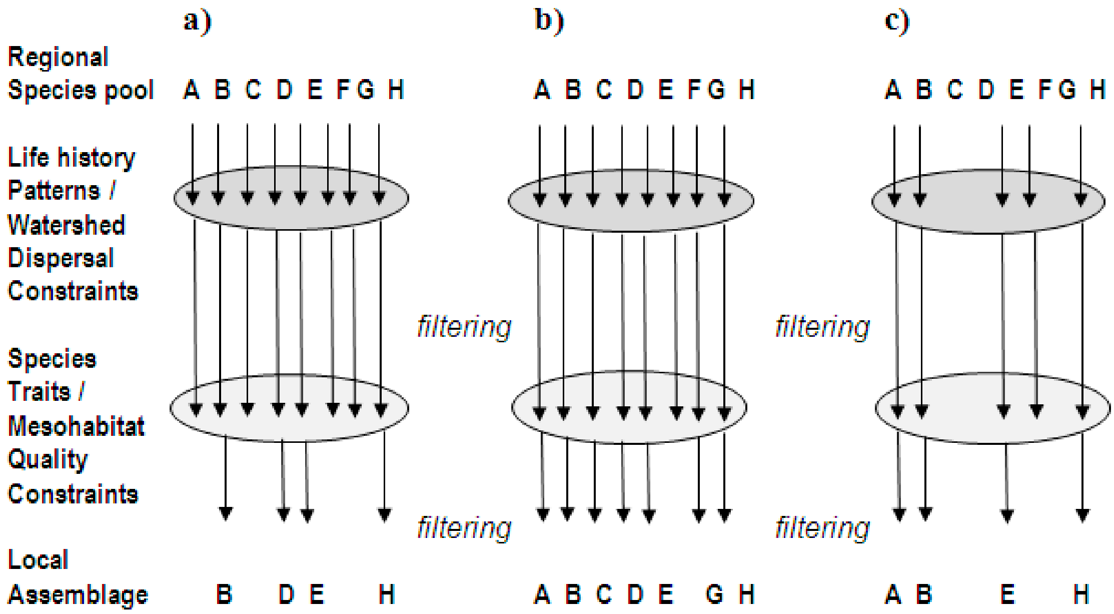

Figure 2. Conceptual basis for a gap analysis for a reach-scale habitat restoration using hypothetical outcomes for: (**a**) no watershed-scale stressors or dispersal constraints and mesohabitat degradation; (**b**) no watershed-scale stressors or dispersal constraints and mesohabitat restoration; and (**c**) watershed-scale stressors and mesohabitat restoration (adapted from Lake et al. (2007) [33]; Poff (1997) [114]; and Belya and Lancaster (1999) [115]).

Flow variability and its effect on stability of fish assemblages have been extensively discussed in relation to extreme flow events, i.e., floods and droughts [181,182]. During floods, habitat selection by fish in Midwestern rivers have been grouped by preference guilds consisting of flood-exploitative species that move onto inundated floodplain and flood-quiescent species that remain in the channel with reduced activity [183,184]. The spatial arrangement of flow refuge within a watershed, and in particular in floodplain areas, appears to be essential for resilience and recovery of fish communities from natural flow disturbances [185–187]. In headwater streams, fish assemblages were observed to be stable and persist over years even after catastrophic floods [188–190], and severe drought conditions [191]. During floods, physical habitat complexity in pools create hydraulic eddies providing shelter as flow refugia. During severe droughts, deep pools provided refuge sites with sufficient water after stream flows ceased and riffles have dried. Fish community structure has evolved over eons adapting to hydrological frequency of extreme flow events correlated with the local geomorphological structure that can provide refuge.

Geomorphological structure, as a scale-dependent abiotic environmental factor strongly regulates fish distribution in watersheds and habitat use patterns that are hierarchically nested [122,125,192]. Within the mesohabitat scale, differential habitat use by fish between pools and riffles has been extensively studied [77,123,175,193–199]. It was observed from these studies that pools and riffles locally diversify lotic conditions providing strong abiotic environmental controls on fish distribution and abundance. For example, in the Pacific Northwest US, coho salmon juveniles and cutthroat trout occupy pools whereas steelhead juveniles occupy riffles [200]. In the Midwest US for example, centrarchid species occupy pools and darter species will occupy riffles [179,197]. Spatial segregation by fish between pool and riffle habitats is also influenced by several biotic factors including predator-prey interactions [194,201], interspecific competition or aggression [202,203], differential body size and body morphology related to energetics of maintaining position in different hydraulic conditions [78,200,204], and innate habitat preferences. Riffles and lateral shallow areas such as submerged point bars provide cover for smaller fish from larger predatory fish [205,206]. Organization of fish assemblages are also associated longitudinally within ecotones between pools and riffles, and laterally per microhabitat complexity, i.e., cover or substrate [77,124,196,207–211].

Recognizing the influence of local hydraulics at the local channel scale, velocity and water depth were used together to associate fish assemblages among pool, riffle, and glide habitats [197,200,203,206,212,213]. Fish preference relationships with local hydraulics are typically measured as depth-averaged velocities in the downstream direction at a single location, along with the total water depth [93]. Based on these same fluvial attributes of velocity and depth, Bain et al. [207] separated fish preference guilds into a habitat specialist that preferred slow velocity and shallow depth, and a habitat generalist that preferred fast or slow water and deep depths. In other studies, habitat preference guilds included differentiating life stage of a fish species, as young-of-the-year and juveniles selected slow velocity, shallow water habitats [197,204]. Local hydraulics influence fish habitat use directly or indirectly based on various biological needs, such as food resources [209,214,215], predation cover [210,216], and spawning requirements [217]. These studies referenced above provide the ecohydraulics perspective for fish habitat use and application for restoration design [80,218–220].

4. Species Functional Traits

In the previous section on ecological concepts, species functional traits were interrelated with species-habitat relationships, species distribution and abundance, and suitability criteria for preferential mesohabitat use, i.e., water depth, velocity, substrate; proximity to instream structural elements; and bank vegetative cover [113,116,221–226]. This section expands on the review of fish trait-based concepts because of its key role for the development of multi-stage ecohydraulic-based mesohabitat classification schemes. Importantly, classification needs to recognize species-habitat relationships within the variable nature of lotic environments and habitat favorability per organism as reflected in the Patch Dynamics Concept.

Frimpong and Angermeier (2010) [113] provided a detailed review of fish species traits and the theoretical and applied use in studies supporting the development of bioassessment protocols with indices of biotic integrity (IBI), linking species responses to habitat degradation, and interpreting mechanisms of assemblage structure and community ecology. They also suggested that species traits could be used in general assessment rules forming the basis of management and conservation tools, including species recovery through restoration. A key objective of this review is to demonstrate how species traits, with the integration of geomorphic and ecohydraulic principles can be used to better define mesohabitat units for restoration assessment and design. Understanding basic definitions associated with traits supports this review's objective. Formally, a trait is defined biologically as the physiological requirements, morphological adaptations, and life histories innate to a species; and ecologically as the species' environmental preferences and associated behaviors [113,227,228]. McGill et al. (2006) [228] defines a functional trait as a species trait that strongly influences organism performance, fitness, and/or survival; and that it must be measurable. The use of the terms, species traits and functional traits has been used interchangeably in literature [113].

With fish community ecology, the Guild Concept is most applicable where co-occurring species are aggregated based on their exploitation of a common resource [113,229–231]. The term "functional groups" used primarily for macroinvertebrate communities differs from guilds in that co-occurring species perform a common ecosystem function by their mode of resource utilization, i.e., shedders, scrapers, and collectors. Fish guilds can be grouped by the dominant strategies or daily activities of resource use including feeding (food habitat, diet choices, and/or trophic structure); reproduction (spawning), resting, escape from predation (evasion), and shelter (flow refugia). These biological needs or strategies are reflected in Table 1, which define the framework for classifying mesohabitat units in Midwest headwater streams (Section 5 below).

The Guild Concept was applied in the development of the IBI by Karr (1991) [232]. IBI are broadly used in state biomonitoring programs to biologically assess environmental from poor water quality and habitat alteration [233–236]. It compresses categorical metrics for various fish traits (i.e., feeding and reproductive guilds, physiological tolerance) and other ecological indicators (i.e., richness and diversity) into a single score, in which the assessment score is compared with state reference condition scores [237]. The single IBI score is valuable as a screening tool to scope potential restoration projects, but is inadequate for design purposes. Differing from the IBI bioassessment approach, trait-based analyses have been specifically applied to assess habitat degradation by observing shifts in fish community composition, statistically [227,238–243]. Assessing levels of degradation with or without the use of a reference comparison, trait-based approaches reduce dimensionally overcoming the cumbersomeness of multispecies statistics. Overall, it is trait-based data interrelated to physical habitat structure within guild categorical metrics that potentially provide the useful information for restoration design.

Further study associated with fish species traits will certainly improve our knowledge of fish ecology and applications for management. Frimpong and Angermeier (2010) [113] suggest future research should aim to advance our understanding of how trait breadth and plasticity relate to fish recruitment and population performance in episodic fluvial environments. In addition, improved statistical techniques for assessing impairment and modeling tools for predicting fish assemblages among local habitat gradients are suggested [242–244]. Though this area has potential for advancement, species traits can effectively be used in stream restoration design by using presence/absence data from field surveys and utilizing a trait database [245]. These data are assessed to determine whether traits are expressed at a proposed project site, or should be based on a reference condition and barring no filtering by watershed-scale stressors (Figure 2). Species traits can be applied in channel restoration designs with the goal of enhancing mesohabitat heterogeneity and fish assemblage diversity, but in doing so it is required that classified mesohabitat units have a functional relationship with trait strategies. Conceptually, trait strategies are associated with mesohabitat structure as defined by unit types, and associations are developed based on HSC and other preference information that are available (Figure 3).

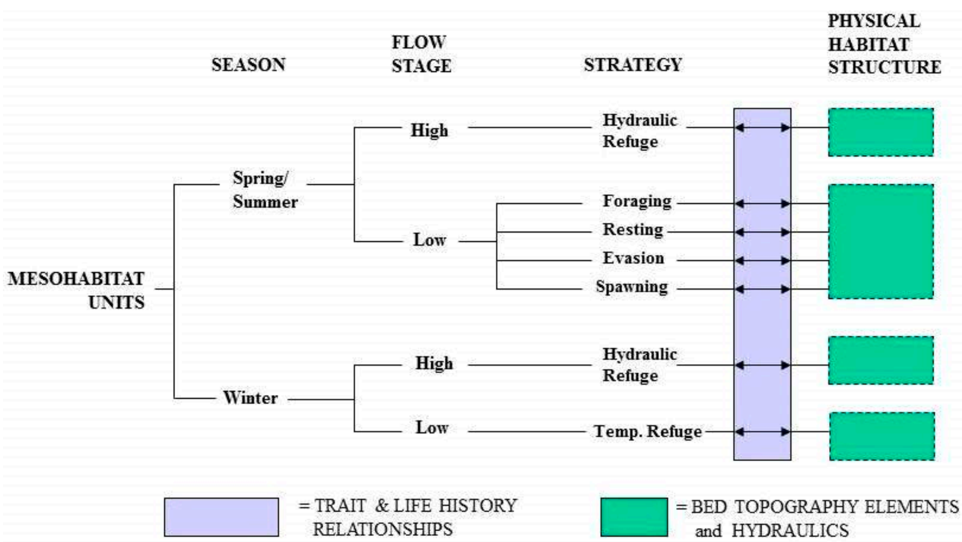

Figure 3. Conceptual framework for developing a mesohabitat classification scheme for low-gradient Midwestern headwater streams applying species trait and life history relationships.

5. Multi-Stage Ecohydraulics-Based Mesohabitat Classification

5.1. Framework for Classification of Multi-Stage Ecohydraulics-Based Mesohabitat Units

Mesohabitat unit types are commonly classified as different pool types for slow water, and glides, riffles, rapids, and cascades for fast water [61,63]. In-stream delineation criteria for mesohabitats based on low-flow stages rely on water depth, water surface slope and visual turbulence conditions, water velocity, substrate characteristics, and instream structural controls. Pools are differentiated by formative structures, for example LWD that causes formation of a scour hole in the bed during high flows, or a beaver dam that causes a backwater pool at all flow stages [162]. Many mesohabitat classification schemes have been developed presenting modifications to this basic terminology though delineation criteria remain essentially the same [58–61,64,77,246,247]. In general, these existing delineation criteria for mesohabitat unit types among the units rely on geomorphic structures and a 1D view of channel flow at low-flow stages.

Flow or physical biotopes have been used as a term to describe these same mesohabitat units emphasizing hydraulic condition and biota unit use [120,121,246–249]. Based on varying low-flow conditions, ecological criteria have been linked to the mesohabitat classification of "functional habitat units" [120]. Functional habitat units conceptually recognized the importance of varying local hydraulics and its influence on biotic environmental factors. Kocik and Ferreri (1998) [248] conducted a field study applying the Patch Dynamics Concept, and related the spatial arrangement of functional habitat units to fish dispersion and spawning. Though these classification schemes begin to integrate physical habitat space with ecological functions at low flow stages, 3D mesoscale hydraulics patterns are not applied to habitat delineation at both low- and high-flow stages. At higher flow stages, channel hydraulics for the same habitat space change, as well as the fish use and survival strategies [120,250–253]. For example, Wadson and Rowntree (1998) [251] applied the biotope classification system to three different flow stages and reported percentages of pool and riffle units decreased with higher flow stages, while percent glide units increased. Because low-flow habitat units are maintained geomorphologically during the high flow events, there is a direct spatial relationship between habitat units classified at both these flow stages; however little attention has been given to classifying high-flow habitat refugia within a geomorphic process framework [32].

The advantage of applying 3D hydraulic models to mesohabitat classification is that they better represent the fluvial environment experienced by aquatic biota at multiple flow stages. This is a fundamental principle in ecohydraulic applications [88,90,91]. Classically, mesohabitat classification schemes have been developed by biologists applying their knowledge of spatial patterns of biota occupancy related to published geomorphic river forms [38,58,61]. Compared with biologists, hydraulic engineers view the fluvial environment through the application of computational fluid dynamic (CFD) models, routing water mass and momentum among a modeler defined numerical mesh space [99]. Turbulence modeled at a micro-scale are a function of Reynolds stresses of fluid motion and boundary layer resistance are scaled to topography and in stream structures [254–259]. Discipline differences are best exemplified by the use of the term "turbulence", where biologists refer to it as "wavy" surface waters as criteria for mesohabitat classification and hydraulic engineers apply CFD at the micro-scale noted above [58,63]. When applying ecohydraulics to mesohabitat classification, it appears that there is a neglected ecohydrogeomorphic scale that occurs between the microhabitat and channel unit (pool-riffle) scales, as defined by the hierarchical habitat framework in Frissell et al. (1986) [38]. Microhabitats are scaled to features on the stream bed <1 m, i.e., rocks, woody debris, macrophytes, etc., where channel units are scaled to geomorphic forms greater than 1–10 channel unit widths [35,36,260]. Relevant to fish use of habitat space and termed as a mesohabitats in this article, 3D hydraulic and turbulence patterns are scaled to large roughness elements (e.g., boulders, LWD) and a length dimension less than one channel unit width [160,261].

In order to improve on existing classification schemes, mesohabitat units should be viewed as patches of irregularly-shaped, three-dimensional space that: (1) vary in shape as a function of flow stage consisting of 3D constructs orientated longitudinally and laterally within the channel; (2) provide for the basic resource needs of organisms as a function of species traits; (3) are bounded by bed topography elements regulated by geomorphic processes associated with self-maintenance; and (4) associate habitat suitability with ecohydraulic relationships reflecting mesoscale 3D hydraulic and turbulence patterns. These criteria are founded in the conceptual framework proposed in Figure 3 recognizing how the fluvial environment meets the biological resource needs of fish, specifically for the following strategies: feeding, resting, spawning, escape from predation, temperature refuge, and flow refuge; and organized by streamflow stage and seasonal period. Key background information on these elements and existing mesohabitat classification schemes are summarized in the following subsections.

5.2. Mesohabitat Units at Low-Flow Stages

Mesohabitat units at the low-flow stage represent bed topography elements characterized by geomorphological and hydraulic characteristics, relative flow depths, and relations to trait strategies (Table 2). Based on formative geomorphic processes, mesohabitat units were grouped into erosional and depositional subcategories [79]. Formative geomorphic processes refer to the aggradation and degradation of bed sediments during high-flow discharges that create and maintain the complexity of the channel bed morphology, termed herein as bed topography elements [74,75]. Hydraulic characteristics associated with the different morphologies were based on 3D acoustic Doppler velocimeter (ADV) measurements [147,262]. Fish mesohabitat use was determined by PAEDs specifically designed to collect fish within exact unit boundaries and without fright bias [93,96]. Collectively, the classification scheme was based on field observations of geomorphic structure, hydraulics, and fish spatial occupancies; and published studies on geomorphic processes and species trait-based analyses [32].

Mesohabitat units, categorized by the formative geomorphic process as erosion, include a main channel pool and a scour pool (Table 2). The main channel pool is subdivided longitudinally into three hydraulic regions as the front, mid, and rear areas [79]. These pool area subdivisions are also relevant to pool-riffle maintenance processes as described above [154–157]. Geomorphologically, a main channel pool is differentiated from a scour pool in that its length is greater than its channel width. In contrast, a scour pool is smaller in size with its length less than the channel width. Its minimum length, width and depth are about 1.5 m, 1.2 m. and 0.25 m, respectively [79]. The pool front unit represents the entrance slope to a local topographic low along the streambed, as observed by the downward-directed bed slope orientated with flow. The pool mid unit is the level bed area represented as a local topographic low. The pool-rear unit represents the exit slope, as observed by the upward-directed bed slope orientated with flow.

Table 2. Geomorphological and hydraulic characteristics of low-flow mesohabitat units in low-gradient streams of the US Midwest. Classification characteristics adapted from [79]; and example ecological traits/strategies based on species occupancy [32].

Formative Geomorphic Process: Erosion			
Mesohabitat Unit	**Geomorphic Characteristics**	**Hydraulic/Flow Depth Characteristics**	**Ecological Trait/Strategies**
Pool Front	Entrance slope to a pool; downward-directed bed slope oriented with flow.	Flow acceleration, and strong outward velocities in meanders; relatively high turbulence [147,154,159]. Moderately deep (0.25–0.35 m).	Feeding by insectivores
Pool Mid	Topographic low along streambed; level bed.	Transition from flow acceleration to deceleration flow, and strong secondary circulation; submergence of high-velocity core; moderate turbulence [136,147,150,154,159]. Deep (0.4–1.2 m).	Feeding by piscivores and topminnows. Broadcast spawners.
Pool Rear	Exit slope to a pool; upward-directed bed slope oriented with flow.	Flow deceleration, and diminishing secondary circulation; relatively low turbulence [147,154,159]. Moderately deep (0.25 m).	Gravel nesting spawners.
Local Scour Pool	Small area of topographic low in bed; length smaller than channel width.	Local flow acceleration due to deflection and constriction of flow field [63,261,263–265]. Moderately deep (0.3 m).	Feeding by omnivores.
Formative Geomorphic Process: Deposition			
Mesohabitat Unit	**Geomorphic Characteristics**	**Hydraulic/Flow Depth Characteristics**	**Ecological Trait/Strategies**
Glide	Intermediate bed topographic elevation; level and uniform bed.	Uniform downstream velocity vectors; minimal secondary circulation [63,212,246,251]. Moderately Shallow (0.25 m).	Feeding by omnivores, herbivores. Spawning by nest builders, other
Riffle without Raceway	Topographic intermediate to high along streambed; lateral bed morphology diversity.	Downstream velocities accelerate from increasing bed slope, weak surface-divergent secondary circulation; relatively moderate turbulence [63,136,150]. Moderately shallow (0.20 m).	Feeding by generalist and benthic insectivores.
Riffle with Raceway	Topographic high along streambed; sinuous flow path through alluvium during low flow; diverse bed morphology with small depressions.	Downstream velocities accelerate from increasing bed slope, weak surface-divergent secondary circulation relatively moderate turbulence [63,136,147]. Very shallow with deep "pockets" (0.1–0.3 m).	Feeding by omnivores and herbivore. Spawners by egg adherence to gravel; darter resting
Submerged Bar	Lateral topographic high adjacent to pool, and extending into riffle structure.	Low velocities due to shoaling and lateral deflection of flow by the point bar; flow separation adjacent to or in lee of the point bar [136,147,149]. Shallow (0.15 m).	Evasion from predation by cyprinid young-of-the-year
Lateral Area in Lee of an Obstruction	Intermediate topographic elevation laterally positioned behind instream or bank structural element; area in lee of obstruction.	Separated, stagnant water or recirculating flow in lee of obstacle [251,261,263]. Shallow (0.15 m).	Evasion—escape from predators; resting; spawners by egg adherence to vegetation

Distinct flow structures occur through the three areas of a main channel pool, particularly in pools associated with a meandering channel in which the flow field is influenced by curvature [136,147,163,266–269]. Convective acceleration of the flow occurs at the front of the pool, with flow in meanders strongly directed towards the outer bend [154]. In the deeper mid-area of the pool, the flow structure begins to transition from convective acceleration to deceleration generating strong secondary circulation. Convective deceleration occurs at the exit slope of the pool, along with diminishing secondary circulation. Turbulence, as turbulent kinetic energy (TKE), is greatest in the front of the pool and weakens through the pool areas as secondary circulation redistributes energy and momentum [147,259,264]. Similar hydraulic conditions occur through the pools in low-sinuosity channels where the main channel flow is deflected by lateral structures [263]. The scour pool unit hydraulically is similar to that of pool front unit where convective acceleration generates velocities directed downward towards the bed [269]. They differ in that the small size of the hydraulic units likely limits development of secondary circulation. In-stream structures control the location of scour pools, and in prairie streams they include sod blocks from bank failures, LWD, exposed tree root wads, rock, and human-deposited debris.

Mesohabitat units, categorized by the formative geomorphic process of deposition, include two types of riffles, a glide, a bar platform, and a lateral area in the lee of an obstruction (LAT) unit (Table 2). These units are generally considered as topographic highs on the streambed compared to the pool-type units [63,74,79,128,262]. Riffle units were observed as those with and without a raceway. A raceway consisted of a sinuous thalweg forming a low-flow channel deeper than very shallow or non-wetted, exposed lateral and mid-channel bars (Figure 4). Small, deep pockets of water sometimes form in the bed along the thalweg (0.15 m depth), though typically the water depth was very shallow over gravel-sand mix (<0.1 m). A riffle with a raceway typically had a unit length in the order of 3 to 10 times the active channel width. In contrast to a riffle without a raceway, unit lengths were approximately equal to the active channel width, and laterally-deposited sediment was submerged during baseflow. Water depth in riffle units without a raceway was moderately shallow and comparable to a glide at the deepest side laterally, ranging in depth from 0.17 to 0.30 m. Glides have variable unit lengths with uniform bed topography. Bar platforms consisted of lateral sediment deposits including point bars along the inner bank of meanders, and alternative bars in straight channels. LAT habitat units include areas behind bank failures, and lateral margin areas where the channel abruptly expands including floodplain sloughs and early stages of concave-bank bench planform development [32].

Flow structures differ among the depositional habitat units and consist of either main channel hydraulic patterns in riffles and glides, or hydraulically separated, low-velocity areas of a bar platform and a LAT unit [79,136]. This classification scheme recognized the fluvial dynamics of a geomorphic bar unit by incorporating the Bar Unit Concept [36]. As a single geomorphic unit consisting of pool-riffle-bar morphology, the fluvial dynamics is characterized by a 3D convergent-divergent helical flow pattern [147,149,150,153]. In riffles during low flow, downstream-directed velocities accelerate slightly from the reduced water depth, and turbulence is moderate in relative comparison to high TKE observed in the front of pool [152,156]. Over bar platforms, low velocities are due to shoaling and lateral deflection of flow by the point or alternate bar with possible flow separation adjacent to or in the lee of the bar [136,147,149,154,157]. Glides are assumed to represent uniformly-directed downstream velocities with minimal secondary circulation [63,213]. The LAT habitat unit occurs downstream of a structural constriction to flow, and lies laterally adjacent to a scour pool formed by the structure [160]. Hydraulically during baseflow, this lateral habitat unit consists of separated, stagnant water or possibly low-velocity recirculating water in some locations (Figure 4).

Within the framework of ecological traits and strategies as shown in Figure 3, relationships between general trait expressions and mesohabitat unit type are demonstrated in Table 2. These relationships were based on statistically distinct patterns of fish occupancy and a trait-based analysis [63,79]. The greatest richness and density occurred during the summer and fall periods, with a total of 23 species and average unit densities ranging from 4.9 to 218.6 fish per 100 m^2. Others found the same seasonal patterns of use where feeding, resting, evasion from predation, and spawning were the dominant trait strategies [172,178,179,193,194,197,198,201,203,214–216]. Schwartz and Herricks (2008) [79] found that feeding strategy could be summarized as: insectivores mainly occupying the pool-front unit, omnivores in the scour pool unit, piscivores in the pool-mid unit, and herbivores in the glide and riffle with raceway unit. Feeding strategy was weakly expressed in the other unit types. Evasion and escape from predation were observed in the LAT unit and submerged point bar. Resting behavior was dependent on body morphology with centrarchids in the LAT unit, and darters and some cyprinids in the riffle with raceway unit. Spawning behavior was highly varied and different strategies related to the unit hydrogeomorphic conditions. For example, broadcast spawners would generally be found in pool-mid units, whereas gravel nest spawners will be found in the pool-rear unit, riffle, and glide units. More focused research is needed to generate direct spawning trait-habitat relationships, but general information is available from literature and trait databases [179,245]. During the harsh winter months, most fish species found refuge in the deep pool-mid units, through the submerged bar and riffle with raceway units were used to a greater extent compared to the summer-fall season [32].

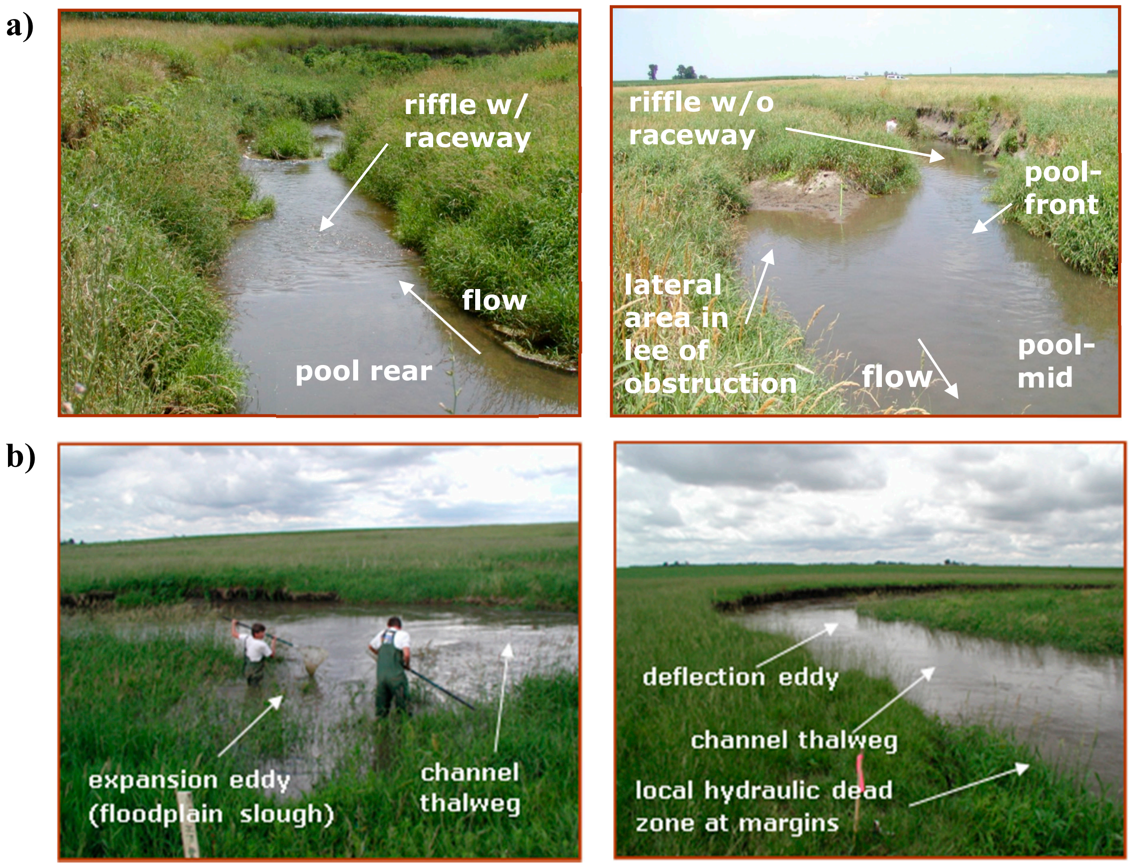

Figure 4. Photo showing examples of mesohabitat units during (**a**) low-flow and (**b**) high-flow stages in the Embarras River headwaters (third-order stream with 476 km^2 drainage basin); located approximately 15 km south of Urbana, IL, USA.

5.3. Mesohabitat Units at High-Flow Stages

Mesohabitats units at high-flow stages represent different hydrodynamic conditions as channel areas of high- and low-velocities (Table 3). These areas develop as flows interact with the channel morphology including planform sinuosity, floodplain-channel morphology, bed topography and large roughness elements influencing the 3D hydraulic characteristics [71,128,135,137,253,262,270–273].

Three hydraulic categories were used to classify high-flow mesohabitat units; they include: (1) the high-velocity corridor within the active channel; (2) low-velocity areas along the active channel margins and (3) low-velocity areas at the channel-floodplain interface [253]. In the main active channel area, topography and hydraulic zones of separated flow direct a high-velocity sinuous corridor. During flood flows, stage height determines what high-flow mesohabitat units are available for fish occupancy. Velocities in the high-velocity corridor ranged from 0.56 to 1.49 $m \cdot s^{-1}$, and they were mostly zero in the low-velocity areas though velocities between 0.03 and 0.08 $m \cdot s^{-1}$ were measured at some units [253].

Within the active channel during high flows, the "high-velocity corridor" habitat unit follows the channel thawleg, the longitudinal path of maximum depth (Table 3; Figure 4). The downstream-directed velocities are swift within this habitat unit creating a harsh environmental for many fish species [181–183]. Spatially, this high-flow habitat unit overlies with the bed topography elements at the low-flow stages consisting of following habitat units: the four pool units, scour pool, the two riffles, and glide (Figure 5). Along the thawleg and high-velocity corridor, pools and riffles are maintained by the geomorphic processes described above per the velocity reversal hypothesis and flow acceleration-deceleration concept [141,142,156,159].

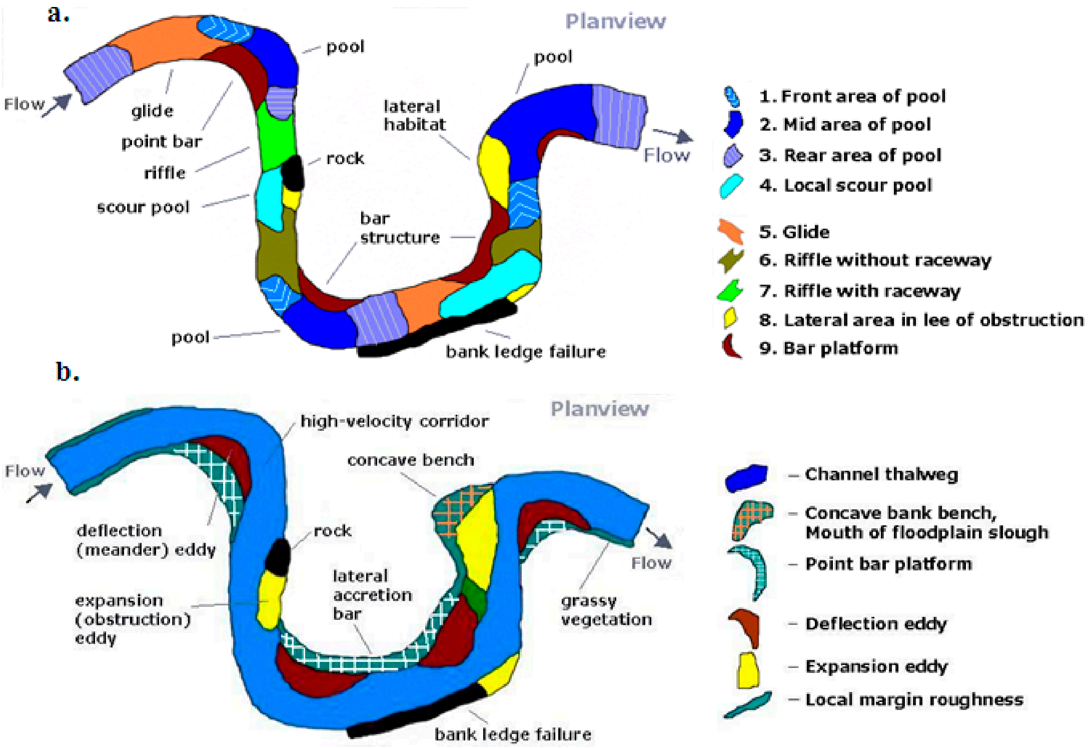

Figure 5. Illustration of a spatial arrangement of mesohabitat units at: (**a**) baseflow stage, changing to units; and (**b**) high-flow stage for the same channel reach.

Table 3. Geomorphological and hydraulic characteristics of fluvial habitat units during high-flow stages in small, low-gradient streams in the Midwest, USA. Table modified from [253].

Habitat Unit	Geomorphological Characteristics	Topographic Elevation	Hydraulic Characteristics
Hydrodynamic Condition: High-velocity corridor within the main channel			
Channel Thalweg	Path of maximum depth and velocity within the channel; often shifts laterally across channel in conjunction with pool-riffle-bar morphology [71]	Lowest bed elevation in active channel [71,156]	Convergent-divergent flow pattern associated with pool-riffle-bar morphology; helical flow in pools; strong downstream velocities; high shear stress in pools [71,136,147]
Hydrodynamic Condition: Low-velocity areas along active channel margins			
Deflection Eddy	Strong topographic deflection of flow laterally by elevated point-bar head, especially in sharp bends, resulting in an elongated zone of flow separation along inner bank [147,263].	Intermediate bed elevation at margin of active channel along interface of point-bar face and platform; inundated with flow.	Separated, recirculating flow [136,147,150]
Expansion Eddy	Abrupt expansions of channel width at local re-entrants associated with remnant channels (floodplain sloughs) [137] or early stages of concave bank bench development in meandering channels [134], local bank ledge failures or other large structures that create local lateral channel constrictions [263,264].	Local topographic low along channel bank, producing intermediate bed elevation within active channel; inundated above baseflow [270,273].	Separated, recirculating flow within expansion zone [136,147,150].
Local Hydraulic Dead Zone at Margins	Channel margins adjacent to thalweg in straight and meandering channels with high hydraulic roughness consisting of local bank irregularities and dense vegetation.	Vertical areas along bank at margins of active channel; wetted inundation slightly above baseflow [262,272].	Stagnant or low-velocity areas produced by high hydraulic roughness [261,262,265].
Hydrodynamic Condition: Low-velocity areas at channel-floodplain transition			
Remnant Point-bar Platforms, Vegetated	Grassy, vegetated zones on surface of point-bar platform along inner (convex) bank of meander bends [71].	Elevated surface above active channel; inundated at bankfull or overbank flows [273].	Low velocities or recirculating flow from high hydraulic roughness during bankflow flow [264].
Concave-bank Bench	Crescent-shaped depositional area at location corresponding to upstream limb of concave bank in the next bend downstream [134] bench becomes vegetated with grass.	Elevated surface about active channel; flood inundation only during bankfull or overbank flows [134,135].	Separated, recirculating flow resulting from enlargement of expansion eddy during bankflow flow [134,270].
Remnant channels; floodplain slough mouth	Remnant channels lateral to active channel; gradually slope towards at re-entrants locations at the mouth of floodplain sloughs [137,270,271].	Elevated surface about active channel; flood inundation only during bankfull or overbank flows [135,137].	Separated, recirculating flow resulting from enlargement of expansion eddy during bankflow flow [270].

When floodwaters rise above baseflow, low-velocity areas form along the channel margins, including a "local hydraulic dead zone at margins" unit parallel to the bank with vegetation, and hydraulic recirculation zones classified as either a deflection or expansion eddy (Table 3; Figure 4). Deflection eddies occur in meanders where a strong lateral deflection by the point bar, along with abrupt changes in channel direction create a zone of flow separation and large recirculation area in the lee of the point bar [147,149]. Helical flows in the downstream direction also play a role in this process by redistributing momentum across the channel, and influence overall 3D velocities and turbulence patterns [147,259,264]. Expansion eddies occur where accelerated flow due to a constricted cross-sectional area is followed by an abrupt lateral expansion of channel morphology forming recirculating fluid [263,266]. In low-gradient streams, large bank ledge failures can laterally impinge the flow field forming a hydraulic recirculation zone in the lee of the obstruction. Channel expansions also occur at planform morphological features, i.e., mouth of a remnant channel [137].

Morphological surfaces that become inundated during very high flows nearing or exceeding top of bank provide short-term, but essential habitat for fish refugia [32]. Three fluvial habitat units are classified; they are remnant point bar platforms, concave-bank benches, and old remnant channels that lead to the mouth of floodplain sloughs (Table 3). These habitat units are shallow, low-velocity patches with emergent grass vegetation less than a meter in depth. Remnant point bar units are a lateral extension of the in-channel bar structure where the deflection eddy occurs. Knighton (1998) [71] refers to them as lateral accretion bars, where sediment deposition vertically builds the geomorphic surface as the channel bend migrates in the floodplain. Concave-bank benches differ from point bar development in that they are not laterally accreting geomorphic platforms [134]. Rather, concave-bank benches form through the deposition of fine sediments in an over widened channel bend immediately upstream of the point of maximum curvature in a meander. Over-widening of the channel at this location is facilitated by rapid erosion of the upstream concave bank, and during high flows forms an expansion eddy unit in the active channel. In general, meandering processes over time leave remnant channels at elevations above the active channel forming local geomorphic platforms at the transition between the channel and the floodplain [135,137,270,271]. These remnant channels form a slough feature at the exit of a former active channel. Floodplain locations of sloughs are areas where the channel width expands abruptly; forming expansion eddies at the active channel margin during high flows [253].

Ecologically, fish species differentially use high-flow habitats but the strategy is singular finding refugia from swift flows in lateral hydraulic recirculation zones [253]. During the flood period, half to bankfull stages, fish densities were greatest in the deflection and expansion eddy units. Also, fish densities and biomass were greater in the deflection eddies than the expansion eddies, averaging 3.33 fish/m^2 and 6.87 g/m^2; and 1.13 fish/m^2 and 2.57 g/m^2; respectively. Schwartz and Herricks (2005) [253] reported that average TKE was greater in the deflection eddy (52.3 cm^2·s^{-2}) than the expansion eddy (20.0 cm^2·s^{-2}), which poses an interesting question of whether fish during flood flows respond to this hydraulic property. Overall, fish assemblages significantly differed among the different high-flow habitat units, providing evidence to their ecological relevance for use in stream restoration design. Literature indicates some species exploit food resources on the episodic submerged floodplain [52,184,188,223]. In general, the importance of flood refugia has been recognized in stream restoration for agricultural Midwest streams with two-stage cross-sectional designs [274–276]. Further research is needed to enhance of understanding of trait expression associated with these high-flow mesohabitat units.

6. Ecohydraulic-Based Stream Restoration: Proposed Application

Advancing stream restoration design with ecological performance outcomes requires a pre-design integration of fluvial geomorphic, hydraulic, and ecological principles incorporated into an applicable mesohabitat classification scheme (Figure 1b). Classification schemes should be unique to an ecoregion and watershed longitudinal position (headwater to large river segments). Most restoration projects are implemented in small streams at the reach-scale (second to third stream order) reconfiguring bedforms as mesohabitat structure [2,4,44,277,278]. As this review suggests the ecological component to restoration design may be advanced through the use of mesohabitat classification that reflects trait-habitat relationships for key biological resource needs, utilizing a functional traits database (Figure 3). Use of fish species traits is applicable for restoration design because trait-habitat relationships scale to constructible habitat patches as geomorphic bedforms and elevated channel-floodplain surfaces.

A proposed restoration design strategy is illustrated in Figure 6 that applies a multi-stage ecohydraulic mesohabitat classification scheme developed specifically for an ecoregion. This review demonstrated a classification scheme for the prairie Midwest (Ecoregion 54), thus would not solely be applicable in other ecoregions. For example in the Pacific Northwest Coast Range (Ecoregion 1), side channel habitat for winter rearing is dominant mesohabitat, in addition to cascades and other high-gradient type units are utilized by various trout species for feeding [65,279]. However, some units will be more ubiquitous such as the pool-front, -mid, and -rear units, and glides.

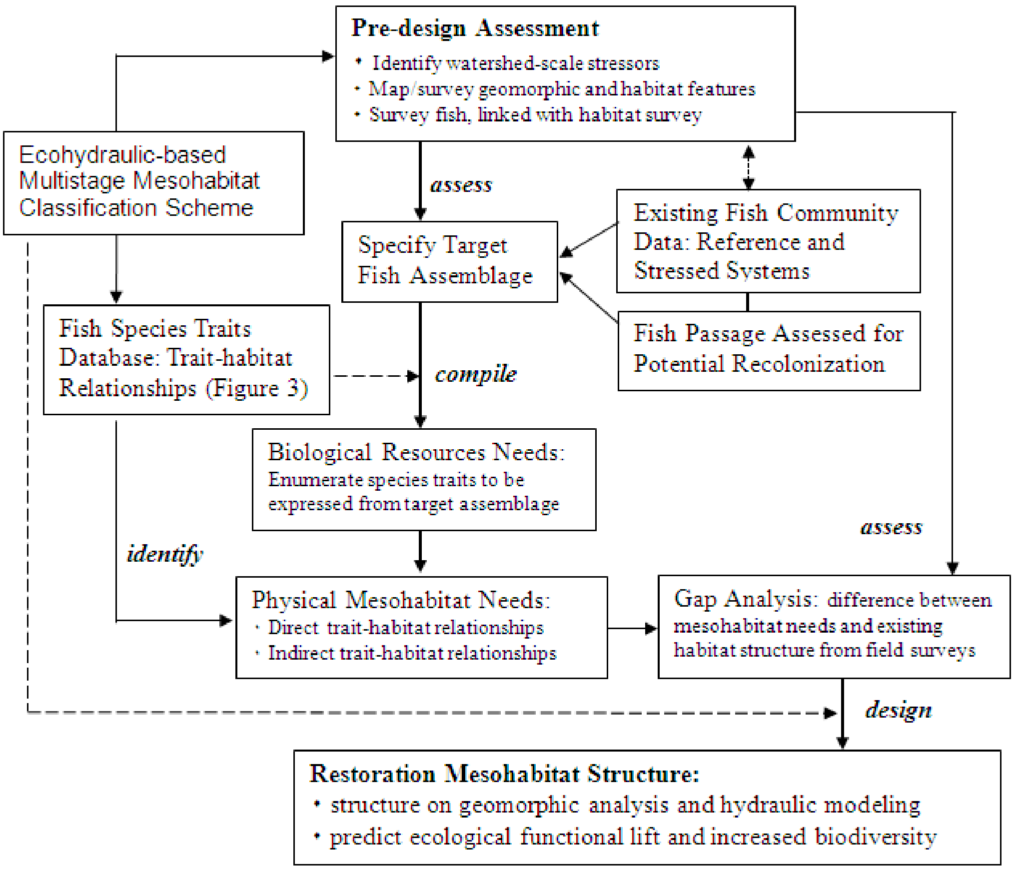

Figure 6. Proposed design protocols for multi-stage ecohydraulic stream restoration using an ecoregion-specific mesohabitat classification scheme and species functional traits.

The stream restoration design strategy as shown in Figure 6 begins with a pre-design assessment consisting of a watershed-scale stressor analysis (Figure 2), standard fish surveys [280], and mesohabitat surveys mapping habitat units in sequence [63–65]. Implementation of a functional traits analysis with a mesohabitat classification scheme first requires a target fish community [108,111]. By identifying the target species, traits and strategies can be summarized from available databases [113,245]. The suggested target community relies on professional judgement, which is supported by fish surveys from both local reference conditions and ecologically impaired streams, in addition to recolonization potential of different species [211,237,281,282]. After the target fish assemblage (community) has been identified, procedures utilizing species functional traits for restoration design are suggested as follow:

(1) Enumerate the functional traits expressed per fish species in the target community, summarizing the frequency of traits expressed because various traits will be expressed by multiple species in the target assemblage;
(2) Summarize physical habitat needs based on the enumerated functional traits of the target assemblage, which constitutes the functional traits analysis (Figure 3); it should be noted that habitat needs could be direct or indirect, where a direct need is the explicit space occupancy for a specified trait expression (e.g., mid-pool resting) and indirect need is space used by another organism needed for a target species, for example pool-front feeding with the food source (benthic macroinvertebrates) generated in the adjacent upstream riffle;
(3) Compile data from field surveys of stream habitat, and summarize the proportion of each mesohabitat unit types per proposed restoration reach; this includes both low- and high-flow units [19,63,64];
(4) Compare the existing mesohabitat units from the stream surveys with a set of habitat units derived from the functional traits analysis, identifying any departures between the two (gap analysis); and
(5) Of the mesohabitat unit types found to be limited, summarize measures of physical structural heterogeneity and complexity from field surveys, and design the restored habitat based on trait-habitat relationships, and geomorphic and hydraulic principles.

This trait-based mesohabitat procedure for stream restoration assumes degraded channel morphology can be modified by adjusting planform and slope, cross-sectional area, or adding roughness and grade control structures to achieve a channel near a geomorphic 'dynamic' equilibrium state. In addition, the procedure assumes there is a regional species pool for recolonization of species based on the proposed target fish assemblage, which accounts for the existing multiple stressors in the watershed. It accomplishes the overall goal where mesohabitat units represent unique process-based relationships of geomorphic maintenance and ecosystem function.

7. Conclusions

Ecological restoration of streams is quite challenging, particularly in human-dominated watersheds with multiple stressors. There is a need to advance our current science-based restoration tools in order to better integrate ecological information into the planning and design phases of stream restoration projects. In addition, there is a growing need in the US to quantify ecological outcomes in order to meet compensatory mitigation requirements, referred to as "functional lift" [83]. The European Union has similar goals as defined in the 2000 Water Framework Directive Framework, whereby ecological condition is to be restored and quantified through assessments [283]. The proposed application of an ecohydraulic-based design approach is suggested for the stream restoration practice, which utilize an ecoregion-specific mesohabitat classification scheme and a 2D hydraulic habitat model. Multidimensional hydrodynamic models can be effectively integrated with ecological design [99]. These models can predict flow patterns at multiple stages, and a mesohabitat template can be overlaid and enumerated with the design reach. Analysis of model outcomes can include summing the potential traits strategies that may be expressed based the mesohabitat classification scheme as described above in Section 6. The overall aim with the use of these tools is to improve ecological outcomes of channel restoration projects.

The key points of this review suggesting the use of multi-stage ecohydraulic-based mesohabitat classification schemes to improve stream restoration design practices by integrating geomorphic, hydraulic and ecological principles are summarized as follow:

(1) physical habitat space is specifically linked with species functional traits so that mesohabitat units form the basic "building blocks" for stream restoration design, recognizing that habitat unit use shifts with season and flow stage governed by life histories and trait strategies;

(2) high-flow refugia must be considered in restoration design, characterized by elevated geomorphic surfaces at the channel-floodplain interface;
(3) mesohabitat units must be associated with mesoscale 3D hydraulic and turbulence patterns that relate to trait strategies, i.e., feeding and spawning positions; and
(4) the restoration design process must recognize the self-maintenance geomorphic processes for both low- and high-flow mesohabitats, the spatial-process linkages for reach-scale bed topography, bank, and elevated floodplain-channel geomorphic surfaces.

The classification scheme presented in this review was developed for Midwest prairie streams, and used as a demonstration of how these key principles can be considered to other ecoregions. It is acknowledged that the design procedures described here within need further development, including fish preferences to new, uniquely defined mesohabitat unit delineations, and spatial considerations associated to unit juxtaposition. Overall, these procedures applying species functional traits appear promising to advance of practice of ecological restoration of streams where enhanced mesohabitat structure specifically meets the biological needs of a target biota assemblage.

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