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ARENA

THE MESOHABSIM MODEL REVISITED

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ABSTRACT

The MesoHABSIM simulation model was developed in 2000 as an enhancement of the habitat descriptions used in the physical habitat simulation model (PHABSIM). MesoHABSIM integrates system-scale assessment of ecological integrity in flowing waters with quantitative information on physical habitat distribution to simulate habitat changes at the watershed scale. The goal was better integration of physical habitat models into river management by 'upscaling' to address issues relevant at management levels. This paper describes the most updated version of the MesoHABSIM approach resulting from the experience gained during the application of the model in projects since 2000. Copyright © 2007 John Wiley & Sons, Ltd.

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INTRODUCTION

MesoHABSIM is an approach to modelling instream habitats. It consists of a data collection strategy and analytical techniques that allow a user to compute how much habitat is available for selected fauna under specific environmental circumstances. To allow for flexibility, it utilizes a variety of input data. The underlying philosophy of MesoHABSIM is the recognition that fauna reacts to the environment at different scales related to the size and mobility of the species as well as the time of use. Meso-scale units can be defined as areas where an animal can be observed for a significant portion of their diurnal routine, and it roughly corresponds with the concept of 'functional habitat' (Kemp et al., 1999). Because of the natural mobility of fish, observation at the meso-scale is less affected by coincidence than at the micro-scale and can be expected to provide relatively meaningful clues about an animal's selection of living conditions (Hardy and Addley, 2001).

As shown in many studies (e.g. Lobb and Orth, 1991; Aadland, 1993; Bain and Knight, 1996), hydromorphic units (HMUs) and mesohabitats commonly correspond in size and location, at least for adult resident fish. Subsequently, 'mesohabitat' has almost become a synonym for HMU (Maddock and Bird, 1996; Bovee et al., 1998; Parasiewicz, 2001). From the perspective of the MesoHABSIM method, we make the distinction that *mesohabitats are species- and life-stage specific areas where the configuration of hydraulic patterns together with attributes that provide shelter* create favourable survival and development conditions. As mentioned above, the size of mesohabitats depends on the size and mobility of the investigated individuals, hence mesohabitats of juvenile fish or macroinvertebrates are usually smaller than those of adult fish. In contrast, HMUs reflect only the interplay between hydraulics and riverbed topography, and their size is dependent upon the size of the river. Still, because hydraulics drives the organizational framework for riverine habitat, the correspondence between the HMUs and mesohabitats is not coincidental. Consequently, the spatial distribution of HMUs accompanied by associated cover attributes can be used for the quantification of summer habitat use by adult fish. For other life stages (or seasons) the functional habitats may be different and need to be considered separately.

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The MesoHABSIM approach follows the typical structure of habitat models described by Parasiewicz and Dunbar (2001) and is an aggregation of three models:

1. A hydromorphologic model that describes the spatial mosaic of fish-relevant physical features.
2. A biological model describing habitat use by animals.
3. A habitat model quantifying the amounts of usable habitat and relating it to flow.

The MesoHABSIM approach has been under development since 2000. The early version served as a template for developing the MesoHABSIM software, a tool useful in data management, data quality control and performing basic calculations. In this paper, I describe the method as our research group uses it now in terms useful to an audience broader than the habitat modelling community, and will also share my experience of working with the application.

HYDROMORPHOLOGIC MODEL

Parasiewicz (2001) described the advantages of the MesoHABSIM model for rapid data collection in the coverage of longer river distances. Compared with the collection of physical data by other modelling approaches (e.g. PHABSIM) this larger spatial scale requires a smaller expenditure of resources (e.g. 10 days to collect data from a 20 km-long [12.5 mi] reach with MesoHABSIM as opposed to 50 days of using physical habitat simulation model (PHABSIM), assuming 37 transects, Payne et al., 2004). Another advantage is a spatially explicit quantification of habitat change, much like that provided by the dual flow analysis module in PHABSIM. On the other hand, the use of hydrodynamic models to predict depth and velocities is limited within the MesoHABSIM, and it has to be supplemented with multiple observations of the same areas to develop a flow/habitat relationship. With the exception of one project on the Stony Clove Creek (Parasiewicz et al., 2003), we have combined repeated mapping of the whole length of the stream with the representative site approach. The selection of the most effective procedure depends on the size of the area to be surveyed.

Table I presents the hierarchical river delineation framework applied in the MesoHABSIM approach. The hydromorphologic model applies following ways to describe this hierarchy:

1. A reconnaissance survey (on-the-ground or aerial) to delineate the stream segments by quantifying the distribution of HMUs and hydraulic estimates. It is similar to the stream habitat stratification method for the PHABSIM model described by Bovee (1994). Subsequent selection of representative sites is supported by cluster analysis (Kaufmann and Rousseeuw, 1990) of the recorded attributes. This type of survey may also be used to investigate transferability of developed models to different study areas (e.g. similar rivers).
2. Alternatively mesohabitat survey of the entire study area and delineation into sections based on macroscale characteristics (gradient, flow, dominant substrate, cover type, etc.). A sensitivity analysis of mesohabitat or HMU distributions is used to select representative sites. In other words, the approach is to select sites representative of the shortest possible segment of the river reflecting the quantitative distribution of the HMUs in the segment.
3. Repeated mapping of the entire length of the study area.

Table I. Hierarchy of spatial river delineation applied within the MesoHABSIM framework

Spatial unit	Description
Study area	Encompasses entirely the investigated river length, preferably from the headwaters to the river mouth. It can also include the entire watershed
Reach or segment	River length with prevalent macro-morphological characteristics between larger tributaries, gradient discontinuities, etc.
Sections	Portions with uniform hydromorphologic patterns and therefore a specific HMU mosaic
Representative site	The shortest portion of a section encompassing HMU distribution
Hydromorphologic units	Areas with consistent hydraulic patterns described by water velocity and depth

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Table II. Definitions of hydromorphologic units (HMU; modified from Dolloff et al., 1993; Bisson & Montgomery, 1996; Perkins, 2002)

HMU	Description of characteristics
Riffle	Shallow stream reaches with moderate current velocity, some surface turbulence and higher gradient. Convex streambed shape
Rapid	Higher gradient reaches with faster current velocity, coarser substrate, and more surface turbulence. Convex streambed shape
Cascade	Stepped rapids with small waterfalls and very small pools behind boulders
Glide	Moderately shallow stream channels with laminar flow, lacking pronounced turbulence. Flat streambed shape
Ruffle	Dewatered rapids in transition to either run or riffle
Run	Monotone stream channels with well-determined thalweg. Streambed is longitudinally flat and laterally concave
Fast run	Uniform fast-flowing stream channels
Pool	Deep water impounded by a channel blockage or partial channel obstruction. Slow. Concave streambed shape
Plunge pool	Main flow passes over a complete channel obstruction and drops vertically to scour the streambed
Backwater	Slack areas along channel margins, caused by eddies behind obstructions
Side arm	Channels around islands, smaller than half river width, frequently at different elevation than main channel

Reconnaissance survey

The goal of the reconnaissance survey is to identify significant changes in spatial distribution of habitat units in order to delineate habitat-consistent river segments. The focus is on the overall distribution of the habitat units, and for each river segment we estimate the proportions of hydromorphologic units (see Table II), mesohabitat characteristics, cover types (woody debris, shallow margins, canopy cover shading, submerged vegetation, etc.), shallow ($<\sim 30$ cm), deep ($>\sim 1.5$ m) and moderately deep areas and slow ($<\sim 20\,\mathrm{cm\,s^{-1}}$), fast ($>\sim 80\,\mathrm{cm\,s^{-1}}$) and moderately flowing areas. Within each river section the average stream and bankfull width are also estimated and noted, along with streambed and bank characteristics. With the help of cluster analysis the sections are then combined into segments and within each segment one or more representative sites are selected for further surveys.

Mesohabitat survey

The purpose of the mesohabitat survey is to determine spatial proportions of the mesohabitat units in selected sections. For each HMU, the location and size are determined with GPS and ArcPAD software in conjunction with high-resolution aerial photographs, creating a detailed map of selected sites on the river. The outlines of each HMU are drawn as geo-referenced polygons on a Pocket PC (e.g. Hewlett-Packard iPAQ) running ArcPAD software.

The physical attributes in Tables III and IV are estimated for each HMU using three categories: absent, present, abundant. Note these categories are also a function of unit size, for example, in smaller units, less woody debris is necessary to classify woody debris as ‘abundant’. Within each HMU, mean column and bottom velocity, depth and estimated substrate are measured in seven random locations. The number of measurements is empirically chosen as the smallest statistically relevant quantity. Measurements for depth and mean column velocity are usually taken with a Dipping Bar (Jens, 1968) in areas shallower than 1 m, but it is equally possible to use other techniques to gather velocity data. For deeper locations, a Marsh-McBirney Flo-Mate is used. Data are entered into a GIS table associated with the corresponding polygon. For substrate definitions, I referred to the choriotop classification system according to Austrian Standard ÖNORM 6232 (1995; Table IV).

Repetitive mapping

These data are collected at three to four flow conditions over the range of investigated flows. The range of flows is determined by the river management purpose and goals, and is defined with the help of the indices of hydrological

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Table III. Physical attributes used to establish logistic regression with fish absence and presence (from Parasiewicz, 2001)

Attribute (value)	Categories
Hydromorphologic units (yes/no)	(See Table II)
Cover sources (no/some/much)	Undercut bank, woody debris, overhanging vegetation, submerged vegetation, boulder, riprap, canopy cover shading, shallow margin
Choriotop (% of random samples)	Pelal, psammal, akal, microlithal, mesolithal, macrolithal, megalithal, phytal, xylal, sapropel, detritus (for exact definitions see Austrian Standard ON6232)
Depth (% of random samples)	6 classes in 25 cm increments (range 0–125 cm and above)
Mean column velocity (% of random samples)	8 classes in 15 cm s^{-1} increments (range 0–105 cm s^{-1} and above)
Froude number	Average

Table IV. Natural choriotop types describing river bottom (modified from Austrian Standard ÖNORM 6232)

Nomenclature	Grain size range	Choriotop description
Megalithal	>40 cm	Upper sides of large cobbles and blocks, bedrock
Macrolithal	>20–40 cm	Coarse blocks, head-sized cobbles, variable percentages of cobbles, gravel and sand
Mesolithal	>6.3–20 cm	Fist to hand-sized cobbles with a variable percentage of gravel and sand
Microlithal	>2–6.3 cm	Coarse gravel, (size of a pigeon egg to child's fist) with percentages of medium to fine gravel
Akal	>2 mm–2 cm	Fine to medium-sized gravel
Psammal	0.063–2 mm	Sand
Pelal	<0.063 mm	Silt, loam, clay and sludge
Biotic choriotop		
Detritus		Deposits of particulate organic matter; distinguished are: CPOM (coarse particulate organic matter), as for example, fallen leaves and FPOM (fine particulate organic matter)
Xylal		Tree trunks (dead wood), branches, roots, etc.
Sapropel		Sludge
Phytal		Submerged plants, floating stands or mats, lawns of bacteria or fungi, tufts, often with aggregations of detritus, moss or algal mats (interphytal: habitat within a vegetation stand, plant mats or clumps)
Debris		Organic and inorganic matter deposited within the splash zone area by wave motion and changing water levels, for example, mussel shells, snail shells

alteration (Richter et al., 1997). For example, to study low flow conditions we use low pulse thresholds as an upper limit of the mapped flow range. This is also expected to roughly encompass the range of fish behaviour associated with low flows.

The data collected during the four habitat surveys are checked for errors and merged in a GIS database. Digital maps showing the spatial distribution of HMUs within each section and each representative site are constructed. Each record associated with an HMU polygon in the ArcGIS map consists of 46 field observations describing the mesohabitat. Attributes with many categories (e.g. HMU type) are broken down into multiple variables in binary (yes/no) format. For each measurement of depth and velocity, the Froude number is calculated according to the following equation:

$$\mathrm{Fr} = \frac{V_\mathrm{m}}{(9.81D)^{0.5}}$$

where Fr is the Froude's number, V_m is the mean column velocity and D the depth.

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The Froude number is a good indicator of surface turbulence and has been shown to strongly correlate with species and HMU distribution (Jovett, 1993; Vadas & Orth, 1998). The seven velocity and depth measurements and choriotop estimates are transferred into categories of relative abundance. The bin size is 25 cm for depth and 15 cm s^{-1} for velocity, and all values above 125 cm and 105 cm s^{-1} are lumped together into one category. These categories are established to reflect the estimated habitat use by adult fish derived from analysis of most common suitability curves for salmonids. I also assume that after reaching certain velocity or depth, further increase in these values has little effect on habitat suitability.

BIOLOGICAL MODEL

In the MesoHABSIM approach, there are several options for obtaining the data necessary to calculate functions describing fish response to environmental conditions. I prefer to use electrofishing grids in shallow (<1 m) water using a habitat-sampling technique developed by Bain et al. (1985). In deeper water we snorkel or use an electro-fishing boat to sample predetermined buoy-marked grids. For shallow areas in wadeable rivers, each grid consists of two cables running upstream and parallel to each other for a distance of 6 m (20 ft) in small rivers or 12 m (40 ft) in large rivers. A PVC pipe is attached at each end to maintain a distance of 1 m (3.3 ft) (or 2 m [6.6 ft] for larger rivers) between the cables at all times. The grids are sampled with a 1000 W generator and 15 Amp transformer using 350 V of alternate current. All fish captured within the grid are identified and measured to the nearest millimetre before release.

In deep and clear waters the same sampling strategy can be applied to snorkelling surveys where the grids are demarcated with coloured stones, and the standard procedures for underwater observations are applied (as described in Bovee, 1986). However, the fish estimates for entire HMU are also possible. If underwater visibility is poor, boat electro-fishing is used. Instead of a grid, two buoys attached to bricks and connected by a rope are placed in the river. The boat moves upstream along the rope, and fish are captured from this area only. This is the least precise method, and therefore the fishing time needs to be standardized. The generator settings need to be similar to those in grid sampling.

The data on HMU type, mesohabitat characteristics (as described above), stream location, cover, gradient, substrate, choriotop, stream depth and stream velocity are collected for each grid location. Each grid is described by the same environmental attributes used to develop the habitat database, and also by the number and size of fish species captured. The environmental attributes are used as independent variables and the fish data as dependent variables in regression models describing fish habitat use. Before calculating response functions, we frequently perform a cross correlation analysis to eliminate redundant parameters from the calculations. We employ a stepwise forward logistic regression model to identify the habitat characteristics mostly used by the target fish. To distinguish between unsuitable and suitable habitat, we used binary-dependent variables indicating fish presence or absence. To distinguish between suitable and suitable-optimal habitat, we construct two binary models for every species: one using species presence/absence and another for high/low fish abundance as dependent variable. All available data are used for the first model; only data from the grids where fish were caught are used for the second. To take behavioural differences into account, we determine a separate cut-off value distinguishing high and low abundance for each species by analysing fish density histograms derived from the electrofishing data. Gregarious species such as fallfish (*Semotilus corporalis*), common shiner (*Luxilus cornutus*) and white sucker (*Catostomus commersoni*) might, for example, have a cut-off value of 0.3 fish/m^2, while solitary dace species (*Rhinichthys* sp.) could have a cut-off value of 0.15 fish/m^2. These calculations are used to develop regression coefficients for significant environmental attributes in both models. The model uses likelihood ratios to determine which parameters should be included in the following regression formula:

$$R = e^{-z}$$

where: e is the natural log base; $z = b_1 \cdot x_1 + b_2 \cdot x_2 + \cdots + b_n \cdot x_n + a$; $x_{1 \ldots n}$ are significant physical variables; $b_{1 \ldots n}$ are regression coefficients and a is a constant.

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LITERATURE-BASED MODEL

When data collection is very difficult or not feasible (e.g. winter habitat use or high flow spawning) we search the literature and seek expert opinion for habitat use estimates.

Literature-based information is used to form the foundation of the habitat model and subsequent analyses. When specific information is not available and only vague references regarding an attribute are made, professional experience, in conjunction with the literature, is used to set a parameter's value or range.

To determine suitability for a discrete HMU as defined by hydraulics, the HMU's depth and velocity distribution, choriotop distribution and HMU type are compared to the ranges specified in the literature. We presume that all selected attributes need to be in acceptable ranges for the discrete HMU to be suitable. With regard to hydraulic measurements (7 for depth, 7 for velocity and 7 choriotop descriptions) the unit is considered to have acceptable ranges for the target fauna (i.e. suitable) if at least one of the measured/mapped values (e.g. depth) were within selected limits.

With regard to HMU type, a discrete HMU is considered as acceptable if its type is often associated with the other attributes of interest to the fauna. For example, a backwater was not considered to be an acceptable HMU for spawning by a species that uses fast-water areas.

Where suitability curves are available in the literature, the acceptable attribute range is considered to be equal to the range listed for all values above 50 per cent suitability. For example, if a species is reported to use velocities between 0.5 and 4.0 $m\,s^{-1}$ (1.7 and 13.2 $ft\,s^{-1}$) but had suitability indices above 50 per cent only for a range of 1.0–2.5 $m\,s^{-1}$ (3.3–8.3 $ft\,s^{-1}$), then the latter range would be acceptable for this evaluation. This allows the conversion of continuous suitability functions into binary format, which is necessary in categorical habitat classification (i.e. suitable vs. not suitable). The method is similar to the literature-based criteria described in Bovee (1986).

HABITAT MODEL

For each mesohabitat mapped during the survey of representative sites we specify if it is not suitable, suitable or suitable optimal. For literature-based criteria suitable habitat needs to have three of four attribute types (depth, velocity, substrate and cover) within specified range and the optimal habitat must have all four attributes in this range. For empirical data analysed with logistic regression the categories are a function of the probability of fish presence and of high abundance. The probability of fish presence is determined using the following equation:

$$p = \frac{1}{(1 + e^{-z})}$$

where p is the probability of presence/high abundance; $z = b_1 \cdot x_1 + b_2 \cdot x_2 + \cdots + b_n \cdot x_n + a$; $x_{1\ldots n}$ = significant physical variables and $b_{1\ldots n}$ are the regression coefficients. The probability is classified to suitability categories by analysing the relative operating characteristic (ROC) curve for presence and abundance predictions (Metz, 1986; Pearce & Ferrier, 2000). The curve examines the discrimination performance of the model over a range of threshold levels, by plotting proportion of grids correctly predicted to be occupied (sensitivity or true positive rate), and the proportion of grids incorrectly predicted to be occupied (false positive rate). Separate cut-off probabilities (Pt) are selected for the presence and abundance models. The habitats with a probability of presence greater than Pt are classified as suitable. The suitable habitats with a probability of high abundance greater than selected Pt are deemed optimal. Using these guidelines, digital maps of the sites can be constructed showing areas of highly suitable habitat at measured flow conditions.

The proportion of river channel area with suitable or optimal habitat for a species and life stage is summarized for each site and plotted against mapped flow. Two rating curves are created: one for suitable and one for optimal habitat. They can be aggregated into effective habitat by weighting the optimal habitat with 0.75 and suitable with 0.25. These weighting factors are selected to assure high contribution of optimal habitat in the river. The factors can be freely adjusted. Because most often the flows during the surveys at the different sites cannot be regulated and are therefore not the same at all sites, we use interpolation to compute habitat values at commonly occurring flows. A linear curve fit function is applied to interpolate habitat values at a range of flows to construct flow/habitat rating

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curves for the target species and life stages. These results are used to analyse the suitability of the river sections for each fish.

To determine habitat quantity for the fish community and to take into account that the same habitat is frequently suitable for more than one species, I developed the concept of a 'generic fish', a hypothetical species that uses the same habitat as all investigated species in the community. Hence, I count 'multiple-occupant' areas only one time, without addressing competitive interactions among the species. This approach describes the present conditions more realistically than trying to assign the habitat to one species over another with very limited life history information. However, to take into account the intensity of habitat overlaps we calculate the average number of species per site that could use the same locations by adding amounts of habitat suitable for all investigated species and dividing it by 'generic fish' habitat. This metric can be used to identify competitive stress if the amount of available habitat is low (and species compete for space). On the other hand, a low overlap factor indicates better conditions because of reduced competitive pressure (e.g. the habitat for juvenile and adult fish is separated). Another option is to compute community habitat by weighting the habitat of each species by their expected proportion in the target fish community.

To construct composite rating curves that represent suitable habitat throughout the study river, we summarize the suitable habitat in the sections, weighted by the section-length ratio. Habitat for each species is analysed individually and cumulatively as generic fish or community habitat. I also compare the distributions of available habitat among the selected species with the distribution of the habitat that is assumed to best support the target community structure. Here, we assume that habitat structure corresponds to community structure in a 1:1 ratio. To compare the desired target habitat structure with the actual structures occurring under the selected flows, we apply an affinity index (Novak and Bode, 1992).

CONTINUING DEVELOPMENT

Increasing surveying effectiveness was one of the original goals of MesoHABSIM design. This happened gradually by incremental reductions in data density. Incorporation of topographic survey principles into transect-based habitat surveys (Parasiewicz, 1996), and studies on the effect of transect density on habitat model output (Parasiewicz et al., 1999) led to the logical step to the meso-scale. The prototype design of MesoHABSIM included detailed mapping of HMU size and location by surveying river traverses with a laser range finder (LRF) and real time (RTK) GPS as described in Parasiewicz (2001). The survey speed during the first application on the wadeable Quinebaug River was about a kilometre (0.6 mi) a day, and the most time-consuming task was collecting high-resolution GPS location. Review of the data from this project shows that habitat variation among various flow conditions results mostly in the change of HMU type and not habitat size or location. Therefore, the resolution of data collection can be further reduced and aerial photography used as a mapping background loaded into the PDA. Sketching units as polygons in ArcPAD addresses the primary mapping, and low-resolution GPS is used only for orientation. River width measurements should be included to allow for correction of area estimates on the aerial photography. With this design those in the field can map an average of 30 HMUs in a day; the distance covered depends on the size of the stream or river. A general rule for mapping is 2 km (1.2 mi) per day hiking a wadeable stream, and 7 km (4.3 mi) per day working from a boat on a larger river.

The application of MesoHABSIM on a larger river (a few hundred metres in width) is underway. The process of HMU mapping is similar but differs in higher reliance on aerial photography and data collection techniques for selected physical variables. Hydraulic data (depth and velocity) are being collected using an acoustic doppler current profiler (ADCP) that continuously samples cross-section hydraulic data in a downstream distance equivalent to a river width. Seven or more measurements are randomly selected from ADCP data for every unit. The surveys of representative sites are being accompanied by high-resolution digital aerial photography of the entire river, which is being analysed with image processing software (ERDAS Imagine & Leica Photogrammetry Suite, Leica Geosystem Geospatial Imaging LLC, Norcross, GA) to determine HMU distribution. An on-the-ground survey is being used for calibration and evaluation of image processing.

With regard to hydromorphologic unit types, after several surveys I decided to introduce one more type of habitat that was not only observed in the field, but also stood out during statistical analysis of hydraulic data (Perkins,

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2002). I called it a *ruffle* and defined it as a dewatered rapid (i.e. relatively turbulent units, with clearly defined thalweg). Cover attributes mapped during the MesoHABSIM survey are defined in Tables I and II. I evaluated the inclusion of vegetation structure, but cross correlation analysis has shown clear redundancy with the parameters already in use.

The survey for describing habitat-use by fish has evolved from the MesoHABSIM prototype. During the first MesoHABSIM study on the Quinebaug River, the hydraulic habitat use data were described at the micro-scale of a sampling grid. Instead of taking seven measurements of depth, velocity and choriotop in randomly selected locations within the HMU, measurements were taken at each of the four corners of the grid. With the data collected during another project we statistically compared the models created using micro- (i.e. grid corners) and meso-scale hydraulic data and observed significant correlation (Pearson $r = 0.9$, $p < 0.01$) between the two models. Therefore in later projects we used only the meso-scale approach for biological model development. I continue to measure hydraulics at the grid corners, but mostly to assure compatibility with the earlier data collections of Bain *et al.*, (1985).

The fish collection survey is the most effort-intensive component of MesoHABSIM. At present, standard data collection of 500 grids takes about 25 days of fieldwork (three people). Because we have already gathered a large database describing habitat use in similar rivers for the most common New England species of fish, we are in the process of evaluating the transferability of habitat use models among rivers.

DISCUSSION

MesoHABSIM is a move from models driven by human recognition of riverine hydraulics and subsequent classification to a model that bases ‘functional habitat’ classification on the way animals react to their environment (Kemp et al., 1999). Acknowledging that these two perspectives may be different is central for evaluating habitat suitability. We use hydromorphologic classification because the relationship between HMUs and functional habitat for adult fish has already been documented. It does not preclude using a different classification scheme that identifies only key habitats for investigated species or life stage, for example, determination of shallow margins as a predetermined key habitat for young-of-the-year fish. Therefore, the approach presented above is not the ultimate one and can be easily adapted to serve modelling of different species and/or life stages.

Even within the framework established for adult resident fish, it is of the essence that the model supports the use of many non-hydraulic variables as habitat descriptors. This is because many non-salmonid species may be associated with habitat attributes different from depth, velocity and substrate (e.g. large woody debris). These features help significantly in applying MesoHABSIM to entire aquatic communities rather than to single species.

The meso-scale better facilitates model validation than the micro-scale by using a snapshot of fish distributions, which is less affected by factors such as time of observation. This is because fish are naturally mobile and do not wait to be seen in one microhabitat. This creates great scatter in the validation data, requiring many observations to document use patterns. It should be less of an impact if we lump the observation to the scale encompassing diurnal range of the mobility. It may be that this is an important reason for the little success with the transferability of microhabitat models.

The greatest advantage of the MesoHABSIM method is its ability to quickly collect detailed information about physical conditions from long river sections. This allows a reduction in second stage error caused by extrapolation, when compared with hydraulic simulations using microhabitat approaches. The scale applied in the model is more consistent with the scale of biological response reflecting functional habitats. The underlying concept is more driven by biological principles than by the data requirements of hydrodynamic models. However, it does not exclude the use of hydraulic models as long as they are embedded in the concept above. Moreover, for projects with very limited spatial scope and high precision requirements microhabitat models may prove to be more appropriate.

As is the case with microhabitat models, the output of MesoHABSIM can be used for sophisticated analyses of habitat time series (Parasiewicz, 2007). In contrast with microhabitat models, MesoHABSIM can easily simulate large-scale management actions, allowing for predicting the effects of measures such as dam removals or extensive channel restoration. Another advantage is the ability to create GIS maps of suitable habitats that describe scientific information in simple terms.

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A mesohabitat model is appealing because it links science and the decision making process (Acreman, 2005) while maintaining a rigor acceptable to the scientific community. Because of this, MesoHABSIM has received attention from resource agencies and is being applied to several projects for the development of instream flow standards in New England. Several researchers have begun to develop similar approaches such as the meso-scale habitat classification method Norway (Borsányi et al., 2004) and rapid habitat mapping (Maddock et al., 2001). Eisner et al. (2005) compared these three models on two river sections and used their findings in the development of MesoCASiMiR; I will use their experiment to explore MesoHABSIM's potential shortcomings. The conclusion was that MesoHABSIM was the most detailed and most effort-intensive of the three methods. The need to measure seven random velocities is the major drawback of the habitat mapping. In future I hope to find a way to predict hydraulic distribution in various HMU types that would not require making these measurements.

Conversely, reducing hydraulic measurements could increase the subjectivity of HMU classification. In MesoHABSIM, the disagreement in HMU classes between two surveyors has little consequence for the habitat type, because both components are included in the mesohabitat description. In other words, a slow-flowing riffle may create the same habitat as a fast-flowing glide. These are the most common inconsistencies as it is unlikely that someone will call a 'pool' a 'rapid'.

The same study points out that although the subjectivity of the hydraulic measurements is low due to the use of random locations, the repeatability is not necessarily so. This may be correct if the absolute values of the seven measurements were compared. However, in MesoHABSIM the velocity and depth measurements serve only to estimate the relative distribution of these attributes within one bin, and therefore the discrepancies in comparing them are much lower. In other words, the seven random measurements serve to estimate the proportion of HMU area having depth or velocity within specified range. It remains to be documented if the increase in the number of randomly collected values has an influence on the results.

Another issue is the necessity of mapping the same site over a range of flows. This is probably the greatest shortcoming of the model, especially when the flows in the river cannot be regulated. Experience indicates that the creation of a good flow-habitat rating curve requires four surveys, since at present it is not possible to predict how the HMU mosaic will evolve with changes in flow.

Though MesoHABSIM does have a limited ability to extrapolate habitat predictions over the range of measured flows, it is important to consider that if the purpose is to define habitat use at flows higher than mean annual, the question of validity of habitat suitability functions (usually obtained at low flow conditions) becomes critical for model accuracy. It is possible that at high flows, very different mechanisms govern fish behaviour (e.g. under such circumstances a fish may search for velocity refuge instead of foraging).

Last is the question of the applicability of the model to large rivers. As mentioned above, the model is being applied to the Upper Delaware River in New York and Pennsylvania, USA. The application and hydromorphologic features are similar to wadeable streams; the major difference is the size, which calls for different instrumentation and equipment. This may be advantageous because using boats, Acoustic Doppler Profilers and aerial or satellite photography is easier with large units, greater depths and less closed canopy. The MesoHABSIM model has not yet been applied to a large floodplain river. I expect that the same principles can be followed, and the major challenge will be the availability of appropriate instrumentation. Remote data collection is likely an option, along with hydrodynamic models that predict hydraulic change such as River2D (Ghanem et al., 1996).

The MesoHABSIM model was developed from the PHABSIM model concepts by successively reducing the field data collection while examining the effect of those modifications on model output. Its development was a response to a need for tools for habitat assessment applicable to river management at the watershed scale. It was essential to create a modelling framework that would provide reasonable results, with the intent of addressing detailed questions in subsequent improvements. In many cases it is necessary to use professional judgment to fill gaps in scientific knowledge. Such cases are related to collection strategy for hydraulic data (Are seven random points enough to describe hydraulic distribution of an HMU? Should cross-sectional measurement be used instead?); the number of HMUs types and the probability of fish presence necessary to declare an HMU suitable. Because of these unknowns it is important to validate model predictions in the early phase of development and document model validity.

In conclusion, MesoHABSIM offers new opportunities for applying habitat models in river management frameworks. It overcomes the high effort and expense of physical habitat models, which are often not applicable for

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large-scale watershed management efforts. MesoHABSIM also bridges the gap between the qualitative synthesis approaches frequently used in impact assessment, and the quantitative models used by 'incrementalists'.

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