Spatial Scales in Instream Flow Modeling:
Why and How to Use Ecologically Appropriate Resolutions

Running title: Spatial Resolution of Instream Flow Models

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ABSTRACT

This paper discusses why and how to use ecologically appropriate spatial resolutions (e.g., cell size or range of cell sizes) when modeling instream flow effects on aquatic animals. Resolution is important because relations between habitat and animal habitat use vary with spatial resolution, and different habitat variables may best predict habitat use at different resolutions. Using appropriate resolutions consistently would bring clarity and coherence to how we quantify and model habitat characteristics and habitat use by fish, facilitate the use of standard and more credible measures of habitat preference, incorporate more fisheries knowledge to improve models for different kinds of fish, and avoid well-known (and perhaps unknown) biases. Doing so involves describing habitat, and habitat use by fish, with spatially explicit measures with clear resolutions; using the same resolution for physical habitat and fish habitat use; selecting that resolution for ecological reasons; and using habitat variables and fish observation methods appropriate for the resolution. The choice of resolution considers factors such as how much space fish use for specific activities and the size of important habitat patches. For drift feeders, cell sizes and fish habitat use observations should use a resolution no smaller than feeding territories. Piscivores typically hunt over large areas so should be modeled with larger habitat units. Models of small and less-mobile organisms (e.g., benthic invertivores) may need fine resolutions to capture the small areas of unusual habitat they depend on. Because of such differences, instream flow studies (like any spatial ecology exercise) should clearly state what resolution(s) they use and why.

1 WHY SPATIAL RESOLUTION IS IMPORTANT

The importance of using appropriate spatial scales is widely understood in ecological modeling but rarely considered in instream flow modeling, especially in traditional PHABSIM-based methods (e.g., Bovee et al. 1998). To address this gap, I summarize the literature and standard practice to help instream flow practitioners avoid scale-related errors and biases. Not every instream flow study needs an elaborate scale-selection exercise, but we should always use habitat unit (cell) sizes that make biological sense. I focus on habitat models of fish, but the same ideas apply generally to mobile aquatic species and other model types.

To ecological modelers, “spatial scale” refers to the “extent”—the total area represented in a model—and the “resolution”—the size pieces, or units or cells, that area is divided into. I focus only on resolution. When we model habitat by dividing it into discrete units, as in instream flow assessment, we assume that (a) variation in habitat within a unit is less important than variation among units, and (b) individuals are only affected by habitat within their unit. The basic resolution question is: what habitat unit sizes make these two assumptions most reasonable? Clearly, the answer for a stationary drift feeder will be different than the answer for a piscivore hunting prey in various habitat types over large distances.

This resolution question is important because ecological relations—including suitability or preference functions in instream flow models—change with the scale at which they are observed. Habitat use by drift-feeding fish illustrates this “scale-dependence” and why resolution is important. Models of net energy intake by drift feeders (Piccolo et al. 2014) assume that two key mechanisms—delivery of drift to the fish and the fish’s ability to catch it—are driven by velocity at the scale of the fish’s “reactive distance”: the distance over which the fish can see and capture food particles. However, drift feeders often wait for prey in velocity shelters that reduce swimming speed. Therefore, if we measure water velocity at a fish’s waiting position we underestimate the larger-scale velocity it needs to deliver food, thereby biasing instream flow recommendations toward lower flows (Railsback 1999, 2016; Rosenfeld and Naman 2021). Drift-feeders also avoid cover that would interfere with prey capture but prefer cover further away but close enough to escape predators in. Hence, observations at the scale of the feeding area would show avoidance of cover while observations over a larger area would show preference for it. These problems are eliminated by using an explicit and appropriate resolution for both the habitat and fish components of the model. The InSTREAM model (Railsback et al. 1999, 2021a) represents drift-feeding habitat using cells that are no smaller than the feeding territory of an adult trout but sometimes larger to represent patches of uniform habitat, with cell variables for the availability of velocity shelter within the cell and the distance to escape cover, which can be outside the cell (Figure 1).

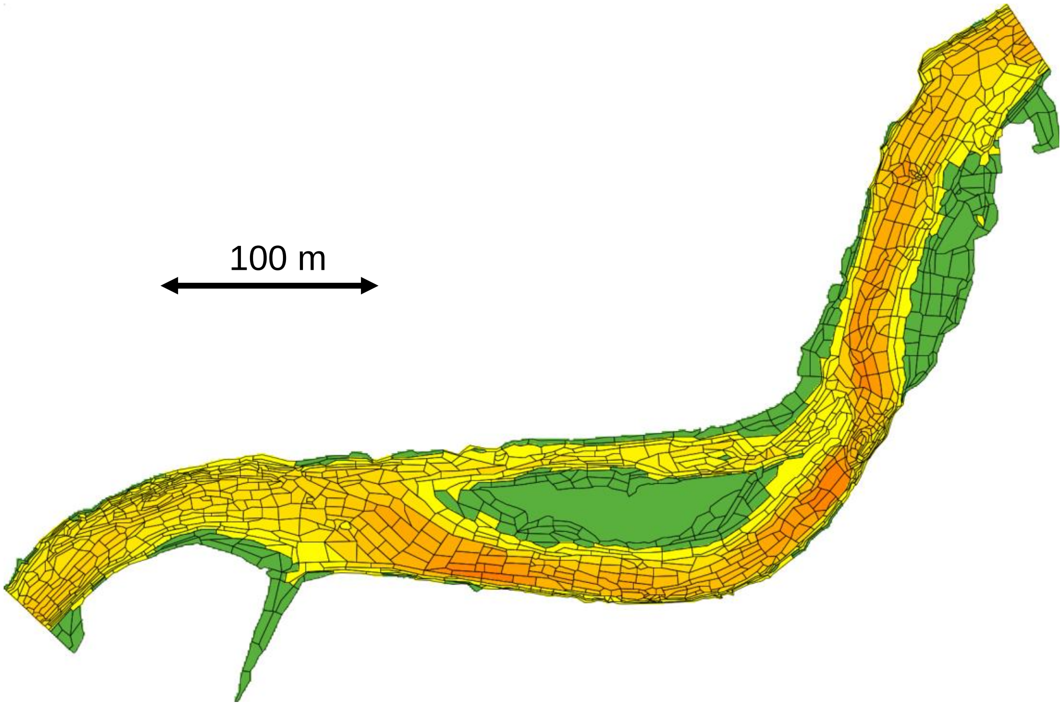

Figure 1. InSTREAM (Railsback et al. 2021a) represents habitat as irregular polygons, here shaded by velocity. In this example, 17,300 m2 of stream is represented via 1373 cells with mean size of 12.6 m2. Large polygons (>100 m2) represent large areas of relatively uniform habitat while smaller ones (down to 1 m^2) represent habitat that changes rapidly over space, especially along channel margins.

In addition to causing such biases, use of inappropriate and mixed resolutions prevents use of standard, more-meaningful measures of habitat preference, and limits our ability to use fisheries knowledge to reflect how flow affects different kinds of fish (e.g., drift-feeders vs. piscivores) differently (Railsback 2016).

The literature on scale dependence is extensive. Key issues relevant to habitat modeling are discussed by Bissonette (1997), Boyce (2006), Northrup et al. (2022), Scott et al. (2002), and

Wu and Li (2006). In stream fisheries, Boisclair (2001) and Bult et al. (1998) addressed appropriate scales in fish habitat models, Fausch et al. (2002) identified research and management principles focused on using appropriate scales, Durance et al. (2006) reviewed 658 river fisheries publications and concluded that scale-dependence of relationships between fish populations and habitat is widely neglected, and Dunbar et al. (2012) reviewed spatial scale issues in environmental flow assessment.

Stream habitat, and fish use of it, is spatially hierarchical: throughout their life cycle, fish make different decisions about habitat for different behaviors, at different spatial and temporal scales. These decisions range from which microhabitat to forage or hide in for the next few minutes to when and where to migrate for annual spawning. We cannot model all these decisions and scales; therefore, we need to explicitly decide which behaviors and life stages we address when selecting resolutions and parameterizing models.

2 GUIDANCE FOR SPATIAL RESOLUTION

The kinds of errors and biases discussed above can be avoided by the following measures related to spatial resolution, which are adapted from the ecological modeling literature (e.g., Grimm and Railsback 2005; Haefner 2005; Manly et al. 2002).

Describe habitat, and habitat use by fish, using spatially explicit measures with clear resolution. Original PHABSIM methods described habitat as points on transects, and fish habitat use via observations made at points where fish were observed. These practices are a problem because habitat is space, but points and transects (being zero- and one-dimensional) cannot represent space. Instead, habitat should be described as units of area or volume with specific boundaries and areas. (When ecologists use “transect” or “point” sampling methods, they specify the area sampled by stating the distance from the transect or point over which observations were made.) Habitat variables should be measured and described with a clear resolution: instead of “depth,” we should refer to “cell average depth” to make it clear that the value represents the cell. We can also use variables like cell maximum velocity and cell area with concealment cover. Habitat variables should be measured and modeled so they represent units of space, not points.

Use the same resolution for habitat and fish habitat use. The original PHABSIM practice of basing “suitability” functions on habitat measurements made at the point where fish are observed makes biases due to mixed spatial resolutions (like those noted above for drift-feeding fish) inevitable. Biases due to mixed resolutions can be strong yet nonintuitive. Therefore, we need to make habitat use observations at the same resolution used to model habitat. Overlaying observed fish locations and habitat unit boundaries in GIS is a simple way to do so.

Select appropriate spatial resolution(s) for each study, during study design. Sections 3 and 4 discuss how the best spatial resolution (or resolutions) depends on the situation being modeled; convenience and tradition are not credible reasons to use a resolution. Selecting the resolution early allows us to avoid measuring and modeling habitat at finer (or coarser) resolutions than we need. Because spatial resolutions are critical elements of study design, they should be fully documented.

Use habitat variables and fish observations appropriate for the resolution. Often, different variables are best for predicting habitat use at different resolutions. Traditional variables such as depth, velocity, and substrate type become much less meaningful for larger habitat units. Sections. 4 and 5 discuss variables meaningful at larger scales.

Alternative ways of observing fish habitat use may be more appropriate at larger scales. When modeling habitat use for foraging, PHABSIM's traditional instantaneous fish observations may be appropriate for stationary feeders but cannot be reliable for fish (e.g., piscivores) that forage over large areas and multiple habitat types; other methods such as tracking individuals over time may be much more informative (e.g., Harvey and Nakamoto 1999). The use of tracking data to understand habitat selection is an active research topic (Northrup et al. 2022).

3 GUIDANCE FOR SELECTING RESOLUTIONS

These steps to selecting appropriate spatial resolutions are adapted from standard ecological modeling practice.

3.1 Preliminary steps

Before we can identify appropriate spatial resolutions, we need to determine exactly what we are modeling, via three steps.

(a) Defining the problem. Characteristics of an instream flow model that must be defined before we select spatial resolutions include: (1) The species and life stages to be modeled. (2) The activities assumed most important, because fish use habitat differently for different activities (Boisclair 2001). Foraging is often of primary importance, but other activities to consider include concealment (hiding for extended periods instead of foraging, e.g., in winter), spawning, and holding while not feeding (e.g., by adult salmon and the grazers discussed in Sect. 4). (3) Time scales: what season, time of day, and time period does the model represent? Fish often use different activities and habitat at different times of day and year (e.g., Harvey and Nakamoto 1999; Railsback et al. 2021b).

(b) Choosing a fish response variable. PHABSIM traditionally evaluates habitat value as "suitability," a vague term that lacks specific meaning (Railsback 2016). Ecologists instead use specific measures of habitat value such as occupancy (probability of a cell being occupied), density (expected number of fish per unit area), and other "selection indices" (Manly et al. 2002; Northrup et al. 2022). Naman et al. (2020) used growth rate as the response variable. Occupancy is most useful for fish that do not share habitat, such as those defending territories, while density is useful when multiple fish use the same habitat unit. Occupancy and density have the important advantage that they can be summed across habitat units to produce meaningful and testable predictions of abundance.

(c) Identifying key mechanisms and variables linking habitat to fish response. Next, we can identify mechanisms through which flow affects the response variable. We implicitly assume that fish select habitat that provides fitness, so we can think about how habitat varies with flow in ways that affect growth and risk. For example, when modeling foraging fish, which flow-dependent habitat variables affect food intake, growth, and predation risk, and how? The mechanisms of how habitat affects drift-feeding salmonids (Sect. 1) provide a good example: velocity within the reactive distance provides food, velocity at the fish's holding position determines its energy cost, depth can limit the volume of catchable food, and predation risk is affected by depth and distance to escape cover. However, quite different mechanisms and variables can be important for other fish. Harvey and Nakamoto (1999) observed warmwater piscivores using depth to reduce predation risk during daytime, but foraging at night in many habitat types, including riffles. This step lets us use our biological expertise instead of blindly following cookbook procedures.

3.2 Selecting resolutions

Now we are ready to select spatial resolutions and the habitat variables that relate fish responses to flow. While we need to identify a biologically reasonable resolution for a model's habitat unit size, we can also use habitat variables at different resolutions: a model for trout can use cells the size of an adult trout feeding territory while each cell has variables for availability of velocity shelter within the cell (a smaller-scale variable) and the distance to escape cover (a larger-scale variable because this cover can be useful even if outside the cell).

The primary consideration in selecting resolutions is how much area fish use for the activities of concern, over the time scale. Some fish use well-defined feeding stations or territories, while others move over large distances while hunting prey or digesting grazed food. In general, it makes no sense to model habitat at a resolution smaller than the area individuals use for the activity we model, over the time scale we consider.

Second is considering the areas over which the key mechanisms and habitat variables affect fish. Drift feeding again illustrates how important mechanisms act over different distances (Sect. 1). Salmonid spawning provides a second example. We could assume that the key mechanisms and variables driving how salmonids select spawning habitat are: substrate size that allows redd construction, depths sufficient to make dewatering unlikely, and velocities sufficient to aid redd construction without undue scour risk. All of these mechanisms act at a small scale, indicating that habitat units should be close to redds in size. But if we also consider intragravel flow to oxygenate eggs and remove waste, then a larger resolution is essential: intragravel flow depends on larger-scale habitat characteristics such as bed slope and permeability of a gravel bed.

The third consideration is the response variable we use to represent habitat benefits to fish. Modeling occupancy works when habitat units approximate the area used by one individual, while modeling fish density lets us use larger units occupied by multiple fish. The growth response model of Naman et al. (2020) demands cell sizes at least as large as the feeding stations it represents.

The final consideration is the scales at which key habitat types occur. If important habitat occurs in large patches, large habitat units may represent it well. However, capturing small but important patches requires small habitat units. Margin habitat is often important for fry; representing that habitat, and how its availability varies with flow, can require smaller cells along channel margins (Figure 1). However, we can represent small-scale habitat features as characteristics of larger units when the location of those features within a unit is not important; e.g., if we model at the mesohabitat unit scale, the area of shallow margin habitat could be a variable of pool units.

These steps can produce different results for different life stages and species, so we often need a compromise resolution. Preferring larger resolutions over smaller ones seems reasonable: using a larger-than-optimal resolution for some life stages or species is less likely to induce serious errors than using smaller-than-appropriate resolutions for others. But some combinations of species could be impossible to model credibly at the same resolution. For example, the mechanisms driving fitness of juvenile salmon occur at much smaller scales than those driving fitness of piscivores that prey on them, so we should not model both at the same resolution.

4 EXAMPLES AND GENERALIZATION

The process of selecting appropriate spatial scales is not inherently site-specific and need not be repeated in detail for each instream flow study—studies addressing the same kinds of fish in similar streams are likely to need similar spatial scales. As examples, I draw general conclusions about resolutions for three kinds of fish, focusing specifically on modeling foraging habitat.

4.1 Stationary drift feeders

Sect. 1 discusses the variables and mechanisms commonly assumed to drive selection of habitat by drift feeders such as trout. That discussion explains why models of such fish need a spatial resolution at least as big as a typical feeding territory. A model could use uniform cells approximately the size of a territory (e.g., ~1 m square grids, for adult trout) and use occupancy probability as the fish response variable. Alternatively, cells could be nonuniform and larger than one territory in patches of relatively uniform habitat (e.g., Figure 1), and fish density used as the response variable.

4.2 Benthic invertivores

Benthic invertivores, including many darters, are not stationary feeders but associated with particular habitat types, typically feeding by searching the substrate over areas of similar habitat (Page 1983). Species appear specialized, with adults of different species adapted to (e.g.) substrate and hydraulic conditions at the heads, tails, or middles of riffles. If we assume such a fish needs only its special habitat, is non-territorial, and can find and use patches too small to support even one fish, then it is reasonable to use small cells (Figure 2) and evaluate habitat by whether it meet the species' requirements. If cells are too small to support one fish, we cannot use occupancy as the response variable but we can use density (by assuming, e.g., that each adult requires 4 m^2 of suitable habitat).

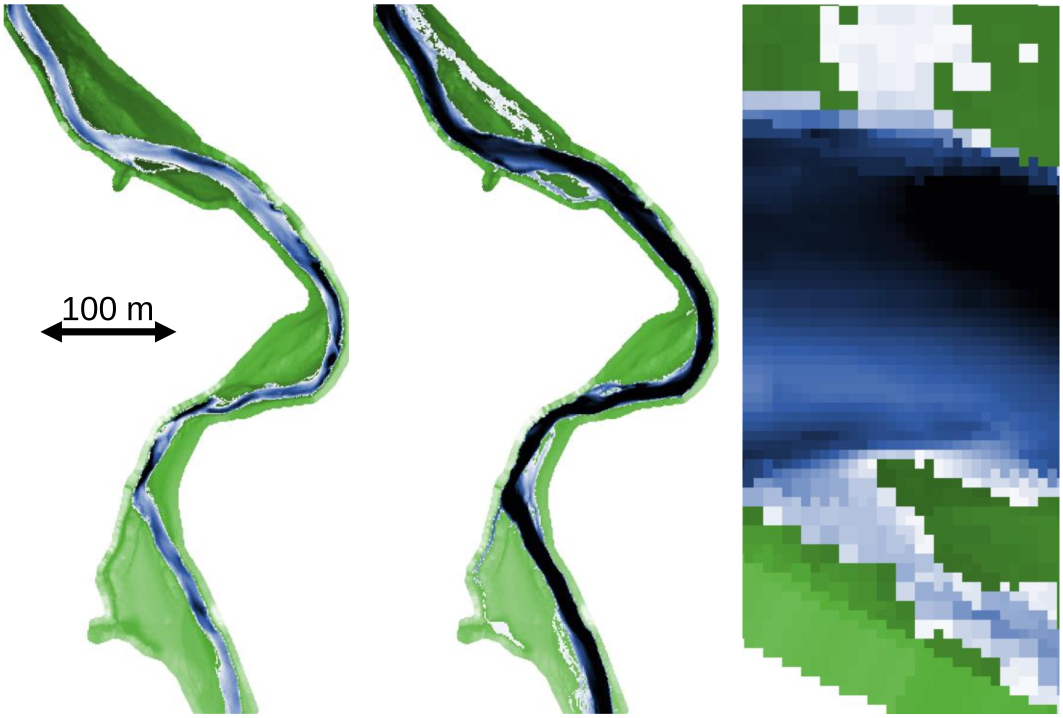

Figure 2. Example model representing habitat as a fine grid of square cells. This application uses >108,000 cells that are 1.5 m wide. Cells are shown shaded by depth at a low and high flow (left, center), and a zoom that shows individual cells (right).

4.3 Piscivores

Large piscivores typically feed over large areas and can rely on several kinds of habitat. The pikeminnow observed by Harvey and Nakamoto (1999) were inactive in deep pools during the day but at night ranged long distances to hunt in riffles. Therefore, small-resolution, short-term, daytime observations would produce highly biased models of habitat use and flow effects. Meaningful models of flow effects on large piscivores must use variables that relate flow to fish fitness at large scales. Examples could include the availability of deep pools for daytime holding (but not necessarily pool *size*, if holding fish are nonterritorial), and the area of habitat productive of important prey (e.g., riffle-feeding fish, crayfish)—variables that cannot be evaluated only by observing the target fish. (The most important effects of flow on piscivores could actually be indirect, on production of their prey.) These variables can be evaluated meaningfully at the mesohabitat or stream reach resolution (Figure 3).

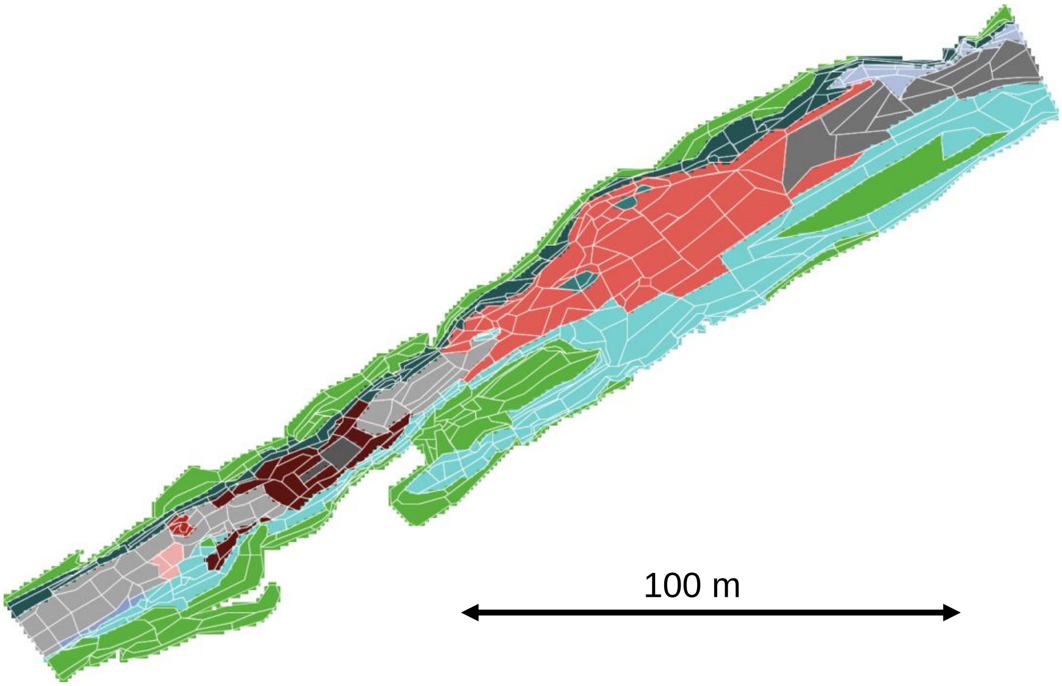

Figure 3. Example representation of habitat as dynamic mesohabitat units. Reach-scale habitat variables can include the areas of deep pool habitat (blue), food-producing riffle (red), and shallows suitable for juveniles (light blue). These areas are delineated dynamically from the depth and velocity of hydraulic model cells (outlined in white). Dry cells are green.

5 PRACTICAL CONSIDERATIONS

Modeling at scales other than PHABSIM's microhabitat resolution may seem alien, but doing so does not always require major changes in methods or throwing away information observed at finer resolutions. For example, we represent InSTREAM's habitat cells by aggregating fine-resolution hydraulic model results in combination with field data, in GIS (Railsback et al., in press, provide several methods). Standard hydraulic model output can also be analyzed to determine how flow affects the areas of mesohabitat types and mesohabitat or reach variables such as the area of shallow pool habitat; Hauer et al. (2009) provide methods that could be adapted for this. And large habitat units can have variables describing finer-scale habitat within them, such as the percentage of a unit providing spawning gravel or velocity shelter.

Sometimes, though, when we know we will use coarser resolutions, we can save work by avoiding unnecessarily detailed data collection and analysis.

6 CONCLUSIONS

Habitat models for instream flow assessment are inherently spatial, and spatial modeling has advanced a great deal since PHABSIM was developed. Ecologists now know that using inappropriate resolutions can strongly bias models, and that fine resolutions are not always best. While a range of scales have been used in instream flow models, the question of which resolution makes ecological sense for a particular application is rarely addressed.

Here, I promote credible treatment of spatial resolution by providing practical guidance. Following this guidance may initially seem burdensome, but shared experience should rapidly lead to standard approaches for different kinds of streams and fish. More importantly, handling spatial resolution properly can alleviate the kinds of problems identified in Sect. 1..

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DATA AVAILABILITY STATEMENT

This study produced no original data.