Chapter 3

Scale and Fisheries Management

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3.1 INTRODUCTION

Scale is an issue of central importance to fisheries managers. This chapter provides an overview of what "scale" is and why its consideration is essential for effective fisheries management. The overview is followed with illustrations of approaches for identifying different scales at which ecological processes may operate and how these approaches relate to incorporating scale into management practices. In contrast to the current trend of providing standard methods for sampling fishes or describing habitat in inland waters (Bain and Stevenson 1999; Bonar et al. 2009), the point of this chapter is that scaling is unique to the question and management situation at hand. With this view in mind, it becomes clear there is no single common protocol or approach that applies to inland fisheries management. Rather it is the question and the scale or scales at which questions are addressed that drive the approach. In a sense, scale is both the question and the answer in fisheries biology and management applications. A primary goal of this chapter is to explore this notion and motivate readers who are relatively new to ideas about scaling in natural systems to appreciate what many view as one of the most daunting challenges in both basic and applied biology. The range of issues and examples covered herein are far from comprehensive, but hopefully the point is made that scale fundamentally controls how fisheries managers see and understand the challenges they confront.

3.2 DEFINING SCALE AND ITS IMPORTANCE

The literature on scale can be confusing and is littered with what King (1997) referred to as "conceptual clutter." This lack of a clear and consistent articulation of basic concepts and terms related to scaling hampers understanding (e.g., Morrison and Hall 2002). This is partly because scale is inherently difficult to define and partly because of disparity on how researchers and practitioners in and among disciplines treat the issue of scaling. We address what we view to be a critical subset of terms, definitions, and considerations for scaling applications in fisheries management.

In the simplest terms, scale is defined by the "grain" and "extent" of observation (Figure 3.1). Grain refers to the finest spatial or temporal resolution possible in a given data set, usually a sample unit. For example in terms of space, grain size may represent the minimum resolution at which a fish length was measured (e.g., millimeter) or the pixel size in geographic data (e.g., square meter). In terms of time, grain size may represent the temporal resolution of

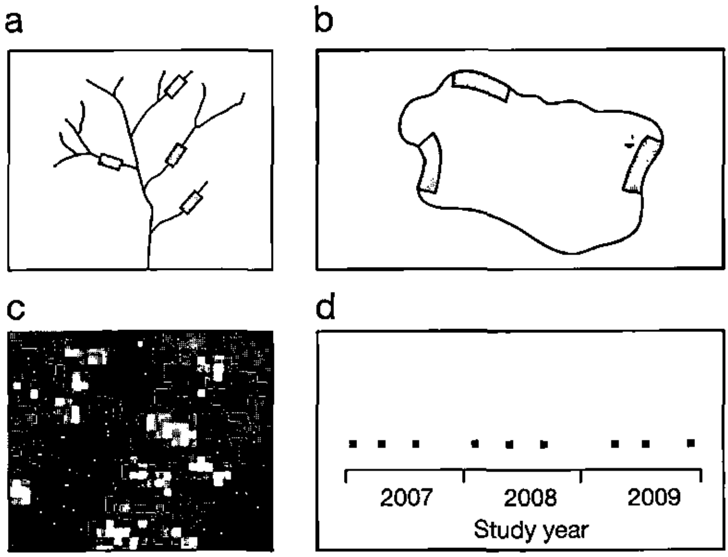
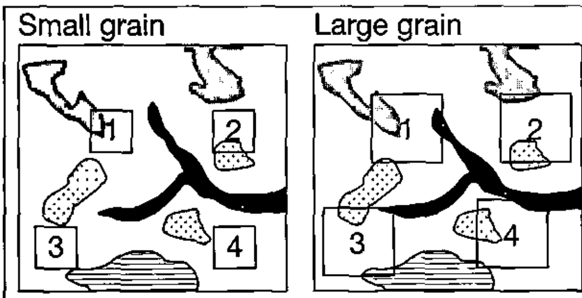


Figure 3.1. Common examples of grain and extent used in fisheries management applications where (a) the spatial extent is a stream network within a watershed and grain is the length of stream sampled (gray rectangles); (b) the spatial extent is a lake and the grain is the area of the individual shoreline electrofishing sites (gray areas); (c) the spatial extent is a geographical information system (GIS) coverage and the grain is represented by three two week sampling periods (squares); and (d) the temporal extent is a 3-year study and the grain is a 2-week sampling period represented by black squares.

a measurement of water temperature (e.g., measured at intervals of 30 min) or time intervals at which populations of fish are monitored (e.g., daily, weekly, or annually). Extent refers to the spatial dimensions or period of time over which observations are made. Common uses include the area of a particular study (e.g., watershed, lake, or in a park boundary) or the "period of record" for stream discharges or lake levels.

The issue of grain and extent of observation determine a fishery manager's ability to observe a phenomenon of interest. Consider, for example, the seemingly simple task of measuring stream temperatures with a digital thermograph. The scale of observation is determined by how frequently the thermograph is set to record measurements (grain) and the temporal interval over which measurements are made (extent). If measurements are made at a relatively coarse grain (e.g., greater than 2-h intervals), daily maximum temperatures may be underestimated by more than 2°C (Dunham et al. 2005). This is obviously more likely in cases in which temperatures can change very quickly (less than 2-h intervals). If the temporal extent of measurement does not include the warmest time of year, daily maximums may similarly be missed in the sample. The spatial grain at which temperatures are measured may also constrain a fishery manager's ability to detect small thermal anomalies that may be important to fish. For example, in warmer streams salmonids may use relatively small patches of cold water ($\leq 10^1$-m grain) in warmer reaches (e.g., extents of 10^1–10^2 m; Torgersen et al. 1999; Ebersole et al. 2001) or larger patches (10^3-m or greater grain) of cold water in the headwaters of river networks by moving over large extents (extents of 10^3 m or greater; Dunham et al. 2002). Smaller patches of cold water may serve as important thermal refugia for short-term survival of individuals or as stopover habitats during migration, whereas larger patches may be more important for persistence of populations. Consequently, different spatial and temporal scales may provide strongly-contrasting views of habitat use and implications for individuals and populations.

The preceding example involving water temperatures indicates that the ratio of grain to extent influences perception of how habitat and other factors influence fish. Within-grain heterogeneity (variability) tends to increase as relative grain size increases (Figure 3.2). For example, the depth, velocity, and substrate composition of a 1-m-long section of a small stream are likely to be homogeneous relative to a 100-m-long section of stream, which is more likely to contain a wide variety of habitat types. As larger grains are considered, differences among them typically decrease owing to increasing variability within grains. For instance, in temperate zones, differences in average annual temperature (large grain) are much less variable from year to year compared with variation from month to month in average monthly temperatures (smaller grain). The ability to detect relationships and patterns in data are weakest when the within-grain heterogeneity is high and between-grain differences are low (Fuller 1987). This means that fisheries managers could arrive at very different conclusions about the relationship between a factor (e.g., habitat characteristics) and fish population response (e.g., abundance) depending on the choice of grain size alone. A good example is coexistence of native and nonnative fish species where both may coexist when considering large grains, but local segregation (e.g., in portions of a lake or stream) occurs and is not detected by coarse-grained analysis (Melbourne et al. 2007). Another common scale dependency is described by "scale–area" curves that examine the effect of grain size on estimates of the area of occupied habitat for different species (Box 3.1). The consequence is that the fishery manager's view of the area of habitat occupied by different species could actually reverse between species for reasons



Small grain: Sample number	Habitat types	Large grain: Sample number	Habitat types
1	2	1	4
2	2	2	3
3	1	3	4
4	1	4	4

Mean Jaccard's SI = 0.56   *Mean Jaccard's SI = 0.63*

Figure 3.2. An example of a fixed study site (extent) with different habitats shown as shapes (with varying patterns) and two different grain sizes (heavy boxes). Each sample collected with the small grain size (a) contains only one to two habitat types, whereas each sample collected with the large grain size (b) contains three to four habitat types. As grain size increases relative to the extent, within-grain heterogeneity in habitats increases and between-sample differences in habitat types decrease. Jaccard's similarity index (SI) is a measure of similarity among samples.

Box 3.1. Scale–Area Curves

Kunin (1998) demonstrated that the grain of observation can influence the view of how species are distributed across landscapes. Consider the example below that illustrates three sampling scenarios for a species with a patchy distribution (occurrences indicated by dots). In (a) a fine-grained sampling grid indicates occupancy of 39% (percent area of white or occupied grid cells) of the area within the sampling frame (all cells, overall extent). In (b) a doubling of the cell size within the grid indicates an occupied area of 75%, whereas in (c), with only four large cells, the occupied area is 100%. This phenomenon leads to a scale–area curve that defines how the grain (scale) of observation influences the estimate of the area of occupancy (d). Given the patterns of rarity we observe among inland fishes (Box 3.2), this effect should be a cause for concern. The importance of scale–area curves and relevance for assessing rarity and risk was explored by Fagan et al. (2005) for desert fishes in the southwestern USA.

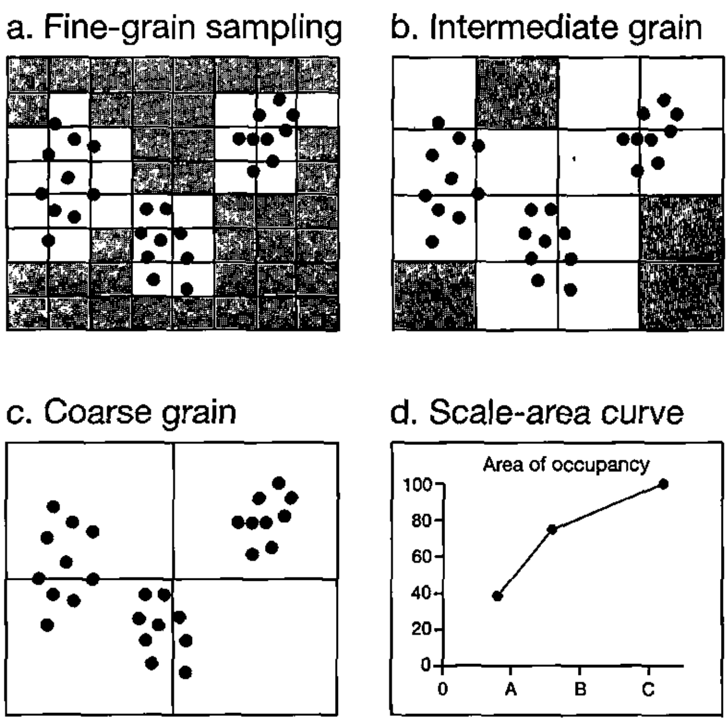


Figure. Illustration of scale–area curve, which defines how the grain (scale) of observation influences the estimate of the area of occupancy.

none other than simply changing the grain size (i.e., sample unit size) of observation (Kunin 1998).

Another issue related to scale is that many processes operate on different temporal or spatial scales. Stream characteristics can influence fish growth, survival, or reproduction over relatively short time spans compared with decades and centuries over which geomorphic processes often operate. For example, interannual or seasonal variation in temperatures of streams in the Missouri Ozarks influences annual variation in fish growth. However, growth in these same streams is currently affected by excessive sediment due to land use changes that occurred more than 150 years ago (Jacobson and Gran 1999). Additionally, variation in both productivity and nutrient availability among these streams has occurred over millions of years due to differences in underlying geologic features and local weathering rates.

A single process may operate on multiple scales. For example, consider the process of gene flow due to dispersal of individuals among local populations of fishes. In some cases, gene flow may be realized through a relatively-constant rate of movement of individuals among populations. A common pattern of gene flow is isolation by distance, by which gene flow is more likely among neighboring populations (Neville et al. 2006). In other cases, infrequent pulses of dispersal or isolation may occur over a wide range of distances in response to episodic disturbances (e.g., extreme floods or droughts). When averaged over multigenerational time scales, patterns of gene flow may appear similar between these two different scenarios. For example, if 10 individuals disperse among locations each year for 10 years or 100 individuals in 1 of 10 years, the average level of dispersal is 10 per year, but the pattern of dispersal is very different between these two scenarios. If gene flow is analyzed at a finer temporal grain, the signatures of these distinctive scenarios may be observable. Over longer time frames (e.g., postglacial colonization), the legacy of gene flow from influences dating back thousands of years may be evident in evolutionary relationships among populations observed today (Avise 1994). The implication is that a clear understanding of fish dispersal requires careful consideration of the processes that influence dispersal at different temporal and spatial scales, as well as the consequences (e.g., gene flow at different scales).

To complicate matters further, it is clear that both pattern and process interact. For example, fish populations that are closer together in space or time may be more likely to interact via dispersal and are more likely to be influenced by common environmental factors (e.g., local climate). The spatial extent occupied by populations also may be important. For instance, *those fish populations occupying a greater spatial extent may experience a broader range of* environmental conditions that can stabilize populations through time (Bisson et al. 2009). In fact, the view of what processes are important may change with scale. When viewing the distribution of fishes at a broad scale, the influences of climatic variability on temperature may be more evident, whereas observing individual fish at a local scale may highlight the importance of biotic interactions (Fausch et al. 1994). In general, processes at large spatial extents operate over longer time frames and processes at smaller extents operate over shorter time frames. For example, the distribution of freshwater fishes in North America is *largely the result of glaciation and fish dispersal operating over thousands of years* (Hocutt and Wiley 1986), whereas the distribution of fish in a stream reach is often the result of diel and seasonal habitat use modified by species interactions (Matthews and Heins 1987). This general relationship between spatial and temporal extents indicates that short-term studies are likely to conclude that small-scale processes have greater effects on fishes than do processes operating over larger scales. Thus, local fishery management efforts, such a changing harvest regulations, are likely to fail if the primary processes responsible for modifying the fishery are occurring at larger scales and are not adequately addressed (Lewis et al. 1996; Maceina and Bayne 2001).

Scale determines how fisheries managers perceive patterns and processes believed to be important (Figure 3.3). Scale may not refer to a constant spatial or temporal dimension but may vary according to the process under consideration (Wiens 1989). Because both fisheries and freshwater ecosystems are highly variable in space and time, there is no standardized sampling approach that can provide a consistent frame of observation. This should be a major cause for concern in fisheries management, but the good news is that considerable progress has been made in the acknowledgment of scale as a central issue, along with concurrent developments in methods for understanding scale. Practical approaches to working with scale in fisheries management are discussed in following sections.

3.3 WORKING WITH SCALE

Incorporating scale into practice is not an easy task, but fisheries managers can benefit greatly by adopting a multiscale perspective (Lewis et al. 1996; Fausch et al. 2002). A multiscale perspective means that managers consider the effects of physical and biological factors operating at large to small spatial scales and short- to long-term temporal scales. Then by means of data and (or) theory, the processes and associated scales that have the greatest influence on a fishery and the scales at which management is likely to be most successful are identified. The complexity of ecological systems and the potentially large number of interacting factors operating over multiple spatial and temporal scales makes this quite challenging. There are, however, a few practical steps that fisheries managers can take to facilitate the incorporation or consideration of scale into fisheries management strategies.

Assuming that management objectives have been clearly and explicitly identified (a crucial first step!), the next step to working with scale is to create a conceptual model of system dynamics. By conceptual model, we are referring primarily to ideas, notions, or hypotheses about how the system works rather than mathematical expressions, although the latter can be extremely useful. The best approach is to create a conceptual model with all of the important relationships and processes that influence the management objective. The structure of the conceptual model should be based on local observations, expert opinion, and other salient information and guided by contemporary theories of system dynamics. Ideally, the conceptual model should be in a graphical form called an influence diagram with arrows between components representing causal relationships (Figure 3.3). Often this is not as straightforward as it may seem as most initial model-building attempts result in conceptual models that are very large, unwieldy, and difficult to interpret. However, the conceptual model is crucial for facilitating communication among managers as well as among team members when used in an interdisciplinary effort that involves decision makers and the general public. Accordingly, managers should attempt to make the conceptual model as simple as possible with only key processes, relationships, and outcomes. In practice, it usually takes several iterations to get to the final conceptual model (Box 3.2). Once the conceptual model is complete, the next step is to use the conceptual model as a guide to identify the most important factors and scales influencing the system of interest. Below are some useful approaches for identifying these scales.

3.4 IDENTIFYING THE APPROPRIATE SCALES

The various approaches to identify the most important scales can be roughly classified as theoretical and empirical. Theoretical approaches rely primarily on ecological theory and published studies to identify the most important factors and associated scales influencing the fishery. In contrast, empirical approaches use existing data to identify the most important fac-

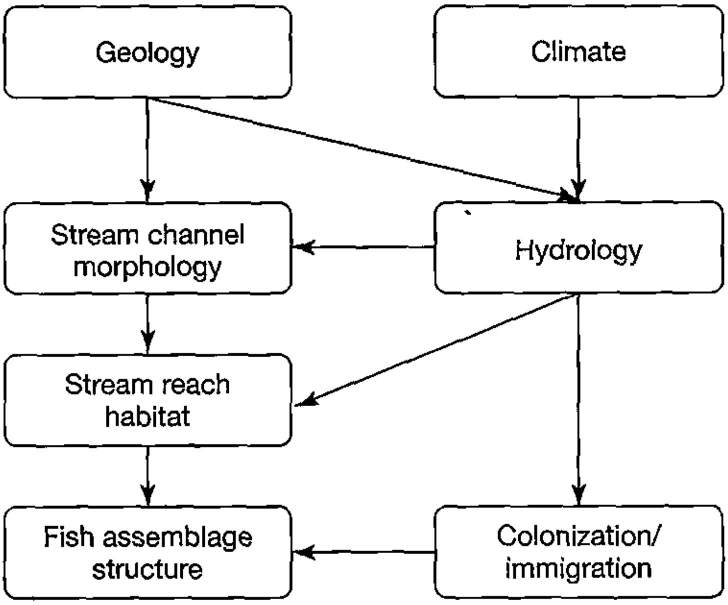


Figure 3.3. A simple conceptual model of the factors affecting the structure of stream fish assemblages in a stream reach. Here the structure of local fish assemblages is influenced by (small scale) stream habitat characteristics, such as the structure and availability of physical habitats, and (larger scale) colonization and immigration dynamics of fishes from connected water bodies. Arrows imply directions of hypothesized causal relationships.

tors and scales. In general, an empirical approach, guided by theoretical considerations, may be more defensible, but when data or available resources for analyses are limited, theoretical approaches may be the only practical means available for identifying appropriate management scales.

3.4.1 Theoretical Approaches

Theory on the role and importance of scale in ecology is large and rapidly expanding (e.g., Allen and Starr 1982; Peterson and Parker 1998; Holyoak et al. 2005). Of the many contemporary theories, hierarchy theory is among the most useful and widely used in fisheries and aquatic ecology (e.g., Frissell et al. 1986; Durance et al. 2006; Cheruvelil et al. 2008). In hierarchy theory, structure and function of biotic communities are viewed as a response to a hierarchical system of constraints in which processes operating at upper levels constrain those operating at lower levels. These levels may correspond roughly to a range of different spatial or temporal dimensions, but in a strict sense the idea of biotic or physical organization is not equivalent to a fixed scale (King 1997). In an oversimplified sense, organization can be thought of as structured interactions among processes, whereas scale in the narrowest sense refers to spatiotemporal dimensions of a phenomenon.

The dual influences of organization at different levels and relationships with scale can be illustrated with examples. Consider that the organization of native stream fish assemblages in local reaches is typically the result of constraints on the fish species pool occurring at larger spatial and temporal scales (e.g., ecoregions; Figure 3.4). In a strict hierarchy, upper-level

Box 3.2. Conceptual Model Development

The first step in evaluating the influence of scale and the response of fisheries to management actions is to create a conceptual model of the system dynamics. The process usually begins with a very complicated and detailed diagram, which is then refined in an iterative process. Below is the initial conceptual model of Rieman et al. (2001) that was used to evaluate the response of native salmonids to land management in the interior Columbia River basin. The initial model contained 45 components, called nodes, with four management action inputs (boxes) and one predicted response, fish population trend.

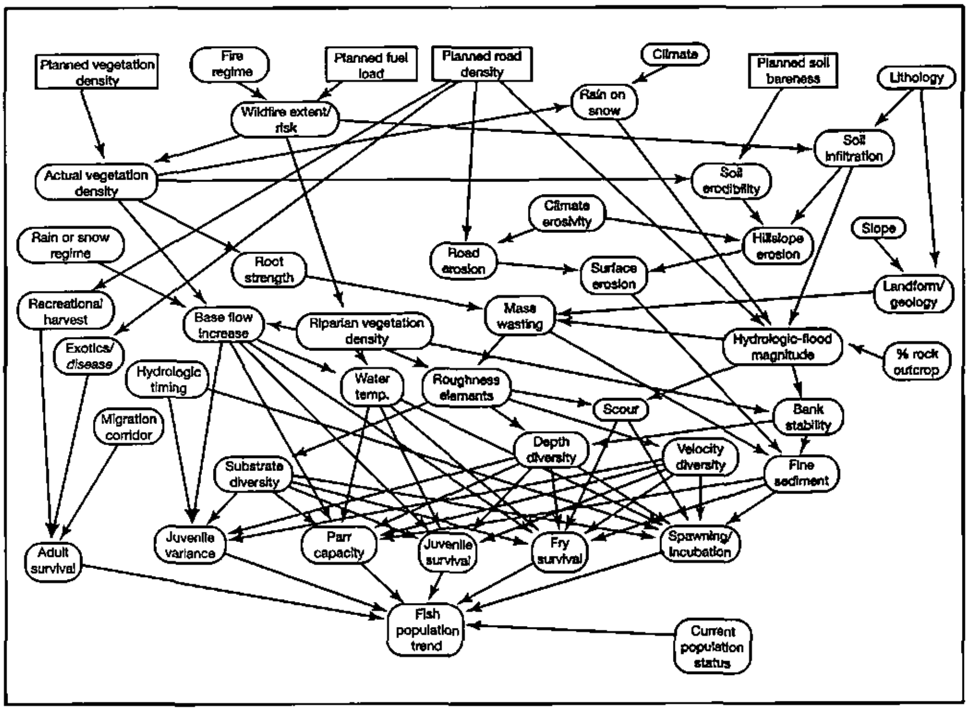


Figure A. Initial conceptual model of Rieman et al. (2001) to evaluate response of native salmonids to land management.

This initial conceptual model was subsequently modified by an interdisciplinary team of scientists and managers over a 3-month period resulting in a much simpler 23-node model (shown below) with four management inputs and one predicted response, future population status. Such substantial changes from initial model to final conceptual model are typical of multiscale evaluations.

(Box continues)

Box 3.2. Continued

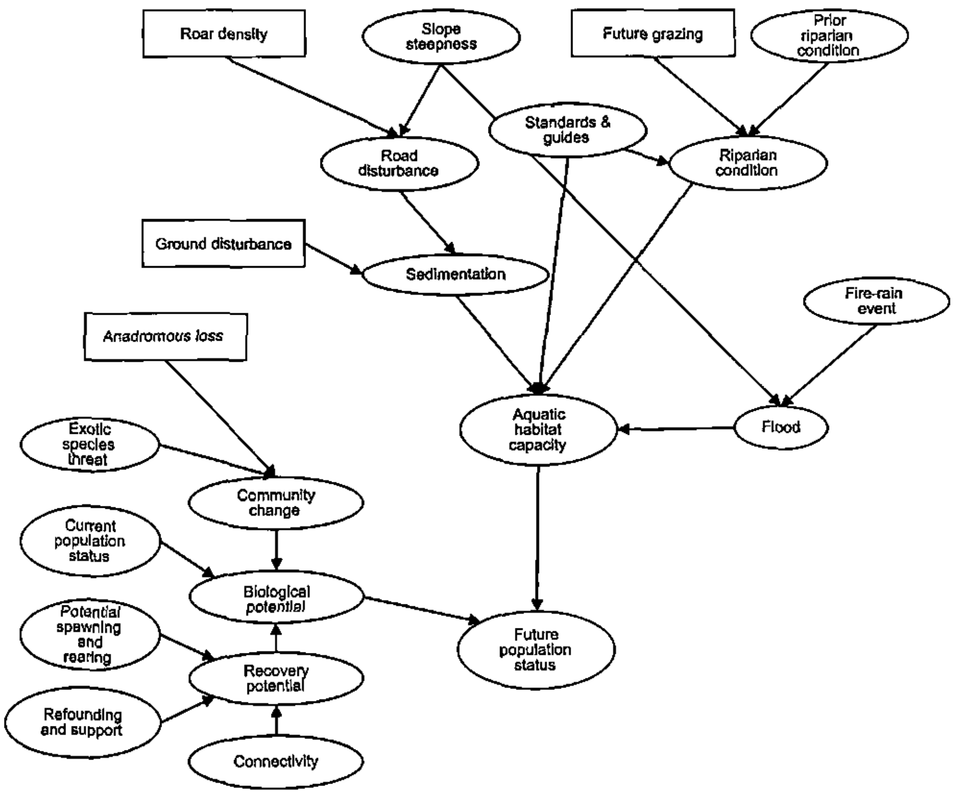


Figure B. Final conceptual model to evaluate response of native salmonids to land management.

factors correspond to larger spatial and longer temporal scales, whereas lower-level factors correspond to smaller spatial scales and shorter temporal scales. Thus, processes operate over shorter spatial extents and with greater frequency at lower levels compared with upper levels. By identifying the hierarchical levels of organization and understanding the relationships among levels (and spatiotemporal dimensions or scales), fisheries managers may identify the primary constraint acting on a fishery and evaluate the feasibility of management actions (Box 3.3). For example, the growth and condition of fishes and population size at a local scale are directly related to the productivity of the larger water body (Waters et al. 1993; Kwak and Waters 1997). Processes influencing water chemistry and productivity of a water body are, in turn, largely controlled by processes tied to watershed geologic features and climate at larger scales (Fetter 2001). In regions where geologic influences constrain productivity, local attempts to increase fish population size, perhaps by installing artificial habitat structures or changing harvest regulations, are likely to fail because population size is constrained by processes operating at a regional scale (Maceina and Bayne 2001). Managing these higher-level processes often requires greater effort or may be impossible (Figure 3.3). For example, consider a situation in which a stream fishery on locally-managed lands is negatively affected

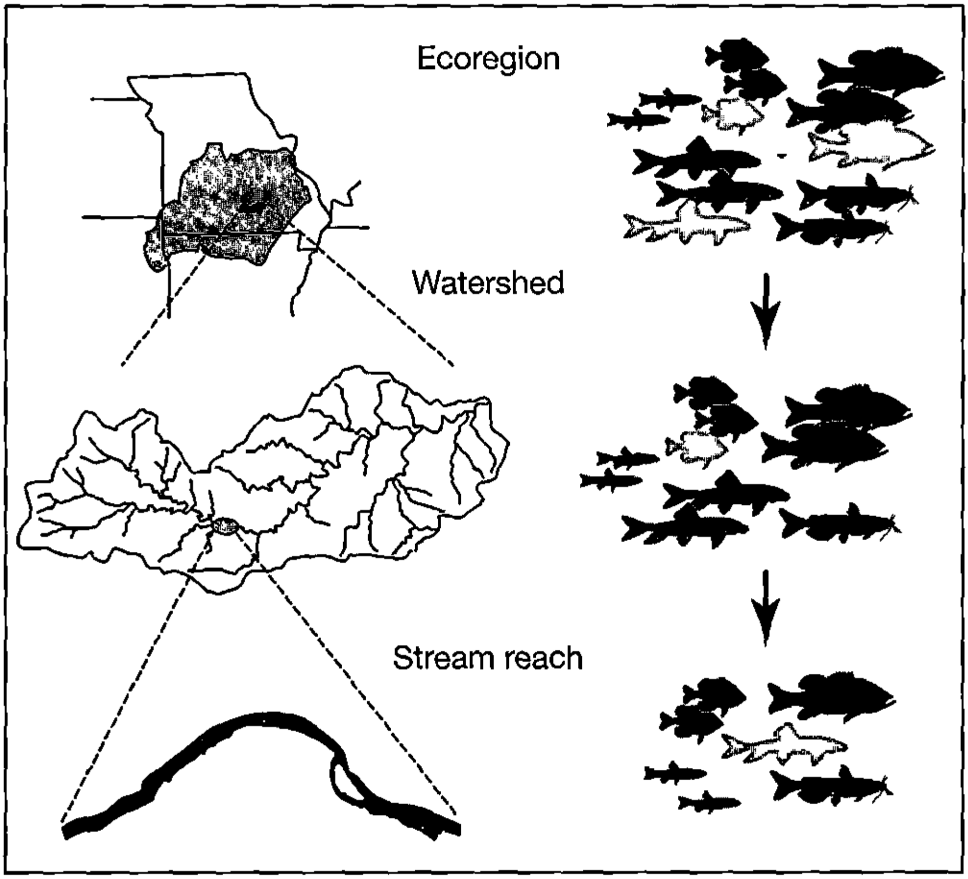


Figure 3.4. An example of the factors influencing fish assemblage structure at three hierarchical levels. At the largest spatial scale of an ecoregion, the fish species pool is the result of geologic and evolutionary processes operating over long time scales. Within the ecoregion, watershed characteristics determine the amount and type of discharge and sediment delivery patterns. At this scale, the watershed places constraints on the assemblage structure by determining the types and amounts and sizes of habitats available. At the smallest scale shown, longitudinal position of a stream reach influences the disturbance regime (i.e., frequency and intensity), which places a constraint on the fish assemblage by limiting the assemblage to the pool of available species that can survive or cope with the disturbance regime.

by habitat degradation. Riparian and stream habitat restoration at the stream reach (local) level, such as replanting riparian vegetation or adding artificial instream structures, are likely to be successful in improving the fishery if the habitat was degraded due to the loss of adjacent riparian vegetation at the local level. However, this scale of restoration is likely to be ineffective if the local habitat is degraded due to larger-scale land uses in the watershed or broad climatic patterns (Bond and Lake 2003).

In addition to these theoretical considerations, the most appropriate scales for management often differ with species-specific characteristics. For example, behavior and life history activities of a species can influence how a species interacts with its environment. Fish species with migratory life histories generally use discrete and often distant areas in a stream system

Box 3.3. An Example of Scale-Dependent Levels of Organization in Fisheries Management

Fisheries management objectives and activities may be scale dependent. The example of threatened bull trout illustrates possible relationships between conceptual scales at which natural populations of salmonid fishes are structured (Dunham et al. 2002) and units of conservation as defined in practice (see table below based on the draft bull trout recovery plan, U.S. Fish and Wildlife Service 2002; table modified from Fausch et al. 2006). Both spatial and temporal scales are implied here: as larger spatial extents are considered, longer time frames become more relevant. For example, local populations in patches can fluctuate substantially either seasonally or from year to year, but the overall range occupied by a species or distinct population segment may remain relatively constant for thousands of years under natural conditions. Specific management objectives may also vary according to unique characteristics that can be identified at each scale. For example, individual habitat patches may be the focus in managing local populations, but individual patches may be less important in considering the species or distinct population segment as a whole. Potential management activities also vary accordingly, with shorter-term actions at smaller scales (e.g., local habitat improvements or removal of nonnative species) and longer-term actions at larger scales (e.g., reintroductions to increase extent of historical habitat occupied or removal of major barriers to restore network connectivity).

(Box continues)

or beyond (e.g., marine migrations; Gross et al. 1988) to complete various life history requirements, such as spawning or juvenile rearing (Schlosser 1991). To identify the most appropriate scales for management, therefore, fisheries managers must also account for the ecological attributes of the species of interest to identify critical elements of the species' biology. The spatial extent over which these activities occur should also be considered when defining the most appropriate spatial and temporal scales for management (Box 3.4).

3.4.2 Empirical Approaches

There are a variety of empirical approaches to identifying relevant scales associated with a fishery, and those most appropriate scales for management are roughly categorized as qualitative or quantitative. Qualitative approaches use classification and ordination techniques to detect patterns in physical and biological data and infer the relative influence of small- and large-scale factors on fishes (Figure 3.5). Quantitative approaches use more detailed measures of fish abundance or community structure (e.g., species richness) to quantify relationships within and among scales and identify those having the greatest influence on fishes. Quantitative approaches are generally superior to qualitative approaches because they can estimate the magnitude of differences and strengths of relationships among scales (see Kwak and Peterson 2007).

Many of the quantitative approaches to dealing with scale are based on the idea that places (e.g., lakes or study sites) close to one another are more similar than are places farther apart. Similarly in the temporal dimension, two observations (e.g., samples) that are made at

Box 3.3. Continued

Table. Possible relationships between conceptual scales at which natural populations of salmonid fishes are structured (Dunham et al. 2002) and units of conservation as defined in practice (based on the draft bull trout recovery plan, U.S. Fish and Wildlife Service 2002; table modified from Fausch et al. 2006).

Conceptual scale	Unit of conservation	Description	Measurable characteristics
Patch	Local population	A discrete unit of suitable habitat, which may or may not be occupied; occupied patches approximate local populations; local populations are characterized by frequent (daily to seasonal) interactions among individuals within them	Patch occupancy, local population size, habitat size (watershed area or stream network length), quality (e.g., habitat conditions within a patch, presence of nonnative species, or barriers), and connectivity as related to fish movement or transport of materials and energy (e.g., water, sediment, or nutrients)
Patch network or metapopulation	Core area	Local aggregation of patches or local populations characterized by less frequent (annual to decadal) interactions	Total number or collective size of patches, rates of occupancy, numbers of individuals summed across patches, overall patterns of connectivity, habitat quality, and variability in the distribution of conditions among patches or local populations
Subbasin	Recovery unit	Naturally discrete aggregations of patch networks or core areas within larger drainage basins that interact potentially over long time frames (hundreds to thousands of years)	Distribution of characteristics among patch networks, network connectivity, and overall habitat conditions (e.g., climate, landform, and geology)
Region	Distinct population segment	Major biogeographic units that characterize distinct evolutionary lineages	Contemporary and historical location and geographic extent of species distributions, suitable habitat conditions, connectivity, and disposal

Box 3.4. Patterns of Rarity among Inland Fishes

The importance of the pattern of rarity for inland fishes was recognized by Minckley and Deacon (1968) for the case of desert fishes in the southwestern USA. Minckley and Deacon (1968) classified these fishes into four categories: (1) species that are widely distributed and positively influenced by human alteration of aquatic systems; (2) species that have not been influenced by human activities and remain widespread; (3) species that require large, special habitats; and (4) species that occupy small and unique habitats or occur as relicts or isolated endemics. Clearly fishes in these different categories have distinctive geographic and biological characteristics and present different management issues. Rabinowitz (1981) expanded these concepts into the "seven forms of rarity" (Rabinowitz et al. 1986) that are possible by considering patterns in the geographic distribution, habitat specificity, and abundance. Rey Benayas et al. (1999) expanded this framework to include habitat occupancy as an additional criterion to yield 10 different potential forms of rarity, and one of "commonness," as follows in the table below.

The implications of these concepts for inland fishes are multifold. First, as indicated earlier (e.g., Box 3.1), patterns of occupancy, and therefore rarity, are strongly scale dependent, and determination of occupancy should be approached with due caution. Second, if there is confidence in the assessments of the criteria recognized by Rabinowitz (1981) or Rey Benayas et al. (1999), it is clear that spatial scaling is critical in terms of both the grain (habitat occupancy) and extent (geographic range) of a species distribution and the inferred pattern of rarity. Finally, whereas the fundamental ideas about scale and pattern of rarity have been known for inland fishes for more than 40 years (Minckley and Deacon 1968), they have rarely been applied (Gaston and Lawton 1990; Fagan and Stephens 2006).

(Box continues)

a single location closer together in time are generally more similar than those made at longer time intervals. These similarities can be due to several factors, such as shared history, climate, and geologic features, intra- and interspecific interactions, and movements of fish. For example, fish assemblages inhabiting two proximate streams often have similar geomorphologic features; hence, there are similar habitats and the fish experience the same weather events, such as floods and droughts. Given that these factors often influence stream fish assemblage structure (Larimore et al. 1959; Matthews 1986; Bayley and Osborne 1993), fish assemblages in these two streams are likely to be similar compared with assemblages in more distant streams. This similarity or dependence among observations located closely in space or time has been defined by statisticians as spatial or temporal autocorrelation, respectively (Sokal and Rohlf 1995). Many statistical techniques have been developed to examine and describe the degree of spatial or temporal autocorrelation and patterns of dependence that may be used to identify characteristic scales of relevance to fish populations (Fortin and Dale 2005; Wagner and Fortin 2005). Of these, hierarchical models are discussed because they are related to linear regression and analysis of variance (ANOVA), two statistical techniques commonly used by fisheries biologists.

Box 3.4. Continued

Table. Framework for patterns of rarity based on Rey Benayas et al. (1999).

Criterion	State							
Geographic range	Wide				Narrow			
Habitat specificity	Broad		Restricted		Broad		Restricted	
Abundance	Large	Small	Large	Small	Large	Small	Large	Small
Habitat occupancy high	Common	Widespread	Specialist[a]		Locally common	Nonexistent	Endemic specialist[a]	
Habitat occupancy low	Highly dispersed	Sparse	Locally endangered		Potentially endangered		Endangered	

[a] Rey Benayas et al. (1999) used the term "indicator" (retained here for accuracy), but the term "specialist" is used here to avoid potentially misleading implications or interpretations of what an "indicator" means (Carignan and Villard 2002).

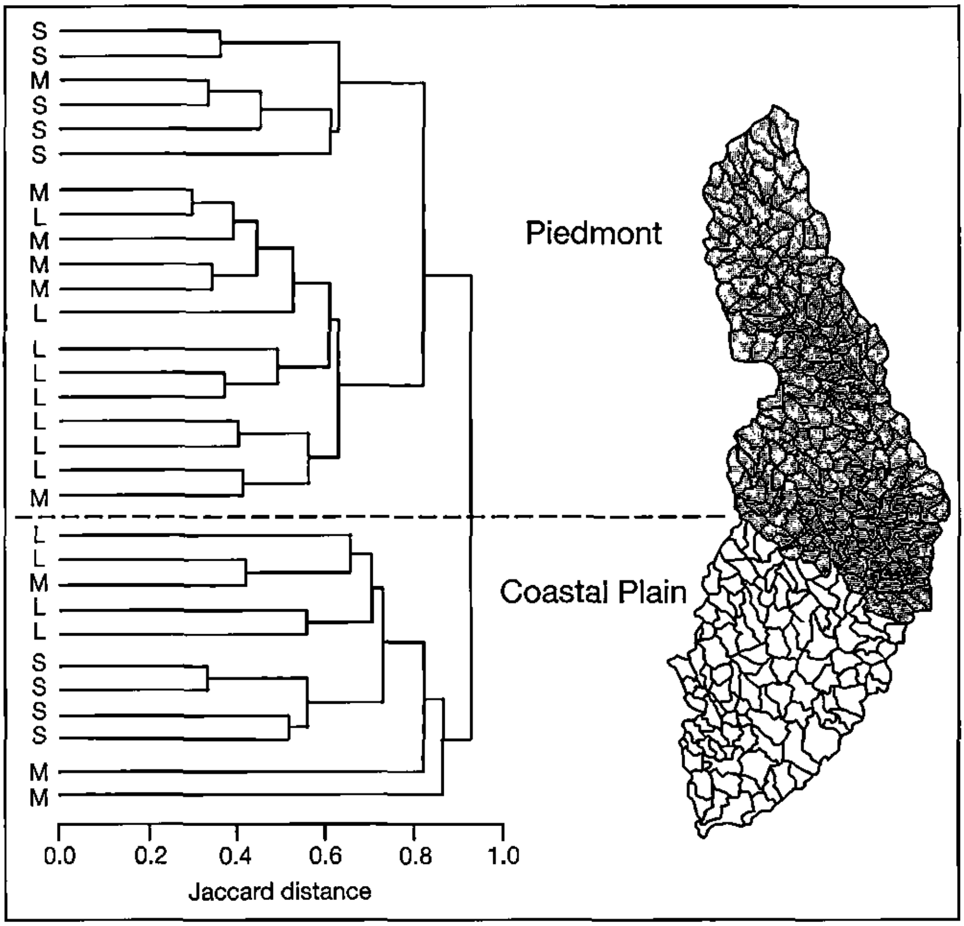


Figure 3.5. A hierarchical cluster analysis of fish assemblages in small (S), medium (M), and large (L) streams in the Flint River basin, Georgia. The cluster analysis shows that assemblages initially cluster most strongly based on physiographic province, with the streams located in the Piedmont and Coastal Plain clustered above and below the broken line, and secondarily by stream size. This suggests that factors at the physiographic province scale have the greatest influence on stream fish assemblage structure, and stream size influences assemblage structure within physiographic province. Jaccard's distance measures the dissimilarity between assemblages.

Hierarchical models are techniques that have been developed to analyze hierarchically-structured data. They may encompass any number of nested levels (i.e., given sufficient data), with each level corresponding to a spatial or temporal scale. In hierarchical model terminology, lower-level units are nested within upper-level units (e.g., streams nested within watersheds) and lower levels correspond to smaller scales and upper levels to larger scales. Hierarchical models include both linear and nonlinear forms, such as logistic and Poisson regression. Here, the description is restricted to a linear form that provides an example of a simple two-level model. Readers interested in additional details on hierarchical models should consult Snijders and Bosker (1999), Bryk and Raudenbush (2002), or Royle and Dorazio (2008).

To describe the hierarchical linear model, we begin with an ordinary linear regression model with one predictor (independent) variable:

$$Y_i = \beta_0 + \beta_1 X_{1i} + r_i, \tag{3.1}$$

where Y_i is the response (e.g., fish density), and X_{1i} is the predictor variable (e.g., stream width or elevation) for observation i, β_0 is the intercept, β_1 is the regression coefficient (i.e., slope), and r is the residual. Collectively, the residuals are assumed to be normally distributed with a mean of 0 and variance (Bryk and Raudenbush 2002). This model is appropriate for examining the relationship between the response and predictor variable when all observations (i) are independent. However, when observations are collected from within different groups (e.g., fish collected from multiple streams in different watersheds), the observations from a group may be more similar to one another simply due to their close proximity (in time or space) or due to similar environments within each group. As discussed above, this is known as dependence or autocorrelation of observations. Hierarchical models can represent this dependence by modeling the variability in the response within and among groups. To illustrate, suppose that J groups (e.g., watersheds) were randomly selected, and sample units within each group (e.g., streams within watersheds) were randomly selected and sampled. A separate regression model can be fit for each of the groups. Mathematically, this can be represented in a single equation with subscript j as

$$Y_{ij} = \beta_{0j} + \beta_{1j} X_{1ij} + r_{ij}, \tag{3.2}$$

where the variables are defined above. In hierarchical modeling, this is a level-1 model where observations (i) and groups (j) are defined as level-1 and level-2 units, respectively. The model coefficients can be treated as fixed, that is, their value is assumed equal across level-2 units (e.g., $\beta_{01} = \beta_{02} = \beta_{03}$), or, alternatively, they can be treated as randomly varying, that is, their values differ among level-2 units (e.g., $\beta_{01} \neq \beta_{02} \neq \beta_{03}$). Thus, models with randomly varying coefficients (i.e., intercepts and slopes) differ from single-level models (equation 3.1) in that each level-2 unit (group) can have unique coefficients.

Simpler and more familiar forms of hierarchical models can be obtained when selected terms in equation (3.2) are replaced by 0s. For example, when there is 0 variability among coefficients, equation (3.2) is equivalent to ordinary linear regression (equation 3.1). One of the hierarchical model forms that is widely used by fisheries biologists is a random effects ANOVA, which is a hierarchical model without predictors (i.e., slopes, or β_1, β_2, and so on):

$$Y_{ij} = \gamma_{00} + u_{0j} + r_{ij}, \tag{3.3}$$

where γ_{00} is the grand mean across groups and u_{0j} is an estimate of how much the response of the jth group differs from the grand mean. Collectively, the values of u_{0j} have a mean of 0 and variance τ_{00}, which is an estimate of variability among groups (i.e., the level-2 variance), whereas the residual variance, σ^2, is an estimate of the variability within groups (i.e., the level-1 variance). The total variance of Y_{ij} is the sum of the estimated variance at levels 1 and 2 ($\hat{\tau}_{00} + \hat{\sigma}^2$) and is used to estimate the intraclass correlation coefficient as

$$\rho = \frac{\hat{\tau}_{00}}{\hat{\tau}_{00} + \hat{\sigma}^2} \tag{3.4}$$

The intraclass correlation coefficient is a measure of the proportion of variance that is accounted for by the group level (Bryk and Raudenbush 2002). In the context of hierarchical multiscale models, the intraclass correlation coefficient is used to estimate the amount of variance in the response variable that is due to (unknown) factors at the level-2 spatial scale. An example of fitting and interpreting hierarchical models can be found in Box 3.5.

3.5 INCORPORATING SCALES INTO MANAGEMENT

In this section, two approaches that fisheries managers have taken to incorporate scaling considerations into fisheries management are described—expert judgment and process modeling. As discussed above, delineation of spatial or temporal dimensions of a management problem is possible via a variety of means, but these scales will often lack sufficient details about processes that are ultimately of concern in fisheries management. Lacking these process details, it may not be clear why certain outcomes occur after a management action is implemented. Whenever possible, therefore, managers should formulate competing hypotheses about how management may influence processes at different scales and measure management

Box 3.5. Hierarchical Modeling of Stream Fish Density

The use of hierarchical models is illustrated by identifying and quantifying scales of influence with empirical fish abundance and habitat data collected from 236 streams in 23 watersheds (6–16 streams per watershed) in central Idaho (Rieman et al. 2006). Here the level-1 units are streams nested within level-2 units, watersheds, and the response of interest is the density (number/100 m) of Westslope cutthroat trout. The analysis was begun by partitioning the variance in trout density within and among watersheds by means of a random effects ANOVA. The variance among watersheds, $\hat{\tau}_{00}$, was 2,972.5 and within watersheds, σ^2, was 1,706.2, which means that $\frac{2972.5}{2972.5+1706.2} = 0.635$ or 63.5% of the variation in Westslope cutthroat trout density was due to factors at the watershed scale. Previous studies reported that salmonid density is related to the geology of the watershed, particularly the amounts of productive lithology (Thompson and Lee 2000). To quantify the influence of a large-scale factor, watershed geology, a level-2 model was fit with a single predictor, percent mafic (productive) lithology. After fitting the model, the level-2 variance, $\hat{\tau}_{00}$, was 1,227.9, which means that $\frac{2972.5-1227.9}{2972.5} = 0.587$, or 58.7% of the variability in Westslope cutthroat trout density among watersheds, and $\frac{2972.5-1227.9}{2972.5+1706.2} = 0.373$, or 37.3% of the total variability, was accounted for by differences in lithology. Previous studies also have suggested that the density of stream-dwelling salmonids is influenced by the characteristics of stream sample reaches. Thus, a complete two-level hierarchical model was fitted by including stream gradient in the mafic lithology model, a (smaller-scale) level-1 predictor. After fitting the model the level-1 variance, σ^2, was 1,305.3, indicating that gradient accounted for $\frac{1706.2-1305.3}{1706.2} = 0.235$, or 23.5% of the variation among streams within a watershed, and $\frac{1706.2-1305.3}{2972.5+1706.2} = 0.086$, or 8.6% of the total variability in Westslope cutthroat trout density. The fact that most variability in density was related to large-scale factors was fairly strong evidence that the greatest influences in Westslope cutthroat populations are large-scale, watershed-level factors.

outcomes against predictions from these hypotheses. It is recognized that not every management action can be elevated to the level of a research project, but it can be stressed that a clear articulation of processes and testable hypotheses (e.g., Box 3.2) is essential for accurate identification, refinement, and functional understanding of management scales. In that spirit, some practical advice and methods for incorporating scale into inland fisheries management are offered.

3.5.1 Expert Judgment Approaches

Fisheries managers are sometimes reluctant to use models because they (1) distrust models and only believe "data" or (2) believe that creating explicit models is too difficult when existing data and knowledge of system dynamics are incomplete. In response to the first concern, it can be argued that data are only numbers until a human brain (using a model) interprets them. Thus, data and model are in essence equivalent if data are to have meaning. The second concern is more challenging to address. One means of coping with the chronic lack of information and uncertainty that characterizes fisheries management is through the use of modeling approaches based on expert judgment, which have a long history in economic applications (Clemen 1996), but are only recently beginning to be used in inland fisheries management. Expert models are based on how people think ecological systems work and require an explicit definition of relationships or key processes and uncertainties. Usually, these models are represented graphically as influence diagrams (Figure 3.3). The models need not be excessively large and should represent only those key processes believed to influence the fishery of interest. The most common expert models take the form of probabilistic networks (Haas 1991). Probabilistic networks, also known as Bayesian belief networks (BBNs), consist of model components defined as nodes and causal links between components represented by directional arcs. Each node consists of a set of mutually-exclusive states, and the relationships between components (nodes) are modeled using probabilistic (conditional) dependencies. To illustrate, consider a simple three-node model for which pool habitat availability in a stream is modeled as a function of stream channel morphology and streamflow (Figure 3.6). Here habitat availability is represented by three states: low, moderate, and high; channel morphology by two states: unconfined and confined channel; and streamflow by three states: low, normal, and high. In practice, each node state would be delineated by a value or range of values that are mutually exclusive, such as less than 4.9 pools/km (low pool habitat availability), 5.0–14.9 pools/km (moderate pool availability), and greater than 15 pools/km (high pool availability). In the pool habitat BBN, the probability that pool habitat availability is low, moderate, or high is conditional (dependent) on the stream channel morphology and streamflow (Figure 3.6). When the channel morphology is unconfined and streamflow is low, the BBN estimates that the probabilities of low, moderate, or high pool habitat availability are 80, 15, and 5%, respectively (Figure 3.6a). In contrast, when the stream channel is confined the probability that pool habitat availability is low, moderate, or high is 50, 40, and 10%, respectively (Figure 3.6b).

Although the conditional probabilities that produced these estimates are hypothetical, in real-world applications conditional probabilities are based on judgments of one or more experts in the field (Clemen 1996; Marcot et al. 2001). The drawbacks of using expert judgment approaches are that a substantial burden of proof is placed on the decision maker (Morgan and Henrion 1990) and model development can be a time consuming process where modifications are made as assumptions are evaluated and changed in an iterative process (Clemen 1996).

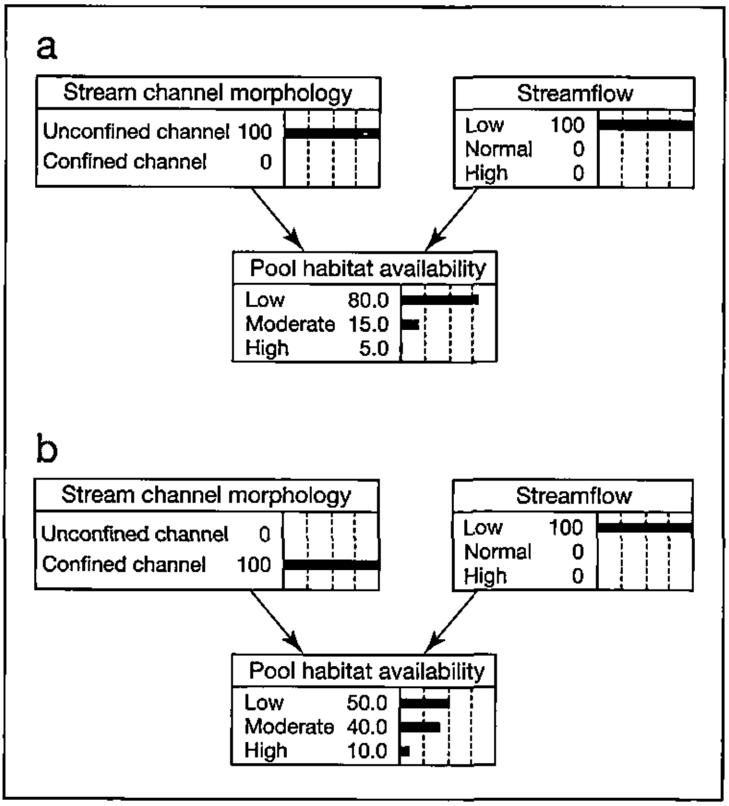


Figure 3.6. Bayesian belief network for pool habitat availability in stream reach as a function channel morphology and streamflow for two combinations of probabilities: (a) unconfined stream channel 100% and low streamflow 100%, and (b) confined stream channel 100% and low streamflow 100%. Numbers in the boxes are probabilities of a particular state expressed as a percentage.

The benefits of expert models are that they convey how managers believe a system functions, how key assumptions may be tested, and where uncertainties are greatest. In practice, uncertainties about a system may play a greater role in decision making. Thus, identifying key areas of uncertainty can be critical. Greater detail about BBNs and expert models can be found in Clemen (1996), Marcot et al. (2001), and Martin et al. (2005).

A recent example of an expert judgment approach was an assessment of alternative conservation strategies for salmonids in the inland northwestern USA (Rieman et al. 2001). This study evaluated the effects of conservation strategies and management actions at multiple scales ranging from stream reach to watershed to large river basins. The study faced difficulties regarding a lack of data on and knowledge of the effects of multiple physical, biological, and anthropogenic factors operating over multiple spatial and temporal scales. Interdisciplinary teams developed and modified conceptual models of the study system (Box 3.2). These models were modified and refined by external reviewers and parameterized by groups of area-specific experts. For example, conditional dependencies for hydrologic and geomorphic nodes were parameterized by hydrologists and geomorphologists familiar with the respective management areas. Following parameterization, a sensitivity analysis was performed on the models to identify key components (i.e., those with the greatest influence on the estimated change in fish populations) and model assumptions were tested. Investigators then evaluated whether the best management strategy for recovering migratory Pacific salmon populations could be influenced by the removal of large hydroelectric dams on the Snake River in Idaho. The effects of management actions with and without dams were assessed, and the expert model suggested the influence of the dams did not change the relative benefits of conservation actions. Through the use of BBNs, this study communicated how the scientists believed the ecological system functioned, quantified the relative value of conservation actions, predicted the outcome of alternative conservation scenarios, evaluated the sensitivity of their predictions to assumptions, and identified key uncertainties. Identifying these uncertainties is important for prioritizing future monitoring and research efforts aimed at increasing the understanding of processes operating at multiple scales and thereby improving future management.

3.5.2 Process-Based Simulations

A less common approach to incorporating scale into fisheries management uses process-based simulations. These models often relate rates of change in both physical and biological components of aquatic systems to factors such as management actions, land use, and climate change. The relative scarcity of empirical simulation modeling approaches is presumably due to a lack of knowledge of and data on the combined effects of large- and small-scale ecological processes. The most common use of process models is as a guide during development of management strategies (Box 3.3). Direct estimation of fish population (e.g., presence and abundance) and assemblage (e.g., species richness) responses to multiscale processes is relatively uncommon. This is because accurate predictions about complex nonlinear responses across multiple spatial and temporal scales often require process-based models. Given the complexity of aquatic systems, development of multiscale process-based models requires interdisciplinary collaboration and matching of spatial and temporal scales from outputs of physical and ecological models.

An example of a process-based simulation is described by Peterson and Kwak (1999). They simulated the effects of large-scale land use and climate change on riverine smallmouth bass populations based on empirical precipitation runoff models, climate projection models, and an age-structured smallmouth bass population dynamics model parameterized by means of a 13-year data set. Another example is the across trophic level system simulation (ATLSS) project in the Florida Everglades. The ATLSS project is a multidisciplinary effort that includes scientists from a variety of fields, including hydrologists, landscape ecologists, and fisheries managers. One objective is to develop multiscale simulation models for predicting the abundance of fishes in response to restoration activities in the Everglades (Gaff et al. 2004). Simulation models were based, in part, on empirical field observations and laboratory studies combined with expert opinion as to how demographic processes scale up to the entire Everglades. These and other studies highlight the need for greater interdisciplinary collaboration (Vaughan et al. 2007).

3.5.3 Adaptive Approaches to Management

An important theme of this chapter is the influence of scale on how fisheries managers perceive fish populations and communities. Significant uncertainties are associated with even the simplest management decision and managers can never be 100% confident of achieving desired outcomes. This uncertainty stems from three basic sources (following Williams et al. 2002): (1) environmental uncertainty, which is composed of environmental and demographic variation and has both spatial and temporal components; (2) statistical uncertainty, due to the use of sample data to estimate model parameters; and (3) structural (or ecological) uncertainty, due to an inability to determine accurately the processes or models that best represent system dynamics (e.g., the relationship between geomorphology, streamflow, habitat availability, and fish population demographics). Consequently, special attention is devoted to structural uncertainty because it represents the main source of uncertainty associated with managing across multiple spatial and temporal scales. Overviews of several approaches for describing and estimating multiscalar systems have been given, but because structure and function of aquatic systems are so complex, there are often several plausible hypotheses to explain observed ecological patterns and processes. Sorting through these hypotheses to determine those that are most accurate can reduce structural uncertainty.

Several methods are available for reducing structural uncertainty. The gold standard is experimentation, which involves replication, randomization, and treatments. Conducting experiments, however, is labor intensive, which precludes application at large spatial scales and long time frames that are often necessary in fisheries management. In contrast to experiments, observational studies use statistical control to describe patterns in data that may be collected across broad spatial or temporal extents. These types of studies often provide the basis for constructing the empirical, theoretical, or simulation models discussed above. Relationships derived from observed data, however, are often confounded with other factors. Thus, a third, complementary approach is advocated, adaptive resource management (ARM; Walters 1986), which is a technique well-suited to reducing structural uncertainty and improving decision making in management.

In ARM, structural uncertainty is explicitly considered by postulating feasible alternative models, with each model representing a hypothesized relationship among multiscale inputs, system dynamics, and objectives (Williams et al. 2002). Each model is assigned a plausibility or probability of being "true." The best management decision then is selected based on the current-system state (e.g., population size) and a prediction of the expected future state taking into account environmental, structural, statistical, and other sources of uncertainty. Model probabilities are updated through time by comparing each of the model-specific predictions to conditions as they are realized. The updated model probabilities are again used to predict future conditions and the "best" management decision made for the following time step. This feedback facilitates adaptive learning and the resolution of competing hypotheses over time. Thus, ARM allows managers to make decisions and enables them to learn about the nature of scale.

3.6 CONCLUSIONS

It should be clear by now that scale is an essential consideration for effective fisheries management. Scale is not just an "academic" issue but one that profoundly influences all stages of management, from the interpretation of patterns in research or monitoring data to the creation and implementation of management strategies. Because the scales at which fisheries managers observe ecological systems directly influence the scales that are perceived to be important, it is sometimes difficult to know whether the proper scales for management have been identified. Lacking this knowledge, managers may incorrectly identify and diagnose the source of problems with a fishery and potentially waste resources and management efforts implementing ineffectual or harmful actions. Potential problems can be avoided if careful thought is given to processes and scales influencing the problem of interest. Uncertainties regarding how physical and ecological processes operate over multiple scales can be specified and incorporated into the process. Experience has proven this is much easier said than done (e.g., Walters 1997), but examples here show that scaling in practice is possible and most definitely desirable in fisheries management. Many of the chapters in this book provide essential background and information on the key scales and processes influencing inland fisheries and can provide guidance regarding multiscale approaches. Finally, fisheries managers are encouraged to consider the importance of scale and incorporate an adaptive approach to management as a means to improve ecological knowledge and future management.

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