

Assessing the Habitat Requirements of Stream Fishes: An Overview and Evaluation of Different Approaches

JORDAN ROSENFELD*

*Fisheries Research, Province of British Columbia,
2204 Main Mall, Vancouver, British Columbia V6K 2M9, Canada*

Abstract.—With the widespread decline and endangerment of freshwater fishes, there is a need to clearly define habitat requirements for effective species management and habitat restoration. Fish biologists often infer habitat requirements on the basis of correlative habitat associations in the wild. This generates descriptive models that predict species presence or abundance at a hierarchy of scales: distributional (macrohabitat) models predict the presence/absence of species at large scales, capacity models predict the abundance at the reach or channel unit scale when a species is present, and microhabitat models predict the distribution of individual fish at smaller spatial scales (e.g., instream habitat suitability curves for velocity, depth, and substrate). However, relationships based on habitat associations in the wild rarely give definitive insight into the absolute requirement for a particular habitat (i.e., necessity of a habitat for the persistence of individuals and populations). The assumption that habitat selection accurately reflects the fitness consequences of habitat use is rarely validated; more rigorous assessment of habitat requirement usually involves manipulative experiments or measurements of fitness (individual growth, survival, or reproductive success) in different habitat types. Bioenergetic habitat models offer a promising mechanistic alternative to correlative habitat suitability models for drift-feeding fish and have the potential to predict habitat-specific growth rates on the basis of swimming costs and energy intake. Once smaller-scale habitat requirements of individuals are well defined, the final step is to determine when and how the requirements of individuals limit populations. Extrapolating smaller-scale habitat requirements to the population level requires either large-scale (ecosystem) manipulations of habitat, adaptive management, or habitat-explicit population models. For species with distinct ontogenic shifts in habitat requirements, the concept of optimal habitat ratios may be useful for identifying limiting habitat factors and defining baselines for habitat restoration. Defining optimal habitat configurations for different species may also provide a basis for predicting how habitat change differentially affects species with contrasting habitat needs.

Many species of fish are endangered because of habitat change caused by human development, and many more will be affected as alteration of habitat and human appropriation of freshwater resources continue (Postel et al. 1996; Sala et al. 2000; Tilman et al. 2001). Understanding and managing human impacts on fish require a clear understanding of the relationship between a species and its environment. Identifying the suite of conditions that defines the habitat requirements of a species is therefore a primary goal of aquatic research. The concept of habitat requirement, however, is poorly defined. Broadly speaking, requirements can be defined as features of the environment that are necessary for the persistence of individuals or populations (e.g., Bjornn and Reiser 1991). When faced with conflicting land uses in a drainage, it is essential to accurately identify the subset of critical habitats on which the persistence of a species

or population depends. Without this knowledge, managing habitat either defaults to educated guesswork, which often fails, or a conservative strategy of protecting everything, which often has economic and social consequences that are difficult to justify.

Although the importance of defining habitat relationships of endangered or managed species is widely recognized, information on habitat use is often collected in a haphazard way, correlative habitat associations are often confused with habitat requirement, and the significance of habitat relationships from field studies is often unclear or misinterpreted (Van Horne 1983; Hobbs and Hanley 1990). In particular, there is ambiguity surrounding the meaning and use of habitat selection, habitat preference, and habitat requirement.

Even when the habitat requirements of individual life stages are well defined, there is often uncertainty surrounding the population-level consequences of habitat change because only a subset of habitats will typically limit a population at any given time. Translating the habitat requirements of

* Corresponding author: jordan.rosenfeld@gems4.gov.bc.ca

Received October 5, 2001; accepted March 3, 2003

individuals to population-level effects then becomes the necessary challenge for fisheries scientists and managers. Solutions are usually limited to whole-scale ecosystem manipulations (e.g., Hartman and Scrivener 1990; Carpenter et al. 1995; Carpenter 1996) or to population models that link the dynamics and habitat requirements of individual life stages (e.g., Minns et al. 1996; Nickleson and Lawson 1998).

In this article I review the various approaches that have been used to describe the habitat requirements of stream fishes as well as their management implications. My objectives are to clarify the significance of different types of habitat information routinely collected by fish biologists but sometimes confused in the literature (i.e., habitat selection versus habitat requirement), to summarize different methodologies for quantifying the habitat requirements of fish, and to provide a clearer conceptual framework for interpreting the significance of habitat information from field studies.

Definition of Habitat Requirements

Habitat requirements are abiotic features of the environment that are necessary for the persistence of individuals or populations. This definition is intended to distinguish between requirements and other features of the environment that are less critical, insofar as their loss or alteration will have minimal effect on organism abundance or population persistence. This simplistic definition of requirement is more or less equivalent to the familiar Hutchinsonian niche, the n -dimensional hypervolume occupied by a species in "habitat-space," where habitat axes are environmental factors ranging from temperature to system productivity (Hutchinson 1957). This hypervolume of environmental factors needed for species persistence will include the range of environmental factors where individuals experience positive growth and reproduction at low densities. If the species of interest has a complex life history—for instance, larvae, juveniles, and adults that occupy different habitats—then different life history stages can be defined by different habitat requirements and corresponding niches (e.g., Minns et al. 1996; Bardonnet and Baglinière 2000).

It is useful to apply the concept of habitat requirements at both the individual and population levels. At the population level, the niche for a species will be the hypervolume in environmental space where populations can achieve a positive intrinsic rate of increase at low densities. In practical terms, habitat requirements for a population

(the fundamental niche) will include the niche occupied by individuals (e.g., habitats must be present where individuals will achieve positive growth and reproduction) but will additionally include metapopulation requirements. The presence of appropriate habitats for individuals does not ensure the persistence of a population, which also depends on landscape-scale features related to immigration and emigration rates between populations and the minimum viable population size (Pulliam 1988; Dunning et al. 1992), as well as broader regional abiotic constraints acting as conditional filters on species presence (Poff 1997). In this review I consider the relationship between habitat requirements of individuals and population persistence, but I do not review metapopulation dynamics. This focus reflects both a need to limit the scope of the review for practical reasons and the presence of recent reviews on the latter subject (Rieman and Dunham 2000).

Similarly, I focus on a narrow definition of habitat requirements based on the physical habitat (the "habitat templet" of Southwood [1977]). Physical habitat requirements may be strongly modified by biotic factors—for instance, system productivity, the requirement for refuges in the presence of predators (Chapman et al. 1996), or narrower thermal tolerances in the presence of competitors (Taniguchi and Nakano 2000). I do not explicitly consider the influence of biotic factors on habitat requirements, but the approaches outlined for assessing physical habitat requirements should apply equally well to assessing biotic influences on habitat needs.

Habitat Selection (or Use) versus Preference versus Requirement

The concepts of habitat selection, preference, and requirement are sometimes confused in habitat studies, and information on habitat selection is frequently used to infer habitat requirement. Habitat selection (i.e., differential occupancy) occurs when an organism avoids a particular habitat (negative selection) or uses a habitat in greater proportion than its availability in the environment (positive selection). Habitat selection can be demonstrated if fish occur at higher densities in particular habitats (e.g., Figure 1), or if fish occur at higher frequencies in particular microhabitats to relative frequency of that microhabitat in the environment; for instance, selection occurs when the frequency distribution of depths at which fish are observed differs from the distribution of depths available (Figure 2). Selective use of different hab-

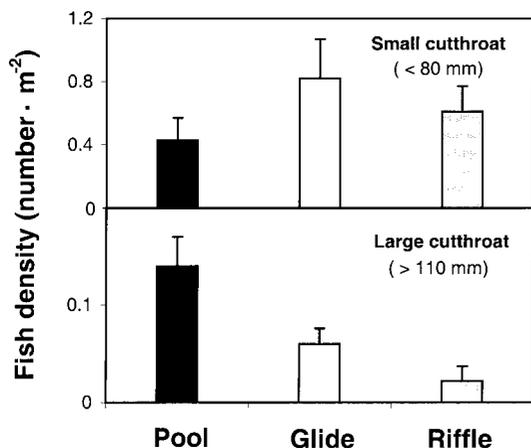


FIGURE 1.—Density (mean + SD) of small and large juvenile cutthroat trout in pool, glide, and riffle channel unit types (modified from Rosenfeld et al. 2000).

itats is often used to infer habitat preference, but true preference is best determined in habitat choice experiments in which extraneous factors (e.g., predation risk, competition, availability of different habitats) are controlled; differential use of habitats in the wild is therefore usually referred to as habitat selection rather than preference. Habitat selection in the wild represents habitat preference under the prevailing biotic and abiotic conditions in any particular stream (the realized niche) and may differ greatly among streams, but true habitat preference in the absence of predation and competition (the fundamental niche; Hutchinson 1957) should be relatively invariant for fixed conditions and will be a function of a species ecology, physiology, and behavior.

It is often assumed that habitat selection indicates a requirement for a particular habitat, but this assumption is rarely validated. Even if fish select one habitat over another, the consequences of losing a strongly selected habitat and occupying a less selected one are usually unclear. Will individual growth rate decrease but remain positive in the less selected habitat, or is the less selected habitat a metabolic sink where a fish will actually lose weight and die (Sogard 1994)? Habitat selection based on differences in density or frequency of use (e.g., Figures 1 and 2) give little quantitative information as to the requirement (in terms of growth and survival) for different habitats. Problems associated with using density as an index of habitat quality are well documented (Van Horne 1983; Hobbs and Hanley 1990; Winker et al. 1995). At very low densities, many suitable hab-

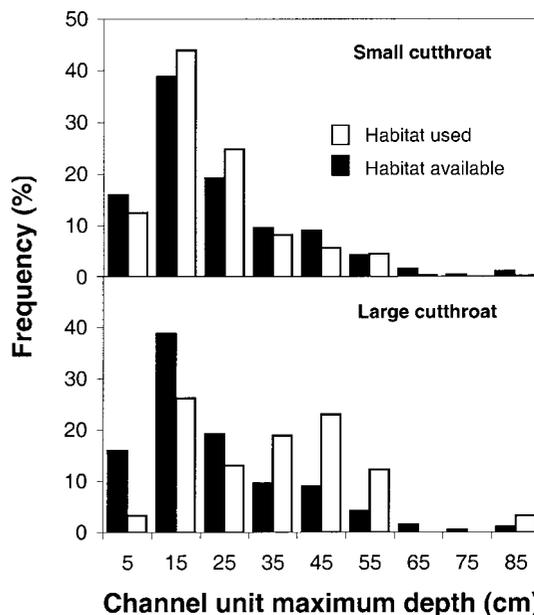


FIGURE 2.—Frequency of occurrence of small (<80-mm) and large (>110-mm) juvenile cutthroat trout in channel units of different maximum depths relative to the distribution of maximum channel unit depths available in the environment.

itats may be unoccupied, resulting in the erroneous conclusion that they are undesirable and seriously altering conclusions based on ratios of abundance between habitats. At the other extreme of very high densities (as with young-of-year fish in high recruitment years), fish may be observed in habitats that are potentially metabolic sinks in which fish will die. This will be especially true if individuals are territorial, and floaters are displaced at high densities into suboptimal habitat (Van Horne 1983). Thus inferring requirement based on habitat selection in the wild may give different results from year to year, depending on overall organism abundance (Hobbs and Hanley 1990).

The true requirement for a preferred habitat depends on the fitness consequences of using that habitat, or equivalently, the fitness consequences if a preferred habitat is lost and a fish is forced to use a less preferred one (e.g., Sogard 1994). For instance, if fish prefer or select pools, then the best measure of their requirement for pools is their ability to survive and grow in other habitats, such as riffles or glides. If individuals of a particular species of fish are incapable of growth and survival in riffles, then pools are required (e.g., pools are necessary for the persistence of individuals and populations).

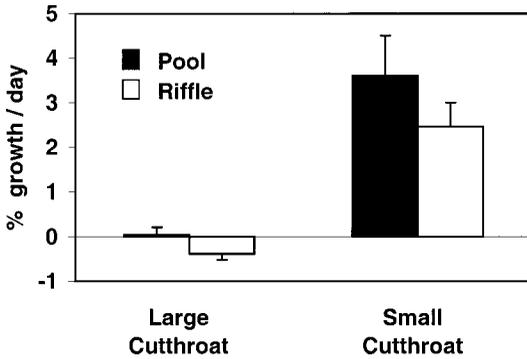


FIGURE 3.—Growth of small (<80-mm) and large (>110-mm) juvenile cutthroat trout confined to pool and riffle habitats in the absence of predators (from Rosenfeld and Boss 2001).

Despite the fact that data on habitat selection in the wild form the basis for most quantitative habitat models, the assumption that habitat selection in the wild accurately reflects requirement (the fitness consequences of habitat use) is rarely validated. Rosenfeld and Boss (2001) examined the relationships between habitat selection in the wild, habitat preference, and habitat requirement in terms of the growth and survival of juvenile cutthroat trout *Oncorhynchus clarki* in different habitats. Based on habitat use information from field surveys, juvenile cutthroat parr longer than 110 mm strongly selected deeper pool habitat, whereas young-of-year fish smaller than 80 mm avoided pools and selected shallower habitats (Figures 1 and 2). To validate whether this pattern of habitat selection accurately reflected preference and requirement for juvenile trout in terms of growth, we performed a series of simple manipulative experiments in a natural stream channel (Rosenfeld and Boss 2001).

Habitat choice experiments demonstrated that young-of-year cutthroat trout strongly preferred pools to riffles in the absence of predators and competitors, despite occurring at their lowest densities in pools in field surveys (Rosenfeld et al. 2000), probably a result of predator avoidance and competition from larger juvenile coho salmon *O. kisutch*. Young-of-year fish grew in both pool and riffle habitats, although growth rates were higher in pools (Figure 3), which was consistent with the results of the young-of-year habitat preference experiment. In contrast, larger juvenile trout lost weight in riffles but grew in pools. This example indicates that pools are a habitat preference for young-of-year cutthroat trout but probably are not a requirement because they are capable of positive

growth in riffles. In contrast, pools are a requirement for larger trout at summer low flow, as fish consistently lost weight in riffle habitat.

The statement that pools are a preference rather than a requirement for young-of-year fish needs to be qualified, given that positive growth in riffles does not necessarily ensure future reproductive success. Young-of-year fish survival is typically a positive function of body size (Quinn and Peterson 1996) with a minimum threshold (e.g., Shuter et al. 1980) that may or may not correspond to the maximum size achieved in riffles. Habitats may often represent a continuum of quality rather than a bimodal distribution of required versus unsuitable habitats. Ideally, the "requirement" for any habitat at a given life stage has to be evaluated within the context of the entire life cycle of the organism to see how it affects future survival and final probability of reproduction.

The experiments with juvenile cutthroat trout described above demonstrate that strong habitat selection (i.e., of pools by larger cutthroat trout) is consistent with the fitness consequences of habitat use. However, it is conceivable that an apparently strong preference may have trivial fitness consequences for individuals, and a shift from preferred habitat may have minimal effects at the population level. Research directed at understanding the potential impacts of sediment inputs on the spawning habitat of lake trout *Salvelinus namaycush* serves as an instructive example (Gunn and Sein 2000). Lake trout spawn with high fidelity at specific sites year after year, over cumulative areas as small as 40 m² in a single lake. To evaluate the requirement of trout for these highly selected spawning habitats, Gunn and Sein (2000) covered the strongly selected spawning sites with plastic tarpaulins and monitored subsequent egg hatching success and population trends.

Although lake trout showed strong fidelity to traditional spawning locations before they were covered, they successfully spawned throughout much of the nearshore area of the experimental lake. Many of the alternative spawning sites (~50%) successfully produced alevins, and there was no measurable population level effect of removing access to the original spawning habitat over the 8-year course of the experiment (Gunn and Sein 2000). This indicates that the strongly selected traditional spawning sites were not required habitat over the duration of the experiment, because successful spawning was possible in alternative locations where sufficient juveniles could be recruited to maintain the adult population. Gunn

and Sein (2000) concluded that negative impacts from angling were far more serious than potential loss of spawning habitat for lake trout, given that angling mortality produced a 70% decline in adult abundance within a year in a nearby lake trout population experiencing no reduction in spawning habitat. In this case, loss of a strongly selected habitat did not have population-level consequences, an outcome that would have been impossible to predict without experimental manipulation. However, it remains conceivable that potentially higher egg survival at traditional sites may contribute to a faster population recovery following episodes of high adult mortality and that the adaptive significance of a habitat preference is manifest only during episodic population “crunches”; when this is true, even longer-term studies or experiments are required to detect the adaptive significance of habitat preference. This lake trout experiment does not necessarily argue against protecting spawning habitat; rather, it demonstrates that angler mortality is a far greater conservation concern for lake trout and that an apparently strong selection for a habitat may give a misleading indication of its significance at either the individual or population level.

Juvenile cutthroat trout represent a case where habitat use and selection in the wild are congruent with the fitness consequences of habitat use. To some extent this validates the use of habitat associations observed in the wild to infer habitat requirements; the lake trout example, however, should serve as a cautionary note that strong habitat associations in the wild do not always imply strong population-level effects of habitat change. Below I review the different types of habitat information and models that fish biologists typically use to describe the distribution and abundance of stream fishes, and by implication their habitat requirements, based on habitat associations in the wild.

Habitat Models

Most habitat models are descriptive as opposed to mechanistic and are based on covariation between environmental variables and habitat use in the wild. Stream habitats are strongly hierarchical (Frissel et al. 1986; Hawkins et al. 1993), and habitat associations can be modeled at a variety of spatial scales. At least three fundamental types of predictive models can be used to define habitat requirements from correlative data: distributional or macrohabitat models, which predict the presence or absence of species at large spatial scales

(e.g., within different drainage basins); capacity models, which predict density or population size when a taxon is present (usually at the reach or channel unit scale); and microhabitat models, which predict habitat associations at a fine spatial scale (e.g., focal velocities and depths selected by juvenile salmonids). Bioenergetic microhabitat models for stream fishes have recently emerged as an additional class of habitat model (Hughes and Dill 1990; Guensch et al. 2001). These models differ fundamentally from other model types in that they are inherently mechanistic (i.e., their predictions are based on explicit biological mechanisms rather than observational data). These four types of models are considered below.

Presence/Absence Models

Models predicting fish presence use binary (presence/absence) response data, whereas multiple regression (capacity) models are used when continuous data are available (fish biomass or density). Although presence/absence models can be used to predict fish presence at smaller spatial scales (e.g., Guay et al. 2000), they are more often used at a landscape scale for defining fish distribution (i.e., when particular taxa are likely to be present in different drainages or stream reaches). These models can be based on either logistic regression (Watson and Hillman 1997; Porter et al. 2000; Harig and Fausch 2002; Olden et al. 2002) or discriminant function analysis (Bozek and Hubert 1992), both of which predict membership in different classes (i.e., present versus absent) on the basis of a suite of independent predictor variables such as drainage basin area, basin gradient, elevation, or latitude. Logistic regression (Manly et al. 1993; Tabachnik and Fidell 1996; Boyce and McDonald 1999) generates an equation predicting the probability (from 0 to 1) of presence as a function of any suite of environmental variables, which need not be normally distributed (Tabachnik and Fidell 1996). Figure 4 illustrates a logistic regression model predicting the presence of anadromous cutthroat trout as a function of a single variable (stream channel width), where there is a 90% probability of presence in channels less than 7 m wide. Although logistic regression and discriminant function analysis are commonly used for modeling species presence, classification trees and artificial neural networks are alternative nonlinear approaches that may provide more robust models of species distribution (Guisan and Zimmermann 2000; Olden and Jackson 2002).

Presence/absence models quantify a process that

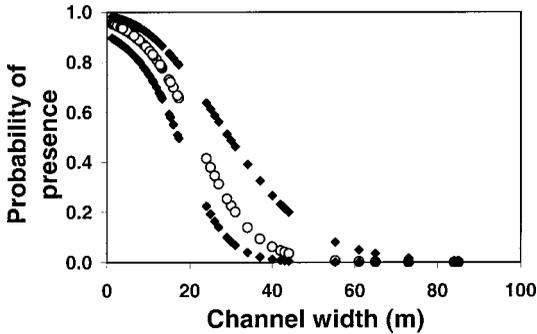


FIGURE 4.—Probability of cutthroat trout presence as a function of stream channel width based on logistic regression ($P = e^{(-0.148 \text{ bfw} + 3.22)} / (1 + e^{(-0.148 \text{ bfw} + 3.22)})$), where bfw is bank-full channel width; see Rosenfeld et al. 2000). Black diamonds represent upper and lower 95% confidence intervals.

occurs in an informal sense whenever a biologist makes a judgment about whether to expect a particular species at a site (i.e., expert opinion). Formal presence/absence models may be redundant for species about which biologists can make accurate personal judgments or when sampling is easy, but represent a more objective approach for defining the probability of occurrence of species about which little is known. Logistic regression models can be linked to geographical information systems (GIS) to predict the distribution of taxa in unsampled locations (Boyce and McDonald 1999; Mladenoff et al. 1995), and can also be used to identify which environmental variables exert the strongest influence on the presence or absence of species (Mladenoff et al. 1995; Watson and Hillman 1997). Harig and Fausch (2002) provide a good example of applying logistic regression to assess the characteristics of streams that are suitable for translocating endangered Rio Grande and greenback cutthroat trout. By comparing the basin scale and instream features of successful and unsuccessful transplant streams, quantitative models were developed for guiding future transplants. However, logistic regression models remain entirely correlative and therefore provide only indirect evidence for causative relationships between habitat variables and fish presence.

Habitat Capacity Models

Capacity (e.g., multiple-regression) models use continuous rather than binary response data to describe the relationship between the abundance of fish and habitat variables such as water temperature, conductivity, channel width, or basin-scale features such as land use or forest cover (e.g., Jow-

ett 1992). Regression models can be applied at any scale but are typically used to model fish abundance at the reach or channel unit scales. Similar to logistic regression, multiple regression models are correlative and therefore tend to be predictive rather than process-oriented, although they can give some insight into factors that influence capacity. For instance, a high correlation between fish abundance and the number of pools in a reach or stream (e.g., Connolly and Hall 1999) provides indirect evidence that pools are an important habitat, but a positive association may also be due to an unmeasured correlate of pools. Manipulative experiments are necessary to establish underlying mechanisms whereby habitat change affects either individuals or populations. Manipulative experiments to understand the significance of pools at the individual scale would measure growth and survival of fish in pools versus other habitats (Lonzarich and Quinn 1995; Rosenfeld and Boss 2001), whereas experiments at the larger population scale would apply treatments to watersheds that would alter pool frequency (e.g., logging; Hartman and Scrivener 1990). Like presence/absence models, capacity models also have the potential to be linked to GIS-based map projections for estimating population abundance in unsampled reaches (Toepfer et al. 2000) or at larger landscape scales (Thompson and Lee 2000).

Although fish abundance is most often modeled as a function of continuous environmental predictor variables (depth, water velocity, channel width, etc.), discrete predictor variables are also useful, particularly at the habitat (channel) unit scale. Channel units represent discrete and regular habitat types (e.g., pools or riffles) formed by natural fluvial processes in streams (Hawkins et al. 1993; Rabeni and Jacobson 1993; Peterson and Rabeni 2001a, 2001b), and many studies have shown that fish have strong associations with discrete habitat types (e.g., Schlosser 1991; Nickleson et al. 1992; Rosenfeld et al. 2000). Predicting fish density by habitat classes (e.g., riffle versus pool habitat units) is often more accurate than predicting density based on continuous variables (e.g., water depth), which suggests that discrete habitat classifications may characterize habitats in a more biologically meaningful way than continuous measurements. Estimated fish abundance in any given stream reach can then be modeled as a simple function of the summed abundance of different habitat types multiplied by habitat-specific densities (Hankin 1984; Hankin and Reeves 1988). This approach has potential as a simplistic but powerful

method to model how changes in habitat (e.g., pool frequency) will affect fish abundance, given that changes in the frequency of channel units is the currency that geomorphologists often use for measuring changes in channel structure (e.g., Grant et al. 1990; Montgomery et al. 1995).

Microhabitat Models

Microhabitat models predict habitat associations at a fine spatial scale within the stream channel. The three variables typically used to characterize microhabitat in streams are current velocity, total depth, and substrate type below the focal point where a fish is observed or collected (Moyle and Baltz 1985; Frissel and Lonzarich 1996). Because microhabitat observations are based on the scale of habitat likely to be used by individuals, as natural history observations they can give insight into how fish exploit different habitats, and how habitat is partitioned among species or age-classes of fish. However, their primary application in stream ecology and fisheries management has been to generate habitat suitability curves (Orth and Maughan 1982) or habitat probability indices (Guay et al. 2000) for different species of fishes. Habitat suitability curves are intended for use with instream flow assessments (e.g., instream flow incremental methodology [IFIM]) which model changes in habitat availability for fish (and by implication, population size) in regulated rivers in relation to various discharges (Bovee 1982). Physical simulations of the availability of different microhabitats at different stream flows are linked to habitat suitability curves for current velocity, substrate, and depth, which are then used to define the extent of suitable habitat under different flow regimes.

The use of habitat suitability curves has been both widely criticized (e.g., Mathur et al. 1985) and defended (e.g., Gore and Nestler 1988) on both technical and theoretical grounds. A review of IFIM is beyond the scope of this paper, and habitat suitability curves are later considered only in the context of the potential biases of different habitat models.

An additional class of microhabitat models predicts the exact distribution of fish at smaller scales within individual channel units or reaches, as opposed to predicting the general characteristics (velocity, depth, and substrate) of a fish's focal location with habitat suitability curves. These microhabitat models are primarily bioenergetic rather than correlative and are discussed below.

Bioenergetic Models

Unlike the preceding models, which are based on habitat associations, bioenergetic models are mechanistic and therefore can contribute to a more definitive understanding of the causations underlying correlates of fish abundance. Bioenergetic models predict individual microhabitat choice based on the energetic costs and benefits of using different habitats (e.g., Fausch 1984; Hughes and Dill 1990; Guensch et al. 2001; Railsback and Harvey 2002) and have been shown to accurately predict microhabitat choice by a variety of drift-feeding fishes, including rosyside dace *Clinostomus funduloides* and rainbow trout *O. mykiss* (Hill and Grossman 1993), brown trout *Salmo trutta* and mountain whitefish *Prosopium williamsoni* (Guensch et al. 2001), Arctic grayling *Thymallus arcticus* (Hughes and Dill 1990), and Atlantic salmon *S. salar* (Nislow et al. 1999, 2000). Although bioenergetic models have been applied to predict habitat choice and growth primarily at microhabitat scales, Hughes (1998) has recently extended a bioenergetic microhabitat model for drift-feeding fish to predict reach and whole-stream size distributions of salmonids, and Hayes et al. (2000) have shown that a bioenergetics model can generate a precise lifetime growth trajectory for brown trout in New Zealand. Bioenergetic models have been successful in part because the biomechanics of drift-foraging are relatively easily modeled, with swimming costs a simple function of velocity at the focal point and energy intake a function of size of the foraging window, reactive distance, and energy concentration of invertebrates in the drift (Hughes and Dill 1990; Hayes et al. 2000; Nislow et al. 2000; Guensch et al. 2001).

Bioenergetic models have the potential to predict not only fish habitat choice but also growth and density. Rosenfeld and Boss (2001) showed that a simple bioenergetic model for drift-feeding cutthroat trout generated average predictions of net energy intake that were consistent with observed patterns of growth in both pool and riffle habitats, and Nislow et al. (2000) demonstrated that bioenergetic modeling provided a reasonable prediction of Atlantic salmon growth rate potential in different habitats. Bioenergetic models have yet to be applied to predict density, which will require linking spatially explicit growth rate potential to salmonid territory-size relationships (e.g., Clark and Rose 1997) to predict density and growth in different habitat types. The main limitations of

present bioenergetic models relate to uncertainty in the efficiency with which fish harvest drifting invertebrates, and how foraging behavior and stream hydraulics influence swimming costs (Boisclair 2001).

Bioenergetic models also have the potential to integrate the effects of both habitat structure (through swimming costs) and system productivity (through invertebrate drift intake). Because habitat suitability models are based solely on physical parameters, they cannot predict how fish growth or abundance will change with increased invertebrate drift (system productivity). In contrast, bioenergetic models of drift-foraging fishes take into account both physical habitat and food abundance and should be able to predict the effects of increased invertebrate drift on individual habitat choice and growth (Nislow et al. 2000), thereby providing a theoretical basis for anticipating the effects of nutrient additions to salmon streams (Hayes et al. 2000). At present, bioenergetic models of stream fishes are restricted to drift-foragers, largely because of the huge pool of detailed information available on the ecology and physiology of stream salmonids; it is unclear whether a similar pool of information exists to adequately parameterize bioenergetic models for benthic fishes.

Disadvantages of bioenergetic models relate to uncertainty concerning the time and effort necessary (in terms of sampling and evaluation of drift samples) to generate reasonable estimates of prey abundance. Any requirement for significant temporal and spatial replication could limit application for general management purposes. Certainly bioenergetic modeling has the potential to provide insight into the mechanisms underlying patterns of habitat use and production by stream fishes, but whether it proves useful for management or remains primarily a research tool remains to be seen.

To date, bioenergetic models of habitat use have seen limited application in stream ecology, and correlative habitat models remain the dominant method for describing fish distribution and abundance. Regardless of which model is applied for describing how habitat changes affect individual fitness, the fitness consequences of habitat change for individuals need to be scaled up to understand population-level effects. This becomes complicated for species that have multiple life history stages, with different habitat requirements, as considered in the following section.

Scaling Habitat Requirements of Individuals up to the Population Level

Defining habitat requirements of all life history stages is a necessary step for species management,

but requirements of any particular life stage will not always be limiting at the population level. It is more often the case that the habitat requirements of only one or two life stages will create limiting bottlenecks for populations. For informed species management, it is often crucial to know which of many habitat factors limit a population, factors that also are likely to vary over space and time within a species range. Small-scale experiments (like those described above for cutthroat trout) are useful for identifying habitat requirements of particular life stages but provide only limited insight into which habitat or life stage limits a population. The lake trout study described above is a good example of how apparent habitat requirements for one life stage (availability of premium spawning habitat) may not translate into population-level effects because the population is limited at a later stage.

There are generally two approaches for sorting out which of many complex factors limit populations and for measuring the population-level consequences of habitat change. The first is to perform habitat manipulations that affect whole populations and ecosystems—for instance, manipulating the availability of spawning habitat for an entire lake (Gunn and Sein 2000) and measuring the population response, or manipulating the abundance of different stream habitats by logging an entire watershed (Hartman and Scrivener 1990) or by re-introducing floods to a regulated river (Patton et al. 2001). Although ecosystem-level manipulations are definitive and can give unique insight into habitat impacts and population dynamics that smaller-scale experiments cannot (Carpenter et al. 1995; Carpenter 1996), few agencies can provide the necessary long-term commitment of time and resources for their completion. Even when time and resources are available, ecosystem-scale manipulations by their nature preclude significant replication and consequently limit possibilities for multiple treatments or management scenarios.

The other option for understanding when and how different habitat factors limit populations is to construct realistic models of population dynamics. Population models for species with discrete life stages use information on individual-scale habitat requirements to parameterize submodels for different life stages, which are then sequentially linked to provide a whole life cycle model for a population (e.g., Holtby and Scrivener 1989; Nickleson and Lawson 1998; sometimes referred to as habitat supply models [Minns et al. 1996]). Submodels for different life history stages can be

understood simplistically in terms of the extent and quality of available habitat, which is related to cohort size by fitness functions relating organism growth and survival to habitat characteristics. For instance, recruitment of juvenile salmonids from the egg to fry stage will depend on both the extent (area) and quality of spawning habitat (e.g., dissolved oxygen, proportion of fine sediment). Population models can draw on an existing knowledge base to extract appropriate model parameters, and they readily permit evaluation of population sensitivity to habitat change, including multiple management scenarios, which are difficult to replicate in whole-ecosystem experiments. However, models are rarely definitive, given that different model configurations can often produce similar population dynamics, and evaluating their biological realism may be difficult if confidence in parameters is low. In practice, ecosystem-scale experiments and population models are complementary, but expediency dictates that controlled whole-system manipulations will be few. Adaptive management provides a more applied variant of ecosystem experimentation that minimizes interruption of resource extraction (Walters and Holling 1990).

Discussion

The development of quantitative models (Manly et al. 1993; Boyce and McDonald 1999) to describe habitat relationships reflects a need to move beyond expert opinion in the identification of habitat requirement. A simple hierarchical framework provides a useful way of organizing habitat information in terms of (1) presence/absence functions to describe distribution at a large spatial scale, complemented by (2) capacity models to understand correlates of organism abundance where populations occur, and (3) habitat or individual-based microhabitat models (based on observational, experimental, or bioenergetic modeling approaches) to understand the mechanisms whereby habitat influences individual fitness at a smaller spatial scale. Development of habitat models must be placed within the context of the life history of the organism when different habitat requirements are associated with different life stages (Minns et al. 1996; Rose 2000).

Recently, correlative resource selection functions (e.g., logistic regression) have been used to model the presence of wildlife populations at a landscape scale (Boyce and McDonald 1999). Just as use of density may distort the fitness consequences of using different habitats at a small scale (e.g., pools versus riffles), failure to distinguish

between source and sink populations may result in severely biased landscape-scale models of habitat requirement. Resource selection functions that predict presence/absence at a landscape scale do not typically distinguish between source and sink populations. If a significant proportion of the populations used to generate a resource selection function are sink populations, then the resource selection function may be severely biased towards sink habitats, and the identification of sink habitats as useable may be an artifact of model generation based on purely correlative data. Harig and Fausch (2002) partially address this problem by modeling separate functions for high- and low-density populations, but the only unambiguous measures of the suitability of a habitat at any scale are direct measurements of fitness—average population growth (reproductive success) in the case of populations or growth and survival of individuals (as correlates of reproductive success) at the microhabitat scale.

The degree to which habitat suitability curves accurately reflect habitat quality is poorly understood, given that curves are rarely evaluated in terms of the true fitness consequences (growth and survival) of the use of different habitats. Concordance between habitat suitability and the fitness consequences of habitat use can be evaluated by superimposing actual measurements of fitness (e.g., growth) on habitat suitability curves. This is illustrated in Figure 5, where we plot growth rates of young-of-year cutthroat trout in pool and riffle habitats over suitability curves for depth and velocity that were developed for young-of-year cutthroat trout from south coastal British Columbia (from Burt and Horchik 1998). Note that growth rates are standardized so that the maximum has a value of 1 and that the observed focal velocity and depth in experimental habitats did not exceed 13 cm/s and 22 cm, respectively (data from Rosenfeld and Boss 2001). Figure 5 demonstrates that there is considerable deviation between the suitability curve and the actual fitness consequences of using different habitats. This does not necessarily discount the use of habitat suitability curves to estimate habitat availability (Gore and Nestler 1988) but does demonstrate that they may be of limited use for defining habitat quality (the fitness consequences of habitat use) beyond coarse generalities; for example, habitats with velocities in excess of 30 cm/s are clearly unsuitable for young-of-year cutthroat trout.

Bioenergetic models for drift-foraging fish are worth exploring as a mechanistic alternative to

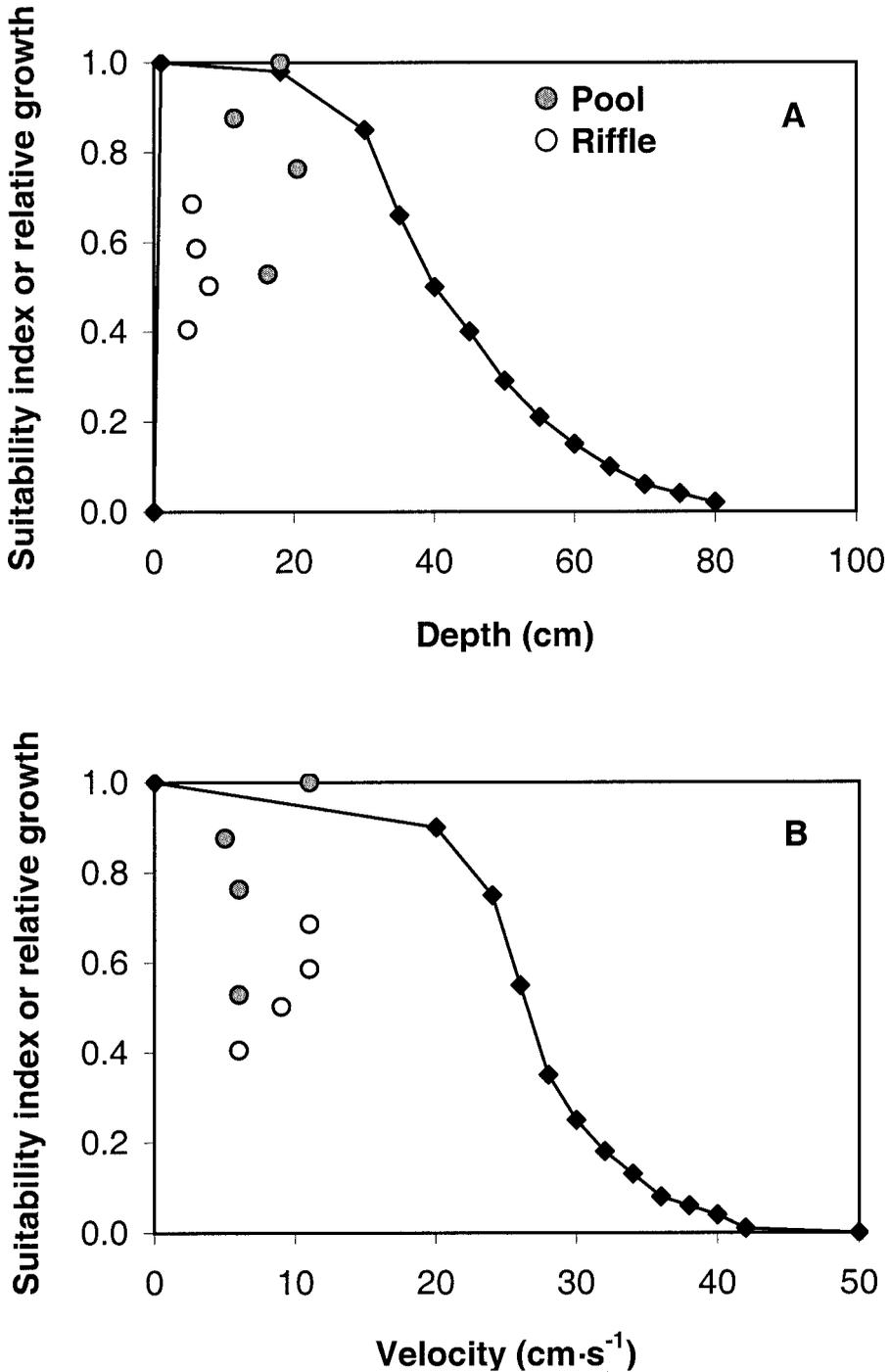


FIGURE 5.—Comparison of young-of-year cutthroat trout habitat suitability curves (from Burt and Horchik 1998) to the fitness consequences (relative growth rates) of using different habitats. Growth rates are averages of cutthroat trout growth rates in replicate pool or riffle enclosures (from Rosenfeld and Boss 2001); focal velocities and depths are based on observations of one individual per enclosure. Relative growth rates are standardized so that the maximum has a value of 1. The maximum observed focal velocity and depth in pool and riffle habitats did not exceed 13 cm/s and 22 cm, respectively.

correlative habitat suitability functions, but they will require significant refinement and validation to assess their ability to accurately predict fish growth and abundance (Boisclair 2001). Similarly, the resources required to perform detailed fitness experiments may also limit their application, and for endangered species, where both opportunity and funding are often available, restrictions against harming individuals may further constrain research options. Clearly, experiments that involve mortality, such as tethering (White and Harvey 2001) or enclosures (Power et al. 1989), to estimate survival in different habitats may not be appropriate (unless performed on surrogate species not at risk). However, short-term growth experiments (e.g., Rosenfeld and Boss 2001) may be acceptable, given that any decrease in fitness (growth) could be offset by supplemental feeding of individuals after the experiments.

Information Needs for Different Management Scenarios

Defining habitat requirements is a multistage process of increasing rigor. Information accrual for any species typically goes through a progression (Regier 1976) from natural history studies documenting basic life history, followed by identification of apparently critical habitats (spawning, juvenile rearing, overwintering, etc.) based on correlative habitat associations, to detailed research on the ecology and physiology of a species. However, the wealth of information necessary to generate complex (e.g., bioenergetic) models is typically available only for species of significant commercial or social interest (e.g., salmonids) with a long history of research. In contrast, information is lacking for many nongame species, which are only recently being explicitly managed as agencies expand their mandates to include stewardship of biodiversity. However, the urgency of threats to many species (Ricciardi and Rasmussen 1999) and limited agency resources will inevitably limit the information available for making timely decisions, and researchers and managers will have to carefully identify the subset of information that is optimal for informed management decisions concerning species at risk.

Basic information on life history and habitat use is essential for even the most rudimentary species management. Lack of resources and the need to act immediately may preclude a more rigorous evaluation of habitat requirement (e.g., beyond correlative relationships). However, it is important to recognize that although a mechanistic under-

standing of the fitness consequences of using different habitats may not be necessary for the initial precautionary stages of habitat protection, it is critical for more advanced stages of management such as habitat restoration. Implementing habitat protection measures that result in significant loss of economic opportunity will also be difficult without credible evidence of the negative impacts of habitat loss, and protection measures based on a weak understanding of habitat requirement are likely to be challenged.

Informational needs for managing any particular species will depend on species distribution, biology, and major threats, many of which will differ among species at risk. For species such as bull trout *Salvelinus confluentus*, for which habitat fragmentation appears to be a major limiting factor on population persistence, assessment of metapopulation dynamics is a key issue (Dunham and Rieman 1999; Rieman and Dunham 2000). For extremely narrow endemic species such as the Devils Hole Pupfish *Cyprinodon diabolis*, which is known from only one location in Nevada (Deacon and Williams 1991), metapopulation dynamics are irrelevant. In this case, detailed information on habitat use or fish physiology is probably not essential for management decisions; narrow endemic species are clearly at risk by nature of their highly restricted distributions (Moyle 1995), and protected area status is appropriate. If their habitat is degraded, then research on habitat use and requirements becomes necessary to inform management and restoration activities or translocation of populations to new habitats (Harig et al. 2000).

Where a particular habitat threat can be identified as the primary factor placing a species at risk, then the impact of the factor on required habitats should clearly become the primary research focus. The effects of flow regulation on the endangered razorback sucker *Xyrauchen texanus* in the Colorado River is a good example (Minckley et al. 1991). In this case, the primary information issue is not a metapopulation one concerning which streams or watersheds are suitable across a landscape, but rather which habitats are critical within the single large endemic habitat, and how they are affected by flow regulation (Modde et al. 2001).

Optimal Habitat Configurations for Restoration and Management

From the standpoint of habitat restoration and management, there are often implicit trade-offs between the abundance of different habitat types in

a stream. For instance, creation of pools will usually come at the expense of riffles (although habitat enhancement activities can sometimes create entirely new habitat [e.g., side-channels; Sheng et al. 1990]). Even when one habitat type is not destroyed to create another, restored habitat needs to be correctly identified as limiting; otherwise, enhancement will be ineffective. One useful way of thinking about limiting habitat factors and restoration goals is in terms of optimal habitat configurations. Poff and Huryn (1998) considered optimal habitat configurations for juvenile Atlantic salmon in terms of trade-offs between "trophic" habitat (juvenile Atlantic salmon feed in faster riffle/run habitats, which have higher invertebrate production) and "nontrophic" habitat (pools for overwintering or low-flow refugia). They postulated a hypothetical ratio of pool : riffle habitat that would maximize juvenile salmon production and that the optimal ratio would be sensitive to both invertebrate production (which governs how many juveniles will be produced from a given riffle area) and the quantity of pool habitat necessary to ensure overwinter survival of juveniles rearing in riffles.

Conceptualizing limiting habitats (e.g., spawning, rearing, overwintering, etc.) as occurring in discrete ratios is a concrete way of defining optimal habitat configurations. Although Poff and Huryn (1998) conceptualized a trade-off between trophic and nontrophic habitat, the concept can also be applied to any species for which different life stages have minimal habitat overlap, and a theoretical optimal ratio of habitats (e.g., spawning : rearing : adult : overwintering) will maximize population size. When an essential habitat required by one life stage is limiting, its proportional abundance will deviate below the optimal ratio, which is conceptually equivalent to Redfield ratios used in limnology as a rule-of-thumb to identify which nutrient (C:N:P) is limiting primary production (Redfield 1958). Reeves et al. (1989) provide a particularly good example of using this approach to identify limiting habitat factors for juvenile coho salmon. The optimal habitat configuration for a species may be thought of as encompassing a range rather than a single value because changes in habitat quality (e.g., prey availability in juvenile rearing habitat, or percent fine sediment in spawning gravel) will alter optimal habitat ratios. Streams are also clearly dynamic systems, and static measures of habitat quality need to be complemented by metrics that capture the effect of disturbance regimes (e.g., floods) and stochastic events on population persistence (Young 1995).

Nevertheless, optimal habitat ratios may serve as a useful conceptual foundation for synthesizing physical habitat requirements of a species for guiding habitat restoration and management. Optimal habitat ratios may also provide a simple way to differentiate physical habitat requirements of different species, and for visualizing trade-offs in the management of sympatric species that have contrasting habitat needs (e.g., lotic versus lentic specialists).

While this review highlights the need to identify the critical stream habitats necessary for the persistence of species, it is equally important to identify and protect the processes that ultimately generate and maintain these features (Imhoff et al. 1996; Roni et al. 2002). For instance, the importance of natural flow regimes is widely recognized as critical for the maintenance of scour pools, off-channel rearing habitat, and clean spawning gravel (Poff et al. 1997). Ensuring sufficient discharge for juvenile rearing at base flow will not ensure healthy populations if the peak flows that maintain channel structure are absent (Barinaga 1996) or if natural recruitment of large woody debris is interrupted by destruction of riparian zones (McIntosh et al. 2000). This does not imply that the identification of critical habitats is unnecessary, but rather that the overriding management priority must be to protect and maintain the processes that create them. Similarly, although the focus of this paper has been on habitat, it is important to recognize that there are critical nonhabitat factors (e.g., fishing and invasions by exotic species) that will also strongly influence species persistence.

Informed management of fish and wildlife remains centered on an accurate understanding of habitat requirements. Biologists need to more critically assess the consequences of using potentially biased correlative habitat relationships as surrogates of the true fitness consequences of habitat use. Although incomplete knowledge should not be used as an excuse for delaying immediate conservation action on critical habitat issues (Ludwig et al. 1993; Pister 1999), research efforts need to be directed at defining less ambiguous metrics of habitat requirement; these include functions relating fitness to habitat structure, the identification of limiting habitat factors by the use of mechanistic population models, and gaining a better understanding of optimal habitat configurations for different species of fishes.

Acknowledgments

I thank Marc Porter and Mike Pearson and several anonymous reviewers for providing helpful

comments on an earlier draft of this manuscript. Discussions with Marc Porter and Eric Parkinson contributed to the development of the ideas presented in this paper. This research was supported in part by the Save the Salish Sucker Foundation.

References

- Bardonnet, A., and J. Baglinière. 2000. Freshwater habitat of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:497–506.
- Barinaga, M. 1996. A recipe for river recovery? Science 273:1648–1650.
- Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.
- Boisclair, D. 2001. Fish habitat modeling: from conceptual framework to functional tools. Canadian Journal of Fisheries and Aquatic Sciences 58:1–9.
- Bovee, K. D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. U.S. Fish and Wildlife Service, Instream flow information paper 12, FWS/OBS-82/26.
- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.
- Bozek, M. A., and W. A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. Canadian Journal of Zoology 70: 886–890.
- Burt, D. W., and J. W. Horchik. 1998. Habitat, abundance, and rearing capacity of salmonids in the Bella Coola watershed. British Columbia Ministry of Fisheries, Victoria.
- Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677–680.
- Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. Science 269:324–327.
- Chapman, L. J., C. A. Chapman, R. Ogutu-Ohwayo, M. Chandler, L. Kaufman, and A. E. Keiter. 1996. Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. Conservation Biology 10:554–561.
- Clark, M. E., and K. A. Rose. 1997. Individual-based model of stream-resident rainbow trout and brook char: model description, corroboration, and effects of sympatry and spawning season duration. Ecological Modelling 94:157–175.
- Connolly, P. J., and J. D. Hall. 1999. Biomass of coastal cutthroat trout in unlogged and previously clearcut basins in the Central Coast Range of Oregon. Transactions of the American Fisheries Society 128:890–899.
- Deacon, J. E., and C. D. Williams. 1991. Ash Meadows and the legacy of the Devils Hole pupfish. Pages 69–87 in W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson.
- Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9:642–655.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169–175.
- Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.
- Frissel, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.
- Frissel, C. A., and D. G. Lonzarich. 1996. Habitat use and competition among stream fishes. Pages 493–510 in F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Academic Press, San Diego, California.
- Gore, J. A., and J. M. Nestler. 1988. Instream flow studies in perspective. Regulated Rivers: Research and Management 2:93–101.
- Grant, G. E., F. J. Swanson, and M. G. Wolman. 1990. Pattern and origin of stepped-bed morphology in high-gradient streams, Western Cascades, Oregon. Geological Society of America Bulletin 102:340–352.
- Guay, J. C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:2065–2075.
- Guensch, G. R., T. B. Hardy, and R. C. Addley. 2001. Examining feeding strategies and position choice of drift-feeding salmonids using an individual-based, mechanistic foraging model. Canadian Journal of Fisheries and Aquatic Sciences 58:446–457.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distributions models in ecology. Ecological Modelling 135:147–186.
- Gunn, J., and R. Sein. 2000. Effects of forestry roads on reproductive habitat and exploitation of Lake Trout (*Salvelinus namaycush*) in three experimental lakes. Canadian Journal of Fisheries and Aquatic Sciences 57(Supplement 2):97–104.
- Hankin, D. G. 1984. Multistage sampling designs in fisheries research: applications in small streams. Canadian Journal of Fisheries and Aquatic Sciences 41:1575–1591.
- Hankin, D. G., and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834–844.
- Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications 12:535–551.
- Harig, A. L., K. D. Fausch, and M. K. Young. 2000.

- Factors influencing success of greenback cutthroat trout translocations. *North American Journal of Fisheries Management* 20:994–1004.
- Hartman, G. F., and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. *Canadian Bulletin of Fisheries and Aquatic Sciences* 223.
- Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman, and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18(6):3–12.
- Hayes, J. W., J. D. Stark, and K. A. Shearer. 2000. Development and test of a whole-lifetime foraging and bioenergetics model for drift-feeding brown trout. *Transactions of the American Fisheries Society* 129: 315–332.
- Hill, J., and G. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology* 74:685–698.
- Hobbs, N. T., and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? *Journal of Wildlife Management* 54:515–522.
- Holtby, B. L., and J. C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging and fishing on the number of chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) returning to Carnation Creek, British Columbia. *Canadian Special Publication of Fisheries and Aquatic Sciences* 105:62–81.
- Hughes, N. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. *Ecology* 79:281–294.
- Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2039–2048.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- Imhoff, J. G., J. Fitzgibbon, and W. K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1):312–326.
- Jowett, I. G. 1992. Models of the abundance of large brown trout in New Zealand rivers. *North American Journal of Fisheries Management* 12:417–432.
- Lonzarich, D. G., and T. P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of fishes. *Canadian Journal of Zoology* 73:2223–2230.
- Ludwig, D., T. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260:17.
- Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London.
- Mathur, D., W. H. Bason, E. J. Purdy, and C. A. Silver. 1985. A critique of the Instream Flow Incremental Methodology. *Canadian Journal of Fisheries and Aquatic Sciences* 42:825–831.
- McIntosh, B. A., J. R. Sedell, R. F. Thurow, S. E. Clarke, and G. L. Chandler. 2000. Historical changes in pool habitats in the Columbia River basin. *Ecological Applications* 10:1478–1496.
- Minckley, W. L., P. C. Marsh, J. E. Brooks, and B. L. Jensen. 1991. Management towards recovery of the razorback sucker. Pages 303–357 in W. L. Minckley and J. E. Deacon, editors. *Battle against extinction: native fish management in the American West*. University of Arizona Press, Tucson.
- Minns, C. K., R. G. Randall, J. E. Moore, and V. W. Cairns. 1996. A model simulating the impact of habitat supply limits on northern pike, *Esox lucius*, in Hamilton Harbour, Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1):20–34.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* 9:279–294.
- Modde, T., R. T. Muth, and G. B. Haines. 2001. Floodplain wetland suitability, access, and potential use by juvenile razorback suckers in the middle Green River, Utah. *North American Journal of Fisheries Management* 130:1095–1105.
- Montgomery, D. R., J. M. Buffington, R. D. Smith, K. M. Schmidt, and G. Pess. 1995. Pool spacing in forest channels. *Water Resources Research* 31: 1097–1105.
- Moyle, P. B. 1995. Conservation of native freshwater fishes in the Mediterranean-type climate of California, USA: a review. *Biological Conservation* 72: 271–279.
- Moyle, P. B., and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. *Transactions of the American Fisheries Society* 114: 695–704.
- Nickleson, T. E., and P. W. Lawson. 1998. Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: application of a habitat-based life cycle model. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2383–2392.
- Nickleson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49:783–789.
- Nislow, K. H., C. L. Folt, and D. L. Parrish. 1999. Favourable foraging locations for young Atlantic salmon. *Ecological Applications* 9:1085–1099.
- Nislow, K. H., C. L. Folt, and D. L. Parrish. 2000. Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. *Transactions of the American Fisheries Society* 129:1067–1081.
- Olden, J. D., and D. A. Jackson. 2002. A comparison

- of statistical approaches for modeling fish species distributions. *Freshwater Biology* 47:1976–1995.
- Olden, J. D., D. A. Jackson, and P. R. Peres-Neto. 2002. Predictive models of fish species distributions: a note on proper validation and chance predictions. *Transactions of the American Fisheries Society* 131: 329–336.
- Orth, D. J., and O. E. Maughan. 1982. Evaluation of the incremental methodology for recommending in-stream flows for fishes. *Transactions of the American Fisheries Society* 111:413–445.
- Patten, D. T., D. A. Harpman, M. I. Voita, and T. J. Randle. 2001. A managed flood on the Colorado River: background, objectives, design, and implementation. *Ecological Applications* 11:635–643.
- Peterson, J. T., and C. F. Rabeni. 2001a. Evaluating the physical characteristics of channel units in an Ozark stream. *Transactions of the American Fisheries Society* 130:898–910.
- Peterson, J. T., and C. F. Rabeni. 2001b. The relation of fish assemblages to channel units in an Ozark stream. *Transactions of the American Fisheries Society* 130:911–926.
- Pister, E. P. 1999. Professional obligations in the conservation of fishes. *Environmental Biology of Fish* 55:13–20.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391–409.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769–784.
- Poff, N. L., and A. D. Huryn. 1998. Multi-scale determinants of secondary production in Atlantic salmon (*Salmon salar*) streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55(Supplement 1):201–217.
- Porter, M., J. S. Rosenfeld, and E. A. Parkinson. 2000. Predictive models of fish species distribution in the Blackwater drainage, British Columbia. *North American Journal of Fisheries Management* 20: 349–359.
- Postel, S. L., G. C. Daily, and P. R. Ehrlich. 1996. Human appropriation of renewable fresh water. *Science* 271:785–788.
- Power, M. E., T. L. Dudley, and S. D. Cooper. 1989. Grazing catfish, fishing birds, and attached algae in a Panamanian stream. *Environmental Biology of Fishes* 26:285–294.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1555–1564.
- Rabeni, C. F., and R. B. Jacobson. 1993. The importance of fluvial hydraulics to fish-habitat restoration in low-gradient alluvial streams. *Freshwater Biology* 29:211–220.
- Railsback, S. F., and B. C. Harvey. 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* 83:1817–1830.
- Redfield, A. C. 1958. The biological control of chemical factors in the environment. *American Scientist* 46: 206–226.
- Regier, H. A. R. 1976. Environmental biology of fishes: emerging science. *Environmental Biology of Fishes* 1:5–11.
- Reeves, G. H., F. H. Everest, and T. E. Nickleson. 1989. Identification of physical habitats limiting the production of coho salmon in western Oregon and Washington. U.S. Department of Agriculture, Forest Service Pacific Northwest Research Station, General Technical Report PNW-GTR-245, Portland, Oregon.
- Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* 13:1220–1222.
- Rieman, B. E., and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. *Ecology of Freshwater Fish* 9:51–64.
- Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. *North American Journal of Fisheries Management* 22:1–20.
- Rose, K. A. 2000. Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecological Applications* 10:367–385.
- Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 585–593.
- Rosenfeld, J. S., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:766–774.
- Sala, O., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. M. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704–712.
- Sheng, M. D., M. Foy, and A. Y. Fedorenko. 1990. Coho salmon enhancement in British Columbia using improved groundwater-fed side channels. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* 2071.
- Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass.

- Transactions of the American Fisheries Society 109: 1–34.
- Sogard, S. M. 1994. Use of suboptimal foraging habitats by fishes: consequence for growth and survival. Pages 103–131 *in* D. J. Strouder, K. L. Fresh, and R. J. Feller, editors. Theory and application in fish feeding ecology. University of South Carolina Press, Columbia.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337–365.
- Tabachnik, B. G., and L. S. Fidell. 1996. Using multivariate statistics. Harper Collins, New York.
- Taniguchi, Y., and S. Nakano. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology* 81:2027–2039.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental changes. *Science* 292:281–284.
- Toepfer, C. S., W. L. Fisher, and W. D. Warde. 2000. A multistage approach to estimate fish abundance in streams using geographic information systems. *North American Journal of Fisheries Management* 20:634–645.
- Thompson, W. L., and D. C. Lee. 2000. Modeling relationships between landscape-level attributes and snorkel-counts of chinook salmon and steelhead parr in Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1834–1842.
- Van Horne, B. 1983. Density as misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893–901.
- Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060–2068.
- Watson, G., and T. W. Hillman. 1997. Factors affecting the distribution and abundance of bull trout: an investigation at hierarchical scales. *North American Journal of Fisheries Management* 17:237–252.
- Winker, K., J. H. Rappole, and M. A. Ramos. 1995. The use of movement data as an assay of habitat quality. *Oecologia* 101:211–216.
- White, J. L., and B. C. Harvey. 2001. Effects of an introduced piscivorous fish on native benthic fishes in a coastal river. *Freshwater Biology* 46:987–995.
- Young, M. K. 1995. Synthesis of management and research considerations. U.S. Forest Service General Technical Report RM-GTR-256.