

ECOLOGICAL CONSIDERATIONS IN THE DEVELOPMENT AND APPLICATION OF INSTREAM FLOW-HABITAT MODELS

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ABSTRACT

Methodologies for recommending instream flows for protecting lotic ecosystems are evolving amid constructive criticism. During this period of change it is important that all concerned parties are aware of the ecological factors that control stream ecosystems and fish populations. Ecological factors relating to stream ecology, population dynamics, energetics, predation, and competition are reviewed to explain why indices of microhabitat availability are not expected to be consistent predictors of fish population density. Implications of these concepts for development and application of instream flow-habitat models for recommending instream flow regimes are discussed. Current ecological theory and empirical studies support the hypothesis that microhabitat availability may limit fish populations but not continuously. Therefore, assessments must consider the limiting habitat events as well as temperature and water quality constraints. Also, invertebrates and non-game fishes must be considered in instream flow assessments because of their importance in stream ecosystems.

INTRODUCTION

Effects of flow modifications on stream habitat and biota have become the focus of an emerging science in the last decade as evidenced by exponential growth in numbers of publications (Petts, 1984). Conservation and regulatory agencies routinely deal with the questions of what effects various stream flow alterations will have on aquatic life and fisheries. Recent efforts to encourage small hydropower development in the United States have intensified the interest; the Federal Energy Regulatory Commission (FERC) received over 6,000 applications since 1979 compared with less than 3,000 in the preceding 60 years (Tanner and Hickman, 1985). The regulatory process for hydropower development and regional water resources planning is thwarted by lack of agreement on methods for recommending appropriate instream flows to meet management objectives.

The lack of agreement on methods and interpretation is understandable because the present state of the art developed largely within the last 10 years (see reviews by Stalnaker and Arnette, 1976; Stalnaker, 1979; Loar and Sale, 1981; Trihey and Stalnaker, 1985). The current state of the art is incorporated in the Instream Flow Incremental Methodology (IFIM), outlined by Bovee (1982). The IFIM process includes evaluation of effects of incremental changes in stream flow on channel structure, water quality, temperature, and availability of suitable microhabitat in order to recommend a flow regime that will maintain existing habitat conditions. The physical habitat component (PHABSIM; Milhous *et al.*, 1984) of the IFIM process is the most frequently used component, often to the exclusion of other components. Criticisms of PHABSIM and the interpretation and application of the weighted usable area (WUA) index focus on the lack of evidence that fish populations respond to changes in WUA (Mathur *et al.*, 1985; Shirvell, 1986; Scott and Shirvell, in press). Consequently, frustration among biologists exists because fish population responses to flow alterations cannot be predicted. This frustration will continue until intensive, long-term research efforts can advance the state of the art with methods to reliably assess instream flow needs based on biological responses (Loar and Sale, 1981). New and more complex models will be needed to address biological responses to altered stream flow regimes.

In the meantime, decisions that affect the future of many stream fisheries will be made without the benefit of predictions of fish population responses to alternative flow regimes. In the near future the IFIM process will continue to play a major role in instream flow assessments and components of IFIM will be modified to accommodate new situations (e.g. hydropeaking, Bovee, 1985). Therefore my purpose in this paper is to (1) review ecological concepts that may explain why WUA is an inconsistent predictor of fish population abundance, (2) suggest cautious applications of PHABSIM models, (3) encourage application of all available models and knowledge in the assessment process, and (4) suggest areas of needed research.

STREAM ECOLOGY AND FLOW ALTERATION

At least six primary factors influence the structural and functional characteristics of stream ecosystems with respect to distribution and abundance of stream fishes. These are energy source (food), water quality, temperature, physical habitat structure, flow regime, and biotic interactions (Karr and Dudley, 1981). Too often, instream flow assessments focus only on changes in physical habitat structure (e.g. WUA) due to flow alteration and ignore potential temperature and water quality changes despite the availability of water temperature and water quality models (Grenney and Kraszewski, 1981; Theurer and Voos, 1984). Variables related to energy source and biotic interactions are typically ignored even though such changes frequently occur following certain types of flow regulation (Ward and Stanford, 1983). Consequently, most instream flow assessments represent incomplete analyses of potential impacts of flow regulation.

Improved instream flow models must address all of the six primary factors affecting stream ecosystems in order to avoid unanticipated effects. Assessment of potential effects of regulation requires a knowledge of how these factors interact and the time scale required before the full effects may be recognized. Petts' (1984) hierarchical framework (Figure 1) describes these effects in terms of three orders

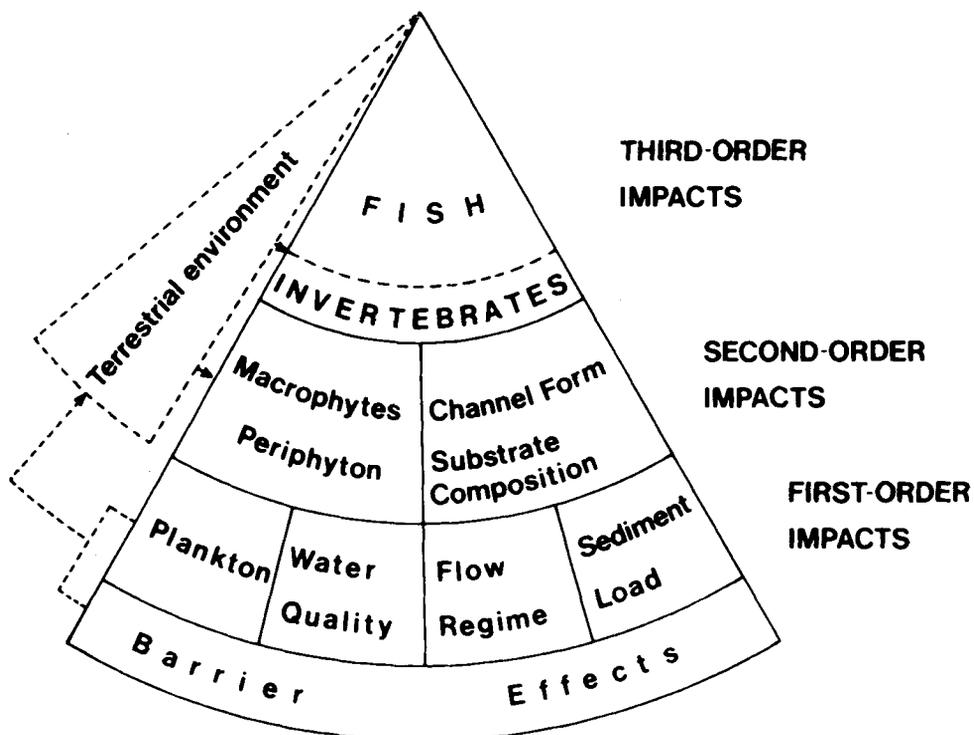


Figure 1. Hierarchical framework for examining the impacts of river impoundment. From Petts (1984). Copyright by John Wiley & Sons Ltd.

of impacts. First-order impacts occur immediately after a dam is built and include effects on energy sources and transport, flow regime, water quality and temperature, and sediment transport. Second-order impacts occur as a result of first-order impacts and include changes in habitat structure (channel form and substrate composition), riparian vegetation and sources of organic matter, and periphyton and macrophyte communities. Assessment of impacts after regulation is complicated because the second-order impacts may require 1–100 years to achieve a new equilibrium (Petts, 1984). Changes in fish and invertebrate communities, which are the most critical concerns for resource management agencies, are third-order impacts which arise as a consequence of first- and second-order impacts. For example, Lehmkuhl (1972) demonstrated that changes in the thermal regime following flow regulation eliminated several species of mayflies. Also, Smith (1976) reported that steelhead trout (*Salmo gairdneri*) runs were significantly reduced after flow regulation because of sand accumulation in the riffles. The time scale for third-order impacts to be manifested is extremely variable depending on the time required for second-order impacts to become significant and the generation time of the organisms of concern.

POPULATION DYNAMICS

The effects of first- or second-order impacts on fish population abundance can be understood by considering the conceptual model which includes the six population parameters that determine numerical changes in fish stock biomass — growth of individual fish, recruitment, natural mortality, fishing mortality, immigration, and emigration. Any of these population parameters may be influenced by first-, second-, or third-order impacts. For example, temperature is a major determinant of growth in fishes and this relationship has been well studied (Brett and Groves, 1979). The amount of suitable winter cover (habitat structure) influences numbers of stream salmonids that will emigrate and numbers that can survive over winter (Bjornn, 1971). Extreme low flows can decimate warmwater stream fish and invertebrates and higher flows may permit rapid recolonization (Larimore *et al.*, 1959). Recruitment success is strongly influenced by the flow regime during and after the breeding season (Schlosser, 1985).

This conceptual model of population dynamics permits the development of hypotheses concerning population regulation. The hypothesis that microhabitat availability limits population abundance is a basic assumption in recommending flow regimes using PHABSIM. However, recent critiques document that WUA is not a consistent predictor of abundance (Shirvell, 1986; Scott and Shirvell, in press). Weighted usable area is an index that represents the amount of acceptable (or suitable) habitat for a given species and life stage (see Bovee, 1982 for formula). Suitability can be defined based on microhabitat (depth, velocity, substrate, and cover) and macrohabitat (temperature, water quality) variables. However, most studies cited by Scott and Shirvell (in press) calculated WUA on the basis of only three microhabitat variables (depth, velocity, and substrate). At least three hypotheses for stream fish population regulation can be offered to explain why WUA does not predict population size. These three hypotheses assume that habitat availability (WUA) and population abundance can be adequately quantified.

First, many validation studies have been on exploited game fish populations; all but one of eleven studies reviewed by Scott and Shirvell (in press) focused exclusively on game fish. Adult game fish populations may be limited by exploitation rather than available microhabitat. Consequently, many of these studies were inadequate tests because the effects of exploitation were not measured.

A second hypothesis is that microhabitat availability does not regulate population abundance but only determines where stream fishes will be. Therefore, food availability, or biotic interactions (competition or predation) may be the major determinants of population size within suitable habitat patches. For example, high availability of food can reduce emigration and thereby increase densities of salmonids (Mason and Chapman, 1965; Wilzbach, 1985). Also, predators (rock bass *Ambloplites rupestris*) can reduce the densities of prey fish (sculpins *Cottus* spp.) even when suitable microhabitat is available (Anderson, 1985).

A third hypothesis to explain population dynamics of stream fishes is that microhabitat availability limits populations only during short periods due to extreme variations in stream flow (Horwitz, 1978;

Orth and Maughan, 1982, 1986). Temporal variations in stream flow can limit populations of stream fish by affecting emigration, growth, survival, or recruitment. Consequently, population size at a given time is determined by past habitat limitations for any life stage and instantaneous measures of microhabitat availability will not be related to instantaneous population size. It is, therefore, not surprising that many attempts to correlate instantaneous WUA and instantaneous fish standing crop have been unsuccessful (Scott and Shirvell, in press).

For stream fishes, survival during the early life stages is critical in determining adult population size, and for many species, these stages can tolerate only near-zero water velocities (Larimore, 1975; Ottaway and Clark, 1981; Ottaway and Forrest, 1983). Therefore, fish densities may be strongly related to habitat conditions during the critical early life stages. Anderson and Nehring (1985) found strong negative relationships between juvenile trout (*Salmo gairdneri* and *S. trutta*) numbers and peak flows during the time when fry have emerged from the gravel, presumably due to excessive water velocities. Loar *et al.* (1985) found that rainbow trout densities were correlated with minimum incubation habitat (minimum WUA during incubation period) in southern Appalachian streams without brown trout. However, the lack of a significant relationship for sites where rainbow trout occurred with brown trout suggests a potential competitive interaction. In populations where recruitment is highly responsive to flow conditions, which may be unpredictable, population densities may exhibit stochastic annual variability. Consequently, adult population densities cannot be predicted on the basis of present WUA measures alone; knowledge of past limiting habitat events and past population densities would be needed to predict population density.

It is crucial that those involved in negotiating stream flow regimes in regulated rivers recognize that microhabitat availability is not the only regulatory factor and does not operate continuously to limit stream fish populations. The prevailing limiting factors vary widely among streams and may vary temporally within the same stream. Moyle and Vondracek (1985) found that despite variable flow conditions in a small stream, stream fish assemblage structure was persistent, suggesting that biotic interactions play an important role in fish population regulation. However, in other streams, stochastic factors (e.g. variable flow) may be equally important, resulting in more variable fish assemblage structure (Grossman *et al.*, 1985; Schlosser, 1985).

ENERGETICS AND FOOD LIMITATION

The usual omission of aquatic invertebrates from instream flow assessments presumes that either food availability does not normally limit fish production in streams or adequate flows for fish result in suitable flows for invertebrates. At the present time, there is insufficient evidence to support either of these assumptions. Furthermore, evidence indicates that some aquatic insects are quite sensitive to small changes in flow and should be included in instream flow assessments (Gore, in press). Stream hydraulics has been proposed as a major determinant affecting stream invertebrate assemblages (Statzner and Higler, 1986). In recent years several studies have described the microhabitat requirements for several stream insects for application in instream flow assessments (Gore and Judy, 1981; Orth and Maughan, 1983; Teague *et al.*, 1985). Morin *et al.* (1986) has critically evaluated methods for developing habitat suitability criteria for stream insects and Newbury (1984) described the measurement of important hydraulic characteristics.

One line of evidence that supports a regulatory influence of prey availability on biomass of stream fish populations is the indication that fish predators depress the density of their invertebrate prey, subsequently resulting in reduced growth of individual fish (Brocksen *et al.*, 1968; Flecker, 1984; Anderson, 1985; Angermeier, 1985). In laboratory streams, Brocksen *et al.* (1968) found that reticulate sculpins (*Cottus perplexus*) and cutthroat trout (*Salmo clarki*) could overexploit their invertebrate prey. Increased fish biomass reduced the density of food organisms, which directly reduced growth rate of trout and sculpins. Anderson (1985) also observed that growth rates in wild populations of sculpins were inversely related to population density. In enclosure experiments, Angermeier (1985) demonstrated that predation by stream fish depressed invertebrate densities in silt-sand habitats but not in gravel-cobble

habitats. In a similar experiment Flecker (1984) found that the presence of fish (mainly dace *Rhinichthys* and sculpins *Cottus*) depressed the densities of midges (Chironomidae) and the stonefly *Leuctra*, but not other invertebrate taxa. These studies suggest that stream fish production may be strongly influenced by invertebrate production or availability. In fact, Warren *et al.* (1964) demonstrated that an increase in biomass of aquatic insects following sucrose enrichment resulted in a seven-fold increase in trout production in experimental streams.

However, other studies demonstrate that fish predators do not always exert an influence on invertebrate densities in natural streams (Allan, 1982; Reice, 1983; Culp, 1986). Allan (1982) reduced trout densities between 10 and 25 per cent of initial levels for four years and observed no increase in invertebrate densities. Reice (1983) found that stream invertebrate communities were unaffected by the exclusion of fish. Culp (1986) increased the densities of coho salmon (*Oncorhynchus kisutch*) fourfold and found no measureable effect on macroinvertebrate density and suggested that salmonid predators are only weak interactors in the food web. The effect of fish predation on invertebrate densities is expected to be slight at all but the highest fish densities (Brocksen *et al.*, 1968) and in silt-sand (i.e., structurally simple) substrate (Angermeier, 1985); therefore, substrate complexity or lack of precision in estimating densities may explain why density reductions were not detected in some field experiments.

A second approach to study the relative roles of food availability and habitat structure involves experiments on microhabitat choice. Theoretically, the optimum habitat is one that minimizes the ratio of mortality (predation risk) to growth rate. Concerning growth rates, Fausch (1985) demonstrated that position choice in three juvenile salmonids maximized the potential for net energy gained (available prey energy minus energy costs for swimming). Bachman (1984) suggested that availability of preferred foraging sites was a major limiting factor for salmonid populations at high population densities. When not feeding, trout select resting microhabitats that provide cover from predators and minimize energy expenditure for swimming; availability of these resting microhabitats may also act as a limiting factor (White, 1975). The unique characteristics of foraging sites and resting sites are probably not adequately described by present habitat suitability criteria which do not distinguish between activities or seasons.

The relative importance of food and cover in determining position choice varies with body size, temperature, and time of day (predator activity) or light level; this variability further complicates the process of developing suitability criteria for instream flow assessments. Smith and Li (1983) found that, for juvenile steelhead trout, increased fish size or increased temperature resulted in selection of microhabitats with higher water velocities, presumably due to increased metabolic needs. This would suggest that availability of prey and preferred foraging sites is probably most critical during summer, a time when invertebrate prey availability is declining (Angermeier, 1985). In fact, Wilzbach (1985) documented that food abundance was more important than cover in determining the numbers of cutthroat trout remaining in laboratory stream channels at summer temperatures. However, microhabitats for resting and protection from predation or displacement may be more critical at other times of the year since salmonid abundance is often related to cover alone (Boussu, 1954; Bjornn, 1971; Hunt, 1976). Rainbow trout show dramatic seasonal shifts in habitat use (Campbell and Neuner, 1985), which suggest that habitat and food requirements change seasonally.

The importance of prey availability suggests that increased efforts be made to incorporate criteria for stream invertebrates into instream flow assessments. Efforts must include riffle invertebrates, which are well studied, as well as inhabitants of woody debris that are often the preferred food items for fish in low-gradient streams (Angermeier and Karr, 1984; Benke *et al.*, 1985). Habitat variables that adequately describe food availability must be sought since abundance of invertebrates is related to the detritus food base (Culp *et al.*, 1983) and quality of food (Brown and Brown, 1984) as well as to substrate or velocity characteristics of the microhabitat.

PREDATION RISK

Consideration of predation risk in instream flow assessments is important because (1) microhabitat utilization may vary due to the presence of predators and their activity pattern (i.e. time of day) and (2)

predation pressure, rather than microhabitat availability, may act to regulate population density. Several studies indicate how predators can affect microhabitat use. Power and Matthews (1983) demonstrated that stonerollers (*Campostoma anomalum*) and piscivorous bass (*Micropterus* spp.) had complementary distributions due to either elimination of stonerollers by bass predation or active avoidance by stonerollers. Power (1984) found that armoured catfish (Loricaridae) avoided shallow areas of stream where they were susceptible to avian predation even though their food, attached algae, was abundant there. At night, these catfish tended to utilize shallower water. Juveniles of two minnows (*Semotilus atromaculatus* and *Rhinichthys atratulus*) also actively avoided locations that contained fish predators (adult *S. atromaculatus*) (Fraser and Cerri, 1982). In that study, the structural complexity (i.e. presence of shade, plastic pipes, and dendritic roots) and time of day affected the response of prey fish to the presence of predators. Presence of structure was the most important determinant of patch choice by these two minnows (Fraser and Cerri, 1982), presumably because predation rates were reduced in structurally complex habitats (Newsome and Gee, 1978).

Changes in habitat use by some forage species with time of day may reflect inactivity of predators and reduced predation risk. Cerri (1983) demonstrated that, in daylight, prey fish were more aggregated and predator fish were concealed in refuges; therefore, predation rates were lowest in daylight. Furthermore, prey fish had a greater reactive distance to predators, but this advantage was reduced under low light conditions. Therefore, prey fish must alter their behaviour and habitat selection in low light conditions. These cover seeking and diel activity patterns are common in stream fishes and likely represent adaptive responses to predation. In some stream fishes the role of predation in influencing habitat choice may be independent of food availability (Cerri and Fraser, 1983; Power, 1984). Presence of fish predators reduced the patch utilization by juvenile *R. atratulus* by the same proportions at low and high food levels; therefore, the benefits of increased food were not balanced against risk of predation (Cerri and Fraser, 1983). Power (1984) concluded that avoiding predators was a more adaptive strategy than obtaining maximum energy intake because fish can withstand periods of starvation (Brett and Groves, 1979). Therefore, improved assessments of instream flow changes must be based on site-specific habitat suitability criteria, which reflect the local adaptations of fishes to the indigenous predators. Also, cover availability must be included in instream flow assessments where cover is strongly influenced by river stage.

The other important consideration of predation to instream flow assessment is whether predators, rather than microhabitat availability, limit the population densities of fishes at the site under study. Lemly (1985) showed with removal experiments that green sunfish (*Lepomis cyanellus*) predation on young-of-year fishes was a dominant force in determining the fish assemblage structure in first-order streams; when green sunfish were removed, most native fishes increased in numbers and biomass. Anderson (1985) hypothesized that factors that regulate stream fish populations vary with stream size and found that sculpin population densities were lower in larger stream sites that also contained rock bass and suggested that predation limited sculpin population density at these sites. In smaller stream sites without rock bass, sculpin densities were higher and growth rates and fecundities were lower suggesting that food availability played a more dominant role than predation in limiting population size in smaller streams. If available microhabitat was limiting, one would expect growth, fecundity, and density to be similar among populations within patches of suitable microhabitat.

In summary, predation risk will influence instream flow assessments and development of new models in four ways. First, habitat suitability criteria may not be applicable to streams with different predation risks. Second, structural complexity is an important characteristic to incorporate into models for stream fishes. Third, the effects of flow regulation on fishes will likely depend in part on the type of predators (terrestrial and aquatic) that occur in the riparian/stream ecosystem and how the predation rate is influenced by flow. Finally, if predation is limiting, availability of microhabitat will not be directly related to population density.

COMPETITIVE INTERACTIONS

Competitive interactions complicate instream flow assessments because: (1) species-specific analyses of microhabitat availability ignore the effects of crowding at low flows and (2) presence of competing species can influence microhabitat selection. Although multiple species and life stages are considered in most instream flow assessments, effects of flow regulation on the outcome of competitive interactions is seldom considered. However, it is generally agreed that many fishes in small streams are habitat specialists (Gorman and Karr, 1978) and reductions in flow will decrease the range of habitats available. Consequently, low flows, especially those of unprecedented duration and magnitude, may increase the intensity of competitive interactions. Because fish are crowded into the same limited physical space at low flows, the influence of resource sharing on microhabitat availability must be considered. The degree to which habitats are partitioned among similar species varies for Cyprinidae (Gibbons and Gee, 1972; Mendelson, 1975), Percidae (Page and Schemske, 1978; Smart and Gee, 1979; Paine *et al.*, 1982; Wynes and Wissing, 1982; Englert and Seghers, 1983; Schlosser and Toth, 1984) and Cottidae (Finger, 1982; Matteson and Brooks, 1983).

The most critical concern for determining habitat suitability criteria is that the abundance and presence of competitors may influence the microhabitat selection. If microhabitat shifts occur in presence of competitors, habitat suitability criteria are not transportable to sites with different assemblages of competitors. Habitat utilization by sculpins (*Cottus* spp.) was strongly influenced by the presence of other sculpin species in an Oregon stream (Finger, 1982); microhabitat shifts were also documented in manipulative experiments in laboratory streams. Fausch and White (1981) demonstrated that removal of brown trout allowed brook trout (*Salvelinus fontinalis*) to occupy more advantageous resting positions. Baltz *et al.* (1982) observed high similarity in microhabitat use between two morphologically dissimilar species (riffle sculpin *C. gulosus* and speckled dace *R. osculus*) in sympatry. Abundance of dace was negatively correlated with abundance of sculpins in the field, and sculpin abundance affected utilization of limited refugia by dace in laboratory experiments. Since the outcome of the competitive interaction between the sculpin and dace was influenced by temperature, habitat suitability criteria developed for either of these species would be limited to the site of development.

SELECTION OF TARGET SPECIES

Selection of appropriate species and life stages on which to base analyses of instream flow needs is a critical step, especially in warmwater streams which have diverse fish faunas. Microhabitat preferences vary greatly among the fish species and life stages in a given stream (Moyle and Baltz, 1985). Species and life stages with the narrowest range of habitat preference will generally be most sensitive to flow alterations. Target species with restricted habitat preferences should be selected to encompass the range of habitat-use guilds (or reproductive guilds) represented by the faunal assemblage in the stream. Fish in different habitat-use guilds exhibit dissimilar habitat responses to discharge and, consequently, recommended flows will represent a compromise between the needs of inhabitants of slack water and inhabitants of fast water (Leonard *et al.*, 1986). Therefore, species most restricted to fast water and slow water would be most useful as target species.

SUMMARY OF IMPLICATIONS

Consideration of other ecological factors that affect stream fishes must be made during the IFIM process. The development of new models either dependent upon or independent of IFIM must incorporate the critical determinants of stream fish population dynamics. Because of the long time scales involved in second- and third-order impacts of flow regulation, the use of field manipulations of low flows to determine an appropriate flow regime may not be an appropriate alternative to the use of some type of

instream flow–habitat model. The following suggestions are offered for future instream flow assessments and research:

1. Microhabitat availability is not the only factor limiting fish populations and does not operate continuously. Therefore, persons using IFIM must identify the time(s) when microhabitat is most critically limited and avoid the mistake of assuming that WUA is positively related to fish abundance at all levels of WUA at all times.
2. Because food availability may limit abundance, habitat suitability criteria for invertebrates must be developed and used in PHABSIM applications. New approaches for assessing instream flow needs for invertebrate production must be developed and tested.
3. Habitat suitability criteria can vary with body size, season, time of day, activity, predators, and competitors. Therefore, the applicability of habitat suitability criteria is limited to sites with similar fish assemblages and thermal regimes. Furthermore, seasonal (or size-related) differences in habitat needs and limiting factors must be identified and incorporated in assessments.
4. Structural complexity plays a major role in position choice by stream fishes through the need to feed efficiently and avoid predators. Greater emphasis must be placed on developing reliable criteria for defining suitable habitat for fishes and invertebrates.
5. Assessments must address the needs of a wider array of target species, especially non-game fishes and invertebrates in order to recommend flows to maintain ecological integrity of stream ecosystems.
6. Temperature and water quality limitations on fish and invertebrate populations are potentially severe and should be evaluated in instream flow assessments.

Although the need for more research is obvious and the complicating factors which I have discussed may seem to make the problem intractable, the benefits of improved stream management are undeniable. In the near future, assessments can be greatly improved by applying our present knowledge of stream fish ecology. The IFIM is not intended to be a panacea. However, IFIM has the potential to identify limiting habitat events and avoid them in developing flow regimes in regulated rivers. The IFIM is a process, not a model, and the process allows the consideration of the other ecological factors that I have discussed. As new models are developed and tested they can be incorporated into the IFIM process. However, it is still not possible, with our current knowledge base, to accurately predict fish population sizes under various flow regulation scenarios — this remains as a goal for research. The additional cost for studying all the factors that I have discussed may not be feasible for all agencies to consider, except in a research mode; the pressure to take short cuts in assessments will continue. More detailed, comprehensive studies of stream fish and invertebrate responses to altered flow regimes will be needed before simpler and less costly methods evolve. In the meantime, flow recommendations developed on the basis of incomplete assessments should, by necessity, be overly conservative to protect stream resources.

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