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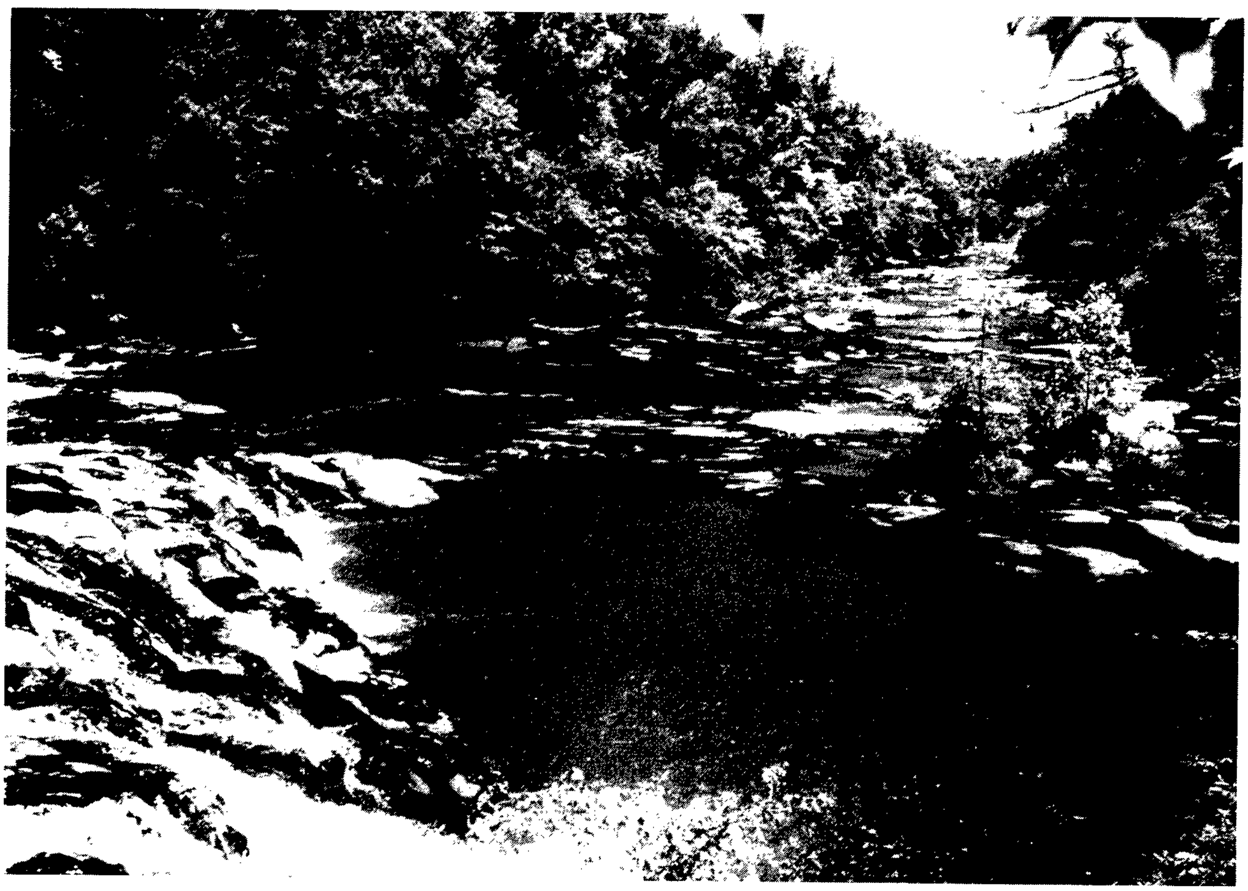
REGULATED STREAMFLOW AND WARMWATER STREAM FISH: A GENERAL HYPOTHESIS AND RESEARCH AGENDA



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Regulated Streamflow and Warmwater Stream Fish: A General Hypothesis and Research Agenda

by

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PREFACE

This review of literature and research needs was prepared at the request of the Chief of the Aquatic Branch, National Ecology Research Center, as part of the warmwater stream habitat research program of the Alabama Cooperative Fish and Wildlife Research Unit at Auburn University. It is also part of a new cooperative research effort involving faculty of Auburn University and the Auburn Field Station of the National Ecology Research Center. This report reviews literature relevant to impacts of streamflow modification on fishes and invertebrates in warmwater streams, outlines a broad hypothesis and testable predictions of modified streamflow effects, and identifies research needed for to develop impact assessment methods. Although this report is a product of the National Ecology Research Center funded program at the Alabama Cooperative Fish and Wildlife Research Unit, the research needs identified in this report are not limited to studies intended for the Alabama Unit and Auburn University. Rather, the broad research agenda provided here is intended to guide future agency efforts to thoroughly study, understand, and assess the consequences of streamflow alterations in warmwater streams.

Any questions, comments, or suggestions regarding technical and scientific aspects of this report should be sent to the authors at the address shown on the cover. Information regarding the current status and plans for warmwater stream research should be directed to:

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Introduction

Natural resource agencies in the eastern United States face continued pressure to develop and defend recommendations for preserving aquatic resources in warmwater streams and rivers. These demands are expected to increase markedly during the next several years as many hydropower projects undergo Federal relicensing. In surveys conducted to identify the stream research and assessment needs of Southeastern State and Federal agencies (Crance 1988) and of the Southeastern field offices of the U. S. Fish and Wildlife Service (Henriksen 1988), the most prominent issue related to warmwater streams appeared to be streamflow regulation associated with new hydropower development and the relicensing of existing facilities. Rapidly fluctuating flows, periodic dewatering, low flows, and reduced quality and quantity of habitat were the specific effects considered to be the most pervasive and significant threats to fish in warmwater streams and rivers.

Orth (1987) identified the Instream Flow Incremental Methodology (IFIM), described by Bovee (1982), as the state of the art in stream habitat assessment, and this methodology has frequently been used in warmwater streams for a decade (early applications were described by Orth 1980; Orth and Maughan 1981, 1982; and Stalnaker 1981). However, the IFIM approach and its basic components were developed on coldwater streams in the Western States where the primary issue was water withdrawal and minimum streamflow needs for coldwater fishes. Permanent allocation of stream water for off-stream uses threatened Western stream habitat for fish and aquatic life. Consequently, the development of assessment methodology emphasized minimum flow needs and the prediction of habitat conditions for specific flows. In the East, water withdrawal issues have been relatively uncommon or have involved short stream reaches bypassed by hydropower facilities. More important is the daily or weekly redistribution of streamflow for power production. Dramatically fluctuating streamflows make stream habitat unstable, and this instability appears to be more important than habitat limitations at low flows. Therefore, stream impact assessment needs in the East are much different from those that motivated earlier stream habitat assessment and the IFIM.

In the arid West, streamflow issues have been historically recognized as important and worthy of thorough scrutiny, probably because of the widespread concerns over water rights. Consequently, Western agencies are accustomed to complex, time-consuming, and expensive studies associated with decisions regarding water allocations and streamflow regimes. Although the protection and management of stream and river habitat is now an important natural resource concern in the East, the abundance of streams, rivers, and water in the region has helped make the impacts on individual streams seem relatively minor. Only recently has the effect of cumulative losses of stream habitats become apparent. In addition, the relicensing of many old hydropower facilities during the next decade presents opportunities for mitigating past impacts on streams and rivers impacts in almost all eastern States. However, many natural resource agencies in the East are not accustomed to expensive, time-consuming stream habitat studies.

A recent survey of Service field offices (Armour and Taylor 1988) indicated that many biologists believe that the application of IFIM is hampered by lack of trained staff and by high time and cost requirements. Wide acceptance and use of IFIM in the East cannot be expected unless the validity of the methodology is clearly demonstrated on Eastern warmwater streams, thereby justifying the cost of using the methodology and developing appropriate staff expertise. Stream assessment needs in the East require a method that is practical and can cope with species-rich, physically complex, and often large warmwater streams. Abundant evidence (discussed later) has shown that existing habitat assessment methods such as IFIM are not directly applicable to warmwater streams in the East. Rather than testing existing methods on warmwater streams, a more productive approach for Service and State biologists appears to be the development of a simpler, less costly stream habitat assessment method that incorporates some aspects of IFIM. This view is reinforced by considerations of the large number and diversity of hydropower sites to be evaluated in the next decade, the regulatory environment of Eastern stream assessment issues, and the resources traditionally available to agency biologists for warmwater stream protection.

The primary challenge in developing an impact assessment method for warmwater stream habitat is to appropriately capture the complexity of diverse fish communities in highly variable habitats in a practical, widely applicable model. A generalized and relatively simple model of a complex system is needed so that an assessment method can be developed for use by agency field biologists who have limited time, staff, and equipment. The appropriateness of any simplification depends on the degree to which it retains essential biological properties important in the mechanisms of stream impact. High species complexity can be reduced by using indicator species to represent the entire community, or by using multispecies groups (guilds) to reduce the number of fish types. Likewise, habitat complexity can be reduced by focusing on specific types of microhabitat or by categorizing habitat into broad types. Once warmwater stream systems are simplified into a general model, quantitative analysis can be conducted to determine the effects of streamflow regulation on habitat quality. Research results reviewed here suggest that a stream habitat assessment method could be developed that requires less precise and intensive modeling than commonly used in IFIM and still be predictive, quantitative, and biologically justified.

The National Ecology Research Center and the Alabama Cooperative Fish and Wildlife Research Unit have begun a 5-year research program to develop methods for assessing habitat changes caused by flow regulation in warmwater streams and rivers. Our general approach is to conduct studies on wamwater stream fish to identify general patterns of habitat use within fish communities, to use these patterns to quantify fish community response to habitat change from streamflow regulation, and to incorporate the findings into new or modified warmwater stream habitat assessment methods. In this report we have the following objectives:

- establish the need for new or modified warmwater stream assessment models,
- summarize past research on habitat use by fish in warmwater streams,
- evaluate multi-species groupings (guilds) for representing diverse warmwater fish communities,
- review present knowledge of regulated streamflow effects on warmwater stream fish,
- identify the importance of invertebrates to fish habitat research,
- develop a general hypothesis explaining the effects of flow regulation on fish communities, and
- outline specific research needs including studies beyond our capabilities and resources.

The integrity of aquatic habitats can be reduced by causes other than changes in physical structure and modifications in streamflow. Alteration of thermal regimes and degradation of water quality frequently have important impacts on stream fishes and their habitats. However, we are concerned here with changes in the composition and temporal variability of stream habitat. Water quality issues have received considerable study in the past and are relatively well understood; criteria for impact assessment are generally available and accepted (e.g., U. S. Environmental Protection Agency 1986). In contrast, the response of warmwater fish to physical habitat modifications is poorly understood, and there are no accepted models of fish-habitat relations for warmwater stream communities. Also, for the purposes of this report, we use the term habitat to refer to the physical structure of the aquatic environment used by a fish, and we do not include the chemical and biological factors associated with the environment used by fish. This definition of habitat has been the traditional one used in most of the habitat modeling literature. Throughout this report, the term coldwater is used to refer to streams characteristically thought of as upland, northern, salmonid streams and the term warmwater to refer to lowland, southern, species diverse streams. Whereas warmwater systems encompass a broad array of stream types, coldwater streams are commonly regarded as those that sustain significant populations of salmonids.

Need For Warmwater Stream Habitat Models

The Instream Flow Incremental Methodology is the most widely used stream habitat assessment method (Reiser et al. 1989); it is the accepted instream flow method in several western states (e.g., California, Washington, and Idaho), is well documented in agency manuals and handbooks, and is frequently discussed in published conference proceedings (e.g., Stalnaker 1979, 1981; Milhous 1984; Trihey and Stalnaker 1985). The papers in major journals that report on IFIM tests and applicatons have been written primarily by Donald Orth, who began working with the methodology in Oklahoma as part of his doctoral research (Orth and Maughan 1981, 1982, 1983, 1986). Orth's papers have been well received (Orth and Maughan 1982 was awarded best paper of the year in Transactions of the American Fisheries Society) and strongly criticized in some of the same journals (Mathur et al. 1983, 1985, 1986). More recently, Orth (1987) and Gore and

Nestler (1988) reviewed the criticisms of IFIM and fish habitat modeling. Controversies over IFIM have identified significant issues that should be considered when determining the need for stream habitat models. Beyond the controversies, there are clear biological reasons for expecting that models used to assess warmwater stream habitat will differ from models developed for coldwater streams of the western United States. Finally, the need for any habitat model is contingent on effectively relating model elements to the assessment of impacts. We review these topics (summarized in Table 1) to justify new research and the development of habitat models for assessing effects of flow regulation on warmwater stream fish.

Probably the most persistent and established criticism of habitat models, especially IFIM, is the lack of an established relation between predicted habitat quantity and population size (fish numbers or biomass). The complicated nature of population regulation for almost all species has long been recognized and was an important justification for the Fish and Wildlife Service adoption of a habitat-based impact assessment philosophy (outlined in U. S. Fish and Wildlife Service 1980). The Service approach for assessing fish and wildlife impact on the basis of changes in habitat quality and quantity acknowledged that many factors affect population levels, and that measures of habitat will not explain population levels at all times or even most of the time. Nevertheless, many biologists and IFIM critics maintain that a habitat model is not valid unless it can reliably predict at least relative population size (a highly rated research need by natural resource agencies [Reiser et al. 1989]). By accepting the charge to produce a quantitative, predictive relation between habitat and population size (generally expected to be linear), proponents of habitat-based assessment methods have created a seemingly inescapable situation: defending models with relations that the original modeling philosophy intended to circumvent. Professionally accepted and clearly defined interpretations of model outputs should preceded any future modeling efforts, and model outputs should not go beyond that needed to assess impacts of habitat change.

We regard habitat models as incomplete representations of factors controlling populations, and we acknowledge that habitat quality and quantity estimates will correlate with population levels under limited conditions that may not typically occur. This does not mean that habitat quality and quantity are not important. Whether populations are always or occasionally limited by physical habitat does not affect the need to preserve and assess habitat changes. In addition, habitat models used for impact assessment will not incorporate every habitat parameter that could be important at some time. Habitat models for impact assessment need only relate those habitat characteristics affected by a proposed action to the potential for a given area to support a species. Streamflow changes alter the composition of the available stream habitat for fish, so assessment methods need only relate anticipated changes in aquatic habitat to the potential of that habitat to support fish. This is a much narrower objective than commonly attributed to IFIM model output (a weighted area statistic with a positive, linear relationship with biomass or density), but one that satisfies the needs of biologists assessing stream habitat changes.

An issue related to the commonly expected habitat-population link is the lack of consideration given to biological factors such as predation, competition, and food (e.g., Moyle and Baltz 1985; Bowlby and Roff 1986). Undoubtedly, these biological factors and others are important determinants of fish population size, and research that we review later suggests how these factors influence habitat use by fish. Warmwater stream fish populations are controlled by multiple factors, including habitat, and the primary controlling factors often vary from year to year and from species to species. The modeling of all factors that determine the density of a species is rarely possible without extensive research. Comprehensive models that enable the prediction of fish densities should be the aim of research on understanding population regulating mechanisms and identifying appropriately simplified models of habitat. Only with detailed knowledge can researchers confidently develop generalized and practical models for use in regulatory studies by agency biologists who have limited time, staff, and budgets. In short, researchers should strive to quantify all factors commonly important to a species and use this information to develop practical assessment methods that focus on altered habitat characteristics and the consequences for fish habitat.

The IFIM incorporates species biology into established hydraulic models by using univariate functions labeled with terms such as probability-of-use, preference, suitability, and utilization. These univariate functions, which relate habitat quality to physical habitat conditions, have been one of the major aspects of IFIM that are frequently criticized. Many studies have demonstrated that fish respond to composite habitat conditions rather than to each habitat variable independently (e.g., Bain et al. 1982, 1988; Orth and Maughan 1982; Shirvell and Dungey 1983; Moyle and Baltz 1985). Therefore, multivariate habitat functions seem to be needed in both research and assessment. Multivariate habitat functions are not incompatible with existing hydraulic models and do not prohibit the development of practical assessment methods. Univariate functions were initially developed to easily combine species biology with existing hydraulic models

Table 1. Issues and criticisms involving habitat models with responses indicating necessary changes in modeling philosophy, protocols, or assumptions. See text for references to papers that discuss the issues summarized here.

Issues	Criticism of current models	Response to criticisms and necessary future changes
Population-habitat link	Little evidence that habitat units correlate with population levels.	Frequently true; this relation is not expected nor is it necessary for effective habitat modeling.
Role of biological factors	Habitat models neglect biological relations that influence habitat use.	True; habitat models are incomplete representations of a species environment and are intended to relate physical changes to the potential for a habitat to support a species.
Integrating habitat attributes with fish needs and preferences	Univariate suitability curves are overly simplified and inadequate.	Multivariate modeling format can be used without sacrificing model practicality. Relations need to be determined before model structure is selected.
Transferability of species-habitat relations	Models need to be parameterized on each system of interest and cannot be transferred from one case to another.	Models developed using common properties of diverse fish-habitat systems could be made general and transferable. Comparative research involving varied systems is needed to develop robust, transferable models.
Target species	The indicator species approach lacks a firm foundation and incorporates biases.	Target species should be used only when necessary and could be replaced by generic, multi-species groups indicative of natural system properties.
Warmwater vs. coldwater systems	Warmwater streams are fundamentally different from coldwater streams in both physical and biological properties.	The role of the physical environment in determining species populations probably does differ, and any differences need recognition. One type of model would not be expected to work in all types of streams.

and this development preceded the detailed studies of fish-habitat relations. Future method development should first identify fish-habitat relations and then select appropriate simplifications that capture essential biological responses.

Critics of IFIM have stressed that species-specific information used in the models is not transferable among different streams and regions, and many proponents of IFIM agree. The basic concern is the robustness of habitat models over varied geographic settings. There is little clear information to suggest the limitations for a set of species-habitat relations. Species-habitat studies have generally involved intensive studies at one or a few stream sites, rather than comparative research under varied stream habitat settings. The development of habitat models should involve studies in streams that vary widely in physical habitat characteristics, so that robust patterns of fish-habitat relations can be identified and used in model development.

Current stream habitat models and impact assessment methods rely on indicator (target) species for analysis. This practice has been effective in coldwater streams because the largest fish and top food chain species are frequently salmonids. Fortunately, salmonids have high public appeal, are sought by anglers, and support important commercial fisheries. The selection of target species for warmwater streams poses a major dilemma. The large fishes in most rivers and streams are species that draw little public interest (e. g., gars *Lepisosteus* spp., catfishes *Ictalurus* spp., and freshwater drum *Aplodinotus grunniens*) and support only limited fisheries. The primary sport species (many *Micropterus* spp., and various other centrarchids) do not appear sensitive to stream habitat change, thrive in impoundments, and tolerate degraded habitats. The indicator species approach leaves natural resource agency biologists two unappealing choices: (1) develop a position by using species of high public and angler interest and thereby risk a convincing counter argument that natural streamflow and habitat conditions are not needed, or (2) develop a position by using obligate riverine species generally regarded as rough fish or unimportant species (redhorses *Moxostoma* spp., cyprinids, darters, etc.) and risk being considered trivial. In arguing for preservation of native stream fishes, Sheldon (1988) summarized this problem by writing that "the common perception of all non-game fishes as 'minnows' and their existence in environments where few people ever see them makes it difficult to muster public support for their conservation." Therefore, a stream impact assessment method that relies on species-specific analyses may pose difficult problems for natural resource agencies dealing with warmwater streams. A method that is based on general riverine system values and characteristics, rather than on indicator species of high public interest, may provide a defensible and biologically sound argument for habitat protection and impact mitigation.

Landres et al. (1988), who reviewed the conceptual bases, assumptions, and guidelines for using indicator species, concluded that the approach is generally ineffective, lacks credibility, and should be avoided. Warmwater stream fish communities are typically species rich, further confounding the selection of appropriate indicator species. In addition, Leonard and Orth (1988b) demonstrated that species selection in IFIM studies can be misleading and intentionally biased. Habitat models developed for warmwater streams should not rely on target or indicator species because of practical problems associated with specific choices, varied fish responses to habitat change, and the difficulty selecting one or a few species to represent a diverse fauna. Rather, habitat models can be developed on the basis of co-occuring groups of species that use similar habitats (guilds). This approach would emphasize the diversity of warmwater stream fishes and contribute to the protection of general system properties and values.

The final issue related to the need for new or modified stream habitat models comes from the differences among coldwater and warmwater stream systems and fishes. There is clear evidence that the primary determinants of fish community characteristics differ between warmwater and coldwater streams. Research in warmwater streams reviewed later describes some properties that can be regarded as typical: large numbers of morphologically similar species that overlap frequently in microhabitat use; species composition that is influenced by atypical flow events (floods and droughts) and predation, and little apparent competition for food and space. Moyle and Vondracek (1985) described very different properties for a fish community in a small California stream and argued that these characteristics reflect coldwater stream fishes throughout North America. Their findings and a review of coldwater stream research portrayed coldwater fish communities as being relatively stable through time with strong segregation in use of space and food among relatively few morphologically and physiologically distinct species.

The differences between warmwater fishes in the East and coldwater fishes in the West are not simply regional variations. Observations of Grossman and his associates, who conducted extended studies on high elevation, coldwater streams in western North Carolina (Grossman and Freeman 1987; Freeman et al. 1988), reflected some aspects of coldwater streams in other regions (e.g., community stability of Moyle and Vondracek 1985) and contrasted patterns in many warmwater streams (e.g., flood- and drought-limited community as in Grossman et al. 1982). Unlike the observations in warmwater streams, the findings in coldwater studies in North Carolina indicated that relative species abundances were stable and probably regulated by density-dependent mechanisms. In general, the density-dependent control of coldwater fish populations through competition seems very different from warmwater fish dynamics that appear contolled by different factors over time ranging from brief climatic extremes (floods, droughts) to the predation effects of large piscivorous fish. Because control mechanisms in warmwater and coldwater communities frequently differ, it is unlikely that an impact assessment method suitable for coldwater systems will be directly appicable to warmwater streams, even if population prediction is not the objective.

Aside from mechanisms that structure fish communities, coldwater streams of mountain regions differ from Eastern warmwater streams in many important ways. Generally, coldwater streams are smaller, the gradients are higher, and the seasonal flow regimes are more stable than in warmwater streams. Streamflow in most warmwater streams is not heavily influenced by gradual, seasonal snowmelt. In contrast, Eastern warmwater streams are influenced more by short-term rainfall patterns and evapotranspiration rates. In general, the wetter, warm climate of the East, combined with differences in regional geology, makes stream and river hydrology very different from that in Western States. Consequently, stream impact assessment methods developed where seasonal flow regimes and channel characteristics are predictable may not be sensitive to short-term habitat dynamics in many warmwater streams. Therefore, future warmwater habitat models and assessment methods should be expected to depart from existing methods, and researchers should anticipate the need for innovation.

Some controversies of IFIM cannot be entirely avoided, but the process used to develop assessment methods can be designed to reduce problems of the past. Given that modified or new assessment methods are needed, thorough research identifying common properties of warmwater fish communities and their relations to habitat should precede the critical phase of constructing simplified, practical assessment tools. By presenting community-habitat findings, methods, and models to fisheries biologists throughout the research process and during the development of assessment methods, one should be able to (1) recognize potential and real problems before the assessment methods are defined, (2) identify necessary changes and options in assessment techniques, and (3) reduce criticism by building positive professional acceptance during the research and development effort. To us, this is the proper and most effective research mode for developing credible, effective, and practical methods for impact assessment.

Patterns Of Habitat Use In Warmwater Fish Communities

Moyle and Li (1979), who reviewed research on warmwater stream fish ecology, developed a general model of factors determining community structure. In Eastern streams with complex fish communities, habitat conditions and habitat variability appear to be the primary factors shaping community structure. In contrast, the structure in coldwater Western streams appears to be heavily influenced by the aggressive spacing behavior of salmonids. Moyle and Li outlined a lottery model for species-rich streams where the composition of species groups varies in response to recent environmental conditions. Under any particular set of habitat conditions, some species dominate and others remain uncommon. As conditions change, a new set of species dominates, although the general structure and relative abundance of different species groups remain fairly stable. This model of Moyle and Li (1979) was recognized as speculative because little information was then available at that time on many properties of warmwater fish communities.

In the Warmwater Streams Symposium (Krumholz 1981) only one paper (Paragamian 1981) included any quantitative data on species-habitat relations. Since that time, research on species-habitat relations for fish in warmwater streams has greatly increased. Syntheses by Ross (1986) and Schlosser (1987a) indicated that habitat may be the most important factor influencing fish composition and abundance, these studies also indicated that competition for food, and especially predation, can be important. Rather than attempt to summarize the broad and diverse literature on stream fish communities, we selectively review research that addresses patterns of habitat use, emphasizing results obtained in warmwater streams over several years.

James Karr and his students (primarily at the University of Illinois) have made several major contributions on fish-habitat relations in warmwater streams. The earliest well-known paper from this group (Gorman and Karr 1978) has been frequently cited as the justification for microhabitat studies organized around depth, velocity, and substrate use by stream fishes. The field studies they reported were conducted on streams in Indiana and Panama and indicated that habitat -- particularly horizontal heterogeneity -- was the primary determinant of community characteristics. Most species were found to require a particular set of microhabitat conditions, and human modifications of these habitats altered the nature (composition and temporal stability) of fish communities.

Gorman (1987, 1988a, 1988b), reporting on an Ozark stream, described how a group of five common minnows (e.g., *Notropis zonatus, N. boops, Campostoma* spp.) that numerically dominated the stream fish community, differed in the use of microhabitat. Large adult minnows used open-water, low-velocity areas (midstream sections of large pools) and were segregated on the basis of depth. Intermediate-sized fish used smaller scale, transitional habitats such as small pools and runs and small fish (mostly young-of-the-year) tended to live along the shallow margins of large pools. Gorman (1987) described the adult and small-size groups as complementary habitat-use guilds that were stable over time. The pattern of habitat use observed was attributed largely to predation risk where shallow edge waters provided refuge for small fish from fish predators and deep water provided large fish refuge from both aquatic and terrestrial predators. Later, detailed analyses of the pool fishes (Gorman 1988a) emphasized the importance of both vertical (depth) and horizontal (edge, open water) separation of size groups and species. Artificial stream experiments (Gorman 1988b), matching the field studies, indicated that community habitat use patterns were the product of species-specific habitat selection, modified by interspecific interactions. Overall, Gorman's work suggested that stream fish continually adjust their use of microhabitat in response to habitat configurations and encounters with other fish -- particularly potential predators.

After the initial work by Gorman and Karr (1978), stream fish research continued on low-order streams in central Illinois. Studies by Paul Angermeier (1982, 1983, 1985) and Angermeier and Karr (1984) directly addressed species-habitat associations in natural, modified, and experimental stream settings. The fish studied clearly preferred specific multivariate habitat configurations that varied somewhat by stream reach and year. In general, species-specific results could be summarized at the family level. Adult centrarchids tended to use deep, slow waters (large pools) and were less specific in microhabitat use in deep and slow stream reaches. Juvenile centrarchids and cyprinids were less specific in habitat use and occupied areas that balanced the benefits of food availability against the risk of predation. Some species, such as grass pickerel (*Esox americanus*), had no clear microhabitat preference. Angermeier (1987) concluded that fish community-habitat organization patterns can be detected when data are collected at the appropriate spatial and temporal scales and in the context of resource availability and use.

Extensive research on warmwater stream fishes in Illinois (Schlosser 1982a, 1982b, 1985, 1987a, 1987b) showed that channel morphology and flow regime appeared to be primary factors affecting a broad range of fish community characteristics. In terms of guilds defined by Schlosser (1982a), deep and slow stream reaches with large habitat volume were dominated by species classified as members of a pool guild (e.g., centrarchids, catostomids, bullheads *Ictalurus* spp.), raceway-pool guild (e.g., redhorses *moxostoma* spp., chubsucker *Erimyzon oblongus*, topminnows *Fundulus* spp.), and an insectivore-piscivore trophic guild (centrarchids, esocids). Shallow, low volume, riffle habitats were dominated by species in the riffle and raceway-riffle habitat guilds (primarily cyprinids, percids) and the generalized insectivore trophic guild (cyprinids). An overriding pattern of community-level habitat partitioning became evident (Schlosser 1982a, 1982b, 1985). Shallow riffle habitats further upstream were dominated by all ages of small species (cyprinids, percids) and the young of large species (centrarchids, catostomids). Large fish were concentrated in deep, pool habitats in the more downstream areas. For a particular stream site, variations in streamflow appeared to adjust the dominance of the two general types of fish. Later experimental stream studies (Schlosser 1987a, 1988a, 1988b) supported the hypothesis that small fish are restricted by predators to shallow waters and upstream low-volume areas.

Schlosser (1987b) developed a generalized pattern of habitat use and fish community structure for warmwater streams. In relatively shallow, low-volume, simple stream habitats, fish densities and species richness are low and dominated by small species and the juveniles of many species and the fish are distributed widely among available microhabitats. In relatively deep, high-volume, complex stream habitats, fish densities and species richness are both high, due to the addition of large fish. In these large and more stable stream areas, large fish are in deep, midstream waters and small fish are restricted to shallow water at the margins of pools. Stream areas that are intermediate between these extremes have the highest fish density because both small and large fishes are represented. The most important factors hypothesized to affect fish density and species richness for small fish in shallow habitats are physical stresses such as unusual streamflow events, whereas large fish are affected primarily by biological factors such as competition for food.

Extensive habitat-oriented research on stream fishes in low-gradient blackwater streams has been conducted on the souhtheastern coastal plain (Baker and Ross 1981; Ross et al. 1987). This research has produced a large set of habitat use data that suggest that different fish families followed a consistent pattern in using stream habitat. Centrarchids were in water with abundant cover (vegetation) and slow to moderate current. Cyprinids used areas of moderate current speed and smaller amounts of cover and, among cyprinids, habitat use differed most by vertical position in the water column. Percids lived in swift areas with coarse substrate. During the study period, the structure of the stream fish community (rank order of species abundances) remained basically consistent but microhabitat use patterns varied among stream sections and years.

Other investigators have reported significant data on habitat use by warmwater stream fishes. Multivariate analyses of habitat use by species in various stream reaches were conducted by Felley and Hill (1983) in the Illinois River, Oklahoma and by Felley and Felley (1987) in the Calcasieu River basin, Louisiana. Current velocity and cover were important for all species, and stream size was important to cyprinids. Many investigators (Fraser and Cerri 1982; Fraser et al. 1987; Power and Matthews 1983; Power et al. 1985; Gilliam and Fraser 1987) demonstrated that large predatory fish (e.g., spotted bass *Lepomis punctatus*) alter the habitat use of small fishes and that the effect is important enough to explain community-wide species-habitat relations in some streams. Other studies have reported that habitat variables such as cover, woody debris, water depth, and velocity are important habitat determinants for specific warmwater fishes -- e.g., smallmouth bass *Micropterus dolomieui* as reported by Probst et al. (1984) and McClendon and Rabeni (1987).

Because studies reviewed here differed considerably in study objectives, in field sampling methods and design, and in investigators background and interpretation, close agreement among the findings could not have been anticipated. Nevertheless, some general patterns of habitat use in stream fish communities became evident. Almost all the investigators indicated that habitat use in warmwater stream fish communities is clearly size related (small fish - shallow water, large fish - deep water). The hypothetical model of Schlosser (1987a) summarized this pattern and many investigators provided strong evidence that predation was the primary cause of it. The importance of vertical microhabitat position, and thus habitat volume, was seen in several studies, and non-traditional habitat variables (lateral position, vegetation, etc.) were sometimes important.

Implications For Impact Assessment

The findings of several independent investigators reflected a general pattern of habitat use for warmwater stream fish communities: small fish in shallow water, large fish in deep water. Current velocity and several other habitat variables were sometimes important but generally secondary to water depth. Several studies indicated that habitat variables need to be analyzed in combination rather than independently. Finally, though habitat characteristics appeared to be important in determining fish community characteristics, biological interactions such as predation may be important and could be the cause of the observed patterns of habitat use. In general, the research findings indicated that the complex relations between warmwater fish communities and stream habitat may be reduced by simple factors like fish size and broad habitat types -- suggesting that practical and biologically realistic assessment methods can be developed.

Research Recommendation

Patterns of habitat use within warmwater stream fish communities should be identified by using data from streams differing in morphology, flow regime, and species composition. By using data from diverse streams and communities, generalized patterns may be identified that could be used for developing robust impact assessment methods. Habitat variables need to be analyzed on a multivariate basis because past studies have indicated that fish respond to habitat configurations rather than to individual habitat variables. Finally, it appears likely that stream habitat analyses will need to be expanded from a two-dimensional (habitat area) to a three-dimensional (volume) format, due to the importance of depth and vertical habitat partitioning. Although a habitat volume orientation will complicate research and assessment analyses, the added complexity may be offset by using a few generalized groups of fish to represent fish communities.

Use Of Guilds In Stream Habitat Models

A practical impact assessment method for warmwater streams will require some means of simplifying the complexity of a fish community by reducing a large number of species to a relatively few types. The key to solving this problem lies in aggregating species into groups that represent the essence of the relations among stream habitat, flow regime, and fish communities. Aggregating species into functional or community structure groups is a common practice in ecology (e.g., herbivores) and fisheries management (e.g., coldwater fishes, forage species) but the relevance of a particular type of grouping is not frequently scrutinized relative to research and prediction objectives (Orians 1980). Stream fishes have been categorized into similar groups or guilds on the basis of trophic status (Grossman et al. 1982; Schlosser 1982a, 1982b; Angermeier and Karr 1983), foraging modes (Horowitz 1978), life history characteristics (Mahon 1984), and morphology (Gatz 1979a, 1979b, 1981; Mahon 1984). However, Orians (1980) argued that the prime consideration for species groupings should be the physical environment where a species evolved and to which it is presumably adapted. For impact assessment, species groupings should be sensitive to the environmental factors changed by the impacts being assessed.

Root (1967) introduced the term "guild" to label a group of species that use a resource in a similar way. Similarity of microhabitat can be used to form habitat resource groups or habitat-use guilds. Although this solution to high species diversity in warmwater streams seems intuitive and comfortable, the disadvantages should be reviewed to insure recognition of the trade-offs involved. In addition, there are important differences in what different researchers mean by guilds and how the concept can be validly and usefully applied to impact assessment.

Severinghaus (1981), who suggested a basis for using the guild concept in impact assessment, stated that "actions that affect environmental resources will similarly affect the members of the guilds using those resources. Once the impact on any one species in a guild is determined, the impact on every other species in that guild is known." He then developed a guild classification for mammals based on factors such as feeding strategy (for example, carnivorous, herbivorous) and behavioral patterns (e.g., gregarious or solitary). He concluded that the use of guilds in impact assessment would reduce study costs by eliminating the need to study the impact response of all members in a guild to a given environmental change. The guild concept as developed by Severinghaus and applied by others (e.g., Balon 1975; Johnson 1981) has been strongly criticized by Landres (1983) and Szaro (1986). We next review their main points and discuss some additional ones to indicate how the guild concept can be used for impact assessment.

Guilds are artificial constructs developed by investigators for specific analyses. Different species may overlap on some resource gradient such as habitat use or food type, but any observed similarity does not imply that a guild functions as a single ecological entity. Guild members may be closely similar in their response to one type of resource such as water depth, but differ with regard to other resources such as food items, feeding times, or reproductive habitat. Consequently, the response of one guild species to an impact does not mean that all guild members will have a similar response, and extrapolations from one species to a guild cannot be made.

To be consistent with the guild concept as defined by Root (1967) and further developed by others (Jaskic 1981; MacMahon et al. 1981), one must define guild membership on the basis of resource use -- not on other behavioral or functional characteristics such as feeding or reproductive behaviors (e.g., "broadcast spawner" does not refer to any resource use that would be shared among species displaying this reproductive behavior). For assessing stream habitat changes, a fruitful approach would be to identify habitat use for all species in a fish community and group similar ones into habitat-use guilds. This approach has been effectively used to simplify community complexity and elucidate community-level habitat use patterns (e.g., Pianka 1980; Short and Burnham 1982; Gorman 1987, 1988a; Bain et al. 1988). The response of habitat-use guilds to habitat change might then be used to assess the effects of habitat impacts on fish communities, without repeating detailed field studies on habitat use by fish.

Habitat-use guilds have been discussed relative to instream flow studies (Bovee 1982, 1986; Leonard and Orth 1988a, 1988b), although the recommendations provided have not been entirely consistent with the use of guilds as defined above. Bovee (1982) defined a guild as "a group of species having similar habitat requirements and exhibiting similar responses to changes in streamflow." The first part of his definition is consistent with the concept of a resource-based guild but the portion suggesting similarity of response to streamflow is not. The response of a habitat-use guild to streamflow can be established but it does not necessarily mean that all guild members will have the same response. The response observed for a guild of fish applies only to the guild as a whole and not necessarily to every guild member. The varied response by members of a habitat-use guild to habitat change was acknowledged by Leonard and Orth (1988a, 1988b) when they recommended studying more than one habitat-use guild species because of "within-guild variability." Again, a guild can be defined on basis of habitat use and its response to habitat change quantified; a guild then can be used for assessing habitat impacts.

Many investigators have defined fish guilds on the basis of habitat-use, others have suggested that responses to flow change could be used to define guilds. When considering this approach, Bovee (1986) recognized a "curious paradox": "the reason for identifying a guild is to develop criteria for the group as a whole, rather than studying each species individually. Without some knowledge about an individual species' habitat preferences, however, it is impossible to determine the guild it belongs in." In making these statements, Bovee suggested that species should be grouped on the basis of both their response to streamflow and their habitat use, which is consistent with his definition of a guild (Bovee 1982). Landres (1983) argued that strict adherence to the concept of resource-use guilds is necessary to avoid circularity in reasoning that seemed to be the cause of Bovee's "curious paradox." To be consistent, one should define guilds on the basis of habitat use and not on the basis of response to streamflow. If species are grouped on the basis of responses alone, the guild concept does not apply and the group should be termed something else (a "response group" perhaps).

One relatively minor problem with developing habitat-use guilds noted by Bovee (1986) relates to the spatial scale and animal range. By tradition, guilds have been discussed in terms of species groups and most past work has involved large areas relative to adult home range (e.g., birds in prairies or shiners in streams). However, habitat use changes considerably with life stage in many species. Consequently, many investigators have divided species into size groups or life stages that can be used as members in guild identification (e.g., Schlosser 1982a; Bain et al. 1988). Identifying guilds on the basis of life stages or size groups does not compromise the guild concept because these subcategories of a species can be considered as "ecological species" (Polis 1984).

A habitat-based assessment method for warmwater stream fishes should be based on models that transcend species-level population fluctuations and center on habitat needs to preserve community-level properties. A multispecies modeling framework may circumvent the habitat-population controversies of the past. First, it seems reasonable that a group of species using habitat in a similar manner (i.e., habitat-use guild) may show a more clear response to habitat change than that shown by any individual species in that group. When extraneous factors alter the abundance of one species (e.g., a small flood during the spawning season in one year, a disease outbreak, peak abundance of a key predator) during some brief life stage or time period in a manner inconsistent with habitat quality for that species, other guild members may not be affected in the same way and may compensate for the changing densities of other guild members. Extraneous variation in the abundance of guild members should also be ameliorated by averaging density across species. Finally, the effect of major habitat quality changes, of the type we wish to assess, should be strong on the majority of guild member species at any one time. The combined effect of several species responding in the same qualitative way (plus or minus) but to different degrees (quantitative response) may yield satisfactory whole-guild responses.

Implications For Impact Assessment

Application of the guild concept to habitat assessment offers a means of handling the typically large number of fish species and complex communities in warmwater streams. Research could identify microhabitat guilds that would probably reduce a fish community of 40 to 60 species to several groups (habitat-use guilds). Research that we reviewed earlier indicated that habitat-use guilds appear to be somewhat consistent among different warmwater streams, and that habitat-use guilds effectively summarize information on many species and may persist despite changes in fish density and species composition. The response (abundance or density) of these guilds to streamflow and habitat changes could be quantified at an affordable cost. On the basis of data collected in a variety of stream habitats, habitat-use guilds could be identified that have regional application. Future impact assessments would first anticipate changes in habitat and then predict changes in the abundance or density of different habitat-use guilds to indicate community-level consequences. The important trade-off that must be recognized is that stream impact predictions will not be attributable to individual species. An advantage of this trade-off is that predicted guild density changes are more likely to be realized because the effect of extraneous factors affecting a few species in a guild may be compensated by density changes in other guild members (the averaging effect of guilds).

Research Recommendation

The use of guilds for stream habitat research and the development of impact assessment methods appears warranted if the interest in community-level habitat assessment expressed by biologists of the U. S. Fish and Wildlife Service (Henriksen 1988) is to be pursued. Evidence suggesting that this approach has merit was demonstrated in the work by several investigators that we previously reviewed. The alternative of using indicator species would be complicated by the selection of useful species. Another alternative -- streamflow response groups -- would require long-term studies (≥10 years) to develop, and that alternative is a population modeling approach rather than a habitat-based approach.

Changes in streamflow or channel structure have a direct effect on habitat available for fish. Consequently, research and assessment based on habitat-use guilds is a relatively straightforward approach and appears less likely than the target species approach to be confounded by unmeasured and extraneous factors.

Fish Community Responses To Flow Regime

Quantitative studies on the response of warmwater fish communities to streamflow changes are rare. Observations and results from studies on species-habitat relations in stream fish communities provide some information on community-level responses to flow regimes. Researchers have documented the effects of unusual natural streamflow events (such as floods and droughts), and these results have some implications for the role of streamflow on fish communities. Finally, limited direct research has linked flow regime with habitat dynamics and warmwater stream fish communities. We next review the available evidence concerning the effects of natural and modified streamflow regimes on warmwater stream fish communities.

Major streamflow events such as large floods and extended droughts are known to cause significant change in the structure of warmwater fish communities (e.g., Starrett 1951; Larimore 1954; Lotrich 1973; Matthews and Hill 1980; Matthews and Styron 1981). More detailed analyses of large streamflow effects indicated that, although the relative abundance of different species changed in response to floods, the most abundant species remained as dominant community species (Matthews 1986) and many dominant species were flexible in microhabitat use (Harrell 1978). Similarly, Ross et al. (1985), who compared fish community structure in two Oklahoma streams differing in environmental stability (high streamflow variation versus more constant conditions), reported that species composition was persistent, but that relative abundances varied more in the stream with harsh, variable habitat conditions.

Warmwater stream research in Illinois (Schlosser 1982a, 1982b) related the relative abundance of small and large fish to seasonal stream discharge. Fish size closely corresponded with shallow and deep habitat guilds (Schlosser did not use the term guild, probably because he also analyzed fish abundances in terms of trophic guilds). Low streamflows in summer and early fall reduced the abundance of large, deep-water species and periods of high streamflow were associated with reductions in small, shallow-water fishes. In a Minnesota headwater stream, the abundance of small cyprinids increased with increased discharge, probably because of a variety of factors such as increases in food availability, habitat space and volume, and ease of upstream colonization (Schlosser and Ebel 1989). However, the intensity of predation on small fish by large cyprinids was not altered by increased discharge. Overall, changes in discharge appeared to affect stream fish abundance, although predator-prey relations and habitat use patterns were not strongly altered.

Bain et al. (1988), who investigated the effects of artificial flow fluctuations on a warmwater fish community, classified small species and some early life stages of large species as members of a shallow, slow-water guild found primarily along stream margins. This guild included over 90% of all fish in the natural New England warmwater stream. Other fish included generally large individuals that used deep or fast water primarily in midstream areas, or were species with no specialized use of microhabitat. Artificial streamflow fluctuations appeared to reduce and eliminate shallow, slow guild fishes and increase the abundance of other species. Evidence for this pattern of effects was developed by comparing guild and non-guild fish densities between regulated and unregulated streams and study sites along a gradient of flow fluctuation intensity. Therefore, the research results from the Midwest and Northeast indicate that warmwater stream fish communities respond to flow changes consistently, and that community-level response can be explained by using a few habitat-use guilds.

Specific mechanisms responsible for flow-related reductions in fish abundances are poorly documented. For large fish in deep water, emmigration to downstream areas is a likely mechanism explaining reduced densities found during low flow periods (Schlosser 1982a). The reduction of small, shallow-water fishes associated with flow changes could be attributed to several causes: peak flows could displace small fish downstream (Harvey 1987); and reductions in streamflow could make small, shallow-water fishes vulnerable to predation (Schlosser 1982a, 1987; Schlosser and Toth 1984; Bain et al. 1988) and susceptible to stranding (Kroger 1973; Bain et al. 1988). Despite uncertainty about how fish abundances are changed when streamflows change, research reviewed here suggests that consistent patterns of community-level responses can be identified.

Implications For Impact Assessment

Warmwater fish communities appear to respond to streamflow changes, and a few habitat-use guilds could be used to model these responses. If the soundness of this approach can be demonstrated by additional field studies in a variety of stream types, a simple framework for describing community-level responses to flow changes can be developed. Once a simplified and biologically meaningful community-habitat framework is defined, predictions of the effect of stream habitat impact can be developed without repeating detailed field studies in every case.

Research Recommendation

Enough evidence is available to justify research on the detection and prediction of community-level responses to flow changes. In previous stream fish community studies, the guilds were defined on the basis of trophic status and habitat use. The habitat-use guilds appear to be more relevant and sensitive to streamflow patterns and should be used in future studies aimed at developing a habitat-community analysis framework. Fish size has been implicated as an important factor correlated with habitat use. This finding needs further study as part of any effort to identify fish community responses to streamflow changes based on habitat-use guilds. If fish size and habitat use seem to be related in future studies, this relation could justify dividing fish communities into a few habitat use guilds. This decision would produce a simple format for analyzing streamflow modification effects.

Importance Of Macroinvertebrates

In a major textbook on stream ecology, The Ecology of Running Waters, Hynes (1970) heavily emphasized macroinvertebrates. This emphasis may be partly attributed to the author's research interests but was justified by the extensive research on invertebrates by stream ecologists before the 1970's. Hynes thoroughly reviewed the existing literature and formulated some general conclusions that now encompass many of the accepted concepts of the ecology of stream invertebrates. Because studies discussed were conducted primarily on coldwater and coolwater streams of Europe and North America, many of the generalizations developed may not apply to warmwater streams.

Hynes (1970) focused largely on the aquatic life stages of insects because this group generally constitutes the majority of stream macroinvertebrates. Among the many physicochemical factors that may affect invertebrate biomass in streams, the most important ones are generally water velocity, substrate, and temperature. Temperature is probably more important for coldwater stream invertebrates where their distribution is limited by warm-water. Velocity and substrate are interrelated and together explain the distribution of invertebrate biomass fairly well. The densities of invertebrates are highest in areas of moderate water velocity and are depressed in stagnant areas that only occasionally have current during spates or floods. The most productive substrates are coarse (cobble and pebble), stable, and have a high surface area in contact with water; the least productive ones are fine, shifting substrates such as silt and sand. The combination of moderate water velocity and coarse substrate are usually the productive stream habitat and the poorest conditions are still waters and fine substrates in backwaters and large pools. This general pattern is used to explain the dogma that riffles are the high productivity microhabitats that drive stream systems.

Hynes also described other patterns of invertebrate distribution in streams. His "width effect" referred to the midstream-bank pattern of invertebrate biomass density documented in many streams. In streams wider than about 7 to 10 m, invertebrates are densest in shallow water along the stream margins. In smaller streams, the pattern is reversed, the invertebrate biomass being highest in midstream. Observations by Elliot (1971), Hayden and Clifford (1974) and Peckarsky (1983) also indicated that a midstream to bank pattern occurs in streams of different size. The general distribution of water velocity and substrate composition in different-sized streams probably explains the width effect pattern. Streamflow regime is also recognized as an important stream property affecting invertebrate biomass and species composition. Hynes concluded that droughts and floods generally deplete the biomass and diversity of stream invertebrates by stranding organisms of flushing them out of a specific stream reach.

Most studies of invertebrates reviewed by Hynes (1970) were conducted on high gradient, coldwater streams; relatively few were made on warmwater streams. However, several studies on high gradient streams in the South (e.g., Gurtz et al. 1980; Haefner and Wallace 1981a, 1981b; O'Hop and Wallace 1983; Webster et al. 1983; Gurtz and Wallace 1984; Huryn and Wallace 1987) generally agreed with Hynes' generalizations by indicating that velocity and substrate are key factors influencing the distribution of invertebrates and that riffle areas are the most productive habitats. In addition, stream habitat changes in flow regime and sediment erosion and deposition resulting from forest cutting selectively effected invertebrates that depended on substrate stability. When a watershed was logged, the density of stream invertebrates declined in unstable sand substrate but increased in stable substrates composed of cobble and pebbles.

Although invertebrates in high gradient southern streams appear to have typical distribution patterns, the patterns differ in warmwater streams of the Atlantic coastal plain (Cudney and Wallace 1980; Wallace and Benke 1984; Benke at al. 1984a, 1984b; Benke et al. 1985; Smock et al. 1985; Benke et al. 1986; Benke and Meyer *in press*). Coastal plain streams have low gradients, little or no stable coarse substrates (cobble, pebble, gravel), abundant shifting-sand substrates, annual floodplain inundation, and significant instream woody debris. Estimates for invertebrate production are high -- contrary to the general notion that coastal plain streams are unproductive. The estimated production of invertebrates on woody debris is as high as estimates published for any stream habitat and appears to be limited only by the availability of wood surface (woody debris constituted <10% of stream substrate surface). On a surface area basis, the invertebrate biomass is 20-50 times higher in woody debris than in sandy substrates and 5-10 times higher in muddy habitats. Invertebrate communities on woody substrates are diverse and include most of the invertebrate species found in the study rivers. Finally, invertebrate drift primarily originates from woody debris substrates and constitutes most of the food eaten by drift-feeding fishes. Obviously, woody debris in low-gradient, coastal plain streams is a key to overall biological productivity.

Woody debris is concentrated along the margins of coastal plain rivers and streams, especially in erosional areas such as the outside edge of stream bends. During low-flow periods, much of this productive habitat may be dewatered, but invertebrates quickly recolonize woody surfaces when they are re-inundated. The concentration of wood debris on the edges causes stream margins to be areas of high invertebrate productivity. Midstream habitat is composed largely of rather unproductive sandy substrate. This distribution pattern coincides with the width-effect generalization of Hynes (1970) that predicted high edge productivity in wide streams.

Stream fishes are known to feed heavily on invertebrates, both on the stream substrate and in the drift. However, there is little clear evidence that the availability of invertebrates is limiting to fish production in streams or that fish have a significant effect on invertebrate densities in streams (Allan 1983; Reice 1983; Flecker and Allen 1984; Culp 1986; Reice and Edwards 1986). Recently though, Gilliam et al. (1989) demonstrated that fish can alter the composition and abundance of invertebrates in warmwater, soft-sediment streams. They attributed their atypical results to habitat differences (primarily in substrate) because most past studies showing weak fish effects were conducted on high gradient, coarse substrate streams. Schlosser and Ebel (1989) found that fish in a small, warmwater stream reduce invertebrate abundance, though the effects were significant only in pool habitats. These recent studies indicated that the repeatedly documented ineffectiveness of fish predation on invertebrates may be limited to stony, high gradient streams and that significant predation occurs in warmwater streams with low gradient and fine substrates. Consequently, fish production in warmwater streams may depend on invertebrate production, and factors that reduce invertebrate abundance or habitat quality could adversely affect fishes.

Flow fluctuations have been shown to alter invertebrate communities, even though many invertebrates have adaptations for streamflow variability such as high rates of migration, drought-resistant eggs, and use of the hyporheic zone as a refuge from dessication (Delucchi 1988). Artificial flow fluctuations have been found to alter the periodicity of insect drift (Minshall and Winger 1968; Gore 1977; Matter et al. 1983; Irvine 1985) and change the composition of invertebrate communities (Armitage 1978; Hauer and Stanford 1982). Community changes typically involve reductions in the abundance of insects from families adapted to swift currents (e. g., some Ephemeroptera and Plecoptera) and increased abundance of taxa tolerant of stressful aquatic conditions such as Diptera and especially chironomids (Trotzky and Gregory 1974; Williams and Winget 1979]). The rate of dewatering along nearshore areas is related to the extent of diversity and density reductions (Fisher and LaVoy 1972; Gersich and Brusven 1981), and desiccation is a clearly documented mechanism (Fisher and LaVoy 1972; Kroger 1973). In a review of fluctuating streamflow impacts, Cushman (1985) concluded that past research has demonstrated that the diversity, density, biomass, and mean size of invertebrates are all reduced by rapidly changing streamflows, and that the patterns of change are generally evident at the family level.

Implications For Impact Assessment

Invertebrates are clearly an important component of warmwater stream systems and are susceptible to alteration by regulated streamflow. Protection of this resource may be important for retaining the natural biological organization of warmwater streams but the influence of invertebrates on fish communities remains ambiguous. The streams in which invertebrates appear to be most vulnerable to flow fluctuations are slow, sandy, and low-gradient with wide, gradually sloping shores. In these systems, invertebrate diversity and biomass are concentrated in nearshore areas, especially on wood debris, and invertebrates are vulnerable to stranding when water levels recede. Invertebrates would be least vulnerable in small, high gradient streams because biomass is concentrated in coarse substrate of midstream areas.

Research Recommendation

Although flow regulation has been clearly shown to alter invertebrate communities, few studies have documented that invertebrates constitute a limiting resource for fish populations in warmwater streams. However, there is almost no thorough research to document this for all components of a stream fish community, and there is no thorough research on interactions between invertebrates and fish in highly modified and flow-regulated streams. Research on invertebrate production in nearshore habitats of large streams, especially coastal plain rivers, that are affected by dramatic flow fluctuations should produce clear results on invertebrate impacts.

A General Hypothesis

Research findings to date, combined with some reasonable assumptions, could be used to develop a general hypothesis or conceptual framework of the effects of regulated flow on fish and invertebrate communities. Such a general hypothesis -- an informed but unaccepted explanation of effects and relations based on a synthesis of existing knowledge -- would provide a basis for designing research composed of a series of specific and related hypothesis tests. Like any hypothesis, the one presented here requires objective testing, modification, and evaluation by the fisheries biology and aquatic ecology professions before it can be accepted as useful and valid. We pose a general hypothesis to justify research outlined later and to begin a critical evaluation of presumed relations.

Following the management issues identified by Armour and Taylor (1988), Crance (1988), and Henriksen (1988), we direct the general hypothesis of flow regulation effects at rapidly fluctuating streamflows generally associated with hydroelectric dams and peaking discharges. From the research reviewed, we offer the following general conclusions.

- The pattern of fish community structure and habitat in warmwater streams is simple: small fish are heavily concentrated in shallow, low velocity, nearshore microhabitats and large fish are concentrated in deep, midstream habitats.

- The simple size-related pattern of habitat use by fish is most likely caused by predation of large fish on smaller fish that seek refuge in shallow, nearshore areas. In addition, fish predation and variability in physical habitat generally reduce the density of small, shallow-water fishes to lower levels than would be imposed by only food availability and competition.

- Sensitive to flow change is greater in small, shallow-water fishes than in large, deep water fishes because of the habitat of small, shallow-water fishes is strongly affected by flow changes.

- The three most likely adverse effects of rapidly changing streamflows on small, shallow-water fish are increased predation during flow changes, stranding during declining flows, and downstream flushing during rapidly increasing flows.

- In large streams, high concentrations of invertebrates coincide with high concentrations of fish: small, shallow water fish and most invertebrates live in nearshore areas, especially where there is coarse substrate, cover, and wood debris.

- The diversity and density of inverteberates are severely reduced by fluctuations in flow in nearshore areas periodically dewatered.

In addition to the conclusions supported by the research reviewed earlier, the following generalizations can be made from common knowledge about stream processes.

- Streamflow changes more adversely affect shallow, nearshore habitats than midstream habitats because the shoreline areas move laterally as stream discharge increases or decreases.

- Some fish species are habitat generalists and are able to persist in highly variable, stressful physical environments. Such species frequently maintain viable populations in lakes and streams. In general, centrarchids are habitat generalists because they not only live in lotic and lentic systems but also persist or increase in relative abundance, in stressed and modified habitats (e.g., Goldstein 1981; Pflieger and Grace 1987; Rutherford et al. 1987; Bain et al. 1988).

- Some fish are obligate riverine species that have very specific requirements for flowing water at some life stage. On average, these species will be most affected by flow fluctuations and other modifications in stream habitat. Many percids (darters), catostomids and cyprinids are in this group.

- In stream reaches below peaking hydroelectric facilities, there is a gradient in severity of habitat modification as the frequency and severity of flow fluctuations decreases downstream.

The above conclusions and assumptions constitute the elements of a general hypothesis of the effects of streamflow regulation on warmwater stream fishes. A concise statement of the general hypothesis follows:

> Fluctuating streamflows change the densities and species composition of fish and invertebrates differently in nearshore and midstream habitats, and the extent of that change depends on the characteristics of the unmodified habitat and flow regime.

From this general hypothesis, we make several specific predictions that are themselves hypotheses to be tested.

Prediction 1: Fluctuating streamflows reduce the diversity and biomass of fish and invertebrates in nearshore habitats.

Shallow, nearshore habitats are used by many small fish species and early life stages of large size species. These fish appear to be restricted to shallow-water for refuge from predators until they attain a size that minimizes predation risk. Under fluctuating flow regimes, shallow habitats move laterally in the stream channel, requiring small fish to move accordingly (Figure 1). On rising flows, shallow areas move away from the stream center, and areas that were shallow become deep. Fish that do not move to maintain position in shallow water are exposed to higher water velocities that may displace them downstream, and become increasingly vulnerable to predation as water depth increases. When flows decline, shallow habitats become dewatered and fish using these areas must move toward midstream or be stranded. Rapid flow fluctuations force small fish to move continually and thus expose them to increased risks of displacement, stranding, and predation. Flow fluctuations would similarly affect invertebrate populations in large streams, where biomass and production are highest in nearshore habitats. Because invertebrates are less mobile than fish, stranding during low flows is almost certain in periodically dewatered areas.

Density reductions affect small species most because these fish complete their entire life cycle in shallow water and thus are exposed to variable habitats throughout life. Large species that grow quickly to sizes large enough to safely occuppy midstream habitats should be less affected. In general, the species composition of the nearshore fish assemblage should shift from one dominated by small species (e.g., cyprinids and percids) to juveniles of species that use midstream habitats as adults (e.g., *Micropterus* spp.).

Prediction 2: Fluctuating streamflows will not markedly effect the biomass of midstream fish and invertebrates although species composition will be dominated by habitat generalists or species that migrate at some life stage.

Streamflow changes generally alter midstream depths and velocities but do not cause deep, main channel habitat to move as nearshore habitats do (Figure 1). While large, midstream fish that prefer specific water depths and velocities, reduced streamflows only make their habitat shallower or deeper and current slower or faster. Consequently, the direct effects of streamflow changes on midstream fish can be expected to be much less than those on nearshore fish. However, midstream fish densities would probably change due to the indirect effects of reduced recruitment from the juvenile life stage (generally shallow, nearshore fish) and possibly reduced the abundance of forage fish (shallow, nearshore fish).

Species with broad habitat requirements or high stress tolerance would probably dominate midstream fish assemblages with fluctuating flows and might increase in density relative to streams with unregulated flows. Species that migrate upstream for spawning (e.g., during spring high flows) or that tend to move about considerably as adults may be an important part of the midstream fish assemblages in highly regulated streams. Migration tendency may be a very important factor in determining midstream fish populations in stream reaches that are unable to support conditions for all life stages (in particular, juveniles). Obligate riverine fishes, species sensitive to stress, and microhabitat specialists would tend to be most affected by flow regulation at some point during the life cycle and might be absent or reduced in midstream habitats.

The biomass, diversity, and productivity of invertebrates are lower in midstream substrates of large streams than they are in nearshore habitats. The same reasons used to hypothesize that midstream fish would experience relatively low stress from flow changes can be applied to invertebrates. Midstream invertebrates of large streams are probably adapted to fine, unstable substrates and various water depths and velocities; consequently, a qualitative change in these habitats would be less of a problem than a habitat that physically moves as nearshore areas do.

Prediction 3: In regulated rivers, a gradient in species composition and biomass of fish and invertebrates will be evident as the effects of flow regulation diminish downstream.

Predictions 1 and 2 are hypotheses of fish and invertebrate communities at sites of high flow fluctuation near peaking hydroelectric plants. Downstream from these facilities, flow regulation attenuates as tributary inflows reduce low flow conditions and the rise and fall of streamflows spread out over time and distance. Consequently, fish and invertebrate communities should gradually change from highly modified in river reaches near peaking hydroelectric dams to unmodified in areas where streamflows approximate natural conditions (Figure 2).

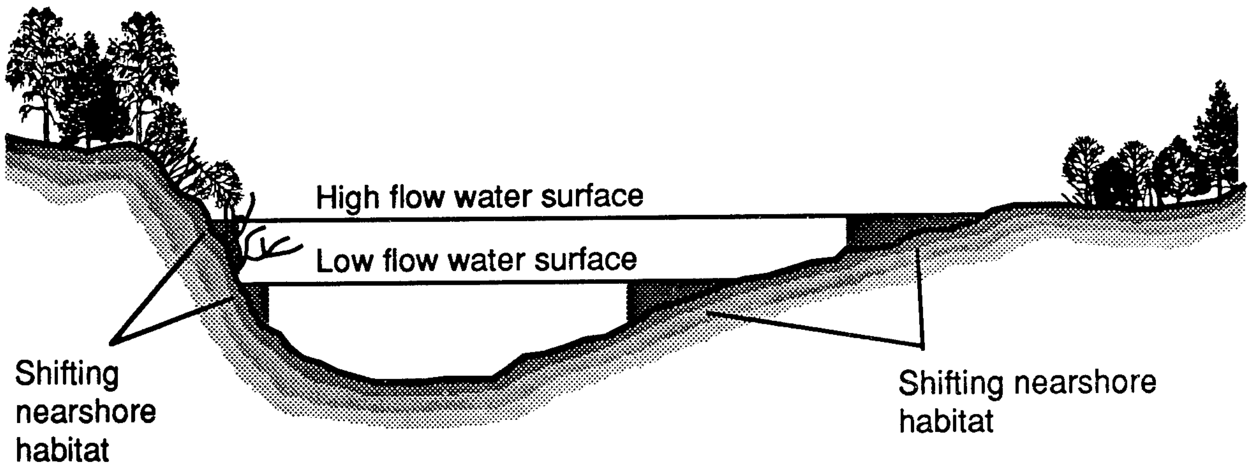

Figure 1. Hypothetical stream cross-section showing shallow, nearshore microhabitats that relocate in response to stream discharge. Fish using these microhabitats are forced to move to maintain constant habitat conditions.

Upstream river reaches should have sparse and low-diversity fish assemblages in shallow, nearshore habitats and midstream fish assemblages should be present in moderate or low densities and be dominated by habitat generalists and species common in lentic habitats. The biomass and diversity of invertebrates should be low in upstream nearshore areas and typical in midstream habitats, where invertebrate fauna is dominated by inhabitants of soft, low stability substrate (e.g., chironomids). Downstream from a peaking hydroelectric dam, nearshore fishes and invertebrates should increase in abundance and diversity and a similar, but much less pronounced, trend should be found in midstream habitats. No clear gradient would be expected the composition or biomass of midstream invertebrates. Overall, the relative abundance of obligate riverine fishes should increase downstream from peaking hydroelectric dams.

Prediction 4: Stream sensitivity to flow regulation effects will be determined by the characteristics of the physical habitat and the flow regime.

Physical habitat characteristics and flow regime should determine the sensitivity of a stream fish fauna to the effects of streamflow regulation impact in regions where potential species lists are as large as those commonly found in warmwater streams (frequently more than 20 species). Variability in natural habitat conditions influence fishes and invertebrates and would therefore be important in determining the sensitivity of a stream fauna to habitat change. Although mid-size warmwater streams (between coldwater, small order streams and large floodplain rivers) are characterized as having highly variable habitat conditions, these streams differ in habitat variability as a consequence of the composition of channel material and flow regime. Streams with highly stable flows (such as those in a forested watershed with abundant groundwater inflow) and stable streambeds (bedrock, boulder composition) provide a nearly constant stream environment. Such streams should have a fish and invertebrate fauna that is consistent through time and dominated by species adapted to the conditions usually present. Deviations from the usual habitat conditions in a fairly constant environment could be expected to result in marked faunal changes. As stream habitat increases in natural variability, either due to variable flows or unstable stream bed structure, fish and invertebrate communities could be expected to vary more over time and be less sensitive to habitat changes. Under changing stream habitat conditions, some species increase as a given set of conditions occurs and others decline. Artificial habitat variability would need to be large and continual to overshadow natural levels of habitat variability.

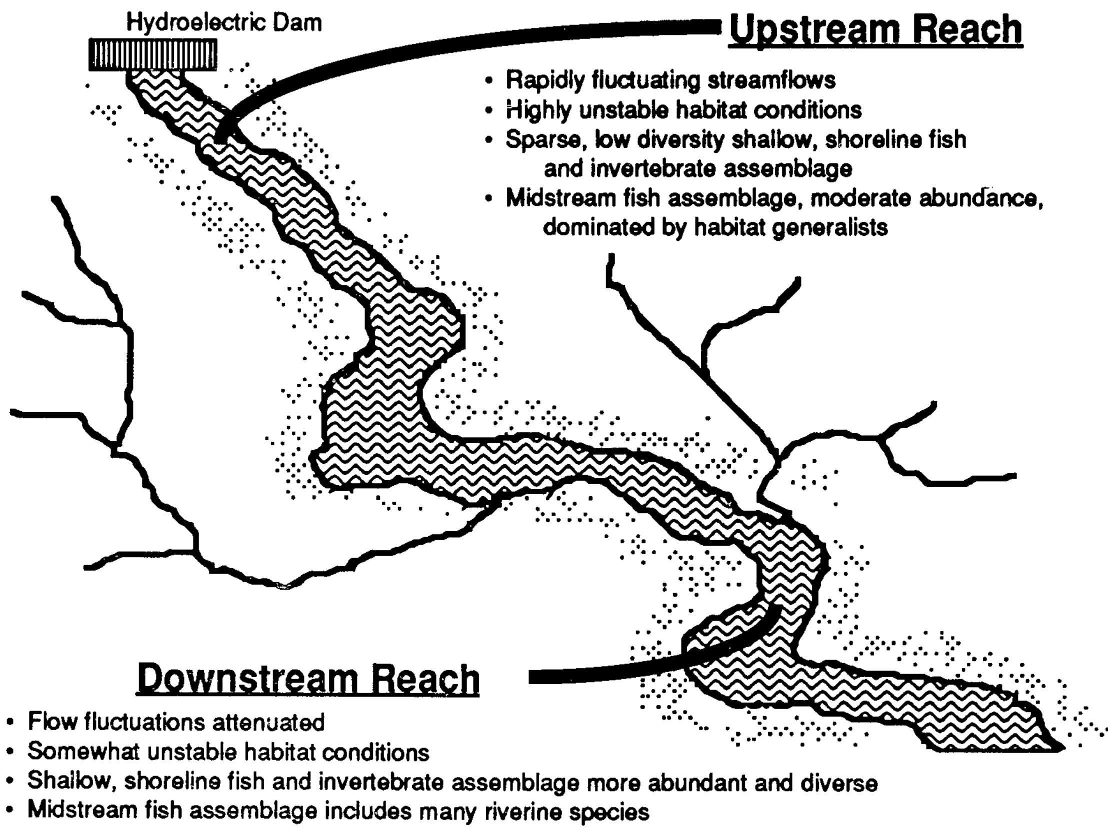

Figure 2. Hypothetical characteristics of stream reaches near and well downstream from peaking hydroelectric dams. Characteristics listed for each area represent extremes of a gradient that would gradually change through a modified river reach.

Because both stream channel structure and flow regime contribute to the stability of stream habitat, a generalized framework can be used to identify stream types most sensitive to the effects of artificial flow regulation (Table 2).

Another factor that would influence the susceptibility of stream fauna to the effects of flow regulation would be the size and number of tributary inflows in a given river reach. Rivers with numerous and large tributaries near peaking hydropower dams could be expected to have short gradients of faunal recovery. Tributaries would not only contribute flow volume to reduce the effects of low flows in the mainstream but would also be sources of fish and invertebrates for mainstream colonization by immigration. Overall, the configuration of the drainage basin and habitat stability interact to determine the susceptibility of a particular stream reach to the adverse effects of flow fluctuation (Table 2).

Prediction 5: The composition of fishes and invertebrates will be less stable in regulated than in unregulated rivers.

Although it is accpeted that biological communities in streams vary over time, the extent and type of variation (random versus cyclic) has been actively debated by ecologists. There is general agreement, however, that changes in the stream environment result in faunal changes that persist for a measurable length of time. Changes in stream habitat caused by streamflow events (e.g., droughts, floods) and seasonal changes in streamflows are accompanied by changes in biological communities. In spring, for example, many species repopulate stream segments previously abandoned during summer low flow periods.

Some factors responsible for variability in species composition in natural streams are likely to remain important in regulated streams. Many peaking hydroelectric dams have little effect on natural spring streamflows, since river discharge can exceed plant capacities. The usual spring fish migrations and spring post-flood fish and invertebrate re-distributions are likely to occur in a regulated river. However, the start of fluctuating streamflows in late spring or early summer will then effects stream faunas. The artificial plus natural variability brings total variability to very high levels.

The reduction in biomass and species diversity predicted earlier would create underused habitats that might be rapidly colonized during periods of non-fluctuating streamflows. For example, adult fish may spawn and produce larvae during a short period of stable streamflow (<1 week) and these larvaemay occur in large numbers for some time. Also, tributaries may serve as a source of fish that are regularly extirpated from a regulated river reach. Consequently, some species may colonize a regulated river reach and persist there temporarily, thereby adding to variability in faunal composition.

Research Needs

Understanding and modeling the relations between streamflow regime, warmwater stream ecology, and fish and invertebrate populations will require considerable research on many aspects of the biology of fish and invertebrates. Past information and models on hydraulics (aquatic habitat simulation) and water quality were developed for a broad range of lotic systems and can be used on warmwater streams. In contrast, many ecological properties of warmwater streams and rivers have been poorly studied and may differ from the typical coldwater streams most often studied in the past. Research needs identified below address either the general hypothesis developed in the preceding section or biological aspects of regulated stream systems poorly documented in the existing literature.

General Hypothesis Testing And Modeling

The general hypothesis and associated predictions offered are an outline for research directed toward understanding the effects of flow regulation on warmwater stream habitat and fish communities. However, to satisfy U. S. Fish and Wildlife Service needs to assess the impacts of streamflow regulation,

Table 2. Stream characteristics hypothesized to influence the sensitivity of the fauna to regulated streamflow impacts. The fish and invertebrates of high sensitivity streams would be expected to have a clear, negative response to flow regulation while low sensitivity streams would be resistant to regulated flow effects.

Characteristics	Streams with low sensitivity to flow regulation effects	Streams with high sensitivity to flow regulation effects
Annual discharge variance	High	Low
Low flow conditions (natural)	Low	High
Groundwater seepage	Low	High
Flood frequency and magnitude	High	Low
Channel stability	Low, meandering	Stable, bedrock
Substrate	Fine material	Large elements
Tributary frequency and size	High	Low
Channel form	Narrow	Broad
Pool/riffle structure	Well developed	Indistinct
Average depth	Deep	Shallow
Depth variance	High	Low

research would have two additional objectives: (1) to develop a model of fish community-habitat relations, and (2) to simplify the model for practical use in stream impact assessment studies. All objectives could be achieved in a three-phase research program (Figure 3):

(1) Quantify fish community-habitat relations and express them as a model,

(2) Quantify fish and invertebrate community responses to flow regime changes in the context of the model, and

(3) Develop a practical and generalized model for warmwater stream impact assessment.

The first phase would quantify species-habitat relations for common fishes, identify community-level patterns of habitat use, and reduce the complex fish fauna to a few fish types (habitat-use guilds). This can be done with data collected by sampling stream microhabitats for all fish and measuring habitat characteristics. Multivariate statistical procedures could be used to determine if species presence or abundance is related to microhabitat characteristics and to classify fish into habitat-use guilds. Once a generally applicable set of habitat-use guilds is identified, stream microhabitat could be classified into general categories. To identify the role of macrohabitat factors such as stream channel stability, productivity, and flow regime, stream sites could be selected in different ecoregions within a large river basin. If stream macrohabitat was not a significant variable, fish and habitat relations would hold for a broad range of warmwater streams and if macrohabitat is important, very generalized relations would need to be identified. Taken together, a guild-habitat classification would constitute a model of fish community-habitat relations in warmwater streams.

The second research phase would identify fish community responses to flow regulation by using the community-habitat model (habitat-use guilds and habitat types) and field data from regulated and unregulated streams. Estimates of fish density and diversity for each habitat-use guild in each habitat type would show how flow regulation affects warmwater fish communities. In addition, the responses of invertebrates would be investigated as a component of fish habitat. As in fish, the density and diversity of invertebrates would be quantified in each habitat type and compared among sites differing in flow regime. Together these tests would determine the pattern of impact from fluctuating flows on fish and invertebrates so that more detailed work could quantify the relation between severity of flow regulation and effect on the fish community.

To quantify the relation between the extent of flow fluctuation and the severity of impact, investigators would use the gradient of flow regulation intensity that occurs on regulated streams. By intensively sampling along a gradient of regulated flow impact, sites with different degrees of impact could be identified. Through detailed studies at a few sites, one might relate some measure of habitat availability and stability to guild fish density. This would provide a quantitative relation between the degree of flow regulation, change in habitat quality, and effect on the fish community. The model and quantitative habitat-flow criteria would constitute the basis of an impact assessment methodology.

The final phase would produce a practical, documented, and transferable impact assessment method. This phase would center on simplifying previously quantified relations so that essential fish community aspects and responses are represented in models with practical application value. Refinement and additional field testing would be expected, although studies preceding this step should justify the utility of the methods.

Regulated Stream Biology

Many aspects of the biology of warmwater streams are inadequately documented and may have significant implications for assessing the effects of streamflow regulation. The research needs outlined in Table 3 and reviewed here may explain patterns in the response of warmwater stream fish communities to streamflow regulation or identify necessary modifications to the general hypothesis proposed above. Although recommended studies tend to be more specific than the testing of a general hypothesis and development of an impact assessment method, the studies are important to an understanding of the mechanisms of impact and consequences of flow regulation.

Many stream fishes, particularly obligate riverine species, have specific stream habitat requirements and environmental tolerances. Recognizing and predicting the impacts of streamflow changes on individual species will be important for endangered species and species of high public concern. Studies are needed to determine the mechanism of impact and life history stage of sensitivity to environmental change. Species-specific studies will be able to address only a few species because of the wide variety of potential species for investigation. Consequently,

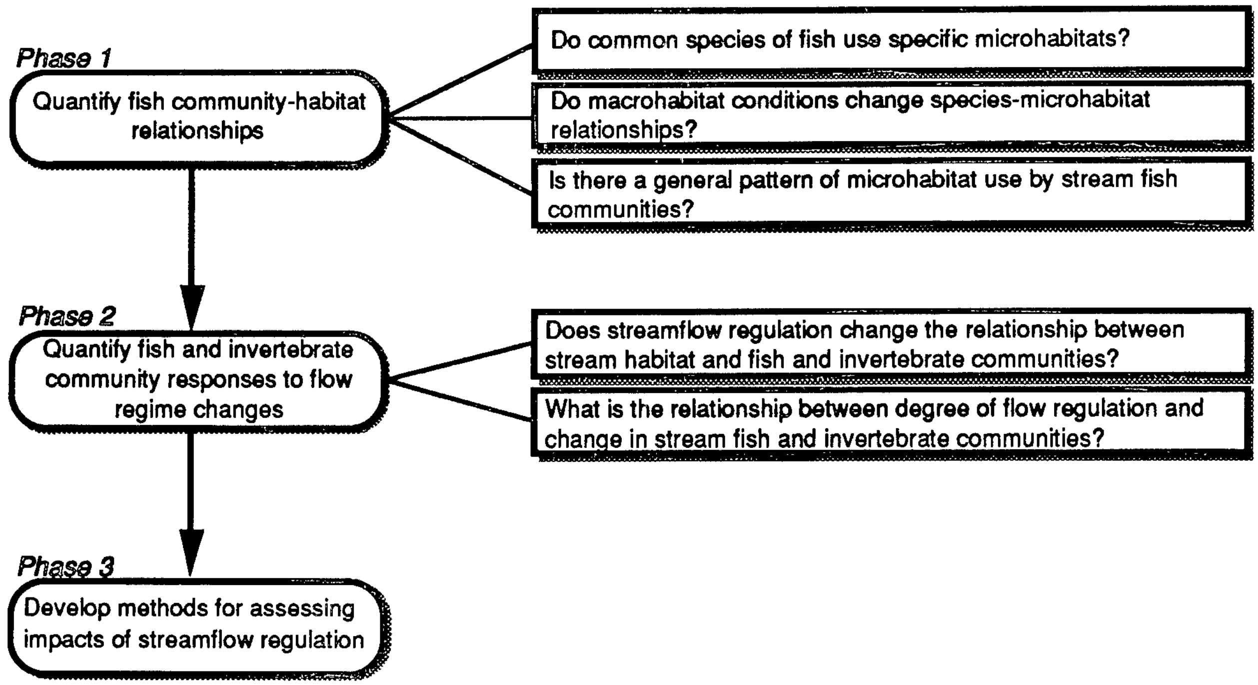

Figure 3. Overview of research strategy to identify and quantify the effects of flow regulation on warmwater fish communities and to develop a practical method for assessing the impacts of flow modifications.

species-specific research should be directed at only the species warranting unusual attention and those expected to be sensitive to regulated flow impacts (i.e., obligate riverine fishes). Studies should not be limited to physical habitat change but would also include indirect effects such as reduced food availability, susceptibility to predation and competition, and interference with migration and early life dispersal. Species-specific research may be time-consuming, expensive, and of limited value outside the environments studied.

Many riverine species that migrate or move extensively as adults (e.g., mooneyes *Hiodon* spp., redhorses *Moxostoma* spp., paddlefish *Polyodon spathula*, freshwater basses *Morone* spp.) may be effected differently by flow regulation than hypothesized earlier for resident or localized stream fishes. Altered steamflows may affect the timing, duration, and extent of migration by altering behavioral cues and stream passage ability. Although low streamflows are known to block fish passage in some rivers, quantitative information on the extent and duration of high streamflows are lacking. Studies are needed to determine streamflow regimes required for migrations and consequences of curtailed migrations. Research on migratory species will probably be expensive, time consuming, and possible for relatively few fishes, though findings may have wide application.

Despite the recognition that early life stages of fish are important in population dynamics, few studies of stream habitat have dealt with fish reproduction and larval fishes. Quantitative studies on reproductive habitats are less common because of the brief periods involved in spawning. Larval fish habitat studies are limited by the difficulty of identifying specimens and the highly variable occurrence of most larvae. However, many stream fishes may be most sensitive to flow regulation effects during reproduction and the first several weeks of life. Quantitative research is needed for these life history stages for most warmwater stream fishes. Field studies would be intensive but of short duration and findings may have wide application and importance for understanding the effects of streamflow regulation.

Little evidence is available to suggest the season or time-periods when warmwater fish communities are most limited by instream habitat availability. Studies are therefore needed to indicate which seasons typically pose the greatest resource limitations on warmwater stream fish. Research directed at seasonal survival rates for juvenile and adult stream fish would greatly

Table 3. Research needs beyond testing the general hypothesis of regulated streamflow effects.

Research need	Justification	Expected benefits
Single species biology	Endangered species, species of high public concern.	Stream habitat needs, impact assessment criteria, and protective measures for single species.
Migratory behavior	Migrations may alter the significance of habitat effects and impose different constraints than apply to localized fishes.	Identification of impacts to fishes that undertake migrations as a normal life history behavior.
Early life history studies	Little quantitative information on reproduction and larval ecology of many warmwater fishes.	Identification and modeling of reproduction and larval habitat.
Limiting seasons	Seasons and time-periods limiting warmwater fish populations have not been adequately documented.	Focused attention on seasons or time-periods where habitat changes may have the greatest influence.
Spatial scale of habitat models	Estimates of the spatial scale that fish perceive have not been documented.	Definition of the appropriate spatial resolution needed in physical habitat models.
Invertebrate and fish production	The link between invertebrate production and fish production has not been established in warmwater streams.	Identification of the importance of invertebrates to fish and the frequency that invertebrate production limits fish production.
Warmwater vs. coldwater systems	Warm headwaters may have fish communities and limiting factors similar to coldwater streams.	Recognition of the applicability of stream impact assessment methods to different types of streams.

contribute to identifying mechanisms involved in the effects of flow regulation. Results from this research could focus impact assessment on time periods when fish are most sensitive to habitat changes and would therefore have wide application to habitat modeling.

Little quantitative information is available to suggest the spatial resolution needed for stream habitat models. The IFIM is based on hydraulic models with physical habitat inputs such as depth measured to the hundredths of a foot. Fish habitat use studies generally measure habitat at fish locations and some investigators have debated whether velocity should be measured at the nose of a fish or at the mean of the water column. However, all these practices could involve measurements far more precise than necessary for modeling habitat relevant to many species. Research is needed on the size of habitat areas percieved by fish (i.e., perceptual realm) to estimate the spatial scale of habitat analysis most appropriate to stream fish. Although this research may be expensive and tedious, it could result in great time savings in impact assessment studies if the resolution of habitat models could be greatly reduced.

The relations between invertebrate production and fish production have not been clearly documented in past studies, and findings have not been consistent. Research should be directed at determining the general importance of invertebrate production and when it may be a limiting factor to warmwater stream fishes. If invertebrate production is more important in warmwater streams than has been suggested from work on coldwater streams, the indirect effects of flow regulation on invertebrates may be important for impact assessment. Indirect mechanisms of impact are difficult to document and model although there is some evidence that reduced invertebrate production may be a limiting factor. Findings from this research would have broad value and application to assessing flow regulation effects on fish communities.

We have repeatedly drawn a distinction between coldwater streams and warmwater streams because there is abundant evidence that fish communities and limiting factors differ between them. However, virtually no community level work has been done on high gradient warmwater streams where the physical habitat, canopy closure, and species diversity may be similar to the typical coldwater streams most often studied in the past. High gradient, warm headwater streams are common in the southeastern United States and these streams tend to have relatively few, morphologically dissimilar species and a few large insectivore-piscivore fishes (e.g., *Micropterus coosae*). It is possible that high gradient, well-shaded, warm headwaters have fish community characteristics and limiting factors similar to in the familiar mountain, salmonid dominated streams. If true, the distinction between coldwater and warmwater streams may be more an artifact of human biases, and a stream continuum classification (after Vannote et al. 1980) may be more appropriate. Research on warm headwaters could determine if this hypothesis has merit and may be important in determining the applicability of different stream impact assessment methods.

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16. Abstract (Limit: 200 words)

Natural resource agencies face continued pressure to develop and defend recommendations for preserving aquatic resources in warmwater streams and rivers. This report reviews the effects of steamflow modification on fishes and invertebrates in warmwater streams, outlines a broad hypothesis and testable predictions, and identifies research needed for the development of stream impact assessment methods. Fish communities in warmwater streams appear strongly affected by habitat configuration and predator-prey relations. Grouping species by habitat use, habitat-use guilds, provides a way to analyze the complex communities in warmwater streams. Research indicates that fish respond to modified streamflows and the community-level effects may be predicted using habitat guilds. Invertebrates are susceptible to streamflow changes although more studies are needed to determine if invertebrate production limits fish densities. A coordinated research plan is presented to test the general hypothesis that fluctuating streamflows change the densities and species composition of fish and invertebrates differently in nearshore and midstream habitats. Additional research tasks address the biology of single species that are endangered or migrate extensively, the appropriate spatial and temporal scale of habitat models, the relations between fish and invertebrate communities, and warmwater versus coldwater stream ecology.

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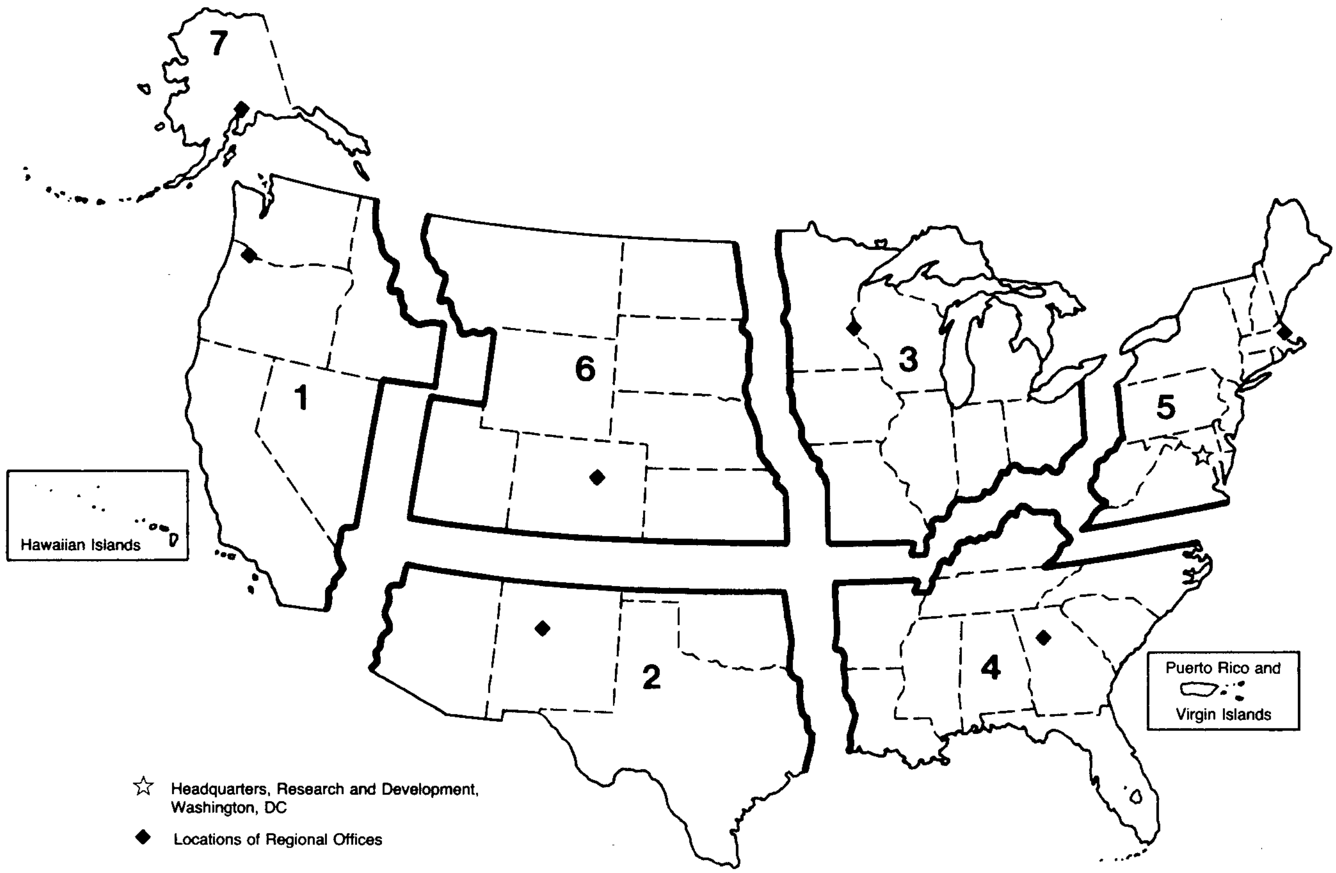

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