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Minimum flows and levels criteria development

Evaluation of the importance of water depth and frequency of water levels/flows on fish population dynamics

Literature review and summary

The Effects of Water Levels on Fish Populations

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Executive summary

This report summarizes published and unpublished literature concerning the effects of water flow and level changes on fish populations, with an emphasis on freshwater fishes in Florida and the adjacent southeast USA. This information will be used by the St. John's River Water Management District Water Supply Management Division for the development of ecological criteria for its Minimum Flow and Levels (MF&Ls) Program. Ecological research concerning the required hydrologic regimes of aquatic and wetland fauna is needed to set meaningful MF&Ls. These MF&Ls will protect water resources from significant ecological harm caused by water withdrawal or diversion and, at the same time, assure water for non-consumptive uses.

Included references were found by computer database searches, discussion with agency personnel, and perusal of the authors' personal libraries. Over 10,000 potential citations were examined and about 300 were obtained and annotated. This literature review summarizes the pertinent findings of these papers.

Water level fluctuations can have significant effects on overall fish production and system productivity. Changes in fish production can be detected in fish biomass, fish numbers, or catch-per-effort for anglers or sampling gear. Many studies have documented broad effects on fish production, but few of these have investigated the mechanisms responsible for observed changes. Periodic high water events are generally thought to enhance fish production in estuaries, lakes, and rivers. On the other hand, a number of studies have failed to find direct evidence of enhanced fish production associated with high water periods. Research also has documented decreased fish production during and after high water events such as acute flooding and unusually prolonged high lake stages. Low water levels, often associated with drought, often decrease fish production. Water level manipulation is a management tool that may be used to increase the production of fish.

Increased growth of fishes is commonly anticipated following floodplain inundation or high water periods. Nevertheless, fishes may be expected to differ in their growth response to water level fluctuations based on coincidence of fluctuations and spawning or nursery periods, diet of the fish, and patterns of habitat use. Growth of fishes may not be significantly effected regardless of water level changes, especially when density-dependent mechanisms due to higher survival cancel out growth benefits. Under specific circumstances, high water can be detrimental to fish growth, such as during acute flooding or for systems where primary productivity originates within the system and allochthonous inputs are unimportant. Timing, especially relative to temperature and fish life history characteristics, may influence any effect on fish growth linked to high water events.

The effects of water level fluctuations on fish mortality may be divided into those associated with specific flood events and those that occur over broader time scales. Acute flooding events may displace, strand, or physically damage fishes, effectively removing them from their source population. Broad scale water level increases may enhance survival through a variety of mechanisms such as increased productivity, food resources, or habitat availability. Extended low water levels generally increase mortality.

Recruitment processes are often complex and overall recruitment may be effected by a number of mechanisms. Several studies have documented changes in fish recruitment relative to water levels or water level fluctuations. Enhanced recruitment of fishes has been associated with high water periods for marshes, reservoirs, and rivers. Although marine fish recruitment may be inhibited during periods of high freshwater inflow, it is generally found that freshwater discharge from rivers enhances overall recruitment of fish in estuaries and nearby marine waters. The effect of fluctuations in water level on recruitment is mixed. Fluctuations inhibit recruitment by disrupting spawning or stranding individuals. Fluctuations enhance recruitment by maintenance of habitat and increasing food and habitat resources.

Hydrology influences fish populations and may therefore play a role in determining the characteristics of fish assemblages. Stability of hydrology was found to be a significant factor in many stream systems. Ontogenetic stage and life history modify the role that stochastic environmental variables play in the regulation of fish populations and assemblages. For wetlands in the floodplain, fish assemblage structure is largely determined by degree of connection with the stream. Several authors have documented reduced species richness and fish assemblage complexity associated with flow regulation of rivers. Artificially maintained high water levels in Florida lakes may also result in decreases in fish species richness and assemblage complexity. Freshwater discharge from rivers influences fish assemblages of estuaries, reducing species richness but increasing productivity.

Traditional concepts of river-floodplain ecology stress the importance of floodplains as spawning habitat for fishes. Studies have repeatedly reported spawning by fishes in flooded areas. Nevertheless, there is relatively little evidence of floodplain pool use for spawning by riverine fishes. Floodplain-associated species and centrarchids, however, have been documented reproducing in floodplain pools. Flow and water level changes may influence initiation of spawning and reproductive success. Many fish spawn during periods of high or rising water. However, acute flooding events may be detrimental to spawning success. Fluctuations in water levels can also disrupt spawning, especially for nest-building species. The use of habitat for spawning requires sufficient depth for the fish to move into the habitat and build a nest or initiate courtship. Floodplains may serve as important nursery areas as well. Larvae or young-of-year of numerous fish species have been documented on floodplains, including species that spawn in river channels. Flooded areas of reservoirs or lakes may serve a similar purpose to floodplains. Lower portions of tributaries have also been shown to function as nursery areas, especially where floodplains are lacking. In certain systems, however, floodplains may be unimportant as fish spawning or nursery areas due to unpredictable and poorly timed flooding.

A major benefit to fishes of inundated floodplain is access to additional food resources. Several studies reported on fish feeding in flooded areas and numerous other studies provide circumstantial evidence of fishes feeding in floodplains by the extensive use of this habitat by larvae, juveniles, and adults. High water levels may increase the food supply for fishes. Floodplain inundation not only provides more habitat for aquatic invertebrates, but also allows fish access to floodplain pools. These wetlands may be rich sources of invertebrate prey, depending on pool size and degree of isolation from channels. Herbivorous fishes may also benefit from a new food source in the form of flooded terrestrial vegetation. Nevertheless, high water can also reduce the food supply of fishes. Acute flooding events may decrease invertebrate numbers. In systems that depend on riverine productivity, low water increases productivity and leads to greater abundance of invertebrate and fish prey.

Water levels have major effects on fish habitat characteristics. A main effect is determining the amount of available habitat. Within limits, high water levels result in more fish habitat and much of the variability in habitat availability in streams may be explained by variability in hydrology. Indeed, critical fish habitat in streams decreases rapidly below certain minimum flow values. Riffles and shallow, low velocity habitats are more susceptible to loss than are pools. Although fish abundance may be related to habitat availability, above certain threshold values, other factors may outweigh habitat limitation, especially for large, predatory species. For lakes that have had historic water level fluctuations stabilized by water control structures, water level manipulation can be an important fisheries management tool, resulting in improved fish spawning and nursery habitat.

There is substantial documentation of inundated floodplain use by fishes and some fishes may be considered floodplain-associated species. Stream flow can influence fish movements as well as specific habitat use. Many species undergo lateral migrations onto floodplains and longitudinal migrations up or down rivers in response to increases in stream flow. For estuaries, salinity, which is influenced by stream flow, can also effect fish habitat use. Furthermore, groundwater discharge can be important to fishes because its consistent, relatively cool temperature provides a thermal refuge for fishes near their southern range limit in the southeast USA.

Import of nutrients or energy from terrestrial systems to aquatic systems (i.e., land-water subsidy), from wetlands to lakes and streams, and from rivers to estuaries can be important in maintaining or enhancing system productivity and therefore, fish production. There is a direct link between swamps and floodplain forests and the productivity of estuaries in the southeast USA. Timing of inundation of floodplains influences the importance of allochthonous nutrient inputs.

Water flows and levels can effect fish populations through degradation of water quality and impacts on fish health. Two of the most common water quality issues related to water levels are hypoxia and salinity. Hypoxia may occur in inundated floodplains due to the decomposition of organic material, limiting use of these areas by most fishes and causing fish kills. Varying river discharge causes variability in salinity gradients in estuaries, influencing fish distribution and habitat use. Marine fishes may be sensitive to changes in salinity and this sensitivity is life stage, species, and estuary-specific. Changes in flow or water levels can also alter the effect of pollutants in aquatic systems such as the bioavailability and fish tissue concentration of mercury in coastal plain wetlands.

It is clear from the literature that water level changes have profound implications for fish populations. However, the effects of water level fluctuations are dependent on numerous factors. The interaction of factors may well prove to influence fish more than any factor in isolation. Regional fish fauna composition is an important factor because certain species benefit more than others from high water (e.g., species that spawn on floodplains). Life stage structure can determine general effects of flow events on fishes. The nature of the habitat plays a role in effects of water levels. Rising waters more likely effect fishes if a floodplain or wetland is connected to the system. Magnitude of the high water events must be sufficient to cause a response in fishes. High water depth and duration must be such that fishes can meaningfully access the flooded habitat. It takes time for fishes to spawn, eggs to hatch, and larvae or juveniles to move off the floodplain. This critical time interval is life history dependent. In particular, nursery functions require a relatively long hydroperiod. Little is know about how frequency of water level events influences fish populations. Logically, the importance of frequency to spawning and overall recruitment should differ based on life history. Long-lived fishes should be influenced less overall than short-lived species. Predictability is a critical factor in long-term responses of fishes to hydrology. Timing is perhaps the most important factor affecting the response of fishes to water level changes. If temperatures are too low or changes do not coincide with spawning or growing seasons, potential benefits of high water for fishes may be lost.

Several basic model types (e.g., Instream Flow Incremental Methodology/IFIM) and thousands of their variants have been used to predict the responses of fishes to water level and instream flow changes. Almost all of these models predict the amount of available fish habitat over a range of flows using hydraulic variables and fish habitat use or preference data. The basic assumptions underlying all these models are that more habitat equals more fish and that habitat availability is the most important factor in determining fish populations in streams. The models have met with mixed results when used for warmwater systems. They seem to work best with small fishes and overestimate abundance of large species of higher trophic levels. The applicability of the present habitat models developed mostly for coldwater streams and salmonids to Florida systems and species is in question. On the other hand, models predicting fish responses to fluctuating water levels, some qualitative, have been applied to Florida systems (e.g., Everglades and Kissimmee River).

The primary ecological paradigm applied to large river systems stresses the importance of floodplains for river productivity and fish populations (i.e., the basis of flood-pulse and river continuum concepts). Nevertheless, the riverine productivity model is an alternative stating that within channel productivity is far more important than allochthonous inputs to productivity in systems with limited floodplains or where floodplain inundation is poorly timed to provide for fish spawning, fish growth, or entrance of allochthonous materials into foodwebs (i.e., floods occur in cold weather).

Water level fluctuations have numerous management implications. Fisheries regulations can be set or modified based on historic, observed, or anticipated hydrology. For systems where flow or water level manipulation is a possibility, water management can be used for fisheries management purposes. Lastly, given the past history of hydrology alteration for water management and the present and future demands for ground and surface water resources in Florida, fisheries implications can be an important consideration for water management projects and policies.

Relatively little information is published concerning the effects of water flows and levels on fishes in Florida. The ecological principles relating high water events (e.g., floodplain inundation) and the responses of fishes are generally known. However, documentation supporting these concepts is often lacking or equivocal. Less structured, but perhaps better documented, is the body of knowledge concerning mechanisms for potential effects of water level changes on fishes (e.g., fish spawning on floodplains). Although there are numerous empirical studies demonstrating that the potential mechanisms operate, there are relatively few studies linking these mechanisms with fish population responses relative to water levels.

There is a general lack of quantitative predictive ability concerning fish responses to water level changes in Florida. Critical information about minimum necessary inundation values (e.g., duration, frequency, percent floodplain inundation), life stage-specific warm-water fish habitat and life history requirements, and fish assemblage and demographic characteristics relative to hydrology is needed to make the leap from qualitative to quantitative predictive ability. In particular, there is very little published information concerning the life history of many nongame fish species. General predictive models may be developed for water bodies in the state or specific models may need to be applied to each system type (e.g., by trophic state of lake), each region, or individual water body. It may be possible to develop regression models predicting recruitment or production from lake or stream stage values. More complex models incorporating time lags, temperature, percent floodplain inundation, or other factors may be necessary to provide the level of precision required for fisheries management. Alternately, habitat type models (e.g., IFIM) could be tested for Florida systems. On a broad scale, more habitat certainly equates to more fish. Nevertheless, there are numerous technical and theoretical obstacles to the widespread use of present habitat models in Florida's warm-water streams and lakes. Clearly, much research is needed in all Florida aquatic habitats to provide needed information for fisheries and water resource management decisions.

The Effects of Water Levels on Fish Populations

Introduction

As human populations increase, greater demands are being placed on both surface and groundwater resources. Water withdrawals can reduce stream discharge, alter lake and wetland hydroperiod, dampen historic water level fluctuations, and ultimately reduce habitat for fishes (e.g., Stalnaker 1980; Tyus 1990; Power et al. 1999). Alteration of flow or water levels due to channelizing streams, digging canals, or constructing water-control structures can have similar effects (e.g., Cushman 1985; Tyus 1990; Steele and Smokorowski 2000). The responses of freshwater and estuarine fishes to water level changes and altered hydrology may be complex and involve both direct and indirect mechanisms. Water level fluctuations can enhance or degrade fish populations depending on the timing, duration, interval, and magnitude of the changes. Given the high socioeconomic value of fisheries in Florida and the southeast USA, understanding effects of hydrology on fishes is an important step in maintaining fisheries in the face of increasing demands for the fishes and the water upon which those fisheries depend.

Florida has a diverse array of freshwater and coastal habitats (Seaman 1985). South Florida is dominated by the Kissimmee River-Lake Okeechobee-Everglades system. This drainage contains diverse freshwater and estuarine habitats, including broad-leaf and grassy marshes, cypress swamps, a large meandering river with associated floodplain, small to massive, shallow natural lakes, drainage canals, sloughs, mangrove creeks, and estuarine bays. Southwest Florida contains numerous small coastal drainages and associated estuaries. Central and northeast Florida are characterized by natural lakes, spring-fed streams, and extensive marshes, mostly associated with the large St. Johns River system. This system has hardwood floodplains along some tributaries and much of its lower portion is considered an estuary. The Suwannee River and tributaries and small coastal drainages feed into the Gulf of Mexico in the Big Bend region of north Florida. The Suwannee River has numerous springs, a hardwood-dominated floodplain, and a large estuary at its mouth. The Panhandle region of west Florida is characterized by coastal plain streams with associated hardwood floodplains and estuaries. The Apalachicola River system supports an extensive hardwood floodplain and a large estuarine bay and is the only Florida system that originates in upland areas.

The composition of the fish fauna effects how water level changes will influence fish populations. The freshwater fish fauna of Florida has its affinity with the southeast USA (Gilbert 1987). Most fishes are either coastal plain-associated species or those with wide distributions and broad habitat requirements. A few species are endemic, or nearly so, to peninsular Florida. Many resident fishes are considered floodplain-associated species, although the numerous wetlands that provide them favorable habitat in Florida make this designation less true than elsewhere. The region has anadromous species such as sturgeon *Acipenser* spp., shad *Alosa* spp., and striped bass *Morone saxatilis* and the catadromous American eel *Anguilla rostrata*. On the other hand, Florida has relatively few fluvial species, with most occurring in Panhandle streams.

Water level fluctuations include both increasing and decreasing levels that may occur rapidly. Water flows and levels may also change gradually. High water events result in greater stream depth, flow, and discharge, inundation of floodplains, and increased depth in permanent or long hydroperiod marshes and swamps. Droughts or excessive water withdrawals can lead to low stream depth, flow, and discharge, salinity intrusion into lower reaches of streams, decoupling of streams and floodplains, decreased depths or dessication of lakes, marshes, and swamps, and degraded water quality.

The primary focus of this review is the effect of changes in water level on freshwater fishes and, to a lesser extent, estuarine fishes, with an emphasis on Florida and the southeastern USA. We included papers identified in computer database searches of the Aquatic, Wetland, and Invasive Plants database, Cambridge Aquatic Science and Fisheries Abstracts, Biological Abstracts, Biological and Agricultural Index, St. Johns River Water Management District (SJRWMD) Library database, and Zoological Record. The period of database coverage varied, but searches typically covered the period of 1980 to 2000. Additional sources of literature, especially for gray literature, included personal communications with state and federal agency personnel and the authors' personal libraries. The searches produced over 10,000 potential citations, about 300 of which were found to be of direct relevance and included in an annotated bibliography (Hill and Cichra 2002). The present review is a summary of the information from this annotated bibliography concerning the effects of water level changes on fishes. The review is organized to first cover the broad level of fish production and system productivity, fish population dynamics, and fish assemblage characteristics before delving into the mechanisms responsible for effects that occur within these broad categories and the factors that can modify these effects. Next, we include habitat and predictive models that use instream flow or water levels.

Given the extent that water levels can influence fish populations, it is important in fisheries ecology to understand both the general relationships as well as the mechanisms responsible for the observed patterns. Using this information, fisheries managers can predict responses of fish populations to water management activities and natural water level cycles and thus implement management actions based on sound empirical and mechanistic grounds. Moreover, this review points out numerous information gaps and suggests topics of research to address those needs. This information will be used by the SJRWMD Water Supply Management Division for the development of ecological criteria for its Minimum Flow and Levels (MF&Ls) Program. Ecological research concerning the required hydrologic regimes of aquatic and wetland fauna is needed to set meaningful MF&Ls. These MF&Ls will protect water resources from significant ecological harm caused by water withdrawal or diversion and, at the same time, assure water for non-consumptive uses.

Production

Water level fluctuations can have significant effects on overall fish production and system productivity. Changes in fish production can be detected in fish biomass, fish numbers, or catch-per-effort for anglers or sampling gear. Productivity or trophic status relates to the ability of a system to produce fish. Productivity is measured as nutrient or phytoplankton concentrations (e.g., Forsberg and Ryding 1980). Many studies have documented broad effects on fish production, but few of these have investigated the mechanisms responsible for observed changes.

Periodic high water events are generally thought to enhance fish production. This has been demonstrated for rivers (Zalumi 1976; Ali and Kathergany 1987), including the Mississippi

River (Tibbs and Galat 1998) and Kissimmee River (Toth 1991, 1993), lakes (see Jude and Pappas 1992), and reservoirs (see Keith 1975; Summerfelt and Shirley 1978; Karenge and Kolding 1995). Increases in fish abundance, especially for small-bodied species, correlated with high water periods in Florida marshes (Toth 1991, 1993; DeAngelis et al. 1997; Jordan et al. 1998). This relationship is also well-established for fish and shellfish given high freshwater discharge from rivers into estuaries. Abundance or fisheries landings of pink shrimp *Penaeus duorarum* (Browder 1985) and fish (Lorenz 1999) in Florida Bay, and oyster *Crassostrea* sp. (Wilber 1992) and fish (Livingston 1997) in Apalachicola Bay were enhanced during or after periods of high freshwater inflow. Estuarine productivity of Apalachicola Bay is also greater under high and normal flow regimes than during drought conditions (Livingston 1997; Livingston et al. 1997). Grimes (2001) reviewed the importance of Mississippi River freshwater discharge in maintaining productivity and fisheries in the northern Gulf of Mexico.

On the other hand, a number of studies have failed to find direct evidence of enhanced fish production associated with high water periods. For the Mississippi River, Risotto and Turner (1985) found little direct evidence of an influence of spring floods on fish abundance, although there was a weak, positive correlation of fish abundance and bottomland hardwood acreage. Also, Rutherford et al. (1995) concluded that mainstem productivity was more important than floodplain productivity for this system, perhaps because of the loss of so much of the historic floodplain. A similar conclusion regarding the dominance of riverine productivity for the Ohio River was reached by Thorp et al. (1998).

Research also has documented decreased fish production during and after high water events. Severe floods can reduce population size of small fishes through direct mortality and displacement (Chapman and Kramer 1991). Seasonal flooding of marshes, even those used for fish spawning and nursery areas, can lead to stranding, mortality, and a net negative demographic balance (Poizat and Crivelli 1997). Sustained high water levels in Lake Okeechobee, Florida, were correlated with lower sport fish abundance and standing crop (Aumen and Gray 1995). In river systems with limited floodplains, flood-associated reductions in mainstem productivity may reduce fish growth and production (Rutherford et al. 1995).

Low water levels, often associated with drought, often decrease fish production. Fish abundance was negatively affected during low water in Arkansas (Jackson et al. 1982), Florida (DeAngelis et al. 1997; Jordan et al. 1998), and South Carolina (Paller 1997). However, low flow conditions in mainstem reservoirs of the Cumberland and Tennessee rivers resulted in increased fish standing crop, probably due to increases in primary productivity associated with longer reservoir retention times and release of phytoplankton from light limitation (Buynak et al. 1991).

Water level manipulation is a management tool that may be used to increase the production of fish. The use of drawdowns followed by reflooding is a common management practice in reservoirs to enhance largemouth bass *Micropterus salmoides* and other sport fish production (Keith 1975; Ploskey 1982). This strategy has also been used in association with muck removal in Florida with rapid, if short term, benefits for sport fish in lakes that experience reduced water level fluctuations due to water control structures (Moyer et al. 1995).

Population dynamics

Growth

Increased growth of fishes is commonly anticipated following floodplain inundation or high water periods. Nevertheless, fishes may be expected to differ in their growth response to water level fluctuations based on coincidence of fluctuations and spawning or nursery periods, diet of the fish, and patterns of habitat use. Cone et al. (1986), Bayley (1988), Staggs and Otis (1996), Gutreuter et al. (1999), and Schramm et al. (2000) documented faster growth of select fishes during high water years. Most of these studies, however, illustrate that mixed effects on growth are often observed. Cone et al. (1986) found that striped bass did not grow faster during a flood year, possibly because of a winter kill of threadfin shad *Dorosoma petenense*, the major prey species in Lake Texoma. In the Amazon River, omnivores experienced faster growth but detritivores did not during high water (Bayley 1988). Staggs and Otis (1996) reported mixed growth results for Lake Winnebago, Wisconsin, with high water periods during the year being beneficial to some species and detrimental to others. Of several species and life stages investigated, Putnam et al. (1995) reported only one significant relationship of a hydrological variable and growth (i.e., velocity and large channel catfish *Ictalurus punctatus* growth).

Some of the most compelling support for flood-pulse principles can be found in Gutreuter et al. (1999), where mixed results for different species were predicted. The authors hypothesized that fish species would differ in growth response to high water based on broad habitat use in the upper Mississippi River. Bluegill *Lepomis macrochirus* and largemouth bass are littoral, white bass *Morone chrysops* are limnetic, and black crappie *Pomoxis nigromaculatus* are intermediate in habitat use. The authors documented increased growth of bluegill and largemouth bass, no effect for white bass, and ambiguous results for black crappie, consistent with theory.

Growth of fishes may not be significantly effected regardless of water level changes. In an upper Missouri River reservoir, Martin et al. (1981) failed to detect differences in growth of the four most abundant species between high and low water years. On the other hand, abundance of age-0 fishes was significantly higher during high water years and density-dependent mechanisms may therefore explain the lack of increased growth. Similarly, gizzard shad *Dorosoma cepedianum* growth in Missouri was not related to water levels (Michaletz 1997).

Under specific circumstances, high water can be detrimental to fish growth. In West Point Reservoir, Alabama and Georgia, high water levels led to increased survival of age-0 largemouth bass and decreased growth due to density-dependence (Miranda et al. 1984). In lakes Barkley and Kentucky, Kentucky and Tennessee, low flow led to increased reservoir productivity, increased food availability, and increased growth of age-0 largemouth bass (Buynak et al. 1991). In the lower Mississippi River, Rutherford et al. (1995) reported negative correlations between fish growth and total hectares flooded (age-0 gizzard shad) and river discharge (age-0/age-1 freshwater drum *Aplodinotus grunniens*). In the latter two cases, mainstem productivity is dominant over allochthonous inputs. Flooding during early life can also result in lower growth for fishes (e.g., Atlantic salmon *Salmo salar* parr; Jensen and Johnsen 1999).

Timing may influence any effect on fish growth linked to high water events. High water was associated with increased growth in blue catfish *Ictalurus furcatus*, channel catfish, and flathead catfish *Pylodictis olivaris* in the lower Mississippi River (Schramm et al. 2000).

However, no single hydrologic variable explained a significant amount of the variation in annual growth. A composite variable of duration of floodplain inundation when water temperatures exceeded the minima for active feeding was significant, indicating that the importance of floodplain inundation to growth varies on a temporal scale. High water in reservoirs from late winter to early summer may increase largemouth bass growth by increasing productivity and increasing invertebrate prey availability for age-0 fish whereas lower water conditions during late summer and fall can enhance largemouth bass growth by concentrating prey fish (Keith 1975).

Mortality/survival

The effects of water level fluctuations on fish mortality may be divided into those associated with specific flood events and those that occur over broader time scales. Acute flooding events may displace, strand, or physically damage fishes, effectively removing them from their source population. Broad scale water level increases may enhance survival through a variety of mechanisms such as increased productivity, food resources, or habitat availability. Extended low water levels generally increase mortality.

Flooding either increased mortality or had no detectable effect. Stream flooding increased mortality of juvenile centrarchids and cyprinids (Harvey 1987; Schlosser and Angermeier 1990), poeciliids (Chapman and Kramer 1991), and juvenile salmonids (Jensen and Johnsen 1999). Conversely, flooding had no effect on survival of larval white bass (Starnes et al. 1983) or juvenile rainbow trout *Oncorhynchus mykiss* (Simpkins et al. 2000). Harvey (1987) found the loss of juvenile centrarchids and cyprinids to be size dependent, with larger individuals better able to withstand floods.

Survival of age-0 largemouth bass was greater during high water years in West Point Reservoir, Alabama and Georgia (Miranda et al. 1984). On the other hand, Michaletz (1997) found no relationship between water levels and age-0 gizzard shad survival in Missouri.

Low water periods resulted in decreased survival of striped bass eggs and larvae in the Savannah River, Georgia, due to saltwater intrusion (Van den Avyle and Maynard 1994). Mortality of cyprinodontiform fishes was related to water levels in the Big Cypress and Everglades systems of Florida, with massive losses of fishes during drying periods (DeAngelis et al. 1997). In southern France, high water allowed access to marshes where fish reproduced and fed, enhancing production, only to result in a net negative demographic balance for all species except three-spined stickleback *Gasterosteus aculeatus* and, occasionally, western mosquitofish *Gambusia affinis* due to stranding when the water receded (Poizat and Crivelli 1997).

Recruitment

Recruitment processes are often complex and overall recruitment may be effected by a number of mechanisms. Recruitment is a broad term and is here used to describe survival to any specified age (e.g., larval stage, age-5). Several studies have documented changes in recruitment relative to water levels or water level fluctuations.

High water periods often correlate with enhanced recruitment of fishes, especially in reservoirs. Gizzard shad (Michaletz 1997), largemouth bass (Keith 1975; Summerfelt and

Shirley 1978; Miranda et al. 1984; Fisher and Zale 1991; Meals and Miranda 1991; Kohler et al. 1993), crappie *Pomoxis* spp. (Beam 1983; Meals and Miranda 1991), sunfish *Lepomis* spp. (Meals and Miranda 1991), and overall fish assemblage (Zalewski et al. 1990) recruitment increased with high water periods in reservoirs. Conversely, largemouth bass recruitment was depressed during high water years in mainstem Cumberland River (Buynak et al. 1999) and Tennessee River reservoirs (Maceina and Bettoli 1998; Buynak et al. 1999). Low water periods may also correlate with increased recruitment in reservoirs by allowing terrestrial vegetation to grow in areas that will be flooded the next spring (Keith 1975; Fisher and Zale 1991).

Much less is documented for water level effects on recruitment for other systems. Enhanced recruitment of fishes has been associated with high water periods for marshes (Jordan et al. 1998) and rivers (Raibley et al. 1997). In marshes, low water limits recruitment of fishes (Poizat and Crivelli 1997; Jordan et al. 1998). Although marine fish recruitment may be inhibited during periods of high freshwater inflow (Rogers et al. 1984; Fraser 1997), it is generally found that freshwater discharge from rivers enhances overall recruitment of fish in estuaries and nearby marine waters (Stevens 1977; Funicelli and Rogers 1981; Bennett et al. 1995; Grimes 2001).

The effect of fluctuations in water level is mixed. Recruitment of sport fish in Florida lakes benefitted from water level fluctuations (Hill et al. 1994; Moyer et al. 1995). Zalewski et al. (1990) found that recruitment of the larval fish assemblage of a Polish reservoir was positively correlated with water level fluctuations. For largemouth bass, fluctuations in water level were determined to have no effect in some reservoirs (Kohler et al. 1993; Maceina and Bettoli 1998; Jackson and Noble 2000). Other research has indicated that water level fluctuations may be detrimental to fish recruitment in reservoirs (Beam 1983) and rivers (Stalnaker et al. 1996; Raibley et al. 1997). Generally, fluctuations inhibit recruitment by disrupting spawning or stranding individuals. Fluctuations enhance recruitment by maintenance of habitat and increasing food and habitat resources.

Assemblage characteristics

Hydrology influences fish populations and may therefore play a role in determining the characteristics of fish assemblages. Stability of hydrology was found to be a significant factor in many stream systems (Horowitz 1978; Poff and Ward 1989; Poff and Allan 1995; Grossman et al. 1998). Nevertheless, Bass (1990) found stable and persistent fish assemblages in the Escambia River, Florida, over a 6-year period despite large fluctuations in stream flows and salinity intrusions. Matthews et al. (1994) concluded that although flooding may alter fish assemblage composition of individual pools, there was little change on the scale of stream reach in an Oklahoma stream. Ontogenetic stage and life history modify the role that stochastic environmental variables play in the regulation of fish populations and assemblages (Schlosser 1985).

For wetlands in the floodplain, fish assemblage structure was largely determined by degree of connection with the stream (Halyk and Balon 1983; Dunson et al. 1997; Galat et al. 1998; Pezold 1998). For instance, Galat et al. (1998) reported that recently isolated floodplain pools have a characteristic riverine fauna which converts to a lacustrine fauna over time.

Conversely, Rodriguez and Lewis (1997) concluded that only transparency, conductance, depth, and surface area predictably related to fish assemblage structure for Orinoco River floodplain lakes.

Flow regulation alters historic hydrology and fish assemblages. Regulated rivers often have drastic, unpredictable changes in flow. Several authors have documented reduced species richness and fish assemblage complexity associated with flow regulation of rivers (Bain et al. 1988; Travnichek and Maceina 1994; Travnichek et al. 1995; Bowen et al. 1996). Travnichek et al. (1995) reported increases in species richness below Thurlow Hydroelectric Dam on the Tallapoosa River, Alabama, following the implementation of a minimum flow release schedule. Construction of water control structures on natural lakes alters historic hydrology, in this case by dampening water level fluctuations and providing hydrological stability. Removal of a coffer dam on Dead Lake, Florida, resulted in increased species richness (Hill et al. 1994). Similarly, in regulated Lake Okeechobee, Florida, sustained high water levels resulted in a decline of species richness in vegetated areas.

Freshwater discharge from rivers influences fish assemblages of estuaries. Fraser (1997) reported a more diverse assemblage of fishes in the upper Charlotte Harbor, Florida, during periods of low flow from the Peace River. Salinity was found to the primary determinant of fish assemblage structure in mangrove habitats in Florida Bay (Lorenz 1997). In Apalachicola Bay, Florida, periods of low freshwater discharge resulted in higher species richness, but lower overall productivity (Livingston et al. 1997).

Mechanisms

Reproduction

Traditional concepts of river-floodplain ecology stress the importance of floodplains as spawning habitat for fishes. Studies have repeatedly reported spawning by fishes in flooded areas. Several species, including centrarchids, have been observed or surmised to spawn on river floodplains (e.g., Guillory 1979; Martin et al. 1981; Miranda et al. 1984; Meals and Miranda 1991; Reimer 1991; Baker and Killgore 1994; Mol 1996; Poizat and Crivelli 1997; Galat et al. 1998; Snedden et al. 1999). In the most extensive study of a forested floodplain system in Florida, Leitman et al. (1991) concluded that the Apalachicola River floodplain is an important spawning habitat based on collection of 11 fish species as adults in spawning condition. There is relatively little evidence of floodplain pool use for spawning by riverine fishes (Leitman et al. 1991; Galat et al. 1998; Pezold 1998). Floodplain-associated species and centrarchids, however, have been documented reproducing in floodplain pools (Leitman et al. 1991; Galat et al. 1998; Pezold 1998).

Floodplains may serve as important nursery areas as well. Larvae or young-of-year of numerous fish species have been documented on floodplains (e.g., Guillory 1979; Martin et al. 1981; Kwak 1988; Poizat and Crivelli 1997; Snedden et al. 1999), including species that spawn in river channels (Baker and Killgore 1994; Turner et al. 1994; Araujo-Lima and Oliveira 1998). The Apalachicola River, Florida, floodplain serves as a nursery area for at least nine species (Leitman et al. 1991). Floodplain pools (Halyk and Balon 1983; Leitman et al. 1991) may be used for nursery functions, but Pezold (1998) found few larvae of any type in isolated pools.

Flooded areas of reservoirs or lakes may serve a similar purpose to floodplains and are used as spawning and nursery areas for fishes, including largemouth bass (Keith 1975; Miranda et al. 1984; Fisher and Zale 1991). Lower portions of tributaries have also been shown to function as nursery areas, especially where floodplains are lacking (Brown and Coon 1994).

In certain systems, floodplains may be unimportant as fish spawning or nursery areas. The Murray-Darling River system of Australia is an example of a system with an extensive floodplain that is not heavily used for fish reproduction due to unpredictable and poorly timed flooding (Humphries et al. 1999). In other systems, floodplain wetlands may represent population sinks. In a marsh in southern France, Poizat and Crivelli (1997) reported that although fish used flooded areas for spawning and nursery habitat, due to the unpredictable nature of water levels, most species exhibited a net negative demographic balance as larvae, juveniles, and adults were often stranded. This situation is also implied for floodplain pools with long periods of isolation. Galat et al. (1998) documented successions of fish assemblages in floodplain pools from a riverine assemblage immediately after isolation to a characteristic lacustrine assemblage over time as riverine species dropped out.

Flow and water level changes may influence initiation of spawning and reproductive success. Many fish spawn during periods of high or rising water. For example, brown hoplo *Hoplosternum littorale* begin building floating nests in newly flooded areas during rising water (Winemiller 1987; Ramnarine 1995; Mol 1996). American shad *Alosa sapidissima* spawning runs into freshwater rivers correlate with increased flow, although temperature may be a more important factor (Quinn and Adams 1996). Gizzard shad exhibit intense reproductive activity associated with rising water levels (Michaletz 1997). Higher reproductive success of fish assemblages in floodplain systems has been documented during high water years (e.g., Baker and Killgore 1994; Galat et al. 1998). However, acute flooding events may be detrimental to spawning success (Helfrich et al. 1991; Lukas and Orth 1993; Carmichael et al. 1998). Fluctuations in water levels can also disrupt spawning, especially for nest-building species such as largemouth bass (e.g., Mitchill 1982; Kohler et al. 1993). Indeed, largemouth bass (Mitchill 1982; Kohler et al. 1993)and redbreast sunfish *Lepomis auritus* (Davis 1971; Lukas and Orth 1993) experience higher nesting success under conditions of stable flow or water levels. Gulf of Mexico sturgeon *Acipenser oxyrhincus desotoi* may also require stable flows for spawning (Sulak and Clugston 1998).

The use of habitat for spawning requires sufficient depth for the fish to move into the habitat and build a nest or initiate courtship. Relatively little information is available on critical depths for passage or minimum nesting depths. Mosely (1982) concluded that most estimates of minimum passage depths for fishes are conservative and not derived with a consideration of both fish morphology and behavior. Almost no minimum nest depth values are reported in the literature, but Heidinger (1975) gave a figure of 15 cm for largemouth bass and Lukas and Orth (1993) reported 0.5 m for redbreast sunfish. Certain minnows spawn in shallow, vegetated riffles (e.g., flagfin shiner *Pteronotropis signipinnis*; Albanese 2000), a habitat vulnerable to loss during low water periods (e.g., Aadland 1993).

Feeding

A major benefit to fishes of inundated floodplain is access to additional food resources. Several studies reported on fish feeding in flooded areas (Keith 1975; Summerfelt and Shirley

1978; Bowen and Allanson 1982; Dudgeon 1983; Reimer 1991; Garutti and Figueiredo-Garutti 2000). Numerous other studies provide circumstantial evidence of fishes feeding in floodplains by the extensive use of this habitat by larvae, juveniles, and adults (e.g., Leitman et al. 1991). Conversely, Humphries et al. (1999) failed to find evidence that floodplains were important feeding habitat for fishes in the Murray-Darling River, Australia, even though the system has an extensive floodplain.

High water levels may increase the food supply for fishes. Coomer et al. (1997) found that the density of macroinvertebrates was not related to stream flow, therefore more prey is available at high flows (i.e., more habitat at high flows yields more prey). A number of fish species feed on terrestrial invertebrates (e.g., Cloe and Garman 1996) and flooding may allow fish greater access to these prey. Floodplain inundation not only provides more habitat for aquatic invertebrates, but also allows fish access to floodplain pools. These wetlands may be rich sources of invertebrate prey, depending on pool size and degree of isolation from channels (Corti et al. 1997). Invertebrate prey numbers increase as water levels increase on the floodplain and then drop off after peak inundation (Theiling and Tucker 1999). Herbivorous fishes may also benefit from a new food source in the form of flooded terrestrial vegetation (Dudgeon 1983). Nevertheless, high water can also reduce the food supply of fishes. Acute flooding events may decrease invertebrate numbers (Schlosser and Angermeier 1990). In systems that depend on riverine productivity, low water increases productivity and leads to greater abundance of invertebrate and fish prey (e.g., Buynak et al. 1991). During sustained high lake levels in Lake Okeechobee, Florida, Aumen and Gray (1995) found reduced diversity of macroinvertebrates.

Habitat characteristics

Water levels have major effects on fish habitat characteristics. A main effect is determining the amount of available habitat. Within limits, high water levels result in more fish habitat (see Orth and Maughan 1982) and much of the variability in habitat availability in streams may be explained by variability in hydrology (Grossman et al. 1998). Indeed, critical fish habitat in streams decreases rapidly below certain minimum flow values (Heggenes et al. 1996). Riffles (Aadland 1993) and shallow, low velocity habitats (Bain et al. 1988) are more susceptible to loss than are pools. For braided rivers, in contrast to single strand rivers, Glova and Duncan (1985) found that reduced flow caused relatively little change in weighted usable area (WUA; see Habitat and predictive models, below) over a broad range of flows, except for losses in side channel habitats. Floodplain pool and backwater habitat characteristics are largely determined by the degree of isolation from river channels (Ellis et al. 1979; Dunson et al. 1997). Although fish abundance may be related to habitat availability, above certain threshold values, other factors may outweigh habitat limitation, especially for large, predatory species such as black basses *Micropterus* spp. (Orth and Maughan 1982).

In lakes, sustained high water may induce declines in submerged vegetation and expansion of emergent vegetation (Aumen and Gray 1995). Water level changes have been associated with shifts between alternative stable states in lakes (e.g., Blindow et al. 1993). Prolonged high water may lead to green, phytoplankton-dominated lakes whereas low water promotes clear, macrophyte-dominated lakes (Blindow et al. 1993). Changes in habitat can alter fish assemblage characteristics. For example, sport fish abundance is generally greater during the macrophyte stage (Blindow et al. 1993).

For lakes that have had historic water level fluctuations stabilized by water control structures, water level manipulation can be an important fisheries management tool. Lake Tohopekaliga, Florida, has undergone drawdowns to improve fish habitat (Holcomb and Wegener 1971; Moyer et al. 1995). These water level manipulations, once supplemented with muck removal (Moyer et al. 1995), resulted in improved fish spawning and nursery habitat (Holcomb and Wegener 1971; Moyer et al. 1995).

Movements/habitat use

Increasing water levels provide new habitat for many species of fishes. There is substantial documentation of inundated floodplain use by fishes (e.g., Guillory 1979; Bowen and Allanson 1982; Kwak 1988; Baker and Killgore 1994; Turner et al. 1994; Flotemersch et al. 1997; Woodward and Noble 1997; Snedden et al. 1999; Garutti and Figueiredo-Garutti 2000). In Florida, Leitman et al. (1991) documented extensive use of Apalachicola River floodplain habitats by nearly 40 fish species. Several species have been collected from the Kissimmee River, Florida, floodplain (Toth 1991, 1993; Furse et al. 1996). Sport fish, including largemouth bass, were among those species using floodplains in Florida. Several small fish species, many common in Florida, have been considered by different authors to be floodplain-associated species (Leitman et al. 1991; Toth 1991; Pezold 1998).

Hydrology can play an important role in determining fish distributions and habitat use in other habitats besides floodplains. Lake levels influence fish distributions in Lake Okeechobee, Florida (Aumen and Gray 1995). Flow and connectivity also mediate use of side channel habitats along rivers (Ellis et al. 1979; Toth 1993). VanGenechten (1999) found hydrological variables (i.e., depth and velocity), along with vegetation, to be significant predictors of species-specific fish habitat use in the Wekiva River, Florida. Hydraulic variables also have been correlated with microhabitat preferences of fish in other regions (e.g., Beecher et al. 1993; Conklin et al. 1995). During flooding, many fish species will move to areas with less current, leaving only fluvial specialists in relatively exposed habitats (Kelsch 1994). Peterson and Meador (1994) reviewed the effects of salinity on freshwater fishes and found that salinity, which is influenced by stream flow, can effect fish habitat use.

Stream flow can influence fish movements as well as specific habitat use. Largemouth bass may move into side channels with increased flow (Furse et al. 1996). Channel catfish move to river sections that maintain connectivity with floodplains during high flow (Flotemersch et al. 1997). Movements of Gulf of Mexico sturgeon (Wooley and Crateau 1985; Chapman and Carr 1995), spotted gar *Lepisosteus oculatus* (Snedden et al. 1999), American eel (Martin 1995), striped bass (Lamprecht and Shelton 1986), white bass larvae (Starnes et al. 1983), and hybrid striped bass x white bass (Yeager 1982) have been correlated with increased stream flow. Conversely, Foster and Clugston (1997) failed to find a relationship between movements of Gulf of Mexico sturgeon and river discharge. Also, Freeman (1995) found that 40 % of long distance movements of juvenile redbreast sunfish and adult blackbanded darter *Percina nigrofasciatum* were not associated with high flow events.

Groundwater discharge can be important to fishes because its consistent, relatively cool temperature provides a thermal refuge for fishes near their southern range limit in the southeast

USA. Such summertime use of springs as thermal refugia has been reported for Gulf of Mexico sturgeon (Chapman and Carr 1995; Carr et al. 1996; Foster and Clugston 1997) and striped bass (Wooley and Crateau 1983; Braschler et al. 1988; Weeks and Van Den Avyle 1996).

Nutrient/energy inputs

Import of nutrients or energy from terrestrial systems to aquatic systems (i.e., land-water subsidy), from wetlands to lakes and streams, and from rivers to estuaries can be important in maintaining or enhancing system productivity and therefore, fish production. Allochthonous inputs occur and may be substantial even under low or normal flow conditions (e.g., Cloe and Garman 1996). Benke et al. 2000 described the land-water subsidy for the Ogeechee River, Georgia, a coastal plain stream with an associated floodplain. High lake levels can also lead to increased chlorophyll concentrations partly due to greater nutrient availability (Maceina 1993). Furthermore, Day et al. (1981) reported on the direct link between swamps and floodplain forests and the productivity of estuaries in the southeast USA.

From a management perspective, nutrient inputs from flooding can be used to enhance fish production. The common reservoir management practice of autumn drawdown and spring flooding of terrestrial vegetation uses the nutrient pulse to stimulate system productivity (Keith 1975).

Timing of inundation of floodplains influences the importance of allochthonous inputs. For example, in the Ohio River, flooding occurs at times of low temperatures and minimal plant production. Allochthonous organic material is too depleted to support a food web and most productivity originates in the river itself (Thorp et al. 1998).

Water quality/fish health

Water flows and levels can effect fish populations through degradation of water quality and impacts on fish health. Two of the most common water quality issues related to water levels are hypoxia and salinity. Hypoxia may occur in inundated floodplains due to the decomposition of organic material, limiting use of these areas by most fishes (Toth 1993; Furse et al. 1996; Sabo et al. 1999; Fontenot et al. 2001) and causing fish kills (Sabo et al. 1999). Varying river discharge causes variability in salinity gradients in estuaries. Peterson and Meador (1994) reviewed the effects of salinity on freshwater fishes in the southeast USA, noting that salinity, especially in combination with other environmental and physiological factors, can influence fish distribution and habitat use. Marine fishes may be sensitive to changes in salinity and this sensitivity is life stage, species, and estuary-specific (Christensen et al. 1997).

Changes in flow or water levels can also alter the effect of pollutants in aquatic systems. Bennett et al. (1995) discovered that larval striped bass in the San Francisco Bay estuary showed signs of toxic exposure during periods of low freshwater input (i.e., drought conditions). They concluded that this condition resulted from undiluted run-off of toxic materials from the land. Water level fluctuations have also been shown to effect the bioavailability and fish tissue concentration of mercury in coastal plain wetlands (Snodgrass et al. 2000). Streever (1992) documented a kill of cave fauna, including fish and invertebrates, following inundation of Peacock Cave by flood waters of the Suwannee River, Florida. The mechanism was unknown, but the author suggested hypoxia or toxins as possibilities.

Modifying factors

It is clear from the literature that water level changes have profound implications for fish populations. However, the effects of water level fluctuations are dependent on numerous factors. The interaction of factors may well prove to influence fish more than any factor in isolation (e.g., Schramm et al. 2000).

Regional fish fauna composition is an important factor because certain species benefit more than others from high water (e.g., species that spawn on floodplains). Some southeast USA coastal plain fishes are considered floodplain-associated species (e.g., Leitman et al. 1991). These fishes may largely rely on floodplains for their persistence in portions of the Florida Panhandle. A great variety of wetland habitats are widespread throughout peninsular Florida, however, perhaps lessening these species reliance on traditional floodplains. Unlike the Mississippi River system (e.g., Baker and Killgore 1994), Florida has relatively few main channel species that are commonly considered to require wooded floodplains as spawning or nursery habitat. Forested floodplain habitat is more common along Florida Panhandle streams, the Suwannee River, and a few tributaries of the St. Johns River than elsewhere in the state (Seaman 1985). Nevertheless, Florida has numerous fish species which will use broad-leaf or wooded floodplains as habitat or for feeding. These include species that support important recreational fisheries (e.g., catfish and sunfish). Many fishes also benefit from flow-related nutrient inputs to system productivity, especially in estuaries (Livingston 1997; Livingston et al. 1997; Lorenz 1999).

Life stage structure can determine general effects of flow events on fishes. Floods can increase mortality and displace fishes. However, larger fishes are less susceptible to flooding than are small fishes (Harvey 1987; Jensen and Johnsen 1999). Growth effects may also be stage-dependent (e.g., Putnam et al. 1995; Jensen and Johnsen 1999).

The nature of the habitat plays a role in effects of water levels. Rising waters more likely effect fishes if a floodplain or wetland is connected to the system. Systems with steep banks and small floodplains (e.g., portions of the upper Suwannee River) potentially have fewer benefits than areas with extensive floodplains (e.g., Apalachicola River and the lower Suwannee River). Large marshes are associated with many Florida lakes. Fish will respond more to water level changes in these systems than, for instance, the sand-hill lakes of central Florida or constructed phosphate pits, many of which completely lack a floodplain. The broad marshes of the upper St. Johns River and the greater Everglades region experience some of the most extensive changes in fish populations associated with water level changes. These systems undergo alternating periods of flood and drought. Fish numbers, often dominated by small-bodied cyprinodontiform fishes, dramatically expand as rising waters inundate thousands of hectares of marsh and drastically decline during low water as fish are then relegated to refugia offered by canals, sloughs, and solution holes (e.g., DeAngelis et al. 1997).

Magnitude of the high water events must be sufficient to cause a response in fishes. High water depth and duration must be such that fishes can meaningfully access the flooded habitat. It takes time for fishes to spawn, eggs to hatch, and larvae or juveniles to move off the floodplain. This critical time interval is life history dependent. In particular, nursery functions require a relatively long hydroperiod. Even fishes that are not traditionally considered as floodplain dependent will spawn in flooded areas if the highwater period is long enough (e.g., largemouth bass; see Keith 1975). Furthermore, growth benefits of feeding on inundated floodplains also take time. On the other hand, temporal dynamics of nutrient inputs from flood events are less certain.

Little is know about how frequency of water level events influences fish populations. Logically, the importance of frequency to spawning and overall recruitment should differ based on life history. Long-lived fishes should be influenced less overall than short-lived species. Striped bass are long-lived and periodic flow-related recruitment failures do not broadly effect their populations (Van Den Avyle and Maynard 1994). On the other hand, small, short-lived fishes in Everglades marshes may take up to a year to recover from a major drought (DeAngelis et al. 1997). Exploitation rate of fisheries might modify this general relationship. Even long-lived fishes may require frequent water level-related recruitment boosts if exploitation mortality is high.

Predictability is a critical factor in long-term responses of fishes to hydrology. Predictable hydrology is more likely to effect fishes in a positive manner because life history strategies may then exploit the water level fluctuations. Unpredictability was concluded to be a major reason that Murray-Darling River fishes lacked much response to flooding and failed to use floodplains extensively for feeding or reproduction (Humphries et al. 1999). The stochastic nature of flows of regulated rivers is often the cause of deleterious effects on fishes in these systems (see Stalnaker 1980).

Timing is perhaps the most important factor affecting the response of fishes to water level changes. If temperatures are too low or changes do not coincide with spawning or growing seasons, potential benefits of high water for fishes may be lost. Flooding on the Ohio River occurs in winter, the temperature is too low for fish spawning or growth, and nutrient inputs are lost to the food web (Thorp et al. 1998). Schramm et al. (2000) found that catfish growth in the Mississippi River was positively correlated only with the combination of floodplain inundation and temperatures high enough for catfish feeding. On the other hand, rapid water level fluctuations during spawning may cause reproduction failures (e.g., Mitchill 1982; Lukas and Orth 1993).

Timing and predictability are two factors about which much information is generally known. Otherwise, little is understood concerning the minimum magnitude, duration, and interval of high water events needed to maintain fish populations and fisheries. In particular, life history influences, nutrient pulse dynamics, and trophic linkages need research. On the other hand, additional research into empirical relationships of fish population responses to the factors of timing, duration, interval, and magnitude can more directly lead to a better understanding of the effects of water management on fisheries.

Habitat and predictive models

The importance of instream flows to fish populations is becoming more recognized, especially for river sections below dams and coldwater streams. Several basic model types (e.g., Instream Flow Incremental Methodology/IFIM) and thousands of their variants have been used to predict the responses of fishes to water level and instream flow changes (e.g., Hatfield and Bruce 2000). Almost all of these models predict the amount of available fish habitat over a range of flows using hydraulic variables and fish habitat use or preference data. The output is often in the form of habitat curves showing weighted usable area (WUA; the amount of usable habitat for a specific fish species defined by flows). The basic assumptions underlying all these models are that more habitat equals more fish and that habitat availability is the most important factor in determining fish populations in streams (Zorn and Seelbach 1995). They have been heavily applied to salmonids with some degree of success (Zorn and Seelbach 1995). On the other hand, instream flow models have been little applied to warmwater streams. The models have also met with mixed results when used for warmwater systems. They seem to work best with small fishes and overestimate abundance of large species of higher trophic levels (e.g., smallmouth bass *Micropterus dolomieu*) (Zorn and Seelbach 1995). Quantitative habitat models are little used for southeast USA coastal plain streams.

There are additional problems associated with use of habitat models. Many models are data-intensive and it is therefore expensive to estimate model parameters. Moreover, there is substantial evidence that general models are not accurate over a wide range of streams and that stream and species-specific models may be necessary (e.g., Waite and Barnhart 1992). Furthermore, the habitat models generally have not been adequately linked to biological responses (E. A. Engineering and Technology, Inc. 1986), although coupling habitat models with population response (Cheslak and Jacobson 1990) or individual-based population models (Van Winkle et al. 1998) shows promise. Indeed, Kondolf et al. (2000) cautioned that information from hydraulic models is not a substitute for biological understanding. Therefore, the applicability of the present habitat models developed mostly for coldwater streams and salmonids to Florida systems and species is in question.

On the other hand, models predicting fish responses to fluctuating water levels, some qualitative, have been applied to Florida systems. Restoration projects in the Everglades and the Kissimmee River have provided the impetus for the development of these models. For the Kissimmee River, Dahm et al. (1995) and Trexler (1995) made qualitative predictions based on concepts of river-floodplain ecology. Both anticipated increased primary productivity due to influx of floodplain nutrients and expanded fish assemblages using reopened channel and inundated floodplain habitats. Small-bodied fishes in Everglades marshes have been the subjects of quantitative models predicting seasonal fish production based on hydrology (DeAngelis et al. 1997; Gaff et al. 2000).

Alternative hypothesis

The primary ecological paradigm applied to large river systems stresses the importance of floodplains for river productivity and fish populations (i.e., the basis of flood-pulse and river continuum concepts). Nevertheless, there is an alternative hypothesis that seeks to explain river productivity and riverine fish ecology. The riverine productivity model is an alternative which has received attention and has garnered supporting data. For example, Thorp et al. (1998) rejected flood-pulse and river-continuum concepts in favor of the riverine productivity model for the Ohio River. This concept states that within channel productivity is far more important than allochthonous inputs to productivity in systems with limited floodplains or where floodplain inundation is poorly timed to provide for fish spawning, fish growth, or entrance of allochthonous materials into foodwebs (i.e., floods occur in cold weather) (see Thorp and Delong 1994). There is evidence to suggest that some rivers have shifted more to the riverine productivity pathway due to loss of historic floodplains (Rutherford et al. 1995).

Management implications

Water level fluctuations have numerous management implications. Fisheries regulations can be set or modified based on historic, observed, or anticipated hydrology. For systems where flow or water level manipulation is a possibility, water management can be used for fisheries management purposes. Lastly, given the past history of hydrology alteration for water management and the present and future demands for ground and surface water resources in Florida, fisheries implications can be an important consideration for water management projects and policies.

Fisheries managers may modify recreational fishing regulations in response to low water conditions, typically in order to protect valuable brood and trophy fish (e.g., during reservoir drawdowns). If models of fish responses to river and lake hydrology were developed, managers would have powerful tools to protect and promote fisheries. Buynak et al. (1999) developed regression models to predict changes in largemouth bass recruitment based on reservoir discharge. They suggest the implementation of management actions based on these predictions prior to the occurrence of undesirable changes in the fish population. A proactive management style could be used if dependable, general or water body-specific models can be developed for Florida systems. A proactive approach to fishery management using hydrology-based models has advantages over a reactive approach by possibly dampening downward cycles in fish recruitment or size structure and by preserving fishery quality over extended periods.

Water level manipulation for fisheries management purposes is a common tactic for the regulation of reservoir fisheries (Keith 1975; Ploskey 1982). Water levels are usually dropped in late summer or autumn to allow growth of terrestrial vegetation on exposed bottom. Reservoir levels are then increased in late winter or early spring, flooding the vegetation and increasing reservoir size. This approach favors reproduction, early survival, and recruitment of sport fish such as largemouth bass (Keith 1975) and white crappie (Beam 1983). In Florida lakes, restoration of historic water level fluctuations by coffer dam removal can enhance fisheries (e.g., Hill et al. 1994). Furthermore, for lakes where dam removal is not desirable or possible, periodic drawdowns, perhaps with accompanying muck removal, can enhance fish habitat and temporarily reverse deleterious consequences of water level stabilization (Holcomb and Wegener 1971; Moyer et al. 1995). In Florida lakes and reservoirs, water level manipulation seems to promote fisheries mainly through habitat enhancement (i.e., aquatic plant manipulation). Lastly, evaluations of habitat enhancement or restoration efforts can be made within the framework of fish responses to water levels. Trexler (1995) used ecosystem function relative to floodplain use by fishes to make predictions and suggest goals for the Kissimmee River Restoration Project..

Many aquatic systems in Florida have altered hydrology due to canal building, channelization, water control structures, or water withdrawals. Some projects have been undertaken with little or no consideration of their effect on fish populations or fisheries. With a better understanding of the socioeconomic and ecological value of fishes and a generally greater environmental awareness by water resource managers, politicians, and the public, fish and other biotic components of aquatic systems are being given more consideration during design and implementation of water management programs. For example, instream flow requirements of fishes are becoming more recognized in water release schedules of dams and hydropower facilities (Tyus 1990). Fisheries managers often do not have authority over water quantity issues, but cooperation between fisheries managers and water resource managers can result in projects that not only meet water management objectives, but do so in ways that produce minimal negative impacts to fisheries. Cardwell et al. (1996) used simulations based on an optimization model to provide resource managers with a range of alternatives involving trade-offs between water storage and fish populations. In certain cases, water regulation projects can be modified to enhance fisheries. A recent example is the Yolo Baypass, California, a project demonstrating the compatibility of water regulation and fisheries (Sommer et al. 2001). This project maintained floodplain connectivity and function (e.g., fish spawning and nursery habitat and nutrient export to the San Francisco Bay estuary) while simultaneously providing flood control.

Multiple use of aquatic resources and human population growth require that management decisions be based on timely scientific evaluation. Poor resource management harms one resource to control or deliver another when compatible alternatives are present. Effective management of water resources for consumptive uses should therefore consider individual biotic components (e.g., fishes), ecosystem function, and natural resource stakeholders.

Conclusions and future research

The ecological principles relating high water events (e.g., floodplain inundation) and the responses of fishes are generally known. The flood pulse concept (Junk et al. 1989), the river-continuum (Vannote et al. 1980; Sedell et al. 1989), and other ecological concepts provide theoretical frameworks for linking rivers and floodplains relative to fish and riverine ecology. At their core, each of these concepts stresses the importance of water level fluctuations and river-floodplain connectivity for fishes. However, it is apparent in the literature that, although the ecological concepts are understood, documentation supporting these concepts is often lacking or equivocal. Crance (1988) noted that quantification of nutrient inputs, productivity, and trophic relationships is especially needed. Less structured, but perhaps better documented, is the body of knowledge concerning mechanisms for potential effects of water level changes on fishes (e.g., fish spawning on floodplains). Many researchers have measured some difference in fish populations correlated with a water level change and then reported inferred mechanisms. Although there are numerous empirical studies demonstrating that the potential mechanisms operate, there are relatively few studies linking these mechanisms with fish population responses relative to water levels.

The hypothesis that river and lake fish populations benefit from periodic floodplain inundation is well-supported theoretically and generally supported empirically. This holds for a broad range of fish species, habitats, and geographic areas. It is equally clear empirically that water level fluctuations can have both positive and negative effects on fishes. Timing of water level changes seems to be the most critical factor in determining the direction and extent of any effect. Also important are duration and magnitude of flooding events, habitat characteristics, and regional fish fauna composition.

A lack of quantitative predictive ability is a general criticism of much of ecology (Peters 1991) and may be applied to our present understanding of fish responses to changes in instream flow and lake levels in Florida and the adjacent southeast USA. What is generally lacking in the literature are estimates of the magnitude of effect on fish populations induced by specific changes in water level. Critical information about minimum necessary inundation values (e.g., duration, frequency, percent floodplain inundation), life stage-specific warm-water fish habitat and life history requirements, and fish assemblage and demographic characteristics relative to hydrology is needed to make the leap from qualitative to quantitative predictive ability. In particular, there is very little published information concerning the life history of many nongame fish species.

General predictive models may be developed for water bodies in the state or specific models may need to be applied to each system type (e.g., by trophic state of lake), each region, or individual water body. Simple, empirical models are used to predict fish biomass from trophic state indicators such as phosphorus concentration in lakes (Bachmann et al. 1996) and streams (Hoyer and Canfield 1991). It may be possible to develop similar regression models predicting recruitment or production from lake or stream stage values. More complex models incorporating time lags, temperature, percent floodplain inundation, or other factors may be necessary to provide the level of precision required for fisheries management. Alternately, habitat type models (e.g., IFIM) could be tested for Florida systems. On a broad scale, more habitat certainly equates to more fish. Nevertheless, there are numerous technical and theoretical obstacles to the widespread use of present habitat models in Florida's warm-water streams and lakes. Additional hurdles to overcome for any modeling effort will be unexpected contrary responses in observed data (e.g., high water resulting in lowered fish production) and how best to incorporate stochastic events into the models (e.g., hurricane effects).

Relatively little is published concerning the effects of water level changes on fishes in Florida systems. Floodplain use is important for fishes in the two most studied river systems, the Apalachicola and Kissimmee rivers. River discharge is also important for maintaining productivity of estuaries such as Apalachicola Bay and Florida Bay. Water level in Florida marshes is the dominant factor influencing populations of small fishes. Also, water level fluctuations seem to be important in natural lakes for maintaining fish habitat (i.e., aquatic macrophytes) and fish populations. Clearly, much research is needed in all Florida aquatic habitats to provide needed information for fisheries and water resource management decisions.

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APPENDIX A

Keywords and taxa searched

Keywords

allochthonous
cohort
dispersal
drought
duration
essential fish habitat
feeding
fish
flood
Florida
habitat
high
hydraulic regime
hydrobiology
hydroperiod
instream flow
inundation
level
MFL
minimum flow
minimum depth
periodicity
pulse
recruitment
reproduction
spate
spawning
stage
timing
use/utilization
water
year class

Taxa

brown hoplo *Hoplosternum littorale*
redbreast sunfish *Lepomis auritus*
spotted sunfish *Lepomis punctatus*
largemouth bass *Micropterus salmoides*
striped bass *Morone saxatilis*
bluenose shiner *Pteronotropis welaka*
Unionidae