# Potential Impacts of Global Climate Change on Warmwater Fisheries of the USA

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## Executive Summary

Warmwater fishes are a valuable component of freshwater ecosystems and support important recreational fisheries in the United States. Angling effort for warmwater sport fishes provided a large portion of the $21.3 billion spent in 2001 on freshwater sport fishing in the United States. We reviewed the scientific literature to evaluate the potential impacts of global warming on warmwater fisheries of the USA. We focused the review on the most popular warmwater sport fish in the US, including potential impacts to populations of largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomeui*, spotted bass *M. punctatus*, black crappie *Pomoxis nigromaculatus*, white crappie *P. annularis*, walleye *Sander vitreus*, white bass *Morone chrysops*, striped bass *M. saxatilis*, channel catfish *Ictalurus punctatus*, flathead catfish *Pylodictis olivaris*, and blue catfish *I. furcatus.* Global warming would intuitively be expected to benefit these warmwater fishes, but effects of climate change on fish ecology and distribution may be large, and in some cases, counterintuitive.

Perhaps the strongest impacts of global warming on aquatic ecosystems will result from changes in precipitation. There is a general consensus in the literature that there will be a rise in the severity and duration of both drought and high water periods. With exaggerated weather patterns, the frequency of dry days has been predicted to increase. Several key studies concluded that summer droughts will increase in severity and duration, and these droughts will be followed by pulses of extreme high-water events. Thus, a consistent trend in the literature predicts that global warming will increase variability in inter-annual water flows for rivers, and water levels in lakes. Although variability is a natural component of ecosystems, highly variable hydrologic regimes can disrupt the shape of river channels, decrease shoreline stability, increase sediment loads, and decrease cover of aquatic vegetation.

As temperatures increase, many warmwater sport fish will benefit from longer periods with temperatures favorable to growth and a significant decrease in winterkill, allowing occupation of areas previously less favorable. This will most likely mean an expansion of range northward and to higher elevations for many warmwater fishes. However, warmer water temperatures are also associated with lower dissolved oxygen, which can be a powerful determinant of species composition in lakes and rivers. The combination of low dissolved oxygen and high temperatures can be especially problematic in deep, stratified water bodies where fish adapted to cooler, more oxygen rich waters can become squeezed between low

oxygen and high temperature layers.  Thus, a contraction of suitable territory will occur in areas where species are currently at the warmest extent of their ranges.  The implications of this could be dramatic for some popular fisheries, such as walleye fisheries in Arkansas and smallmouth bass fisheries in Alabama.  However, the overall effect of warmer temperatures will result in a net expansion of favorable habitats for most species of warmwater sport fish.  Threats from exotic fishes, most of which are tropical in origin, are expected to increase as the thermal environment becomes closer their optimal range.

Because of the preeminent role of aquatic macrophytes in aquatic ecology, warmwater sport fish are often vitally dependent upon their dynamics.  Aquatic macrophytes provide habitat for macroinvertebrates, a food resource for many warmwater fishes, and critical refugia from predation for juvenile fishes including many important warmwater sport fish.  Variable water level conditions would tend to favor generalist and fast growing species over species which thrive in late-succession stages of aquatic systems.  The increased advantage afforded plants suited to warmer conditions is an important factor when considering the future expansion of noxious exotic plant species such as giant salvinia *Salvinia molesta*, hydrilla *Hydrilla verticillata* and eurasion watermilfoil *Myriophyllum spicatum*.  Many exotic and invasive aquatic plants are tropical in origin and would benefit from warmer temperatures.  Thus, global warming would be expected to increase the occurrence and growth rates of tropical aquatic plants.  Methods to prevent new invasive species from entering the US, as well as control the spread of currently established species, will be more important in the future as climate conditions become more suitable for their growth.

Our review revealed some region-specific predictions that will be useful as fisheries management agencies begin to plan for the future.  Higher water temperatures are predicted in all regions of the US. Regions across the US will also experience supply and demand issues with increasingly limited water resources due to regional combinations of rapidly expanding human populations (particularly in the Northeast and Southeast), high demand water uses (agriculture, industrial and commercial, etc.),  and more variable rainfall patterns.  However, other impacts of higher temperatures and altered precipitation trends will vary by region.  For example, the Great Lakes are predicted to have stronger lake stratification, decreased occurrence of winter anoxia, and lower lake levels.  The western US states are expected to have lower snow volumes resulting in lower spring/summer streamflows.  Arid regions in the western US are expected to have more variable flows and critically warmer stream temperatures. Variable conditions are expected to affect the Northeast as well. The Midwest is predicted to have increased salinity of lake waters, decreased area of the pothole lake region, and more variable precipitation patterns. Eutrophication and anoxia (low dissolved oxygen) should increase in the Southeast. Thus, the review indicated potential for different challenges in different parts of the US, and fisheries management agencies should consider these challenges as they initiate new monitoring and management programs.

Coastal rivers and lakes will likely be influenced by sea level rise around the US. The literature contains substantial evidence that sea levels will rise, with predicted rise being about 0.4 m increase by the year 2100. Higher sea levels will influence estuaries and cause higher salinity water to encroach into freshwater portions of rivers, overland into low lying areas, and into freshwater aquifers. This salinization of freshwater habitats will cause a contraction of suitable habitat for obligate freshwater species. Low elevation gradient coastal areas and areas where organisms have no escape options from high salinity conditions, such as coastal wetlands and dammed coastal rivers, will be most susceptible to the effects of sea level rise.

In summary, our review revealed a number of predicted impacts to warmwater sport fish in the US. The strongest impacts are predicted to be changes in precipitation levels, which can have dramatic influence on fishing quality across large spatial scales. The literature provides strong evidence that water levels in lakes and rivers will be more variable in the future, with more extreme highs and lows. Because fish recruitment to adulthood is frequently tied to water levels in lakes and rivers, we surmise that more extreme drought and high-water events would cause larger fluctuations in the quality of recreational fisheries. The implications of more variable water levels for anglers means that travel distance to reach quality fisheries may increase substantially, and occurrence of “boom and bust” fisheries would become more common. Fisheries managers will need to consider management actions that stabilize fisheries, such as use of harvest regulations to protect adult fish, water use and water allocation measures to protect fish habitat, and habitat enhancement efforts to improve fish recruitment during periods of poor habitat conditions (e.g., low water). Warmer water temperatures will alter fish distributions and the threat of exotic plants and animals will increase. These scenarios present unique challenges in different parts of the country, with different implications for maintaining water quality and quantity necessary for healthy fisheries. Fisheries management agencies should consider these points as they develop new management strategies in the future.

## Introduction

Climate change has produced changes to the environmental conditions of the United States and will continue to do so in this century (Houghton et al. 2001; Wigley and Raper 2001). A defining element of this climate change is an increase in mean temperature. Increases in temperatures will cause numerous impacts that may have serious consequences for freshwater ecosystems.

Warmwater fishes are a valuable component of freshwater ecosystems and support important recreational fisheries in the United States. The effects of climate change on warmwater fish ecology and distribution may be large, and in some cases counterintuitive. Because changing climate will likely influence management options in the future, resource managers should be aware of the potential impacts of global climate on fisheries resources.

Temperature is an important driver of all global systems. Meteorological systems are intricately tied to the thermal characteristics of the atmosphere. Increases in global mean temperature are expected to alter rain and snowfall patterns (Cubasch et al. 1995; McCarthy et al. 2001) across the United States. Coupled with increased temperatures, the changes to meteorological cycles will have serious effects on hydrology. Ice and snowfall dynamics, river flows, lake levels, runoff, and drought and flood events are all expected to undergo changes (Carpenter et al. 1992; Meyer et al. 1999; Murdoch et al 2000). Water quality variables including dissolved oxygen (DO), temperature, turbidity, dissolved solutes, and pH of surface waters are expected to respond as well (Schindler et al. 1997; Murdoch et al. 2000). These changes will be beneficial or detrimental to current conditions in freshwater environments depending upon the species and systems considered (Hurd et al. 1999; Lettenmaier 1999; Poff et al. 2002).

## Warmwater Fishes

Warmwater fishes are defined simply as a group of fishes that are biologically adapted to maintain optimal functioning within a range of temperatures about 7-10$^{o}$C around 30$^{o}$C (Magnuson et al. 1979; Wehrly et al. 2003). In terms of economic and ecological significance, some of the primary species include largemouth bass *Micropterus salmoides,* smallmouth bass

*M. dolomeui*, spotted bass *M. punctatus*, black crappie *Pomoxis nigromaculatus*, white crappie *P. annularis*, sunfishes *Lepomis spp.*, walleye *Sander vitreus* , white bass *Morone chrysops*, striped bass *Morone sexatilis,* channel catfish *Ictalurus punctatus*, flathead catfish *Pylodictis olivaris*, and blue catfish *I. furcatus*. The range of these fishes extends north past the Canadian border, south into the far southern states, west to the western of the Mississippi drainages, and east into many of the water bodies of the Atlantic Coastal Plain (Mettee et al. 1996; Carlander 1969). Some populations have been established in western states including California, Nevada, New Mexico, and Arizona (Mette et al. 1996; Carlander 1969). Smallmouth bass, walleye, and striped bass are frequently described as cool water fishes (e.g. Eaton and Scheller 1996), but we considered these species given their association with many warmwater fisheries. Because of their preference for slightly cooler habitats their range does not extend as far south as many of the other species, with the exception of the striped bass.

Like all fishes, warmwater fish are dependent on the quality and quantity of water. Warmwater fishes are adapted to a specific range of chemical and physical conditions, as dictated by species tolerances. The meteorological and hydrological changes that will occur with climate change will produce changes, in some cases drastic changes, to the chemical and physical habitats that these species currently use. Mechanisms used to cope to these new environments have potential to stress fish if certain tolerance ranges are exceeded. This stress, or lack of stress given proper conditions, in turn, will determine the metrics of populations and individuals within a species.

Warmwater sport fishes are extremely important species economically and ecologically. Angling effort for warmwater sport fishes provided a large portion of the $21.3 billion spent in 2001 on freshwater sport fishing in the United States (Census Bureau, 2002). Some species (e.g., catfishes) also support important commercial fisheries throughout their range. As ecological resources, they are upper trophic level predators. Their presence or absence can have serious consequences for the vitality and structure of aquatic communities (Carpenter et al. 1992).

## Objectives

Our objectives were to 1) evaluate the broader literature to elucidate predicted trends in climate change with respect to temperature, hydrology and aquatic plants, 2) review the spawning temperatures of warmwater fishes and discuss potential range changes, 3) describe how fish abundance could change as a result of altered habitat conditions and subsequent species interactions, and 4) outline research and monitoring needs in the future.

## Predicted Trends in Temperature and Hydrology

Throughout the earth's history there have been global mean temperature fluctuations over many different magnitudes and timeframes. Many of these changes have occurred over the range of only a few degrees Celsius. Although seemingly small, changes of this size have been shown to produce large effects on Earth's physical and biological systems (Houghton et al 2001; Walther et al. 2002; Regonda et al. 2005)

Currently there is a trend of increasing temperatures, yielding the warmest temperatures in the last thousand years (Jones et al. 1999). Several studies have concluded that global mean temperatures have increased 0.3$^{o}$C-0.6$^{o}$C in the last century (Jones et al. 1999; Peterson et al. 1999; Houghton et al. 2001). Average North American temperatures have risen about 0.7$^{o}$C over the same period (Houghton et al. 2001).

This increasing trend is expected to continue in the next century. Many climate models have been used to evaluate various warming scenarios, producing a diversity of projected climate responses. Nevertheless, there is a trend and a general consensus of projections. Based on the results of several climate forcing models, the Intergovernmental Panel on Climate Change (Houghton et al. 2001) projected that, between 1990 and 2100 global warming of 1.4-5.8$^{o}$C can be expected. The report adds that it is most likely that actual temperature rise during this time period will occur at a level between these two values, and not towards their extremes. Other studies have produced similar results (Wigley and Raper 2001), with an average expected warming of about 3$^{o}$C over the next century. In addition to increases in mean temperatures, extreme heat events will also become more common and intense (Kharin and Zwiers 2000; Meehl and Tebaldi 2004). Diurnal temperature ranges will also decrease (Houghton et al. 2001).

Predictions of regional temperature changes are difficult to make because of the scale of the grids used in atmospheric climate models. However, some scenarios have been produced on models tuned to finer resolutions. Scenarios considering low emissions of greenhouse producing gasses yield estimates of temperature increase for the North America of 1-3$^{o}$C, whereas estimates assuming higher emissions in the future predict 3.5-7.5$^{o}$C increases (McCarthy et al. 2001).

Most studies agree on a scenario of warming of 2-4$^{o}$C for North America over the coming century.

Meteorological and hydrological processes (as they deal with the properties of water in the atmosphere and on the land surface, respectively) are intricately interconnected with atmospheric temperature. Each is also extremely complex and not fully understood, resulting in high uncertainty in predicting the responses of precipitation and surface water patterns to temperature changes. Nevertheless, as with temperature, there are trends common to much of the literature on the subject. Some of these trends can be seen in Table 1. These predictions are applicable over much of the United States, but there will be variation in intensity by region, as well as unique trends within regions due to the natural variability of climate between areas (see Figure 1). Owing to unique regional resource dependencies, population attributes, and land use characteristics, each region will also exhibit different vulnerabilities to these changes (Meyer et al. 1999; Murdoch et al. 2000).

Table 1. Predicted responses to global warming for the atmosphere, meteorological, and hydrological components of aquatic ecosystems.

| **System** | **Response** |
|---|---|
| Atmosphere | Increased temperatures (Houghton et al. 2001; Wigley and Raper 2001) |
| | Increased severity of heat events (Kharin and Zwiers 2000; Meehl and Tebaldi 2004) |
| Meteorological | More extreme precipitation events (Cubasch et al. 1995; Houghton et al. 2001; Benestad 2006) |
| | Increased amount of winter precipitation as rainfall (Huntington et al. 2004; Leung et al. 2004; Regonda et al. 2005) |
| | Decreased snowfall (Leung et al. 2004) |
| | Increased/decreased mean precipitation (uncertain) (Cubash 1995; Chao 1999; Kharin and Zwiers 2000; McCarthy et al. 2001) |
| Hydrological | Higher lake, river temperatures (Fang and Stefan 1997; Schindler 1997; Meyer et al. 1999) |
| | Exaggerated hydrological patterns (Karl and Knight 1998; Groisman et al. 2001) |
| | Decreased dissolved oxygen during summer (Fang and Stefan 1997; Mulholland et al. 1997; Meyer et al. 1999; Murdoch et al. 2000) |
| | Earlier snowmelt and peak spring streamflow (Hodgkins et al. 2003; Stewart et al. 2004; Regonda et al. 2005) |
| | Decreased late spring runoff (Dettinger and Cayan 1995; Hodgkins et al. 2003) |
| | Decreased snowpack, less summer snow storage (Leung et al. 2004) |
| | Earlier lake ice retreat, less ice cover (Scrimgeour et al. 1994; Vavrus et al. 1996) |
| | Longer clear period in lakes that experience (Schindler 1997) |
| | Increased waterbody productivity (Regier et al. 1990; Meyer et al. 1999; Magnuson et al. 1997; Mulholland 1997) |
| | Increased strength of lake stratification (Fang and Stefan 1997; Schindler 1997; Winder and Schindler 2005) |
| | Decreased water quality (Carpenter et al. 1992; Cruise et al. 1999) |
| | Increased saltwater intrusion into coastal rivers (McCarthy et al. 2001; Meehl et al. 2005) |
| | Lower river levels during summer, especially in areas driven by snowmelt (Hurd et al. 1999) |
| | Increased frequency of dry days (Cubash et al. 1995; Gregory et al. 1997) |
| | Decreased lake levels (uncertain) (Magnuson et al. 1997) |
| | Increased evaporation (uncertain) (Gregory et al. 1997; Wetherald and Manabe 1999; McCarthy et al. 2001). |

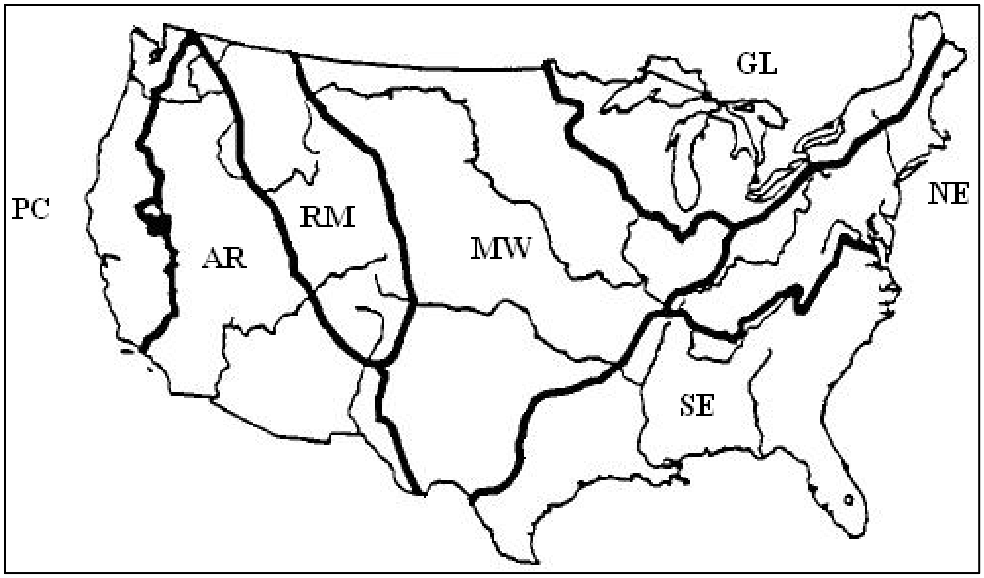


Figure 1. Summary of predicted regional effects of global warming on aquatic systems for the USA. Figure was adapted from (Leavesley et al. 1997). Regions and the predicted responses are as follows:

All Regions:

- Higher water temperatures (Hurd et al. 1999)
- Supply and demand issues stemming from limited water resources due to combinations of rapidly expanding human populations (particularly in the Northeast and Southeast), high demand water uses (agriculture, industrial and commercial, etc.), and more variable rainfall patterns (Hurd et al. 1999; Meyer et al. 1999; Murdoch et al. 2000)

AR = Arid

- High stream sensitivity to declines in spring and summer flows, variable precipitation patterns (Grimm et al. 1997; Hurd et al. 1999)
- Decreased snow volume, earlier snow thaw, higher percentage winter rainfall (Leung et al. 2004; Regonda et al. 2005)
- Increased salinity of lake waters (Covich et al. 1997)

GL = Great Lakes

- Strengthened lake stratification, altered mixing (Schindler 1997)
- Decreased winter anoxia (Fang and Stefan 1997)
- Decreased lake levels (Chao et al. 1999)

MW = Midwest and Great Plains

- Increased salinity of lake waters (Covich et al. 1997)
- Decreased area of pothole region lakes (Hurd et al. 1999)
- High stream sensitivity to declines in spring and summer flows, variable precipitation patterns (Grimm et al. 1997; Hurd et al. 1999)

Figure 1, continued.

NE = Northeast

- Decreased spring and summer river flows (Hurd et al. 1999; McCarthy et al. 2001)
- Decreased snow volume, earlier snow thaw(Huntington et al. 2004; Leung et al. 2004; Regonda et al. 2005)
- Strengthened lake stratification, altered mixing (Schindler 1997)

PC = Pacific Coast and Western Great Basin

- Decreased spring, summer river flows (Hurd et al. 1999; McCarthy et al. 2001)
- Decreased snow volume, earlier snow thaw, higher percentage winter rainfall (Leung et al. 2004; Regonda et al. 2005; Dettinger and Cayan 1995)
- Increased flow variability (Lettenmaier et al. 1999)

RM = Rocky Mountains

- Decreased snow volume, earlier snow thaw, higher percentage winter rainfall (Leung et al. 2004; Regonda et al. 2005)
- Decreased spring and summer flows (Hurd et al. 1999; McCarthy et al 2001)

SE = Southeast

- Increased anoxia, eutrophication (Meyer et al. 1999; Mulholland et al. 1997; Fang and Stefan 1997)
- Strengthened lake stratification, altered mixing (Mulholland et al. 1997)

Studies have demonstrated an increase in occurrence of extreme precipitation events over the continental United States over the last 100 years due to an increase in precipitable moisture (Karl and Knight 1998; Groisman et al. 2001). Kunkel et al. (1999) also found a statistically significant increase in short duration (1-7d) heavy precipitation events. As climates continue to warm, extreme events are forecast to increase in frequency and intensity (Cubasch et al 1995; Houghton et al. 2001; Benestad 2006).

Higher temperatures will also cause a shift in winter precipitation patterns over the areas that receive snowfall, increasing rainfall at the expense of snowfall. Leung et al. (2004) and McCabe and Wolock (1999) modeled a large decrease in future snowpacks in the Rocky Mountains as a result of increased winter temperatures and rainfall. Similar patterns, attributed to increased temperatures, have already been observed in the Rocky Mountains (Regonda et al. 2005; McCabe and Wolock 1999). On the eastern seaboard, Huntington et al. (2004) also demonstrated a significant decrease in the ratio of snow to total precipitation with increasing temperatures.

Predictions about mean yearly precipitation patterns are less consistent than trends in extreme rainfall events (Cubash 1995; Kharin and Zwiers 2000; Houghton et al. 2001). Studies involving the future behavior of evapotranspiration are also conflicting, although there seem to be indications that a future escalation could occur, especially near areas that currently tend to be arid or semiarid, as the result of increased temperatures and altered precipitation patterns (Gregory et al. 1997; Wetherald and Manabe 1999). There are many factors that moderate the level of evapotranspiration (Gregory et al. 1997), and a better understanding of these is needed before a representative projection can confidently be made.

The interaction of precipitation with temperature and evapotranspiration is key to determining the behavior of surface water hydrology, such as mean runoff amounts (McCarthy et al. 2001), drought (Gregory et al. 1997), and ultimately, lake levels and river flows. The connectivity between these variables, and their respective uncertainties, causes ambiguity in predictive models regarding their individual behaviors (Gregory et al. 1997; McCarthy et al. 2001). However, there is consistency in the literature as to the behavior of certain elements of surface waters and their direct inputs, such as snowpacks, ice cover dynamics, and pulse flooding, as well as patterns that emerge that provide a picture of the behavior of other elements.

For example, decreases in snow pack volume, combined with elevated air temperatures and increased winter precipitation as rainfall, will cause a change in timing and volume of spring snowmelt. The shift in precipitation patterns, in combination with reduced snow volume will combine to cause a larger winter portion of annual runoff (McCabe and Wolock 1999; Leung et al. 2004). As a result of the decreased snowpack storage volume, spring runoff volume will decrease (Dettinger and Cayan 1995; Hodgkins et al. 2003). Peak spring streamflows will also occur significantly earlier as warmer temperatures cause an advancement of the spring snow thaw (Hodgkins et al. 2003; Stewart et al. 2004; Regonda et al. 2005). These changes will be most felt in basins that are primarily fed by snowmelt or that have dynamics dependent upon spring snowmelt, such as the Rocky Mountain drainages and the Northeast (Lettenmaier et al. 1999; Barnett et al. 2005).

Winter ice cover will also be affected by the elevated air temperatures. Although it is unclear as to the effect of warming on ice-on dates, there is confidence that the ice-off date will be greatly advanced on lakes and rivers (Vavrus et al. 1996; Gao and Stefan 2004). With an earlier ice-off date there would be fewer total days of ice cover (Scrimgeour et al. 1994; Vavrus et al. 1996). In systems retaining ice cover, the thickness of the ice layer will be reduced. This could influence the physical and chemical transformations that occur as a result of ice cover and ice-breakup patterns (Scrimgeour et al. 1994; McCarthy et al. 2001). Ice dynamics in cold regions frequently produce the most significant hydrologic events in those systems, and alterations to ice patterns could influence nutrient dynamics, stream flow regimes, and thus biotic interactions (discussed below).

Another important projection deals with the variability of hydrological regimes. There is a general consensus that there will be a rise in the number of high water volume flooding events as the product of high runoff from single-event heavy precipitation (Groisman et al. 2001; McCarthy et al. 2001), regardless of mean precipitation levels. The increase of winter precipitation as rainfall will also contribute to the pulse inputs of water. Higher variability of flows and levels could pose greater impacts than changes in mean precipitation in many areas (Meyer et al. 1999; Murdoch et al. 2000). This prediction may be most significant for arid and semiarid regions, where runoff response to precipitation is amplified (Carpenter et al. 1992; Grimm et al. 1997). Flooding and disturbance are natural components of ecosystems, and as such, communities become dependent upon the ecological benefits they provide and the patterns of perturbation associated with them. For example, in both river and lake systems that include floodplains, flood events serve as a vital source of energy and nutrients (Poff et al. 1997). Although variability is a natural component of ecosystems, highly variable precipitation and hydrologic regimes can cause disruption of river channel morphometry, decrease shoreline stability, increase sediment loads, decrease cover of aquatic vegetation, and disrupt fish and invertebrate community structure (Tucker and Slingerland 1997; Meyer 1999).

With exaggerated weather patterns the frequency of dry days has been predicted to increase (Cubash et al. 1995; Gregory et al. 1997). Some confidence lies in the predictions of summer drought (Wetherald and Manabe 1999; Meehl et al. 2000). Studies that include increased evapotranspiration as part of their parameters indicate that increased soil moisture deficits would increase the intensity of droughts.

The quality of water in waterbodies is also sensitive to changing climates. The most obvious effect of increased air temperatures is an increase in water body temperature. Temperature is a fundamental component of chemical and biological activity in aquatic systems (Regier et al. 1990). In its most basic function, it controls the rate of chemical reactions. In this capacity higher temperature can stimulate higher nutrient cycling through higher chemical, and thus biological, activity (Regier et al. 1990). This stimulated activity has the potential to increase the productivity of systems (Carpenter et al. 1992; Magnuson et al. 1997; Mulholland 1997; Meyer et al. 1999). The resulting higher temperature and productivity would foster increased cycling of both nutrients and pollutants (Moore et al. 1997).

In addition to temperature, precipitation and hydrology patterns also have a strong effect on water qualityl. High runoff events are characterized by high levels of dissolved and suspended constituents, including nutrients, acidic components, silt, and pollutants (Carpenter et al. 1992; Meyer and Pulliam 1992; Cruise et al. 1999). Extreme high water events followed by dry periods would cause high nutrient inputs followed by extended water retention times and decreased water volumes, thus concentrating nutrients and toxins (Carpenter et al. 1992). The increase of temperatures, decrease or absence of winter ice, and altered nutrient dynamics will lead to earlier, more intense summer stratification and weakening, or even elimination of winter stratification in lakes (Fang and Stefan 1997; Schindler 1997; Winder and Schindler 2005). Increased summer stratification, possibly higher phytoplankton production, and warmer temperatures will reduce the amount of oxygen in the water during summer (Fang and Stefan

1997; Mulholland et al. 1997; Meyer et al. 1999; Murdoch et al. 2000), creating anoxic conditions for a larger portion of lake water columns. However the opposite could occur in winter where lakes experience ice-over. During ice-over in the winter, lakes frequently experience anoxic conditions highly stressful or even lethal to many biota. This condition would be ameliorated or eliminated owing to shorter ice cover periods and the subsequent weakening of winter stratification (Fang and Stefan 1997).

As with other changes, there are some general water quality patterns reflected by region and waterbody type, some of which have already been mentioned. There is a concern that lakes in the southern United States could experience increased trophic status as a result of increased nutrient contributions from sediments, resulting from elevated nutrient cycling and higher temperatures (Mulholland et al. 1997). Alternately, some northern lakes may exhibit larger euphotic zones and longer clear periods from decreased nutrient inputs (Schindler 1997). Closed basin lakes, especially prominent in the Midwest, are very vulnerable to climate change conditions because they are solely dependent on atmospheric and near-basin runoff inputs or from groundwater inputs (Covich et al. 1997).

One very important consideration for freshwaters proximate to or influenced by ocean water is the influence of sea level rise. Houghton et al. (2001), project sea level rise over the coming century to be between .09m-0.88m, with an average increase of 31 to 49 mm (Figure 2). Meehl et al. (2005) also model a similar change. The increase in sea level will cause a push of high salinity water farther into freshwater portions of rivers, overland in to low-lying areas, and in to freshwater aquifers (Gornitz 1991; Cruise et al. 1999). This salinization of freshwater habitats will cause a contraction of suitable habitat for saltwater-intolerant species (Jassby et al. 1995; Catalano et al. 2006). Low elevation gradient coastal areas (Gornitz 1991) and areas where organisms have no escape options from high salinity conditions, such as coastal wetlands and dammed coastal rivers will be most susceptible to direct effects of sea level rise.

The environmental changes resulting from elevated temperatures must be considered in the context of increasing human population growth and associated manipulation of water resources. Consumptive and non-consumptive uses, including use for industrial cooling, industrial and municipal wastewater assimilation, irrigation, and municipal consumption, all impact water resources (Hurd et al. 1999; Gleick et al. 2000; Murdoch et al. 2000; Jackson et al. 2001). Landscape manipulations from agriculture, channelization, damming, and development further alter aquatic systems. These activities affect the quality and quantity of water as much, or in excess of, the changes wrought by climate change (Dale 1997; Minns and Moore 1992; Xenopoulos et al. 2005). In watersheds that are currently stressed by these and other natural stressors, future changes in climate could magnify negative effects on the services waterbodies provide (Jackson et al. 2001). Although human manipulation of water resources can be detrimental to water resources, it is by direct human management and stewardship that there is also the most potential to ameliorate the effects of climate change (Grimm et al. 1997; Poff et al. 2002; Murdoch et al. 2000; Jackson et al. 2001).

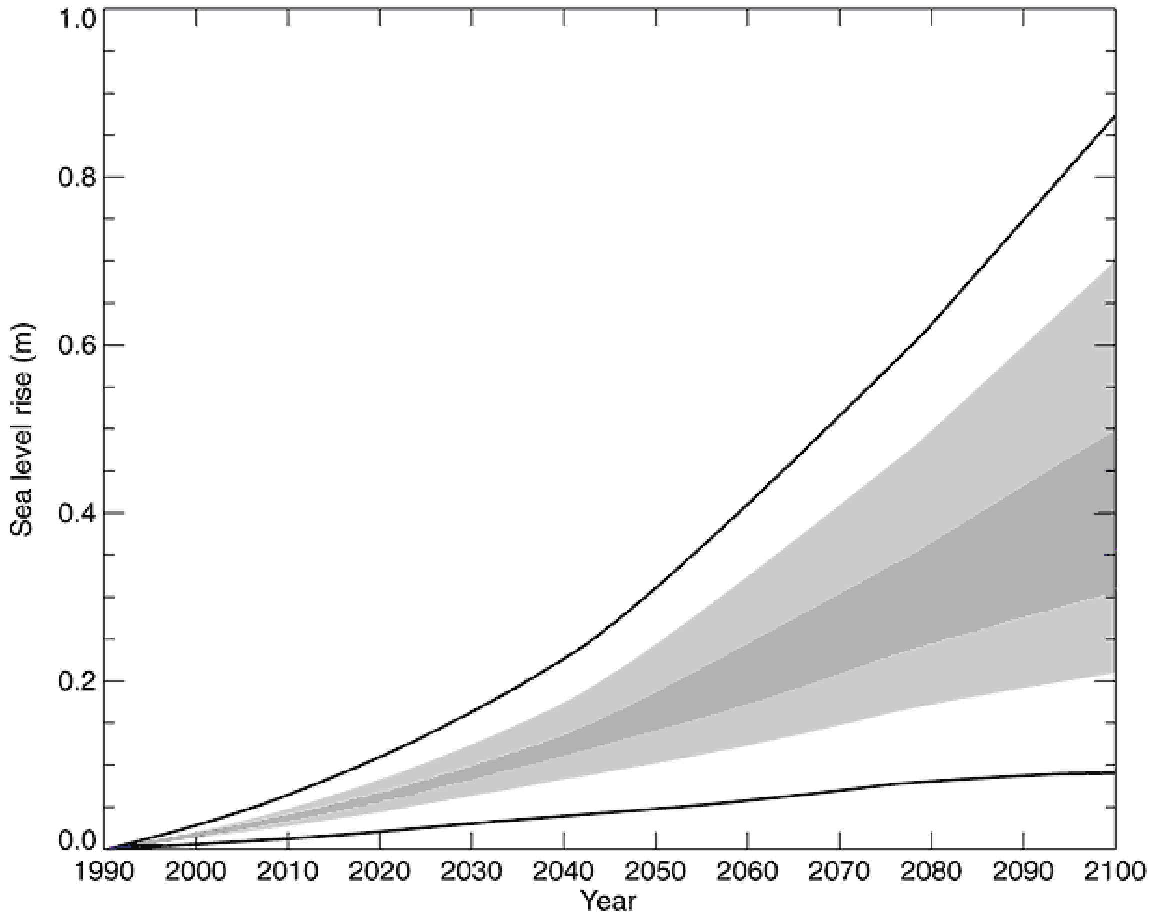


Figure 2. Global mean sea level rise. Dark region indicates mean sea level rise modeled from 35 climate models. Light region indicates full range from climate models. Dark lines indicate range of sea level rise predicted by additional scenarios (Adapted from Houghton et al. 2001).

## Effects on Aquatic Plants

The biota that is characteristic of aquatic ecosystems reflects the typical environmental conditions in those habitats. Average conditions as well as characteristic departures from those conditions are critical components in maintaining the health and diversity of systems (Poff et al. 1997). When alterations, such as those predicted to occur with climate change, are made to the regimes under which species have become established, shifts in community composition are expected to occur. Though disturbances stemming from climate change will occur on various temporal and spatial scales, they will all reshape population dynamics of aquatic communities to some degree. Changes in many different plant and animal populations have been noted already (Walther et al. 2002).

Freshwater aquatic and wetland plants (hereafter aquatic macrophytes) are important elements of freshwater environments. They contribute to ecosystem productivity and stability by providing crucial habitat and food for aquatic fauna, enhancing stability of aquatic areas, altering water flow and temperature, and influencing water quality by affecting sedimentation, cycling of chemicals including nutrients, and contributing to dissolved oxygen (Carpenter and Lodge 1986; Poff et al. 1997). Because of the preeminent role of aquatic macrophytes in aquatic ecology, it follows that fish, including warmwater sportfish, are vitally dependent upon their dynamics. Aquatic macrophytes provide habitat for macroinvertebrates, important food resources for many warmwater fishes, and critical refugia from predation for juvenile fishes including many important warmwater sportfish (Carpenter and Lodge 1986).

There is a multitude of plants associated with aquatic zones, each with specific habitat and environmental requirements. The following projections are meant to cover the response of plant communities as a whole, with some emphasis on specific groups (e.g. submerged, emergent, etc.). Although the overall picture of plant response contains uncertainty, some predictions can be made. Overall indications are that conditions will be advantageous for the growth of fast growing, generalist species suited to warm temperatures. The shift in vegetation could have important implications for warmwater fishes (Carpenter et al. 1992; Poff et al. 2002).

Because many aquatic macrophytes in the United States are limited in range and growth rate by minimum temperature, higher temperatures may prove beneficial to many species (Haag and Gorham 1977; Walther 2003; Lacoul and Freedman 2006). Higher temperatures will relieve the limitations placed on plants by cold temperatures (e.g. frost kill, dormancy) and extend the total number of days that plants experience temperatures warm enough to permit growth (Walther 2003). Accordingly, Jansson et al. (2000) associated longer growing seasons with higher diversity and plant cover.

Favorable growing conditions will also be extended in areas that experience diminished ice cover. As temperatures increase, the associated loss of ice cover will allow light conditions favorable to growth to exist a greater percentage of the year. This will foster earlier colonization and higher overwintering success of aquatic macrophytes (Haag and Gorham 1977). Less ice cover will also foster plant growth by relieving the scouring of shallow riverine habitats (Bunn and Arthington 2002). This is especially important for herbaceous macrophytes because they are typically the ones that are affected most by sheering stress and scouring caused by ice (Scrimgeour et al. 1994).

The above effects of warming temperatures will allow certain plants to more successfully compete in their traditional habitats as well as expand into new areas, most notably higher altitudes and latitudes (Walther 2003). The increased advantage afforded plants suited to warmer conditions is an important factor when considering the future expansion of exotic plant species such as giant salvinia *Salvinia molesta*, hydrilla *Hydrilla verticillata* and eurasion watermilfoil *Myriophyllum spicatum* (Madsen and Owens 2000). Many exotic and invasive aquatic plants, such as these, in the United States are tropical in origin and would benefit from warmer temperatures.

Hydraulic variability is also a primary variable controlling abundance of aquatic macrophytes (Resh et al. 1988; Poff et al. 1997; Lacoul and Freedman 2006). Highly variable hydrological patterns, like those forecast to occur from climatic warming, minimize exposure of macrophytes to the proper physical and chemical conditions necessary for establishment and reproduction. Variable conditions tend to favor generalist and fast growing species over species which thrive in late-succession, stable stages of aquatic systems (Hudon 1997; Lacoul and Freedman 2006). Invasive and/or exotic species may become favored because of their fast growth rates and lack of natural competitors. The results of Hudon (1997), support this idea, finding that large water-level variations favored generalist and exotic species in the St. Lawrence, New York, waterway.

However, the intensity of deviations can be as important as their periodicity. Large water level draw downs tend to reduce submersed and floating-leaved macrophyte abundance.

Because they inhabit the shallow littoral zone, they quickly die when exposed, but propagules may remain (Cooke 1980). Long periods of drawdown could cause regional declines in total aquatic macrophyte abundance, and would favor emergent and woody species growth in the floodplain. Thus, although more variable precipitation trends could favor fast growing invasive/exotic species, the effects of extreme water level variation could be a reduction in overall submersed and floating plant coverages.

Increased flood intensity can also alter conditions for aquatic macrophtye growth. Periods of high water level and high water inputs tend to disrupt fluvial morphology and decrease shoreline stability (Tucker and Slingerland 1997). Shifting substrates inhibit establishment of macrophytes by disrupting rooting zones and seedbeds and uprooting established plants (Hudon 1997). The effects of flooding are exacerbated during winter, when vegetation is absent or senescent and exhibits reduced ability to moderate flow and stabilize substrates.

Extreme water levels also create unfavorable light conditions for submersed plants via increased turbidity. Light availability is one of the most critical environmental factors determining the maximum depth of establishment of aquatic macrophytes (Chambers and Kalff 1985; Lacoul and Freedman 2006). The predicted exaggeration of water input to systems has the potential to increase sediment loads in lakes and rivers. Increased waterbody productivity resulting from higher temperatures could also increase turbidity by stimulating phytoplankton growth. Thus, decreased water transparency from either abiotic (i.e., sediment) or biotic (i.e., phytoplankton) sources would reduce the size of the littoral zone, which could lower aquatic plant abundance and reduce highly productive littoral fish habitat.

The services that macrophytes provide aquatic systems are numerous and many times other organisms become dependent upon a specific macrophyte species or combination of species for the unique services they provide. Lake et al. (2000) and Mulholland et al. (1997) examined the interaction of altered flows, riparian vegetation, sediments, and the biota in ecosystems and concluded that conditions consistent with those predicted from climate change could cause disturbances in the critical linkages between terrestrial vegetation, the sediments that they create, the infauna, and the above sediment biota of an area that are dependent upon them.

## Warmwater Fish Spawning Temperatures

Because fish are poikilothermic, their metabolism and activity levels are directly linked to temperature. Near the upper limit of a fish's fundamental thermal niche optimal metabolic rates are typically achieved. When ideal metabolic function is achieved, growth, fitness, and reproductive capability are maximized (Magnuson et al. 1979). In addition to increasing the growth rate of many warmwater sportfish, a warmer climate will also decrease the length of time to maturation, and hence reproductive age (Regier et al. 1990; Winder and Schindler 2005). Although there are many factors that contribute to successful reproduction, for fish it must usually first be initiated by the proper temperatures. With overall warmer environmental conditions and an earlier onset of spring, the date at which waters will achieve a temperature suitable to spawn will be advanced. The advancement of breeding and spawning dates has already been observed in many plant and animal species (Walther et al. 2002). Reported water temperatures necessary for the onset of the warmwater fishes included in this review are shown in Table 2. In general, the minimum spawning temperatures ranged from about 12.5 $^{o}$C to 22 $^{o}$C among species, with maximum values of 16 $^{o}$C to 29 $^{o}$C.

Table 2. Reported spawning temperatures ($^{o}$C) of common warmwater sportfish. Parentheses indicate peak spawning times. Values without parentheses indicate range of various temperatures observed in the literature.

| **Species** | **Authors** | | | |
|---|---|---|---|---|
| | Carlander (1969) | Becker (1983) | Mette et al. (1996) | Others |
| largemouth bass *Micropterus salmoides* | 12.8-21.1 (15-17) | 15.6-18.3 (16.7-18.3) | 17-20 | 15-24 Heidinger(1975) |
| spotted bass *M. punctatus* | 15.6-21 | | | 14-23 Vogele (1975) |
| black crappie *Pomoxis nigromaculatus* | (14.4-20) | 14.4-20 (17.8-20) | | |
| white crappie *P. annularis* | 14-23 (16-20) | 14-23 (16-20) | | |
| redbreast *Lepomis auritus* | 20-29 | | 20 | |
| pumpkinseed *L. gibbosus* | 13-18, 20-29 | 19.4 | | |
| warmouth *L. gulosus* | ~26 | 21.5 | | |
| bluegill *L. macrochirus* | 17-32 (17-26) | 19.4-26.7 | | |
| redear sunfish *L. microlophus* | 21-32 (21) | | | |
| channel catfish *Ictalurus punctatus* | 21-27(27) | >23.9 (26.7) | | 21-29(27) Hubert(1999) |
| flathead catfish *Pylodictis olivaris* | | 22.2-23.9 | | 19-24 Jackson (1999) |
| blue catfish *I. furcatus* | | | | ~21-24 Graham(1999) |
| smallmouth bass *M. dolomeui* | 13-21 | 13-23.9 (16-18) | 15-17 | |
| striped bass *Morone sexatilis* | (15-20) | | | |
| white bass *Morone chrysops* | (17-21) | 12.5-26.1 (16.9-22.6) | | |
| walleye *Sander vitreus* | 3-13 | 5.6-17.2 (5.6-10) | | |

## Potential Range Changes

As environmental conditions across the country change so to will the nature of the stressors placed on fish. Accordingly, altered environmental characteristics will create a dynamic situation in which conditions will become favorable for expansion of range of certain species in a region while at the same time acting negatively against other species (Carpenter et al. 1992; Lodge 1993; Mulholland et al. 1997; McCarthy et al. 2001). Whether or not these changing conditions will result in the expansion or contraction of ranges will depend on a variety of factors.

When considering range changes it is first important to think about the nature of the habitats inhabited by freshwater fish. Many freshwater habitats have explicitly defined borders on a local scale that do not permit movement over large distances. Small ponds, isolated wetlands, and lakes are prime examples, but rivers, especially when oriented in an east-west manner can be considered to be locally finite environments when climate change is considered to occur primarily on a north-south gradient (Matthews and Zimmerman 1990). Because fish are typically unable to move spatially over long distances to more environmentally amiable habitats, they can be faced with physiologically burdensome local environments due to drying, high temperatures, or low dissolved oxygen, among other things, causing stress (Coutant 1987). Where conditions exceed the adaptive capability of the fish, death of individuals, and eventually local species extirpations, will occur. Habitats that permit movement to more favorable environs allow fish to avoid physiologically stressful conditions. If populations can move the distance needed to find favorable environmental conditions this will cause seasonal or permanent abandonment of some species' traditional localities and new interactions in their new environments. Other species will likely fill the void formed in their abandoned habitats, but it will mean a change of population structures. It is also important to consider the time scale of change when thinking about the impacts of higher temperatures. If change proceeds slowly enough then it may be possible for organisms to adapt in some areas (Matthews and Zimmerman 1990).

Extended periods of cold create conditions of starvation and intense cold periods below a fish's physiological threshold can be acutely lethal, in particular for the thermophilic warmwater sportfish. This winterkill frequently acts in a size selective manner against smaller fish. Hence, the northern limits of species can be largely determined by the ability of the young of the year to maximize growth during warmer months and to survive cooler conditions (Shuter and Post 1990). As temperatures increase, many warmwater sportfish will benefit from more favorable growth conditions and a significant decrease of winterkill, allowing them more successful occupation of areas previously less favorable (Minns and Moore 1992; Scheller et al. 1999; Stefan et al. 2001). This will most likely result in an expansion of range northward and to higher elevations (Regier and Meisner 1990; Shuter and Post 1990; Meyer et al. 1999; Stefan et al. 2001; Chu et al. 2005)

Although warmer temperatures will prove beneficial to many warmwater sportfish populations, higher temperatures may prove detrimental at extremes. High temperatures can be taxing to a fish when they exceed the temperatures that a fish is adapted to. Low dissolved oxygen, commonly associated with warmer temperatures, can also be extremely stressful, and thus a powerful determinant of species composition in an area (Smale and Rabeni 1995). Although the minimum amount of oxygen required by fish changes with acclimation history and species, it is generally accepted that below about 5 mg/L most fish become stressed and at 2 mg/L conditions can become lethal.

Because of the effects of high temperatures and low dissolved oxygen a contraction of suitable territory will occur in areas where species are at the warmest extent of their ranges. Smallmouth bass, striped bass, and walleye will be particularly vulnerable to range reductions because of their preference for cooler waters (Coutant 1987; Eaton and Scheller 1996; Mohseni et al. 2003). The combination of low dissolved oxygen and high temperatures will be especially problematic in deep, stratified water bodies where fish adapted to cooler, more oxygen rich waters can become squeezed between cool, low oxygen and high temperature, low oxygen layers (Coutant 1987; Stefan et al. 2001). Problems for many species could also be particularly acute in the shallow rivers of the Southwest (Matthews and Zimmerman, 1990). Despite the range contractions in some areas, the overall effect of warmer temperatures will cause a net expansion of favorable habitats for most species of warmwater sportfish (Minns and Moore 1992; Stefan et al. 2001; Mohseni et al. 2003).

As the conditions most favorable for growth of a certain species shift poleward and to higher elevations, areas that experience high yields of that species will also shift (Carpenter et al. 1992). This is particularly the case for species that rely on slightly cooler water such as walleye, smallmouth bass, and striped bass (Coutant 1987; Shuter and Post 1990; Minns and Moore 1992;

Eaton and Scheller 1996). At the northern extent of a species' range the increase in production will tend to be highest (King et al. 1999).

## Effects of Invasive and Exotic Species

As altered environmental conditions make areas more suitable to invasions by foreign organisms there will be more cases of species native and exotic to the United States invading new environments (Allan and Flecker 1993; Walther 2002). Although only a small percent of invasions will result in the permanent establishment of a species in an area (Whittier and Kincaid 1999; Rahel 2002), each invasion will assuredly force new interactions within communities (Meyer et al. 1999). The results of these interactions will range from having no long term effects on the system to incorporation of species into an environment to widespread ecosystem disruption or suppression or extinction of native species (Miller et al. 2001).

There are many aspects of environmental conditions and traits of species that will favor invasion of habitats (Table 3). The literature contains large discussion about the relative of importance of biotic and abiotic factors but there is a general agreement that both play a role and must be considered when examining the initiation, pathways, and endpoints of invasions (Moyle and Light 1996). Because of their large, diverse human populations and amiable climates, Florida, California, and Texas possess many of the environmental characteristics that favor invasion, and thus currently have the highest levels of introduced fish species (Fuller 2003). In these and other nearby states with conditions favorable to invasion particular vigilance must be paid to avoid establishing foreign organisms. Human introductions, through intentional releases by well intentioned government agencies and anglers, aquaria releases, escapes or releases from aquaculture facilities, and unintentional transport through commerce, contribute to a large portion of translocations of both native and exotic fish (Lodge 1993; Nico and Fuller 1999; Fuller 2003). Coupled with the fact that in many cases once a species is established it is extremely difficult to remove, it is important to focus on preventing introductions to minimize species invasions (Lodge 1993; Benson 2000; Fuller 2003). Because many of the exotic species in the United States are from the tropics, increasing temperatures will greatly favor their ability to expand occupied areas. The suitable habitats for many exotic fishes such as the jaguar guapote, *Cichlasoma manguense*, blue tilapia *Oreochromis aureus*, and butterfly peacock bass

*Cichla ocellaris* are greatly limited by minimum temperatures and any elevation of temperatures would permit expansion of the species' ranges.

As warmwater sportfish expand ranges they will likely occupy the upper trophic level and be the dominant predator in the system. For example, the introduction of smallmouth bass in to areas with trout can disrupt trophic patterns and negatively affect trout populations (Whittier and Kincaid 1999). The interaction of warmwater sportfish with other species may be particularly evident in streams as the warmwater species that typically occupy downstream reaches move into the areas that were traditionally cool or cold water areas (Scott and Helfman 2001).

The effects that invasive and exotic species can have on native systems can be wide ranging. In most cases invasions fail and even when they do not there is a chance that the species could be incorporated into the existing communities either through filling an underutilized niche, or through replacement of another species' role (Moyle and Light 1996; Rahel 2002). When viewed from different standpoints some invasions have proven to be beneficial, although not necessarily ecologically. For example, the introduction of the peacock cichlid in South Florida has created a large sport fishery. The spread of many sunfish and black bass species has also created very valuable fisheries. Some less positive results of an invasion can include predation upon native species, alteration of habitat, competition for resources, introduction of diseases or parasites, and hybridization with native populations (Magnuson 1976; Ross 1991; Allan and Flecker 1993; Lodge 1993; Benson 2000). As invasions and environmental changes continue, homogenization of environments, communities and genetics will also increase, with the more tolerant, generalist species becoming increasingly represented (Scott and Helfman 2001; Rahel 2002). In some cases invaders can cause the extinction of native species (Ross 1991).

Table 3. Characteristics of species and habitats that favor successful invasions or invasions with large impacts (Adapted from Lodge 1993; also Magnuson 1976; Moyle and Light 1996; Nico and Fuller 1999; Scott and Helfman 2001; Rahel 2002).

| **Species Characteristics** | **Habitat Characteristics** |
|---|---|
| Short generation time | Disturbed system (natural or anthropogenic) |
| High fecundity | Vacant niche |
| High growth rate | Simple food web, low diversity of native species |
| High short-range dispersal | Lack of competitors, predators to invading species |
| High genetic variability | Climatically similar to habitat of invading species |
| Phenotypically plastic | |
| Tolerant of a wide range of physical conditions | |
| Broad diet | |
| Gregarious | |
| Aggressive, highly competitive for resources | |
| Predatory, piscivorous | |

## Fisheries Implications

A cursory evaluation could suggest that global warming would benefit warmwater fishes, but the potential impacts on habitat and hydrology outlined above clearly show that effects may be counterintuitive. The general trend from the literature is that with warming temperatures precipitation will become more variable, with more severe wet and drought periods through time. Much research has shown that fish recruitment (i.e., the number of young fish that survive to adulthood) is influenced by changes in river flow and lake stage (e.g., Matthews 1986; Bain et al. 1988; Bonvechio and Allen 2005) and the habitat modifications that result. Based on the previous discussion of predicted temperature and precipitation trends, we surmise that more extreme drought and high-water events would cause larger fluctuations in the quality of recreational fisheries. We reiterate that the literature contains substantial uncertainty about the specific effects of climate change on aquatic systems. However, we believe we were able to identify some consistencies among the studies that can help fisheries agencies plan management strategies for the future.

Our review would suggest less severe winters in the future, meaning that warmwater fisheries may move to higher latitudes. Popular fishes such as walleye, smallmouth bass, and striped bass could have more restricted ranges in the south as water temperatures favor species better adapted to mild winters (e.g., largemouth bass). Efforts to protect habitat (e.g., substrate and river flows) for species requiring cooler winters at the southern end of their range could help offset effects of rising temperature.

The implications of more variable water levels for anglers means that travel distance to reach quality fisheries may increase substantially, and occurrence of “boom and bust” fisheries would become more common. Fisheries managers will need to consider management actions that stabilize fisheries, such as use of harvest regulations to protect adult fish, water use and water allocation measures to protect fish habitat, and habitat enhancement efforts to improve fish recruitment during periods of poor habitat conditions (e.g., low water). Establishment of minimum flows and levels for rivers and lakes will be important to protect fisheries resources, and increasing temperatures may exacerbate problems with invasive and exotic species. These challenges will require fisheries management agencies to adapt to more variable fisheries and modify management plans accordingly.

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