POTENTIAL IMPACTS OF GLOBAL CLIMATE CHANGE ON FRESHWATER FISHERIES

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ABSTRACT

The purpose of this review is to explore the likely effects of climate change on the world's freshwater fisheries. Global warming will affect fish populations through direct temperature effects on physiology. All freshwater fish are cold-blooded, and their physiological mechanisms are directly or indirectly temperature – dependent. The optimal physical and biological ranges of a fish species are determined by temperatures that are required for efficient metabolism, reproductive success, and disease resistance. Any changes in those temperatures, including those predicted to result from global climate change, will result in range shifts and local species extirpations.

Climate change is also expected to affect fish populations through its influence on physical factors such as water chemistry and limnology. Oxygen solubility decreases with increasing water temperature, so warmer water holds less oxygen. Given the thermally-regulated nature of fish metabolic rates, increases in environmental temperature will result in increased oxygen demand, while at the same time the amount of available O_2 will be reduced. Higher temperatures will tend to increase duration and strength of thermal stratification in temperate zones. Lentic (lake) environments also depend upon wind – driven mixing, so changes in weather patterns will affect their function. Mixing regimes strongly influence the community of primary producers that in turn influence lentic food webs and their associated fish communities.

Hydrologic regimes may also be affected. The timing, frequency, duration, and interannual variability of peak and low flows may be altered with a change in weather patterns. Fish have evolved with their current local hydrologic conditions—possible changes in these environmental constraints will present them with new challenges to survival and reproductive success. Melting of polar ice caps and thermal expansion of seawater will result in a sea level rise that would inundate important freshwater habitats in low-gradient rivers and river deltas. Finally, increased temperatures could also affect the toxicity and bioaccumulation of anthropogenic pollutants. Billions of people worldwide receive benefits from the exploitation of fish populations. Developing countries rely upon freshwater fish as a source of inexpensive protein and as a revenue source. Industrialized countries primarily use freshwater fisheries as a source of recreation, which also produces revenue and employment opportunities. Given that declines or changes in fish populations can have far-reaching socioeconomic impacts, we have yet another compelling reason for the proper management of greenhouse gas emissions.

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INTRODUCTION

Water temperature is one of the “master variables” in freshwater systems because of its widespread effects on the life history, physiology, and behavior of most freshwater organisms, including fishes. Water temperature can also alter the physical habitat available to a species, primarily through thermal stratification and heterogeneity within a system. Freshwater fishes are all poikilothermic, or “cold-blooded”, and rely on behavioral thermoregulation (Nevermann and Wurtsbaugh 1994; Nielsen et al. 1994; Brio 1998) to modify their internal body temperatures. Their ability to behaviorally thermoregulate is constrained by the thermal heterogeneity of their immediate environment, because their body temperatures will match the temperature of the water they currently occupy. This inextricable linkage to the local water temperature makes fish (and most other aquatic organisms) particularly susceptible to even small-scale perturbations in environmental thermal regimes. One such perturbation is the increase in mean global temperatures brought about by the accelerated release of “greenhouse gases”, carbon dioxide (CO_2), nitrous oxide (NO_X), and methane (CH_4), largely from the combustion of fossil fuels (Bolin et al. 1986; ACIA 2004).

How will changes in mean global temperatures affect fish? Most studies that attempt to predict the effects of anthropogenic perturbances on the rate of climate change have used air temperature as their response variable (IPCC 2001; ACIA 2004). The magnitude of the predicted increases range from 1°C to over 7°C (IPCC 2001; ACIA 2004), but it is generally accepted that mean global air temperatures have increased rapidly in the recent past and will continue to do so. Temperatures in lakes, ponds, and streams are closely coupled to air temperature (Meisner et al. 1988; Boyd and Tucker 1998), so increases in air temperature are expected to be followed by similar increases in water temperature, though the magnitude may be somewhat lower. For example, Northcote (Northcote 1992) predicted that a 4°C increase in air temperature would result in a 3-8°C increase in the surface temperature of a 10-m deep lake in British Columbia, Canada. Changes in global air temperatures will also affect some groundwater sources. The temperatures of shallow aquifers that recharge some of these systems usually approximates the mean annual air temperature for that region (Meisner et al. 1988; Boyd and Tucker 1998).

Another “master variable” in freshwater systems is hydrology. As with temperature, freshwater organisms have evolved to survive under a specific set of hydrologic conditions that help define and shape their habitats. While temperature can have effects at all levels of organization (from the individual to the ecosystem), hydrology tends to act at the broader levels. Like water temperatures, hydrologic regimes in freshwater ecosystems will likely be altered by global climate change. These changes will result from differences in the spatiotemporal distribution and rates of precipitation and evaporation (Roessig et al. 2004). Precipitation is expected to increase globally, but much of this increase may come in the form of more frequent “extreme” events (Palmer and Räisänen 2002). On a regional scale, winter rainfall will increase in the mid and high latitudes of the Northern Hemisphere, reducing the size of the snowpack and reducing the duration and magnitude of spring and summer flows. Precipitation is also expected to increase in the African tropics, and expected to decrease in Australia, South America, and southern Africa. Summer rainfall is expected to increase in southern and eastern Asia (IPCC 2001). Current trends also show a decrease in snowpack and ice cover. In the high latitudes of the Northern Hemisphere, snowpack has decreased by approximately 10% since the late 1960's, and rivers and lakes have lost, on average, 2 weeks of ice cover (IPCC 2001). These changes in global hydrologic regimes and thermal regimes will impact the majority of aquatic ecosystems, including those that support freshwater fisheries.

Most climate models have global or regional resolution, so it is difficult to predict the effects of climate change on individual fish populations, including those that support fisheries. Changes in hydrologic regimes will affect species whose life histories require a larger scale (migratory species, big river fishes) in a different manner than those that are limited to a small scale (endemic species, headwater species).

The global effects of climate change mean that freshwater ecosystems, and the fisheries therein, will be affected to some degree. The stated purpose of this review is to address the question of how global climate change will impact a variety of freshwater fisheries. These fisheries range from small subsistence efforts to large commercial endeavors, often under artificial conditions, where millions of pounds of fish are produced. Freshwater fisheries are typically based on one or more species from the salmon family (Salmonidae), the minnow and carp family (Cyprinidae), the cichlid family (Cichlidae), and multiple families within the catfishes (Siluriformes). Though we will focus on these families, we will occasionally illustrate key concepts using other freshwater fishes.

TEMPERATURE AND FISH PHYSIOLOGY

All freshwater fishes are ectotherms that cannot regulate their body temperature through physiological means (Moyle and Cech 2004) and whose body temperatures are identical to, or very close to the environmental temperature at their specific location. These fishes do thermoregulate behaviorally, moving between thermally heterogeneous microhabitats to “select” the most advantageous temperature for their current physiological state (Nevermann and Wurtsbaugh 1994; Nielsen et al. 1994; Brio 1998). However, unlike physiological thermoregulation, behavioral thermoregulation is constrained by the range of temperatures available in the environment. Because biochemical reaction rates are largely a function of body temperature, all aspects of an individual fish’s physiology, including growth, reproduction, and activity are directly influenced by changes in temperature. Biochemical and physiological reactions that occur can be quantified by the Q_{10}, a dimensionless number that measures the magnitude of the rate change over a 10°C range (Wohlschlag et al. 1968; Schmidt-Nielsen 1990; Franklin et al. 1995). The consequences of this are obvious: global warming will affect individual fish by altering physiological functions such as thermal tolerance, growth, metabolism, food consumption, reproductive success, and the ability to maintain internal homeostasis in the face of a variable external environment (Roessig et al. 2004). If the net effects on individual fish are amplified to the population level and beyond, it becomes apparent that a change in environmental temperature will have cascading effects on ecosystems and the fisheries that depend on them. We will now examine the potential effects of an increase in temperature on specific aspects of fish physiology, including thermal tolerance and metabolism before looking at specific examples for temperate and tropical fishes.

If one thinks in extreme terms, the most severe potential effect of global warming is that the water temperatures in specific ecosystems would increase to levels that are lethal for the resident fishes. All fish have a thermal range bounded on the upper end by their critical thermal maxima (CT_{Max}) and on the lower end by their critical thermal minima (CT_{Min}) (Fry 1971; Becker and Genoway 1979). These critical thermal limits represent temperatures that the fish can tolerate for a few minutes, at best, and they can be slightly increased or decreased if the fish is acclimated to a sub–lethal temperature approaching the lethal temperature (Myrick and Cech 2000; Myrick and Cech 2003). Temperatures that fish can tolerate for a few minutes to a few days are referred to as the incipient lower lethal temperatures (ILLT) and incipient upper lethal temperatures (IULT) (Myrick and Cech 2000). Although fish will eventually perish at these temperatures, they can tolerate them for longer intervals than their critical thermal limits. As temperatures move farther away from the incipient lethal temperatures, they enter the suboptimal range where physiological performance may be reduced, but the fish is not going to die. Finally, there is a narrow range where physiological performance is near the optimum; temperatures within this range are known as the optimal temperatures. Given enough time to acclimate to a changing thermal regime, most fishes can adjust the ranges of their critical, incipient lethal, suboptimal, and optimal temperatures up or down by a few degrees, but there are limits to the magnitude and rate of thermal acclimation.

Thermal ranges are species–specific, as there are stenothermal (narrow thermal range) species like lake trout (*Salvelinus namaycush*) and peacock pavon (*Cichla ocellaris*), and eurythermal (wide tolerance range) species like common carp (*Cyprinus carpio*) and bluegill (*Lepomis macrochirus*) (Table 1). Increases in global temperature are a concern because ambient thermal conditions may encroach on suboptimal conditions for certain fishes, or bring them closer to their incipient lethal temperatures. Faced with such changes, one can expect fish populations to achieve new equilibrium dictated largely by the energetic costs of coping with a new thermal environment. Some species may increase or decrease in abundance, others may experience range expansions or contractions, and some species may face extinction. The fate of a species will depend on the following factors:

1. Whether it is stenothermal or eurythermal and what region it inhabits (arctic, subarctic, temperate, subtropical, or tropical).
2. The magnitude of the thermal change in that ecosystem.
3. The rate of the thermal change.
4. Opportunities to move to areas with appropriate thermal conditions (narrow endemics in small lakes or in rivers with impassable barriers may not be able to move to avoid lethal conditions).

5. Changes in the abundance or distribution of sympatric species that may be prey, predators, or competitors for resources.

Table 1.—Temperature tolerances of some common coldwater, coolwater, warmwater, and tropical fish species. All temperature values are given in degrees Celsius (°C). ILLT is the lower incipient lethal temperature, or the temperature below which a fish cannot survive for an indefinite time, and UILT is the upper incipient lethal temperature, or the temperature above which a fish cannot survive indefinitely. Variations in these values most likely occur because incipient lethal temperatures depend somewhat upon acclimation temperature. (Adapted from Stickney 2000 and McLarney 1996.)

Temperature Guild	**SPECIES**	**ILLT**	**Optimum temperature range**	**UILT**
Coldwater	Rainbow trout (*Oncorhynchus mykiss*)	1	13–21	24–28
Coolwater	Yellow perch (*Perca flavescens*)	0–3.7	19–21	21.3–29.7
	Bluegill (*Lepomis macrochirus*)	0–1.1	20.5–29	28–39
Warmwater	Largemouth bass (*Micropterus salmoides*)	0–11.8	22.8–30	28.9–38.9
	Channel catfish (*Ictalurus punctatus*)	0–6	21–27	30.3–35
Warmwater/ tropical	Common carp (*Cyprinus carpio*)	0–0.7	26.7–29.4	31–35.7
Tropical	Blue tilapia (*Tilapia aurea*)	8.9–12.8	22.8–30	28.9–38.9

When exposed to temperatures that fall within the sublethal range (bounded by the upper and lower incipient lethal temperatures), fishes can still be affected, positively or negatively, by the environmental temperature. The majority of these effects result from the close coupling of fish metabolic rates with water temperature. All fishes must allocate energy from consumed food to their energy budget, represented by the metabolic equation developed by (Warren and

Davis 1967):

$$C = (M_r + M_a + SDA) + (F + U) + (G_s + G_r);$$

where C = energy consumption rate, M_r = standard metabolic rate, M_a = metabolic rate increase because of activity, SDA = energy allocated to specific dynamic action (food digestion and processing), F = waste losses due to fecal excretion rates, U = waste losses due to urinary excretion rates, G_s = somatic tissue growth rate, and G_r = reproductive tissue growth rates.

The amount of energy allocated to each of these compartments is temperature–dependent, with increases in temperature generally increasing allocation to all areas except somatic and reproductive growth if the fish is given a fixed ration. These two compartments are the equivalent of storage compartments for surplus energy, so if a fish is forced to allocate more energy to the other compartments, logically less is available for growth and reproduction. Figure 1 shows the energy budget for yellow perch (*Perca flavescens*) as a function of temperature. Note that all components of the budget increase with temperature to a point, primarily because the total amount of energy available through consumption (C_{max}) is also increasing. However, once the temperature increases past the point where consumption and growth are maximized, the increased cost of respiration and decreased consumption rate result in a rapid decline in growth rates. This “surplus” energy is known as the “metabolic scope”, and this tends to be highest at the fish’s metabolic optimum temperature. Increases in temperature decrease the metabolic scope (Brett 1971; Elliot 1975a), through a variety of mechanisms including cardiac inefficiency

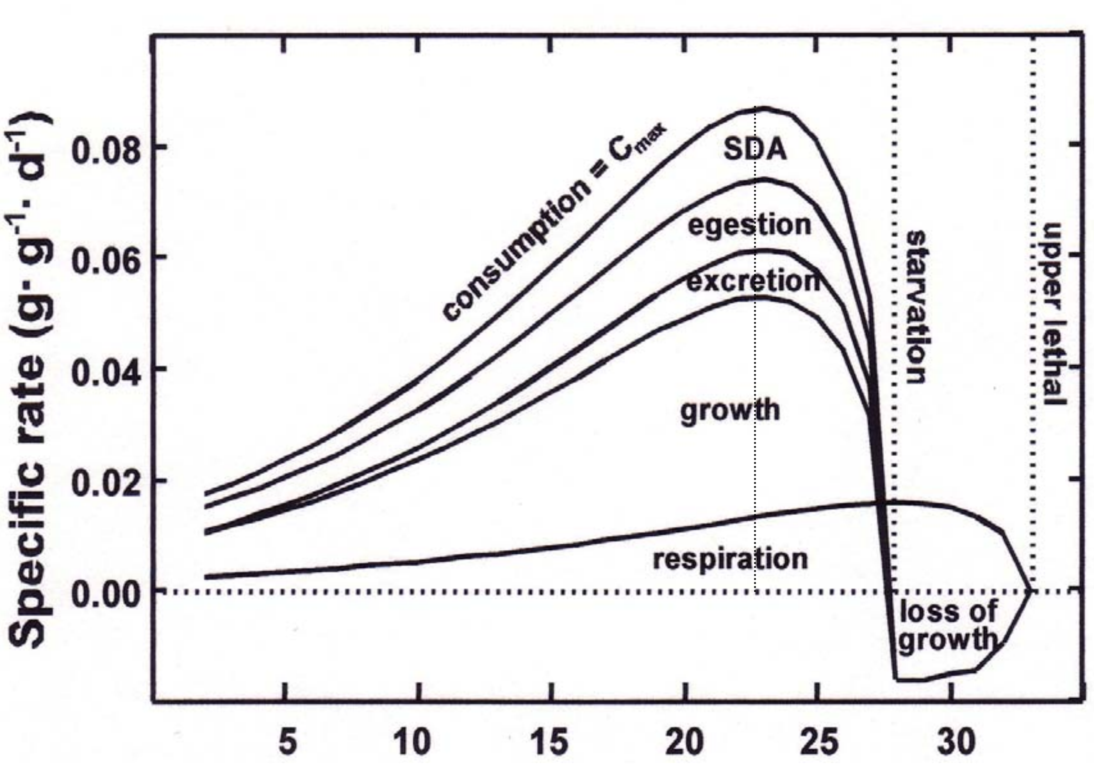

Figure 1.—The energy budget of a yellow perch as a function of temperature. Note the rapid decline in growth as temperature increases beyond 25°C. The vertical dotted line at 23°C indicates the optimal temperature and maximum metabolic scope for this species. From Kitchell et al. 1977.

(Taylor et al. 1997) and an increased cost of repairing heat–damaged proteins (Somero and Hofmann 1997). If fish are exposed to temperatures high enough to thermally stress them (approaching or exceeding IULT) they experience problems with osmoregulation (Boyd and Tucker 1998), possibly due to increased gill permeability at higher temperatures (Somero and Hofmann 1997). In general, a reduction in metabolic scope leads to decreased swimming performance (Brett 1971), reduced reproductive output (Van Der Kraak and Pankhurst 1997; Webb et al. 2001), lower growth rates (Brett 1971; Kitchell et al. 1977), and, in extreme cases, mortality (Kitchell et al. 1977).

Temperate fishes

Fish growth is temperature–dependent and generally increases with temperature to an optimal level before decreasing again (Kitchell et al. 1977; Myrick and Cech 2000). Fish in temperate ecosystems undergo about 90% of their annual growth in the summer months (Wrenn et al. 1979) because food availability tends to be highest and water temperatures approach growth optimums. In these cases, a slight increase in water temperature could be beneficial because the growing season is extended (Hill and Magnuson 1990; Kling et al. 2003). This scenario only would apply if food resources can support a higher consumption rate (Shuter and Meisner 1992) and interspecific interactions are not increased. Milder winters could also reduce overwintering stresses, such as food limitation, that can be significant for some temperate fishes (Boyd and Tucker 1998). This increase in over–winter survival combined with slightly elevated water temperatures could increase the productivity of fisheries that are currently limited by temperatures below the species' growth optimum. In the Great Lakes region, suitable habitat for cold, cool, and warmwater fish would increase under four global circulation model (GCM) warming scenarios, provided that oxygen supplies remain adequate. This increase in thermal niche is possible for large, deep lakes and for medium-sized lakes in this region (Magnuson et al. 1997).

Regardless of the state of food resources, an increase in temperature causes an increase in metabolic rate, and a subsequent increase in the amount of energy needed. For example, food intake was found to be highly temperature dependent for five cyprinids from Lake Balaton (Hungary). The daily intake of bream *(Abramis brama*), silver bream *(Blikka bjoerkna*), roach *(Rutilus rutilus*), gibel (*Auratus gibelio*), and common carp increased exponentially when temperatures were increased from 5 to 25°C (Specziár 2002). In sockeye salmon (*Oncorhynchus nerka*), food consumption triples between 2.5 and 17.5°C, but decreases at temperatures above 17.5°C because like yellow perch, this fish will reduce food intake at temperatures above its thermal optimum (Brett 1971). Elliot (1975a, 1975b) found similar results in his studies of brown trout (*Salmo trutta*). In food–limited environments, food intake cannot keep pace with metabolic demand. For example, common carp cultured at 35°C developed a vitamin C deficiency and grew more slowly than those cultured at 25°C when both experimental groups received the same rations (Hwang and Lin 2002). In 1975, a pair of studies using brown trout found that the temperature for optimum growth was 13–14°C when fish were fed on maximum rations (Elliot 1975b) and 9–10°C when fish were fed on 50% rations (Elliot 1975c). A 1999 study using rainbow trout (*O. mykiss*) found that fish fed limited rations experienced significantly lower growth rates when held in water 2°C warmer than ambient temperatures (Morgan et al. 1999). Since trout are often food–limited in the summer months (Morgan et al. 1999), climate change will probably lower the carrying capacity of trout–dominated systems. Studies on cold– and cool–water species like lake trout, whitefish (*Coregonus commersoni*), and perch (*Perca spp.*) only predict increased fish growth rates if the food supply can sustain the increased demand. Otherwise, decreased growth rates can be expected (Hill and Magnuson 1990; Gerdaux 1998). It should be noted, however, that if the temperature increase is large enough, no increase in food availability will be sufficient to meet increased metabolic demand because feeding activity is depressed at temperatures above a species optimal temperature (Brett 1971; Kitchell et al. 1977).

The reproductive success of temperate fishes will be affected by global warming. Low overwinter temperatures are often essential for the spawning success of cold water stenotherms such as salmonids (Langford 1983; Gerdaux 1998). Even temperate zone eurytherms require relatively low temperatures to ensure reproductive success. Channel catfish (*Ictalurus punctatus*), which support the largest commercial aquaculture industry in the United States, require several weeks of water temperatures below 15°C to stimulate gametogenesis (Boyd and Tucker 1998). Female white sturgeon (*Acipenser transmontanus*), now the cornerstone of a valuable commodity industry (culture caviar production), held at water temperatures of 12°C during vitellogenesis and follicle maturation experience lower rates of ovarian regression and the ability to retain mature oocytes for a longer period of time than those kept at higher temperatures (14.5±2.3° C) (Webb et al. 2001). Similar responses are likely for other sturgeon species, including the critically threatened Caspian Sea species. Given the need for “cold-tempering” among many temperate species, increases in temperature, especially in the colder months, may reduce the reproductive output of commercially important fishes near the lower latitudinal bounds of their distributions.

Recruitment of juveniles may also be affected by changing thermal regimes. Juvenile fishes often occupy different thermal niches than adults of the same species; higher temperatures decreased mortality and encouraged faster growth in juvenile northern pike (*Esox lucius*) and Eurasian perch (*Perca fluviatilis*) in Lake Windermere, England (Craig and Kipling 1983). However, Craig and Kipling (1983) studied these species and found that, with respect to age-1+ fish, faster–growing cohorts had a shorter lifespan and lower reproductive potential than slow–growing cohorts. The reduction in juvenile mortality might compensate for the decreased reproductive capacity, but this was not been experimentally tested. The paucity of data on the reproductive physiology of most fishes, including many commercially important species, means that it is difficult to accurately predict the impacts of even slight changes in environmental temperature. If one draws inferences from the physiology of the few well-studied species, it appears that some reduction of reproductive output may occur, leading to a decline in rates of population growth, or, in the case of heavily exploited species, potential rates of population recovery.

Tropical Fishes

Tropical fishes have evolved to survive in very warm water and may seem less likely to suffer negative impacts from increases in global temperatures. For example, spotted tilapia,

(*Tilapia mariae*), native to the west central coast of Africa, prefer temperatures between 25 and 33°C, depending upon acclimation temperature, and have a critical thermal maxima of 37°C (Siemien and Stauffer 1989). Instead of having exceedingly high metabolic rates and energy demands, tropical fish held at their optimal temperatures have metabolic rates similar to those of temperate fishes (Val and Almeida-Val 1995). Unlike most temperate fishes, however, tropical species live in systems where diurnal water temperature fluctuations regularly approach their incipient upper lethal limits (United Nations Economic Commission for Asia and the Far East 1972; Irion and Junk 1997). Though tropical fishes can endure temperatures very near their IULT (Milstein et al. 2000), a slight (1 – 2°C) increase in regional temperatures may cause the daily temperature maxima to exceed these limits, particularly for populations that currently exist in thermally marginal habitats (Roessig et al. 2004). However, some recent work by Chaterjee et al (2004) on common carp and rohu (*Labeo rohita*), two fish that feature prominently in capture and aquaculture fisheries on the Indian subcontinent and are well adapted to increases in temperature, shows increased tolerance to elevated temperatures following acclimation to water temperatures of 30 and 35°C (Chatterjee et al. 2004). However, the authors do note that the common carp is more thermally tolerant than the rohu (Chatterjee et al. 2004), so this would be one case where an increase in temperature could result in a change in species composition. If fish are currently living in marginal habitats, the effects of global warming would be similar to those predicted for temperate systems because tropical fish exhibit similar physiological symptoms when subjected to elevated temperatures. For example, temperatures of 39 – 40°C inhibited swimming ability in the tilapia (*Tilapia mossambica*) (Kutty and Sukumaran 1975) despite the fact that many other tilapia species can survive at temperatures up to 41–42°C (Chervinski 1982). Nile tilapia (*Oreochromis niloticus*) experienced higher oxygen debts after exhaustive exercise at 33°C than 23°C (McKenzie et al. 1996). Common carp and rohu had increased oxygen consumption rates at temperatures of 30 and 35°C, and if food intake is not increased concurrently, this elevated metabolism would decrease the growth rates of these fish. The consequence of this for aquaculture systems is that it would take longer for the fish to reach a harvestable size or it would require more food to grow them to the harvestable size in the same amount of time. Though lethal effects of increasing water temperature are possible, particularly if multiple stressors related to temperature (e.g., high water temperature, low dissolved oxygen concentrations, increased pathogen virulence) occurred simultaneously, the sublethal effects of warming could be equally damaging to fisheries through the reduced productivity of natural and artificial aquatic systems.

Current climate change models cannot determine whether the amplitude of diel temperature oscillations will also be affected by climate change (Figure 2). If the amplitude increases, it is possible that an increase in fish kills will ensue. If the amplitude of the fluctuations decrease, the new thermal regime may either offset or exacerbate the effects of a mean annual temperature increase. If this dampening effect involves a rise in the minimum daily temperatures, fish would experience less time at optimal temperatures and fisheries productivity would likely decrease.

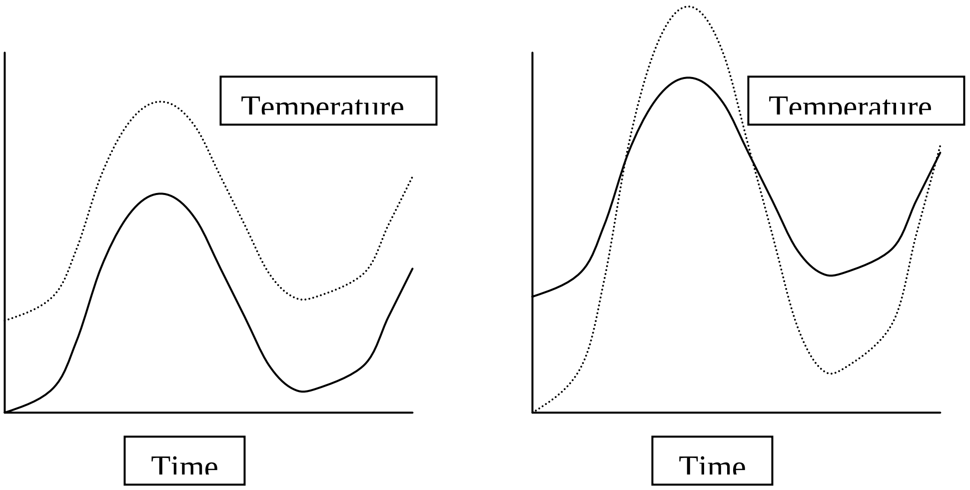

Figure 2.—The distinction between an increase in average temperature (graph A) and an increase in the amplitude of daily fluctuations (graph B). The average temperature in graph B remains the same, but the daily maximum and minimum temperatures increase and decrease respectively.

Few studies have been conducted to determine the effects of temperature on the reproductive success on tropical fishes. Though temperature cues are not thought to play a large role in gametogenesis and spawning behavior of tropical fishes (Moyle and Cech 2004), there are some cases where reproductive output was reduced at higher temperatures. The commercially raised guppy (*Poecilia reticulata*) achieved the highest fry production rates at 25 – 27°C. At 30°C, these fish experienced increased fry and (female) adult mortality, degeneration of ovaries, and reduced brood size (Dzikowski et al. 2001). Grass carp (*Ctenopharyngodon idella*) also experienced lower ovulation rates at 28°C (10%) than at 24°C (36%) (Glasser 2003). These limited studies suggest that reduced reproductive output may be yet another sublethal effect of elevated water temperatures, but comprehensive investigations in this area, particularly on species that form the basis of the major commercial and subsistence fisheries (i.e., the carps, tilapia, and catfishes), are sorely needed.

Small increases (1 – 2°C) in temperature may be sufficient to have sublethal effects on tropical fish physiology, and reproduction in particular, especially when they are combined with the possible effects of an altered hydrologic regime. Spawning in many tropical fishes (and some temperate species) is cued by rising water levels (Val and Almeida-Val 1995; Hori 2000). Tropical fishes that spawn in seasonally flooded areas experience a recruitment bottleneck caused by the loss of juveniles entrained in off–channel areas and desiccation of eggs exposed by receding water levels (Welcomme 1979). Changing hydrographs could increase the magnitude of this recruitment bottleneck by exposing more eggs to desiccation, or, if flows increase, immersing eggs in water too deep and too cool for the survival of eggs and juvenile fish (Welcomme 1979). The effects of altered hydrographs will be discussed in further detail in a subsequent section.

Unfortunately, though the tropics have a wealth of freshwater fish fauna, few physiological studies have examined them: most studies have focused upon a few economically important fishes, such those used in aquaculture or the aquarium trade. Therefore, estimating the impacts of climate change on tropical species is difficult. Some research indicates that these fishes are resilient to poor environmental conditions such as high temperatures and low levels of dissolved oxygen (Kramer et al. 1978; Welcomme 1979; Val and Almeida-Val 1995), but there is considerable uncertainty regarding the direction and magnitude of the possible changes to their environment. This adds to the difficulty of predicting the response of these species to climate change. In tropical systems it is quite possible that the effects of global climate change on local freshwater ecosystems may be overshadowed by other, larger disturbances such as deforestation and land–use changes (Val and Almeida-Val 1995; Verschuren et al. 2002). Recent studies using GCMs suggest that deforestation in the Amazon basin has the potential to increase precipitation in the Parana and Paraguay River basins and decrease precipitation in the Uruguay and Negro River basins (Genta et al. 1998). If these predictions hold true, then fisheries productivity will be altered by the change of the flow regime. With an ambient temperature increase of only 1-2°C, the disturbances brought about by deforestation, such as additional temperature increases (Abell and Allan 2002) would likely pose a larger and more immediate threat to fish populations. However, a larger temperature increase will have heightened effects upon fish physiology, up to and including lethal temperature effects. Again, these effects will be species–specific and will depend upon the frequency and magnitude of high-temperature events for a given population.

Polar and High-Latitude Fishes

Most freshwater fishes of high-latitude regions have ranges that extend into temperate zones. These fishes include coldwater stenotherms such as salmonids and riverine sculpins (Family Cottidae). Because fresh water freezes at 0°C, these fishes are limited on the upper latitudinal boundaries of their ranges by a lack of available habitat, winterkill and a short growing season. Shallow bodies of water, including ponds, flowing rivers, and streams can freeze solid at higher latitudes, temporally eliminating potential habitat for fish in these regions (Jørgensen and Arnesen 2002). Winterkill occurs when a body of water is covered with ice and the dissolved oxygen cannot be replenished by photosynthesis or by diffusion from the atmosphere. However, biological oxygen demand continues, and the resultant environmental hypoxia or anoxia proves lethal to the aquatic organisms. Freshwater systems at the highest latitudes cannot support fish because of their permanent, or near-permanent ice cover. Where fish do occur, their growing seasons are severely limited by the short period of (relatively) warm water temperatures and light levels sufficient to support primary production. Because of these constraints, almost all obligate polar fishes are marine species like the Antarctic plunderfish (*Harpagifer antarcticus*) and the Arctic cod (*Arctogadus glacialis*), though the Alaska blackfish (*Dallia pectoralis*) does occur up to 71°N in North America. Unlike the scenarios presented for temperate and tropical fishes, it is possible that an increase in global temperatures could actually increase the amount of habitat available for colonization by coldwater stenotherms. However, at the same time that their ranges may be expanding into higher latitudes, they may contract at the lower latitudinal bounds as they face competition from temperate fishes whose own ranges are expanding. Changing temperatures may also reduce habitat for these fishes: because they have evolved to survive in polar regions, they may be extremely vulnerable to temperature changes. Preliminary studies on polar saltwater fishes indicate that they have lost the ability to manufacture heat shock proteins, which repair cellular structures damaged by high (relatively) temperatures (Roessig et al. 2004). Further research is required to determine whether this is also true of the freshwater fishes in these regions. A lack of heat shock proteins would increase their vulnerability to climatic change.

Changes in global temperature will affect fish communities and the fisheries dependent on those communities through direct effects on fish physiology and indirectly through effects on water quality, water chemistry, and hydrographs. Even when the increase in temperature is not sufficient to prove acutely or even chronically lethal, the sublethal impacts on fish physiology, particularly on growth and reproduction, may be sufficient to cause significant changes in the structure and composition of fish faunas from the tropics to the arctic regions. The impacts of global climate change on the critical physical and chemical characteristics will likely prove to be the driving factors in determining the well–being and composition of fish communities and thus cannot be discounted in discussions concerning global climate change.

WATER CHEMISTRY

Most water chemistry parameters, including dissolved oxygen (DO) levels, pH, nutrient concentrations, and the toxicity of natural and anthropogenic pollutants are affected by water temperature. In addition, climate change will affect hydrographs that in turn influence water chemistry through changes in water volume over the year and by season, introduction of nutrients, and flushing of pollutants and metabolic byproducts. Outside of water temperature, dissolved oxygen concentrations are perhaps the most critical aspect of water chemistry from the fishes' standpoint.

Dissolved Oxygen

Adequate dissolved oxygen (DO) concentrations are essential for most fishes, aquatic insects, algae, and macrophytes. Oxygen enters the water column through diffusion from the atmosphere, introduction by turbulence, and by photosynthetic production (Kalff 2000; Stickney 2000). Plant, animal, and microbial aerobic respiration all require DO, lowering its concentration in the water column. Dissolved oxygen concentrations of 5 mg O_2/L or more are acceptable for most aquatic organisms (Stickney 2000). When oxygen concentrations drop below 2 – 3 mg O_2 /L, hypoxic conditions are present (Doudoroff and Warren; Kalff 2000).

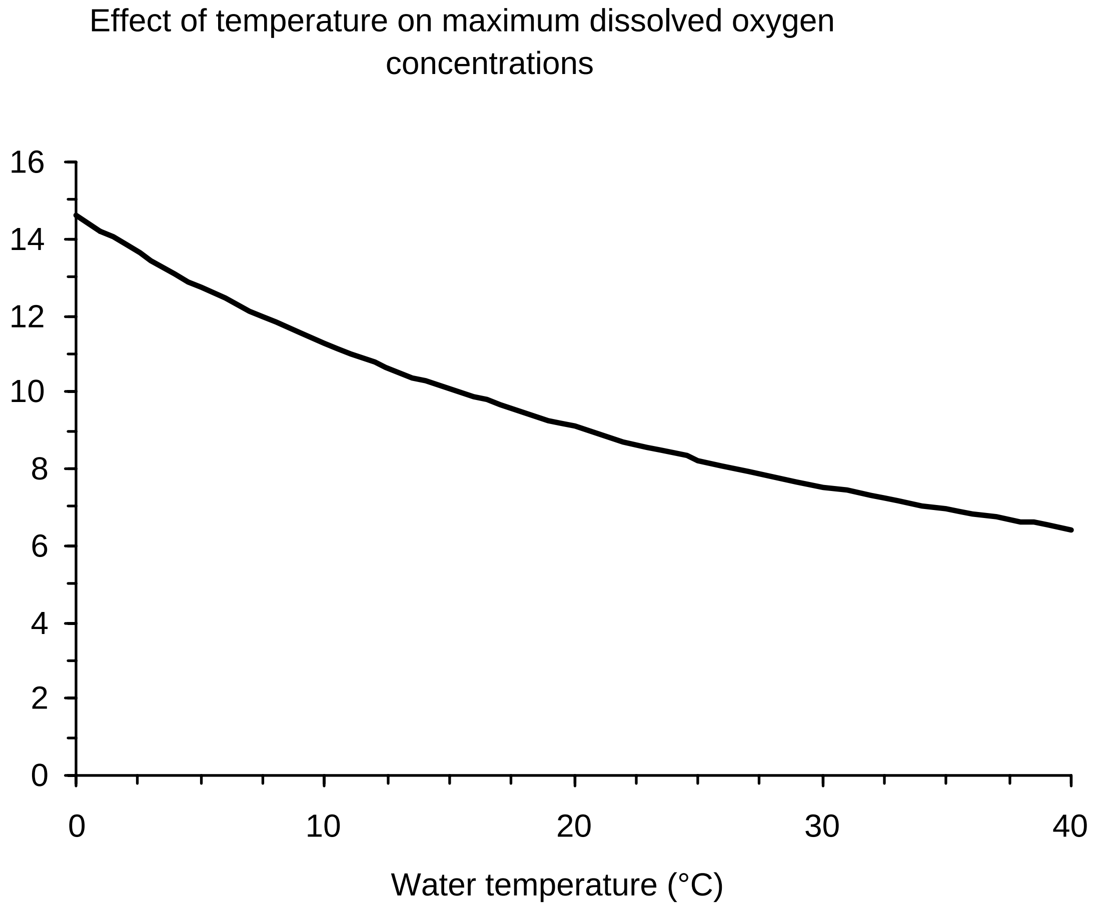

Figure 3.—Relationship between dissolved oxygen solubility and water temperature. Modified from Goldman and Horne 1986.

Oxygen solubility in water has an inverse relationship with water temperature (Figure 3). For example, water at 0°C holds about 14.6 mg O_2/L , but water at 25°C can only hold about 8.3 mg O_2/L (Kalff 2000). Because the aerobic metabolic rates of most cold-blooded aquatic organisms increase with temperature, an increase in temperature both reduces the supply (through reduced saturation concentrations) and increases the biological oxygen demand (BOD) (Kalff 2000). Fishes exposed to elevated water temperatures can face an “oxygen squeeze” where the decreased supply of oxygen cannot meet the increased demand. For example, an anomalously warm year (1983) in southern Canada produced anoxic conditions in the hypolimnion of Lake Erie (Schertzer and Sawchuk 1990) because the BOD exceeded the supply. Dissolved oxygen concentrations in Lake Erie could be reduced by 1 – 2 mg/L under a 3 –4°C warming scenario conducted by Blumberg and Di Toro (Blumberg and Di Toro 1990). This study indicated that warming of this magnitude would lead to DO levels below 5 mg/L in the summer months (July-September) and below 2 mg/L in late August to early September. Climate models predict July DO levels in Lake Suwa, Japan to decrease from the current value of 6.1 mg/L to 2.0 mg/L under a 2°C warming scenario (Hassan et al. 1998). The ayu (*Plecoglossus altivelus altivelus*), the endemic masu salmon (*Oncorhynchus rhodurus*), and the kokanee salmon (*Oncorhynchus nerka*) are three fishes found in the lacustrine environments of Japan. These species are valuable because they are fished commercially, are cultural art symbols in art, and are targeted in a recreational fishery (Fausch and Nakano 1998). A drop in DO concentrations to this level would result in extirpation of these species as salmonids cannot tolerate DO levels lower than 3 mg/L for an indefinite period of time (Avault 1996).

The extent and strength of lake stratification is also a major driving factor in determining DO concentrations (Klapper 1991). The effects of this phenomenon will be discussed in subsequent sections. However, it is important to note that current models predict that stratification will increase in strength and duration (Topping and Bond 1988), thereby impacting the spatial and temporal distribution of adequate dissolved oxygen levels temperate lakes.

Environmental dissolved oxygen levels must be high enough to support aerobic metabolism in fishes (Moyle and Cech 2004). As mentioned above, most fishes can maintain adequate levels of oxygen uptake at DO concentrations above 5 mg/L (Brett and Groves 1979). When concentrations drop below 5 mg/L, many species employ physiological and behavioral adaptations to maintain adequate rates of oxygen uptake, but as DO concentrations drop below 2 – 3 mg/L, these adaptations often prove insufficient. Adaptations for dealing with hypoxia are most advanced in tropical fishes, but temperate species that naturally occur in habitats where environmental hypoxia is commonplace, such as the crucian carp (*Carassius carassius*) and Sacramento blackfish (*Orthodon microlepidotus*) (Campagna and Cech 1981; Cech and Massengill 1995) also show similar adaptations (Walker and Johannsen 1977). For example, some fish resort to air breathing through modified swim bladders (the arapaima, *Arapaima gigas* (Val and Almeida-Val 1995) and the alligator gar *Lepisosteus spatula* (Jenkins and Burkhead 1993)). Others, like the commercially important (both capture fisheries and aquaculture) South American tambaqui, *Colossoma macroponum* obtain O_2 from the oxygen-rich air-water interface (Val and Almeida-Val 1995). Other fishes employ metabolic downregulation, anaerobic metabolic pathways, or the ability to move short distances over land in search of better habitat (United Nations Economic Commission for Asia and the Far East 1972; Val and Almeida-Val 1995). The ability to persist in hypoxic or even anoxic environments is not without cost. The physiological and behavioral adaptations fish use to deal with hypoxia can be energetically expensive, reducing the amount of energy available for growth and reproduction (Campagna and Cech 1981). Therefore, if increased water temperatures result in an increased frequency or duration of hypoxic episodes, it is likely that fish that persist will experience reduced growth rates and reduced reproductive output. This will be of particular concern for aquaculture species, because of the need for culturists to produce fish of a harvestable size as economically and quickly as possible. Anything (like hypoxia) that hinders this need is detrimental. Although some intensive culture operations could use aeration to offset lower oxygen levels, many of the world’s cultured fishes are grown in outdoor ponds, where aeration is either logistically difficult or extremely expensive.

Dissolved oxygen concentrations do not have to drop to very low levels before physiological functions are affected. Sublethal hypoxia (2-3 mg/L) causes reduced feeding activity (Stickney 2000), reduced swimming performance, and reduced fitness of emerging larvae (Doudoroff and Warren). Low DO levels have also been linked to immunosuppression in fish (Boyd and Tucker 1998; Stickney 2000); this is particularly important in aquaculture systems where the high fish densities increase the risk of disease transmission. Fish exposed to hypoxic conditions are less tolerant of environmental stresses (e.g. disease, crowding, food limitation, thermal stress, and natural and anthropogenic toxins) than fish in normoxic (O_2-saturated) water (Langford 1983).

Shallow ponds, lakes and all tropical systems are highly dependent on photosynthesis to replenish their DO supply because of their high productivity and biological oxygen demand (Liang et al. 1981; Val and Almeida-Val 1995). In these systems, critically low dissolved oxygen concentrations are encountered overnight, and particularly just before sunrise (United Nations Economic Commission for Asia and the Far East 1972; Liang et al. 1981; Val and Almeida-Val 1995). A temperature–related increase in biological oxygen demand could increase the magnitude and duration of this critical period, potentially altering the community structure and carrying capacity of these systems. Larger systems such as the African and Laurentian Great Lakes display some eplilimnetic dissolved oxygen cycles, but these concentrations are most affected by changes in strength of stratification and wind–driven mixing (Welcomme 1979; Klapper 1991; Kurki et al. 1999). Tropical systems such as the Amazon River in South America and the Mekong River in southeast Asia contain extremely diverse fish faunas. The Amazon River system contains economically important characins such as the trahira (*Hoplias malabaricus*), tambaqui, a host of smaller species that support large subsistence and artisanal fisheries, and approximately 1000 species of catfish, some of which are also economically important. The Mekong River in southeast Asia is home to commercially important species such as the milkfish (*Chanos chanos*), various carps and catfishes, and featherbacks (*Notopterus spp.*) (Lowe-McConnell 1975; Val and Almeida-Val 1995). These systems have naturally low oxygen levels due to high nutrient cycling, high rates of bacterial decomposition, and macrophyte shading and water turbidity (Val and Almeida-Val 1995). Though most of the fishes in these systems have evolved to cope with moderate levels of hypoxia, they are still dependent on aquatic respiration, and are hence vulnerable to prolonged periods of hypoxia or anoxia. Air-breathing fishes will be less affected by hypoxia or anoxia in the water column, but increased metabolism will probably necessitate more frequent surfacing, which, in turn increases energetic costs and predation risk.

Increased incidence of hypoxia and anoxia in freshwater systems is a likely result of climate change due to the decreased DO concentrations and increased biological oxygen demand that are associated with of increasing temperatures.

EUTROPHICATION, PRIMARY PRODUCERS, AND LIMNOLOGY

In temperate and subarctic zones, researchers have found that changes in the global climate can profoundly affect primary production and the trophic state of inland waters (Roessig et al. 2004). In temperate zones, temperature increases and stratification have appreciable impacts, whereas in the tropics, wind, precipitation, and stratification may have a greater effect on the status of inland water bodies.

Eutrophication

The trophic status of aquatic systems are defined by nutrient concentration. An oligotrophic system has a low nutrient concentration, a mesotrophic system has a moderate nutrient concentration, and a eutrophic system has a high nutrient concentration (Kalff 2000). The natural trophic state of an aquatic system is a function of volume, water residence time, and nutrient input from the surrounding watershed (Kalff 2000). However, human activity can also alter the trophic status of aquatic systems through anthropogenic enrichment or nutrient depletion, and climate change.

Most cases of eutrophication result from the input of excess nutrients from urban and agricultural runoff and from sewage discharge (Lammens 1990; Klapper 1991; Karabin et al. 1997; Nicholls 1998). However, increases in temperature can also augment the productivity of a body of water by increasing algal growth, bacterial metabolism, and nutrient cycling rates

(Klapper 1991). When coupled with the input of anthropogenic pollutants, temperature changes can accelerate the eutrophication process (Klapper 1991; Adrian et al. 1995) and delay recovery from anthropogenic eutrophication. For example, in the El Niño years of 1983, 1987, and 1992, anomalously warm winters in Lake Huron, North America caused reduced ice cover and allowed wind and wave disturbance of the water column during winter, thereby allowing increased transport of pollutants containing phosphorus. These pollutants are capable of affecting the productivity of aquatic systems, and their introduction into relatively pristine areas has caused eutrophication in some of Lake Huron's (formerly) oligotrophic waters (Nicholls 1998).

Increases in temperature may enhance eutrophic conditions by stimulating explosive macrophyte growth. A 2002 study found that a 2 – 3°C temperature increase could cause a 300–500% increase in shoot biomass of the aquatic macrophyte *Elodea canadensis* (Kankaala et al. 2002). A biomass increase of this magnitude would affect the system in various ways. First, because macrophytes take up the phosphorus sequestered in the sediment, the amount of phosphorus immediately available for other primary producers would decline. However, when the macrophytes die and decompose, they release nutrients such as nitrogen and phosphorus into the water column (Cooper 1996; Kankaala et al. 2002). This influx of nutrients can stimulate algal blooms and help perpetuate high macrophyte production. Additionally, the increased oxygen demand during the bacterial and fungal decomposition of these macrophytes increases the amplitude of the diel oxygen cycle (Figure 4). This can lead to depressed levels of DO in the system, raising the likelihood of anoxia–related fish kills (Klapper 1991) or of chronically stressful hypoxic conditions.

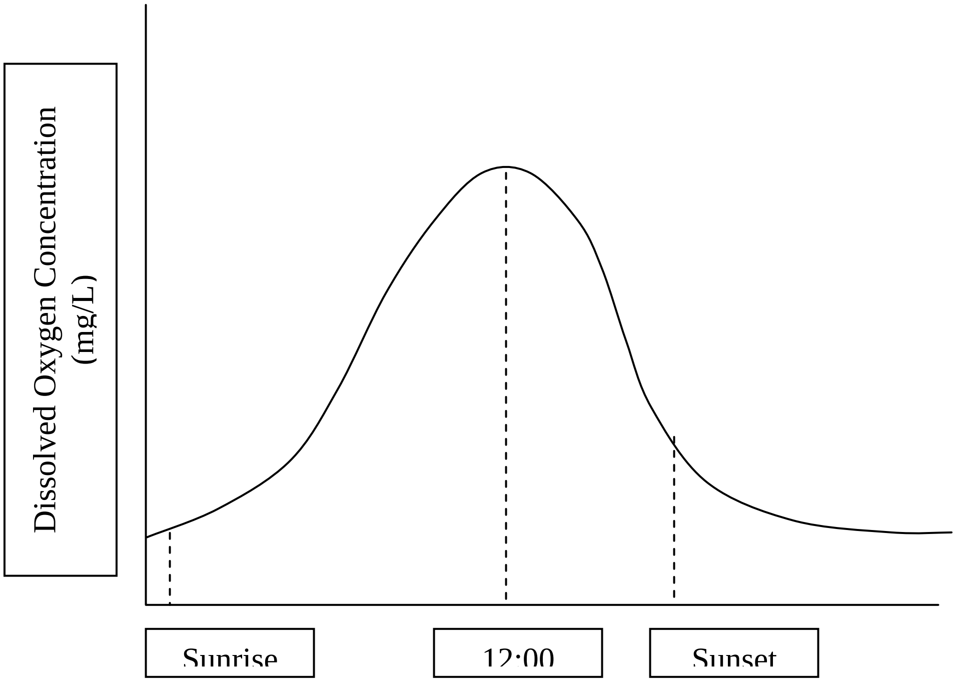

Figure 4.—Diurnal fluctuation in a small warm aquatic system. Due to high temperatures, community respiration would quickly deplete the O_2 introduced into the system by surface turbulence or by diffusion from the atmosphere. Therefore, all of the aquatic organisms in a system such as this depend heavily upon algal or macrophytic photosynthesis to supply adequate oxygen. As a result, oxygen concentrations are highest during the day when photosynthetic rates are maximal and lowest at night when photosynthesis does not occur and the entire aquatic community consumes O_2 through respiration. (Adapted from Kalff 2002 and Goldman and Horne 1983.)

Finally, increased macrophyte growth pushes aquatic systems toward a eutrophic state by trapping sediment and preventing flushing of excess nutrients from the system.

Increased production of aquatic macrophytes can have other indirect effects. Large rafts of emergent, floating, or subsurface macrophytes can reduce wind mixing, increasing the duration of periods of stratification (Welcomme 1979). An overabundance of macrophytes can reduce the amount of fish habitat. This was the case in two Estonian lakes where increases in macrophyte density resulting from eutrophication reduced the amount of northern pike (*Esox lucius*) habitat (Kangur et al. 2002).

Australian freshwater systems appear to be particularly susceptible to eutrophication. When Europeans first traveled to Australia, they observed signs of eutrophication, such as persistent algal blooms. This implies that, in addition to the present environmental issue of anthropogenic eutrophication, the “slow flowing rivers of Australia’s arid inland” are naturally susceptible to eutrophication (Banens and Davis 1998). Australian fishes have evolved to withstand a specific set of harsh environmental conditions (Young 2001). For example, juvenile spangled perch (*Madigania unicolor*) can tolerate temperatures between 5.3 and 39°C without experiencing significant mortality rates (Llewellyn 1973), and when ephemeral pools desiccate in the dry season, the Australian salamanderfish (*Lepidogalaxias salamandroides*) survive by burrowing into moist substrate and breathing air by cutaneous respiration (Martin et al. 1993). However, should eutrophication exceed pre–settlement levels, negative impacts on both native and introduced fishes should be expected (Young 2001).

Changes in trophic state often negatively affect fish communities through direct effects on macroinvertebrate prey and through effects on the algal community that support the zooplankton (Adrian 1998). The general result of eutrophication in temperate lakes appears to be the replacement of economically important species such as salmonids and centrarchids with smaller, less desirable species such as some cyprinids (Persson et al. 1991) and gizzard shad (*Dorosoma cepedianum*) (Bays and Chrisman 1983).

Water Temperature Effects on Limnology

In temperate and subarctic zones, small annual temperature increases have a pronounced effect on the timing and strength of stratification in lotic systems (Gaedke et al. 1998). As global temperatures rise, stratification in temperate zone lakes will strengthen (Topping and Bond 1988; Gaedke et al. 1998). The deeper portion of large lakes, the hypolimnion, contains water that is not directly heated by solar radiation (Kalff 2000). At the same time, the warmer water in the relatively thin epilimnion is continually heated by the sun, and the density gradient between the two layers prevents mixing between them (Kalff 2000). An increase in global temperatures will strengthen stratification because increased heating of the epilimnion will intensify the temperature and density gradients between the two compartments, making mixing more difficult. Climate change will also prolong stratification events by heating the epilimnion sufficiently to form a density gradient earlier in the year. For example, Lake Geneva in Switzerland has not experienced a complete turnover since 1986; this is thought to be a result of climate warming (Gerdaux 1998).

Why does this matter? The epilimnion is exposed to the atmosphere and experiences turbulence–induced mixing of O_2 and sufficient light to stimulate algal photosynthesis.

However, since algal growth requires nutrients such as NO_X, PO_4, and Mg^{+2}, the epilimnion is characterized by limited amounts of nutrients (Goldman and Horne 1983). The hypolimnion does not receive oxygen from the atmosphere, and low light prevents photosynthesis and algal use of nutrients so it is characterized by a limited DO supply and a large store of nutrients (Goldman and Horne 1983). Lake mixing is essential for the movement of oxygen to the hypolimnion and nutrients to the epilimnion, where they can be incorporated into the food web (Klapper 1991; George and Hewitt 1998; Straile and Geller 1998).

Thermal stratification is a major driving force in determining algal assemblages. Longer periods of stratification create favorable conditions for blue–green algae because these species are naturally buoyant and have the ability to fix nitrogen in amictic, nutrient–limited conditions (George et al. 1990; de Souza et al. 1998; Jones and Poplawski 1998). Blue–green algae are inedible to most species of zooplankton that planktivorous fishes feed on (George et al. 1990; Kangur et al. 2002), so such a shift in phytoplankton composition can negatively affect fisheries productivity. In addition, some species of blue–green algae produce alkaloids that are toxic to fish (de Souza et al. 1998) or their prey items (Bucka 1998). Sublethal concentrations of these toxins can remain in an organism for up to three months and have the potential to enter the human food chain (Banens and Davis 1998). In a four–year study (1996–1999), tilapia (*Tilapia rendilli*) harvested from Jacarepaguà Lagoon in Brazil were analyzed to determine the concentration of cyanobacterial hepatotoxins in their liver, viscera, and muscle tissue. The analyzed muscle tissues contained microcystin levels that reached or exceeded maximum concentrations recommended for safe human consumption (de Magalhães et al. 2000). Changes in mixing regimes could increase the success of toxic cyanobacteria: these undesirable organisms may dominate the algal community for a greater part of the year if stratification increases in strength and duration. This could lead to increased accumulation of toxins such as microcystins in the flesh of edible fish.

The suitability of the hypolimnion, an important refuge for numerous cold stenothermal fishes (Brett 1971; Coutant 1985) can be compromised by prolonged and more distinct periods of stratification. An increase in mean temperature will affect hypolimnetic dissolved oxygen concentrations in two ways: increased metabolism of fish and other organisms in a slightly warmer hypolimnion will lead to the faster depletion of the limited oxygen supply, and lake overturn, the primary means of replenishing hypolimnetic dissolved oxygen, will occur less frequently.

There are some dramatic examples of how stratification also affects fisheries productivity in tropical systems. Because tropical water temperatures do not fluctuate seasonally as in temperate and subtropical zones, turnover, and therefore, nutrient cycling to the biota of the lake, is a function of wind–induced mixing (Kurki et al. 1999; Vuorinen et al. 1999). The African Great Lakes contain deep anoxic hypolimnia that serve as nutrient stores. The anoxic hypolimnia of tropical lakes also contain high concentrations of hydrogen sulfide. This chemical compound is a byproduct of anaerobic decomposition of organic matter and is highly toxic to fish. Moderate amounts of mixing allow nutrient influx into the epilimnion and benefit fisheries productivity without introducing high concentrations of toxic hydrogen sulfide into the epilimnion. For example, the stratified northern end of Lake Tanganyika, Africa supports a less productive fishery than the well–mixed southern arm and the main basins (Vuorinen et al. 1999). A comparative study of historical and current levels of primary production in the north end of Lake Tanganyika indicated that current levels are much lower as a result of strengthened stratification (Verburg et al. 2003). This lack of mixing is attributable to a tripling in density gradients between 110-200 m and between 200-800 m of depth since 1913 (Verburg et al. 2003). Because a small temperature difference greatly affects water density at higher temperatures (22-26°C in this case), this increase in gradient is attributable to a 0.7°C differential in heating between 100 and 900 m of depth (Verburg et al. 2003). Recent changes in the limnology of Lake Victoria have also negatively affected its fishery. In the 1980’s decreased turnover in the lake led to low levels and dissolved oxygen and, consequently, fish kills. Stratification in this lake now appears to be permanent (Kaufman et al. 1996).

It is important to note that fish kills are common in tropical lakes and often result from natural events such as storms. Sudden perturbation of the water column and the resulting introduction of large amounts of anoxic water and hydrogen sulfide into the epilimnion suffocate and poison aquatic organisms. Data on these fish kills are scarce, but a 1984 storm in the

Nyanza Gulf of Lake Victoria resulted in the deoxygenation of the water column and the subsequent death of 400,000 fish, mostly Nile perch and Nile tilapia (Ochumba 1990). Many authors argue that effects of anthropogenic eutrophication is a primary cause of many of these fish kills because they increase the incidence of water column hypoxia and anoxia (Ochumba 1990; Verschuren et al. 2002). However, climate change has the ability to alter limnological characteristics such as stratification and trophic status. Therefore, its contribution to fish kills may be small at present but is still worthy of consideration especially in coming years.. It is likely that other tropical lakes will begin to exhibit limnological changes similar to those seen in lakes Tanganyika and Victoria. Though the biological record for Lake Malawi is poor in comparison to that of Tanganyika, recent studies suggest that its mixing rates have also declined (Verburg et al. 2003).

The amplitude and nature of changes in tropical weather patterns are the source of considerable disagreement. Decreased incidence of wind in the tropics may lead to the prevalence of conditions seen in Lake Victoria and their subsequent impacts on the fishery. On the other hand, an increase in wind–driven overturn could have mixed effects. The increased mixing would increase the productivity of lakes by cycling more nutrients, but this could accelerate the rate of eutrophication. If changing weather patterns produce stronger winds, then there is the risk that the increased mixing will resuspend anoxic sediments. Total turnover of these lentic systems can result in a massive infusion of hydrogen sulfide into the epilimnion, causing fish kills (Welcomme 1979). Turnovers resulting in fish kills currently occur in the Amazon basin during friagem events. A friagem event occurs when cold winds decrease the surface water temperature in lentic systems and force mixing. The resulting fish kills are caused by the sudden introduction of large amounts of anoxic water and hydrogen sulfide from the hypolimnion into the epilimnion (Val and Almeida-Val 1995).

THERMAL HABITAT SPACE, THERMAL REFUGES, AND CHANGES IN FISH COMMUNITIES

An increase in mean annual temperature will significantly alter the geographical ranges of temperate and subarctic fish. This will occur through the compression or expansion of thermal habitats, the alteration of thermal refuges, and the migration towards the poles of the isolines that determine present species distributions.

In the temperate and subarctic lakes of North America and Europe, cold water stenotherms such as arctic charr (*Salvelinus alpinus*), lake trout (*Salvelinus namaycush*), and whitefish (*Coregonus* spp.) use the hypolimnion as a thermal refuge (Christie and Regier 1988; Gerdaux 1998). However, more pronounced and longer–lasting stratification will reduce the amount of oxygen exchange to the hypolimnion from the oxygen–rich epilimnion. When the oxygen demand in the hypolimnion exceeds the supply, hypoxic or anoxic conditions will occur. Fishes that depend upon these thermal compartments are then faced with a "temperature–oxygen squeeze" (Figure 5); they are confined to a habitat whose boundaries are defined by the warm temperatures in the epilimnion and the low levels of dissolved oxygen in the hypolimnion (Matthews et al. 1985). This severely limits their available spring and summer habitat, because increased ambient temperatures thicken the epilimnion and cause accelerated oxygen depletion in the hypolimnion (Christie and Regier 1988; Gerdaux 1998). This principle is also applicable to fishes introduced beyond the edge of their optimal ranges.

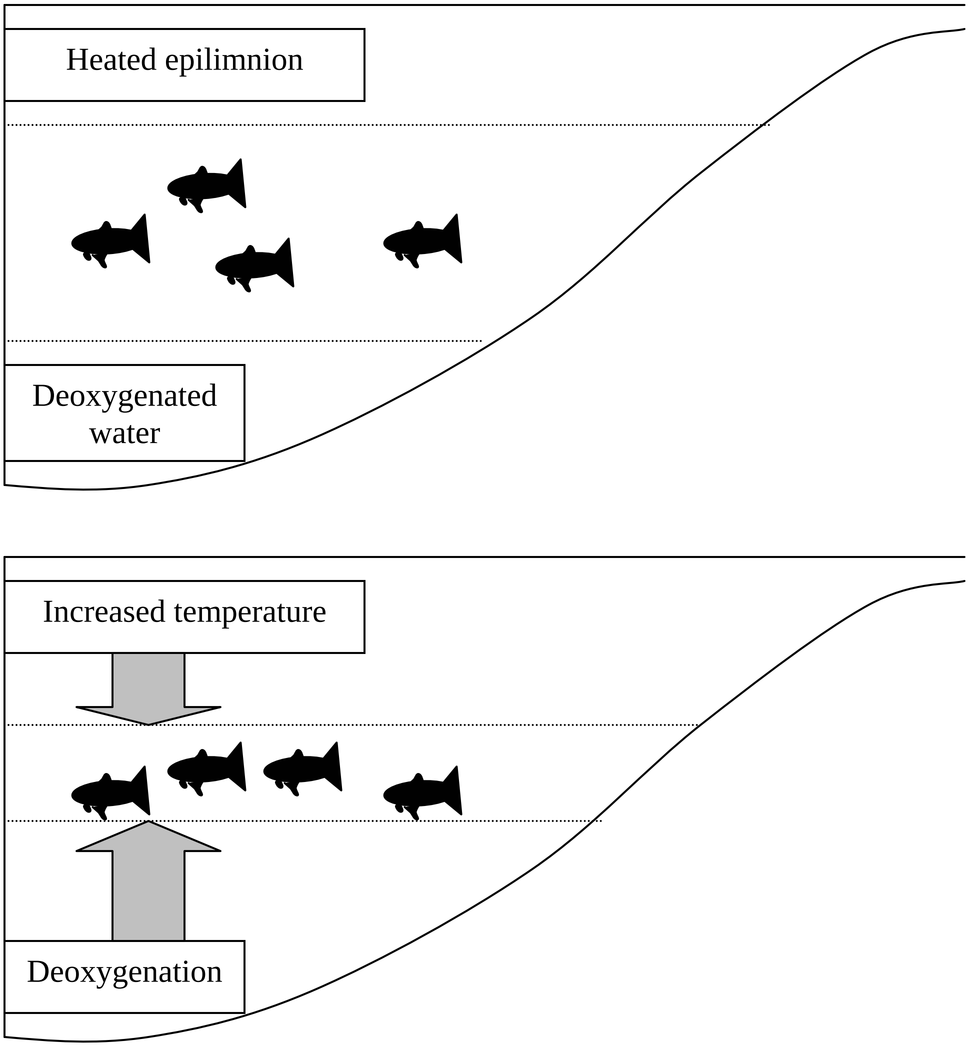

Figure 5.—Due to species–specific temperature and oxygen requirements, climate change may restrict pelagic habitat availability for many species. Increased solar radiation will thicken the epilimnion, and increased fish metabolism will result in decreased concentrations of dissolved oxygen. Adapted from Coutant 1985

For example, reservoirs in the southeastern United States contain striped bass (*Morone saxatilis*), the target species of a lucrative sport fishery. Striped bass naturally occurred in some of the rivers impounded by these reservoirs and have been widely introduced into others in the southeastern US and in other regions of the United States. Striped bass survive in the reservoirs of the southeastern U.S. by using thermal refugia such as springs and dam tailwaters during the summer months (Cheek et al. 1985; Moss 1985; Coutant 1990). As was discussed above, the size of these thermal refugia can be reduced by increased water temperatures. When thermal refugia are reduced in size, the fish are crowded into a smaller volume of water where factors such as rapid oxygen depletion, low prey availability, stress, and the probability of increased disease transmission are present (Coutant 1985).

Increased strength and duration of thermal stratification could decrease access to prey for cool and coldwater species or decrease the ability of a prey species to use the epilimnion as a refuge. The kokanee salmon (landlocked sockeye salmon; *Oncorhynchus nerka*), an important sport and forage fish in western North America, makes diel vertical migrations, partially to avoid encounters with predatory lake trout that are largely confined to the hypolimnion during summer stratification (Stockwell and Johnson 1999). If surface water temperatures become too warm, kokanee salmon may not be able to use the epilimnion as a refuge from predators.

Coolwater fishes such as the native yellow perch (*Perca flavescens*) may experience an increase in thermal habitat because of increased global temperatures. The hypolimnion of the Laurentian Great Lakes is too cold for this species, but global warming would thicken the epilimnion, thus increasing the size of their thermal niche (Kling et al. 2003). Yellow perch are native to the Great Lakes region, but their possible northward range expansion causes some concern because they would compete with the current fish assemblage for limited resources. The effects of this competition on yellow perch or on the fishes currently inhabiting these lakes is not known, but yellow perch have been branded a nuisance species in other areas where they have been introduced. Because the coolwater systems would still be subject to density–dependent controls such as inter– and intraspecific competition, disease, and resource availability, careful modeling would be required to determine if an increase in coolwater fish production would occur.

In North American stream systems, salmonid genera including *Salmo, Oncorhynchus*, and *Salvelinus* rely on groundwater discharge for a summer refuge (Meisner et al. 1988), especially in lower latitude and lower elevation streams (Meisner 1990). The availability of cold refugia will decrease as groundwater temperatures increase concurrently with mean global temperatures(Meisner et al. 1988). Warming of 3.8°C is expected to drastically reduce the range of brook trout (*S. fontinalis*) in the southeastern United States (Flebbe 1993; Mulholland et al. 1997) and in southern Canada (Meisner 1990). Specifically, 89% of thermally suitable brook trout habitat in North Carolina and Virginia, U.S.A. could be lost (Flebbe 1993). A study of two headwater streams in the Humber and Rouge river systems in southern Ontario indicated that a 4.1°C increase in summer air temperature would reduce thermally suitable brook trout habitat by 42% and 30% respectively (Meisner 1990). These findings suggest that this pattern of habitat loss would also be experienced in other temperate and subtropical areas. Trout (both brown and rainbow) populations that support substantial recreational fisheries exist throughout the world's temperate regions with concentrations in Australia (Young 2001), New Zealand, southern South America, the United States, and Europe (Dill 1993). While there may actually be an ecological benefit from reducing the range of exotic species in some locations (such as might happen as water temperatures increase), it is important to remember that the native fishes most impacted by the introduced salmonids (e.g., the galaxiids in Australia and New Zealand) are likely to be cold-water stenotherms as well, and would experience further contractions of their already limited ranges. We use trout as an example but any stenothermal fishes living at the lower latitudinal edge of their range will probably experience a range contraction as global temperatures increase.

FISH DISTRIBUTIONS AND TEMPERATURE BARRIERS

The distributions of many temperate zone freshwater fish species are determined by temperature isolines instead of physical barriers. These isolines are both elevational and latitudinal in nature (Moyle and coauthors 1982; Baltz et al. 1987). Fishes are limited at the highest latitudes and altitudes of their range by cold temperatures, primarily because the growing seasons are too short to allow juveniles to attain sufficient size in their first summer to stave off overwinter starvation (Shuter and Post 1990; McCauley and Beitinger 1992; Kling et al. 2003). The warm water temperatures at the lowest latitudes and elevations of their range also become limiting factors.

In some cases, the predicted shifts in range are quite dramatic. McCauley and Beitinger (1992) argue that a temperature increase of 1°C would shift the range of channel catfish (*Ictalurus punctatus*), the most common commercially raised fish in the United States, 240 km north; the northward expansion of the range would also be accompanied by a parallel northward retreat of the southern edge of the range. A global warming trend would result in the northward expansion of warmwater species in North America, Europe (Roessig et al. 2004), and Asia, and the southward expansion of warmwater species in Australia and South America. Species such as Eurasian perch in Europe and Australia, and yellow perch (Shuter and Post 1990) and smallmouth bass (*Micropterus dolomieui*) (Jackson and Mandrak 2002) in North America would be able to use habitats closer to the poles. These fish would compete for space in their “new” ecosystems, possibly at the expense of native species that share similar thermal requirements. The northern migration of predatory species could also have a deleterious effect on native prey fish. Jackson and Mandrak (2002) argue that a northward migration of species such as smallmouth bass would cause the extinction of as many as 25,000 populations of native cyprinids (*Phoxinus* spp*.*, *Pimephales promelas, Margariscus margarita*) in the province of Ontario. Though the four cyprinid species are common to Ontario, smallmouth bass are limited to environments where the average July temperature is in excess of 16°C (Jackson and Mandrak 2002). Increasing annual temperatures would also force a northward retreat in the species range of economically valuable fishes such as northern pike, whitefish, and lake trout (Kling et al. 2003). Because global climate change will shift the ranges of temperate fishes in a poleward direction, it could have potentially serious impacts on some stream fishes, fishes in geographically isolated environments, and fish in lentic systems. The ranges of all species will shift on a north–south axis, so fishes in lotic systems with an east–west orientation, geographically isolated systems (i.e., those without connections to north–south oriented waterways), springs, and lakes will be essentially trapped and therefore faced with extinction. For example, the diverse assemblage of fishes in the southwestern United States (Ono et al. 1983) would not be able to migrate in response to climate change because…. The size of the stream systems in the southern Great Plains of the United States precludes the possibility of migration. In order to “track” their optimal thermal range as temperatures increased, these fishes would have to undertake westward or eastward migrations of thousands of miles to reach more suitable watersheds (Matthews and Zimmerman 1990). Even if these fish were to somehow "understand" the necessity of migration and undertake these journeys, they would be hindered by man–made barriers, such as dams, water diversions, and flood control structures (Porto et al. 1999; Clarkson and Childs 2000; Bednarek 2001; Winter and Van Densen 2001; Gehrke et al. 2002; Morita and Yamamoto 2002). Though some fishes in streams with an east-west orientation could migrate toward high-elevation headwaters in search of cooler temperatures, they would likely be faced with an entirely new set of environmental challenges such as smaller stream size and unfamiliar habitat (e.g. higher gradient, larger substrate, changes in turbidity). Similarly, fishes forced to seek optimal temperatures in north-south oriented systems would probably also have to cope with a new physical environment. The magnitude of these differences would depend upon factors such as the extent of the range shift and the size and longitudinal profile of the stream. Although fish in small, coastal east-west oriented streams could attempt migration to cooler waters by leaving their natal stream and seeking habitat in higher latitudes. In this case, the ultimate barrier for these migrating fishes would be the ocean, which they are physiologically ill-adapted to enter, even temporarily, in an attempt to locate suitable freshwater habitat (McDowall 1992). Fishes native to the Arctic Circle such as broad whitefish (*Coregonus nasus*), Arctic cisco (*Coregonus autumnalis*), and wild and commercially–raised Arctic char (*Salvelinus alpinus*) will also face new challenges. These species are largely restricted to the near-Arctic and

Arctic latitudes and are obligate coldwater stenotherms: they will be unable to migrate elsewhere when temperatures approach suboptimal conditions (ACIA 2004). Increasing temperatures are likely to cause declines and regional extinctions of these Arctic-adapted fish (ACIA 2004).

Fishes in relatively closed systems such as lakes will also be affected with potentially detrimental results. Fisheries managers could alleviate this phenomenon by translocating “trapped” fishes into more suitable watersheds. The introduction of fish to new environments is not always successful and raises environmental, political, and ethical questions. When various Colorado subspecies of cutthroat trout (*Oncorhynchus clarki* spp.) were introduced into fishless or reclaimed waters, they experienced a success rate of less than 50% (Harig et al. 2000). The introduction of fish into naive waters is not a decision to be made lightly because of the possible negative consequences for organisms already in that environment. History has taught us that introduction of nonindigenous species into natural ecosystems can have disastrous results. For example, the Nile perch (*Lates niloticus*) was introduced into Lake Victoria in a well–meaning effort to improve the fishery. The endemic cichlids had not evolved with a large, cursorial predator and were subsequently decimated (Ribbink 1987).

Predictions of the effects climate change will have on the distribution of tropical fishes are few, because though the topic is of interest, relatively little is known about tropical systems compared to those in temperate regions. However it is likely that tropical species will experience a poleward expansion as the thermal isolines are shifted (Mulholland et al. 1997). Resource managers should be concerned because a small increase in temperature could be sufficient to shift thermally optimal ranges.

Regardless of the type of system (tropical, subtropical, temperature, polar), it is important to note that range shifts will occur at the species level, but not necessarily at the community or ecosystem level. Fishes (and other organisms) in the same community may not share the same thermal optima and tolerance limits. Stenothermal species (e.g., salmonids) are most likely to experience range shifts while eurythermal species (e.g., common carp) may be capable of adapting to a new thermal regime. This raises the possibility that ecosystem components like food webs, interspecific competition, and host–parasite interactions will be altered. Though the altered ecosystems will, eventually, achieve a new steady state, the form this state will take or the amount of time required to do so is completely unknown.

DISEASE AND PARASITISM

Parasite transmission depends on host condition, the presence of intermediate hosts necessary for the parasite life cycle, water quality, and temperature (Marcogliese 2001) (Figure 6). Climate change will alter host–parasite dynamics by changing transmission opportunities and changing host susceptibility (Roessig et al. 2004).

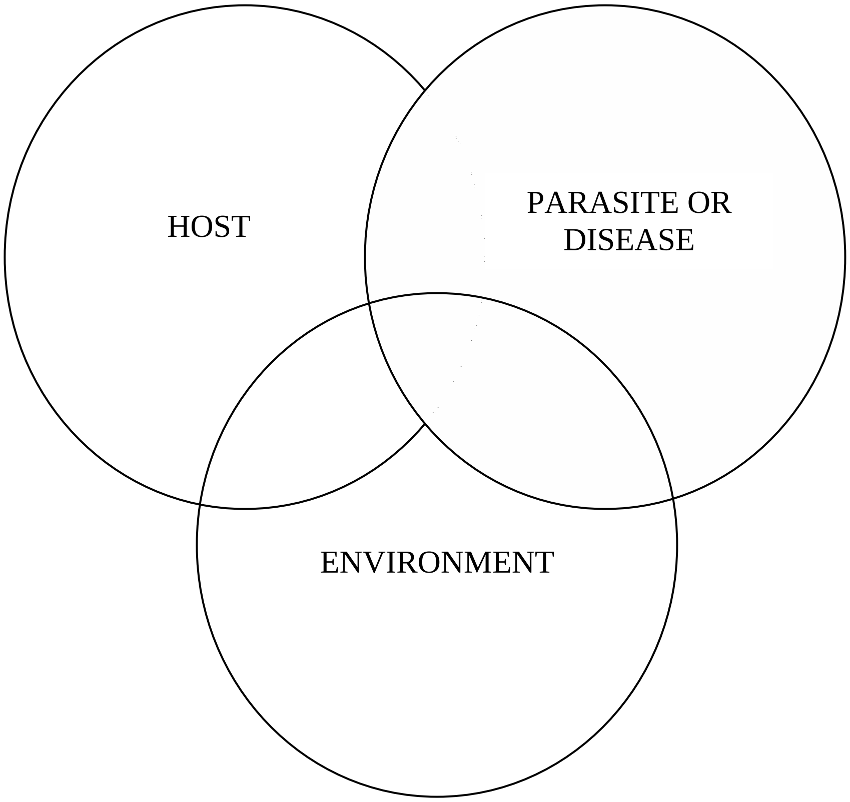

Figure 6.—In order for a host fish to be infected by a parasite or disease organism, the two organisms must overlap in space and time. Large–scale environmental changes such as global warming will affect the host–parasite relationship by altering host and parasite range, host susceptibility, and transmission rates. Direct temperature effects upon the parasite may also affect this relationship.

Temperate and subarctic zones fishes may experience increased parasite loads due to increased transmission opportunity. Warmer winter temperatures may allow for higher parasite survival, increasing the possibility of year–round infection and multiple generations of parasites in a single year (Marcogliese 2001). In temperate and subarctic zones, overwinter temperatures are a major limiting factor on the standing stock of parasites (Marcogliese 2001), through both direct and indirect mechanisms. Conversely, in some situations warmer winter temperatures could reduce the impact of disease and parasitism. In temperate zones with large annual temperature ranges, many opportunistic parasites infect fishes in the early spring, when they are still weakened from harsh winter conditions (Hefer and Pruginin 1981; Ozer and Erdem 1999). Therefore, higher temperatures associated with milder winters may lower infection rates by decreasing the stress experienced by overwintering fishes. However, the possible larger standing stock of parasites and their own abilities to survive the minimum temperature may outweigh the benefits of a warmer winter.

Changing global temperatures will also affect fish susceptibility as parasite abundances and infectivity change. The immune function of fish is compromised in the presence of stressors, including crowding, high temperatures, and osmotic stress. For example, rates of bacterial disease (such as furunculosis) in aquaculture systems often peak at high temperature (Hefer and Pruginin 1981; Wedemeyer 1996). The impact of whirling disease (*Myxobolus cerebralis*) on juvenile rainbow trout and cutthroat trout (*O. clarki* subspp.) in the Rocky Mountain region of the United States, is likely to become more severe as summer water temperatures in the Rocky Mountains increase (Hiner and Moffitt 2001). Whirling disease was introduced into North

America from Europe, and it infects most North American salmonids. Rainbow trout are the most susceptible to the disease, which causes skeletal deformities and death in severe cases (Gilbert and Granath 2003). Whirling disease is particularly detrimental to juvenile salmonids (Gilbert and Granath 2003), and can therefore severely limit recruitment in wild situations or production of fish under aquaculture conditions. A field study conducted in the Colorado River, Colorado found that experimental infection of juvenile trout (rainbow, brook, brown, and four cutthroat subspecies) resulted in mortality rates of approximately 89% within 4 weeks of infection (Gilbert and Granath 2003). Similar levels of mortality can occur under aquaculture conditions, and because of the ease with which whirling disease is transmitted, states like Colorado have imposed strict regulations (and in some cases quarantines) on aquaculture facilities that are whirling disease positive. In Colorado, at least, the commercial trout aquaculture industry has experienced a drastic decline in size, largely because of the effects of whirling disease and their subsequent inability to sell infected fish. Overall, it is difficult to quantify the effects of this disease throughout western North America. However, due to its ability to severely curtail recruitment, this disease threatens the viability of wild trout populations, commercial production, and even small-scale production of native trout (e.g., cutthroat trout) for restoration purposes. Furthermore, stress associated with increasing temperatures may degrade the ability of coldwater stenotherms to resist and survive infection (Marcogliese 2001).

The changes in lake limnology accompanying climate change may also influence transmission rates. The crowding of cool and coldwater fishes into a smaller hypolimnion could bolster parasite transmission (Marcogliese 2001) by virtue of the increased density of potential hosts. Stream and river systems may also experience more frequent parasite epizootics. Extended periods of low flows and elevated temperature have been linked to increased parasitism and disease in rainbow and brown trout (Schisler et al. 1999; Hiner and Moffitt 2001). The changes in fish communities brought about by individual species' range shifts will likely alter the composition of the parasite fauna of specific systems. Fish migrating from warmer regions may serve as hosts or vectors for parasites and diseases that are novel to species in the receiving environment (Font 2003).

Current data are insufficient to allow accurate predictions of the impacts of global climate change on parasite and disease outbreaks. However, the observed thermal effects on parasites, fishes, and water quality suggest that global warming may well increase the virulence of certain fish pathogens and the transmission of some parasites. The implications of this are global in nature and involve both wild and cultured fish. Parasitism and disease outbreaks can cause increased mortality, slower growth rates, and lower marketability in fishes (Hefer and Pruginin 1981).

WATER BALANCE: THE HYDROLOGIC CYCLE AND REGIME

Global climate change will also affect aquatic systems through changes in the hydrologic cycle: evaporation, evapotranspiration, and precipitation . Changes in evaporation and evapotranspiration rates will have significant effects in both tropical and temperate zones. Increased temperatures and exposure to solar radiation will accelerate the rate of water loss from lakes, rivers and swamps. History has not linked increased evapotranspiration with lower water levels in temperate lakes (Kling et al. 2003). However, higher temperatures and insolation should increase current water loss rates from these systems; lower water levels would occur if evaporation rates outstrip input from increased precipitation. Though precipitation is expected to increase in North America, the continent will receive rain in fewer but more pronounced rainstorms; this is expected to lead to a general drying of watersheds (Kling et al. 2003). This increase in water loss and probable decrease in input does suggest a net reduction in lake levels; GCM models predict that water levels in the Laurentian Great Lakes will drop by 0.23 to 2.48 m within the next 100 years (Magnuson et al. 1997).

In tropical systems, evaporation and evapotranspiration often already exceed precipitation in the dry season (Welcomme 1979; Irion and Junk 1997); it is also not known if increased water loss to the atmosphere will be offset by rising precipitation rates (Hulme 1994). Evaporation rates are a driving factor in tropical lakes. Lakes Malawi and Tanganyika are endorheic; their only “outlet” is to the atmosphere. Therefore, changes in their water chemistry are largely driven by inflows, evaporation and precipitation. Tropical systems may well experience faster water loss to the atmosphere; GCMs indicate that a 2 – 3°C increase in ambient temperature in the Mekong system would bring about a 10 – 15% increase in evapotranspiration (Jacobs 1992).

Small changes in water levels of lentic systems will likely have minimal impacts on freshwater pelagic fishes. Changes in water level will have more serious consequences for species with narrow bathymetric ranges, such as some of the cichlids in the African Great Lakes. The traditional fishery in Lake Victoria consisted of two tilapiine species (*Oreochromis esculentis, Oreochromis variabilis*) and about 300 species of the genus *Haplochromis.* Within the last 30–40 years, many of these fishes have become extinct or are near extinction due to overfishing and introduction of nonnative fishes (Kudhongania and Chitamwebwa 1995). A majority of the remaining species (a major food source for local peoples) inhabit shallow, sandy areas that form a small percentage of the total lake habitat (Ribbink 1987). Small changes in water levels will eliminate this habitat, forcing these fishes to use areas devoid of their vital habitat structures; this would likely lead to population declines and might set off a cascade of new interspecific interactions.

Large lakes tend to be fairly resistant to physical and chemical changes, primarily because of the inertia or buffering capacity provided by their large volume. This environmental stability is in part responsible for the large numbers of endemic fishes found in such systems;

Lakes Victoria, Tanganyika, Malawi, and Baikal have the highest number of endemic fishes in the world (Ribbink 1987). Unfortunately, the same stability that allows for high biodiversity is also a liability for aquatic organisms in these systems, because they are not adapted to widely fluctuating conditions (Ribbink 1987). Should global climate change manage to alter the physical or chemical characteristics of large systems like the Laurentian Great Lakes, the African Great Lakes, and Lake Baikal, an overall loss in biodiversity would result because many endemic species would be incapable of adapting to the changing conditions.

Obviously, precipitation is a major driving factor in aquatic systems; changes in annual rain and snowfall totals can drastically affect lotic ecosystems by changing their hydrologic regime. The hydrologic regime of a stream involves the timing of flows of different magnitudes. Flood or peak flows and low flows vary regionally and by watershed with respect to duration, frequency, and magnitude, and interannual variability. Again, fishes living in lotic systems have adapted to a specific set of hydrologic conditions: changes in these conditions can result in increased success of invasive species, reduced recruitment, and poor survival of individuals. In most major river systems worldwide, the size of the seasonal flood is determined by precipitation. Most large river systems are pulse–dominated; the extent and duration of the seasonal flood determines the success of the system’s fisheries (Welcomme 1979).

Temperate rivers will experience changes in the timing and composition of precipitation. Reduced snowpacks will decrease spring flows, especially in systems that occupy regions that are marginal with respect to snow storage; major rivers such as the Mississippi and the Severnaya Dvina will be affected by the decrease in snowpack (Nijssen et al. 2001). In high latitude rivers, the expected increase in precipitation and decrease in snowpack will result in an earlier, smaller flood pulse (ACIA 2004). Without high spring flows, these stream systems may experience lower minimum flows (Nijssen et al. 2001). This could negatively affect populations of economically important fishes. For example, introduced Chinook salmon (*Oncorhynchus tshawytscha*) in New Zealand migrate during low flow periods; a further decrease in stream discharge during seasonal low flows may block their migration (McDowall 1992).

Tropical “blackwater” habitats such as the Amazon varzèa lakes are inundated during flood stages and may become isolated from the main channel during the dry season (Val and Almeida-Val 1995). Seasonal floods flush toxins out of these peripheral systems and reintroduce massive amounts of allochthonous material that forms the base of the system’s food chain (Welcomme 1979). Regular, predictable annual flooding also ensures reproductive success; most tropical fishes leave the main river channel and enter the inundated floodplain to spawn (Welcomme 1979; Harper and Mavuti 1996).

Tropical fishes and artisanal and commercial fisheries are adapted to this “feast–or–famine” cycle and are equipped to deal with conditions that vary with season. During the flood stage, opportunistic feeders build fat reserves to survive the dry season (Val and Almeida-Val 1995), spawning occurs, and human fishing activities are negligible due to the difficulties associated with fishing at high water (Welcomme 1979). During the dry season, fish take refuge in floodplain lakes (Val and Almeida-Val 1995) and large pools (United Nations Economic Commission for Asia and the Far East 1972). Here they endure crowding, low DO, increased levels of ammonia and nitrite, and increased risk of disease transmission (Welcomme 1979). The confinement of fishes in these refuges provides increased foraging opportunities for obligate piscivores (Val and Almeida-Val 1995) and better fishing success for artisanal and commercial fisheries (Welcomme 1979; Harper and Mavuti 1996).

Predictive models do not agree on the exact effects of climate change on tropical systems. Several models predict an increased flow amplitude for the Mekong River system; it would experience higher flood stages and lower minimum flows (Nijssen et al. 2001). The implications of an increased flow amplitude on the Mekong system are not insignificant; high flows would bring an increase in catastrophic flooding, and low flows may affect the fishery by increasing the length and severity of crowded, stressful conditions in refuge pools. On the other hand, a decrease in flow amplitude may also negatively impact the fisheries in tropical systems. Smaller flood stages would decrease the allochthonous input of material into the aquatic system. In addition, a smaller inundated floodplain would also translate into reduced spawning habitat. It is not known whether or not climate change has resulted in the decrease of the seasonal pulse in tropical systems. This phenomenon has been observed in four major rivers in southern South America, but it may be the result of land use changes and deforestation (Genta et al. 1998). Some

GCMs do agree on a small decrease in precipitation for the Amazon basin (Meisner 1992; Labraga 1997). If these predictions are accurate, the Amazon fisheries may indeed suffer because a change in rainfall of 2 or 3 mm/day over the Amazon drainage basin is enough to drastically alter stream flows (Meisner 1992).

Lower flows in tropical and temperate rivers may also present problems with respect to seawater intrusion. For example, the Mekong and the Amazon are both extremely low gradient rivers. In dry years, when the Mekong River's discharge drops below 1500 m^3/s, seawater penetrates the Mekong system as far as 50 km from the coast (Hori 2000) and inhibits rice production in 1.7 – 2.1 million hectares (Jacobs 1992). The Amazon River also has a very low slope (100 m per 4000 km) (Salati and Marques 1984), so a decrease in flows could profoundly affect their lowland and deltaic regions by altering the water chemistry and allowing more saltwater intrusion. This change in flows would be further exacerbated by a small rise in sea level (Roessig et al. 2004). Sea levels rose by 1 – 2 mm per year during the 20th century, much faster than prehistoric fluctuation rates . Furthermore, sea level is expected to rise between 10 and 80cm by 2100 according to IPCC scenarios (IPCC 2001). Though this rise would be partially attributable to the melting of ice, the majority of sea level rise would occur due to the thermal expansion of seawater (ACIA 2004).

TEMPERATURE AND TOXICOLOGY

The effects of temperature on toxicity have been tested with a myriad of chemical compounds and a diverse array of fish species. Unfortunately, much of the testing has involved short–term acute toxicity determinations, often at concentrations higher than those found in ecosystems (Nussey et al. 1996). In addition, the temperature–related toxicity effects often decrease with time (Seegert et al. 1979; Nussey et al. 1996). There are some general trends that can be identified with respect to toxicity, especially when considering the effect of temperature on poikilotherm metabolism. Studies that examine the toxicity of common pollutants (e.g., organophosphates and heavy metals) to fish have generally found that toxic effects increase at higher temperatures (Murty 1986b) (Figure 7). The increases in toxicity may result from the increased production of bioactivated free radicals that are more toxic than the parent compound (Nemcsók et al. 1987). Studies on bioaccumulation have shown a positive correlation between temperature and pollutant uptake (Figure 7); this increased uptake is thought to result from increased gill ventilation rates at warmer temperatures (Roch and Maly 1979; Köck et al. 1996).

An increase in fish metabolism also facilitates a faster depuration of toxicants (MacLeod and Pessah 1973; Huey et al. 1984) (Figure 7). For example, MacLeod and Pessah (1973) reported that rainbow trout placed in mercury–contaminated water and subsequently moved to clean water reduced their body burdens of the metal faster at higher temperatures; at 20°C, the reduction of mercury concentrations in fish tissue became apparent after 10 days, as opposed to

20 to 30 days for fish held at 5 and 10°C (MacLeod and Pessah 1973). However, despite their increased ability to metabolize pollutants at warmer temperatures, fishes may still experience increased negative effects at higher temperatures, but these effects may be toxicant–specific. Köck et al. (1996) suggest that inessential metals such as cadmium and lead are difficult for fish to depurate because no specific metabolic pathway exists to process them. Therefore, fish accumulate heavy metals more quickly at higher temperatures. Köck et al. (1996) documented this effect with arctic char. Fish exposed to cadmium and lead were unable to completely metabolize the metals, resulting in positive correlations between metal body burdens and water temperature, as well as metal concentrations and the age of the fish. The temperature–dependent accumulation of heavy metals has large economic implications for the developed world. For example, mercury accumulation in fish flesh is a common problem in areas of southern Canada, Japan, and Scandinavia; it accumulates in muscle tissue, rendering it unfit for human consumption (Wobeser et al. 1970). The discovery of mercury contamination in Canada's fish led to a significant decline in recreational and commercial fisheries in the early seventies (Uthe and Bligh 1971).

Fish will accumulate mercury in greater concentrations at higher temperatures, even if the water contains only low concentrations of the metal (MacLeod and Pessah 1973; Bodaly et al. 1993). Although fish tested under laboratory concentrations can depurate metals faster at higher temperatures, they can only do so if they are held in clean water. It is likely then that higher temperatures will cause mercury accumulation rates in wild fish to outstrip the increased excretion rates.

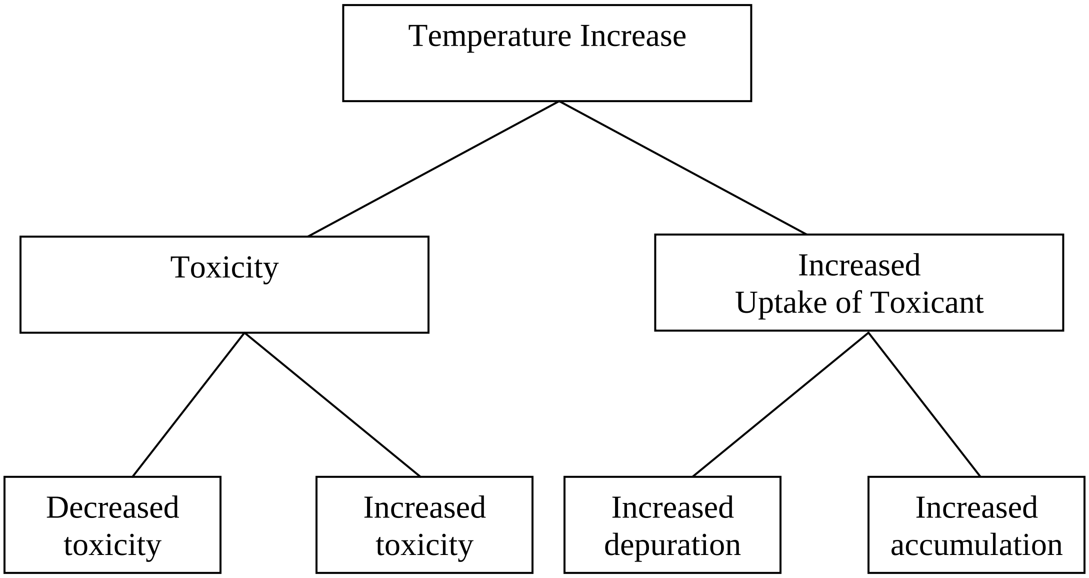

Figure 7.—The possible effects of climate change on toxicity of pollutants to fish are specific to the toxicant and the fish species. It is important to note that stress synergy, or the combined effects of increased temperature, decreased dissolved oxygen, and pollutant presence will have a deleterious effect on fish populations regardless of temperature effects on toxicity. (Adapted from Langford 1983 and Murty 1986.)

Even when fish can physiologically process toxicants present in the water or their food, the processes used to depurate these compounds are energetically costly, and require energy that could have been allocated to some other compartment of the energy budget. For example, detoxification of ammonia in the common carp requires ATP (Jeney and Nemcsók 1992); this increased cost of maintenance metabolism leaves less energy for other processes such as growth and reproduction.

Increasing water temperatures will also alter the toxicity and uptake of ammonia (and other natural toxicants). Accumulation of ammonia and its metabolites is a serious issue in aquaculture systems. Increased temperatures lead to increased nitrite uptake rates in cultured fishes such as channel catfish (*Ictalurus punctatus*) (Huey et al. 1984) and grass carp (*Ctenopharyngodon idella*) (Alcaraz and Espina 1995). A combination of high temperature, low dissolved oxygen concentration, and sublethal ammonia concentrations have been shown to cause gill necrosis in common carp (Jeney and Nemcsók 1992). Increased uptake of natural toxicants such as ammonia and the synergy existing between high temperatures, poor environmental conditions, and the presence of ammonia suggest that an increase in global temperatures has the potential to lower productivity in intensive aquaculture systems.

An increase in toxicant uptake rates has the potential to affect the quality of fish populations worldwide. For example, though the acute toxicity of organochlorines decreases at warmer temperatures (Murty 1986b), accumulation of these compounds in fish tissue increases (Murty 1986a). These elevated tissue concentrations can have sublethal effects, including the reduction of reproductive output. Westin et al. (1985) found that striped bass carrying a high parental load of organochlorines produced fewer viable offspring. Similar results have also been reported in lake trout (*Salvelinus namaycush*) exposed to DDT (Westin et al. 1985).

SOCIOECONOMIC EFFECTS

The preceding sections have discussed how global climate change will affect freshwater systems and the fishes therein. Because many of these freshwater systems support artisanal, sport, and commercial fisheries, global climate change will impact those fisheries. Changes in fishery productivity will in turn affect the human populations and economies that are reliant on those resources.

Billions of people depend upon fish as their primary source of protein. Fish can be easily harvested, or can often be produced quickly, cheaply, and with a minimum of husbandry. For example, China has the world's largest population and produces the world's largest supply of freshwater fish. China produces table–size fish primarily by stocking fingerlings in lakes and reservoirs early in the year and collecting them by organized capture later in the year (Martin 2001). In developing countries, farmers often use small aquaculture ponds as part of an integrated subsistence system. In Vietnam, fish are raised on agricultural waste products such as rice hulls; this practice is also used in the Philippines (Pekar et al. 2002; Prein et al. 2002). Cage aquaculture is also employed in the lakes and rivers of Indonesia (Munzir and Heidhues 2002) and China (Lu 1992). Because fish protein is affordable and easy to grow, many of the world's people depend heavily on freshwater fisheries. For example, in Manaus, Brazil, 70% of the average annual animal protein intake comes from fish (Bayley 1981), and in Cambodia, fish is the most important staple food after rice (van Zalinge 2002).

In addition to providing an essential affordable food source, fisheries also contributes to economies around the world. For example, fishing is the second–highest producer of foreign exchange in Bangladesh at 12% (Hossain 1994). India is the world's second–largest producer of freshwater fish, which contributes a significant amount to the economy (Chauhan 1994): in 1998, culture production totaled just over 2 million metric tons valued at over 2.2 billion U.S. dollars (New 2003). Freshwater fisheries generated 8.8% of the Cambodian GNP in the mid–1960's (Hori 2000).

Industrialized countries also benefit financially from commercial–scale fisheries; the channel catfish farming industry in the United States produces several hundred million dollars in marketable product annually (not including satellite businesses) (McCauley and Beitinger 1992; NASC 2005). The freshwater recreational fisheries of the industrialized world produce far more revenue than the freshwater commercial capture industries. It is difficult to attach a dollar value to recreational fisheries because people participate in the sport for unquantifiable reasons such as enjoyment of nature and relaxation (Rudd et al. 2002). Nevertheless, the economic benefits of recreational fisheries are clear when considering the money spent by anglers. In the Great Lakes region, revenues from recreational freshwater fisheries are an integral component of local economies. Nearly 10 million recreational anglers spent approximately 9.3 billion US dollars annually while fishing the Great Lakes (and the inland rivers, streams, and lakes in the surrounding area) in the 1990's (Kling et al. 2003). In the United Kingdom, recreational anglers spend about 3.41 billion US dollars per year (Lyons et al. 2002). The levels of participation in recreational fishing vary among developed countries, ranging from 1 – 2% of the population in Germany (Rudd et al. 2002) to 24% of the population in Sweden (Dill 1993) and 50% in Norway (Toivonen 2002).

Loss of productivity in or total collapse of subsistence or recreational fisheries poses serious threats to humans worldwide. For example, a 2°C rise in temperature on the North American continent may result in a major northward shift in the ranges of economically important fish species. As both the northern and southern boundary of their ranges move toward the poles, North American fishes will either migrate northward or face extirpation. Endemic species, particularly those in the species–rich southeastern United States, will likely become extinct due to their specialized ecological niches. The Suwanee bass (*Micropterus notius*), for example, is restricted to the Suwanee (Florida, USA) and the Ochlocknee Rivers (Florida and Georgia, USA). Unlike many of its cogeners, this fish prefers a riverine environment over lentic habitats (Hurst et al. 1975). In addition to its value as a sport fish, this species contributes to the biodiversity of the southeastern United States fish fauna. However, its restricted geographic range makes it vulnerable to extinction brought about by increasing temperatures or altered flow regimes. If this species were extirpated, anglers could direct their efforts toward a more cosmopolitan species, but the loss in biodiversity would be permanent. The southern United States may lose the ability to farm catfish. The valuable coldwater fish species of the Great

Lakes region, such as the lake trout (*Salvelinus namaycush*), may migrate northward, leaving behind the local businesses such as resorts, restaurants and fishing equipment retailers that depend upon them (Kling et al. 2003; Roessig et al. 2004).

CONCLUSION

Currently, the magnitude of global climate change is such that most of its effects on freshwater fisheries could be easily masked by or attributed to other anthropogenic influences, such as deforestation, over–exploitation and land use change (McDowall 1992; Genta et al. 1998; Nobre et al. 2002). At this juncture, global climate change appears to represent an additional stressor to the suite that includes pollution, overfishing, water diversion, and introduction of nonnative fishes. For example, two formerly abundant tilapiine species in Lake Victoria, *Oreochromis esculentis* and *O. variabilis*, have been subject to fishing pressure, competition with introduced tilapiine species (e.g. *O. niloticus*) (Goudswaard et al. 2002), and other anthropogenic changes such as pollution (Verschuren et al. 2002). These challenges predispose these populations for collapse, and climate change could create sufficient additional disturbance to extirpate these species. Though these native populations have been much more heavily impacted than many of the world's fisheries, this principle of predisposition can be applied worldwide. Large–scale human activities like water diversion, land–use changes, and deforestation often have dramatic and rapid impacts on fish populations, while the effects presently attributable to climate change exist in the background and may go unnoticed. However, even though the effects of climate change have not yet manifested themselves through large and widespread fish kills, the sublethal effects experienced by the world's fish populations have been, and will be, detrimental. Temperature increases, decreased DO levels, changes in disease transmission, changes in toxicant stresses, and alterations to hydrographs all contribute to the decreased productivity of native fish populations. Although each of these changes has been discussed separately, they are highly correlated and will not act alone. Fishes will have to cope with some combination of these factors. Though the small changes seen in current years have not yet significantly decreased the productivity most fisheries, global climate change is expected to increase in magnitude in the near future (IPCC 2001), at which point it will exert more influence upon the fishes of the world. Furthermore, human response to a hotter planet will lead to secondary effects on fisheries. For example, increased demand for water will lead to further water diversion, and increased waste heat loading that will exacerbate existing environmental challenges (Mulholland et al. 1997; Vörösmarty et al. 2000). Some regions of the world will receive more water as precipitation increases. The fishes in these regions will face challenges presented by structures built to control increased floods and higher flows (Abell 2002). However, dam construction is expected to increase worldwide regardless of regional and global precipitation change. Dams produce “clean” hydroelectric power, and they help meet the irrigation and sanitation needs of a growing population (Schelle et al. 2004). Therefore, developing countries are building dams at an alarming rate. For example, there are 46 large dams (> 60 m high) that are currently planned or under construction in the Yangtze River basin (Schelle et al. 2004). The benefits of these projects do come with a cost as dams impact river systems through large-scale changes. Dams alter water temperature and quality, and destroy natural hydrographs. They also block fish migration, thereby preventing many riverine species from completing their life cycles. These detrimental effects on fish populations will in turn affect the human populations which depend upon them for subsistence and recreation (Schelle et al. 2004). The anticipated effects of climate change are yet another criteria that must be included in designing criteria for more environmentally agreeable dams, as well as in the review process for individual projects.

Fish are vitally important as a protein source in developing countries. In industrialized countries, fish provide a food source and numerous recreational opportunities. Loss of productivity in the world’s fisheries could result in increasing food shortages in nonindustrialized countries, many of which are experiencing rapid human population growth. For example, the population of the Lake Victoria basin is expected to reach 53 million people by the year 2020, a two–fold increase from 1995 levels (Verschuren et al. 2002). Though decreased fishery productivity would probably not cause a crisis in industrialized countries, loss of recreational fisheries would have profound negative economic effects. Given these stakes, it is vitally important to manage our emission of greenhouse gases.

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