RESEARCH PAPER

Potential impacts of global climate change on freshwater fisheries

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Abstract Despite uncertainty in all levels of analysis, recent and long-term changes in our climate point to the distinct possibility that greenhouse gas emissions have altered mean annual temperatures, precipitation and weather patterns. Modeling efforts that use doubled atmospheric CO_2 scenarios predict a 1–7°C mean global temperature increase, regional changes in precipitation patterns and storm tracks, and the possibility of ''surprises'' or sudden irreversible regime shifts. The general effects of climate change on freshwater systems will likely be increased water temperatures, decreased dissolved oxygen levels, and the increased toxicity of pollutants. In lotic systems, altered hydrologic regimes and increased groundwater temperatures could affect the quality of fish habitat. In lentic systems, eutrophication may be exacerbated or offset, and stratification will likely become more pronounced and stronger. This could alter food webs and change habitat availability and quality. Fish physiology is inextricably linked to temperature, and fish have evolved to cope with specific hydrologic regimes and habitat niches. Therefore, their physiology and life histories will be affected by alterations induced by climate change. Fish communities may change as range shifts will likely occur on a species level, not a community level; this will add novel biotic pressures to aquatic communities. Genetic change is also possible and is the only biological option for fish that are unable to migrate or acclimate. Endemic species, species in fragmented habitats, or those in east–west oriented systems will be less able to follow changing thermal isolines over time. Artisanal, commercial, and recreational fisheries worldwide depend upon freshwater fishes. Impacted fisheries may make it difficult for developing countries to meet their food demand, and developed countries may experience economic losses. As it strengthens over time, global climate change will become a more powerful stressor for fish living in natural or artificial systems. Furthermore, human response to climate change (e.g., increased water diversion) will exacerbate its already-detrimental effects.

Model predictions indicate that global climate change will continue even if greenhouse gas emissions decrease or cease. Therefore, proactive management strategies such as removing other stressors from natural systems will be necessary to sustain our freshwater fisheries.

Keywords Climate change · Freshwater · Fisheries · Physiology · Socioeconomic

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Introduction

Climate change and uncertainty

The study of global climate change is fraught with uncertainty at each level of analysis: emissions scenarios, the response of the climate to this forcing, the linkage between global circulation and regional models, and the resulting impacts of these changes (Loaiciga et al. 1996; Baede et al. 2001; Viner 2002). However, the evidence that our climate is changing more rapidly now than in periods in the past is becoming overwhelming. Following the Industrial Revolution, humans have increasingly relied on fossil fuels as an energy source. Currently, about 80% of the world's power is generated from fossil fuels (Bolin et al. 1986; ACIA 2004). The benefits of such power use are obvious, but fossil fuel combustion does produce greenhouse gases that can affect the global climate (Bolin et al. 1986). Although the earth's climate changes naturally in response to differences in solar radiation, volcanic eruptions, and aerosol concentrations, our modern climate is also subject to forcing from greenhouse gases, and this forcing will increase in importance as emissions continue (Mann et al. 1998).

The purpose of this review is to present current knowledge about climate change and its potential effects upon freshwater fish populations. Although a complete discussion of every possible effect is beyond the scope of this paper, the global effects of climate change mean that freshwater ecosystems, and the fisheries therein, will probably be affected to some degree. Freshwater 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, carp, and barb 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.

What do we know about climate change?

Predicting trends in the Earth's climate is difficult, but it can be done using a variety of techniques. Mathematical simulations of the Earth's climate such as global circulation models (GCMs) are commonly used to predict changes in the earth's climate. Global climate circulation models, like any simulation, require validation and sensitivity analyses, most commonly achieved by comparing their predictions with observed climatic conditions (Rodo and Comin 2003). These tests have revealed that GCMs work reasonably well on a global scale, but their inability to work at a finer resolution limits their ability to simulate climate on a regional scale (Bolin et al. 1986; Melack et al. 1997). The Intergovernmental Panel on Climate Change (IPCC 2001) employed several GCMs and found an increased likelihood of a 1–7°C increase in mean global temperature within the next hundred years. The magnitude of the regional temperature increase appears to be correlated with latitude; higher latitudes are predicted to experience a larger temperature change than tropical and subtropical latitudes (ACIA 2004). Advances in modeling techniques and computer technology over the last decade have increased the accuracy of global circulation models, and they are viewed as powerful tools for tracking and predicting climate change. While these models provide insight into future climate change scenarios, they do not predict what that altered climate will mean for natural systems.

Paleoclimatic data, or information about prehistoric climatic conditions, can be obtained from trees, glacial ice cores, sediment cores, and corals (Melack et al. 1997; Spray and McGlothlin 2002). Data from these sources have shown that Post-Industrial human actions have greatly changed atmospheric greenhouse gas concentrations. The concentrations of greenhouse gases like CO_2, NO_2, and CH_4 remained more or less stable in the tens of thousands of years preceding the industrial revolution. However, once fossil fuel combustion increased, concentrations of these gases began to rise. For example, the concentration of atmospheric carbon dioxide is now higher than any observed in the last 160,000 years (Dobson 2001). Judging from paleoclimatic data, current temperatures have reached maxima seen in other interglacial periods; this provides some evidence that further warming is not natural (Spray and McGlothlin 2002).

The effects of global climate change can also be studied through the examination of recent trends in the earth's climate. For example, the 1990's was the warmest decade on record, 1998 was the warmest year

ever recorded (Houghton 2004), and the mean global temperature has risen by 0.3–0.4°C in the last 60–70 years (Mann et al. 1998). There is some evidence that this increase in temperature is attributable to a decrease in intra-annual variability; winter low temperatures in many areas appear to be increasing more than summer high temperatures (Folland and Karl 2001). An increase in inter-annual variability in temperature is not supported by an analysis of the available data (Folland and Karl 2001).

There is less consensus concerning the direction and magnitude of changes in weather patterns and the resulting effects on hydrologic regimes. Precipitation is expected to increase globally, but much of this increase may come in the form of more frequent "extreme" events (Folland and Karl 2001; Palmer and Räisänen 2002). In extratropical areas, a shortening of the return period between "great floods," (i.e., floods that exceed the estimated 100-year flood mark) has been predicted (Milly et al. 2002). However, the authors could not attribute this change to anthropogenic forcing of the climate. Winter rainfall may increase in the mid and high latitudes of the Northern Hemisphere (Nijssen et al. 2001; Palmer and Räisänen 2002). In this area, 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). Although data are limited and many areas have not yet been analyzed (Folland and Karl 2001), the IPCC predictions indicate possible increases in precipitation in the African tropics, and southern and eastern Asia, and precipitation decreases in Australia, South America, and southern Africa (IPCC 2001). Precipitation could increase over northern and central Europe and in large river basins in western Asia, while Mediterranean regions (e.g., southern Europe and northern Africa) could become drier (Palmer and Räisänen 2002). These examples are not a complete list, but they suggest that precipitation and hydrologic regimes are changing on a global scale. These alterations could impact any of the world's aquatic ecosystems, including those that support freshwater fisheries.

Global climate change may also involve "surprises" or sudden ecological changes (Meyer et al. 1999; Magnuson 2002b). Regimes, or periods of relatively stable means in a set of physical climate data (e.g., global oscillations such as the North Atlantic Index, NAO, and El Niño/Southern Oscillation,

ENSO) shifted in 1966 and possibly again in the 1990's (Beamish et al. 1999). Such changes in the amplitude and period of global circulations such as the El Niño-Southern Oscillation (Timmermann et al. 1999) may alter global weather because of the influence of ENSO on temperature and precipitation patterns (Shukla and Paolino 1983; Ropelewski and Halpert 1987; Simpson et al. 1993). There is no indication that these regime shifts are cyclic, and they may represent new "steady states" (McFarlane et al. 2000). Changes in thermohaline circulation could also profoundly affect the atmospheric circulations that drive weather patterns (reviewed in Roessig et al. 2004). Sudden, irreversible events have occurred in the past as a result of climate change. For example, glacial melting 7,150 years ago increased the level of the Mediterranean Sea so that it flowed over the Bosporus Isthmus (the location of Istanbul, Turkey) into the (formerly) freshwater Black Sea (Lodge 2001).

The concept of feedback is also very important. The multitude of factors that structure our climate (albedo or ice reflectivity, vegetation, soil, oceans, atmospheric gases, and aerosols) interact to form positive and negative feedback loops (Loaiciga et al. 1996; Baede et al. 2001). This further hinders our ability to make predictions about changing temperatures, precipitation patterns, and climate variability. However, the fact remains that the climate is changing, and significant climate shifts will affect freshwater fish communities and fisheries.

Changes in fish habitat

Climate change will present fishes with new environments through a number of mechanisms. These will not necessarily operate independently, and the possibility of synergy or interactions between them is probable. For the purpose of clarity however, they will be discussed separately.

General effects

Increased temperature

All freshwater fishes are exotherms that cannot regulate their body temperature through physiological means (Moyle and Cech 2004) and whose body temperatures are virtually identical to their environ-

mental temperatures. These fishes may thermoregulate behaviorally, by selecting thermally heterogeneous microhabitats (Brett 1971; Nevermann and Wurtsbaugh 1994; Nielsen et al. 1994; Brio 1998), but they are constrained by the range of temperatures available in the environment. Because biochemical reaction rates vary as 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 (Wohlschlag et al. 1968; Schmidt-Nielsen 1990; Franklin et al. 1995). Therefore, increasing global temperatures can 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 (Fry 1971). Temperature tolerance ranges are species-specific and include both stenothermal (narrow thermal range) species such as Arctic charr (*Salvelinus alpinus*), and eurythermal (wide tolerance range) species such as common carp (*Cyprinus carpio*) (Table 1). Fish populations that are faced with changing thermal regimes may increase or decrease in abundance, experience range expansions or contractions, or face extinction.

Decreased dissolved oxygen

Biologically available (dissolved) oxygen (DO) is much less concentrated in water than in air (Moyle and Cech 2004). Oxygen enters the water column through diffusion from the atmosphere (this is potentially facilitated via turbulence and mixing) and by photosynthetic production (Kalff 2000; Stickney 2000). Plant, animal, and microbial aerobic respiration may decrease DO in the water column, especially at night when photosynthesis stops. Dissolved oxygen concentrations of 5 mg/l or more are acceptable for most aquatic organisms (Stickney 2000), and concentrations below 2–3 mg/l are considered hypoxic (Doudoroff and Warren 1965; Kalff 2000).

Oxygen solubility in water has an inverse relationship with water temperature. For example, water at 0°C holds about 14.6 mg/l, but water at 25°C can only hold about 8.3 mg/l (Kalff 2000). Because the aerobic metabolic rates of most cold-blooded aquatic organisms increase with temperature, an increase in temperature both decreases the DO supply (through reduced saturation concentrations relative to air) and increases the biological oxygen demand (BOD) (Kalff 2000). Fishes exposed to elevated water temperatures (e.g., from climate change) can face an "oxygen squeeze" where the decreased supply of oxygen cannot meet the increased demand.

Changes in dissolved oxygen levels will depend on a multitude of factors such as ambient temperatures, biological oxygen demand, and local climate (e.g., wind mixing). Whether or not the incidence of hypoxia or anoxia increases in individual systems remains to be seen. Given the probability of higher temperatures and increased biological oxygen demand, it is possible that levels of dissolved oxygen will decrease in at least some systems.

Table 1 Temperature tolerances of some common coldwater, coolwater, warmwater, and tropical fish species

Temperature Guild	Species	ILLT, ULLT	Optimal range	Reference
Coldwater	Arctic charr (*Salvelinus alpinus*)	0–19.7	6–15	(Johnston 2002)
	Atlantic salmon (*Salmo salar*)	−0.5–25	13–17	(Wallace 1993)
Coolwater	Walleye(*Stizostedion vitreum*)	0–30	20–23	(Nickum and Stickney 1993)
	Striped bass(*Morone saxatilis*)	2–32	13–24	(Stickney 1994)
Warmwater	European eel (*Anguilla anguilla*)	0–39	22–23	(Sadler 1979)
	Channel catfish (*Ictalurus punctatus*)	0–40	20–25	(Tucker 2000)
Warmwater/ tropical	Common carp (*Cyprinus carpio*)	0–35.7	26.7–29.4	(McLarney 1998)
Tropical	Redbelly tilapia(*Tilapia zillii*)	7–42	28.8–31.4	(Phillipart and Ruwet 1982)
	Guinean tilapia (*Tilapia guineensis*)	14–34	18–32	(Phillipart and Ruwet 1982)

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, and other abiotic factors

Increased toxicity of pollutants

The effects of temperature on toxicity have been tested in the laboratory with myriad chemical compounds and a diverse array of fish species, but many experiments have used short exposure times and 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). Despite these complications, there are general trends that can be identified with respect to toxicity, especially when considering the effect of temperature on poikilotherm metabolism. The toxicity of common pollutants (e.g., organophosphates and heavy metals) to fish generally increases at higher temperatures (Murty 1986b). These 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) or from the increased uptake of the original toxin (Murty 1986a). Studies on bioaccumulation have shown a positive correlation between temperature and the uptake of anthropogenic (e.g., mercury (MacLeod and Pessah 1973), and natural (e.g., nitrite, Huey et al. 1984; Alcaraz and Espina 1995) pollutants (Fig. 1)). 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) (Fig. 1). For example, MacLeod and Pessah (1973) reported that rainbow trout (*Oncorhynchus mykiss*) placed in
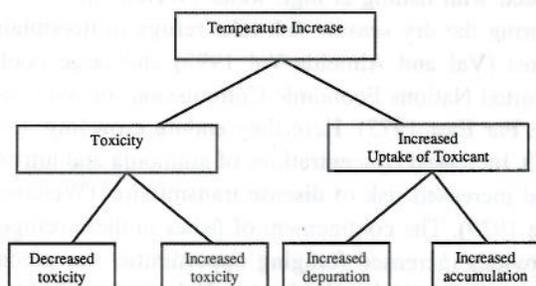
mercury-contaminated water and subsequently moved to clean water reduced their body burdens of the metal two to three times faster at 20°C than at 10°C or 5°C, respectively.

Despite their increased ability to metabolize pollutants at warmer temperatures, fishes may still experience increased negative, toxicant-specific effects at higher temperatures. Köck et al. (1996) suggested that non-essential metals such as cadmium and lead are difficult for fish to depurate because no specific metabolic pathway exists to process them. Therefore, fish accumulate these toxins more quickly at higher temperatures. Köck et al. (1996) documented this effect with wild arctic charr (*Salvelinus alpinus*). Fish exposed to cadmium and lead were unable to completely metabolize the metals, which accumulated in fish tissue and organs. This resulted in positive correlations between metal body burdens and water temperature, and the age of the fish. An increase in toxicant uptake rates has the potential to affect the quality of fish populations worldwide. Even when fish can physiologically process toxicants present in the water or their food, the processes used to depurate these compounds are energetically expensive and increase the cost of maintenance metabolism (Jeney and Nemcsók 1992). Therefore, elevated toxicant concentrations in fish tissues can have sublethal effects, including the reduction of reproductive output. Westin et al. (1985) found that striped bass (*Morone saxatilis*) 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).

The temperature-dependent accumulation of toxicants has large economic implications. For example, accumulation of endogenously produced ammonia and its metabolites is a serious issue in aquaculture systems. 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 exogenous toxicants 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 wild fish populations and in intensive aquaculture systems worldwide. For example, mercury accumulation in

Fig. 1 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

the flesh of fishes in areas of southern Canada, Japan, and Scandinavia is already sufficient to render the flesh 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 1970s (Uthe and Bligh 1971). Continued atmospheric deposition and natural production of mercury in combination with increased water temperatures could exacerbate existing conditions in industrialized countries or create new problems in unaffected areas.

Effects on lotic systems

Hydrologic regimes

Local hydrology is a function of land use, precipitation, soil moisture, and evapotranspiration (Wood et al. 2002; Jiongxin 2005). Therefore, it is difficult to predict the effects of climate change on the hydrologic regime of individual streams, and quantitative estimates of the effects of climate change are few (Poff et al. 2001; Allan et al. 2005). However, it appears that climate change has already begun to affect the flow regime of the world's streams (Mauget 2003; Ye et al. 2003).

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, magnitude, and inter-annual variability. 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 (Baltz and Moyle 1993; Ross et al. 2001; Annear et al. 2004), reduced recruitment (Mion et al. 1998; Modde et al. 2001), and extirpation of locally specialized species (Cross and Moss 1987). 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 (Magnuson 2002b); major rivers such as the Mississippi (USA) and the Sever-

naya Dvina (Russia) 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 (Welcomme 1979; Meisner 1992). During the flood stage, opportunistic feeders store energy 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 concentrations of ammonia and nitrite, and increased risk of disease transmission (Welcomme 1979). The confinement of fishes in these refuges provides increased foraging opportunities for predatory species (Val and Almeida-Val 1995) and better fishing success for artisanal and commercial fisheries (Welcomme 1979; Harper and Mavuti 1996). Tropical river 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). Increased evapotranspiration could reduce the volume and quality of available fish habitat during the dry season. Careful modeling would be necessary to determine whether this would be beneficial to piscivores and artisanal or commercial fishers. Though prey fish could be more susceptible to capture, harsh abiotic conditions in isolated habitats could also lead to increased fish kills and reduced survival of these fishes (Meisner 1992).

Predictive models do not agree on the exact effects of climate change on tropical systems (IPCC 2001). 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 (Welcomme 1979). 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 if 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 have resulted from 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 would be enough to drastically alter stream flows (Meisner 1992).

Hydrologic variability

Because fish are often adapted to a certain level of hydrologic variability (Poff and Allan 1995), a change in this variability could have negative effects on fish populations. In the North American Midwest, fish community composition depends upon the degree of hydrologic stability in a given stream (Poff and Allan 1995). Streams characterized by extreme variability (such as those of the North American Great Plains)

contain generalist fish species that are able to exploit a wide array of resources and tolerate changing environmental conditions; environmental specialists are virtually non-existent (Fausch and Bestgen 1997). Many climate models predict increased variability or extreme events in weather (Magnuson 2002b; Milly et al. 2002; Palmer and Räisänen 2002). Floods or exceptionally large seasonal pulses can displace adults and displace or injure juveniles and larvae (Harvey 1987), and droughts or prolonged dry spells can cause population declines, reduced abundance, and altered species composition (Matthews and Marsh-Matthews 2003). As a result, changes in variability could select for generalist species or those with the ability to rapidly colonize defaunated habitats and possibly lead to a loss of locally adapted ones (Poff et al. 2001).

Lower dry-season 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 1,500 m^3/s, seawater penetrates the river 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 4,000 km) (Salati and Marques 1984), so a decrease in flows could profoundly affect its 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 cm and 80 cm 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). Rising sea levels could also increase erosion and inundate important habitat in deltaic regions of temperate coastal streams (Wood et al. 2002).

Changes in stream and groundwater temperatures

Increases in stream and groundwater temperatures will likely have more pronounced effects in temperate zones because groundwater temperatures in

tropical streams are not significantly lower than summer stream temperatures (Meisner 1992). On the other hand, increasing temperatures in North American streams could result in a decrease in cold and coolwater fish habitat of nearly 50% (Eaton and Scheller 1996). In temperate stream systems, salmonid genera including *Salmo, Oncorhynchus*, and *Salvelinus* (Meisner et al. 1988) and warmwater fishes such as smallmouth bass (*Micropterus dolomieu*) (Whitledge et al. 2006) rely on groundwater discharges for summer thermal refugia, 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, Canada 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, *Salmo trutta*, 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 also be cold-water stenotherms, 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.

Effects on lentic systems

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 through changes in water temperature and stratification patterns (Lofgren 2002). In the tropics, wind, precipitation, and stratification may affect trophic status of inland water bodies (Bootsma and Hecky 2003).

Eutrophication

The trophic status of aquatic systems is 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 (Klapper 1991), and climate change (Mulholland et al. 1997; Bertahas et al. 2006).

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). Although the complex relationship between climate change and eutrophication makes prediction difficult, increased temperatures will likely result in a general increase in lake trophic status (Allan et al. 2005). Lower stream flows could increase water residence times and reduce flushing of nutrients from lake systems, thereby increasing trophic status (Bertahas et al. 2006). When coupled with the input of anthropogenic pollutants, climate change can accelerate the eutrophication process (Klapper 1991; Adrian et al. 1995) or delay recovery from anthropogenic eutrophication (Nicholls 1998; Jankowski et al. 2006). On the other hand, climate change could reduce anthropogenic eutrophication; increased strength and duration of stratification could

lead to an increased sequestration of nutrients in the hypolimnion, where they are not biologically available to primary producers (Magnuson 2002a). Likewise, an increase in stream flows and pollutant flushing rates could reduce eutrophication rates (Magnuson 2002a).

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. 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. 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 decrease 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).

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

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). The extent and strength of lake stratification is also a major driving factor in determining DO concentrations (Klapper 1991). 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 in temperate lakes.

In larger lakes, 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).

The epilimnion is exposed to the atmosphere and experiences turbulence-induced mixing of O_2 and sufficient light to stimulate algal photosynthesis. However, because 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 levels at depths below the compensation point prevent 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 eat (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 (e.g., *Anabaena flos-aquae*) 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 4-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 thermal 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:
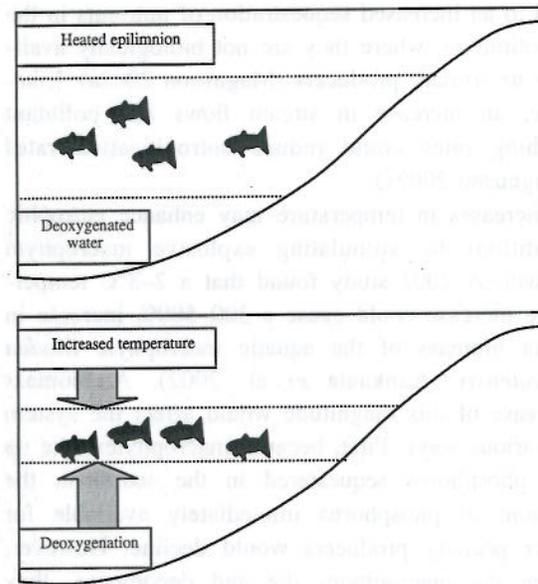

Fig. 2 Due to species-specific temperature and oxygen requirements, climate change may restrict pelagic habitat availability for many species. Increased solar radiation will thicken the epilimnion, and increased fish metabolism will result in decreased concentrations of dissolved oxygen

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 (Regier and Meisner 1990; Gerdaux 1998). In the temperate and subarctic lakes of North America and Europe, cold water stenotherms such as arctic charr (*Salvelinus alpinus*), lake trout (*Salvelinus namaycush*), whitefish (*Coregonus* spp.), and striped bass use the hypolimnion as a refuge from high summer water temperatures (Cheek et al. 1985; Moss 1985; Christie and Regier 1988; Coutant 1990; Gerdaux 1998). 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'' (Fig. 2); 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). 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).

Loss of hypolimnetic habitat has been observed in some temperate lakes and predicted for others. An anomalously warm year (1983) in southern Canada produced anoxic conditions in the hypolimnion of Lake Erie (Schertzer and Sawchuk 1990) because the biological oxygen demand exceeded the supply. Dissolved oxygen concentrations in Lake Erie could be reduced by 1–2 mg/l under a 3–4°C warming scenario (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). This change would result in the extirpation of the economically and culturally important ayu (*Plecoglossus altivelus altivelus*), the endemic masu salmon (*Oncorhynchus rhodurus*), and the kokanee salmon (*Oncorhynchus nerka*) (Fausch and Nakano 1998) because salmonids cannot tolerate DO levels below 3 mg/l for an indefinite period of time (Avault 1996).

Increased strength and duration of thermal stratification could increase 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. A stronger, deeper thermocline may also benefit economically important fishes by increasing their access to forage species such as alewife (*Alosa pseudoha-*

rengus), bloater (*Coregonus hoyi*), and rainbow smelt (*Osmerus mordax*). The thermal requirements of these forage species would confine them to the thermocline. This could increase prey encounter rates and therefore increase growth potential (a function of prey availability and water temperature) by 74% for Chinook salmon (*O. tshawytscha*), 73% for lake trout, and 114% for striped bass (Brandt et al. 2002). 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). Warm and coolwater fishes such as the native yellow perch (*Perca flavescens*), striped bass, and white perch (*Morone chrysops*) may experience an increase in thermal habitat because of increased global temperatures. The hypolimnion of the Laurentian Great Lakes is too cold for these species, but global warming would thicken the epilimnion, thus increasing the size of their thermal niche (Kling et al. 2003). These fishes 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 (Kling et al. 2003). The effects of this competition on potential invaders or on the fishes currently inhabiting these lakes is not known. Because the coolwater systems would still be subject to density-dependent controls such as inter- and intraspecific competition, disease, and resource availability, careful modeling efforts or well-designed micro- and mesocosm studies would be required to determine if an increase in coolwater fish production would occur.

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). Tropical systems such as the African Rift Lakes and the Amazonian varzéa lakes contain anoxic hypolimnia (Kaufman et al. 1996; Beeton 2002). The anoxic hypolimnia of tropical lakes also contain high concentrations of hydrogen sulfide (Welcomme 1979; Val and Almeida-Val 1995). Hydrogen sulfide 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 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 m 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 or seasonal mixing because perturbation of the water column introduces large amounts of anoxic water and hydrogen sulfide into the epilimnion (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, because climate change may alter limnological characteristics (e.g., more extreme storms would cause sudden and complete overturns in systems with anoxic hypolimnia), its contribution to fish kills may increase 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 (IPCC 2001; Houghton 2004).

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; Val and Almeida-Val 1995).

Ultraviolet light (UV-B)

Climate change will result in increased ultraviolet light penetration into bodies of water (Lodge 2001; Allan et al. 2005). UV-B affects survival of primary producers, the bioavailability of dissolved organic carbon, and the survival of zooplankton species (Häder et al. 1998). Although the effects of UV-B have been documented, the interaction between acidification or pollution, UV-B penetration, and eutrophication has been little studied and is expected to have significant impacts on lake systems (Lodge 2001; Magnuson 2002a; Allan et al. 2005). A pair of laboratory and outdoor studies of *Ceriodaphnia dubia* concluded that increased exposure to UV-B light increased the crustacean's sensitivity to arsenic (Hansen et al. 2002). Synergy between increased UV-B and the bioavailability of zinc has also been documented in natural systems (Kashian et al. 2004). These studies both suggest that this phenomenon may negatively affect natural systems, and it warrants further study.

Water loss from lentic systems

Global climate change will also affect aquatic systems through changes in the hydrologic cycle: evaporation, evapotranspiration, and precipitation. Although history has not linked increased evapotranspiration with lower water levels in temperate lakes (Kling et al. 2003), higher temperatures and insolation could increase current water loss rates from these systems because evaporation rates may outstrip input from increased precipitation (Allan et al. 2005).

Though precipitation is expected to increase in North America under two model scenarios (the Parallel Climate Model, PCM, and the Hadley Centre for Climate Modeling Model, HadCM3), 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 0.23–2.48 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 unknown 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 (Melack 1996). Therefore, changes in their water chemistry are largely driven by inflows, evaporation and precipitation.

Small changes in water levels of lentic systems will likely have minimal impacts on freshwater pelagic fishes but could have more serious consequences for species with narrow bathymetric ranges, such as some of the cichlids in the African Great Lakes. These fish, a major food source for local peoples, inhabit shallow, sandy areas that form a small percentage of the total lake habitat (Ribbink 1987). Similarly, temperate fishes that rely upon littoral vegetation for reproductive success often fail to produce strong year classes in drought years when lake levels are low (Moyle and Cech 2004). Small changes in water levels will eliminate these crucial habitats, forcing these fishes to use areas devoid of their vital habitat structures. This change would likely lead to population declines and might set off a cascade of new interspecific interactions.

Effects on fishes

Fish physiology

We will now examine the potential effects of climate on specific aspects of fish physiology, including thermal tolerance and metabolism before looking at

specific examples for temperate, tropical, and polar fishes. A possible effect of global warming is that the water temperatures in specific ecosystems would increase to levels that are suboptimal or lethal for resident fishes with a limited dispersal ability or for those living in systems that prevent migration. 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). Although acclimation to higher-than-ambient or near-lethal temperatures (under laboratory or natural conditions) allows fish to adjust these critical limits by a few degrees (Meffe et al. 1995; Myrick and Cech 2000, 2003), there are limits to the magnitude and rate of thermal acclimation (Taniguchi and Nakano 2000).

When exposed to temperatures 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 in the simplest form 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. For a fixed ration, the amount of energy allocated to each of these compartments is temperature-dependent (Fig. 3), with increases in temperature generally increasing allocation to all areas except somatic and reproductive growth. Allocation pathways are plastic and allow fish to adjust to changing environmental conditions such as temperature (Nicieza and Metcalfe 1997; Sogard and Spencer 2004), but in general, exotherms dedicate more energy to respiration as temperatures increase (Kitchell et al. 1977; Mayfield and Cech 2002; Britton and McMahon
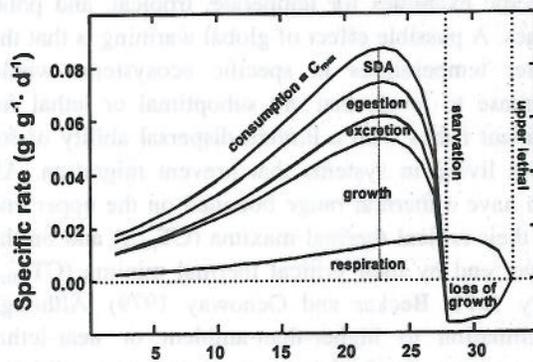
Fig. 3 The energy budget of a yellow perch as a function of temperature. Note the rapid decline in growth as temperature increases beyond 25°C. The vertical dotted line at 23°C indicates the optimal temperature and maximum metabolic scope for this species. From Kitchell et al. (1977), used with permission

2004). At the cellular level, repairing proteins is an important component of maintenance metabolism. Proteins are vulnerable to heat damage because the chemical bonds that allow biologically necessary conformational changes are weak; these repairs consume 25–30% of cell ATP for fish in their normal thermal range (Somero and Hofmann 1997). As temperatures increase, more protein repairs become necessary (Somero and Hofmann 1997). Because these minimum metabolic requirements are met before energy is channeled into somatic or reproductive growth (Sogard and Spencer 2004), increasing ambient temperatures may affect the ability of fishes to grow, reproduce, and maintain homeostasis. Increases in temperature beyond the species' optimal range decrease the scope for activity and growth (Brett 1971; Elliot 1975a) through a variety of mechanisms including cardiac inefficiency (Taylor et al. 1997) and an increased cost of repairing heat-damaged proteins (Somero and Hofmann 1997). In general, a reduction in this 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, osmoregulatory problems (Boyd and Tucker 1998) and mortality (Kitchell et al. 1977).

Thermal ranges are species-specific, and one can expect fish populations faced with changing thermal regimes to achieve new equilibria (e.g., altered

abundances and ranges) dictated largely by the energetic costs of coping with a new thermal environment and a new set of interspecific interactions. Whether species increase or decrease in abundance, experience range expansions or contractions, or face extinction 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 and rate of the thermal change in that ecosystem.
3. The genetic response of the population to new selective pressures.
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.
6. The availability of necessary physical resources such as habitat and water quality parameters.

Temperate fishes

Temperate and polar regions are expected to experience larger changes in temperature than tropical areas, so fishes inhabiting these areas will be more affected by this aspect of climate change. Given sufficient rations and good water quality, fish growth is temperature-dependent and generally increases with temperature to an optimal level before decreasing again (Elliot 1975b; 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, and overwintering stress is decreased (Hill and Magnuson 1990; Kling et al. 2003; Coleman and Fausch In Press). 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.

Regardless of the state of food resources, an increase in temperature causes some increase in metabolic rate, and a subsequent increase in the amount of energy needed. Given time to thermally acclimate, fishes show the ability to compensate for some of the temperature-related increase in metabolic rate, but the general trend is upwards. For example, food intake increases exponentially with temperature for fishes in natural (Brett 1971; Specziár 2002) and laboratory (Elliot 1975a) conditions. 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 may 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 (Hill and Magnuson 1990; Shuter and Meisner 1992; 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 (cold-tempering) are often essential for the spawning success of temperate fishes such as salmonids (Langford 1983; Gerdaux 1998), channel catfish (*Ictalurus punctatus*) (Boyd and Tucker 1998), and white sturgeon (*Acipenser transmontanus*) (Webb et al. 2001). 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. This will affect species in natural systems differently depending upon their reproductive strategy. Equilibrium species (large eggs, small clutches, late sexual maturity) are most vulnerable to environmental change, periodic species (late maturity, small eggs, large clutches) are less vulnerable, and opportunistic species (early maturity, small eggs, small clutches, frequent spawning) are the least vulnerable (Poff et al. 2001).

Reproductive success of adults and 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, these faster-growing cohorts had lower reproductive potential than slow-growing ones (Craig and Kipling 1983). In general, measures of reproductive potential such as egg size (which has a positive effect on juvenile survival), egg quality, and clutch size are highest in fish of intermediate size and age, but this is not universal (Kamler 2005). Brook trout in Colorado's Rocky Mountains use one of two life history strategies depending upon temperature regime: in high-elevation streams, fish grow more slowly and mature later than those living in lower elevation (i.e., warmer) streams. This plasticity in reproductive strategies allows these fish to successfully colonize streams of varying temperature (Kennedy et al. 2003). Roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) near the southern edge of their distribution spawn at the same temperature and for the same duration as more northern populations, but they spawn earlier in the year to exploit optimal water temperatures (Tarkan 2006). The reproductive response of fishes to climate change will be species-specific. However, given the plasticity in reproductive strategies, some fish species may be able to adapt to a changing environment by using alternate life history strategies and adjusting spawning dates.

Environmental dissolved oxygen levels must be high enough to support aerobic metabolism in fishes (Moyle and Cech 2004). 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. 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) have physiological adaptations that allow them to tolerate environmental hypoxia (Walker and Johannsen 1977). For example, the alligator gar *Lepisosteus spatula* breathes air through a modified swim bladder (Jenkins and Burkhead 1993). However, for most fishes, dissolved oxygen concentrations do not have to drop to very low levels before physiological functions are affected. Sublethal hypoxia (2–3 mg/l) decreases feeding activity (Stickney 2000), swimming performance, and fitness of emerging larvae (Doudoroff and Warren 1965). Low DO levels have also been linked to immunosuppression in fish (Boyd and Tucker 1998; Stickney 2000). 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 (air-saturated) water (Langford 1983).

Decreased levels of dissolved oxygen can reduce the growth and reproductive success of individual fishes and prevent them from dealing as effectively with other environmental challenges. Therefore, if climate change results in reduced levels of dissolved oxygen, it is possible that individual fish could be smaller, less fecund, and less likely to survive. However, it is also possible that some fish could become acclimated to lower levels of dissolved oxygen. For example, fishes are capable of producing varying amounts of red blood cells depending upon the season, and they can produce multiple types of hemoglobin that have different affinities for oxygen (Moyle and Cech 2004). These compensatory mechanisms may prove sufficient in generalist species that can tolerate a wide range of environmental conditions. However, there are again limits to acclimation and adaptation. For example, rainbow trout (*Oncorhynchus mykiss*) produce four types of hemoglobin (Binotti et al. 1971) but are still confined to well-oxygenated waters. The response to changing dissolved oxygen levels will be species-specific and dependent upon other environmental stressors.

Tropical fishes

Tropical fishes have high critical thermal maxima (e.g., the spotted tilapia, *Tilapia mariae*, has a critical thermal maximum of 37°C (Siemien and Stauffer 1989)) and an ability to adjust to increasing temperatures. Zebrafish (*Danio rerio*) embryos reared at 33°C produced more heat shock proteins than those held at 21°C or 26°C, to cope with thermal stress (Hallare et al. 2005). 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). Given this and the fact that current climate change scenarios predict small temperature increases for the tropics (IPCC 2001), it seems possible that tropical fish will not suffer the effects of climate change as much as temperate or polar fishes. 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 currently endure these temperatures (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). Recent work by Chaterjee et al. (2004) on common carp and rohu (*Labeo rohita*), important eurythermal aquaculture species on the Indian subcontinent, showed increased tolerance to elevated temperatures following acclimation to water temperatures of 30°C and 35°C (Chatterjee et al. 2004). This suggests that there may be physiological adjustments to a new climate by eurythermal species in low latitudes. However, for fish 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). In a laboratory study of temperature and swimming costs, 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°C and 35°C (Chatterjee et al. 2004), which suggests that higher temperatures and a fixed ration would result in decreased growth rates. 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. Given their effects on growth, sublethal temperature increases could reduce productivity of natural and artificial aquatic systems by slowing individual growth rates.

Although model predictions and observations are complicated by land use or land cover changes (Bounoua et al. 2004; Zhang et al. 2005), daily temperature ranges appear to be decreasing. This is largely due to an increase in minimum temperatures and the fact that aerosols partially offset the maximum temperature increase (Braganza et al. 2004; Caminade and Terray 2006). Similarly, examination of recent climate records indicate that seasonal temperature variations are decreasing due to an increase in cool season low temperatures (Folland and Karl 2001). Fish that do not migrate to cooler areas could experience less time at established optimal temperatures because of this dampening effect and increases in daily minima.

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 higher temperatures decrease reproductive output. 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). High temperatures (28°C and 32°C) caused elevated deformity rates in 5-day-old tilapia (*Oreochromis mossambicus*) raised under laboratory conditions (Wang and Tsai 2000). These studies suggest that reduced reproductive output may be yet another sublethal effect of elevated water temperatures. The spawning seasons of some tropical fish species correspond with the lower water temperatures seen during the wet season (Chellappa et al. 2004) or with the rising limb of the hydrograph (Smith 1991), so there is a possibility that increased cool season

temperatures could inhibit successful reproduction. Because increased temperatures can have sublethal effects on tropical fish, 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; this has occurred with temperate fishes (Parmesan and Yohe 2003).

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. The annual growth patterns and spawning dates of equatorial carp (*Labeo dussumieri*) correspond to local flow regimes (Smith 1991). Spawning in many tropical fishes is cued by rising water levels (Val and Almeida-Val 1995; Hori 2000). Tropical fishes that spawn in seasonally flooded areas may 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). Some research indicates that tropical 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 (IPCC 2001; Houghton 2004). Furthermore, the lack of information on the status and biological needs of many tropical species makes predictions about the effects of climate change difficult (Dudgeon 2003). However, it is likely that the effects of altered flow regimes will be more detrimental than a change in temperature (Meisner 1992; Poff et al. 2001). In tropical systems it is also possible that the effects of global climate change will 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 may be altered by the change of the flow regime. With an ambient temperature increase of only 1–2°C, disturbances such as deforestation (Abell and Allan 2002), pollution, and overfishing (Dudgeon 2003) would likely pose a larger and more immediate threat to fish populations. On the other hand, examination of multiple taxa suggests that climate change is already affecting natural populations as much as other anthropogenic disturbances (McCarty 2001). Again, these effects will be species-specific and will depend upon mean temperatures and their variability, changes in magnitude, duration, and variability of seasonal stream flows, and the interactions of these climate-caused changes with other anthropogenic stressors.

Many tropical 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). Shallow ponds and lakes depend 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) (Fig. 4). A temperature-related increase in biological oxygen demand could increase the magnitude (by further depleting the low pre-dawn DO levels) or duration of this critical period (by depleting the DO supply sooner), thereby selecting for species that are more tolerant of hypoxic conditions. This could potentially alter the community structure and carrying capacity of these systems.

Adaptations for dealing with hypoxia are most advanced in tropical fishes. For example, some fish resort to air breathing through modified swim bladders (e.g., the arapaima, *Arapaima gigas,* Val and Almeida-Val 1995). Others, like the commercially important (both capture fisheries and aquaculture) South American tambaqui, *Colossoma macroponum* exploit 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
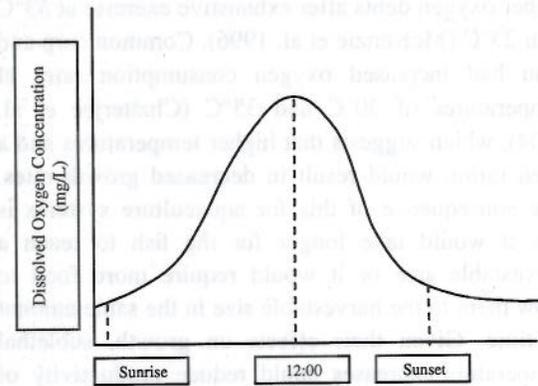

Fig. 4 Diurnal fluctuation in a small warm aquatic system. Due to high temperatures, community respiration would quickly deplete the O_2 introduced into the system by surface turbulence or by diffusion from the atmosphere. Therefore, all of the aquatic organisms in a system such as this depend heavily 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

(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 surviving species 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.

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, may increase energetic costs and predation risk (Kramer et al. 1983).

Polar and high-latitude fishes

Most freshwater fishes of high-latitude regions have ranges that extend into temperate zones (Reist et al. 2006). These fishes include coldwater stenotherms such as salmonids and riverine sculpins (family Cottidae). Some freshwater fishes are confined to the Arctic and live at high latitudes: the Alaska blackfish (*Dallia pectoralis*) does occur up to 71°N, and the arctic charr can be found as far north as 79°N in Eurasia (Gulseth and Nilssen 2000). Otherwise, almost all obligate polar fishes are marine species like the Antarctic plunderfish (*Harpagifer antarcticus*) and the Arctic cod (*Arctogadus glacialis*). Despite the physiological (Reist et al. 2006) and behavioral (Gulseth and Nilssen 2000; Jørgensen and Arnesen 2002) adaptations that provide resistance to freezing, these fish are limited by lack of available habitat. Because fresh water freezes at 0°C, these fishes are limited on the upper latitudinal boundaries of their ranges by 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, albeit at a reduced rate, and the resultant environmental hypoxia or anoxia proves lethal to most 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. Fish that have antifreeze proteins and an ability to breathe atmospheric air could potentially survive such conditions, as is suggested by anecdotal evidence on Alaska blackfish (*Dallia pectoralis*). The blackfish has the ability to use a modified swimbladder as a respiratory organ (Crawford 1974), and an unpublished report suggests it has unusual tolerance of freezing conditions (USGS

2002). Though the literature is replete with studies on the presence of antifreeze proteins and antifreeze glycoproteins in marine fish (Harding et al. 2003), there is only a single published report on the presence of these compounds in a strictly freshwater fish, the Japanese smelt (*Hypomesus nipponensis*) (Yamashita et al. 2003). Unlike the scenarios presented for many 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 moving toward the poles (ACIA 2004; Reist et al. 2006). Changing temperatures may also reduce habitat for these fishes; because they have evolved to survive in polar regions (Reist et al. 2006), 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 relatively high 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 could 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 that determine the available niche for a fish species will likely prove to be the driving factors in determining the well-being and composition of fish communities.

Changing aquatic communities

Although other factors such as geomorphology and hydrologic regime also determine available fish habitat (Poff et al. 2001; Thomas 2005), distributions

of many temperate zone freshwater fish species are determined by temperature isolines that are elevational and latitudinal in nature (Moyle et al. 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 (Reist et al. 2006).

There may also be local movements within drainages where fish from lower elevations are able to move upstream into stream reaches that were previously too cold for them. These fish would compete for space in their "new" ecosystems, possibly at the expense of native species that share similar thermal requirements, or, in some cases, have lower thermal tolerances (Carveth et al. 2006).

A global warming trend would result in the northward expansion of warmwater and coolwater species in North America (e.g., smallmouth bass, *Micropterus dolomieui*, Jackson and Mandrak 2002; yellow perch, Shuter and Post 1990), Europe (Parmesan and Yohe 2003), and Asia, and the southward expansion of warmwater species in Australia and South America. These fish would also compete for space in their "new" ecosystems, possibly at the expense of native species. 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, lake trout (Kling et al. 2003), and channel catfish, *Ictalurus punctatus* (McCauley and Beitinger 1992).

Parasite transmission depends on host condition, the presence of intermediate hosts necessary for the parasite life cycle, water quality, and temperature

(Fig. 5), so climate change may alter host-parasite dynamics by changing transmission opportunities and host susceptibility (Marcogliese 2001). Temperate and subarctic zones fishes may experience increased parasite loads due to increased transmission opportunity. 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, so warmer winters could allow the possibility of year-round infection and multiple generations of parasites in 1 year (Marcogliese 2001). 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 overwinter stress. Although intra-annual variability appears to have decreased in recent years (through elevated winter temperatures) (Folland and Karl 2001), the frequency of extreme weather has increased (Magnuson 2002b; Milly et al. 2002).
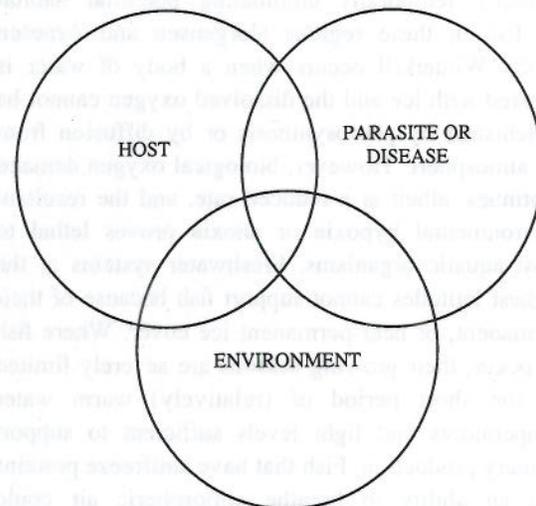

Fig. 5 In order for a host fish to be infected by a parasite or disease organism, the two organisms must overlap in space and time. Large-scale environmental changes such as global climate change will affect the host-parasite relationship by altering host and parasite range, host susceptibility, and transmission rates. Direct temperature effects upon the parasite may also affect this relationship

These extreme events may put additional stress on fish, parasite, and pathogen populations, and warmer winters could have variable effects.

Changing global temperatures will also affect fish susceptibility to disease because 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 may become more severe as summer water temperatures and periods of low flow in the Rocky Mountains increase (Schisler et al. 1999; Hiner and Moffitt 2001). Whirling disease was introduced into North America from Europe, and it infects most North American salmonids. Whirling disease is particularly detrimental to juveniles (Gilbert and Granath 2003), and can severely limit recruitment in wild situations or production of fish under aquaculture conditions. A field study conducted on 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 (Thompson et al. 1999).

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 (Cheek et al. 1985; 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). Although many pathogens or parasites may not become established in a novel environment, those that do so can affect native fish populations (Brouder 1999).

Current data are insufficient to allow accurate, site-specific 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 and decrease it for others (Wakabayashi 1991; Watson et al. 1998; Decostere et al. 1999; Cairns et al. 2005). 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).

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, and their competitive ability can be affected by temperature (Taniguchi et al. 1998; Taniguchi and Nakano 2000). 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. Therefore, aquatic communities will have to adjust to new biotic pressures in addition to altered abiotic conditions. Though the altered ecosystems will, eventually, achieve a new steady state, the form this state will take, and the amount of time required to adjust, are completely unknown.

Possible responses to new challenges

Fish faced with a changing environment must adapt, migrate, or perish. Fish populations, especially large or widely distributed ones often have high heterogeneity that varies within their geographic range (Laikre et al. 2005). For example, genetic loci in the European hake (*Merluccius merluccius*) (Cimmaruta et al. 2005) and the mummichog *Fundulus heteroclitus* (Smith et al. 1998) vary along a latitudinal cline. The current rate of climate change rivals or surpasses all other rates recorded in the fossil record (Allan et al. 2005), so it is likely that the

changing climate will outstrip the ability of some fish populations to respond to new selective pressures. Historic and fossil records indicate that animals and plants tend to shift their range in response to climate change, indicating that some genetic traits are relatively intractable (Thomas 2005). The ability of species to adapt will depend upon their genetic plasticity and degree of specialization. Specialists adapted to local conditions will be more likely to go extinct than generalists (Allan et al. 2005).

Because global climate change will shift the ranges of temperate fishes towards higher latitudes, it could have potentially serious impacts on some stream fishes, fishes in geographically isolated environments, and fish in lentic systems. Migration towards the poles may be an option for some species, but fishes in east–west oriented stream systems (e.g., the southwestern United States (Matthews and Zimmerman 1990), eastern Africa (Allan et al. 2005), and New Zealand (McDowall 1992) would be prevented from moving to higher latitudes by excessive distance and physiological barriers like the ocean. 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. Furthermore, physical barriers to migration will prevent colonization of new habitats. Worldwide, streams and lake chains have been fragmented by man-made barriers, such as dams, water diversions, and flood control structures (Porto et al. 1999; Clarkson and Childs 2000; Bednarek 2001; Lodge 2001; Winter and Van Densen 2001; Gehrke et al. 2002; Morita and Yamamoto 2002). These alterations will hinder the ability of fishes to move to new habitat. Fish populations in geographically isolated systems such as springs and lakes will be essentially trapped and therefore faced with extinction (Lodge 2001). Fishes native to the Arctic Circle such as broad whitefish (*Coregonus nasus*), Arctic cisco (*Coregonus autum-*

nalis), and wild and commercially raised Arctic charr 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 (Shuter et al. 2002a). The introduction of fish to new environments is not always successful and raises environmental, political, and ethical questions (Beeton 2002). 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 non-indigenous species into natural ecosystems can have disastrous results (Zaret and Paine 1973; Courtenay 1997). 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).

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). However, a 2°C warming of the North American continent may prevent the efficient farming of this fish in the southeastern United States (McCauley and Beitinger 1992), and the species' range shift may not coincide with the resources (land and water) needed to shift the industry northward. 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 Laurentian Great Lakes region, revenues from recreational freshwater fisheries are an integral component of local economies. Nearly 10 million recreational anglers spent approximately $US 9.3 billion 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). Climate change may threaten this economy by shifting the ranges of target fish northward; the valuable coldwater fish species of this area, such as the lake trout, may migrate northward, leaving behind the local businesses such as resorts, restaurants and fishing equipment retailers that depend upon them (Shuter et al. 2002b; Kling et al. 2003; Roessig et al. 2004). In the United Kingdom, recreational anglers spend about $US 3.41 billion annually (Lyons et al. 2002). The levels of participation in recreational fishing vary among developed countries, ranging from 1% to 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).

Endemic species or those with limited ranges are naturally prone to extinction (Brown and Kodric-Brown 1977; Stacey and Taper 1992; Hanski 1994; Angermeier 1995). Therefore, another possible effect of climate change is the loss of biodiversity through the extinction of specialized or endemic fish species. It is difficult to quantify this loss in financial terms, but there is some evidence that people are willing to pay to preserve native fish species (Nishizawa et al. 2006), even those that are not commercially or recreationally exploited (Loomis and White 1996). Furthermore, it can be argued that biodiversity has intrinsic and ecological value and should be preserved whenever possible.

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). Global climate change appears to represent an additional stressor to the suite that includes pollution, overfishing, water diversion, and widespread introduction of non-native

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, climate change has already affected natural populations (McCarty 2001; Parmesan and Yohe 2003) and will likely continue to do so. Temperature increases, decreased DO levels, changes in disease transmission, changes in toxicant stresses, and alterations to hydrographs could all contribute to the decreased productivity of native fish populations. Although each of these changes has been discussed separately, they are highly correlated, and fishes will have to cope with some combination of these factors. Furthermore, the effects of climate change will interact with other anthropogenic impacts such as land use change, habitat fragmentation and destruction, and the introduction of non-indigenous species (Lodge 2001). Though the small changes seen in current years have yet to cause significant decreases in the productivity of most fisheries, global climate change is expected to increase in magnitude in the near future (IPCC 2001), and measurable changes may soon occur. Furthermore, human response to increased temperatures will lead to secondary effects on fisheries (Vörösmarty et al. 2000). For example, increased demand for water will lead to further water diversion and development, and increased waste heat loading that will exacerbate existing environmental challenges (Mulholland et al. 1997; Vörösmarty et al. 2000). Fishes inhabiting regions that receive more precipitation will face new challenges as humans respond by building flood control structures (Abell

2002). Regardless of local changes in precipitation, dam construction is expected to increase worldwide. 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 (Blinn et al. 1998; Porto et al. 1999; Wohl 2001). They also block fish migration, thereby preventing many riverine species from completing their life cycles (Winston et al. 1991; Peter 1998). 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 criterion 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. Though decreased fishery productivity would probably not cause a crisis in industrialized countries, loss of recreational fisheries would have profound negative economic effects (Post et al. 2002; Chen et al. 2003; Stoeckl et al. 2006). Loss of productivity in the world's fisheries could be exacerbated by rapid human population growth and subsequent high demand for fish protein. Often, freshwater fish stocks in countries with burgeoning populations are already heavily exploited (Thompson 1996; Etim et al. 1999; De Jesus and Kohler 2004). 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). Given these stakes, it is vitally important to confront the looming effects of climate change. As an alternative to coping with the results of a changing environment, we can actively manage for the inevitable. Possible strategies include removing other anthropogenic stressors so that fishes can better adjust to climate change (Casselman 2002; Magnuson 2002a) and decreasing greenhouse gas

emissions to decrease future climate change. Although a thorough discussion of this is beyond the scope of this paper, it is apparent that a proactive response to managing fisheries in the face of a changing climate will better ensure functional fish communities in the future.

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