Effects of Global Climate Change on Marine and Estuarine Fishes and Fisheries

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Abstract

Global climate change is impacting and will continue to impact marine and estuarine fish and fisheries. Data trends show global climate change effects ranging from increased oxygen consumption rates in fishes, to changes in foraging and migrational patterns in polar seas, to fish community changes in bleached tropical coral reefs. Projections of future conditions portend further impacts on the distribution and abundance of fishes associated with relatively small temperature changes. Changing fish distributions and abundances will undoubtedly affect communities of humans who harvest these stocks. Coastal-based harvesters (subsistence, commercial, recreational) may be impacted (negatively or positively) by changes in fish stocks due to climate change. Furthermore, marine protected area boundaries, low-lying island countries dependent on coastal economies, and disease incidence (in aquatic organisms and humans) are also affected by a relatively small increase in temperature and sea level. Our interpretations of evidence include many uncertainties about the future of affected fish species and their harvesters. Therefore, there is a need to research the physiology and ecology of marine and estuarine fishes, particularly in the tropics where comparatively little research has been conducted. As a broader and deeper information base accumulates, researchers will be able to make more accurate predictions and forge relevant solutions.

Introduction

One fascinating feature of global climate change is how it relates so many facets of science that are so often segregated. To fully understand how this phenomenon affects fish, we must consider atmospheric science, chemistry, oceanography, physiology, and ecology. Taken a step further in relating these to people and communities, we must also consider geography, economics, and sociology. With the context so broad, one review paper cannot fully encapsulate the spectrum of implications. We focus on how global changes (particularly temperature-related ones) impact marine and estuarine fish and fisheries, and the people who depend on them.

The amazing aspect of global climate change is the magnitude of the impact of a relatively small temperature change. An increase of a few degrees in atmospheric temperature will not only raise the temperature of the oceans, but also cause major hydrologic changes affecting the physical and chemical properties of water. These will lead to fish, invertebrate, and plant species changes in marine and estuarine communities (McGinn, 2002). Fishes have evolved physiologically to live within a specific range of environmental variation, and existence outside of that range can be stressful or fatal (Barton et al., 2002). These ranges can coincide for fishes that evolved in similar habitats (Attrill, 2002). We approach these patterns of existence by looking at three different regions of the world’s oceans: temperate, polar, and tropical. Within each region, we examine physiological characteristics common to its fishes and relate them to regional habitat characteristics. After examining predicted changes that fish and their populations will encounter, we attempt to bridge the gap between the science information and models and fish-dependent societies. Three types of harvesters exploit fish stocks: subsistence (artisanal), commercial, and recreational. These all may be impacted (negatively and/or positively) by changes in fish stocks due to climate change. Other issues affected by these global changes include boundaries of marine protected areas, low-lying island countries dependent on coastal economies, and disease (in aquatic organisms and humans). All stem from a relatively small rise in temperature.

By examining the physiological and ecological effects on fishes in these regions, we are made aware of how much is not known about fishes and their ecosystems. There is a great need for research on the physiology and ecology of fishes, particularly in the tropics. Without an understanding of how these organisms and systems function and interact, we cannot predict how they will react to perturbation, including global climate change-related disturbances. These gaps lead to uncertainties about future fish stocks and for people depending on them.

The Situation

Many naturally occurring compounds from the Earth's crust and waters are continuously added to the atmosphere. Until recently, chemical influx and efflux have been driven by non-anthropogenic processes (Fig. 1) over geological time spans, allowing organisms to evolve with their environments. However, since the Industrial Revolution (19th Century), many compounds that naturally existed in small quantities have been mass produced and added to our atmosphere through anthropogenic activities (Sarmiento and Gruber, 2002). This comparatively rapid introduction of compounds has caused profound environmental alterations. Greenhouse gases, such as carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), chlorofluorocarbons (CFCs), and volatile organic compounds (VOCs), absorb incoming solar energy and outgoing (reflected) radiant energy. Changes in the concentrations of these and other atmospheric gases, therefore, alter the global radiation budget (Gribbin 1988; Fig. 1). The retention of additional radiant energy raises atmospheric temperatures and impacts climates. These climatic changes affect the entire earth system, including ecosystems, community and population structures, and organismal ranges (Bernal, 1993; Daniels et al., 1993; Parmesan, 1996; Booth and Visser, 2001; McCarthy, 2001; Walther et al., 2002). Recent evidence outlines the magnitude of such changes in terrestrial systems (Root et al., 2003; Parmesan and Yohe, 2003).

Global atmospheric temperatures and CO_2 concentrations have risen throughout the last 50 years (Fig. 2; Trenberth, 1997; Quay, 2002). Simultaneously, the world's oceans have experienced a net warming (Levitus et al., 2000; Sheppard, 2001; Fukasawa et al., 2004). Regional increases in temperature have been documented in the southwest Pacific Ocean and North Atlantic Ocean (Bindoff and Church, 1992; Parrilla et al., 1994). For the last 20-30 years the western Mediterranean Sea temperatures have been rising (Bethoux et al., 1990), which is reflected in the presence and abundance of ectothermic marine life (Francour et al., 1994). For example, off the coast of France, two thermophilic algal species, several thermophilic echinoderm species, and some thermophilic fishes have increased in abundance, while other thermophilic species are being observed for the first time (Francour et al., 1994).

Model Predictions

Several models have been produced recently suggesting outcomes to various global climate change situations. Models incorporate and combine knowledge about individual processes in a quantitative way, yet they typically have intrinsic limitations because they are simplifying a complex system, and using often incomplete and inaccurate knowledge (Trenberth, 1997; Rahmstorf, 2002). Ultimately, modeling is a compromise among inclusion of processes, level of complexity, and desired resolution (Rahmstorf, 2002). Assessment of their accuracy is possible by comparing model outcomes to climate reconstructions. Climate reconstructions are based on proxies such as pollen, ocean-sediment cores, lake-level reconstructions, glacial moraines, terrestrial, and ice-borehole data (for coarse, long time scales), and tree rings, corals, ice cores, lake sediments, and historical records (for shorter time scales; Mann, 2002). Each proxy has advantages and disadvantages, leaving no single proxy adequate for all climate reconstruction purposes (Mann, 2002).

Estimates of future surface air temperature increases range from 1 to 7ºC, depending on the hypothesized atmospheric CO_2 contents (Daniels et al., 1993; Kwon and Schnoor, 1994; Manabe et al., 1994; Woodwell et al., 1998). Air temperatures are expected to increase ocean warming, most significantly in the upper 500-800 m (Bernal, 1993). However, even slight warming of deeper oceanic layers will have a huge impact on the Earth's energy budget due to the mass of water they contain (Bernal, 1993; Levitus et al., 2000; Stevenson et al., 2002). Ocean circulations are predicted to shift, possibly interacting with land masses, creating a north-south thermal asymmetry (Bernal, 1993). For example, the northern boundary of the Gulf Stream has shifted slightly northward in recent decades (Taylor and Stephens, 1998).

Potential Effects of Global Climate Change on Marine and Estuarine Environments

It is widely accepted that due to greenhouse gases a profound change in climate will occur (Palmer and Räisänen, 2002; Schnur, 2002). How will this affect the physical environments of oceanic and estuarine ecosystems? Change in climate means there is a change in precipitation and evaporation rates, constituents of the hydrologic cycle, which affect surface runoff, and groundwater and ocean levels (Klige, 1990; Zestser and Loaiciga, 1993; Loaiciga et al., 1996). A rise in global temperature, generally, would increase regional evaporation in the lower latitudes and increase regional precipitation in the higher latitudes (Klige, 1990; Zestser and Loaiciga, 1993; Manabe et al., 1994; Palmer and Räisänen, 2002). Shifts in the evaporation/precipitation regime could have significant consequences to the continents, including worsening conditions for flood control and water storage (Loaiciga et al., 1996; Milly et al., 2002). In addition, excess runoff (in relation to evaporation) will contribute to groundwater levels (Zestser and Loaiciga, 1993; Manabe et al., 1994). Approximately 6% of the total water influx to the oceans and seas comes from direct groundwater discharge (Zestser and Loaiciga, 1993). An increase in the amount of groundwater entering the ocean would lead to a net gain in oceanic volume. In addition to increased groundwater discharge, meltwater from glaciers may contribute to increasing ocean volume (Klige, 1990; Daniels et al., 1993; Schøtt Hvidberg, 2000; Stevenson et al., 2002). Finally, as water temperatures rise, the volume of the oceans will also increase due to thermal expansion (Daniels et al., 1993; Stevenson et al., 2002).

Increased oceanic volume and concomitant sea level rise have tremendous implications for coastal environments. Sea levels have risen (0.1-0.3 m over the past century) in conjunction with the rising global temperature (Wigley and Raper, 1987; Liu, 2000; IPCC, 2001), but with a time lag of 19 years (Klige, 1990). Depending on model factors, predicted increases range from 0.3 to 5.0 m, possibly inundating almost 1 million km^2 of coastal land (Klige, 1990; Daniels et al., 1993; Liu, 2000). This rise is occurring at a faster rate than plants can colonize and establish wetland habitat (Daniels et al., 1993; Stevenson et al., 2002). Therefore, many tidal wetlands, estuaries, mangroves, and other shallow-water habitats may be lost if climate change continues at the predicted rates. An increasing water column depth affects the complex interactions of the hydrodynamic processes that take place in the coastal environment. Tides and tidal currents, distribution of turbulent energy, shoreline configuration, near-shore depth distribution, sedimentation patterns, and estuarine-river interactions will be affected (Liu, 2000).

Another major consequence of a changing climate is the likely perturbation of oceanic circulations. Currents are driven directly by winds (upper layer of ocean), fluxes of heat and freshwater (thermohaline circulation), or by the gravitational pull of the sun and moon (tides; Rahmstorf, 2002). Thermohaline circulation is the deep ocean water (> 200 m) that is conveyed in slow large-scale circulations, driven by water density, which is dependent on heat and salinity (Fig. 3; Garrison, 1996). Although there is much debate on the predicted future of this circulation (Hansen et al., 2004), many global climate change models suggest weakening, and possibly complete breakdown, of the thermohaline circulation, particularly in the Atlantic Ocean (Bernal, 1993; Manabe et al., 1994; Sarmiento et al., 1998; Plattner et al., 2001; Vellinga and Wood, 2002). Furthermore, suggestions that a rise in sea level may also decrease the formation of North Atlantic deep water (NADW) will directly impact massive ocean water circulations (Mikolajewicz et al., 1990). This is caused, in part, to increased density-driven stratification of the upper water column in the higher latitudes, which decreases vertical mixing and convective overturning (Sarmiento et al., 1998).

Evidence of this has been uncovered in the Gulf of Alaska. Here, surface temperatures have been rising from warmer air temperatures, while salinities have been decreasing from melting ice, thereby decreasing the water's density. Meanwhile, deep waters have had little change in density, leading to increased ocean stratification and decreased formation of mixed layers (Whitney and Freeland, 1999; Freeland and Whitney, 2000). This halts the convective flow that drives thermohaline circulation, and consequently disturbs the circulation of nutrients and heat that these deep waters contain.

In the Pacific Ocean, increased stratification could increase the frequency of El Niño/Southern Oscillation (ENSO) events and more extreme climatic variations (Timmermann et al., 1999). ENSO events are characterized by an intrusion of warm water from the western equatorial Pacific into the eastern equatorial Pacific, where it causes a rise in sea level, higher sea surface temperatures, and a weakened thermocline, which is associated with reduced primary productivity (Miller and Fluharty, 1992). Thermohaline circulation is intimately linked to the carbon cycle and deep ocean ventilation, and any change in either would further disrupt the carbon cycle and biogeochemistry of the coupled system (Bernal, 1993; Manabe et al., 1994; Sarmiento et al., 1998).

The oceans act as an immense carbon sink. The amount of carbon stored in the oceans is regulated by atmosphere-sea gas exchange, carbonate equilibria, ocean circulation, and marine organisms (Plattner et al., 2001; Sarmiento and Gruber, 2002; Sabine et al., 2004). Increasing water temperature decreases the solubility of CO_2, resulting in the slowed uptake of atmospheric CO_2 (Kwon and Schnoor, 1994; Sarmiento et al., 1998; Plattner et al., 2001). For example, the solubility coefficient for CO_2 in seawater is 1.57 mL · L^{-1} · mm Hg^{-1} at 5ºC, and shifts to 1.34 mL · L^{-1} · mm Hg^{-1} at 10ºC (Randall, 1970). Plattner et al. (2001) reviewed many studies that predict the CO_2 uptake by oceans to be reduced by 4-28% during the 21st century. There has already been an 8-10% decrease in CO_2 uptake during the 20th century, attributed to increasing surface water temperatures (Joos et al., 1999). Reduced oceanic uptake, along with deforestation (decreasing CO_2 uptake via photosynthesis and CO_2 storage in living plant biomass), decreases the effectiveness of natural CO_2 buffering systems, which exacerbates the accumulation of anthropogenic CO_2 emissions in the atmosphere (Chambers et al., 2001).

When CO_2 is introduced to ocean waters and hydrated, more hydrogen ions are produced, and this equation shifts to the right:

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^- \leftrightarrow 2H^+ + CO_3^{2-}.$$

When the CO_2 concentration increases, the equilibrium of the equation shifts such that more carbonic acid (H_2CO_3) is formed, which partially dissociates into bicarbonate (HCO_3^-) and hydrogen (H^+) ions, lowering water pH. Bicarbonate may further dissociate so that 2 H^+ are created for one molecule of CO_2. The pH is a measure of H^+ activity, and is an important water quality indicator because fish and other organisms are sensitive to pH. Ocean surface pH has already decreased by 0.1 pH units in colder waters and almost 0.09 pH units in warmer waters (Haugen, 1997). If atmospheric CO_2 concentrations continue to increase, another 0.3 pH unit decrease of oceanic surface waters may occur (Haugen, 1997). Furthermore, as temperature increases, an increased proportion of the water molecules dissociate to H^+ and OH^-, decreasing water pH.

It has been suggested that CO_2 should be intentionally stored in the ocean, as a mechanism to stabilize atmospheric concentrations (Bacastow et al., 1997; Haugen, 1997; Wong and Matear, 1997; Gnanadesikan et al., 2003). This could be accomplished by several methods, including: A) creating a detritus flux, with CO_2 attached, to transport the CO_2 into deep waters, B) direct disposal into certain known deep water currents, and C) fertilizing nutrient-rich regions with iron to increase CO_2 utilization (Wong and Matear, 1997; Gnanadesikan et al., 2003). Obviously, one consequence of CO_2 disposal in the ocean is decreased pH (Haugen, 1997; Wong and Matear, 1997), which could be detrimental to affected organisms. This is especially true for bathypelagic organisms that are adapted to a very stable environment.

Salinity is another important factor that is greatly affected by climate. Because the oceans contain such a massive amount of water, net changes in salinity have not been much of an issue to this point. However, it may be a significant issue in the future, considering that although groundwater discharge to the ocean floors contributes only 6% of total water influx, it's salt load is 50% that of rivers, and groundwater discharge is expected to increase with increasing precipitation (Zestser and Loaiciga, 1993). Therefore, oceanic salinity could rise if the salt load introduced by groundwater discharge is not offset by water volume increases (Zestser and Loaiciga, 1993). It is also likely that the upper oceanic layers near the higher latitudes may become more dilute due to increased precipitation (Manabe et al., 1994) and river discharge (Peterson et al., 2002). A slight decrease in salinity has been observed in the northern Pacific, although a definite causal link has not been established (Wong et al., 1999; Freeland and Whitney, 2000). Changes in salinity have important implications on thermohaline circulation and on the formation of dense water (Peterson et al., 2002).

A possible consequence of ocean warming is clathrate outgassing. Clathrates (or gas hydrates) are gases that under the proper temperature and pressure conditions have stabilized as ice-like solids (Wilde and Quinby-Hunt, 1997). Clathrates of greenhouse gases (carbon dioxide and methane) and toxic gases (hydrogen sulfide) exist on the ocean floors near the higher latitudes, and it is thought that they could exist at the lower latitudes as well (Wilde and Quinby-Hunt, 1997). It is possible that an influx of warmer water could destabilize these clathrates, causing release of these gases into the water column, potentially adding more greenhouse gases to the atmosphere (Wilde and Quinby-Hunt, 1997).

The increase in greenhouse gas concentrations is likely causing global climate changes (Watson et al. 2001, Hughes et al. 2003) and consequent changes in the physical characteristics of the oceans. Recent evidence from model simulations is consistent with relevant anthropogenic effects of greenhouse gases on a warming climate (Watson et al. 2001). However, controversy remains and there are conflicting analyses and insufficient data to explain some phenomena, including intensities of tropical storms, leading to other explanations of more regional-scale impacts (Watson et al. 2001). Warmed marine and estuarine waters (and consequent changes in dissolved gases, pH, and salinity), from global climate change-related (or other) effects could be expected to affect many fish species and life stages. Fish, as ectotherms, are intimately connected to their environment, and significant changes in oceanic conditions regionally and globally will likely have both direct and indirect effects on individuals, their populations, and communities (Fig. 4).

Effects on Fishes

Climate change will affect individuals, populations and communities through the individuals' physiological and behavioral responses to environmental changes (Boesch and Turner, 1984). Extremes in environmental factors, such as elevated water temperature, low dissolved oxygen or salinity, and pH, can have deleterious effects on fishes (Moyle and Cech, 2004). Suboptimal environmental conditions can decrease foraging, growth, and fecundity, alter metamorphosis, and affect endocrine homeostasis and migratory behavior (Barton and Barton, 1987; Donaldson, 1990; Pörtner et al., 2001). These organismal changes directly influence population and community structure by their associated affects on performance, patterns of resource use, and survival (Ruiz et al., 1993; Wainwright, 1994).

Estuarine and coastal regions are extremely productive because they receive inputs from several primary production sources and detrital food webs. Yet, these systems present the biota with a harsh environment, forcing organisms to evolve physiological or behavioral adaptations to cope with wide ranging physical and chemical variables (Horn et al., 1999). Due to water circulation and oceanic volume changes, estuarine and coastal systems are predicted to experience a loss of marsh and intertidal habitat, a greater marine intrusion or freshwater plumes, and increased eutrophication, hypoxia, and anoxia (Officer et al., 1984; Kennedy, 1990; Ray et al., 1992; Schwartz, 1998). The close relationship between laboratory-based measurements of fishes' responses to temperature and the same species' thermal distributional limits in their native habitats has been demonstrated (Cech et al., 1990). Because many native organisms currently live near their tolerance limits, estuarine and coastal ecosystems will likely exhibit responses earlier to regional changes, including native species loss and exotic species increases (Kennedy, 1990; Carlton, 1996).

Marine pelagic systems are susceptible to climate change through extreme events and the contraction or expansion of oceanic zones. For example, sea temperature changes driven by variations in the North Atlantic Oscillation (NAO) have been linked to fluctuations in cod (*Gadus morhua*) recruitment and habitat shifts off Labrador and Newfoundland (Rose et al., 2000). On the west coast of Canada and Alaska, the Gulf of Alaska is exhibiting increased temperature and decreased salinity levels. The result is seen in shallower mixed layers, which lead to a reduced nutrient supply (Whitney and Freeland, 1999), impacting primary production levels and changing food webs (Bjørnstad and Grenfell, 2001; Zabel et al., 2003; Richardson and Schoeman, 2004). In the next sections, we focus on marine ecosystems where global climate change-related influences are predicted to have significant impacts on fishes and their populations.

Temperate Regions

Attempts to identify the impacts to fishes in the temperate (spanning subtropical to subpolar) regions are complicated, due to the diversity of life history patterns, trophic relationships, and variations in local habitats. Therefore depending on the environmental change, a broad range of fish responses can be expected (Table 1). Because many lucrative commercial fisheries are situated in the temperate regions, global climate change-related effects could have dramatic economic impacts. Consequently, comparatively more research has been conducted on potential effects of global climate change on temperate region species. However, because continual exploitation affects fish stock abundance and recruitment, detecting global climate change-related effects is difficult. Before examining temperature and other climate-related effects on populations, it is useful to understand global climate change effects on individual fishes.

Physiological and Behavioral Effects on Temperate Fishes

Temperature tolerances (including lethal limits) and the associated rates of thermal acclimation of fishes are critical data when predicting fishes' responses to global climate changes. Fishes have shown varying abilities to adjust their upper temperature tolerance limits with increased acclimation temperatures. For example, Young and Cech (1996) found that the estuarine splittail (*Pogonichthys macrolepidotus*) increased their critical thermal maximum (CTM; temperature where equilibrium is lost after rapid heating) from 29 ºC, when acclimated to 17 ºC, to 32-33 ºC, when acclimated to 20 ºC. This contrasts with golden shiners (*Notemigonus crysoleucas*), which increased their incipient lethal temperature only 4 ºC (from 30 to 34 ºC) when their acclimation temperature was increased by 15 ºC (from 15 to 30 ºC; Hart, 1952). Laboratory data can be used to determine the environmental temperatures a fish can survive, and by combining this information with observational data, researchers can predict fishes responses to thermal changes.

Sudden shifts in temperature can have disastrous effects on fish populations (e.g., thermal stress), especially if shallow water or long distances prevents the fish from finding a thermal refuge. For example, Gunter and Hildebrand (1951) described a massive die-off of fishes and crabs associated with a weather cold front that lowered water temperatures in the shallow Gulf of Mexico bays and estuaries of the Texas coast to 3 ºC (with ice forming along the shorelines). Overstreet (1974) described a similar occurrence in Mississippi coastal waters, and attributed the death of mullets (*Mugil* spp.), tarpon (*Megalops atlanticus*), and other species to the sudden cold temperatures and other factors (e.g., low dissolved oxygen and the presence of toxic pesticides in the water). Burton et al. (1979) showed that fast temperature decreases are correlated with increased mortality rates in Atlantic menhaden (*Brevoortia tyrannus*). There are several mechanisms of temperature-related mortality in fishes, ranging from molecular (e.g., heat-related damage to vital enzymes; Somero, 1995) to systemic (e.g., cardiac insufficiency, Cech et al., 1975).

Many marine fishes exhibit behavioral thermoregulation, in that they seek preferred temperatures, depending on environmental conditions. The practice of "fishing with thermometers," concentrating fishing efforts on areas characterized by particular sea-surface temperatures, has been used to locate pelagic stocks since the mid-Twentieth Century. Although multiple factors influence organisms' positions in natural environments, skipjack tuna (*Katsuwonus pelamis*) data from the 1950s and 1960s show that catches were optimal in the 20 - 29 ºC surface temperature range (Williams, 1970). Subsequent laboratory studies found that the lower and upper tolerance limits (18 and 30 ºC respectively) on the same species (Barkley et al., 1978) closely brackets the field temperature-preference data. Tsuchida (1995) found a close correlation between the preferred temperature and the upper temperature tolerance limit of 14 marine fishes found in Japan's coastal waters. Yet, temperature preferences can be modified by environmental factors. Fishes with restricted food supplies tend to seek cooler water, consequently lowering their metabolic demands (Moyle and Cech, 2004). For example, food-deprived threespine sticklebacks (*Gasterosteus aculeatus*) preferred significantly cooler sea water (15.9 ºC) than fed fish (20.1 ºC), when both were acclimated to the same temperature (10-

12 ºC) at 33 ppt salinity (Magee et al., 1999). Similarly, Atlantic cod preferred lower temperature conditions when fed lower rations (Despatie et al., 2001), and the intertidal fish, *Girella laveifrons*, selected lower temperatures when fed a poor-quality diet (Pulgar et al., 2003). Thus, on a population level, decreased food availability (e.g., from decreased productivity and therefore decreased prey fish) could lead to a shift in the distribution of predatory fishes to cooler waters.

With the notable exceptions of partial endothermy in some pelagic tunas (Scombridae), sharks (Lamnidae), and billfish (Xiphiidae; Block et al., 1993), fish are poikilothermic. Thus, environmental temperature increases elevate their biochemical reaction rates, which translates into increased metabolic rates. Every species has its temperature tolerance range, and, typically, energy allocation towards growth and reproduction declines at temperatures near the range extremes (Miller et al., 1988; Sogard and Olla, 2002). For example, the maximum attainable size of the Atlantic cod decreases with increasing water temperature (Brander, 1995; Björnsson et al., 2001; Björnsson and Steinarsson, 2002). This trend was also documented in periods of slow growth with juvenile Atlantic salmon (*Salmo salar*) induced by either food deprivations or low temperatures (Nicieza and Metcalfe, 1997). Large juvenile California halibut (*Paralichthys californicus*) were far less tolerant than smaller juveniles of temperature and salinity variations, resulting in weight loss, water-balance problems, and increased mortality (Madon, 2002).

Temperature can exert significant direct (e.g., via metabolic processes) or indirect (e.g., via distribution and abundance of prey species) effects on fish growth and mortality (Brett, 1970; Anderson and Dalley, 2000). Laboratory studies on the growth of juvenile plaice

(Pleuronectidae), sole (Soleidae), and English sole (*Pleuronectes vetulus*; United States, northern Pacific coast populations) demonstrated that growth strongly correlated with ambient temperatures (Williams and Caldwell, 1978; Fonds, 1979; Yoklavich, 1982; Shi et al., 1997). In contrast, Anderson and Dalley (2000) found that temperature had no effect, or an easily discernable effect, on cod growth in Newfoundland waters. Bioenergetic models have suggested that the higher metabolic costs associated with elevated water temperatures, and tied with poor foraging ability or diet quality, could decrease growth and increase mortality of sockeye salmon (*Oncorhynchus nerka*; Hinch et al., 1995). Interspecific competition for common prey items may also determine the ration consumed, which in turn influences growth and survival, as in Asian pink salmon (*O. gorbuscha*) and Alaskan sockeye salmon (Ruggerone et al., 2003). Therefore, foraging success and diet quality, along with temperature changes, will be critical to predicting responses to global climate change.

Ecological Effects on Temperate Fishes

Many fishes experience high mortality (due to predation or fishing pressure) and high growth rates (dependent on environmental quality) during larval and juvenile stages, which influences the subsequent survival and abundance of these fishes (Houde, 1987; Rose, 2000). This often results in young-of-the-year abundances that do not correlate with adult abundances. For example, increases in the abundance of young-of-the-year cod in the northern range of Arctic-Norwegian stocks were associated with water temperature elevation. Conversely, a large drop in North Sea young-of-the-year cod abundances was partly attributed to elevated sea temperatures (O'Brien et al., 2000). Yet, cold temperature seemed to limit growth of young cod in the Barents Sea (Nakken, 1994; Pörtner et al., 2001; Pörtner, 2002) and is associated with weak year-classes of North Sea cod when spawning-stock biomass is also low (O'Brien et al., 2000). These confounded findings illustrate the diversity of responses, and therefore, the importance of population- and area-specific research to understand global climate change effects (McFarlane et al., 2000).

Long-term trends in phytoplankton records in the North Sea showed a regime break in 1988, when satellite images of phytoplankton pigmentation exhibited seasonal and intensity level changes. The break was associated with atmospheric changes in the area (including increased wind circulation), oceanic flow, and higher sea surface temperatures in the North Sea. Reid et al. (2001) suggested that these changes may have increased northerly advection in this region, causing phytoplankton (and associated zooplankton) to increase their distribution ranges. Horse mackerel (*Trachurus trachurus*) which feed on these zooplankton changed their migratory patterns, following food availability, and fishery landings increased to a record high (Reid et al., 2001). Though it is difficult to conclusively state that the increased landings were the direct result of the expanded season and abundance of phytoplankton, the correlations among these factors were very strong (Reid et al., 2001). This serves as an example how changes in ocean conditions can affect the food web base, which in turn affects the behavior and distribution of fishes, and ultimately translates to changes in fisheries production.

Temperature-induced shifts may also affect fish distribution ranges (McFarlane et al., 2000; Table 1). Sockeye salmon stock, in the marine phase, may encounter increasing warmer water temperatures. Welch et al. (1998) hypothesized that if the surface mixed layer warms past the fishes' thermal limits, then sockeye salmon will need to: 1) develop the ability to migrate to the

Bering Sea; 2) vertically migrate to stay below the thermocline during the day and migrate to the surface waters for short time periods to forage; or 3) deal with the energetic costs and consequences associated with unfavorable thermal environments. In North Carolina, the numbers and abundance of tropical species in the temperate reef habitats are slowly increasing because of increases in bottom water temperatures (1-6 ºC) over the last 15 years (Parker and Dixon, 1998). Two new families and 29 new species of tropical fishes have been documented. However, no new temperate species were observed, and the most abundant temperate species have declined (Parker and Dixon, 1998).

Many pelagic fishes (e.g., anchovies [Engraulidae] and sardines [Clupeidae]) are strongly affected by regional environmental cues. In the Adriatic Sea, long-term changes in the landings of small pelagic fish (e.g., anchoveta [*Cetengraulis mysticetus*], sardines, sprat [*Sprattus sprattus*]) were suggested to be partially due to the advection cycle of the Levantine Intermediate Water (Grbec et al., 2002), which resulted in hydrological changes. Similarly in Trieste Bay, the mackerel stock reduction may be linked to mismatched timings of the larvae's arrival and the production of sustainable food in the nursery ground, due to the recent modification in the hydrological cycle of the area (Grbec et al., 2002). In addition, recent analyses indicate that the distribution and abundance of tuna (particularly bluefin, *Thunnus thynnus*) larvae, and the migratory patterns and seasonal availability of skipjack and bigeye (*T. obesus*) tunas, have changed in concert with a 3-4 ºC temperature increase and other environmental changes (Lehodey et al., 1997; ICCAT, 2002). These examples demonstrate how individual responses can lead to population level changes, resulting from changing oceanic conditions. Similar changes, but with greater magnitude, can be expected if predicted global warming scenarios occur.

Polar Regions

Polar regions already have exhibited effects of rapid climate changes. For example, collapsing ice sheets over the past thirty years have resulted in surges of icebergs into the North Atlantic Ocean. Furthermore, relatively sudden temperature changes (increases or decreases of 5-10 ºC) in Greenland are thought to be caused by the gradual shutdown (temperature increase) or retention (decreases) of the NADW, an oceanic-atmospheric circulation (Rahmstorf, 2002). Through thousands of generations polar organisms have evolved cold-water tolerance, possibly leaving these fishes vulnerable to relatively small environmental temperature or salinity changes (Eastman, 1993).

Physiological Effects on Polar Fishes

Polar marine habitats are characterized by well-oxygenated waters with narrow, cold temperature ranges (Rose et al., 2000). Some fish species can exist in a super-cooled state, where their blood remains fluid to one degree below the normal freezing point (De Vries and Lin, 1977). Fishes employing this strategy live at depths to avoid contacting ice. Other fishes are able to inhabit areas with ice, thus being exposed to temperatures < -2.2 ºC (Eastman and De Vries, 1986). To better withstand the low temperatures, many of the fishes have antifreeze peptides or glycopeptides in their blood and tissues, which allow their body temperatures to drop to < -0.8 ºC without freezing (De Vries and Lin, 1977; De Vries, 1988). If they are capable of producing these special molecules, most of these fishes can tolerate temperatures to -1.9 ºC (Kock, 1992;

Eastman, 1993; Pörtner, 2002). Fishes in the Antarctic region produce these compounds year-round, while Arctic Ocean fishes produce them only in the winter, as regulated by temperature and photoperiod (Duman and De Vries, 1974; Kock, 1992). Among species, subtle differences between types and amounts of peptides/glycopeptides produce variations in lower temperature tolerances. If polar waters warm due to global climate shifts, antifreeze peptide/glycopeptide production would likely decrease, thereby increasing available energy for growth or reproduction, if food consumption stayed constant. However, warming polar waters would increase maintenance metabolic (oxygen and energy) requirements, possibly offsetting such energetic gains.

Cold temperatures increase oxygen solubility in polar waters and decrease the oxygen requirements (oxidative metabolic rates) of polar ectothermic organisms, including fishes. The high environmental oxygen concentrations (and corresponding plasma oxygen levels in polar fishes) are associated with reduced numbers of red blood cells, and lower hemoglobin and myoglobin concentrations, compared to temperate fishes. Fewer red blood cells and less oxygen-binding proteins are needed to satisfy the lower metabolic rate of the polar fishes (Kock, 1992; Nikinmaa, 2002). In addition, polar fishes show reduced hemoglobin polymorphism, compared with many fishes. While some polar species have three hemoglobins types (e.g., *Trematomus* spp.), other species (e.g., bathydraconids) have only one type. The temperate Chinook salmon (*O. tshawtscha*) has at least three hemoglobin types (Fyhn and Withler, 1991; Fyhn et al., 1991). Reduction of hemoglobin types is, presumably, the evolutionary result of stable environmental conditions and polar fishes' stable metabolic rates (di Prisco et al., 1990; Kunzmann, 1991). Antarctica's famous icefishes (Channichthyidae) have no hemoglobin or red blood cells in their blood (Kunzmann, 1991). Because polar fishes have lower levels of hemoglobin polymorphism than temperate species, they are likely ill-prepared to cope with even minor elevations in environmental temperature.

Other physiological data indicate that polar fishes are well adapted to only a narrow range of cold temperatures (i.e., highly stenothermic). For example, Somero and DeVries (1967) found that *Trematomus hansoni* has a lethal upper temperature near 5 ºC. Some polar fishes have highly temperature-sensitive enzymes (e.g., lactate dehydrogenase) and enzyme-ligand interactions (Kock, 1992). Preliminary investigations show that Antarctic fishes in the family Nototheniidae lack heat shock proteins (HSPs). The HSPs, which repair or re-fold damaged proteins (from cellular insults like heat), and are present in most other animals (e.g., amphibians, mammals, some fishes). The loss of HSPs further indicates the relative warm-temperature vulnerability of Antarctic fishes (Kock, 1992; Hofmann et al., 2000).

Ecological Effects on Polar Fishes

Because of their narrow temperature limits, even slight changes in polar temperatures may cause fish populations to shift their migratory patterns and geographical ranges, and affect physiological performance (Table 1). Cold-water adapted fishes may need to seek deeper water for cooler temperatures. Depending on how the ocean currents change, if some areas become isolated and remain very cold, the potential for horizontal migration exists. The effects, however, of such migrations on their foraging patterns and life history strategies are unknown. In addition, increasing temperatures are predicted to accelerate polar ice melting rates. For instance, the Antarctic bottom waters in the Argentine Basin experienced a cooling (0.05 ºC) and freshening (0.008 ppt) during the 1980s (Coles et al., 1996). At present, there is little information available on the salinity tolerances or preferences of polar fishes. If polar fishes are stenohaline, they will be limited to life below the halocline or migrate to more haline areas. On the other hand, these polar waters may eventually resemble the physical conditions in our present-day temperate waters. This may allow temperate fishes to colonize these areas, but at the expense of the polar species.

Indirect temperature-related effects (e.g., changes in the distribution and abundance of polar fishes' food organisms) could have dramatic effects on the polar fishes and fisheries. The food chains in the polar regions are short and depend on relatively few species. In the Antarctic Ocean, zooplankton and associated nekton are trapped by the Antarctic convergence, permitting little passage north (Loeb et al., 1997). Most Antarctic fishes' behavioral patterns are linked with the life cycles of an important euphausid shrimp, krill, although energy may also be acquired from fish remains, bird regurgitated pellets, and seal feces (Stark, 1994; Loeb et al., 1997). A warming trend has been documented for the Antarctic Peninsular region since the 1940s, with a corresponding decreased frequency of extensive winter-ice conditions (Loeb et al., 1997). The less extensive winter sea-ice cover does not favor krill recruitment and abundance, and Adelie penguin (a krill predator) abundance has decreased 30% since 1987 (Stark, 1994; Loeb et al., 1997). Thus, warming air temperatures, resulting in less frequent winters with extensive sea-ice conditions, may limit food availability for krill-eating fishes, also.

Tropical Regions

The tropical oceans are comprised of structurally distinct habitats with distinct fish communities. Unfortunately, physiological studies of tropical fishes are comparatively few. Therefore, in this section, we examine the effects on tropical fishes by looking at comparatively well-studied coral reef ecosystems and their fish communities.

Effects on Coral Reef Communities

Coral reefs occur within well-defined, physical and environmental limits. Radiation, water quality (physical and chemical properties, including temperature), bathymetry, and natural history all help determine the composition, distribution, and diversity of these ecosystems. The hypothesis that coral reef communities are among the first to show signs of adverse climate change-related effects has been widely stated in the literature (Glynn and D'Cruz, 1990; Hughes and Connell, 1999; Whitney and Freeland, 1999; Fitt et al., 2001; Brown et al., 2002). To date, the study of potential effects of global climate change and inter-annual variation on coral reef communities have focused almost entirely on hermatypic (reef-building) corals, including "bleaching" events (Lough, 1998; Fitt et al., 2001; Brown et al., 2002; Loch et al., 2002). "Bleaching" events are a classic response of tropical hermatypic corals to a variety of environmental stressors (Fig. 6; Fitt et al., 2001).

The scientific community has recently begun to collect physiological tolerance limits of corals (Fig. 5), but data for reef fishes and non-structural invertebrates are almost non-existent (Urban, 1994; Mate, 1997; Mora and Ospína, 2001). Consequently, more direct measurements from coral reef communities, and knowledge of the upper and lower temperature tolerance limits of marine organisms, especially non-coral invertebrates and fishes, in the tropical oceans are necessary for future response predictions of these organisms to environmental, inter-annual, and global climate changes. Mora and Ospína (2001) examined the critical thermal maximum (CTM) of fifteen fishes from the tropical eastern Pacific Ocean. Their CTM ranged from 34.7 to 40.8 ºC, greater than temperatures recorded during the last El Niño event (averaging 32 ºC).

Although CTM data are useful as an indicator, other factors (e.g., magnitude and duration of high temperature exposure) are also important for predicting a fish's response and survival. For instance, temperature changes (e.g., increases) may affect immune system function, and decrease fecundity in coral reef fishes (Bevelhimer and Bennett, 2000; Mora and Ospína, 2001).

Coral bleaching and the loss of reef complexity may be a critical factor reducing abundances and biodiversity of invertebrates and fishes. Corals interact with fishes in a variety of manners. Some species forage on the gametes or larvae of corals (Prachett et al., 2001). Others use coral as refuge and protection, forage on non-structural invertebrates and fishes using corals, and eat algae that are overgrowing on corals, while many fishes provide nutrients to coral (Mora and Ospína, 2001; Prachett et al., 2001). In coral reef communities where intense bleaching has occurred, significant changes in the abundance of some fishes were observed (Table 1). Species intimately tied to live coral for shelter and sustenance have shown little recovery from severe bleaching events (Williams, 1986; Spalding and Jarvis, 2002).

Socio-economic Effects

In 2000, the world's fishery production (excluding aquaculture) totaled 130,434,000 metric tons (live weight; FAO, 2002). About 70% of the annual catch was eaten directly by people, while the rest was reduced to fish oil or meal, or processed into non-food products (e.g., jewelry, cosmetics, and pets; Miller and Johnson, 1989; FAO, 2002). Marine and estuarine fish provide an important portion of the world's food supply (UNEP, 1994). With global climate change, these fish will experience a change in their physical environment, as outlined in the previous sections. An inherent feature of climate is variability, although the ranges of variability may change, leading to less predictable marine resources (McGoodwin, 1992; Miller and Fluharty, 1992). Possible oceanic condition scenarios would produce three expected responses by motile fish: 1) areas where favorable conditions exist will increase in size, allowing a species to expand its range and/or proliferate; 2) areas where favorable conditions exist may move, causing a population's numbers to decline in certain areas and increase in others, effectively shifting the population's range; and 3) favorable conditions for a species may disappear, leading to a population crash and possible extinction. Each species has its physiological tolerance limits, optima, and ecological needs, thus within a community you can expect different responses from different organisms. Here we examine the environmental effects on fishing, rather than the fishing effects on populations. Because marine and estuarine systems are complex, and our knowledge of how they work is in its infancy, we can only speculate at the possible consequences of global climate change on their fishable stocks and the people who depend on them.

Harvesting fish is often connected to family and community traditions that may date back several thousand years (Ross, 1997). Generally, there are three types of harvesters who utilize fisheries resources: subsistence (artisanal) fishers, commercial fishers, and recreational fishers. Subsistence harvesters typically stay within their regional community, and fish mainly to feed themselves and their families, or to sell to local consumers. Fishing is often an expression of their cultural heritage, and the center of economic and cultural activity for an area (McGoodwin, 1990; Miller and Fluharty, 1992; Ross, 1997; Kramer et al., 2002). Commercial harvesters fish to earn money, and spread earnings throughout community and regional economies by paying for supportive services (e.g., equipment, boating supplies, fuel, etc.; Ross, 1997). Recreational harvesters (anglers) fish for the enjoyment of the outdoor experience or landing a fish, not out of necessity, and are usually from industrialized nations with time and money to enjoy fishing as a sport (Royce, 1987; Ross, 1997). These categories are not mutually exclusive; a subsistence or commercial fisher may enjoy the outdoors and the thrill of landing a fish just as much as a recreational angler. Conversely, recreational anglers may use their catch to feed themselves and their families. For our discussion on social and economic aspects of fisheries impacted by climate change, we will refer to these harvester groups as separate entities.

Subsistence Harvesters

In many parts of the world, particularly in non-industrialized countries, subsistence harvesters make up a substantial portion of the total harvesters. For example, in 1994 the total annual fish catch in Indonesia was 2.5 million metric tons, 90% of which was harvested by artisanal fishers (Kramer et al., 2002). Along with being part of a culture's identity, fisheries provide food for many people in certain regions, where local fish are the main source of animal protein (Miller and Johnson, 1989; McGoodwin, 1990). In the Southern Indian Ocean Biosphere Reserve in the Gulf of Mannar, approximately 1/3 of the population (ca. 200,000 people) depend on the sea to earn their livelihood, 90% of which rely on nearshore reef-related fisheries and seaweed resources (Wilkinson et al., 1999). In the Maldives, reef fishes are eaten by tourists and used as bait for fishers supplying tuna, the staple food for the region and main export (Wells and Edwards, 1989). Peruvian fisheries can be divided into artisanal and commercial fisheries, with the artisanal fishery consisting of about 50,000 people who typically have low socio-economic status, are self-employed, and consume and sell their catch locally (Pfaff et al., 1999).

Possible impacts of global climate change on artisanal fishers include changes in the current harvested fish stocks' distribution and abundance. As outlined in the previous sections, global climate change may alter oceanic currents and, consequently, the physical environment experienced by fish. Not only would these changes affect fish at the individual level (i.e., physiology), but changes would also have population-level effects. For example, changing currents may affect larval dispersal, retention, and recruitment. Larvae may be passively transported to unfavorable areas, decreasing recruitment and, consequently, stock size (Iles and Sinclair, 1982; Fortier and Leggett, 1984; Cowen et al., 2000; Soto, 2002). Temperature, along with other variables, causes active movement of mobile species to areas encompassing the preferred range of environmental variables, influencing migration patterns (Rose and Leggett, 1988; Murawski, 1993; Soto, 2002).

Artisanal harvesters typically do not have the necessary resources or equipment to fish areas far from their homes and, therefore, are forced to harvest local species. If species' ranges shift and/or migration routes change, fish that were once readily available to these fishers may become scarce or non-existent. On the other hand, fishes that once were not able to thrive in nearshore habitats, and therefore have not traditionally been utilized by the local people, may become more abundant. Artisanal harvesters may have to adapt their fishing habits (e.g., gear, methods, or species fished) in order to continue providing enough food for themselves and their families. Whereas commercial fishers typically exploit areas further from shore, artisanal harvesters tend to fish in areas that are more accessible from shore. Thus, in tropical areas, artisanal fishers utilize fish stocks that are dependent on shallow and near-shore coral reef systems. In the Minahasa district of North Sulawesi (Indonesia), artisanal harvesters mostly catch reef fishes (Kramer et al., 2002). If global climate changes create conditions that affect the coral reefs (e.g., temperature increases that cause bleaching), artisanal harvesters may witness a sharp decrease in exploitable fish stocks.

Commercial Harvesters

Globally, the open oceans are harvested by commercial fishers. Commercial fisheries contribute billions of dollars (US) to the worldwide economy and create thousands of jobs (Salz and Loomis, 2004). This includes people employed in harvesting, processing, and marketing, as well as those involved in producing supplies used in each of these. In the US alone, commercial fisheries produce billions of dollars in economic activity and employ over 300,000 people (Ross, 1997). The Peruvian commercial fishery employs approximately 20,000 individuals who staff fishing fleets, fish-meal plants, canneries, and large firms, that have diversified and now hold influence in all levels of government (Pfaff et al., 1999).

For many countries, commercial fisheries provide a large percentage of traded goods. In 2000, Seychelles, Maldives, Kiribati, Greenland, Iceland, and the Faeroe Islands had fisheries product exports that ranged between 54 and 94% of their total merchandise exported (FAO, 2002). Fisheries products also made up a substantial (10-35%) percentage of exported goods for Peru, Morocco, Panama, Viet Nam, Ecuador, Nicaragua, Belize, Guyana, and Madagascar (FAO, 2002). In 1999, the US had a domestic catch of 4,235,347 metric tons (live weight) valued at $3.5 billion (US). The exported portion of this catch brought in approximately $2.6 billion (US; USCB, 2002). In addition, the US also imported another 3,645,805 metric tons (live weight), worth an estimated $8.1 billion (US; USCB, 2002). Other countries, such as Samoa, Japan, and Micronesia, also are net importers, with 4-8% of their total merchandise imported consisting of fisheries products (FAO, 2002).

The money generated and the jobs created by the commercial fishing industry is obviously very important to the individuals involved and to countries that rely on fishery products exports. The overall economic importance of fisheries tends to be low in industrialized countries, but is important at the regional level (e.g., in Åland, Finland; Virtanen et al., 2001). In Finland, the total value of the commercial fisheries (including fishing, aquaculture, processing, and wholesaling) in 1997 was approximately $38,530,000 (US), 80% of which was contributed by marine fishing (Baltic herring, salmon, sprat, and cod; Virtanen et al., 2001). Although, this accounted for < 1% of the nation’s gross domestic product (GDP), there were 4200 registered fishers, with 1200 of them deriving > 30% of their total income from fishing (Virtanen et al., 2001).

As with the artisanal fishers, commercial fishers may experience a decrease and/or movement of stocks currently being exploited. Stocks may have different reactions to fishing pressure under changing environmental conditions, and many examples exist of climatic factors affecting fish stocks. For example, increased stratification of the oceans may lead to less primary production, which translates to less energy overall for fish production (Frank et al., 1990). The well-mixed waters will shift towards shallower zones, decreasing their overall area. This change will decrease suitable spawning habitat for many species, such as Atlantic herring (*Clupea harengus*), ultimately leading to decreased stock size (Frank et al., 1990). Changing currents may affect larval dispersal and retention (e.g., passively transporting larvae to unfavorable areas), also leading to decreased stock sizes (Iles and Sinclair, 1982; Fortier and Leggett, 1984; Cowen et al., 2000; Soto, 2002). Many species' successes may depend on their ability to disperse to more favorable habitats. It is widely recognized that temperature change causes mobile species to move and redistribute themselves into areas of thermal preference, potentially changing migration routes (Rose and Leggett, 1988; Krovnin and Rodionov, 1992; Murawski, 1993; Soto, 2002).

Large-scale climatic fluctuations, such as the NAO, have been shown to affect the timing of life history events of various species from phytoplankton to birds (Blenckner and Hillebrand, 2002). The NAO can also affect fish, directly or indirectly. For instance, when temperatures fluctuate, marked changes occur in the plankton community structure off of Britain's southwest coast and western English channel, and it is predicted that a latitudinal range shift of 322-644 km will occur with a 2 ºC increase in temperature. This would be accompanied by a restructuring of the planktonic, pelagic, and benthic communities, including fish (Southward et al., 1995). Many commercially important species, such as Atlantic cod, American plaice (*Hippoglossoides platessoides*), Atlantic halibut (*Hippoglossus hippoglossus*), cusk (*Brosme brosme*), redfish

(*Sebastes* spp.), Atlantic menhaden, butterfish (*Peprilus triacanthus*), and red hake (*Urophycis chuss*), off the eastern Canadian coast are predicted to shift their ranges due to redistribution and change in recruitment patterns (Frank et al., 1990). In the early 1990s, northern cod shifted their range southwards, following favorable environmental conditions and food sources (Rose et al., 2000). Fluctuations of Atlanto-Scandian herring populations in the Norwegian Sea have been attributed to intensity and temperature of the Norwegian Current (related to the NAO), which affects the distribution patterns of the larvae and juveniles, along with growth rates, maturation age, and recruitment (Krovnin and Rodionov, 1992). Regarding the harvesting of affected species, their ranges may shift to an area equally favorable for harvesting. Although, it is also possible that the areas to which their ranges shift either may be not feasible to fish or may require new equipment purchases for efficient fishing.

The predicted increase in major climatic events, such as ENSO (Timmermann et al., 1999; IPCC, 2001), may have drastic effects on fish stocks, especially when combined with other factors, such as overfishing (Pauly and Christensen, 1995). It has been suggested that reduced survival, reduced growth rate, and diversions of traditional migratory routes can all be caused by ENSO events, exacerbating the effects of intensive harvesting (Miller and Fluharty, 1992). This was the case with the Peruvian anchoveta fishery during the 1972-73 and 1997-98 ENSO events (Caviedes and Fik, 1992; Pfaff et al., 1999; Pontecorvo, 2000). Between 1960 and 1999, the anchoveta catch ranged from 12.3 to 23 thousand metric tons (Pontecorvo, 2000), and today accounts for 4% of Peru's gross national product (GNP) and $1 billion (US) in foreign exchange earnings (Pfaff et al., 1999). During the 1972-73 ENSO event, nearly 1,500 fishing boats and 200 fish-processing plants were forced to cease operations, causing more than 100,000 people to be unemployed (Jordán, 1991). In September 1998, during a particularly strong ENSO event, Peru's largest fishing port (Chimbote) had so many unemployed people that food was distributed to thousands of fishermen and their families (Pfaff et al., 1999). The 1983-84 ENSO is implicated in both the poor salmon harvest along the western coast of the US (and the subsequent economic distress of these fishers), and the strong salmon harvest in Alaskan waters (Miller and Fluharty, 1992). ENSO events temporarily displace individuals and shift populations, and introduce changes in reproductive physiology, egg and larvae survival, recruit and adult biomass, and fish schooling behavior (Jordán, 1991). If ENSO events become frequent, these temporary changes may become permanent.

Recreational Harvesters

It has been estimated that, in 1990, 36 million people over the age of 16 fished recreationally in the US (Ross, 1997). In 1991, 36 million anglers in the US fished for a total of 115 million days, 15% of which were spent in saltwater systems (Ross, 1997; Gentner and Lowther, 2002). The money spent while fishing produced the equivalent of 600,000 full-time jobs in tourism and recreation-based industries (Ross, 1997). In South Africa, almost 500,000 people participate in recreational fishing, providing 81% of the employment and generating 82% of the revenue from fishing activities (including commercial; Griffths and Lamberth, 2002). In the US, in 1991, anglers spent $24 billion (US; 25% of it in saltwater systems) to fish, including spending money on boats, motors, electronic equipment, rods, reels, lures, baits, supplies, marinas' services, fuel at gas stations, meals at restaurants, rooms at hotel/motels, and guides' and party-boat operators' services (Ross, 1997). Recreational fishing is variable according to region. For example, it has been modeled that if Florida was closed to recreational angling, it would experience a $4.3

billion loss (US; Gentner and Lowther 2002). If species popular to anglers shift their ranges to an extent that they cannot be found in traditional fishing areas (or near resorts and businesses that cater to anglers), these areas will suffer due to less money being put into local economies. In this case, the people supporting these recreational activities will be affected economically by global climate change more than the fishers, some of whom would travel to new fishery access points. Other regions may benefit from the influx of popular recreationally-fished species, as business niches are created in that area.

Marine Protected Areas

The active movement of fishes to more favorable regions as oceanic conditions change has implications for marine protected areas (MPAs). As food sources, currents, temperatures, and salinities change, fish are likely to move to more favorable habitats, rendering the anthropogenically-determined boundaries of MPAs useless. The range shifts of these fishes do not necessarily mean the population will be negatively affected, but their movement outside of designated MPA boundaries renders them more vulnerable to anthropogenic disturbances. Marine protected areas can serve dual functions as biodiversity conservation and fisheries management tools, and the “open” nature of fish populations and other marine organisms causes one to question whether there should be the establishment of networking marine reserves (Bohnsack, 1996). Soto (2002) provides a thorough review on the potential impacts of global climate change on MPAs.

Effects of Rising Sea Levels

Rising sea levels could be a particular threat to countries such as Bangladesh, Guyana, and the Maldives, and to low-lying islands like Tuvalu, Tonga, and Kiribati (Dickson, 1989). Most low-lying coral islands in the Pacific and Indian Oceans also have economies tied to coastal and marine systems, in the form of fishing and tourism (Wells and Edwards, 1989). In the Maldives, 45% of GNP stems directly and indirectly from tourism revenues (Wilkinson et al., 1999). It has been predicted that Subang's fish and shrimp harvest would be decreased by 4318 metric tons, affecting the livelihood of 14,500 households (Hunt, 1992). A rise in sea level would increase the depth of water above coral reefs (optimum being 2-30 m; Wells and Edwards, 1989). This would result in lower light penetration to support the photosynthetic algae living within the coral. If the water depth increases faster than the corals can grow, they could effectively "drown," destroying habitat for fish upon which many artisanal fishers are dependent (Wells and Edwards, 1989). Reefs are also vitally important as breakwaters (Wells and Edwards, 1989), and areas that have experienced coral die-offs due to temperature increases or anthropogenic disturbances, such as Sri Lanka, are now having to spend millions of dollars to develop and implement revetments, groynes, and breakwater schemes (Wilkinson et al., 1999).

Disease

Disease risks, for marine organisms and humans, represent another potential impact of global climate change. There have been studies linking human disease (e.g., human cholera) to changing ocean temperatures (Colwell, 1996; Pasual et al., 2000; Harvell et al., 2002) and climatic factors (Anderson, 1997; Hales et al., 1999; Epstein, 2000). Many pathogens are temperature-sensitive. For example, growth rates of marine bacteria and fungi are positively correlated with temperature (Shiah and Ducklow, 1994; Harvell et al., 2002), whereas certain cold-water salmonid diseases are favored by low temperatures (Holt et al., 1989; Harvell et al., 2002). In tropical areas, warmer waters may increase the susceptibility of fish (and other hosts) to pathogens because they are already expending energy dealing with thermal stress (Harvell et al., 2002). As with any organism, pathogens have preferred temperatures, and will expand or contract ranges depending on their tolerances. Range changes may affect biodiversity either by introducing a new pathogen or parasite to a population, or by releasing hosts from a major source of population regulation (Harvell et al., 2002).

Coral diseases may have wide influences on coral reef ecosystems. Three coral pathogens (*Aspergillus sydowii*, *Vibrio shiloi*, and Black Band Disease) grow well at temperatures close to or exceeding probable host optima, suggesting that their population sizes would increase in warmer waters (Harvell et al., 2002). Certain bacteria (e.g., *V. shiloi*) cause bleaching of certain coral species (e.g., *Oculina patagonica*), while fungi grow optimally at temperatures that coincide with thermal stress and bleaching in corals (Harvell et al., 2002). This may lead to a co-occurrence of bleaching and infection (Harvell et al., 2002). Along with disrupting the fish communities associated with these corals, the leftover dead coral surfaces can become colonized by macroalage, which support the proliferation of toxic dinoflagellates (de Sylva, 1994; Hales et al., 1999).

Ciguatera is the most frequent source of human illness caused by ingesting marine toxins, although many marine organisms produce toxins that affect humans (Hales et al., 1999). Ciguatoxins are produced by marine dinoflagellates that inhabit the surface of macroalgae. Herbivorous fish feed on this macroalgae, become contaminated, and the toxins bioaccumulate enough to cause illness when fish (e.g., groupers [Serranidiae], snappers [Lutjanidae], and jacks [Carangidae]) are consumed by humans (de Sylva, 1994; Hales et al., 1999). Fish poisoning is therefore related to physical disturbances of coral reefs, which are sensitive to changes in environmental variables such as temperature and pollutants (Hales et al., 1999). An increase in ciguatera poisoning was seen around French islands in the Indian Ocean and was linked to coral bleaching (Wilkinson et al., 1999). Annual reports of fish poisonings in the South Pacific are positively correlated with ENSO events, and there is a linear relationship between fish poisoning and sea-surface temperatures (Hales et al., 1999). Blooms of algae, called red tides, can also occur in marine and estuarine environments, causing poisoning of fish and humans eating contaminated fish (Anderson, 1997). These blooms are very variable, lasting anywhere from weeks to years, and can stay localized in a specific area, or can be massive, covering thousands of square miles (Anderson, 1997). More intense rains wash more fertilizer and sewage into coastal waters, and this runoff triggers algal blooms and consequent poisoning of fish and humans (Epstein, 2000). Countries that farm their coastal waters heavily (e.g., Japan, China, and Korea) are also exposed to economic losses from red tides (Anderson, 1997). Because poisonings and algal blooms have been correlated with ENSO events and excessive rain, their frequency and severity are likely to increase with the predicted increasing climatic variability associated with global climate change.

Although we have proposed many possible socio-economic effects of global climate change, they are based on statistical correlations and model-derived predictions. Although some fishers will suffer losses, others will experience gains. The shift in fish distribution may just shift the economic benefits to another group, resulting in no net loss. This is very hard to predict. Little peer-reviewed literature has been produced that directly connects global climate change with socio-economic conditions because these connections are all very complex and somewhat elusive. The research base needs to expand to elucidate the interactions among climate, biological processes, and socio-economic activities dependent on these processes (Miller and Fluharty, 1992).

Conclusions

Global climate change is impacting and will likely increasingly impact marine and estuarine fish and fisheries. Current data show global climate change effects ranging from changes in metabolic rates to changes in fish behavioral patterns in polar seas to fish community changes associated with bleached tropical corals. Projections of future conditions show further impacts on the distribution and abundance of fishes associated with a relatively small temperature change. Changing fish distributions and abundances will undoubtedly affect communities of humans who harvest these stocks. Harvesters (subsistence, commercial, recreational) may be impacted (negatively or positively) by changes in fish stocks due to climate change. Marine protected area boundaries, low-lying island countries dependent on coastal economies, and disease incidence (in aquatic organisms and humans) are also affected by a relatively small rise in temperature. The evidence on hand still includes many uncertainties about the future of affected fish species and their harvesters. Therefore, there is a great need for research on fish physiology and ecology, particularly in the tropics where relatively little research has been conducted. With a broader and deeper information base, researchers will be able to more accurately predict future situations.

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Table 1. Predicted changes in various fish populations associated with warmed habitats, according to geographical region.

Region	**Species**	**Prediction**	**Source**
Polar	North Sea cod, haddock, herring, and sardines	Possible shift in spawning times; alteration of bioenergetics; changes in transport of larvae	Svendsen et al., 1995; Alheit and Hagen, 1997; Ottersen et al., 2001
	Barents Sea cod and haddock	Changes in early life stages growth rates and recruitment levels	Ottersen et al., 1994; Ottersen, 1996; Ottersen et al., 2001
	Cod, haddock, plaice	Recruitment decreases off West Greenland with increasing temperature; changes in growth rates	Stein, 1991; Ottersen et al., 2001
Temperate	Pacific salmon *(Oncorhynchus spp.*)	Distribution shifts northward; changes in size; decreased population	Ishida et al., 2001; McFarlane et al., 2000; Swansburg et al., 2002
	Sockeye salmon *(O. nerka)*	Distribution shifts towards the sub-Arctic	Welch et al., 1998
	Skipjack tuna	Spatial shifts with temperature	Stenseth et al., 2002
	Atlantic salmon	Distribution and survival changes	Friedland et al., 1998
	Horse mackerel (*Trachurus trachurus* L.)	Distribution changes in accordance to food shifts	Reid et al., 2001
	Atlantic tropical reef spp.: porgies, snappers, sea bass	Species shift into new areas and change in abundance	Parker and Dixon, 1998
Tropical	Pacific reef spp.	Decreases in corallivore and coral nester abundance; increases in invertebrate feeders	Spalding and Jarvis, 2002

Figure 1. Earth’s radiation budget. Some energy is absorbed and re-radiated downwards by the atmosphere (from Gribbin, 1988 with permission).

Figure 2. Estimated changes in annual global mean temperatures (red) and carbon dioxide (green) from a 135-year period. Earlier values for carbon dioxide are from ice cores (dashed line) and for 1957 to 1995 from direct measurements made at Mauna Loa, Hawaii. The scale for carbon dioxide is in parts per million by volume (p.p.m.v.) relative to a mean of 333.7 p.p.m.v. (from Trenberth, 1997 with permission).

Figure 3. Highly simplified cartoon of the global thermohaline circulation. Near-surface waters (red) flow towards three main deep-water formation regions (yellow ovals) - in the northern Atlantic, the Ross Sea, and the Weddell Sea - and recirculation at depth. Deep currents are shown in blue, bottom currents in purple. Green shading indicates salinity above 36‰, blue shading indicates salinity below 34‰. (from Rahmstorf, 2002 with permission)

Figure 4. The variable effects of climate on oceanographic processes and production are shown. Signs (+/-) indicate the correlation between any two factors (modified from Soto, 2002 with permission).

Figure 5. Bleached and partly bleached *Acropora* sp., *Pocillopora* sp., and various reef fishes, including butterfly fishes, emperors, cleaner wrasse, and sturgeon fishes. The photo was taken at 15 m depth at St. Pierre, Farquhar Group, Seychelles, in April 1998. The temperature in the water was 31 to 34 ºC (from Wilkinson et al., 1999 with permission).

Figure 6. Coral physiological stress to two stressors, salinity and temperature. In combination, these factors profoundly diminish the photosynthetic capacity of this species. (from Porter et al., 1999 with permission).