Climate Change in the U.S. Atlantic Affecting Recreational Fisheries

L. A. KERR, W. J. CONNELLY, E. J. MARTINO, A. C. PEER, R. J. WOODLAND, and D. H. SECOR

University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, Solomons, Maryland, USA

This review provides an examination of the consequences of climate change in the coming century to saltwater sport fishing. We emphasized recreational fisheries in the U.S. Atlantic, but draw from the broader national and international literature where appropriate. Three themes were addressed: (1) climate change in the U.S. Atlantic, with a focus on increases in temperature, precipitation, sea level, the frequency and intensity of storms, and changes in ocean circulation; (2) the response of marine and estuarine fishes to climate change on an individual, population, and community-level; and (3) the response of marine and estuarine recreational fisheries to climate change. In addition, we provide strategies for the future of fisheries assessment and management in response to climate change.

Keywords climate change, Atlantic Ocean, fish populations, recreational fisheries

1. INTRODUCTION

Climate change along the Atlantic coast of the United States is predicted to affect atmospheric and water temperature, sea level, the frequency and severity of storm systems, and ocean circulation. Each of these factors has the potential to dramatically affect fish populations and the recreational fisheries they support (Table 1). For example, temperature increases of small magnitude can have significant impacts on fisheries resources in coastal environments, causing shifts in species distributions and altering the accessibility of a fisheries resource to specific fishing ports. Likewise, changes in precipitation and stream flow, which are closely linked to the reproductive success of anadromous species (e.g., American shad Alosa sapidissima and striped bass Morone saxatilis) can dramatically impact, both positively and negatively, the abundance of fish populations that are targeted by recreational fisheries. Increased intensity and frequency of storms can have negative effects on the early life history stages of fish, which are highly sensitive to rapid changes in environmental conditions, resulting in decreased abundance and catchability of recreationally important fish. Additionally, rising sea levels could adversely affect recreational fisheries directly by flooding and damage to recreational fishing facilities and indirectly by reducing the extent and quality of nearshore habitats important to many fish populations. The severity of climate change effects will depend on both the magnitude of climate change and the sensitivity of fish and fisheries to changing environmental conditions.

Recreational fisheries are of great social, cultural, and economic importance in the United States, with nearly 13 million individuals participating in marine recreational fisheries in 2006 (National Marine Fisheries Service [NMFS], Fisheries Statistics Division, personal communication). Recreational fishing contribute substantially to local economies, spending nearly $8.9 billion on saltwater fishing and related activities (primarily trip-related and equipment expenditures) in 2006 and generating $30 billion in economic benefits (USFW, 2006; American Sportfishing Association, 2008). The saltwater recreational fishing industry supports nearly 300,000 jobs in tourism and recreational fishing-associated industries nationwide (American Sportfishing Association, 2008) and, in the process, helps define the cultural identity of coastal regions. Sportfishing plays a particularly important role in the economy of Atlantic coast states, a region responsible for over 60% of saltwater fishing-related retail sales (American Sportfishing Association, 2008). Because of the economic importance of recreational fishing to Atlantic states, this region may suffer disproportionately from economic losses if climate change negatively impacts participation and effort in recreational fisheries.
### Table 1
Matrix of interrelated climate effects on fishes and possible impacts and responses of recreational fisheries. Potential impacts of climate change to fishes are denoted by lowercase letters. Superscript letters associated with impacts on fisheries and responses of fisheries correspond to the lettered impacts to fishes. Superscript numbers are impacts to and responses of the fishery that are independent of the impact to fish.

<table>
<thead>
<tr>
<th>Climate change</th>
<th>Impact to fishes</th>
<th>Impact on fisheries</th>
<th>Response of fisheries</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increase in temperature</td>
<td>a) Change in spatial distribution of fish populations (extension/contraction of range)</td>
<td>Increases/decreases in catchability and/or accessibility&lt;sup&gt;1,4,5,8,9&lt;/sup&gt;</td>
<td>Change in regional distribution of fishing&lt;sup&gt;6&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>b) Increased/decreased growth rate of fish</td>
<td>Economic losses (cool water fisheries) and gains (warm water fisheries)&lt;sup&gt;5&lt;/sup&gt;</td>
<td>Shift in target species&lt;sup&gt;6,7,8,9&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>c) Change in timing of migration and reproduction (early spawning season)</td>
<td>Increase in unpalatable and non-consumable catch&lt;sup&gt;5&lt;/sup&gt;</td>
<td>Management for increased/decreased fishery yields&lt;sup&gt;6,7&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>d) Habitat squeeze</td>
<td>Biomass and yield increase for some species and increase for others&lt;sup&gt;9&lt;/sup&gt;</td>
<td>Increased travel by individuals to fish for preferred species. Increase cost of</td>
</tr>
<tr>
<td></td>
<td>e) Change in reproductive success</td>
<td>Increased biomass at low trophic levels&lt;sup&gt;5&lt;/sup&gt;</td>
<td>retaining fish&lt;sup&gt;9&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>f) Increased prevalence of disease</td>
<td>Increased number of days with &quot;good&quot; weather conditions&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Increased/decreased effort and participation in the fishery&lt;sup&gt;6,7&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>g) Increased/decreased mortality rates and recruitment of fish populations</td>
<td></td>
<td>Change in timing and duration of the recreational fishing season&lt;sup&gt;6&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>h) Increased productivity at lower trophic levels</td>
<td></td>
<td>Changes in mode and gear of fishing&lt;sup&gt;8,9&lt;/sup&gt;</td>
</tr>
<tr>
<td>Increase in precipitation</td>
<td>a) Increased streamflow will have positive/negative effects on recruitment of</td>
<td>Increased number of days with &quot;bad&quot; weather conditions&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Increased number of days fished&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>anadromous species</td>
<td></td>
<td>Increased/decreased effort and participation in the fishery&lt;sup&gt;8&lt;/sup&gt;</td>
</tr>
<tr>
<td>Increase in sea level</td>
<td>a) Loss of fish habitat</td>
<td>Decreased catchability and accessibility&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Decreased number of days fished by anglers&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Increase in frequency</td>
<td>a) Increased mortality of early life stages</td>
<td>Flooding and damage to recreational fishery-associated facilities&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Decreased effort and participation in the fishery&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td>and intensity of storms</td>
<td>b) Advantages/disadvantages transport of larval stage fish</td>
<td></td>
<td>Relocation and economic losses incurred by fishery-associated facilities&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>c) Variable recruitment with different consequences to long- vs. short-lived species</td>
<td>Increased/decreased catchability&lt;sup&gt;1,4,6&lt;/sup&gt;</td>
<td>Decreased effort and participation in the fishery&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Damage to boats and shoreline facilities&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Decreased number of days fished&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

This article addresses the consequences of climate change in the coming century to recreational fisheries in the U.S. Atlantic. We focus on the Western Atlantic, with particular attention to the mid-Atlantic region (MAR). This region is likely to undergo large environmental and faunal changes because it represents a transition zone situated between the temperate northeast and sub-tropical southeast Atlantic. This region has a high diversity of recreationally important species, including several highly migratory fish. Further, many species occur at the limit of their range in this region. Thus, we propose that fish populations in the MAR will likely exhibit large responses associated with climate change. Here, we first provide a synopsis of likely climate change along the U.S. Atlantic coast, addressing temperature, precipitation, sea level rise, the frequency and intensity of storms, and ocean circulation. We then examine likely responses in resource populations at an individual, population, and community level. Based upon coupled fish and human responses to climate (Table 1), we suggest how recreational fisheries may respond in marine and estuarine environments.

## 2. CLIMATE CHANGE IN THE U.S. ATLANTIC

### 2.1. Temperature

#### Atmospheric Temperature

Recent predictions by the Intergovernmental Panel on Climate Change (IPCC) of temperature increase over eastern North America range from 2–7°C by 2100, depending upon the specific climate model and global population growth scenario used (Trenberth et al., 2007); however, all 21 climate models examined predict a minimum of 2°C increase by 2100. Researchers have refit these global models to allow for predictions to be made at regional scales and successfully calibrated them against historical observations and trends in temperature and precipitation for both the MAR (Polisky et al., 2009; Najjar, 1999) and the NE U.S. (Frumhoff et al., 2007). No such regional predictions are available for the SE U.S., but predictions for the entire Atlantic coast should be applicable (Trenberth et al., 2007). The range of temperature increase in air temperatures for the MAR by 2095, as given by the Hadley Center and Canadian Climate Center models, is 2.3 to 5.3°C (Polisky et al., 2000). Temperature increase for the NE was predicted using a high carbon dioxide emissions scenario and a low-emissions scenario developed by the IPCC. In the higher-emissions scenario, atmospheric CO₂ concentrations reach 940 ppm in 2100, whereas, in the lower-emissions scenario, concentrations reach 550 ppm in the same timeframe (Frumhoff et al., 2007). By 2099, the annual temperatures in the NE are predicted to increase by 3.6 to 6.9°C under the high-emissions scenario and 1.9 to 3.6°C under the low-emissions scenario (Frumhoff et al., 2007).

Based upon long-term environmental records, there exists considerable evidence that climate change has already occurred during the 20th century along the Atlantic coast. Mean air temperature in the MAR increased 0.5°C from 1895 to 1997.
CLIMATE CHANGE IN THE U.S. ATLANTIC AFFECTING RECREATIONAL FISHERIES

(Polsky et al., 2003). In the NE, annual temperatures have increased by nearly 1.0°C since 1900, most of which occurred since 1970 (Frumhoff et al., 2007). Much of the warming occurred during winter, which warmed 2.2°C since 1970 (Frumhoff et al., 2007). While annual and seasonal temperatures are increasing regionally and globally, the global diurnal temperature range (difference between daytime and nighttime temperatures) has declined by 2.6°C from 1979–2004 (Trenberth et al., 2007). Furthermore, 11 of the last 12 years have been among the warmest years on record worldwide since 1850 (Trenberth et al., 2007).

Water Temperature

Water temperatures in estuaries and in the coastal ocean have shown trends similar but dampened compared to the atmosphere (see reviews by Najjar et al., 2000; Frumhoff et al., 2007; Trenberth et al., 2007). The ocean’s large heat capacity and ability to redistribute heat plays an important role in climate change as the rate and distribution of warming is influenced by the uptake of heat by the ocean (Stanton, 1991). Increasing water temperatures have been documented over the last century, with shallow water environments, such as estuaries, showing a higher magnitude response to warming compared to continental shelf waters. Increasing surface water temperatures have been observed at the Patapsco River, Chesapeake Bay, U.S. (Chesapeake Biological Laboratory), based on measurements from 1938–2006. This 69-year temperature record reveals an increase of 1.5°C or 0.22°C per decade when averaged across all seasons (D. Secor and R. Wingate, personal communication). However, winter and spring exhibited even higher rates of temperature rise, ~0.5°C per decade during the most recent 20 years. Sea surface temperatures along the continental shelf of the NE have also increased, although to a lesser degree, by 0.6°C during the 20th century (Frumhoff et al., 2007). Additionally, there are geographic patterns in warming showing increased warming at high northern latitudes (Meehl et al., 2005).

Projections of water temperature increase require an understanding of the heat capacity of water, air-sea heat flux, circulation, and mixing; limits in our understanding of these processes contribute to uncertainty in modeling future climate change (Stanton, 1991). Under the high carbon dioxide emission scenario, sea surface temperatures are expected to increase 3.3 to 4.4°C by 2099 and 2.2 to 2.8°C under the low-emissions scenario in the NE U.S. (Frumhoff et al., 2007). Similar rates of change are expected for the MAR (V. Celes and D. Kimmel, personal communication). Chesapeake Bay water surface temperatures are predicted to increase 1.7 to 2.2°C by 2050 and 2.5 to 4.7°C by 2090 (V. Celes and D. Kimmel, personal communication).

2.3. Frequency and Severity of Storm Systems

Ocean-atmosphere models predict that global warming will cause increased storm intensity globally (Emanuel, 2005a, 2005b; Trenberth et al., 2007). A significant positive trend in the potential destructiveness of hurricanes has occurred since the mid 1970s. This trend is reinforced by the conspicuous increase in both numbers and proportion of hurricanes worldwide reaching category 4 and 5 levels (Trenberth et al., 2007). North Atlantic hurricane activity has also been above normal in 9 of the last 11 years (Trenberth et al., 2007). Further, in 2005 the North Atlantic experienced the most active tropical storm season on record (Levinson, 2005).

Although it is difficult to attribute increased storm activity throughout the world to global climate change, a growing body of evidence supports the argument that global warming is responsible. For instance, sea surface temperatures have already increased throughout the world’s oceans (Levitus et al., 2000; Barnett et al., 2001, 2005; Biadoff et al., 2007), and this is generally accompanied by increased water vapor in the lower atmosphere. Increased water vapor in turn results in additional energy to fuel convection and thundersstorms (Trenberth et al., 2007). But, many other factors, such as wind forces in the atmosphere, determine where storms form and what path they follow. More direct evidence of the link between global warming and storm activity is based on a power dissipation index (PDI) that largely reflects recorded wind speeds. The PDI shows significant positive trends (power increasing by 75%) within the North Atlantic beginning in the mid 1970s (Emanuel, 2005b), indicating longer storm lifetimes and increased storm intensity. Further, the PDI has a strong association with tropical sea surface temperatures and, as such, supports the link between recent storm activity and global warming (Trenberth et al., 2007).
2.4. Sea Level

Global sea level rise is a result of several factors, but is primarily driven by the thermal expansion of seawater and melting of ice from glaciers and land (Trenbath et al., 2007). The magnitude of sea level rise at particular locations will largely depend on the degree of land subsidence, a result of both the extraction of groundwater and glacial rebounding (Gaffin, 1997). Land subsidence is occurring in many locations along the Atlantic coast, accelerating the rate of sea level rise for these areas (Gaffin, 1997).

Sea levels are rising along the U.S. Atlantic coast and will continue to rise throughout this century. Forecasted rates of sea level rise are lowest in New England, higher in southern states, including Florida, and highest in the MAR (Thieler and Hammar-Krøse, 1999). Sea levels in the MAR are rising at almost two times the global average, rising at 3-4 mm per year due to land subsidence (Titus and Narayanan, 1995). Compared to 1996 baseline levels, sea level in the mid-Atlantic coastal region is expected to rise 19 cm by 2030 and 66 cm by 2095 (Warrick et al., 1996; Najjar et al., 2000). However, these estimates are being re-evaluated based on new evidence showing increased rates of Antarctic ice melting (Stroeve et al., 2007) and decreased efficiency of carbon dioxide uptake and storage in the southern ocean (Le Quéré et al., 2007). In light of these recent findings, current predictions of sea level rise could be best-case scenarios and higher levels might be more likely.

2.5. Impact of Climate Change on Coastal and Oceanic Circulation

Large-scale water movement along continental coasts is driven by interactions among wind forces, tides, and differences in density between water masses (Epifanio and Garvine, 2001). Differences in density can arise from lower-salinity flow emanating from estuaries, heating and cooling of surface waters, and the interaction of coastal and oceanic water masses (Epifanio and Garvine, 2001). Wind-driven circulation and buoyancy-driven flow are the primary forces that influence the passive transport of fish larvae, and both forces can be affected by global climate change. For example, in the MAR Atlantic, menhaden, blue crab, and bluefish utilize these physical forces for across-shelf transport in the MAR and South Atlantic Bight (Epifanio and Garvine, 2001). A southwestern buoyant flow occurs close to shore as a result of lower density water exiting the Hudson, Delaware, and Chesapeake estuaries (Figure 1; Epifanio and Garvine, 2001). Farther offshore on the continental shelf, wind-driven flow dominates, with the direction of this flow depending upon the direction of prevailing winds (Figure 1; Epifanio and Garvine, 2001). At the edge of the continental shelf is the Gulf Stream (Figure 1), a strong, wind-driven current (Wunsch, 2002) that begins in the Gulf of Mexico, and flows through the Florida Strait northward along the southeast coast of the U.S. (Lund et al., 2006). Climate change will influence ocean circulation through changes in temperature and salinity of water masses that affect the density of water masses and shifts in the direction and intensification of wind-driven circulation (Epifanio and Garvine, 2001; Toggweiler and Russell, 2008). Warmer temperatures and regional decreases in salinity have been documented. The temperature of the upper 700 m of the ocean has increased since 1955 (Levitus et al., 2000; Barnett et al., 2001, 2005; Bindoff et al., 2007), and there is evidence that the temperature of the world ocean down to 3000 m has increased (Bindoff et al., 2007). Additionally, the salinity of the coastal ocean near Labrador and Greenland has been decreasing as a result of increased precipitation, as well as increased glacial melting and runoff (Bindoff et al., 2007). Climate models have predicted that warming ocean temperatures and a freshening of the oceans may dampen thermohaline circulation; however, there is no evidence of this occurring to date (Toggweiler and Russell, 2008). Strengthening of wind intensity may be compensating for the effects of slowed ocean circulation due to density differences (Toggweiler and Russell, 2008). There is still much uncertainty regarding the effects of global climate change on ocean circulation (Bindoff et al., 2007; Trenberth et al., 2007); however, changes in ocean circulation will have implications for locations of fish spawning grounds, reproductive success, and larval transport (Drinkwater et al., 2003).

2.6. Separating the Effects of Natural Climate Variability from Anthropogenic-Induced Climate Change

Large ocean currents are primarily wind and buoyancy driven, but teleconnections—complex interactions between atmospheric and oceanic circulation—that also influence the variability of these currents in a number of ways. Two teleconnections that influence the climate and fisheries of the United States are the El Niño/Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO), both of which have exhibited multi-decadal changes during the 20th century (Trenberth et al., 2007). These oscillating climate patterns control annual variability in regional weather, complicating the detection of long-term climate change. Teleconnections can explain up to 44% of the observed northern hemisphere temperature increase since 1935 (Hurrell, 1996). However, the variability of the teleconnections cannot be used to explain the warming that has occurred from 1999 to the present (Hurrell et al., 2003), indicating that human-induced warming has been accelerating and now overwhelms many natural signals.

3. RESPONSE OF MARINE AND ESTUARINE FISHES TO CLIMATE CHANGE

The numerous environmental changes expected under climate change will affect fish populations and communities in
complex ways depending on the geographic region, a species' tolerance to environmental change, life history requirements (e.g., spawning and feeding migrations), and predator-prey relationships. Because warming is the most certain of future climate changes and has well-known effects on fishes, we focus primarily on the effect of temperature change on fish. Other changes in climate that will likely affect fishes include increased precipitation, sea level rise, storm frequency and intensity, and changes in ocean circulation, which will be given additional discussion where appropriate. Beyond the direct effects of climate change on water quality and habitat availability, fish will also respond to indirect effects such as changes in the abundance and distribution of predators and prey.

3.1. Individual Fish Responses

The ability of a species to successfully grow and reproduce depends on its tolerance range, which is bounded by upper and lower thresholds of environmental conditions that define the habitat suitability for a given species (Fry, 1971). Pertinent environmental conditions include water temperature, dissolved oxygen concentrations, salinity, and water acidity. Long-term disruption of environmental conditions, as expected under most climate change scenarios, can make habitats less productive or completely unsuitable for fish, especially in nearshore areas. Additionally, the prevalence of disease in individuals may increase as environmental conditions are altered, habitat availability decreases, and conditions become stressful.
Physiology

Laboratory and field studies indicate that fish growth is heavily influenced by water temperature. As water deviates from a fish’s optimum temperature, growth decreases from a maximum, either due to depressed metabolic rates at lower temperatures or the increased cost of oxygen respiration at higher temperatures (Wootton, 1998). Changes in thermal optima and energy partitioning often occur through ontogeny, with older, larger fish typically tolerating a wider range of temperatures than smaller larvae or early juveniles (Haines and Able, 2001). Striped bass from the mid-Atlantic exhibit different temperature tolerances across life stages, with tolerance ranging from 14–23°C for egg stage, 10–25°C for larval stage, 10–27°C for juvenile, and 9–30°C for adult striped bass (Fay et al., 1983). Thus, the effect of increasing temperature will depend on the physiological tolerance of individual life stages as well as the availability of suitable habitat.

In addition, species with overlapping distributions often exhibit divergent optimal temperature ranges (Figure 2). For example, optimal growth of juvenile striped bass occurs between 18.5 and 28°C, depending on the latitude of the nursery along the Atlantic Coast (Cox and Coutant, 1981; Hartman and Brandt, 1995; Spero et al., 2000). Growth rate declines at temperatures greater than 29°C, and fish begin to lose weight at temperatures greater than 33°C (Cox and Coutant, 1981). In the case of juvenile bluefish Pomatomus saltatrix and weakfish Cynoscion regalis collected from Chesapeake Bay, optimum growth occurs at 20°C and 23.5°C, respectively (Hartman and Brandt, 1995). Increasing temperatures beyond the optima for these two species lead to weight loss at 30°C for bluefish and 27°C for weakfish (Hartman and Brandt, 1995). These examples illustrate differences in the responses of co-occurring species to summer temperatures in coastal nursery habitats.

While temperate species typically experience declining growth with increasing temperatures, tropical and subtropical species have elevated thermal ranges and optimum temperatures, and are likely to benefit from seasonal increases in water temperatures in temperate Atlantic regions. In the case of the subtropical red drum Sciaenops ocellatus, growth of larval and juvenile red drum increases up to 32°C (Brightman et al., 1997; Rooker and Hoit, 1997). Similarly, juvenile mullet grow more rapidly when held at 25–30°C than 20°C (Peterson et al., 2004). Additionally, adult spotted sea trout Cynoscion nebulosus along the Atlantic coast migrate offshore to avoid low temperatures, and spawning from Texas to Florida is restricted to waters ≥21°C (Lassuy, 1983). These relationships suggest that these and other subtropical species may benefit from warming of temperate U.S. coastal and estuarine areas, potentially experiencing higher growth and survival rates. However, it is important to note that we are only emphasizing direct temperature effects on growth, without considering coincident changes in prey or other food web properties. Food web changes are far more difficult to predict and could mask direct temperature effects on fish growth rates by changing foraging conditions (Ries and Perry, 1995).

Fish rarely respond to only a single factor such as temperature in their environment; rather, it is usually the interaction of multiple factors that control metabolic responses. For instance, warm water absorbs less dissolved oxygen than cooler water,
and because warmer temperatures raise the oxygen demand of fish and other components of the ecosystem (e.g., phytoplankton and microbes), hypoxic or anoxic conditions in estuarine and other inland coastal waters can occur during summer months. The combined effects of rising temperature and decreasing oxygen will alter habitat suitability for fish and their prey (e.g., amphipods; Wu and Or, 2005). In extreme cases, interactions between temperature and oxygen can result in acute stress and fish kills. Less severe environmental stress can still be lethal by forcing fish out of preferred habitats and into smaller less suitable areas (i.e., habitat squeeze), where predation risk or competition may be high (Coutant, 1985; Shimp et al., 2005; Reist et al., 2006).

In a review of striped bass distribution under several climate change scenarios, Coutant (1990) found that productive southern estuaries may no longer provide suitable nursery habitat due to increasing temperatures, especially in summer. Rising temperatures can lead to unsuitably warm surface and shallow water, as well as hypoxic conditions in bottom water through a variety of physical and biological mechanisms (Figure 3). Together, these habitat constraints may preclude summertime survival in the northern Gulf of Mexico and Florida waters (regions at the species’ southern range), while reducing the overall contribution of the Chesapeake Bay nursery to the adult stock, a region of historically high abundance for this species (Coutant, 1990). Additionally, high densities of fish in the few remaining suitable areas can increase the risk of disease and parasitic infestation, contributing additional stress to fish that are already compromised physiologically. Because early life stages are generally more sensitive to environmental changes, they may be more severely impacted by these types of habitat squeezes.

3.1.1 Reproduction

To maximize the probability of reproductive success, fish have evolved reproductive cycles that are timed to seasonal events in specific locations. Timing of reproduction likely has two components: an endogenous cycle (i.e., driven by internal factors such as hormones) and behavioral mechanisms that synchronize this cycle with environmental cues such as temperature or photoperiod (Wooton, 1998). Historically, photoperiod was believed to be the dominant external cue driving reproductive timing (van der Kraak and Pankhurst, 1997, Brotzage, 2001); however, current research suggests that temperature is likely the more important cue among most temperate species (Bye, 1984; Horvath, 1986). For example, recent experiments on striped bass show that the onset and progression of maturation is regulated by water temperature, even when photoperiod is held constant (Clark et al., 2005).

Given the influence of temperature as a reproductive cue for many fishes, climate change is likely to impact reproductive cycles. To date, Lake Geneva (jurisdiction in France and Switzerland) provides the backdrop for the only known research that shows direct evidence for the effects of global warming on fish reproductive timing. During the period 1980–2000, the roach Rutilus rutilus, a recreationally important fish of the minnow family, developed ovaries faster and spawned earlier in more recent and warmer years (Gillet and Quelin, 2006). Surprisingly, this change coincided with a mere 1°C increase in annual surface water temperature. Warmer winter temperatures in particular were associated with earlier egg ripening (Gillet and Quelin, 2006). Future research will be necessary to determine the extent to which the results for roach apply to other species, but it is clear that global warming can have substantial effects on reproductive timing and possibly on overall reproductive success.

Disease

In recent decades, reports of diseases affecting marine organisms have increased globally (Williams and Bunkley-Williams, 1990; Ward and Lafferty, 2004; Havell et al., 2004). Although several climatic or anthropogenic factors are possible, there is accumulating evidence that increasing water temperature is an important factor influencing the prevalence of some marine
diseases. Growth rates and reproduction of potential pathogens such as marine bacteria (Shiah and Ducklow, 1994), fungi (Holmquist et al., 1983), and parasites (Barse and Secor, 1999) increase with temperature. Thus, the severity of infections or infestations of fish is expected to increase with temperature (Lafferty et al., 2004).

Although disease incidence among many types of marine taxa (e.g., eelgrass, shrimp, fish, turtles) has been linked to temperature, the best known cases come from corals and oysters. For example, elevation of water temperature by as little as 1°C has contributed to coral bleaching, the result of corals expelling zooxanthellae that normally live symbiobically within their tissue (Goreau and Hayes, 1954; Brown, 1997; Bellwood et al., 2004). Additionally, the northern expansion of several oyster diseases (e.g., Dermo and MSX) has been linked to warming temperatures (Powell et al., 1996; Cook et al., 1998; Hofmann et al., 2001). Although the impact of global warming on corals and oysters do not directly affect recreational fisheries, these living reefs harbor important food resources and provide refuge for early-life stages of important recreational species. Therefore, any negative impacts to these reefs are expected to have indirect effects on fish populations and fisheries that depend upon them. Loss of living coral is associated with less diverse fish assemblages than those that existed prior to bleaching, sedimentation, and starfish outbreaks (Jones et al., 2004). Oyster reefs are also well known for their historical association with and valuable habitat function for many important species in the U.S. Atlantic region such as striped bass, black drum (Harding and Mann, 2001).

Curiously, a recent study that surveyed reports of disease across nine marine taxonomic groups found that disease reports for bony fish actually decreased during the past 30 years, in contrast to increased or similar disease levels documented for corals, seagrasses, sea urchins, mollusks, crustaceans, sharks/rays, turtles, and mammals (Ward and Lafferty, 2004). One possible explanation is that disease transmission is lower among many fish species due to low abundances caused by years of fishing pressure (Ward and Lafferty, 2004). Another explanation is that some stressors, such as temperature, may have greater negative effects on the disease agents than the potential hosts (Ward and Lafferty, 2004). For example, signs of infection of coldwater disease in Pacific salmonids (Chinook salmon Oncorhynchus tshawytscha, coho salmon Oncorhynchus kisutch, and rainbow trout Oncorhynchus mykiss) occur between 4°C and 10°C and disappear at water temperature greater than 10°C (Hol et al., 1989). Thus, although Pacific salmon tolerate temperatures above 10°C, the bacteria that cause coldwater disease will die.

Fish are also affected by harmful algal blooms, which appear to have increased globally in the past several decades coincident with warmer water temperatures (Mudie et al., 2002; Edwards et al., 2006), and can serve as a disease vector for humans. For example, ciguatera poisoning is caused by consuming fish that contain ciguatoxins. These neurotoxins are produced by marine dinoflagellates, which live on the surface of seaweed species (Baden et al., 1995). Plant-eating reef fish become contaminated when feeding, and the toxins bioaccumulate as they move up the food chain (Baden et al., 1995). Higher incidence of ciguatera poisoning was observed in the South Pacific concurrent with higher sea surface temperatures associated with El Niño conditions (Hales et al., 1999). Thus, warmer conditions in regions that support ciguatoxin-producing organisms could lead to increased health risk to anglers.

3.2. Population Level Response

As environmental conditions change, the habitat requirements and preferences that we observe at an individual fish level translate to distributional shifts of entire populations and species (Pearson and Dawson, 2003). This prediction is supported by large regional shifts in the distribution of fish populations over decadal periods of environmental change (Murawski, 1993; Davis and Shaw, 2001). In extreme cases, reduction in available habitat could result in extirpation of fish species. Because of the critical role temperature plays in cueing fish behaviors, population level responses to climate change will include shifts in the distribution, migration patterns, and recruitment of fishes.

Range Expansion and Contraction

Whether or not a population shifts its distribution in response to climate change depends on whether the new conditions fall within the tolerance limits of the species. There are three basic responses a population can exhibit under changing climatic conditions: range expansion, range contraction, or no response. Range expansion is typically associated with temperate, sub-tropical, or tropical species, which have temperature tolerances that overlap with temperatures in temperate and boreal waters (Kennedy, 1990; Shuter and Post, 1990). The ranges of northern temperate and boreal species, such as North Atlantic cod (Gadus morhua; Rose, 2005a) and Atlantic salmon (Salmo salar; Power, 1990), are predicted to contract toward the poles with increasing temperatures, especially in light of larger temperature changes predicted for northern latitudes (Trenberth et al., 2007).

Expansion and contraction can occur simultaneously for a population or species as habitats are lost at one end of its distribution and gained at the other end. In this case, a species may maintain a relatively constant latitudinal range that is simply north-shifted to account for the overall northward shift of temperature thresholds (here we are referencing Northern Hemisphere changes only). Some populations may exhibit little to no response in their distribution to climate change. This is most likely to occur when (a) the new conditions lie within a species' tolerance range, or (b) the negative effects of climate change are compensated by other factors such as increased prey availability, increased reproductive success, or decreased predation pressure (Pearson and Dawson, 2003; Perry et al., 2005).
In order for a species to shift its distribution in response to climate change, populations must be able to relocate and move in concert with changes in the environment. Thus, sedentary species or fish that associate with a specific habitat may be more negatively impacted by climate change than migratory fish (Murawski, 1993). Additionally, as fish colonize new environments, they face new food webs: changes in the suite of predators, competitors, and prey. For example, several key forage species of the northwest Atlantic Ocean (e.g., short-finned squid Illex illecebrosus, Atlantic mackerel Scomber scombrus, Atlantic herring Clupea harengus) shift their distributions northward or southward depending on annual water temperatures (Murawski, 1993). More mobile predators, such as bluefish and summer flounder Paralichthys dentatus, will be able to shift in concert with the forage base, while more sedentary predators such as Atlantic cod may be less flexible. Similarly, reef-based fish that are strongly associated with structure (e.g., black sea bass Centropristis striata, tautog Laturus acutus) are expected to lag behind the distributional shifts of prey species under changing environmental conditions. In some cases, populations or species that lack the means to easily shift their overall range could become extirpated. For example, estuarine-dependent fish that are restricted by salinity tolerance from marine migrations (e.g., white perch Morone americana) will be unable to colonize more northerly estuaries as temperatures increase and the habitat available to them in the estuary is reduced (Kennedy, 1990). This could lead to species extirpation and reduced species diversity in a given estuary or coastal region.

Although global temperature change is unlikely to be reversible over the next hundred years, biological responses by fishes and marine food webs can show resiliency to climate change. A fish population that has been exposed to a new environmental stress can remain stable in its current condition or be forced toward a different stable ecosystem state from which it cannot directly return to the previous one: an ecological phenomenon termed hysteresis.

Extirpation

Populations at the southern end of a species range are likely to be most strongly affected by climate change, particularly to the direct effects of increasing temperature. Many species across diverse taxonomic groups (i.e., corals, insects, amphibians, birds, mammals) have already suffered large-scale contractions in range due to recent climate warming (Parmesan, 1996; Hoegh-Guldberg, 1999; Pounds et al., 1999; Croxall et al., 2002; Beever et al., 2003). Some equatorial species are now extinct (e.g., cloud-forest dependent amphibians, tropical corals); of those species that persist, some have either failed to expand to higher latitudes or are unable to expand due to geographic barriers (Parmesan, 2006). These absolute reductions in range size put species at greater risk of extinction in the near future (Parmesan, 2006).

Range reductions due to decreased abundance at lower latitudes are currently most evident in boreal and polar species, which typically have greater latitudinal range restrictions than more temperate species. Fish species in this group generally exhibit narrower ranges of temperature preference and tolerance, and thus have reduced capacity to adapt to the effects of warming climate (Reist et al., 2006). In addition, higher latitudes have warmed more than lower latitudes in the past half century (Roo et al., 2003; Trenberth et al., 2007), and thus impacts may be greater for species with ranges nearer the poles.

North American Atlantic salmon, which ranges from distribution extending from Connecticut to northern Quebec, represents a stenothermal coldwater species that may have already shown local extinctions due to global warming. Local extinctions have been witnessed in the Connecticut and Merrimack Rivers, and most populations in Maine are endangered (NRC, 2003). Poor juvenile production and low stock abundance have been associated with warm surface water temperatures (SST) in the spring off the coasts of northeastern U.S. and Nova Scotia (Friedland et al., 2003) and in their overwintering environment near the Grand Banks (Condron et al., 2005). Warmer ocean conditions are associated with poor post-smolt survival, and this association is thought to be due to insufficient food to support increased metabolism at warmer temperatures (Friedland et al., 2005). Although the historical declines (beginning in the mid-1960s) and localized extinctions at the southern end of the range in North America may or may not be related to climate change (Parrish et al., 1998), the negative correlation between SST and post-smolt survival suggests that increases in ocean temperatures could lead to further declines and localized extinctions in Maine and other southern populations unless Atlantic salmon are able to adapt quickly to local changes.

Although cold-water, stenothermal species are likely more prone to extirpations in their southern range, cool-water and even warm-water species may also face extirpation risk in southern latitudes with continued climate warming. For example, the Atlantic sturgeon Acipenser oxyrhynchus), which has a wide distribution from Florida to Labrador, is considered a cool-water species due to its sensitivity to warmer temperatures. Existence in more southern latitudes is made possible by thermal refuges in deeper, colder portions of estuaries. However, as shown in a model simulating juvenile Atlantic sturgeon summertime habitat in the Chesapeake Bay, increases in temperature due to warming by as little as 1°C can lead to significant reductions in suitable habitat (Niklitscheck and Secor, 2005). Furthermore, increases in temperature are likely to be accompanied by decreases in dissolved oxygen and increases in salinity in deeper water, which may lead to additional reductions in suitable habitat. Thus, even temperate species with relatively wide geographic distributions can face large population declines and possible extirpations with moderate increases in temperature.

Fish Migration

Many recreationally important species, including salmonids, tunas, striped bass, bluefish, and shads exhibit long-distance
migrations. For these species, movements between different habitats are related to seasonal changes in temperature. Temperature-related movements are often associated with seasonal prey availability and changes in feeding requirements. In addition, spawning migrations for many species are linked to changes in water temperature, effectively timed to provide the best chance of growth and survivorship for their offspring. Both predators and prey respond to temperature cues, and climate change can cause migrations to be displaced or occur out of synchrony with prey availability. Indeed, the temperature triggers for spawning are thought to have evolved to ensure that first-feeding larvae are produced in synchrony with plankton blooms, which support early growth and survival.

Climate and other factors that cause mismatches between the production of larvae and feeding conditions can contribute to lower or failed reproductive success for a population of fish. For example, American shad move north along the Atlantic seaboard in the spring, staying in their preferred water temperatures of 13–18°C (Leggett and Whitney, 1972). American shad spawn within a specific temperature range (14–23°C) in freshwater portions of rivers and estuaries along the Atlantic coast, and their timing of spawning matches the temperature when food for their young is most likely to be abundant (Walburg and Nichols, 1967; Leach and Houde, 1999). Additionally, temperature acts as a key stimulus in the initial oceanic migration of Atlantic salmon smolts (Jonsson and Ruud-Hansen, 1985; Holtby et al., 1990; Salminen et al., 1995). This temperature cue presumably indicates favorable survival and growth conditions in adjacent coastal habitats, reducing the likelihood of entering the ocean at inopportune times and enhancing the chances of survival (Jonsson and Ruud-Hansen, 1985; Holtby et al., 1990; Salminen et al., 1995). Temperature also serves as a cue for movement into estuaries for many juvenile fish that are spawned at sea, including recreationally important species such as bluefish, Atlantic croaker Micropterus undulatus, spotted Leithosomus xanthus, and red drum (Maes et al., 2005).

Given the strong role of temperature in cueing fish migrations, there can be little doubt that global warming will alter migrations. For example, spawning migrations by Atlantic salmon in the Connecticut River are now over 10 days earlier than in 1978, corresponding to warming in that watershed (Juanes et al., 2004). In the Columbia River, American shad migrated more than five weeks earlier in 1993 than in 1949, corresponding to a long-term warming trend in the Columbia River (Quinn and Adams, 1996). Sockeye salmon Oncorhynchus nerka in the same river have also shifted their spawning runs to earlier dates, albeit not to the same degree. Climate change is not solely responsible for the warming of the Columbia River; dams too have played a large role in causing warmer conditions (Quinn and Adams, 1996). Still, the correlation between migration timing and temperature change observed in the Columbia River forecasts the likely influences of global warming on fish migrations.

Long-distance oceanic migrations, such as bluefin tuna Thunnus thynnus, can also be responsive to climate change. Long-term fluctuations in Atlantic bluefin tuna trap catches collected from Mediterranean trap fisheries appear to be closely related to long-term trends in temperature, suggesting shifts in migratory patterns associated with changes in climate (Ravier and Fromentin, 2004). In the Pacific Ocean, there is evidence for climate (and associated SST) induced changes in an important prey species, Japanese sardine Sardinops melanostictus (Yasuda et al., 1999), which in the recent decades has been associated with increased trans-oceanic migration of Pacific bluefin tuna Thunnus orientalis (Polovina, 1996). Associations between catches and sea surface temperature have also been shown for skipjack tuna (Katsuwonus pelamis; Fiedler and Bernard, 1987), yellowfin tuna (Neothunnus macropterus; Zagaglia et al., 2004, Torres-Orozco et al., 2006), and swordfish (Xiphias gladius; Podesta et al., 1993).

Global warming may differentially influence the migrations of southern versus northern populations of a species, especially if higher latitudes continue to warm more rapidly (Root et al., 2003). One of the earliest observations of latitudinal trends in migrations was among American shad populations. This species spawns earlier in southern latitudes than northern latitudes, resulting in upriver spawning migrations that occur at relatively consistent temperatures (15.5–20.0°C) at each location (i.e., St. Johns River, Florida; York River, Virginia; Connecticut River, Connecticut; Leggett and Whitney, 1972). These latitudinal trends place the maximum number of spawning adults on the spawning grounds when the temperature is optimum for the survival of eggs and larvae (Leggett and Whitney, 1972).

In contrast to American shad, sockeye salmon spawn in interior streams and lakes that require more distant migrations. Sockeye salmon exhibit the opposite trend to shad, migrating earlier at northern latitudes than southern latitudes (Hodgson and Quinn, 2002). Here, migrations likely occur earlier due to the longer egg incubation times in the colder waters associated with northern latitudes (Hodgson and Quinn, 2002). To hatch at the appropriate time in an environment suitable for larval and juvenile growth and survival, spawning must occur earlier in northern latitudes.

Although the consequences of global warming among southern and northern populations can only be speculated given the current state of our knowledge, some predictions can be made in light of the present trend of greater warming at higher latitudes. For instance, American shad in the Connecticut River and York River, which spawn as temperatures begin to increase in the early spring and early summer, respectively, will likely begin migrating and spawning earlier, much like those in the Columbia River example discussed earlier. However, shad spawn at southern latitudes, such as in the St. Johns River, Florida, may actually spawn later, as they typically spawn during late autumn and winter, when temperatures are falling (Leggett and Whitney, 1972). In addition, if temperatures warm faster at northern latitudes, the rate of change in the timing of migration may be much greater in the Connecticut River than the St. Johns River.

For sockeye salmon, which display strong genetic control (and thus less environmental control) over the timing of migrations (Quinn and Adams, 1996), migration timing may not
change as rapidly as the timing in American shad. Thus, if they are unable to adjust their spawning with changing temperatures, sockeye salmon at northern latitudes may spawn at inopportune times, leaving fry to hatch at times that are “mismatched” with the emergence of prey and favorable environmental conditions. Similar consequences may also occur at southern latitudes; however, the degree of mismatch is expected to be less pronounced due to predictions of less extreme changes in temperature.

**Recruitment**

Because severe cold temperatures during winter can negatively influence survival of young-of-the-year temperate and sub-tropical marine and estuarine fishes, increasing winter temperatures may enhance survival of some species. Most often overwinter mortality is explained by reduced food availability and cessation of feeding at low temperatures. Species such as striped bass (Hurst and Conover, 1998), white perch *Morone americana* (Johnson and Evans, 1996), and Atlantic croaker (*Lumpenus* and Targett, 2001) show increased first-year mortality and lower recruitment in their northern ranges during colder than average winters. With global warming, winters will become less severe at all latitudes, and recruitment success will likely improve in regions where population abundance is currently limited by winter mortality. Thus, population expansions in more northern latitudes associated with improved recruitment related to climate warming are expected and have already taken place in some cases. For example, white perch, a species with a northern limit in the Mirimachi Estuary in the Gulf of St. Lawrence (Scott and Crossman, 1959), exhibits poor survival during severe winters. White perch invaded Lake Ontario around 1946 with the aid of both transportation canoes in New York and warmer than average winter temperatures (Johnson and Evans, 1990). Global warming may lead to improved white perch recruitment and range expansion throughout the Great Lakes due to longer growth seasons for juveniles and reduced winter severity.

Predictions similar to those for white perch have been made for Atlantic croaker along the U.S. Atlantic coast. This region is important, as it includes the northern range limit (i.e., Massachusetts; Mercer, 1987) of this fish—a sub-tropical species that is subject to cold-induced mortality as juveniles (Lankford and Targett, 2001). Warmer winters are thought to contribute to high abundances of juveniles in spring, leading to “outbursts” of Atlantic croaker (Hare and Able, 2007). Outbursts cause croaker to expand their overall distribution. Thus, it is expected that warming winters would lead to a more permanent northerly range extension for this species to coastal and estuarine regions north of Delaware Bay and Hudson River.

In contrast to sub-tropical species, such as Atlantic croaker, and temperate species, such as white perch, boreal and cold-temperate species are expected to experience negative effects on recruitment due to warming trends. For North American Atlantic salmon populations in the Gulf of St. Lawrence, warm SST during spring are negatively correlated with recruitment (Friedland et al., 2003). Higher temperatures in the Gulf of St. Lawrence may lower growth due to increased metabolic demands and insufficient prey availability (Friedland et al., 2003). Warmer conditions in the Gulf of St. Lawrence also may be associated with greater predation pressure (e.g., macrourids) or the depletion of available benthic energy reserves due to the increased swimming necessary to seek optimal temperatures (Friedland et al., 2003).

Similar to Atlantic salmon, yellowtail flounder (*Limanda ferruginea*) recruitment is negatively influenced by warm temperatures. In this case, however, warmer winters appear to decrease juvenile survival (Sullivan et al., 2005) due to loss of essential cold bottom water (4–8°C) habitat and possibly decreased productivity of their primary prey (copepods) as larval (Sutcliffe et al., 1977; Johnson, 2000; Sullivan et al., 2000). Likewise, warmer winters result in less productive nursery habitats for juvenile winter flounder (*Pseudopleuronectes americanus*; Keller et al., 1999), as well as increased activity of predators of juvenile flatfish (Taylor and Collie, 2003). During warmer winters in Narragansett Bay, Rhode Island, juvenile winter flounder experienced higher predation by transient migrants (silver hake *Mallotus villosus* and red hake *Urophycis chuss*) that preferred higher temperatures (Jeffries and Tercero, 1985).

In addition to the role of temperature, climate-induced changes in the magnitude and timing of peak streamflow may positively or negatively affect the reproductive success of many species of recreationally important fish, especially anadromous fishes such as American shad and striped bass. Higher streamflows tend to support higher reproductive success of striped bass and other anadromous fishes (Turner and Chadwick, 1972; Jung and Hoede, 2003; Kimmerer et al., 2001; North and Hoede, 2003; Martino and Hoede, 2004). In contrast, American shad in the Connecticut River respond negatively to increased streamflow (Savoy et al., 2004). Increased winter temperatures associated with climate change can result in the snow melt occurring earlier or in winter precipitation falling as rain instead of snow. Either of these scenarios can result in the peak streamflow occurring earlier in spring or even during winter, which may be too soon to provide the necessary environmental conditions for the reproductive success of anadromous fishes. Peak streamflow in the Northeast U.S. now occurs 7–14 days earlier since 1850 and is projected to occur an additional 10–14 days earlier by end of the century (Frumhoff et al., 2007).

Intense storms and associated strong winds and precipitation can also have major effects on recruitment of fish populations. Many species that spawn along the continental shelf, including Atlantic menhaden, Atlantic croaker, and blue crab, utilize estuarine and coastal ocean nursery habitats (Able, 2005). These species rely on winds and ocean currents to move their offspring from offshore spawning areas to inshore nurseries, and storms can disrupt this dispersal (Beardsley and Boicourt, 1981; Epifanio and Garvine, 2001). Certain fish populations might actually benefit from increased severe storm activity. For instance, there is a positive relationship between the abundance
of young Atlantic croaker in Chesapeake Bay and hurricane activity (Montane and Austin, 2005). The largest abundances of young croaker in the Chesapeake Bay occurred during 2003 and were related to persistent onshore winds associated with Hurricane Isabel. During hurricanes, the dispersal of croaker larvae from offshore areas into the Chesapeake Bay is favored by strong northeasterly winds and westward currents (Montane and Austin, 2005; Houde et al., 2005).

3.3. Community Level Response

Fish communities are characterized by constant fluctuations that are linked to climate, food web dynamics, fishing, recruitment processes, and other factors. Climate change can stimulate changes in fish communities through changes in the abundance or composition of species, altered interactions among species, and pressure from non-native species from outside the local area. Complicating the situation is the fact that the response of fish communities to climate change occurs in the face of continued harvest, pollution, and human development (Scavia et al., 2002).

Community Composition

As opposed to the global nature of climate change, changes in fish communities occur at regional to local scales. We anticipate that even communities that are seemingly similar will show differences in their response to climate change based on the manner in which the complex interactions within the community are impacted. For example, a European study looked at the effect of regional climate warming on two fish communities from the southwest of England in the Bristol and English channels (Genner et al., 2004). The researchers found an overall pattern of increasing abundance by dominant species within both communities; however, the same species responded differently between the two habitats due to local conditions (e.g., bathymetry, local atmospheric weather patterns, oceanic currents, and river plumes; Genner et al., 2004). Thus, the responses of individual species to changes in their local climate will translate to changes in the composition and dynamics of a fish community.

Shifts in community composition have already been observed in some systems. At "210 rock," a popular reef targeted by North Carolina recreational and headboat fishermen, a substantial turnover in community composition was observed between 1975 and 1990 (Figure 4; Parker and Dixon, 1998). The shift from a temperate subtropical community to one dominated by tropical species occurred in conjunction with a 1–6°C increase in average bottom water temperature during winter. Similarly, from 1977 to 2001, approximately two-thirds of the groundfish community of the North Sea showed a response to warming by shifting the center of their distribution away from the warming areas and into colder waters (Perry et al., 2005). These species accomplished this by either moving latitudinally toward cooler waters or retreating into deeper waters while maintaining their latitudinal position. These data show that the component species of 210 Rock, NC

![Diagram of fish species]

Figure 4 Species compositional changes at a popular recreational and commercial headboat fishing location off the coast of North Carolina from a survey conducted in the late 1970s and again in the 1990s. Relative abundance for each species is depicted by the size of the open (1970s) and solid black (1990s) bars. Data come from visual SCUBA surveys and headboat fishery logbooks presented by Parker and Dixon (1998).
of the North Sea groundfish community responded differently to changes in their environment, an indication that community structure can be altered by climate change.

As fish adjust their distributions to evolving habitat conditions (Rose, 2005b; Murawski, 1993), changes in component species will result in an alteration in trophic structure and energy flow within communities (Holbrook et al., 1997; Edwards and Richardson, 2004). The loss of predator and prey species alike has the potential to temporarily or permanently alter food webs, depending on whether functionally similar species are able to replace those that are lost.

Invasive Species

The "natural" level of variability in fish communities can be disturbed by the introduction of non-native species. Disruption of marine and fresh water ecosystems can create new habitats that are suitable for invasive species, while reducing the ability of native species to compete with the invasive species. For example, the invasive Indo-Pacific lionfish Pterois volitans, introduced to coastal waters of Florida in the early to mid 1990s, has expanded its range northward to Cape Hatteras, North Carolina, and established population abundances equal to that of native groupers (Whitefield et al., 2007). Lionfish have the potential to adversely affect native fishes through competition for prey and habitat and by directly eating native juveniles. As nearshore coastal water temperatures increase with global warming, lionfish may invade more temperate waters. Similarly, warm water invasive species such as northern snakehead Channa argus, which recently took up residence in the Potomac River, Maryland, may become increasingly prevalent in other U.S. temperate rivers. In addition, zebra mussels, a well known invasive species that has had large-scale ecological and commercial impacts in rivers and lakes of the Eastern seaboard, colonizes new habitats faster in warmer waters (Drake and Bossembroek, 2004), in the Hudson River, zebra mussel colonization has resulted in slower growth (e.g., striped bass, American shad, blueback herring Alosa aestivalis) and reduced abundance (e.g., American shad, alewife Alosa pseudoharengus, blueback herring) among juveniles of several important recreational and forage species (Strayer et al., 2004). Thus, climate change can create new niches for invasive species and thereby affect the fish community structure upon which current recreational fisheries depend.

4. RESPONSE OF MARINE RECREATIONAL FISHERIES TO CLIMATE CHANGE

4.1. Current State of Recreational Fisheries

Recreational fisheries are of great economic, social, and cultural importance in the United States. In 2006, nearly 13 million individuals participated in the marine recreational fishery making over 89,000 recreational fishing trips (including the Atlantic, Gulf, and Pacific coast regions; NMFS, 2007). The total marine recreational catch was estimated at more than 475 million fish, a large portion (55%) of which was released alive (NMFS, 2007). Drums dominated the catch (~66,550,000 lb.), followed by tunas and mackerels (44,885,000 lb.), and temperate basses (~50,915,000 lb.; NMFS, 2007). The majority of trips (>61%) and catch (>53%) were attributed to the Atlantic coast fishery, followed by the Gulf coast fishery (~28% of trips and >40% of the catch), and the Pacific coast fishery (almost 7% of trips and 5% of the catch; NMFS, 2007). In 2006, the recreational catch came primarily from inland waters (59%), with a smaller contribution from state territorial seas (32%) and federal waters (9%). The major modes of recreational fishing in 2006 included private/fishing boat (53% of trips), shore fishing (38% of trips), and party/charter boat (4% of trips), with private/rental boat being the most common mode in the North Atlantic and Mid-Atlantic regions (NMFS, Fisheries Statistics Division, personal communication).

Nationally, the number of recreational fishing trips was relatively stable from 1987 to 1998, followed by an increasing trend to 2006 (NMFS, Fisheries Statistics Division, personal communication). Across years the Atlantic coast fishery dominates in the number of U.S. recreational trips (NMFS, Fisheries Statistics Division, personal communication). Estimates of the percentage of total fish landings attributable to the recreational fishery averaged 4% nationally in 2002; however, on a regional basis, the recreational sector can comprise a much greater proportion of the total landings (e.g., 64% of Gulf of Mexico landings are recreational; Coleman et al., 2004). We anticipate changes in recreational fishery landings associated with climate change due to the factors discussed previously that will influence fish at the individual, population, and community level.

4.2. The Impact of Climate Change on Recreational Fishing Economies

Climate-induced changes to the environment will undoubtedly affect fish populations and fishing conditions and consequently have socioeconomic impacts on recreational fishing. As recreational fishing is a non-profit endeavor, the economic impacts will be primarily experienced by the industries that service recreational fishers. For example, sea level rise and coastal flooding may require relocation of fishery-associated facilities (e.g., marinas, bait shops, and charter boat operations; Watson et al., 1997; NRC, 2001). In addition, an increase in the frequency and intensity of storms will cause property damage to boats and shoreline facilities and may decrease the number of days fished by anglers.

Not all effects of climate change are expected to be negative. Based on the positive relationship between temperature and number of days fished, initial warming associated with climate change may effectively increase the number of days fished. Overall, regions that target cool water fisheries are expected to experience economic losses, whereas regions where
warm water fisheries dominate are expected to experience gains (Watson et al., 1997). The potential of both economic gains and losses associated with climate change makes the calculation of net losses complicated. Projected economic losses of global warming on U.S. recreational fishing are wide-ranging, estimated at $85–$320 million annually, with potential gains estimated at $80 million (in 1991 dollars; Watson et al., 1997). Based on current differences in the distribution of effort in the recreational fishery (Figure 5) and predicted changes in fish populations, recreational fishery losses will not be distributed evenly across regions. Some regions will sustain significant losses, and other regions will experience gains that will compensate for losses.

4.3. The Impact of Climate Change on the Catchability and Accessibility of Recreational Fishes

Climate change is predicted to affect the catchability and accessibility of fish in the recreational fishery. The catchability of fish by recreational fishers depends not only on the abundance of fish, but how they are distributed in space and time. Shifts in the overall spatial distribution of fish populations based on thermal preferences and other habitat requirements will affect the availability of a particular species to recreational anglers. Additionally, climate-induced shifts in the timing of migration may impact the timing and duration of the recreational fishing season for affected species.

Increasingly, shifts in the timing of migration and earlier spawning seasons have been documented for recreationally fished species, such as American shad and sockeye salmon (Quinn and Adams, 1996) and possibly striped bass (A. Peer, personal communication), and have been linked to increasing average spring temperatures over the past decades. Expectations are that recreational catches of these species will be earlier, assuming management regulations do not interfere. Valiente et al. (2004), however, observed a significant positive association between first-angling catch date of Atlantic salmon and the local mean annual temperatures in Spanish rivers from the 1950s to 2003. These results indicate that the first catch in this region was delayed by increasing temperatures—a trend opposite to that expected based on migratory trends observed in North America. One explanation for this perplexing trend is that the Atlantic salmon are leaving their Greenland nursery areas early in response to warming, in turn shortening their feeding period and reducing their potential energetic reserves. This migration is the longest of any Atlantic salmon worldwide, and the reduction in energy reserves may cause a slower migration and a later arrival to their spawning grounds (Valiente et al., 2004). Despite most predictions indicating that increasing temperatures will result in earlier recreational catches, the Spanish Atlantic salmon example illustrates the complex and potentially unpredictable impacts of global warming on fish populations and their associated fisheries.

If changes in the timing of migration are sufficiently large, they may impact the timing and duration of the recreational fishing season for affected species. In the case of a fixed recreational season designed to allow escapement of fish from the fishery after spawning, early spawning may effectively reduce the fishing season. The Maryland "tranny" stripers bass recreational fishery is an example of a fishery that targets post-spawning individuals and has a fixed start date. In response to increasing temperatures, management agencies may need to explore temperature-specific regulations, rather than fixed fishing seasons, to compensate for shifts in behavior. Maryland Department of Natural Resources (MDDNR) has considered fishery seasons based upon temperatures >18°C (temperature at which the majority of spawning has already occurred), rather than a fixed spring date.

Another projected impact of climate change is a shift in the distribution of fish populations (Parmesan and Yohe, 2003).
2003). Several studies have shown distributional shifts in Atlantic cod associated with climate variability, with their range expanding northward under warming regimes and southward during cold regimes (Drinkwater, 2005). Changes in the distribution patterns of recreationally important fishes will result in shifts in the center of distribution for a given fishery. Regional declines in catch-per-trip of traditionally targeted recreational species may negatively impact the number of angler trips and decrease the value of the recreational fishery. Alternatively, anglers may adapt to new conditions (i.e., targeting new species or increased travel by individuals to fish for preferred species). Thus, the loss of a species from a portion of their historical range will decrease its regional catchability; however, colonization of newly suitable habitats by species may present new recreational fishing opportunities (Kennedy et al., 2002). Such shifts in community composition have been documented at a North Carolina recreational fishing site (see Section 3.3: Community Composition), where the catch of temperate subtropical species decreased and tropical species increased with increasing water temperatures.

Accessibility of fish to recreational fishers will be affected by climate change and may lead to changes in the mode or gear used in the recreational fishery. Shifts in the distribution and abundance of popular recreational fish species, such as skipjack tuna, have been associated with a 3–4°C temperature increase during ENSO events (Lehodey et al., 1998; Roessig et al., 2004). Shifts in the spatial distribution of these populations result in changes in their availability to fishers and serves to forecast how climate change might bring about spatial shifts in effort by recreational fisheries. Additionally, nearshore regions, such as estuaries and coastal bays, which see highest use by recreational fishers, may be differentially affected by warming due to their shallow, semi-closed nature (see Section 2.1: Water Temperature). Decreased habitat suitability of shallow water habitat may prompt a population shift into deeper cooler waters, preventing access of shore fishers to fish (Reist et al., 2006).

A potential consequence of large-scale shifts in fish population distribution may be increased travel to reach fishing destinations (Roessig et al., 2004). In the future, participation in the fishery may be decided based on the increased costs (i.e., fuel costs) of reaching target species and factors such as shoreline accessibility and the location of harbor facilities. Individuals who lack mobility will suffer disproportionately from changes in the accessibility of fish. In some regions, such as where shore fishing dominates, we may see a decrease in overall participation in the fishery if new species do not move into the warmer, nearshore waters. In addition, as accessibility to fish becomes a problem, charter fishing may increase in popularity over private boating, as this will be the less costly mode of reaching some target species. Further research into the effects of climate change on catchability and accessibility of fish populations is needed to fully understand the potential consequences to the recreational fishery.

4.4. Effect of Climate Change on Gear Used in Recreational Fishing

Changes in the gear used in the recreational fishery may also be required to adapt to new climate conditions (Reist et al., 2006). Catch and release is a large component of the recreational fishery, and, in general, post-release mortality has been found to be low for a variety of species (Atlantic salmon, ~12%; summer flounder, ~10%; weakfish, ~4%; tautog, ~2%; red drum, <2%; and black sea bass, ~12%; Bartholomew and Bohaska, 2005). A study of hooking mortality of striped bass found that catch-and-release mortality was generally low for shallow-hooked fish (3.5% shallow-hooked, 53.1% deep-hooked); however, mortality increased dramatically with increasing temperature (Lukacovic, 1999). The mortality of shallow-hooked striped bass when air temperatures were below 35°C was 0.8%, whereas when air temperatures ranged from 35–41°C, mortality rose to 17.2% (Lukacovic, 1999). A switch from conventional hooks to circle hooks (0.8% mortality) could be an option for offsetting increased mortality associated with increasing temperatures. Consideration of potential changes in recreational fishing mortality in response to increasing temperature will have to be included in the management plans of recreational species.

4.5. The Affect of Climate Change on Fish Population Dynamics

The direction of changes in productivity of populations will vary between species based on their habitat requirements and sensitivity to climate-induced changes. Opposite trends in population abundance associated with increasing temperature, such as those documented in Atlantic croaker and Atlantic salmon populations, will require recreational fishers to be adaptable to changing conditions and to shift target species with shifts in population abundance. Shifts in fish community structure are also expected with an increase in temperature, requiring adaptation by the recreational fishery to increased productivity of fish that may not have been traditionally targeted in the region (Watson et al., 1997).

In some instances, mortality rates may increase due to an overall loss of species habitat, such as in the case of striped bass that experience a "habitat squeeze" in response to the combined effects of increasing temperature and decreasing dissolved oxygen in nearshore waters (Coutant, 1990). Loss of habitat ultimately reduces the population density that can be supported in the area, and, as a consequence, the availability of fish to fishers is reduced (Coutant, 1990). In the short term, however, habitat squeezes can result in higher local densities and increased accessibility of fish to anglers (Coutant, 1990). Increased density of fish is oftentimes associated with increased prevalence of disease and poor condition of those fish that are available to recreational fishers, making them undesirable to catch, unpalatable, or a potential risk to human health (Harvell et al., 2002).
Climate-induced changes to the dynamics of fish populations will require adjustment of management practices, specifically the designation of target species and magnitude of recreational and commercial harvest.

Tracking temporal changes in fishery landings can inform us as to the way fisheries adapt to changing environmental conditions (Figure 6). Changes in fishery landings may reflect changes in the environment, in management (i.e., establishment of total allowable catch in commercial fishery), or the dynamics of the fisheries (i.e., dominance of commercial fishery over recreational fishery or vice versa). For example, during the early to mid 1980s, striped bass landings along the Atlantic coast were dominated by the commercial fishery; however, from 1985 onward we see both recreational and commercial landings increase incrementally (Figure 6A). This increase in landings is associated with the recovery of striped bass stocks following the enactment of a moratorium on fishing and several years of favorable environmental conditions for recruitment (Richards and Rago, 1999; Secor, 2000). In the late 1990s to early 2000s, we see a rise in recreational landings that outpaces the rise in commercial landings. Thus, a decadal scale shift in environmental conditions favorable to recruitment was associated with...
a large change in the structure of fisheries that resource supported. Although commercial quotas explain much of this, we also speculate that recreational fisheries can be more responsive to increased abundances to striped bass than commercial ones. In the case of Atlantic croaker (in Delaware and New Jersey), low landings of both the recreational and commercial fisheries in the 1980s reflect a period of record low landings in a fishery that has been harvested intensively for several generations (highs of 64 million lb landed in 1945; Figure 6B). A subsequent increase in both the recreational and commercial fisheries occurred in the 1990s in response to increased population abundance. A circular trend in landings occurred in the 2000s, indicative of periodic high recruitment of Atlantic croaker during this period and the response of both fisheries. In this case, the drop in commercial landings was followed by a decrease in recreational landings. Tracking landings as in these phase plots provides a historical perspective on how fisheries respond to changing conditions, their ability to adapt, and take advantage of changes: important factors in understanding the response of recreational fisheries to climate change.

4.6. The Impact of Climate Change Impact on the Assessment and Management of Fish Populations

The impact of climate change on marine and estuarine fishes will require a change in the way we assess and manage fish populations. Population assessment will undoubtedly become more difficult as climate deviates from historic baselines and fishery scientists are forced to cope with increasing uncertainty (Watson et al., 1997). There is increased recognition by recreational and commercial fishers, managers, scientists, and the public that fisheries management must be done from an ecosystem perspective, considering the interactions of fishery resources with the habitats and food webs upon which they depend, other resource species, climate change, fishery management actions, and exploitation. Ecosystem-based fisheries management includes increased cooperation in the regional management of fish populations to deal with such issues as shifting fish distributions and how these are likely to affect fishing behaviors (Watson et al., 1997).

Given the uncertainty of changes in fish populations with climate, management strategies will need to be informed by past approaches in management when faced with long-term fluctuations in fisheries resources due to inter-annual (e.g., ENSO) and decadal scale (e.g., Pacific Decadal Oscillation) climate variability. When information is scarce, erring on the side of caution and enacting management to avoid the likelihood of stock collapse (i.e., implementation of the precautionary principle) is prudent (FAO, 1996). Walters and Parma (1996) suggested a fixed exploitation rate for management of fisheries that fluctuate in response to environmental change, a strategy that is in keeping with a precautionary approach. Such a strategy has been applied in the management of Atlantic salmon fisheries through a fixed escapement strategy (Potter et al., 2003). In addition to the consideration of risk, managers must also consider opportunities associated with climate change, such as the possibility of new sustainable fisheries in a region (Scheraga and Grambsch, 1998).

Adaptive management, a systematic process designed for decision-making and improving management strategies through learning and adaptation, may be increasingly employed in the management of fish under the influence of climate change. Its most effective form, active adaptive management, involves the implementation of a suite of management actions on different portions of a population and subsequent monitoring of the biological and economic responses, thus enabling managers to evaluate the optimal management action (Walters and Holling, 1990). In this manner, feedback from the fishery is used to shape and improve policy. This method is responsive to change in the status of the fishery and thus may be appropriate as we experience the effects of climate change (Walters and Holling, 1990).

Changes in the way we manage fisheries will not be able to prevent climate-induced changes, but can play an important role in the mitigation of its effects (Watson et al., 1997). Mitigation of the effects of climate change by management will require conservation of characteristics that promote population resiliency and stability. The long lifespan of some recreationally important species (e.g., striped bass and red drum) ensures survival of the population over periods of recruitment failure (Secor, 2000; Walther et al., 2002). However, recreational targeting of the largest individuals of a population leads to truncated age structure, and the loss of age structure compromises the resiliency of these populations (Walther et al., 2002; Coleman et al., 2004; Berkeley et al., 2004). The spatial distribution of fish populations can also play a role in a population’s resilience to environmental variability. Similar to diversifying an investment portfolio to reduce risk, diversifying habitat use within a population has a stabilizing effect, reducing the population’s risk of extinction (Ray, 1997). Thus, conservation of age structure and patterns of habitat use in populations should be a management objective (Secor, 2007). In addition, there is ample theoretical and empirical evidence that biodiversity contributes to community stability and production (Hilborn et al., 2003). For example, focused harvest on the upper levels of the food web can affect the structure of a community and compromise community stability (Berkeley et al., 2004). Consideration of and management for factors that contribute to resiliency of fish populations will be essential to the sustainable management of populations in a changing environment.

A critical component in the future of fisheries assessment and management is increased involvement of stakeholders, including recreational fishers. Recreational anglers and their representatives have been involved through invited public comment and active participation in fisheries assessments at state, regional, federal, and international levels. In addition, recreational anglers are oftentimes involved in fish tagging programs, which contribute to vital knowledge on population abundance and movement of fish. As fishing behaviors change, it will be important to incorporate these changes accurately into assessment efforts.
and goals of future single-species and ecosystem-based fishery management plans. Increased collaboration of anglers, scientists, and fisheries managers are needed to educate participants in the recreational fishery as to the consequences of fishing pressure and management action on populations, as well as to take advantage of the valuable local knowledge fishers possess.

**SUMMARY**

**Climate Change in the U.S. Atlantic**

1. Temperature Change—Climate change along the U.S. East Coast has already occurred. Air temperatures have increased by 0.5–1.0°C since 1900, and water temperatures in both the coastal ocean and principal U.S. Atlantic estuaries have warmed 0.6–1.5°C since the middle of the 20th century. Water temperatures along the U.S. East Coast are predicted to increase by another 2–4°C by 2099.

2. Change in Precipitation and Ocean Circulation—Precipitation is forecasted to increase by 6–24% by 2099, with heavy precipitation events becoming more common. Increased streamflow from higher annual precipitation, additional glacial melting, and higher ocean temperatures could alter ocean circulation along the coast.

3. Sea Level Rise—Historical data reveal that global sea levels have been rising (~2 mm/yr−1 since the late 19th century). Rates of sea level rise will differ substantially among regions. In some locations, sea level rise will result in the near-term loss of coastal marsh and submerged aquatic vegetation, habitats important to many fish populations.

4. Storminess—Ocean atmosphere models predict that global warming will cause increased storm frequency and intensity both globally and for the U.S. Atlantic region. Storms are characterized by spikes in wind velocity and precipitation for a relatively brief period of time disrupting prevailing environmental conditions. Increased storminess can cause direct mortality of fish eggs and larvae and may disrupt successful transport of larval fishes by prevailing winds.

**Response of Marine and Estuarine Recreational Fisheries to Climate Change**

1. Accessibility and Catchability of Target Species—Climate-driven responses, such as distributional shifts and shifts in the timing of migrations, can change the accessibility and catchability of target species. Recreational fishery landings, participation, and economic output will be affected by this displacement.

2. Fishery Sector Changes—Climate-induced changes to the dynamics of fish populations will require recreational fishers to be adaptable to changing conditions and to shift target species with shifts in species abundance. Participation in the fishery may be decided based on changes in catch-per-trip of preferred species and the increased costs of reaching target species.

3. Management—An ecosystem-based approach to fisheries management is required to address complex shifts in community and population dynamics due to climate change. Increased collaboration of recreational anglers, scientists, and fisheries managers will promote the effectiveness of future fisheries assessment and management.

4. Resiliency and Stability as Management Targets—Management to mitigate the effects of climate change will require conservation of characteristics that insure population and community resiliency and stability (e.g., age structure, patterns of habitat use, biodiversity) to promote long-term persistence.

**ACKNOWLEDGMENTS**

We thank T. Irle and R. Wingate for their contribution to this work. This work was supported by the American Sportfishing Association. The writing of this manuscript was stimulated by a student-led seminar focused on the consequences of climate change held at the Chesapeake Biological Laboratory. This is
CLIMATE CHANGE IN THE U.S. ATLANTIC AFFECTING RECREATIONAL FISHERIES

Contribution No. 4248 of the University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory.

REFERENCES


Sullivan, M. C., R. K. Cowen, and B. P. Steves. Evidence for atmospheric-ocean forcing yellowtail flounder (Limanda...


