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ARCTIC CLIMATE CHANGE AND ITS IMPACTS ON THE ECOLOGY OF THE NORTH ATLANTIC

Charles H. Greene,[1,4] Andrew J. Pershing,[1,2] Thomas M. Cronin,[3] and Nicole Ceci[1]

[1]*Ocean Resources and Ecosystems Program, Snee Hall, Cornell University, Ithaca, New York 14853 USA*
[2]*Gulf of Maine Research Institute, 350 Commercial Street, Portland, Maine 04101 USA*
[3]*U.S. Geological Survey, 12201 Sunrise Valley Drive, Reston, Virginia 20192 USA*

Abstract. Arctic climate change from the Paleocene epoch to the present is reconstructed with the objective of assessing its recent and future impacts on the ecology of the North Atlantic. A recurring theme in Earth's paleoclimate record is the importance of the Arctic atmosphere, ocean, and cryosphere in regulating global climate on a variety of spatial and temporal scales. A second recurring theme in this record is the importance of freshwater export from the Arctic in regulating global- to basin-scale ocean circulation patterns and climate. Since the 1970s, historically unprecedented changes have been observed in the Arctic as climate warming has increased precipitation, river discharge, and glacial as well as sea-ice melting. In addition, modal shifts in the atmosphere have altered Arctic Ocean circulation patterns and the export of freshwater into the North Atlantic. The combination of these processes has resulted in variable patterns of freshwater export from the Arctic Ocean and the emergence of salinity anomalies that have periodically freshened waters in the North Atlantic. Since the early 1990s, changes in Arctic Ocean circulation patterns and freshwater export have been associated with two types of ecological responses in the North Atlantic. The first of these responses has been an ongoing series of biogeographic range expansions by boreal plankton, including renewal of the trans-Arctic exchanges of Pacific species with the Atlantic. The second response was a dramatic regime shift in the shelf ecosystems of the Northwest Atlantic that occurred during the early 1990s. This regime shift resulted from freshening and stratification of the shelf waters, which in turn could be linked to changes in the abundances and seasonal cycles of phytoplankton, zooplankton, and higher trophic-level consumer populations. It is predicted that the recently observed ecological responses to Arctic climate change in the North Atlantic will continue into the near future if current trends in sea ice, freshwater export, and surface ocean salinity continue. It is more difficult to predict ecological responses to abrupt climate change in the more distant future as tipping points in the Earth's climate system are exceeded.

Key words: Arctic; climate change; marine ecosystems; North Atlantic; regime shift.

Introduction

For centuries, Arctic explorers searched in vain for the Northwest Passage linking the North Atlantic and North Pacific Oceans. Sea ice impeded their efforts to sail from the Atlantic to the Pacific just as it has been a factor in impeding the movements of flora and fauna between these two major ocean basins since the mid-Pleistocene. With increasing concerns about the impacts of global warming at high latitudes, it has been proposed that the Arctic Ocean may become entirely ice-free during summer months sometime before the next century (Johannessen 1999, 2004). Recent studies suggest that rapid climatic and oceanographic changes in the Arctic may already have (1) impacted shelf ecosystems downstream in the Northwest Atlantic, and (2) breached the barrier to trans-Arctic exchanges of plankton between the two ocean basins (Greene and Pershing 2007, Reid et al. 2007).

Relative to the 1980s, the decade of the 1990s was characterized by an increase in the amount of low-salinity water exiting the Arctic Ocean and entering the North Atlantic through the Canadian Archipelago and Fram Strait (Proshutinsky et al. 2002, Steele et al. 2004). This enhanced discharge of low-salinity water freshened shelf waters from the Labrador Sea to the Middle Atlantic Bight (Loder et al. 2001, Smith et al. 2001, Häkkinen 2002, Mountain 2002, 2003, Frank 2003, Belkin 2004). The freshening altered stratification and circulation patterns and can be linked to a dramatic regime shift in the shelf ecosystems of the Northwest Atlantic (Greene and Pershing 2007). Later in the decade, boreal planktonic species from both the Pacific and Arctic Oceans started to appear and spread throughout the North Atlantic (Sundt and Melle 1998, Reid et al. 2007). This biogeographic range expansion of boreal plankton has been both rapid and extensive. In this paper, we will briefly review the extensive literature

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[4] E-mail: chg2@cornell.edu

Box 1. Glossary of Earth Climate System Terminology

Albedo: the Earth's reflectance of incoming solar radiation, defined as the ratio of reflected to incident electromagnetic radiation.

Buoyancy forcing: upward forcing due to differences in density associated with variations in salinity and/or temperature.

Cryosphere: ice components of the Earth system, including sea ice, lake and river ice, snow cover, glaciers, ice caps and ice sheets, permafrost.

Eccentricity: deviation of the Earth's orbit from a circle.

Glacial/interglacial: geological interval of ice age conditions/geological interval of warmer conditions that separates glacials or ice ages.

Ice rafting: transport of sediments by icebergs.

Insolation: amount of solar radiation incident on the Earth's surface.

Meridional overturning circulation: density-driven circulation of the global ocean.

Obliquity: Earth's axial tilt expressed as the inclination angle of its rotational axis relative to a line drawn through the planet's center perpendicular to its orbital plane.

Precession: slow wobbling motion of Earth's rotational axis caused by the gravitational attraction of the Sun and the Moon on the Earth's equatorial bulge.

Stadial/interstadial: a relatively brief interval of colder temperatures during an interglacial of insufficient duration or intensity to be considered a glacial transition/a relatively brief interval of warmer temperatures during a glacial interval of insufficient duration or intensity to be considered an interglacial transition.

of Arctic climate change in the past to provide insights for interpreting the ecological responses to changes in climate recently observed in the Northwest Atlantic. We will then attempt to predict what additional ecological changes might be expected in response to future alterations in climate.

Arctic and Global Climate Change in the Past

Cenezoic overview: an era in transition from greenhouse to icehouse conditions

The Arctic is very sensitive to changes in the Earth system's climate. During the Cenozoic era, 65 million years ago (Ma) to the present, the Arctic has undergone a transition in extremes from the ice-free greenhouse conditions of the late Paleocene and early Eocene epochs, approximately 55–48 Ma, to the icehouse conditions of the Quaternary, culminating in the extensive continental ice sheets and Arctic Ocean sea ice of the Last Glacial Maximum, approximately 24–20 ka (Moran et al. 2006). (To review relevant climate terminology, see Box 1; to review the geological time scale, see material *available online*.)[5] During the past 55 million years of global cooling, since the Palaeocene-Eocene Thermal Maximum (Zachos et al. 2001, Sluijs et al. 2006), atmospheric CO_2 concentrations have declined roughly in parallel with declines in temperature (Pagani et al. 2005, Stoll 2006). The somewhat erratic nature of this global cooling has been attributed to continental drift, changes in ocean-basin geometry, mountain building, volcanism, and other geological processes that interact with the primary drivers of long-term, natural climate variability: changes in greenhouse gas concentrations, planetary albedo, and incident solar radiation. A dramatic drop in CO_2 concentration took place between approximately 45–25 Ma, coinciding with the onset of a major episode of global cooling (Pagani et al. 2005). In the Antarctic, ice-sheet, ice-shelf, and sea-ice formation began at approximately the same time, creating icehouse conditions that have persisted to the present. In contrast, while there is new evidence for ice-rafted sediments in the Arctic Ocean as early as 45 Ma (Moran et al. 2006), the onset of true Arctic icehouse conditions appears to have been delayed, with major expansions in continental glaciers, ice sheets, and sea ice occurring approximately 14 and 3 Ma (Stoll 2006).

The second transition in the Arctic cryosphere, from seasonally ice-free conditions during the middle Pliocene epoch (Cronin et al. 1993) to true icehouse conditions characterized by the development of perennial Arctic Ocean sea ice and continental ice sheets in North America and Eurasia, occurred approximately 3 Ma. This transition is particularly intriguing because initial CO_2 concentrations, incident solar radiation, and global geological conditions were comparable to those of

[5] ⟨http://vulcan.wr.usgs.gov/Glossary/geo_time_scale.html⟩

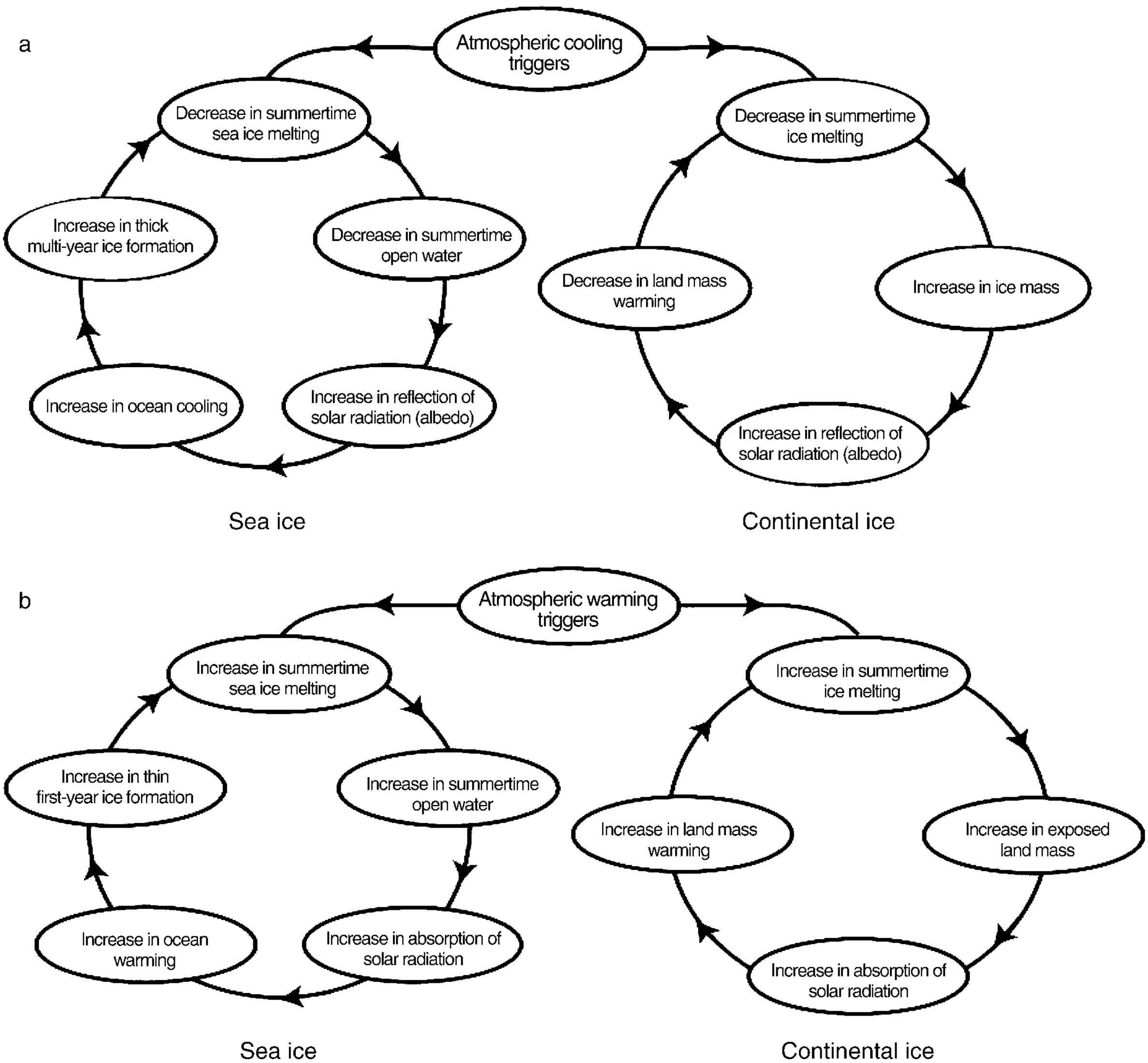

FIG. 1. Ice–albedo feedback mechanisms that form the basis for (a) accelerated ice formation and cryosphere expansion and (b) accelerated ice melting and cryosphere contraction.

today, yet global temperatures were significantly warmer, Northern Hemisphere ice sheets were largely absent, and sea levels were approximately 25 m higher (Dowsett and Cronin 1990). Based on palaeoclimate records (Cane and Molnar 2001, Molnar and Cane 2002) and modeling studies, Fedorov et al. (2006) suggest that the cooling at higher latitudes reached a tipping point during the Pliocene, driving the Earth system from warmer, continuous El Niño-like conditions to the cooler, intermittent El Niño conditions of more recent times. A complex scenario, involving positive-feedback mechanisms between the high-latitude and tropical regions of the global ocean, is proposed by these authors to explain the transition. In their scenario, high-latitude cooling enhanced the global ocean's meridional overturning circulation, expanded the volume of cold water in the deep ocean, and resulted in a shoaling of the thermocline in the tropical Pacific and Atlantic Oceans. By raising the Eastern Tropical Pacific's thermocline to depths where the cold water could be entrained by upwelling processes, a strong zonal sea surface temperature (SST) gradient was established in the Equatorial Pacific. This strong SST gradient is essential to the ocean-atmosphere interactions that support intermittent rather than continuous El Niño conditions. The SST gradient is also associated with increased cloud cover and albedo in the Eastern Tropical Pacific. Fedorov et al. (2006) suggest that such changes in the tropics during the Pliocene provided a cooling feedback to high-latitude regions, which resulted in the expansion of continental ice sheets and sea ice. In their interpretation, the combination of tropical ocean–atmosphere and Arctic ice–albedo feedback mechanisms (Fig. 1) triggered the final shift to Arctic icehouse conditions.

Quaternary overview: a period of glacial/interglacial climate cycles

The Arctic icehouse has played an important role in the Earth system's climate and its variability throughout the Quaternary period, beginning approximately 1.8 Ma. On time scales of 10^4 to 10^5 years, glacial/interglacial climate cycles are driven primarily by responses of the cryosphere to insolation changes forced by variations in the Earth's orbital parameters associated with eccentricity, obliquity, and precession (Ruddiman 2006). However, changes internal to the climate system can alter its responses to such orbital forcing. For example, between approximately 1.2 and 0.7 Ma, the mid-Pleistocene transition occurred and, in the absence of any significant changes in orbital forcing, the amplitude of glacial-interglacial climate cycles increased while their quasi-periodicity changed from an approximately 41-kyr cycle to one of approximately 100 kyr (Clark et al. 2006). Clark et al. (2006) reviewed a number of competing hypotheses that have been proposed to explain this transition. While most invoke a response to long-term cooling, possibly induced by declining CO_2 concentrations, Clark et al. (2006) prefer an alternative hypothesis, one suggesting that alterations in the climate system's responses to orbital forcing were the consequence of repeated glaciations exposing the base of continental ice sheets to unweathered Precambrian Shield crystalline bedrock (Clark and Pollard 1998). According to this hypothesis, a thick layer of relatively low friction regolith favored the development of thin, but areally extensive ice sheets that responded linearly to the 41-kyr insolation forcing characteristic of the early Pleistocene. Successive glaciations eventually eroded this regolith layer, exposing the Precambrian Shield bedrock beneath. Clark and Pollard (1998) proposed that this unweathered crystalline bedrock provided a higher frictional substrate, thereby supporting the development of thicker ice sheets with a fundamentally different response to orbitally forced changes in insolation.

Subsequent to the mid-Pleistocene transition, glacial/interglacial climate cycles exhibited greater amplitudes and a slower, broad-band pacing centered on 100 kyr (Clark et al. 2006). Martrat et al. (2007) recently characterized the centennial- to millennial-scale variability associated with the four major climate cycles of the past 420 kyr. Each of these climate cycles commenced with a rapid warming phase over a few centuries, which completed deglaciation. During this initial part of the climate cycle, a warm and relatively stable interglacial period was maintained. The warming phase was followed by gradual cooling over several thousand years and often ended in a relatively abrupt cooling episode leading to the subsequent glaciation. Martrat et al. (2007) related such relatively abrupt cooling episodes to the ocean's bipolar behavior. North Atlantic Deep Water (NADW) formation and its role in the global ocean's meridional overturning circulation are thought to be essential to the maintenance of stable interglacial periods (Broecker 1997). When NADW formation is disrupted and the predominance of deepwater formation shifts to southern hemisphere sources (Antarctic Bottom Water), less heat is transported to higher latitudes in the northern hemisphere and a rapid plunge into glacial conditions is triggered (Clark et al. 2002).

The most recent interglacial, the Eemian, extended from the end of the penultimate glaciation, approximately 130–120 ka, to when the last glacial period began, approximately 107 ka. The Eemian was a typical interglacial event characterized by reduced global ice sheets and relatively high sea levels. According to most proxy data, the Eemian exhibited slightly warmer temperatures than today and a global sea level approximately 6 m higher (IPCC 2001). Brigham-Grette and Hopkins (1995) suggest that during this interglacial the winter sea-ice limit in the Bering Strait was at least 800 km farther north than today and some summers in the Arctic Ocean may have been entirely ice free. High-resolution records from North Atlantic sediment cores indicate that the Eemian ended rapidly, over a period of less than 400 years, in response to a surge of cold, low-salinity water entering the Norwegian Sea (McBean et al. 2005). This low-salinity water would have reduced NADW formation and slowed the global ocean's meridional overturning circulation. With less heat transported to higher latitudes by the North Atlantic Drift, the stage was set for a return to glacial conditions.

After the Eemian, the Earth system entered a glacial period of declining temperatures punctuated by a series of rapid warm and cold oscillations, referred to as Dansgaard–Oeschger (DO) events (Dansgaard et al. 1993). Oxygen isotope records from Greenland ice cores demonstrate that DO events were associated with abrupt climate swings, over only a few decades, from glacial conditions to conditions about as warm as today. The warm interstadial conditions lasted for varying periods of time, usually a few centuries up to approximately 2000 years, before cooling returned conditions to their previous glacial state. High-resolution records from North Atlantic sediment cores provide evidence that DO events were correlated with SST variations (Bond et al. 1993) and, at least during the past 30 000 years, interstadial conditions tended to occur at the warmer points of an approximately 1500-year North Atlantic temperature cycle (Bond et al. 1997).

Closely coinciding in time with certain DO events are the ice-rafting cycles referred to as Heinrich events (Heinrich 1988). Heinrich events correspond to the most extreme of a series of sudden, but brief cold events that occurred frequently over the past 115 000 years. In most cases, Heinrich events were triggered by the massive discharge of icebergs from the Laurentide Ice Sheet through Hudson Strait into the North Atlantic. As they melted, these icebergs deposited characteristic layers in deep-sea sediments. The melting of these icebergs during Heinrich Events also led to a reduction in NADW

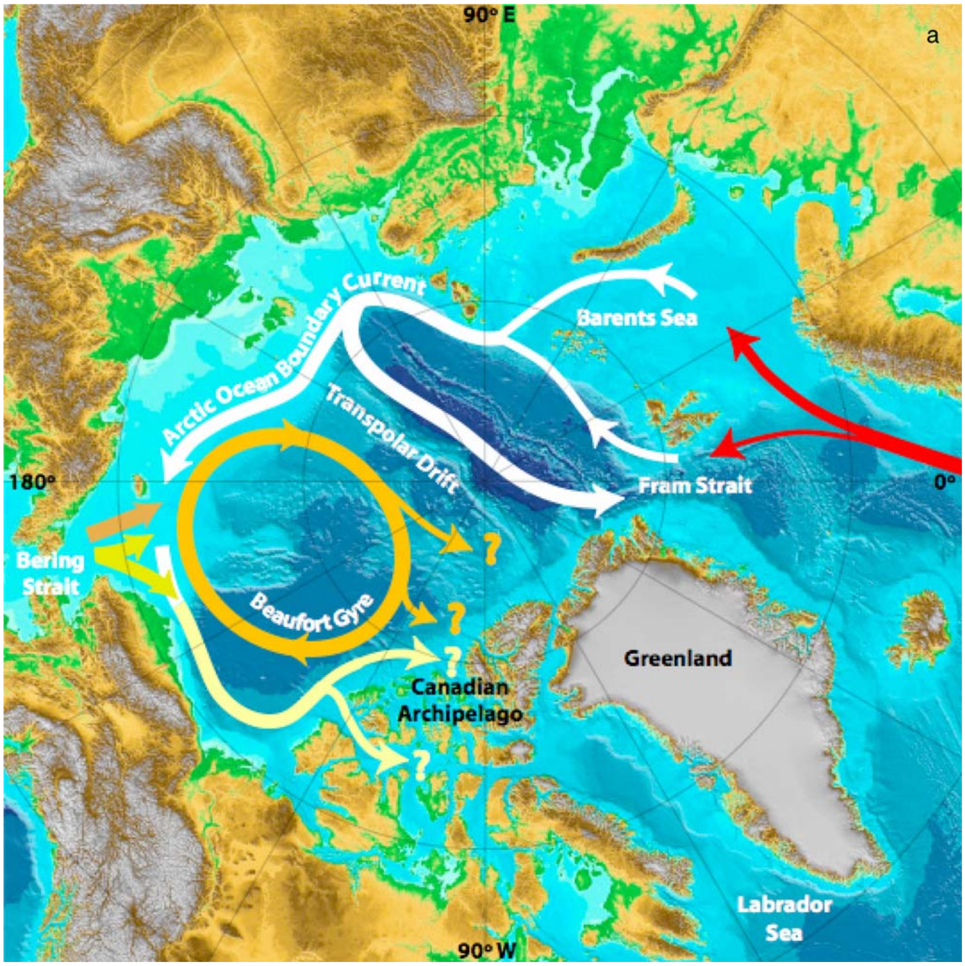

FIG. 2. Upper ocean circulation patterns in the Arctic Ocean (a) before and (b) after the shift to a strongly cyclonic atmospheric circulation regime. Red arrows indicate inflow of Atlantic water into the Arctic Ocean through the Barents Sea and Fram Strait. White arrows indicate surface flows of polar water. Yellow and orange arrows indicate inflow of Pacific water into the Arctic Ocean through the Bering Strait. Pale yellow and orange arrows indicate mixtures of polar- and Pacific-derived waters.

formation and a slowing of the global ocean's meridional overturning circulation. By slowing down thermohaline circulation on a global scale, Heinrich events promoted climate cooling in the Northern Hemisphere and enhanced the Arctic ice–albedo feedback mechanisms that support ice sheet expansion during glacial periods (Fig. 1).

The greatest global ice extent of the Quaternary period occurred approximately 24–21 ka during the Last Glacial Maximum (Clark and Mix 2000). During the Last Glacial Maximum, extensive ice sheets were found on the continents surrounding the Arctic Ocean. At its maximum extent, the Laurentide Ice Sheet stretched from the Arctic Ocean north of the Canadian Archipelago to the midwestern United States in the south and from the Canadian Cordillera in the west to the Atlantic Ocean in the east.

The most abrupt climate changes documented in the geological record for the Quaternary period occurred during the transition from full glacial conditions, approximately 24 to 21 ka, to full interglacial conditions, attained approximately 10 ka at the onset of the Holocene epoch (IPCC 2001). Proxy data indicate that the average warming occurred at a rate of about 2°C per millennium between approximately 20 and 10 ka in Greenland, with lower rates found for other regions. However, abrupt temperature increases at the start of the Bølling-Allerød period, approximately 14.5 ka (Severinghaus and Brook 1999), and at the end of the Younger Dryas, approximately 11.5 ka, may have occurred at rates as high as 10°C in less than half a century over extensive areas of the Northern Hemisphere. In addition, although this was a period of warming in general, abrupt temperature decreases were also observed. A short-term cold event, the Younger Dryas, occurred approximately 12.8 to 11.5 ka, temporarily plunging the Arctic back into conditions of advancing ice sheets. It has been hypothesized that a

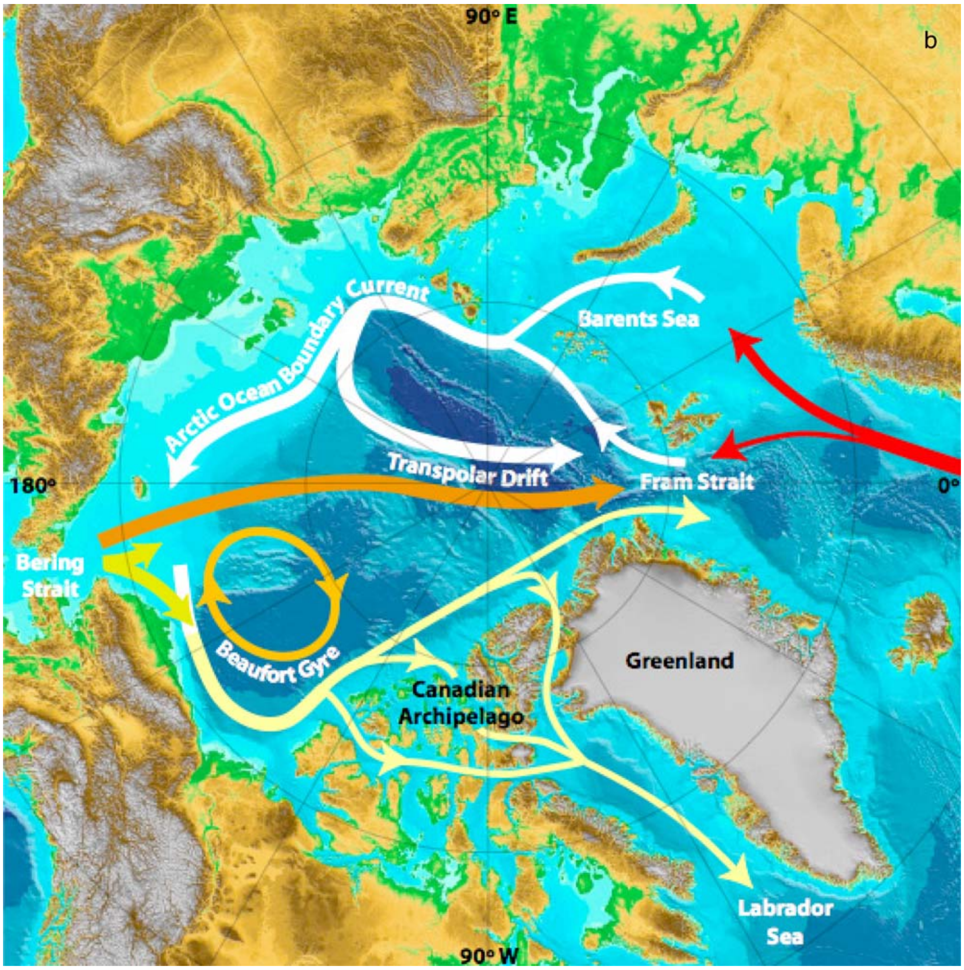

FIG. 2. Continued.

catastrophic release of meltwater from an enormous glacial lake entered the North Atlantic and triggered the Younger Dryas' rapid onset (Broecker 1997, Clark et al. 2001). Hypothetically, this massive inflow of freshwater would have reduced North Atlantic Deep Water formation, slowed the global ocean's meridional overturning circulation, and resulted in the abrupt cooling that occurred in less than a century. Although uncertainties remain, such as the exact timing and routing of the drainage (Teller et al. 2005, Broecker 2006), glacial lake discharge into the high latitude North Atlantic remains the leading hypothesis for the onset of abrupt climate change associated with the Younger Dryas.

Holocene overview: an epoch of relative stability in Earth's climate system

The Holocene epoch began once the present interglacial was fully established approximately 10 ka. The Holocene has been remarkably stable when compared to the previous glacial period. Only two major cooling episodes have been documented in the geological record during this epoch, and both were associated with what has been referred to as the 8.2 ka Event (Alley et al. 1997). Similar to the Younger Dryas, the trigger for the 8.2 ka Event is hypothesized to be the catastrophic release of meltwater from large glacial lakes during the decay of the Laurentide Ice Sheet (Barber et al. 1999). Apparently this release of meltwater from Lakes Agassiz and Ojibway occurred in two pulses, one at approximately 8.5 ka and the other at approximately 8.3 ka (Ellison et al. 2006). Both pulses resulted in a slowing of the global ocean's meridional overturning circulation and an abrupt cooling of the Northern Hemisphere.

Although stability has been a hallmark of the present interglacial, the last millennium has exhibited some periods of marked climate warming and cooling. The Medieval Warm Period, from approximately the early 9th to mid-15th centuries, brought warm temperatures to areas in and around the North Atlantic. In contrast, the Little Ice Age, from approximately the mid-16th to early 20th centuries, may have brought the coldest temperatures of the entire Holocene to these same areas

(Bradley 1990). Variations in solar insolation (Bond et al. 2001), atmospheric circulation (O'Brien et al. 1995), and thermohaline circulation (Keigwin and Pickart 1999) have been suggested as possible forcing mechanisms behind this centennial-scale variability in the North Atlantic. These forcing mechanisms interact most strongly in the Arctic and higher latitudes of the North Atlantic, where solar forcing may excite different modes of atmospheric variability, which in turn amplify and transmit basin- to global-scale changes in climate through their effects on thermohaline circulation in the Labrador and Nordic Seas (McBean et al. 2005).

During the past two centuries, the advent of calibrated instruments providing reliable atmospheric and hydrographic data has enabled scientists to detect annual- and decadal-scale modes of climate variability that are difficult to resolve from ice- or sediment-core data. In the North Atlantic, the North Atlantic Oscillation (NAO) is the principal mode of annual- to decadal-scale climate variability (Hurrell et al. 2003). Recently, it has been suggested that the NAO is the North Atlantic manifestation of a more widespread hemispheric climate mode referred to as the Arctic Oscillation (AO) or Northern Hemisphere Annular Mode (Thompson and Wallace 1998, Thompson et al. 2000). Alterations in atmospheric circulation patterns associated with the NAO force changes in the North Atlantic's wind-driven and thermohaline circulation. Keigwin and Pickart (1999) noted that the positive and negative phases of the NAO appear to share certain processes in common with the Medieval Warm Period and Little Ice Age. However, the exact relationship between the NAO and these centennial-scale events is poorly understood at present.

Another mode of decadal-scale ocean variability, likely related to the AO and NAO, is recognized by the discharge of large salinity anomalies from the Arctic Ocean into the North Atlantic (Dukhovskoy et al. 2006). Referred to as Great Salinity Anomalies (GSAs), these pulses of freshwater from the Arctic have been well documented during the past three decades and may have occurred earlier in the 20th century as well (Dickson et al. 1988, Belkin et al. 1998, Belkin 2004, Sundby and Drinkwater 2007). Each of the four GSAs since 1970 has had its own distinctive characteristics. Most have entered the North Atlantic from Fram Strait, while it appears that at least one may have entered from the Canadian Archipelago. When viewed in the context of the instrumental record, these GSAs from the Arctic are aptly named. When viewed in the context of the geological record, there is nothing particularly "great" about these salinity anomalies of the 20th century.

Recurring themes in Earth's paleoclimate record

In summary, a reconstruction of Earth's history from its ice and sedimentary records demonstrates that changes in the Arctic atmosphere, ocean, and cryosphere can regulate climate on a variety of spatial and temporal scales. One recurring theme in Earth's history is the importance of Arctic ice expansion and melting in regulating global climate. When the extent of sea ice and continental ice sheets begins to expand, positive ice-albedo feedback mechanisms serve to accelerate an expansion of the cryosphere (Fig. 1a). When melting begins to reduce the extent of sea ice and continental ice sheets, the same ice-albedo feedback mechanisms run in reverse and accelerate a contraction of the cryosphere (Fig. 1b). Processes that trigger these ice-albedo feedback mechanisms can operate on time scales of millions of years, such as the transition from greenhouse to icehouse conditions over much of the Cenozoic era, to time scales of decades to millennia, such as the transitions from interstadial to stadial conditions during the last ice age.

A second recurring theme in Earth's history is the importance of freshwater discharge from the Arctic and adjacent continental ice sheets in regulating global- to basin-scale ocean circulation patterns and climate. On a global scale, large discharges of freshwater into the North Atlantic's subarctic seas can lead to intense stratification of the upper water column and a disruption of NADW formation. A reduction in the formation of NADW can lead to a slowing down of the global ocean's meridional overturning circulation. This can have climatic ramifications for the entire Earth system. On a basin scale, smaller discharges of freshwater from the Arctic, such as the GSAs of recent decades, also can impact ocean circulation patterns and climate; however, these impacts are largely confined to the North Atlantic Basin and its adjacent landmasses.

Ecological Responses to Recent Climate Change

After reviewing Arctic climate change in the past, we are in a better position to interpret the ecological responses to climate change observed recently in the North Atlantic. Two types of ecological responses have been observed in the North Atlantic since 1989. The first of these responses has been a series of biogeographic range expansions by boreal plankton, including renewed trans-Arctic exchange of the North Pacific diatom species *Neodenticula seminae* with the North Atlantic (Reid et al. 2007). During the late 1990s, this diatom indicator species from the Pacific began to reappear throughout the North Atlantic. This reappearance has coincided with a southward expansion in the biogeographic ranges of a number of boreal North Atlantic planktonic species (Johns et al. 2001, Reid and Beaugrand 2002). Such biogeographic range expansions of boreal plankton have been overshadowed by a second response of perhaps greater ecological significance. During the early 1990s, a dramatic regime shift occurred in the shelf ecosystems of the Northwest Atlantic, with both physical and biological processes affected from the Labrador Sea to the Mid-Atlantic Bight. Although we do not have the instrumental nor proxy records to document similar responses far into the past, we can use these observations and our knowledge of climate-change processes to predict future ecosystem responses under different climate-change scenarios.

Biogeographic range expansions of boreal plankton

Trans-Arctic exchanges of boreal plankton between the Pacific and Atlantic are among the more extreme biogeographic range expansions. Such Trans-Arctic exchanges are affected by changes in sea level, ice cover, and ocean circulation. Sea level varies with the amount of ice locked up in continental ice sheets and glaciers. During periods of reduced ice cover, sea level is higher, and the Bering Strait serves as a gateway between the Pacific and Arctic Oceans for the exchange of organisms. In contrast, during periods of extensive ice cover, sea level is lower, and flow through the Strait can be restricted or even completely blocked by the Bering Land Bridge. Once Pacific organisms are in the Arctic Ocean, sea ice cover and circulation patterns determine whether or not they are advected into the North Atlantic through either the Canadian Archipelago or Fram Strait.

The first opening of the Bering Strait dates back to the late Miocene/early Pliocene, between approximately 4.8 to 7.4 Ma (Marincovich and Gladenkov 2001). Despite an apparently open Strait, there is no evidence for trans-Arctic exchanges of organisms from the Pacific to the Atlantic prior to the late Pliocene, approximately 3.5 Ma (Einarsson et al. 1967). It appears that currents may have flowed from east to west during this period and were therefore unfavorable for the advection of organisms from the Pacific to the Atlantic. There is evidence for several faunal invasions during the late Pliocene, before the Strait was closed off again by the emergence of the Bering Land Bridge near the time of the late Pliocene/early Pleistocene boundary. Subsequent invasions during the early to middle Pleistocene enabled *N. seminae* to invade the North Atlantic and contribute to its sedimentary record from approximately 1.2 Ma to 800 ka (Reid et al. 2007). After 800 ka, *N. seminae* disappeared from the sedimentary record of the North Atlantic, implying that trans-Arctic exchanges between the Pacific and Atlantic have been rare or absent until very recently.

Continuous Plankton Recorder (CPR) samples collected from the Labrador Sea during May 1999 contained large numbers of *N. seminae* (Reid et al. 2007). This species has spread rapidly to become a common and abundant member of the phytoplankton flora in the North Atlantic. The spatial distribution of *N. seminae* has increased in subsequent years, extending to the Irminger Sea by 2000 and reaching as far south as 42° N along the North American shelf by 2001. The reappearance of *N. seminae*, after being absent in the sedimentary record for 800 000 years from a region where it was abundant during the early to middle Pleistocene, indicates that a major reorganization of circulation patterns in the Arctic and Atlantic Oceans has occurred during recent decades.

Since the 1980s, dramatic changes have occurred in the Arctic (Arctic Climate Impact Assessment 2005). In 1989, sea level pressure dropped precipitously in the central Arctic, leading to the emergence of a strongly cyclonic atmospheric circulation (Dickson 1999). This cyclonic atmospheric circulation resulted in increased transport of relatively warm, high-salinity Atlantic water into the Arctic Ocean primarily through the Barents Sea (Dickson 1999, McLaughlin et al. 2002). Associated with the cyclonic atmospheric circulation and enhanced inflow of Atlantic water, an extensive reorganization of upper-ocean circulation patterns occurred in the Arctic Ocean (Fig. 2; Dickson et al. 2000). This reorganization brought about the following changes (McLaughlin et al. 2002, Steele et al. 2004, Leong et al. 2005): a shift from the Lomonosov Ridge to the Mendeleyev Ridge of the front separating Atlantic and Pacific water masses, a weakening and deflection of the Transpolar Drift, a weakening and shrinking of the Beaufort Gyre, a intensification and thickening of the Arctic Ocean Boundary Current, and a significant redirection of the shallow Arctic Ocean outflow entering the North Atlantic. The last of these changes was particularly significant because it meant that Fram Strait could no longer be considered the only major route for Pacific-derived halocline and surface waters entering the North Atlantic. Instead, it became clear that a significant fraction of the low-salinity waters entering the North Atlantic, at least during the early 1990s, had emerged from the Canadian Basin via the Canadian Archipelago (Steele et al. 2004).

Dramatic climate-associated changes in the cryosphere accompanied these major shifts in the circulation patterns of the Arctic atmosphere and ocean. Over the past three decades, the melting of permafrost, snow, and ice has increased substantially, which in combination with increased precipitation, has resulted in greater river discharge into the Arctic Ocean (Arctic Climate Impact Assessment 2005, Peterson et al. 2006). Large reductions in the extent and thickness of Arctic sea ice have been observed as well, with satellite imagery revealing extensive summertime ice-free conditions to the north of Canada and Russia during the period 1978–2005 (Hassol and Corell 2006, Serreze et al. 2007). Lindsay and Zhang (2005) have hypothesized that the atmospheric regime shift in 1989 and its subsequent effects on Arctic Ocean circulation pushed the cryosphere beyond a tipping point and triggered a new, internally perpetuating state of accelerated sea ice melting. Their hypothesis suggests that the reorganization of upper ocean circulation forced an extensive flushing of thicker, multi-year sea ice out of the Arctic Basin, which, in turn, increased the amount of summertime open water. By increasing summertime open water beyond a critical threshold, such atmosphere-ocean-cryosphere interactions can initiate the ice-albedo feedback process

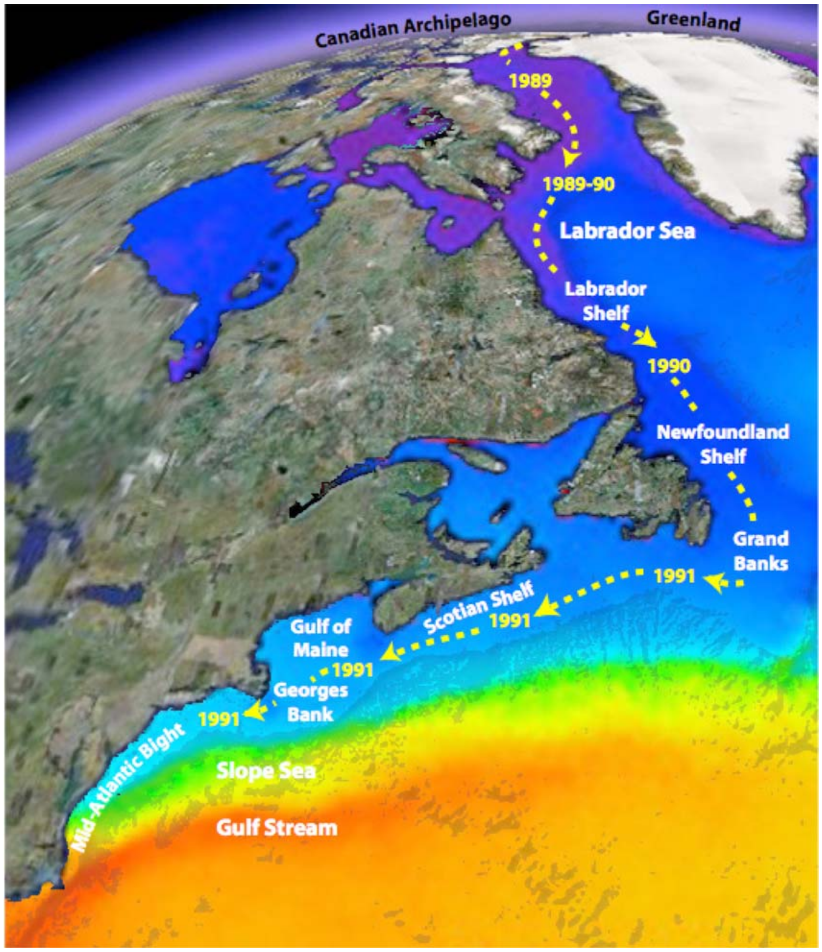

FIG. 3. Shelf waters from the Labrador Sea to the Mid-Atlantic Bight. Colors correspond to mean sea surface temperatures for the decade of the 1990s (from orange [warmest] to purple [coldest]). The dashed yellow line illustrates progression of first low-salinity pulse after it exited the Arctic in 1989 and was advected downstream. Arrival dates, labeled in yellow, are indicated at each of the major shelf ecosystems, labeled in white.

illustrated in Fig. 2b. Once initiated, this internal feedback process may have continued to drive the accelerated melting of Arctic sea ice even after the climate regime shifted out of its strongly cyclonic mode during the late 1990s (Morison et al. 2006).

Changes in the wind-driven circulation of the Beaufort Gyre (Proshutinsky and Johnson 1997, Proshutinsky et al. 2002, Dukhovskoy et al. 2006), in combination with changes in river inflow and sea ice melting (Peterson et al. 2006), have resulted in alternating periods of enhanced freshwater export and enhanced freshwater storage in the Arctic. As mentioned in a previous section, GSAs have been entering the North Atlantic from the Arctic Ocean approximately every decade since the early 1970s (Belkin 2004). Each GSA has its own distinctive characteristics, with most entering the North Atlantic primarily from Fram Strait. The GSA of the early 1990s was unusual, apparently emerging primarily from the Canadian Archipelago during 1989 and sequentially impacting shelf ecosystems downstream from the Labrador Sea to the Mid-Atlantic Bight. The first pulse of low-salinity water reached the Mid-Atlantic Bight by 1991 (Fig. 3). A second GSA advected even lower salinity waters downstream several years later (Fig. 4a). This second GSA, although moving downstream from the Labrador Sea as well, appears to have entered the North Atlantic from Fram Strait rather than the Canadian Archipelago (Belkin 2004). A Fram Strait entry point is supported by the abundance of Pacific-derived halocline and surface waters observed in Fram Strait during the second half of the 1990s (Jones et al. 2003, Falck et al. 2005). After entering Fram Strait, these waters from the Arctic are typically entrained in the East Greenland Current and advected around the southern tip of Greenland where the West Greenland Current carries them the rest of the way to the northern reaches of the Labrador Sea. At present, a definitive entry point for the second 1990s GSA has not been determined.

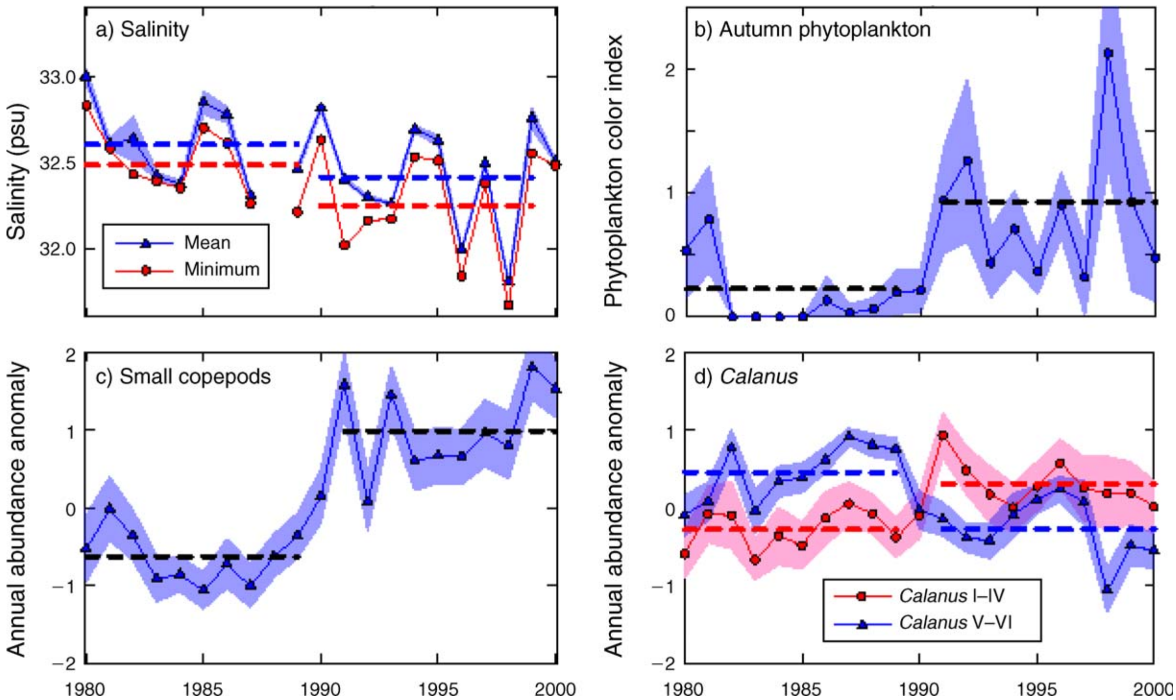

FIG. 4. Northwest Atlantic time series of salinity, phytoplankton, and zooplankton data from Gulf of Maine/Georges Bank Region. Dashed lines indicate mean values during the decades 1980–1989 and 1990–1999; shaded areas correspond to 95% confidence intervals. (a) Time series of annual mean (blue) and minimum (red) salinities as determined with data derived from National Marine Fisheries Service hydrographic surveys. (b) Time series of autumn phytoplankton color index values as determined with data derived from continuous plankton recorder (CPR) surveys. (c) Time series of annual small copepod abundance anomaly values as determined with data derived from CPR surveys. (d) Time series of annual abundance anomaly values for fifth copepodid and sixth adult stages of the large copepod species, *Calanus finmarchicus* (red), and abundance anomaly values for earlier copepodid stages (blue) as determined with data derived from CPR surveys (figure modified from Greene and Pershing [2007]).

This ambiguous entry point for the second GSA also has ecological implications. One might assume that if most of the low-salinity water of Pacific origin entering the North Atlantic during the second half of the 1990s came through Fram Strait, then this would be the logical entry point for *N. seminae* as it invaded during spring 1999. However, during summer 1998, sea ice cover enveloped the northern and northeastern coasts of Greenland into Fram Strait. At the same time, sea ice cover along the northern coast of Canada and into the Canadian Archipelago was at its summertime minimum for the decade from 1996 to 2005 (Reid et al. 2007). This pattern of sea ice cover led Reid et al. (2007) to conclude that *N. seminae* likely invaded the North Atlantic via the Canadian Archipelago despite the large pulse of Pacific-derived waters observed in Fram Strait during the previous two years (Jones et al. 2003, Falck et al. 2005). Hopefully, additional information will clarify this point as the interaction between ocean circulation and ice cover may have important biogeographic consequences.

One final point on recent climate-associated biogeographic range expansions in the North Atlantic is worth noting. While boreal plankton have been shifting further south in the Northwest Atlantic (Johns et al. 2001, Reid and Beaugrand 2002, Reid et al. 2007), the opposite pattern has been observed in the Northeast Atlantic, with subtropical and temperate plankton shifting further north by as much as 1000 km during the past four decades (Beaugrand et al. 2002). Comparable southward shifts by boreal fish species in Northwest Atlantic (Rose et al. 2000, Vilhjálmsson et al. 2005) and northward shifts by subtropical and temperate fish species in the Northeast Atlantic have also been observed (Perry et al. 2005, Vilhjálmsson et al. 2005). Reid and Beaugrand (2002) provide a more complete discussion of the relationship between these shifts in distributional patterns and the hydrometeorological processes driving them.

Regime shift in the Northwest Atlantic

With the enhanced discharge of low-salinity waters from the Canadian Archipelago, shelf waters from the Labrador Sea to the Mid-Atlantic Bight freshened significantly during the 1990s (Loder et al. 2001, Smith et al. 2001, Hakkinen 2002, Mountain 2002, 2003, Frank 2003, Belkin 2004). This freshening occurred in two pulses associated with the two GSAs of the 1990s. Smith et al. (2001) reported the salinity anomaly's first appearance in the Gulf of Maine and Western Scotian Shelf. Subsequent studies reported the salinity anomaly's presence in the Labrador Sea (Hakkinen 2002, Belkin 2004), Middle Atlantic Bight (Mountain 2002, 2003), and Eastern Scotian Shelf (Frank 2003).

The arrival of low-salinity waters throughout the decade increased water-column stratification and appears to have been responsible for a regime shift observed in the Scotian Shelf and Gulf of Maine ecosystems of the Northwest Atlantic (Fig. 4a) (Greene and Pershing 2007). Similar bottom-up ecosystem responses might have been expected elsewhere in the Northwest Atlantic during the 1990s, but have not been reported yet. Enhanced stratification resulted in greater phytoplankton abundance over the year but especially during the autumn and winter when light availability typically limits primary production (Fig. 4b) (Durbin et al. 2003). The increased stratification and associated phytoplankton production coincided with a reorganization of the zooplankton assemblage, with populations of smaller, shelf-associated copepods, like *Centropages typicus*, *Metridia lucens*, *Oithona* spp., and *Pseudocalanus* spp., increasing significantly in abundance (Fig. 4c) (Durbin et al. 2003, Pershing et al. 2005). Early copepodid stages of *Calanus finmarchicus* also increased in abundance with these smaller species; however, later copepodid stages of this more oceanic species declined in abundance (Fig. 4d). Pershing et al. (2005) have suggested that increased size-selective predation by herring may have been behind these paradoxical observations for *C. finmarchicus*. The largest increases in small copepod abundance were observed during late autumn/early winter, a change associated with the enhanced autumn phytoplankton blooms (Durbin et al. 2003). This is also the time of year when most of the *C. finmarchicus* population is diapausing in deep water as late copepodites and not feeding (Marine Ecosystem Responses to Climate in the North Atlantic 2003, 2004).

Commercially harvested fish and crustacean populations in the Northwest Atlantic also underwent large changes in abundance during the 1990s (Frank et al. 2005, 2006, Pershing et al. 2005, Vilhjálmsson et al. 2005). Relative to the 1980s, cod stocks collapsed during the early 1990s. Although overfishing was the predominant cause of this collapse, the cold, low-salinity Arctic waters entering the northern portion of their range from the Canadian Archipelago have hampered the subsequent recovery of cod (Rose et al. 2000, Vilhjálmsson et al. 2005). Other species of fish and crustaceans have increased in abundance during this period (Frank et al. 2005, Pershing et al. 2005, Vilhjálmsson et al. 2005). For certain species, such as snow crab and shrimp, a release from cod predation has been proposed to account for their increased abundances (Frank et al. 2005). While this explanation appears likely (Worm and Myers 2003), it is also important to recognize that these are cold-water boreal species extending their ranges southward as shelf waters become colder and fresher.

Related to the last point, it should be noted that an alternative hypothesis was proposed previously to explain the Northwest Atlantic's regime shift of the 1990s. While we have emphasized Greene and Pershing's (2007) interpretation of this regime shift as a bottom-up ecosystem response to changes in climate, Frank et al. (2005) originally hypothesized that it could be attributed to a top-down trophic cascade initiated by the overfishing of cod and other demersal predatory fish. While some of the direct effects of reduced cod and demersal fish predation on higher trophic levels seem likely (Frank et al. 2006), Greene and Pershing (2007) suggest that bottom-up processes linked to climate change provide a more parsimonious explanation for the observed changes in nutrients, phytoplankton, and zooplankton.

Ecological Responses to Future Climate Change

Throughout much of the Cenozoic era, the cryosphere has played a key role in global climate change. The Quaternary, in particular, has been a period in which the Earth system's climate has undergone dramatic changes in response to fluctuations in the extent of continental ice sheets, sea ice, and NADW formation in the Northern Hemisphere. While the Holocene epoch has exhibited remarkable climate stability relative to the previous glacial period, recent observations of Arctic warming and ice melting have caused scientists to raise serious concerns about the potential for abrupt climate change and dramatic cooling in the Northern Hemisphere, especially in the Northeast Atlantic and northern Europe. These concerns, first raised during the 1990s (Broecker 1997, Rahmstorf 1997), were based on the hypothetical scenario that increases in ice melting and freshwater discharge brought about by greenhouse warming could disrupt NADW formation, diminish the global ocean's meridional overturning circulation, and reduce oceanic heat transport to the Northeast Atlantic and northern Europe (Clark et al. 2002). Although the geological record provides ample evidence for comparable processes operating in the past (McBean et al. 2005), results from more recent climate-change models have downplayed the likelihood of this scenario, at least in the near future, as NADW formation in the Nordic Seas appears to be less sensitive to the kinds of buoyancy forcing anticipated during the present century (Weaver and Hillaire-Marcel 2004). However, results from these same climate-change models do suggest that the Labrador Sea may be a region that is especially sensitive to the effects of greenhouse warming in the Arctic and its associated surface-water freshening (Hillaire-Marcel et al. 2001, Weaver and Hillaire-Marcel 2004). Given its recently recognized sensitivity and role as the gateway into the Northwest Atlantic for remote, buoyancy-driven forcing from the Arctic, the Labrador Sea is now being viewed as the center of action for climate change in the North Atlantic during the 21st century (Dickson et al. 2007). By understanding the

Labrador Sea's role in amplifying and transmitting climate change signals to the surface and intermediate waters of the Northwest Atlantic, scientists will be in a better position to predict the impacts of global climate change on marine ecosystems throughout the North Atlantic basin.

It is reasonable to predict that the recently observed ecological responses to Arctic climate change in the North Atlantic will continue into the near future. In the Northwest Atlantic, we can expect that biogeographic range expansions to the south by boreal plankton and fish species will continue, including new trans-Arctic invasions by boreal species from the Pacific. This southward expansion of biogeographic ranges for boreal species in the Northwest Atlantic will continue to contrast sharply with the northward expansion of biogeographic ranges for subtropical and temperate species in the Northeast Atlantic. The general pattern of northward range expansions in the Northeast Atlantic is unlikely to change significantly in the near future despite the increasing discharge of cold, low-salinity waters from the Arctic. However, if this discharge were to alter surface and thermohaline circulation patterns in a manner that impacted the intensity and/or trajectory of the Gulf Stream (Lund et al. 2006), then biogeographic range changes in the Northeast Atlantic might occur abruptly.

Similar to the biogeographic range responses described above, we can expect ecosystem responses to Arctic climate change to be greater in the Northwest Atlantic than the Northeast Atlantic. The recent regime shift that altered Northwest Atlantic shelf ecosystems during the 1990s may be a good indication of things to come. During periods of enhanced freshwater export from the Canadian Archipelago and Fram Strait, we can expect these ecosystems to support regimes characteristic of the fresher, more stratified conditions observed during the 1990s. Such periods are likely to become more common as climate warming increases the supply of freshwater to the Arctic Ocean through higher rates of precipitation as well as glacial, permafrost, and sea ice melting (Peterson et al. 2006). In addition, the phase of the AO appears to play an important role in regulating freshwater storage in the Beaufort Gyre (Dukhovskoy et al. 2006) as well as the magnitude and pathways of Pacific-derived freshwater export from the Arctic Ocean to the North Atlantic (Morison et al. 2000, Steele et al. 2004). The strongly cyclonic atmospheric circulation, characteristic of highly positive AO conditions, favors periods of greater freshwater export through the Canadian Archipelago and Fram Stait, with proportionally greater increases in the former (Steele et al. 2004). A weakening of this cyclonic circulation, as AO conditions become less positive or negative, appears to favor periods of reduced freshwater export and increased storage in the Beaufort Gyre (Falck et al. 2005, Dukhovskoy et al. 2006). For the past three decades, the AO has exhibited predominantly positive conditions, and several studies have suggested that this may be a response to anthropogenic climate forcing (reviewed by McBean et al. 2005). This provides an additional mechanism for anthropogenic climate change in the Arctic to increase freshwater export to the Northwest Atlantic, thereby supporting the trend towards ecosystem regimes characteristic of fresher, more stratified conditions.

It becomes more difficult to predict ecological responses to climate change in the more distant future as the Earth's climate system is changing so rapidly and scientists are only beginning to understand its inherent nonlinearities. One tipping point in the climate system does deserve special attention because it has been the subject of so much interest and speculation. While it has been generally agreed upon that NADW formation and the global ocean's meridional overturning circulation are likely safe from abrupt change during the 21st century, most models show that both are very sensitive to continued buoyancy forcing from the Arctic as greenhouse warming continues unabated (Schlesinger et al. 2006). Therefore, a great reduction or even a complete shutting down of NADW formation and the global ocean's meridional overturning circulation are real possibilities in the coming centuries. If these were to happen, then many of the atmospheric, cryospheric, and oceanic processes that have been relatively stable over the Holocene would change, and the change would likely be quite abrupt.

In the event of such abrupt climate change, major ecological responses would likely be observed first in the Northeast Atlantic, where reduced heat transport associated with a decrease in the Gulf Stream's intensity would begin to counterbalance the effects of greenhouse warming. It seems reasonable to predict that this change would impede and perhaps even reverse some of the northward biogeographic range expansions that have been observed recently for subtropical and temperate species in the Northeast Atlantic. In addition, it is difficult to believe that a major regime shift would not take place as ecosystems in Northeast Atlantic responded to such dramatic changes in ocean circulation.

The ecological responses in the Northwest Atlantic to such abrupt climate change are more difficult to predict. A decrease in the Gulf Stream's intensity would likely reduce the transport of relatively warm, high-salinity Atlantic water into the Arctic Ocean through the Barents Sea and Fram Strait. How this change would impact the Arctic Ocean's heat and salt budgets and influence its circulation patterns is unknown. In addition, it is unclear how a reduction of oceanic heat transport to the Arctic Ocean would interact with greenhouse warming to alter the cryosphere. If significant ice melting were to continue, then it would likely sustain high levels of freshwater export from the Arctic Ocean into the North Atlantic (Curry et al. 2003, Peterson et al. 2006, Dickson et al. 2007). Should ice melting diminish, then that export would likely decline.

The magnitude and sign of the change in freshwater export from the Arctic Ocean, in addition to the primary route that this freshwater export takes, either via the Canadian Archipelago or Fram Strait, will determine whether biogeographic and ecosystem responses in the Northwest Atlantic continue along the same trajectories as at present or begin to shift in new directions.

Concluding remarks

As we enter the 21st century and face the likelihood of climate changes unprecedented in human history (IPCC 2007), society must anticipate changes in the structure and function of the ecosystems on which we have come to depend. For marine ecosystems, scientists confront a daunting challenge: we must take our modest understanding of marine ecosystem responses to previously observed changes in climate and try to develop models capable of forecasting the fate of these ecosystems in a future shaped by both natural as well as anthropogenic climate forcing. During the past decade, there have been significant advances in our understanding of the linkages between the NAO, a natural mode of climate variability, and observed changes in marine ecosystems on both sides of the North Atlantic (Marine Ecosystem Responses to Climate in the North Atlantic 2001, Ottersen et al. 2001, Drinkwater 2003, Stenseth 2005). In the coming decades, scientists must begin to distinguish between the responses of marine ecosystems to such natural modes of climate variability and their responses to anthropogenic climate change. The Arctic appears to be an important key to understanding the past, present, and future ecological responses of the North Atlantic to climate change.

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