Limnol. Oceanogr., 58(3), 2013, 803–816
© 2013, by the Association for the Sciences of Limnology and Oceanography, Inc.
doi:10.4319/lo.2013.58.3.0803

Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems

Charles H. Greene,[a,*] Erin Meyer-Gutbrod,[a] Bruce C. Monger,[a] Louise P. McGarry,[a] Andrew J. Pershing,[b,c] Igor M. Belkin,[d] Paula S. Fratantoni,[e] David G. Mountain,[f] Robert S. Pickart,[g] Andrey Proshutinsky,[g] Rubao Ji,[h] James J. Bisagni,[i] Sirpa M. A. Hakkinen,[j] Dale B. Haidvogel,[k] Jia Wang,[l] Erica Head,[m] Peter Smith,[m] Philip C. Reid,[1,n] and Alessandra Conversi[n,o,p]

[a] Ocean Resources and Ecosystems Program, Cornell University, Ithaca, New York
[b] Gulf of Maine Research Institute, Portland, Maine
[c] School of Marine Sciences, University of Maine, Orono, Maine
[d] Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island
[e] National Oceanic and Atmospheric Administration National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts
[f] Independent oceanographer, Tucson, Arizona
[g] Department of Physical Oceanography, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts
[h] Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts
[i] School for Marine Science and Technology, University of Massachusetts Dartmouth, New Bedford, Massachusetts
[j] National Aeronautics and Space Administration Goddard Space Flight Center, Greenbelt, Maryland
[k] Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey
[l] Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, Michigan
[m] Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada
[n] Sir Alister Hardy Foundation for Ocean Science, Plymouth, United Kingdom
[o] Institute of Marine Sciences, Italian National Research Council, La Spezia, Italy
[p] Marine Institute, University of Plymouth, Plymouth, United Kingdom

Abstract

Decadal-scale regime shifts in Northwest Atlantic shelf ecosystems can be remotely forced by climate-associated atmosphere–ocean interactions in the North Atlantic and Arctic Ocean Basins. This remote climate forcing is mediated primarily by basin- and hemispheric-scale changes in ocean circulation. We review and synthesize results from process-oriented field studies and retrospective analyses of time-series data to document the linkages between climate, ocean circulation, and ecosystem dynamics. Bottom-up forcing associated with climate plays a prominent role in the dynamics of these ecosystems, comparable in importance to that of top-down forcing associated with commercial fishing. A broad perspective, one encompassing the effects of basin- and hemispheric-scale climate processes on marine ecosystems, will be critical to the sustainable management of marine living resources in the Northwest Atlantic.

An ecosystem regime shift occurs when some perturbation leads to an abrupt restructuring of the ecosystem from one relatively persistent, quasi-equilibrium state to another (Scheffer et al. 2001; Bakun 2005; DeYoung et al. 2008). In large marine ecosystems, regime shifts have often been associated with bottom-up forcing by climate, top-down forcing by commercial fishing, or some combination of the two (DeYoung et al. 2004; Steele 2004). Determining the relative roles of climate and fishing in forcing such regime shifts can be challenging because of our limited understanding of marine ecosystem dynamics and their responses to both natural and anthropogenic perturbations. Here, we focus our attention on the role of climate in forcing decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. Specifically, we explore the processes linking the dynamics of these ecosystems to two sources of high-latitude climate variability and change, one associated with climate forcing within the North Atlantic Basin and the other associated with climate forcing from the Arctic. We conclude by discussing the implications of our findings for the management of marine living resources within these ecosystems during the coming decades. Table 1 lists acronyms used in the present paper.

Shelf ecosystem responses to climate forcing within the North Atlantic Basin

In the North Atlantic Ocean, the major basin-scale mode of interannual to inter-decadal climate variability is the North Atlantic Oscillation (NAO) (Hurrell et al. 2003; Hurrell and Deser 2010). As quantified by the station-based NAO index (Table 2) (Hurrell 1995), this mode is

* Corresponding author: chg2@cornell.edu

[1] Present address: Marine Institute, University of Plymouth, Plymouth, United Kingdom, Marine Biological Association of the United Kingdom, Plymouth, United Kingdom

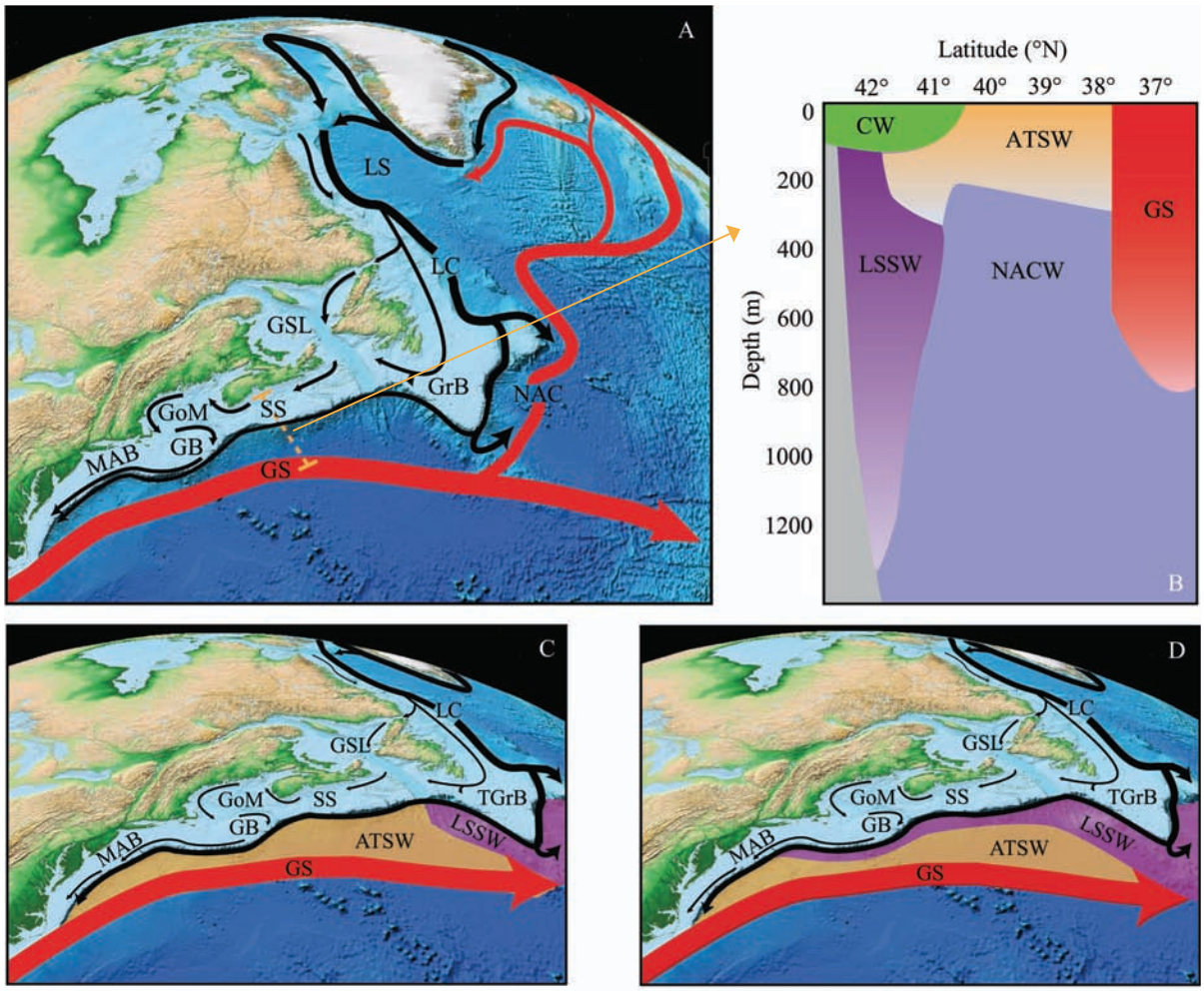
Table 1. List of acronyms.

AO	Arctic Oscillation
AOO	Arctic Ocean Oscillation
ATSW	Atlantic Temperate Slope Water
CAA	Canadian Arctic Archipelago
CPR	Continuous Plankton Recorder
CSWS	Coupled Slope Water System
GSA	Great Salinity Anomaly
LSSW	Labrador Subarctic Slope Water
NAO	North Atlantic Oscillation
RSWS	Regional Shelf Water Salinity
RSWT	Regional Slope Water Temperature
STARS	Sequential *t*-Test Analysis of Regime Shifts

characterized by shifts in the atmospheric pressure gradient over the North Atlantic Basin during winter. Positive values of the NAO index correspond to an enhanced pressure gradient between centers of the two major atmospheric pressure systems in the North Atlantic, the Azores subtropical high and Icelandic subpolar low; negative values correspond to a reduced pressure gradient between these two atmospheric centers of action (Jones et al. 2003). Shifts in the NAO have been linked to basin-scale changes in storm track and wind field patterns, heat transport, precipitation, sea ice, and major reorganizations of ocean circulation (Hurrell et al. 2003; Visbeck et al. 2003; Drinkwater et al. 2009). These changes also have been correlated with significant regional responses of marine

Table 2. Time series analyzed in this paper.

Index	Description	References
AO index	The first mode derived from an empirical orthogonal function analysis of the winter sea level pressure field in the Northern Hemisphere above 20°N	Thompson and Wallace 1998; Thompson et al. 2000
AOO index	The model-derived sea surface height gradient near the center of the Arctic Basin; it provides a measure of geostrophic circulation in the Arctic Ocean, with positive (negative) values corresponding to anticyclonic (cyclonic) circulation	Proshutinsky and Johnson 1997; Dukhovskoy et al. 2006
Autumn Phytoplankton Color index	The mean color index anomaly calculated each autumn from Gulf of Maine CPR survey data	Greene and Pershing 2007
Calanus finmarchicus Abundance index	The mean abundance anomaly calculated each year from Gulf of Maine CPR survey data; it is calculated separately for early juveniles (copepodites 1–4) and late stages (copepodite 5 and adults) of this species	MERCINA 2001; Pershing et al. 2005
NAO index	The mean atmospheric pressure difference during winter between the North Atlantic subtropical high-pressure system, measured in Lisbon, Portugal, and the subpolar low-pressure system, measured in Stykkishólmur, Iceland	Hurrell 1995
Right Whale Calving index	The annual calving rate anomaly per reproductively viable female in the population relative to the climatological mean rate from 1980 to 2010. The annual calving rate is the number of individually identified females accompanied by calves observed during a year beginning in December of the preceding calendar year	Greene et al. 2003; Waring et al. 2011
RSWS index	The first mode derived from a principal components analysis of shelf-water salinity data from the Scotian Shelf–Gulf of Maine–Georges Bank region. Salinity time-series data are derived from two databases, the most comprehensive of which only covers the period 1950–2003. The analysis was extended through 2009 by using a less comprehensive database archived at the Northeast Fisheries Science Center in Woods Hole, Massachusetts. This extended analysis was done by conducting a linear regression analysis between the two data sets during their period of overlap, 1977–2003, and using this regression relationship ($y=0.347x$; $r^2=0.82$) to transform values from the less comprehensive data set, x, to values on the same scale as those from the more comprehensive data set, y, over the period 1950–2009	MERCINA 2012; further information on less comprehensive time series available from author P.S.F. (paula.fratantoni@noaa.gov)
RSWT index	The first mode derived from a principal components analysis of slope water temperature data from the region; it serves as an indicator of the state of the CSWS, with positive (negative) values corresponding to maximum and warmer (minimum and cooler) modal state conditions	MERCINA 2001
Small Copepod Abundance index	The first mode derived from a principal components analysis of abundance index values calculated each year from Gulf of Maine CPR survey data for the small copepod species *Centropages typicus*, *Metridia lucens*, *Oithona* spp., and *Pseudocalanus* spp.	Pershing et al. 2005; MERCINA 2012



ATSW	Atlantic Temperate Slope Water	LS	Labrador Sea
CW	Coastal Water	LSSW	Labrador Subarctic Slope Water
GB	Georges Bank	MAB	Middle Atlantic Bight
GoM	Gulf of Maine	NAC	North Atlantic Current
GrB	Grand Banks	NACW	North Atlantic Central Water
GS	Gulf Stream	SS	Scotian Shelf
GSL	Gulf of St. Lawrence	TGrB	Tail of the Grand Banks
LC	Labrador Current		

Fig. 1. (A) Circulation patterns for the Northwest Atlantic Ocean, emphasizing the Gulf Stream and Labrador Current systems. (B) Hydrographic section corresponding to dashed line shown in panel A. (C) Maximum modal state of CSWS. (D) Minimum modal state of CSWS. Acronyms for geographic features, water masses, and currents are listed below figure panels. Illustrations are copied or revised with permission from MERCINA (2001, 2012).

ecosystems on both sides of the North Atlantic, including the Baltic Sea (Hanninen et al. 2000; Alheit et al. 2005); Barents Sea (Ottersen and Stenseth 2001; Sirabelli et al. 2001; Mueter et al. 2009); Bay of Biscay, Celtic Sea, and English Channel (Beaugrand et al. 2000); Mediterranean Sea (Molinero et al. 2005; Conversi et al. 2010); North Sea (Reid et al. 2001; Sirabelli et al. 2001; Lynam et al. 2004); Georges Bank (MERCINA 2004); Gulf of Maine (Conversi et al. 2001; MERCINA 2001; Piontkovski and Hameed 2002); and Scotian Shelf (Sameoto 2001, 2004). The abundance and recruitment of commercially important fish stocks in these ecosystems also have been correlated with phase changes in the NAO (Attrill and Power 2002; Drinkwater et al. 2003; Ottersen et al. 2004, 2010).

The region of the Northwest Atlantic most sensitive to direct atmospheric forcing associated with the NAO is the Labrador Sea (Fig. 1). Winds out of the Canadian Arctic, which strengthen during positive phases of the NAO and weaken during negative phases, regulate heat flux and deep convection in the central Labrador Sea. In turn, these open-ocean processes influence circulation patterns in the North Atlantic's Deep Western Boundary Current as well as its subpolar and subtropical gyres (Curry and McCartney 2001; Yashayaev et al. 2008). Closer to the North American

continent, precipitation, runoff, and ice freezing and melting processes associated with the NAO influence the Labrador Current's hydrography and transport along the outer shelf and slope of the Labrador Sea's western margin. These upstream processes are the primary source of NAO-associated remote forcing on shelf ecosystems extending from Labrador to the Middle Atlantic Bight.

Being buoyancy driven, the Labrador Current responds to processes in the Canadian Arctic and Atlantic Provinces that alter its freshwater and salt content. Near Newfoundland's Grand Banks, the offshore component of the Labrador Current splits in two, with most of its volume transport veering eastward to join the North Atlantic Current, while a smaller branch veers westward around the Tail of the Grand Banks towards the Gulf of St. Lawrence and Scotian Shelf (Fig. 1A). Before reaching this bifurcation point, the Labrador Current's offshore component tends to run colder and fresher during positive phases of the NAO (Petrie and Drinkwater 1993; Loder et al. 2001). These positive NAO-associated hydrographic characteristics result from increased ice melting and runoff in the Canadian Arctic and Labrador.

Paradoxically, hydrographic responses to the NAO appear reversed in shelf and slope waters downstream of the Grand Banks. These waters tend to be warmer and saltier during positive phases of the NAO and colder and fresher following prolonged periods of the negative phase (Petrie 2007). These counterintuitive observations are the result of NAO-associated changes in the Labrador Current's volume transport at the shelf break, west of the bifurcation point near the Tail of the Grand Banks. During positive phases of the NAO, a lesser volume of the colder and fresher Labrador Current water turns southwest and mixes with the warmer and saltier shelf and slope waters downstream. In contrast, during negative phases of the NAO, a greater volume of Labrador Current water veers to the west along the shelf break, leading to greater cooling and freshening of the shelf and slope waters downstream (Petrie and Drinkwater 1993; Loder et al. 2001; Petrie 2007). This phenomenon appears to be related to a southward expansion of the wind-driven subpolar gyre during negative NAO conditions as well as an increase in the Labrador Current's baroclinic component at the shelf break in the Labrador Sea (Myers et al. 1989; Marsh et al. 1999; Marsh 2000). In addition, a wind-driven seasonal cycle in that component preferentially enhances the westward volume transport at the Tail of the Grand Banks during winter (Marsh 2000).

The NAO-associated remote forcing of shelf ecosystems downstream from the Grand Banks is often mediated by the Northwest Atlantic's Coupled Slope Water System (CSWS) (Pickart et al. 1999; MERCINA 2001). The CSWS refers to the dynamic interplay of two slope-water masses, the Labrador Subarctic Slope Water (LSSW; previously referred to as Labrador Slope Water [Gatien 1976]) and Atlantic Temperate Slope Water (ATSW; previously referred to as Warm Slope Water [Gatien 1976]) (Fig. 1B–D). The relatively cold and fresh LSSW extends from the northeast and is a mixture of Labrador Current Water and North Atlantic Central Water situated below the Coastal Water along the upper continental slope. The ATSW is a relatively warmer and saltier mixture of Coastal Water and Gulf Stream Water. In hydrographic sections to the southwest and beyond the range of LSSW, the ATSW is situated below the Coastal Water along the upper continental slope and occurs at the surface further offshore. In hydrographic sections to the northeast in which it co-occurs with LSSW, the ATSW lies further offshore, located between the Gulf Stream on its oceanic side and the Coastal Water and LSSW on its continental margin side (Fig. 1B).

Two modal states have been identified for the CSWS (Pickart et al. 1999; MERCINA 2001). The maximum mode corresponds to a state in which Labrador Current transport around the Tail of the Grand Banks is reduced, and the frontal boundary of ATSW advances upstream along the continental margin as far as the Gulf of St. Lawrence (Fig. 1C). The minimum mode corresponds to a state in which Labrador Current transport around the Tail of the Grand Banks is increased, and the frontal boundary of LSSW advances downstream along the continental margin as far as the Middle Atlantic Bight, displacing the ATSW offshore (Fig. 1D).

The Regional Slope Water Temperature (RSWT) index was developed to quantify the state of the CSWS (Table 2) (MERCINA 2001). During periods when this index is positive, the contribution of LSSW is reduced, and slope waters are warmer. During periods when the RSWT index is negative, the contribution of LSSW is greater, and slope waters are cooler. Greene and Pershing (2003) demonstrated that it is possible to forecast with considerable skill the RSWT index in a given year from a model incorporating the previous year's RSWT index and NAO index. In their interpretation of the model, they suggested that the value of the previous year's RSWT index captures the CSWS's inertia and resistance to change, while the value of the previous year's NAO index provides the forcing necessary to shift the system from one modal state towards the other.

Trends in the NAO have been linked to shifts between the two modes of the CSWS (MERCINA 2001) (Fig. 2A,B). During the decade of the 1960s, the NAO index was predominantly negative, and the CSWS exhibited conditions characteristic of its minimum modal state. In contrast, from 1972 to 1995, the NAO index was predominantly positive, with especially high values observed from the late 1980s to mid-1990s (Fig. 2A), whereas the CSWS exhibited conditions characteristic of its maximum modal state. A pronounced, 1 yr shift from the maximum to minimum modal state occurred during 1998 in response to the 20th century's largest drop of the NAO index during winter 1996. Subsequently, the North Atlantic entered a period of positive but unusual NAO conditions during the late 1990s (Hurrell and Dickson 2004), followed by fluctuating positive and negative NAO conditions during the decade of the 2000s (Fig. 2A). Strongly negative NAO conditions returned during the recent winters of 2010 and 2011; however, no evidence has emerged yet for the CSWS returning to the minimal modal state conditions last observed during 1998.

NAO-associated changes in the CSWS over the past 50 yr have had major effects on marine ecosystems throughout

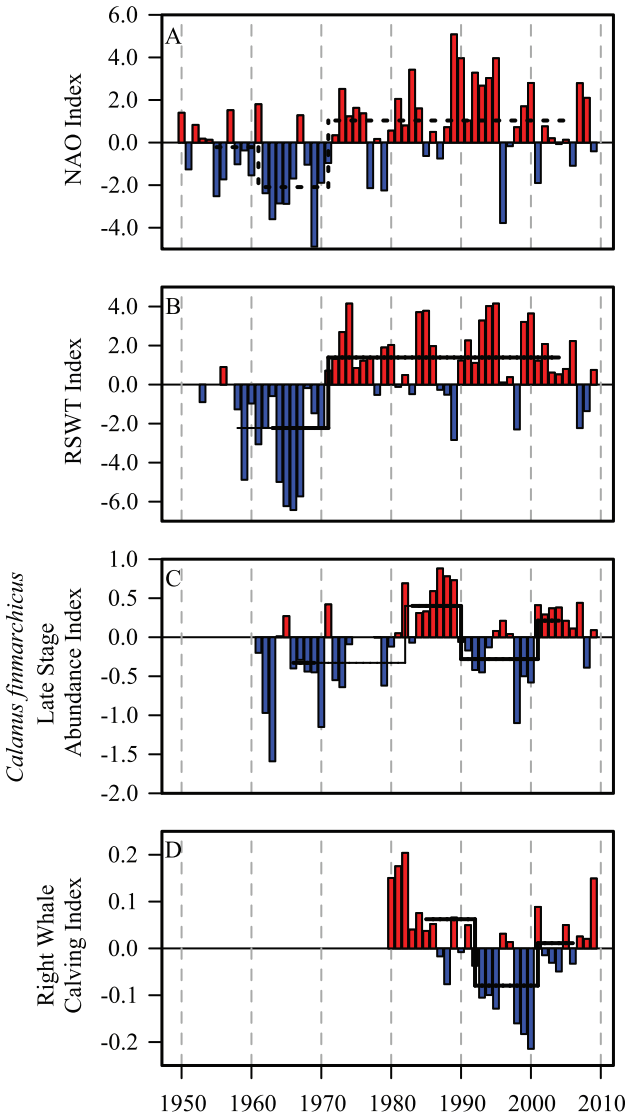


Fig. 2. Time series from the North Atlantic Ocean: (A) annual values of the NAO index, (B) annual values of the RSWT index, (C) annual values of the *Calanus finmarchicus* Late Stage Abundance index, (D) annual values of Right Whale Calving index (Table 2). Positive values of indices above the climatological mean are shaded in red; negative values below the climatological mean are shaded in blue. A sequential *t*-test analysis of regime shifts (STARS; Rodionov 2004) was applied to each of the time series. For analyses of decadal-scale regime shifts, cutoff lengths of L = 5 and L = 10 yr were tested. L = 10 yr provided the best fit for all time series. Regime shifts significant at the $p = 0.05$ level are shown by thick solid black lines; those significant at the $p = 0.10$ level are shown by thick dashed black lines. A STARS was applied conservatively when gaps appeared in the time-series data. Regimes were indicated with thick lines 0.5L before such gaps and 0.5L after such gaps; thin lines were used in gaps where data were interpolated for the STARS.

the Northwest Atlantic (Fig. 2) (MERCINA 2001; Drinkwater et al. 2003; Pershing et al. 2004). The springtime zooplankton biomass and secondary production in much of this region is dominated by the copepod species *Calanus finmarchicus* (MERCINA 2003). An annual *C. finmarchicus* Abundance index (Table 2) (MERCINA 2001), derived from continuous plankton recorder (CPR) surveys conducted in the Gulf of Maine, provides one indicator of ecosystem responses to NAO-forced changes in the CSWS (Fig. 2A–C). During the 1960s, when the NAO index was in a negative regime, and the CSWS was in its minimum modal state, slope-water temperatures and *C. finmarchicus* abundance were relatively low. During the 1980s, when the NAO index was predominantly positive and the CSWS was predominantly in its maximum modal state, slope-water temperatures and *C. finmarchicus* abundance were relatively high. As will be described in the next section, interpretations since the early 1990s have been more complicated due to the increasing importance of remote climate forcing from the Arctic. Nevertheless, the pronounced, single-year drop in the NAO index during winter 1996 triggered an intense modal shift of the CSWS during 1998, which in turn was associated with very low abundances of *C. finmarchicus* during 1998 and early 1999. The physical–biological coupling underlying these climate-driven changes in *C. finmarchicus* abundance have not been fully resolved; however, they appear to be linked to the advective supply of this species into the Gulf of Maine–Scotian Shelf region from slope-water intrusions and/or shelf transport processes further upstream (Greene and Pershing 2000; MERCINA 2001; Pershing et al. 2009). Ongoing research is attempting to document the timing and mechanisms underlying these processes.

Marine ecosystem responses to NAO-associated oceanographic changes also have been detected at trophic levels higher than the one occupied by *C. finmarchicus*. Drinkwater et al. (2003) noted that Atlantic cod (*Gadus morhua*) is a good choice for investigating the responses of commercially exploited fish populations to NAO-associated forcing because climate variability has been shown to affect its recruitment, growth, and distribution on both sides of the North Atlantic. Cod recruitment and growth responses vary by region, with northern (southern) stocks responding more favorably to oceanographic changes that result in warmer (cooler) temperatures (Beaugrand and Kirby 2010). During the recent decades of predominantly positive NAO conditions, Labrador–Newfoundland stocks have tended to exhibit reduced recruitment and growth rates in response to the region's colder temperatures. The unfavorably cold waters have suppressed the recovery of these heavily overfished stocks even after a complete moratorium on their harvesting was implemented during the 1990s (Drinkwater et al. 2002). In contrast, on the opposite side of the North Atlantic, the predominantly positive NAO conditions of recent decades have resulted in warmer waters and more favorable conditions for the recruitment and growth of Arcto-Norwegian cod stocks in the Barents Sea (Ottersen and Stenseth 2001). Warmer waters also have characterized this time period in the Gulf of Maine, Georges Bank, and southern New England where Brodziak and O'Brien (2005) found significant cross correlations between the NAO index time series lagged by 2 yr and the recruit per spawner index time series for two cod stocks and seven of 10 other commercially important groundfish stocks. These authors hypothesized that the observed 2-yr lag corresponds to the time it takes the CSWS to respond to NAO forcing and alter

hydrographic conditions in a manner that affects larval and early juvenile groundfish survival.

Population responses of the highly endangered North Atlantic right whale (*Eubalaena glacialis*) also have been linked to the NAO. Greene and colleagues (Greene et al. 2003; Greene and Pershing 2004) demonstrated that a rapid decline followed by a sharp spike in right whale calving rates during the late 1990s could be linked to climate-associated fluctuations in *C. finmarchicus* abundance (Fig. 2C,D). Using a stochastic reproduction model, in which the transitional probabilities among female reproductive states depended only on *C. finmarchicus* abundance, these authors were able to demonstrate the model's potential for accurately forecasting right whale calving rates. The model not only reproduced the rapid decline in calving rates during 1999 and 2000, it also predicted the dramatic increase in right whale calves born during 2001. Subsequent demographic modeling by Samuel (2008) has assessed the sensitivity of right whale population projections to different feeding conditions under various climate scenarios. Her model results demonstrate that climate-associated changes in feeding conditions can determine whether this endangered population is on a trajectory to recovery or extinction.

Shelf ecosystem responses to climate forcing from the Arctic

Anthropogenic greenhouse warming has contributed to historically unprecedented changes in the Arctic's cryosphere and hydrological cycles during the past three decades. The massive loss of multiyear sea ice and the rapid decline of summertime sea-ice extent have been the most obvious changes observed (Serreze et al. 2007; Stroeve et al. 2011). In addition, the elevated levels of high-latitude warming have led to significant increases in precipitation, river runoff, and glacial discharge (Peterson et al. 2006; Serreze et al. 2008). These phenomena have arisen from both the amplification of processes associated with the Arctic's natural modes of climate variability as well as from the introduction of processes not clearly associated with such modes (Greene 2012). Regardless of their exact origin, the processes responsible for the observed changes in the Arctic's cryosphere and hydrological cycles have had major effects on the Arctic Ocean's salt budget and freshwater export to the North Atlantic (Dickson et al. 2008). This export of freshwater has been episodic and often characterized by large discharges of ice and low-salinity liquid water that subsequently have gone on to form the Great Salinity Anomalies (GSAs) observed in the North Atlantic since the late 1960s (Belkin et al. 1998; Belkin 2004). It is the downstream propagation of these GSAs along North America's eastern seaboard that completes the teleconnection between the Arctic's climate system and the shelf ecosystems of the Northwest Atlantic. In this section, we will review our current understanding of (1) the role of the Arctic's climate system in regulating freshwater export to the North Atlantic, (2) the effects of this freshwater export on the shelf circulation and hydrography of the Northwest Atlantic, and (3) the responses of the region's shelf ecosystems to such remote forcing from the Arctic.

The Arctic Oscillation (AO) is the most important mode of interannual to inter-decadal climate variability above the Arctic Circle (Thompson and Wallace 1998; Thompson et al. 2000). Sometimes referred to as the Northern Annular Mode in the climate dynamical literature, the AO can be quantified by the AO index, the first empirical orthogonal function of the Northern Hemisphere's sea level pressure field from 20°N to the pole (Table 2). It has been suggested that the NAO is a North Atlantic manifestation of the AO; however, the former corresponds to variability in the pressure field between the subtropical high and subpolar low in the North Atlantic, whereas the latter is hemispheric in scale and extends all the way to the pole. Thus, while indices of the NAO and AO are strongly correlated (r^2 = 0.85 [Hurrell and Deser 2010]), the AO better reflects atmospheric phenomena occurring at higher latitudes (Greene 2012).

The phase of the AO index can play an important although variable role in regulating the salt budget of the Arctic Ocean (Houssais and Herbaut 2011) and the magnitude of freshwater export from the Arctic Ocean to the North Atlantic (Steele et al. 2004). In 1989, sea level pressure dropped precipitously in the central Arctic and a strongly cyclonic atmospheric circulation anomaly occurred, coinciding with the most positive AO index of the 20th century (Fig. 3A) (Dickson 1999). This atmospheric circulation anomaly persisted as a cyclonic regime until 1996 and affected circulation patterns both below and above the Arctic Ocean's halocline throughout this period (Fig. 4). Below the halocline, there was enhanced transport of relatively warm, high-salinity North Atlantic water into the Arctic Ocean primarily through the Barents Sea (Dickson 1999; McLaughlin et al. 2002). Above the halocline, there was a major reorganization of upper-ocean circulation patterns, especially in the Beaufort Gyre. Since a cyclonic atmospheric circulation regime runs counter to the Beaufort Gyre's anticyclonic circulation, the gyre began spinning down, a process indicated by the shift to negative values of the Arctic Ocean Oscillation (AOO) index (Table 2; Fig. 3B) (Proshutinsky and Johnson 1997; Dukhovskoy et al. 2006). With the gyre spinning down, freshwater was released from storage, resulting in an increase in the Arctic Ocean's freshwater export above the halocline into the North Atlantic (Steele et al. 2004). These conditions reversed themselves abruptly in 1996 when a strongly anticyclonic atmospheric circulation anomaly occurred, putting an end to the 6 yr long cyclonic regime (Fig. 3A).

It has been proposed that anthropogenic climate change played an important role in generating the strongly positive AO (and NAO) conditions observed between 1989 and 1995. Modeling studies suggest that greenhouse warming of the troposphere results in cooling of the stratosphere, and such stratospheric cooling can amplify positive AO conditions (Shindell 2003). The extremely positive AO conditions observed during the late 1980s to mid-1990s were associated with pulsed discharges of low-salinity water from the Arctic Ocean into the North Atlantic (Dukhovskoy et al. 2006). The two freshwater pulses observed during the 1990s are part of a series of GSAs that have been

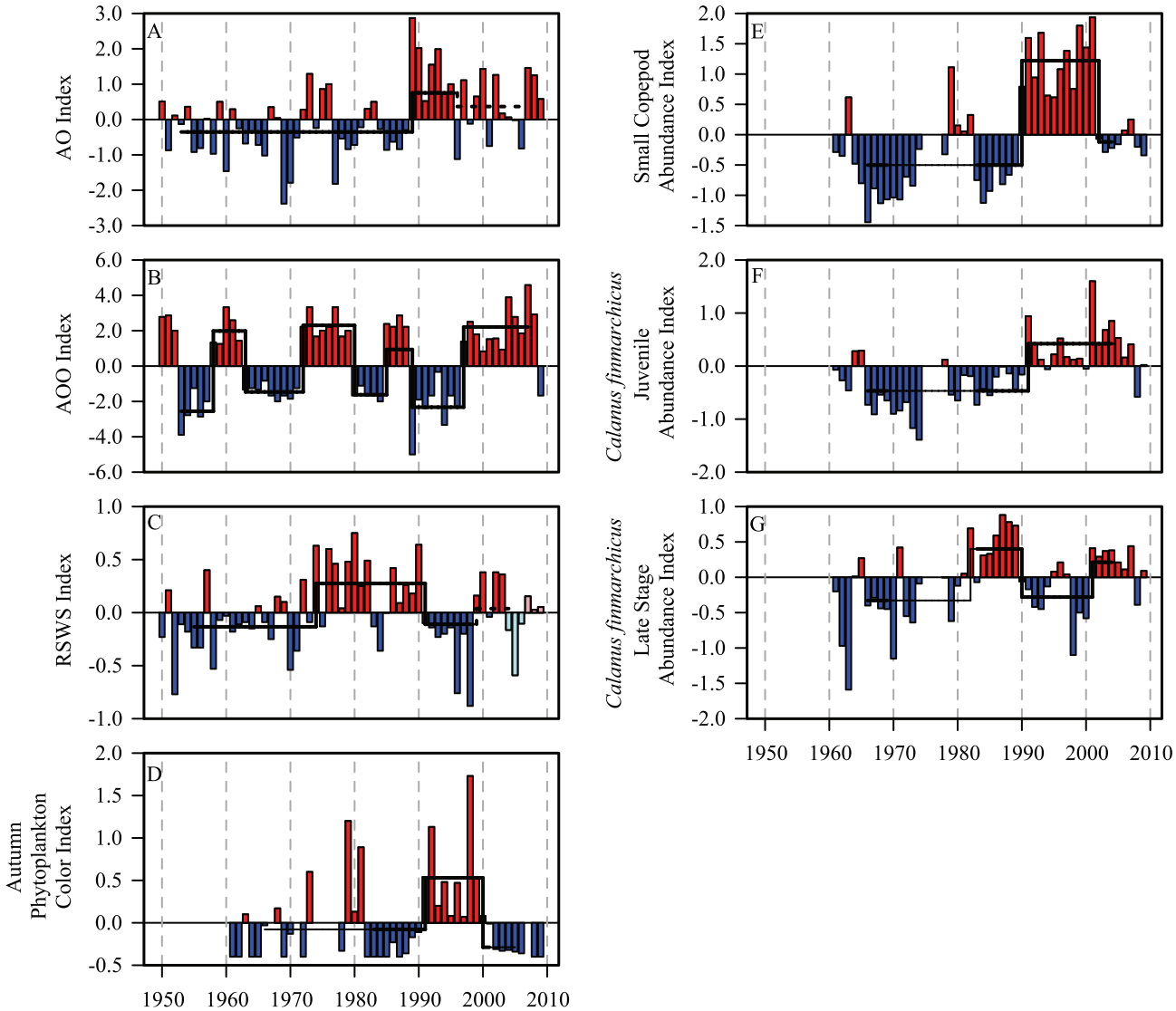


Fig. 3. Time series from the Arctic and North Atlantic Oceans: (A) annual values of the AO index, (B) annual values of the AOO index, (C) annual values of the RSWS index, (D) annual values of the Autumn Phytoplankton Color index, (E) annual values of the Small Copepod Abundance index, (F) annual values of the *Calanus finmarchicus* Early Juvenile Abundance index, (G) annual values of the *C. finmarchicus* Late Stage Abundance index (Table 2). Positive values of indices above the climatological mean are shaded in red; negative values below the climatological mean are shaded in blue. Different shades of red and blue were used to distinguish the RSWS index calculated from the more comprehensive data set collected prior to 2003 and the RSWS index calculated from the less comprehensive data set collected after 2003 (Table 2). A STARS was applied to each of the time series. For analyses of decadal-scale regime shifts, cutoff lengths of L = 5 and L = 10 yr were tested. L = 5 yr provided better fits for the AO index and AOO index time series; L = 10 yr provided better fits for all other time series. Statistically significant regime shifts were detected in all time series at $p = 0.05$. Regime shifts significant at the $p = 0.05$ level are shown by solid black lines; those significant at the $p = 0.10$ level are shown by dashed black lines. A STARS was applied conservatively when gaps appeared in the time-series data. Regimes were indicated with thick lines 0.5L before such gaps and 0.5L after such gaps; thin lines were used in gaps where data were interpolated for the STARS.

documented since the late 1960s (Belkin et al. 1998; Belkin 2004; Greene et al. 2008). Three GSAs have been recognized in the literature (1970s GSA, 1980s GSA, 1990s GSA), each with its own distinctive characteristics (Belkin 2004). All of these GSAs appear to have resulted primarily from the export of ice and low-salinity liquid water from the Arctic Ocean to the North Atlantic via either Fram Strait or the Canadian Arctic Archipelago (CAA). Relative to the earlier GSAs, the first pulse of the 1990s GSA was characterized by a large contribution of low-salinity liquid water from the CAA (Houssais and Herbaut 2011). This observation is consistent with recent modeling results, which suggest that one consequence of anthropogenic climate change may be an increase in liquid freshwater export out of the CAA (Koenigk et al. 2007).

This first GSA pulse of the early 1990s sequentially affected shelf ecosystems downstream from the Labrador Sea, with its leading edge of low-salinity water eventually

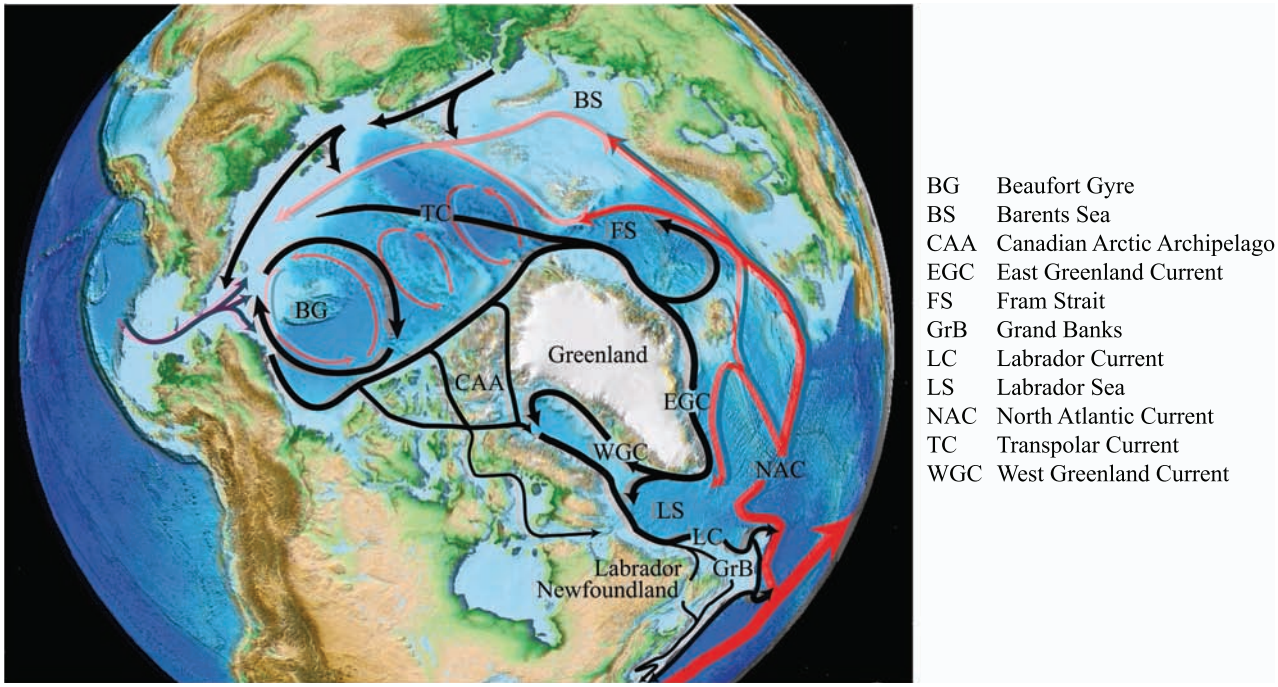


Fig. 4. Circulation patterns for the Arctic Ocean, emphasizing upper ocean inflows and outflows with North Pacific and North Atlantic Oceans. Acronyms for geographic features and currents are listed beside the figure panel. Illustration is copied with permission from MERCINA (2012).

reaching the Scotian Shelf–Gulf of Maine–Georges Bank region by 1991 (Fig. 3C) (Greene and Pershing 2007; Greene et al. 2008; MERCINA 2012). The MERCINA Working Group hypothesized that increased volume flux from the Arctic Ocean into the North Atlantic remotely forced the movement of fresher water masses downstream, well in advance of the arrival of any Arctic-derived water (MERCINA 2012). They estimated that, with an advective speed of 4 cm s^{-1}, such Arctic-derived waters would not have reached the Scotian Shelf–Gulf of Maine–Georges Bank region until 1993 or 1994. These are the years during the early 1990s when the lowest salinities were observed as boundary fluxes into the Gulf of Maine from the Western Scotian Shelf (Smith et al. 2001).

A second GSA pulse, one associated with even lower salinities, propagated downstream several years later (Fig. 3C). This subsequent pulse, although propagating through the Labrador Sea as well, appears to have had a greater contribution from the Fram Strait than from the CAA (Belkin 2004; MERCINA 2012). Atmospheric pressure conditions in the Arctic, as quantified by the Dipole Anomaly index, produced a wind-driven meridional transport of sea ice and upper ocean waters across the Arctic Ocean Basin and into the North Atlantic's Greenland Sea through Fram Strait (Wang et al. 2009). A Fram Strait entry point is further supported by the abundance of Pacific-derived halocline and surface waters observed in the strait during the second half of the 1990s (Falck et al. 2005). After entry into the Greenland Sea, principally as sea ice but also as low-salinity water of both Arctic and Pacific origin, this salinity anomaly would likely have followed the path of the 1970s GSA, first along the East Greenland Current, subsequently around the southern tip of Greenland, and then along the West Greenland Current to the northern reaches of the Labrador Sea (Fig. 4).

Both GSA pulses of the 1990s produced significant freshening in the shelf waters from the Labrador Sea to the Mid-Atlantic Bight (Fig. 3C) (Loder et al. 2001; Hakkinen 2002; Mountain 2003). By enhancing water-column stratification during the autumn and winter, this freshening is thought to be largely responsible for the ecosystem regime shifts observed in the Scotian Shelf, Gulf of Maine, and Georges Bank ecosystems during the 1990s (Greene and Pershing 2007; Greene et al. 2008; MERCINA 2012). Typically in high-latitude pelagic ecosystems, thermal stratification of the water column breaks down with atmospheric cooling during autumn, and phytoplankton primary production becomes light limited until thermal stratification returns during the subsequent spring. However, the freshening of Northwest Atlantic shelf waters during the 1990s appears to have provided sufficient buoyancy to maintain water-column stratification and extend the phytoplankton growing season throughout the autumn and into the winter (Fig. 3D). Greene and colleagues (Greene and Pershing 2007; Greene et al. 2008; MERCINA 2012) hypothesized that this extended phytoplankton growing season led to more favorable feeding conditions and an increase in the abundance of small copepod species like *Centropages typicus*, *Metridia lucens*, *Oithona* spp., and *Pseudocalanus* spp. (Fig. 3E) (Pershing et al. 2005). The younger copepodid stages of *C. finmarchicus* also increased in abundance with these smaller species;

however, the older copepodid and adult stages were observed to decline (Fig. 3F,G). Pershing et al. (2005) hypothesized that increased size-selective predation on the larger and older stages of *C. finmarchicus* during an outbreak in the herring (*Clupea harengus*) population may help explain this apparent paradox.

Large changes in the abundance of commercially exploited fish and crustacean populations were also observed in the Northwest Atlantic during the 1990s (Pershing et al. 2005; Vilhjálmsson et al. 2005; Greene et al. 2008). While overfishing was largely responsible for the collapse of cod stocks during the early 1990s, recovery of these stocks in much of Atlantic Canada was inhibited by the cold waters advected into the region (Rose et al. 2000; Drinkwater et al. 2002) and possibly by a reversal of predator–prey interactions with forage fish populations (Frank et al. 2011). With a release from cod predation, other fish and crustacean species increased in abundance during this time period, including capelin (*Mallotus villosus*), herring, and sand lance (*Ammodytes dubius*) (Frank et al. 2005, 2011) as well as snow crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*) (Worm and Myers 2003). For the snow crab and northern shrimp, it is also important to recognize that environmental conditions become more favorable for these more northern species as shelf waters become colder and fresher (Greene and Pershing 2007; Greene et al. 2008, 2009).

Farther south on Georges Bank, elevated heat flux from the atmosphere to ocean counteracted the advection of colder waters from the north, eliminating consistent differences in shelf-water temperatures between the decades of the 1980s and 1990s (Mountain 2003). Nevertheless, Mountain and Kane (2010) reported that first-year survivorship of Georges Bank cod declined during the 1990s relative to the previous decade. By analyzing first-year survivorship based on the ratio of first-year recruitment to hatched egg abundance, these authors demonstrated that larval and juvenile survivorship for cod was lower in the 1990s than in the 1980s. In contrast, first-year survivorship of Georges Bank haddock (*Melanogrammus aeglefinus*) increased between the 1980s and 1990s. Mountain and Kane (2010) hypothesized that these contrasting survivorship responses were associated with differences in the nutritional ecology of cod and haddock. Specifically, they hypothesized that, as mediated by the limited availability of juvenile benthic habitat, the prey and feeding conditions were more favorable for larval and juvenile cod prior to the ecosystem regime shift and were more favorable for larval and juvenile haddock after it.

After 1996, the Arctic's atmospheric circulation regime became more neutral, with the AO index fluctuating between positive and negative values (Fig. 3A). With a strengthening of the Arctic High over the Canada Basin, the Beaufort Gyre began spinning up, a process indicated by the shift to positive values of the AOO index (Fig. 3B). With the gyre spinning up, the Arctic Ocean entered an extended period of increased freshwater storage and reduced export to the North Atlantic. This reduction in freshwater export resulted in elevated salinities throughout Northwest Atlantic shelf waters (Fig. 3C). In response to this remote forcing, lower trophic levels in the shelf ecosystems of the Scotian Shelf–Gulf of Maine–Georges Bank region shifted back at the beginning of the new millennium to a regime comparable to that of the 1980s, characterized by reduced phytoplankton and small copepod production during the autumn and a resurgence of *C. finmarchicus* (Fig. 3D–G) (MERCINA 2012).

Higher trophic level responses to this regime shift at the beginning of the new millennium were more complex. Populations of planktivorous forage fish such as herring, capelin, and sand lance collapsed from their earlier outbreak during the 1990s. Frank et al. (2011) hypothesized that this collapse can be attributed to the oscillatory, runaway consumption dynamics of these forage fish populations in the absence of predator control. A simpler alternative hypothesis, one emphasizing bottom-up processes, suggests that climate-forced changes in the plankton assemblage reduced the environmental carrying capacity for these planktivorous populations and led to their collapse (MERCINA 2012; Greene 2013). Further analyses are necessary to assess the relative merits of these alternative hypotheses.

Among commercially exploited fish and crustacean populations, the responses to changes in climate forcing and fishing pressure have been more gradual. With regard to cod, there has been little evidence until recent years that stocks from Atlantic Canada are starting to recover from their collapse during the early 1990s despite a dramatic reduction in fishing pressure (Frank et al. 2011). In contrast, stocks of northern shrimp and snow crab remain at high levels of abundance relative to those observed prior to the collapse of cod. The MERCINA (2012) authors suggest that these delayed population responses may be explained in part by the longer life cycles of these higher trophic level species and in part by the complex food web interactions resulting from the lingering and ongoing effects of multispecies fisheries.

Implications of remote climate forcing for ecosystem-based management of the Northwest Atlantic's marine living resources

The importance of climate in forcing Northwest Atlantic ecosystems and their associated fisheries has been recognized for many years (Koslow 1984; Koslow et al. 1987). Nevertheless, management plans for commercially exploited and protected marine species typically ignore the role of climate and focus instead on mitigating the demographic consequences of anthropogenic sources of mortality (Beaugrand and Kirby 2010). Since such mortality sources can often be regulated directly through management practices, this focus is understandable. However, a failure to take into account environmental factors regulating reproduction, growth, and non-anthropogenic sources of mortality can lead to "ecological surprises" (Berkes et al. 2000; Beamish and Riddell 2009). Such surprises can occur when managed populations do not respond as expected. During recent decades, ecological surprises have arisen in the fisheries management of cod stocks in Atlantic Canada as well as in the conservation management of North Atlantic right whales. Here, we will examine these examples

to determine what lessons can be learned from such surprises and how the resulting lessons might be used to better inform future ecosystem-based management practices.

During the early 1990s, most cod stocks in Atlantic Canada (Labrador–Newfoundland, Scotian Shelf) collapsed in response to overfishing and, despite a moratorium on fishing implemented in 1993, the stocks have shown little evidence of recovery until very recently (Frank et al. 2011). The failure of these cod stocks to recover for more than a decade despite the fishing moratorium surprised fisheries managers and has encouraged scientists to propose several hypotheses to explain the observed failure. The earliest hypotheses focused on climate-associated cooling of the region's shelf waters, which encouraged distributional shifts of cod stocks to the south and suppressed their recovery by slowing recruitment and growth rates (Rose 2000; Drinkwater et al. 2002). More recently, Frank et al. (2011) have proposed that, at least on the eastern Scotian Shelf, the recovery of these stocks was suppressed primarily by planktivorous forage fish predation on the younger stages of cod. Since these forage fish populations were formerly held in check by cod predation, such a predator–prey reversal after the collapse of cod could explain the prolonged failure of the stocks to recover.

Evaluating the relative merits of these alternative hypotheses will require a close examination of changes in cod stock structure and demography as ecosystems in Atlantic Canada continue to undergo their own changes, including decadal-scale regime shifts. Cod stocks in some parts of the region have begun to recover in recent years, and this recovery is consistent with both a warming of ocean conditions as well as a reduction in predation pressure on the younger stages of cod after the collapse of forage fish populations during the mid-2000s (Frank et al. 2011). It is unclear whether the collapse of forage fish populations was due to their own oscillatory, runaway consumption dynamics (Frank et al. 2011) or due to a climate-forced reduction in prey availability (Greene 2013; MERCINA 2012). Until such fundamental ecological issues are resolved, successful ecosystem-based fisheries management in Atlantic Canada will continue to be elusive.

The decade of the 1990s was a difficult period for North Atlantic right whales as well. Demographic projections produced by Fujiwara and Caswell (2001) suggested that the population was on a trajectory towards extinction within 200 yr. With the attention of conservation biologists focused almost exclusively on the elevated mortality rates associated with ship strikes and entanglement in fishing gear, a consensus view emerged that the population was in crisis and would continue to spiral downwards unless these sources of mortality could be held in check (Fujiwara and Caswell 2001; Kareiva 2001; Waring et al. 2001).

During the decade of the 2000s, the right whale population confounded this consensus view, increasing in abundance from ~ 300 animals at the beginning of the decade to ~ 400 animals by 2010 (Waring et al. 2011). Therefore, despite higher mortality rates and even more dire demographic projections (Kraus et al. 2005), the population grew throughout the decade at ~ 2.5% per year. This ecological surprise was the result of a doubling of calf production between 2001 and 2010 relative to the previous decade (Fig. 2D), a result leading to the obvious question—what caused such a dramatic increase in right whale reproduction?

Building upon earlier modeling studies (Greene et al. 2003; Greene and Pershing 2004; Samuel 2008), E. Meyer-Gutbrod (unpubl.) has developed a more sophisticated demographic model for right whales with the population's calving rate dependent on bimonthly- and geographic-specific abundances of *C. finmarchicus*, its primary food resource. Results from the model demonstrate that the observed increase in right whale reproduction during the 2000s can be attributed to a resurgence of *C. finmarchicus* associated with the regime shift observed at the beginning of the new millennium (Fig. 3F,G). It appears that a substantial increase in food availability provided the nutritional advantage necessary for the population to recover despite elevated mortality rates.

In both the cod and right whale examples, changes in climate led to ecological surprises that the federal agencies responsible for their management had not anticipated. In the cod example, managers could not have done much more for the fishery than the moratorium that was imposed in Atlantic Canada. However, in the more general case, an appropriate management response would be to reduce fishing quotas when stocks are challenged by less favorable environmental conditions. In the context of decadal-scale ecosystem regime shifts, one might see great advantage in the development of regime-dependent management strategies.

In the right whale example, it is difficult to conceive what other options managers might have employed to enhance the population's recovery other than to impose regulations that reduce the effects of anthropogenic sources of mortality. However, the federal agencies responsible for managing exploited and protected marine species also have a responsibility to manage the expectations of stakeholders and the general public. The concept of regime-dependent management may be relevant in this context, too. It is important that stakeholders and the general public understand that even with the best management plans in place, less favorable environmental conditions may prevent populations from recovering. When those less favorable environmental conditions are the result of ecosystem regime shifts associated with natural climate variability, then it might be reasonable to assure the public that conditions may improve in the future. On the other hand, when those less favorable environmental conditions are the result of ecosystem regime shifts associated with anthropogenic climate change, then prospects for the future are much more uncertain.

As the 21st century unfolds, society is facing the likelihood of climatic changes unprecedented in human history (IPCC 2007). Ocean scientists, resource managers, and policy makers will rely on our understanding of marine ecosystem responses to previously observed changes in climate to try to predict the fate of these ecosystems and their living resources in a future shaped by both natural as well as anthropogenic climate forcing.

The retrospective studies of Northwest Atlantic shelf ecosystems reviewed here demonstrate that a broad

perspective, one encompassing basin- and hemispheric-scale processes, will be necessary to understand the role of climate in forcing the dynamics of such ecosystems. Specifically, these studies have taught us that ocean advective processes provide the teleconnections linking atmosphere–ocean interactions in the North Atlantic and Arctic Ocean Basins to the dynamics of Northwest Atlantic shelf ecosystems thousands of kilometers downstream. Clearly, the scope of the problem is far greater than we could have imagined only a few years ago.

Another important lesson from these retrospective studies is that we must be cautious in extrapolating from the past in trying to predict the future. During recent decades, anthropogenic climate forcing has steadily increased, introducing new elements to Earth's climate system as well as projecting itself on the system's preexisting modes of natural climate variability. For example, the recent declines in Arctic summer sea-ice extent are altering ocean–atmosphere heat fluxes and thereby changing AO-associated teleconnections between the Arctic and middle latitudes (Overland et al. 2008; Overland and Wang 2010; Overland 2011). These changes in Arctic climate are increasing the likelihood of negative AO conditions during winter as well as the frequency of extreme weather events (Francis and Vavrus 2012; Greene and Monger 2012; Liu et al. 2012). Since the forcing behind these changes is different than in the past, it is uncertain at present how ocean circulation in the North Atlantic will respond. This uncertainty will make it even more difficult to predict when the next decadal-scale ecosystem regime shifts are likely to occur.

Acknowledgments

We thank the Gulf of Maine Research Institute, Cornell University's Shoals Marine Laboratory, and the University of Washington's Friday Harbor Laboratories (FHL) for hosting the research workshops at which the ideas in this paper were developed. C.H.G. thanks FHL for hosting him as a Whiteley Center Scholar during the preparation of this manuscript. Funding for this research was provided by the National Science Foundation as part of the Regional and Pan-Regional Synthesis Phases of the U.S. Global Ocean Ecosystem (GLOBEC) Program.

References

Alheit, J., C. Mollmann, J. Dutz, G. Kornilovs, P. Loewe, V. Mohrholz, and N. Wasmund. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES J. Mar. Sci. **62:** 1205–1215, doi:10.1016/j.icesjms.2005.04.024

Attrill, M. J., and M. Power. 2002. Climatic influence on a marine fish assemblage. Nature **417:** 275–278, doi:10.1038/417275a

Bakun, A. 2005. Regime shifts, p. 971–1026. *In* A. R. Robinson and K. Brink [eds.], The sea, v. 13, The global coastal ocean: Multiscale interdisciplinary processes. Harvard Univ.

Beamish, R. J., and B. E. Riddell. 2009. The future of fisheries science on Canada's west coast is keeping up with the changes, p. 567–596. *In* R. J. Beamish and B. J. Rothschild [eds.], The future of fisheries science in North America. Springer Science.

Beaugrand, G., F. Ibañez, and P. C. Reid [eds]. 2000. Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. Mar. Ecol. Prog. Ser. **200:** 93–102, doi:10.3354/meps200093

———, and R. R. Kirby. 2010. Climate, plankton and cod. Global Change Biol. **16:** 1268–1280, doi:10.1111/j.1365-2486.2009.02063.x

Belkin, I. M. 2004. Propagation of the "Great Salinity Anomaly" of the 1990s around the northern North Atlantic. Geophys. Res. Lett. **31:** L08306, doi:10.1029/2003GL019334

———, S. Levitus, J. Antonov, and S.-A. Malmberg. 1998. "Great Salinity Anomalies" in the North Atlantic. Progr. Oceanogr. **41:** 1–68, doi:10.1016/S0079-6611(98)00015-9

Berkes, F., C. Folke, and J. Colding [eds.]. 2000. Linking social and ecological systems: Management practices and social mechanisms for building resilience. Cambridge Univ.

Brodziak, J., and L. O'Brien. 2005. Do environmental factors affect recruits per spawner anomalies of New England groundfish? ICES J. Mar. Sci. **62:** 1394–1407, doi:10.1016/j.icesjms.2005.04.019

Conversi, A., S. Piontkovski, and S. Hameed. 2001. Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US shelf) with reference to the North Atlantic Oscillation. Deep-Sea Res. II **48:** 519–539, doi:10.1016/S0967-0645(00)00088-6

———, S. F. Umani, T. Peluso, J. C. Molinero, A. Santojanni, and M. Edwards. 2010. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other European basins. PLoS ONE **5:** e10633, doi:10.1371/journal.pone.0010633

Curry, R. G., and M. S. McCartney. 2001. Ocean gyre circulation changes associated with the North Atlantic Oscillation. J. Phys. Oceanogr. **31:** 3374–3400, doi:10.1175/1520-0485(2001)031<3374:OGCCAW>2.0.CO;2

DeYoung, B., M. Barange, G. Beaugrand, R. Harris, R. I. Perry, M. Scheffer, and F. Werner. 2008. Regime shifts in marine ecosystems: detection, prediction and management. Trends Ecol. Evol. **23:** 402–409, doi:10.1016/j.tree.2008.03.008

———, R. Harris, J. Alheit, G. Beaugrand, N. Mantua, and L. Shannon. 2004. Detecting regime shifts in the ocean: Data considerations. Progr. Oceanogr. **60:** 143–164, doi:10.1016/j.pocean.2004.02.017

Dickson, R. R. 1999. All change in the Arctic. Nature **397:** 389–391, doi:10.1038/17018

———, J. Meincke, and P. Rhines [eds]. 2008. Arctic-subarctic ocean fluxes: Defining the role of the northern seas in climate. Springer Science.

Drinkwater, K. F., F. Mueter, K. D. Friedland, M. Taylor, G. L. Hunt, Jr., J. Hare, and W. Melle. 2009. Recent climate forcing and physical oceanographic changes in Northern Hemisphere regions: A review and comparison of four marine ecosystems. Progr. Oceanogr. **81:** 10–28, doi:10.1016/j.pocean.2009.04.003

———, B. Petrie, and P. C. Smith. 2002. Hydrographic variability on the Scotian Shelf during the 1990s. Northwest Atlantic Fisheries Organization SFO Document 02/42, Serial No. N4653. Northwest Atlantic Fisheries Organization.

———, and others. 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation, p. 211–234. *In* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck [eds.], The North Atlantic Oscillation: Climatic significance and environmental impact. Geophysical Monograph 134. American Geophysical Union.

Dukhovskoy, D., M. Johnson, and A. Proshutinsky. 2006. Arctic decadal variability from an idealized atmosphere-ice-ocean model: Simulation of decadal oscillations. J. Geophys. Res. **111:** C06029, doi:10.1029/2004JC002820

Falck, E., G. Kattner, and G. Budéus. 2005. Disappearance of Pacific Water in the northwestern Fram Strait. Geophys. Res. Lett. **32:** L14619, doi:10.1029/2005GL023400

Francis, J. A., and S. J. Vavrus. 2012. Evidence linking Arctic amplification to extreme weather. Geophys. Res. Lett. **39:** L06801, doi:10.1029/2012GL051000

Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science **308:** 1621–1623, doi:10.1126/science.1113075

———, ———, J. A. D. Fisher, and W. C. Leggett. 2011. Transient dynamics of an altered large marine ecosystem. Nature **477:** 86–89, doi:10.1038/nature10285

Fujiwara, M., and H. Caswell. 2001. Demography of the endangered North Atlantic right whale. Nature **414:** 537–541, doi:10.1038/35107054

Gatien, M. G. 1976. A study of the slope water region south of Halifax. J. Fish. Res. Board Can. **33:** 2213–2217, doi:10.1139/f76-270

Greene, C. H. 2012. The winters of our discontent. Sci. Am. **307:** 50–55, doi:10.1038/scientificamerican1212-50

———. 2013. Towards a more balanced view of marine ecosystems. Fish. Oceanogr. **22:** 140–142, doi:10.1111/fog.12006

———, and B. C. Monger. 2012. An Arctic wild card in the weather. Oceanography **25(2):** 7–9, doi:10.5670/oceanog.2012.58

———, ———, and L. P. McGarry. 2009. Some like it cold. Science **324:** 733–734, doi:10.1126/science.1173951

———, and A. J. Pershing. 2000. The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: Basin-scale forcing associated with the North Atlantic Oscillation. ICES J. Mar. Sci. **57:** 1536–1544, doi:10.1006/jmsc.2000.0966

———, and ———. 2003. The flip-side of the North Atlantic Oscillation and modal shifts in slope-water circulation patterns. Limnol. Oceanogr. **48:** 319–322, doi:10.4319/lo.2003.48.1.0319

———, and ———. 2004. Climate and the conservation biology of North Atlantic right whales: The right whale at the wrong time? Front. Ecol. Environ. **2:** 29–34, doi:10.1890/1540-9295(2004)002[0029:CATCBO]2.0.CO;2

———, and ———. 2007. Climate drives sea change. Science **315:** 1084–1085, doi:10.1126/science.1136495

———, ———, T. M. Cronin, and N. Cecci. 2008. Arctic climate change and its impacts on the ecology of the North Atlantic. Ecology (suppl. 2008) **89:** S24–S38, doi:10.1890/07-0550.1

———, ———, R. D. Kenney, and J. W. Jossi. 2003. Impact of climate variability on the recovery of endangered North Atlantic right whales. Oceanography **16(4):** 96–101, doi:10.5670/oceanog.2003.16

Hakkinen, S. 2002. Freshening of the Labrador Sea surface waters in the 1990s: Another great salinity anomaly? Geophys. Res. Lett. **29:** 2232, doi:10.1029/2002GL015243

Hanninen, J., I. Vuorinen, and P. Hjelt. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. Limnol. Oceanogr. **45:** 703–710, doi:10.4319/lo.2000.45.3.0703

Houssais, M.-N., and C. Herbaut. 2011. Atmospheric forcing on the Canadian Arctic Archipelago freshwater outflow and implications for the Labrador Sea variability. J. Geophys. Res. **116:** C00D02, doi:10.1029/2010JC006323

Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. Science **269:** 676–679, doi:10.1126/science.269.5224.676

———, and C. Deser. 2010. North Atlantic climate variability: The role of the North Atlantic Oscillation. J. Mar. Syst. **78:** 28–41, doi:10.1016/j.jmarsys.2008.11.026

———, and R. R. Dickson. 2004. Climate variability over the North Atlantic, p. 15–31. *In* N. C. Stenseth, G. Ottersen, J. W. Hurrell, and A. Belgrano [eds.], Marine ecosystems and climate variation. The North Atlantic, Oxford.

———, Y. Kushnir, G. Ottersen, and M. Visbeck. 2003. An overview of the North Atlantic Oscillation, p. 1–36. *In* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck [eds.], The North Atlantic Oscillation: Climatic significance and environmental impact. Geophysical Monograph 134. American Geophysical Union.

[IPCC] Intergovernmental Panel on Climate Change. 2007. Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ.

Jones, P. D., T. J. Osborn, and K. R. Briffa. 2003. Pressure-based measures of the North Atlantic Oscillation (NAO), a comparison and an assessment of changes in the strength of the NAO and in its influence on surface climate parameters, p. 51–62. *In* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck [eds.], The North Atlantic Oscillation: Climatic significance and environmental impact. American Geophysical Union.

Kareiva, P. 2001. When one whale matters. Nature **419:** 493–494, doi:10.1038/35107167

Koenigk, T., U. Mikolajewicz, H. Haak, and J. Jungclaus. 2007. Arctic freshwater export in the 20th and 21st centuries. J. Geophys. Res. **112:** G04S41, doi:10.1029/2006JG000274

Koslow, J. A. 1984. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. **41:** 1722–1729, doi:10.1139/f84-212

———, K. R. Thompson, and W. Silvert. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: Influence of stock size and climate. Can. J. Fish. Aquat. Sci. **44:** 26–39, doi:10.1139/f87-004

Kraus, S. D., and others. 2005. North Atlantic right whales in crisis. Science **309:** 561–562, doi:10.1126/science.1111200

Liu, J., J. A. Curry, H. Wang, M. Song, and R. M. Horton. 2012. Impact of declining Arctic sea ice on winter snowfall. Proc. Natl. Sci. Acad. USA **109:** 4074–4079, doi:10.1073/pnas.1114910109

Loder, J. W., J. A. Shore, C. G. Hannah, and B. D. Petrie. 2001. Decadal-scale hydrographic and circulation variability in the Scotia-Maine region. Deep-Sea Res. II **48:** 3–35, doi:10.1016/S0967-0645(00)00080-1

Lynam, C. P., S. J. Hay, and A. S. Brierley. 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol. Oceanogr. **49:** 637–643, doi:10.4319/lo.2004.49.3.0637

Marsh, R. 2000. Modeling changes in the North Atlantic circulation under NAO-minimum wind forcing of 1877–81. Atmos.-Ocean **38:** 367–393, doi:10.1080/07055900.2000.9649653

Marsh, R. B., and others. 1999. The 1882 tilefish kill—a cold event in shelf waters off the northeastern United States? Fish. Oceanogr. **8:** 39–49, doi:10.1046/j.1365-2419.1999.00092.x

McLaughlin, F., E. Carmack, R. Macdonald, A. J. Weaver, and J. Smith. 2002. The Canada Basin, 1989–1995: Upstream events and far-field effects of the Barents Sea. J. Geophys. Res. **107(C7):** 3082, doi:10.1029/2001JC000904

[MERCINA] Marine Ecosystem Responses to Climate In the North Atlantic Working Group. 2001. Oceanographic responses to climate in the Northwest Atlantic. Oceanography **14(3):** 76–82, doi:10.5670/oceanog.2001.25

———. 2003. Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. Prog. Oceanogr. **58:** 301–312, doi:10.1016/j.pocean.2003.08.009

———. 2004. Supply-side ecology and the response of zooplankton to climate-driven changes in North Atlantic Ocean circulation. Oceanography **17(3):** 60–71, doi:10.5670/oceanog.2004.31

———. 2012. Recent Arctic climate change and its remote forcing of Northwest Atlantic shelf ecosystems. Oceanography **25(3):** 208–213, doi:10.5670/oceanog.2012.64

Molinero, J. C., F. Ibanez, P. Nival, E. Buecher, and S. Souissi. 2005. North Atlantic climate and northwestern Mediterranean plankton variability. Limnol. Oceanogr. **50:** 1213–1220, doi:10.4319/lo.2005.50.4.1213

Mountain, D., and J. Kane. 2010. Major changes in the Georges Bank ecosystem, 1980s to the 1990s. Mar. Ecol. Prog. Ser. **398:** 81–91, doi:10.3354/meps08323

Mountain, D. G. 2003. Variability in the properties of Shelf Water in the Middle Atlantic Bight, 1977–1999. J. Geophys. Res. **108:** 3014, doi:10.1029/2001JC001044

Mueter, F. J., and others. 2009. Ecosystem responses to recent oceanographic variability in high-latitude Northern Hemisphere ecosystems. Prog. Oceanogr. **81:** 93–110, doi:10.1016/j.pocean.2009.04.018

Myers, A. A., J. Helbig, and D. Holland. 1989. Seasonal and interannual variability of the Labrador Current and West Greenland Current. ICES C.M. 1989/C:16. International Council for the Exploration of the Sea.

Ottersen, G., J. Alheit, K. Drinkwater, K. Friedland, E. Hagen, and N. C. Stenseth. 2004. The responses of fish populations to ocean climate fluctuations, p. 73–94. *In* N. C. Stenseth, G. Ottersen, J. W. Hurrell, and A. Belgrano [eds.], Marine ecosystems and climate variation: The North Atlantic. Oxford Univ.

———, S. Kim, G. Huse, J. J. Polovina, and N. C. Stenseth. 2010. Major pathways by which climate may force marine fish populations. J. Mar. Syst. **79:** 343–360, doi:10.1016/j.jmarsys.2008.12.013

———, and N. C. Stenseth. 2001. Atlantic climate governs oceanographic and ecological variability in the Barents Sea. Limnol. Oceanogr. **46:** 1774–1780, doi:10.4319/lo.2001.46.7.1774

Overland, J. E. 2011. Potential Arctic change through climate amplification processes. Oceanography **24(3):** 176–185, doi:10.5670/oceanog.2011.70

———, and M. Wang. 2010. Large-scale atmospheric changes are associated with the recent loss of Arctic sea ice. Tellus **62A:** 1–9, doi:10.1111/j.1600-0870.2009.00421.x

———, ———, and S. Salo. 2008. The recent Arctic warm period. Tellus **60A:** 589–597, doi:10.1111/j.1600-0870.2008.00327.x

Pershing, A. J., C. H. Greene, J. W. Jossi, L. O'Brien, J. K. T. Brodziak, and B. A. Bailey. 2005. Interdecadal variability in the Gulf of Maine zooplankton community with potential impacts on fish recruitment. ICES J. Mar. Sci. **62:** 1511–1523, doi:10.1016/j.icesjms.2005.04.025

———, ———, B. Planque, and J.-M. Fromentin. 2004. The influence of climate variability on North Atlantic zooplankton populations, p. 59–69. *In* N. C. Stenseth, G. Ottersen, J. Hurrell, and A. Belgrano [eds.], Ecological effects of climatic variations in the North Atlantic. Oxford Univ.

———, N. R. Record, B. C. Monger, D. E. Pendleton, and L. A. Woodard. 2009. Model-based estimates of *Calanus finmarchicus* abundance in the Gulf of Maine. Mar. Ecol. Prog. Ser. **378:** 227–243, doi:10.3354/meps07828

Peterson, B. J., J. McClelland, R. Curry, R. M. Holmes, J. E. Walsh, and K. Aagaard. 2006. Trajectory shifts in the Arctic and subarctic freshwater cycle. Science **313:** 1061–1066, doi:10.1126/science.1122593

Petrie, B. 2007. Does the North Atlantic Oscillation affect hydrographic properties on the Canadian Atlantic continental shelf? Atmos.-Ocean **45:** 141–151, doi:10.3137/ao.450302

Petrie, B. D., and K. Drinkwater. 1993. Temperature and salinity variability on the Scotian Shelf and in the Gulf of Maine 1945–1990. J. Geophys. Res. **98:** 20079–20089, doi:10.1029/93JC02191

Pickart, R. S., T. K. Mckee, D. J. Torres, and S. A. Harrington. 1999. Mean structure and interannual variability of the slope water system south of Newfoundland. J. Phys. Oceanogr. **29:** 2541–2558, doi:10.1175/1520-0485(1999)029<2541:MSAIVO>2.0.CO;2

Piontkovski, S. A., and S. Hameed. 2002. Precursors of copepod abundance in the Gulf of Maine in atmospheric centers of action and sea surface temperature. Global Atmos. Ocean Syst. **8:** 283–291, doi:10.1080/10236730290030932

Proshutinsky, A. Y., and M. A. Johnson. 1997. Two circulation regimes of the wind-driven Arctic Ocean. J. Geophys. Res. **102:** 12493–12514, doi:10.1029/97JC00738

Reid, P. C., N. P. Holliday, and T. J. Smyth. 2001. Pulses in the eastern margin current and warmer water off the northwest European Shelf linked to North Sea ecosystem changes. Mar. Ecol. Prog. Ser. **215:** 283–287, doi:10.3354/meps215283

Rodionov, S. N. 2004. A sequential algorithm for testing climate regime shifts. Geophys. Res. Lett. **31:** L09204, doi:10.1029/2004GL019448

Rose, G. A., B. DeYoung, D. W. Kulka, S. V. Goddard, and G. L. Fletcher. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): A view from the ocean. Can. J. Fish. Aquat. Sci. **57:** 644–663, doi:10.1139/f00-004

Sameoto, D. 2001. Decadal changes in phytoplankton color index and selected calanoid copepods in continuous plankton recorder data from the Scotian Shelf. Can. J. Fish. Aquat. Sci. **58:** 749–761, doi:10.1139/f01-033

———. 2004. The 1990s—a unique decade for plankton change in the Northwest Atlantic. Canadian Science Advisory Secretariat Research Document 2004/074. Canadian Science Advisory Secretariat.

Samuel, Y. 2008. Climatic impacts on marine ecosystems: A study of climate variability and conservation oceanography. Ph.D. thesis. Cornell Univ.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413:** 591–596, doi:10.1038/35098000

Serreze, M. C., A. P. Barrett, and A. G. Slater. 2008. Variability and change in the atmospheric branch of the Arctic hydrologic cycle, p. 343–362. *In* R. R. Dickson, J. Meincke, and P. Rhines [eds.], Arctic-subarctic ocean fluxes: Defining the role of the northern seas in climate. Springer Science.

———, M. M. Holland, and J. Stroeve. 2007. Perspectives on the Arctic's shrinking sea-ice cover. Science **315:** 1533–1536, doi:10.1126/science.1139426

Shindell, D. 2003. Whither Arctic climate? Science **299:** 215–216, doi:10.1126/science.1080855

Sirabelli, P., A. Giuliani, A. Colosimo, and J. Dippner. 2001. Breaking down the climate effects on cod recruitment by principal components analysis and canonical correlation. Mar. Ecol. Prog. Ser. **216:** 213–222, doi:10.3354/meps216213

Smith, P. C., R. W. Houghton, R. G. Fairbanks, and D. G. Mountain. 2001. Interannual variability of boundary fluxes and water mass properties in the Gulf of Maine and on Georges Bank: 1993–1997. Deep-Sea Res. II **48:** 37–70, doi:10.1016/S0967-0645(00)00081-3

Steele, J. 2004. Regime shifts in the ocean: Reconciling observations and theory. Prog. Oceanogr. **60:** 135–141, doi:10.1016/j.pocean.2004.02.004

Steele, M., J. Morison, W. Ermold, I. Rigor, M. Ortmeyer, and K. Shimada. 2004. Circulation of summer Pacific halocline water in the Arctic Ocean. J. Geophys. Res. **109:** C02027, doi:10.1029/2003JC002009

Stroeve, J. C., M. C. Serreze, M. M. Holland, J. Kay, J. Maslanik, and A. P. Barrett. 2011. The Arctic's rapidly shrinking sea ice cover: A research synthesis. Clim. Change **110:** 1005–1027, doi:10.1007/s10584-011-0101-1

Thompson, D. J. W., and J. M. Wallace. 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. Geophys. Res. Lett. **25:** 1297–1300, doi:10.1029/98GL00950

Thompson, D. W. J., J. M. Wallace, and G. C. Hegerl. 2000. Annular modes in the extratropical circulation. Part II: Trends. J. Clim. **13:** 1018–1036, doi:10.1175/1520-0442-(2000)013<1018:AMITEC>2.0.CO;2

Vilhjálmsson, H., and others. 2005. Fisheries and aquaculture, p. 691–780. *In* Arctic climate impact assessment (ACIA). Cambridge Univ. Press.

Visbeck, M., E. P. Chassignet, R. G. Curry, T. L. Delworth, R. R. Dickson, and G. Krahmann. 2003. The ocean's response to North Atlantic Oscillation variability, p. 113–145. *In* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck [eds.], The North Atlantic Oscillation: Climatic significance and environmental impact. Geophysical Monograph 134. American Geophysical Union.

Wang, J., and others. 2009. Is the Dipole Anomaly a major driver to record lows in the Arctic sea ice extent? Geophys. Res. Lett. **36:** L05706, doi:10.1029/2008GL036706

Waring, G. T., E. Josephson, K. Maze-Foley, and P. E. Rosel. 2011. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments—2011. NOAA Technical Memorandum NMFS-NE-219. National Oceanic and Atmospheric Administration.

———, J. M. Quintal, and S. Swartz. 2001. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments—2001. NOAA Technical Memorandum NMFS-NE-168. National Oceanic and Atmospheric Administration.

Worm, B., and R. A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology **84:** 162–173, doi:10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2

Yashayaev, I., N. P. Holliday, M. Bersch, and H. M. van Aken. 2008. The history of the Labrador Sea Water: Production, spreading, transformation and loss, p. 569–612. *In* R. R. Dickson, J. Meincke, and P. Rhines [eds.], Arctic-subarctic ocean fluxes: Defining the role of the northern seas in climate. Springer Science.

Associate editor: Jonathan J. Cole

Received: 11 August 2012
Accepted: 21 January 2013
Amended: 22 January 2013