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Ecosystem effects of the Atlantic Multidecadal Oscillation

Janet A. Nye ^{a,*}, Matthew R. Baker ^b, Richard Bell ^c, Andrew Kenny ^d, K. Halimeda Kilbourne ^e, Kevin D. Friedland ^c, Edward Martino ^f, Megan M. Stachura ^g, Kyle S. Van Houtan ^{h,i}, Robert Wood ^f

^a United States Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Atlantic Ecology Division, 27 Tarzwell Dr, Narragansett, RI 02882, USA

^b NOAA National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way N.E., Seattle, WA 98115, USA

^c NOAA National Marine Fisheries Service, Northeast Fisheries Science Center, 28 Tarzwell Dr., Narragansett, RI 02882, USA

^d Centre for Environment, Fisheries & Aquaculture Science, Lowestoft, UK

^e Chesapeake Biological Laboratory, Center for Environmental Science, University of Maryland, Box 38, Solomons, MD 20688, USA

^f National Oceanic and Atmospheric Administration, Cooperative Oxford Laboratory, Oxford, MD 21654, USA

^g School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195–5020, USA

^h NOAA Fisheries Service, Pacific Islands Fisheries Science Center, Honolulu, HI 96822, USA

ⁱ Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708, USA

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ABSTRACT

Multidecadal variability in the Atlantic Ocean and its importance to the Earth's climate system has been the subject of study in the physical oceanography field for decades. Only recently, however, has the importance of this variability, termed the Atlantic Multidecadal Oscillation or AMO, been recognized by ecologists as an important factor influencing ecosystem state. A growing body of literature suggests that AMO-related fluctuations are associated with shifts in ecological boundaries, primary productivity, and a number of ecologically and economically important coastal and marine populations across the Atlantic basin. Although the AMO is a basin-wide index of SST, the drivers of ecosystem change encompass more than temperature anomalies and the mode of action differs within each ecosystem. A common theme in assessing ecosystem change indicates that fluctuations in water masses and circulation patterns drive shifts in ecosystem states, but the magnitude and rate of change is dependent on the physical characteristics of the region. Because of the wide ranging geographic effects of the AMO, and considering its multidecadal nature, a more complete understanding of its causes and effects would allow scientists and managers to more effectively inform ecosystem-based management across the Atlantic Basin.

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1. Introduction

There are several modes of climatic variability in the North Atlantic that affect ecosystem processes, but one mode of variability that has received relatively little attention until recently is the Atlantic Multidecadal Oscillation (AMO sensu Kerr, 2005) also known as Atlantic Multidecadal Variability (AMV sensu Delworth et al., 2007; Knight et al., 2005). It is hypothesized that fluctuations in the strength of Atlantic Meridional Overturning Circulation (AMOC) cause internal variability in sea surface temperature (SST), sea level pressure, and ocean circulation all of which are represented by the AMO index (Knight et al., 2005; Ting et al., 2011). Many biological oceanographers are familiar with the AMO index and refer to this large-scale phenomenon as the AMO. For consistency we will use this terminology throughout this review of its effect on ecosystems. However, the AMO index represents a wide variety of processes such that AMV is perhaps the more appropriate terminology for this

phenomenon. In particular, records of past climate variability indicate that the AMO is not an oscillatory cycle with regular periods of fixed length (Gray et al., 2004; Knudsen et al., 2011). Instead it appears to be a climate system feature with variance concentrated at multidecadal scales.

The AMO index (Fig. 1) is typically defined as the SST anomaly from 0–60°N linearly detrended to account for the increase in temperature associated with anthropogenic climate change (Enfield et al., 2001; Sutton and Hodson, 2005). Modern observations of SST indicate that the AMO switches between positive and negative phases on the order of 65–70 years (Schlesinger and Ramankutty, 1994), but the length and consistency of the oscillatory cycle is the subject of considerable debate. The 65–70 year cycle is based on only ~130 years of observed and reconstructed SST data for which there are only 1.5–2 complete cycles of the AMO. Smoothing or detrending of SST to calculate the AMO index results in oscillations of different frequencies (Vincze and Janosi, 2011). Although the exact timing of the switch from the positive to negative phase depends on how the index is calculated, it is generally agreed that negative/cold phases occurred from approximately 1900–1925 and 1971–1994 while positive/warm phases occurred from 1875–1899, 1926–1970 and 1990–present (Goldenberg et al., 2001).

* Corresponding author at: School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY 11794–5000, USA. Tel.: +1 401 782 3165.

E-mail address: janet.nye@stonybrook.edu (J.A. Nye).

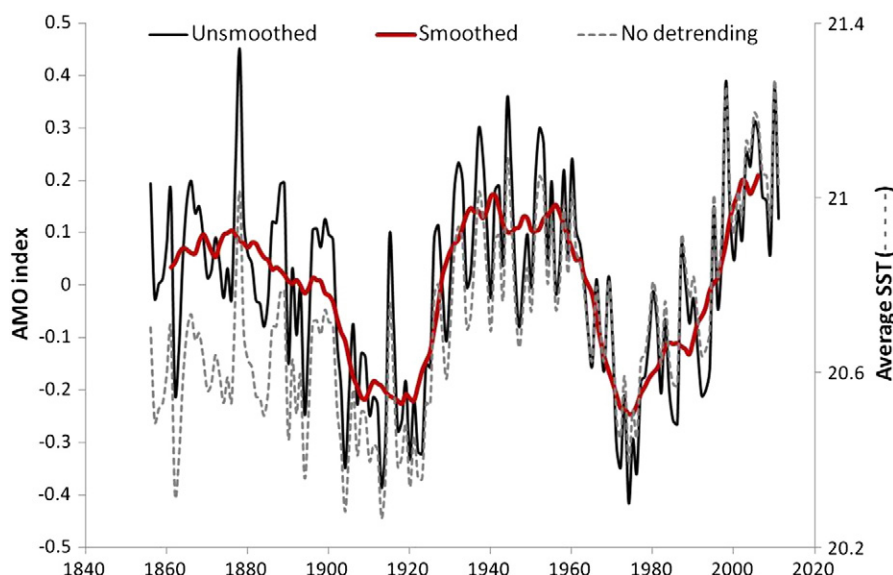


Fig. 1. The unsmoothed and smoothed AMO index calculated from Kaplan SST dataset detrended for the effects of climate change (Enfield et al., 2001). The dashed line is the unsmoothed, undetrended SST data with the 1951–1980 NOAA ERSST climatology added back in. All data obtained from the NOAA ESRL website (<http://www.esrl.noaa.gov/psd/data/timeseries/AMO/>).

The large scale warming and cooling related to the AMO interacts with anthropogenic warming. It has been suggested that the combined effects of anthropogenic climate change and the positive phase of the AMO since the 1990s has caused a more rapid warming than would be expected from climate change alone (Andronova and Schlesinger, 2000; Belkin, 2009; Knudsen et al., 2011). Similarly, cool (negative) phases of the AMO in the past may have masked the effects of climate change. The combination of warming trends from AMO and from anthropogenic climate change since the 1970s makes it difficult to distinguish the cause of changes in ecological time series unless the record length extends back before the mid to late 20th century.

The purpose of this review is to first explain the physical phenomena associated with the AMO so as to elucidate how this broad scale climatic index may be associated with more localized ecosystems in the Atlantic basin. Because the AMO index is usually presented as a time series in the ecological literature, we focus on the spatial aspects of the AMO to better understand the more proximate mechanisms by which this large scale process affects local ecosystem dynamics. Secondly, we review published ecological studies where the AMO was found to influence populations and ecosystems or where we suspect that the AMO may have influenced ecosystem dynamics. Lastly, we will discuss how the AMO affects large marine ecosystems (LMEs) around the Atlantic and how understanding this process is fundamental for informing Ecosystem Based approaches to Management (EBM).

2. Spatial patterns of the AMO

In contrast to the time series of the AMO index, the spatially explicit representation of the AMO suggests that the mechanisms through which this phenomenon affects ecosystems varies in different areas of the Atlantic and perhaps in other parts of the globe (Fig. 2). As in previous studies (Delworth et al., 2007; Grossmann and Klotzbach, 2009), a horseshoe-shaped spatial pattern (warm colors in Fig. 2) is generated in the Atlantic when the AMO is correlated with SST in the positive phase of the AMO. Thus, the regional effects of the AMO can vary throughout the Atlantic basin, but the positive phase of the AMO generally indicates a period of warmer temperatures. Whereas the AMO is primarily defined by oceanic phenomena (SST anomalies), it is related to atmospheric processes as well, since the ocean and atmosphere interact closely to form the Earth's climate system. During the positive phase of the AMO the position of the Intertropical Convergence Zone (ITCZ)

shifts from the south (Fig. 2, brown ellipse), where precipitation is reduced, to the north, where precipitation is increased (Fig. 2, green ellipse). This ITCZ shift is associated with weaker northeast trade winds and a stronger cross equatorial wind flow from the southern equatorial zone. The weaker northern hemisphere winds are the result of a weakening of the Bermuda High and Icelandic Low atmospheric pressure zones. The AMO also appears to generate remote effects with anomalously low pressure over Eastern Europe and perhaps also over the northeast Pacific. The position of high and low pressure cells results in easterly winds over the central North Atlantic that influence the position and strength of the Gulf Stream and North Atlantic current. The mixed layer depth (MLD) is also shallower in the positive phase. The negative phase of the AMO has roughly opposite sign anomalies, but given the very long time scale of the AMO, there is not enough data to determine how linear the signal is (i.e. the extent to which the positive and negative phases are equal and opposite).

While it may be tempting to assume from this schematic that the areas with highest spatial correlations are the areas where ecosystem changes related to the AMO are most frequently found, the AMO's influence is still very strong in areas where correlations are low. For example, the highest correlations occur to the east of Spain (Delworth et al., 2007), while low correlations occur near the Chesapeake Bay, Northwest Atlantic and the continental US. However, strong ecosystem effects are observed in North America in part because of the influence of SST on atmospheric processes such as precipitation and wind patterns.

3. Links between AMO and other modes of climate variability

In addition to the AMO, other patterns of climate variability interact with the AMO to elicit ecosystem response. Such climatic processes include the North Atlantic Oscillation (NAO), Arctic Oscillation (AO) or Northern Annular Mode (NAM), Atlantic Meridional Mode (AMM), El Niño and the Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). The NAO is a north–south dipole in sea level pressure (SLP) that is primarily governed by internal atmospheric dynamics, although it can be influenced by both local and nonlocal SST anomalies (Hurrell and Deser, 2009; Hurrell et al., 2003). It affects the ocean via a number of processes, including surface heat fluxes, which drives a SST tripole pattern in the North Atlantic and influences deep water formation in the Labrador Sea, and the wind stress curl, which can alter the

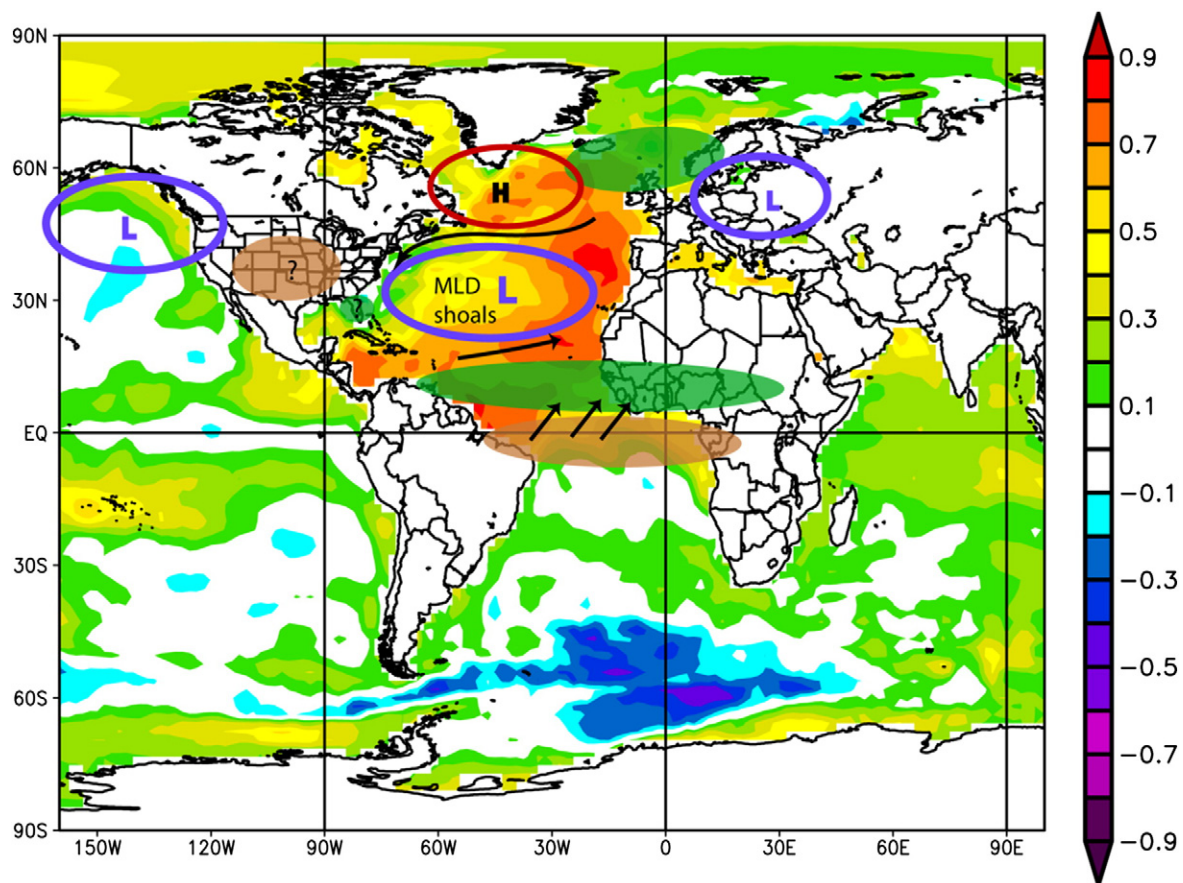


Fig. 2. Schematic of climate perturbations associated with AMO warm phase. The shaded base map represents the correlation of annual SST anomalies from NCEP/NCAR reanalysis 1948–2007 with the AMO index. Drier and wetter conditions are indicated by brown and green ellipses, respectively. Wind anomalies are represented by thick black arrows and a shallower ocean mixed layer in the North Atlantic Gyre is indicated by the text “MLD shoals”. Open blue and red ellipses represent low and high pressure regions, respectively. Base map image provided by the NOAA/ESRL Physical Sciences Division, Boulder Colorado from their Web site at <http://www.esrl.noaa.gov/psd/>. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

gyre circulations (Häkkinen and Rhines, 2004; Häkkinen et al., 2011). The NAO may influence the AMO through changes in sea ice dynamics and North Atlantic Deep Water formation (Grossmann and Klotzbach, 2009). Both of these processes influence thermohaline circulation and thus, the AMO. The AMO may in turn influence the NAO via changes in SST that affect pressure gradients (Grossmann and Klotzbach, 2009). The AO is closely associated with the NAO, but is defined as the dominant pattern of non-seasonal sea-level pressure variations north of 20°N.

Two processes in the Pacific may relate to the Atlantic climate variability through complex teleconnections, the extent to which is unclear (but see McKinnell paper, this volume). ENSO is centered in the tropical Pacific, but can impact the global ocean including the North Atlantic. The PDO, defined by the first Empirical Orthogonal Function (EOF) of North Pacific SST, exhibits variability on multiple time scales with enhanced variability at a period of ~20 years. The PDO is likely controlled by several factors including random fluctuations in the Aleutian Low, ENSO teleconnections, and coupled atmosphere–ocean interaction in the North Pacific. Both the AMO and PDO exhibit multidecadal variability and while it appears that one may lag the other, no mechanism to link the two currently exists (d’Orgeville and Peltier, 2007). However, both are influenced by Western Boundary Currents, the Kuroshio in the Pacific (Kwon and Deser, 2007) and the Gulf Stream in the Atlantic (Frankignoul et al., 2001; Joyce et al., 2009). Thus, analogous internal ocean dynamics may influence these basin-scale processes in similar ways to give rise to multidecadal climate variability, but how the AMO and PDO directly influence each other remains unclear (Kwon et al., 2010).

The AMO is newer to the scientific community, but already has a presence in the scientific literature on par with other often cited indices of climate variability. Fig. 3a shows the results of our survey of the ISI Web of Science publications for the NAO, PDO, and AMO since their first record in this database. Since 1987, the NAO has been the central topic of 3661 publications, and these studies have been cited 90,726 times. The PDO, since 1997, has 785 publications that have been cited 13,065 times. And since 2000, the AMO has 210 publications that have been cited on 2859 occasions. As the AMO is increasingly understood and appreciated, its scientific importance as expressed in the literature may equal that of the NAO and the PDO. Because the AMO is an emerging research topic, most AMO publications to date describe the index itself and its relationship to local and regional climate. Far fewer studies address its significance to biological populations and ecosystems.

4. Taxa-specific responses to AMO

There are several mechanisms by which the AMO may influence marine species. Temperature affects all physiological processes of organisms, especially ectotherms (Fry, 1971; Hoar, 1953). Thus, growth, consumption, metabolism, migration and reproductive output may be affected by AMO-related temperature changes. Changes in temperature alone may affect the population growth rates of lower trophic levels (phytoplankton and zooplankton) much more than upper trophic levels, by reducing generation time under optimal temperature conditions, changing dormancy cycles for certain planktonic species, and altering phenology. These changes in lower trophic levels could cascade through the food web and fundamentally alter ecosystem state. Mobile

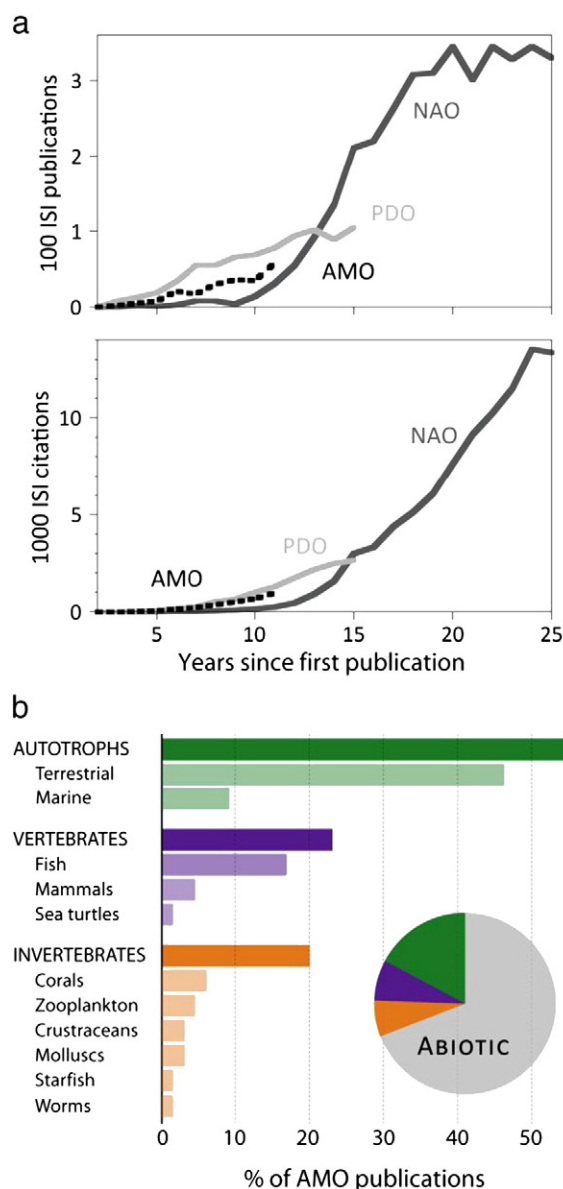


Fig. 3. Publication rate and topics researched for published AMO studies. Using the ISI Web of Science database, we compare the publications and citations for the North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), and the AMO. (a.) After 25 years in the literature, roughly 300 NAO publications and 13,000 citations appear annually. Though not as mature in the scientific literature, PDO and AMO studies are steadily increasing on pace with the NAO. (b.) Most AMO studies (69%) address the index itself and its relationship to regional climate indicators, such as rainfall or temperature. Less than one third (30%) of AMO publications directly relate the AMO to ecological population metrics, and most of these publications (14%) investigate precipitation through the proxy series of terrestrial vegetation records. The relationship of the AMO to terrestrial and marine populations is still a young research field.

marine organisms may respond to temperature by moving away from suboptimal temperatures.

The AMO is also associated with changes in wind and current regimes (Delworth et al., 2007; Häkkinen et al., 2011). Thus, passive dispersal of marine organisms, many of which are planktonic or have planktonic larvae, will be affected resulting in changes in spatial distribution, survival, and population abundance. The response of each species to the physical changes caused by the AMO will depend on life history, spawning behavior, and temperature preferences/tolerances. These individual species responses to the AMO and their subsequent interactions with other components in the ecosystem may lead to unexpected consequences.

The majority of AMO publications (144 or 69%) did not research the influence of the AMO on any taxonomic group, reflecting that by far most AMO studies address the index itself and its relationship to climate indicators, such as rainfall or temperature (Fig. 3b). Of the 210 total AMO publications recognized through our ISI search, 36 (17%) dealt with autotrophs, 15 (7%) with vertebrates, and 13 (6%) with invertebrates. Less than one third (64 or 30%) of AMO publications directly relate the AMO to ecological population metrics, and most of these publications (30 or 14%) investigate precipitation through the proxy series of terrestrial vegetation records. The relationship of the AMO to terrestrial and marine populations is still a developing research field.

4.1. Phytoplankton

Shifts in global and basin-specific primary production and phytoplankton abundances are related to large-scale climatic variability in the physical environment. Despite the lack of a definitive period associated with the AMO, the relationship between the atmospheric variability associated with the NAO and thermohaline circulation characterized by the AMO suggests a coupling of ocean and atmospheric processes on time scales that will facilitate understanding and prediction of inter-annual weather, precipitation, fluvial output and estuarine and marine productivity. Several studies have documented shifts related to the AMO in oceanic (Martinez et al., 2009), coastal and continental shelf (Rodrigues et al., 2009; Schofield et al., 2008) and estuarine (Hubeny et al., 2006) productivity and responses in forage fish populations to this increase in planktonic productivity (Tourre et al., 2007).

Correlations between the AMO indices and marine productivity have been documented at immediate (Schofield et al., 2008), historical (Martinez et al., 2009; Tourre et al., 2007), and pre-historical (Hubeny et al., 2006; Rodrigues et al., 2009) scales. There are several mechanisms through which this might occur. Stratification within the water column separates nutrients at lower depths from entering the euphotic zone, thus limiting primary productivity. Long-term climate oscillations may augment or suppress seasonal conditions that promote or erode stratification and regulate mixing. Schofield et al. (2008) have demonstrated links between the AMO and phytoplankton blooms in the Mid-Atlantic Bight, such that increased nutrient availability during the annual fall transition were augmented by increased winter winds associated with a positive phase in the AMO. Martinez et al. (2009) demonstrated that global phytoplankton productivity is linked to multi-decadal oscillations in both the Atlantic and Pacific, suggesting that links between chlorophyll and sea surface temperature are driven by interactions between the pycnocline and mixed surface layers. The influence of large-scale climate fluctuations on surface stratification has particular influence on phytoplankton productivity in the tropics and mid-latitudes, waters which are often nutrient-limited. Alternatively, warmer sea surface temperatures themselves may influence productivity. Shifts in fluvial inputs associated with altered precipitation patterns will also alter river-induced fertilization of marine productivity.

There are several means to evaluate correlations between marine productivity and multi-decadal shifts in climate. Chlorophyll concentrations and SST may be monitored through satellite observations and imaging. Photosynthetic pigments and organic compounds such as alkenones present in sediments provide historical time-series on primary production among autotrophs. Alternatively proxies for primary productivity such as survey or landing indices of forage fish abundance or biomass may be indicators of changes in productivity. Multi-decadal low frequency signals in the populations of small pelagics and the relative synchrony in these populations across ocean basins suggest populations respond not only to basin-wide climatic patterns but to changes in lower trophic levels (Chavez et al., 2003; Tourre et al., 2007).

4.2. Zooplankton

Zooplankton is especially susceptible to oceanographic changes driven by the AMO because of their short life-cycles and high dispersal rates within their bioclimatic envelope (Beaugrand et al., 2009). Northward geographical shifts of northeast Atlantic calanoid copepods have been observed in response to changes in SST, positively correlated with the AMO (Beaugrand et al., 2009). However, analysis for several regions within the northeast Atlantic of the abundance and the timing of peak abundance of copepod groups showed varied relationships with SST and AMO by region, indicating region-specific responses should be considered (McGinty et al., 2011). In the Mid-Atlantic of the US Northeast Continental Shelf, increasing abundance of certain zooplankton taxa was also positively correlated with the AMO and warm water temperatures (Kane, 2011).

Influences of the AMO on zooplankton may have important ecosystem implications through indirect effects on higher trophic level organisms. Multidecadal variability of North American salmon abundance correlated with the AMO is hypothesized to be a result of influences on the abundance, concentration, and location of key zooplankton species (Condrón et al., 2005). Survival of Atlantic salmon in southern Europe is correlated with the AMO and the abundance of several prey species of zooplankton (Friedland et al., 2009). The copepod *Calanus finmarchicus* is a key food item of cod and other organisms in the northeast Atlantic (Beaugrand et al., 2003). It is expected to decline in some regions with increasing summer temperatures, due in part to the AMO, and the decline could lead to broad ecosystem impacts (Kamenos, 2010).

4.3. Invertebrates

The AMO influences larger invertebrate species through both direct and indirect effects. The observed decline of several demersal fish species in Narragansett Bay, Rhode Island from 1959 to 2005 in correlation with the AMO has had consequences for other species in this ecosystem (Collie et al., 2008). Several of these demersal fish species feed primarily on crustaceans and their decline may have triggered an increase in crab (*Cancer irroratus*, *C. borealis*) and lobster (*Homarus americanus*) species through a release from predation. Increases in squid (*Loligo pealeii*) positively correlated with the AMO also correspond to a shift from demersal to pelagic species, resulting from decreasing chlorophyll *a* and increasing zooplankton grazing (Collie et al., 2008). Hydrological regimes impacting juvenile blue crab (*Callinectes sapidus*) abundance in the north central Gulf of Mexico were related to the AMO (Sanchez-Rubio et al., 2011). High abundance of juvenile blue crab during the early part of the time series corresponded with a cold AMO and positive NAO phase. The abundance was low however during the later part of the time series when the AMO had changed to a warm phase and the NAO had switched to a negative phase (Sanchez-Rubio et al., 2011).

Assemblages of invertebrate rocky intertidal assemblages around the British Isles have also changed over the last 100 years in response to temperature. With 100 years of data, these changes may be associated with climate change, but several patterns suggest the AMO contributes to these observations. Since the 1990s the abundance of warm water species has increased. For instance, the limpet *Patella depressa* was at high abundance during a warm phase of the AMO in the 1950s then declined during a cold AMO phase, and increased in abundance during the recent warm AMO phase (Hawkins et al., 2009).

Multidecadal variability may contribute to extreme conditions that can impact reef-building corals. For example, anomalously high sea surface temperatures in the Caribbean, partly attributed to high background SSTs during the positive phase of the AMO, were responsible for a recent mass coral bleaching event (Simonti and Eastman, 2010). Additionally, the strong relationship between Atlantic tropical cyclone frequency and AMO (Goldenberg et al., 2001), indicates that coral reefs are more at risk from storm damage during warm phases of

AMO, when tropical cyclones are more prevalent (Mendoza et al., 2006).

Historical reconstructions of the AMO behavior can be gathered from several invertebrates such as the bivalve *Arctica islandica*, foraminifera, and several species of scleractinian coral. Oxygen isotope analysis of *Arctica islandica* was used to investigate historical Gulf of Maine water temperatures (Wanamaker et al., 2008). Findings indicated the AMO accounts for about 6–19% of local water temperature variability from 1950 to 2003 (Wanamaker et al., 2008). The AMO impacts ocean temperature, salinity and potentially many other environmental parameters, which can manifest as changes in growth rates or in skeletal chemistry (Kilbourne et al., in review).

4.4. Fish

On both sides of the Atlantic there have been large scale shifts in the distribution of fish species over the last century (Nye et al., 2009; Perry et al., 2005; Simpson et al., 2011; Sundby and Nakken, 2008; ter Hofstede et al., 2010). Large-scale coherence among different species or different populations suggests external factors are important drivers of population dynamics (Moran, 1953). Multidecadal climate oscillations exhibit forcing on basinwide scales and can have important impacts on the distribution and abundance of marine fish (Collie et al., 2004, 2008). During positive phases of the AMO there is generally a poleward shift in the distributions of marine organisms and a subsequent equatorial shift during negative phases. Range shifts can be curtailed depending on the dispersal potential of the species, the connectivity of suitable habitat patches and the rate of temperature change (Genner et al., 2004; ter Hofstede et al., 2010). Several potential mechanisms explaining observed shifts in fish spatial distribution include directed movement to remain within preferred habitat, population level processes such as spatial differences in recruitment or ecosystem changes in productivity or trophic interactions.

The spawning intensity of Arcto-Norwegian cod off the coast of Norway has covaried with the AMO over the last hundred years. The northern spawning areas have been the most important during the warm phases of the AMO (~1930–1950, ~1980–present) while the southern spawning areas were most important during the cold phases (~1900–1920, ~1960s–1970). The stock is at the northern extent of its range and is thus thermally limited. High temperatures increase fecundity and juvenile growth rate resulting in higher recruitments and abundance. The higher fecundity in Arcto-Norwegian cod is linked to their hepatosomatic index and their condition factor which are both a function of feeding conditions. During positive phases of the AMO, warm, productive water is advected from the Norwegian Sea reducing ice coverage. This copepod-rich water increases growth rates of cod creating conditions conducive for Arcto-Norwegian cod to recruit well and increase in abundance (Sundby and Nakken, 2008). Although the AMO was not implicated specifically, long term fluctuations (1908–1998) in Norwegian spring spawning herring is positively correlated with winter water temperatures (Toreisen and Østvedt, 2000).

Along the east coast of the United States most stocks captured in a fishery independent trawl survey exhibited a shift in response to the warming conditions associated with the AMO (Nye et al., 2009). In general, stocks at the southern edge of their range decreased in abundance and their center of abundance shifted poleward. In contrast, stocks at the northern edge of their range typically increased in abundance and their range expanded northward. Those species constrained by the lack of connected suitable habitat, such as those confined to the Gulf of Maine, shifted their biomass to deeper water over the course of the time series. The distribution of fish stocks appeared to shift in order to remain within their preferred temperature range (Nye et al., 2009).

In the northeast Atlantic, distributional studies showed that southern fishes moved north into the English Channel, Celtic Sea and North Sea and within the North Sea species moved poleward over the last few decades (Perry et al., 2005; Simpson et al., 2011;

ter Hofstede et al., 2010). Since 1993, both winter bottom temperatures and species richness have increased in the North and Celtic Sea. However, species richness off the west coast of Scotland has declined in response to the warmer temperatures (ter Hofstede et al., 2010). Lusitanian (warm-water) species have expanded their range into the North and Celtic Seas and their abundance is correlated with a five year running mean of bottom temperature. Boreal species have showed no trend over the same time period resulting in an increase in species richness. The boreal species off the west coast of Scotland have declined however and Lusitanian species have not moved into the area. The temperature has increased more rapidly than expected in these areas leading to the assertion that the AMO has intensified warming attributed to global warming. Fishing mortality has declined in the northeast Atlantic since 1993 suggesting that the climate and not overfishing is playing a more dominant role in patterning fish abundances (ter Hofstede et al., 2010). European anchovy and sardine, warmer water species, have shifted north and reinvaded the North Sea and adjacent seas (Alheit et al., 2012). The NAO allows sardines to close its life cycle in the North Sea while the warmer summer temperatures associated with the AMO lead to anchovy spawning in the North Sea.

The AMO can also have a direct effect on the total biomass of fish species. Atlantic salmon stocks are doing poorly in the eastern and western Atlantic despite limited or no fishing over the past two decades (Friedland et al., 2009; Friedland et al., in review). The low frequency signal of Atlantic salmon catch, a proxy for abundance, was significantly correlated with the AMO from 1917–2009. Catch was higher during the two cool periods 1905–1925 and 1970–1990 and lower during the bracketing warm periods. The mortality of juveniles during their first year at sea appears to be an important bottleneck for this species. In the northeast Atlantic, the AMO impacts the marine food web supporting juvenile salmon, resulting in lower growth during the warm phase and lower survivorship that is assumed to be driven by size mediated mortality. The warm phase of the AMO is believed to affect northwest Atlantic salmon by a different mechanism. Juvenile marine growth does not appear to play a role, instead AMO related warming modifies the predator field affecting the mortality rate of salmon at ocean entry and during the early marine phase. Climate also appears to affect the accumulation of adult biomass by thermal related mechanisms (Friedland and Todd, 2012).

The AMO has been linked to recruitment in other fishes using time series methodologies. Gröger and Fogarty (2011) developed ARIMAX time series models to predict recruitment in cod and found that models incorporating the AMO index, the NAO index and Spawning Stock Biomass (SSB) vastly outperformed all other models. Across the Atlantic basin, the recruitment of North Sea herring was analyzed with a similar method and the ARIMAX model again outperformed the traditional stock recruitment models. The best fit model included the AMO and NAO, but did not include SSB. Variations in herring recruitment appear to be better explained by climate than by SSB. While the exact mechanisms regulating recruitment are not always known, climate oscillations capture large scale oceanographic processes which can have major impacts on the early life stages of fish (Gröger et al., 2010).

Year class strength is typically determined during the first year of life (Houde, 1987) and influenced by environment conditions, which are known to be more variable at the edges of a species range (Grinnell, 1922; Myers, 1998). This recruitment variability is often related to a species ability to extend its range in a poleward or anti-poleward fashion (Hare and Able, 2007; Hare et al., 2010). The proposed mechanisms affecting recruitment in marine fishes include direct temperature effects and/or changes in food availability. In coastal systems, rainfall has substantial impacts on river flow, coastal nutrients and salinity, which can regulate the scale and timing of primary production. Fishes are known to time spawning to coincide with the spring bloom productivity to enhance cohort survival, thus

changes to bloom phenology may adversely affect recruitment (Cushing, 1969; Platt et al., 2003). Warmer temperatures can also alter the activity or spatial and temporal distribution of potential predators (Keller and Klein-MacPhee, 2000; Taylor and Collie, 2003). Though the mechanisms are still undescribed for many species, the accumulated body of evidence points to the AMO as a regulator of fish biomass through bottom-up effects on recruitment dynamics (Drinkwater, 2006, 2011; Gröger and Fogarty, 2011; Gröger et al., 2010).

4.5. Sea turtles, birds, and marine mammals

The effect of the AMO on populations of higher order vertebrates is poorly understood. Our lack of knowledge stems from a poor understanding of the effect of the AMO on primary production and fish populations, which provide the forage for sea turtles, birds, and marine mammals. Despite an absence of comprehensive information, progress on relating the AMO to higher vertebrates is being made. A population model formulated with the AMO as an independent variable explained up to 88% of the observed variability in loggerhead sea turtle (*Caretta caretta*) nesting over the past several decades (Van Houtan and Halley, 2011). It was hypothesized that the AMO had a controlling effect on juvenile recruitment in the North Atlantic. Like most taxa, hatchling and neonatal sea turtles have physiological constraints (Bostrom et al., 2010; Prange, 1976) that limit their capacity to exploit and endure resource variability. As the AMO index is positively correlated with atmospheric and thermohaline circulation in the subtropical-temperate North Atlantic (Knight et al., 2005), the study found a positive AMO was linked to enhanced juvenile recruitment (Van Houtan and Halley, 2011). These ideas were recently applied to explain the historical population variability of loggerhead turtles in the Pacific Ocean and to forecast environmental baselines (based on decadal oscillations) and model proposed fishery actions (Van Houtan, 2011). Knowledge of how the AMO relates to oceanographic processes and marine ecology will advance the understanding of the long-term population dynamics in higher order marine taxa.

5. Ecosystem level responses to the AMO

5.1. Terrestrial systems

The AMO is derived from the variable dynamics of the marine environment, yet some of the best examples of linkages between AMO and ecosystem dynamics come from terrestrial systems. When the AMO was first described by Schlesinger and Ramankutty (1994) as a phenomena that occurs primarily in the North Atlantic Ocean, the description included correlations with effects in terrestrial ecosystems in North America, Eurasia, and Africa. Warm phases of the AMO have been associated with low precipitation, droughts, reduced stream flow and elevated temperature in the southern continental US (Enfield et al., 2001; Sutton and Hodson, 2005, 2007). Because temperature and precipitation greatly affect plant growth, many proxy time series for the AMO are derived from tree ring chronology (Gray et al., 2004). Indeed, ~47% of the citations about effects of the AMO on autotrophs are for terrestrial species (Fig. 2).

The warm phase of the AMO is also associated with droughts in Mexico, wet conditions in Europe, Africa, and India, and frequency and intensity of Atlantic hurricanes (Feng et al., 2011; Goldenberg et al., 2001; Hu and Feng, 2008; Sutton and Hodson, 2005; Zhang and Delworth, 2006). Many studies of the AMO's effects on human populations (Fig. 2), relate North American drought conditions to the persistence of civilizations (Benson et al., 2007; Mendoza et al., 2006). Melting of glaciers in the Swiss Alps (Huss et al., 2010), snow cover in the Tibetan Plateau (Shen et al., 2011), and sea ice cover in Hudson Bay (Tivy et al., 2010) are all correlated with the

AMO; though the changes in the physical environment were well documented in these studies, the consequences for associated terrestrial and aquatic ecosystems have seldom been documented.

Because temperature and precipitation greatly affect plant growth, the AMO has dramatic effects on both agriculture and plant growth in the wild. Forest growth is correlated with the AMO to the extent that many of the proxy time series for the AMO are derived from tree ring chronology (Gray et al., 2004). Tourre et al. (2011) showed that the AMO influences growing season and harvest times of grapes by the viticulture industry in France. In a meta-analysis of AMO related publications, we found that ~47% of the citations about effects of the AMO on autotrophs were for terrestrial species (Fig. 3b).

5.2. Estuarine and aquatic ecosystems

The AMO has a direct effect on estuarine ecosystems mainly due to its linkage to precipitation patterns and resultant river flows and estuarine mixing dynamics. The positive phase of the AMO is generally associated with reduced precipitation across the continental United States although there are exceptions in the southeast and parts of the mid-Atlantic region where precipitation is positively correlated with the AMO (Enfield et al., 2001). Moisture reconstructions from a freeze core at a lake in New Jersey partly supports the positive association of AMO and wet climate patterns in the Mid-Atlantic region over the last ~240 years (Zhao et al., 2010). Cronin et al. (2003) note salinity oscillations in the Chesapeake Bay on time scales of 60–70 years. Further, lake level records derived from long cores revealed an association between US northeast moisture conditions and Atlantic sea surface temperatures at the multidecadal scale for the last ~7000 years (Li et al., 2007). Water transparency and thus light availability in Florida lakes was strongly correlated with AMO, the more proximate mechanism being the influence of the AMO on rainfall (Gaier et al., 2009).

Estuarine fossil pigments indicate that productivity and runoff were lower in a Northeast US estuary when the AMO was in a cold, dry phase (Hubeny et al., 2006). Striped bass abundance increased while shad abundance declined in the Hudson River Estuary during positive AMO time periods (Buchsbbaum and Powell, 2008; O'Connor, 2010). Chesapeake Bay anadromous fish recruitments have been linked to inter-annual variability in hydroclimate conditions and associated effects on the spatial and temporal availability of zooplankton prey for striped bass larvae (Martino and Houde, 2010; Wood, 2000). The strongest recruitments of striped bass and other anadromous fishes in Chesapeake Bay occur during wet years (Martino and Houde, 2010; North and Houde, 2003; Wood, 2000). At decadal time scales, Chesapeake Bay striped bass landings and juvenile recruitments are positively correlated with the AMO while Chesapeake Bay menhaden landings and recruitments are negatively correlated with the AMO (Wood et al., in preparation). The AMO influences the production of Chesapeake Bay striped bass and other fishes through atmospheric forcing and weather effects on hydrographic structure, the subsequent timing and magnitude of zooplankton prey production, and the quantity and quality of habitat (Wood et al., in preparation). Collie et al. (2008) showed that species assemblages in Narragansett Bay, Rhode Island had shifted over the last 50 years and these shifts were strongly associated with the AMO. There were increases in the ratio of pelagic to demersal fish within the bay and an increase in the number of warm water species over time. Similarly, the species assemblage in Bristol Channel, an estuarine environment in southwest England, also changed with SST (Genner et al., 2004).

5.3. Northwest Atlantic

In the Northwest Atlantic, the AMO has been associated with shifts in spatial distribution of fish stocks (Nye et al., 2009), loggerhead sea turtle *Caretta caretta* population dynamics (Van Houtan and Halley,

2011), recruitment of marine and anadromous fishes (Gröger and Fogarty, 2011) and shifts in fish assemblages (Collie et al., 2008; Lucey and Nye, 2010). Landings and population abundance are coherent among most stocks of Atlantic salmon and correlated with the AMO (Friedland et al., in review). Growth in northeast Atlantic salmon stocks was highly correlated with sea surface temperature measurements when post-smolts enter the marine environment (Friedland et al., 2009). Poor growth under warm conditions may be a result of temperature-induced growth reduction and/or declines in productivity associated with the positive phase of the AMO since the 1990s and may be one reason that Atlantic salmon has not recovered despite reduced exploitation.

Much of the research relating the AMO to ecosystem change has been done in the current warm phase of the AMO. However, historical studies indicate similar changes in species assemblages in the previous warm phase of the AMO that occurred in the 1950s. Landings of yellowtail flounder *Limanda ferruginea*, silver hake *Merluccius bilinearis* and lobster *Homarus americanus*, declined in the southern parts of their ranges (south of Cape Cod), but increased in northern parts of their range (Taylor et al., 1957). Menhaden was absent from Massachusetts waters from 1900 to 1922, but reappeared and supported a fishery in 1945. New reports of southern species in northern waters increased as well and these changes seemed to be associated with warm temperatures (Taylor et al., 1957). After 1953, temperatures declined again in this region, but southward shifts in distribution were not documented in the same manner as the northward shifts observed during the warming phase (Colton, 1972). A disease of the Eel grass *Zostera* spread rapidly along the Atlantic coast of North America during an earlier warm phase when cultural eutrophication was less of a dominate driver of seagrass decline (Petersen, 1935).

Steele et al. (2007) noted that low nitrate levels associated with lower fish productivity prevailed during the 1960s followed by an increase in the early 1970s. These nutrient levels may have been associated with climatic conditions related to NAO, particularly the effects of Labrador Current transport. However, the AMO and its effect on circulation patterns may have also played a role.

Several whole-ecosystem analyses have identified the AMO as an important factor regulating ecosystem state. A multivariate analysis of the Northeast US LME found that anthropogenic factors, primarily fishing, caused large scale changes in the ecosystem. An array of climate and physical indicators were examined and revealed a transition beginning in the mid-to-late 1990s, reflecting an increase in the both the NAO and AMO along with associated temperature, river flow, and wind stress metrics in the more northerly locations (Fig. 4). In Canadian systems similar patterns were also observed on the Scotian Shelf (Frank et al., 2005) and a coastwide analysis of trends in ecosystem variables revealed that fishing was the dominant pressure on the ecosystem, but that the AMO was also an important factor (Shackell et al., 2012). In these systems, it appears that overfishing triggered a cascading effect which has been amplified and maintained by environmental change even as fishing pressure has been reduced on many ecosystem components. The persistent positive AMO and NAO state in this region may explain why many fish stocks have not recovered, while others have.

The local mechanism in the Northwest Atlantic that links AMOC and the AMO to these observed ecosystem changes is the interplay between warm slope water influenced by the Gulf Stream and cold Labrador slope water and the resulting spatial pattern in temperature. This process affects the entire shelf, but particularly affects nutrient and temperature regime in the Gulf of Maine. Bottom water enters the Gulf of Maine through the narrow Northeast Channel. If the volume of cold Labrador slope water is large relative to warm Gulf Stream water, bottom water temperatures in the Gulf of Maine and outer continental shelf will be relatively cold. However, when the Gulf Stream is in a more northerly position, shelf waters tend to be warmer. The exchange between these two water masses has been

shown to affect distribution of commercially important fish, abundance of *Calanus finmarchicus*, and right whale calving success (Green and Pershing, 2003; Nye et al., 2011).

5.4. Northeast Atlantic

Although the AMO was not formally named prior to the 1990s, historical records indicate that shifts in species distributions occurred in the 1930s in European waters during a positive phase of the AMO (Southward, 1980). Russell and Kemp (1932) reported the appearance of *Veilella*, *Ianthina*, and *Salpa fusiformis* at Plymouth, UK. Whales and dolphins were more common in Scottish water (Stephen, 1938). Strandings of whales and dolphins, uncommon in Scottish waters, became much more frequent in 1931–1933. Several Kemp's Ridley

and loggerhead turtles were caught in the English Channel perhaps carried by surface water penetrating the English Channel and/or by strong westerly winds (Parker, 1939; Russell, 1939). During this time, tropical tunicates and blue sharks also were more abundant in northern waters (Farran, 1933) and a disease of the eelgrass *Zostera* spread throughout Europe (Petersen, 1935). Several marine species were found in European waters that had never been recorded previously or had been found on only one or two occasions (Stephen, 1938). Dense patches of diatoms apparently affected the herring fishery by forming a barrier that herring avoided during their migration (Savage and Wimpenny, 1936). These shifts in species assemblages throughout the food chain were attributed to a 1.5–3 °C increase in water temperatures in the North Sea in the early 1930s, but salinities were also high, indicating a change in circulation. At the time, it was suggested that this general warming in air and water temperatures was caused by greater northward flow of Atlantic water of southern origin (Farran, 1933; Stephen, 1938). Anomously high egg production of Atlantic herring and oysters were attributed to these high temperatures. A more detailed explanation of changes in the English Channel are given in Meiszkowska et al. (this edition).

Monitoring off Plymouth, England since the 1920s indicate that during periods of positive AMO there were high abundance of chaetognaths *Sagitta elegans*, but low abundance of fish larvae, particularly sardine *Sardina pilchardus* and the opposite being true during periods of negative AMO (Hawkins, 2003; Mieszkowska et al., this issue; Russell, 1973; Southward, 1980; Southward et al., 2005). Squid (*Loligo*) arrived earlier in the warmer 1950s than the cooler 1960s and 1970s (Sims et al., 2001). This phase shift was termed the “Russell Cycle”, but further monitoring found that these ecosystem phase changes were not truly cyclical. The phase shifts associated with the “Russell Cycle” appear to be driven by AMO forcing, which as described above has not been established as a cycle with regular oscillations either. Härkönen et al. (2006) reviewed the potential causes of two recent outbreaks of phocine distemper in the North Sea and parts of the Baltic. Whilst the specific causes are not clear, both coincide with large changes in the cod and blue whiting stocks at a time when the AMO and NAO were in positive phases.

During the 1920s and 1930s a large scale warming event occurred in the northern North Atlantic ocean which altered marine ecosystems of the Barents, Norwegian, and Icelandic Seas (Drinkwater, 2006, 2011). Warm polar water temperatures reduced the amount of sea ice and enhanced the flow of warm Atlantic water into the area. The changes in oceanographic condition are thought to have caused an increase in phytoplankton and zooplankton and actuated cascading effects on upper trophic levels of the ecosystem. The ranges of cod, haddock, and herring expanded northward while capelin and polar cod were excluded from the area. The phenology of migrations changed with species entering these waters earlier and warm-water Atlantic benthic species were colonized the region for some time.

In the Barents Sea, the distribution of Atlantic cod, capelin and polar cod shifted northward while the distribution of haddock and Norwegian spring-spawning herring shifted eastward. The abundance of herring increased over the prolonged warming period and their range expanded, supporting fisheries in both Russia and Iceland where these fisheries did not exist before (Drinkwater, 2011). During the same time period, in the Norwegian Sea, the location of the spawning sites of Atlantic cod shifted to more northerly regions (Sundby and Nakken, 2008).

During positive phases of the AMO the proportion of cod spawning in northern regions increased as did recruitment while catches were poor in fisheries that targeted cod from the southernmost spawning grounds. During negative phases of the AMO, the southernmost spawning grounds have been more important, but overall recruitment and year class strength tended to be lower. Since 2003, spawning has been more active in northern Norway, in areas where it has not been observed for 40 years (Sundby and Nakken, 2008). Species richness of fish in 3 regional seas in the eastern North Atlantic Ocean has changed over time (1997 to

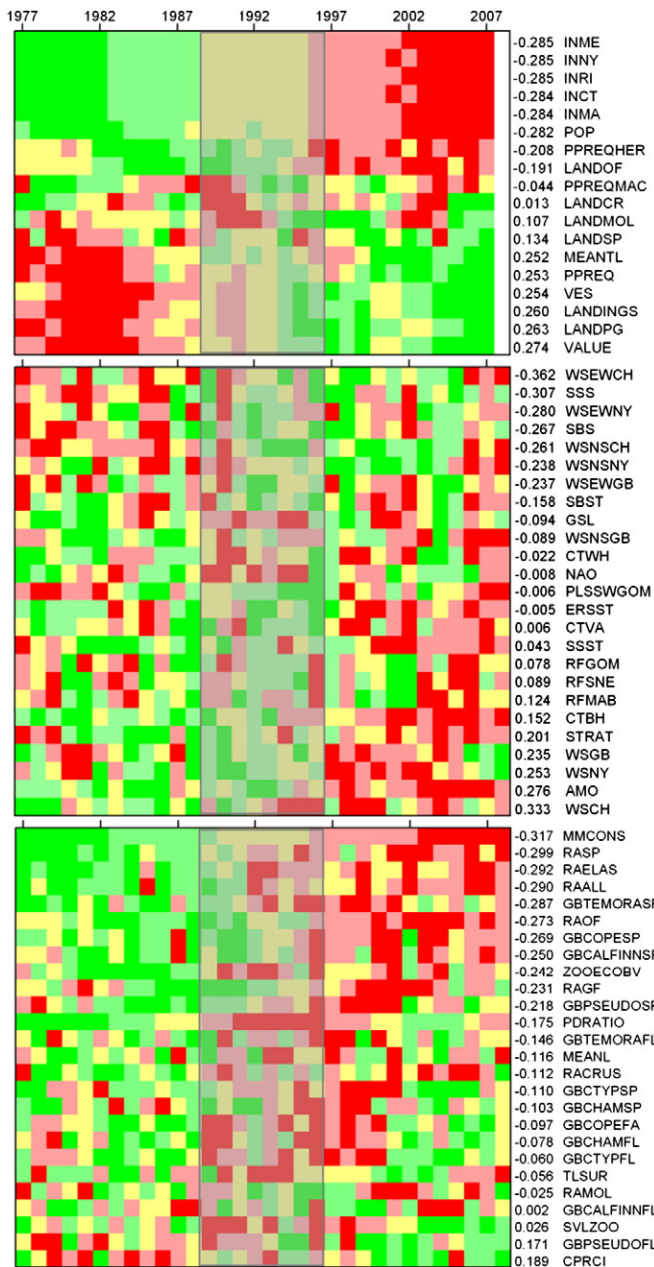


Fig. 4. Results from PCA analysis of a Northwest Atlantic ecosystem (Northeast US LME) showing anthropogenic factors (top panel), climate stressors including the AMO (middle panel) and ecosystem responses (bottom panel). The gray highlighted area indicates the time period where a shift in ecosystem status occurred. Modified from Ecosystem Status Report for the Northeast US LME (For more details see Ecosystem Assessment Program, 2009).

2008) in response to higher water temperatures and the biogeographic affinity of the species (ter Hofstede et al., 2010). In the North and Celtic Seas, species richness increased due to increases in the number of warm-adapted Lusitanian species. In the area west of Scotland, species richness decreased because the number of cold-adapted Boreal species decreased. In the Irish Sea, off-shelf regions showed a progressively later timing in the seasonal peak of *chl-a* measurements moving northwards loosely associated with the AMO (McGinty et al., 2011). Both the NAO and AMO were important to understand ecosystem changes at these high latitudes, but the role of warm water advected from the south associated with the AMO into these northern areas is critical to understanding ecosystem changes.

The key factor to understand the physical oceanography of the Northeast Atlantic is the extent of the subpolar gyre. The subpolar gyre rotates counterclockwise and is composed of relatively cold and low saline water. During negative phase of the AMO, the circulation is intense and cold water from the gyre dominates the northern Northeast Atlantic (Benson et al., 2007; Hatun et al., 2005). Warm, saline water from the North Atlantic Current (NAC) originating from the Gulf Stream and Eastern North Atlantic Water (ENAW) originating from the Biscay region is prevented from moving northward by the eastern limb of the subpolar gyre. During positive phases of the AMO, the circulation of the gyre weakens and the gyre retracts, allowing the warm, saline waters of the NAC and ENAW to move northward leading to a rapid warming and salinification of the northern Northeast Atlantic. Warm subtropical water is allowed to enter these areas. A recent study suggests that the subtropical gyre contracts as a result of changing winds that can occur anywhere over the Atlantic. Changes in wind patterns or “blocking events” vary decadal with the AMO (Häkkinen and Rhines, 2004; Häkkinen et al., 2011). Changes in strength and extent of the subpolar gyre lead to variations in the community assemblage of the Northeast Atlantic through bottom-up processes. A numerical ocean general circulation model links these changes in circulation with phytoplankton, zooplankton, blue whiting, and pilot whales (Hatun et al., 2009).

5.5. North Sea

Long-term shifts in species assemblages and distribution attributable to climate variability have been detected in the North Sea. An increase in the inflow of generally warmer and more saline NAC water occurred in the late 1980s. This caused changes at all trophic levels including increases in dinoflagellates and decapods (Edwards et al., 2002). As is the case in other ecosystems, both fishing and warming have caused shifts in abundance and distribution of fish. For example, plaice *Pleuronectes platessa* showed a northward and deepening shift in distribution that could be attributed to climate, but not to fishing pressure, whereas sole *Solea solea* showed a southward shift and shallowing that was related to both climate change and fishing pressure (Engelhard et al., 2011). Northward latitudinal shifts in species distribution consistent with climate change have been detected (Perry et al., 2005) as well as utilization of deeper waters by the North Sea fish assemblage driven by increasing bottom water temperatures (Dulvy et al., 2008). The correlative relationships to the AMO were not developed in these studies. However, the AMO may affect the North Sea ecosystem via its influence on warm water entering from the south through the English Channel and by warm North Atlantic Water entering from the north. Thus, southward shifts in distribution and invasions of new species from the north have been observed (Dulvy et al., 2008; Ehrich and Stransky, 2001; Perry et al., 2005).

The most recent analysis of the North Sea ecosystem covers a period from 1983 to 2009 and it shows a continued and intensified decline in the status cod and skate stocks (Kenny et al., 2009). The signal for these species groups were embedded in the groundfish trend of a meta-analysis for the North Sea system (Fig. 5). However, the trends in variables showing an increase in dominance (e.g. certain pelagic fish stocks, bottom temperature and *Calanus helgolandicus*)

have not intensified to the same extent over the same period (Fig. 5). Indeed, the more recent data (2007–2009) indicates that the intensification of positive anomalies associated with temperature and some of the pelagic fish stock variables (notably herring) have actually started to decline. It is also apparent that many variables changed state between 1994 and 1996, which coincides with peaks in the positive phase of the NAO and SST in the North Sea (Fig. 5).

In an attempt to better understand the causes driving this change during the last 30 years, Kenny et al. (2009) used a type of ecosystem network analysis (Heath, 2005; Mackinson et al., 2009). The trend in bottom-up forcing corresponds very well with the trend in the SSB of herring for the North Sea (Fig. 6). From this we conclude that the principal controlling mechanism regulating the direction of the trend in the status of the North Sea herring stock is bottom-up, that is it is responding primarily to changes in the prevailing environmental conditions. Clearly this trend (in terms of its rate of change) is modified by fishing pressure as is the absolute level of SSB. The relative importance of bottom-up vs. top-down forcing is further emphasized by examining long time-series of environment, stock and fisheries data. By comparing the trends of North Atlantic sea surface temperature (SST-AMO), herring SSB and the herring landings there is clear correspondence between the multi-decadal trend in the AMO and herring SSB, whilst the fishery appears to correspond more closely to decadal variations in herring stock yield (Fig. 6).

6. Conclusions

There is increasing evidence that the AMO is important to many trophic levels and to overall ecosystem state, but several factors prevent a full understanding of how and to what extent the AMO affects ecosystems around the Atlantic basin. First, many of the observed effects are based on detected changes in fish abundance surveys. While fish surveys provide time series longer than those typically available for most other taxa, they are still limited to only a few decades and document changes in species assemblages only for the last positive phase of the AMO. Much qualitative and some quantitative evidence suggest that similar changes in the ecosystem occurred in warm periods in the 1930s–50s throughout the North Atlantic. Without long time series of multiple ecosystem metrics it is difficult to establish the link between the AMO, changes in ecosystem state, and the more proximate causes of these changes. Only two studies have sufficient data to quantify population level changes occurring over more than one full AMO cycle (Sundby and Nakken, 2008; Toresen and Østvedt, 2000). Most works only describe the recent half cycle in the AMO. Secondly, fish populations and communities have been subject to high fishing pressure in these ecosystems. Fishing pressure is a more dominant driver in many of these ecosystems, complicating our ability to disentangle fishing effects from the AMO. It is likely that additional factors including other climate variability patterns like the NAO interact with the AMO making it difficult to discern the effect of the AMO itself. As such, a priority research area should be to coordinate research efforts to investigate the effects of other pressures (e.g. fishing) in combination with the AMO.

Although fish trawl surveys provide valuable time series, much of the published literature on the ecological effects of the AMO are focused on autotrophs in terrestrial and marine environments. In marine systems, several studies suggest that ecosystem changes related to the AMO are “bottom up” (Drinkwater, 2006, 2011). The growing body of evidence linking large-scale climate oscillations to marine productivity emphasizes the need for greater inclusion and more accurate representation of multi-decadal climate regimes in ecosystem and global ocean models. The physical processes governing ocean productivity patterns operate at multiple scales, including anthropogenic climate shifts at the scale of centuries, decadal and multi-decadal atmospheric and oceanic climate regimes, and inter-annual and seasonal variability. Understanding multiple processes overlapping at different scales and how

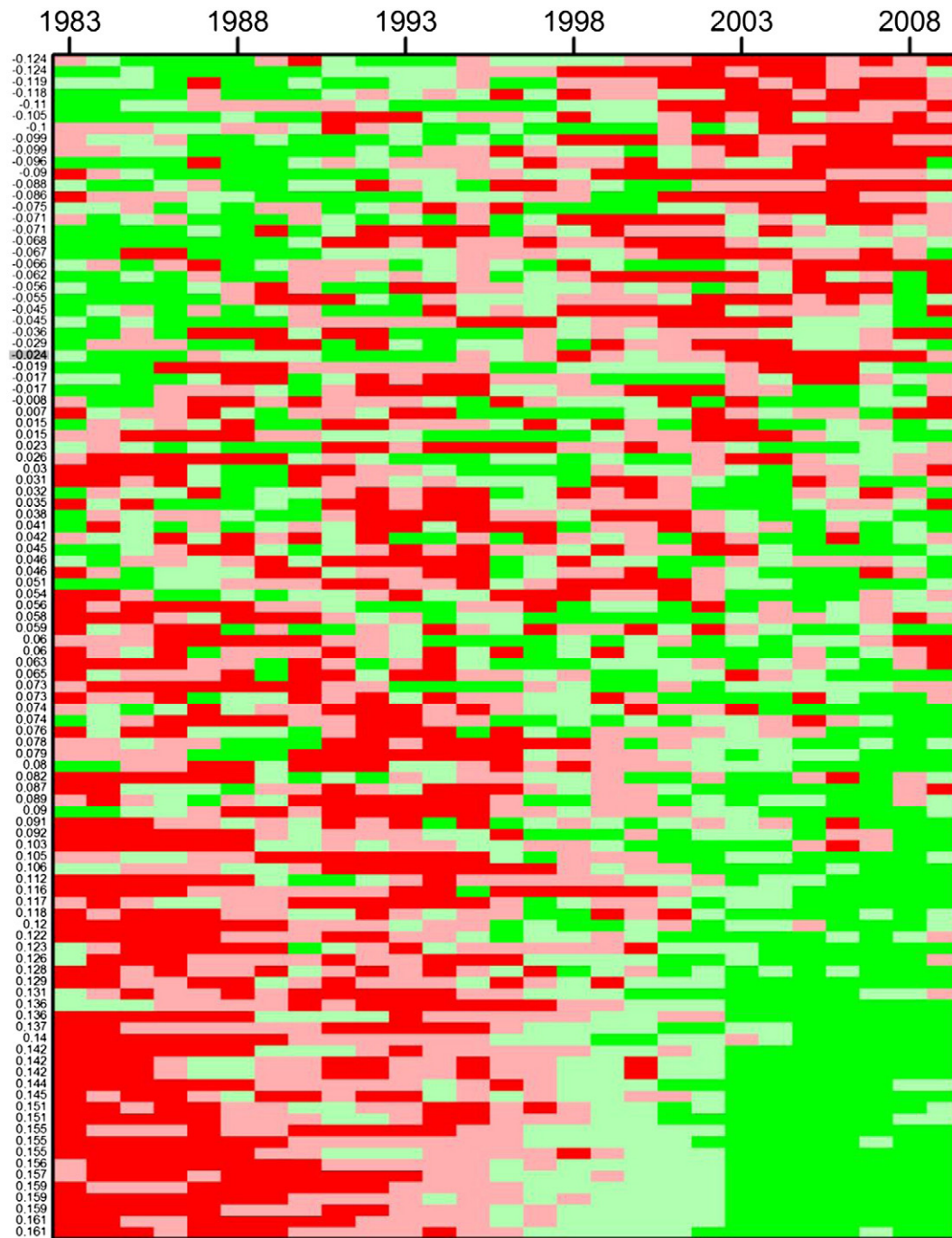


Fig. 5. A composite and ordered plot of North Sea variable anomalies between 1983 and 2009. PC scores for each variable are given on the vertical axis and the AMO is highlighted in gray. Green indicates negative anomalies and red indicates positive anomalies. Note the intensification of negative anomalies in recent years compared to the status of the same variables in 1983. The variables with the highest loadings and negative anomalies (top 5 variables) at the beginning of the time series were *Calanus helgolandicus* biomass, Horse mackerel landings, bottom silicate ($\mu\text{mol l}^{-1}$), Atlantic herring spawning stock biomass, and average pelagic fish length. The variables with positive anomalies at the start of the time series (bottom 5 variables) were North Sea plaice CPUE, Atlantic cod landings, Whiting CPUE, North Sea plaice landings, and otter trawling effort. For more details on methodology and variables used please see [Appendix 1](#) and [Kenny et al., 2009](#).

these processes influence ocean conditions and primary productivity requires multi-decadal or centennial time series. Building, maintaining and analyzing relevant long-term time series data should be a priority ([Martinez et al., 2009](#)).

Changes in the character of several ecosystems across the Atlantic occurred in the 1990s indicating a large-scale process was at work. Closer examination of the proximate causes of these ecosystem changes emphasizes that the AMO has different modes of action throughout the Atlantic basin. For example, in the Northeast Atlantic, the primary effect

seems to stem from a change in the subpolar gyre related to more frequent blocking events ([Häkkinen and Rhines, 2004](#); [Häkkinen et al., 2011](#); [Hatun et al., 2005, 2009](#)). In the Northwest Atlantic, the primary effect stems from changes in the relative strength of cold Labrador slope water and warm Gulf Stream water. In terrestrial and estuarine ecosystems, changes in precipitation rather than temperature associated with the AMO, are more important variables for ecosystem change. Although the AMO index is defined by SST, the AMO should not be thought of only as an indicator of temperature change. Thus referring to the

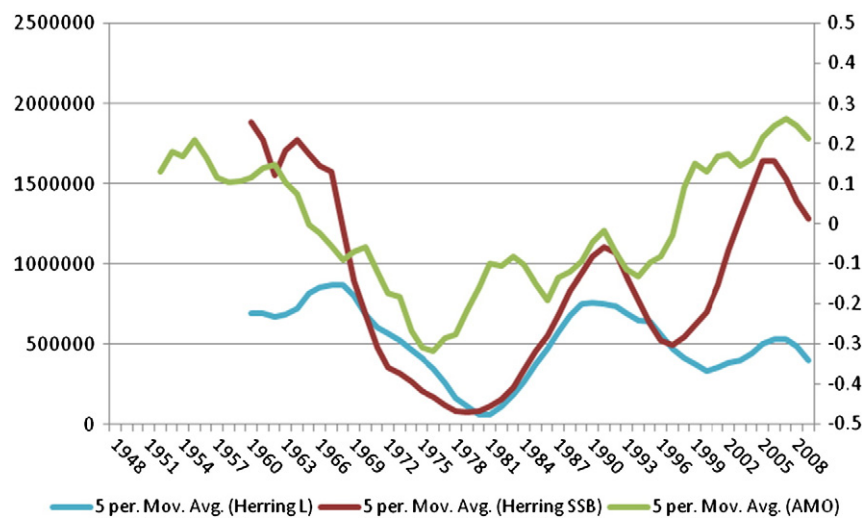


Fig. 6. Long-term trends in North East Atlantic spring spawning herring biomass, AMO and herring landings. The herring landings follow almost exactly the limits set by the Total Allowable Catch (TAC).

“warm” and “cold” phase of the AMO is misleading. Rather, the AMO is an indicator of basin-wide shifts in water masses and associated changes in atmospheric processes.

Because the AMO index represents changes in the character of water masses within ecosystem boundaries, we recommend that researchers use the AMO index as a leading indicator of large-scale climate variability. Once a link between ecosystem state and climate variability is established, the more proximate mechanism/s can be identified. When identifying proximate mechanisms, it is also important to consider the combined effect of other modes of climate variability as many studies that we reviewed highlight the importance of both the AMO and NAO (Gröger and Fogarty, 2011; Gröger et al., 2010). Furthermore, the rate of change in each ecosystem is likely a function of whether it is a closed systems and to what degree it is closed. Relatively closed systems vary much more rapidly than more open systems such as the North Sea and West of Scotland/Ireland ecosystems; comparative analysis of the Baltic Sea, North Sea and Irish Seas suggest different rates of change (McGinty et al., 2011; ter Hofstede et al., 2010).

A key question resulting from this review of the AMO's impact on ecosystem dynamics is whether the AMO can be incorporated into a resource management framework, particularly EBM. The AMO and other modes of climate variability have been successfully incorporated into single-species assessments. Recent modeling efforts with sea turtles (Van Houtan, 2011; Van Houtan and Halley, 2011), for example, have already developed population forecasts using oscillation indices. Furthermore, incorporating the NAO and AMO in single species assessment models improves the predictability of recruitment and reduces a major source of uncertainty in stock assessments (Gröger and Fogarty, 2011; Gröger et al., 2010). A recent study (De Oliveira and Butterworth, 2005) demonstrated that recruitment–environmental relationships can be useful for management even if the correlations and associated predictability are only of moderate strength ($r^2 > 0.5$). While it may not currently be feasible to incorporate environmental indices into every single-species population model, the AMO is a promising metric for use in EBM.

The current body of ecological studies suggests that the AMO is associated with multidecadal changes in ecosystem state, but can we use the multidecadal signal of the AMO to inform EBM? If environmental factors can be incorporated into management a certain degree of predictability is beneficial (Walters and Collie, 1988). Because the AMO does not fluctuate as widely as other modes of climate variability such as the NAO, the positive and negative phases of the AMO index can be used to predict ecosystem patterns at a coarse level. For

example, when both the AMO and NAO are in a positive phase a more rapid warming at high latitudes in the North Atlantic might be expected and management can be adjusted depending on a species' biogeography and temperature preferences. Because the variability in the AMO operates on longer time scales than the NAO or annual changes in temperature, there may be some predictability in the cycle. An analysis using global climate models indicates that AMOC and the AMO might be predictable at decadal scales (Msadek et al., 2010). Having an indicator of climate state and an understanding of the mechanism of its effect on different components of the ecosystem will likely inform the management process, especially on EBM decisions at decadal timescales. Recent advances in simulating the dynamics of the subpolar gyre suggests a potential for predicting the distribution of the main faunistic zones in the northeastern Atlantic a few years into the future, which might facilitate management of the commercially important fisheries in this region (Hatun et al., 2009).

In a management context, the AMO should be viewed as an indicator of ecosystem state. For example, in the North Sea there is a tendency towards an ecosystem state dominated by small pelagics during the positive phase of the AMO, which then has a negative impact on demersal stocks; management could adjust fishing limits appropriately. The length of the cycle makes this hard to test statistically, but there are mechanisms which describe how sprat and herring biomass in the North Sea are responding positively to increases in SST (Kenny et al., 2009). High pelagic SSB will in turn have a large negative predation pressure on the larvae of many other fish species. This multi-decadal pattern of system variability highlights some important issues relevant to fisheries and potentially ecosystem management, namely that trajectories in ecosystem state (determined by long-term oscillations in carrying capacity) are probably the norm and they ultimately determine the type and quantity of resource we can exploit. If the AMO is associated with “bottom-up” forcing, total ecosystem production and by extension, fisheries production, may change with the phase of the AMO. It therefore follows that management approaches which assume a fixed yield or level of ecosystem service provision are inappropriate. Given that many regional management strategies now extend to cover multi-decadal periods, knowledge of such trajectories is essential, especially as we reach the carrying capacity of many coastal systems.

Although the AMO is a mode of natural climate variability, it will interact with and exacerbate or mitigate the effects of anthropogenic climate change. Thus, understanding the physical aspects of this phenomenon and its effects on ecosystems is of utmost importance. Furthermore, many of the ecosystem responses we see in the positive

phase of the AMO may be predictors of ecosystem changes to come as global climate change progresses. A key component of the Earth's climate system is the AMOC to which the AMO is closely associated. Global climate models predict that AMOC will weaken by 2100 by about 25% (Meehl, 2007; Schmittner et al., 2005). For the Northwest Atlantic, this means that the position of the north wall of the Gulf Stream will be in a more northerly position (Joyce and Zhang, 2010), volume of Labrador slope water will lessen, and the Northwest Atlantic ecosystems will be warmer due to the direct effects of anthropogenic warming and to subsequent changes in circulation. With a decline in AMOC, circulation of the subpolar gyre may weaken allowing warm water from the south to influence the ecosystems of the Northeastern Atlantic. For this reason, continued and increased monitoring to improve understanding of environmental influences on ecosystems is especially important. Such research should be trans-disciplinary, involving physical oceanographers, climate scientists, and ecologists to fully understand this broad-scale phenomenon and its effects on ecosystems. Such holistic understanding will contribute to the effective management of natural resources through an Ecosystem-based approach.

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Appendix 1

PC1	Variable Name	PC1	Variable Name	PC1	Variable Name	PC1	Variable Name
–0.124	CalheINS	–0.024	AMO	0.060	nop-R	0.123	dinoNS
–0.124	MUR_L	–0.019	Herring	0.063	calfinNS	0.126	HER_L
–0.119	Bottom SLCA (umol/l)	–0.017	JOD_L	0.065	Bottom AMON (umol/l)	0.128	cod-R
–0.118	SCOPHTHALMUS RHOMBUS	–0.017	Mackerel	0.073	ple-TB	0.129	POK_L
–0.110	her-SSB	–0.008	MAC_L	0.073	had-R	0.131	SOL_L
–0.105	Ave.P.Fish.L	0.007	Bottom PHOS (umol/l)	0.074	RAJIDAE	0.136	ANF_L
–0.100	HOM_L	0.015	SOLEA SOLEA	0.074	her-47d3	0.136	HAD_L
–0.099	DiaNS	0.015	her-TB	0.076	SPR_L	0.137	SKA_L
–0.099	HAL_L	0.023	TRISOPTERUS ESMARKI	0.078	GADUS MORHUA	0.140	PT
–0.096	SCOMBER SCOMBRUS	0.026	Saithe	0.079	Sole	0.142	had-34
–0.090	Sprat	0.030	euphNS	0.080	SCOPHTHALMUS MAXIMUS (PSETTA MAXIMA)	0.142	NOP_L
–0.088	Bottom PSAL	0.031	had-TB	0.082	sai-3a46	0.142	nop-34
–0.086	had-SSB	0.032	Bottom DOXY (umol/l)	0.087	nop-TB	0.144	cod-SSB
–0.075	Bottom NTRI (umol/l)	0.035	AMMODYTES MARINUS	0.089	sol-SSB	0.145	copsNS
–0.071	meroNS	0.038	MELANOGRAMMUS AEGLEFINUS	0.090	BT	0.151	cod-TB
–0.071	SPRATTUS SPRATTUS	0.041	ANARHICHAS LUPUS	0.091	cladNS	0.151	cod-347d
–0.068	TRACHURUS TRACHURUS	0.042	sol-R	0.092	Bottom TPHS (umol/l)	0.155	TUR_L
–0.067	POLLACHIUS VIRENS	0.045	CLUPEA HARENGUS	0.103	WHG_L	0.155	DS
–0.066	MERLUCCIIUS MERLUCCIIUS	0.046	Bottom PHPH	0.105	sol-TB	0.155	Cod
–0.062	Bottom NTRA (umol/l)	0.046	NAO	0.106	BLL_L	0.156	ple-nsea
–0.056	NEP_L	0.051	MERLANGIUS MERLANGUS	0.112	Haddock	0.157	Plaice
–0.055	Bottom Temp	0.054	nop-SSB	0.116	Norway pout	0.159	CAA_L
–0.045	Bottom CPHL (mg/m ³)	0.056	ple-R	0.117	sol-nsea	0.159	COD_L
–0.045	LOPHIUS PISCATORIUS	0.058	Ave.D.Fish.L	0.118	her-R	0.159	Whiting
–0.036	PLEURONECTES PLATESSA	0.059	Bottom NTOT (umol/l)	0.120	MT	0.161	PLE_L
–0.029	HIPPOGLOSSUS HIPPOGLOSSUS	0.060	ple-SSB	0.122	HKE_L	0.161	OT

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