The Influence of Climate Variability on North Atlantic Zooplankton Populations

Andrew J. Pershing and Charles H. Greene Cornell University

Benjamin Planque and Jean-Marc Fromentin IFREMER

Introduction

Considerable attention has been focused in recent years on how ecosystems respond to natural climate variability, with the understanding that this knowledge will be useful for managing natural resources in the face of anthropogenic climate change. This work has shown that climate variability influences the ecology of many species and can play an important role in ecosystem dynamics (McGowan et al., 1998,Ottersen et al., 2001). Here, we review the influence of interannual to interdecadal climate variability on zooplankton populations in the North Atlantic.

Because of the economic importance of North Atlantic fish stocks, there is a long history of research on the variability in the fisheries and ecosystems in this region (Mills, 1989). Time series from this research provide a unique opportunity to study population responses to climate variability. The best example of such time series are those derived from the Continuous Plankton Recorder (CPR) surveys conducted by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). The SAHFOS surveys provide a detailed picture of long-term variability in the ecosystems of the North Atlantic, particularly the eastern Atlantic (Gamble, 1994). The SAHFOS surveys, which began in the late 1940's, rely on commercial ships traveling on their usual routes. The CPR sieves plankton on to a silk gauze that is periodically advanced, thereby providing a quantitative record of the abundance of zooplankton and large phytoplankton in discrete segments along the ship's path. Traditional oceanographic surveys complement the CPR surveys, and together, these techniques are beginning to provide a detailed picture of the influence of climate variability on zooplankton populations in the North Atlantic.

Variations in zooplankton populations in regions throughout the North Atlantic have been tied to changes in the Atlantic atmosphere-ocean system (Figure 1). Recent work has tended to focus on the impact on zooplankton of one particular climate mode, the North Atlantic Oscillation (NAO) (Ottersen et al., 2001), although it is important to remember that the NAO is only one measure of the climatic conditions in this region. Rather than describe the details of each of these climate-zooplankton associations, we will focus on two particularly well-known regions, the North Sea and the Gulf of Maine. These examples characterize the range of mechanisms by which climate may influence zooplankton. This approach will allow us to categorize the important processes linking zooplankton populations and climate.

Climate Variability and Zooplankton Populations in the Northeast Atlantic

Most results linking the NAO to variability in marine ecosystems come from studies in the

Northeast Atlantic. Starting with the study by Fromentin and Planque (1996) which related variability in the North Sea populations of the copepods *Calanus finmarchicus* and *C. helgolandicus* to the NAO, researchers have documented NAO-associated changes in marine ecosystems throughout the region (Ottersen et al., 2001). However, the importance of the NAO in the eastern Atlantic should not be surprising, given the strong influence the NAO has on European weather.

Environmental Conditions and the NAO

The state of the NAO is a good indicator of weather patterns over the eastern Atlantic and Europe. When the NAO is positive, the strong pressure difference between the subpolar low and subtropical high enhances the westerly winds and shifts their track to the north (Figure 2) (Hurrell, 1995; Dickson et al., 1996). The shift in the westerlies brings warmer air to northern Europe and Scandinavia, but also more precipitation and winter storms. When the NAO reverses, the westerlies shift to the south, and northern Europe is colder and less stormy (Hurrell, 1995; Dickson et al., 1996).

The atmospheric and circulation changes associated with the NAO are further reflected in the correlations between winter sea surface temperature and the NAO (Reid and Planque, 1999). When the NAO is positive, a large area in the center of the North Atlantic is cooler, and areas to the south and east are warmer. Sea surface temperature in the North Sea is positively correlated with the NAO. The correlation is similar to that for air temperature over the North Sea, but is also related to NAO-associated changes in the water flowing into the North Sea from the Atlantic. When the NAO is negative, the inflow increases in the eastern section, bringing cool water from the Norwegian Sea (Stephens et al., 1998; Reid et al., 2001). When the NAO is positive, the inflow is restricted to a small section off the Scottish coast, and the water entering is warmer.

In addition to the direct, year-to-year influence of the NAO on conditions in the eastern Atlantic, there is evidence for a cumulative effect of the NAO on this region. The 1980's were the first sustained period of positive NAO-conditions since the 1920's. Reid et al. (2001) report the presence of unusually warm water in the North Sea during the late 1980's. This water was associated with a coastal jet that intensified during this period, bringing very warm water and warm-water species into the vicinity of the British Isles. They propose that several years of very positive NAO conditions were required to alter the flow in this jet.

Response of Zooplankton Populations

Calanus finmarchicus Variability

Of all the species in the North Atlantic, few have received more attention than the calanoid copepod, *Calanus finmarchicus*. *C. finmarchicus* is a large copepod that dominates the spring zooplankton biomass in areas across the N. Atlantic (Marshall and Orr, 1955; Astthorsson and Gislason, 1995, Planque and Batten, 2000). To understand many of the associations between this species and climate, it is necessary to understand its seasonal patterns. *C. finmarchicus* is most abundant during late spring and early summer, following the spring bloom. Starting in early

summer, some *C. finmarchicus* postpone their development to adults, descend to depths of 400-2000 m, and enter diapause, a state of reduced activity (Hirche, 1996; Heath et al., 2000). By autumn, most *C. finmarchicus* have entered diapause and their abundance near the surface is greatly reduced. The copepods begin to emerge from diapause and enter the surface waters in winter, in anticipation of the spring bloom (Miller et al., 1991). Because their overwintering strategy requires deep water, most areas on the continental shelf are too shallow to support large numbers of diapausing *C. finmarchicus*. Thus, even though *C. finmarchicus* dominates the springtime biomass in shelf regions such as the North Sea (Williams et al.; 1994), the populations of this species in shelf ecosystems should be viewed as expatriates from the openocean populations (Greene and Pershing, 2001).

C. finmarchicus in the Northeast Atlantic, together with its cogener *C. helgolandicus*, were the first zooplankton species whose fluctuations in abundance were directly correlated with the NAO (Fromentin and Planque, 1996). Starting in the 1960's, the NAO Index exhibited a consistent trend towards more positive conditions (Figure 3a). During this time, the abundance of *C. helgolandicus* increased (Figure 3b) along with the total abundance zooplankton and phytoplankton as measured by the CPR (Planque and Taylor, 1998). The *C. finmarchicus* population exhibited an opposite trend, declining by 37% between 1962 and 1992 (Figure 3c). *C. helgolandicus* abundance is positively correlated with the NAO, and exhibits the same pattern as total zooplankton and phytoplankton (Planque and Taylor, 1998) (Figure 4a). *C. finmarchicus* abundance is negatively correlated with the NAO (Figure 4b), and the correlation is stronger than that for *C. helgolandicus*.

Several hypotheses have been advanced to explain the NAO-associated fluctuations in the North Sea between populations of these two copepods. Fromentin and Planque (1996) proposed that changes in temperature associated with the NAO (warmer during positive years, colder during negative) drive the species shifts, with *C. helgolandicus*, which is typically found in warmer waters, flourishing during warmer conditions and *C. finmarchicus*, which is typically found in cold waters, flourishing during colder conditions. They also suggest that the influence of temperature on these species could alter the competitive interaction between them. Stephens et al. (1998) suggest that increased flow from the north and west during negative NAO conditions advects large numbers of *C. finmarchicus* to the shelf region from their principle overwintering habitat in the deeper waters. If temperature changes in the North Sea are determined by water mass movements, then these two hypotheses may be related. Specifically, increased flow from the North Sea and bring *C. finmarchicus* on to the shelf while displacing *C. helgolandicus* to the south.

From 1958 until 1995, the phase of the NAO was a good predictor of *C. finmarchicus* abundance in the North Sea (Planque and Reid, 1998). However, the dramatic drop in the NAO in the winter of 1996 did not lead to a dramatic increase in *C. finmarchicus* abundance as predicted. The correlation between the NAO and *C. finmarchicus* seems to have broken down in 1996 and 1997 (Planque and Reid, 1998), and there are two hypotheses that may explain the anomalous relationship in those years.

The first hypothesis concerns the nature of the NAO Index. The NAO Index is based on the difference in sea-level pressure between Lisbon, Portugal and Stykkisholmur, Iceland (Hurrell,

1995). In most years, these locations are near the centers of the low and high pressure cells over the Atlantic. However, in both 1996 and 1997, the subpolar low shifted from Iceland to northern Norway (Ulbrich and Christoph, 1999). Thus, even though the NAO Index was low in 1996, it is likely that the conditions in the eastern Atlantic were atypical of negative NAO conditions, possibly explaining the unpredictable response of the North Sea *C. finmarchicus* population.

The second hypothesis is based on the interaction between deep-water circulation patterns and the diapausing strategy of C. finmarchicus. In 1994 Backhaus et al. (1994) offered a detailed hypothesis to explain the persistence of C. finmarchicus in the regions surrounding the British Isles in the face of strong advection. They postulated that the North Sea population of C. finmarchicus is formed by animals (and their descendents) that overwinter in the Faroe-Shetland Channel and are advected into the North Sea via wind-driven surface currents similar to the flows investigated by Stephens et al (1998). These ideas prompted the formation of the ICOS (Investigation of Calanus finmarchicus migrations between Oceanic and Shelf seas) project which investigated the ``Backhaus" hypothesis using both field observations and numerical modeling (Heath, 1999). A key result of the modeling efforts was the identification of relative contributions that various deep-water source regions make to the North Sea population under different wind conditions. When the winds are from the southwest or southeast, the important source region is to the west of Scotland, southwest of the Wyville-Thomson Ridge (Gallego et al., 1999) (Figure 5, outlined in red). When the winds are from the northwest, the source region shifts to the northeast, extending into the Faroe-Shetland Channel and southern Norwegian Sea(Figure 5, outlined in blue). The field observations suggest that diapause stocks south of the Wyville-Thompson Ridge are lower than in the Faroe-Shetland Channel, and within the Channel, the concentration of C. finmarchicus closely follow the distribution of Norwegian Sea Deep Water (NSDW) (Heath and Jonasdottir, 1999). Combining these results provides an explanation for the relationship between C. finmarchicus and the NAO that accounts for the low abundance of C. finmarchicus in the North Sea in 1996. According to the model, advection of animals from the Faroe-Shetland Channel requires northwest winds, a condition that is associated with negative NAO winters (Dickson, 1997). However, the concentration of diapausing C. finmarchicus in the Faroe-Shetland Channel is influenced by the flow of NSDW across the Wyville-Thompson Ridge. When NSDW production is high as it was during the 1960's, this water mass flows into the Faroe-Shetland Channel (Figure 5, light blue), leading to increased abundance of C. finmarchicus in the source region and eventually, in the North Sea. The persistant positive NAO conditions during the 1980's and 1990's lead to reduced NSDW formation (Figure 5, pink) and reduced concentrations of C. finmarchicus in the Faroe-Shetland Channel. Thus, even though conditions in 1996 were favorable for advecting C. finmarchicus from the chief source region, the actual concentrations there were depressed (Heath et al., 1999a). The transport of NSDW into the Faroe-Shetland Channel is likely related to the NAO; however, several years of negative NAO conditions my be required for this transport to increase.

Broader Patterns

The diapause strategy of *C. finmarchicus* implies that shelf populations of this species must be closely tied to oceanic populations. Thus, this species can be considered an indicator of the degree to which a shelf ecosystem reflects an oceanic versus neritic zooplankton community. This idea was first articulated for the North Sea by (Glover, 1957), who described a shift in the

North Sea zooplankton community from one composed of mostly neritic species such as copepods in the genera Pseudocalanus, Paracalanus, and Acartia as well as Centropages hamatus, to a more oceanic community with Calanus, Centropages typicus, and the pteropod Clione limacina. The community change in the early 1950's was associated with decreased biomass in the zooplankton community, a delayed spring bloom, and years with progressively more negative NAO values. The oceanic community dominated through much of 1970's, until the NAO shifted into a consistently positive phase. In the mid-1980's, the North Sea zooplankton shifted to a strongly neritic community (Reid et al., 2001). The ``regime shift" observed by Reid et al. (2001) included a dramatic increase in the number of horse mackerel in the North Sea as well as an earlier spring bloom, more phytoplankton, and more frequent observations of species typically found much farther south. Reid et al. (2001) propose that the ecosystem shift was caused by an extension of the northward-flowing warm water jet along the shelf break. The changes in this current brought warm water and warm water species into the region, and this water was then transported into the North Sea. Thus, the interannual abundance patterns of individual species must be interpreted in the light of dramatic shifts in the state of the physical environment and ecosystem of the North Sea.

Climate Variability and Zooplankton Populations in the Northwest Atlantic

The relationship between the NAO and the weather over the Northwest Atlantic Shelf is less clear than in the North Sea. In maps of the correlation between the NAO and atmospheric properties such as wind speed or sea-level pressure, the Gulf of Maine/Scotian Shelf region appears as an area of low or zero correlation (Hurrell, 1995; Reid and Planque, 1999). However, the Northwest Atlantic Shelf lies near the intersection of two major current systems (Figure 6), the Labrador Current and the Gulf Stream, both of which are influenced by the NAO (Dickson et al., 1996; Taylor and Stephens, 1998). Thus, any effects that the NAO has on ecosystems of the NW Atlantic Shelf are likely to be mediated by oceanographic processes, specifically, the dynamical interaction of the subpolar and subtropical gyres.

The Gulf of Maine/Scotian Shelf region, including Georges Bank is one of the most heavily studied areas in the Northwest Atlantic. The US National Marine Fisheries Service and the Canadian Department of Fisheries and Oceans have conducted CPR surveys throughout the region since the 1960's. These studies have followed the same protocols as the SAHFOS surveys, but the temporal and spatial coverage of the western surveys is more limited.

As in the eastern Atlantic, much of the analysis of the CPR data has focused on *C. finmarchicus*. Jossi and Goulet (1993) were the first to note a trend towards increased abundance of *C. finmarchicus* from 1961 to 1989 in the Gulf of Maine (Figure 7c). They noted that this trend ran counter to the pattern for this species in the North Sea. After Fromentin and Planque (1996) established the influence that the NAO can have on *C. finmarchicus*, Conversi et al. (2001) reanalyzed the CPR time series from the Gulf of Maine. They specifically looked for a connection between the *C. finmarchicus* and NAO Index time series and found a positive cross-correlation with the NAO at a lag of four years. Furthermore, Conversi et al. (2001) established cross-correlations between the NAO and sea surface temperature at a lag of 2 years and between sea surface temperature and *C. finmarchicus* at a lag of 2 years. These results were supported by Greene and Pershing (2001) who linked changes in *C. finmarchicus* abundance to the

temperature in the bottom waters (150-250 m) in the Gulf of Maine/Scotian Shelf region with changes in slope water circulation patterns following the NAO. Both studies suggest a chain of events that starts with a phase shift in the NAO, is followed next by hydrographic changes in the Gulf of Maine/Scotian Shelf region, and ends with a response in the *C. finmarchicus* population.

Environmental Conditions and the NAO

Both Conversi et al. (2001) and Greene and Pershing (2001) found a correlation between C. *finmarchicus* abundance in the Gulf of Maine and a measure of regional temperature. These results raise two questions: what processes account for the C. *finmarchicus*-temperature correlation, and which temperature measure is a better proxy for these processes? Addressing these questions requires a more detailed understanding of the physical and climatic environment of the Northwest Atlantic.

Petrie and Drinkwater (1993) established an idea that is key to connecting physical changes in the Gulf of Maine to the NAO. In their analysis of temperature and salinity data from the Gulf of Maine and Scotian Shelf, Petrie and Drinkwater (1993) found that the amplitude of the interannual temperature oscillations increased with depth and was especially strong below 100 m. When searching for a mechanism, they found little correlation between water temperatures and interannual differences in winter heat flux. Instead, the variability was related to the volume transport of water from the Labrador Sea around the Tail of the Grand Banks. When the transport is high, the waters below 100 m in this region are cooler, and when the transport is reduced, these waters are warmer.

Because of the strong influence of the NAO on winter conditions over the Labrador Sea, it seems reasonable to connect the mechanism proposed by Petrie and Drinkwater (1993) to the NAO. Recent observations following the dramatic drop in the NAO during 1996 have solidified our understanding of the connection between the NAO and physical and biological processes in the Gulf of Maine. Prior to 1996, the bottom water found in the deep basins of the Gulf of Maine and Scotian Shelf was derived from relatively warm and saline Atlantic Temperate Slope Water (ATSW)¹. This water mass extended northeast to the Laurentian Channel during much of the 1980's and 1990's (Drinkwater et al., 2001) (Figure 8 a). Following the drop in the NAO during the winter of 1996, the front separating ATSW from the cooler, fresher Labrador Subarctic Slope Water (LSSW) was pushed to the southwest as the transport of LSSW around the Tail of the Bank increased. By the end of 1998, the LSSW had reached the Mid-Atlantic Bight and had intruded into the deep basins on the shelf (Drinkwater et al., 2001) (Figure 8 b). The subsequent years saw a return to positive NAO conditions, and the front between the two water masses returned to the northeast.

The changes in the distribution of the Slope Water masses described above suggest that a large area centered on the Gulf of Maine should have a common response to the NAO. The changes in

¹ Atlantic Temperate Slope Water (ATSW) and Labrador Subarctic Slope Water (LSSW) which Gatien (1976) originally named Warm Slope Water and Labrador Slope Water, respectively, were renamed by us to reflect their origins and avoid confusion with Labrador Sea Water (Greene and Pershing, 2001).

the distribution of ATSW and LSSW are accompanied by changes in the water mass signal in the Deep Western Boundary Current and in the position of the Gulf Stream (Pickart et al., 1999, Dickson et al., 1996, Taylor and Stephens, 1998, Rossby and Benway, 2000). There is evidence that the changes in these currents and water masses have been operating for millennia (Keigwin and Pickart, 1999). The consistency of the changes in these water masses as currents led Pickart et al. (1999) to refer to the variability in this region as a ``coupled slopewater mode." MERCINA, 2001INA (2001) applied these ideas and terminology to interpret the association between conditions in the Gulf of Maine region and the NAO. As a proxy for the modal state of this ``Coupled Slope Water System" (CSWS; MERCINA, 2001), we developed the Regional Slope Water Temperature Index (RSWT Index, Figure 7b), which is the dominant mode from a principle components analysis of the temperature between 150-250 m in 8 regions in the Gulf of Maine, Scotian Shelf, and over the continental slope (MERCINA, 2001; Pershing, 2001). The RSWT Index has its strongest cross-correlation with the NAO at a lag of 1 year, although the correlation at lags of 0 and 2 years are also high (MERCINA, 2001; Pershing, 2001) (Figure 9a).

From the description above, the deep-basin temperatures that Greene and Pershing (2001) linked to *C. finmarchicus* variability in the Gulf of Maine should be strongly influenced by the state of the CSWS. Furthermore, the strong winter mixing in the Northwest Atlantic implies that the sea surface temperatures analyzed by Conversi et al. (2001) are also influenced by the CSWS. The cold, continental air masses which pass over the Northwest Atlantic lead to large heat fluxes out of the surface waters, creating cold, dense waters and deep winter mixed layers (Brown and Beardsley, 1978; Dickson et al., 1996). The formation of Labrador Sea Water is an extreme example of this phenomenon. A consequence of this winter mixing is that variability in winter temperature, even in the surface waters, is strongly dependent on the temperature at the base of the mixed layer (Petrie and Drinkwater, 1993).

An analysis of the relationship between *C. finmarchicus* abundance in the Gulf of Maine and the state of the CSWS confirmed the results of Conversi et al. (2001) and Greene and Pershing (2001). From 1961 to 1999, *C. finmarchicus* abundance in the Gulf of Maine is strongly correlated with the state of the CSWS, as indicated by the RSWT Index. A cross-correlation analysis suggests that the copepod population increases after a shift in the CSWS from cold to warm, with the strongest correlation at a lag of three years (Figure 9b). However, *C. finmarchicus* abundance declined in the same year as the dramatic change in the state of the CSWS that occurred in 1997.

As in the eastern Atlantic, the NAO's value in predicting changes in the abundance of *C*. *finmarchicus* in the Gulf of Maine decreased in the 1990's. There is no significant relationship between the NAO time series and *C. finmarchicus* abundance in the Gulf of Maine, if the data from the 1990's are incorporated. However, the relationship between copepods and the state of the CSWS still holds. The increasing trend in the NAO values over the time period studied by Conversi et al. (2001) and Greene and Pershing (2001) likely made the effect of the NAO on the copepods easier to detect. The NAO was predominantly positive during the 1990's, although not as high as in the late 1980's. Adding data from the 1990's to the analysis decreases the sensitivity of the correlation analysis to the large changes (1960's vs. 1980's) and increases the focus on smaller, year-to-year fluctuations. Because the NAO's influence on the conditions in the Gulf of Maine is indirect—mediated by the CSWS, the Gulf of Maine should be less sensitive to subtle

changes in the NAO.

As in the eastern Atlantic, the mechanisms that could account for the climate-induced fluctuations in *C. finmarchicus* fall into two categories: those involving changes in local biological processes and those involving circulation changes. There is evidence to support both possibilities. In addition to their different temperature and salinity signatures, the two water masses associated with the CSWS have distinct nutrient concentrations (Petrie and Yeats, 2000). LSSW is a relatively young water mass that is formed by cooling of winter surface waters in the Labrador Sea; thus, this water mass has relatively low concentrations of nitrate and silicate (Petrie and Yeats, 2000). ATSW forms by mixing between LSSW, Gulf Stream and coastal water masses (Gatien, 1976), and consequently, it has higher nutrient concentrations. The CPR Color Index data from the Gulf of Maine indicate higher phytoplankton standing stocks when ATSW is present (Figure 7c), and this could lead to higher growth rates for the *C. finmarchicus* population. This hypothesis assumes that *C. finmarchicus* is always abundant on the Northwest Atlantic Shelf; however, this species preference for deep water during winter calls this assumption into question.

Variability in *C. finmarchicus* transport into the Gulf of Maine from different source areas is another hypothesis. Unlike the North Sea, the Gulf of Maine and Scotian Shelf have a few deep areas (>250 m) that provide habitat for diapausing *C. finmarchicus* (Sameoto and Herman, 1990). Simulations of *C. finmarchicus* in climatological flow fields indicate that the summer population in the Gulf of Maine--the population to which the CPR is most sensitive--is composed of animals that were on the Scotian Shelf in late-winter and spring (Miller et al., 1998). Thus, the abundance observed by the CPR in the Gulf of Maine in a given year is determined by a combination of the size of the initial late-winter population on the Scotian Shelf and the growing conditions during the spring. Sameoto and Herman (1990) found high concentrations of diapausing *C. finmarchicus* in the Emerald Basin on the Scotian Shelf in 1985 and 1986 and hypothesized that these stocks seed the Scotian Shelf population. However, a longer study in this region suggests that conditions in 1985-86 were exceptional, and that in most years, the initial population on the Scotian Shelf is derived from the Slope Water (Head et al., 1999).

The scenario described above suggests two transport pathways that could affect the Gulf of Maine population: the transport of *C. finmarchicus* onto the Scotian Shelf, and the transport of *C. finmarchicus* from the Scotian Shelf to the Gulf of Maine. Modeling studies comparing the circulation over of the Northwest Atlantic shelf between positive and negative NAO conditions found little change in the shelf circulation (Loder et al., 2001). This suggests that any transport mechanism linking *C. finmarchicus* abundance in the Gulf of Maine and the state of the CSWS likely affects the coupling between the Scotian Shelf and Slope Waters. To get from the continental slope region on to the Scotian Shelf, *C. finmarchicus* must be advected across the shelf-break front. When LSSW is present in the region, the density gradient across this front is stronger (Pickart et al., 1999) and may provide a barrier to cross-shelf exchange.

Broader patterns

In the North Sea, *C. finmarchicus*'s negative association with the NAO sets it apart from most other zooplankton populations in the region. In the Gulf of Maine, the abundance time series of

several other zooplankton species including *Metridia lucens* and *Pseudocalanus* spp., had a similar pattern to that of *C. finmarchicus* with highs in the early 1960's and throughout most of the 1980's and lows during the late 1960's, early 1970's and a brief period in the early 1980's (Jossi and Goulet, 1993). However, *C. finmarchicus* was the only species Jossi and Goulet (1993) found that had a significant trend; and despite the similarities among the time series, the *C. finmarchicus* time series stood apart from the other species. Their work suggests a common mechanism that allows for increased zooplankton production in the Gulf of Maine during positive NAO/ATSW-dominated conditions. The differences in nutrient concentrations between the two Slope Water masses and the resulting changes in phytoplankton abundance could influence the abundance of a wide range of zooplankton species. This could account for the commonalities among the copepod time series. If the modal shifts in the CSWS are associated with circulation changes, espeically changes in the coupling between the shelf and slopewater regions, then *C. finmarchicus*'s sensitivit to advective changes would enhance this species' association with the CSWS.

Discussion

The examples presented above suggest that the effects of Atlantic climate variability on zooplankton populations fall into two categories. *C. finmarchicus* exemplifies the first class of effects which we call *translations* (Pershing, 2001). Translations involve movements of organisms from one place to another such as the advection of *C. finmarchicus* from the continental slope on to the shelf. These changes are based entirely on the physical changes produced by climate variability. We will refer to the other class as *indirect* effects. Indirect effects link a population to climate only through its effect on another species, such as climate-induced changes in its prey or predators.

Indirect effects have been recognized in many ecosystems and by many authors (Ottersen et al., 2001); however, translations are a unique class of climate effects that have not been recognized previously. Zooplankton populations are very sensitive to translational effects because their horizontal distributions are often determined by advection. C. finmarchicus, in particular, is especially susceptible to circulation changes because of its requirement for deep water during the fall and early winter diapause period. In both the Gulf of Maine and North Sea, a significant portion of the interannual variability of this species--and its association with the NAO, is associated with physical changes that could alter the coupling between shelf and deep water populations. The variability in C. finmarchicus abundance is also linked to circulation in other Atlantic regions. In the Barents Sea, the abundance of C. finmarchicus is closely tied to the supply of warm Atlantic Water flowing from the Norwegian Sea (Skjoldal et al., 1992; Helle and Pennington, 1999). When the flow increases, it advects C. finmarchicus and other Norwegian Sea zooplankton into the Barents Sea. Although the abundance of C. finmarchicus in the Barents Seahas not been formally correlated with the NAO, the transport of Norwegian Sea water is associated with positive NAO conditions (Dickson et al., 2000). The abundance of C. finmarchicus around Iceland has been linked to changes in the distribution of water masses; however, it is unclear if the association is related to direct advection of C. finmarchicus in the water masses or differing patterns of primary productivity associated with them (Astthorsson and Gislason, 1995).

Translations associated with frontal shifts have an especially strong effect on species with

distributions tied to a specific geographic feature, provided the shift passes over the feature. The nesting grounds of marine birds and breeding grounds of seals are limited to a few locations. During frontal shifts such as those occurring during El Nino in the Pacific, these species are often the most heavily impacted (Graybill and Hodder, 1985). Many commercially important fish species have similar restrictions, spawning only at a few locations, principally submarine banks (Mann and Lazier, 1996). The dramatic nature of these indirect effects results from the species sampling their environment from a fixed point. Shelf ecosystems are similarly fixed relative to adjacent circulation features; thus, they should be particularly sensitive to changes in circulation. This may explain the strong response of shelf populations such as those in the North Sea to climate variability, and the predominance of translational effects linking climate variability to population changes in the ocean.

The changes in the Gulf of Maine suggest that translations and indirect effects are independent and not exclusive of each other. Conditions favorable for the transport of *C. finmarchicus* into the Gulf occur concurrently with increased primary production, and both likely play a role in the connection between the variability in the *C. finmarchicus* population and the NAO. Distinguishing the relative influence of physical processes such as climate-induced translations versus biological processes is a fundamental problem in biological oceanography, one that increases the complexity of uncovering the mechanisms linking population changes to climate. Because translational effects are due entirely to physical processes, recognizing the importance of translational effects offers the potential to simplify these investigations.

A third class of effects known as *direct effects* was not obviously present in the examples discussed above, although this is a key class in other categorizations of population responses to climate (Ottersen et al., 2001). Direct effects include the influence of physical factors controlled by climate, temperature being the most obvious, on a population's vital rates. An example of this class is the association between the growth rate of larval cod and temperature in the Barents Sea (Ottersen et al., 2001). In the Baltic, salinity changes associated with the NAO appear to determine the proportion of oceanic versus freshwater zooplankton (Viitasalo et al., 1995; Hanninen et al., 2000); however, the community changes may result from an alteration in the inflow of Atlantic water (a potential translation) or differences in phytoplankton dynamics caused by buoyancy changes (an indirect effect) rather than the direct influence of salinity of zooplankton growth and survival.

Interannual vs. Longer Time Scales

The North Sea responds to the NAO on two main time scales. The longest scale involves the large regime shifts reported by Glover (1957) and Reid et al. (2001). These shifts are similar to the changes associated with the Russell Cycle (Cushing and Dickson, 1976; Cushing, 1982). Although these interdecadal shifts can occur abruptly, at least for some species (Reid et al., 2001), many species exhibit a more gradual rise and fall between the extreme states. The long-term changes are likely driven by a combination of physical and biological mechanisms. Physical features such as the extension of the coastal jet described by Reid et al. (2001) and the decline in *C. finmarchicus*'s overwintering habitat described by Heath et al. (1999) likely require several years of consistent environmental conditions for their effects to be detected. Imposed on the interdecadal changes in the North Sea are interannual fluctuations. These changes involve

year-to-year differences in the circulation field or the timing or magnitude of spring stratification. The physical changes lead to changes in the abundance of various species, but are rarely strong enough to lead to regime shifts in any one year.

Conclusion

Climate variability, especially the NAO, is an important process determining the distribution and abundance of zooplankton populations around the North Atlantic. These examples suggest that climate influences zooplankton populations in two main ways. Through its effect on ecosystem properties such as the timing or magnitude of the spring bloom, clmate variability can cause changes zooplankton populations. Effects of this kind, known as indirect effects, are likely present in all of the ecosystems reviewed, but the complexity of marine ecosystems can mask their influence. Climate variability can have a significant effect on ocean circulation patterns, and thus, the distribution of zooplankton. Effects of this kind, known as translations depends solely on physical processes and thus, are easier to detect. Translations are especially important in shelf ecosystems and for the copepod *C. finmarchicus*.

There are still relatively few examples of the influence of climate on zooplankton populations. Partly, this is due to the rarity of biological time series long enough to compare with the NAO pattern, but it is also influenced by our incomplete knowledge of the physical aspects of climate variability. Enhanced knowledge of ecosystem-climate interactions is a prerequisite for sustainable management of the marine resources in the in the North Atlantic.

References

- Astthorsson, O. S. and Gislason, A. (1995).Long-term changes in zooplankton biomass in Icelandic waters in spring. *ICES Journal of Marine Science*, 52:657–668.
- Backhaus, J. O., Harms, I. H., Krause, M., and Heath, M. R. (1994). An hypothesis concerning the space-time succession of *Calanus finmarchicus* in the northern North Sea. *ICES Journal of Marine Science*, 51:169–180.
- Brown, W. S. and Beardsley, R. C. (1978). Winter circulation in the western Gulf of Maine. part 1: Cooling and water mass formation. *Journal of Physical Oceanography*, 8:265–277.
- Conversi, A., Piontkovski, S., and Hameed, S. (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 Research II*, 48:519–520.
- Cushing, D. H. (1982). Climate and Fisheries. Academic Press, New York.
- Cushing, D. H. and Dickson, R. R. (1976). The biological response in the sea to climatic changes. *Advances in Marine Biology*, 14:1–122.
- Dickson, R. (1997). From the Labrador Sea to global change. Nature, 386:649-650.
- Dickson, R., Lazier, J., Meincke, J., Rhines, P., and Swift, J. (1996). Long-term coordinated changes in the convective activity of the North Atlantic. *Progress in Oceanography*, 38:241–295.
- Dickson, R. R., Osborn, T. J., Hurrell, J. W., Meincke, J., Blindheim, J., Adlandsvik, B., Vinje, T., Alekseev, G., and Maslowski, W. (2000). The Arctic Ocean response to the North Atlantic Oscillation. *Journal of Climate*, 13:2671–2696.
- Drinkwater, K. F., Mountain, D. B., and Herman, A. (2001). Variability in the slope water properties off eastern North America and their effects on the adjacent seas. *Journal of Geophysical Research*, In press.
- Fromentin, J. and Planque, B. (1996). Calanus and the environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on C. finmarchicus and C. helgolandicus. Marine Ecology Progress Series, 134:111–118.
- Gallego, A., Mardaljevic, J., Heath, M. R., Hainbucher, D., and Slagstad, D. (1999). A model of the pring migration into the North Sea by *Calanus finmarchicus* overwintering off the Scottish continental shelf. *Fisheries Oceanography*, 8:107–125.
- Gamble, J. C. (1994). Long-term planktonic time series as monitors of marine environmental change. In Leigh, R. A. and Johnston, A. E., editors, Long-term Experiments in Agriculture and Ecological Sciences: Proceedings of a Conference to Celebrate the 150th Anniversary of Rothamsted Experimental Station, held at Rothamsted, 14-17 July, 1993, pages 365–386. CAB International, Wallingford, U. K.
- Gatien, 1976, M. (1976). A study in the slope water region south of Halifax. *Journal of the Fisheries Research Board of Canada*, 33:2213–2217.
- Glover, R. S. (1957). An ecological survey of the drift net herring survey off the northeast coast of Scotland II: the planktonic environment of the herring. *Bulletin of Marine Ecology*, 5:1–43.
- Graybill, M. R. and Hodder, J. (1985). Effects of the 1982-83 El Nino on reproduction of six species of seabirds in Oregon. In Wooster, W. S. and Fluharty, D. L., editors, *El Nino North: El Nino Effects in the Eastern Subarctic Pacific Ocean*, pages 205–210. University of Washington, Seattle.
- Greene, C. H. and Pershing, A. J. (2001). The response of Calanus finmarchicus populations to

climate variability in the Northwest Atlantic: Basin-scale forcing associated with the North Atlantic Oscillation. *ICES Journal of Marine Science*, 57:1536–1544.

- Hanninen, J., Vuorinen, I., and Hjelt, P. (2000). Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnology and Oceanography*, 45:703–710.
- Head, E. J. H., Harris, L. R., and Petrie, B. (1999). Distribution of *Calanus* spp. on and around the Nova Scotia Shelf in April—evidence for an offshore source of *Calanus finmarchicus* to the mid- and western regions. *Canadian Journal of Fisheries and Aquatic Science*, 56:2463—2476.
- Heath, M. R. (1999). Introduction. Fisheries Oceanography, 8:vii-viii.
- Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J. G., Gallego, A., Hainbucher, D., Hay, S., Jonasdottir, S., Madden, H., Mardaljevic, J., and Schacht, A. (1999a). Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fisheries Oceanography*, 8:163–176.
- Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J. G., Gellego, A., Hainbucher, D., Hay, S., Jonasdottir, S., Madden, H., Mardaljevic, J., and Schacht, A. (1999b). Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fisheries Oceanography*, 8 (Suppl. 1):163–176.
- Heath, M. R., Fraser, J. G., Gislason, A., Hay, S. J., Jonasdottir, S. H., and Richardson, K. (2000). Winter distribution of *Calanus finmarchicus* in the Northeast Atlantic. *ICES Journal of Marine Science*, 7:1628–1635.
- Heath, M. R. and Jonasdottir, S. H. (1999). Distribution and abundance of overwintering *Calanus finmarchicus* in the Faroe-Shetland Channel. *Fisheries Oceanography*, 8:40–60.
- Helle, K. and Pennington, M. (1999).
- The relation of the spatial distribution of early juvenile cod (*Gadus morha* L.) in the Barents Sea to zooplankton density and water flux during the period 1978-1984. *ICES Journal of Marine Science*, 56.
- Hirche, H.-J. (1996). The reproductive biology of the marine copepod *Calanus finmarchicus*—a review. *Ophelia*, 44:111—128.
- Hurrell, J. (1995). Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, 269:676–679.
- Jossi, J. and Goulet, J. (1993). Zooplankton trends: US North-east shelf ecosystem and adjacent regions differ from north-east Atlantic and North Sea. *ICES Journal of Marine Science*, 50:303–313.
- Keigwin, L. and Pickart, R. (1999). Slope water current over the Laurentian Fan on interannual to millenial time scales (vol 285, pg 520, 1999). *Science*, 286:1479–1479.
- Loder, J. W., Shore, J. A., Hannah, C. G., and Petrie, B. D. (2001). Decadal-scale hydrographic and circulation variability in the Scotia-Maine region. *Deep-Sea Research II*, 48:3–36.
- Mann, K. H. and Lazier, J. R. N. (1996). *Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans*. Blackwell Science, Cambridge, MA.
- Marshall, S. M. and Orr, A. P. (1955). *The Biology of a Marine Copepod*. Oliver and Boyd, Edinburgh.
- McGowan, J. A., Cayan, D. R., and Dorman, L. M. (1998). Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science*, 281:210–217.
- MERCINA (2001). Gulf of Maine/Western Scotian Shelf ecosystems respond to changes in

ocean circulation associated with the North Atlantic Oscillation. Oceanography, in press.

- Miller, C. B., Cowles, T. J., Wiebe, P. H., Copley, N. J., and Grigg, H. (1991). Phenology of *Calanus finmarchicus*—hypotheses about control mechanisms. *Marine Ecology Progress Series*, 72:79—91.
- Miller, C. B., Lynch, D. R., Carlotti, F., Gentleman, W. C., and Lewis, C. (1998). Coupling of an individual-based population dynamical model for stocks of *Calanus finmarchicus* with a circulation model for the Georges Bank region. *Fisheries Oceanography*, 8:219–234.
- Mills, E. L. (1989). *Biological Oceanography. An Early History*, 1870-1960. Cornell University Press, Ithaca, NY.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., and Stenseth, N. C. (2001). Ecological effects of the North Atlantic Oscillation. *Oecologia*, in press.
- Pershing, A. J. (2001). Response of large marine ecosystems to climate variability: patterns, processes, concepts and methods. PhD thesis, Cornell University, Ithaca, NY.
- Petrie, B. and Yeats, P. (2000). Annual and interannual variability of nutrients and their estimated fuxes in the Scotian Shelf-Gulf of Maine region. *Canadian Journal of Fisheries and Aquatic Science*, 57:2536–2546.
- Petrie, B. D. and Drinkwater, K. (1993). Temperature and salinity variability on the Scotian Shelf and in the Gulf of Maine, 1945-1990. *Journal of Geophysical Research*, 98:20,079–20,089.
- Pickart, R., McKee, T., Torres, D., and Harrington, S. (1999). Mean structure and interannual variability of the slopewater system south of Newfoundland. *Journal of Physical Oceanography*, 29:2541–2558.
- Planque, B. and Batten, S. D. (2000). Calanus finmarchicus in the North Atlantic: the year of Calanus in the context of interdecadal change. ICES Journal of Marine Science, 57:1528-1535.
- Planque, B. and Reid, P. C. (1998). Predicting *Calanus finmarchicus* abundance from a climate signal. *Journal of the Marine Biological Association U. K.*, 78:1015–1018.
- Planque, B. and Taylor, A. H. (1998). Long-term changes in zooplankton and the climate of the North Atlantic. *ICES Journal of Marine Science*, 55:644–654.
- Reid, P. C., Borges, M. D., and Svendsen, E. (2001). A regime shift in the North Sea circa 1988 linked to changes in the North Sea fishery. *Fisheries Research*, 50:163–171.
- Reid, P. C. and Planque, B. (1999). Long-term planktonic variations and the climate of the North Atlantic.
- In Mills, D., editor, *The Life of the Atlantic Salmon*, pages 153–169. Blackwell Science, Oxford.
- Rossby, T. and Benway, R. L. (2000). Slow variations in mean path of the Gulf Stream east of Cape Hatteras. *Geophysical Research Letters*, 27:117–120.
- Sameoto, D. D. and Herman, A. W. (1990). Life cycle and dsitribution of *Calanus finmarchicus* in deep basins on the Nova Scotia shelf and seasonal changes in *Calanus* spp. *Marine Ecology Progress Series*, 66:225–237.
- Skjoldal, H. R., Gjøsæter, H., and Loeng, H. (1992).
- The Barents Sea ecosystem in the 1980s: ocean climate, plankton, and capelin growth. *ICES Marine Science Symposia*, 195:278–290.
- Stephens, J. A., Jordan, M. B., Taylor, A. H., and Proctor, R. (1998). The effects of fluctuations in North Sea flows on zooplankton abundance. *Journal of Plankton Research*, 20:943–956.

- Taylor, A. H. and Stephens, J. A. (1998). The North Atlantic Oscillation and the latitude of the Gulf Stream. *Tellus*, 50:134–142.
- Ulbrich, U. and Christoph, M. (1999). A shift of the NAO and increasing storm track activity over Europe due to anthropogenic greenhouse gas forcing. *Climate Dynamics*, 15:551-559.
- Viitasalo, M., Vuorinen, I., and Saesmaa, S. (1995). Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. *Journal of Plankton Research*, 17:1857–1878.
- Williams, R., Conway, D. V. P., and Hunt, H. G. (1994). The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas. *Hydrobiologia*, 293:521-530.

Figure Captions

- Figure 1. Examples of zooplankton populations in the North Atlantic whose variability is associated with regional climate.
- **Figure 2.** Atmospheric conditions over the North Atlantic associated with the NAO. During the NAO's positive phase (indicated by dark gray), the Icelandic Low and Azores High are intensified, producing strong westerlies (dark gray arrow) that are shifted to the north. When the NAO is in the negative phase (light gray), the difference between the pressure centers is diminished and both shift to the east. The westerlies are weakened and shift to the south (light gray arrow). The scalar wind speeds in areas northeast of the dashed line are positively correlated with the NAO (windy during positive phases---dark region), while wind speeds south are negatively correlated (light region).
- **Figure 3.** The relationship between (a) the NAO and the copepods (b) *Calanus helgolandicus* and (b) *C. finmarchicus* (c) in the eastern Atlantic.
- **Figure 4.** Correlations between the NAO and the abundance of (a) *Calanus helgolandicus* and (b) *C. finmarchicus* in the eastern Atlantic.
- Figure 5. Hypothesis explaining interannual and interdecadal variability in *C. finmarchicus* abundance in the North Sea developed by the ICOS study (Heath, 1999; Heath et al., 1999). Southerly winds associated with negative NAO conditions tend to advect *C. finmarchicus* from an area west of Scotland (red outline). Winds with a more northerly component tend to advect animals from a region further east, in the Faroe-Shetland Channel (blue outline). The concentration of *C. finmarchicus* in the Faroe-Shetland Channel is characteristically higher than that further west; thus, negative NAO conditions should lead to more *C. finmarchicus* in the North Sea. However, this mechanism is complicated by the distribution of NSDW which is believed to carry *C. finmarchicus* into the Faroe-Shetland Channel. When NSDW production is high, a typical condition during negative NAO winters, the flow of NSDW into the Faroe-Shetland Channel is higher and leads to greater abundance of *C. finmarchicus* in the source region (light blue patch). When the volume of NSDW is reduced, the flow of this water mass and *C. finmarchicus* into the Faroe-Shetland Channel is reduced.
- **Figure 6.** The major circulation features of the Northwest Atlantic. LC = Labrador Current, GS = Gulf Stream, DWBC = Deep Western Boundary Current. Land is indicated by shades of green, and the sea floor is indicated by shades of gray (light gray on the continental shelf, dark gray in deeper areas).
- **Figure 7.** The three time series analyzed: a. The winter NAO time series, b. The first principal component of the regional temperature, c. *Calanus* abundance index (line and the color index (triangles). The shading underneath the curve indicates whether the anomalies are positive (light) or negative (dark).

Figure 8. The distribution of Labrador Subarctic Slope Water (LSSW), Atlantic Temperate

Slope Water (ATSW), and the position of the Gulf Stream (GS) during the warm (a) and cold (b) states of the CSWS. The numbers in (b) show the first observations of LSSW following the 1996 drop in the NAO: (1) = September 1997, (2) = January 1998, (3) = February 1998, (4) = August 1998 (Drinkwater et al, 2001). Land is indicated by shades of green, and the sea floor is indicated by shades of gray (light gray on the continental shelf, dark gray in deeper areas).}

Figure 9. The significant relationships between NAO and temperature (a) and temperature and *Calanus* (b) identified by the cross-correlation analysis. All of the best-fit lines have slopes significantly different from zero.









Geography and Circulation of the NW Atlantic







