The Response of Marine Ecosystems to Climate Variability Associated With the North Atlantic Oscillation

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A strong association is documented between variability of the North Atlantic Oscillation (NAO) and changes in various trophic levels of the marine ecosystems of the North Atlantic. Examples are presented for phytoplankton, zooplankton, benthos, fish, marine diseases, whales and seabirds. NAO variability is shown to influence abundance, biomass, distribution, species assemblages, growth rates, and survival rates. Examples are drawn from across the North Atlantic. The impacts of the NAO are generally mediated through local changes in the physical environment, such as winds, ocean temperatures, and circulation patterns. The spatial variability in the physical oceanographic responses to NAO forcing leads to spatial differences in biological responses.

1. INTRODUCTION

It is well known that fish respond to changes in ocean climate. This is suggested from sedimentary records, which in the absence of fishing indicate large variability in the abundance of fish. For example, *Baumgartner et al*. [1992] pieced together a 2000-year record of Pacific sardines

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(*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) in the upwelling area off southern California that suggests their abundances varied 10–100 fold with a period of approximately 20–50 years. Historical records also offer insight into the effects of climate change on fish stocks. One of the best documented is the response to the dramatic warming of the 1920s and 1930s along the coast of West Greenland [*Jensen and Hansen*, 1931; *Hansen*, 1949]. As the waters warmed, there was a noticeable northward extension in range and an increase in abundance of several "warm-water" species, including Atlantic cod (*Gadus morhua*), Atlantic salmon (*Salmo salar*) and haddock (*Gadus aeglefinus*). White whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) were observed to arrive earlier off West Greenland during their annual migration and to leave later. Numerous other studies have reported relationships between environmental conditions and changes in recruitment, abundance, distribution or the growth of fish and shellfish [e.g., *Shepard et al*, 1984; *Sharp*; 1987, *Brander*, 1996]. One of the difficulties using historic records has been separating the response to climate variability from the effects due to fishing. However, in spite of this difficulty, evidence continues to mount that climate plays a significant role in most life history stages of fish.

The impact of climate on the marine ecosystem is not limited to fish but also extends to the lower trophic levels as well. For example, it is known that interannual variability of both phytoplankton and zooplankton reflects changes in winds and ocean temperatures [*Colebrook*, 1982]. In the case of phytoplankton, temperature determines the rate at

which phytoplankton cells divide (their turnover rates) and wind-induced turbulent mixing is important in controlling the onset of the spring phytoplankton bloom [*Sverdrup*, 1953]. Climate affects zooplankton partially through its influence on phytoplankton production. In addition, temperature determines development rates of the zooplankton, and wind, through turbulent mixing, affects the contact rates of zooplankton with their food.

The North Atlantic Oscillation (NAO) is the dominant mode of recurrent atmospheric variability over the North Atlantic [*Hurrell*, 1995]. The NAO influences atmospheric variables such as wind speed and direction, air temperatures, heat and moisture transports, and precipitation [*Hurrell et al.*, this volume]. The atmospheric variables in turn exert strong forcing on the ocean leading to changes in the temperature and salinity characteristics of the water, vertical mixing, circulation patterns and in northern areas, ice formation [*Visbeck et al.*, this volume]. Given that these ocean variables exert demonstrable influences upon marine biology and fish stocks, it is therefore not surprising that the fluctuations in the NAO would be reflected in the variability of many components of the marine ecosystem. It is important to stress that the biology is not responding directly to the NAO but rather indirectly through changes in the local physical or chemical characteristics of the water that are themselves associated with variability in the NAO [*Ottersen et al.*, 2001]. It is also important to remind the reader that the physical response to NAO forcing varies spatially across the North Atlantic. We thus expect spatial variability in the biological response to the NAO.

In this chapter we provide numerous examples of biological variability linked to the NAO and present hypotheses proposed to explain these linkages. We proceed up the food chain beginning with phytoplankton, then through zooplankton, benthos, fish, whales and finally to seabirds. For the lower trophic levels, we provide some background information to help the unfamiliar reader better understand the role the environment might play in influencing their distribution, abundance and community composition.

Unless otherwise stated, the NAO index referred to below is the boreal winter index. This is because the NAO pattern is strongest in boreal winter and generally is considered to exert it greatest influence on the ocean environment at this time. No distinction is made herein between studies using the NAO index based upon December to February averages of sea level pressure differences between the Azores and Iceland [*Rogers*, 1985] or December to March averages between Lisbon, Portugal and Iceland [*Hurrell*, 1995]. Although there are slight differences in the numerical values of these two indices, the patterns tend to be quite similar. Studies using NAO indices other than these will be noted.

2. PHYTOPLANKTON

2.1. Background

Phytoplankton are passively floating plants that are responsible for the vast majority of primary production and photosynthetic activity in the marine environment. They form the base of the marine food web, thereby playing a fundamental role in marine trophodynamics. To grow and reproduce, phytoplankton require sufficient light and nutrients. Growth and production generally tend to increase with higher temperatures. In North Atlantic temperate waters during winter, low light levels limit phytoplankton production while strong winds mix high nutrient concentrations into the near surface waters. Indeed, winter mixing determines the nutrient levels available for new production during the following production season. With spring, the increasing light and vertical stability of the water column result in a phytoplankton "bloom". Stratification is necessary to prevent the plankton from being mixed below the necessary light levels. The 'critical depth' is where the average light intensity within the water column is such that the energy production from photosynthesis equals the energy losses through respiration. Once the mixed-layer becomes shallower than the critical depth, photosynthesis exceeds respiration thereby resulting in net production, and the onset of the bloom can occur. This is known as *Sverdrup's* [1953] critical depth hypothesis.

The initial stages of the spring bloom tend to be dominated by diatom species. In late spring and summer, a reduction in the wind-induced vertical mixing, coupled with nutrient uptake by the phytoplankton, depletes the upper layer nutrients in most areas. Phytoplankton production slows down and there is a shift in community composition favoring small flagellates and eventually dinoflagellates that can cope with lower nutrient concentrations and reduced turbulence levels. This relatively stable system continues until the autumn when the pycnocline gradually begins to break down, triggered by surface cooling and enhanced by windstorms. Increased nutrients due to more intense mixing generally lead to an autumn bloom of dinoflagellates (which often dominate at the end of summer) and an increase in some diatom species. Hence, the transition from a turbulent to a stable environment is associated with a phytoplankton succession from diatoms (opportunists), through flagellates (competitors) to dinoflagellates (stress-tolerators). As winter sets in, phytoplankton production decreases, with light becoming the limiting factor due to the shortening of daylight hours.

Given the importance of vertical mixing and stratification in both the timing of the spring bloom and the succession of the phytoplankton species, it is perhaps not unexpected that

the NAO might be linked to interannual variability in primary production through its relationship to winds and air temperatures. To detect such linkages requires long-term datasets of marine phytoplankton. These are generally rare; however, one invaluable dataset is that collected by the Continuous Plankton Recorder (CPR) survey. This survey began during 1931 in England and presently consists of a network of CPR transects towed monthly across the major geographical regions of the North Atlantic. Although the majority of the data through the years has been collected from the North Sea and the Northeast Atlantic, data are available throughout the North Atlantic. The sampling protocol basically has remained unchanged [*Hardy*, 1939; *Colebrook*, 1975; *Hays and Warner*, 1993; *Warner and Hays*, 1994]. Due to changes in the method of counting, however, consistent phytoplankton data are available only from 1958 on. A United States run CPR program across the Gulf of Maine uses identical protocols. It began in 1961 but early on samples were not taken every month, and there was almost no sampling between 1974 and 1977 [*Jossi and Goulet*, 1993]. From the CPR data, a visual index of phytoplankton color is derived that indicates relative changes in phytoplankton production [*Reid et al.*, 1998] along with quantification of the abundance of phytoplankton and zooplankton by taxa.

Initial analyses of the CPR phytoplankton data revealed abundance patterns that were similar over large geographic areas and were interpreted as most likely indicating a response to climate-induced variability [*Colebrook*, 1972; *Reid*, 1977; 1978]. Later, statistical analyses showed phytoplankton abundance in the Northeast Atlantic and the North Sea increasing with rising sea surface temperatures and decreasing frequency of westerly winds over the British Isles [*Colebrook*, 1982; *Aebischer et al.*, 1990]. The relationship with weather systems was also suggested from monthly sampling (1963–1986) of phytoplankton off southern England using standard net tows [*Maddock et al.*, 1989]. A decline in phytoplankton from the late 1950s to the 1980s in the Northeast Atlantic based upon abundance of various taxa [*Colebrook et al.*, 1984] was related to increased winds through intensification of the large-scale pressure systems [*Dickson et al.*, 1988]. The hypothesis was that increased storminess led to more intense vertical mixing, which delayed the initiation of the spring bloom. This shortened the growing season and hence decreased phytoplankton abundance. None of these early studies referred to the NAO specifically, but they were the precursors of future NAO-related studies.

2.2. Relationship with NAO

By the 1990s, ecological investigations began to focus on the association with the NAO. Following *Dickson et al.*

[1988], strong winds accompanying the high NAO index years of the late 1980s and early 1990s were hypothesized as possibly delaying the spring bloom and reducing phytoplankton production on both sides of the Atlantic; in the Labrador Sea by *Mann and Drinkwater* [1994] in a study of the decline of the northern cod, and in the North Sea by *Fromentin and Planque* [1996] in a study of zooplankton variability. The CPR color index for the North Sea did not support this hypothesis, however. It revealed a noticeable increase after 1985 and was interpreted as increased production [Plate 1; see also *Reid et al.*, 1998]. The interpretation was based on observations from the North Sea that show the color index has comparable variability to that of calculated annual primary production averaged over seven years [*Reid et al.*, 1998]. Note, however, that the color index also has been shown to have the opposite response to the pattern of abundance of diatoms and several other taxa [*Reid*, 1978] and questions remain as to the link between the color index and phytoplankton biomass or production. In any event, a similar increase in the color index as that observed in the North Sea and the Northeast Atlantic was observed in the 1990s over the Scotian Shelf in the Northwest Atlantic [*Sameoto*, 2001] but not in the area to the northeast of Newfoundland [D. Sameoto, Bedford Institute of Oceanography, personal communication]. The Scotian Shelf results were based upon comparisons between data collected during the 1990s and 1961–1976. The absence of data from the late 1970s through the 1980s when the CPR survey was discontinued in the region did not allow precise determination of when the change in phytoplankton production occurred on the Scotian Shelf.

While the increased color index in the 1990s was also observed in the Northeast Atlantic to the west of Ireland, in the oceanic region to the northwest of the Scotland it decreased [*Reid et al.*, 1998; *Edwards et al.*, 2001]. Noting the similarity in the trends of the CPR color index and sea surface temperature (SST), *Edwards et al.* [2001] concluded that the major effect of the NAO on the phytoplankton was likely through temperature-related influences rather than through the winds. Consistent with this, correlation analysis of the NAO index with both SST and phytoplankton biomass showed positive relationships in the North Sea and to the west of Ireland, but negative relationships to the northwest of Scotland (Plate 2).

Temperature directly influences the metabolic rate of organisms and thus higher temperatures could account for increased phytoplankton production by shortening the turnover time of the plankton. Temperature also influences plankton indirectly through its effect on stratification. Warmer surface temperatures promote earlier or more intense stratification of the upper water-column that can

Means of phytoplankton colour
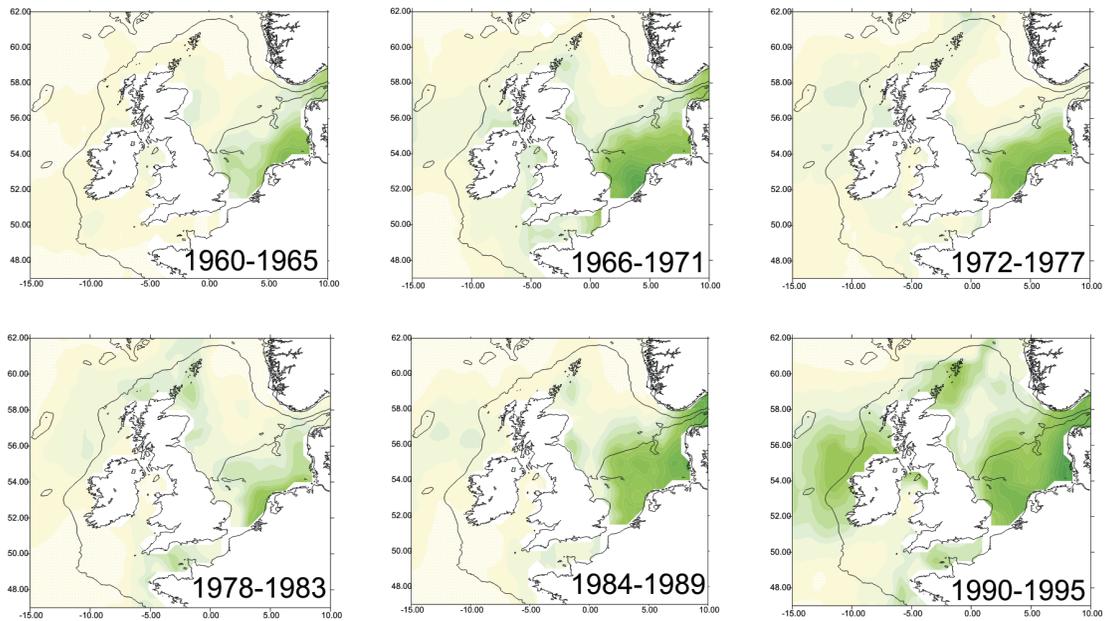
Means of phytoplankton colour - the long-term mean (anomaly plots)
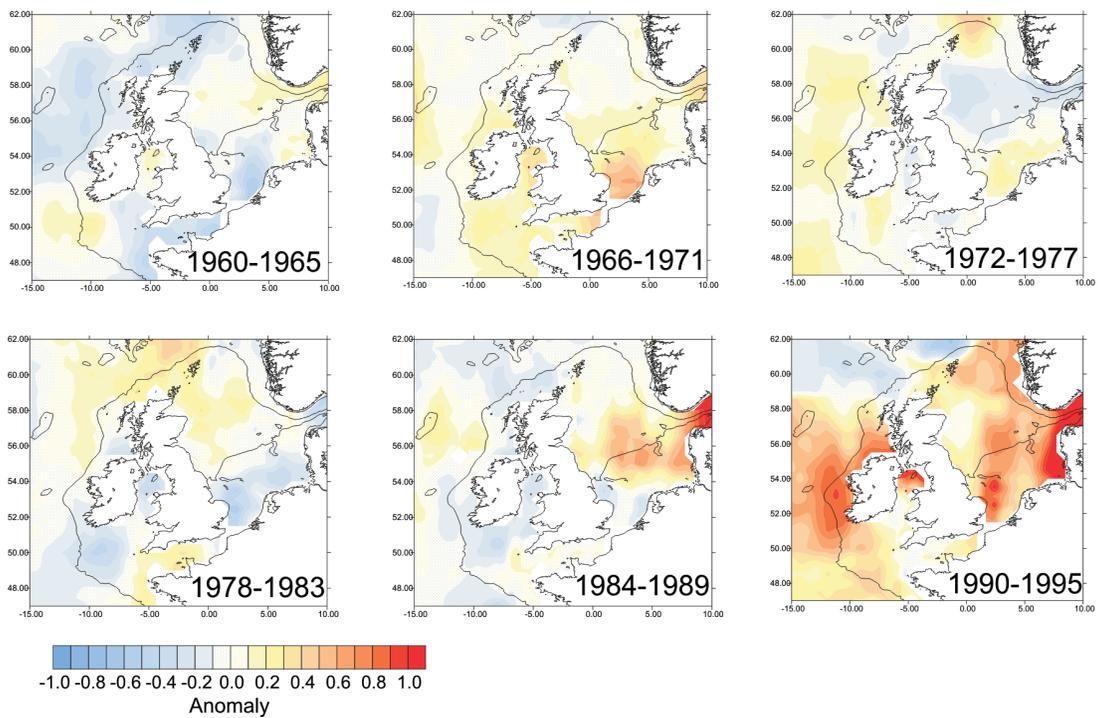
Plate 1. Geostatistical estimates of the mean spatial distribution of phytoplankton color in six-year periods from 1960-1995 (top six panels). Anomaly maps show the mean spatial distribution of phytoplankton color minus the long-term mean (bottom six panels). From *Edwards* [2000].
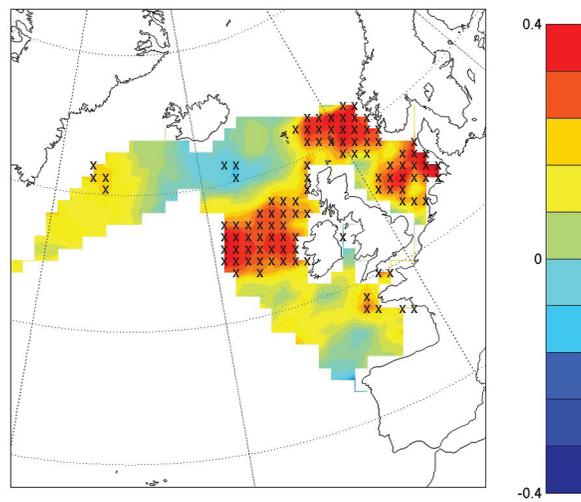
Plate 2. Correlations between phytoplankton color (biomass) and the NAO index. The crosses indicate significant correlations (p=≤0.01). From *Edwards* [2000].

lead to an earlier spring bloom. While an earlier bloom could not be detected from an analysis of the CPR data in the Northeast Atlantic, the monthly temporal resolution was considered insufficient to detect the expected small change [*Edwards et al.*, 2001]. An earlier stratification or increased intensity in stratification also would be expected to lead to a change in the phytoplankton community structure. Indeed, there is evidence from the CPR data that this occurred. Dinoflagellates appeared earlier and were more abundant in the 1990s than in the 1960s [*Edwards et al.*, 2001]. They also disappeared earlier in the year, with the result that their duration remained relatively unchanged. *Edwards et al.* [2001] also observed that long-term trends in dinoflagellate abundance in the Northeast Atlantic and the North Sea were positively correlated with the NAO index, whereas diatom abundance was negatively correlated. This provides nominal support for the contention that the temperature influence on the plankton may be through its influence on stratification. This result contrasts with that of *Irigoien et al.* [2000], however, who found a positive relationship of the NAO index with May-April concentrations of diatoms in a 50 m deep station off Plymouth in the English Channel from 1993–1999. They argued that the deeper mixed layer caused by high wind stresses during a high NAO index and reduced light from increased cloud cover would tend to favor diatoms. The cause of the differences between the two studies remains unclear.

Barton et al. [2002] have examined the color index from the CPR data throughout the North Atlantic. They noted an apparent relationship between the color index and the NAO index but found that the detrended time series were not significantly correlated. They suggested that the long-term trends in the phytoplankton color index are likely linked to the NAO index, but the correlation of the two time series at higher frequencies are not strong.

NAO-induced variability also extends into the coastal embayments. One of the best studied is Gullmar Fjord on the west coast of Sweden. *Lindahl et al*. [1998] found that primary production at a monitoring site at the mouth of the fjord was positively related to the NAO. They suggested that stronger winds during a positive NAO index led to an increase in the northward transport of low salinity waters from the Kattegat area. These waters enhance the nutrient concentrations at the mouth of the fjord, leading to higher primary production. *Belgrano et al*. [1999] showed that the NAO index could account for approximately 45% of the variance in the May primary production and 63% in the population growth between April and May in Gullmar Fjord. In a statistical modelling study of primary production in the Fjord, *Belgrano et al*. [2001] found that the NAO was one of the significant explanatory climate variables at a lag

of one month. The other variables included nutrient concentrations and stratification related indices such as density, precipitation and winds.

During the late 1980s, large phytoplankton blooms were observed along the Swedish coast with the main species being toxic flagellates. These blooms coincided with a positive NAO index and, for the period 1986–1996, the NAO index accounted for over 90% of the variability in the abundance of the three toxic *Dinophysis* species found in the fjord [*Belgrano et al.*, 1999]. The NAO also affects the plankton biodiversity in Gullmar Fjord. Biodiversity of a community is usually measured as the number of species or species richness, S, and their relative abundances known as species evenness, E [*Magurran*, 1988]. Adding the ln(E) to the ln(S) produces the biodiversity information function, H [*Buzas and Hayek*, 1996]. As part of the present study, a statistically significant positive correlation was found between the NAO and H for Gullmar Fjord. Between the early and late 1990s there was a noticeable shift from larger to smaller phytoplankton in Gullmar Fjord, especially an increase in dinoflagellates. This corresponded in time to a change from very high NAO to low NAO index values and is a similar response to that reported by *Edwards et al*. [2000] for the North Sea and the Northeast Atlantic but opposite to that reported by *Irigoien et al*. [2000] in the English Channel.

On the other side of the Atlantic, changes in the phytoplankton species composition at Narragansett Bay have also been linked to climate variations [*Karentz and Smayda*, 1998; *Smayda,* 1998]. Major changes were observed among the boreal-Arctic diatom bloom species, *Detonula confervacea* and *Thalassiosira nordenskioeldii*, and the diatoms, *Skeletonema costatum* and *Asterionellopsis glacialis*. The shifts in species abundance were in part related to a warming trend in annual SST beginning in the early 1960s associated with the increasing positive trend in the NAO index, as well as to increasing copepod grazing pressure [*Durbin and Durbin*, 1992].

Primary production determined from C^{14} measurements at a site southeast of Bermuda was negatively related to the NAO index [*Bates*, 2001]. In this location, during periods of low NAO index, storm tracks shift southward, more frequent outbreaks of cold air come off North America, surface waters cool, and the winter mixed layer deepens [*Dickson et al.*, 1996]. *Bates* [2001] suggested that the deeper mixed layer during low NAO index years led to elevated nutrient levels in the near-surface layer, which ultimately led to higher primary production. This argument linking winds and primary production is opposite that often given for the more northern areas where increased mixing has been suggested as leading to reduced

production. This difference was explained by *Dutkiewicz et al.* [2001] from modelling studies. They showed that the relationship between mixing and production depends upon the ratio of the Sverdrup's critical depth in spring (h_c) to the mixed layer depth (h_m) at the end of the winter. Where h_c/h_m is approximately 1, such as in the subtropics, strong mixing does lead to enhanced production through nutrient enhancement, but in subpolar regions where the ratio is <<1, increased mixing should lead to lower production because of reduced light levels.

The above examples have focused upon linkages between the phytoplankton and the NAO through air-sea fluxes. However, the phytoplankton community is also affected by circulation changes related to variability in the NAO index. For example, during the late 1980s when the NAO index was strongly positive and the strength of the westerly winds increased in the Northeast Atlantic, there was an increase of oceanic inflow into the North Sea. Subsequently, the phytoplankton biomass in the North Sea was the highest ever recorded [*Edwards et al.*, 2001]. Phytoplankton biomass in 1989 was nearly three standard deviations above its long-term mean. At this time there was also an influx of unprecedented numbers of oceanic species into the North Sea, including the diatom *Thalassiothrix longissima* and a succession of short-lived exceptional phytoplankton blooms occurred. Many of the phytoplankton species recorded their peak abundance one to three months in advance of their normal seasonal peak. The inflowing Atlantic water is thought to have possibly brought a pulse of oceanic-derived nutrients, which when coupled with very mild atmospheric conditions, produced an exceptionally favorable period for phytoplankton growth [*Edwards et al.*, 2001].

3. ZOOPLANKTON

3.1. Background

Zooplankton are small, passively floating animals that generally feed on phytoplankton, or in some cases, other smaller zooplankton. They are important food for most fish larvae and some small adult fish. There are numerous species of zooplankton, each adapted to particular oceanographic characteristics. In the North Atlantic, one of the most important zooplankton species is *Calanus finmarchicus* because of its pan-Atlantic distribution and large biomass. It has been estimated to reach up to 92% of the total zooplankton biomass in Icelandic waters [*Gislason and Astthorsson*, 1995]. In the Northwest Atlantic, on continental shelves off the United States, this species, together with *Pseudocalanus* spp. and *Centropages typicus*, account for

75% of the total zooplankton abundance [*Sherman et al.*, 1987; 1998]. In addition, *C. finmarchicus* has been identified as the prominent prey for fish larvae such as cod and haddock in the Barents Sea [*Helle*, 1994], off Iceland [*Astthorsson and Gislason*, 1995] and in U.S. waters [*Marak*, 1960; *Sherman et al.*, 1981]. The abundance of herbivorous (phytoplankton eating) zooplankton, such as *C. finmarchicus*, usually follows a similar cycle to that of the local phytoplankton production cycle but lagged slightly. Carnivorous zooplankton, which eat other smaller zooplankton, tend to be tuned to the abundance cycles of their particular prey. Zooplankton generally produce one to several generations per year and many species diapause through the winter. Some, such as *C. finmarchicus*, spend this diapause period in deep waters in the open ocean. Awaking in early spring, they ascend to the surface where they feed on the spring bloom, mate and reproduce.

During the last 20 years there has been increasing interest among marine scientists in understanding the relationship between zooplankton and climate because of the fact that most marine fish and invertebrates feed-on zooplankton during some stage of their life. Early studies documented large fluctuations in zooplankton in the Northeast Atlantic and the North Sea from the CPR records [*Colebrook*, 1972; *Gieskes and Kraay*, 1977]. Long-term patterns of variability in the zooplankton were found to be similar over large geographic areas of the North Atlantic, and often across trophic states [*Colebrook et al.*, 1984; *Aebischer et al.*, 1990; *Cushing*, 1990]. The magnitude of the spatial scale was the first suggestion that hydrographic or climatic factors most likely drive interannual variability in these marine species.

3.2. Relationship with NAO

Fromentin and Planque [1996] were the first to document linkages between NAO variability and interannual changes in zooplankton in the North Atlantic. They found significant correlation between the NAO index and two major copepod species in the eastern Northeast Atlantic and the North Sea. A negative relationship ($R^2 = 0.58$) with *C. finmarchicus* was attributed to the association of the NAO to the wind and SST. It was argued that higher wind stresses under a high NAO index lead to reduced stratification, lower phytoplankton, and ultimately lower abundance of zooplankton because of less food. The warmer temperatures were also considered to inhibit production of this cold-water species. A weaker but positive relationship ($R^2 = 0.28$) of the NAO was found with the abundance of *C. helgolandicus* with a delay of one year. Differences between the responses of the two species were attributed to differences in seasonal cycles, temperature affinities and geographical locations

coupled with the spatial heterogeneity in the wind and temperature responses to NAO forcing and competition between the two species.

Planque and Reid [1998], based upon the results of *Fromentin and Planque* [1996], generated a regression model of the abundance of *C. finmarchicus* from the NAO using data from 1958–1992 (Figure 1). They went on to predict the abundances for the years 1993 to 1997. There was reasonable agreement between predicted and observed abundances for 1993–1995, but when the NAO index dropped precipitously in 1996, they predicted a corresponding increase in the *C. finmarchicus* abundances. The observed abundance, on the other hand, fell to its lowest value in the entire time series. Acknowledging a lack of understanding as to why such a large discrepancy existed, they speculated that it might have been due to very low overwintering stocks. They suggested this could have been a consequence of a prolonged period of poor years or a lag response in the establishment of circulation to colonize favorable feeding grounds following the new phase of the NAO. Another possibility is related to the unusual eastward shift in the position of both the Icelandic Low and Azores High in 1996, which might have caused a different response than under normal low NAO index conditions when the pressure systems were located more towards the central North Atlantic.

Several studies have shown a strong positive relationship between the interannual variability in the latitudinal posi-
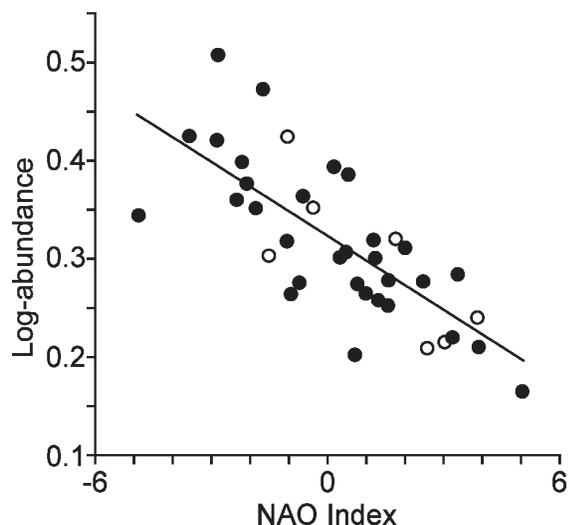
Figure 1. Log-abundance of *Calanus finmarchicus* in the Northeast Atlantic against the NAO winter index for the period 1958-1995 used to generate the linear regression model to predict the *Calanus* abundances. Open circles indicate data for 1958-1961 and 1993-1995 that were not included in the analysis by *Fromentin and Planque* [1996]. Taken from *Planque and Reid* [1998].

tion of the northern edge or "wall" of the Gulf of Stream and zooplankton indices around the United Kingdom, including the central North Sea [*Taylor and Stephens*, 1980; *Taylor et al.*, 1992; *Hays et al.*, 1993; *Taylor*, 1995]. The lack of any lag and similar relationships between the Gulf Stream and zooplankton from a freshwater lake (Windermere) in the northwest of England lead to the conclusion that the connection must be via the atmosphere. That link was later shown to be through the NAO. *Taylor and Stephens* [1998] noted a strong positive relationship between the NAO index and the Gulf Stream position such that the "north wall" was located farther north following high NAO index years and farther south when the NAO index is low. *Curry and McCartney* [2001] found that the Gulf Stream transport covaries with its position such that a more northward location occurs during increased transport and a southward location when the Stream weakens. They too noted the positive relationship between the NAO index and the Gulf Stream transport, and therefore its position. *Planque and Taylor* [1998] suggested that the relationship between the NAO (and hence the Gulf Stream) and zooplankton around the U.K. was due to several mechanisms. In the case of *C. finmarchicus*, these included direct advection of zooplankton into the North Sea through increased Atlantic inflow as well as changes in stratification and temperature that affected the timing and intensity of the spring phytoplankton bloom and subsequently the zooplankton.

Studies of zooplankton along the CPR transect that crosses the Bay of Biscay, the Celtic Sea and the English Channel during 1979–1995 were carried out by *Beaugrand et al.* [2000]. They found a negative relationship between the NAO index and the zooplankton (primarily copepod) abundance in the English Channel, similar to that for *C. finmarchicus* in the North Sea and Northeast Atlantic found by *Fromentin and Planque* [1996]. *Beaugrand et al.* [2000] argued that the stronger winds associated with a high NAO index produce greater wind-induced turbulence leading to more intense vertical mixing. While higher levels of turbulence increase contact rates between the zooplankton and its prey [*Rothschild and Osborn*, 1988] and hence feeding rates [*Mackenzie and Leggett*, 1991; *Sundby et al.*, 1994], they also increase metabolic rates [*Alcaraz et al.*, 1994]. High metabolic rates also result from the higher temperatures associated with a high NAO index. *Beaugrand et al.* [2000] proposed that the increased feeding does not compensate for these higher metabolic costs. The resulting lower net energy consumption translates into higher mortality of adult copepods and lower fecundity, implying fewer eggs and a delay in their spring production. No relationship was found between the NAO and zooplankton in the Celtic Sea or the Bay of Biscay. Although not commented on by *Beaugrand*

et al. [2000], this may be due to the observed southward reduction in the effect of the NAO on the atmospheric and physical oceanic variables in this region as discussed by *Planque and Taylor* [1998].

NAO-associated changes in current transport have also been suggested as a control on zooplankton abundances. Persistent anomalies in the wind field associated with the NAO causes variability in the direction and strength of surface currents. Off northern Norway, a high NAO index is associated with stronger northeastward flow of warmer Atlantic water into the Barents Sea [*Ådlandsvik and Loeng*, 1991; *Dickson et al.*, 2000]. *Helle and Pennington* [1999] have shown that in this region, the abundance of zooplankton (primarily *C. finmarchicus*) is positively related to the volume of the Atlantic inflow and that this effect is propagated through the food web up to at least juvenile cod. A similar relationship between zooplankton and Atlantic inflow is suggested for the North Sea [*Planque and Taylor*, 1998; *Stephens et al.*, 1998; *Gallego et al.*, 1999; *Heath et al.*, 1999; *Edwards et al.*, 1999].

Variability in both the extent of the large-scale convection and the circulation of the deep waters in the North Atlantic are associated with the NAO [*Dickson*, 1997]. Such changes appear to affect zooplankton populations over long time scales. The North Sea population of *C. finmarchicus* is seeded from the Faroe-Shetland Channel, where it overwinters in Norwegian Sea Deep Water. Changes in convective intensity over the latter decades of the 1900s have been associated with a decrease of the volume of Norwegian Sea Deep Water [*Schlosser et al.*, 1991; *Hansen et al.*, 2001]. *Heath et al.* [1999] proposed that this reduction in the volume of *C. finmarchicus* overwintering habitat is partly responsible for the decline in abundance of the species observed in the North Sea since the late 1950s. They further suggested that such changes occur on decadal time scales but that interannual fluctuations in the NAO, which are accompanied by immediate changes in the northwesterly winds, do not necessarily lead to corresponding changes in the abundance of *C. finmarchicus* in the North Sea.

Beare and McKenzie [1999] noted significant changes in the seasonality of both the NAO and the abundance of stage 5 and 6 of *C. finmarchicus* in the North Sea off northeastern Scotland from the CPR surveys beginning in 1967 (Figure 2). The *C. finmarchicus* population densities were relatively high between 1958 and 1965 but collapsed in 1967 and did not recover through to the mid-1990s. Associated with this collapse was a change in the bimodal pattern of abundance. The earlier high abundances were associated with a dominant spring peak whereas after the collapse, the autumn peak dominated until the mid-1980s. Using the NAO index of *Jones et al.* [1997], *Beare and McKenzie*

[1999] noted increasing abundance in winter and decreasing in spring and they contended that this was a major contributor to the collapse of *C. finmarchicus* in 1967 although they were unable to provide the mechanism. They speculated that it might be related to changes in physical conditions or currents in April when these copepods are ascending to the surface waters after their winter diapause.

Conversi et al. [2001] investigated the relationship between the NAO index and *C. finmarchicus* (copepodites 5 and adults) abundance from the CPR records in the Gulf of Maine for the period 1961-1991. They found a positive relationship at all scales studied. The seasonal cycle of *C. finmarchicus* showed a clearer cycle (less variability) and there was higher overall abundance during high NAO versus low NAO index years. There was a 30-year increasing linear trend (accounting for 39% of the total variability of *C. finmarchicus* abundance), confirming the pattern described by *Jossi and Goulet* [1993]. Similar increasing trends were observed in the Gulf of Maine SST (39% of total variability) and the NAO index (20% of total variability). Cross correlation of detrended series showed the variations in the NAO index
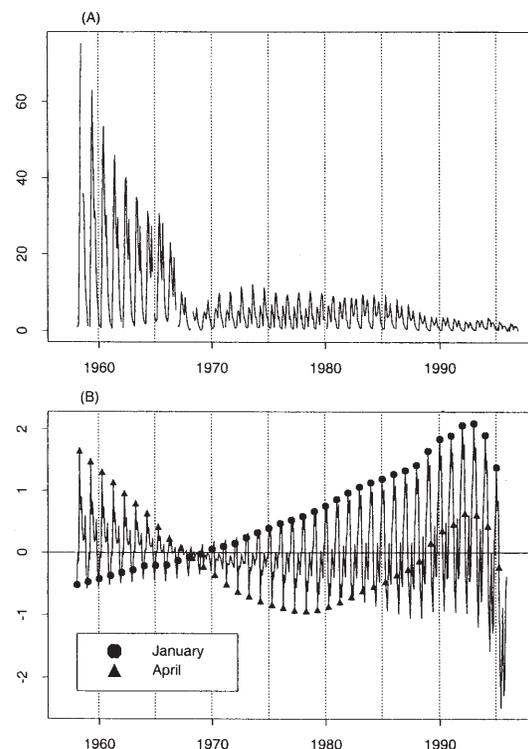
Figure 2. Long-term and seasonal changes in (a) *Calanus finmarchicus* abudance to the north-west of Scotland (57º to 61.4ºN, 0º to 4ºW) and (b) the North Atlantic Oscillation index. Both time series were analyzed using decomposition techniques that separate the long-term trend and seasonal structure. Taken from *Beare and McKenzie* [1999].

were positively correlated with and preceded the winter SST fluctuations by 2 years ($R^2 = 0.22$) and the *C. finmarchicus* summer abundance by 4 years ($R^2 = 0.25$). Winter sea surface temperatures preceded summer *C. finmarchicus* by 2 years ($R^2 = 0.38$). A stepwise regression indicated that the winter SST alone accounted for a third of the observed variability in *C. finmarchicus* summer abundance.

Greene and Pershing [2000], using GLOBEC (GLOBal ocean ECosystems dynamics) field data, found that *C. finmarchicus* abundance in the Gulf of Maine was related to variations in bottom temperature. They suggested this was because the species is tightly coupled to the conditions of the Slope Water [see also Marine Ecosystem Response to Climate in the North Atlantic *MERCINA*, 2001]. Slope Water occupies the area between the continental shelf and the Gulf Stream and penetrates into the Gulf at depth through the deep gullies and channels. The Slope Water characteristics adjacent to the Gulf vary on time scales of years to decades between cold (4º–8ºC), fresh conditions indicative of a northern (Labrador Current) origin and warm (8º–12ºC), salty waters of a southern (North Atlantic Current) origin. The appearance of the Labrador-type Slope Water off the Gulf of Maine appears to be related to the NAO [*Worthington*, 1964; *Marsh et al.*, 1999; *Drinkwater et al.*, 1999]. During the decade of the 1960s, when the NAO index was predominantly negative, cold Labrador Slope Water extended as far south as the Middle Atlantic Bight. As a result, both bottom water temperatures and *C. finmarchicus* abundance in the Gulf of Maine were relatively low. In contrast, during the 1980s when the NAO index was predominantly positive, warm Slope Water lay off the shelf, the temperature of the lower layers of the Gulf was warm, and *C. finmarchicus* abundances were relatively large. The Labrador-type Slope Water during this period was largely confined to an area north of the Laurentian Channel. During each southward intrusion of Labrador Slope Water along the Scotian Shelf to the Gulf of Maine after 1980, *C. finmarchicus* abundance in the Gulf declined in subsequent years. For example, the very low abundances of *C. finmarchicus* during 1998 and early 1999 are believed to be linked to the largest annual decline in the NAO index in the past century that occurred in 1996. It was followed two years later by the furthest southward extension of Labrador Slope Water along the shelf and the coldest waters in the Gulf since the 1960s. The CPR data revealed several arctic boreal zooplankton species associated with the 1998 southward excursion of the Labrador Slope Water, including the southern most record of *C. hyperboreus* [*Johns et al.*, 2001].

The differences and similarities in the relationship between the NAO index and *C. finmarchicus*, as observed in the western Gulf of Maine and the eastern Atlantic including and North Sea are striking. *C. finmarchicus* abundance in the Northeast Atlantic tends to be lower during high NAO index years and the overall 30-year trend of *Calanus* is downward while that of the NAO index is upward. In the Gulf of Maine, the opposite occurs as the relationship between the NAO index and *Calanus* abundance is positive. To verify whether the relationship between the NAO index and *C. finmarchicus* abundance found in the eastern and western North Atlantic corresponded to opposite patterns in the long-term variations of the copepods' populations, Conversi, Licandro and Ibanez (unpublished data) compared *C. finmarchicus* time series sampled on the opposite sides of the ocean. CPR abundance data of *C. finmarchicus,* stages 5–6, from the Gulf of Maine and from the Northern North Sea (area A2), over the 38 year period 1961–1998 were converted to the same units (ln(counts)/10 n.mile). The first modes of temporal variations of the two series represent, respectively, 25.8% of the temporal variability of *Calanus* populations in the Gulf of Maine and 26.4% off western Ireland and represent the general trends of the series. An out-of-phase relationship becomes evident when comparing the first mode of *C. finmarchicus* in the Gulf of Maine with that in the North Sea. Generally, years when *C. finmarchicus* increased in the western Atlantic corresponded to years in which it decreased in the North Sea, and vice versa. The correlation (r = -0.28) between detrended series for the period Feb. 1978 – Dec. 1998 (a period with reduced number of missing data) confirms the inverse relationship but indicates that it is relatively weak. The year-to-year changes in *C. finmarchicus* abundance that are coupled across the North Atlantic are considered to be a result of atmospheric forcing linked to the NAO.

4. BENTHOS

Benthos refers to those animals living on or beneath the sea floor. Although there has been less research conducted on the benthos compared to phytoplankton and zooplankton, several studies provide evidence of relationships between the NAO and benthic populations. *Cohen and McCartney* [2000], examining chemical and structural variations in the skeletons of small brain corals (*Diploria labyrinthiformis*) collected at 50-ft depth on the south-east edge of the Bermuda platform, constructed seasonally-resolved oxygen isotope records and examined changes in skeletal density (calcification rate). These parameters were strongly correlated with the instrumental record of the NAO over a 40-year period covering the late 1900s.

On the opposite side of the Atlantic, *Nordberg et al.* [2000], working with benthic foraminiferal records between

1930 and 1996, showed a significant change in faunal composition during the mid-1970s. In those years, *Stainforthia fusiformis*, an opportunistic indicator of low oxygen environments in the Scandinavian fjords, became the most common Skagerrak species in the foraminiferal fauna assemblage. The timing of this faunal change coincided with a severe low oxygen event in the Gullmar Fjord, which *Nordberg et al.* [2000] related to changes in the NAO. Positive NAO index values in the early 1970s were marked by strong westerly winds in the Skagerrak region, thereby preventing the exchange of bottom-water in the fjords and decreasing the oxygenation of the sea floor and its benthic community. Working in the same area, *Tunberg and Nelson* [1998] monitored soft sediment macrofauna in depths from 10 to 300 m for periods of 12 to 20 years. The variability in macrobenthic abundance was in phase over the upper 100 m but out of phase with that at 300 m. Abundances and biomasses varied with a 7 to 8 year periodicity, which approximated that of the NAO index (7.9 years as determined from spectral analysis). The NAO index over the period 1970 to 1990 was positively correlated with Skagerrak deep-water (600 m) temperatures and negatively correlated with stream flow from western Sweden. Stream flow, in turn, was positively correlated with benthic abundance and biomass at stations down to 100 m, but negatively correlated with bottom water oxygen content. *Tunberg and Nelson* [1998] proposed that the NAO association with the benthos occurs by bottom-up control of the population through influences on primary production. They further suggested that climatic variability in the region is likely the most important factor in controlling the variability in the benthos.

Hagberg and Tunberg [2000] continued the work in Gullmar Fjord and the Swedish Skagerrak. They compared a 7 to 13 year data series (covering 1983-1995) of mean macrobenthic abundance data from eight stations (25 to 118 m) to the freshwater runoff to the fjord, temperature at 600 m in the Skagerrak and the NAO index. The macrobenthic abundances at 3 of the innermost fjord stations were positively correlated with the NAO index ($R^2 = 0.6$-0.7, p<0.05) with a delay of up to 1 year. The authors proposed that this was due to stronger stratification as a result of higher freshwater runoff under a low NAO index. This in turn reduced primary production and hence there was less food input to the benthos (Figure 3). At the three stations outside the fjord and the remaining two stations inside the fjord, the highest correlations of the macrobenthic abundances were with Skagerrak temperatures at 600 m. The authors suggested the negative correlations with temperature might be related to the NAO. This could occur, they stated, through periodic upwelling of deep colder water, rich in dissolved inorganic nutrients, resulting in an increase in primary production and subsequently more food for the benthos.

Kroencke et al. [1998] examined long-term (1938–1995) macrofauna data in the subtidal zone (10 to 20 m) off Norderney, one of German's East Frisian barrier islands. They found strong positive correlations between abundance, species number and to a lesser extent the biomass of macrofauna in spring and the NAO index. They suggested that the mediator is probably the SST in late winter and early spring. Mild meteorological conditions, probably acting in conjunction with eutrophication, were believed to result in the observed increase in total biomass from 1989–1995. The authors concluded that climate variability explains most of the interannual variability in macrozoobenthos off Norderney.

5. FISH

5.1. Atlantic Cod (Gadus morhua L)

Atlantic cod is an ideal candidate for examination of the relationship between the NAO and fish because of its pan-Atlantic distribution and the fact that climate variations have been shown to affect recruitment [*Planque and Frédou*, 1999], growth [*Brander*, 1994; 1995] and distribution [*Jensen and Hansen*, 1931; *Rose et al.*, 2000]. The disadvantage is that they are heavily exploited. This has led to a general decline in numbers, especially during the last half of the 1900s, which sometimes has made it difficult to separate climate from fisheries effects. In spite of this, several studies have provided convincing evidence of NAO associated variability of cod.

Cod eggs, larvae and early juveniles are generally distributed in the upper water column where they are free-floating before settling on the bottom as half-year olds. It is principally during these early life stages that the year-class strength of cod (the number of fish that reach commercial size) is determined [*Sundby et al.*, 1989; *Myers and Cadigan*, 1993]. This is also a stage at which climate is considered to have its most profound effect [*Cushing*, 1966; *Ellertsen et al.*, 1989; *deYoung and Rose*, 1993; *Dickson and Brander*, 1993; *Ottersen et al.*, 1994; *Ottersen and Sundby*, 1995].

The south and central Barents Sea is a highly productive region, being home to one of the largest cod stocks in the North Atlantic, the Arcto-Norwegian or Northeast Arctic cod. Recruitment varies extensively with the ratio between strong and weak year classes evaluated at age 3 being about 15 [*Ottersen*, 1996], and as high as 70 based on early juveniles [*Ottersen and Sundby*, 1995]. Interannual variability in the thermal conditions in the areas of the Barents Sea inhabited by cod are principally determined by winter conditions [*Ottersen and Stenseth*, 2001] through changes in the temperature and quantity of the Atlantic inflow from the south-

west [*Loeng*, 1991] and regional air-sea heat exchanges [*Ådlandsvik and Loeng*, 1991; *Loeng et al*., 1992]. The impact of interannual and decadal shifts in sea temperatures in the Barents Sea on cod recruitment has been well documented with high recruitment associated with warm years [*Sætersdal and Loeng*, 1987; *Ottersen et al*., 1998; *Ottersen and Loeng*, 2000]. This is thought to be because of (i) higher primary production due a larger ice-free area, (ii) a larger influx of zooplankton carried by the increased Atlantic inflow and (iii) higher temperatures that promote higher biological activity at all trophic levels [*Sakshaug*, 1997].

Ottersen and Stenseth [2001] demonstrated a positive association between the NAO and Barents Sea cod recruitment (1970–1998). They evaluated several statistical mod-

els that predicted year-class strength from climate variables during the winter the year-class was spawned. The single most important variable was the NAO index that alone accounted for 53% of the recruitment variability. The mechanistic link (Figure 4) was considered to be through effects on regional sea temperatures and food availability. Higher NAO index values are associated with warmer temperatures through both increased atmospheric heat transfer to the ocean and an increased Atlantic inflow. The latter transports more *Calanus finmarchicus* into the Barents Sea and hence more food for cod. On the other hand, the year-class strength of cod in the much warmer North and Irish Seas is negatively related to both the NAO index and temperature. This is believed to result from a limitation in energy resources neces-
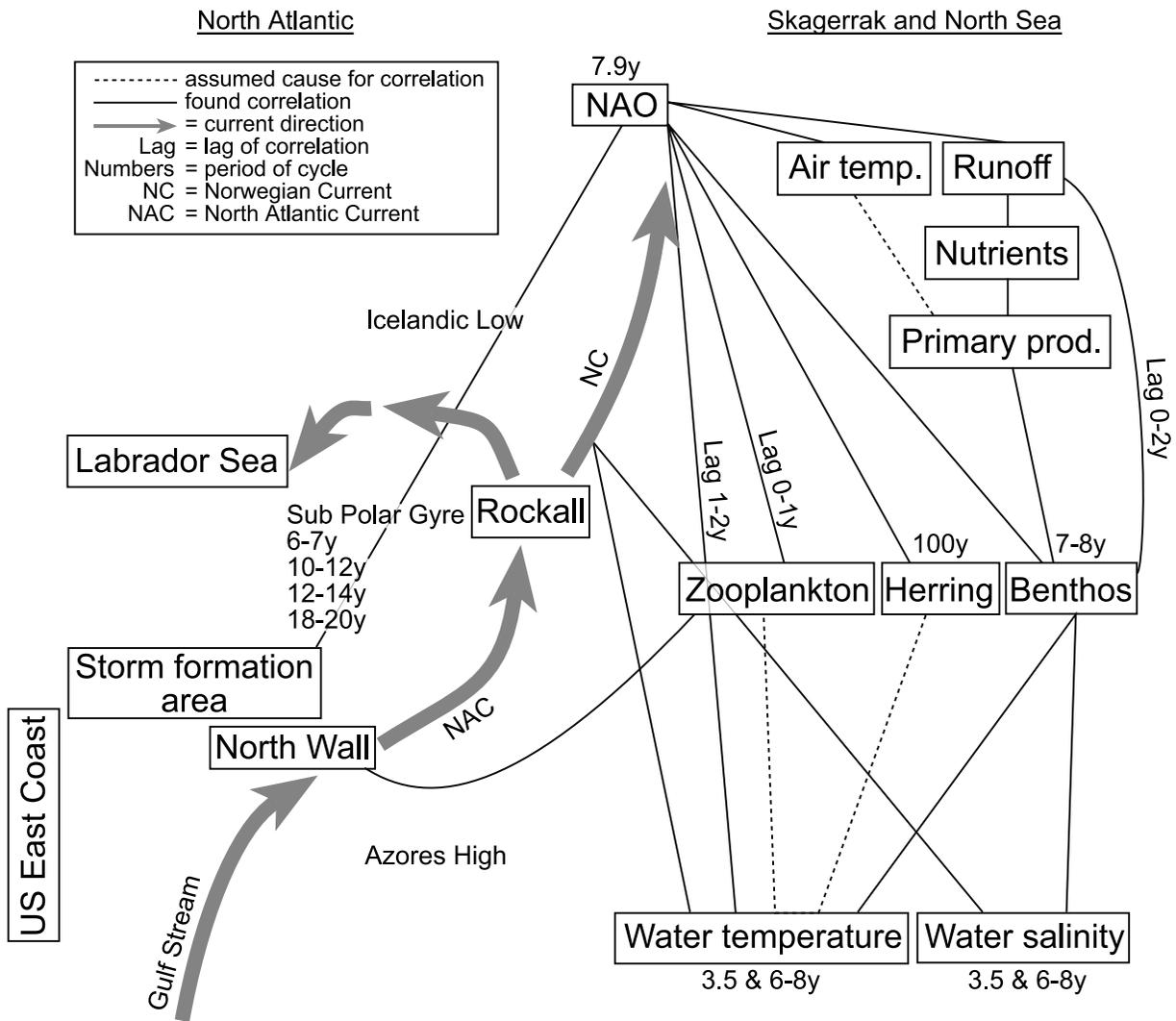
Figure 3. Schematic diagram describing the assumed cause for correlation between the NAO and physico-chemical and biological interactions courtesy of J. Hagberg, Department of Marine Ecology, Goteborg University, Sweden and based upon *Hagberg and Tunberg* [2000]. Note the number of years indicate the dominant periods of variability.
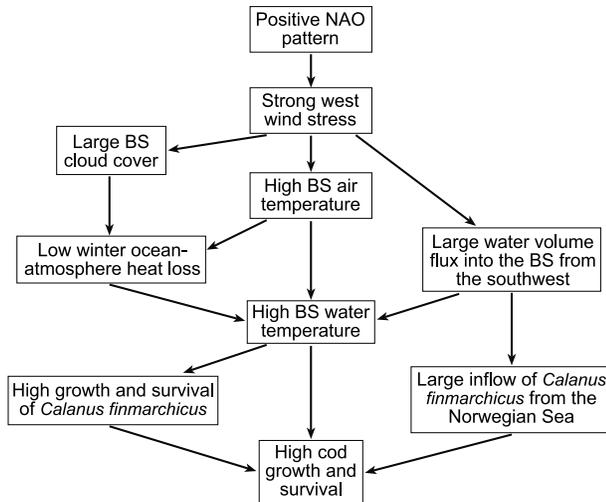
Figure 4. Mechanisms linking the NAO to variability in Barents Sea (BS) oceanography and ecology. A positive NAO index phase results in increased westerly winds over the North Atlantic. This increases BS water temperatures through enhanced volume flux of relative warm Atlantic water from the southwest, higher air temperatures, and increased cloud cover. Higher BS water temperature improves growth and survival of cod larvae both directly through faster development rates and indirectly through regulating the production of their main prey, nauplii of the copepod Calanus finmarchicus. Increased inflow from the zooplankton rich Norwegian Sea further increases availability of food for the cod larvae. High food availability for larval and juvenile fish results in higher growth rates and greater survival through the vulnerable stages when year-class strength is determined. Modified from *Ottersen and Stenseth* [2001].

sary to achieve higher metabolic rates during warm years [*Planque and Fox*, 1998]. These results are consistent with *Planque and Fredou* [1999] who found that recruitment was positively related to temperature for stocks occupying relatively cold waters and negative if in relatively warm waters.

Dippner and Ottersen [2001] also related cod recruitment to large-scale climate variability and Barents Sea temperatures. They showed that the temperature anomalies at the Kola section across the southern Barents Sea are significantly correlated to the anomalies of the NAO index. Furthermore, a statistically significant CCA (canonical correlation analysis) correlation was found between the Kola section temperature and both the number of 0-group cod (R^2 = 0.44, unlagged) and recruitment measured at age 3 (R^2 = 0.37, lag of 2 years).

Opposing year-class strengths of cod between the eastern and western regions of the North Atlantic was hypothesised [*Izhevskii*, 1964; *Templeman*, 1972], and was suggested to be related to the NAO [*Rodionov*, 1995]. Links between

strongly negative NAO index events and good recruitment and growth for the Northern cod stock off southern Labrador and northern Newfoundland in Canada were discussed by *Mann and Drinkwater* [1994] while positive NAO index anomalies have been linked to favorable conditions for Arcto-Norwegian cod [*Ottersen and Stenseth*, 2001; *Ottersen et al.*, 2001]. Both regions are characterised by sea temperatures towards the lower end of the overall range inhabited by cod. The NAO index accounts for approximately 50% of the interannual variability in atmospheric, oceanic and sea-ice indices both in the Labrador Sea Region [*Drinkwater and Mountain*, 1997] and the Barents Sea [*Ottersen and Stenseth*, 2001], but the signs of the correlation are opposite [e.g., *Hurrell et al.*, this volume]. Years of high NAO index values produce cold temperatures in the Newfoundland-Labrador area and warm temperatures in the Barents Sea and visa versa. Such inverse fluctuations in Barents and Labrador Sea temperatures were pointed out by *Izhevskii* [1964] and the association of the NAO with this "seesaw" pattern in temperatures was demonstrated by *van Loon and Rogers* [1978]. Recruitment in both areas tends to be higher in warmer years than in colder years, thus during a high NAO index recruitment is good in the Barents Sea and poor in the Labrador while during low NAO index years, the reverse is true [*Ellertsen et al.* 1989; *DeYoung and Rose*, 1993].

Cod growth also is linked to NAO variability. *Brander* [1994; 1995] showed that temperature accounts for both the mean differences in size-at-age for cod throughout the North Atlantic and the interannual variability in mean size within individual stocks. Higher size-at-age occurs under warmer conditions for most stocks. Consistent with this, *Drinkwater* [2002] showed that the NAO accounted for over 50% of the variability in growth increment between 3 and 5 year olds from the Northern Cod stock off Newfoundland (Figure 5).

Changes in climate patterns associated with the NAO also affect predator-prey interactions. In the Barents Sea, an increase in the basic metabolic rate of cod, associated with higher temperature during years of high NAO index values, results in an increase in the consumption of capelin (*Mallotus villosus*) by 100 thousand tonnes per degree centigrade [*Bogstad and Gjøsæter*, 1994].

The effects of NAO-associated events on cod can be sustained for several years [*Ottersen et al.*, 2001]. For example, the increase in survival of Arcto-Norwegian cod through the vulnerable early stages during warm, high NAO index years historically results in stronger year classes in later years. As such year-classes mature, the number of spawners tends to remain higher-than-normal, enhancing the potential for good recruitment to the next generation. Furthermore, if
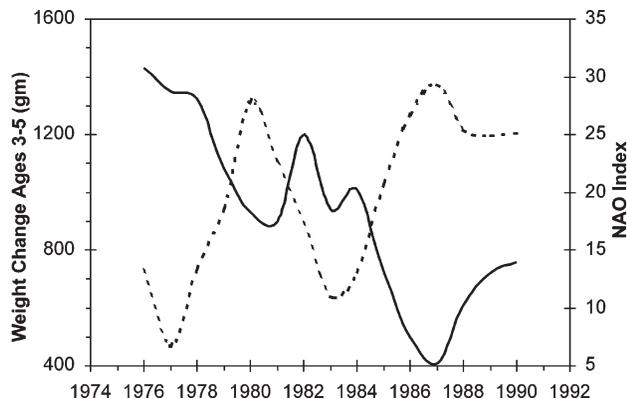
Figure 5. The time series of the weight gain between ages 3-5 and the three year-average of the NAO index for the equivalent years. Redrawn from *Drinkwater* [2002].

individuals in a cohort of Arcto-Norwegian cod are larger-than-average as half-year olds, they tend to remain large as they grow older and the cohort abundance tends to be high [*Ottersen and Loeng*, 2000].

5.2. Herring (Clupea harengus) and Sardines (Sardina pilchardus)

Small pelagic fishes such as sardine and herring are widespread and represent about 20–25% of the total annual catch of the world fisheries. Most are highly mobile and have short, plankton-based food chains, with a few species feeding directly upon phytoplankton. They are also short-lived (3–7 years, except herring) and highly fecund. Catch records of several hundreds of years for herring and sardines in northern Europe show that the fisheries oscillate between times of very high yields and other times when the fish were totally absent. These periods of high and low catches varied spatially. Such fluctuations occur on decadal time scales and in part can be explained as a response to different regimes of prevailing wind directions corresponding to related phases of the NAO [*Alheit and Hagen*, 1997; 2001]. Herring stocks off Bohuslän on the Swedish West coast, off southwestern England, in the eastern English Channel and the Bay of Biscay were favored during periods of low NAO index when the westerly winds were shifted to the south and the sea temperatures in these regions were low. In contrast, the Norwegian spring spawning herring, the sardines of southwestern England and the sardines caught by the French fleet in the English Channel exhibit high catches during the high index phase of the NAO, i.e. when the westerly winds intensified and high local temperatures prevailed.

Guisande et al. [2001] showed that higher sardine recruitment off northern Spain occurs during low NAO index

years. During such conditions, the winds tend to be more southerly, bring warmer-than-normal temperatures to this region as well as promoting onshore Ekman transport. The higher temperatures result in faster growth rates and the onshore drift in greater larval retention inshore. Lower recruitment occurs during high NAO index years due to the colder temperatures and offshore drift.

5.3. Tuna and Other Large Pelagics

Santiago [1997] and *Borja and Santiago* [2001] examined the relationship between the NAO index with tuna in the eastern Atlantic for the period 1969–1995. The mean recruitment was estimated for three stocks during years of low and high NAO index (Figure 6). For bluefin tuna (*Thunnus thynnus*) in the eastern Atlantic, mean recruitment during high NAO index situations was near double that during low NAO index conditions. The opposite occurred in the case of northern albacore (*Thunnus alalunga*), with recruitment during high NAO index years being approximately half that of low NAO index years. These differences were estimated to be statistically significant. In contrast, there was no difference in recruitment of bluefin tuna from the western Atlantic between the two phases of the NAO. Standard correlation analysis confirmed a negative relationship between the NAO index and recruitment of northern albacore ($R^2 = 0.52$, $p<0.05$) but no statistically significant relationship ($p>0.05$) was found for either eastern or western bluefin tuna.

Borja and Santiago [2001] suggested that the mechanism linking the NAO to albacore recruitment is through the temperature of the spawning-overwintering area. Also, during positive NAO index winters, the storm activity increases, especially in a narrow band following the main eastern U.S.
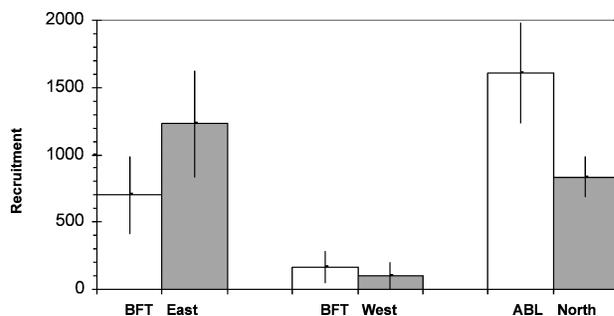
Figure 6. Mean recruitment of eastern and western bluefin (times 1000) and northern albacore (times 10000) estimated for low NAO index years (1969, 1970, 1977, 1979) and high NAO index years (1973, 1981, 1983, 1989, 1990, 1992, 1993, 1994, 1995). Low NAO index situations are expressed as blank boxes; high NAO index situations as filled boxes. 95% confidence intervals are indicated.

coastal baroclinic zone, which increases mixed-layer depth [*Dickson et al*., 1996]. The stronger winds are thought to be responsible for increased upwelling and mixing, eventually leading to a higher concentration of food organisms.

Opposite to the albacore tuna, the relationship between the NAO index and eastern bluefin tuna is positive but the NAO only accounts for 13% of the recruitment variability. However, this rises to 49% when the recruitment lags the NAO index by 1 year. The different sign of the responses of the two species can be explained by differences in their overwintering areas. Whereas the albacore overwinters along the western side of the Atlantic, the eastern bluefin overwinters on the eastern side (along the Moroccan coast and in the Canary Islands). The NAO effect on SST differs in sign between the two overwintering areas *Krovnin* [1995].

Another possible factor linking the NAO to the eastern bluefin recruitment is the observation of *Fromentin and Planque* [1996] that the abundance of *C. helgolandicus* was significantly higher during high NAO index years than during low NAO index years and the degree of significance increased when the NAO index lagged the zooplankton by one year. If the abundance of this dominant zooplankton group is compared with bluefin year-class strength estimated for the same year, the relationship is statistically significant, suggesting a possible direct connection between zooplankton abundance and recruitment success of bluefin.

Climate variability seems to play a minor role in the recruitment success of western bluefin tuna, at least during the analyzed period. It should be noted, however, that the number of western bluefin has been extremely low since the 1970s, which could account for a low signal to noise ratio.

Other links between the NAO and changes in abundance and distribution of large pelagic fish have been observed. The Norwegian bluefin fishery developed after the Second World War, peaked in 1952 (11,400 t) and collapsed in the mid-1960s [*Tiews*, 1978] coinciding with a period of low NAO index. The same collapse was observed in the Danish and German fisheries in the North Sea that dropped from 2,400 t in 1952 to less than 100 t by the mid-1960s. According to *Tiews* [1978], it was the lack of recruit year classes to the Northeast Atlantic tuna fishery that led to the absence of bluefin tuna in the central North Sea after 1962.

Mejuto and de la Serna [1997] found a statistically significant relationship (p<0.05) between North Atlantic swordfish (*Xiphias gladius*) year-class strength and the NAO index. As in the case of northern albacore, high NAO index years were associated with low recruitment and low NAO index years with high recruitment levels. The model explains 33% of the variability of swordfish recruitment. Standardized catch per unit fishing effort indices of age 1 corresponding to the Spanish longline fleet from 1983–1995 were used as estimates of swordfish year-class strength.

Cushing [1982] refers to an increased abundance of bluefin tuna in the Northeast Atlantic during a period of warming, between the 1920s and 1950, and bluefin tuna, together with swordfish, appeared off the Faroe Islands and Iceland. This period was typified by high NAO winter index values. After disappearing in the 1960s during low NAO index years, the bluefin again appeared in high latitude waters during the 1990s. In the western Mediterranean, the abundance of age-0 bluefin in 1996, when the NAO index fell dramatically to the lowest value since 1969, was extremely low [*de la Serna*, 1997].

5.4. Atlantic Salmon (Salmo salar)

Atlantic salmon is another pan-Atlantic species. It is affected by climate variability in all of its many stages, from the parr through the smolt, marine post-smolt and mature stages. Parr is the name for juvenile salmon in freshwater, smolt is the juvenile stage adapted to life in the ocean and post-smolt is the name for juveniles during their first year in the ocean. The similarity in the return rates of salmon to different and wide spread rivers throughout the North Atlantic indicates that the highest mortality affecting Atlantic salmon populations occurs in the marine phase. The largest component of the natural mortality tends to occur during the first year at sea, with the result that the post-smolt period emerges as the critical stage for salmonids [*Pearcy*, 1992]. The temperature and productivity of the coastal waters that the salmon enter as they leave their rivers varies from year to year and may be critical in determining their ultimate survival rate. However, post-smolts rapidly migrate through coastal waters, and commence large-scale oceanic migrations. During their marine phase, salmon achieve upwards of 90% of their somatic growth and will reach sexual maturity before making their return migration to their native river [*Dickson and Turrell*, 2000]. Long-term patterns of stock abundance for regional and continental stock complexes, which are defined by post-smolt survival, are often associated with climate forcing [*Friedland*, 1998].

Reddin and Shearer [1987] demonstrated that the abundance of salmon off West Greenland was related to the area enclosed by 4ºC to 10ºC in the Northwest Atlantic. Quantitative thermal habitat concepts were further developed and applied to European salmon by *Friedland* [1998] who found that survival rates of one-seawinter and two-seawinter salmon in the North Sea were correlated with the area of 8º-10ºC water in May. The first study to link variability in the thermal habitat indices of Atlantic salmon to the NAO, was that by *Friedland et al*. [1993]. They found that during years of high NAO index, the 4ºC isotherm was

positioned to the south and east of its mean location in the area of the Labrador Sea, Davis Strait and Norwegian Sea and conversely in low index years it was located to the north and west. The thermal habitat index of Atlantic salmon was shown to covary with the NAO, with the thermal habitat index decreasing during the years of positive NAO index and expanding during negative index phases [*Friedland et al.*, 1993; *Dickson and Turrell,* 2000].

Dickson and Turrell [2000] suggest that salmon in European waters are linked to the NAO variability in many different ways, including at first entry to the sea, while leaving the European shelf and in distant oceanic waters. During the last few decades of the 1900s, the NAO index correlates with SST and winds in the coastal waters around the U.K., both key variables likely to determine the environment of fish leaving the European Shelf for middle and distant waters [*Dickson and Turrell*, 2000; *Ottersen et al.*, 2001]. *Dickson and Turrell* [2000] admit that although the factual basis for ascribing importance to any particular set of environmental properties as a control on salmon is scanty, there is strong circumstantial evidence that salmon variability is linked to the NAO.

5.5. Winter Flounder (*Pseudopleuronectes americanus*)

The positive phase of the winter NAO index leads to warmer and wetter winters along the U.S. east coast [*Hurrell*, 1995; *Shindell et al.*, 1999]. From 1960 to 1990, as the winter NAO index moved from persistent negative to persistent positive values, the winter temperatures increased in Narragansett Bay, Rhode Island by 3ºC. This in turn altered marine food webs [*Keller et al.*, 1999] and may have impacted negatively upon the winter flounder, the formerly dominant commercial fish [*Keller and Klien-MacPhee*, 2000]. Warmer winters result in smaller winter-spring phytoplankton blooms, an observation experimentally reproduced in marine mesocosms [*Keller et al,* 1999]. During the past 25 years winter flounder abundances in southern New England have been in decline. One hypothesis is that warmer sea water temperatures result in more of the winter marine phytoplankton bloom being consumed in the water column by pelagic food chains, with reduction in the amount of fixed carbon available to benthic (bottom dwelling) food chain members, such as flounder. In contrast to the winter flounder, Atlantic herring stocks, which feed in the upper water column, have been on the increase. Another hypothesis is that temperature increases affect predation and survival of winter flounder during critical early life stages [*Keller and Klein-MacPhee*, 2000].

There is still debate, however, about how much of the observed decline is due to warmer winters and how much may be attributed to heavy fishing pressure. The physiology and ecology of winter flounder provides some interesting clues. The winter flounder is a former dominant member of the bottom dwelling fish community in southern New England [*Cooper and Chapleau*, 1998]. Most adult fish migrate into inshore waters in the late fall and early winter, and spawn in late winter and early spring when seawater temperatures are quite cold [*Klein-MacPhee*, 1978]. To accomplish this feat, winter flounder make use of unique antifreeze proteins found in a number of polar fish which allow them to survive cold temperatures, even as low as -1.9ºC [*Wen and Laursen*, 1992]. Winter flounder spawning occurs at night in the upper portions of estuaries. Eggs are attached to the bottom. Hatching rate, larval development rate, and mortality rates due to predation are all temperature dependent. Variations in egg and larval survival during the first year determine the age-1 year-class strength. Observations suggest that a significant component of the decline in winter flounder abundance in southern New England is associated with a shift from a period with cold winters and sea water temperatures in Southern New England during the 1960s, into a period of relatively warmer winters during the following three decades. February sea temperatures from the three years prior to recruitment of age 1 winter flounder is associated with about 70% of the interannual variation in the abundance (year-class strength) of age-1 winter flounder in Niantic Bay. The series of warm winters such as experienced in southern New England during the 1990s is clearly unfavorable for winter flounder.

6. MARINE DISEASES

Climate variability and change is also associated with variations in the geographic range of marine diseases [*Harvell et al.*, 1999]. Off the eastern seaboard of the United States, a positive NAO index and the associated winter warming of coastal marine waters favor a northward extension of marine species typically found to the south. For example, in the past several decades, *Dermo* disease in oysters has progressively moved northward from off the mid-Atlantic states into New England [*Ford*, 1996; *Cook et al.,* 1998]. Also, at lower latitudes in the North Atlantic, there are disturbances in coral ecosystems, involving coral bleaching and a variety of coral diseases that are associated with NAO variations [*Barber et al.,* 2001; *Sherman*, 2001; *Sherman and Epstein*, 2001; *Hayes et al.,* 2002]. *Hayes et al.* [2002] and *Barber et al.* [2001] advanced the hypothesis that observed increases in aeolian dust transport into the western North Atlantic, associated with increased persistence of a positive phase of the winter NAO index, may "release" coral disease organisms from an iron–limited state.

7. WHALES

Present day right whales (*Balaena glacialis*) in the western North Atlantic rely almost exclusively on feeding grounds in the Gulf of Maine/western Scotian Shelf region [*Winn et al.*, 1986]. These are a small remnant of a much larger population that existed on both sides of the North Atlantic but that were drastically reduced through harvesting [*Reeves and Mitchell*, 1986; *Aguilar*, 1986]. The population growth rate of the right whales declined from the 1980s to the 1990s [*Caswell et al.*, 1999]. As reported by *O'Connell* [2001], Wood's Hole scientists Caswell and Fujiwara examined the effects of shipping, gillneting, the Southern Oscillation and the NAO on the survival rates of the right whales and found that the NAO index was the most important factor.

The Gulf of Maine/Western Scotian Shelf region presents right whales with a highly variable feeding environment. Physically, the region lies within a transient oceanographic transition zone, located between cold subpolar waters influenced by the Labrador Current to the northeast and warm temperate waters influenced by the Gulf Stream to the south (Loder et al., 2001; MERCINA, 2001). The transitions that occur within this zone are not only physical, as reflected in hydrographic changes, but also biological, as reflected in the changes in composition and relative abundance of plankton (see zooplankton section). The shifting nature of this transition zone makes the Gulf of Maine and Western Scotian Shelf regions especially vulnerable to climate-driven changes in North Atlantic circulation patterns.

Since *C. finmarchicus* is the principal source of nutrition for right whales in the region [*Kenney et al.*, 1986; *Wishner et al.*, 1995], it has been proposed that the response of right whale populations to climate variability may be mediated by trophic interactions with this prey species [*Kenney et al.*, 1986]. Although the mechanisms underlying the climate-driven changes in *C. finmarchicus* abundance are not fully resolved, they appear to be linked to the NAO through advective processes from the Slope Water [*Greene and Pershing*, 2000; *MERCINA*, 2001; see section 3].

Since consistent data were first collected in 1982, declines in right whale calving rates have generally tracked declines in *C. finmarchicus* abundance [*Greene et al.*, unpublished data]. From 1982 to 1992, calving rates were relatively stable with a mean total rate of 12.4 ± 0.9 (standard error) calves per year, consistent with the relatively high abundance of *C. finmarchicus*. From 1993 to 2001, calving rates exhibited two major declines, and the mean rate dropped to 11.2 calves per year and became more variable (± 2.7 calves per year). They followed large declines in *C. finmarchicus* abundance although their timing varied. During the first

event in the early 1990s, the lower calving rates occurred two years after *C. finmarchicus* abundances fell. During the second event in the late 1990s, calving rates exhibited a steep decline in the same year that abundances began to fall. Although these differences cannot presently be explained, some hypotheses based on right whale reproductive physiology and behavior may help reconcile the different responses.

Right whale reproductive physiology typically requires at least three years between births – one year for lactation, one year to amass fat stores to support the next pregnancy, and one year during the pregnancy [*Knowlton et al.*, 1994]. Hence, feeding conditions over several years are likely integrated when determining if a given female will reproduce or not. Since the first multi-year decline in calving rates occurred two years after a period of relatively stable reproduction and good feeding conditions, the time-lagged response may have required two years of poor feeding conditions before taking effect. When *C. finmarchicus* abundance increased in the mid-1990s, many females in the right whale population had not given birth recently and were available for reproduction. Hence, when good feeding conditions returned, calving rates nearly doubled during 1996 and 1997. This rapid increase in reproduction limited the number of females available for reproduction in the immediate years following and, in combination with the poor feeding conditions during the late 1990's, calving rates plummeted from 1998 to 2000. When *C. finmarchicus* abundance increased again in 2000, many females in the right whale population had not given birth recently and were available for reproduction. With the combination of many females available for reproduction and good feeding conditions, the annual calving rate reached an historical high in 2001.

8. SEABIRDS

Few published studies of the relationship between the NAO and seabirds exist. An exception is that by *Thompson and Ollason* [2001]. Using 50 years of data on the northern fulmar (*Fulmarus glacialis*) collected on Eynhallow in Scotland, they showed a statistically significant negative relationship between the proportion of breeding adult fulmars present at the colony each summer and the NAO index. In addition, the hatching success and the fledging success in the summer were both negatively related to the previous winter's NAO index. The variances accounted for by the NAO were between 10–20% ($p \leq 0.05$). The authors suggested that all three fulmar indices might be linked to the NAO through *C. finmarchicus* as the latter increase in the North Sea during a negative NAO index phase. More zooplankton was assumed to lead to an increase in the crustaceans and small fish eaten by fulmars.

The Seabird Ecology Working Group within ICES (Anonymous, 1998) had earlier examined the relationship between the NAO index and the seabird breeding numbers and success in the Northeastern Atlantic (United Kingdom and German Wadden Sea). From 1983 through 1996, there were no significant correlations between the NAO index and breeding population sizes or breeding success of seven species (guillemot (*Uria aalge*), razorbill (*Alca torda*), puffin (*Fratercula arctica*), fulmar, gannet (*Sula bassana*), shag (*Phalacrocorax aristotelis*) and kittiwake (*Rissa tridactyla*)) at several U.K. seabird colonies. In the Wadden Sea, no significant relationship was found between the NAO index and breeding numbers of cormorant (*Phalacrocorax* spec.), Arctic tern (*Sterna paradisaea*) or common tern (*Sterna hirundo*). However, there were significant correlations (p<0.02) between the NAO and the breeding number of several other species , including fulmars, herring gulls (*Larus argentatus*), lesser black-backed gulls (*Larus fuscus*), common gulls (*Larus canus*), black-headed gulls (*Larus ridibundus*), kittiwakes, sandwich terns (*Sterna sandvicensis*), guillemots and razorbills. These time series consisted of 44 years of data from the early 1950s to the early to mid-1990s for all species except the sandwich tern, where data were available from 1907 to 1996. The variance accounted for by the NAO ranged from 7 to 32%. These relationships may occur through the influence of the NAO on food resources; however, the feeding requirements and general feeding ecology of these species are so diverse that the authors thought this highly unlikely.

9. SUMMARY

Over the past decade, numerous investigations have established links between the NAO index and the biology of the North Atlantic. Our review has included studies of the changes in the biomass and species composition of phytoplankton and zooplankton, the biomass, distribution and growth of several commercial species of fish, the abundance of benthos, the spread of marine diseases, the survival rates of right whales and the hatching success of certain seabirds. These studies span the North Atlantic and include the deep ocean basins, the continental shelves and coastal embayments. This reflects the extent of the physical oceanographic responses to the NAO-associated forcing [*Visbeck et al.*, this volume] through which the links to the biology occur. The relationship to the NAO results in large-scale coherency between certain biological phenomena. However, different physical responses in different regions lead to differences in the biological responses. For example, during a high NAO index phase, the Barents Sea warms through increased heat exchange with the atmosphere and increased

Atlantic inflow. These result in higher abundances of *C. finmarchicus* and increased recruitment of cod [*Ottersen et al.*, 2001]. On the other side of the Atlantic, off Newfoundland, a high NAO index is associated with stronger northwesterly winds, cold conditions and generally poor recruitment of cod [*Mann and Drinkwater*, 1994]. Such relationships are not limited to fish but have also been shown to hold for zooplankton, with opposite trends in the abundance of *C. finmarchicus* on both sides of the Atlantic (see section 3).

Some of the studies presented in this review are of short duration or have significant long-term trends, which were not removed in the statistical analyses. This sometimes brings into question the statistical reliability of these studies. However, the sheer number of studies linking the NAO to biological variability in the North Atlantic, plus that they occur at different trophic levels, for different species, and different aspects (abundance, distribution, growth, speciation, etc.), is convincing evidence that the biology is definitely linked to the climate variability associated with the NAO. The majority of the studies have been carried out on fish, or the lower levels of the food chain, i.e. phytoplankton and zooplankton. This is due to the availability of long-term time series that are needed to establish such relationships with any statistical reliability. One of the reasons for the large quantity of the work on phytoplankton and zooplankton has been the CPR data. They confirm the importance of maintaining consistent, long-term monitoring programs.

While it is clear that biotic changes are linked to NAO variability, much work still remains in determining the precise mechanisms through which the linkages occur. Many hypotheses have been proposed. For zooplankton, the association with the NAO is often assumed to be mediated through phytoplankton and for higher trophic levels, through the zooplankton. The responsible mechanism ultimately must be linked to changes in the physical environment, however. These usually occur either from changes in advection by ocean currents or through regional atmospheric forcing.

Changes in the geographical distribution and abundance of plankton through advective processes have been well demonstrated [*Edwards et al.*, 1999; *Johns et al.*, 2001; *MERCINA*, 2001; *Ottersen and Stenseth*, 2001]. Advection can also lead to changes in the water properties, such as temperature, or vertical structure (i.e., depth of the mixed layer). For phytoplankton abundance, the NAO is typically assumed to be mediated through changes in meteorological forcing, such as temperature or wind mixing. The phytoplankton response to variability in these variables can be complex, however. For example, higher temperatures can raise phytoplankton production directly by increasing turnover rates but can suppress production through

increased stratification, if nutrients are limiting. On the other hand, stratification early in the production season can be beneficial by limiting the depth to which the phytoplankton cells are mixed. Wind affects are generally assumed to be through their affect on vertical mixing. The response to wind mixing varies, however, depending upon the ratio of the mixed layer depth to the critical depth in spring [*Dutkiewicz et al.*, 2001]. This results in increased primary production from deeper mixing in the subtropics but decreased production in the subpolar gyre. No one process is able to explain phytoplankton production linkages to the NAO throughout the North Atlantic. While studies in the Northeast Atlantic and North Sea presently suggest temperature to be the overriding factor [*Edwards et al.*, 2001], wind is suggested as the principal mechanism off Bermuda [*Bates*, 2001]. Even where temperature is thought to be the dominant factor, it is often unclear whether it is through increased turnover rates, temperature effects on stratification or some other process. Sorting out the precise mechanisms and relationships between the NAO and phytoplankton is extremely important, given that it is often assumed that the links between zooplankton and the NAO are through the phytoplankton.

Other hypotheses linking zooplankton to the NAO, besides through phytoplankton and advection, include direct temperature effects on development times of the zooplankton and the effects of wind on the contact rates between the zooplankton and their food through turbulent mixing. For fish and other higher trophic levels, the links of abundance levels to the NAO are often considered to occur through the association between the NAO and zooplankton production. Growth effects are generally felt to be through temperature, while distribution effects for phytoplankton, zooplankton and fish are usually hypothesized to occur through either advection or from hydrographic changes that favor certain species over others.

Given that the NAO is not directly responsible for the changes observed in the biological components of the ecosystem, but rather are usually driven by local physical changes associated with NAO variability, one may ask, why is the NAO index so useful in accounting for changes in the marine ecosystem? Why not use the local characteristics instead? First, in some cases long-term data of the necessary local physical variables are unavailable and thus the NAO index provides an excellent proxy. Second, the NAO has been found to account for as much, and in some cases more, of the variance of biological phenomena than local physical climate indices. This may be because the NAO is linked to changes in several physical characteristics of a particular ecosystem, including its hydrographic characteristics, mixed-layer depth, or circulation patterns. In such cases, the NAO captures more of the overall physical variability than any individual local climate index. In such cases it can be considered as an integrator of the local climate changes. Third, the NAO provides a conceptual framework and a broader understanding of the observed changes in the local physical environment.

While the NAO research has helped to advance the field of climate-induced impacts on the marine ecosystems of the North Atlantic Ocean, future strides will require not only expanding the list of NAO-associated linkages but also going beyond the correlations and establishing the precise mechanisms through which the NAO acts. Critical to achieving these objectives are the continuance of the present long-term data sets such as the CPR surveys and the establishment of new time series, such as for benthos. The challenge is to continue improving our understanding of the links of climate with the marine ecosystem to allow us to predict what might happen under future climate change scenarios.

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