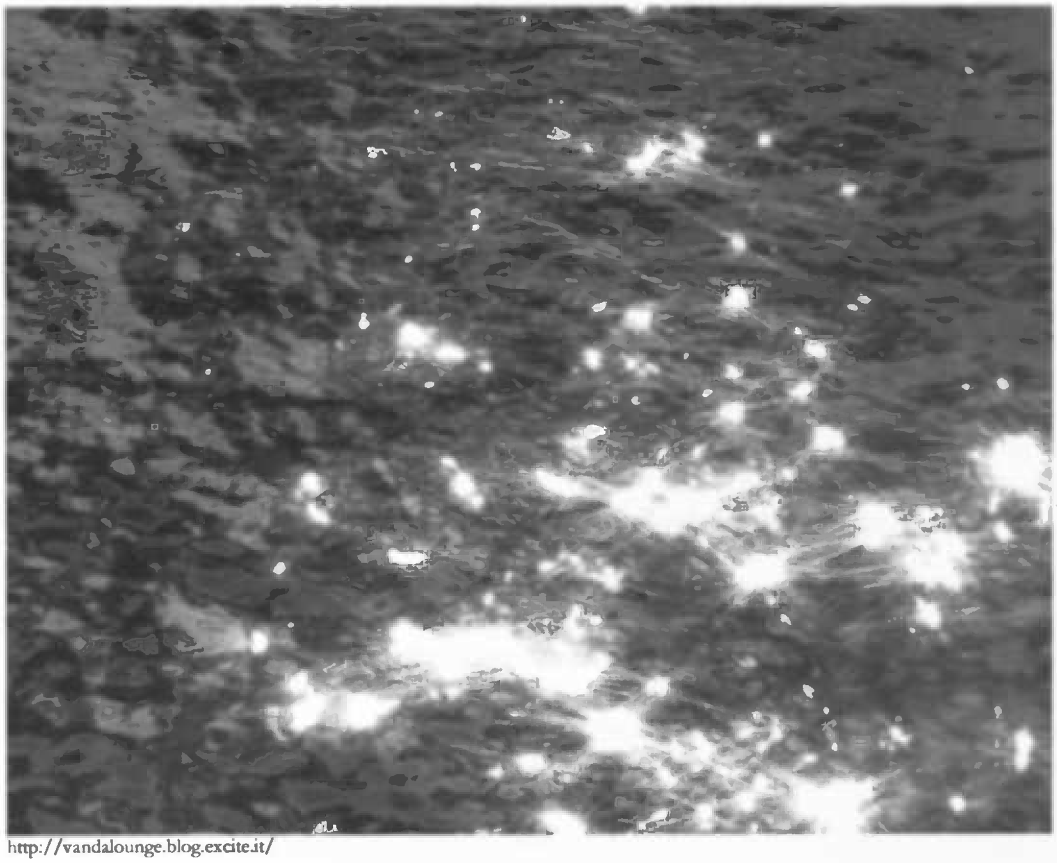
# North Atlantic climate variability: consequences for pelagic ecosystems



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## Abstract

When considering policies and management plans for the conservation of endangered marine animals there is often a focus on anthropogenic activities that may be harmful for their safety and therefore increase the mortality rate. As a consequence environmental factors such as variability in climate that affect birth rates are overlooked, yet climate variability has considerable effects on the conservation prospects of endangered animals. The changes in zooplankton composition (the abundance of the copepod *Calanus finmarchicus* decreases) on the feeding grounds of the right whale (*Eubalaena glacialis*) following years with a negative NAO (North Atlantic Oscillation) Index have detrimental effects on the calving rates of this mammal. There is a tight coupling between the NAO Index and the coupled slope water system (CSWS) affecting the Regional Slope Water Temperature in the Northwest Atlantic. This in turn has a tight coupling with the abundance of *C. finmarchicus*, probably caused by the changes in advective transport. Because of the reproductive physiology of right whales, years with drops in abundance of prey result in years with almost no births. When prey returns the opposite happens: birth peaks. The past decade there has been a predominantly low abundance of *C. finmarchicus*, resulting in bad conditions for calving. When *C. finmarchicus* returned many female right whales were ready to become pregnant, because of the preceding years without pregnancy. Knowing the results of certain climate conditions and the stage female whales are in, it might become possible to predict calving rates with reasonable certainty. Periods with very high or very low calving rates can be explained using this knowledge.

Also commercial fish stocks are influenced by climate variability through the changes in plankton composition. The example of cod in the North Sea shows the importance of water temperature. During the relatively warm past decade cod larvae were not able to grow up because of low prey abundances. In 1996 the recruitment was higher because of lower temperatures, but the following years low recruitments returned. The 1996 year-class lacks the ability to become mature, as most cod are fished before their fourth year. During the past decade the amount of cod diminished because of a combination of low recruitment and fisheries that kept on their high fishing pressure. As the environmental conditions are thought to remain, the only way to give the North Sea cod population a chance for recovery is by prohibiting cod fisheries for indefinite time.

The examples used in this report show the importance of long-term monitoring of the marine environment. Even though nothing seems to happen at first sight, over longer periods fluctuations, changes, and shifts can become visible, which could be useful in explaining unexpected events, like rapid diminishing or fast growth of populations. Using this knowledge can result in more suitable management measures and conservation policies, because of having the ability to utilize the obtained knowledge directly as a certain event occurs or tends to occur.

# Contents

## Introduction

Nowadays, many marine animals and even ecosystems are endangered as a result of anthropogenic activities. There has been over-fishing, over-hunting, and different kinds of unintentional threats. One of these threats is climate change, which is thought to be caused mainly by burning of fossil fuels (IPCC, 2001). The change or variability in climate, or global change, results in melting polar ice, rising sea levels, and changes in sea current patterns, water temperatures and other physical characteristics. Subsequently, abundances and distribution of phytoplankton and zooplankton species in basins and estuaries are changing, resulting in harsh situations for organisms at higher trophic levels (i.e. marine mammals and fish). The conservation of endangered species and ecosystems can best be achieved when there is adequate knowledge of the ecological and environmental requirements necessary for sustained population growth. However, there is a tendency to focus on direct anthropogenic factors affecting mortality rates when looking for conservation efforts, especially when dealing with populations of endangered species that were commercially harvested, while factors affecting birth and growth rates are frequently overlooked. Since sustained population growth is determined by the age-weighted balance between birth and mortality rates, it is important that both will be considered when the recovery prospects of a certain endangered mammal are to be assessed (Boyce, 1992).

Here, the case of the North Atlantic right whale (*Eubalaena glacialis*; Figure 1) will be reviewed, with focussed attention on the influence of the North Atlantic Oscillation on the population dynamics. The North Atlantic right whale is a critically endangered species, due to extensive whaling in the past. Right whales are rich in oil and baleen, slow swimming, and have a tendency to float after being harpooned. These traits led early whalers to give them their common name, as they were clearly the "right" whales to hunt. Prior to commercial exploitation, right whales were distributed widely throughout the subtropical to subpolar regions of the Atlantic Ocean (Best *et al.*, 2001). The North Atlantic right whales occurred in both the western and eastern sectors of the North Atlantic Basin. Intense harvesting pressure first drove the eastern population to near extinction and subsequently reduced the western population to a small fraction of its former size (Reeves and Mitchell, 1986). In 1935 right whales were among the first cetaceans to receive international protection (Best *et al.*, 2001). Commercial harvesting reduced whale abundance as well as it impacted the distribution of right whales.
Whalers took whales of Newfoundland and Labrador in the 16th and 17th centuries and the population has never reoccupied these former feeding grounds. The remnant population of today relies almost exclusively on feeding grounds in the Gulf of Maine/Western Scotian Shelf (GOM/WSS) region (Winn *et al.*, 1986). Nowadays, only 300 individuals are left in the western North Atlantic (Caswell *et al.*, 1999). In the 1980's growth rate was gradually increasing and shifted during the 1990's to gradually declining (Caswell *et al.*, 1999; Fujiwara and Caswell, 2001). If mortality and growth rate remain comparable to those observed in the 1990's the species will become extinct within 200 years (Fujiwara & Caswell, 2001). It is suggested that prevention of one or two female deaths per year would be sufficient to support the slow recovery of the species. It is thought that climate variability is an important factor in the rate of recovery of the North Atlantic right whale population, but it is also important to interpret the demographic projections of right whale populations in the context of climate-driven oceanographic variability (Fujiwara and Caswell, 2001).

In this report attention will be focussed on climate variability on the northern hemisphere and its influence on plankton composition in the Atlantic Ocean. Subsequently attention is focussed on how much the right whale population status is influenced by climate variability and subsequent changes in plankton abundance and what nature conservationists and policy makers can do with this information. Finally attention is focussed on the influence of climate variability and subsequent plankton composition changes on commercial fish stocks. Detrimental changes in these fish stocks could affect valuable nutrition sources for human consumption as well as the economy: "global change" may well become a problem that should be considered seriously in the future.

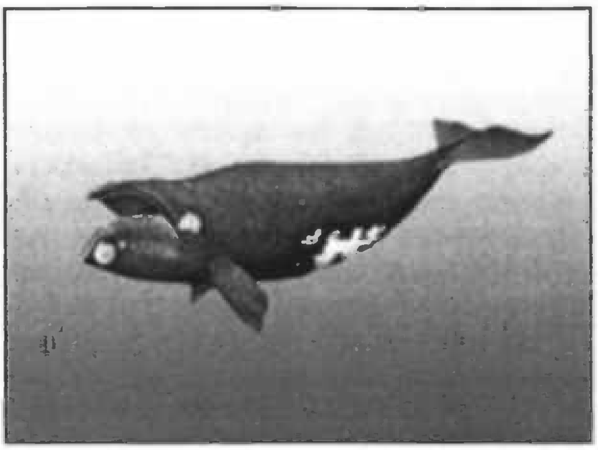

*Figure 1*: Drawing of a right whale (*Eubalaena glacialis*). Only 300 individuals are left in the western North Atlantic (http://www.terrambiente.org/fauna/Mammiferi/cetacea/balaenidae).

# 1 Climate variability

The climate on the northern hemisphere is mainly regulated by the North Atlantic Oscillation (NAO). The NAO is characterized by an oscillation of atmospheric mass (pressure) between the Arctic (Iceland) and the subtropical Atlantic (Azores). When the NAO is in its "positive" phase, the wintertime gradient over the North Atlantic is large because the Icelandic low-pressure centre and the high-pressure centre at the Azores are both enhanced. Both centres are weakened during its "negative" phase (Figure 2). Changes in pressure gradient from one phase to another, produces changes in wind speed and direction over the North Atlantic, thereby altering the heat and freshwater exchange at the ocean surface. Subsequently, changes in the NAO have wide range effects on marine ecosystems, including phytoplankton and zooplankton production, and distribution of populations of fish, shellfish and marine mammals. A substantial part of the increasing surface temperatures over the past 40 years or so are believed to be caused by the remarkable upward trend of the NAO. The NAO dictates climate variability from the eastern seaboard of the United States to Siberia and from the Arctic to the subtropical Atlantic, especially during winter. Scientists remain puzzled about which climate processes govern the NAO variability, how the phenomenon has varied in the past or will vary in the future, and whether it is predictable (Hurrell *et al.*, 2001). A small but useful percentage of atmospheric changes might be predictable. Predictability could arise from the influence of slow changes in the ocean or from external factors. There are patterns in Atlantic sea surface temperatures (SSTs) that precede specific phases of the NAO by up to 6 months, therefore it is thought that the ocean may have an appreciable influence on the atmosphere (Hurrell *et al.*, 2001). Hoerling *et al.* (2001) suggest the predominantly positive NAO to be forced by warming of the tropical (Indian and Pacific) oceans during the past half-century.

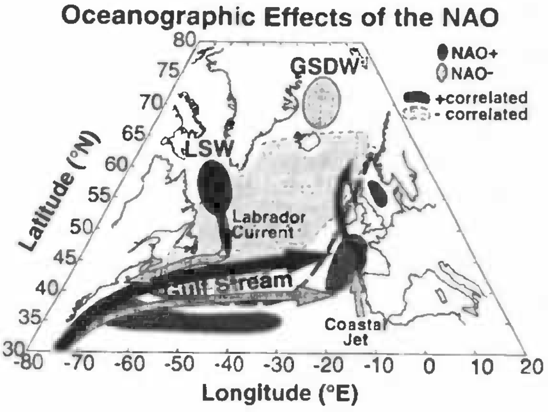

*Figure 2*: Oceanographic changes in the North Atlantic associated with the NAO. During positive phases, Labrador Sea Water (LSW) production increases, the coastal jet on the European shelf intensifies, and the Gulf Stream is shifted to the north. During negative phases Greenland Sea Deep Water production increases, the Labrador Current increases and the Gulf Stream shifts to the south. Sea surface temperatures south and east are positively correlated (dark area) and north and east are negatively correlated (light area) (Pershing, 2001).

phases of the NAO; a relatively cool, fresh, and thick layer of Labrador Sea Water (LSW) is formed, while volume transport in the Labrador Current diminishes (Dickson *et al.*, 1996; Dickson, 1997). When the NAO reverses to negative, convection becomes shallower and weaker in the Labrador Sea; the LSW layer becomes warmer, saltier and thinner, and volume transport in the shallow Labrador Current increases (Dickson *et al.*, 1996; Dickson, 1997).

The Gulf of Maine/Western Scotian Shelf (GOM/WSS) region in the north-western area of the Atlantic Ocean, south of the Labrador Sea, is an important feeding ground of North Atlantic right whales and appears to be influenced by the NAO as stated above. The GOM/WSS region is located between cold sub-polar waters influenced by fluctuations in the Labrador Current to the northeast and warm temperate waters influenced by fluctuations in the Gulf Stream to the south. The transitions that occur are not only physical but also biological, as reflected by changes in the composition and relative abundance of plankton (Greene and Pershing, 2000; MERCINA, 2001). Physical responses are often mediated by the NW Atlantic's coupled slope water system (CSWS). The CSWS has two characteristic modes (Figure 3). The minimum mode corresponds with an intensified Labrador Current, and the frontal boundary of relatively cool, fresh Labrador Sub-arctic Slope Water (LSSW) advances further downstream than usual (all the way to Boston), displacing warmer, saltier Atlantic Temperate Slope Water (ATSW) offshore. The maximum mode corresponds to a state of reduced transport of the Labrador Current and the frontal boundary retreats upstream, allowing ATSW to move onshore towards the shelf. Recently it has been shown that the shifts in CSWS are often associated with phase changes in the NAO. From the early 1970's to the present, the NAO index has been predominantly positive (Hurrell *et al.*, 2001, 2003), and CSWS has exhibited conditions characteristic of its maximum modal state (MERCINA, 2001). Five times (1977, 1979, 1985, 1987, 1996) during these 30 years the NAO Index dropped to negative for a single year. In each case the CSWS responded to a drop of the NAO Index by shifting toward its minimal modal state after a one- to two-year time lag (1978, 1981, 1987, 1989, 1998). The response to the drop of 1996 was the most dramatic and the best documented modal shift to date. During this modal shift (1998) the Labrador Current intensified, with LSSW advancing along the shelf break, and penetrating to the southwest as far as the Middle Atlantic Bight. By early winter 1998, LSSW had replaced the deep waters of Emerald Basin on the WSS and began entering the GOM through Northeast Channel. By early autumn 1998, the hydrographical properties of the GOM deep basins reflected the advective replacement and mixing that had occurred between the invading LSSW and the resident deep waters which derive largely from ATSW. The observed hydrographical changes were short-lived. Similar to the NOA Index becoming positive again the CSWS shifted back to its maximum modal state for the remainder of the 1990's (Green *et al.* 2003a).

Similar water temperature shifts did occur in the California Current along the western coast of the United States, according to the interdisciplinary ecosystem research of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) (Ohman and Venrick, 2003). CalCOFI is presently a consortium of three partners: the Southwest Fisheries Science Center of the National Marine Fisheries Service (NMFS)/National Oceanic and Atmospheric Administration, the California Department of Fish and Game (CDF&G), and Scripps Institution of Oceanography/University of California, San Diego (Scripps/UCSD). Thanks to long-term monitoring that began in the 1950's (from the 1920's to the 1950's it was mainly focussed on research for sardine fisheries), climate shifts influencing the marine ecosystems were recognized in 1976-77 and 1999. These shifts can be distinguished when looking at springtime temperature stratification in the California Current and the Pacific Decadal Oscillation (PDO) Index. From 1950 to 1976-77 PDO was predominantly negative, then there was a shift to predominantly positive values until 1999. After the shift of 1999 the PDO Index was negative again (Ohman and Venrick, 2003).

From 1958 to 2002 Richardson and Schoeman (2004) observed a slight cooling of 0.1°C in some northern areas, but a substantial warming of 0.5°C in the southern regions. Ocean temperatures are likely to be further affected by anthropogenic climate change: the IPCC predicts a rise in temperature of between 2° and 4°C in the northeast Atlantic by 2100, with greater increase in the north than in the south. It seems inevitable that fish, seabirds, and marine mammals will need to adapt to a changing spatial distribution of primary and secondary production within pelagic marine ecosystems.

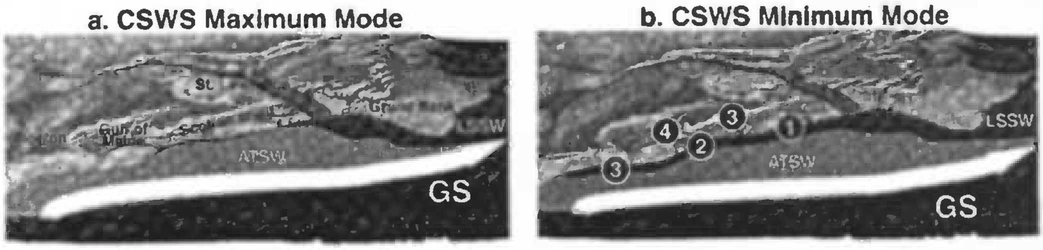

*Figure 3*: The two modes of the coupled slope water system (CSWS): maximum (a) and minimum (b). Circled numbers indicate 1997-1998 advance of Labrador Subarctic Slope Water (LSSW) frontal boundary along the continental margin pushing away Atlantic Temperate Slope Water (ATSW): (1) September 1997; (2) January 1998; (3) February 1998; (4) August 1998 (Green *et al.* 2003b).

## 2 Influence of climate variability on zooplankton abundance

The changes in climate and ocean circulation patterns associated with the NAO provide a context for interpreting population responses of plankton species in the North Atlantic Ocean. There is evidence of climate-mediated (warming of the Northern Hemisphere and NAO) shifts among some groups of marine plankton like calanoid copepods (such as *Calanus finmarchicus*) (Beaugrand *et al.*, 2002). In the north-eastern North Atlantic and European seas there have been biogeographical shifts for all species assemblages since the early 1980's. The number of southern and pseudo-oceanic temperate species has increased by 10° of latitude. In contrast, the diversity of colder-temperate, sub-arctic and arctic species has decreased in the north. All the biological associations show consistent long-term changes, which may reflect a movement of marine ecosystems toward a warmer dynamical equilibrium (Beaugrand *et al.*, 2002). Sub-arctic and arctic species are negatively correlated with Northern Hemisphere temperature (NHT) anomalies and the NAO Index in the North Sea and the European shelf edge north of Ireland. The opposite occurs in the north-western North Atlantic, where the number of arctic species is positively correlated with NHT and NAO Index in the south Labrador Sea (Beaugrand *et al.*, 2002).

The climate-driven changes in ocean circulation observed over the past 40 years also have a considerable impact on the plankton ecology in the GOM region, according to the Continuous Plankton Recorder (CPR) data collected since the late 1950's. The abundance of *Calanus finmarchicus*, a copepod species that dominates the spring and summertime zooplankton biomass in the GOM, which is the main food source of North Atlantic right whales, is tightly coupled to the modal status of the CSWS (Greene *et al.*, 2003a). Trans-Atlantic responses of *C. finmarchicus* shelf populations to the NAO are thought to be driven primarily by changes in advective transport processes (Greene and Pershing, 2000; MERCINA, 2001). A cross-correlation between *C. finmarchicus* abundance in the GOM and the NAO Index reveals a weak positive correlation from 1961 to 1989, with evidence for a time lag of approximately 4 years (Figure 4a,b,c). However, this correlation breaks down and becomes non-significant when data from the 1990's are included (Greene *et al.*, 2003b). During the 1960's, when NAO index was predominantly negative and the CSWS was in its minimum modal state, slope water temperatures and *C. finmarchicus* abundance were relatively low. This was an unusual period in the past 50 years (MERCINA, 2001). During the 1980's, when the NAO index was predominantly positive and the CSWS was predominantly in its maximum modal state, slope water temperatures and *C. finmarchicus* abundance were relatively high. During each of the maximum- to minimum-modal shifts in the CSWS after 1980, *C. finmarchicus* abundance declined in the subsequent years. The modal shift during 1981-1983 preceded a large, single-year decline in abundance during 1983. The modal shift during 1988-1991 preceded a large decline in abundance that persisted throughout the early 1990's. The, after the abundance building up again during the mid-1990's, the NAO Index underwent its largest drop of the century in 1996. This event triggered the intense modal shift of the CSWS during 1997, which led to very low abundances of *C. finmarchicus* during 1997 and early 1998 (Greene *et al.*, 2003a). Although the CSWS typically undergoes modal shifts in response to large changes in the NAO Index, the time lag of the response and the intensity of the phase change necessary to elicit a response (i.e. threshold effect) appear to be variable (Greene *et al.*, 2003b). The mechanisms underlying these climate-driven changes in *C. finmarchicus* abundance have not been fully resolved, but they appear to be linked to the advective supply of this species into the GOM/WSS region from the slope waters Greene and Pershing, 2000; MERCINA, 2001). Head *et al.* (1999) have shown that slope-water incursions can be an important source of *C. finmarchicus* recruiting to the WSS. Since the major inflows into the GOM from the WSS also occur during spring (Smith *et al.*, 2001), the timing is right for these incursions of slope water to affect the advective supply *of C. finmarchicus* into the GOM (Greene *et al.*, 2003b).

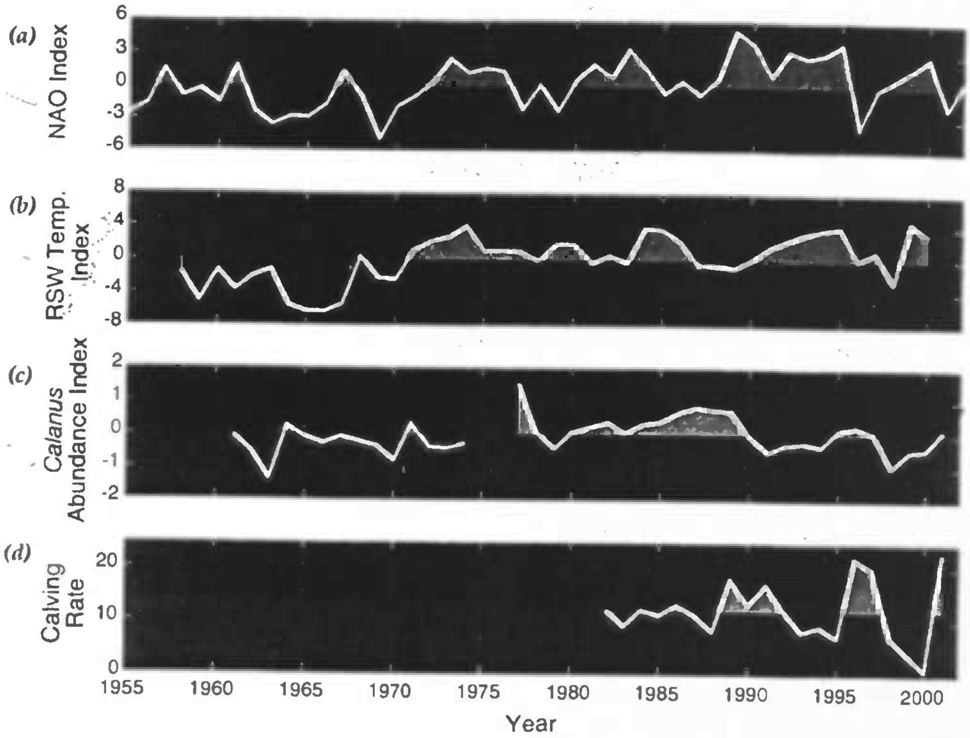

*Figure 4*: Time series from the North Atlantic. a) Annual values of the winter NAO Index. b) Annual values of the Regional Slope Water Temperature Index. c) Annual values of the *Calanus finmarchicus* Abundance Index. d) Annual values of right whale calving rate. The winter NAO Index is the mean atmospheric pressure difference between the North Atlantic's subtropical high-pressure system and the subpolar low-pressure system. The RSW Temp. Index is an indicator of the modal state of the CSWS, with positive (negative) values corresponding to maximum (minimum) modal state conditions. The *Calanus finmarchicus* Abundance Index is the mean abundance anomaly for this species. Right whale calving rate is the number of individually identified females accompanied by calves observed during a year beginning in December of the preceding calendar year. There is a time lag of approximately 4 years between changes in NAO Index and *Calanus finmarchicus* Abundance Index and about 1 year between *Calanus finmarchicus* Abundance Index and Calving Rate (Greene *et al.*, 2003a).

In contrast with the GOM population, the *C. finmarchicus* population in the North Sea region (Irish Sea, shelf waters north and west of Scotland and Ireland) has had a negative trend since the early 1970's (Greene *et al.*, 2003b). This is based on Continuous Plankton Recorder (CPR) data collected since the late 1940's. A cross-correlation analysis between the abundance of *C. finmarchicus* in the North Sea and the NAO Index reveals a strong negative correlation, with little evidence for a time lag exceeding 1 year (Greene *et al.*, 2003b). The negative response of *C. finmarchicus* in the North Sea has been attributed to several physical mechanisms associated with the NAO, each operating on a different time scale. The first of these mechanisms involves year-to-year fluctuations of advective transport into the North Sea. Years with a positive NAO Index are characterised by an increased inflow of relatively warm upper-layer water from the North Atlantic into the North Sea (Reid *et al.*, 2001a). This increased inflow of warmer North Atlantic water is thought to bring in fewer recruits of *C. finmarchicus* from the oceanic habitat, where they diapause during autumn and winter, into the North Sea (Hirche, 1996). It also provides a less favourable environment for growth and reproduction of this cold-water species (Fromentin and Planque, 1996). In contrast, during negative NAO years there is an increased inflow of relatively cool deep water from the Norwegian Sea into the North Sea (Reid *et al.*, 2001a), bringing an increased number of recruits and providing them with cooler and more favourable conditions for growth and reproduction (Fromentin and Planque, 1996). Also long-term changes in ocean circulation associated with NAO are thought to be linkable with *C. finmarchicus* abundance patterns, like regional deep-water circulation (Greene *et al.*, 2003b). Heath *et al.* (1999) proposed that during the predominantly positive NAO conditions of the past quarter century (Hurrell *et al.*, 2001), the production and transport of Norwegian Sea Deep Water has steadily declined, leading to a reduced flux of this water mass across the Iceland-Scotland Ridge through the Faeroe-Shetland Channel (Hansen *et al.*, 2001). These changes are thought to reduce the supply of late copepodites available for recruitment into the North Sea, further contributing to the decline in the abundance of *C. finmarchicus* (Greene *et al.*, 2003b). Another proposed mechanism is that of intensification of the slope current, which transports warm water into the vicinity of the British Isles and the North Sea (Reid *et al.*, 2001b). Reid *et al.* (2001a) think that several years of highly positive NAO conditions during the late 1980's and early 1990's lead to an intensified flow of the shelf edge jet. This jet advects both warm water and warm-water species into the region, which is unfavourable for *C. finmarchicus* (Reid *et al.*, 2001a,b). These longer-term mechanisms together with the annual mechanisms complicate the predictability of year-to-year circumstances. Due to the longer-term mechanisms shown above, consequences of a shift in the NAO Index may not be as predictable as it may seem at first sight (Greene *et al.*, 2003b).

Richardson and Schoeman (2004) have shown that there is tight coupling between the plankton trophic levels in marine pelagic ecosystems over large time and space scales in the eastern North Atlantic. The overall response of phytoplankton and zooplankton communities, which is likely to depend on the form and strength of the linkages between successive trophic levels, is not known. We have to understand these to know how resilient such food webs are to global-scale impacts, such as climate change. Without this knowledge it will be difficult to manage marine sources sustainably (Richardson and Schoeman, 2004). To predict the response of the base of the marine food web to climate change, understanding of the type and degree of coupling between trophic levels in marine systems is necessary. Complex biological systems are generally controlled by their top predators through top-down control, by their producers through bottom-up control, or by a number of key species in the middle through wasp-waist control (Cury *et al.*, 2000). For the plankton ecosystem in the marine pelagic realm, there is currently conflicting evidence on when these types of control operate, and on what scales (Richardson and Schoeman, 2004). In their research on plankton ecosystems in the Northeast Atlantic Richarson and Schoeman (2004) found mainly positive linkages between copepod herbivores and their phytoplankton prey, although most of the correlations were not significant individually. However, a meta-analysis indicated that the overall relation between the abundances of herbivorous copepods and phytoplankton is positive and highly significant. These positive correlations are unlikely to be a consequence of both trophic levels responding directly to sea surface temperature (SST), because there was no significant relation between copepod herbivores and SST. The relationship therefore is likely to be the result from bottom-up control of herbivorous copepods by their phytoplankton prey, although production/biomass ratios between predators and their prey might also be important in this link (Richardson and Schoeman, 2004). To assess whether the signal goes as far as secondary consumers, the relationship between zooplankton carnivores and herbivorous copepods was also investigated. All correlations were strongly positive and all but one were individually significant. These findings suggest a possible mechanism underlying previously observed relationships between fish ecology and climate (Richardson and Schoeman, 2004).

Also in the Pacific Ocean there are indications for plankton ecosystem changes induced by climate variability. In the California Current zooplankton abundances coincidentally changed with the shifts of the PDO Index. The springtime biomass of the euphausid *Nyctiphanes simplex* was predominantly below average during negative PDO periods and predominantly above average during the positive PDO period. These species appear to be linked tightly to the PDO. The doliolid species *Doliolum denticulatum* did not have such a tight linking to the PDO and stayed near its average abundance, but when the PDO was positive during 1977-1999 the species had several outbursts in abundance around 1980 and three times in the 1990's (Ohman and Venrick, 2003).

## 3 Influence of variability in prey abundance on right whale population

*Calanus finmarchicus* is recognized as the most important nutrition source for right whales in the GOM/WSS region (Kenney *et al.*, 2001). Therefore Greene *et al.* (2003a) hypothesized that right whale population responses to climate variability are brung about primarily by trophic interactions with this prey species. To check their hypothesis right whale calving rate patterns since the early 1980s were examined. Considerable multi-year declines in right whale calving rates followed after considerable multi-year declines in *C. finmarchicus* abundance (Figure 4c,d). From 1982 to 1992, calving rates exhibited no multi-year declines and were relatively stable. These findings correspond with the relatively high abundance of *C. finmarchicus* during the 1980s. From 1993 to 2001, calving rates exhibited two major, multi-year declines. These findings correspond with the two preceding drops in *C. finmarchicus* abundance during the early and late 1990s. Although both major declines in right whale calving rates were associated with drops in *C. finmarchicus* abundance, the timing of the responses varied. During the first event, calving rates dropped steeply two years after *C. finmarchicus* abundance had begun to fall. During the second event calving rates dropped steeply the same year that *C. finmarchicus* abundance began to fall. The right whale reproductive physiology supports these different responses. Female right whales require at least three years between births: one year for lactation, one year to amass fat reserves to support the next pregnancy and one year during the pregnancy (Knowlton *et al.*, 1994). Feeding conditions over several years have to be integrated when determining whether a given female will reproduce or not. Since the first decline in calving rate 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 mid-1990s, many females in the right whale population had not given birth recently and were available for reproduction. When good feeding conditions returned, calving rates nearly doubled during 1996 and 1997. This high number of reproduction reduced the number of females available for reproduction. When this is combined with the poor feeding conditions during the late 1990s, this leads to calving rates going down during 1998 to 2000. When *C. finmarchicus* abundance increased again in 2000, many right whale females had not given birth recently and therefore were available for reproduction (Greene *et al.*, 2003a).

# 4 Projections on right whale conservation

In discussing the projected decline of the North Atlantic right whale population, Fujiwara and Caswell (2001) demonstrate that it is driven primarily by the recent trend towards a higher female mortality rate. Collisions with ships and entanglement in fishing gear are considered to be the most important causes (Knowlton and Kraus, 2001). Fujiwara and Caswell (2001) suggest that if mortality rates would be reduced by a few female deaths per year, then this improvement would be sufficient to support a slow recovery of the population. If the increasing female mortality rate can be attributed largely to anthropogenic activities, conservation policies become clearer. It is tempting, therefore, to take the results of Fujiwara and Caswell (2001) and suggest that conservation policies leading to a modest reduction in female mortality rates would be sufficient to ensure the population's gradual recovery. This suggestion is argued by Greene and Pershing (2004); the population may be more vulnerable and facing a far more uncertain future than the projections of Fujiwara and Caswell (2001) would suggest. The major source of uncertainty is the limited demographic data set upon which these population projections were based. The data analyzed by Fujiwara and Caswell (2001) were collected during the period, from 1980 to 1995, the North Atlantic right whale population not only experienced increasing female mortality rates, but also during an unusual climate regime in the North Atlantic with a predominantly positive NAO Index (Hurrell *et al.*, 2001, 2003). Paradoxically, during this period environmental conditions were generally favourable for nutrition and reproduction (Greene *et al.*, 2003a). During a positive NAO Index the right whale feeding grounds in the GOM/WSS region typically exhibited warmer ocean temperatures, higher standing stocks of phytoplankton, and higher abundances of *Calanus finmarchicus* (Greene and Pershing, 2000, 2003a,b). Given the interdecadal-scale climate variability of the NAO and its dramatic effects on the marine environment of right whales, population projections many decades into the future must be interpreted with a considerable degree of caution (Greene and Pershing, 2004).

The Intergovernmental Panel on Climate Change (IPCC) has concluded that it is highly likely that anthropogenic forcing, due to increasing greenhouse gas concentrations, will lead to an increase in global mean temperature, although the regional effects are far more difficult to predict (IPCC, 2001). The NAO Index has been predominantly positive during the past quarter century, and a number of investigators have suggested that this may be associated with greenhouse forcing (Hurrell *et al.*, 2003). Given the generally favourable conditions for right whale nutrition and reproduction associated with positive phases of the NAO, one might see this as the best-case scenario for right whale conservation biology. Under such a scenario, Fujiwara and Caswell's (2001) population projections should provide a solid foundation for setting appropriate right whale conservation goals (Greene and Pershing, 2004). The IPCC however, has concluded that it is likely that continually rising greenhouse gas concentrations will lead to an increase in climate variability (IPCC, 2001). During the late 1990's, North Atlantic climate exhibited some unusual behaviours, including a north-eastward shift in the sub-polar low-pressure center towards the Greenland Sea (Ulbrich and Christoph, 1999). Several investigators have suggested that rising greenhouse gas concentrations may have been responsible for this unusual behaviour (Hurrell *et al.*, 2001, 2003). In this context, one must ask whether the extreme drop of the NAO Index in 1996 was an unusual event or an omen of the larger swings that we might expect in the future, due to rising greenhouse gas concentrations. The flip-side of the NAO, when a large phase reversal occurs from a positive to a negative NAO Index (Greene *et al.*, 2003a), appears to have had a highly detrimental effect on calving rates of right whales in the late 1990's. The strongly negative NAO conditions observed in winter 2003 may have similar effects in the coming years. It is important that the effects of increased climate variability on right whale calving rates be incorporated into future demographic modelling studies as they have major effects on the sustainability of the right whale population (Greene and Pershing, 2004).

What if North Atlantic climate were to enter a long period of negative NAO conditions? While there is no evidence yet of such an event to happen in the near future, paleoclimatic records indicate that such conditions have occurred in the past (Cook, 2003). Some investigators have suggested that we might expect a return to such conditions in the not-too-distant future (Wood *et al.*, 1999; Hillaire-Marcel *et al.*, 2001). If right whale calving rates were depressed to low levels for a considerable period of time, then the projected time to extinction would occur much sooner than Fujiwara and Caswell (2001) have predicted. Under such a climate scenario, even a large decline in the female mortality rate associated with anthropogenic activities might not be sufficient to help these animals recovering (Green and Pershing, 2004).

## 5 Projections on fish stocks

Climate variability also results in shifts in abundance and distribution of fish stocks that are commercially interesting. The North Sea cod stock is under pressure because of over-fishing, but also by a decline in the production of young cod that has paralleled warming of the North Sea over the past ten years as O'Brien *et al.* (2000) have shown. Over the last decade the annual number of one-year-old cod in the population has been at or below the long-term average. The recruitment of cod in the North Atlantic appears to be related to sea temperature for stocks located at the latitudinal limits of the species distribution (Planque and Frédou, 1999). Cod in the North Sea are near the southern boundary of their range and strong-year classes have been associated with lower-than-average temperatures during the first half of the year (O'Brien *et al.*, 2000). Weak year-classes have also occurred, but only when the spawning-stock biomass was low. A change in temperature patterns might prevent the stock from being able to produce high recruitments as in the 1960's and 1970's, even if the spawning-stock biomass were to rebuild to the abundances of that period. The survival of cod larvae is determined by the abundance of its zooplankton prey, thus determining long-term changes in cod recruitment (Beaugrand *et al.* 2003). Since 1988, mean sea temperatures during the first half of the year in the North Sea have been higher than during the previous three decades. During this period annual recruitment levels have been low, with exception of 1996, when cold conditions prevailed. Since 1997, warmer conditions have returned to the North Sea and the 1997 and 1998 year-classes have coincidentally been the poorest ever monitored. The findings of Richardson and Schoeman (2004) suggest a possible mechanism underlying the deminished cod recruitment. The bottom-up control that was found between trophic levels in plankton suggests that there is a linkage between water temperature, plankton abundance and cod recruitment (Richardson and Schoeman, 2004). Cod in the North Sea has been a valuable fishery. Over the past 40 years it yielded an average of 200.000 tonnes per year. Nowadays, the catch mainly contains immature fish younger than three years old. Few individuals survive to reach sexual maturity. Both the stock and fishery are dependant upon years of strong recruitment. The only way to reduce the risk of collapse is by reducing fishing pressure as sea temperature is not manageable. The combination of a diminished stock and disadvantaging warm conditions is endangering the long-term sustainability of cod in the North Sea (O'Brien *et al.*, 2000). In 1999 the International Council for the Exploration of the Sea (ICES) advised a reduction of 40-60% in cod catches. Last years ICES even recommended a prohibition on cod fisheries in the North Sea.

There are also examples from other regions that are influenced by climate variability. In the 1990's the northern cod stock of southern Labrador and northeast Newfoundland collapsed and fishing was stopped. Although over-fishing is believed to be the main cause, severe climate conditions also contributed. Almost half of the decline in stock biomass in the 1980's and 1990's was due to changes in the mean weight of fish. This was due to reduced growth rates, largely caused by cold temperatures that also affect cod recruitment (Drinkwater, 2002). A decade later there is little evidence of recovery, even with the moratorium still in place. In the north-east Atlantic management was succesful for the recovery of other fish species at the same trophic level as cod: the niche of cod seems to be taken by haddock, herring, mackerel, and others. Over-fishing is certainly decimating many stocks, but the influences of climatic forces are also clear (Barange *et al.*, 2003).

During the 1970's a large shift occurred in a community in the northeast Pacific, having dramatic results for fishery yields. A community that was dominated by invertebrate shrimps, changed into one dominated by cod and other ground fishes. The cause for these changes is unknown, but they were coincident with a large climate shift (Anderson and Piatt, 1999).

In 1992 Pacific sardines appeared in catches off British Columbia for the first time in 45 years. By 1995 an experimental fishery was initiated and by 1997 the stock size off the west coast of Vancouver Island was about 60,000 tonnes. Equally, the current abundance of Pacific halibut in this area is considered to be highest in history (McFarlane *et al.*, 2000).

## Discussion

The associations between the variability in climate, especially the NAO, and plankton composition and abundance appear to be clear. There is very tight coupling between the NAO Index (and modal state of the CSWS) and *Calanus finmarchicus* abundance in the Gulf of Maine/Western Scotian Shelf region. During the 1990's the *C. finmarchicus* Abundance Index was predominantly negative following the RSW Temperature Index with a time-lag of about four years (Greene *et al.*, 2003a). As *C. finmarchicus* is their most important food source, the right whale population responded to these detrimental feeding conditions with years containing hardly any births. When the *C. finmarchicus* Abundance Index was positive again for one year (1996) following a period of a positive RSW Temperature Index, the right whale population responded with a peak of births as most females had not given birth for more years in a row (Greene *et al.*, 2003a). Climate variability evidently has an influence on the whole food chain in the northwestern Atlantic up to the right whales.

Fujiwara and Caswell (2001) suggested that the decline of North Atlantic right whales could be stopped by reducing a few female deaths, caused by collisions with ships or entanglements in fishing gear, per year. But probably the low birth rates caused by detrimental prey abundances are also attributing to this decline. If the increasing female mortality rate can be attributed largely to anthropogenic activities, conservation policies become clearer. It is tempting, therefore, to assume the results of Fujiwara and Caswell (2001) and suggest that conservation policies leading to a modest reduction in female mortality rates would be sufficient to ensure the population's gradual recovery. This suggestion is questioned by Greene and Pershing (2004): the population may be more vulnerable and facing a far more uncertain future than the projections of Fujiwara and Caswell (2001) would suggest. Their major source of uncertainty is the limited demographic data set upon which these population projections were based. The data analyzed by Fujiwara and Caswell (2001) were collected during the period, from 1980 to 1995, that North Atlantic right whale population not only experienced increasing female mortality rates, but also during an unusual climate regime in the North Atlantic with a predominantly positive NAO Index (Hurrell *et al.*, 2001, 2003). In contrast, during this period environmental conditions were generally favourable for nutrition and reproduction (Greene *et al.*, 2003a). During a positive NAO Index the right whale feeding grounds in the GOM/WSS region typically exhibited warmer ocean temperatures, higher standing stocks of phytoplankton, and higher abundances of *C. finmarchicus* (Greene and Pershing, 2000, 2003). It is therefore thinkable that Fujiwara and Caswell (2001) overestimated the chances of recovery for right whales. When the climate variability is not taken into account, it is easy to underestimate or overestimate the future prospects of the population. It is possible that in the near future there will be a period of predominantly negative NAO conditions, being very detrimental for the right whale reproduction. In such a period the number of right whales could diminish very rapidly. As long as long-term monitoring programs are kept up measures can be taken beforehand when such harsh periods are ahead.

Not only plankton composition in the western North Atlantic is influenced by climate variability, also plankton composition in the eastern part, notably the North Sea region, is correlated with climate shifts. The North Sea population of *C. finmarchicus* is correlated strongly negative with the NAO Index (Greene *et al.*, 2003b). This negative response is attributed to several physical mechanisms associated with the NAO: changes in advective transport bringing fewer recruits of *C. finmarchicus* from the oceanic habitat into the

North Sea. The inflow of warmer North Atlantic water provides a less favourable environment for growth and reproduction (Fromentin and Planque, 1996). Heath *et al.* (1999) proposed that during positive NAO conditions, the production and transport of Norwegian Sea Deep Water declines, leading to a reduced flux of this water across the Iceland-Scotland Ridge through the Faeroe-Shetland Channel, reducing the supply of late copepodites available for recruitment into te North Sea. The intensification of the shelf edge jet strengthens the advectation of both warm water and warm-water species into the region, being disadvantageous for C. finmarchicus (Reid *et al.*, 2001a,b). These events together amplify the negative effect of positive NAO conditions on *C. finmarchicus* abundance in the North Sea. The interaction between long-term and short-term mechanisms makes it harder to make predictions and results of shifts in the NAO Index may not be as predictable as it may seem (Greene *et al.*, 2003b). The unfamiliarity with the linkages between trophic levels of plankton (Richardson and Schoeman, 2004) may make predictions even more uncertain. To predict the response of the base of the marine food web to climate change, there is more knowledge needed on the coupling between trophic levels in marine systems. There is conflicting evidence on which type of control (top-down, bottom-up, or wasp-waist) is operational at which moment and on what scale. But research on the relationship between trophic levels of plankton in the eastern North Atlantic suggests that there is bottom-up control (Richardson and Schoeman, 2004). This supports the idea of positive NAO conditions being detrimental for cod recruitment.

There are clear indications that the North Sea cod stock is under pressure because of higher temperatures over the last decade (O'Brien *et al.* 2000). Recruitments are lower because of deminished prey abundances during positive NAO conditions (Beaugrand *et al.* 2003; Richardson and Schoeman, 2004). Low frequency climate variability forcing requires changes in harvesting policies to accommodate changes in production levels, to avoid over-fishing during periods of lower productivity. This is a principle not widely accepted and even less widely implemented. Synchronicity between fisheries managers and the fish environment is paramount for management to succeed (Barange *et al.* 2003). The only way to let the North Sea cod population recover is by prohibiting cod fisheries for several years. Furthermore it is recommendable to keep up the monitoring, so the recovery can be followed and policies can be better adapted to environmental changes.

The importance of long-term monitoring is evident in all cases shown in this report. Thanks to long-term monitoring changes and forces can be recognized while it is also possible to make reasonable predictions for future developments. There is a great danger of misunderstanding variations in ecosystems in the absence of long-term observations. When years are looked at seperately it could give a misleading picture of a dynamic ecosystem. Policy decisions and management guidelines would fail because they did not take the underlying long-term variability in account (Ohman and Venrick, 2003). Because changes in community structure reflect the adjustment of pelagic ecosystems to modifications in the water masses and currents, it is clearly important to continue to monitor plankton associations, which provide valuable means of checking the well-being of marine ecosystems in the North Atlantic Ocean (Beaugrand *et al.*, 2002). The findings of Richardson and Schoeman (2004) suggest that any effects of a temperature rise of 2° to 4°C as the IPCC predicts, will have a large impact on phytoplankton, copepod herbivores, and zooplankton carnivores. The direct consequences of these changes for fisheries are not clear, but it seems inevitable that fish, seabirds and marine mammals will need to adapt to a changing spatial disribution of primary and secondary production (Richardson and Schoeman, 2004).

## References

Anderson, P.J. & J.F. Piatt (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189: 117-123 *(in Barange et al., 2003)*

Barange, M., F. Werner, I. Perry & M. Fogarty (2003) The tangled web: global fishing, global climate, and fish stock fluctuations. *Global Change NewsLetter* No. 56: 24-27

Beaugrand, G., P.C. Reid, F. Ibañez, J.A. Lindley & M. Edwards (2002) Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. *Science* 296: 1692-1694

Beaugrand, G., K.M. Brander, J.A. Lindley, S. Souissi & P.C. Reid (2003) Plankton effect on cod recruitment in the North Sea. *Nature* 426: 661-664

Best, P.B., J.L. Bannister, R.L. Brownell & G.P. Donovan (editors) (2001) *Right whales: worldwide status.* J. Cetacean Management. Spec. Issue 2 *(in Greene and Pershing, 2004)*

Boyce, M.S. (1992) Population viability analysis. *Annual Review of Ecology and Systematics* 23: 481-506 *(in Greene and Pershing, 2004)*

Caswell, H.., M. Fujiwara & S. Brault (1999) Declining survival probability threatens the North Atlantic right whale. *Proceedings of the National Academy of Science USA* 96: 3308-3313

Cury, P., A. Bakun, R.J.M. Crawford, A. Jarre-Teichmann, R.A. Quiñones, L.J. Shannon, H.M. Verheye (2000) Small pelagics in upwelling systems: Patterns of interaction and structural changes in 'wasp-waist' ecosystems. *Academic Press, ICES Journal of Marine Science, Symposium Edition* 57(3): 603-618 *(in Richardson and Schoeman, 2004)*

Dickson, R. (1997) From the Labrador Sea to global change. *Nature* 386: 649-650

Dickson, R., J. Lazier, J. Meincke, P. Rhines & J. Swift (1996) Long-term coordinated changes in the convective activity of the North Atlantic. *Progress in Oceanography* 38: 241-295

Drinkwater, K.F. (2002) A review of the role of climatic variability in the decline of northern cod. *American Fisheries Society Symposium* 32: 113-130 *(in Barange et al., 2003)*

Fromentin, J.M. & B. Planque (1996) Calanus and 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 *(in Greene et al., 2003b)*

Fujiwara, M. & H. Caswell (2001) Demography of the endangered North Atlantic right whale. *Nature* 414: 537-541

Greene, C.H. & A.J. Pershing (2000) The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: Basin-scale forcing associated with the North Atlantic Oscillation (NAO). *International Council for the Exploration of the Sea Journal of Marine Science* 57: 1536-1544

Greene, C.H. & A.J. Pershing (2003) The flip-side of the North Atlantic Oscillation and modal shifts in slope-water circulation patterns. *Limnol. Oceanogr.* 48: 319-322

Greene, C.H. & A.J. Pershing (2004) Climate and the Conservation Biology of North Atlantic Right Whales: Being a Right Whale at the Wrong Time? *Frontiers in Ecology and the Environment,* 2

Greene, C.H., A.J. Pershing, R.D. Kenney & J.W. Jossi (2003a) Impact of Climate Variability on the Recovery of Endangered North Atlantic Right Whales. *Oceanography* 16 (No. 4): 98-103

Greene, C.H., A.J. Pershing, A. Conversi, B. Planque, C. Hannah, D. Sameoto, E. Head, P.C. Smith, P.C. Reid, J. Jossi, D. Mountain, M.C. Benfield, P.H. Wiebe & E. Durbin (2003b) Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. Progress in *Oceanography* 58: 301-312

Hansen, B., W.R. Turrell & S. Osterhus (2001) Decreasing overflow from the Nordic seas into the Atlantic Ocean through the Faeroe Bank Channel since 1950. *Nature* 411: 927-930

Head, E.J.H., L.R. Harris & B. Petrie (1999) Distribution of *Calanus* spp. on and around the Nova Scotia Shelf in April – evidence for offshore source of *Calanus finmarchicus* to the mid- and western regions. *Canadian Journal of Fisheries and Aquatic Science* 56: 2463-2476 *(in Greene and Pershing, 2000)*

Heath, M.R., J.O. Backhaus, K. Richardson, E. McKenzie, D. Slagstad, A. Gallego, H. Madden, J. Mardaljevic, D. Hainbucher, A. Schacht, S. Jónasdóttir, D. Beare, J. Dunn & S. Hay (1999) Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus. Fisheries Oceanography* 8: 163-176 *(in Greene and Pershing, 2000)*

Hillaire-Marcel, C., A. de Vernal, G. Bilodeau & A.J. Weaver (2001) Absence of deep-water formation in the Labrador Sea during the last interglacial period. *Nature* 410: 1073-1077

Hirche, H.J. (1996) Diapause in the marine copepod, *Calanus finmarchicus* – a review. *Ophelia* 44: 129-143 *(in Greene et al., 2003b)*

Hoerling, P.H., J.W. Hurrell & T. Xu (2001) Tropical Origins for Recent North Atlantic Climate Change. *Science* 292: 90-92

Hurrell, J.W. (1995) Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. *Science* 269: 676-679

Hurrell, J.W., Y. Kushnir & M. Visbeck (2001) The North Atlantic Oscillation. *Science* 291: 603-605

Hurrell, J.W., Y. Kushnir, G. Ottersen & M. Visbeck (2003) An overview of the North Atlantic Oscillation. *The North Atlantic Oscillation: Climatic Significance and Environmental Impact.* American Geophysical Union, Washington, D.C., p. 1-35

IPCC (2001) *Climate change 2000: The Science of Climate Change, the Contribution of Working Group 1 to the Second Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK *(in Greene and Pershing, 2004)*

Kenney, R.D., C.A. Mayo & H.E. Winn (2001) Migration and foraging strategies at varying spatial scales in western North Alantic right whales: a review of hypotheses. *Journal of Cetacean Resource Management*, Special Issue 2: 251-260 *(in Greene and Pershing, 2004)*

Knowlton, A.R., S.D. Kraus & R.D. Kenney (1994) Reproduction in North Atlantic right whales (*Eubalaena glacialis*). *Canadian Journal of Zoology* 72: 1297-1305 (*in Greene et al., 2003a)*

Knowlton, A. & S. Kraus (2001) Mortality and serious injury of northern right whales (*Eubalaena glacialis*) in the western North Atlantic Ocean. *Journal of Cetacean Resource Management*, Special Issue 2: 193-207 *(in Greene and Pershing, 2004)*

McFarlane, G.A., J.R. King & R.J. Beamish (2000) Have there been recent changes in climate? Ask the fish. *Progress in Oceanography* 47: 147-169 *(in Barange et al., 2003)*

MERCINA (2001) Oceanographic responses to climate in the Northwest Atlantic. *Oceanography* 14: 76-82 *(in Greene and Pershing, 2004)*

O'Brien, C.M., C.J. Fox, B. Planque & J. Casey (2000) Climate variability and North Sea cod. *Nature* 404: 142

Ohman, M.D. & E.L. Venrick (2003) CalCOFI in a Changing Ocean. *Oceanography* 16 (No. 3): 76-85

Pershing, A.J. (2001) *The Climate Variability Response Hierarchy: A General Approach for Understanding the Ecology of Climate.* Response of Large Marine Ecosystems to Climate Variability: Patterns, Processes, Concepts, and Methods, thesis Cornell University, p. 1-26

Planque, B. & T. Frédou (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2069-2077 *(in O'Brien et al., 2000)*

Reeves, R.R. & E. Mitchell (1986) The Long Island, New York, right whale fishery: 1650-1924. *Reports of the International Whaling Commission*, Special Issue 10: 201-220 *(in Greene et al., 2003a)*

Reid, P.C., M.D. Borges & E. Svendsen (2001a) A regime shift in the North Sea circa 1988 linked to changes in the North Sea fishery. *Fisheries Research* 50: 163-171 *(in Greene et al., 2003b)*

Reid, P.C., N.P. Holliday & T.J. Smith (2001b) Pulses in the eastern margin current and warmer water off the north west European Shelf linked to North Sea ecosystem changes. *Marine Ecology Progress Series* 215: 283-287 *(in Greene et al., 2003b)*

Richardson, A.J. & D.S. Schoeman (2004) Climate Impact on Plankton Ecosystems in the Northeast Atlantic. *Science* 305: 1609-1612

Smith, P.C., R.W. Houghton, R.G. Fairbanks & D.G. Mountain (2001) Interannual variability of boundary fluxes and water mass properties in the Gulf of Maine and Georges Bank: 1993-1997. *Deep-Sea Research I* 48: 37-70 *(in Greene et al., 2003b)*

Ulbrich, U. & M. Christoph (1999) A shift in the NAO and increasing storm track activity over Europe due to anthropogenic greenhouse gas forcing. *Climate Dynamics* 15: 551-559 *(in Greene and Pershing, 2004)*

Winn, H.E., C.A. Price & P.W. Sorensen (1986) The distributional biology of the right whale (Eubalaena glacialis) in the western North Atlantic. *Reports of the International Whaling Commission*, Special Issue 10: 129-138 *(in Greene and Pershing, 2004)*

Wood, R.A., A.B. Keen, J.F.B. Mitchell & J.M. Gregory (1999) Changing spatial structure of the thermohaline circulation in response to atmospheric $CO_2$ forcing in a climate model. *Nature* 399: 572-575