Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation

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Abstract

Populations of the copepod species *Calanus finmarchicus* often dominate the springtime biomass and secondary production of shelf ecosystems throughout the North Atlantic Ocean. Recently, it has been hypothesised that interannual to interdecadal fluctuations observed in such populations are driven primarily by climate-associated changes in ocean circulation. Here, we compare evidence from the North Sea and Gulf of Maine/Western Scotian Shelf (GoM/WSS) linking fluctuations in *C. finmarchicus* abundance to changes in ocean circulation associated with the North Atlantic Oscillation (NAO). A particularly striking contrast emerges from this Trans-Atlantic comparison: whereas the North Sea *C. finmarchicus* population exhibits a negative correlation with the NAO index, the GoM/WSS population exhibits a more complex, positive association with the index. The physical processes underlying these contrasting population responses are discussed in the context of regional- to basin-scale circulation changes associated with the NAO.

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Keywords: *Calanus finmarchicus*; Climate variability; Gulf of Maine; North Atlantic Oscillation; North Sea

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1. Introduction

*Calanus finmarchicus* dominates the zooplankton biomass found throughout the cold temperate and subpolar oceanic waters of the North Atlantic Ocean (Raymont, 1983; van der Spoel & Heyman, 1983; Mauchline, 1998). Although considered an oceanic species, *C. finmarchicus* frequently achieves high levels of abundance in many North Atlantic shelf ecosystems. For example, although not self-sustaining, expatriate populations of *C. finmarchicus* dominate the springtime biomass and secondary production in the shelf ecosystems of the North Sea, the Northeast Atlantic, and Gulf of Maine/Western Scotian Shelf (GOM/WSS) region of the Northwest Atlantic. Since these expatriate shelf populations must be replenished every year or every few years by advection from some oceanic source (Longhurst, 1998), it has been hypothesised that their interannual to interdecadal fluctuations in abundance are driven primarily by climate-associated changes in ocean circulation (Greene & Pershing, 2000). Such fluctuations in the abundance of *C. finmarchicus* have been documented in the North Sea and attributed to changes in ocean circulation patterns associated with the North Atlantic Oscillation (NAO) (Reid, Planque, & Edwards, 1998; Stephens, Jordan, Taylor, & Proctor, 1998; Heath, Backhaus, Richardson, McKenzie, Slagstad, Gallego et al., 1999). More recently, fluctuations in abundance observed in the GOM/WSS region also have been linked to NAO-associated changes in ocean circulation (Greene and Pershing, 2000; Conversi, Piontkovski and Hameed, 2001; MERCINA, 2001). Here, we compare these trans-Atlantic responses of *C. finmarchicus* to basin-scale NAO forcing and document how regional- to basin-scale changes in ocean circulation account for the striking differences observed in the population ecology of this species in shelf ecosystems on both sides of the North Atlantic.

2. Trans-Atlantic patterns in *C. finmarchicus* abundance and the NAO

The North Sea population of *C. finmarchicus* has exhibited a general decline in abundance since the early 1970s (Fig. 1a). This negative trend has been observed in the Irish Sea and shelf waters north and west of Scotland and Ireland as well (Fromentin & Planque, 1996; Planque & Taylor, 1998). In contrast, the GoM population of *C. finmarchicus* increased from relatively low levels of abundance during the 1960s to very high levels of abundance during the 1980s (Fig. 1b) (Jossi & Goulet, 1993; Greene & Pershing, 2000). This positive trend halted abruptly in 1990. From 1991 to 1994, the abundance levels of *C. finmarchicus* in the GoM were an order of magnitude lower than those observed during the 1980s and comparable to levels observed during the 1960s. A brief increase in the population occurred during the mid-1990s, but
Fig. 1. Time series of *C. finmarchicus* abundance from (a) the North Sea and (b) the Gulf of Maine/Scotian Shelf region. Time series are based on Continuous Plankton Recorder (CPR) data collected for *C. finmarchicus* from the North Sea since the late 1940s and from the Gulf of Maine/Scotian Shelf region since the late 1950s. Data from the Gulf of Maine are indicated by circles and from the Scotian Shelf by triangles. Methods of sample collection and processing have been described by Hardy (1939); Colebrook (1975), and Jossi and Goulet (1993). (c) Time series of the NAO index from 1955 to 1999. The NAO index is the mean difference, expressed as an anomaly from the long-term mean, in atmospheric pressure during winter between the subtropical high pressure system of the North Atlantic, measured in Lisbon, Portugal, and the subpolar low pressure system, measured in Stykkisholmur, Iceland (Hurrell, 1995). (d) Cross-correlation analyses between *C. finmarchicus* abundance and the NAO index. Results of the analyses of data from the North Sea are indicated by rectangles and from the Gulf of Maine during 1961–1989 and 1961–1999, respectively by triangles and circles. (e) Regression between *C. finmarchicus* abundance in the North Sea and the NAO index with no time lag. (f) Regression between *C. finmarchicus* abundance in the Gulf of Maine and the NAO index with a time lag of 4 years, 1961–1989 (dashed) and 1961–1999 (continuous).

this was followed by another decline to extremely low levels in 1998. The abundance levels of *C. finmarchicus* on the WSS largely mirrored those observed in the GoM for the periods of 1961–1975 and 1991–1994 (Fig. 1b); however, the brief resurgence of the GoM population during the mid-1990s was not observed on the WSS (Sameoto, 2001). Unfortunately, a gap in the time series from the WSS does not allow comparisons during the critical decade of the 1980s, when the *C. finmarchicus* population in the GoM exhibited its highest abundance.

Relationships between *C. finmarchicus* abundance trends in these ecosystems and the NAO can be examined by comparing the above time series with a time series of the NAO index (Fig. 1c). 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 (Fig. 1d and e). In contrast, a similar cross-correlation analysis 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 (Fig. 1d and f). However, this correlation breaks down and becomes non-significant when data from the 1990s are included (Fig. 1d and f). To reconcile these contrasting population responses, it is necessary to examine how basin-scale changes in climate and ocean circulation associated with different phases of the NAO manifest themselves in physical and biological processes at the regional scale.

3. Basin- and regional-scale changes in climate, ocean circulation, and the NAO

The phase of the NAO has important effects on climate throughout the North Atlantic. During positive phases, the planetary westerly winds intensify, and the North Atlantic storm track shifts to the north. These changes lead to milder conditions in the western Atlantic and east coast of the United States; colder, stormier conditions in the northwest Atlantic and Greenland; and milder conditions in the northeast Atlantic and coasts of northern Europe and Great Britain (Hurrell, 1995; Dickson, Lazier, Meincke, Rhines, & Swift, 1996). In contrast, during negative phases of the NAO, the westerly winds diminish in intensity and the storm track shifts to the south. These changes lead to colder, stormier conditions in the western Atlantic and east coast of the United States; milder conditions in the northwest Atlantic and Greenland; and colder, drier conditions in the northeast Atlantic and coasts of northern Europe and Great Britain (Hurrell, 1995; Dickson, Lazier, Meincke, Rhines & Swift, 1996).

The phase of the NAO also has important effects on the formation and spreading of deep water, as well as the near-surface circulation patterns of the North Atlantic. In the subpolar northwest Atlantic, during positive phases, convection is deeper and more intense in the Labrador Sea; a relatively cool, fresh, and thick layer of Labrador Sea Water is formed and volume transport in the Deep Western Boundary Current increases, while volume transport in the shallow baroclinic component of the Labrador Current decreases (Fig. 2a) (Dickson, Lazier, Meincke, Rhines & Swift, 1996; Dickson, 1997; Curry, McCartney, & Joyce, 1998; Loder, Shore, Hannah, & Petrie, 2001). In the subpolar northeast Atlantic, convection during positive phases of the NAO is shallower and weaker in the Greenland Sea; the deep-water layers are warmer, saltier, and thinner; and the formation and volume transports of Greenland Sea Deep Water and Norwegian

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Fig. 2. Ocean circulation responses to (a) positive and (b) negative phases of the NAO. Areas with increased deep convection and water mass formation are darkly shaded; those with decreased deep convection and water-mass formation are lightly shaded. Water masses and currents are labeled as follows: GSDW, Greenland Sea Deep Water; LC, Labrador Current; LSW, Labrador Sea Water.
Sea Deep Water decrease (Fig. 2a) (Dickson, Lazier, Meincke, Rhines & Swift, 1996; Dickson, 1997). When the phase of the NAO reverses to negative, these patterns of convection and deep-water formation in the Labrador and Greenland Seas also reverse (Fig. 2b). Hence, convection becomes shallower and weaker in the Labrador Sea, the Labrador Sea Water layer becomes warmer, saltier and thinner, and volume transport in the Deep Western Boundary Current decreases while volume transport in the near-surface baroclinic component of the Labrador Current increases (Dickson, Lazier, Meincke, Rhines & Swift, 1996; Dickson, 1997; Curry, McCartney & Joyce, 1998; Loder, Shore, Hannah & Petrie, 2001). Synchronous with the above events in the Labrador Sea, convection becomes deeper and more intense in the Greenland Sea; the deep-water layers are cooler, fresher, and thicker; and the formation and volume transports of Greenland Sea Deep Water and Norwegian Sea Deep Water increase (Dickson, Lazier, Meincke, Rhines & Swift, 1996; Dickson, 1997). The deep, intense convection observed in the Greenland Sea during negative phases of the NAO is mirrored by shallow, intense ventilation in the western Sargasso Sea and increased formation and spreading of 18° Mode Water (Dickson, Lazier, Meincke, Rhines & Swift, 1996).

Interactions between the major western boundary currents of the subpolar and subtropical gyres have also been linked to the NAO (Rossby & Benway, 2000; Loder, Shore, Hannah & Petrie, 2001). Associated with these NAO-linked gyral interactions are changes in the Coupled Slope Water System (CSWS) of the Northwest Atlantic (Pickart, McKee, Torres and Harrington, 1999; MERCINA, 2001). During positive phases of the NAO, the CSWS tends to operate in its maximum modal state, with relatively warm and salty Atlantic Temperate Slope Water (ATSW) taking a position adjacent to the shelf break and forming a front near the mouth of the Gulf of St. Lawrence with Labrador Subarctic Slope Water (LSSW) (Fig. 3a) (MERCINA, 2001). This advance of ATSW coincides with a decrease in shallow Labrador Current transport around the Tail of the Grand Banks and an enhanced hydrographic signature of Labrador Sea Water in the Deep Western Boundary Current (Pickart, McKee, Torres & Harrington, 1999). When the phase of the NAO reverses to negative, the CSWS typically shifts to its minimum modal state (Fig. 3b). This mode is characterised by relatively cool and fresh LSSW advancing along the shelf break as far to the southwest as the Middle Atlantic Bight (MERCINA, 2001). This advance of LSSW along the shelf break displaces the warmer, saltier ATSW further offshore and coincides with an increase in shallow Labrador Current transport around the Tail of the Grand Banks and a reduced hydrographic signature of Labrador Sea Water in the Deep Western Boundary Current (Pickart, McKee, Torres & Harrington, 1999).
4. Population responses of *C. finmarchicus* to changes in ocean circulation

4.1. The North Sea

The changes in climate and ocean circulation patterns associated with the NAO provide a context for interpreting the contrasting population responses of *C. finmarchicus* on the two sides of the North Atlantic. The response of this species in the North Sea has been attributed to several physical mechanisms associated with the NAO, each operating on a different time scale (Fig. 4). The first of these mechanisms involves year-to-year fluctuations of advective transport into the North Sea. Positive NAO years are characterised by an increased inflow of relatively warm upper-layer water from the North Atlantic into the North Sea (Fig. 4) (Reid, Borges, & Svendsen, 2001a). This increased inflow of warmer North Atlantic water is hypothesised to supply the North Sea with fewer recruits of *C. finmarchicus* from the oceanic habitat where they diapause during autumn and winter (Hirche, 1996). It also provides a less favourable environment for growth and reproduction of this cold-water species (Fromentin & Planque, 1996). In contrast, negative NAO years are characterised by an increased inflow of relatively cool deep water from the Norwegian Sea into the North Sea (Fig. 4) (Reid, Borges & Svendsen, 2001a). This increased inflow of cooler water is hypothesised to supply the North Sea with an increased number of recruits from the oceanic diapause habitat and provide the population with cooler, more favourable conditions for growth and reproduction. Both of these advection-based hypotheses provide reasonable explanations for the strong negative correlation between the abundance of *C. finmarchicus* in the North Sea and the NAO index (Fig. 1d and e) (Planque & Reid, 1998), as well as the general decline in abundance of the species observed there since the early 1970s (Fig. 1a) (Fromentin & Planque, 1996; Planque & Taylor, 1998; Reid, Planque & Edwards, 1998).

Additional mechanisms have been proposed that link abundance patterns of *C. finmarchicus* in the North Sea to longer-term changes in ocean circulation associated with the NAO. One of these mechanisms involves changes in regional deep-water circulation. Heath et al. (1999) hypothesised that the main source of late copepodites in diapause that recruits to the North Sea shelf in spring occurs at depths greater than

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![Image](https://example.com/image.png)

**Fig. 4.** NAO-associated changes in ocean circulation patterns thought to affect *C. finmarchicus* abundance in the North Sea. The first mechanism involves year-to-year fluctuations in advective transport into the North Sea. Positive NAO years are characterised by an inflow of relatively warm water from the North Atlantic into the North Sea. Negative NAO years show an inflow of relatively cool water from the Norwegian Sea. A second mechanism involves changes in deep-water circulation. During negative NAO conditions, the production and transport of Norwegian Sea Deep Water (NSDW) increases, leading to an increased flux of this water mass across the Iceland-Scotland Ridge through the Faroe-Shetland Channel (FSC). The third mechanism involves an intensification of a jet at the shelf edge, which transports warm water into the vicinity of the British Isles and North Sea.
600 m in the Faroe-Shetland Channel. During the predominantly positive NAO conditions of the past quarter century (Hurrell, Kushnir, & Visbeck, 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 Faroe-Shetland Channel (Fig. 4) (Hansen, Turrell, & Osterhus, 2001). These changes in deep-water circulation have been hypothesised to reduce the supply of late copepodes available for recruitment into the North Sea, further augmenting the decline in the abundance of *C. finmarchicus* observed there in recent years.

Another proposed mechanism involves the intensification of the slope current, which transports warm water into the vicinity of the British Isles and the North Sea (Fig. 4) (Reid, Holliday, & Smyth, 2001b). Reid, Borges and Svendsen (2001a) hypothesised that several years of highly positive NAO conditions during the late 1980s and early 1990s were necessary to intensify the flow of this shelf edge jet. Since the jet advects both warm water and warm-water species into the region, it has resulted in a regime shift that is unfavourable to *C. finmarchicus* (Reid et al., 2001a,b). As in the previous case, this mechanism would further augment the recent declining trend in the abundance of *C. finmarchicus* observed in the North Sea.

Although each of the mechanisms described above would tend to reinforce the declining trend in *C. finmarchicus* abundance in the North Sea, the longer-term mechanisms may interact with the annual one to complicate year-to-year predictability. For example, Planque and Reid (1998) found that their predictions of the abundance of *C. finmarchicus* in the North Sea, based on a regression with the NAO index, proved accurate through most of the CPR time series until the mid-1990s. A pronounced drop in the NAO index during the winter of 1996 led them to predict a year of high *C. finmarchicus* abundance after a steady decline through the early part of the decade. This predicted increase did not occur, and one explanation may be that a single-year drop in the NAO index, even as in this case the largest drop of the century, may not be sufficient to overcome the effects of changing circulation patterns that were years in the making.

### 4.2. The Gulf of Maine/Western Scotian Shelf region

The more complex, positive association between *C. finmarchicus* in the GoM/WSS region and the NAO index has also been attributed primarily to advective–supply mechanisms (Greene and Pershing, 2000; MERCINA, 2001). These mechanisms, suggested after recent observations emerged from the Global Ocean Ecosystem Dynamics (GLOBEC) Northwest Atlantic/Georges Bank Field Programme, link fluctuations in *C. finmarchicus* abundance to NAO-triggered modal shifts in the northwest Atlantic’s CSWS. In the section that follows, we will first describe the events observed during the years of the GLOBEC Field Programme, then place these observations in the context of relevant time-series data collected over the past half century.

The drop of the century in the NAO index during the winter of 1996 led to a modal shift in the CSWS, an intensification of the shallow baroclinic component of the Labrador Current around the Tail of the Grand Banks, and the most extensive intrusion of LSSW into the GoM/WSS region since the 1960s (MERCINA, 2001). This cooler, fresher LSSW steadily advanced along the Scotian Shelf break and replaced or significantly altered the deep basin waters of the WSS and GoM over the subsequent 2 years (Fig. 3b). By the early autumn of 1998, all of the warmer, saltier ATSW, typical of the GoM deep basins since the 1970s, had been replaced by LSSW or rendered significantly cooler and fresher through mixing. Coinciding with this major advective event and change in the regional hydrography, *C. finmarchicus* exhibited an order-of-magnitude decline in abundance in the GoM during 1998 (Fig. 5). The NAO index returned to positive values after the winter of 1996, and by December 1999 the LSSW had been replaced in most of the WSS and GoM deep basins by ATSW (MERCINA, 2001). Again, coincident with the physical changes, *C. finmarchicus* in the GoM/WSS region during December 1999 returned to a level comparable to that observed before the dramatic decline of 1998 (Fig. 5).

The oceanographic events observed in the Northwest Atlantic during the latter part of the 1990s provide
Fig. 5. Depth-integrated abundance of *C. finmarchicus* C5 copepodites sampled in the deep basins of the Gulf of Maine during the autumns of 1997 to 1999. One night-time MOCNESS sample was collected from each basin on each of the five cruises. Abundances from samples taken in Georges Basin are indicated by circles, those from Jordan Basin by squares, and from Wilkinson Basin by triangles. Mean values from all basins during a given year are indicated by a diamond with bars corresponding to ±1 SE.

an important piece of the puzzle for interpreting the historical abundance of *C. finmarchicus* in the GoM/WSS region over the past half century. During the decade of the 1960s, the NAO index was predominantly negative and the CSWS operated in its minimum modal state (Fig. 6) (MERCINA, 2001). This was an unusual period during the past 50 years when the deep waters of the GOM/WSS region were derived primarily from cool and fresh LSSW (Loder et al., 2001; MERCINA, 2001) and numbers of *C. finmarchicus* were relatively low (Greene and Pershing, 2000; MERCINA, 2001). Subsequent to the 1960s, the NAO index shifted to a predominantly positive phase and the CSWS to its maximum modal state (Fig. 6). Associated with these changes, the deep waters of the GoM/WSS region became warmer and saltier, derived primarily from ATSW, and *C. finmarchicus* numbers increased significantly. These coincident increases in the NAO index and *C. finmarchicus* account for the significant positive correlation observed between them during the period of 1961–1989 (Greene & Pershing, 2000). In the context of these long-term trends, the events of the late 1990s fit the pattern consistently: the NAO index dropped dramatically during the winter of 1996, the coupled slope water system shifted from its maximum to minimum modal state during 1997, and *C. finmarchicus* abundance declined by an order of magnitude during 1998.

The puzzle is more complicated than this, however. Although the CSWS typically undergoes modal shifts in response to large phase 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. After the 1960s, the coupled slope water system shifted from its maximum to minimum modal state on only a few brief occasions, including 1981–1983, 1988–1991, and 1996–1998 (Fig. 6) (MERCINA, 2001). While the 1996–1998 modal shift was clearly in response to the large phase change in the NAO index during the
winter of 1996, the circumstances leading up to the modal shifts in the early and late 1980s are less clear. Both of these modal shifts were weaker than the one observed in the late 1990s. In addition, although both of them occurred within a few years of a positive to negative phase change in the NAO index, the time lag in each case was different (Fig. 6) (MERCINA, 2001). We conclude from analyses of these time-series data that, although physical responses of the CSWS are significantly correlated with the NAO index, a large proportion of the variance in the relationship remains unexplained as a result of variable time lags and potential threshold effects (MERCINA, 2001). This conclusion is consistent with the weak positive correlation observed between *Calanus finmarchicus* abundance in the GoM and the NAO index from 1961 to 1989, a relationship that subsequently became non-significant when data from the 1990s were included (Fig. 1d and f).

While retrospective analyses of the time series data yield correlative relationships that are informative, they provide few details of the underlying physical and biological processes linking population responses of *Calanus finmarchicus* in the GoM with NAO-associated modal shifts in the CSWS. We hypothesise that springtime incursions of slope water onto the WSS play a central role in linking the two. Head, Harris and Petrie (1999) have shown that slope-water incursions can be an important source of *C. finmarchicus*

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### Table: Normalized Abundance

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<tr>
<th>Year</th>
<th>NAO Index</th>
<th>Regional Slope Water Temperature Index</th>
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**Fig. 6.** 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 in the GoM. Positive anomalies in each of the time series are lightly shaded and negative anomalies darkly shaded. Lines connecting the figures are offset by the time lags determined in the cross-correlation analyses. The NAO index is defined in the caption to Fig. 1. The Regional Slope Water Temperature index was developed as an indicator of the modal state of the CSWS, with positive (negative) values corresponding to maximum (minimum) modal state conditions (MERCINA, 2001). It is the dominant mode derived from a principal component analysis of eight slope–water temperature–anomaly time series from the GoM/WSS region. The *Calanus finmarchicus* abundance index is the mean abundance anomaly for this species calculated each year as the mean difference between log-transformed observed abundances and log-transformed expected abundances (MERCINA, 2001). Expected abundances were determined from the climatological mean seasonal cycle of *C. finmarchicus* in the Gulf of Maine. These abundance index values, connected by the solid line, have been calculated differently from the abundance values shown here and in Fig. 1b as circles. Those values were calculated by the standardised procedures described by Colebrook (1975) and therefore are comparable to other values presented in the literature. The abundance index values displayed only in this figure are valuable in that they can be used to fill in gaps in the time series when data are insufficient to meet the SAHFOS standards.
recruiting to the WSS. Since the major inflows into the GoM from the WSS also occur during spring (Smith, Houghton, Fairbanks & Mountain, 2001), the timing is right for these incursions of slope water to affect the advective supply of _C. finmarchicus_ into the GoM.

There are several potential mechanisms that could explain the relationship between the modal state of the CSWS and _C. finmarchicus_ in the GoM/WSS region. During the minimum modal state of the CSWS, LSSW advances southwestward along the WSS, displacing ATSW offshore (Fig. 3b). If the abundance of _C. finmarchicus_ is lower in LSSW than in ATSW, then source waters with reduced abundance of this species could provide a simple explanation for the regional decline of _C. finmarchicus_ during minimum modes of the CSWS. We are unaware of any evidence supporting this hypothesis at present. An alternative hypothesis is that cross-frontal exchange is impeded by intensification of the slope-water front during minimum modal conditions, reducing the frequency and/or intensity of slope-water incursions. Pickart, McKee, Torres and Harrington (1999) provided evidence that the gradient of this front is intensified during minimum modal conditions; however, we are unaware of any observations confirming that the frequency and/or intensity of slope-water incursions are reduced under these conditions. Clearly, future field studies will be necessary to fill in the gaps in our knowledge.

5. Discussion

We have reviewed evidence from the North Sea and GoM/WSS linking fluctuations in the abundance of _C. finmarchicus_ to changes in ocean circulation associated with the NAO. A noteworthy finding of this review is the regional dependence of the population responses of _C. finmarchicus_. In the North Sea, the species exhibits a negative correlation with the NAO index, whereas the GoM/WSS population exhibits a more complex, positive association with the index. Since ocean–circulation responses to the NAO vary in different regions of the North Atlantic, it should come as no surprise that the population responses of _C. finmarchicus_ vary by region as well.

The responsiveness of _C. finmarchicus_ to changes in ocean circulation, combined with its ecological importance throughout the North Atlantic, makes this species a good indicator of climate change and a suitable target species for global climate-change research (GLOBEC, 1991; MERCINA, 2001). While this review has focused primarily on linking regional population responses of _C. finmarchicus_ to circulation changes associated with the NAO, our findings are also relevant to predicting the future responses of the species to global climate change.

During the past quarter century, the NAO index has exhibited a persistently increasing trend, a trend that some have associated with greenhouse warming (Hurrell, Kushnir & Visbeck, 2001) and the recently documented rise in oceanic heat content (Hoerling, Hurrell, & Xu, 2001; Barnett, Pierce, & Schnur, 2001; Levitus et al., 2001). While we have shown that positive NAO conditions appear unfavourable for _C. finmarchicus_ in the North Sea and favourable in the GoM/WSS region, the increased climate variability predicted by some models as a consequence of rising greenhouse-gas concentrations (IPCC, 2001) makes long-term predictability difficult at present. The NAO has exhibited unusual behaviour during the latter half of the 1990s, including a shift in the subpolar low-pressure centre towards the Greenland Sea (Ulbrich & Christoph, 1999). Several investigators have suggested that rising greenhouse-gas concentrations may be responsible for this unusual behaviour (Langenberg, 2000). In addition, the extreme drop of the NAO index during 1996 may represent an unusual event or perhaps a sign of the larger swings in climate that we might expect in a greenhouse future. The uncertainty surrounding these recent events also raises the issue of what we might expect if the NAO were to enter a long, persistently negative phase. Palaeoclimate records indicate that such conditions have occurred in the past (Appenzeller, Stocker, & Anklin, 1998; Jones, Osborn, & Briffa, 2001), and some investigators have suggested that we might expect a return to such conditions in a greenhouse future (Wood, Keen, Mitchell & Gregory, 1999; Hillaire-Marcel, de Vernal,
Ultimately, the fate of *C. finmarchicus* populations on both sides of the North Atlantic will depend on how regional circulation patterns respond to natural, as well as anthropogenically forced changes in global climate.

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