

# Pattern and scale of variability among Northwest Atlantic Shelf plankton communities

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Continuous plankton recorders (CPRs) have been used in the Northwest Atlantic for almost 50 years. While data collected by these surveys have provided valuable information on long-term variability in plankton populations, all previous analyses have been limited to only a portion of the geographic range of the available data. Here we present an analysis of the CPR data from the Mid Atlantic Bight to the Labrador Sea. Across this wide geographic range, we found many common associations among the taxa. In particular, the changes in most regions were strongly size structured, with small and medium copepods varying together and often positively related to indicators of phytoplankton abundance. The time series from nearby regions were strongly correlated; however, after 1990, the spatial pattern became more complex. During this period, several of the copepod taxa, noticeably *Calanus finmarchicus* and *Centropages typicus*, experienced a series of anomalies that appeared to propagate from northeast to southwest. Although the direction of propagation was consistent with the shelf circulation, the anomalies propagated at a rate much slower than typical current speeds. The timing of the copepod anomalies and their phase speed were similar in character to observed changes in salinity and the position of the Shelf Slope Front. The correspondence between the changes in the plankton community and changes in the physical environmental suggests that physical conditions are a strong driver of interannual variability in Northwest Atlantic Shelf ecosystems.

**KEYWORDS:** zooplankton; phytoplankton; continuous plankton recorder; Gulf of Maine; Scotian Shelf; Middle Atlantic Bight; North Atlantic; climate variability

## INTRODUCTION

Surveys with the continuous plankton recorder (CPR) were started by Sir Alister Hardy and expanded by his eponymous foundation, SAHFOS. For this reason, the vast majority of CPR lines terminate at ports in the UK and northern Europe. Not surprisingly, the majority of CPR-based studies have focused on patterns in the

central and eastern Atlantic. The first UK-managed CPR route off eastern Canada began in 1957, with additional routes in the 1960s, 1970s and 1990s. The first route connecting to the eastern USA began in 1961. The US National Marine Fisheries Service assumed management of this route, across the Gulf of Maine, in 1974, and added more routes across the US northeast shelf in the 1970s and 1990s (Jossi *et al.*, 2003).

Compared with the eastern Atlantic, relatively few studies have used CPR data from US and Canadian waters. Most of these studies have examined one subset of the data, such as the Gulf of Maine (e.g. Jossi and Goulet, 1993; Conversi *et al.*, 2001) or the Eastern Scotian Shelf (e.g. Frank *et al.*, 2005) or several regions within one country's waters (Head and Sameoto, 2007). This study is the first comprehensive analysis of the entire North American Shelf CPR data set.

Previous analyses of data from the Gulf of Maine and Canadian Shelf have identified significant interannual and interdecadal variability. Following work by Planque and colleagues (Fromentin and Planque, 1996; Planque and Reid, 1998), work on the Gulf of Maine CPR data focused on the influence of the North Atlantic Oscillation (NAO) on late stage *Calanus finmarchicus* abundance (Conversi *et al.*, 2001; MERCINA, 2001). These studies identified a marked increase in *C. finmarchicus* abundance between the 1960s and late 1980s and a dramatic drop in abundance in 1998. The time series was found to be weakly correlated with the NAO Index at a lag of 2–4 years, and both studies found that *C. finmarchicus* abundance was more strongly correlated with a temperature index than the NAO.

Continuing work by Jossi and Goulet (Jossi and Goulet, 1993), Pershing *et al.* (Pershing *et al.*, 2005) conducted a multivariate analysis of the most common zooplankton taxa in the Gulf of Maine CPR record. They found that the zooplankton community exhibited two main modes of variability. The first mode, which included most of the small- and medium-sized copepods, was characterized by a strong interdecadal signal, with low abundance in the 1980s, an abrupt transition to high abundance in 1990 and a rapid decline in 2001. The second mode included *Calanus finmarchicus* and euphausiids, and not surprisingly, looked very much like the *C. finmarchicus* time series. Although the *C. finmarchicus* mode had stronger interannual variability, it also possessed a step change in 1990, but from high to low values. Pershing *et al.* (Pershing *et al.*, 2005) proposed that the 1990s community shift was related to the reduced salinities on the shelf, both in the Gulf of Maine (Smith *et al.*, 2001) and on the Labrador Shelf (Häkkinen, 2002; Belkin, 2004). A more extensive review of the salinity observations on the North Atlantic Shelf indicated that the reduced salinities observed in the Gulf of Maine likely originated in the Arctic (Greene and Pershing, 2007). The changes in the 1990 zooplankton community in the Gulf of Maine were also found in a time series of net samples collected on Georges Bank (Kane, 2007).

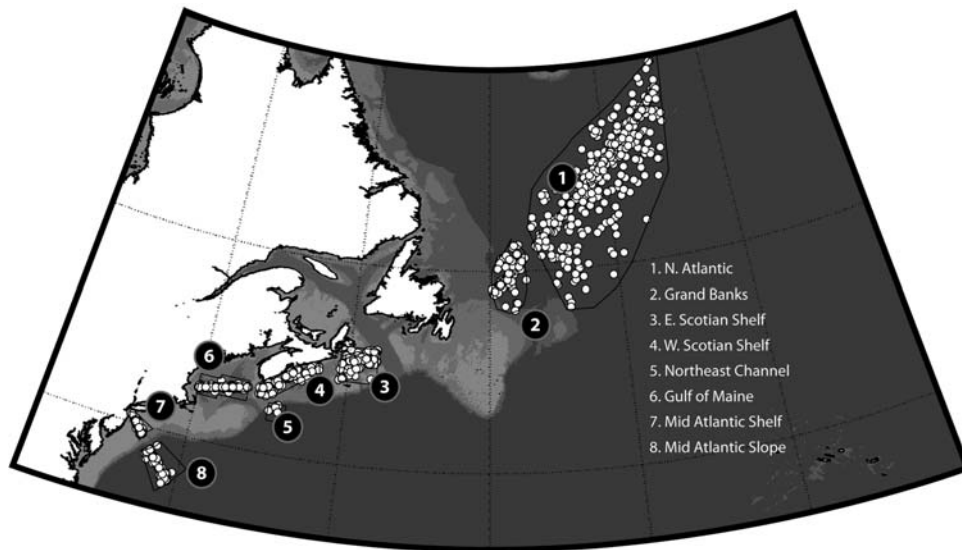
One high profile paper using the Canadian Shelf CPR data was Frank *et al.*'s (Frank *et al.*, 2005) study of

the Eastern Scotian Shelf. They found a marked change between the plankton community during the 1990s and observations from the early 1970s. The change included an increase in phytoplankton colour index (PCI) and small copepods and a decrease in large copepods, including *Calanus finmarchicus* and *C. glacialis*, and they attributed these changes to a trophic cascade precipitated by the collapse of groundfish stocks. More recently, Head and Sameoto (Head and Sameoto, 2007) analyzed the entire Canadian Shelf CPR data set. They noted a large increase in phytoplankton (diatoms, dinoflagellates and PCI) between the 1960s and the 1990s. The phytoplankton changes occurred in all regions and persisted into the next decade. The changes in the copepod community were similar to those observed in the Gulf of Maine, including elevated *Oithona* spp. and *Centropages typicus* populations and reduced *C. finmarchicus* during the 1990s. They attributed the increase in phytoplankton, and the response of the smaller copepods, to reduced salinity and enhanced stratification.

The similarities between the plankton community changes in the 1990s documented for the Gulf of Maine and Canadian Shelf suggest that these regions may be closely linked. However, differences in the methodology between the US and Canadian studies limit a reviewer's ability to directly compare these studies. This difficulty is the motivation behind our current study. Here, we present an analysis of the zooplankton and phytoplankton data from the Northwest Atlantic Shelf CPR data. Our primary goal is to understand the covariation between taxa and between regions. Although our study is primarily descriptive, documenting patterns and scales of community change can provide insights into the mechanisms that drive variability in these ecosystems.

## METHODS

For this study, we assembled data on zooplankton and phytoplankton abundance from CPR collections from the Northwest Atlantic. We divided the data into eight regions (Fig. 1). The sampling on the Canadian Shelf and North Atlantic has been organized by the Sir Alister Hardy Foundation for Ocean Sciences (SAHFOS) and its predecessors, with funding from both Canada and the USA. Data from the Gulf of Maine CPR transect prior to 1977 was processed in the UK alongside the North Atlantic data. From 1977 to 1999, data from the Gulf of Maine and Mid Atlantic Bight were processed by the US National Marine Fisheries Service (NMFS). After 1999, US samples were sent to the Plankton Sorting and Identification Center in



**Fig. 1.** Northwest Atlantic Shelf. The CPR data were partitioned into the eight regions marked on the figure. Shades of gray represent depth: white, land; light gray, 0–80 m; gray, 80–200 m; dark gray, 200–1000 m; very dark gray, 1000+ m.

Gdynia, Poland for counting. Although every effort has been made to ensure that the collection and handling of the US samples was consistent with SAHFOS protocols, we cannot rule out subtle differences between the two programs. Regardless, collections from each of the eight regions should be internally consistent.

Our analysis focuses on 11 zooplankton taxa: euphausiids, *Calanus hyperboreus*, *Calanus glacialis*, *Calanus finmarchicus*, early copepodid stages of *Calanus* (includes all *Calanus* species), *Metridia lucens*, *Pseudocalanus* spp., *Paracalanus* and *Pseudocalanus* spp., *Centropages typicus*, *Centropages hamatus* and *Oithona* spp. These taxa were selected based on their consistent presence in the database. Most of these groups include the adult stage (C6) and often one or two sub-adult stages (Table I). We also analyzed three indices of the phytoplankton community: total diatoms, total dinoflagellates and the PCI. Not all of the plankton variables were available for each region (Table I). Notably, the Arctic *Calanus* species *C. glacialis* and *C. hyperboreus* were not found in significant numbers in the Gulf of Maine and Mid Atlantic Bight. Furthermore, diatom and dinoflagellate counts were not available for the surveys operated by NMFS.

We used a consistent methodology to create standardized time series for each taxa-region combination. Annual abundance anomalies were created for the zooplankton taxa and for diatoms and dinoflagellates using the methods described in Pershing *et al.* (Pershing *et al.*, 2005). Briefly, an annual cycle represented by a periodic spline function was fitted to the log-transformed abundance data from all data after 1990. Each sample was then expressed as an

anomaly from this cycle, and the mean of the anomalies was computed for each year. The time series were further standardized by subtracting the post-1990 mean and dividing by the standard deviation of the annual anomalies from this time period. The PCI categorizes a sample into one of the four greenness levels that have been related to chlorophyll concentrations (Richardson *et al.*, 2006). The categorical nature of the PCI data did not produce reasonable annual spline functions. Thus, time series for PCI were computed by taking the mean value in each year. All time series were then standardized to the post-1990 mean and standard deviation.

The main goal of our study is to understand patterns of covariance among species and regions. We focused on simple descriptive statistics, namely linear correlation and principal component analysis (PCA). These two techniques are closely related, with PCA extracting the dominant patterns (the principal components) from a set of correlations. We began by computing a correlation matrix. Each entry in the matrix represents the correlation between two time series for their commonly sampled years. These correlations included both correlations between the same taxa from different regions, different taxa within a region or different taxa from different regions. The principal components were computed by taking the singular value decomposition of the correlation matrix. Each principal component is then a vector of weightings for the set of time series. The principal components can then be ordered based on the amount of the total variance they explain, indicated by the magnitude of the singular values. The PCA

Table I: Summary of the availability and staging of the plankton taxa considered in this study

	Mid Atlantic Slope Operated by NMFS	Mid Atlantic Shelf Operated by NMFS	Gulf of Maine Operated by NMFS	Northeast Channel Operated by SAHFOS	Western Scotian Shelf Operated by SAHFOS	Eastern Scotian Shelf Operated by SAHFOS	Grand Banks East Operated by SAHFOS	North Atlantic Operated by SAHFOS
Years sampled	1977–2006	1977–2006	1961–1974, 1974, 1977–2006	1961–1974, 1976, 1991–2006	1961–1974, 1976, 1991–2006	1961–1974, 1976, 1991–2006	1962–1978, 1991–2006	1958–1986, 1991–2006
Euphausiids	Post-calyptosis		All forms					
<i>Calanus hyperboreus</i>	Not present		C3–6					
<i>Calanus glacialis</i>	Not present		C5–6					
<i>Calanus finmarchicus</i>	C5–6		C5–6					
<i>Calanus</i> C1–4	C1–4		C1–4					
<i>Metridia lucens</i>	C6		C6					
<i>Pseudocalanus</i> spp.	C6		C6					
<i>Paracalanus-Pseudocalanus</i>	Small copepodids not assigned to another taxa		Small copepodids not assigned to another taxa					
<i>Centropages typicus</i>	C4–6		C6					
<i>Centropages hamatus</i>	C4–6		C6					
<i>Oithona</i> spp.	C4–6		C4–6					
Phytoplankton color index	Available		Available					
Diatoms	Not available		All species					
Dinoflagellates	Not available		All species					

The boundaries of the eight regions are defined in Fig. 1 (MAB, Mid Atlantic Bight). For the copepod stages, the prefix “C” indicates copepodids and C6 is the adult stage. For most taxa, the identification and staging between the NMFS and SAHFOS data are the same. The main exceptions are the two *Centropages* species. We choose to use the C4–6 staging of these species from the US regions to maintain consistency with prior work in these regions (e.g. Pershing *et al.*, 2005).

procedure guarantees that the first component explains the maximum amount of the total variance and that the other components are orthogonal. We performed the analysis first for the entire data set and then for the period 1990–2005, the only period during which all regions were sampled.

We first computed the correlation matrices and principal components for the entire set of 100 time series (8 regions × 14 taxa, minus the four missing time series from each of the three southern regions). We then merged the data in two different ways and recomputed the analysis. The first merging combined all taxa within a region into a single time series. Since the order of the taxa was the same within each region, the correlation between each region was the mean of the correlation of each taxon within a region with the same taxon from the second region. The second merging combined all time series for each taxon.

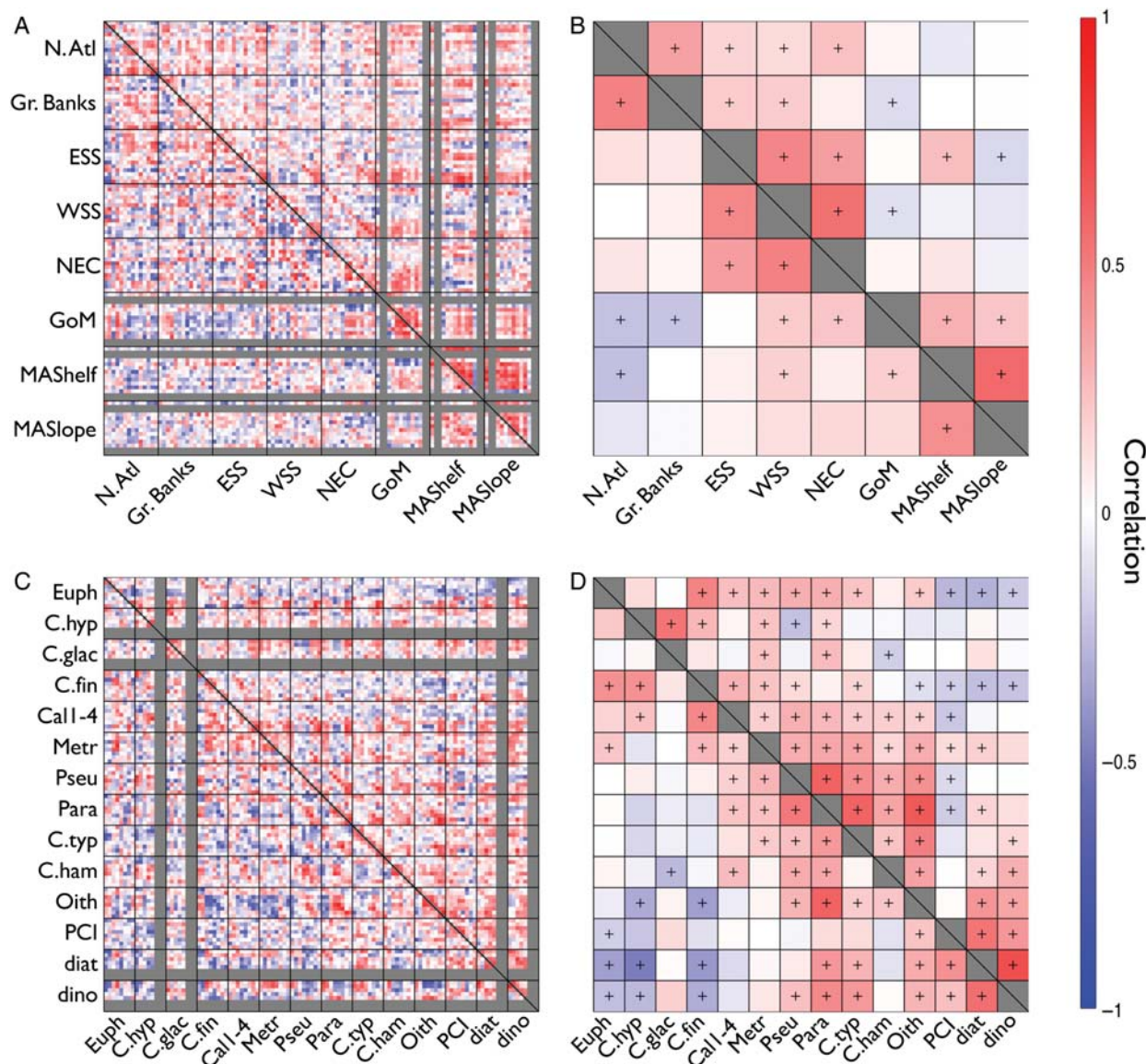
## RESULTS

### Correlations

A complete matrix of the correlations contain 4950 unique combinations of time series, and identifying patterns in this quantity of data is a challenge. We first

sorted the correlations by region and then, within each region, by taxon. This creates an 8-by-8 array of boxes, with each box containing a 14-by-14 array of correlations (Fig. 2A). Pooling the data by regions and computing the overall correlations is the same as averaging the correlations along the main diagonal within each box, provided the variance of the time series included in the average is the same. This criterion is true for the post-1990 portion of the matrices (lower triangular part of Fig. 2A and C); however, the uneven sampling before 1990 breaks this assumption in the full data set. Nevertheless, the relationship between the diagonals and the values in the panels at the right is still a useful guide. We will use the resulting 8-by-8 matrices (Fig. 2B) as a guide to interpreting the more detailed matrices.

The most apparent features of the regional correlation matrices are the blocks of strong positive correlations surrounding the main diagonal. The correlations on the main diagonal are trivial and have been grayed out. That the blocks extend on both sides of the main diagonal indicates that the relationships are present in both the 1990s (lower triangular portion) and throughout the data sets (upper triangular portion). Moving from east to west, the first block links the North Atlantic with the Grand Banks region. The correlation between these two regions is slightly stronger in the post-1990 data. The second block links the two Scotian Shelf



**Fig. 2.** Correlation matrices for the data organized by region (top panels, **A** and **B**) and taxon (bottom panels, **C** and **D**). In all panels, the upper triangular part contains the correlations using the full time series, while the lower triangular part contains the correlations using the post-1990 data. The matrices on the left (**A** and **C**) contain all of the correlations and only differ in how the correlations are organized. The matrices on the right (**B** and **D**) contain the correlations using the data binned by region (**B**) or taxon (**D**). The color of the cells in the matrices indicates the sign (red, positive; blue, negative) and magnitude of the correlation according to the color bar on the right. Correlations significant at the 5% level are indicated by a “+”. The significance of the matrices on the left is not shown. Region abbreviations: N. Atl, North Atlantic; Gr. Banks, Grand Banks; ESS, Eastern Scotian Shelf; WSS, Western Scotian Shelf; NEC, Northeast Channel; GoM, Gulf of Maine; MAShelf, Mid Atlantic Shelf; MA Slope, Mid Atlantic Slope. Taxon abbreviations: Euph, euphausiids, *C. hyp*, *Calanus hyperboreus*; *C. glac*, *C. glacialis*; *C. fin*, *C. finmarchicus*; Call-3, *Calanus* spp. copepodids; Metr, *Metridia lucens*; Pseu, *Pseudocalanus* spp.; Para, *Paracalanus-Pseudocalanus*; *C. typ*, *Centropages typicus*; *C. ham*, *Centropages hamatus*; Oith, *Oithona*; PCI, phytoplankton color index; diat, diatoms; dino, dinoflagellates (for high-resolution Fig. S2A and B, see Supplementary data online).

regions and the Northeast Channel. The third block contains the three US regions. The US correlations are weaker after 1990, with the Gulf of Maine-Mid Atlantic Slope correlation no longer significant.

The fully resolved matrices (Fig. 2A) are complex. Rather than describing each correlation, our

presentation will highlight the more interesting patterns. To aid with the interpretation, an 8-by-8 grid representing the regions has been overlain on top of the fully resolved matrices. The values along the diagonals (upper left to lower right) in each box partition the corresponding region-region correlation in Fig. 2B among

the taxa. For example, the positive correlation between the Western Scotian Shelf and Northeast Channel appears as a distinct red diagonal line in Fig. 2A.

Each box in Fig. 2A contains a 14-by-14 array of correlations between the taxa from two regions, or in the case of the boxes on the main diagonal, a single region. One of the most prominent features in the correlation matrices is that the pattern within a box is often similar to nearby boxes. This is especially true for the boxes within the regional blocks in Fig. 2B. For example, the US block (Gulf of Maine, Mid Atlantic Shelf and Slope) is characterized by strong positive correlations among most of the taxa. The most notable exceptions to this are *Calanus finmarchicus* (Gulf of Maine and Mid Atlantic Shelf), euphausiids (also Gulf of Maine and Mid Atlantic Shelf) and the PCI (all boxes involving the Mid Atlantic Shelf). For the 1990s, the correlations are weaker, and there is a strong band of negative correlations between *Calanus* and the euphausiids on the Mid Atlantic Shelf and the small copepods in the Gulf of Maine.

The boxes within the eastern block (N. Atlantic and Grand Banks) have a similar structure to those in the US block. Notably, they have positive correlations among the smaller taxa and phytoplankton and among the larger taxa, but many negative correlations between large and small. This pattern is enhanced (stronger positive and negative correlations) when the post-1990 data is used. The Scotian Shelf block contains more negative correlations, especially between the phytoplankton and some of the mid-sized copepods. The post-1990 correlations are less organized.

The regional-averaged matrices (Fig. 2B) also contain several long-range correlations. The North Atlantic and Grand Banks regions are linked to the Eastern and Western Scotian Shelves for the full data set, but not for the post-1990 period. In the full data set, the only correlation between the eastern and US blocks is the negative correlation between the Gulf of Maine and Grand Banks. During the 1990s, this negative correlation is stronger, and negative correlations also appear between the North Atlantic and both the Gulf of Maine and Mid Atlantic Shelf. The Scotian Shelf block and US blocks have no clear pattern in the full data set. The Eastern Scotian Shelf is positively correlated with the Mid Atlantic Shelf but negatively correlated with the Slope. The Western Scotian Shelf is negatively correlated with the Gulf of Maine. During the 1990s, the correlations between Scotian Shelf regions and the US regions are consistently positive, with significant correlations between the Gulf of Maine and both the Western Scotian Shelf and Northeast Channel and between the Mid Atlantic Shelf and Western Scotian Shelf.

The full correlation matrices possess a richer array of long-range correlations. In the full data set, the most noticeable features are the horizontal bands of high positive correlations between the US regions and many of the upstream regions. The horizontal bands indicate correlations between most of the taxa in the downstream region and one or more taxa in the upstream region. The strongest bands in the Gulf of Maine column appear in the rows for the smaller copepods and phytoplankton in Northeast Channel and both Scotian Shelf regions. Bands also appear for the *Calanus hyperboreus* and *C. glacialis* rows in the two eastern rows. These bands indicate that the abundance of these large species is strongly correlated with the abundance of the smaller copepods in the Gulf of Maine. The bands in the columns for the two Mid Atlantic regions are strongest in the Eastern Scotian Shelf and eastward. The dominant bands are for the phytoplankton rows and the *C. hyperboreus* and *C. glacialis* rows. The phytoplankton correlations decrease towards the east while the *Calanus* correlations increase.

The long-range correlation pattern is less consistent in the post-1990 data. The horizontal bands in the full data set should appear as columns in the post-1990 data. In the west, the Gulf of Maine taxa are no longer uniformly correlated with the small copepods and phytoplankton in the Northeast Channel. While the smaller taxa from each region are still positively correlated, the larger taxa (euphausiids and *Calanus*) are now negatively correlated with the small species in the Northeast Channel. This correlation pattern is also present in the Mid Atlantic Shelf during the 1990s, but breaks down for the Gulf of Maine and Scotian Shelf, and by the Grand Banks, many of the correlations have changed signs. For example, the small taxa in the Gulf of Maine and Grand Banks are now negatively correlated. The association between most of the Gulf of Maine taxa and the largest species is still present in both the N. Atlantic and Grand Banks boxes.

The correlation matrices in Fig. 2C are simply a reorganization of the correlations in Fig. 2A. This new ordering emphasizes the associations among the taxa. Merging the data by taxa and computing the correlations corresponds to the mean of the correlations along the diagonals in the taxa–taxa boxes in the fully resolved matrices. Like the regional correlations, this simplified correlation matrix (Fig. 2D) has a block-like structure. The largest block unites all of the medium and small copepods, including the *Calanus* copepodids. In the full data set, all of the correlations in the block are positive and significant, while in the post-1990 data, some of the correlations between widely separated taxa are no longer significant. The other main block

contains the three phytoplankton indices. The patterns for the euphausiids and late-stage *Calanus* taxa are less clear. In the full data set, *C. finmarchicus* and euphausiids are strongly correlated with each other and both are positively correlated with many taxa in the central block. While the correlation between these two taxa is present in the 1990s, many of the correlations with the central block taxa disappear. The only exceptions are the correlations with *Metridia lucens* (both taxa) and with *Calanus* copepodids (*C. finmarchicus* only). *Calanus hyperboreus* and *C. glacialis* are both correlated with each other and with both *M. lucens* and the *Paracalanus* group in the full data set. All of these correlations become non-significant in the post-1990 data. *Calanus hyperboreus* is also positively correlated with *C. finmarchicus* in both time periods.

The correlations between the two main blocks (phytoplankton and small-medium copepods) are less clear. In the full data set, the diatoms are positively correlated with *Oithona* and the two *Centropages* species. Diatoms are also correlated with *Oithona* and *C. hamatus* and add correlations with *Paracalanus* and *Metridia lucens*. Although the PCI is positively correlated with *M. lucens*, it tends to be negatively correlated with many of the other taxa. Furthermore, all of the phytoplankton indices are negatively correlated with both *C. finmarchicus* and euphausiids. After 1990, the phytoplankton correlations are largely unchanged. The main differences are the addition of positive correlations with *Pseudocalanus* (dinoflagellates) and *Paracalanus* (dinoflagellates and diatoms) and negative correlations with *C. hyperboreus* (all but PCI). In addition, after 1990, *Oithona* is negatively correlated with *C. finmarchicus* and *C. hyperboreus*. Additionally, *C. hamatus* is negatively correlated with *C. glacialis*.

The fully resolved matrices (Fig. 2C) allow one to explore which regions are driving the correlations in the merged data and whether these correlations occur in other region–region combinations. Since the information in this figure is the same as that in Fig. 2A, we will only highlight a few of the most interesting patterns. Readers interested in exploring these patterns further are encouraged to examine the high-resolution images in the online material. The most prominent feature in Fig. 2C is the quantity of red in the central block of species. This indicates that the taxa–taxa patterns shown in the simplified matrix occur over a broad collection of regions. However, even in this block, the red tends to be clustered near the lower right corner of the boxes, reflecting the strong correlations among the US regions. The diatom and dinoflagellate boxes are also largely positive, suggesting strong, large-scale correlations between these phytoplankton indicators and the small- and medium-sized species. Negative correlations

are more prominent after 1990. These indicate that, while two taxa may be positively correlated within a region (for example, the red diagonal line in the *Paracalanus-Pseudocalanus* box), the taxa are negatively correlated with regions up or downstream.

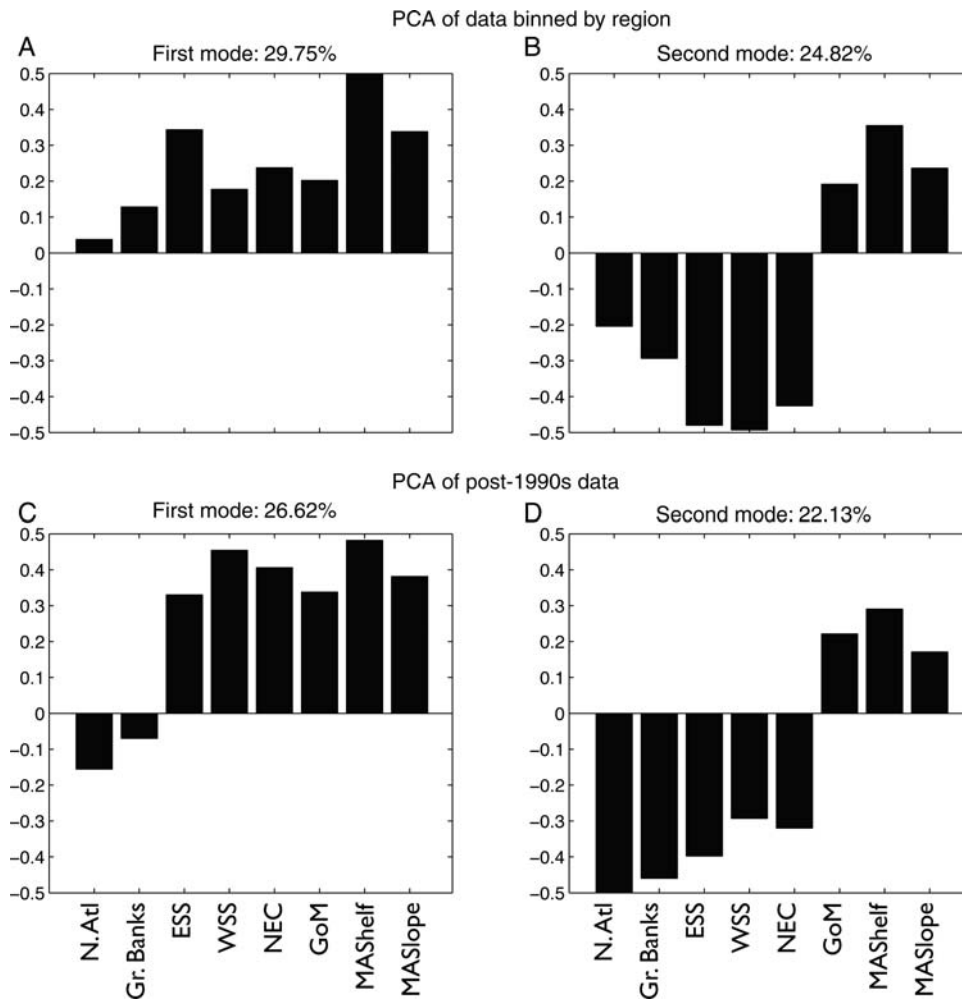
### Principal component analysis

The PCA of the region-pooled correlation matrices confirms the patterns described above (Fig. 3A and B). The first principal component from the whole-data set analysis is simply a weighted mean of the entire time series. This component explains 29.7% of the total variance in the data set. The second component contrasts the three western regions (block three above) with the other regions. This component is nearly as strong as the first and explains 24.8% of the variance. The first two modes from the post-1990 data are similar to those for the entire data set. The leading mode explains 26.6% of the variance and distinguishes the two easternmost time series from the rest of the data. The second mode, which explains 22.1% of the variance, again contrasts the US regions against the more easterly regions.

The first principal component of the taxon-pooled data explains 26.1% of the variance (Fig. 4A). This mode contrasts the zooplankton, especially the euphausiids, *Calanus* spp. and *Oithona* spp., with the phytoplankton indices. This mode is driven by the negative correlations between the PCI and many of the zooplankton taxa. The second mode, which explains 18.5% of the variance, contrasts *Paracalanus*, *Centropages typicus* and *Oithona* with the larger copepods and the phytoplankton (Fig. 4B). For the post-1990 data, the two modes are reversed. The leading mode for this data contrasts *Paracalanus*, *C. typicus* and *Oithona* with the other taxa (Fig. 4C), whereas the second mode contrasts the zooplankton against the phytoplankton (Fig. 4D).

### Time series

Displaying the time series for the eight regions and 14 taxa is a challenge. Four representative taxa were selected to give a sense of the variability in the data (both in time and space) as well as sampling history for each region (Fig. 5). The strongest signal in the post-1990 *Calanus finmarchicus* data is the transition from negative anomalies to positive anomalies found in all regions west of the Grand Banks (Fig. 5A). The transition occurred after 1997 on the Eastern Scotian Shelf, after 1999 on the Western Scotian Shelf and Northeast Channel, after 2000 in the Gulf of Maine and after 2001 in the Middle Atlantic Bight. This pattern suggests that the transition propagated down the shelf at a rate



**Fig. 3.** Principal component analysis for the region-pooled data using the full time series (**A** and **B**) and post-1990 data (**C** and **D**). For each PCA, only the two leading modes are shown. Region names are abbreviated as in Fig. 2.

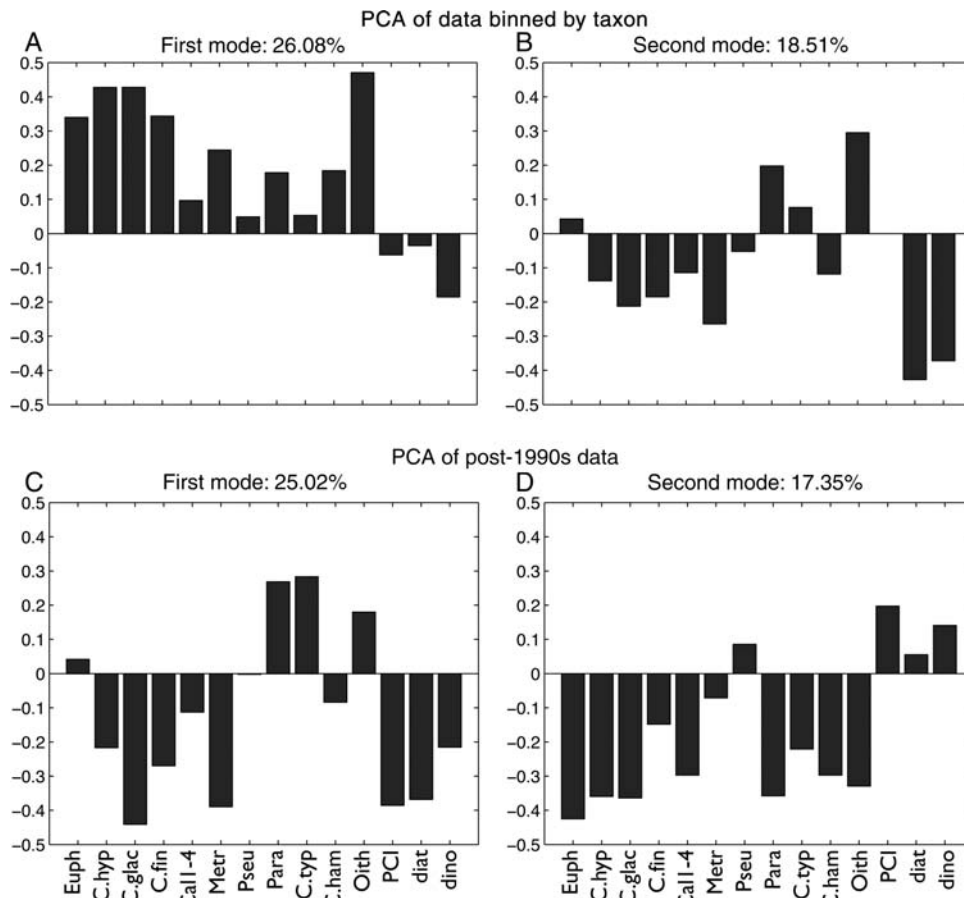
of  $200 \text{ km year}^{-1}$  ( $0.6 \text{ cm s}^{-1}$ ). The time series in the two eastern-most time series have the opposite pattern, with generally positive values prior to 2001 and negative values thereafter.

Moving back in time, the data become more sparse, with data from the Canadian Shelf absent during the 1980s, while sampling in the Mid Atlantic did not begin until 1976. This makes it difficult to assess whether the apparent propagation in the 1990s is unique to that time period or is a ubiquitous feature of *Calanus finmarchicus* dynamics on the Northwest Atlantic Shelf. Considering the 1980s, we see a strong correspondence between *C. finmarchicus* in the Gulf of Maine and in the Mid Atlantic (Fig. 5A). There is also generally good agreement between the Gulf of Maine and Scotian Shelf time series during the 1960s. The exception is the strong positive anomaly in the Canadian data during the early 1970s that is not present in the Gulf of Maine data.

Despite different sizes and ecological niches of *Centropages typicus* and *Oithona*, Pershing *et al.* (Pershing *et al.*, 2005) found a strong correspondence between these two taxa in the Gulf of Maine. This relationship also holds for the Mid Atlantic data (Fig. 5B and C), and the time series from these regions are also very similar to those from the Gulf of Maine. Both taxa have a prominent series of negative anomalies during the 1980s in the US surveys. The association between these two taxa east of the Gulf of Maine is less clear. The main exception is the negative *C. typicus* anomaly in the early 1990s, which occurred during a period of enhanced *Oithona* abundance. As with *Calanus finmarchicus*, anomalies of both *C. typicus* and *Oithona* during the 1990s had a tendency to propagate from east to west.

The PCI was less spatially and temporally coherent during the 1990s than any of the three copepod taxa (Fig. 5D). Over the entire data set, the dominant signal





**Fig. 4.** Principal component analysis for the taxon-pooled data using the full time series (**A** and **B**) and post-1990 data (**C** and **D**). For each PCA, only the two leading modes are shown. Taxon names are abbreviated as in Fig. 2.

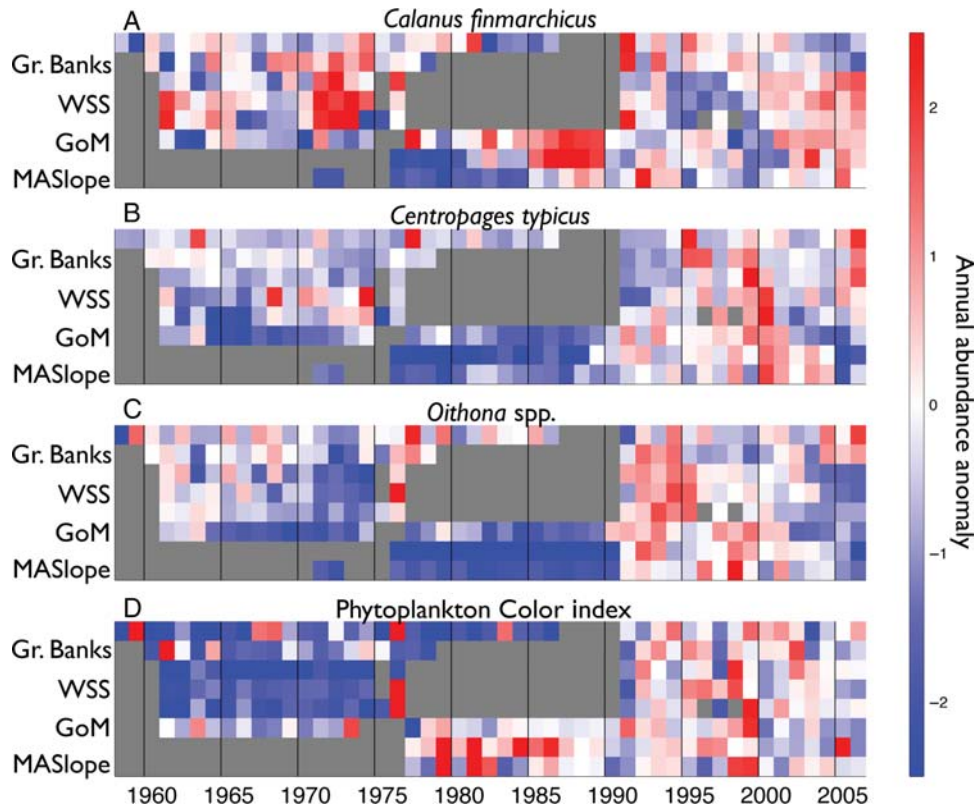
is the strong tendency for negative anomalies during the 1960s and 1970s. The negative anomalies persisted in the North Atlantic through the 1980s, while the values in the Gulf of Maine and Mid Atlantic were more likely to be positive. In the Gulf of Maine and Mid Atlantic Shelf, all but 2 years since 2000 had below average PCI values. After 2005, negative anomalies occurred in all regions except for the North Atlantic.

Perhaps the most intriguing result in our analysis is the apparent propagation of the zooplankton anomalies, especially those for *Calanus finmarchicus* and *Centropages typicus*. To examine this signal more thoroughly, we computed correlations between the *Calanus finmarchicus* and *Centropages typicus* time series from the Gulf of Maine and the time series at the other regions at time lags ranging from  $-3$  to  $3$  years (Fig. 6). The main pattern in these plots is a band of positive correlations that is tilted to the left (towards negative lags) upstream of the Gulf of Maine and to the right (positive lags) downstream. For *C. finmarchicus*, the strongest upstream correlations are with the Eastern Scotian Shelf 2 and 3 years earlier and

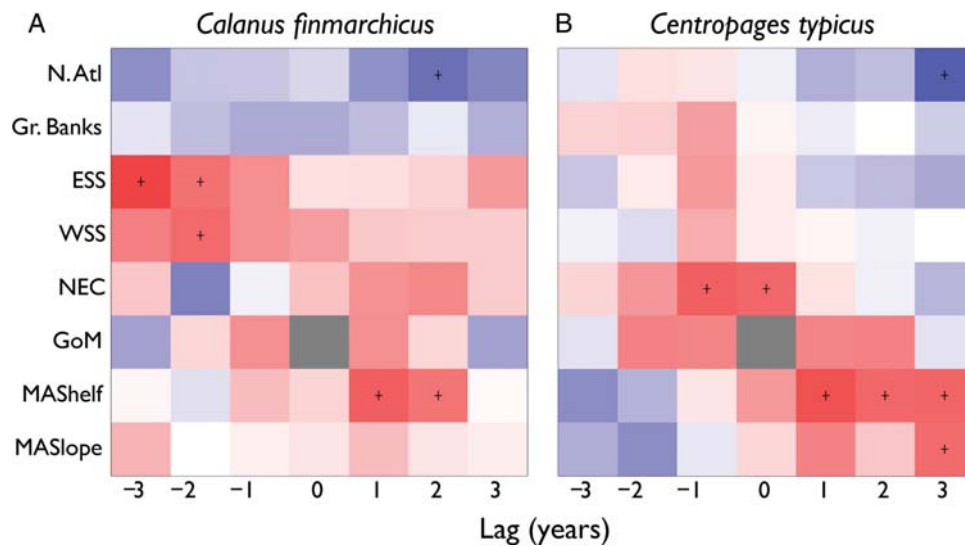
the Western Scotian Shelf 2 years earlier. The strongest downstream correlations are on the Mid Atlantic Shelf 1 or 2 years later. *Centropages typicus* has a similar correlation pattern downstream, with significant correlations with the Mid Atlantic Shelf (lags 1–3) and the Mid Atlantic Slope (lag 3). The only significant upstream correlations are with the Northeast Channel during the same year (lag 0) and the previous year. The previous year ( $-1$  year) correlations are positive, moderately strong and extend up to the Grand Banks.

## DISCUSSION

The cross-shelf density gradient across the Northwest Atlantic Shelf creates a general equator-ward flow that transports Arctic and subarctic water masses down the shelf. This flow is modified by the banks, channels and basins on the shelf that set up cross-shelf currents and some measure of recirculation. The other major contributor to the shelf current system is the outflow from the



**Fig. 5.** Time series of annual abundance anomalies for four representative taxa: *Calanus finmarchicus* (A), *Centropages typicus* (B), *Oithona* spp. (C) and PCI (D). Each colored box represents the anomaly for a particular year and region using the color bar on the right. The time series were standardized to the post-1990 mean and variance, so a positive anomaly should be interpreted as “larger than the 1990–2005 mean.” Regions are organized from northeast (top) to southwest (bottom) as in the previous figures, and the names are abbreviated as before.



**Fig. 6.** Correlation between the post-1990 Gulf of Maine *Calanus finmarchicus* (A) and *Centropages typicus* (B) time series and the other seven regions at lags from  $-3$  to  $3$  years. A lag of  $n$  means that the Gulf of Maine data in year  $j + n$  was compared with the other region's data in year  $j$ . Thus, a positive correlation at a negative lag means that a change in the region in question appears later in the Gulf of Maine. Correlations significant at the 5% level are indicated by a “+”. Region names are abbreviated as in Fig. 2.

Gulf of St Lawrence. This outflow combines both freshwater from the St Lawrence river and oceanic waters entering through the Strait of Belle Isle and along the east side of the Laurentian Channel (Loder *et al.*, 1998).

The correlations among the plankton communities in the eight regions we examined are consistent with the system of currents. The three regional blocks we identified are separated by the Laurentian Channel and the Northeast Channel, the two largest channels on the Northwest Atlantic Shelf. Based on the contribution of the Gulf of St Lawrence outflow to the Scotian Shelf, we might expect a sharp division between the regions on either side of the Laurentian Channel. In the post-1990 data, the Scotian Shelf block is in fact not correlated with the eastern block (Fig. 2B). However, in the fully resolved matrix (Fig. 2A), the Eastern Scotian Shelf appears more closely aligned with the North Atlantic and Grand Banks. The longer range correlations are harder to explain, especially since the correlations at these larger spatial scales change between the two time periods.

Our choice to sort the taxa in the correlation matrices by size was based on our earlier observations in the Gulf of Maine, especially the contrast between *Calanus finmarchicus* and euphausiids and smaller copepods (Pershing *et al.*, 2005). The analysis presented above found evidence for strong size-structuring in all regions.

The generally positive correlations between the phytoplankton indices and the smaller copepods suggest that the interannual variability in these taxa is driven by bottom-up processes. The negative correlations between the larger taxa (euphausiids, *C. finmarchicus* and after 1990s, *C. hyperboreus*) and the phytoplankton are certainly consistent with top-down forcing. However, it is unclear how top-down processes would appear in annual anomalies, given the short generation times of the species in question. For example, if *C. finmarchicus* becomes abundant, we might expect it to reduce phytoplankton stocks through grazing. However, the low phytoplankton abundance should then limit reproduction in *C. finmarchicus* later in the year. Furthermore, the main euphausiids in the study area, *Meganyctiphanes norvegica* and *Thysanoessa longicaudata*, are omnivorous and both can be important predators on *C. finmarchicus* (Dalpadado *et al.*, 2008).

Perhaps the most compelling observation in our analysis is the series of propagating anomalies during the 1990s. Using  $6 \text{ km day}^{-1}$  as a representative current speed for the Scotian Shelf (Smith, 1989), a water parcel, and the plankton community embedded within it, should take just over 3 months to travel from the Laurentian Channel to the Gulf of Maine. The phase

speed of the copepod anomalies is much slower, with a positive *Calanus finmarchicus* anomaly on the Scotian Shelf requiring 2 years to reach the Gulf of Maine (Fig. 6A). This presents an interesting paradox. Water and plankton are traveling through the region at one rate, but the community properties are traveling at a much slower rate.

The phase speed of the copepod anomalies is, however, consistent with the speed at which anomalies in the position of the Shelf-Slope Front move down the shelf (Bisagni *et al.*, 2009). Based on the analysis of Bisagni *et al.* (Bisagni *et al.*, 2009), many of the changes in the physical environment on the Northwest Atlantic Shelf appear to be linked. When the Shelf Slope Front is located further offshore, as it was during the early and late 1990s, the volume of Shelf Water (e.g. Mountain, 2003) is larger and salinity on the shelf is lower (e.g. Smith *et al.*, 2001). The fresh conditions and offshore position of the slope front are also associated with increased transport in the shelf current system (Smith *et al.*, 2001). At present, the exact mechanism that drives the physical anomalies and what processes determine their speed is not known; however, there is strong evidence that the anomalies originate upstream of the Grand Banks (Smith *et al.*, 2001; Greene and Pershing, 2007; Bisagni *et al.*, 2009). Furthermore, the changes observed on the Scotian Shelf and downstream appear to be decoupled from the outflow of the St. Lawrence River (Smith *et al.*, 2001), suggesting that variability in the transport and water properties on the shelf has an oceanic origin.

The copepod abundance anomalies in the Gulf of Maine and Georges Bank were associated with salinity anomalies during the 1980s and 1990s (Greene and Pershing, 2007; Kane, 2007; Greene *et al.*, 2008; Mountain and Kane, 2010). The results from the Gulf of Maine, together with the correspondence between the phase speeds of the salinity events and copepod anomalies, suggest that the changes in the plankton are associated with the physical changes. Previous studies have linked changes in the plankton communities on the Northwest Atlantic Shelf to physical forcing. Motivated by work in the eastern Atlantic, early studies examined the relationship between the North Atlantic Oscillation (NAO) and *Calanus finmarchicus* abundance in the Gulf of Maine (Conversi *et al.*, 2001; MERCINA, 2001). MERCINA (MERCINA, 2001) pointed out that conditions in the Labrador Sea are more closely associated with the NAO than are conditions near the Gulf of Maine. While the influence of the NAO has weakened in recent years (Pershing *et al.*, 2004), changes in physical conditions upstream are still a major driver of changes in the plankton community farther down the shelf.

The biological response we observed, with increased phytoplankton and small copepods and decreased *Calanus* and euphausiids, is broadly consistent with previous studies in the Gulf of Maine. In an analysis of the Gulf of Maine zooplankton data, Pershing *et al.* (Pershing *et al.*, 2005) identified two zooplankton groups with opposite responses. The first group corresponds to our small copepods, while the second group included *C. finmarchicus* and euphausiids. Kane (Kane, 2007) found a similar grouping on Georges Bank. Both studies suggested that the zooplankton changes were associated with reduced salinity in the 1990s. The impact of the community shift in the Gulf of Maine/Georges Bank region extends beyond zooplankton and is associated with increased haddock and decreased cod recruitment (Mountain and Kane, 2010) and decreased right whale reproduction (Greene and Pershing, 2004).

Still, the exact mechanism that links the physical changes and biological changes remains elusive. Most studies have considered the impact of reduced salinity on stratification and phytoplankton as the main driver of the pattern. The influx of freshwater to the Gulf of Maine during the 1990s resulted in increased stratification, at least during the winter (Mountain, 2004). Durbin *et al.* (Durbin *et al.*, 2003) found that the influx of fresh Scotian Shelf water during January of 1999 stimulated a winter phytoplankton bloom and supported an actively reproducing copepod community. Modeling work also suggests that reduced salinities could lead to an earlier spring bloom but that the stratification may reduce total annual productivity due to reduced nutrient supplies (Ji *et al.*, 2008).

The influence of reduced salinity on stratification and phytoplankton could explain the positive relationship we found between phytoplankton and small copepods. However, this simplified bottom-up mechanism cannot account for the observed reduction in *Calanus finmarchicus* and euphausiids. Frank *et al.* (Frank *et al.*, 2005) used the negative association between large copepods (principally *Calanus finmarchicus*) and phytoplankton on the Eastern Scotian Shelf as evidence for a top-down trophic cascade. They proposed that the collapse of cod stocks in this region led to predatory release of shrimp and small pelagic fish which, in turn, grazed down the large copepods. An increase in the abundance of mid-trophic level planktivores could certainly explain a reduction in *C. finmarchicus*. Indeed, herring stocks increased in the Gulf of Maine and Georges Bank during the 1990s (Overholtz and Friedland, 2002). While predation rates on large zooplankton may have been higher in the 1990s, it seems unlikely that herring predation would propagate down the shelf.

Two other mechanisms could explain the *Calanus*-phytoplankton relationship. Our processing of the zooplankton and phytoplankton data into annual anomalies obscures any changes in the annual cycles. The increase in the small copepods in the Gulf of Maine during the 1990s was due to unusually high abundance during the fall and early winter (Pershing *et al.*, 2005). During fall and early winter, the majority of *C. finmarchicus* are diapausing at depth and are not actively feeding. If, as Ji *et al.* (Ji *et al.*, 2008) hypothesize, the enhanced winter phytoplankton blooms lead to reduced spring blooms or summer phytoplankton abundance, then annual productivity in *C. finmarchicus* would decline. Indeed, the summer period accounts for the lower *C. finmarchicus* abundance during the 1990s relative to the 1980s (Pershing *et al.*, 2005).

The second mechanism is more directly related to the wave-like nature of the 1990s physical anomalies. The concentration of plankton at a particular location represents the net effect of population dynamics and advection. In an Eulerian framework, advection operates on horizontal gradients. If there is no gradient around a point, then the concentration of plankton at that point will never change. Increased horizontal transport seems to underlie the physical changes observed on the Northwest Atlantic Shelf, with increased transport associated with reduced salinity (Smith *et al.*, 2001). On average *Calanus finmarchicus* is more abundant in the Gulf of Maine than on the Scotian Shelf (Meise and O'Reilly, 1996), thus increased down-shelf transport should lead to a negative *C. finmarchicus* anomaly in the Gulf of Maine. This mechanism is identical to the one Sundby and Drinkwater (Sundby and Drinkwater, 2007) offered to explain the persistence of salinity anomalies in the North Atlantic. However, *Centropages typicus* abundance also increases down the shelf (Head and Sameoto, 2007). Thus, the negative association we found between *C. typicus* and *C. finmarchicus* would seem to argue against an advection-based explanation. If the transport changes have a seasonal component, then it is possible that differences in the timing of the annual abundance peaks could account for different responses to a transport change. Furthermore, the typically shorter generation times of the smaller copepods could allow their population dynamics to overwhelm any advective signal (e.g. Aksnes and Blindheim, 1996).

Due to their broad spatial range, consistent sampling and long duration, the CPR surveys provide a rich data set to examine patterns of variability in plankton communities across space and time. For example, our study identified similar associations among taxa across the Northwest Atlantic Shelf and found evidence for propagating anomalies in some of

the copepod taxa. While we have done our best to identify mechanisms that could account for the observed patterns, observational work alone cannot uncover processes. Many of the hypotheses presented above could be tested using coupled physical biological models. For example, the ability of transport changes to generate copepod anomalies could be modeled using existing single-species models (e.g. Lynch *et al.*, 1998; Zakardjian *et al.*, 2003; Ji *et al.*, 2009; Pershing *et al.*, 2009). Other hypotheses such as the relationship between stratification, phytoplankton abundance and small copepod abundance would require more complex models that represent the interactions of different ecosystem components.

## SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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